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UNTERSUCHUNGEN ÜBER DETERMINATION UND DIFFERENZIERUNG

2. ÜBER DIE WACHSTUMSVORGÄNGE IN DER SPITZE DER WURZELHAARE VON *PHLEUM*

VON

P. BOYSEN JENSEN

With an English Summary

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1. Einleitung.

Bei dem Flächenwachstum der pflanzlichen Zellwand wird nur das Areal der Zellwand (oder am häufigsten nur ein Teil desselben) vergrössert, während die Dicke im grossen und ganzen unverändert bleibt. Hinsichtlich der Weise, in der die Arealvergrösserung der Zellwand erreicht wird, sind zwei Theorien aufgestellt worden. Nach der einen Theorie ist der erste Wachstumsschritt eine durch den Turgordruck hervorgerufene elastische oder plastische Dehnung der Zellwand, wobei dieselbe dünner wird. Die ursprüngliche Dicke wird dann entweder durch Einlagerung neuer Teile (Intussusception) oder durch Anlagerung neuer Schichten (Apposition) wiederhergestellt. Nach der zweiten Theorie ist das Flächenwachstum der Zellwand ein aktiver Vorgang. Die zum Wachstum notwendige Energie stammt von den Kräften, die bei der Ausscheidung neuer Zellwandbestandteile zwischen den vorhandenen wirksam sind. Der Turgordruck hat nur insofern Bedeutung, als er das Protoplasma in Verbindung mit der Zellwand hält, aber er wirkt nicht als Energiequelle. Dass diese letztere Wachstumsweise tatsächlich vorkommen kann, hat Fitting (1900) in seinen Untersuchungen über das Wachstum der Membran der *Selaginella*spore zeigen können.

Es ist die Aufgabe der vorliegenden Untersuchung, die Wachstumsvorgänge in den Wurzelhaaren von *Phleum* im Lichte dieser zwei verschiedenen Theorien des Flächenwachstums näher zu erhellen.

2. Methodisches.

Drei Samen von *Phleum* werden ohne eingeweicht zu sein auf einen etwa 1 cm breiten Streifen von Japonaispapier, der auf einen Objektträger etwa 3 mm von dem unteren Ende desselben

angebracht ist, gelegt. Vier solche Objektträger werden senkrecht in ein Färbekästchen, dass mit einer 6 mm hohen Schicht von sterilisierter, mit atmosphärischer Luft gesättigter Nährlösung (I_b + II, vgl. Boysen Jensen 1950) beschickt ist, gestellt. Die Samen befinden sich etwa 3 mm über der Oberfläche der Nährlösung, so dass die Wurzeln in dieselbe hineinwachsen, ohne in Berührung mit Papier zu gelangen (Abb. 1). Nach 4—5 Tagen haben die Wurzeln eine passende Länge erreicht; 24 Stunden bevor die Wurzeln benutzt werden sollen, wird die Nährlösung erneuert.

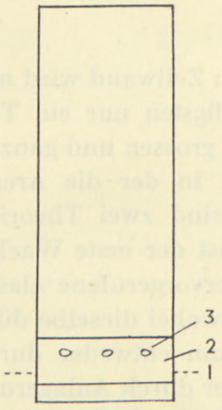

Abb. 1. Objektträger mit *Phleum*samen. 1 Oberfläche der Nährlösung, 2 Japonaispapier, 3 Samen.

Es ist von grosser Bedeutung, dass die Samen einigermassen steril sind. Eine Sterilisation wird am besten vermieden. Hinsichtlich der Sterilität können grosse Unterschiede zwischen den verschiedenen Jahrgängen von Samen vorhanden sein. Wenn man aber einmal einen guten Jahrgang gefunden hat, kann derselbe mehrere Jahre hindurch benutzt werden.

Bei der Untersuchung der Wurzelhaare unter dem Mikroskop ruht das Deckglas auf dem Samen, so dass die Wurzel nicht gedrückt wird. Bei starken Vergrösserungen kann es jedoch notwendig sein, das Deckglas direkt auf die Wurzel zu legen. Bei der Untersuchung verwendet man am besten dieselbe Nährlösung, in der die Wurzeln gewachsen sind. Soll diese durch eine andere Lösung ersetzt werden, wird die letztere mit Hilfe von Filtrierpapir, ohne das Deckglas zu entfernen, durchgesaugt. Die Lage der Wurzel wird dadurch nicht gestört, so dass man leicht die Wurzelhaare, die man beobachtet, wiederfinden kann.

3. Das Verhältnis zwischen Flächen- und Dickenwachstum in der Spitze der Wurzelhaare.

Das Wachstum der Wurzelhaare ist mit einer Bildung von Zellwandbestandteilen, Zellulosen und Hemizellulosen verschiedener Art, verknüpft. Man muss annehmen, dass diese Stoffe

mit Hilfe von Enzymen aus Glukose oder vielleicht wahrscheinlicher aus Glukosephosphaten in ähnlicher Weise wie Stärke gebildet werden. Die Enzyme, die bei der Zellulosenbildung beteiligt sind, habe ich Zellulosenbildner genannt.

Man wird nun zwei Gruppen von Zellulosenbildern unterscheiden können, einmal diejenigen, die in dem Plasma in einem bestimmten Zeitpunkt anwesend und tätig sind, und ferner diejenigen, die unter gewissen Umständen (z. B. bei Plasmolyse) neugebildet werden können. Es soll in dieser Abhandlung nur die erstere Gruppe von Zellulosenbildnern behandelt werden.

Das Wachstum der Wurzelhaare findet, wie HABERLANDT und andere nachgewiesen haben, ausschliesslich in der Spitze statt. Die wachsende Zone ist sehr kurz, sie beträgt bei *Polygonum fagopyrum* nur 0.013 mm. Man muss daher annehmen, das die Zellulosenbildner der ersten Gruppe in der Spitze des Plasmas lokalisiert sind.

Wenn die Wurzeln mit den Wurzelhaaren in eine Lösung von Kongorot gelegt werden, hört das Flächenwachstum auf. Es entsteht dann in der Spitze der Wurzelhaare auf der inneren Seite der Zellwand eine Verdickung. In einer schwach hypotonischen Dextroselösung können ebenfalls Verdickungen gebildet werden. Bei schwacher Plasmolyse kann die freie Plasmakuppe sich mit einer neuen Zellwand umgeben. Die Entstehung dieser Gebilde erklärt sich am leichtesten durch die Annahme, dass die Zellulosenbildner, die bei dem Flächenwachstum beteiligt sind, nach der Behandlung mit Kongorot oder bei Plasmolyse ihre Tätigkeit fortsetzen und dabei die Verdickung in der Spitze der Wurzelhaare oder eine neue Zellwand erzeugen.

Es soll nun untersucht werden, ob diese Annahme richtig ist.

1. Das zeitliche Auftreten der Verdickung. Die beginnende Verdickung manifestiert sich durch einen schwarzen Saum innerhalb der Primärwand. Dieser Saum ist der Anfang des schwarzen Schattens in der Verdickung, der später erwähnt werden soll. Es kann festgestellt werden, dass man schon 4—6 Minuten, nachdem die Wurzeln in Kongorot gelegt sind, eine beginnende Verdickung nachweisen kann, dass somit die Zellulosenbildung an der inneren Seite der Zellwand fast unmittelbar nach der Behandlung mit Kongorot beginnt. Nach 15 Minuten

ist die Verdickung sehr deutlich, die Grösse derselben ist aber noch nicht messbar.

2. Ein quantitativer Vergleich zwischen der bei dem Flächen- und Dickenwachstum erzeugten Zellulosenmasse. Um die Zellulosenmenge, die während des Flächenwachstums gebildet wird, zu bestimmen, muss man die Diameter des Wurzelhaares, die Dicke der Zellwand, und die Wachstumsgeschwindigkeit des Wurzelhaares kennen. Der gesamte Diameter der Wurzelhaare ist bei *Phleum* etwa 8,64 μ. Die Dicke der Zellwand kann nur schätzungsweise bestimmt werden, sie liegt zwischen 0,5 und 1 μ und wurde auf 0,6 μ veranschlagt. Das Querschnittareal der Zellwand ist dann π. $4{,}32^2 - \pi$. $3{,}72^2 = 15{,}1\ \mu^2$. Wenn man diese Grösse mit dem Zuwachs in μ pro Stunde multipliziert, erhält man die Zellulosenbildung bei dem Flächenwachstum in μ^3 pro Stunde.

Die Zellulosenmasse, die bei dem Dickenwachstum entsteht, bildet eine gegen den Basalteil des Wurzelhaares offene Schale; sie kann nur schätzungsweise bestimmt werden. Man betrachtet die Verdickung als ein Kugelsegment und misst die Höhe (m) und den grössten Radius desselben. Um den Inhalt des Kugelsegmentes zu berechnen, muss man von dem Volumen des umschriebenen Zylinders ($\pi\ r^2\ m$) eine Grösse abziehen, die von dem Verhältnis $\frac{m}{r}$ abhängig ist und aus einer von Höfler errechneten Tabelle (vgl. Strugger 1949) gefunden werden kann.

Das berechnete Volumen des Kugelsegmentes ist einerseits zu gross, weil die Höhlung in demselben nicht berücksichtigt wird, andererseits zu klein, weil auch Verdickungen an der Zellwand unterhalb des Kugelsegmentes vorhanden sind. Es wurde angenommen, dass diese Fehler sich gegenseitig aufheben.

Nachdem die Wachstumsgeschwindigkeit und der Flächenzuwachs in μ^3 pro 30 Minuten eines Wurzelhaares mittlerer Länge gemessen war, wurde die Wurzel 15 Min. lang in eine Lösung von Kongorot in Nährlösung (etwa 0,01 %) gelegt und nachher ausgewaschen. Es wurde dann das Volumen der Verdickung in Zeitintervallen von 30 Minuten gemessen (Tab. 1).

Es geht aus der Tabelle hervor, dass das Dickenwachstum schon 60 Min. nach der Behandlung mit Kongorot beendet ist. Der durchschnittliche Dickenzuwachs betrug in der ersten

Tab. 1.

Nr. der Versuchspflanzen	Flächenzuwachs μ^3 pro 30 Min.	Dickenzuwachs, μ^3 pro 30 Min. Minuten nach dem Aufhör der Behandlung mit Kongorot		
		0—30 Min.	30—60 Min.	60—75 Min.
1	245	20	78	
2	285	10	88	
3	144	62	54	23
4	260	64	0	
5	455	53	45	
6	326	35	40	0
7	390	60	70	10
8	580	60	80	0

Periode 16 %, in der zweiten Periode 19 % des Flächenwachstums.

Die Geschwindigkeit der Zellulosenbildung ist somit, wie zu erwarten war, bedeutend grösser während des Flächenwachstums als während des Dickenwachstums. Die Ursache hierfür ist einmal, dass ein Teil der Zellulosenbildner in der Zellwand zurückbleibt und dadurch inaktiviert wird, und ferner, dass die Zellulosenbildner wahrscheinlich durch das Kongorot ziemlich schnell zerstört werden. Jedenfalls hört das Dickenwachstum bald auf; die Zellen werden jedoch nicht getötet.

3. Ein qualitativer Vergleich zwischen der bei dem Flächen- und Dickenwachstum erzeugten Zellulosenmasse. Es sollen später die Reaktionen der Verdickungen und der jungen Primärwand eingehend besprochen werden. Es wird sich zeigen, dass diese Reaktionen im grossen und ganzen identisch sind, und dass eine weitgehende chemische Übereinstimmung zwischen den bei dem Flächen- und Dickenwachstum erzeugten Zellulosenmassen vorhanden ist.

Es geht aus dem angeführten hervor, dass das Dickenwachstum seinen Anfang unmittelbar nach dem Aufhör des Flächenwachstums nimmt, dass die Geschwindigkeit der Zellulosenbildung während des Dickenwachstums zwar bedeutend kleiner als während des Flächenwachstums, aber immerhin doch ziemlich gross ist, und ferner, dass die Verdickungen ungefähr dieselbe chemische Zusammensetzung wie die Spitze der primären Zellwand haben. Man wird somit folgern müssen, dass die Zellulosenbildner, die das Dickenwachstum er-

zeugen, mit denjenigen, die das Flächenwachstum hervorrufen, identisch sind. Diese Folgerung ist von entscheidender Bedeutung für die folgenden Untersuchungen.

4. Die Umschaltung des Flächenwachstums zu Dickenwachstum.

Die nächste Aufgabe muss sein zu ermitteln, was eigentlich geschieht, wenn das Flächenwachstum zu Dickenwachstum um-

Tab. 2. Die Wurzel wurde 1 Stunde in 0,2 mol. Dextroselösung gelegt und nachher in 0,05 mol. Dextroselösung überführt. Länge einiger Wurzelhaare in μ (vgl. Abb. 2).

	1	2	3	4	5
10^{17}	17	24	58	63	54
10^{37}	17	24	58	65	54
10^{57}	22	24	58	65	54
11^{17}	45	24	58	65	54
		0,05 mol. Dextr.			
11^{27}	54	24	58	65	54
12^{07}	61	24	58 + 15	65	54
12^{37}	95	24 + 2	58 + 54	65 + 13	54 + 4
13^{17}	122	24 + 6	58 + 76	65 + 33	54 + 11
13^{59}	130	24 + 9 (Plasmoptyse)	58 + 83	65 + 37	54 + 15

Tab. 3. Die Wurzel wurde 1 Stunde in 0,25 mol. Dextroselösung gelegt und nachher in 0,05 mol. Dextroselösung überführt. Länge einiger Wurzelhaare in μ (vgl. Abb. 3).

	1	2	3	4	5	6
10^{22}	19	48	67	62	85	133
10^{42}	19	48	67	62	85	133
11^{02}	19	48	67	62	85	133
11^{22}	19	48	67	62	85	133
			0,05 mol. Dextrose			
11^{36}	19	48	67	62	85	133
11^{56}	19	48	67	62	85	133
12^{36}	19 + 19	48	67	62	85	133
13^{16}	19 + 33	48	67	62	85	133
13^{56}	19 + 33	48	67	62	85	133

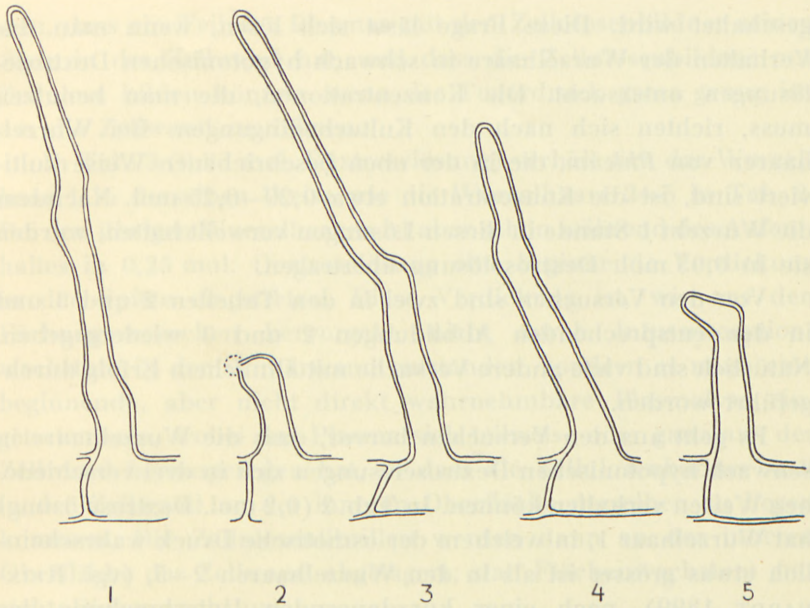

Abb. 2. Wurzelhaare von *Phleum*, 1 Stunde in 0,2 mol., nachher in 0,05 mol. Dextroselösung (Vergr. $\frac{460}{1}$).

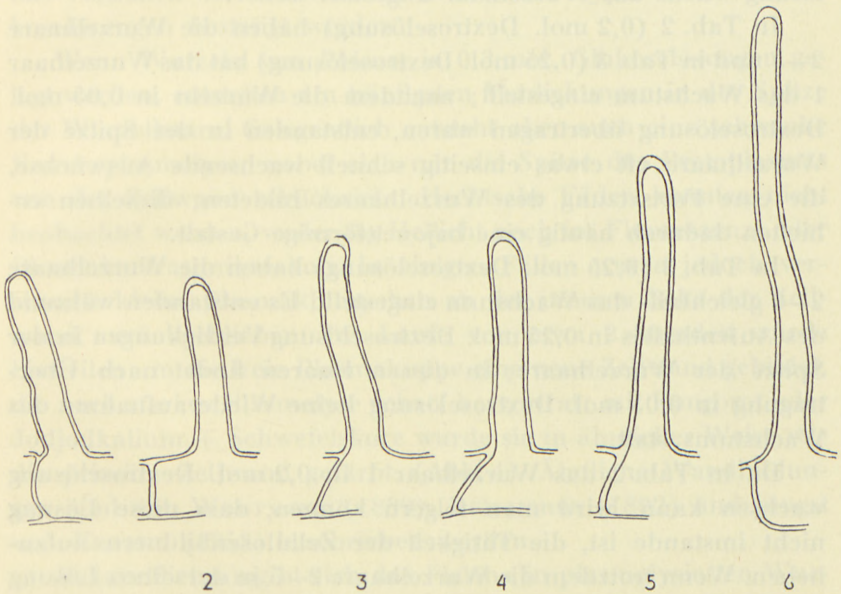

Abb. 3. Wurzelhaare von *Phleum*, 1 Stunde in 0,25 mol., nachher in 0,05 mol. Dextroselösung (Vergr. $\frac{460}{1}$).

geschaltet wird. Diese Frage lässt sich lösen, wenn man das Verhalten der Wurzelhaare in schwach hypotonischen Dextroselösungen untersucht. Die Konzentrationen, die man benutzen muss, richten sich nach den Kulturbedingungen. Bei Wurzelhaaren von *Phleum*, die in der oben beschriebenen Weise kultiviert sind, ist die Konzentration etwa 0,20—0,25 mol. Nachdem die Wurzeln 1 Stunde in diesen Lösungen verweilt hatten, wurden sie in 0,05 mol. Dextroselösung übertragen.

Von den Versuchen sind zwei in den Tabellen 2 und 3 und in den entsprechenden Abbildungen 2 und 3 wiedergegeben. Natürlich sind viele andere Versuche mit ähnlichem Erfolg durchgeführt worden.

Es geht aus den Versuchen hervor, dass die Wurzelhaare in schwach hypotonischen Dextroselösungen sich in drei verschiedenen Weisen verhalten können. In Tab. 2 (0,2 mol. Dextroselösung) hat Wurzelhaar 1, in welchem der osmotische Druck wahrscheinlich etwas grösser ist als in den Wurzelhaaren 2—5, (vgl. REINHARDT 1899), nach einer kurzdauernden Unterbrechung das Wachstum fortgesetzt; nach Übertragung in 0,05 mol. Dextroselösung wuchs das Wurzelhaar ungestört weiter.

In Tab. 2 (0,2 mol. Dextroselösung) haben die Wurzelhaare 2—5 und in Tab. 3 (0,25 mol. Dextroselösung) hat das Wurzelhaar 1 das Wachstum eingestellt; nachdem die Wurzeln in 0,05 mol. Dextroselösung übertragen waren, entstanden in der Spitze der Wurzelhaare oft etwas einseitig schnell wachsende Auswüchse, die eine Fortsetzung des Wurzelhaares bildeten; dieselben erhielten dadurch häufig eine bajonettförmige Gestalt.

In Tab. 3 (0,25 mol. Dextroselösung) haben die Wurzelhaare 2—6 gleichfalls das Wachstum eingestellt. Es entstanden während des Aufenthaltes in 0,25 mol. Dextroselösung Verdickungen in der Spitze der Wurzelhaare; in diesen Haaren findet nach Übertragung in 0,05 mol. Dextroselösung keine Wiederaufnahme des Wachstums statt.

Da in Tab. 2 das Wurzelhaar 1 in 0,2 mol. Dextroselösung wachsen kann, wird man folgern können, dass diese Lösung nicht imstande ist, die Tätigkeit der Zellulosenbildnern aufzuheben. Wenn trotzdem die Wurzelhaare 2—5 in derselben Lösung aufhören zu wachsen, während sie nach Übertragung in 0,05 mol. Dextroselösung das Wachstum fortsetzen, muss die Ursache dafür

sein, dass ein Teil des Plasmas mit den Zellulosenbildner seinen Platz in der Zellwand hat, und dass die Zellulosenbildner nur Zellulose bilden können, wenn der Tugordruck gross genug ist, um die Zellwand zu dehnen.

In Tab. 3 (0,25 mol. Dextroselösung) verhält sich das Wurzelhaar 1 in derselben Weise wie die Wurzelhaare 2—5 in Tab. 2. Bei den übrigen Wurzelhaaren ist aber schon während des Aufenthaltes in 0,25 mol. Dextroselösung eine beginnende Verdickung in der Spitze eingetreten. Diese Verdickung ist, wie aus den Färbungsversuchen hervorgeht, nicht durch Intussusceptionwachstum in der Primärwand entstanden, sondern es muss eine beginnende, aber nicht direkt wahrnehmbare Plasmolyse eingetreten sein, wobei das Plasma sich teilweise oder ganz aus der Zellwand herausgezogen hat, so dass die Zellulosenbildner statt in der Zellwand an der inneren Oberfläche derselben zu liegen kommen. Die Zellulosenfibrillen werden dann an der inneren Oberfläche der Zellwand abgelagert; statt Flächenwachstum entsteht Dickenwachstum.

Diese Schlussfolgerungen konnten durch Untersuchungen über das Verhalten der Wurzelhaare in schwach hypertonischen Glukoselösungen bestätigt werden.

Wenn Wurzeln von *Phleum* in 0,3 mol. Glukoselösungen gelegt werden, entstehen am häufigsten Verdickungen in der Spitze der Wurzelhaare. Gelegentlich entsteht aber auch eine schwache Konvexplasmolyse, wobei sich nur die Spitze des Protoplasmas von der Zellwand zurückzieht. Hechtsche Fäden konnten nicht beobachtet werden, weder im Hellicht noch im Fluoreszenz- oder Phasenkontrastmikroskop. In einigen Fällen waren jedoch vereinzelte kleine Plasmaklümpchen an der inneren Seite der Zellwand zurückgeblieben. Im Laufe von etwa 2 Stunden wurde bisweilen um die freie Plasmakuppe eine neue Zellwand gebildet, die nach starker Plasmolyse scharf hervortrat; mit Kongorot oder Jodjodkalium + Schwefelsäure wurde sie in ähnlicher Weise wie die primäre Zellwand gefärbt. (Abb. 4). Ähnliche Wandbildungen sind von Wortmann (1889), Reinhardt (1892) und jüngst von Ekdahl (1953) beschrieben worden.

Bekanntlich umgibt sich das Plasma in plasmolysierten Wurzelhaaren häufig mit einer neuen Zellwand. Es ist nun die Frage, ob die oben erwähnte neugebildete Zellwand von den in dem

intakten Wurzelhaar anwesenden oder von neugebildeten Zellulosenbildnern erzeugt wird. Da sie wie oben erwähnt in einigen Fällen im Laufe von zwei Stunden entstand, muss man annehmen, dass sie von Zellulosenbildnern, die vor der Plasmolyse in der Zellwand anwesend waren, gebildet wurde. Die neugebildete Zellwand entspricht somit vollkommen den Verdickungen, die in hypotonischen Glukoselösungen auf der Innerseite der Zellwand gebildet werden können. Es finden sich tatsächlich alle möglichen

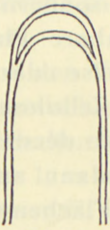

Abb. 4.

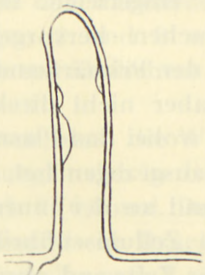

Abb. 5.

Abb. 4. Ein Wurzelhaar von *Phleum* in 0,3 mol. Glukoselösung. Bildung einer neuen Zellwand.

Abb. 5. Ein Wurzelhaar von *Phleum* in 0,5 mol. Glukoselösung. Beginnende Plasmolyse im basalen Teil des Wurzelhaares.

Übergänge zwischen Verdickungen und Zellwänden, die frei im Zellraum liegen.

Wenn die Wurzel kurz nach dem Beginn der Plasmolyse in Nährstofflösung oder in 0,1 mol. Glukoselösung zurückgebracht wird, wird das Flächenwachstum der Wurzelhaare, das während der Plasmolyse abgebrochen war, nicht fortgesetzt. Es geht hieraus hervor, dass die Verbindung zwischen Zellwand und Plasma, wenn sie einmal abgebrochen worden ist, nicht wiederhergestellt werden kann.

Die Plasmolyse in 0,3 mol. Dextrose tritt langsam ein. In 0,5 mol. tritt dagegen häufig ziemlich plötzlich eine Plasmolyse im Basalteile der Haare ein, in der Spitze dagegen nicht (vgl. Reinhardt 1899) (Abb. 5). Aus diesem Versuche kann man schliessen, dass in dem wachsenden Teil des Wurzelhaares eine starke Adhäsion zwischen dem Plasma in der Zellwand und der Zellwand vorhanden ist; in dem basalen Teil des Wurzelhaares

ist die Adhäsion schwächer[1]. Vielleicht zieht das Plasma sich nach dem Abschluss des Wachstums aus der Zellwand heraus. In der Spitze von Wurzelhaaren, die in 0,5 mol. Dextroselösung in der Basis schwach plasmolysiert gewesen sind, scheint bisweilen nach Deplasmolyse ein schwaches Wachstum wieder eintreten zu können.

Tab. 4. Länge der Wurzelhaare in μ

10^{00}	52	66
10^{15}	80	90
10^{35}	111	118
Plasmolyse		
10^{52}	114	123
11^{05}	123	130
11^{22}	157	163
11^{50}	200	213
12^{05}	216	226

Die Wurzelhaare von *Lepidium* (Wasserhaare) verhalten sich etwas anders als diejenigen von *Phleum*.

In schwach hypertonischen Lösungen tritt eine Konvexplasmolyse ein. An der freigelegten Zellwand liegen kleine Plasmaklümpchen, die durch Hechtsche Fäden mit dem Plasma verbunden sind. Gelegentlich kann man beobachten, dass die Plasmakuppe in eine Spitze ausgezogen wird; diese wird später abgeschnürt und an die Zellwand hingezogen (vgl. Reinhardt 1899).

Bei den Plasmolyseversuchen mit *Lepidium* wurde niemals eine neue Zellwand um die freie Kuppe des Plasmas gebildet.

Das Verhalten der Wurzelhaare nach einer kurzdauernden Plasmolyse geht aus der beigefügten Tabelle 4 hervor. Nachdem die Wachstumsgeschwindigkeit von zwei Wurzelhaaren gemessen war, wurde die Wurzel in 0,3 mol. Glukoselösung gelegt. Es trat eine schwache Plasmolyse ein, die etwa 10 Minuten dauerte. Nachher wurde die Wurzel wieder in Nährlösung übertragen. Es geht aus dem Versuche hervor, dass eine Wiederaufnahme des Wachstums der Wurzelhaare nach der Plasmolyse stattfindet. Man wird hieraus schliessen müssen, dass bei *Lepidium* das Plasma bei schwacher Plasmolyse in der Zellwand liegen bleibt, und dass es sich nach Deplasmolyse wieder mit dem übrigen Plasma, mit dem es durch Hechtsche Fäden verbunden ist, verschmelzen kann.

[1] Man ist somit jedenfalls in einigen Fällen imstande, die Orte zu bestimmen, an denen die Adhäsion zwischen dem in der Zellwand vorhandenen Plasma und der Zellwand am grössten ist, indem bei Plasmolyse das Plasma an diesen Orten an der Zellwand haftet, während es sich an den übrigen Orten von der Zellwand abhebt. Die Orte der stärksten Adhäsion können durch Wundreize verändert werden (vgl. Strugger 1949 S. 91).

Aus den mit *Phleum* ausgeführten Versuchen wird man folgern können: Während des normalen Flächenwachstums in der Spitze der Wurzelhaare liegt die Plasmaoberfläche mit den Zellulosenbildnern in der Zellwand, und es ist zwischen dem in der Zellwand liegenden Plasma und der Zellwand eine starke Adhäsion vorhanden. Die neu erzeugten Zellulosefibrillen werden zwischen den schon vorhandenen eingelagert. Durch verschiedene Mittel, namentlich durch Behandlung mit Kongorot, β-Indolylessigsäure, Trijodbenzoesäure und vielen anderen Stoffen, kann die Adhäsion aufgehoben werden, und die Plasmaoberfläche mit den Zellulosenbildnern zieht sich aus der Zellwand heraus. Dasselbe kann durch schwach hypertonische Dextroselösungen erreicht werden. Wenn die Zellulosenbildner auf der inneren Seite der Zellwand zu liegen kommen, entsteht eine Verdickung; bei schwacher Plasmolyse kann eine neue Zellwand um die freie Plasmakuppe gebildet werden.

Die Umschaltung des Flächenwachstums zu Dickenwachstum kommt somit dadurch zustande, dass das Plasma sich aus der Zellwand herauszieht.

5. Das Dickenwachstum in der Spitze der Wurzelhaare.

a. *Die chemische Beschaffenheit der Verdickungen.*

Um Verdickungen hervorzurufen wurden Pflanzen, die in der oben beschriebenen Weise in der Nährlösung I_b + II auf Japonaispapier kultiviert waren, in 0,25 mol. Glukoselösung gelegt. Nach 4 Stunden wurden sie in 1 mol. Glukoselösung übertragen und am nächsten Tage untersucht. In den meisten jüngeren Haaren waren Verdickungen vorhanden.

1. Methylenblau. Sowohl die Primärmembran als die Verdickungen färben sich stark blau. Die Grenze zwischen Primärmembran und Verdickung war sehr undeutlich.

2. Kongorot. Während die Verdickungen, die mit Kongorot erzeugt werden, intensiv rot sind, ist die Färbung der Verdickungen, die in 0,25 mol. Dextroselösung entstehen, etwas ungleichmässig, bisweilen schwach, bisweilen stark rot. Im Anfang ist die Grenze zwischen Primärmembran und Verdickung deutlich, später kann sie kaum beobachtet werden.

3. Resorcinblau. Die Verdickungen entweder ungefärbt oder sehr schwach blau.

4. Rutheniumrot. Die Verdickungen färbten sich etwas ungleichmässig bisweilen schwach, in einigen Fällen stark rotviolett. Eine Grenze zwischen Primärmembran und Verdickung war nicht vorhanden.

5. Jod-jodkalium + Schwefelsäure. Die Wurzeln wurden einige Minuten in Jod-jodkalium gelegt, nachher wurden eine Mischung von 2 Teilen conc. Schwefelsäure und 1 Teil Wasser am Rande des Deckglases zugesetzt. Die Verdickungen quellen stark und färben sich schwach blau. Eine Grenze zwischen Primärmembran und Verdickung war nicht nachweisbar.

6. Behandlung mit Salzsäure und Ammoniak. Wurzeln mit Verdickungen in den Wurzelhaaren wurden 12 Stunden in eine Mischung von 2 Teilen conc. Salzsäure und 8 Teilen Alkohol gelegt. Nachher wurden sie gründlich ausgewaschen, mit 2 % iger Ammoniaklösung 30 Minuten extrahiert und wieder ausgewaschen. Bei diesem Verfahren sollten alle Pektinverbindungen gelöst werden, die Verdickungen waren aber nach der Behandlung nicht verschwunden, sie können somit nicht ausschliesslich aus Pektinverbindungen gebildet sein. Wenn die Wurzeln nachher mit Jod-jodkalium und Schwefelsäure behandelt wurden, färbten sich die Verdickungen bisweilen schön blau oder violett.

Es soll hinzugefügt werden, dass die Verdickung nicht immer ganz homogen ist, indem die Reaktionen des inneren Randes derselben häufig kräftiger sind als diejenigen der übrigen Verdickung. Dies deutet wahrscheinlich daraufhin, dass der innere Rand mehr Zellulose enthält als der übrige Teil der Verdickung.

7. Dunkelfeldbeleuchtung. Wenn man mit Dunkelfeld arbeiten will, ist es vor allem notwendig, das Gesichtsfeld gleichmässig beleuchtet zu haben. Man erreicht dies am besten, wenn man ein Präparat mit verdünnter Milch unter dem Mikroskop anbringt, und die Beleuchtung so einstellt, dass die Fettkügelchen von einer gleichmässigen, leuchtenden Zone umgeben sind.

Bei der Deutung des Bildes, das man bei Dunkelfeldbeleuchtung erhält, muss man sich bewusst sein, dass nicht die Dinge selbst, sondern nur die Grenzflächen als leuchtende Linien hervortreten. Die Zellwand wird somit als zwei leuchtende Linien abgebildet. Ist eine Verdickung in der Spitze des Wurzelhaares vorhanden,

läuft die innere leuchtende Linie der Zellwand an dem inneren Rand der Verdickung herum (Abb. 6).

Es geht aus dem angeführten hervor, dass eine scharfe Grenze zwischen Primärmembran und Verdickung bisweilen nicht vorhanden ist, im grossen und ganzen weisen diese beiden Gebilde dieselben Reaktionen auf, und man darf daher schliessen, dass ihre chemische Zusammensetzung auch dieselbe ist.

Über die chemische Zusammensetzung der jungen Zellwand besteht noch viel Unklarheit (vgl. Whaley, Merle und Heimsch 1952, Wood, Gold, Rawlins 1952). Es kann mit Sicherheit nachgewiesen werden, dass Zellulose sowohl in der Primärmembran als auch in der Verdickung vorhanden ist. Die Zellulosefibrillen sind in eine Masse eingelagert, die wahrscheinlich aus pektinähnlichen Substanzen besteht. Der Zellulosegehalt in den Zellwänden der Wurzelhaare ist wahrscheinlich ziemlich gering.

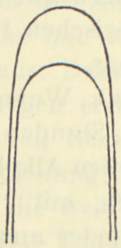

Abb. 6. Wurzelhaar mit einer Verdickung in der Spitze in Dunkelfeldbeleuchtung.

8. Die Orientierung der Fibrillen in den Verdickungen. Durch polarisationsmikroskopische Untersuchungen kann mit Sicherheit festgestellt werden, dass in dem basalen Teil der Primärmembran die Mehrzahl der Fibrillen parallel der Längsachse des Wurzelhaares orientiert ist. Dagegen ist es mit grossen Schwierigkeiten verbunden, zu ermitteln, wie die Fibrillen in den Verdickungen orientiert sind. In einem Falle, wo in einem jungen, sehr dicken Wurzelhaar eine kräftige sekundäre Zellwand gebildet worden war, konnte jedoch mit ziemlich grosser Sicherheit festgestellt werden, dass die Mehrzahl der Fibrillen in der Mitte der Zellwand senkrecht auf die Längsachse des Wurzelhaares hin, d. h. parallel mit der Oberfläche des Plasmas, orientiert war (vgl. Gorter 1945).

b. *Das Protoplasma.*

1. Das strömende Plasma. Der grösste Teil des Plasmas befindet sich in starker Bewegung. Die Protoplasmaströmungen sind ziemlich regellos, grosse Protoplasmamassen werden verschoben, dünne Protoplasmafäden schiessen aus der inneren Plasmawand hervor und bilden neue Plasmastränge, welche die Zentral-

vakuole durchsetzen. Immer entstehen neue Konfigurationen, bald ist die Spitze des Wurzelhaares ganz mit Plasma gefüllt, bald bilden sich im Plasma kleinere oder grössere Vakuolen, bisweilen kann die Spitze von einer grossen Vakuole fast ganz ausgefüllt sein, aber immer bleibt eine dünne Schicht von Plasma an der inneren Seite der Zellwand zurück.

Das strömende Plasma enthält Körner von sehr verschiedener Grösse und Gestalt. Der Körnchengehalt schwankt sehr stark; er nimmt, namentlich wenn die Wurzelhaare geschädigt werden, stark zu. Eine Analyse der Körnchen ist nicht durchführbar. Im

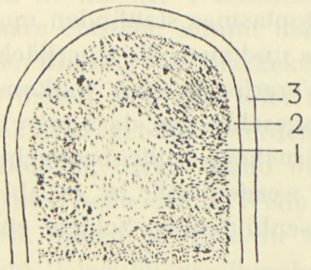

Abb. 7. Die Spitze eines Wurzelhaares. 1 Gekörntes Plasma. 2 Hyaloplasma. 3 Zellwand. Die Plasmafortsätze, die sich in die Zellwand hineinstrecken, sind nicht gezeichnet.

Dunkelfelde beobachtet man neben grösseren kugelförmigen oder etwas eckigen Körnern kleine, stäbchenförmige, stark leuchtende Körperchen, wahrscheinlich Chondriosomen. Auch Plastiden sind ziemlich sicher vorhanden. Es wurde versucht, ob man pektinähnliche Substanzen in dem strömenden Plasma nachweisen konnte. Wurzeln, die mit Alkohol getötet waren, wurden mit Rutheniumrot gefärbt. Die Zellwände wurden violett gefärbt, gefärbte Körner konnten im Plasma nicht nachgewiesen werden.

2. Das Hyaloplasma. Das strömende Plasma ist von der Zellwand durch eine sehr dünne, körnchenfreie Schicht von Hyaloplasma getrennt. Die Dicke derselben beträgt nur 0,5—0,7 μ, d. h. sie ist ungefähr dieselbe oder ein wenig kleiner als diejenige der Zellwand (Abb. 7). Im Hellicht ist sie grünblau gefärbt, im Phasenkontrastmikroskop dunkel; am deutlichsten sieht man sie vielleicht in Wurzelhaaren, die in einer Lösung von Kongorot liegen, sie tritt dann als eine klare rote Schicht zwischen der Zellwand und dem körnigen Plasma hervor, und man kann sie

bis an die Basis des Wurzelhaares verfolgen. In der Spitze entsteht dann nach und nach eine Verdickung, die das Hyaloplasma überdeckt; wenn man dann aber mit 0,5 mol. Glukose plasmolysiert, sind die Plasmaklümpchen von einem hellen Saum, dem Hyaloplasma, umgeben.

Es kann mit ziemlich grosser Sicherheit festgestellt werden, dass die in dem strömenden Plasma vorhandenen Körner nicht in das Hyaloplasma übertreten[1]. Dies ist von grosser Wichtigkeit. Man wird hieraus schliessen können, dass die Körner in dem strömenden Plasma nicht direkt bei der Zellulosenbildung in der Primärwand oder in den Verdickungen, wie sie auf der äusseren Overfläche des Hyaloplasmas stattfinden muss, beteiligt sind.

Das Hyaloplasma und auch die Oberfläche desselben ist selbst bei den stärksten Vergrösserungen vollkommen homogen, und es ist somit ganz ausgeschlossen, dass man die Zellulosenbildner direkt (z. B. als Körnchen) sollte beobachten können. Wie im folgenden dargetan werden soll, ist es aber möglich, über die Struktur der zellulosenbildenden Schicht etwas auszusagen.

e. *Der schwarze Schatten.*

Wenn ein Wurzelhaar mit Kongorot behandelt wird, entsteht, wie wiederholt erwähnt wurde, in der Spitze des Wurzelhaares an der inneren Seite der Zellwand eine Verdickung. Diese bildet entweder eine Halbkugel oder eine nach unten offene Schale. An der Grenze zwischen Verdickung und Plasma findet sich ein tiefschwarzer Schatten. Wenn die Verdickung halbkugelförmig ist, tritt derselbe als eine schwarze Linie hervor, wenn die Verdickung schalenförmig ist, als eine schwarze Fläche. In Wurzelhaaren, die auf Fliesspapier in Luft kultiviert sind, und in denen die Verdickung durch Übertragung in Wasser erzeugt wird, findet sich ein ähnlicher Schatten, der jedoch grau und nicht schwarz ist.

Der schwarze Schatten ist nicht gleichmässig, man hat den Eindruck, dass er fein gekörnt ist. Dass dieser Eindruck richtig ist, wird klar, wenn man eine ganz junge Verdickung, wo der Schatten eine schwarze Linie bildet, betrachtet. Diese Linie ist nämlich am Rande gezahnt.

Bei Plasmolyse bleibt der schwarze oder graue Schatten

[1] Auch nicht in Wurzelhaaren von *Lepidium* konnte ein Übertreten der Körner aus dem flüssigen Plasma in das Hyaloplasma beobachtet werden.

liegen, er gehört somit der Verdickung an und nicht dem Plasma. Man muss schliessen, dass die innere Oberfläche der Verdickung fein gekörnt ist.

Hieraus folgt weiter, dass auch die Oberfläche des Plasmas nicht plan ist, sondern mit Papillen oder Kämmen, die zwischen die Körner an der Oberfläche der Verdickung hineinragen, besetzt ist. Auf diesen hervorragenden Teilen des Plasmas haben die Zellulosenbildner ihren Platz.

d. *Die Theorie des Dickenwachstums.*

Um zu verstehen, in welcher Weise die Verdickung in der Spitze der Wurzelhaare entsteht, nimmt man am besten seinen Ausgangspunkt in der Bildung der Stärkekörner.

In jeder Plastide finden sich eine oder mehrere Organellen, in denen die Stärkekörner gebildet werden. Diese sind wahrscheinlich kleine Vakuolen, deren Wand mit einer Tapete von stärkebildenden Enzymen bekleidet ist. Wenn Glykose- oder Rohrzucker zugeführt wird, bilden die Enzyme Fadenmoleküle. Wie aus Beobachtungen im Polarisationsmikroskope hervorgeht, sind diese senkrecht auf die Oberfläche der Stärkekörner und somit auch auf die Tapetenoberfläche hin orientiert. Allmählich, wenn die Stärkekörner wachsen, dehnt sich die Tapetenoberfläche aus, behält aber ihre Kontinuität. Nur in pathologischen Fällen kann eine Sprengung der Tapetenoberfläche eintreten, so dass man verzweigte Stärkekörner erhält.

In ähnlicher Weise verläuft wahrscheinlich das Dickenwachstum in der Spitze der Wurzelhaare. Wenn das Plasma sich aus der Zellwand herauszieht, ist es, wie oben beschrieben, mit Papillen oder Kämmen, an denen die Zellulosenbildner sich befinden, bekleidet. Diese Schicht erzeugt in ähnlicher Weise wie die Tapetenschicht in den Plastiden Zellulosefibrillen. Diese entstehen wahrscheinlich intraplasmatisch. Da sie aber extraplasmatisch abgelagert werden, müssen sie durch die Plasmahaut herauswachsen. Die Fibrillen stehen annähernd senkrecht auf der Oberfläche der Papillen und sind daher parallel mit der Oberfläche des Plasmas orientiert (Abb. 8). Es entstehen dadurch kleine Warzen auf der

inneren Seite der Zellwand, die nach und nach zu der Verdickung zusammenschmelzen.

Wenn die Verdickung eine gewisse Grösse erreicht hat, hört sie auf zu wachsen, wahrscheinlich weil das zellulosenbildende System in der einen oder anderen Weise inaktiviert wird.

Dass diese Auffassung richtig ist, wird durch die Untersuchungen von ZACHARIAS (1889) über die Bildung der Verdickungen in

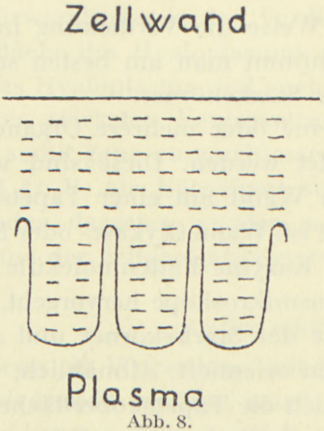

Abb. 8.

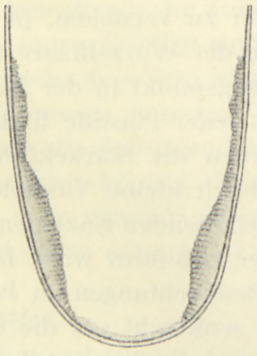

Abb. 9.

Abb. 8. Bildung der Verdickung in der Spitze eines Wurzelhaares (Schematische Darstellung).

Abb. 9. Verdickung in einem Wurzelhaar von *Chara* nach ZACHARIAS (1889), Taf. VII, Fig. 5.

den Wurzelhaaren von *Chara*, wenn diese in Brunnenwasser gelegt werden, bestätigt. Er fand, dass diese Verdickungen ursprünglich von Stäbchen, die senkrecht auf der Plasmaoberfläche stehen, und die später zu einer kompakten Verdickung zusammenwachsen, gebildet werden. Zwischen den Stäbchen sind Plasmafortsätze vorhanden. Es muss somit die Oberfläche des Plasmas ein Netzwerk bilden; in jeder Masche findet sich eine zylinderförmige Vertiefung, die einem. Stäbchen in der Verdickung entspricht (Abb. 9).

6. Das Flächenwachstum der Zellwand.

a. *Die Abhängigkeit des Flächenwachstums von einigen äusseren und inneren Bedingungen.*

1. Baumaterial. Bekanntlich kann Stärke aus Glykose-l-phosphat unter Mitwirkung von Stärkephosphorylase gebildet werden. Man kann sich vorstellen, dass die Zellulosen der Zellwand in ähnlicher Weise durch Zellulosenphosphorylasen aus Glukose-l-phosphat, das durch Hydrolyse von Stärke in Gegenwart von Phosphat entstehen kann, gebildet werden.

2. Zellulosenbildner. Obwohl es noch nicht gelungen ist nachzuweisen, dass tote Wurzelhaare Zellulosen bilden können, muss man annehmen, dass die Zellulosen in der Zellwand von Enzymen oder Enzymsystemen, die ich Zellulosenbildner genannt habe, gebildet werden. Über die Lage derselben in der Oberfläche des Hyaloplasmas wurde oben gesprochen. Im Gegensatz zur Stärkesynthese ist die Zellulosensynthese nicht reversibel.

3. Osmotischer Druck. Aus den im Abschnitt 4 erwähnten Versuchen geht hervor, dass eine Dehnung der Zellwand durch den osmotischen Druck des Wurzelhaares notwendig ist, damit ein Flächenwachstum in der Spitze des Haares stattfinden kann.

4. Sauerstoff. Von besonderer Bedeutung ist es, den Einfluss des Sauerstoffs auf das Flächen- und Dickenwachstum zu untersuchen.

Aus Tabelle 5 geht hervor, dass das Flächenwachstum der Wurzelhaare sofort aufhört, wenn die Wurzel in ausgekochte,

Tab. 5. Die Wurzel wurde 20 Minuten in sauerstoffhaltige Nährlösung, 20 Minuten in sauerstofffreie und nachher wieder in sauerstoffhaltige Nährlösung gelegt. Länge der Wurzelhaare in μ.

sauerstoffhaltige N.	10^{40}	24	10	33	57
sauerstofffreie N.	11^{00}	47	19	47	81
sauerstoffhaltige N.	11^{20}	47	19	47	83
—	11^{45}	47	19	62*	81
	12^{25}	47	19	62	81

* das Wurzelhaar wahrscheinlich gedreht, ein Wachstum hat nicht stattgefunden.

sauerstofffreie Nährlösung, die in einem kleinen Präparatenglas untergebracht ist, übertragen wird. Wird die Wurzel nach 20 oder 40 Minuten wieder in sauerstoffhaltige Nährlösung gelegt, fangen die Wurzelhaare nicht wieder zu wachsen an. Die Wurzel ist jedoch nicht tot; unterhalb der Zone der Wurzelhaare werden neue gebildet. In den Wurzelhaaren, die in sauerstofffreier Nährlösung verweilt haben, entstehen später schwache Verdickungen. In einem einzigen Versuche begannen die Wurzelhaare nach einem Aufenthalt von 20 Minuten in sauerstofffreier Lösung wieder zu wachsen.

Werden Wurzeln $^1/_2$ Stunde in sauerstofffreie Kongorotlösung gelegt und nachher in sauerstofffreie Nährlösung übertragen, entstehen im Laufe von 24 Stunden sichere Verdickungen, die jedoch meistens bedeutend kleiner sind als diejenigen, die in sauerstoffhaltigen Lösungen gebildet werden. Auch wenn die Wurzeln nach einem Aufenthalt von 1—2 Stunden in sauerstofffreier Nährlösung in derselben Weise behandelt werden, entstehen Verdickungen, ja auch ohne Behandlung mit Kongorot können Verdickungen in sauerstofffreier Lösung gebildet werden.

Es geht aus dem oben erwähnten hervor, dass das Flächenwachstum in sauerstofffreier Lösung sofort aufhört, das Dickenwachstum dagegen nicht. Es kann somit auch ohne Sauerstoff Zellulose gebildet werden, jedenfalls wenn Baumaterial vorhanden ist. Die Bedeutung des Sauerstoffs für das Flächenwachstum ist daher wahrscheinlich darin zu suchen, dass die Respiration notwendig ist, um osmotisch wirksame Substanz in die Vakuole hineinzupressen, so dass der Tugordruck trotz der Volumenvergrösserung während des Wachstums aufrecht erhalten wird. Doch dürfte auch die Bildung des Baumaterials (Glykosephosphate?) von der Respiration abhängig sein.

5. Wuchsstoff. Lundegårdh (1946) hat nachgewiesen, dass die Wachstumsgeschwindigkeit der Wurzelhaare von *Triticum* durch Zusatz von β-Indolylessigsäure in Konzentrationen von 10^{-8} bis 10^{-5} n bei pH = 6 nicht merkbar beeinflusst wird. Ich habe untersucht, ob es möglich ist nachzuweisen, dass Wuchsstoff für das Wachstum der Wurzelhaare von *Phleum* notwendig ist, bisher aber ohne Erfolg. Die Ursache hierfür dürfte wohl sein, dass in Wurzelhaaren ein so grosser Vorrat von Wuchsstoffen vorhanden ist, dass man nicht imstande ist, das Wachstum der Wurzelhaare

durch Eliminierung der Wuchsstoffzufuhr, z. B. durch Abschneidung der Spitze, zum Aufhör zu bringen. Wahrscheinlich dürfte jedoch der Wuchsstoff für das Wachstum der Wurzelhaare ebenso notwendig sein wie für das Wachstum der übrigen Zellwände.

Eine Theorie, die die Wirkung des Wuchsstoffes auf das Flächenwachstum in der *Avena*koleoptile und in Sprossen erklären soll, wird zwei Tatsachen berücksichtigen müssen, die zu Auffassungen führen, die jedenfalls scheinbar mit einander unvereinbar sind. Einmal besteht in der *Avena*koleoptile ein genauer quantitativer Zusammenhang zwischen Wachstumsgeschwindigkeit und β-Indolylessigsäurekonzentration; diese Tatsache wird am besten verständlich, wenn man annimmt, dass die β-Indolylessigsäure an einer chemischen Reaktion, die begrenzend auf die Wachstumsgeschwindigkeit wirkt, teilnimmt. Auf der anderen Seite kann aber eine ähnliche Wachstumsbeschleunigung wie diejenige, die durch β-Indolylessigsäure erzeugt wird, durch Stoffe mit einer ganz anderen chemischen Konstitution, z. B. durch α-Napthylessigsäure, hervorgerufen werden. Dies spricht dafür, dass die Wirkung des Wuchsstoffes nicht eine chemische, sondern eine physikalische ist, z. B. eine Oberflächenwirkung, wie Veldstra (1944) annimmt.

Wenn man annimmt, das das Flächenwachstum in der *Avena*koleoptile und in Sprossen in ähnlicher Weise verläuft wie in der Spitze der Wurzelhaare, könnte man sich denken, dass die oben mehrmals erwähnte Adhäsion zwischen dem in der Zellwand vorhandenen Plasma und der Zellwand durch eine Einwirkung des Wuchstoffes auf die Oberfläche des Plasmas aufrecht erhalten wurde. Diese Auffassung wird durch die Versuche von Wortmann (1887) und Bücher (1906) gestützt (Abb. 10). Wenn Sprossen in horizontaler Lage durch Zugspannung verhindert wurden, sich aufwärts zu krümmen, traten nach 36—48 Stunden anatomische Veränderungen in den Geweben ein; die Zellen der Unterseite wurden dünnwandig und grösser als normal, während die Zellen der Oberseite klein und dickwandig wurden, d. h. es fand an der Unterseite hauptsächlich Flächenwachstum der Zellwände statt, auf der Oberseite dagegen Dickenwachstum. Die verschiedene Wachstumsweise der Zellen der Ober- und Unterseite ist zweifellos dadurch bedingt, dass der Wuchsstoff sich auf der Unterseite der Sprossen ansammelt (Boysen Jensen 1936),

so dass die Zellen der Oberseite sehr wuchsstoffarm sind. Da jedoch ein Dickenwachstum in diesen Zellen stattfindet, würde man wohl schliessen können, dass der Wuchsstoff für die Bildung des Zellwandmaterials nicht notwendig ist. Die Umschaltung des Flächenwachstums zu Dickenwachstum an der Oberseite kann dadurch erklärt werden, dass das Plasma, wenn nicht genügend

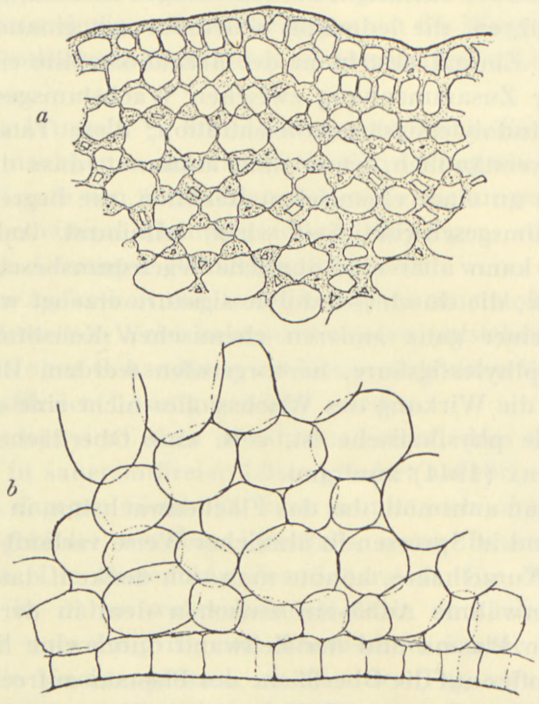

Abb. 10 a und b. Querschnitt durch die geotropisch reaktionsfähige Zone eines 18 Tage in horizontaler Lage gehaltenen Hypokotyls von *Ricinus communis*. a Oberseite (o), b Unterseite (u). Vergr. 137. (BÜCHER).

Wuchsstoff vorhanden ist, sich aus der Zellwand herauszieht. Die Funktion des Wuchsstoffes sollte dann sein, den Kontakt zwischen dem Plasma in der Zellwand und der Zellwand aufrechtzuhalten.

Schwierig ist es jedoch mit Hilfe dieser Hypothese die quantitative Abhängigkeit der Wachstumsgeschwindigkeit von der Wuchsstoffkonzentration in der *Avena*koleoptile zu erklären. Man könnte sich denken, dass die Adhäsion zwischen Plasma und Zellwand nicht gleichmässig über die ganze Zellwand ver-

teilt wäre. Diese Annahme wird dadurch gestützt, das die Adhäsion in der äussersten Spitze der Wurzelhaare etwas kleiner ist als in dem basalen Teil derselben. In 0,25 mol. Dextroselösung tritt nämlich häufig eine schwache Verdickung in der äussersten Spitze ein, so dass der Neuzuwachs, der eintritt, wenn die Wurzel in 0,1 mol. Lösung übertragen wird, einseitig angesetzt wird; das Wurzelhaar erhält dadurch eine bajonettförmige Gestalt (Abb. 2 (3 und 4)). Die Proportionalität zwischen Wuchsstoffkonzentration und Wachstumsgeschwindigkeit könnte daher dadurch zustande kommen, dass die Verbindung zwischen Plasma und Zellwand bei geringer Wuchsstoffkonzentration über einen grösseren Teil der Zellwand gelockert würde, so dass nur ein kleiner Teil der Zellwände an dem Wachstum teilnähme, mit wachsender Wuchsstoffkonzentration müsste dann der wachsende Teil der Zellwände und somit auch die Wachstumsgeschwindigkeit der Koleoptile vergrössert werden.

b. *Die Theorie des Flächenwachstums.*

Während das Dickenwachstum jedenfalls in grossen Zügen erhellt sein dürfte, begegnet man dagegen den allergrössten Schwierigkeiten, wenn man das Flächenwachstum zu verstehen versucht.

In einer früheren Abhandlung (1950, 2) habe ich gezeigt, dass eine Anhäufung von Zellulosenbildnern an dem Ort, wo ein Wurzelhaar gebildet werden soll, stattfinden muss. Ferner wurde oben erwähnt, dass man durch Verminderung des Turgordrucks das Wachstum zum Aufhör bringen kann. Es geht hieraus hervor, dass sowohl Turgordruck als auch Zellulosenbildung notwendige Bedingungen für das Flächenwachstum sind. Sie sind gewöhnlich so genau mit einander verbunden, dass sie nicht getrennt werden können[1], und sie liefern wahrscheinlich gemeinsam die für das Wachstum notwendige Energie.

Die Frage, wo die Zellulosenbildner ihren Platz haben, wurde auch schon oben beleuchtet. Es geht aus den im Abschnitt 4 angeführten Versuchen unzweideutig hervor, dass eine Auflagerung neuer Schichten auf der inneren Seite der Zellwand immer

[1] Gelegentlich kan jedoch, wie viele Forscher beobachtet haben, eine Dehnung ohne Wachstum in der Spitze der Wurzelhaare stattfinden, z. B. wenn eine Wurzel von einer mehr konzentrierten in eine weniger konzentrierte Lösung übertragen wird (vgl. Abb. 2 (3 und 4)).

von einem Aufhör des Flächenwachstums begleitet ist. Man wird daher schliessen müssen, dass bei dem Flächenwachstum die neugebildeten Fibrillen in der Zellwand eingelagert werden, und das ist nur möglich, wenn die Zellulosenbildner ihren Platz innerhalb der Zellwand haben, d. h. es müssen Plasmapapillen oder -kämme sich in die Zellwand hineinstrecken. Das Flächenwachstum in der Spitze von *Phleum* kommt somit durch plastische Dehnung in Verbindung mit Intussusceptionswachstum zustande.

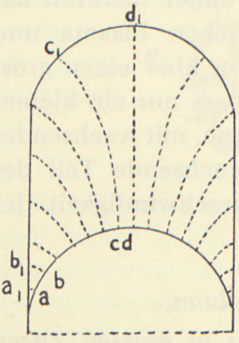

Abb. 11. Schematische Darstellung des Wachstums der einzelnen Teile der Membrankuppe einer Pilzhyphe (nach REINHARDT 1892).

Die Plasmapapillen und Zellulosenbildner sind jedoch nicht gleichmässig in der Membrankuppe verteilt. REINHARDT (1892) hat in einem Schema, das in Abb. 11 wiedergegeben ist, darzustellen versucht, wie das Wachstum der einzelnen Teile der halbkugeligen Membrankuppe verläuft. Wenn die Membran wächst, werden die Punkte a und b nach a_1 und b_1 verschoben, die Punkte c und d dagegen nach c_1 und d_1, d. h. die Wachstumsgeschwindigkeit ist in den apikalen Teilen der Membrankuppe weit grösser als in den basalen Teilen. Hieraus muss man folgern, dass auch die Anzahl der Zellulosenbildner in dem apikalen Teil am grössten ist.

Es ist nun wahrscheinlich, dass die Umfänglichkeit der Verdickung, die man z. B. durch Kongorot hervorrufen kann, mit der Anzahl der Zellulosenbildner in den einzelnen Teilen der Membrankuppe ungefähr proportional ist. Tatsächlich findet man am häufigsten, dass die Verdickung eine nach unten offene Schale bildet, deren Basis an der Grenze der halbkugeligen Spitze liegt; die Dicke der Schale nimmt von dem apikalen Teil nach unten ab. Die Form der Verdickung bildet somit eine Bestätigung der Annahme, dass die Anzahl der Zellulosenbildner in dem apikalen Teil der Membrankuppe grösser als in dem basalen Teil ist.

Man wird somit, wie ich glaube, mit ziemlich grosser Sicherkeit schliessen können, dass bei dem Flächenwachstum die Plasmaoberfläche mit den Zellulosenbildnern als Papillen oder Kämme in die Zellwand hineinragt, dass zwischen Plasma und Zellwand eine starke Adhäsion vorhanden ist, und dass die Menge der

Zellulosenbildner gegen die Spitze der Membrankuppe stark zunimmt.

Der nächste Schritt muss sein zu untersuchen, in welcher Weise das Plasma innerhalb der Zellwand verteilt ist.

Es erhebt sich dabei die Schwierigkeit, zu verstehen, wie die Zellwand gleichzeitig wachsen und eine genügende Festigkeit besitzen kann, um dem recht bedeutenden Turgordruck zu widerstehen[1].

Am einfachsten wäre es sich vorzustellen, dass die Plasmakämme, die in die Zellwand hineinragen, netzförmig mit einander verbunden wären. In diesen Falle würden nämlich die Zellulosenmassen wie Inseln in einer Plasmamasse verteilt sein, und könnten jede für sich durch Anlagerung neuer Fibrillen an den Kanten wachsen. Eine solche Auffassung wird man jedoch ablehnen müssen. Ein Gebilde dieser Art ist nicht existenzfähig, es würde sofort zerreissen.

Wenn die Zellwand eine genügende Festigkeit haben soll, müssen die Zellulosefibrillen ein zusammenhängendes Gerüst bilden. In diesem müssen Kanäle oder Hohlräume, die mit Plasma gefüllt sind, vorhanden sein. Das Plasma ist, wenn es erlaubt ist sich so auszudrücken, die disperse Phase, die in einem dehnungsfähigen Medium, dem Zellulosefibrillengerüst, untergebracht ist.

Zuletzt muss man dann untersuchen, ob in einem solchen Gebilde ein Flächenwachstum möglich ist.

Weil das Plasma nicht gleichmässig in der Zellwand verteilt ist, wird auch die Bildung der neuen Zellulosefibrillen, die an der Oberfläche der Plasmapapillen stattfindet, an bestimmten, scharf begrenzten Orten in der Zellwand lokalisiert sein. Durch die Tätigkeit der Zellulosenbildner werden die Kanäle und Hohlräume mit Zellulosefibrillen gefüllt und vergrössert, d. h. es findet ein Wachstum an vielen scharf lokalisierten Orten statt. Dieses Wachstum bewirkt in Verbindung mit dem Turgordruck, das an anderen Orten der Zellwand eine Auflockerung eintritt, wodurch neue Kanäle und Hohlräume gebildet werden; in diese fliesst

[1] Sehr interessant ist es zu sehen, wie dieses Problem bei verschiedenen Algen gelöst wird. In den *Oedogoniumz*ellen wird bekanntlich die neue Zellwand in dem apikalen Ende der Zellen als ein ringförmiger Wulst angelegt. Die alte Zellwand öffnet sich mit einem kreisförmigen Riss, und der Ring wird zu einer neuen, zylindrischen Zellwand, die eine Verlängerung der ursprünglichen Zellwand bildet, ausgezogen. Ein Intussusceptionswachstum findet somit bei dieser Alge nicht statt, die Bildung der neuen Zellwand ist scharf lokalisiert.

Plasma ein, und es findet nun an diesen Stellen Bildung von Zellulosefibrillen und Wachstum statt. Namentlich in der Spitze der Membrankuppe, wo die Wachstumsgeschwindigkeit am grössten ist, müssen immer neue Papillen in die Zellwand hineingeschoben werden.

Die elektronenmikroskopische Untersuchung der Wurzelhaare von Mais, die von FREY-WYSSLING und MÜHLETHALER (1950) ausgeführt ist, zeigt, dass die Zellwand ausserordentlich locker gebaut ist. Dass die Zellulosefibrillen vor allem in der Spitze der

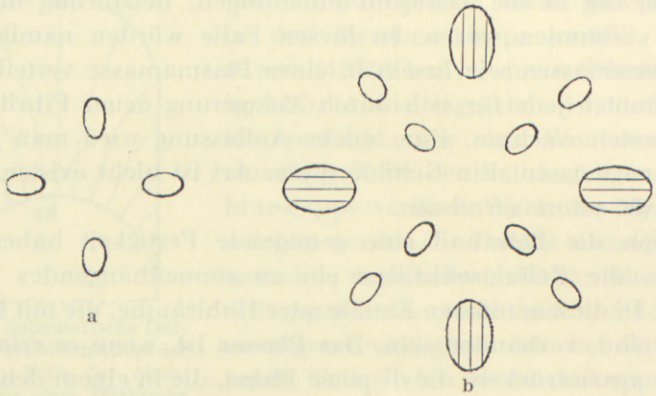

Abb. 12 a und b. Schematische Darstellung der Bildung neuer Plasmapapillen in der Membrankuppe der Wurzelhaare. Wie die Kanäle in der Zellwand verteilt sind, weiss man natürlich nicht. In den Abbildungen sind sie in Ringsystemen geordnet (vgl. übrigens den Text).

Membrankuppe besonders lose verflochten sind, geht aus verschiedenen Tatsachen hervor. Wenn Wurzelhaare in eine stark saure Nährlösung gelegt werden, tritt häufig eine Plasmoptyse ein, d. h. es wird ein Tropfen Plasma durch die Zellwand in der Spitze des Wurzelhaares, wo die Festigkeit der Zellwand offenbar am kleinsten ist, herausgepresst. Dasselbe geschieht, wenn Wurzeln von *Lepidium* oder *Phleum*, die auf feuchtem Filtrierpapir kultiviert sind, in Wasser gelegt werden. Es ist daher wohl nicht schwierig zu verstehen, dass Plasmapapillen oder -kämme an dem apikalen Teil der Membrankuppe in die Zellwand hineingeschoben werden können.

In Abb. 12 habe ich versucht, schematisch darzustellen, wie man sich die Bildung neuer Kanäle vorstellen kann. Die Abb. a und b stellen die Membrankuppe in zwei Entwicklungsstadien

von oben gesehen dar. Die Kreise bedeuten Kanäle, die mit Plasma gefüllt sind. Wenn die Kanäle in a mit Zellulosefibrillen gefüllt und erweitert werden, treten Sprengungen zwischen den Kanälen ein. Gleichzeitig wird, wie in b gezeigt, das Ringsystem in a und damit die Fläche innerhalb desselben erweitert. Als Folge der Erweiterung muss in dieser Fläche ein neues System von Kanälen innerhalb des ursprünglichen gebildet werden.

Diese neugebildeten Plasmapapillen müssen natürlich mit Zellulosenbildnern besetzt sein. Diese können entweder neugebildet sein oder es könnte eine Verschiebung der Zellulosenbildner vom basalen Teil der Membrankuppe gegen die Spitze hin stattfinden. Wenn das letztere der Fall wäre, würde der Aufhör des Wachstums an der basalen Grenze der Membrankuppe durch das Verschwinden der Zellulosenbildner an dieser Stelle zu Stande kommen. — Dass eine Verschiebung der Zellulosenbildner tatsächlich vorkommen kann, hoffe ich später zeigen zu können.

Zuletzt hört auch das Wachstum in der Spitze des Wurzelhaares auf, indem die Zellulosenbildner allmählich zerstört werden. Durch Behandlung mit Kongorot kann man nachweisen, dass in den ausgewachsenen Wurzelhaaren meistens keine Zellulosenbildner vorhanden sind.

Ebenso wie bei dem Dickenwachstum stehen die neugebildeten Zellulosenfibrillen mehr oder weniger senkrecht auf der Oberfläche der Papillen, und sind daher annähernd parallel mit der Oberfläche des Wurzelhaares orientiert, was mit der polarisationsmikroskopischen Untersuchung der Wurzelhaare im Einklang steht.

Die oben geschilderte Theorie des Flächenwachstums kann in folgender Weise zusammengefasst werden. Das Wachstum, das unter Mitwirkung von Turgordruck und Intussusceptionswachstum zustande kommt, findet in jedem Augenblick an vielen, scharf begrenzten Orten, nämlich an der Oberfläche der in die Zellwand hineinragenden Plasmapapillen statt; die Wachstumsorte wechseln aber unaufhörlich, indem immer neue Plasmapapillen namentlich in der Spitze der Membrankuppe gebildet werden.

Diese Theorie vermag zwar nicht alle Einzelheiten des Flächenwachstums in der Spitze der Wurzelhaare zu erklären; sie wird

aber durch so viele Tatsachen gestützt, dass sie wahrscheinlich in den Hauptzügen richtig sein dürfte. Ob sie sich auf das Flächenwachstum in anderen Zelltypen übertragen lässt, muss vorläufig dahingestellt bleiben.

Über andere Theorien des Flächenwachstums vgl. STECHER (1952) (Keimwurzel von Mais), FREY-WYSSLING (1952) (Koleoptilen von Hafer und Mais), EKDAHL (1953) (Wurzelhaare) und KETELLAPPER (1953) (Haferkoleoptile).

Meine Theorie des Flächenwachstums ähnelt anscheinend am meisten derjenigen von STECHER, ist aber nicht mit derselben identisch. In den elektronenmikroskopischen Bildern der Zellwände in der Wurzelrinde von Mais, die von STECHER aufgenommen und von FREY-WYSSLING veröffentlicht sind, finden sich Auflockerungen mit einer Grösse von etwa 0,5—1 μ. Diese Auflockerungen sind nicht mit den oben erwähnten Kanälen oder Hohlräumen identisch, indem die letzteren weit kleiner und wahrscheinlich auch tiefer sind. Wären solche Auflockerungen in der Zellmembran der Wurzelhaare vorhanden, würde man sie auch im Hellichtmikroskop beobachten können. Das ist aber nicht der Fall. Die innere Seite der Zellwand bildet eine ganz ebene Fläche.

Dem Carlsbergfond, der mir die für die Untersuchungen notwendigen Instrumente zur Verfügung gestellt und mich auch in anderer Weise unterstützt hat, spreche ich meinen besten Dank aus.

7. Summary.

The following conclusions may be drawn from the experiments reported in this paper:

The cytoplasm in the root hairs consists of the streaming, granulated plasma, which is surrounded by a thin, clear layer of plasma, the hyaloplasm. From this papillae or crests of plasma protrude into the cell wall in the tip of the root hair.

Elongation arises through a cooperation of two factors, viz. turgor pressure and intussusception, i. e. production of new cellulose fibrils by cellulose-building enzymes on the surface of the papillae. As these are localized in definite places in the cell wall of the tip, growth also takes place at a certain moment on many, sharply defined spots. Through the activity of the cellulose-building

enzymes the hollows in which the papillae are situated are filled out by cellulose fibrils and enlarged. In consequence of turgor pressure and growth new channels and hollows arise especially in the extreme tip of the cell wall. In these hollows new papillae protude, and thus the growth places are shifting incessantly.

There is a strong adhesion between the plasma in the cell wall and the substances of the cell wall. By different means, Congo red, a weak plasmolysis, and so on this adhesion can be broken and the plasma with the cellulose-building enzymes will withdraw from the cell wall. The enzymes continue to build cellulose. The cellulose fibrils will then be deposited on the inner side of the cell wall and a thickening arises, i. e. the elongation is changed to a thickening growth.

Investigations (WORTMANN, BÜCHER) and considerations cited in the text afford some evidence that the significance of the growth substance consists in maintaining the adhesion between the plasma in the cell wall and the cell wall itself.

Pflanzenphysiologisches Laboratorium
der Universität, Kopenhagen.

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MATURE LARVAE OF THE BEETLE-FAMILY ANOBIIDAE

BY

ADAM G. BÖVING

København
i kommission hos Ejnar Munksgaard
1954

CONTENTS

The drawings have been made by the author.

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The present work is dedicated
to
Doctor R. E. Snodgrass
Outstanding Investigator of the Anatomy of Arthropods.
Author, Teacher and Illustrator.
Upright and noble in his dealing with
other men of science.

Preface.

This paper has been prepared for the purpose of presenting the results of an anatomical analysis and taxonomic investigation of the mature larvae of the species belonging to the beetle-family Anobiidae, which are kept in the collection of immature Coleoptera in the U. S. National Museum. It is by no means intended or planned to be a monograph about the anobiid larvae on the whole.

The general taxonomic characterization and the special descriptions of the larvae are considered the core of the study, and the aim of the anatomical dissections, observations and comparisons has been primarily to procure reliable systematic characters to separate the different forms and, in addition, to arrive at a terminology based on a rational comparative anatomical evaluation of the general organization of the body and its special appendages.

It is principally the exterior of the body which has been studied, its cranial parts, many appendages, and the areas of the body-trunk, while most of the internal organization has been little considered because specific and generic taxonomic characters could not be obtained from them. Only the musculature has been investigated in detail on account of the intimate connection which exists between different categories of muscles and certain component parts of the cranium, or certain sulci which limit and define important regions and areas of the trunk, or the various elements of the leg. The muscles have therefore both indicative and corroborating qualities when it comes to defining the exterior body parts.

The taxonomically important feeding apparatus includes both external and internal elements, and the appendicular organs, the

epipharyngeal and hypopharyngeal structures and the alimentary canal have been thoroughly studied.

The taxonomic part of the paper has been elaborated exclusively from my own dissections of material before me. Supplementary information has not been found in the literature, and reference to previous taxonomic papers on the subject has therefore been deemed unnecessary[1]. The actual data given in the comparative anatomical part are likewise brought out by examinations of my own dissections but in the search for the location of single muscles and muscle-associations and what they might mean for the interpretation of the fundamental anatomical organization, I have constantly consulted and been guided by information obtained from publications by Voss[2], Korschelt[3], Snodgrass[4], Anderson[5], and Dorsey[6].

Preliminary studies of the anobiid larvae were made from time to time when I was in charge of the collection of immature stages of Coleoptera in the U. S. National Museum but I began first to occupy myself continuously with the group after my retirement from official work in 1945. From then on I did all my research in a small laboratory in my home, which is located in a quiet and more or less remote part of the city. On account of some heart- and sight-difficulties I did not often risk the trip downtown to the Museum in the heavy traffic of the city center, and it would not have been easy for me to have continued my

[1] Attention should, however, be called to the very useful, weighty paper by E. A. Parkin on the larvae of eight wood-boring european Anobiidae (Bull. Ent. Res., vol. XXIV, pp. 33–68, 1933) in which, besides excellent descriptions of the eight larvae, several items not considered in the present contribution have been dealt with, f. inst. the technique of preparing the larval material, the economic importance and the various shapes of the excremental pellets. It also contains an annotated list of literature on anobiid larvae.

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[6] Dorsey, C. K.: The musculature of the Labrum, Labium and pharyngeal region of adult and immature Coleoptera, Smithson. Misc. Coll., vol. 103, 1943.

contact with it without the unceasing help of my successor, Dr. Wm. H. Anderson. He brought me the books and larval specimens I needed, went over essential parts of my manuscript giving me the benefit of his criticism and suggestions, he even dissected and mounted some rare or difficult to handle material which I hesitated to tackle myself.

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I wish to acknowledge with thanks the gift of larvae from Denmark, which my old friend, the late Mr. J. P. Kryger, had sent me, and which now are included in the collection of the Museum, and I wish also to express my gratitude to Mr. R. A. Crowson of the University of Glasgow who most graciously has presented me with larvae, pupae and imagines of the species *Ochina ptinoides* Marsh., from Ivy in Scotland; this material has likewise been incorporated in the collection of the Museum.

To the members of the "Kongelige Danske Videnskabernes Selskab" ("Royal Danish Academy of Sciences and Letters") who have consented to do me the honour of printing my paper in the series "Biologiske Meddelelser" (bibliographic abbreviation: Dan. Biol. Medd.) of their publications, I am respectfully obliged.

Adam G. Böving
221 Rock Creek Church Road
Washington, D. C.
U. S. A.

Introduction.

It is evident from what was emphasized in the beginning of the preface that a discussion cannot be undertaken in this paper about so wide-ranging a problem as the morphological and taxonomic position of the superfamily Bostrichoidea to which the family Anobiidae belongs. In fact, in the present state of our knowledge, the best that can be done concerning the classification of the larvae of the Bostrichoidea is to give them a preliminary place in the beetle order that merely reflects the current opinions of the majority of competent taxonomists.

On the other hand, the superfamily Bostrichoidea is in itself, regardless of its uncertain position in the order, one of the best defined family-groups in the system, at least according to the larval forms. These larvae possess namely, together with other fundamental characters, the unique one of being equipped in front of anus with the so-called nates, a buttockslike, double-folded and elongate elevation that bears between the folds a sclerotized ribbonlike prolongation of the ventral wall-part of rectum (Pl. 1 and Pl. 11, figs. 1–4).

The taxonomic arrangement of the families which are included in the well-defined superfamily is, however, less settled as, at least, the validity of the family *Ptinidae* is questionable according to the characters of the larvae which are so closely related to the larvae of the Anobiidae that they can be separated from the latter only by the two specific, but weak, characters that the first thoracic spiracle is located laterally close to the anterior margin of prothorax in the known ptinid larvae but not in the anobiid larvae and that their buttockslike anal cushion is somewhat asymmetrical in the known ptinid larvae, symmetrical in all anobiid larvae. But, in addition to this couple of special characters, the ptinid larvae can be separated from the anobiid

larvae by a combination of characters derived from a set of features, each found in one or other of the anobiid larvae but never combined in any member of this family in the way they are in all ptinid larvae. The characters which constitute the combination are the following: Frontal cleavage lines always absent, mandible with only a single apical tooth and the rather short subapical margin produced posteriorly into a toothshaped process, marginal brush absent, lacinia vestigial, only represented by a strong spine, the prodorsal areas of the body trunk and sides of ninth abdominal segment hairy and never armed with hook shaped asperities, pretarsus provided with arolium and a single seta[1].

Leaving the family Ptinidae and the question of its doubtful taxonomic position out of consideration, the larvae of the family Anobiidae, as generally conceived, constitute a very well-marked group of genera and species which readily can be recognized by the combination of the following characters[2]:

1) The *mandibles* are, normally, dentate, at least with two apical teeth and never possess a veritable mola which grinds against an anvillike hypopharyngeal sclerotization.

2) A single *ocellus* equipped with a convex, round cornea is located on each side in many species.

3) The *mesothoracic spiracle* has moved foreward into prothorax but not as far as to near the anterior margin of prothorax.

4) The *body trunk* is more or less curved, soft and, subcircular in cross-section, and the thoracic and abdominal segments are, as a rule, of nearly equal thickness; each segment has no more than two distinct dorsal transverse folds.

5) *Legs* are always present.

[1] Compare: Hall, D.W. and Howe, R.W.:—
A revised key to the larvae of the Ptinidae associated with store products (Bull. Ent. Research, vol. 44, part 1, April 1953). In this paper the authors refer to some previous articles on the subject and notably to an important contribution by S. M. Manton with an introduction by H. E. Hinton (Bull. Ent. Research, vol. 35, 1945, pp. 341–365) in which is given a list of characters for the determination of the larvae of Ptinidae. Included in the list as distinctive features are the different setal arrangements on the adoral side of tibio-tarsus. These items may have potential value also in the classification of the anobiid larvae but I have not paid attention to them in the present study, possibly underestimating their significance.

[2] A detailed taxonomic family characterization will be found on pages 57–61.

6) The *spiracles* are annular but often peculiarly aberrant; airsacs from main tracheal branches are lacking.

An anatomical analysis and comparison of the external and internal structural elements of the bodies of the different genera and species reveal an unexpectedly great variation in the development of many of their organs compared with the standard types displayed in the majority of the larval forms of the family. Thus, the head which usually is hypognathous and protracted is wellnigh prognathous and retracted in a few genera (Pl. 44, figs. 2, 10). The epipharynx and the mandibles are adapted to participate jointly in grinding the spores in the fungivorous genera. In these the usual spines on the sidemargins of epipharynx have disappeared and a molalike enlargement has been developed on the dorsal subapical margin of each mandible (Pl. 48, figs. 3, 4–6, 17). In some genera the maxillary lobes are represented by a lacinia and a galea of equally large size (Pl. 32, fig. 5), in others the lacinia is much the smaller (Pl. 14, fig. 4), and in a few genera almost vestigial (Pl. 16, fig. 5). Generally the lobes sweep the masticated food from the sides of hypopharynx into the preoral cibarium but in the genus *Caenocara* the inner, adoral edge of each lacinia is expanded and hard and grinds the spores of the fungus in which the larva lives against one of two sclerotizations at the base of hypopharynx (Pl. 49, figs. 1, 10, 15). In the majority of the larval forms most of the segments carry asperities on their anterior dorsal folds and a patch of similar asperities on the sides of the ninth abdominal segment (Pl. 1), but in the larvae of a single genus additional asperities are found on most of the tergal epipleural areas and on the tenth abdominal segment (Pl. 50, fig. 20). On the other hand, in several genera the body is completely without asperities (Pl. 41, fig. 6). In the majority of the larvae the legs are not strong but developed normally and each leg has five distinct articles and a single claw. But in several species the claw is lacking and has been substituted by a soft pretarsal bladder (Pl. 45, figs. 8, 14), and in some of the fungivorous larvae the legs as a whole are much reduced (Pl. 49, figs. 3, 19, 20). The fundamentally annular spiracles are transformed in several genera in the most changing and complicated ways unlike anything observed in the larvae

of other coleopterous families (Pls. 15, fig. 8; 35, figs. 6–8; 36, figs. 6–8).

As in any other living larvae, the form and structures of the anobiid larvae undergo a series of changes during the successive periods of their existence but these changes are small, judging from the occasions in which a species is known in all its stages, and, with exception of the first instar, the different instars, always living under the same conditions, are pretty well recognized by the taxonomic characters by which the larger, fully developed larva is determined. For this reason it is assumed to be sufficient to deal exclusively with the mature larvae in the present paper.

The variations from the common anatomical pattern of the nerve-system, the tracheal system and the circulatory apparatus in all members of the anobiid family are so insignificant that no taxonomic characters for the identification of the genera and species can be obtained from them, and no study of these systems has therefore been undertaken, as previously mentioned in the preface.

CHAPTER I

Anatomy.

Division 1. External and Internal Structures of Head Capsule, Ocelli and Antennae.

The head is protracted and hypognathous and the plane of the foramen magnum almost perpendicular on the horizontal midplane of thorax in most anobiid larvae (Pl. 1). But in a few forms, as *Cryptorama minutum* Lec. (Pl. 44, fig. 10), it is quite retracted, almost prognathous, and the plane of foramen magnum is oblique to the posterior part of the cranial roof or vertex (Pl. 2, Vx, fig. 1). Foramen magnum opens widely into the neck-region and is limited posteriorly and laterally by the postoccipital sulcus (Pl. 2, pos, fig. 1) which on each side terminates anteriorly with the long pit (Pl. 2, pt, fig. 1) of the posterior tentorial arm. Posteriorly and laterally the inner wall of the sulcus is deeply inflected in its entire length forming a large endoskeletal apophysis (Pl. 2, PoR, fig. 1) which gradually continues into the bases of the posterior tentorial arms. These proceed from each side to the middle of the head where they meet, fuse and form a broad, transverse tentorial bar or bridge (Pl. 2, Tnt, fig. 1). The anterior tentorial arms are reduced to a pair of membranous, blindly ending, distally obtuse, short projections from the anterior margin of the bridge. They do, however, supply sufficient space for the attachment of the strong maxillary ventral adductor muscles of stipes and cardo (Pl. 6, Tnt, fig. 1). Dorsal tentorial arms are not developed, and there is no sclerotized hypostomal bridge in any anobiid larva.

The open space which is framed by the shelflike postoccipital apophyses (Pl. 2, PoR, fig. 1) and the tentorial bridge (Pl. 2, Tnt, fig. 1) is approximately oval and about half as long and half as wide as the foramen magnum. The cranium is generally suboval,

not fully as broad as long, broadest at the middle but can be subglobose as in *Lasioderma serricorne* F. (Pl. 43, fig. 19) and *Anobium punctatum* Deg. (Pl. 26, fig. 8) or shaped as a round, flattened door-knob, as in *Oligomerus sericans* Melsh. and *Ptilinus basalis* Lec. (Pl. 50, fig. 20) or be elongate suboval with the sides converging strongly behind the middle in a few forms, as *Ptilineurus marmoratus* Reitter (Pl. 50, fig. 2) and the above mentioned *Cryptorama minutum* Lec. (Pl. 44, fig. 2).

The dorsal and lateral parts of the cranial roof form a capsule with continuous wall in most of the larvae, because they lack frontal cleavage lines (= frontal sutures, auct.) and, therefore, a distinct frons well separated from the parietalia (= epicranial halves, auct.). Only in a few larvae, notably *Ernobius mollis* L., *Ernobius abietis* F., and some other species of this genus (Pl. 19, fig. 3; Pl. 20, figs. 2 and 10; Pl. 21, figs. 2 and 9) and in an undetermined larva in an orchid from Mexico, apparently related to genus *Lasioderma*, (Pl. 43, fig. 6) do the frontal lines (Frl) occur, terminating anteriorly outside of the antennal fossae. A distinct midcranial epicranial sulcus (= coronal suture, auct.) is the external groove corresponding to a well-developed internal ridge (Pl. 2, EpicrR, fig. 1) which extends from the foramen magnum to about the middle of the cranium where it often ends at a little dimple in the surface. In cross-section the ridge is shaped as an inverted Y and serves as the attachment place for bundles of mandibular muscle fibers. From the inside of the terminal impression of the epicranial sulcus some fibers of the posteriorly converging labral depressor muscles (Pl. 3, #3 and Pl. 5, fig. 1, #3) originate. The anterior foramen of the cranial capsule is braced by a continuous, usually distinct, strong and well-pigmented facial frame composed of a single epistoma (Pl. 2, Est, fig. 2) and paired pleurostomata (Pl. 2, Pst, fig. 2) and hypostomata (Pl. 2, Hst, fig. 2). Epistoma, morphologically a clypeal derivative between the upper mandibular articulations (Pl. 2, Cat, fig. 1), is separated from the anteclypeus (Pl. 3, Acl, and Pl. 4, Acl, fig. 1) by a transverse anteclypeal sulcus (Pl. 4, Acls, figs. 1, 8) which has a deep inflexion giving rise to an internal ridge to which the base of the anteclypeus is fastened. In several species a transverse row of setae is found on epistoma along the anteclypeal sulcus, numbering, on each side, from two as in

Microanobium sp. (Pl. 46, fig. 4) to many as in *Catorama tabaci* (Pl. 39, fig. 1). The cups of the setae are generally close to the sulcus but from each of them a fine canal can be traced internally through the solid body of the epistoma toward its posterior margin (Pl. 2, scn, fig. 2). The pleurostomata are located between the upper and lower processes with the mandibular articulations (Pl. 2, Cat and Anap, fig. 2). Each pleurostoma is strongly arched around the outer base of the mandible and bears the antenna (Pl. 2, Ant, fig. 2) and a single ocellus (Pl. 2, O, fig. 2). The hypostomata, extending posteriorly from the cups for the lower mandibular condyles, are somewhat weaker and paler at their terminal inner ends than are the other parts of the cranial frame, but these weaker parts are recognizable by small, quite dark sockets (Pl. 2 and Pl. 6, Hst, fig. 1) for the articulations of the maxillary cardines. The posterior boundary line of submentum (Pl. 2, Smt, fig. 1) at the base of labium lies, generally speaking, between and slightly behind these sockets.

In many species, for instance *Catorama tabaci* Guér. (Pl. 39, fig. 1) and *Eucrada humeralis* Melsh. (Pl. 15, fig. 1) the cranial wall behind the mouth frame appears as a rugose, darkly pigmented field often pitted with many round deepenings, each with a seta at the bottom, and in *Ernobius mollis* L. (Pl. 19, fig. 3), and the other species of the genus *Ernobius* which have frontal cleavage-lines, the whole clypeo-frontal region is dark and rather smooth. In *Cryptorama minutum* Lec. a single pointed projection is found in the pigmented field half-way between the anteclypeal sulcus and the terminal impression of the epicranial sulcus (Pl. 44, figs. 1 and 2). A similar projection occurs also in *Holcobius haleakalae* Perk. (Pl. 32, fig. 1) although the two species have no close relationship. In contrast to the condition in the species just described the cranium behind the sclerotized epistoma is entirely smooth and slightly or not pigmented in many other larvae, for instance *Petalium seriatum* Fall (Pl. 42, fig. 11), *Priobium tricolor* Oliv. (Pl. 35, fig. 1) and *Xeranobium macrum* Fall (Pl. 33, fig. 1).

The cranial region behind the epistomal frame, whether pigmented or not, belongs to a common clypeo-frontal unit whose component clypeal and frontal elements are completely fused. Laterally the fronto-clypeal region is, as mentioned, rarely

separated from the parietal parts of the cranium because the frontal lines are lacking in most of the larvae, and transversely the region is not divided by a fronto-clypeal sulcus as the case is in many other larvae. However, the clypeal component contains and is identified by the clypeal dilator muscles of the cibarium (Pl. 3, #5, #6, #7) which are attached to the undersurface of the wall and run anterior to the connecting branches of the frontal ganglion (Pl. 3, FrGng); and the frontal component lies posteriorly to these muscles and extends to the anterior end of the epicranial sulcus. In most anobiid larvae the cranium is provided with many, often very long, soft setae but in a few the number is quite limited. The upper and lower projections with articular surfaces for the mandibles are present and strong in all anobiid larvae. Each of the upper projections, named the catapophyses (Pl. 2, Cat, figs. 1 and 2)[1] is more or less flattened and rounded in outline and marked off from the antennal fossa by a narrow groove in the undersurface of the frame, and also marked off from epistoma by a similar, but wider, inward bent groove (Pl. 2, fig. 2). The inner adoral surface of the catapophysis is smooth, but the outer surface varies in the different species and may be rugulose, or punctured, or setae-bearing, or smooth without setae. The outer groove is indicated externally, often by a series of about five (Pl. 38, figs. 1 and 10), sometimes only by one or two setae and in some species none occur.

The lower articular projection (Pl. 2, Anap, figs. 1 and 2) for the mandible, which may be called "the anapophysis," is subcylindrical with a hemispherical cup or fossa on top. In most species the outer surface is smooth, but in some granulose or rugose or strigate (Pl. 50, fig. 3), and in the genus *Dorcatoma* a rounded, subconical, rugose projection occurs under the articulating fossa (Pl. 48, figs. 11 and 15).

The antennae (Pl. 2, Ant, fig. 2) and *eyes* (Pl. 2, O, fig. 2) are, as mentioned, located in the pleurostomata between the upper and lower mandibular articulations, the antennae nearer the catapophyses and the ocelli nearer the anapophyses. The antennae (Pl. 4, figs. 3, 4, 5, 6), are inserted in funnel-shaped sockets (or fossae) and protected ventrally by a subtriangular casing (Pl. 4,

[1] The term catapophysis has been proposed by Wm. H. Anderson, Proc. Ent. Soc. Wash., vol. 48, 1947.

fig. 5) which usually is thin but sometimes, as in *Coelostethus* (Pl. 22, fig. 2), heavily sclerotized and higher than the catapophysis. In many species, for instance *Ernobius mollis* L. (Pl. 19, fig. 2), each antenna has two distinct articles and a basal membrane which possibly could be interpreted as including elements of a basal article because it often bears two or one large sensilla placodea and because the two distinct antennal articles evidently are homologous with the apical and the second articles of the plainly three-articulated antenna of the larvae of the closely related Bostrichidae family. (See Wm. H. Anderson, 1939; with a picture of the antenna of *Lichenophanes bicornis*.) Of the two distinct articles of *Ernobius mollis* L., the one implanted in the basal membrane is drum-shaped with a broad, well-sclerotized cylindrical barrel-part and terminally covered by a soft membrane. The membrane carries exteriorly one large, ovate sensory papilla, a long sensory hair, a few sensory pores and minute setae and, interiorly toward the sagittal midline of the head, the apical antennal article. The latter is also drum-shaped but not wider than the sensory papilla and about as long as wide. Terminally it is covered, like the first article, with a soft membrane in which two sensory setae are seated. In other species the first article is also barrel-shaped and long, as in *Ptilinus basalis* Lec. (Pl. 4, fig. 6) but very low in other species such as *Ozognathus cornutus* Lec. (Pl. 4, fig. 4) and *Lasioderma serricorne* F. (Pl. 43, fig. 13), the apical article, however, is always low in these larvae and the sclerotization at their bases incomplete or absent. Both articles bear the usual hairs and punctures. Finally in the genus *Anobium* (Pl. 26, fig. 1), genus *Vrilletta* (Pl. 4, fig. 5) and many others, the antenna is reduced to a simple, undifferentiated, completely membraneous, dome-shaped elevation but it carries, nevertheless, the ovate, sometimes conical papilla, the regular sensory setae and punctures besides large sensilla placodea (Pl. 4, S.plac, fig. 5). A remarkable development of the tactile papilla is found in *Nevermannia* (Pl. 28, fig. 10), *Dorcatoma dresdensis* Herbst (Pl. 4, fig. 3), *Eutylistus intermedius* Lec. (Pl. 47, fig. 1) and related dorcatomoid forms. In these larvae the papilla is not ovate, or short and conical, but sausage-shaped or elongate oval. Two small bundles of muscle-fibers, a depressor and a levator, have

been observed inserted at the base of the antenna and attached on the cranial wall (Pl. 4, fig. 3 and Pl. 19, fig. 2).

Some anobiid larvae appear to have a well-developed, simple, lateral ocellus on each side of the head, provided with a strongly arched, clear cornea and a great amount of black pigment, except in the termitophilous *Nevermannia* in which cornea is flattened and the black pigment seemingly lacking. In other anobiid larvae no ocelli can be detected.

Division 2. Labrum and Anteclypeus.

Labrum (Pl. 4, Lm, fig. 1) and *Anteclypeus* (Pl. 4, Acl, fig. 1) are two separate parts of a flat lobe whose outer surface in anobiid larvae is approximately on the level with the dorsal surface of the head, while the inner surface gradually slopes down posteriorly to the entrance of pharynx (Pl. 3, Phy). The outer or dorsal surface of anteclypeus is, on the whole, a naked, smooth, uniform, membranous connecting feature separated from the clypeofrontal region by a distinct anteclypeal sulcus (Pl. 4, Acls, figs. 1 and 8)[1]. However, in many larvae the posterior anteclypeal margin is enforced by a narrow sclerotized transverse band which expands at each end into a small pigmented plate (Pl. 4, Aclp, fig. 1) with well-developed setae, varying in number and lengths according to species. In some larvae the band is lacking but the plates with setae are present, and in *Eutylistus intermedius* Lec. (Pl. 4, fig. 8) two long setae are found on each side at the base of anteclypeus but there are no sclerotized band or plates. A different development is, on the other hand, met with in *Coelostethus notatus* Say (Pl. 22, fig. 2) where the whole anteclypeus is heavily sclerotized and set with deeply impressed punctures. Posteriorly, in each corner, a group of about ten fairly long setae is present as customary in many of the other larvae of the family. *Trypopitys* (Pl. 24, fig. 3) [and the doubtful *Hadrobregmus carinatus* Say (Pl. 23, fig. 2)] are also provided with a posterior anteclypeal covering but it is much smaller than in *Coelostethus*.

The labrum (Pl. 4, Lm, fig. 1) is moveably connected with

[1] Probably not identical with an "epistomal sulcus" which is understood to be located to the rear of clypeus, or the rear of postclypeus when clypeus is divided into ante- and postclypeus.

clypeus (i.e. postclypeus) by the normally membranous anteclypeus. Proximally it is prolonged into a pair of tormae (Pl. 2, torma, fig. 1: and Pl. 5, figs. 1 and 3) which extend back under anteclypeus and carry the strong labral depressor muscles (Pl. 3, #3 and Pl. 5, fig. 1, #3) from the anterior end of the ridge of the epicranial sulcus. There are a few small labral compressor muscles (Pl. 3, #1). The outline of labrum varies in the different larval forms from subrectangular with rounded corners and the width greater than the length (Pl. 4, fig. 1) to subcircular (Pl. 4, fig. 10) and to longer than wide with a strongly arched front margin (Pl. 4, fig. 11). The subrectangular type is the most common, sometimes showing a slightly concave anterior emargination, and differing in the relation between width and length. It is for instance comparatively broad in *Catorama* (Pl. 39, fig. 1), *Ernobius* (Pl. 19, fig. 3) and related genera but more narrow in *Anobium* (Pl. 26, fig. 3), *Hadrobregmus* and *Ptilinus* (Pl. 50, fig. 15). The subcircular type is found notably in *Nicobium* (Pl. 33, figs. 10 and 11), *Trichodesma* (Pl. 34, figs. 2 and 3) and related genera, in *Oligomerus* (Pl. 31, figs. 12 and 14) and *Ptilineurus marmoratus* Reitter (Pl. 50, figs. 1 and 2) from Japan. The elongate type is characteristic of many, but not all, of the fungivorous larvae and occurs for instance in *Eutylistus* (Pl. 47, figs. 4 and 12) and *Dorcatoma* (Pl. 48, figs. 14 and 15). However, in the genus *Caenocara* the labrum varies from subcircular as in *Caenocara oculata* Say (Pl. 49, figs. 11 and 13) to broadly heart-shaped in *Caenocara bovistae* Hoffm. (Pl. 4, fig. 2 and Pl. 49, fig. 2). The labral surface is well sclerotized, shieldlike, commonly covered with rather numerous moderately long setae, and in larvae with subcircular labrum with particularly numerous, long and fine ones. Only a few setae are found in *Microanobium* (Pl. 4, fig. 9), namely, three long and one short on each side; one or two setae on each side are found in most of the fungivorous genera as in *Dorcatoma* and *Eutylistus* (Pl. 4, fig. 8).

In many larval forms but particularly distinct in *Ernobius mollis* L. (Pl. 5, Mark, fig. 1) and *Microbregma emarginatum* Dufts., (Pl. 27, figs. 1 and 3) a pair of pyriform or oval wartlike thickenings occur on the other side of the labral shield at its anterior margin on each side of the sagittal line, and from each of the thickenings a weak and colorless, frayed strand, the

beginning of a labral rod, appears to originate, continuing its course through the inner space of labrum toward the terminal anterior part of one of the tormae with which it finally combines to a joint feature (Pl. 27, fig. 3). In many larvae similar, but usually less distinct, labral marks and labral rods have been found, and it would seem plausible to expect that structural elements, homologous with the described items, would occur in all anobiid larvae, but this seems not to be the case.

Division 3. Epipharynx, Hypopharynx, Preoral Cibarium and Pertinent Muscles.

Epipharynx (Pl. 2, Ephy, fig. 1), the inner surface of the combined labrum, anteclypeal and postclypeal regions which form the upper and facial surface, appears as a continuous membrane extending, as mentioned, from the anterior and lateral margins of labrum to the entrance of pharynx. It contains, however, two clearly distinguishable parts corresponding to the two main component parts of the upper surface. The anterior part (Pl. 3, LmEphy, and Pl. 5, LmEphy, fig. 1) lies beneath labrum and anteclypeus ending at a transverse low ridge between the terminal tips of the tormae, and the posterior part (Pl.3, ClpEphy, and Pl. 5, ClpEphy, fig. 1), corresponding to the clypeal region, extends from this ridge to where pharynx begins at a transverse fold between the lateral angles of the pharyngeal orifice (Pl. 5, Mouth, fig. 1). With reference to their location in relation to the labrum with anteclypeus and the clypeus, the anterior part of epipharynx will be termed the labral epipharyngeal area (LmEphy) and the posterior part the clypeal epipharyngeal area (ClpEphy).

The labral epipharyngeal area comprises a complex of several regions which on the whole correspond to the epipharyngeal regions of scarabaeid larvae as they have been defined and named by Böving[1] and Ritcher[2] and the same terms will therefore be applied to the homologous regions, structural details and setal arrangements of the anobiid larvae. In the following de-

[1] Böving, Adam G.: Description of the larva of *Plectris aliena* Chapin and explanation of new terms applied to the epipharynx and raster. Proc. Ent. Soc. Wash., vol. 38, pp. 169–185, 1936.

[2] Ritcher, P. O.: a) Coprinae of Eastern North America, Kentucky Agric. Exp. Station, University of Kentucky, Lexington; Bull. 477, pp. 1–23, June, 1945.
b) North American Cetoniinae, ibidem, Bull. 476, pp. 1–39, June 1945.

scription of the labral epipharyngeal region the one found in *Ernobius mollis* L. has been chosen as a convenient general type to start with. In this larva two pairs of small, simple, coryphal setae are present inside the middle of the anterior margin of epipharynx (Pl. 5, Co, fig. 1) but in other larvae similar but several setae are found in this region and in *Ptilineurus marmoratus* Reitt. (Pl. 4, fig. 10) a great number of small but hook-shaped setae occurs, and in many of the fungivorous dorcatomoid larvae (Pl. 4, Co, fig. 11) the region is strongly sclerotized and armed with robust toothlike setae. However, in most anobiid larvae the region merges with and becomes an integral part of the combined acroparial and acanthoparial marginal arrangement of spiny setae (Pl. 4, Acr, and A, fig. 7). In *Ernobius mollis*, and most of the anobiid larvae, a naked gymnoparial region (Pl. 4, G, fig. 7) lies on each side between the acanthoparial setae and the chaetoparial setae (Pl. 4, C, fig. 7) which in *Ernobius mollis* as in most of the other larvae extend back to the anterior end of the torma on the same side. The chaetoparial setae correspond to a region which exterio-laterally borders the central hairless region of pedium (Pl. 4, P, fig. 7). The posterior part of the labral epipharynx lies between the paired labral rods plus tormal features, and extends back to the transverse line separating it from the clypeal epipharyngeal area. It (Pl. 4, Cri, fig. 7) is homologous with the crepidal region of scarabaeid larvae which essentially has a sense function, is velvety pubescent, and often provided with sensory pores[1]. The general pattern of the described labro-epipharyngeal area is repeated in the majority of the larvae but is obscured or completely eliminated in larvae with subcircular labrum in which the entire or almost entire labro-epipharyngeal surface is covered with long, uniform setae (Pl. 4, fig. 12). Neither are V- or Y-shaped rod-plus-tormal features found in these larvae but only short, curved and cornuiform tormae. Simple, non-combined tormal sclerites are also found in *Petalium* (Pl. 42, fig. 12) and in *Cryptorama* (Pl. 4, fig. 7) where they are straight, rather long and slender, and in *Eutylistus* (Pl. 4, fig. 11) and other

[1] It is noteworthy that the posterior ends of the tormae bend strongly toward each other in many anobiid larvae (Pl. 4, figs. 2 and 12), carrying the labral depressor muscles with them. This corresponds to what is found in scarabaeid larvae where the sagittally fused tormae form a bowed transverse sclerite to which the muscle-fibers of the labral adductor muscle are attached.

fungivorous larvae in which they are straight but very long, pointed and robust. Acanthoparial setae are not developed in the latter larvae and their gymnoparial regions are usually large. In many of the anobiid species the chaetoparial setae are arranged in a single oblique series of six on each side (Pl. 4, fig. 7), in others as in *Ernobius mollis* (Pl. 5, fig. 1) in a small patch and in *Ptilineurus* (Pl. 4, fig. 10) in a large patch. A distinct crepidal region is lacking in *Caenocara* (Pl. 4, fig. 2). The backwards- slanting clypeo-epipharynx (Pl. 3, ClpEphy; and Pl. 5, fig. 1), lined with a smooth, shining intima, forms the hindwall of the cibarium (Pl. 3, Cb) and has the three pairs of upwards-extended muscles (Pl. 3, #5, #6, #7) to raise it. A sheet of circular and longitudinal muscle fibers covers the epithelium of the intima exteriorly.

The hypopharyngeal area (Pl. 3, Hphy, and Pl. 5, Hphy, figs. 2, 5) occupies the median upper part of the lower portion of the head. It is well developed, fleshy, somewhat pyriform and widest anteriorly. It rests upon labium above prementum (Pl. 3, Prmt) and lies behind the often large dorsal part of ligula (Pl. 3, Lig, and Pl. 5, figs. 2, 5) with which it is fused anteriorly. Salivary labial glands are absent. Posteriorly the hypopharyngeal area reaches back to the beginning of pharynx (Pl. 3, Phy, and Pl. 5, Phy, figs. 2, 5). On each of its lateral walls a suspensorial bar (= fultura, auct.) is lodged (Pl. 3, Su, and Pl. 5, fig. 2) which extends from the base of hypopharynx near where the latter joins the ligula and goes to the entrance of pharynx (Pl. 5, Mouth, figs. 2–5). It consists of a shoe-shaped part and a rod that stretches obliquely upward (Pl. 3, Su). A branched muscle, the retractor of the angle of the pharyngeal mouth opening (Pl. 3, #10) arises from the dorsal end of the bar and is inserted on the inner surface of the posterior region of the frontal area behind the frontal ganglion (Fr.Gng). Another muscle runs between the base of hypopharynx at the bar and the tentorial bridge (Pl. 3, #19). The adoral surface of hypopharynx is completely membranous in all of the investigated larvae of the family, except in genus *Eutylistus* (Pl. 47, figs. 3, 6, 9) in which the distal part has become conical and sclerotized, and in *Caenocara bovistae* Hoffm. and *Caenocara oculata* Say (Pl. 49, figs. 1, 10, 15). In these two latter larvae it is the proximal end of each of the suspensorial bars

which has been enlarged to a strong, rounded, well-sclerotized swelling (Su) on the upper surface of hypopharynx, and together the two swellings form a bilobed inculus, or anvil, against which the inner margins of the lacineas (Pl. 49, Lc, figs. 1 and 10) can grind effectively because they, too, are swollen and strongly sclerotized.

Medially the longitudinal adoral surface of hypopharynx may become somewhat concave, and in many larvae, for instance in *Xyletobius walsinghami* Perkins (Pl. 5, fig. 2), is furnished with long, threadlike hairs and a few sensorial pores. Above the shoe-shaped part of the suspensorium the border of hypopharynx is fringed on each side with fine short setae from the curved paragnathal lobe (= superlingual lobe, auct. = maxillula, auct.) (Pl. 5, Slin, fig. 2).

Division 4. Appendages of Head with Muscles and Gland.

Section 4 a. Mandibles.

The mandible (Pl. 5, Md, fig. 4) is proximally full and heavy from the subquadrangular base as high up as on the level with an archshaped, bristle-bearing thickening (arch.elv) in the subapical dorsal margin of the mouthpart. Distally it is more compressed with a convex aboral outer surface and concave adoral inner surface. It is implanted in membrane at the cibarium and is strongly attached to the cranium by two large, freely projecting articulating processes at its base. Its length, width and depth measure about equal. It has no typical mola acting against a hypopharyngeal sclerotization and, contrary to what is the case in the bostrichid larvae in which the entire distal edge is simple, toothless and gouged, it is dentate or pointed in all anobiid larvae, except in *Catorama gracilis* Fall (Pl. 13, fig. 6), in an undetermined closely related larva, and possibly in the *Eucrada* larva (Pl. 15, fig. 3) in which it is quite similar to the distal edge of a bostrichid mandible. The number of the teeth is never more than four but often less. Two apical teeth are usually present and often claw-shaped, and only in a few larvae as *Gastrallus laevigatus* (Pl. 40, figs. 3 and 5) is the second apical tooth absent. The subapical dorsal margin of the distal part of the mandible is more variable than the apical. Thus, in many larvae (Pl. 5, fig. 4 and Pl. 31,

figs. 4, 13) no subapical teeth are present but the edge is low, approximately straight and scraperlike with only a short projection above the arched marginal elevation. In other larvae the edge may be humplike (Pl. 45, fig. 12), or form a pseudomola with a broad, multistriate surface which grinds against the epipharynx (Pl. 47, figs. 10, 10*). In *Hedobia imperialis* (Pl. 16, fig. 3), *Microbregmum emarginatum* (Pl. 27, fig. 4) and *Ernobius champlaini* (Pl. 27, fig. 10) the subapical part of the edge is produced into a single third tooth, and in *Utobium* (Pl. 14, fig. 3), the typical *Ernobius* larvae (Pl. 19, figs. 4, 5) and some other species there are both a third and a fourth tooth.

Adorally the inner concave surface of the mandible is raised, at least from under the two apical teeth, into longitudinal keels which at the ends form a wall around oblong cavities (Pl. 22, fig. 5 and Pl. 43, figs. 1, 12). In some cases, notably in *Nevermannia dorcatomoides* (Pl. 28, fig. 11), the dental keels arise into elongate, flat enlargements. Below the adoral cavities the rest of the inner surface is rather convex all the way to the basal margin. This margin itself is often reinforced by a ribbon-shaped sclerotization (Pl. 22, fig. 5).

The convex exterior side of the mandible is generally smooth. It is adorned by a series of setae (Pl. 5, fig. 4) often from under a small, straight or curved wall located either near the basal margin of the side, or in the middle of the side or, as in *Caenocara bovistae* (Pl. 49, fig. 8) nearer its apex. Another and smaller group of, sometimes bifurcate, setae is usually found at a considerable distance in front of the first, but sometimes close to it (Pl. 5, fig. 4). In a few species, notably *Vrilletta blaisdelli* (Pl. 34, fig. 12) each seta of the first group sits on top of a dome-shaped, small elevation, and in *Caenocara bovistae* (Pl. 49, fig. 8) the region has been developed into a thin-skinned, rather large, transverse elevation with a spray of fine, very long, curved hairs. In several species a single ovate setula (sl), possibly a sense organ, occurs in the space between the proximal and distal setae. The ventral condyle is globe-shaped but the dorsal pivot which fits into the inner surface of the catapophysis is horseshoe shaped and smooth (Pl. 5, fig. 4). From the exterior corner of the basal rim of the mandible between the two articulations a projection extends downward. To this the mandibular abductor (= "retractor")

muscle is attached, coming from the lateral part of the cranium. From the interior basal corner a similar feature projects with which the tendon of the adductor (= "protractor") muscle is connected (Pl. 5, fig. 4). The muscle is very strong and consists of various bundles of muscle fibers which originate from the dorsal and lateral regions of the cranium. The motion of the mandible is regulated by the positions of the articulations and produced by the actions of the adductor and abductor muscles. The end of each mandible is moved in a curve obliquely outward by the abductor muscle and obliquely inward by the adductor muscle. The mandibular edge between the apical teeth and the brush-bearing, arched elevation passes below the lateral part of the labral epipharyngeal area. And this marginal edge may in several larvae, among them larvae with a pseudomolar feature (Pl. 47, figs. 4, 12) act against a large and somewhat hollow gymnoparial region outside of which the acanthoparial setae are lacking. The mandibular first and second apical teeth often wear out by use (Pl. 18, figs. 4, 6), and in *Caenocara bovistae* the apical part and the membranous pad with the long hairs break off early and give place to a lower, new, smooth, and curved margin (Pl. 49, fig. 8). The different shapes of the mandibles of the various species are useful in the classification. Thus, as mentioned above in another connection, most of the larvae of the genus *Ernobius* (Pl. 19 to Pl. 21) have four well-developed teeth but *Ernobius champlaini* (Pl. 27, fig. 10) has only three distinct teeth and *Ernobius marginicollis* (Pl. 45, fig. 4) has but two teeth and the subapical part of the edge has been transformed to a low, long edge; *Xeranobium macrum* (Pl. 33, fig. 4) has two apical teeth and a rounded, compressed, strong, subapical edge, and the fungivorous *Dorcatoma-Eutylistus-Caenocara* species (Pls. 47, 48, 49) have strong pseudomolar structures.

A large gland on each side opens in the membrane in which the mandible is imbedded right behind the inside of the catapophysis and the corresponding dorsal mandibular pivot (Pl. 5, fig. 3).

Section 4 b. Maxillae.

The maxillae (Pl. 6, Mx, figs. 1 and 3 and Pl. 19, fig. 7) are located latero-ventrally to the cranium (Pl. 24, fig. 1; Pl. 29, fig. 4)

with the adoral surfaces of the maxillary lobes facing hypopharynx, usually in a position vertical to the horizontal upper side of the hypopharynx.

Cardo (Cd) and stipes (St) are well developed and movable toward each other in the transverse hinge (Pl. 6, Hng, fig. 3) between the anterior margin of cardo (Pl. 6, Cd III, fig. 3) and the posterior margin of stipes. In outline the scutiform cardo is subtrapeziform with the inner ventrolateral (Cd II) and outer dorsolateral (Cd IV) margins subparallel. The dorsolateral margin ends with an articular process (Pl. 6, a**, fig. 1) which fits into the small maxillary articular sclerite of hypostoma (Hst), and the ventrolateral margin (Cd II) terminates posteriorly with a projection on which a dorsocranial muscle (I) is inserted. The rather short posterior margin (Cd I) is located between the piece with the articulating process (a**) and the insertion place for the dorsally directed muscle to the cranium (I). Across the inner concave bottom of cardo a strong ridge (r) extends obliquely from the middle of the dorsolateral wall to the corner between the ventrolateral (Cd II) and the anterior (Cd III) margins of cardo. A groove (Pl. 6, r, fig. 3) in the exterior surface of the wall corresponds to the ridge (r, fig. 1).

The stipes (Pl. 6, st, fig. 3) is subrectangular, as wide as the anterior margin of cardo and about twice as long as wide. Dorsolaterally the wall is weakly sclerotized and its membranous margin (Pl. 29, D-LMg, fig. 4, and Pl. 19, fig. 7) attached to the strong frame of hypostoma (Hst). The ventrolateral wall of stipes (Pl. 19, V-LMg, fig. 7) is more strongly sclerotized and pigmented than the dorsolateral part and is usually provided immediately inside the thin lateroventral margin with a long and strong bar (Pl. 6, q, fig. 3 and Pl. 19, q, fig. 6) which anteriorly bends upward to the dorsal margin of stipes ending in a somewhat conelike process (Pl. 6, *, figs. 1 and 3). The margin of the ventrolateral wall of stipes joins the soft and pale membrane of the cushioned maxillary articulating area (Pl. 6, Mxamb, fig. 3) which itself joins the membranous submentum (Pl. 6, Smt, fig. 3). Stipes carries in most larvae long and moderately long setae which vary in number according to the genus. Cardo, on the other hand, has usually only a few or no setae.

The lacinia (Pl. 6, Lc, fig. 1) extends from the inside of the

distal part of stipes, and the galea (Pl. 6, Ga, fig. 1) sits on top of stipes together with the maxillary palpus (Pl. 6, Plp, fig. 1) implanted outside the galea and slightly posterior to it. In some larvae as *Nicobium* (Pl. 33, fig. 15) *Dorcatoma* (Pl. 48, figs. 8, 16), *Caenocara* (Pl. 49, fig. 1) and *Ptilinus* (Pl. 50, fig. 24) a transverse armlike sclerotization (Lc-Ga arm) occurs at the base of the adoral surfaces of lacinia and galea extending from the proximal end of the lacinial margin remote from galea to the galeal margin near the palpus. The lacinial margin near galea has a sclerotized edging the proximal end of which articulates with the distal part of the stipital bar (Pl. 6, q, fig. 3) below the top of its conical projection, and the proximal end of the galeal margin toward lacinia articulates with the top of the conical projection (*). The opposite margin of galea has also a sclerotized edging which is particularly strong where it faces the basal article of the palpus. Framed posteriorly by the adoral transverse arm, a soft-skinned region occurs which frequently, as in *Dorcatoma* (Pl. 48, fig. 16) may carry an abundance of very long, fine and soft hairs. The galea is always well developed while lacinia is distinctly smaller in the majority of the genera and even vestigial as in *Hedobia* (Pl. 16, figs. 4, 5) and *Microanobium* (Pl. 46, fig. 8). It is only in the genera *Nicobium* (Pl. 33, fig. 15), *Trichodesma* (Pl. 34, fig. 5), *Oligomerus* (Pl. 31, fig. 17), *Dorcatoma*, with its closely related forms (Pl. 48, fig. 8), and in a few other larvae as the species *Xyletinus fucatus* L., and *Xyletinus mucoreus* Lec. (Pl. 31, fig. 3), that it is as large as galea or at least approximately as large. In genera like *Lasioderma* (Pl. 43, fig. 15), *Catorama* (Pl. 36, fig. 5), *Anobium* (Pl. 26, fig. 10) and many other larvae it is, on the other hand, only half as large or still smaller than galea. In larvae with a small lacinia some, as *Utobium elegans* Horn (Pl. 14, figs. 4, 5), *Ernobius abietis* F. (Pl. 20, fig. 4) and *Gastrallus* (Pl. 40, fig. 4), possess one or a few strong spines on the end of the lobe in addition to the normal lacinial setae on both the inner and the outer side.

The special development of the posteriorly-facing, heavily-sclerotized, inner margin of lacinia in *Caenocara bovistae* Hoffm., and *Caenocara oculata* Say, which previously has been mentioned under the discussion of the hypopharynx, p. 19, l. 36, may properly be recalled here, and attention should also be called to a horizontal

splitting of the anterior marginal part of the galea which is found in the genus *Caenocara* (Pl. 49, figs. 1, 10). The galea extends about as far foreward as the middle of the distal article of the maxillary palpus. It is flat with round outline, usually as wide as long but in a few larvae, as *Gastrallus laevigatus* Oliv. (Pl. 40, fig. 4), only half as wide as long. The distal margin of the lobe is armed with particularly strong setae and the outside and inside are covered, at least partly, with setae which are stiffer and stronger on the outside than on the inside. The lacinia is similarly equipped, as indicated above. Both lobes can be pressed against the sides of the upper part of ligula and of hypopharynx by special muscles (Pl. 6, fga and flcs, fig. 1) whether the stipes is moving forward or obliquely backward.

The maxillary palpus (Pl. 6, Plp, fig. 1) is well developed and can be moved as an entity; but its single articles can also move independently. It consists of either two, three or four articles. An incomplete ring-shaped sclerotization is developed on the bases of the proximal, the second and eventually, in larvae with four articles, of the third article; the terminal article is completely but thinly sclerotized. Three articles occur in most genera, two in *Cryptorama minutum* (Pl. 44, figs. 5, 6) and four are present in the genera *Trichodesma* (Pl. 34, fig. 5), *Nicobium* (Pl. 33, fig. 15), *Microbregma* (Pl. 27, fig. 5) and *Eucrada* (Pl. 15, fig. 4). The terminal article has fine and very short sensory hairs and papillae on the top, and a longitudinal impression into which a setalike rod is imbedded is found exteriorly on the dorsal side (Pl. 19, fig. 7). The function of this organ is probably of sensorial nature.

The two subdivisions of the maxilla, the cardo and the stipes as well as the lobes and the maxillary palpus can perform a number of motions either independently or jointly and a reasonable idea about these movements can be obtained from a study both of the places where the muscles are inserted and attached, and of how the different special articulations are arranged.

The muscle which runs from the end of the ventrolateral marginal process of cardo (Pl. 6, I, fig. 1) to the posterior part of the frontoparietal region of the cranium is the only retractor muscle of the maxilla and probably produces, besides the retraction of the mouthpart, an additional function by assisting in regulating other movements as the rolling of the whole maxilla

toward a side of the hypopharynx. From the hollow inside of cardo and its transverse ridge numerous fibers unite into a strong ventral adductor muscle of cardo (Pl. 6, adcd, fig. 1). It is attached to one of the small anterior tentorial arms (Pl. 6, Tnt, fig. 1). A similar collection of many muscle-fibers constitutes the strong ventral adductor muscles of stipes (Pl. 6, adst, fig. 1). They are inserted principally on the longitudinal ventrolateral bar (q) of stipes and are attached, like the ventral adductor muscles of cardo, to one of the anterior tentorial arms. With the tip of cardo (a**) anchored to the hypostoma (Hst), a simultaneous contraction of the strong ventral adductor muscles of cardo and stipes will straighten the two pieces from the angular position in which they were bent, and thereby push the whole maxilla foreward, including the lobes and the palpus. The pressing of the lobes against hypopharynx is, as said above, performed by contraction of two adducting flexor muscles. One, the stipital flexor muscle of lacinia (flcs) is attached to the posterior part of the stipital wall and inserted on the proximal part of lacinia. The other, the stipital flexor muscle of galea (fga) is, like the corresponding lacinial muscle, entirely intrastipital, is also attached to the posterior part of the stipital wall and is inserted on the proximal part of galea. The two muscles of lacinia and galea lie often close together and may fuse into a single muscle. Coinciding with the pressure exercised by the lobes against hypopharynx the lobes perform a backwards- directed sweeping along the sides of hypopharynx when stipes and cardo move backward and outward into the position of a bent knee. This movement is probably caused mainly by an increase of the blood-pressure when the labial sections are drawn together, but is aided by the contraction of the cranial flexor muscle of lacinia (flcc). The muscle is inserted in the lobe close to the stipital lacinial flexor muscle but diverges from it in a dorsal direction and is, as mentioned previously, attached to the back of the cranium.

The movement of the entire palpus is accomplished by alternating contractions of a depressor (dplp) and a levator muscle (lplp). Both are intrastipital and attached with the flexor of galea (fga) and the flexor of lacinia (flcs) in the posterior region of stipes. Tiny, single muscles may or may not be found running from the base of one palpal article to the base of the next.

The maxillary articulating region (Pl. 6, Mxamb, fig. 3), intermediate between the ventrolateral margin of cardo (Cd II), the posterior ventral corner of stipes and the submentum (Smt), is softskinned, fleshy, and usually carries setae.

Section 4 c. Labium.

The labium (Lb) lies ventrally between the maxillae. The postlabial region, or submentum (Pl. 3, Smt; Pl. 6, Smt, figs. 2, 3), is sessile, rather large and fleshy, trapezoidal in outline, wider posteriorly and usually bearing about ten setae on each side. It is connected, as just stated, laterally with the maxillary articulating membrane and is posteriorly contiguous with the cervical membrane of the neck. Anteriorly the submentum is separated from the prelabium by a transverse infolding, the labial sulcus (Pl. 6, Lbs, fig. 2) which contains and is determined by the anterior points of insertion of the subparallel, ventral, median labial retractor muscles (Pl. 3, #22 and Pl. 6, rst, #22, fig. 3) from the posterior margin of submentum.

The prelabial region is divided into the two labial areas here termed the mesomentum (Pl. 3, Msmt, and Pl. 6, Msmt, fig. 2) (= mentum, auct.) and the prementum (Pl. 3, Prmt and Pl. 6, Prmt, fig. 2) with its ligula (Pl. 3, Lig, and Pl. 6, Lig, fig. 2) and labial palpi (Pl. 6, Lbplp, fig. 2). Mesomentum is, like submentum, trapezoidal in outline and wider behind than in front but somewhat shorter and narrower than submentum. It is fleshy, as the submentum, without sclerites, and bears the same number of about ten setae on each side. Anteriorly it is limited by a transverse, in most larvae arched and narrow, sclerite on the hindmargin of prementum (Pl. 6, PrmtScl, fig. 2), and on this sclerite a pair of ventral labial adductor muscles (Pl. 3, #21, and Pl. 6, vadlb, fig. 3) are inserted sagittally, each muscle composed of two bundles of muscle-fibers. These muscles diverge posteriorly, run quite horizontally through mesomentum and submentum and are attached posteriorly on the tentorial bar (Pl. 3, Tent). Anterolaterally to the distal point of insertion of these ventral adductor muscles, a pair of dorsal labial adductor muscles (Pl. 3, #20, and Pl. 6, dadlb, #20, fig. 3) is inserted a short distance behind the bases of the labial palpi where the ligula

meets the hypopharynx. They run, like the ventral adductor muscles, through mesomentum and submentum but are subparallel and, sloping in a ventral direction, cross and pass below the ventral adductor muscles. They are attached, apparently to the middle of the tentorial bar, or possibly to the internal surface of the base of submentum very close to the bar.

The transverse premental sclerite which, as said above, is arched, narrow and somewhat expanded sagitally in almost all of the anobiid larvae, is strong, elongate and triangular with apex directed backward in the genus *Ptilinus* (Pl. 50, fig. 19).

Ligula (Pl. 3, Lig, and Pl. 6, Lig, fig. 2) is ventrally rather short and conical, dorsally contiguous posteriorly with the hypopharynx (Pl. 5, Lig, fig. 2) in front of the paragnatha (Slin) (= superlinguae, auct. = maxillulae, auct.). In most genera the conical lobe and the dorsal part in front of hypopharynx are set with numerous, pointed, often stiff, setae, and prementum at the bases of the labial palpi may carry a marginal group of long setae.

Each of the labial palpi (Pl. 6, Lbplp, fig. 2) consists of two well-developed articles which generally are slightly smaller than the two distal articles of the maxillary palpus. The terminal article has numerous minute hairs at the end and one or a few sensory papillae like the terminal article of the maxillary palpus but there is no rod-shaped organ on the dorsal side; as a rule a sensory pore is present but no setae. A single seta is found on the proximal article in several of the larvae; some have more than one and in others like *Ernobius mollis* the article is dorsally furnished with a patch of setulae (Pl. 6, fig. 3). Two small muscles, one a levator, (Pl. 3, # 24, and Pl. 6, levplp. # 24, fig. 3), one a depressor (Pl. 3, # 23, and Pl. 6, dep.plp, # 23, fig. 3) are inserted on the base of the proximal article and attached posteriorly to the premental sclerite; they are difficult to discover in many cases.

The movements of the whole labium accompany the protractions and retractions of the maxillae and the movements of the prelabial region may assist the upward, foreward and backward motions of hypopharynx. It is evident that the foreward motion of the free part of labium must be produced exclusively by added bloodpressure as there are no labial protractor muscles.

A distinct *gular area* or a median gular sulcus do not occur

between the neck and the posterior margin of submentum, the latter determined by the places for attachment of the labial retractor muscles (Pl. 6, rst, # 22, fig. 3).

Divisivon 5. Exterior of Neck and Body Trunk.

The *neck or cervical region* is smooth, flexible and shaped like a flat ring which is divided by a median constriction into two parts, an anterior, connected with the hindmargin of the head, and a posterior, connected with the anterior margin of prothorax. The region is short in the anobiid larvae, largest in the few genera with semiretracted heads as *Ptilineurus* and *Cryptorama* (Pl. 44, fig. 10), and its anterior and posterior parts are folded together and hidden under the overlapping anterior margin of prothorax when the head is withdrawn.

The trunk of the body is membranous, soft and pale whitish, usually subcylindrical, of nearly equal thickness throughout, and curved. Only rarely are the larvae elongate, slender and not strongly curved as in *Petalium* (Pl. 42, fig. 16) and *Catorama vestitum* (Pl. 41, fig. 6), or the thoracic part considerably larger than the abdominal as in *Xyltobius* and *Cryptorama*. There are no plate-shaped sclerites, the separation of the segments is obvious and the subdivisions of the principal regions more distinct by segmental grooves than in many other coleopterous larvae in which they are obscured by large sclerites, and there are no urogomphi or similar structures in any of the larvae, except in the first larval stage which is known in a few species. In the inside of the body wall the grooves have usually low ridges but nowhere are these raised to strongly-projecting phragmata, conspicuous apodemes or apophyses. Thus, there are no strong pleural ridges and the pleural apophyses (Pl. 9, PlA, fig. 3) are short, the furcae (= sternal apophyses, auct.) (Pl. 9, furc, fig. 3) are absent and no medioventral apodemal processes, usually named spinae, extend from the spinasternal areas (Pl. 7, Ss, fig. 4; Pl. 8 and Pl. 9, spin, fig. 3) of pro- and mesothorax. Minor upper and lower nodal swellings may project from the upper and lower junctions (Pl. 9, ujc and ljc, fig. 3) of the intersegmental conjunctivae.

The different segmental areas are furnished with setae in all

anobiid larvae, but to a varied degree. In some species all areas are covered profusely with long, soft hairs, as in *Nicobium*, *Gastrallus*, *Trichodesma*, *Lasioderma* and *Ptilineurus*. In most species only some of the segmental areas are well supplied with setae, usually of moderate lengths, and in some of the fungivorous larvae as *Caenocara* (Pl. 49, fig. 4) and *Eutylistus*, the setae are sparse on all the areas and lacking on some of them.

In the majority of the anobiid larvae the prodorsal tergal areas (Pl. 7, PrD, fig. 4) of metathorax and a number of the abdominal segments, varying according to species, are armed with a few or with a single row or a patch of hook-shaped asperities. In a few species, as *Catorama gracilis* Fall and *Utobium elegans* Horn (Pl. 14, fig. 6) asperities are also found on mesothorax, but on the contrary, asperities are completely lacking in several species as in *Catorama vestitum* Fall., *Ozognathus cornutus* Lec. (Pl. 42, fig. 3), *Petalium seriatum* Fall. (Pl. 42, fig. 16), *Microanobium* sp. from China (Pl. 46, fig. 1), *Neogastrallus librinocens* Fisher and *Lasioderma serricorne* F. Aberrantly the asperities are minute, som obtuse others with flat scraperlike top in *Nevermannia dorcatomoides*. With the exception of the genera *Platybregmus* (Pl. 25, fig. 6) and *Anobium* (Pl. 26, fig. 8), all the larvae which possess prodorsal asperities on some of the body segments have also asperities on the lateral tergal regions of the ninth abdominal segments, but prodorsal asperities are always absent on this segment.

A great number of asperities is found on most of the epipleural tergal areas (EPI) of a single genus, *Ptilinus* (Pl. 50, fig. 20), in addition to numerous prodorsal asperities on most of the segments and a large patch on the sides of the ninth abdominal segment. Asperities on the tenth abdominal segments are rarely present but occur in the larvae of *Xestobium rufovillosum* (Pl. 17, fig. 7), *Ernobius mollis* and some other species of the genus *Ernobius*, in *Eucrada humeralis*, *Hedobia imperialis*, *Ochina ptinoides* (Pl. 18, fig. 13 and 14) and a few more larvae. In *Nicobium castaneum* strong, short, but not hook-shaped asperities are present on this last abdominal segment.

The tergal areas of prothorax are fused together to a great extent and cannot be clearly homologized with the areas of the more typical segments.

In meso- and metathorax the composing elements of the two lateral tergal areas, the paradorsal area (= alar area, auct.) (Pl. 7, ParD, fig. 4), including the spiracular area (Pl. 7, SpA, fig. 4) and the epipleural (Pl. 7, Epi, fig. 4) area are in the main united and adapted to accomodate within them the pupal wing-pads. All the three thoracic segments are furthermore somewhat modified in keeping with the presence and functions of the legs. For these reasons the thoracic areas cannot be so precisely identified and defined as the areas of the more simple and typical first to seventh abdominal segments. Even on the somewhat reduced eight abdominal segment the single areas are quite determinable, and only the ninth and tenth abdominal segments are radically changed, the ninth for the purpose of being able to perform special locomotory motions, and the tenth with its nates (see p. 54, J) for aiding the final elimination of the dry excrements.

The tergal region with its areas is separated in *all segments* from the combined pleural and sternal regions by a longitudinal dorsopleural sulcus (Pl. 7 a–a) which dorsally above pleurum extends throughout the entire length of the body from one segment to the next between the lower junctions (Pl. 7, ljc) of the intersegmental conjunctivae (Pl. 7, IMB). In front of each segment a marginal lip is inflected from the intersegmental conjunctiva, and to these low phragmata the segmental longitudinal dorsal muscle-bands (Pl. 8, #1a + 2, and Pl. 10, #A1a + A2) are attached, indicating the beginning and the end of each segment.

The intersegmental conjunctivae in a hasty view appear exteriorly merely as ring-formed grooves between the segments but on the inside their generally simple and continuous walls are interrupted on each side by the upper and lower junctions (Pl. 10, ujc and ljc). These junctions are limited spaces located where the ends of some of the sulci which deliminate different areas approach or join the conjunctiva and are of particular importance as terminological landmarks. The upper junction lies at the ventral tip of the subtriangular half of the prodorsal area (Pl. 7, PrD, fig. 4) where the anterior end of the epipleural sulcus (Pl. 10, EPIs) of the segment and the posterior end of the same sulcus of the preceeding segment approach the conjunctiva.

The lower junction (Pl. 10, ljc) is located where the con-

junctiva crosses the dorsopleural sulcus (Pl. 10a–a), and from this junction the externally rather indistinct anterior and posterior sternal sulci (Pl. 10, ASts and PSts) pertaining to two succeeding segments extend obliquely down in opposite directions. The intersegmental conjunctival ring is simple and quite regular between the abdominal segments but in front of the mesothoracic spiracular area (Pl. 7, SpA, fig. 4) and, less pronounced, in front of the metathoracic spiracular area it is somewhat indistinct and curved forward. Between metathorax and the first abdominal segment it is fashioned as between the abdominal segments.

The tergal region of a *typical abdominal segment* is divided into two dorsal and three lateral areas. The dorsal areas are the prodorsal (Pl. 7, PrD, fig. 4) and postdorsal (Pl. 7, PsD, fig. 4) areas, both mediodorsal and partly laterodorsal. The areas are separated by the oblique prodorsal sulcus (Pl. 10, PrDs). The lateral areas comprise the paradorsal (Pl. 7, ParD), the spiracular (Pl. 10, SpA) and the epipleural (Pl. 7, EPI) tergal areas. The paradorsal and postdorsal areas are fused and the boundary between them only qualified by an imaginary line located approximately outside the longitudinal paradorsal muscle (Pl. 10, Alb) (see: Abdominal muscles p. 40, l. 17) and well above the spiracle. Ventrally the paradorsal area is separated from the epipleural area by the curved epipleural sulcus (Pl. 10, EPIs) below the spiracle. The spiracular area (Pl. 10, SpA) is small, indistinct, located in front of the paradorsal area and contains the spiracle. The epipleural area (Pl. 10, EPI) lies above the dorsopleural sulcus (a–a). More or less centrally it is raised into an often profusely setose lobe and in front of the lobe a triangular small section is present. Behind the lobe lies a similar but larger section the posterior epipleural triangle (Pl. 10, EpT) the apex of which extends up to the rear of the paradorsal area. The pleural and sternal regions below the dorsopleural sulcus (a–a) consist in each segment of a pleural area (= "hypopleurum," auct.) (Pl. 7, Pl) with a lobelike elevation and a ventral boundary marked by a longitudinal pleuroventral sulcus (Pl. 7, b–b), and below the pleural area, of three sternal areas, namely the basisternal area (Pl. 7, BSt), the pedal area (Pl. 7, PdA) and the sternellar area (Pl. 7, Stl). The latter three areas are separated by the oblique anterior (Pl. 10, ASts) and posterior (Pl. 10, PSts) sternal sulci. In each

typical abdominal segment the two sulci converge, and consequently the anterior basisternal, the median pedal and the posterior sternellar areas are more or less distinctly subtriangular, the basisternal and the sternellar areas vaguely right-angled with apices toward the dorsopleural sulcus and the pedal area vaguely isosceles triangular with the apical part directed toward the midventral sagittal line.

In the *meso- and metathoracic segments* an oblique linear depression, the paradorsal line (Pl. 7, ParDL) is found between the postdorsal and paradorsal tergal areas. It has apparently no corresponding ridge on the inside but is a constant feature lacking in the abdominal segments and constitutes a rather indistinct dorsal indication of the meso- and metathoracic paradorsal areas.

The distinct separation between the paradorsal and epipleural tergal areas of the typical abdominal segments is, on the other hand, not found in the meso- and metathoracic segments and the two areas have, as mentioned previously, to a considerable degree been combined into a single large composite area eventually covering a pupal wingpad. To be sure, a curved line corresponding to the distinct epipleural sulcus (Pl. 7 and Pl. 10, EPIs) in the abdominal segments below the spiracles is also present here but it is indistinct and shallow, and no muscle is attached to it corresponding to muscle 13b–b in the abdominal segments. The epipleural component of the unified area has also changed from what its abdominal counterpart looks like, for the lobed part has moved forward and downward. In many larvae this can be recognized readily by the position of a dense patch of setae lowered from the position of the corresponding patch on the lobes of the abdominal segments (Pl. 1 and Pl. 7, fig. 4). The anterior epipleural triangular section is insignificant, but the posterior (Pl. 7, EPT, fig. 4) is as large as in the abdominal segments.

Ventral to the dorsopleural sulcus (a–a) the thoracic pleurum is located and characterized by a large, round subcoxal division which consists of an anterior (Pl. 7, Scx′, fig. 4) and a posterior (Pl. 7, Scx″) crescent-shaped lobe. The anterior lobe carries the episternal part (Pl. 7, Eps) and the posterior, the epimeral part (Pl. 7, Epm) of a poorly developed pleural sclerite. A pleural sulcus (Pl. 7, Pls) with a low pleural ridge on the inside separates

the episternal and epimeral parts and bears an articulating condyle (Pl. 9, c, figs. 1 and 2) which fits into a fossa or cup in the upper corner of the ovate, ring-shaped, sclerotized base of coxa. Adjacent to the base of coxa a lip-shaped fold, the meron (Pl. 7, m, fig. 4), is separated from the epimeral lobe, and a similar fold is separated from the episternal lobe on the opposite side.

The sternal region is divided by a transverse sternocostal line (Pl. 8, Stco) between the infracoxal furca-spots (Pl. 7, furc) into an anterior area, the basisternal area (Pl. 7, BSt) and a posterior one, the sternellar area (Pl. 7, Stl). Presternal sections are not found in anobiid larvae.

The composition of the prothoracic pleural and sternal regions with their areas and subdivisions deviates little from that of the same regions in meso- and metathorax, but the *prothoracic* tergal areas were as mentioned fused or obliterated to such an extent that any homology is obscured and indefinite between the prothoracic tergal elements and the meso- and metathoracic tergal areas.

Even more modified than prothorax is the *ninth abdominal segment*, and it differs from the preceding segments not so much in size as in the general appearance. This is due, partly to the predominance of the tergal region in comparison with the insignificant pleurosternal region, and partly to the disappearance by fusion of all the tergal areas. Only by help of the lower junction of the intersegmental conjunctiva anterior to the segment is it possible to locate and follow a weak dorsopleural sulcus and thus define the tergal region. But in a very general way the places can, nevertheless, be pointed out which are equivalent to the well-characterized areas of the typical segments. It is evident that the simple smooth dorsal part of the ninth segment corresponds to a combination of the two ordinary pro- and postdorsal areas and that the large patch of hook-shaped asperities, usually present on each side of the segment, is not homologous with the prodorsal hooks. But judging from the presence of a series of vertical muscles attached to the dorsopleural sulcus and affixed above the hook-bearing part this could be considered as a combination of paradorsal and epipleural elements and the hooks consequently be paradorso-epipleural. They could, however, hardly be homologous with the particular patch of hooks which are found on the epipleural lobes in the genus *Ptilinus*.

The *tenth abdominal segment* carries a ventral bilobed, symmetrical, oval cushion termed "the nates"[1] in front of anus. In some of the larvae, for instance, *Ptilineurus marmoratus* Reitter from Japan and several species of the genus *Ernobius*, in *Hedobia imperialis* L., *Ochina ptinoides* March. and *Xestobium rufovillosum* Deg. the tenth segment is, as previously mentioned on p. 30, l. 30, armed with asperities.

Division 6. Muscles of Body-Trunk.

The Neck Musculature.

The principal dorsal and ventral longitudinal bands of the muscles of the body trunk pass through the neck and attach themselves in the posterior part of the cranium, but there are no intrinsic longitudinal cervical muscles. Cervical plates are not found, but short dorsal and ventral oblique muscles are present, homologous with the ones which move the plates up and down in the insects which possess plates. Minor muscles are also inserted in the cervical membrane coming from both the cranium and the anterior marginal regions of the tergum and the sternum of prothorax, probably to aid the infolding of the neck.

Thoracic and Abdominal Muscles.

The locomotion of the body is a comparatively minor function in the anobiid larvae just as in other curved and soft-bodied larvae. The legs are weak and, in the genus *Caenocara*, even minute, and sclerotizations, such as a prothoracic shield and pleural plates, are insignificant or entirely absent; strong internal apodemes and apophyses are lacking, as previously mentioned. But the prodorsal areas and the sides of the ninth abdominal segment, armed in several species with asperities, aid the larvae considerably in making their way in wood, or beans, or other material in which they live. Nevertheless, the ordinary locomotory muscles of the legs are all present, and the dorsal muscles which produce the movements of the asperate body-parts are not essentially different in distribution and development from the

[1] The morphological origin, the construction and the function of the nates will be treated separately in a special section (p. 54, J) of the chapter dealing with the structures of the alimentary canal.

dorsal muscles known in other coleopterous larvae, including the curved larvae with more than two dorsal folds and the well-sclerotized running and swimming larvae. However, some of the special, supplementary muscles to the additional folds in some of the curved larvae are not present in the anobiid larvae and some of the muscles which occur in running and swimming larvae have not been found, whether the muscles have been fused with other muscles or are obscured in the small anobiid larvae, or are absent, as some peculiar transverse adductor coxae muscles are which occur in the thoracic segments of several other larvae. In these they start from a lower junction, run over the entire sternum, enter the coxa on the opposite side of the body and on the way through the segment cross their counterpart in the sagittal midline. The muscles are fairly strong where they occur, and it seems therefore noteworthy that they are completely absent here in the anobiid larvae.

The whole assemblage of muscles in the body and the sulci and areas to which the muscles are attached belongs undoubtedly to two different anatomical categories but the two systems are intimately correlated; to special sulci and areas special muscles are fastened. Thus it becomes possible to distinguish anatomically and orismologically important sulci and areas from similar but occasional features with different or no muscle associations[1].

The arrangement of the sulci and areas is fairly uniform in mesothorax, metathorax and the majority of the abdominal segments and can consequently be considered in common. But in prothorax and the greatly modified ninth and tenth abdominal segments many areas are fused and significant muscles rearranged or reduced so much that an homologization with those present in the typical segments is uncertain or impossible. In prothorax, however, it is to a certain extent the special shape and size, anterior insertions on the head and the altered course of single

[1] In several of my papers published at different times I have intepreted and termed the dorsal areas of the scarabaeid larvae differently from the current opinion. However, Dr. Wm. H. Anderson has shown me that the pertinent musculature did not substantiate my view as the prothoracic dorsal sulcus, which I had considered to be the separating boundary line between the pro- and mesothoracic segments, was an occasional secondary feature without any determining muscle association. The terms designated by authors, as R. B. Friend, Wm. Hayes, P. O. Ritcher and F. H. Butt, to the body areas of the scarabaeid larvae are correct according to the attachment of the determining musclebands and my own erroneus naming of same should be disregarded.

muscle-units which create the immediate, but not entirely correct impression that the pattern of the prothoracic muscle system has little in common with the arrangement of, even, the meso- and metathoracic musculature. Yet, several of the muscles are exclusively prothoracic and, on the other hand, some muscles which are common in the other body segments are lacking here. For these reasons the details of the prothoracic muscle-arrangement will be described separately.

The anterior and posterior margins of the mediodorsal part of each body segment are determined by internal dorsal longitudinal muscles (Pl. 8, # 1a, and Pl. 10, # A1a) which run from the low phragma or ridge in front to the phragma lying behind the segment, except in prothorax, where the anterior insertions are on the postoccipital ridge (Pl. 2, pos, fig. 1). These internal longitudinal muscles are in most of the body segments arranged, sometimes quite indistinctly, in four flat, parallel bands, and underneath and crossing them is a layer of similar muscles (Pl. 8, # 2, and Pl. 10, # A2). A distinct longitudinal band, termed the paradorsal muscle (Pl. 8, # 1b, and Pl. 10, # A1b), runs between the upper junction in front of one segment to the upper junction behind it. It consists of but one layer of fibers. Exterior to all these segment-long muscles and close to the body wall are external mediodorsal and laterodorsal sectional muscles (Pl. 8, # 3, and Pl. 10, # A3) which characterize and determine the prodorsal sulci. One set of these external dorsal muscles (Pl. 8, # 3) extends from the anterior margin of the segment to its prodorsal sulcus (Pl. 10, PrDs) and another set (Pl. 8, # 3′, and Pl. 10, A3′) from the sulcus goes to the conjunctiva behind the segment. The ends of the muscles of the set in front are often connected with the ends of the muscles of the posterior set where they are fastened to the sulcus. The imaginary line which, as described in the preceding chapter (p. 32, l. 20), forms the boundary between the postdorsal area and the paradorsal area in the abdominal and, to a certain degree, also in the thoracic segments, is determined by the paradorsal longitudinal muscle band (Pl. 8, # 1b and Pl. 10, # A1b) over which the line is to be located on the outer surface of the body. The lateral section of each of those conjunctivae which limit a typical segment anteriorly and posteriorly is defined by a strong, upright tergopleural conjunctival muscle

(Pl. 8, #12c, and Pl. 10, #A12). This muscle is slightly intersegmental and located posteriorly in the thoracic segments, running from the anterior side of a lower junction to the posterior side of an upper junction, but it is segmental and placed anteriorly in the abdominal segments, except in the first one in which the muscle is absent.

In each of the thoracic segments a long, upright, lateral intersegmental muscle (Pl. 8, #11) lies between the upper junction and the postcoxal pleurosternal region at the furca spot and follows the somewhat shorter conjunctival muscle (12c) quite closely, but it is absent in the abdominal segments. In these there are, on the other hand, two strong oblique lateral muscles (Pl. 10, #A7a and A7b) which, supplementing the conjunctival muscle, extend from the lower end of it (A12) all the way through the segment in an upward posterior direction. Two, similarly supplementary muscles (12a and 12b), are found in thorax but here they extend from the lower end of each conjunctival muscle in an upward anterior direction. Both the latter and former sets of supplementary muscles belong to the same category of strong oblique and counterwise-running muscles (7d, A7c, A7d) which occupy the flanks of the body trunk both in thorax and the abdomen and may run through two or more segments and even continue into the ventral areas below the dorsopleural sulcus (A7c). They are functionally essential for the purpose of forcing the tergal and pleurosternal elements together and accomodate the breathing and the shifting of blood pressure, but they have no particular orismological value because, speaking in general, they are unassociated with any of the sulci by which the different areas are determined. Of the sulci, which in the lateral part of the body limit the individual tergal areas, the distinct and curved epipleural sulcus in the abdominal segments (Pl. 10, EPIs) is characterized by the dorsal end of a vertical muscle (Pl. 10, #13bb) whose ventral end is affixed to the abdominal pleuroventral sulcus (Pl. 10, b–b). In meso- and metathorax where the paradorsal area (Pl. 7, ParD) and the lobe bearing part of the epipleural area (Pl. 7, EPI) are fused to form a composite area, no homologous muscle is inserted on the very vaguely-indicated epipleural sulcus (Pl. 7, EPIs). But to the sulcus which limits the posterior epipleural triangle (Pl. 7, EPT)

anteriorly, and which also is conspicuous in the abdominal segments, a fan-shaped group of small muscles (Pl. 8, #13) radiates from the lower junction and often spreads into the small anterior epipleural triangle of the next segment (compare Pl. 10, #13a and 13c). A thin muscle (Pl. 9, S) is fastened to the spiracle immediately under the peritrema on and around the so-called neck of the spiracle both in the thoracic and the abdominal segments (Pl. 10, #S) extending down in the direction of the dorsopleural sulcus (a–a) in the segment to which the spiracle belongs.

The anterior and posterior margins of the pleurosternal ventral part of a segment are determined, like the margins of the mediodorsal part, by internal longitudinal segment-long muscles (Pl. 8, 4b, and Pl. 10, #A4b) between the conjunctiva in front and the conjunctiva behind. In meso- and metathorax additional strong, flat muscles (Pl. 8, #4a) form a horizontal band running between the sternocostal lines (Pl. 8, Stco) which are interposed between the furca-spots of each segment both in mesothorax and metathorax (Pl. 7, furc, fig. 4). An oblique diagonal muscle (Pl. 8, #4c) runs, furthermore, from the lower junction in front of mesothorax to the spina spot (Pl. 9, spin, fig. 3) behind the segment. It crosses a similar oblique diagonal muscle (Pl. 8, #4d) which runs contrawise and external to it from the lower junction behind to the spina spot in front. A muscle homologous with the latter is found in the metathoracic segment, but this muscle crosses internally an oblique, external muscle (Pl. 8, #4e) which runs in a posterior direction from the lower junction in front of the segment to near the sagittal line. Still, in the same segment, a short, oblique posterior muscle (Pl. 8, #4f) comes from the lower junction behind and extends to the furcal spot at the third leg.

In the abdomen the entire inner ventral surface of the body wall is covered by horizontal, flat muscle bands, and two vertical tergopleural muscles also occur in each segment. The horizontal muscles include both internal and external longitudinal muscles. The internal longitudinal muscles (Pl. 10, #A4b) run between subsequent conjunctivae, defining the ventral anterior and posterior margins of the segment. They form more or less distinct bands along the whole ventral region of the abdomen. A single band of likewise internal muscle fibers, but intersegmental (Pl. 10,

#A4a), is also found. The external muscles (Pl. 10, A4g) lying close to the integument are only a little shorter than the segment in which they occur. Of the two vertical tergopleural muscles, one has already been described as running from the abdominal pleuroventral sulcus (b–b) to the abdominal epipleural sulcus (Pl. 10, EPIs), thus determining both sulci, and the other (Pl. 10, #A10), which consists of a couple of bundles of long muscle fibers, extends from the dorsopleural sulcus (a–a) to the dorsal boundary region of the paradorsal area (Pl. 10, ParDl) covered here internally by the paradorsal longitudinal muscle band (Pl. 10, #A1b). It may correspond to some of the long upright bundles of tergopleural muscles in each of the thoracic segments which run from the pleural ridge (Pl. 8, #10c, 10d, 10f) to the weak paradorsal line, and this is the reason why the abdominal muscles in question are considered not simply as tergal muscles but as associated also with the pleurosternal regions.

With the exception of the latter bundle of muscle fibers, none of the many following muscles are represented by homologous muscles in the abdominal segments. They are all thoracic and directly or indirectly produce and regulate the movements of the legs, or support the features with which the legs are connected. A few thin postcoxal tergopleural muscles (Pl. 8, #10g and Pl. 9, #10g, fig. 1) come from the posterior marginal part of the fused paradorsal-epipleural areas and are fastened, one to or close to the epipleural ridge, and the others to epimeron and the adjacent pleurosternal membranous field. Attached to the pleural ridge a very small muscle (Pl. 9, #20, fig. 1 and Pl. 9, #20, fig. 3) goes to the lower junction in front of the ridge and another, somewhat larger (Pl. 9, #21) to the lower junction behind it. A small pleurocoxal muscle (Pl. 9, #18) connects the ridge with the opposite coxal margin at the furca-spot, and from the episternum and the side of the ridge small pleurocoxal muscles (Pl. 9, #19, figs. 1 and 3) go to the basal rim of coxa anterior to the coxal articulation. The long tergopleural muscles (Pl. 8 and Pl. 9, fig. 1, #10c, 10d, 10f), alluded to above (p. 40, l. 11) extend from the pleural ridge to the thoracic incomplete paradorsal line, and to the same category as these muscles a single tergopleural muscle (Pl. 8 and Pl. 9, fig. 1, #10b) probably belongs, but it is inserted in the membrane anterior to the coxal rim close to

the coxal articulation. Dorsally it is attached to near the middle of the anterior margin of the lateral tergal region. The long ascendant, dorsoventral promotor (Pl. 9, figs. 1 and 3, #14) and remotor (15) muscles of coxa, as well as the extracoxal depressor of trochanter (Pl. 9, figs. 1 and 3, Trm) are dorsally attached in the same horizontal level as the long tergopleural muscles from the pleural ridge. The ascendant promotor of coxa is single and affixed anteriorly somewhat above the middle of the coxal rim. The remotor muscle is double, V-shaped and inserted by a common single short tendon on the posterior side of coxa opposite to and nearer the sagittal middle line (Pl. 9, sagit, fig. 3) of the body than the promotor. The sternal anterior (Pl. 9, #16) and posterior (Pl. 9, #17) rotator muscles of coxa are inserted respectively on the anterior and posterior side of coxa, closer to the sagittal line than the ascendant promotor and remotor muscles. In mesothorax the anterior rotator runs to the prothoracic spina spot and in metathorax to the mesothoracic spina spot. In prothorax where an anterior rotator has not been found it may possibly be obscured by the segmental or the sternocostal ventral depressors of the head (Pl. 8, #4a, 4b). The posterior rotator muscles run to the spina spots behind or, referring to the rotator of the third leg, to the middle of the ventral part of the conjunctiva behind. Both the anterior and posterior rotators are either covered internally by or run closely parallel with the diagonal, oblique ventral muscles to the spina spots (Pl. 8, #4c, 4d).

With the exception of the just-described muscles of the legs which are almost identical in all thoracic segments, the pattern of the muscle system in prothorax is manifestly different from that of the two other thoracic segments because, as said before, (p. 36, l. 26) several of the principal muscles are considerably changed in shape and in places of insertion from the homologous ones in the other thoracic segments and because new muscles have been developed and others, present in meso- and metathorax, have disappeared.

The prothoracic muscle bands attenuate gradually forward and usually bend more or less strongly toward the cranium, either upward or downward. Only one of the principal bands, a dorsally located levator of the head (Pl. 8, #1*) is horizontal. It extends from the first phragma to the top of the cranium and

belongs evidently to the same category as the mediodorsal longitudinal internal muscles (1a) of the other segments. Two rotators of the head (Pl. 8, #2*) come from the posterior upper part of tergum and the conjunctival membrane immediately behind, and they run obliquely down to the upper part of the postoccipital apophysis. The muscles correspond possibly to the oblique ones, (Pl. 8, #2) which lie beneath the mediodorsal internal longitudinal bands in meso- and metathorax. External oblique prothoracic muscles (Pl. 8, #3*) from the first phragma, dorsally of its upper junction, extend upward to about the middle of the prothoracic roof. They are similar to and probably homologous with the mediodorsal, sectional external muscles (Pl. 8, #3) from the phragmata behind meso- and metathorax to the prodorsal sulci in front. Parallel with these muscles a long muscle (Pl8, #1**) attached at the upper junction runs upward to near the head. Three long muscles (Pl. 8, #7a, 7b, 8), which are depressors of the head, belong to the muscles which, unlike the just mentioned, are exclusively prothoracic. They are attached in the tergum approximately on the same level with the paradorsal longitudinal muscle bands (Pl. 8, #1b) in meso- and metathorax and continue obliquely downward to the lateral margin of the throat where they become inserted. Another special prothoracic muscle group (Pl. 8, #6) is a levator of the head. It consists of rather long but thin muscles which, lying close together, extend from near the posterior margin of acrosternum (Pl. 9, Acrst, fig. 3) and are inserted low in the lateral part of the postoccipital apophysis. Running counterwise of this bundle of muscles and crossing it in front of coxa, a second but shorter bundle of dorsoventral muscles comes from the acrosternal vicinity (Pl. 8, #9), and the single elements of the bundle are inserted on the ventral margin of tergum.

From the lower junction behind the segment two long and strong muscles come which, diverging from a common starting place, extend upward through the tergum. The upper branch (Pl. 8, #12b) becomes implanted in about the same horizontal level as the tergal motor muscles of the coxa, and the lower branch (Pl. 8, #12a) is fastened nearby but more ventrally in the anterior part of tergum.

The vertical tergopleural conjunctival muscle (Pl. 8, #12c),

formerly described, belongs apparently to the same unit, and the whole set may or may not be homologous with the muscles (marked 12a, 12b and 12c) which originate from the lower junction in the rear of both meso- and metathorax.

The forward attenuating horizontal ventral depressor of the head (Pl. 8, #4a*) from the prothoracic sternocostal line (Pl. 8, Stco) to the throat is evidently a continuation of the longitudinal ventral muscle bands between the meso- and metathoracic sternocostal lines. In a similar manner a second ventral depressor of the head (Pl. 8, #4b*) appears as an oblique prolongation of the ventral longitudinal muscles between the lower junctions of meso- and metathorax (Pl. 8, #4b). It originates also from a lower junction, in this case the lower junction of prothorax behind the leg, thus above and somewhat to the rear of the place where the first ventral depressor of the head is attached. In addition to the three long tergopleural muscles from the pleural ridge (Pl. 8, #10c, 10d, 10f) which the prothorax has in common with the other thoracic segments, a fourth muscle (Pl. 8, #10a) runs from the pleural ridge to the cervical membrane. Finally, two muscles issue from the first spinal spot and run obliquely forward to the base of the leg, one on top of the other. The one above (Pl. 8, #5) is inserted in the furcal spot and is a special prothoracic muscle but the other is a typical leg muscle, present in all thoracic segments, for it is the posterior sternal rotator of coxa (Pl. 9, #17, fig. 3), inserted, as noted above, on the posterior side of the basicoxal rim.

The musculature of the ninth and tenth segments will be discussed p. 55 K) in a following chapter about the alimentary canal and has already been referred to on p. 34, l. 33.

Division 7. Legs and Leg-Muscles.

The legs (Pl. 9, figs. 1 and 2) are present in all anobiid larvae. They are generally fairly well developed although their function as locomotory organs is limited to aiding the larvae either in moving inside their galleries in old furniture, old books and objects of similar nature or, according to the different habitats of the species, in changing of place within dry beans, puffballs etc. With the exception of the species of *Caenocara*, in which the

legs are either minute and indistinctly segmented or mere warts without claw (Pl. 49, figs. 3, 19, 20), all the anobiid genera and species have five segments in each leg as normally found in the polyphagous beetle-larvae. The trochanter (Tr) is distinctly separated from femur (Fm), tibia and tarsus united to one segment (Tb–Ta) and pretarsus (Ptar) always present though its terminal claw-shaped part (Dac) is absent in several of the species (Pl. 44, fig. 17, and Pl. 45, fig. 8). Coxa (Cox) is short and broad. Its procimal end is enforced by an annular basicoxal sclerotization which has a single articular cup hinged to the condyle (C) of the pleural ridge, and also bears a pair of small processes (Pl. 9, pr, fig. 2) which articulate with trochanter. The other segments of the leg are generally smooth, thinly sclerotized and pale. In two places only, apart from the claws, distinctly colored and fairly thick sclerotizations are found, one on the ventral broad side of trochanter where the proximal margin projects as a round, beaklike lobe which at each end of its base has a small articular socket for the coxal processes (pr) and the second on the dorsal side of tibia where the proximal margin is hardened to a semicircular expansion. Trochanter is shaped as a signet ring with the face turned ventrally. It joins the femur closely but is, as stated above, distinctly separated from it by a boundary line and contains also a short muscle (R) which is attached to the proximal end of femur. Femur and tibio-tarsus are either about of the same length, or femur is slightly the longer in some species, tibio-tarsus distinctly longer in others, but femur is always thicker than tibio-tarsus which gradually tapers from its proximal base to the distal end; and this is about as wide as the base of pretarsus. Pretarsus (Ptar) is characterized by a small unguitractor plate (Untr) at its proximal end and consists regularly of two parts, one a basal part armed with from two to many setae, and the other a claw. The claw (Dac) varies in shape and size according to genus and even to species as in the genus *Ernobius* (Pls. 19 to 21, 44, 45). It may be long, pointed and rather straight or awl-shaped, as in *Eucrada* (Pl. 15, fig. 7), *Hedobia* (Pl. 16, fig. 6), *Holcobius* (Pl. 32, fig. 4) and *Nicobium* (Pl. 33, fig. 12), with gradual transition in width and sclerotization toward the membranous basal part, which is armed with several setae. But in most of the other larvae the proximal membranous

part of pretarsus is distinctly set apart from the claw and carries only two setae. The claw may be short, strong and slightly curved downward or straight as in *Anobium* (Pl. 26, fig. 9) and *Platybregmus* (Pl. 25, fig. 9) or distinctly curved as in *Catorama tabaci* (Pl. 39, fig. 6), or it may be long and awl-shaped as in *Stegobium* (Pl. 28, fig. 9), or thin and spinelike as in *Cryptorama* (Pl. 44, fig. 9), *Eutylistus* (Pl. 47, fig. 16) and *Dorcatoma* (Pl. 48, fig. 18). Intermediate forms are frequently found between all of the types. In some of the larvae, for instance *Ernobius mollis* (Pl. 19, fig. 8) and *Catorama vestitum* (Pl. 41, fig. 10) a soft arolium (Ar) is found in continuation of the ventral side of the membranous part of pretarsus, and in several species as in *Ernobius marginicollis* (Pl. 45, fig. 8), *Neogastrallus librinocens* (Pl. 45, fig. 14) and *Microanobium* sp. a claw is completely absent. In these latter species pretarsus with two setae unites with arolium into an oval, soft bladder. A unique development of the legs is found in *Ptilineurus marmoratus* (Pl. 50, figs. 9 and 10), for while the three pairs of legs are similar in size and shape in all other anobiid larvae, the front legs differ in this species considerably from the second and third pairs. The latter are entirely normal legs of the type in which the claw is long and straight and the membranous basal part conical with many setae, but the legs of the first pair have a particularly strong and completely sclerotized basal pretarsal part, recognized by a distinct unguitractor plate, and carries numerous short, thick and ovate setae all over. The claw is very slender, awl-shaped and turned upward. With the exception of this strange pretarsus, the other segments of the first leg are generally proportioned and shaped as those of the second and third pairs, only a little more robust.

A noticeable change in shape and reduction in size from the common type of anobiid larval legs occurs in a small group of species related to the fungivorous genera *Eutylistus* and *Dorcatoma*, both of which, however, have normal legs. The group includes *Anitys rubens* Hoffm., *Caenocara bovistae* Hoffm. and *Caenocara oculata* Say. In *Anitys rubens* (Pl. 48, fig. 10) the legs have become short and thick; femur and tibio-tarsus being particularly reduced in length, but all the regular segments are present and pretarsus is distinct, has a membranous base armed with two setae and a long, awl-shaped claw. In *Caenocara bovistae*

Hoffm. (Pl. 49, fig. 3), the entire leg is membranous and soft, very short and thick and has a bristlelike claw; the single segments are only indicated and their setae are few. In *Caenocara oculata* Say (Pl. 49, figs. 19 and 20) the legs are vestigial and represent the last step in the retrograde development. They are reduced to mere warts with the segmentation almost eliminated, the setae are few, and the claw is practically gone.

The muscles of the leg conform in general to the pattern in which they are arranged in other beetle larvae, but are in some of the larvae, particularly of the genus *Caenocara*, so reduced in number and development that most of them seemingly are absent. The many muscles from the wall of the thoracic segments to the bases of the legs, not always easy to distinguish individually, have been described previously (pp. 40, l. 17 to 41, l. 25) and, therefore, only the muscles located strictly within the legs will be dealt with here.

The main movement between coxa and trochanter is up and down around an imaginary quite horizontal axis between the anterior and posterior coxo-trochanteral small articulations (Pl. 9, pr, fig. 2). For the performance of the movement two groups of trochanteral muscles from the coxa to the proximal margin of trochanter oppose each other. The first group, the levator muscles of trochanter (Pl. 9, O, figs. 1 and 2) includes muscle-sets which are inserted close together on the dorsal, narrow side of trochanter and are attached to the hind side of coxa. The second group, the intracoxal depressor muscles of trochanter (Q) includes also separate sets of muscles. They are inserted jointly on the ventral beaklike process, and one of them is attached to the front side of the coxal wall near the pleural articulation of the leg, the others somewhat more distal from it. The long tergal depressor muscle of trochanter (Trm) which as previously described (p. 41, l. 4) arose in the tergal region is also inserted on the beak. In trochanter a single, short muscle (R) is affixed to its ventral broad face and inserted on the opposite proximal corner-part of femur. When contracted the muscle may aid in pressing the adjacent margins of trochanter and femur securely together. The femur (Fm) with little or no independent movement needs no strong levator and depressor muscles but many and strong tibio-tarsal muscles are attached to its wall. The tibio-tarsal levator muscle (S) is inserted

on the dorsal projection from the proximal margin of tibia and consists of two bundles of muscles both arising on the dorsal side of femur at the line separating it from trochanter. The tibio-tarsal depressor muscle (T) is inserted ventrally where tibia and femur meet; it consists also of two bundles of fibers but they form a somewhat stronger muscle than the levator. The weaker of the depressor bundles arise from about the same place on the wall of femur as the levator but the other, more ventral, bundle is attached to the broad face of trochanter. A long threadlike apodemal tendon (Tend, fig. 1) runs from the unguitractor plate (Untr) all the way into the femur through the tibio-tarsal segment, and on the proximal half of this tendon two bundles of long depressor muscles of pretarsus (U) are inserted coming from the proximal part of the dorsal side of femur, and, more distally, two much shorter and weaker bundles are inserted coming from the tibial part of the segment. All of these pretarsal depressor muscles cooperate as a flexor of the claw, but levator muscles to raise the claw do not exist.

Division 8. Spiracles.

The spiracles (Sp) of the anobiid larvae are all found on the sides of the body in the laterally-located spiracular areas of tergum. The first thoracic spiracle has its place in the rear of prothorax somewhat more ventral than the abdominal spiracles which follow in a horizontal row, but it is, strictly speaking, a forward-moved mesothoracic spiracle as its spiracular muscle (Pl. 9, S) shows. The second thoracic spiracle is reduced to a minute, dark dot in or close to the conjunctiva between meso- and metathorax and at the level with the first thoracic spiracle. The spiracles in each of the succeeding eight abdominal segments are well developed even if they are somewhat, and in a few species much, smaller than the first thoracic. The first abdominal spiracle may occasionally be noticeable larger than the rest in the abdomen but usually they are all of equal size. When the spiracles have special extensions from the rim, the common rule is that these extentions point forward toward the head in thorax and backward toward the anus in the abdomen. The spiracles vary greatly in appearance in the different members of the family and, yet,

can all be considered either as typical annular spiracles or as manifold variations of this principal type. They have a wide spiracular opening, set off from the body-skin by a distinct but thin marginal peritremal rim, and leading directly into a well-developed atrium. In its basic simpleness this annular type occurs in species as *Xeranobium macrum* Fall (Pl. 33, figs. 6 and 7), *Catorama punctatum* Lec. (Pl. 37, figs. 6–8), *Caenocara bovistae* Hoffm., (Pl. 49, figs. 5, 6) and others. However, in the majority of the species one or two or many closed or more often widely open and smooth spouts extend from the rim which consequently loses its regular annular appearance. An annular spiracle with a single spout has occasionally been observed also in larvae of other families, for instance in the curculionoid *Platypus compositus* Say and *Proterhinus anthracias* Perkins and has even been given the special name of uniforous or unicameral spiracle. In anobiid larvae, however, this variation of the annular type is common and found for instance in *Hedobia imperialis* L. (Pl. 16, figs. 7–9), *Ernobius abietis* F. (Pl. 20, figs. 5 and 6) and other species of *Ernobius*, in *Ozognathus cornutus* Lec. (Pl. 42, figs. 6–8), *Stegobium panicum* L. (Pl. 28, figs. 3–6), and *Catorama herbarium* Gorh. (Pl. 38, figs. 7–9). In species as *Anobium punctatum* Deg. (Pl. 26, figs. 5–7), and *Gastrallus laevigatus* Oliv. (Pl. 40, figs. 7 and 8) the spout is long and sausagelike. Spiracles with two well separated spouts are found at least in the thorax of several species as *Catorama tabaci* Guér. (Pl. 39, figs. 7 and 9), *Anobium gibbicollis* Lec. (Pl. 26, fig. 11), *Oligomerus sericans* Melsh. (Pl. 31, fig. 15) and others. Spiracles with from three to numerous spouts occur in *Trypopitys sericeus* Say (Pl. 24, figs. 7–9) and *Eucrada humeralis* Melsh. (Pl. 15, figs. 8–10). In several species an extraordinary development of the annular spiracle has taken place, appearing in a very characteristic way in *Cryptorama minutum* Lec. (Pl. 44, figs. 7 and 8) and *Eutylistus intermedius* Lec. (Pl. 47, figs. 7 and 8) in which one part of the rim forms a loop away from the entrance to the spiracular trachea which is two or more times longer than the opposite part, and also in *Catorama nigritulum* Lec. (Pl. 36, figs. 6–8) and *Eutylistus facilis* Fall (Pl. 47, figs. 14 and 15) in which the circumference of the entire annular rim has been greatly extended. That part of the wall of the atrium which is nearest the rim follows the extension of the

rim and forms a horizontal floor flush with the surface of the body. Generally the floor retains the appearance, common to the inside of an atrium in many insects, being laid with a covering of a multitude of minute, pointed swellings, but here interspersed with many suboval and irregularly ring-shaped, clear spots or arranged as a mosaic of geometrical figures. These spiracles ressemble superficially the cribriform type and have mistakenly been so named. As the last offshoot of the polymorphic spiracular development in the anobiid larvae the remarkable looking spiracles of *Priobium tricolor* Oliv. (Pl. 35, figs. 6–8) will be mentioned. Its features can morphologically be derived from those found in species like *Eucrada humeralis* Melsh. (Pl. 15) in which a part of the otherwise straight rim is convoluted into a series of low loops and curves. However, in *Priobium tricolor* the rim has only a single extension but the latter is long and from its margin obtuse, open branches crop out whose edges roll in over the floor of the structure. The floor itself is a prolongation from the wall of the atrium and like the atrium provided with numerous fine pointed projections. It might be suggested that the marginal flexions of this strange spiracle constitutes a stage in the development of the common bicameral spiracular type and if that is the case it would make a good point in favor of the much discussed claim that the airtubes at least of the typical bicameral spiracle have open linear fissures on top and are not to be regarded as wholly closed outshoots from the sidewall of the atrium.

Division 9. Organ of Ingestion and Nates.

The organ of ingestion of the anobiid larvae (Pl. 12) is divisable into the following sections: A – The preoral cibarial cavity (Cb); B – the pharynx (Phy); C – the oesophagus (Oe); D – the ingluvies (or "crop") (Cr); E – the proventriculus (Pvent), and the cardiac valve; F – the ventriculus (Vent); G – the pyloric section (Pyl); H – the anterior intestine (AInt); I – the posterior intestine with two subdivisions, namely the rectal sac (rsc) and the rectum proper (Rect); J – the nates (or "anal cushion") (Nat) and; K – anus (An).

A – The preoral cibarial cavity (Cb) is well developed, with the posterior part built as a pump to convey, together with

pharynx, the masticated solid food in the anterior part of the cavity into the subsequent sections. The roof is formed by the labro-epipharyngeal region (Pl. 3, LmEphy, Pl. 4, and Pl. 5, fig. 1), anteriorly armed with strong, curved setae or, in some species, long, soft bristlelike hairs, and posteriorly covered with minute, densely set papillae and, often sensory pores. The floor is represented by the fleshy upper surface of hypopharynx (Hphy), and the hind wall by the clypeo-epipharyngeal region (Pl. 3, ClpEphy and Pl. 5, fig. 1) which slants back to the entrance to Pharynx (Phy) and is lined with a smooth, shiny and elastic intima. The mandibles and maxillae are within the cibarium, bounding it laterally (Pl. 24, fig. 1). When functioning the cavity is alternately dilated and compressed. In dilation (Pl. 3) the labrum together with the labro-epipharyngeal region is raised, the hypopharynx is lowered and the clypeo-epipharyngeal hind-wall pulled upward. The raising of labrum is done mainly by the increase of the blood pressure; the lowering of hypopharynx, on the other hand, is performed by the contraction of the muscle (Pl. 3, # 19) which arises on the tentorial bridge and is inserted laterally on the base of hypopharynx, and the pulling back and up of the hindwall (Pl. 3, ClpEphy) is done by the contraction of the three dorsal dilator muscles on each side of the cibarium (Pl. 3, # 5, 6 and 7) which are inserted in a longitudinal row, one behind the other, at the lateral margin of the hindwall. At the same time when the dilation of the cibarial wall takes place, the mandibles rotate outwards with their bases raised and separated from each other, and the maxillae are thrust out to the sides. The compression of the cibarial cavity results from opposite movements of the same component parts. The labrum with the labro-epipharyngeal region is bent downward by contraction of the muscles from torma to the inside of the posterior part of frons (Pl. 3, # 3), the hypopharynx is raised by contraction of the muscle (Pl. 3, # 10) of the hypopharyngeal suspensorial bar (Pl. 3, Su) to the frons immediately lateral of the place where the dorsal dilator of pharynx (Pl. 3, # 9) is attached, and the clypeo-epipharyngeal hindwall of the cibarium is bulged into the cavity by the elasticity of the wall after relaxation of the dorsal dilator muscles (Pl. 3, # 5, 6, 7). Simultaneously the mandibles and maxillae return to their closed positions. The salivarium,

usually associated in other insects with the cibarium both in position and function, is here reduced to an inconspicuous concavity in the skin between the hypopharynx and the labial wall above prementum, and salivary (or "labial") glands and a duct are absent as they supposedly are in all coleopterous larvae and imagines.

B – The entrance to pharynx from the cavity of the cibarium is marked by the place of insertion on the dorsal wall (immediately behind the pharyngeal opening) of the muscle (Pl. 3, # 9) which arises on frons and lies posterior to one of the paired connectives of the frontal ganglion. Pharynx (Pl. 3, Phy) is about twice as long as the hindwall of the cibarium and has anteriorly the shape of a flat tube; posteriorly it is more circular in cross section. The dorsal wall of the anterior part is convex toward the lumen of pharynx and covered by a boat-shaped posteriorly tapering portion of intima which is smooth, shiny and elastic like the cibarial hindwall. The ventral wall is softer. The pumping action which started in the posterior part of the cibarium in order to transmit the food into the digestive system proceeds in the pharynx and is accomplished by dilating and compressing the section alternately. To dilate it the dorsal and ventral walls are drawn in opposite directions. The dorsal wall is lifted by the dorsal dilator muscle (Pl. 3, # 9) to the anterior region of pharynx and by the group of dorsal dilator muscles (Pl. 3, # 11) which arise from the posterior part of frons immediately lateral of where the depressor muscles of labrum arise; and the ventral wall is lowered partly by the midventral group of dilatores of pharynx (Pl. 3, # 30) which extend from the anterior part of pharynx to the tentorium (Pl. 3, Tnt) and partly by the lateral group of dilators (Pl. 3, # 31) which, inserted in the wider posterior part of pharynx, comes from the inside of each parietale (= "epicranial half"). The compression of pharynx, following the dilation of it, is performed by increasing the convexity of the elastic intima of the dorsal wall, pressing it against the opposite ventral wall which moves upwards at the same time. And the compression is performed by the layer of small transverse and oblique muscles (Pl. 3, # 12) which spreads over the wall.

C – The oesophagus (Pl. 3, Oe, and Pl. 12) begins immediately, and without any essential histological and anatomical changes,

behind the last group of the dilator muscles of pharynx (Pl. 3, #31). It is about as long as the first thoracic segment, is straight, tube-shaped, and circular in cross section; posteriorly it enlarges gradually and continues into the crop (Pl. 12, Cr). The wall is extensible and has, as typical in insects, six longitudinal main folds, and the intima is set with colorless, hairlike filaments especially on top of the folds. Around the epithelium of the wall is a sheath of longitudinal (Pl. 3, lmcl) and circular (Pl. 3, cmcl) muscles. The longitudinal muscles lie mainly in the folds of the epithelium and the circular muscles cover them on the outside. Besides these muscles, which perform the important peristaltic movements of the oesophagus, no other group of muscles is found inserted on and radiating away from the wall of the oesophagus, and the latter differs in this respect distinctly from the pharynx.

D – The crop (or "ingluvies") (Pl. 12, Cr) is usually well developed in the anobiid larvae and has an average length corresponding to the combined lengths of the meso- and metathoracic segments, but in some species as *Dorcatoma dresdensis* it is barely as long as one of the segments. It is round, mostly ovate or pyriform, posteriorly abruptly constricted anterior to the narrow proventriculus (Pl. 12, P.vent). The intima (Pl. 7, Int) is well developed, elastic, and provided with hairlike filaments (Pl. 7, Fil). These are pointing forward and arranged in several longitudinal, collateral rows. Between the rows the wall space is moreover densely set with minute, rounded granulae (Pl. 7, Grl) with asperate tops which are directed posteriorly. The epithelial cells of the crop are covered by a sheath of longitudinal musclefibers (Pl. 7, lmcl) and outside of them by circular muscles (Pl. 21, cmcl) arranged in many transverse bands.

E – The proventriculus (Pl. 12, P.vent) which narrows the alimentary canal between the crop and the large ventriculus (Pl. 12, Vent) is short in anobiid larvae. Posteriorly it in invaginated into the lumen of the ventriculus forming the funnel-shaped cardiac valve (Pl. 12, Cardv) in the initial region of the ventriculus. Its intima differs from the intima of the crop in that the usual six longitudinal main folds of the stomadaeum are very well developed here while they are weak in the crop. At the hind end the folds are swollen into six rather soft lobes which lie

against each other and thus are able to hold back the food in the crop when required and also to prevent regurgitation from the ventriculus. The epithelial cells are almost as large as those of the crop and the covering sheath of muscles is thick.

F – The ventriculus (or "stomach") (Pl. 12, Vent) is long, generally tube-shaped and circular in transverse section, but anteriorly bladderlike in most of the species. It extends parallel with and close to the curved dorsal outline of the body from the cardiac valve (Cardv) to the end of the ninth abdominal segment where it forms a loop. From here it ascends along the venter of the ninth, eighth and part of the seventh abdominal segments, and, bending toward the inside of the tergum of the eighth abdominal segment, ends near where the malpighian tubules enter the pyloric region (Pl. 12, Pyl) of the intestine. Large gastric coeca (Pl. 12, Gla) open into ventriculus immediately behind the cardiac valve. They are arranged in paired clusters and contain bacteria, supposedly to aid the digestion.[1] The wall of ventriculus is soft and fragile, and this section of the digestive system is therefore difficult to dissect and remove unbroken. The epithelial cells are large but not lined with a distinct, continuous sclerotized intima as in the foregoing and most of the subsequent sections of the alimentary canal, and the surrounding layer of muscles has also a different character, being weak and prevalently composed of longitudinal muscle-fibers lying outside the poorly developed circular ones.

Peritrophic sacs enveloping the food appear to be present (Pl. 11, Peritrs, fig. 5).

G – Following ventriculus is a distinct but short pyloric region (Pl. 12, Pyl) which is separated from ventriculus by a pyloric valve. The swollen bases of six malpighian tubules (Pl. 7, Mal, figs. 1 and 3) open into the pyloric region immediately behind the valve, and a circular layer of muscles behind the bases of the malpighian tubules marks the posterior boundary, separating it from the subsequent anterior intestinal section (Pl. 12, A.Int). The six long malpighian tubules (Pl. 12, Mal), present in anobiid larvae, wind through the entire interior of the larva but do not end freely in the cavity, the terminal parts being gathered together

[1] Compare: Phyllis Gardiner: Morphology and biology of *Ernobius mollis* L. Trans. Ent. Soc. London, vol. 104, pp. 1–24, 1953.

and enclosed in a membrane (Pl. 12, malsc) which adheres to the side of the rectal sac (Pl. 12, rsc) throughout the whole length of the sac. The membrane forms a ribbon-shaped sheath with a bulblike posterior swelling, and an elongate thickening, a socalled rectal pad (Pl. 12, rpd) is seen inside the membrane.

H – The anterior intestine (Pl. 12, AInt) beyond the pyloric region extends to the place where the malpighian tubules enter into the ribbon-shaped sheath on the rectal sac. It has a thin intima, without longitudinal folds, is provided with only weak circular muscle-fibers, and appears in the anobiid larvae as a uniform ensemble which is not divided into an anterior ilium and posterior colon.

I – The two parts of the posterior intestine, the socalled rectal sac (Pl. 12, rsc) and rectum proper (Pl. 12, Rect) are almost of equal lengths. Like the anterior intestine, the rectal sac has a thin intima, weak circular muscle-fibers and can be dilated considerably. It is bent as a letter U and fits into the curve between the sac-shaped and tubular portions of the ventriculus. The rectal sac can be recognized by the membranous sheath (Pl. 12, malsc) with the malpighian tubules which is present on the side of the wall along its entire inner curvature. The rectum proper (Pl. 12, Rect) is straight, rather stiff, has a strong intima with six distinct longitudinal folds and a well-developed muscular covering composed of a continuous series of rings of circular fibers with less conspicuous longitudinal fibers on the outside. Many strands of dilatory muscles, the socalled suspensorial muscles of proctodeum, (Pl. 11, spms) radiate from the rectal wall to the skin of the body and attach themselves here.

J – The nates (Pl. 11, figs. 1–4 and Pl. 12, Nat) or anal cushion is located on the underside of the curved end of the body below the terminal part of rectum proper. It consists of a tongue-shaped prolongation of the ventral side of rectum (Pl. 11, figs. 1 and 4) flexed over and imbedded in the surface of an elongate, oval, bilobed, symmetrical, padlike elevation of the skin of the last abdominal segment, and could perhaps be interpreted as an enlarged lower anal lip. When raised by increase of the blood pressure the elevation becomes blisterlike with the rectal prolongation resting on top of it (Pl. 11, fig. 2). But under lessened blood pressure and contraction of the many thin suspen-

sorial muscle fibers (Pl. 11, spoms) which radiate right and left from the rail to the base of the tenth segment (Pl. 11, fig. 1) the upper eversible part of the elevation (Pl. 11, cv, figs. 2 and 3) is invaginated into the basal not eversible (incv) part. Together the two parts form a case with the rail at the bottom covered from each side by the double wall, only with a longitudinal opening left sagittally (Pl. 11, open, fig. 3). The rectal prolongation (Pl. 11, rail, fig. 1) is suboval, varying somewhat in length according to species. It forms an angle with rectum proper of about 90° (Pl. 11, fig. 4), is well sclerotized, smooth and shiny being a direct continuation of the rectal intima. A pair of thickenings (Pl. 11, rail, figs. 1 to 5) on the lateral borders of the rail are homologous with the thickening on the right and left ventral rectal folds (Pl. 11, v.rectf, fig. 4). Opposite anus the rail is linked to a strongly sclerotized bow (Pl. 11, Bow, fig. 1) which supports some longitudinal sternal muscles (Pl. 11, stmsc, fig. 1) of the ninth abdominal segment. These diverge to the right and left, and are fairly strong. The unchanged simple dorsal anal lip is short and fleshy. The integument on its inside is a continuation of the dorsal side of the wall of rectum proper but is without any folds corresponding to the dorsal folds of the rectum.

K – Anus (Pl. 11, An, figs. 1, 4 and 5) is a transverse slit when firmly closed coinciding with the invagination of the nates but becomes a wide, round aperture during the period of the elimination of the excrements. This opening of anus and the elimination are undoubtedly produced, as in other coleopterous larvae, by contraction of the numerous thin socalled suspensorial dilator-muscles (spoms) from the rectal wall to the inside of the body-wall in combination with the intestinal peristaltic movements. However, it appears probable that in anobiid larvae a lifting of the rectal prolongation on top of the inflated cushion will protract the coalescent end of the rectum and drag it somewhat outward, a motion which a contraction of the diverging muscles from the bow-shaped symphysis will support by fixing the distal end of the rail at the same time the proximal end moves in an outward curve.

CHAPTER II

Taxonomy.

The preceding anatomical research was undertaken, as stated in the introduction, not only to study the structural differences found in the available larval material for suitable taxonomic characters to separate the various forms but also for the purpose of investigating the true morphological nature of the component elements of the body in order to decide on a rational terminology to be used in the technical descriptions. Thereafter the present chapter could then be outlined and was divided into the following sections: 1) A brief taxonomic account of the general exterior appearance of a typical anobiid larva, 2) a family characterization, 3) precursory remarks about the segregation of the larvae into groups, 4) a key to species, 5) descriptions of species, 6) an alphabetically arranged list of the described species.

Division 10. General Taxonomic Description of the Exterior Appearance of an Anobiid Larva.

(See Plate 1).

Mature larvae of the family small to moderately large varying in length from about three mm. to fifteen mm. according to the different species.

Head usually protracted and hypognathous, suborbicular to oval, rarely much longer than wide.

Body-trunk more or less curved, subcylindrical in cross-section, equally thick throughout in the majority of the larvae. Skin pliable, not sclerotized, pale-whitish and generally abundantly hairy. Various prodorsal areas armed with hookshaped asperities in most of the larvae.

Ninth abdominal segment well developed, obtusely rounded at the end and lacking urogomphi[1], laterally with asperities in the majority of species.

Tenth abdominal segment small, with a pair of symmetrical, soft, longitudinal, oval lobes, separated sagittally by a sclerotized groove in front of anus.

Legs present in all larvae and provided with a distinct claw in the majority of the larvae. Vestigial legs only in the genus *Caenocara*.

Division 11. Taxonomic Family-Characterization.

Cranium uniformly pale yellowish with darker epistoma, pleurostoma and hypostoma, often with a pigmented field behind epistoma; exceptionally with dark cranium variegated by light patches (*Lasioderma*) or with completely pigmented cranium and lighter setal cups. Pigmented field behind epistoma varying according to species both in extent and texture, armed in a few species with a small process sagittally at the anterior end of the epicranial sulcus. Frontal cleavage lines present only in a few forms, notably in some species of *Ernobius*. Epicranial sulcus distinct, usually half as long as cranium. Catapophyses varying in size, shape and texture of surface. Epistoma usually with setae, arranged differently and present in different numbers according to species. Main surface of cranium normally bearing evenly scattered, short to long setae.

A single, rather conspicuous *ocellus* with strongly arched cornea often present and located in a smooth or rough or conically protruding part of pleurostoma near fossa for the ventral mandibular condyle.

Antenna placed in pleurostoma close to the catapophysis, protected ventrally by a thin-walled shield projecting from the cranial frame. Number of antennal articles varying from two well developed, cylindrical articles borne by a membranous, dome-shaped base, to two short articles, to no articles at all. A sensory papilla, usually suboval, rarely sausage-shaped, pre-

[1] Ninth abdominal segment in first-stage larvae terminating with a single pointed, hard projection, not found in the larvae of the other stages.

sent on top of the proximal article and exterior to the dista article; minute sensory hairs present in the end of both articles. Tactile papilla and other sensorial organs borne by the base when articles are absent.

Anteclypeus well developed, attached to underside of clypeal epistomal margin between the catapophyses, without pigmentation, but often provided with a small, setae-bearing plate at each end of the anteclypeal sulcus. Exceptionally, in *Coelostethus* and a few other larvae, a great posterior part of anteclypeus, or the entire anteclypeus, darkly sclerotized.

Labrum hard and well pigmented, with an outline varying from subtrapezoidal and transverse to subcircular or to elongate pyriform. Each torma and labral rod either forming together a Y- or V-shaped structure or fused entirely to a simple stalk. A pair of dark marks often found on the labral surface. Labrum usually bearing an abundance of setae but in some larvae only a moderate number, and, in a very limited group of genera, as few as two or three setae on each side.

Epipharynx divided into a labral epipharynx and a clypeal epipharynx. *Labral epipharynx* located below labrum and extended to a transverse border line between the posterior ends of tormae. *Clypeal epipharynx* reaching from the border line to the entrance of pharynx. Labral epipharynx by itself divided into an anterior and posterior subdivision. Anterior subdivision, ending at an imaginary line between the anterior ends of tormae, armed (1) with numerous *acanthoparial* setae either of cultriform shape or slender, circular in cross section and very pointed, (2) with *chaetoparial* setae arranged in many different ways but practically always present and (3) *coryphal* setae, seldom strong, often lacking, and large only in *Dorcatoma*-like larvae; in the latter tooth-shaped and attached to a plate. *Pedium* often well developed, rarely lacking. *Posterior subdivision* of labral epipharynx, the socalled crepidal field, located between the tormae, always softskinned, set with minute papillae and frequently with some sensory pores.

Hypopharyngeal bracon absent.

Hypopharynx lacking a sclerite at base except in genus *Caenocara* in which the upper ends of the suspensorial bars are swollen and hard.

Mandible adorally concave, aborally convex; dorsal articulation horse-shoe-shaped, large and flat, ventral articular ball globular and strong. *Marginal brush* of stiff setae located where the adoral and aboral sides meet above the protractor muscle of the mandible, present in most larvae, and indicating the posterior beginning of the distal part of the mandible. *Distal part of mandible* (1) *apically* projecting into two distinct teeth, except in a few forms with vestigial second tooth or with simple, rounded margin, (2) *subapically with dorsal margin* built in various ways, being either produced into two teeth, or into one tooth, or into a long wall extending from base of second apical tooth to the marginal brush, the wall low and straight in some larvae, convex in outline in others, often projecting above the brush into a more or less tooth-shaped corner, or transformed into a broad, strong pseudomola with grinding surface. Aboral side of mandible furnished with proximal setae in various numbers and of different lengths and with distal, sometimes bifurcate, or very long and soft setae gathered in a small group; occasionally, with a single ovate setula.

Mandibular glands present, paired, each with opening at base of mandible.

Maxilla with cardo as a rule about half as large as stipes or smaller but almost as large as stipes in a few genera. Setae usually few or absent on cardo, long and moderately long on stipes, and present in various number, always most numerous in the indistinctly limited distal stipital region which corresponds to palpiger in other larvae. *Lacinia* differing much in size, setal arrangement and presence of spines. Genus *Caenocara* with swollen hard inner lacinial margin fitted for masticating spores of puffball against the hypopharyngeal sclerite. *Galea* always comparatively large, with rounded outline; marginal setae strong, moderately long and often cultriform. Adoral and aboral sides of both lobes with many setae, stronger and stiffer on aboral side, softer and thinner on adoral side. Particularly long and fine, hairlike setae present in some larvae issuing from a membranous adoral region at a bridgelike bar between the lacinial margin away from galea and the margin of galea adjacent to the proximal article of palpus. *Maxillary palpus* usually consisting of three articles, but of four in several species and only of two in *Cryptorama minutum* Lec.

Apical article always without setae and provided dorsally and externally with a rod imbedded in a niche in the wall; subapical article usually with two setae and a pore; proximal article with a varying number of setae approximately equal to the number on the distal part of stipes; an extra article, occasionally present between the proximal and subapical articles, carrying few setae.

Maxillary articulating area generally narrow and indistinct.

Submentum and *mesomentum* (= mentum, auct.) separated by the transverse *labial sulcus*. Both subdivisions large and fleshy and carrying a group of setae on each side, setae present in about same number on both submentum and mesomentum. *Prementum* membranous, limited posteriorly by a narrow, arched or, in *Ptilinus*, triangular sclerotization. *Proximal article of labial palpus* usually with one, sometimes with several setae or setulae; *distal article* without setae but with minute sensory papillae and a pore. *Ligula* rather short and obtusely conical between palpi, dorsally enlarged in front of hypopharynx in several species.

Gular region and gular sulcus absent.

Body-trunk with areas distributed and developed essentially as in other curved larvae. Dorsum of each segment, except, the dorsally simple prothorax and the last three abdominal segments, divided by a transverse groove, the *prodorsal sulcus*, into a *prodorsal* and *postdorsal area*.

Prothorax, generally isormophous in all the anobiid larvae, and therefore, offering no characters of taxonomic value, except, in a few genera with considerably larger prothoracic than abdominal segments; sometimes provided with an oblique linear groove on each side.

Prodorsal areas of meso- and metathorax with or without hook-shaped asperities, mesothorax ordinarily without.

Asperities present or absent on prodorsal areas of first to eighth abdominal segments, on sides of ninth abdominal segment and on the tenth abdominal segment; present on the epipleural lobes of genus *Ptilinus*.

First thoracic spiracle located laterally in posterior part of prothorax; second thoracic spiracle vestigial; eight pairs of abdominal spiracles always present, all located laterally. Thoracic spiracle much larger than abdominal spiracles in several species, but more often of about the same size. All spiracles annular,

varying much in details, being simple without airtubes, or having from one to many open or apparently closed, non-annulated airtubes or, possessing a pseudocribrate plate with atrial surface texture.

Legs with sessile coxa and usually distinct trochanter, femur, tibio-tarsus and pretarsus. *Pretarsus* consisting of a membranous or, in *Ptilineurus marmoratus* Reitt., sclerotized proximal part, and ordinarily a claw. Claw lacking in several species, and membranous part of pretarsus combined with arolium changed in these into a bladder. Membranous part characterized in most species by having two or more setae. Claw-forming part varying in length, strength and form according to species and genus. *Arolium* present in several larvae but more often absent. Segments of legs barely separated, lacking distinct claw as well as arolium and a bladder in the vestigial, subconical, completely membranous leg of the genus *Caenocara*.

Ingluvies or crop varying in size according to genus, but varying little in general shape.

Airsacs from main tracheal branches not found.

Malpighian tubes six in number.

Hypometamorphosis unknown in the family.

Division 12. Precursory Remarks about Segregation of Larvae into Groups.

The majority of the known anobiid larvae lend themselves to a taxonomic grouping which conforms pretty well with the current classification of the imagines as far as the sequence in which they are listed in the leading catalogues is concerned and therefore supposedly reflects the natural interrelationship of the species and genera. But a significant minority of the larvae cannot be included in the same genera and tribes in which their imagines usually are placed. Thus the tribe Dorcatomini of Reitter[1] includes the genera *Catorama*, *Dorcatoma* and *Caenocara*, and to these Leng[2] has added the American genera *Petalium*, *Protheca* and *Eutylistus*; but, according to the larvae, the genus

[1] L.V. Heyden, E. Reitter, I. Weise: Catalogus Coleopterorum Europae, 1906, edit Edmund Reitter, Paskau editio secunda pp. 427–433.

[2] Charles W. Leng: Catalogue of the Coleoptera of America north of Mexico, 1920, Mont Vernon, N.Y., John D. Sherman jr., pp. 241–244.

Catorama and the genera *Petalium* and *Protheca* are only distantly related to the larvae of *Dorcatoma*, *Eutylistus* and *Caenocara* which together form a natural group.

In addition to other similar cases in which it has been found that the imagines and their larvae cannot be placed in the same tribe, different taxonomic perplexities have to be contended with as when certain larval species cannot be included in the same genera in which the imagines are placed. Thus the larva of *Ernobius marginicollis* Lec. is fundamentally different from the larvae of the other species of the genus *Ernobius* and, likewise, the larva of *Catorama vestitum* Fall cannot be classified as a *Catorama* larva because it is entirely without asperities and comes very close to the larva of *Ozognathus cornutus* Lec. in this respect as well as in almost all other characters, and *Catorama gracilis* Fall occupies a remarkably isolated position in the family. Such lack of conformity in the taxonomic arrangement of the imagines and the corresponding larvae may arise from some inadequacy of the characters used in the grouping of the imagines but in some cases can also be due to the fact that the available determined material of the larvae is too scanty for a full understanding of their true interrelationship. Less than one fifth of the circa 235 North American species and about one third of the genera listed by LENG are known in the larval stages.

For these reasons no premature attempt shall be made in this paper to segregate the larvae into new genera or to create new tribes, and in the following key and descriptions the commonly known generic and specific names of the reared imagines will be kept and used in the identification of the larvae.

The different larval species have, however, been arranged in the key and the succeding series of descriptions in a sequence which as far as possible will reflect the natural relationship between them. Unfortunately not always with much success, for, to mention a few examples, the casual grouping together of all the larvae with a terminal bladder instead of a claw is evidently artificial and, therefore, phylogenetically irrelevant; and so is the convenient lumping together of the miscellaneous larvae without asperities on the body trunk. It is also noteworthy that the larvae of the *Dorcatoma*-group and the species *Ptilineurus marmoratus* Reitter and the genus *Ptilinus*, readily recognized in themselves

are mutually very different and each strikingly isolated taxonomically.

On the other hand, the great bulk of the anobiid larvae presents a homogeneous association of interrelated forms which, nevertheless, are separable, in most cases easily, into the following seven subdivisions.

The *first subdivision* includes the larvae of the genera *Hedobia* and *Eucrada* whose imagines constitute the tribe Hedobiini in the current classification, but it includes also the larva of *Utobium* and perhaps the aberrant larva of *Catorama gracilis* Fall. It is a diversified group but apparently quite natural.

The *second subdivision* includes besides *Xestobium rufovillosum* Deg. and *Ochina ptinoides* Marsh., the majority of the species of genus *Ernobius*. It is readily characterized by the presence of asperities on the tenth (= "anal") abdominal segment, and in the here-placed *Ernobius* species also by the presence of distinct frontal cleavage lines.

The *third subdivision* includes *Coelostethus*, *Trypopitys* and, according to reared larvae, possibly but doubtfully *Hadrobregmus carinatus* Say[1] in which anteclypeus is completely or half-way covered by a plate.

The *fourth subdivision* includes *Platybregmus* which resembles *Vrilletta* more than it resembles *Anobium*, and the genus *Anobium*, in both of which the lateral asperities on ninth abdominal segment are lacking.

The *fifth subdivision* includes *Microbregma emarginatum* Dufts. and *Ernobius champlaini* Fisher; both forms, in other characters quite heterogeneous, have tridentate mandibles.

The *sixth subdivision* includes *Trichodesma*, *Nicobium*, *Xeranobium*, *Holcobius*, *Oligomerus*, *Xyletinus fucatus* L., and *Xyletinus* sp. (which, according to reared imago, is either *Xyletinus mucoreus* Lec. or a very close species) in all of which the maxillary lacinia is as large or almost as large as galea and epipharynx to a great extent or completely covered with long, centripetal chaetoparial setae. As a minor part the subdivision contains also *Xyletinus peltatus* Harris and *Xyletobius walsinghami* Perkins

[1] A mistaken identification of the larva of this species may have happened by associating a reared imago with all the larval specimens in a material which accidentally was mixed.

plus *Xyletobius sykesi* Perkins and conditionally *Hadrobregmus umbrosus* Fall plus *Hadrobregmus thomsoni* Kraatz, in which lacinia is distinctly smaller than galea and the chaetoparial setae less numerous, even if usually arranged in patches of up to ten or more on each side. The species *Xyletinus peltatus* Harris and the genus *Xyletobius* mark, in fact, a gradual transition from the larvae of the major part of this sixth subdivision in which the other two species of *Xyletinus*, viz. *X. fucatus* L. and *X. mucoreus* Lec., unquestionably belong, to the larval type of the large seventh subdivision; the principal difference between them and this subdivision being a contrasting number of prodorsal asperities on the fifth and sixth abdominal segments (cp. key couplet 29).

The *seventh subdivision* includes the genera *Vrilletta*, *Priobium*, *Protheca*, *Catorama*, *Stegobium* and *Nevermannia* in which lacinia is distinctly smaller than galea, each side of epipharynx usually provided only with a single oblique row of chaetoparial setae and the prodorsal area of the seventh abdominal segment furnished with only a small number of asperities ranging from 15 or a few more to much less or none at all.

Division 13. Key to Species.

1. Either (61, first alternative) with proximal pretarsal part of prothoracic leg long, sclerotized and beset with numerous ovate setae, or, (61, second alternative) with epipleural areas of most segments of body trunk armed with hook-shaped asperities and with a premental sclerite formed as a triangular plate 61

   Proximal pretarsal part of prothoracic leg usually much shorter than tibio-tarsus and membranous, without ovate setae, and epipleural areas lacking asperities 2

2(1). Mandible with grinding, broad and long pseudomola. (Outer surface of labrum usually with a single transverse series of, altogether, four or six long, stiff setae; coryphal setae often strong and claw-shaped.) 56

   Mandible without grinding, broad and long pseudomola. (Surface of labrum with numerous, moderately long setae except in *Microanobium*; coryphal setae small when present.) 3

3(2). Leg terminating with a balloon-shaped bladder; two pretarsal setae proximally; claw absent 53

   Leg with distinct claw, no bladder 4

4(3). Prodorsal asperities absent 47

Prodorsal asperities present on most segments..... 5

5(4). Second thoracic segment with a large patch of ten or more asperities on each side of prodorsal area..... 6

Second thoracic segment with a few, or, usually with no prodorsal asperities 7

6(5). 8th abd. segment with fifteen or more asperities on each side; mandible without teeth but with a simple, gouge-shaped apical edge..... 1. *Catorama gracilis* Fall

8th abd. segment without asperities; mandible with two apical teeth and two subapical teeth. 2. *Utobium elegans* Horn

7(5). Spiracles with numerous short airtubes on one side of peritrema; maxillary palpus with four articles. (Distal part of mandible apparently with simple terminal edge, without distinct teeth.) ..... 3. *Eucrada humeralis* Melsh.

Characters different..... 8

8(7). Lacinia maxillaris vestigial, represented by a single strong spine and a few setae. (Pretarsus almost as long as tibiotarsus, membranous part longer than the straight thin, very pointed claw and provided with at least three setae.) 4. *Hedobia imperialis* L.

Lacinia of varying size according to different species but always present and distinct..... 9

9(8). Anal (tenth abdominal) segment armed with hook-shaped asperities; frontal cleavage lines present or absent..... 10

Anal (tenth abdominal) segment without asperities; frontal cleavage lines always absent..... 16

10(9). Cranium without frontal lines..... 11

Cranium with frontal lines 12

11(10). Chaetoparial setae about ten in two rows on each side; tormae short and clubshaped, loosely connected with labral rods..... 5. *Xestobium rufovillosum* Deg.

Chaetoparial setae four (or five) in one oblique row on each side; tormae long, straight, terminally pointed, labral rods insignificant..... 6. *Ochina ptinoides* Marsh.

12(10). Epipharynx with about twenty short and moderately long, slender chaetoparial setae on each side; prodorsal asperities about forty five on third thoracic segment and about thirty on sixth abdominal segment. (Spiracles with one short airtube.) ..... 7. *Ernobius mollis* L.

Epipharynx with less than fifteen chaetoparial setae on each side; prodorsal asperities twenty five or fewer on third thoracic segment and less than twenty on sixth abdominal segment 13

13(12). Six chaetoparial setae in a regular curved series on each side. (Spiracles with one short airtube.) 8. *Ernobius abietis* F.

More than six chaetoparial setae present on each side of epipharynx..... 14

14(13). Spiracles without airtubes; chaetoparial setae on each side about fourteen; chaetoparial setae from right and left side intermingled into a median patch in posterior half of epipharynx ..... 9. *Ernobius* sp. (ex spruce cones from Canada)

Spiracles with at least one well-developed airtube; chaetoparial setae on each side numbering from eight to fourteen; chaetoparial setae from right and left side of epipharynx not intermingled into a median patch posteriorly 15

15(14). Thoracic spiracle with one airtube; chaetoparial setae numbering fourteen on each side. 10. *Ernobius granulatus* Lec.

Thoracic spiracle with one distinct and one small airtube; chaetoparial setae numbering about eight on each side. 11. *Ernobius punctulatus* Lec.[1]

16(9). Anteclypeus covered either completely or on its posterior half by a single large plate 17

Anteclypeus either without a plate or with a small, setae-bearing plate at each end of the anteclypeal sulcus 20

17(16). Anteclypeus completely covered by a strongly pigmented and deeply pitted plate ..... 12. *Coelostethus notatus* Say

Anteclypeus with posterior plate shorter than anteclypeus. 18

18(17). Abdominal spiracles with vestigial or no airtubes. (Number of asperities generally around fifty on each side of main abdominal segments.) .... 13. ?*Hadrobregmus carinatus* Say (probably wrong determination. See footnote p. 96)

Abdominal spiracles with distinct airtubes 19

19(18). Abdominal spiracles with short airtube; number of asperities generally more than seventy on each side of main abdominal segments ..... 14. *Trypopitys sericeus* Say

Abdominal spiracles with larger airtubes; number of asperities generally around thirty on each side of main abdominal segments ..... 15. *Trypopitys punctatus* Lec.

20(16). Lateral asperities absent on ninth abdominal segment.... 21

Lateral asperities present on ninth abdominal segment... 24

21(20). Epipharynx with a patch of chaetoparial setae on each side; acroparial and acanthoparial setae recurved over the margin of epipharynx; labral rods and tormae fused together into short, curved, robust features (compare identical epipharyngeal and other structures in genus *Vrilletta* (Pl. 34, figs. 8–17) which, however, has hook-shaped asperities on ninth abdominal segment.) 16. *Platybregmus canadensis* Fisher

[1] Some larvae in the U.S.N.M. collection are labelled: "*Ernobius pallitarsis* Fall, in *Pinus lambertiana*; the city "Misteltoe" in Oregon, 7.XII.1917." No information is available about how the identification was obtained or by whom. But the larvae appear identical in all taxonomic characters with the larval species *Ernobius punctulatus* Lec.

Epipharynx with an inwardly convex single series of six chaetoparial setae on each side; acanthoparial setae straight; numerous small coryphal setae; labral rods and tormae forming long, strong Y-shaped features 22

22(21). Abdominal spiracles with one long, curved airtube. 17. *Anobium punctatum* Deg.

Abdominal spiracles with a short airtube 23

23(22). First to sixth abdominal segments each with four or five irregular rows of prodorsal asperities. 18. *Anobium gibbicollis* Lec.

First to sixth abdominal segments each with two to three to four rows of prodorsal asperities. 19. *Anobium nitidum* Herbst also *Anobium pertinax* L.

24(20). Mandible with three teeth, terminally placed and distinctly distant from the marginal brush 25

Mandible with two teeth apically and subapically either with smooth concave edge, or with subtriangularly projecting ledge 26

25(24). Maxillary palpus with four articles, seventh abdominal segment with few or no prodorsal asperities. 20. *Microbregma emarginatum* Dufts.

Maxillary palpus with three articles, seventh abdominal segment with about twelve prodorsal asperities. 21. *Ernobius champlaini* Fisher

26(24). Lacinia distinctly smaller than galea; epipharynx with a single (or mainly single) row, or a narrow triangular patch of not more than fifteen chaetoparial setae on each side.. 27

Lacinia as large or almost as large as galea; epipharynx with a broad patch of more than fifteen setae on each side, or, covered completely by curved, centripetal, rather soft hairs. (No arolium.) 32

27(26). With a series, on each side of six conspicuously short chaetoparial setae, series hardly reaching the middle of epipharynx; claw slender, pointed, somewhat curved and half as long as tibio-tarsus; abdominal prodorsal asperities distributed in double rows on some of the segments and in a single row on others ..... 22. *Stegobium paniceum* L. (= *Sitodrepa panicea*)

Different combination of characters 28

28(27). Adoral mandibular surface with projecting longitudinal carinae; prodorsal asperities minute and flattened on top, distributed in a single regular, transverse series of not more than ten on each of first to seventh abdominal segsegments; claw short.. 23. *Nevermannia dorcatomoides* Fisher (In termites nests, Costa Rica)

Different combination of characters 29

29(28). Prodorsal asperities of fifth and sixth abdominal segments

each numbering from at least thirty to many more on each side. (Arolium absent; tormae slender, as long as labrum.) 30

Prodorsal asperities of fifth and sixth abdominal segments each numbering from a few to no more than twenty five on each side. (Arolium commonly present.) 38

30(29). Seventh abdominal segment with not more than twelve prodorsal asperities ..... 24. *Hadrobregmus thomsoni* Kraatz
also 25. *Hadrobregmus umbrosus* Fall
(and perhaps *Hadrobregmus carinatus* Say)[1]

Seventh abdominal segment with twenty five or more prodorsal asperities 31

31(30). Spiracles pseudocribriform; chaetoparial setae in a long, subtriangular patch of about twelve on each side; short pigmented field present behind epistoma.
26. *Xyletobius walsinghami* Perkins
also *Xyletobius sykesii* Perkins

Spiracles simple, annular with a single minute or no airtubes; chaetoparial setae in a single, regular, curved series of six setae on each side; pigmented field absent.
27. *Xyletinus peltatus* Harris
also *Xyletinus* sp.

32(26). Asperities present on sixth and seventh abdominal prodorsal areas; maxillary palpus three-articulate 33

Asperities absent on sixth and seventh abdominal prodorsal areas; maxillary palpus four-articulate 37

33(32). Tormae long or short, narrowly conical and pointed; seventh abdominal prodorsal area with about fifteen or less asperities; membranous base of pretarsus with two setae 34

Tormae long, either with upward ascending branches or sausage-shaped; seventh abdominal prodorsal area with about twenty five or many more asperities; membranous base of pretarsus with four of five setae 36

34(33). Sixth and seventh abdominal prodorsal areas with, respectively, about twenty five and twelve asperities; spiracles oval, without airtubes. (Tormae almost as long as sagittal length of epipharynx anterior to crepidal field.)
28. *Xyletinus* sp., near *mucoreus* Lec.

Sixth and seventh abdominal prodorsal areas with, respectively, twelve or less and eight or less asperities; spiracles oval, with one or two short airtubes 35

35(34). Tormae almost as long as sagittal length of epipharynx anterior to crepidal field ..... 29. *Xyletinus fucatus* Lec.

Tormae about half as long as sagittal length of epipharynx anterior to crepidal field .... 30. *Oligomerus sericans* Melsh.

36(33). Field behind epistoma strongly pigmented and large, cen-

[1] See p. 63.

trally with a single, conical process; tormae long, robust, anteriorly irregularly branched, posteriorly curved toward each other, no labral rods; prodorsal asperities on third thoracic segment and subsequent seven abdominal segments in five or more series at the sagittal line of the body.
31. *Holcobius haleakalae* Perkins
also *Holcobius glabricollis* Perkins
and *Holcobius hawaiensis* Perkins

Field behind epistoma not pigmented, no median cranial process; tormae sausage-shaped, about as long as sagittal length of epipharynx anterior to crepidal field; no labral rods; prodorsal asperities on third thoracic and subsequent seven abdominal segments in less than five series at the sagittal line of the body ..... 32. *Xeranobium macrum* Fall

37(32). Spiracles pseudocribriform..... 33. *Nicobium castaneum* Oliv.
Spiracles simple, annular, without airtubes.
34. *Trichodesma klagesi* Fall
also 35. *Trichodesma gibbosa* Say

38(29). Chaetoparial setae anteriorly in a narrow patch of two irregular rows of setae and posteriorly in a longer, oblique single row on each side; pigmented field behind epistoma absent; tormae short, robust, strongly converging; no labral rods; marginal brush of mandible present. (Claw curved, moderately large.) ..... 36. *Vrilletta convexa* Lec.
also *Vrilletta blaisdelli* Fall
and *Vrilletta* sp.

Different combination of characters. (Chaetoparial setae usually in a single row on each side; pigmented field present in some species; marginal brush often lacking.)..... 39

39(38). Abdominal spiracles with a single long, multibranched airtube. (Pigmented field not present; prodorsal asperities of third thoracic segment absent.).. 37. *Priobium tricolor* Oliv.
also *Priobium eichhoffi* Seidl.

Spiracles different. (Prodorsal asperities of third thoracic segment usually present.)..... 40 and 41

40(39). The larva of 38. *Protheca hispida* Lec. may be closely related to larvae of the genus *Catorama*. See description of single, imperfect larval skin p. 132.

41(39). Spiracles pseudocribriform; arolium absent. (Prodorsal areas of third to seventh abdominal segments with a single, regular row of ten or fewer asperities on each side.)
39. *Catorama nigritulum* Lec.

Spiracles different; arolium present..... 42

42(41). Annular spiracles simple, circular without airtubes..... 43
Annular spiracles with a single or two distinct airtubes. (Mandible without marginal brush.) 44

43(42). Seventh abdominal segment with an irregular, partly double

row of about 12 asperities on each side. (Mandibular marginal brush present; epipharynx with numerous small coryphal setae anterior to an irregular, posteriorly diverging row of six long chaetoparial setae and some fine ordinary setae in space behind.) ..... 40. *Catorama* sp. (from ivy together with imagines not determinable to species)

Seventh abdominal segment without asperities. (Mandibular marginal brush absent; epipharynx with two pairs of minute coryphal setae and a regular, posteriorly converging row of six moderately long, curved chaetoparial setae.) 41. *Catorama punctatum* Lec.

44(42). Field behind epistoma poorly pigmented and indistinct. (Third thoracic segment with from about eight to less or no asperities on each side.) 45

Field behind epistoma strongly pigmented. (Third thoracic segment with from about nine to more asperities on each side.) 46

45(44). Prodorsal asperities of each of first to fourth abdominal segments in a single straight row of about five asperities on each side ..... 42. *Catorama* sp. near *C. conjunctum* Fall[1]

Prodorsal asperities of each of first to fourth abdominal segments in an irregular single or two rows of generally ten or more asperities on each side ..... 43. *Catorama* sp.[1] probably *C. herbarium* Gorh. (= *C. mexicanum* Chev.)

46(44). Third thoracic segment on each side with about ten dorsal asperities generally arranged in a single row; first and second abdominal segments each with about twenty asperities in two irregular rows ..... 44. *Catorama* sp. probably *C. inaequale* Fall[1]

Third thoracic segment on each side with about sixteen dorsal asperities in two irregular rows; first and second abdominal segments each with about twenty five asperities in two to three irregular rows... 45. *Catorama tabaci* Guér.[1] (= *C. impressifrons* Fall) also 46. *Catorama grande* Fall

[1] A great many larvae in the collection of U.S.N.M. are referable to the second alternative of couplet #42 but only the four larval forms listed in couplets #45 .and #46 are associated with imagines (determined conditionally by W. S. Fisher). These four can be separated from each other by the characters given in the key, when considered without regard to the specimens not associated with imagines. But one group of these unidentified larvae is very close to one or the other of the two species listed in couplet #45 and another group is intermediate between the two species of couplet #46. In both cases it is impossible at present to know whether they are mere larval varieties of the named species or belong to closely related, generally recognized species. It may even become a problem to find out how to separate the larvae of the two categories defined in couplet #42 because some of the non-identified larvae tend to link them together.

47(4). Spiracles annular with a single or no airtubes 48
Spiracles pseudocribriform 50

48(47). Mandible with one apical tooth; lacinia terminally with a single long, strong spine and a few stiff setae; galea half as wide as long ..... 47. *Gastrallus* sp. (probably *G. laevigatus* Oliv.)
Mandible with two apical teeth; lacinia terminally without spine and with about eight densely set stiff setae; galea as wide as long 49

49(48). Body elongate, not strongly curved, with all areas hairy, and epipleural area in particular provided with numerous long hairs; epistoma on anterior margin with a series of, altogether, sixteen long setae; anteclypeus at each end of anteclypeal sulcus with a small plate bearing five long setae. (Mandible without marginal brush.) 48. *Catorama vestitum* Fall
Body short, thick and curved, with all areas sparsely furnished with hairs; epipleural areas each with about three hairs; anterior margin of epistoma with a series, of, altogether, six (or eight) long setae; anteclypeus without a setae-bearing plate or any setae at each end of the anteclypeal sulcus. (Mandible with a marginal brush.) 49. *Ozognathus cornutus* Lec.

50(47). Clypeofrontal region without distinct pigmented field behind epistoma (Body elongate, cylindrical and fairly straight.) 50. *Petalium seriatum* Fall
Clypeofrontal region behind epistoma either dark and bearing posteriorly a conical process in the sagittal line, or, head-capsule provided with both a large pigmented field and additional pigmented spots on parietalia, or, entire head dark with light pits or pale yellowish 51

51(50). Frontal cleavage lines distinct; head capsule strongly sclerotized with setae all over, regularly arranged, in deep pits. (Cranium reddish brown.) 51. *Unknown genus near Lasioderma* (with orchids from Mexico)
Frontal cleavage lines either incomplete or lacking; head capsule not particularly thick-walled and setae not set in regularly arranged deep pits 52

52(51). Head capsule protracted, almost orbicular, covered completely with long, fine setae and without a conical process sagittally; mandible with two apical teeth and a long subapical, somewhat concave edge; maxillary palpus with three articles; arolium present ..... 52. *Lasioderma serricorne* F.
(Cranium without frontal cleavage lines, particolored with longitudinal whitish bands.) 53. *Lasioderma* sp.
(Cranium with incomplete frontal cleavage lines, uniformly brownish.)

Head capsule retracted, elongate oval, naked posteriorly; a conical process present at end of pigmented field; distal part of mandible ending with three distinct teeth (two apical and one subapical); maxillary palpus with two articles; arolium absent ..... 54. *Cryptorama minutum* Lec.

53(3). Prodorsal asperities present on most segments; antenna with two articles; spiracles ring-shaped, with one airtube..... 54

All body segments without asperities; antenna without articles; spiracles ring-shaped, without airtubes..... 55

54(53). Chaetoparial setae in a single, oblique row of five on each side; mandible with four teeth, and marginal brush present; lacinia with two strong curved and claw-shaped hooks and a few long, fine setae. . 55. *Genus and species unknown* (resembles genus *Ernobius* of the *Ernobius mollis* type)

Chaetoparial setae numerous, in a patch on each side; mandible with two apical teeth and an elongate, subtriangular, low subapical wall; marginal brush lacking; lacinia with many straight, stiff terminal setae but no hooks.
56. *Ernobius marginicollis* Lec.

55(53). Chaetoparial setae numerous, irregularly distributed, long fine and curved; numerous hook-shaped, small coryphal setae; labrum covered with many setae; lacinia distinct, terminally with about five stiff setae.
57. *Neogastrallus librinocens* Fisher

Chaetoparial setae in a single regular series of four thick, club-shaped, rather short setae on each side of epipharynx; a transverse row of, altogether, four short, thick coryphal setae; labrum on each side with only one short and three long setae; lacinia vestigial with one spine.
58. *Microanobium* sp. (from China)

56(2). Prodorsal areas of many segments with hook-shaped asperities; lacinia typical in shape and function; legs of normal build 57

Prodorsal areas without hook-shaped asperities but with straight, pointed spines, each on top of a tubercle, tubercles arranged in a single transverse row; lacinia with swollen strongly sclerotized inner margin grinding against a hypopharyngeal callosity; legs poorly developed, claw weak or lacking..... 60

57(56). Chaetoparial setae in a single, longitudinal inwardly concave row; coryphal setae two, large, median, each fused exteriorly with a vestigial one. (Spiracles slightly pseudocribriform; laterally at ventral fossa for mandible with a flat, granulated field.)..... 59. *Eutylistus intermedius* Lec.

Chaetoparial setae on each side arranged in an anterior patch of many setae and posteriorly in a single longitudinal row; coryphal setae at least four, large ones..... 58

58(57). Pseudocribriform part of spiracles much larger than width of spiracular trachea. (With flat, granulated field at fossa for mandible.) ..... 60. *Eutylistus facilis* Fall

Spiracles not pseudocribriform 59

59(58). Cranium ventrolaterally with flat, granulated field at fossa for mandible; spiracles regular, annular without air tubes; coryphal setae four altogether.... 61. *Anitys rubens* Hoffm.

Cranium ventrolaterally with a large, granulated, conical process at fossa for mandible; spiracles annular with a very short air tube; coryphal setae, altogether, six or more.

62. *Dorcatoma dresdensis* Herbst

also: 62* *Dorcatoma chrysomelina* Sturm

60(56). Mandible apically with one distinct tooth and minute and indistinct second tooth; labrum broad, cordiform; chaetoparial setae in a single inwardly convex row, numbering about twenty five on each side; leg reduced but with a setalike, curved claw..... 63. *Caenocara bovistae* Hoffm. (from Denmark)

also: *Caenocara* sp. (from Maryland, U.S.A.)

Mandible apically with two distinct teeth; outline of labrum two-thirds of a circle; chaetoparial setae in a single, straight, somewhat oblique row of about ten setae on each side; leg vestigial without distinct claw ... 64. *Caenocara oculata* Say

61(1). Proximal part of prothoracic pretarsus very long, sclerotized and set with many short, ovate setae; proximal part of meso- and metathoracic pretarsus fairly long with many straight and pointed setae; claw of first leg rather small, slender and upturned; epipharynx covered with long hair-like setae; epipleural area without asperities; premental sclerite weak and curved as a bow.

65. *Ptilineurus marmoratus* Reitter

Proximal part of prothoracic pretarsus very short, carrying a single seta; proximal part of meso- and metathoracic pretarsus similar to the prothoracic; claw of first leg rather small, slender but straight to slightly curved downward; epipharynx on each half with a single, inwardly convex series of six chaetoparial setae; epipleural area of most segments with a patch of asperities; premental sclerite formed as an elongate, triangular plate.

66. *Ptilinus basalis* Lec.

(also: *P. ruficornis* Say,
P. fuscus Geoffr.
and *P. pectinicornis* L.)

Division 14. Description of Species.

1. *Catorama gracilis* Fall.

Plate 13.

Described material labeled:

Catorama gracilis Fall., in fungus in bark of dead maple; University Park, Md. 27.VIII.1944, W. H. Anderson coll.; W. S. Fisher det. imago.

Size of larva[1]*:* Small (c. 4 mm.).

Head capsule (Fig. 2) subcircular, slightly longer than broad, broadest at the middle, rounded posteriorly, without frontal lines; pigmented field behind epistoma about three times longer sagittally than epistoma; epistoma (fig. 1) provided in anterior margin with, altogether, about sixteen fairly long and rather short, straight setae behind the entire base of anteclypeus, and also with a few fairly long setae rearward; rest of cranium with some moderately long and many short, soft setae. Antenna (fig. 1) without articles, sensory organs born by dome-shaped membranous base. Anteclypeus (fig. 1) with a group of about six rather long setae on a thin plate at each end of anteclypeal sulcus, plates connected by a thinly sclerotized band. Labrum (figs. 1 and 2) transverse, about two and one half times as broad as long, anterior margin quite straight, anterior corners and the side margins rounded, surface densely set with short, fine setae and on the side margins with somewhat longer ones; paired dark marks absent. Epipharynx (fig. 3) naked with exception of about three minute setae in an oblique row on each side, probably corresponding to the chaetoparial setae in other larvae; tormae fairly long and straight, somewhat convergent; labral rods vestigial, reduced to a membranous little projection from the tormal stem

[1] W. H. Anderson: Larvae of some genera of Anthribidae, Annals Entomological Society of America, vol. XL, 1947, p. 490.

"No satisfactory was has been devised for measuring and expressing the size of the larvae. The over-all length of mature specimens of a given species will vary considerably depending upon the method of killing before preservation. General statements have been made, however, in an attempt to indicate the comparative sizes of the larvae; as small, moderately large, and large. The length of the larvae studied ranges from about 2.5 mm.... to about 15 mm."

The length of anobiid larvae ranges from:

small	about 2 mm. to 4 mm.
moderately large	5 mm. to 10 mm.
large	11 mm. to 15 mm.

at the posterior end of its anterior half; crepidal field broad, covered with soft papillae, apparently no pores. *Mandible* (fig. 6) not dentate, with a gouge-shaped distal end as in larvae of the Bostrichidae and the dermestid Attageninae; aboral surface with a proximal transversal group of about a dozen short setae, irregularly arranged, and a distal group of some minute setae. Maxillary lacinia (fig. 5) small, about one third as large as galea, armed with a thin spine and about five terminally placed, long, stiff setae; galea with rather slender, terete setae in the distal margin, and on the aboral surface with several setae; maxillary palpus with three articles, proximal article with about five setae ventrally, second article with one seta, apical article with a pore on ventral side and a sensory rod dorso-exteriorly; stipes with a moderate number of setae. Prementum proximally with simple, arched sclerite (fig. 7) and prementum, mesomentum and submentum with several setae.

Body trunk (fig. 4) curved; thoracic segment somewhat larger than the abdominal; asperities (fig. 11) conical, some slightly curved, others straight.

Number of asperities[1] *on each side of:*

Thoracic segment II	15
„ „ III	25
Abdominal segment 1	30
„ „ 2	30
„ „ 3	32
„ „ 4	33
„ „ 5	30
„ „ 6	25
„ „ 7	22
„ „ 8	20

9th abdominal segment with a large patch of about 70 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 8 and 9) small, annular with circular orifice

[1] In the descriptions of the present and the following species, the prodorsal asperities have as a rule been counted on a single specimen which was selected as typical of the larvae of the material on which the descriptions of the species are based. The recorded numbers of asperities should therefore be considered merely as guiding symbols, being only approximately, but not exactly, the numbers found in all specimens of the various species in the collection of the U.S.N.M.

and two very small and one vestigial airtubes; all spiracles of almost same size.

Leg (fig. 10) reduced in size; segments not sharply formed, length of pretarsus in proportion to length of tibio-tarsus as one to one and a half; claw longer than the membranous part of pretarsus and shaped like a slightly curved sting; no arolium.

2. *Utobium elegans* Horn

Plate 14,

Described material labeled:

1) *Utobium elegans* Horn, ex lodgepole pine killed by Dendroctonus monticolae, Sequoia Natl. Park, California, 2.XI.1933, H. H. Keifer coll.
2) *Utobium elegans* Horn, in Pinus contorta, boring between bark and wood, Crater Lake, Or., Hopk. U. S. 1881, 3a.

Size of larva: Moderately large (c. 8 mm.).

Head capsule as broad as long, broadest at the middle, rounded posteriorly, without frontal lines, pigmented field (fig. 1) behind epistoma present, sagittally about twice as long as epistoma; epistoma (fig. 1) glabrous; cranium, including pigmented field covered with a moderate number of fairly long, rather dark setae. Antenna (fig. 1) with two distinct articles. Anteclypeus (fig. 1) with about five rather long setae at each end of anteclypeal sulcus and borne by a small plate. Labrum (fig. 1) with free margin semicircular and with numerous fine setae on anterior part of surface; paired marks present. Epipharynx (fig. 2) with two pairs of small coryphal setae, acroparial and acanthoparial setae long; chaetoparial setae fairly numerous, four to five of them on each side rather short, slightly curved and arranged in an inwardly convex, oblique row extending from anterior margin to near center of epipharynx, remainder of chaetoparial setae generally somewhat longer and straight, scattered in an irregular double row; labral rods long, straight and subparalle, not firmly united with short, strong, corniform tormae; crepidal field velvety pubescent without pores. *Mandible* (fig. 3) with four distinct, not widely separated teeth; setae of marginal brush dense and long; aboral mandibular surface with a proximal group of many setae, some very long; about five distal setae. Maxillary lacinia (figs.

4 and 5) small, terminally armed with one strong, thornlike spine and in addition with about four long and stiff and several finer setae; galea with a series of strong, cultriform setae on anterior margin, aboral and adoral surfaces with numerous setae; maxillary palpus with three articles, proximal article with a transverse series of about five long setae on both dorsal and ventral surfaces; distal part of stipes with about five long setae.

Body trunk curved, subcircular in cross-section, of nearly same thickness throughout.

Number of asperities on each side of:

Thoracic segment	II (fig. 6)	10 in two rows
„ „	III (fig. 6)	29 in three rows
Abdominal segment	1	23 „
„ „	2	24 „
„ „	3	20 „
„ „	4	16 „
„ „	5	15 in two rows
„ „	6	15 „
„ „	7	5 in one row
„ „	8	none

9th abdominal segment with a patch of 35 lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (fig. 8) annular with oval peritrema, the thoracic and some of the abdominal spiracles with two very short air-tubes; thoracic spiracle about twice as long as the abdominal.

Leg (fig. 7) with pretarsus about half as long as tibic-tarsus; claw two-thirds the length of entire pretarsus, strong, sharp and curved; membranous proximal part of pretarsus with two setae; no arolium.

3. *Eucrada humeralis* Melsh.

Plate 15.

Described material labeled:

1) *Eucrada humeralis* Melsh., in Quercus alba, Springfield, Mass., Nov. 3. 1901; Dimmock #2048, inside of clear thin-walled oval cocoon.
2) *Eucrada humeralis* Melsh., in bark of oak, College Park, Md., 11.X.1942, W. H. Anderson coll.

Size of larva: Moderately large (c. 7 mm.).

Head capsule widest near the middle, oval posteriorly, without frontal lines; pigmented field behind epistoma sagittally about twice as long as epistoma; epistoma (fig. 1) armed with a transverse anterior, regular series of densely set, fairly long and fine, straight setae; rest of cranium, including pigmented field covered with numerous, mostly moderately long and straight setae in small pits. Antenna without articles; tactile papilla and sensory hairs on membranous base. Anteclypeus (fig. 1) with a group of about ten, rather long, straight setae at each end of anteclypeal sulcus, setae borne by a small sclerite. Labrum transverse oval with free margin almost semicircularly rounded; anterior part of surface with numerous fine setae; without paired marks. Epipharynx (fig. 2) with numerous small hook-shaped coryphal setae medianly and in front of chaetoparial setae; acroparial and acanthoparial setae long and densely set; chaetoparial setae rather short, filiform or slightly fan-shaped, numerous, and well dispersed in an inwardly slightly convex, broad longitudinal patch; tormae and labral rods forming together a pair of Y-shaped, strong, parallel features; crepidal field with a few minute setae. *Mandible* (fig. 3) (apparently not worn, similarly shaped in all examined specimens) without teeth, apical corner incorporated in the thick, crenulate and finely striate edge of the entire distal part of the mandible; setae of marginal brush short; proximal and distal groups of setae on aboral mandibular wall poorly developed. Maxillary lacinia (figs. 4 and 5) small, terminally armed with one strong spine and in addition bearing a few moderately long and short setae; dorsally many fine hairs; galea with fairly strong, curved, simple marginal setae, aboral surface with many rather stiff setae, and adorally numerous soft ones; maxillary palpus (fig. 4) with four articles, proximal article somewhat wider than long, next article about half as wide and half as long as proximal; subapical article and apical article subequal in length and approximately as long as proximal article, subapical article about half as wide as proximal, and apical about two thirds as wide as subapical; proximal article anteriorly with a transverse group of ten irregularly placed long and moderately long setae on the dorsal surface and about as many on the ventral surface; next article with two long setae and one or two

small ones; subapical article anteriorly with two setae; apical article without setae and dorsally with rod-shaped accessory organ; sensory pores present but few on all articles; stipes with numerous setae, particularly long on its distal part. Prementum with a broad group of moderately long setae in each anterior corner, meso- and submentum with numerous long lateral setae.

Body trunk curved, abdominal segments of nearly same thickness throughout, the thoracic segments somewhat thicker; asperities small, more conical than hook shaped.

Number of asperities on each side of:

Thoracic segment II	1	(or none)
„ „ III	40	in two to three rows
Abdominal segment 1	46	
„ „ 2	45	
„ „ 3	45	
„ „ 4	43	
„ „ 5	44	
„ „ 6	45	
„ „ 7	19	in two rows
„ „ 8	5	

9th abdominal segment with a patch of very numerous asperities on each side laterally.

10th abdominal segment with about 10 asperities on each side.

Spiracles (figs. 8 and 9) annular with oval orifices and a great number of short open spout-shaped airtubes from one side of peritrema; airtubes directed toward the head on the thoracic spiracle, toward anus on the abdominal ones; latter, half as large as thoracic.

Leg (fig. 7) with pretarsus slender, conical and two-thirds as long as tibio-tarsus; claw one-third the length of the whole pretarsus, straight and not strong; proximal membranous part bearing five strong but rather short setae; no arolium.

4. *Hedobia imperialis* L.

Plate 16.

Described material labeled:

1) *Hedobia imperalis* L., in bark of ash and elm, near Copen-

hagen, Denmark, from coll. Zool. Mus. Copenhagen, F. Meinert, 1890, #145.

Size of larva: Moderately large (c. 6 mm.).

Head capsule as broad as long, broadest at the middle, rounded posteriorly, without frontal lines; pigmented field behind epistoma (fig. 1) sagittally about twice as long as epistoma; epistoma (fig. 1) with a single transverse, regular series of about thirty four altogether, densely set, rather long and fine setae; rest of cranium, including pigmented field, covered with numerous moderately long and fine, straight setae. Antenna (fig. 1) without articles, ovate tactile papilla and sensory hairs borne by membranous base. Anteclypeus (fig. 1) with two rather long straight setae on each end of thinly sclerotized basal ribbon. Labrum (figs. 1) with almost semicircular free margin, anterior part of surface with numerous fine setae; without paired marks. Epipharynx (fig. 2) with numerous small obtuse, coryphal setae medianly in front of chaetoparial setae; acroparial and acanthoparial setae long, slender, slightly curved and densely set; chaetoparial setae long and filiform, well dispersed over most of the epipharyngeal surface; tormae and labral rods forming together a pair of Y-shaped, strong features; crepidal field broad with several small setae in the velvety pubescent surface. *Mandible* (fig. 3) with three teeth slightly projecting from the edge of the moderately wide distal part of the mandible; setae of marginal brush present, surrounded by distinct marginal elevation; aboral surface of mandible (probably) with proximal and distal setae (but broken off on material examined). Maxillary lacinia (figs. 4 and 5) vestigial, terminally armed with one strong spine and, in addition, furnished with a few long setae; galea (fig. 4) with narrow, long cultriform setae in the margin and dorsally and ventrally with numerous setae on the entire surface, stronger ventrally; long, soft, hairlike dorsally; maxillary palpus with three articles of about equal length, proximal article both dorsally and ventrally with a transverse series of about ten setae, next article both dorsally and ventrally with about five anterior setae, two behind them and in addition a few minute ones, apical article without setae, with dorsal rod-shaped accessory organ and a sensory pore; stipes with numerous setae, particularly long ones on its distal part. Prementum with a dense group of

setae in each anterior corner, meso- and submentum with numerous setae on each side.

Body trunk curved, abdominal segments of nearly same thickness throughout, the thoracic somewhat thicker; asperities rather flat, slightly curved, not sharp and not hook-shaped.

Number of asperities on each side of:

Thoracic segment II	3	
„ „ III	25	
Abdominal segment 1	40	in four to five rows
„ „ 2	45	
„ „ 3	45	
„ „ 4	48	
„ „ 5	47	
„ „ 6	35	in three to four rows
„ „ 7	18	
„ „ 8	a few	

9th abdominal segment with a patch of very numerous lateral asperities.

10th abdominal segment with a few asperities.

Spiracles (figs. 7 and 8) annular with broadly oval to circular orifices, each with a single short air tube directed toward the head on thoracic spiracle, toward anus on abdominal ones, the latter two-thirds as large as the thoracic.

Leg (fig. 6) with pretarsus slender and conical, somewhat more than two-thirds as long as tibio-tarsus; proximal membranous part about two-thirds as long as entire pretarsus, armed with six well-developed but rather short setae; claw thin, straight and setalike; no arolium.

5. *Xestobium rufovillosum* Deg.

Plate 17.

Described material labeled:

1) *Xestobium rufovillosum* Deg. (= *X. pulsator* Schall. = *X. tesselatum* Oliv.) in oak stump, Dyrehaven near Copenhagen, Denmark, 1.IV.1915, J. P. Kryger coll. et reared.
2) *Xestobium* sp. West Kingston, Rhode Island, Dr. A. E. Stone coll. et det.
3) *Xestobium rufovillosum* Deg. from floorbeams of house at

least 100 years old; Foxboro, Mass., Mrs. EGGLESTON coll.

Size of larva: Moderately large (c. 8 mm.).

Head capsule as broad as long, broadest at the middle, rounded posteriorly, without frontal lines; pigmented field behind epistoma absent (fig. 1); epistoma (fig. 1) with a single transverse series of densely set, altogether twelve setae, located between catapophyses; rest of cranium with moderately long, densely set setae all over the surface. Antenna (fig. 2) with two distinct articles. Anteclypeus (figs. 1 and 2) with a group of about ten long setae on a thin plate at each end of anteclypeal sulcus; plates connected with a thin, narrow, ribbonlike sclerotization. Labrum (figs. 2 and 3) transverse, suboval, nearly twice as broad as long, anterior part of surface covered with fine setae; paired dark marks merely indicated. Epipharynx (fig. 3) with several small curved and sharp coryphal setae medianly in front of chaetoparial setae; acroparial and acanthoparial setae long, slender, curved and densely set; chaetoparial setae numbering about ten on each side in an oblique, inwardly convex series extending from anteroexterior corner of epipharynx to near the sagittal line; anterior six of the chaetoparial setae in a double row, rest in a single row, all moderately long, some straight, others slightly curved, terminally obtuse; tormae (fig. 3) short, strong, terminally rounded, not connected with thin labral rods except by a membranous ligament; labral rods parallel; crepidal field broad with a series of, altogether, four sensory pores distributed between anterior bases of labral rods and with another irregularly arranged group of about eight pores in the posterior part of the velvety pubescent field. *Mandible* (figs. 4 and 5) with two apical teeth, each deeply hollowed adorally, followed by a subapical bicuspidate, strong tooth; marginal brush present; aboral mandibular surface with a proximal group of about ten fine, short setae in two parallel rows and a distal group of five similar setae in an oblique row. Maxillary lacinia (fig. 6) small, terminally armed with one strong spine and in addition with four stiff setae; dorsally many fine hairs; galea (fig. 6) with long cultriform setae in margin; dorsally and ventrally with numerous setae, stiff ventrally, soft and hairlike dorsally; maxillary palpus with three articles of approximately same length; proximal article ventrally with a group of

about ten long setae and dorsally with a similar number of setae; second article with two setae; apical article without setae; stipes with numerous long setae. Prementum with a group of about ten setae in each anterior corner and several smaller setae on rest of surface; meso- and submentum with many long setae, most numerous laterally.

Body trunk curved, segments generally of same thickness; asperities strong, hook-shaped.

Number of asperities on each side of:

Thoracic segment II	none
„ „ III	46 in two and three rows
Abdominal segment 1	63 in three and four rows
„ „ 2	57
„ „ 3	48 in two and three rows
„ „ 4	43
„ „ 5	41
„ „ 6	42
„ „ 7	13
„ „ 8	2

9th abdominal segment with a patch of very numerous, vaguely estimated as one hundred, lateral asperities.

10th abdominal segment (fig. 7) with about ten asperities on each side.

Spiracles (figs. 9 and 10) annular with oval orifice and one very short air tube; thoracic spiracle about three times as large as the abdominal ones.

Leg (fig. 8) with pretarsus about one-third as long as tibiotarsus; proximal membranous part about as long as wide, with two setae; claw about two-thirds the length of entire pretarsus, quite strong and somewhat curved; no arolium.

6. *Ochina ptinoides* Marsh.

Plate 18.

Described material labeled:

1) *Ochina ptinoides* in dead ivy stem, Dunblane, Perthshire, Scotland. March 1952, N.W. Hussey coll. (reared) (Roy A. Crowson ded. 13.X.1952).

Size of larva: Moderately large (c. 6 mm.).

Head capsule (fig. 5) as broad as long, broadest at the middle, rounded posteriorly, without frontal lines; pigmented field behind epistoma (fig. 1) present but sagittally only about half as long as epistoma; epistoma naked; rest of cranium with moderately long and short, fairly densely set setae all over the surface (fig. 5). Antenna (fig. 2) with two distinct articles. Anteclypeus (fig. 1) with a group of about six rather long and short setae on a thin plate at each end of anteclypeal sulcus. Labrum (figs. 3 and 5) transverse, suboval, nearly twice as broad as long, surface densely set with fine setae; paired dark marks absent. Epipharynx (fig. 3) with several (about eight) minute coryphal setae medianly in front of chaetoparial setae; acanthoparial setae slender, long and pointed, somewhat curved, about five on each side; chaetoparial setae four or five on each side in an oblique, inwardly convex series extending from anterior-exterior margin of epipharynx to near the sagittal line at a point removed not more than one-third of the length of epipharynx from anterior margin to the beginning of tormae; chaetoparial setae moderately long, slightly curved and club-shaped; tormae rather long and strong, straight with irregular, rough surface and slightly converging; labral rods vestigial, reduced to a thin membrane projecting from the tormal stem at the posterior end of its anterior third part; crepidal field broad, with a few pores and covered with velvety papillae. *Mandible* (figs. 4 and 6) with two apical and two subapical teeth (teeth worn down on mandible, fig. 6); marginal brush with many well-developed stiff bristles; aboral mandibular surface with a proximal group of about ten short setae in two parallel rows and a distal group of about four similar, short setae. Maxillary lacinia (figs. 7 and 8) small, terminally armed with one strong spine and in addition five stiff, mostly somewhat curved setae; galea (figs. 7 and 8) with long, cultriform setae in margin; aboral surface with numerous, normal setae; adorally, posteriorly fused surfaces of lacinia and galea bearing a transverse group of many densely set, curved, well-developed setae (fig. 8); another smaller group of short, fine, soft setae present along the adoral marginal region at the palpus; maxillary palpus (fig. 8) with three articles, proximal article with three long setae ventrally, second article with two setae, apical article with a pore and dorso-exteriorly the usual sensory rod; stipes with a moderate

number of setae. Prementum, meso- and submentom with several setae.

Body trunk (fig. 13) curved; segments of same general thickness; asperities hook-shaped.

Number of asperities on each side of:

Thoracic segment II	none
„ „ III	23
Abdominal segment 1	20
„ „ 2	20
„ „ 3	18
„ „ 4	15
„ „ 5	15
„ „ 6	13
„ „ 7	5
„ „ 8	none

9th abdominal segment (fig. 14) with a patch of 14 lageral asperities.

10th abdominal segment (fig. 14) with 19 asperities on each side.

Spiracles (figs. 10 to 12) annular with oval orifice and one well-developed air tube; thoracic spiracle (fig. 10) about twice as long as the abdominal (figs. 11 and 12); air tubes of the thoracic and the anterior five abdominal spiracles about as long as the orifices of the spiracles are broad; air tubes of the posterior spiracles (fig. 12) about twice as long as the spiracular orifices are broad.

Leg (fig. 9) with pretarsus about one-third as long as tibiotarsus; proximal membranous part about as long as wide, with two short setae; claw about two-thirds the length of entire pretarsus, distinct but not particularly strong and somewhat curved; no arolium.

7. *Ernobius mollis* L.

Plate 19.

Described material labeled:

1) Sweden, intercepted at New York, 27.XI.1937.
2) Cincinnati, Ohio, 1.II.1932. White pine in bark and sapwood, C. F. Shields coll., larvae associated with reared imagines.

3) Russia, N.Y. #42630, 8.V.1935. Pine from cargo crating of barrel staves.

4) France, N.Y. #82455, 7.VIII.1939. Pine wood used as cask.

Size of larva: Moderately large (c. 7 mm.).

Head capsule (fig. 3) subcircular, slightly broader than long, with complete frontal cleavage lines, anteriorly extending through cranial socket around antenna; clypeo-frons pigmented all over; parietals light colored; epistoma with finely rugose catapophyses and a row of, altogether, about twelve irregularly placed, small setae; cranium beset with numerous evenly distributed setae, many as long as labrum and anteclypeus together. Antenna (fig. 2) with two, rather short, sclerotized articles. Anteclypeus (fig. 3) with four well-developed setae at each end of anteclypeal sulcus. Labrum (fig. 3) transverse, suboval, approximately twice as wide as long; on anterior margin with a series of densely set, long setae and with an antero-lateral group of moderately long and thin setae on each side; paired marks elongate-oval and pale. Epipharynx (fig. 1) on each side with two small coryphal setae, one behind the other and a patch of from fifteen to twenty curved, moderately long and short chaetoperial setae; crepidal space between the labral rods covered with minute velvety pubescent projections and having a single pore on each side near base of torma; tormae (fig. 1) obtusely corniform and well sclerotized, labral rods slightly sclerotized, straight and parallel; each torma and labral rod connected by a thin ligament, thus forming a defective Y-shaped feature. *Mandible* (figs. 4 and 5) with two apical and two subapical teeth; marginal brush present above tendon of mandibular adductor muscle; proximal and distal groups of setae on the aboral surface of the mandible present but short (fig. 4). Maxillary lacinia (figs. 6 and 7) rather small, terminally armed with a single, moderately strong spine and bearing four or five setae about as long as the spine and, in addition, with numerous soft, fine hairs on the adoral dorsal surface (fig. 7); stipes with about twenty five setae of various sizes spread over the whole surface but particularly numerous at the distal end; maxillary palpus with three articles, proximal article with an anterior transverse group of about ten setae on ventral side and as many, but much smaller, dorsally. Prementum with about ten setae in each anterior corner and several

setae on remainder of surface; meso- and submentum each with ten or a few more long and moderately long setae on each side.

Number of prodorsal asperities[1] *on each side of:*

Thoracic segment II	none
„ „ III	42 to 47
Abdominal segment 1	40 to 47
„ „ 2	45 to 48
„ „ 3	34 to 44
„ „ 4	36 to 40
„ „ 5	33 to 39
„ „ 6	25 to 38
„ „ 7	6 to 12
„ „ 8	6 to 15

9th abdominal segment with a large patch of lateral asperities, vaguely estimated to 50 on each side.

10th abdominal segment with 10 to 14 asperities on each side.

Spiracles (figs. 9 and 10) annular with oval orifice and a single short air tube; thoracic spiracle (fig. 9) about twice as long as the abdominal ones (fig. 10), and with the air tube directed upward and toward the head, while the air tubes of the abdominal spiracles are directed upward and toward the end of the body.

Tibio-tarsus (fig. 8) two and one-half times longer than pretarsus; proximal membranous part of pretarsus as long as claw; membranous part with two setae; claw somewhat curved; arolium present.

8. *Ernobius abietis* F.

Plate 20.

Described material labeled:

1) Germany, N.Y. #82602, 17.VIII.1939. Spruce cone.
2) *Ernobius abietis* F. Suomi, Karjalohja, in cones of Picea excelsa, 1.IX.1915, U. Saalas.

Size of larva: Moderately large (c. 6 mm.).

Head capsule (fig. 2) subcircular, slightly broader than long, with complete frontal lines anteriorly extending through the

[1] In the present record the extreme minor and major numbers have been given of asperities found in a great many examined specimens, because, an unusually abundant amount of larvae of this species are kept in the collection of U.S.N.M., thus demonstrating that the average number of asperities is fairly constant in the specimens of the same species.

cranial socket around the antenna; clypeo-frons and rest of cranium pigmented, with the exception of a fairly whitish subtriangular spot anteriorly on each parietal behind antenna; epistoma (fig. 2) with finely rugose catapophyses and a transverse continuous row of about six setae altogether. Clypeo-frons and rest of cranium set with numerous evenly distributed setae of moderate lengths. Antenna (fig. 2) without distinct, sclerotized articles; ovate tactile papilla and sensory hairs on membranous base. Anteclypeus (fig. 2) with a series of four setae at each end of anteclypeal sulcus. Labrum (fig. 2) transverse, suboval, anteriorly rounded, occasionally slightly concave sagittally; anterior margin with a series of densely set setae and with an antero-lateral group of rather long and thin setae on each side; paired marks faint or absent. Epipharynx (fig. 1) in middle of anterior margin with a series of several short hook-shaped coryphal setae, and on each side six short, strong, curved, obtuse chaetoparial setae arranged in an oblique inwardly curved regular series extending from antero-exterior corner of epipharynx to near its center; crepidal space between the labral rods covered with minute velvety pubescent projections and, on each side anteriorly, a few pores; well sclerotized robust tormae and membranous light colored labral rods forming imperfect Y-shaped features with tendonlike posterior extensions parallel with sagittal line. *Mandible* (fig. 3) with two apical and two subapical teeth; marginal brush, proximal and distal groups of setae on aboral mandibular surface well developed. Maxillary lacinia (fig. 4) rather small, terminally with a single moderately strong spine surrounded by five stiff setae about as long as the spine, and in addition, with other much finer setae especially on dorsal surface; stipes with many setae on the whole surface but particularly numerous and long at the distal end; maxillary palpus with three articles (fig. 4); proximal article with an anterior transverse series of about six setae on the ventral surface and a similar number of much finer setae dorsally. Prementum with several setae in each anterior corner; meso- and submentum, each with about ten long setae on each side.

Number of prodorsal asperities on each side of:

Thoracic segment II ..... none
„ „ III 23

Abdominal segment	1	40
„	„ 2	39
„	„ 3	39
„	„ 4	29
„	„ 5	28
„	„ 6	13
„	„ 7	9
„	„ 8	9

9th abdominal segment with a large patch of lateral asperities vaguely estimated as about 35 on each side.

10th abdominal segment with about 9 asperities on each side.

Spiracles (figs. 5 and 6) oval with a single air tube less than half as long as spiracular orifice; thoracic spiracle not fully three times as large as abdominal; air tube of thoracic spiracle directed obliquely upward and toward head, air tubes of abdominal spiracles directed obliquely upward and toward the end of body.

Tibio-tarsus (fig. 7) more than twice as long as pretarsus; proximal membranous part of pretarsus slightly longer than claw and provided with two setae; claw rather weak and short, slender and somewhat curved; small arolium present.

9. *Ernobius* sp.

Plate 20.

Described material labeled:

1) Canada, 42–11399, Boston #16306, 21.IX.1942, in spruce.

Size of larva: Moderately large (c. 6 mm.).

Head capsule with complete frontal cleavage lines (fig. 10), anteriorly extending through cranial socket around antenna; clypeo-frons and rest of cranium pigmented, except for a longitudinal fairly large, whitish spot anteriorly on each parietal and adjacent to frontal sulcus; epistoma (fig. 10) with smooth catapophyses and an irregular transverse series of, altogether, eight setae; clypeo-frons and rest of cranium set with numerous evenly distributed setae of different lengths. Antenna (fig. 10) with two indistinct articles. Anteclypeus (fig. 10) with a series of eight long setae at each end of anteclypeal sulcus. Labrum (fig. 10) transverse, suboval anterior margin densely set with fine setae, some straight others curved, and with an antero-lateral group of fairly long setae on each side; paired marks faint or absent.

Epipharynx (fig. 8) with two pairs of small coryphal setae, and on each side an oblique, inwardly curved series of about fourteen short, strong, slightly curved or straight chaetoparial setae arranged in a small group anteriorly; posteriorly combined with setae of the opposite series into a median patch; crepidal space with minute sensory papillae and two or three pores; well sclerotized robust tormae (fig. 8) and membranous, light colored labral rods forming imperfectly Y-shaped features with posterior extensions parallel with sagittal line. *Mandible* (fig. 9) with two apical and two subapical teeth; marginal brush well developed, proximal setae numerous and very long; distal setae about five, well developed, moderately long. Maxillary lacinia (fig. 15) rather small, terminally with a single moderately strong spine and many well developed, rather stiff setae as long as the spine and seated in a membranous region surrounded by a broad, well sclerotized basal ring; stipes at distal end with about ten long setae; maxillary palpus with three articles; proximal article with an anterior transverse group of about ten setae on each side. Prementum with about ten setae in each anterior corner, and meso- and submentum each with a similar number of setae.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	15
Abdominal segment 1	19
„ „ 2	17
„ „ 3	14
„ „ 4	14
„ „ 5	16
„ „ 6	14
„ „ 7	9
„ „ 8	5

9th abdominal segment with a patch of lateral asperities vaguely estimated at 30 on each side.

10th abdominal segment with 5 asperities on each side.

Spiracles (figs. 12, 13 and 14) oval without any air tubes; thoracic spiracle (figs. 12 and 13) not more than one and one-half times as large as the abdominal ones (fig. 14).

Tibio-tarsus (fig. 11) about three times as long as pretarsus; proximal membranous part of pretarsus slightly longer than claw

and armed with two setae; claw rather weak and slightly curved; small arolium present.

(*Note:* A larva, not reared or determined by association with imago, and labeled: "British Columbia, San Francisco #22358, 46–20214, 29.XI.'46, in *Picea* sp. cone," is identical with the above described larva in all characters, except in the number of the prodorsal asperities. These are on each side: II th.: none, III th.: 23, 1st abd. segm.: 24, 2nd abd. segm.: 27, 3rd abd. segm.: 22, 4th abd. segm.: 23, 5th abd. segm.: 22, 6th abd. segm.: 16, 7th abd. segm.: 16, 8th abd. segm.: 12, 9th abd. segm.: c. 30 lateral asperities, 10th abd. segm.: on each side 10 asperities.)

10. *Ernobius* (*granulatus* Lec.)?

Plate 21.

Described material labeled:

1) *Ernobius* sp. (probably *E. granulatus* Lec. A. G. B. det) Big Pine Key, Fla., Spec. Surv. #24083, 45–7967, 6.III.1945. Ex *Pinus caribeae*, GRISWOLD coll.
2) Probably *Ernobius granulatus* Lec., A. G. B. det.; no association with adults. In dying tip of *Pinus palustris*. Starke, Florida, Marsh 1929, F. C. CRAIGHEAD coll.

Size of larva: Small (c. 4 mm.).

Head capsule subcircular with complete frontal lines anteriorly extending through cranial socket around antenna; clypeo-frons (fig. 2) and rest of cranium pigmented with exception of a broad, longitudinal subtriangular not pigmented spot anteriorly on each side of parietale adjacent to the frontal line; epistoma (fig. 2) with rugulose cataophyses and a transverse row of approximately, altogether, six setae, located in the posterior faint limiting line of epistoma; clypeo-frons and rest of cranium rather sparingly set with long setae but with many short setae between. Antenna (fig. 2) without articles, sensory organs borne by dome-shaped membranous base. Anteclypeus (fig. 2) with a series of five long and short setae at each end of anteclypeal sulcus. Labrum (fig. 2) transverse, suboval; paired marks indistinct or indiscernible; anterio-lateral margin with a series of densely set, fine, long, curved setae. Epipharynx (fig. 1) in the middle of anterior margin with a series of coryphal setae; on each side about fourteen short, strong, hook-shaped chaetoparial setae

in an oblique, irregular, subtriangular patch, about four setae wide in front, followed by a single row behind; crepidal area covered with minute sensory papillae and bearing one pair of pores anteriorly; well sclerotized tormae (fig. 1) and membranous, light colored labral rods forming imperfect Y-shaped features. *Mandible* (fig. 3) with two apical and two subapical teeth; marginal brush well developed; aboral surface with proximal and distal groups of long and moderately long setae. Maxillary lacinia (fig. 4) rather small, terminally with a single spine surrounded by about six stiff setae as long as the spine, in addition, with finer and curved setae on dorsal surface; stipes with about 6 long setae at distal end ventrally; maxillary palpus with three articles; proximal article ventrally with an anterior transverse series of three long and three short setae. Prementum with four or five setae in each anterior corner; meso- and submentum each with a number of long setae.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	16 to 23
Abdominal segment 1	29 to 33
„ „ 2	31
„ „ 3	24 to 30
„ „ 4	24 to 28
„ „ 5	20 to 28
„ „ 6	10 to 13
„ „ 7	9 to 11
„ „ 8	4 to 6

9th abdominal segment with a patch of lateral asperities vaguely estimated as about 40 on each side.

10th abdominal segment with about 12 asperities on each side.

Spiracles (figs. 5 and 6) circular with one air tube about half as long as spiracular orifice or somewhat longer; thoracic air tube (fig. 5) directed almost straight upward; abdominal ones (fig. 6) extending obliquely upward and toward the end of body; abdominal spiracles about one-third the size of the thoracic.

Tibio-tarsus (fig. 7) about three times as long as pretarsus; proximal membranous part of pretarsus slightly longer than claw and provided with two setae; claw rather weak, and somewhat curved; small arolium present.

11. *Ernobius punctulatus* Lec.

Plate 21.

Described material labeled:

1) Ernobius punctulatus Lec., Cathlamet, Washington State, Special Surv. #19853, 44–24138, 14.IX.1944, Douglas fir in cone scales, C. G. Anderson coll., W. S. Fisher det. the associated adults.
2) *Ernobius* sp. (probably *E. punctulatus* Lec.), Wisconsin, Hopk. U. S. 32807 ♀, 41–3900. Jack pine cones. A. G. Boving det. larva.

Size of larva: Small to moderately large (4 to 5 mm.).

Head capsule subcircular, with complete frontal cleavage lines (fig. 9), anteriorly extending through cranial sockets around antennae; clypeo-frons and rest of cranium pigmented, with exception of a broad, longitudinal, not pigmented spot on the sides of parietalia and adjacent to the frontal lines; epistoma with catapophyses bearing very few setae; clypeo-frons and rest of cranium rather sparingly set with long setae but with several short setae between them. Antenna (fig. 9) with two very low articles bearing the ordinary sensory organs. Anteclypeus (fig. 9) with a series of about six short and long setae at each end of anteclypeal sulcus. Labrum (fig. 9) transverse, suboval, paired marks very pale; antero-lateral margin with a series of densely set fine, long, terminally curved setae on each side. Epipharynx (fig. 8) in middle of anterior margin with some short, hook-shaped coryphal setae; on each side about eight short, straight or slightly curved chaetoparial setae in an oblique inwardly convex, irregular series; crepidal area between the labral rods covered with minute soft projections and bearing anteriorly a pair of pores; well sclerotized tormae (fig. 8) and membranous light colored labral rods forming imperfect Y-shaped features. *Mandible* (fig. 10) with two apical and two subapical teeth; marginal brush present; aboral surface of mandible with proximal and distal groups of long setae. Maxillary lacinia (fig. 11) rather small, terminally with a single spine surrounded by about six stiff setae as long as the spine, and in addition, with much finer setae on dorsal surface; stipes with many setae on the whole surface but particularly with long, strong ones at distal end; maxillary palpus with three articles; proximal article with an

anterior transverse series of about six setae ventrally, and a similar number of finer setae dorsally. Prementum with four or five setae in each anterior corner; meso- and submentum each with about ten long setae on each side.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	15
Abdominal segment 1	30
„ „ 2	30
„ „ 3	33
„ „ 4	25
„ „ 5	22
„ „ 6	18
„ „ 7	8
„ „ 8	9

9th abdominal segment with a patch of lateral asperities, vaguely estimated as about 40 on each side.

10th abdominal segment with about 10 asperities on each side.

Spiracles (figs. 13, 14) broadly oval with one air tube less than half as long as spiracular orifice; on thoracic spiracle with an additional second short air tube; both thoracic air tubes (fig. 13) directed toward the head, the single abdominal (fig. 14) toward the end of the body; abdominal spiracles about two-thirds the size of the thoracic one.

Tibio-tarsus (fig. 12) almost twice as long as pretarsus; proximal membranous part of pretarsus slightly longer than claw and provided with two setae; claw rather weak, short, slightly curved; small arolium present.

12. *Coelostethus notatus* Say.

Plate 22.

Described material labeled:

1) *Coelostethus notatus* Say, Jackson Isl. Md., 18.VIII.1914. In red rotten oak, SCHWARZ and BARBER coll. et det. (Note No. 134 ♀).
2) Amherst, Mass. 5.X.1944. In ash, chestnut and oak, also in pine-boards in cellar partitions, W. B. BECKER [received material from Mr. Ernst Watson's summer place at Monterey, Mass.].

3) Vienna, Va. 7.II.1937. In dry rotten standing pine, BRIDWELL coll. W. S. FISHER det. imagines.

Size of larva: Moderately large (c. 6 mm.).

Head capsule subcircular, without frontal cleavage lines; pigmented field (fig. 2) behind epistoma distinct, sagittally about three times as long as epistoma; epistoma (fig. 2) with some short, fine setae near the sagittal line, otherwise smooth, not pitted with round depressions; cranium with numerous evenly distributed fine, long, and moderately long setae. Antenna (fig. 2) with two distinct articles. Anteclypeus (fig. 2) with eight, mainly long setae at each end of anteclypeal sulcus, and covered completely with a pigmented, densely punctured sclerite. Labrum (fig. 2) transverse, suboval, about three times as wide as long; anterior margin and most of surface densely set with moderately long setae; paired marks not noticeable. Epipharynx (fig. 1) with, altogether, four small coryphal setae, and on each side an oblique, inwardly convex, single, regular row of six slender, curved, rather long chaetoparial setae; tormae (fig. 1) and labral rods forming strong Y-shaped, somewhat converging features; crepidal region between them covered with minute papillae and provided with a few irregularly placed pores. *Mandible* (figs. 3 and 5) with two apical strong, sharp teeth and two smaller, more obtuse subapical teeth; marginal brush present but with short bristles; aboral mandibular surface bearing a proximal series of about seven rather long setae and a distal group of about five similar setae. Maxillary lacinia (fig. 4) a little larger than half the size of galea, lacking any special robust spines but beset with about twelve strong, straight setae, each as long as one of the similar marginal setae of galea and, clustered adorally in a bundle behind, with many rather long but finer setae; maxillary palpus with three articles; proximal article with about seven long setae ventrally; distal part of stipes with a similar number of like setae. Prementum, meso- and submentum each with about ten setae on the sides.

Prothorax laterally with an oblique sulcus.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	15
Abdominal segment 1	25

Abdominal segment	2	25
„ „	3	25
„ „	4	23
„ „	5	20
„ „	6	16
„ „	7	a few or none
„ „	8	none

9th abdominal segment with a patch of 15 to 20 lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (figs. 7, 8 and 9) annular, the thoracic (fig. 7) broadly oval with two minute air tubes facing the head and some small beadlike bubbles emerging from the peritremal frame; abdominal spiracles (figs. 8 and 9) circular with a single short air tube directed toward the end of body, (exceptionally one of the abdominal spiracles may be without air tube (fig. 9)); length of thoracic spiracle about three times longer than the diameter of an abdominal spiracle.

Tibio-tarsus (fig. 6) one and one-half times longer than pretarsus; proximal membranous part of pretarsus subconical about as long as wide, armed with two strong setae; claw very long and slender, spinelike, somewhat curved, three times longer than membranous part; arolium absent.

13. *Hadrobregmus carinatus* Say
(Identification doubtful, onus probandi).

Plate 23.

Described material labeled:

Hadrobregmus carinatus Say; in decaying roots of live hemlock, Black Pond, Fairfax, Va., March 24, 1920. F. C. Craighead coll. et reared[1].

[1] The following description is based on the above mentioned material, labeled as collected and reared by F. C. Craighead but without explanation about who made the determination of the imago. More and similar material of larvae but without determination are also in the collection of U. S. Natl. Mus. These larvae have an anteclypeal sclerite of the same shape as the larvae of genus *Trypopitys* and look on the whole like them. However, in the collection of the Museum another lot of larvae, also collected by F. C. Craighead, is present which, too, is named *Hadrobregmus carinatus* but, differing from the former, have a simple anteclypeus without any sclerite, and in this and all other characters coincide with the larvae of *Hadrobregmus umbrosus* Fall and *Hadrobregmus thomsoni* Kraatz in *Picea excelsa* from Finland, collected and determined by Professor Uunio Saalas. It is therefore impossible to determine which of the larvae in the Museum are the true *H. carinatus* until new material will be available for rearing and determination.

Size of larva: Moderately large (c. 7 mm.).

Head capsule subcircular, slightly longer than broad, without frontal cleavage lines; pigmented field behind epistoma (fig. 2) distinct, sagittally about twice as long as epistoma, provided with many setae in small pits; epistoma (fig. 2) smooth, without setae; rest of cranium with numerous, evenly distributed, moderately long and short setae. Antenna (fig. 2) with two distinct articles. Anteclypeus (fig. 2) with about ten mostly moderately long, stiff setae at each end of the anteclypeal sulcus and with a pigmented, anteriorly convex, smooth, thick sclerite on the posterior half of anteclypeus. Labrum (fig. 2) transverse suboval, about twice as wide as long; anterior margin and much of surface behind the margin densely set with long and fairly long setae; paired marks faint. Epipharynx (fig. 1) with two pairs of small coryphal setae; on each side six long, slender, almost, straight chaetoparial setae in an oblique curved row; tormae and labral rods forming a pair of long, sclerotized, Y-shaped, straight features; crepidal region covered by minute sensory papillae and with some irregularly distributed pores. *Mandible* (fig. 3) with two strong apical teeth and two small almost confluent, subapical, obtuse projections; marginal brush lacking, bristles substituted by some minute granules; aboral mandibular surface bearing a proximal series of fairly long setae and a distal group of five similar setae. Maxillary lacinia (fig. 4) more than half as large as galea, lacking a robust spine but distally bearing a considerable number of strong, ensiform setae, each as long as one of the similar marginal setae of galea; dorsally with numerous long but finer and softer setae; maxillary palpus with three articles; proximal article with an irregular double series of about ten long setae anteriorly placed across the ventral surface; distal part of stipes with about same number of similar setae. Prementum, meso- and submentum each with about a dozen setae on each side.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	41
Abdominal segment 1	48
„ „ 2	49
„ „ 3	47
„ „ 4	43
„ „ 5	44

Abdominal segment	6	51
„ „	7	13
„ „	8	13

9th abdominal segment with a patch of about 55 lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (figs. 5, 6, 7 and 8) simple annular; both thoracic and abdominal subcircular, without air tubes, or with very short or vestigial air tubes; orifice of thoracic spiracle (fig. 7) with a diameter about three times longer than the diameter of an abdominal spiracle (figs. 5, 6 and 8).

Pretarsus (fig. 10) about half as long as tibio-tarsus; proximal membranous part of pretarsus subconical, about as long as wide, armed with two setae; claw almost three times as long as proximal part, slender, slightly curved; arolium absent.

14. *Trypopitys sericeus* Say.

Plate 24.

Described material labeled:

1) *Trypopitys sericeus* Say, In hickory, Pennsylvania, Hopk. U. S. 10264 S.
2) *Trypopitys sericeus* Say. Ex fallen dead holly branch, Snow Hill, Md., larvae: 21.X.1949, adults out 1950, W. H. Anderson coll., reared, and det.

Size of larva: Moderately large (c. 8 mm.).

Head capsule subcircular, slightly longer than broad, without frontal cleavage lines; pigmented field (figs. 1 and 3) behind epistoma distinct, sagittally about two and one-half as long as epistoma, provided with a multitude of moderately long setae seated in small pits; epistoma (fig. 3) rather smooth, without setae; rest of cranium with numerous, evenly distributed, long and moderately long setae. Antenna (fig. 2) with two distinct articles. Anteclypeus (fig. 3) with eight mostly long, stiff setae at each end of anteclypeal sulcus and with a pigmented, in anterior outline convex, smooth, thick sclerite covering the posterior half of anteclypeus. Labrum (fig. 3) transverse, suboval, about three times as wide as long; anterior margin and most of surface densely set with fairly long setae, paired marks very faint but present.

Epipharynx (fig. 5) medially with a transverse row of, altogether, four small, club-shaped coryphal setae; on each side with six long, slender, slightly curved chaetoparial setae arranged in an arched, irregular, partly double row; tormae and labral rods forming a pair of long, sclerotized, Y-shaped, straight and somewhat converging features (fig. 5); crepidal region between them covered by minute sensory papillae with a few irregularly placed pores. *Mandible* (fig. 4) with two strong apical teeth and two small, almost confluent subapical projections; marginal brush lacking, bristles substituted by a few minute granules; aboral mandibular surface bearing a proximal series of fairly long setae and a distal group of five similar ones. Maxillary lacinia (fig. 6) somewhat more than half as large as galea, lacking a robust spine but terminally bearing about ten strong, ensiform setae, each as long as one of the similar marginal setae of galea; in addition, with many, as long and almost as strong setae behind them on the ventral surface and with numerous long, but fine and soft setae on the dorsal side; maxillary palpus with three articles; proximal article with about ten long setae in an irregular, double, transverse row on the ventral side; distal part of stipes with about same number of similar setae. Prementum, meso- and submentum (fig. 1) each with about a dozen setae on either side. Prothorax laterally with an oblique long, straight groove on each side.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	50
Abdominal segment 1	87
„ „ 2	83
„ „ 3	88
„ „ 4	114
„ „ 5	102
„ „ 6	76
„ „ 7	44
„ „ 8	23

9th abdominal segment with c. 80 lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles annular, the thoracic (fig. 7) broadly oval with several winding air tubes, three distinct, a few additional small and simple; atrium projecting below the larger ones as a tongue-

shaped expansion; abdominal spiracles (figs. 8 and 9) subcircular with one or two quite regular, short air tubes, orifice of thoracic spiracle about three times as long as the diameter of an abdominal one.

Pretarsus (fig. 14) about half as long as tibio-tarsus; proximal membranous part of pretarsus subconical, about as long as wide, armed with two setae; claw almost three times as long as proximal part, slender and somewhat curved; arolium absent.

15. *Trypopitys punctatus* Lec.

Plate 24.

Described material labeled:

Trypopitys punctatus Lec. In decayed wood building timber, Los Angeles, Calif. 20.XI.1928, Dr. A. W. Merril, coll. et det.

Size of larvae: Moderately large (c. 8 mm.).

Characters of larva identical with those of *Trypopitys sericeus*, except, that the number of prodorsal asperities on the body segments is considerably less and the spiracles somewhat different.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	22
Abdominal segment 1	28
„ „ 2	31
„ „ 3	31
„ „ 4	29
„ „ 5	27
„ „ 6	22
„ „ 7	17
„ „ 8	11

9th abdominal segment with a patch of about 25 lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles annular, the thoracic (fig. 11) circular with three short and simple air tubes and vestiges of one or two more; abdominal spiracles (figs. 12 and 13) circular with two or three short, simple air tubes close together; orifice of thoracic spiracle not fully twice as long as the diameter of an abdominal spiracle.

16. *Platybregmus canadensis* Fisher.

Plate 25.

Described material labeled:

Platybregmus canadensis Fisher. Basswood-shelf in basement of farmhouse, So. Onondaga, N.Y. 17.VI.1950, I. B. Simeone coll., associated imago det. by W. S. Fisher.

Size of larva: Large (c. 12 mm.).

Head capsule subcircular, as broad as long, without frontal lines; pigmented field (fig. 1) behind epistoma absent (or indistinct and faint); epistoma (fig. 1) with some setae irregularly distributed on the surface and with a double row of about twelve densely set, moderately long setae on each side of anterior margin; rest of cranium with well-developed, fine setae, rather densely distributed. Antenna (fig. 1) without distinct articles; fossal ring around antennal base with some long setae. Anteclypeus (fig. 1) with six setae at each end of anteclypeal sulcus, attached to a small sclerite; corresponding sclerites connected with a very low, ribbon-shaped sclerotization. Labrum (fig. 1) suboval, about twice as wide as long; anterior margin and much of surface behind it densely set with fairly long setae; paired marks present. Epipharynx (fig. 2) with marginal acanthoparial setae numerous and bent in over epipharyngeal surface; two pairs of minute coryphal setae present; on each side with a subtriangular patch of moderately long and short, slender, curved and pointed chaetoparial setae anteriorly arranged in a group of about fifteen setae and posteriorly in a single row of about five setae extending to posterior end of torma; labral rods and tormae (fig. 2) united to short, robust, curved, V-shaped features. *Mandible* (fig. 3) with two apical teeth and two small, almost confluent, rounded subapical projections. Maxillary lacinia (fig. 4) about half as large as galea, without spine, covered terminally and ventrally with numerous straight, strong setae and with additional finer setae dorsally; galea (fig. 4) with marginal and ventral setae similar to the corresponding lacinial setae, dorsal setae very long and fine particularly in the region near palpus; maxillary palpus with three articles; proximal article ventrally with about fifteen rather fine and long, irregularly distributed setae; ventral side of stipes with a great number of similar setae all over. Prementum on

each side with fifteen or more long, fine setae, meso- and submentum each with at least twenty similar setae on either side.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	30
Abdominal segment 1	45
„ „ 2	45
„ „ 3	25
„ „ 4	21
„ „ 5	23
„ „ 6	5
„ „ 7	none
„ „ 8	none

9th abdominal segment (fig. 6) without lateral asperities[1].

10th abdominal segment without asperities.

Spiracles (figs. 7 and 8) annular, oval, simple without air tubes; thoracic spiracle (fig. 7) only slightly larger than the abdominal ones (about as five to four).

Pretarsus (fig. 9) about half as long as tibio-tarsus; proximal membranous part subconical, about as long as wide, armed with two setae; claw same length as proximal part, almost straight, quite strong; segments of leg richly furnished with long setae; arolium absent.

17. *Anobium punctatum* Deg. (= *A. striatum* Oliv.).

Plate 26.

Described material labeled:

1) *Anobium striatum* Oliv. South Germany; [bought from] Dr. K. W. Verhoeff; received 25.VIII.1922.
2) *Anobium punctatum* Deg., In twig of *Salix* sp. England, 19.I.1948; N.Y. #100389, 48–1259, imago det. by W. S. Fisher.
3) *Anobium punctatum* Deg. In *Laurus* sp. stem. France, 9.V.1939; N.Y. #81534.
4) *Anobium punctatum* Deg. In oak beams and spruce flooring, Middletown, R. I., 12.X.1944, Rau coll., Spl. Sur. #20412.

Size of larva: Moderately large (c. 6 mm.)

[1] In other characters very similar to genus Vrilletta (Pl. 34, figs. 8 to 14).

Head capsule subcircular, slightly longer than broad, widest in the middle, without frontal lines; pigmented field (fig. 2) behind epistoma distinct; in sagittal line not much longer than epistoma, bearing three long and a few small setae on each side; epistoma (fig. 2) with a single seta on each side of sagittal line; rest of cranium with long and short setae distributed evenly over the whole surface. Antenna (fig. 1) without distinct articles, sensory organs borne by membranous basal membrane, ring-shaped sclerotization around antennal base with one very long seta. Anteclypeus (fig. 2) with two long, stiff setae at each end of anteclypeal sulcus, attached to a small plate. Labrum semi-circular, anterior margin and much of surface behind it set with setae; paired marks distinct. Epipharynx (fig. 3) with well-developed acanthoparial setae; a curved, double series of short hook-shaped coryphal setae inside of and parallel with anterior margin; six fairly robust, curved, obtuse chaetoparial setae arranged in a regular, convex arch; labral rods and tormae (fig. 3) forming long, sclerotized, distinctly Y-shaped features; crepidal region between them apparently without pores and setae. *Mandible* (fig. 4) with two rather short apical teeth and subapical edge developed into a distinct toothlike projection connected with a minute, pointed tip at marginal brush by a thin, in outline convex wall; a marginal brush, proximal and distal groups of setae present but rather inconspicuous. Maxillary lacinia (fig. 10) about one-third as large as galea, without spine but terminally with six stiff, strong setae of same length and shape as the marginal setae of galea; dorsally with almost as long but finer setae; maxillary palpus with three articles; proximal article with about six transversely placed, long ventral setae and a few additional short ones. Prementum, mesomentum and submentum each with about five long setae, often transversally arranged on each side, and in addition with a few fine setae scattered on the surface.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	30
Abdominal segment 1	40
„ „ 2	38
„ „ 3	35
„ „ 4	35

Abdominal segment	5	20
„	„ 6	20
„	„ 7	15
„	„ 8	none

9th abdominal segment without lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 5, 6 and 7) annular, oval; thoracic spiracular orifice (fig. 5) about twice as long as orifice of an abdominal spiracle (figs. 6 and 7); thoracic spiracle with a short, single, simple or heart shaped air tube, abdominal spiracles also with a single air tube but this is about as long as or longer than the orifice.

Segments of leg rather short; pretarsus (fig. 9) half as long as tibio-tarsus; proximal membranous part subconical, about as long as wide, armed with two setae; claw same length as proximal part, slightly curved, quite strong; arolium absent.

18. *Anobium gibbicollis* Lec.

Plate 26.

Described material labeled:

Anobium (*"Hadrobregmus"*) *gibbicollis* Lec., In dead alder, Seattle, Wash. 12.IV.1942; E. I. Smith coll., Fisher det. imagines, Seattle #10016 — 42–5350.

Size of larva: Moderately large.

Characters of larva identical with those of *Anobium punctatum* Deg., except, in having differently formed spiracles and a different number of prodorsal asperities.

Spiracles (figs. 11, 12, and 13) annular with very short air tubes; thoracic spiracle with two air tubes, abdominal spiracles with one air tube.

Number of prodorsal asperities on each side of:

Thoracic segment	II	none
„	III	35
Abdominal segment	1	74
„	„ 2	76
„	„ 3	67
„	„ 4	57
„	„ 5	48

Abdominal segment	6	46
„ „	7	20
„ „	8	none

9th abdominal segment without lateral asperities.
10th abdominal segment without asperities.

19. *Anobium nitidum* Herbst and *Anobium pertinax* Linnaeus (nec. F.)

Plate 26.

Described material labeled:

1) *Anobium nitidum* Herbst, In piece of branch of wood; grove at Dragör, Amager, Denmark, 16.II.1935, J. P. Kryger leg. and reared.
2) *Anobium pertinax* L. Silver fir, Dyrehaven, Denmark, 23.XI.1938, J. P. Kryger.

Size of larva: Moderately large (c. 6 mm.).

Characters of larva identical with those of *Anobium punctatum* Deg., except, having short spiracular tubes and a different number of prodorsal asperities; characters also identical with those of *Anobium gibbicollis* Lec., except, in that all of the spiracles have only one air tube and the prodorsal asperities are present in a different number.

Spiracles (figs. 15, 16, 17) annular with very short air tubes; thoracic spiracle (fig. 15) with one air tube (*A. nitidum*), or apparently none (*A. pertinax*); abdominal spiracles (figs. 16 and 17) with one air tube (both in *A. nitidum* and *A. pertinax*).

Number of prodorsal asperities on each side of:

Thoracic segment	II	... none	(in *nitidum*)	... none	(in *pertinax*)
„ „	III	 27	„	 31	„
Abdominal segment	1	 40	„	 50	„
„ „	2	 40	„	 54	„
„ „	3	 28	„	 30	„
„ „	4	 28	„	 31	„
„ „	5	 22	„	 27	„
„ „	6	 20	„	 20	„
„ „	7	 14	„	 11	„
„ „	8	.. none	„	... none	„

9th abdominal segment without lateral asperities.
10th abdominal segment without asperities.

20. *Microbregma emarginatum* Dufts.

Plate 27.

Described material labeled:

Microbregma emarginatum (Dufts.). In bark of Picea, Gaspé-Quebec, Canada, 27.VIII.1921, F. C. Craighead coll. and reared.

Size of larva: Moderately large (c. 7 mm.).

Head capsule subcircular without frontal lines; pigmented field (fig. 1) behind epistoma distinct, but sagittally not much longer than epistoma and provided with long setae; epistoma (fig. 1) bearing a few long setae in the middle of surface and a single row of about seven rather long setae on each side of anterior margin; rest of cranium with numerous long setae evenly distributed. Antenna (fig. 1) with two very low ring-shaped articles. Anteclypeus (fig. 1) with a ribbonlike sclerotization proximally at the anteclypeal sulcus and a sclerotization at each end of it bearing about five fairly long, fine, stiff setae. Labrum subovate (fig. 1), only one and one-half times wider than long; anterior margin and a great part of the surface densely set with fairly long setae; paired marks present. Epipharynx (fig. 3) with long acanthoparial setae and two pairs of small coryphal setae; on each side an inwardly convex, somewhat irregular row of six curved, strong, rather short chaetoparial setae and anterior to the crepidal region with a pair of straight, fine setae; tormae and labral rods (fig. 3) forming distinct, Y-shaped features; crepidal region covered with minute papillae and with, altogether, about ten, irregularly placed pores. *Mandible* (fig. 4) with fairly narrow distal part ending with three distinct teeth of nearly same shape and size, marginal brush well developed; aboral mandibular surface with a proximal and a distal group of setae. Maxillary lacinia (fig. 5) about half as large as galea, distally bearing four strong setae similar to the marginal setae of galea, no spine but ventrally with additional finer setae; maxillary palpus with four articles; proximal article with about seven long setae ventrally, and a transverse anterior series of much finer setae dorsally, next article without setae, subapical article with two setae, and apical article without setae but with accessory rod-shaped organ dorsally, a single pore, and terminally, minute sensory projections; distal part of stipes with about twelve long setae. Prementum,

meso- and submentum each with about ten setae on either side.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	25
Abdominal segment 1	30
„ „ 2	38
„ „ 3	42
„ „ 4	47
„ „ 5	30
„ „ 6	16
„ „ 7	none (or a few)
„ „ 8	none

9th abdominal segment on each side with a patch of lateral asperities amounting to about 50.

10th abdominal segment without asperities.

Spiracles (fig. 6) annular, oval, about twice as long as wide, with one air tube half as long or less than half as long as length of spiracle.

Pretarsus (fig. 7) almost as long as tibio-tarsus; proximal membranous part of pretarsus subconical, about as long as wide, armed with one strong seta, about two-thirds as long as claw and one much shorter but robust; claw almost three times as long as membranous part, slender and slightly curved; arolium absent.

21. *Ernobius champlaini* Fisher.

Plate 27.

Described material labeled:

Waldo Canyon, Colo., Hopk. U. S. 10061, b, Dec. 1914, dead limbs of Pinus flexilis, A. B. Champlain coll. and reared.

Size of larva: Small to moderately large (4 to 6 mm.).

Head capsule (fig. 9) subcircular, slightly longer than broad, broadest in the middle, sides convergent behind the middle, without frontal lines; pigmented field (fig. 9) behind epistoma absent; capsule light colored; epistoma without setae; cranium (fig. 9) set with numerous evenly distributed, mostly long setae. Antenna (fig. 9) without articles, sensory organs borne by membranous base. Anteclypeus (fig. 9) with four (or five) long setae

at each end of anteclypeal sulcus. Labrum (fig. 9) oval, twice as wide as long, on anterior margin with a multitude of fine, fairly long, curved setae; paired marks not found. Epipharynx (fig. 8) with densely set, long, fine, curved combined acroparial and acanthoparial setae; two pairs of small coryphal setae; on each side a subtriangular patch of chaetoparial setae with about seven setae grouped together anteriorly and five setae in a single, irregular row posteriorly; some chaetoparial setae long and others short, all slender, curved and pointed; crepidal space covered with minute sensory papillae and having a single pair of pores anteriorly located near base of each torma; tormae (fig. 8) rather short, well sclerotized and elongate conical; labral rods slightly sclerotized, long, straight and parallel; each torma and labral rod poorly connected, forming a defective Y-shaped feature. *Mandible* (fig. 10) with three teeth distally, namely two apical teeth and one subapical tooth; marginal brush, proximal and distal groups of setae on aboral mandibular surface all present but short. Maxillary lacinia (fig. 12) small, terminally with one rather short, moderately strong spine and three stiff setae longer than spine and placed close to it; in addition with seven fine, short setae on both dorsal and ventral surfaces; stipes with about ten long ventral setae and shorter setae dorsally; maxillary palpus with three approximately equal, long articles; proximal article ventrally with about ten long and moderately long setae, dorsally with about the same number of setae but fine and short; second article with two setae and one pore; distal article without setae. Prementum with about seven long and short setae in each anterior corner; meso- and submentum each with about ten, mostly long setae on each side.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	27
Abdominal segment 1	30
„ „ 2	30
„ „ 3	24
„ „ 4	22
„ „ 5	24
„ „ 6	25
„ „ 7	12
„ „ 8	none

9th abdominal segment with a patch of lateral asperities amounting to about 35.

10th abdominal segment with no asperities.

Spiracles (figs. 13 and 14) of moderate size, broadly oval and without air tubes, thoracic spiracle (fig. 13) a little shorter than the claw, abdominal spiracles (fig. 14) not much smaller than the thoracic.

Tibio-tarsus (fig. 11) about twice as long as pretarsus; proximal membranous part of pretarsus about half as long as the claw and carrying two setae; claw well developed, somewhat curved; arolium absent.

22. *Stegobium paniceum* L.
(= Sitodrepa panicea L).

Plate 28.

Described material labeled:

1) *Stegobium paniceum* L., from *Crataegus* fruits from Erfurt, Germany, Inspection house, Wash. D. C. 4.V.1926, H.V. Goldman.
2) *Stegobium paniceum* L., in thyme seed from New York State, N.York #34474, 20.I.1935.
3) *Stegobium paniceum*, in nutmeg seed, from Mexico; Laredo, Texas #36978, 45–13530.

Size of larva: Small (c. 4 mm.).

Head capsule somewhat longer than broad, widest slightly behind the middle, tapering gradually posteriorly, without frontal lines; pigmented field behind epistoma (fig. 1) quite distinct, sagittally about as long as epistoma; epistoma (fig. 1) with a transverse series of a total of about ten long, straight, rather fine setae in anterior margin and five or six long and stronger setae behind them; epistomal surface smooth; a group of about six setae at inner margin of antennal fossa; rest of cranium including pigmented field with long and short setae all over. Antenna (fig. 1) without articles, sensory elements borne by dome-shaped base. Anteclypeus (fig. 1) with a group of five long, straight, fine setae at each end of anteclypeal sulcus; not borne by a special small plate. Labrum (fig. 1) transverse, broadly oval, about twice as wide as long, with fairly long setae on anterior half of

surface; paired marks present. Epipharynx (fig. 2) with long, strong acanthoparial setae and on each side five short chaetoparial setae in a curved, regular row extending posteriorly only to the middle of the area; two pairs of coryphal small setae present anteriorly; tormae (fig. 2) and labral rods forming short, strong, V-shaped features; crepidal area with a few pores anteriorly. *Mandible* (fig. 7) with two apical teeth; subapical edge forming a triangularly projecting wall; marginal brush with short setae; on aboral surface with a proximal group of many long setae and a distal smaller group of similar setae. Maxillary lacinia (fig. 8) less than half as large as galea, lacking special spine but with about five, slightly curved, strong terminal setae similar to the marginal setae of galea; maxillary palpus with three articles; proximal article with about eight long, curved setae; stipes anteriorly with the same number of similar setae.

Number of prodorsal asperities on each side of:

Thoracic segment II	none	
„ „ III	2	
Abdominal segment 1	13	
„ „ 2	12	in an irregular,
„ „ 3	13	in some places
„ „ 4	11	double but prevalently
„ „ 5	10	single series
„ „ 6	8	
„ „ 7	6	in a single series
„ „ 8	4	

9th abdominal segment on each side with a patch of about 20 lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 3, 4, 5, and 6) small, circular, with an air tube generally at least as long as diameter of spiracular orifice; thoracic spiracle (fig. 3) half as long as pretarsus and its diameter about twice as long as the diameter of the abdominal ones (figs. 4, 5 and 6).

Leg (fig. 9) with pretarsus half as long as tibio-tarsus; membranous basal part of pretarsus subconical, a little longer than wide, armed with two moderately long setae; claw very long and slender, somewhat curved and almost three times as long as basal part; arolium absent.

23. *Nevermannia dorcatomoides* Fisher.

Plate 28.

Described material labeled:

1) *Nevermannia dorcatomoides* Fisher, in termites nest; Hamburg Farm, Costa Rica, NEVERMANN coll. et dedit., 27.VIII 1926.

Size of larva: Moderately large (c. 6 mm.).

Head capsule (fig. 10) about twice as long as broad, widest slightly behind middle, tapering gradually posteriorly; no frontal lines; pigmented field behind epistoma absent; epistoma (fig. 10) with a transverse series of, altogether, eight long setae in anterior margin close to anteclypeal sulcus; one long seta present at inner side of antennal fossa; rest of cranium with long and short setae distributed over entire surface. Antenna (fig. 10) without articles; sensory papilla subconical and at least as long as diameter of basal, dome-shaped membrane. Anteclypeus (fig. 10) without plate and without setae at each end of anteclypeal sulcus. Labrum (fig. 10) oval, fully twice as broad as long, with transverse series of, altogether, about ten long setae; paired marks absent. Epipharynx (fig. 12) with numerous long, straight acroparial and cultriform acanthoparial setae; on each side six short, strong cultriform chaetoparial setae in a regular, curved row extending posteriorly to the middle of the epipharyngeal area; weak labral rods and tormae forming V-shaped features; crepidal field velvety pubescent with a couple of pores. *Mandible* (figs. 11 and 13) with two very short, almost fused apical teeth; subapical part raised into a conspicuous, thin, triangular wall; adoral surface with high, longitudinal carina; marginal brush with many fine, well-developed setae; aboral mandibular surface with two (or a few more) long proximal and two long distal setae. Maxillary lacinia (fig. 15) about half as large as galea, lacking spine; latero-terminally with about six cultriform and strong setae and in addition a few longer and finer setae behind them; galea (fig. 15) ventrally with some long setae; maxillary palpus with three articles; proximal article with about five setae. Asperities (fig. 14) minute, some obtuse, others with flat, scraperlike top.

Number of prodorsal asperities on each side of:

Thoracic segment II ..... none
„ „ III 6

Abdominal segment	1	8	
„	„ 2	8	
„	„ 3	8	
„	„ 4	8	in single
„	„ 5	8	regular rows
„	„ 6	8	
„	„ 7	3	
„	„ 8	none	

9th abdominal segment with four minute asperities in a single row on each side of body.

10th abdominal segment without asperities.

Spiracles (figs. 16 and 17) simple, ring-shaped, broadly oval to circular, without air tubes; diameter of thoracic spiracle (fig. 16) one and a half times as long as diameter of each abdominal spiracle (fig. 17).

Leg (fig. 18) with a reduced number of setae, but setae very long and fine; pretarsus about one-fourth as long as tibio-tarsus; basal membranous part about twice as wide as long, armed with two setae; claw short, but twice as long as membranous base, somewhat curved and quite robust; arolium absent.

24. *Hadrobregmus thomsoni* Kraatz[1]
25. *Hadrobregmus umbrosus* Fall.[1]

Plate 29.

Described material labeled:

1) *Anobium thomsoni* Kraatz; Suomi, Korpiselkä, in *Picea excelsa*, 7.VI.1913, Uunio Saalas coll. et det.
2) *Hadrobregmus umbrosus* Fall., in *Fagus*, Conn., U. S. A., F. C. Craighead coll., Hopk. U. S. 10082 j.
3) *Hadrobregmus carinatus* Say, in *Quercus*, Conn., F. C. Craighead coll., Hopk. U. S. 10082 h.

Size of larva: Moderately large (c. 7 mm.).

Head capsule slightly longer than broad, broadest before middle, sides convergent behind; pigmented field behind epistoma (fig. 1) present, but length sagittally less than that of epistoma; provided with a few fine setae but not pitted; epistoma (fig. 1)

[1] The larvae of *H. thomsoni* from Finland and *H. umbrosus* from U. S. A. are identical, even the number of asperities in the prodorsal areas differs only slightly and cannot be considered as a separating character. Concerning *Hadrobregmus carinatus* Say see: footnote to the description of this larva on p. 96.

fairly smooth and without setae; rest of cranium (fig. 4) with numerous, evenly distributed, moderately long and short setae. Antenna (fig. 4) with two distinct articles. Anteclypeus (fig. 4) simple, with five moderately long, stiff setae at each end of anteclypeal sulcus. Labrum (fig. 4) transverse, suboval, about twice as wide as long; anterior margin and much of surface behind it densely set with long and fairly long setae; paired marks present. Epipharynx (fig. 1) on each side with six slender, almost straight chaetoparial setae in a subtriangular, anteriorly wider group on each side, and near each torma a smaller additional seta; Tormae and labral rods (fig. 1) forming a pair of long, Y-shaped, straight features; crepidal region covered by minute papillae and with a few indistinct pores. *Mandible* (fig. 2) with two apical teeth and two small, rounded, almost confluent subapical projections; marginal brush well-developed in *H. thomsoni* but lacking (possibly broken off) in the two other species; aboral mandibular surface bearing a proximal series of fairly long setae and a distal group of five similar setae (fig. 4) (absent, probably broken off in *H. thomsoni*, fig. 2). Maxillary lacinia (fig. 3) about half as large as galea, lacking a robust spine but distally bearing a considerable number of strong, ensiform, slightly curved setae, each as long as one of the similar marginal setae of galea; in addition with some straight but weaker setae on ventral side behind the distal setae; dorsally with numerous fine, soft, and long setae; maxillary palpus with three articles; proximal article with an irregular series of about ten long setae on ventral side, and about the same number of similar setae on distal part of stipes. Prementum, meso- and submentum, each with about a dozen setae on either side.

Number of prodorsal asperities on each side of:

	thomsoni	*umbrosus*	*carinatus*
Thoracic segment II	none	none	none
„ „ III	21	26	23
Abdominal segment 1.....	38	41	31
„ „ 2.....	49	42	41
„ „ 3.....	47	50	50
„ „ 4.....	70	56	66
„ „ 5.....	98	109	90
„ „ 6.....	84	75	71
„ „ 7.....	8	9	11
„ „ 8.....	none	none	none

9th abdominal segment on each side with a patch of lateral asperities amounting to about 77 (*thomsoni*); about 77 (*umbrosus*); and about 80 (*carinatus*).

10th abdominal segment without asperities.

Spiracles (fig. 4) annular, both thoracic and abdominal broadly oval, without air tubes; orifice of thoracic spiracle more than twice as long as one of the abdominal spiracles.

Pretarsus (fig. 4) about half as long as tibio-tarsus; proximal membranous part of pretarsus subconical sometimes slightly swollen, about as wide as long, armed with two setae; claw almost three times longer than proximal part, slender, only a little curved; arolium absent.

26. *Xyletobius walsinghami* Perkins.[1]

Plates 1 and 29.

Described material labeled:

Xyletobius walsinghami Perk., ex *Perrottetia*, Mt. Tantalus, Oahu, 7.VI.1930, O. H. Swezey coll. et det.

Size of larva: Moderately large to large (c. 10 mm.).

Head capsule circular, without frontal lines; pigmented field behind epistoma (fig. 5) present, sagittally almost twice as long as length of epistoma; epistoma (fig. 5) on each side with a transverse series of about seven long, stiff, closely-set setae; rest of cranium, including pigmented field, with numerous rather short, evenly distributed setae (Pl. 1). Antenna (fig. 5) without articles; sensory organs borne by dome-shaped membranous base. Anteclypeus (fig. 5) thin walled, with about seven stiff, rather long, fine setae borne by a small plate at each end of anteclypeal sulcus. Labrum (fig. 5) transverse, not fully twice as wide as long, with shallow, broad anterior emargination; anterior margin and half of surface behind it set with moderately long and rather short, fine setae; paired marks present. Epipharynx (fig. 6) with two pairs of coryphal setae; well-developed marginal acanthoparial setae; on each side a narrow, subtriangular, oblique patch of about thirteen chaetoparial setae; most of the anterior eight setae moderately long, straight and

[1] *Xyletobius sykesii* Perkins is characterized at the end of the description of *Xyletobius walsinghami*.

arranged in two irregular rows; posterior five setae very short, robust and in a single row; tormae (fig. 6) strongly sclerotized and straight, labral rods rather membranous and light colored, together forming indistinct Y-shaped features; crepidal area velvety pubescent with about twelve pores dispersed over entire surface. *Mandible* (fig. 9) with two apical teeth; subapical marginal edge forming an, in outline, approximately subtriangular ledge, followed by the enclosure around the marginal brush; setae of proximal group on aboral mandibular surface about six long ones, setae of distal group three, of moderate size. Maxillary lacinia half as large as galea, distally without spine but with about a dozen densely set, stiff setae of similar shape and length as the marginal setae of galea, and dorsally at base (fig. 7) with a tuft of about four long, fine hairs; maxillary palpus with three articles, proximal article ventrally with about ten setae and dorsally (fig. 7) with a few minute setae at base and about four long ones more anteriorly; distal part of stipes with about ten setae on ventral surface.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	100
Abdominal segment 1	116
„ „ 2	107
„ „ 3	89
„ „ 4	78
„ „ 5	67
„ „ 6	77
„ „ 7	44
„ „ 8	none

9th abdominal segment on each side with a patch of at least 70 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 8, 10, 11) pseudocribriform, broadly oval; thoracic spiracle (fig. 8) about twice as long as one of the abdominal (figs. 10 and 11).

Leg (Pl. 1 and Pl. 29, fig. 12) well provided with setae, especially at distal end of tibio-tarsus; pretarsus about one-third the length of tibio-tarsus; proximal membranous part and claw

of the same length; membranous part with six well-developed setae; claw rather short, narrow, conical and straight; arolium absent.

Addenda: 26. *Xyletobius sykesii* Perkins; ex Xanthoxylum (Hawaii)? O. H. Swezey coll. et det. (1 larva, 1 pupa, 1 reared imago). Differs from *X. walsinghami* by being much smaller and having approximately only half as many asperities on the segments.

Size of larva: Small (c. 3 mm.). Head circular.

27. *Xyletinus peltatus* Harris and *Xyletinus* sp. (near *peltatus*).

Plate 30.

Described material labeled:

1) *Xyletinus peltatus* Harris; in pine wood, Griffin, Ga., 10.VIII. 1937, Th. Bissell coll., W. S. Fisher det. imago.
2) *Xyletinus peltatus* Harris; from infested pine joists in 40-year old house in McLean, Va., 6.XII.1938.
3) *Xyletinus peltatus* Harris; in shop timbers made of so-called Swamp Maple, Farmingdale, N. Jersey, Novbr. 1938.
4) *Xyletinus* sp. (near peltatus Harris); ex barn timbers, Tiffin, Ohio (letter 26.VIII.1941), T. H. Parker coll., 41–14691, W. H. Anderson det.
5) *Xyletinus* sp. (near peltatus Harris) from wood of a book case, Thomasville, Ga., 20.IV.1938, B.V.Travis coll.
6) *Xyletinus* sp. (near peltatus Harris); in pine sills, Atlanta, Ga., 3.V.1937 (with letter from State Entomologists's office, Atlanta, Ga.).

Size of larva: Moderately large (c. 6 mm.).

Head capsule somewhat longer than broad, widest in the middle, posteriorly oval, without frontal lines; pigmented field behind epistoma absent; epistoma (fig. 1) with transverse anterior series of, altogether, two long median setae and on each side two small setae; rest of cranium with numerous long and short, evenly distributed setae. Antenna (fig. 2) without articles; sensory organs borne by dome-shaped membranous base. Anteclypeus (fig. 1) thin walled with a single, long seta, borne by a small sclerite at each end of anteclypeal sulcus. Labrum (fig. 1) transverse, about

twice as wide as long, anterior half densely set with moderately fine setae; paired marks present. Epipharynx (fig. 3) with well-developed marginal acanthoparial setae, two pairs of small coryphal setae, and on each side an oblique, curved series of six rather short, robust chaetoparial setae; tormae and labral rods united into long, straight, somewhat Y-shaped features; crepidal area between tormae velvety pubescent with numerous larger and smaller pores. *Mandible* (fig. 4) with two apical teeth; subapical marginal edge forming a rather short and low, convex ledge, followed by a well-developed, oval enclosure around the marginal brush; aboral setae of proximal group about eight, rather long, of distal group three (or four) of moderate size. Maxillary lacinia (fig. 6) half as large as galea, distally without spine but with about a dozen long, stiff, strong setae, similar to the marginal setae of galea; maxillary palpus with three articles, proximal article ventrally with about seven well-developed, anteriorly placed setae in two irregular, transverse series; distal part of stipes with about same number of similar setae.

Number of prodorsal asperities (fig. 7) *on each side of:*

— *Xyletinus peltatus.*

1) Griffin, Ga. 2) McLean, Va. 3) Farmingdale, N. Jersey. —

Thoracic segment II	none	none	none
„ „ III	27	31	32
Abdominal segment 1	37	48	53
„ „ 2	31	47	51
„ „ 3	33	47	47
„ „ 4	37	42	43
„ „ 5	35	39	38
„ „ 6	33	41	44
„ „ 7	43	38	36
„ „ 8	none	none	none

— *Xyletinus sp.* (*near X. peltatus*) (fig. 11).

4) Tiffin, Ohio 5) Thomasville, Ga. 6) Atlanta, Ga. —

Thoracic segment II	none	none	none
„ „ III	48	42	41
Abdominal segment 1	86	64	66
„ „ 2	96	68	75
„ „ 3	79	55	70

Abdominal segment 4	64	57	66
„ „ 5	48	50	66
„ „ 6	61	55	76
„ „ 7	65	61	69
„ „ 8	6	7	9

9th abdominal segment on each side with a patch of at least 70 lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 8, 9 and 10) oval with a single, minute air tube; thoracic spiracle (fig. 8) about twice as long as the abdominal ones (figs. 9 and 10).

Leg (fig. 5) well provided with setae, especially at the distal end of tibio-tarsus; pretarsus about one-fourth the length of tibio-tarsus, proximal membranous part and claw of same length, membranous part with three setae; claw rather short, narrow conical, and straight; arolium absent.

28. *Xyletinus fucatus* L. and 29. *Xyletinus* sp. (near *X. mucoreus* Lec.).

Plate 31.

Described material labeled:

1) *Xyletinus fucatus* L., in dead oak twigs, Westboro, Ont., Canada, 11.III.1921, F. C. Craighead coll., reared and det. Dom. Can. Ent. Br. #15043 E.
2) *Xyletinus* sp. (perhaps *X. fucatus* L.), ex small dead branch, College Park, Md., 28.II.1942, W. H. Anderson coll. et det.
3) *Xyletinus* sp. (near *X. mucoreus* Lec.), in fallen dead holly branch, Snow Hill, Md., 21.X.1949 and 6.III.1950, W. H. Anderson coll. and reared, W. S. Fisher det. imago.

Size of larva: Moderately large (c. 7 mm.).

Head capsule subcircular, very little longer than broad, widest in the middle, sides slightly convergent posteriorly, without frontal lines; a pigmented field behind epistoma absent (fig. 1); epistoma with transverse series of, altogether, eight well-developed setae (fig. 1); rest of cranium bearing moderately long and short, evenly scattered setae. Antenna (fig. 1) without articles, sensory organs borne by dome-shaped, membranous base. Anteclypeus

(fig. 1) bearing a group of five long setae attached to a small plate at each end of anteclypeal sulcus. Labrum (fig. 1) semicircular, anteriorly densely set with fine setae; paired marks present. Epipharynx (fig. 2) with numerous fine, rather short and recurved acanthoparial setae; anteriorly in front of paired marks with short, curved coryphal setae in two parallel, transverse series; chaetoparial setae numerous, well developed, awl-shaped, somewhat curved and assembled in a subtriangular patch on each side in front of tormae and also between the tormae; the latter setae short, arranged in a single, longitudinal, irregular series of about eight setae; tormae solid, straight, elongate conical; no distinct labral rods; crepidal area velvety pubescent with about a dozen pores scattered over the entire area. *Mandible* (fig. 4) with two apical teeth; subapical margin formed as a long, strong, subtriangular wall with cut-off top near marginal bristles; adoral surface swollen at base; marginal brush present; aboral surface with a double series of about twelve well-developed proximal setae and a small group of about four distal setae. Maxillary lacinia (fig. 3) almost as large as galea, terminally set with numerous strong, straight setae; galea similarly armed; dorsal surface of both lobes (fig. 3) furnished with many fine, short setae and proximally with some very long, soft and fine setae; maxillary palpus with three articles, proximal article ventrally with about seven long setae, dorsally with many short setae; distal part of stipes with many long setae.

Number of prodorsal asperities (fig. 9) *on each side of:*

Thoracic segment II	none
„ „ III	18
Abdominal segment 1	18
„ „ 2	14
„ „ 3	10
„ „ 4	9
„ „ 5	7
„ „ 6	8
„ „ 7	5
„ „ 8	none

9th abdominal segment on each side with a patch of 20 lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 10 and 11) oval with a single, short air tube; thoracic spiracle (fig. 10) slightly less than twice as long as one of the abdominal spiracles (fig. 11).

Leg (fig. 7) with many long setae; pretarsus about one-third the length of tibio-tarsus, proximal membranous part only a little more than half as long as claw and bearing two long setae; claw slender, strong, pointed and slightly curved; arolium absent.

29. *Xyletinus* sp. (near *mucoreus* Lec.).

This species differs from *Xyletinus fucatus* L. only in having oval spiracles without any air tubes (figs. 5 and 6) and the following larger *number of prodorsal asperities* (fig. 8) *on each side of:*

Thoracic segment II	none
„ „ III	48
Abdominal segment 1	55
„ „ 2	46
„ „ 3	30
„ „ 4	30
„ „ 5	30
„ „ 6	25
„ „ 7	12
„ „ 8	none

9th abdominal segment on each side with a patch of 35 lateral asperities.

10th abdominal segment without asperities.

30. *Oligomerus sericans* Melsh.

Plate 31.

Described material labeled:

1) *Oligomerus sericans* Melsh., in chestnut, West Virginia, Hopk. U. S. #13807.
2) *Oligomerus sericans* Melsh., in end of twig of English Walnut, Salem, Oregon, 4.V.1944, Spl. Surv. #15441.

Size of larva: Moderately large (c. 8 mm.).

Head capsule a little longer than broad, widest slightly behind the middle, posteriorly somewhat convergent, without frontal

lines; a pigmented field behind epistoma absent (fig. 14); epistoma (fig. 14) with transverse series of, altogether, fourteen fine, well-developed setae and about four setae at each antennal fossa; rest of cranium bearing long and short, evenly scattered setae. Antenna (fig. 14) without articles; sensory organs on membranous base. Anteclypeus (fig. 14) with a group of six straight, long, fine setae borne by a small plate at each end of anteclypeal sulcus. Labrum (fig. 14) broadly oval, slightly wider than long, densely set with small setae on anterior half of surface; paired marks present. Epipharynx (fig. 12) with numerous fine, recurved acanthoparial setae; chaetoparial setae on each side anteriorly in a broad, longitudinal patch of numerous awl-shaped setae continued in an irregular posterior row of similar but shorter setae and extending behind tips of tormae; tormae solid, subconical, somewhat curved, strongly converging, and about one-third the length of epipharynx in front of crepidal area; crepidal area velvety pubescent with about ten pores irregularly distributed all over. *Mandible* (fig. 13) with two apical teeth; subapical marginal edge strong and fairly straight; adoral surface swollen at base; marginal brush present; aboral mandibular surface with a double series of about twelve well-developed proximal setae and a small group of about four distal setae. Maxillary lacinia (fig. 17) almost as large as galea, terminally densely set with numerous strong, stiff setae similar to the marginal setae of galea; ventral surfaces (fig. 17) of both lobes with strong, stiff setae; dorsal surfaces with fine, short setae and proximally with some very long, soft and hairlike setae; maxillary palpus with three articles; proximal article with about seven long setae; distal part of stipes with many similar setae.

Number of prodorsal asperities (fig. 19) *on each side of:*

Thoracic segment II	none
„ „ III	23
Abdominal segment 1	26
„ „ 2	22
„ „ 3	17
„ „ 4	18
„ „ 5	15
„ „ 6	10
„ „ 7	8
„ „ 8	none

9th abdominal segment on each side with a patch of 24 lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 15 and 16) oval, with two very short air tubes on thoracic (fig. 15) and on a few of the abdominal spiracles (fig. 16), only a single short air tube on most abdominal spiracles; thoracic spiracle about twice as long as an abdominal one.

Leg (fig. 18) with many long setae; pretarsus about one-third the length of tibio-tarsus; proximal membranous part about as long as claw and bearing two long setae; claw slender, pointed and slightly curved; arolium absent.

31. *Holcobius haleakalae*, var. *chrysodytus* Perkins[1].

Plate 32.

Described material labeled:

1) *Holcobius haleakalae* var. *chrysodytus* Perkins, ex dead branch of *Acacia koa*, 1500 ft., Waipio, Oahu, 9.X.1929, O. H. Swezey coll. et det.

Size of larva: Large (c. 14 mm.).

Head capsule (fig. 1) subcircular, without frontal lines, pigmented field behind epistoma (fig. 1) very large, extending over more of cranial surface than half the distance from base of anteclypeus to distal end of epicranial sulcus; centrally armed with a single cone-shaped projection; epistoma (fig. 1) anteriorly with a transverse series of, altogether, sixteen fine, moderately long and straight setae; a group of several long and short setae present interiorly of antennal fossa; rest of cranium with long and fairly short setae scattered over the surface. Antenna (fig. 1) without distinct articles. Anteclypeus (fig. 1) with a group of six fairly long, straight setae on a small sclerotization at each end of anteclypeal sulcus. Labrum (fig. 1) almost circular, densely set with setae on anterior half of surface; paired marks distinct. Epipharynx (fig. 2) with numerous, fine, rather short and recurved

[1] Present in collection of U.S.N.M. are the larvae of the following species, reared and determined by O. H. Swezey, but not (or, "Holcobius sp.", only by a different size) to be separated from larvae of *H. haleakalae*: 1) *Holcobius glabricollis* Perk., ex *Acacia koa*, Mt. Tantalus, Oahu, 4.VII.1930, O. H. Swezey [large larvae]; 2) *H. hawaiiensis* Perk., ex *Suttonia kilauea*, Hawaii, 20.VII.1934, O.H.S. [large larvae]; 3) *Holcobius* sp., reared, imago in vial, ex Kukui-wood, Ukumohame Val., Maui, 29.VIII.1929, O. H. S. [moderately large, c. 6 mm].

acanthoparial setae; chaetoparial setae on each side numerous, fine, curved and awl-shaped, assembled in a dense patch in front of torma and continued parallel with the torma in a double and irregular row; tormae almost as long as sagittal line of epipharynx in front of crepidal area, forceful, anteriorly irregularly branched, posteriorly curved in an inside concave, semicircular arch; no distinct labral rods; crepidal area with six, or a few more, pores, irregularly distributed. *Mandible* (fig. 3) with two apical teeth; subapical margin forming a low, somewhat bent, slightly granulated, strong wall; marginal brush present but setae short; a series of about twelve proximal setae and a few distal setae on aboral mandibular surface. Maxillary lacinia (fig. 5) as large as galea, terminally with a multitude of densely set, strong, straight setae similar to marginal setae of galea; ventral surfaces of both lobes with strong setae, dorsal surfaces with fine setae and proximally with some very long and soft hairs; maxillary palpus with three articles; proximal article ventrally with about seven long setae, and a similar number of long setae on distal end of stipes.

Number of prodorsal asperities (fig. 6) *on each side of:*

Thoracic segment II	5
„ „ III	99
Abdominal segment 1	118
„ „ 2	100
„ „ 3	84
„ „ 4	65
„ „ 5	52
„ „ 6	64
„ „ 7	93
„ „ 8	none

9th abdominal segment on each side with a patch of about 190 lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 7 and 8) oval with a single small air tube; thoracic spiracle (fig. 7) about twice as long as an abdominal one (fig. 8).

Leg (fig. 4) with many long setae; pretarsus about half as long as tibio-tarsus; membranous part about as long as claw and carrying five setae; claw slender, pointed and slightly curved; no arolium.

32. *Xeranobium macrum* Fall.

Plate 33.

Described material labeled:

1) *Xeranobium macrum* Fall., in iodine bush *Spirostachys occidentalis* Walson, Los Banos, Calif., P. Ting coll., 28.IX.1935; W. S. Fisher det. imago (16.VII.1937).

Size of larva: Moderately large (c. 7 mm.).

Head capsule subcircular, slightly longer than broad, widest in the middle, without frontal lines; pigmented field behind epistoma (fig. 1) absent; epistoma (fig. 1) with transverse series of, altogether, twelve fine, well-developed, straight setae in anterior margin, about six long, fine setae at inner outline of antennal fossa, and a few small setae in middle of epistoma; rest of cranium with fine, long and short setae over the entire surface. Antenna (fig. 1) without articles. Anteclypeus (fig. 1) with a group of about twelve long, fine setae seated at each end of anteclypeal sulcus on a small plate. Labrum (fig. 1) approximately circular, set with setae on anterior half of surface; paired marks present. Epipharynx (fig. 2) with a multitude of fine, recurved acanthoparial setae; chaetoparial setae on each side assembled in a broad, longitudinal patch of numerous awl-shaped setae and continued in two very irregular rows of short, some fan-shaped, others hook-shaped setae along inner line of torma; tormae (fig. 2) long, quite slender, sausage-shaped, and somewhat S-bent; no labral rods; crepidal area velvety pubescent with about four pores irregularly placed. *Mandible* (fig. 4) with two apical teeth; subapical margin forming a humplike, thick wall with granulated surface; marginal brush not found; proximal aboral group of setae with ten very long setae, distal group with few and short setae. Maxillary lacinia (fig. 5) almost as large as galea, terminally with numerous strong, stiff setae similar to the slender cultriform marginal setae of galea; ventral surfaces of both lobes with many strong setae, dorsal surfaces covered with fine, short setae and proximally furnished with very long, soft hairs; maxillary palpus with three articles; proximal article ventrally with about four moderately long setae; distal part of stipes with a similar number of like setae.

Number of prodorsal asperities (fig. 3) *on each side of:*

Thoracic segment II	none
„ „ III	52
Abdominal segment 1	66
„ „ 2	53
„ „ 3	43
„ „ 4	38
„ „ 5	36
„ „ 6	33
„ „ 7	29
„ „ 8	none

9th abdominal segment on each side with a patch of about 65 lateral asperities.

10th abdominal segment without asperities.

Spiracles (figs. 6 and 7) oval, simple, without air tubes; thoracic spiracle (fig. 6) twice as long as one abdominal (fig. 7).

Leg (fig. 8) with many long setae; pretarsus about one-third the length of tibio-tarsus; proximal membranous part not fully as long as claw and bearing four setae; claw slender, pointed and slightly curved; arolium absent.

33. *Nicobium castaneum* Oliv.

Plate 33.

Described material labeled:

1) *Nicobium* sp. ex wood from packing case, Azores, New York, 14.III.1922, #953.
2) *Nicobium castaneum* Oliv. from flooring of house, Baton Rouge, Louisiana, 17.III.1931.
3) *Nicobium* sp., in box containing dried persimmon from Japan, Hawaii #3003.
4) *Nicobium castaneum* Oliv., in wood strip, trunk-enforcement, from Italy, New York #82224, Juni 1939.
5) *Nicobium castaneum* Oliv., in wooden box from New Caledonia, Australia, Boston ..16342, 7.X.1942.

Size of larva: Moderately large (c. 7 mm.).

Head capsule circular, without frontal lines; pigmented field behind epistoma (fig. 10) absent, epistoma (fig. 10) with a transverse group of, altogether, about twelve scattered, moderately long and short setae; about three long setae inside from antennal fossa; rest of cranium with long and short setae all over the

surface. Antenna (fig. 9) with two articles; proximal article a low ring. Anteclypeus (fig. 10) with a group of about ten well-developed, straight, fine setae at each end of anteclypeal sulcus, seated on a small plate; the two plates connected by a narrow, ribbon-shaped sclerotization. Labrum (fig. 10) transversally broadly oval, pigmented, set with long, fine, curved setae; paired marks absent. Epipharynx (fig. 11) with a multitude of recurved, fine marginal setae and almost completely covered by more or less curved, pointed, rather short chaetoparial setae; tormae short, subcylindrical, somewhat hooked terminally, no distinct labral rods; crepidal area with about ten sensory pores. *Mandible* (fig. 13) with two apical teeth and subapical margin forming a long, robust, fairly high, straight wall with fine longitudinal striae and minute granulae; marginal brush with short setae; a group of many long proximal setae and a row of five distal setae of moderate lengths on aboral mandibular surface. Maxillary lacinia (fig. 15) slightly larger than galea both lobes terminally covered with a multitude of densely set, strong, straight setae; adorally reinforced by sclerotized bar (Lc-Ga arm, fig. 15) and bearing many thin, soft setae; maxillary palpus with four articles; proximal article with many long, curved setae, next article with four much shorter setae, penultimate article with two setae and distal article without setae; stipes bearing numerous long, curved setae distally, ventro-lateral stipital bar (q, fig. 15) at the maxillary articulating area weakly sclerotized, except distally at the lobes.

Number of prodorsal asperities on each side of:[1]

	— 1) Azores	2) Louisiana	3) Japan	4) Italy	5) Australia. —
Thoracic segment II	none	none	none	none	none
„ „ III	3	2	none	4	4
Abdominal segment 1	27	30	23	28	37
„ „ 2	25	34	35	49	47
„ „ 3	28	35	42	50	45

[1] The number of prodorsal asperities varies more in the single larval specimens of this species than of other anobiid species. Several samples of different groups of larvae, determined as *Nicobium castaneum*, from many parts of the world have therefore been examined in order to discover whether more than one species might be listed under the same name. However, a positive result of the investigation was not obtained because the variations in the number of the prodorsal asperities appeared to fluctuate quite indiscriminately as shown in the following tabulations. It was also found that in the majority of the specimens all of the prodorsal asperities were not typically hook-shaped, but many reduced to either pointed or obtuse minute, dark granulae.

Abdominal segment	4	24	36	33	43	45
„ „	5	16	16	18	30	30
„ „	6	none	none	none	none	none
„ „	7	none	none	none	none	none
„ „	8	none	none	none	none	none

9th abdominal segment on each side with a patch of from 20 to 50 lateral asperities (roughly estimated).

10th abdominal segment without asperities.

Spiracles (figs. 14, 16 and 17) pseudocribriform, thoracic spiracle (fig. 14) about one and one-half as long as an abdominal (figs. 16 and 17).

Leg (fig. 12) with pretarsus half as long as slender tibio-tarsus; membranous basal part of pretarsus rather long, bearing eight setae; claw as long as basal part, straight, very slender and pointed; no arolium.

34. *Trichodesma klagesi* Fall and 35. *Trichodesma gibbosa* Say.

Plate 34.

Described material labeled:

1) *Trichodesma klagesi* Fall in *Benzoin* sp. (Fever bush), Lyme, Conn., 29.XII.1916, A. B. Champlain coll. et det. (Hopk. U. S. #10083b).
2) *Trichodesma gibbosa* Say, in dead trunk of *Persea*, Nicholson, Miss., 9.II.1945, Gordon coll., (Spl. Surv. #23189).

Size of larva: Large (c. 11 mm.)

Head capsule subcircular, without frontal lines; pigmented field behind epistoma absent; epistoma (fig. 2) with a transverse group of, altogether, about sixteen scattered, moderately long and short setae, about four long setae inside from antennal fossa; rest of cranium with long and short setae over the whole surface. Antenna (fig. 1) with two articles; proximal article a low ring. Anteclypeus (fig. 2) with a group of about twenty-five well-developed, fine, setae on a small plate at each end of antec lypeal sulcus; the two plates connected with a transverse, low sclerotization. Labrum (fig. 2) almost circular, somewhat pointed anteriorly, pigmented, with numerous, rather strong and stiff setae; paired marks absent. Epipharynx (fig. 3) with a multitude

of somewhat recurved marginal setae and almost completely covered by more or less curved, pointed, generally fine, well-developed and short chaetoparial setae; tormae short, subcylindrical; no labral rods; crepidal area velvety pubescent with about ten sensory pores irregularly distributed over the whole field. *Mandible* (fig. 6) with two apical teeth and subapical margin forming a long, fairly high, subtriangular wall; marginal brush with short setae; proximal and distal groups of setae present on aboral surface. Maxillary lacinia (fig. 5) slightly broader distally than the more oval galea; both lobes densely set with strong, straight setae on terminal margins, and with long, strong, curved setae on aboral surfaces; adorally reinforced by sclerotizations and bearing many fine, soft setae; maxillary palpus with four articles; proximal article with many long, curved setae; next article with four much shorter setae; penultimate article with two setae and distal article without setae; stipes bearing numerous long, curved, strong setae; ventro-lateral stipital bar weakly sclerotized except distally at the lobes.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	3
Abdominal segment 1	25
„ „ 2	33
„ „ 3	27
„ „ 4	32
„ „ 5	19
„ „ 6	none
„ „ 7	none
„ „ 8	none

9th abdominal segment on each side with a patch of about 35 lateral asperities.

10th abdominal segment without asperities but with short, stiff, straight and pointed setae.

Spiracles annular, simple, oval, without air tubes; thoracic spiracle (fig. 7 a) two and one-half times longer than one of the abdominal (fig. 7 b).

Leg (fig. 4) with pretarsus half as long as slender tibiotarsus; basal part of pretarsus rather long, bearing eight setae of different lengths; claw as long as membranous basal part, straight, very slender and pointed; no arolium.

35. *Trichodesma gibbosa* Say.

Large (c. 11 mm.), with subcircular head, appears identical with the larva of *Trichodesma klagesi* Fall.

36. *Vrilletta blaisdelli* Fall
Vrilletta sp.,
Vrilletta convexa Lec. and
Vrilletta expansa Lec.

Plate 34.

Described material labeled:

1) *Vrilletta blaisdelli* Fall, in live oak, Irvine Park, Calif., 15.XII.1943, PROLE and BYERS coll., Spl. Surv. #23594.
2) *Vrilletta* sp., under apple bark, Monteray County, Calif., 1944, ROMSAY and CAMERON coll., Spl. Surv. #23629 45-6916.
3) *Vrilletta convexa* Lec., in white alder, Ashland, Oregon, 2.V.1913, U. S. Hopk. #11074a, imago det. April 1944 by W. S. FISHER.
4) *Vrilletta expansa* Lec., Los Angeles, Calif., COQUILLETT coll. et det.

Size of larva: Large (c. 11 mm.).

Head capsule circular, without frontal lines; pigmented field behind epistoma absent; epistoma (fig. 8) with transverse anterior series of, altogether, ten stiff, fine setae and a few or no setae behind; rest of cranium with numerous, evenly distributed, moderately long and short setae. Antennal triangular casing extending beyond catapophysis; antenna (fig. 8) without articles. Anteclypeus (fig. 8) thin walled with about six setae from a small sclerite at each end of anteclypeal sulcus. Labrum (fig. 8) transverse, suboval, about twice as wide as long, anterior margin with broad, shallow, concave curvature, densely set with moderately long, fine setae; paired marks present. Epipharynx (fig. 9) with numerous long, recurved acanthoparial setae; immedially behind them with a patch of hook-shaped, comparatively long coryphal setae; on each side with a long, oblique series of short, cultriform chaetoparial setae, anteriorly arranged in a small group of about five setae and posteriorly in a single row of about eight extending to proximal end of torma; crepidal field with about six pores; tormae short, robust, curved toward sagittal line; no labral rods. *Mandible* (fig. 12) with two short apical

teeth; subapical margin raised to a moderately high, subtriangular wall; aboral mandibular surface covered proximally with small granules; marginal brush well-developed, proximal aboral group of setae containing about twelve long setae, each setae in a pit on top of a little round elevation, distal aboral group with about four well-developed setae. Maxillary lacinia (fig. 10) about half as large as galea, distally without spine but with about twelve long, stiff, strong setae similar in shape to the marginal setae of galea; dorsal surface of both lacinia and galea, in addition to numerous fine, moderately long setae, with many proximally located, very long and fine hairs; maxillary palpus with three articles; proximal article bearing on ventral surface twelve long setae; distal part of stipes with about as many similar setae.

Number of prodorsal asperities on each side of:

	blaisdelli	sp.	expansa
Thoracic segment II	none	none	none
„ „ III	17	20	19
Abdominal segment 1	21	21	24
„ „ 2	21	22	20
„ „ 3	16	17	16
„ „ 4	13	15	15
„ „ 5	13	14	14
„ „ 6	13	15	21
„ „ 7	9	11	15
„ „ 8	none	none	none

9th abdominal segment on each side with the following number of lateral asperities: *blaisdelli:* 30; sp.: 32; *expansa:* 32.

10th abdominal segment without asperities.

Spiracles (figs. 13 and 14) broadly oval, with a single air tube of small size, resting in a thin-walled enlargement of peritrema; orifice of thoracic spiracle (fig. 13) about twice as long as orifice of an abdominal spiracle (fig. 14), thoracic air tube winding, abdominal air tubes straight.

Pretarsus about one-third of tibio-tarsus in length, proximal membranous part and claw equally long, membranous part with two setae; claw rather short, quite robust and curved; arolium as long as membranous part.

37*. *Priobium tricolor* Oliv.

Plate 35.

Described material labeled:

1) *Priobium tricolor* Oliv., in wood of oak, Dyrehaven, Denmark, ex Mus. Zool. Copenhagen, #145, MEINERT, 1890.

2) *Priobium tricolor* Oliv., Denmark, 23.VI.1936, J. P. KRYGER coll. and reared.

Size of larva: Moderately large (c. 7 mm.).

Head capsule slightly longer than broad, broadest before the middle, sides convergent behind the middle, without frontal lines, pigmented field behind epistoma absent; epistoma (fig. 1) anteriorly with a transverse, irregular series of, altogether, eight long setae; a few long setae present at innerside of antennal fossa and rest of cranium with rather long and short setae on the entire surface. Antenna (fig. 1) without distinct articles, sensory cone short. Anteclypeus (fig. 1) with three long, straight setae at each end of anteclypeal sulcus, not borne by any small plate. Labrum (fig. 1) with semicircular anterior margin; about as wide as long, with many long, fine, straight setae on each side; paired marks present. Epipharynx (fig. 2) anteriorly with numerous, recurved acanthoparial setae; behind them several rather short, hooked coryphal setae and on each side with an oblique series of five (or six) short, mostly ovate chaetoparial setae; labral rods and tormae forming robust, long, subparallel, Y-shaped features; crepidal field velvety pubescent without pores. *Mandible* (fig. 4) with two apical teeth, subapical margin raised into a strong, subtriangular wall with a short, toothlike process at the second apical tooth; marginal brush present; aboral surface with proximal and distal groups of four setae each. Maxillary lacinia (fig. 5) about half as large as galea, lacking spine, but terminally with many straight, slightly cultriform, stiff setae and some straight, rather stiff setae behind them; galea with similar setal arrangement; maxillary palpus with three articles; proximal article with six long setae on ventral side; distal part of stipes bearing same number of similar setae.

Number of prodorsal asperities on each side:

Thoracic segment II..... none
„ „ III..... none

Abdominal segment 1	22	
„ „ 2	25	in one or two
„ „ 3	20	irregular rows
„ „ 4	18	
„ „ 5	17	
„ „ 6	16	in one row
„ „ 7	9	
„ „ 8	none	

9th abdominal segment with about 30 lateral asperities on each side of body.

10th abdominal segment without asperities.

Spiracles (figs. 6, 7 and 8) almost circular, with a single, large air tube of T-shape on thoracic spiracle (fig. 6) and multibranched, single air tube on each abdominal spiracle (figs. 7 and 8).

Leg (fig. 3) with pretarsus only one-third or less as long as tibio-tarsus; proximal membranous part of pretarsus subconical, about as wide as long, armed with two setae; claw not longer than membranous part, rather robust and slightly curved; arolium small but distinct, a little longer and wider than membranous part.

37*. *Priobium eichhoffi* Seidl.

The larva of this species is identical in all characters with *P. tricolor*. Material in collection labeled: *Priobium eichhoffi* Seidl., Denmark; in dead moist branches on east shore of Fuur-sö; E. C. Rosenberg coll. and reared; received from Mus. Copenhagen, March, 1915—through Böving.

Size of larva: c. 7 mm.

38. *Protheca hispida* Lec.

Plate 35.

Described material labeled:

1) *Protheca hispida* Lec., in *Liriodendron*, Virginia, Hopk. U.S. #10036, c (single, imperfect larval skin).

Size of larva: . . . ?

Head capsule without frontal lines, pigmented field behind epistoma present and sagitally about as long as epistoma (fig. 9); epistoma with a transverse series of, altogether, six long setae; rest of cranium, including pigmented field, with evenly scattered,

moderately long and short setae. Antenna (fig. 9) without articles, sensory cone about as high as membranous, dome-shaped base. Anteclypeus (fig. 9) with a group of three long setae at each end of anteclypeal sulcus; no supporting plates. Labrum (figs. 9 and 10) transverse, broadly oval, set with numerous setae, apparently no paired marks present. Epipharynx (fig. 10) with a multitude of moderately long acanthoparial setae; on each side six cultriform, rather short chaetoparial setae in a single, curved row; tormae and well-developed labral rods forming strong, moderately long, Y-shaped features. *Mandible* (fig. 11) with two apical teeth; subapical margin narrow, raised into a short, tooth-like process; marginal brush lacking, possibly rubbed off; aboral surface with proximal and distal fairly long setae. Maxillary lacinia (fig. 12) about half as large as galea, both lobes with long, curved marginal setae and well-developed straight setae on aboral surfaces; no lacinial spine; maxillary palpus with three articles; proximal article and distal end of stipes each with five long setae.

Prodorsal, hook-shaped asperities present, arranged at least in two rows (fig. 13), and a group of several lateral asperities distinguishable on skin of ninth abdominal segment (fig. 14). The exact number of prodorsal asperities on each segment cannot be determined from the single, crumbled cast skin on hand.

Spiracles (figs. 15 and 16) oval, simple, without air tubes.

Legs missing on partly mutilated cast skin.

39. *Catorama nigritulum* Lec.

Plate 36.

Described material labeled:

1) *Catorama nigritulum* Lec., ex dead wood, University Park, Md., 28.II.1943, W. H. Anderson coll., W. S. Fisher det. imago.
2) *Catorama nigritulum* Lec., in wood of *Ulmus americana* L., growing at U. S. National Mus., Washington, D. C., 27.III. 1943, W. H. Anderson coll.
3) *Catorama nigritulum* Lec., ex dead *Wisteria*, Ridgely, Md., 15.IX.1942, W. H. Anderson coll.
4) *Catorama nigritulum* Lec., in dead Elm branch, Washington,

D. C. near U.S.N.M., 28.I.1945, W. H. Anderson coll. and det.

Size of larva: Small (c. 4 mm.).

Head capsule subcircular, without frontal lines, pigmented field behind epistoma (fig. 1) distinct, sagittally about twice as long as epistoma; epistoma (fig. 1) with long, straight, fine setae in anterior margin; cranium covered with short to moderately long setae on entire surface, including pigmented field. Antenna (fig. 1) without articles. Anteclypeus with three to four long, straight, fine setae from small plate at each end of anteclypeal sulcus. Labrum (fig. 1) almost three times as wide as long, anterior margin slightly concave medianly, densely set with fairly long, fine setae; paired marks present. Epipharynx (fig. 2) anteriorly with several short, curved coryphal setae; acanthoparial setae numerous, well developed, somewhat curved; chaetoparial setae on each side in a single, oblique, inwardly convex series of seven to eight, rather short, curved and pointed setae; tormae and labral rods forming Y-shaped, fairly long features; crepidal field velvety pubexcent with a few pores. *Mandible* (fig. 4) with two broad and low apical teeth, subapical part of mandible raised into a low, somewhat arched wall between second apical tooth and arched elevation around marginal brush; marginal brush small, or in most specimens examined, absent; aboral surface of mandible with a series of about seven long proximal setae and three long distal setae. Maxillary lacinia (fig. 5) about half as large as galea, terminally armed with a group of about ten strong, cultriform setae, no spine, ventrally with well-developed, straight setae; maxillary palpus with three articles; proximal article with about six setae ventrally; distal part of stipes similarly armed.

Number of prodorsal asperities on each side of:

Thoracic segment II	none	
„ „ III	3	
Abdominal segment 1	11	partly in two irregular rows
„ „ 2	8	
„ „ 3	6	in one row
„ „ 4	6	
„ „ 5	4	
„ „ 6	3	
„ „ 7	1	
„ „ 8	none	

9th abdominal segment with a lateral patch on each side of about twelve asperities.

10th abdominal segment without asperities.

Spiracles (figs. 6, 7 and 8) pseudo-cribriform with large, oval, slightly irregular peritrema surrounding a flat atrium raised to near level of body-surface; thoracic (fig. 6) and abdominal spiracles (figs. 7 and 8) of about same size.

Leg with pretarsus about one-third as long as tibio-tarsus; proximal membranous part of pretarsus short, armed with two moderately long setae; claw curved and pointed, twice as long as basal part; arolium not present.

40. *Catorama* sp.

Plate 36.

Described material labeled:

1) (*Catorama* sp.)?, in stem of Ivy from residence of Mr. E. M. Funkhausen, Roanoke, Va., 10.IV.1933, W. S. Fisher det. imago.
2) Genus? ex English Ivy stem, Coatesville, Pa., 28.V.1948 S.W. Bromley coll., #48—7933 (one associated adult with sample of work pinned).

Size of larva: Small (c. 4 mm.).

Head capsule widest near middle, suboval, slightly longer than broad, without frontal lines; pigmented field behind epistoma sagittally a little longer than epistoma, heavy, distinctly set off posteriorly, with many moderately long setae in small pits; epistoma (fig. 9) anteriorly with transverse series of, altogether, ten long, fairly straight setae; cranium with a great number of short to moderately long setae. Antenna (fig. 9) without articles. Anteclypeus (fig. 9) lacking setae at each end of anteclypeal sulcus. Labrum about as wide as long, anterior margin semicircular, densely set with fine setae; paired marks not visible. Epipharynx (fig. 10) anteriorly with several short, hook-shaped coryphal seta; acanthoparial setae numerous, well developed, somewhat curved; chaetoparial setae on each side in a single, irregular row of six; about four small setae scattered behind chaetoparial series of setae; tormae long, straight, strong, somewhat converging, labral rods indistinct; crepidal field velvety

pubescent, without pores. *Mandible* (fig. 12) with two short apical teeth, subapical part forming a low wall with somewhat arched outline between second apical tooth and a small projection near the arched elevation around the marginal brush; marginal brush with several, rather short setae; aborally a proximal series of about five short, fine setae and a small group of about four short distal setae. Maxillary lacinia (fig. 13) less than half as large as galea, terminally armed with approximately ten stiff, straight, strong setae, but no spine; galea of normal build and size with marginal setae strong and spatulate, adoral surface (fig. 13) with a group of very fine, long setae distally; maxillary palpus with three articles; proximal article with about five long setae on aboral surface; distal part of stipes with about seven long setae ventrally.

Number of prodorsal asperities on each side of:

Thoracic segment II	none	
„ „ III	17	
Abdominal segment 1	16	
„ „ 2	17	in single, or partly double irregular rows
„ „ 3	15	
„ „ 4	15	
„ „ 5	16	
„ „ 6	17	
„ „ 7	12	
„ „ 8	none	

9th abdominal segment with a lateral patch on each side of about 16 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 14 and 15) simple, circular without air tubes; diameter of thoracic (fig. 14) peritrema one and one-half times as long as diameter of peritrema of an abdominal spiracle (fig. 15).

Leg (fig. 11) with pretarsus only a little more than one-third the length of tibio-tarsus; proximal part of pretarsus short, armed with two moderately long setae; claw small, slender, somewhat curved, pointed, about as long as proximal part; arolium well developed.

41. *Catorama punctatum* Lec.

Plate 37.

Described material labeled:

1) *Catorama punctatum* Lec., in grape vine, New Jersey (box 9, 188).

Size of larva: Moderately large (c. 6 mm.).

Head capsule suboval, widest near middle, somewhat longer than broad, without frontal lines; pigmented field behind epistoma (fig. 1) present but with posterior margin indistinct, sagittally about as long as epistoma, densely set with long, straight setae; epistoma (fig. 1) anteriorly with transverse series of, altogether, twelve long, straight setae; in the middle with one long seta on each side; cranium with a great number of short to long setae. Antenna (fig. 1) without articles, ventrally protected by a thin casing. Anteclypeus (fig. 1) with five long seta attached at each end of anteclypeal sulcus, not borne by a distinct little plate. Labrum (fig. 1) subrectangular with rounded anterior corners, slightly concave medially, many fine setae on surface; paired marks indistinct. Epipharynx (fig. 2) anteriorly with several straight, moderately long setae and two pair of very short coryphal setae; acanthoparial setae numerous, well developed, somewhat curved; chaetoparial setae six on each side, in an oblique, single series extending from anterior border to near the sagittal line posteriorly, slender, somewhat curved and pointed; tormae straight, labral rods reduced, united Y-shaped features barely indicated; crepidal field velvety pubescent, without pores. *Mandible* (fig. 3) with two short apical teeth, subapical part of mandible forming a low wall with fairly straight, slightly convex margin extending from near the top of second apical tooth to an obtuse projection near the elevation around the place where marginal brush usually occurs; marginal brush not found in specimens studied, aborally with a proximal series of about six setae and a distal group of three long setae. Maxillary lacinia (fig. 4) somewhat less than half as large as galea; terminally armed with about seven stiff, strong and long setae; no spine; maxillary palpus with three articles.

Number of prodorsal asperities on each side of:

Thoracic segment II	none	
„ „ III	23	
Abdominal segment 1	24	in two somewhat irregular rows
„ „ 2	23	
„ „ 3	19	
„ „ 4	17	
„ „ 5	17	
„ „ 6	11	
„ „ 7	none	
„ „ 8	none	

9th abdominal segment with a lateral patch on each side of about 30 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 6, 7 and 8) circular without air tubes; diameter of thoracic spiracle (fig. 6) one and one-half times as long as the diameter of an abdominal spiracle (figs. 7 and 8).

Leg (fig. 5) with pretarsus about one-third the length of tibiotarsus; proximal part of pretarsus short, armed with two moderately long setae; claw three times as long as proximal part, somewhat curved, slender, narrow at base and pointed; arolium distinct, about half as long as claw.

42. *Catorama* sp. (near *C. conjunctum* Fall).

Plate 37.

Described material labeled:

1) *Catorama* sp. (near *C. conjunctum* Fall); in gall in stem of white sage (*Artemisia ludoviciana*), Calexico, Calif., 15.XII. 1944, (—455028) C. G. Anderson coll., W. S. Fisher det. imago.

Size of larva: Moderately large (c. 6 mm.).

Head capsule subcircular, without frontal lines; pigmented field behind epistoma (fig. 9) somewhat longer sagittally than epistoma, indistinctly limited posteriorly and lightly colored, bearing many long setae; epistoma (fig. 9) anteriorly with transverse marginal series of long, fine, straight setae, totaling twelve; behind the series with several long setae scattered over the surface; rest of cranium with numerous moderately long to long setae. Antenna (fig. 9) without articles. Anteclypeus with six long,

straight setae borne by a small plate at each end of anteclypeal sulcus (fig. 9). Labrum (fig. 9) subrectangular with largely rounded corners; most of exposed part of surface covered with long, fine, curved and straight setae; paired marks visible but faint. Epipharynx (fig. 10) with two pairs of small coryphal setae anteriorly; acanthoparial setae numerous, well developed, somewhat curved; chaetoparial setae small and hook-shaped, on each side six in a single regular, oblique, inwardly convex series; tormae solid, simple, rather short and somewhat thorn-shaped; no epipharyngeal rods; crepidal field velvety pubescent with a few pores. *Mandible* (fig. 12) with short, distinct first apical tooth, second apical tooth almost fused with subapical part of mandible into a quite low, straight wall ending abruptly near the marginal arched elevation; marginal brush itself lacking, replaced by rugose surface; aborally with a proximal patch of several long, fine setae and a small distal group of about four moderately long setae. Maxillary lacinia (fig. 13) about half as large as galea, terminally armed with approximately ten stiff setae similar to the strong marginal setae of galea, but no spine; adorally from bases of lacinia and galea a group of very long and fine hairs present; maxillary palpus with three articles; proximal article with about five long and a few short setae; distal part of stipes with about seven long setae.

Number of prodorsal asperities (fig. 11) *on each side of:*

Thoracic segment	II	none	
„	III	2 (1)	
Abdominal segment	1	5	
„	2	5	in single regular row
„	3	6	
„	4	4	
„	5	3	
„	6	1	
„	7	none	
„	8	none	

9th abdominal segment with a lateral patch on each side of about 8 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 14, 15 and 16) small, circular, with an air tube generally somewhat shorter than the spiracular diameter; thoracic

spiracle (fig. 14) twice to three times as large as an abdominal spiracle (figs. 15 and 16).

Leg (fig. 17) with pretarsus about one-third the length of tibio-tarsus; proximal membranous part of pretarsus very short, armed with two setae of moderate size; claw quite strong, hook-shaped and about three times as long as proximal part; arolium present, extending to middle of claw.

43. *Catorama* sp. (probably *C. herbarium* Gorham) (= *C. mexicanum* Chev.—teste W. S. Fisher).

Plate 38.

Described material labeled:

1) *Catorama* sp., in seed husk of the palm *Livistona chinensis*, Key West, Florida, 11.IV.1945, O. D. Link coll., Spec. Surv. #24862, 45—8746, W. H. Anderson det., July 1945.
2) *Catorama* sp. (probably herbarium Gorh.) in partially decayed fruits of pear, El Paso, Texas, 28.VIII.1943, A.G.B., det.

Size of larva: Small (c. 4 mm.).

Head capsule widest near the middle, subcircular, posteriorly slightly oval, without frontal lines; pigmented field behind epistoma (fig. 1) sagittally somewhat longer than epistoma, indistinctly limited posteriorly, rather thinly pigmented and with many short to long setae; epistoma (fig. 1) anteriorly with transverse marginal series of long, fine, straight setae totaling about twelve, no setae behind them; rest of cranium with numerous moderately long to long setae. Antenna (fig. 1) without distinct articles; sensory appendage and projections borne by membranous dome-shaped base. Anteclypeus (fig. 1) with six long, straight setae borne by a small plate at each end of anteclypeal sulcus. Labrum (fig. 1) subrectangular with large rounded corners, most of exposed part of surface covered with long, fine, curved setae and shorter, more straight ones; paired marks not visible. Epipharynx (fig. 2) with short, coryphal setae anteriorly; acanthoparial setae numerous, strong, curved, in irregular, in places double, rows; chaetoparial setae short, hook-shaped, on each side in an oblique inwardly curved, regular row of six or seven; tormae moderately long and straight, no distinct labral

rods; crepidal field velvety pubescent with four anterior and two posterior pores. *Mandible* (fig. 4) with short, distinct first apical tooth, second apical tooth fused with subapical part of mandible into a quite low, straight wall with thin edge and ending with a toothlike projection near the arched marginal elevation; marginal brush lacking, replaced by small granules and wrinkles; aborally with a large proximal patch of long, fine setae and a small distal group of about four long setae. Maxillary lacinia (fig. 5) about half as large as galea, terminally armed with approximately ten stiff setae similar to the strong marginal setae of galea, but no spine; adorally (fig. 5) with weaker setae and, present at bases of both lacinia and galea, a bunch of very long, fine hairs; maxillary palpus with three articles; proximal article with five setae; distal part of stipes with about same number of long setae.

Number of prodorsal asperities (fig. 3) *on each side of:*

Thoracic segment	II	none	
„	III	7	
Abdominal segment	1	16	in two irregular rows
„	3	16	
„	3	14	
„	4	12	
„	5	10	in one irregular row
„	6	7	
„	7	3	
„	8	none	

9th abdominal segment with a lateral patch on each side of about 30 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 7, 8 and 9) small, circular with a single air tube; air tube of thoracic spiracle (fig. 7) a little shorter than diameter of peritreme, those of abdominal spiracles (figs. 8 and 9) almost twice as long as diameter of their peritremes; thoracic spiracle about three times as large as an abdominal spiracle (fig. 6).

Leg (fig. 6) with pretarsus about one-third the length of tibiotarsus; proximal membranous part of pretarsus very short, armed with two setae of moderate sizes; claw quite strong, hook-shaped and about three times as long as proximal part; arolium present, extending to middle of claw.

44. *Catorama* sp. (probably *C. inaequale* Fall).

Plate 38.

Described materal labeled:

1) *Catorama* sp. (probably *C. inaequale* Fall), imago det. by W. S. Fisher; in ebony bean; Mexico, 26.XII.1937, Brv., Tx., # 20779.
2) *Catorama* sp. (*C. inaequale* Fall?), in garlic bulb, Mexico, Brv., Tx., # 5463, c.
3) *Catorama* sp., in pod *Acacia farnesiana*, Brownsville, Tex., 21.IV.1945, Harrison and Fraser collrs., Spec. Surv. # 25407, 45—8944.

Size of larva: Small (c. 4 mm.).

Head capsule widest near the middle, subcircular, posteriorly slightly oval, without frontal lines, pigmented field behind epistoma (fig. 10) sagitally at least three times longer than epistoma, strongly pigmented, with many moderately long to long setae evenly distributed over the entire surface; epistoma (fig. 10) anteriorly with transverse marginal series totaling twelve long, fine, straight setae; catapophysis rugose, bearing long setae, mostly at base behind antenna; rest of cranium with numerous, moderately long to long setae. Antenna without articles. Anteclypeus (fig. 10) with about ten long setae attached to a small sclerite at each end of anteclypeal sulcus. Labrum (fig. 10) subrectangular with largely rounded corners and slightly concave anterior margin; most of exposed part of surface covered with setae; paired marks visible but faint. Epipharynx (fig. 11) with two pairs of small coryphal setae anteriorly; acanthoparial setae well developed, slender and curved; chaetoparial setae hook-shaped, in an oblique, inwardly convex, somewhat irregular, single row of about ten setae; tormae quite short, well sclerotized, forming indistinct V or Y-shaped features with weak labral rods; crepidal field velvety pubescent, anteriorly with a somewhat irregular transverse series of four pores and posteriorly two pores. *Mandible* (fig. 13) with distinct first apical tooth, second apical tooth almost fused with subapical part of mandible into a quite low, straight, thinly edged wall ending with a toothlike process at the arched marginal elevation; marginal brush lacking, replaced by a rugose, somewhat striate surface; aborally with a proximal patch of several long setae and a small distal group of

four long, fine setae. Maxillary lacinia (fig. 14) about half as large as galea, terminally armed with about ten stiff setae, adorally (fig. 14) with fairly short, soft setae similar to those on galea, and from bases of both lacinia and galea with many very long and fine hairs; maxillary palpus with three articles; proximal article aborally with about ten long setae; distal part of stipes with about ten long setae.

Number of prodorsal asperities (fig. 12) *on each side of:*

Thoracic segment II	none	
„ „ III	11	
Abdominal segment 1	20	in two irregular rows
„ „ 2	21	
„ „ 3	18	
„ „ 4	16	
„ „ 5	12	
„ „ 6	10	
„ „ 7	3	
„ „ 8	none	

9th abdominal segment on each side with a lateral patch of about 25 asperities.

10th abdominal segment without asperities.

Spiracles (figs. 16, 17 and 18) small, almost circular; thoracic spiracle (fig. 16) with a single short, rather broad air tube, abdominal spiracles (figs. 17 and 18) each with a single air tube about as long as diameter of peritrema.

Leg (fig. 15) with pretarsus about one-third the length of tibio-tarsus, proximal membranous part of pretarsus short, armed with two setae of moderate size; claw quite strong, hook-shaped and twice as long as proximal part; arolium present extending to middle of claw.

45. *Catorama tabaci* Guér.
(= *C. impressifrons* Fall, teste W. S. Fisher).

and

46. *Catorama grande* Fall.

Plate 39.

Described material labeled:

1) *Catorama tabaci* Guér. (= *C. impressifrons* Fall), imago det. by W. S. Fisher, in garlic bulbs, Mexico, Brv., Tex., 14.XI.1942, 42·14614.

2) *Catorama* sp. (near *tabaci*), on lettuce in baggage, Mexico, Brv., Tex., 6.VI.1938, #25052.

3) *Catorama tabac* Guér., in Poinciana seed, West Indies; New York #39968, 2.IV.1935.

4) *Catorama tabaci* Guér., in tobacco received at Key West, Fla., 16.XI.1912 by Ruy Lopez, probably from Cuba, H. S. Barber det.

5) *Catorama grande* Fall, in flower stalk of *Yucca*, Langtry, Texas, 5.XI.1936, W. H. Anderson coll.

Size of larva: Moderately large (c. 7 to 10 mm.).

Head capsule (fig. 1) widest near the middle, subcircular, posteriorly slightly ovate, without frontal lines, pigmented field behind epistoma (fig. 1) sagittally about three times longer than epistoma, strongly pigmented, with many moderately long to long setae; epistoma (fig. 1) anteriorly with transverse marginal series totaling twelve or more, long, fine, straight setae; catapophysis rugose with long setae at base behind antenna; rest of cranium with numerous moderately long to long setae. Antenna (fig. 1) without articles. Anteclypeus (fig. 1) with about ten long setae attached to a small sclerite at each end of anteclypeal sulcus. Labrum (fig. 1) subrectangular with largely rounded corners and slightly concave anterior margin, most of exposed part of surface covered with setae; paired marks present but not distinct. Epipharynx (fig. 2) with comparatively long, hooklike coryphal setae anteriorly; acanthoparial setae rather long, slender and curved; chaetoparial setae in an oblique, inwardly convex, fairly regular single row of from eight to ten moderately long, pointed and curved setae; tormae rather short, well sclerotized, forming indistinctly Y-shaped features with weak labral rods; crepidal field velvety pubescent with four irregularly arranged pores in an anterior transverse series and two pores posteriorly. *Mandible* (fig. 3) with distinct first apical tooth, second apical tooth almost fused with subapical part of mandible into a rather low, straight, thin-edged wall which ends abruptly at the arched marginal elevation; marginal brush lacking, replaced by a rugose, somewhat striate surface; aborally with a proximal patch of several long setae and a small distal group of four long, fine setae. Maxillary lacinia (fig. 4) about half as large as galea; terminally armed with ten stiff, strong setae, about as long as lobe, and adorally

from bases of both lacinia and galea with many very fine and long hairs besides fairly short, soft setae on the whole surface; maxillary palpus with three articles; proximal article with about ten long setae ventrally (fig. 4); distal part of stipes also with ten similar, long setae.

Number of prodorsal asperities on each side of:

	tabaci	grande	
Thoracic segment II	none	none	
„ „ III	16	16	
Abdominal segment 1	30	28	in two
„ „ 2	25	25	to three
„ „ 3	20	26	irregular
„ „ 4	20	22	rows
„ „ 5	10	10	
„ „ 6	10	10	
„ „ 7	8	6	
„ „ 8	4	4	

9th abdominal segment on each side with a lateral patch of from 40 (*tabaci*) to 45 (*grande*) asperities.

10th abdominal segment without asperities.

Spiracles (figs. 7, 8 and 9) circular to broadly oval; thoracic (figs. 7 and 9) with one short but distinct air tube and an additional indication of a second; abdominal spiracles (fig. 8) each with an air tube about half as long as diameter of peritrema.

Leg (fig. 6) with pretarsus about one-third the length of tibiotarsus; proximal membranous part of pretarsus short, armed with two setae, one long, the other of moderate size; claw quite strong, hook-shaped and more than twice as long as proximal part; arolium present.

Note concerning the description of *Catorama tabaci* Guér, *Catorama grande* Fall and *Catorama inaequale* Fall.

The larvae of *Catorama tabaci* Guér. and *Catorama grande* Fall, determined according to reared imagines, are identical in all their specific characters, and in general the larvae of *Catorama tabaci* (**Catorama grande*) and *Catorama inaequale* Fall are very similar, but typical larval specimens of the two species can, nevertheless, be separated, especially, by the different average number of asperities on the prodorsal areas (Pl. 38, fig. 12; Pl. 39, fig. 5). However, a number of other larvae have been collected which form a gradual transition between the two species. Among these intermediate larval forms the most significant are some intercepted from Mexico in bulbs of garlic and, according to their

reared imagines, determined by Mr. W. S. Fisher as *Catorama* sp., near *Catorama tabaci* Guér. Generally considered, the whole group of these gradually modified larval forms seems to belong to a single, very unstable species with several subspecies and varieties.

47. *Gastrallus* sp., probably *G. laevigatus* Oliv.

Plate 40.

Described material labeled:

1) *Gastrallus* sp., probably *G. laevigatus* Oliv., (imago det. by W. S. Fisher) in seeds of *Callistemon lanceolatum* (related to *Eucalyptus*), from France; U. S. Seed house, 2.XII.1929.
2) *Gastrallus* sp., probably *G. laevigatus* Oliv., in thin clear cocoons in burlap around bales of stockfish from Norway; Dr. Don C. Mote coll., 9.XI.1932, Portland, Oregon Ent. Dept.
3) *Gastrallus* sp., in beans from Twin Falls, Idaho, W. H. White coll., 30.III.1944.
4) *Gastrallus* sp., in wall of house lined with fir lumber covered with heavy paper; Snohomish, State of Washington.
5) *Gastrallus* sp., "internal worms" passed from time to time, sent in by Dr. E. H. Strickland, Edmonton, Alberta, Canada, 4.I.1939.

Size of larva: Small (3 to 4 mm.).

Head capsule subcircular, slightly broader than long, widest in the middle, without frontal lines; pigmented field behind epistoma (fig. 1) large, more than three times as long as sagittal length of epistoma, anteriorly rather light colored and set with few setae, rest of field well furnished with long and moderately long setae; epistoma (fig. 1) on each side of sagittal line with an oblique series of eight fine, straight and fairly long setae; cranium with quite a limited number of setae. Antenna (fig. 1) without articles. Anteclypeus (fig. 1) with a group of about five fine, fairly long setae on plate at each end of anteclypeal sulcus. Labrum (fig. 1) with semicircular free margin, with numerous setae and with indistinct or no paired marks, medio-posteriorly with three pores. Epipharynx (fig. 2) anteriorly with several short, hook-shaped coryphal setae; acanthoparial setae long, curved and slender; chaetoparial setae on each side in an oblique arched series of six robust, rather short and some-

what curved setae, a few minute additional setae scattered irregularly immediately behind them; tormae strong, straight, subparallel, combined with labral rods to form well-sclerotized, Y-shaped features; crepidal field velvety pubescent with fine, very pointed, small setae varying in number from two to five in different specimens. *Mandible* (figs. 3 and 5) with only a single apical tooth, second apical tooth obliterated; subapical part forming a strong wall with a generally straight, slightly convex, and a little serrated edge; wall terminating with a sharp, toothlike projection near a weak, indistinct, arched marginal elevation; marginal brush lacking; aboral surface of mandible (fig. 3) with a large proximal group of about twelve long, strong setae and a distal group of about ten similar setae. Maxillary lacinia (fig. 4) small, carrying distally a well-sclerotized, somewhat gouged, strong spine as long as the lobe, also two long, stiff setae and a few additional short, fine setae; galea only half as wide as long; maxillary palpus with three articles; proximal article ventrally with about five long setae; distal part of stipes with about seven long setae.

Body trunk covered with long, soft, hairlike setae; asperities lacking completely.

Spiracles (figs. 7 and 8) circular with a single air tube; air tube of thoracic spiracle (fig. 7) shorter than diameter of peritrema, air tube of each abdominal spiracle (fig. 8) about as long as the peritremal diameter.

Leg (fig. 6) with pretarsus about one-third the length of tibiotarsus; proximal membranous part of pretarsus short, furnished with two fine, moderately long setae; claw well developed, curved, pointed and slender; arolium present, extending to near the middle of claw.

48. *Catorama vestitum* Fall.

Plate 41.

Described material labeled:

1) *Catorama vestitum* Fall (Imago in coll., det. by W. S. F.), in pith of dried Okra-Stalks, Calexico, Calif., 14.IV.1945, C. G. Anderson coll. (Spec. Surv. # 26594).
2) *Catorama* sp., near *vestitum* Fall (W. H. A. det. July 1945)

in grass stem, Blythe, Calif., 23.III.1945, C. G. Anderson and Hanson collrs. (Spec. Surv. # 24647).

Size of larva: Moderately large (c. 6 mm.).

Head capsule (fig. 6) about as broad as long, subcircular, without frontal lines; pigmented field behind epistoma (fig. 1) distinct, sagittally about as long as epistoma, bearing several long setae; epistoma (fig. 1) with transverse anterior series of, altogether, sixteen fairly long, fine, straight setae; cranium covered with densely set, long and moderately long setae. Antenna (fig. 1) without distinct articles. Anteclypeus (fig. 1) with five long, fine, straight setae from small plate at each end of anteclypeal sulcus. Labrum (fig. 1) almost three times as wide as long, anterior margin convex, surface densely set with setae; paired marks absent. Epipharynx (fig. 2) anteriorly with several short, curved coryphal setae; acanthoparial setae slender, long, more or less curved; chaetoparial setae on each side in a single, oblique, inwardly convex series of eight rather short, curved and pointed setae; tormae and labral rods forming rather long, Y-shaped features; crepidal field velvety pubescent, without pores. *Mandible* (fig. 3) with two sharp apical teeth; subapical part of mandible forming a slightly concave wall with thin edge impressed by numerous parallel, transverse, very fine lines and terminatino with a sharp toothlike process near arched marginal elevation; marginal brush absent; mandibular surface between dorsal articulation and marginal elevation granulate; aboral proximal setae numerous and long; distal setae, numbering about four, also long. Maxillary lacinia (fig. 4) less than half as large as galea, terminally with about ten densely set, long, stiff setae; also with smaller, but well developed, stiff setae on ventral surface and softer on dorsal surface; maxillary palpus with three articles; proximal article with about eight long setae ventrally; distal part of stipes similarly armed with about ten setae.

Body-trunk (fig. 6) elongate, not strongly curved, all areas set with many moderately long, fine setae; epipleural areas, in particular (fig. 5), provided with numerous very long ones; asperities lacking completely.

Spiracles (figs. 7, 8 and 9) simple, annular, each with a single, short air tube; thoracic spiracle (fig. 7) oval with peritrema not

fully twice as long as peritrema of an abdominal spiracle (figs. 8 and 9).

Leg (fig. 10) with pretarsus less than one-third as long as tibio-tarsus; proximal membranous part of pretarsus short, furnished with two moderately long setae; claw well developed, strongly curved and pointed; arolium present, extending to the middle of claw.

49. *Ozognathus cornutus* Lec.

Plate 42.

Described material labeled:

1) *Ozognathus cornutus* Lec., Imagines reared from dried terminal growth and flowers of Avocado and identified by Arnett, Los Angeles, Calif., Febr. 1950. Roy J. PENCE coll.
2) *Ozognathus* sp., in bark of pine lumber, Durango, Mexico, Brownsv., Tex. coll. 42—335, 29.X.1942.
3) *Ozognathus cornutus* Lec., Los Angeles, Calif., D. W. COQUILLETT coll.

Size of larva: Small (c. 3 mm.).

Head capsule about as broad as long, subcircular, without frontal lines; pigmented field behind epistoma (fig. 1) distinct, sagittally slightly longer than epistoma, bearing a few, long setae; epistoma (fig. 1) with transverse anterior series of, altogether, eight fairly long, fine, straight setae; cranium with moderately dense, long and short setae. Antenna (fig. 1) without distinct articles. Anteclypeus without plate, and no setae at each end of anteclypeal sulcus. Labrum (fig. 1) about twice as wide as long, anterior margin convex, labral surface bearing comparatively few (on each side less than ten) long and short setae; paired marks absent. Epipharynx (fig. 4) anteriorly with several short, curved coryphal setae; acanthoparial setae slender, long, more or less curved; chaetoparial setae on each side in a single, oblique, inwardly convex series of six rather short, curved and pointed setae, a pair of minute setae between the bases of tormae; tormae well developed and pigmented; labral rods weak, joining tormae to form incomplete Y-shaped features; crepidal field velvety pubescent, without pores. *Mandible* (fig. 5) with two sharp apical

teeth; subapical part forming a slightly concave wall with a thin, transversally striate edge and terminating with a sharp, tooth-like process near arched marginal elevation; marginal brush present, surrounded by the elevation; mandibular surface between dorsal articulation and marginal elevation smooth; aboral proximal setae numerous and long, distal setae, numbering four, also long. Maxillary lacinia (fig. 2) less than half as large as galea, terminally with about ten, densely set, long, stiff setae, also with smaller setae on rest of both dorsal and ventral surfaces; at base both lacinia and galea furnished dorsally with very soft, curly hairs (fig. 2). Maxillary palpus with three articles, proximal article with about eight long setae on ventral surface; distal part of stipes similarly armed.

Body-trunk (fig. 3) thick, short and curved, body areas sparsely furnished with setae, epipleural areas (fig. 10) with only five or less setae; asperities lacking completely.

Spiracles (figs. 6, 7 and 8) simple, annular, with a single, minute air tube each; abdominal spiracle (figs. 7 and 8) remarkably small; thoracic spiracle three times larger than an abdominal.

Leg (fig. 9) with pretarsus less than one-third as long as tibiotarsus; proximal membranous part of pretarsus short, furnished with two setae, one short the other moderately long; claw well developed, curved and pointed; arolium present, extending to the middle of claw.

50. *Petalium seriatum* Fall.

Plate 42.

Described material labeled:

1) *Petalium seriatum* Fall, in *Juglans*, Virginia, Hopk. U. S. # 10084 1 (reared imago in coll.).
2) *Petalium seriatum* Fall, ex small dead branch, College Park, Md., 28.II.1942, W. H. Anderson coll.
3) *Petalium seriatum* Fall, Hopk. U. S. # 12605 x.

Size of larva: Small (c. 4 mm.).

Head capsule slightly longer than broad, broadest before the middle, sides convergent behind the middle; head slightly retracted (fig. 16), without frontal lines; pigmented field behind epistoma lacking or very feeble; epistoma (fig. 11) on each side

with a marginal series of four fine, straight and moderately long setae; cranium immediately behind epistoma with a single transverse series of about six moderately long setae on each side, rest of cranial surface anteriorly quite sparsely provided with scattered, fairly long setae, and posteriorly without setae (fig. 16). Antenna (fig. 11) without articles. Anteclypeus (fig. 11) with two long, fine, straight setae at each end of anteclypeal sulcus, but not borne by any plate. Labrum (fig. 11) with semicircular, free margin and set all over the surface with setae; no paired marks. Epipharynx (fig. 12) with several very short coryphal setae medioanteriorly; acanthoparial setae few, long, curved and slender; chaetoparial setae, numbering six on each side, moderately strong, slightly curved, and arranged in an oblique row; tormae straight, conical, slender, moderately long and convergent; labral rods absent; crepidal field without pores. *Mandible* (figs. 14 and 15) with two apical teeth; subapical part of mandible forming a rather high, subtriangular wall terminating above the arched elevation around the marginal brush and having a thin, convex, small, projecting enlargement anteriorly; marginal brush well developed; aboral mandibular surface with a few, long proximal and distal setae. Maxillary lacinia (fig. 17) much reduced in size, not fully as long as distal article of maxillary palpus, armed with a single, fairly long, slightly pigmented spinelike seta and bearing in addition a few, fine, ordinary setae; galea of normal size, armed marginally with a row of about seven, slender, curved and sharply pointed setae, ventral surface with a few, long and small setae; maxillary palpus with three articles, proximal article ventrally with three setae; distal part of stipes with about five setae.

Body-trunk (fig. 16) elongate, cylindrical and almost straight, covered with quite a limited number of moderately long to long, fine, soft setae; asperities lacking completely.

Spiracles (fig. 18) pseudocribriform.

Leg (fig. 13) with short pretarsus, only about one-third as long as tibio-tarsus, proximal membranous part very short, armed with two small setae; claw rather narrow and curved; arolium present extending to near the middle of claw.

51. *Unknown genus possibly near Lasioderma.*

Plate 43.

Described material labeled:

1) Unknown genus, possibly near *Lasioderma*, single specimen with Orchid plants (A. G. B. det.), Mexico, intercepted at Brownsville, Texas, 4.IX.1946, (46·15196).

Size of larva: Small (c. 4 mm.).

Head capsule (fig. 6) subcircular, with distinct frontal lines, thickly sclerotized, uniformly dark all over; surface of cranium, epistoma included, set with regularly arranged long setae, each seta in a round, comparatively large pit; epistoma (fig. 6) indistinctly limited posteriorly, with anterior margin scalloped, provided with a transverse series of, altogether, about fourteen long, stiff setae. Antenna (fig. 6) without articles. Anteclypeus with a narrow, weakly sclerotized band adjacent to the anteclypeal sulcus, bearing two setae at each end. Labrum (fig. 6) subrectangular, about two and one-half times broader than long, sparsely set with short setae; paired marks apparently lacking. Epipharynx (fig. 2) anteriorly with some small, curved, obtuse coryphal setae; acanthoparial setae, about six on each side, inserted in anterior epipharyngeal margin, lacking laterally; chaetoparial setae on each side in a single, arched and oblique series of six setae, the three anterior of them slender, curved and pointed, the three posterior short, robust, curved, more or less fan-shaped; tormae moderately long, awl-shaped, rather straight and pointed, posteriorly convergent; no distinct labral rods. *Mandible* (figs. 1 and 3) with two apical teeth; subapical part of mandible forming a low, slightly concave, and comparatively short wall with serrated edge and terminating at a strong, long, convex marginal thickening; no marginal brush; abdoral mandibular surface (fig. 3) with a proximal transverse series of six long setae and a distal small group of four long setae. Maxillary lacinia (fig. 9) somewhat less than half as large as galea, distally with a number (about five) moderately long and strong setae, no spine; maxillary palpus with three articles; proximal article ventrally (fig. 9) with about six setae; distal part of stipes with same number of well-developed setae.

Body-trunk robust and curved, densely covered with long, fine setae, asperities lacking completely.

Spiracles (figs. 4, 5, 7 and 8) pseudocribriform with a comparatively small, ill-defined cribrate field; thoracic spiracular peritrema (fig. 4) about two and a half times as long as abdominal peritremata (figs. 5, 7 and 8).

Leg (fig. 10) with pretarsus about one-third as long as tibiotarsus; proximal membranous part short, only half as long as wide, armed with two short setae; claw weak, slender, curved and sharp; arolium well-developed, extending beyond tip of claw.

52. *Lasioderma serricorne* F.

Plate 43.

Described material labeled:

1) *Lasioderma serricorne* F., from tobacco, Harpers Ferry, West Va., 8.II.1914, F. C. Craighead coll.
2) *Lasioderma serricorne* F., in dried Chamomile flowers, Italy. 11.VIII.1939, N.York # 82493.

Size of larva: Moderately large (c. 6 mm.).

Head capsule (fig. 19) subcircular, without frontal lines, but on each side with a light-colored band limiting a dark clypeofrontal field; each parietal light with one dark spot parallel with epicranial sulcus and a similar dark spot in the middle of the parietal wall; epistoma (fig. 19) with a transverse anterior series of, altogether, about sixteen fine, straight and moderately long setae; some setae present on each catapophysis; cranium behind epistoma with densely set, long and short, soft setae all over, each seta placed in a minute pit. Antenna (fig. 13) without articles. Anteclypeus without setae and without a small sclerite at each end of anteclypeal sulcus. Labrum (fig. 19) subrectangular with broadly rounded corners, about twice as broad as long, densely set with setae; paired marks indicated, but small and indistinct. Epipharynx (fig. 11) anteriorly with some small, straight coryphal setae; acanthoparial setae long, curved and slender; chaetoparial setae on each side six, the two anterior rather slender and moderately long, the four posterior short, robust and curved, together forming an oblique, arched, single series; tormae short and

strong; labral rods and tormae united posteriorly into V-shaped features; crepidal field without pores. *Mandible* (figs. 12 and 14) with two, rather short apical teeth, subapical part of mandible forming a wall with serrated, almost straight edge terminating with a toothlike projection above the marginal arched elevation around a distinct but small brush; aboral mandibular surface (fig. 14) with a proximal group of seven long, curved setae and a bunch of four, rather long distal setae. Maxillary lacinia (fig. 15) somewhat less than half as large as galea, distally with a number (about five) of moderately long and stiff setae and laterally a small number of smaller, similar setae; no spine; maxillary palpus with three articles, proximal article ventrally with about six setae, distal part of stipes with the same number of well-developed setae.

Body-trunk quite robust and strongly curved, densely covered with long, fine, mostly curved setae; asperities lacking completely.

Spiracles (figs. 18, 20 and 21) pseudocribriform with comparatively narrow cribrate field.

Leg (fig. 17) with pretarsus about one-third as long as tibiotarsus; proximal membranous part short, armed with two moderately long setae; claw curved and sharp; arolium present, extending somewhat beyond the middle of the claw.

53. *Lasioderma* sp.

Plate 43.

Described larva labeled:

Lasioderma sp., in *Eragrostis curvula* seeds, coll. D. C., 27.VI. 1939, 39—11866 (Single larva, not reared).

Head capsule (fig. 16 (*L.* sp.)) subcircular with faint indication of incomplete frontal lines, uniformly colored light brownish; epistoma (fig. 16) with a transverse anterior series of, altogether, about twelve fine, straight, moderately long setae, about seven long setae on each catapophysis; cranium behind epistoma densely set with from short to long setae. Anteclypeus (fig. 16) with a minute sclerite bearing two long setae at each end of anteclypeal sulcus. Epipharynx (fig. 22) anteriorly with several minute coryphal setae; acanthoparial setae long and curved;

chaetoparial setae on each side about twelve, fairly short, curved and pointed, arranged in an oblique, arched, irregular double series; tormae and labral rods forming rather strong Y-shaped features. Other characters as in *Lasioderma serricorne* F.

54. *Cryptorama minutum* Lec.

Plate 44.

Described material labeled:

1) *Cryptorama minutum* Lec. (imago det. by W. S. Fisher), in dry mesquite wood, Mexico, intercepted Brownsville, Texas, 14.X.1939, (39·16766).
2) *Cryptorama minutum* Lec. (10 larvae); in mesquite twigs, local, Brownsville, Tex., 14.III.1944, G. F. Callaghan coll. (44—12042).

Size of larva: Small (c. 4 mm.).

Head capsule (fig. 2) about twice as long as broad, sides nearly straight before and convergent behind the middle, partly retracted, without frontal lines; pigmented field behind epistoma (fig. 1) well developed, sagittally about twice as long as epistoma, armed at posterior end of field with a single, conical projection and bearing an irregular series of long setae along the hind margin; epistoma (fig. 1) with a transverse anterior series of, altogether, ten long, strong setae; non-pigmented part of head capsule in front of anterior end of epicranial sulcus (fig. 2) provided with several, very short to long setae, scattered irregularly over the surface; behind anterior end of sulcus without setae. Antenna (fig. 1) without articles. Anteclypeus (fig. 1) thin walled, apparently without setae-bearing plate and without setae. Labrum (figs. 1 and 2) semicircular, densely set with setae; paired marks indicated but insignificant. Epipharynx (fig. 3) anteriorly with a group of small, stubby coryphal setae; acanthoparial setae long, curved and slender; chaetoparial setae on each side six, short and somewhat fan-shaped, in a regular, single, oblique series; tormae slender, straight, somewhat convergent; no distinct labral rods; crepidal field without pores. *Mandible* (fig. 4) ending distally with three teeth, namely: apically two teeth and subapically a toothlike large projection at the end of a very short wall above large, elongate, marginal arched elevation; small marginal

brush present; aboral mandibular surface with a few long proximal setae and about three similar distal setae. Maxillary lacinia (figs. 5 and 6) about one-third the size of galea, distally with about ten closely set, long and stiff setae, no spine; dorsally and ventrally with minor setae; maxillary palpus with two distinct articles, the subapical article absent, represented only by a single seta on a minute wartlike projection at base of distal article; proximal article ventrally with about four long and a few smaller setae; distal part of stipes with about the same number of similar setae.

Body-trunk (fig. 10) robust and curved, with thoracic segments much larger than abdominal segments; body setae inconspicuous, except on the epipleural areas, the sternal areas and ninth abdominal segment; asperities lacking.

Spiracles (figs. 7, 7* and 8) pseudocribriform with large cribrate field.

Leg (fig. 9) with pretarsus about half as long as tibio-tarsus; proximal membranous part of pretarsus small, about as long as wide, with two setae; claw slender and somewhat curved; arolium absent.

55. *Unknown genus and species, perhaps Ernobius sp.*

Plate 44.

Described material labeled:

1) Unknown larva, perhaps genus Ernobius, in spruce buds at tip of stem; from Norway, intercepted N.York, 10.VIII.1936 (N.Y. #62610); one specimen; not reared.

Size of larva: Moderately large (c. 7 mm.).

Head capsule (fig. 11) orbicular, no definite, sharp frontal lines but clypeo-frontal region limited by a non-pigmented, narrow, uneven, and oblique stripe on each side; anteriorly confluent, with a likewise non-pigmented, large spot on parietale; rest of cranium pigmented; epistoma (fig. 11) not distinct; entire surface of cranium set with moderately numerous, well-developed setae, each usually as long as labrum and anteclypeus combined. Antenna (fig. 11) with two articles. Anteclypeus (fig. 11) with three long setae at each end of anteclypeal sulcus. Labrum (fig. 11) transverse, somewhat less than twice as broad as long,

outline gently rounded; surface with straight, fine, small setae both anteriorly and on each side; paired marks not visible. Epipharynx (fig. 12) with two pairs of minute coryphal setae; comparatively few, slender and moderately long acanthoparial setae and on each side an oblique, inwardly convex series of four, fairly short, slender, curved and pointed chaetoparial setae; tormae and labral rods forming Y-shaped features; crepidal area with two minute pores. *Mandible* (figs. 13 and 15) with two apical and two subapical teeth; marginal brush present; on aboral surface with four proximal setae and apparently only one distal seta. Maxillary lacinia (fig. 16) rather small, terminally with two strong, pointed, claw-shaped spines, several fine, short and two long, stiff setae behind them; maxillary palpus with three articles; proximal article with three long setae; distal part of stipes with a few more similar setae.

Number of prodorsal asperities (fig. 14) *on each side of:*

Thoracic segment II	none
„ „ III	2
Abdominal segment 1	9
„ „ 2	7
„ „ 3	6
„ „ 4	7
„ „ 5	5
„ „ 6	none
„ „ 7	none
„ „ 8	none

9th abdominal segment with a patch of six lateral asperities on each side.

10th abdominal segment with two asperities on each side.

Spiracles (figs. 18 and 19) circular, each with one air tube; air tube almost as long as diameter of peritrema on the thoracic spiracle (fig. 18), twice as long on the abdominal spiracles (fig. 19).

Leg (fig. 17) with membranous part of pretarsus somewhat longer than broad, carrying two minute setae; no claw; arolium elongate, balloon-shaped, twice as long as membranous part.

56. *Ernobius marginicollis* Lec.

Plate 45.

Described material labeled:

1) San Francisco, Calif., Sand dunes, 10.VII.1934. In rotten dry lupine wood, P. TING coll. & det., confirmed by FISHER (Larva: 10.VII.1934, imagines emerged 24.V.1935, 26.V.1935, 31.V.1935; pupae taken out of remaining wood by P. TING).
2) *Ernobius marginicollis* Lec. (A. G. B. det.), Washington State, 8.XII.1943. In *Ribes sanguineum* stalk. WILBUR coll., Spl. Surv. # 7348.

Size of larva: Moderately large (c. 7 mm.).

Head capsule oval, slightly longer than broad, broadest in the middle, without frontal lines; pigmented field behind epistoma (fig. 1) indistinctly limited posteriorly, sagittally about twice as long as epistoma; epistoma (fig. 1) anteriorly on each side with a transverse row of, altogether, six moderately long setae; cranium with many evenly distributed, mostly fine setae, each as long as labrum and anteclypeus together. Antenna (fig. 1) with two distinct articles. Anteclypeus (fig. 1) with a small sclerite bearing a group of about ten moderately long to long setae at each end of anteclypeal sulcus. Labrum (fig. 1) transverse suboval, approximately twice as wide as long; anterior margin with a series of numerous, densely set, fine, curved setae and on each side behind them with a group of rather short, thin setae; paired marks distinct. Epipharynx (fig. 2) on each side with recurved, soft acanthoparial setae and a long, inwardly concave row of numerous, irregularly arranged, slender and curved chaetoparial setae; tormae strong, short, sausagelike; labral rods not present; crepidal space covered with minute papillae, but no pores. *Mandible* (fig. 4) with two apical teeth; subapical part of mandible low and subtriangular, with a long, straight distal edge equipped with a row of minute, grainlike elevations; marginal brush lacking; aboral surface (fig. 4) bearing a proximal series of about ten long setae and a distal group of about five shorter setae. Maxillary lacinia (fig. 5) about half as large as galea, distally carrying about a dozen long, stiff, straight setae, clustered in a bundle, and behind them several additional but much weaker setae; no spine; maxillary palpus with three articles, proximal article

ventrally with three or four long setae; distal part of stipes with a similar number of long setae. Prementum with a transverse series of about eight short setae on each side, meso- and submentum each with a similar number of much longer setae.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	20
Abdominal segment 1	21
„ „ 2	15
„ „ 3	11
„ „ 4	11
„ „ 5	11
„ „ 6	9
„ „ 7	none
„ „ 8	none

9th abdominal segment (fig. 3) with a patch of about twenty-four lateral asperities on each side.

10th abdominal segment (fig. 3) without asperities.

Spiracles (figs. 6, 7 and 9) circular, each with one air tube about half as long as diameter of peritrema or, in some of the abdominal spiracles (fig. 7), as long as the peritremal diameter; thoracic spiracle (fig. 5) including air tube not fully as long as distal article of maxillary palpus; diameter of abdominal spiracles (figs. 7 and 9) about two-thirds as long as thoracic spiracle.

Leg (fig. 8) with pretarsus less than one-fourth as long as tibio-tarsus; membranous part of pretarsus with two setae, forming together with arolium an elongate balloon-shaped feature; claw absent.

57. *Neogastrallus librinocens* Fisher

Plate 45.

Described material labeled:

1) *Neogastrallus librinocens* Fisher, larvae, associated with imagines, attacking books, Notre Dame Seminary, New Orleans, Louisiana, 28.VII.1939.

Size of larva: Small to moderately long (c. 5 mm.).

Head capsule oval, slightly longer than broad, broadest near the middle, without frontal lines; pigmented field behind epistoma lacking; epistoma (fig. 10) on each side of sagittal body line with

a transverse series of about ten fairly long setae anteriorly, and another transverse series with fewer setae posteriorly; rest of cranium with a limited number of mostly short setae. Antenna (fig. 10) without articles; sensory organs borne by dome-shaped membranous base. Anteclypeus (fig. 10) apparently without setae. Labrum (fig. 10) with semicircular free margin, surface densely set with setae; paired marks absent. Epipharynx (fig. 11) anteriorly with several short, hook-shaped coryphal setae in two transverse series; acanthoparial setae slender, almost straight and pointed; chaetoparial setae on each side numerous, long, fine, somewhat curved and arranged in a subtriangular patch; tormae solid, straight and corniform; labral rods not developed; crepidal field without pores. *Mandible* (figs. 12 and 17) apically with first tooth distinct, second tooth indistinct and fused with long subapical part of mandible into a large, convex wall, overhanging the adoral surface (fig. 17); marginal brush well developed; aboral surface with two long proximal and no distal setae. Maxillary lacinia (fig. 13) much smaller than galea, terminally with six moderately long and stiff setae and a few minute setae behind; galea with well-developed more or less dagger-shaped marginal setae, and parallel with them, ventrally a series of short, ovate setae; maxillary palpus with three articles; proximal article ventrally with five setae; distal part of stipes with a similar number.

Body-trunk curved, covered with fine setae; prodorsal and lateral asperities lacking.

Spiracles (figs. 15 and 16) somewhat irregularly ring-shaped, no air tubes; thoracic spiracle (fig. 15) considerably larger than abdominal spiracles (fig. 16).

Leg (fig. 14) comparatively short, with pretarsus about one-third as long as tibio-tarsus; proximal membranous part small with two setae; claw lacking; proximal part and arolium fused into a balloon-shaped feature.

58. *Microanobium* sp.

Plate 46.

Described material labeled:

1) *Microanobium* sp. (= *Microsternus* sp.), (imago det. by W. S.

Fisher) in bark of dried wood stump from China; intercepted Hawaii, 6.III.1933 (Hawaii # 541).

Size of larva: Small (3 to 4 mm.).

Head capsule oval, about as long as broad, without frontal lines; pigmented field behind epistoma (fig. 4) small, quite light, sagittally somewhat longer than epistoma; epistoma (fig. 4) on each side with two well-developed setae; cranium, including pigmented field, with a moderate number of fine, short to quite long setae scattered over the whole surface. Antenna (fig. 4) without articles; sensory organs on membranous dome-shaped base. Anteclypeus (fig. 4) without plate and no setae at each end of anteclypeal sulcus. Labrum (fig. 4) with free margin semicircular, and three long setae on each side of surface; a pair of minute fine setae anteriorly; no paired marks. Epipharynx (fig. 7) with a transverse series of, altogether, four club-shaped, short coryphal setae near middle of front margin; acanthoparial setae lacking; chaetoparial setae on each side four, club-shaped, rather small, in an oblique series; labral rods and tormae united into strong V-shaped features; crepidal field quite narrow, with a pair of pores. *Mandible* (fig. 6) with first apical tooth distinct, second apical tooth entirely fused with subapical part of mandible into a convex, fairly high wall ending with a low conical projection; marginal brush well developed; aboral mandibular surface with a single long seta proximally and two small distal setae. Maxillary lacinia (fig. 8) almost vestigial carrying a single straight, pointed spine terminally and two minute setae; galea of normal size, with dagger-shaped marginal setae much shorter than lacinial spine; ventral surface with two small setae; dorsal galeal surface bearing a fringe of very long, soft hairs; maxillary palpus with three articles; proximal article with two long setae; distal part of stipes with three long and a short seta.

Body-trunk (fig. 1) subcylindrical and curved, set with a moderate number of fine, soft setae on all areas; no asperities present.

Spiracles (figs. 2 and 3) circular, without air tubes.

Leg (fig. 5) with very short pretarsal membranous part carrying two small setae; claw absent; arolium comparatively large and balloon-shaped.

59. *Eutylistus intermedius* Lec.

Plate 47.

Described material labeled:

1) *Eutylistus intermedius* Lec., in *Fomes fomentarius*, White Heath, Ill., 29.II.1932, H. H. Ross coll. et det.
2) *Eutylistus intermedius* Lec., ex *Fomes* sp., Landley, Va., 29.X.1939, W. H. Anderson coll. (Div. Ins. Id. # 01—39 c.l.).
3) *Eutylistus* sp. (intermedius Lec.?), in fungus, Rosslyn, Va., 24.IV.1913, R. C. Shannon coll. (A.G.B. det.).

Size of larva: Small (c. 4 mm.).

Head capsule oval, about as long as broad, without frontal lines; pigmented field behind epistoma (fig. 1) about twice as long as epistoma, rather pale and indistinctly limited behind; epistoma (fig. 1) densely pitted; with, altogether, five straight setae in a transverse series and a single long seta at base of each catapophysis; ventro-laterally at base of fossa for mandible (fig. 2) with surface flat and granulated; cranial surface, including pigmented field, with a moderate number of short to long, fine setae. Antenna (fig. 1) without articles; tactile papilla long and sausage-shaped. Anteclypeus (fig. 1) with two well-developed, straight setae at each end of anteclypeal sulcus, not borne by any plate. Labrum (fig. 1) elongate pyriform, armed with a median transverse series of, altogether, four straight, well-developed setae and bearing some small, lanceolate, flat, transparent setae in anterior margin; no dark marks. Epipharynx (fig. 4) with a heavily sclerotized, single, triangular coryphal plate bearing a pair of strong, curved, sagittally adjacent, tooth-like setae with a rudimentary, somewhat similar seta on each side, partly fused with them; four long, recurved acroparial setae on each side of coryphal plate; no acanthoparial setae; chaetoparial setae numerous, cultriform, rather small, on each side arranged in a single, longitudinal, inwardly concave series; pedium large, slightly scabroseous; tormae strong, straight, elongate, subconical, fairly close together; no labral rods; crepidal field quite narrow, without pores. *Mandible* (figs. 10, 10*) apically with two teeth and a long, broad subapical mandibular wall, forming a grinding pseudomola (fig. 10*) with a series of about twenty crescent-

shaped, downward-turned, parallel grooves alternating with granulated crests; marginal brush lacking, but oval arched marginal wall large and heavily sclerotized; aboral surface of mandible (fig. 10) proximally with a row of about five long setae and distally with two long setae. Maxillary lacinia (fig. 6) as large as galea; on adoral side (fig. 9) bases of the two lobes reinforced by an armlike sclerotization (LcGa.arm) extending from posterior end of the lacinial edge farthest from galea to the galeal edge adjacent to proximal article of palpus; distal to armlike bar with a membranous pad carrying a profuse number of very long, soft, fine hairs; marginal setae of lacinia and galea strong and cultriform; aboral (fig. 5) and adoral (fig. 9) surfaces of both lobes with setae of usual shape; maxillary palpus with three articles; proximal article carrying five setae on the outside. Hypopharynx (figs. 3, 6) ending distally with an arrowlike projection (x) on top of its large anterior face above ligula (Lig); the latter with a wartlike swelling armed with sharp setae.

Body-trunk (fig. 11) subcylindrical and curved.

Number of prodorsal asperities (fig. 11) *on each side of:*

Thoracic segment II	none
„ „ III	3
Abdominal segment 1	11
„ „ 2	10
„ „ 3	7
„ „ 4	7
„ „ 5	4
„ „ 6	none
„ „ 7	none
„ „ 8	none

9th abdominal segment with a patch of about twelve lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (figs. 7, 8) pseudocribriform with a small, in some of the abdominal spiracles (fig. 8) exiguous, cribrate field.

Leg with short pretarsal membranous part about as long as broad, carrying two setae; claw slender, somewhat curved and setalike, half as long as tibio-tarsus; arolium absent.

60. *Eutylistus facilis* Fall.

Plate 47.

Described material labeled:

1) *Eutylistus facilis* Fall, Victoria, Texas, E. A. Schwarz coll. et det.

Size of larva: Small (c. 4 mm.).

Differing from *Eutylistus intermedius* Lec. only by characters pertaining to pigmented field behind epistoma, epistoma itself, epipharynx and spiracles.

Pigmented field behind epistoma insignificant or entirely absent; epistoma (fig. 13) smooth with an irregular transverse series of, altogether, twelve setae. Anteclypeal setae absent. Epipharynx (fig. 12) with two pairs of well-developed, toothlike coryphal setae borne by triangular plate; apparently no recurved acroparial setae; acanthoparial setae absent; chaetoparial setae numerous, short, somewhat curved and slender, on each side arranged in a large anterior patch followed by a single, longitudinal row of setae.

Spiracles (figs. 14, 15) pseudocribriform with a large cribrate field, four or five times longer than diameter of spiracular trachea.

61. *Anitys rubens* Hoffm.

Plate 48.

Described material labeled:

1) *Anitys rubens* Hoffm. (= *Dorcatoma rubens* Hoffm.), ex coll. Zool. Mus., Copenhagen, Denmark (in exchange from F. Meinert 1890 # 148).

2) *Anitys rubens* Hoffm., in red moulded oak, Dyrehaven near Copenhagen, 6.I.1935, J. P. Kryger coll. and reared.

Size of larva: Moderately large (c. 6 mm.).

Head capsule oval, slightly longer than broad, without frontal lines; pigmented field behind epistoma (fig. 2) small, indistinct; epistoma (fig. 2) smooth, except with rugose catapophyses, with, altogether, seven setae, in a single, transverse row and one long seta externally at base of each catapophysis; flat and granulated surface ventro-laterally at fossa for mandibular condyle (fig. 1); cranium with a moderate number of fine setae. Antenna (fig. 2)

without articles; tactile papilla of medium size and ovate. Anteclypeus (fig. 2) with one long seta at each end of anteclypeal sulcus, not borne by a plate. Labrum (fig. 2) pyriform, armed with a median transverse series of, altogether, four straight, well-developed setae and bearing some small, lanceolate, flat setae in anterior margin; no paired dark marks. Epipharynx (fig. 3) with a sclerotized, subtriangular coryphal plate bearing four strong, claw-shaped setae; acroparial setae numerous, long and recurved; no acanthoparial setae; chaetoparial setae numerous, cultriform, somewhat curved, pointed and small; on each side in a large anterior patch followed by a single, longitudinal, rather straight row of many setae; pedium large and subtriangular, with slightly granulose surface; tormae strong, straight, elongate subconical and almost adjacent; no labral rods; crepidal field obliterated. *Mandible* (figs. 4, 5, 6) apically with two strong teeth and a broad, long, thick subapical wall forming a grinding pseudomola; marginal brush lacking but marginal elevation (fig. 5), usually surrounding it, heavily sclerotized; aboral surface of mandible (figs. 5, 6) proximally with an irregular row of about fifteen moderately long setae, and distally with a group of about five similar setae. Maxillary lacinia (fig. 8) as large as galea, on adoral side (fig. 8) bases of both lobes supported by a bar between inner marginal edge of lacinia and galeal edge adjacent to proximal article of palpus; lobes with a common, soft-skinned pad covered by a profusion of very long, fine, soft hairs situated in front of the bar; margins of both lobes armed with slender, cultriform, rather short setae; aboral and adoral surfaces of both lobes with a moderate number of setae; maxillary palpus with three articles; proximal article carrying five setae. Hypopharynx ending in an arrowlike projection placed over anterior large wall (compare Pl. 47, fig. 3).

Body-trunk subcylindrical and curved.

Number of prodorsal asperities on each side of:

Thoracic segment II	none
„ „ III	5
Abdominal segment 1	9
„ „ 2	8
„ „ 3	10
„ „ 4	9

Abdominal segment	5	8
„ „	6	4
„ „	7	none
„ „	8	none

9th abdominal segment with a patch of about fifteen lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (fig. 7) simple, annular, without air tubes.

Leg (figs. 9, 10) with short pretarsal membranous part about as long as broad, carrying two setae; claw slender, a little curved and setalike, half as long as the comparatively short tibio-tarsus; arolium absent.

62. *Dorcatoma dresdensis* Herbst.

Plate 48.

Described material labeled:

1) *Dorcatoma dresdensis* Hbst., ex woody fungus, Cummington, Mass., 24.XI.1939, A. B. Gurney & W. H. Anderson coll., W. S. Fisher det. imago (Div. Ins. Id. # 87—39).
2) *Dorcatoma dresdensis* Hbst., Patuxent Game Preserve, Md., 17.IX.1944, W. H. Anderson coll.
3) *Dorcatoma dresdensis* Hbst., in woody fungus, Crab Lake, Wisc., H. S. Barber coll. 1907—1908.
4) *Dorcatoma dresdensis* Hbst., ex *Fistulina hepatica* on *Quercus*, Fuglsang, Lolland, Denmark, 27.III.1945, reared 25.IV.1945, J. P. Kryger, coll.

Size of larva: Moderately large (c. 5 mm.).

Head capsule subcircular, about as long as broad, without frontal lines; pigmented field behind epistoma rather pale and indistinct, not sharply set off from posterior part of large, rugose epistoma (fig. 15); epistoma with, altogether, about sixteen long, evenly distributed setae, each in a small pit; ventro-laterally at fossa for mandibular condyle with a large, granulated, conical process (figs. 11, 13); rest of cranium with a moderate number of setae. Antenna (figs. 12, 15) without articles, tactile papilla sausagelike. Anteclypeus with one long seta at each end of anteclypeal sulcus (fig. 15), seta borne by an insignificant sclerotiza-

tion. Labrum (fig. 15) pyriform, armed with a median, transverse row of, altogether, six long setae and bearing some small, flat, lanceolate, transparent setae in anterior margin; no paired dark marks. Epipharynx (fig. 14) with a heavily sclerotized, oblong, transverse coryphal plate bearing a row of four well-developed, curved, toothlike setae and two quite similar but smaller setae on each side of them; acroparial setae numerous, strong and recurved; no acanthoparial setae; chaetoparial setae numerous, short, somewhat curved, on each side in a large anterior patch followed by a single, longitudinal, slightly inwardly concave row of setae; pedium large, suboval, with slightly granulose surface; tormae strong, subconical, about one-third as long as rest of epipharynx, terminally as far apart from each other as length of one torma; no distinct labral rods; crepidal field fairly wide, with two minute setae. *Mandible* (fig. 17) apically with two strong teeth followed by a broad, long, thick subapical wall which forms a grinding pseudomola; no marginal brush; aboral surface of mandible proximally with an irregular row of approximately eight moderately long setae and distally with a small group of about four similar setae. Maxillary lacinia (fig. 16) as large as galea; on adoral side bases of both lobes enforced by a bar between the inner marginal edge of lacinia and the outer galeal edge adjacent to the proximal article of palpus; lobes with a common soft-skinned pad, covered with very long and soft hairs, situated in front of bar; margins of both lobes armed with slender, cultriform setae; aboral and adoral surfaces of both lobes with a moderate number of ordinary setae; maxillary palpus with three articles; proximal article carrying five setae.

Body-trunk subcylindrical and curved.

Number of prodorsal asperities on each side of:

Thoracic segment	II	none	
„ „	III	5	
Abdominal segment	1	10	
„ „	2	8	in two transverse rows
„ „	3	9	
„ „	4	7	
„ „	5	8	
„ „	6	4	
„ „	7	none	
„ „	8	none	

9th abdominal segment with a patch of about fifteen lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (figs. 19, 20, 21) annular with a single, very short air tube; thoracic spiracle (fig. 19) much larger than abdominal spiracles (fig. 21).

Leg (fig. 18) with short pretarsal membranous part about as long as broad, carrying two setae; claw slender, slightly curved, setalike and half as long as tibio-tarsus; arolium absent.

62*. *Dorcatoma chrysomelina* Sturm.

Described material labeled:

1) *Dorcatoma chrysomelina* Sturm, from *Quercus ruber*, Turku, Suomi, 11.VII.1918, Uunio Saalas coll. et det.
2) *Dorcatoma chrysomelina* Sturm, fungus on *Quercus*, Knuthenborg, Denmark, Larva—July 1947, imago out 12.IV.1948, J. P. Kryger, coll. and reared.

Size of larva: Small (c. 4 mm.) to moderately large (c. 5 mm.).

Larva identical in all characters and in size with *Dorcatoma dresdensis* Hbst., except in the number of the prodorsal asperities.

Number of prodorsal asperities on each side of:

Thoracic segment II	none	
„ „ III	6	
Abdominal segment 1	19	in two
„ „ 2	19	and in
„ „ 3	18	some places
„ „ 4	17	three
„ „ 5	14	transverse
„ „ 6	4	rows
„ „ 7	none	
„ „ 8	none	

9th abdominal segment with a patch of about twenty lateral asperities on each side.

10th abdominal segment without asperities.

62**. Preserved in collection of U.S.N.M. is the larva of *Dorcatoma flavicornis* F.

Fortunens Indelukke, near Copenhagen, Denmark, larvae and one pupa, 10.V.1940, J. P. KRYGER coll. et det.

Size of larva: c. 4 mm.

63. *Caenocara bovistae* Hoffm.

Plate 49.

Described material labeled:

1) *Caenocara bovistae* Hoffm., in *Bovista* sp. (reared), Vester Fælled, Copenhagen, Denmark, larva: 10.XI.1895; pupa: 23.XII.1895; imago: out 5.I.1895, E. ROSENBERG coll.
2) *Caenocara* sp. (probably *C. bovistae* Hoffm., ex *Lycoperdon*, Greenbelt, Md., 27.X.1940, W. H. ANDERSON coll.

Size of larva: Small (c. 3 mm.).

Head capsule subcircular, about as long as broad, without frontal lines, pigmented field behind epistoma present but pale and indistinct; epistoma with low catapophyses, epistomal setae absent; ventro-laterally at fossa for mandibular condyle without process or granulations; pigmented field and rest of cranium with a moderate number of setae. Antenna without articles, tactile papilla of normal, moderate size and shape. Anteclypeus with one small seta at each end of anteclypeal sulcus. Labrum cordiform (fig. 2), armed with a median, transverse row of, altogether, four moderately long setae, and in the concave anterior margin with four moderately long, stiff setae in a transverse row; no paired dark marks. Epipharynx (fig. 2) with a transverse coryphal plate bearing a row of, altogether, four well-developed, somewhat curved, toothlike setae; acroparial setae reduced to one in each anterior corner; acanthoparial setae lacking; chaetoparial setae numerous, short, slightly curved and pointed, arranged in an inwardly convex, long row on each side, reaching from anterior epipharyngeal corner to posterior end of torma; pedium narrow; tormae and labral rods fused into converging, pointed, flat, elongate triangular features with a globular, dark ball anteriorly on exterior side; crepidal field between tormae occupied by the posterior half of the two rows of chaetoparial setae. *Man-*

dible (figs. 7, 8) apically with a distinct first tooth and a minute second; and subapically with a broad, grinding pseudomola; marginal brush absent; aboral mandibular surface (fig. 8) with a profusion of long, fine, soft setae in a row from under a-low, thin-walled, transverse ridge at the base of anterior part of mandible. (Eventually this part, including the long setae, breaks off along a weak line posterior to the ridge.) Maxillary lacinia (fig. 1) about as large as galea; adorally basal padlike region of both lobes set with numerous soft hairs; distal margins of lobes armed with short, pointed setae; lacinia (Lc) overhanging upper surface of hypopharynx (Hphy); inner lacinial margin heavily sclerotized working against the equally heavily sclerotized, enlarged upper end of each lateral hypopharyngeal bar (Su); galea with a single series of strong, cultriform setae on the adoral surface, seated in a furrow parallel with and considerably behind the anterior margin of the lobe; maxillary palpus with three articles; proximal article with one or two setae.

Body-trunk (fig. 4) curved, subcircular in cross section, somewhat thicker behind the middle than anteriorly and posteriorly; prodorsal areas of most segments carrying on either side two or three tubercles each with one straight seta on top (figs. 4, 9); asperities lacking.

Spiracles (figs. 5, 6) circular, simple, without air tubes.

Leg (fig. 3) very short, tibio-tarsus thick and conical; membranous part of pretarsus vestigial; claw tiny, somewhat curved; no arolium.

64. *Caenocara oculata* Say.

Plate 49.

Described material labeled:

1) *Caenocara oculata* Say (imago det. by W. S. Fisher), in puffballs, Greenbelt, Md., 28.IX.1941, W. H. Anderson coll.
2) *Caenocara oculata* Say, ex fresh puffballs, College Park, Md., 21.VII.1942, W. H. Anderson coll.
3) *Caenocara oculata* Say, in puffball, Falls Church, Va., August 1920.

Size of larva: Small (c. 3 mm.).

Head capsule subcircular, about as long as broad, without frontal lines; pigmented field behind epistoma (fig. 11) present but pale; catapophyses low; epistomal setae absent; without a ventro-lateral process or granulations at the fossa for mandibular condyle; pigmented field (fig. 11) and rest of cranium with a moderate number of setae. Antenna without articles; tactile papilla of normal shape and moderate size. Anteclypeus (fig. 11) with one seta at each end of a sclerotized band in front of anteclypeal sulcus. Labrum (fig. 11) with outline as three quarters of a circle, surface armed medially with a transverse series of, altogether, four moderately long setae; in addition bearing four closely set, stiff setae in a row on the middle of the anterior part of the margin; no paired dark marks. Epipharynx (fig. 13) with a transverse row of, altogether, four well-developed, toothlike coryphal setae and on each side some short acroparial setae; acanthoparial setae lacking; chaetoparial setae short and pointed, in a single, slightly inwardly concave series of about ten setae on each side; pedium rather large; tormae and labral rods fused into converging, posteriorly united, flat, elongate features with a globular projection anteriorly; crepidal field not present. *Mandible* (fig. 18) with two marginally crenulated apical teeth and subapically a broad, long pseudomola; marginal brush absent; aboral mandibular surface with numerous long, straight setae in a row inserted under cover of a low transverse ridge at base of anterior part of mandible. Maxillary lacinia (figs. 10, 14, 15) slightly smaller than galea; both lobes provided adorally with many fine hairs from a soft membranous pad anterior to the bar at the bases of the lobes; distally, margins of lobes armed with stiff short setae (fig. 15); lacinia overhanging upper surface of hypopharynx (fig. 10); inner lacinial margin heavily sclerotized, working against an equally heavy sclerite of hypopharynx (Su) at the entrance to pharynx; the hypopharyngeal sclerite being an element of the enlarged and transformed ends of the lateral hypopharyngeal bars; galea on adoral side (fig. 10) with a series of numerous setae lodged in a transverse convex groove in some distance behind anterior margin of lobe; maxillary palpus with three articles; proximal article with two ventral setae; distal end of stipes with a few more, similar setae.

Body-trunk curved, subcircular in cross-section, thicker some-

what behind middle of trunk than anteriorly and posteriorly; prodorsal areas without asperities; but most of the body segments bear two or three tubercles with a strong seta on top (fig. 12).

Spiracles (figs. 16, 17) circular, simple without air tubes; diameter of thoracic spiracle (fig. 16) about twice as long as diameters of abdominal spiracles (fig. 17).

Leg (figs. 19, 20) very short, thick and conical; segments not distinct; terminally with two long setae; claw vestigial or apparently lacking in some specimens.

65. *Ptilineurus marmoratus* Reitter.

Plate 50.

Described material labeled:

1) *Ptilineurus marmoratus* Reitter, Japan.

Size of larva: Large (c. 11 mm.).

Head capsule (fig. 2) somewhat longer than broad, broadest before the middle, sides convergent behind the middle, without frontal lines; pigmented field behind epistoma not present; epistoma smooth, with numerous long and fine setae densely set in a transverse row in the anterior margin (fig. 2) latero-ventrally at fossa behind ocellus with a longitudinal, narrow, ridged region like a file (fig. 3); cranial surface densely covered with short and long, fine setae, except, posteriorly on each side of epicranial sulcus. Antenna without articles; tactile papilla short and ovate. Anteclypeus (fig. 2) with a considerable number of long, fine setae at each end of anteclypeal sulcus and attached to a narrow, transverse, ribbon-shaped thinly sclerotized plate on posterior anteclypeal margin. Labrum (fig. 2) with semicircular free margin and distally with many short and moderately long setae; no paired dark marks. Epipharynx (fig. 1) with a median patch of about twenty very short, robust, hook-shaped coryphal setae; acroparial and acanthoparial setae forming a continuous fringe of moderately long and long, straight and curved setae; chaetoparial setae mostly long and hairlike covering the whole epipleural surface, except, a narrow pedial sagittal region; torma and labial rod forming a V-shaped feature; crepidal field without pores. *Mandible* (figs. 4 and 5) apically with two teeth, both low, the first with gouge-shaped edge, the second smaller and sub-

triangular; subapical part of mandible short, almost of same size and shape as second apical tooth; marginal elevation well developed around distinct marginal brush; aboral surface (fig. 4) with a proximal group of about eight fairly short setae and three long distal setae. Maxillary lacinia (fig. 8) much smaller than galea, distally armed with three strong, pointed spines and for the rest provided with many weak, straight setae; galea with strong, cultriform marginal setae and dorsally and ventrally with numerous smaller setae; maxillary palpus with four articles; proximal article with five long ventral setae, next article with one seta and penultimate article with two setae; stipes densely furnished with long setae.

Body-trunk curved, subcircular in cross section, of nearly same thickness throughout. Asperities hook-shaped.

Number of asperities on each side of:

Thoracic segment II	25	in three or more transverse rows
„ „ III	25	
Abdominal segment 1	20	
„ „ 2	25	
„ „ 3	35	
„ „ 4	35	
„ „ 5	35	
„ „ 6	15	in two transverse rows
„ „ 7	12	
„ „ 8	10	

9th abdominal segment with a patch of very numerous lateral asperities on each side.

10th abdominal segment with about 25 rather fine and only slightly curved asperities.

Spiracles (figs. 6, 7, 7*) annular, without air tube; oval; thoracic spiracle (fig. 6) about twice as long as abdominal spiracles (figs. 7, 7*).

Leg of prothorax (fig. 9) a little stronger than legs of meso- and metathorax (fig. 10); proximal parts of pretarsi of all the thoracic legs approximately as long as their tibio-tarsi, well sclerotized and furnished with a multitude of setae, ovate on prothoracic pretarsus, straight and pointed on meso- and metathoracic pretarsi; claw of prothoracic leg (fig. 9) somewhat curved with forward-turned concavity and about one-fourth as long as

proximal part of pretarsus; claw of a mesothoracic and a metathoracic leg (fig. 10) rather straight and about one-third as long as proximal part; arolium absent.

66. *Ptilinus basalis* Lec.

Plate 50.

Described material labeled:

1) *Ptilinus basalis* Lec., in Laurel from Calif., 6.II.1919, Hopk. U. S. #15280d; reared imago.

Also examined are:

2) *Ptilinus ruficornis* Say (imago det. by E. A. Schwarz) removed from powder-posted cotton-wood—*Populus deltoides* March., Worthington, Minn. and Menasha, Wisc., 28.VI. 1923, Watten's Paper Co.
3) *Ptilinus fuscus* Geoffr. (det. Reitter) bought from Reitter, Paskau, Europe, 1922 (no data).
4) *Ptilinus pectinicornis* L., ex Mus. Zool., Copenhagen, Denmark, in exchange from F. Meinert, 1890 (#146).
5) *Ptilinus pectinicornis* L., ex wood of *Populus* sp. from Italy, intercepted 26.I.1948 by M. H. Sartor; N.Y. #101946; 48—6328. Imago in coll. U.S.N.M.; det. by Arnett.

Size of larva: Moderately large (c. 7 mm.).

Head capsule widest near the middle, oval posteriorly, somewhat longer than wide, without frontal lines; pigmented field behind epistoma poorly developed; epistoma (fig. 15) with long wavy fine furrows on its entire surface, without setae; latero-ventrally quite smooth (fig. 11) at fossa for mandibular condyle; pigmented field and rest of cranium with many short and fine setae. No ocellus. Antenna (fig. 15) with two articles; tactile papilla ovate and short; cylindrical fossa containing antenna wide, with diameter about as long as sagittal length of epistoma. Anteclypeus (fig. 15) with three small setae at each end of anteclypeal sulcus. Labrum (fig. 15) with free margin approximately semicircular, antero-laterally with a patch of small setae on each side; paired dark marks present at anterior ends of labral rods. Epipharynx (fig. 12) with two pairs of minute coryphal setae and a fringe of fine setae on anterior margin; no acanthoparial setae; chaetoparial setae slender, fairly long, six present on each side in an

inwardly convex single row; tormae well developed forming together with labral rods a pair of Y-shaped features; crepidal field with several (about seven) sensory pores. *Mandible* (fig. 16) apically with a short, obtuse tooth, second apical tooth completely amalgamated with subapical part of mandible into a large, thick wall with convex outline; marginal brush present but short; aboral surface with a single, long seta. Maxillary lacinia (fig. 19) somewhat smaller than galea, distally with several straight, strong setae, adorally (fig. 24) with a longitudinal single series of about seven well-developed setae in margin toward galea; centrally a few long setae; galea with a series of cultriform setae in anterior margin, adorally (fig. 24) with several long setae anteriorly, and an oblique, single series of well-developed setae behind; at base of both lobes another series of similar setae; aborally surfaces (fig. 19) of both lobes with many setae; maxillary palpus with three articles; proximal article ventrally with four setae; stipes with several moderately long setae. Labium (fig. 19) with several fine setae on submentum and mesomentum; prementum with a large, triangular, arrow-shaped, well sclerotized plate posteriorly; distal part and ligula covered with short, strong setae.

Body-trunk (fig. 20) curved; subcircular in cross-section, thoracic segments somewhat thicker than abdominal segments; as perities not hook-shaped but short, conical and minute (figs. 13, 14), present both on most prodorsal areas on lateral areas of ninth abdominal segment and on most of the epipleural areas.

Number of asperities on each side of:

	prodorsal	epipleural
Thoracic segment II	10	none
„ „ III	15	few
Abdominal segment 1	numerous	numerous
„ „ 2	numerous	numerous
„ „ 3	numerous	numerous
„ „ 4	numerous	numerous
„ „ 5	numerous	numerous
„ „ 6	numerous	numerous
„ „ 7	25	numerous
„ „ 8	20	none

9th abdominal segment with a patch of numerous lateral asperities on each side.

10th abdominal segment without asperities.

Spiracles (figs. 21, 22, 23) varying from oval to circular, simple, annular, without air tubes; thoracic spiracle (fig. 21) about twice as long as an abdominal spiracle; first abdominal spiracle (fig. 22) a little larger than the rest of the abdominal spiracles (fig. 23).

Leg (figs. 17, 18, 25) regularly built and of normal length; pretarsus with membranous proximal part about as long as broad, armed with a single short, strong seta (fig. 26); claw slender, pointed, very slightly curved, about one-third as long as tibiotarsus; no arolium.

Note: The larvae of
66. *Ptilinus pectinicornis* L,
66. *Ptilinus ruficornis* Say, and
66. *Ptilinus fuscus* Geoff. are not specifically separable from
66. *Ptilinus basalis* Lec.

Explanation of Plates.

All figures pertain to mature anobiid larvae.

PLATE 1

External structures of the body of an anobiid larva.
(*Xyletobius walsinghami* Perkins).

Xyletobius walsinghami Perkins.

PLATE 2

Fig. 1. Structures of head with ventral appendages removed; posterior view.

Anap	anapophysis
Cat	catapophysis
Ephy	epipharynx
EpicrR	epicranial ridge
Hst	hypostoma
Oc	occiput
Poc	postocciput
PoR	postoccipital apophysis
pos	postoccipital sulcus
pt	pit of posterior tentorial arm
Smt	submentum
Tnt	tentorial bridge
Torma	torma
Vx	vertex

Fig. 2. Facial frame around the anterior cranial foramen.

Anap	anapophysis
Ant	antenna
Cat	catapophysis
Est	epistoma
Hst	hypostoma
O	ocellus
Pst	pleurostoma
scn	internal canal of epistomal seta

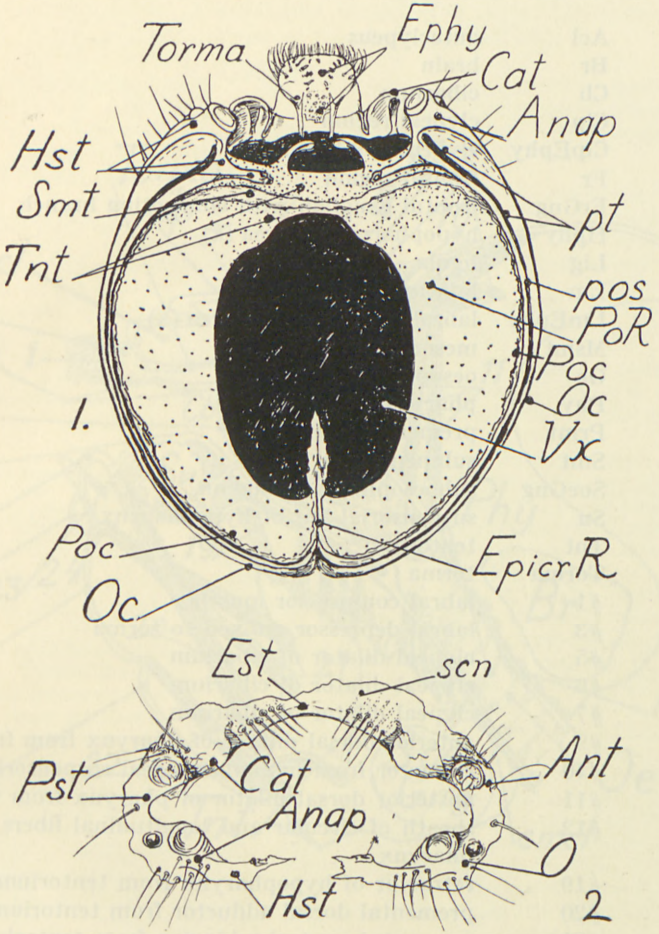

Torma
Ephy
Cat
Anap
Hst
Smt
Tnt
pt
pos
PoR
Poc
Oc
Vx
1.
Poc
Oc
EpicrR
Est
scn
Pst
Cat
Ant
Anap
O
Hst
2

PLATE 3

Section of head showing muscles and structural details. View from inside of right half of head.

Acl	anteclypeus
Br	brain
Cb	cibarium
Clp	clypeal region
ClpEphy	clypeal epipharynx
Fr	frontal region
FrGng	frontal ganglion with connecting branch
Hphy	hypopharyngeal area (x)
Lig	ligula
Lm	labrum
LmEphy	labral epipharyngeal area (x)
Msmt	mesomentum
Oe	oesophagus
Phy	pharynx
Prmt	prementum
Smt	submentum
SoeGng	suboesophageal ganglion
Su	suspensorial bar of hypopharynx
Tnt	tentorium
Torma	torma
#1	labral compressor muscle
#3	labral depressor adfixed to torma
#5	clypeal dilator of cibarium
#6	clypeal dilator of cibarium
#7	clypeal dilator of cibarium
#9	anterior dorsal dilator of pharynx from frons
#10	retractor from hypopharyngeal suspensorial bar
#11	posterior dorsal dilator of pharynx from frons
#12	sheath of circular and longitudinal fibers of pharynx
#19	retractor of hypopharynx from tentorium
#20	premental dorsal adductor from tentorium
#21	premental ventral adductor from tentorium
#22	mesomental ventral median retractor from posterior margin of submentum
#23	levator of labial palpus
#24	depressor of labial palpus
#30	ventral dilator of pharynx from tentorium
#31	lateral dilator of pharynx from parietale

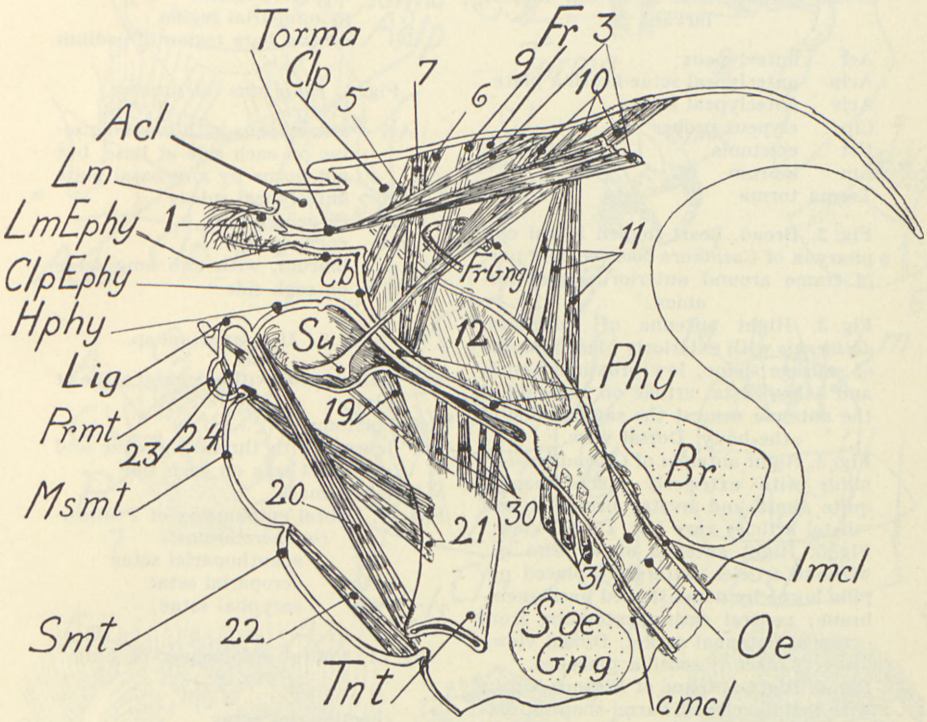

Torma
Clp
Fr
3
5
7
9
6
10
Acl
Lm
LmEphy
1
11
ClpEphy
Cb
FrGng
Hphy
Su
12
Phy
Lig
19
Prmt
23
24
Br
Msmt
20
21
30
Imcl
31
Soe
Gng
Oe
Smt
22
Tnt
cmcl

Plate 4

Examples of epistoma, anteclypeus and labrum, labral epipharynx and antenna as developed in various species.

Fig. 1. Diagram illustrating the type of labral and anteclypeal parts and epistoma characteristic of certain anobiid larvae.

Acl anteclypeus
Aclp anteclypeal setae-bearing plate
Acls anteclypeal sulcus
Clp clypeus proper
Est epistoma
Lm labrum
Torma torma

Fig. 2. Broad, heart-shaped labral epipharynx of *Caenocara bovistae*, and part of frame around anterior cranial foramen.

Fig. 3. Right antenna of *Dorcatoma dresdensis* with exteriorly placed papilla of sausage shape; low proximal article and a low distal article on the side of the antenna nearest the sagittal line of the body. Dorsal view.

Fig. 4. Right antenna of *Ozognathus cornutus* with exteriorly placed papilla quite short and ovate; proximal and distal articles very low. Dorsal view.

Fig. 5. Right antenna of *Vrilletta* sp., without articles, externally placed papilla borne by dome-shaped basal membrane; ventral casing extending from rim of antennal socket. Dorsal view.
S.plac sensilla placodea.

Fig. 6. Right antenna of *Ptilinus basalis* with well-developed, barrel-shaped proxmal article and low but distinct distal article inserted internally on top of proximal article; short and fine antennal muscle fibers originate from wall of cranium. Dorsal view.

Fig. 7. Labral epipharynx of *Cryptorama minutum*; torma simple not combined with labral rod.

A marginal acanthoparial region
Acr acroparial region
C chaetoparial region
Co corypha
Cri crepidal region
G gymnoparial region
P central bare region of pedium

Fig. 8. *Eutylistus intermedius.*

Acl anteclypeus with two long setae on each side at base, but not borne by any basal plate
Acls anteclypeal sulcus
Clp clypeus proper
Est epistoma
Lm labrum, with two long setae on each side

Fig. 9. *Microanobium* sp.

Acl anteclypeus without basal setae or plate
Est epistoma
Lm labrum with three long setae and one short seta on each side
M labral mark

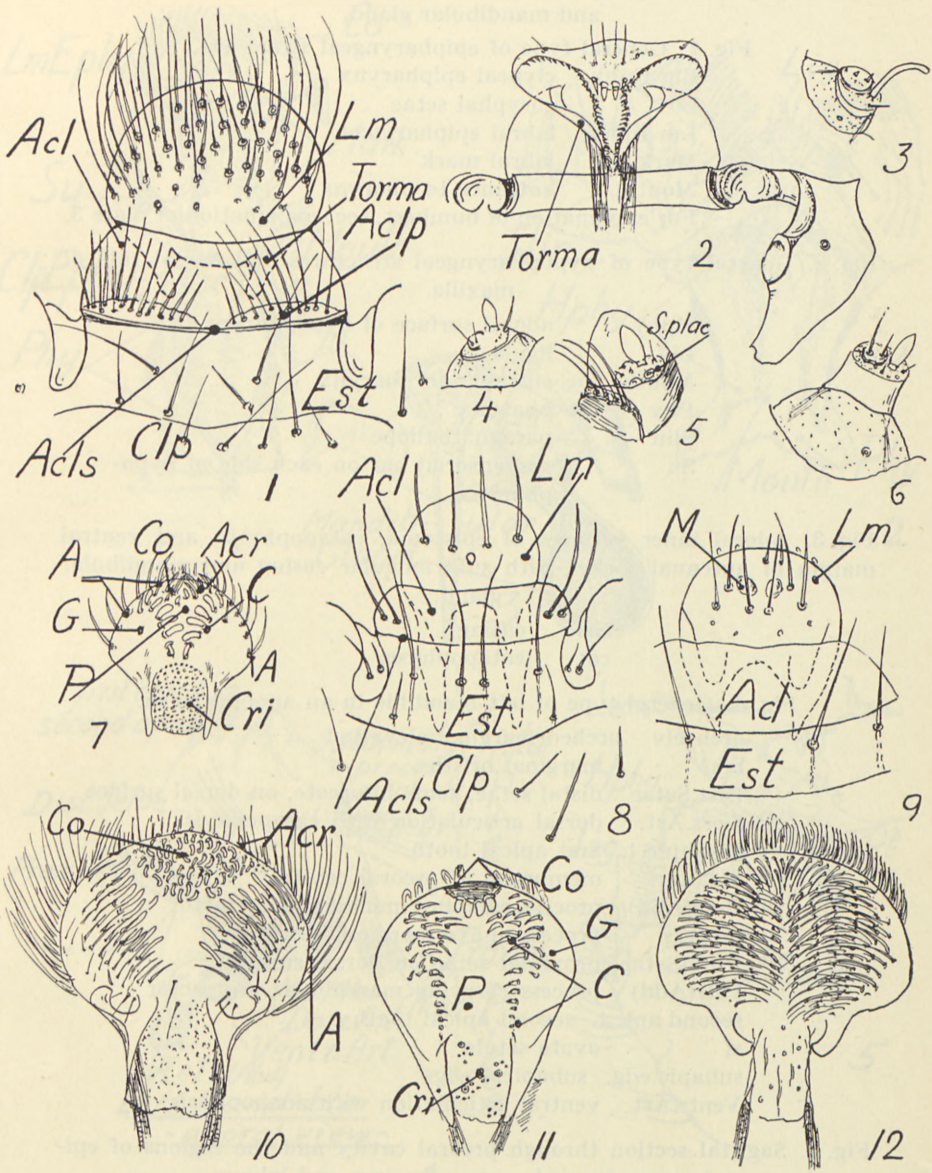
Fig. 10. Labral epipharynx of *Ptilineurus marmoratus.*

A acanthoparial setae
Acr acroparial setae
Co coryphal setae

Fig. 11. Labral epipharynx of *Eutylistus* sp.

C chaetoparial setae
Co heavily sclerotized coryphal plate bearing, altogether, four strong toothlike setae
Cri crepidal region
G gymnoparial region
P pedium

Fig. 12. Labral epipharynx of *Nicobium castaneum*, sub-circular in outline, entire surface covered with long setae.


Acl
Lm
Torma
Aclp
Est
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Acl
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Acls
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Cri
11
12

Plate 5

Epipharyngeal and hypopharyngeal structures, preoral cavity, mandible and mandibular gland.

Fig. 1. General type of epipharyngeal structures.

Clp-Ephy	clypeal epipharynx
Co	coryphal setae
Lm-Ephy	labral epipharynx
Mark	labral mark
Mouth	entrance to pharynx

For explanation of numbers, see: explanation of plate 3.

Fig. 2. General type of hypopharyngeal structures and dorsal side of maxilla.

Hphy	adoral surface of hypopharynx
Lig	ligula
Mouth	entrance to pharynx
Phy	pharynx
Slin	paragnathallobe
Su	suspensorial bar on each side of hypopharynx

Fig. 3. Adoral inner surfaces of epistoma, catapophysis, and ventral margin of antennal socket with subtriangular casing and mandibular gland.

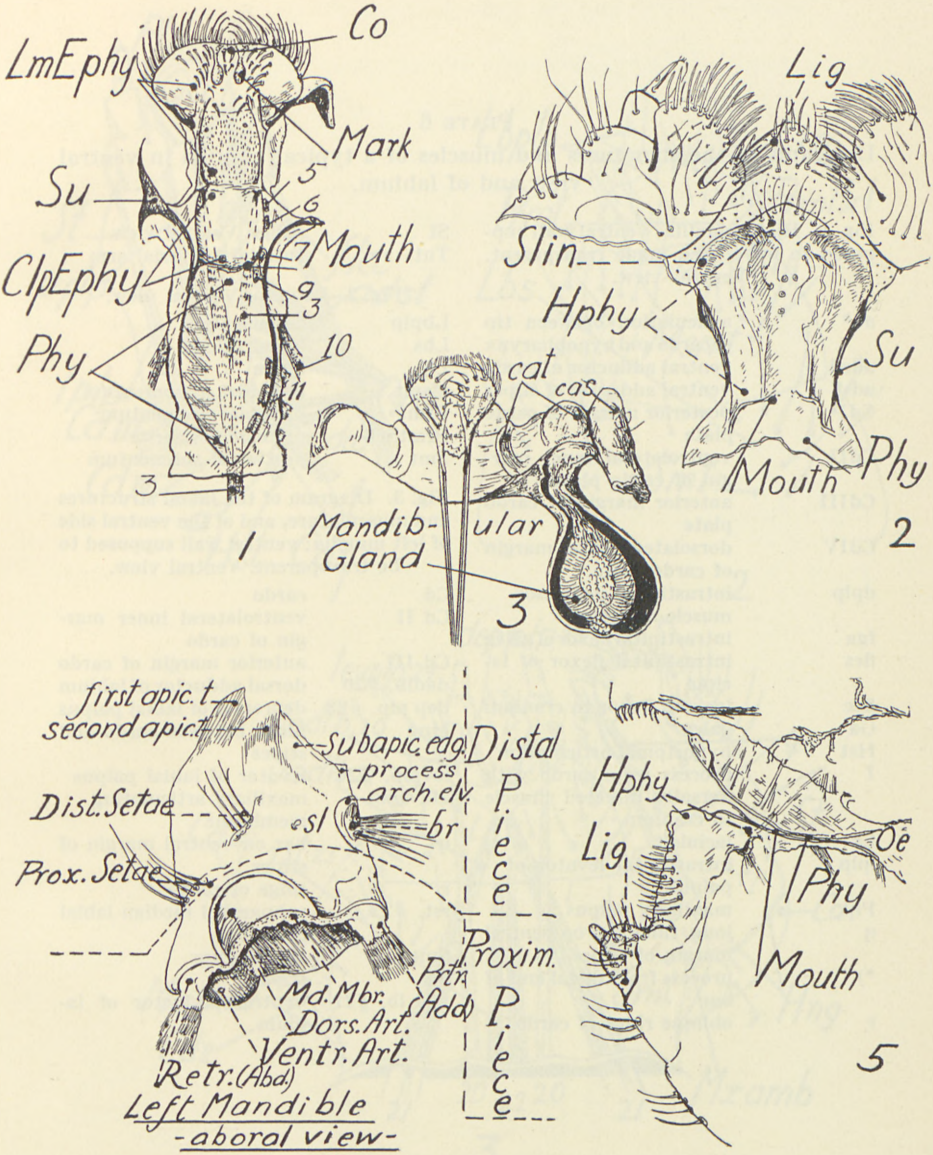
cas	casing
cat	catapophysis

Fig. 4. General type of left mandible in an anobiid larva.

arch elv	arched marginal elevation
br	marginal bristles
Dist.Setae	distal setae, some bifurcate, on dorsal surface
Dors.Art.	dorsal articulation with catapophysis
first apic. t.	first apical tooth
Md.Mbr.	membrane of preoral cavity
Retr(Abd) process	process carrying mandibular retractor
process	process above marginal elevation
Prox-Setae	proximal setae on dorsal surface
Prtr(Add)	process carrying mandibular protractor
second apic.t.	second apical tooth
sl	ovate setula
subapic.edg.	subapical edge
Ventr.Art	ventral articulation with anapophysis

Fig. 5. Sagittal section through preoral cavity and the regions of epipharynx, hypopharynx, pharynx and labium.

Hphy	hypopharynx
Lig	ligula
Mouth	entrance to pharynx
Phy	pharynx
Oe	oesophagus


LmEphy
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Mouth
ClpEphy
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Dist. Setae
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Prox. Setae
Proxim.
Ptr. (Add)
Piece
Md. Mbr.
Dors. Art.
Ventr. Art.
Retr. (Abd)
Left Mandible
-aboral view-
4
Hphy
Lig.
Oe
Phy
Mouth
5

Plate 6

Diagrams of the structures and muscles of a typical maxilla in ventral view and of labium.

Fig. 1. Right maxilla; ventral wall supposed to have been made transparent. Ventral view.

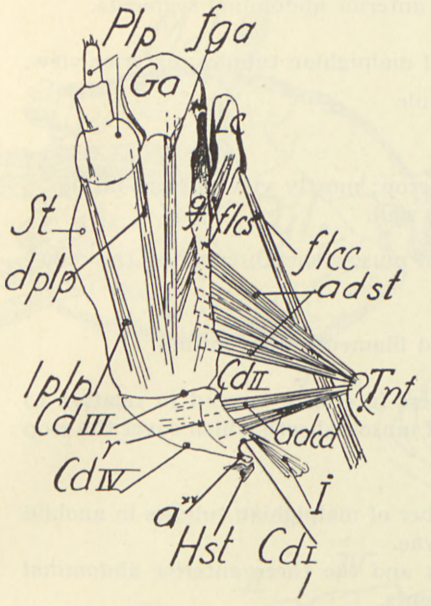
a**	articulation between tip of cardo and hypopharynx
adcd	ventral adductor of cardo
adst	ventral adductor of stipes
CdI	posterior margin of cardo plate
CdII	ventrolateral inner margin of cardo plate
CdIII	anterior margin of cardo plate
CdIV	dorsolateral outer margin of cardo plate
dplp	intrastipital depressor muscle of palpus
fga	intrastipital flexor of galea
flcs	intrastipital flexor of lacinia
flcc	lacinial flexor to cranium
Ga	galea
Hst	hypostomal articulation
I	process from cardo with dorsally directed muscle to cranium
Lc	lacinia
lplp	intrastipital levator of palpus
Plp	maxillary palpus
q	long, thick bar on ventral margin of stipes
*)	process from distal end of bar
r	oblique ridge of cardo
St	stipes. Ventral view
Tnt	anterior tentorial arm

Fig. 2. Labium. Ventral view.

Lbplp	labial palpus
Lbs	labial sulcus
Lig	ligula
Msmt	prelabial mesomentum
Prmt	prelabial prementum
PrmtScl	premental sclerite
Smt	postlabial submentum

Fig. 3. Diagram of the labial structures and musculature, and of the ventral side of left maxilla; ventral wall supposed to be transparent. Ventral view.

Cd	cardo
Cd II	ventrolateral inner margin of cardo
Cd III	anterior margin of cardo
dadlb, #20	dorsal adductor of labium
dep plp, #23	depressor of labial palpus
Hng	hinge between cardo and stipes
levplp, #24	levator of labial palpus
Mx amb	maxillary articulating membrane
q	bar on ventral margin of stipes
r	ridge of cardo
rst, #22	subparallel median labial retractors
Smt	submentum
St	stipes
vad lb, #21	ventral adductor of labium


Plp
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lplp
CdII
Tnt
CdIII
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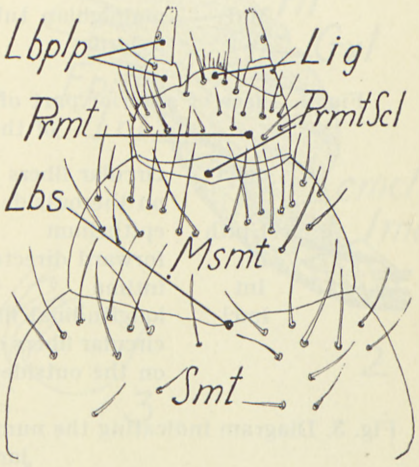
adcd
CdIV
a
i
Hst
CdI
1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Prmt
PrmtScl
Lbs
Msmt
Smt
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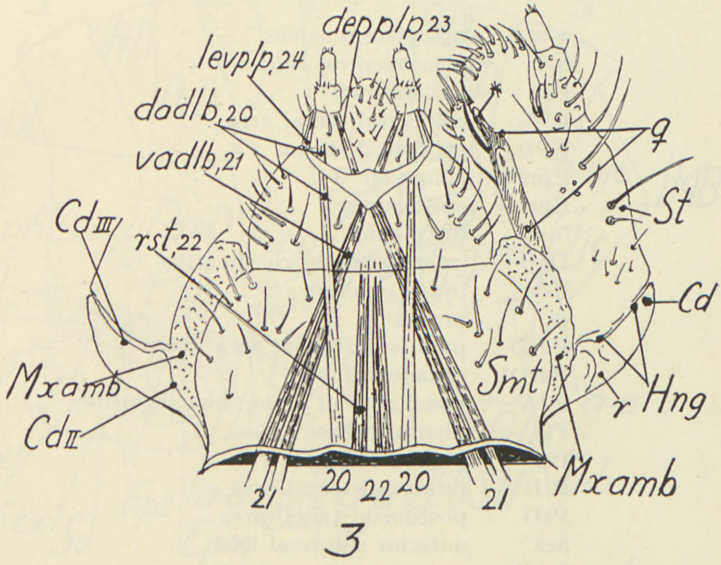
depplp,23
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CdIII
rst,22
q
St
Cd
Mxamb
CdII
Smt
r
Hng
Mxamb
21
20
22
20
21
3

Plate 7

Structures of the pyloric region with malpighian tubules; the crop; areas of thorax and the three anterior abdominal segments.

Fig. 1. Piece of pylorus with bases of malpighian tubules; exterior view.

Mal	malpighian tubule
Pyl	pylorus

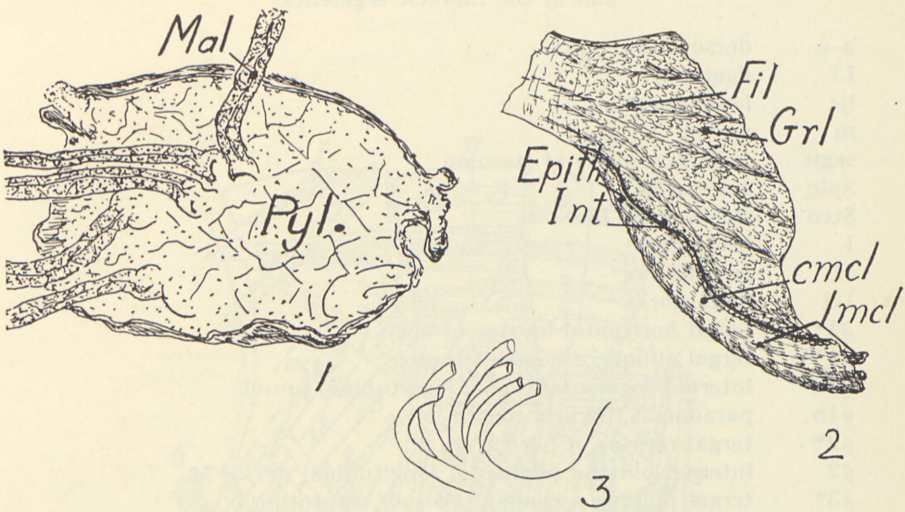
Fig. 2. Piece of anterior part of crop; mostly viewed from inside of the wall.

cmcl	circular fibers of muscle sheath covering the crop on the outside
Epith	epithelium
Fil	forward directed filaments from intima
Int	intima
lmcl	longitudinal fibers interiorly located in relation to circular fibers of muscle sheath which cover the crop on the outside

Fig. 3. Diagram indicating the number of malpighian tubules in anobiid larvae.

Fig. 4. Areas of the wall of thorax and the three anterior abdominal segments.

a–a	dorsopleural sulcus
b–b	pleuroventral sulcus
BSt	basisternum
EPI	epipleural tergal area
EPIs	epipleural sulcus
Epm	epimeron
Eps	episternum
furc	furca spot
IMB	intersegmental conjunctiva
ljc	lower junction
m	meron
ParD	paradorsal tergal area
ParDL	paradorsal line
PdA	pedal area of abdominal segment
Pl	pleural region
Pls	pleural sulcus
PrD	prodorsal tergal area
PsD	postdorsal tergal area
Scx′	anterior subcoxal lobe
Scx″	posterior subcoxal lobe
Sp	spiracle
SpA	spiracular area
Ss	spina spot
Stl	sternellar area
ujc	upper junction


Mal
Pyl.
1
Fil
Grl
Epith
Int
cmcl
lmcl
2
3

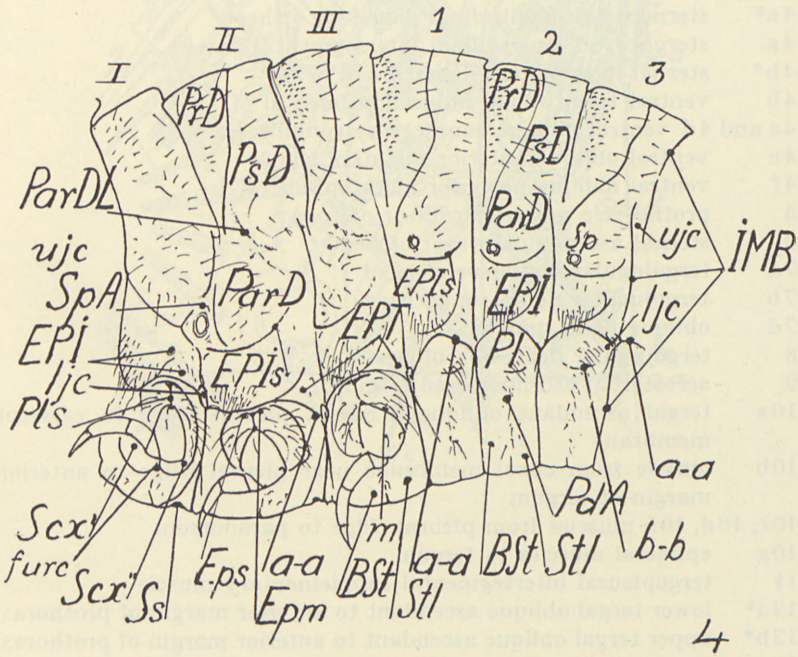

I
II
III
1
2
3
PrD
PsD
ParDL
ujc
SpA
EPi
ljc
Pls
ParD
EPIs
EPI
Pl
Sp
IMB
a-a
PdA
b-b
Scx
furc
Scx'
Ss
E.ps
Epm
m
BSt
Stl
4

Plate 8

Diagram of the ventral musculature and the musculature of the right half of the thoracic segments.

a–a dorsopleural sulcus
Li ligament
ljc lower junction
m meron
sagit sagittal midline of sternum
Spin spina spot
Stco sternocostal line
I prothorax
II mesothorax
III metathorax
#1* tergal horizontal levator of head
#1** tergal oblique ascendant muscle
#1a internal segmental dorsal longitudinal muscle
#1b paradorsal thoracic muscle
#2* tergal rotator of head
#2 internal oblique segmental longitudinal dorsal M.
#3* tergal oblique ascendant to roof of prothorax
#3 and 3′ external sectional dorsal muscles
#4a* sternocostal longitudinal depressor of head
#4a sternocostal longitudinal intersegmental muscle
#4b* sternal longitudinal depressor of head
#4b ventral longitudinal internal segmental M.
#4c and 4d ventral oblique counterwise running spina M.
#4e ventral oblique anterior metathoracic M.
#4f ventral oblique posterior metathoracic M.
#5 prothoracic posterior rotator of coxa
#6 sternal ascendant levator of head
#7a tergojugular depressor of head
#7b tergojugular depressor of head
#7d oblique flank muscle
#8 tergojugular depressor of head
#9 acrosternal ascendants to tergum
#10a tergal ascendant oblique M. from pleural ridge to cervical membrane
#10b muscle from coxal membrane near pleural ridge to anterior margin of tergum
#10c, 10d, 10f muscles from pleural ridge to paradorsum
#10g epimeral muscles to tergum
#11 tergopleural intersegmental supplementary muscle
#12a* lower tergal oblique ascendant to anterior margin of prothorax
#12b* upper tergal oblique ascendant to anterior margin of prothorax
#12a, 12b oblique flank muscles in meso- and metathorax
#12c thoracic conjunctival muscle
#13 epipleural fan-shaped bundle of muscle fibers

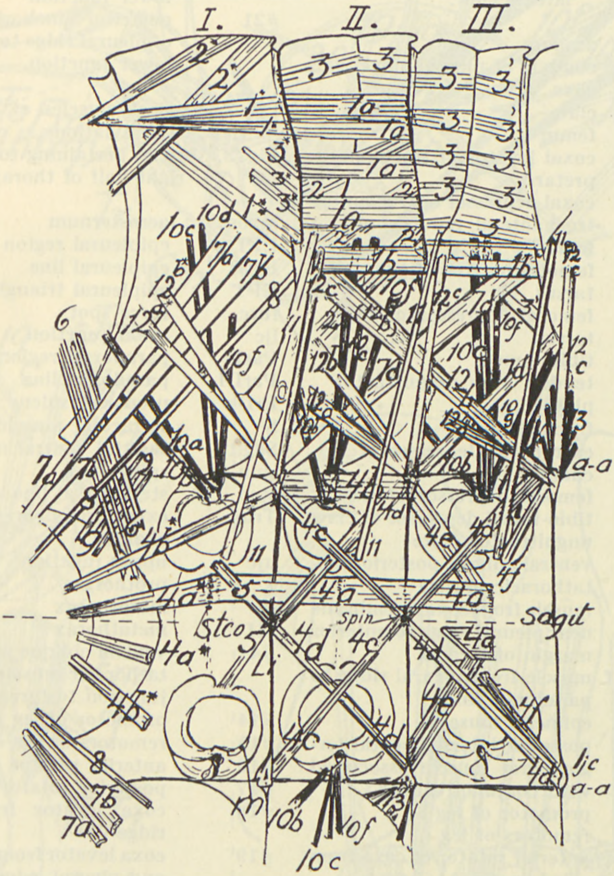

I.
II.
III.
Sagit
spin
stco
a-a
ljc
Li
M

Plate 9

Diagrams of the musculature of the legs.

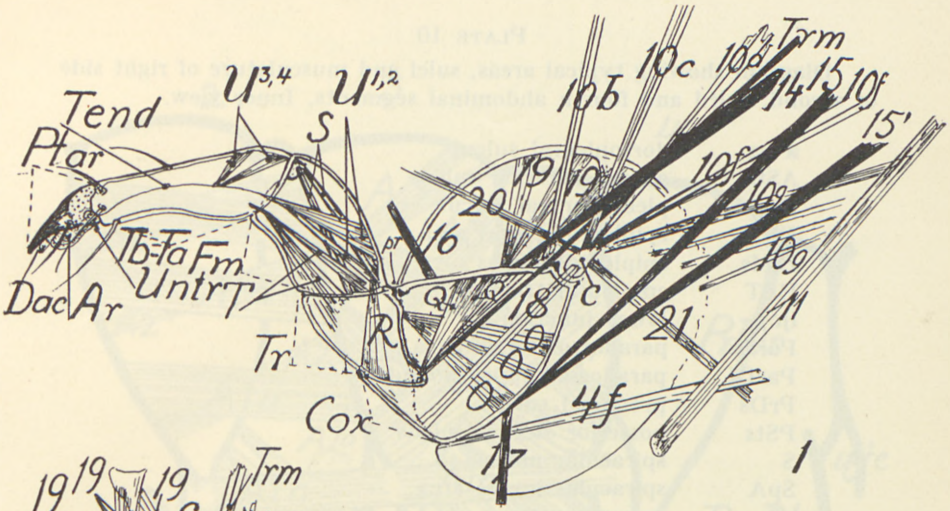
Fig. 1. Typical muscles of the third leg; lateral view.

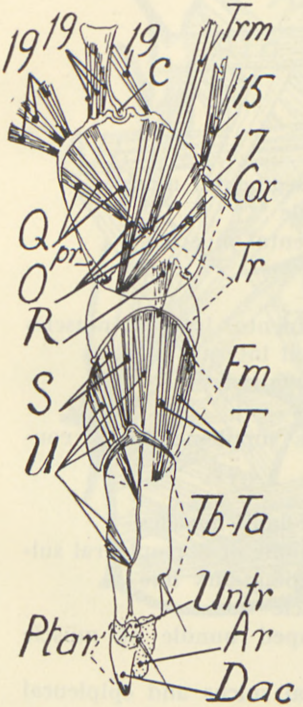
Ar	arolium
c	condyle of pleural ridge
Cox	coxa
Dac	claw
Fm	femur
O	coxal levator of trochanter
Ptar	pretarsus
Q	coxal depressor of trochanter
R	trochanteral reductor of femur
S	femoral levator of tibio-tarsus
T	femoral depressor of tibio-tarsus
Tb-Ta	tibio-tarsus
Tend	tendon from unguitractor plate
Tr	trochanter
Trm	extracoxal depressor of trochanter
$U^{1, 2}$	femoral depressor of claw
$U^{3, 4}$	tibio-tarsal depressor of claw
Untr	unguitractor plate
#4f	ventral oblique posterior metathoracic muscle
#10b	muscle from coxal membrane near pleural ridge to anterior margin of tergum
#10c, d, f	muscle from pleural ridge to paradorsal line
#10g	epimeral muscles
#11	posterior intersegmental tergopleural muscle associated with conjunctival M.
#14	promotor of leg
#15, 15'	remotors of leg
#16	anterior rotator of coxa from spina spot
#17	posterior rotator of coxa
#18	levator of coxa from pleural ridge
#19	levator of coxa from episternum and pleural ridge
#20	anterior anchoring muscle of pleural ridge to preceeding lower junction
#21	posterior anchoring muscle of pleural ridge to succeeding lower junction

Fig. 2. Typical muscles of leg. Dorsal view. (Abbreviations as of fig. 1).

Fig. 3. Muscles pertaining to the legs of right half of thorax.

acrost	acrosternum
EPI	epipleural region
EPIs	epipleural line
EPT	epipleural triangle
furc	furca spot
ljc	lower junction
ParD	paradorsal region
ParDL	paradorsal line
PrDs	prodorsal sulcus
S	spiracular muscle
Sagit	sagittal ventral midline
spin	spina spot
stco	sternocoxal line
Trm	extracosal depressor of trochanter
ujc	upper junction
I	prothorax
II	mesothorax
III	metathorax
#4f	ventral oblique posterior metathoracic muscle from lower junction to furca spot
#14	promotor of leg
#15	remotors of leg
#16	anterior rotator of coxa
#17	posterior rotator of coxa
#18	coxa levator from pleural ridge
#19	coxa levator from episternum and pleural ridge
#20	anterior anchoring muscle of pleural ridge to preceeding lower junction
#21	posterior anchoring muscle of pleural ridge to succeeding lower junction


Tend
Ptar
U3,4
U1,2
S
Tb-Ta
Fm
Untr
T
Dac
Ar
Tr
R
Q
pr
16
20
19
19
10b
10c
10d
Trm
14
15
10f
15'
10e
10g
18
c
21
11
Cox
4f
17
1


19
19
19
c
Trm
15
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Cox
Q
pr
O
R
Tr
S
Fm
U
T
Tb-Ta
Untr
Ptar
Ar
Dac
2

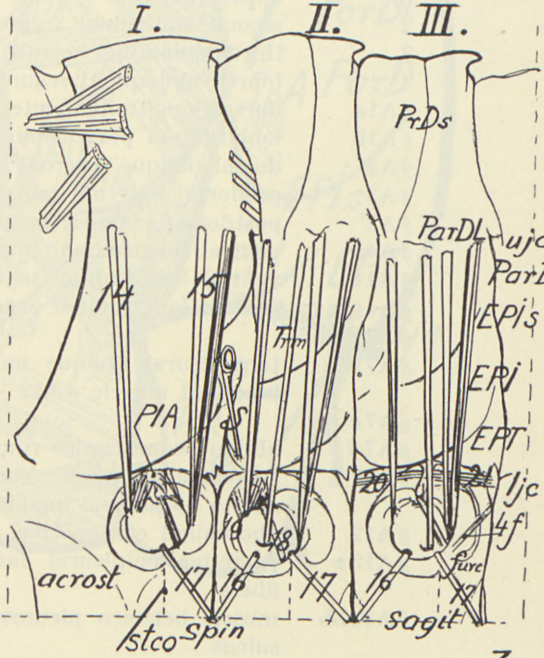

I.
II.
III.
PrDs
ParDL
ujc
ParD
EPi's
EPi
EPT
ljc
4f
furc
14
15
Trm
9
PlA
20
21
18
17
16
acrost
Stco
Spin
sagit
3

Plate 10

Diagram showing typical areas, sulci and musculature of right side of second, third and fourth abdominal segments. Inner view.

a—a	dorsopleural sulcus
ASts	anterior sternal sulcus
b—b	pleuroventral sulcus
EPI	epipleural tergal area
EPIs	epipleural sulcus
EPT	epipleural triangle
ljc	lower junction
ParD	paradorsal tergal area
ParDl	paradorsal upper boundary
PrDs	prodorsal sulcus
PSts	posterior sternal sulcus
S	spiracular muscle
SpA	spiracular tergal area
ujc	upper junction
2	second abdominal segment
3	third abdominal segment
4	fourth abdominal segment
#A1a	dorsal longitudinal internal segmental muscle
#A1b	longitudinal paradorsal muscle
#A2	dorsal oblique internal segmental muscles
#A3	prodorsal external muscles
#A3′	postdorsal external muscles
#A4a	ventral longitudinal intersegmental internal muscles
#A4b	ventral longitudinal segmental internal muscles
#A4g	ventral longitudinal external muscles
#A7a and #A7b	tergopleural oblique muscles supplemental to conjunctival muscle #A12
#A7c and #A7d	oblique counterwise running flank muscles
#A10	tergopleural muscles from middle of dorsopleural sulcus to paradorsal imaginary boundary line
#A12	abdominal conjunctival muscle
#A13a	posterior epipleural fan-shaped bundle of muscle fibers
#A13bb	muscle between pleuroventral sulcus and epipleural sulcus
#A13c	anterior epipleural fan-shaped bundle of muscle fibers

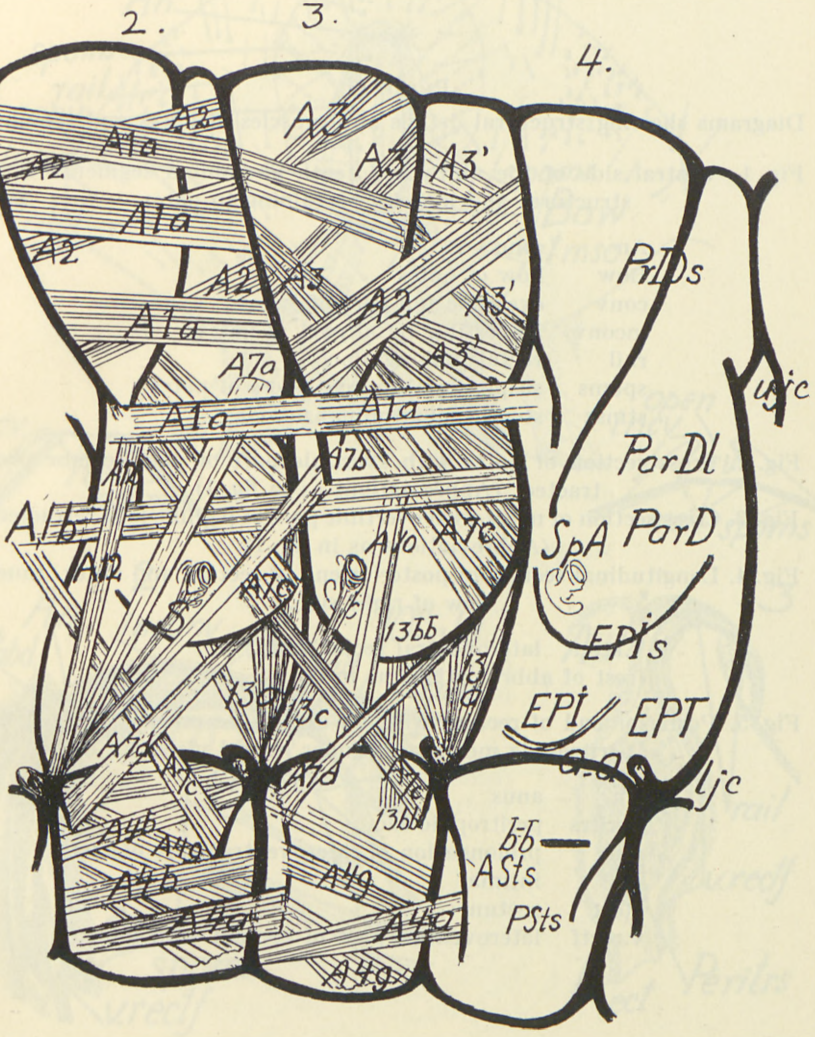

2.
3.
4.
A1a
A2
A3
A3'
A7a
A7b
A7c
A4a
A4b
A4c
A4d
PrDs
ParDl
ParD
SpA
EPIs
EPI
EPT
ljc
ujc
bb
ASts
PSts

Plate 11

Diagrams showing structural details and muscles of nates and rectum.

Fig. 1. Ventral side of the ninth and tenth abdominal segments with structures and muscles pertaining to nates.

An	anus
Bow	bow of nates
conv	evertible top-part of nates
inconv	inevertible basal part of nates
rail	rectal prolongation
spoms	suspensorial muscle fibers of nates
stmsc	sternal longitudinal muscles

Fig. 2. Cross section of nates with evertible part of padlike lobe protracted. (Abbreviations as in fig. 1).

Fig. 3. Cross section of nates with evertible part of padlike lobe retracted. (Abbreviations as in fig. 1).

Fig. 4. Longitudinal section of posterior end of rectum and nates. Inner view of right side.

v.rectf	lateroventral rectal fold

(rest of abbreviations as in fig. 1)

Fig. 5. Posterior end of rectum with an excremate mass enveloped by peritrophic membrane. Inner lateral view.

An	anus
Peritrs	peritrophic sac
rail	prolongation of lateroventral part of rectal intima
Rect	rectum
v.rectf	lateroventral part of rectum with fold

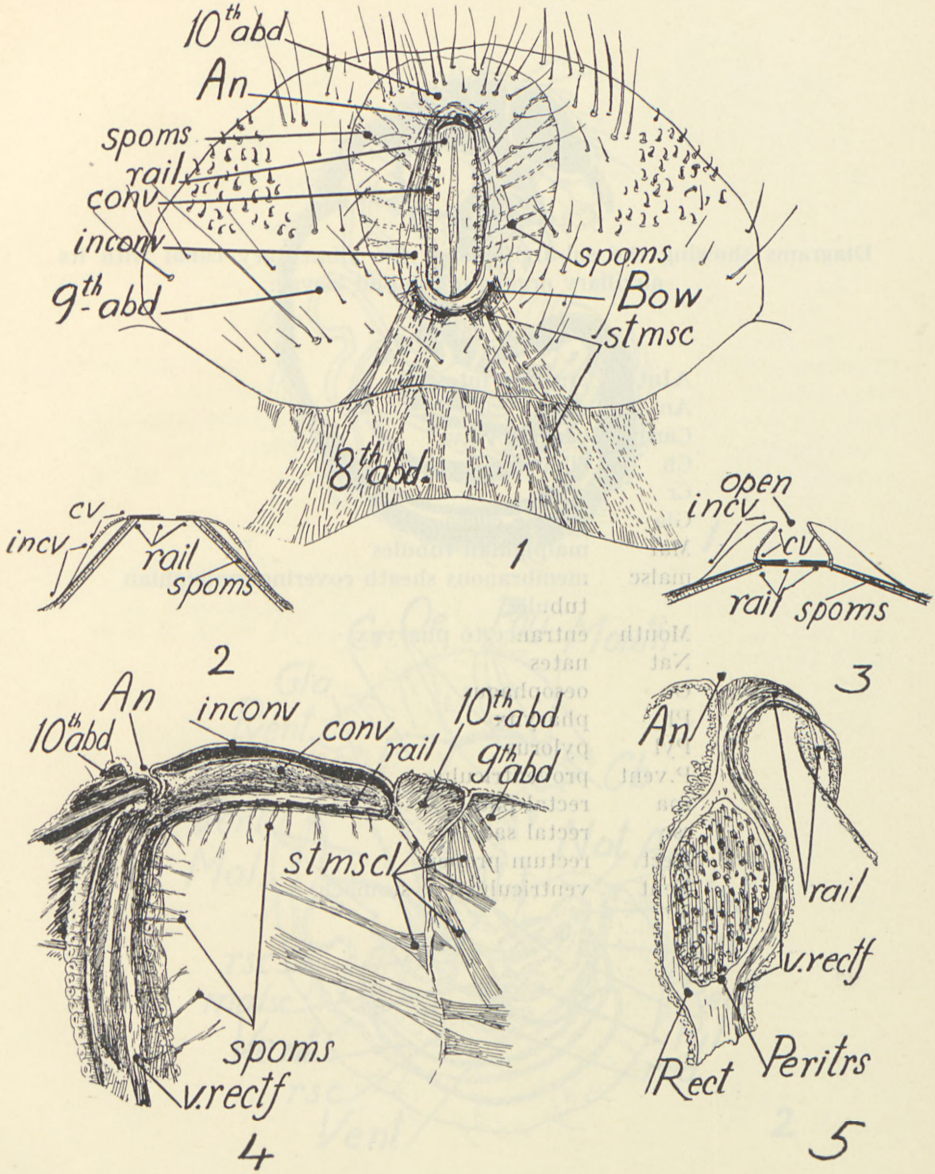

10th abd
An
spoms
rail
conv
inconv
9th abd
spoms
Bow
stmsc
8th abd.
1
cv
incv
rail
spoms
2
open
incv
cv
rail
spoms
3
An
10th abd
inconv
conv
rail
10th abd
9th abd
stmscl
spoms
v.rectf
4
An
rail
v.rectf
Rect
Peritrs
5

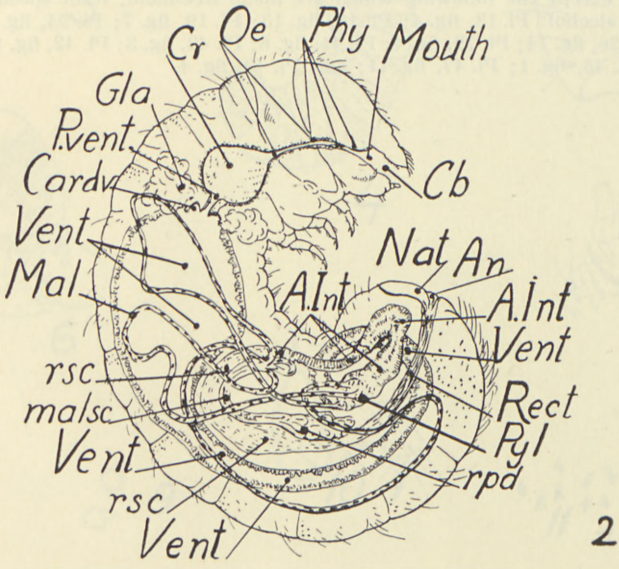
PLATE 12

Diagrams showing the subdivisions of the alimentary canal with its auxiliary organs in anobiid larvae.

Figs. 1 and 2.

AInt	anterior intestine
An	anus
Cardv	cardiac valve
Cb	cibarium, preoral cavity
Cr	crop
Gla	gastric coeca
Mal	malpighian tubules
malsc	membranous sheath covering malpighian tubules
Mouth	entrance to pharynx
Nat	nates
Oe	oesophagus
Phy	pharynx
Pyl	pylorus
P.vent	proventriculus
rpa	rectal pad
rsc	rectal sac
Rect	rectum proper
Vent	ventriculus (= stomach)

1

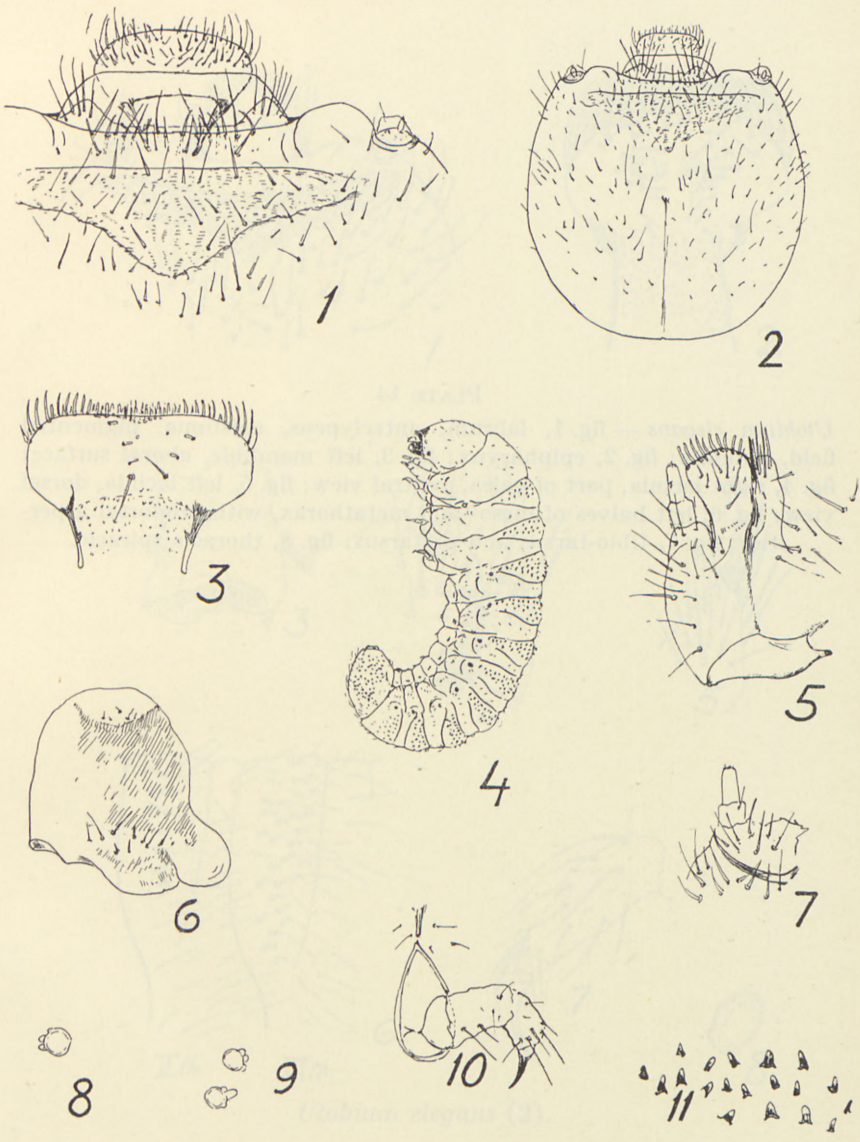

Cr
Oe
Phy
Mouth
Gla
P.vent
Cardv
Vent
Mal
Cb
Nat An
A.Int
A.Int
Vent
Rect
Pyl
rpd
rsc
malsc
Vent
rsc
Vent

2

Plate 13[1]

Catorama gracilis — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 2, cranium, dorsal view; fig. 3, epipharynx; fig. 4, larva, left side; fig. 5, right maxilla, ventral view; fig. 6, right mandible, aboral surface; fig. 7, right half of prelabium, ventral view; fig. 8, thoracic spiracle; fig. 9, two abdominal spiracles; fig. 10, leg; fig. 11, asperities.

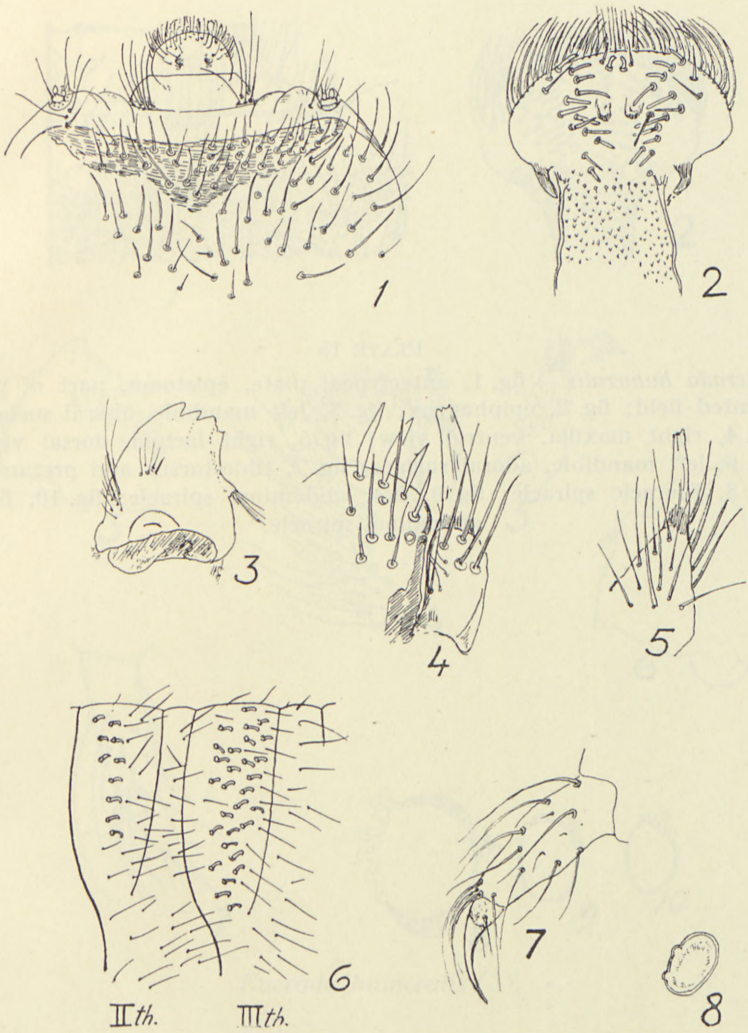
[1] All figures on plate 13 to 50 are drawn with camera lucida from structures on slides, except the following which are made free-hand, from specimens preserved in alcohol: Pl. 13, fig. 4; Pl .18, fig. 13; Pl. 19, fig. 7; Pl. 24, fig. 1; Pl. 26, fig. 8; Pl. 26, fig. 14; Pl. 29, fig. 4; Pl. 41, fig. 6; Pl. 42, fig. 3; Pl. 42, fig. 16; Pl. 44, fig. 10; Pl. 46, fig. 1; Pl. 47, fig. 11; and Pl. 49, fig. 4.



Catorama gracilis (1).

Plate 14

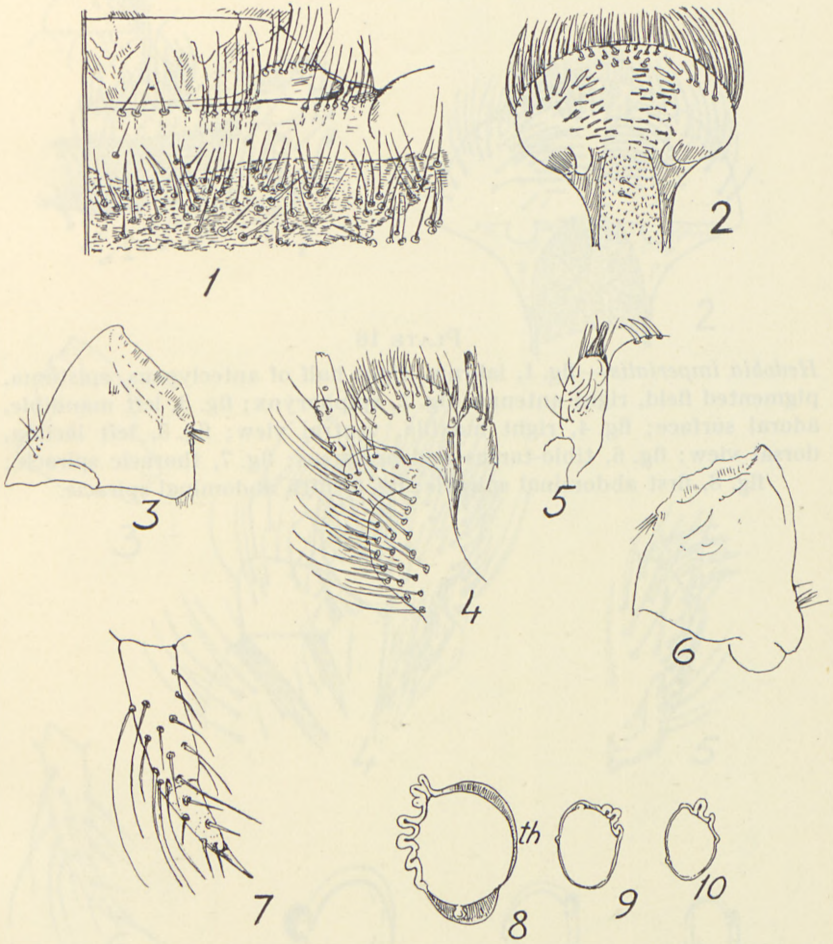
Utobium elegans — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, right lacinia, part of galea, ventral view; fig. 5, left lacinia, dorsal view; fig. 6, left halves of meso- and metathorax, with prodorsal asperities; fig. 7, tibio-tarsus and pretarsus; fig. 8, thoracic spiracle.



Utobium elegans (2).

PLATE 15

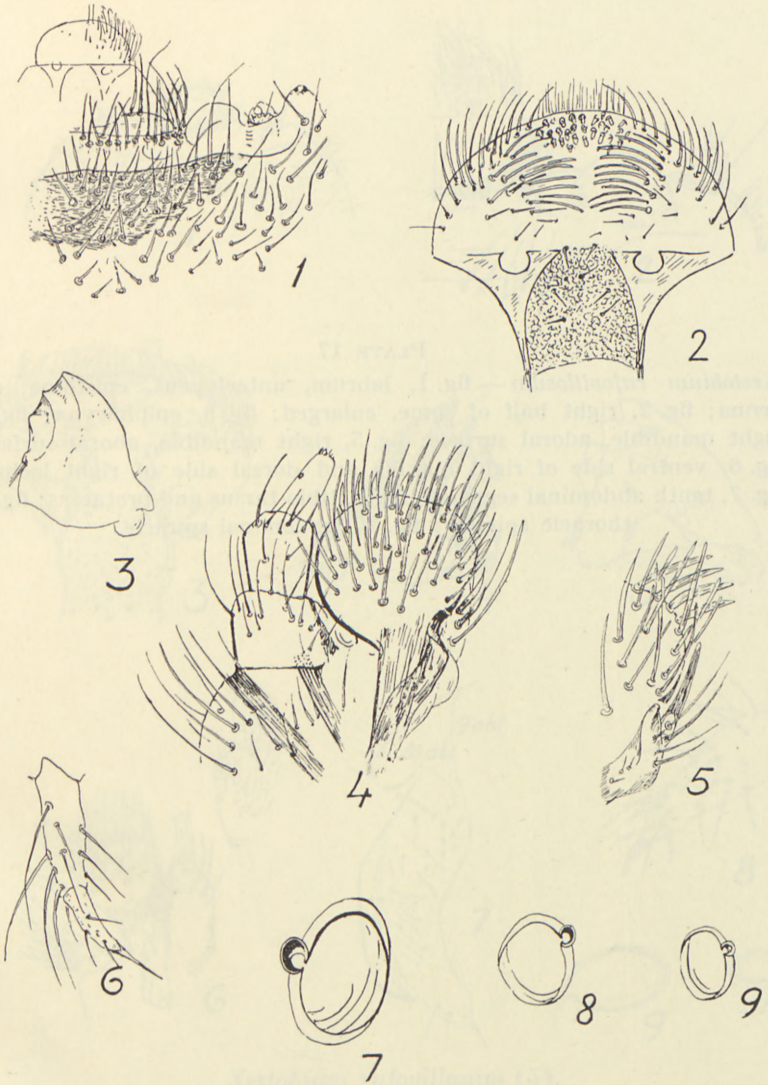
Eucrada humeralis — fig. 1, anteclypeal plate, epistoma, part of pigmented field; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, right maxilla, ventral view; fig. 5, right lacinia, dorsal view; fig. 6, left mandible, adoral surface; fig. 7, tibio-tarsus and pretarsus; fig. 8, thoracic spiracle; fig. 9, first abdominal spiracle; fig. 10, fifth abdominal spiracle.



Eucrada humeralis (3).

PLATE 16

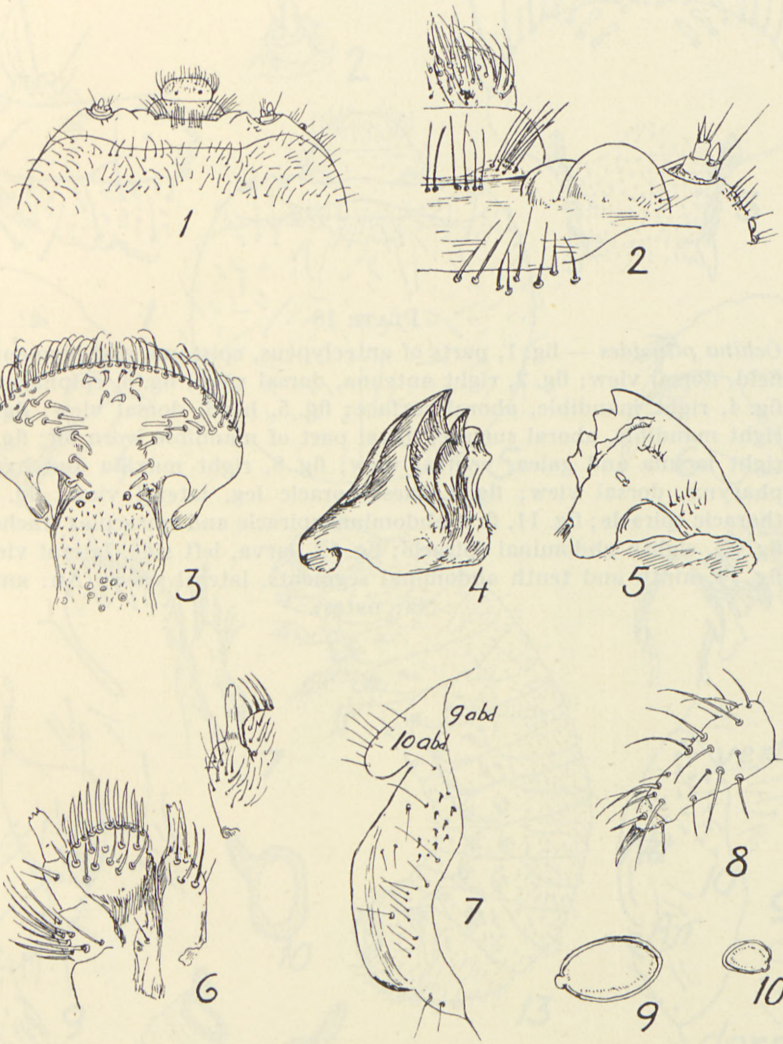
Hedobia imperialis—fig. 1, labrum, right half of anteclypeus, epistoma, pigmented field, right antenna; fig. 2, epipharynx; fig. 3, left mandible, adoral surface; fig. 4, right maxilla, ventral view; fig. 5, left lacinia, dorsal view; fig. 6, tibio-tarsus and pretarsus; fig. 7, thoracic spiracle; fig. 8, first abdominal spiracle; fig. 9, fifth abdominal spiracle.



Hedobia imperialis (4).

PLATE 17

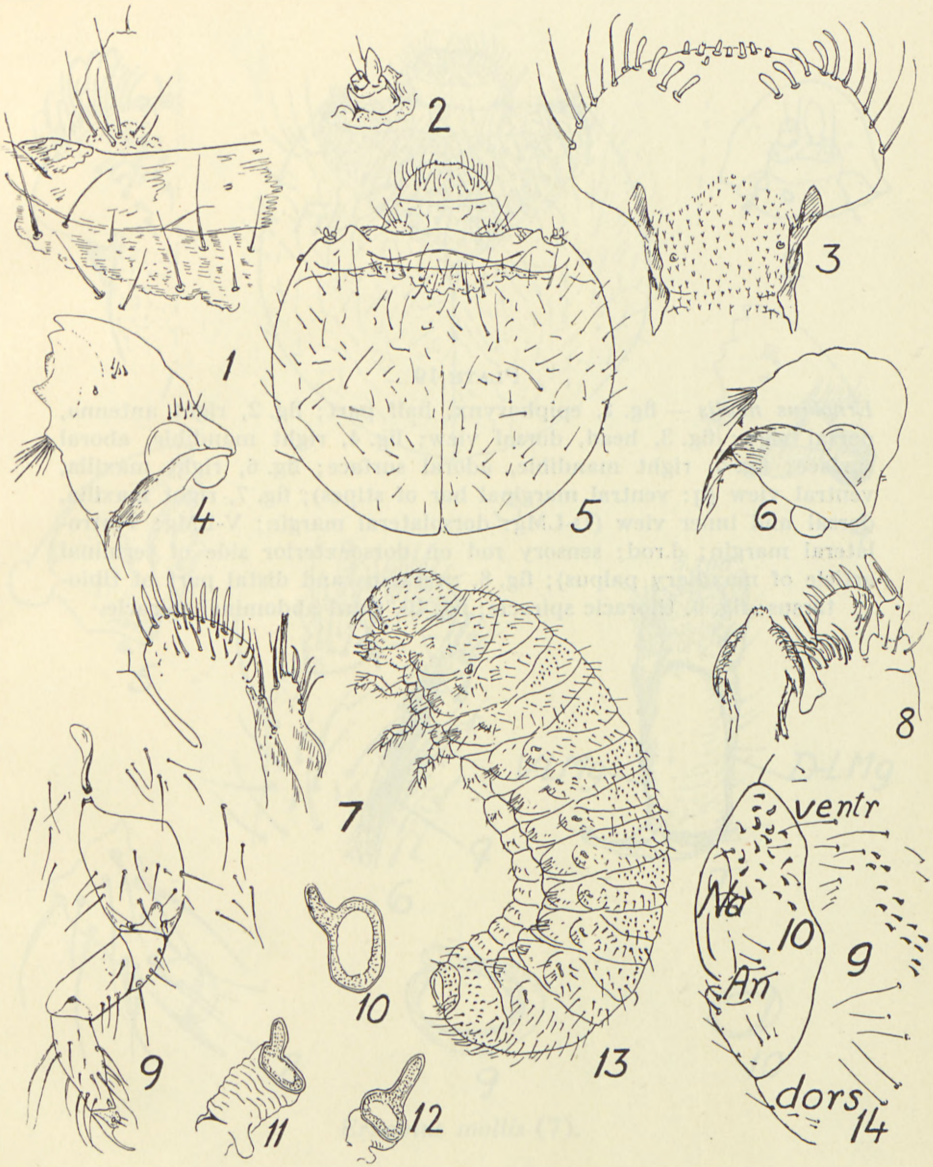
Xestobium rufovillosum — fig. 1, labrum, anteclypeus, epistoma, antenna; fig. 2, right half of same, enlarged; fig. 3, epipharynx; fig. 4, right mandible, adoral surface; fig. 5, right mandible, aboral surface; fig. 6, ventral side of right maxilla and dorsal side of right lacinia; fig. 7, tenth abdominal segment; fig. 8, tibio-tarsus and pretarsus; fig. 9, thoracic spiracle; fig. 10, abdominal spiracle.



Xestobium rufovillosum (5).

Plate 18

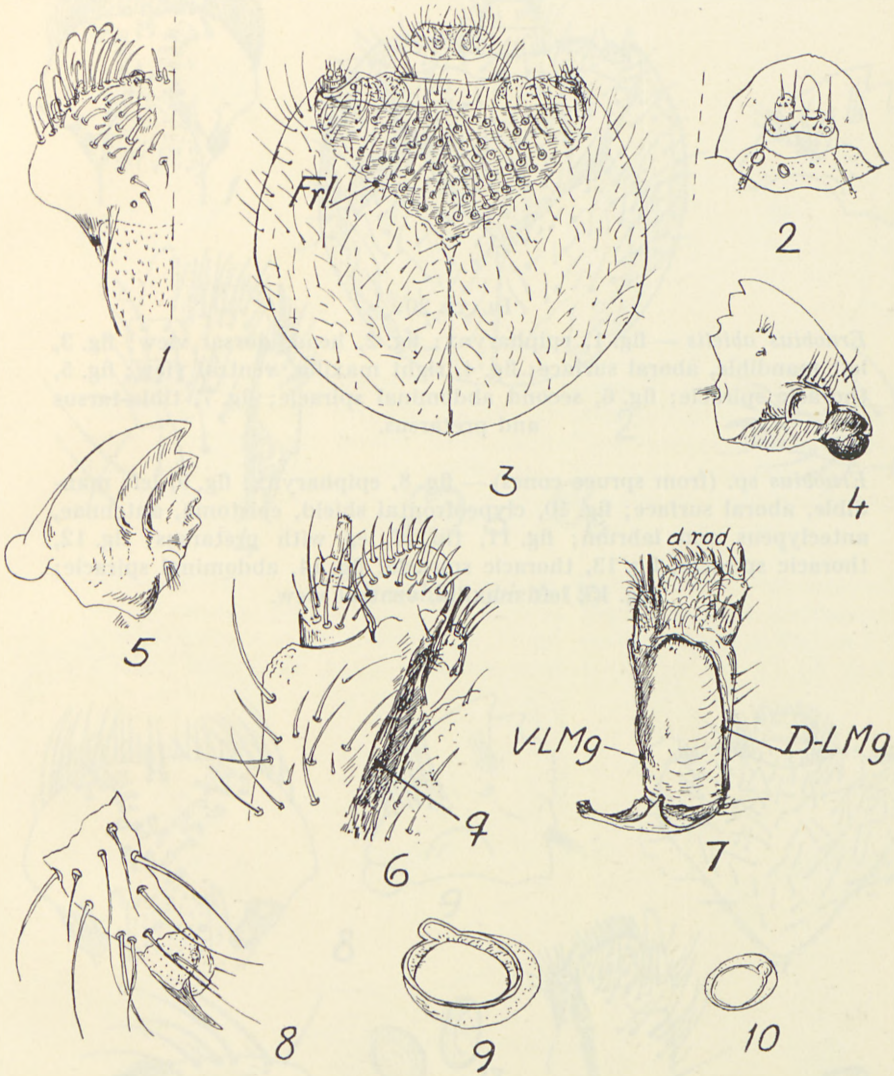
Ochina ptinoides — fig. 1, parts of anteclypeus, epistoma and pigmented field, dorsal view; fig. 2, right antenna, dorsal view; fig. 3, epipharynx; fig. 4, right mandible, aboral surface; fig. 5, head, dorsal view; fig. 6, right mandible, aboral surface, distal part of mandible worn off; fig. 7, right lacinia and galea, ventral view; fig. 8, right maxilla and hypopharynx, dorsal view; fig. 9, mesothoracic leg, lateral view; fig. 10, thoracic spiracle; fig. 11, first abdominal spiracle and spiracular trachea; fig. 12, eighth abdominal spiracle; fig. 13, larva, left side, lateral view; fig. 14, ninth and tenth abdominal segments, lateral view; (An: anus; Na: nates).



Ochina ptinoides (6).

Plate 19

Ernobius mollis — fig. 1, epipharynx, half part; fig. 2, right antenna, dorsal view; fig. 3, head, dorsal view; fig. 4, right mandible, aboral surface; fig. 5, right mandible, adoral surface; fig. 6, right maxilla, ventral view (q: ventral marginal bar of stipes); fig. 7, right maxilla, dorsal and inner view (D-LMg: dorsolateral margin; V-LMg: ventrolateral margin; d.rod: sensory rod on dorsoexterior side of terminal article of maxillary palpus); fig. 8, pretarsus and distal part of tibiotarsus; fig. 9, thoracic spiracle; fig. 10, third abdominal spiracle.

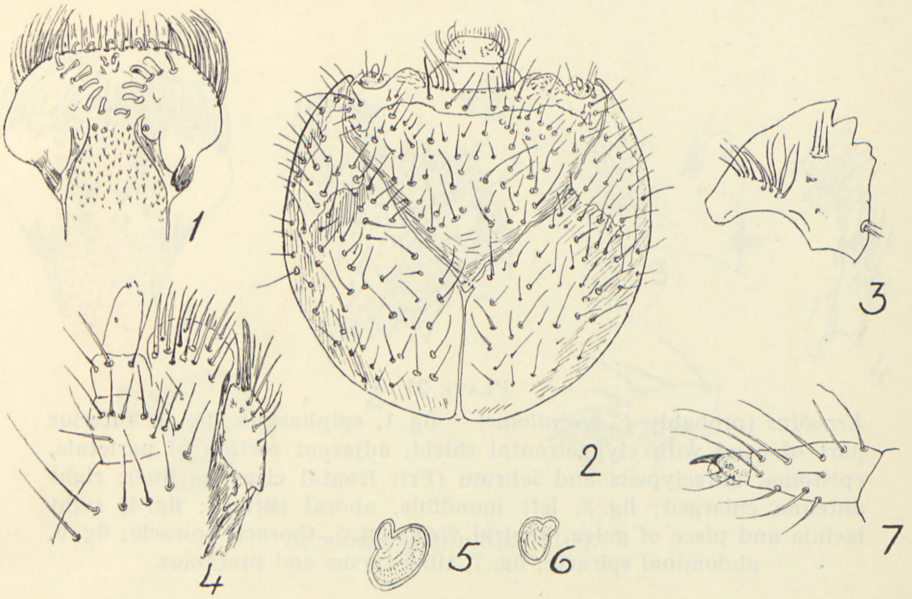


Ernobius mollis (7).

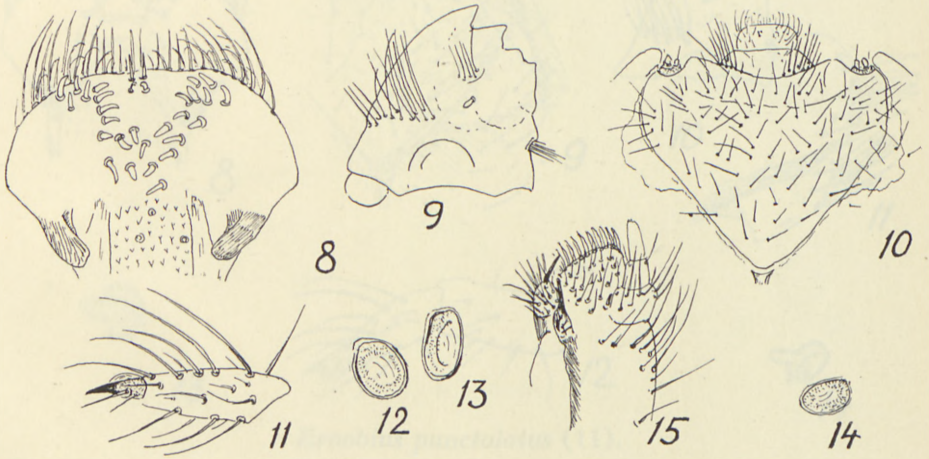
Plate 20

Ernobius abietis — fig. 1, epipharynx; fig. 2, head, dorsal view; fig. 3, left mandible, aboral surface; fig. 4, right maxilla, ventral view; fig. 5, thoracic spiracle; fig. 6, second abdominal spiracle; fig. 7, tibio-tarsus and pretarsus.

Ernobius sp. (from spruce cones) — fig. 8, epipharynx; fig. 9, left mandible, aboral surface; fig. 10, clypeofrontal shield, epistoma, antennae, anteclypeus and labrum; fig. 11, tip of leg with pretarsus; fig. 12, thoracic spiracle; fig. 13, thoracic spiracle; fig. 14, abdominal spiracle; fig. 15, left maxilla, ventral view.



Ernobius abietis (8).

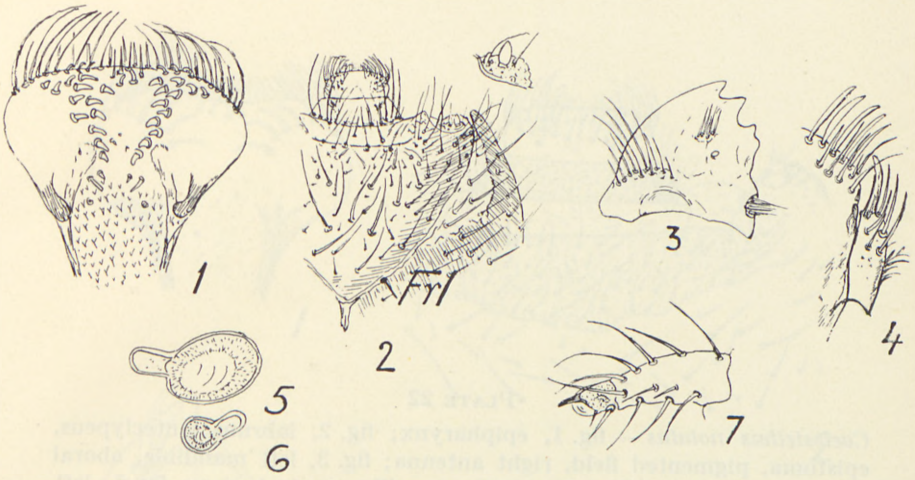


Ernobius sp.-ex spruce cone (9).

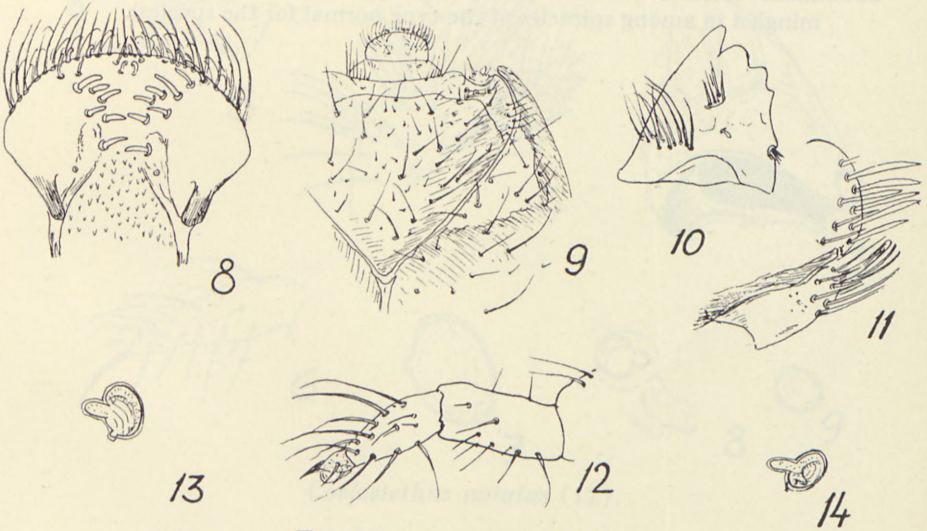
PLATE 21

Ernobius (probably *E. granulatus*) — fig. 1, epipharynx; fig. 2, anterior part of head with clypeofrontal shield, adjacent section of parietale, epistoma, anteclypeus and labrum (Frl: frontal cleavage line); right antenna enlarged; fig. 3, left mandible, aboral surface; fig. 4, right lacinia and piece of galea, ventral view; fig. 5, thoracic spiracle; fig. 6, abdominal spiracle; fig. 7, tibio-tarsus and pretarsus.

Ernobius punctulatus — fig. 8, epipharynx; fig. 9, piece of right parietale, clypeofrons, epistoma, right antenna, anteclypeus and labrum; fig. 10, left mandible, aboral surface; fig. 11, right lacinia, piece of galea, ventral view; fig. 12, leg; fig. 13, thoracic spiracle; fig. 14, abdominal spiracle.



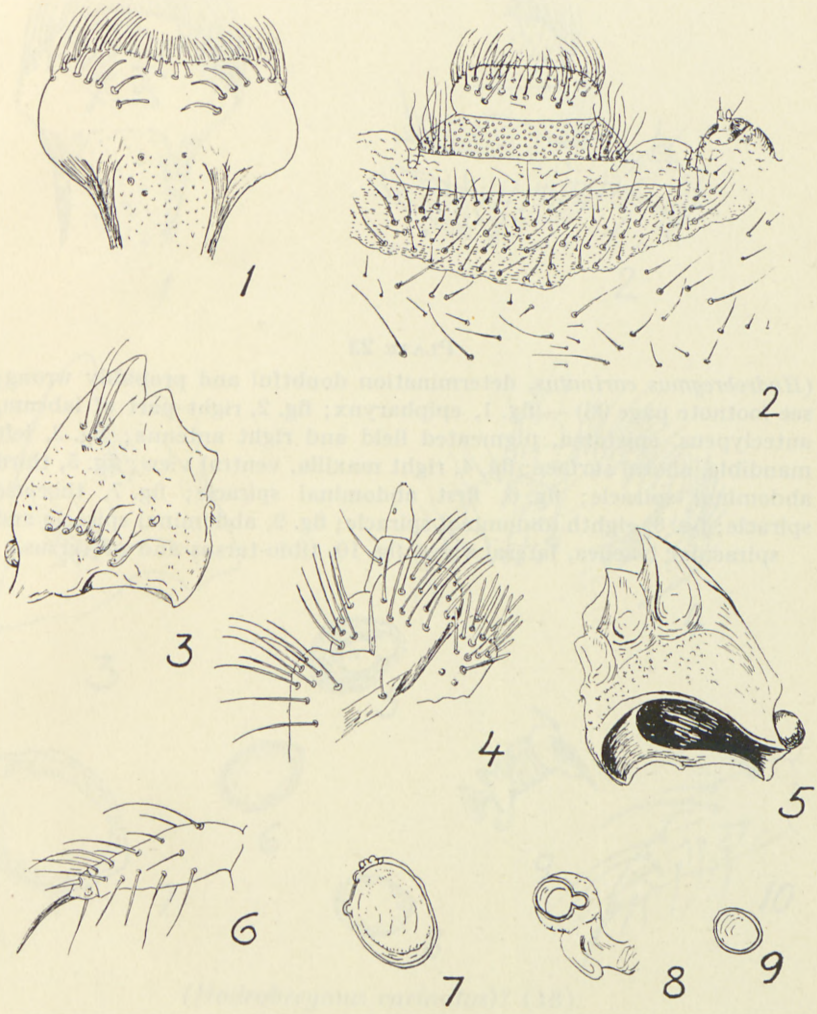
Ernobius granulatus (10).



Ernobius punctulatus (11).

PLATE 22

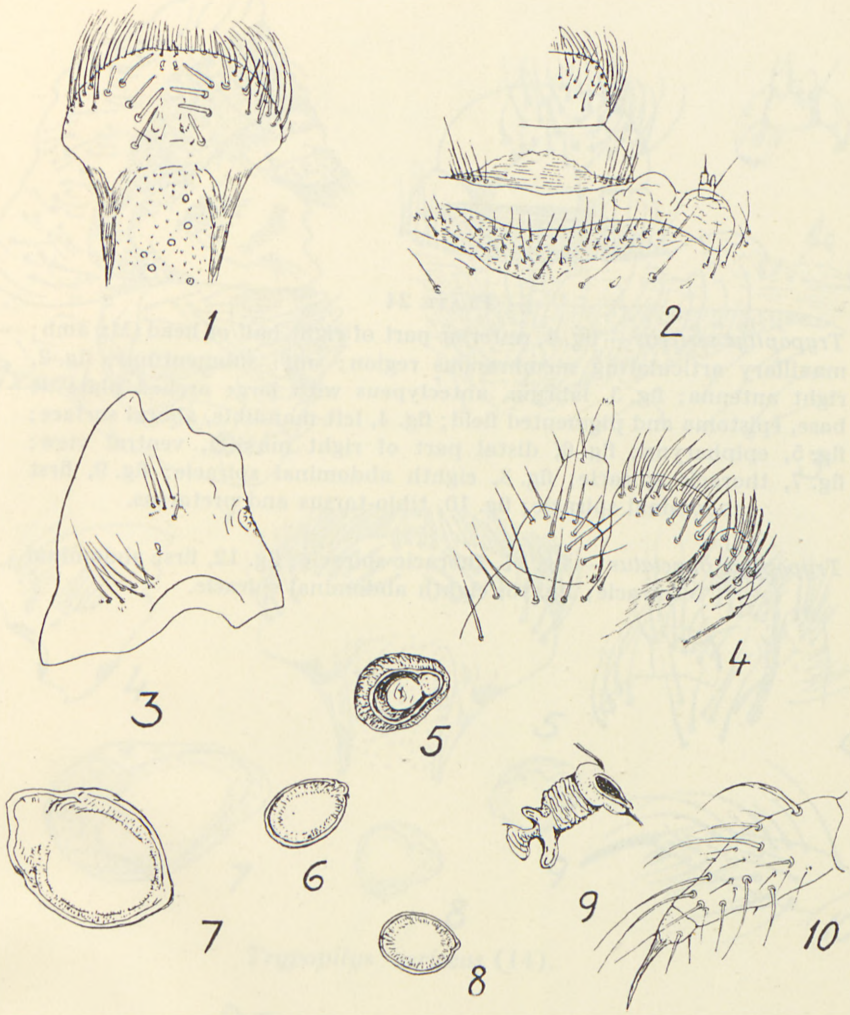
Coelostethus notatus — fig. 1, epipharynx; fig. 2, labrum, anteclypeus, epistoma, pigmented field, right antenna; fig. 3, left mandible, aboral surface; fig. 4, distal part of right maxilla, ventral view; fig. 5, left mandible, adoral view; fig. 6, tibio-tarsus and pretarsus; fig. 7, thoracic spiracle; fig. 8, abdominal spiracle (normal type in this species); fig. 9, abdominal spiracle (as it occasionally appears in some specimens, mingled in among spiracles of the type normal for the species).



Coelostethus notatus (12).

PLATE 23

(*Hadrobregmus carinatus*, determination doubtful and probably wrong; see footnote page 96) — fig. 1, epipharynx; fig. 2, right part of labrum, anteclypeus, epistoma, pigmented field and right antenna; fig. 3, left mandible, aboral surface; fig. 4, right maxilla, ventral view; fig. 5, third abdominal spiracle; fig. 6, first abdominal spiracle; fig. 7, thoracic spiracle; fig. 8, eighth abdominal spiracle; fig. 9, abdominal spiracle and spiracular trachea, lateral view; fig. 10, tibio-tarsus and pretarsus.

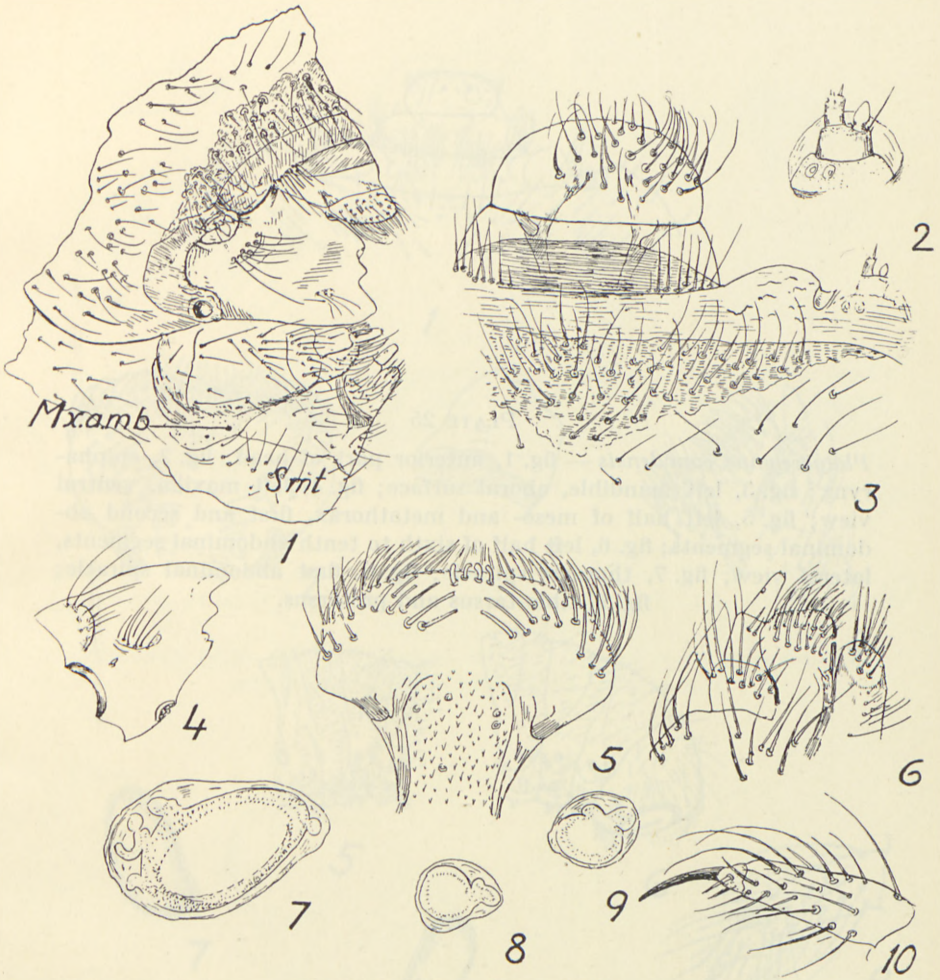


(Hadrobregmus carinatus)? (13).

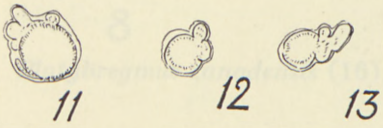
Plate 24

Trypopitys sericeus — fig. 1, anterior part of right half of head (Mx amb: maxillary articulating membranous region; smt: submentum); fig. 2, right antenna; fig. 3, labrum, anteclypeus with large arched plate at base, epistoma and pigmented field; fig. 4, left mandible, aboral surface; fig. 5, epipharynx; fig. 6, distal part of right maxilla, ventral view; fig. 7, thoracic spiracle; fig. 8, eighth abdominal spiracle; fig. 9, first abdominal spiracle; fig. 10, tibio-tarsus and pretarsus.

Trypopitys punctatus — fig. 11, thoracic spiracle; fig. 12, first abdominal spiracle; fig. 13, eighth abdominal spiracle.



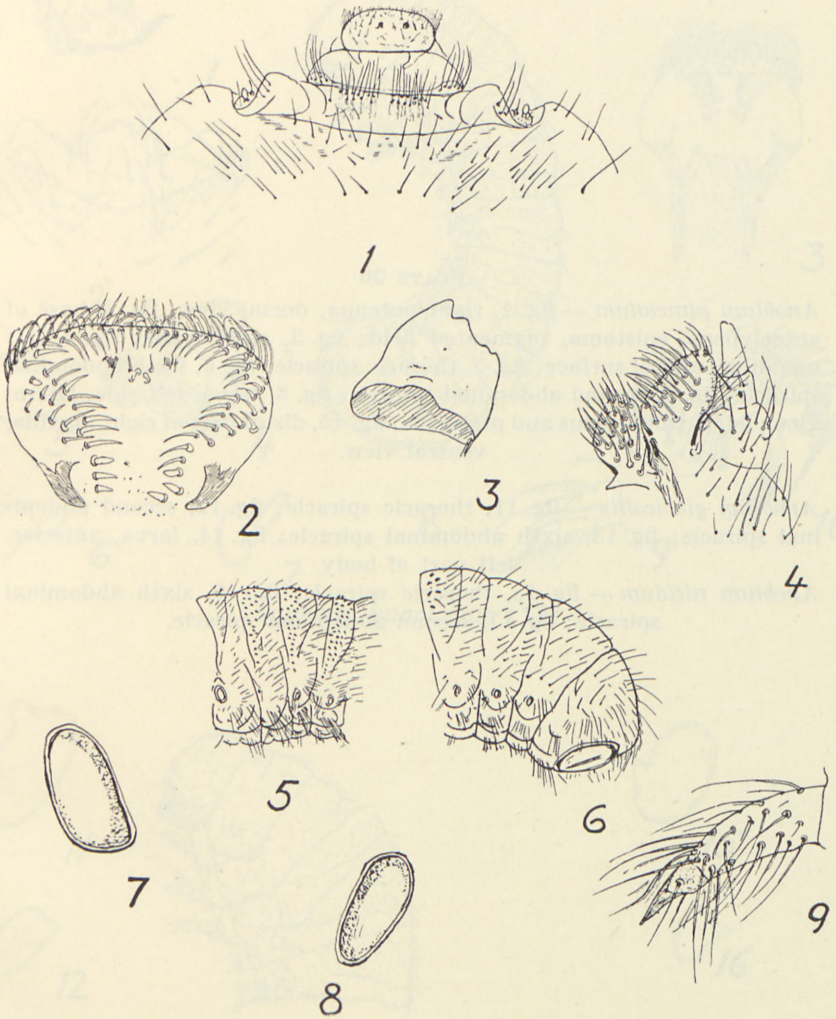
Trypopitys sericeus (14).



Trypopitys punctatus (15).

PLATE 25

Platybregmus canadensis — fig. 1, anterior part of head; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, left maxilla, ventral view; fig. 5, left half of meso- and metathorax, first and second abdominal segments; fig. 6, left half of sixth to tenth abdominal segments, lateral view; fig. 7, thoracic spiracle; fig. 8, first abdominal spiracle; fig. 9, tibio-tarsus and pretarsus.



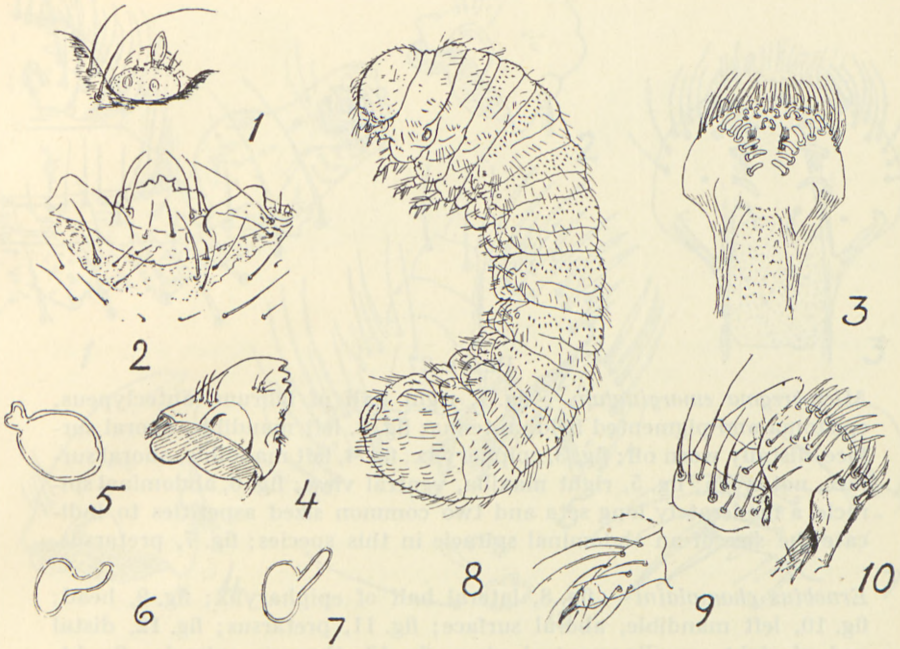
Platybregmus canadensis (16).

PLATE 26

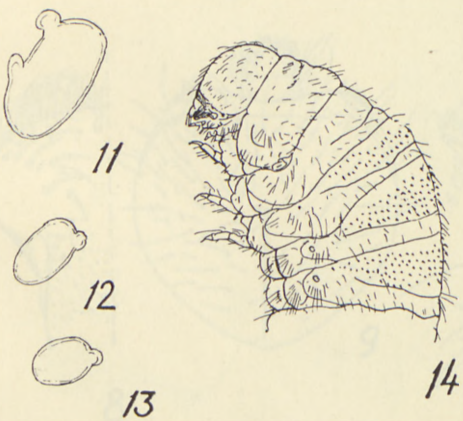
Anobium punctatum — fig. 1, right antenna, dorsal view; fig. 2, base of anteclypeus, epistoma, pigmented field; fig. 3, epipharynx; fig. 4, left mandible, aboral surface; fig. 5, thoracic spiracle; fig. 6, sixth abdominal spiracle; fig. 7, second abdominal spiracle; fig. 8, larva, left side, lateral view; fig. 9, tibio-tarsus and pretarsus; fig. 10, distal part of right maxilla, ventral view.

Anobium gibbicollis — fig. 11, thoracic spiracle; fig. 12, second abdominal spiracle; fig. 13, sixth abdominal spiracle; fig. 14, larva, anterior, left part of body.

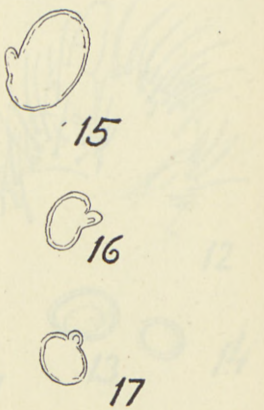
Anobium nitidum — fig. 15, thoracic spiracle; fig. 16, sixth abdominal spiracle; fig. 17, second abdominal spiracle.



Anobium punctatum (17).



Anobium gibbicollis (18).

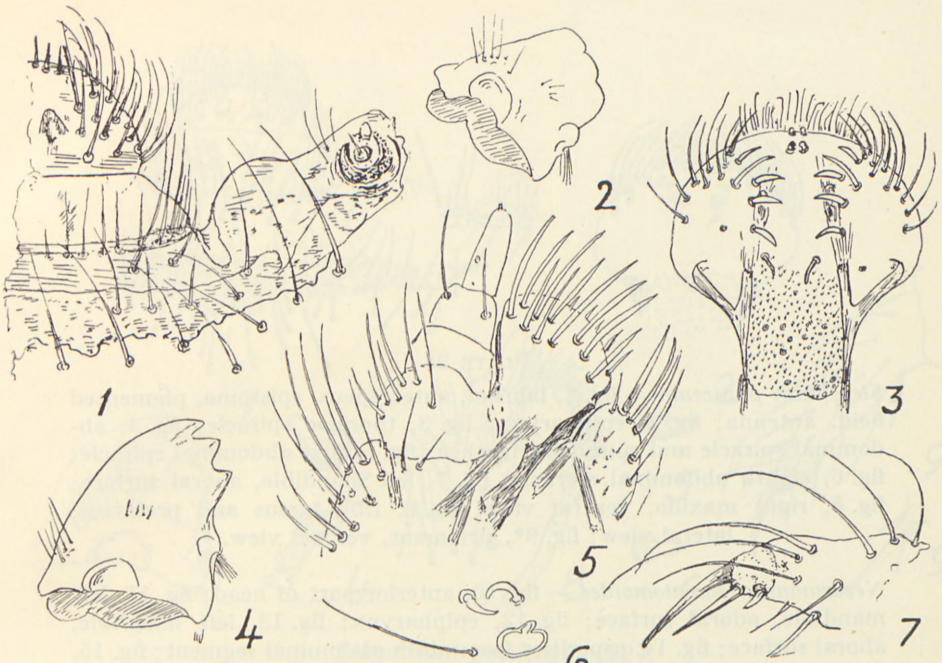


Anobium nitidum (19).

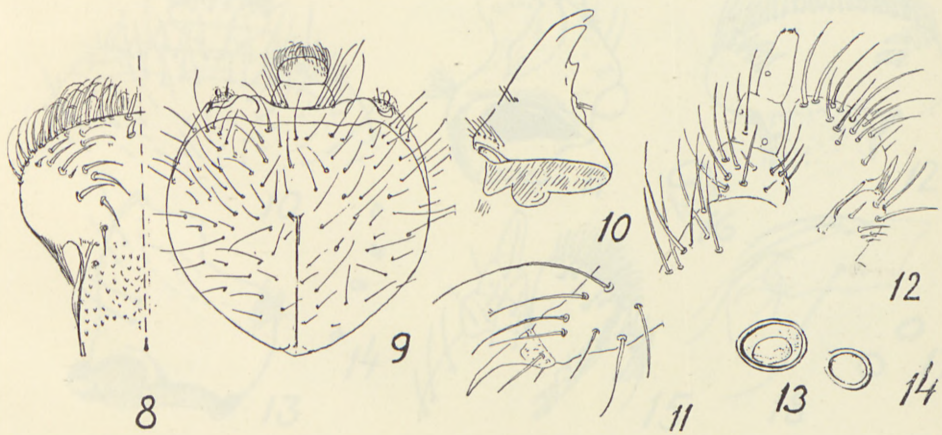
PLATE 27

Microbregma emarginatum — fig. 1, right half of labrum, anteclypeus, epistoma and pigmented field, antenna; fig. 2, left mandible, aboral surface, distally worn off; fig. 3, epipharynx; fig. 4, left mandible, aboral surface, not worn; fig. 5, right maxilla, ventral view; fig. 6, abdominal spiracle, a moderately long seta and two common sized asperities to indicate the size of an abdominal spiracle in this species; fig. 7, pretarsus.

Ernobius champlaini — fig. 8, lateral half of epipharynx; fig. 9, head; fig. 10, left mandible, aboral surface; fig. 11, pretarsus; fig. 12, distal end of right maxilla, ventral view; fig. 13, thoracic spiracle; fig. 14, abdominal spiracle.



Microbregma emarginatum (20).

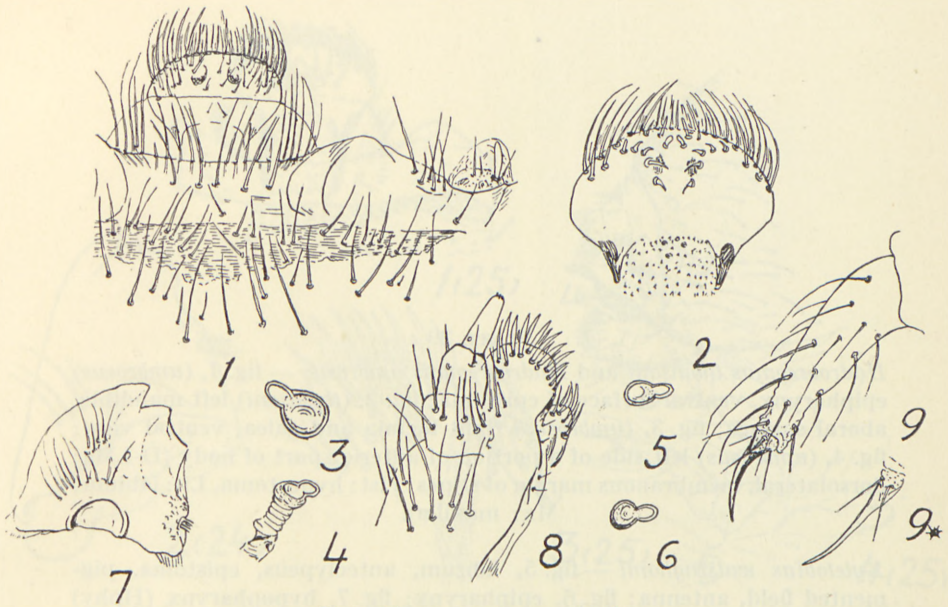


Ernobius champlaini (21).

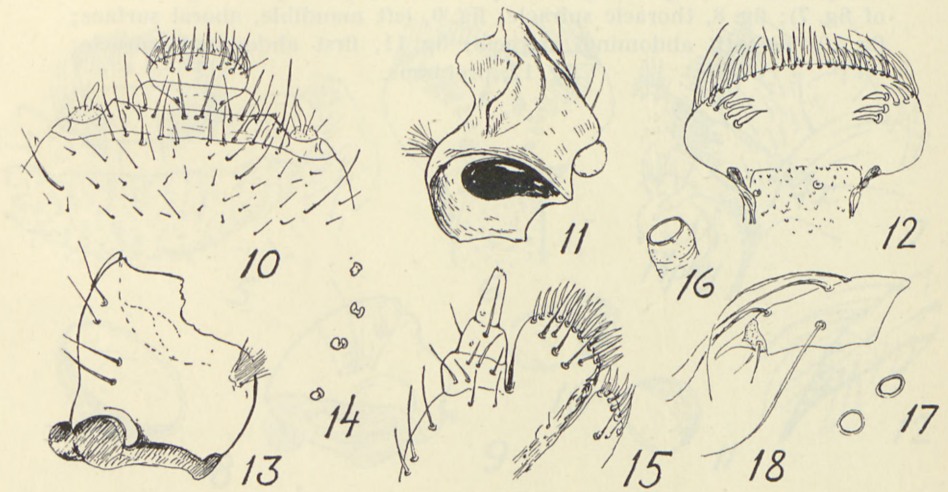
PLATE 28

Stegobium paniceum — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 2, epipharynx; fig. 3, thoracic spiracle; fig. 4, abdominal spiracle and spiracular trachea; fig. 5, first abdominal spiracle; fig. 6, eighth abdominal spiracle; fig. 7, left mandible, aboral surface; fig. 8, right maxilla, ventral view; fig. 9, tibio-tarsus and pretarsus, lateral view; fig. 9*, pretarsus, ventral view.

Nevermannia dorcatomoides — fig. 10, anterior part of head; fig. 11, left mandible, adoral surface; fig. 12, epipharynx; fig. 13, left mandible, aboral surface; fig. 14, asperities from ninth abdominal segment; fig. 15, right maxilla, ventral view; fig. 16, thoracic spiracle; fig. 17, first and seventh abdominal spiracles; fig. 18, tibio-tarsus and pretarsus.



Stegobium paniceum (22).

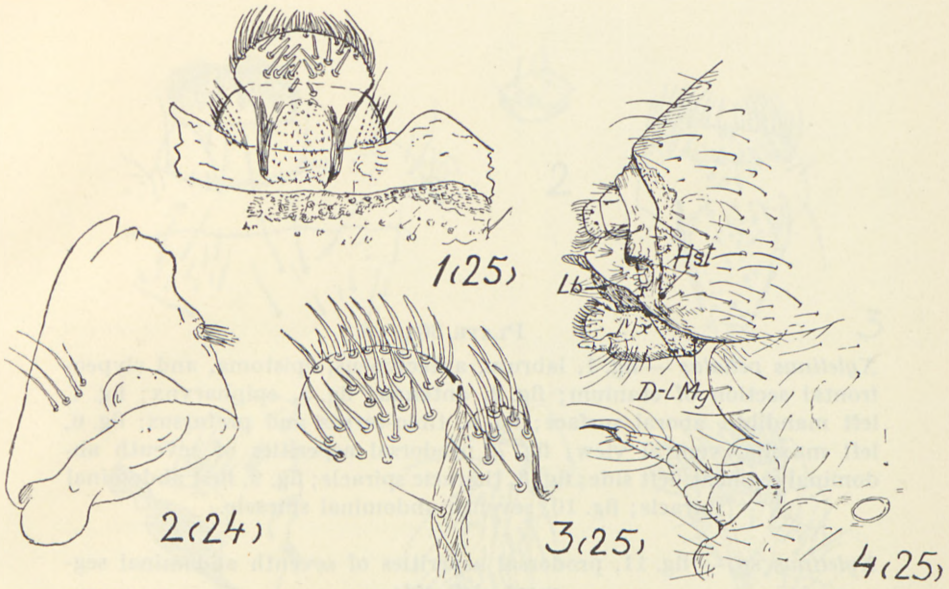


Nevermannia dorcatomoides (23).

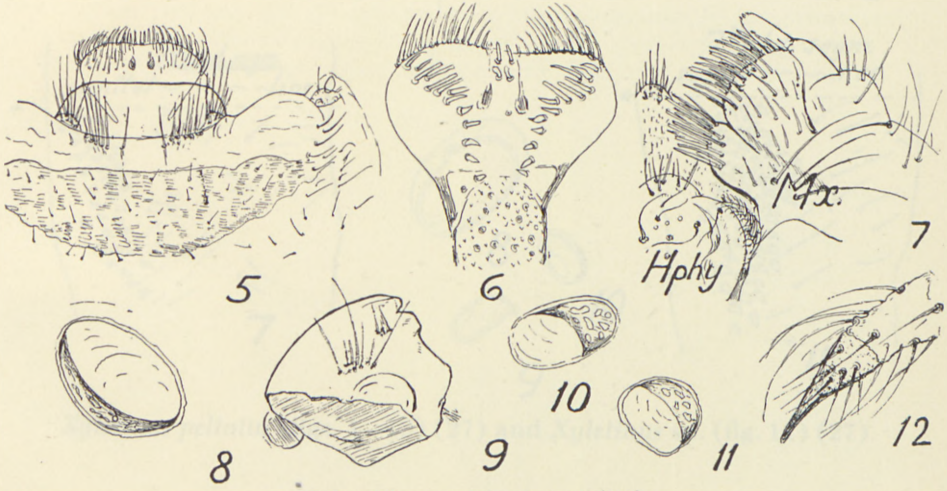
PLATE 29

Hadrobregmus thomsoni and *Hadrobregmus umbrosus* — fig. 1, (*umbrosus*) epipharynx, ventral surface of epistoma; fig. 2, (*thomsoni*) left mandible, aboral surface; fig. 3, (*umbrosus*) right lacinia and galea, ventral view; fig. 4, (*umbrosus*) left side of a portion of anterior part of body (D-LMg: dorsolateral, membranous margin of stipes; Hst: hypostoma, Lb: labium; Mx: maxilla).

Xyletobius walsinghami — fig. 5, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 6, epipharynx; fig. 7, hypopharynx (Hphy) and right maxilla (Mx) showing ventral aboral surface of lobes (compare fig. 7 with fig. 4 on this same Plate 29, where a left maxilla is drawn in a position corresponding to the position occupied by the right maxilla of fig. 7); fig. 8, thoracic spiracle; fig. 9, left mandible, aboral surface; fig. 10, seventh abdominal spiracle; fig. 11, first abdominal spiracle; fig. 12, pretarsus.



Hadrobregmus thomsoni (24). *Hadrobregmus umbrosus* (25).

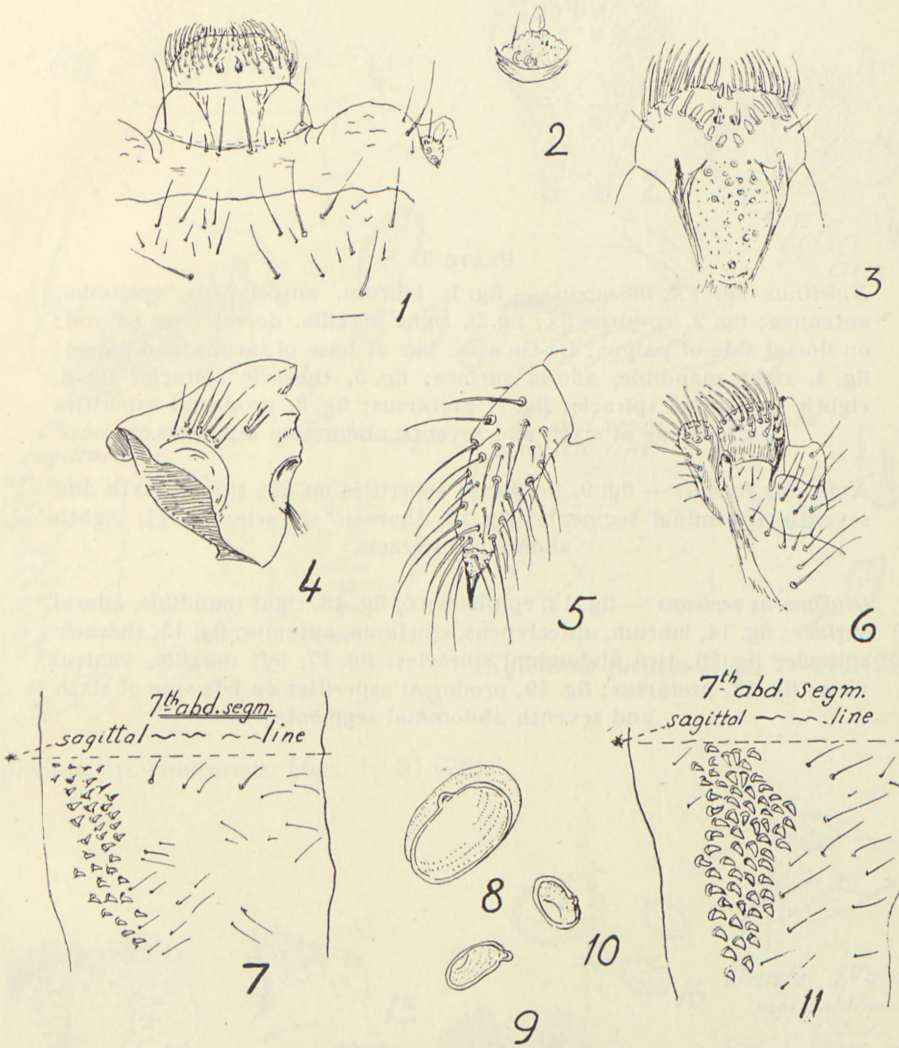


Xyletobius walsinghami (26).

Plate 30

Xyletinus peltatus — fig. 1, labrum, anteclypeus, epistoma, and clypeofrontal section of cranium; fig. 2, antenna; fig. 3, epipharynx; fig. 4, left mandible, aboral surface; fig. 5, tibio-tarsus and pretarsus; fig. 6, left maxilla, ventral view; fig. 7, prodorsal asperities of seventh abdominal segment, left side; fig. 8, thoracic spiracle; fig. 9, first abdominal spiracle; fig. 10, seventh abdominal spiracle.

Xyletinus sp. — fig. 11, prodorsal asperities of seventh abdominal segment, left side.



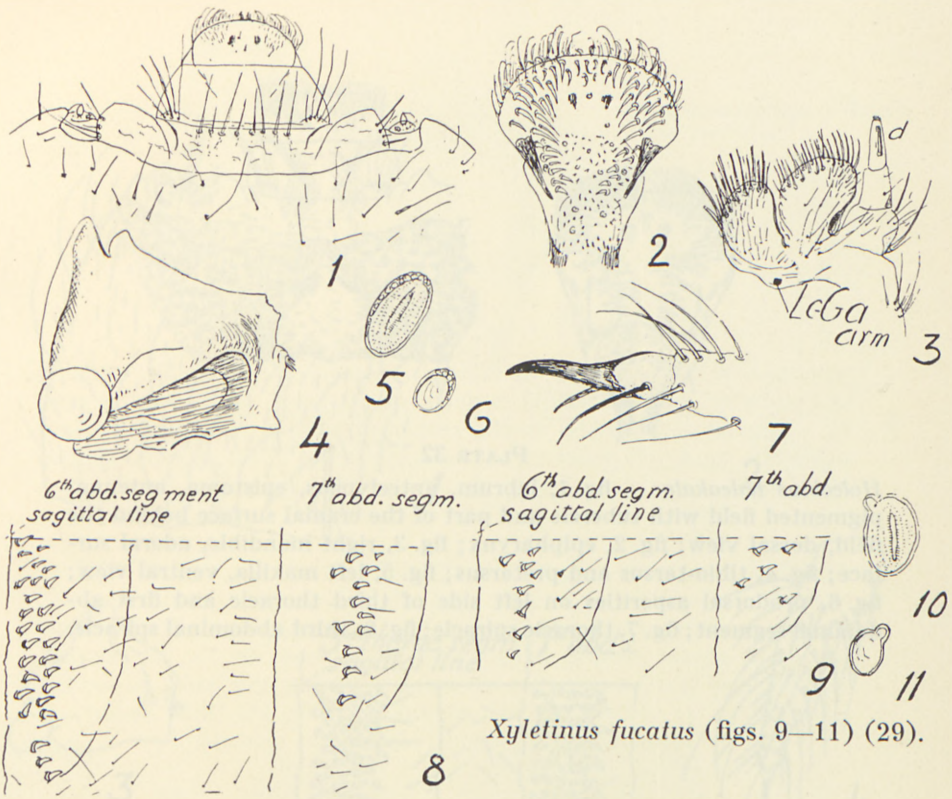
Xyletinus peltatus (figs. 1—10) (27) and *Xyletinus* sp. (fig. 11) (27).

PLATE 31

Xyletinus sp. (*X. mucoreus*) — fig. 1, labrum, anteclypeus, epistoma, antennae; fig. 2, epipharynx; fig. 3, right maxilla, dorsal view (d'-rod: on dorsal side of palpus; Lc-Ga arm: bar at base of lacinia and galea); fig. 4, right mandible, adoral surface; fig. 5, thoracic spiracle; fig. 6, eighth abdominal spiracle; fig. 7, pretarsus; fig. 8, prodorsal asperities on left side of sixth and seventh abdominal segments.

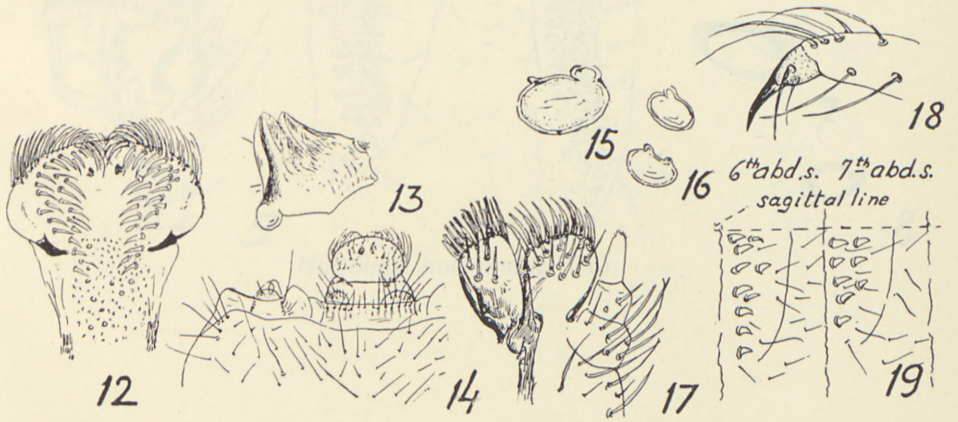
Xyletinus fucatus — fig. 9, prodorsal asperities on left side of sixth and seventh abdominal segments; fig. 10, thoracic spiracle; fig. 11, eighth abdominal spiracle.

Oligomerus sericans — fig. 12, epipharynx; fig. 13, right mandible, adoral surface; fig. 14, labrum, anteclypeus, epistoma, antenna; fig. 15, thoracic spiracle; fig. 16, two abdominal spiracles; fig. 17, left maxilla, ventral view; fig. 18, pretarsus; fig. 19, prodorsal asperities on left side of sixth and seventh abdominal segments.



Xyletinus fucatus (figs. 9—11) (29).

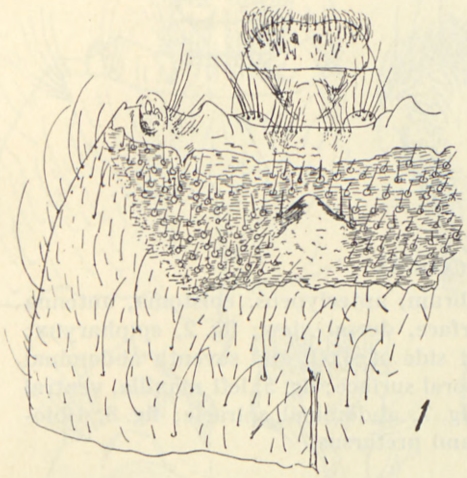
Xyletinus sp. *(mucoreus)* (figs. 1—8) (28).

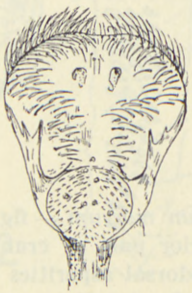


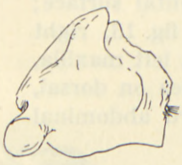
Oligomerus sericans (30).

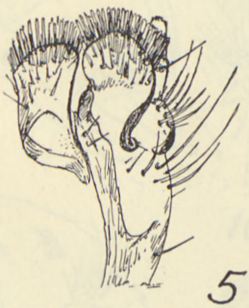
PLATE 32

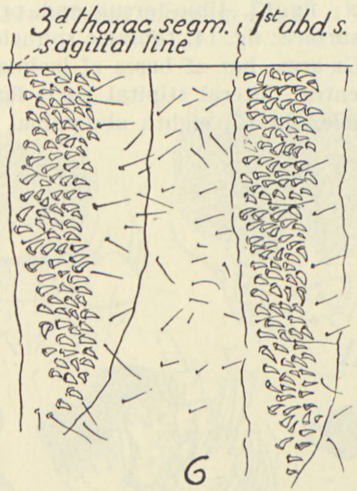
Holcobius haleakalae — fig. 1, labrum, anteclypeus, epistoma, antenna, pigmented field with tubercle and part of the cranial surface behind the field, dorsal view; fig. 2, epipharynx; fig. 3, right mandible, adoral surface; fig. 4, tibio-tarsus and pretarsus; fig. 5, left maxilla, ventral view; fig. 6, prodorsal asperities on left side of third thoracic and first abdominal segment; fig. 7, thoracic spiracle; fig. 8, third abdominal spiracle.

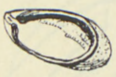


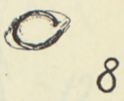










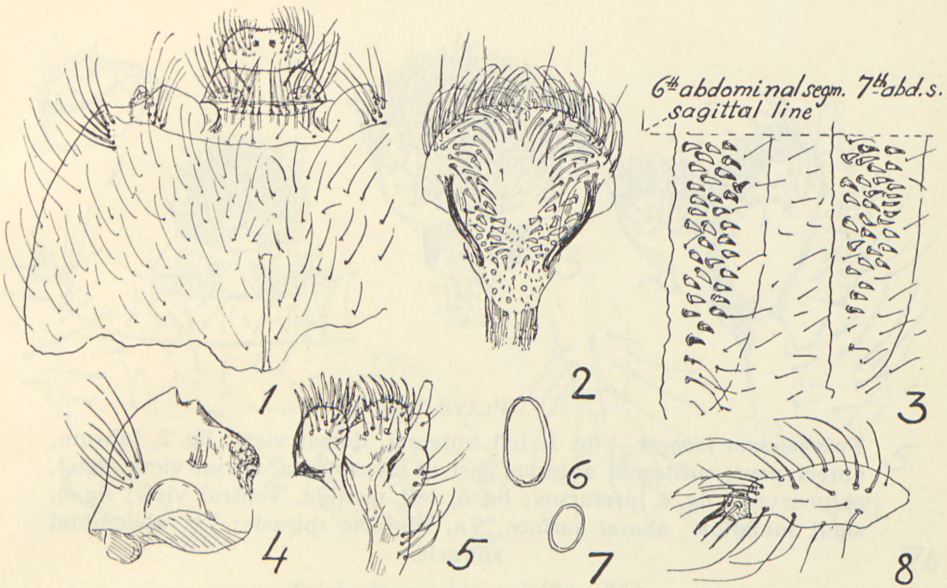


Holcobius haleakalae (31).

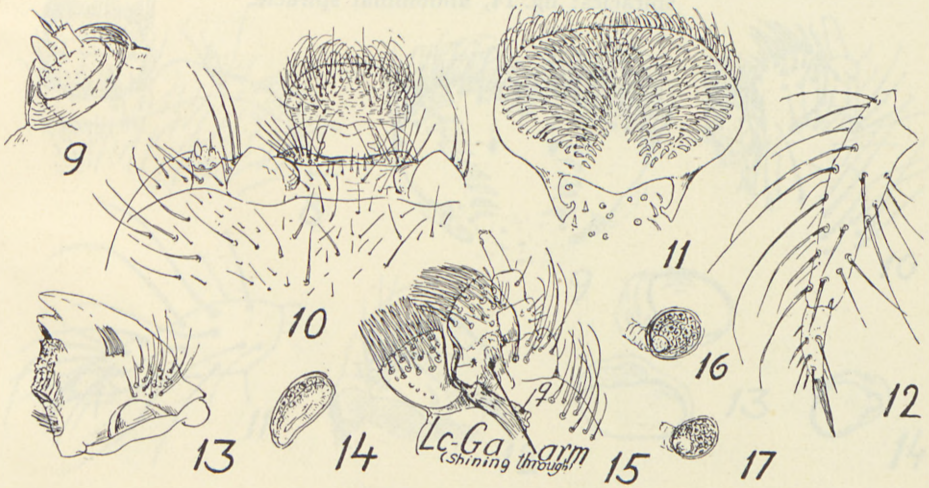
PLATE 33

Xeranobium macrum — fig. 1, labrum, anteclypeus, epistoma, antenna and anterior part of cranial surface, dorsal view; fig. 2, epipharynx; fig. 3, prodorsal asperities on left side of sixth and seventh abdominal segments; fig. 4, left mandible aboral surface; fig. 5, left maxilla, ventral view; fig. 6, thoracic spiracle; fig. 7, abdominal spiracle; fig. 8, tibio-tarsus and pretarsus.

Nicobium castaneum — fig. 9, left antenna, dorsal view; fig. 10, labrum, anteclypeus, epistoma, anterior part of cranial clypeofrontal surface; fig. 11, epipharynx; fig. 12, tibio-tarsus and pretarsus; fig. 13, right mandible, aboral surface; fig. 14, thoracic spiracle; fig. 15, left maxilla, ventral view (Lc-Ga arm: bar at bases of lacinia and galea on dorsal, adoral side; q: ventral, lateral stipital bar); fig. 16, third abdominal spiracle; fig. 17, eighth abdominal spiracle.



Xeranobium macrum (32).

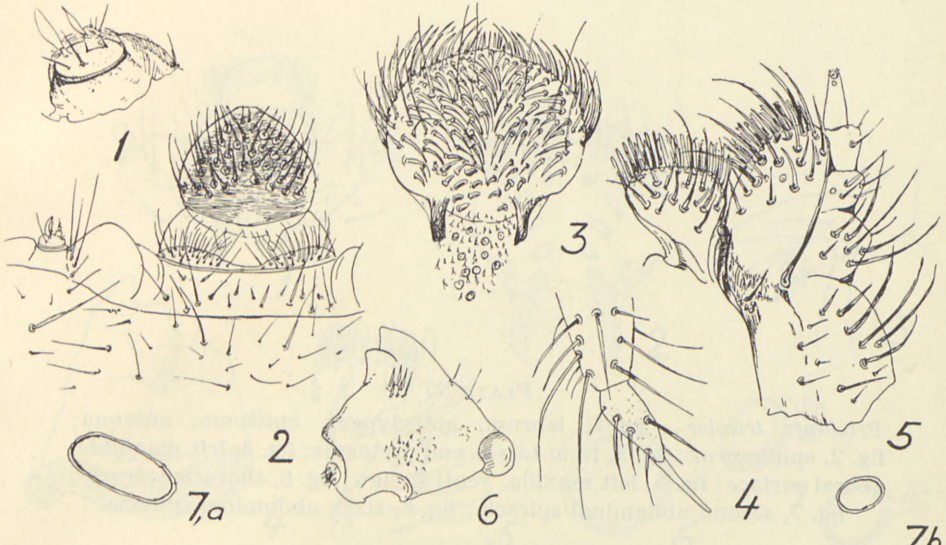


Nicobium castaneum (33).

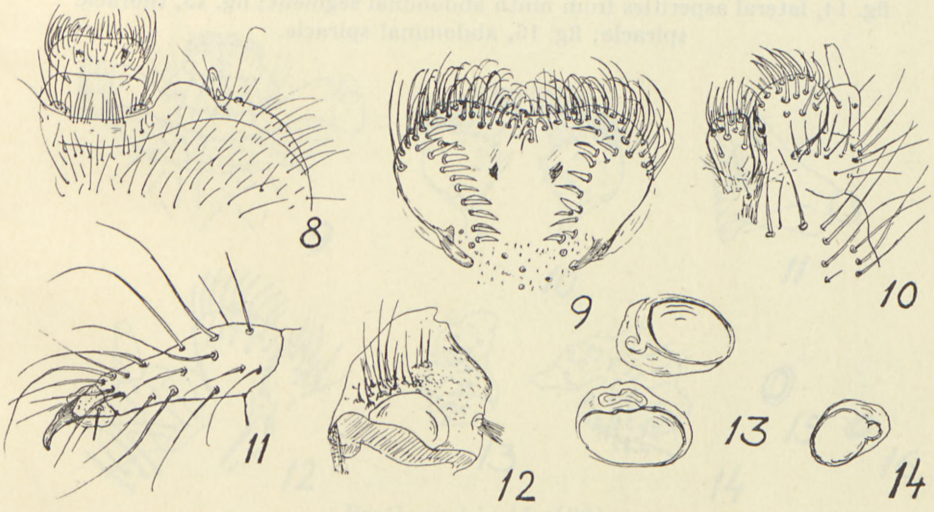
PLATE 34

Trichodesma klagesi — fig. 1, left antenna, dorsal view; fig. 2, labrum, anteclypeus, epistoma, anterior part of clypeofrons, dorsal view; fig. 3, epipharynx; fig. 4, pretarsus; fig. 5, left maxilla, ventral view; fig. 6, right mandible, aboral surface; 7a, thoracic spiracle; 7b, abdominal spiracle.

Vrilletta blaisdelli — fig. 8, labrum, anteclypeus, epistoma, antenna; fig. 9, epipharynx; fig. 10, left maxilla, ventral view; fig. 11, tibio-tarsus and pretarsus; fig. 12, left mandible, aboral surface; fig. 13, two thoracic spiracles; fig. 14, abdominal spiracle.



Trichodesma klagesi (34—35).

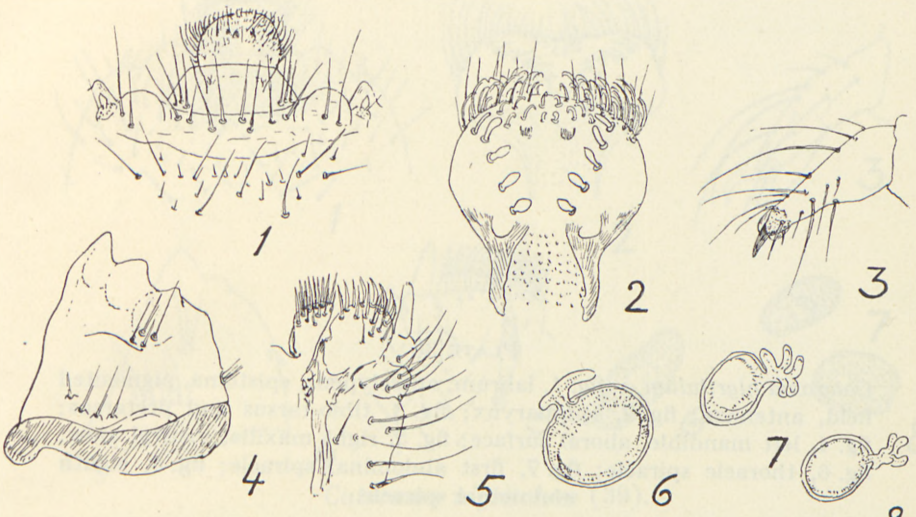


Vrilletta blaisdelli (36).

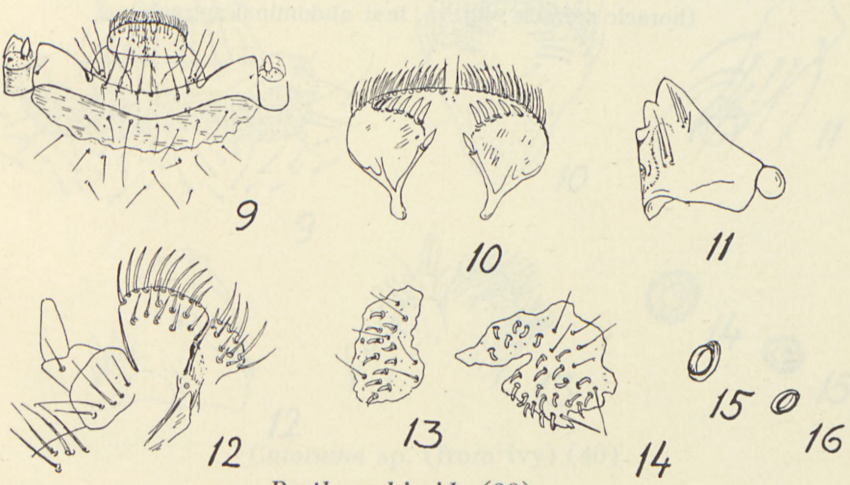
PLATE 35

Priobium tricolor — fig. 1, labrum, anteclypeus, epistoma, antenna; fig. 2, epipharynx; fig. 3, tibio-tarsus and pretarsus; fig. 4, left mandible, aboral surface; fig. 5, left maxilla, ventral view; fig. 6, thoracic spiracle; fig. 7, second abdominal spiracle; fig. 8, sixth abdominal spiracle.

Protheca hispida — fig. 9, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 10, epipharynx; fig. 11, right mandible, aboral surface; fig. 12, right maxilla, ventral view; fig. 13, prothoracic asperities; fig. 14, lateral asperities from ninth abdominal segment; fig. 15, thoracic spiracle; fig. 16, abdominal spiracle.



Priobium tricolor (37).

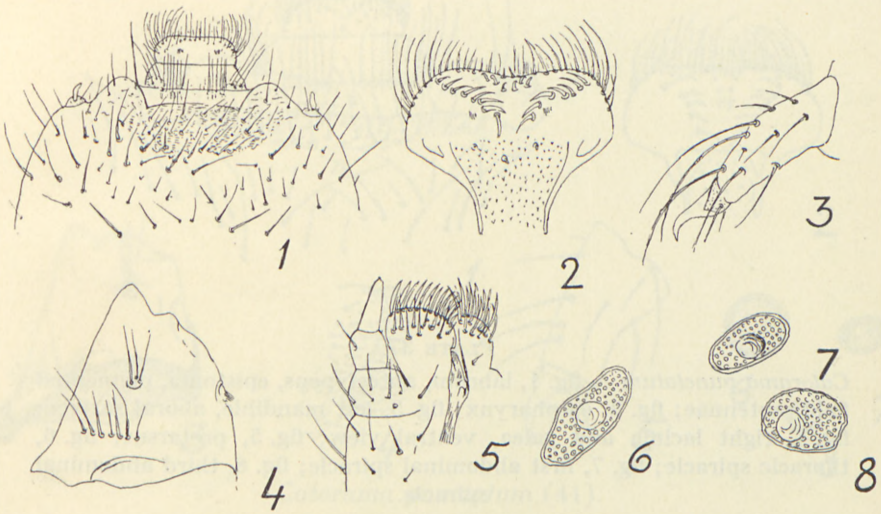


Protheca hispida (38).

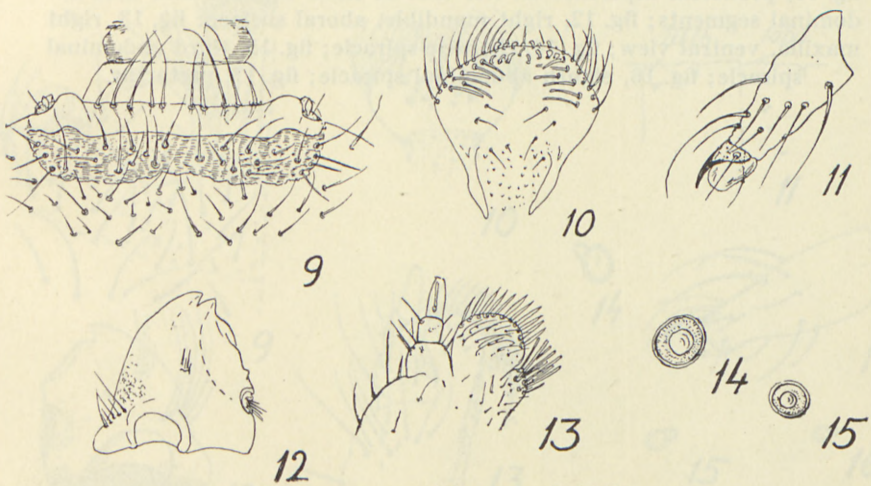
PLATE 36

Catorama nigritulum — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 2, epipharynx; fig. 3, tibio-tarsus and pretarsus; fig. 4, left mandible, aboral surface; fig. 5, right maxilla, ventral view; fig. 6, thoracic spiracle; fig. 7, first abdominal spiracle; fig. 8, eighth abdominal spiracle.

Catorama sp. (ex ivy) — fig. 9, anteclypeus, epistoma, pigmented field, antenna; fig. 10, epipharynx; fig. 11, tibio-tarsus and pretarsus; fig. 12, left mandible, aboral surface; fig. 13, left maxilla, dorsal view; fig. 14, thoracic spiracle; fig. 15, first abdominal spiracle.



Catorama nigritulum (39).

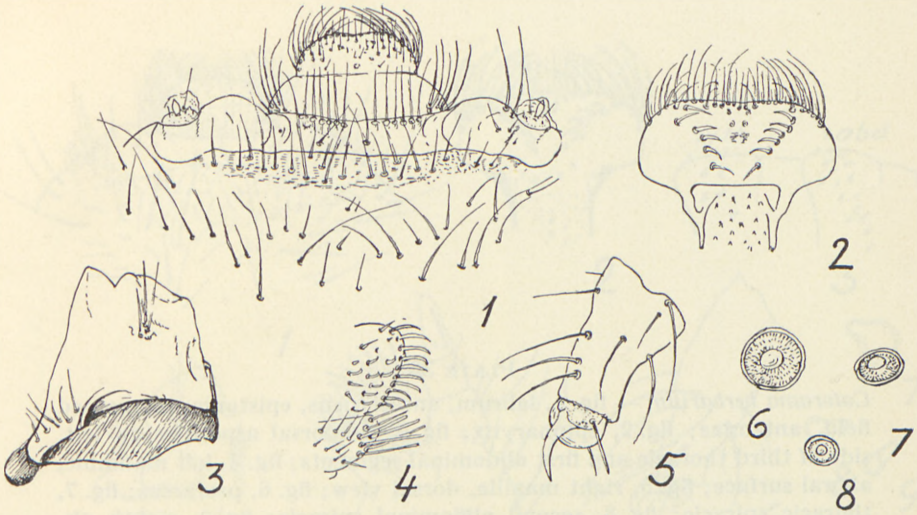


Catorama sp. (from ivy) (40).

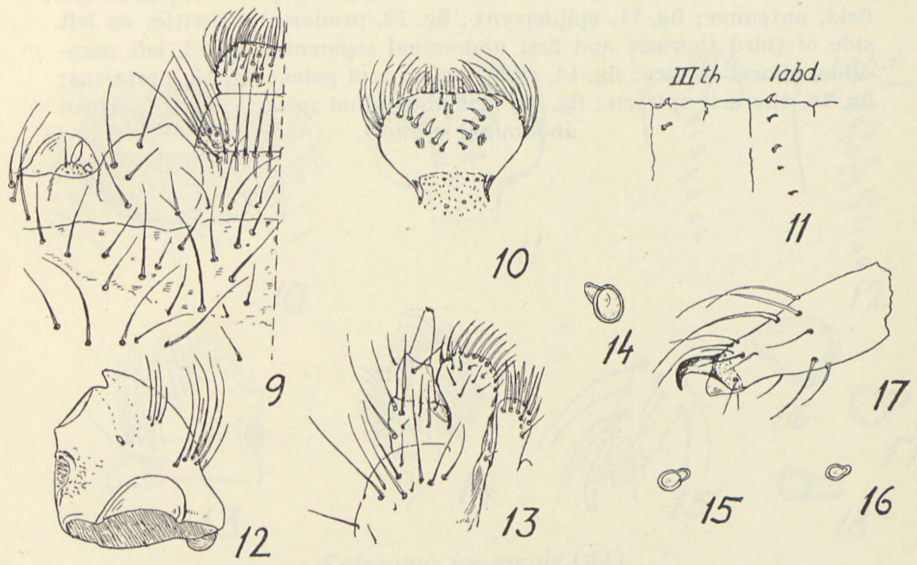
PLATE 37

Catorama punctatum — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, right lacinia and galea, ventral view; fig. 5, pretarsus; fig. 6, thoracic spiracle; fig. 7, first abdominal spiracle; fig. 8, third abdominal spiracle.

Catorama sp. (near *C. conjunctum*) — fig. 9, left half of labrum, anteclypeus, epistoma, pigmented field, left antenna; fig. 10, epipharynx; fig. 11, prodorsal asperities on left side of third thoracic and first abdominal segments; fig. 12, right mandible, aboral surface; fig. 13, right maxilla, ventral view; fig. 14, thoracic spiracle; fig. 15, third abdominal spiracle; fig. 16, eighth abdominal spiracle; fig. 17, pretarsus.



Catorama punctatum (41).

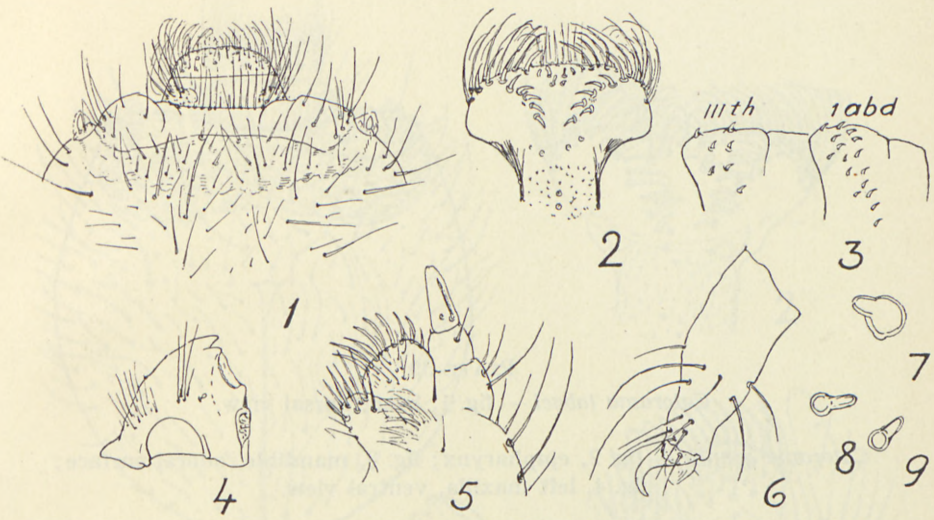


Catorama sp. (near *C. conjunctum* (42).

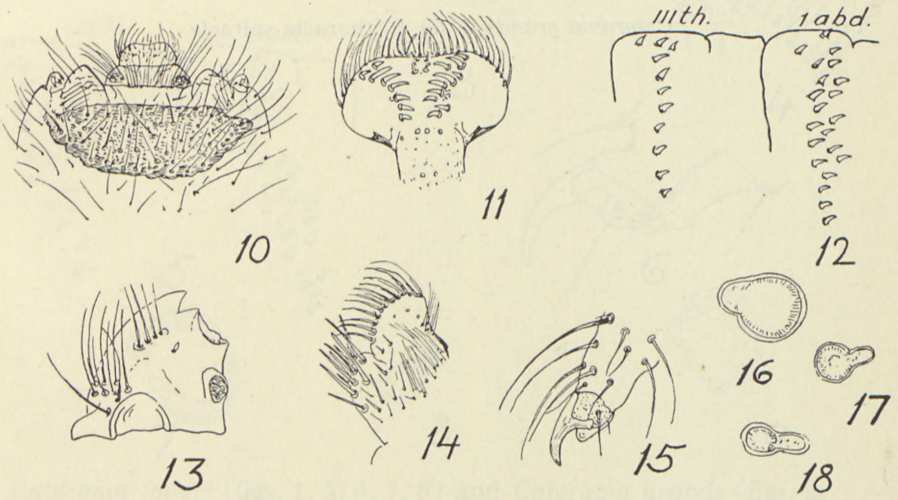
PLATE 38

Catorama herbarium — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 2, epipharynx; fig. 3, prodorsal asperities on left, side of third thoracic and first abdominal segments; fig. 4, left mandible, aboral surface; fig. 5, right maxilla, dorsal view; fig. 6, pretarsus; fig. 7, thoracic spiracle; fig. 8, second abdominal spiracle; fig. 9, eighth abdominal spiracle.

Catorama inaequale — fig. 10, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 11, epipharynx; fig. 12, prodorsal asperities on left side of third thoracic and first abdominal segments; fig. 13, left mandible, aboral surface; fig. 14, right lacinia and galea; fig. 15, pretarsus; fig. 16, thoracic spiracle; fig. 17, first abdominal spiracle; fig. 18, eighth abdominal spiracle.



Catorama herbarium (43).



Catorama inaequale (44).

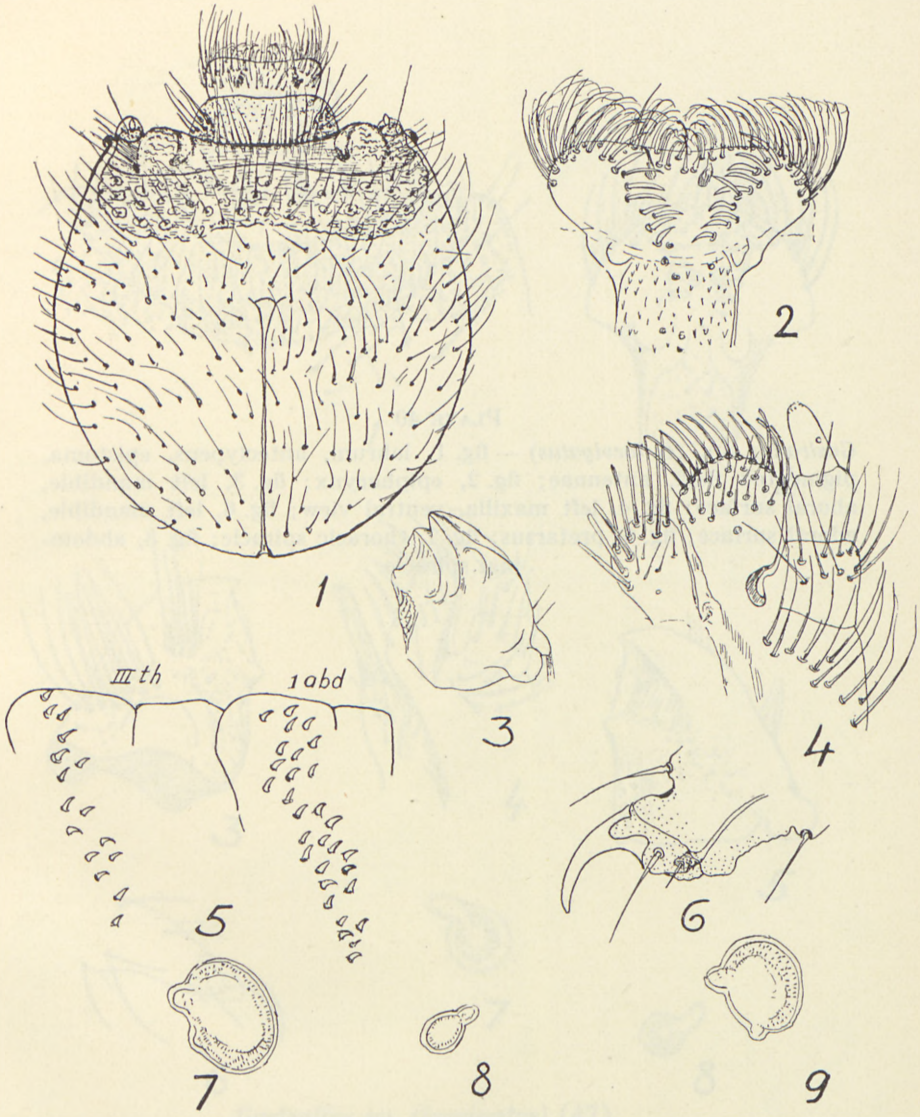
PLATE 39

Catorama tabaci — fig. 1, head, dorsal view.

Catorama grande — fig. 2, epipharynx; fig. 3, mandible, adoral surface; fig. 4, left maxilla, ventral view.

Catorama tabaci — fig. 5, prodorsal asperities on left side of third thoracic and first abdominal segments; fig. 6, pretarsus; fig. 7, thoracic spiracle; fig. 8, abdominal spiracle.

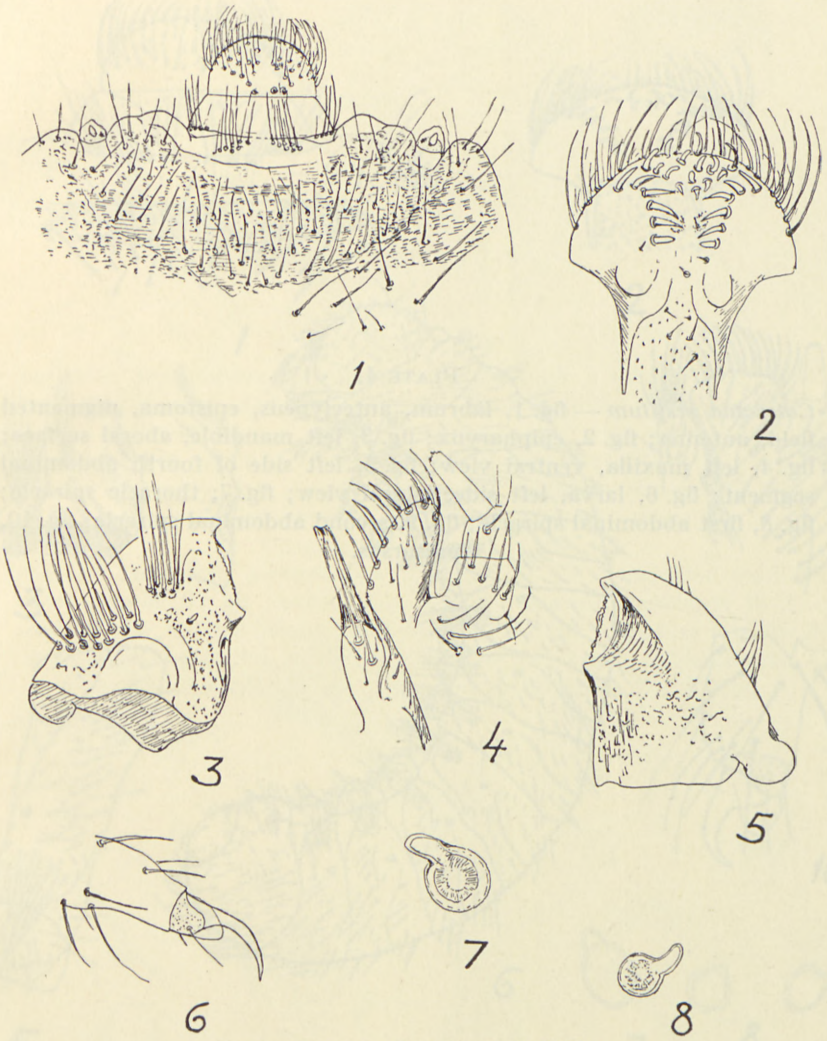
Catorama grande — fig. 9, thoracic spiracle.



Catorama tabaci (figs. 1, 5, 6, 7, 8) and *Catorama grande* (figs. 2, 3, 4, 9) (45).

PLATE 40

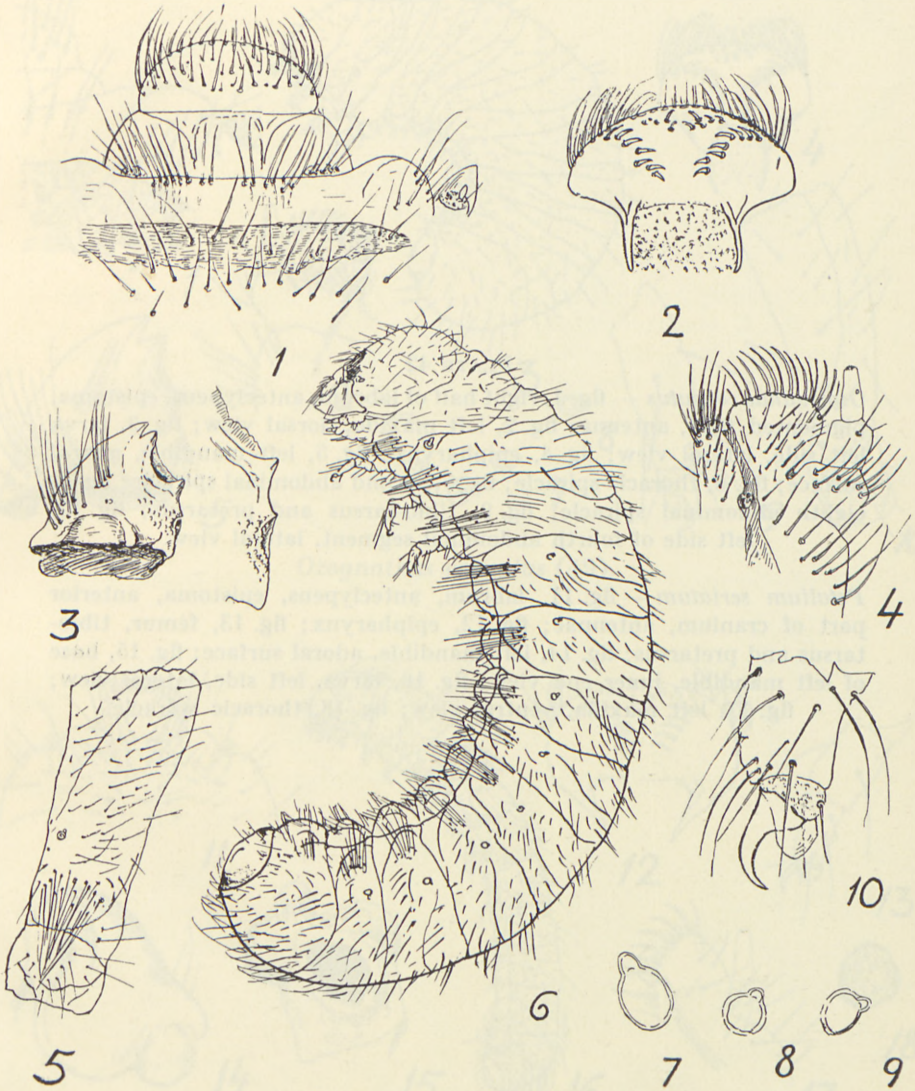
Gastrallus sp. (*G. laevigatus*) — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, left maxilla, ventral view; fig. 6, left mandible, adoral surface; fig. 6, pretarsus; fig. 7, thoracic spiracle; fig. 8, abdominal spiracle.



Gastrallus sp. *(laevigatus)* (47).

PLATE 41

Catorama vestitum — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, left maxilla, ventral view; fig. 5, left side of fourth abdominal segment; fig. 6, larva, left side, lateral view; fig. 7, thoracic spiracle; fig. 8, first abdominal spiracle; fig. 9, second abdominal spiracle; fig. 10, pretarsus.

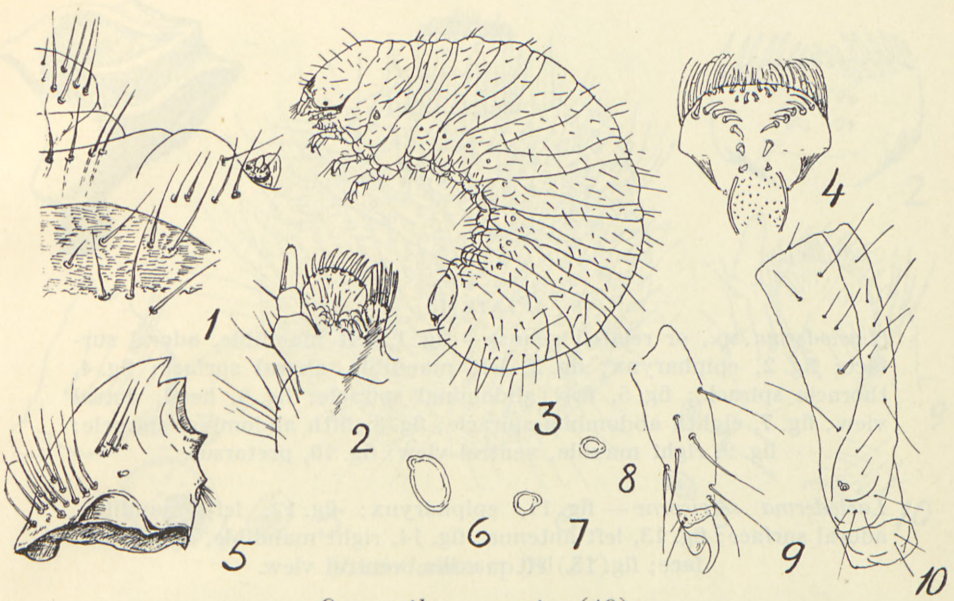


Catorama vestitum (48).

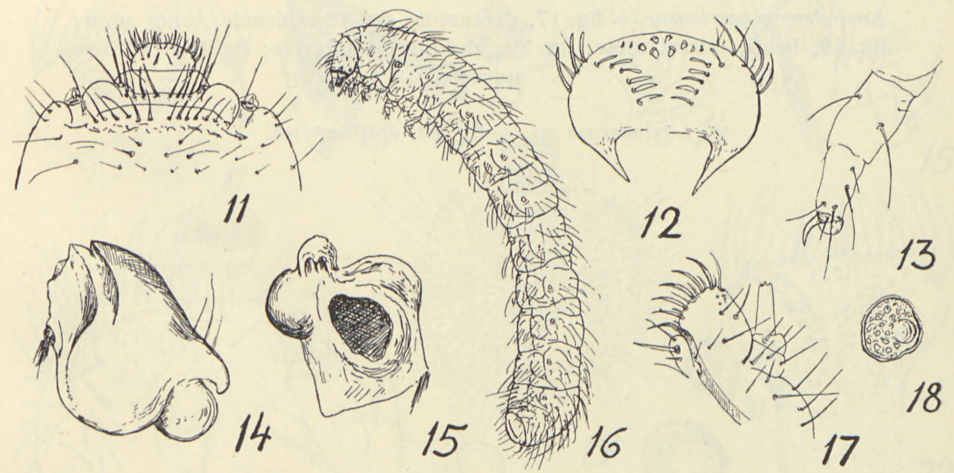
Plate 42

Ozognathus cornutus — fig. 1, right half of labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 2, left maxilla, dorsal view; fig. 3, larva left side, lateral view; fig. 4, epipharynx; fig. 5, left mandible, aboral surface; fig. 6, thoracic spiracle; fig. 7, second abdominal spiracle; fig. 8, eighth abdominal spiracle; fig. 9, tibio-tarsus and pretarsus; fig. 10, left side of fourth abdominal segment, lateral view.

Petalium seriatum — fig. 11, labrum, anteclypeus, epistoma, anterior part of cranium, antennae; fig. 12, epipharynx; fig. 13, femur, tibio-tarsus and pretarsus; fig. 14, left mandible, adoral surface; fig. 15, base of left mandible, inner end view; fig. 16, larva, left side, lateral view; fig. 17, left maxilla, ventral view; fig. 18, thoracic spiracle.



Ozognathus cornutus (49).



Petalium seriatum (50).

Plate 43

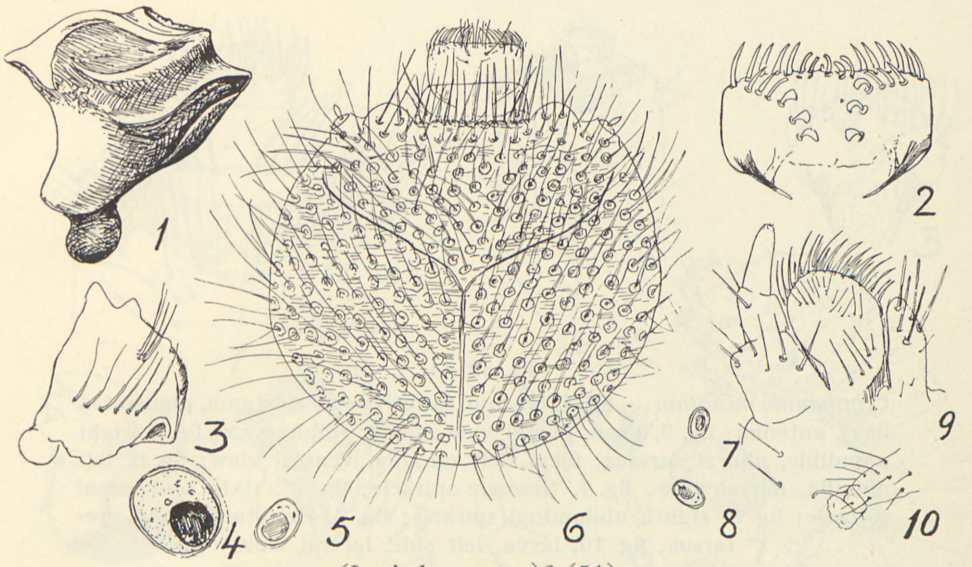
(*Lasioderma* sp., or related genus) — fig. 1, left mandible, adoral surface; fig. 2, epipharynx; fig. 3, left mandible, aboral surface; fig. 4, thoracic spiracle; fig. 5, first abdominal spiracle; fig. 6, head, dorsal view; fig. 7, eighth abdominal spiracle; fig. 8, fifth abdominal spiracle; fig. 9, right maxilla, ventral view; fig. 10, pretarsus.

Lasioderma serricorne — fig. 11, epipharynx; fig. 12, left mandible, adoral surface; fig. 13, left antenna; fig. 14, right mandible, aboral surface; fig. 15, left maxilla, ventral view.

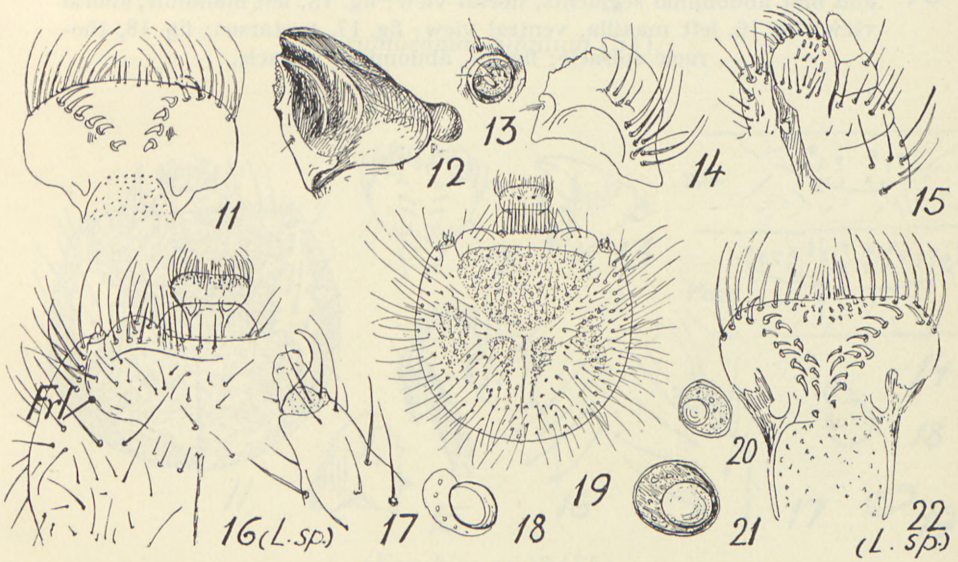
Lasioderma sp. — fig. 16, left anterior part of head (Frl: frontal cleavage line).

Lasioderma serricorne — fig. 17, pretarsus; fig. 18, spiracle, inner view; fig. 19, head, dorsal view; fig. 20, abdominal spiracle; fig. 21, thoracic spiracle.

Lasioderma sp. — fig. 22, epipharynx.



(*Lasioderma* sp.)? (51).

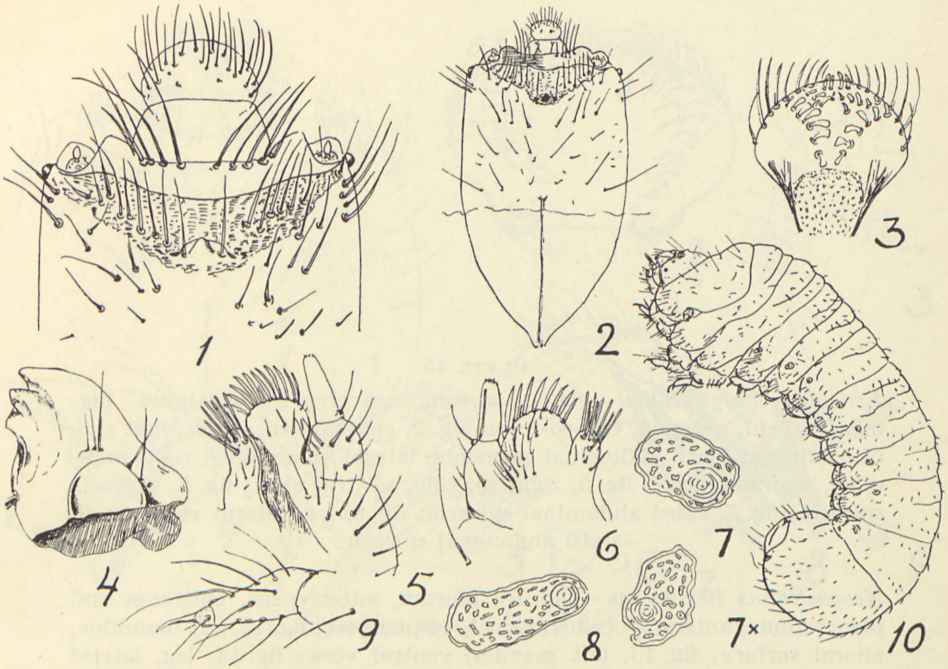


Lasioderma serricorne (52) *Lasioderma* sp. (53).

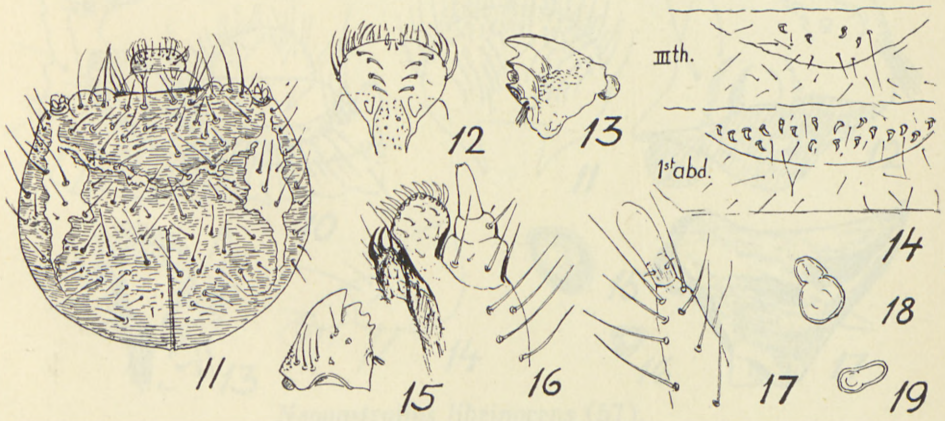
PLATE 44

Cryptorama minutum — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antenna; fig. 2, head, dorsal view; fig. 3, epipharynx; fig. 4, right mandible, aboral surface; fig. 5, left maxilla, ventral view; fig. 6, left maxilla, dorsal view; fig. 7, thoracic spiracle; fig. 7*, sixth abdominal spiracle; fig. 8, eighth abdominal spiracle; fig. 9, tibio-tarsus and pretarsus; fig. 10, larva, left side, lateral view.

(*Ernobius* sp.)? — fig. 11, head, dorsal view; fig. 12, epipharynx; fig. 13, left mandible, adoral surface; fig. 14, prodorsal asperities of third thoracic and first abdominal segments, dorsal view; fig. 15, left mandible, aboral view; fig. 16, left maxilla, ventral view; fig. 17, pretarsus; fig. 18, thoracic spiracle; fig. 19, abdominal spiracle.



Cryptorama minutum (54).

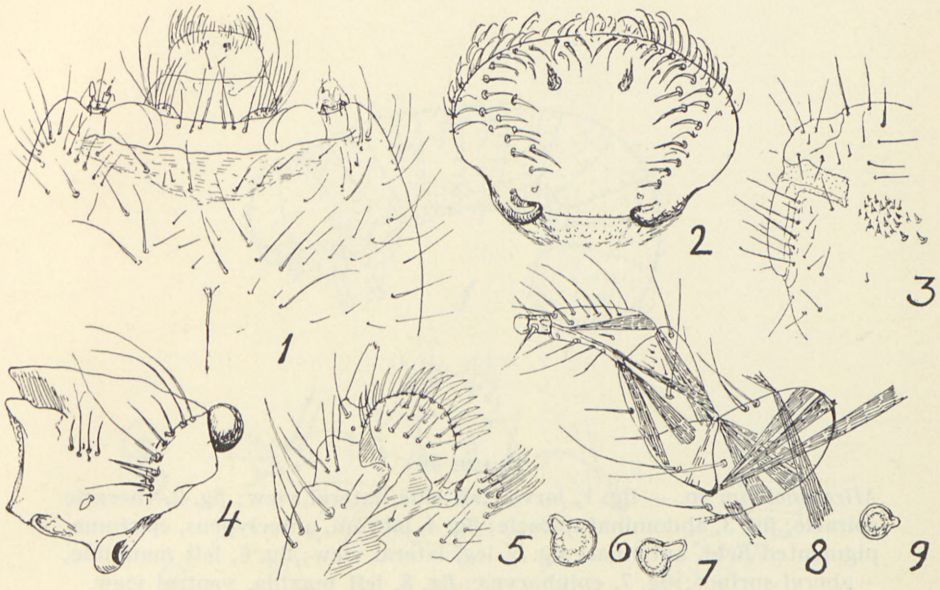


(*Ernobius* sp.)? (55).

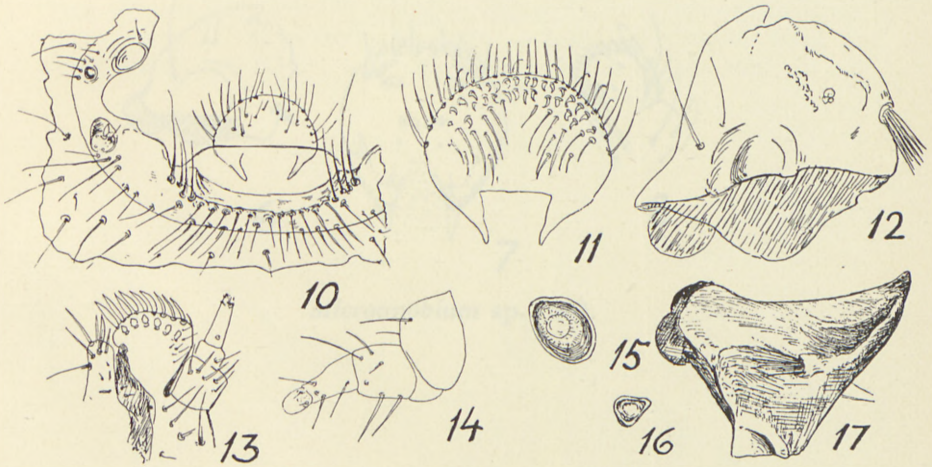
PLATE 45

Ernobius marginicollis — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antenna, clypeo-frons; fig. 2, epipharynx; fig. 3, right side of ninth and tenth abdominal segments, lateral view; fig. 4, right mandible, aboral surface; fig. 5, right maxilla, ventral view; fig. 6, thoracic spiracle; fig. 7, third abdominal spiracle; fig. 8, leg, lateral view; fig. 9, sixth abdominal spiracle.

Neogastrallus librinocens — fig. 10, labrum, anteclypeus, epistoma and pleurostoma, antenna, ocellus; fig. 11, epipharynx; fig. 12, left mandible, aboral surface; fig. 13, left maxilla, ventral view; fig. 14, leg, lateral view; fig. 15, thoracic spiracle; fig. 16, abdominal spiracle; fig. 17, right mandible, adoral and small part of aboral surfaces showing the scraper-shaped subapical margin.



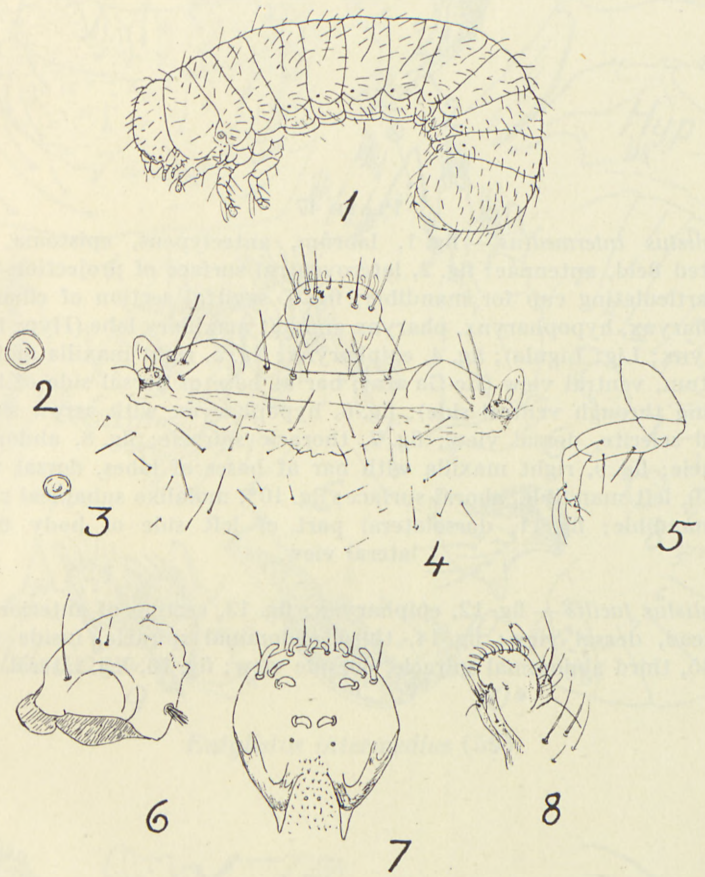
Ernobius marginicollis (56).



Neogastrallus librinocens (57).

PLATE 46

Microanobium sp. — fig. 1, larva, left side, lateral view; fig. 2, thoracic spiracle; fig. 3, abdominal spiracle; fig. 4, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 5, leg, lateral view; fig. 6, left mandible, aboral surface; fig. 7, epipharynx; fig. 8, left maxilla, ventral view.

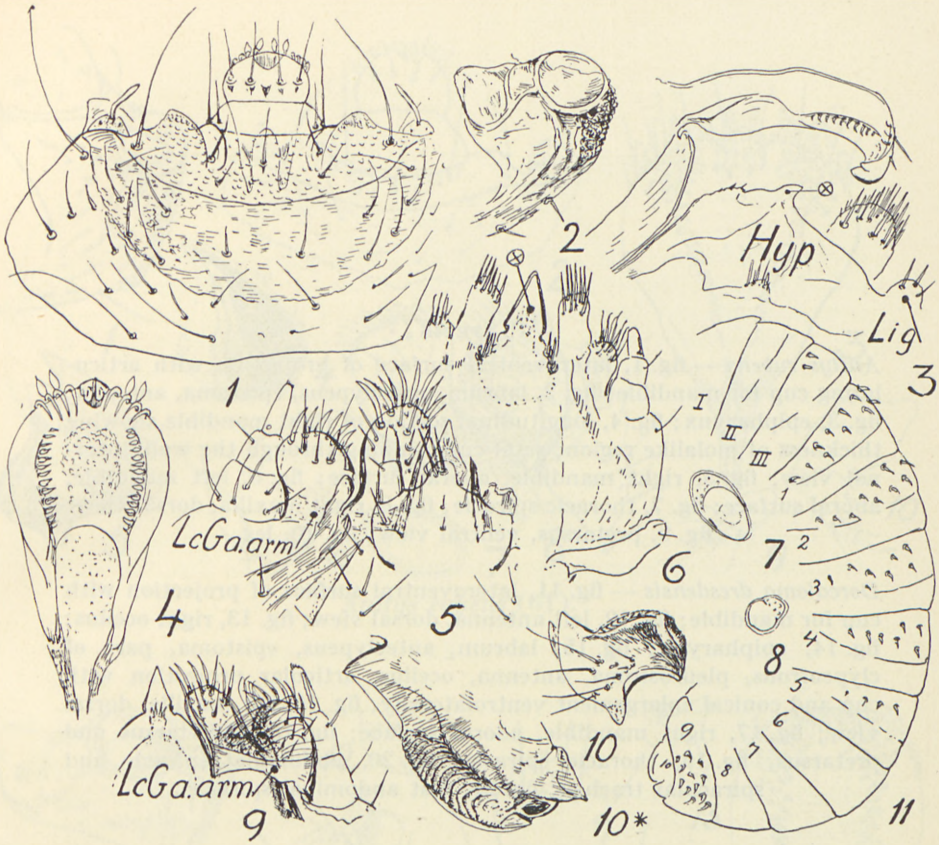


Microanobium sp. (58).

Plate 47

Eutylistus intermedius — fig. 1, labrum, anteclypeus, epistoma, pigmented field, antennae; fig. 2, lateroventral surface of projection bearing articulating cup for mandible; fig. 3, sagittal section of cibarium, epipharynx, hypopharynx, pharynx and left maxillary lobe (Hyp: hypopharynx; Lig: Ligula); fig. 4, epipharynx; fig. 5, right maxilla and prementum, ventral view (Lc-Ga arm: bar at base of dorsal side of lobes, shining through ventral side); fig. 6, hypopharynx with arrow shaped distal sclerite, dorsal view; fig. 7, thoracic spiracle; fig. 8, abdominal spiracle; fig. 9, right maxilla with bar at bases of lobes, dorsal view; fig. 10, left mandible, aboral surface; fig. 10*, molalike subapical region of mandible; fig. 11, dorsolateral part of left side of body trunk, lateral view.

Eutylistus facilis — fig. 12, epipharynx; fig. 13, section of anterior part of head, dorsal view; fig. 14, third abdominal spiracle, inside view; fig. 15, third abdominal spiracle, outside view; fig. 16, leg, lateral view.



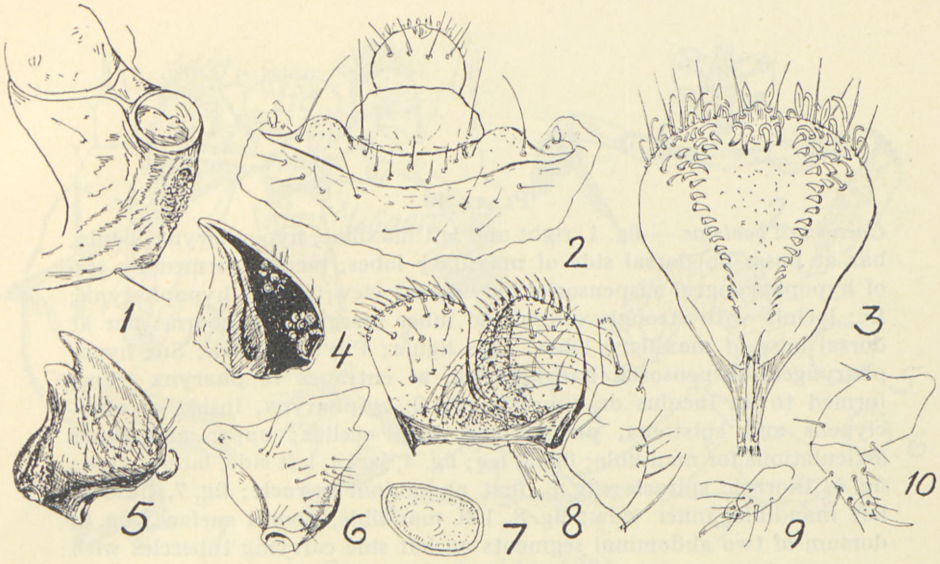
Eutylistus intermedius (59).

Eutylistus facilis (60).

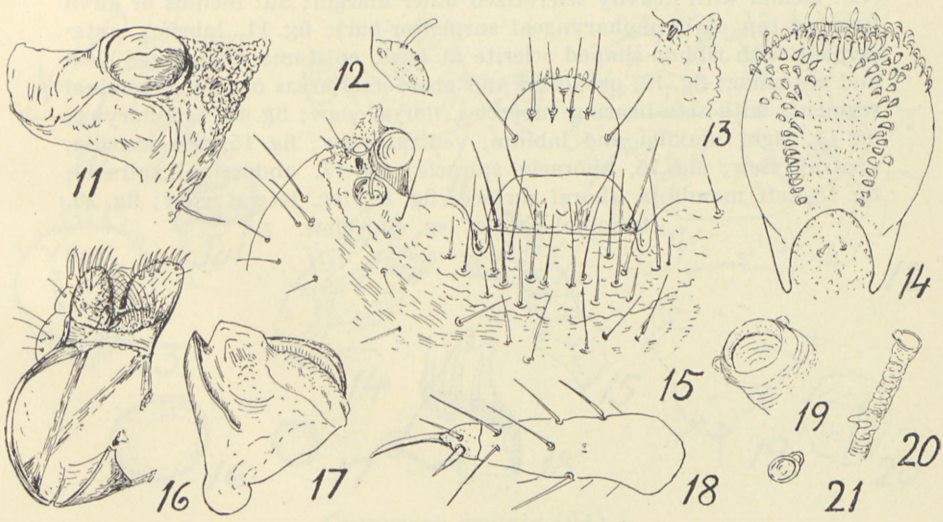
Plate 48

Anitys rubens — fig. 1, lateroventral surface of projection with articulating cup for mandible; fig. 2, labrum, anteclypeus, epistoma, antenna; fig. 3, epipharynx; fig. 4, longitudinal section of right mandible showing thickness of molalike region; setal cups shining through the wall, internal view; fig. 5, right mandible, aboral surface; fig. 6, left mandible, aboral surface; fig. 7, thoracic spiracle; fig. 8, right maxilla, dorsal view; fig. 9, pretarsus, ventral view; fig. 10, leg.

Dorcatoma dresdensis — fig. 11, lateroventral surface of projection with cup for mandible; fig. 12, left antenna, dorsal view; fig. 13, right ocellus; fig. 14, epipharynx; fig. 15, labrum, anteclypeus, epistoma, part of clypeofrons, pleurostoma, antenna, ocellus, articular projection with cup and conical enlargement ventrolaterally; fig. 16, left maxilla, dorsal view; fig. 17, right mandible, adoral surface; fig. 18, tibio-tarsus and pretarsus; fig. 19, thoracic spiracle; fig. 20, abdominal spiracle and spiracular trachea; fig. 21, first abdominal spiracle.



Anitys rubens (61).

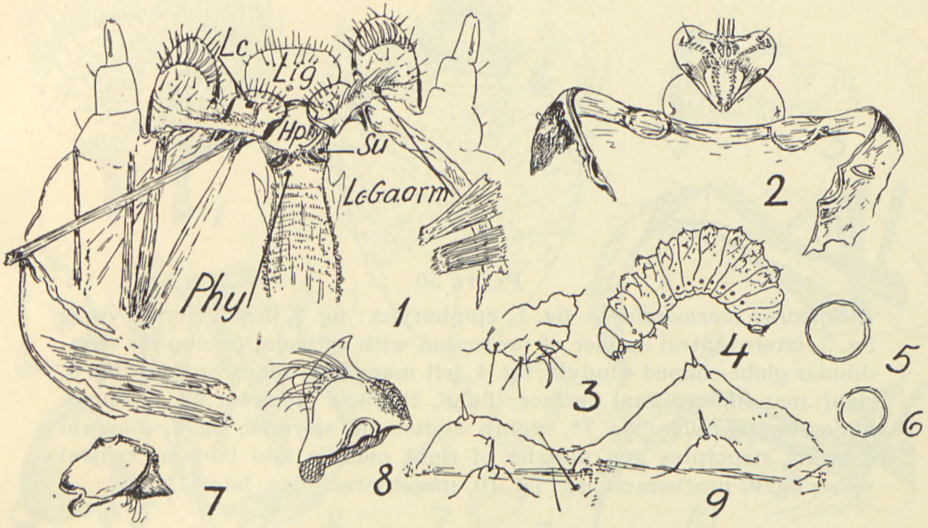


Dorcatoma dresdensis (62).

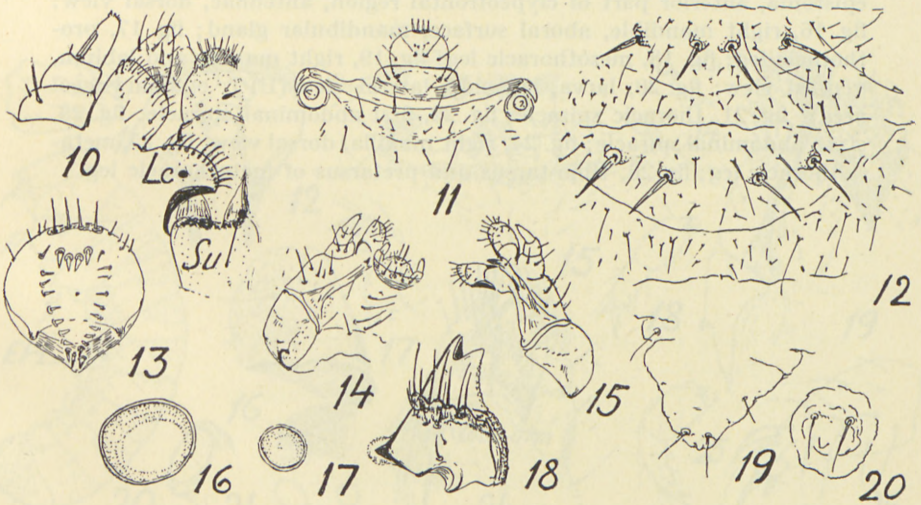
Plate 49

Caenocara bovistae — fig. 1, right and left maxillae, hypopharynx, ligula, bar at bases on dorsal side of maxillary lobes, inculus formed by top of hypopharyngeal suspensorial bar, dorsal view (Hphy: hypopharynx; Lc: lacinia with strongly sclerotized inner margin; Lc-Ga arm: bar at dorsal base of maxillary lobes; Lig: ligula; Phy: pharynx; Su: hypopharyngeal suspensorial bar with top at entrance to pharynx transformed to an inculus or "anvil"); fig. 2, epipharynx, inside of anteclypeus and epistoma, pleurostoma with ocellus; upper and lower articulations for mandible; fig. 3, leg; fig. 4, larva, left side, lateral view; fig. 5, thoracic spiracle; fig. 6, first abdominal spiracle; fig. 7, base of left mandible, inner view; fig. 8, left mandible, aboral surface; fig. 9, dorsum of two abdominal segments on left side carrying tubercles with a single seta on top.

Caenocara oculata — fig. 10, left maxilla and hypopharynx, dorsal view (Lc: lacinia with heavily sclerotized inner margin; Su: inculus or anvil forming top of hypopharyngeal suspensor-bar); fig. 11, labrum, anteclypeus with ribbon-shaped sclerite at base, epistoma, pigmented field and antennae; fig. 12, prodorsal and postdorsal areas of two abdominal segments with seta-bearing tubercles, dorsal view; fig. 13, epipharynx; fig. 14, right maxilla and labium, ventral view; fig. 15, left maxilla, ventral view; fig. 16, thoracic spiracle; fig. 17, abdominal spiracle; fig. 18, left mandible, aboral surface; fig. 19, leg, lateral view; fig. 20, terminal part of leg, end view.



Caenocara bovistae (63).

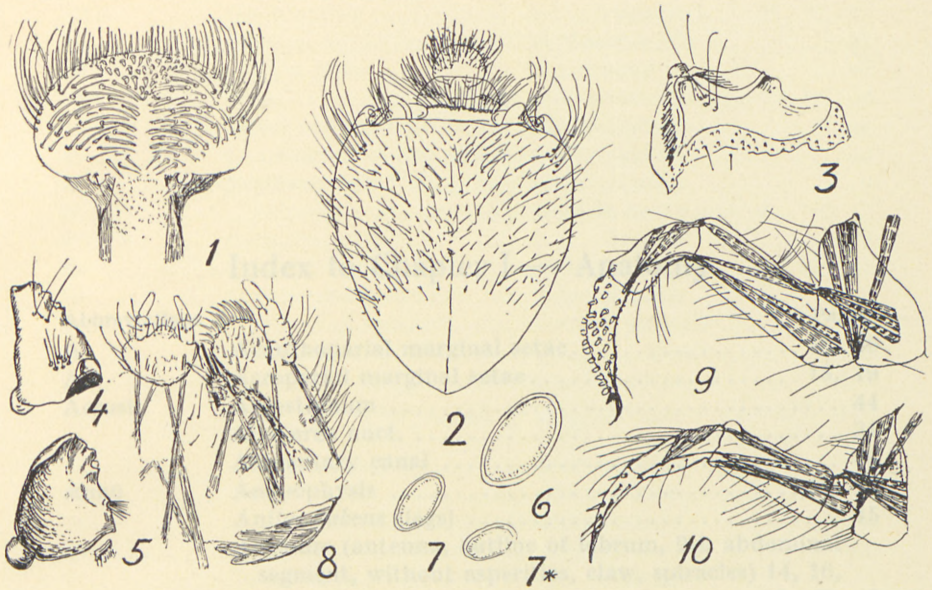


Caenocara oculata (64).

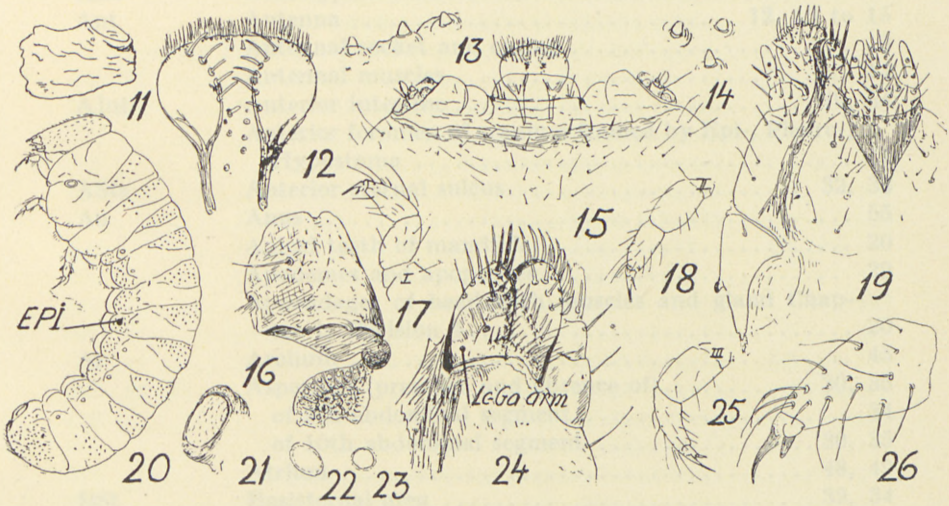
Plate 50

Ptilineurus marmoratus — fig. 1, epipharynx; fig. 2, head, dorsal view; fig. 3, lateroventral surface of projection with articulating cup for mandibular globe-shaped condyle; fig. 4, left mandible, aboral surface; fig. 5, right mandible, adoral surface; fig. 6, thoracic spiracle; fig. 7, fourth abdominal spiracle; fig. 7*, eighth abdominal spiracle; fig. 8, diagram showing structures and muscles of right maxilla and labium, ventral view; fig. 9, prothoracic leg; fig. 10, mesothoracic leg, lateral view.

Ptilinus basalis — fig. 11, projection with articulating cup for mandibular globe-shaped condyle; fig. 12, epipharynx; fig. 13, prodorsal asperities; fig. 14, epipleural asperities; fig. 15, labrum, anteclypeus, epistoma, anterior part of clypeofrontal region, antennae, dorsal view; fig. 16, right mandible, aboral surface, mandibular gland; fig. 17, prothoracic leg; fig. 18, mesothoracic leg; fig. 19, right maxilla and labium, ventral view; fig. 20, larva, left side, lateral view (EPI: epipharyngeal area); fig. 21, thoracic spiracle; fig. 22, first abdominal spiracle; fig. 23, sixth abdominal spiracle; fig. 24, right maxilla, dorsal view; fig. 25, metathoracic leg; fig. 26, tibio-tarsus and pretarsus of metathoracic leg.



Piilineurus marmoratus (65).



Ptilinus basalis (66).

Index to Chapter I — Anatomy

Abbreviations Pages

Index to Chapter II — Taxonomy

An alphabetically arranged list of genera and species.

Indleveret til selskabet den 14. oktober 1953.
Færdig fra trykkeriet den 27. juli 1954.

Errata.

p. 20, line 29:	for	*C. gracilis*	read	*C. gracile*
p. 28, line 13:	"	*paragnatha*	"	*paragnaths*
p. 29, line 19:	"	*Xyltobius*	"	*Xyletobius*
p. 30, line 12:	"	*C. gracilis*	"	*C. gracile*
p. 62, line 14:	"	"	"	"
p. 63, line 10:	"	"	"	"
p. 65, line 8:	"	"	"	"
p. 74, line 2:	"	"	"	"
p. 74, line 5:	"	"	"	"
p. 74, line 32:	"	was	"	way
p. 100, line 23:	"	equal,	"	equally
p. 280, line 23:	"	*C. gracilis*	"	*C. gracile*
plate 13:	"	"	"	"

Det Kongelige Danske Videnskabernes Selskab

Biologiske Meddelelser, bind **22**, nr. 3

Dan. Biol. Medd. **22**, no. 3 (1954)

POSSIBLE MATHEMATICAL RELATION BETWEEN DEOXYRIBONUCLEIC ACID AND PROTEINS

BY

G. GAMOW

København

i kommission hos Ejnar Munksgaard

1954

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»Die Methoden der Polypeptidsynthese gestatten den Aufbau langer Ketten mit vielfachen Variationen in der Reihenfolge. Es ist drum kein blosses Spiel mit Zahlen, wenn man die gegebenen Möglichkeiten berechnet.«

(EMIL FISCHER, Sitzungsber. der Kgl. Preuss. Akad. der Wiss., p. 990, 1916.)

It was recently shown by WATSON and CRICK (1) that the molecules of *Deoxyribonucleic Acid* (DNA), which constitute chromosome fibers of living cells, are formed by double sequences of four basic compounds (*Adenine*, *Thymine*, *Guanine*, and *Cytosine*) held together by two parallel sugar-phosphate chains. Since, according to that scheme, *Adenine* can pair only with *Thymine*, and *Guanine* only with *Cytosine*, one half of that double sequence of bases is completely determined by the other half. Thus, if we denote the four bases by figures 1, 2, 3, 4 (a mathematician would prefer 0, 1, 2, 3), all hereditary properties of any living organism should be characterized by *a long number* ("number of the beast") *written in a four digital system*, and containing many thousands of consecutive digits. The numbers describing two different members of the same species must be very similar to each other (though not quite identical, unless they belong to a pair of identical twins), whereas the numbers representing the members of two different species must show larger differences. Since the number of all possible arrangements of four elements in sequences of several thousand is incredibly large*, we must conclude that all living organisms represent only a negligible fraction of all "mathematically possible" forms of life. For example, it is extremely unlikely that any organism which ever lived on the surface of the earth was represented by such familiar numbers as π, or $\sqrt{3}$ written in the four digital system. WATSON and CRICK

* For a chain which is, for example, 10,000 steps long, the number of possible arrangements is $4^{10,000} = 10^{6,000}$, which is much (much!) larger than the number 10^{76} representing the number of all atoms in the Universe within range of the 200" telescope at Palomar Mountain Observatory.

TABLE I. The list of Amino acids.

1. *Glu*temic acid	14. *Phe*nylalanine
2. *Leu*cine	15. *Cys*tine
3. *Asp*artic acid	16. *His*tidine
4. *Ser*ine	17. *Meth*ionine
5. *Lys*ine	18. *Tryp*tophane
6. *Gly*cine	19. *Cyst*eic acid
7. *Val*ine	20. *Hydr*oxyproline
8. *Pro*line	21. (Norvaline)
9. *Arg*inine	22. (Hydroxy glutamic acid)
10. *Ala*nine	23. (Asparagine)
11. *Thr*eonine	24. (Glutamine)
12. *Iso*leucine	25. (Cannine)
13. *Tyr*osine	

also suggest a very plausible mechanism by which the replication of DNA molecules may take place, with a provision for occasional mutations, i. e. the change of some digits in the original "number of the beast".

It is well known, however, that, while the chromosomes are responsible for carrying all (or, at least, most of) the hereditary information from the parents to the progeny, the actual work of the growing and the development of any organism are carried out by enzymes which catalyze various biochemical reactions in the cytoplasm of the cell. In fact, while a chromosome can be compared with the file cabinet in the director's office of a large factory where all the blueprints are stored, the enzymes play the role of engineers, foreman, and workers constituting the major part of the entire outfit. It follows that there must exist a very precise mechanism which shapes the enzymes produced in any given organism, exactly according to the hereditary information carried by chromosomes. The enzymes, being proteins, possess, however, an entirely different constitution than DNA molecules, and are formed by long sequences of many different amino acids. The number of different amino acids which participates in the structure of proteins is usually taken as 20, although actually there may be a few more. In Table I these amino acids are listed in order of their relative abundance in proteins.

If one assigns a letter of the alphabet to each amino acid, each protein (and, in particular, each enzyme) can be considered

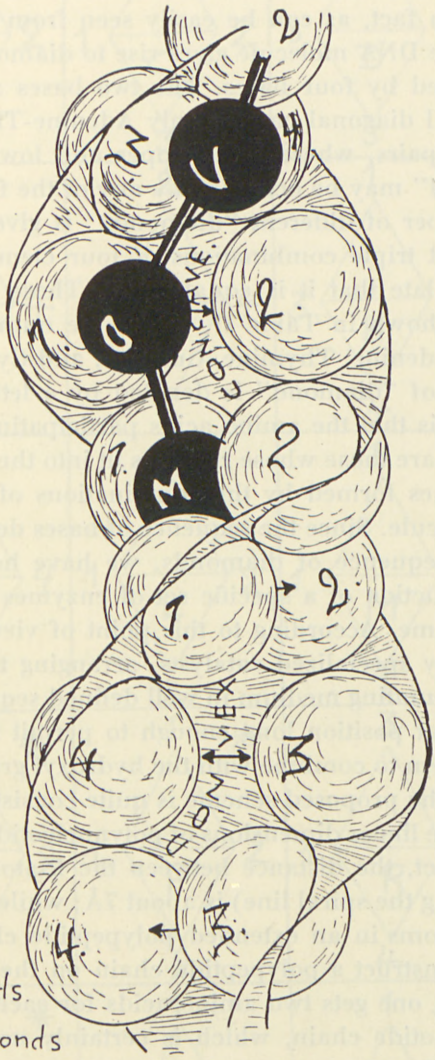


Fig 1.

White balls: bases.
Black balls: amino acids.
Arrows: H bonds.
Bars: Peptide bonds

as *a long word based on an alphabet with 20* (or somewhat more) *different letters.*

It was recently suggested by the author (2) that a simple relation between the order of bases in chromosome fibers, and the

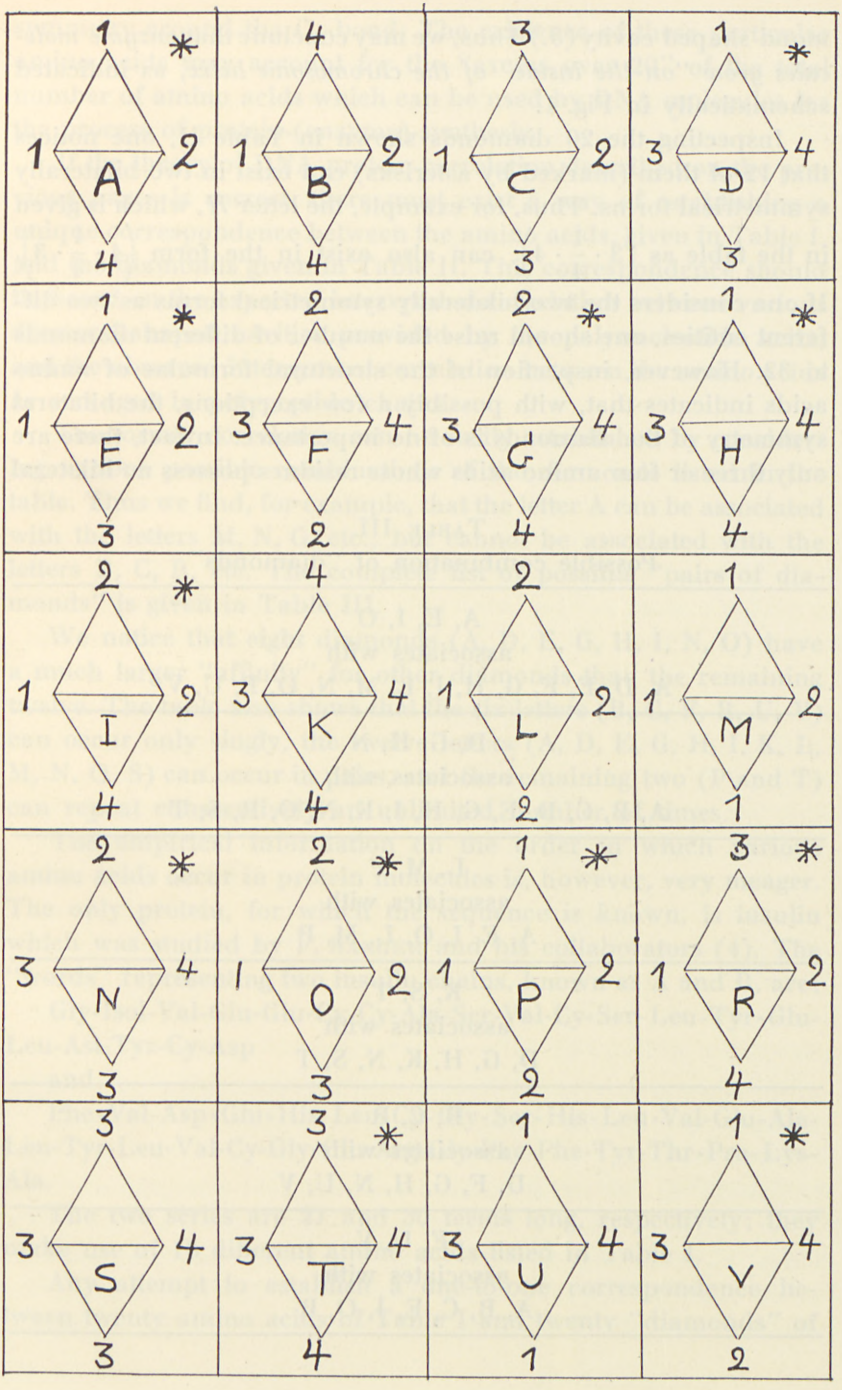
order of amino acids in the corresponding enzymes, can be established by considering basic geometrical features of the WATSON and CRICK model of a DNA molecule.

In fact, as can be easily seen from Fig. 1, the helical nature of the DNA molecule gives rise to diamond-shaped configurations formed by four bases. The two bases at both ends of the horizontal diagonal can be only Adenine-Thymine or Guanine-Cytosine pairs, whereas the upper and lower corners of each "diamond" may be occupied by any of the four bases. Thus, the total number of different "diamonds" is given by the number of different triple combinations of four elements, and one can easily calculate that it is equal to *20*. These 20 different "diamonds" are shown in Table II, where the numerals 1, 2, 3, and 4 stand for Adenine, Thymine, Guanine, and Cytosine, respectively. Each type of "diamond" is denoted by a letter of the alphabet*. The idea is that the amino acids participating in the structure of proteins are those whose residues fit into the various diamond-shaped cavities formed by the combinations of four bases in the DNA molecule. Since the sequence of bases determines in a unique way the sequence of diamonds, we have here a mechanism for the production of a specific set of enzymes by each particular chromosome. According to this point of view, DNA molecules act as highly specialized catalysts, arranging the amino acids from the surrounding medium in well defined sequences, and holding them in that position long enough to permit the amino group of each of them to combine with the hydroxyl group of its next neighbour.

The proposed scheme is quite consistent with the existing data on the linear dimensions of polynucleotide and polypeptide chains. In fact, the distance between the P-atoms in the DNA molecule (along the spiral line) is about 7Å, while the distance between two C_α-atoms in an extended polypeptide chain is 3.6 Å. If one tries to construct a polypeptide chain on the *convex* side of the DNA helix, one gets two amino acids for each "diamond" in the polynucleotide chain, which is certainly not correct. However, constructing the same chain on the *concave* side of the DNA helix, one gets the correct relationship of one amino acid for each dia-

* The assignment of letters in Fig. 2 is different from that given in the author's original article (Ref. 2). The new assignment associates more probable diamonds with more abundant letters of the alphabet in the English text, which makes the "words" made up by various diamond sequences more pronounceable.

TABLE II.


1 * 1 A 2 4
4 1 B 2 4
3 1 C 2 3
1 * 3 D 4 3
1 * 1 E 2 3
2 3 F 4 2
2 * 3 G 4 4
1 * 3 H 4 4
2 * 1 I 2 4
4 3 K 4 4
2 1 L 2 2
1 1 M 2 1
2 * 3 N 4 3
2 * 1 O 2 3
1 * 1 P 2 2
3 * 1 R 2 4
3 3 S 4 3
3 * 3 T 4 4
1 3 U 4 1
1 * 3 V 4 2

mond-shaped cavity (3.) Thus, we may conclude that *enzyme molecules grow "on the inside" of the chromosome helix*, as indicated schematically in Fig. 1.

Inspecting the 20 diamonds shown in Table II, one notices that 12 of them (marked by asterisks) can exist in two bilaterally symmetrical forms. Thus, for example, the letter *H*, which is given in the table as $\left(3 \cdot \frac{1}{4} \cdot 4\right)$, can also exist in the form $\left(4 \cdot \frac{1}{4} \cdot 3\right)$. If one considers the two bilaterally symmetrical forms as two different entities, one should raise the number of different diamonds to 32. However, inspection of the structural formulae of amino acids indicates that, with possibly a few exceptions, the bilateral symmetry of the diamonds is of no importance. In fact, there are only three or four amino acids whose residues possess no bilateral

TABLE III.
Possible combination of "diamonds".

A, E, I, O associates with A, D, E, F, G, H, I, L, M, N, O, P, U, V
D, G, H, N associates with A, B, C, D, E, G, H, I, K, N, O, R, S, T
L, M, P associates with A, E, I, O, L, M, P
K, S, T associates with D, G, H, K, N, S, T
B, C, R associates with D, F, G, H, N, U, V
F, U, V associates with A, B, C, E, I, O, R

symmetry around the C_α-bond. The existence of these particular amino acids may account for the "excess over 20" of the total number of amino acids which can be used by DNA molecules for the process of protein-(enzyme)-synthesis.

If the theory of DNA protein correlation described on the previous pages is correct, there must exist a way of establishing a unique correspondence between the amino acids, given in Table I, and the diamonds given in Table II. This correspondence should be based on the expected intersymbol correlation between various diamond-shaped cavities provided by the polynucleotide helix, and the observed intersymbol correlation between the amino acids as arranged in polypeptide chains.

The former correlation can be easily established by considering various possible combinations of the diamonds listed in the table. Thus we find, for example, that the letter A can be associated with the letters M, N, G, etc., but cannot be associated with the letters B, C, R, etc. The complete list of possible "pairs of diamonds" is given in Table III.

We notice that eight diamonds (A, D, E, G, H, I, N, O) have a much larger "affinity" for other diamonds than the remaining twelve. The table also shows that the six letters (B, C, F, R, U, V) can occur only singly, the twelve letters (A, D, E, G, H, I, K, L, M, N, O, S) can occur in pairs, and the remaining two (P and T) can repeat consecutively an unlimited number of times.

The empirical information on the order in which various amino acids occur in protein molecules is, however, very meager. The only protein, for which the sequence is known, is insulin which was studied by F. SANGER and his collaborators (4). The "words" representing two insulin chains, known as A and B, are:

Gly-Isol-Val-Glu-Glu-Cy-Cy-Ala-Ser-Val-Cy-Ser-Leu-Tyr-Glu-Leu-Ast-Tyr-Cy-Asp

and

Phe-Val-Asp-Glu-His-Leu-Cy-Gly-Ser-His-Leu-Val-Glu-Ala-Leu-Tyr-Leu-Val-Cy-Gly-Glu-Arg-Gly-Phe-Phe-Tyr-Thr-Pro-Lys-Ala.

The two series are *21* and *30* terms long, respectively; they make use of 16 different amino acids listed in Table I.

Any attempt to establish a one-to-one correspondence between twenty amino acids of Table I and twenty "diamonds" of

Table II must face the fact that the number of possible assignments is immensely large, being given by: $20! = 2.3 \cdot 10^{17}$. However, due to highly restricting intersymbol correlation rules given in Table III, such an attempt becomes possible. Thus, for example, there are only sixteen different possible cases in which a double letter is followed by another double letter. These sixteen cases break up into four groups in such a way that the members

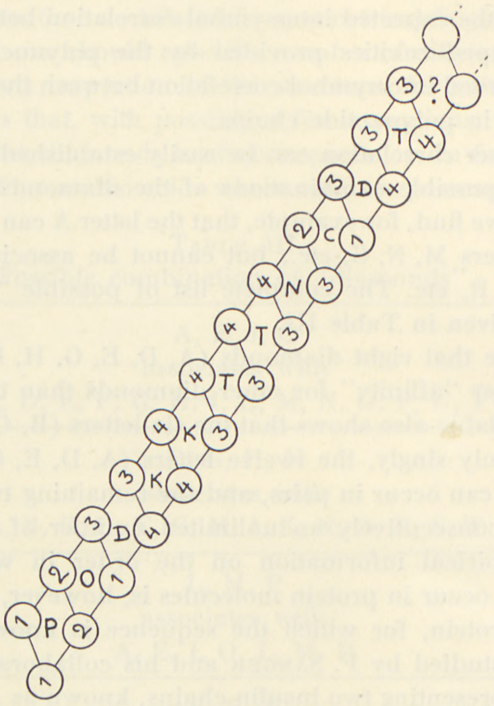


Fig. 2.

of the same group can be transformed into each other by a simple internal permutation. Thus, in order to explain the sequence:

Glu-Glu-Cy-Cy

in insulin A, one must try only four different possibilities (A-A-N-N; L-L-M-M; K-K-T-T, and T-T-S-S). In each of these four cases, we also know the letter-assignment of the fourth amino acid to the right from Cy-Cy, since it is also a Cy. This restricts the choice of the letter for Val since it must precede both Glu and Cy.

Proceeding in this way, it is possible to "decipher" the first eleven places in insulin A as:

P-O-D-K-K-T-T-N-C-D-T- (cf. Fig. 2).

The choice of nine letters from the first K to the last T is unique, except for the above-mentioned internal permutations. However, the next step runs into a difficulty. The 12th amino acid is *Ser*, which was already assigned the letter *C*. But, according to Table III, the letter *C* cannot follow the letter *T*. Thus, at least in this particular case, the correspondence between amino acids and "diamonds" cannot be established, although one comes rather close to it.

It is possible that the difficulty encountered in "deciphering" the structure of insulin in terms of "diamonds" is due to over-simplification of the situation in the proposed form of the theory. For example, it is not impossible that some of the "diamonds" can accommodate more than one amino acid, or that some amino acid can fit into more than one diamond. The answer can be given only by actually constructing a model of a DNA molecule from an atomic-model-kit, and comparing it with the models of various amino acids.

But it looks more likely that insulin is not a good case for testing the validity of the proposed theory. In fact, the theory pertains primarily to "hereditary proteins", i. e. the proteins whose structure is directly and completely determined by genes in the chromosomes. Thus, for example, it should apply directly to the substances primarily responsible for colour vision, or coagulation of blood which are subject to strict laws of heredity. It is not at all certain that insulin falls into this category of organic proteins, especially because diabetes, a sickness connected with insulin deficiency, does not seem to possess hereditary characteristics. Unfortunately, however, we have no information concerning amino acid sequence in any other protein.

A somewhat different approach to the problem can be provided by the study of relative abundances of different amino acids in various proteins. One would, in fact, expect that different types of "diamonds" are affected in different ways by the variation of *Adenine-Thymine* to *Guanine-Cytosino* ratio. Suppose that, within a particular group of living organisms, the abundance of the first pair of bases varies between the limits of $(X - \Delta X)$ and

$(X + \Delta X)$, so that the abundance of the second pair lies within the limits $(1 - X \pm \Delta X)$. It is easy to see that, in such a case, the expected variability of different types of "diamonds" will be different. The "diamonds" defined entirely by the numbers of the first pair (α-type), such as, for example, $\left(1\frac{1}{1}2\right)$ or $\left(1\frac{1}{2}2\right)$, will appear with the relative probability X^3 (since there are only three free choices), whereas the diamonds of the type $\left(3\frac{3}{3}4\right)$ or $\left(3\frac{3}{4}4\right)$ (δ-type) will have the relative probability $(1 - X)^3$. The dia-

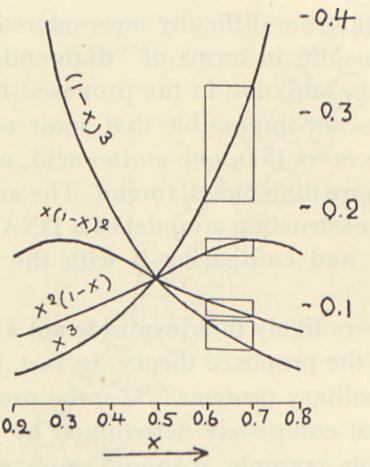


Fig. 3.

monds of the *mixed* type, such as $\left(1\frac{1}{4}2\right)$ (β-type), with the excess of first pair of bases, or such as $\left(3\frac{2}{3}4\right)$ (γ-type) with the excess of second pair of bases, will have relative probabilities given by $X^2(1 - X)$, and $X(1 - X)^2$, respectively. These four functions are plotted in Fig. 3 in respect of X. We notice that, in case that X varies, let us say, within the limits 0.65 ± 0.05, the relative probability of α-type diamonds varies in rather wide limits, whereas the probability of β-type diamonds remains almost constant because the corresponding curve passes through a maximum near $X = 0.65$. This theoretical result may be correlated with observations (5) which seem to suggest that some of the amino

acids show wider variations in different proteins than some others. It would be interesting to undertake a special investigation by comparing the relative abundances of various amino acids in the cytoplasm of cells with the ratios of base-pairs in the corresponding nuclei.

It is the author's pleasant duty to express thanks to Dr. F. H. C. CRICK, and also to the members of the Cyclotron Laboratory (D.T. M.) of the Carnegie Institution of Washington, for helpful discussion of the problems.

Note added in the proof (June, 1954):

Since this article was sent to print, several alternative attempts were made to decipher the sequences of amino-acids in protein molecules in terms of base-sequences in the molecules of nucleic acids. Although no finite solution of that basic problem has as yet been found, a number of interesting possible relationships came to light. The work in this direction is now being continued, and will be reported in due time.

The George Washington University.
Washington, D. C.
U. S. A.

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(1) I. D. WATSON and F. H. C. CRICK, Nature **171**, 964 (1953).
(2) G. GAMOW, Nature **173**, 318 (1954).
(3) This remark is due DR. F. H. C. CRICK.
(4) F. SANGER and H. TUPPY, Biochem. Journal, **49**, 481 (1951); F. SANGER and O. P. THOMPSON, Biochem. Journal, **53**, 336 (1953).
(5) Information theory in Biology. Edited by H. QUASTLER, University of Illinois Press (1953).

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Det Kongelige Danske Videnskabernes Selskab
Biologiske Meddelelser, bind **22**, nr. 4

Dan. Biol. Medd. **22**, no. 4 (1954)

SOME MARINE ALGAE FROM MAURITIUS

ADDITIONS TO THE PARTS PREVIOUSLY PUBLISHED, **VI**

BY

F. BØRGESEN

København 1954
i kommission hos Ejnar Munksgaard

Printed in Denmark.
Bianco Lunos Bogtrykkeri A-S.

As in former years I have also in the past year received collections of algae from Mauritius, and the result of the examination of these is published in this part. Besides some species not previously found in the island, among which two are described as new, I have been able to give some additions and corrections to some species mentioned in earlier parts.

For their continual great interest in collecting the algal material I want most heartily to thank Director, Dr. R. E. Vaughan and his Assistant, Mr. G. Morin.

For very valuable assistance I am much indebted to several specialists.

Thus Mme, Dr. Geneviève Feldmann has most kindly examined some few fragments of *Ceramium* found among other algae.

I also feel much indebted to the well-known specialist in *Corallinaceae*, Mme, Dr. Paul Lemoine, who has been kind enough to work out some specimens of this group received from Mauritius.

And my best thanks are likewise due to Professor T. Segi, University of Mie, Japan, for having examined the material of *Polysiphonia* sent from Mauritius.

Furthermore I owe thanks to cand. mag. Tyge Christensen for his valuable help with the Latin diagnoses.

And likewise I want to thank stud. polyt. Jens Th. Keiding for producing some of the drawings.

To the Trustees of the Carlsberg Foundation I am much indebted for a continued grant.

CHLOROPHYCEAE

I. Siphonocladales.

Fam. 1. ***Boodleaceae.***

Microdictyon Decsne.

1. **Microdictyon Agardhianum** Decsne.

Alg. Mauritius, I, 1940, p. 25, fig. 7. Addit. List, 1946, p. 18.

In a collection of algae received in April 1953 from Mauritius some fine large specimens of this species were contained.

Referring to the more detailed description in Part I of some specimens of this species I shall with regard to the specimens now received mention only that they have a diameter up to about 7 cm. The outline of the specimens is very irregularly sinuated and lobed.

The colour of the specimens in a dried condition is greyish green.

The specimens were "epiphytes on stems of *Cymodocea*".

Mauritius: Point aux Roches, 22-9-52, R. E. V. no. 1289.

II. Siphonales.

Fam. 1. ***Bryopsidaceae.***

Bryopsis Lamour.

1. **Bryopsis indica** A. & E. S. Gepp.

Alg. Mauritius, I, 1940, p. 44; Additions V, 1953, p. 6, fig. 1.

In lately received collections of algae two gatherings contain a small *Bryopsis* which I think is referable to *Bryopsis indica*.

The arrangement of the ramuli, characteristic of this species, in two double, oppositely placed rows up along both sides of the rachis is not always so regular as was the case in the specimens previously examined. But according to the description of A. and E. S. GEPP some variations as to this character are often present, for instance it often happens that the ramuli now and then are placed in a single row only.

As to the locality it is said: "epiphyte on various algae, *Sargassum*, etc."

Mauritius: Riambel, 6-7-52, R. E. V. nos. 1245, 1247.

Fam. 2. Caulerpaceae.

Caulerpa Lamour.

1. Caulerpa Vickersiae Børgs.

Alg. Mauritius, Additions I, 1949, p. 6, figs. 1—2. Additions V, 1953, p. 6.

Entangled among the thallus of *Halodictyon* spec. a small specimen of this little *Caulerpa* was found.

About the locality it was said: "In cavities of rocks mixed with other algae."

Mauritius: Pointe aux Roches, 6-9-52, G. MORIN, no. 1282.

2. Caulerpa crassifolia (Ag.) J. Ag.

Alg. Mauritius, Additions IV, 1952, p. 9, figs. 4—5.

Of this species I have from the island seen only some few small and more or less abnormally developed specimens having besides the usual rows of opposite pinnules some irregularly placed ones in between them.

It was therefore of interest from Dr. VAUGHAN to receive a large specimen (Fig. 1) in which the assimilators nevertheless are small, ovate-oblong in shape, about $1\frac{1}{4}$—$1\frac{1}{2}$ cm long and $\frac{1}{2}$ cm broad, rarely more; and the pinnules, being longest in the middle of the assimilators, where they are about $1\frac{1}{2}$ mm long, become shorter upwards and downwards. The shape of the

Fig. 1. *Caulerpa crassifolia* (Ag.) J. Ag. forma *expositа* Børgs. × 1.

pinnules is obliquely oval (Fig. 2) to more elongate, tapering towards the base and the mucronated or also often rounded apex.

The assimilators are borne upon quite a short stipe about 1 mm high only.

About the locality it is said: "Creeping over rocks in rough water exposed to strong surf near reef." The character of the

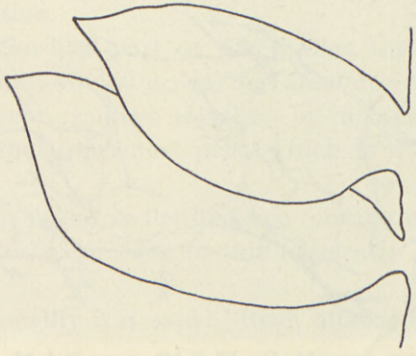

Fig. 2. *Caulerpa crassifolia* (Ag.) J. Ag. forma *expositа* Børgs. Two pinnules. (About 20:1).

locality explains the appearance of the Mauritian plant, which differs highly from that of specimens growing upon soft bottom in tranquil localities, as for instance in lagoons in the West Indies.

In the Canary Islands in similar localities as in Mauritius, where the Atlantic rollers thundered over the reefs a very similar small form was found; cf. BØRGESEN, Alg. Canary Islands, I. Chlorophyceae, 1925, p. 111, fig. 26.

This characteristic form I propose to call forma *exposita*.

Mauritius: Riambel, 24-7-52, G. MORIN, no. 1259.

3. **Caulerpa racemosa** (Forssk.) Weber v. Bosse. var. **microphysa** (Weber) Taylor.

Alg. Mauritius, Additions IV, 1952, p. 11.

A small form (no. 1265) with vesicles about 1 mm broad or a little more comes near to var. *microphysa* (Weber) Taylor, 1928, p. 102.

About the locality it is said: "in lagoon exposed at low tide, on old coral."

Another very much reduced small form (no. 1266) consisting mostly of the much ramified, thin rhizome, the thickest ones about $\frac{1}{2}$ mm thick, is, I think also referable to forma

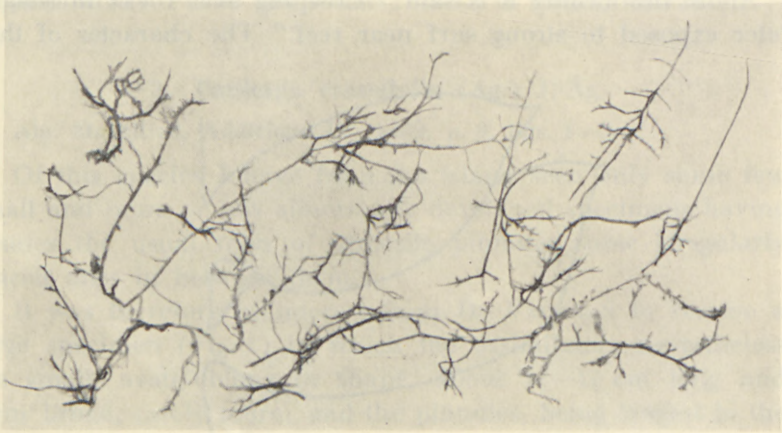

Fig. 3. *Caulerpa racemosa* (Forssk.) Web. v. Bosse var. *microphysa* (Weber) Taylor ad f. *reductam* Børgs. vertens. ×1.

microphysa (Fig. 3). The assimilators are very much reduced, carrying often a single or a few small subpyriform or more spherical vesicles only, which rarely are more than $\frac{1}{2}$—$\frac{3}{4}$ mm broad.

This small form reminds very much of the forma *reducta* which many years ago I found near the harbour of Charlotte Amalia, St. Thomas (in Kgl. Danske Vidensk. Selsk. Skrifter, 7. Række, Bd. IV, 5, København 1907, p. 393—4, figs. 36—7 and Mar. Alg. D. W. I., 1913—4, p. 150—3, figs. 122—3).

About the locality it is said: "forms dense cushions exposed at low tide, calm water."

Mauritius: Cassis, 8-8-52, G. Morin, nos. 1265, 1266.

Fam. 3. Codiaceae.

Udotea Lamour.

1. Udotea javensis (Mont.) A. and E. S. Gepp.

A. and E. S. Gepp in Journ. of Bot., XLIII, 1904, p. 363, tab. 417, figs. 1—4. The Codiaceae of the Siboga Expedition, 1941, p. 110, fig. 36a—c. Okamura, Icon. Jap. Alg. I, 1908, p. 228, pl. XLV, figs. 1—7. — *Rhipidosiphon javensis* Montagne, Prdr. Phycolog. Antarct., 1848, p. 14.

This nice little species was found in a recently received batch of algae. The specimens are in good accordance with Gepp's description.

In the fan-like part of the thallus the filaments had a breadth of about 40—60 μ; in the greater part of the thallus they are coherent, knitted together by means of a chalk incrustation; in the uppermost part, which is not incrusted, they are free.

Having been found in the Red Sea (compare Alg. Mauritius I, 1940, p. 44), the occurrence of this species in Mauritius was to be expected.

About the locality it is said: "Reef, attached to dead corals."

Mauritius: Mahébourg, 21-3-51, G. Morin, no. 1074.
Geogr. Distr.: Indian & Pacific Oceans, Red Sea.

Codium Stackh.

1. **Codium Bartlettii** Tseng and Gilbert.

Alg. Mauritius, Additions V, 1953, p. 11, fig. 3.

Some specimens, which I take to be referable to this characteristic species, being in good accordance with the description of this species and likewise with the specimen mentioned in Part V, have recently been received from Mauritius.

Two gatherings are present and of both some material is preserved in formol and sea water and has thus kept its natural shape, in one of these (no. 1286) a sample has been taken below a division of the thallus and on examination shows that it is broadly flattened, in the other gathering (no. 1258) originating from the upper part of the thallus, this is subterete; the shape of the thallus is thus in good accordance to the description of the species.

As to the locality it is said: "Sandy pools submerged at low tide."

Mauritius: Riambel, 6-7-52, R. E. V. no. 1246. Same locality, 24-7-52, R. E. V. no. 1258.

PHAEOPHYCEAE
HETEROGENERATAE
Polystichineae.
Punctariales.
Fam. 1. Encoeliaceae.
Chnoospora J. Ag.

1. **Chnoospora fastigiata** J. Ag.

Alg. Mauritius, II, 1941, p. 63. Additional List, 1948, p. 50.

Some fine specimens of this species have lately been received from Mauritius. The specimens form up to about 14 mm high, much ramified tufts composed of the repeatedly furcated filaments; these are more or less flattened, about twice as broad as thick.

In my paper: Marine Algae from Easter Island, 1920, p. 263 I have given some illustrations of specimens found there. The habit figure (Fig. 11) shows much developed clusters of hairs. These are not so large in the specimens from Mauritius and while the thallus in the Easter Island plant was very little compressed, that of the plant from Mauritius, as said above, is more flattened. Otherwise the anatomy of the plant from Mauritius exhibits quite well the same character as that found in the plant from Easter Island; cp. Fig. 12, p. 264, l. c.

Two collections were found of which no. 941 was collected "in rocky pools near shore", these specimens being closely covered by large tufts of *Ectocarpus Mitchellae* Harv. About the locality of the other collection no. 1253 it is said: "On large rocks exposed at low tide and subjected to strong surf."

Mauritius: Savinia, 17-9-50, R. E. V. no. 941. Riambel, 24-7-52, G. Morin, no. 1253.

RHODOPHYCEAE

FLORIDEAE

I. Nemalionales.

Fam. 1. Helminthocladiaceae.

Liagora Lamouroux.

1. **Liagora rugosa** Zan.

Alg. Mauritius, III, 1, 1942, p. 30, fig. 14; Additions IV, 1952, p. 21, fig. 10.

Some specimens recently received from Mauritius are by their habit and structure in good accordance with the plant mentioned in Additions IV, 1952, p. 21.

The material was sterile.

As to its habitat it is said: "Firmly attached to large basalt rocks exposed at low tide."

Mauritius: Pointe aux Roches, 22-9-52, R. E. V. no. 1288.

II. Cryptonemiales.

Fam. 1. Corallinaceae.

Subfam. 1. Melobesieae.

Par Mme Paul Lemoine.

Dans la précédente liste, M. F. Boergesen (1943, p. 16) avait seulement mentionné les algues signalées par Jadin (1934) recueillies: sur récifs, *Lithophyllum incrassatum* Foslie à Port Louis et Mahébourg, et (sous le nom de *Lithophyllum incrustans* Phil.) à Flacq; sur coquilles, *Melobesia* (*Pliostroma*) *mauritiana* Foslie, à Flacq; sur algues, *Melobesia farinosa* Lamour., à Flacq;

enfin en épaves, à Flacq, sur la plage, *Porolithon onkodes* (Heydr.) Foslie et *Lithothamnium Lenormandii* (Aresch.) Foslie.

L. incrassatum ayant d'abord été considéré par Foslie (New or crit. calc. alg. p. 29, 1900) comme une forme de *L. incrustans*, ce dernier nom est par suite à supprimer de la liste des algues de Maurice.

Les récoltes de R. E. Vaughan et Dr. Th. Mortensen apportent une intéressante contribution à la connaissance des Algues de Maurice, par la découverte des deux espèces: *Mesophyllum crispescens* (Fosl.) Lem. et *Archaeolithothamnium Schmidtii* Foslie.

A. LITHOPHYLLIEAE

Lithophyllum Philippi.

1. **Lithophyllum moluccense** Fosl.
forma *pygmaea* Heydr.

Cette espèce a déjà été signalée à Maurice par Heydrich (1901, p. 533) sous le nom de *Lithophyllum pygmaeum*, d'après les échantillons de la Collection Agassiz du Muséum de Paris; puis par Mme Lemoine (1938, p. 306) d'après l'étude de la collection Henri Michelin (n° 187 in Herbier Muséum Paris). La forma *pygmaea* est figurée par Heydrich (Kalkalg., 1897, p. 3, fig. 1, pl. I, fig. 8 à 10 et par Foslie ("Siboga", 1904, pl. XII, fig. 7, 12, 13). D'autre part des échantillons de la Collection Agassiz, dans l'Herbier Farlow, de provenance incertaine, mais probablement de Maurice, nommés par Foslie ("New Melob", 1900 (1901), p. 11) *Lithophyllum torquescens* Fosl. ont été ensuite rattachés au *L. moluccense* comme forma *torquescens* (Siboga, p. 70, pl. XII, fig. 11; 1929, pl. LV, fig. 17); cependant un échantillon de l'Herbier du Muséum de Paris déterminé par Foslie *Lithophyllum torquescens*, ne m'a pas montré les rangées alternativement longues et courtes caractéristiques de *L. moluccense*. La réunion des deux espèces reste à élucider par l'étude d'autres échantillons.

Maurice: Flic en Flacq, 3 mai 1950, R. E. Vaughan, no. 925 "seaward edge of reef".

Distr. géogr.: Océans Indien et Pacifique.

2. **Lithophyllum Kaiserii** Heydr.

Heydrich. Corall. insb. Melob. 1897, p. 64, pl. III, fig. 8, 12, 13.

Un massif jeune a été recueilli sur récif; l'espèce avait déjà été signalée à Maurice par Foslie (Stanley Gardiner, 1907, p. 188).

Maurice: Flic en Flacq, 3 avril 1950, R. E. Vaughan, no. 913 "sur le bord externe du récif".

Distr. géogr.: Mer Rouge, Océan Indien (La Réunion etc.) Pacifique.

B. ARCHAEOLITHOTHAMNIEAE

Archaeolithothamnium Rothpletz.

1. **Archaeolithothamnium Schmidtii** Fosl.

Foslie, Flora Koh Chang, p. 16; Siboga Exp., 1904, p. 43, pl.VIII, fig. 15—17.

L'unique échantillon recueilli correspond comme aspect extérieur à la description de Foslie; la structure concorde, mais les cellules dépassent en des points localisés, la dimension extrême indiquée par Foslie, 22 μ, et atteignent 27 μ en coupe transversale et 30 μ en coupe longitudinale; il est stérile.

Maurice: Ile Flat, 16 octobre 1929, Dr. Th. Mortensen, Java, S. Africa Exp., 1929—1930, St. 44, 25 br. (= 45 m.), sables coralliens.

Distr. géogr.: Océans Indien (Maldives, Addu Atoll) et Pacifique, (Golfe de Siam 9 m., Arch. Sulu 15 m., Nouvelle-Guinée, récif).

C. LITHOTHAMNIEAE

Mesophyllum Lemoine.

1. **Mesophyllum crispescens** (Fosl.) Lem. mscr.

Cette espèce, décrite comme forme de *Lithothamnium simulans* Foslie, (Siboga, 1904, p. 16, pl. I, fig. 21—23) se différencie par des cellules plus longues dans l'hypothalle et le périthalle, ce qui me paraît justifier la distinction des deux

espèces qui toutes deux appartiennent au genre *Mesophyllum* Lem. (1928).

L'échantillon est voisin de la fig. 22, pl. I, Siboga.

Cette espèce était inconnue à Maurice et dans l'Océan Indien.

Maurice: Flic en Flacq, 3 avril 1950, R. E. VAUGHAN, no. 913, "sur le bord externe du récif, fixée sur la croûte de *L. Kaiserii*".

Distr. géogr.: Archipel Malais, sur récifs et de 27 à 54 m.

Subfam. 2. Corallinae.

Jania Lamour.

1. Jania tenella Kütz.

Cette espèce avait été recueillie par R. E. VAUGHAN, n° 354, Août 1939, Pointe aux Sables, sur *Galaxaura* (F. BOERGESEN, 1943, p. 26). Je l'ai retrouvée fixée sur *L. Kaiserii* et *Mes. crispescens*.

Dans les sections décalcifiées, les rameaux ont un diamètre de 53 à 63 μ et seulement 47 μ à la partie supérieure. Ainsi qu'il est de règle dans les *Jania*, les cellules de l'article et de l'articulation ont à peu près la même longueur.

L'articulation est formée d'une rangée de cellules de 45 à 60 μ de haut et 5 à 9 μ de large; les cellules des articles, disposées en rangées rigoureusement horizontales, mesurent 40 à 46 $\mu \times$ 3 à 7 μ; dans les rameaux supérieurs la disposition en rangées s'efface et les cellules deviennent plus petites; celles des filaments centraux n'ont que 10 à 17 $\mu \times 2\,^1/_2\,\mu$ à $4\,^1/_2\,\mu$; celles de la partie externe 6 à 7 μ de large.

Maurice: Flic-en-Flacq, 3 Avril 1950, R. E. VAUGHAN, no. 913, "sur le bord externe du récif".

Distr. géogr.: Mexico, Méditerranée, Océans Indien et Pacifique.

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JADIN, Algues des Iles de la Réunion et de Maurice. Ann. Crypt. exotique, t. VII. Paris 1934.

LEMOINE, Un nouveau genre de Mélobésiées: Mesophyllum Bull. Soc. Bot. Fr. 5e sér., t. IV, 1928, p. 251.

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WEBER VAN BOSSE et FOSLIE, Siboga Expeditie 1904.

III. Gigartinales.

Fam. 1. Solieriaceae.

Tenaciphyllum Børgs.

1. **Tenaciphyllum lobatum** Børgs.

Alg. Mauritius, Additions V, 1953, p. 28, figs. 8—10.

In a gathering of algae quite recently received from Mauritius a large well developed dried specimen of this species, besides some fragments in formol and sea water, was included.

An examination of the material in formol has shown that the material is sterile, but the structure is quite in conformity with that of the type specimen no. 905.

Regarding the external conditions in which the formerly found plant lives, nothing was said by the collector (1953, p. 29). And as to the locality in which the latest received specimen occurred, it is said only: "Growing on old coral in lagoon." This must, I think, be indicative of a tranquil locality, and not, as I presumed, an exposed one.

Mauritius: Riambel, 4-11-52, G. Morin, no. 1304.

2. **Tenaciphyllum rotundilobum** Børgs.

Alg. Mauritius, Additions V, 1953, p. 32, figs. 11—12, pl. III, the two figures below.

Also of this species (Fig. 4), in all respects smaller than that mentioned above, some fine specimens were present in a lately received batch of algae.

An examination of some material preserved in formol and sea water has shown that the specimens are built up quite in accordance with those first received.

The material examined was sterile.

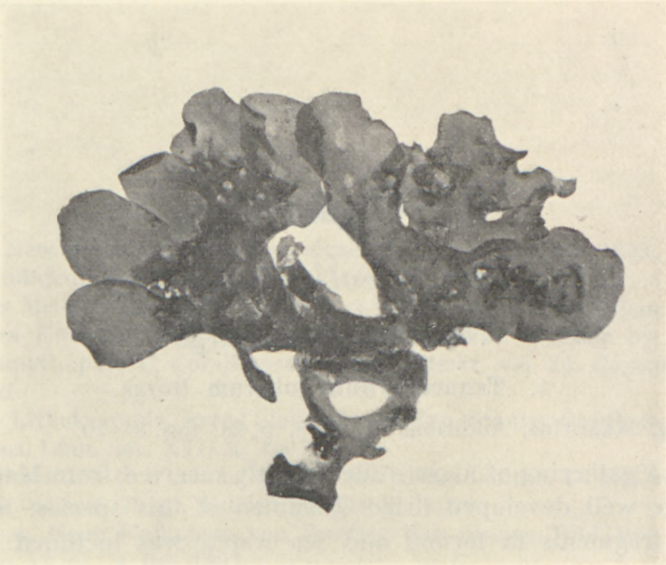

Fig. 4. *Tenaciphyllum rotundilobum* Børgs. Habit of a specimen. Natural size.

As to the locality it is said only: "creeping upon rocks and other algae." Whether or not the locality was exposed to strong surf is not mentioned; nor was this mentioned about the type-specimen formerly received.

Mauritius: Riambel, 20-7-52, G. Morin, no. 1257.

Fam. 2. ***Rhodophyllidaceae.***

Gelidiopsis Schmitz.

1. **Gelidiopsis acrocarpa** (Harv.) Schmitz.

Schmitz, Fr., Marine Floridun von Deutsch Ostafrika, 1895, p. 148. Feldmann, J., Remarques sur les genres *Gelidium* Lamour., *Gelidiopsis* Schmitz et *Echino caulon* (Kütz.) emend., 1931, p. 7. — *Gelidium acrocarpum* Harv., Friendly Island Algae no. 40.

Some few small specimens (no. 1285), having a structure like that of *Gelidiopsis*, are found in a batch of algae recently received from Mauritius.

Fig. 5 shows 3 of the specimens.

Fig. 5. *Gelidiopsis acrocarpa* (Harv.) Schmitz (× 1).

From prostrate creeping filaments fixed to the substratum the erect parts of the thallus are given out; these are in their basal parts terete, about 500 μ thick and of variable length, up to about two cm, rarely more; the upper part of the thallus becomes broadened out more or less ribbonlike, elongate ellipsoidal, getting a length of about 3 cm and up to about 2 ½ mm broad where they are broadest, from there tapering towards both ends, the apical ones being obtuse.

The specimens from Mauritius have some likeness to KÜTZING's figure of a plant which he calls *Gelidium repens* in Tab. Phycolog., vol. 18, pl. 60, figs. a, b, a figure to which FELDMANN refers in his paper quoted above, when mentioning *Gelidiopsis acrocarpa* (Harv.) Schmitz and as "échantillon authentique" FELDMANN quotes HARVEY's Friendly Island Algae no. 40. Most regrettably no specimen of this is found in the herbarium of the Botanical Museum, Copenhagen, nor any of HARVEY's Ceylon Algae no. 34, which is the same species.

SETCHELL in "American Samoa", 1924, p. 163 says that he has examined both specimens in HARVEY's Herbarium in Trinity

Fig. 6. *Gelidiopsis acrocarpa* (Harv.) Schmitz. A specimen from Tahiti (× 1).

College, Dublin, and compared some specimens which he has collected in Tutuila Island with HARVEY's specimens, and has found, that they are the same species. And later SETCHELL has also referred a plant collected in Tahiti ("Tahitian Algae", 1928, p. 99) to this species; of the plant from Tahiti I have from SETCHELL received some specimens (no. 5192). Fig. 6.

A comparison of this plant with that from Mauritius shows, however, rather essential differences not only is the plant from Mauritius much smaller and more delicate, but the flat parts of the thallus are proportionally much broader; and in the Tahitian plant the flat parts run out into some more or less long, whiplike prolongations. About the Tahitian plant SETCHELL points out that it has much likeness to *Sphaerococcus angustifolius* Kütz., Tab. Phycol., vol. 18, pl. 99 from New Caledonia, and this figure has also some likeness to the plant from Mauritius.

SETCHELL in the same paper, p. 99, also refers to *Gelidium*

samoense Reinbold in Denkschr. Akademie d. Wissensch., Bd. 81, Wien 1908, p. 204, and gives an illustration of a specimen from Tahiti which he finds "clearly answering to REINBOLD's description". REINBOLD about his plant says that it reminds of *Acrocarpus pulvinatus* Kütz., Tab. Phycol., vol. 18, tab. 37 and of *Sphaerococcus angustifolius* Kütz., Tab. Phycol., vol. 18, tab. 99, but to this SETCHELL remarks: "Our plant bears some resemblance to the former but the latter is more clearly resembling the plant we have referred to *Gelidium acrocarpum* Harv.", and this is also in accordance with my view.

And yet it must be mentioned that SETCHELL in the same paper gives two figures (pl. 18, figs. 1—2) of a plant which he refers to *Gelidium acrocarpum* Harv.; their likeness to the specimens from Mauritius seems not very striking.

In this connection it should be added also that GRUNOW in "Algen der Fidschi-, Tonga- und Samoainseln", 1873, p. 39, mentions *Gelidium acrocarpum* Harv., (Ceylon Algae No. 34, Kg., Tab. Phyc. Bd. XIX, tab. 23), as found "An Korallenriffe von Ovalau", and GRUNOW adds: "*G. repens* Kg. tab. phyc. Bd. XVIII, tab. 60, welches VEILLARD bei Neu-Caledonien sammelte, scheint mir gar nicht von *G. acrocarpum* verschieden zu sein, und entsprechen die Exemplare von Ovalau beiden citierten Abbildungen."

And finally I want to mention that HAUCK in Hedwigia, 1888, p. 89 about *Gelidium acrocarpum* Harv. says: "Die Tetrasporangien tragenden Pflanzen entsprechen die KÜTZING'schen Abbildungen von *Gelidium acrocarpum*, Tab. Phyc., XIX, tab. 23 und *Gelidium repens*, Tab. Phyc., XVIII, tab. 60, während die sterilen Pflanzen und Thallusstücke sehr gut mit den KÜTZING'schen Habitusbildern von *Gelidium variabile* Tab. phyc., XIX, Tab. 23 und *Acrocarpus setaceus* Tab. phyc., XVIII, tab. 33 übereinstimmen."

As appears from what is said above, the apprehensions of the different investigators of these very variable but closely related forms are rather deviating and to reach a satisfactory result a large material from localities with different external conditions is surely necessary.

But as our knowledge of these forms is now, and as I have very little material to base any construction upon, I am at present

inclined to consider most of these forms, perhaps all, as members of a single very variable and polymorphous species: *Gelidiopsis acrocarpa* (Harv.) Schmitz.

About the locality it is said: "growing in crevices of large rocks in lagoon."

Mauritius: Pointe aux Roches, 22-9-52, R. E. V. no. 1285.

2. **Gelidiopsis scoparia** (Mont. et Millard.) Schmitz.

Alg. Mauritius, Additions IV, 1952, p. 26, figs. 13—14. Additions V, 1953, p. 36.

A small and tender form with much developed furcations of the thallus giving it a very elegant appearance has recently been received from Mauritius.

The plant forms low, 4—5 cm high, tufts upon rocks.

While in former collections the base has been wanting, this is present here. It consists of decumbent filaments fixing themselves to the substratum by small discs.

From this base the erect stem-like shoots are given out; these are terete below, becoming gradually flattened upwards and broader up to where the furcations take place, forming an often very regular fanlike upper part. Some of the rays may again continue the growth, becoming furcated and forming a new fan.

Fig. 7. *Gelidiopsis scoparia* (Mont. et Millard.) Schmitz. A specimen (× 1).

The specimens were sterile.

About the locality it is said: "Rock crevices, exposed to surf on reef."

Mauritius: Flic en Flacq, 3-4-51, R. E. V. no. 904.

Fam. 3. ***Hypneaceae.***

Hypnea Lamour.

1. **Hypnea chordacea** Kütz.

Kützing, F., Regensb. Flora, 1847; Spec. Alg., 1849, p. 760. Weber, A., Algues Siboga, p. 448. Tanaka, T., The genus *Hypnea* from Japan, 1941, p. 230, figs. 2, 3.

In a collection of algae recently received a rather characteristic small *Hypnea* is found which I think is referable to *Hypnea chordacea* Kütz. as it agrees very well with the description in Kützing, Species Algarum, 1849, p. 760. (Fig. 8).

Fig. 8. *Hypnea chordacea* Kütz. A specimen (× 1).

This species, which De Toni in Sylloge Algarum II, p. 473 takes with a ? as a synonym of *Hypnea spicifera*, is, as is pointed out by Mme Weber l. c., well characterized in three respects from *H. spicifera* (Suhr) Harv., the most closely related species, namely by its more compact consistence, its curved erect stem-

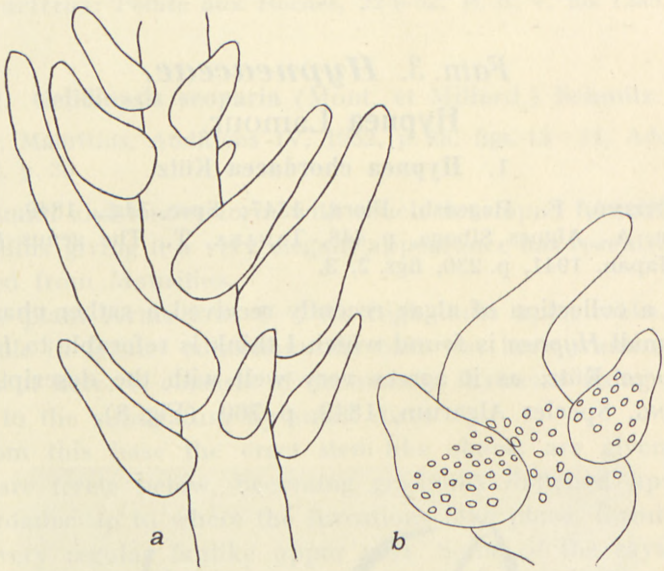

Fig. 9. *Hypnea chordacea* Kütz. *a*, part of a stemlike filament with branchlets yet sterile; *b*, branchlet with sporangia (× c. 30).

like filaments and its quite short branchlets covering the upper part of the erect filaments.

The Mauritian plant forms tufts up to a height of 5—6 cm; the tufts are composed of a number of erect, curved filaments about 1 mm thick, tapering upwards to an acute apex. Some of the filaments are sparingly branched, some not all.

From their middle or a little lower the erect filaments become densely clad with short branchlets of different shape and size, the younger ones subcylindrical or obliquely pear-shaped; the older ones are more irregularly shaped and often provided with smaller outgrowths (Fig. 9); in the lower parts of these branchlets the tetrasporangia are formed. These are of variable shape, some nearly cylindrical with broadly rounded ends, about 50 μ

long and 20 μ broad, others are shorter and broader. The colour of the dried specimens is dark red, nearly blackish.

Being built in this way our plant reminds much of the two *Hypnea*-species: *H. spicifera* (Suhr) Harv. and *H. Harveyi* Kütz. from Cape, and about *H. Boergesenii* Tanaka from Japan; but a more detailed comparison with these species nevertheless shows essential differences.

Thus the Japanese species, according to the description (see Tanaka, The Genus Hypnea, 1941, p. 233) and two specimens most kindly sent me from Professor Tanaka, is a much taller and more ramified plant and furthermore carrying densely placed fertile branchlets from near the base of the plant up to the apices of the branches.

Hypnea spicifera is likewise a taller plant and its thallus is often much ramified. Furthermore, the fertile branchlets are given out in the upper parts of the thallus only; yet it must be mentioned that its colour in most of the specimens I have seen is a rather light red.

And finally as to Kützing's species I want to point out that I know it only from the description by Kützing in "Species Algarum", p. 760 and from his figure in Tab. Phycol., vol. 18, tab. 28, figs. a, b, c. According to the description the more or less ramified thallus is densely clad with short, fructiferous, acute branchlets from base to apex and thus in this respect very different from the plant from Mauritius mentioned here.

In Part III, 2, 1943, p. 55 I have referred some small specimens found in Jadin's collection to this species of Kützing.

And lastly, when mentioning these and related forms, I also want to remind of some specimens from Karachi which in Kew Bulletin, 1934, p. 189 I referred to *H. spicifera*, following, as I did at that time, J. Agardh in his supposition that *H. Harveyi* Kütz. is to be considered a synonym of *Hypnea spicifera*; but if one does not agree with J. Agardh, the plant from Karachi has perhaps better be referred to Kützing's species.

The specimens have been gathered "in rock crevices exposed to strong surf".

Mauritius: Riambel, 24-7-52, G. Morin, no. 1251.
Geogr. Distr.: Java, Japan.

2. **Hypnea musciformis** (Wulf.) Lamour.

Alg. Mauritius, III, 2, 1943, p. 54.

A fine, large specimen of this species is found in a collection of algae recently received.

As to the locality it is said: "Usually epiphytic on *Sargassum* etc. in lagoon."

Mauritius: Riambel, 4-11-52, R. E. V. no. 1302.

3. **Hypnea (?) pectinella** nov. spec.[1]

Thallus parvus ca. 1.5 cm altus, caespitosus, ramosus, compositus ex partibus decumbentibus, repentibus, teretibus, rhizoidibus disciformibus ad saxa adfixis et partibus erectis, basi teretibus supra planis, ex marginibus ramulos teretes, ca. 1 mm longos, plus minus regulariter oppositos pectinatim gerentibus, quorum plurimi semper simplices, nonnulli autem indefinite crescentes ramigeri.

Tetrasporangia zonatim divisa, ca. 17—20 μ longa et 6—7 μ lata, in superficie thalli formata.

Mauritius: Riambel, 24-7-52, R. E. V. no. 1254.

This nice little species (Fig. 10) forms upon rocks small tufts up to about $1\frac{1}{2}$ cm high.

Fig. 10. *Hypnea*? *pectinella* nov. spec. (× 1).

The base of the thallus consists of decumbent creeping terete filaments (Fig. 11 b) fixed to the substratum by short roundish

[1] When putting a? after the generic name it is because I have not seen any female or male organs, but also because the thallus is flattened.

discs formed by groups of coherent rhizoids issuing here and there from the underside of the filaments.

From the upper side of these filaments the erect shoots are given out. Below, these are terete, becoming flattened upwards,

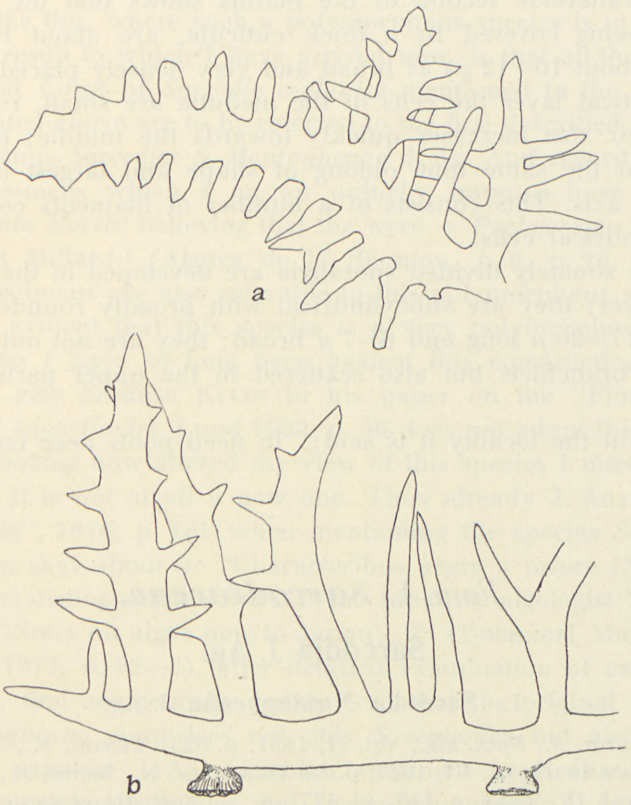

Fig. 11. *Hypnea* (?) *pectinella* nov. spec. *a*, upper part of the thallus, *b*, apex of basal filament with young erect shoots (× ca. 15).

about $\frac{1}{2}$ mm broad and 200 μ thick. From the edges of these shoots terete branchlets issue more or less regularly, oppositely placed, giving the thallus a nice, pectinate appearance; most of these branchlets remain undivided, reaching a length of about 1 mm or a little more; some of them get a single or a few branchlets near their upper ends, and now and then a side-branch with indefinite growth is given out by means of which the ramification of the thallus is carried out (Fig. 11 a). The branchlets

are nearly cylindrical, tapering in their upper ends towards the acute apex.

The epidermal cells in the younger parts of the thallus are provided with hairs.

A transverse section of the thallus shows that the cortical cells, being covered by a thick cuticula, are about twice as long (about 10—12 μ) as broad and very densely placed. Below the cortical layer the cells of the medulla are small, roundish, but their size increases quickly towards the middle; they become at the same time oblong of shape and largest near the central axis. This consists of a number of filaments composed of cylindrical cells.

The zonately divided sporangia are developed in the epidermal layer; they are subcylindrical with broadly rounded ends, about 17—20 μ long and 6—7 μ broad; they are not only found in the branchlets but also scattered in the upper parts of the thallus.

About the locality it is said: "in deep pools near reef."

Fam. 4. Sarcodiaceae.

Sarcodia J. Ag.

1. Sarcodia Montagneana J. Ag.

Agardh, J., Spec. alg., vol. II, 1851, p. 623. Yendo, K., Notes on Algae New to Japan, VI, 1917, p. 82. Okamura, K., Icones of Japanese Algae, vol. IV, 1923, p. 110, pl. 177—8. — *Sarcodia ceylanica* Harv., Alg. Ceylon Exsicc. no. 27. Børgesen, F., Alg. Mauritius, III, 2, 1943, p. 66, where literature is quoted; Additions II, 1950, p. 21; Additions V, 1953, p. 37, fig. 13. — *Callymenia Morelii* Børgs., Additions, III, 1951, p. 39, pl. V. — *Sarcodia mauritiana* Børgs., Additions, IV, 1952, p. 29, pl. III.

A short time ago, in a letter dated Port Louis Dec. 21, 1953, Dr. Vaughan asked me about some of the specimens previously received. About two of them he writes as follows: "I cannot distinguish between *Callymenia Morelii* no. 957 and *Sarcodia Ceylanica* var. *Mauritiana* no. 1037; this material comes from the same locality."

Owing to this I have taken the question up for renewed examination and not only that about the two gatherings mentioned above, but practically all the material received of this species.

However, the material has not been particularly extensive in a case like this, where such a polymorphous species is involved.

The result to which I have arrived now, is that all the specimens and forms of *Sarcodia ceylanica* mentioned in the papers enumerated above are to be referred to the first described species of the genus *Sarcodia: S. Montagneana* J. Ag. And regarding the few specimens which I on an unlucky impulse have called *Callymenia Morelii* believing that the were = *Pachycarpus Morelii* Mont. et Millard.[1] (Algues de la Réunion, p. 6, p. 26, fig. 2), these specimens are also referable to this polymorphous species.

It is evident that this species is a very polymorphous one, and when I have so long been against this construction, it is perhaps also because KYLIN in his paper on the "Florideengattung" *Gigartinales*, Lund 1932, p. 56 does not adopt this view.

But having now altered my view of this species I must point out that it is not at all a new one. Thus already J. AGARDH in "Epicrisis", 1876, p. 431, when mentioning the species *Sarcodia ceylanica*, says about it: "Characteribus aegre a priore (*S. Montagneana*) distinguenda". But it is the Japanese algologist YENDO, who in "Notes on algae new to Japan", VI (Botanical Magazine, vol. 31, 1917, p. 82—3), after detailed examination of extensive material, first energetically pointed out that the original species *S. Montagneana* comprises not only *S. ceylanica* but also *Meristotheca papulosa* J. Ag. (Arabian specimen in Herb. J. Ag.), *Sarconema palmata* Sonder and *Sarconema capensis* J. Ag., however, putting a ? after the two latter species. And the Japanese algologist OKAMURA in his "Icones of Japanese Algae", vol. IV, p. 110, pl. 177—8 likewise referred *Sarcodia ceylanica* to *S. Montagneana*.

Having tried myself also without any happy result to distinguish between some of the most characteristic forms of this

[1] What the above-mentioned species of MONTAGNE et MILLARDET is, does not seem to have been cleared up yet. DE TONI in Sylloge Alg., vol. IV 1897, p. 254 says about it: "est forsan *Callymenia* spec."; however, in *Callymenia* the tetrasporangia are cruciately divided, but that pictured in MONTAGNE et MILLARDET's paper seems to be tetrahedrally divided.

polymorphous species I now refer not only *S. ceylanica* Harv. but also, as done above, *S. mauritiana* Børgs. to *S. Montagneana* J. Ag.

1. **Sarcodia multifida** Børgs.

Alg. Mauritius, Additions V, 1953, p. 39, fig. 11.

Since this species was described in 1953 I have had an opportunity to examine some more material, and this has shown that this species is rather polymorphous; but I have difficulty in believing in the possibility that it should be a form of the above-mentioned species.

Figs. 12 a, b shows some specimens of the plant.

As was the case with the material formerly examined, the specimens now received are all fragments without bases, but as was said already in the description of the species, I have no

Fig. 12 a. *Sarcodia multifida* Børgs. Fragment of a specimen (× 1).

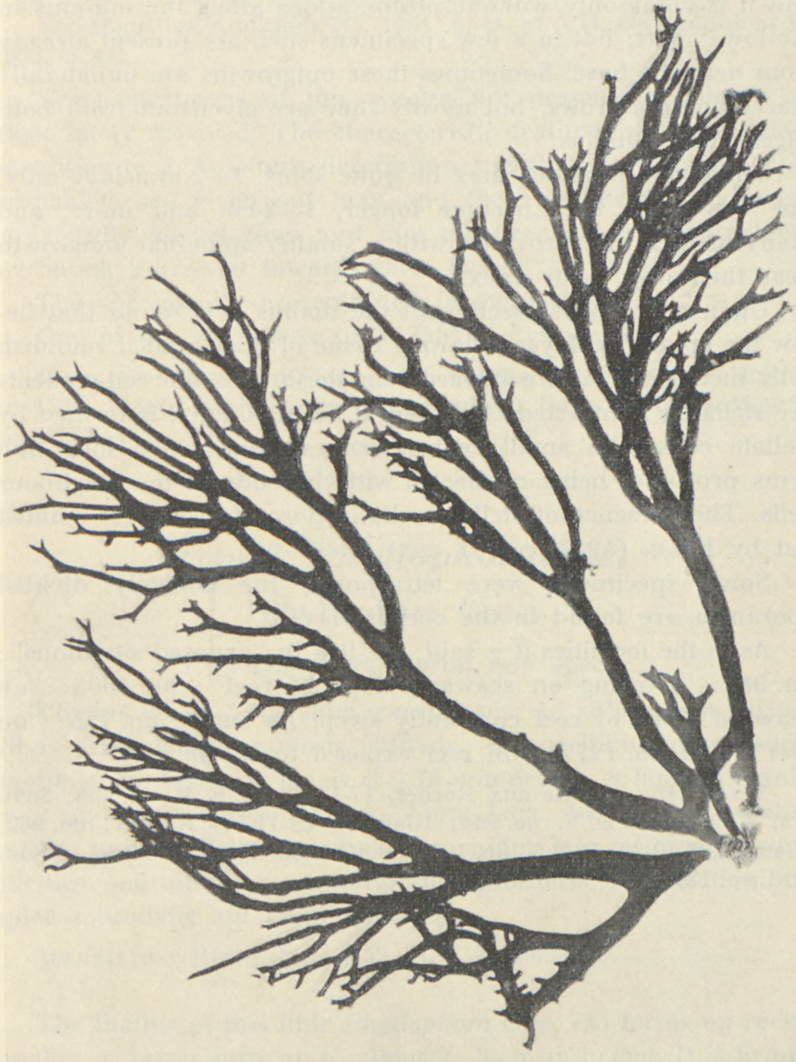

Fig. 12 b. *Sarcodia multifida* Børgs. Fragments of a specimen (× 1).

doubt that the present specimens have had an irregularly lobed disc firmly fixed to the rocks, from which a number of erect shoots are given out; in some of the specimens fragments of the disc are also present. Near the base the thallus is flattened and it is commonly without proliferations along the margins in the lower part; but in a few specimens such are present already from near the base. Sometimes these outgrowths are unilaterally placed in short rows, but mostly they are given out from both edges of the thallus.

These proliferations may be quite short, 1—2 mm long only, but very often they become longer, 1—2 cm and more, and many of them are provided with a smaller spine-like outgrowth near their own acute apex.

Upon a transverse section of the thallus it is found that below the epidermal layer follows a tissue of thick-walled roundish cells increasing in size inwards; in these cells the cell-contents are stellately contracted. The central tissue, finally, is formed by stellate cells with small central bodies from which long thin arms protrude, being connected with the ends of the neighbour cells. The presence of stellate cells in *Sarcodia* was first pointed out by KYLIN (1932, p. 56).

Some specimens were tetrasporic; the zonately divided sporangia are found in the cortical layer.

As to the localities it is said: no. 944 in "exposed situations"; no. 982: "growing on seaward slope of reef"; no. 1003: "on seaward slope of reef constantly swept by surf"; no. 755: "on reef", and no. 1277: "on reef exposed to strong surf".

Mauritius: Pointe aux Roches, 17-11-47, R. E. V. no. 755; Savinia, 17-9-50, R. E. V. no. 944; Riambel, 23-11-50, R. E. V. no. 982; Riambel, 8-12-50, R.E.V. no. 1003; Pointe aux Roches, 6-9-52, G. MORIN, no. 1277.

Fam. 5. Gracilariaceae.

Gracilaria. Grev.

1. **Gracilaria dura** (Ag.) J. Ag.

Alg. Mauritius, Additions III, 1951, p. 41, pl. VII, and Additions V, 1953, p. 41.

Some specimens of this species are present in batches of algae lately received. The characteristic features of this species, according to J. AGARDH's description, are that the branches and branchlets are given out here and there in shorter or longer unilaterally placed rows and that the branches and branchlets are much narrowed towards their bases.

The specimens were collected in lagoons.

One of the specimens (no. 1258) is cystocarpic.

Mauritius: Pointe d'Eesny, near Mahébourg, 15-11-51, G. MORIN, no. 1176. Pointe Roche Noire near Tombeau Bay, 9-7-52, G. MORIN, nos. 1237—8.

Fam. 6. Phyllophoraceae.

Phyllophora Grev.

1. **Phyllophora Morini** nov. spec.[1]

Thallus ad 2—3 cm altus, caespitosus, ad substratum rhizoidibus irregulariter ramosis adfixus, ex stipitibus compositus teretibus, ca. 1—3 mm longis et 0.75 mm crassis et laminis planis ca. 2 cm longis, medio ca. 1.5—2 mm latis, deorsum attenuatis, sursum subaequilatis, apicibus plus minus late rotundatis, simplicibus, sed interdum ex marginibus proliferis, prolificationibus apice rotundatis aut saepe furcatis.

Mauritius: Riambel, 24-7-52, R. E. V. no. 1255.

The thallus of this little *Phyllophora* (Fig. 13) forms on rocks smaller or larger tufts up to about 2—3 cm in height. It is firmly

[1] Named in honour of Mr. G. MORIN, Taxidermist at the Mauritius Institute, who, according to kind information from Director R. E. VAUGHAN, is a very keen worker and preparator and who has collected a great number of the algae enumerated in this and previous papers dealing with the algal flora of Mauritius.

Fig. 13. *Phyllophora Morini* nov. spec. Some specimens × 1.

fixed to the substratum by means of irregularly ramified hapters issuing from the short stem-like, basal, terete part of the erect thallus. From this stem the ribbon-like part of the thallus is given out, reaching a breadth of $1\frac{1}{2}$—2 mm, where it is broadest, from where it tapers gradually downwards and less upwards or not at all, becoming in cases even a little broader towards the upper, more or less broadly rounded apex.

The erect thallus mostly is not branched; but some specimens are provided with adventitious shoots or proliferations, shorter or longer, issuing from the margins; the apices of these shoots are often bifurcate.

The consistency of the thallus is very tough.

A transverse section of the thallus shows that it is built in good accordance with that of *Phyllophora*.

The peripheral layer is covered by a thick cuticula and composed of densely placed palissade-like cells, about 7—8 μ long and about half as broad; then follows a layer of small roundish densely placed cells surrounding the medulla, the cells

of which are proportionally large, oblong, thick-walled, about 50 μ long and half as broad.

Any concentric cortical layers as found in the stipe of *Phyllophora Brodiaei* (compare ROSENVINGE Mar. Alg. Denmark, p. 524, fig. 500) are not observed in the tiny stipe of this little species; the tissue found here is composed of densely placed cells in transverse section, roundish, in longitudinal ones subcylindrical, and have thick walls.

Most regrettably the specimens are sterile.

As to the locality it is said: "on rocks exposed to strong surf."

IV. Ceramiales.

Fam. 1. Ceramiaceae

Subfam. 1. Griffithsieae.

Griffithsia. C. Ag.

1. **Griffithsia subcylindrica** Okamura.

Alg. Mauritius, Additions V, 1953, p. 53.

In the paper quoted above it is mentioned that this species occurs in the island; in a batch of algae lately received from Mauritius another specimen of this species was present.

An examination of it has shown that it is a male plant.

As to the locality it is said: "Lagoon, epiphytic on *Cymodocea*, etc."

Mauritius: Riambel, 4-11-52, G. MORIN, no. 1305.

Fam. 2. Rhodomelaceae.

Subfam. 1. Polysiphonieae.

Polysiphonia Grev.

By Professor T. Segi.

1. **Polysiphonia subtilissima** Montagne.

"Centurie II, n. 6 in Ann. Sc. Nat. Avr. 1840, Syll. p. 442"; Kützing, Spec. Alg. (1849) p. 804; Id., Tab. Phyc. vol. 13 (1863) pl. 28, figs. a—e; Harvey, Ner. Bor. Amer. (1853) p. 34; J. Agardh, Spec. Alg. vol. 2 (1863) p. 962; Farlow, Mar. Alg. New Eng. (1881) p. 178; Phyc. Bor. Amer. Fas. 1 (1892) No. 45; De Toni, Syll. Alg. vol. 4 (1903) p. 874; l. c. vol. 6 (1924) p. 393; Pilger, Meeresalg. Kamerun (in Engler's Jahrb. vol. 46, 1911) p. 304; Taylor, Mar. Alg. Northeast. coast of North Amer. (1937) p. 365; Tseng, Mar. Alg. Hong Kong, VI. Polysiphonia (Papers Michigan Acad. Sci. Arts and Lett. vol. 29, 1944) p. 70, pl. 1; Segi, Polysiphonia from Japan (Jour. Fac. Fish. Pref. Univ. Mie, vol. 1, No. 2, 1951) p. 197, pl. III, 6, fig. 8.

This plant has four siphons without cortical cells.

In the Mauritian specimen (Fig. 14) the cystocarps (Fig. 15) are almost globose (ca. 260—320 × 270—340 μ) as figured, but in the Japanese one they are broadly urceolate (Segi, *l. c.*). It seems to the writer that there are two types of cystocarps as noted by De Toni (*l. c.* vol. 6).

Fig. 14. *Polysiphonia subtilissima* Montagne. A specimen. About natural size.

The present specimens agree with Kützing's figure (Tab. Phyc. *l. c.*) and on the whole with the American specimen (Phyc.

Bor. Amer. Fasc. 1, 1892, No. 45). But the frond is not so finely branched as that of the Japanese plant (Samani).

The plant is purplish red or almost blackish in drying.

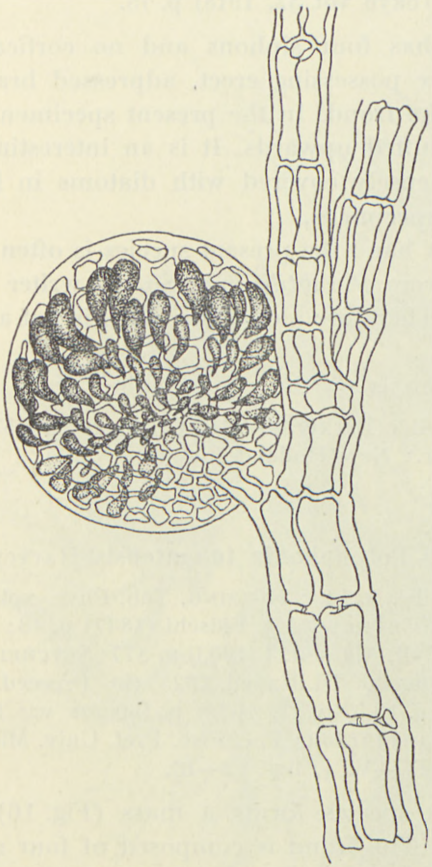

Fig. 15. *Polysiphonia subtilissima* Mont. A cystocarp × ca. 120.

Mauritius: Ilôt Barkly, 3-10-48, G. Morin, no. 737, no. 782.

Geogr. Distr.: Atlantic coast of France and America; Hong Kong; Japan.

2. **Polysiphonia scopulorum** Harvey?

"Mar. Bot. of West Austr. n. 88 in Trans. Irish Ac. vol. 22, p. 540; Id., Austr. Alg. n. 186"; J. Agardh, Spec. Alg. vol. 2 (1863) p. 940; Kützing, Tab. Phyc. vol. 14 (1864) p. 12, pl. 37, figs. a—c;

De Toni, Syll. Alg. vol. 4 (1903) p. 1065; Segi, Polysiphonia from Japan (Jour. Fac. Fish. Pref. Univ. Mie, vol. 1, No. 2, 1951) p. 200, pl. III, 7, fig. 9.

Syn. *P. ferulacea* (non Suhr) Yendo, Notes on Alg. New to Japan VIII (Bot. Mag. Tōkyō vol. 32, 1918) p. 75.

This plant has four siphons and no cortical layers. It is characterized by possessing erect, adpressed branchlets on the upper part of the frond. In the present specimen the branchlets are somewhat tufted upwards. It is an interesting fact that the branches are densely covered with diatoms in both Mauritian and Japanese specimens.

On the other hand the present species is often rather difficult to distinguish from *P. subtilissima*. So the writer remains somewhat in doubt. Therefore a question mark is put after the specific name.

The specimen is on the whole rather grey.

Mauritius: Ilôt Barkly, 1-4-46, G. Morin, no. 522.
Geogr. Distr.: New Holland; Japan.

3. **Polysiphonia tongatensis** Harvey.

"Alg. Friend. Isl. n. 14"; Kützing, Tab. Phyc. vol. 14 (1864) p. 14, pl. 41, figs. a—d; Grunow, Alg. Fidschi (1847) p. 48; Id., "Alg. Kelan p. 4"; De Toni, Syll. Alg. vol. 4 (1903) p. 877; Setchell and Gardner, Mar. Alg. Revillagigedo Isl. Exped. 1925 (in Proceed. Calif. Acad. Sci. Fourth Series, vol. 19, No. 11, 1930) p. 160 (as var. (?)); Segi, Polysiphonia from Japan (Jour. Fac. Fish. Pref. Univ. Mie, vol. 1, No. 2, 1951) p. 207, pl. IV—V, 1, figs. 12—13.

The present species forms a mass (Fig. 16), expanded in every direction. The frond is composed of four siphons, having no cortical layers.

In the specimen at hand the writer could observe a connection between branches and trichoblasts in the origin as figured (Fig. 17). The branches do not arise in connection with the trichoblasts. Sometimes they occur in the place of the trichoblasts. It is noticeable that in the Mauritian plant one trichoblast arises per two segments, with $\frac{1}{4}$ divergence in a left-hand spiral, while in the Japanese plant there is one per segment in the same manner. The writer wants to study this interesting point further.

In outward appearance this specimen agrees with the Ja-

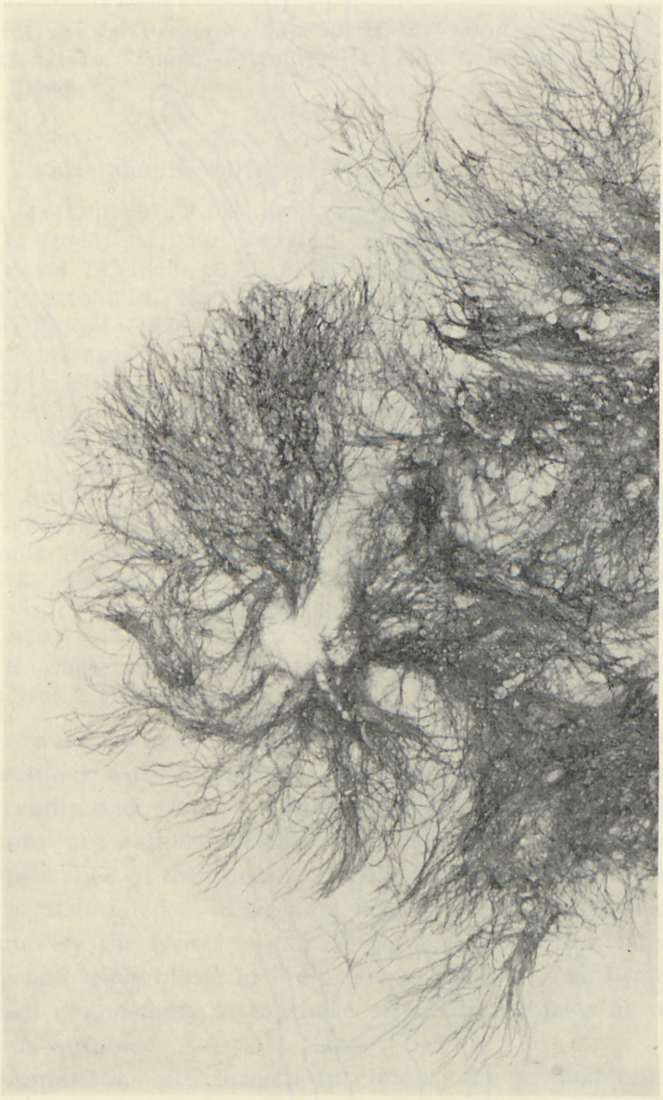

Fig. 16. *Polysiphonia tongatensis* Harv. ($\times \frac{4}{5}$).

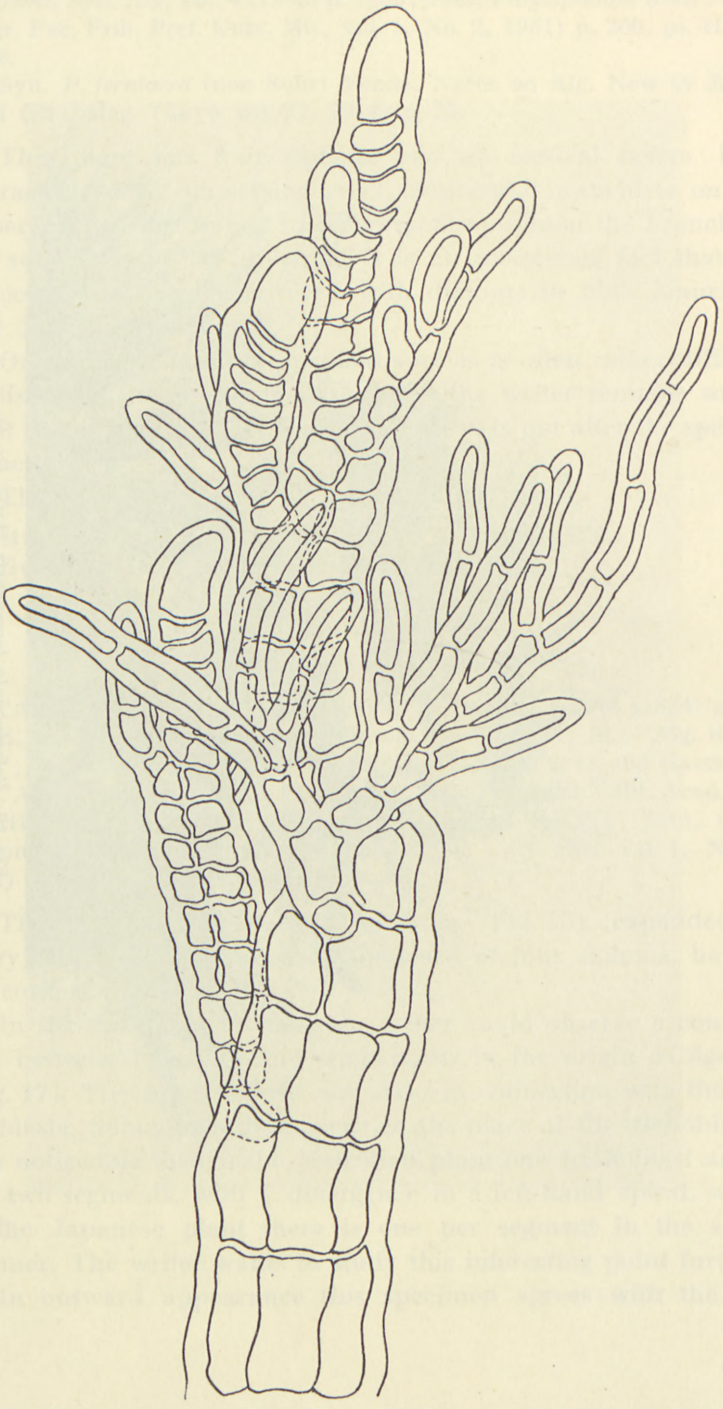

Fig. 17. *Polysiphonia tongatensis* Harvey. Tip of a branch showing trichoblast and branchlet which issue independently of each other × ca. 700.

panese (Segamiike) and the American one (Herb. Univ. Calif. No. 261338, Port Phaeton, Tahiti Isl. det. Setchell).

The plant is purplish red in drying.

Mauritius: La Preneuse, 12-4-52, R. E. VAUGHAN, no. 1211.

Geogr. Distr.: Tonga (Friendly) Isl.; New Caledonia; Tahiti Isl.; Fiji Isl.; Japan.

4. **Polysiphonia variegata** (C. Agardh) Zanardini.

"Syn. (1841) p. 60"; J. AGARDH. Alg. Med. (1842) p. 129; Id., Spec. Alg. vol. 2 (1863) p. 1030; KÜTZING, Spec. Alg. (1849) p. 821; Id., Tab. Phyc. vol. 13 (1863) pl. 81, figs. d—f; HARVEY, Phyc. Brit. vol. 2 (1846—51) pl. 155; Id., Ner. Bor. Amer. (1853) p. 45; THURET et BORNET, Etud. Phycol. (1878) pl. 42; FARLOW, Mar. Alg. New Eng. (1881) p. 173; ARDISSONE, Phyc. Mediter. vol. 1 (1883) p. 390; HAUCK, Meeresalg. (1885) p. 236; FALKENBERG, Rhodomelac. (1901) p. 119, t. 21, fig. 30; DE TONI, Syll. Alg. vol. 4 (1903) p. 922; l. c. vol. 6 (1924) p. 398; BØRGESEN, Mar. Alg. of Dan. West Ind. vol. 2 (1918) p. 269, figs. 264—266; Id., Ind. Rhodophyc. IV (1934) p. 26, fig. 18; Id., Mar. Alg. Nor. Part Arabian Sea Geogr. Distr. (1934) p. 48; Id., List Mar. Alg. Bombay (1935) p. 62; Id., Mauritius (1945) p. 35; BATTEN, The Genus Polysiphonia (in Journ. Linn. Soc. Bot. vol. 46, 1923) p. 307, pl. 25, figs. 74—76; FELDMANN et MAZOYER, Addit. Fl. Alg. mar. l'Algerie (1937) p. 319; TAYLOR, Mar. Alg. Northeast. Coast of North Amer. (1937) p. 370.

Syn. *Hutchisia variegata* C. Agardh, Syst. Alg. (1824) p. 153; Id., Spec. Alg. vol. 2 (1828) p. 81.

There were six dried specimens at hand and they have all been identified with *P. variegata*. In the present specimens the frond is composed of 5—7 siphons without cortical cells. Thus the siphons are rather variable in number as well as in the outer appearance of the species. DE TONI, HARVEY, and THURET et BORNET also noted 5—8 siphons with or without cortical cells.

Fortunately the writer could ascertain a connection between branches and trichoblasts in the origin as figured. The branches are formed connectedly at the base of the trichoblasts as noted by various authors.

In comparison with foreign specimens, the present ones on the whole agree with them. Specimen no. 887 coincides with the European specimen (Herb. LENORMAND, Communicat. ex Herbario Lungduno-Batavo "*Hutchinsia variegata* Ag." côtes atlantiques de France, en Herb. CHAUVIN), no. 624 with the American

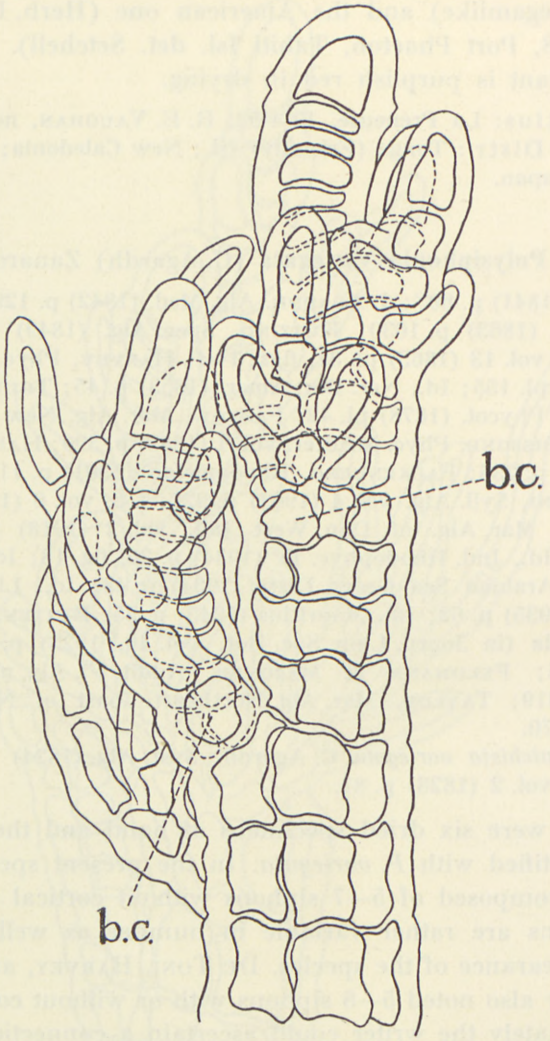

Fig. 18. *Polysiphonia variegata* (C. Agardh) Zanardini. Tip of a branch showing trichoblast and branchlet which issue connectedly in the origin × ca. 600. *b.c.* basal cell of both trichoblast and branchlet common to both.

one (Duplicates from the Herbarium of Mrs. M. A. Booth, Distrib. by the New York Bot. Garden. "*P. variegata* Ag." Orient, Long Island) and no. 912 with indistinctive locality (*S. Suliae*).

This species seems to be distributed widely in Europe and America, but not in Japan.

The plant is light or dark purplish red in drying.

Mauritius: Near Ilôt Barkly, 9-10-48, no. 887. Flic-en-Flacq, R. E. VAUGHAN, no. 912. Ile aux Aigrettes, 14-1-52, G. MORIN, no. 1204. Ile aux Aigrettes, 12-5-52, G. MORIN, no. 1222. R. E. VAUGHAN, no. 624. Ile Maurici, Daruty 1892, Herb. E. JADIN.

Geogr. Distr.: Adriatic Sea; Mediterranean Sea; European and North American Coasts; West Indies.

5. **Polysiphonia nigrescens** (Smith) Greville.

In "HOOKER, Br. Fl. vol. 2 (1833) p. 322"; HARVEY, Phyc. Brit. (1846—51) pl. 277; Id., Man. (1849) p. 88; KÜTZING, Spec. Alg. (1849) p. 813; Id., Tab. Phyc. vol. 13 (1863) pl. 56, figs. f—i; J. AGARDH, Spec. Alg. vol. 2 (1863) p. 1057; Id., Florid. Morphol. (1879) pl. 33, fig. 14; FARLOW, Mar. Alg. New End. (1881) p. 174; HAUCK, Meeresalg. (1885) p. 244; FALKENBERG, Rhodomelac. (1901) p. 129; DE TONI, Syll. Alg. vol. 4 (1903) p. 940; l. c. vol. 6 (1924) p. 401; OLTMANNS. Morph. u. Biol. Alg. II (1922) p. 309, fig. 525, p. 404, fig. 596; BATTEN, The Genus Polysiphonia (in Journ. Linn. Soc. Bot. vol. 46, 1923) p. 306, pl. 25, figs. 67—73; KYLIN, Stud. Ent. Florid. (1923) p. 116—123, figs. 73—76; Id., Rhodo. schwed. Westküste (1944) p. 84, fig. 52, A. B., pl. 28, figs. 80, 81, pl. 29, fig. 82.

Syn. *Conferva nigrescens* Smith, Engl. Bot. (1806) pl. 1717.

Syn. *Hutchinsia nigrescens* Ag., Syst. Alg. (1824) p. 15; Id., Spec. Alg. (1828) p. 69; LYNGBYE, Hydro. Dan. (1819) p. 109, pl. 33.

There were two dried specimens at hand. Among them no. 1 (Fig. 19) is cystocarpic and no. 2 not female.

The frond is composed of 6 siphons (no. 1), 7—8 ones (no. 2) and ecorticated (no. 1, no. 2). The lower part of the frond is branched in a decompound-dichotomous manner.

According to the description and plates of *P. nigrescens* given by KYLIN (*l. c.* 1944), this species includes three forms, *f. fucoides* (Hudson) J. Agardh, *f. protensa* J. Agardh and *f. flaccida* Areschoug. In his opinion, no. 1 seems to be related to *f. protensa* and no. 2 to none of the three forms.

On the other hand no. 2 (Fig. 20) seems to show a resemblance to *P. fastigiata*, especially in the dichotomous ramification. But the former has fewer siphons (7—8) than the latter (12—24) (DE TONI, *l. c.* vol. 4).

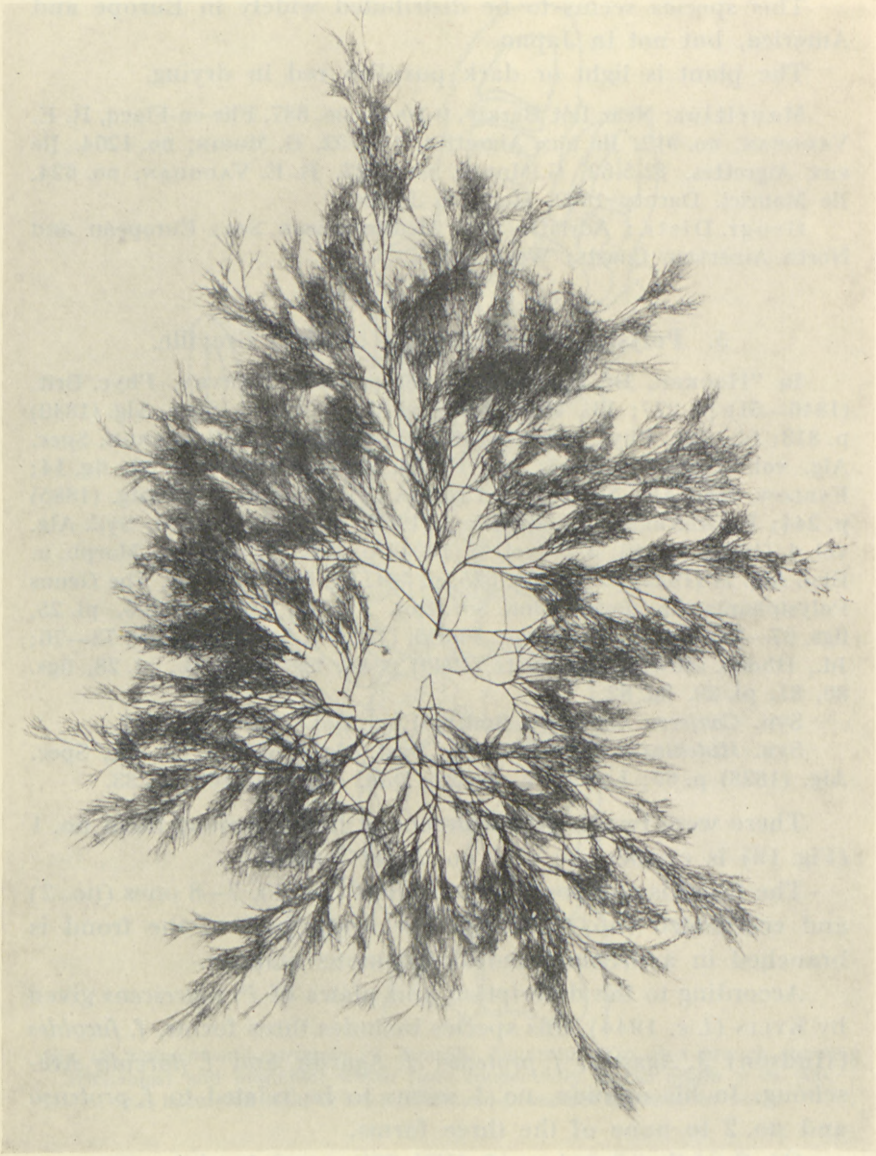

Fig. 19. *Polysiphonia nigrescens* (Smith) Grev. A cystocarpic specimen. No. 1. Herb. JADIN. × 1.

Fig. 20. *Polysiphonia nigrescens* (Smith) Grev. A sterile specimen. No. 2. Herb. JADIN. × 1.

In *P. nigrescens* the siphons are rather variable in number (8—20, generally 16), according to DE TONI's description (*l. c.*). In general, however, there are fewer than in *P. fastigiata*. The branches in *P. nigrescens* are not dichotomous, being different from those of the Mauritian plant. On this point, however, the writer considers that it is only a question of individual variation.

It seems to the writer more reasonable to refer these two specimens to *P. nigrescens* than to *P. fastigiata*.

The plant is dark purplish red in drying.

Mauritius: Ile Maurice, envoi Daruty 1892, Herb. F. JADIN, no. 1. Ile Maurice, envoi Daruty 1892, Herb. F. JADIN, no. 2.

Geogr. Distr.: Europe; Canary Isl.; Australia; New Zealand (?).

Subfam. 2. Laurencieae.

Laurencia Lamour.

1. **Laurencia papillosa** (Forssk.) Grev.

Alg. Mauritius, III, 4, 1945, p. 47.

Of this species surely common in Mauritius I have, since it was first mentioned in the paper quoted above, received several gatherings of which I shall mention some of the most essential.

No. 537; 543; 660 "rocky pools"; 661, "attached to rocks in deep pools"; 676; 906, "in shallow water near the shore attached to old coral and rocks".

Mauritius: Grand Baie, 16-2-46, G. MORIN, no. 537. Cassis, 4-2-46, G. MORIN, no. 543. Ilôt Brocus, 25-8-46, R. E. V. nos. 660—661. Pointe aux Sables, 7-4-47, G. MORIN, no. 676. Flic-en-Flacq, 3-4-50, R. E. V. no. 906.

2. **Laurencia decumbens** Kütz.

Alg. Mauritius, III, 4, 1945, p. 50, figs. 25—27; Additions IV, 1952, p. 65.

Some small specimens very like those I have formerly referred to this species have recently been received from Mauritius.

As to the locality it is said: "in lagoon, firmly attached to large rocks."

Mauritius: Pointe aux Roches, 22-9-52, G. MORIN, no. 1292.

3. **Laurencia flexilis** Setchell.

Alg. Mauritius, III, 4, 1946, p. 56, figs. 31—33; Additions IV, 1952, p. 66, fig. 33; Additions V, 1953, p. 55.

Some few specimens of this species are included in a collection of algae recently received.

About the locality it is said: "In rock crevices, exposed to waves."

Mauritius: Riambel, 24-7-52, R. E. V. no. 1252.

4. **Laurencia obtusa** (Huds.) Lamour.

Alg. Mauritius, III, 4, 1945, p. 58; Additions IV, 1952, p. 67.

var. *divaricata* (J. Ag.) Yamada.

Yamada, K. Notes on Laurencia, 1931, p. 223. *Laurencia divaricata* J. Ag., Epicris, p. 649.

Some specimens recently received are, I think, referable to this variety. The specimens are tetrasporic; the tetrasporangia are developed densely round the apices of the fertile branchlets as described by J. Agardh.

About the locality it is said: "on rocks and old coral near reef."

Mauritius: Pointe aux Roches, 6-9-52, G. Morin, no. 1278.

Subfam. 3. Polyzonieae.

Leveillea Decsne.

1. **Leveillea jungermannioides** (Mart. et Her.) Harv.

Alg. Mauritius, III, 4, 1945, p. 42.

In a batch of algae recently received some fragments of this species are found; it was creeping upon a specimen of *Vidalia fimbricata*.

About the locality it is said: "In rock crevices near reef submerged at low tide."

Mauritius: Riambel, 8-12-50, R. E. V. no. 1005.

Subfam. 4. Amansieae.

Vidalia Lamouroux.

1. **Vidalia fimbriata** (R. Br.) J. Ag., Falkenb. emend.

Alg. Mauritius, III, 4, *Ceramiales*, 1945, p. 44, fig. 20.

While treating this species in the paper quoted above I had very little material to work with, namely two small specimens

from JADIN's collection and some fragments dredged in deep water and sent from Dr. VAUGHAN.

It was therefore of interest in a collection of algae received later from the island to find several specimens of this species.

Referring to the list of literature mentioned in the paper quoted above and likewise to the list of synonyms and what is said about the right naming of this species according to SCHMITZ and the detailed description of FALKENBERG as to the structure of the thallus, I shall only mention here, that an examination of the specimens now received has shown that there is great variation in the development of the adventitious shoots.

Thus the endogenous marginal shoots are sometimes present only as short spines, or they are much more developed, getting 2—3 curved branchlets; in Tab. Phycol., vol. 14, tab. 97, fig. b KÜTZING gives a good figure of such a branchlet. Now and then a branchlet may grow out into a long shoot. Also the most probably exogenous short shoots, growing out from the flat sides of the thallus, as a rule in 2 rows one on each side of the midrib, but sometimes also more scattered, often become large and well developed like the marginal ones.

The characteristic rather robust hairs were often found upon the branchlets.

Fructiferous organs were not observed in the specimens.

Leveillea jungermannioides (Mert. et Her.) Harv. was an epiphyte upon it.

As to the locality it is said: "In rock crevices near reef submerged at low tide."

Mauritius: Riambel, 8-12-50, R. E. V. no. 1005.

Subfam. 5. Dasyeae.

Dictyurus Bory.

1. **Dictyurus purpurascens** Bory.

Alg. Mauritius, III, 4, 1945, p. 30.

Of this species, of which I have previously seen very little material, some fine specimens are found in a batch of algae recently received.

FALKENBERG, in "Rhodomelaceen", p. 675, bases his detailed description of this species upon material from Mauritius collected by K. MOEBIUS.

The specimens were collected "in cavities in rocks near reef exposed at low tide".

Mauritius: Pointe aux Roches, 6-9-52, G. MORIN, no. 1281.

Halodictyon Zanard.

1. Halodictyon spec.

Some small specimens (Fig. 21) of a *Rhodophycea* have after examination turned out to be a *Halodictyon*. As we in the Botanical Museum, Copenhagen, have only some few specimens of *Halodictyon mirabile* Zan. to compare with, I have sent a specimen of the plant to Mme, Dr. G. FELDMANN, Paris, who most kindly answered me that it most probably was a new species. But as the material is sterile, I have let it remain as *Halodictyon* spec.

The cells in the reticulate tissue are up to about 250 μ thick with walls about 30—50 μ. The short apical subpyramidal cells are about 50 μ broad below.

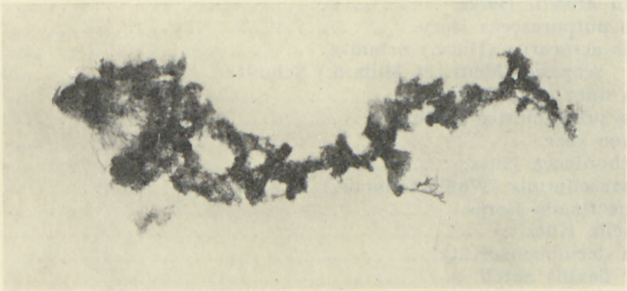

Fig. 21. *Halodictyon* spec. Habit of a specimen × 1.

About the locality it is said: "In cavities of rocks mixed with other algae."

Mauritius: Pointe aux Roches, 6-9-50, G. MORIN, no. 1282.

Index specierum.

with some few synonyms, the latter italicized.

Chlorophyceae.

Phaeophyceae.

Rhodophyceae.

Indleveret til selskabet den 11. maj 1954.
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UNTERSUCHUNGEN ÜBER DETERMINATION UND DIFFERENZIERUNG

3. ÜBER DIE WIRKUNGSWEISE DES DETERMINIERENDEN FAKTORS, DER BEI DER BILDUNG DER WURZELHAARE VON *LEPIDIUM, SINAPIS* UND *PHLEUM* TÄTIG IST

VON

P. BOYSEN JENSEN

With an English Summary

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1. Einleitung.

Die Gestaltung eines Tieres oder einer Pflanze ist die Summe einer Reihe von oft ganz geringfügigen Veränderungen des sich entwickelnden Organismus. Eine solche mikro- oder makroskopische Veränderung, die sich darin äussert, dass Zellen oder Zellteile, die ursprünglich gleichartig sind, gegen einander ungleichartig werden, nennt man einen Differenzierungsvorgang. Bevor ein solcher eintritt, muss aber ein nicht unmittelbar sichtbarer Vorgang eingetreten sein, der den betreffenden Differenzierungsvorgang hervorruft. Diesen Vorgang nennen wir eine Determination.

Das Ergebnis der Determinations- und Differenzierungsvorgänge ist die Entstehung der verschiedenen Gewebe- und Zelltypen, die den fertigen Organismus ausmachen und in demselben auf bestimmte gesetzgebundene Weise angeordnet sind. Wenn man nun versuchen will zu ermitteln, in welcher Weise die Determinations- und Differenzierungsvorgänge zustande kommen, beginnt man am besten damit zu untersuchen, worin der Unterschied zwischen den verschiedenen Zelltypen bei höheren Organismen besteht.

Schon bei einzelligen Organismen kann eine Differenzierung innerhalb des Zytoplasmas vorhanden sein. In einem *Paramaecium*, einem *Stentor* finden sich reizleitende Plasmastränge, die die Basalkörner der einzelnen Cilien verbinden, und bei dem letzteren auch kontraktile Fibrillen, Myonemen. Solche kontraktile Fibrillen sind ferner in den Cilien von Zoosporen, Gameten und einigen vegetativen Zellen von Thallophyten vorhanden.

Die Entwicklung der Somatozoen kommt nun dadurch zustande, dass die verschiedenartigen Zytoplasmabestandteile, die bei den Infusorien in einer einzelnen Zelle vorhanden sind, auf verschiedene Zelltypen verteilt werden.

In Muskelzellen besteht die Hauptmenge des Zytoplasmas aus kontraktilen Fibrillen. Das Zytoplasma der Nervenzellen hat gleichfalls einen sehr spezifischen Bau. Von besonderer Wichtigkeit sind die Neurofibrillen, die sich im Zellkörper in der mannigfaltigsten Weise durchkreuzen und sich in den Dendriten und Neuriten fortsetzen. Die Sekretzellen haben die Fähigkeit, spezifische Sekrete, z. B. Verdauungsenzyme, zu erzeugen, und besitzen einen dementsprechenden, spezifischen, zytoplasmatischen Bau. Dasselbe ist ferner der Fall mit Sinneszellen, z. B. in der Retina, u. s. w.

Auch in höheren Pflanzen können zytoplasmatische Ungleichartigkeiten in den verschiedenen Zellmodifikationen vorhanden sein.

In der Epidermis von Blättern und jungen Stengeln sind nur die Schliesszellen imstande, Chlorophyll zu bilden, die übrigen Epidermiszellen dagegen nicht. Auch die Wurzelzellen vermögen nicht Chlorophyll, dagegen bisweilen andere Farbstoffe, z. B. Carotin, in grosser Menge zu bilden. Die Zellen der Kleberschicht, der äussersten Schicht des Endosperms der Gräser, sind mit Proteinkörnern gefüllt, die übrigen Zellen dagegen mit Stärkekörnern. In der Kleberschicht werden während der Keimung grosse Mengen Amylase gebildet.

Wenn auch Unterschiede zwischen den Zellmodifikationen in Bezug auf den Gehalt an Mikromolekylen und Jonen in dem Zytoplasma vorhanden sein können, ist die zytoplasmatische Ungleichartigkeit der verschiedenen Zelltypen unzweifelhaft hauptsächlich an die Makromolekyle, d. h. vorzugsweise an Eiweissstoffe und an eiweisshaltige Gebilde geknüpft. Die Spezifität der Eiweisskörper der Zellmodifikationen kann darin bestehen, dass sie kontraktil oder reizleitend sind, wie in den Muskel- und Nervenzellen, oder dass sie bestimmte Enzyme zu erzeugen vermögen, wie die Sekretzellen im Darmkanal oder die Zellen der Kleberschicht der Gräsersamen. Daneben kommen natürlich auch Eiweisskörper vor, die allen lebenden Zellen gemeinsam sind, z. B. die Enzyme, die an dem Abbau der Kohlenhydrate, der Eiweissstoffe und verschiedener anderer Stoffe beteiligt sind.

Neben dem Zytoplasma finden sich in den verschiedenen Zelltypen auch ein oder mehrere Zellkerne. Dieselben sind durch Äquationsteilungen entstanden und sind, selbst wenn neben den

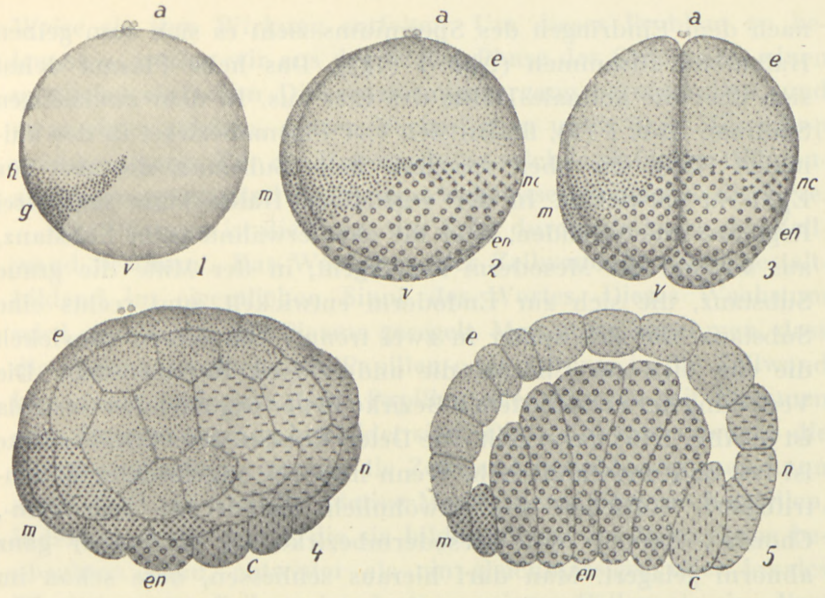

Abb. 1. Die ersten Entwicklungsstadien von *Styela partita*. 1 Ungefurchtes Ei, 2 Zweizellenstadium, 3 Vierzellenstadium, 4 Beginnende Gastrula, 5 Längsschnitt durch die Gastrula. g gelber Halbmond, h heller Zytoplasmabezirk, m präsumptive Mesoderm, e präsumptive Epiderm, en präsumptive Endoderm, nc präsumptiver Neuro-Chordalbezirk, n Neuralbezirk, c Chordalbezirk. (Conklin nach Dürken, halbschematisch).

normalen diploiden auch polyploide Kerne vorkommen können, im grossen und ganzen äquivalent. Eine Differenzierung der Kerne findet nach unserem heutigen Wissen nicht statt.

Wir kommen somit zu dem Ergebnis, dass die Ungleichartigkeit der verschiedenen Zelltypen mit einer Ungleichartigkeit im Gehalt an Makromolekylen und an makromolekularen Gebilden im Zytoplasma zusammenhängt und durch dieselbe bedingt wird.

Die nächste Aufgabe muss daher sein zu untersuchen, in welcher Weise die zytoplasmatische Ungleichartigkeit der verschiedenen Zelltypen entsteht. Diese Frage lässt sich durch Verfolgung der Entwicklung von Mosaikeiern (z. B. von *Styela*) lösen (Conklin 1905).

In dem unbefruchteten Ei von *Styela* kann man drei verschiedene Zytoplasmatypen, die gelbe, die graue und die helle, die konzentrisch geordnet sind, unterscheiden. Die gelbe liegt gleichmässig verbreitet in der Oberfläche des Eies. Unmittelbar

nach dem Eindringen des Spermiums zieht es sich zum gelben Halbmond zusammen (Abb. 1 (1g)). Das helle Plasma dehnt sich über die animale Hälfte des Eies aus. In dem zweizelligen Stadium, Abb. 1 (2), finden sich vier Plasmabezirke, in der animalen Hälfte die oben erwähnte helle Substanz, die sich zur Epiderm entwickelt. In der vegetativen Hälfte kann man drei Regionen unterscheiden, links die oben erwähnte gelbe Substanz, aus welcher die Mesoderm hervorgeht, in der Mitte die graue Substanz, die sich zur Endoderm entwickelt, und rechts eine Substanz, die sich später in zwei trennt; von diesen entwickelt die eine sich zur Chorda, die andere zum Nervensystem. Die Verteilung der verschiedenen Bezirke in der beginnenden Gastrula ist in Abb. 1 (5) dargestellt. Die Determination der Plasmabezirke ist fest und unveränderlich. Wenn man ein ungefurchtes Ei zentrifugiert, entstehen wie gewöhnlich Ektoderm-, Entoderm-, Chorda-, Nerven- und Mesodermbezirke, sie sind aber ganz abnorm gelagert. Man darf hieraus schliessen, dass schon im Zytoplasma des ungefurchten Eies mehrere, stoffliche verschiedene, fest determinierte Gewebe- und Organrepräsentanten vorhanden sind, und dass dieselben durch eine Verlagerung von Zytoplasmaelementen in dem unbesamten Ei entstanden sind.

Diese Umlagerungen werden durch die Besamung in Gang gesetzt, sind aber, soweit man beurteilen kann, vollkommen autonom.[1]

Nachdem somit durch die Untersuchungen von Conklin und anderen festgestellt worden ist, dass Umlagerungen im Plasma differenzierungsbestimmend wirken können, muss der nächste Schritt sein, wenn möglich zu ermitteln, wie solche Umlagerungen (d. h. Determinationen) zustande kommen können, und in welcher

[1] Neben den autonomen Determinationsvorgängen hat man auch induzierte. Diese können entweder von Induktionszentren, die während der Ontogenese entstanden sind, ausgehen oder es können äussere Faktoren induzierend wirken. Namentlich hat W. Johannsen hervorgehoben, dass die äusseren Faktoren für die Gestaltung der Organismen mitbestimmend sind, und dass sie auch in die ontogenetischen Entwicklungsvorgänge eingreifen können. Jedoch darf man die Bedeutung der äusseren Faktoren nicht überschätzen; tatsächlich ist sie namentlich bei Tieren ziemlich gering. Man kann die Entwicklungsbedingungen innerhalb weiter Grenzen variieren und man erhält doch im grossen und ganzen einen normalen Organismus. Bei den Pflanzen, die in viel höherem Grade als die Tiere plastisch sind, spielen die äusseren Faktoren eine nicht unbedeutende Rolle, sie können direkt Determinierungsvorgänge auslösen und sie können bewirken, dass eine Zellenmodifikation in eine andere umschlagen kann. Ich hoffe, später auf diese Determinationen zurückkommen zu können.

Weise sie ihre Wirkung entfalten. Um dieses Problem zu beleuchten, wollen wir aus der letzten Phase der Ontogenese einen möglichst einfachen Differenzierungsvorgang herausgreifen, und zwar einen solchen, dessen Verlauf man unter dem Mikroskop verfolgen kann. Für die Untersuchung solcher einfacher Differenzierungsvorgänge sind die Pflanzen weit besser geeignet als die Tiere.

Bei Pflanzen ist die Form der Zelle durch die Form der Zellwand bestimmt. Das Wachstum der Zellwand ist somit gestaltbildend im eigentlichen Sinne des Wortes. Dieses Wachstum wird aber durch das Plasma geregelt. Man muss annehmen, dass die Plasmaoberfläche als Papillen oder Kämme in die Zellwand hineinragt, und dass diese Papillen oder Kämme mit Enzymen oder Enzymsystemen bekleidet sind. Diese Enzyme erzeugen die Zellulosenfibrillen, woraus die Zellwand besteht, und man kann somit die Lage und die relative Menge dieser Enzyme feststellen, indem man die Stoffe, die sie bilden, direkt im Mikroskope beobachten kann, entweder als ein gleichmässiges oder lokales Wachstum der Zellwand (oder in gewissen Fällen als eine Verdickung auf der inneren Seite der Zellwand). Findet nun eine lokale Änderung der Wachstumsgeschwindigkeit statt oder wird eine Verdickung gebildet, so wird man, wie später gezeigt werden soll, diese Vorgänge auf eine Umlagerung der Zellulosenbildner zurückführen können. Diese Umlagerung ist somit die Determination, die das lokale Wachstum oder die Verdickung hervorruft.

In einer früheren Abhandlung (Boysen Jensen 1950) habe ich gezeigt, dass die Bildung der Wurzelhaare, die als Ausstülpungen der Zellwand in dem apikalen Ende einer Epidermiszelle der Wurzel entstehen (Abb. 3), durch eine vorhergehende Anhäufung von Zellulosenbildnern an der betreffenden Stelle hervorgerufen wird. Diese Anhäufung entsteht durch eine Umlagerung der Zellulosenbildner in dem Plasma, und sie ist somit ein Beispiel für die oben erwähnten Determinationsvorgänge. Es ist die Aufgabe dieser Abhandlung zu untersuchen, ob man möglicherweise die Anhäufung der Zellulosenbildner in dem apikalen Ende der Trichoblasten und später in der Spitze der Wurzelhaare durch äussere Faktoren beeinflussen oder hervorrufen kann, um auf diese Weise näher zum Verständnis der Determinationsvorgänge vorzudringen.

2. Methodisches.

Die Kultur der Pflanzen ist früher beschrieben worden (Boysen Jensen 1954); sie wurden diesmal in Färbekästchen, in denen die Objektträger horizontal lagen, gezüchtet. Als Nährlösungen wurde entweder $I_b + II$ oder das sehr kalkhaltige Kopenhagener Leitungswasser benutzt.

*Sinapis*keimpflanzen werden besser in Petrischalen (Diam. 10 cm), deren Boden mit zwei Schichten Filtrierpapier das mit $I_b + II$ oder Leitungswasser befeuchtet ist, kultiviert. Die Samen werden in einer Reihe mitten in die Schale gelegt; die Schalen werden senkrecht gestellt, so dass die Wurzeln nach unten wachsen. In ähnlicher Weise kann man auch *Lepidium*- und *Phleum*keimpflanzen züchten.

Die meisten Versuche sind in schwachem Tageslicht ausgeführt, in der letzten Zeit wurden sowohl die Kulturen als die Versuche im Dunkeln gehalten. Obwohl kein entscheidender Unterschied zwischen den zwei Versuchsgruppen vorhanden ist, habe ich doch den Eindruck, dass die Versuche am besten im Dunkeln gelingen.

Bei der Untersuchung des Wachstums und der Neubildung der Wurzelhaare benutzt man am besten ein Präpariermikroskop mit verschiebbarem Tubus (z. B. Reichert, Mak M, Vergrösserung 8×4,1). Die Wurzel wird parallel mit dem Okularmasstab und mit einer der Verschiebungsrichtungen orientiert. Wenn man dann nach und nach den Nullstrich auf die Zonengrenzen einstellt, kann man die Länge der unten erwähnten Zonen und der Wurzel an dem Masstab mit Nonius in mm ablesen.

Die Länge der *Phleum*wurzeln, die für die Versuche benutzt wurden, betrug 5—9 mm. Wenn man eine solche Wurzel unter das Präpariermikroskop legt, sieht man, dass die Wurzel aus zwei Zonen besteht, der Zone, die mit Wurzelhaaren bekleidet ist, und der Spitze. Die erstere Zone (die primäre Wurzelhaarzone) wollen wir Zone I nennen (Abb. 2 a). Die Länge der Wurzelhaare nimmt gegen die Spitze hin allmählich ab; in dem äussersten Teil der Zone sollen die Wurzelhaare zerstreut sein. Ist die Wurzelspitze beschädigt, bilden die Wurzelhaare einen dicken Filz, und die Wurzel kann nicht verwendet werden. Die

wurzelhaarfreie Zone, die die Spitze bildet, wollen wir Zone IV nennen; in derselben können vereinzelte Wurzelhaarinitiale vorhanden sein.

Es soll nun das Aussehen der Wurzel 24 Stunden später beschrieben werden (Abb. 2 b).

Wenn die Wurzel in einer etwa 2 mm hohen Schicht von

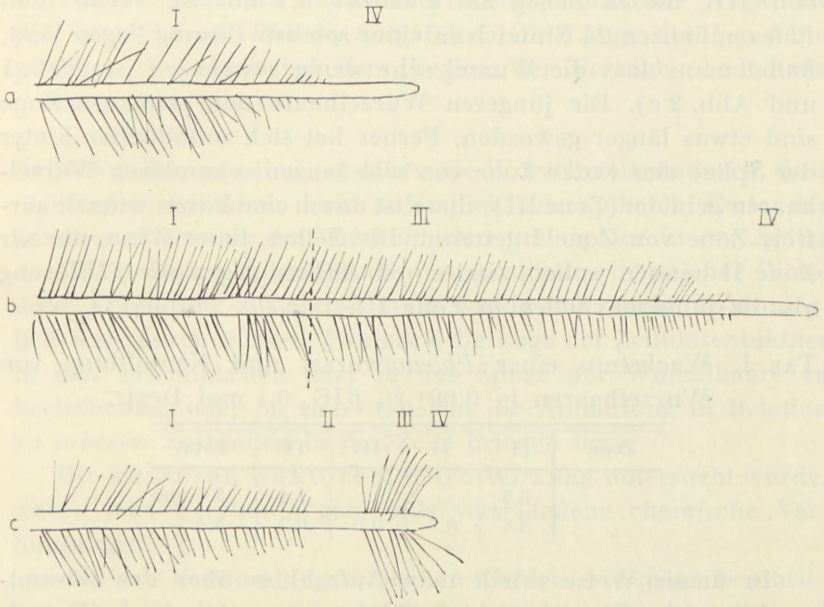

Abb. 2. Wachstum der Wurzeln von *Phleum*. a Wurzel am Anfang des Versuches, b dieselbe Wurzel 24 Stunden später, c Wurzel, die 24 Stunden in 0,001 % β-Indolylessigsäure gelegen hat.

Nährlösung in einer kleinen Petrischale gelegen hat, ist sie um etwa 3—5 mm länger geworden. Die jüngeren Wurzelhaare sind ausgewachsen, und im Anschluss an die primäre Wurzelhaarzone hat sich eine Zone mit neuen Wurzelhaaren entwickelt, die wir als die sekundäre Wurzelhaarzone (Zone III) bezeichnen wollen. Die Grenze zwischen Zone I und Zone III ist nicht scharf.

Wünscht man nun die Wirkung einer Lösung von β-Indolylessigssäure (der meistens so viel Dextrose zugesetzt wurde, dass die Konzentration 0,1 mol betrug)[1] auf das Wachstum der

[1] Ob die Dextrose irgendwelche Bedeutung für die Versuche hat, weiss ich jedoch nicht.

Wurzel und die Bildung von Wurzelhaaren zu untersuchen, stellt man z. B. eine 0,002 % ige Lösung von βIE in $I_b + II$ her. Aus dieser Lösung kann man durch Verdünnung mit $I_b + II$ 0,0002 und 0,00002 % ige Lösungen herstellen. Wenn man gleiche Mengen einer 0,002 % igen Lösung mit einer 0,2 mol Dextroselösung (in $I_b + II$) mischt, erhält man eine 0,001 % ige Lösung von βIE, die in Bezug auf Dextrose 0,1 mol ist. Wenn man *Phleum*pflanzen 24 Stunden in einer solchen Lösung liegen lässt, findet man, dass die Wurzel sehr wenig gewachsen ist (Tab. 1 und Abb. 2 c). Die jüngeren Wurzelhaare der primären Zone sind etwas länger geworden. Ferner hat sich unmittelbar hinter der Spitze eine kurze Zone von sehr langen sekundären Wurzelhaaren gebildet (Zone III); diese ist durch eine kurze, wurzelhaarfreie Zone von Zone I getrennt. Die Zellen dieser Zone, die wir Zone II nennen wollen, sind empfindlicher gegen die βIElösung als die jüngeren Zellen in Zone III.

Tab. I. Wachstum einer *Phleum*wurzel und Neubildung von Wurzelhaaren in 0,001 % βIE, 0,1 mol Dextr.

Zone	I	II	III	IV	Total
	3.6	..	..	1.4	5.0 mm
	3.6	0.9	0.6	0.3	5.4

In dieser Weise erhält man Aufschluss über das Gesamtwachstum der Wurzel, über die Bildung der sekundären Wurzelhaarzone u. s. w. Häufig kann man auch sehen, ob die primären Wurzelhaare gewachsen sind oder nicht. Wenn man jedoch das Wachstum derselben in $I_b + II$ oder in einer anderen Lösung näher zu verfolgen wünscht, legt man eine Wurzel auf einen Objektträger in der betreffenden Lösung unter ein gewöhnliches Mikroskop. Man arbeitet am besten ohne Deckglas mit einer Vergrösserung von 8×20 (×1½). Man misst die Länge einiger der jüngsten Wurzelhaare in Zeitintervallen von 20 oder 30 Minuten. Um zu verhüten, dass die Flüssigkeit, worin die Wurzel liegt, verdampft, wird der Objektträger mit der Wurzel zwischen den Messungen in einer Petrischale mit feuchtem Papier in dem Deckel untergebracht. Wenn der Objektführer nicht verschoben wird, ist es leicht, die Wurzelhaare, mit denen man arbeitet, wiederzufinden.

Wenn die Versuche abgeschlossen sind, werden die Wurzeln

in verdünntem Glyzerin aufbewahrt. Man untersucht dann mit Vergrösserungen von 240—500, ob Missbildungen (Verdickungen, Verzweigungen oder Anschwellungen) in den Wurzelhaaren entstanden sind, ob die Insertion der Wurzelhaare normal ist u. s. w. Solche Missbildungen sind von grosser Bedeutung, wenn man die Verschiebungen der Zellulosenbildner untersuchen will.

Die Versuche mit *Lepidium* werden in ähnlicher Weise wie die Versuche mit *Phleum* ausgeführt. Die Länge der *Lepidium*-pflanzen ist jedoch bei dem Beginn der Versuche bedeutend grösser, etwa 1—2 cm.

Wie früher erwähnt entstehen die Wurzelhaare dadurch, dass die Zellulosenbildner sich anfänglich am apikalen Ende der äusseren Zellwand der Trichoblasten und später in der Spitze der Wurzelhaare anhäufen. Um zu ermitteln, in welcher Weise diese Anhäufung zustandekommt, wurde untersucht, ob es möglich war, durch äussere Faktoren die Lage der Zellulosenbildner in den Trichoblasten oder in der Spitze der Wurzelhaare zu beeinflussen, oder ob sich vielleicht die Anhäufung in Relation zu inneren Zuständen in der Zelle bringen liess.

Die äusseren Faktoren, deren Wirkung untersucht wurde, waren teils Verwundungen, teils verschiedene chemische Verbindungen.

Bei den Verwundungsversuchen wurden, wie später beschrieben werden soll, verschiedene Teile der Spitze abgeschnitten und 24 Stunden in 0,1 mol Dextrose gelegt. Nachher wurde die Wurzelhaarbildung untersucht.

Die chemischen Verbindungen, deren Wirkung auf die Entwicklung der Wurzelhaare untersucht wurde, waren Colchicin, Rhodanammonium, β-Indolylessigsäure und Sublimat. Daneben wurden auch einige Versuche mit Chloralhydrat, Aethylurethan, Monojodessigsäure und 2-3-5 Trijodbenzoesäure ausgeführt. Die Pflanzen wurden 16—24 Stunden in verschiedene Konzentrationen der betreffenden Stoffe, die in Bezug auf Dextrose o,1 mol waren, gelegt und nachher untersucht.

Die genannten Stoffe wirken als Gifte. In höheren Konzentrationen werden die Wurzelhaare getötet, in niedrigeren wachsen sie ziemlich ungestört. Man ist in den Versuchen bestrebt, mit den kritischen Konzentrationen zu arbeiten, d. h. mit solchen, in welchen die Wurzelhaare sich zwar entwickeln können, aber

mehr oder weniger deformiert werden. Die kritischen Konzentrationen sind für Colchicin etwa 0,02—0,05 %, für Rhodanammonium 0,02—0,1 %, für β-Indolylessigsäure 0,00001—0,0001 % und für Sublimat 0,0001 %.

Die Ergebnisse der Versuche sind häufig etwas launisch. Einmal kann die Resistenz der Versuchspflanzen gegen die Giftwirkung ziemlich verschieden sein; man hat den Eindruck, dass die Pflanzen um so resistenter sind, je schneller sie wachsen. Pflanzen von alten Samen geben daher, z. B. bei *Phleum*, häufig bessere Ergebnisse als solche von neuen Samen. Ferner findet oft eine starke, aber ungleichartige Anpassung an die Giftwirkung statt. Häufig beobachtet man, dass die primären Wurzelhaare das Wachstum schnell einstellen, und dass später aus den Epidermiszellen, die vor der primären Wachstumszone liegen, eine sekundäre Zone von Wurzelhaaren gebildet wird. Diese letzteren Wurzelhaare müssen somit imstande sein, sich in einer Lösung zu entwickeln, in welcher die primären Wurzelhaare nicht wachsen können. Aber auch die Anpassungsfähigkeit der Epidermiszellen ist ungleichartig, was daraus hervorgeht, dass normale und deformierte Wurzelhaare zwischen einander vorkommen können. Wie später ausgeführt werden soll, besteht ein Kampf zwischen der lämenden Wirkung des Giftes und dem Entwicklungsstreben der Wurzelhaare. Der Ausfall dieses Kampfes ist in dem Bereich der kritischen Konzentrationen ganz zufällig.

Von den inneren Faktoren, die für die Ausbildung und das Wachstum der Wurzelhaare von Bedeutung sein könnten, ist vornehmlich an die Lage des Zellkerns zu denken.

Dass der Zellkern eine notwendige Bedingung für das Wachstum der Zellwand ist, geht daraus hervor, dass in plasmolysierten Zellen, z. B. in Wurzelhaaren, nur Plasmateile, die einen Zellkern enthalten oder durch einen dünnen Plasmafaden mit einem kernhaltigen Teil verbunden sind, sich mit einer neuen Zellwand umgeben. In welcher Weise der Zellkern bei der Bildung der Zellwand wirkt, weiss man nicht. Man kann sich denken, dass der Zellkern entweder bei der Erzeugung der Zellulosenbildner oder der für die Zellulosenbildung notwendigen plastischen Stoffe beteiligt ist.[1]

Bekanntlich hat Haberlandt (1887) nachgewiesen, dass der

[1] Bei *Acetabularia* können Zellulosen jedoch auch in kernfreien Stielen gebildet werden (Hämmerling).

Zellkern in vielen Fällen seinen Platz in nächster Nähe des wachsenden Teils der Zellwand hat. Z. B. werden die Wurzelhaare bei *Pisum* an der über dem Zellkern liegenden Partie der Aussenwand gebildet; ferner liegt häufig der Zellkern in der Spitze der Wurzelhaare. HABERLANDT schliesst hieraus, dass der Zellkern das Wachstum der Zellwand bewirkt oder fördert, und dass er deshalb seinen Platz dort hat, wo ein besonders starkes Wachstum der Zellwand stattfindet.

Durch spätere Untersuchungen hat sich doch gezeigt, dass die Theorie von HABERLANDT über die Lage des Zellkerns bei weitem nicht allgemeingültig ist. In vielen Wurzelhaaren liegt der Zellkern nicht in der Spitze, sondern an der Basis der Wurzelhaare (vgl. die Darstellung bei KÜSTER 1935 p. 143 ff.). FARR (1928) hat gefunden, dass die Lage des Zellkerns in Wurzelhaaren von *Brassica oleracea* sehr wechselnd sein kann. Häufig liegt er in einiger Entfernung von der Spitze, kann aber auch seinen Platz in dem Zellkörper haben.

In den Wurzelhaaren von *Lepidium* und *Phleum* kann man im Mikroskope bisweilen einen Zellkern in den lebenden Wurzelhaaren und bei *Phleum* im Zellkörper beobachten.

Eine Färbung des Zellkerns mit Karminessigsäure ist häufig mit Schwierigkeiten verbunden, weil das Plasma sich zusammenballt. Die besten Ergebnisse erhält man nach meinen Erfahrungen in folgender Weise. Die Pflanzen werden zwei Stunden in einer kleinen Petrischale in Carnoy gelegt. Der Same wird entfernt und die Wurzel auf einen Objektträger in Karminessigsäure übertragen und mit einem Deckglas bedeckt. Die Färbung dauert eine halbe Stunde, nachher saugt man, ohne das Deckglas zu entfernen, Wasser hindurch, und schliesslich wird Glyzerin am Rande des Deckglases zugesetzt. Man kann dann leicht sehen, ob der Zellkern im Wurzelhaare liegt. Wenn er sich im Zellkörper befindet, kann man bei *Phleum* in wenigen günstig gelegenen Zellen seine Lage im Verhältnis zum Wurzelhaar feststellen.

Wie später erwähnt werden soll kann man die Lage der Zellulosenbildner in der Spitze von Wurzelhaaren und bisweilen in Trichoblasten durch Behandlung mit Kongorot nachweisen. Die Wurzeln werden eine halbe Stunde in eine etwa 0,01 %-ige Lösung von Kongorot in 0,1 mol Dextroselösung gelegt; nach-

her werden sie ausgewaschen und mindestens 2 Stunden in einer 0,1 mol Dextroselösung untergebracht. An den Orten, wo die Zellulosenbildner liegen, entstehen Verdickungen an der inneren Seite der Zellwand.

3. Über Versuche, die Zellulosenbildner in getöteten Zellen nachzuweisen.

Es ist in der Einleitung und in früheren Abhandlungen anscheinend hypothetisch von Zellulosenbildnern, d. h. von Enzymen oder Enzymsystemen, die zur Zellulosenbilddung imstande sein sollen, gesprochen worden; die Lage derselben soll für das Wachstum der Zellwand und der Wurzelhaare und somit für viele Determinations- und Differenzierungsvorgänge entscheidend sein. Bevor wir nun auf den Verlauf dieser Vorgänge näher eingehen, ist es angezeigt zu untersuchen, ob diese Zellulosenbildner überhaupt eine reelle Existenz haben.

Aus Abbildung 5 geht hervor, dass in Trichoblasten in Wurzeln, die in 0,15—0,20 mol Dextroselösung gelegen haben, eine Zellulosenmasse an dem apikalen Ende der Aussenwand gebildet werden kann. Eine solche Zellulosenmasse entsteht natürlich nicht von selbst, man muss annehmen, dass sie unter Mitwirkung von Enzymen oder Enzymsystemen gebildet wird.

Das erste Problem, nämlich wo diese Enzyme lokalisiert sind, wurde schon in einer früheren Abhandlung (Boysen Jensen 1954) behandelt. Es wurde gezeigt, dass das körnige Plasma in den Wurzelhaaren durch eine dünne Schicht von Hyaloplasma von der Zellwand getrennt ist, und dass die Körner nicht in das Hyaloplasma heraustreten. Die Enzyme, die die Zellulosenfibrillen in der Zellwand erzeugen, müssen in dem Hyaloplasma ihren Platz haben, und zwar auf Kämmen oder Papillen des Hyaloplasmas, die in die Zellwand hineinragen.

Es wäre nun natürlich von grosser Bedeutung, wenn man nachweisen könnte, dass eine Zellulosenbildung auch an totem Plasma stattfinden kann. Ich habe viele Versuche über dieses Problem angestellt. Obschon diese Versuche ohne Erfolg blieben, möchte ich doch das Verfahren, dass ich angewendet habe, kurz besprechen.

Es werden für die Versuche *Phleum*pflanzen, die in Glasschachteln auf Japonaispapier in $I_b + II$ gezüchtet waren, verwendet. Der Same wird abgeschnitten, und die Wurzel wird eine Minute in eine Lösung von zu gleichen Teilen Kongorotlösung und 0,2 mol Dextrose gelegt. Bei dieser Behandlung wird die Adhäsion zwischen Plasma und Zellwand abgebrochen, und das Plasma zieht sich aus der Zellwand heraus. Nachher wird die Kongorotlösung durch die Versuchslösung ersetzt, die Wurzel wird mit Deckglas bedeckt und unter das Mikroskop gelegt. Die Lage der äussersten zehn Wurzelhaare wird gezeichnet, und es wird für jedes Wurzelhaar vermerkt, ob Plasmaströmungen oder Verdickungen bei dem Anfang des Versuches vorhanden waren.

In Lösungen von 0,1 mol Dextrose entstehen im Laufe von einer Stunde Verdickungen in vielen Wurzelhaaren.

Die eigentlichen Versuchslösungen waren:

0,1 mol Dextroselösung mit Toluol gesättigt
0,2 mol Glyzerinlösung mit Toluol gesättigt
2 mg K_2 Glukose-1-phosphatlösung[1] in 0,2 ccm $I_b + II$ gelöst, und mit Toluol gesättigt (pH etwa 7,3).
Dieselbe Lösung durch Zusatz von 1 % iger Essigsäure auf ein pH von 5,2 gebracht.

In diesen Lösungen hörten die Plasmaströmungen sofort auf, das Plasma wurde steif und körnig; wenn nach dem Versuche Glyzerin zugesetzt wurde, trat keine Plasmolyse ein.

Ich meine, in zwei (von etwa 100) Wurzelhaaren sehr schwache Verdickungen beobachtet zu haben, aber es ist nicht möglich, aus den Versuchen irgendwelche Schlüsse zu ziehn.

Obgleich es nicht gelungen ist, die zellulosenbildenden Enzyme in mit Toluol getöteten Zellen direkt nachzuweisen, kann jedoch das Vorkommen derselben in lebenden Zellen nicht bezweifelt werden. Hierfür sprechen nicht nur die im Eingang des Kapitels erwähnten Tatsachen, sondern auch einige frühere Versuche (Boysen Jensen 1954), aus denen hervorgeht, dass Wurzelhaare, die sich in sauerstofffreier Nährlösung befinden,

[1] Der verwendete Stoff war wahrscheinlich eine α-Verbindung. Da Zellulose aus β-Glukose aufgebaut ist, wäre es vielleicht besser gewesen, ein β-Glukose-1-phosphat zu verwenden. Diese Verbindung stand mir aber nicht zur Verfügung.

und in welchen die Wachstumsfähigkeit schnell erlischt, dazu imstande sind, Zellulosenverdickungen zu erzeugen. Ich habe diese Versuche mit demselben Ergebnis wie früher wiederholt. Wenn *Phleum*pflanzen, deren Wurzelhaare keine Verdickungen enthalten, $2^1/_2$ Stunden in einer sauerstofffreien Lösung von 0,1 mol Dextrose mit Kongorot untergebracht werden, entstehen in der Spitze der Wurzelhaare starke Verdickungen. Die Wurzelhaare sind nicht tot, es finden in ihnen sehr schwache Bewegungen im Plasma statt, und es entsteht nach Zusatz von Glyzerin Plasmolyse. Es geht aus den Versuchen hervor, dass die Zellulosenbildung ohne Mitwirkung der bei der oxybiotischen Respiration produzierten Energie zustande kommen kann. Diese Tatsache wird wohl nur verständlich, wenn man annimmt, dass die Zellulosen durch Enzyme gebildet werden.

Man wird somit die folgenden Sätze aufstellen können.

Wenn in Wurzelhaaren neue Zellwand oder Verdickung gebildet wird, sind Zellulosenbildner vorhanden an der Stelle, wo die Neubildung stattfindet.

Wenn keine neue Zellwand gebildet wird, können Zellulosenbildner in dem Plasma in der Zellwand vorhanden sein, indem dieselben durch einen fehlenden osmotischen Druck verhindert werden, ihre Wirkung zu entfalten. Durch Zusatz von Kongorot kann man dann eine Verdickung an der inneren Seite der Zellwand hervorrufen.

Wenn durch Zusatz von Kongorot keine Verdickung in Wurzelhaaren gebildet wird, sind auch keine Zellulosenbildner vorhanden.

4. Die Differenzierung der Zellen in der Wurzelepidermis.

Es gibt zwei verschiedene Typen von Wurzelepidermen. Bei der einen Type sind alle Zellen gleichartig und alle dazu imstande, Wurzelhaare zu bilden, selbst wenn sie es nicht immer tun. Bei der anderen Type besteht die Epidermis aus wechselweise kurzen und langen Zellen; nur die ersteren, die Trichoblasten, bilden Wurzelhaare; die anderen dagegen normalerweise nicht. Der Unterschied zwischen den beiden Typen kann mehr oder weniger scharf sein.

Der Verlauf der Differenzierung der Epidermiszellen in einer

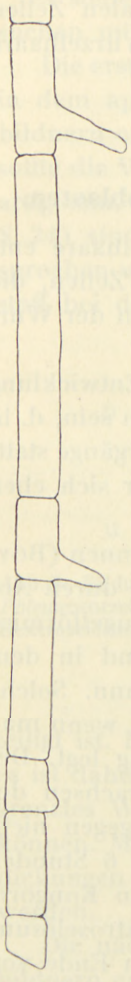

Abb. 3 Differenzierung der Zellen in der Wurzelepidermis und Bildung der Wurzelhaare bei *Phleum*.

Wurzel der letzteren Type ist von SINNOTT und BLOCH (1939 (1) und (2)) untersucht worden. Sie haben gezeigt, dass z. B. bei *Phleum* gewöhnlich bei der vierten Zellteilung von der Spitze zwei ungleichartige Zellen gebildet werden; sie unterscheiden sich darin, dass die apikale Zelle mehr Plasma enthält als die basale. Die apikale Zelle wächst langsam und bildet schliesslich ein Wurzelhaar, während die basale Zelle schnell wächst und kein Wurzelhaar bildet (Abb. 3).

Die Frage ist nun, was bei dieser ungleichartigen Zellteilung eigentlich geschieht.

Wenn man eine Wurzel in eine Lösung legt, in welcher das Wachstum der Wurzel aufhört, oder wenn man die Spitze der Wurzel durch Lapis tötet, kann man erreichen, dass Wurzelhaare auch von den noch nicht gestreckten Zellen gebildet werden (Abb. 4). In den äussersten Zellen bis etwa 0,2—0,3 mm von der Spitze ist es jedoch niemals gelungen, Wurzelhaarbildung hervorzurufen, sie sind wahrscheinlich noch vollkommen embryonal. Kurz nach der inäqualen Zellteilung erhalten die Zellen die Fähigkeit, an dem apikalen Ende ein Wurzelhaar zu bilden, und zwar können, wie aus Abbildung 4 hervorgeht, alle Zellen ursprünglich Wurzelhaare bilden. Während aber diese Fähigkeit in der apikalen Zelle, die bei der inäqualen Zellteilung entsteht, erhalten bleibt und schliesslich zur Wurzelhaarbildung führt, geht sie dagegen in der basalen Zelle nach und nach verloren, indem dieselbe sich streckt, ohne ein Wurzelhaar zu bilden.

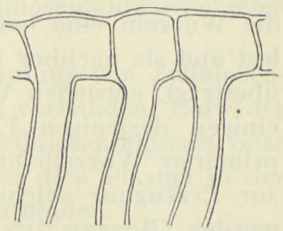

Abb. 4. Bildung von Wurzelhaaren in Zellen, die noch nicht gestreckt sind, bei *Phleum*, Kult. I_b + II. Bhdl. Die Spitze durch Berührung von einer Sekunde mit einem Lapiskristall getötet. Zeichenapp. $\frac{400}{1}$.

Es muss jedoch bemerkt werden, dass die Differenzierung der Zellen nicht immer so schematisch verläuft,

wie es hier geschildert ist. Es können in den basalen Zellen Teilungen eintreten, gelegentlich können auch sie Wurzelhaare bilden.

5. Die Determinierungsvorgänge in den Trichoblasten.

Die Trichoblasten sind polär gebaut, die Wurzelhaare entstehen an dem apikalen Ende derselben. Selbst in Zellen, die nicht mehr als 20 μ lang sind, ist die apikale Insertion der Wurzelhaare deutlich (Abb. 4).

Es muss nun der Differenzierung, der sichtbaren Entwicklung des Wurzelhaares, eine Determination vorausgegangen sein, d. h. es müssen in der Zelle nicht unmittelbar sichtbare Vorgänge stattgefunden haben, die bewirken, dass ein Wurzelhaar sich eben an dem apikalen Ende der Zelle entwickelt.

In einer früheren Abhandlung habe ich zeigen können (Boysen Jensen 1950), dass man in verschiedener Weise durch Abbruch der Entwicklung kegelförmige oder halbkugelförmige Verdickungen an der inneren Seite der Aussenwand in dem apikalen Ende von Epidermiszellen hervorrufen kann. Solche apikalen Verdickungen kann man bisweilen erzeugen, wenn man *Phleum*wurzeln in eine 0,15—0,2 mol Dextroselösung legt. Der osmotische Druck dieser Lösung hindert das Auswachsen der Wurzelhaare, d. h. den Differenzierungsvorgang, dagegen nicht den Determinationsvorgang. Wenn man daher nach 6 Stunden die Wurzeln eine halbe Stunde in eine Lösung von Kongorot legt und sie nachher 16 Stunden in eine 0,1 mol Dextroselösung überträgt, entstehen Verdickungen an dem apikalen Ende von einigen derjenigen Epidermiszellen, die unmittelbar vor der primären Wurzelhaarzone liegen (Abb. 5). Andere Methoden zur Erzeugung solcher Verdickungen sind früher beschrieben worden (Boysen Jensen 1950).

Diese Verdickungen bestehen aus Zellulosen; bei der normalen Entwicklung würden diese Zellulosen die Zellwand eines Wurzelhaares gebildet haben; bei Abbruch der Entwicklung entsteht dagegen eine Verdickung. Der Erfolg der Determination ist somit eine vermehrte Zellulosenbildung in dem apikalen Ende der Trichoblasten.

Es stellen sich nun zwei Fragen, die wir zu beantworten versuchen müssen.

Die erste dieser Fragen ist, ob die vermehrte Zellulosenbildung in dem apikalen Ende durch eine Anhäufung von Zellulosenbildnern oder von Wuchsstoff zustande kommt. Im letzten Falle sollte die Verteilung der Zellulosebildner in der Zellwand gleichartig sein. In einer früheren Abhandlung (Boysen Jensen 1954 S. 24) sind einige Versuche von Wortmann und Bücher besprochen worden, aus denen man folgern kann, dass der Wuchsstoff bei der Zellulosenbildung wahrscheinlich nicht direkt be-

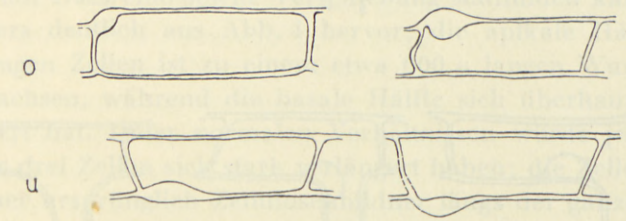

Abb. 5. Bildung von Verdickungen in dem apikalen Ende von Trichoblasten in *Phleum*wurzeln. Kultur Leitungswasser, Behdl. 6 Stunden in einer 0,15—0,2 mol Dextroselösung, eine halbe Stunde in Kongorot, nachher 16 Stunden in Leitungswasser, o Oberseite, u Unterseite. Zeichenapp. $\frac{400}{1}$.

teiligt ist. Ferner weiss man, dass Wuchsstoffe schnell wandern, es ist daher ausgeschlossen, dass sie ein lokales, sehr scharf begrenztes Wachstum oder Zellulosenbildung sollten hervorrufen können. Man muss daher schliessen, dass die kegelförmige Verdickungen durch eine Anhäufung von Zellulosenbildnern erzeugt werden.

Die nächste Frage ist, wie diese Anhäufung von Zellulosenbildnern entsteht. Zwei Möglichkeiten sind vorhanden. Entweder muss eine lokalisierte Neubildung von Zellulosenbildnern oder eine Verschiebung der Zellulosenbildner in dem Plasma in der Zellwand gegen das apikale Ende hin stattfinden.

Eine lokalisierte Neubildung von Zellulosenbildnern könnte unter Mitwirkung des Kerns zustandekommen. Wie oben angeführt hat Haberlandt gezeigt, dass die Wurzelhaare von *Pisum* unmittelbar über den Zellkern angelegt werden. Bei *Phleum* ist das nicht der Fall. In *Phleum*wurzeln, die ohne jede Behandlung unter das Mikroskop gelegt werden, kann man in günstig ge-

legenen Zellen sehen, dass der Zellkern in den Trichoblasten an der Rückwand ungefähr in der Mitte seinen Platz hat. Dieses wird durch Färbung mit Karminessigsäure bestätigt (Abb. 6 a). Nur selten liegt der Zellkern im Wurzelhaar. In einer abgeschnittenen Wurzelspitze, die 20 Stunden in 0,1 mol Dextrose gelegen hatte, lag jedoch in vielen Fällen der Zellkern im Wurzelhaar. Die Einwanderung des Kerns fand aber erst statt, nachdem das

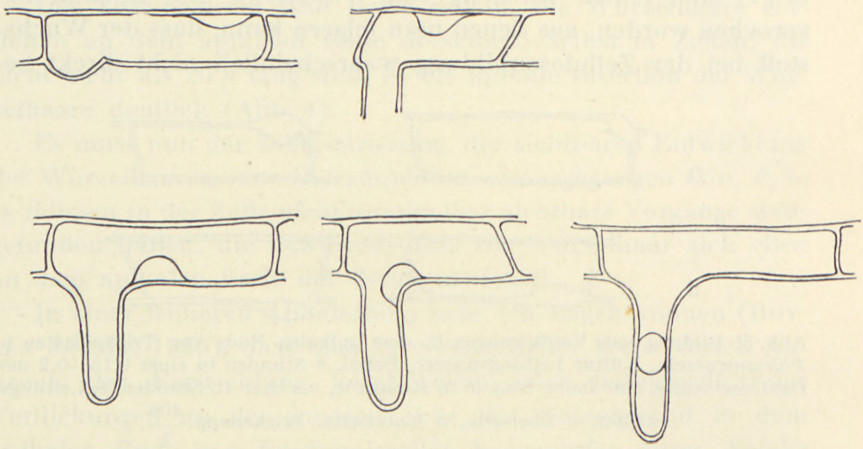

Abb. 6. Die Lage des Zellkerns in den Trichoblasten, a in intakten Wurzeln, b in abgeschnittenen Spitzen, die 20 Stunden in einer 0,1 mol Dextroselösung gelegen haben.

Wurzelhaar eine Länge von etwa 40 μ erreicht hatte (Abb. 6 b). In einer anderen abgeschnittenen Wurzelspitze, die in ähnlicher Weise behandelt wurde, lagen die Zellkerne nicht in den Wurzelhaaren.

Es ist somit nicht gelungen, eine Beziehung zwischen der Lage des Zellkerns und der Entwicklung des Wurzelhaares, dessen Bildung mit derjenigen einer Verdickung analog ist, nachzuweisen, und es ist daher wahrscheinlich, dass die Anhäufung der Zellulosenbildner in dem apikalen Ende der Trichoblasten durch eine Verschiebung derselben im Plasma entsteht. Diese letztere Auffassung wird durch die folgenden Tatsachen bestätigt.

Es geht aus einer Reihe von Untersuchungen hervor, dass die Entwicklung eines Wurzelhaares von einer Abnahme des Längenwachstums des übrigen Teils der Zellwand begleitet ist.

Cormack gelangt geradezu zu dem Schluss, dass »each epidermal cell has a certain capacity for growth which may be expressed in either a longitudinal or horizontal direction« (Cormack 1949). Die Richtigkeit dieses Schlusses kann ich vollkommen bestätigen. Die Länge der Wurzelhaare in der sekundären Zone, die von ganz kurzen Zellen entwickelt werden, ist weit grösser als diejenige der Wurzelhaare in der primären Zone (Abb. 2 c).[1] Man muss dann weiter folgern, dass die Entwicklung der Wurzelhaare durch eine lokale Anhäufung aller oder jedenfalls des grössten Teils der Zellulosenbildner in der Zellwand ermöglicht sein muss. Dass eine solche Verschiebung stattfinden kann, geht besonders deutlich aus Abb. 4 hervor; die apikale Hälfte der 20 μ langen Zellen ist zu einem etwa 600 μ langen Wurzelhaar ausgewachsen, während die basale Hälfte sich überhaupt nicht verlängert hat. Unter normalen Verhältnissen würde jedenfalls eine der drei Zellen sich stark verlängert haben; die Zellen müssen daher ursprünglich Zellulosenbildner längs der ganzen Aussenwand enthalten haben. Das Ausbleiben des Wachstums in der basalen Hälfte kann daher nur dadurch erklärt werden, dass die Zellulosenbildner apikalwärts verschoben worden sind. Wie später gezeigt werden soll, kann auch in der Spitze der Wurzelhaare eine Verschiebung der Zellulosenbildner stattfinden.

Wir können somit feststellen, dass die Polarität der Trichoblasten, die in der Ausbildung einer Verdickung oder eines Wurzelhaares an dem apikalen Ende zum Ausdruck kommt, in einer Fähigkeit besteht, die Zellulosenbildner in dem Plasma in der Aussenwand der Zelle gegen das apikale Ende zu verschieben. Diese Verschiebung ist eben der Determinationsvorgang in den Trichoblasten.

Wir müssen sodann untersuchen, ob sich erhellen lässt, welche Faktoren diese Verschiebung hervorrufen.

Es wurde zunächst geprüft, ob es möglich ist, die Polarität durch äussere Faktoren umzukehren, so dass die Wurzelhaare an dem basalen Ende gebildet wurden.

Zuerst wurde die Wirkung traumatischer Reize untersucht.

[1] Wahrscheinlich findet eine Neubildung von Zellulosenbildnern während des Wachstums des Wurzelhaares überhaupt nicht statt.

Es wurde entweder die äusserste Spitze (< 1 mm) oder die äussersten 3—5 mm abgeschnitten. Im ersteren Fall befand sich die Schnittfläche unterhalb, im zweiten Falle oberhalb des wurzelhaarbildenden Teils. Ferner wurde an abgeschnittenen Spitzen (Länge 3—5 mm) die äusserste Spitze (< 1 mm) abgeschnitten, so dass Schnittflächen sowohl unterhalb als oberhalb des wurzelhaarbildenden Teils vorhanden waren. Endlich wurde auch versucht, den wurzelhaarbildenden Teil (ohne die äusserste Spitze) in umgekehrter Lage an die Wurzel anzusetzen. In allen Fällen wurden die Versuchsobjekte 24 Stunden in eine 0,1 mol Dextroselösung gelegt. Das Ergebnis der Versuche war vollkommen eindeutig. In allen Fällen wurden reichlich neue Wurzelhaare gebildet. Die Insertion derselben war immer die normale apikale, eine Umkehrung der Polarität gelang es nicht zu erzwingem.

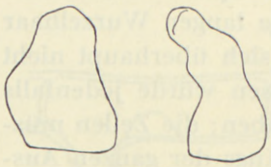

Abb. 7. Apoläre Wurzelhaarbildung bei *Phleum*. Kultur I_b + II, Behdl. a 24 Stunden in 0,02 %, b in 0,01 % Colchicin. Zeichenapp. $\frac{400}{1}$.

In nächsten Abschnitte sollen Versuche über die Einwirkung einer Reihe verschiedener Stoffe auf die Gestalt der Wurzelhaare besprochen werden. Gleichzeitig mit diesen Untersuchungen wurde auch geprüft, ob die normale, apikale Insertion der Wurzelhaare verändert wurde. In keinem Falle wurden die Wurzelhaare an das basale Ende angelegt, aber es gelang bei Wurzelhaaren von *Phleum* in einer 0,01—0,02 % igen Lösung von Colchicin, 0,1 mol Dextrose, die Polarität aufzuheben, so dass in ganz kurzen, noch nicht gestreckten Zellen die ganze Aussenwand sich auswölbte. Aber auch in diesem Falle sammelten die Zellulosenbildner sich schliesslich an einer bestimmten Stelle, so dass die ursprüngliche halbkugelige Bildung in eine Spitze auslief (Abb. 7).

Es konnte somit nicht ermittelt werden, welcher Faktor die Verschiebung der Zellulosenbildner in den Trichoblasten gegen das apikale Ende hervorruft. Dagegen ist es vielleicht möglich festzustellen, welche Faktoren nicht beteiligt sein können.

Zunächst kann man, da die Wurzeln in den Versuchen immer horizontal lagen, die Schwerkraft ausschliessen. Ebensowenig dürften elektrische Potentiale und stoffliche Wirkungen in Betracht kommen können. Durch die Einschnitte dürften diese

Faktoren in so tiefgehender Weise verändert worden sein, dass eine sichtbare Wirkung dieser Veränderungen nicht ausbleiben könnte, falls die betreffenden Faktoren irgendwelche Bedeutung für die Verschiebung der Zellulosenbildner hätten.

6. Die Verschiebungen der Zellulosenbildner in den Wurzelhaaren.

Der Umfang der Verdickung, die man durch Kongorot im Laufe 1—2 Stunden in der Spitze der Wurzelhaare hervorrufen kann, dürfte mit der Anzahl der Zellulosenbildner in den einzelnen Teilen der Membrankuppe ungefähr proportional sein. Tatsächlich findet man am häufigsten, dass die Verdickung anfänglich eine nach unten offene Schale bildet, deren Basis an der Grenze der halbkugeligen Spitze liegt; die Dicke der Schale nimmt von dem apikalen Teil nach unten zu ab, und man wird daher folgern können, dass dasselbe mit der Anzahl der Zellulosenbildner der Fall ist. Später kann die Spitze von der Verdickung ganz ausgefüllt werden.

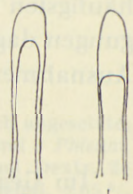

Abb. 8. Normale Verdikkungen in der Spitze von Wurzelhaaren. a *Phleum*, Kultur Leitungswasser, Behdl 0,00001 % β-Indolylessigsäure, 0,1 mol Dextr. in 24 Stunden, b *Lepidium*, Kultur Leitungswasser, Petrischale, Behdl. 0,05 % Colchicin, 0,1 mol Dextr. 24 Stunden Zeichenapp. $\frac{400}{1}$.

Ausser durch Kongorot können ähnliche Verdikkungen durch β-Indolylessigsäure, Colchicin und viele andere Stoffe, jedoch erst im Laufe von 24 Stunden, erzeugt werden (Abb. 8).

Während man in den Trichoblasten, wie im vorigen Abschnitt dargestellt wurde, verfolgen kann, wie eine bestimmte Anordnung der Zellulosenbildner entsteht, ist dagegen in den Wurzelhaaren eine solche bestimmte Anordnung vorhanden; in diesem Falle kann man daher untersuchen, wie diese Anordnung durch äussere Faktoren, namentlich durch die Einwirkung der oben angeführten chemischen Verbindungen, beeinflusst wird.

Schon längst hat man die Erfahrung gemacht, dass man durch chemische Stoffe Wachstumsanomalien in Wurzelhaaren hervorrufen kann. Die ältere Literatur über diese Frage findet sich z. B. bei Küster (1916). In neuerer Zeit hat Farr (1928), die Wirkung von Kalksalzen auf Wurzelhaare un-

tersucht und dabei eine lange Reihe abnormer Formen erhalten.

Die Abnormitäten, die man bei Behandlung der Wurzelhaare von *Lepidium*, *Sinapis* und *Phleum* mit verschiedenen chemischen Verbindungen erhalten kann, können in zwei Hauptgruppen eingeteilt werden, nämlich verschobene Verdickungen und Wachstumsanomalien. Jede dieser Gruppen umfasst wieder zwei einander entsprechende Untergruppen, auf der einen Seite verschobene allseitige Verdickungen und Anschwellungen und auf der anderen Seite verschobene lokale Verdickungen und Verzweigungen. Die verschobenen Verdickungen finden sich am häufigsten in den primären, die Anschwellungen und Verzweigungen dagegen in den sekundären Wurzelhaaren. Es gibt jedoch Ausnahmen von dieser Regel.

a. *Die verschobenen Verdickungen.*

Im Gegensatz zu den oben erwähnten in Abb. 8 dargestellten Verdickungen, die man als normale bezeichnen kann, entstehen unter dem Einfluss verschiedener Stoffe (β-Indolylessigsäure, Colchicin, Sublimat) Verdikkungen, die unterhalb der Spitze liegen, und die man daher als verschobene Verdickungen bezeichnen kann.

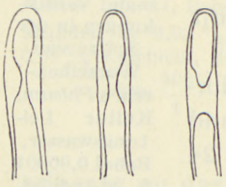

Abb. 9. Verschobene allseitige Verdickungen in der Spitze von Wurzelhaaren von *Phleum*. Kultur Leitungswasser, Behdl. 0,0001 % β-Indolylessigsäure, 0,1 mol Dextr. 24 Stunden, Zeichenapp. $\frac{400}{1}$.

1. Verschobene allseitige Verdikkungen. Relativ selten tritt die Verdickung als ein mehr oder weniger dicker ringförmiger Wulst mit ausfliessender Basis hervor, der an der inneren Seite der Zellwand ungefähr an der unteren Grenze der Membrankuppe liegt (Abb. 9 a, b).[1] Der Wulst kann sich in der Mitte vollkommen schliessen, so dass die Höhlung der Membrankuppe durch eine Zellulosenplatte von der Höhlung im unteren Teil des Wurzelhaares getrennt wird (Abb. 9 c).

2. Verschobene lokale Verdickungen. Weit häufiger als die allseitigen sind die lokalen Verdickungen. Diese sind meistens halbkugeliche Zellulosengebilde von verschiedener Grösse, die an

[1] Eine verschobene allseitige Verdickung in einem Wurzelhaar von *Chara* ist von Zacharias abgebildet (vgl. Boysen Jensen 1954 Abb. 9).

der inneren Seite der Zellwandkuppe in verschiedener Höhe, doch niemals unterhalb der Grenze der Membrankuppe liegen (Abb. 10).[1] Auch die lokalen Verdickungen können so stark entwickelt sein, dass sie die Höhlung des Wurzelhaares fast ganz verschliessen (Abb. 10 b).

Die verschobenen Verdickungen sind mit den in Abb. 8 dargestellten Verdickungen durch Übergänge verbunden, und man

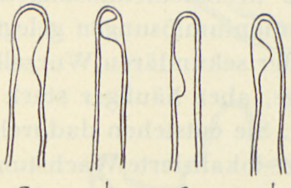

Abb. 10. Verschobene lokale Verdickungen. a schiefe, allseitige, b hoch angesetzte, c tropfenförmig herabgleitende, d regelmässige, tiefe Verdickung. a und c *Phleum*, Kultur Leitungswasser, Behdl. 0,0001 % β-Indolylessigsäure, 0,1 mol Dextr. 24 Stunden. b und d *Lepidium*, Kultur Leitungswasser Petrischale, Behdl. 0,05 % Colchicin, 0,1 mol Dextr. 24 Stunden. Zeichenapp. $\frac{400}{1}$.

muss daher schliessen, dass sie in ähnlicher Weise wie diese von den in dem intakten Wurzelhaar anwesenden und nicht von neugebildeten Zellulosenbildnern erzeugt worden sind. Da Verdickungen von bedeutender Grösse statt in der Spitze an der unteren Grenze der Membrankuppe, wo in normalen Wurzelhaaren die Wachstumsgeschwindigkeit sehr langsam und die Anzahl der Zellulosenbildner sehr klein ist, erzeugt werden, muss man schliessen, dass eine Verschiebung der Zellulosenbildner nach unten stattfinden kann. Sehr bemerkenswert ist es, dass diese Verschiebung nach unten nicht immer gleichmässig verläuft, sondern dass die Zellulosenbildner sich an einer bestimmten Stelle anhäufen, wo dann die Verdickung entsteht. Ob die Verschiebung der Zellenbildner stattfindet, bevor oder nachdem das Plasma sich aus der Zellwand herausgezogen hat, kann nicht festgestellt werden.

[1] In einem Falle war jedoch wahrscheinlich eine Verdickung im Basalteil eines Wurzelhaares vorhanden.

b. *Wachstumsanomalien.*

Während das Aussehen der Wurzelhaare mit Verdickungen vollkommen normal ist, sind dagegen die Wachstumsanomalien mit einer Gestaltänderung der Wurzelhaare verknüpft. Man kann zwei Typen unterscheiden, die Anschwellungen und die Verzweigungen.

1. Die Anschwellungen (Abb. 11). Wenn Wurzeln von *Lepidium* und *Sinapis* in Colchicinlösungen und Wurzeln von *Phleum* in Rhodanammoniumlösungen gelegt werden, werden in der Regel an einigen der sekundären Wurzelhaare eigentümliche, bisweilen kugelförmige, aber häufiger stark unregelmässige Anschwellungen gebildet. Sie entstehen dadurch, dass das normale, in der äussersten Spitze lokalisierte Wachstum, durch ein diffuses, über die ganze Membrankuppe verteiltes Wachstum ersetzt wird. Es besteht jedoch in dem abnorm gestalteten Wurzelhaar eine Tendenz, zur normalen Wachstumsweise zurückzukehren. An einer oder mehreren willkürlichen Stellen der Anschwellungen entstehen bisweilen wurzelhaarähnliche Auswüchse mit Spitzenwachstum, die jedoch häufig bald zu wachsen aufhören.

b. Verzweigungen. Unter denselben Bedingungen wie oben können statt Anschwellungen Verzweigungen an verschiedenen Stellen der Membrankuppe gebildet werden. Liegt die Verzweigung in der Nähe der Spitze, erhält man entweder gabelige oder bajonettförmige Wurzelhaare, liegt sie weiter unten, ist der Neuzuwachs mehr oder weniger schräg im Verhältnis zu dem basalen Teil des Wurzelhaares, und liegt sie an der Grenze der Membrankuppe, ist der Zweig winkelrecht zum Wurzelhaare (Abb. 12 a, b, c). In allen Fällen kann sich ein Wurzelhaar wiederholt verzweigen. Da der Neuzuwachs nach allen Richtungen ausgehen kann, kann die schliessliche Gestalt des Wurzelhaares sehr verwickelt werden (Abb. 12 d, e, f).

Die Wachstumsanomalien entstehen in ähnlicher Weise wie die Verdickungen dadurch, dass die Zellulosenbildner nach unten herabgleiten. Der Unterschied zwischen den Verdickungen und Wachstumsanomalien kommt dadurch zustande, dass das Plasma sich bei der Bildung der Verdickungen aus der Zellwand herauszieht, während es bei der Bildung der Wachstumsanomalien

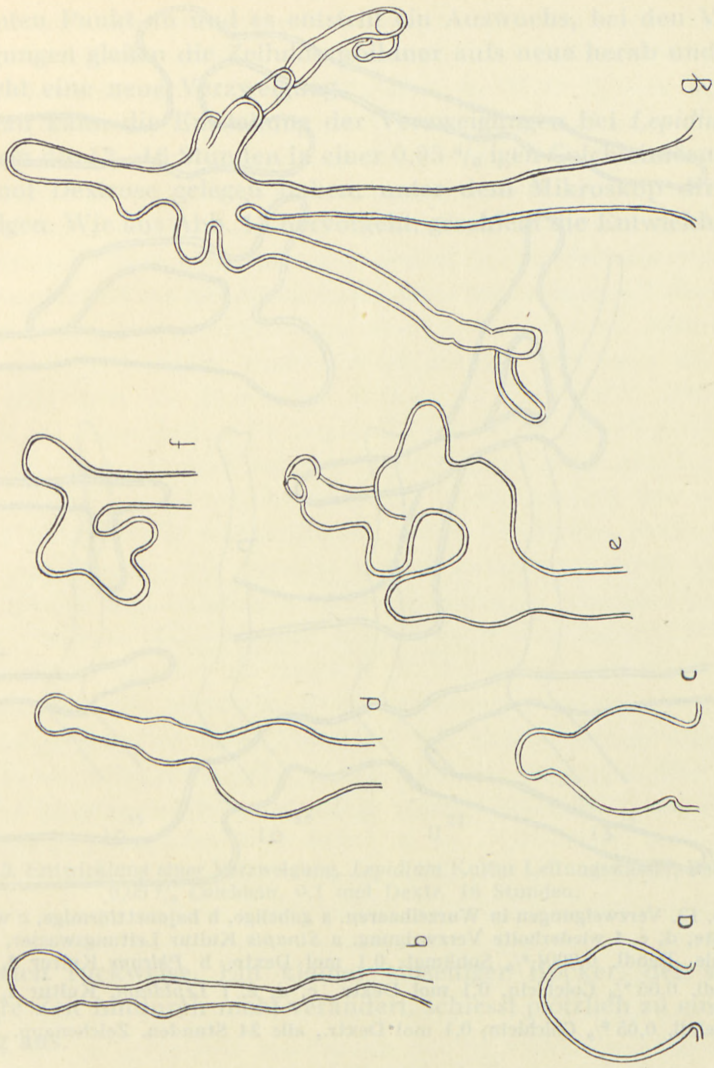

Abb. 11. Anschwellungen in Wurzelhaaren. a kugelförmige, b keulenförmige, c, d kolbenförmige Anschwellungen, e und f verästelte Köpfe, g verästelter Kopf mit wurzelhaarähnlichen Auswüchsen. a, b, c, d *Phleum*, Kultur I_b + II, Behdl. 0,1 % Rhodanammonium, 0,1 mol Dextr., e *Sinapis*, Kultur Leitungswasser, Petrischale, Behdl. 0,05 % Colchicin, 0,1 mol Dextr., f *Lepidium*, Kultur I_b + II Behdl. 0,05 % Colchicin, 0,1 mol Dextr., g *Lepidium*, Kultur Leitungswasser, Petrischale, Behdl. 0,05 % Colchicin, 0,1 mol Dextr., alle 24 Stunden. Zeichenapp. $\frac{400}{1}$.

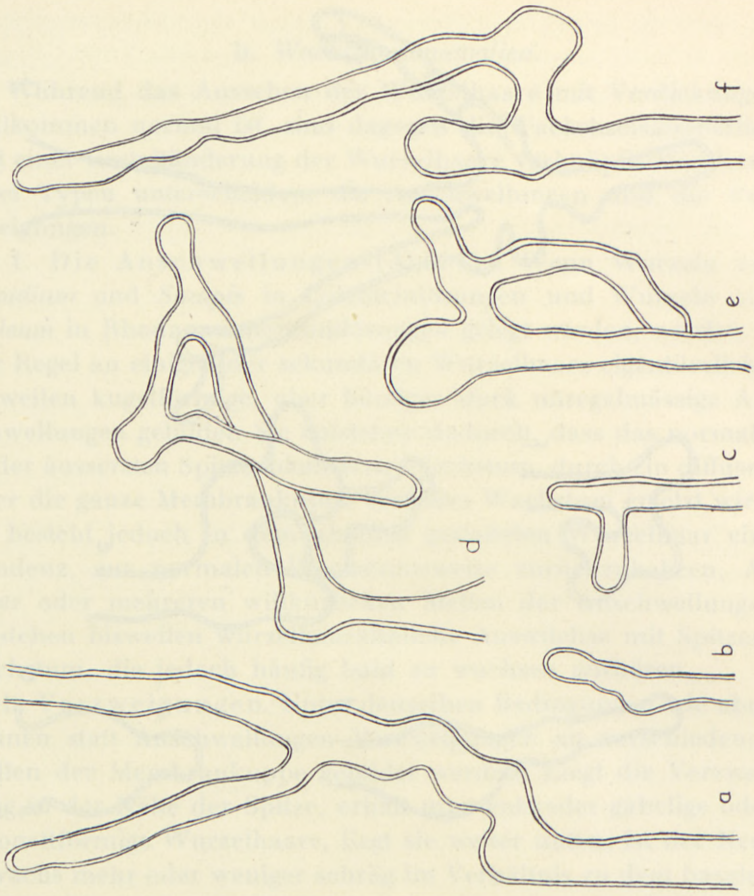

Abb. 12. Verzweigungen in Wurzelhaaren. a gabelige, b bajonettförmige, c winkelrechte, d, e, f wiederholte Verzweigung. a *Sinapis* Kultur Leitungswasser, Petrischale, Behdl. 0,0001 % Sublimat, 0,1 mol Dextr. b *Phleum* Kultur I_b + II, Behdl. 0,05 % Colchicin, 0,1 mol Dextr., c, d, e, f *Lepidium*, Kultur I_b + II, Behdl. 0,05 % Colchicin, 0,1 mol Dextr., alle 24 Stunden. Zeichenapp. $\frac{400}{1}$.

in der Zellwand liegen bleibt. Wenn das Herabgleiten der Zellulosenbildner allseitig erfolgt, entsteht eine Anschwellung; wenn dagegen die Zellulosenbildner sich an einem scharf begrenzten Ort anhäufen, muss ebenso wie in den Trichoblasten eine wurzelhaarähnliche Ausstülpung mit einer apikalen Anordnung der Zellulosenbildner erzeugt werden. Wie oben angeführt sind diese Anordnungen der Zellulosenbildner jedoch nicht stabil. Bei den Anschwellungen häufen die Zellulosenbildner sich an einen be-

stimmten Punkt an und es entsteht ein Auswuchs, bei den Verzweigungen gleiten die Zellulosenbildner aufs neue herab und es entsteht eine neue Verzweigung.

Man kann die Entstehung der Verzweigungen bei *Lepidium*-wurzeln die 13—16 Stunden in einer 0,05 % igen Colchicinlösung, 0,1 mol Dextrose gelegen haben, unter dem Mikroskop direkt verfolgen. Wie aus Abb. 13 hervorgeht, geschieht die Entwicklung

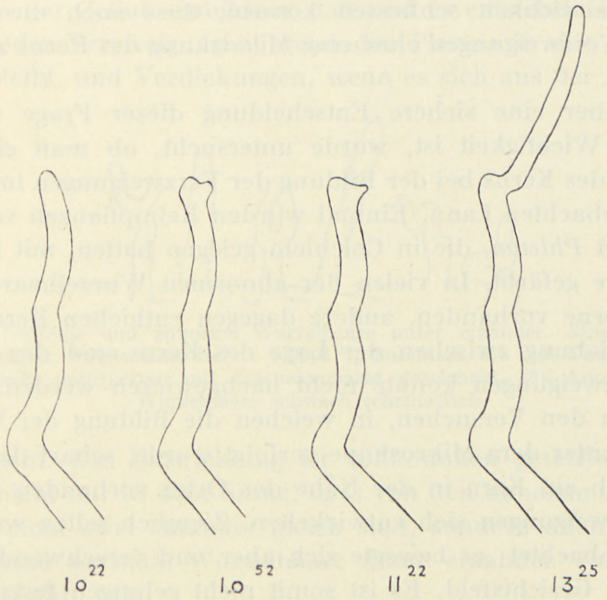

Abb. 13. Entwicklung einer Verzweigung. *Lepidium* Kultur Leitungswasser, Behdl. 0,05 % Colchicin, 0,1 mol Dextr. 16 Stunden.

bisweilen ruckweise. Ein kleiner einseitiger Höcker, der sich längere Zeit hindurch nicht verändert, schiesst plötzlich zu einem Zweig aus.

c. *Bedeutung des Kerns.*

Das wichtigste Ergebnis der Untersuchungen ist wohl, dass die Zellulosenbildner dazu imstande sind, sich an einem bestimmten Ort anzuhäufen, und es ist daher von entscheidender Bedeutung zu klären, ob der Zellkern bei dieser Anhäufung beteiligt ist. Es ist wohl ausgeschlossen, dass der Zellkern bei der Entstehung der verschobenen allseitigen Verdickungen und der

Auschwellungen sollte mitwirken können. Bei den letzteren ist das Wachstum so unregelmässig über grössere Bezirke der Zellwand verteilt, dass es nicht auf die Wirkung eines an einem bestimmten Ort gelegenen Zellkerns zurückgeführt werden kann. Ebenso wenig kann die Entstehung der gabeligen Verzweigungen und der beiden Wurzelhaargebilde in Abb. 11 g durch die Wirkung des Kerns verursacht sein, und man wird daher mit grosser Wahrscheinlichkeit schliessen können, dass auch die winkelrechten Verzweigungen ohne eine Mitwirkung des Kerns zustande kommen.

Da aber eine sichere Entscheidung dieser Frage von der grössten Wichtigkeit ist, wurde untersucht, ob man eine Mitwirkung des Kerns bei der Bildung der Verzweigungen im Mikroskop beobachten kann. Einmal wurden Keimpflanzen von *Lepidium* und *Phleum*, die in Colchicin gelegen hatten, mit Karminessigsäure gefärbt. In vielen der abnormen Wurzelhaare waren keine Kerne vorhanden, andere dagegen enthielten Kerne, aber eine Beziehung zwischen der Lage des Kerns und der Bildung der Verzweigungen konnte nicht nachgewiesen werden. Ferner wurde in den Versuchen, in welchen die Bildung der Verzweigungen unter dem Mikroskope verfolgt wurde, scharf darauf geachtet, ob ein Kern in der Nähe des Ortes vorhanden war, wo die Verzweigungen sich entwickelten. Ziemlich selten wurde ein Kern beobachtet; er bewegte sich aber und verschwand schnell aus dem Gesichtsfeld. Es ist somit nicht gelungen festzustellen, dass der Kern bei der Bildung der Verzweigungen beteiligt ist.

Für die Beurteilung der Bedeutung des Kerns für die Gestaltbildung ist es von grossem Interesse, dass *Acetularia*stiele einen Hut bilden können, selbst wenn sie keinen Kern enthalten (Hämmerling).

7. Schlussfolgerungen.

Die Entwicklung der Wurzelhaare verläuft ganz gesetzmässig, sie geschieht wie oben erwähnt dadurch, dass ein Teil der Zellulosenbildner in den Trichoblasten nach dem apikalen Ende hin verschoben werden. Es entsteht dann an dieser Stelle eine Ausstülpung, ein Wurzelhaar,[1] und die Zellulosenbildner sam-

[1] Damit ein Wurzelhaar gebildet werden kann, muss jedoch auch ein osmotischer Druck in den Trichoblasten vorhanden sein.

meln sich in der Spitze desselben. Die Entwicklung kommt somit durch ein bestimmtes Verteilungsmuster der Zellulosenbildner zustande; dieses Muster entsteht durch die Wirkung des determinierenden Faktors.

Wie im vorigen Abschnitt erwähnt wurde, kann man durch verschiedene Stoffe dieses Verteilungsmuster in der Spitze der Wurzelhaare aufheben oder zerstören. Es findet dann ein Herabgleiten der Zellulosenbildner statt und es entstehen Anschwellungen oder Verzweigungen, wenn das Plasma in der Zellwand liegen bleibt, und Verdickungen, wenn es sich aus der Zellwand

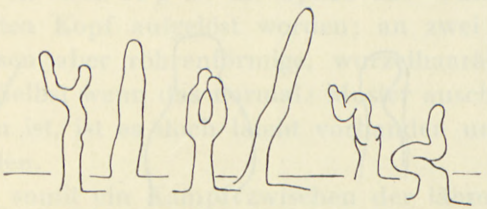

Abb. 14. Normale und abnorme Wurzelhaare unter einander. *Sinapis* Kultur Leitungswasser, Petrischale, Behdl. 0,0001 % Sublimat, 0,1 mol Dextr. Die einzelnen Haare naturgetreu mit Zeichenapparat gezeichnet, die Anordnung der Wurzelhaare schwach schematisch.

herauszieht. Die Entwicklung ist vollkommen gesetzlos, — gesetzlos nicht nur in dem Sinne, dass von den abnormen Wurzelhaaren nicht zwei einander gleich sind, sondern auch weil abnorme und normale Wurzelhaare unter einander vorkommen können (Abb. 14).

Namentlich Colchicin, Rhodanammoinum, β-Indolylessigsäure, aber ausserdem viele andere Stoffe sind imstande, solche Wachstumsanomalien hervorzurufen. Es sind unzweifelhaft kleine Unterschiede hinsichtlich der Wirkung dieser Stoffe auf die Wurzelhaare von verschiedenen Pflanzen vorhanden. Man erhält z. B. am leichtesten Anschwellungen bei *Phleum* mit Rhodanammonium, bei *Sinapis* und *Lepidium* dagegen mit Colchicin oder Sublimat. Diese Unterschiede treten aber gegenüber der Übereinstimmung in der Wirkungsweise der verschiedenen Stoffe ganz in den Hintergrund. Wie gross diese Übereinstimmung ist, geht aus Abb. 15 hervor. Mit allen vier Stoffen kann man alle Typen von Verdickungen und Wachstumsanomalien erhalten.[1] In der

[1] Selten können auch in *Lepidium*pflanzen, die in Leitungswasser gelegen haben, ähnliche Typen von Anomalien auftreten wie in Giftlösungen.

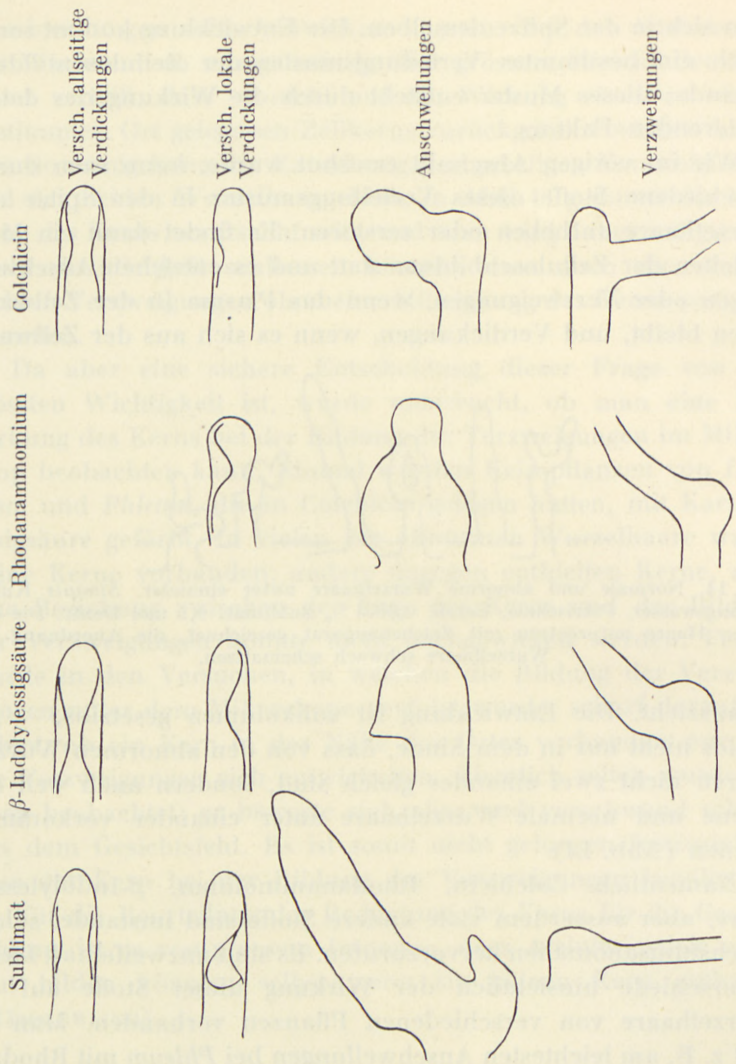

Abb. 15. Abnormitäten, die durch Colchicin, Rhodanammomium, β-Indolylessigsäure und Sublimat in Wurzelhaaren von *Phleum* erzeugt worden sind.

chemischen Konstitution haben diese Stoffe nichts gemeinsam, und es ist daher auch nicht möglich eine Beziehung zwischen Konstitution und Wirkungsweise festzustellen. Nur in einer Eigenschaft stimmen diese Stoffe überein, indem sie in der einen oder anderen Weise als Gifte auf die Wurzelhaare wirken.

Man muss sich daher damit begnügen festzustellen, dass wenn die Wurzel normal ist, auch das Verteilungsmuster der Zellulosenbildner normal ist, wenn aber die Wurzel vergiftet wird, wird das normale Verteilungsmuster zerstört und es entstehen Verdickungen und Wachstumsanomalien der einen oder anderen Art.

Es ist nun von besonderer Wichtigkeit hervorzuheben, dass in den abnorm wachsenden Wurzelhaaren eine Tendenz besteht, den normalen Zustand wiederherzustellen. In Abb. 12 d ist das Wachstum dreimal abgebrochen und dreimal wieder aufgenommen worden. In Abb. 11 g ist die Spitze des Wurzelhaares in einen verästelten Kopf aufgelöst worden; an zwei Stellen des Kopfes schiessen aber röhrenförmige, wurzelhaarähnliche Gebilde heraus. Selbst wenn das normale Muster auscheinend verloren gegangen ist, ist es doch latent vorhanden und kann regeneriert werden.

Es besteht somit ein Kampf zwischen der lähmenden Wirkung des Giftes und dem determinierenden Faktor. Unter dem Einfluss des Giftes tritt eine diffuse Verteilung der Zellulosenbildner in der Spitze des Wurzelhaares ein, unter der Einwirkung des determinierenden Faktors wird aber das normale Verteilungsmuster der Zellulosenbildner wiederhergestellt, indem dieselben an einem bestimmten Ort angehäuft werden, so dass in ähnlicher Weise wie in dem apikalen Ende der Trichoblasten ein Wurzelhaar gebildet werden muss.

Es ist nun von entscheidender Bedeutung, dass der Ort, wo die Zellulosenbildner sich sammeln oder wo sie angehäuft werden, ein ganz zufälliger ist, jedoch liegt er immer innerhalb der Membrankuppe, am häufigsten an der Basis derselben. Die Wachstumsrichtung der abnormen Wurzelhaare ist daher auch eine ganz zufällige. Das geht wieder deutlich aus Abb. 12 hervor. In Abb. 12 e, f ist in beiden Fällen ein Ast nach rechts gebildet worden, von diesem gehen wieder Äste aus, in Abb. 12 e basalwärts, in Abb. 12 f dagegen apikalwärts. Das Wurzelhaar in Abb. 12 d, das dreimal seine Wachstumsrichtung verändert hat, bildet ein Dreieck.

Das Problem ist nun, ob man den determinierenden Faktor mit einem physikalischen Faktor identifizieren kann, d. h. ob es möglich ist, einen physikalischen Faktor zu finden, der die An-

häufung der Zellulosenbildner an einem bestimmten, aber willkürlichen Ort bewirken könnte.

Äussere Faktoren kommen natürlich nicht in Frage, man wird die Faktoren innerhalb der Zelle suchen müssen.

Von inneren Faktoren wäre zuerst an die Lage des Kerns zu denken, es ist aber nicht gelungen, eine Beziehung zwischen der Ausbildung der Wachstumsanomalien und der Lage des Kerns nachzuweisen.

Es bleibt dann die Möglichkeit übrig, dass in den Zellulosenbildnern eine Neigung vorhanden sein könnte, sich an einem willkürlichen Ort zu sammeln.

Man könnte sich vorstellen, dass die Zellulosenbildner ein zusammenhängendes, verschiebbares, kontraktiles System ausmachten. In normalen Wurzelhaaren sollte dieses System sich aus der einen oder anderen Ursache in der Spitze lagern und sich dort halten, indem es sich während des Wachstums der Spitze vorwärts geschoben hätte. In vergifteten Wurzelhaaren sollte es aus unbekannten Ursachen[1] nach unten herabgleiten, doch nur bis zur unteren Grenze der Membrankuppe. Da das System kontraktil ist, könnte es sich an einem zufälligen Ort ansammeln, wo dann ein Seitenzweig gebildet würde. Obwohl eine solche Auffassung in vielen Beziehungen rätselhaft ist, harmoniert sie doch ganz gut mit den gefundenen Tatsachen.

Die grössten Schwierigkeiten entstehen aber, wenn man versucht, diese Auffassung auf andere Zelltypen auszudehnen, indem das Muster der Zellulosenbildner in den verschiedenen Zellen ein ganz verschiedenes ist. In den Zellen, die sich strecken, sind sie ziemlich gleichmässig in der Zellwand verteilt, in den Trichoblasten sammeln sie sich in dem apikalen Ende, in den Wurzelhaaren in der Spitze, und in den Sternparenchymzellen an regelmässig verteilten Orten an der Plasmaoberfläche. In Zellen, wo die Zellulosenbildner sich aus der Zellwand herausziehen und in welchen daher Verdickungen gebildet werden, verteilen sie sich entweder gleichmässig (Steinzellen) oder in Ringen oder Schraubenbändern (Tracheiden und Gefässen). Es wird kaum möglich sein, diese verschiedenartigen Verteilungs-

[1] Die Ursache des Herabgleitens kann kaum eine Lähmung der Respiration sein. In sauerstofffreier Atmosphäre erhält man nämlich Verdickungen, die normal gelagert sind. Ferner wird, wie aus Abb. 12 hervorgeht, das Wachstum nach dem Herabgleiten aufs neue in einer anderen Richtung fortgesetzt.

muster durch physikalische Verschiedenheiten in den betreffenden Zellen zu erklären.

Wenn man den Bau eines lebenden Organismus zu verstehen versucht, begegnet man vornehmlich zwei Probleme: Das erste, welche Stoffe sich in den lebenden Organismen vorfinden und in welcher Weise sie gebildet werden, und das zweite, in welcher Weise diese Stoffe zu dem fertigen Organismus zusammengebaut werden.

Das erste Problem ist allgemeiner Art. Die Gruppen von Baustoffen sind im grossen und ganzen bei allen lebenden Organismen dieselben. Innerhalb der Eiweisstoffe findet sich jedoch eine grosse Anzahl verschiedener arts- und gewebespezifischer Verbindungen. Die Eiweisskörper bilden in der Zelle vielfach bestimmte Muster, und es ist wahrscheinlich, dass die Art der Muster durch die Konstitution der Eiweisskörper bedingt ist. Über die Aufbauvorgänge in den lebenden Zellen wissen wir noch ziemlich wenig. Sicher ist, dass viele plastische Stoffe unter Mitwirkung bestimmter Gene gebildet werden. Auch bei der Bildung der Zellulosen ist der Kern indirekt beteiligt. Die Zellulosen werden jedoch im Plasma gebildet; wie aus den Versuchen mit kernlosen *Acetabularia*stielen (Hämmerling 1953) hervorgeht, können Proteinstoffe gleichfalls in Plasma gebildet werden.

Das zweite Problem, die Sammenfügung der Baustoffe, ist sehr spezifischer Art. Jede Art, in vielen Fällen jedes Individuum, jedes Gewebe und viele Zellen haben je ihr eigenes Muster. Aufgabe der determinierenden oder gestaltbildenden Faktoren, die an das Plasma geknüpft sind, ist es, durch Verteilung der Plasmakomponenten die Entstehung dieser Muster zu ermöglichen. Selbst in dem einfachen Falle, der in dieser Abhandlung behandelt worden ist, ist es nicht gelungen, die Wirkungsweise des determinierenden Faktors zu erhellen. Nichts spricht dafür, dass dieser Faktor, der die Verteilung der Zellulosenbildner hervorruft, ein Stoff ist, der Ausdruck »gestaltbildende Stoffe« ist meiner Meinung nach am besten zu vermeiden.[1]

Die Möglichkeit, dass man in Zukunft die Art und Wirkungs-

[1] Ebensowenig kann man β-Indolylessigsäure, die die Bildung von Seitenwurzeln hervorruft, oder Blühhormone, als gestaltbildende Stoffe bezeichnen. Die betreffende Stoffe lösen nur Wurzel- und Blütenbildung aus, die Gestaltbildung selbst liegt tiefer.

weise der determinierenden Faktoren wird erhellen können, kann natürlich nicht abgewiesen werden. Es ist jedoch nicht ausgeschlossen, dass wir uns hinsichtlich der Lösung dieser Probleme an der Grenze der Forschungsmöglichkeiten befinden.

Dem Carlsbergfond, der mir die für die Untersuchungen notwendigen Instrumente zur Verfügung gestellt und mich auch in anderer Weise unterstützt hat, spreche ich meinen besten Dank aus.

Meiner Tochter, Frau Margrete Ehlers, möchte ich auch an dieser Stelle für ihre gewissenhafte Hilfe bei der Ausführung der Versuche herzlich danken.

8. Summary.

In the root hair the cellulose-building enzymes accumulate on papillae or crests of plasma which protrude into the cell wall in the tip of the root hair. If the root is placed in a solution of Congored the plasma in the tip of the root hair will withdraw from the cell wall, the enzymes will continue their agency and a layer of cellulose will be deposited on the inside of the cell wall. Usually the thickness of the layer is greatest in the extreme part of the hemispherical tip and decreases to its basis. We must therefore conclude that also the amount of cellulose-building enzymes decreases from the extreme part of the tip in a similar manner as the thickening.

If a root is placed in solutions of colchicin, 3-indole-acetic-acid, rhodanammonium, etc., the pattern in which the cellulose-building enzymes are distributed in the tip, can be changed, the enzymes gliding down from the extreme part of the tip to its basis. If the gliding down takes place regularly on all sides of the tip a girdle of cellulose arises at its basis, when the plasma withdraws from the cell wall (fig. 9); if the plasma remains in the wall a more or less regular swelling of the wall arises (fig. 11). More frequently the enzymes gather in an accidental place. If the plasma withdraws from the cell wall a unilateral thickening will be formed (fig. 10), if the plasma remains in the cell wall a ramification takes place (fig. 12). As will be seen in fig. 12 d-f this state is not stable. When the lateral branch has grown a

short distance the enzymes will again glide down from the tip, and having gathered in a place at the basis of the tip a new branch is formed. A struggle is going on between the determinative factor which aims at forming a normal root hair and the paralysing effect of the poison in the solutions.

The mode of action of the determinative factor consists in collecting the cellulose-building enzymes at a definite place. The problem is whether it is possible to identify the determinative factor with a known physical factor. Hitherto it has not been possible to do so, and the possibility exists that concerning this problem we are on the border of the reach of scientific investigation.

Pflanzenphysiologisches Laboratorium
der Universität, Kopenhagen.

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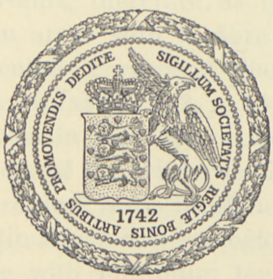
THE EVOLUTIONARY SIGNIFICANCE OF BIRD-MIGRATION

BY

FINN SALOMONSEN



København 1955
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CONTENT

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Adaptive Variation and Migration.

The geographical variation in homoiothermous organisms is not fortuitous, but follows certain ecological rules, of which the most important ones are Bergmann's rule, Allen's rule and Gloger's rule (cf. HUXLEY 1942, p. 211, MAYR 1942, p. 90, DOBZHANSKY 1951, p. 152, RENSCH 1929, p. 131; 1936, p. 317; 1938, p. 364; 1947, p. 40; 1952, p. 137). These rules express correlations between geographical variation and environmental factors. Populations of different species respond to the selective forces of the environment in a parallel way and develop a number of morphological (and physiological) adaptive characters. In species with extensive continuous ranges the variation usually takes place as character gradients (clines), in which the correlation between the geographical differentiation and the gradually changing environment is often very accurate. The ecological rules are apparently of minor importance in the tropics, where the selection pressure of the environment is smaller and the mutation pressure is the main evolutionary factor. In tropical species random fixation of variants, therefore, is much more frequent than in species living in areas with a more severe climate, and consequently environmentally correlated characters are generally of much less significance (RENSCH 1952, p. 141). This corresponds very well with the fact that in birds the ecological rules generally reflect the selective effects of the winter-environment. The character-gradients in non-tropical birds must be regarded primarily as adaptations to the climatical and ecological conditions in the most severe winter-time with minimum temperatures and lack of food as the critical factors; cf. RENSCH 1939, p. 103; 1947, p. 42; 1952, p. 148. HEMMINGSEN (1951, p. 204) in a comprehensive paper on the birds of N. China has stressed similar

points, stating that "if the validity of Bergman's rule for migrants is to be tested—not only in this connection, but on a broad scale—with reference to latitudes, it should be to their winter ranges rather than to their breeding ranges (where also many spend so relatively little of their time)", a conclusion completely in agreement with the view-points which will be advanced in this paper.

The situation, extension and environmental conditions of the wintering grounds of a species is, therefore, of the outmost importance when analysing the evolutionary trends and processes of the species concerned. In migratory species the wintering grounds are completely or partially separated from the breeding area. The evolutionary consequences of this separation form the subject of the following discussion.

Subspeciation in Resident and Migratory Birds.

It is a well-known fact that the geographical variation is distinctly smaller in migratory than in resident birds. Among the palæarctic Passeres the migratory polytypic species possess on an average 3.2 subspecies, while the sedentary ones have 7.2 subspecies (Rensch 1933, p. 19).

The fact that the migratory populations leave the breeding areas and therefore are not subject to the influence of the winter conditions is of importance when discussing the evolution of different species breeding in the same climatical zone. When comparing, as an example, sedentary species of parids and picids, which are distributed over the greater part of the palæarctic region and which are split up in a large number of subspecies, with migratory species like *Jynx torquilla* and *Phylloscopus trochilus* with a breeding range as extensive as that of the former groups but with a very slight geographical variation, it appears that the sedentary species in winter time are exposed to extremely varying life-conditions, ranging from the mild Atlantic climate of Portugal and Ireland to the icy cold of Kamtchatka, while the said migratory species spend the winter in the uniform climate of tropical Africa.

Still more important is no doubt the fact that the scattering

of the migrants in the winter-quarter is much greater than that which takes place in strictly sedentary birds. Almost all results of ringing have demonstrated that the individual scattering in the winter-quarter of migratory birds originating from a circumscribed breeding area is much greater than that of the sedentary birds inhabiting the same area. As an example can be mentioned that sedentary birds inhabiting the Danish island Zealand rarely leave this island (7000 km^2) in winter, while specimens of the migratory Song-Thrush (*Turdus philomelos*), ringed as nestlings in Zealand, have been recovered in the wintertime (Dec.—Feb.) in entire France, Spain and Portugal, and Linnets (*Carduelis cannabina*), breeding in Zealand, have been recovered in winter in an area extending from Belgium to Algeria, just to quote a few examples. The same extensive area is in winter inhabited by a number of other populations of the said species. This shows that the "synhiemic unit", *i.e.* the populations which mix freely in winter, is much greater in migratory than in resident birds, and consequently the populations of migratory birds are not in winter subject to the great differences in the selective influences due to local environmental factors as are the sedentary birds.

The difference in the extent of geographical variation between sedentary and migratory species is usually given another explanation. "It indicates", to quote Mayr (1942, p. 246), "that migration produces greater dispersal and hence decreased subspeciation." When the dispersal, *i.e.* the interchange of individuals in local breeding-populations, is increased, the gene-flow may outweigh the selection-pressure and in this way impede or completely prevent adaptive differentiation. It has, however, not been demonstrated with certainty that the dispersal is particularly greater in migratory than in resident species, although it appears that the area of the effective breeding units[1] is slightly smaller in the latter. The dispersal of the resident species is a result mainly of the individual movements in the off-season, while that of the migratory species depends on their capacity of homing. The adult birds are known generally to return to their nest or its immediate surroundings in spring, but the young birds scatter more or less in the breeding area and in this way give rise to

[1] The "panmictic unit" of Dobzhansky & Wright (1943, p. 335).

a certain diffusion of genes in the population. Boyd & Landsborough Thomson (1937, p. 278) in a study on the recoveries of ringed Swallows (*Hirundo rustica*), an extreme long-distance migrant, found that 72 % of the one-year old birds bred within a radius of 25 km from the nest in which they were hatched, the greater part (38 %) within a radius of 3 km. The remaining young birds scattered in a larger area, but only exceptionally settled beyond 100 km from their place of hatching. In a partly sedentary population of the Song-Sparrow (*Melospiza melodia*) the dispersal of the yearlings was distinctly smaller, the young birds settling usually less than 1.4 km from the nest, the greater part within a radius of 500 m (Miller 1947, p. 188). A similar result was recently achieved by Kluijver (1951, p. 13) as far as the Great Tit (*Parus major*) was concerned, in a population which was strictly resident. He found that the majority of the young birds settled to breed withing 2 km of their place of hatching, but a few were recovered in the breeding-season as far as 25 km from the area in which they were hatched. Compared with the dispersal of the Swallow there is a pronounced difference. Von Haartman (1949, p. 52) in a comprehensive paper on homing in the Pied Flycatcher (*Muscicapa hypoleuca*) gives the percentage of vernal returns of young birds in a number of species in which the movements have been thoroughly studied by means of ringing (usually with coloured rings). There is a considerable variation, but the difference between resident and migratory species is negligible. In migratory species returns of young birds in spring to a limited check area amount to 3 % (*Sturnus vulgaris*, Letland), 8 % (*Fringilla coelebs*, Finland), 1 % (*Muscicapa hypoleuca*, Finland), 6 % (*Phoenicurus phoenicurus*, Holland), 10 % (*Iridoprogne bicolor*, Connecticut), etc., while the corresponding figures in resident birds are 12 % (*Melospiza melodia*), 1 % (*Parus inornatus*, California), 10 % (*Erithacus rubecula*, England). I agree with Haartman when he says that the percentage of returns is scarcely higher in the resident than in the migratory species. Nevertheless, there may possibly be a somewhat greater percentage of returns in the sedentary species studied, but a number of grave sources of error, enumerated by Haartman p. 54, obscure the comparison.

Although far from conclusive the results of the investigations on ringed birds, so far carried out, show a tendency in sedentary populations to smaller dispersal and hence greater probabilities for adaptive differentiation. The tendency, however, is too slight to explain the pronounced difference in geographical variation between migratory and sedentary birds. This difference is probably mainly due to the much larger size of the "synhiemic units" in the migratory than in the sedentary species. In addition, it is of importance that the migratory populations evade the pessimum conditions of the winter season by moving to areas with a milder climate, where the selection-pressure is much smaller, and where life-conditions are more uniform. The comparative size of the synhiemic unit is a more essential evolutionary factor than the environmental differences. This is demonstrated in species belonging to migration-type VI, discussed on p. 28, below.

The Rôle of Competition.

The evolutionary significance of interspecific competition has been emphasized particularly by Lack (*e.g.* 1944, 1949, 1951). Subsequent to geographical isolation and development of full specific diversity the next step in speciation, when the two hitherto isolated species come into contact, will be—and necessarily must be—development of differences in ecology, usually in habitat selection. This theory appears to give a satisfactory explanation of the ecological diversification of closely related sympatric species. The selective effect of inter-specific competition must consequently be considerable, a view-point which is not shared by all students, however. Udvardy (1951, p. 113) sharply criticises the competition concept, concluding that "it has not been possible to prove in one single case that the competition between species has any important influence upon the distribution ecology of European bird life". It must be admitted that it is difficult to demonstrate competition in action, "because its importance becomes obvious only when it is either lacking or reduced to a minimum" (Mayr 1942, p. 272). The reason for this is no doubt

that competition is not a "proximate" but an "ultimate" factor[1], which in a stable environment has produced a balanced equilibrium among the synecological species. Every change would therefore be a disadvantage and would result in a reversion to the original condition.

An analogous phenomenon is the appearance in wild populations of mutations; these are usually deleterious and the mutants are eliminated. This fact in former days gave rise to one of the main objections against the acceptance of mutations as being of any significance for evolution. The critics against the competition concept has a similar background.

The importance of competition appears when a change takes place between the competing species. Changes of this kind can be found when a species is followed to other geographical areas, just as the principles of speciation can be studied by following the geographical variation. Very little is gained in this respect by studying a local fauna, neither concerning speciation nor competition. It is necessary to compare the local conditions with those which are present in other localities. It can be demonstrated in a number of cases that in areas where a competitor is present a shift in ecology takes place in the species concerned. LACK (1944) has enumerated a number of the known cases and particularly draws attention to the geospizids, species of *Zosterops*, *Acanthiza*, *Dicrurus* and *Lalage* and the well-known case of *Fringilla coelebs* and *F. teydea*. I have added a number of cases of competition among arctic birds (*Somateria mollissima* and *S. spectabilis*, *Phalaropus lobatus* and *Ph. fulicarius*, *Falco peregrinus* and *F. rusticolus*, *Rissa tridactyla* and *Sterna paradisaea*, the *Stercorarius* species, and others (SALOMONSEN 1951). Finally, VAURIE (1951, p. 163) has presented a very fine example, *viz.* the two Nuthatches *Sitta tephronota* and *S. neumayer*. Cf. also MAYR (1948, p. 212—218), who recently has discussed the problem of competition.

It is most likely to assume that the ecological differences be-

[1] These handy terms were coined by BAKER (1938, p. 161) for a special situation, but used in a wider sense by LACK (1950, p. 307) and others. The ultimate factors denote the biological expediency or aim (the survival value), the proximate factors the releasing mechanisms. However, the number of causalities in biological phenomena are not exhausted by the distinction between proximate and ultimate factors.

tween two sympatric species are preceded by a certain degree of pre-adaptation. This took place while the two species were geographically isolated and was an unavoidable result of intra-specific competition. It is highly improbable that the ecological development should be exactly similar in two completely isolated species.

LACK (1944, p. 276) has drawn attention to the important point that related species, which in the breeding season are separated from each other by habitat differences in the wintering grounds are isolated geographically. On the basis of this evidence he draws the conclusion "that such closely related species are potential food competitors in winter and so have evolved geographical isolation at this season as a result of differential adaptation". Independently of LACK I have arrived at the same result. I want to quote this paragraph here in full as it contains certain statements which will be further dealt with below.

"It appears as if the extensive bird-migrations involve an unnecessary waste of time and energy. The irresistible urge of migration no doubt carries the birds further than it seems necessary when the question is to find an adequate climate and sufficient food. Why continue to S. Africa when the subtropical N. Africa offers just as good life-conditions? However, the migration of a species should not be singled out, but must be viewed in comparison with that of its relatives. With an even distribution of the different allied species over extensive continents the food resources can be utilized in much larger areas than if all migratory species were crowding in a smaller but not so distant region. The segregation of the migratory species is not arranged in conformity with the taxonomic units, in the sense that each family or genus has its own wintering area. On the contrary. The different species within a genus are generally the closest competitors for food, and hence they segregate in winter over as large areas as possible, each species occupying a separate part of the area. Typical examples are found in the genera *Anas*, *Larus*, *Calidris*, *Anthus*, *Phylloscopus*, *Lanius*, *Emberiza*, etc., the members of which often vary from being residents in arctic or temperate regions to long-distance migrants which move to the tropics or even further. In many instances the greatest differences in the migration pattern is found between the most closely related species, *e. g. Larus fuscus* and *L. argentatus*." (SALOMONSEN 1950, p. 311; translated from Danish).

It can safely be assumed that the spatial segregation in the wintering grounds in some way or other has influenced the

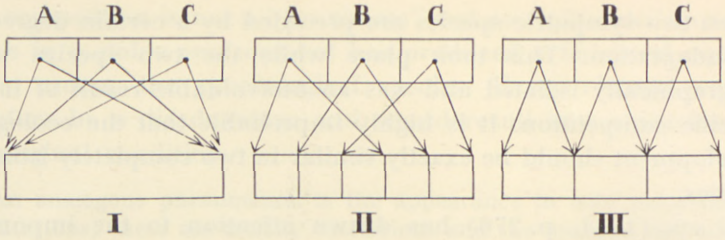

Fig. 1. Migration of three neighbouring populations (A, B, and C), left (I) showing synhiemy, right (III) allohiemy, centre (II) being intermediate. The upper rectangles symbolize the breeding areas, the lower ones the winter-quarters. The scattering in winter of the individuals belonging to the different populations is shown by the arrows.

evolution of the species in question, *i.e.* has contributed to change the genotype. In order to further elucidate this problem it is necessary to study the phenomenon at a more elementary stage and turn the attention to the intraspecific competition in wintering populations.

Spatial Segregation of Wintering Populations.

It would be very inconvenient if all populations of a given migratory species spent the winter in a restricted area. This would result in a devastating competition for the limited resources of the wintering ground and give rise to other deleterious effects of overcrowding. Most species avoid this development by scattering over so wide an area as possible. The limits of the winter range are conditioned mainly by competition with other species (cf. above, p. 9), geographical barriers and various extrinsic (*e.g.* climatical) factors.

Competition for food is probably the primary reason for the wide dispersal in the off-season. In a number of species breeding in the Arctic, scarcity of food in the breeding-places in summer keeps the population size within narrow limits, and hence their winter-quarters are often of a modest extension (many diving ducks and geese)[1]. This is, however, not the normal situation.

In many species the different populations mix freely in the

[1] STRESEMANN (1934, p. 668) gives some other instances of a restricted winter-quarter.

entire wintering ground. Populations which in this way are united in a common winter-quarter (are components of a "synhiemic unit") I propose to call *synhiemic*. Ordinarily the dispersal in winter has been achieved by a spatial division of the available wintering grounds among the different populations. Such populations, which have separate winter-quarters, are here called *allohiemic*. In some species the populations hold an intermediate position between the state of synhiemy and allohiemy, in other species some populations are synhiemic while others are allohiemic. To make the difference between these concepts clear a case of synhiemy, a case of allohiemy and an intermediate stage in three neighbouring populations (A, B, and C) are shown in fig. 1[1].

The distinction between synhiemic and allohiemic populations is important when discussing the evolutionary significance of migration. Both synhiemy and allohiemy have certain advantages, as will be shown below. In most species a certain degree of allohiemy will no doubt gradually be established. Selection will produce various hereditary differences between individuals belonging to different allohiemic populations, in direction and choice of migration route, in time and speed of migration, *i.e.* in the strength of the urge or instinct of migration, and finally in the adaptation to local climatic and other environmental factors in the winter ground. Ringing of American Passeres (*e. g. Zonotrichia albicollis*) has shown that the same individuals return year after year to a restricted winter-quarter (Baldwin 1921, p. 236, and others). Similarly, recent experiments with transported birds have demonstrated that a number of species (gulls, Coot, etc.) possess a homing faculty also in the wintering grounds, just as in the breeding grounds (Rüppell & Schifferli 1939, p. 224; Petersen 1953, p. 153). It is important, however, that the homing capacity in winter was much greater in adult birds than in young birds in their first winter (Petersen, *l. c.*). Consequently, the immature birds to a considerable extent scatter in the wintering grounds and in this way strongly reduces the effects of allohiemy. This phenomenon can be compared

[1] When nothing else is stated the figures are original. I am indebted to Mr. Erik Petersen for his careful drawing of the diagrams and maps. My thanks are also due to Ejnar Munksgaard, Publishers, for the loan of the block to fig. 8.

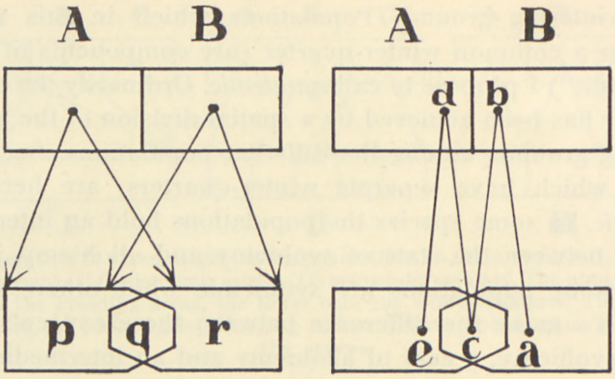

Fig. 2. Migration of two partly allohiemic populations (A and B). For further explanation cf. text p. 12—13.

with the dispersal of young birds in the breeding area, as discussed above (p. 6).

Isakov (1949, p. 54), on the evidence of ringing results, is of the opinion that most species of birds form minute fixed, so-called elementary populations. The members of these populations not only breed in the same limited area but follow the same migration route and winter in the same area. They have a synchronous biological rhythm just as is the case in various micropopulations of certain migratory fish. However, in birds such conditions are developed only in rare instances. What concerns us here is the fact that only in species which are divided into so small units the populations display virtual allohiemy in the strictest sense of the word (without scattering). It should be borne in mind that the difference between allohiemy and synhiemy is one of degree. No doubt the greater part of migratory birds display a partial allohiemy, holding an intermediate position, as shown in fig. 1, II. Allohiemy does not need to be complete in order to affect evolution. In winter (which here means the non-breeding season) selection is the only genetic factor involved, and the influence of the selection-pressure cannot be hampered or impeded by disturbing mutations or by gene-flow.

Let is now consider two populations, A and B, which are partially allohiemic, *i. e.* of the intermediate type shown in fig. 1, II. In fig. 2, left, is shown the scattering in the winter grounds of the individuals coming from a locality in the breeding area of

A and from one in the breeding area of B, respectively. It appears that the two populations overlap considerably in the winter grounds. This is one of the most common distributional types among migratory birds. If adaptive differences have developed between A and B owing to selection in the winter-quarters, the populations of p and r will never reach a stage of stability under the circumstances presented in fig. 2. Dispersal from the zone of overlap (q) will steadily tend to counteract the work of selection by mixing the populations A and B. If the differences in selection-pressure are sufficiently great such stragglers will be eliminated owing to the minor survival value of their genotype. Before this, however, they may very well have contributed to gene-flow between A and B. This situation is shown in fig. 2, right. A specimen belonging to population B, having wintered at "a" breeds at "b". Owing to the normal scattering of the immature birds the offspring of the said individual winters at "c", which locality is situated in the zone of overlap, where the survival value of the B-genotype is not virtually reduced. Next spring the bird migrates from "c" to "d", which is situated in the breeding area of A. This is a normal procedure, due to the usual dispersal of first year birds. The locality "d" is the breeding place of our bird, which originally was a member of the population B. In this way the individual in question contributes to furnish the gene-pool of A with genes of B. Some of the offspring, carriers of B-genes, may winter at "e", where their genotype will be inferior if the difference in selection-pressure between A and B is strong. The steady mixing of A- and B-genes will in a case like that shown in fig. 2 prevent subspeciation, at least in the sense in which it is usually applied in ornithology. However, the selection in the winter-quarters will nevertheless leave its mark and produce a cline, but with a broad overlap of its characters. Under the circumstances discussed above a subspeciation will be possible only when the zone of overlap (q in fig. 2) is sufficiently narrow or in any other way the interchange of individuals between A and B is limited, *i. e.* if the differences in selection-pressure between the population of p and r, respectively, outweigh the effects of dispersal.

The evolutionary effects, described above, have been due to the influence of selective forces in winter only. Naturally this

does not imply that conditions in summer (*i. e.* the breeding time) are without importance. The discussion has shown, however, that notwithstanding the evolutionary activity in the breeding population, alone the spatial segregation of the populations in the winter-quarter may have important evolutionary consequences and suffices to change the genotype, provided that the degree of allohiemy is tolerably great.

When discussing the variation in migratory birds it is necessary to consider the conditions both in the breeding area and in the wintering grounds. In accordance with this view we can conclude that the evolutionary processes in a migratory bird is influenced by the following factors:

1. Rate of mutations (mutation-pressure).
2. Selective processes (selection-pressure).
3. Degree of dispersal, causing gene-exchange (being nil in completely isolated populations).
4. Numerical size of the breeding unit (Sewall Wright effect).
5. Limitation of the synhiemic unit, *i. e.* the degree of allohiemy.

Granted that the mutation-pressure is negligible, that the numerical size of the population is fairly large, that allohiemy is present and that random dispersal in the breeding area is slight, the following four possibilities exist for the development of adaptive diversity between two populations (A and B) of a migratory species:

I. The difference in selection-pressure (by environment) between A and B is great in the breeding area but slight in the wintering ground. In this case the adaptive variation will be a result mainly of the conditions in the breeding area.

II. The difference in selection-pressure by environment between A and B is great in the wintering grounds but slight in the breeding area. In this case the adaptive variation will be a result mainly of the conditions in the wintering ground.

III. The difference in selection-pressure (by environment) between A and B is great both in the breeding area and in the wintering ground. In cases like this the adaptive variation will reflect the conditions in both areas, sometimes with both in-

fluences equally manifested, sometimes one more prominently than the other.

IV. The difference in selection-pressure (by environment) between A and B is slight both in the breeding area and in the wintering ground. In this case the adaptive variation will be slight and the possibility for fixation of random variants is considerable.

Of these four theoretical possibilities, present in "ideal" populations, the second is the one which is most often realized in nature, thus demonstrating that the selective forces in the winter grounds are among the most potent agencies in the evolution of migratory birds.

Synhiemic populations follow the first possibility (evolutionary type I). They are subject to the influences of the same environment in winter and, consequently, the natural selection by environment must be much reduced. Any differences in the adaptive variation of A and B must be due to differences between the selective influences in the respective breeding areas.

Synhiemic Populations.

When individuals belonging to different populations do not show any morphological differences the only way to decide whether they are allohiemic or synhiemic is by means of recoveries of ringed birds. The results of ringing have demonstrated that the populations in a number of sea-birds are synhiemic. As a good example of this the European populations of the Sandwich Tern (*Sterna s. sandvicensis*) can be mentioned. In fig. 3 the recoveries of birds ringed in Denmark, N. Germany, Holland and England are plotted, and it appears distinctly that all these populations winter in the Benguella Current along tropical W. Africa and S.W. Africa, where they mix freely. So far as can be judged on the evidence of the ringing records the populations in question are completely synhiemic. This is no doubt the case also in many other terns, in which, however, ringing has not yielded equally conclusive results. It is worth

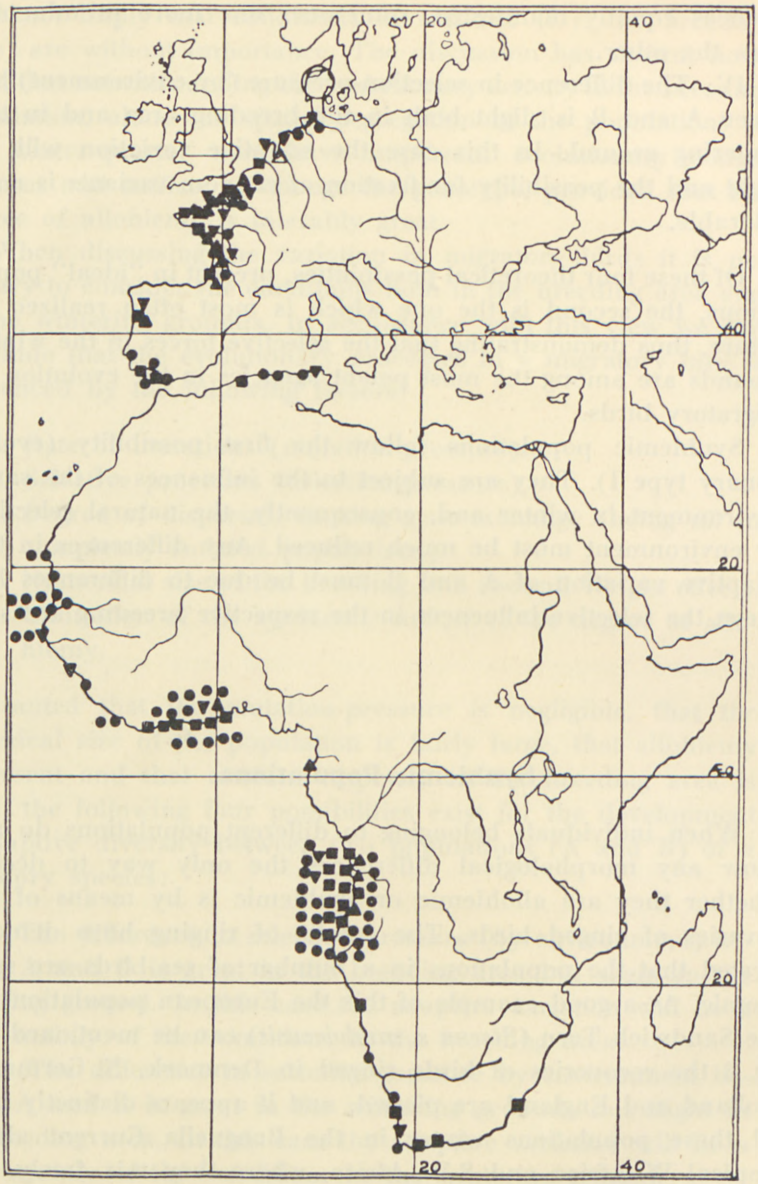

Fig. 3. Recoveries abroad of Danish, German, Dutch and English Sandwich Terns (*Sterna sandvicensis*). Open signatures indicate areas of ringing, solid signatures corresponding recoveries. (After F. Salomonsen 1953.)

mentioning that all Scandinavian populations of the Common Tern (*Sterna hirundo*) appear to winter in the coastal waters of S. Africa. In the Cape Province there are winter recoveries (Oct.–April) of 1 Danish, 1 Norwegian, 4 Swedish and 7 Finnish specimens. Of the closely allied Arctic Tern (*Sterna paradisaea*) there are winter recoveries in S. African waters not only of birds originating from European breeding-places but also from N. America and Greenland. Probably all Atlantic populations of this species are synhiemic, wintering in S. African and antarctic waters. The American populations of the Common Tern differ in their migration pattern considerably from the species mentioned. AUSTIN (1951, p. 1), on the basis of very extensive ringing, concludes that the Common Tern of the Western Hemisphere displays a certain amount of "group-adherence" which persists even in the winter-quarter. Presumably this phenomenon will gradually lead to allohiemy. AUSTIN in another paper (1953, p. 39) demonstrated that this development has actually taken place. The birds from the colonies on the Atlantic coast winter in the W. Indies going southwards to Brazil, those from the interior breeding-places winter at the Gulf coast westwards to Florida, while a certain number continue to Central America where some individuals even cross the isthmus of Panama to winter at the Pacific coast south to Peru. The allohiemy of the two populations is partial; there is some overlapping. "Even when the bulk of the recoveries from any group has been made in one restricted area, some of the others are frequently scattered in faraway places" (AUSTIN 1953, p. 44).

The populations of a number of N. Atlantic sea-birds show a pronounced synhiemy. Ringing has shown that this is the case in *Rissa tridactyla*, *Uria lomvia*, *Fulmarus glacialis*, *Gavia stellata* and others. European specimens cross readily the ocean and have been recovered along the N. American coasts.

The type of synhiemy developed among the populations of terns and other sea-birds mentioned above is outlined in fig. 4, I. It shows that neighbouring populations (or rookeries) intermingle in a common extensive winter-quarter, where the individuals mix freely. There is no spatial segregation of the different populations, but the adequate utilization of the available food-resources is secured by an even dispersal of the individuals over

wide areas, in this way preventing large concentrations in any one locality[1].

The most important consequence of synhiemy is the fact that the populations involved share the same habitat in winter and hence are subject to similar environmental influences. Consequently, selection cannot give rise to any adaptive differentiation. The result will be that species with synhiemic populations are monotypic or, at most, show only a slight geographical variation.

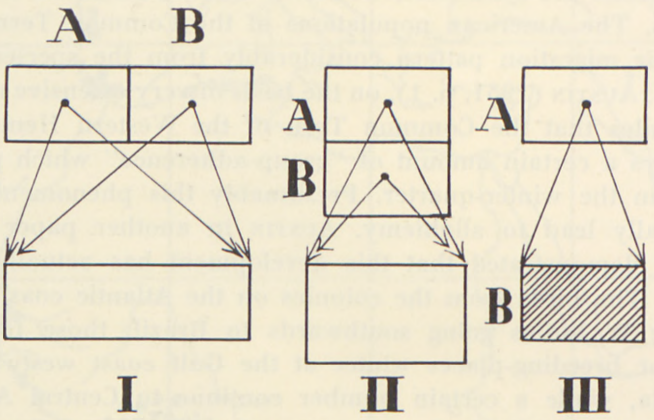

Fig. 4. Three types (I—III) of migration in synhiemic populations. Hatching indicate a resident population. For further explanation cf. text to fig. 1, p. 10.

The adaptive differentiation in these species is due exclusively to selective forces working in the breeding-area (cf. below, p. 21, on *Fulmarus*).

It is possible that the dispersal of the individuals in the breeding area is greater in synhiemic than in allohiemic populations, but the evidence available does not favour this view. As far as we know the homing faculty is equally finely developed in both groups. Ringing of a large number of *Rissa tridactyla* in Greenland has shown that the immature birds wander far and wide on the Atlantic and do not return to the breeding place in the first summer. However, in spite of the long absence and the extensive movements on the ocean, when they are two years old they return regularly to the area in which they hatched (Ber-

[1] This is of course dependent on the distribution of the food. In areas rich in food (like the Newfoundland waters) large concentrations of birds may occur.

TELSEN 1932, p. 37); the places of recovery were all situated within 50 km of the place of hatching. It appears, however, that the adherence to the breeding-place is rather unstable in many colonially breeding sea-birds, *e. g.* the Sandwich Tern. In this species the dispersal is rather wide. There are two instances of a specimen ringed in northern Jutland, Denmark, in subsequent years being recovered as breeding in N. W. Germany (Mellum). Species, in which this phenomenon is common, have few possibilities of development of geographical races. Only few instances of long-distance dispersal in the breeding area are known. A very pronounced example offered a Ruff (*Philomachus pugnax*) ringed as nestling in Denmark, recorded in the breeding-time at Archangelsk in N. Russia[1]. This case may be indicative. The Ruff has an enormous breeding area and yet does not show any geographical variation. However, we do not know whether its populations are allohiemic or synhiemic.

Strict synhiemy is developed in the populations of the herbivorous birds which like the Waxwing (*Bombycilla garrulus*), the Crossbill (*Loxia curvirostra*) and a number of finches, tits, etc., undertake irregular irruptions over wide areas in correlation with fluctuations in the crop of their food-plants. Ringing has revealed some facts about the movements of such species. In the case of the Waxwing a specimen ringed in winter in Poland was recovered the subsequent winter at Chita in eastern Siberia, 5700 km distant. This implies synhiemy among widely scattered populations. In the Crossbill a case of long-distance dispersal is known, *viz* a specimen ringed as nestling in Denmark, recovered two years later breeding in Czeckoslovakia. A similar case is known in the Coal-Tit (*Parus ater*), of which species a Czeckoslovakian specimen was found breeding in Switzerland after an irruption. The nomadic populations of these species are characterized by absolute synhiemy and excessive dispersal, hence they do not show any subspeciation[2].

A sort of synhiemy is found in the populations of most ducks, this holding good of both surface-feeding and diving ducks. The populations are often allohiemic, but the dispersal (of the males)

[1] STRESEMANN (1934, p. 686) mentions a few other examples of long-distance dispersal.

[2] Many of these species possess a number of resident or normally migratory populations, which may form distinct subspecies.

in the breeding areas is extraordinarily great, and this results in a subsequent mixture of the populations in the winter-quarters, which makes the allohiemy illusory. The extensive dispersal is due to a peculiar migration pattern in these birds for which LANDSBOROUGH THOMSON (1931, p. 382) has proposed the term "abmigration". The chance for adaptive differentiation in species with abmigration is practically nil. In most ducks the populations of the New and Old World keep separate and often form distinct subspecies. In some few species, however, the abmigration covers all populations, which implies that the panmictic unit ranges through the entire holarctic region. The Long-tailed Duck (*Clangula hiemalis*) exhibits probably the most extreme case of this development. This is evidenced by some interesting recoveries of ringed birds. A number of nestlings were ringed at Disko Bay, West Greenland in 1947. Of these birds one was recovered in 1950 as a breeding-bird in N.W. Canada, not far from the Alaskan border, where the local populations move to the Pacific in winter. Another specimen was recovered in Jan. 1951, wintering in the southern Baltic Sea, where the winter-visitants of this species usually originate from N. Russia, as evidenced by ringing (cf. SALOMONSEN 1952, p. 113; & 1953, p. 134). Russian birds will easily mix with Siberian birds wintering in the Pacific. This shows that the Long-tailed Duck in a few years' time obviously is capable of undertaking a circumpolar "migration".

A pronounced synhiemy appears to be present among the populations of a number of waders, just as in most sea-birds, but the ringing results are usually not conclusive. Owing to extensive ringing of the Dunlin (*Calidris alpina*) it is possible to say that the populations passing Denmark, Sweden and Norway, respectively, on migration, mainly are synhiemic, although the Norwegian birds differ slightly from the Swedish-Danish ones (SALOMONSEN 1953, p. 156).

Lack of recoveries in the tropics makes it difficult to form any idea of the type of wintering in the African winter-visitants. Ringing has yielded good results only in a few cases. The populations of the Stork (*Ciconia c. ciconia*) are synhiemic, while those of the Swallow (*Hirundo rustica*) display a distinct allohiemy (maps and description by SCHÜZ 1952, p. 53).

Allohiemy is present in the greater part of the polytypic species with more than one subspecies wintering in tropical Africa, sometimes, as in the case of *Phylloscopus trochilus* and its races (*trochilus*, *acredula* and *yakutensis*) with a broad zone of overlap (q in fig. 2) between the winter-ranges of the races (cf. TICEHURST 1938, p. 33—38). The subspecies of its near ally *Ph. borealis* (*viz: borealis*, *examinandus*, *xanthodryas* and *kennicotti*), which all winter in Malaysia and the Philippines, appear to be synhiemic, but the winter-range is not properly worked out. A pronounced synhiemy is displayed also by the members of the variable group *Motacilla flava*. In Kenya Colony in British East Africa no less than 5 forms are known to winter (*flava*, *thunbergi*, *beema* (rare), *lutea* and *feldegg*). The synhiemy is not absolute, but two forms at least appear to share the same winter-quarter in most districts of Africa and India. The evolutionary history of *Motacilla flava* is very complicated. The capricious combination of clear-cut colour patterns is apparently due to random fixation of mutants, but the plumage design can of course form the exterior manifestation of the presence of genes with certain pleiotropic effects on adaptation. At any rate, the geographical differentiation in this puzzling group of birds has a historical background and is due to factors which have worked in several isolated breeding areas. It is hardly possible that influences originating from conditions in the winter habitat have played any part in this development.

When synhiemic populations display morphological differences and these are not the result of a former isolation of the populations, they must be due to adaptive variation in the present breeding areas. A subspecific differentiation often takes place when the breeding areas of the two populations are situated in widely differing life-zones. An example of this type is shown in fig. 4, II. The breeding areas of the two synhiemic populations A and B are situated in different latitudes and therefore, presumably, must be subject to considerable differences in temperature conditions, etc.

A development along these lines has taken place in a number of palæarctic and nearctic birds. The two Atlantic populations of the Fulmar (*Fulmarus glacialis*), *viz*: *F. g. glacialis* and *F. g. minor*, are synhiemic in the off-shore and pelagic zones of Labrador and Newfoundland. The short-billed *F. g. minor* (which follows Allen's rule) breeds in the high-arctic region, the nominate form in low-arctic and boreal environments. The races of *Phylloscopus borealis* form another example. The populations breeding

in various Pacific areas (Japan, Kamtshatka, Alaska) differ from those breeding in Siberia[1].

In some species the synhiemic subspecies follow Bergmann's rule. This rule denotes that in a species the body-size (in birds usually measured by the wing-length) increases with decreasing air-temperature of the habitat. In populations inhabiting more northern regions the body-size is therefore often larger than in those living further south. An example of synhiemic populations which follow Bergmann's rule is offered by the Cuckoo (*Cuculus canorus*). The larger northern subspecies (*C. c. canorus*) and the smaller Mediterranean one (*C. c. bangsi*) are apparently synhiemic, both wintering in tropical Africa.

A special case of synhiemy is developed in species in which a northern migratory population winters in the area of a southern sedentary form (cf. fig. 4, III). In the following examples the synhiemic populations follow Bergmann's rule:

	Northern migratory form:	Southern sedentary form:
Acrocephalus orientalis	*orientalis*	*harterti*
Pyrrhula pyrrhula	*pyrrhula*	*minor*
Anthus richardi	*richardi*	*rufulus*
Dicrurus leucophaeus	*leucogenis*	*bondi*
Ninox scutulata	*scutulata*	*borneensis*
Butorides striatus	*amurensis*	*javanicus*
Egretta alba	*alba*	*modesta*
Ixobrychus minutus	*minutus*	*payesii*

A number of other instances might be cited, but they are not all as typical as those mentioned above. In some cases the morphological differences among the synhiemic populations are very great, as *e. g.* in the forms of the Paradise Flycatcher (*Terpsiphone paradisi*), in which the distinct *T. p. incei* and *T. p. atrocaudata*[2] winter in Malaysia among the sedentary *T. p. affinis*. In other cases the synhiemic populations do not differ at all, as *e. g.* in a number of species of which the Scandinavian migratory populations winter in Great Britain among the in-

[1] I want again to emphasize that this is not a good example since the winter distribution of the populations of *Phylloscopus borealis* is not properly worked out; some of them may be allohiemic.

[2] *Terpsiphone paradisi incei* and *T. p. atrocaudata* are allopatric, but the latter is usually considered a full species.

digenous resident birds; in the Starling (*Sturnus v. vulgaris*), however, the two populations display important differences in physiology (cf. Bullough 1946, p. 165).

When comparing the status of allohiemic and synhiemic populations it is obvious that the greatest amount of evolutionary potentiality is available to allohiemic populations. In synhiemic populations, on the other hand, the intrapopulational variability in winter is much greater (best to be seen, of course, when the populations are subspecifically different), because the variability is not reduced by local differences in the selection pressure in winter-time (cf. p. 15). The main advantage of synhiemy is consequently to be sought in the fact that a larger number of gene-combinations, with a greater variation in adaptive value, will be preserved than under the rigid system of allohiemy. This is of particular importance in case of environmental changes.

Longitudinal Migration of Allohiemic Populations.

The arrangement of allohiemic populations in the winter grounds is much more varied and more complicated than in the case of the synhiemic populations[1]. The forms of migration which lead to allohiemy can be divided into four groups: 1. Longitudinal Migration, 2. Parallel Migration, 3. "Leap-frog" Migration, and 4. Crosswise Migration. These terms are rather inappropriate and have been chosen only for the sake of brevity. The longitudinal and parallel types of migration occur much more frequently than the two other types.

The term "Longitudinal Migration" is just a brief designation for the type of migration in which the migratory populations move along the same degree of longitude. Actually, this category comprises the cases in which one of the two populations concerned breeds under more unfavourable life-conditions, primarily at lower air-temperatures, than does the other population. Such conditions are generally found further north, but the term "longitudinal" should not be applied too literally. The lower

[1] "Allopatric diversity has one more dimension than the sympatric one"; Dobzhansky 1951, p. 136.

temperatures may prevail to N.E., as is very often the case in Europe.

In the following discussion the adaptive variation will be tested in its accordance with Bergmann's rule. This rule, working with quantitative measurements, is the most suitable for a comparison of populations, and the size differences are obviously of adaptive significance.

Types of longitudinal migration are shown in fig. 5. In migration type IV the population (A) which has the northernmost

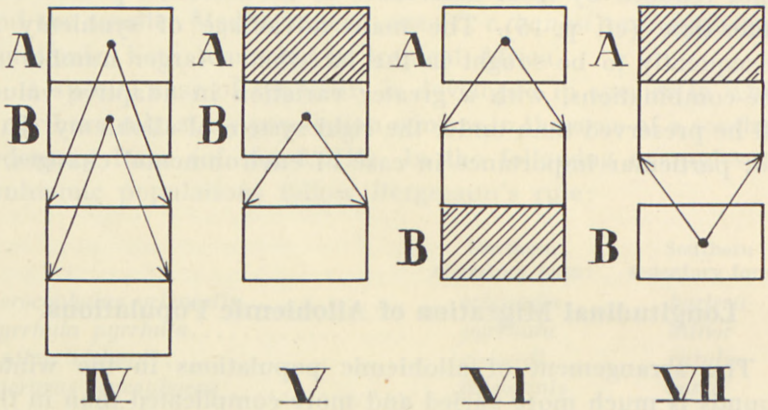

Fig. 5. Four types (IV—VII) of longitudinal migration in allohiemic populations. Hatching indicates a resident population. For further explanation cf. text to fig. 1, p. 10.

breeding area has also the northernmost wintering ground, *i. e.* the winter-quarters of the two populations A and B are situated in the same latitudinal sequence as are the breeding areas. In this migration type the selective forces in the breeding area and in the winter-quarter, respectively, affect the populations in a parallel way and hence sum up their influences. Good examples of species which follow this type of migration are found among American fringillids, as *e. g. Carduelis hornemanni* (*hornemanni* and *exilipes*)[1], *Carduelis flammea* (*rostrata* and *flammea*) and *Aimophila aestivalis* (*bachmanni* and *aestivalis*). *Anser caerulescens* (*atlanticus* and *caerulescens*) could also be mentioned. Of Old World instances can be mentioned *Tringa totanus* (*robusta* and *totanus*), *Turdus musicus* (*coburni* and *musicus*), and *Muscicapa*

[1] The populations are given in brackets, "A" being the first mentioned.

parva (*albicilla* and *subrubra*). The variation in all these species are in agreement with Bergmann's rule.

This migration type (IV, in fig. 5) is not so commonly established as should be expected. The populations frequently have a tendency to synhiemy in such cases, as shown by ringing in the Scandinavian and Central European populations of *Fringilla doelebs, Turdus philomelos, Ardea cinerea, Anas platyrhynchos, Anas crecca, Columba palumbus, Vanellus vanellus* and many others. In other cases the southern population (B in fig. 5) is resident and is synhiemic with the northern one (A), which winters in the area of B. This gives the migration type III (cf. fig. 4). Of the numerous examples of this type can be mentioned the large number of species in which the Scandinavian populations winter among their sedentary congeners in the British Isles (cf. above, p. 22), and among American birds the Alaskan species wintering among the sedentary populations of California.

In another type of migration (V in fig. 5) the northern population (A) is resident, while the southern one (B) is migratory. In such cases the difference in selection-pressure (by environment) between A and B is greater in the wintering grounds than in the breeding areas, and consequently the adaptive variation will be a result mainly of the conditions in the wintering grounds (evolutionary type II; cf. p. 14). The following species can be mentioned as examples:

	Northern, resident form:	Southern, migratory form:
Melospiza melodia	*sanaka*	*melodia*
Anthus spinoletta	*kleinschmidti*	*littoralis*
Sturnus vulgaris	*faroensis*	*vulgaris*
Anas platyrhynchos	*conboscas*	*platyrhynchos*
Mergus serrator	*schioleri*	*serrator*
Phalacrocorax carbo	*carbo*	*sinensis*
Haematopus ostralegus	*occidentalis*	*ostralegus*
Fratercula arctica	*naumanni*	*grabae*
Uria aalge	*hyperborea*	*aalge*
Plotus alle	*polaris*	*alle*

In all species in this list the populations have responded in conformity with Bergmann's rule, the northern form being the larger. In some of these species, however, the two populations are not quite comparable from an evolutionary point of view.

This holds good of the species with an endemic sedentary population in the Faeroes (*Sturnus vulgaris*, *Anthus spinoletta*) and the Aleutians (*Melospiza melodia*). These populations are completely isolated (*i. e.* dispersal from neighbouring populations is practically non-existent) and are numerically small and therefore subject to the Sewall Wright effect. In the large continental populations, with which they are compared, these factors are of no influence. A similar difference, although not so pronounced, exists between the Central European and the Iceland populations of *Tringa totanus* and *Turdus musicus*, dealt with above (p. 24). Most of the other "A"-populations are northern sea-birds in which the breeding-area usually is isolated from that of the southern migratory B-population. However, this does not necessarily need to be so. In the North American Herring-Gull (*Larus argentatus smithsonianus*) three groups can be distinguished, according to Eaton (1934, p. 70). The populations breeding along the Atlantic coast from New Brunswick to Massachusetts undertake extensive first-year migrations southwards along the coast, often reaching the Gulf States. The populations breeding in the interior continent, around the Great Lakes, are characterized by a wide dispersal during the first winter throughout eastern North America, from James Bay south along the rivers to the Gulf Coast of Texas and Mexico. Finally, the northern populations, breeding in the St. Lawrence region, are resident, or at least have no true habit of migration. The three groups are typically allohiemic, their winter ranges only slightly overlapping. Eaton is of the opinion that the three groups may show morphological differences.

In the Cormorant (*Phalacrocorax carbo*) there is a gradual increase in the distance of migration from north to south. The population of low-arctic W. Greenland is resident, in so far as it never leaves the country and in winter moves so far to the south only that it avoids the un-broken ice-cover. The population breeding at the northern shore of St. Lawrence is migratory, but the movements are short, the winter range covering the southern coast of Newfoundland, the southern and western coast of Nova Scotia and the northern coast of Maine (Lewis 1937, p. 11). Finally, the boreal population breeding at the Danish waters and belonging to *P. c. sinensis* winters in the subtropic

environment of the Mediterranean countries (SALOMONSEN 1953, p. 142 and fig. 46).

The migration type VI (fig. 5) is the opposite of V. The northern population (A) is migratory, but does not reach the area of the southern form B, which is resident. The Linnet (*Carduelis cannabina*) can be given as an example. Ringing in Scandinavia has shown that the breeding population spends the winter in Belgium and France, rarely south to Algeria. South of the winter-quarter of the Scandinavian population (Spain, North Africa) the subtropical, sedentary *C. c. mediterranea* lives. The wing-length of the latter is 75—80 mm, compared with 78—82, rarely 85, in the Scandinavian population (HARTERT 1910—38, p. 2052). Still smaller forms (*nana, harterti,* etc.) inhabit the Canary Islands and Madeira. *C. c. cannabina* and *C. c. mediterranea* are usually allohiemic, although there is a slight overlap. The difference in environment between the ranges of *C. c. cannabina* and *C. c. mediterranea* is probably greater in summer than in winter, although generally not much. At any rate, the difference in body-size between the two subspecies is no doubt a response to the combined effect of the natural selection in the breeding area and the winter ground. The well-marked subspecies of the Canaries owe their racial characters not only to adaptive variation, but also to the complete isolation and the limited number of individuals (cf. the Faeroe races mentioned above, p. 26). The same holds good of the other insular forms (of the species *Falco tinnunculus, Turdus merula* and *Asio otus*) mentioned in the list below. Other examples of this type of migration, all in conformity with Bergmann's rule:

	Northern, migratory form:	Southern, resident form:
Corvus corone	*cornix*	*sardonius*
Carduelis carduelis	*carduelis*	*africana*
Carduelis cannabina	*cannabina*	*mediterranea*
Turdus merula	*merula*	*cabrerae*
Falco tinnunculus	*tinnunculus*	*canariensis*
Asio otus	*otus*	*canariensis*
Pipilo erythrophthalmus	*erythrophthalmus*	*alleni*
Agelaius phoeniceus	*phoeniceus*	*floridanus*
Gallinula chloropus	*chloropus*	*parvifrons*
Phalacrocorax pelagicus	*pelagicus*	*resplendens*

This type of migration grades into type III (fig. 4), in which the two populations in question are synhiemic. It was already stressed that in *Carduelis cannabina* a slight synhiemy is present between the two subspecies discussed (*cannabina* and *mediterranea*). A good example of the transition to type III is offered by *Agelaius phoniceus*, in which the winter-quarter of the northern migratory forms (*e. g.* the nominate form of eastern North America) extends south into the area of the southern sedentary forms (*e. g. littoralis* at the Gulf Coast; cf. Oberholser 1938, p. 584). In this wide-spread and very plastic species a northern partly migratory form (*A. p. phoeniceus*) is replaced in the south by a number of sedentary forms with small body-size and of restricted ranges in southern U.S. and in the West Indies. The coastal regions of Florida alone is inhabited by three forms. The environmental differences between the habitats of these forms are certainly much smaller than those present in the huge area inhabited by the nominate form, extending from southern Canada to the Gulf States. The reason for this phenomenon is no doubt that racial differentiation is favoured in the extreme sedentary populations in the south, while it is prevented or at least considerably inhibited in the northern populations which in winter scatter over extensive areas and are largely synhiemic. This demonstrates how adaptive variation is impeded by synhiemy.

Among the longitudinal types of migration should finally be mentioned type VII (fig. 5), which is a special case, established, as far as I know, in some alcids only. In birds following this migration type the northern population (A) is sedentary as in type V, but the southern population (B) moves northwards in winter, approaching the range of A. The environmental differences between the winter-quarters of the two populations are thus considerably reduced. This migration type is realised *e. g.* in *Uria aalge*, in which the southern population (*U. a. albionis*) of Heligoland and England undertakes a first-winter migration northwards to southern Norway. Here they mix with the indigenous population (*U. a. aalge*), which, however, partly moves southwards in winter. All these populations keep strictly off the wintering grounds of the large-sized northern resident *U. a. hyperborea*; the populations are completely allohiemic (cf. Holgersen 1951, p. 53).

Parallel Migration of Allohiemic Populations.

In these types of migration the two populations A and B are neighbouring, living approximately in the same latitude, and migrate side by side in a parallel way, as outlined in the different types shown in fig. 6. The greater part of migratory species with allohiemic populations display this type of migration. In both the Old and the New World a great number of species inhabit the continent in its entire breadth and, moving south, segregate in winter in an area which has a huge extent in east-western direction. In many species the different populations have de-

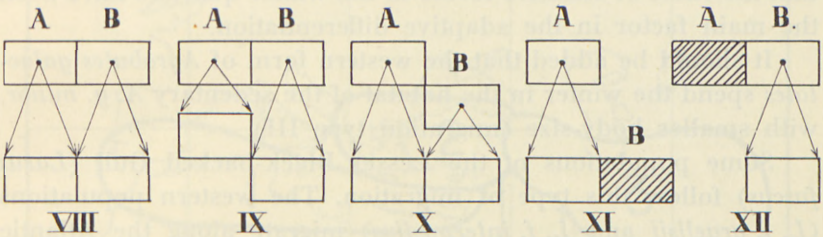

Fig. 6. Five types (VIII—XII) of parallel migration in allohiemic populations. Hatching indicates a resident population. For further explanation cf. text to fig. 1, p. 10.

veloped a high degree of allohiemy and hence are subject to the influence of widely different environmental factors in the winter-quarters. There is a considerable variation in this form of migration.

In type VIII (fig. 6) the two neighbouring populations undertake a migration of almost the same extent, that of "A" not being appreciably shorter or longer than that of "B". Among the numerous examples the superspecies *Lanius collurio—L. cristatus* forms one of the most beautiful cases. According to the map prepared by Stresemann (1927, tafel II) the Asiatic subspecies demonstrate a practically complete allohiemy. When combining this map with that prepared by Geyr (1926, p. 388), concerning the distribution of *L. c. collurio*, it appears that the populations wintering in Africa are allohiemic also. A zone of overlap is present only in N.E. Africa, where *L. c. phoenicuroides* (belonging to the *collurio* group) is partly synhiemic with *L. c. isabel-*

linus (belonging to the *cristatus* group). The superspecies *Luscinia luscinia—L. megarhyncha* offers another good example of almost absolute allohiemy of the two populations, according to the map issued by NIETHAMMER (1937, Vol. I, p. 415). A number of similar cases could be mentioned, but I shall restrict myself to that of *Agrobates galactotes*. The breeding areas and winter-quarters of the three migratory subspecies of *Agrobates galactotes* are shown in fig. 7. This example is particularly interesting because the breeding areas of the said races are contiguous while the winter-quarters are mutually isolated. Hence the populations are probably subject only to an insignificant interpopulational dispersal in winter. In such cases it is obvious, in my opinion, that the effect of selective forces in the winter-quarters have been the main factor in the adaptive differentiation.

It should be added that the western form of *Agrobates galactotes* spend the winter in the habitat of the sedentary *A. g. minor*, with smaller body-size (migration type III).

Some populations of the Lesser Black-backed Gull (*Larus fuscus*) follow this type of migration. The western populations (*L. f. graellsii* and *L. f. intermedius*) migrate along the Atlantic coasts, the East Danish *L. f. fuscus* through Central Europe to the eastern Mediterranean and tropical Africa, and the Swedish and Finnish *L. f. fuscus* via Russia to the Black Sea and sometimes to Africa. There is some overlapping in the winter-quarters of the populations of *L. f. fuscus*, but the allohiemy, nevertheless, is marked; cf. fig. 8, based on recoveries of ringed birds.

In a number of waders the subspecies are allohiemic, although in most cases there is some overlapping of the respective winter-quarters. Such cases are *Pluvialis dominica* (*dominica* and *fulva*, which are absolute allohiemic), *Numenius arquata* (*arquata* and *lineatus*), *N. phaeopus* (*phaeopus* and *variegatus*), *Haematopus ostralegus* (*ostralegus* and *osculans*), *Limosa limosa* (*limosa* and *melanuroides*) and so forth. In *Limosa l. lapponica* and *L. l. baueri*, which apparently are completely allohiemic, the morphological differences are greater than in the other waders mentioned. *Sterna hirundo* (*hirundo* and *longipennis*) forms a similar case.

The tendency to allohiemy is seen in smaller units too. Ringing in European populations of a number of species has demonstrated that the populations scatter in a fan-like manner, moving

to the nearest areas with a mild winter-climate, segregating into partly allohiemic units. A good example is the Starling (*Sturnus vulgaris*) as shown in a figure in Schüz 1952, fig. 12, p. 46 (with winter-isotherms drawn). Another example is the Redshank (*Tringa totanus*), as shown in fig. 12 in this paper. The degree of allohiemy of the populations in this species is pronounced, but many other species are similar. In fig. 9 is shown the distribution of a number of populations of the Black-headed Gull

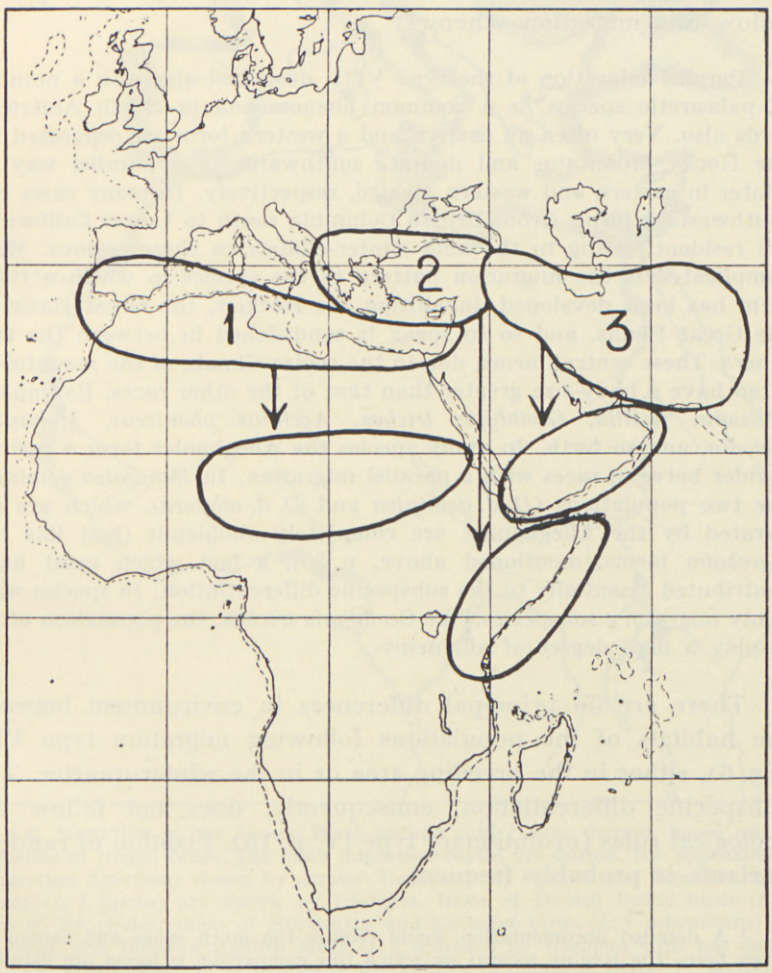

Fig. 7. Breeding areas and winter-quarters of the palaearctic forms of *Agrobates galactotes*. 1: *A. g. galactotes*, 2: *A. g. syriacus*, 3: *A. g. familiaris*.

(*Larus ridibundus*) in Europe, based on ringing records. The different populations demonstrate a marked allohiemy, although the overlapping is considerable.

A situation similar to that found in *Larus ridibundus* is widespread among Scandinavian birds. A comparison of Danish Swedish and Finnish populations of migratory birds reveals that a pronounced allohiemy is established in no less than 22 species, as demonstrated by recoveries of ringed birds[1]. A greater number of recoveries would no doubt show that still many other species follow this migration scheme.

Parallel migration of the type VIII, described above in a number of palæarctic species, is a common phenomenon in North American birds also. Very often an eastern and a western form are separated by the Rocky Mountains and migrate southwards in a parallel way to winter in eastern and western Mexico, respectively. In many cases the southwestern forms (from British Columbia south to Lower California) are resident, owing to the mild winter-climate in these regions. More complicated is the migration pattern in the species in which a third form has been developed, inhabiting the Rockies, the Great Basin or the Great Plains, and so to speak is sandwiched in between the two others. These central forms, due to the cooler climate of the mountains, often have a body-size greater than that of the other races. Examples: *Wilsonia pusilla*, *Geothlypis trichas*, *Agelaius phoniceus*, *Melospiza melodia*, and so forth. In many species the Alleghanies form a further divider between races with a parallel migration. In *Dendroica dominica* the two populations (*D. d. dominica* and *D. d. albilora*), which are separated by the Alleghanies, are completely allohiemic (just like the *Agrobates* forms, mentioned above, p. 30), a fact which must have contributed essentially to the subspecific differentiation. In species with many migratory subspecies, like *Geothlypis trichas*, the population often display a high degree of allohiemy.

There are no principal differences in environment between the habitats of the populations following migration type VIII (fig. 6), either in the breeding area or in the winter-quarter. The subspecific differentiation, consequently, does not follow the ecological rules (evolutionary type IV, p. 15). Fixation of random variants is probably frequent.

[1] A detailed documentation would require too much space and cannot be given here. The ringing records on which this comparison is based are listed in my book SALOMONSEN 1953.

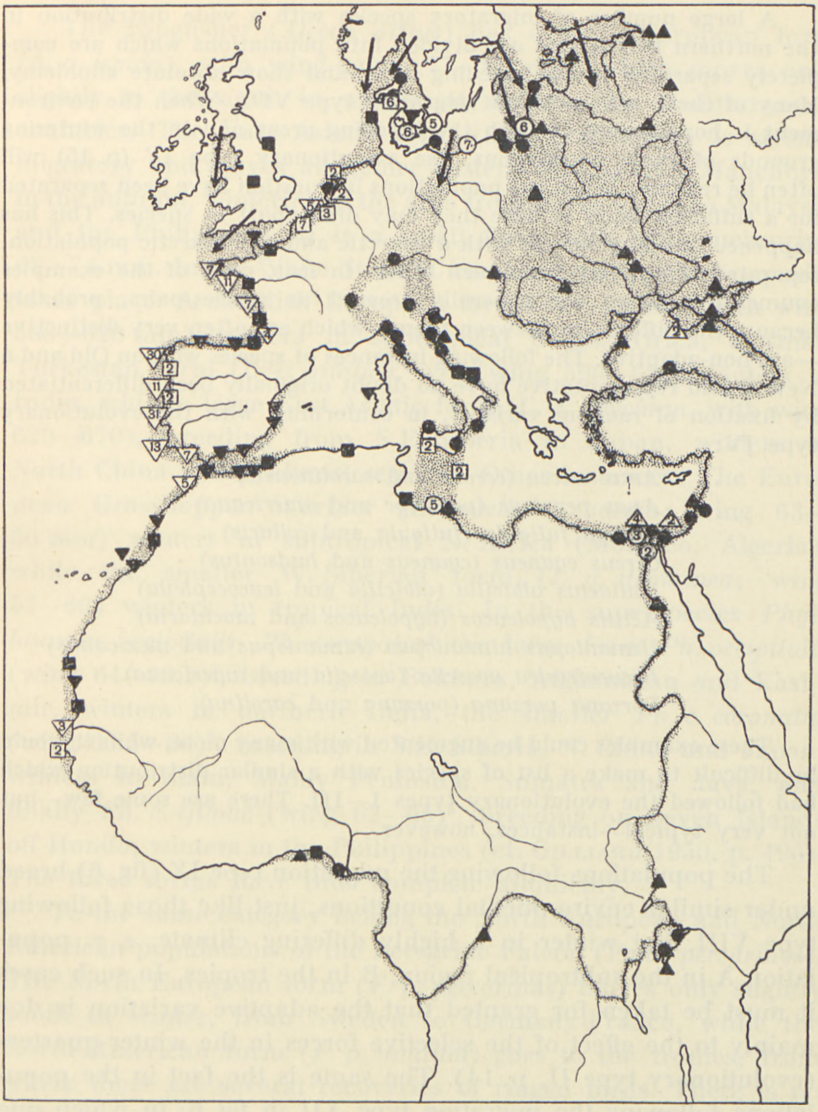

Fig. 8. Migration of the Lesser Black-backed Gull (*Larus fuscus*), based on recoveries of ringed birds. The main migration routes are dotted, the approximate migration directions shown by arrows. Recoveries of Finnish and Swedish Baltic birds (*L. f. fuscus*) are shown by triangles, those of Danish Baltic birds (*L. f. fuscus*) by circles, those of Norwegian and Cattegat birds (*L. f. intermedius*) by squares, and those of English birds (*L. f. graellsii*) by triangles with top down. Figures give number of recoveries in the locality in question. (After F. Salomonsen 1953.)

A large number of migratory species with a wide distribution in the northern hemisphere are divided into populations which are completely separated in the breeding areas and show absolute allohiemy. Many of these species follow migration type VIII. When the environment is homogenous in both the breeding areas and in the wintering grounds of these populations, the evolutionary type IV (p. 15) will often be realized. When the populations in question have been separated for a sufficient lapse of time they may drift apart as species. This has happened in many species with a nearctic and a palæarctic population, separated completely from each other. In fact, most of the examples enumerated below are generally treated as species-pairs, probably because the differences between them—which are often very distinctive—are non-adaptive. The following instances of species with an Old and a New World representative have no doubt originally been differentiated by fixation of random variants, in conformity with the evolutionary type IV:

Anas crecca (*crecca* and *carolinensis*)
Anas penelope (*penelope* and *americana*)
Aythya fuligula (*fuligula* and *collaris*)
Circus cyaneus (*cyaneus* and *hudsonius*)
Haliaetus albicilla (*albicilla* and *leucocephala*)
Actitis hypoleucos (*hypoleucos* and *macularia*)
Himantopus himantopus (*himantopus* and *mexicanus*)
Recurvirostra avosetta (*avosetta* and *americana*)
Porzana porzana (*porzana* and *carolina*)

These examples could be augmented with many more, while it would be difficult to make a list of species with a similar distribution which had followed the evolutionary types I—III. There are some few—but not very typical—instances, however.

The populations following the migration type IX (fig. 6) breed under similar environmental conditions, just like those following type VIII, but winter in a highly differing climate, *e. g.* population A in the subtropical region, B in the tropics. In such cases it must be taken for granted that the adaptive variation is due mainly to the effect of the selective forces in the winter-quarters (evolutionary type II, p. 14). The same is the fact in the populations following the migration type XII in fig. 6, in which one of the populations (A) is resident, while in type IX it carries out a short migration.

In the species dealt with below the adaptive variation follows Bergmann's rule, *i. e.* the population wintering more northernly (A) attains larger body-size than population B wintering further south.

The Kingfisher (*Alcedo atthis*) has a large European form (*A. a. ispida*), with wing-length 77—81 mm[1], which moves only slightly to the south in winter, at most to the Mediterranean countries. The East Asiatic form (*A. a. bengalensis*) is strictly migratory and leaves altogether eastern Siberia and Manchuria in the autumn, wintering in the area from North China to Malaysia and the Philippines. It is a small form with wing measuring 68—74 mm. In the White Stork (*Ciconia ciconia*) just the opposite takes place. A smallish European form (*C. c. ciconia*, with wing 560—620 mm) winters in subtropical South Africa, a small Turkestan form (*C. c. asiatica*, with wing 590—620) winters in India, while a large East Asiatic form (*C. c. boyciana*, with wing 620—670), breeding from S.E. Siberia to Japan, winters in North China and is almost resident. Other instances: The European Grasshopper Warbler (*Locustella n. naevia*; wing 63—66 mm) winters in subtropical N. Africa (Morocco, Algeria), while the smaller W. Siberian form (*L. n. straminea*; wing 57—60) winters in tropical India. In the superspecies *Phylloscopus occipitalis—Ph. coronatus*[2] the large form *Ph. occipitalis* (wing 64—70.5)[3], breeding in Bokhara, Afghanistan and Kashmir, winters in northern India, the smaller *Ph. c. coronatus* (wing 60.5—66)[3], breeding in S.E. Siberia, N. China and Japan, winters in Siam, Malay Peninsula, Sumatra and Java, and finally *Ph. c. ijimae* (wing 62—65)[3], breeding on Seven Islands off Hondo, winters in the Philippines (cf. Gilliard 1950, p. 496). The three forms have thus complete allohiemy.

To the same category belong the North European and North American populations of the Peregrine Falcon (*Falco peregrinus*). The North European form (*F. p. peregrinus*) moves only slightly south in winter, from Sweden to Germany-France, while the North American form (*F. p. anatum*) goes to the tropics, from where there are several recoveries of ringed birds. There is no difference in body-size between the two populations, but *F. p. anatum* is much darker than *F. p. peregrinus* in the juvenile

[1] According to Hartert (1910—38, p. 881). When nothing else is stated the measurements given in this paper are based on the figures given by Hartert (*l. c.*) concerning palæarctic birds, and by Ridgway (1901—14), concerning nearctic birds.

[2] These two forms are usually regarded as conspecific, but Ticehurst (1938, p. 162) holds them to be closely allied allopatric species.

[3] Measurements from Ticehurst (1938).

plumage (which is kept for a year). This is probably an adaptive character, the variation agreeing with Gloger's rule. This rule denotes that populations inhabiting areas with a higher temperature and a higher degree of moisture tend to be darker.

As an example of migration type XII some populations of

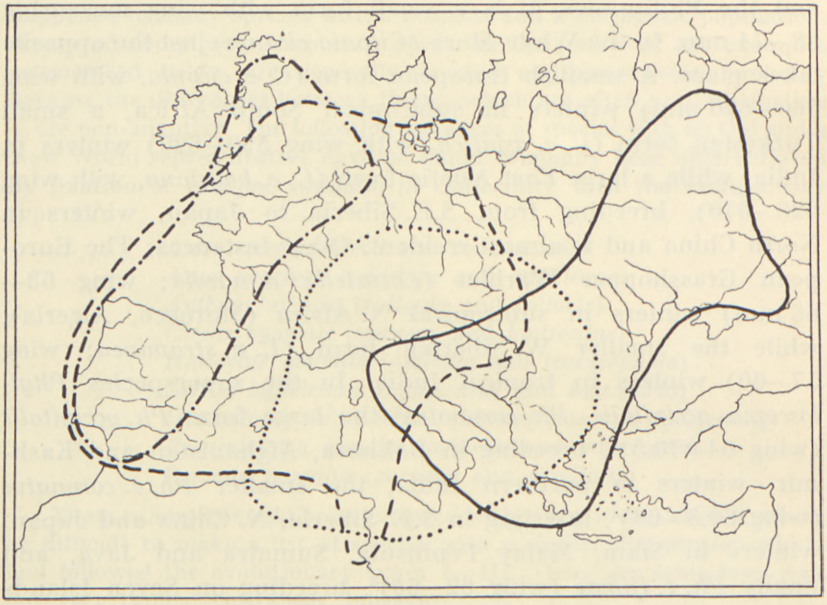

Fig. 9. Distribution of a number of European populations of the Black-headed Gull (*Larus ridibundus*), based on recoveries of ringed birds. Breeding areas: – · – · – · –: Cumberland, England, – – – – – – –: Oberlausitz, Germany, · · · · · · · · · : Ungarn, ———— : Moscow, Russia. (Redrawn after SCHÜZ & WEIGOLD 1931.)

the Redshank (*Tringa totanus*) can be mentioned. The British population (*T. t. britannica*) is mainly resident, while the Danish one (*T. t. totanus*) is strictly migratory, wintering in the subtropics. Another example is offered by the Herring-Gull (*Larus argentatus*). The European populations are usually resident, while a number of the North American ones are highly migratory (cf. above, p. 26).

The migration type X (fig. 6) is just contrary to type IX. Populations A and B have contiguous winter-quarters, situated in about the same latitude, while the breeding area of A is situated much farther north than that of B. Consequently, A makes a

longer migration than B. Migration type XI differs only in the fact that population B is resident. Adaptive variation in populations following types X—XI must be the result of the selection in the breeding area (evolutionary type I, p. 14).

The Lesser Black-backed Gull (*Larus fuscus*) offers a clear example of migration type X. The arctic form *L. f. taimyrensis*, breeding in North Russia, is slightly larger than the boreal Scandinavian *L. f. fuscus*. Both winter in the tropics, *taimyrensis* in Indian waters, *fuscus* from the Black Sea to Central Africa. The difference in body-size demonstrates that these gulls follow Bergmann's rule. Some other examples from the New World: *Pinicola enucleator* (*alascensis* and *flammula*) and *Passerella iliaca* (*iliaca* and *schistacea*). *P. e. flammula* and *P. i. schistacea* are the "B"-forms with smaller body-size than the "A"-forms, thus demonstrating that they follow Bergmann's rule.

Finally, I shall mention two species in which migration type XI is established. *Buteo r. rufinus*, breeding from southern Russia to Turkestan and W. Mongolia, winters in northern India and N.E. Africa from Egypt to Abyssinia. *B. r. cirtensis* breeds from Morocco to Tunisia and southern Algeria, where it is resident. Being much the smaller it follows Bergmann's rule. In addition, the largest form, *B. r. hemilasius*, can be mentioned. It breeds in Central Asia eastwards to S.E. Siberia and winters in N. China. This form and *B. r. rufinus* display migration type IX (p. 34), demonstrating a close resemblance to the migration of the forms of *Ciconia ciconia*, described above (p. 35). Another example of migration type XI is offered by the Little Ringed Plover (*Charadrius dubius*). The European form (*Ch. d. dubius*) winters mainly in tropical Africa and have larger proportions than the resident Indian and Malaysian form (*Ch. d. jerdoni*), thus following Bergmann's rule. There is a tendency to synhiemy, the winter ranges of the two forms overlapping in N.W. India.

"Leap-Frog" Migration.

In many migratory birds the northern populations winter south of the southern ones, *i. e.* the northern and southern popu-

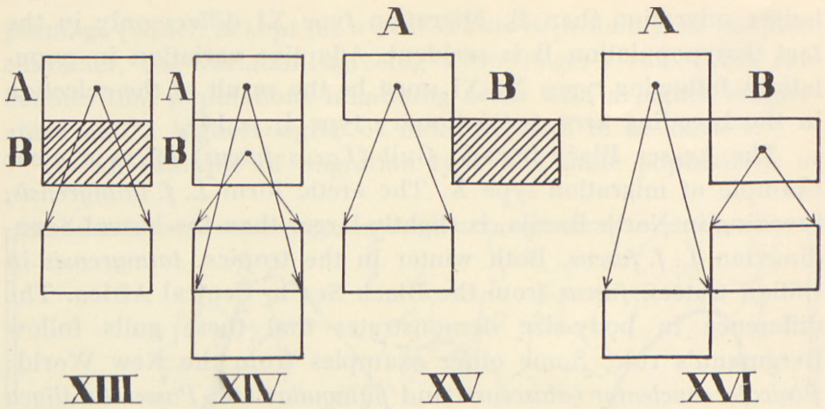

Fig. 10. Four types (XIII—XVI) of leap-frog migration in allohiemic populations. Hatching indicates a resident population. For further explanation cf. text to fig. 1, p. 10.

lations so to speak play at leap-frog with each other during migration. This is shown as migration type XIV in fig. 10. Type XIII is very similar, only is the southern population (B) resident. Leap-frog migration has been developed as well in species with "longitudinal" migration as in those with parallel migration. Type XIII and XIV in fig. 10 show leap-frog migration of the "longitudinal" type, and type XV and XIV the corresponding "parallel" types.

Type XIII and XIV can be combined, as can type XV and XVI. This is demonstrated in a species in which a population C is resident, a population B, breeding north of C, winters south of C, and finally a population A, breeding north of B, winters south of B. Cf. *e.g. Geothlypis trichas, Passerella iliaca, Charadrius hiaticula, Tringa totanus* and other species mentioned below.

There is a wide-spread tendency among migratory species to develop this form of migration. I have studied the recoveries of birds ringed in Scandinavia and found that among the comparatively few species in which ringing has given a fairly good idea of the migration, leap-frog movements are carried out, to a varying extent, in 12 species[1]. The origin of this type of migration might be a development of a certain "prolongation" of the migration among the northern populations, as postulated by

[1] For documentation cf. footnote on p. 32.

some students, but in my opinion it is primarily a result of the intraspecific (intergroup) competition, which will necessarily lead to allohiemy. To give an example, which shows the initial stage of leap-frog migration: The Danish population of the Oyster-Catcher (*Haematopus ostralegus*) moves slightly to the S.W. along the Northsea coasts, some being resident. The main winter-quarter extends from Denmark proper along the German and Dutch coasts to North France; only one recovery was made in Vendée, W. France, while 50 % of the recoveries were made in Holland. The Norwegian and Swedish Oyster-Catchers winter in the same area and, consequently, the density of individuals may reach the point of crowding. Owing to this population pressure the individuals arriving later continue slightly longer and settle just south of the others, where the wintering population is more scattered. There are several recoveries of Norwegian birds in Vendée and one of a Swedish bird even in Gironde. In cases like the Oyster-Catcher, where the leap-frog migration is still in its being, the phenomenon may be purely phenotypical and the guiding influence may still be the intraspecific competition. In species with a well-marked leap-frog migration the populations differ genetically in their migration habits, the releasing factors (the proximate causes)[1] no longer being competition (which now is relegated to an "ultimate cause"), but a fixed and stabilized system of inherent mechanisms built up by means of selection.

The first to draw attention to this form of migration was Swarth (1920, p. 75) in his study of the Fox-Sparrow (*Passerella iliaca*) in western North America. His results have been quoted and commented on in most handbooks on migration (*e. g.* Stresemann 1934, Schüz 1952, Salomonsen 1953, etc.). Stresemann (1934, p. 666) adds some characteristic examples, *viz*: *Hirundo rustica* (*savignyi* resident in Egypt, *transitiva* breeding in Palestine, wintering in N.E. Africa, *rustica* breeding in Europe, wintering in tropical and southern Africa), *Motacilla flava* (*pygmaea* resident in Egypt, *feldegg* breeding in S.E. Europe, wintering in N.E. Africa south to Kenya and Uganda, *flava* breeding in Central Europe, wintering in entire tropical E. Africa and South Africa) and a few others.

[1] Cf. footnote p. 8.

When discussing the adaptive variation in a species with leap-frog migration, following *e. g.* type XIV in fig. 10, it is important to draw attention to the fact that selection by environment in the winter-quarters influences the populations in just the opposite way of that in the breeding areas. According to Bergmann's rule the population A when under the conditions of the breeding area will tend to attain larger proportions than B, but in the winter-quarter it will, on the contrary, tend to be smaller. Populations with leap-frog migration will generally follow the evolutionary type III (p. 14), *i. e.* the adaptive variation will be the result of the influences of the selective forces in both the breeding area and the winter-quarter. However, in species with leap-frog migration these two influences counteract each other. In some species the summer-influences, in other species the winter-influences are the superior ones and stamp the morphology of the populations, while in other instances a certain balance between the two influences is reached. The result of the fight between the counterworking influences is dependent upon the degree of difference in the selection pressure in the breeding areas and in the winter-quarters, respectively. The selection pressure is the result of various influences. Significant in this respect is the degree of difference in climate and other environmental factors between the habitats of the populations (both in summer and winter) and the extension of the period spent in the breeding area and winter-quarter, respectively. It is obvious that the winter-influences will be the more important when the populations in question spend a long time in the winter-quarter, while the stay in the breeding area is short and ephemeral, like in many waders. If, on the other hand, the environmental differences between the breeding habitats of the populations in question are considerable, while those between the respective wintering grounds are slight, the adaptive variation will mainly be due to influences of the selective forces in the breeding area.

The adaptive variation in species with leap-frog migration has usually evolved in accordance with the above considerations, which therefore probably express something essential.

Swarth's classic study of the Fox-Sparrow, mentioned above, deals with the migratory subspecies inhabiting the coastal areas of western North America. In the table below the variation in

this species is compared with that in its near ally, the Song-Sparrow (*Melospiza melodia*), which is as "plastic" as the Fox-Sparrow, *i. e.* just as readily respond to the comparatively small differences in environment in the extreme maritime climate of N.W. America. The figures in the table give the average wing-lengths of adult males.

	Passerella iliaca		*Melospiza melodia*	
Shumagin Islands	*unalaschkensis*[1]	84	*sanaka*	85
Kodiak Island	*insularis*[1]	84	*insignis*	82
Kenai Peninsula	*sinuosa*[1]	82	*kenaiensis*	78
S.E. Alaska (islands)	*townsendi*[1]	81	*rufina*	72
S.E. Alaska (coast)	*annectens*[1]	82	*caurina*[3]	69
Brit. Columbia-Oregon	*fuliginosa*[2]	82	*morphna*	68
N.W. California, Middle California	Various forms[1]	80—84	*cleonensis*	62
			samuelis	61
Santa Barbara Islands			*graminea*	60

[1] Migratory, wintering in California, lowland.
[2] Mainly resident.
[3] Migratory, wintering south to North California.

The Fox-Sparrow forms dealt with breed from the islands and coasts of S. Alaska south to the mountains of eastern California, where it inhabits the Canadian zone. Most populations winter in the Californian lowland, where the local differences in climate are small, much smaller indeed than those present between the respective summer habitats extending from Alaska to California (although these differences are not particularly pronounced either). The populations inhabiting the region from Alaska to Oregon make a pronounced leap-frog migration. It appears from the table that the subspecies breeding in the northern areas are slightly larger than the southern ones (wing-length 84 mm, as compared with 81—82). According to Bergmann's rule (other ecological rules are not considered here) this shows a slight preponderance of the influences due to the selective forces in the summer habitats, while the "winter-influences"[1] are negligible. In the resident *Melospiza melodia* the northern populations, likewise, are the larger, but the adaptive variation is enormous compared with that in the Fox-Sparrow. From Oregon

[1] A brief term to signify the adaptive influences due to selection by environment in the winter-quarters.

to South Alaska the average wing-length increases from 68 to 85 mm, forming a gradual cline[1]. This is due to the combined effects of the summer- and winter-influences and demonstrates that the "winter-influences"—which the migratory Fox-Sparrow avoids—are much the stronger of the two.

A similar difference in the variation between resident forms and migratory populations which evade the cold season, has recently been demonstrated in the Drongo *Dicrurus leucophaeus* by MAYR and VAURIE (1948, p. 238). In the resident subspecies there is a gradual cline for increasing size from Malaysia to southern China, *viz*:

D. l. stigmatops	(Borneo),	wing-length	127—134 (129.4) mm
— *bondi*	(Siam),	—	128—138 (132.9) —
— *salangensis*	(S. China),	—	139—145 (143.0) —

The North China form, *D. l. leucogenis*, is migratory, and its proportions are similar to those of the South China form *salangensis* (wing-length of *leucogenis*: 138—148 (average 142.8) mm), *i. e.* the size-gradient is not continued into the N. China population, which is probably due to the fact "that the northern populations are migratory and spend the cold season in the subtropical and tropical parts of eastern Asia" (quotation from MAYR and VAURIE, *l. c.*).

The counteracting influences of the selective forces in the breeding areas and winter-quarters, respectively, in species with leap-frog migration make the pattern of adaptive variation extremely complicated. In some species the "summer-influences", in others the "winter-influences" predominate. Populations belonging to the same species may differ in their response to the environmental influences. When the northern population (A in fig. 10, XIV) has attained larger body-size than the southern one (B), it will be explained, below, as a reaction on the "summer influences", in accordance with Bergmann's rule. If, on the contrary, population A, which winters south of B, is smaller than B, it will be interpreted as a response to the "winter-influences".

[1] The Californian forms of the two species are not comparable since in this state the Fox-Sparrow is a mountain bird, the Song-Sparrow a lowland bird. The Californian populations of the Song-Sparrow have very small proportions; the smallest body-size is attained in *M. m. pusillula* of the San Francisco salt-marches, with an average wing-length of 58.4 mm. The southern forms, including a number of Mexican populations, have again somewhat greater proportions.

I. Positive reaction to "summer-influences" (A > B):

Muscicapa s. sibirica, breeding S.E. Siberia, wintering Malaysia, wing 76—82 mm; *M. s. fuliginosa*, resident on southern slopes of Himalaya, wing 70—75 mm. (Migration type XIII).

Motacilla f. flava, breeding Central Europe, wintering tropical Africa, wing 80—85; *M. f. pygmaea*, resident in Egypt, wing 72—79. (Type XIII).

Jynx t. torquilla, breeding Europe, wintering tropical Africa, wing 86—92; *J. t. mauretanica*, resident in Algeria, wing 76—82. (Type XIII).

Turdus m. migratorius, breeding from tree-limit in Alaska to northern U.S.A., wintering in southern U.S.A. and northern Mexico, wing (average of ♂♂) 134; *T. m. achrusterus*, resident in middle U.S.A., wing 122; greatly synhiemic with *T. m. migratorius*. (Type XIII).

Hylocichla ustulata swainsoni, breeding from N.W. Alaska to Pennsylvania, wintering from southern Mexico to Argentine, wing 101; *H. u. ustulata*, breeding west-coast of N. America south to California, wintering from Mexico to Ecuador and British Guiana, wing 98. (Type XVI, but the two subspecies are largely synhiemic and the difference in wing-length is slight).

Geothlypis trichas brachydactyla, breeding N.E. America from southern Labrador to Pennsylvania, wintering Bahamas, West Indies and entire eastern Mexico, wing 55; *G. t. trichas*, breeding from Pennsylvania to Texas, wintering from North Carolina to Bahamas and Haiti, wing 53; *G. t. ignota*, resident from South Carolina to Florida. (Type XIII and XIV combined, but geographical variation slight).

Geothlypis trichas occidentalis, breeding S.E. Alaska to California, wintering from Lower California to S.W. Mexico, wing 58; *G. t. sinuosa*, resident in California, wing 53, darker plumage. (Type XIII).

A number of birds have developed in the same way as the western *Geothlypis*, e. g. *Falco columbarius*: *F. c. bendirei*, breeding from N. Alaska to N.E. California, wintering from California to North Mexico, wing 191; *F. c. suckleyi*, resident in W. British Columbia, wing 189, plumage darker. A similar example offers *Hylocichla guttata*: *H. g. guttata*, breeding from Alaska to British Columbia, wintering in California and northern Mexico, wing 88; *H. g. nana*, breeding British Columbia, wintering California, wing 87, darker plumage. The two subspecies are partly synhiemic and share their winter-quarter also with the still smaller Californian *H. g. slevini* (wing 84). There is a large number of similar instances.

II. Positive reaction to "winter-influences" (A < B):

Motacilla f. flava, breeding Central Europe, wintering tropical Africa, wing 80—85; *M. f. feldegg*, breeding in Balcan, wintering in N.E. Africa, mainly Sudan and Abyssinia, wing 84—90. (Type XIV; the two subspecies overlap largely in the winter-quarters).

Otus s. scops, breeding in Mediterranean region, wintering in Africa

south to Uganda, wing 144—162; *O. s. cyprius*, resident in Cyprus, wing 153—167. (Type XIII).

Ceryle a. alcyon, breeding eastern North America (north to tree-limit), wintering in southern U.S.A., Central America to Columbia and British Guiana, wing 156; *C. a. caurina*, breeding from Alaska to California, wintering from California to North Mexico, wing 163. There is apparently absolute allohiemy. (Type XVI).

Piranga r. rubra, breeding in eastern U.S.A., wintering from Central Mexico to Ecuador, Peru and Guiana, wing 95; *P. r. cooperi*, breeding in southwestern U.S.A. and northern Mexico, wintering in central Mexico, wing 100. Almost full allohiemy. (Type XVI).

Guiraca c. caerulea, breeding eastern U.S.A., wintering from southern Mexico to Costa Rica, wing 86, darker plumage; *G. c. interfusa* and *G. c. salicaria*, breeding in southwestern U.S.A., wintering in northern Mexico, wing 90, paler plumage. (Type XVI).

Vireo s. solitarius, breeding Canada and northeastern U.S.A., wintering from the Gulf States to Nicaragua, wing 74; *V. s. alticola*, breeding in the Alleghanies, wintering from South Carolina to Florida, wing 80. (Type XIV). There is a pronounced allohiemy among all the 5 subspecies of this species.

Passerculus sandwicensis alaudinus, breeding Alaska and N.W. Canada, wintering from California to Guatemala, wing 72; *P. s. sandwicensis*, breeding Unalaska, wintering southwards to Central California, wing 76. (Type XIV).

Passerculus sandwicensis princeps, breeding on Sable Island, Nova Scotia, wintering at the Atlantic coast to Georgia, wing 76, paler plumage; *P. s. savanna*, breeding boreal zone of eastern Canada and north-eastern U.S.A., wintering from southeastern U.S.A. to north-eastern Mexico and the West Indies, wing 69, darker plumage. (Type XIV).

Falco c. columbarius, breeding in eastern Canada, wintering from Gulf States to Ecuador and northern Venezuela, wing 189; *F. c. richardsoni*, breeding in the Great Plains, wintering from Colorado to north-western Mexico, wing 198. (Type XVI).

The interpretation of the facts set forth above is somewhat schematical, it is true. A much closer analysis of each species is required in order to explain the correlation between migration and geographical variation. There are many sources of error. Island forms of restricted distribution and small population size (like those mentioned of *Passerculus sandwicensis*) are not well suited to be compared with continental forms with a wide range, owing to their different evolutionary history. When comparing mountain forms, like those breeding in the Great Basin of N.W. America, with lowland populations it must be kept in mind that microclimatical, edaphic and other factors are very different in

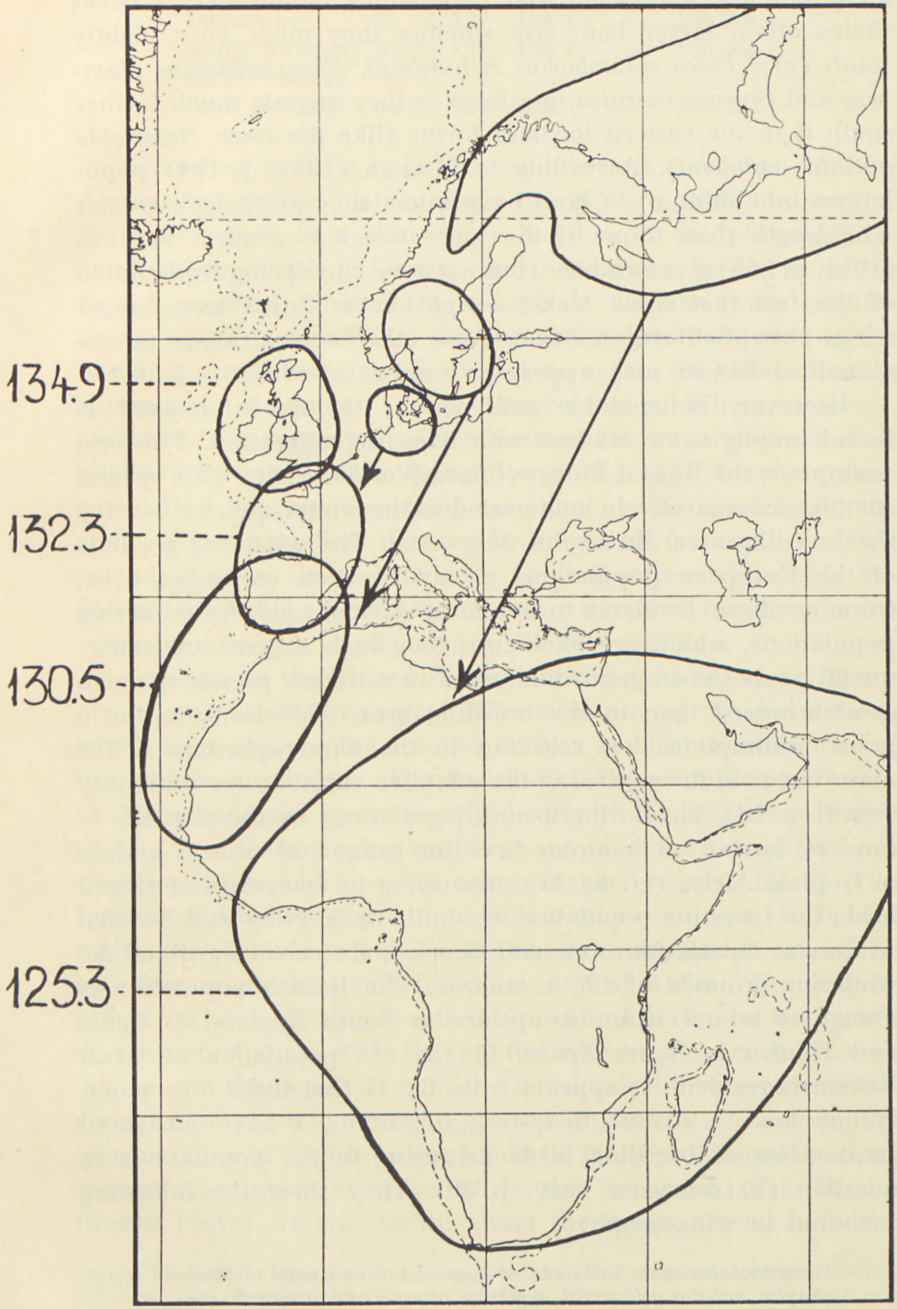

Fig. 11. Breeding-areas and winter-quarters of a number of populations of the Ringed Plover (*Charadrius hiaticula*), partly based on recoveries of ringed birds. Breeding-areas and corresponding winter-quarters are connected by arrows; the British population is resident. Figures insertedt a left give average wing-length of the population wintering in the area in question.

their habitats. It appears that populations inhabiting the Great Plains attain larger body size whether they move only slightly south (like *Falco columbarius richardsoni, Vireo solitarius plumbeus* and *Guiraca caerulea interfusa*) or they migrate much further south than the eastern lowland forms (like the huge *Hylocichla guttata auduboni*). According to MILLER (1931, p. 104) populations inhabiting open land have a tendency to attain a greater wing-length than those of the more wooded country. PITELKA (1951, p. 366) gives another, but not very convincing explanation of the fact that some Mexican *Aphelocoma* forms have longer wings than Californian ones[1]. Also other ecological or microclimatical factors may appear as sources of error.

However, indisputable evidence of "winter-influences" is found among some waders with leap-frog migration. The best example is the Ringed Plover (*Charadrius hiaticula*). This species spends a comparatively long period in the winter-quarter, leaving the breeding area already in July—Aug. The wintering grounds of the European populations extend over an enormous area, from northern Scotland to southern Africa, and the wintering populations, which are allohiemic to a high degree, are consequently exposed to great differences in selection pressure, much greater indeed than in the breeding area. This leads to the *a priori* assumption that selection in the winter-quarters is the main factor in the control of the adaptive variation (evolutionary type II, p. 14). The northern-most population, separated as *Ch. h. tundrae*, has an arctic-alpine breeding range and winters mainly in tropical Africa (cf. fig. 11). According to recoveries of ringed birds the breeding population of southern Norway and Sweden winters in Spain, Morocco and Senegal, *i. e.* northwards of the wintering grounds of *Ch. h. tundrae*. The Danish population is known to winter from Hampshire in South England to Cadiz and Huelva in South Spain. Finally the population of Great Britain is resident. It appears from fig. 11 that these four populations have a distinct leap-frog migration. I have measured great series of breeding birds belonging to the populations in question (SALOMONSEN 1949, p. 30). They show the following variation in wing-length:

[1] There are also other instances of increased wing-length in Mexican forms, *viz*: *Melospiza melodia goldmanni, Agelaius phoeniceus sonoriensis*, etc.

England:	36 ♂♀	130—140	(average	134.89) mm
Denmark:	73 ♂♀	127—139	(—	132.30) —
South Sweden:	30 ♂♀	127—135	(—	130.46) —
Arctic Sweden and Russia:	44 ♂♀	121—132	(—	125.21) —

According to these measurements there is a regular cline for decreasing wing-length running from S.W. to N.E. in Europe. Similarly, there is a cline for coloration of the plumage; the small northern *Ch. h. tundrae* are the darkest birds, while the British resident birds form the palest extreme with greyish-brown upper-parts[1]. When the populations are compared in the breeding areas this variation makes no sense, the clines running contrary to Bergmann's and Gloger's rules. When, however, arranged in their proper winter-quarters the populations in their adaptive variation follow both rules (cf. fig. 11). There is a close correlation between the clinal variation in this species and the environmental gradient dictated by climatical factors in the area extending from Great Britain to tropical Africa. The only explanation of this phenomenon is that adaptive selection in the wintering grounds is responsible for the variation.

The case of the Ringed Plover is extraordinarily clear. There are no appreciable ecological differences among the populations which may obscure the results; neither are historical factors of importance any longer. The Redshank (*Tringa totanus*) offers a similar example. I have recently dealt with the migration of this species, based on ringing results (Salomonsen 1954, p. 94) and shall restrict myself to a few comments, referring to fig. 12. The Iceland and British populations follow migration type IV (fig. 5), while the Scandinavian—North Russian population makes a leap-frog migration and winters in tropical Africa. The geographical variation in wing-length is shown in fig. 12, and it appears that it corresponds with that of the Ringed Plover. Just as in this species the populations of the Redshank are subject to much greater differences in selection pressure in their respective winter-quarters than in their breeding habitats. The distributional pattern is, however, more complicated in the Redshank than in the Ringed Plover. In the North, about the Arctic Circle, both the

[1] The British form has been separated as *Ch. h. major* Seebohm, recently renamed *Ch. h. harrisoni* by Clancey (1949, p. 319).

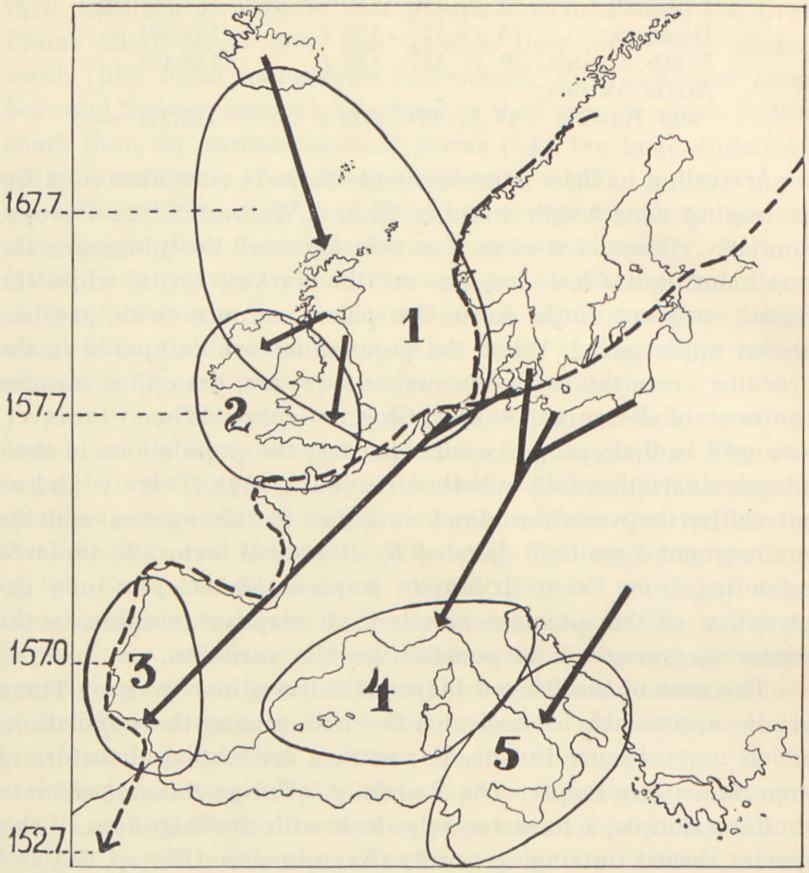

Fig. 12. Main winter-quarters of various European populations of Redshank (*Tringa totanus*). 1: Iceland, 2: British, 3: Belgian-Dutch-W. German, 4: Danish-E. German, 5: Hungarian population. Broken line: Migration route of Swedish and Norwegian (and ?Russian) populations to tropical Africa. Figures inserted at left give average wing-length of the population wintering in the area in question. (After F. Salomonsen 1954.)

Redshank population with the biggest proportions (in Iceland) and that with the smallest proportions (in Norway) breed, which indicates that any "summer-influence" cannot be involved in the adaptive variation. In winter, however, the smallest form inhabits the tropics, the largest one the Northsea countries, which gives a satisfactory explanation of the variation in body-size.

Finally, the case of the Common Buzzard (*Buteo buteo*) should be mentioned. The northeastern form (*B. b. intermedius*) is small

(wing-length ♂♂ 340—380) and has a dark, reddish-brown plumage. It migrates from northern Scandinavia and from Russia to tropical Africa. The southwestern form (*B. b. buteo*) is larger (wing-length ♂♂ 370—395) and paler. It remains within the boundary of Europe in winter. The Danish *B. b. buteo* are partly resident, partly migrants which winter in N.W. Germany, the Netherlands and N. France, according to recoveries of ringed birds. The population of Central Sweden, which is intermediate between the two races, winters in France and Spain. Finally, *B. b. intermedius* from northern Sweden early in the autumn pass on the migration southern Europe (from where there is a number of recoveries) and winter in Africa (one recovery in Morocco). The case is quite similar to that of *Charadrius hiaticula*, the smallest and darkest forms breeding farthest north and wintering in the tropics[1].

Apparently a number of geese follows this scheme. Owing to their strict family adherence and their tendency to winter colonially in isolated restricted areas the geese are subject to the selective influence of widely differing environments during their hibernation. When the species are sufficiently "plastic" as is the case in the Canada Goose (*Branta canadensis*) this will give rise to adaptive variation. In this and other species (*Anser albifrons, A. fabalis*) size-mutations occur at a considerable rate and give rise to a remarkable individual variation in proportions. In my opinion selection in the winter-quarters forms the main control and regulation of this variation. The populations of the Canada Goose form a wide continuum in the breeding-time, but have often isolated winter ranges. The smallest forms breed highest to the north and, making a leap-frog migration, winter farthest south. According to the newest hand-list (Hellmayr and Conover 1948, p. 297) the small and dark *B. c. minima* (wing-length 350—390 mm)—which is now usually given full specific rank—from its Alaskan breeding range migrates south to California, where it mainly winters in San Joaquin and Sacramento Valleys. Of the two forms of the *leucopareia* group *B. c. leucopareia* is the smaller (wing 378—410); it breeds from N. Alaska to the Aleutians and winters from Washington to northern Mexico. The

[1] The case of the Ringed Plover and that of the Common Buzzard have previously been described by me (Salomonsen 1951, p. 184).

larger *B. c. occidentalis* (wing 451—485) breeds from S. Alaska to British Columbia, where it is mainly resident. Of the eastern forms the smallest one, *B. c. hutchinsii* (wing 370—405), breeds in the Eastern Arctic and winters in Texas and Mexico. The intermediate *B. c. parvipes* (wing 420—430) breeds in the interior of northern Canada and winters in the southern U.S.A. from California to Louisiana. The regions south of the breeding area of *B. c. parvipes* are inhabited by the largest forms (*moffitti*, *interior* and *canadensis*) with wing measuring 465—495. They are partly resident, but the greater part move southwards along the Atlantic States, sometimes to the Gulf Coast westwards to Louisiana. Recent ringing of *B. c. interior* on the breeding places at the southeastern coast of Hudson Bay has shown that this population winters along the Atlantic coast from Cheasapeake Bay to the Lake Mattamuskeet area in North Carolina (Hanson and Griffith 1952, p. 1—22).

In the Bean-Geese (*Anser fabalis*) the northern "Tundra-Geese" are slightly smaller than the southern "Taiga-Geese". The latter winter from Turkestan westwards to Central and South Europe, while the Tundra-Geese mainly winter in S.E. China and Japan (cf. also Johansen 1945, p. 119). The smallest form, *A. f. brachyrhynchus*, is partly high-arctic and winters in temperate Europe.

Above such cases only have been discussed in which the populations differed in body-size. There are of course many other instances of leap-frog migration, and in some of them the populations involved do not differ in proportions. As an example can be mentioned *Phylloscopus inornatus*, in which the nominate form breeds in Siberia and winters in the area from Burma and South China to Malaya, while *P. i. mandelli* breeds in Kansu and Szeshwan and winters in Sikkim and North Burma. The two races are identical as regards body-size.

In most species more than one migratorial trend can be distinguished. In the Mallard (*Anas platyrhynchos*), the migration of which has been thoroughly studied by means of ringing, the Greenland and the boreal population show a clear example of migration type V (cf. the table, p. 25), and the European population demonstrates both synhiemy (based on abmigration) and local allohiemy, and, in addition, some populations have a tendency to leap-frog migration.

Crosswise Migration.

In a small number of birds the migration routes of neighbouring populations cross each other, as shown as migration type XVII in fig. 13. This is a rare form of migration; I know of a few cases only. There is no particular evolutionary interest attached to the crosswise migration, only it symbolizes an urgent need for allohiemy; the populations attempt, so to speak, with all means to keep clear of each other in the wintering grounds,

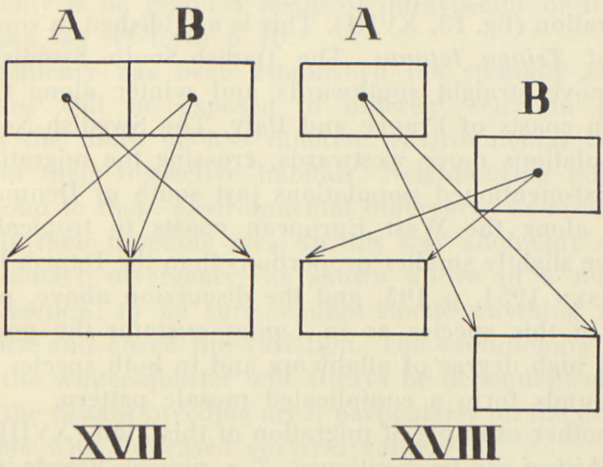

Fig. 13. Two types (XVII—XVIII) of Crosswise migration in allohiemic populations. For further explanation cf. text to fig. 1, p. 10.

and this sometimes results in complicated arrangements. This is most clearly seen in the East Astatic forms of *Lanius* (*collurio*) *cristatus*, as demonstrated by STRESEMANN (1927, map tafel II). The East Siberian *L. c. cristatus* winters in India, western Burma and the Malayan Peninsula, the Japanese *L. c. superciliosus* in Indochina, Sumatra, Java and the Lesser Sunda Islands. In order to reach to Sumatra from Indochina *L. c. superciliosus* crosses Malaya, which is inhabited in winter by *cristatus*. The Chinese *L. c. lucionensis* has two isolated wintering grounds. The first one, which is much the larger, is situated on the Philippines, northern Borneo and northern Celebes. In order to get there it has to cross the migration route of *superciliosus* in southern China. The other wintering ground of *lucionensis* is the Andaman and Nicobar Islands, which are reached by an overcrossing in Burma

of the winter-ground of *cristatus*. The information about this restricted and isolated winter-quarter rests on HUME's and RICHMOND's notes, according to STRESEMANN (1927, p. 72). It appears that *lucionensis* is very common in winter on the Andamans and Nicobars. It can be added that the Zoological Museum in Copenhagen possesses 8 skins of this form collected on the Andamans by F. A. DE ROEPSTORFF. The only clear-cut examples of crosswise migration so far known in American birds is found in *Dendroica p. palmarum* and *D. p. hypochrysea*.

In a few cases crosswise migration is combined with leapfrog migration (fig. 13, XVIII). This is established in some populations of *Tringa totanus*. The Danish-South Swedish populations move straight southwards and winter along the Mediterranean coasts of France and Italy. The Swedish-North Russian populations move westwards, crossing the migration route of the first-mentioned populations just south of Denmark, and continue along the West European coasts to tropical Africa. They have slightly smaller proportions than the Danish birds (cf. SALOMONSEN 1954, p. 105, and the discussion above, p. 47 and fig. 12). In this species as in *Lanius cristatus* the populations display a high degree of allohiemy and in both species the wintering-grounds form a complicated mosaic pattern.

As another example of migration of this kind (XVIII, fig. 13) *Turdus sibiricus* can be mentioned. *T. s. sibiricus* breeds in Siberia and winters in the region from South China and Burma south to Java and Borneo. *T. s. davisoni* breeds in Japan and winters in Burma; it is slightly larger than the nominate form.

Discussion and Conclusion.

I have endeavoured to demonstrate the evolutionary significance of natural selection by environment in the winter-quarters of migratory birds. The extrinsic factors of importance for evolution operate in a similar way in the breeding area and in the winter-quarter. It is now a well-established fact that the spatial replacement of populations tends to modify the members of the panmictic units and may lead to morphological differen-

tiation. A similar spatial segregation in the winter-quarter is achieved in species with allohiemic populations. A development of allohiemy, consequently, is a necessary requirement if the environmental factors in the winter-quarter have to contribute to the development of diversity. Although in many species the populations are synhiemic a certain degree of allohiemy has been established in the greater part of migratory species, as has been shown in this paper. In a number of species the allohiemy is complete or almost complete. This widespread development of allohiemy is no doubt a result of intraspecific or intergroup competition, as set forth p. 10.

If allohiemy has been established the spatially segregated populations will be exposed to different selection pressures owing to the more or less different environmental conditions present in their respective habitats. Neighbouring populations will respond to these environmental differences as accurately as they do in their breeding area. In this way allohiemy may lead to evolutionary divergence, as shown above in a number of cases. Selection, to be sure, cannot create anything new, but only adjust and check the variation. The evolutionary development in the winter-quarter will always be dependent on phenomena in the distant breeding area, particularly on the occurrence of mutants with increased survival value.

The absence of gene-flow between populations will accelerate adaptive differentiation. A similar effect will be achieved by absence of dispersal in the winter-quarters of allohiemic populations. In this respect it is possible to distinguish between four situations:

1. The populations in question form a continuum both in the breeding area and in the winter-quarter (*e. g. Haematopus ostralegus ostralegus* and *H. o. osculans*).

2. The populations have separated breeding areas but form a continuum in the winter-quarters (*e. g. Tringa t. totanus, T. t. britannica* and *T. t. robusta*).

3. The populations form a continuum in the breeding area but have separated winter-quarters (*e. g. Sterna h. hirundo* and *S. h. longipennis*).

4. The populations are separated both in the breeding area

and in the winter-quarter (*e. g. Ciconia c. ciconia* and *C. c. boyciana*).

Only in the latter case is gene-flow completely prevented and selection is allowed full scope. This does not necessarily mean that the adaptive variation is greater than in other cases, also other factors being involved (the time factor, differences in selection pressure, mutation rate).

The selection in the breeding area and that in the winter-quarter may cooperate or may counteract each other. Significant for the evolutionary trend in a migratory bird is mainly the degree of difference in selection pressure to which the populations are exposed in their breeding area and winter-quarter, respectively. This leads to the establishment of the four evolutionary types, described on p. 14–15.

Allohiemy does not need to be complete in order to be of evolutionary significance. In populations with partial synhiemy, as outlined in fig. 1, II, an isolation by distance is present between the individuals inhabiting the extreme areas of the wintering ground. If the environmental differences between the extreme areas are sufficiently great, selection will tend to shift the gene frequencies in the populations inhabiting these areas. Even when selection is of a weak order it will be capable of adjusting the populations somewhat to local conditions. In this way random dispersal will be checked, because it would result in maladaptation in the individuals which strayed too far away. Consequently, the degree of allohiemy will be stabilized or may even be increased until a certain equilibrium has been established.

The state of synhiemy have certain evolutionary advantages also, which have been mentioned on p. 23.

It may be objected that too much emphasis has been laid on the evolutionary significance of allohiemy, while other factors have been neglected. It is of course well-known that influence of environmental conditions in earlier geological periods, operating for instance in isolated refugia during the glacial epoch, have been of immense importance for the evolution in holarctic birds. Rand (1948, p. 315) has drawn attention to these factors in regard of the evolution in the Canada Geese, Johansen (1945, p. 122) similarly in regard to the variation in the Bean-Geese.

I do not wish to underestimate the historical factors and am well aware that the differences between various populations in body-size which in this paper have been ascribed to selection by the present day environment in many cases may be due to isolation in previous epochs in refugia with a different climate. However, evolution was not brought to a stand still in the periods subsequent to the isolation, and in many cases adaptive diversities due to selection in recent periods have been superimposed on the more fundamental morphological characters achieved during an isolation in a distanct past. The variation in a species will usually not remain unchanged when it has been exposed to the selective forces of the environment for thousands of generations.

May allohiemy in its extreme form, when the populations in question are completely isolated in their respective winter-quarters, lead to speciation? I do not think so. Speciation requires an establishment of discontinuity in the breeding area in order to perform a complete reproductive isolation of the populations; cf. discussion by Mayr 1947, p. 263 on ecology and speciation. It is thinkable, but highly improbable, that in certain species, like geese, with strongly social wintering habits, populations isolated in the wintering grounds subsequently choose separate breeding grounds and in this way secondarily attain a reproductive isolation. I have the Canada Geese in mind particularly. In recent treatises (Aldrich 1946, p. 94; Hellmayr and Conover 1948, p. 297) these geese are split up into a number of separate species (*Branta minima, canadensis, leucopareia* and *hutchinsii*) on somewhat slender grounds. They are partly sympatric, to be sure, but hybrids are common and there is a gradual transition between some of the species; alleged ecological differences are indistinct or uncertain.

However, the importance of the principles set forth in this paper is evidenced by the fact that they hold good also in units on the species level. There is an interspecific allohiemy almost as pronounced as the intraspecific one, dealt with above, and, further, the allohiemic species follow the same rules as do the populations within the same species.

The presence of allohiemy among closely related species has been stressed by Lack and myself, as mentioned above, p. 9,

where a number of genera in which the species displayed a particular high degree of allohiemy, were enumerated. Interspecific competition was given as the cause of this development. In the Scandinavian members of the genus *Larus*, for instance, *L. fuscus* migrates to the tropics (and the subspecies are allohiemic; cf. p. 30), *L. ridibundus* to S.W. Europe, *L. canus* to the Northsea coasts, while *L. argentatus* is resident (and *Rissa tridactyla* moves to the pelagic zone of the Atlantic). In North America, where *L. argentatus* is exempted from competition with the closely allied *L. fuscus*, it moves far to the south, just as *L. fuscus* in the Old World.

The spatial segregation of related species in the winter-quarters has been emphasized also by STRESEMANN (1934, p. 666), who draws attention particularly to the fact that the northernmost species often choose the southernmost wintering grounds, *i. e.* he describes leap-frog migration carried out by a number of species (within the genera *Sylvia*, *Phylloscopus*, *Hippolais* and *Acrocephalus*), just as it was described above (p. 39) to take place in intraspecific units.

The significance of selection by environment in the winter-quarters is evident also when comparing units with specific rank, as will be demonstrated by a few examples. The Ringed Plover (*Charadrius hiaticula*), which was dealt with above (p. 46), is closely related to two other species, *Ch. semipalmatus* and *Ch. placidus*, both being monotypic. As a matter of fact, they are so nearly allied that I formerly considered them members of the same superspecies (SALOMONSEN 1930, p. 71), a view which is now known to be incorrect. The separation of the different forms of Ringed Plovers is due to historical factors, no doubt to isolation in different refugia during the glacial epoch, *Ch. hiaticula* in Europe[1], *placidus* in China and *semipalmatus* in America. *Ch. semipalmatus* breeds in the arctic of the New World, and winters in the tropics, from Louisiana to Patagonia and Chile. From a migratorial point of view it is a counterpart to *Ch. h. tundrae* of the Old World. It is even smaller than this form, the wing measuring less than 125 mm. *Ch. placidus* breeds from south-eastern Siberia far down in China, where it is partly resident, wintering from Central China to northern Burma and Tonkin, only rarely

[1] *Ch. h. tundrae* possibly in Central Siberia.

passing beyond these areas. It is very similar to *Ch. hiaticula*, but is even larger than the British population, the wing measuring 139—146 mm. When comparing all these forms it appears that they fit in with the same pattern. The smallest forms (*Ch. h. tundrae* and *Ch. semipalmatus*) spend the winter in areas in which the mean-temperature of the coldest winter month is not lower than 20° C. and where night-frost does not occur, while the biggest forms (*Ch. h. hiaticula* and *Ch. placidus*) winter in areas in which the monthly mean-temperature varies in winter between zero and 20° C. and in which night-frost may occur more or less frequently, at least in the northern part of the areas. It is noteworthy that the interspecific differences are greater than those present between the populations of *Ch. hiaticula, i. e. Ch. semipalmatus* and *Ch. placidus* have drifted farthest apart both genetically and morphologically.

In the sympatric species *Larus argentatus* and *L. fuscus* the former, resident in a temperate climate, is distinctly larger than the latter, which winters in the tropics.

A final example: In the closely allied species of North American Tanagers (*Piranga*), which has developed a considerable degree of allohiemy, the winter-quarters are distributed as follows:

		Average Wing-length:
P. flava hepatica:	Sonora to State of Mexico	103
P. rubra cooperi:	Sonora to Colima-Morelos	100
P. ludoviciana:	Central Mexico to Costa Rica	96
P. rubra rubra:	Central Mexico to Ecuador-Guiana ..	96
P. erythromelas:	Colombia to Bolivia-Peru	96

The three latter forms winter in a slightly hotter climate (mean winter-temperature higher than 25° C.) than the two former ones, which do not on the migration surpass Central Mexico, where the mean winter-temperature is 20°—25° C. These forms are of slightly larger body-size than the three others which winter further south.

Examples like these are not common, because even closely allied species are physiologically different units and morphologically have drifted so far apart that their adaptive differentiation is usually not comparable. The tendency is clear, however. In

many species-pairs which now differ considerably it is obvious that the adaptive differentiation is due to the influence of selection in allohiemic populations. The separation of the two species in such pairs is due to isolation in separated areas and is in itself not the result of allohiemy. However, allohiemy is responsible for some of the morphological characters of the present species, and this development thus forms the logical continuation of the phenomena described in this paper. In a recent paper HEMMINGSEN (1951, p. 138) draws attention to these facts, demonstrating that in a pair of closely allied species that one which winters in a warmer climate attains the smallest proportions. He gives a number of examples of such species-pairs, of which many carry out a leap-frog migration, *e. g. Sturnus* (*Spodiopsar*) *cineraceus* and *S.* (*Agriopsar*) *sturninus* (p. 148), *Erythrina rosea* and *E. erythrina* (p. 151), *Circus cyaneus* and *C. melanoleucus* (p. 153), *Ardea cinerea* and *A. purpurea* (p. 154), *Calidris tenuirostris* and *C. canutus* (p. 184), *Numenius arquata* and *N. phaeopus* (p. 184), and some more. HEMMINGSEN also draws attention to the fact that the smaller species of a pair, wintering furthest south, is the latest in spring to migrate to the north, *i. e.* it is exposed to a higher temperature also during migration. After a collective treatment of a large number of migratory East Asiatic species HEMMINGSEN (p. 204) arrives at the conclusion that "there is thus apparently in the majority of the species an association between, on the one hand, early spring migration, great body size, and relatively northern (colder) winter quarters, and, on the other hand, late spring migration, small body size and relatively southern (warmer) winter quarters«.

In order to get a closer knowledge of the evolutionary significance of bird migration it is necessary to make a detailed analysis of single species, including a study of the adaptive variation, the ecological amplitude and the influence of the environmental factors. What has been given in this paper has been only an adumbration. Nevertheless, the theories set forth may open up new possibilities and add to the understanding of the mechanisms in avian evolution.

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URIDYL TRANSFERASES, THEIR OCCURRENCE AND PHYSIOLOGICAL ROLE

BY

AGNETE MUNCH-PETERSEN, HERMAN M. KALCKAR, AND EVELYN E. B. SMITH

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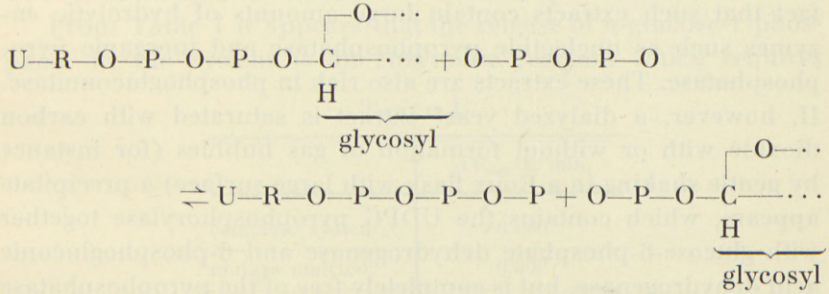
LELOIR *et al.* (1) in 1950 reported the isolation and identification of uridine diphosphoglucose as a coenzyme for the enzymic conversion of glucose-1-phosphate in extracts of galactose-adapted yeast (*Saccharomyces fragilis*). Since then increasing interest has centered around the uridine compounds, and the isolation of a number of other uridine compounds have already been reported (2), (3), (4), (5), (6), (7) as well as the demonstration of enzymic reactions in which these compounds participate (8), (9), (10), (11), (12). Mention will be made here only of one other uridine diphosphoglycosyl compound, which is present in yeast together with UDPG and was identified by LELOIR as uridine diphospho N-acetylglucose-amine (13).

In the present article we will describe an enzymic reaction which gives rise to the formation of uridine triphosphate from UDPG. The enzyme which we have classified as a uridyl transferase most likely brings about the following type of reaction:

$$\text{UDPG} + \text{PP} \rightleftharpoons \text{UTP} + \text{G-1-P} \quad (1)$$

or, more general



The following abbreviations are used: UDPG for uridine diphosphoglucose, UTP for uridine triphosphate, UDP for uridine diphosphate, UMP for uridine monophosphate, UDPAG for uridine diphospho N-acetylglucosamine, UDPGal for uridine diphosphogalactose, ATP for adenosine triphosphate, ADP for adenosine diphosphate, TPN for triphosphopyridine nucleotide, DPN for diphospho pyridine nucleotide, G-1-P for glucose-1-phosphate, gal-1-P for galactose-1-phosphate and PP for pyrophosphate.

This particular type of reaction has been observed as an important step reaction in the reversible biosynthesis of diphospho pyridine nucleotide from adenosine triphosphate and nicotinamide monoclucleotide (14), and has been called pyrophosphorolysis (14). In a similar manner flavine adenine dinucleotide can undergo pyrophosphorolytic cleavage, producing ATP and flavine mononucleotide (15). These enzymes bring about a transfer of the adenyl group and may consequently be termed adenyl transferases (16).

In this paper a detailed account will be given of the uridyl transferase reaction, and evidence will be presented that uridine triphosphate is a primary product of pyrophosphorolysis of UDPG and correspondingly that UTP incubated with α-glucose-1-phosphate in the presence of the same enzyme can give rise to the formation of UDPG. Methods for quantitative and highly specific determination of UDPG will also be presented.

Enzyme preparation.

The UDPG pyrophosphorylase is present in extracts from fresh baker's yeast as well as from dry yeast. Assay of the enzyme, as described in detail below, is based upon the determination of the glucose-1-phosphate liberated in reaction (1). If unfractionated extracts from yeast are used, observations are complicated by the fact that such extracts contain large amounts of hydrolytic enzymes such as nucleotide pyrophosphatase and inorganic pyrophosphatase. These extracts are also rich in phosphoglucomutase. If, however, a dialyzed yeast extract is saturated with carbon dioxide with or without formation of gas bubbles (for instance by gentle shaking in a Roux flask with large surface) a precipitate appears, which contains the UDPG pyrophosphorylase together with glucose-6-phosphate dehydrogenase and 6-phosphogluconic acid dehydrogenase, but is completely free of the pyrophosphatase as well as the phosphoglucomutase.

It is in general more advisable to use Warburg-Christian's Zwischenferment (17) (18), dried over phosphorus pentoxide and stored as a powder. This preparation is not only devoid of pyrophosphatase and phosphoglucomutase, but also of the 6-

phosphogluconate dehydrogenase. The pyrophosphorylase as well as the clucose-6-phosphate dehydrogenase are insoluble in water, but soluble in dilute salt solutions. Precipitation at 45 % saturation with ammonium sulphate removes large amounts of nucleoprotein and pigments, and further addition of ammonium sulphate to 60 % saturation accomplishes a precipitation of the active fraction. This fraction is dissolved in 0.05 M Tris-hydroxymethyl-aminomethane, pH 7.8; 10 mg. protein per ml. yields a clear solution which is stable with respect to the pyrophosphorylase for a couple of days when stored at 0°.

As will be described in another article by one of us (A. M-P) it is possible not only to obtain glucose-6-phosphate dehydrogenase which is free of uridyl transferase, but also to obtain highly active UDPG pyrophosphorylase without glucose-6-phosphate dehydrogenase and with very high specific activity. This was accomplished through ethanol fractionation (see (19)).

UDPGlucose assay.

The assay, as performed routinely, is an estimation of α-glucose-1-phosphate liberated from UDPGlucose upon addition of the UDPG pyrophosphorylase and inorganic pyrophosphate. The indicator system consists of TPN, phosphoglucomutase and glucose-6-phosphate dehydrogenase; the equimolar reduction of TPN is measured as an increase in density at 340 mμ.

From Table I it appears that the release of α-glucose-1-phosphate in the system is an enzymatic reaction which requires

Table I.

	ΔE_{340}/30 min.
complete system . .	0.080
mutase omitted . . .	0.003
UDPG omitted . . .	0.009
PP omitted	0.000

Participation of UDPG and PP in the uridyl transferase reaction.
Complete system: 1 ml 0.05 ml tris-hydroxymethyl aminomethane HCl, pH 7.5, 0.02 μ mol UDPG, 0.5 μmol PP. 0.5 μmol P, 0.5 μmol TPN, 10 μl mutase (0.5 mg/ml), 100 μl Zwischenferment (0.5 mg/ml).

UDPGlucose as an α-glucose-1-phosphate donor and inorganic pyrophosphate as an uridyl acceptor. Hence the reaction is decidedly a pyrophosphorolysis and not a phosphorolysis. For each 0.1 micromole/ml of UDPGlucose undergoing fission an increase of 0.622 (20) in density at 340 mμ should be observed if glucose-6-phosphate is oxidized only one step, i.e. to 6-phosphogluconic acid. This is the case in most Zwischenferment preparations as well as in assays performed with the more purified UDPGlucose pyrophosphorylase and glucose-6-phosphate dehydrogenase.

However, in unfractionated extracts from dry yeast such as are used in many experiments with *S. fragilis*, a more than one step oxidation of glucose-6-phosphate is encountered; this is also the case in the active CO_2-precipitate obtained by shaking as described above. Therefore, if a known amount of α-glucose-1-phosphate is added to the reaction mixture, it turns out that the molar increase in extinction at 340 mμ reaches a higher value than expected, but is not quite doubled. In order to get reproducible values under the latter circumstances it is advisable to add excess phosphogluconate dehydrogenase to bring about an almost complete oxidation of 6-phosphogluconic acid. In this case the average value of the factor is 1.75, i. e. for each micromole glucose-1-phosphate metabolized 1.75 micromoles of TPN is reduced (cf. (21)). The same applies if this indicator system is used in connection with the pyrophosphorolysis of UDPGlucose as seen in Table II.

As illustrated in a later section, the assay system here described has served as a specific and quantitative micromethod for deter-

TABLE II.

substrate added	ΔE_{340} calculated	ΔE_{340} found	factor	μmol true UDPG $\left(\frac{\Delta E_{340}}{0.622 \times 1.76}\right)$
0.1 μmol G-1-P	0.622	1.085	1.75	
0.04 μmol G-1-P ...	0.249	0.443	1.77	
0.04 μmol UDPG ..		0.405	(1.76)	36.8
0.02 μmol UDPG ..		0.203	(1.76)	18.4

Analysis of UDPG with crude enzyme solutions.

mination of UDPGlucose. With the recent isolation of UDPG-dehydrogenase (22) an independent and highly sensitive alternative specific method has become available.

Identification of UTP.

The fact that inorganic pyrophosphate is required in stoichiometric amounts points strongly towards the possibility of a pyrophosphorolysis (Table I). This is further supported by the fact that radioactive pyrophosphate could be shown to be incorporated gradually into a new compound which is adsorbable on norite. If the norite is eluted with 50 % ethanol, containing 0.1 % concentrated ammonia, and this eluate is subjected to paper

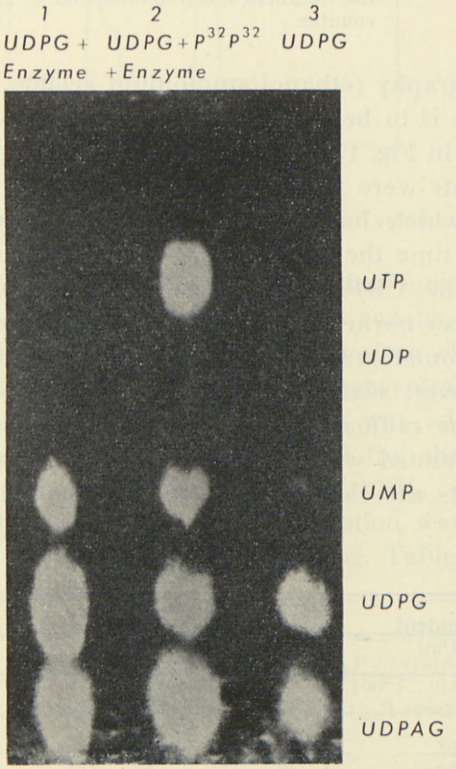


Fig. 1. Chromatogram, showing the formation of UTP from UDPG and PP. (Photographed in ultraviolet light).

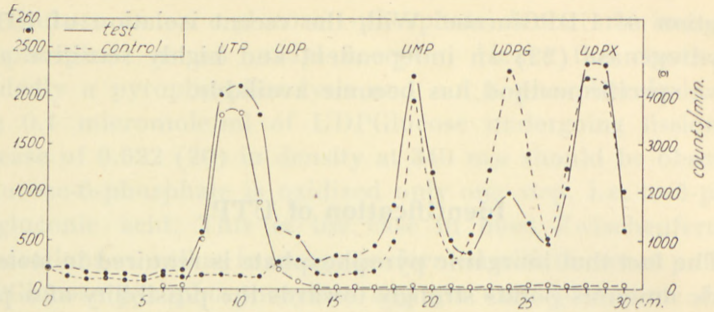


Fig. 2. Paper chromatogram of norite eluate from UDPG-pyrophosphorylase digest.
Reaction mixture: 0.2 μmol UDPG, 2 μmol inorganic pyrophosphate (8×10^4 cts./min.), 50 μl Zwischenferment (3 mg/ml), 3 ml tris-hydroxymethyl aminomethane HCl, pH 8.0, M/10, $MgCl_2$ M/100.
Control mixture: Same without pyrophosphate.
After 45 min. incubation the digest were acidified, adsorbed on norite and eluted with 50 % ethanol. Chromatographed 44 hours in neutral solvent (23). Chromatogram scanned in the Beckman spectrophotometer at 260 mμ and in the Geiger counter.

chromatography (ethanol/ammonium acetate, pH 7.5 (23); a 40 hours run is to be recommended), a chromatogram is obtained as shown in Fig. 1. It is seen that in the sample in which all the components were present during the incubation a marked spot appears which migrates slower than uridine diphosphate. At the same time the UDPGlucose spot has decreased in intensity whereas the UDPAG spot has essentially remained unaltered. This is also borne out by the results obtained by scanning the paper chromatogram with respect to ultraviolet absorption (Fig. 2). Moreover, scanning for radioactivity shows (cf. same Fig.) that all the radioactivity is confined to the new spot. The new spot was eluted with distilled water and subjected to analyses. The results are shown in Table III. The UTP-concentration of

Table III.

UTP-content μmol/ml	counts/min/μmol		P_7 μg/ml	
(calculated from E_{260})	UTP	P^{32}-P^{32} added	found	calculated from E_{260}
0.133	42×10^3	40×10^3	8.95	8.23

Analysis of UTP-solution, obtained from paper chromatogram (Fig. 1).

the solution was derived from the absorption value at 260 mμ, and it is seen that with respect to both radioactivity and 7 min.'s hydrolysable phosphate the values found agree with those calculated for UTP.

When larger amounts of UTP were prepared, the incubation mixture was adsorbed on an anion exchange column (Dowex

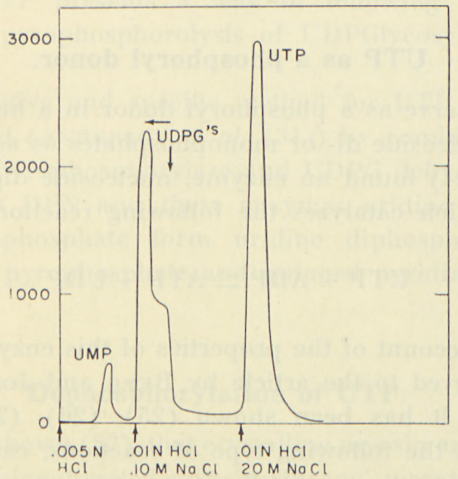


Fig. 3. Elution of UTP from a Dowex 2 Cl^- column.

No. 1) and eluted with solvents of increasing ionic strength. The results are shown in Fig. 3. In general it can be stated that UTP requires 0.2 M sodium chloride or potassium chloride for elution, while ATP is eluted at lower salt concentrations. The uridine polyphosphate present in the eluate was adsorbed on charcoal which was washed with water, and the charcoal was eluted with 50 % ethanol, containing 0.1 % NH_3. After evaporation of the ethanol the concentrated solution was analyzed for uracil and for total and labile phosphorus. Table IV shows

Table IV.

uracil/PP	uracil/P total	% P liberated per hour at 100° C., 0.01 M HCl
1.18	2.7	50

Analysis of uridine polyphosphate, eluted from Dowex 2 Cl^- with 0.01 M HCl, 0.2 M NaCl (Fig. 3).

that the new compound contains close to three phosphorus atoms per uracil molecule, and that the two phosphate groups are acid labile, although less so than those of ATP. It is known that UDP possesses an organic pyrophosphate linkage which likewise is more acid stable than the corresponding linkage in ADP (cf. LELOIR *et al.* (1)).

UTP as a phosphoryl donor.

UTP can serve as a phosphoryl donor in a number of reactions with nucleoside di- or monophosphates as acceptors. BERG and JOKLIK (24) found an enzyme, nucleoside diphosphokinase ('nudiki'), which catalyzes the following reaction:

$$UTP + ADP \rightleftharpoons ATP + UDP$$

For detailed account of the properties of this enzyme system the reader is referred to the article by BERG and JOKLIK (24).

Moreover, it has been shown (25), (26), (27), that UTP participates in the following type of reactions, catalyzed by enzymes present in yeast and liver extracts.

$$UTP + 5\text{-}AMP \rightleftharpoons ADP + UDP$$

$$ATP + UMP \rightleftharpoons ADP + UDP$$

These enzymes were named 5-nucleotide kinases (28).

In those reactions, i. e. the 'nudiki' and the 5-nucleotide kinases, UTP serves as a primary phosphoryl donor. However, in a number of other transphosphorylating reactions UTP seems to play a secondary role only as shown by BERG and JOKLIK (28). In the creatine kinase UTP is totally inactive without the ADP-'nudiki' system as participants, i. e. ATP is the primary phosphoryl donor. The same seems to be the case with yeast hexokinase although a very slow direct reaction seems not to be excluded.

UTP can be formed from UDP by phosphorylation with phosphopyruvate (KORNBERG (29)). It is not yet quite certain whether this phosphorylation is direct or goes through the ATP-ADP system.

Enzymic assay of UTP.

Assay of UTP can be carried out by the method of BERG and JOKLIK (24) using nucleoside diphosphokinase and catalytic amounts of ADP. The ATP formed is estimated by the hexokinase method of KORNBERG and PRICER (30). This method of determining UTP presents a way of following spectrophotometrically the pyrophosphorolysis of UDPGlycosyls other than UDPG.

A new sensitive and specific method for UTP estimation is being developed (ANDERSON *et al.* (31)) by combining two enzymes, UDPG pyrophosphorylase and UDPG dehydrogenase. In the presence of DPN and these enzymes uridine triphosphate plus glucose-1-phosphate form uridine diphospho glucuronic acid, inorganic pyrophosphate and reduced pyridine nucleotide.

Dephosphorylation of UTP.

It has been shown (32), that crystalline myosin and the 'heavy' fraction of trypsine-digested myosin ('heavy' meromyosin) bring about a dephosphorylation of UTP which is 3 to 5 times faster than that of ATP. The mechanism of this dephosphorylation must be more complex than one would anticipate, and will be the subject of discussion in a separate paper (33). STROMINGER *et al.* (34) have found recently that extract from acetone powder of pigeon liver brings about a dephosphorylation of UTP and UDP which is about 20 times faster than that of ATP to ADP. The mechanism of this reaction is definitely complex; it seems that UDP and not UTP serves as a phosphoryl donor in this system.

Action of UTP on various biological systems.

The reported action of UTP on the superprecipitation of actomyosin and on bioluminescence seems most likely to be indirect and to go through the ATP system by means of 'nudiki' although the mechanism of action in the case of actomyosin is still under discussion.

UTP as uridyl donor.

The transfer of the uridyl moiety of UTP to acceptors like α-glucose-1-phosphate and α-galactose-1-phosphate seems to be a specific reaction for UTP.

$$UTP + \alpha\text{-glucose-1-phosphate} \rightarrow UDPGlucose + PP$$

If UTP is incubated with α-glucose-1-phosphate in the presence of the uridyl transferase described above, UDPGlucose is

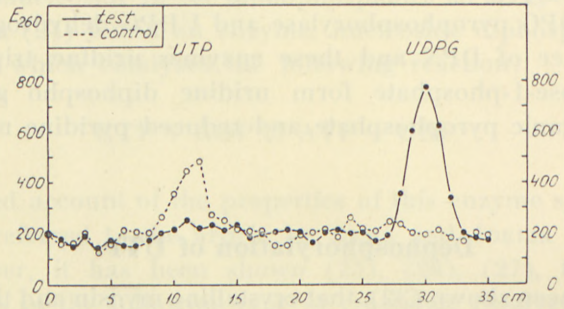


Fig. 4. Paper chromatogram of norite eluate from UTP-pyrophosphorylase digest.
Reaction mixture: 0.2 μmol UTP, 10 μmol α-glucose-1-phosphate, 100 μl inorganic pyrophosphatase, 50 μl Zwischenferment (3 mg/ml), 1 ml tris-hydroxymethyl aminomethane HCl, pH 8.0, M/10, $MgCl_2$ M/100.
Control mixture: Same without α-glucose-1-phosphate.
After 50 min. incubation the digests were acidified, adsorbed on norite and eluted with 50 % ethanol. Chromatographed 44 hours in neutral solvent (23). Chromatogram scanned in the Beckmann spectrophotometer at 260 mμ.

In the norite filtrates inorganic phosphate was precipitated as Mg-NH_4 salt, washed with dilute NH_3 and dissolved in 150 μl 0.2 M H_2SO_4. Counting of the samples in the Geiger counter gave the following results, expressed as counts per minute:

Control	Test
186	3660

formed as appears from the chromatogram scanned in U. V. (Fig. 4). It can be seen that in the sample which is incubated with all components present, the UTP spot has disappeared, and a U.V. absorbing spot located corresponding to UDPGlucose has appeared. The formation of UDPGlucose can also be demonstrated by enzymatic assay of the digest. It is seen from Table

TABLE V.

	% G-1-P consumed	μmoles present in norite-eluate		% UDPG formed
		UDPG	UV-absorbing compound	
control		0.00	0.200	
complete.....	46	0.135	0.315	43

Enzymatic synthesis of UDPG.

Equimolar amounts of UTP and G-1-P were incubated with the UDPG-pyrophosphorylase. After 30 min. the digest was acidified, spun and treated with norite. In the norite filtrate G-1-P was determined by addition of phosphoglucomutase, Zwischenferment and TPN. The norite eluate was analyzed for UDPG by means of pyrophosphorylase, phosphoglucomutase, Zwischenferment and TPN. In the control G-1-P was omitted.

V that the α-glucose-1-phosphate was consumed to an extent which corresponds to a reaction in which half of the UTP is consumed. The assay of the norite eluate with UDPGlucose pyrophosphorylase showed correspondingly that 43 % of the total uridine compounds appeared as UDPGlucose in the filtrates from the complete digest.

The application of a P^{32}-labeled uridyl acceptor was used as a third approach. In this case, illustrated in Fig. 5, P^{32}-labeled

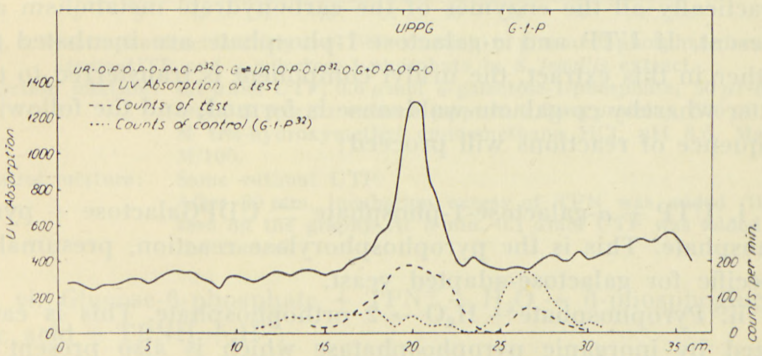


Fig. 5. Formation of P^{32}-labeled UDPG.

Paper chromatogram showing the reaction of UTP with G-1-P^{32}. Abscissa: Distance from starting line; ordinate: Extinction × 10^3 at 260 mμ. Reaction mixture: 0.5 μmol UTP, 8.5 μmol G-1-P^{32} (6500 cts./min.), 100 μl inorganic pyrophosphatase, 50 μl Zwischenferment (3 mg/ml), 1 ml tris-hydroxymethyl aminomethane HCl, pH 7.5, M/10. Control mixture: Same without UTP. After 45 min. incubation the digest were treated as described in Fig. 2. Chromatographed 22 hours in acid solution (23).

α-glucose-1-phosphate was used as uridyl acceptor and UTP as uridyl donor. It can be seen that in the filtrate from the complete digest an intensive U.V. absorbing spot carrying radioactive P^{32} appears at the location corresponding to UDPGlucose. At the same time the radioactivity at the location corresponding to glucose-1-phosphate has decreased markedly. Experiments with various uridyl acceptors and in which the UTP phosphorus is P^{32}-labeled show that larger amounts of pyrophosphate were liberated when an active uridyl acceptor was present than in a control without acceptor. In this way it could be shown that a Zwischenferment from ordinary brewer's yeast with UTP as uridyl donor could not use only α-glucose-1-phosphate as acceptor, but also, although to a much smaller degree, α-galactose-1-phosphate; β-glucose-1-phosphate, however, was totally inactive. In *S. fragilis* the same technique can be used.

By means of the recently isolated UDPG-dehydrogenase (22) the *de novo* formation of UDPG can be followed spectrophotometrically.

The fourth approach was to see whether UTP could serve as precursor for co-galacto-waldenase in a dialyzed extract of galactose-adapted yeast. In such an unfractionated dialyzed extract from *S. fragilis* a number of co-enzymes are absent, but practically all the enzymes of the carbohydrate metabolism are present. If UTP and α-galactose-1-phosphate are incubated together in this extract, the uridyl component is transferred to the latter whereby co-galacto-waldenase is formed, and the following sequence of reactions will proceed:

i. UTP + α-galactose-1-phosphate $\rightleftarrows$ UDPGalactose + pyrophosphate. This is the pyrophosphorylase reaction, presumably specific for galactose-adapted yeast.

ii. Pyrophosphate + $H_2O \rightarrow$ 2 orthophosphate. This is catalyzed by inorganic pyrophosphatase which is also present in crude *S. fragilis* extracts.

iii. UDPGalactose $\rightleftarrows$ UDPGlucose. This is catalyzed by an inversion enzyme (Galacto-waldenase), specific for galactose-adapted yeast (35).

iv. UDPGlucose + α-galactose-1-phosphate $\rightleftarrows$ UDPGalactose

+ α-glucose-1-phosphate. This is catalyzed by a non-pyrophosphorolytic uridyl transferase presumably specific for galactose-adapted yeast (11).

v. α-glucose-1-phosphate ⇄ glucose-6-phosphate; catalyzed by phosphoglucomutase, which is also present in unfractionated *S. fragilis* extracts. Glucose-6-phosphate accumulates, and upon addition of TPN a very rapid reduction takes place corresponding to step vi.

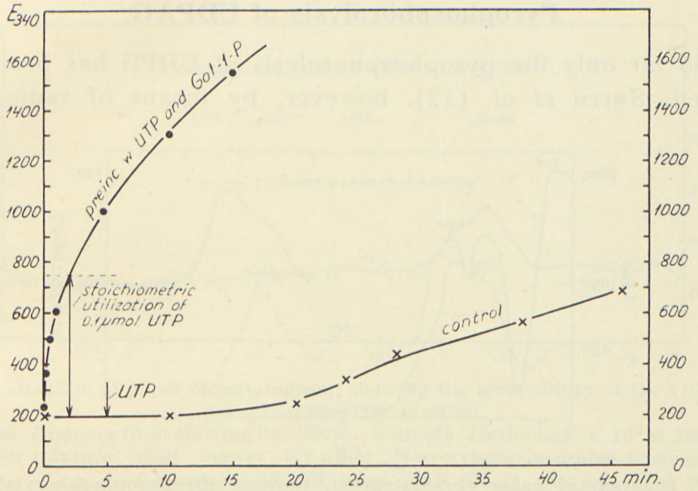


Fig. 6. Spectrophotometric analysis (TPN reduction) of glucose-6-phosphate formed from UTP and α-galactose-1-phosphate in *S. fragilis* extract.

Reaction mixture: 0.1 µmol UTP, 0.6 µmol α-galactose-1-phosphate, 50 µl dialyzed *S. fragilis* extract (approx. 2,5 mg protein), 500 µl 0.1 M tris-hydroxymethyl aminomethane HCl, pH 8.0, $MgCl_2$ M/100.

Control mixture: Same without UTP.

After 30 min. incubation excess of TPN was added (time zero on the graph). At 5 min. 0.1 µmol UTP was added to the control.

vi. Glucose-6-phosphate + TPN^+ + H_2O → 6-phosphogluconic acid + TPNH + H^+.

That the reaction, as measured by the reduction of TPN, proceeds beyond stoichiometric amount of UTP added (see Fig. 6), is caused by the non-pyrophosphorolytic uridyl transferase in step iv, which in conjunction with step iii tends to convert all the α-galactose-1-phosphate present into glucose-1-phosphate.

Incubation of extracts of *S. fragilis* with each component separately does not yield glucose-6-phosphate.

The presence of 'nudiki' in crude *S. fragilis* extracts in addition to the six other step enzymes mentioned above should account for the fact that ATP + UDP + α-galactose-1-phosphate also bring about formation of co-galacto-waldenase (36).

Pyrophosphorolysis of UDPAG.

So far only the pyrophosphorolysis of UDPG has been discussed. Smith *et al.* (12), however, by means of radioactive

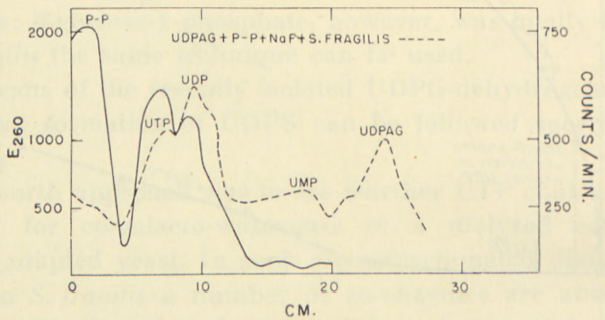


Fig. 7. Diagram of paper chromatogram, showing the pyrophosphorylation of UDPAG in extract of *S. fragilis*.
Abscissa: Distance from starting line; ordinate: Extinction $\times 10^3$ at 260 mμ.
Reaction mixture: 0.2 μmol UDPAG, 1 μmol PP (54 $\times 10^3$ cts./min.), 20 μmol NaF, 150 μl enzyme, 1 ml tris-hydroxymethyl aminomethane HCl, pH 7.5, 0.05 M.
After 30 min. incubation the digest was treated as described in Fig. 2.
Legend: - - - - - - - - - - Extinction $\times 10^3$ at 260 mμ
———— counts/min.

pyrophosphate reported the presence in liver nuclei of an enzyme which catalyzes the pyrophosphorylation of uridine diphospho (-N-acetyl)-glucosamine. This enzyme has later been isolated and purified, and the pyrophosphorolysis was demonstrated spectrophotometrically (37).

Furthermore, it is found that yeast extracts catalyze the formation of UTP from UDPAG and PP; if UDPAG and P^{32}-labeled pyrophosphate are incubated with extracts of *S. fragilis*, the formation of radioactive UTP can be demonstrated by paper

chromatography and subsequent scanning of the chromatogram (Fig. 7). Fluoride was added to the incubation mixture to suppress the activity of inorganic pyrophosphatase which is present in abundant amounts in the crude extracts of *S. fragilis*.

Also this reaction can be reversed. N-acetyl-glucosamine-1-phosphate was prepared from purified UDPAG in the following way: 0.5 μmoles of UDPAG were hydrolyzed with 0.1 M $Ba(OH)_2$ for 15 min. and neutralized with H_2SO_4. The centrifuged solution

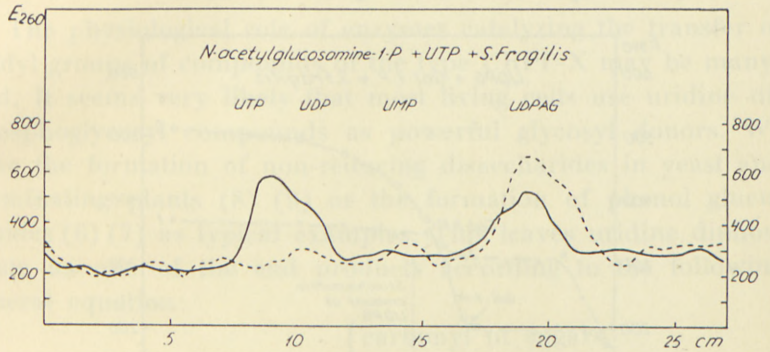


Fig. 8. Diagram of paper chromatogram, showing the reversibility of the UDPAG pyrophosphorylase reaction.
Abscissa: Distance from starting line in cm.; ordinate: Extinction $\times 10^3$ at 260 mμ.
Reaction mixture: (full curve) 0.2 μmol N-acetylglucose-amine-1-phosphate; 0.5 μmol UTP, 20 μmol NaF, 20 μl enzyme, 1 ml 0.05 M tris-hydroxymethyl aminomethane HCl, pH 7.5.
Control mixture: (dotted curve) 0.1 μmol UDPAG.
After 30 min. incubation the digest was treated as described in Fig. 2.

was passed through a column of Dowex 50 and evaporated to a small volume. The solution was chromatographed on paper for 20 hours in acid solvent (23). The N-acetyl-glucosamine-1-phosphate was localized by spraying a simultaneously run marker-chromatogram with $HClO_4$-molybdate mixture (38) followed by heating at 85° for 7 min. An aqueous eluate of the original spot contained no U.V. absorbing compounds. When the N-acetyl-glucosamine-1-phosphate was incubated with UTP in the presence of *S. fragilis* extract and sodium fluoride as above, formation of UDPAG could be demonstrated as seen in Fig. 8.

Non-pyrophosphorolytic transfer of uridyl groups.

It has been shown (11) that extracts of galactose-adapted *S. fragilis* contain an enzyme which catalyze the following reaction:

$$\text{UDPGlucose} + \alpha\text{-gal-1-P} \rightarrow \text{UDPGal} + \alpha\text{-G-1-P}$$

An example of this reaction is given in Fig. 9. It is seen (curve 2) that upon addition of gal-1-P to UDPG and with no

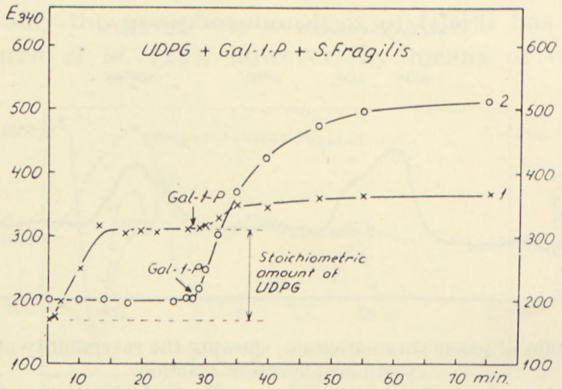


Fig. 9. Spectrophotometric demonstration of non-pyrophosphorolytic transfer of uridyl groups.
Abscissa: Time in min.; ordinate: Extinction $\times 10^3$ at 340 mμ.
Reaction mixture: 1. 0.025 μmol UDPG, 1 μmol PP, 30 μl dialyzed *S. fragilis* extract, 0.5 μmol TPN, 1 ml tris-hydroxymethyl aminomethane HCl, pH 8, 0.05 M.
2. same without PP.
After 28 min. incubation 0.5 μmol α-gal-1-P was added to each cuvette.

PP present a rapid reduction of TPN occurs, indicating that G-1-P is formed and subsequently converted to G-6-P and 6-phosphogluconic acid according to the sequence on page 14; here also the reaction will proceed beyond the stoichiometric amount of UDPG, due to the presence of galacto-waldenase. The stoichiometric amount of UDPG is derived from curve 2, where addition of PP causes pyrophosphorolysis of the compound with subsequent reduction of TPN. Addition of gal-1-P to this sample caused no appreciable further reduction of TPN, although a reaction between gal-1-P and the UTP formed was expected.

This must mean that either the proper uridyl transferase was not active in this particular *fragilis* extract, or, more likely, the UTP was rapidly broken down in the crude *fragilis* extract. Hence, at the time when gal-1-P was added, only small amounts of UTP were present, insufficient to yield significant amounts of UDPGal (and subsequent formation of UDPG) with gal-1-P.

Discussion.

The physiological role of enzymes catalyzing the transfer of uridyl groups of compounds of the type URPP-X may be manyfold. It seems very likely that most living cells use uridine diphosphoglycosyl compounds as powerful glycosyl donors. We have the formation of non-reducing disaccharides in yeast and germinating plants (8) (9) or the formation of phenol glucuronides (6) (7) as typical examples. This leaves uridine diphosphate as one of the end products according to the following general equation:

$$\text{U—R—P—O—P—O-glycosyl} + \left\{\begin{array}{c}\text{carbonyl of sugars}\\ \text{or}\\ \text{phenol groups}\end{array}\right. \rightleftharpoons \text{U—R—P—O—P—O} + \left\{\begin{array}{l}\text{nonreducing disac-}\\ \text{charides or}\\ \text{phenol glucuronides}\end{array}\right.$$

The 'discharged' uridine nucleotide (U-R-P-O-P-O, i.e. UDP) can be 'recharged' by the following enzymic mechanism operating in most cellular systems (24)

$$\text{U—R—P—O—P—O} + \text{A—R—P—O—P—O—P—O} \rightleftharpoons \text{U—R—P—O—P—O—P—O} + \text{A—R—P—O—P—O}$$

The UTP (U-R-P-O-P-O-P-O) reacts subsequently with α-glucose-1-phosphate (and presumably also with other glycosyl-1-phosphates) according to the equation:

$$\text{U—R—O—P—O—P—O} + \text{O—P—O-glycosyl} \rightleftharpoons \text{U—R—O—P—O—P-O-glycosyl} + \text{O—P—O—P—O}$$

Since the reaction is most adequately described as a transfer of the uridyl groups (U-R-O-P-) from pyrophosphate to a glycosyl-1-phosphate the class of enzymes was called uridyl transferases.

It can be seen that in the presence of ATP, the proper glycosylphosphate compound and glycosyl acceptor the uridine diphosphate acts catalytically, since it is formed through a cycle (the UDP cycle).

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DEDICATED TO PROFESSOR NIELS BOHR ON THE OCCASION OF HIS 70TH BIRTHDAY

ON INFORMATION TRANSFER FROM NUCLEIC ACIDS TO PROTEINS

BY

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København 1955
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One of the most important problems of today's theoretical biology is the problem of the transfer of the hereditary informations from the chromosomes, where they are presumably stored in the form of long polynucleotide sequences, to the enzymes which, as all other proteins, are represented by long polypeptide chains. Mathematically the problem reduces to finding a procedure by which a long number written in fourdigital system (four bases forming the molecules of nucleic acid) can be translated in a unique way into a long word formed by twenty different letters (twenty amino acids which form protein molecules). The fact that number 20 represents the number of different triplets (with disregard to order) which can be formed out of 4 different elements suggests that each amino acid in the resulting polypeptide sequence is determined by a group of three bases in the corresponding section of polynucleotide chain. Some time ago the author attempted to establish such a translation mechanism on the basis of Crick and Watson's model of Deoxyribonucleic Acid (DNA) molecule[1]. It turned out, however, that the translation mechanism suggested by DNA structure ("diamond code") leads to a contradiction with the actually observed sequences of amino acids in certain protein molecules. This negative result is presumably due to over-simplification of the original picture, since it seems, indeed, that the transfer of informations from chromosomes to enzymes is a two-step process. First the informations stored in DNA molecules are transmitted to the molecules of RNA (Ribonucleic Acid) which move out into the cytoplasm of the cell and form the so-called microsomes. The second part

[1] G. Gamow. Dan. Biol. Medd. 22, no. 3 (1954).

of the process consists in synthesizing the proteins according to the informations carried by RNA-base sequences. The presence of such double coding makes the analysis of information transfer much more difficult.

The most promising biological material for the study of information transfer is presented by viruses, since it has been shown that in this case (at least for bacterial viruses, or phages) the virus protein for the progeny is synthesized directly by the nucleic acid of the original virus particles which had penetrated into the cytoplasm of the host cell[1]. If we limit our studies to plant viruses in which nucleic acid is of RNA-type (rather than DNA-type, as in all animal viruses or phages), we may also hope that we are dealing with only one-step information transfer.

Very careful analysis of both nucleic acid and protein constitution is available in the case of Tobacco Mosaic Virus[2], and is shown in Tables I and II.

TABLE I.

Relative amounts of bases (in moles) in RNA from TMV.

	1. Adenine	2. Guanine	3. Cytosine	4. Urosil
TMV	0.31	0.25	0.18	0.26

TABLE II.

Relative amounts of amino acids (in moles) in proteins from TMV.

Amino Acid	TMV	Amino Acid	TMV
1. Alanine	0.070	11. Leucine	0.087
2. Arginine	0.069	12. Lysine	0.012
3. Asp. acid	0.030	13. Methionine	0.000
4. Asparagine	0.090	14. Phenylalanine	0.062
5. Cysteine	0.010	15. Proline	0.061
6. Glu. acid	0.047	16. Serine	0.083
7. Glutamine	0.047	17. Threonine	0.102
8. Glycine	0.031	18. Tryptophane	0.012
9. Histidine	0.000	19. Tyrosine	0.026
10. Isoleucine	0.061	20. Valine	0.097

[1] A. D. HARSHEY and M. CHASE. J. Gen. Physiol. **36**, 39 (1952).
[2] C. A. KNIGHT. J. Biol. Chem. **171**, 297 (1947); **197**, 241 (1952).

If we assume the hypothesis that each amino acid in the protein structure is determined by a triplet of bases in RNA chain, we may expect that relative abundance of different amino acids

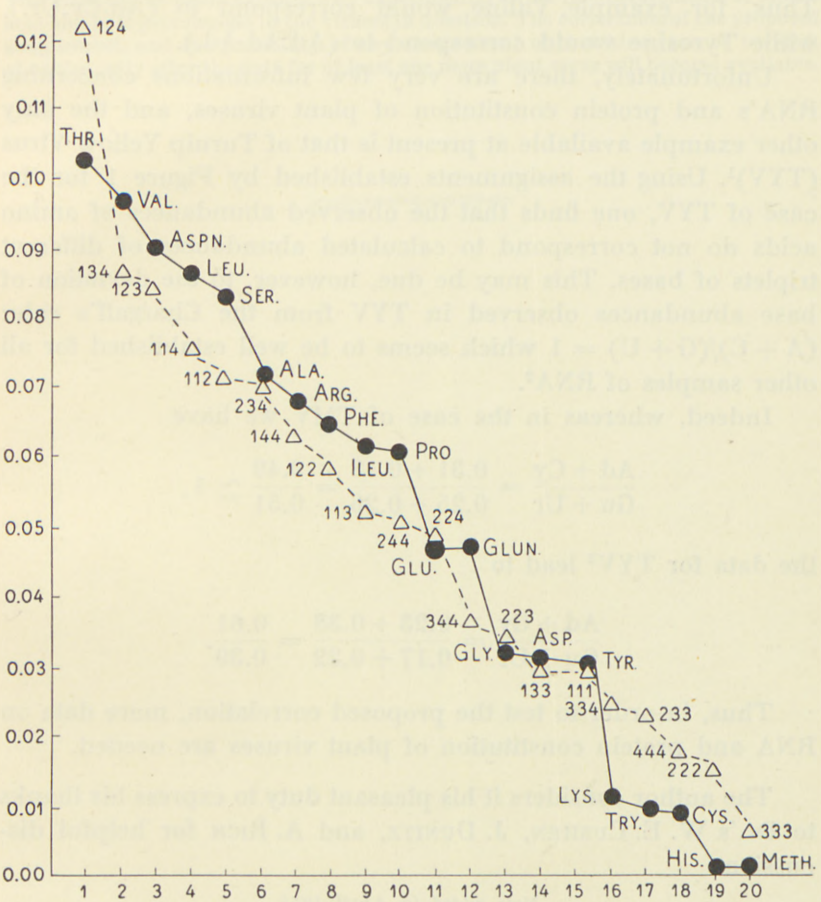

Fig. 1

will be given by the products of relative abundances of the three corresponding bases. (Because of multiplicity of various types of triplets the probability of *aaa*, *aab*, and *abc* types of triplets should be given the weights 1, 3, and 6).

The calculated abundance of various triplets, and the observed abundances of various amino acids, are plotted in Figure 1

in decreasing order, and we see that two sets of data are in a reasonably good agreement. If this agreement is not coincidental, it should permit the establishment of a correlation between individual units forming polynucleotide and polypeptide chains. Thus, for example, Valine would correspond to (Ad.Cy.Ur.), while Tyrosine would correspond to (Ad.Ad.Ad.).

Unfortunately, there are very few informations concerning RNA's and protein constitution of plant viruses, and the only other example available at present is that of Turnip Yellow Virus (TYV)[1]. Using the assignments established by Figure 1 for the case of TYV, one finds that the observed abundances of amino acids do not correspond to calculated abundances of different triplets of bases. This may be due, however, to the deviation of base abundances observed in TYV from the Chargaff's rule: $(A + C)/(G + U) = 1$ which seems to be well established for all other samples of RNA[2].

Indeed, whereas in the case of TMV we have

$$\frac{Ad + Cy}{Gu + Ur} = \frac{0.31 + 0.18}{0.25 + 0.26} = \frac{0.49}{0.51} \simeq 1,$$

the data for TYV[2] lead to

$$\frac{Ad + Cy}{Gu + Ur} = \frac{0.23 + 0.38}{0.17 + 0.22} = \frac{0.61}{0.39}.$$

Thus, in order to test the proposed correlation, more data on RNA and protein constitution of plant viruses are needed.

The author considers it his pleasant duty to express his thanks to Dr.'s W. E. Cushen, J. Dunitz, and A. Rich for helpful discussion.

Note added in April 1955.

It was indicated to the author by his colleague Dr. M. Yčas that a reasonable agreement between amino acid constitution of *both* viruses (TMV and TYV), and the probabilities of base-triplets can be achieved if the "burden of fit" is distributed equally between the two caces. Indeed, if one makes the following assignments of the most abundant amino acids to the most probable base-triplets:

[1] R. Markham and J. D. Smith. Bioch. J. 49, 401. (1951); E. Roberts and G. B. Ramasarma. Proc. Soc. Exp. Biol. Med. 80, 101 (1952).

[2] D. Elson and E. Chargaff. Biochim. et Biophys. Acta (in press). The author is grateful to Dr. Chargaff for the opportunity to see this manuscript prior to publication.

Ala → 113; Arg → 122; Asp + Aspn → 124 + 222 (?); Glu + Glun → 144 + 223; Gly → 344; Jleu → 133; Leu → 123; Lys → 233; Phe → 244; Pro → 334; Ser → 234; Thr → 134; Vol → 114,

the observed abundances of these amino acids in both TMV and TYV agree with the calculated probabilities of base-triplets with a mean error of 20 per cent. This error can be easily explained by experimental errors in measurements of amino acid and base percentages in the viruses in question. The correctness of the proposed assignement, and the possibility of any assignement of that kind, can be verified, of course, only after the data for at least one more plant virus will become available.

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DEDICATED TO PROFESSOR NIELS BOHR ON THE OCCASION OF HIS 70TH BIRTHDAY

CONSERVATION OF SKELETAL CALCIUM ATOMS THROUGH LIFE

BY

G. HEVESY

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i kommission hos Ejnar Munksgaard

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From the earliest beginning, Professor NIELS BOHR has shown great interest in the application of radioactive indicators to the study of the conservation of skeletal atoms through life. This fact has induced the writer to contribute to this volume with a communication of the results obtained in an investigation on the conservation of skeletal calcium atoms in the adult mouse and on the fate of maternal calcium atoms through generations.

The first application of an artificially radioactive isotope as a tracer in 1934 was that of P^{32} in a study of the problem whether and to what extent the mineral constituents of the skeleton of the adult organism are replaced during lifetime[1,2,3,3a]. By using this radioactive indicator it was possible to demonstrate the dynamic nature of the building up of bone tissue. It was found that an initial rapid location of the circulating labelled phosphate in the mineral constituents of the skeleton is followed by a much slower second effect. The first effect was interpreted by us to be due to an interchange between the phosphate ions located in the surface layer of the bone apatite and in the plasma, the second one, however, to the fact that "the bone is destroyed at certain places and rebuilt under incorporation of labelled phosphate at others". Emphasis was given to the analogy between these phenomena and those observed when, in early experiments, naturally radioactive isotopes were applied as tracers. PANETH[4], when shaking solid lead sulfate with a solution containing labelled lead ions, observed an interchange of lead ions only between the uppermost molecular layer of the solid salt and the dissolved ions. In studies in which the interchange between the atoms of lead metal and the labelled lead ions of a solution, or vice versa, was investigated, the present author and others[5,6,7] found that many hundreds of atomic layers of the lead foil were converted into ions, and a corresponding number of ions into atoms,

making out the lead foil. Thus, a renewal of the constituents of a metal foil, involving dissolution and reprecipitation due to "local currents", was found to be a much deeper going process than that occurring between solid lead salts and the lead ions of the surrounding solution. In the early investigations mentioned above, it was pointed out that the rapid uptake of P^{32} during the early phase of the experiment recalls the behaviour of a lead salt placed in the solution containing labelled lead ions, the recrystallization of the mineral constituents of the skeleton reminds of the behaviour of a lead foil immerged into a solution containing labelled lead ions, however, with the difference that, in the latter case, enzymic actions are involved. Or, as it was expressed later[8], "A restricted extent of renewal of the skeleton is due to the fact that, while the P atoms of the uppermost molecular layer of the bone apatite crystals can promptly interchange with the free P atoms of the plasma (actually not the P atoms, but the phosphate ions interchange), a renewal of the main part of the apatite P can take place only when the crystal is dissolved and when new crystals are formed from the plasma; from labelled plasma, labelled crystals are formed". Subsequent experiments confirmed the correctness of these early conclusions, showing that both a surface exchange between plasma phosphate and bone phosphate, and a recrystallization, thus a dissolution of some of the apatite crystals and the formation of new ones, take place in the skeleton. Different workers, however, arrived at divergent results about the share of both processes in the interaction of plasma and bone constituents.

The introduction of autoradiographic methods into the study of bone formation by LEBLOND and assoc.[9] was a very important advance, since it became possible to visualize the rapid formation and destruction of some parts of the calcified tissue. Numerous autoradiographic investigations such as those by LEBLOND and assoc. applying P^{32}, those by COMAR et al.[10] using Ca^{45}, Sr^{89}, and P^{32}, by SKIPPER et al.[11] with C^{14}, by KIDMAN et al.[12] with Sr^{89}, by ENGFELDT et al.[13] with P^{32}, by AMPRINO and ENGSTRÖM[14] with Ca^{45}, and by BAUER[15] with Na^{22}, clearly demonstrate that a great part of the bone salt crystals are more or less unchanged until they are reached by the process of resorption.

LEBLOND's autoradiographs clearly indicate that the cir-

culating phosphate enters the skeleton either by *exchange* or by *precipitation* in definite areas with the formation of new bone. While, in the autoradiographs, the exchangeable phosphate is depicted as diffuse reactions disappearing rapidly with time, the precipitated or stable phosphate appears as localized persistent reactions.

In contradistinction to all workers in this field, ENGFELDT, ENGSTRÖM, and ZETTERSTRÖM[13] arrived at the result that even the initial uptake of P^{32} by the bone is due exclusively to some kind of recrystallization. This conclusion is based on their observation that the autoradiographic patterns of cross sections from long bones show an uneven distribution of radioactive phosphate. They found the fastest uptake of labelled phosphate to take place in Haversian systems with a low content of mineral salts. Since the major part of the tracer is found in limited areas, the initial rapid uptake of labelled phosphate –according to their view– cannot be due to an ion exchange on the crystal surface of the bone minerals, such an exchange being prevented by the organic constituents of the bone.

While there can hardly be any doubt that the main part of the renewal of the bone apatite of the skeleton is due to a recrystallization process, to a degradation and new formation of the mineral constituents of the skeleton, objections may be raised against the view that the initial uptake of P^{32} is due exclusively to some kind of recrystallization.

Uneven distribution of radioactive phosphate as shown in autoradiographic patterns of cross sections from long bones cannot be interpreted as an absence of surface interchange. According to PANETH[4,16], the whole uppermost molecular layer of crystalline salt powders interchanges with the ions of a surrounding solution, while properly crystallized surfaces like those of natural crystals fail to do so. He states that his investigations suggest that the radioactive method of determining surfaces, based on the assumption that the whole uppermost layer molecular interchanges, should be employed in those cases only for which it is established that the fundamental supposition of kinetic exchange of the entire surface is valid. If we assume the bone apatite, or part of it, as occurring in vivo, to be a properly crystallized substance, we arrive at another explanation than

that of ENGFELDT, ENGSTRÖM, and ZETTERSTRÖM, according to which the organic constituents of fresh bone are responsible for preventing surface exchange. This alternative explanation is that the bone apatite, or large parts of it, behaves like a properly crystallized substance in Paneth's experiments and not like a crystal powder.

The exchange of ions on a crystal surface is thus far from being absent and, though restricted to a fraction of that surface, is responsible for an appreciable part of the early uptake of labelled ions by the mineral constituents of the skeleton. As shown by ARMSTRONG and assoc.[17], in the course of the first ten minutes, 2 % of the skeletal calcium of the dog are replaced by labelled calcium of the plasma; this is $^1/_{10}$ only of the amount which, according to FALKENHEIM's[18, 18a] calculations, would be necessary to replace the whole uppermost molecular layer of the bone apatite, or $^1/_6$ of the amount estimated by HENDRICKS and HILL[19]. A large part of these 2 % –or even 2 %– could be due to a surface interchange in spite of the uneven autoradiographic patterns of cross sections of long bones observed by ENGFELDT, ENGSTRÖM, and ZETTERSTRÖM. In view of the high specific activity of the plasma calcium in an early stage of the experiment, to a 2 % interchange corresponds a very much higher percentage decrease in the Ca^{45} content of the plasma in the course of the first two minutes, more than 50 % of the injected radiocalcium leaving the circulation. From Ca^{45} injected into the circulation of growing hogs, COMAR and assoc.[10] found only 2 % to be present after the lapse of an hour.

In the experiments of ENGFELDT and assoc., three hours was the shortest time after which the P^{32} injected rats were sacrificed. The early phase of the experiment, in which a very rapid interchange of the mineral constituents of the bone takes place, is much shorter than three hours. When investigating the uptake of Sr^{89} by the skeleton of outgrown rabbits during the first 30 seconds, 11.7 % were found to be taken up[20], while during the first six hours –thus a 720 times longer period– only about twice as large an uptake was observed. ARMSTRONG and assoc.[17] found during the first 20 minutes an interchanges of 4 % of the skeletal calcium with plasma calcium, this amount increasing less than three times during the following 160 minutes.

A change in the concentration of the bone apatite constituting ions, and still more a variation in the concentration of enzymes involved in recrystallization of the plasma and the lymph, is bound to influence the rate of recrystallization of the skeleton. Repeated administration of bone phosphatase extract by intravenous injection was found to lead to a decrease of the mineral constituents of the bone tissue[21], which are replenished after removal of the excessive phosphatase. HASTINGS[22], when replacing the plasma of a dog by plasma of low calcium content, found that the mobilization of bone calcium increased the calcium level of the plasma almost momentarily to a normal level. Parathyroid hormon is known to exert a direct action on bone[22a]. In this connection, also CARLSSON's[23] investigation should be mentioned; he found vitamin D deficient rats to be unable to utilize their bone stores for maintaining a normal serum calcium. However, in view of the very great difference in the distribution of the mineral constituents in the bone tissue and the corresponding tendency to remove these differences, the biological recrystallization of the skeleton, as rightly emphasized by ENGFELDT and ass.[13], is not due exclusively to these processes[24].

KING raised the idea that, though conventionally, the bony framework of the body is regarded as a means of making locomotion possible, it may be that this is no more than a secondary development, the primary function of bone in the body being to act as a reservoir for the maintenance of a constant blood calcium level.

At a very early date[25, 26, 3], it has already been observed that the diaphysial phosphate is replaced by administered labelled phosphate at an appreciably lower rate than epiphysial phosphates, and similar observations were made in the investigation of the incorporation of Ca^{45} into the skeleton[27, 29]. Since the transition between diaphysial and epiphysial bone tissue is almost continuous, the specific activity of bone phosphorus or bone calcium varies considerably through the whole bone tissue. This great heterogeneity of the specific activity of the bone apatite phosphorus could be demonstrated by ZETTERSTRÖM and LJUNGGREN[30] by isolating bone fractions of different solubility and measuring their specific activity. The most soluble bone phosphorus was found to show the highest specific activity, thus the

most rapid rate of renewal. X-ray absorption and diffraction studies by AMPRINO and ENGSTRÖM[14] revealed also that the distribution of mineral components in the bone tissue is far from being uniform.

Size of the Non-Renewable Part of the Skeleton.

The extent of renewal of apatite phosphate of the skeleton can be calculated from the mean value of the specific activity of the plasma phosphate during the experiment and the value of the specific activity of the apatite phosphate at the end of the experiment. During the early part of the experiment, the sensitivity of the radioactive indicator is comparatively low, thus a strong decline in the plasma activity corresponds to a comparatively low interchange figure. In the later part of the experiment, the same activity which indicated at the start the presence of 1 mg. of phosphorus in the plasma, for example, indicates 1/100 mg., thus the sensitivity of the radioactive indicator is strongly increased. Now, a further interchange will be indicated by a very small further loss of activity. Furthermore, following the interchange of plasma and bone phosphate for a longer time interval, increase and decrease in the specific activity of the plasma phosphate may alternate due to a variation in the phosphate intake or other reasons. Thus, it encounters great difficulties, by comparing the mean specific activity of the plasma phosphate during the experiment and the specific activity of the apatite phosphate at the end of the experiment, to find a reliable value for the extent of the renewable part of the mineral phosphate of the skeleton, and similar considerations apply to the determination of the renewable part of bone calcium in contrast to that of the bone sodium. Sodium, being mainly an extracellular element, is distributed between plasma and extracellular fluid within a few minutes, a distribution which results in a decrease in the specific activity of plasma sodium to about $^1/_6$ of its original value, followed by a very slow decrease with time only. Thus, as discussed on p. 16, the extent of the renewable part of the mineral bone sodium could be calculated from specific activity data. We can, however, determine the extent of renewal of bone phosphate from specific activity data when keeping the specific activity of

the plasma phosphate at a constant level during the experiment. This result was obtained by the author and his associates[31] by daily injecting the rabbit repeatedly with labelled phosphate. After the lapse of 50 days, the phosphorus of the femur epiphysis found to have a specific activity of 30 % of that of the plasma inorganic P, thus indicating that 30 %, and only 30 %, of the epiphysial bone apatite had been renewed, a much lower renewal figure (7 %) being obtained for the diaphysial phosphorus.

This method has the disadvantage of being cumbersome. Furthermore, the results may be influenced by the time that passes between the last injection of the rabbit and the killing of the animal. Therefore, when determining the renewable fraction of the skeleton calcium of the mouse, we have chosen another procedure. Mice were bred whose skeleton was labelled throughout with Ca^{45} and the loss of the activity in the skeleton was followed with increasing age of the animals. Such mice can be obtained by administering to the mother food containing labelled calcium already weeks before gestation and continuing to feed the lactating mother and the growing offsprings with food containing labelled calcium. We assume every one of the offsprings to have the same Ca^{45} content. If we stop administering labelled food after these offsprings are outgrown, they start to interchange their labelled bone calcium with the unlabelled calcium from the food with the result that the Ca^{45} content of the skeleton decreases and, when the offspring is killed after two months, its Ca^{45} content is lower than that of another offspring killed after one month. By killing members of a litter at different dates, we can follow the processes in the skeleton for years, viz. through the lifetime of the animal.

TABLE I.

Weight and activity of new-born mice.

No.	Weight in gm.	Relative activity
1	1.8	100
2	1.3	98.5
3	1.4	93.5
4	1.2	99.5

The Ca^{45} content of every member of a litter is not strictly the same, and this applies also to the growth rate. The evidencee that a part of the curve depicted in Fig. 1 is discontinuous may presumably be due to a difference in the uptake of maternal Ca^{45} by the offspring of the same litter. The variation in the radioactivity of different members of a litter, however, is restricted and does not suffice to frustrate the applicability of the method described (cf. Table I).

Experimental.

In view of the difficulties in replacing all food calcium by labelled calcium, we added the labelled calcium as $CaCl_2$ (150 mg. per liter) to the drinking water, on the assumption that the quantity of water drunk by the mouse, kept at constant temperature, is about proportional to the intake of food which consisted of standard cakes. We started to administer two to ten weeks before parturition to 20—30 gm. mice the labelled $CaCl_2$ and continued administration of such drinking water till weaning. Then, the growing mice were given labelled drinking water until they were outgrown. From that date (when the mice were about 100 days old), administration of Ca^{45} was discontinued. The offsprings were killed at different times, and the radioactivity of the ash of their skeletons was compared. 20 mg. of bone ash were placed under the Geiger counter, and the total activity of the skeleton was calculated from the measured activity and the total ash weight. In other experiments, the radioactivity of the total body ash samples was compared.

The ratio of the activity of 20 mg. of bone ash of outgrown and of newborn mice is not a correct measure of their relative Ca^{45} content. The calcium content of the ash of the newborn being appreciably lower than that of the adult, the backscattering of the β-rays emitted by the Ca^{45} of the first mentioned samples will be lower, furthermore the consistency of the samples and, thus, the distance of the sample from the counter window may slightly differ. By measuring once the activity of a 20 mg. sample of the bone ash of newborn mice, and then that of a small known aliquot of this sample brought up to 20 mg. through addition of inactive bone ash of an adult mouse, we arrive at the result

that the activity measured of the ash of the newborn mouse has to be multiplied by 1.05 in order to make it comparable with the activity of the bone ash of adult mice.

In other experiments, new-born mice were shifted from their active mothers to inactive mothers shortly after birth; determinations were made of the percentage of maternal labelled calcium taken up by the offspring after birth and the rate of loss of these calcium atoms during growth and later.

The Ca^{45} activity of the mice remained below 0.05 μC per gm. and, in most cases, it was very appreciably less. SIMMONS and assoc.[32] observed the effect of radiation produced in mice during 108 weeks. When a dose of 0.034 μC was administered, they could not find anaemia; when the dose was raised to 0.068 μC, moderate changes in heterophylous values could be detected. In our experiments, no effect on growth or fertility due to the presence of Ca^{45} could be observed. Our main litter size was 5.7. As shown by RUSSELL[33], the litter size of mice at term is reduced as a result of irradiation during preimplantation stages with 100 r or more, and when exposed shortly after implantation, by a minimum dose of 200 r.

The composition of standard cakes fed to our mice is seen from Table II.

TABLE II. Composition of cakes fed to our mice ("Gard-bred").*

100 gm. cakes contain	
Water	7.6 gm.
Ash	2.9 -
Proteins (5.7 × N)	6.3 -
Carbohydrates	67.6 -
Ca	188 mg.
P	424 -
Fe	24 -
Combustion value (calculated according to Rubner)	400 cal.

* In Sweden, mice and rats are fed almost exclusively on these cakes, the exact composition of which was hitherto unknown. The author is much indebted to Professor E. BRUNIUS and Mrs. ESTHER SIHLBOM who most kindly made the analysis of these cakes at Statens Institut för Folkhälsan.

Results.

The results of experiments in which mice born from mothers kept on a Ca^{45} diet for weeks prior to and after parturition, and continuously kept on a Ca^{45} diet till they reached an age of about 100 days, thus were outgrown, are shown in Table III.

TABLE III.

Loss of Ca^{45} by the uniformly labelled skeleton of mice with time, indicated by measurements of the radioactivity of the skeleton of different members of a litter killed at various times. The mice were born from active mothers and were administered Ca^{45} until the first member of the litter was killed.

No. of litter	Age in days	Ca^{45} content
I	111	100
	329	66.7
	519	57.0
II	108	100
	327	90.7
	517	78.8
III	108	100
	326	88
	501	69.4
IV	115	100
	220	79.9
	393	64.4
V	106	
	106	100
	231	66
	325	63.8
VI	56	100
	129	81.4
	266	69.7
VII*	99	100
	214	77.7
	308	55.5
	392	55.9
	503	50.1

* Cheese and egg shells were added ad libitum to the standard bred diet.

The mean conservation of Ca^{45} by the uniformly labelled skeleton of the mice in the course of 390 days, representing a mean value of the duration of the experiments, works out to be 64.7 ± 7.34 per cent, the standard error of the mean being 2.78. If we disregard the last experiment in which the mice were

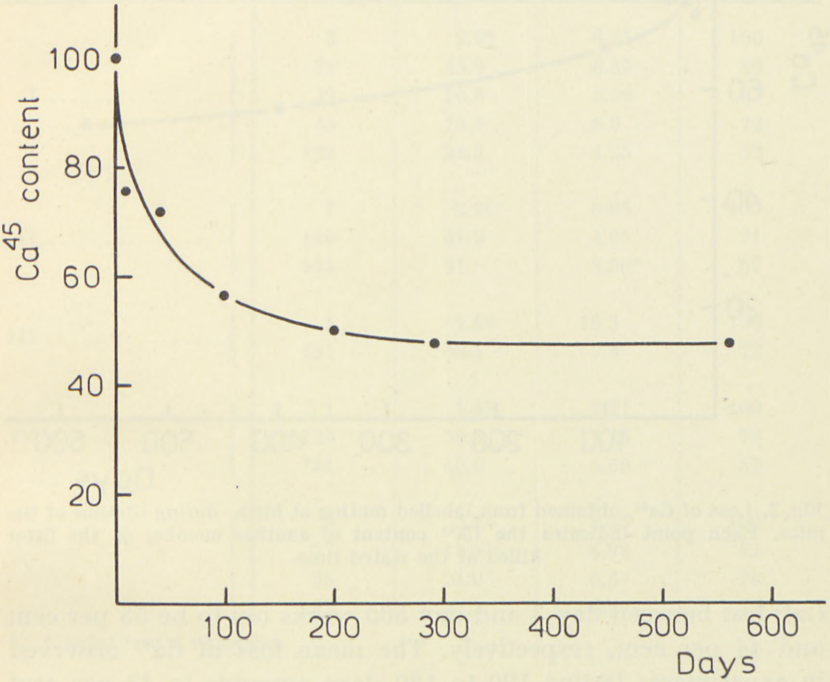

Fig. 1. Loss of Ca^{45}, obtained from labelled mother at birth, during lifetime of the mice. Each point indicates the Ca^{45} content of another member of the litter killed at the stated time.

kept on a high calcium diet, the mean value is 67.2 ± 7.86 per cent, the standard error of the mean being 3.23. Thus, $^2/_3$ of the calcium atoms present in the skeleton of the outgrown mice are present after the lapse of more than a year and can thus be considered to be unreplaceable during life.

Figs. 1 and 2 and Table IV show the results of some of our experiments in which the litter, born from active mothers, was kept from birth on a Ca^{45}-free diet. These experiments include the results obtained between the third and the 560th day after birth, thus almost the lifetime of the mouse. The percentage of

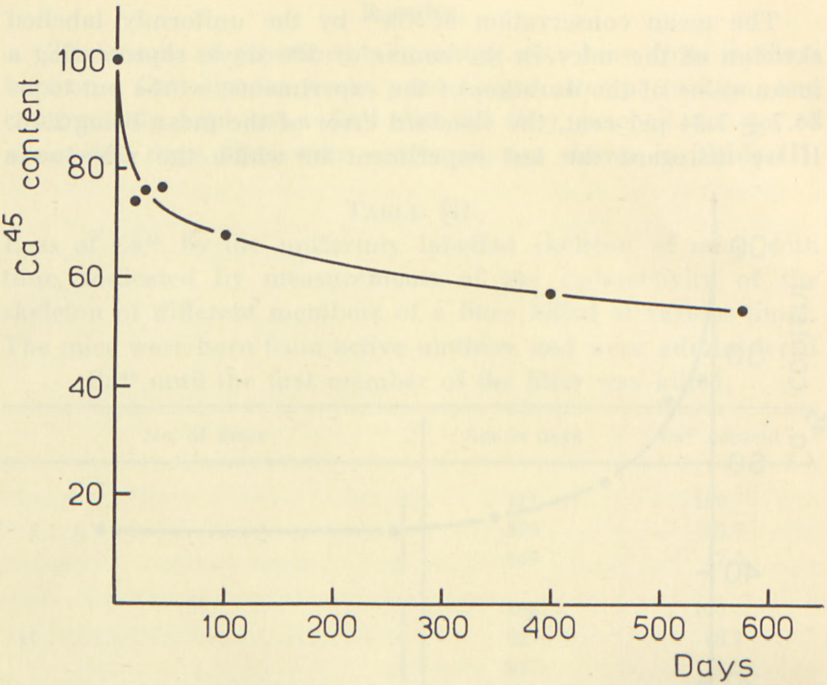

Fig. 2. Loss of Ca^{45}, obtained from labelled mother at birth, during lifetime of the mice. Each point indicates the Ca^{45} content of another member of the litter killed at the stated time.

Ca^{45} lost between day 3 and day 560 works out to be 53 per cent and 44 per cent, respectively. The mean loss of Ca^{45} observed in experiments lasting 100 to 180 days amounts to 43 per cent (Table IV). The loss of Ca^{45} during the first three days of life is less than 10 per cent; thus half of the maternal calcium atoms are preserved during life.

The calcium content of our newly born mice, weighing 1.23—1.37 gms. varied between 0.28 and 0.35 per cent of the body weight, not much differing from the calcium content of the new-born rat (4.7 gm.) for which data varying between 0.27 and 0.35 per cent are reported[42]. The calcium content of 1 gm. fresh weight of newly born mouse amounts to 0.3 times that of 1 gm. of the adult animal, which is 1.05 per cent. If all the maternal calcium atoms had the same chances to supply calcium to the offspring, and all were labelled, we would find 1 gm. of newly born mouse to be 0.3 times as active as 1 gm. of the mother.

TABLE IV. Retention of maternal calcium atoms by the offsprings.

No. of litter	Age in days	Weight in gms.	Per cent of mothers' activity present in the offspring	Number of maternal atoms present
I	3	2.95	8.25	100
	31	13.9	6.59	80
	39	16.8	5.50	67
	43	18.6	6.0	72
	103	24.3	4.25	52
II	1	2.20	6.95	100
	129	41.9	4.95	71
	181	31	3.96*	57
III	1	1.80	10.3	100
	131	38.1	7.4	72
IV	1	1.45	9.91	100
	128	39.6	7.25	73
	181	40.0	5.69	57
V	3	3.1	8.55	100
	27	11.5	6.98	82
	35	21.0	6.67	78
	42	24.2	6.27	73

* Incl. C^{45} of 3 offsprings.

We find the Ca^{45} content of 1 gm. of new-born mouse to amount to 1.7 times that of 1 gm. of the adult mouse. The Ca^{45} taken in by the mother has thus only an opportunity of interchanging in the average with about $^1/_5$ to $^1/_6$ of the body calcium before being utilized in the building up of the embryo.

Discussion.

a) Conservation of the calcium atoms of the outgrown skeleton through life.

The fact that a very appreciable part of the skeletal calcium is preserved in the outgrown animal throughout its lifetime results

from experiments carried out by SINGER, ARMSTRONG, and PREMER[34], by CARLSON[28,35], and by BAUER[15]. Similar results werse obtained in investigations on the renewal of the mineral constituents of the skeleton, performed by the present author and his assoc. who used P^{32} as an indicator[31].

From specific activity data of the plasma and the skeleton of the outgrown rat, the percentage of renewable skeletal sodium was calculated by BAUER[36] to amount to 30—40 per cent of the sodium present (disregarding the extracellular sodium); a similar figure – 45 per cent – is reported by EDELMAN[38] and by BADEN and MOORE[39]. Since sodium is mainly an extracellular element, the specific activity of plasma sodium decreases only slowly with time, not so the specific activity of calcium. The calculation of the percentage of renewable skeletal calcium from specific activity data is therefore encumbered with great difficulties (cf. p. 8). From data collected during five days, BAUER[15] estimates, however, that less skeletal calcium than skeletal excess sodium is exchangeable in the rat, thus less than 30—40 per cent. As it was shown above (p. 13), the mobilization of some further skeleton calcium is still going on in the mouse after the lapse of more than 100 days and the non-exchangeable part of the skeleton amounts to 67 per cent.

It is interesting to note that, when injecting Ca^{45} at the start of the experiment interperitoneally to outgrown rats whose skeletal calcium content was increased appreciably during the experiment, SINGER and ARMSTRONG[40] found a Ca^{45} retention of 42—45 per cent in the skeleton after the lapse of 52 days and the release of only small amounts of radiocalcium after that date. BUCHANAN[41], who exposed mice to air containing $C^{14}O_2$, found that 30 per cent of the bone carbonate are replaced within 12 days, while 45 per cent only are renewed in the course of three months.

b) *Conservation of maternal calcium atoms by the offspring through life.*

Our results demonstrate the very pronounced ability of the skeleton to conserve maternal atoms.

In the first mentioned experiments, one third of the Ca^{45} content of the outgrown mouse was found to be replaceable by

inactive food calcium. In the latter experiments with growing mice, released Ca^{45} had a further outlet, viz. utilization in the formation of additional skeleton, which takes place in the growing organism.

Investigations were carried out earlier on the loss of P^{32} through the lifetime of mice born from active mothers[37]. Some results of these investigations are shown in Table V.

TABLE V.

Loss of P^{32} through the lifetime of mice born from active mothers. Mother injected with P^{32} on February 9. Gestation: February 18. Replacement of the active by an inactive mother: February 22.

No. of offspring	Killed: date	Relative activity	Weight in gm.
1.....	22/2	100	3
2.....	3/3	82	7
3.....	16/3	73	15
4.....	30/3	48	18
5.....	13/4	41	25
6.....	13/5	40	35

Loss of P^{32} in the course of 81 days: 60 per cent.

The fact that a very appreciable percentage of the maternal phosphate is preserved –though less than of the maternal calcium– is presumably due to the lower share of the bone phosphorus in the total body phosphorus than the part of bone calcium in body calcium. 17 per cent of the phosphorus content of the mouse are present in the soft tissues, but only 1 per cent of its calcium content is located there. The phosphorus and calcium atoms present in various components of the soft tissues –with the exception of desoxyribo nucleic acid phosphorus of some tissues– are poorly conserved and, consequently, maternal calcium may be expected to be better conserved than maternal phosphorus.

From the fact that during the first 40 days of life –thus during a phase of intense skeleton formation– only less than a third of the maternal calcium atoms of the mouse is lost, we can conclude that the largest part of the calcium atoms leaving the circulation is utilized to skeleton formation and remains largely conserved in the skeleton.

Le Blond and assoc.[9] injected labelled phosphate into newborn rats and followed the P^{32} uptake by the humerus and the lower jaw. Denoting the total P^{32} taken up by the humerus in the course of the first hour by 100, the uptake after eight hours was found to be 150, after one day 117, and after three days 116. In spite of the rapid growth of the humerus, the P^{32} present after the lapse of a day is thus conserved through the following days; similar results were obtained in investigations on the P^{32} uptake by the lower jaw.

The incorporation of calcium atoms in the rapidly growing bone tissue can also be studied by following its uptake into the incisor of outgrown animals. Carlson[23, 28, 35] performed extensive and highly instructive studies on the calcium metabolism of outgrown rats, among others with the result that the calcium atoms incorporated with the rapidly growing incisors are conserved to a very large extent in contrast to those incorporated with the outgrown skeleton.

It is rather difficult to determine the calcium intake and excretion by the suckling mouse. Our adult mice (36—37 gm.), however, were found daily to consume 4 ± 0.6 gm. of standard bread containing 8.3 ± 1.2 mg calcium; further 0.2 mg. calcium was contained in the 4 ml. of daily consumed water. The calcium recovered daily in the feces amounted to 8 mg. A very appreciable part of the feces calcium may be assumed to be of endogenous origin, thus having passed the circulation before excretion. The share of endogenous phosphorus in the feces phosphorus was calculated from the specific activity of feces P and urine (plasma) P[44, 45]; these calculations lead to the result that 74 per cent of the phosphorus of the human food and 72 per cent of the rat food are absorbed into the circulation. About the same percentage of the food P can be expected to be taken up by the mouse. As to the utilization of calcium, data are available only for the uptake by humans[43]. Here, the mean percentage uptake was found to be 56. From the above data it follows that, out of the daily uptake of 8 mg. calcium by our mice, at least 4 mg. have passed the circulation, representing a minimum amount of 2 gm. in the course of 500 days. From our results it thus follows that these 2 gm. were prevented from interchanging with $^2/_3$ of the 370 mg. calcium present in the skeleton of a mouse weighing 36 gm. The pro-

tected part of the skeleton calcium did not come into contact with the plasma or lymph and, correspondingly, an exchange between the unlabelled food calcium and labelled skeleton calcium could not take place; the same is true for the new-formation of the protected apatite crystals of this part of the skeleton under participation of food calcium. A possible rearrangement within the protected area would not manifest itself in our experiment.

The inaccessibility of parts of the skeleton minerals manifests itself also by the observation that radium, which like calcium is a strongly bone-seeking element, can find a life-long abode in the skeleton. The fact that a large fraction of radium administered to human subjects remains for decades in the skeleton is due presumably to the incorporation of the radium into parts of the skeleton which are covered by apatite layers and thus become inaccessible and, even if released, are incorporated again with the apatite structure. Aub and associates[46] report a case in which no decrease in the radium content of a woman was found to take place between 1934 and 1945. This woman had been administered radium in 1924.

Conservation of Ancestoral Atoms.

The radiocalcium atoms going over from the first generation of mice into the second (cf. p. 14) do not indicate the total amount of maternal calcium atoms passing from the mother to the offspring, since the mother is not uniformly labelled. Chemical data indicate a passage of about 1.3 per cent. Since the calcium of the second generation is uniformly labelled, the passage of the ancestoral calcium atoms from the second into the third generation is properly indicated by the radioactive tracer. About one third of the Ca^{45} content of the second generation is lost prior to gestation, while about 0.5 per cent or less of the remainder passes into the third generation. From the calcium atoms present at birth in each generation, thus $^1/_{300}$ part or less goes over to the following generation. As our mice contained 6.10^{21} calcium atoms, the eleventh generation did no longer contain a single ancestoral calcium atom.

It is of interest to compare the life cycle of the ancestoral

calcium atoms of the mouse with that of easily accessible water molecules. Applying deutoriated or tritiated water as an indicator first the half life of water molecules present in the rat was found to vary between 3.6 and 2.5 days[35, 36], that of the mouse is expected to be somewhat shorter. Thus, in the course of 165 days, all 10^{24} water molecules present at the start of the experiment in the mouse are replaced. About 4 per cent of the maternal water molecules go over to the offsprings and, from these, the second and third generations of offsprings will take up a share which depends on the age of gestation; the fourth generation, however, will hardly contain any more ancestoral water molecule.

When the rate of disappearance of labelled water was followed in the rat during a long period, which was made possible by using tritiated water as an indicator, it was observed[36] that, after the lapse of 30 days, the labelled water disappeared at an appreciably slower rate than with a half life of 2.5 days. The controlling factor of the disappearance of labelled water from the organism is now the release of firmly bound tissue tritium which again becomes a constituent of the water molecules. Due to this fact, it lasts 60 days until the number of labelled water molecules of this type, present in the mouse, decreases to a 10^{-2}th of its initial value.

If we disregard those water molecules whose hydrogen atoms were temporarily incorporated in tissue constituents and released appreciably later to become constituents of water molecules again, then all ancestoral water molecules are lost by the mouse during two generations.

While the loss of ancestoral calcium is determined mainly by the loss at birth, many ancestoral water molecules are lost during the lifetime of a generation, none of them reaching the third generation of offsprings.

Summary.

Since it was desirable to obtain uniform labelling of all calcium present in the skeleton of the mouse, $^{45}CaCl_2$ was added to all water administered to mice for weeks before and after gestation. Such water was also given to new-born mice after weaning until adult age was reached. The members of the litter, having almost the same radiocalcium content, were then sacrificed at different dates within 560 days.

From the labelled calcium atoms present in the skeleton of the outgrown mice, 67.2 ± 7.9 per cent were found still to be present in the skeleton of sister mice sacrificed after the lapse of 390 days.

When administration of Ca^{45} was interrupted after the birth of the litter, and its members reared by inactive mothers were sacrificed at different dates within 560 days, a mouse killed shortly after birth contained 8 per cent of the maternal Ca^{45} atoms, another mouse killed after 510 days contained 4 per cent. Half of the calcium atoms present at birth is thus conserved during the lifetime of the mouse.

From the figures obtained for the passage of labelled calcium from one generation to the next, it follows that the eleventh generation does not contain a single calcium atom present in the first generation of its ancestors.

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