

GEORG NØRGAARD HANSEN

ON THE STRUCTURE AND
VASCULARIZATION OF THE PITUITARY
GLAND IN SOME PRIMITIVE
ACTINOPTERYGIANS

(*Acipenser, Polyodon, Calamoichthys,*
Polypterus, Lepisosteus and Amia)

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Synopsis

An anatomical and histological description is given of the hypothalamus-hypophyseal region of *Acipenser stellatus*, *Acipenser güldenstaedti*, *Polyodon spathula*, *Polypterus senegalus*, *Calamoichthys calabaricus*, *Lepisosteus productus* and *Amia calva*. The distinctive features of the hypophysial vascularization have been studied in the same species with the exception of *Acipenser güldenstaedti* and *Polypterus senegalus*.

The neurohypophysis comprises three parts: 1) a rostral part, which is regarded as homologous with the eminentia mediana of the tetrapods, 2) a hypophyseal stem, only comparable with the oral wall of the infundibular stem in the tetrapods and 3) a hollow caudal part, the lobus nervosus, comparable with the lobus nervosus of tetrapods. Crown cells have been described in the eminential ependymal layer in *Chondrostei* and in the same layer in the lobus nervosus in all the species except for *Calamoichthys*.

The adenohypophysis comprises in *Chondrostei* and *Holostei* three histologically different regions and in *Brachiopterygii* two regions. The chromophilic cell types in the adenohypophysis have been described and compared with those of the teleosts. In the *Chondrostei* a hypophyseal cavity is present, and in the *Brachiopterygii* a buccohypophyseal duct.

The adenohypophysis has no direct arterial supply but is supplied exclusively from a pituitary portal system, basically comparable with that of tetrapods. The primary plexus covering the eminentia mediana is fed through aa. infundibulares, which on their way give off some small branches, supplying the post-chiasmatic region. In addition the primary plexus also receives supplementary vessels from the adjacent hypothalamic plexus in *Holostei* and *Calamoichthys*. The primary plexus comprises a rostral and a caudal region which are not sharply delineated. In the *Chondrostei* the primary plexus merges into the secondary plexus of the adenohypophysis, while vv. portae originating from this plexus are developed in *Brachiopterygii* and *Holostei*. The plexus intermedius is mainly fed through the superficial hypophyseal stem plexus. In addition the plexus intermedius is supplied in *Lepisosteus* through lateral afferent veins.

The neurohypophysis and the vascularization of the pituitary gland in the primitive actinopterygians have been compared with that of other vertebrates. This comparison gives a reason to conclude, among other things, that the subdivision of the neurohypophysis into an eminentia mediana and a lobus nervosus region, and a pituitary portal system represent primitive features that must have been present in a gnathostome ancestor, probably with a pattern similar to that in *Chondrostei*. In the light of this hypothesis it is pointed out that the structural pattern of the neurohypophysis and the vascular arrangement in the teleosts represents a secondary pattern.

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I. Introduction

The pituitary gland in *Amia* and *Lepisosteus* has been studied by GREEN (1951), who gives a brief description of the vascular system. Green points out that a well marked vascular plexus in the teleosts, as well as in the Elasmobranchs, separates the pro- and the meso-adenohypophysis from the neurohypophysis, and that vessels branch from this plexus to the adenohypophysis. GREEN has suggested that there is an evolutionary relationship between this (primitive) vascular plexus and the portal system of higher vertebrates.

Since GREEN put forward his hypothesis of the evolution of the pituitary portal system, a great deal of interest has been attached to the study of the pituitary vascularization and the hypothalamic control of the adenohypophysis. A pituitary portal system, although in some species of simple configuration, exists in all tetrapods. MEURLING (1960, 1967 a, b) and MELLINGER (1960 a-c, 1963) have proved that the neurohypophysis of Chondrichthyes consists of a neural lobe, a hypophysial stem and a median eminence with histological and vascular characteristics similar to that of other eminences. On the basis of this observation it is evident that the division of the neurohypophysis into a median eminence and a neural lobe and the evolution of the pituitary portal system are more primitive features than supposed by GREEN. This brings into question the interpretation of the pituitary gland, and in particular the neurohypophysis, in the primitive actinopterygians.

1) Does there exist, among the primitive actinopterygians, a division of the neurohypophysis into a median eminence and a neural lobe, and is a pituitary portal system developed? (WINGSTRAND (1966 a) has suggested that these structures are present in *Polypterus* and *Acipenser*).

2) Alternatively, is the hypothalamic-neurovascular link built up in the same way as in the teleosts? (This possibility is assumed by GREEN (1951)).

3) Should the hypothalamic-hypophysial link and the elaboration of the neurohypophysis in the teleosts be interpreted as primary or secondary developments?

In an attempt to answer some of these questions, the following primitive actinopterygians have been examined: *Acipenser stellatus* and *güldenstaedti*, *Polyodon spathula*, *Polypterus senegalus*, *Calamoichthys calabaricus*, *Lepisosteus productus* and *Amia calva*, with special reference to a description of the pituitary gland and its vascularization.

Acknowledgements: The specimens in the list of material marked +) were kindly placed at my disposal by Professor K. G. WINGSTRAND. The 5 μ section series of *Polypterus senegalus* was generously given by Laborator RAGNAR OLSON (Stockholm). I am grateful to Dr. S. L. TUXEN, who arranged the contact with Rumania, and my sincere thanks are due to Dr. I. ANDRIESCU and Dr. STANCIU in Rumania for their great efforts and help in obtaining the sturgeons. Dr. O. MUNK was especially helpful in obtaining *Polyodon*, *Lepisosteus* and *Amia* which were most kindly sent as gifts by Dr. W. J. WISBY (National Fisheries Center and Aquarium Department of the Interior, Washington 25, D.C.).

II. Material and Methods

1. Material

The different methods of preparation used in the investigation are indicated in the list below. The abbreviations used are as follows:

- AFA: fixed in alcohol-formalin-acetic acid.
 B: fixed in Bouin's mixture.
 C: celloidin sections.
 Ii: Indian ink injection of the vascular system.
 Ii, S-V: double injection with Indian ink-starch-vermilion solution of the vascular system.
 ls: longitudinal sections.
 P: paraffin sections.
 P-C: plastic injection into the arterial system and corrosion.
 sp: specimen.
 S-V: starch-vermilion injection into the arterial system.
 T: tissue sections.
 T-B: total preparation, cleared in benzol.
 Tl: total length.
 trs: transverse sections.

Order: *Chondrostei*

Family: *Acipenseridae*

Acipenser stellatus

PALLAS, 1771	1 sp	Tl, 450 mm	B	P	ls, 8 μ
	1 sp	Tl, 430 mm	B	P	trs, 8 μ
	1 sp	Tl, 400 mm	Ii	AFA	C ls, 75 μ
	1 sp	Tl, 410 mm	S-V	AFA	T-B

Acipenser güldenstaedti

BRANDT, 1833	+).....	1 sp	B	P	ls, 8 μ
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Family: *Polyodontidae*

Polyodon spathula

(WALBAUM, 1792)	1 sp	Tl, 215 mm	B	T	ls, 8 μ
	1 sp	Tl, 200 mm	B	T	trs, 8 μ
	1 sp	Ii	AFA	C ls, 50 μ

Order: *Brachiopterygii*Family: *Polypteridae**Polypterus senegalus*

CUVIER, 1829	+).....	1 sp	trs, 10 μ
	1 sp	B ..	ls, 5 μ

Calamoichthys calabaricus

(SMITH, 1865)	+).....	1 sp	TL, 320 mm	B P	trs, 8 μ
	+).....	1 sp	TL, 260 mm	B P	trs, 8 μ
	+).....	1 sp	B P	ls, 5 μ
	+).....	1 sp	TL, 325 mm	B P	ls, 5 μ
	+).....	1 sp	TL, 350 mm	Ii, S-V ..	AFA C	trs, 100 μ
	+).....	1 sp	TL, 370 mm	Ii, S-V ..	AFA C	ls, 75 μ
	+).....	1 sp	TL, 300 mm	Ii	AFA C	ls, 100 μ
	1 sp	TL, 331 mm	P-C		

Order: *Holostei*Family: *Lepisosteidae**Lepisosteus productus*

(COPE, 1865)	1 sp	TL, 200 mm	B P	ls, 8 μ
	1 sp	TL, 260 mm	B P	trs, 8 μ
	1 sp	TL, 290 mm	Ii	AFA C	ls, 75 μ

Family: *Amiidae**Amia calva*

LINNÉ, 1766	1 sp	TL, 470 mm	B P	ls, 8 μ
	1 sp	TL, 420 mm	B P	trs, 8 μ
	1 sp	TL, 440 mm	Ii	AFA C	ls, 75 μ

2. Methods

Anaesthesia: *Acipenser* and *Calamoichthys* were anaesthetized with a solution of urethane. The other fishes were anaesthetized with a solution of MS 222 (Sandoz).

Fixation: Specimens for histological investigation were fixed in Bouin's mixture (ROMEIS, 1948). The specimens were fixed by injection through aorta dorsalis. Fixation with alcohol-formalin-acetic acid was used for specimens injected with Indian ink and starch-vermilion.

Vascular injection: The Indian ink and starch-vermilion injections of the vascular system of the head were done according to the method given by WINGSTRAND (1951).

Decalcification: The Indian ink and starch-vermilion injected specimens were hardened in alcohol and decalcified in alcoholic hydrochloric acid or in aqueous nitric acid (ROMEIS, 1948).

Embedding: The specimens fixed with Bouin's mixture were embedded in paraffin or tissuemat, whereas the Indian ink and starch-vermilion specimens were embedded in celloidin (Pro-Fluka).

Staining of the histological material: For histological use the paraffin and tissuemat material were stained in: 1) Aldehyd-fuchsin, AF (GABE, 1953), 2) Aldehyd-fuchsin-HALMI (GABE, 1953; HALMI, 1952), 3) HEIDENHAIN'S azocarmine-aniline blue stain (Azan), 4) periodic acid SCHIFF (PAS), 5) Alcian blue-PAS (1 % AB in 1 vol. % acetic acid), 6) PAS-orange G (HERLANT, 1956), 7) AB-PAS orange G (ox. with KMnO_4) pH 3 or pH 0.2 (HERLANT, 1960), 8) EHRLICH'S hematoxylin and eosin (H-E), 9) Trichrome stain of CLEVELAND and WOLFE (1931-32), and according to BODIAN'S protargol method. The celloidin sections were mounted as recommended by WINGSTRAND (1951: p. 14-15) and stained with H-E.

Graphic reconstructions of the vascular system were made from the celloidin sections. The schematic cross sections were reconstructed from the celloidin and paraffin (tissuemat) sections.

III. General Anatomy and Terminology of the Pituitary Region

This general description of the pituitary region is based on common characters among the species examined. The deviations and variations between the species will be noted during the individual descriptions.

1. The Hypothalamo-neurohypophysial Region

The *recessus praeopticus* lies immediately in front of the chiasma opticum. The ventral surface is here quite thin and covered by a dense capillary plexus. *Nucleus praeopticus* is morphologically differentiated into two regions: the dorsal, *pars magnocellularis*, and the ventral region, *pars parvocellularis*. The neurosecretory cells lie close to the ependyma which bounds the recessus praeopticus.

The *lobi inferiores* (*lobi laterale*) enclose the recessus lobi inferiores. They constitute the main part of the ventral hypothalamus. The *lobi inferiores* lie close to the lateral part of hypothalamus, and to the ventral part of the lobus nervosus.

The *lobus medius* in *Amia* and *Lepisosteus* is described by KAPPERS (1907) as that part of the ventral hypothalamic wall which is situated between the *lobi inferiores* and bounded rostrally by the chiasma opticum. The homologies of the region including the lobus medius and the neurohypophysial part are described by WINGSTRAND (1959, 1966). The *lamina postoptica* is, in the species examined, caudally proliferated while the rostral part is undifferentiated brain wall. This undifferentiated brain wall, the *postchiasmatic region*, is called the *pars oralis tuberis* in the reptiles and mammals where it is very distinct (SPATZ, DIEPEN and GAUPP, 1948).

The *differentiated part of the lobus medius*, separated by a more or less distinct furrow, the *sulcus tubero-infundibularis* (SPATZ, DIEPEN and GAUPP, 1948) from the rest of the lobus medius, is characterized in the following way.

1) The region is separated from the adenohypophysis only by a layer of connective tissue.

2) It is covered by a dense vascular plexus. The capillaries of this plexus may, in some of the species, form loops into the rostral or lateral part of the wall. In other species these capillaries run in shallow furrows on the surface. The blood from this vascular plexus (pial plexus—eminential plexus—primary plexus) is drained to the adenohypophysis and to the plexus intermedius along the oral surface of the hypothalamus.

3) The brain wall in the region consists of three histological zones: an inner ependymal layer, an intermediate fibre layer and an outer cortical layer covered by the pial plexus. In the ependymal layer there are only a few nerve fibres and nerve cells. From the ependymal cells, processes run to the external surface through the other layers. The fibre layer is dominated by the AF positive nerve fibres which come from the nucleus praeopticus. In the cortical layer there are no coarse nerve fibres but an accumulation of AF positive material in connection with the capillaries of the pial plexus. The fine ependymal processes are, in this layer, branched and end on the endomeninx with “vascular feet”.

4) There is, in connection with the pial plexus, an accumulation of AF positive material.

The median eminence is defined by GREEN (1947 a, according to WINGSTRAND, 1966 a) as that part of the postoptic hypothalamic wall which is coextensive with the primary capillary net of the hypophysial-portal system of blood vessels. In 1951 GREEN defined the eminentia mediana as that part of the neurohypophysis which receives its blood supply from the hypophysio portal circulation or which has a common vascularization with the adenohypophysis. This requirement is fulfilled in the case of this differentiated region.

In addition this region fulfils the histological requirement established for the eminentia mediana (NOWAKOWSKI, 1951; WINGSTRAND, 1951). The same histological characteristics are described in sharks and rays (MEURLING, 1960, 1967 a, b; POLENOV, 1968), in *Hydrolagus* (JASIŃSKI and GORBMAN, 1966; SATHYANESAN, 1965) in *Chimarea* (FUJITA, 1963; MEURLING, 1967 b) and also in *Acipenser* (POLENOV, 1966 and 1968).

For this reason it is assumed that an eminentia mediana is developed in the primitive actinopterygians.

The *eminentia mediana* of the primitive actinopterygians may thus be defined as *that part of the ventral hypothalamic wall* (in some instances bounded by a sulcus tubero-infundibularis) *which consists of three histological layers* (ependymal-fibre- and cortical layer), *and whose superficial vascular plexus is drained toward the adenohypophysis* (in some instances by typical vv. portae).

This description is in agreement with MEURLING's (1967 a) definition of the eminentia mediana of the elasmobranchs. As with the elasmobranchs it is necessary

that both structural criteria are fulfilled because: 1) The characteristic histological structure may continue rostrally from the eminentia mediana, without its pial plexus being drained to the adenohiphysis and 2) the primary plexus may be continuous with the surrounding plexus of the brain wall, which does not contain the three histological layers.

The boundary between the eminentia mediana and the postchiasmatic region (pars oralis tuberis) and the hypophysial stem is not sharp.

The *hypophysial stem* connects the lobus nervosus with the eminentia mediana. Its wall consists of an inner ependymal layer and an outer layer, occupied mainly by the AF positive nerve fibres passing down to the lobus nervosus. A layer which corresponds to the eminentiae medianae cortical layer, is only found in *A. güldenstaedti*. The pial plexus which covers the hypophysial stem continues in the plexus intermedius. The hypophysial stem is only comparable with the oral wall of the infundibular stem in tetrapods.

The majority of the AF positive neurosecretory fibres which constitute the tractus praeroptico-hypophyseus fibres terminate in the *lobus nervosus* (the neural lobe). The lobus nervosus which is in close contact with the meta-adenohiphysis is externally surrounded by a connective tissue membrane and the plexus intermedius. The lobus nervosus is more or less lobulated. The lobuli are solid or contain hollow diverticules from the recessus infundibularis. The hollow lobuli subdivide gradually into numerous solid processes. The walls in the hollow lobuli consist of three histological layers: 1) the ependymal layer nearest the ventricle contains ependymal cells and in some cases crown cells, 2) the intermediate fibre layer with the coarse neurosecretory fibres and in some cases pituicytes and 3) the superficial cortical layer containing the ends of the neurosecretory fibres and the fine ramified ends of the ependymal processes.

The *saccus vasculosus* which is found in all the species examined, is a thin-walled, strongly folded and richly vascularized sac in which the epithelium contains crown cells with supporting cells in between. In some of the species the central cavity of the saccus vasculosus is in direct wide connection with the recessus infundibularis. In others there is a hollow stem, through which the recessus infundibularis communicates with the central cavity of the saccus vasculosus.

2. The Adenohiphysis

With the exception of *Calamoichthys* and *Polypterus* the adenohiphysis consists of three histological divisions: the *pro-*, the *meso-* and the *meta-adenohiphysis*. The terms are proposed by PICKFORD and ATZ (1957). The adenohiphysis of *Calamoichthys* and *Polypterus* can be subdivided into only two typical parts, designated the *pars intermedia* (meta-adenohiphysis) and the *pars distalis*.

According to OLIVEREAU (1954, 1963) the subdivision of the pars distalis into two zones (pro- and meso-adenohiphysis) in the teleosts depends on the distribution of two types of acidophil cells: 1) the erythrophil cell generally found in the pro-

adenohypophysis and 2) the Orange-G positive cell generally localized in the meso-adenohypophysis.

In *Salmo* (OLIVEREAU, 1954) the pro-adenohypophysis contains numerous regular follicles, composed mainly of erythrophil. A corresponding follicular structure of the pro-adenohypophysis is found in other primitive teleosts (PICKFORD and ATZ, 1957; WINGSTRAND, 1966). In teleost species without a follicular pro-adenohypophysis, and in the elasmobranchs, in which the pro-adenohypophysis contains vesicles or follicles, the dominant cell type is an acidophil, fuchsinophil and erythrophil cell.

In accordance with this, the part of the pars distalis (in the examined species), which has a follicular structure and where the dominating cell type is erythrophil, is called the *pro-adenohypophysis*.

The *meso-adenohypophysis* which forms the posterior part of the pars distalis is composed of more or less typical cell-columns, which either are compact or made up of follicles and tubules. The cell-columns are separated by the secondary vascular plexus of the pars distalis and by connective tissue.

The *meta-adenohypophysis* consists of more or less irregular cell-columns or cell groups, separated from the lobus nervosus by connective tissue and a capillary plexus (plexus intermedius).

In *Acipenser* and *Polyodon* a hypophysial cavity is present between the meta-adenohypophysis and the pro- and meso-adenohypophysis. The pars distalis in *Polypterus* and *Calamoichthys* has a medio-ventral hypophysial lumen, connected with the oral roof through a hypophysial duct.

An attempt has been made to classify the cell types in the adenohypophysis in spite of the imperfection of the material and the difficulty in trying to compare cell types in the absence of appropriate physiological tests.

The pars distalis may contain two types of acidophil cells, four basophils and chromophobes. The meta-adenohypophysis may contain one type of acidophil cells, two basophils and chromophobes. The acidophils are PAS negative or only weak PAS positive. The basophils are AF and PAS positive.

In the light of a comparison with the histological description of the adenohypophysis in the teleosts (PICKFORD and ATZ, 1957; OLIVEREAU, 1963) the following grouping is made.

The pars distalis:

a. Acidophil cells

1) Erythrophil (A_1). These cells, the dominant cell type in the pro-adenohypophysis, are PAS and AF negative and are stained with erythrosine and azocarmine (possibly epsilon-cells).

2) Orange G or fuchsinophils (A_2). These cells may be found everywhere in the adenohypophysis. The A_2 cells are generally smaller than the A_1 , and are in some cases weakly PAS positive (possibly alfa-cells).

b. Basophil cells

3) B_1 cells (possibly delta-cells) are most often "cone shaped", angular, AF and PAS positive cells, with coarse granules. These cells are present in the medio-ventral part of the meso-adenohypophysis. According to OLIVEREAU (1963) they are found in the pro- as well as the meso-adenohypophysis. In the specimens examined B_1 cells are considered to be restricted to the meso-adenohypophysis.

4) and 5) B_2 and B_3 cells probably correspond to the gonadotrophs. The material does not permit classification into gamma and beta cells. It is also possible that these two "cell types" may not be functionally different but represent various stages in the secretory activity of the same cell type. Both of them are AF and PAS positive. The B_2 cell is bigger than the B_3 cell and dominates the medio-dorsal or the central part of the meso-adenohypophysis.

6) B_4 are small AF and PAS positive cells. They are only present in the pro-adenohypophysis in *A. güldenstaedti*.

7) B_7 are big ovoid, only weakly AF and PAS positive cells. They are found only in the ventro-rostral region of the pars distalis in *Calamoichthys*.

8) Chromophobes are found throughout the adenohypophysis; they are small degranulated faintly stainable cells, with only a small amount of plasma around the nucleus.

The meta-adenohypophysis:

1) In many cases small acidophils were seen in this part of the adenohypophysis. These cells are possibly identical with the A_2 cells.

2) B_5 is the predominant cell type in the meta-adenohypophysis. The cell is AF and PAS positive.

3) B_6 are only found in *Acipenser*. These cells are AF and PAS positive, with a coarser granulation than found in B_5 .

3. The Arteries

The paired *aa. carotides internae* which do not anastomose mutually supply the brain and the hypophysial region with blood. The *a. carotis interna* continues in the investigated specimens (with the exception of *Calamoichthys*) intracranially as *a. carotis cerebialis*, which divides into a *ramus anterior* and a *ramus posterior*. In *Calamoichthys* the *a. carotis interna* bifurcates extracranially into these main stems, which then continue intracranially.

The *ramus anterior* gives off the following branches: a) the *a. cerebialis anterior* which supplies the ventral part of the telencephalon, b) the *a. cerebialis media* to the olfactory brain region, plus c) the *a. mesencephali dorsalis* (GRODZIŃSKI, 1948) the main branch of which runs to the mesencephalon, the cerebellum and the dorsal part of medulla oblongata.

The *ramus posterior* (*a. cerebialis posterior*, MEURLING, 1967 a) runs caudally and joins its "twin" ventrally of the medulla oblongata. From this union the unpaired median *a. basilaris* or the paired *aa. basiliares* continue caudally ventral of the medulla

oblongata. The a. cerebialis posterior gives off small branches which supply the superficial part of the diencephalon, the cerebellum, the mesencephalon and the medulla oblongata.

The *circulus arteriosus Willisi* is complete caudally, where the rami posteriores fuse, but it is incomplete rostrally because there is no anastomosis between the paired rami anteriores. Some anastomotic vessels between aa. cerebrales anteriores are present but have the dimensions of capillaries.

The aa. *infundibulares* supply the postchiasmatic region and the primary capillary plexus. The source and the course of these arteries are very variable.

4. The Hypophysial Blood System

The pituitary portal system consists in the tetrapods of a *primary plexus*—a dense capillary plexus in connection with the eminentia mediana—and portal vessels which drain this plexus, and which pass the blood to the secondary plexus in the pars distalis. The primary plexus, which is supplied by the aa. *infundibulares* (aa. *hypophyseae*), is often quite distinct, and is only slightly in connection with the hypothalamic capillaries.

In the species examined, this system is differentiated in various degrees. For the description it is intended to follow the terminology used by MEURLING (1967 a).

In connection with the *eminentia mediana* a *pial plexus* is developed (= *eminential plexus* = *primary plexus*). This plexus is fed by aa. *infundibulares* and by the plexus which covers the postchiasmatic region. Further there is in some cases connection between the primary plexus and the surrounding hypothalamic plexus via supplementary vessels. From the *rostral part of the primary plexus* the blood continues to the secondary plexus in the pro- and meso-adenohypophysis, while the blood from the *caudal part of the primary plexus* is led to the meta-adenohypophysis and to the *hypophysial stem plexus* which is emptied into the *plexus intermedius* (BENDA, 1927; WINGSTRAND, 1966 b). In addition to this blood supply of the plexus intermedius there are in *Lepisosteus* developed *lateral afferent veins*. These veins arise from the hypothalamic superficial vessels, and terminate in the plexus intermedius.

In the light of the elaboration of the primary plexus it is possible, in the species examined, to distinguish between two eminential types: 1) a “*simple eminential type*”, with only a few or no loops at all in the rostral part of the eminentia mediana and 2) a “*differentiated eminential type*”, with well-developed “*deep*” loops into the rostral part of the eminentia mediana.

5. The Veins

Only the draining of the pituitary gland and of the saccus vasculosus is described to an extent determined by the available material.

For descriptive purposes the following terms are used: The *v. hypophyseos media* drains the ventral part of the adenohypophysis and leads into the *v. interorbitalis* (*v. pituitaria*). The plexus intermedius and saccus vasculosus may be drained through the *v. hypophyseos lateralis*. The *v. hypophyseos* collects blood from the adenohypo-

physis, the plexus intermedius and the saccus vasculosus. In some instances there is developed a *v. sacci vasculosi* which drains only the saccus vasculosus. The lobi inferiores and the diencephalon are drained towards the *vv. infundibulares*.

IV. *Acipenser güldenstaedti* and *Acipenser stellatus*

Material and methods (see p. 6).

Literature.

The early embryonal development of the pituitary gland in *A. sturio* and *A. ruthenus* has been described respectively by VON KUPFFER (1906) and HOLMGREN (1932). Both of these authors point out that the hypophysial cleft forms as a schizocoel in the original compact hypophysial anlage. STENDEL (1913, 1914) gives a morphological and an embryological description of the pituitary gland in *A. sturio*. JOHNSTON (1902) gives a complete survey of the brain of *A. rubicundus* and in connection with this a brief morphological description of the pituitary gland. KERR (1949) gives a detailed morphological and histological account of the pituitary gland in *A. fulvescens*. There is agreement in the present work with the morphological description but some discrepancy as to the position and number of cell types. BARANNIKOVA (1949, 1950) considers the gonadotropic function in the hypophysis in *A. stellatus* and the histophysiology of the basophil cells in the hypophysis in *A. güldenstaedti persicus*. POLENOV and BARANNIKOVA (1958) describe the preoptico-neurohypophyseal neurosecretory system in *Acipenser*. The general structure of the pituitary gland is given by WINGSTRAND (1966 a). POLENOV 1966 (*A. stellatus*) and 1968 (*A. stellatus*, *A. güldenstädti*) examined the vascularization of the pituitary gland and pointed out the presence of an eminentia mediana and a primitive portal system. JASIŃSKI (1964) describes the structure and vascularization of the pituitary gland in *A. stellatus*. This author denies the existence of an eminentia mediana and a portal system although his illustrations give a hint of a portal system. GRODZIŃSKI (1948) gives a detailed picture of the arteries and veins in the head of *A. ruthenus*. Embryological and comparative information on jugular and cerebral veins is given by BERTMAR (1965). (This material includes the species, *A. güldenstaedti*, *ruthenus* and *stellatus*).

1. The Hypothalamo-neurohypophysial Region (Figs. 1–3, Pls. I–IV)

The *recessus praeopticus* in front of the chiasma opticum is V-shaped, and continues ventro-caudally below the chiasma opticum as a thin-walled sac. The ependymal processes run to the surface, which is covered by a dense capillary plexus. The cells of the *nucleus praeopticus*, are definitely neurosecretory and differentiated into the dorso-caudal region, pars magnocellularis, plus the bigger ventro-rostral region, pars parvocellularis. In *A. stellatus* a corresponding division of the cells in the nucleus praeopticus has not been found. This might possibly be due to the juvenile character of the specimens examined. The *lobi inferiores* are well developed and the recessus lobi inferiores have a wide open medial connection with the recessus infundibularis. The lobi inferiores merge into the lobus medius. The *lobus medius* consists of a rostral *postchiasmatic region*, and a caudal region, the eminentia mediana.

The *eminentia mediana* (Figs. 1–2, Pls. I, III) is bounded by a sulcus tubero-infundibularis faintly discernable. Between the ependymal cells in the whole eminentia mediana crown cells are visible. In the fibre layer there are, besides the tractus praeoptico-hypophyseos fibres, some pituicytes. In the rostral part of the eminentia

mediana the cortical layer is well developed and contains abundantly AF + material, concentrated around the primary capillaries. Between the ependymal processes in the cortical layer a few small glia cells are found.

The eminentia mediana continues caudally in the *hypophyseal stem*, which on the inner side is dominated by crown cells. The hypophysial stem is bounded laterally by two longitudinal grooves.

The *lobus nervosus* is folded down into a "pocket" on either side of the median plane but the "pockets" are asymmetrically constructed. The recessus infundibularis continues into the lobus nervosus as a primary lumen in each of the pockets. The primary lumen gives off secondary lumina which in turn are subdivided. The outermost lobi nervosi processes are solid and run out in all directions. In the hollow lobuli (Pl. II) the wall is composed of the ependymal, fibre- and cortical layers. The ependymal layer contains ependymal cells, with oval or circular nuclei, and crown cells in between.

The *saccus vasculosus* is limited ventrally by the hypophyseal stem and the lobus nervosus, and dorsally by the lobus posterior. The saccus vasculosus is thin-walled and richly vascularized, with a central cavity from where two ventral, two lateral and two dorsal protuberances (which in turn subdivide) branch off.

2. The Adenohypophysis

a) *The adenohypophysis in A. güldenstaedti* (Fig. 1, Pl. III)

The pituitary gland is elongated and flattened dorso-ventrally, with the longitudinal axis parallel to the recessus infundibularis. The gland consists of the pro- and meso-adenohypophysis plus the meta-adenohypophysis which is separated from the other parts by the hypophysial cavity. This cavity runs forward between the pro- and meso-adenohypophysis. Laterally, dorso-caudally and ventro-caudally the meta-adenohypophysis is continuous with the meso-adenohypophysis, but the two parts are histologically clearly separated.

The *pro-adenohypophysis* is built of cell-groups, radially situated around vesicles or follicles, which in some instances contain colloidal material. In addition tubules are found which likewise may contain colloidal material. These tubules are possibly derived from the tubular extensions of the hypophysial cavity. The latter do not hold colloidal material. All transitions from tubules in connection with the hypophysial cavity to isolated tubules (with or without colloidal material) and typical vesicles or follicles are found. Therefore the last-mentioned possibly represent, as suggested by KERR (1949) and OLIVEREAU (1954), separated diverticula from the hypophysial cavity. The cell groups are surrounded by connective tissue and by the secondary capillary plexus.

The *meso-adenohypophysis*: The medio-dorsal part of this region is built up of cell-columns. The cells in the columns surround projections from the hypophysial cavity. The cell-columns are enclosed by connective tissue and the secondary capillary plexus. The ventral and the lateral parts of this region are more irregularly constructed of cell-columns and cell-groups.

The *meta-adenohypophysis* encloses the lobus nervosus and fills up the spaces between the branches of this. Medially are found some vesicles and tubules. There is no special structure associated with the superficial cells which line the cleft.

The *pro-adenohypophysis* is almost solely composed of A_1 cells. In between these cells a few A_2 , B_4 and chromophobic cells are found. The acidophil A_1 cells are elongated and grouped around the follicles, with the nucleus located in the basal part of the cells and with the granules concentrated in the perinuclear plasm. The small B_4 cells adjoin the capillary walls. In addition there are a few scattered A_2 cells and chromophobic cells.

The *meso-adenohypophysis* contains B_1 , B_2 , B_3 , A_1 , A_2 plus chromophobic cells. The B_1 cells are "cone shaped", the nucleus circular and eccentrically placed.

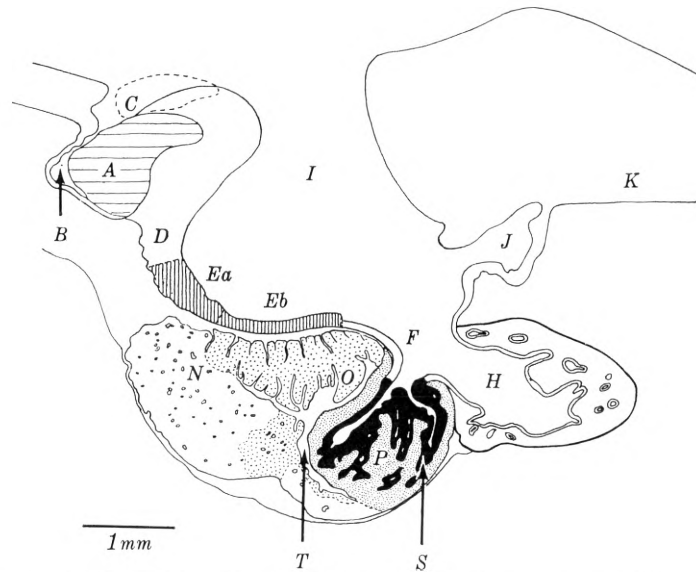


Fig. 1. *Acipenser güldenstaedti*. Median diagrammatic section. — A = chiasma opticum, B = recessus praeopticus, C = nucleus praeopticus, D = postchiasmatic region, Ea = rostral part of the eminentia mediana, Eb = caudal part of the eminentia mediana, F = hypophysial stem, H = saccus vasculosus, I = recessus infundibularis, J = recessus posterior, K = medulla oblongata, N = pro-adenohypophysis, O = meso-adenohypophysis, P = meta-adenohypophysis, S = lobus nervosus, T = hypophysial cavity.

This cell type is confined to the ventro-medial part of the meso-adenohypophysis. The B_2 cells which predominate in the dorso-medial part are ovoid in shape. Medially there are only a few B_3 cells, but they are prevalent laterally. A_2 is the predominant acidophil cell type in this part of the adenohypophysis. It is an ovoid cell, with an eccentrically placed nucleus. In addition to A_2 cells a few A_1 cells are found. The chromophobic cells are mainly aggregated in the central part of the cell-columns.

In the *meta-adenohypophysis* B_5 and B_6 are found together with chromophobic cells. The B_5 is the conspicuous cell type. They are ovoid or elongated cells, with

SCHEME I. Staining affinities of the chromophilic cell-types in the adeno-hypophysis in *Acipenser güldenstaedti*.

staining method	cell-type								
	A ₁	A ₂	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	colloidal material
Gabe's AF			+	+	+	+	+	+	+
AF — Halmi's counterstain	yellowish green	yellowish green	violet	brown	pale violet	pale brownish violet	pale brown (with violet shade)	pale violet	violet
PAS	—	((+))	+	+	+	+	+	+	+
Azan	red	pale orange	pale blue	red	bluish (red)	red	pale violet	violet	blue
Trichrome stain. Cleveland — Wolfe	reddish brown	yellowish red	dark blue	yellowish green	bluish violet	reddish violet	purple	violet	blue

the nucleus eccentrically situated. Dorso-rostrally and medially is found an area with B₆ cells. These are small elongated cells. There are only a few A₂ and chromophobic cells.

b) *The adeno-hypophysis in A. stellatus* (Fig. 2–3, Pl. IV)

The longitudinal axis of the oval dorso-ventrally flattened pituitary gland is parallel to that of the recessus infundibularis. The gland is situated in a deep fossa hypophyseos surrounded by connective tissue. Only the rostral part of the fossa hypophyseos is ossified. Caudally the fossa hypophyseos is bounded by a well-developed, cartilaginous dorsum sellae. The adeno-hypophysis can be divided into three zones; the pro-, meso- and meta-adeno-hypophysis. The meta-adeno-hypophysis is separated from the former parts by the hypophysial cavity. The hypophysial cavity extends forward to the pro-adeno-hypophysis, and envelops caudally the neuro-intermedia lobe, which “hangs” into the hypophysial cavity. The hypophysial cavity gives off tubules penetrating the pro- and meso-adeno-hypophysis.

The *pro-adeno-hypophysis* is strongly folded and consists of cell-strands and cell-groups, separated by connective tissue and capillaries. The cell-strands and groups contains vesicles, follicles and tubules, with or without colloidal material.

The *meso-adeno-hypophysis* is essentially of the same structure as in *A. güldenstaedti*, although the ventral part is quite thin, and consists of irregular cell-strands, penetrated by protuberances from the hypophysial cavity.

The cell-strands of the *meta-adeno-hypophysis* lie towards the hypophysial cavity and the plexus intermedius is surrounded by connective tissue. There is no special differentiation of the cells lining the hypophysial cleft.

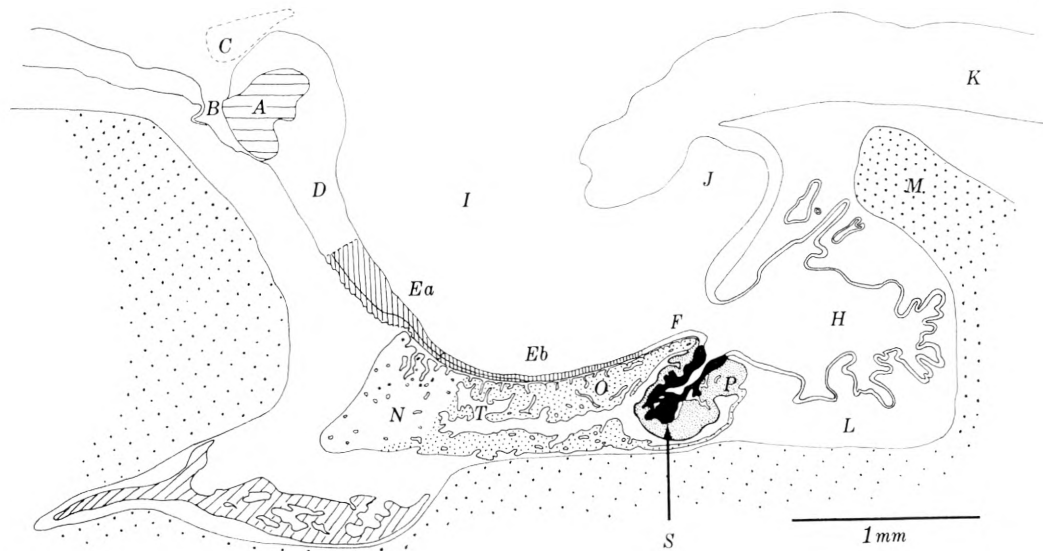


Fig. 2. *Acipenser stellatus*. Median diagrammatic section. — L = fossa hypophyseos, M = dorsum sellae coarsely stippled = cartilage, coarsely striated = bone. Other labels see fig. 1.

The cell type A_1 in the *pro-adenohypophysis* are small ovoid or elongated cells, with faint cell-boundaries. In the specimens examined these cells are weakly stainable.

In the *meso-adenohypophysis* are found B_1 , B_2 , B_3 , A_2 and a few small chromophobic cells. The B_1 cells are "cone shaped" with the circular nucleus eccentrically placed at the base of the "cone". This cell type is found mainly in the ventro-medial area. B_2 is the predominant cell type. The cell is ovoid, with the nucleus located in

SCHEME II. Staining affinities of the chromophilic cell-types in the adenohypophysis in *Acipenser stellatus*.

staining method	cell-type							colloidal material
	(A_1)	A_2	B_1	B_2	(B_3)	B_5	B_6	
Gabe's AF			+	+	+	+	+	+
AF — Halmi's counterstain		yellowish green	violet	brown (with violet shade)	pale violet	greyish violet	greyish violet	violet
PAS	—	—	+	+	+	+	+	+
Azan		orange red	pale blue	purple	bluish	pale violet	dark blue	blue
Trichrome stain. Cleveland — Wolfe		yellow		yellowish green	bluish grey	reddish brown	dark blue	blue

that part of the cell which is nearest to the capillaries. There are only a few ovoid B_3 cells. The A_2 's too are few, small and ovoid.

The *meta-adenohypophysis* contains B_5 and B_6 cells, the former being the main type. B_6 cells are found only in the dorso-rostral and the medial part. The B_5 cells are ovoid with an eccentrically placed nucleus and faint cell boundary. The B_6 cells are ovoid with a distinct cell boundary.

3. The Arteries in *A. stellatus*

a) Carotid and cerebral arteries (Fig. 3)

The two *aa. carotides internae* penetrate the basis cranii rostro-laterally to the pituitary gland. The *a. carotis cerebralis* divides between the n. opticus and the lobus inferior, into two main stems: the ramus anterior and the ramus posterior. The *ramus anterior* gives off the *a. ophthalmica interna* and after a short distance it splits into the *a. cerebralis anterior* and *media* plus the *a. mesencephali dorsalis*. The paired *aa. mesencephali dorsales* anastomoses medio-dorsal to the mesencephalon and continue caudally as an unpaired vessel. *A. cerebralis posterior* passes caudally and dorso-medially, lateral to the lobus inferior. Medio-ventral to the n. oculomotorius, in the fissure between the saccus vasculosus and the base of the brain, the *a. cerebralis posterior* joins its twin from the other side to form the paired *aa. basilares*.

b) Infundibular arteries (Fig. 3)

The *aa. infundibulares* originate from the *aa. carotides cerebrales*, the *rami anteriores* and from the *aa. cerebralis anteriores* and *mediae*. Compared with JASIŃSKI'S (1964) description it is evident that the courses and origins of the *aa. infundibulares* are variable within the species. The *aa. infundibulares*, emitted from the *aa. carotides cerebrales*, pass to the rostral part of eminentia mediana, while the other *aa. infundibulares* run to the postchiasmatic region.

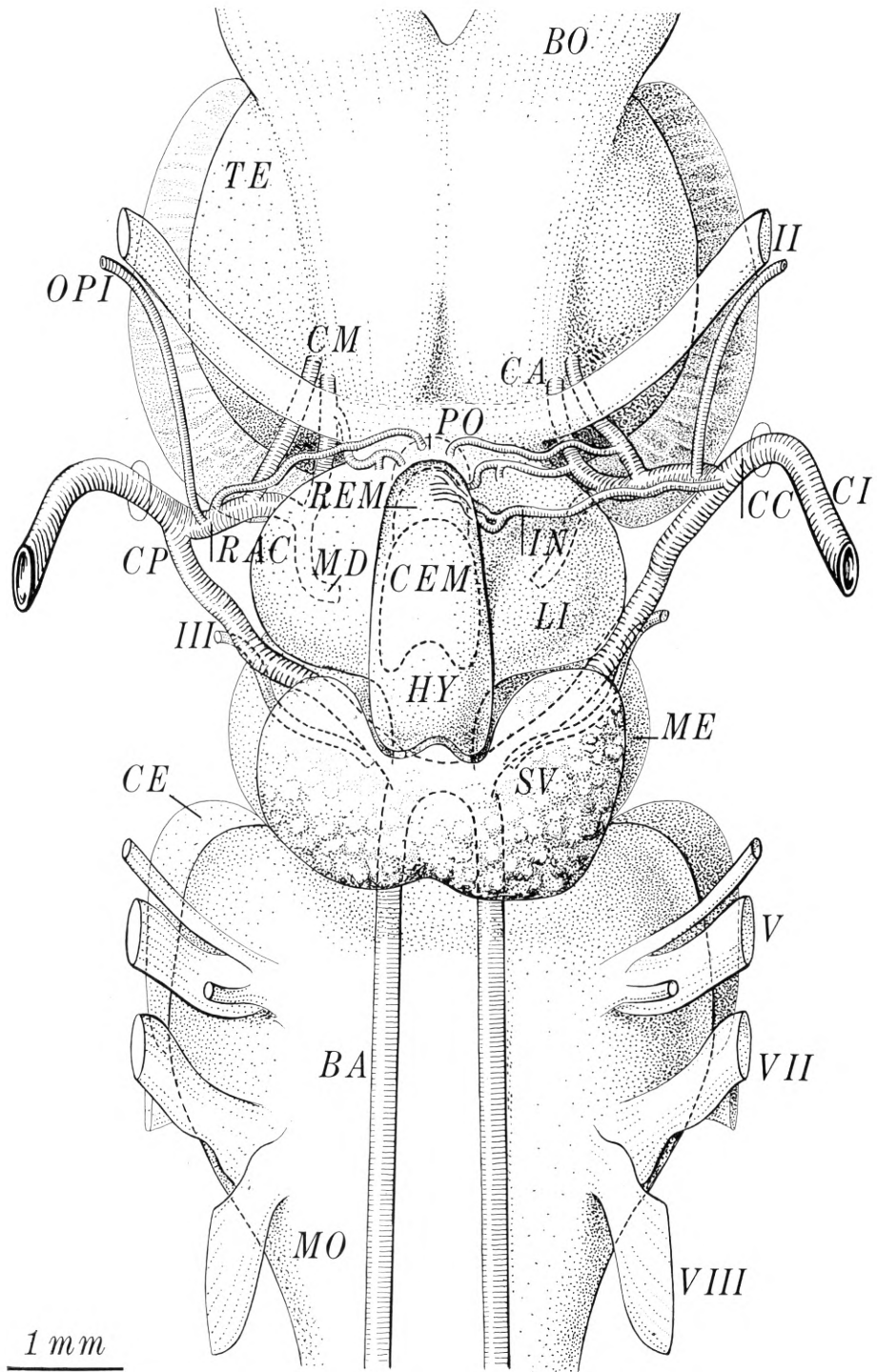
4. The Hypothalamo-hypophysial Blood System in *A. stellatus* (Fig. 3, Pls. IV-V)

a) Pituitary portal system

There is a hypophysial portal system, but no supplementary vessels and no, or only minor, connection between the hypothalamic superficial capillaries and the plexus intermedius via lateral afferent veins.

Arriving at the postchiasmatic region the *aa. infundibulares* split into capillaries, some of which supply the profound part of the hypothalamus, whilst others run as superficial capillaries ventro-caudally to the primary plexus. From the postchiasmatic plexus additional capillaries run to the deeper and superficial part of the chiasma opticum.

The *primary plexus* consists of a rostral and a caudal part. There are no connections between the profound capillaries and the superficial plexus in the eminentia mediana.



In the *rostral part* of the primary plexus the capillaries lie mainly in flat longitudinal furrows, and loops are only faintly developed at some places — a “simple eminentia type”. The medial part of the primary plexus is drained to the pro- and meso-adenohypophysis, but real portal vessels are not developed. In consequence the primary plexus continues directly into the secondary plexus. Additionally, some capillaries from the rostral plexus run to the caudal eminential plexus.

In the *caudal part* of the primary plexus the capillaries lie superficially, medially in flat grooves without any special orientation, laterally in somewhat deeper furrows. Loops in the strict sense are not developed. The capillaries from the medial part of the primary plexus continue into the secondary plexus of the meso-adenohypophysis. The lateral part of the primary plexus is drained to the adenohypophysis via a few typical *vv. portae* (Pl. V: 1). The primary plexus merges posteriorly into the hypophysial stem plexus, which continues into the plexus intermedius. Some of the capillaries from the hypophysial stem plexus are also in connection with the capillaries of the saccus vasculosus.

b) *Vessels in the pro- and meso-adenohypophysis*

There is no direct arterial supply to the pro- and meso-adenohypophysis, which are supplied exclusively from the primary plexus. The primary plexus is, as mentioned above, connected with the secondary plexus either directly or via the *vv. portae*.

In the pro-adenohypophysis the capillaries of the secondary plexus form a dense network which surrounds the cell-strands and cell-groups. In the meso-adenohypophysis the main direction of the capillaries are along the more or less vertically aligned cell-columns. In neither of the two parts of the adenohypophysis do the capillaries penetrate between the cells which constitute the cell-groups.

c) *Vessels in the neuro-intermedia area*

The *plexus intermedius* is well developed and supplied with blood from the hypophysial stem plexus. From the plexus intermedius a few capillaries pass through the meta-adenohypophysis to the superficial plexus which covers this part of the adenohypophysis. This gives a hint of an *intermedia sinusoid system* (Pl. V).

d) *Saccus vasculosus*

The dense capillary net in the saccus vasculosus receives a few capillaries from the hypophysial stem plexus and from the plexus intermedius. Furthermore, there exists a vascular connection between the plexus of the saccus vasculosus and the superficial capillaries of the hypothalamus.

Fig. 3. *Acipenser stellatus*. Ventral view of the brain showing the distribution of the arteries. — BA = a. basilaris, BO = bulbus olfactorius, CA = a. cerebialis anterior, CC = a. carotis cerebialis, CE = cerebellum, CEM = caudal part of the eminentia mediana, CI = a. carotis interna, CM = a. cerebialis media, CP = a. cerebialis posterior, HY = hypophysis, IN = a. infundibularis, LI = lobus inferior, MD = a. mesencephali dorsalis, ME = mesencephalon, MO = medulla oblongata, OPI = a. ophthalmica interna, PO = postchiasmatic region, RAC = a. carotis cerebialis ramus anterior, REM = rostral part of the eminentia mediana, SV = saccus vasculosus, TE = telencephalon, II = n. opticus, III = n. oculomotorius, V = n. trigeminus, VII = n. facialis, VIII = n. acusticus.

5. The Venous System (Fig. 4, Pls. V–VI:1)

The unpaired *v. hypophyseos* (which drains the pituitary gland only) arises medio-ventrally on the hypophysis in the superficial venous plexus which covers the ventral part of the pars distalis (Fig. 4). The *v. hypophyseos* communicates with the terminal

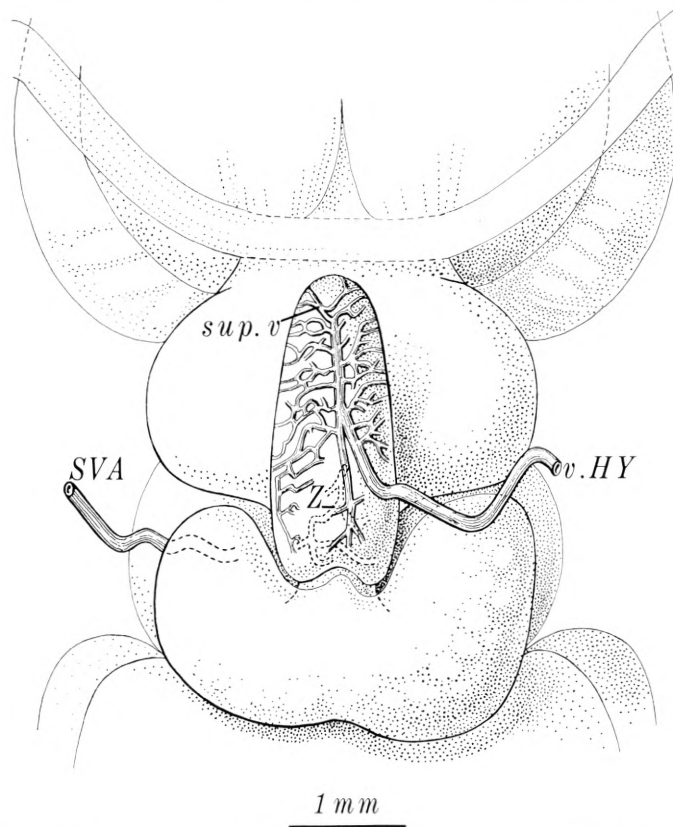


Fig. 4. *Acipenser stellatus*. Ventral view of the brain showing the venous drainage of the pituitary gland. — sup. v. = superficial venous plexus, SVA = v. sacci vasculosi, v. HY = v. hypophyseos, Z = capillary connection between the plexus intermedius and the superficial venous plexus of the hypophysis. Brain parts see fig. 3.

part of the *v. cerebralis anterior* immediately before this fuses with the left *v. cerebralis media* (BERTMAR, 1965).

The lateral parts of the plexus intermedius are drained by veins (Pl. VI: 1) directed dorsally. These veins run into the *v. cerebralis media ramus anterior*. JASIŃSKI (1964) found only one vein draining the plexus intermedius and entering the *v. cerebralis media*.

The saccus vasculosus is drained by small veins running dorsally and communicating with the *v. cerebralis media ramus anterior*. In addition there is a single well developed *v. sacci vasculosi* (Fig. 4) which enters the terminal part of the right

v. cerebralis anterior, immediately before this unites with the v. cerebralis media. The course of the v. sacci vasculosi and of the v. hypophyseos is the same and for this reason these veins are possibly right and left half of a divided v. *interorbitalis* (v. pituitaria).

V. *Polyodon spathula*

Material and methods (see p. 6).

Literature.

The paired aa. carotides internae were described by ALLIS (1911) and DANFORTH (1912). HOCHE HOOGENBOOM (1929) gives a complete survey of the brain of *P. folium* and in connection with this a brief morphological description of the pituitary gland. LAGIOS (1968 a) gives a description of the pituitary gland of *P. spathula*. There is in the present work disagreement with this last description, as to 1) the morphology of the adenohypophysis, 2) the number of cell types and 3) LAGIOS's opinions of the hypothalamus-hypophysial vascular system.

1. The Hypothalamo-neurohypophysial Region (Figs. 5-6, Pl. VII)

The cells of the *nucleus praeopticus* are easily-stained neurosecretory cells differentiated into a dorsal group, the pars magnocellularis and a bigger ventral group, the pars parvocellularis. The boundaries of the *lobi inferiores* and the *lobus medius* are only weakly defined. The medial part of the lobus medius consists of the post-chiasmatic region and the eminentia mediana.

The *postchiasmatic region* is covered by a dense vascular plexus. In between the ependymal cells crown cells are visible.

The *eminentia mediana* is not bounded by a sulcus tubero-infundibularis. In the eminentia mediana crown cells are visible between the ependymal cells (Pl. VI: 2), with a few in the rostral part and more in the caudal part. In the fibre layer there are a few pituicytes. In the cortical layer a few small glia cells are found between the ependymal processes. Neurosecretory material appears close to the superficial capillaries in this layer.

The *hypophysial stem* is on the inner side (toward the recessus infundibularis) bounded rostrally and laterally by furrows. Between the ependymal cells are seen crown cells. The hypophysial stem is covered by a superficial capillary plexus.

The *lobus nervosus* is morphologically and histologically similar to that in *A. stellatus*. The ependymal layer contains ependymal cells with crown cells in between.

The *saccus vasculosus* is a thin-walled and richly vascularized sac, with a central cavity in connection with the recessus infundibularis. A ventral, two lateral and a well-defined dorsal protuberance branch off from the central cavity.

2. The Adenohypophysis (Figs. 5-6, Pl. VII)

The oviform, dorso-ventrally flattened pituitary gland is situated, surrounded by connective tissue, in a relative flat fossa hypophyseos, which is bounded caudally by an inconspicuous dorsum sellae. The adenohypophysis comprises a pro- and meso-

adenohypophysis plus a meta-adenohypophysis separated from the first-mentioned parts by a well-developed hypophysial cavity. The hypophysial cavity extends rostrally to the pro-adenohypophysis and surrounds caudally the ventral and lateral parts of the meta-adenohypophysis. Laterally the hypophysial cavity is bounded by the meso-adenohypophysis which communicates dorso-caudally and medially with the meta-adenohypophysis. The hypophysial cavity gives off tubules which penetrate into the meso-adenohypophysis.

The *pro-adenohypophysis* is folded and consists of cell groups containing follicles and tubules with or without colloidal material.

The *meso-adenohypophysis* consists medio-dorsally of more or less vertically orientated cell strands. These cell strands contain follicles and protuberances from the hypophysial cavity. The lateral and ventral parts are very thin-walled and are composed of cell groups with central lumina.

The *meta-adenohypophysis* occupies the spaces between the folds of the lobus nervosus. Tubules and follicles are not found in this part, and the cells lining the hypophysial cavity are similar to those deeper in the tissue.

In the *pro-adenohypophysis* are found two types of PAS-negative cells. One is a small ovoid cell, with a globular nucleus, whilst the other is an elongated cell, with an eccentrically placed nucleus. Neither can be stained specifically which might possibly be due to immaturity of the animals.

The *meso-adenohypophysis* contains A_2 , B_1 , B_2 , B and chromophobic cells. The B_1 's are irregular in form, with the globular nucleus eccentrically placed and filled with coarse granules. This cell type, which is not frequently seen, occurs in the medio-ventral area. The B_2 's are ovoid or elongated cells, which predominate dorso-medially and laterally. The cells are filled with amorphous material and the nucleus is eccentrically placed. The B cell is a small ovoid cell, with a globular nucleus, around which the PAS-positive material is concentrated. This cell type is found in the rostral part of the medio-ventral area. The A_2 's are small and ovoid and filled with amorphous material.

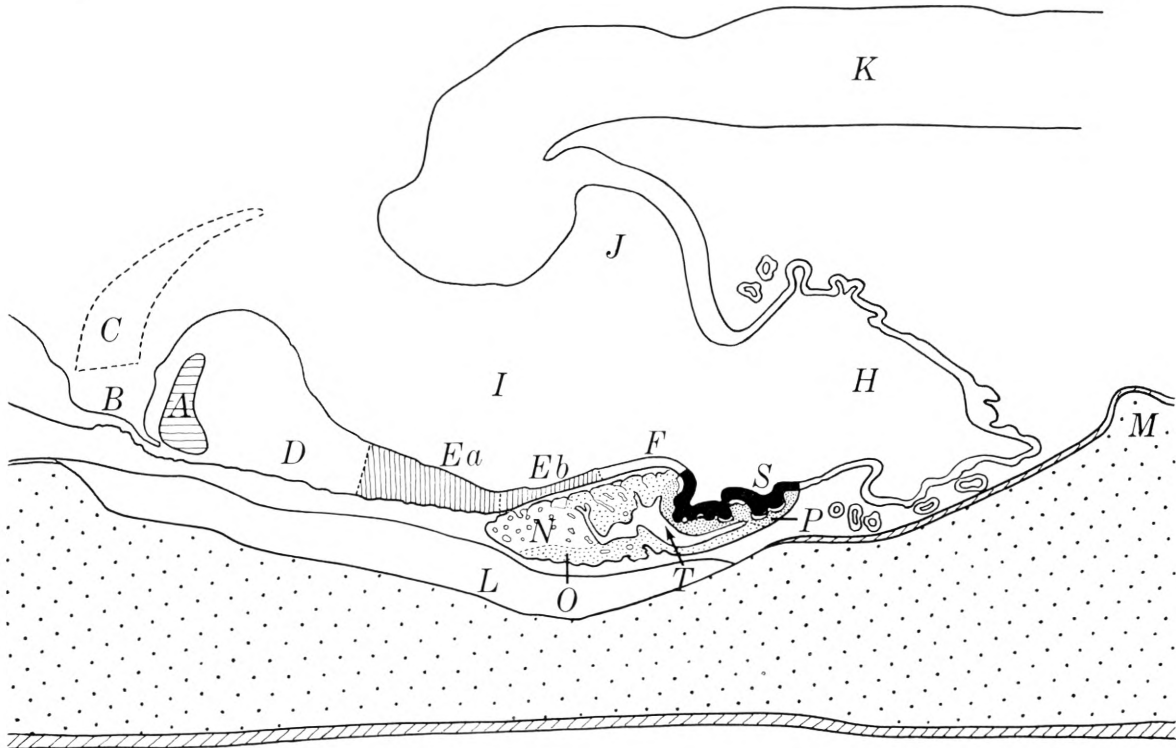
In the *meta-adenohypophysis* the B_5 's and the A_2 's are found. The B_5 's are elongated and filled with distinct but small granules uniformly scattered in the cytoplasm. There are only a few A_2 cells.

3. The Arteries

a) Carotid and cerebral arteries (Fig. 6)

There is in the present material no deviation from the description of the origin of the paired aa. carotides internae given by ALLIS (1911) and DANFORTH (1912).

The paired aa. carotides internae penetrate the basis cranii ventro-laterally to the pituitary gland. In the area between the n. opticus and the lobus inferior the a. carotis cerebialis divides into the ramus anterior and the ramus posterior (= a. cerebialis posterior). Caudally to n. opticus the ramus anterior gives off the a. ophthalmica interna and after a short distance splits further into the a. cerebialis anterior



0.5 mm

Fig. 5. *Polyodon spathula*. Median diagrammatic section. — Labels see figs. 1-2.

SCHEME III. Staining affinities of the chromophilic cell-types in the adenohipophysis in *Polyodon spathula*

staining method	cell-type					
	A ₂	B ₁	B ₂	B	B ₅	colloidal material
Gabe's AF		+	+		+	+
AF — Halmi's counterstain	yellowish green	violet	yellowish brown (with or without a violet shade)		pale greyish violet	violet
PAS		+	+	+	+	+
Azan	orange	pale blue	pale purple		pale greyish blue	blue
Trichrome stain. Cleveland — Wolfe	greenish yellow	blue	greenish yellow		pale greyish blue	blue

and *media* plus *a. mesencephali dorsalis* which is the largest branch. The *a. mesencephali dorsalis* runs dorsally and meets its contralateral partner medio-dorsally to the mesencephalon to form an unpaired vessel which continues caudally. Rostro-ventrally to the n. oculomotorius the *a. cerebralis posterior* joins its twin to form the unpaired *a. basilaris* which continues below the medulla oblongata. (According to DANFORTH (1912) the *a. basilaris* is a paired vessel).

b) Infundibular arteries (Fig. 6)

The *aa. infundibulares* originate from the *aa. cerebralis anteriores* and *mediae* and can be followed to the caudal part of the eminentia mediana. The *aa. infundibulares* send off capillaries to the postchiasmatic region and to the rostral part of the eminentia mediana.

4. The Hypothalamo-hypophysial Blood System (Fig. 6, Pls. VII–VIII)

a) Pituitary portal system

There is a pituitary portal system, but no supplementary vessels and no lateral afferent veins.

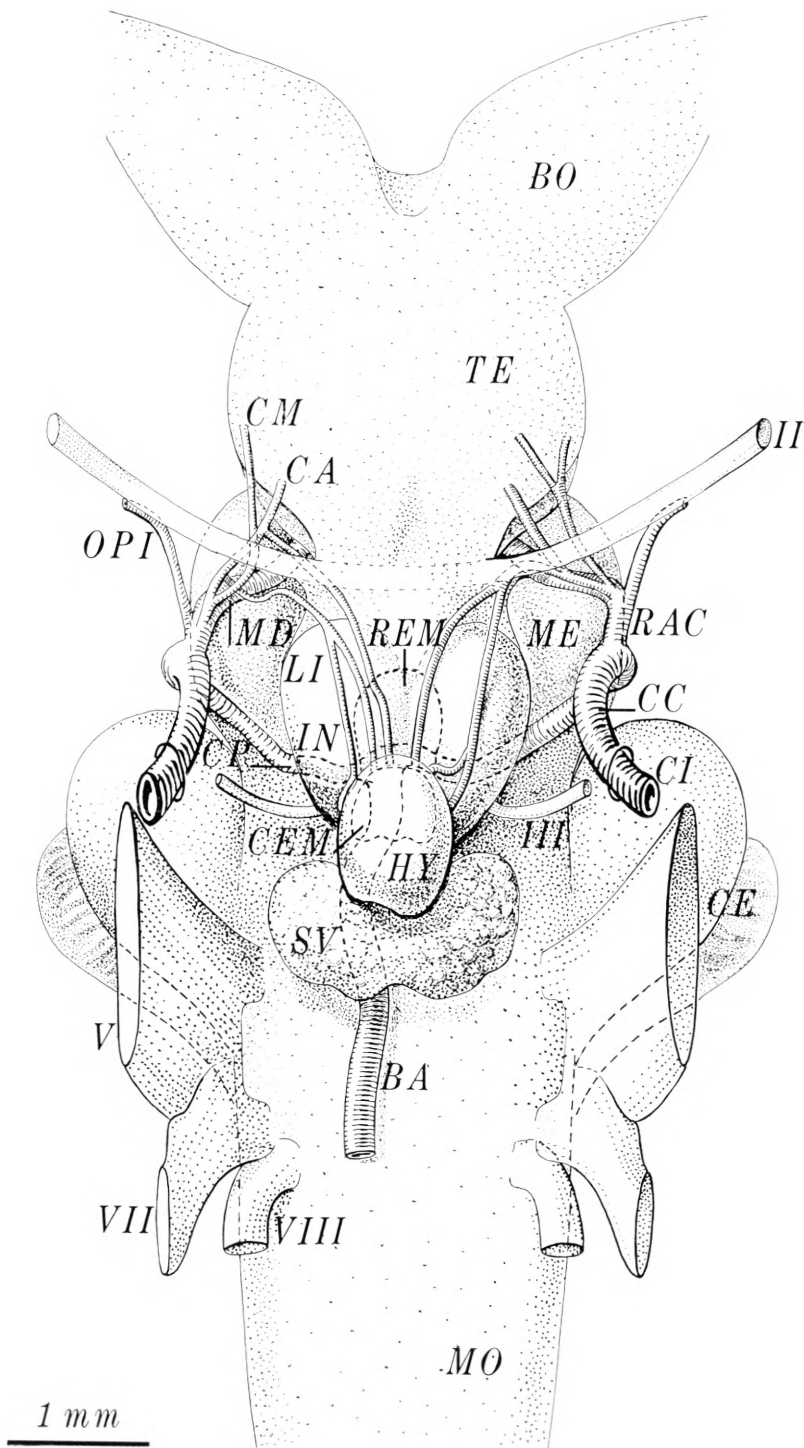
The postchiasmatic plexus, which is fed by the *aa. infundibulares*, is more open than the plexus of the eminentia mediana. In this region there are connections between the superficial and deeper capillaries. The posterior delimitation to the eminentia mediana is not distinct, and the capillaries from the postchiasmatic plexus continue both to the chiasma opticum and to the eminentia mediana.

The *primary plexus* comprises a rostral and a caudal part (Fig. 6). There are no connections between the deeper capillaries and the superficial plexus of the eminentia mediana.

In the *rostral part* of the eminentia mediana the capillaries run in flat longitudinal grooves, and loops are not found—"simple eminential type". The lateral part of the plexus is drained to the pro-adenohypophysis via a few "*vv. portae*" (Pl. VIII: 1). The capillaries from the medial part of the plexus continue into the caudal eminential plexus.

In the *caudal region* of the eminentia mediana the capillaries also lie in longitudinal grooves, but the grooves in this part of the eminentia are deeper than in the former part. The capillaries (Pl. VIII: 2–3) continue directly into the secondary plexus in the pro- and meso-adenohypophysis (real portal vessels are not developed).

Fig. 6. *Polyodon spathula*. Ventral view of the brain, showing the distribution of the arteries. — BA = a. basilaris, BO = bulbus olfactorius, CA = a. cerebralis anterior, CC = a. carotis cerebralis, CE = cerebellum, CEM = caudal part of the eminentia mediana, CI = a. carotis interna, CM = a. cerebralis media, CP = a. cerebralis posterior, HY = hypophysis, IN = a. infundibularis, LI = lobus inferior, MD = a. mesencephali dorsalis, ME = mesencephalon, MO = medulla oblongata, OPI = a. ophthalmica interna, RAC = a. carotis cerebralis ramus anterior, REM = rostral part of the eminentia mediana, SV = saccus vasculosus, TE = telencephalon, II = n. opticus, III = n. oculomotorius, V = n. trigeminus, VII = n. facialis, VIII = n. acusticus.



The capillaries from the caudal part of this plexus continue into the hypophysial stem plexus, which in turn passes into the plexus intermedius and to the saccus vasculosus.

b) Vessels in the pro- and meso-adenohypophysis

The secondary plexus in the pars distalis is fed exclusively from the primary plexus.

The general vascular pattern in the pars distalis resembles that in *Acipenser*. As in *Acipenser* the capillaries of the secondary plexus surround, in the form of a dense network, the cell groups, but do not penetrate between the cells.

c) Vessels in the neuro-intermedia area

The *plexus intermedius* is well developed (Pl. VIII). There is no hint of an intermedia sinusoid system, and the plexus intermedius does not send off capillaries to the lobus nervosus.

d) Saccus vasculosus

The capillary plexus of the saccus vasculosus is fed from the hypophysial stem plexus and from the superficial capillaries of the hypothalamus.

5. The Venous System (Fig. 7, Pl. VIII:1)

The unpaired *v. hypophyseos* (*v. interorbitalis*) (Fig. 7) which drains the pituitary gland and the saccus vasculosus unites with the *v. cerebralis media*. The vein arises in the superficial capillary plexus which covers the ventral surface of the pars distalis. After a short distance it communicates with an unpaired "*v. hypophyseos lateralis*" which drains the plexus intermedius. In addition the *v. hypophyseos* communicates with several small vessels coming from the saccus vasculosus.

VI. *Polypterus senegalus* and *Calamoichthys calabaricus*

Material and methods (see p. 7).

Literature.

The pituitary gland of the *Brachiopterygii* was examined and briefly described by WALDSCHMIDT (1887, *Polypterus*), BICKFORD (1895, *Calamoichthys*), DE BEER (1926, *Polypterus*; according to WINGSTRAND 1966 a), GERARD and CORDIER (1936 a, b, *Polypterus*) and GERARD (1937, *Polypterus*). These authors agreed in finding a persistent buccohypophyseal duct. DORN (1955) alleges (referring to BICKFORD, 1895) that the saccus vasculosus is absent in *Calamoichthys*. DODD and KERR (1963, *Calamoichthys* and *Polypterus*) described the pituitary gland and suggested the existence of a pituitary portal system in *Polypterus*, which superficially recalls the portal arrangement in amphibians. The general structure of the pituitary gland in *Polypterus* is given by WINGSTRAND (1966 a). This author describes a "morphological" eminentia

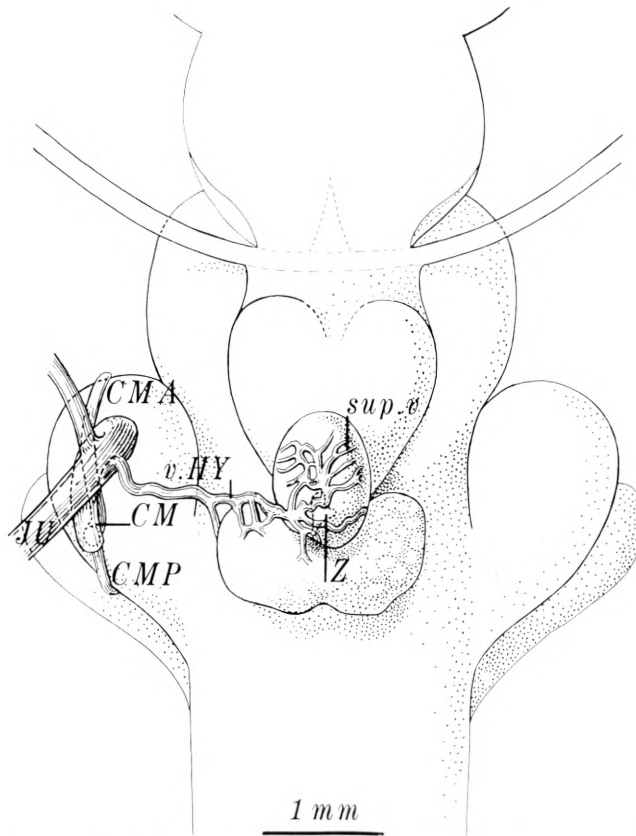


Fig. 7. *Polyodon spathula*. Ventral view of the brain showing the venous drainage of the pituitary gland. — CM = v. cerebialis media, CMA = v. cerebialis media ramus anterior, CMP = v. cerebialis media ramus posterior, JU = v. jugularis, sup. v. = superficial venous plexus, v. HY = v. hypophyseos, Z = capillary connection between the plexus intermedius and the superficial venous plexus of the hypophysis. Brain parts see fig. 6.

mediana in the brain wall between and in front of the meso-adenohypophysis. LAGIOS (1968b, c, *Calamoichthys* and *Polypterus*) gives a description, based on light and electron microscopy, of the pituitary gland and of the eminentia mediana. KERR (1968, *Calamoichthys* and *Polypterus*) likewise gives a morphological and histological description of the pituitary gland. The last mentioned author also describes the pituitary gland of two larvae (*Polypterus*). ALLIS (1908, *Polypterus*) describes the pseudobranch and the carotid arteries.

The descriptions given by LAGIOS and KERR are in nearly all respects in agreement regarding the morphology but discrepant concerning the cell types. The following description confirms in nearly all respects the morphological description given by these authors, but the interpretation of the number of cell types diverges.

As a consequence of the similar morphological structure of the pituitary gland and of the neurohypophysial region in *Polypterus* and *Calamoichthys*, the two species will be treated together below.

1. The Hypothalamo-neurohypophysial Region (Figs. 8–10, Pl. IX)

The cells of the *nucleus praeopticus* are differentiated into a dorso-caudal group, the pars magnocellularis, and a bigger ventro-rostral group, the pars parvocellularis. The *lobi inferiores* are not very prominent. The medial part of the *lobus medius* includes the postchiasmatic region and the eminentia mediana.

The *eminentia mediana* (Figs. 8–10, Pl. IX: 1) is bounded by a vague sulcus tubero-infundibularis. In the angle between the rostral part of the eminentia mediana and the pars distalis a pad of connective tissue is found containing *vv. portae* (“the vascularized ligament” of WINGSTRAND, 1966 a). The caudal part of the eminentia mediana is separated only by a thin layer of connective tissue and capillaries from the pars distalis. The brain wall in the eminentia mediana may be divided into the three histological layers. The fibre layer in *Polypterus* contains Herring bodies but no pituicytes. In *Calamoichthys* pituicytes are found in the margin between the fibre and cortical layer. Neurosecretory material is found in the cortical layer, localized around the capillaries of the primary plexus.

Caudally the eminentia mediana continues in the thin but distinctly marked *hypophysial stem*, which is covered superficially by a capillary plexus.

The recessus infundibularis continues with a primary lumen into the *lobus nervosus* (Pl. IX: 2), on each side of the median plane. The primary lumen is short and gives off only a few secondary lumina. The outermost lobi nervosi processes appear solid and are irregularly dispersed in all directions in intimate association with the pars intermedia. In the hollow proximal part of the lobus nervosus, the wall consists of the ependymal-, fibre- and cortical layers. The ependymal cells continue from here as a central cell-mass into the solid processes, so that the three histological layers, somewhat atypically, are found also in these parts of the lobus nervosus. In *Polypterus* some crown cells are found in between the ependymal cells, but not in *Calamoichthys*. In both *Calamoichthys* and *Polypterus* the ependymal cells (of which there are two types) include some cells in all respects equal to the crown cell, but lacking the characteristic “crown”. In the fibre layer Herring bodies and pituicytes are found. The cortical layer contains a lot of small neurosecretory granules and some Herring bodies.

The *saccus vasculosus* is limited rostro-dorsally by the lobus posterior, and ventrally by the lobus nervosus. The recessus infundibularis continues as a central cavity into the saccus vasculosus which in turn subdivides. The walls of the saccus vasculosus are thin, and the epithelium contains crown cells with supporting cells in between.

2. The Adenohypophysis (Figs. 8–10, Pls X–XI:2)

The oviform pituitary gland lies rostrally between the caudal parts of the lobi inferiores. The pituitary gland and the saccus vasculosus are situated in a flat fossa hypophyseos bounded ventrally by the parasphenoid and caudally by the dorsum sellae, which dorsally is completely ossified. The adenohypophysis comprises the pars distalis, the pars intermedia (the meta-adenohypophysis) and a duct (the bucco-

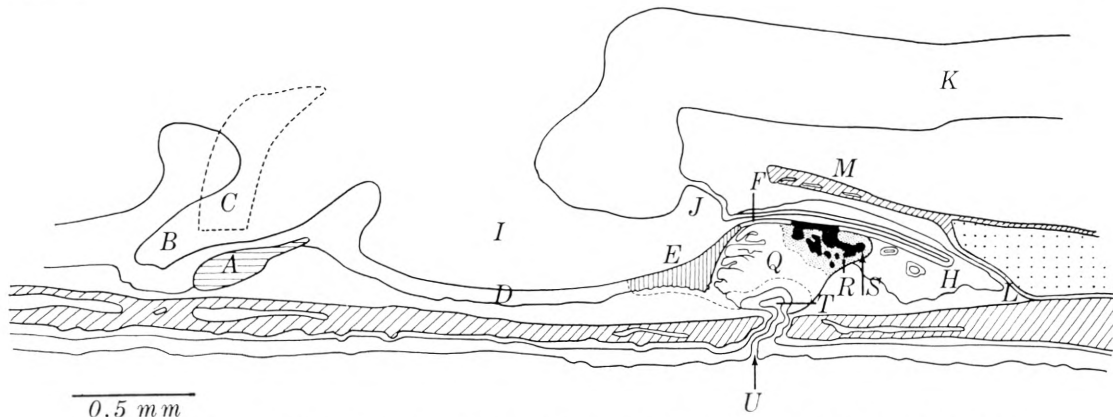


Fig. 8. *Calamoichthys calabaricus*. Median diagrammatic section. — Labels see figs. 1-2, 9.

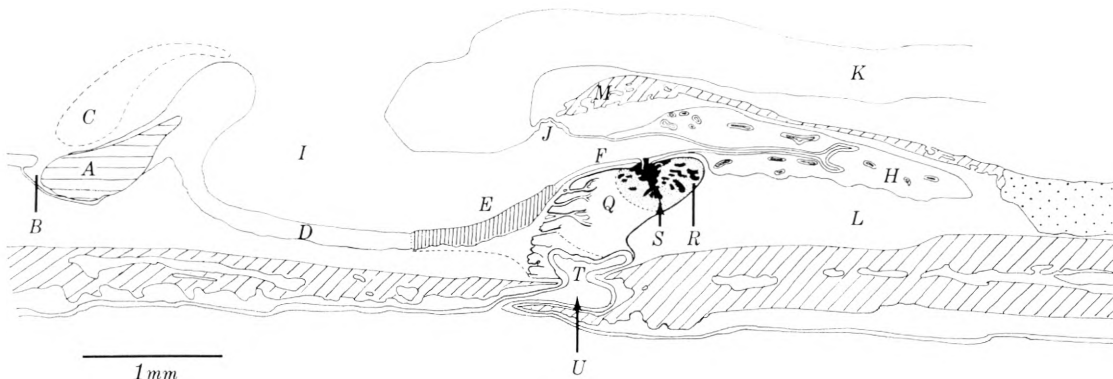


Fig. 9. *Polypterus senegalus*. Median diagrammatic section. — E = eminentia mediana, Q = pars distalis, R = pars intermedia. Other labels see figs. 1-2.

hypophysial duct) connecting the cavity in the adenohypophysis with the buccal cavity (Figs. 8-9). (A subdivision of the pars distalis into a pro- and meso-adenohypophysis is not possible after the criteria given on p. 11). The irregular cavity of the adenohypophysis gives off short hollow protuberances which in turn are subdivided. The cells lining the cavity are long and narrow basophils, comparable with ordinary mucus-producing cells. The cells lining the duct are, in the proximal part, identical with the cells of the cavity epithelium, but in the distal part the cells become reduced in length, and are identical with the mucus cells of the buccal cavity. The lumen contains a small quantity of PAS positive substance.

The greater part of the *pars distalis* (interpreted by WINGSTRAND and KERR as a possible meso-adenohypophysis) is built up of regular horizontally placed compact

SCHEME IV. Staining affinities of the chromophilic cell-types in the adenohypophysis in *Calamoichthys calabaricus*.

staining method	cell-type					
	A	B ₁	B ₂	B ₃	B ₇	B ₈
Gabe's AF	—	(+)	+	+	+	+
AF-Halmi's counterstain	pale green	greyish violet	brown	violet	pale violet	pale violet
PAS — orange G	orange		brownish red		pale pink	bordeaux red
Azan	orange	blue	red	blue	pale blue	pale blue
Trichrome stain. Cleveland — Wolfe	greenish yellow	greenish blue, or pale blue	yellowish orange	blue	pale violet	pale blue

cell-columns surrounded by connective tissue and separated by capillaries. Around the hypophysial cavity the pars distalis is made up mainly of separate cell-groups. The rostro-medio-ventral part of the pars distalis is irregularly constructed and bounded rostrally by the "vascularized ligament". (The two last-mentioned parts of the pars distalis are interpreted by WINGSTRAND and KERR as a possible pro-adenohypophysis). In *Polypterus* the dorso-lateral part of the "meso-adenohypophysis" extends into a pair of lobules, which touch the lobi inferiores, and which embrace the lateral parts of the "pro-adenohypophysis".

The *neuro-intermedia* lobe is sharply demarcated histologically from the pars distalis. Dorso-rostrally the lobe extends on either side of the median plane above the pars distalis. A single layer of intermedia cells (radially arranged) surrounds the irregular neurohypophysial processes. The capillaries of the plexus intermedius are found between the lobus nervosus and the intermedia cells. The single neuro-intermedia "rosettes" are separated by capillaries and connective tissue.

The *pars distalis* in *Calamoichthys* contains A, B₁, B₂, B₃, B₇ and chromophobic cells. The B₁ cells are small round cells, with only a little cytoplasm. These cells are chiefly grouped together in separated clones in the area around the hypophysial cavity. Nearest to the mucus cells of the cavity the B₁ cells form a layer, one or two cells thick. In the rostro-medio-ventral part of the pituitary gland the B₁ cells are found together with some indefinable, weakly stainable cells the B₇. The B₂'s are big ovoid cells filled with amorphous material, with or without vacuoles. This cell type is prevalent in the central part of the pars distalis, whilst B₃ cells are predominant in the dorso-medial part. The latter are elongated, smaller than the B₂ cells, and filled with granules of medium size. The B₇'s are big ovoid cells, with granules of medium size, with or without vacuoles. This cell type is found in the rostro-medial and lateral part of the pars distalis in a faintly stainable form. In the central part the B₇ cells are found in

SCHEME V. Staining affinities of the chromophilic cell-types in the adenohypophysis in *Polypterus senegalus*.

staining method	cell-type				
	A	B ₁	B		B ₅
			B ₂	B ₃	
Gabe's AF	—	(+)	+	+	+
Gomori's chrome hematoxylin	— red	(+)	+	+	(+)

a more distinctly stainable form. The A cells are very small, somewhat elongated and less numerous than the other cells in the pars distalis. They are found mainly in the rostral periphery of the pars distalis, and in addition occur in small numbers in the rest of the pars distalis. The chromophobic cells are small and found throughout the pars distalis.

In the *pars intermedia* the B₅ cells are found. They are small and elongated, with the nucleus eccentrically situated in the basal part of the cell.

On the basis of the nature of the material, the following classification of the cell types in *Polypterus*, must be taken with reservations.

The *pars distalis* contains the basophil B cells (which probably may be classified into B₂ and B₃) and a "doubtful" basophil cell type B₁, the acidophil cell type A plus chromophobic cells. The B₁ cells correspond with the B₁'s in *Calamoichthys* as far as the morphology and the location relative to the hypophysial cavity are concerned. The B cells are ovoid or elongated and uniformly scattered in the pars distalis. The "B₂" cells are elongated with the nucleus eccentrically placed and the cytoplasm filled with amorphous material. This "cell type" is predominant in the central part. The "B₃" is ovoid, of a size similar or smaller than the "B₂" and filled with irregular medium size granules. This "cell type" is prevalent in the medio-dorsal part. Laterally the two "cell types" are uniformly scattered. The A cells are equivalent in morphology and location to the A cells of *Calamoichthys*.

The *pars intermedia* contains a single basophil cell type B₅ which likewise corresponds with the B₅ cells described in *Calamoichthys* with respect to morphology and location.

3. The Arteries in *Calamoichthys*

a) Carotid and cerebral arteries (Fig. 10)

The paired *aa. carotides internae* divide extracranially into the ramus anterior and the ramus posterior (= a. cerebralis posterior). The extracranial part of the ramus posterior gives rise to the *a. ophthalmica interna* and the *a. ophthalmica* (FRANTZ, 1934). Intracranially the *a. mesencephali dorsalis* branches off from the *ramus anterior* which after a short distance splits into the *a. cerebralis anterior* and *media*. The paired *aa. mesencephali dorsales* anastomose medio-dorsally to the mesencephalon. This

anastomosis gives off vessels to the telencephalon and a vessel which continues caudally. Lateral to the lobus inferior the *a. cerebialis posterior* gives off a vessel "Y" which continues to the pars dorsalis hypothalami and pars ventralis thalami. Ventrally of the medulla oblongata the *a. cerebialis posterior* joins its twin from the other side to form the unpaired *a. basilaris*. Lateral to the pituitary gland the *a. cerebialis posterior* gives off an artery "X", which meets its collateral partner behind the *n. oculomotorius* and dorso-medial to the pituitary gland. This anastomosis is with respect to the position and the area of supply equal to the anastomosis formed by the *aa. cerebialis posteriores* as seen in the other species, but it lacks the *a. basilaris* which normally continues from this anastomosis.

b) *Infundibular arteries* (Fig. 10)

The paired *aa. infundibulares* originate from the arteries "Y". The *aa. infundibulares* give off vessels to the postchiasmatic region and to the *lobi inferiores*. On arrival at the *eminentia mediana* the *aa. infundibulares* divide into capillaries which continue into the primary plexus.

4. The Hypothalamo-hypophysial Blood System in *Calamoichthys* (Fig. 10, Pls. X–XI)

a) *Pituitary portal system*

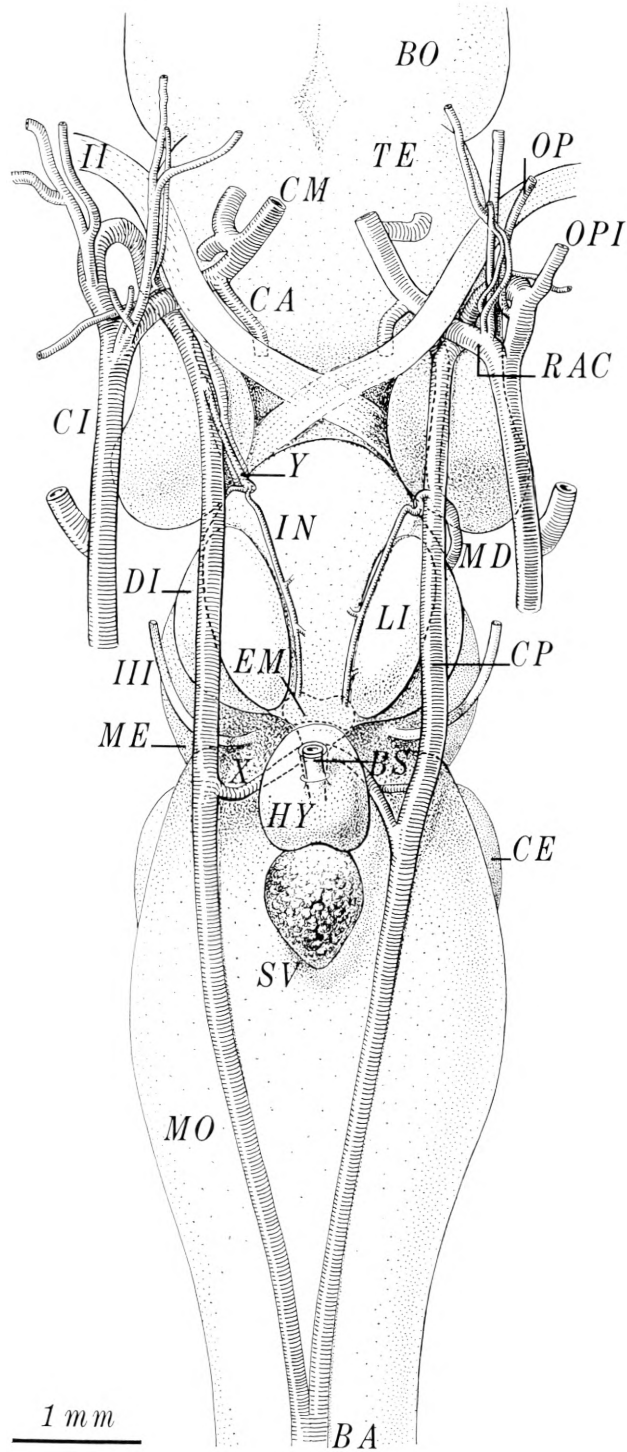
There is a pituitary portal system and a suggestion of supplementary vessels, but no lateral afferent veins.

The postchiasmatic superficial and deep-lying capillary plexus are fed by the *aa. infundibulares*. Some of the superficial capillaries continue into the plexus of the *eminentia mediana*.

The *primary plexus* of the *eminentia mediana* comprises a rostral part in connection with a caudal part. The capillaries of the *rostral part* of the primary plexus lie medially in flat furrows, but form laterally some capillary loops. This *eminentia* type represents approximately a "transitional stage" between the simple and the differentiated *eminentia* type. The rostral part of the primary plexus is drained to the *pars distalis* via typical *vv. portae* running in the pad of connective tissue (Pl. X).

The primary plexus of the *caudal part* of the *eminentia mediana* consists of slender capillaries, which lie in slightly undulated furrows. Real portal vessels are not developed, and the capillaries of the plexus continue nearly directly into the secondary plexus of the *pars distalis*. There is also a slight connection between the capillaries of the primary plexus and the deep-lying capillaries of the hypothalamus. In addition some capillaries of this plexus merge posteriorly into the hypophysial stem plexus, which in turn passes into the plexus *intermedius* and to the *saccus vasculosus* (Pl. X).

Fig. 10. *Calamoichthys calabaricus*. Ventral view of the brain, showing the distribution of the arteries. — BA = *a. basilaris*, BO = *bulbus olfactorius*, BS = *buccohypophysial stem*, CA = *a. cerebialis anterior*, CE = *cerebellum*, CI = *a. carotis interna*, CM = *a. cerebialis media*, CP = *a. cerebialis posterior*, DI = *diencephalon*, EM = *eminentia mediana*, HY = *hypophysis*, IN = *a. infundibularis*, LI = *lobus inferior*, MD = *a. mesencephali dorsalis*, ME = *mesencephalon*, MO = *medulla oblongata*, OP = *a. ophthalmica*, OPI = *a. ophthalmica interna*, RAC = *a. carotis cerebialis ramus anterior*, SV = *saccus vasculosus*, TE = *telencephalon*, X = *a. X*, Y = *a. Y*, II = *n. opticus*, III = *n. oculomotorius*.



b) *Vessels in the pars distalis*

The secondary plexus in the pars distalis is a well developed system of capillaries fed exclusively from the primary plexus. The capillaries of the secondary plexus are surrounded by connective tissue and run between the cell "columns" in the form of a dense network, without penetrating between the individual cells in the "columns".

c) *Vessels in the neuro-intermedia area*

The *plexus intermedius* is well developed and associated with the outer faces of the lobus nervosus processes. In connection with this plexus an intermedia sinusoid

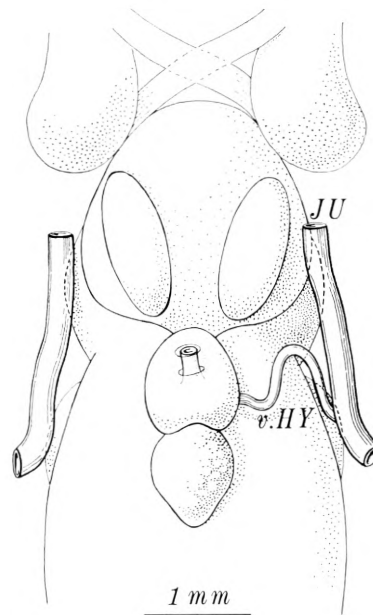


Fig. 11. *Calamoichthys calabaricus*. Ventral view of the brain showing the venous drainage of the pituitary gland. — JU = v. jugularis, v. HY = v. hypophyseos. Brain parts see fig. 10.

system is developed. The sinuses form a dense network throughout the intermedia around the "rosettes" and reunite with the secondary plexus of the pars distalis.

d) *Saccus vasculosus*

The capillary plexus of the saccus vasculosus is as previously mentioned fed from the hypophysial stem plexus.

5. The Venous System in *Calamoichthys* (Fig. 11, Pl. XI:2)

The unpaired *v. hypophyseos*, which drains the pituitary gland, arises in the ventral fissure between the saccus vasculosus and the pars distalis. This vein receives some small veins from the saccus vasculosus, and communicates extracranially with

the v. jugularis. In the specimens examined only a left v. hypophyseos was found. Furthermore the saccus vasculosus is drained by small veins running dorsally and communicating with the vv. infundibulares, which in turn run into a venous plexus ventral to the medulla oblongata.

VII. *Lepisosteus productus*

Material and methods (see p. 7).

Literature.

The early developmental stages of the pituitary gland are described by BALFOUR and PARKER (1882) (these authors point out that the hypophysial cleft is formed as a schizocoel), and by DEAN (1895). Further embryological investigations were carried out by LINDAHL (1944). This author indicates that the adenohypophysis of the holosteans and chondrosteans develops approximately like that of elasmobranchs. The adult pituitary gland is briefly described by TILNEY (1911). KERR (1949) gives a detailed morphological and histological account of the pituitary gland. As in the case of *Acipenser* there is agreement in the present work with the morphological description, but some discrepancy as to the number of cell types. A brief description of the vessels in and around the pituitary gland is given by GREEN (1951), who points out that a well marked vascular plexus separates the pro- and meso-adenohypophysis from the brain wall, and that this plexus continues into the area between the lobus nervosus and the meta-adenohypophysis. A recent review by WINGSTRAND (1966 a) surveys the literature dealing with the pituitary gland. SATHYANESAN and CHAVIN (1967) describe the hypothalamo-hypophyseal neurosecretory system in the primitive actinopterygians (which includes among others *Lepisosteus*). These authors suggest the presence of a pituitary portal system in *Amia* and *Lepisosteus*. Information on the aa. carotides internae is given by WRIGHT (1885).

1. The Hypothalamo-neurohypophysial Region (Figs. 12–13, Pls. XII–XIII)

The ventral brain wall of the recessus praeropticus is thin and covered by a dense capillary plexus, with typical capillary loops. The general structure of this wall recalls that of the eminentia mediana but without the neurosecretory material. The cells of the *nucleus praeropticus* are differentiated into a dorsal group, the pars magnocellularis, and a ventral group, the pars parvocellularis. The *lobi inferiores* are distinct. The medial area of the *lobus medius* consists of the postchiasmatic region and of the eminentia mediana.

The *postchiasmatic region* is covered by a superficial capillary plexus.

The sulcus tubero-infundibularis is distinct (Pl. XII: 1). The rostral part of the *eminentia mediana* is crescent-shaped and lies rostrally and laterally to the caudal part. The brain wall in the eminentia mediana comprises the ependymal- the fibre and the cortical layer. In the fibre layer some glia cells are found, and in the cortical layer some small glia cells can be discerned in between the ependymal processes.

The *hypophysial stem* is distinctly marked, and covered by a dense capillary plexus.

The *lobus nervosus* is bifid and asymmetrically lobulated (Pl. XII: 2). A pair of hollow protuberances from the recessus infundibularis continue into the lobus nervosus. These primary lumina are restricted to the proximal part of the lobus nervosus and only to a small extent subdivided. The outermost processes of the lobus nervosus are solid. In the hollow parts of the lobus nervosus, the wall consists of the three histological layers. As in the *Brachiopterygii* the ependymal cells continue as a central mass into some of the solid processes. In the ependymal layer some crown cells are found, in the fibre layer pituicytes appear, and the cortical layer contains small neurosecretory granules and some small glia cells.

The *saccus vasculosus* (Figs. 12–13, Pl. XIII) lies ventrally to the medulla oblongata, as a transverse hollow sac in connection with the hypothalamus-hypophysial area via a stem. The lumen of the stem links the recessus infundibularis to the central cavity of the saccus vasculosus. This central cavity gives off hollow protuberances to the rest of the saccus vasculosus. The walls of the saccus vasculosus contain crown cells with supporting cells in between.

2. The Adenohypophysis (Figs. 12–13, Pl. XIII)

The elongated, dorso-ventrally flattened pituitary gland is situated, surrounded by connective tissue, in a flat fossa hypophyseos, close to the parasphenoid, and bordered caudally by a distinct dorsum sellae, which is completely ossified dorsally. The gland comprises the three histological zones (the pro-, the meso- and the meta-adenohypophysis). A hypophysial cavity is not developed.

The *pro-adenohypophysis* is built of follicular cell groups, with or without colloid material. The cell groups are surrounded by connective tissue and by capillaries.

The *meso-adenohypophysis* consists dorsally of solid, perpendicularly arranged cell columns surrounded by capillaries. The ventral part is irregular in construction and consists of separated cell strands and groups. Ventral to the pro-adenohypophysis this irregular part (which corresponds to KERR's "mixed zone") extends to the tip of the adenohypophysis. Latero-ventrally this "zone" covers the meta-adenohypophysis.

The *meta-adenohypophysis* consists of cell strands which are separated from the lobus nervosus by the plexus intermedius. The cell strands are separated mutually by sinusoid capillaries.

The *pro-adenohypophysis* contains A_1 , A_2 , B_3 and some chromophobic cells. A_1 is the predominant cell type, radially arranged around the follicles. This is a typical elongated cell, with the nucleus in the basal part of the cell, surrounded by granules. The A_2 cells are found less frequently, and are ovoid, with eccentric nuclei and a cytoplasm packed with small granules. The ovoid B_3 cells lack a sharply defined cell boundary, and the granules of medium size are scattered irregularly in the cytoplasm.

The *meso-adenohypophysis* contains one acidophil cell type (A_2), possibly three

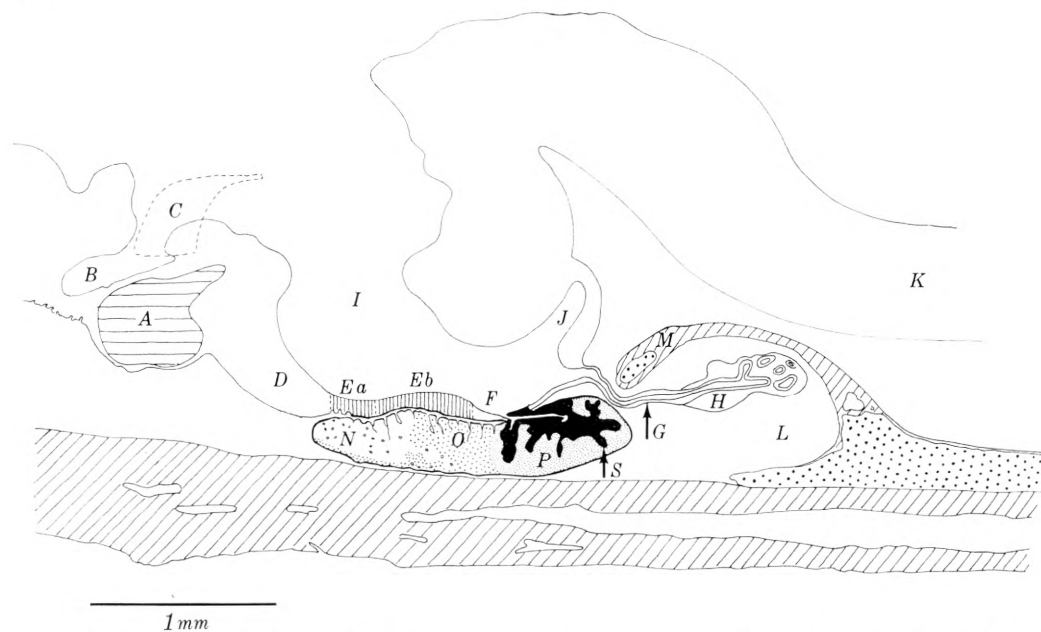


Fig. 12. *Lepisosteus productus*. Median diagrammatic section. — G = sacci vasculosi stem. Other labels see figs. 1-2.

basophil cell types (B_1 , B_2 and B_3) together with some chromophobic cells. The B_1 cells, which are confined to the medio-ventral region are elongated and have an eccentrically placed nucleus. The granules are fairly coarse and irregular in shape. The B_3 's are distributed in considerable number throughout the remaining part of the meso-adenohypophysis. The B_2 cells are only prevalent in the dorsal region. This "cell type" is smaller than the "type" marked B_3 , and contains fewer granules.

SCHEME VI. Staining affinities of the chromophilic cell-types in the adenohypophysis in *Lepisosteus productus*.

staining method	cell-type					colloidal material
	A_1	A_2	B_1	$B_2 \leftrightarrow B_3$	B_5	
Gabe's AF	—	—	+	+	+	+
AF — Halmi's counterstain	green	yellowish green	violet	brownish violet	pale violet	violet
PAS	—	—	+	+	+	+
Azan	red	orange	dark blue	pale blue	blue violet	purple
Trichrome stain. Cleveland — Wolfe	yellowish brown	yellow	dark blue	blue - violet	blue violet	blue

(The B_2 and B_3 may be two different cell types, but this is not precisely demonstrated by the staining results). Further, a few A_2 cells are present in this part of the adeno-hypophysis.

In the *meta-adenohypophysis* B_5 is the conspicuous cell type, and only a few A_2 cells are encountered. The B_5 cells are somewhat elongated with the nucleus eccentrically placed. The granules are coarse and distributed uniformly in the cytoplasm.

3. The Arteries

a) Carotid and cerebral arteries (Fig. 13)

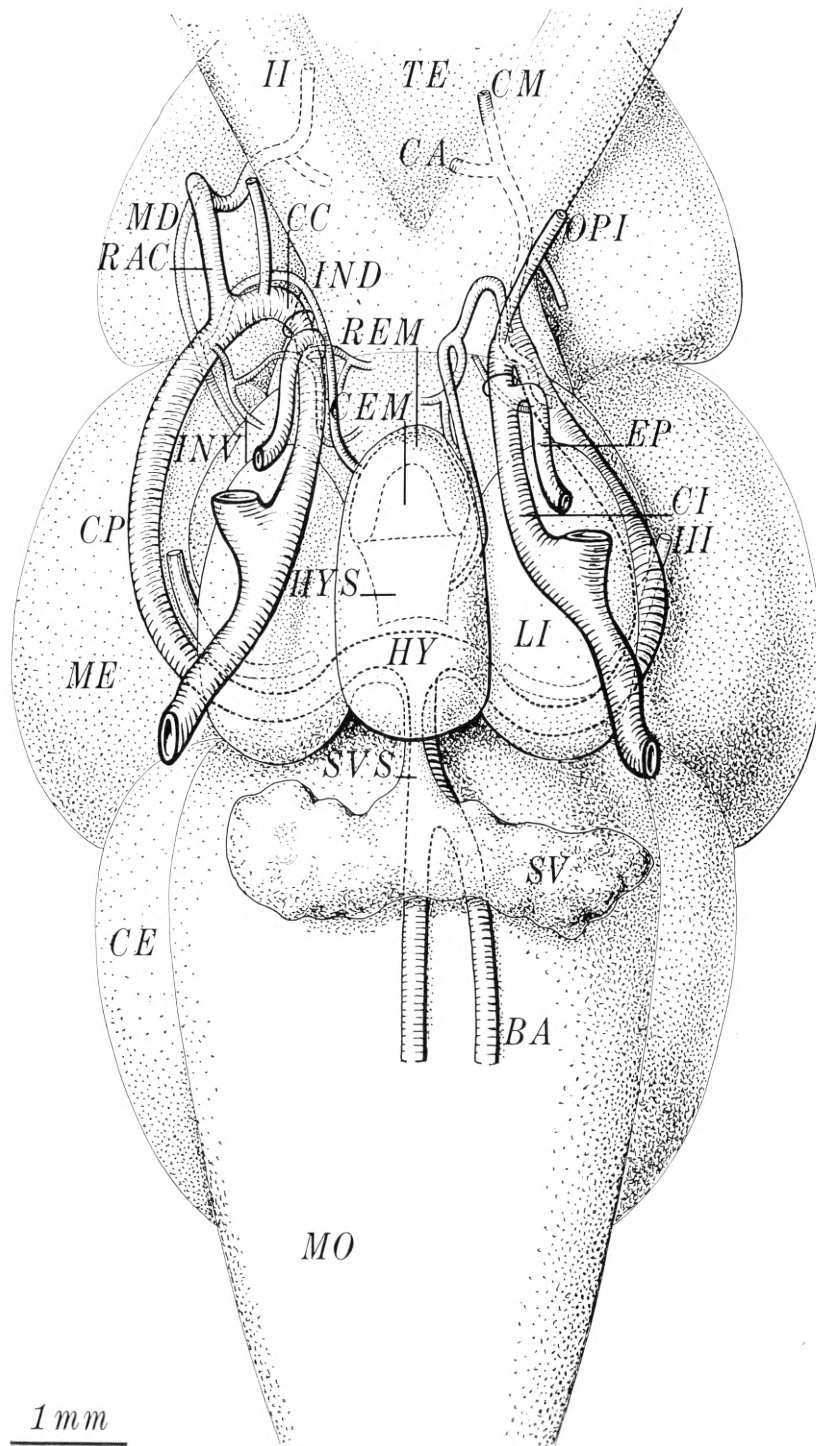
There is in the present work agreement with the description of the aa. carotides internae given by WRIGHT (1895).

The paired aa. carotides internae unite with the efferent pseudobranch arteries immediately before the former pierce the basis cranii. The a. carotis cerebralis sends off the a. ophthalmica interna laterally to the chiasma opticum. Somewhat further rostrally it splits into the two main stems: the ramus anterior and the ramus posterior (a. cerebralis posterior), which is the more prominent of the two. The ramus anterior gives off the a. mesencephali dorsalis, after which it passes above the n. opticus and gives rise to the a. cerebralis anterior and media. The paired aa. mesencephali dorsales do not anastomose dorsally to the mesencephalon. The a. cerebralis posterior runs caudally and joins its partner from the opposite side, behind and below the n. oculomotorius, to form an unpaired strong trunk, which after a short course subdivides into the paired aa. basillares.

b) Infundibular arteries

It is possible to distinguish between the a. infundibularis ventralis, which arises from the ventral side of the a. cerebralis posterior, and the a. infundibularis dorsalis which arises from the dorsal side of the a. cerebralis posterior. The a. infundibularis ventralis proceeds forward giving off small branches supplying the capillary plexus of the postchiasmatic region. From this plexus pial capillaries continue into the median part of the primary plexus. The a. infundibularis dorsalis supplies the lateral part of the primary plexus and the hypophysial stem plexus, and in addition it gives off some small branches to the postchiasmatic region. There is a marked difference in the course of the paired vessels on the two sides.

Fig. 13. *Lepisosteus productus*. Ventral view of the brain showing the distribution of the arteries. — BA = a. basilaris, CA = a. cerebralis anterior, CC = a. carotis cerebralis, CE = cerebellum, CEM = caudal part of the eminentia mediana, CI = a. carotis interna, CM = a. cerebralis media, CP = a. cerebralis posterior, EP = efferent pseudobranch artery, HY = hypophysis, HYS = hypophyseal stem plexus, IND = a. infundibularis dorsalis, INV = a. infundibularis ventralis, LI = lobus inferior, MD = a. mesencephali dorsalis, ME = mesencephalon, MO = medulla oblongata, OPI = a. ophthalmica interna, RAC = a. carotis cerebralis ramus anterior, REM = rostral part of the eminentia mediana, SV = saccus vasculosus, SVS = sacci vasculosi stem, TE = telencephalon, II = n. opticus, III = n. oculomotorius.



4. The Hypothalamo-hypophysial Blood System (Fig. 13, Pls. XIV–XV)

a) Pituitary portal system

There is a pituitary portal system which includes supplementary vessels and a lateral afferent vein on each side.

Medially the postchiasmatic plexus continues into the *primary plexus* of the eminentia mediana, which comprises a rostral and a caudal region.

In the *rostral region* of the primary plexus (Pls. XIV: 2, XV: 1) distinct capillary loops are found (“differentiated eminentia type”). The lateral parts of the plexus receive some supplementary vessels (Pl. XIV: 1). From the plexus typical *vv. portae* arise and pass to the pro-adenohypophysis. Furthermore many of the capillaries pass to the caudal part of the primary plexus.

In the *caudal region* (Pls. XIV:2, XV:1) of the primary plexus the capillaries lie in narrow undulated furrows. (There is no distinct border between the caudal and the rostral eminential parts). Some supplementary vessels make contact with the lateral part of the plexus. Blood from the plexus passes to the meso-adenohypophysis. Real portal vessels are not developed, and the primary and the secondary plexus are more or less continuous. From the posterior part of the primary plexus the capillaries converge toward the hypophysial stem plexus, which in turn continues into the plexus intermedius and the plexus of the saccus vasculosus.

b) Vessels in the pro- and meso-adenohypophysis

As mentioned above the pars distalis receives blood from the primary plexus of the eminentia mediana. In addition the adenohypophysis receives direct arterial supply via a few small capillaries (Pl. XIV:1), branching off from the a. infundibularis. This supply is probably of no special functional significance compared with the supply coming from the primary plexus. The general capillary pattern is determined by the different glandular proliferation in the pro- and meso-adenohypophysis, i.e.: with an irregular network in the pro-adenohypophysis and more longitudinal meshes in the meso-adenohypophysis (Pl. XIV:2).

c) Vessels in the neuro-intermedia area

The *plexus intermedius* is distinct. It gives rise to some small capillaries which penetrate into the interior of the lobus nervosus. A pair of prominent *lateral afferent veins* (Pl. XV:2) collect blood from the lobi inferiores, the lobi posteriores and the adjacent area of the hypothalamus. Reaching the pituitary gland the afferent vein joins the lateral part of the plexus intermedius. The plexus intermedius gives rise to some small capillaries which penetrate the meta-adenohypophysis. These capillaries unite with the superficial capillary plexus of the meta-adenohypophysis, i.e. a hint of an intermedia sinusoid system is developed (Pl. XV:2).

d) Saccus vasculosus

The capillary plexus of the saccus vasculosus receives capillaries from the hypophysial stem plexus, plexus intermedius and the superficial parts of the hypothalamus.

5. The Venous System (Fig. 14, Pl. XV:2)

An unpaired *v. hypophyseos media* arises at the medio-ventral surface of the pituitary gland. This vein communicates with the *v. interorbitalis*.

The paired *vv. hypophyseos laterales* collect blood from the plexus intermedius. The veins pass dorso-caudally and enter a venous plexus below the medulla oblongata.

The saccus vasculosus is drained by an unpaired *v. sacci vasculosi*, which empties into the *v. hypophyseos lateralis*.

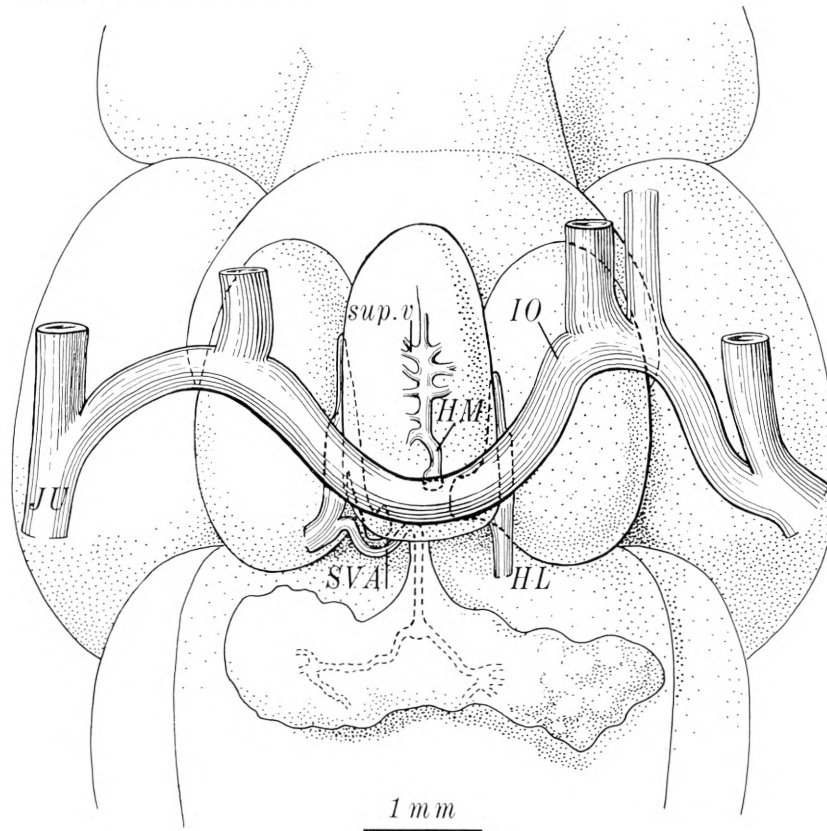


Fig. 14. *Lepisosteus productus*. Ventral view of the brain showing the venous drainage of the pituitary gland. — HL = *v. hypophyseos lateralis*, HM = *v. hypophyseos media*, IO = *v. interorbitalis*, JU = *v. jugularis*, sup. v. = superficial venous plexus, SVA = *v. sacci vasculosi*. Brain parts see fig. 13.

VIII. *Amia calva*

Material and methods (see p. 7).

Literature.

Notes on the embryonic development of the pituitary gland are given by DEAN (1896), SMITH (1914) and DE BEER (1923). The two last-named indicate that a schizocoelic cavity appears in the compact anlage but is reduced in the adult. KERR (1949) and GREEN (1951) fur-

nish information about the hypophysial structure in the adult animal. Neither of these authors describes an eminentia mediana structure. GREEN points out that a vascular plexus separates the adeno-hypophysis from the brain wall, and that this plexus gives rise to capillaries which pass into the plexus intermedius. KERR describes the structure, the histology and the blood supply of the pituitary gland. WINGSTRAND (1966 a) gives a survey of the literature dealing with the pituitary gland. SATHYANESAN and CHAVIN (1967) describe the hypothalamo-hypophysial neurosecretory system, and suggest the presence of a pituitary portal system. The carotides in the larvae are described by WRIGHT (1885). The main arteries in the head and brain are described by ALLIS (1897, 1900 and 1912). ALLIS (1897) gives a complete survey of the cranial muscles and nerves including the first spinal nerves. The main veins are described by ALLIS (1897). Embryological and comparative information on jugular and cerebral veins are given by BERTMAR (1965).

1. The Hypothalamo-neurohypophysial Region (Figs. 15–16, Pls. XVI–XVII)

The structure of the praeoptic region is rather similar to that of *Lepisosteus*. The *lobi inferiores* are prominent, and lie rostrally fairly close to the pituitary gland. There is a clear boundary between the lobus medius and the lobus inferiores. The medial part of the lobus medius comprises the postchiasmatic region and the eminentia mediana.

The structure of the *postchiasmatic region* is fairly similar to that of *Lepisosteus*.

The *eminentia mediana* is bounded by a distinct sulcus tubero-infundibularis. In the eminentia mediana (Fig. 16) one can distinguish between a rostral and a caudal region. The rostral region is crescent-shaped, and the brain wall is rather thick compared with that of the caudal region. In addition capillary loops are found in the rostral region. The brain wall of the eminentia mediana (Pl. XVI:1) comprises the ependymal, the fibre and the cortical layer. In the outer part of the fibre layer some pituicytes are found. The cortical layer contains neurosecretory material and some small glia cells. In addition pituicytes are found although less abundantly in the caudal than in the rostral region.

The eminentia mediana joins the *hypophysial stem* posteriorly. The boundary between the hypophysial stem and the adjacent parts of the hypothalamus is not distinct.

The lobus nervosus is asymmetrically bifid and is folded down as lobulated pockets on either side of the median plane into the meta-adeno-hypophysis. The recessus infundibularis continues with a pair of hollow protuberances (the primary lumens) into the lobus nervosus. These lumens are in turn subdivided, pushing out ramified hollow protuberances, but the outermost processes of the lobus nervosus are solid. The general histological pattern of the lobus nervosus corresponds to that of *Lepisosteus* (p. 38).

The *saccus vasculosus* consists of a stem and a considerable caudal part (Fig. 16). The hollow stem connects the caudal part with the hypothalamus-hypophysial area. In the caudal part there is a central cavity. This gives off blind-ending hollow ramified protuberances. In the hollow stem as well as in the large caudal part the epithelium contains crown cells with supporting cells in between.

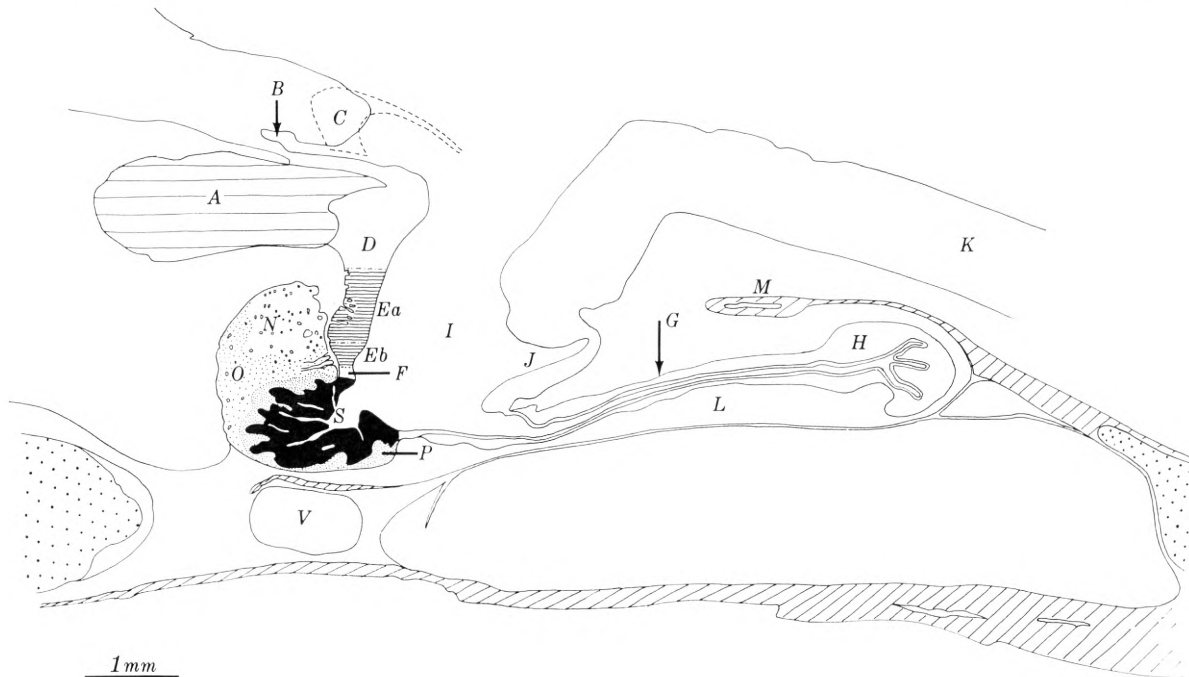


Fig. 15. *Amia calva*. Median diagrammatic section. — Labels see figs. 1–2, 6.

2. The Adenohypophysis (Figs. 15–16, Pl. XVII)

The pituitary gland is “dorso-ventrally” flattened, heart-shaped, with the “apex” toward the chiasma opticum. The gland is dislocated rostrally, lying in front of the lobi inferiores. The longitudinal axis is approximately perpendicular to that of the recessus infundibularis. The gland is situated surrounded by connective tissue, in the fossa hypophyseos, which is bounded caudally by a distinct dorsum sellae. The adenohypophysis is subdivided into three histological regions (the pro-, the meso- and the meta-adenohypophysis). A hypophysial cavity is not found.

The *pro-adenohypophysis* consists of follicles and occupies the dorso-caudal part of the gland. It embraces part of the meso-adenohypophysis from the sides with two lobules facing backwards. The follicular cell groups are surrounded by connective tissue and capillaries.

The *meso-adenohypophysis* consists “dorsally” of cell columns lying approximately perpendicular to the longitudinal axis of the gland. These cell columns are mutually separated by connective tissue and capillaries. “Ventrally” the cell columns disintegrate into irregular cell groups which constitute the remaining portion of the

SCHEME VII. Staining affinities of the chromophilic cell-types in the adenohypophysis in *Amia calva*.

staining method	cell-type						
	A ₁	A ₂	B ₁	B ₂	B ₃	B ₅	colloidal material
Gabe's AF	—	—	+	+	+	+	+
AF — Halmi's counterstain	greenish yellow	yellowish green	dark violet	greyish violet	violet	greyish violet	violet
PAS		((+))	+	+	+	+	+
Azan	red	orange	red-violet reddish	pale blue	blue-violet	red-violet reddish	purple
Trichrome stain. Cleveland — Wolfe	brown	yellow	dark blue	blue-violet	blue-violet	red-violet reddish	blue

meso-adenohypophysis. The irregular cell masses, enclosed by connective tissue and capillaries, are devoid of distinct orientation. That part of the meso-adenohypophysis which is irregular in structure corresponds to the mixed zone described by KERR.

The *meta-adenohypophysis* forms a dense cell mass, containing a few vesicles, around and between the processes of the lobus nervosus. Laterally the meta-adenohypophysis is covered of the meso-adenohypophysis.

The *pro-adenohypophysis* contains A₁, A₂, B₂ and some small chromophobic cells. The A₁ cells are radially orientated around the vesicles and are the prevailing cell type. They are typically elongated, with the globular nucleus eccentrically located in the basal part of the cells and with the fine granules concentrated around it. The A₂ cells are oval in shape and are found less frequently than the A₁. The nucleus is globular and the cytoplasm is packed with homogeneous fine granules. In between the acidophils a few B₂ cells are found. These cells are oval, with scattered medium size granules.

The *meso-adenohypophysis* contains A₂, B₁, B₂, B₃ and some small chromophobic cells. The B₁ cells are confined to the "medio-ventral" part. They are cone-shaped and without a sharply defined cell boundary. The ovoid nucleus is typically at the base of the "cone", and the granules are coarse and somewhat irregular in shape. The above-mentioned B₂ cells are mainly confined to the more "dorsal" part of the meso-adenohypophysis. The B₃ cells occur throughout the meso-adenohypophysis, and form laterally the predominant cell type. These cells are oval, the nuclei are ovoid and irregular, and the medium size granules are scattered throughout the cytoplasm, but are more clumped together than in the B₂ cells. The cell type A₂ occurs only in small number.

The *meta-adenohypophysis* contains B₅ and A₂ cells. The B₅ cells make up the

predominant cell type. These cells are oval or elongated, with the nucleus typically at one end of the cell, and with the fine granules mainly concentrated around it. The A_2 cells previously mentioned are relatively few in number.

3. The Arteries

a) Carotid and cerebral arteries (Fig. 16)

The paired *aa. carotides internae* pierce the basis cranii lateral to the n. opticus. Intracranially and ventral to the n. opticus the a. carotis cerebialis divides into two main stems: the *ramus anterior* and the *ramus posterior* (a. cerebialis posterior).— (It has not been possible to give a general description of the ramus anterior, due to incorrect trimming of the celloidin block)—. The *a. cerebialis posterior* runs dorso-medially, dorsal to the lobus inferior and ventral to the n. oculomotorius. The a. cerebialis posterior meets its contralateral partner above the saccus vasculosus to form an unpaired *a. basilaris*. (ALLIS (1897) points out that from the median point of this anastomosis one branch is sent forward and another backward)—. The presence of the antrorse vessel has not been verified. In addition ALLIS indicates that a. cerebialis posterior sends off *a. auditiva*, this artery, in the material examined, is sent off by the a. basilaris. Immediately before the a. cerebialis posterior meets its partner from the opposite side, it gives rise to an *artery "X"* which turns inwards behind the lobus inferior and meets its collateral partner. The anastomosis gives rise to some vessels which supply parts of the diencephalon, the mesencephalon and the cerebellum. This anastomosis appears to be analogous to the "X" anastomosis described in *Calamoichthys* (p. 34).

b) Infundibular arteries

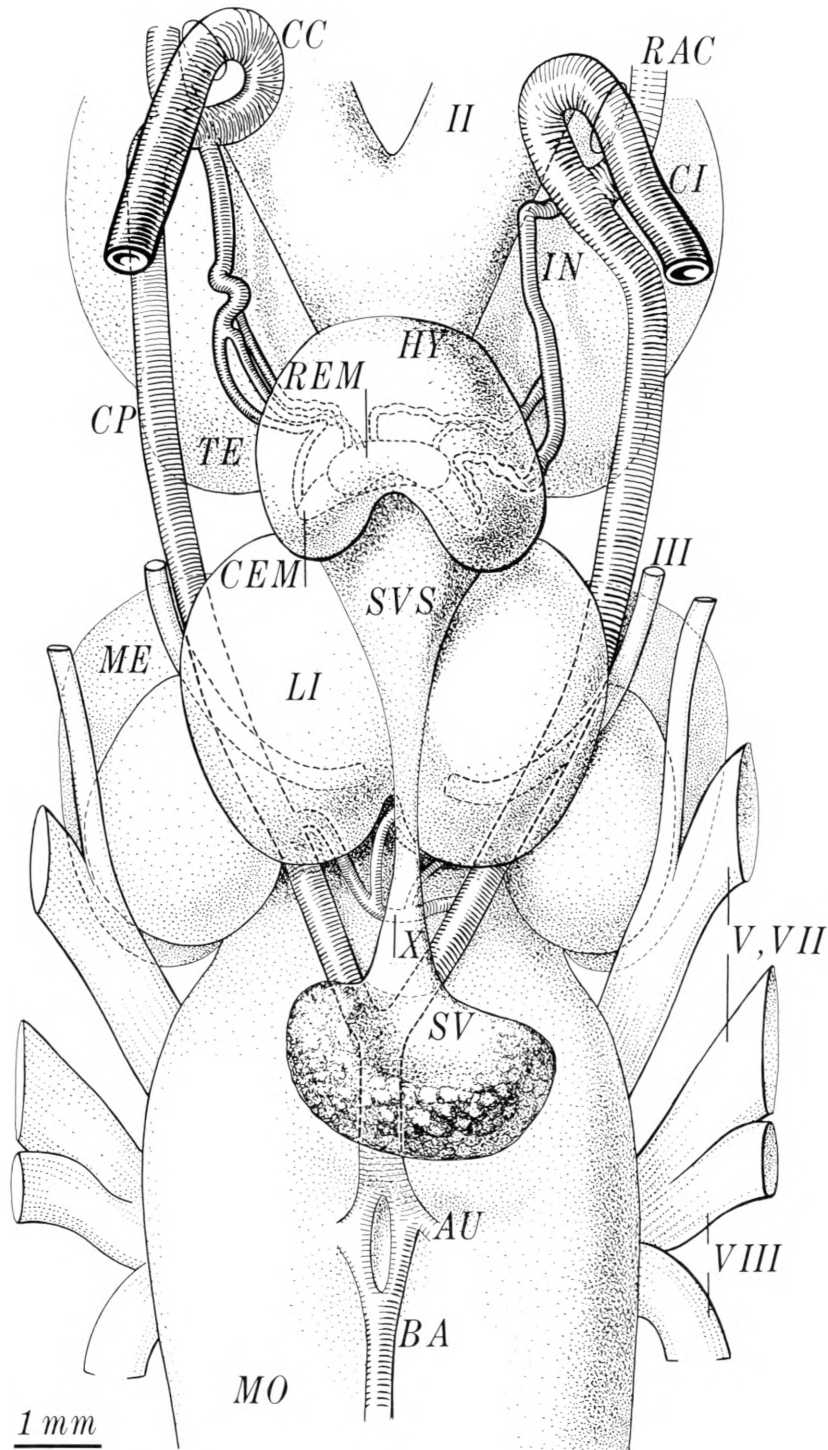
The proximal part of a. cerebialis posterior emits, fairly close to the point where the a. carotis cerebialis ramifies into the two main stems, the paired *aa. infundibulares* which continue caudally. Reaching the lateral part of the hypophysis the a. infundibularis splits into smaller branches which supply both the rostral and the caudal part of the primary plexus and the hypophysial stem plexus. In addition some branches may reach the plexus intermedius. Also the median part of the postchiasmatic capillary plexus is fed by branches from the *aa. infundibulares*.

4. The Hypothalamo-hypophysial Blood System (Fig. 16, Pls. XVI:2, XVII-XVIII)

a) Pituitary portal system

There is a pituitary portal system which includes a few supplementary vessels, but no lateral afferent veins.

As mentioned above, the median part of the *postchiasmatic capillary plexus* is mainly supplied by small branches from the *aa. infundibulares*. The lateral parts



are according to ALLIS supplied by small arteries emitted from the "aa. olfactoriae". The postchiasmatic plexus continues into the *primary plexus* of the eminentia mediana which comprises a rostral and a caudal region (Pl. XVIII:2).

In the *rostral region* of the eminential plexus the capillaries give rise to some peculiar capillary loops or "wads" (Pls. XVI:2, XVIII). The individual "wad" consists of a complex of capillary loops, framed in such a way that it is this bundle of loops and not the single loop which are enclosed by the cortical layer of the eminentia. In the light of the material examined it is very probable that the individual complex of loops originates from a single capillary and is drained through a single v. porta. The lateral parts of the primary plexus receive some supplementary vessels from the deep and superficial part of the adjacent area. From this plexus some typical vv. portae arise and pass to the pro- and meso-adenohypophysis. Further, this plexus continues on to the caudal eminential plexus.

In the *caudal region* the capillaries run in superficial undulating furrows. This part of the primary plexus more or less merges with the secondary plexus in the meso-adenohypophysis (Pl. XVIII). From the caudal part of this plexus, capillaries continue into the hypophysial stem plexus which in turn is connected with the plexus intermedius and the plexus of the saccus vasculosus plus the superficial capillary plexus of the hypothalamus.

b) *Vessels in the pro- and meso-adenohypophysis*

The general vascular pattern of the pars distalis is, as in the other 4 species, determined by the different glandular arrangement in the pro- and the meso-adenohypophysis. Only an insignificant direct arterial supply occurs, via some small arteries branching off from the "aa. olfactoriae". The general structure of the capillaries of the secondary plexus also resembles that of the other species i. e. the capillaries do not penetrate between the individual cells in the cell columns or cell groups.

c) *Vessels in the neuro-intermedia area*

A typical *plexus intermedius* occurs interposed between the lobus nervosus and the meta-adenohypophysis. Around its margins this plexus is connected with the capillary plexus of the hypophysial stem and of the saccus vasculosus stem. The plexus intermedius gives rise to some small capillaries which penetrate into the lobus nervosus. An intermedia sinusoid system does not exist.

d) *Saccus vasculosus*

The capillary plexus of the saccus vasculosus is connected with the hypophysial stem plexus and the plexus intermedius. In addition the plexus receives capillaries from the superficial plexus of the hypothalamus.

Fig. 16. *Amia calva*. Ventral view of the brain showing the distribution of the arteries. — AU = a. auditiva, BA = a. basilaris, CC = a. carotis cerebialis, CEM = caudal part of the eminentia mediana, CI = a. carotis interna, CP = a. cerebialis posterior, HY = hypophysis, IN = a. infundibularis, LI = lobus inferior, ME = mesencephalon, MO = medulla oblongata, RAC = a. carotis cerebialis ramus anterior, REM = rostral part of the eminentia mediana, SV = saccus vasculosus, SVS = sacci vasculosi stem, TE = telencephalon, X = a. X, II = n. opticus, III = n. oculomotorius, V = n. trigeminus, VII = n. facialis, VIII = n. acusticus.

5. The Venous System (Fig. 17, Pls. XVII–XVIII:2)

The unpaired *v. hypophyseos media* (Fig. 17) arises in the ventro-medial part of the pituitary in connection with the superficial capillary plexus. In addition the vein is joined by a pair of veins coming from the internal parts of the pro- and the meso-adenohypophysis. The *v. hypophyseos media* communicates rostrally and dorso-medially with the *v. interorbitalis*.

The *vv. hypophyseos laterales* (Fig. 17, Pl. XVIII:2) drain the plexus intermedius and, before they communicate with the venous plexus below the notochord, receive some small veins coming from the lobi inferiores and the saccus vasculosus. In addition the plexus of the saccus vasculosus is in connection with the above-mentioned venous plexus via several small veins.

IX. The Pituitary Gland and its Blood Supply in the Primitive Actinopterygians Compared with that of other Vertebrates

The morphological descriptions given in the preceding chapters made it possible to compare the pituitary gland and its vascularization in the primitive actinopterygians with that of other vertebrates.

The comparative anatomy of the hypophysis (in particular the neurohypophysis) and its blood supply was reviewed by GREEN (1951). WINGSTRAND (1966 a) gives a survey of the comparative anatomy of the hypophysis and aspects of its evolution. The vascularization of the pituitary gland has recently been reviewed by MEURLING (1967 a).

A. Comparison with Cyclostomata

1) Neurohypophysis

The neurohypophysis of the primitive actinopterygians comprises the saccus vasculosus, the lobus nervosus, the hypophysial stem and the eminentia mediana. In the cyclostomes a saccus vasculosus is not found. In *Petromyzon* the caudal part of the hypothalamic floor is slightly thickened and is similar histologically to a lobus nervosus (although primitive). An eminentia mediana area does not appear. The neurohypophysis of the *Myxine* is more differentiated and comprises a ventral part called "Infundibulum" (= eminentia mediana and hypophysial stem (WINGSTRAND, 1966 a)), and a dorsal part "the lobus nervosus".

2) Adenohypophysis

The adenohypophysis of the *Chondrostei* and the *Holostei* is histologically differentiated into the pro-, the meso- and the meta-adenohypophysis. In *Petromyzon* the adenohypophysis consists of three histological parts, designated after their situation the pro-, the meso- and the meta-adenohypophysis. According to WINGSTRAND (1966 a)

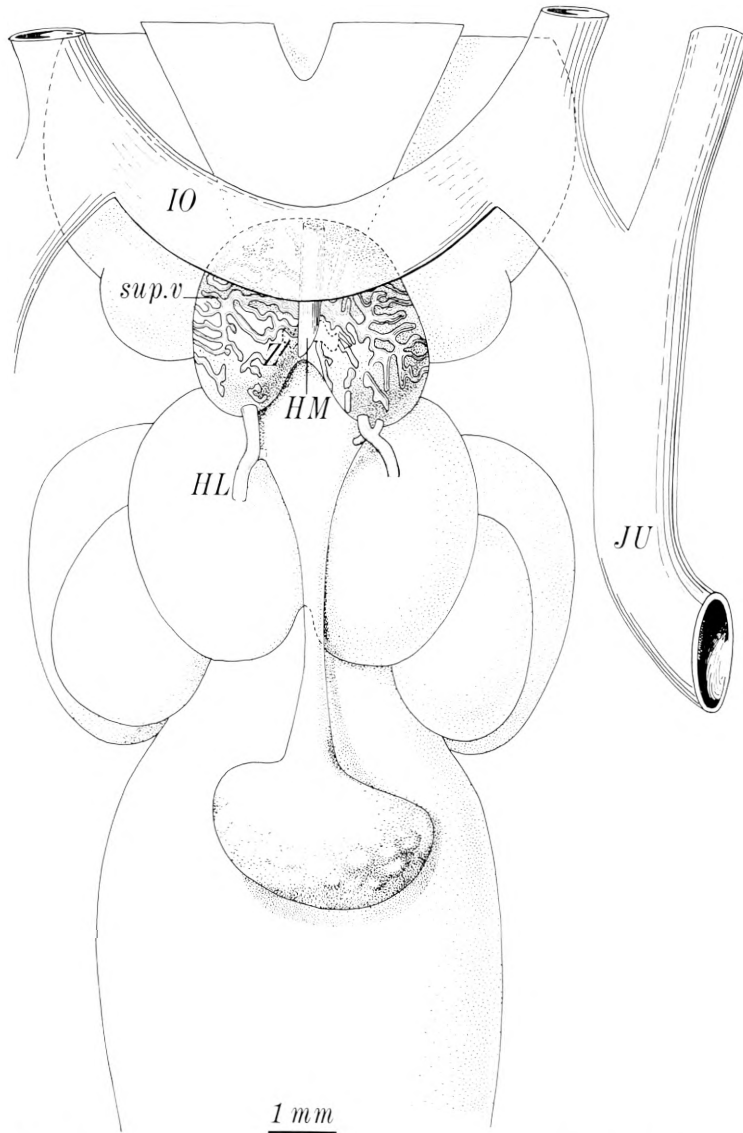


Fig. 17. *Amia calva*. Ventral view of the brain showing the venous drainage of the pituitary gland. — HL = v. hypophyseos lateralis, HM = v. hypophyseos media, IO = v. interorbitalis, JU = v. jugularis, sup. v. = superficial venous plexus, Z = vein from the internal parts of the pro- and meso-adenohypophysis. Brain parts see fig. 16.

the pro- and the meso-adenohypophysis are hardly homologous with the similarly situated parts in the actinopterygians. In *Myxine* the histological differentiation of the adenohypophysis is not apparent.

3) *Vascularization of the pituitary gland*

A pituitary portal system like that in the primitive actinopterygians is not found in the cyclostomes.

According to GORBMAN (1965) the area between the lobus nervosus and the meta-adenohypophysis of the lamprey is fed with blood through arteries branching off from the carotids. In addition the carotids send off some arteries which run to "the pro- and the meso-adenohypophysis". In the area between these two regions and the hypothalamic floor only a few capillaries are found.

A description of the vascularization of the pituitary gland in *Polistotrema* (a *Myxinoidea*) is given by GORBMAN et al. (1963). According to these authors the adenohypophysis and the neurohypophysis (the lobus nervosus) are fed through a pair of arteries branching off from the internal carotids. The "eminencia mediana" is drained via some neurohypophysial portal veins running to the lobus nervosus. Consequently this eminentia area has little in common with the eminentia mediana in the primitive actinopterygians.

B. Comparison with Chondrichthyes

1) *Neurohypophysis*

The general embryology, structure and differentiation of the neurohypophysis in the primitive actinopterygians and the Chondrichthyes are very much alike.

According to MEURLING (1962) it is possible in the selachians to distinguish between two lobus nervosus types a) the "*Squalus type*" which represents a primitive type and b) the "*Scyllium type*". The lobus nervosus of the primitive actinopterygians corresponds morphologically and histologically to the "*Squalus type*". Crown cells in the ependymal layer in the lobus nervosus and the eminentia mediana are not found in the selachians. An eminentia mediana area with a structure similar to that of the primitive actinopterygians exists in the selachians. The eminentia mediana of the selachians approximate to the "simple type" described in the *Chondrostei*.

2) *Adenohypophysis*

The adenohypophysis of the selachians is differentiated into three histological regions. The hypophysial cavity in the *Chondrostei*, the *Brachiopterygii* and the selachians (belonging to the *Squaloid type*) can be considered as homologous even though they are of different embryological origin (WINGSTRAND, 1966 a).

The *Euselachii* have a ventral lobe, the *Holocephali* a "Rachendach-Hypophyse" (MEURLING, 1967 b). In the primitive actinopterygians nothing occurs which could be interpreted as homologous with the ventral lobe.

3) *Vascularization of the pituitary gland*

In the primitive actinopterygians and in the selachians so far investigated, a pituitary portal system was found. Both in the species examined and in the selachians there are more or less marked structural difference between the anterior and the pos-

terior part of the eminentia mediana. The pro-adenohypophysis is fed mainly from the anterior part, while the posterior part supplies the meso-adenohypophysis. Supplementary vessels are found from adjacent brain parts to the primary plexus in euselachians, in the holosteans and are suggested in *Calamoichthys*. A distinct plexus intermedius occurs in the primitive actinopterygians and in some selachians. In the selachians the plexus intermedius is usually fed through arteries and in certain cases through the hypophyseal stem plexus and the lateral afferent system. In the primitive actinopterygians the plexus intermedius is generally fed through the hypophysial stem plexus; direct arterial supply does not occur, and only in the *Lepisosteus* are lateral afferent veins found. An intermedia sinusoid system is present in some of the selachians and in some of the primitive actinopterygians.

C. Comparison with Teleosts

1) Neurohypophysis

In the light of embryological criteria there is no positive basis to homologize the neurohypophysis in the teleosts and the eminentia mediana and the lobus nervosus in the primitive actinopterygians (WINGSTRAND, 1966 a). On the other hand, in the light of a) the distribution of the Gomori positive and negative fibres in the neurohypophyseal area in the teleosts (DIEPEN, 1953; BARGMAN, 1953), b) the nature of the neurocrine fibres and their connection with "the primary plexus" (FOLLENIUS, 1965 a) and c) the occurrence and variation of the ependymal processes and the glia cells (pituicytes) (DIEPEN, 1953; FOLLENIUS, 1965 a), these authors consider that the neurohypophysis in the teleosts comprises a rostral and a caudal part which are functionally equivalent to the eminentia mediana and the lobus nervosus.

2) Adenohypophysis

The actinopterygian adenohypophysis is subdivided into three histological regions termed the pro-, the meso- and the meta-adenohypophysis. Deviations have been described e.g. there are only two regions in the *Brachiopterygii*, *Fundus* (MATTHEWS, 1936) and *Esox niger* (SCRUGGS, 1939) and according to KOBAYASHI et al. (1959) there are more than three regions in *Lepidogobius lepidus*.

3) Vascularization of the pituitary gland

A pituitary portal system like that in the species examined does not occur in the teleosts. FOLLENIUS (1965, a-b) describes in the teleosts a primary plexus, fed by arteries, surrounding the protuberances of the neurohypophysis and giving off quite a number of capillaries constituting the secondary plexus of the adenohypophysis. According to FOLLENIUS there is a duality in the terminations of the neurosecretory fibres 1) a neurovascular and 2) a neuroglandular termination. In the light of the origin of the neurosecretory fibres, their termination on the capillaries and the average size of their secretory granules, this author supposes: a) that the anterior

part of the neurohypophysis is equivalent to the eminentia mediana and b) that the primary plexus in the teleosts represents a functional and a morphological analogy to the hypophysial portal system in the tetrapods.

D. Comparison with Dipnoi and Tetrapods

1) Neurohypophysis

The neurohypophysis of *Dipnoi* and tetrapods consists of a lobus nervosus, a hypophyseal stem and an eminentia mediana area (WINGSTRAND, 1956). These parts plus the saccus vasculosus have also been identified in the primitive actinopterygians.

The histological structure of the lobus nervosus in the species examined corresponds to the "primitive neural lobe type" which occurs in the case of many reptiles and some birds. The hypophysial stem in the primitive actinopterygians and in the amphibians (except the *Gymnophiona*) corresponds only to the oral wall of the infundibular stem in the *Amniota*. An eminentia mediana area which contains three histological layers and which is covered by a capillary net (the primary capillary plexus) supplying the adenohypophysis, occurs both in the primitive actinopterygians, the *Dipnoi* and in the tetrapods.

In *Chondrostei*, *Protopterus* (WINGSTRAND, 1956), *Cryptobranchus* (GRENNELL, 1939), *Necturus* (GREEN, 1947 b, 1951), *Megalobatrachus* (IMAI, 1960) and *Genenophis* (PILLAI, Thesis, Trivandrum, 1961; according to WINGSTRAND, 1966 a) the eminentia mediana represents a simple type i.e. it is only weakly differentiated, and the primary plexus is superficial and essentially continuous with the secondary plexus (real portal vessels are not or poorly developed).

The eminentia mediana in the *Brachiopterygii*, the anurans and most of the urodelans represents an "intermediate type", i.e. the eminentia mediana is only slightly proliferated, and there is a faint suggestion of capillary loops, formed by the primary plexus, which is drained by vv. portae.

A "differentiated eminentia mediana type" occurs in the holosteans and in most of the mammals. In this type, the eminentia mediana is thick, the capillaries of the primary plexus are buried in deep furrows formed as loops, and typical vv. portae are found.

2) Adenohypophysis

In the light of the material examined it is not possible to compare the histologically different regions of the adenohypophysis in the primitive actinopterygians with those of the *Dipnoi* and tetrapods. A general discussion of the adenohypophysis in the vertebrates is given by WINGSTRAND (1966 a). In his interpretation the metaadenohypophysis of the primitive actinopterygians is homologous with the pars intermedia in the *Dipnoi* and the tetrapods. In addition WINGSTRAND considers the hypophysial cavity of the actinopterygians as homologous with the cavity which occurs in some reptiles and mammals. A pars tuberalis which is found in most of the tetrapods (WINGSTRAND, 1956) does not occur in the primitive actinopterygians.

3) *Vascularization of the pituitary gland*

In all the species investigated a pituitary portal system was found. The hypophysial stem plexus enters the plexus intermedius, which in *Lepisosteus* is also fed through the lateral afferent veins. Supplementary vessels are found in the holosteans, and are suggested in *Calamoichthys*.

According to GREEN (1951, 1966) it is possible in the tetrapods to distinguish between two fairly well-defined vascular systems, 1) the primary plexus and 2) the plexus intermedius. The primary plexus is in vascular contact with the adeno-hypophysis, which is practically without direct arterial supply. In the adult tetrapods there are only slight connections between the deeper capillaries of the hypothalamus and the primary plexus. The plexus intermedius receives blood through the aa. infundibulares and/or aa. hypophyseae inferiores. According to ENEMAR (1961) there is in some amniotes a vascular connection between the plexus intermedius and the primary plexus.

X. Discussion

1) *The neurohypophysis*

In the preceding comparison it has been demonstrated that the neurohypophysis in the selachians, the primitive actinopterygians, the lungfish and the tetrapods comprises an eminentia mediana and a lobus nervosus region. In addition it has been suggested in this context, that a pituitary portal system connects the eminential plexus and the secondary plexus of the adeno-hypophysis. In the cyclostomes (p. 50) it is not certain if an analogous subdivision of the neurohypophysis can be made. In the teleosts the solid neurohypophysis gives off branching processes into all three histological regions of the adeno-hypophysis, and a distinct eminentia mediana region, in agreement with the definition given p. 9, has not so far been described.

In the light of the presence of such a subdivision of the neurohypophysis among the gnathostomes, with the exception of the teleosts so far investigated, it may thus be concluded: 1) *that the eminentia mediana and the lobus nervosus represent primitive features and must have been present in the gnathostome ancestor*, and 2) *that the structural pattern of the neurohypophysis in the teleosts constitutes a secondary feature*.

The structural pattern of the lobus nervosus in the primitive actinopterygians led KERR (1949) to conclude that: "the penetration of the lobus nervosus into all three glandular regions in teleosts is shown by the "ganoids" to be a secondary development".

A general survey of the embryology of the neurohypophyseal region is given by WINGSTRAND (1959, 1966 a). In his interpretation the lobus nervosus in the primitive actinopterygians is developed from the oral wall of the saccus infundibuli and the basal part of the lamina postoptica, while the saccus vasculosus develops from the aboral part of the saccus infundibuli. The fact that crown cells occur in the ependymal layer of the lobus nervosus and the eminentia mediana in *Chondrostei*, and in addition in the ependymal layer of the lobus nervosus in the *Holostei* and *Polypterus*, may

possibly be construed to mean that the segregation of the saccus vasculosus and the lobus nervosus in the above-mentioned animals is incomplete (a possible primitive character). Further, the presence of these crown cells outside the saccus vasculosus, supports WINGSTRAND'S (1956) argument against the justification for defining the saccus vasculosus solely on the basis of its content of crown cells, and that: "crown cells cannot be used as a primary criterion for homologies".

In addition the uniform histological feature (with three zones) in the eminentia mediana and the lobus nervosus could be regarded as a support to the hypothesis put forward by WINGSTRAND (1959), and further adopted by JØRGENSEN and LARSEN (1960) and MEURLING (1967 a), that the eminentia mediana and the lobus nervosus have arisen from a uniform undivided neurohypophysis.

There is according to WINGSTRAND (1951, 1956, 1959 and 1966 a) no basis for postulating strict homology of the neurohypophysis of the teleosts with the eminentia mediana and the lobus nervosus of the other gnathostomes. On the other hand from the distribution of the Gomori negative and positive fibres in the neurohypophysis of the teleosts (BARGMANN, 1953 and DIEPEN, 1953) and in the light of the connection of the neurocrine fibres with "the primary plexus" in the teleosts (FOLLENIUS, 1965 a), these authors suggest that it is possible to divide the neurohypophysis of the teleosts into an anterior and a posterior region which morphologically and/or functionally are homologous with the eminentia mediana and the lobus nervosus of the tetrapods, respectively. BARGMANN'S and DIEPEN'S arguments in favour of such a subdivision of the neurohypophysis in the teleosts are weakened, although not convincingly, by the fact that *Etmopterus* (MEURLING, 1963) in which an eminentia mediana and a lobus nervosus are described, has both Gomori positive and negative fibres in the lobus nervosus region.

In the light of the elaboration of the primary plexus and the proliferation of the eminentiae medianae wall in the species examined, three eminential types have been established (fig. 18): 1) The "simple type" found in the selachians, the sturgeons, the lungfish and in some of the amphibians and the *Prototheria*. Here the eminential wall is thin and the capillaries of the primary plexus run in superficial furrows and merge into the secondary plexus. In consequence of its broad distribution, this type represents a primitive pattern and must have been present in a gnathostome ancestor. 2) In the "transitional eminential type", found in the *Brachiopterygii* and in most of the amphibians, the eminential wall is more proliferated. The capillaries run in deep furrows and loops may occur. The primary plexus is drained by vv. portae. 3) The "differentiated eminential type" occurs in the *Holostei* and in most of the mammals. The capillaries of the primary plexus may form well-developed loops into the wall. The primary plexus is drained by vv. portae.

2) *The vascularization of the hypothalamo-hypophysial region*

A pituitary portal system, comprising a primary plexus, more or less typical vv. portae and a secondary plexus in the adenohypophysis, occurs in the selachians,

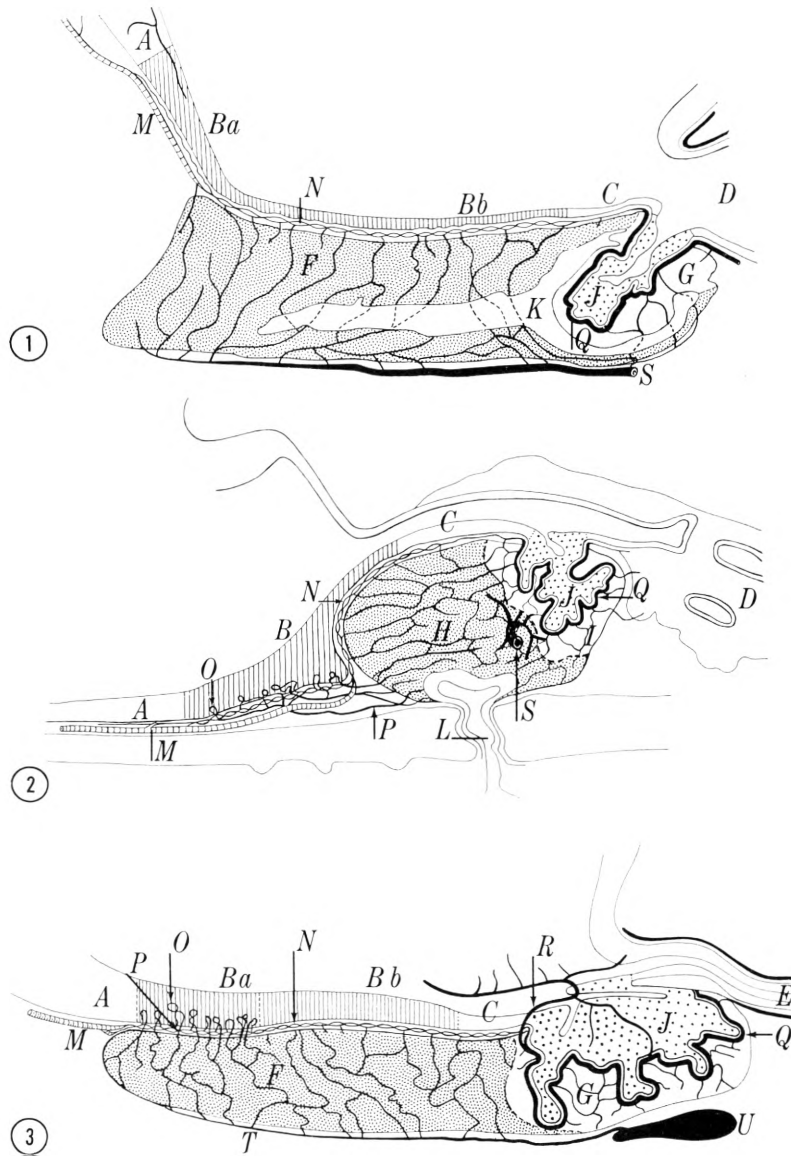


Fig. 18. Median diagrammatic sections through the pituitary region showing the hypothalamo-hypophysial vascular links in *Acipenser* (simple eminential type, fig. 1), *Calamoichthys* (transitional eminential type, fig. 2) and *Lepisosteus* (differentiated eminential type, fig. 3). — A = postchiasmatic region, B = eminentia mediana, Ba = rostral part of the eminentia mediana, Bd = caudal part of the eminentia mediana, C = hypophysial stem, D = saccus vasculosus, E = sacci vasculosi stem, F = pro- and meso-adenohypophysis, G = meta-adenohypophysis, H = pars distalis, I = pars intermedia, J = lobus nervosus, K = hypophysial stem, L = buccohypophysial duct, M = a. infundibularis, N = superficial primary capillary plexus, O = capillary loops of the primary plexus, P = v. porta, Q = plexus intermedius, R = lateral afferent vein, S = v. hypophysios, T = v. hypophysios media, U = v. interorbitalis.

the primitive actinopterygians, the lungfish and the tetrapods. In consequence of this distribution it is probable that: *the pituitary portal system is a primitive feature, and that it has been present in the gnathostome ancestor.* In addition there is reason to suppose that the primary and the secondary plexus have been directly continuous in the gnathostome ancestor. The reason for this supposition is that a portal system with such a structural feature occurs in the selachians, the sturgeons, *Necturus*, *Cryptobranchus* and *Genenophis*. GREEN (1951) is of the definite impression that the pituitary portal system has evolved from a simple superficial plexus situated between the neurohypophysis and the adenohypophysis. This hypothesis presupposes that a vascular plexus of such a pattern is common among fish-like vertebrates. However, the existence of a more typical portal system in the selachians (MEURLING, 1960, 1967 a and MELLINGER, 1960, 1963) and in the primitive actinopterygians as shown in the preceding section proves that the structural feature of the vascular plexus found in the teleosts so far investigated shows something unique for this order. FOLLENIUS (1965 a) is of the opinion that the hypothalamic control of the pro- and the meso-adenohypophysis in the teleosts may be exercised in two ways: 1) via a neurovascular transmission—a vestigial portal system, comprising a “primary plexus” on which neurocrine fibres terminate and from where the majority of the capillaries irrigating the “pars distalis” originate, and 2) via a neuroglandular transmission—exerted through ordinary neurons terminating in contact with the glandular cells.

In the light of the fact that a pituitary portal system occurs in all the gnathostomes except for the teleosts so far investigated, it may be concluded that: *the vascularization of the hypothalamus-hypophysial region in the teleosts, comprising a superficial vascular plexus which continues directly into the secondary plexus, and the direct innervation of the glandular cells of the pro- and the meso-adenohypophysis represent secondary developments.*

In *Amia* a few supplementary vessels are found and in *Lepisosteus* both supplementary vessels and lateral afferent veins occur in connection with the primary plexus and the plexus intermedius, respectively. In addition, supplementary vessels are found in all euselachians investigated and lateral afferent veins occur in some of the selachians (MEURLING, 1967 a). This author assumes that the portal system, including the supplementary vessels, the lateral afferent veins and the neuro-intermedia component of the portal system, in the selachians represent remains of an original drainage pattern common to the hypothalamus hypophyseal region. Thus the primary route of the blood from hypothalamus to the hypophysis is not necessarily of any specific functional significance for the hypothalamic regulation of the hypophysis. In accordance with this JØRGENSEN and LARSEN (1967) indicate that the primitive arrangement of blood vessels in this region: “. . . can be imagined to have been of preadaptive significance in the development of functioning portal system of the type which has been demonstrated in tetrapods”. This is favoured by WINGSTRAND’S (1951) and ENEMAR’S (1960) observations on the embryonic differentiation and development of the pituitary vessels. According to these authors the adenohypophyseal plexus, the eminential plexus

and the portal vessels are successively formed by differentiation of a part of the capillary plexus covering the brain surface. This plexus starts as a cloud of capillaries in connection with the v. interorbitalis (or derivative of this) through the area in which the Rathke's pouch develops.

3. *The adenohipophysis*

A survey of the embryology and the differentiation of the adenohipophysis in the different vertebrate classes is given by WINGSTRAND (1966 a). This author concludes among other things that: . . . "the adenohipophysis of the ancestral vertebrate can be supposed to have developed from the stomodeal ectoderm . . .". In addition the embryological development shows the meta-adenohipophysis in the cyclostomes, the selachians and the actinopterygians to be homologous with the pars intermedia in the lungfish and the tetrapods.

WINGSTRAND (1966 a) discusses some of the advanced theories dealing with comparisons between the histological regions of the adenohipophysis in the different vertebrate classes. An attempt to detect homology between the different histological regions in the adenohipophysis of the primitive actinopterygians with those in the other vertebrates has not been carried out. The reason for this is that the present investigation does not include embryological material, which must be regarded as the only possible basis for deciding homologies.

Neither in the species examined nor in the teleosts so far investigated, has a ventral lobe or a pars tuberalis been developed. Therefore it is still somewhat doubtful whether these parts were present in an ancestral gnathostome form.

In the *Chondrostei* and the *Brachiopterygii* a hypophysial cavity occurs. Tubules and follicles are found in the adenohipophysis in the *Holostei* and some of the isospondylous teleosts (WINGSTRAND, 1966 a). In addition a hypophysial cavity occurs in the lungfish, and in some of the selachians, the reptiles and the mammalians. In spite of the fact that the hypophysial cavity, the tubules and the follicles have different embryological origins (a schizocoele development, or represent the remains of the cavity in the pouch of Rathke) it is highly probable that these structures can be considered as homologous, and indicate that a hollow pituitary gland must have occurred in a gnathostome ancestor as pointed out by KERR (1949) and WINGSTRAND (1966 a).

XI. References

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PLATES

PLATE I

Fig. 1. *Acipenser stellatus*. Transverse section through the caudal part of the eminentia mediana, showing crown cells between the ependymal cells. — a = ependymal layer, b = fibre layer, c = cortical layer, moa = meso-adenohypophysis. Thick arrow points at a crown cell. — $8\ \mu$ section. AF-Halmi. Na: 0.65. The scale represents $50\ \mu$.

Fig. 2. *Acipenser güldenstaedti*. Sagittal section through the eminentia mediana. — d = superficial capillary plexus, e = connective tissue. Other abbreviations, see fig. 1. — $8\ \mu$ section. NA: 0.45. The scale represents $50\ \mu$.

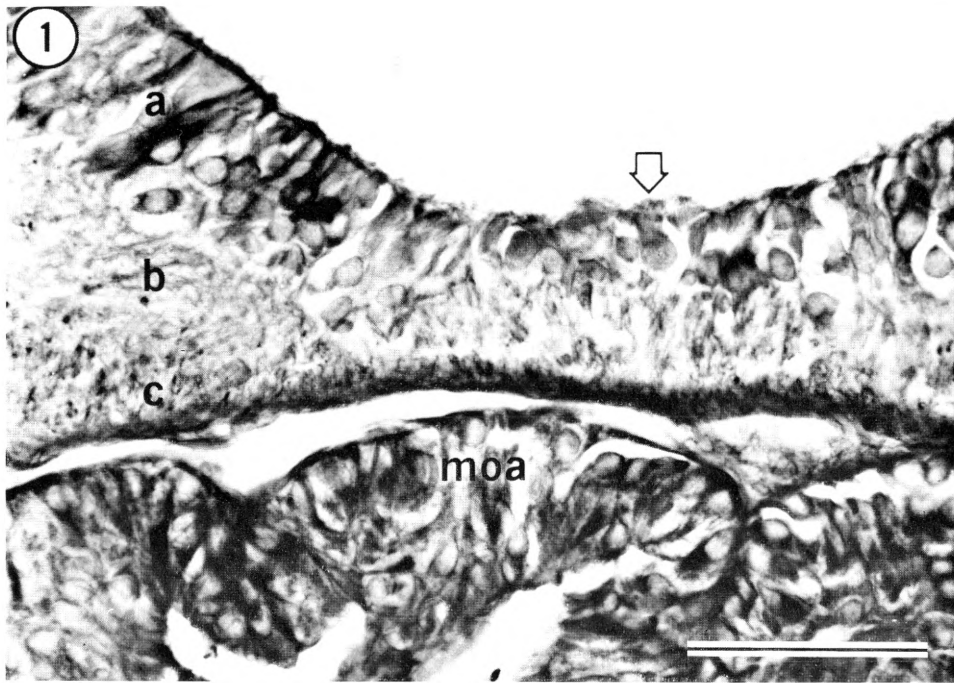


PLATE II

Fig. 1-2. *Acipenser güldenstaedti*. Sagittal section through the lobus nervosus and the meta-adenohypophysis. — a = ependymal layer, b = fibre layer, c = cortical layer, d = secondary lumen, e = decussating ependymal processes, f = accumulated neuro-secretory material (mainly in the fibre layer, see fig. 2), ln = lobus nervosus, maa = meta-adenohypophysis, pli = plexus intermedius. Thick arrow points at a crown cell. — 8 μ section. Fig. 1, Azan; fig. 2, AF-Halmi. NA: 0.65. The scale represents 50 μ .

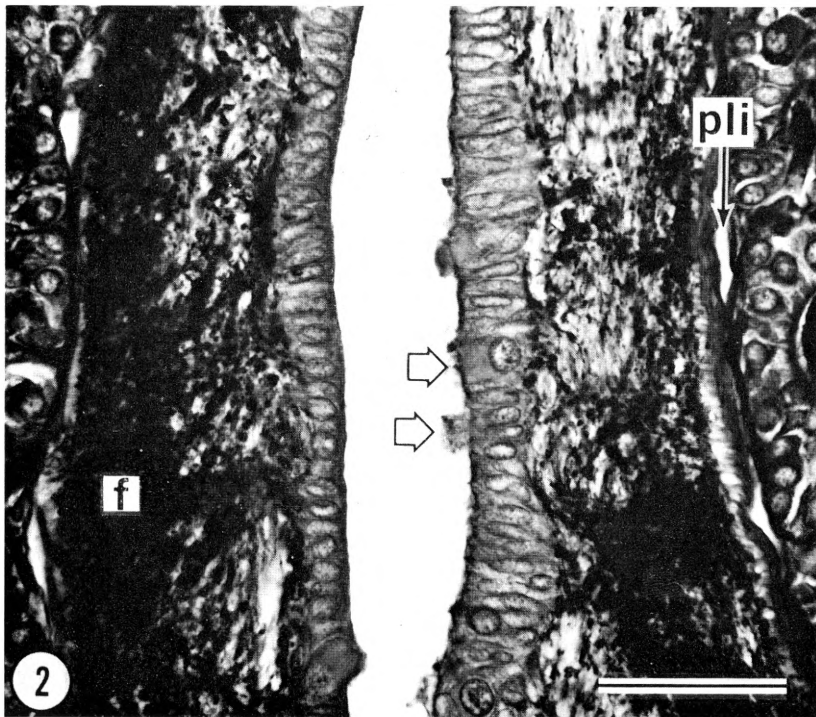
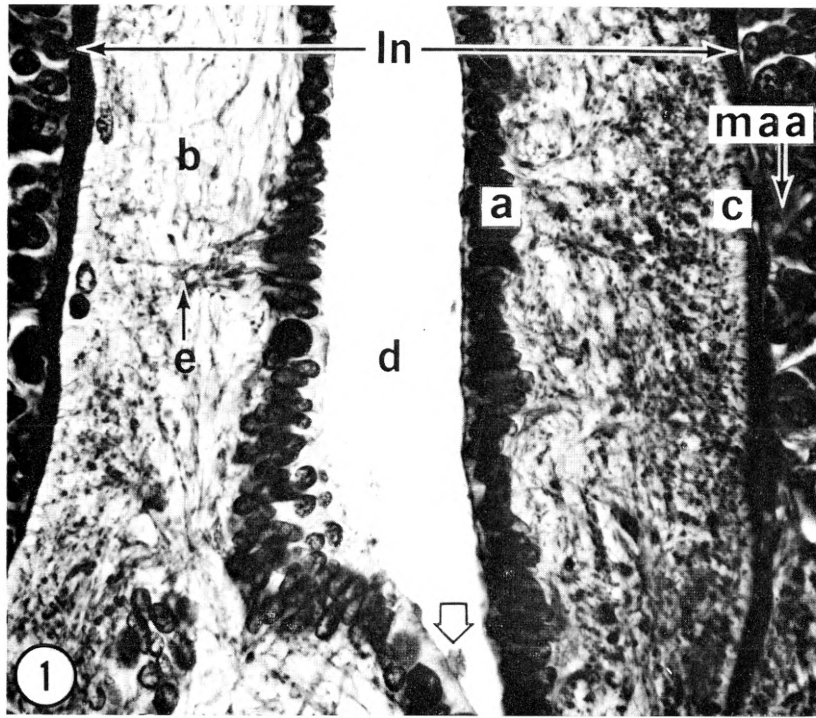


PLATE III

Acipenser güldenstaedti. Paramedian section. — em = eminentia mediana, hc = hypophysial cavity, ln = lobus nervosus, pr = post chiasmatic region, pra, moa and maa = pro-, meso- and meta-adenohypophysis, sv = saccus vasculosus. Arrow points at crown cells in the ependymal layer of the hypophysial stem. — 8μ section. AF-Halmi. The scale represents 500μ .

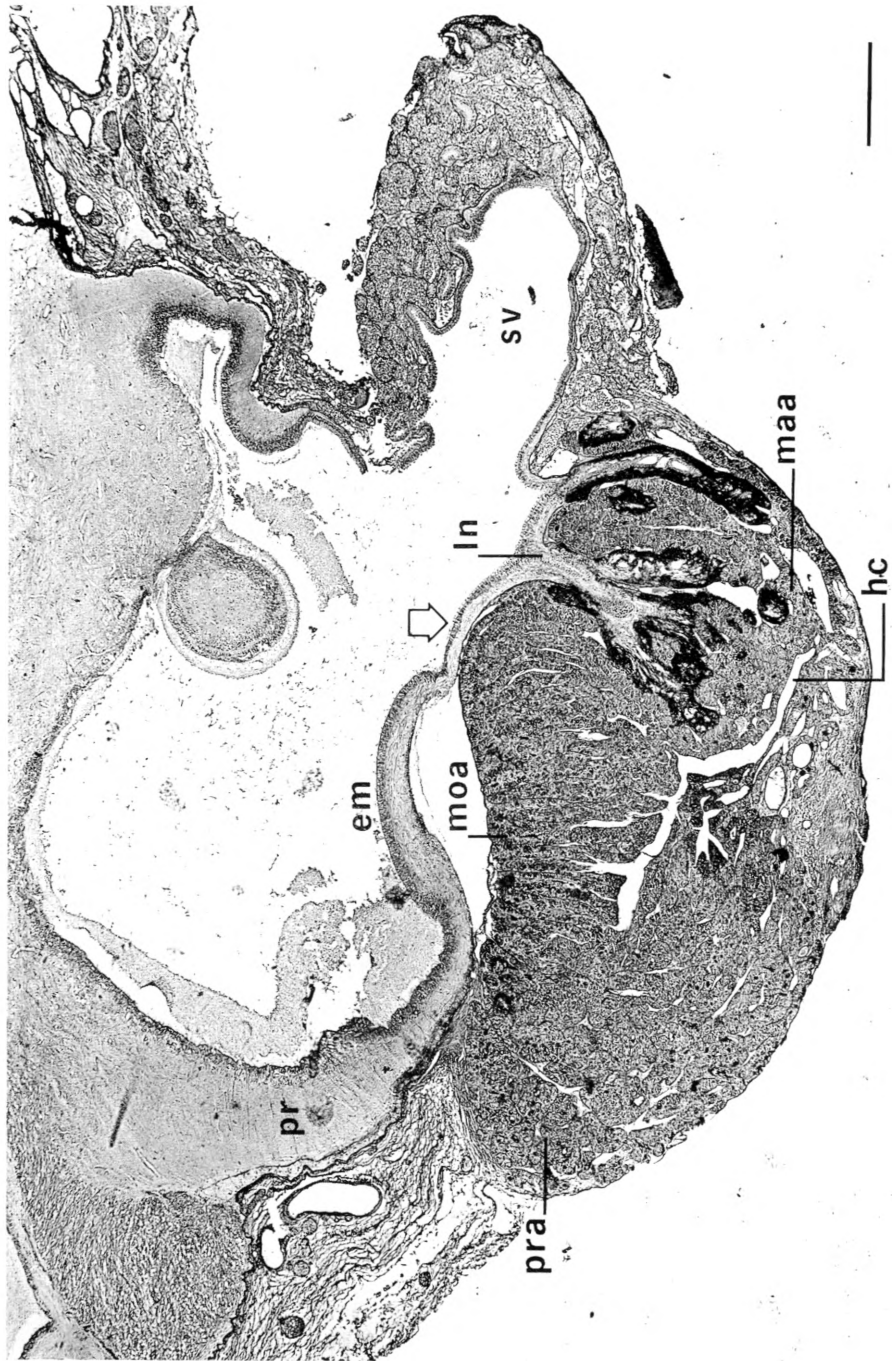


PLATE IV

Acipenser stellatus. Paramedian section. — ds = dorsum sellae, em = eminentia mediana covered by the primary plexus giving off vessels to the adenohipophysis (ad), hc = hypophysial cavity, nil = neuro-intermedia lobe, pli = plexus intermedius, pr = postchiasmatic region, sv = saccus vasculosus. — 75 μ section (celloidin). H-E. The scale represents 500 μ .

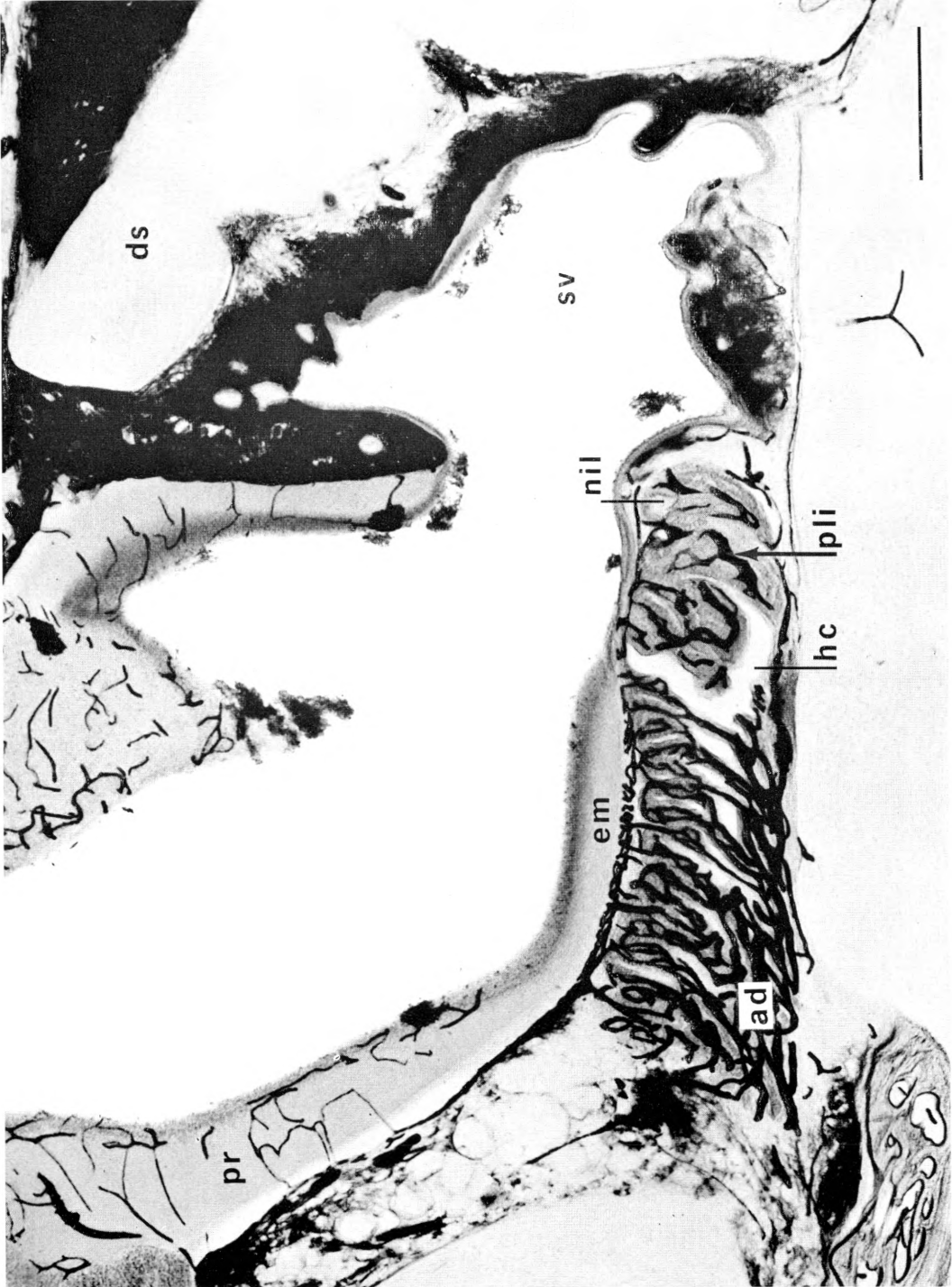


PLATE V
Acipenser stellatus

Fig. 1. Sagittal section, showing how the caudal part of the primary plexus is drained to the adeno-hypophysis via vv. portae. — a = hypophysial stem plexus, b = superficial venous plexus, c = v. hypophyseos, cem = caudal part of the eminentia mediana, d = a. infundibularis, e = primary plexus, hc = hypophysial cavity, ln = lobus nervosus, moa = meso-adenohypophysis, pli = plexus intermedius. Thick black arrow points at vv. portae. — 75 μ section (celloidin). H-E. NA: 0.3. The scale represents 250 μ .

Fig. 2. Median section, showing how the capillaries of the primary plexus merge into the secondary plexus of the adeno-hypophysis. — em = eminentia mediana, f = capillary connecting the plexus intermedius with the plexus of the saccus vasculosus, nil = neuro-intermedia lobe, pra = pro-adenohypophysis. Other abbreviations, see fig. 1. — 75 μ section (celloidin). H-E. NA: 0.3. The scale represents 250 μ .

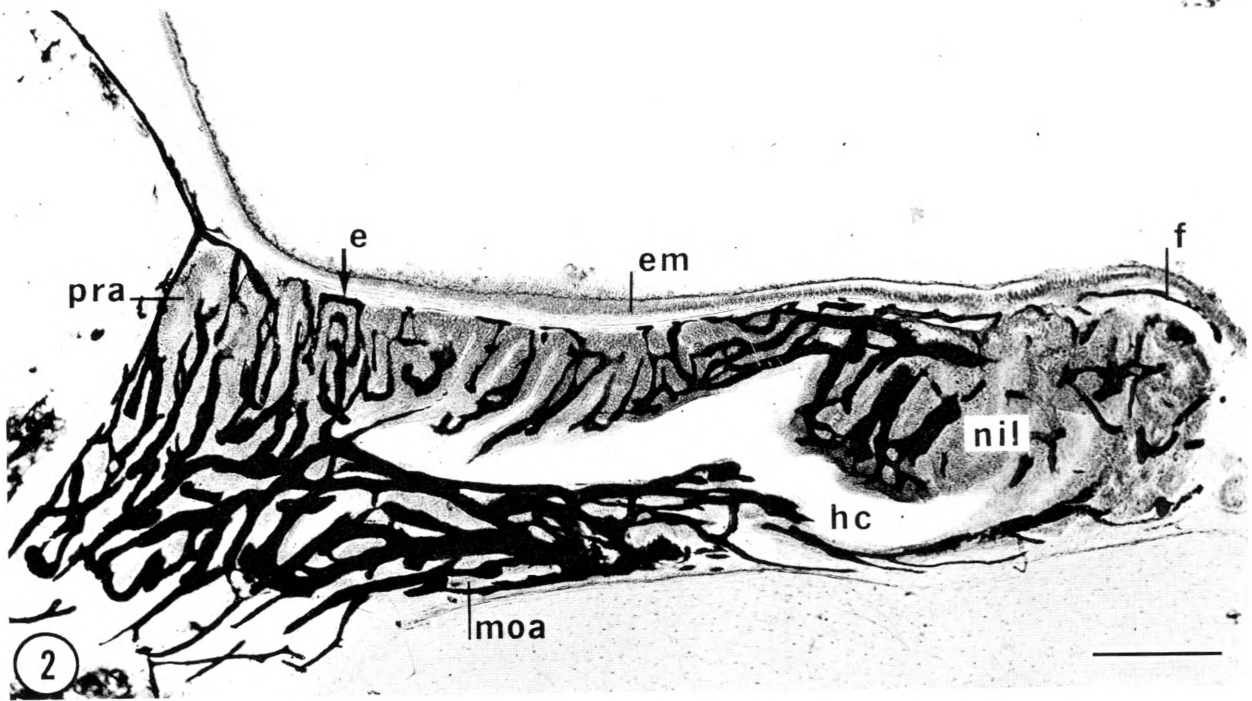
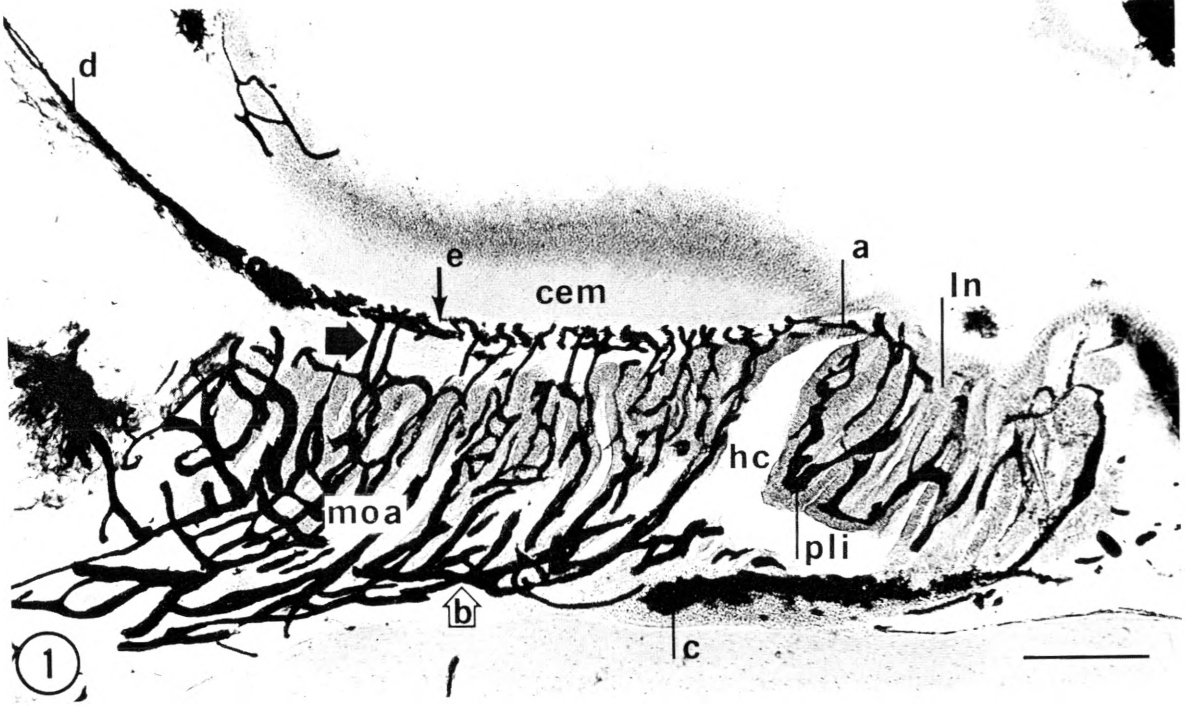


PLATE VI

Fig. 1. *Acipenser stellatus*. Sagittal section through the lateral part of the hypophysis showing the dorsally directed draining (thick arrow) of the plexus intermedius (pli). — a = part of the superficial venous plexus covering the meta-adenohypophysis, hc = hypophysial cavity, nil = neuro-intermedia lobe. — 75 μ section (celloidin). H-E. NA: 0.3. The scale represents 250 μ .

Fig. 2. *Polyodon spathula*. Sagittal section through the eminentia mediana. Thick arrow points at a crown cell. — pra = pro-adenohypophysis, rem = rostral part of the eminentia mediana. — 8 μ section. Azan. NA: 0.65. The scale represents 50 μ .

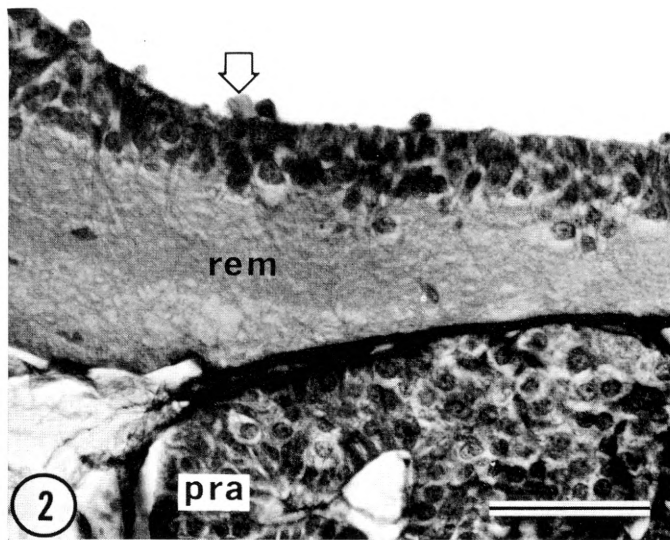
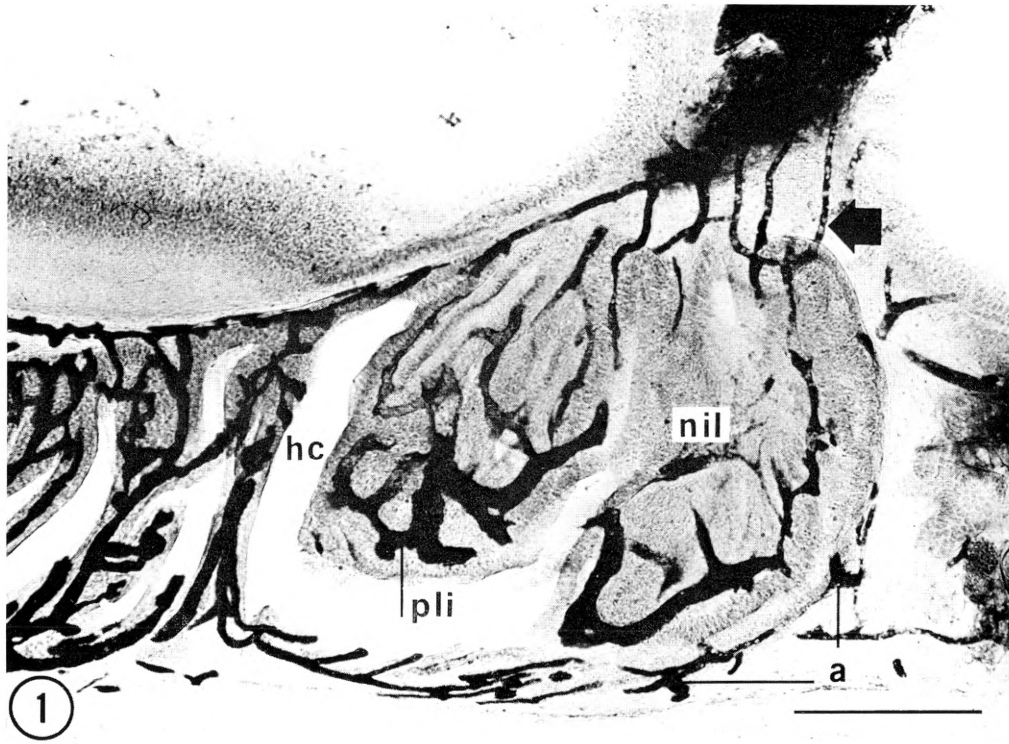


PLATE VII

Polyodon spathula. Paramedian section. — em = eminentia mediana covered by the primary plexus giving off vessels to the secondary plexus of the pro- and the meso-adenohypophysis (ad), fh = fossa hypophyseos, hc = hypophysial cavity, ln = lobus nervosus, maa = meta-adenohypophysis, pli = plexus intermedius, sv = saccus vasculosus. — 50 μ section (celloidin). H-E. NA: 0.3. The scale represents 250 μ .

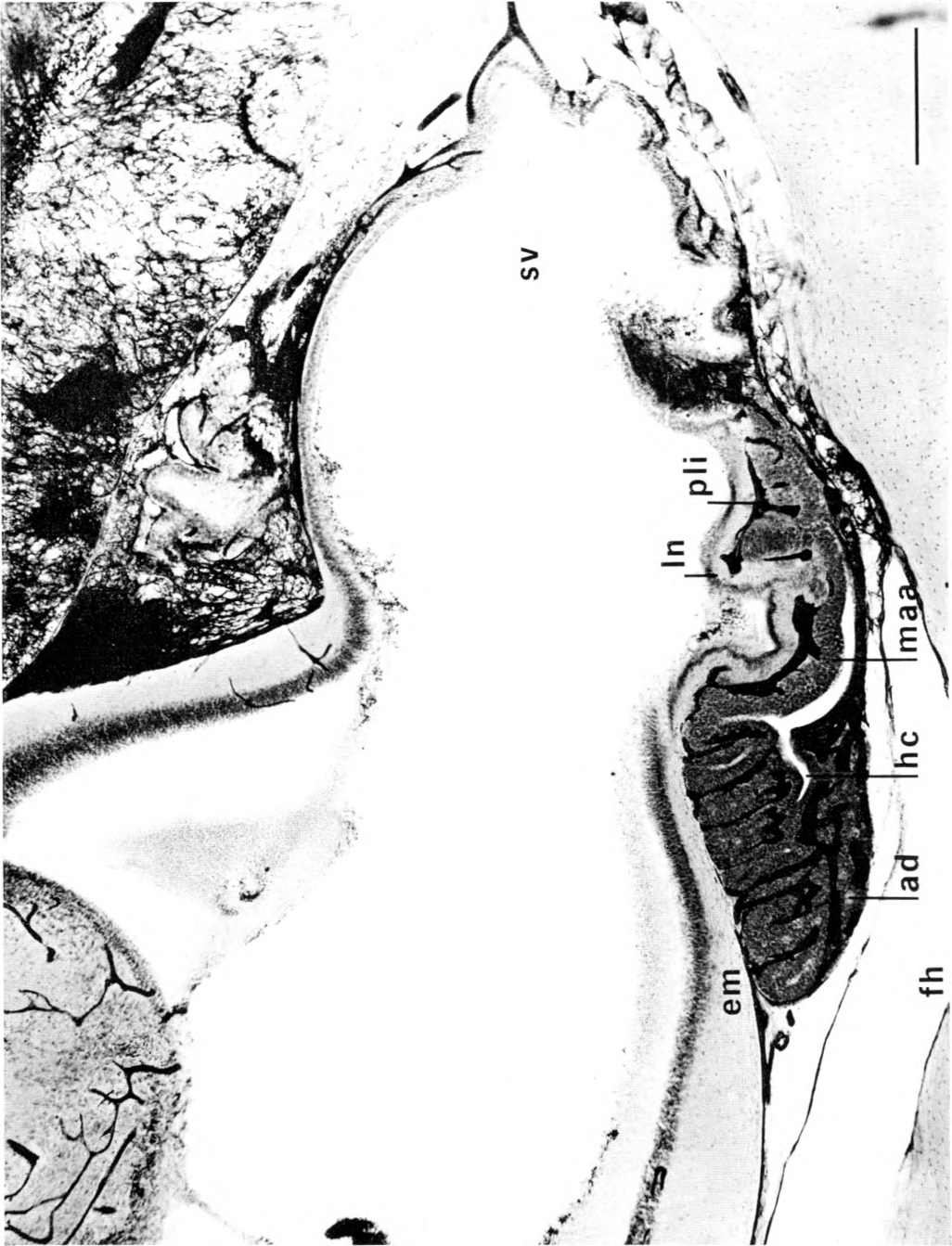


PLATE VIII

Polyodon spathula

Fig. 1. Sagittal section through the lateral part of the pituitary gland, showing how the primary plexus covering the eminentia mediana (em) merges into the secondary plexus of the meso-adenohypophysis (moa). — a = v. porta, b = a. infundibularis, thick black arrow points at v. interorbitalis, hc = hypophysial cavity, maa = meta-adenohypophysis, nil = neuro-intermedia lobe, pli = plexus intermedius.

Fig. 2. Paramedian section. — ad = pro- and meso-adenohypophysis, c = part of the hypophysial stem plexus, ln = lobus nervosus. Other abbreviations, see fig. 1.

Fig. 3. Slightly median section. — d = part of the superficial venous plexus covering the adenohypophysis, fh = fossa hypophyseos. Other abbreviations, see figs. 1 and 2.

Figs. 1–3. 50 μ section (celloidin). H-E. NA: 0.32. The scale represents 250 μ .

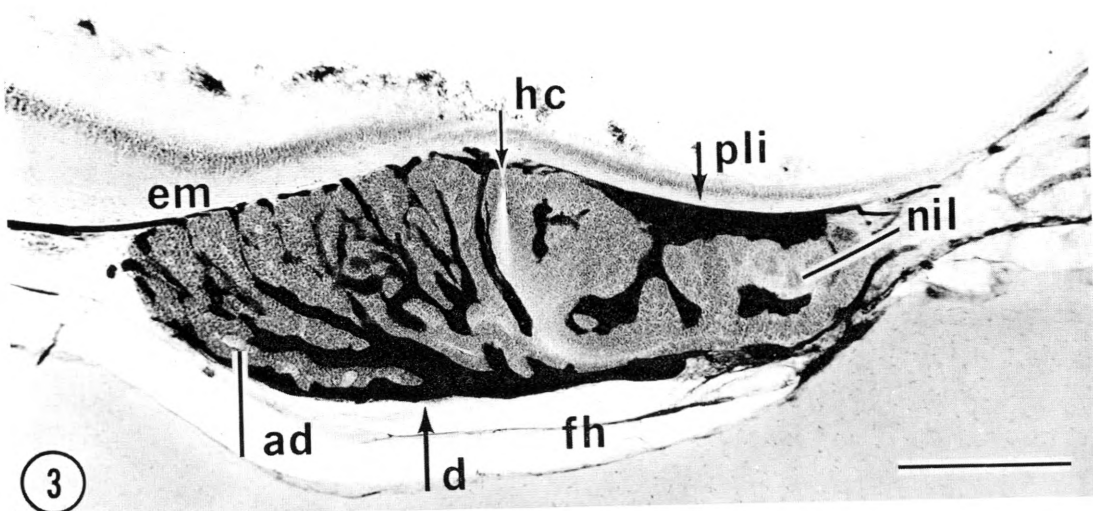
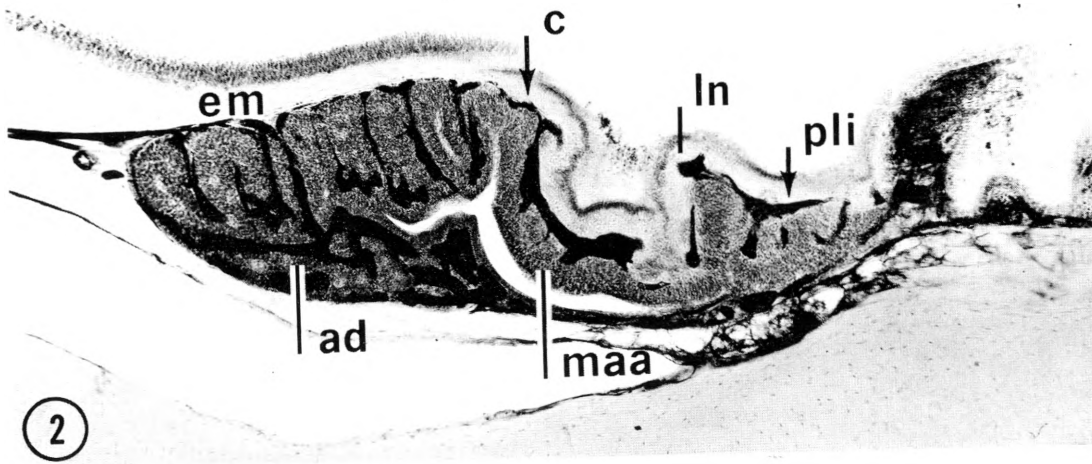
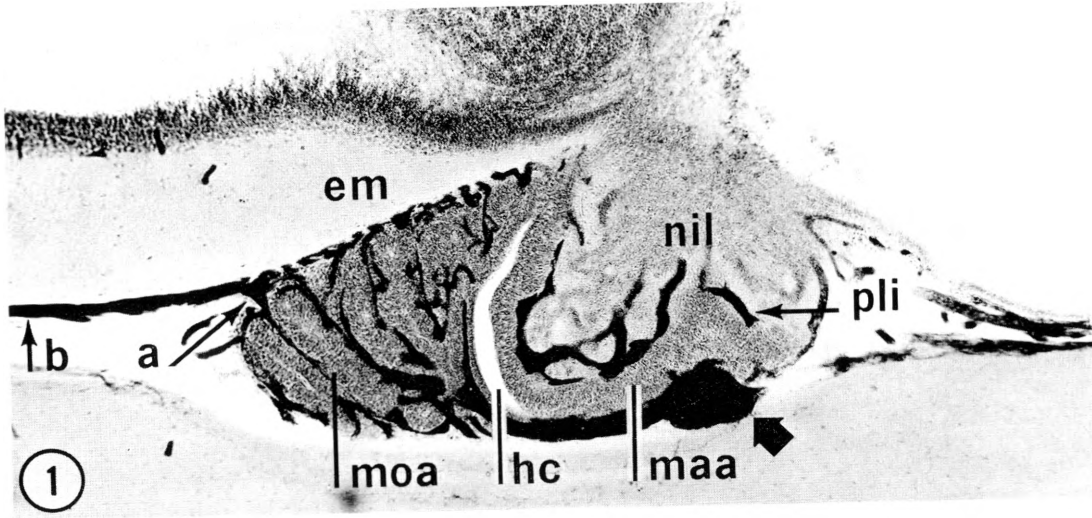


PLATE IX

Polypterus senegalus

Fig. 1. Sagittal section through the eminentia mediana showing the localization of the ependymal layer (a), the fibre layer (b) and the cortical layer (c). — d = connective tissue containing vv. portae (e), pd = pars distalis. — $5\ \mu$ section. Gomori-staining. NA: 0.45. The scale represents $50\ \mu$.

Fig. 2. Transverse section through the neural lobe and the pars intermedia showing how the recessus infundibularis gives off a pair of hollow protuberances (= the primary lumen = a). — ln = lobus nervosus, pd = pars distalis, pi = pars intermedia, thick black arrow points at the dorsal saccus vasculosus wall. — $8\ \mu$ section. AF-Halmi. NA: 0.2. The scale represents $200\ \mu$.

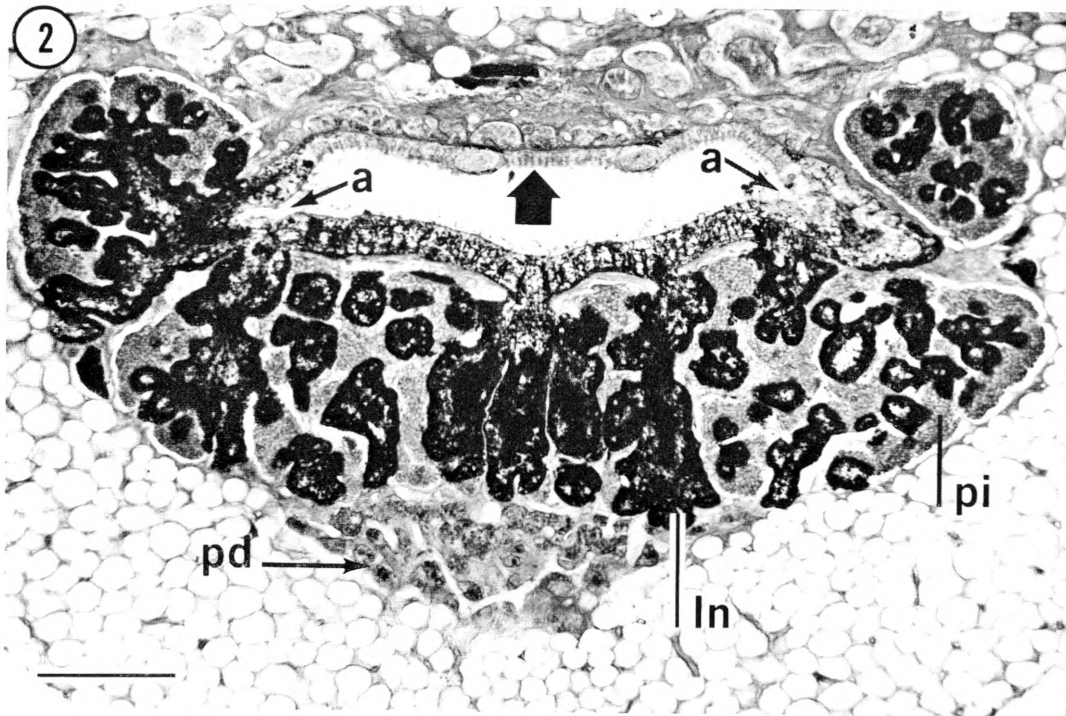
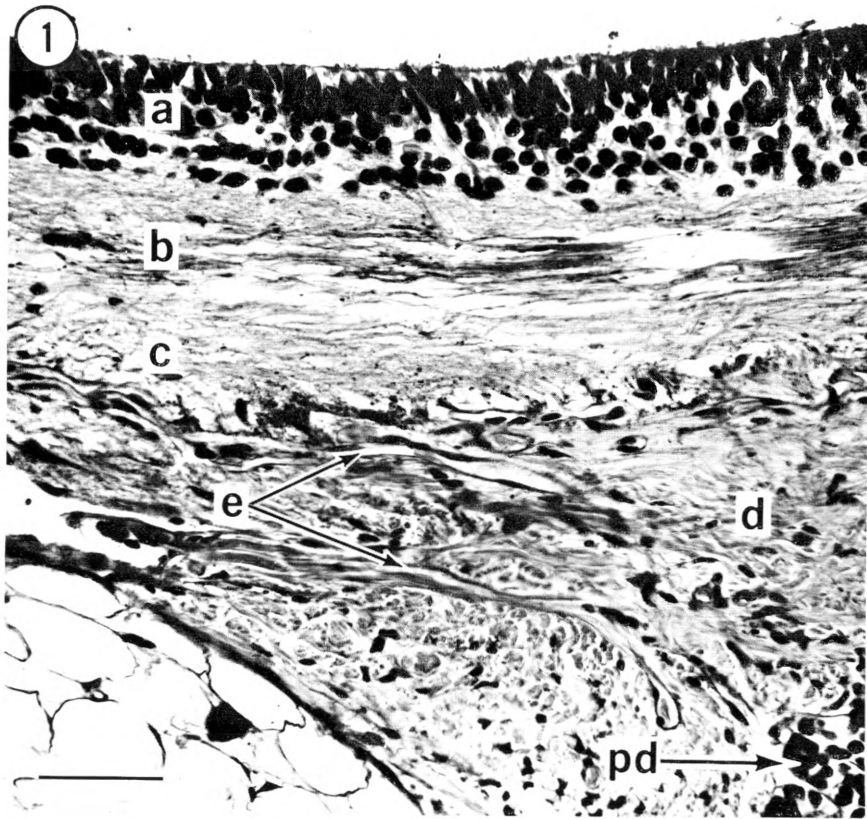


PLATE X

Calamoichthys calabaricus

Fig. 1. Sagittal section. — a = portal vessels collecting blood from the rostral part of the primary plexus, b = capillary connection between the capillaries of the primary plexus and the deeper capillaries of the hypothalamus, ds = dorsum sellae, em = eminentia mediana, hc = hypophysial cavity plus buccohypophysial duct, pd = pars distalis, sv = saccus vasculosus. — $75\ \mu$ section (celloidin). H-E. NA: 0.3. The scale represents $250\ \mu$.

Fig. 2. Paramedian section showing how the capillaries of the caudal part of the primary plexus (= c) merge into the secondary plexus of the pars distalis. — pli = plexus intermedius. Other abbreviations see fig. 1. — $75\ \mu$ section (celloidin). H-E. NA: 0.3. The scale represents $250\ \mu$.

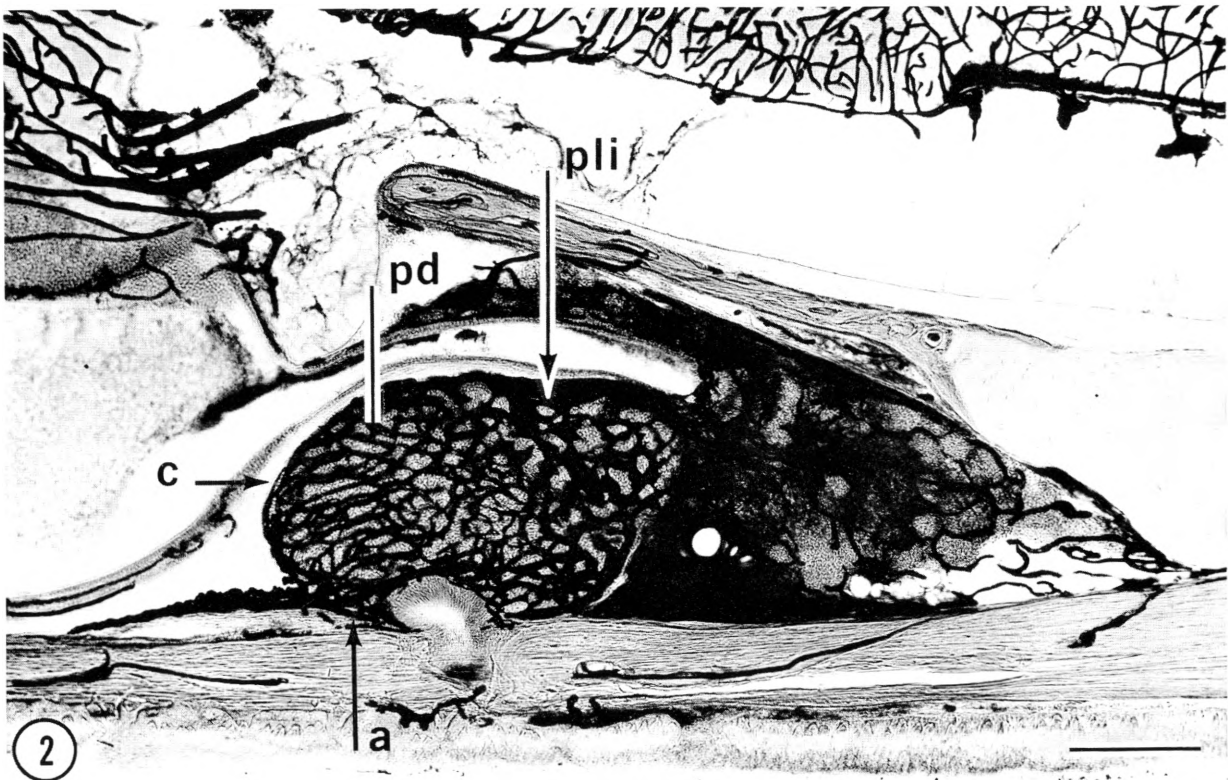
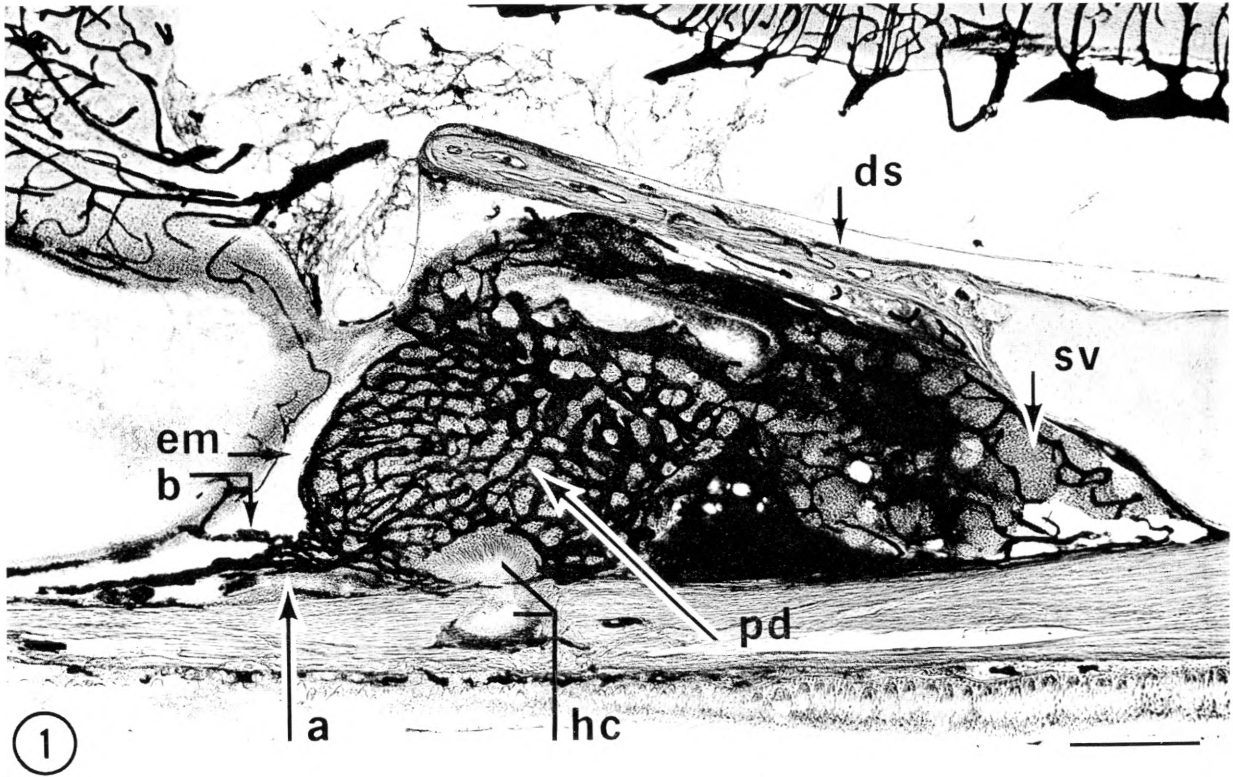


PLATE XI

Calamoichthys calabaricus

Fig. 1. Transverse section through the anterior part of the eminentia mediana. — a = eminential plexus, b = sulcus tubero-infundibularis, c = lobus inferior, d = a. cerebialis posterior, em = eminentia mediana. — 100 μ section (celloidin). Phosphotungstic acid hematoxylin of Mallory. NA: 0.3. The scale represents 250 μ .

Fig. 2. Transverse section through the pituitary gland. — bd = buccohypophysial duct, ds = dorsum sella, e = the unpaired v. hypophyseos, f = osseous floor of the fossa hypophyseos, hs = hypophysial stem, pd = pars distalis. Other abbreviations see fig. 1. — 100 μ section (celloidin). Phosphotungstic acid hematoxylin of Mallory. NA: 0.3. The scale represents 250 μ .

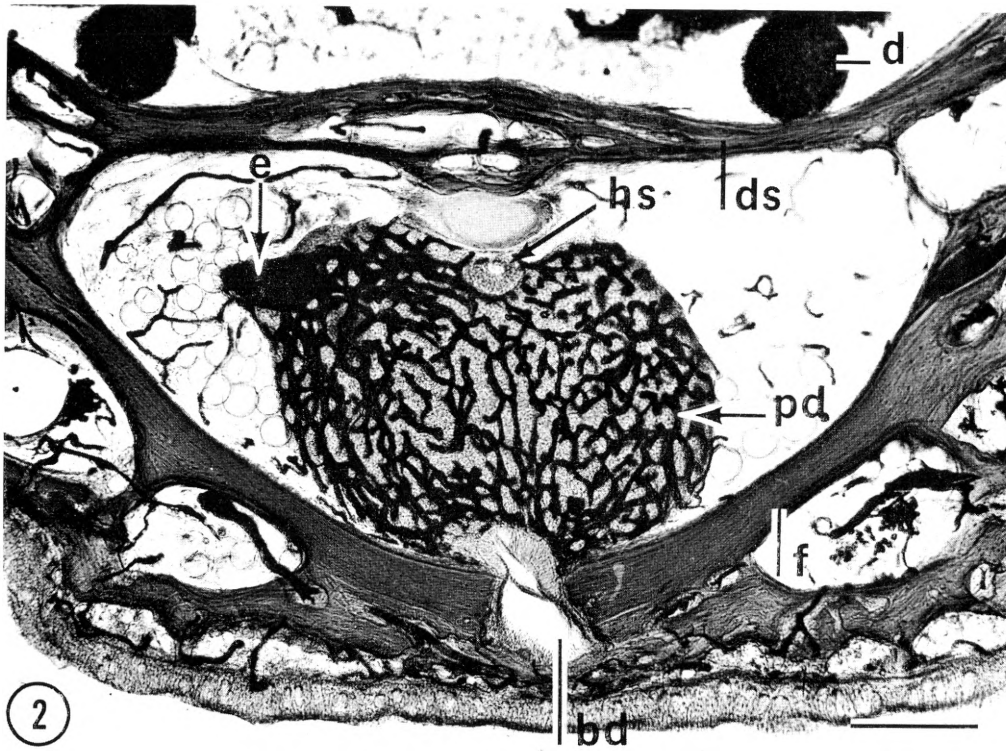
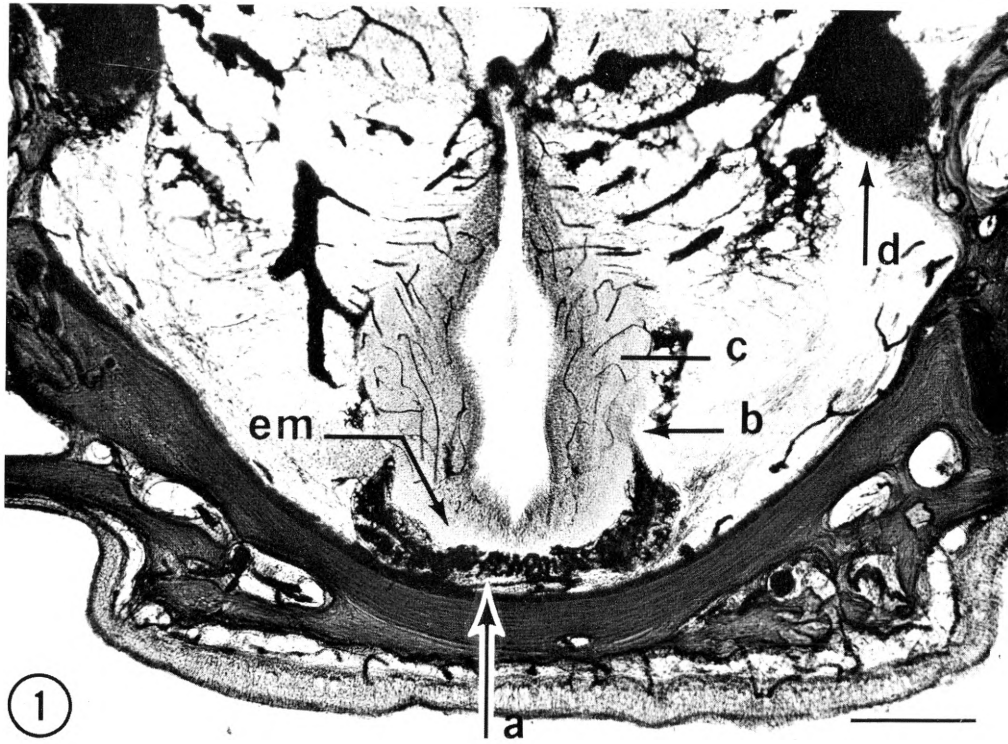


PLATE XII

Lepisosteus productus

Fig. 1. Transverse section through the eminentia mediana and the meso-adenohypophysis. — a = recessus infundibularis, b = eminential plexus, cem = caudal part of the eminentia mediana, moa = meso-adenohypophysis, thick black arrow points at the sulcus tubero-infundibularis. — 8μ section. AF-Halmi. NA: 0.22. The scale represents 100μ .

Fig. 2. Transverse section through the neural lobe and the meta-adenohypophysis. — a = recessus infundibularis, b = primary lumen of the lobus nervosus, ln = lobus nervosus, maa = meta-adenohypophysis. — 8μ section. AF-Halmi. NA: 0.2. The scale represents 150μ .

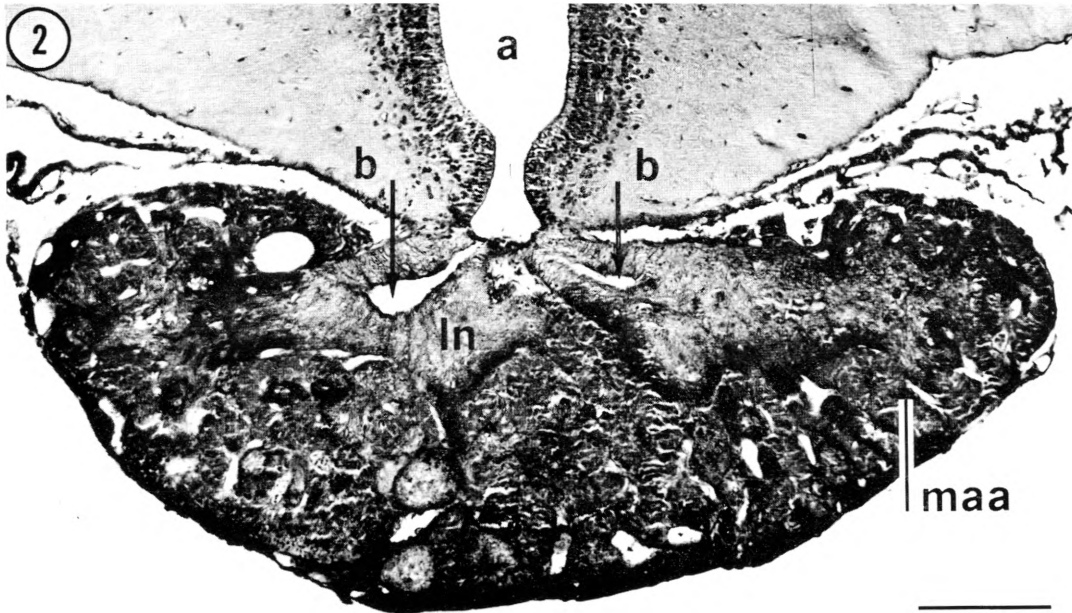
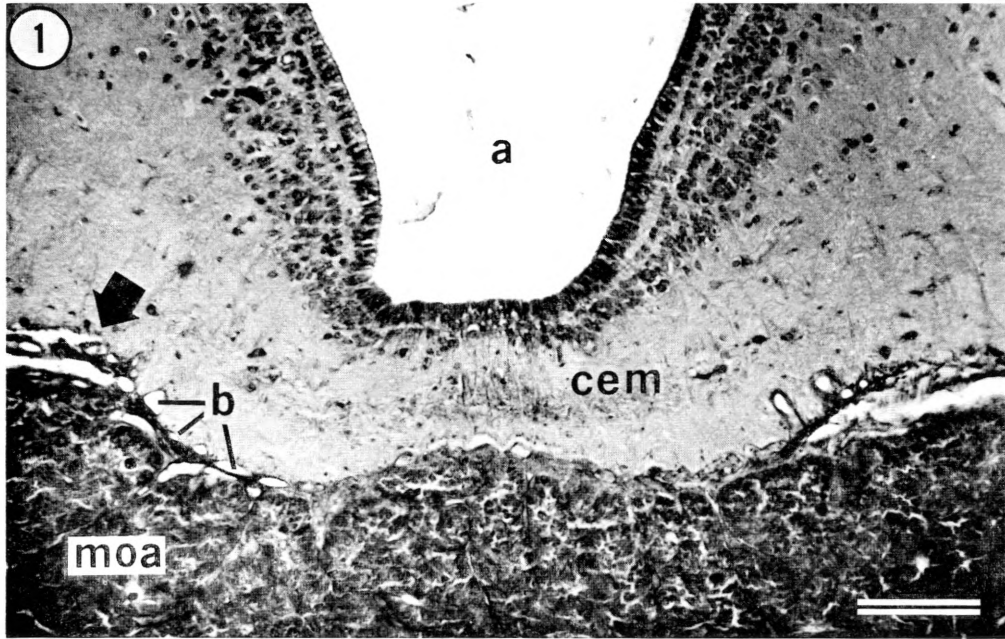


PLATE XIII

Lepisosteus productus. Paramedian section. — a = recessus infundibularis, b = v. interorbitalis, ds = dorsum sellae, em = eminentia mediana, ln = lobus nervosus, maa - moa - pra = meta-, meso- and pro-adenohypophysis, sv = saccus vasculosus, sv_s = saccus vasculosus stem. — 75 μ section (celloidin). H-E. The scale represents 500 μ .

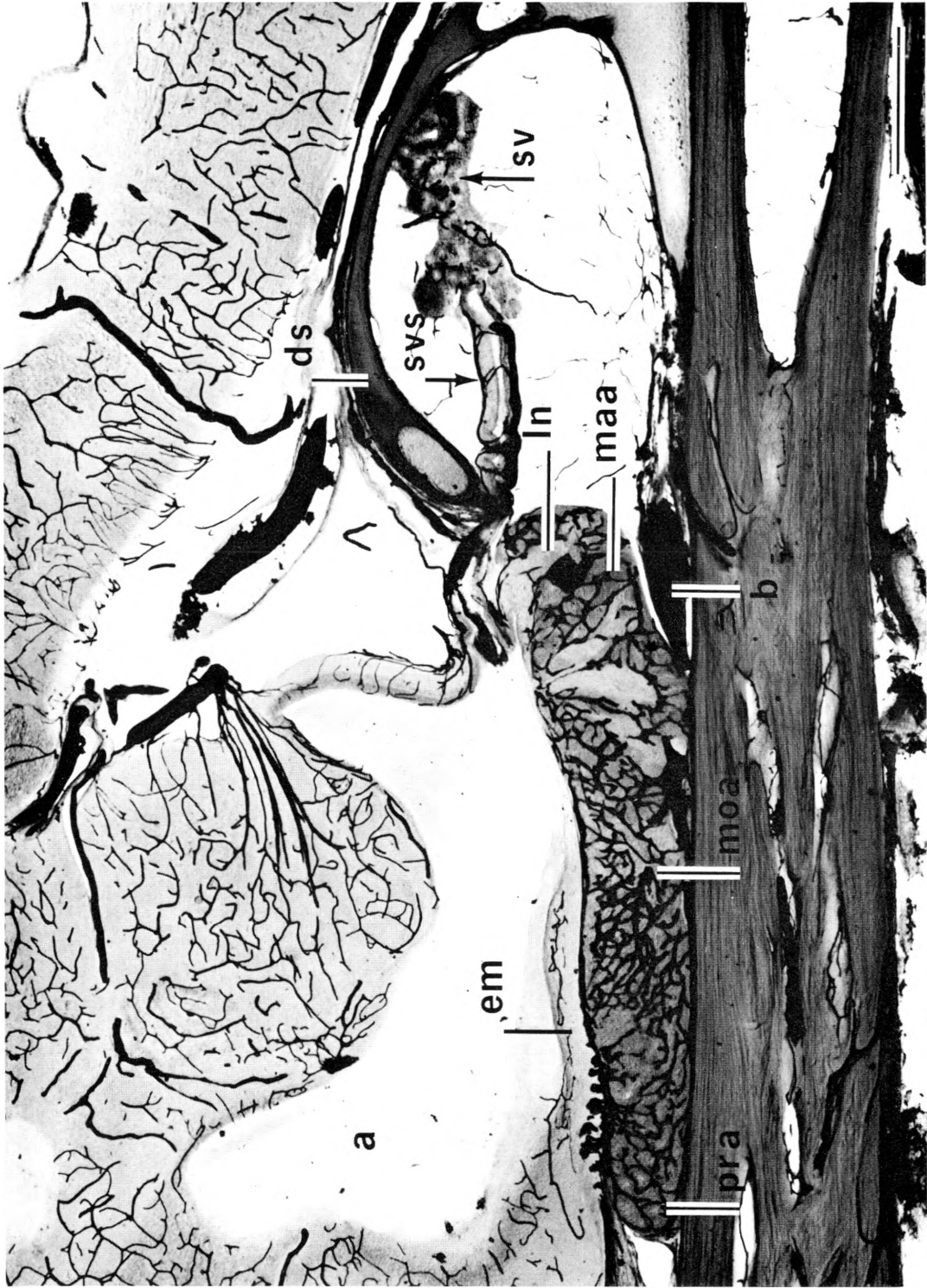


PLATE XIV

Lepisosteus productus

Fig. 1. Sagittal section. — a = a. infundibularis, b = eminential plexus receiving supplementary vessels (= c), d = lateral afferent vein, moa = meso-adenohypophysis. — 75 μ section (celloidin). H-E. NA: 0.3.
The scale represents 150 μ .

Fig. 2. Sagittal section showing the different development of the rostral (= a) and caudal (= b) eminential plexus. — c = hypophysial stem plexus, cem = caudal part of the eminentia mediana, ln = lobus nervosus, maa - moa - pra = meta-, meso- and pro-adenohypophysis, rem = rostral part of the eminentia mediana.
— 75 μ section (celloidin). H-E. The scale represents 200 μ .

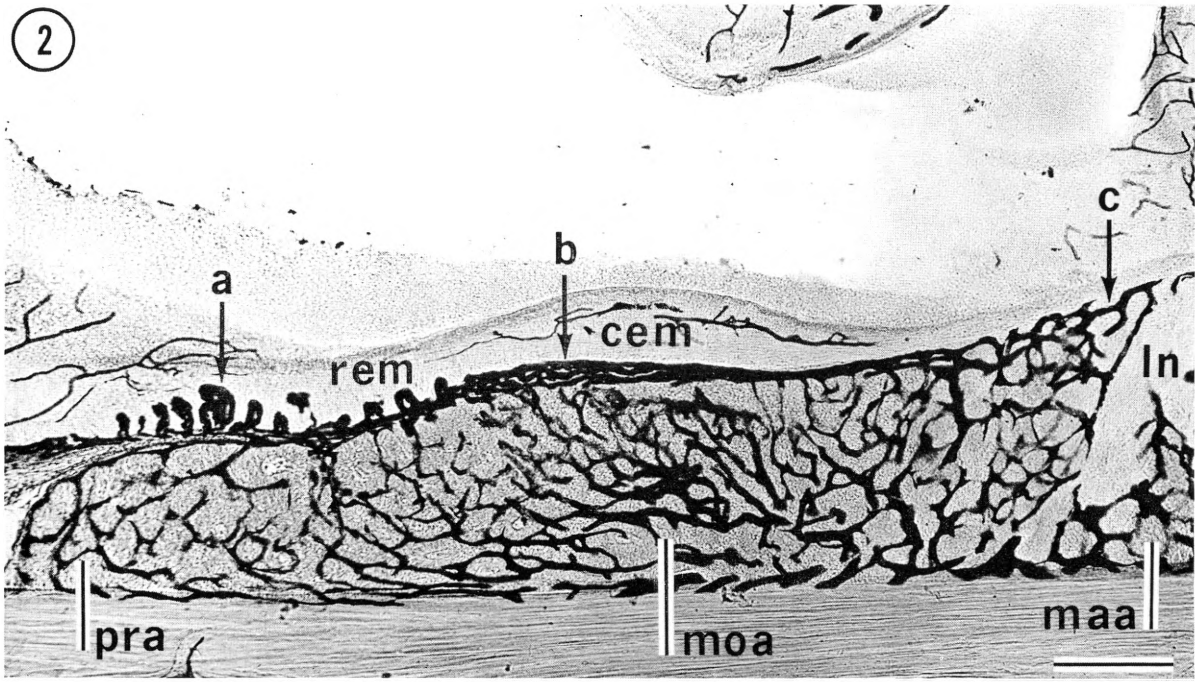
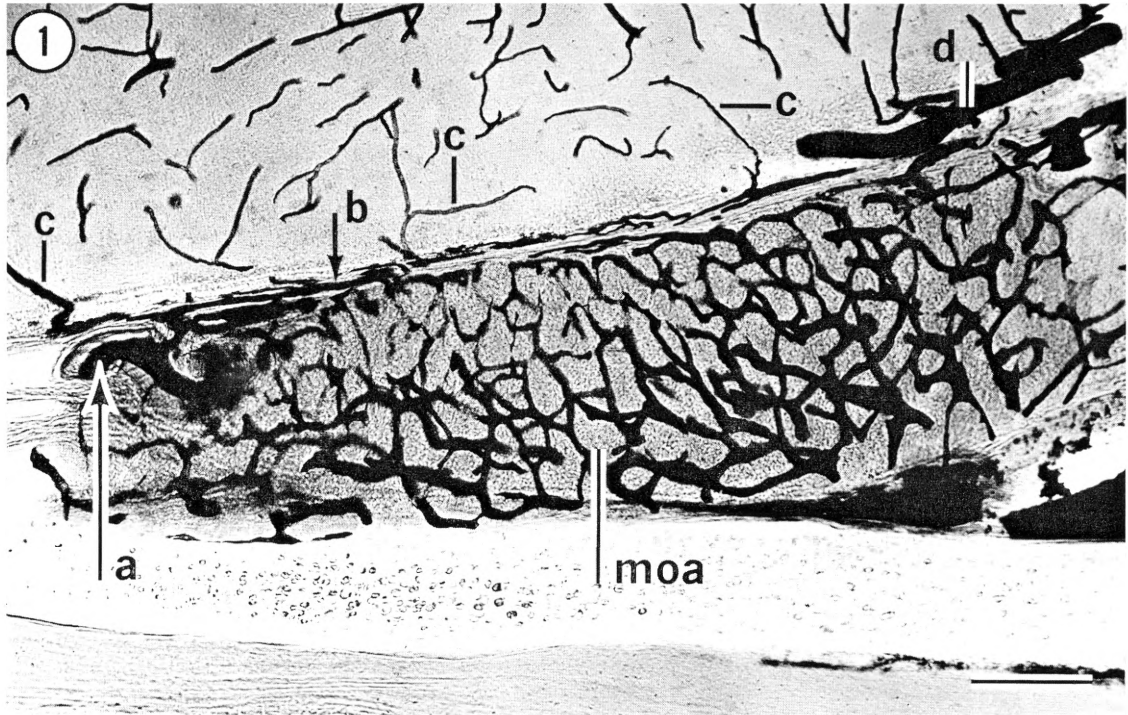


PLATE XV

Lepisosteus productus

Fig. 1. Paramedian section showing the rostral and (part of the) caudal region of the eminential plexus. — a = capillary loops of the primary plexus, b = superficial primary capillaries, c = v. porta, cem = caudal part of the eminentia mediana, d = a. infundibularis, moa - pra = meso- and pro-adenohypophysis, rem = rostral part of the eminentia mediana. — 75 μ section (celloidin). H-E. NA: 0.3. The scale represents 100 μ .

Fig. 2. Sagittal section through the lateral part of the lobus nervosus and the meta-adenohypophysis. — e = lateral afferent vein, f = hypothalami capillaries, g = capillary penetrating the meta-adenohypophysis, h = v. hypophyseos lateralis, i = v. interorbitalis, j = part of the superficial venous plexus covering the adenohypophysis, ln = lobus nervosus, maa - moa = meta- and meso-adenohypophysis, pli = plexus intermedius. — 75 μ section (celloidin). H-E. NA: 0.3. The scale represents 150 μ .

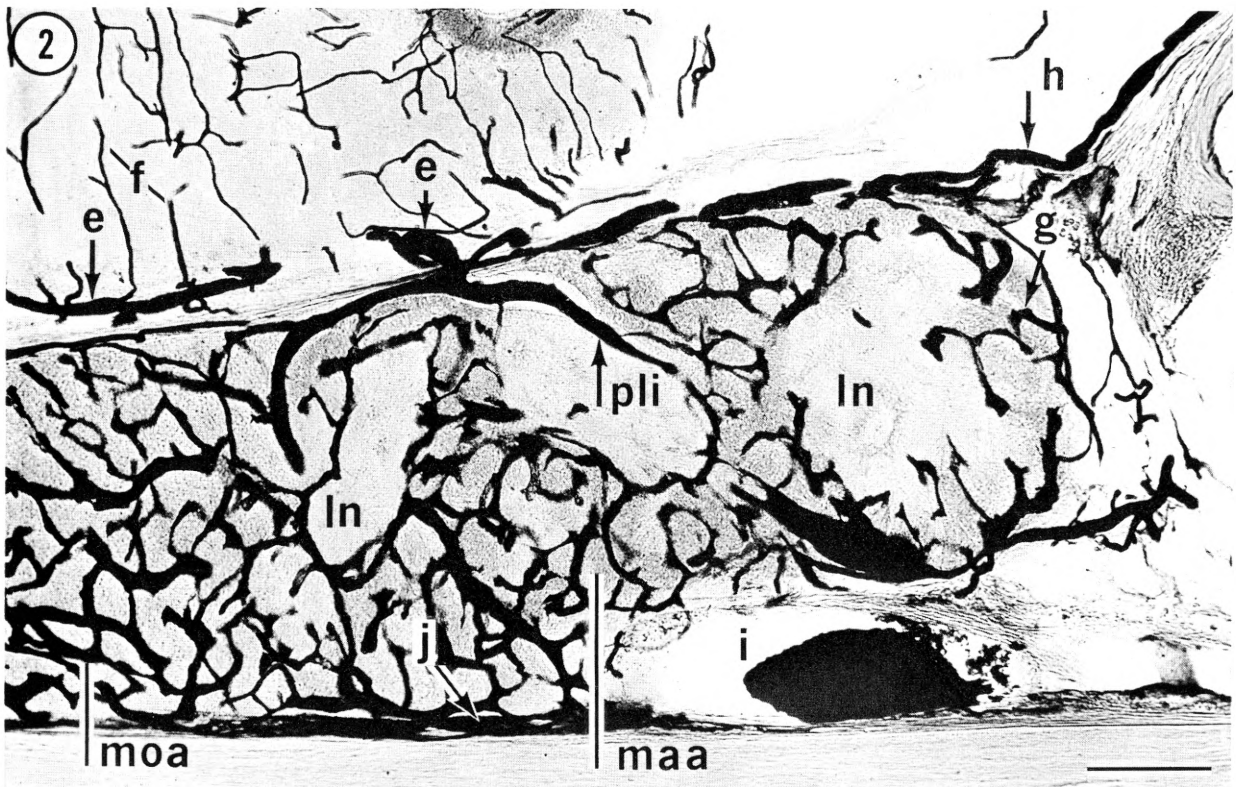
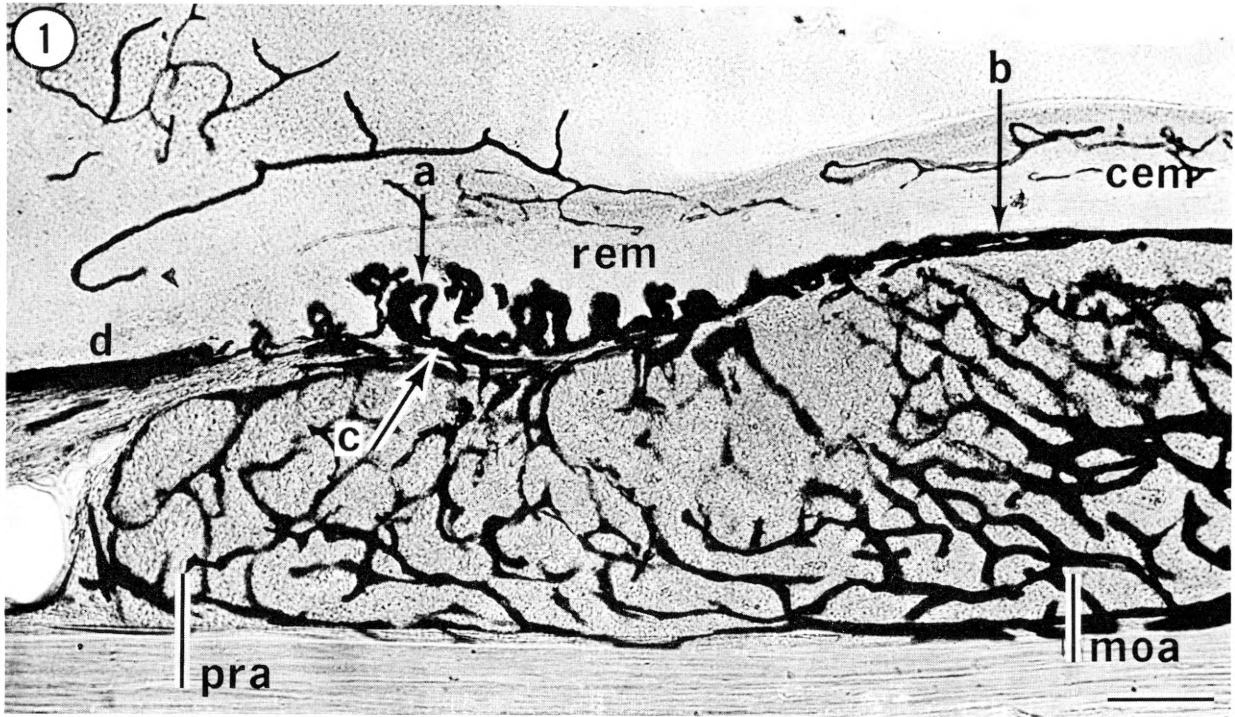


PLATE XVI

Amia calva

Fig. 1. Sagittal section through the rostral part of the eminentia mediana. — a = ependymal layer, b = fibre layer, c = cortical layer, d = capillary loops of the primary plexus (around which neurosecretory material (black) is accumulated). — $8\ \mu$ section. AF-Halmi. NA: 0.32. The scale represents $100\ \mu$.

Fig. 2. Transverse section through the rostral part of the eminentia mediana, showing the capillary loops (or "wads") of the primary plexus. — e = bundle of loops surrounded by tissue of the cortical layer (= c), d = accumulated neuro-secretory material, maa = meta-adenohypophysis. — $8\ \mu$ section. AF-Halmi. NA: 0.22. The scale represents $150\ \mu$.

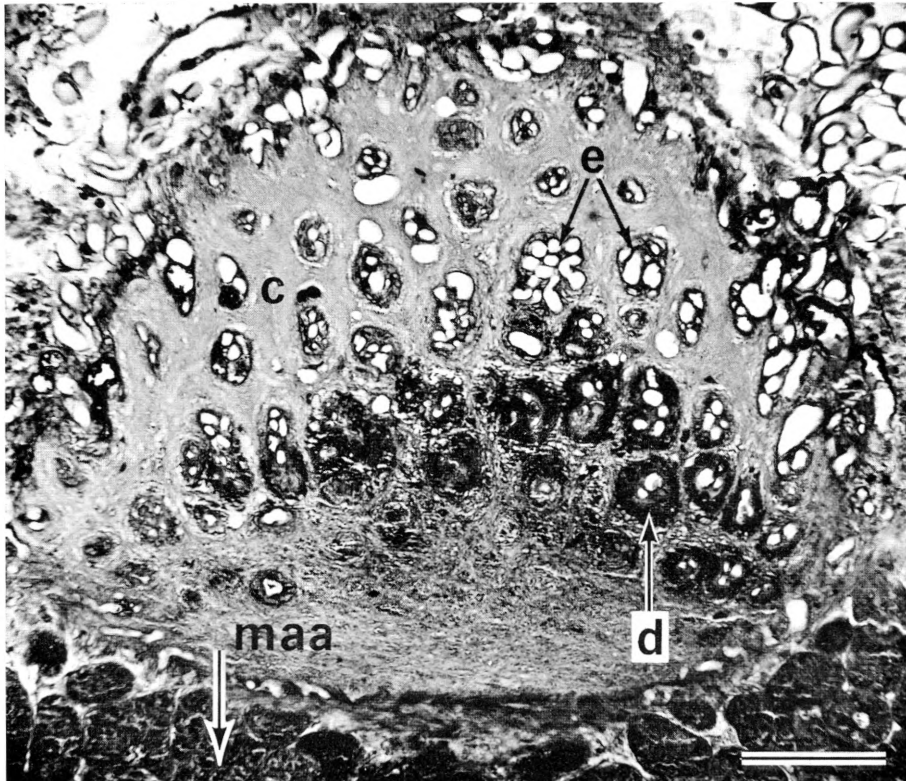
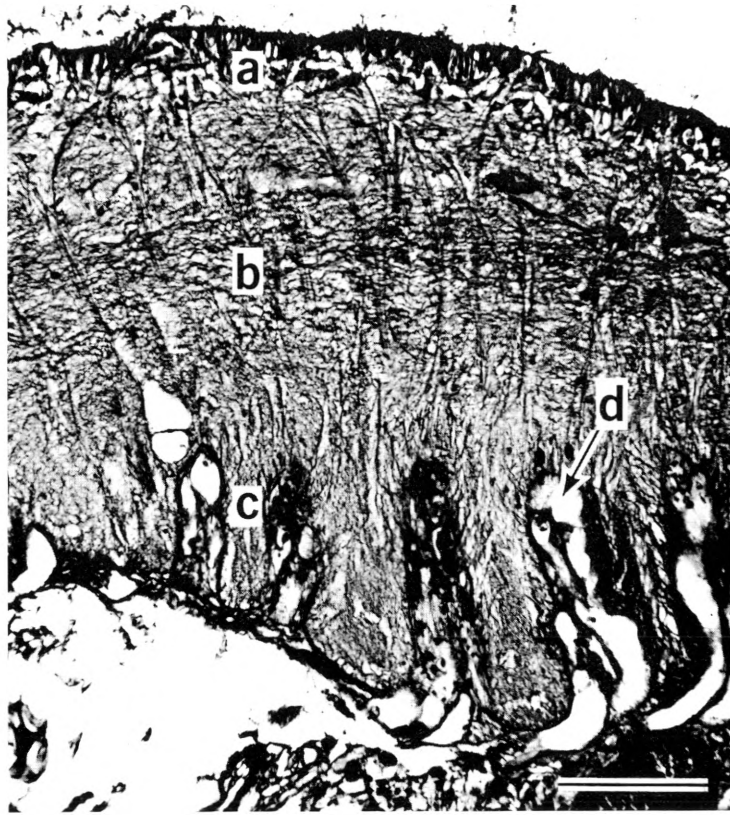


PLATE XVII

Amia calva. Paramedian section. — a = recessus infundibularis, ad = adenohipophysis, b = v. interorbitalis, c = v. hypophyseos media, ds = dorsum sellae, em = eminentia mediana, ln = lobus nervosus, sv = saccus vasculosus, svs = saccus vasculosus stem. — $75\ \mu$ section (celloidin). H-E. The scale represents $100\ \mu$.

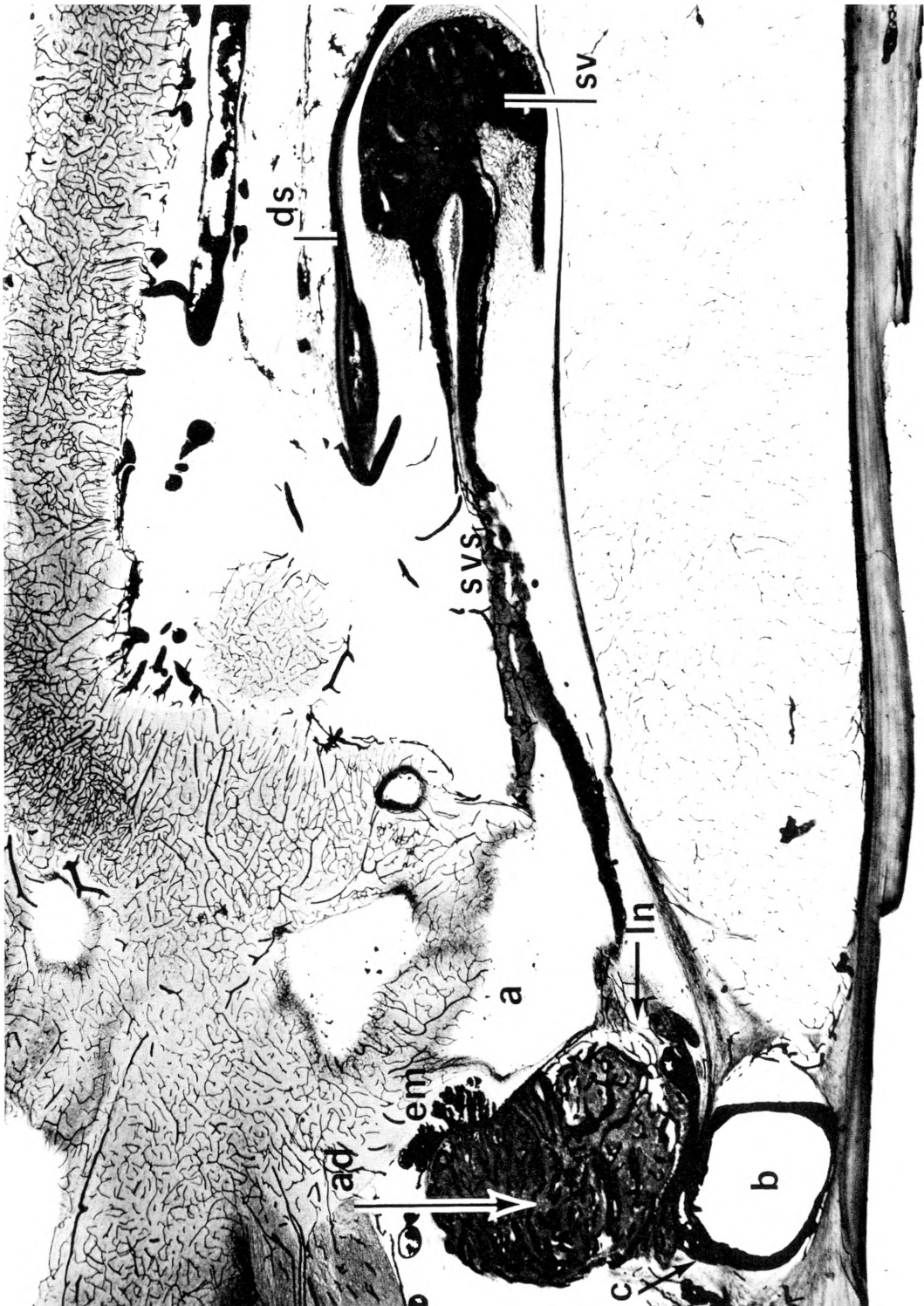
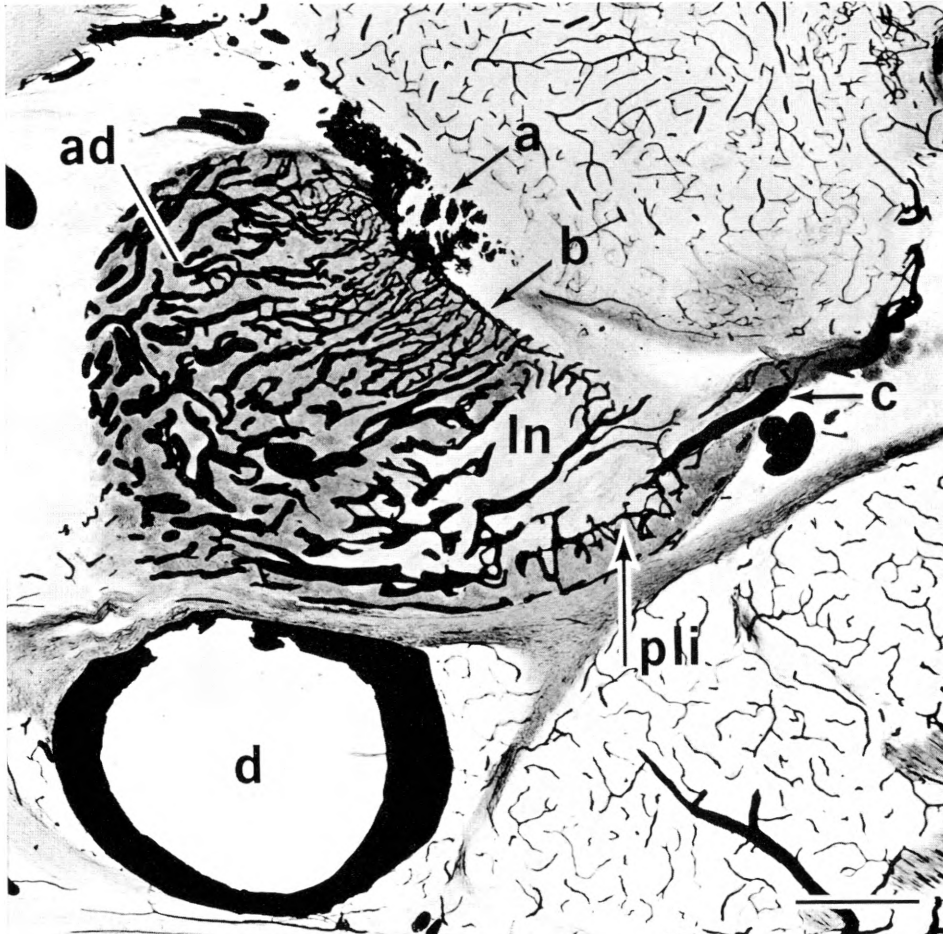
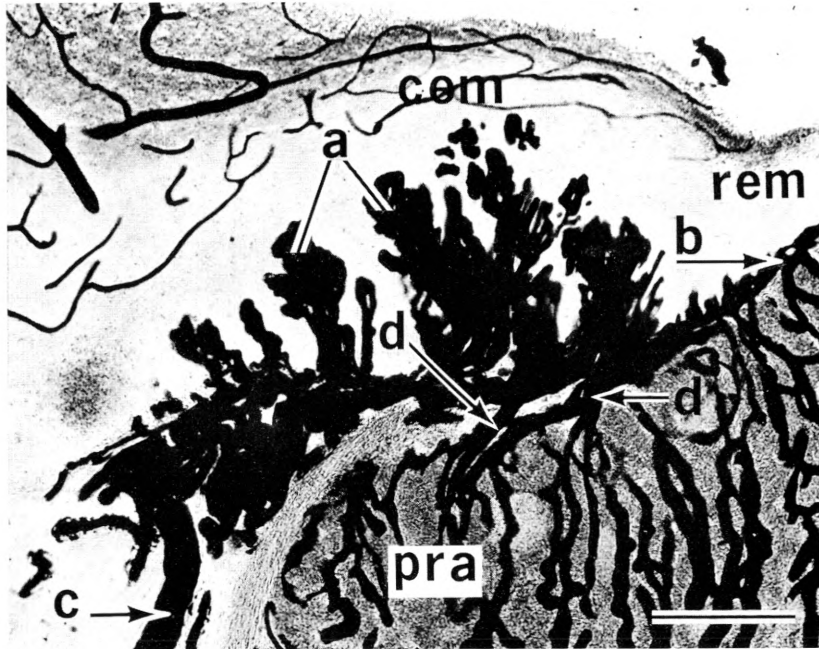


PLATE XVIII

Amia calva

Fig. 1. Median section through eminentia mediana and the adenohipophysis, showing how the rostral region of the primary plexus is drained by vv. portae, while the capillaries of the caudal region merge into the secondary plexus of the adenohipophysis. — a = capillary loops of the primary plexus, b = superficial primary capillaries, c = a. infundibularis, cem = caudal part of the eminentia mediana, d = v. porta, pra = pro-adenohipophysis, rem = rostral part of the eminentia mediana. — 75 μ section (celloidin). H-E. NA: 0.3. The scale represents 200 μ .

Fig. 2. Sagittal section. — a = rostral part of the primary plexus, ad = adenohipophysis, b = caudal part of the primary plexus, c = v. hypophyseos lateralis, d = v. interorbitalis, ln = lobus nervosus, pli = plexus intermedius. — 75 μ section (celloidin). H-E. The scale represents 500 μ .



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