Biologiske Skrifter
udgivet af
Det Kongelige Danske Videnskabernes Selskab
Bind **14,** nr. 5

Biol. Skr. Dan. Vid. Selsk. **14,** no. 5 (1966)

# NEW INVESTIGATIONS ON *HELICOPRION* FROM THE PHOSPHORIA FORMATION OF SOUTH-EAST IDAHO, U.S.A.

BY

SVEND ERIK BENDIX-ALMGREEN

København 1966

Kommissionær: Ejnar Munksgaard

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## Synopsis

The treated material comprises 10 specimens of the genus *Helicoprion* representing the species *H. ferrieri* HAY, *H. ergasaminon* n. sp. and *H. cf. ferrieri*, and *H. sp. indt*, preserved in bituminous, phosphatic limestone boulders, and originating from the lower Upper Permian Phosphoria formation in south-east Idaho, U.S.A.

Descriptions are given of some general traits of the anatomy of the foremost part of the cranial capsule, the lower and the upper jaw (*H. ferrieri*, *H. ergasaminon*), revealing features not previously known. The compound tooth-spiral, occuring in the symphysis of the lower jaw is described and its function discussed (*H. ferrieri*, *H. ergasaminon*, *H. cf. ferrieri*, *H. sp. indt.*), as is also the remains of a weak dentition situated on the very anterior part of the upper jaw (*H. ferrieri*). The tooth-histology is discussed, bringing out a few new details (*H. ferrieri*).

The new evidence found in the anatomy and the tooth-histology in *Helicoprion* are discussed and compared with the same anatomical and histological features, as they occur in some of the better known forms among the so-called *Bradyodonts*. It is concluded that *Helicoprion* systematically can not be placed close to any of these forms but shows indications of a closer relationship to the *Selachians*.



PRINTED IN DENMARK
BIANCO LUNOS BOGTRYKKERI A/S

## Preface

In the autumn of 1961 the material treated in the present paper was handed over to me for investigation by Professor WILLIAM FURNISH, head of the paleontological department at the University of Iowa, Iowa City. For permission to investigate and describe these really valuable finds I wish to express my most sincere thanks to Professor FURNISH.

The material is the property of the University of Idaho and Idaho State College. It was borrowed from these institutions in 1950 and 1951 by Dr. A. K. MILLER and Dr. WALTHER YOUNGQUIST, the latter having himself collected the greater part of it. To both these gentlemen I express my sincere gratitude.

On behalf of Dr. A. K. MILLER, Dr. W. YOUNGQUIST and myself, I would like to take this opportunity to express our grateful thanks to the following persons:

Mr. and Mrs. A. E. THIEL of Montpelier, Idaho, who in different ways have given valuable assistance and also donated one of the specimens investigated.

Professor A. ISOTOFF of Idaho State College, Moscow, Idaho.

Mr. D. L. KING and the authorities of the "San Francisco Chemical Company", Montpelier, Idaho.

Mr. C. W. SWEETWOOD and the authorities of the "Simplot Fertilizer Company", Pocatello, Idaho.

Mr. J. HAEGELE, Mr. CALDWELL and Mr. B. HAWLEY for their assistance to Dr. W. YOUNGQUIST during the collection of the material.

During a one month stay in Moscow and Leningrad for the purpose of carrying out investigations on fossil elasmobranchs, especially the renowned Russian Helicoprion finds, I made the acquaintance of Professor D. OBRUCHEV of Moscow, and Dr. L. S. GLÜCKMAN of Leningrad. I am greatly indebted to these two gentlemen for their assistance in making the fossil material accessible to me, and for valuable discussions with respect to fossil and recent fishes. My thanks are also due to Mr. RASTATUROV, vice-chief of the International Department of the Ministry of Higher and Secondary Education of the U.S.S.R., and to Mr. P. N. VARFOLOMEEV, Director of the Tschernyschev Museum, Leningrad. Financial support for this journey was also received from the Rask-Ørsted Foundation.

The map was drawn by Mrs. E. HANSEN in the Geographical Institute of the University of Copenhagen, and placed at my disposal through lecturer B. FRISTRUP. To both I offer my cordial thanks.

To Dr. EIGIL NIELSEN, head of the Department of Vertebrate Paleontology at the Mineralogical and Geological Institute of the University of Copenhagen, I express my cordial thanks for many discussions on problems related to the subject of the present paper.

To my wife Mrs. BENTE BANG SOLTAU, Conservator in the Department of Vertebrate Paleontology at the Mineralogical Museum, Copenhagen, I am greatly indebted for assistance she has offered me in the preparation of the photographs, and for advice during cleaning and casting of the fossil material.

Mrs. RAGNA LARSEN, artist at the Mineralogical and Geological Institute prepared three of the figures for the text, for which careful work I express my thanks.

I would like, moreover, to thank the authorities of the Mineralogical Museum, Copenhagen, for the excellent working facilities they have afforded me.

Civil engineer V. BUCHWALD, Royal Technical University, Copenhagen and civil engineer BRAM-HANSEN, Danotrix, Copenhagen, are thanked for their considerable technical assistance in the preparation of the thin sections.

Dr. A. K. HIGGINS kindly corrected the English manuscript.

The Mineralogical and Geological Institute of the University of Copenhagen.

*February 1965.*

SVEND ERIK BENDIX-ALMGREEN.

## Material and Methods

The fossil material is preserved in strongly bituminous and phosphatic limestone boulders which may be parts of limestone bands, but more probably are parts of large concretions.

The vertebrate remains are represented by four kinds of hard tissues i. e. bone, dentine and enamel, all belonging to the preserved teeth-structures, and lime prisms from the endoskeletal cartilage elements belonging to the neurocranium and the jaws. Numerous invertebrates, mainly brachiopods, occur in association with the vertebrate fossils.

The hard tissues have, unfortunately, been subjected to a diagenetic process which particularly affected the prismatic calcifications and the enamel. They are therefore not well suited for detailed microscopic analysis, although attempts have been made.

The preparation of thin-sections for these investigations was first attempted in the normal manner employing the adhesives Lakeside and Canada balsam. However, this method was unsuccessful because of the great friability of the material. A second method described by WEBER (1963) was later adopted in which the crystic resin "Palatal" in polymerised condition was used both as the adhering and the embedding medium.

When the suitable material was too small for the normal preparation of thin-sections, the small fossil specimens were first embedded in a clear acrylic resin using a warm pressure agregate manufactured by A. BÜHLER (*A. B. Simplimet Press* 1303). The block was then cut into slices, using a very thin, absolutely precise diamond saw, a process which yielded as many as eight slices from a tooth-fragment not more than 5 mm long and 3 mm broad.

A Leitz Dialux polarisation microscope was used in the microscopical study, and to take the microphotographs.

Other photographic work was carried out utilising a Sinar 9 × 12 cm camera equipped with a Schneider Symmar 135 mm objective. Photograph reproductions were made using the same camera and objective, together with a coldlight adaptor of the Graphlarger type. Perutz Silbereosin negative plates were used and reproductions were made on the paper types Umbrano UB 1 SP and UB 1 N manufactured by LEONARD.

The fossil material was photographed both in dry condition, and also in Xylene to take advantage of the refraction between matrix, fossil and liquid. Some of the

larger specimens are illustrated on the plates in both conditions in order to give a more detailed impression of the material.

In some cases a positive cast was made of a specimen, using the warm polymerising PVC and Dibuthylphtalate. The casts were coated with graphite to bring out the finer details.

Some preparations were made employing a modified dental mallet, and dental cutting and grinding tools. A stereomicroscope of the Zeiss Jena SM XX type was used in this work and in examinations of the fossils.

An attempt to stain the hard tissues using a 0.1 % solution of alizarine in 96 % ethylated spirit was unsuccessful, possibly on account of the previously mentioned diagenetic process, which occurred during fossilisation.

Most of the figures were drawn by the author. A Zeiss Jena drawing instrument attached to the stereomicroscope was utilized for some of this work.

The reconstruction of the section through the lower jaw (fig. 7) and the reconstructions of the shape of this jaw in lateral and ventral aspects (figs. 8–11) were achieved by NIELSEN's method (1952, pp. 13–19).

## Introduction

The fossil material comprises ten specimens. All of them originate from the lower part of the Phosphoria formation, and were collected in two localities in south-east Idaho, where the beds of the formation are mined for the contained phosphatic minerals.

All but one of the specimens are from the so-called "Waterloo Mine", which is owned and worked by the "San Francisco Chemical Company". It is situated in the Montpelier Canyon not far from Montpelier (fig. 1).

The "Waterloo Mine" specimens are:

> Idaho no. 1, Idaho no. 2 and Idaho no. 3, which were collected by Dr. W. YOUNGQUIST and Mr. B. HAWLEY in the summer of 1949.
>
> Idaho no. 4, Idaho no. 6, Idaho no. 7, Idaho no. 8 and Idaho no. 9, which were collected on 11th and 12th july 1950 by Dr. W. YOUNGQUIST and his assistant Mr. J. HAEGELE.
>
> The specimens referred to as Idaho mrk. "Thiel P" and Idaho mrk. "Thiel MP", are counterparts of the same concretion, and were donated by Mrs. A. E. THIEL of Montpelier to the University of Idaho.

Only a single specimen, Idaho no. 5, originates from another locality, and was collected in the so-called "Gay Mine", owned and worked by the "Simplot Fertilizer Company". This mine is situated about 30 miles ESE. of Pocatello at the Fort Hall Reservation (fig. 1). The specimen is the property of Idaho State College, Moscow, Idaho.

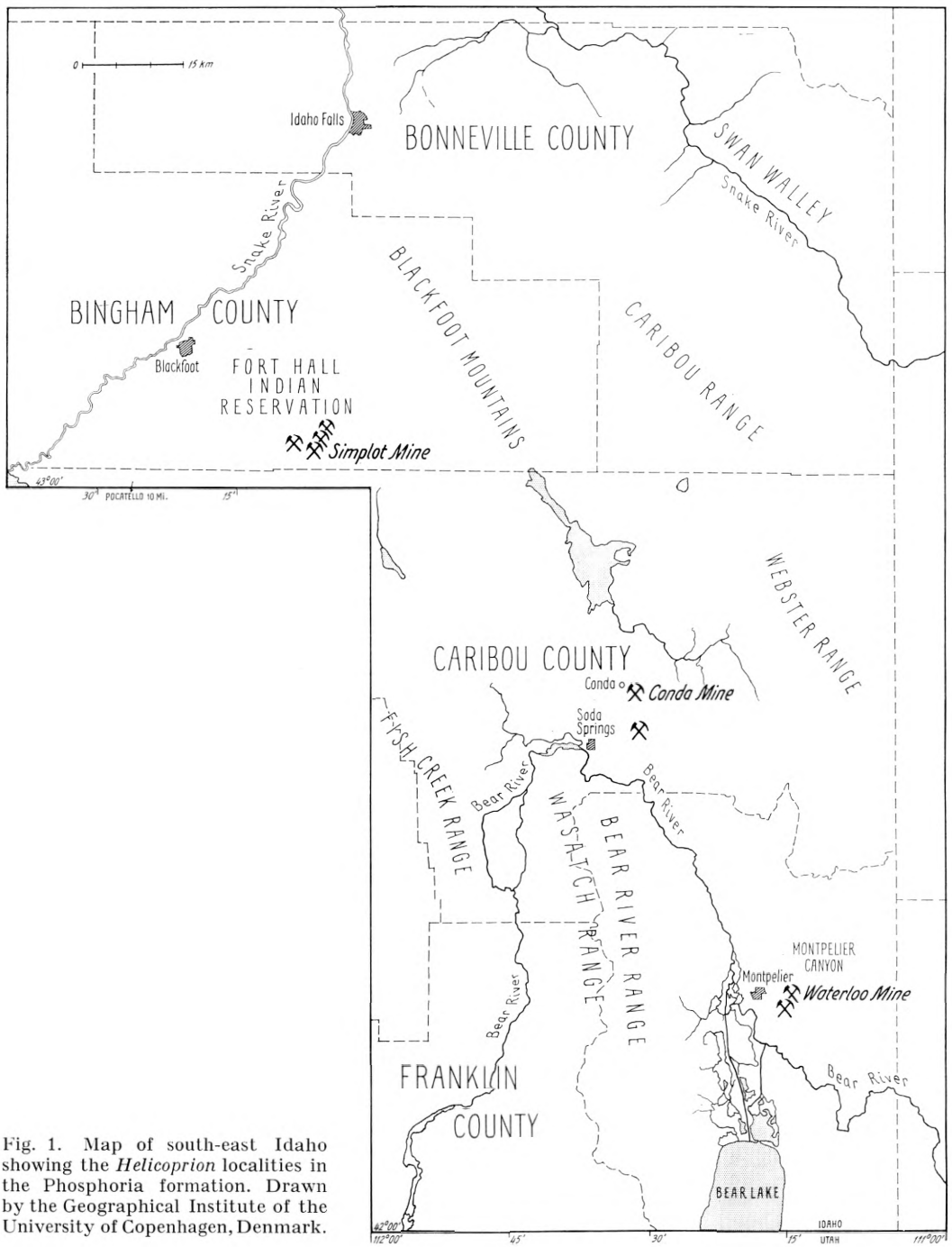


Fig. 1. Map of south-east Idaho showing the *Helicoprion* localities in the Phosphoria formation. Drawn by the Geographical Institute of the University of Copenhagen, Denmark.

A number of documents were received with the fossil material. These partially dealt with the collection of the material, but also gave important information of further, still undescribed, *Helicoprion* finds from the Phosphoria beds in south-east Idaho. These additional finds number at least 17 specimens which, with the material already at hand, bring the total number of specimens known from the U.S.A. to at least 27, not including those previously described in the literature.

Of the 17 undescribed specimens, 10 were collected by Mr. J. SMEDLEY and are stored in the collections of the U. S. Geological Survey and the U. S. National Museum in Washington. Of the remaining 7 specimens one is still at the Idaho State College or the University of Idaho, two are in the possession of Mrs. THIEL, two are owned by Mr. F. W. CHRISTENSEN, Lava Hot Springs, Idaho and two specimens, originating from the "Waterloo Mine", have been reported by Mrs. THIEL as disappeared or destroyed. For three of these specimens a few details, given below, are available concerning the preserved part of the tooth-spirals:

A: *Specimen owned by Mrs.* A. E. THIEL:
Greatest diameter of the symphyseal tooth-spiral: 10 ins.
Number of volutions preserved: 2.
Locality: "Waterloo Mine", Montpelier Canyon, Idaho.

B: *Specimen owned by Mr.* F. W. CHRISTENSEN:
Greatest diameter of the symphyseal tooth-spiral: about 115 mm.
Number of volutions preserved: $2^1/_2$.
Locality: "Waterloo Mine", Montpelier Canyon, Idaho.

C: *Specimen owned by Mr.* F. W. CHRISTENSEN:
Greatest diameter of the symphyseal tooth-spiral: about 142 mm.
Number of volutions preserved: 2.
Locality: Possibly the "Conda Mine", near Soda Springs (fig. 1).

As far as can be ascertained most of the remaining specimens were obtained from the "Waterloo Mine", and a few from the "Gay Mine".

Only eight specimens have previously been described in the literature. Four of these specimens (HAY 1907, 1909), of lower Upper Permian age, were derived from the "Waterloo Mine", as were most of those described in the present paper. WHEELER described two specimens (WHEELER 1939), of which one was collected from beds of Artinskian or Uralian age in Nevada, and the other, which is of uncertain age (possibly Artinskian or Uralian) was found in California. One other specimen, poorly preserved, is known from Nevada and is said to be of certain Leonardian age (LARSON & SCOTT, 1951).

The best preserved specimen hitherto known of those recorded in the literature, is that dealt with by DUNKLE and WILLIAMS in a short note (DUNKLE & WILLIAMS 1948, p. 1362), and it is reproduced as figure 3 in the present paper. This Helicoprion specimen was collected in the "Gay Mine". One of the documents at my disposal

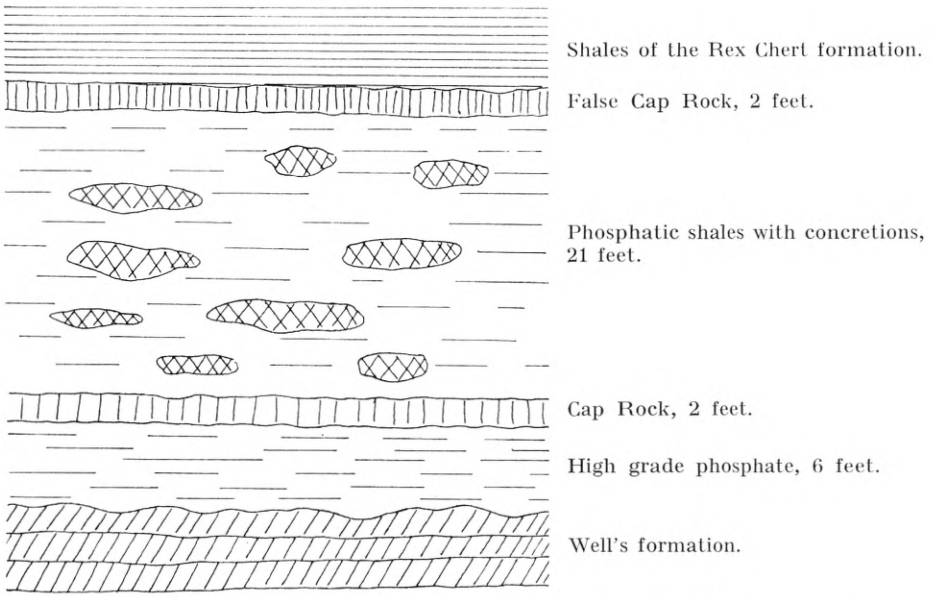


Fig. 2. Sketch showing the sedimentary sequence of the Phosphoria formation and parts of the adjacent formations, as represented in the "Gay Mine", Fort Hall Reservation, about 30 miles ESE of Pocatello, Idaho. Based on a field sketch by Dr. W. YOUNGQUIST.

deals with its position in the sedimentary sequence and includes several photographs of the specimen[1]. According to this document the sedimentary sequence is as shown in fig. 2. The specimen itself was derived from the beds just above, or just below, the "false cap rock", but most probably below such that it represents one of the concretions which are common in the phosphatic shales.

It is worth recording that the sequence of the sediments in the "Waterloo Mine" is almost identical to that shown above. Generally, there are only very small and unimportant variations between the successions at different lower Phosphoria localities in south-east Idaho, and that given in figure 2. It is likely that at least the majority of the finds were derived from the concretions in the phosphatic shales, or from the false cap rock itself.

## Review of previous works

The descriptions and reports concerning the genus *Helicoprion* published before 1940 were briefly but excellently reviewed by WHEELER (1939) and TEICHERT (1940) in their papers on North American and Australian finds respectively.

In addition to these works MOY-THOMAS (1939 a & b) and BERG (1940) deal briefly with *Helicoprion*, as will be referred to below in a discussion of the different classification attempts.

[1] To judge from the photographs the specimen is probably of the species *Helicoprion ferrieri* HAY.

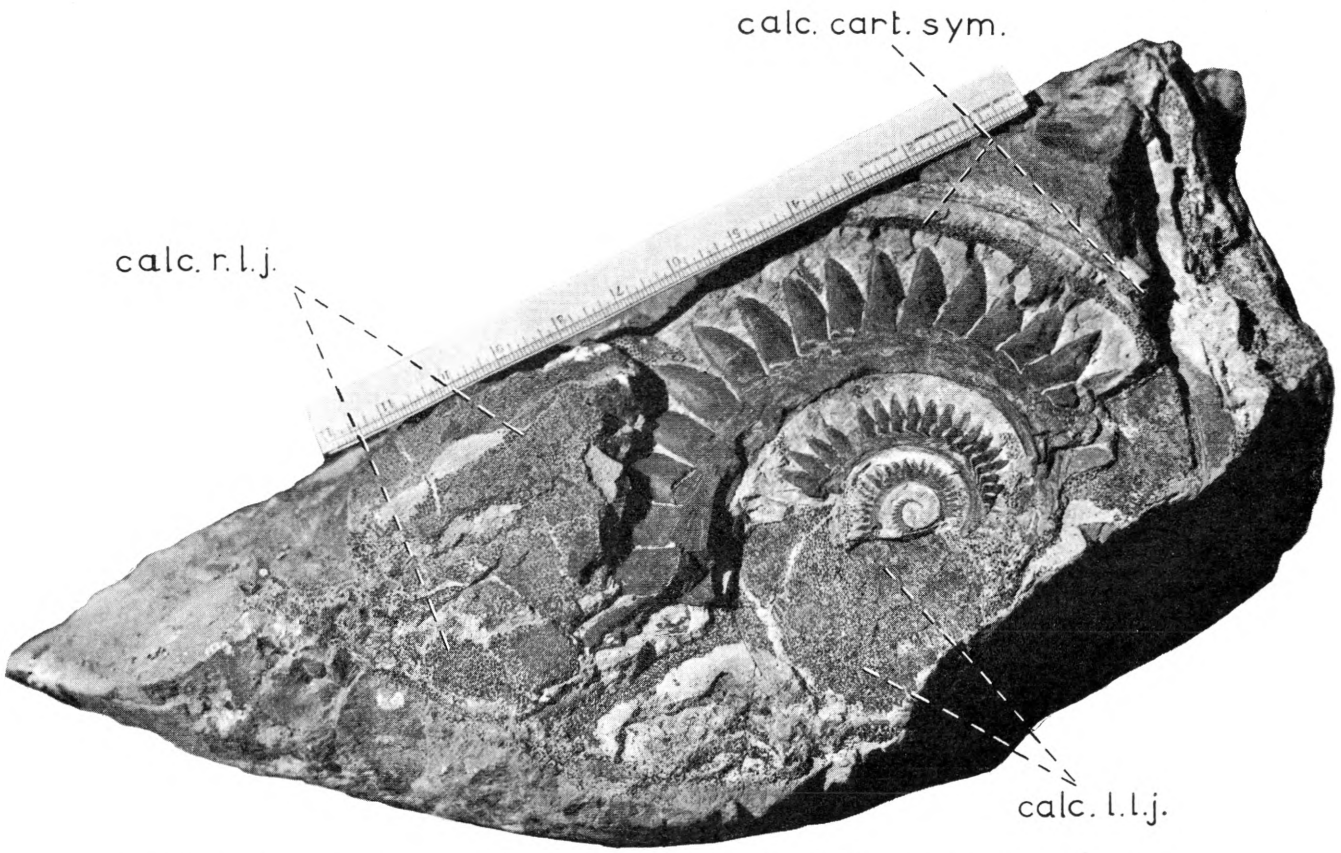


Fig. 3. The *Helicoprion* specimen discovered in 1947 at the "Gay Mine" and briefly discussed by DUNKLE and WILLIAMS in 1948. This exceptionally well preserved specimen shows clearly defined remains of the anterior part of the right lower jaw-branch (calc. r. l. j) and the left lateral wall of the symphyseal cavity, formed by the anterior part of the left lower jaw-branch (calc. l. l. j.). Note the strongly calcified symphyseal crista (calc. cart. sym.), still situated in the groove on the ventral side of the complex root. The oldest part of the tooth-spiral—the juvenile tooth-arch—is preserved. The photograph was donated by Mr. C. SWEETWOOD. Scale in inches.

The Russian paleontologist OBRUCHEV published in 1952 a work dealing with the elasmobranch *Helicoprion*. He dealt with the problems concerning the orientation of the roots of the teeth forming the symphyseal spiral, comparing them to those of *Edestus*. He concluded that the root in *Helicoprion* was directed backwards, that the forward directed narrowed and pointed bases of the crowns were only of secondary origin, and consequently that there were no fundamental differences between the teeth of *Helicoprion* and *Edestus*.

This publication was followed by a work dealing with the complete *Helicoprion* material collected in Russia (OBRUCHEV 1953), which included new finds and the considerable research done by KARPINSKY on this group. OBRUCHEV here attempted a thorough classification of the *Bradyodonts*, including *Helicoprion*.

In connection with investigations on *Edestid* material from East Greenland NIELSEN published an excellent reconstruction of the complete tooth spiral (NIELSEN 1952, fig. 21 p. 50). ØRVIG (1951) dealt briefly with the prismatic calcifications of the endoskeleton.

The few and extremely short reports of American finds since WHEELER have been mentioned above (p. 8). A more detailed up to date list of these finds, as given below, may be of some interest in connection with the material at hand:

1) *Helicoprion ferrieri* (*Lissoprion f.*) HAY 1907 and 1909.
   Montpelier, Bear Lake County, Idaho.
   Phosphoria formation, Permian.
2) *Helicoprion nevadensis*, WHEELER 1939.
   U. N. Loc. 28, Rochester district, Lovelock quadrangle, Perking County, Nevada.
   Rochester trachyte, Uralian or Artiskian.
3) *Helicoprion sierrensis*, WHEELER 1939.
   U. N. Loc. 29, Downieville quadrangle, Plumas County, California.
   Boulder from glacial moraine, possibly originating from beds of Uralian or Artinskian age.
4) *Helicoprion sp.*[1], DUNKLE and WILLIAMS 1948.
   "Gay Mine", Fort Hall Reservation, Bingham County, Idaho, Phosphoria formation, Permian.
5) *Helicoprion sp. indt.*, LARSON and SCOTT 1951.
   China Mountain, SSW. of Contact, Nevada.
   Leonardian age.

## Review of classification and taxonomy

A brief review of the classification of the genus *Helicoprion* KARPINSKY was given by TEICHERT (1940, p. 143). TEICHERT, besides supporting the view of KARPINSKY (1924) and BRANSON (1936) that the genus *Campyloprion* EASTMAN (1902) and the genus *Lissoprion* HAY should be regarded as synonymous with the genus *Helicoprion*, also quoted the four more recent attempts then made, by HAY (1929), NIELSEN (1932), ROMER (1933) and WHITE (1936), to classify this unusual elasmobranch. TEICHERT objects to the suggestion of NIELSEN (op. cit.) that the genus *Helicoprion* should be included in the *Bradyodont* group because of the specialisation of the symphyseal row of teeth and the microscopic tooth structure, since this structure, as far as he could determine from the description given by KARPINSKY (1899), differed fundamentally from that described by NIELSEN for the *Edestids* from the Permian of East Greenland.

[1] See footnote p. 9 and fig. 3 p. 10.

In his review of the fossil elasmobranchs MOY-THOMAS (1939 a) supports NIELSEN's point of view, with some reservations, and classifies the genus *Helicoprion* within the *Bradyodonti* in the following manner:

Subclass: ***Elasmobranchii.***
Division 2: *Bradyodonti.*
Order I: *Eubradyodonti.*
Suborder 6: *Edestidi.*
e. g. *Edestus, Agassizodus, Orodus, ? Helicoprion.*

BERG (1940) lists, also with some reservations, *Helicoprion* among the *Holocephali* in the following way:

Class: ***Holocephali.***
Subclass: *Chimaerae.*
Order: *Chimaeriformes.*
Family: *Edestidae.*
Genus: *Helicoprion* KARPINSKY 1899 has teeth with an enamel layer and according to MOY-THOMAS (1939) may belong to the class *Elasmobranchii.*

TEICHERT's statement, mentioned above, was rejected by NIELSEN (1952). The latter stated that the microscopic structure in *Helicoprion* did not in his opinion "differ in any fundamental respect from the tooth structure in other *Bradyodonti*" (p. 52).

NIELSEN, in the same publication, summarises his views regarding the main lines of evolution within the family *Edestidae,* and illustrates this with the diagram reproduced here as figure 4.

NIELSEN's views were supported by OBRUCHEV (1953, pp. 57–59), who published the following systematic division of the *Bradyodonti* as a whole:

Subclass: ***Holocephali.***
Superdivision: *Chondrenchelyes.*
– : *Chimaerae.*
Division: *Cochliodontiformes.*
– : *Janassiformes* (= *Petalodontidae*).
– : *Psammodontiformes.*
– : *Copodontiformes.*
– : *Menaspiformes.*
– : *Edestiformes.*
Family: *Edestidae*: *Edestus, Protopirata, Edestodus, Lestrodus.*
Family: *Helicoprionidae*: *Campodus, Agassizodus, Fadenia, Parahelicoprion, Helicampodus, Toxoprion, Helicoprion.*
Family: *Orodontidae*: *Orodus.*
Division: *Chimaeriformes.*

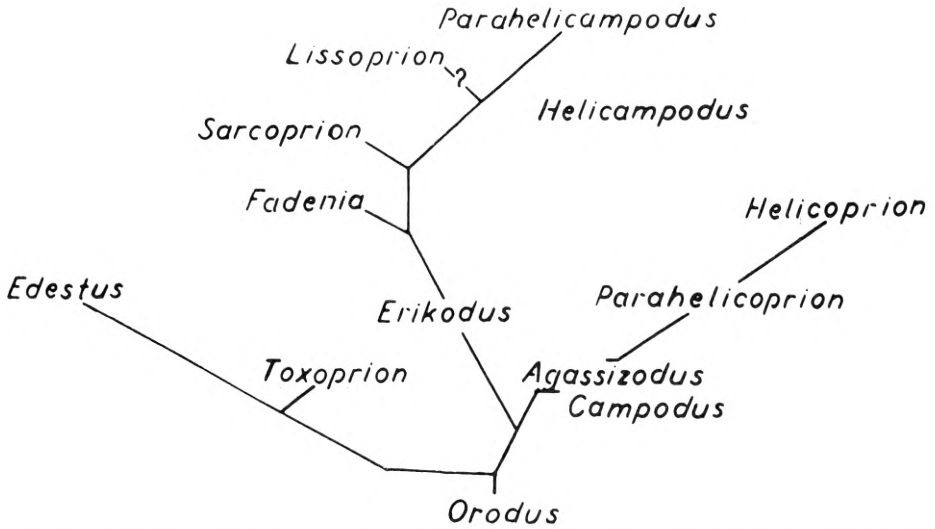


Fig. 4. The main lines of evolution within the family *Edestidae* according to NIELSEN (1952).

In the German translation of BERG's (1940) systematical work, scientifically revised by W. GROSS (BERG 1958), some hesitation is still expressed with regard to the classification of *Helicoprion*.

New investigations in paleohistology (ØRVIG 1965) have revealed facts showing that the microscopic tooth structure, previously regarded as being of some importance in classification within the Elasmobranchs, in this respect is without any significance.

Nevertheless, the present investigations have yielded features of the anatomy of the anterior part of the neurocranium and the mandibular arch. From these features it is evident that *Helicoprion* systematically is not closely related to those Elasmobranchs hitherto grouped as *Bradyodonts* in which corresponding traits of the cranial anatomy are known.

Finally, it should be noted that as a result of new and well preserved finds from Upper Carboniferous limestones in the Moscow region, it has been shown by OBRUCHEV (1964), that *Campyloprion* EASTMAN forms a well defined genus, which is not synonymous with the genus *Helicoprion*; also that *Helicoprion ivanovi* KARPINSKY (1922) is in fact a species of *Campyloprion*.

## Description of the Material

Genus ***Helicoprion*** KARPINSKY 1899.

Syn. *Lissoprion* HAY 1907, 1909, 1929.

*Helicoprion ferrieri* HAY 1907.

Syn. *Lissoprion ferrieri* HAY 1907, 1909, 1929.

Pl. I–VI, VII fig. 2, VIII, IX fig. 1–3, X–XIII, XIV fig. 1–2.
Text-fig. 3, 5, 7–24.

Material: The material representing this species consists of the following specimens: Idaho no. 1, Idaho no. 2, Idaho no. 3, Idaho no. 4, Idaho no. 7, Idaho no. 9 and Idaho mrk. "Thiel P" and "Thiel MP".

Introductory notes on the endoskeleton of the head: Some of the specimens show extensive endoskeletal remains, representing the anterior part of the neurocranium and the upper and lower jaws. This is notably the case with the specimen Idaho no. 4, as may be seen from the illustrations pl. I–IV and fig. 5. They are also present to a lesser extent in specimens Idaho no. 1 (calc. cart.: pl. VIII) and in Idaho mrk. "Thiel P" and "Thiel MP" (r. calc. cart.: pl. X–XII).

The preserved parts are the layers of prismatic calcifications, which were originally located superficially in the cartilage, as can be generally observed both in recent Elasmobranchs and in many well preserved fossil Elasmobranchs. The layers are preserved to some degree in their original positions with regard to each other and to the symphyseal tooth-spiral. These circumstances permit an interpretation of the limitations of the different elements, a reconstruction of the anterior portion of the lower jaw, and an interpretation of the original location of the tooth-spiral.

Unfortunately the layers of calcifications of the neurocranium are so strongly affected by pressure, as seen on pl. IV and fig. 5, that it has proved impossible to make detailed investigations. However, due to a fortunate dorso-ventral section through the preserved parts of specimen Idaho no. 4, which displays a large number of calcification walls (pl. IV & fig. 5), it is possible to give a few general observations on the neurocranium and also the upper jaw. The dislocation which the elements observable in the section have undergone during decay and compaction are shown schematically in figure 6 A, B, C.

Although the calcifications are in close mutual connection, it is possible to distinguish two areas of different complexity. The less complex of these is adjacent to the tooth-spiral. The more complex area is situated partly below some of the younger tooth-crowns of the spiral, partly outside and away from them and has a long extension in a forward direction (calc. cart. n. cr. & r. p. n. cr.: pl. I). These two areas can only be adequately interpreted as representing the lower jaw and the neurocranium

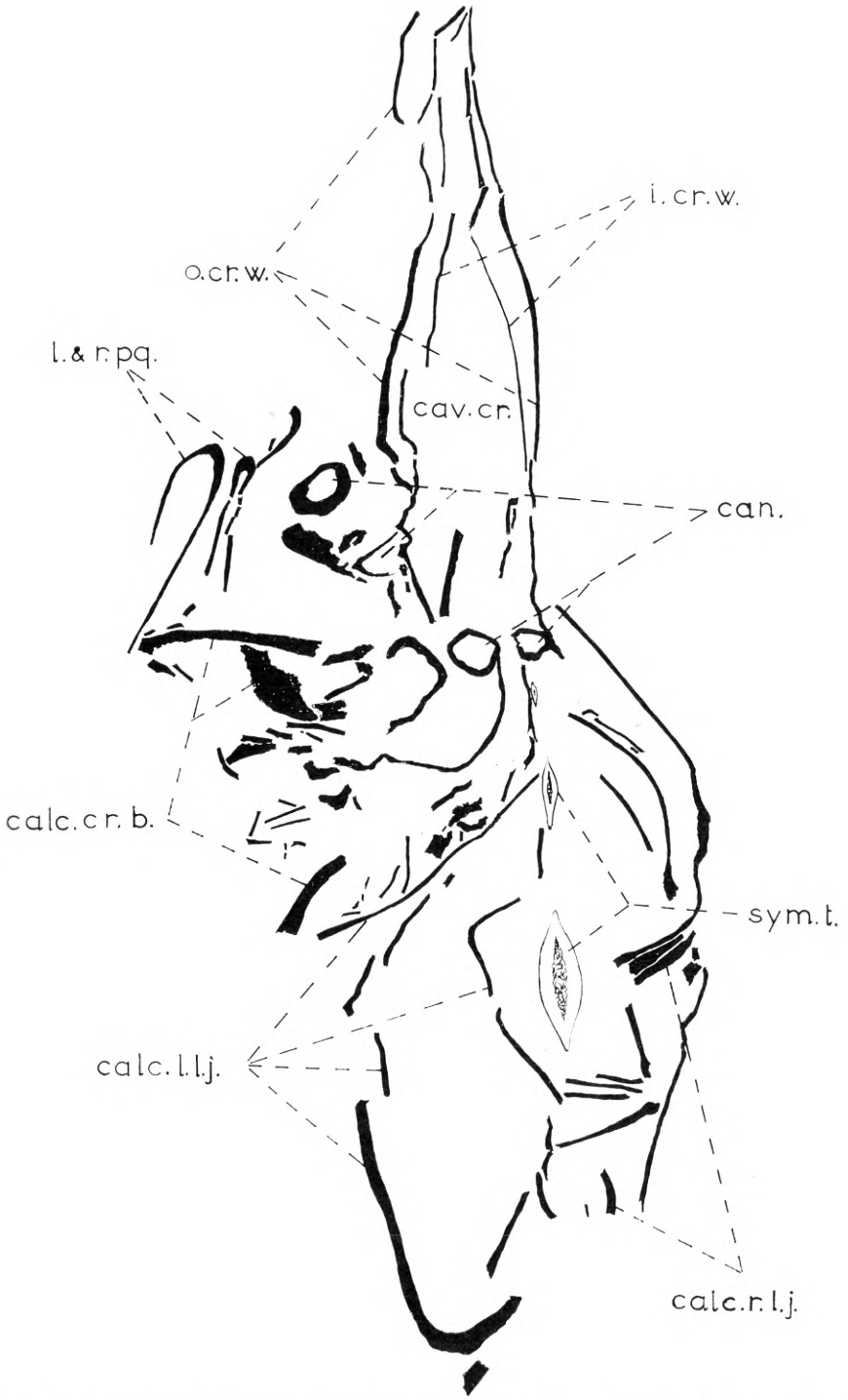


Fig. 5. *Helicoprion ferrieri* HAY: Transverse section through the anterior part of the neurocranium and the palatoquadrates, and through the lower jaw, just caudally to its symphyseal region, as exposed on Idaho no. 4. Only the sections through the calcification layers are shown on the sketch. 1,1× nat. size. calc. cr. b.: layers of calcifications from the broken ventral part of the neurocranial capsule. calc. l. l. j. & calc. l. r. j.: layers of calcifications from the left and the right part of the lower jaw respectively. can.: two pair of canals. cav. cr.: the cranial cavity. i. cr. w. & o. cr. w.: layers of calcifications originally lining the inner and the outer surface respectively of the neurocranial capsule. l. & r. pq.: the left and the right palatoquadrate. sym. t.: sections of tooth-crowns belonging to the youngest part of the symphyseal tooth-spiral.

respectively. The area representing the lower jaw exhibits a rather simple pattern with the calcifications concentrated around the tooth-spiral. The area with the remains of the neurocranium shows, as might be expected, a pattern of great complexity.

## The neurocranium.

The layers of calcifications representing the neurocranium show clearly in their dorsal parts the presence of an inner and an outer wall of calcifications (l. &r. i. cr. w. and l. &r. o. cr. w.: pl. IV; see also fig. 5: i. cr. w. & o. cr. w. and pl. I: calc. cart. n. cr.). The inner wall, which is comparatively thin, lines the inner surface of the cartilaginous cranial capsule along the cavum cerebrale cranii (cav. cr.: pl. IV and fig. 5), while the outer wall is situated superficially in the cartilage along the outer surface.

Ventrally to these walls are situated a number of broken pieces of calcifications, which clearly represent the lower lateral parts and the floor of the cranial capsule (calc. cr. b: pl. IV and fig. 5). It has not been possible to deduce their original pattern. However, the presence of two pairs of rather prominent canals can be demonstrated (can. l. &r.: pl. IV and fig. 5; can. r.: pl. I). These canals run in a forward direction and may originally have been situated with two canals in each lateral wall of the cranial capsule, possibly at the connection between the walls and the cranial floor. It is not possible to state whether they originally conducted some of the main vessels or the stems of nerves, but their presence does suggest that the mentioned cranial cavity represents a portion of the cavum cerebrale cranii proper.

In lateral view the neurocranium tapers in a forward direction. The most anterior part preserved occurs as a strongly calcified cartilage balk, which represents the rostrum. Because of the incompleteness of the specimen in the area where the rostral element is found, it is not possible to state whether or not the rostrum originally consisted of more rostral elements than that observed (r. p. n. cr.: pl. I–III). On the ventral side of the rostral element is found proximally a broad, evenly rounded tuberosity (art. p.: pl. I). This tuberosity may have acted as the area of attachment for the ligaments running to the anterior part of the palatoquadrates, a suggestion which is supported by the fact that the only traces found of a lateral dentition are situated below the neurocranial remains just caudally to the tuberosity (dnt.: pl. I).

It may be concluded, from the above evidences, that the preserved rostral element corresponds to an unpaired ventral rostral balk, similar to that found in many Selachian skulls e. g. *Mustelus, Isurus,* and *Carcharhinus.*

A rather large foramen (f. o. l.: pl. I) is situated in the calcifications of the left wall in the anterior part of the neurocranial capsule just caudally to the rostrum, and thus at the very anterior end of the ethmoidal region. The foramen is divided into three sections by very delicate bars of calcifications. Outside the foramen there occurs a space surrounded by a layer of calcifications. This space is only partially filled by argillaceous sediment, the remainder, as far as the foramen, being occupied

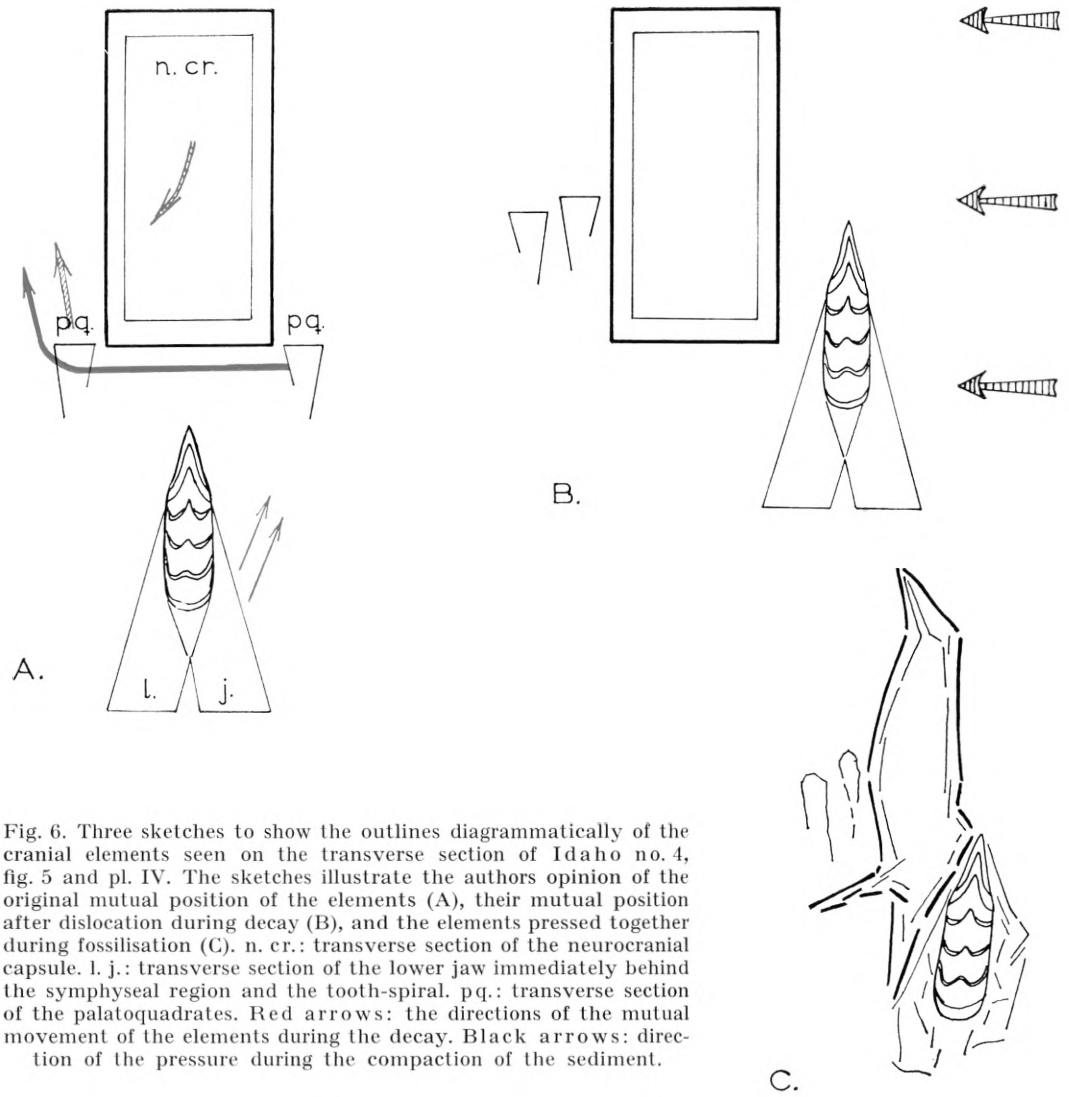


Fig. 6. Three sketches to show the outlines diagrammatically of the cranial elements seen on the transverse section of Idaho no. 4, fig. 5 and pl. IV. The sketches illustrate the authors opinion of the original mutual position of the elements (A), their mutual position after dislocation during decay (B), and the elements pressed together during fossilisation (C). n. cr.: transverse section of the neurocranial capsule. l. j.: transverse section of the lower jaw immediately behind the symphyseal region and the tooth-spiral. pq.: transverse section of the palatoquadrates. Red arrows: the directions of the mutual movement of the elements during the decay. Black arrows: direction of the pressure during the compaction of the sediment.

by an accumulation of calcite crystals, which suggest that originally the communication between the space and its surroundings was somewhat restricted.

These facts suggest that the foramen can be regarded as the divided foramen for the nervus olfactorius; outside this is situated the olfactory capsule, the interior of which would be in only restricted communication with the surroundings through the fenestra endonarina communis, if an annular cartilage was originally present.

If these suggestions are correct, the fila olfactoria entered the nasal capsule through a divided olfactory foramen, and therefore through a very simply formed lamina cribrosa.

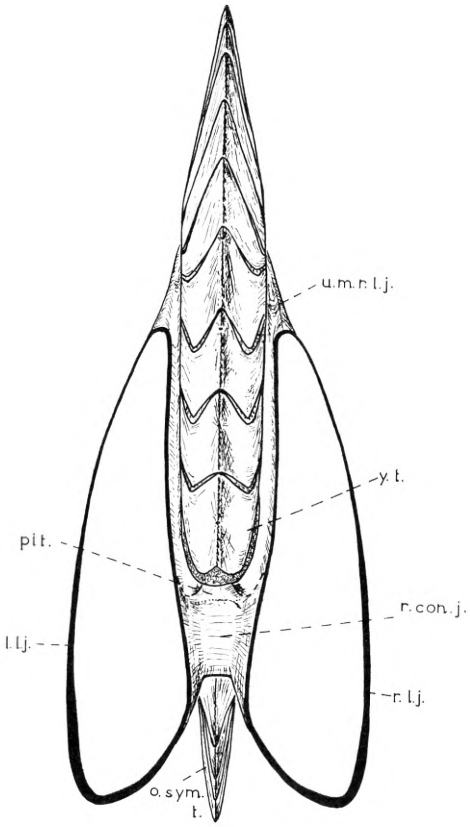


Fig. 7. *Helicoprion ferrieri* HAY. Attempted sketch of the anterior part of the lower jaw and the symphyseal tooth-spiral in lingual view. The jaw is sectioned just caudally to the symphyseal region. The strong layer of prismatic calcifications situated along the surface of the cartilage is indicated by the heavy black line (l. l. j. & r. l. j.). 0.55× nat. size.
o. sym. t.: older part of the symphyseal tooth-spiral exposed on the ventral side. pit.: the pit where the new tooth-members of the spiral are developed. r. con. j.: the rear connection in the symphyseal region between the two branches of the jaw. u. m. r. l. j.: the upper margin of the right lower jaw. y. t.: the youngest tooth in the spiral.

Remarks: – The presence of a type of lamina cribrosa closing the canalis olfactorius toward the nasal capsule is also known in the recent Elasmobranch *Chlamydoselachus anguineus*, although it is here formed by a layer of connective tissue and not by a proper endoskeletal cartilage wall (ALLIS 1923 p. 113). On the other hand a lamina cribrosa formed by proper endoskeletal bony tissue is known in many *Arthrodires* (STENSIÖ 1942; 1963, p. 50, pp. 147–152, fig. 50 A, B, D).

## Visceral skeleton.

The palatoquadrates: On the left side of the neurocranium of Idaho no. 4, and situated below it in the matrix are found two nearly oval shaped, but somewhat compressed, walls of calcifications representing sections through two elements, which now lie close together and apparently parallel with the neurocranium (pq. l. & pq. r.: pl. IV; l. & r. pq.: fig. 5).

These two elements, which as can clearly be seen were originally mirror-images of each other, on account of their size and general shape can only be regarded as sections through the palatoquadrates. During decay and compaction these elements

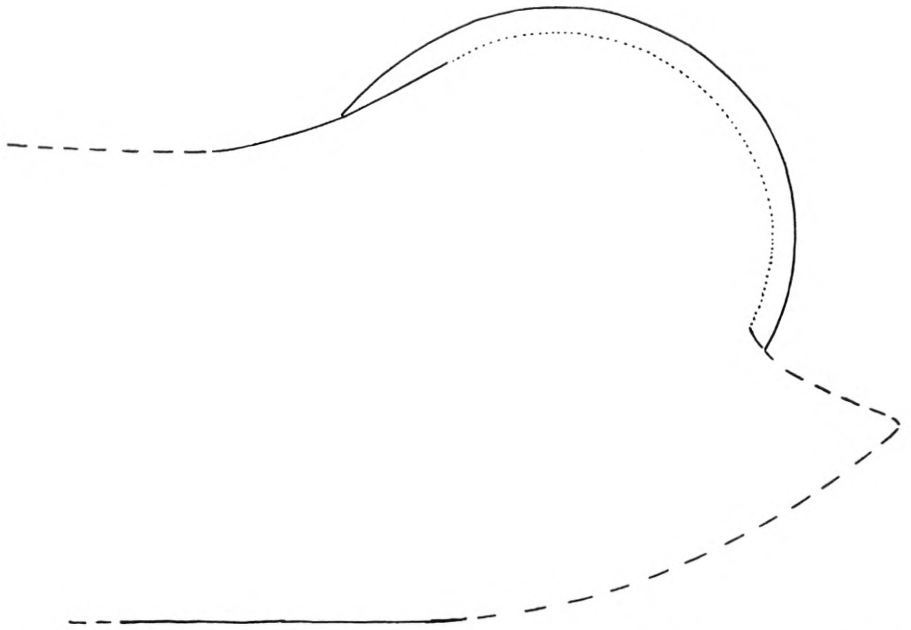

Fig. 8. *Helicoprion ferrieri* HAY. Attempted restoration of the anterior part of the lower jaw. Lateral view. 0.55× nat. size.

appear to have loosened and moved out laterally to the neurocranium (fig. 6 A, B, C). If this assumption is correct, the upper jaw would seem to have been very weak in its anterior portion compared to the lower jaw.

The anterior part of the lower jaw: Just behind the symphyseal region the anterior part of the lower jaw is about $1^1/_2$ times higher than it is wide. Its height increases in the symphyseal region forwards to the midpoint of the symphysis and then gradually decreases, tracing in this distance a circular path along the upper margin of the jaw (fig. 8). The lateral width decreases continuously in a forward direction, although it is always broader ventrally than dorsally (figs. 7, 11).

The prismatic calcifications, which form a continuous layer along and just below the surface of the cartilage, are heavier in the ventral than in the dorsal part of the jaw, except along the symphyseal border (calc. l. l. j. & calc. r. l. j.: pl. IV and fig. 5; r. l. j. & l. l. j.: fig. 7; sym. c.: fig. 9). Here the left and the right branch of the jaw are connected by a strongly calcified cartilage crista (calc. cart. sym.: pl. I; r. calc. cart.: pl. X and XII). This crista runs in a coil forward from the rear point of symphyseal connection of the jaw branches to form a prominent crista—the symphyseal crista—between the two jaw branches along the upper and anterior margin of the symphysis. It then coils backwards and inwards, between the left and the right jaw branches, and terminates at a point just caudally to the vertical diagonal axis of the symphyseal region, leaving an opening on the ventral side between the

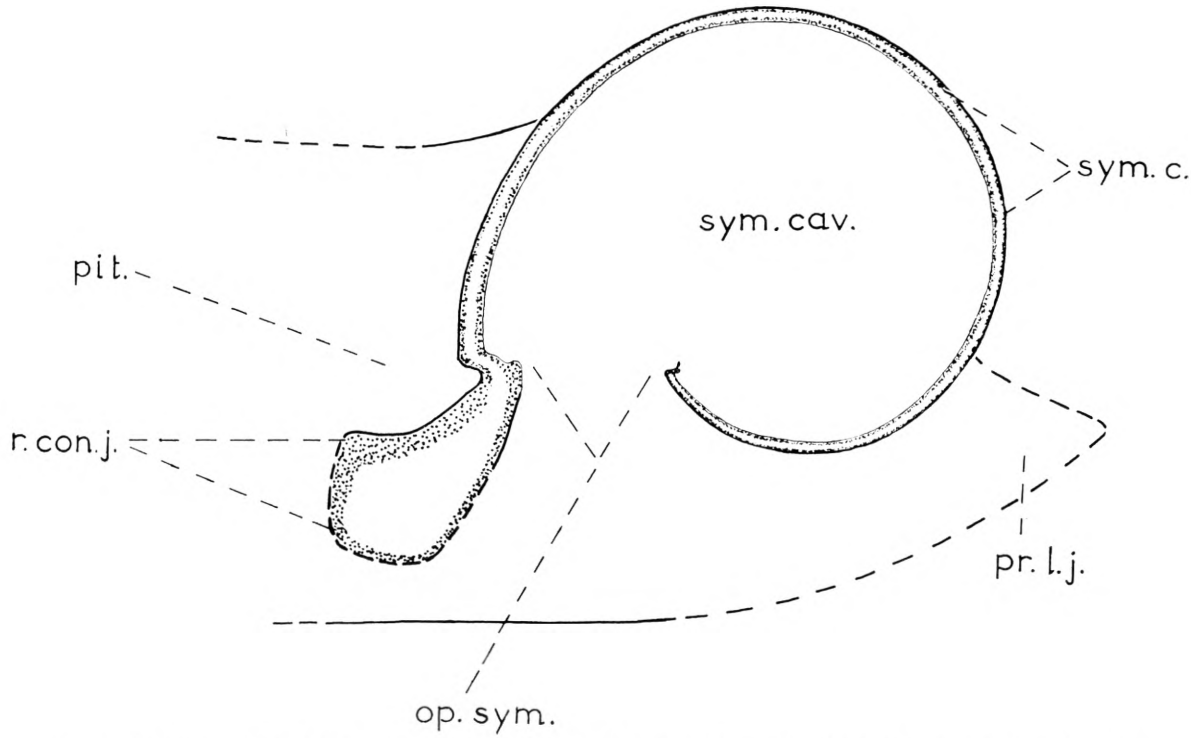


Fig. 9. *Helicoprion ferrieri* Hay. Attempted restoration of a median section through the symphyseal region of the lower jaw. The strong calcifications of the symphyseal crista (sym. c.) and the rear connection (r. con. j.) between the two jaw branches are indicated by dense shading. 0.55× nat. size. op. sym.: the opening through which the older parts of the tooth-spiral enter the symphyseal cavity (sym. cav.). pit.: the pit where the new tooth-members are formed. pr. l. j.: the anterior process of the left half of the lower jaw.

termination of the crista and the rear connection of the jaw branches (op. sym.: figs. 9 and 11).

The upper anterior margins of the two jaw branches follow the symphyseal crista to a level just below the middle horizontal plane of the symphyseal region. Ventrally to this plane each jaw branch is prolongated as nearly triangular, broad based, but comparatively thin processes forming the termination of the jaw (pr. l. j.: pl. I, and fig. 9; and fig. 11).

The ventral border of the symphyseal region is formed by the ventral borders of the two jaw branches which are not here in mutual connection (figs. 7, 9, 11).

This unique construction leaves a cavity in the interior of the symphyseal region within the symphyseal crista. This cavity, the lateral walls of which are formed by the left and the right jaw branch (calc. cart. l. l. j. & calc. cart. r. l. j.: pl. I–III, and fig. 3), contains completely enclosed the older volutions of the tooth-spiral (sym. cav.: fig. 9) which entered it through the opening situated on the ventral side (op. sym.: figs. 9 and 11). In fact the tooth-crowns of the older half part of the last formed volution are already, before entering the symphyseal cavity, protected laterally

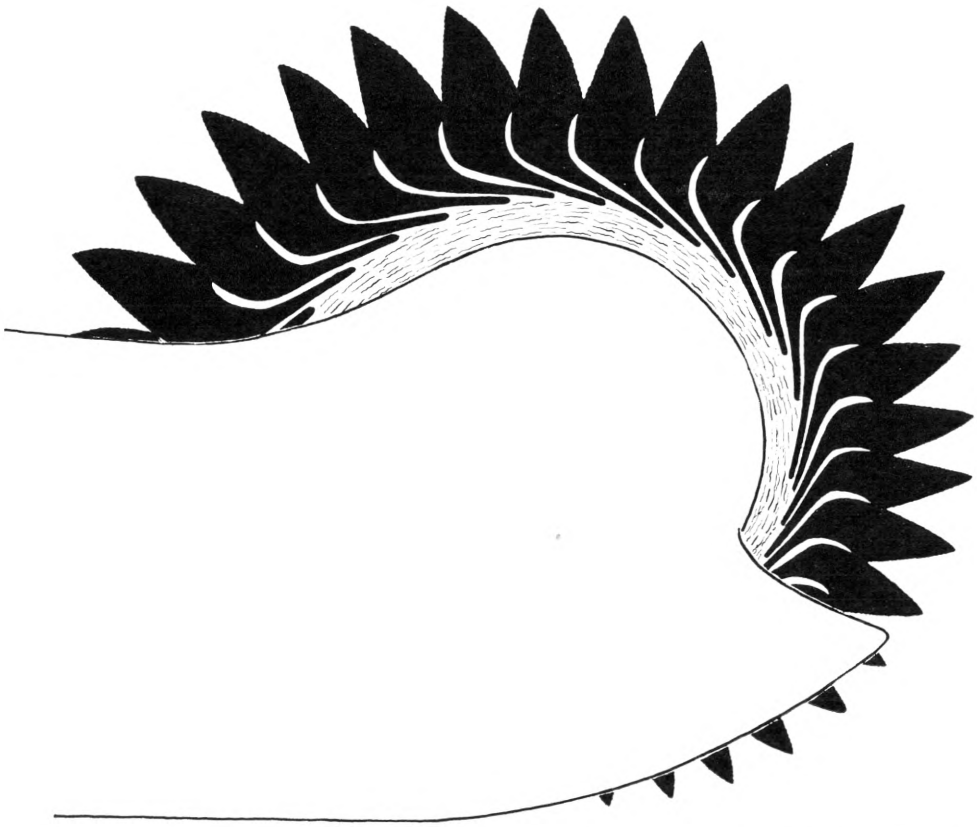

Fig. 10. *Helicoprion ferrieri* HAY: Attempted restoration of the anterior part of the lower jaw and the exposed parts of the tooth-spiral. Lateral view. 0.55×nat. size.

by the anterior processes and the ventral parts of the jaw branches, as shown on fig. 10 and pl. I.

At the lingual end of the symphysis is situated the pit, where the development of the new teeth takes place as normally in the Elasmobranchs.

Remarks: The unusual form of the symphyseal region with the connection between the jaw branches restricted to, and formed by, the symphyseal crista, seems to indicate that the elements present in this region at the embryo stage, during ontogeny developed in a rather special manner.

The symphyseal connection of the Meckelian cartilages is situated caudally to their anterior termination. The connection between them is formed by a coiled, strongly calcified cartilage element which laterally is fused with the Meckelian cartilages. However, it does not fuse their median surfaces completely together but only a part of their dorsal and anterior edges and also a part of their median surfaces, leaving a cavity inside the symphysis. This cavity communicates with the surroundings by an opening on the ventral side of the symphyseal region.

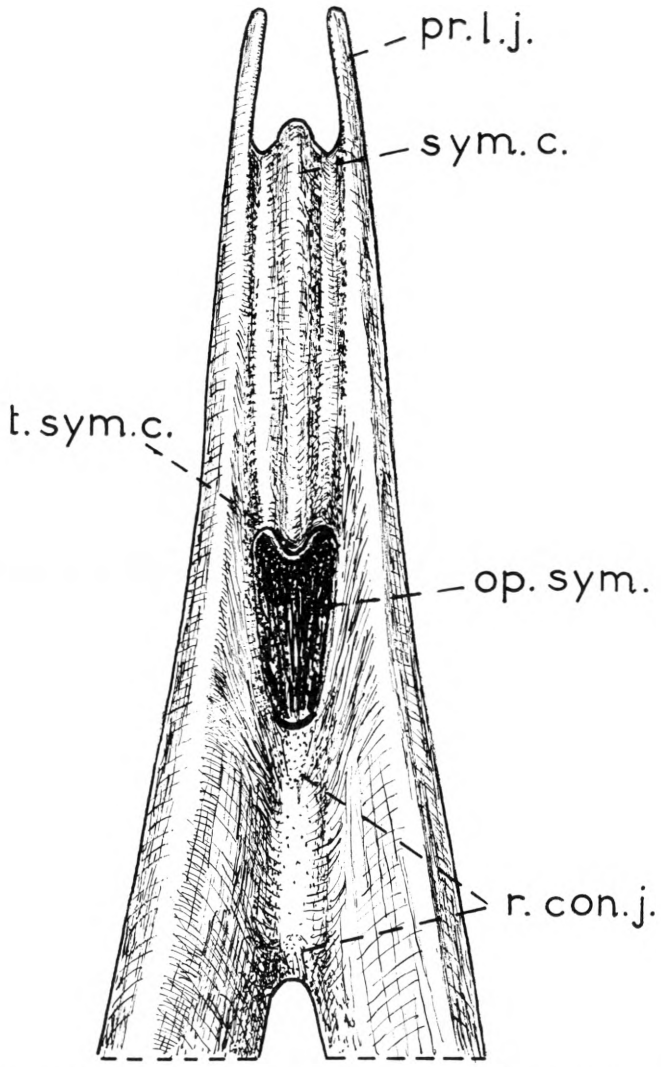


Fig. 11. *Helicoprion ferrieri* HAY: Attempted restoration of the anterior part of the lower jaw in ventral view. The tooth-spiral is omitted to show the symphyseal crista (sym. c.), and the entrance to the symphyseal cavity (op. sym.). 0.7×nat. size. pr. l. j.: the anterior process of the left branch of the lower jaw. r. con. j.: the rear connection of the jaw branches. t. sym. c.: the termination of the symphyseal crista.

These facts seems to suggest that the coiled cartilage element—the symphyseal crista—represents an independantly formed cartilage structure, which during the ontogenetic development fused to the Meckelian cartilages.

A similar position in relation to the anterior end of the Meckelian cartilages is characteristic for the Basimandibular element known in the embryos of several recent Elasmobranchs (HOLMGREN 1940, *Etmopterus* 34 mm stage, p. 132 fig. 90; 43 mm

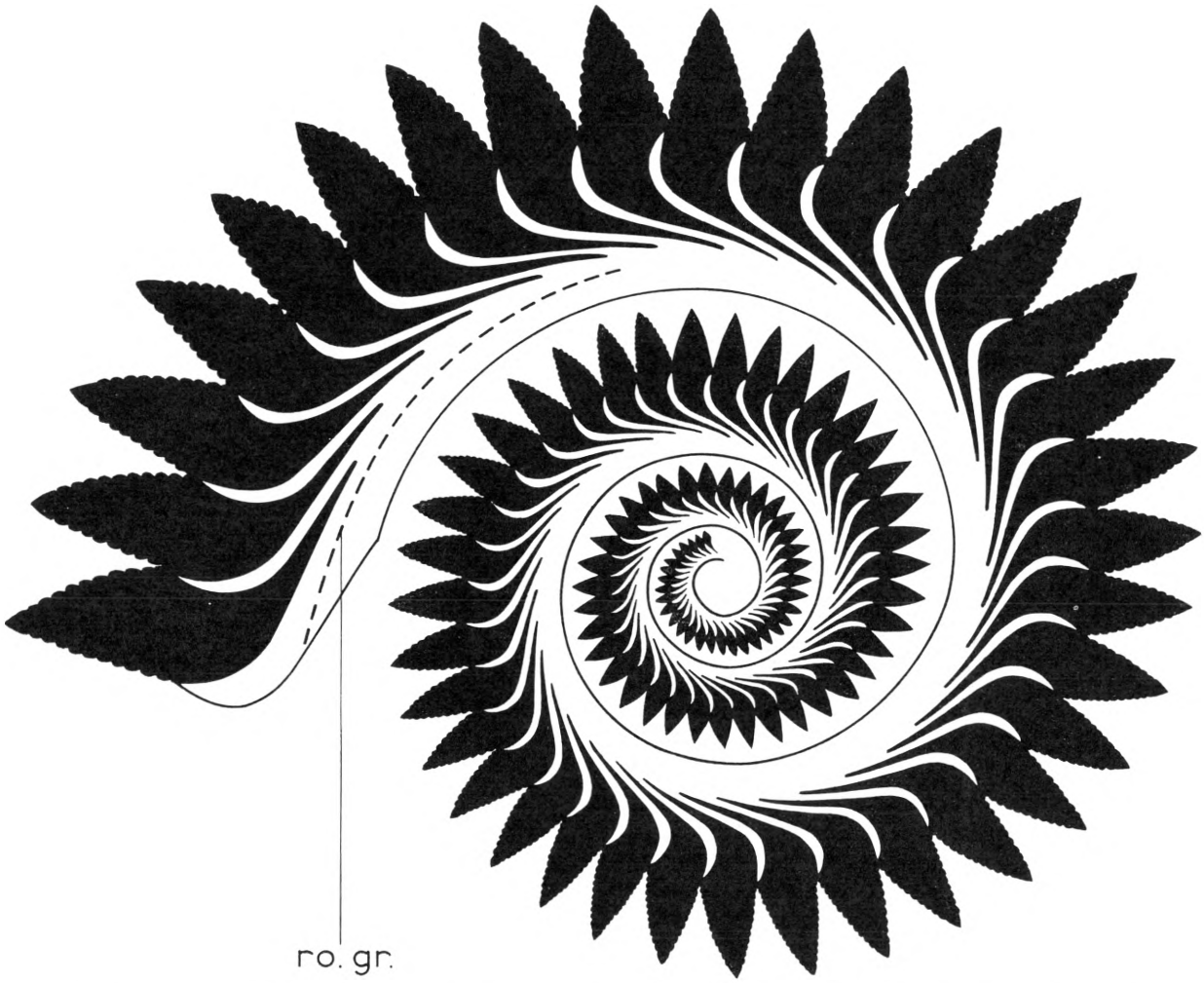


Fig. 12. *Helicoprion ferrieri* HAY: Restoration of the tooth-spiral in Idaho no. 4. The oldest part, the juvenile tooth-arch, is omitted. ro. gr.: the upper limitation of the youngest part of the groove on the underside of the tooth-spiral. 0.7 × nat. size.

stage, p. 139 fig. 96. *Squalus* 38 mm stage, p. 106 figs. 56 & 64; 68 mm stage, p. 113 figs. 68 & 78). It is therefore probable that the symphyseal crista as it occurs in Helicoprion represents a special development of the Basimandibular.

With regard to this discussion the conditions found in the recent Elasmobranch *Lamiostoma belyaevi* GLÜCKMAN may be of some value. In this form an elongated visceral element is present, the posterior end of which articulates with the distal end of the Ceratohyals, while its anterior part is located between the anterior ends of the branches of the lower jaw (GLÜCKMAN 1964 p. 105, fig. 32).

It is clear that this element is of compound origin and represents a Basihyal which is fused distally with a well developed Basimandibular, although no observable traces show the original presence of two elements.

## Dentition.

The symphyseal tooth-spiral: In the description of the tooth-spiral and the individual tooth-crowns of this species by HAY (1907 p. 22, 109 pp. 52–56) many points concerning the shape, the superficial structure, and their mutual relations are excellently described and discussed. However, the new material treated in this paper contributes further detail and justifies the re-description given below.

The dimensions of the same volution in the tooth-spiral vary to some degree from one specimen to another as shown by a comparison of Idaho no. 4 and Idaho mrk. "Thiel P & MP" (pl. I–III & pl. X–XII). The width of the former at $2^3/_4$ volution is 16.5 cm against 18.8 cm in the latter. For the most complete specimen available to HAY (1909 pl. 15) the equivalent measurement is 15.6 cm. However, these circumstances do not appear to affect the mutual relative dimensions within different tooth-spirals at particular stages of growth.

With regard to the number of volutions present in a tooth-spiral, this is naturally mainly dependant upon the lifetime of the particular individual concerned, although the possibility of some individuals producing teeth more or less rapidly than others is to be taken into consideration. In the two specimens Idaho no. 4 and Idaho mrk. "Thiel P & MP", which are the best preserved in the collection at hand, there are $3^3/_4$ volutions, although the oldest part of the latter specimen is not preserved. The complete number of tooth-crowns in Idaho no. 4 is 118 plus the juvenile tooth-arch, and in Idaho mrk. "Thiel P & MP" at least 122, and possibly 124.

The tooth-spiral consists of a number of enamel covered individual parts, which at their bases are attached to a coiled, completely undivided structure. The former has usually been referred to by previous authors as the teeth or the denticles, and the latter has generally been termed the shaft. However, both these terms are in the authors view inadequate, and they have been replaced in the present paper by the terms "the tooth-crowns " and "the compound root".

The oldest part of the tooth-spiral occupies about $^1/_5$ of a volution (pl. V fig. 1–2; pl. VIII: r. em. cr.; fig. 13). It has the form of an enamel covered curved rod and can most adequately be termed "the juvenile tooth-arch". Its crenulation occuring along the upper margin is very delicate but is more coarse in the youngest portion where it to some degree resembles the crenulation on the cutting edge of the smaller tooth-crowns. The juvenile tooth-arch is well preserved in Idaho no. 4, and a part of it is also seen in Idaho no. 1. It is nearly as broad ventrally as it is high, and in section it shows a sigmoidal curving of the surface from the ventral border to the upper cutting edge.

The first formed individual tooth-crowns occur immediately after the juvenile tooth-arch (pl. V fig. 1–2, fig. 13).

Fig. 13. *Helicoprion ferrieri* HAY. The oldest part of the tooth-spiral, the juvenile tooth-arch, in the form of an enamel covered curved rod crenulated along a part of the upper margin, followed by the first formed individual tooth-crowns. 6.3×nat. size. Idaho no. 4.

In the first 6 tooth-crowns there is a discernable angle between the lower and the upper portion of the front cutting edge, but it becomes rapidly inconspicious in later tooth-crowns, and is not apparent after the first half of the first volution. The rear edge of the cutting blades is slightly concave. The lateral tapering parts, which are only slightly bent forwards, are relative short and strong, and are somewhat concave along the front and rear margins (fig. 13).

The height of the cutting blades increases gradually, and in the middle part of the first volution is nearly half the total height of the tooth-spiral. The cutting edges, which on the first tooth-crowns are smooth, show at this stage of growth a feeble crenulation, and both edges are convex. The lateral tapering parts are slender and directed forwards, and terminate at a point below the centre of the next tooth (fig. 14).

Fig. 14. *Helicoprion ferrieri* HAY. Three tooth-crowns from the middle part of the first volution of the tooth-spiral. 5.2×nat. size. Idaho no. 4.

In the second volution the tooth-crowns gradually acquire a shape which can be regarded as the mature form. Here they have strong and pointed cutting blades with crenulated convex cutting edges, and long and slender tapering lateral parts in which

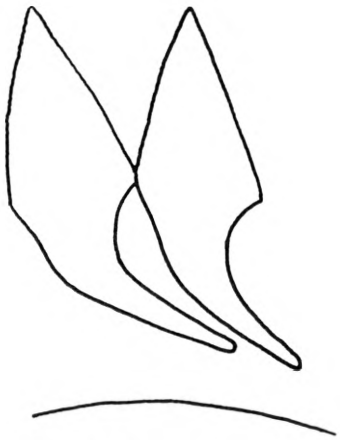

Fig. 15. *Helicoprion ferrieri* HAY. Two tooth-crowns from the last part of the first half of the second volution of the tooth-spiral. 5× nat. size. Idaho no. 4.

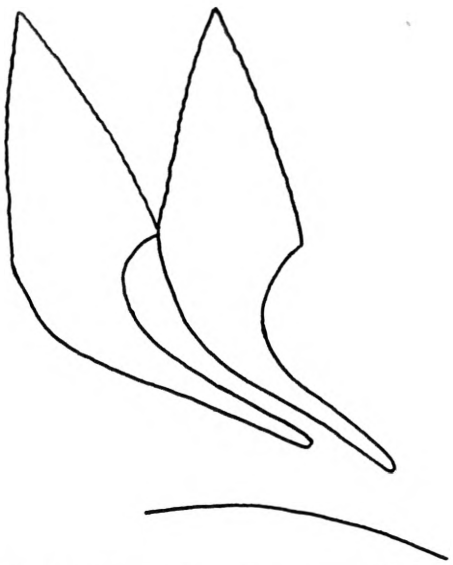

Fig. 16. *Helicoprion ferrieri* HAY. Two tooth-crowns from the middle part of the second half of the second volution of the tooth-spiral. 4.5× nat. size. Idaho no. 4.

"a middle portion" and "a narrowed base" can be distinguished (fig. 15 & 16 and pl. I, V fig. 1, XII, XIII, XV fig. 1–2; terminology after WHEELER 1939). The middle portions posses strongly concave margins in the tooth-crowns of the oldest part of the second volution, while in the younger part the rear margins are almost straight. The narrowed bases become gradually longer and more slender. In the older part of the second volution the narrowed bases terminate at a point below the rear margin of the second tooth-crown in front, but in the younger part the termination point is situated beneath the centre of that tooth-crown (fig. 15 & 16; pls.: op. cit.).

All three portions of the tooth-crowns, i. e. the cutting blade, the middle portion, and the narrowed base, are clearly distinguished in the tooth-crowns of the third volution (fig. 17, pl. I–III). The pointed cutting blades possess convex cutting edges of which the front edge is the most strongly curved, and both edges show a pronounced crenulation. The middle portions have concave margins. The narrowed bases are long and slender, directed towards the older parts of the tooth-spiral and terminate at a point below the centre of the second tooth-crown in front.

The fourth volution of the tooth-spiral is characterised by tooth-crowns with strong and pointed cutting blades with a coarse crenulation along the cutting edges. The front cutting edges are the most strongly convex (fig. 18 & 19; pl. I–III, VIII–X). The middle portions have different characteristics; the front margin is always concave, but the rear margin can in the older parts be slightly concave or straight, and in tne younger parts straight or even a little convex. The narrowed bases are long and very

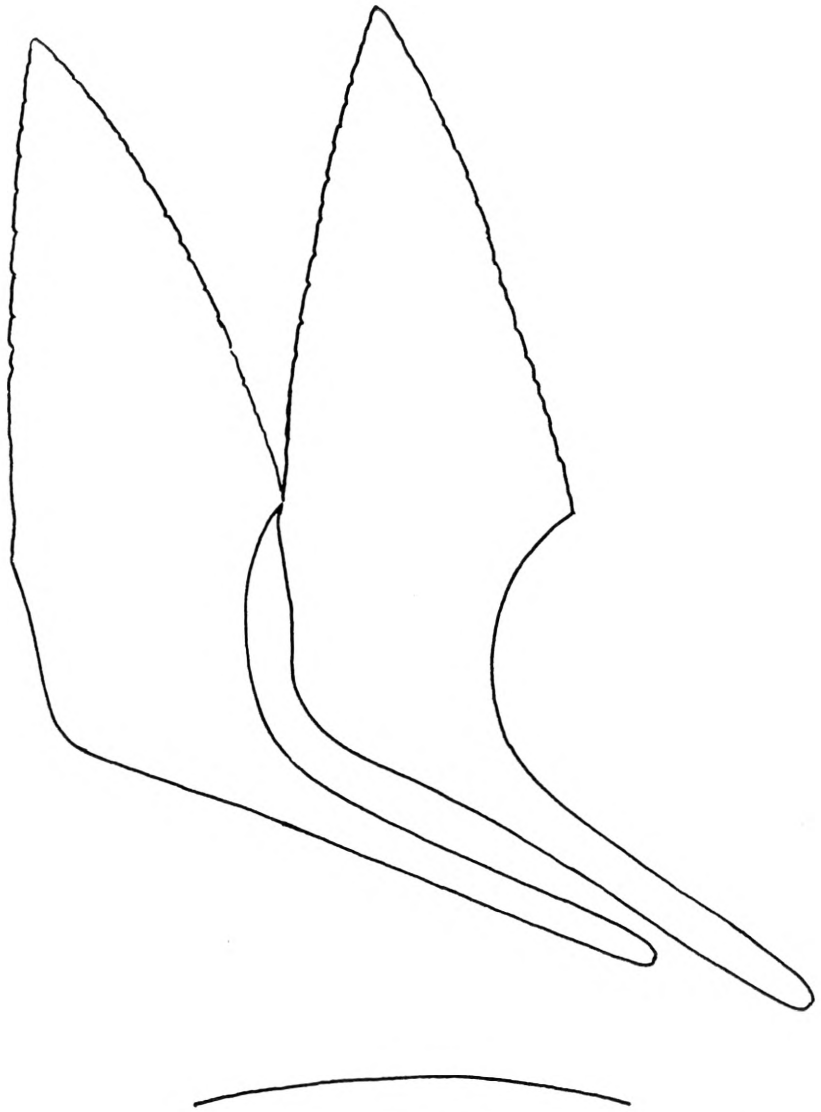

Fig. 17. *Helicoprion ferrieri* HAY. Two tooth-crowns from the middle part of the second half of the third volution. 5× nat. size. Idaho no. 4.

slender compared to the other parts of the tooth-crown. Their point of termination is situated below the front margin of the second tooth-crown in front.

The tooth-crowns are only in contact at the base of the cutting blade, where the front lower corner of the cutting edge fits into a small recess at the lower point of the cutting edge of the tooth-crown in front (pl. I; pl. X fig. 1).

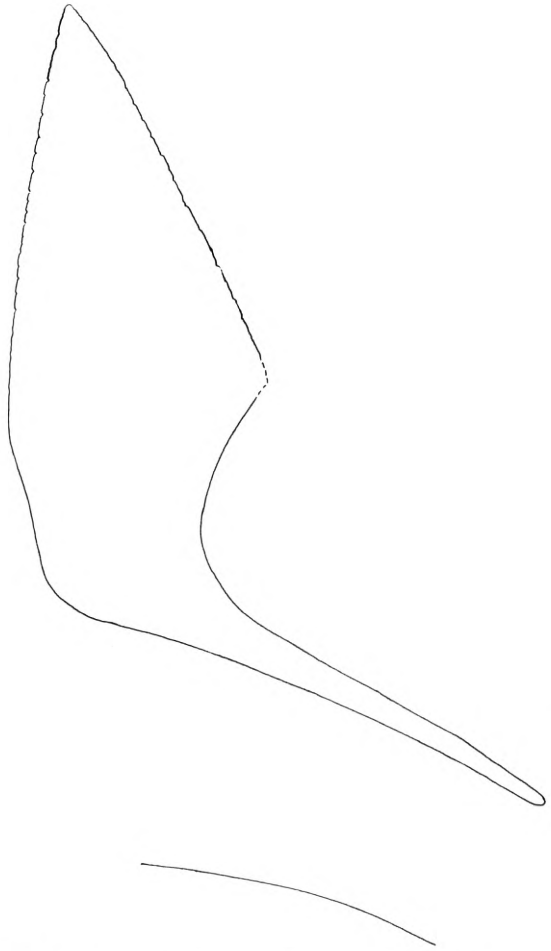

Fig. 18. *Helicoprion ferrieri* HAY. Tooth-crown from the middle of the first half part of the fourth volution of the tooth-spiral. 2.4× nat. size. Idaho no. 4.

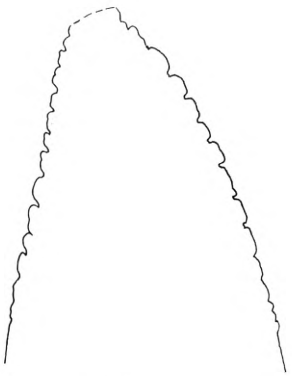

Fig. 19. *Helicoprion ferrieri* HAY. A cutting blade with a rather coarse crenulation from one of the largest tooth-crowns of the fourth volution. 2.1× nat. size. Idaho no. 4.

Originally the tooth-crowns were covered by a layer of enamel-like hard tissue, but in only one specimen, Idaho no. 4, are a few small traces of this layer still preserved. It is impossible, therefore, to state the nature of the original ornamentation of the surface with any certainty. However, as HAY (1909 p. 55) has observed, there may have been a number of narrow ridges radiating from the apex (pl. I & III). The crenulation on the cutting edges also contributes to the surface sculpture, especially in the larger tooth-crowns (pl. IX fig. 1–2).

The tooth-crowns are supported by the solid, undivided and coiled compound root, which has developed through a complete fusion of the tooth-roots. This fusion is already observable in the development of a new tooth (y. t.: pl. I; y. p. t. sp.:

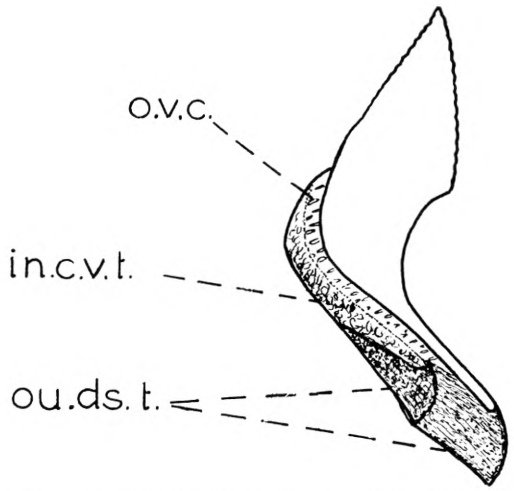


Fig. 20 a. *Helicoprion ferrieri* HAY. Reconstruction of a single complete tooth. in. c. v. t.: inner core of strongly vascular hard tissue of the root. ou. ds. t.: the outer denser hard tissue of the root. o. v. c.: openings for vascular canals on the area exposed between the middle portions and the narrowed bases of successive teeth. 0.7× nat. size. Based on Idaho no. 4.

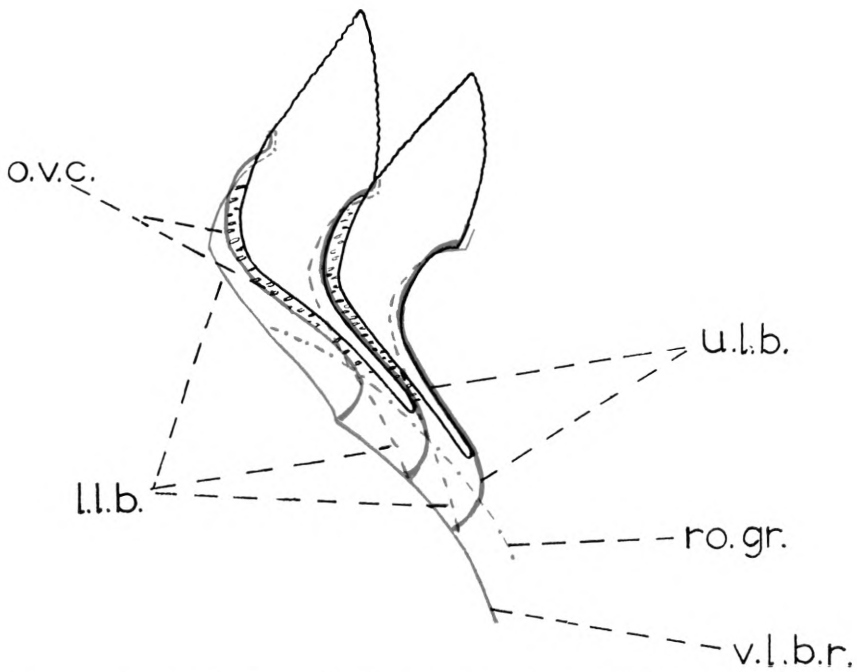


Fig. 20 b. *Helicoprion ferrieri* HAY. Reconstruction of the dividing lines between the roots of two successive teeth, to show the limitation between the root-parts. l. l. b.: the green lines show the lower lingual and labial borders of the roots. o. v. c.: openings of vascular canals. ro. gr.: line showing the location of the dorsal wall of the groove on the ventral side of the roots. u. l. b.: the red lines show the upper lingual and labial borders between the successive teeth. v. l. b. r.: ventro-lateral border of the roots. 0.7× nat. size. Based on Idaho no. 4.

pl. X). The differences which are seen in the structure of the hard tissue below the three last formed tooth-crowns (pl. I), may however, to a certain degree, reflect the original limitation of these members of the tooth-spiral.

These observations, and the fact that the last formed tooth clearly shows the rear border of its root (y. t.: pl. I), have been employed in the reconstruction of a single complete tooth and of two successive teeth (fig. 20 a–b).

The surface of the parts of the compound root situated between the middle portions and the narrowed bases of successive tooth-crowns exhibits a large number of openings of vascular canals (o. v. c.: pl. II–III). These openings are oval and are larger than the openings on the surface of the compound root ventrally to the narrowed bases of the tooth-crowns, where the hard tissue lining them has produced fine ridges running nearly parallel to the lower border of the compound root (a. rdg.: pl. II–III).

On the ventral side of the compound root occurs a prominent longitudinal groove with a smooth surface. The section through the tooth-spiral of fig. 24 b shows the outlines of the groove, which differs in some respects from that figured by HAY (1909, p. 56 fig. 7). In this groove the symphyseal crista of the lower jaw is situated (see pp. 20–21). The lateral parts of the compound root between and below the tooth-crowns were covered only by soft tissue.

A notable feature of the tooth-spirals of this species is that none of the specimens show traces of wear on the tooth-crowns, or other evidence of use or destruction during the life of the animals.

The lateral teeth: In specimen Idaho no. 4 some small tooth-like elements are to be seen. They are located in an area below and just behind the rear part of the rostral region of the neurocranium (dnt.: pl. I; pl. VII fig. 2).

Some of the elements are seen still to be lying in mutual positions and forming parts of rows (r. dnt.: pl. VII fig. 2).

In the present state of preservation the elements are seen in profile or longitudinal section (ct. dnt.: pl. VII fig. 2), except one element which exhibits its lower surface (rt. dnt.: pl. VII fig. 2).

The elements are nearly rectangular in shape as seen in profile or longitudinal section. At the upper and the lower surfaces a layer of dense hard tissue is seen. One of the layers is much heavier than the other, and possibly represents the base of the root. Between these layers the hard tissue is formed as a coarse mesh-work connecting the upper and lower denser layers. The openings in the mesh-work clearly represent openings for the vascular canals (fig. 21 A & B).

It has not been possible to investigate the hard tissue of these elements in thin section, but from the visible structure it may be suggested that the inner part consists of osteodentine, capped by a layer of pallial-dentine and coated by a thin outer layer of an enameloid substance.

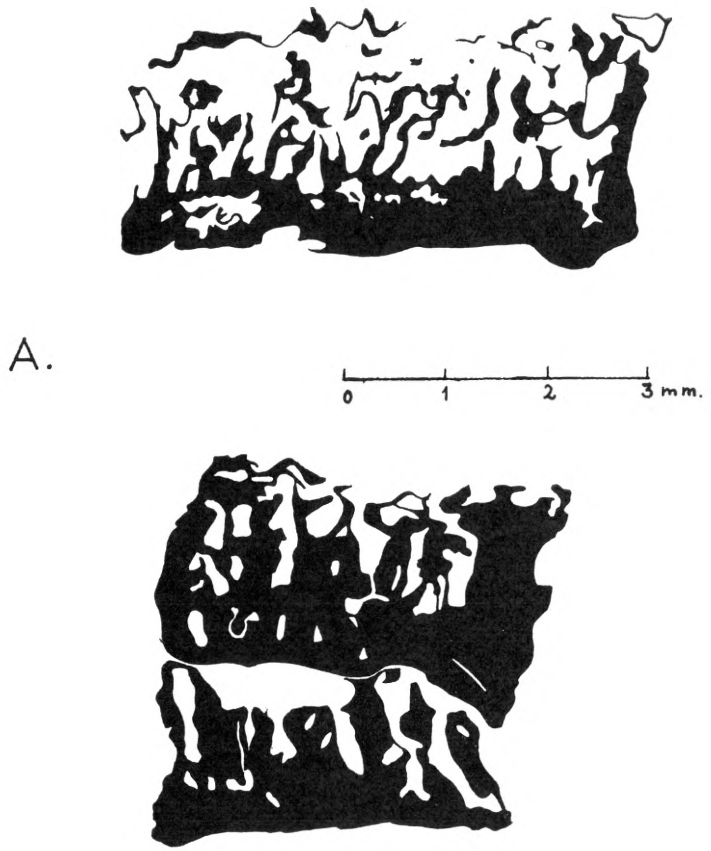


Fig. 21. *Helicoprion ferrieri* HAY. Small lateral teeth from the anterior part of the upper jaw. Lateral view. A: Isolated tooth. B: Two teeth in natural mutual position. 13× nat. size. Idaho no. 4.

It is not certain whether the elements as seen from above were rectangular or rhombic. The nature of their upper surface is not known in detail, but it may be regarded as a crushing surface.

The small elements are interpreted as part of a dentition situated in the anterior part of the upper jaw. No other traces of a lateral dentition have been found in connection with the remainder of the jaws. This may be due to the fact that only remains of the anterior part of the neurocranium and the jaws are preserved. However, it is more likely that it reflects a strong reduction of all other parts of the dentition.

The smallest of the elements is 4.1 mm in length and 1.2 mm high, and the largest is 5.2 mm long and 2.6 mm high.

### Scale covering.

None of the specimens show any traces of a scale covering. Consequently it is proposed that *Helicoprion ferrieri* at least on the anterior part of the head, was completely devoid of scales.

### Histological notes on the tooth-spiral.

The histological structure of the hard tissues which compose the tooth-spiral was treated by KARPINSKY (1899 pp. 44–61, pl. III–IV). His observations were completely verified by TEICHERT (1940 pp. 145–147), although the latter was unable to add further detail on account of the state of preservation of the Australian material.

In the present work only very little can be added to the excellent description by KARPINSKY, the principal features of which are as follows:

1) An inner core of strongly vascular tissue, the so-called "schwammiges Vasodentin", occupies the central part of the compound root, in the centre of which can be observed one, or a pair, of prominent canals. The canals are not distinguishable in the smaller parts of the spiral. The vascular tissue is devoid of cell-spaces, but is concentrically laminated around the vascular canals and penetrated by dentinal tubes.
2) Surrounding the "schwammiges Vasodentin" is a denser type of vascular tissue with smaller vascular canals, termed "faserigen Vasodentin". In its upper part is situated a very prominent longitudinal canal, which runs through the complete extent of the spiral. In polarized light a concentric lamination is observed and dentinal tubes are seen penetrating the surface of the vascular canals at right angles.
3) The interior of the tooth-crowns is occupied by strongly vascular tissue, in the centre of which strong nutritive canals run out nearly at right angles to the spiral. These canals send out smaller dichotomously branching canals, which bend towards and nearly at right-angles to the surface of the tooth-crown terminating just below the surface. They form the layer called "Röhrenvasodentin" or "Parallelröhrendentin" in the periferal parts of the tooth-crown. Dentinal tubes can be observed, running out nearly at right-angles into the hard tissue surrounding the parallel canals, as well as from their termination below the superficial layer of enamel-like hard tissue.
4) An outer layer of comparatively thin enamel-like hard tissue.

This description shows clearly that the tooth-spiral is composed of osteodentine comprising denteons (ØRVIG 1965), penetrated by dentinal tubes, and with an interdenteonal bony substance which lacks bone-cells. Furthermore the tooth-crowns are coated with a thin layer of shiny hard tissue, which, at least in part, may represent an enameloid substance (ØRVIG 1965).

With respect to the observations which can be made on the material of the present study, the histological composition of the tooth-spiral of *Helicoprion ferrieri*

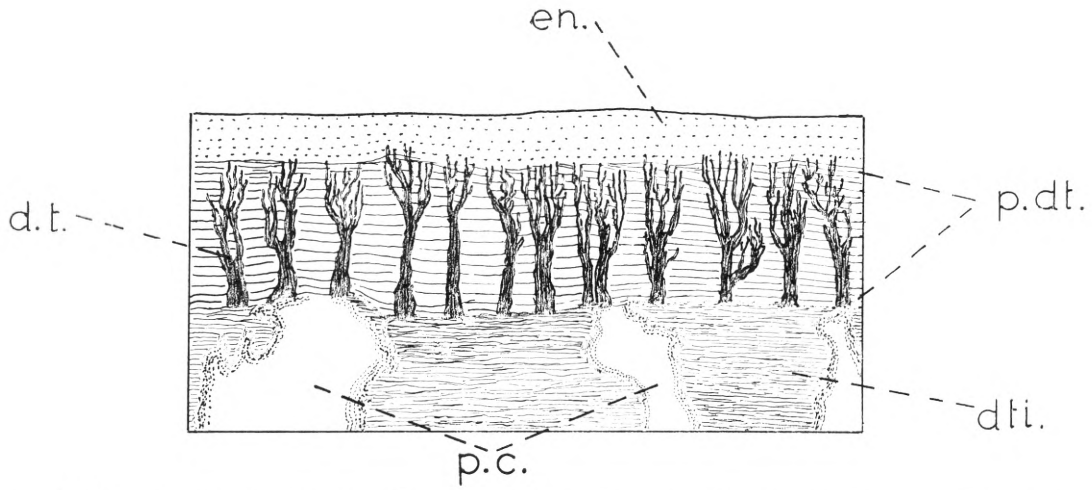


Fig. 22. *Helicoprion ferrieri* HAY. Simplified sketch of a section through the superficial part of a tooth-crown, showing the thin layer of enameloid substance (en.), the layer of pallial dentine (p. dt.) with dentinal tubes (d. t.), the osteodentine (dti.), and the pulp cavities (p. c.). ×580. Idaho no. 4.

Fig. 23. *Helicoprion ferrieri* HAY. Simplified sketch of a vertical orientated section through a part of the compound root, showing the circumvascular denteons (cv. dti. o.) and the interdenteonal bone trabecles (int. s.). v. c.: vascular canals. ×580. Idaho no. 4.

is identical in detail with that described for *Helicoprion bessonowi*. The root and the interior of the tooth-crowns show osteodentine (dti.: fig. 22; pl. VI fig. 1–3) with denteons (c. v. dti. o.: fig. 23; pl. VI fig. 4) surrounding the vascular canals and the pulp cavities (v. c. & p. c.: fig. 22 & 23). The interdenteonal bony substance can also be observed (int. s.: fig. 23). The dentinal tubes can be seen penetrating the denteons surrounding the vascular canals of the root; no traces of them are found in the tooth-crowns where the denteons are badly preserved.

The outer layer, coating the osteodentine in the tooth-crowns, is penetrated by very densely set, strongly branching dentinal tubes. These are more widely spaced in their proximal part (d. t.: fig. 22; pl. VI fig. 1–2). A comparatively thin superfical part of the outer layer is devoid of dentinal tubes. This part is thickest in the area around the cutting edges. Thus the outer part of the tooth-crown of *Helicoprion ferrieri*, as is also the case with *Helicoprion bessonowi*, comprises two distinct layers: an inner layer of pallial dentine (p. dt.: fig. 22; pl. VI fig. 1–2) and an outer thinner layer of enameloid substance (en.: ibid).

The pulp cavities in the most superficial parts of the osteodentine are about 0.06 mm wide; the thickness of the layer composed of the enameloid substance and the pallial dentine is 0.09–0.1 mm, and the diameter of the proximal parts of the dentinal tubes situated in the pallial dentine is about 0.003 mm.

## Comparisons and affinities.

The tooth-spiral of *Helicoprion ferrieri* has previously been compared with that of *Helicoprion bessonowi, Helicoprion nevadensis, Helicoprion sierrensis* and *Helicoprion davisii* in the discussions of Hay (1909), Karpinsky (1912), Wheeler (1939) and Teichert (1940).

Their principal conclusions can be summarised as follows:

1) The apical angle of the tooth-crowns is smaller in *Helicoprion ferrieri* than in *Helicoprion bessonowi, Helicoprion davisii* and *Helicoprion nevadensis*, but about the same as in *Helicoprion sierrensis*.
2) The height of the free lateral lower portion of the compound root (= the shaft, Wheeler, Teichert) is greater in *Helicoprion ferrieri* than in *Helicoprion bessonowi, Helicoprion nevadensis* and *Helicoprion sierrensis*. In *Helicoprion ferrieri* it is equal to about $^1/_5$ to $^1/_7$ of the total height of a volution, while in *Helicoprion nevadensis* and *Helicoprion sierrensis* it is nearly $^1/_{10}$ and in *Helicoprion bessonowi* about $^1/_{15}$ of the total height. It differs also from the equivalent dimension in *Helicoprion davisii*. It most closely resembles the condition found in the Japanese specimen described by Yabe (1903) under the name *Helicoprion bessonowi*.
3) Hay regarded the American species as representing a particular genus *Lissoprion*, but this was rejected by Karpinsky whose statement has since been confirmed by other workers.

4) *Helicoprion ferrieri, Helicoprion sierrensis, Helicoprion nevadensis, Helicoprion davisii* and *Helicoprion bessonowi* apparently form one group of closely allied species.

Several further points can be added to these conclusions concerning the tooth-spiral in *Helicoprion ferrieri* as a result of the present investigation. In *Helicoprion ferrieri* the height of the middle portions of the tooth-crowns is smaller than in *Helicoprion bessonowi* and *Helicoprion nevadensis,* as well as in the new species *Helicoprion ergasaminon* described below. It more closely resembles the dimensions found in *Helicoprion davisii* and *Helicoprion sierrensis,* of which the latter may be rather closely related to *Helicoprion ferrieri.*

The groove on the ventral side of the compound root (fig. 24 b) differs characteristically in shape and in depth from that described and figured for *Helicoprion bessonowi* (KARPINSKY 1899, pp. 37–38, fig. 30–34) and for *Helicoprion davisii* (TEICHERT 1940, pl. 22 fig. 3).

Concerning the endoskeletal remains found in *Helicoprion ferrieri* and in *Helicoprion ergasaminon* n. sp., as described in the present paper, many details of the structure are readily comparable to those described by KARPINSKY for *Helicoprion bessonowi,* thus representing in this form the remains of the symphyseal region of the lower jaw. The so-called "besondern Gefässes" (KARPINSKY 1899, pp. 76–79, fig. 57) represents cartilage-calcifications, as shown by OBRUCHEV (1952, p. 279). These calcifications are located inside the groove on the ventral side of the tooth-spiral and might be regarded as the remains of the symphyseal crista, as are those found in *Helicoprion ferrieri* and *Helicoprion ergasaminon.*

With regard to the layers of cartilage-calcifications preserved laterally to the tooth-spiral on KARPINSKY's specimen no. 1 (1899, pp. 65–76, fig. 47), their relation to the spiral is exactly the same as found in the American material, thus representing the calcifications from the walls of the symphyseal cavity formed by the left and the right lower jaw. The suggestion by KARPINSKY and OBRUCHEV that these elements are forward and upward coiled prolongations of the palatoquadrates has thus been proved to be incorrect.

The anterior part of the lower jaw in *Helicoprion ferrieri* differs from that found in *Helicoprion ergasaminon* n. sp. (p. 40) by the presence of prolongations of the two branches of the jaw rostrally to the symphysis.

## Diagnosis:

The neurocranium consists of cartilage with an inner and an outer layer of prismatic calcifications lining the cranial cavity and the outer surface. A rostrum consisting of at least one strong rod of cartilage situated ventrally in the median line is present. The palatoquadrates are independent elements attached to the neurocranium, possibly in an amphistylic or a hyostylic manner. The lower jaw, consisting of calcified cartilage, possesses a long, high but narrow symphyseal portion,

formed by a spiral-coiled crista lying between the two branches of the jaw which terminates rostrally to the symphysis. Between the branches of the jaw and inside the symphyseal crista is situated a cavity, the symphyseal cavity, which contains the older parts of the symphyseal tooth-spiral. The dentition comprises a strongly developed symphyseal tooth-spiral situated in the lower jaw, and a few rather small crushing teeth in rows on the anterior part of the upper jaw. The symphyseal tooth-spiral is formed in its oldest part as a crenulated curved rod, the juvenile tooth-arch, about $^1/_3$ of a volution long, while the rest of the tooth-spiral consists of isolated tooth-crowns the root-parts of which are completely fused. On the ventral side of the compound root is situated a broad, deep groove with a smooth surface. The tooth-crowns undergo a gradual change in form from the older to the younger part of the spiral in that their three parts, the proportionally broad cutting blades with crenulated cutting margins, the paired middle portions and the paired narrowed bases, tend gradually to become more clearly defined. Histologically the tooth-spiral consists of a thin outer layer of enameloid substance covering a layer of pallial dentine, both restricted to the tooth-crowns, and an inner core of osteodentine composed of denteons and an interdenteonal bony substance. The anterior part of the head is devoid of scales.

## Dimensions.

The measurements given in the schedules below were assessed as outlined in fig. 24 a & b, a system based on that used by Wheeler (1939) and Teichert (1940), and refined by Nielsen (1952).

The number of tooth-crowns in the volutions of the tooth-spiral is counted in each case from the oldest to the youngest preserved part of the specimen. It is to be noted that the numbers with which the tooth-crowns are designated refer not to the number of the tooth-crown in question in the originally complete spiral, but to its number in the sequence of preserved or partly preserved tooth-crowns in the tooth-

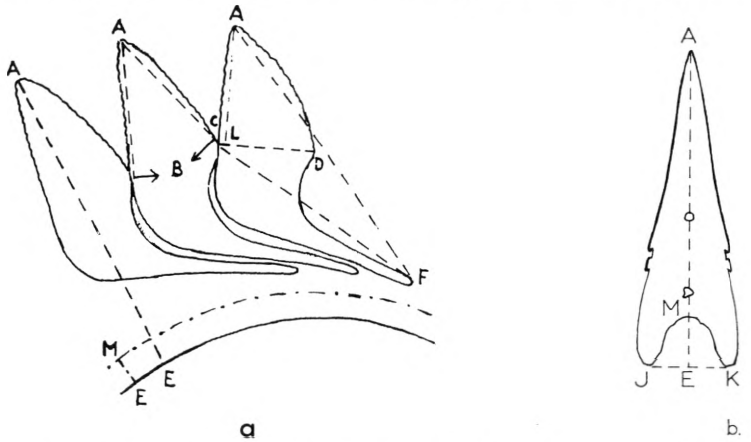


Fig. 24 a & b. The two sketches show the points between which the measurements of the specimens were made. The sketches are based on Idaho no. 4 and Idaho mrk. Thiel "P" and "MP". 0.7× nat. size.

spiral. The symbols S. T. 1–2–3–4 and L. T. 1–2–3–4 are employed in the schedules to indicate the smallest and the largest tooth-crown measured in the first, the second, and subsequent volutions of the tooth-spiral. All linear measurements are given in mm.

Idaho no. 1.

The tooth-spiral consists of $3^1/_6$ volutions, which have the following numbers of tooth-crowns preserved:

1st volution: 26. 2nd volution: 34. 3rd volution: 28. 4th volution: 6.

The greatest width of the preserved part of the spiral measures 170 mm.

| | B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| S. T. 1 (no. 16) | – | 6.5 | 1.5 | – | – | 3.0 | – | – |
| L. T. 1 (no. 26) | – | – | 2.5 | – | – | – | – | 0.75 |
| S. T. 2 (no. 39) | 30° | 12.0 | 3.5 | – | – | 6.5 | – | – |
| L. T. 2 (no. 58) | 35° | 20.0 | 6.5 | – | – | 9.0 | – | 3.0 |
| S. T. 3 (no. 68) | – | – | – | – | 23.0 | – | – | 3.5 |
| L. T. 3 (no. 86) | 40° | 55.0 | 14.5 | – | – | 21.5 | – | 6.2 |
| L. T. 4 (no. 94) | 45° | 56.0 | 17.0 | – | – | 21.5 | – | – |

Idaho no. 2.

Nearly two volutions of the tooth-spiral are preserved, in which the following number of tooth-crowns can be observed:

1st volution: 32. 2nd volution: 28.

The greatest width of the preserved part of the tooth-spiral measures 66 mm.

| | B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| S. T. 1 (no. 11) | 22° | 5.4 | 1.4 | 5.8 | 3.0 | 2.6 | – | – |
| L. T. 1 (no. 29) | 25° | – | 3.0 | – | 6.5 | – | – | – |
| S. T. 2 (no. 43) | 33° | 17.7 | 4.4 | 15.5 | 10.0 | 7.2 | – | – |
| L. T. 2 (no. 56) | 30° | – | 6.0 | – | 6.0 | – | – | 1.5 |

Idaho no. 3.

The specimen shows parts of two volutions, probably the second and the third, in which the following numbers of tooth-crowns are present:

Oldest volution: 11. Youngest volution: 3.

The greatest width of the oldest volution measures 52 mm and the part preserved of the youngest measures 45 mm.

Tooth-crown no. 7 in the oldest volution has the following dimensions:

| B | A-E | C-D | A-E | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|
| 25° | 17.0 | 5.0 | 17.0 | – | 8.0 | – | – |

Idaho no. 4.

This specimen is the best preserved in the collection and consists of $3^2/_3$ volutions with a total of 118 tooth-crowns in addition to the juvenile tooth-arch. The latter forms the first $^1/_3$ of the oldest volution. The following numbers of tooth-crowns can be observed:

1st volution: 23 + the juvenile tooth-arch. 2nd volution: 35. 3rd volution: 37. 4th volution: 23.

The greatest width of the tooth-spiral measures 221 mm.

The height of the juvenile tooth-arch is at the anterior end 0.75 mm and at the posterior end 1.4 mm.

| | B | A-E | C-D | A-E | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| S. T. 1 (no. 2) | 27° | 2.8 | 1.3 | 2.2 | 1.2 | 1.0 | – | – |
| L. T. 1 (no. 19) | 29° | 7.4 | 2.3 | 6.5 | 3.5 | 3.3 | – | 0.8 |
| S. T. 2 (no. 36) | 34° | 10.2 | 3.4 | 11.5 | 7.7 | 5.5 | 2.2 | 1.7 |
| L. T. 2 (no. 49) | 32° | 15.9 | 4.3 | 16.8 | 11.3 | 7.6 | 2.4 | 1.8 |
| S. T. 3 (no. 74) | – | 25.8 | – | 26.5 | 20.4 | 11.0 | – | 2.5 |
| L. T. 3 (no. 84) | 32° | 31.0 | 8.5 | 35.0 | 27.2 | 14.0 | 4.8 | 2.6 |
| S. T. 4 (no. 102) | 40° | 49.1 | 13.7 | 51.0 | 38.0 | 19.1 | – | – |
| L. T. 4 (no. 115) | 45° | – | 18.8 | – | – | 24.0 | – | – |

Idaho no. 7.

A part of a tooth-spiral, probably belonging to the third volution, is preserved and represented by 9 tooth-crowns partially hidden in the matrix.

The greatest width of the part visible measures 63 mm. No other dimensions can be given.

Idaho no. 9.

Parts of $2^1/_2$ volutions of the tooth-spiral are preserved, mostly as a cast. The following numbers of tooth-crowns can be observed:

1st volution: 12. 2nd volution: 23. 3rd volution: 16.

The greatest width of the preserved parts measures 148 mm.

| | B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| S. T. 1 (no. 3) | – | 3.5 | 1.7 | – | – | 1.5 | – | – |
| L. T. 1 (no. 12) | 35° | 12.2 | – | 12.0 | 8.6 | 5.0 | – | – |
| S. T. 2 (no. 14) | 36° | 13.5 | 3.5 | 12.4 | 9.0 | 5.5 | – | – |
| L. T. 2 (no. 35) | 35° | 32.0 | 8.5 | 30.0 | 21.4 | 13.2 | – | 5.0 |
| S. T. 3 (no. 37) | 34° | 33.0 | 9.2 | 31.9 | 22.3 | 14.3 | – | – |
| L. T. 3 (no. 50) | 34° | 44.4 | 11.6 | – | – | 16.3 | – | – |

Idaho mrk. Thiel "P".

The specimen, which is the counterpart to Idaho mrk. Thiel "MP", is represented by $3^3/_4$ volutions. However, a part of the youngest volution is lacking, and it is therefore not possible to state exactly the original number of tooth-crowns. The number of tooth-crowns present is 122, which are distributed in the volutions in the following manner:

1st volution: 33. 2nd volution: 34. 3rd volution: 35. 4th volution: 20.

The greatest width of the tooth-spiral measures 290 mm.

| | B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| S. T. 1 (no. 1) ..... | 35° | 3.7 | 1.4 | – | – | 1.5 | – | – |
| L. T. 1 (no. 33) ..... | 30° | 11.0 | 3.0 | – | – | 4.8 | – | – |
| S. T. 2 (no. 34) ..... | 30° | 11.2 | 3.2 | – | – | 5.0 | – | – |
| L. T. 2 (no. 66) ..... | 35° | 26.4 | 7.8 | – | – | 10.5 | – | – |
| S. T. 3 (no. 71) ..... | 32° | 28.4 | 8.5 | – | – | 13.8 | – | – |
| L. T. 3 (no. 97) ..... | 34° | 57.3 | 14.6 | – | – | 20.7 | – | – |
| S. T. 4 (no. 110) ..... | 40° | 76.8 | 22.0 | 70.8 | 51.9 | 30.1 | 13.8 | 13.2 |

## *Helicoprion ergassaminon* n. sp.

Pl. XV.
Figs. 25–26.

Material: The new species is represented only by specimen Idaho no. 5, thus being the holotype of this species.

Introductory notes: The specimen possesses a tooth-spiral in which most of the tooth-crowns are fairly completely preserved, with the exception of those in the youngest volution. A large part of this volution is missing and for the most part only impressions are found of the tooth-crowns. In the present state of preservation 107 tooth-crowns can be observed, but this number may have been exceeded by about 50 in the complete spiral, giving an estimated total of 150–160 tooth-crowns.

A large number of the preserved tooth-crowns, especially those in the older volutions, are more or less hidden by layers of calcifications from the cartilage. It was decided to preserve these endoskeletal remains because of their importance as representing the symphyseal portion of the lower jaw, and the form of the older tooth-crowns is thus only partially known.

Most of the compound root of the tooth-spiral is also hidden by the endoskeletal remains, but it has been possible to study some of its youngest part in some detail, although it is preserved in a relatively broken condition. This circumstance, however, made it well-suited for studies of the internal structure.

## The endoskeleton.

The anterior part of the lower jaw: This part of the mandibular endoskeleton is represented by layers of prismatic calcifications from the cartilage. The specimen is immediately caudally to the tooth-spiral broken off from the adjoining rock.

The layers of calcification occur laterally to the tooth-spiral on both sides of it and in close connection with it (calc. cart.: pl. XV). Thus the cartilage remains in the anterior part of the jaw show the same pattern as that found in *Helicoprion ferrieri* (pp. 19–22).

The jaw symphysis is formed by a coiled, strongly calcified symphyseal crista (calc. cart. sym.: pl. XV), nearly $^3/_4$ of a volution long, which connects the anterior parts of the branches of the lower jaw along their dorsal and anterior margins and parts of their median surfaces; the connection here is situated dorsally to the ventral borders of the jaw branches. Thus a cavity is formed within the symphyseal region. This symphyseal cavity communicates with the surroundings through an opening on the ventral side of the symphyseal region, where it opens into a relatively deep groove. The lateral walls of this groove are formed by the ventral parts of the jaw branches, while its base is formed by the symphyseal crista.

The symphyseal crista supports the tooth-spiral, the older parts of which are stored in the symphyseal cavity and enter it through the opening on the ventral side of the symphyseal region. The tooth-crowns situated in the older half part of the last formed volution of the tooth-spiral are protected by the lateral walls of the groove on the ventral side of the symphyseal region.

The anterior end of the jaw is formed by the anterior margin of the jaw branches and the adjoining part of the symphyseal crista. Thus no anterior processess, such as those characterizing the anterior part of the lower jaw of *Helicoprion ferrieri* (p. 20, figs. 8–11), are present.

Remarks: The symphyseal region of the lower jaw in *Helicoprion ergassaminon*, it can be seen, is formed in the same way as that of *Helicoprion ferrieri*. Although no traces of anterior processes of the jaw branches are present, the shape and location of the symphyseal crista is essentially the same in both species, as is also the formation of the symphyseal cavity.

Thus, there is no evidence against the assumption put forward above (pp. 21–24) that the symphyseal crista represents a fully developed Basimandibular element highly specialized for the support of the immense tooth-spiral, and which during the ontogenetic development fused completely with the anterior parts of the Meckelian cartilages.

## Dentition.

The symphyseal tooth-spiral: This consists of a large number of individual tooth-crowns situated on a completely undivided, strongly coiled compound root, as is normal in Helicoprion forms (pl. XV).

It has already been mentioned that the greater part of the tooth-spiral is hidden below the remains of the jaw and thus a detailed description of the variation of the tooth-crowns in the different parts of the tooth-spiral cannot be given.

Also no description can be given of the oldest part of the tooth-spiral. It seems probable that as in *Helicoprion ferrieri* (p. 24) it has the form of a curved rod—the juvenile tooth-arch. The shape of the oldest tooth-crowns is unknown.

Some of the tooth-crowns at the beginning of the second volution are visible. A notable feature of these is the strongly worn nature of the cutting blades (fig. 25),

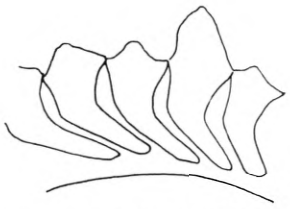

Fig. 25. *Helicoprion ergassaminon* n. sp. A part of the beginning of the second volution, showing tooth-crowns with strongly worn cutting blades. The very narrow, exposed part of the compound root is seen below the narrowed bases of the tooth-crowns. 3× nat. size.

as a result of which the original total height and shape is impossible to reconstruct. The middle portions are rather low and broad and have more or less concave margins. The narrowed bases are broad and comparatively short, forming a rather open angle to the middle portions and point rostro-ventrally. Their terminations vary from gently rounded to angular and are situated below the front margin of the tooth-crown in front (fig. 25).

Since these tooth-crowns were observed in their original place in the symphyseal cavity, covered by the compressed but undisturbed calcifications from the cartilage, the wearing marks are of premortal origin.

In the second volution really marked changes occur in the form of the middle portions and the narrowed bases but could not be studied in detail. However, at the beginning of the third volution these parts of the tooth-crowns have a sharper mutual angle and the middle portions are rather high and narrow with both margins concave, the front margin more strongly so. The narrowed bases are comparatively stout, but long and with nearly pointed terminations situated below the front margin of the second tooth-crown in front. The pointed cutting blades have delicately crenulated cutting edges of which the front edges are more strongly curved than the rear. Some of the cutting blades show undoubted wearing marks.

In the last part of the third volution the tooth-crowns are high with relatively narrow cutting blades. These are only a little greater in height than the middle portions. Their crenulated edges are convex with the stronger curving along the front edge (fig. 26). The middle portions have concave margins with the strongest concavity also along the front margin. The narrowed bases are proportionally narrower than in the preceding volutions and sharply pointed at their terminations, which are

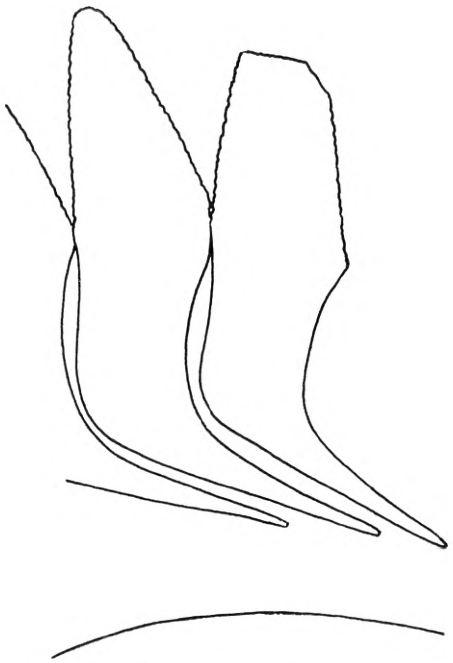

Fig. 26. *Helicoprion ergassaminon* n. sp. Tooth-crowns from the middle part of the third volution. The most complete of them shows a gentle rounding of the apex caused by use. The tooth-crown in front has a broken cutting blade, also originating in actual use during the lifetime of the animal. Note the exposed lower lateral surface of the compound root, which is rather narrow in comparison with the proportions within the tooth-spiral. 2.9× nat. size.

situated anterior to the front margin of the tooth-crown in front. The angle between the middle portions and the narrowed bases is rather acute (fig. 26).

In the last formed part of the tooth-spiral, which amounts to about $^3/_4$ of a volution, the tooth-crowns have nearly the same characteristics as those found in the third volution. The only difference occurs in the form of the narrowed bases, which are somewhat more slender (pl. XV).

The high and narrow tooth-crowns are only in mutual contact at the lower end of the cutting edges. Here the front lower corner of one edge is inserted in a pocket situated at the rear lower corner of the cutting edge of the adjacent tooth-crown.

A very thin layer of enameloid hard tissue originally covered the tooth-crowns, but on the specimen only very small vestiges of this layer are still preserved. From these remains it appears that the surfaces of the tooth-crowns were originally covered all over the surface from the apex to the termination of the narrowed bases by delicate striations.

In cross section the compound root is, like the tooth-crowns, rather narrow. The lateral surfaces of it, exposed below the narrowed bases, exhibit a sculpture of small irregular ridges. The ventral part of this surface is gently curved in a median direction. Moreover, the surface is also exposed in the long and narrow grooves be-

tween the lower parts of the tooth-crowns i. e. between the middle portions and the narrowed bases. The surface displays here a number of large vascular canals (o. v. c.: pl. XV).

On the ventral surface of the compound root is situated a longitudinal groove (ro. gr.: pl. XV), nearly as deep as the height of the exposed lower lateral surface of the root. The surface of this groove is rough due to small delicate tubercles.

The greatest lateral width of the spiral is situated at the level of the terminations of the narrowed bases.

Histologically the compound root consists of osteodentine. Internally in the median dorsal part occurs the characteristic longitudinal nutritive canal (c. can.: pl. XV), which gives off branches to the tooth-crowns. The last formed part of the root has the rather widely spaced meshwork typical for osteodentine in an early stage of development (y. p. t. sp.: pl. XV).

Remarks: Apart from the symphyseal tooth-spiral no other traces of a dentition appears in the specimen.

### Scale-covering:

No traces of placoid scales are found on the preserved part of the lower jaw. As is the case with *Helicoprion ferrieri* and *Helicoprion bessonowi* it appears that *Helicoprion ergasaminon* n. sp. may have been devoid of scales on the anterior part of the head.

### Comparisons and affinities.

The tooth-spiral of the new species differs clearly in its habitual appearance from all other hitherto described *Helicoprion* species. This can readily be seen by a comparison of the figures in the present paper with the previously figured specimens of *Helicoprion bessonowi* (Karpinsky 1899; Yabe 1903; Obruchev 1953), *Helicoprion karpinskii* (Obruchev 1953), *Helicoprion ferrieri* (Hay 1907, 1909), *Helicoprion davisii* (Woodward 1886; Teichert 1940), *Helicoprion nevadensis* (Wheeler 1939) and *Helicoprion sierrensis* (Wheeler 1939).

However, if the different details of the tooth-spiral are compared there are a number of details in which the new species resembles, to a certain degree, some of the species listed above.

The height of the exposed lower lateral part of the compound root is nearly the same as that found in *Helicoprion davisii*, *Helicoprion bessonowi* and especially *Helicoprion nevadensis*. This area is comparatively broad in *Helicoprion ferrieri* and in *Helicoprion sierrensis*.

The height of the cutting blades in relation to the other parts of the tooth-crowns only closely resembles the conditions occurring in *Helicoprion ferrieri*, but in the latter species the tooth-crowns are broader and exhibit a more coarse crenulation.

The height of the middle portions in relation to the other parts of the tooth-crowns bears a close resemblance to the conditions in *Helicoprion nevadensis*, especially

in the younger volutions, but the interspaces separating the tooth-crowns are much narrower in the new species.

The narrowed bases have a large angle between the upper and lower borders, similar to that in *Helicoprion bessonowi*, but they form a more acute angle to the middle portions in the new species, resembling more closely in this respect *Helicoprion ferrieri*.

The proportions between the middle portions and the narrowed bases are very like those occurring in *Helicoprion nevadensis*, although the angle between the two parts is somewhat more acute in the new species, and in particular the rear corner between the two parts is sharper.

The apical angle (25°–35°) is rather small in comparison to *Helicoprion ferrieri* and *Helicoprion sierrensis* (34°–37°), *Helicoprion bessonowi* (45°), and also *Helicoprion nevadensis* (42°–37°–45°).

A further notable feature of the new species is the great number of tooth-crowns represented per volution. This amounts to 48–50, while in most other species between 30 and 39 are found. The highest hitherto known number is 43 found in *Helicoprion bessonowi*.

The lower jaw differs from that found in *Helicoprion ferrieri* by the lack of the anterior processess.

It may be said, in conclusion, that the new species is most closely comparable to *Helicoprion nevadensis*, from which, however, it differs essentially in many respects. It forms a well-defined new species.

The specific name proposed, *Helicoprion ergasaminon*, refers to the distinct wearing marks found on the type specimen, and in translation from the Greek Εργασαμινον means "the one, who has done work".

## Diagnosis.

The endoskeleton consists of cartilage with a superficially situated layer of prismatic calcifications. The lower jaw has a high and long, but narrow symphyseal region. A spiral-coiled, strongly calcified symphyseal crista connects the two jaw branches, which terminate rostrally along the border of the symphyseal crista. These three elements enclose the symphyseal cavity. The known parts of the dentition are represented by the high, narrow symphyseal tooth-spiral, composed of a large number of separated tooth-crowns placed on a solid, spiral-coiled, undivided compound root, which has on the ventral side a narrow, deep, longitudinal groove with a rough surface. The closely set tooth-crowns are high and narrow, and are proximally separated from each other by shallow grooves. Their cutting blades have crenulated cutting edges and are a little higher than the middle portions. The middle portions have concave margins. The form of the narrowed bases varies from short and stout with angular or evenly rounded terminations, to long and narrow with extremely pointed terminations. Histologically the tooth-spiral is composed of osteodentine covered by a thin layer of enameloid substance below which, it is presumed, a layer of pallial dentine was originally present.

### Dimensions.

Parts of $3^3/_4$ volutions of the tooth-spiral are preserved. The greatest width of the tooth-spiral measures 218 mm.

Due to the conditions of preservation it is impossible to give systematic measurements of the tooth-crowns in the spiral. However, in order to give some idea of the proportions between the different parts of the tooth-crowns, and of tooth-crowns in successive parts of the tooth-spiral, the dimensions of some of the more completely preserved tooth-members are given below. All linear measurements are given in mm.

| | B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| I | – | – | 2.7 | – | 5.5 | – | – | – |
| II | – | – | 4.7 | – | 15.0 | – | – | – |
| III | 25° | 31.8 | 6.9 | 29.5 | 21.0 | 13.6 | – | – |
| IV | 35° | 37.3 | 9.1 | – | – | 13.0 | – | 3.8 |
| V | 35° | 41.9 | 9.8 | – | – | 16.2 | – | 5.0 |

I: One of the last tooth-crowns in the first volution.
II: One of the early tooth-crowns in the third volution.
III: One of the intermediate tooth-crowns in the third volution.
IV: One of the last tooth-crowns in the third volution.
V: One of the youngest tooth-crowns in the third volution.

## *Helicoprion cf. ferrieri.*

Pl. VIII fig. 1.
Fig. 27–28.

Material: The material is represented by only a single specimen, Idaho no. 8.

### The symphyseal tooth-spiral.

The specimen preserves parts of $3^1/_6$ volutions of a tooth-spiral, which occurs mainly as impressions of the tooth-crowns and of the compound root (pl. VIII, fig. 1).

All the tooth-crowns, or parts of them preserved, have a more or less prominent long and tapering lower portion, representing the narrowed base. The other parts, the middle portions and the cutting blades, can be observed in detail only in the second, the third and the fourth volutions.

The strong pointed cutting blades are in the younger portions of the tooth-spiral nearly half as high as the complete tooth-crown. The front cutting edges are longer and more strongly convex than the rear edges; both possess a crenulation, which is somewhat coarse in the youngest preserved tooth-crowns.

The tooth-crowns are in mutual contact at the lower part of the cutting edges. This contact is formed by the lower corner of the front cutting edge of one tooth-crown,

Fig. 27. *Helicoprion cf. ferrieri.* Tooth-crowns from the fourth volution showing the mutual dimensions of the three parts of the crown, in particular the short, triangular shaped and strongly pointed narrowed bases. The broad lateral lower part of the compound root is a characteristic feature of the specimen. 1.1× nat. size.

which fits into a small recess in the lower portion of the rear cutting edge of the preceeding tooth-crown.

The middle portions are more clearly defined in the younger than in the older parts of the tooth-spiral. The front margins are strongly concave, and the rear margins are straight or slightly convex.

The narrowed bases are more prominent in the older than in the younger parts of the tooth-spiral. They are in the oldest tooth-crowns directed nearly vertically, but, after a short distance, they are bent more forward, and in the youngest tooth-crowns they are nearly at right-angles to the axis of the remainder of the tooth-crowns.

In the oldest part of the tooth-spiral the narrowed bases terminate at a point below the middle of the second tooth-crown in front, while in the younger parts they only reach below, or just behind, the front margin of the middle portion of the adjacent tooth-crown. The narrowed bases of the younger tooth-crowns have extremely pointed terminations.

The tooth-crowns were probably originally covered by a layer of enameloid substance, but this layer has completely disappeared and nothing can be stated about the presence or absence of any kind of original surface ornamentation.

Undoubted wearing marks occur on a number of the tooth-crowns belonging to the youngest of the preserved volutions (fig. 28). These wearing marks are found as a series of distinct facets bordering broad shallow depressions on the lateral proximal parts of the cutting blades and on the middle portions. The pattern shown by the marks seems to be a compound of systems of alternating directions. This circum-

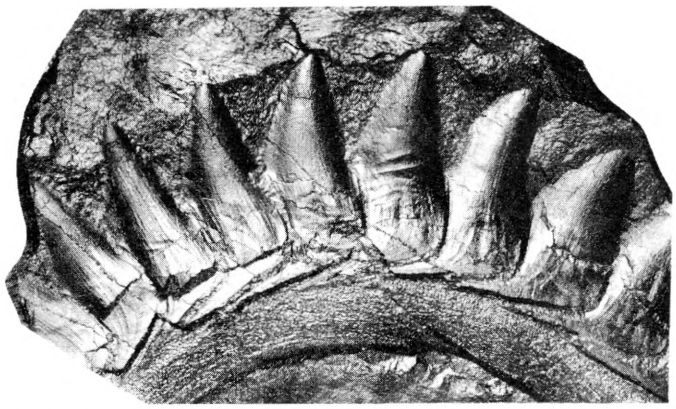

Fig. 28. *Helicoprion cf. ferrieri.* Tooth-crowns from the youngest of the preserved volutions showing distinct wearing marks. Idaho no. 8, Cast in PVC-plastic. 0.7× nat. size.

stance reflects the change of inclination of the tooth-crowns in relation to the rows of small teeth on the upper jaw, and is a consequence of the gradual movement in a labial direction of the symphyseal tooth-spiral.

The lateral surfaces of the compound root are covered by a fine meshwork formed by the walls of hard tissue surrounding the openings of the small vascular canals. In the areas situated between the middle portions and the narrowed bases of adjacent tooth-crowns the openings are larger and fewer, and oval shaped.

A longitudinal groove is present on the ventral side of the compound root, but nothing is known of its original form, size or surface features.

Remarks: No traces of other teeth, scales or calcifications from the cartilage are found in the specimen.

## Discussion.

The tooth-spiral of the described specimen shows in many details a close resemblance to that of *Helicoprion ferrieri* (pp. 24–30). However, there are strong differences with regard to the form and length of the narrowed bases of the tooth-crowns. This is especially the case with the younger tooth-crowns of *Helicoprion ferrieri* in which the narrowed bases reach a point situated below the front margin of the middle portion of the second tooth-crown in front, while in the specimen under discussion they only reach a point below or just behind the front margin of the first adjacent tooth-crown.

Furthermore the shape of the narrowed bases differs in the two species. In *Helicoprion ferrieri* they are long and slender with nearly parallel upper and lower borders, and have a rounded termination (pl. I and fig. 12). In the specimen in question they are rather short and nearly triangular in shape, with a strongly pointed termination.

These differences might be considered as sufficient for the erection of a further new species. This, however, has been rejected on account of the many similarities

between the specimen and *Helicoprion ferrieri*, and the possibility that the observed differences are only of secondary origin. They could in this particular individual have been caused by a local destruction or other alteration of the ectomesodermal tissue which took part in the formation of this portion of the tooth-crown. Therefore, until more and better material becomes available, it has been decided to refer to the specimen as *Helicoprion cf. ferrieri.*

Dimensions.

Parts of $3^1/_6$ volutions are preserved with the following numbers of tooth-crowns occurring in each volution:

1st volution: 30. 2nd volution: 37. 3rd volution: 26. 4th volution: 6.

The greatest width of the preserved part of the spiral measures 181 mm.

The general state of preservation does not permit systematic measurements. No dimensions could be obtained from the first and the fourth volution. For the second and the third volution the following measurements can be stated:

| | B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|---|
| S. T. 2 (no. 36) . . . . . | – | – | 4.0 | – | 9.5 | – | – | – |
| S. T. 3 (no. 70) . . . . . | – | – | 8.0 | – | 16.0 | – | – | – |
| L. T. 3 (no. 86) . . . . . | 40° | 49.6 | 15.5 | 44.2 | 32.0 | 20.5 | – | – |

*Helicoprion sp. indt.*

Pl. XIV fig. 3.

Material: This consists of the specimen Idaho no. 6.

Description: The specimen preserves the remains of 12 tooth-crowns and a part of the compound root. From the size it seems most reasonable to assume that the fragment originally formed a part of a second volution.

Most of the specimen is preserved as a impressions in the matrix. None of the tooth-crowns are complete, and their original form and sculpture cannot be determined. In contrast, the impressions of the middle portions are fairly clearly defined, and show a concave curving along their front margins while the rear margins are straight or slightly convex. The narrowed bases are slender and terminate at a point below the centre of the second tooth-crown in front.

The state of preservation is too poor to permit a specific determination.

Dimensions.

The greatest width measures 57 mm.

Tooth-crown no. 8, counted from the posterior end of the specimen, has the following dimensions:

| B | A-E | C-D | A-F | C-F | A-L | J-K | M-E |
|---|---|---|---|---|---|---|---|
| – | – | 6.0 | – | 15.6 | – | – | – |

## Summary and conclusions

The treated North American Helicoprion material comprises the species *Helicoprion ferrieri*, Hay, *Helicoprion ergasaminon* n. sp. and two other not closely determinable specimens referred to respectively as *Helicoprion cf. ferrieri*, and *Helicoprion sp. indt.*

The investigations have yielded a number of new features in our knowledge of this Elasmobranch.

With respect to the neurocranium details of the rostral and the ethmoidal region are now known.

The rostral region is found to possess one un-paired cartilage rod ventrally. On the posterior part of this rod occurs a smooth rounded, relatively broad tuberosity, to which ligaments apparently have been attached. Because of incompleteness of the material the dorsal part of the rostral region is unknown. However, the presence of a ventrally situated un-paired rod is a character typical of a Selachian skull pattern. Therefore, it is most likely that the rostrum originally has been formed as a basket with a pair of cartilage rods dorsally forming its upper lateral limitation and anteriorly joining the un-paired ventral rod.

The remains of the ethmoidal region of the neurocranium indicate that the nasal capsules are placed at the most anterior part of this region.

Of the visceral skeleton the anterior part of the lower jaw and two dorsal elements are known. The latter are tentatively interpreted as the anterior parts of the palatoquadrates on account of their shape, size and position in relation to the neurocranium, and their relation to the remains of a weak upper dentition. If this interpretation is correct the palatoquadrates are completely independant elements. Consequently they may have been suspended on the neurocranium in an amphistylic or hyostylic manner, both of which characters are typical of the Selachians.

The anterior part of the lower jaw is strongly formed, with an extremely high symphyseal region composed of a strongly developed, coiled Basimandibular element connecting the Meckelian cartilages, and enclosing a cavity in which the older volutions of the symphyseal tooth-spiral are successively stored.

The symphyseal tooth-spiral is described in detail. Its oldest part, not previously known, is found to be a curved rod, which along its dorsal edge is developed as a crenulated cutting crista. The individual tooth-crowns vary to some degree in shape from the oldest part to the youngest part of the tooth-spiral. Considerable but gradual changes are found in the relations between the three principal parts of the tooth-crowns. It has been possible, also, to give an interpretation of the limitations between the roots of the teeth in the youngest portion of the tooth-spiral. This was due to the fact that, although the complete fusion between successive teeth is already at hand at the development of a new tooth, the hard tissue of the compound root in the youngest part of the tooth-spiral exhibits a clear gradual degree of completion of the circumvascular denteons of the vascular canals. On the tooth-spiral of *Helicoprion ergasaminon* n. sp. and *Helicoprion cf. ferrieri* distinct wearing marks are found on the tooth-crowns.

A number of very small crushing teeth form a weak tooth-pavement on the most anterior parts of the upper jaw. Apart from these and the symphyseal tooth-spiral no other traces of dentition have been found. This circumstance may be due to the fact that only the anterior parts of the jaws are present. However, it is more likely that it reflects a very strong reduction of the lateral dentition.

A reduction seems also to have taken place in the dermal skeleton since no traces of scales are found on the anterior part of the head.

Although KARPINSKY had already, in his admirable monograph (1899), given great attention to the histology of the symphyseal tooth-spiral there were still several obscure points, which led to the discussion of its histology (NIELSEN 1932, 1952; MOY-THOMAS 1939 a; TEICHERT 1940). A re-description, such as that given in the present paper, was therefore highly desirable. This re-description has clearly shown that the tooth-crowns consist of typical osteodentine, composed of denteons arranged at right angles to the tooth-surface in its outer parts. The denteons are separated by an interdenteonal bony substance in which dentinal tubes, issuing from the vascular cavities of the denteons, penetrate to a certain degree. The outer coating of the tooth-crowns consists of two layers, an outer very thin layer of an enameloid substance underlain by a thin layer of pallial dentine with strongly developed, irregular branching dentinal tubes.

The new evidence concerning the anatomy of the anterior part of the neurocranium and the palatoquadrate provides good reasons for a closer determination of the systematical position of *Helicoprion ferrieri* and *Helicoprion ergasaminon* as well as for the other known *Helicoprion* species. It is obvious from these anatomical features that this Elasmobranch may be grouped most adequately close to the Selachian Elasmobranchs. However, because of the restriction of the known features, it is necessary provisionally to establish the genus *Helicoprion* in a separate order within the subclass *Elasmobranchii* as follows:

Class: ***Elasmobranchiomorphi.***
Sub-class: *Elasmobranchii.*
Super-order: *Helicoprioni.*
Order: *Helicoprioniformes.*
Family: *Helicoprionidae.*
Genus: *Helicoprion*[1].

This is in strong contrast to previous suggestions put forward by most of the authors who have dealt in details with *Helicoprion* or problems related to this form. Only TEICHERT (1940 p. 143) has maintained a corresponding view, while others (NIELSEN 1932, 1952; MOY-THOMAS 1939 a; OBRUCHEV 1953, 1964; BENDIX-ALMGREEN 1961) have placed *Helicoprion* within the *Edestid* group among the *Bradyodonti*

[1] The genus *Toxoprion* HAY 1909 founded on *Toxoprion lecontei* DEAN 1895 may be regarded as synonymous for *Helicoprion*, as suggested by OBRUCHEV (1953 p. 59).

due to the similar specialisation of the symphyseal tooth-row, and because of the microscopic tooth-structure suggested to be tubular dentine. In this type of dentine the tooth-crowns are composed of denteons clearly separated by an interstitial enameloid substance (Nielsen 1932 pp. 30, 33; Moy-Thomas 1939 a pp. 2–3; Ørvig 1951 pp. 342, 349) thought to be characteristic for all Elasmobranchs grouped as *Bradyodonts*.

However, new investigations in paleohistology (Radinsky 1961; Ørvig 1965) have revealed certain features showing that the tubular dentine is without any significance as a systematical character. It is beyond the scope of this paper to consider this problem, which will be dealt with in detail in a forthcoming publication. Nevertheless, it can be stated that the results of these investigations also involve that the osteodentine found in the tooth-crowns of *Helicoprion* does not provide evidence of value with regard to the systematical position of this Elasmobranch.

On the other hand, the anatomical features of the neurocranium and palatoquadrate show clearly the non-existence of a close relationship with the better known *Edestids* i. e. *Sarcoprion edax* (Nielsen 1952), *Fadenia crenulata* (Nielsen 1952; Bendix-Almgreen 1961; 1962) and *Erikodus groenlandicus* (Bendix-Almgreen 1961). This applies also to the other better known Elasmobranchs hitherto placed as members of the *Bradyodont* group i. e. *Helodus simplex* (Moy-Thomas 1936; Patterson 1965) and *Chondrenchelys problematica* (Moy-Thomas 1935; Patterson 1965). All these forms possess a holostylic jaw suspension and the rostral region has an entirely different configuration.

The facts discussed above show the interesting feature that parallel evolution and specialisation of the teeth in the symphyseal region of the lower jaw has taken place within different Elasmobranch lines during Carboniferous and Permian time. The acme of this form of specialisation was reached in late Carboniferous and Permian time with the complete tooth-spiral found in Helicoprion.

The reasons for the development of such an unusual organ as the *Helicoprion* tooth-spiral are certainly obscure, especially since in all the previously described species no observations of evidence of actual use have been reported. However, during a visit to Moscow and Leningrad, I had the opportunity to study the classical *Helicoprion* material. This study, which also fully confirmed the description of the tooth-histology given above, revealed that some of the specimens of *Helicoprion bessonowi* do, in fact, show weak but clear wearing marks. These occur on the lateral surfaces of the middle portions and on the narrowed bases of the tooth-crowns, and show to some degree a pattern comparable to that found on *Helicoprion cf. ferrieri* described above (pp. 46–47). The strongest wearing marks known from a *Helicoprion* specimen remain, however, those described in the present paper for the specimen known under the new specific name, *Helicoprion ergasaminon*, where they are found, not only on the lateral surfaces of the tooth-crowns, but also on the apex of the cutting blades.

In the past some confusion has prevailed over the question of the original location

of the tooth-spiral in the mouth. The most adequate previous explanation was given by KARPINSKY (1899 p. 107, fig. 72), although it was viewed with great scepticism by many authors (HAY 1909, 1912; WOODWARD 1900 pp. 33–36). OBRUCHEV, in his 1953 work, published a new reconstruction mainly based on Karpinsky's material and original figures, but the tooth-spiral was still placed in the upper jaw symphysis and was thought to have acted as a defence weapon. OBRUCHEV, however, notes, ".... one may hope that new finds will show, how near such a reconstruction is to the truth" (p. 57).

Our present extended knowledge enables us to state with certainty that the tooth-spiral is, in fact, situated in the symphysis of the lower jaw and that no similar organ was developed in the upper jaw.

With regard to the role and function of the symphyseal tooth-spiral many different opinions have been published, in which it has been suggested as a defence weapon, as a cutting device or as a crushing organ. If it was principally a crushing organ, really strong wearing marks would be expected, as occur, for example, in *Fadenia crenulata*, which it is known from a specimen with preserved stomach contents preyed on Brachiopods (BENDIX-ALMGREEN 1961). The proposal that the tooth-spiral acted as a defence weapon was mostly based on its assumed location in the upper jaw symphysis, a now invalid assumption. The most probable function and use of the tooth-spiral on the evidence of the wearing marks seems to have been as a cutting and, probably to some degree, a tearing device, in combination with the rows of small upper jaw teeth.

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Indleveret til Selskabet den 15. februar 1965.
Færdig fra trykkeriet den 2. marts 1966.

# PLATES

PLATE I

*Helicoprion ferrieri* HAY.

Idaho no. 4.

0.5× nat. size.

Photographed in Xylene.

art. p.: the tuberosity on the proximal part of the rostral element. calc. cart. l. l. j. & calc. cart. r. l. j.: the left and the right branches respectively of the lower jaw. calc. cart. n. cr.: frontal part of the neurocranium. calc. con. j.: calcifications from the rear connection between the two branches of the lower jaw at the lingual end of the symphyseal crista. calc. cart. sym.: the symphyseal crista. The calcifications are enclosed in the ventral groove of the compound root of the tooth-spiral. calc. na.?: layers of calcifications possibly belonging to the nasal capsula. can. c.: two canals which were possibly originally situated ventrally in the lateral wall of the neurocranial capsule. dnt.: teeth from the tooth-pavement on the anterior part of the upper jaw. f. o. l.: foramen for the nervus olfactorius. pit.: the cavity where the new tooth-members of the spiral are developed. pr. l. j.: the anterior process of the left branch of the lower jaw. r. p. n. cr.: unpaired ventral rostal balk. y. t.: the last formed tooth in the spiral. The large spaces in the hard tissues forming the crown and corresponding root are clearly seen. This circumstance indicates the incompletely developed state of the tissues and is in strong contrast to the condition found in the older parts of the tooth-spiral.

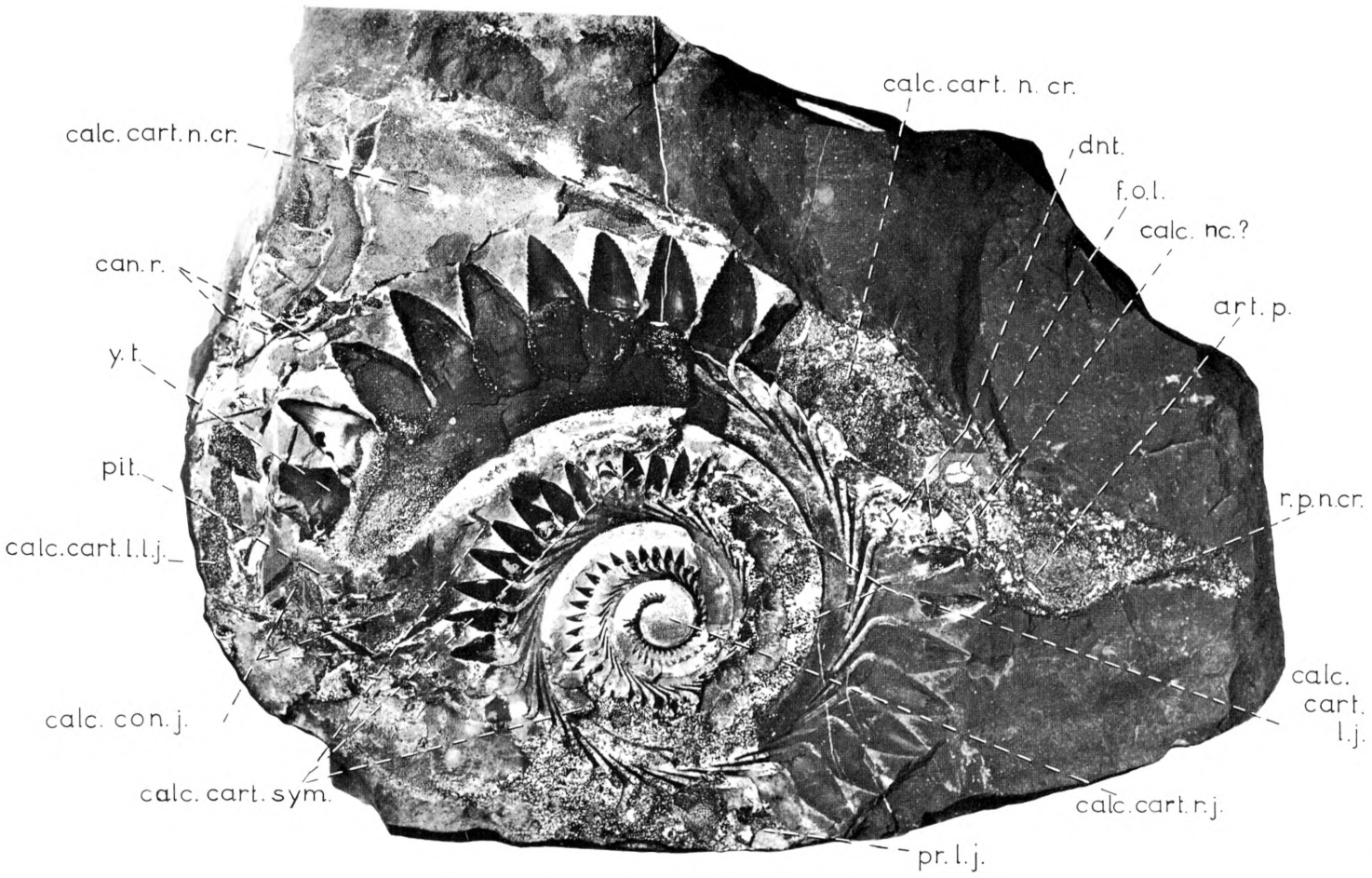

calc. cart. n. cr.
calc. cart. n. cr.
dnt.
f. o. l.
calc. nc.?
can. r.
art. p.
y. t.
pit.
r. p. n. cr.
calc. cart. l. l. j.
calc.
cart.
l. j.
calc. con. j.
calc. cart. sym.
calc. cart. r. j.
pr. l. j.

PLATE I

PLATE II

*Helicoprion ferrieri* HAY.

Idaho no. 4.

0.5× nat. size.

Photographed dry.

a. rdg.: area clearly showing the delicate ridges which characterize the lateral surface of the compound root. calc. cart. r. l. j. & calc. cart. l. l. j.: anterior part of the right and the left branches of the lower jaw forming the lateral walls of the symphyseal cavity. dnt.: teeth from the upper jaw. o. v. c.: fairly widely spaced vascular canals.

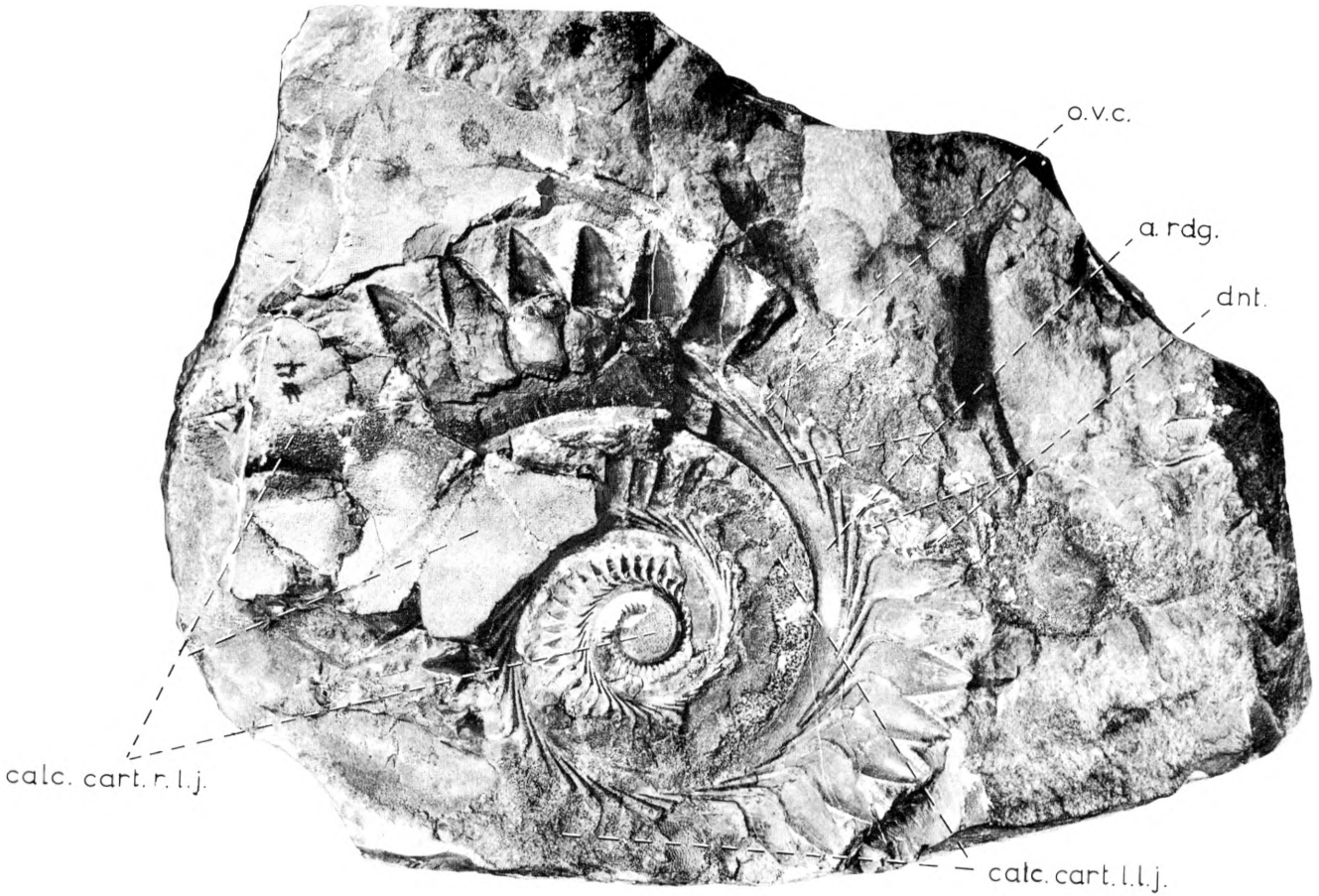



PLATE II

PLATE III

*Helicoprion ferrieri* HAY.

Cast in PVC-plastic.

Idaho no. 4.

0.5× nat. size.

a. rdg.: area showing the delicate ridges on the lateral surface of the complex root. o. v. c.: vascular canals.

o.v.c.
o.v.c.
a. rdg.

PLATE IV

*Helicoprion ferrieri* HAY.

Idaho no. 4.

1× nat. size.

Photograph of the specimen submerged in xylene, showing a transverse section through the anterior portion of the neurocranium, the palatoquadrates and the lower jaw.

calc. cr. b.: layers of prismatic calcifications representing the basal part of the neurocranium. calc. l. l. j. & calc. r. l. j.: prismatic calcifications from the left and the right lower jaw. can. l. & can. r.: two pair of canals which possibly originally were situated close to the base in the left and the right side of the neurocranium. cav. cr.: cavum cerebrale cranii. l. i. cr. w. & r. i. cr. w.: calcification layer lining the inner surface of the neurocranium. l. o. cr. w. & r. o. cr. w.: calcification layer lining the outer surface of the neurocranium. pit.: location of the pit where the symphyseal teeth are developed. pq. l. & pq. r.: transverse section through the supposed left and right palatoquadrates. sym. t.: two tooth-crowns from the symphyseal spiral.

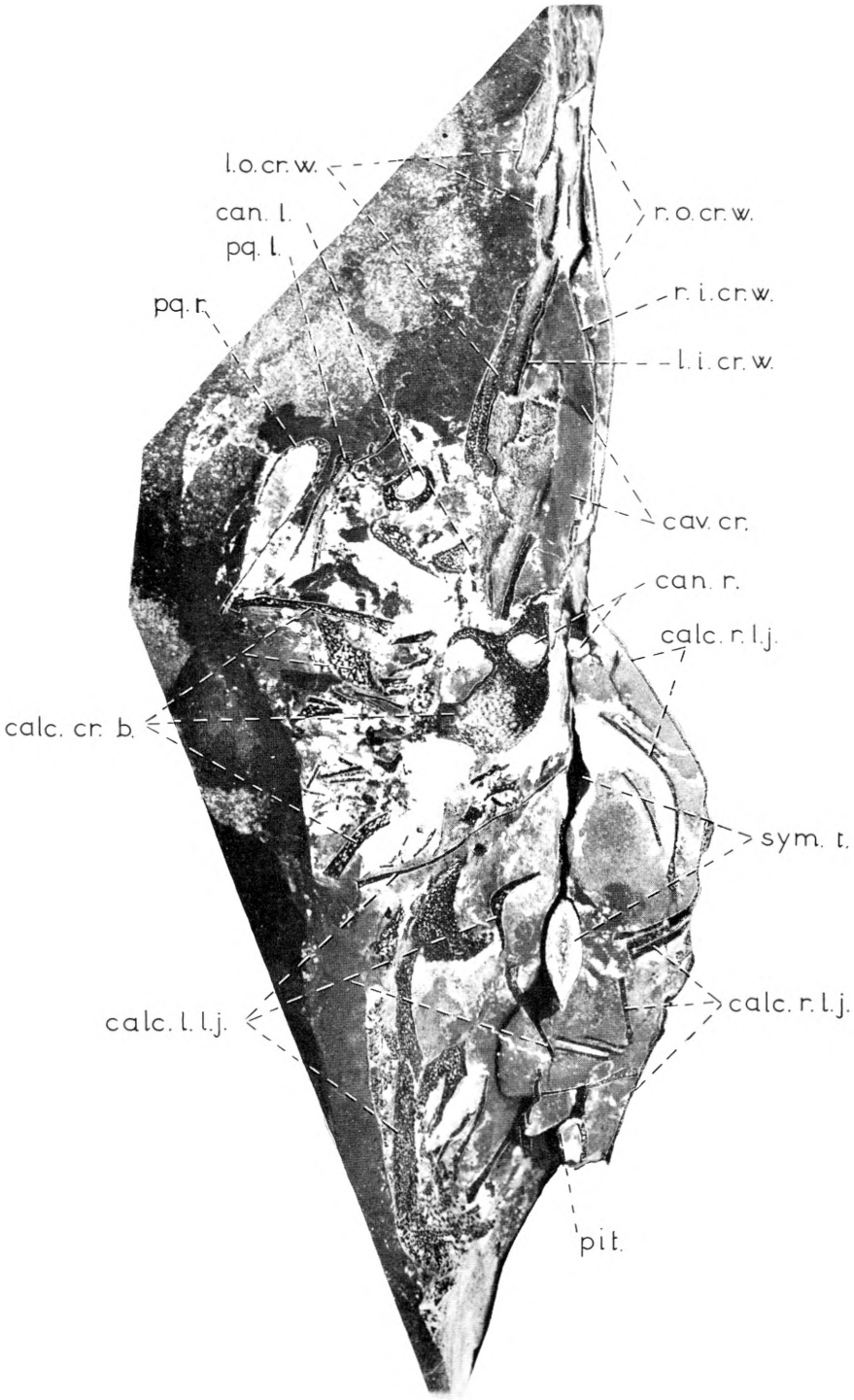

l.o.cr.w.
can. l.
pq. l.
pq. r.
r.o.cr.w.
r. i. cr. w.
l. i. cr. w.
cav. cr.
can. r.
calc. r. l. j.
calc. cr. b.
sym. t.
calc. l. l. j.
calc. r. l. j.
pit.

PLATE V.

*Helicoprion ferrieri* HAY.

Idaho no. 4.

Fig. 1. 4× nat. size.

Fig. 2. 8.2× nat. size.

Photographed in Xylene.

Both figures show the oldest part of the tooth-spiral with the juvenile tooth-arch, and the first developed tooth-crowns. These differ somewhat in general shape from the later tooth-crowns. On figure 2 the crenulation on the cutting edge of the juvenile tooth-arch is visible.

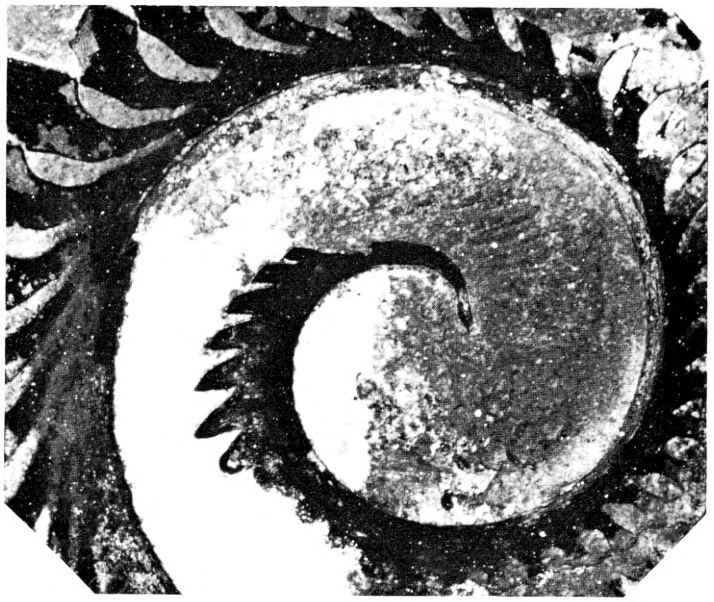


Fig.1

Fig.2

PLATE VI

*Helicoprion ferrieri* HAY.

Fig. 1: Idaho no. 4.
Fig. 2: Idaho no. 4.
Fig. 3: Idaho no. 4.
Fig. 4: Idaho no. 1.
Enlargement: 483×.

Fig. 1: Thin-section through the area of the cutting edge of a tooth-crown showing the osteodentine (dti.) surrounding the pulp cavities (p. c.), the pallial dentine (p. dt.) with strongly branching, densely set dentinal tubes (d. t.), and the outer layer of enameloid substance (en.). Horizontal section.

Fig. 2: Thin-section through an area of the tooth-crown, showing a thin layer of enameloid substance (en.), the osteodentine (dti.), parts of pulp cavities (p. c.), and the layer of pallial dentine (p. dt.) with dentinal tubes (d. t.). Horizontal section.

Fig. 3: Thin-section of the osteodentine (dti.) of the tooth-crown. The osteodentine shows clearly a fairly coarse lamination. No traces of the hard tissue of the circumpulpar denteons are preserved. Horizontal section × Nicols.

Fig. 4: Thin-section through a part of the compound root showing circum-vascular denteons (cv. dti. o.) surrounding the vascular canals (v. c.), and the interosteonal bony substance (int. s.) Vertical section.

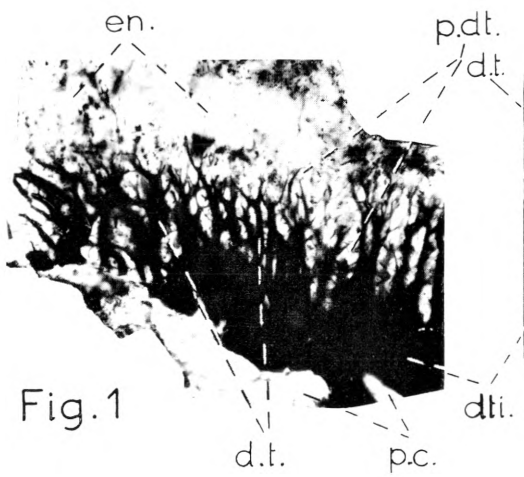



Fig.1

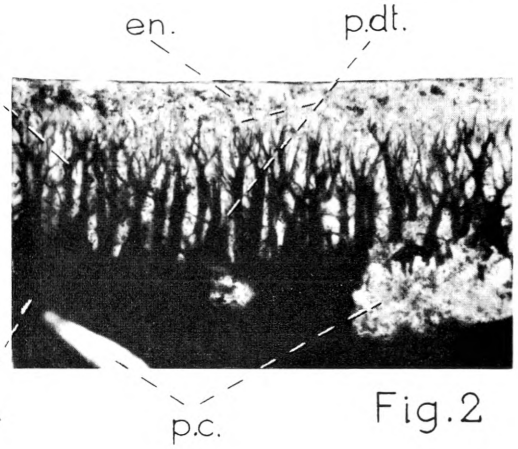



Fig.2

Fig.3

Fig.4

PLATE VII

Fig. 1: *Helicoprion cfr. ferrieri.*

Idaho no. 8.
0.7× nat. size.
Photographed dry.
can. w.: vascular canals.

Fig. 2: *Helicoprion ferrieri* HAY.

Idaho no. 4.
0.9× nat. size.
Photographed in Xylene.

Detail of specimen Idaho no. 4 showing small scattered teeth (dnt.), which represent parts of a strongly reduced tooth-pavement situated on the anterior part of the upper jaw.
ct. dnt.: tooth in lateral view. r. dnt.: teeth forming part of the original rows. rt. dnt. lower surfaee of the root.

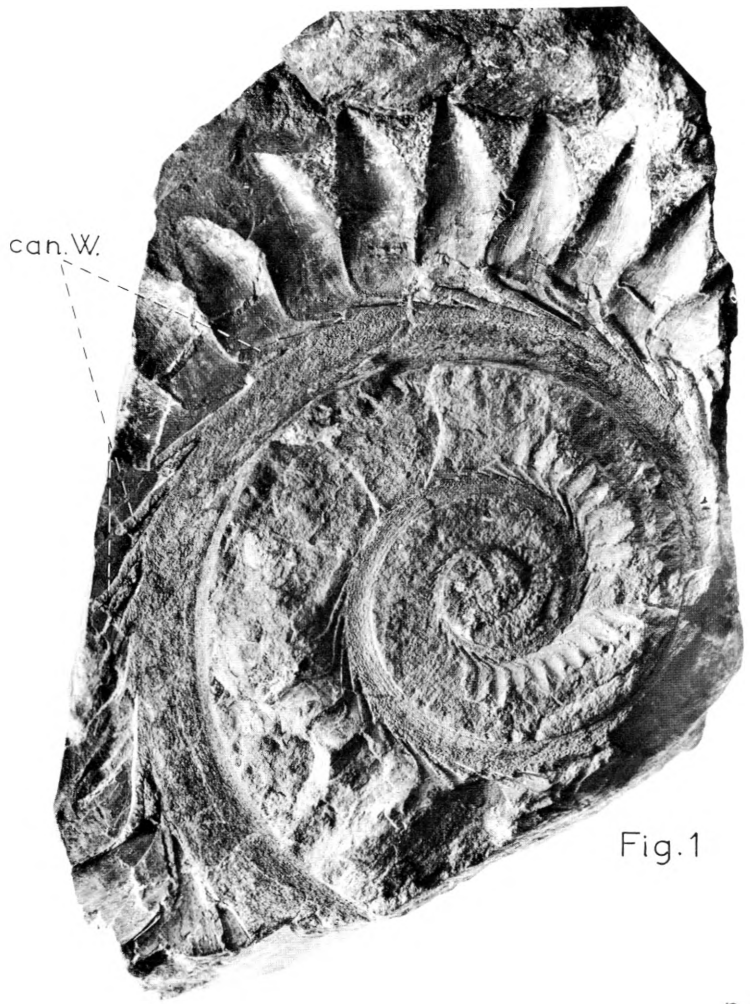



Fig. 1

Fig. 2

PLATE VIII

*Helicoprion ferrieri* HAY.

Idaho no. 1.

0.6× nat. size.

Photographed dry.

calc. cart.: prismatic calcifications from the cartilage of the lower jaw. c. can.: parts of the central canal which runs through the compound root of the tooth-spiral, and originally contained the main nutritive vessel. r. em. cr.: remains of the juvenile tooth-arch.

calc. cart.
r. em. cr.
c. can.

PLATE IX

*Helicoprion ferrieri* HAY.

Idaho no. 1.

0.9× nat. size.

Photographed dry.

Fig. 1: Impressions of tooth-crowns of the fourth volution.

Fig. 2: Cast in PVC-plastic; lateral view from the right.

Fig. 3: Same seen from above.

The coarse crenulations along the cutting edges of the cutting blades are clearly seen, as well as the fine striations characterizing the surface of the dentine. The original layer of enameloid substance, which once covered the tooth-crowns, is not preserved.

Fig. 1

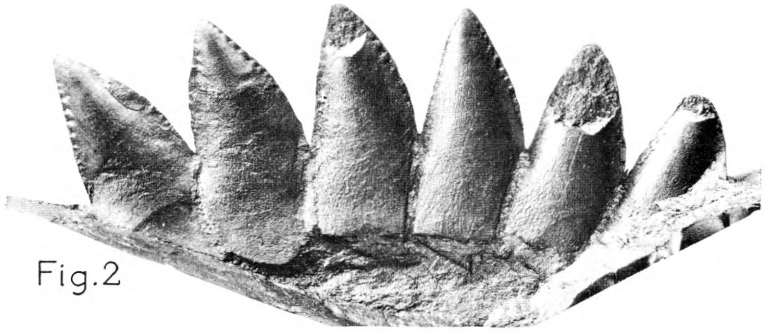


Fig. 2

Fig. 3

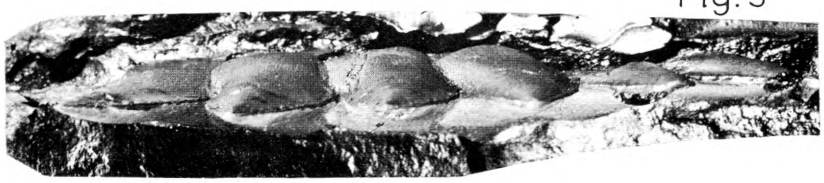


PLATE X

*Helicoprion ferrieri* HAY.

Idaho mrk. "Thiel P".

0.5× nat. size.

Photographed in Xylene.

r. calc. cart.: calcifications from the cartilage of the symphyseal portion of the lower jaw, corresponding to the symphyseal crista. ro. gr.: the right lateral wall of the groove occuring ventrally on the compound root. y. p. t. sp.: remains of the last formed portion of the compound root.

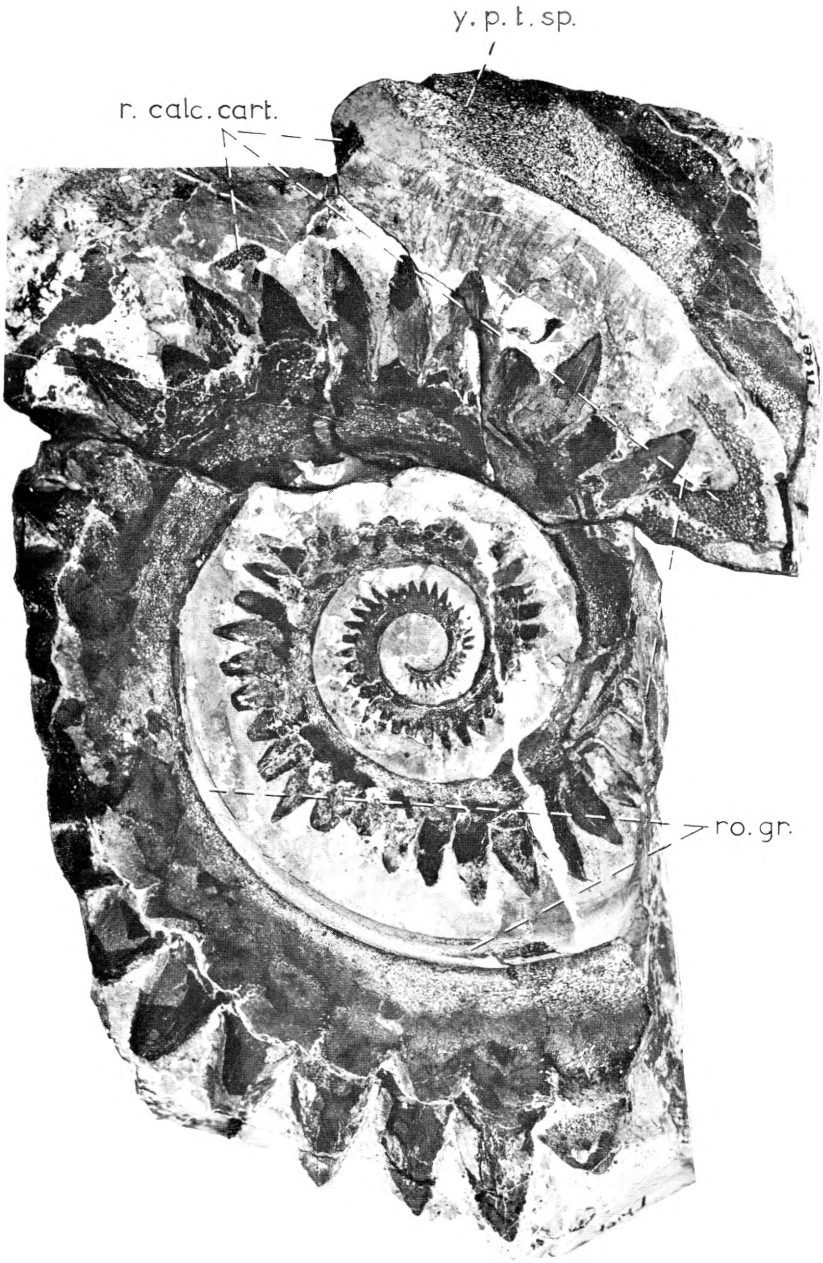

y. p. t. sp.
r. calc. cart.
ro. gr.

PLATE XI

*Helicoprion ferrieri* HAY.

Idaho mrk. "Thiel P".

0.5× nat. size.

As plate X but photographed dry.

h. v. g.: the lateral wall of the ventral groove.

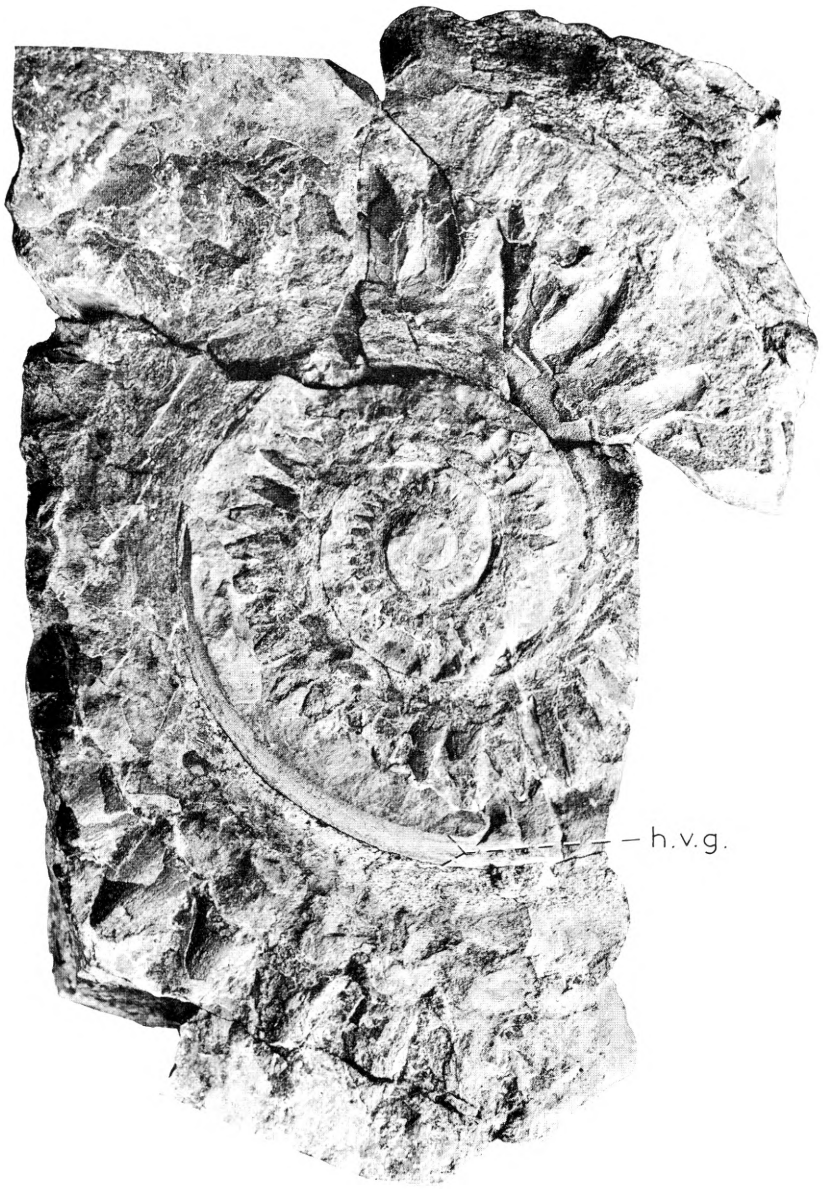

h.v.g.

PLATE XII

*Helicoprion ferrieri* HAY.

Idaho mrk. "Thiel MP".

0.5× nat. size.

Photographed in Xylene.

r. calc. cart.: calcifications from the symphyseal crista.

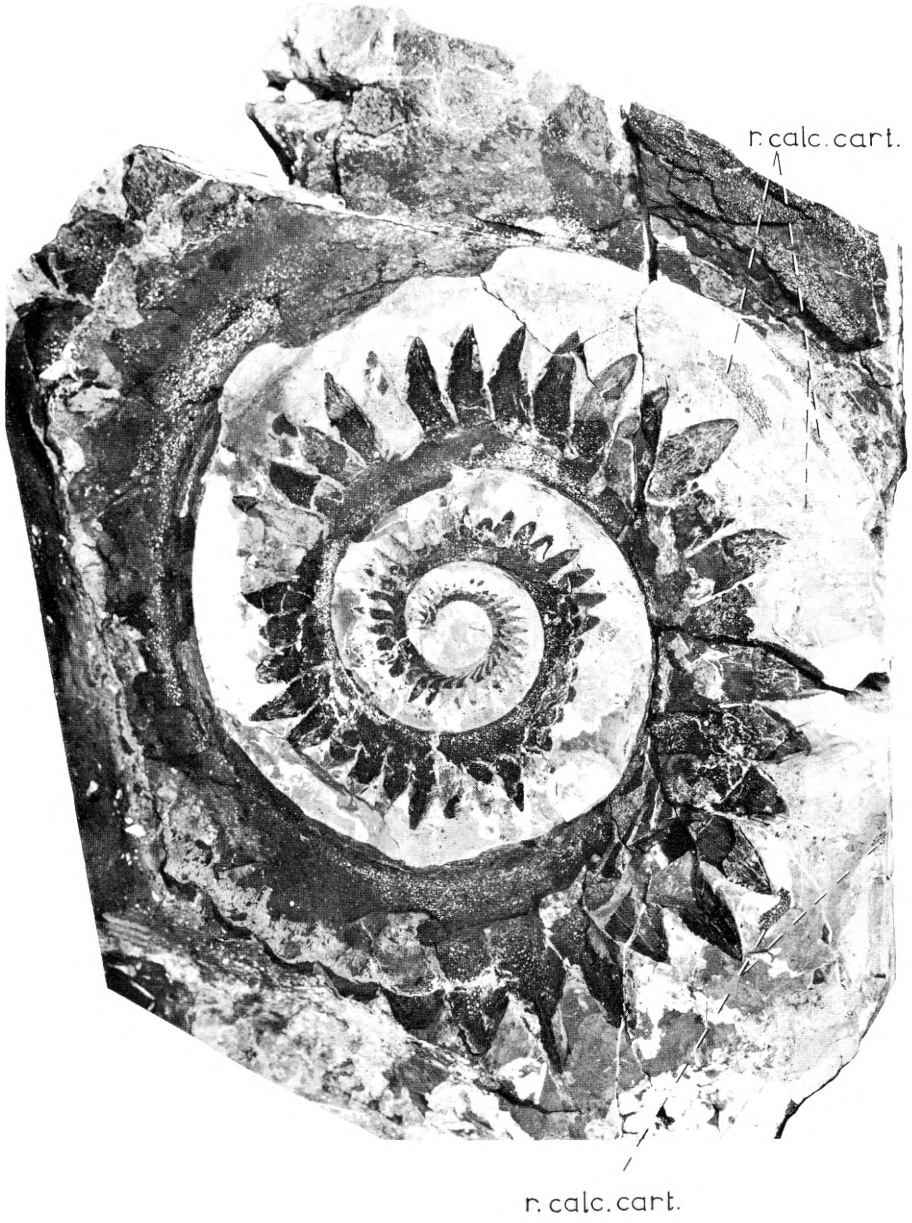

r. calc. cart.
r. calc. cart.

PLATE XIII

*Helicoprion ferrieri* HAY.

Idaho no. 9.

nat. size.

Photographed dry.

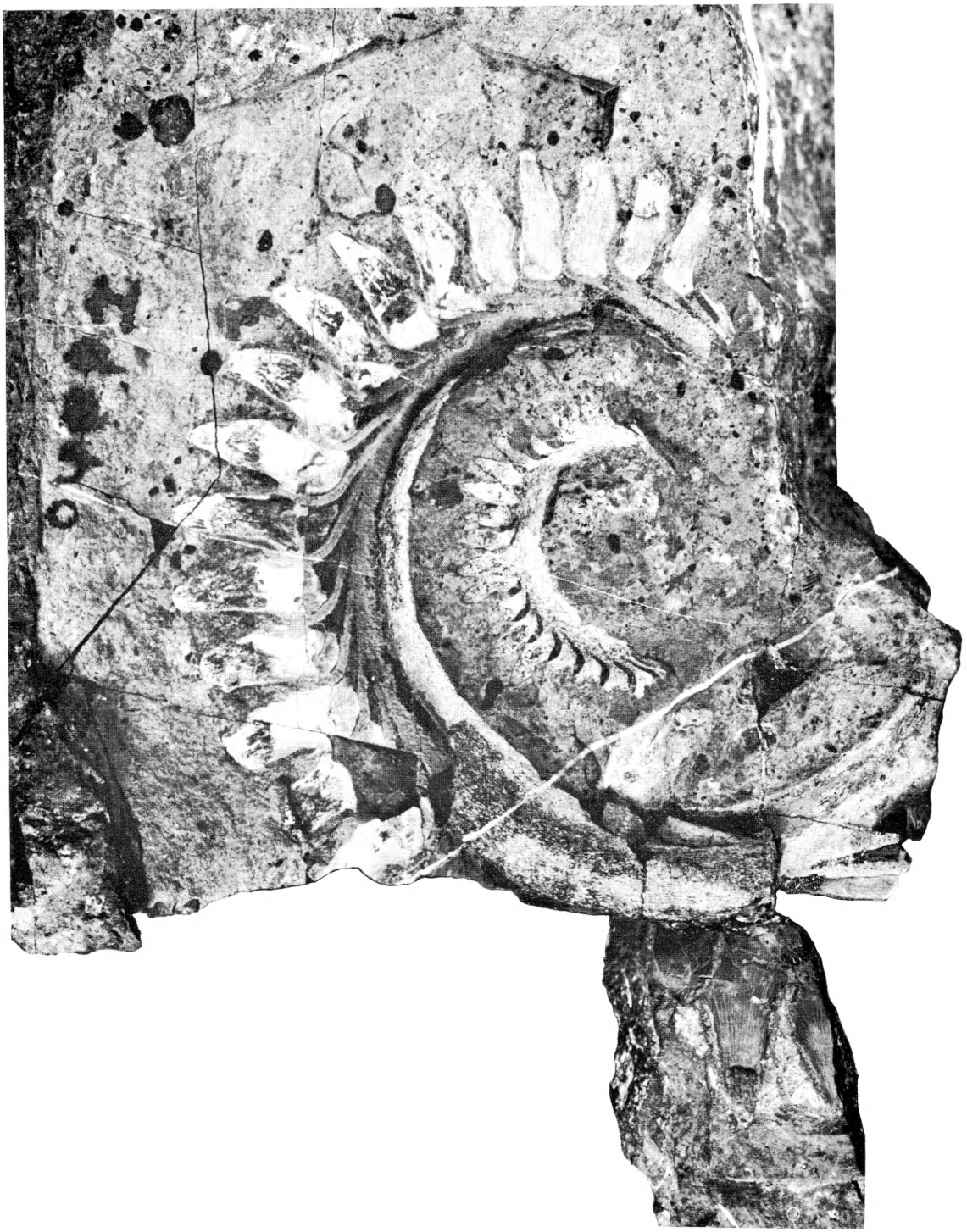


PLATE XIV

*Helicoprion ferrieri* HAY.

Fig. 1–2: Idaho no. 2.
0.8× nat. size.

Original specimen and cast in PVC-plastic. The minute, densely set openings for the vascular canals occuring laterally on the compound root can be seen on the cast.

Fig. 4: Idaho no. 3.
0.5× nat. size.

Badly preserved parts of two volutions of a tooth-spiral, possibly the second and the third.

*Helicoprion sp. indt.*

Fig. 3: Idaho no. 6.
0.7× nat. size.

All specimens photographed dry.

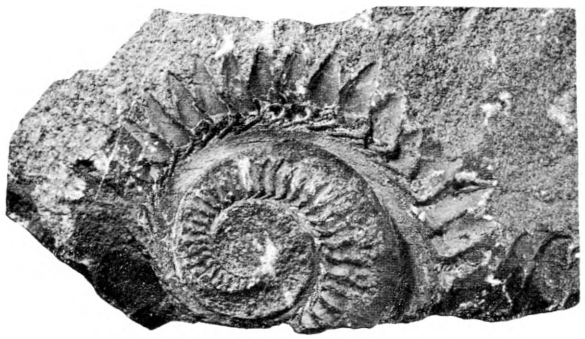


Fig. 1

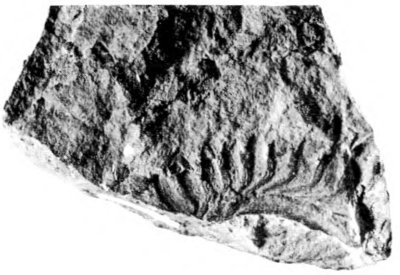


Fig. 3

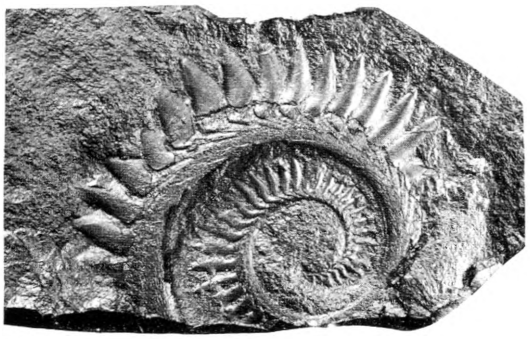


Fig. 2

Fig. 4

PLATE XV

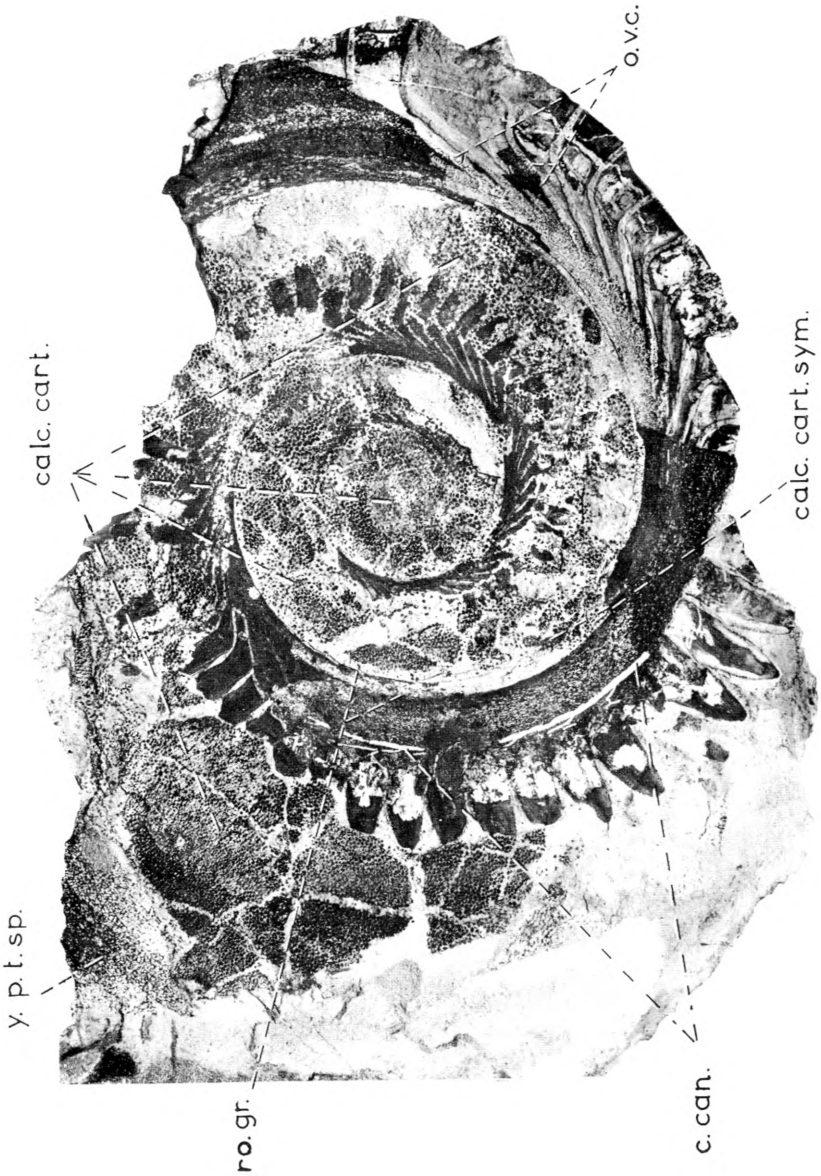
*Helicoprion ergasaminon* n. sp.

Idaho no. 5.

0.6× nat. size.

Photographed in Xylene.

calc. cart.: calcifications from the cartilage of the lower jaw. calc. cart. sym.: calcifications from the symphyseal crista. c. can.: the central canal of the compound root. Some of the branches for the nutritive vessels diverging from the main canal into the tooth-crowns can be seen. o. v. c.: openings for vascular canals. ro. gr.: the groove on the ventral side of the compound root. y. p. t. sp.: the last formed part of the compound root.


o.v.c.
calc. cart.
calc. cart. sym.
y. p. t. sp.
ro. gr.
c. can.

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