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Under Ledelse af Lauge Koch

ON NEW OR LITTLE KNOWN *EDESTIDAE* FROM THE PERMIAN AND TRIASSIC OF EAST GREENLAND

BY

EIGIL NIELSEN

WITH 23 FIGURES IN THE TEXT
AND 13 PLATES

KØBENHAVN
C. A. REITZELS FORLAG
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PREFACE

Most of the material treated in the present paper belongs to the large collections of Permian and Triassic vertebrates secured by the author during his stays in East Greenland in the years 1932—33 and 1936—38 as a member of Dr. LAUGE KOCH's expeditions. A single, especially beautiful specimen of *Erikodus* was added to the collection in 1947, when I participated in Count EIGIL KNUTH's Danish Peary Land Expedition.

I am greatly indebted to Dr. LAUGE KOCH and to Count EIGIL KNUTH for their permission to describe the valuable finds.

Even many years ago some of the specimens dealt with here were cleaned and prepared by the conservators of the Palæozoological Department of the Swedish Riksmuseum. Part of the photographic work as well as some very skilfully done retouch work were likewise carried out in Stockholm, by Mr. AHL and Mr. S. EKBLOM, respectively, both of them members of Professor E. STENSIÖ's trained staff. To these two gentlemen I tender my most cordial thanks, and to Professor E. STENSIÖ I wish to express my sincere gratitude for permitting me to work in his famous institute.

In Copenhagen, the photographic work was done by Mr. CHR. HALKIER, conservator at the Mineralogical and Geological Museum; the text-figures were drawn by Miss INGEBORG FREDERIKSEN. To both of them I express my best thanks for their careful work.

INTRODUCTION

During Dr. LAUGE KOCH's expeditions to East Greenland in 1926—27, 1929, and 1930, remnants of Ganoids and Elasmobranchs were secured from beds then taken to be of Carboniferous age or (LAUGE KOCH 1929a, p. 95, 1929b, p. 244) in part even a little older. The bulk of the material was collected from marine deposits in the Kap Stosch area, at Hirdhavn, and in Margrethedal, while a few specimens were secured from freshwater deposits exposed at the southern part of Kongeborgen on Traill Ø.

Of the fish-bearing deposits mentioned here, those at Kongeborgen are still regarded as Carboniferous, while the marine beds at Kap Stosch, Hirdhavn, and Margrethedal are now generally considered to be of Upper Permian age (cf. p. 48, text-fig. 19.).

The small collection of Permian and Carboniferous fishes obtained on the early East Greenland expeditions was described by me in 1932 immediately before I left for East Greenland as a member of the Danish Three-Year Expedition to undertake a detailed study of the little known vertebrate-bearing Permian and Triassic beds at Kap Stosch and at Hirdhavn. During this stay in Greenland in 1932—33 I succeeded in securing a very large collection of marine Permian fishes including many interesting specimens, and this collection was further increased during my stay in East Greenland in 1936—38 as a member of another of Dr. LAUGE KOCH's expeditions. Finally, in 1947, as a member of the Danish Peary Land Expedition, I was again able to collect from the Permian deposits at Kap Stosch.

The large new collections comprise both Ganoids and Elasmobranchs, but so far only the Ganoids collected in 1932—33 have been described (ALDINGER 1937). The present paper is a study on some of the most important specimens of Edestids contained in the collections from the Permian beds at Kap Stosch, and on a single Triassic Edestid specimen likewise collected in the Kap Stosch area. The remaining part of the material of Permian Elasmobranchs will be dealt with in a later paper.

My reason for publishing my studies on the Edestids in a separate paper is that the fundamental idea—the lepidomorial theory—in a forthcoming paper by STENSIÖ and ØRVIG on the structure of scales, teeth, and dermal bones, is based mainly on investigations of the Danish collections of Permian Edestids from East Greenland (cf. ØRVIG 1951, pp. 366—368, 387—393), and that ØRVIG's histologic studies on the endoskeleton of the *Bradyodonti* (ØRVIG 1951, pp. 416—422), also, are mainly based on the same material.

As regards the numbering of the specimens treated in the present paper, I wish to put forward the following remarks: The enormous Danish collections of fossil vertebrates from Greenland comprise numerous forms belonging to different faunas and derived from several geological periods. The different faunal or systematical units have been distributed for description among a number of scientists, and as a rule these scientists have numbered their parts of the collections independently of each other instead of using a continuous numbering for the whole material. This is much to be regretted from a museum point of view, in so far as the fact that several specimens carry identical numbers may easily cause some confusion. However, until the whole material has been returned to Denmark, it is more or less impossible to re-number the specimens in a satisfactory way. As to the present paper, I have therefore temporarily numbered the Permian specimens dealt with in continuation of my numbering of the specimens treated in my first paper on the Permian fishes (1932). The single Triassic Edestid has not received any number so far, as it will be dealt with again later on in my monograph on the Triassic fishes.

The list of Permian Bradyodonts given in my first paper on the fauna from East Greenland was as follows:

Family *Edestidae*.
Agassizodus groenlandicus n. sp.
Fadenia crenulata n. g. et n. sp.

Family *Copodontidae*.
Copodus (?) sp.

Family *Petalodontidae*.
Janassa kochi n. sp.

The fresh collection necessitates a very considerable revision of this list, thus addition of new forms not represented in the old material as well as re-interpretation of the forms already treated. Of special importance is the identification of complete symphysial teeth of the species previously described as *Agassizodus groenlandicus*. The finds of such complete teeth have shown beyond doubt that the fragmentary teeth previously referred to the family *Copodontidae* and described as *Copo-*

dus(?) sp. are actually symphysial teeth of *A. groenlandicus*, and moreover that this form does not belong to the genus *Agassizodus*, but represents a separate genus, which I have named *Erikodus* in honour of my former teacher, Professor Erik Stensiö. A new, very interesting Edestid genus, *Sarcoprion*, with a single species, *S. edax*, is represented by four specimens, the most complete of which comprises the whole anterior portion of the head, thus being one of the finest specimens of Edestids ever found. New forms of Petalodonts have also been discovered in the material, but they are not dealt with in the present paper.

According to the above, the revised list of Permian Bradyodonts from East Greenland will be as follows:—

Family *Edestidae*.
Sarcoprion edax n. g. et n. sp.
Erikodus groenlandicus (E. Nielsen) n. g.
Fadenia crenulata E. Nielsen.

Family *Petalodontidae*.
Janassa kochi E. Nielsen.
One or two other Petalodonts.

The only Triassic Edestid specimen found represents a new genus, *Parahelicampodus*, with the single species *P. spärcki*, named in honour of Professor Dr. R. Spärck, head of the Zoological Museum of the University of Copenhagen, in recognition of his indefatiguable efforts to provide means and working facilities for Danish vertebrate palæontology.

DESCRIPTION OF THE MATERIAL

Sarcoprion n. g.

Diagnosis: Head with long and tapering preorbital portion represented by a double-walled capsule of calcified cartilage comprising a neurocranial and a palatoquadratal component fused in a holostylic way. External nasal openings presumably placed about midway between the anterior end of the rostrum and the orbit. On the ventral face of the double-walled head capsule a conspicuous longitudinal groove. Lower jaw, also, consisting of calcified cartilage and with an extremely long symphysial part.

Skin of preserved part of head armed with densely set smaller and larger scales of more or less complicated structure. Dentition comprising a single upper and a single lower series of large mutually fused symphysial teeth, numerous lateral series of small simple teeth, and along the lower series of symphysial teeth a pavement of small parasymphysial teeth, the roots of which are in places fused with each other or with the roots of the large symphysial teeth. Lower symphysial series rather strongly curved, though not forming a spiral. Upper symphysial series almost straight. Crowns of both upper and lower symphysial teeth with a very strong cutting blade and a long antero-ventro-laterally directed paired lateral division. Roots of symphysial teeth mainly situated between right and left lateral parts of crown. On basal face of fused roots of lower symphysial series a broad and deep longitudinal groove. Cutting edges of the blades extremely finely serrated. Ornamentation of coronal faces of the crowns of the symphysial teeth consisting of fine ridges, which on the cutting blades have an almost straight course from apex to base, and on the paired lateral parts of the crowns form a more intricate pattern. Lateral teeth of the *Orodus-Campodus-Agassizodus* type. All teeth with strongly folded labial and more finely crenulated lingual margin.

Remarks.—With regard to the general type of its symphysial teeth, *Sarcoprion* decidedly belongs to the *Helicoprion* group within the family *Edestidae*. Among the previously known members of the *Helicoprion* group, *Sarcoprion* shows the closest resemblance to *Helicampodus* and

Lissoprion, especially in the strong development of the cutting blades and in the very fine serration of the cutting edges.

Sarcoprion differs, however, from these two genera in the greater width of its symphysial teeth and in possessing a pavement of para-symphysial teeth along the margin of the lower symphysial series. This latter character is only known in one other Edestid, viz. *Campyloprion*

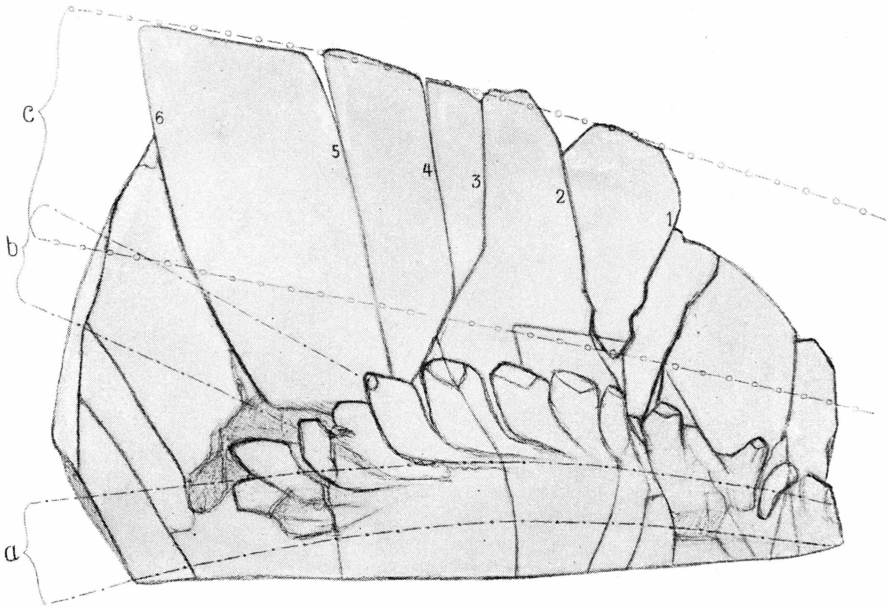

Fig. 1. *Sarcoprion edax* n. sp. Sketch of the holotype (specimen no. 214) in dorsal view. C. 0.3 ×. *a* and *b*, right and left half of the lower jaw; *c*, incomplete preorbital part of the skull; *1—6*, sections nos. *1—6* through the preorbital part of the skull.

(Eastman 1902, pp. 64—69, pl. 4), but the large symphysial teeth of *Campyloprion* are very different in shape from those of *Sarcoprion*.

Sarcoprion edax n. sp.

(Text-figs. 1—7, 10—15; pl. 1, figs. 1—2; pl. 2, figs. 1—3; pl. 3, figs. 1—3; pls. 4—6; pl. 7, figs. 1—3; pl. 8, figs. 1—4; pl. 9, figs. 1—2).

Syn. 1935. An *Edestus*-like symphysial row of teeth. E. Nielsen, p. 97.

Material and localities.—The material comprises four specimens (nos. 214—217), all from the Permian fish-zone in the upper part of the *Posidonomya* beds in the Kap Stosch area (cf. E. Nielsen 1935, pp. 16—21). Specimens nos. 214 and 215 were collected at River 14, and nos. 216 and 217 between River 8 and River 9. Specimen no. 214 consists of a considerable anterior part of a head with most of the dentition, while specimen no. 215 is a series of five beautifully preserved symphysial teeth, parts of the endoskeleton of the head, and numerous scales, specimen no. 216 is the apical end of the cutting blade of a symphysial tooth, and specimen no. 217 consists of fragments of the endoskeleton of the head and numerous scales.

Holotype.—Specimen no. 214, which is by far the best preserved and the most complete of the four specimens, is chosen as a holotype. This unique specimen comprises the incomplete anterior part of a skull with jaws, the lower series and parts of the upper series of symphysial

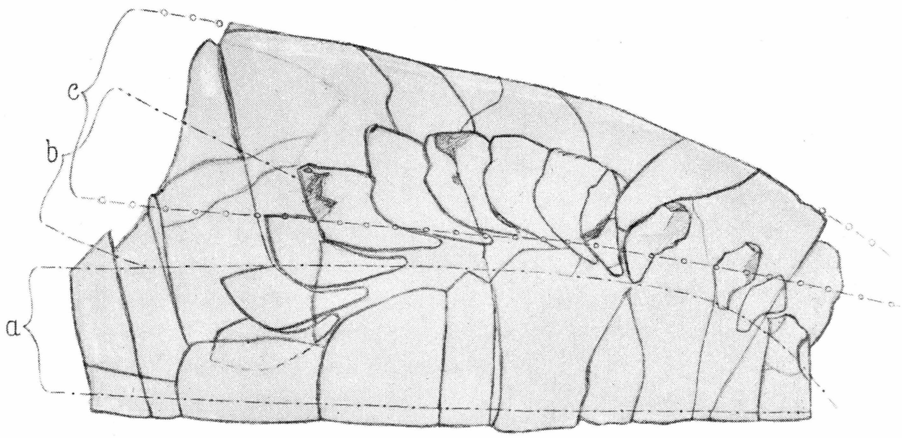

Fig. 2. *Sarcoprion edax* n. sp. Sketch of the holotype (specimen no. 214) in lateral view. C. 0.3 ×. Lettering as in fig. 1.

teeth, a very large number of lateral teeth, and a still larger number of scales of greatly varying size. The endoskeleton of the head consists of strongly calcified cartilage, which, though in places somewhat compressed, is not seriously crushed. The lower row of symphysial teeth is still *in situ*, while the upper symphysial row as well as most of the lateral teeth and many of the scales no longer occupy their original position, neither in relation to each other nor in relation to the preserved parts of the endoskeleton of the head.

General remarks.—Specimen no. 214 was discovered in 1932 in one of the large concretions characteristic of the fish zone in the *Posidonomya* beds. A large part of the concretion was lacking, and although two important fragments were secured during my search in 1937, there is not very much hope that all the lacking pieces will ever be found, for probably they are scattered over a large area of the steep slope of the mountain.

The preserved parts of the concretion (text-figs. 1—2), on the weathered surface of which the fossil was exposed in several places, showed a tendency to splitting almost perpendicularly to the bedding

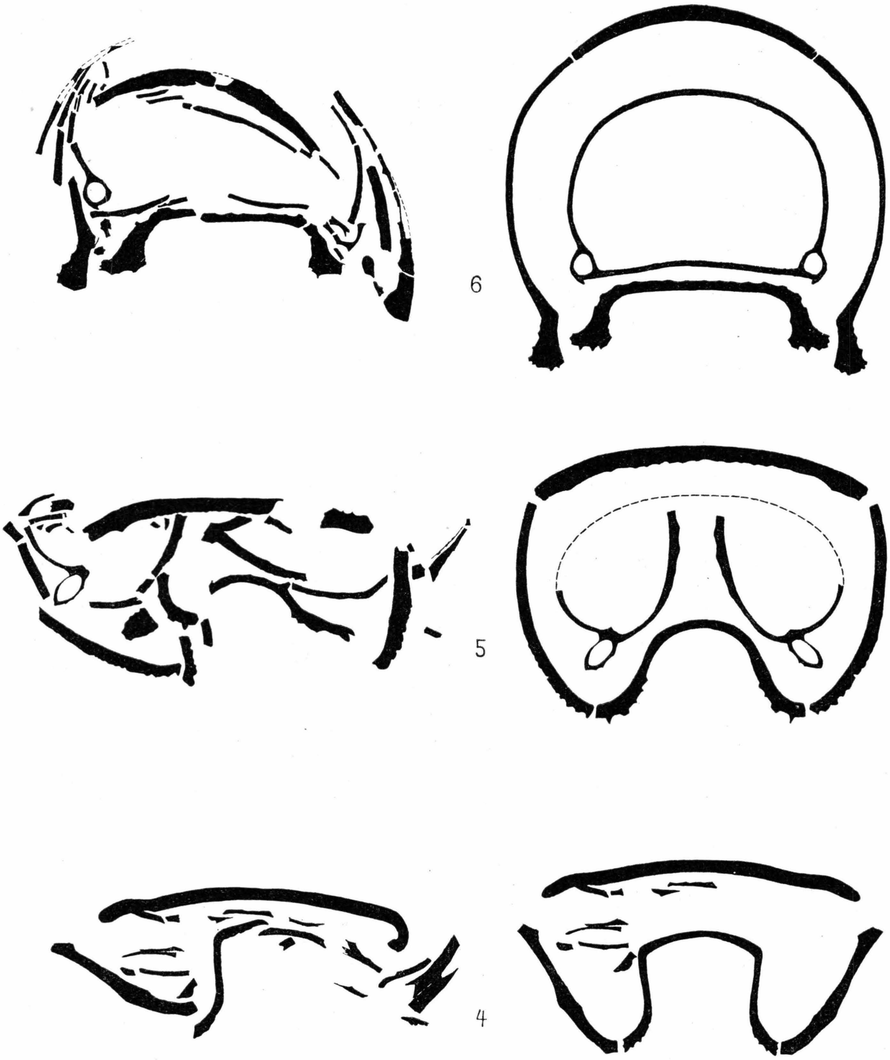

Fig. 3. *Sarcoprion edax* n. sp. Sections nos. 4—6 (left) through the preorbital part of the skull and the corresponding restored cross-sections. Specimen no. 214. 0.4 ×.

planes rather than along these, or along the surface of the fossil, and as, moreover, the matrix of the concretion was very hard, it turned out to be very difficult to get the fossil sufficiently exposed for a detailed examination. Much of this difficult work was carried out at the Swedish Riksmuseum, Stockholm, during my absence, and certain parts of the fossil, especially the big symphysial teeth, were rather seriously damaged during the process. For the present publication I have not carried the preparation very much farther, although parts of the fossil are still hidden in the rock; I have instead utilised the many fresh surfaces obtained by the splitting of the concretion during the preparation in Stockholm, to study a number of sections through the fossil, and in this way I gained quite a satisfactory picture of all the more important structural details. Some of the fresh surfaces obtained by splitting were polished in order to obtain a better contrast between the calcified cartilage and the matrix. Others were, for the same purpose, etched by means of a weak solution of hydrochloric acid.

The following structures have now been localised:

1. A large capsule of calcified cartilage, the hindmost portion of which contains a smaller capsule, likewise of calcified cartilage. The structure, which extends through the whole length of the concretion, and is seen in cross-section both on its anterior and its posterior face, can only be interpreted as the greater part of the preorbital division of the neural endocranium fused in a holostylic manner with the palatoquadrate.
2. The greater part of the lower jaw, likewise of calcified cartilage and with an extremely long unpaired symphysial portion.
3. A small structure of calcified cartilage situated midway between the posterior ends of the right and the left member of the lower jaw and representing a basihyal.
4. The almost complete lower symphysial series with adjoining parasymphysial teeth and parts of the upper symphysial series.
5. Several hundreds of small teeth, which must originally have been arranged in lateral series on the upper and lower jaws, but which, during the decay of the soft tissues, have become detached from their places on the jaws and have subsided towards the lower part of the concretion.
6. Large numbers of scales of varying size and shape, once densely set in the skin, but now only occupying their original mutual positions on the ventral part of the lower jaws, viz. on that part of the head which was probably first buried after the death of the animal.

The remnants of the skull.—The big structure interpreted above as the foremost part of the neural endocranium fused with the underlying part of the palatoquadrate, in its present incomplete state measures about 35 cm in a rostro-caudal direction. Much of the dorsal part of the structure is exposed on the weathered upper surface of the concretion, and other details could be studied from six sections (nos. 1—6), the mutual positions of which are indicated in text-fig. 1. As is evident from this figure, the six sections (text-figs. 3—4; pl. 1, figs. 1—2; pl. 2, figs. 1—3; pl. 3, fig. 1) are not absolutely parallel to one another, nor

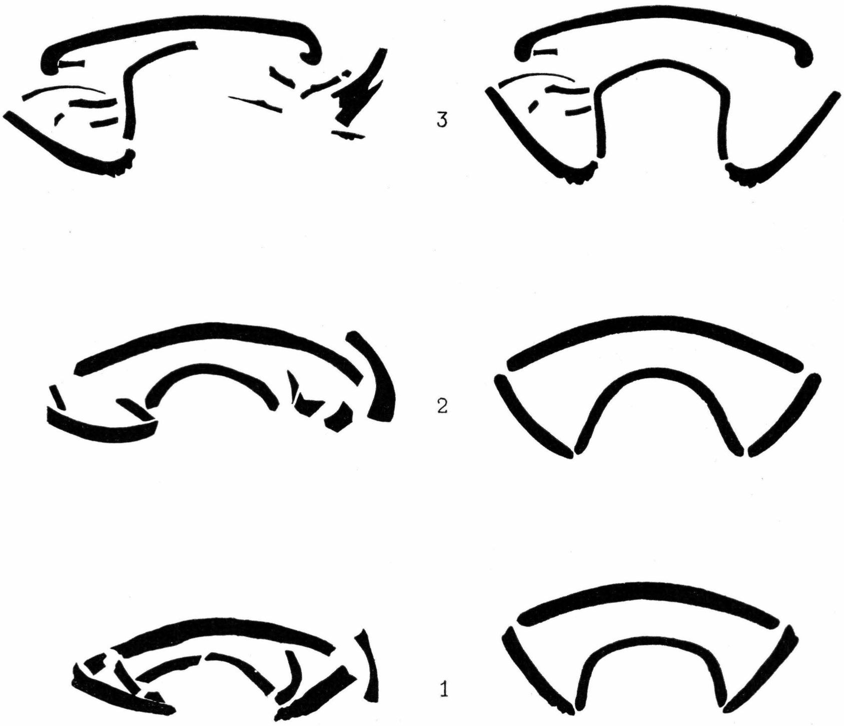

Fig. 4. *Sarcoprion edax* n. sp. Sections nos. 1—3 (left) through the preorbital part of the skull and the corresponding restored cross-sections. Specimen no. 214. 0.4 ×.

are they quite perpendicular to the main axis of the whole structure. Moreover, the outlines of the sections show a considerable deformation owing to post-mortem compression of the animal. In spite of these difficulties it was possible, on the basis of the six sections, to reconstruct six transverse sections (text-figs. 3—4), which, though they can hardly claim to be regarded as anything but rough sketches, offer a sufficient basis for a preliminary reconstruction of the main part of the preorbital division of the skull of *Sarcoprion* (text-figs. 5A and 5B).

As mentioned above, this part of the skull might be described as a big capsule of calcified cartilage, in the hindmost part of which another, smaller, capsule is enclosed. In the following pages these two capsules will be referred to as the outer and the inner capsule, respectively. The outer capsule (text-fig. 5), which, as already mentioned, is cut off abruptly by fractures both anteriorly and posteriorly, has a dorsal, a paired lateral, and a ventral wall. In the reconstructed transverse sections (text-figs. 3—4) these walls are separated from each other by mostly narrow interspaces, which are present on the original sections, but the possibility exists that these interspaces, or most of them, merely represent longitudinal fractures of the wall of the capsule. As far as I can see, however, there can only be little doubt that the interspaces between the ventral wall and the lateral walls in section no. 6 (text-fig. 3) and those between the lateral and the dorsal wall in sections nos. 3 and 4 (text-figs. 3—4) are not due to fractures. Thus, in section 6, both the lateral margin of the ventral wall and the ventral margin of the lateral walls show distinct thickenings, the outlines of which render it impossible to believe that they have been separated by mere fractures, and in section no. 3 the lateral margin of the dorsal wall is bent downward in such a way as seems to indicate that a well-defined opening existed in this place between the dorsal and the lateral wall. As will be discussed below (p. 18), this opening can most adequatedly be interpreted as a fenestra endonarina communis.

The dorsal wall of the outer capsule is slightly curved from side to side, with the concavity facing downward, but it shows no visible curvature in a rostro-caudal direction. From section no. 5 to section no. 1 the dorsal wall decreases in width from 11.0 to 8.3 cm, in section no. 6 the dorsal wall measures only about 8 cm in width, if the fissures separating it from the lateral walls are not mere post-mortem fractures.

In section no. 6 the dorsal wall decreases a good deal in thickness towards its lateral margin; in the other sections the thickness is more uniform, except in section no. 3, where the downward bent marginal zones of the wall show a very distinct thickening.

The paired lateral wall is fairly straight in a rostro-caudal direction, but is slightly curved in a dorso-ventral direction, with the concavity facing inwards. This curvature is especially marked in the two hindmost sections; in section no. 6, however, the ventralmost part of the wall, instead of being bent, extends straight downwards at the same time as it increases very considerably in thickness. A comparison of the six sections shows that the lateral wall, which is roughly vertical farthest posteriorly, assumes an increasingly oblique position towards its anterior end, the width of the ventral wall of the capsule decreasing in a forward direction more strongly than that of the dorsal one. The lateral wall itself decreases gradually in height from about 10.5 cm in section no. 6 to about 3 or 3.5 cm in section no. 1.

The ventral wall shows a distinct rostro-caudal bend with the concavity facing downwards, and is very strongly bent from side to side in such a way that it forms the dorsal and lateral walls for a deep and broad groove extending in a longitudinal direction from the hindmost to the foremost end of the capsule. This groove attains its greatest depths in sections nos. 3—4, whence it decreases gradually in depth both forwards and backwards. There can be no doubt that the dorsal row of symphysial teeth was attached to the bottom of this groove, and that it furthermore lodged the distal parts of the ventral symphysial series when the mouth was closed. Except farthest anteriorly, the outer face of the lateral part of the ventral wall and the outer face of the ventral part of the lateral wall are provided with a pattern of densely set shallow pits, which are distinctly seen in the figures of sections nos. 3—6. Similar pits are present in the jaws of both *Fadenia* and *Erikodus*, and there is no doubt that in these two forms the pits have

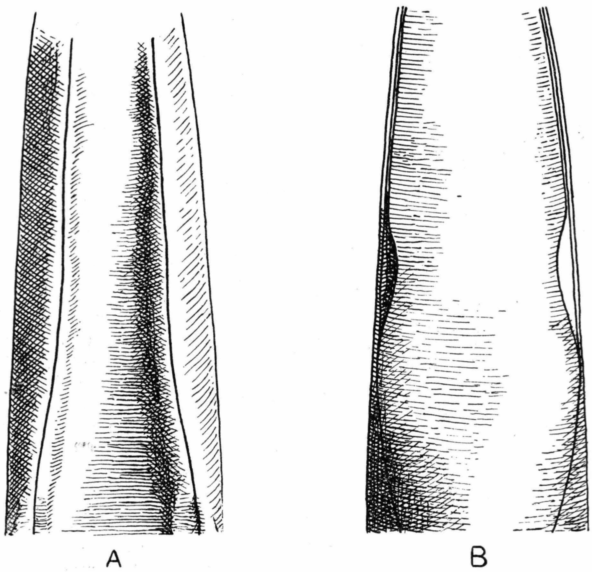

Fig. 5. *Sarcoprion edax* n. sp. Attempted restoration of the preorbital part of the skull in (A) ventral and (B) dorsal view. Based on specimen no. 214. 0.2 ×.

functioned as pockets for the basal ends of the roots of the lateral teeth, for these teeth are often observed in their original position on the jaws. As regards *Sarcoprion*, the pits must have had a similar function, though here the lateral teeth have never been found *in situ*.

The inner capsule, the walls of which are generally less massive than those of the outer capsule, can only be studied on the two hindmost sections. In section no. 6 the dorsal and the lateral walls of the inner capsule pass quite gradually into one another and have a curvature from side to side corresponding closely to that of the outer capsule, from which they are separated by a rather large interspace. The ventral wall is almost straight from side to side, and is only separated by a very narrow interspace from the median part of the ventral wall of the outer capsule. At the place where the ventral and the lateral wall join, the wall of the inner capsule is much thickened and contains a longitudinal canal, the transverse section of which is almost circular.

In section no. 5 the inner capsule is so greatly damaged that anything like an exact restoration is out of the question. As far as can be made out, the capsule was here probably divided more or less completely into a right and a left half, each of which has a rounded outline with a somewhat greater height than width. On its most ventral part the wall of the paired capsule has a conspicuous thickening, appearing in the restored section as a strong process extending in a ventro-lateral direction from the outer face of the paired capsule. The process encloses a space which undoubtedly represents a more anterior section through the longitudinal canal already described from section no. 6. In the more anterior sections, no remnants of an inner capsule can be identified with certainty, although a number of small fragments of calcified cartilage are found enclosed in the outer capsule in sections nos. 3 and 4.

There can be no reasonable doubt that the large bilaterally symmetrical element dealt with above forms part of the calcified endoskeleton of the anterior part of a skull which differs considerably in general shape and detailed structure from all the other Elasmobranch skulls known so far. How far behind the preserved part of the skull the orbits were situated, it is impossible to estimate, and the length of the lacking foremost end of the capsule cannot be ascertained either. It is probable, however, that the preserved part of the capsule represents the main part of the preorbital division of the skull.

The peculiar fact that the preserved structure consists of an outer and an inner capsule well separated from each other, might be explained by assuming that the skull had originally a single very massive wall of cartilage, a thin superficial inner and outer layer of which were impregnated with lime-salts, while the impregnation never spread to the central parts of the wall. The posterior division of the thick-walled capsule contained the foremost part of the cavum cerebrale cranii, which was divided most anteriorly into a right and a left half, each of which contained one of the olfactory lobes. The more anterior part of the capsule was developed as a strong rostrum, which probably contained an unpaired precerebral cavity lined with uncalcified cartilage. The well defined large paired foramen piercing the wall of the outer capsule in the cross-sections nos. 3 and 4 has such relations to the presumed cavities for the olfactory lobes that it is tempting to identify it with the fenestra endonarina communis, and if this identification is correct, the small fragments of calcified cartilage lying just inside this foramen might be interpreted as the remnants of the ala nasalis, the exact shape of which, however, cannot be made out on the basis of the available sections.

In the above consideration of the preorbital part of the skull of *Sarcoprion* as a continuous thick-walled capsule we have disregarded the possible presence of the above-mentioned four longitudinal fissures separating the dorsal, the paired lateral, and the ventral walls of the outer capsule of calcified cartilage. If these fissures are not mere post-mortem fractures, the structure of the capsule must have been somewhat more complicated than sketched above, though there can be little doubt that at least most of the interspace between the inner and the outer capsule was in any case occupied by uncalcified cartilage. Nor have we considered the significance of the presence on the ventral face of the outer capsule of numerous lateral rows of small crushing teeth and of the single median series of large teeth with a laterally compressed cutting blade. The fact that such teeth were situated on the ventral face of the capsule itself, indicates that a palatoquadrate component is included in the capsule, which must therefore be regarded as the preorbital part of the neural endocranium fused in a holostylic manner with the palatoquadrate.

Even if the longitudinal fissures through the outer capsule existed in the living animal, they cannot be explained as sutures between the neurocranial and the palatoquadratal components of the skull, for in that case the palatoquadrate would have occupied a most awkward position in relation to the neurocranium, while most of the teeth would still have been situated on the neurocranial component.

The lower jaw.—From the posterior face of the concretion, which shows cross-sections both of the right and the left half of the lower jaw (text-fig. 6, A and B; pl. 4), we are able by the aid of the sections at hand (pl. 7, fig. 1; pl. 8, figs. 1, 4) to trace the jaw forwards to the anterior end of the concretion and to form a very satisfactory idea of its shape (text-fig. 7). It is not possible to estimate the length of the complete jaw, probably, however, the lacking anterior part has been very short. The length of the preserved part is about 37 cm.

Farthest posteriorly the right and the left half of the lower jaw are well separated, as shown in pl. 4, but their mutual distance decreases rapidly in a forward direction, and already about 12 cm from their posterior ends they join, to continue further forward as a single element without any visible traces of a paired origin.

Thus the preserved part of the lower jaw may be described as an Y-shaped hollow rod of calcified cartilage placed with the stem of the Y directed forward. Probably the cavity of the rod was largely filled with uncalcified cartilage in the living animal, the preserved calcified walls presumably only representing a surface layer of the Meckelian cartilage.

In transverse section the posterior paired portion of the jaw is rounded triangular, with a medial, a dorso-lateral, and a ventro-lateral wall, all three of which are curved in such a way that they pass gradually into one another. The ventro-lateral wall and the ventral part of the medial wall are here especially thick.

Towards the area where the right and the left half of the jaw meet, the medial wall except the most ventral part, grows gradually thinner, to disappear completely just behind the place of junction. No good sections have been obtained through the posterior part of the unpaired portion of the jaw, which is here much damaged by pressure; further

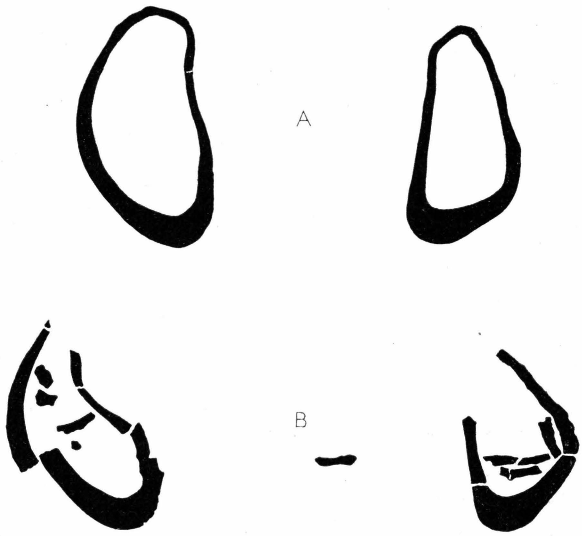

Fig. 6. *Sarcoprion edax* n. sp. Section through the right and the left half of the lower jaw and the basihyal (B), and attempted restorations (A) of the sections through the jaw. Specimen no. 214. 0.4 ×.

forwards, however, the unpaired portion is rounded triangular in transverse section (pl. 7, fig. 1), with a ventral and a right and a left dorsolateral wall, all three of which are fairly massive. At its foremost end the jaw, which farther posteriorly is about 7 cm, and at the point of junction between its right and left halves about 6 cm high, suddenly decreases very rapidly in height, its transverse sections assuming an oval outline with the horizontal diameter about twice as long as the vertical one.

According to the above, the lower jaw of *Sarcoprion* is especially characterised by its extremely long symphysial portion. On this unpaired part of the jaw there still rests the lower row of very large symphysial teeth, while the postsymphysial paired part of the jaw was originally armed with numerous rows of small crushing teeth similar to those of the upper dentition. Most of these lateral teeth have become detached from the jaws and are now found scattered in the surrounding matrix. In places, however, their original positions are still indicated by shallow pits in the surface of the jaw.

The basihyal.—About midway between the sections of the right and the left half of the lower jaw a small plate of calcified cartilage can be observed on the posterior face of the concretion (text-fig. 6B; pl. 4).

The plate has a maximum thickness of 3 mm and a width of 13 mm. From the plate to the right and the left half, respectively, of the lower

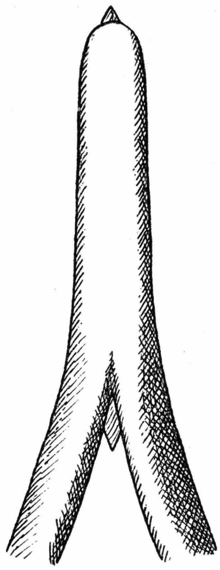

Fig. 7. *Sarcoprion edax* n. sp. Attempted restoration of the lower jaw in ventral view. Specimen no. 214. 0.2 ×.

jaw extends, as shown in pl. 4, an extremely thin, dark, horizontal line, which forms the base of a layer of small scales of the same type as those on the outer surface of the head. Similar scales also occur on the dorsal face of the small plate itself. On both the dark line which may represent the superficial layer of the floor of the mouth, and the small plate, the scales are seemingly still *in situ*, and from the whole arrangement it is evident that the plate, also, occupies its original place. There can be no doubt, therefore, that the plate is the foremost, ventral, unpaired element of the visceral endoskeleton, viz. the basihyal. As seen in pl. 4, another, more dorsally placed, layer of small scales parallel with, but separated by an interspace from, the one just described occurs on the same face of the concretion, and a third layer of scales, and even teeth, with the same direction is found a little more dorsally between the members of the lower jaw. In the two upper layers the scales and teeth lie haphazardly distributed among each other and are not, as in the basal layer, underlain by a black line. As far as I can see, the two upper layers have arisen during the burying of the animal. The mouth cavity has been slowly filled with a mud-like sediment, and twice during this process a larger number of scales and teeth have slipped down from the still unburied part of the head region to the surface of the sediment in the mouth cavity.

The lower and upper symphysial teeth.—The lower series of symphysial teeth is especially well preserved in the holotype (text-figs. 10, 11, 12, 13A; pls. 5—6; pl. 7, figs. 1—3), where it forms the most conspicuous element of the preserved part of the dentition. The series comprises 15 bilaterally symmetrical teeth, forming a gently curved arch still resting *in situ*, or nearly so, on the symphysial portion of the lower jaw. The foremost part of the series has been slightly damaged before the surrounding matrix hardened sufficiently to offer protection against strong pressures. The distal tips of the teeth of the middle part of the row originally protruded from the upper face of the concretion and are now lacking owing to weathering. The distal parts of most of the hindmost teeth were somewhat damaged during the first attempts to remove them from the matrix. Otherwise, however, this symphysial series is in a very fine state of preservation and, as far as can be judged, it is almost complete, i. e. probably only very few teeth are absent from its posterior end, and perhaps none at all have been lost anteriorly since the death of the animal.

Specimen no. 215 shows a series of symphysial teeth (pl. 3, fig. 2), which, according to their shape, must have belonged to a lower symphysial arch. The series comprises only 5 teeth and is evidently a fragment of a much larger series.

In the following description the most complete specimen of the two will first be dealt with.

In this specimen the teeth increase in size from the foremost (and oldest) to the hindmost one, and more rapidly than is normally the case within the *Helicoprion* group. The difference in size from one end of the series to the other is further accentuated by the fact that the crowns of the oldest teeth have been much worn during the lifetime of the animal, so that they are now much shorter than when they first appeared.

For practical reasons I have numbered the teeth, starting from the foremost end of the series, and for a detailed description I have chosen tooth no. 14, because it is almost unworn and has sustained practically no damage either by weathering or by preparation.

Karpinsky, in 1899 and later, and after him several other writers have used a special morphologic terminology in describing the teeth of

Helicoprion and related genera, illustrated here in text-fig. 8 (after TEICHERT 1940 (adapted from WHEELER 1939)).

In *Helicoprion* the crowns of the teeth appear as a series of separate enamelled units, while the roots are completely fused mutually to a solid unsegmented bar, the basal part of which protrudes below the crowns as the so-called shaft. Each "tooth", i. e. each of the enamel-covered units on the shaft, is regarded as consisting of a distal cutting blade, a middle portion, and a narrowed base extending forward below the base of the "tooth" next in front of it.

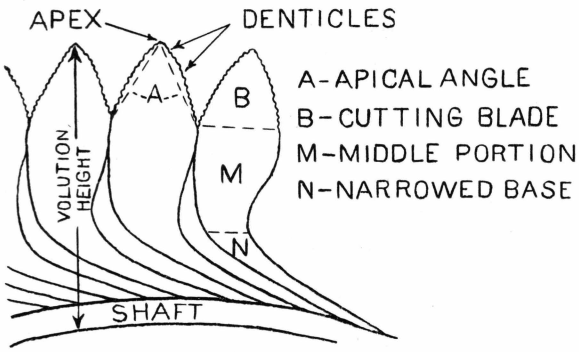

Fig. 8. Morphological terminology of *Helicoprion*. After TEICHERT 1940, fig. 2.

As regards *Sarcoprion*, the crowns of the teeth are also arranged as a series of separate enamelled units with a cutting blade and with homologues to the middle portion and the narrowed base in *Helicoprion*, but it is very difficult to draw a definite boundary between the middle portion and the narrowed base, as the transition between these two divisions is quite gradual. Moreover, the roots of the teeth of *Sarcoprion* are not entirely fused, and no typical shaft is developed.

It has been emphasised by earlier writers, and it is further accentuated by the conditions in the Greenland species of *Fadenia* and *Erikodus*, that the large symphysial teeth of the specialised Edestids might be derived from the simple rectangular lateral teeth of the *Campodus-Agassizodus-Fadenia-Erikodus*-type by compression of such teeth from the ends in such a way that the teeth obtained a sharp bend along a line connecting the lingual and the labial margin and dividing the crown into two equally large divisions. The procedure is shown schematically in text-fig. 9, and it will easily be understood from the figure that what is termed "narrowed base" by WHEELER and TEICHERT (text-fig. 8), corresponds partly to a distal part of a lateral tooth, and that their term "middle portion" does not correspond to the middle portion of the crown of a lateral tooth. In a not compressed tooth placed in a symphysial position it is more natural to distinguish between an unpaired median and a paired lateral part of the crown.

In such cases in which the median part of the crown of the symphysial teeth, besides increasing in height, has developed a cutting edge, as in *Helicoprion*, *Edestus*, *Sarcoprion*, and most other Edestids, the term cutting blade is very convenient, but instead of the two terms "middle portion" and "narrowed base" used by WHEELER and TEICHERT, I prefer, in the following description, to use the new term "paired lateral part of the crown".

The altered terminology is illustrated in text-fig. 10, which also shows the lines along which the various measurements of the teeth

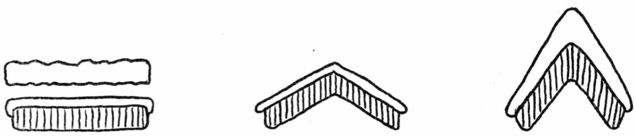

Fig. 9. Sketch illustrating the transition from a simple lateral tooth (A) to a laterally compressed symphysial tooth (C).

mentioned in the subjoined description were made. The figure further introduces the term parasymphysial teeth for some smaller teeth in *Sarcoprion* arranged as a dense pavement in the area ventro-laterally to the forwardly bent, narrowed ends of the paired lateral parts of the crowns (cf. p. 28).

Tooth no. 14 in the lower symphysial series measures 74 mm from the apex to the lateral end of its labial margin (*A*—*F*) and about 44 mm in greatest width (*J*—*K*). The height of the tooth is 65 mm.

The measurements of the cutting blade are as follows: height (*A*—*L*) 23 mm; length of base (*C*—*D*) 27 mm; greatest thickness (*G*—*H*) 13 mm; apical angle 57°. The anterior and posterior cutting edges are slightly convex except farthest dorsally, where the convexity increases a good deal, though the tooth is very little worn. Seen with the naked eye, both the cutting edges appear to be smooth, but examined under a strong lens they turn out to be extremely finely serrated. The lateral surface of the cutting blade is slightly convex in a dorso-ventral, and rather strongly so in a labio-lingual direction except for a narrow area along the cutting edges, where the surface is almost plane. The surface of the blade is ornamented with a system of very fine ridges extending from the apex to the base line and with a number of very short somewhat broader ridges forming short continuations of the small serrations on the cutting edges.

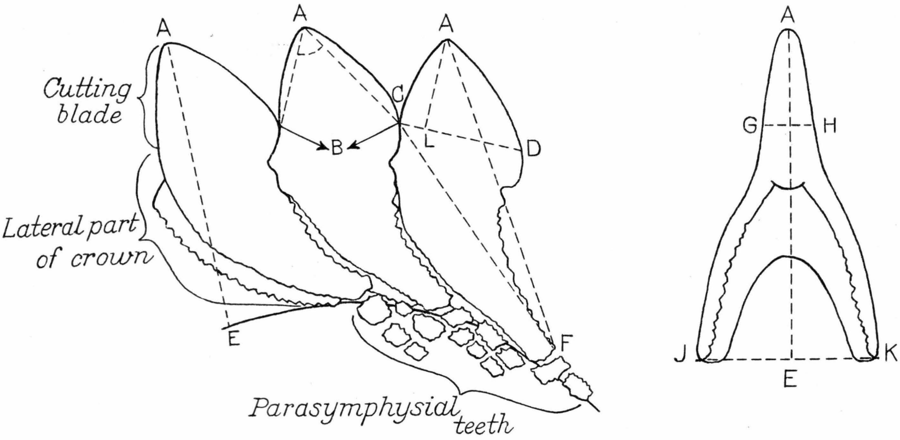

Fig. 10. *Sarcoprion edax* n. sp. Part of the lower symphysial series in lateral view and a single lower symphysial tooth in anterior view. On both figures the lines along which the measurings have been made are inserted. 0.6 ×.
A, apex; *B*, apical angle; *A—E*, height of tooth; *A—F*, distance from apex to lateral end of labial margin of crown; *A—L*, height of cutting blade; *C—D*, length of base of cutting blade; *C—F*, distance from posterior end of base of cutting blade to lateral end of labial margin of crown; *G—H*, greatest thickness of cutting blade; *J—K*, greatest width of tooth.

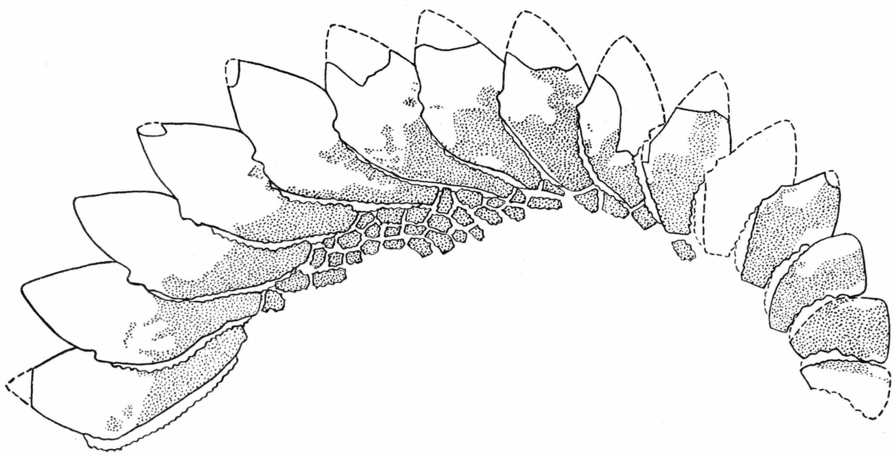

Fig. 11. *Sarcoprion edax* n. sp. Lower symphysial tooth series in lateral view. Slightly restored. Areas of wear dotted. Specimen no. 214. C. 0.4 ×.

The paired lateral part of the crown measures 59 mm from the posterior end of the boundary towards the cutting blade to the lateral end of its labial margin (*C—F*). Apart from its straight-lined boundary towards the cutting blade, it is bounded by a long concave labial, a long convex lingual, and a very short, almost straight, lateral margin.

From the boundary towards the cutting blade the lateral part of the crown extends in a ventro-lateral direction, showing at the same time a forward curvature, which is especially pronounced in its most lateral

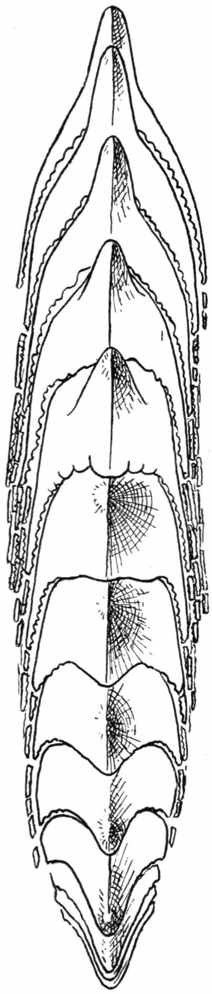

Fig. 12. *Sarcoprion edax* n. sp. Lower symphysial tooth series in dorsal view. Slightly restored. Specimen no. 214. C. 0.5 ×.

half. The width of the lateral part of the crown (i. e. the distance between its labial and its lingual margins) decreases from its medial to its lateral margin, at first slowly, subsequently rapidly, as shown in the figures. As already mentioned, it is not possible, however, to define a line of division between a broader medial and a narrower more lateral portion, corresponding to, respectively, the "middle portion" and the "narrowed base" in *Helicoprion*. In labial or lingual view the lateral part of the crown shows a distinct bend, its broadest part facing more dorsally than its narrow more lateral part. Apart from this distinct bend, the surface of the lateral part of the crown, its delicate ornamentation disregarded, is plane or slightly undulating with a few fairly large shallow depressions, especially near its lingual margin. The ornamentation consists of a pattern of low ramifying ridges running mainly perpendicularly to the labial and lingual margins.

The main part of the root of the tooth is situated in the interspace between the diverging lateral parts of the crown, but a narrow posterior

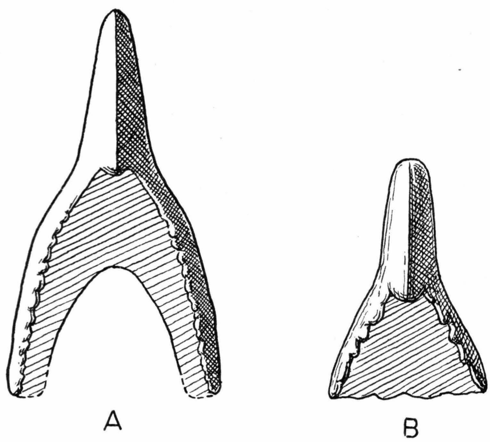

Fig. 13. *Sarcoprion edax* n. sp. Schematic restoration of (A) lower and (B) upper symphysial tooth in anterior view. Roots of teeth ruled. Specimen no. 214. C. 0.8 ×.

part of the root extends beyond the lingual margin of the crown, as shown in the figures. The lateral face of this free part of the root is overlapped by, but not fused with, the foremost part of the root of the tooth next behind. The fissure thus existing between the roots of two adjoining teeth, however, is only a superficial phenomenon, a complete fusion having taken place between the central parts of the adjoining roots throughout the whole series.

The basal face of the root is deeply concave from side to side (text-fig. 13 A), in which respect *Sarcoprion* agrees with most other Edestids. However, a longitudinal canal piercing the more dorsal part of the root, as in *Helicoprion* and other forms, is not developed in *Sarcoprion*.

After this description of one of the youngest teeth in the lower symphysial series, we will briefly consider the alteration in shape and size from one end of the series to the other. As to the alteration in size, it is decidedly more rapid than in *Helicoprion*, but direct comparisons between the smallest and the largest teeth are difficult to carry out, the oldest teeth being very strongly worn. Instead of two sharp cutting edges, these old teeth have a broad, rounded, longitudinal ridge on a much shortened cutting blade, and they are also much worn on their lateral faces.

As the foremost tooth is only a fragment, the following measurements were carried out on tooth no. 2: Distance from top of cutting blade to lateral end of labial margin 28 mm; greatest width approximately 23 mm; height of tooth 25 mm; length of base of cutting blade ca. 18 mm; height of cutting blade ca. 4 mm; length of lateral part of crown (*C—F* on text-fig. 10) ca. 26 mm.

From those of the above measurements which have not been influenced by the wear of the tooth it will be understood that the lateral part of the tooth was considerably smaller compared with the unworn cutting blade than is the case in the largest teeth, and from fig. 11 it will be evident that especially the narrowed end of the lateral paired part of the crown is less developed in the small teeth.

In the area adjoining the ventro-lateral margin of the series of lower symphysial crowns we find, except most anteriorly, where the fossil is damaged, a pavement of smaller flat-crowned teeth, for which I have introduced the term parasymphysial teeth. In fig. 11 only those of the parasymphysial teeth which have been cleaned for matrix are shown. The extent of the not inconsiderable area of parasymphysial teeth not yet exposed has been traced in a number of sections through the concretion, and is shown in the restoration given in fig. 15. As seen in the figures, the parasymphysial teeth are of rather varying size, and although their crowns are in most cases roughly rectangular in outline, some of them are more irregularly polygonal. All the coronal margins are crenulated, and as a rule the crenulations are especially strongly developed on a single margin of each crown. The crowns are ornamented with a pattern of fine ridges of much the same type as those on the crowns of the big symphysial teeth.

The parasymphysial tooth-pavement does not, as might appear at a cursory glance, form a quite haphazardly developed mosaic, but shows unmistakable traces of a serial arrangement. More precisely, the forwardly bent narrowed portion of the lateral part of the crown of each of the bigger main symphysial teeth seems to be continued by one or two series of parasymphysial teeth, which at first extend forwards and then also somewhat downwards. In each series the individual teeth are placed with their main axis parallel to the direction of the series. The arrangement might give the impression that the parasymphysial teeth have arisen by subdivision of the most lateral parts of the main symphysial teeth, and this impression is strengthened by the fact that precisely the margin of each of the small teeth which would represent the labial margin of a large symphysial tooth if a subdivision had taken place, is especially strongly crenulated.

On the other hand, some weighty objections can be raised against the assumption that the parasymphysial teeth have arisen by subdivision of parts of the main symphysial teeth. The general tendency within the Edestids as regards the evolution of the symphysial teeth, as illustrated for instance by the series *Erikodus—Fadenia—Sarcoprion*, goes from small and simple towards large and specialised symphysial teeth, and an initial fragmentation of the large teeth can only be interpreted as an opposite tendency, viz. a tendency toward reduction in size and simplification in shape. That *Sarcoprion*, though a very late member of the Edestid group should show tendencies to degeneration, is not very probable, this form being not by far as specialised as for instance *Edestus* and *Helicoprion*. Another objection against the assumption of a subdivision is that the pavement of parasymphysial teeth passes quite gradually into the pavement of scales arming the skin of the lateral and ventral faces of the jaw (cf. text-fig. 15). The serial arrangement of the parasymphysial teeth decreases in traceability with increasing distance from the main symphysial series, and the teeth quite gradually approach the scales in size.

The crowns of the parasymphysial teeth are separated from each other by narrow interspaces, and normally the same seems to be the case with their well-developed roots. In some places, however, there can be no doubt that more or less extensive fusions have taken place between the roots of adjoining teeth, and fusion has also taken place between the roots of main symphysial teeth and the adjoining parasymphysial teeth. In specimen no. 215 (pl. 3, fig. 2) parasymphysial teeth are completely lacking, but this may be explained solely by the state of preservation of the specimen. In this connection it is very interesting, however, that the surface of the most lateral portions of the lateral parts of the crowns of these teeth are divided into smaller areas by a number of transversely running shallow grooves, which may be interpreted as the last traces of lines of fusion between smaller tooth units, in which case the lack of parasymphysial teeth might be due to their complete fusion with the main symphysial teeth.

Thus, instead of assuming that the main symphysial teeth in *Sarcoprion* decreased in size owing to fragmentation of their most lateral portions, there seems to be strong reasons for assuming that the main symphysial teeth increased in size by fusion with adjoining tooth units.

Of the upper symphysial series, remnants have been discovered of six or perhaps seven consecutive teeth, which in the concretion lay along the left side of the anterior half of the lower symphysial series and rather far from their original place in the longitudinal groove on the ventral face of the preorbital part of the skull (cf. p. 16). Furthermore, two single teeth (pl. 8, fig. 4) from the upper symphysial series were found just behind the posterior end of the lower series.

Of the upper symphysial teeth, nos. 2—5 in the continuous series of six or seven teeth mentioned above have been more or less completely exposed, while all the other upper symphysial teeth appear only as sections. The four well exposed teeth (text-fig. 14; pl. 3, fig. 3), like those in the lower series, consist of independent crowns and partly fused roots, but differ a good deal in the details of shape from the lower symphysial teeth, especially by their relatively stronger cutting blades and

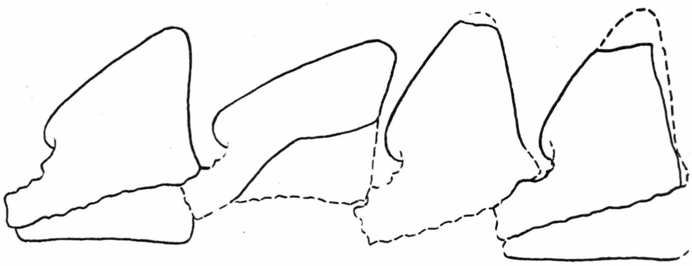

Fig. 14. *Sarcoprion edax* n. sp. Teeth nos. 2—5 from the upper symphysial series. Specimen no. 214. Nat size.

their more dominant roots, on the basal faces of which no longitudinal groove is developed.

For a more detailed description I have chosen tooth no. 2, which is by far the best preserved tooth in the upper series.

The measurements of this tooth, which is only slightly worn, are as follows: Distance from apex to lateral end of labial margin 34 mm, height of tooth 29 mm, greatest width of tooth 22 mm, height of cutting blade 18 mm, length of base of cutting blade 21 mm, greatest thickness of cutting blade 9 mm, and length of lateral part of crown 27 mm.

The cutting blade has a small apical facet of wear, but has quite unworn lateral faces. The cutting edges, the foremost of which is slightly convex, while the hindmost one is faintly S-curved, as shown in text-fig. 14, are serrated in the same degree as those of the lower symphysial teeth. As regards the general shape and ornamentation, the cutting blade agrees well with the lower teeth, the most important difference being that the blade of the upper tooth attains its greatest thickness much nearer the posterior cutting edge than is the case in the lower teeth.

The paired lateral part of the crown, in addition to its boundary towards the cutting blade, has a short, concave, labial, a long convex lingual, and a very short straight lateral margin. As is normal, the labial margin is much more strongly folded than the lingual one. The lateral part decreases gradually in width towards its lateral end, but instead of curving forward, as in the lower symphysial teeth, it extends throughout its whole length in the same antero-ventro-lateral direction. The ornamentation of the crown agrees with that of the lower symphysial teeth.

The root is to a great extent situated in the space between the right and the left diverging parts of the crown, but a comparatively much larger part of the root than in the lower teeth protrudes beyond the lingual border of the crown. This protruding part of the root is to some extent overlapped laterally by the paired lateral part of the tooth next behind, but on account of the shortness of the overlapping part, a greater portion of the protruding part of the root is still visible when the series of teeth is seen from the side (text-fig. 14) than is the case in the lower series.

The overlapping of the protruding part of the root by the tooth next behind takes place without fusion between the overlapped and the overlapping parts, but a real fusion may have existed between the more central parts of the roots of adjoining teeth. Their fusion, however, though consolidating the upper series of symphysial teeth to some extent in the living animal, has not been sufficiently effective to prevent the teeth from being broken apart by post-mortem compression of the structure.

The basal face of the root, as already mentioned, is plane and seems to lie almost on a level with those of the other teeth in the series, which, instead of being strongly curved like the lower series, must have been straight or nearly so, corresponding to the almost plane bottom of the longitudinal groove on the ventral face of the skull, against which it is fitted.

The preserved part of the upper series is too incomplete to permit a study of the alteration in shape and size from the oldest to the youngest teeth.

As mentioned in the above descriptions, many of the symphysial teeth of *Sarcoprion* show distinct traces of wear during life, and, as might be expected, the traces of wear are most marked on the foremost and oldest teeth.

The worn surfaces of the crowns are easily distinguishable, even when they have caused only small alterations in the shape of the teeth, owing to their lack of ornamentation and in most cases also to a difference in colour. In the Greenland Edestids the dominant layer of the crowns, interpreted by me in 1932 as enamel, is usually white or light greyish, while the hard tissue of the root and in many cases also the matrix filling the ascending canals of the crowns are black or darkish brown. The white coronal layer has its maximum thickness in the median part of the cutting blade, growing gradually thinner towards the lateral ends of the crown. On most of the paired lateral parts of the crowns the white layer is very thin, and here the dark deeper-lying substance of the tooth is exposed even by very slight wear. In cases of stronger wear, also the white layer of the cutting blades disappears more or less completely. In normally preserved teeth, therefore, all strongly worn areas are black, while the unworn areas of the coronal surfaces are white. In a few cases, however, the teeth are preserved in such a way that even the superficial layer of unworn crowns is very dark and hardly different in colour from the dark roots. This is, for instance, the case in the posterior teeth in the symphysial series of specimen no. 215. In the holotype the conditions are normal, and in text-fig. 11 I have shown the approximate distribution of the worn black areas of the lower symphysial series of that specimen. The youngest teeth are only worn on the narrowest portion of the paired lateral part of the crowns, and passing forwards through the series, it is easy to see from the figure how the black colour has spread to larger and larger areas of the surface of the lateral parts of the crowns. From tooth no. 8 and forwards the black-coloured area extends to the cutting blade, and in the foremost teeth it spreads over the greater part of the blade. The surface layer of all the parasymphysial teeth is black. The apical ends of almost all the teeth of the specimen considered here are lost, but in most cases sufficiently complete impressions on the adjoining rock are preserved for a study of their original outline. Farthest posteriorly the apical ends of the teeth appear to be quite unworn, from tooth no. 13 and forwards the apices show signs of increasing wear.

The upper symphysial teeth nos. 2–5, which were most probably placed in the foremost half of the upper series, are also worn, both farthest distally and on the surface of the paired lateral parts of their crowns. However, they are comparatively less strongly worn than the teeth in the anterior half of the lower symphysial series, and especially the ornamentation of the lateral faces of their cutting blades is surprisingly little influenced by wear.

As to both the lower and the upper series, it seems to hold good that the degree of wear is the same on both sides of the teeth, and the question which now arises is how this two-sided wear is to be accounted for considering that we are dealing with a single lower row opposing a single upper row. There can be no doubt that the wear of the apical ends of the teeth is not due to direct contact between the points of the upper and the lower teeth, but is rather due to contact with the prey of the animal. The two series must have worked much as a pair of scissors, and the symmetrical wear may have been caused by a regular shifting of one of the series from one side to the other of the opposite series. The cutting edges thus served to cut the prey into smaller pieces, which were afterwards masticated between the broad lateral parts of the upper and lower crowns. The distal parts of the crowns of the lower symphysial series, however, not only worked against those of the upper series, but also against the pavement of smaller teeth on the upper jaw, and probably these small lateral teeth played an important rôle in the development of the rather extensive areas of wear on the lateral faces of the lower symphysial teeth.

The lateral teeth.—As already mentioned (pp. 17, 20), the surface of the calcified cartilage both of the upper and the lower jaw is provided with numerous shallow pits, which should probably be interpreted as the places of insertion for the lateral jaw teeth. The lateral teeth themselves are in no case found *in situ*, but lie disorderly dispersed in the matrix surrounding the jaws (pl. 4; pl. 8, figs. 1, 4). In a few places the dislodged teeth still present traces of a serial arrangement, thus, for instance, section no. 4 (pl. 2, fig. 1) shows a series of teeth from the upper dentition.

The serially arranged teeth, as far as can be judged, originally occurred as a dense pavement partly on the dorsal border region of the posterior two-thirds of the lower jaw, partly on the paired ventro-lateral longitudinal ridge of the skull, where the aforementioned characteristic shallow grooves occur on the posterior five-sixths of the whole length of the ridge.

The number of rows of lateral teeth on the jaws cannot be estimated with certainty, but judging by the length of the dislodged teeth found along different parts of the jaws, we get for the lower jaw a number ranging between 35 and 40 and for the upper jaw a number not far from 60. In both the upper and the lower dentition the longest lateral teeth are found in the area around the posterior part of the lower symphysial series, and from this area the teeth decrease gradually in length both forwards and backwards, as shown in text-fig. 15.

The lateral teeth are of the *Orodus-Campodus-Agassizodus-Erikodus* type, with a low, roughly rectangular crown and a high root. The crown of an unworn tooth (pl. 8, figs. 2, 3) has a rather conspicuous longitudinal ridge, which gives off short transverse ridges towards the labial and the lingual margin. The labial transverse ridges continue in a corresponding number of large projections from the lateral margin, and the more numerous lingual transverse ridges are in the same way continued into small crenulations in the lingual coronal margin. The difference in size between the projection of the lingual and the labial margin is greater than in *Erikodus*, and of about the same magnitude as in *Agassizodus variabilis*, in certain species of *Edestus*, and in *Helicoprion*.

Structure of the teeth.—The teeth of *Sarcoprion edax* as to their structure agree entirely with those of the Greenland genera *Fadenia* and *Erikodus* (*Agassizodus*), and thus belong to the same structural type as the teeth of all well-investigated members of the group *Bradyodonti* (cf. E. NIELSEN 1932). This Bradyodont structural type is especially characterised by possessing a system of numerous, more or less parallel vascular canals ascending through the greater part of the crown, but ending blindly just below the tritoral surface. The ascending canals are lined with layers of dentine, and the dentine around each canal is separated from that around the other canals by a hard tissue, described as enamel by me in 1932. For the coronal tissue found in the Bradyodont teeth MOY-THOMAS has introduced the term tubular dentine (MOY-THOMAS 1939, pp. 2—3, text-fig. 1 B), a term which will also be used in the present paper, though it is not quite logical in so far as the coronal substance to which it refers comprises both dentine and enamel. The development of tubular dentine in durophagous teeth seems in some measure to be analogous to the development of high crowns in teeth of gnawing or grass-eating mammals, and the presence of tubular dentine in specialised symphysial teeth, partly (*Sarcoprion*) or not at all (*Helicoprion*) adapted for crushing, must be due to these teeth having evolved from simple solid durophagous teeth.

The new material of Edestids from Greenland offers ample opportunities for detailed studies of the histology and development of the tubular dentine. Since, however, such studies, based in part on the Danish material, have quite recently been undertaken by ØRVIG (cf. ØRVIG 1950, p. 342), I consider it unnecessary, before his results have been published, to deal further with this matter except for the following brief remarks:—

In my previous paper I put forward the supposition (E. NIELSEN 1932, p. 33) that the peculiar relations between dentine and enamel in the crowns of the Bradyodont teeth might be due to a strong folding of the surface of the pulp cavity, each fold corresponding to one of the ascending canals of the crown.

In a recent work, ØRVIG (1950) briefly summarises the contents of a new theory on the formation of dermal bones, scales, and teeth in lower vertebrates, and this theory throws new light on many puzzling problems relative to these hard tissues.

According to this theory, worked out by STENSIÖ and ØRVIG, the scales, dermal bones, and teeth of lower vertebrates consist of small units (lepidomoria) combined in different ways. Isolated lepidomoria are formed in larger numbers in some Palæozoic Elasmobranchs, i. a. the Edestids from Greenland. According to ØRVIG (1950, p. 366), "each lepidomorium consists of a simple, conical, mostly high crown of dentine and a low basal plate of bone. The crown, which is frequently covered superficially with enamel, or an enamel-like substance, contains a single pulp cavity, the lepidomorial pulp cavity. Like "placoid scales" the lepidomoria did not grow in area".

By means of the lepidomorial theory, a new interpretation of the tubular dentine seems possible, viz. that each of the ascending canals represents a lepidomorial pulp cavity, and that a tooth crown of tubular dentine is thus formed by fusion of a large number of high and slender lepidomorial crowns, each of which was covered with enamel. One of the commonest types of larger composite scales in *Sarcoprion edax* seems to disagree in structure with typical tubular dentine solely in lacking a layer of enamel between the dentine-lined lepidomorial pulp cavities.

Scales.—The scales of *Sarcoprion edax* can be studied both in the holotype and in specimens nos. 215 and 217, but only in the holotype are the scales still found *in situ* in certain areas (cf. p. 14). The largest scales, measuring about 2 mm across their coronal surface, occur on the foremost part of the lower jaw (pl. 9, fig. 2) in an area extending along the parasymphysial tooth pavement, into which it passes quite gradually, as shown in text-fig. 15. Among the very large scales, smaller ones are occasionally found, and also on the more posterior parts of the jaw, where the average size of the scales has decreased considerably, they still show a great variation in size even within quite small areas. On the dorsal part of the head no scales are found, which is probably due to the decay of the skin having been much advanced before this part of the head was buried. Scales belonging to the floor of the mouth, as already mentioned (p. 21), were found a short distance behind the posterior part of the lower symphysial series.

Wherever the scale-covering is intact, the scales form a dense pavement, which evidently offered a very effective protection of the skin.

Among the scales we find many simple lepidomoria, but most of the scales are composite and present a considerable variation in shape and structure. A section through some composite scales are shown in pl. 9, fig. 1, but since studies of the scales in *Sarcoprion* form part of the investigations at present carried out by Stensiö and Ørvig, I shall here abstain from any kind of description. I only wish to point out that it is quite easy by means of the most characteristic types of scales alone to distinguish *Sarcoprion* from both *Fadenia* and *Erikodus*.

Remarks.—As the first species within the Edestid family in which larger uncrushed parts of the endoskeleton of the head have been examined, *Sarcoprion edax* has supplied very important contributions to our knowledge of the organisation of the *Edestidae*. Text-fig. 15 shows an attempted sketch of the anterior part of the head of *Sarcoprion edax*, based mainly on the holotype. The sketch, which can be regarded as a brief summary of the above description, illustrates very beautifully how much still remains to be done before all the problems concerning this part of the head have been solved in a satisfactory way. To one of the unsolved problems illustrated by the sketch, I wish to add the following comments:

It is evident that, as sketched here, the animal was unable to close its mouth completely on account of the relatively large size of its lower

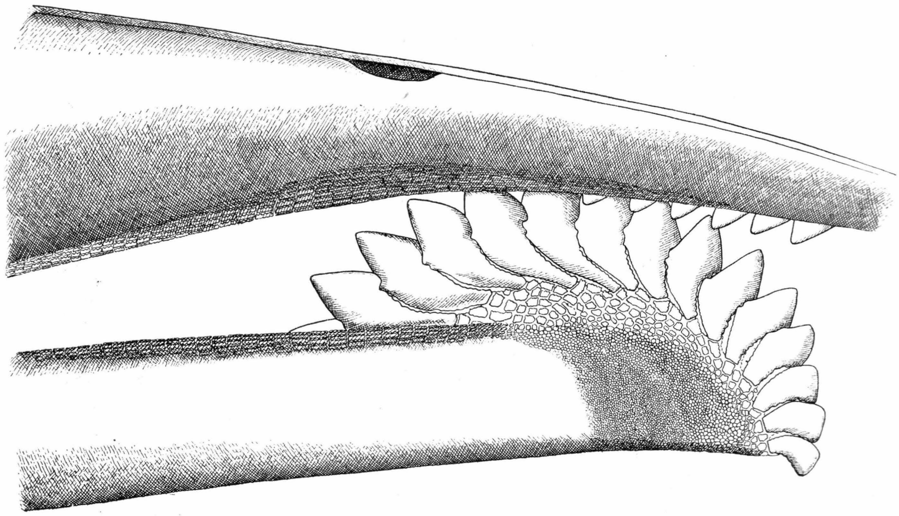

Fig. 15. *Sarcoprion edax* n. sp. Attempted sketch of the anterior part of the head. Scale-covering only indicated on the foremost part of the lower jaw; both this scale-covering and the pavement of the lateral teeth are drawn in a very schematic way. Mainly based on specimen no. 214. C. 0.3 ×.

symphysial teeth. If so, the series of lateral teeth, or most of them, can have served no other purpose than to act as a mere protective covering of the jaws, and, in fact, the small size of the lateral teeth, as compared with for instance those of *Campodus*, *Fadenia*, and *Erikodus*, may well be regarded as a degenerative phenomenon. If this is so, the sketch may not be very far from the truth, even though it must be improved by addition of well developed upper and lower lips serving as lateral walls for the mouth cavity when the gape was closed.

If, on the other hand, the upper and the lower lateral teeth still functioned as crushing teeth, and accordingly must have met when the mouth was closed, the mutual relations between the lower jaw and the lower symphysial series must have been very different from those shown in the sketch. From the material at hand it is impossible to make out how the sketch should be satisfactorily altered, but, of course, the tendency of an alteration must be towards lowering the lower symphysial series in relation to that part of the lower jaw which carries the serially arranged lateral teeth.

Diagnosis.—*Sarcoprion edax* being the genotype and the only species of the genus known so far, its diagnosis is like that of the genus.

Erikodus n. g.

Syn. 1932. *Agassizodus* (in part). E. NIELSEN, pp. 35—42.
1932. ?*Copodus* (in part). E. NIELSEN, pp. 49—51.

In my previous paper on the Permian fishes from Greenland I referred a number of teeth to the genus *Agassizodus* St. JOHN and WORTHEN, which by many investigators, thus quite recently by LEO A. THOMAS and FRANKLIN E. McCLURE (1951), is regarded as synonymous with the genus *Campodus* DE KONINCK.

As pointed out already in 1932 (pp. 35—37), I do not share the view that the American genus *Agassizodus* and the European genus *Campodus* are identical. I especially emphasised that even if the lateral teeth in the European and the American forms agree, this does not necessarily mean that the same is the case with their symphysial teeth, which are so far known from the American *Agassizodus*, only. As regards the species from Greenland, which I referred to *Agassizodus*, its symphysial teeth were, it is true, also unknown in 1932, but the agreement between the lateral teeth of this form and those of the American species *A. corrugatus* and *A. variabilis* was much closer than between the lateral teeth of the American *Agassizodus* and those of the European *Campodus*.

Now, however, the new collections from Greenland include a large number of symphysial teeth of the Greenland species, and as these teeth are of quite another type than those of *Agassizodus variabilis*, and do not agree with those of any other Edestid, either, there can be no doubt that the Greenland form represents a separate genus, which I have given the name of *Erikodus*.

The fresh finds from Greenland furthermore show that the two teeth, referred by me with great doubt to *Copodus* in 1932 (pp. 49—51, text-fig. 4; pl. VII, figs. 1—3; pl. XIII, fig. 1), are nothing but symphysial teeth of *Erikodus* (*Agassizodus*) *groenlandicus*, a possibility which I considered already in 1932, and which I rejected on account of the entirely different shape of the symphysial teeth of *A. variabilis*.

In view of the above new statements I must emphasise, with even greater weight than before, the importance of the symphysial teeth for classificatory purposes within the *Edestidae*.

Diagnosis.—The following diagnosis, based alone on the dentition, can at present be given for the genus *Erikodus*:

Dentition comprising an upper and a lower series of very large symphysial teeth and numerous upper and lower series of smaller lateral teeth. Both upper and lower symphysial series curved, the lower series more strongly so than the upper one. Teeth in both series very large and densely set, but not fused mutually as in *Sarcoprion*, *Helicoprion*, etc. The individual symphysial teeth slightly compressed from side to side, with their coronal face slightly convex and their basal face correspondingly concave from side to side. Width of symphysial teeth much greater than their rostro-caudal extent. Lateral portions of symphysial teeth somewhat forwardly bent, the anterior face of the teeth being concave and the posterior face convex from side to side. Crown of symphysial teeth much lower than the root. Middle portion of crown developed as a blunt elevation, but not as a real cutting blade. Surface of crown ornamented with ramifying sharp ridges. Both labial and lingual margin of crown folded, the labial margin much more strongly so than the lingual one. Lateral teeth of jaws of the same general type as those of *Campodus* and *Agassizodus* and with the same serial arrangement. Teeth in foremost and hindmost lateral rows very small, in some of the middle rows especially large. Ornament of crowns and folding of coronal margins corresponding closely to those of the symphysial teeth.

Remarks.—*Erikodus* differs from all other Edestid genera in the much less pronounced lateral compression of its symphysial teeth, which are developed as typical crushing teeth of an extraordinarily solid type. However, the difference from *Fadenia* as regards the symphysial teeth is not greater than that a rather close relationship is probable, but as to the lateral teeth, *Erikodus* seemingly bears closer affinities to the genera *Campodus* and *Agassizodus* than to *Fadenia*.

Erikodus groenlandicus (E. NIELSEN).

(Text-fig. 16 A, B, and C; pl. 10, figs. 1—4; pl. 11, figs. 1—2; pl. 12, fig. 3; pl. 13, figs. 1, 4.)

Syn. 1932. *Agassizodus groenlandicus.* E. NIELSEN, pp. 37—42, pl. VII, figs. 4—17; pl. VIII, figs. 1—31; pl. X, figs. 1—3; pl. XI, figs. 2—3; pl. XIII, fig. 2.

1932. *Copodus* (?) sp. E. NIELSEN, pp. 49—51; text-fig. 4; pl. VII, figs. 1—3; pl. XIII, fig. 1.

The symphysial teeth.—A considerable number of symphysial teeth of *Erikodus* are at hand. Often they are accompanied by large numbers of lateral teeth, pieces of calcified cartilage, and scales. In addition to the two teeth dealt with in 1932 (specimens nos. 94a and b), the present description is based mainly on specimens nos. 218—222 from the collections made between 1932 and 1947. All the fresh specimens are from the Permian fish-zone in the upper part of the *Posidonomya* beds in the Kap Stosch area. Specimens nos. 220 and 221 were collected between Rivers 8 and 9, and specimens nos. 218, 219, and 222 from the exposures at River 14. Specimens nos. 218 (pl. 10, figs. 3—4) and 222 consist of single teeth, specimen no. 219 (pl. 12, fig. 3; pl. 13, fig. 4) is a series of five, and specimen no. 22 (pl. 10, figs. 1—2) a series of three (four?) teeth; both series are slightly curved. Specimen no. 220 (pl. 11, figs. 1—2; pl. 13, fig. 1) is the greater part of the dentition of a single

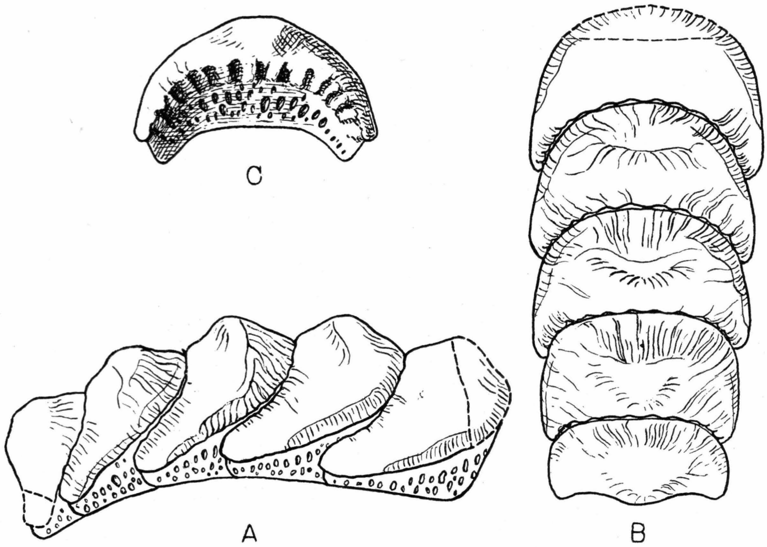

Fig. 16. *Erikodus groenlandicus* (E. Nielsen). Series of symphysial teeth in (A) lateral and (B) coronal view and (C) a single symphysial tooth in anterior view. Based on specimen no. 219. C. 0.6 ×.

animal with portions of both an upper and a lower symphysial series, the presumed lower series in this specimen is rather strongly curved.

For a more detailed description I have chosen specimen no. 218, a single tooth, which is complete except for the most lateral part of its right half. In its present state the tooth measures 48 mm in greatest width (the measurement was taken between the extreme lateral ends of its crown), when complete, the width must have been about 50 mm.

From side to side the tooth is slightly bent in two ways, viz. partly so that the coronal face is slightly convex and the basal face correspondingly concave, and partly so that the anterior face of the tooth is rather strongly concave and the posterior face still more strongly convex. The last-mentioned bend is most pronounced about midway between the mid-line and the lateral ends of the tooth, which might accordingly be regarded as consisting of a transversely placed, almost rectangular unpaired central part, and a paired lateral part extending from the central part in an antero-lateral direction and narrowing gradually towards its lateral end.

The central part of the crown shows a blunt median elevation instead of a real cutting blade. The surface of the crown of the whole tooth is ornamented with a system of ramifying ridges of varying magnitude. The two most conspicuous of these ridges has a mainly transverse course, one of them extending a short distance behind and parallel with the labial margin of the crown, and the other, which has a more posterior position, passing across the highest part of the median elevation of the crown. From these main ridges issue a large number of shorter ridges in all directions towards the coronal margins, which, as normally within the Edestids, are folded, the labial one more strongly than the lingual one.

The root is very stout, and has its greatest height, about 9 mm, below the central part of the crown, while farthest laterally it only measures 5 mm. From side to side as well as in a labio-lingual direction the dimensions of the root are somewhat smaller than those of the crown. The main axis of the root, as can be seen from the figures, is not exactly perpendicular to the basal face of the crown, but extends in a somewhat anterior direction from this face, on which account the posterior face of the root overlaps, to some extent, the anterior face of the root of the tooth next behind. The overlapping takes place without fusion.

Within the whole material of symphysial teeth here considered a rather considerable variation in the degree of transverse curvation of the teeth can be observed. Thus in specimen no. 221 (pl. 10, figs. 1—2) the teeth are very little bent from side to side, compared with those of specimen no. 219 (text-fig. 16 A, B, C; pl. 12, fig. 3; pl. 13, fig. 4). The teeth vary greatly in size from specimen to specimen, but very little within the individual symphysial series. The smallest tooth, specimen no. 222, measures only 19 mm in width, while the largest complete tooth (from specimen no. 221) has a width of no less than 61 mm. The height of the root varies in the normal way, thus in the youngest teeth the root is very low and with very wide vascular spaces, while in the old teeth the root is strong and with narrow vascular spaces.

Most of the teeth show traces of wear during life, and in some cases not only the ornamental ridges of the crown have disappeared, but the whole central elevation of the crown has been worn away, leaving a quite smooth and gently curving coronal surface.

As already mentioned, the series of symphysial teeth are more or less curved, and in one specimen (no. 220), which is interesting in possessing portions of two symphysial series, one of these series (pl. 11, figs. 1—2) is extraordinarily strongly curved. A comparison with the conditions in *Sarcoprion* leaves no great doubt that this strongly curved series belongs to the lower dentition, and if so, it seems highly probable that specimens nos. 219 and 221 are of the upper symphysial series.

The above-mentioned fact, that the oldest and youngest teeth within the same symphysial series differ only very little in size, indicates that a large number of teeth were formed in each series during the growth of the animal, and that the teeth were shed at the labial end of the series at about the same rate as new teeth developed at its lingual end.

Scales.—Large numbers of scales are present in many specimens of *Erikodus*, but they will not be dealt with here, as they have recently been subjected to detailed, still unpublished, studies by Stensiö and Ørvig (cf. p. 8).

Fadenia E. Nielsen.

Fadenia crenulata E. Nielsen.

Text-fig. 17 A, B, and C; pl. 12, figs. 1—2; pl. 13, fig. 2.)

Syn. 1932. *Fadenia crenulata.* E. Nielsen, pp. 43—49, text-figs. 3 B, D, 7 b; pl. II, fig. 1; pl. III, figs. 1—4; pl. IV, figs. 1—12; pl. V, figs. 1—12; pl. VI, figs. 1—18; pl. IX, figs. 1—2; pl. XII, figs. 1—2; pl. XV, figs. 8—10; pl. XVI, fig. 6.

Remarks on the symphysial teeth.—A description of the symphysial teeth of *Fadenia* was already given in 1932 on the basis of a number of specimens from the earlier collections, viz. nos. 129, 133, 134, 176, 177, and others. The new material contains several fine specimens, of which the following, all derived from the Permian fish-zone in the upper part of the *Posidonomya* beds at Kap Stosch, will be dealt with here: specimens nos. 223 and 225—227 from the area between Rivers 8 and 9 and specimens 221 and 228 from River 14. Specimen no. 223 (pl. 12, fig. 1) in addition to numerous lateral teeth and scales shows a slightly curved series of seven symphysial teeth. Specimen no. 224 is a compressed but seemingly almost complete skull with well preserved teeth. Both the upper and the lower symphysial series are at hand, but the upper one is still partially concealed in the rock. The lower row, which contains at least eight teeth, is much more strongly curved than the upper one. The skull and the lateral teeth will be dealt with in a later publication; here it will suffice to mention that the lower jaw measures about 30 cm in length, of which about 8 cm belong to the symphysial portion. Specimen no. 225 (pl. 12, fig. 2; pl. 13, fig. 2) consists of a series of four teeth in an excellent state of preservation. Specimen no. 226 shows, in addition to calcified cartilage of the lower jaw, numerous lateral teeth, well preserved scales, and a fine section through a large symphysial tooth. Specimen no. 227 is the anterior part of a skull with jaws, and it shows well preserved symphysial teeth. Specimen no. 228 shows the greater part of the right and left halves of a lower jaw with most of the teeth still nearly in their original position, and with beautifully preserved symphysial teeth.

The new symphysial teeth of *Fadenia* here considered agree in their main features well with those previously described, although in some cases rather insignificant differences in shape can be observed, thus, for instance, the paired lateral part of the symphysial crowns of specimen no. 225 (pl. 12, fig. 2) is decidedly narrower than that of specimen no. 134 figured in my earlier paper (pl. IV, figs. 1—2).

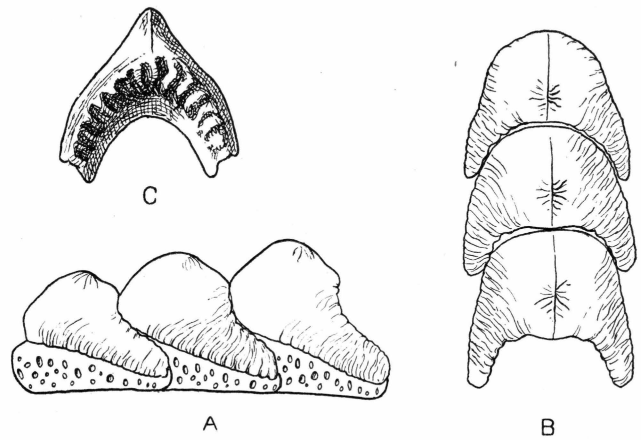

Fig. 17. *Fadenia crenulata* E. NIELSEN. Series of symphysial teeth in (A) lateral and (B) coronal view and (C) a single symphysial tooth in anterior view. Based on specimen no. 225. Nat size.

Judging from the most complete specimens, the symphysial series were relatively shorter in *Fadenia* than in *Sarcoprion*, and the number of teeth in a complete series did not, presumably, exceed 10 or 11. The difference in size between the foremost and the hindmost teeth is quite considerable and much greater than in *Erikodus*. The foremost tooth in specimen no. 223 measures 12 mm from the apex to the lateral end of the labial margin, while the corresponding measurement in the hindmost teeth of the same series is 23 mm. The same specimen also shows a marked difference in shape between the foremost and the hindmost teeth of the same series, the lateral paired part of the crown of the small teeth being relatively much shorter than in the largest teeth, an alteration in shape of much the same nature as observed in *Sarcoprion* (cf. p. 28).

Remarks on the scales.—The scales of *Fadenia crenulata* can be studied in many specimens, and in a number of cases they are still found in their natural mutual position in areas of varying size. A detailed description of the scales, which include both simple lepidomoria and many types of composite scales, is beyond the scope of the present work, so I shall confine myself to a few remarks on the scales of the extreme foremost end of the head, which is well preserved in a few specimens. On this part of the head we find, as the dominant type, scales similar to those figured by me in 1932 on pl. XI, fig. 1, and already then identified as scales of *Fadenia crenulata*. These scales, the smooth external face of which has a much indented outline, measure up to 3—5 mm across and are so close-set that they must have formed a very effective protection of the skin of the snout. As similar scales have not been observed so far in either *Erikodus* or *Sarcoprion*, they are probably usable for identificatory purposes. In a single specimen a number of still larger scales are also present on the extreme tip of the snout. These extraordinarily large scales have a roughly rectangular external face, which measures more than 10 mm in length and 2—3 mm in width and is thus considerably more extensive than the coronal face of the smallest teeth on the jaws. A section through the scale-covering extending from an area with very large teeth to an area where very small scales dominate, gives a very instructive picture of the transition from single lepidomoria to more and more complex composite types of scales, in full accordance with the view on the formation of scales in lower vertebrates summarised in ØRVIG's recent paper (1951).

Parahelicampodus n. g.

Diagnosis.—Symphysial teeth completely fused to a solid, slightly curved rod, the segmented nature of which is indicated by the enamelled tooth-crowns separated from each other by very shallow fissures. Cutting blades of crown large, lateral paired parts of crown narrow and tapering to a point beneath the cutting blade of tooth no. 2 in a forward direction. Labial margin of paired lateral part of crown very slightly crenulated, lingual margin smooth. The fused roots protruding very far beyond the basal margin of the coronal series as a shaft, the height of which far exceeds that of *Helicampodus* BRANSON. Basal surface of shaft with a broad and shallow longitudinal groove, lateral surface of shaft with an ornament of densely placed, ramifying, irregular sinuous ridges.

Remarks.—*Parahelicampodus* in most respects agrees closely with *Helicampodus* BRANSON (text-fig. 20) from the upper *Productus* limestone of the Salt Range (BRANSON 1935, pp. 19—23), and especially as regards the shape and relative dimensions of its tooth crowns. It differs, however, from *Helicampodus* in being less laterally compressed, in having a less strongly crenulated labial, coronal margin, and especially in the much greater height of its shaft. As to the dimensions of the shaft, it bears a closer resemblance to *Lissoprion* HAY from the Phosphoria formation of the United States of America (HAY 1907, pp. 22—24), from which it differs both by the straightness of its antero-ventrally extending paired lateral part of the crown, and by being much less laterally compressed.

Parahelicampodus spärcki n. sp.

(Text-fig. 18 A, B, and C; pl. 12, fig. 4; pl. 13, fig. 3.)

Syn. 1935. Edestid. E. NIELSEN, p. 101.
1936. Undetermined Edestid genus. E. NIELSEN, p. 12.

Material and locality.—The material consists of a single specimen from the lower Triassic beds in the Kap Stosch area, and was collected immediately east of River 13 in the highly fossiliferous Fish-zone II (cf. E. NIELSEN 1935, pp. 100—109).

The fossil consists of five fused teeth arranged in a short and almost straight row, and it is embedded in one of the rounded concretions typical of Fish-zone II. The concretion with the enclosed fossil is rather much damaged by weathering, thus most of the cutting blades as well as the surface layer on the left side of all the five crowns are lacking. Both the anterior and the posterior end of the row, however, were still concealed in the concretion when the fossil was collected, and accordingly the present length of the specimen must be the same as when it was first embedded in the rock. Anteriorly and posteriorly the fossil is bounded by gently rounded surfaces, which, as shown in text-fig. 18, cut across the boundaries between the original tooth units. Judging by their appearance, there can be no doubt that these terminal faces of the row have arisen by wear, but the question whether they were worn during the lifetime of the animal or afterwards, is not easy to answer. The terminal faces share the bilateral symmetry of the whole fossil, and this circumstance speaks rather in favour of their formation during life. On the other hand, the fact that the row of teeth is almost equally strongly worn at both ends, can hardly be explained otherwise than as due to wear after death, in fact, strong wear in the live animal of the posterior end of the series, where new teeth continually formed, would seem quite impossible.

Description.—In its present state of preservation, the unique specimen measures 72 mm in length, about 30 mm in height, and 23 mm in greatest width. With restored cutting blades, the height would probably be about 35 mm. As the height of the shaft is about 8—9 mm, the height of a restored crown would be 26—27 mm. The base of the cutting blade measures about 14—16 mm, and the distance from the posterior end of the base of the cutting blade to the lateral end of the labial margin is about 35 mm (measured on tooth no. 2 in the row). The paired lateral part of the crown extends from the base of the cutting blade in a fairly straight antero-ventro-lateral direction, and narrows gradually towards its lateral end, as shown in text-fig. 18 A. Its labial border is slightly concave, and its lingual border slightly convex. The coronal surface of this part of the tooth is almost plain and is quite smooth except for a number of extremely fine striae extending from

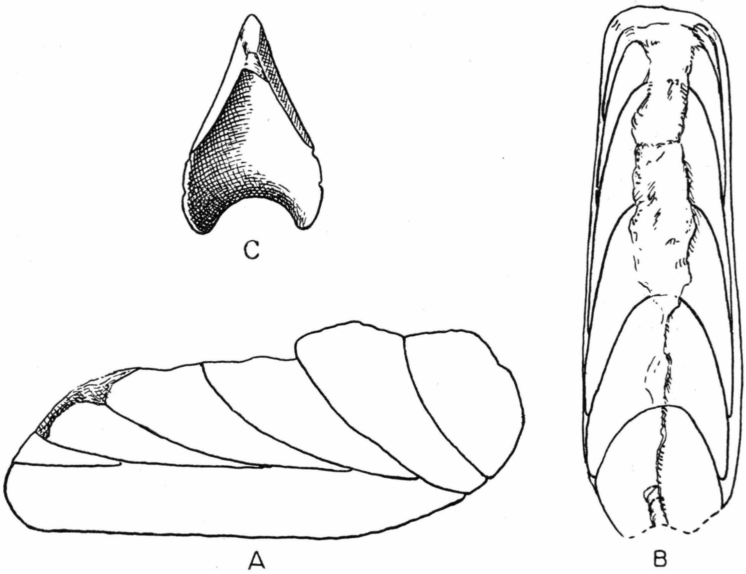

Fig. 18. *Parahelicampodus spärcki* n. sp. The holotype in (A) lateral, (B), coronal, and (C) anterior view. About nat. size.

the base of the cutting blade in a ventro-lateral direction. As far as could be made out, the labial margin of the crown is very finely crenulated, while the lingual margin is quite smooth, The strong shaft, formed by the completely fused roots of the symphysial teeth, has a paired lateral face, which is somewhat convex in a dorso-ventral direction, and a very broad basal face, mainly occupied by a wide and rather shallow longitudinal groove. The lateral surface layer of the shaft consists of an enamel-like substance, and is ornamented with a dense system of broad and rounded ramifying irregular sinuous ridges.

The basal face of the shaft passes very gradually into the anterior terminal face of the fossil, and, most surprisingly, also the basal longitudinal groove continues on to the terminal face, which, as discussed above, must have arisen by wear. A satisfactory explanation of this peculiar phenomenon is not easy to find; the only explanation I can suggest at present is that the presence of the concavity in the terminal face may be accounted for by presuming a difference in hardness between the substance of the roots and that of the crowns.

Diagnosis.—*Parahelicampodus spärcki* being the genotype and the only species of the genus known so far, its diagnosis is like that of the genus.

REMARKS ON THE FAMILY *EDESTIDAE*

The four Greenlandic genera dealt with in more or less detail on the preceding pages form a valuable addition to the brief list of Edestid genera previously known, and considerably increase our understanding of the group as a whole, as will be evident from the following brief review.

As early as 1855, at a time when only vague conjectures as to the interpretation of the nature of the peculiar *Edestus* fossils had been put forward, AGASSIZ assumed that *Edestus* should be referred to a separate family, and the same standpoint was adopted by LEIDY, who in 1857 (p. 302) proposed the name of *Edestina* for this family. Later KARPINSKY (1899, p. 80) introduced the name of *Edestidae* as being in better agreement with the usual terminology, which name had at the same time been chosen by JAEKEL, also.

The admirable work of KARPINSKY (1899) on the family *Edestidae* in general, and especially on the new genus *Helicoprion*, represented a climax within the study of these peculiar fossils. After 1899 other valuable contributions to our knowledge of the *Edestidae* were supplied by EASTMAN (1901, 1903), HAY (1912), WOODWARD (1916), and other workers, and already before 1920 it was generally accepted that the peculiar structure on which the genera *Edestus*, *Helicoprion*, etc., had been erected were the symphysial teeth of some large Elasmobranchs, of which the endoskeletons of the head and body were almost totally unknown. The skin of these Elasmobranchs was armed with densely set small scales, and from a number of successful finds it was ascertained that the jaws in addition to the symphysial teeth were equipped with smaller teeth of a less specialised type.

KARPINSKY, who in 1899, in spite of certain important differences in the shape of their fused symphysial teeth, referred *Edestus* and *Helicoprion* to the same family, later on (1911, 1912) erected a special family, the *Helicoprionidae*, for *Helicoprion*. In this subdivision of the Edestid group he was followed by HAY (1929), but neither by BRANSON (1935) nor by me (1932). In the present paper, also, I use the family name of *Edestidae* in its original wide sense, and especially the fact that both *Edestus* and *Helicoprion* possessed small lateral teeth of principally

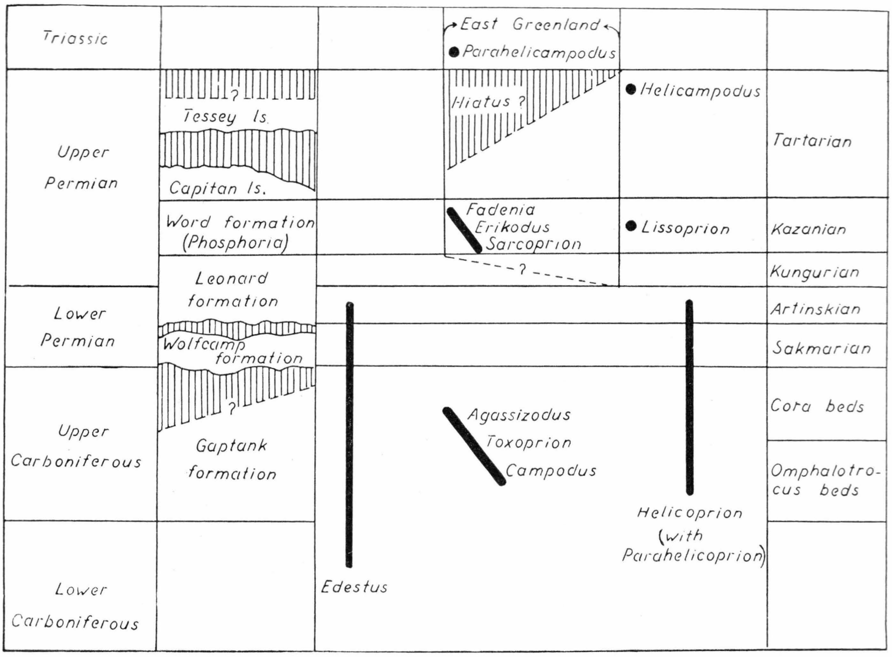

Fig. 19.

similar type, seems to me to tell in favour of a close relationship between the *Edestus* group and the *Helicoprion* group.

At the time when *Fadenia* and *Erikodus* were first described, they fitted well in among the previously known Edestid genera as primitive members of the family. Now, however, we know that instead of being only a little younger than the transition between the Carboniferous and the Permian as then assumed, their age is Upper, or even uppermost, Permian, which means that they are younger than the most specialised members of the family, viz. *Edestus* and *Helicoprion*, and this, of course, necessitates a revision of our view of the relationships within the group.

In text-fig. 19 I have attempted to place the genera of the Edestid family in a stratigraphic table based mainly on Dunbar's investigations (Dunbar 1940, fig. 9) and with the Permian of East Greenland placed in accordance with the results of studies carried out by Maync (1942), Miller & Furnish (1939), and Aldinger (1935).

According to Maync (1942, p. 96), in East Greenland possibly no hiatus exists between the Upper Permian fish-bearing beds and the overlying Lower Triassic series, and if this is actually the case, we will perhaps sooner or later succeed in "die in Ostgrönland heute noch nicht nachgewiesenen Zwischenformen von oberpermischen und eotriassischen Ammoniten aufzufinden und damit gleichzeitig den Beweis zu erbringen, dass in Ostgrönland eine lückenlose Zonengliederung vom Oberperm in die vollständigste Eotrias der Erde durchgeführt werden kann."

From the Upper Permian, apart from the three Greenlandic genera, we know at present only *Helicampodus* (text-fig. 20) from the Chideru beds of India and *Lissoprion* from the Phosphoria formation in the U.S.A. As already mentioned, *Helicampodus* bears a close resemblance to *Parahelicampodus* from the Eotriassic of East Greenland, and both these genera agree with *Sarcoprion* as regards the strong development of their cutting blades. *Sarcoprion* also shows close affinities to *Fadenia*,

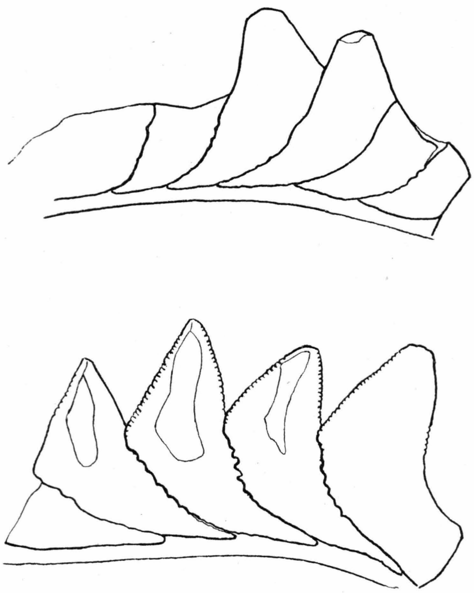

Fig. 20. *Helicampodus kokeni* C. C. BRANSON. Two fragments of the same symphysial series. Re-drawn from C. C. BRANSON 1935, pl. 1, figs. 2—3. C. 0.5 ×.

and this genus, again, to the less specialised *Erikodus*. In fact, it seems to me that no very serious objections can be raised against considering all these five genera as belonging to the same evolutionary line, passing from the primitive *Erikodus* via *Fadenia* to *Sarcoprion* and onwards to *Helicampodus* and *Parahelicampodus*.

The genus *Lissoprion* with the only species *L. ferrieri* HAY, is more difficult to place. KARPINSKY (1912, pp. 90—92) regarded the genus as synonymous with *Helicoprion*, in which view he was joined by BRANSON (1935, p. 20), WHEELER (1939, pp. 103—105), and other authors. However, even as late as 1929 HAY still maintained the name of *Lissoprion*. *L. ferrieri* (HAY 1910, pls. 14, 15) has a spiral row of symphysial teeth with a well developed shaft, the relative dimensions of which are largely the same as in *Parahelicampodus*.

Lissoprion ferrieri differs from the typical *Helicoprion* species especially by its relatively stronger cutting blades and by having nearly smooth cutting edges. In both these characters *Lissoprion* agrees more closely with *Helicampodus* and with *Parahelicampodus*, and I am therefore inclined to connect *Lissoprion* with the *Erikodus*, *Fadenia*, *Sarcoprion*, *Helicampodus*, *Parahelicampodus* line rather than with *Helicoprion*. If I am right in this assumption, all the Upper Permian Edestids

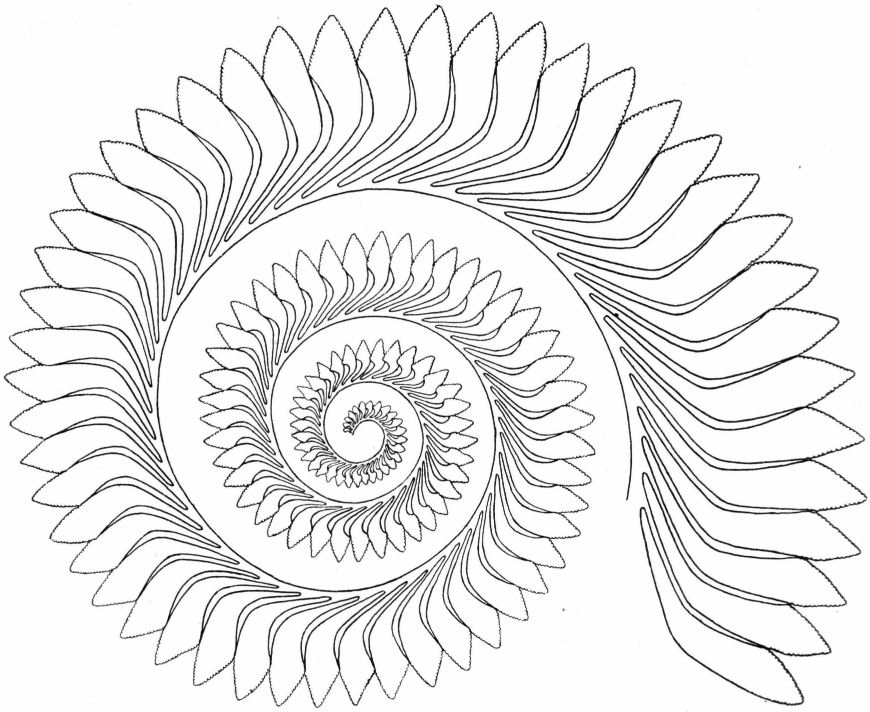

Fig. 21. *Helicoprion bessonowi* KARPINSKY. Re-drawn from A. KARPINSKY 1899, pl. 1. Somewhat restored. C. 0.5 ×.

belong to the same narrow group within the *Edestidae*, a group within which we are able to follow, from form to form, the gradual development of the rows of symphysial teeth, from more or less curved series of unfused crushing teeth to spiral rows of entirely fused teeth with very strong cutting blades.

The Upper Carboniferous and Lower Permian genus *Helicoprion* with its perfect spiral row (text-fig. 21) and with its, in relation to the paired lateral part of the teeth, very small cutting blades, the edges of which are strongly crenulated, must be regarded as an end result of an evolutionary line issuing from primitive Edestids of Upper or Middle Carboniferous age. The ancestral form of this line may quite well have been closely related to *Agassizodus variabilis* with its extraordinarily long and narrow symphysial teeth, in fact, *Helicoprion clerci* (*Parahelicoprion*) was discussed already by KARPINSKY (1924, pp. 128—131) and other workers as a possible connecting link between *Agassizodus* (*Campodus*) and the more typical *Helicoprion* species.

In no case can the *Helicoprion* line have been directly connected

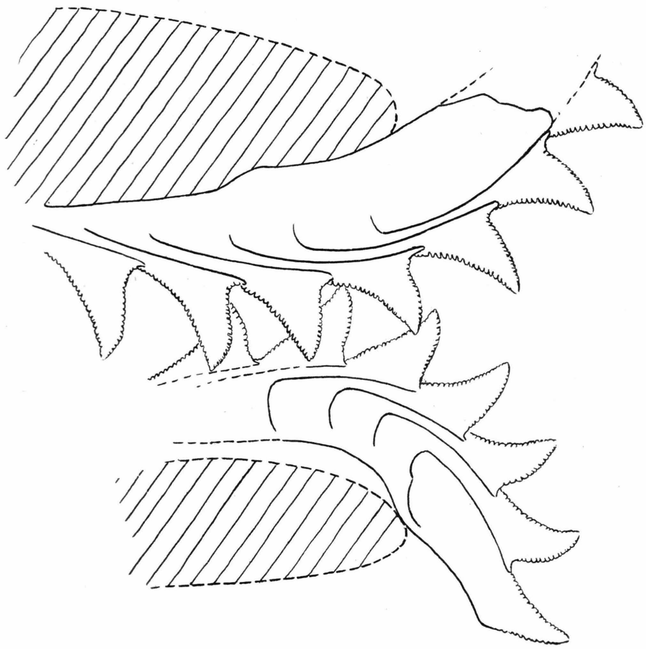

Fig. 22. *Edestus mirus* HAY. Re-drawn from O. P. HAY 1912 pl. 1. Somewhat restored. C. 0.5 ×.

with the Upper Permian Edestid line terminating in *Helicampodus*, *Parahelicampodus*, and probably *Lissoprion*, also. The two lines, however, may have a common starting point in the Lower Carboniferous, to be found, quite possibly, within the primitive genus *Orodus* or within a genus closely related to *Orodus*.

If, as I am inclined to think, the Edestid family is a monophyletic group, a third evolutionary line must have existed within the group, viz. the line leading towards *Edestus* with its typical symphysial teeth characterised by their large, posteriorly directed bases (text-fig. 22). It seems probable that the least specialised genus belonging to the *Edestus* line is *Toxoprion* (BASHFORD DEAN 1898), but a re-description of the only specimen known of the only species referred to *Toxoprion*, *T. lecontei*, will be required before the relationship between this genus and *Edestus* can be seriously considered.

A re-description of *Campyloprion annectans* (EASTMAN 1902), known from a single specimen and even from an unknown locality, is also highly needed. KARPINSKY (1912, p. 86) regarded *Campyloprion* as a synonym of *Helicoprion*, as suggested by EASTMAN as early as 1903. *C. annectans*, however, differs from all typical species of *Helicoprion* in possessing small distinct parasymphysial teeth, while in this respect it agrees more closely with *Sarcoprion* (and possibly with *Agassizodus variabilis*, also (cf. EASTMAN 1902, pp. 68—69)).

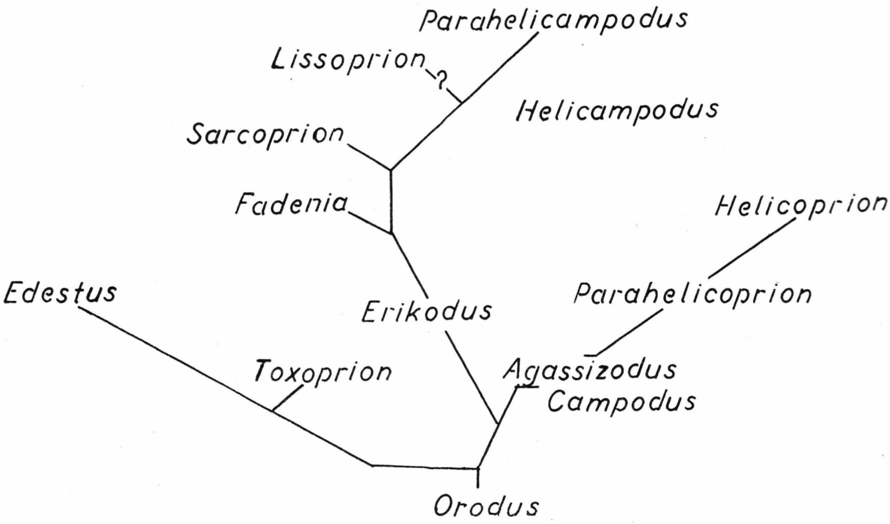

Fig. 23.

In text-fig. 23 I have attempted to summarise what has been said above regarding the main evolutionary lines within the Edestid family. I wish to point out, however, that the figure does not pretend to be anything but an extremely rough sketch, which will probably be altered in many details as a result of future research work.

In my paper from 1932, I referred (pp. 20—21), on the basis of the structure of their teeth, the families *Orodontidae* and *Edestidae* to A. S. WOODWARD's group *Bradyodonti*. In this view I have been joined by MOY-THOMAS (1939, pp. 12, 14—15), who merely expresses some doubt as to *Helicoprion* on account of KARPINSKY's description of a highly "enamel"-like outer layer in that genus, as well as regarding those Edestids in which the structure of the teeth is still unknown. TEICHERT (1940, p. 143), also, objects against including *Helicoprion* in the order of *Bradyodonti* on account of differences in the structure of the teeth. It is to be regretted, however, that he does not state anything about the presumed differences, and therefore, of course, his objection cannot carry much weight.

Neither according to KARPINSKY's nor to TEICHERT's descriptions does the tooth structure of *Helicoprion*, as far as I can see, differ in any fundamental respect from the tooth structure in other *Bradyodonti*. The layer of tubular dentine, it is true, is relatively thin in *Helicoprion*, but the same is the case in *Sarcoprion*, and the "enamel"-like outer layer in *Helicoprion* is easily comparable to the outer shining surface layer of unworn teeth of all the Greenland Edestids.

According to MOY-THOMAS (1939, p. 3), all the Bradyodonts in which the skull is known, have a holostylic jaw suspension, and there is every reason to believe that this is a common character of the whole group. We now know that the jaw suspension in the typical Edestid *Sarcoprion*, also, (as well as in *Fadenia*, judging by well preserved skulls) is holostylic, and this must be regarded as another strong argument for including the Edestids as a whole in the large Bradyodont group.

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Færdig fra trykkeriet den 20. november 1952.

PLATES

Plate 1.

Sarcoprion edax n. sp.

Fig. 1. Section no. 6 through the skull. Specimen no. 214. Nat. size.
Fig. 2. Section no. 5 through the skull. Specimen no. 214. Nat. size.

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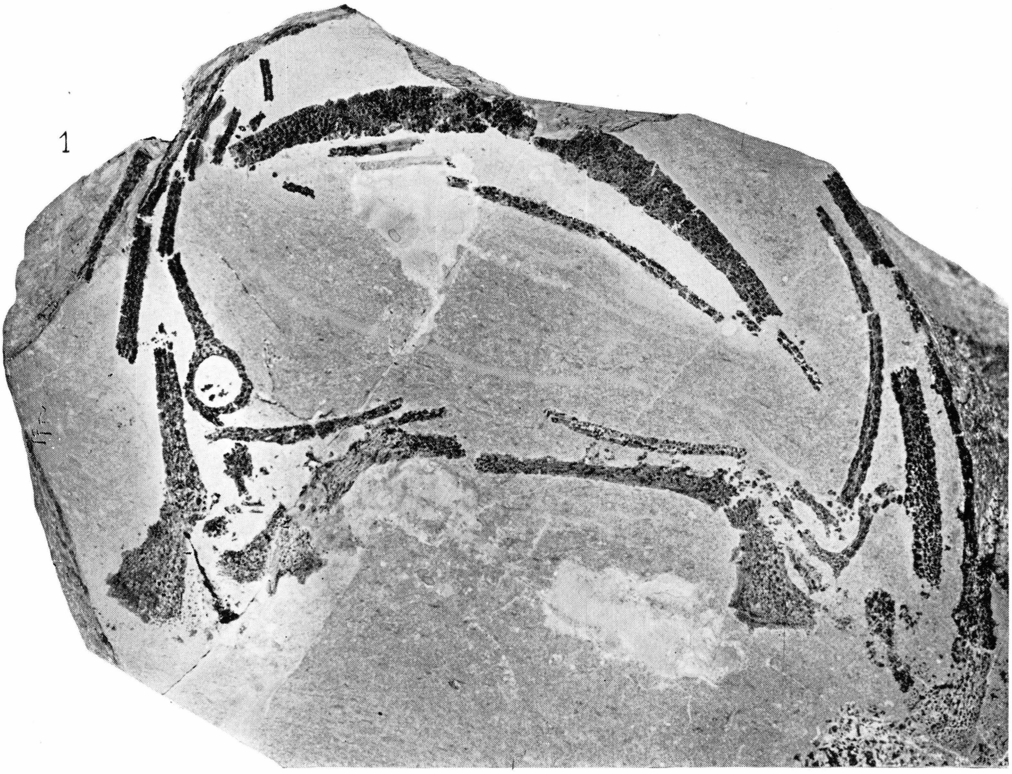

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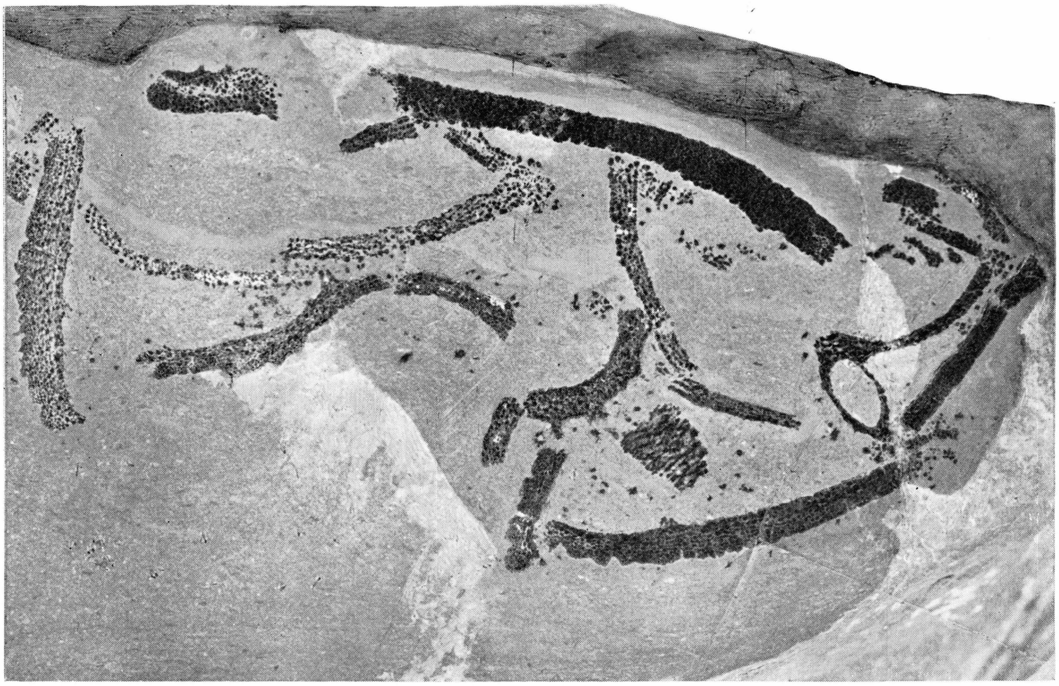

Plate 2.

Sarcoprion edax n. sp.

Fig. 1. Section no. 4 through the skull. Specimen no. 214. Nat. size.
Fig. 2. Section no. 3 through the skull. Specimen no. 214. Nat. size.
Fig. 3. Section no. 2 through the skull. Specimen no. 214. Nat. size.

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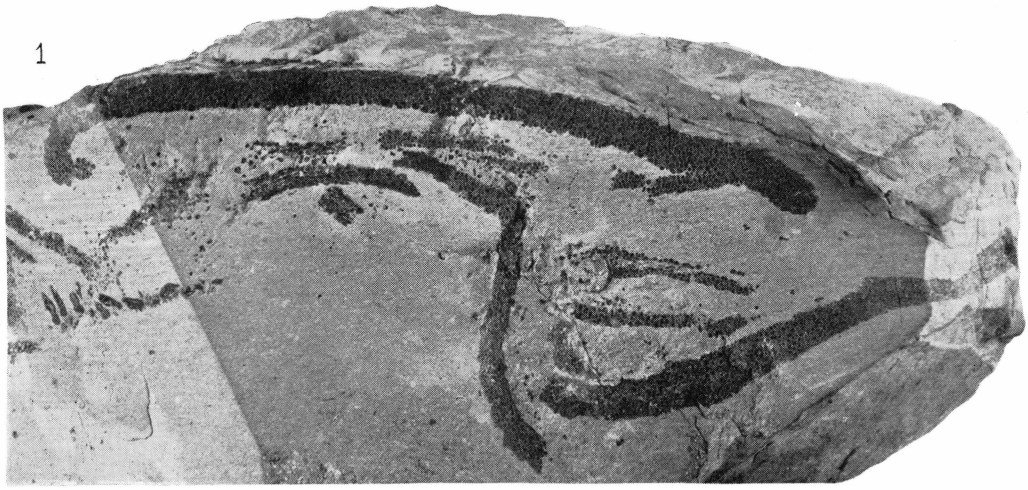

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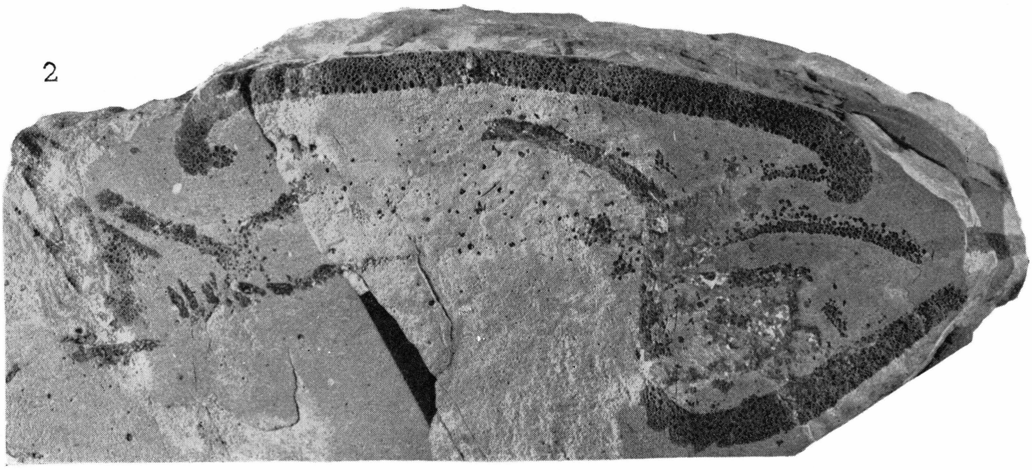

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Plate 3.

Sarcoprion edax n. sp.

Fig. 1. Section no. 1 through the skull. Specimen no. 214. Nat. size.
Fig. 2. Series of symphysial teeth in lateral view. Specimen no. 215. Nat. size.
Fig. 3. Part of the upper series of symphysial teeth in lateral view.
Specimen no. 214. 1.5 ×.

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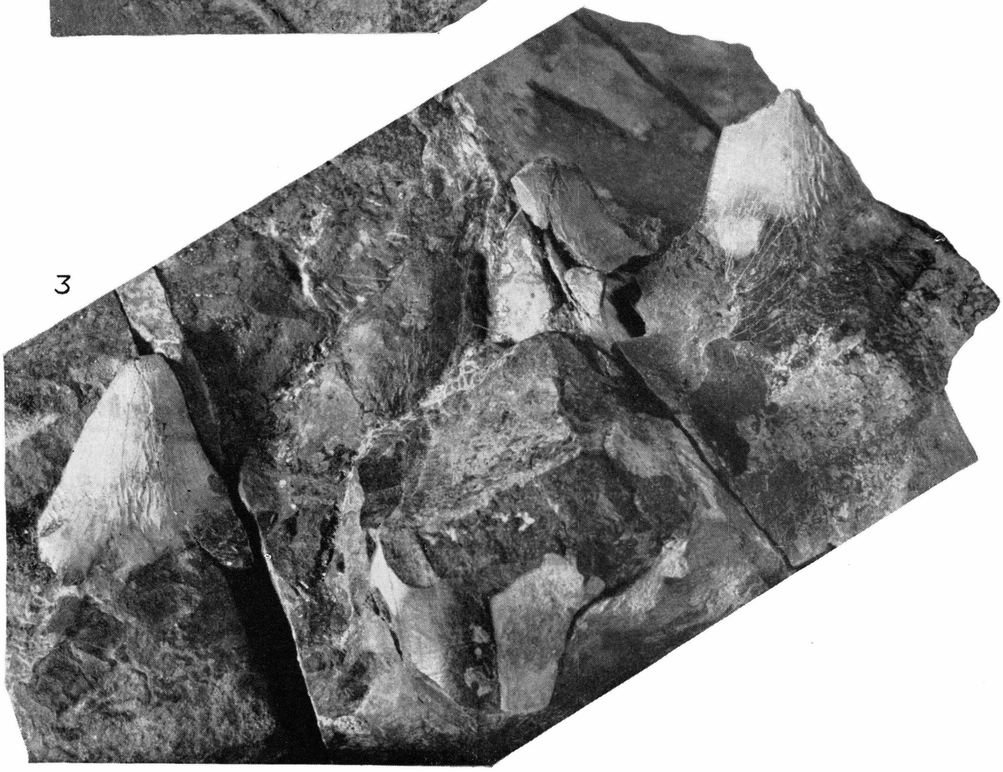

Plate 4.

Sarcoprion edax n. sp.

Two adjoining faces of specimen no. 214 showing sections of the two members of the lower jaw, the small basihyal, and numerous teeth and scales. Nat. size.

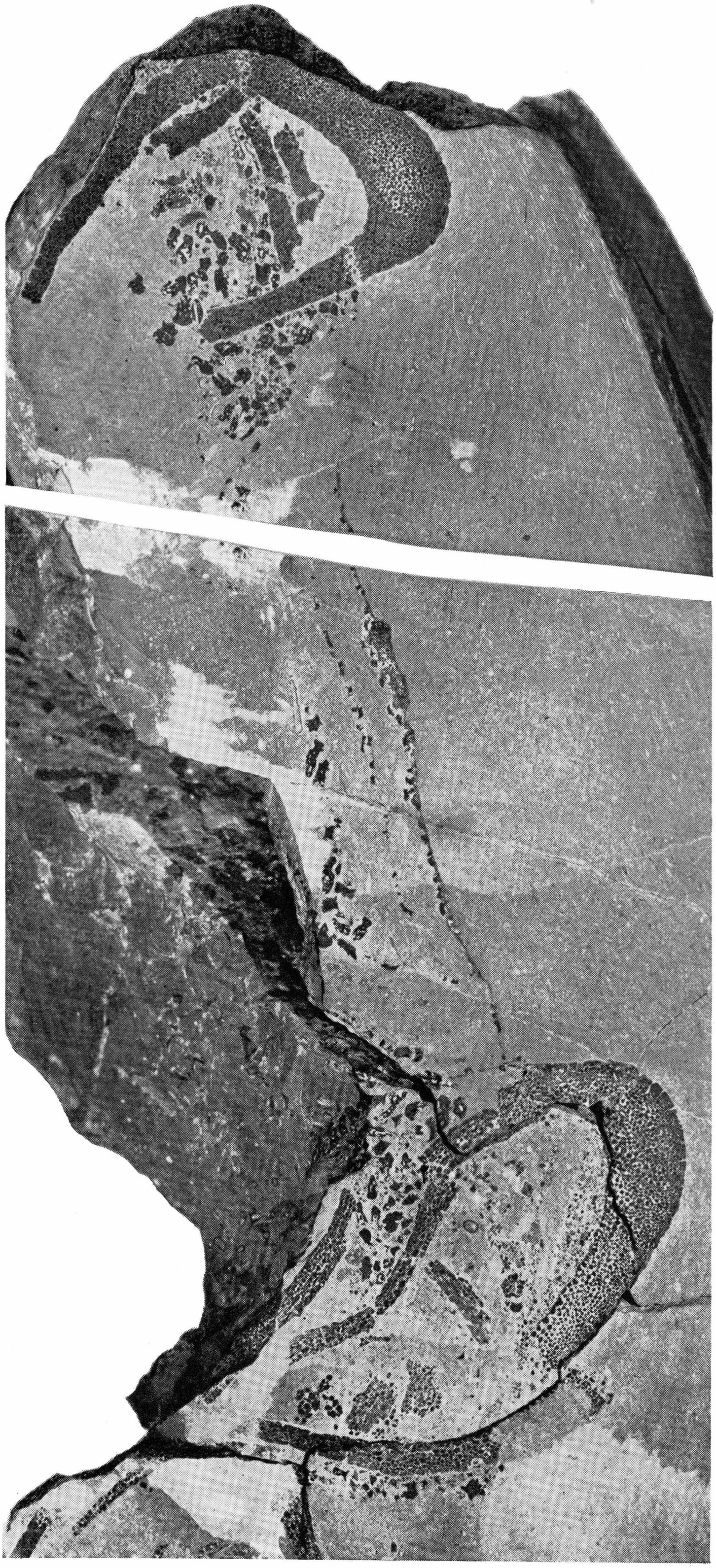

Plate 5.

Sarcoprion edax n. sp.

Lower series of symphysial teeth in lateral view.

Specimen no. 214. 0.75 ×.

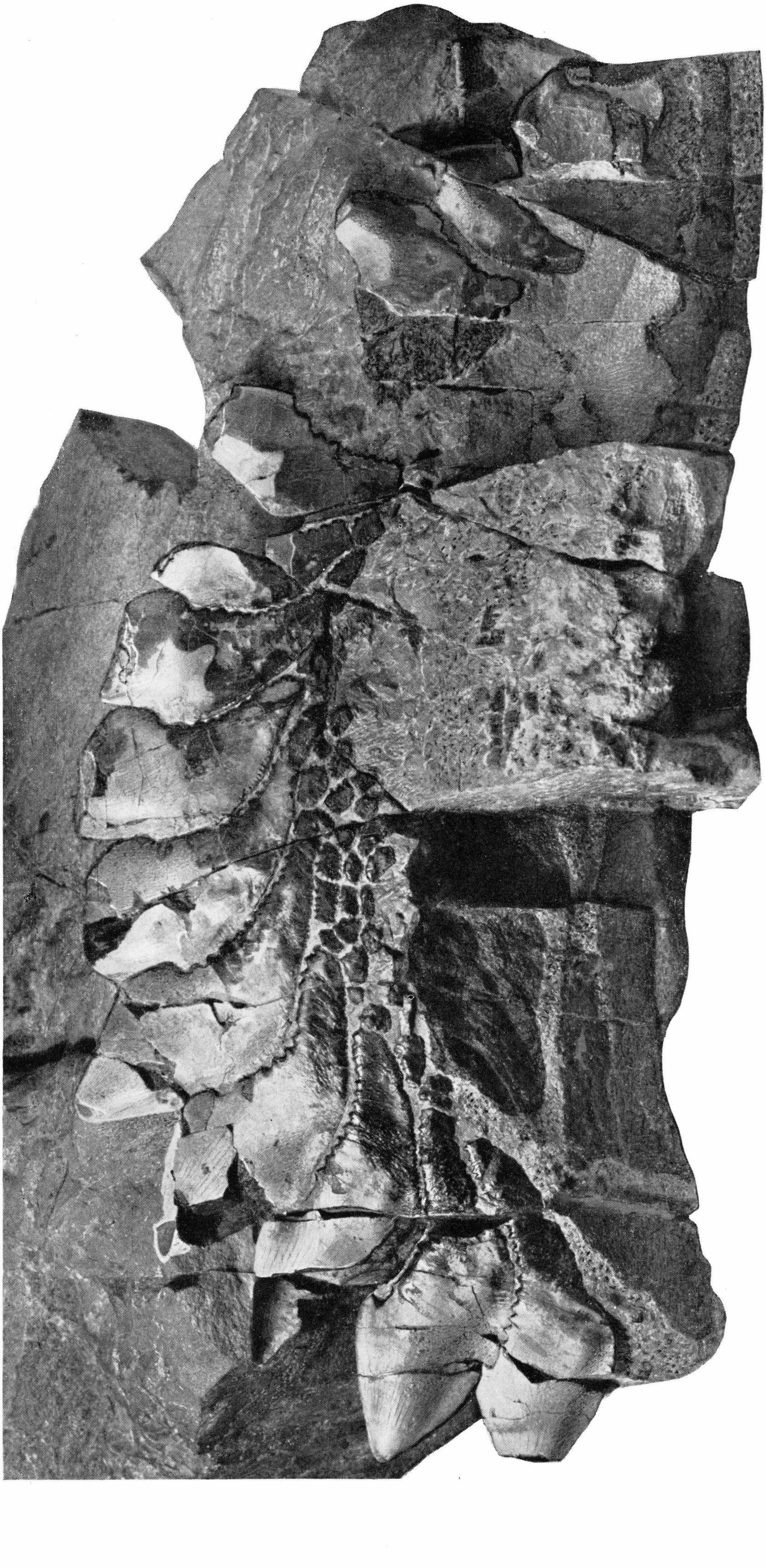

Plate 6.

Sarcoprion edax n. sp.

Part of the lower series of symphysial teeth in lateral view.

Specimen no. 214. C. 1.9 ×.

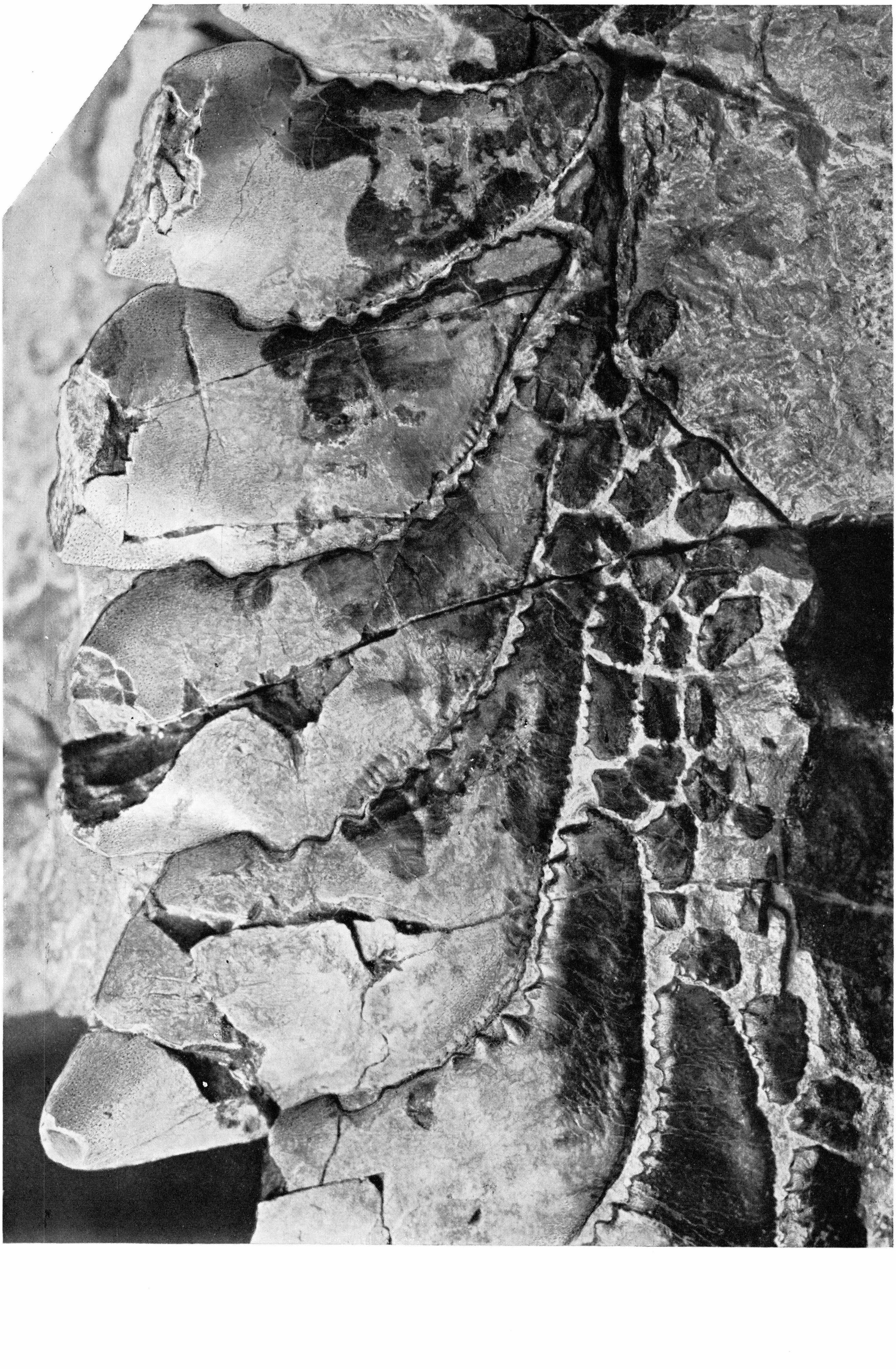

Plate 7.

Sarcoprion edax n. sp.

Fig. 1. Teeth nos. 3 and 4 from the lower symphysial series in anterior view and section through the symphysial portion of the lower jaw.
Specimen no. 214. Nat. size.

Fig. 2. Lower series of symphysial teeth in dorsal view. Specimen no. 214. 0.67 ×.

Fig. 3. Posterior part of lower symphysial series in posterior view.
Specimen no. 214. 0.67 ×.

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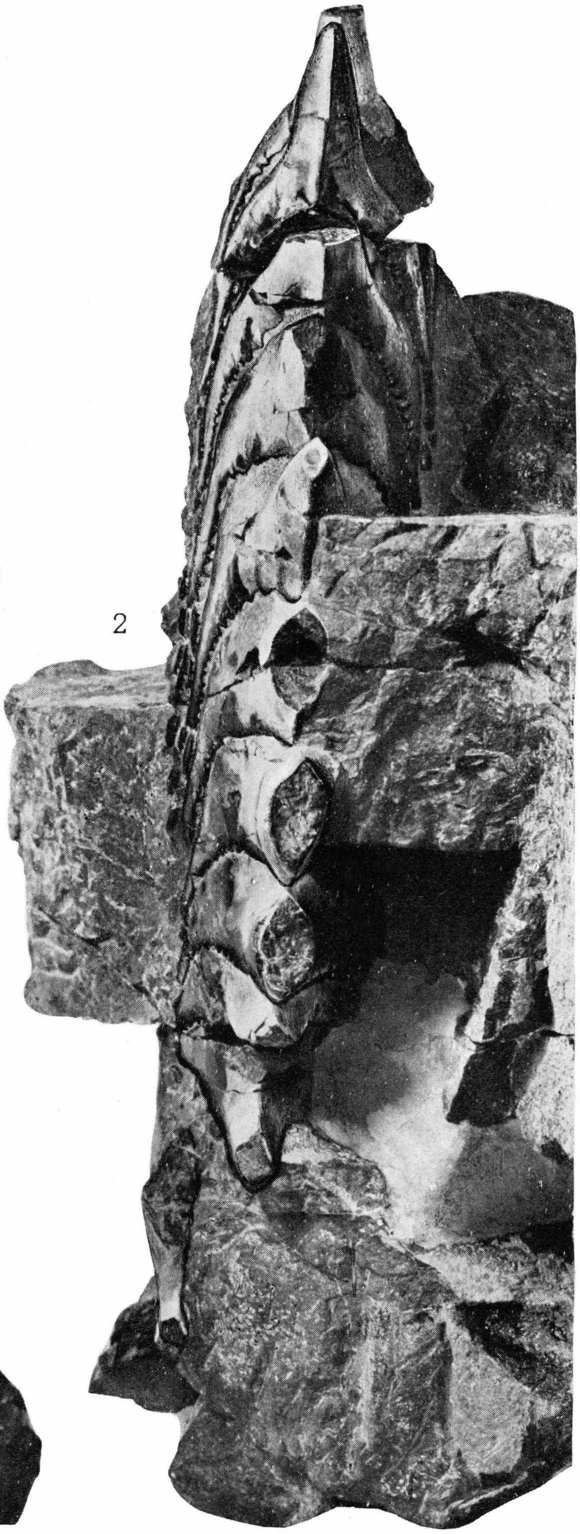

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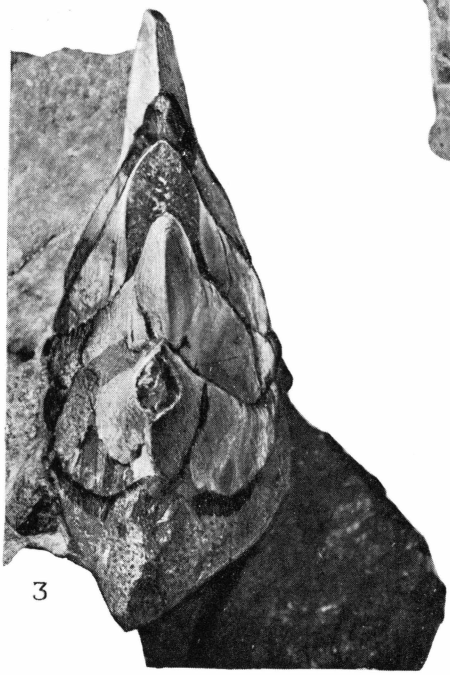

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Plate 8.

Sarcoprion edax n. sp.

Fig. 1. Section through part of the right half of the lower jaw with accumulation of the lateral teeth and scales. Specimen no. 214. Nat. size.

Fig. 2. Two unworn lateral teeth in coronal view. Specimen no. 214. 6.1 ×.

Fig. 3. Worn lateral tooth in coronal view. Specimen no. 214. 6.1 ×.

Fig. 4. Oblique section through the right member of the lower jaw a short distance behind the region where the right and the left member of the jaw fuse. In addition, numerous lateral teeth and scales. The figure also shows sections through two large symphysial teeth probably from the upper series. Specimen no. 214. Nat. size.

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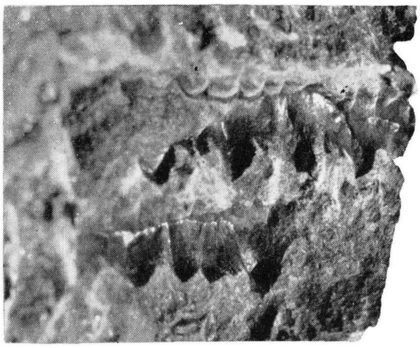

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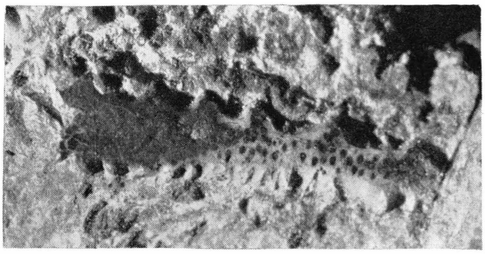

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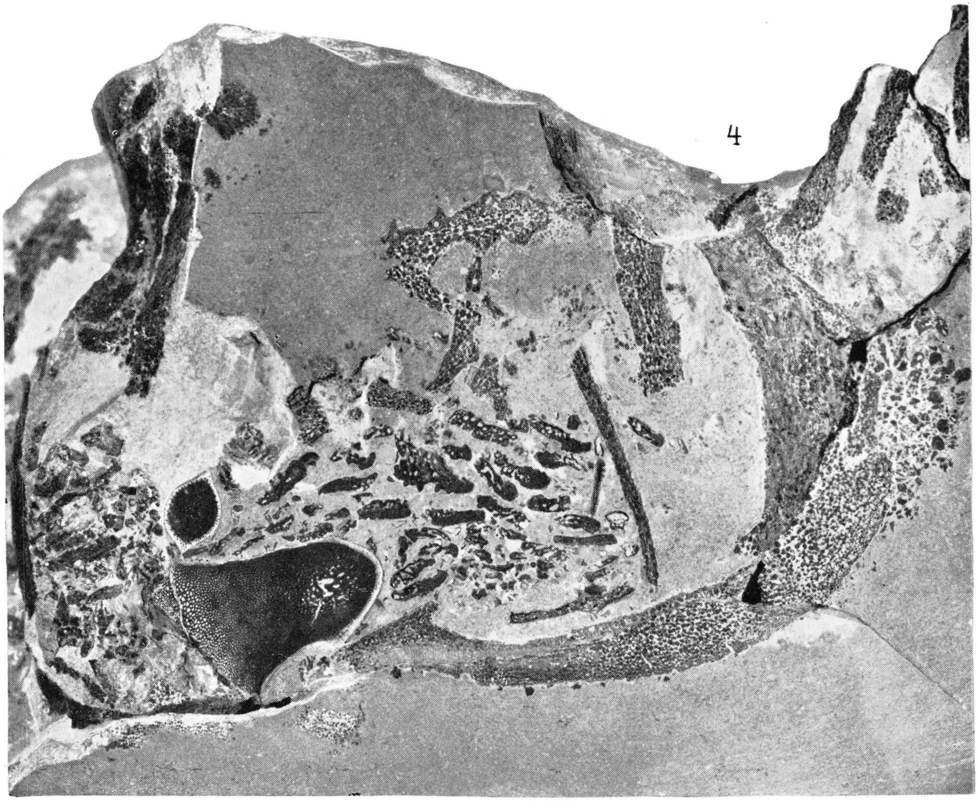

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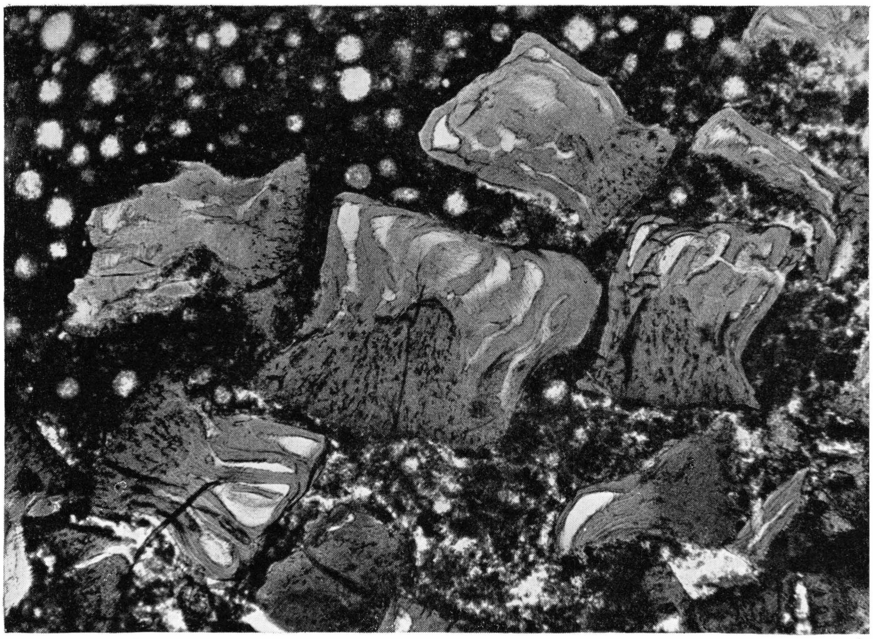
Plate 9.

Sarcoprion edax n. sp.

Fig. 1. Section through a number of large composite scales. Specimen no. 214. 32×.

Fig. 2. Part of the pavement of very large scales on the foremost part of the lower jaw. Specimen no. 214. 6.1×.

1 

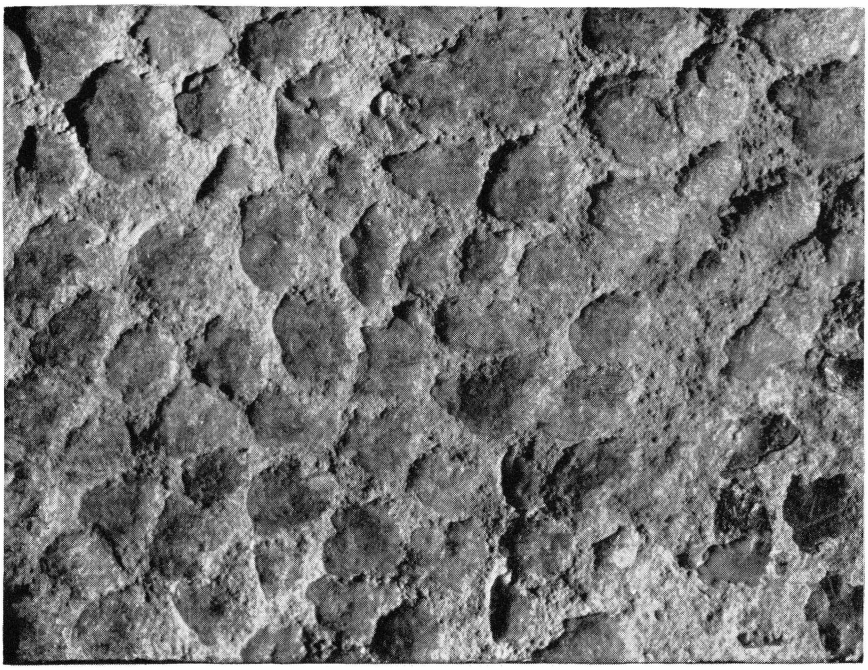
2 

Plate 10.

Erikodus groenlandicus (E. Nielsen).

Figs. 1—2. Part of a symphysial series in lateral and coronal view.
Specimen no. 221. 1.5 ×.

Figs. 3—4. Single symphysial tooth in coronal and basal view.
Specimen no. 218. 1.5 ×.

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Plate 11.

Erikodus groenlandicus (E. NIELSEN).

Figs. 1—2. Lower series of symphysial teeth in lateral view and in sagittal section. Specimen no. 220. 1.5 ×.

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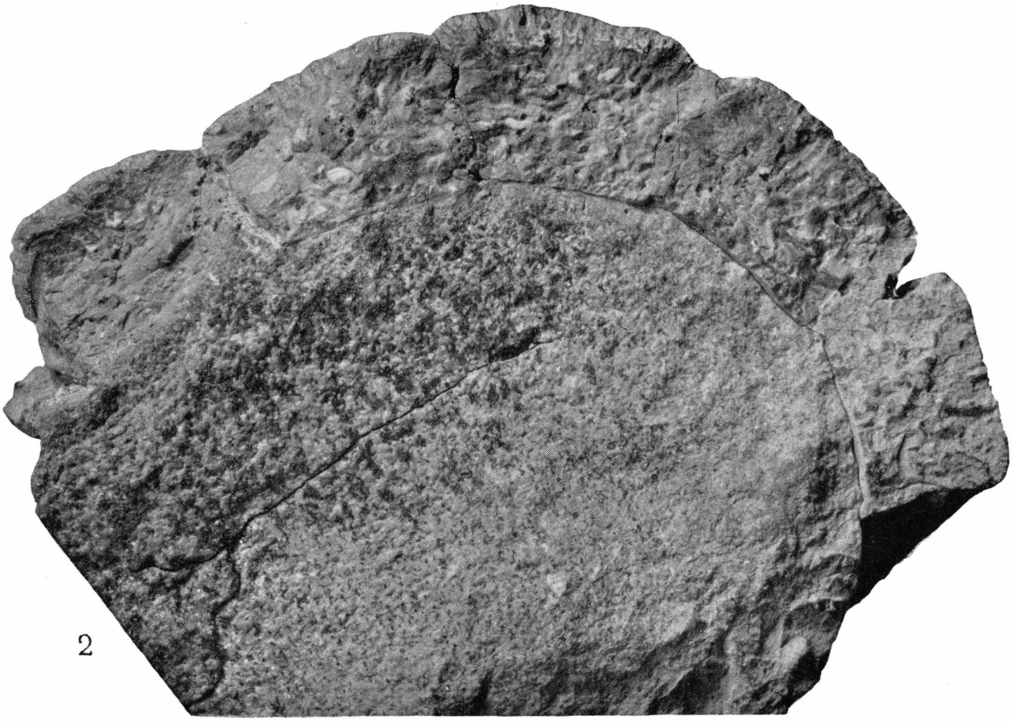

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Plate 12.

Fig. 1. *Fadenia crenulata* E. NIELSEN. Series of symphysial teeth in lateral view. Specimen no. 223. 1.5 ×.

Fig. 2. *Fadenia crenulata* E. NIELSEN. Series of symphysial teeth in lateral view. Specimen no. 225. 1.5 ×.

Fig. 3. *Erikodus groenlandicus* (E. NIELSEN). Series of symphysial teeth in lateral view. Specimen no. 219. Nat. size.

Fig. 4. *Parahelicampodus spärcki* n. sp. Series of symphysial teeth in lateral view. Holotype. 1.5 ×.

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Plate 13.

Fig. 1. *Erikodus groenlandicus* (E. Nielsen). Two presumed upper symphysial teeth in coronal view. Specimen no. 220. 1.5 ×.

Fig. 2. *Fadenia crenulata* E. Nielsen. Series of symphysial teeth in coronal view. Specimen no. 225. 1.5 ×.

Fig. 3. *Parahelicampodus spärcki* n. sp. Series of symphysial teeth in coronal view. Holotype. 1.5 ×.

Fig. 4. *Erikodus groenlandicus* (E. Nielsen). Series of symphysial teeth in coronal view. Specimen no. 219. Ca. nat. size.

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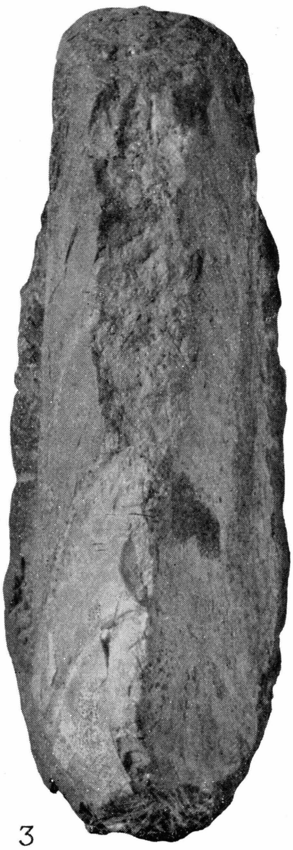

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