# AMERICAN MUSEUM NOVITATES

Number 1017 Published by THE AMERICAN MUSEUM OF NATURAL HISTORY New York City March 2, 1939

## ON *SPERMATODUS PUSTULOSUS* COPE, A COELACANTH FROM THE "PERMIAN" OF TEXAS[1]

BY T. STANLEY WESTOLL, B.Sc., Ph.D.[2]

### I.—INTRODUCTION AND ACKNOWLEDGMENTS

The coelacanth fishes have been the subject of much research during the past fifty years, particularly since the work of Stensiö (1921) on certain Triassic forms from Spitzbergen. Recent work has been, with few exceptions, devoted to Mesozoic types, and any Palaeozoic genera are likely to prove of interest. While discussing certain coelacanths with Prof. D. M. S. Watson, the writer was informed of the existence, in The American Museum of Natural History, of an undescribed coelacanth head from the Texan Red Beds. Later, on examining Hussakof's figure of *Spermatodus pustulosus* Cope (Hussakof, 1911, Pl. XXXII), the writer saw that it probably represented a coelacanth, and it has been possible, through the kindness and courtesy of Prof. W. K. Gregory, to study both specimens in London. The two heads have proved to belong to the same species, and are of almost exactly comparable size. After the specimens had been identified as coelacanths, the writer asked Prof. A. S. Romer, who has been collecting from the Texan Red Beds for some time, if similar material occurred in his collections. At that time he had no material, but in December, 1936, he sent the writer eight bones, more or less fragmentary, which he considered, from their resemblance to the basisphenoid of "*Megalichthys*" (= *Ectosteorachis*), to be remains of a coelacanth. They prove to be basisphenoids of the same species as the original two.

Since that time the writer has been able to visit certain Museums in the United States, with the aid of grants from the Geological Society and the Royal Society of London, and has seen much more material of the fish in the Museum of Geology, University of Michigan, and in the Museum of Comparative Zoölogy at Harvard. As it will be some time before this material can be adequately prepared and studied, the present description is based on the specimens mentioned above, and is offered as a prelimi-

[1] This manuscript was completed November 20, 1937.

[2] Dept. of Geology, Marischal College, Aberdeen, Scotland.

nary description in the hope that other material of the fish may be recognized. The body and much of the front of the head are yet unknown.

The author is indebted to Profs. W. K. Gregory and A. S. Romer for generously lending him the specimens described in this paper. He is very grateful to many other workers who have freely given help and information: in particular he desires to thank Prof. E. A. Stensiö and Dr. E. Nielsen, who have shown him much unpublished material of coelacanths in Stockholm; and Dr. E. I. White of the British Museum of Natural History, who, with Dr. Lang, has been responsible for letting him have the use of comparative material. This work has been done mainly at University College, London. Prof. D. M. S. Watson has been generous with his help and valuable criticism. Finally, the author wishes to acknowledge with thanks a Senior Research Award from the Department of Scientific and Industrial Research.

## II.—HISTORICAL NOTE. PROVENANCE OF MATERIAL, ETC.

*Spermatodus pustulosus* was described by Cope in 1894 as a crossopterygian. His description can be followed quite readily on the type specimen (A.M.N.H. 7245), though naturally many of his descriptive terms are misapplied or are now obsolete. The type was refigured and considered by Hussakof, who believed it to be part of the skull of a fish which he thought should be removed from the crossopterygians and placed in the "Actinopteri," though its affinities were regarded as uncertain (Hussakof, 1911, p. 172, Pl. XXXII). There has been no subsequent redescription of the animal.

In 1877, Cope described a tooth-bearing plate from the Texas "Permian" as *Peplorhina arctata* (1877, p. 54); his genus *Peplorhina* had been recognized first from the Coal Measures of Linton, Ohio. Later (1882, p. 461, footnote) he regarded the fossil as part of a "Theromorph saurian." Case (1900, p. 707) found a second and more complete specimen and regarded it as undoubtedly crossopterygian. Hussakof, in 1911, figured all the known specimens, with some other fragments which may or may not belong to the same animal. He regarded them all as being referable to Fritsch's genus *Sphaerolepis*, founded for an actinopterygian from the Bohemian Gascoal; Hussakof made pertinent criticism of the validity of *Peplorhina*.

In 1915, W. D. Matthew published the plates originally prepared for Cope in 1880–1883 (Cope and Matthew, 1915). Cope figured (Pl. III, fig. 5, 5*a*) the type of *P. arctata* (described as *Sphaerolepis arctata* in the description of the plates); the original specimen from the Walker Museum seems to the writer to be strictly indeterminable, though it may well belong to a coelacanth.

Of these specimens, the tooth-plates figured by Hussakof (1911, Fig. 54 *a, c:* Pl. xxxi, figs. 1, 2) are possibly coelacanth in origin, as similar plates have been seen by the writer in other genera. Strictly speaking, however, all are indeterminate, and it is best to disregard them completely in the synonymy.

The provenances of the type (A.M.N.H. 7245) and referred specimen are uncertain. The basisphenoids lent by Prof. A. S. Romer are from the Admiral Formation of the Wichita group, in Rattlesnake Canyon, Archer County, Texas.

## III.—DESCRIPTION OF MATERIAL

The type specimen (A.M.N.H. 7245) (Fig. 1*a, b*) consists of the disturbed remains of about half a skull, lacking the most posterior region, the snout and most of the cheeks. The bones preserved are very difficult to prepare in a satisfactory way.

The referred specimen (A.M.N.H. 7245*a*) (Fig. 2*a, b*) lacks the snout and the right half of the head, but shows the left cheek very clearly. The matrix is more stubborn than that of the type.

These two specimens are of almost exactly the same size, and indicate an animal with a total skull-length of about 18–20 cms.; the total body-length may thus have reached 1 meter.

The separate basisphenoids lent by Prof. A. S. Romer show a range of size from about 2/3 to 1 1/2 that of the type. When fully adult the fish must have been over a meter long, with a head nearly 30 cms. in length. It is thus of very large size for a coelacanth, though it does not rival *Mawsonia gigas* in this respect. (Woodward, 1907, p. 134.)

Cranium.—As in all coelacanths, the endocranium is divided into two parts by a transverse division: an otico-occipital and a spheno-ethmoid region are thus separated.

The otico-occipital region is almost unknown: in the type specimen no remains can with certainty be referred to it, and in the other skull nothing of the characteristic coelacanth "proötic" can be seen. In the latter specimen, however, two curious elements, lying below the posterior section of the skull-roof, probably belong in some way to the otic region (Fig. 2*b*, "*?Ot*"); so far as the author is aware, nothing quite like them has been described in any other coelacanth, though some comparable

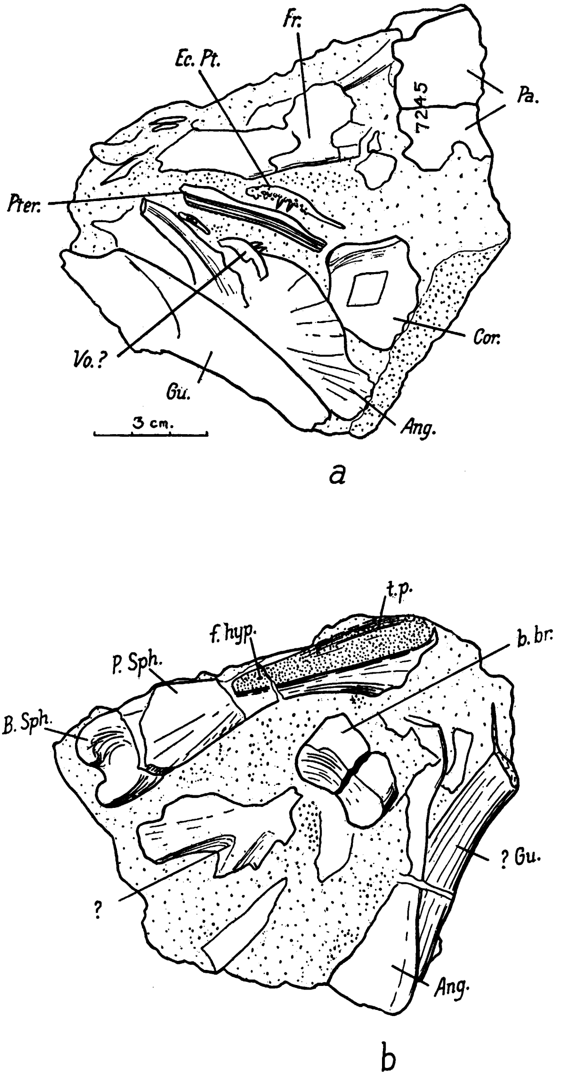


Fig. 1. *Spermatodus pustulosus* Cope.

*a, b.*—The two sides of the holotype, A.M.N.H. 7245. × 2/3

| | | | |
|---|---|---|---|
| *Ang.*, | Angulo-surangular | *P.Sph.*, | Parasphenoid |
| *B.Sph.*, | Basisphenoid | *Pter.*, | Edge of Pterygoid |
| *Cor.*, | Coronoid | *Vo.?* | Possibly a vomer |
| *Ec.Pt.*, | Ectopterygoid | | |
| *Fr.*, | Frontal | *b.br.*, | Basibranchial? |
| *Gu.*, | Gular | *f.hyp.*, | Foramen for hypophysial canal |
| *Pa.*, | "Parietal" | *t.p.*, | Toothplate of parasphenoid |

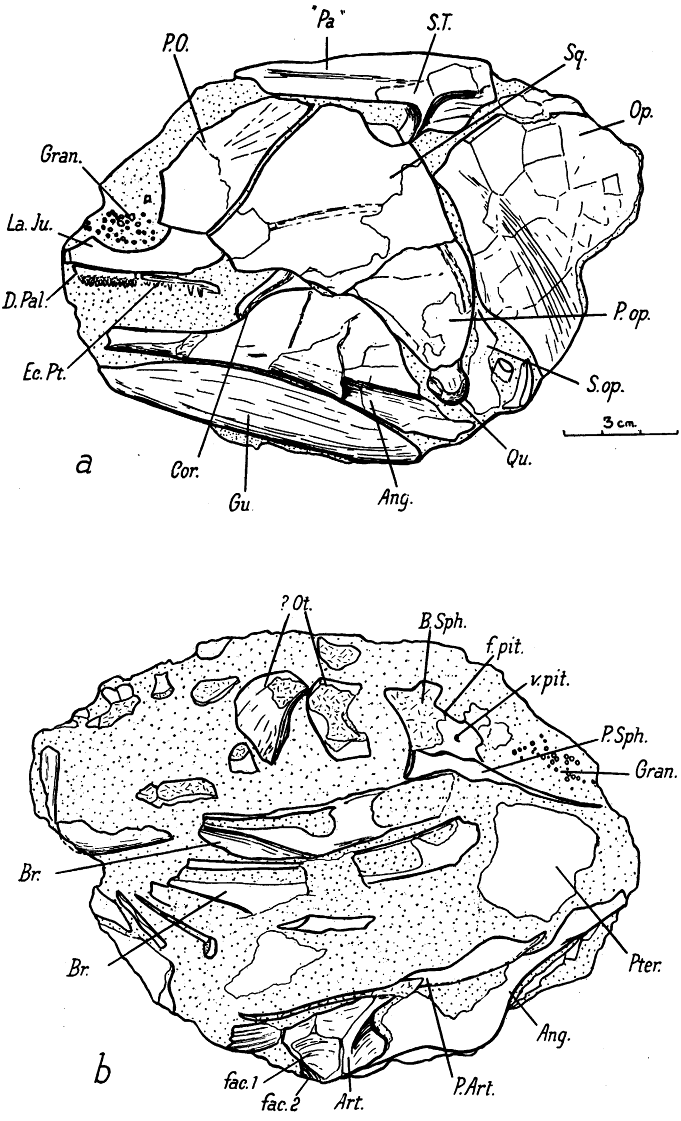


Fig. 2. *Spermatodus pustulosus* Cope.

*a, b.*—The two sides of the referred specimen, A.M.N.H. 7245*a*. × 2/3

| | | | |
|---|---|---|---|
| *Ang.*, | Angulo-surangular | *P.O.*, | Postorbital |
| *Art.*, | Articular | *P.Op.*, | Preopercular |
| *Br.*, | Branchial arch | *P.Sph.*, | Parasphenoid |
| *B.Sph.*, | Basisphenoid | *Pter.*, | Pterygoid |
| *Cor.*, | Coronoid | *Qu.*, | Quadrate |
| *D.Pal.*, | Dermo-palatine | *S.Op.*, | Subopercular |
| *Ec.Pt.*, | Ectopterygoid | *Sq.*, | Squamosal |
| *Gran.*, | Granular ossifications | *S.T.*, | Supratemporal |
| *Gu.*, | Gular | | |
| *La.Ju.*, | Lacrimo-jugal | *fac.1,2*, | Facets for quadrate on articular |
| *Op.*, | Opercular | | |
| *?Ot.*, | Bones perhaps belonging to otic region | | |
| *Pa.*, | "Parietal" | *f.pit.*, | Pituitary fossa |
| *P.Art.*, | Prearticular | *v.pit.*, | Foramen for pituitary vein |

structures may have been present in *Macropoma* (see below). The bones are lying loose, and their proper orientation is a matter of conjecture, but they appear to be a pair. The more "anterior" ossification, as now preserved, is apparently turned upside down with reference to the other, and shows the reverse face. The general nature of these bodies will be seen from figure 2*b*. One face of each body was apparently almost flat, and this is presented in the more anterior specimen; this face is fragmentarily preserved, and may not have been well ossified. It is met along its two narrower margins by a strongly convex bony sheet, and the element was completed by two, apparently rather flat, narrow faces. The whole element is rather like a desk blotter in shape: owing to the bad preservation any possible foramina cannot be distinguished. The auditory capsule seems to be the most likely provenance of these bodies.

The anterior portion of the endocranium is partly preserved in both skulls. The basisphenoid of the type is still partly hidden by matrix, and is in nearly normal relationship with the parasphenoid (Fig. 1*b*). In the other specimen the right side of the basisphenoid has been removed by fracture, and the pituitary fossa is partly open (Fig. 2*b*). The specimens collected by Prof. Romer are, however, the main source of information about this bone. (See Fig. 3, *a–e*, Fig. 4.)

The postero-ventral face of the basisphenoid is concave, resembling a cotylus very markedly; it was called "occipital cotylus" by Cope in his original description. The concave surface is almost circular, but the lateral margins are thickened and produced postero-dorsally into a pair of rounded knobs. These knobs are marked off from the cotylus-like face by shallow grooves, in which there are often small patches of dense bone which may mark the insertion of ligaments connected with the intra-cranial joint. The cotylus itself is marked by a small central hummock, of which the ventral surface is roughened. This probably marks the actual termination of the notochord. Above this hummock is a series of slight grooves and ridges, partly concentric but sloping laterally down to a pair of slight swellings on the lower parts of the lateral ridges. There is never any sign of notches or foramina such as those figured by Aldinger (1930, p. 31, Figs. 1, 6 ("VI")) and believed by him to be for n. abducens. Apart from the two small patches of dense perichondrial (?) bone mentioned above as possibly marking ligamentous insertion, the postero-ventral surface is composed of rather fine-meshed spongy bone.

In front of the postero-ventral face, the basisphenoid consists of a ventral corpus, a pair of lateral lamellae extending forward and upward

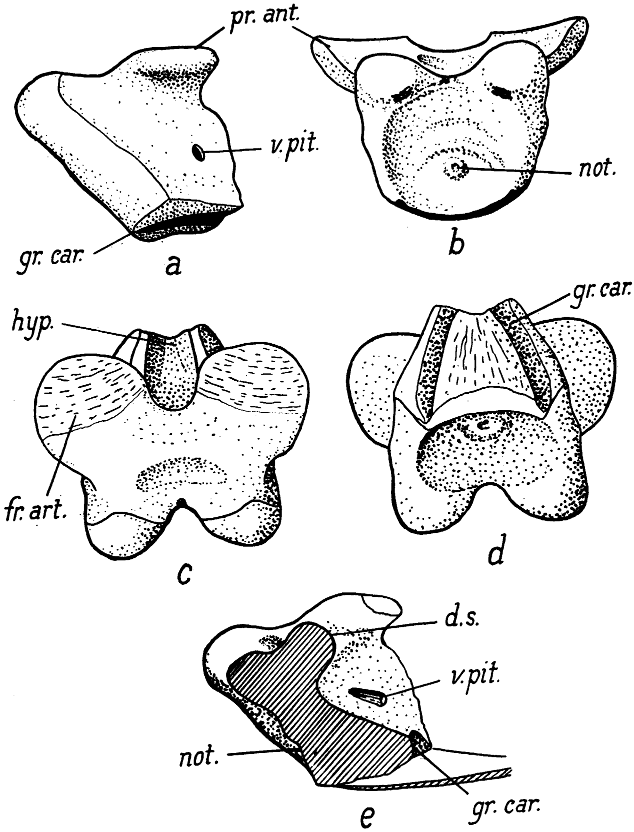


Fig. 3. *Spermatodus pustulosus* Cope.

Basisphenoid; based on specimens from Rattlesnake Canyon, Archer Co., Texas. About × 1.

*a.*—In lateral view.
*b.*—In posterior view.
*c.*—In dorsal view.
*d.*—In ventral view.
*e.*—In median sagittal section, with parasphenoid attached.

| | | | |
|---|---|---|---|
| *d.s.,* | Dorsum sellae | *not.,* | Notochord scar |
| *fr.art.,* | Sutural face against frontal | *pr.ant.,* | Antotic process |
| *gr.car.,* | Groove for internal carotid artery | *v.pit.,* | Foramen for pituitary vein |
| *hyp.,* | Groove for hypophysial canal | | |

from this, and a pair of stout antotic processes rising to the dermal skull-roof and being firmly attached to it in life (Fig. 3*a*, *b*, *c*; "*pr. ant.*," "*fr. art.*").

The ventral aspect of the basisphenoid is convex from side to side, and posteriorly is closely fitted to the rather unusually broad parasphenoid. Anteriorly the bone becomes more slender, and was clearly incompletely ossified antero-ventrally, being continued by cartilage during life. Paired grooves, convergent forward, run from the back of the basisphenoid; they make slight notches in the posterior margin, rapidly become deep as traced forward, and then keep at a more or less uniform depth below the surface (Fig. 3, "*gr. car.*"). These grooves are rather narrow, and the walls are lined with lamellar bone, which curves roughly round the walls. The parasphenoid covers these grooves ventrally, apparently without sending any processes into them. In life, therefore, these grooves were probably made into canals, which may reasonably be regarded as the courses of the internal carotid arteries (see below). The anterior part of the ventral surface of the basisphenoid corpus is, in large specimens, partly covered with dense bone; in young individuals this is absent.

From the pair of postero-dorsal knobs on the basisphenoid, and the slight depression between them, a broad surface runs forward, rising till it forms the dorsum sellae. The lateral margins of this surface are slightly waisted, and anteriorly pass outward into the antotic processes. The middle of the surface is excavated in a shallow transverse hollow, of unknown function, similar to that figured in *Coelacanthus granulatus* Ag. (Moy-Thomas and Westoll, 1935, Fig. 4). The antotic processes arise from the junction of this postero-dorsal surface with the lateral lamellae; at the base each process is thick and massive, but passes antero-laterally and slightly dorsally as a rather wide and flat process, scarfed for the articulation with the frontal (Fig. 3*c*, "*fr. art.*"). The anterior margin of the postero-dorsal surface between the antotic processes is smoothly concave and overhangs a deep excavation, bounded largely by the lateral lamellae. This excavation is the pituitary fossa. The posterior margin is overhung, and the ventral margin slopes gently forward, forming a broadly U-shaped floor between the lamellae. Anteriorly this floor is continued as a narrow groove sloping still more gradually downward and forward, and this was clearly continued in life in cartilage beyond the limits of the bone as preserved. This groove can only have lodged a hypophysial duct or cord.

The lateral lamellae extend ventrally as far forward as the corpus, but the dorsal parts are more incompletely ossified, and the actual margins are imperfect in the available material. Below the anterior junction of the lamella and the antotic process the former is pierced by a foramen directed inward and backward into the pituitary fossa; this is clearly for the pituitary vein (Fig. 3*a*, *e*, "*v. pit.*"). On the internal face of the lamella the foramen is continued posteriorly as a shallow groove; this may lead to a tiny foramen in the bone, showing that the corpus of the basisphenoid was drained of nutritive blood into the pituitary vein.

The cranial aspect of the basisphenoid is formed of smooth lamellar perichondrial bone, somewhat imbricated in detailed structure. The outer faces of the lateral lamellae, the postero-dorsal surface, and the antotic processes are similarly covered, but on the lateral lamellae the bone-structure is coarser and so imbricated as to present almost a flaky appearance. This perichondrial bone ends on a sharp line running just anteriorly to the lateral ridges of the cotylus and the postero-dorsal knobs. Often dense bone penetrates rather deeply into the corpus.

It is clear in the type (A.M.N.H. 7245) that there are well-developed ossifications in the ethmoid region, but these are so confused that no attempt has been made to prepare them. Between this region and the basisphenoid there is scattered a large number of small irregularly rounded nodules of bone, showing concentric structure in section. These can be seen in both specimens, and in no. A.M.N.H. 7245 it seems probable that they form two masses, one on each side of the median plane: they seem to represent ossifications in the side walls of the orbital part of the cranium (Fig. 2*b*, "*gran.*"). Similar nodular ossifications, in a comparable position, were noted by Moy-Thomas and Westoll in *Coelacanthus granulatus* Ag. (1935, p. 457), though as nothing comparable had been described elsewhere they considered them to be possibly extraneous and did not describe them further.

DERMAL BONES OF THE CRANIUM.—The parasphenoid is partly shown in both skulls, almost completely in the type (Fig. 1*b*, "*P.Sph.*"; Fig. 4). It is a strong and broad element closely attached to the basisphenoid posteriorly; no cavity such as that described as a myodome by Aldinger (1930, p. 34 etc., Fig. 5) can be seen. The bone is remarkably broad posteriorly, being there as wide as the basisphenoid. Just behind the middle of its length the bone is narrower, and it expands again anteriorly. A spatulate tooth-plate, about 2/3 of the whole length of the bone, is situated far forward; its shape will be clear from the figure (Fig. 4). The tooth-plate is raised so that it projects ventrally from the main surface of the bone, and the anterior part is very concave. The teeth are small, rounded, and densely packed. Near the posterior end of the tooth-plate the parasphenoid is pierced by a small oval median foramen, which marks the center of the radiate structure of the bone. The foramen can only be for a hypophysial cord; it is surrounded by teeth and must have been just beneath the skin of the roof of the mouth.

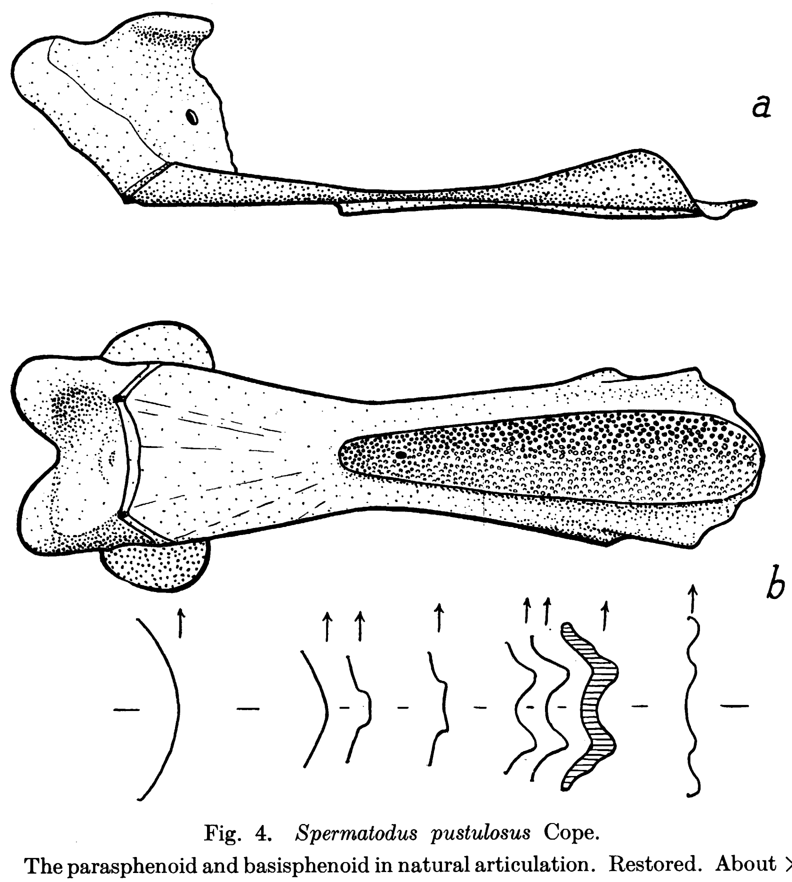


Fig. 4. *Spermatodus pustulosus* Cope.

The parasphenoid and basisphenoid in natural articulation. Restored. About × 1.

*a.*—In lateral view.

*b.*—In ventral view, with a series of profiles and cross sections of the parasphenoid at various points.

The posterior part of the parasphenoid closely fits the basisphenoid, save for the grooves mentioned above. A little farther forward the anterior part of the corpus of the basisphenoid is separated from the parasphenoid by a space which varies much in different individuals, and which is apparently considerably reduced in large specimens. In this region the parasphenoid is convex from side to side in ventral view. Anteriorly the lateral wings of the parasphenoid rise more sharply toward the skull-roof; near the widest part of the tooth-plate, however, is a pronounced lateral flare, which was almost certainly related to the dorso-mesial margin of the primary upper jaw.

The detailed shape of the parasphenoid will be clear from the series of sections given in the figure.

No remains of vomers can be identified with certainty (but see below, p. 13).

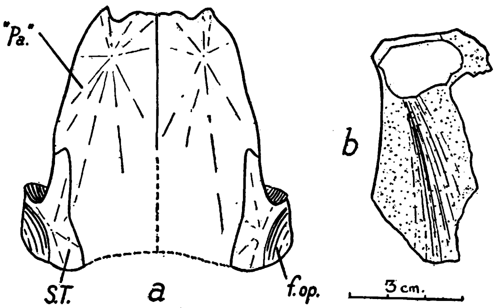


Fig. 5. *Spermatodus pustulosus* Cope.

*a*.—The "parietal shield" restored from specimens A.M.N.H. 7245 and 7245*a*. × 2/3.

| | |
|---|---|
| "*Pa.*," | "Parietal" |
| *S.T.*, | Supratemporal |
| *f.op.*, | Facet for suspension of opercular |

The ornament is omitted and the radiation-centers of the bones are indicated.

*b*.—The opercular removed by preparation from A.M.N.H. 7245*a;* the figure is reversed for ease of comparison with Fig. 2*a*. × 2/3.

Dermal Bones of the Skull-Roof.—The posterior part of the cranium is covered, as is usual in coelacanths, by two pairs of bones: the postero-lateral "supratemporals" and the larger antero-mesial "parietals" (= "parieto-intertemporals" of Stensiö, "fronto-parieto-intertemporals (+ dermosphenotics?)" of Nielsen, 1936).

The supratemporal has a more or less triangular exposure on the skull-roof, and bears a strong lateral process directed antero-ventrally, which was in life connected with the otic region of the endocranium (Fig. 2*a*, "*S.T.*"). Behind this process is a facet on the dorsal surface of the bone, which was probably the insertion of a ligamentous support of the opercular (Fig. 5*a*, "*f.op.*").

Only the front ends of the "parietals" are shown in the type specimen, but No. 7245*a* shows the full length of the left "parietal," which is unfortunately incomplete mesially. The antero-lateral contours of the bones in the two specimens agree so well that the probable median line of No. 7245*a* can be determined with fair certainty, and figure 5*a* shows an attempted restoration of this part of the skull-roof.

Both "parietals" and supratemporals are thick bones, and bear a characteristic ornament of very small, closely-crowded tubercles. A ventrally-directed ridge runs from the radiation-center of each "parietal" toward that of the corresponding supratemporal, and was in life firmly connected with the endocranium.

The dermal bones of the anterior part of the cranium are present only fragmentarily in the type; they are crushed and fractured, but it is clear that the "frontal" was short. These bones were apparently connected to the antotic processes of the basisphenoid by descending lamellae.

DERMAL BONES OF THE CHEEK.—The left cheek is very well shown in No. 7245*a* (Fig. 2*a*) but the type is much disturbed and has very little of this region preserved.

The postorbital is a bone of rather unusual shape; it is incomplete antero-dorsally. It does not touch the supratemporal. The lacrimo-jugal is an element of characteristic coelacanth shape, expanded both anteriorly and posteriorly. The squamosal is very large, with an unusually great dorsal extension. It fits anteriorly between the post-orbital and the lacrimo-jugal. The preopercular is triangular, and is widely separated from the lacrimo-jugal; it has a rather thick posterior margin, in which the latero-sensory canal runs. There is a small supra-squamosal element, now misplaced, but originally probably fitting against the supratemporal as in the figures of *Whiteia* sp. given by Nielsen (1936, Figs. 11 and 12).

So far as their external faces are preserved, the dermal bones of the cheek bear a tubercular ornament similar to that on the skull-roof.

THE PALATE.—Unfortunately neither specimen shows much of this important region. The referred specimen shows the left quadrate lying below the preopercular; there is a lateral, small, antero-ventrally directed articular facet, and a much larger mesial facet which has not been exposed (Fig. 2*a*, "*Qu.*").

A small portion of the right pterygoid was exposed in lateral view on the "reverse" of No. 7245*a;* it was of little morphological importance and badly preserved, and was removed during preparation of the mandible. It showed a small part of the lateral surface, with the beginning of the quadrate at its lower margin. From this a slightly damaged ridge curved forward and upward, as in many coelacanths, on the lateral surface of the bone; near the dorsal margin of the fragment was a small part of the metapterygoid, a thin lamella closely applied to the pterygoid and curled up against the ridge. After removal of the actual bone of the pterygoid an impression of the ornament and dentition of the mesial face was obtained. This showed a thick sprinkling of tubercles covering most of the bone, but leaving a smooth postero-dorsal area; near the margin between smooth and ornamented areas the tubercles become streaked but parallel to the margin.

The grooved lateral margin of the pterygoid is possibly to be seen in No. A.M.N.H. 7245 (Fig. 1*a*, "*Pter.*"); nearby is a long narrow element bearing anteriorly (though its orientation remains somewhat uncertain) a crowded series of small teeth, posteriorly a few larger, pointed teeth (Fig. 1*a*, "*Ec.Pt.*"). The same element is shown under the posterior part of the lacrimo-jugal in the other specimen (Fig. 2*a*, "*Ec.Pt.*"); it is very similar in its relationships to the ectopterygoid in *Macropoma* (Watson, 1921, Fig. 4) and in *Coelacanthus granulatus* Ag. (Moy-Thomas and Westoll, 1935, Fig. 3). In front of this bone in No. A.M.N.H. 7245*a* is another slender element with a close-set dentition of stout, blunt-pointed teeth; it is a dermo-palatine (Fig. 2*b*., "*D.Pal.*").

No. A.M.N.H. 7245 shows a tooth-bearing bone lying loose on the angulo-surangular; it is of quite uncertain provenance, and may belong to the mandible or the upper jaw (premaxillary?) or it may even be a vomer. It is badly damaged, but bears large conical teeth (Fig. 1*a*, "*Vo.?*").

THE MANDIBLE.—The large "angulo-surangular" bone which forms most of the outer aspect of the lower jaw is shown in both specimens. In No. 7245 the anterior portion of the left "angulo-surangular" is concealed: the posterior part was identified as the maxillary by Cope.

In No. 7245*a* the actual bone of the left "angulo-surangular" is largely removed, but the impression fully indicates the shape (Fig. 2*a*, "*Ang.*"). As in most coelacanths the bone has a high dorsal extension, subsiding into more slender anterior and posterior portions. The ventral margin is very thick, transversed longitudinally by the mandibular latero-sensory canal, and extends some way behind the articular. Anteriorly there is a slight dorsal flange on the bone for the reception of the dentary. The ornament of the bone consists of very small closely-crowded tubercles. Neither dentary nor splenial is preserved.

The right mandible in No. 7245*a* is partly disarticulated and is seen in dorsal and mesial aspect (Fig. 2*b*). The angulo-surangular has a strong rounded internal ridge lying below the emplacement of Meckel's cartilage. Only one ossification in the latter is visible—the articular, which is a strongly ossified element. The articulatory surface is in two parts, one directed dorso-mesially and somewhat backward (fac. 1, Fig. 2*b*), the other (smaller than, and external to, the first) is directed somewhat postero-dorsally (fac. 2, Fig. 2*b*). These correspond to the condyles on the quadrate. In front of these facets the dorsal surface of the articular is divided into two parts by a strong ridge, directed antero-mesially and sutured against a special process of the prearticular. Mesial to this ridge the articular is excavated into a pit, bounded mesially by the prearticular. Lateral to the ridge the bone forms a deep groove pitching ventrally and forming the anterior part of the bone; a thin lamina of the articular is applied to the angulo-surangular.

The prearticular is badly preserved, but is clearly a long bone, probably reaching the symphysis. It extends behind the corpus of the articular, and is sutured against the prominent ridge on that bone.

The left coronoid is shown more or less *in situ* in No. 7245*a*, and lying free in No. 7245. It is a surprisingly large element. The antero-dorsal margin is thickened, outwardly rolled, and sinuous. The ventral margin was almost certainly sutured against the prearticular just in front of the ridge to the articular, and during life the bone curved outward and upward so that the thickened margin lay above the "angulo-surangular."

Opercular Apparatus.—The left opercular is shown in No. 7245*a*, in place. The posterior margin is incomplete, but the nature of the impressions shows that little is missing. There is a broad thickened ridge running on the internal surface from the antero-dorsal corner to the most ventral prolongation of the bone, and becoming broader and less distinct ventrally. The left subopercular (cf. Nielsen, 1936, p. 31, Figs. 11, 12; Westoll, 1937, p. 366, Fig. 2) is shown below the quadrate: it is incomplete marginally, but can be restored provisionally. The left gular is preserved as an impression of the inner surface and is very imperfect. On the "reverse" side of No. 7245*a*, part of the right opercular was present, and was removed during preparation. A reversed drawing of this bone, for completing the outline of the antero-dorsal portion of the left opercular, is given in figure 5*b*.

A.M.N.H. 7245 shows only very fragmentary remains of one gular.

The opercular and subopercular have the same ornament as the bones of the skull-roof and cheek: the gulars are too badly damaged to show ornament.

VISCERAL ARCHES.—Neither specimen shows remains which can be referred with certainty to the hyoid arch.

No. 7245*a* has badly preserved remains of several of the branchial arches. The ceratobranchials are ossified only superficially, leaving an internal cavity in each bone. Processes extend ventrally from both lateral and mesial faces of the bone, forming a deep groove on the postero-ventral surface of each element.

No. 7245 shows a large mass of solid bone, divided along what is probably a fracture into nearly symmetrical parts. It may most feasibly be regarded as the homologue of the large basibranchial element described by Nielsen (1936, p. 33) and has the same proportionate size to the cranium (Fig. 1*b*, "*b.br.?*"). The resemblance in detail is not very close, however, and the orientation of the element is doubtful.

LATERO-SENSORY SYSTEM.—The sensory canal traversing the "parietal" and supratemporal is very narrow in comparison with other coelacanths; it is only 2–3 mm. side, and is dorso-ventrally compressed. The canal traverses the center of ossification of the supratemporal, and probably that of the "parietal."

Nothing is known of the supraorbital canal, and the infraorbital canal is seen only in the lacrimo-jugal. The jugal canal anastomosed with the infraorbital canal between the postorbital and the lacrimo-jugal: its course is well shown, partly by positive preparation, partly by the impression of the ridges on the visceral surfaces of the bones. It passes postero-dorsally, curves through or near the radiation center of the squamosal, and is continued as the preopercular canal down the posterior margin of the preopercular. The jugal canal is also narrow and shallow (Fig. 2*a*).

The mandibular canal is narrow and compressed, being only 4 mm. wide. It opens by means of narrow and rather well-separated tubules.

SQUAMATION.—The only remains of the body are a few badly preserved scales visible in No. 7245*a* behind the skull-roof and above the opercular. Their exposed surfaces bear an ornament like that of the dermal bones of the skull.

## COMPARISON WITH OTHER COELACANTHS

In spite of the very fragmentary nature of the material of *Spermatodus* used in this description, the unusual preservation of some of the remains allows certain anatomical deductions to be drawn. These will be discussed systematically.

1. ENDOCRANIUM.—The otic region of *Spermatodus* is almost com-

pletely unknown, but two ossifications are assigned tentatively to the auditory capsule. Similar bodies have not, so far as the writer is aware, been described elsewhere, but it is worthy of note that in other coelacanths in which this region has been described—e.g., *Wimania* (Stensiö, 1921, pp. 53 *et seq.*, Figs. 19, 20), *Macropoma* (Watson, 1921, p. 323, Figs. 1, 2), *Undina* (Aldinger, 1930, p. 25, Figs. 1, 3, 5, etc.)—the "proötic" has mesial and lateral lamellae, with a posteriorly-directed pocket-like space between. In this lay most of the membranous labyrinth. Watson (1921, p. 324, Fig. 2) described two pairs of small bones, apparently mutually related, and probably belonging to the otic region of *Macropoma:* these may be in some way representative of the larger ossifications in *Spermatodus.*

The sphenoid region is of greater interest. The pituitary fossa is here very completely shown, and there can be no doubt of the identification of the foramen for the pituitary vein. No other foramina in the basisphenoid can be seen. It was thus of interest to examine *Macropoma mantelli* Ag., in which Watson had described and figured several foramina in the lateral lamellae of the basisphenoid (Watson, 1921, Figs. 1, 2, p. 322). After an examination of the original material of Watson's description, it is clear that the foramen labelled "III" by Watson is for the pituitary vein; that the foramen labelled "IV" is a false appearance, as is the posterior unlabelled foramen in his figure 2; and that the foramen "*Op.Pr.*" is for the r. ophthalmicus profundus, if the conditions be compared with the figure of *Diplocercides* given by Stensiö (1932, Fig. 8, p. 30). The interpretation of Watson's figures by Stensiö must therefore be modified. No sign of the foramen for r. ophthalmicus profundus can be seen in *Spermatodus;* probably the nerve left the *cavum cerebrale* above the ossified region, just behind the antotic process.

The groove leading forward on the ventral floor of the pituitary fossa can only be for a hypophysial cord or duct, and its line prolonged anteriorly would come to the ventral surface of the parasphenoid very near the foramen at the center of radiation. The center of radiation of the parasphenoid in coelacanths occurs beneath the hinder part of the toothplate, and any small foramen might easily be missed in the matrix adhering to the granular dentition. The writer has examined a number of coelacanths from various formations to try to discover similar foramina.[1]

In specimens of *Coelacanthus* sp. from the Low Main Seam (Middle Coal-measures) of Newsham, Northumberland, the parasphenoid tooth-

[1] Stensiö has recently (1937, p. 10, Figs. 5, 8; Pl. XII, fig. 2) described the occurrence of a foramen for the hypophysial canal in the parasphenoid of several Devonian genera, *Diplocercides*, *Nesides*, and *Euporosteus*.

plate is large and extends very near the back of the bone, and a foramen is present in a rather posterior position. In this form the basisphenoid shows a short and steep groove leading straight downward from the pituitary fossa.

The Triassic form *Wimania sinuosa* Stensiö (1921, p. 51, Figs. 19, 20, 22, 23, etc.) has a groove leading rather steeply down from the pituitary fossa; though it is not described by Stensiö there seems to be a small foramen in the parasphenoid near the center of radiation (*op. cit.*, Pl. VII, Figs. 1, 2), which seems to be near the back of the tooth-plate, which is not well preserved. In *Axelia* (*op. cit.*, p. 89, Figs. 39–42) there is a groove, leading straight down from the fossa hypophyseos, which Stensiö identifies as being probably "in relation to the hypophysis" (*op. cit.*, p. 93). The center of radiation of the parasphenoid is not far in front of this, and is within the area of the very extensive tooth-plate. The teeth may prevent any foramen from being shown here.

In *Undina acutidens* Reis, as described with the aid of other Jurassic coelacanths, by Aldinger, the pituitary fossa leads antero-ventrally with rather slight pitch; no details of the structure of the parasphenoid are given, but the tooth-plate is forwardly situated (Aldinger, 1930, Figs. 6–8).

Finally, in *Macropoma mantelli*, of which the writer has examined good material, the groove for the hypophysis is narrow, sloping downward very gently; there seems to be a canal in the body of the parasphenoid leading toward the hinder part of the very anteriorly-placed tooth-plate, but no foramen is visible in the available material.

This short summary appears to show that a primitive condition, in which the hypophysial fossa was in direct relation with a foramen in the parasphenoid immediately ventrally to it, has been modified in many forms by anterior movement of the center of growth of the parasphenoid, *pari passu* with the palatal end of the hypophysial cord or duct. The significance of this must remain obscure until more is known of the palatal and cranial structures in different forms.

The relationships of the internal carotid artery now call for comment. In the primitive Devonian form *Diplocercides*, the only well-known coelacanth with a basipterygoid process, the foramen for the pituitary vein lies just above and in front of this process, while the foramen for the internal carotid (+ efferent pseudobranchial artery) lies farther forward and more ventrally. Clearly the artery must have run forward between the basisphenoid and the pterygoid and metapterygoid, ventral to the basipterygoid process. Of other genera of coelacanths, only an indeterminate specimen from the Westphalian Carboniferous (Aldinger, 1931, Fig. 15) has been described with a basipterygoid process: however, as noted below, a different interpretation is possible. Nevertheless it is easy to see that the lower part of the ventral ridge on the outer surface of the basisphenoid of *Macropoma mantelli* (Watson, 1921, p. 322, Fig. 1) is in the position of the basipterygoid process. Lying ventrally to this ridge is a "deep smooth groove, running along the side of the bone immediately above the upper edge of the parasphenoid" (*op. cit.*, p. 323). It is not unreasonable to suppose that this groove marks the track of the internal carotid on its way forward into the brain-case: it is even possible that the smooth notches at the lower end of the lamellae of the basisphenoid in this form mark the actual entrance of the artery into the side-wall of the brain-case. Aldinger, in *Undina* (1930, Figs. 4, 5, etc.: "fen"), and Stensiö, in *Wimania* (1921, p. 58, Fig. 19, "fen") and *Axelia* (*op. cit.*, p. 91, Fig. 39, etc.), have figured hypothetical fenestrations in the side-wall of the orbito-temporal region just in front of the basisphenoid, which they took to be the orbital opening of a myodome. Stensiö has more recently withdrawn this view, and his figure of *Wimania* reproduced in 1932 (Fig. 13) is altered in this region. It is noteworthy, however, that the lower part of the lateral lamella in *Wimania* is smoothly notched, and possibly the internal carotid entered the brain-case here. Compared with *Macropoma*, *Spermatodus* has a very much broader parasphenoid, which clasps round much more of the lower face of the basisphenoid, and it seems probable that the internal carotid arteries have been enclosed between the two bones in *Spermatodus*, lying within the deep grooves in the basisphenoid.

The structure of *Spermatodus* and some English Carboniferous coelacanth basisphenoids suggests a different interpretation of the basipterygoid process described by Aldinger in an undetermined Carboniferous specimen (1931, Fig. 15). A basisphenoid from the Scottish Coal-measures belonging to the Geological Survey of Scotland (No. J. S. 18534)[1] shows a pair of grooves on the ventral face resembling those in *Spermatodus*. The lateral boundary of the groove is shorter and stouter than that in the latter fish, however, and possibly this has been mistaken for a basipterygoid process by Aldinger. It corresponds essentially in position with the true basipterygoid process of *Diplocercides*, but lacks its functions.

The identification of the exit of the pituitary vein, and the entrance of the internal carotid into the cranium in *Spermatodus*, *Wimania*, and

[1] Collected by James Smith from the roof of the Ell Coal, Kilwinning.

*Macropoma*, discussed above, seems to dispose of any possibility of a myodome having been present in these forms, and probably in all coelacanths. (Cf. Watson, 1921, p. 335, Stensiö, 1932, p. 25, Holmgren and Stensiö, 1936, p. 349.)

2. Dermal Bones of the Skull-Roof.—The posterior part of the skull-roof in *Spermatodus* is rather unusually narrow in proportion to its length as compared with such forms as *Wimania, Axelia, Whiteia*, and *Macropoma*. Other genera, such as *Laugia, Coelacanthus* (*C. granulatus* Ag.), etc., are rather more like *Spermatodus* in this respect. The constituent bones show no unusual features; unfortunately the extrascapular series is missing. The small diameter of the "cranial section of the main lateral line" as it passes through the bones is remarkable in a coelacanth. Unfortunately the available material of *Spermatodus* does not show the exact conditions of the anastomosis between the supraorbital and infraorbital canals; Nielsen (1936, p. 29, etc.) has recently shown that the representative of the osteolepid dermosphenotic is either reduced or is to be sought in the anterior part of the bone called "parietal" above (= "parieto-intertemporal" of Stensiö and others). Moreover, from the occurrence of the apparent homologue of the anterior pit-line in the same bone Nielsen suggests that part of the frontal is also incorporated. He thus calls the whole elements "fronto-parieto-intertemporals" or "at least in some coelacanthids, perhaps even .... fronto-parieto-intertemporo-dermosphenotics." (*Op. cit.*, p. 30.) It is possible, on other grounds, to show that the element usually contains the equivalents of the rhipidistian dermosphenotic and intertemporal, but the evidence for the presence of frontal and parietal components is very slender, and other investigations by the writer tend to show that they may be completely absent. For the moment, however, it will be convenient to call the bone by the familiar name "parietal," the falsity of the homology being kept in mind. In this connection Watson's reconstruction of *Macropoma* (1921, see Fig. 5 and p. 330) deserves comment. Watson figures a state of affairs in the "parietal shield" which the writer is unable to confirm. The supratemporals can always be distinguished from the "parietals," though the sutures may be extremely interdigitated; the use of immersion fluids will demonstrate the separation. In no specimen is there a sutural separation of the two "parafrontals" described by Watson, they seem to be due merely to fractures. This is of importance, as Stensiö has regarded these elements as representing the intertemporal. In no known coelacanth is there a division of the "parietal" into the two components suggested by the compound name "parie-

to-intertemporal." This matter will be more fully discussed on another occasion.

The bone here called supratemporal is named "supratemporo-extrascapular" by Stensiö and his associates; *Spermatodus* offers no direct evidence in favor of the implied fusion and the element will be called by the simpler name. It may be mentioned that at least some coelacanths seem to have the lateral extrascapulars distinct.

The anterior part of the skull-roof is so fragmentary that it cannot be compared with other forms.

3. Dermal Bones of the Cheek.—*Spermatodus* presents somewhat unusual features in the cheek region and is in many respects rather reminiscent of the osteolepid condition. The squamosal, in all coelacanths hitherto described, is separated by a considerable distance from the "parietal" and "supratemporal," either by the intervention of postorbital and suprasquamosal elements, or by an unossified space (e.g., *Axelia, Laugia*). In *Spermatodus* the squamosal has a broad contact with the skull-roof, and the postorbital is proportionately reduced. The lacrimo-jugal is rather small, and the orbit seems to have been distinctly small for a coelacanth, and set rather anteriorly. But the most notable feature of the cheek is the extreme obliquity of the angle of the "suspensorium." The metapterygoid in coelacanths articulated with the antotic process, and from this point the posterior edge of the pterygoid complex swept down to the quadrate: this slope is indicated by the slope of the back of the postorbital, squamosal, and preopercular elements. In typical coelacanths, such as *Macropoma, Whiteia, Wimania, Axelia*, etc., this margin slopes steeply downward; in some, such as *Coelacanthus granulatus* and *Laugia*, the slope is somewhat less steep. *Spermatodus* shows a comparatively extreme obliquity of suspensorium.

This combination of a high cheek, anteriorly placed orbit and oblique suspensorium suggests that the masticatory musculature was more extensive and powerful than in most coelacanths. Unfortunately nothing of value is known of the palate, and the dentition is poorly preserved.

The latero-sensory canals of the cheek are notably narrow, and the preopercular canal pierces the posterior part of the preopercular. Reasons have been advanced elsewhere (Westoll, 1937, p. 366) for the belief that the quadrato-jugal is completely reduced in coelacanths, contrary to the views expressed by Stensiö (1921, p. 66, etc., p. 125; 1932, p. 36) and Nielsen (1936, p. 30).

The anastomosis of the jugal canal with the infraorbital canal between the lacrimo-jugal and the postorbital is a point of difference between coelacanths and osteolepids. The anastomosis of two different sections of the latero-sensory system, originating as separate ectodermal thickenings, need not always show the same details, however, and this difference between the groups may be of little or no importance.[1]

4. THE LOWER JAW.—This is chiefly interesting for the demonstration of the relationship between the articular and the dermal bones. The articular occurs as a separate ossified element in *Mawsonia* (Woodward, 1907, Pl. VII, fig. 1, Pl. VIII, figs. 1, 2), in certain Carboniferous *Coelacanthus* (Stensiö, 1921, p. 118, Fig. 55) and in *Coccoderma suevicum* Quenst. (Stensiö, 1921, p. 118, Fig. 56). But in *Macropoma*, Smith-Woodward (1909, p. 176), Stensiö (1921, p. 118), and Watson (1921, p. 331) have been unable to find sutures between the articular and the "angular" (= angulo-surangular). *Spermatodus* shows the articular to be completely free from the angulo-surangular, but to be attached to the prearticular by a strong sutural union. The double nature of the articulation with the quadrate is noteworthy.

5. THE OPERCULAR APPARATUS.—The shape and relationship of the opercular seem to be normal. The bone here called subopercular was identified in another form (*Whiteia*) as the preopercular, by Moy-Thomas (1935, pp. 218, 221, Fig. 1, etc.). Reasons for its identification as a subopercular have been given by Nielsen (1936, p. 30) and Westoll (1937, p. 366).

It is now possible briefly to discuss the relationship of *Spermatodus* to other coelacanths. Unfortunately a very large proportion of members of this group so far described is represented by fragmentary material, and it is impossible to compare them adequately with *Spermatodus*, of which only parts of the head are known.

All coelacanths of which the cheek has been described differ from *Spermatodus* in the comparatively limited dorsal extension of the squamosal. Many also differ in the comparatively slight extension of the cheek behind the orbit—e.g., *Whiteia* (Moy-Thomas, 1935, Fig. 1), *Macropoma* (Watson, 1921), *Laugia* (Stensiö, 1932, Fig. 19), *Wimania* (Stensiö, 1921, Fig. 25), *Axelia* (Stensiö, 1921, Fig. 44), *Undina* and *Libys* (personal examination). The genus *Coelacanthus* (Moy-Thomas,

[1] In the Devonian fish *Nesides* and *Diplocercides* Stensiö has recently (1937, Figs. 3,4) described the cheek-bones. In these early forms the preopercular is quite extensive, and in *Nesides* bears a groove for the vertical pit-line of the cheek. Stensiö believes this to be evidence in favor of the fusion of the preopercular with a quadrato-jugal component. The writer has found that pit-lines can often show changes of course without any change in the pattern of the dermal bones, and prefers to regard this as a case of "piracy" rather than of fusion.

1935, Figs. 9, 10; Moy-Thomas and Westoll, 1935) shows conditions more comparable with *Spermatodus*, but no other form so far described has quite such an elongated cheek as the Texan fish.

Probably to be correlated with this is the distinctly elongated and narrow form of the "parietal shield" in *Spermatodus*. It is possible to make a close correlation between the extension of the cheek and the length of the "parietal shield" in coelacanths. The forms with very short cheeks have short and broad parietal shields: those with longer cheeks (e.g., *Coelacanthus* and *Spermatodus*) have proportionately longer and narrower parietal shields. In this way the back of the cranium is in all cases more or less directly over the quadrates.

The reduction of the extent of ossification in the orbital region of the brain-case, shown in *Coelacanthus granulatus* and *Spermatodus*, is of interest. Such small granular ossifications have not been described elsewhere, but the reduction in this region seen in Mesozoic forms was clearly advanced even in Carboniferous and Permian times.

The tubercular ornament on the dermal bones of *Spermatodus* is much finer than that in other coelacanths.

It may be concluded, therefore, that *Spermatodus* represents a well-defined coelacanth genus, without very close resemblance to any form so far described. It seems on the whole to be most closely comparable with *Coelacanthus granulatus* Ag., from the Marl Slate of England and the Kupferschiefer of Germany.

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