proceedings

of the Koninklijke Nederlandse Akademie van Wetenschappen

Orthocormus teyleri nov. spec., the first pachycormid (Pisces, Actinopterygii) from the Kimmeridge lithographic limestone at Cerin (Ain), France; with remarks on the genus Orthocormus Weitzel

by Paul Lambers

Teylers Museum, Spaarne 16, 2011 CH Haarlem, the Netherlands Or: Paleontologische Werkkamer, Biologisch Centrum RUG, Kerklaan 30, 9751 NN Haren, the Netherlands Orthocormus teyleri nov. spec., the first pachycormid (Pisces, Actinopterygii) from the Kimmeridge lithographic limestone at Cerin (Ain), France; with remarks on the genus Orthocormus Weitzel

by Paul Lambers

Teylers Museum, Spaarne 16, 2011 CH Haarlem, the Netherlands Or: Paleontologische Werkkamer, Biologisch Centrum RUG, Kerklaan 30, 9751 NN Haren, the Netherlands

Communicated by Prof. C.W. Drooger at the meeting of September 26, 1988

SUMMARY

The first pachycormid from the lithographic limestone of Cerin (Ain), France is described. It is considered a new species of the genus *Orthocormus* wEITZEL and has been named *Orthocormus teyleri* nov. spec. *Orthocormus cornutus* wEITZEL, 1930 has been reexamined. An emended diagnosis of the genus *Orthocormus* wEITZEL is given.

In a cladogram of the relationships between pachycormids *Orthocormus* is regarded as the sistergroup of *Protosphyraena*.

INTRODUCTION

The Pachycormidae are a family of fossil fishes which is known from the Jurassic and Cretaceous of Europe (Woodward 1895; Wenz 1968; Mainwaring 1978), North-America (Gregory 1923) and Asia (Taverne 1977). Remains of undetermined pachycormids were reported from the Portlandian from Canjuers (dept. Var), France (Ginsburg & Menessier 1970) and from the Toarcian of Lombardy (Italy) (Tintori 1977). Recently, the existence of pachycormids was reported from newly discovered Upper Jurassic Plattenkalke in Argentina (Cione e.a. 1987). The following genera have been attributed to the family:

Pachycormus Saurostomus Prosauropsis Euthynotus Hypsocormus

from the Toarcian of England, France, Germany

from the Oxfordian of England and Tithonian of Germany

from the Oxfordian of Cuba and the Tithonian of Bavaria

from the Tithonian of Bavaria

Asthenocormus Orthocormus Neopachycormus Protosphyraena

Sauropsis

from the Cenomanian of Burma from the Upper Cretaceous of England and the USA.

Protosphyraena is sometimes assigned to a separate family, the Protosphyraenidae (Nicholson & Lydekker 1889; Berg 1958; Danil'chenko 1967; Gardiner 1967). Incompletely known genera assigned to the Pachycormidae are *Eugnathides* (Gregory 1923) and *Leedsichthys* (Woodward 1889a,b; 1895; Martill 1986). Mainwaring (1978), in a review of some European members of the family, doubts the existence of *Prosauropsis* as a distinct genus, regards *Asthenocormus* as *incertae sedis* as to genus and removes *Leedsichthys* from the family.

The pachycormids are characterized by a more or less elongated, toothed rostrum, scythe-like pectoral fins, reduction of the pelvic fins and a powerful, almost symmetrical caudal fin (Patterson 1973; Mainwaring 1978).

Originally, the pachycormids were considered as related to the amioids or caturids (Gregory 1923; Regan 1923; Arambourg & Bertin 1958), or treated as a separate group within the holosteans (Rayner 1941; Berg 1958; Danil'chenko 1967; Wenz 1968; Lehman 1968; McAllister 1968). Patterson (1973) showed the relationship between pachycormids and teleosts and considered these the most primitive teleostean group, being the sistergroup of all other teleosts, a view-point not generally accepted (Taverne 1977).

Mainwaring (1978) found some additional derived characters and showed that their position in Patterson's cladogram lies between the Pleuropholidae and *Ichthyokentema*, thus being the sistergroup of *Ichthyokentema* and succeeding teleosts.

The main subject of this paper is a specimen in the collection of Teylers Museum, Haarlem, the Netherlands, which had been assigned to *Caturus velifer* THIOLLIERE by T.C. Winkler in his catalogue of the paleontological cabinet of the museum (1878a). It is of special interest, as the specimen has been collected from the Kimmeridge lithographic limestone of Cerin, France. So far no members of the Pachycormidae have been recorded from this deposit, which contrasts with the slightly younger (Lower Tithonian) lithographic limestone of Bavaria, from which several species are known. De Saint-Seine (1949) explicitly mentions the absence of this group in his monograph of the Cerin fauna.

The specimen belongs to the genus Orthocormus WEITZEL 1930, of which only the type species O. cornutus was known, from the Tithonian of Bavaria. A new diagnosis of the genus is presented, based on the type specimen Orthocormus cornutus in the Senckenberg Museum, Frankfurt, additional material of O. cornutus in the Juramuseum, Eichstätt and the specimen in Teylers Museum. Some new features are reported concerning O. cornutus; the Teyler specimen is described as a new species, O. teyleri, nov. spec.

SYSTEMATIC PALEONTOLOGY

Infraclass: Neopterygii (sensu Patterson 1973) Division: Halecostomi (loc. cit.) Subdivision: Teleostei (loc. cit.) Family Pachycormidae woodward 1895 Genus Orthocormus WEITZEL, 1930

Diagnosis of genus

Trunk elongate, fusiform. Rostrodermethmoid produced anterior to symphysis of the lower jaw. Pronounced, anteriorly directed boss in the parietal region of the skull. Rostrodermethmoid with a pair of large, laterally compressed teeth, directed obliquely forward. Premaxilla with large teeth, maxilla bearing small teeth. Mandible with a row of large, medial, procumbent teeth and small lateral teeth. Teeth on anterior edge of the dentary procumbent. Rather large pelvic fin, originating nearer to the pectoral than to the anal fin. Large dorsal fin, originating somewhat behind the middle of the trunk, dorsal fin base completely in advance of the anal. Origin of anal fin situated behind the middle of the trunk, anal fin base extended. Caudal fin with long, slender lobes, containing more than 40 rays.

Type species O. cornutus WEITZEL, 1930.

Orthocormus cornutus WEITZEL, 1930

Diagnosis (emended)

Orthocormus of large size, reaching 106 cm standard length (SL). Premaxilla with only one large tooth in its hinder half. Dentary with large, conical teeth, almost vertical. A pair of large, procumbent anterior dentary teeth. Fulcra absent on all fins. Head length 21% of SL/ prepelvic 36% of SL/ preanal 64% of SL/ predorsal 57% of SL. Fin-ray counts: pectoral ± 22 ; pelvic ± 22 ; anal ± 60 ; caudal, both lobes ± 40 ; dorsal ± 40 .

Material. The holotype in Senckenberg-Museum, nr. P. 1863 and a specimen (part and counterpart) in the Juramuseum, Eichstätt, (without number, designated Eich.). In these specimens, the skull anterior to the preoperculum is missing.

Horizon and locality (of type specimen). Tithonian of Langenaltheim, Bavaria, West Germany.

DESCRIPTION

Weitzel (1930a,b) gave a short, but accurate description of the holotype. I will make only additional comments on his findings, based on new observations and new material from the Juramuseum.



General features. plate 1, figure A and B.

The skull (textfigure 1 and plate 2, figure A)

The rostrodermethmoid projects clearly beyond the symphysis of the lower jaw and bears one pair of paramedial teeth, directed obliquely forwards.

The premaxilla bears one large tooth in its posterior half. The premaxilla is bordered dorsally in its posterior half by the antorbital (praeorbitale of Weitzel), and in its anterior half by the nasal. Postero-dorsal to the nasal lies the dermosphenotic, which lines the dorsal margin of the orbit. Posterior to the orbit the dermopterotic is visible. The sutures between these bones and the frontal and parietal are not clear. Weitzel further mentions the presence of two large and thin suborbitals (postorbitalia). It must be pointed out that it is evident that these bones are present, but that there is no clear border between the two.

Although the most posterior border of the maxilla is broken away, there is still a supramaxilla visible, attached to the dorsal margin of the posterior part of the maxilla.

The dentary bears some large, conical teeth, which are situated almost vertically. The anterior border of the dentary possesses one, outwardly projecting tooth. Lateral teeth have not been observed, but this may be due to insufficient preparation. Ventral to the posterior part of the dentary and the angular, a part of ceratohyal I is visible, together with attached branchiostegal rays.

The hyomandibular is almost completely overlain by the suborbitals. Only the uppermost part is uncovered, a little posterior to the dermopterotic, at the insertion in the neurocranium.

Postcranial skeleton

Some additional remarks can be made on the postcranial skeleton, because the specimen in the Juramuseum possesses almost complete fins. For the calculations of the fin-base origin as percentages of SL, I used an average of the values of the holotype and of the Eichstätt specimen, in which the head was assumed to have been 20 cm long.

a/ pectoral fin (plate 2, figure C)

It is difficult to determine accurately, but the pectoral fin seems to have had about 22 rays. The first ray was short and fused at its end to the second ray. All rays have been grooved along their full length and dichotomize distally.

PLATE 1

Figure A: Orthocormus cornutus WEITZEL, holotype nr. P. 1863 in Senckenbergmuseum, Frankfurt.

Figure B: Orthocormus cornutus WEITZEL, specimen in Juramuseum.

Figure C: Orthocormus teyleri nov. sp., holotype nr. 14836 in Teylers Museum, Haarlem.



Figure A: skull of holotype of Orthocormus cornutus WEITZEL



Figure B: skull of holotype of Orthocormus teyleri nov. sp.



Figure C: pectoral fin of Eichstätt specimen of Orthocormus cornutus WEITZEL



Figure D: pectoral fin of holotype of Orthocormus teyleri nov. sp.

b/ pelvic fin (plate 3, figure A)

This fin is almost completely preserved in the Eichstätt specimen. Its origin is situated at $\pm 36\%$ SL, closer to the pectoral than to the anal. The first ray is much shorter than the second. All rays dichotomize, most of them already in their proximal half. Transverse segmentation is not observed. This could be due to the fact that the distal part of the fin is missing and transverse segmentation may have occurred in this part, as in *O. teyleri*, (see below).

c/ anal fin (plate 3, figure C)

In the holotype the anal is rather damaged, but in the Eichstätt specimen this fin is complete. Its origin is completely behind the base of the dorsal and at $\pm 64\%$ of SL. Caudal to the main part, of which about 22 rays have been preserved, an extension consisting of much smaller rays must have been present. About 40 axonosts can be seen in counterpart. Also, assuming a one-to-one ratio of axonosts and fin-rays (as is the case in Eich.), the anal may well have possessed about 60 rays. The Eichstätt specimen possesses about 63 rays, of which ± 38 in the extension towards the caudal. The first six rays are short, rays 7 to 9 are the longest. All rays beyind the 6th dichotomize, the first in its distal 1/3, the rays in the extension from their point of origin. The posterior border of the fin is made of very fine, delicate rays, resulting from repeated dichotomies. All rays are already transversely segmented in their proximal half.

d/ dorsal fin (plate 4, figure A)

The dorsal of the holotype is incomplete, lacking its posterior part. The dorsal of the Eichstätt specimen is complete, but the fin rays are deformed distally probably during life. Its origin is at $\pm 57\%$ of SL. The remaining part of P. 1863 has about 30 rays, behind which 7 axonosts are preserved. From comparison with Eichstätt it is deduced that the fin was composed of 40 to 45 rays. Eich. has about 40 rays. Starting from about the 10th, they all dichotomize distally, in the most posterior rays in their proximal half. Transverse segmentation is observed also, beginning in the first half of most rays.

e/ caudal fin (plate 4, figure C)

In all specimens the caudal fin is complete. P. 1863 has about 40 rays in its upper lobe and 38 in its lower lobe, Eich. 42 and 41 respectively. Between upper and lower lobes are 5 small, ventral rays. The first 13 to 15 rays on the leading edges of the lobes are small and undivided. All other rays dichotomize distally and are transversally segmented, from the proximal half.

The endoskeleton of the tail is not sufficiently preserved in either specimen for anything to be said about it. Anterior to the caudal lobe of the holotype remains of a bony structure can vaguely be seen, covered by the squamation. It will be discussed below, in *O. teyleri*, where is it more clearly preserved.

None of the fins exhibit fulcra.



Fig. 1. Skull of *Orthocormus cornutus* WEITZEL based on the holotype, nr. P 1863 in the Senckenbergmuseum, Frankfurt.



Fig. 2. Skull of *Orthocormus teyleri* nov. sp., based on the holotype, nr. 14836 in Teylers Museum, Haarlem.





Figure A: pelvic fin of holotype of Orthocormus cornutus WEITZEL



Figure B: pelvic fin of holotype of *Orthocormus teyleri* nov. sp. pp = pelvic plate (basipterygium)



Figure C: anal fin of Eichstätt specimen of Orthocormus cornutus WEITZEL



Figure D: anal fin of holotype of Orthocormus teyleri nov. sp.

Orthocormus teyleri, nov. spec. 1878a Caturus velifer THIOLLIERE; Winkler: 153. Derivatio nominis: The species is named after Teylers Museum. Holotype: Specimen in Teylers Museum, Haarlem, nr. 14836. Horizon and locality: Kimmeridgian (lithographic limestone) of Cerin, dept. Ain, France.

Diagnosis

Orthocormus of moderate size, reaching 54 cm. SL and with relatively robust fins. Premaxilla bearing 3 large teeth in its hinder half. Dentary with large, procumbent, conical teeth and small lateral teeth. Three pair of large anterior dentary teeth. Fulcra on dorsal, ventral and anal fins.

Headlength 25% of SL/ prepelvic 41% of SL/ preanal 67% of SL/ predorsal



Figure A: dorsal fin of Eichstätt specimen of Orthocormus cornutus WEITZEL

55% of SL. Fin-ray counts: pectoral \pm 35; pelvic \pm 28; anal \pm 50; caudal upper lobe \pm 50, lower lobe \pm 43; dorsal \pm 48.

Differential diagnosis

Orthocormus teyleri is closely related to Orthocormus cornutus WEITZEL, from which it differs by its dentition on premaxilla and dentary, the larger number of fin rays in the pectoral, ventral, dorsal and caudal fins, the smaller number of rays in the anal fin and the presence of fulcra on the pectoral, pelvic, anal and dorsal fin.

Material. The holotype only.

DESCRIPTION AND COMPARISON

General features (plate 1, figure C)

Orthocormus teyleri is a medium-sized, (54 cm SL) slender, fusiform fish with a clear fronto-parietal boss, large pectoral fin, broad dorsal fin and a caudal fin with long, slender lobes.



Figure B: dorsal fin of holotype of Orthocormus teyleri nov. sp.

The skull (textfigure 2, plate 2, figure B)

a/ the dermal bones of the ethmoid region and skull roof

In lateral view, the margin of the skull roof is almost straight and makes an angle of $\pm 25^{\circ}$ with the upper jaw. In the parietal region a remarkable cranial boss is visible, projecting anteriorly. The ossification of this boss is not so clear as in *O. cornutus*. Its surface is ornamented with very small, fine tubercles. It is not clear which bones form the cranial boss. Weitzel (1930b) interprets this structure, together with the pointed rostrodermethmoid (see below), as an efficient cutwater. The pointed rostrodermethmoid projects forward beyond the symphysis of the lower jaw. Its surface is granulated. It is provided with a pair of large, paramedial teeth, directed obliquely forward out of the mouth.

The skull roof is severely crushed. This makes the remaining dermal bones difficult to recognize. Nevertheless, caudal to the remains of the frontal and ventral to the cranial boss, the remains of a bone are visible which is probably a part of the dermopterotic.



Figure C: caudal fin of Eichstätt specimen of Orthocormus cornutus WEITZEL

b/ the dermal bones of the cheeck and upper jaw

These bones are only fragmentarily preserved. A severely crushed antorbital is situated dorsally to the hinder part of the premaxilla. Caudal to the orbit, remains of the very thin suborbitals can be seen. They overlie the hyomandibular and are bordered posteriorly by the preoperculum. The more dorsal fragments are sparsely granulated, the more ventral completely smooth. It therefore seems probable that the dorsal suborbital (SO 1) had an ornamented surface and the ventral one (SO 2) was smooth.

Caudal to the suborbitals two-thirds of the preoperculum is preserved. It is a rather narrow bone, broadest ventrally and thickening in its anterior edge. Along this thickening branching of the preopercular sensory canal can be seen. Posterior to the preoperculum lies approximately half of the operculum. It seems to have been a rather broad, large bone. Its surface has a sparse ornamentation.



Figure D: caudal fin of holotype of Orthocormus teyleri nov. sp.

aj = additional joint for upper lobe of caudal fin

The upper jaw consists of premaxilla and maxilla. The premaxilla bears six teeth. The three teeth in the posterior half of the bone are especially stout. This is in contrast to *O. cornutus*, which has one large tooth on the premaxilla. The maxilla is a long, slender bone. The hinder part is broken away, so there is no trace of a supramaxilla. It bears a row of conical teeth, which are smaller than the teeth on the maxilla.

c/ the mandible

The dentary is a rather robust bone, with a thick dorsal border that bears large, medial, procumbent, conical teeth. Very small lateral teeth are present. The most anterior part bears three large teeth that project outward the mouth. One of the teeth is preserved in counterpart. In *O. cornutus* there is one large tooth on the anterior border. The caudal part of the dentary is missing, so nothing can be said about the angular or supraangular. The ventral margin cannot be recognized accurately, since it has been crushed on the displaced dentary ramus of the opposite side. Still, a part of the mandibular canal is seen, beginning somewhat caudal to the anterior teeth and running postero-ventrally crossing the displaced ramus.

The anterior part of the displaced ramus bears one large tooth, while the remains of another large tooth are seen immediately dorsal to this one.

d/ palate and suspensorium

The following remains can be recognized: The ectopterygoid is visible between the maxilla and dentary, behind the teeth of the dentary. It bears some very small teeth. The hyomandibular is a long bone, partly overlain by the remains of the suborbitals and anteroventrally overlain by the quadrate. It is set at an angle of approximately 65° to the dentary. At one-third of its length from the insertion in the neurocranium a stout opercular process projects posteriorly. The quadrate is partly preserved, overlying the anteroventral margin of the hyomandibular.

e/ the visceral arch skeleton

Ventral to the posterior half of the dentary a piece of the ceratohyal I can be recognized. It is broadest caudally and has a smooth surface. Immediately behind ChI lies ceratohyal II, to which long, thin branchiostegal rays have been attached. Ventral to the preoperculum underterminable bones are visible, probably remains from the branchiostegal apparatus.

Postcranial skeleton

f/ vertebral column (plate 1, figure C)

The vertebral column is almost completely preserved and has been damaged in only a few places. The notochord was persistant throughout life and there are no ossified vertebral centra. The axial skeleton consists of neural and hemal elements with associated spines. I counted ± 126 vertebral elements, of which about 75 are in the abdominal region. Not all elements can be seen because the first are covered by the shoulder girdle and some are absent because of damage. By comparing the dorsal and ventral part of the vertebral column and combining these results with the number of remains of isolated neural and hemal spines an accurate approximation is possible.

The neural spines are fused with the vertebral arches throughout the length of the vertebral column. Although it is not very clear, they seem to be paired structures in the abdominal region and single in the caudal region, a halecostome feature (Patterson 1973). Up to approximately the first 20 rays of the dorsal fin the neural spines are sigmoid shaped. The paired elements of the hemal arches and spines seem to be separate up to about the 68th element. From the 68th to about the 98th element the hemal spines are fused and the hemal arches appear as deeply forked structures. A very similar situation is known in *Asthenocormus titanius* (Vetter 1881 and personal observation on a specimen in the private collection of Solnhofener Portland Zementwerk in Solnhofen).

g/ pectoral girdle and fin (plate 2, figure D)

Of the cleithrum only the uppermost part is visible, posterior to the fragment of the operculum. According to the thickness of this part the cleithrum must have been a rather robust bone. Posterior to this fragment a piece of bone can be interpreted as the dorsal postcleithrum.

The pectoral fin of the exposed side of the fish is only partly preserved, while the fin of the opposite side is almost complete. It is a large, scythe-like fin, which is typical for the Pachycormids. It possesses approximately 35 fin-rays. The first 2 rays fuse in the proximal 1/3 of the fin and they fuse at $\pm 1/2$ of its total length with the third ray. The length of these fused rays is 2/3 of the finlength. A similar case of fusion is reported by Woodward (1895) in *Hypsocormus tenuirostris*. In the distal 1/3 a row of fused fulcra lies along the forth ray. Rays 4 to 7 are the longest ones. All rays have been grooved along their full length. They dichotomise distally up to 4 times. Transverse segmentation is observed in the distal ends of the 5th to 11th ray. With its 35 fin-rays the pectoral of *O. teyleri* is more robust than that of *O. cornutus*, which is composed of about 22 rays.

h/ pelvic girdle and fin (plate 3, figure B)

Below the squamation the contours are visible of a large bony plate, the basipterygium. It seems to have the same form as the basipterygium in *O. cornutus* (plate 3, fig. A: pp.).

The fin itself is rather large, possessing ± 29 rays. Its origin is situated at 41% of SL, nearer to the pectoral than to the anal fin. The first ray runs from its origin along the second up to half the total length of the fin. Below this ray lies a row of fulcra. All rays dichotomize distally. Transverse segmentation is not very clear.

Pelvic fins are usually very small or absent in Pachycormids, *Sauropsis, Euthynotus*, and *Hypsocormus* being the only genera which possess them (Wenz, 1968, Mainwaring 1978). I observed a small pelvic fin in an undescribed, 1.60 m. giant member of the family from the Tithionian of Solnhofen (a specimen in the private collection of the Solnhofener Portland Zementwerk). *O. cornutus* as well as *O. teyleri* have a relatively large pelvic fin with 20-30 rays and more or less as big as the anal. *Orthocormus* is the only pachycormid with rather well developed pelvic fins.

i/ anal fin (plate 3, figure D)

The anal is only partly preserved. The fin base possessed an extension towards the caudal fin. Posterior to the main part of the fin, of which 33 rays are intact, an extension towards the caudal fin is present, consisting of much shorter rays. The remains of 17 rays can be seen. The origin is at 67% of SL and situated completely behind the base of the dorsal. Dorsal to the fin base 16 axonosts are visible. The first \pm 11 rays are small and undivided. Along the 12th ray runs a row of fulcra. The 13th ray is the longest, the succeeding rays decrease rapidly in length. Starting from the 13th ray all rays exhibit distal dichotomy. From the 11th ray onwards transverse segmentation is observed in the intact rays, beginning in the proximal 1/3 of their length. The anal of *O. cornutus* is a little larger, containing about 60 rays.

j/ dorsal fin (plate 4, figure B)

The dorsal fin possesses ± 49 fin rays. Its origin is at 55% of the SL, a little closer to the pelvic than in *O. cornutus*. The fin base lies completely in advance of the anal. Ventral to the fin base contours of axonosts can be seen below the squamation.

The first 12 rays are very small, the first 14 are undivided. The rays 15 to 17 are the longest, behind these they rapidly decrease in length. Fulcra are present along the leading edge of the fin and are arranged in a row along the distal 1/3 of the 15th ray.

All rays from the 14th to the end exhibit dichotomy, which starts in the first 1/5 of their length. The last 20 rays dichotomize often and end like the hairs of a paint brush. From the 15th ray onwards they are transversely segmented. Compared to *O. cornutus*, (40 rays) the dorsal is somewhat larger.

k/ caudal skeleton and fin (plate 4, figure D)

The caudal fin is deeply forked and almost symmetrical. The lobes are long and slender. The dorsal lobe consists of about 50 rays, of which the first 15 are very small and the first 24 are undivided. The remaining rays dichotomize distally up to 4 times, in the last 10 rays dichotomy starts in their proximal half. They are transversely segmented up to 10 times and more, beginning at approximately half their length. Between the dorsal and ventral lobes there are 6 intermediate fin-rays, each distally dichotomized into very delicate rays and transversely segmented.

The ventral lobe is somewhat smaller, with about 43 rays. As in the dorsal lobe the first 15 are small and the first 24 are undivided. They exhibit the same pattern of dichotomy and segmentation.

In both dorsal and ventral lobes, the rays in the middle are the longest.

The caudal fin of pachycormids has more fin rays than that of other teleosts (Patterson 1973). It is remarkable that the caudal fin of the members of the genus Orthocormus possesses even more rays than the other pachycormids. Hypsocormus insignis has ± 27 rays in both lobes (pers. obs.), Asthenocormus titanius ± 25 in the upper and ± 35 in the lower lobe (pers. obs.), Pachycormus macropterus 25 in the upper and 15 in the lower lobe (Wenz 1968), Euthynotus incognitus ± 20 in both lobes (counted from Wenz 1968), the undescribed pachycormid mentioned before has ± 23 rays in both lobes (pers. obs.) and Winkler's holotype of Pachycormus westermani (1878b) = Saurostomus esocinus (nr. 13230 in Teyler's collection) had certainly not more than ± 25 rays (pers. obs.). O. cornutus has about 40 rays in each lobe, and O. teyleri 50 and 43, their caudal fin possesses many more rays than the fins of their relatives.

Anterior to the base of the upper caudal lobe lies a ± 4.6 cm long bony structure. Its anterior half consists of a bundle of 5 slender, flattened rays that apparently lay in the flesh of the fish (pl. 4, fig. D: aj.). This bundle passes into a stout joint, from which again a bundle of about 5 flattened rays projects towards the caudal. The rays merge into the anterior rays of the caudal lobe. A similar structure is mentioned by Vetter (1881) in *Hypsocormus insignis* and I have seen impressions of it, though not so clear as in this case in *O. cornutus*, in several specimens of *Hypsocormus* and in the type of *Sauropsis longimanus* (specimen AS VII 1089 in the Bayerische Staatssammlung, München). It may have served as an additional structure to facilitate the movements of the powerful caudal fin. The endoskeleton of the tail of the pachycormids is characterized by a large triangular hypural plate (h2 + n of Patterson 1973), at the end of the vertebral column. In *O. teyleri* the hypural plate is for the greater part covered by the rays of the tail lobes, so the exact form cannot be determined.

Patterson (1973) interpreted certain structures in the caudal region as uroneurals that more or less resemble the uroneurals of teleosts. It is difficult to interpret the situation in this specimen, since the caudal skeleton is mostly covered by the fin rays, but, if the hemal arch in front of the hypural plate is assumed to be the first hypural, there are 3 uroneurals visible. They grade into unmodified neural arches anteriorly, as described by Patterson for *Pachycormus macropterus*. Epurals are not discernible.

1/ squamation

The whole body is covered by numerous extremely small (± 1.5 mm) rhombic scales, which lack ganoin. The scales are arranged in rows that are directed in an angle of 60° to the body axis.

RELATIONSHIPS OF ORTHOCORMUS TO OTHER EUROPEAN PACHYCORMIDS

Mainwaring (1978) listed the following 20 derived characters which she found in the genera: *Pachycormus* (Pa.); *Saurostomus* (St.); *Sauropsis* (Sp.); *Euthynotus* (Eu.); *Hypsocormus* (Hy.); *Protosphyraena* (Pr.).

- 1. Large compound rostro-dermethmoid meeting the frontals posteriorly, and separating the paired premaxillae and nasals. (all)
- No supraorbitals; dorsal margin of the orbit formed by the dermosphenotic. (all)
- 3. At least nine rectangular infraorbitals forming the posterior margin of the orbit, and meeting the two large suborbitals posteriorly. (all)
- 4. Extrascapulars absent; dermopterotic enlarged and containing the supratemporal commissural sensory canal. (all)
- 5. Pectoral fins scythelike; the dermal fin rays branching only at their extreme ends. (all)
- 6. Ural neural arches modified as uroneurals of a peculiar type (Pa., St., Sp., Eu., Hy.) Unknown (Pr.)
- 7. Head length equalling one fifth of the total body length, and exceeding the maximum depth of the body. (Eu.) Unknown (Pr.)
- 8. Pelvic fins absent. (Pa., St.). Unknown (Pr.)
- 9. Anal fin base not extended. (Pa., St.) Unknown (Pr.)
- 10. Dorsal fin base completely in advance of the anal fin. (Pa., St.) Unknown (Pr.)
- 11. Anal fin base in advance of the dorsal fin which starts opposite the middle part of the anal fin. (Eu.) Unknown (Pr.)
- 12. Mandible with a single row of teeth. (Pa.)
- 13. Fronto-parietal boss present. (Pa., St., Hy., Pr.)
- 14. Opercular bone trapezoidal in shape. (St.)
- 15. Post-supracleithrum present. (Pa., St.)
- 16. Rostro-dermethmoid with marginal teeth and a pair of paramedial teeth. (Hy., Pr.)
- 17. Anterior coronoid plate inflated. (Pr.)
- 18. Rostro-dermethmoid produced forward beyond the symphysis of the lower jaw. (Pr.)
- 19. Anterior teeth on dentary procumbent. (Pr.)
- 20. Distal ends of pectoral fin-rays fused to form a peculiar rigid zig-zag structure (Pr.)

Character 6 is unknown in *Protosphyraena*, but the presence of a large hypural plate (h2 + n) in this genus, which is known in all other genera, suggests the presence of this character in *Protosphyraena* as well (Mainwaring 1978).

Mainwaring established monophyly of pachycormids on the basis of the first 6 derived characters, which are present in all genera. Concearning *Orthocormus*, character 1, 2, 4, 5, 6, 10, 13, 16, 18 and 19 have been observed.

Character 3 is unknown. I assume that this character must have been present in *Orthocormus* as well, but it cannot be observed because of damage.

Characters 14, 15 and 17 are unknown. According to the remains of the operculum that have been observed, it is unlikely that character 14 was present.

Examining the relationships within the pachycormids, Mainwaring presents the following list of distribution of derived characters:

genus	number of	number of	unknown	
form of the property of	derived characters 12	unique characters	characters	
				Pachycormus
Saurostomus		12	1	0
Sauropsis	6	0	0	
Euthynotus	8	2	0	
Hypsocormus	8	0	0	
Protosphyraena	12	4	5	

The unique characters of *Euthynotus* are nrs. 7 and 11, of *Saurostomus* nr. 14, of *Pachycormus* nr. 12, and of *Protosphyraena* nrs. 17 to 20. From this study it appears that *Orthocormus* also possesses character 18 and 19, so that *Protosphyraena* only has characters 17 and 20 as autapomorphies.

According to this result, *Orthocormus* can be placed in Mainwaring's cladogram of relationships within the Pachycormidae in the following way:



It is remarkable that character 10 (dorsal fin base completely in advance of the anal) is present in *Saurostomus* and *Pachycormus* as well as in *Orthocormus*. This feature may have evolved twice in the pachycormids. It is unknown in *Protosphyraena*, but assuming that genus possessed this character, *Orthocormus* would be placed between *Hypsocormus* and *Protosphyraena*.

ACKNOWLEDGEMENTS

I thank Mr. E. Ebbinge and Dr. J. de Vos of Teylers Museum for giving me the opportunity to study the specimen in their collection. I thank Dr. G.

Plodowski (Senckenbergmuseum, Frankfurt), Dr. N. Rückert and Dr. P. Wellnhofer (Bayer. Staatss. München); Dr. G. Viohl (Juramuseum, Eichstätt); Mr. Bergér (Museum Bergér, Eichstätt); Mr. Güllich, the lord mayor of Solnhofen (Bürgermeister Müllermuseum, Solnhofen); and Dr. Pücker of Solnhofener Portland Zementwerk for allowing me to study specimens in their care.

Furthermore I wish to thank Mr. Gert van Maanen for his help during my stay in Germany; Mr. Joop van Veen (Teylers Museum) for preparing the Teyler specimen, Mr. Ronald Schouten and Mr. Frank Diemel for making the photos and Miss Candida Baskcomb for correcting the English. I am grateful to Prof. Dr. P. Dullemeijer (University of Leiden) for his valuable help and advice. Dr. J. de Vos, Prof. Dr. G.J. Boekschoten (University of Groningen) and Dr. Colin Patterson (Brit. Mus. Nat. Hist.) kindly commented upon the manuscript.

Abbreviations used in figures

AO	=	antorbital
BA	=	remains of branchiostegal apparatus
CB	=	cranial boss
CH 1	=	ceratohyal 1
CH 2		ceratohyal 2
CL	=	cleithrum
DEN	=	dentary
DEN 1	=	dentary (in O. teyleri)
DEN 2	=	dentary ramus from the opposite side (in O. teyleri)
DPC	=	dermal postcleithrum
DPT	=	dermopterotic
DSP	=	dermosphenotic
EPT	=	ectopterygoid
HY	=	hyomandibular
mc	=	mandibular canal
MX	=	maxilla
Ν	-	nasal
OP	=	region occupied by opercular bones
PMX	=	premaxilla
POP	=	preoperculum
PS	Ŧ	parasphenoid
pc	H	preopercular sensory canal
QU 🔤	=	quadrate
ROD	Ŧ	rostrodermethmoid
RBR	=	branchiostegal rays
SC	=	sclerotic ring
SO	=	region occupied by suborbital bones SO 1 and SO 2
SO 1	=	suborbital 1 (in O. teyleri)
SO 2	=	suborbital 2 (in O. teyleri)

REFERENCES

- Arambourg, C. & L. Bertin, 1958 Super-Ordres des Holostéens et des Halécostomes. In: P.P. Grassé (Ed.), Traité de Zoologie 13, 3, 2173-2203. Masson, Paris.
- Berg, L.S., 1958 System der rezenten und fossilen Fischartigen und Fische. VEB Deutscher Verlag der Wissenschaften Berlin. 310 p.
- Cione, A., Z. Gasparini, H. Leanza & A. Zeiss, 1987 Marine oberjurassische Plattenkalke in Argentinien (Ein erster Forschungsbericht). Archaeopteryx 5, 13-22.
- Danil'chenko, P., 1967 Superorder Holostei. In: D.V. Obruchev (Ed.), Fundamentals of Paleontology 11, 586-599, Transl. in English, Israel Program for Scientific Translations, Jerusalem.
- Gardiner, B.G., 1967 Subclass Chondrostei and Holostei. In: W.B. Harland et al. (Eds.), The Fossil Record, 644-654. Geol. Soc. London.
- Ginsburg, L. & G. Menessier, 1970 Découverte d'un important gisement de Vertébrés dans le Jurassique supérieur du Petit Plan de Canjuers (Var). C.R. Acad. Sc. Paris 271, 570-571.
- Gregory, W.K., 1923 A Jurassic fish fauna from Western Cuba, with an arrangement of the families of Holostean Ganoid fishes. Bull. Amer. Mus. Nat. Hist. 48, 223-242.
- Lehman, J.P., 1966 Actinopterygii. In: J. Piveteau (Ed.), Traité de Paleontologie 4, 3, 1-242. Masson, Paris.

Mainwaring, A.J., 1978 - Anatomical and systematic revision of the Pachycormidae, a family of Mesozoic fossil fishes. Unpublished Ph.D. Thesis, Westfield College, London. 127 p.

Martill, D., 1986 - The world's largest fish. Geology Today 2, 2, 61-63.

McAllister, D.E., 1968 - Evolution of branchiostegals and classification of teleostome fishes. Bull. natn. Mus. Can. 221, xiv + 239 p.

Nicholson, H.A. & R. Lydekker, 1889 - A manual of palaeontology. 2nd. ed., 1624 p. Edinburgh & London.

- Patterson, C., 1973 Interrelationships of Holosteans. In: P.H. Greenwood et al. (Eds.), Interrelationships of fishes, 233-305. Academic Press, London.
- Rayner, D.H., 1941 The structure and the evolution of the holostean fishes. Biol. Rev. 16, 218-237.
- Regan, C.T., 1923 The skeleton of *Lepidosteus* with remarks on the origin and evolution of the lower Neopterygian fishes. Proc. Zool. Soc. London, 445-461, 1923.

Saint-Seine, P. de, 1949 - Les poissons des calcaires lithographiques de Cerin (Ain). Nouv. Arch. Mus. Hist. Nat. 2, 1-357, Lyon.

Taverne, L., 1977 - On the Actinopterygian fishes from the Cenomanian of the Kyu River (Burma, Pakokku District). Geol. Jb. 23, B, 47-59.

 Tintori, A., 1977 - Toarcian fishes from the lombardian basin. Boll. Soc. Paleont. Ital. 16, 143-152.
Vetter, B., 1881 - Die Fische aus den lithographischen Schiefern Bayerns im Dresdener Museum. Mitt. k. min. geol. Mus. Dresden 4, 1-118.

Weitzel, K., 1930a – Riesenfische aus den Solnhofener Schiefern von Langenaltheim. Nat. und Mus. 60, 1, 23–31.

 - 1930b - Drei Riesenfische aus den Solnhofener Schiefern von Langenaltheim. Abh. Senckenb. Naturforsch. Ges. 42, 2, 85-113.

Wenz, S., 1968 - Complements à l'étude des poissons Actinopterigièns du Jurassique Français. Cah. Paleont., 1-276, CNRS Paris.

Winkler, T.C., 1878a – Catalogue systématique de la collection paléontologique du musée Teyler Haarlem: Héritiers Loosjes.

- 1878b - Description d'une espèce nouvelle de Pachycormus. Arch. Mus. Teyler 5, 1-9.

Woodward, A.S., 1889a – Preliminary notes on some new and little known British Jurassic fishes. Geol. Mag. 6, dec. 3, 448-455.

- 1889b - Notes on some new and little known British Jurassic fishes. Ann. Mag. nat. Hist. ser. 6, 4, 405-407.

- 1895 - Catalogue of the fossil fishes in the British Museum (Nat. Hist), 3, xlii + 544, Brit. Mus. (Nat. Hist.) London.