Biol. Jb. Dodonaea, 55/1, 1987, 136-145 (31/12/1987).

ON THE CRANIAL AND CAUDAL OSTEOLOGY OF THE CRETACEOUS MARINE TELEOST *PACHYRHIZODUS* (PACHYRHIZODONTIDAE, CROSSOGNATHIFORMES)

by

Louis TAVERNE

SUMMARY. – The author describes some cranial features and the caudal skeleton of the marine Cretaceous teleost *Pachyrhizodus.*

SAMENVATTING. – De auteur beschrijft enkele delen van de schedel en het staartskelet van *Pachyrhizodus*, een mariene beenvis uit het Krijt.

RÉSUMÉ. – L'auteur décrit quelques éléments crâniens et le squelette caudal du téléostéen crétacique marin *Pachyrhizodus.*

INTRODUCTION

Numerous fossil fishes have been collected from the marine Cenomano-Turonian deposits of Cinto Euganeo, North Italy (SORBINI, 1976). They now belong to the collection of the Museo Civico di Storia Naturale of Verona where I examined them.

SORBINI (1976) mentions three species of the genus *Pachyrhizodus* DIXON, 1850 in that material, *Pachyrhizodus magnus* (WOODWARD, 1901), *Pachyrhizodus subulidens* (OWEN, 1840), and *Pachyrhizodus intermedius* n. sp., and also a few caudal fragments belonging to one of these three species but not specifically referable.

The Pachyrhizodontidae were primitive small or big carnivorous teleosts, with a fusiform body, and an elongated head. They lived from the Lower Aptian to the Middle Eocene, in the Euro-African Tethys, the Palaeoatlantic Ocean, the North Transamerican Sea, and the Australian Sea (TAVERNE,

1980, in press a and b). The Pachyrhizodontidae and the South American marine Aptian family Notelopidae form the suborder Pachyrhizodontoidei (FOREY, 1977). These and the Crossognathoidei, another Cretaceous marine teleost suborder, represent the order Crossognathiformes (TAVERNE, in press b).

The skull of *Pachyrhizodus* is rather well known (WOODWARD, 1902-1912 ; BARTHOLOMAI, 1969 ; FOREY, 1977 ; etc.) but not the tail structure. The caudal skeleton is correctly figured in the North American species *Pachyrhizodus caninus* COPE, 1872 only (NELSON, 1973, p. 23, fig. 8A ; FOREY, 1977, p. 187, fig. 36). Other illustrations exist in the scientific literature but are unprecise, incomplete or erroneous.

The fragments of *Pachyrhizodus subulidens* (IG 37491 to IG 37494) and the tails (IG 37530 to IG 37536, IG 37545, and IG 37546) of Cinto Euganeo allow to complete notably our knowledge of the osteology of *Pachyrhizodus*.

The graphical illustrations hereafter are based on camera lucida drawings.

ABBREVIATIONS USED IN THE FIGURES

AN : angular
ART : articular
BO : basioccipital
CM : coronomeckelian
DN : dentary
EC : caudal scutes
EP 1, 2 : epurals
HEM : haemal arch
HEMEP : haemal spine
HETH : hypoethmoid (ventral part of the mesethmoid)
HY 1 + 2 : ventral hypural plate (first and second hypurals)
HY 3 + 4 + 5 : dorsal hypural plate (third, fourth and fifth hypurals)
LEP : caudal rays
MX : maxillary
NA : nasal
NEUR : neural arch
NEUREP : neural spine
NP PU II and III : neural spines of the second and the third preural centra
PHY : parhypural
PMX : premaxilla
PS : parasphenoid

PU I to V : first to fifth preural centra
QU : quadrate
RART : retroarticular
RO : rostral (dermethmoid)
SETH : supraethmoid (dorsal part of the mesethmoid)
SMX : supramaxilla
U I and II : first and second ural centra
UR 1 to 3 : uroneurals
VO : vomer
a. f. : articular facet of the angulo-articular for the quadrate
a. hy. : hypurapophysis of the parhypural
a. p. p. : articular process of the maxilla for the palatine
a. w. : ascending wing of the parasphenoid
c. p. : coronoid process of the angular
f. i. ca. : foramen for the internal carotid in the parasphenoid
i. t. pmx. : inner tooth of the premaxilla
m. c. f. : posterior opening of the mandibular sensory canal on the angular
part. p. : postarticular process of the angular
p. d. pmx. : dorsal process of the premaxilla
pmx. p. : toothless anterior part of the maxilla, overlapped by the premaxilla
p. o. my. : posterior opening of the myodome.

Description

The specimen IG 37491 is a head of *Pachyrhizodus subulidens*. The cranial vault, the bones of the cheek, and the opercular region are severely crushed. Only the jaws, the ethmoid region, and the parasphenoid are well preserved.

The rostral (dermethmoid) is small, moderately broad, and a little wider than long. The posterior margin is divided into two short and wide processes by a little fontanelle. There is no trace of an ethmoid sensory commissure. The mesethmoid appears to have ossified from two centers, a dorsal supraethmoid, and a ventral hypoethmoid. The rostral is fused with the underlying supraethmoid. The anterior face of the supraethmoid bears a small medio-sagittal crest, and a lateral depression on either side for articulation with the dorsal process of the premaxilla. Dorsally the hypoethmoid is sutured with the supraethmoid, and is ventrally fused with the anterior end of the vomer. There is also a small medio-sagittal crest on the anterior face of the hypoethmoid, continuing that on the supraethmoid.

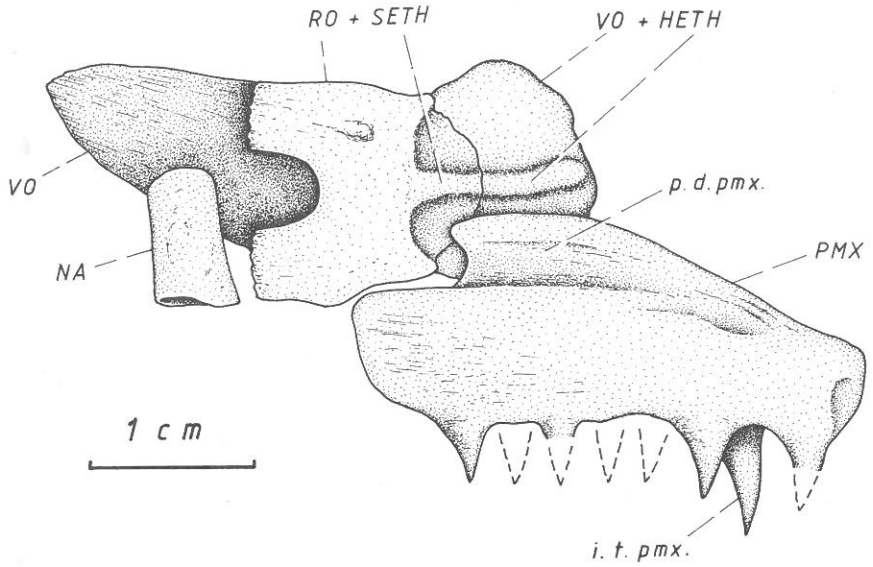

FIG. 1. – *Pachyrhizodus subulidens* (OWEN, 1840). Ethmoid region in right latero-dorsal view, based on the specimen IG 37491.

The premaxilla is elongated, more than twice as long as deep, with a wide, short, and posteriorly bended dorsal process abutting onto the supraethmoid. The maxilla is three times as long as the premaxilla. The facet for articulation with the autopalatine is wide but low. The premaxilla overlaps the large and long toothless anterior part of the maxilla (see also FOREY, 1977, p. 174, fig. 32). Such an important overlapping must considerably limit independent movement between the two bones, and strengthen the upper jaw. There is a single splint-like supramaxilla. The marginal teeth of the upper jaw are sharp, slightly recurved, of moderate size (3-5 mm long in specimen IG 37491), and a little larger on the premaxilla than on the maxilla. The inner tooth on the anterior end of the premaxilla is considerably larger than the other upper jaw teeth.

The lower jaw is slightly longer than the upper one, and 4.4 to 5.1 times as long as deep at its maximum depth. It is composed of the dentary, the angulo-articular, the retroarticular, and the coronomeckelian. The oral margin of the dentary is almost horizontal, and bears a single row of large (5-7 mm long in specimen IG 37491), sharp, distally recurved, and ventrally thickened teeth. The poorly-developed coronoid process is located in the posterior end of the dorsal margin of the angular. A partial fusion of the

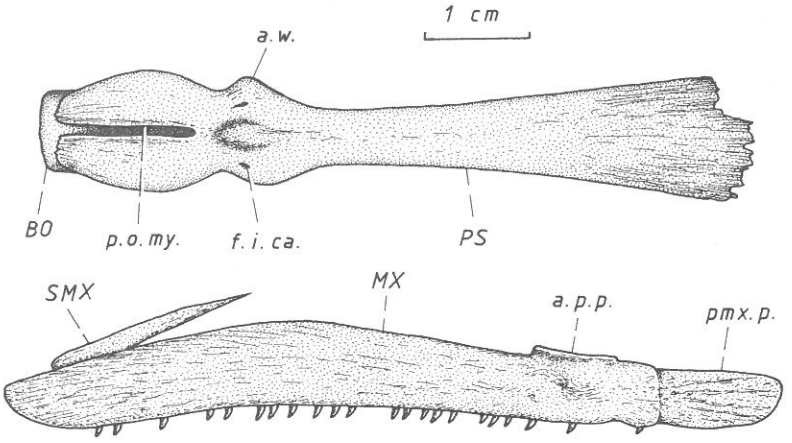

FIG. 2. – *Pachyrhizodus subulidens* (OWEN, 1840). Parasphenoid in ventral view (over), and right maxilla in external view (under), based on the specimen IG 37491.

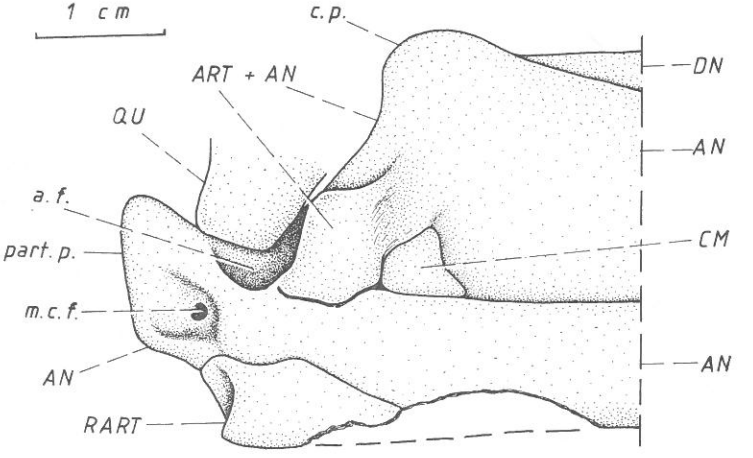

FIG. 3. – *Pachyrhizodus subulidens* (OWEN, 1840). Posterior part of the left lower jaw in medial view, based on the specimen IG 37491.

angular and articular occurs in specimen IG 37491, and a total fusion in specimen IG 37494, which, however, is smaller than the former. In IG 37491, the articular is fused with the angular dorsally, and at the level of the articular facet for the quadrate. But there is still a well marked suture-line between the two bones ventrally. The angulo-articular forms and supports the entire joint-surface with the quadrate. The large, long, and unfused retroarticular is totally excluded from the articular facet for the quadrate. The coronomeckelian is a small independent bone located just before the articular. The postarticular process of the angular is particularly well developed and shields from lateral view the joint-surface with the quadrate. The posterior opening for the mandibular sensory canal is on the medial face of the angular, in a depression of the long postarticular process.

The parasphenoid is long, narrow beneath the orbit, slightly enlarged anteriorly, and toothless. The ascending wings are poorly developed, with the foramen for the internal carotid beneath them. The posterior myodome opens distally in a long and very narrow mid-ventral slit in the posterior part of the parasphenoid. There is no basipterygoid process.

There are short tubular nasals in the ethmoid region.

The caudal skeleton involves five pleural and two ural vertebrae. The first preural centrum is slightly smaller than the anterior vertebrae. The first ural centrum is considerably reduced, and the second one is only a small bony nodule. The last neural and haemal arches are very thin, and become fused with their centra. The last neural spines are narrow bony rods, strongly bent towards the vertebral column. The third pleural centrum bears a half-length neural spine, and the second preural centrum only a rudimentary one, visible in specimen IG 37545 under immersion in water. We know that *Pachyrhizodus* also shows a neural arch on the first preural centrum (NELSON, 1973, p. 23, fig. 8A), but such a structure is hidden by the first uroneural in all the specimens of Cinto Euganeo. The narrow haemal spines of the fourth and the fifth preural centra are bent towards the vertebral axis, like the neural spines. The haemal spines of the second and the third preural centra and the parhypural are robust. The parhypural, which bears a small hypurapophysis, is fused with the first preural centrum, and is characteristically angled. The first and second hypurals form together a broad hypural plate which is fused to the reduced first ural centrum. There is sometimes an hypural foramen in the ventral hypural plate which marks the proximal division between the first and the second hypurals. The dorsal hypurals are also fused together in a dorsal hypural plate, and there is a more (IG 37545, IG 37546) or less (IG 37532) important degree of fusion between the ventral and dorsal hypural plates. There are three uroneurals. The very large

first uroneural is ending anteriorly on the fifth preural centrum, and is expanded ventrally at the level of the first and chiefly the second preural vertebrae, covering the dorsal part of their lateral faces. There is a well marked oblique ridge on the external surface of the first uroneural. The second uroneural is long, and rather wide. It extends forward to the first preural centrum, and overlaps the posterior portion of the first uroneural, and the lateral face of the first preural centrum. The third uroneural is smaller though well developed, and is located behind the reduced second ural centrum. It covers a small portion of the second uroneural. Two epurals are visible in the specimen IG 37545 under immersion in water. There are well developed dorsal and ventral caudal scutes.

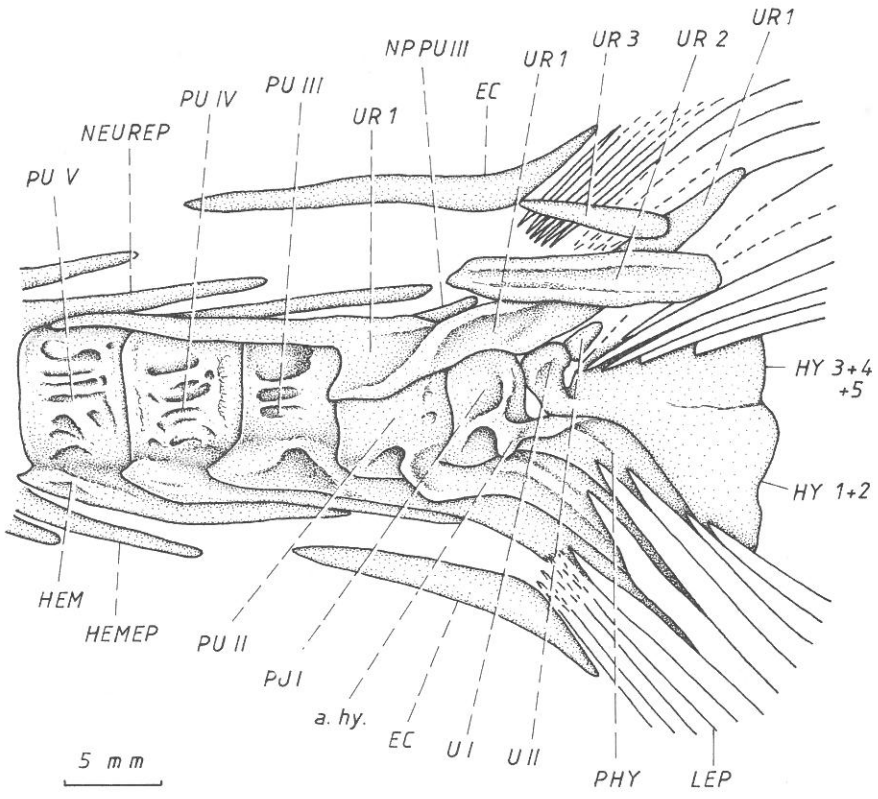

FIG. 4. – *Pachyrhizodus* sp. Caudal skeleton, based on the specimen IG 37546. The dorsal caudal scute is added from the specimen IG 37530. The specimen IG 37546 is labelled IG 37545 in SORBINI (1976, pl. XVII), while the specimen IG 37545 is labelled IG 37546 (*ibid.*, pl. XVIII).

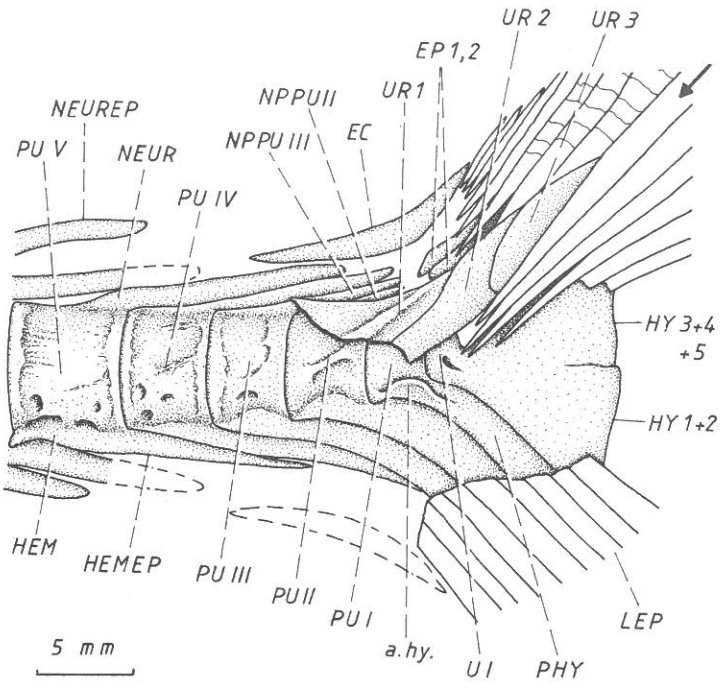

FIG. 5. – *Pachyrh.zodus* sp. Caudal skeleton, based on the specimen IG 37545.

The deep and forked caudal fin exhibits a high degree of hypurostegy, and contains ten principal rays in the upper lobe and probably nine in the lower one. The outer principal rays of each lobe are segmented and moderately branched, except the external unbranched one. The segments are long, and they show denticulate joint-margins. Some of the procurrent rays are also segmented. The inner principal rays are profusely branched, with very short basal undenticulate segments, like those in *Elopopsis microdon* HECKEL, 1856, another Pachyrhizodontid fish (TAVERNE, 1976, p. 488, fig. 1).

DISCUSSION

The fossil fish material of Cinto Euganeo thus provides informations on some unknown osteological features of *Pachyrhizodus*, and confirms other doubtful characters :

1. In some *Pachyrhizodus*, the mesethmoid shows a primitive teleost pattern of ossification, from a dorsal supraethmoid and a ventral hypoeth-

moid (PATTERSON, 1975, pp. 496-503). Other species, like *Pachyrhizodus megalops* (WOODWARD, 1901), lack an ossified mesethmoid (FOREY, 1977, p. 164).

2. Small tubular nasals exist at least in some species.

3. The myodome may open posteriorly in a mid-ventral slit of the parasphenoid or in a hole between the parasphenoid and the basioccipital (FOREY, 1977, p. 167, fig. 27).

4. The articular is not always completely fused with the angular.

5. The coronomeckelian is present.

6. The posterior opening for the mandibular sensory canal is on the medial face of the angular.

7. There is a small independent second ural centrum.

8. The dorsal hypurals may totally fuse in a dorsal hypural plate, more or less attached to the ventral hypural plate. In the American species *Pachyrhizodus caninus*, the dorsal hypurals are free or incompletely fused (NELSON, 1973, p. 23, fig. 8A ; FOREY, 1977, p. 187, fig. 36).

9. Some species still exhibit three uroneurals, in place of only two (FOREY, 1977, p. 187, fig. 36).

10. Some species still possess two epurals, in place of only one (FOREY, 1977, p. 187, fig. 36).

11. There are dorsal and ventral caudal scutes.

FOREY (1977, pp. 192-194) concludes that *Pachyrhizodus* and the Pachyrhizodontid *Rhacolepis* AGASSIZ, 1841 are close relatives, but finds "it impossible to decide which of the two genera is the apomorph". I think that *Pachyrhizodus* is the plesiomorphic sister group of *Rhacolepis*. Indeed, some species of *Pachyrhizodus* still possess a primitive mesethmoid, with well ossified supraethmoid and hypoethmoid, while *Rhacolepis* has an evolved one, small and cartilaginous (FOREY, 1977, p. 150). Some species of *Pachyrhizodus* still exhibit three uroneurals, whereas there are only two in *Rhacolepis* (FOREY, 1977, p. 161, fig. 24).

The skeleton of *Elopopsis* HECKEL, 1856 and *Greenwoodella* TAVERNE and ROSS, 1973, two other Pachyrhizodontid genera, is not sufficiently well known to allow a valid comparison with *Pachyrhizodus*.

ACKNOWLEDGEMENTS

I wish to thank Dr. Lorenzo SORBINI, Director of the Museo Civico di Storia Naturale of Verona, for his kind hospitality.

References

BARTHOLOMAI, A. 1969. The Lower Cretaceous Elopoid fish *Pachyrhizodus marathonensis* (Etheridge Jnr.). In K. S. W. ACAMPBELL edit., "*Stratigraphy and Palaeontology*", pp. 249-263, 4 fig., 2 pl.

FOREY, P. L. 1977. The osteology of *Notelops* Woodward, *Rhacolepis* Agassiz and *Pachyrhizodus* Dixon (Pisces : Teleostei). *Bull. Brit. Mus. (Nat. Hist.), Geol.*, **28** (2) : 123-204, 39 fig.

NELSON, G. J. 1973. Notes on the Structure and Relationships of Certain Cretaceous and Eocene Teleostean Fishes. *Amer. Mus. Novit.*, Nr **2524**, 31 p., 9 fig.

PATTERSON, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philos. Trans. Roy. Soc. London*, B. Biol. Sci., **269**, Nr 899 : 275-579, 108 t. fig., 13 pl.

SORBINI, L. 1976. L'ittiofauna cretacea di Cinto Euganeo (Padova-Nord Italia). *Boll. Mus. Civ. Stor. Nat. Verona*, **III** : 479-567, 23 fig., 31 pl.

TAVERNE, L. 1976. À propos d'*Elopopsis microdon* Heckel, J. J., 1856, du Crétacé moyen de l'Afrique et d'Europe et des affinités systématiques de la famille fossile des *Pachyrhizodontidae* au sein des Téléostéens primitifs. *Rev. Zool. Afr.*, **90** (N° 2) : 487-498, 6 fig.

TAVERNE, L. 1980. Ostéologie et position systématique du genre *Platinx* (Pisces, Teleostei), de l'éocène du Monte Bolca (Italie). *Acad. Roy. Belg., Bull. Cl. Sci.*, **LXVI**, F. 11 : 873-889, 7 fig., 1 pl.

TAVERNE, L. in press a. *Greenwoodella tockensis* Taverne and Ross, 1973 from the marine Lower Aptian (Töck) of Heligoland (West Germany), the oldest known Pachyrhizodontid fish (Teleostei, Crossognathiformes). *Geol. Jahrb.*

TAVERNE, L. in press b. Ostéologie de *Crossognathus* Pictet, 1858 du Crétacé inférieur de l'Europe et affinités systématiques de la famille des Crossognathidae. Position, paléozoogéographie et biologie des Crossognathiformes nov. ord. (Crossognathoïdes et Pachyrhizodontoïdes), Téléostéens marins du Crétacé et du Tertiaire inférieur. *Palaeontographica.*

WOODWARD, A. S. 1902-1912. *The fossil fishes of the English Chalk.* Palaeontogr. Soc. (Monogr.), London, 264 pp., 79 fig., 54 pl.

Prof. Dr. L. Taverne
Université du Burundi,
Faculté des Sciences,
Département de Biologie
B. P. 2700
Bujumbura, Burundi.