

New insights on the osteology and taxonomy of the osteoglossid fishes *Phareodus*, *Brychaetus* and *Musperia* (Teleostei, Osteoglossomorpha)

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Abstract

The author describes the snout osteology of the fossil Osteoglossidae *Phareodus* and *Brychaetus*. He shows that the two genera considerably differ in their naso-ethmoid region. Indeed, *Phareodus encaustus* and *P. queenslandicus* possess a large dermethmoid contacting the frontals and separating the two nasals from each other, which is the primitive condition within teleosts. *P. testis* is a little more specialized. Its dermethmoid still separates partially the two nasals but it begins to lose its contact with the frontals. On the contrary, *Brychaetus muelleri* exhibits a specialized snout pattern. The two nasals, articulated with the frontals, are joined together on almost their entire length, except at their anterior edge where a small dermethmoid, largely separated from the frontals, is inserted between them, as in *Osteoglossum* and *Scleropages*. Thus, *Brychaetus* is a valid genus and not a synonym of *Phareodus*. The author also shows that the osteoglossid *Musperia radiata*, from the Eocene of Indonesia, displays the same advanced snout pattern as *Brychaetus* and the two Recent Osteoglossidae. The caudal skeleton of *Musperia* is described for the first time. The first preural and the first ural centra bear complete neural spines. The five hypurals are autogenous. There is a pair of uroneurals and no epural.

Keywords: Teleostei, fossil Osteoglossidae, *Phareodus*, *Brychaetus*, *Musperia*, osteology.

Résumé

L'auteur décrit l'ostéologie du museau des Osteoglossidae fossiles *Phareodus* et *Brychaetus*. Il montre que les deux genres diffèrent considérablement au niveau de la région naso-ethmoïdienne. En effet, *Phareodus encaustus* et *P. queenslandicus* possèdent un grand dermethmoïde en contact avec les frontaux et qui sépare les deux nasaux l'un de l'autre, ce qui est la situation primitive chez les téléostéens. *P. testis* est un peu plus spécialisé. Son dermethmoïde continue à séparer partiellement les deux nasaux mais il commence à perdre son contact avec les frontaux. À l'inverse, *Brychaetus*

muelleri offre une morphologie évoluée du museau. Les deux nasaux, articulés avec les frontaux, sont jointifs sur presque toute leur longueur, sauf à leur extrémité antérieure où un petit dermethmoïde, largement séparé des frontaux, s'intercale entre eux, comme chez *Osteoglossum* et *Scleropages*. *Brychaetus* est donc un genre valide et non pas un synonyme de *Phareodus*. L'auteur montre aussi que l'ostéoglossidé *Musperia radiata*, de l'Éocène d'Indonésie, présente la même morphologie évoluée du museau que *Brychaetus* et les Osteoglossidae récents. Le squelette caudal de *Musperia* est décrit pour la première fois. Les vertèbres préurales 1 et urale 1 portent des neurépines complètes. Les cinq hypuraux sont autogènes. Il y a une paire d'uroneuraux et pas d'épural.

Mots-clefs: Teleostei, Osteoglossidae, *Phareodus*, *Brychaetus*, *Musperia*, ostéologie.

Introduction

Osteoglossomorpha are a super-order of primitive teleosts existing since the Jurassic-Cretaceous boundary (CHANG & MIAO, 2004: 547). They comprise three orders: the Hiodontiformes, the Osteoglossiformes and the Mormyriiformes (= Notopteriformes). Some authors bring down the last two orders to a subordinal rank, the Osteoglossioidei and the Mormyroidei, and gather them in a larger order of Osteoglossiformes *sensu lato*. Others separate the Lycopteridae from the Hiodontiformes and erect for them a peculiar order: the Lycopteriformes. Some osteoglossomorph fossil genera and families are left *incertae ordinis*. The recent Osteoglossomorpha inhabit fresh-water environments but the fossil species comprise both marine and fresh-water members.

Osteoglossiformes or bonytongues are still represented today by five tropical genera: *Osteoglossum* CUVIER, 1829 and *Arapaima* MÜLLER, 1843, both from South America, *Heterotis* CUVIER & VALENCIENNES, 1846 and *Pantodon* PEETERS, 1876, both from Africa, and *Scleropages* GÜNTHER, 1864 from northern

Australia and south-eastern Asia. These five Recent genera are included in three families, the Osteoglossidae for *Osteoglossum* and *Scleropages*, the Arapaimidae (= Heterotidae) for *Arapaima* and *Heterotis*, and the Pantodontidae for *Pantodon* (TAVERNE, 1979, 1998). Some authors recognize only a subfamilial rank to these families, the Osteoglossinae, the Arapaiminae (= Heterotinae) and the Pantodontinae, and group all three in a family Osteoglossidae *sensu lato* (see for instance NELSON, 2006: 104-106).

The purpose of this paper concerns three fossil genera of Osteoglossidae. I wish to discuss some problems regarding *Phareodus* LEIDY, 1873 (= *Dapedoglossus* COPE, 1877) and *Brychaetus* WOODWARD, 1901, on the one hand, and to complete the study of the genus *Musperia* SANDERS, 1934, on the other hand.

Material and methods

The specimens used for the present study are listed in appendix 1. The material was observed with a stereomicroscope WILD M5 and the drawings made by the author with a camera lucida.

The problem of the snout region of *Phareodus* (Figs 1-8)

The first fossil Osteoglossidae ever discovered in North America was collected from the fresh-water Eocene Green River Formation of Wyoming. It consisted only of a body fragment with some big reticulated scales (COPE, 1884: pl. 6, fig. 1) and was named *Osteoglossum encaustum* by COPE (1871: 430). A little later, LEIDY (1873: 99) described from the same deposits five mandibular fragments. He recognized them as different from *Osteoglossum* and thus erected a new genus and a new species: *Phareodus acutus* LEIDY, 1873. Four years later, COPE (1877: 807) described some new osteoglossid specimens from the Green River Formation and created also a new genus and a new species: *Dapedoglossus testis* COPE, 1877, which he figured later on (COPE, 1884: pl. 7, fig. 1). He included his former *O. encaustum* in the same new genus as *Dapedoglossus encaustus* (COPE, 1877: 808). Other species were described during the same period and also during the following years: *Phareodon* [a misspelling for *Phareodus*] *sericeus* COPE, 1873, *Dapedoglossus aequipinnis* COPE, 1878 and *Phareodus brevicaudatus* THORPE, 1938, all three from the Green River Formation, *Phareodus queenslandicus* HILLS, 1934 from the Eocene of Queensland, Australia, and,

more recently, *Phareodus songziensis* ZHANG, 2003 from the Eocene of the Hubei Province, China (COPE, 1873: 638, 1878: 77; HILLS, 1934: 160; THORPE, 1938: 289; ZHANG, 2003: 328).

HILLS (1934: 160-164), working only on *P. queenslandicus*, was the first to give useful osteological information on *Phareodus*. Later, ROELLIG (1967: 19-49), in his unpublished Ph. D. thesis, TAVERNE (1978: 7-32), LI (1994) and LI *et al.* (1997) have studied thoroughly the osteology of the two North-American and of the Australian species of *Phareodus*.

WOODWARD (1901: 74) was apparently the first to put *Dapedoglossus* and *Phareodus* into synonymy, giving the priority to the former because LEIDY (1873) had left *Phareodus* undefined. THORPE (1938: 289) agreed with this synonymy but, in opposition to WOODWARD (1901), invalidated *Dapedoglossus* because of the priority of *Phareodus*. This use of *Phareodus* instead of *Dapedoglossus* is now currently accepted by all the specialists working on fossil and Recent Osteoglossomorpha.

In his study of the ichthyofauna of the Green River Formation, GRANDE (1984: 70) stated that there were only two valid species of *Phareodus* in those North-American strata: *P. encaustus* (= *P. acutus*, *P. sericeus*, *P. aequipinnis* and *P. brevicaudatus* [pro parte]), the type-species, and *P. testis* (= *P. brevicaudatus* [pro parte]). That was already the opinion expressed by TAVERNE (1978: 7). This view was followed by later authors (LI, 1994; LI & WILSON, 1996; LI *et al.*, 1997; ZHANG, 2006; WILSON & MURRAY, 2008; among many others).

Phareodus is a rather big, fusiform and deep-bodied teleost (Figs 1-2). Some large specimens exceed 50 cm of total length. As in some other fossil Osteoglossidae, the frontal is wide, with a lateral margin presenting a marked expansion above the orbit, and the jaws bear strong, long and acuminate teeth. *Phareodus* certainly was a fast-swimming fish and one of the principal predators present in its lacustrine environment. When seen in side view, *P. encaustus* can be distinguished easily from *P. testis*. Both fishes possess large posterior infraorbitals, as all Osteoglossidae, but the former offers the third infraorbital longer than deep and the fourth one as deep as long (ROELLIG, 1967: fig. 6; TAVERNE, 1978: fig. 8; GRANDE, 1984: fig. II.33a; LI, 1994: figs 5B, 8, LI *et al.*, 1997: fig. 3), while the latter exhibits the third and fourth infraorbitals deeper than long (ROELLIG, 1967: fig. 8; TAVERNE, 1978: fig. 2; GRANDE, 1984: fig. II.33b; LI, 1994: fig. 5C; LI *et al.*, 1997: fig. 8). There are other minor differences between the two North-American species (ROELLIG,

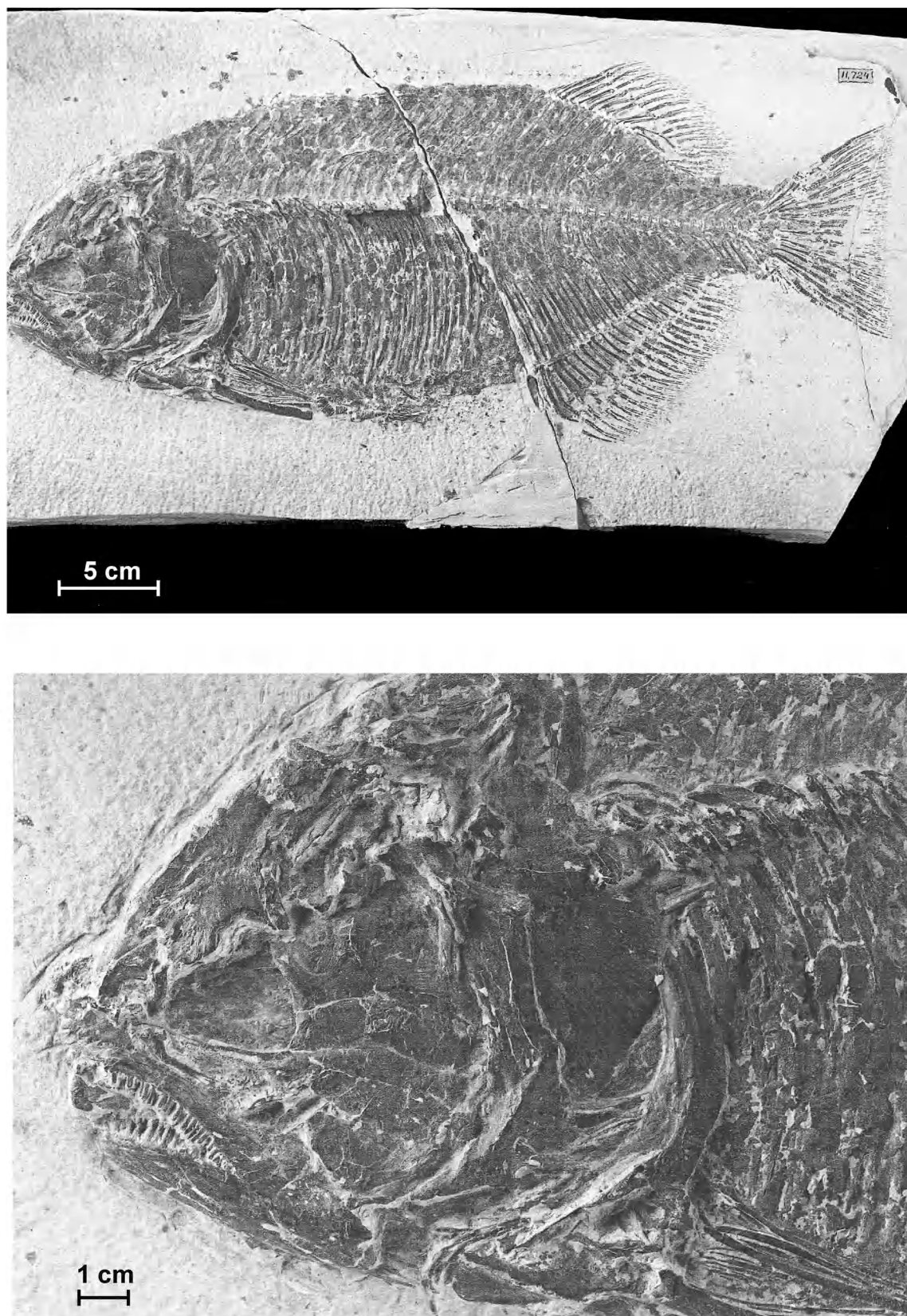


Fig. 1 – *Phareodus encaustus* (COPE, 1871). Specimen USNM 11.724, (above) complete body and (below) head region.

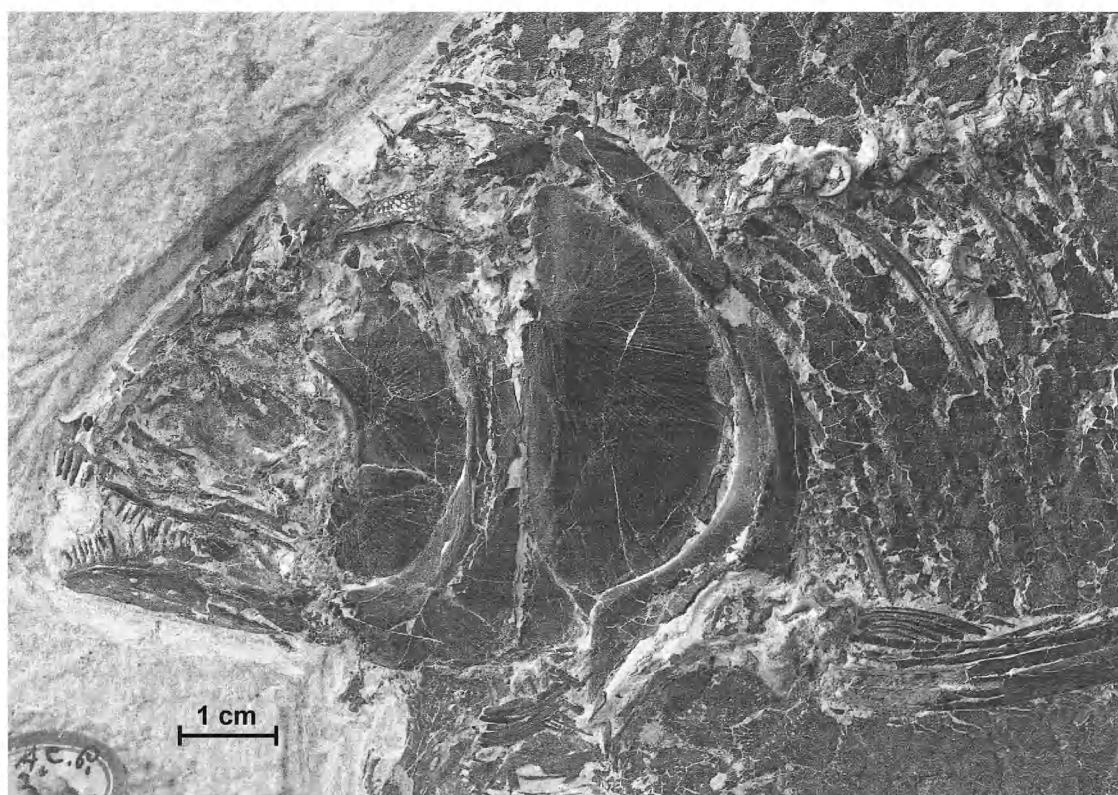
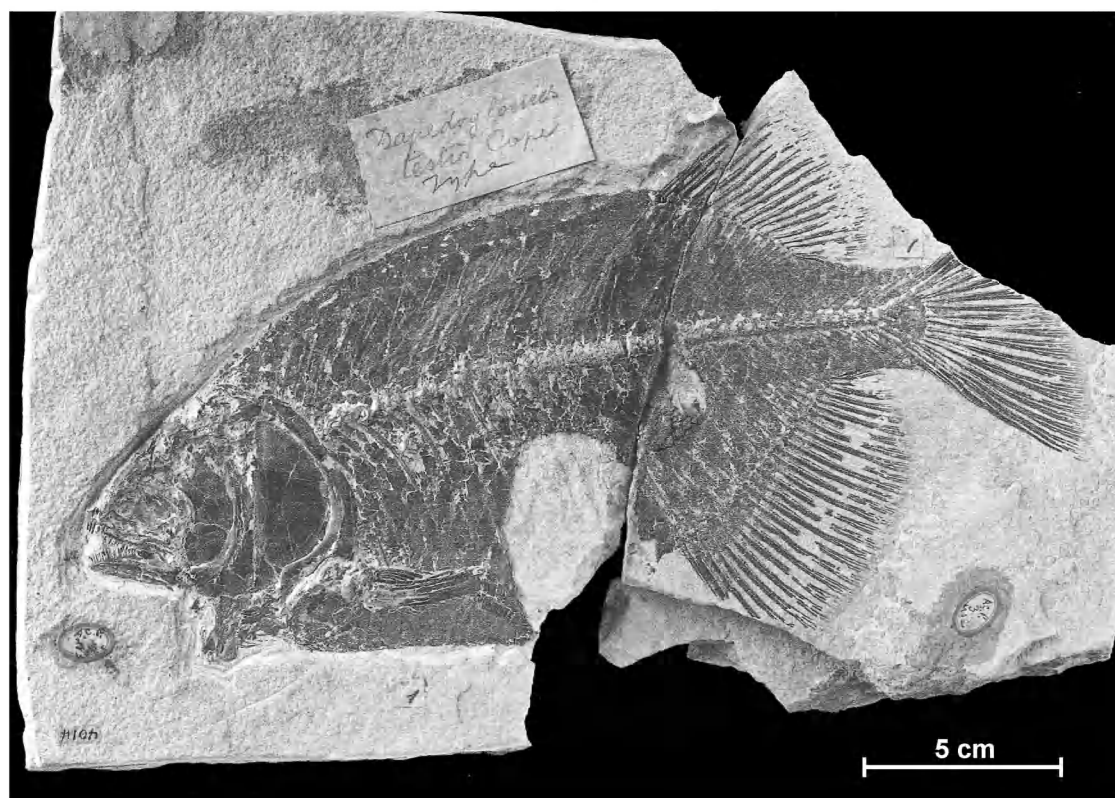


Fig. 2 – *Phareodus testis* (COPE, 1877). Holotype USNM 4014, (above) complete body and (below) head region.

1967; TAVERNE, 1978; GRANDE, 1984; LI *et al.*, 1997). *P. queenslandicus* shares a few osteological characters with *P. encaustus*, particularly the shape of the two posterior infraorbitals, and is thus closer to this species than to *P. testis* (LI, 1994: 297-298). *P. songziensis* differs from the other species by its very short dorsal fin and its caudal skeleton (ZHANG, 2003). But the head of this fish is unknown. So it is quite possible that the Chinese species belongs to another genus of fossil deep-bodied Osteoglossidae than *Phareodus*, for instance the Indonesian *Musperia* or the Indian *Taverneichthys*.

When figuring the skull roof of the North-American *Phareodus*, ROELLIG (1967: fig. 1) used the specimen AMNH 4587 of *P. encaustus* (named *acutus* in his paper) and TAVERNE (1978: fig. 4) the specimen USNM 4916, identified as *P. testis* on the accompanying label (EASTMAN, 1917: pl. 16, fig. 1) but considered as *P. encaustus* by GRANDE (1984: fig. II.35a). In my opinion, USNM 4916 really belongs to *P. testis* and not to *P. encaustus* (compare my Fig. 3 in the present paper and LI, 1994: fig. 1B with my Fig. 4).

Both ROELLIG (1967) and TAVERNE (1978) have represented those two skull roofs with a pair of long and broad nasals meeting each other on the mid-line and articulated with the frontals just before their enlarged anterior parts. A very small dermethmoid (called mesethmoid by ROELLIG and supraethmoid by TAVERNE) was drawn wedged between the anterior extremities of the nasals and so widely separated from the frontals. Such a derived situation is the one existing in the Recent Osteoglossidae *Osteoglossum* and *Scleropages* (TAVERNE, 1977: figs 44, 73; among others).

The Australian *P. queenslandicus* offers a quite different morphology of the snout, as seen on the specimen UQ F 14960. It presents a marked lateral expansion of the anterior half of the frontal, as in the North-American species. A large, anteriorly rounded and posteriorly triangular dermethmoid is embedded in a "V"-shaped notch formed between the anterior borders of the two frontals (Fig. 3; HILLS, 1934: fig. 4; TAVERNE, 1978: fig. 16; LI, 1994: fig. 1A). The mesethmoid endoskeleton is not preserved. The nasals are unknown in this species but they were obligatory separated from each other by the wide dermethmoid reaching the frontals. The loss of the nasals on specimen UQ F 14960 also indicates that these bones were not firmly articulated with the frontals but simply in contact with them. Such a morphology looks like the classic primitive teleostean condition, with the dermethmoid (or mesethmoid) contacting

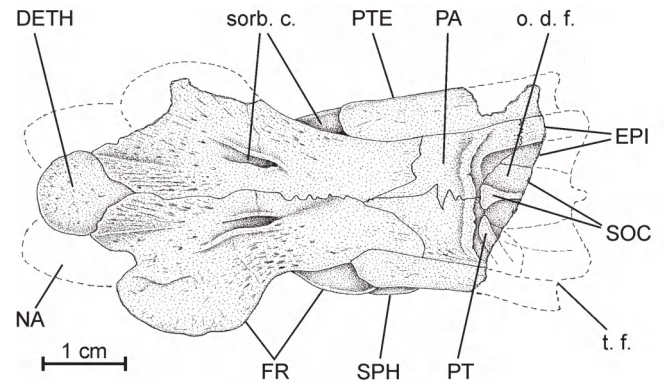


Fig. 3 – *Phareodus queenslandicus* HILLS, 1934. Specimen UQ F 14960, skull roof.

the frontals and located between a pair of nasals, as found in the archaic teleost *Elops* LINNÉ, 1766 (FOREY, 1973: fig. 1; TAVERNE, 1974a: fig. 3). The same primitive morphology seemingly occurs in the archaic Osteoglossidae *Chanopsis lombardi* CASIER, 1961 from the Lower Cretaceous (Valanginian-Barremian) of the Democratic Republic of Congo (Fig. 4), judging by the large "V"-shaped notch between the anterior edges of the two frontals.

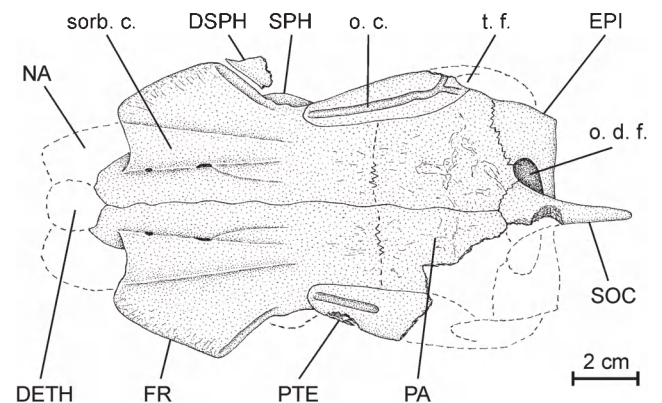


Fig. 4 – *Chanopsis lombardi* CASIER, 1961. Holotype MRAC RG 13.608, skull roof.

Those important differences between the snout morphology figured by ROELLIG (1967) and TAVERNE (1978) for the two North American *Phareodus* and the one of *P. queenslandicus* led to the erection of a new genus, *Phareoides*, by TAVERNE (1975) for the Australian species.

LI (1994) and LI *et al.* (1997) have re-studied *P. queenslandicus*, comparing this fish with the two North-American species. They have shown that

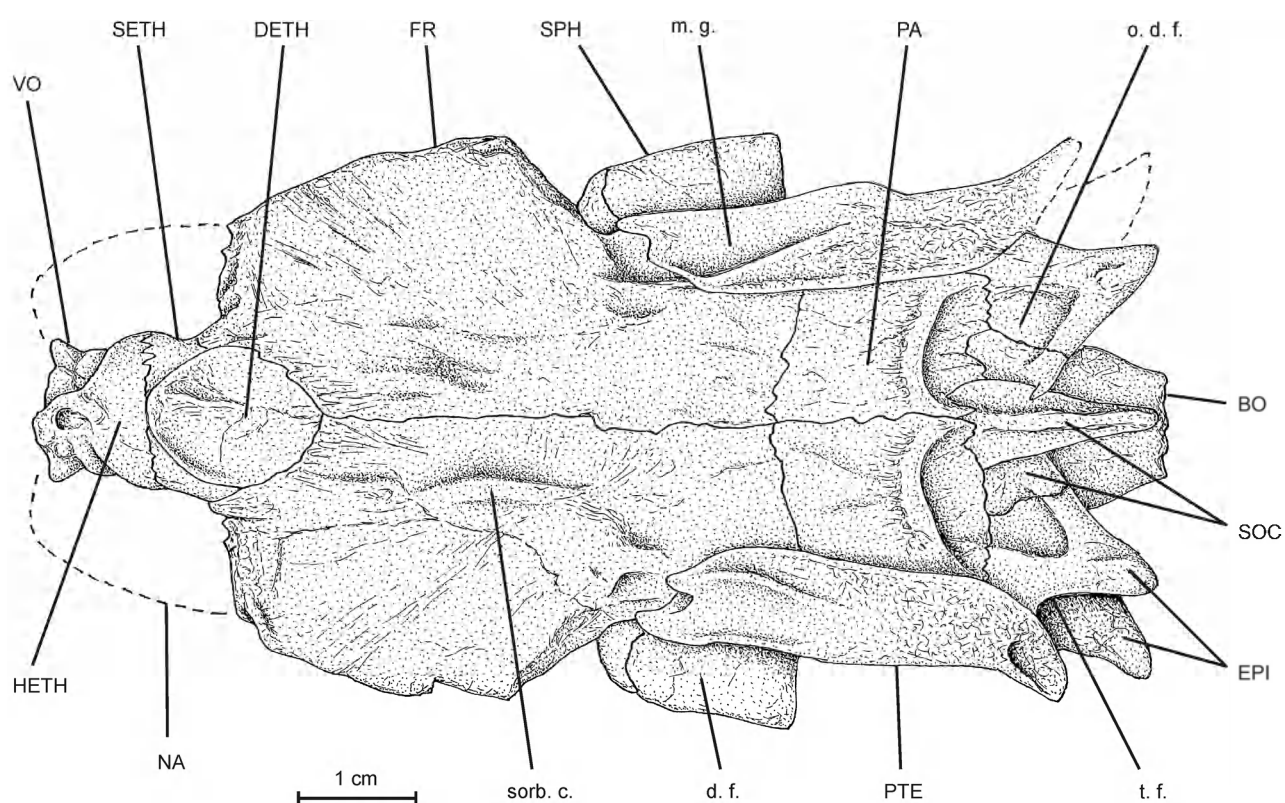
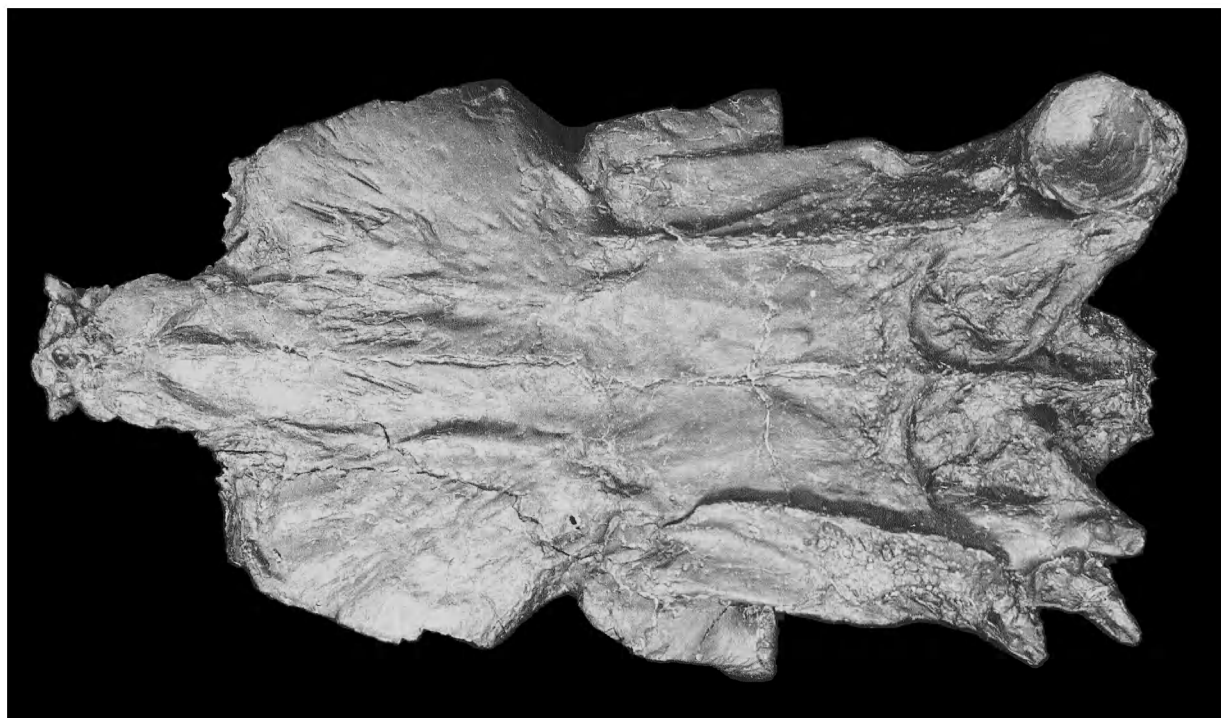


Fig. 5 – *Phareodus encaustus* (COPE, 1871). Specimen AMNH P 4587, skull roof.

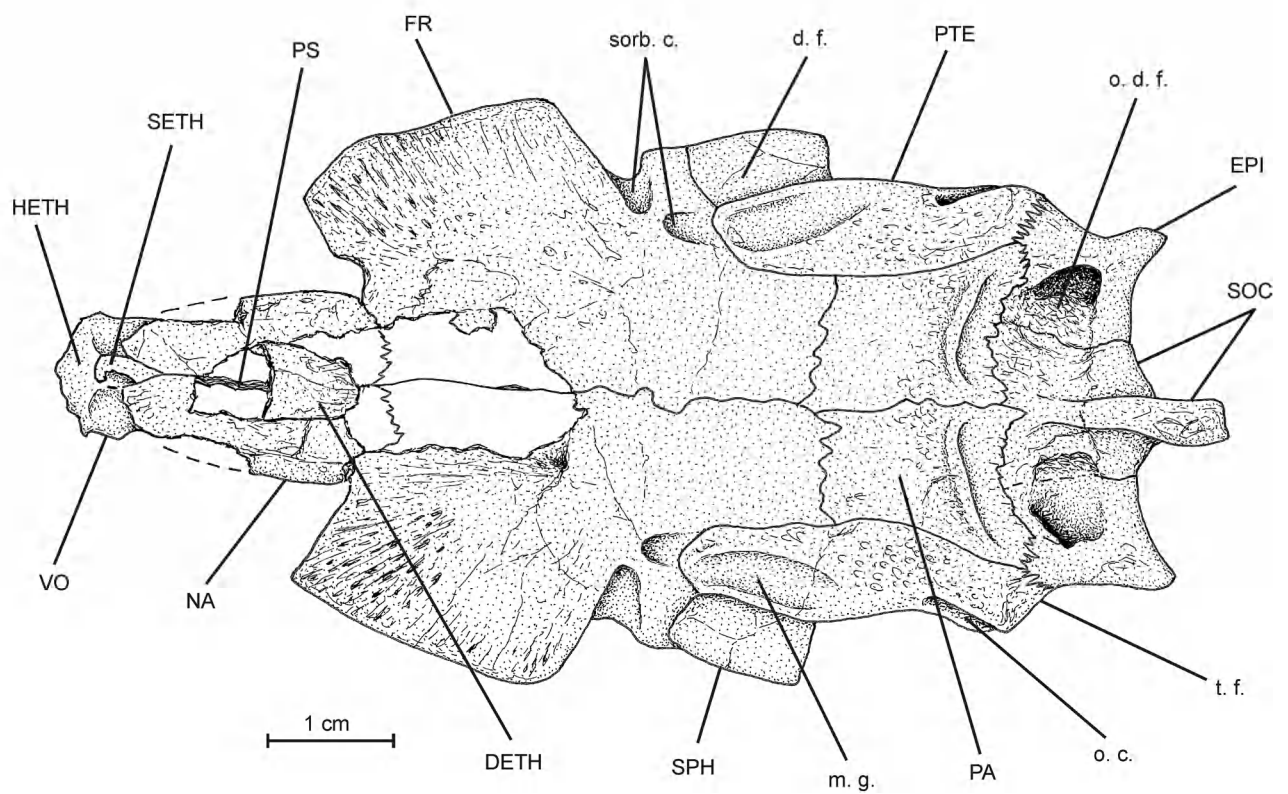


Fig. 6 – *Phareodus testis* (COPE, 1877). Specimen USNM 4916, skull roof.

specimens AMNH 4587 and FMNH P F 14040 of *P. encaustus* (LI, 1994: fig. 1B, 8; LI *et al.*, 1997: fig. 2A, 3) and specimens FMNH P F 14062 and UALVP 447 of *P. testis* exhibit the primitive snout pattern with the dermethmoid separating the left nasal from the right, as in the Australian species. They have thus invalidated the genus *Phareoides*, replacing this species in *Phareodus*, since the only valuable reason invoked by TAVERNE (1975) to justify the erection of a new genus was precisely the differences in the snout morphology.

Today, I can confirm the pertinence of the descriptions of the snout in *P. encaustus* and *P. testis* made by those authors by my own observations (Figs 5-8). It is obvious that ROELLIG (1967) has completely misinterpreted the naso-ethmoid region of *P. encaustus* (compare his fig. 1 with LI, 1994: fig. 1B and Fig. 5 in the present paper for the same specimen AMNH 4587). Concerning the specimen USNM 4916 of *P. testis*, TAVERNE (1978) has been led into error by the bad preservation of its snout region. Indeed, the anterior half of the dermethmoid is lost, revealing a small part of the medio-dorsal crest of the parasphenoid. The posterior part of the dermethmoid exhibits a fine medio-sagittal fissure. Moreover, the limits between the dermethmoid and the nasals are not easily visible. Those crest and fissure have been erroneously considered as the suture between the two nasals and the small anterior endoskeletal supraethmoid has been mistakenly interpreted as the dermoskeletal component of the mesethmoid.

However, the snout morphologies of the two North-American *Phareodus* are not the same. In *P. encaustus*, the naso-ethmoid region is wide but rather short (Fig. 5). There is a large dermethmoid embedded between the two frontals, resting on a broad supraethmoid and completely separating the two nasals. In *P. testis*, the naso-ethmoid region is more elongated (Figs 6-8). The dermethmoid is a little smaller, separating the two nasals only partially, and it begins to lose its contact with the frontals. The hypoethmoid and supraethmoid are very small and clearly separated from the dermethmoid, which was probably resting on an ethmoid cartilage. This more anterior position of the dermethmoid and the reduction of the supraethmoid announce the situation of *Osteoglossum* and *Scleropages* where the dermethmoid is a small bony plate, anteriorly located, largely separated from the frontals and resting on a small supraethmoid.

Those differences in the snout morphology of *P. encaustus* and *P. queenslandicus*, on the one hand, and of *P. testis*, on the other hand, could eventually justify the erection of a new genus for *P. testis*.

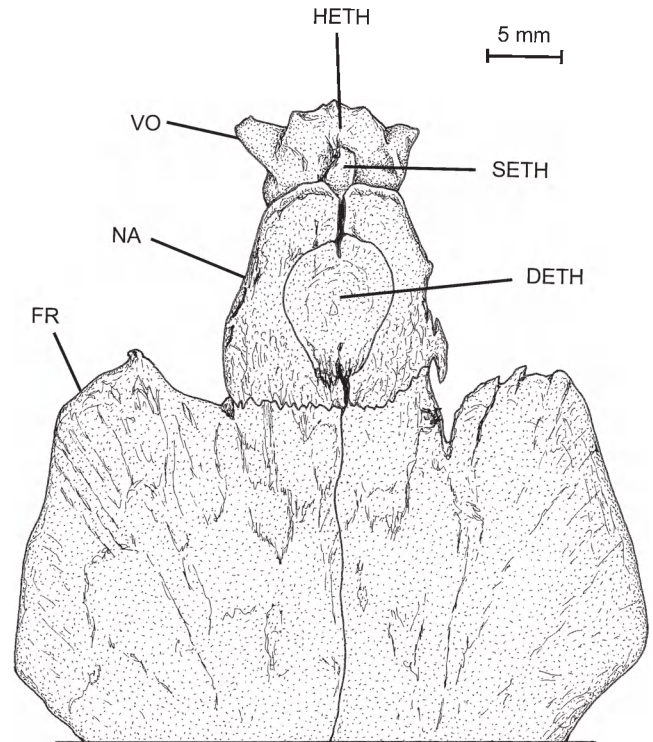


Fig. 7 – *Phareodus testis* (COPE, 1977). Specimen USNM 15608, anterior part of skull roof.

The snout region and the validity of *Brychaetus* (Figs 9-10)

AGASSIZ (1845: 308) was the first to mention the name *Brychaetus muelleri* for some fossil fish remains from the London Clay but without any description or figure. The taxon was thus a *nomen nudum* at that time, until WOODWARD (1901: 76-80, pl. 1) re-uses the names *Brychaetus* and *B. muelleri* and, this time, gives a short diagnosis of both taxa, with some figures. Today, the genus is known as *Brychaetus* WOODWARD, 1901 and the species as *B. muelleri* WOODWARD, 1901.

B. muelleri, from the Ypresian (Lower Eocene) of England, is the first marine osteoglossid ever described. Other marine fossil fishes of this lineage were already known before but not recognized as osteoglossid by their original descriptors, for instance *Monopteros gigas* VOLTA, 1796 and *Thrissopterus catullii* HECKEL, 1856. *B. muelleri* is a large fish probably reaching more than 1 m of total length. Only the head and the beginning of the body are known. The jaws bear the same huge acuminate teeth as in *Phareodus*. The body is not as deep as in *Phareodus*. CASIER (1966: 139-144), ROELLIG (1967: 50-60, 1974) and TAVERNE (1974b,

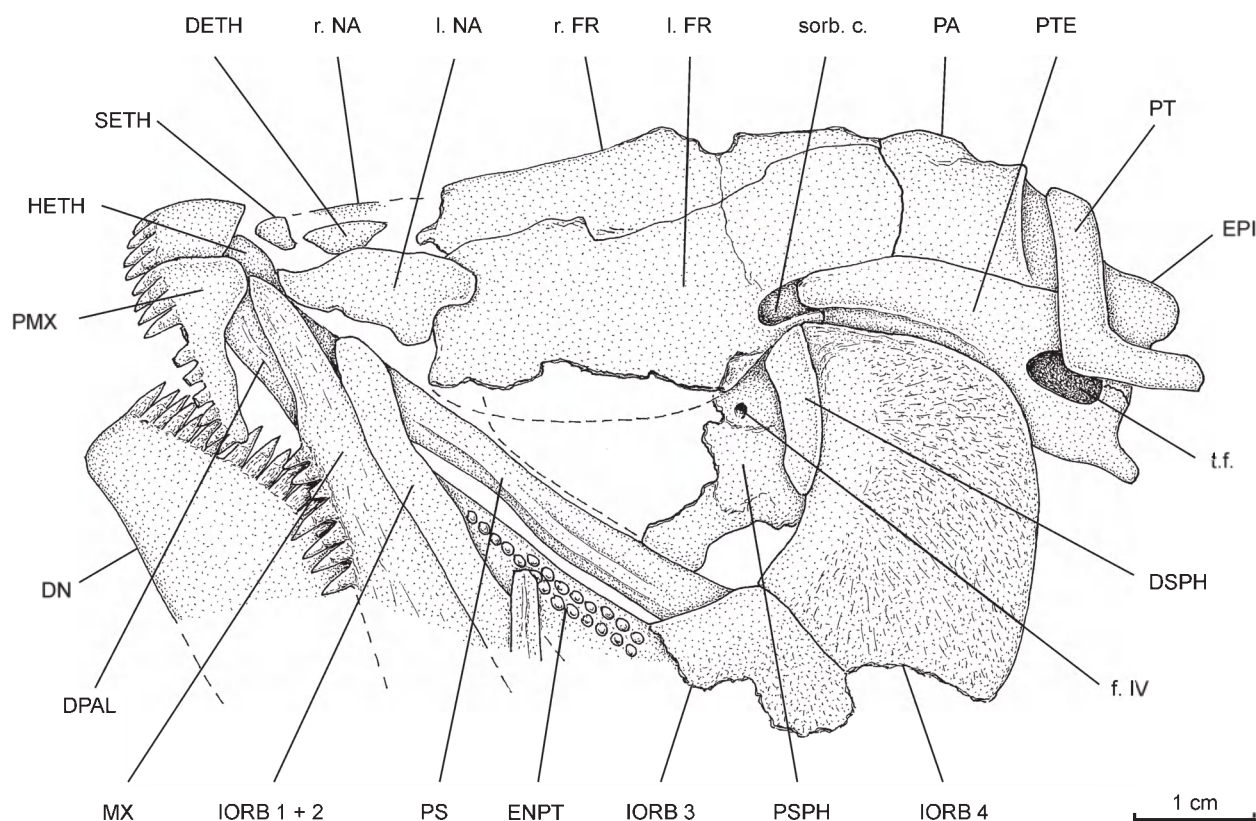


Fig. 8 – *Phareodus testis* (COPE, 1877). Specimen AMNH P 2799, skull in lateral view.

1978: 33-47) have provided a detailed osteological study of *B. muelleri*.

Recently, LI (1994: 297) and LI *et al.* (1997: 498) have suggested that *Brychaetus* was a synonym of *Phareodus*. They have considered however that the British species was valid under the name *Phareodus muelleri*. They think that the British fossil fish is more closely related to *P. encaustus* and *P. queenslandicus* than to *P. testis* because of the shape of its posterior infraorbitals. Their opinion about that synonymy was supported by some (for instance ZHANG, 2006: 51) and refused by others (for instance TAVERNE, 1998: 157-158).

The nasals of the holotype NHM 3893 are long and wide bones but however narrower than the frontals, in front of which they are located and with which they are articulated. They are joined on the mid-line on their entire length (WOODWARD, 1901, pl. 1, fig.1, 1a; pers. obs.). The mesethmoid is not clearly visible in the holotype. In contrast, the paratype NHM 39699 exhibits a perfectly preserved snout with all the concerned bones (nasals, dermethmoid, supraethmoid, hypoethmoid and vomer) present (TAVERNE, 1978: fig.

23). The large nasals contain the most anterior part of the supraorbital sensory canal. They meet each other in the mid-line on their entire length, except at the level of their anterior edge where a small dermethmoid (named supraethmoid in TAVERNE, 1978) is inserted between them (Fig. 9). This dermethmoid rests on a small supraethmoid (named dorsal hypoethmoid in TAVERNE, 1978) and is largely separated from the frontals. Thus *B. muelleri* shows the same specialized type of snout region as the Recent *Osteoglossum* and *Scleropages*, and not the primitive one of *P. encaustus*, *P. testis* and *P. queenslandicus*. The conclusion is clear: *Brychaetus* is not a synonym of *Phareodus* but a valid osteoglossid genus.

LI (1994: 297) also considers as doubtful the reconstruction of the frontal with a marked lateral expansion proposed by TAVERNE (1978: fig. 22) for *Brychaetus muelleri* because “there are too many discrepancies between TAVERNE’s restorations and WOODWARD’s (1901) original illustrations for that species”, as he writes. It is true that generally the lateral margin of the frontal is not well preserved in this fish. But, apparently, LI (1994) has seen neither the holotype

NHM 3893 nor its photographs in CASIER (1966: pl. 16, fig. 1a, b), a book not mentioned in his references. The lateral expansion of the frontal is undoubtedly present and clearly visible on the left side of the skull of this specimen but somewhat downward bent because of the fossilisation. However, this lateral expansion is less important in its anterior part than the one of *Phareodus*. The paratype NHM 638 exhibits the posterior part of the lateral expansion of the frontal but, this time, on the right side of the skull (Fig. 9).

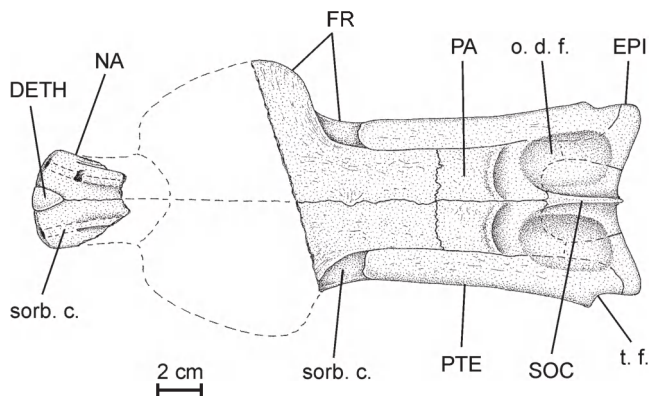


Fig. 9 – *Brychaetus muelleri* WOODWARD, 1901. Nasomethmoid region of specimen NHM 39699 and skull roof of specimen NHM 638. The scale refers to specimen NHM 39699.

There is another osteological character of *Brychaetus muelleri* which is problematic: the respective shape of the two posterior infraorbitals. CASIER (1966: fig. 19A) and ROELLIG (1967: fig. 22, 1974: fig. 1) figure the third infraorbital larger than the fourth one, whereas TAVERNE (1974b: fig. 1, 1978: fig. 20) shows a fourth infraorbital much larger than the third one, as in *Phareodus*. In the holotype NHM 3893, as in almost all the other specimens, the fourth infraorbital is broken more or less obliquely into two separate parts because of the compression due to the fossilisation on a so huge bone. Moreover, the real suture between the third and the fourth infraorbitals is not easy to see. CASIER (1966) and ROELLIG (1967, 1974) have misinterpreted this break as the suture between the two bones. Specimen NHM 39699 presents only a thin breaking line on the fourth infraorbital and the suture between the two bones is well visible. This specimen clearly shows that the fourth infraorbital is much deeper than the third one (Fig. 10), the two bones having the same shape as in *Phareodus encaustus* and *P. queenslandicus*. LI (1994: 298) confirms my observation by his own.

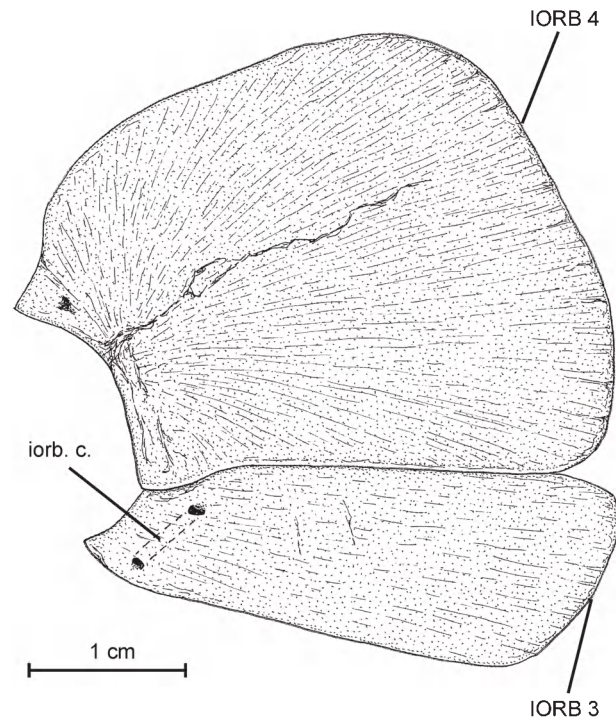


Fig. 10 – *Brychaetus muelleri* WOODWARD, 1901. Left posterior infraorbitals of specimen NHM 39699.

Brychaetus outside of England

Brychaetus schnarrenbergeri ZOTZ, 1928 has been described on the basis of some big bony fragments from the marine Oligocene of Alsace (ZOTZ, 1928). As TAVERNE (1978: 46) wrote, some bones are misinterpreted by the author and nothing in these bones indicates a close relationship with *Brychaetus*.

ARAMBOURG & SIGNEUX (1952: 243, pl. 37, fig. 43, 44) are the first to mention the presence of *Brychaetus muelleri* outside of England. The concerned material comes from the marine Ypresian (Lower Eocene) of Morocco and comprises large isolated teeth and teeth attached to a fragment of a dentary. At that time, *B. muelleri* was the only recognized fossil marine osteoglossid fish and the Moroccan fossil teeth obviously belonged to an Osteoglossidae. That is probably the reason which led those two authors to assign their material to *B. muelleri*. Today, we know two other fossil marine Osteoglossidae, with similar large teeth as *B. muelleri*, occurring in the Tethysean realm during the lowermost Tertiary, the deep-bodied *Monopteros gigas* VOLTA, 1796 from the Lower Eocene of Italy and *Opsithrissops osseus* DANILCHENKO, 1968 from the Paleocene of Turkmenia

(TAVERNE, 1979, 1998). It is not possible to decide on isolated teeth and a small dentary fragment to which of those three species the Moroccan material belongs. Its determination as *B. muelleri* is thus questionable.

DARTEVELLE & CASIER (1959: 351-352) assign some isolated bones and teeth from the marine Paleocene of Cabinda to *Brychaetus* aff. *muelleri*. TAVERNE (1969) adds a caudal skeleton to those bony fragments and erects for them the new species *Brychaetus caheni*. Today, that material is transferred to the new genus *Ridewoodichthys* (TAVERNE, 2009a).

CAPPETTA (1972: 224, pl. 13, fig. 8) mentions the presence of *Brychaetus* aff. *muelleri* in the marine Paleocene of the Republic of Niger on the basis of one premaxilla. However, this bone exhibits a very weakly developed ascending process as in *Scleropages* (TAVERNE, 2009b) while the one of *B. muelleri* is deep (TAVERNE, 2009a: fig. 5B).

WEEMS & HORMAN (1983: 43-45, fig. 4) describe an osteoglossid dentary with large and strong teeth from the marine Eocene of Maryland (U.S.A.) and referred it to *B. muelleri*. This dentary is less deep than in *Phareodus* (TAVERNE, 1978: figs 2, 15, 17; LI, 1994: figs 6, 8) and, indeed, corresponds well to the one of *B. muelleri* (CASIER, 1966: pl. 16, fig. 1a, b).

CASE (1994: 144, pl. 2, figs 392-393) refers to *B. muelleri* some teeth from the marine Paleocene

of Mississippi (U.S.A.). The general shape of those North-American teeth seems effectively very close to the one of the British species.

BONDE (2008: 290-291, fig. 23-24) mentions under the name *Brychaetus* sp. fragmentary jaws and some scales from a big osteoglossid in the marine Lower Eocene of Denmark.

Complement to the study of *Musperia* (Figs 11-13)

Musperia radiata (HEER, 1874) is the unique species of the genus *Musperia* SANDERS, 1934. It is a deep-bodied osteoglossid discovered in the continental Eocene of Sumatra. The biggest known specimen reaches almost 60 cm of total length.

HORA (1938: fig. 8) attributes to *M. radiata* some Indian scales from the Cretaceous/Tertiary boundary. Indeed, their wide squamules seem to be like the ones of *M. radiata* figured by SANDERS (1934: pl. 3, fig. b). However, another deep-bodied osteoglossid, *Taverneichthys bikanericus* KUMAR *et al.* (2005), has been discovered recently in the continental Paleocene of India (KUMAR *et al.*, 2005; TAVERNE *et al.*, 2009). It is thus quite possible than the Indian scales mentioned by HORA (1938) belong to it and not to *Musperia*.

SANDERS (1934: 13-21) has provided a good morphometric study of *M. radiata* but her description

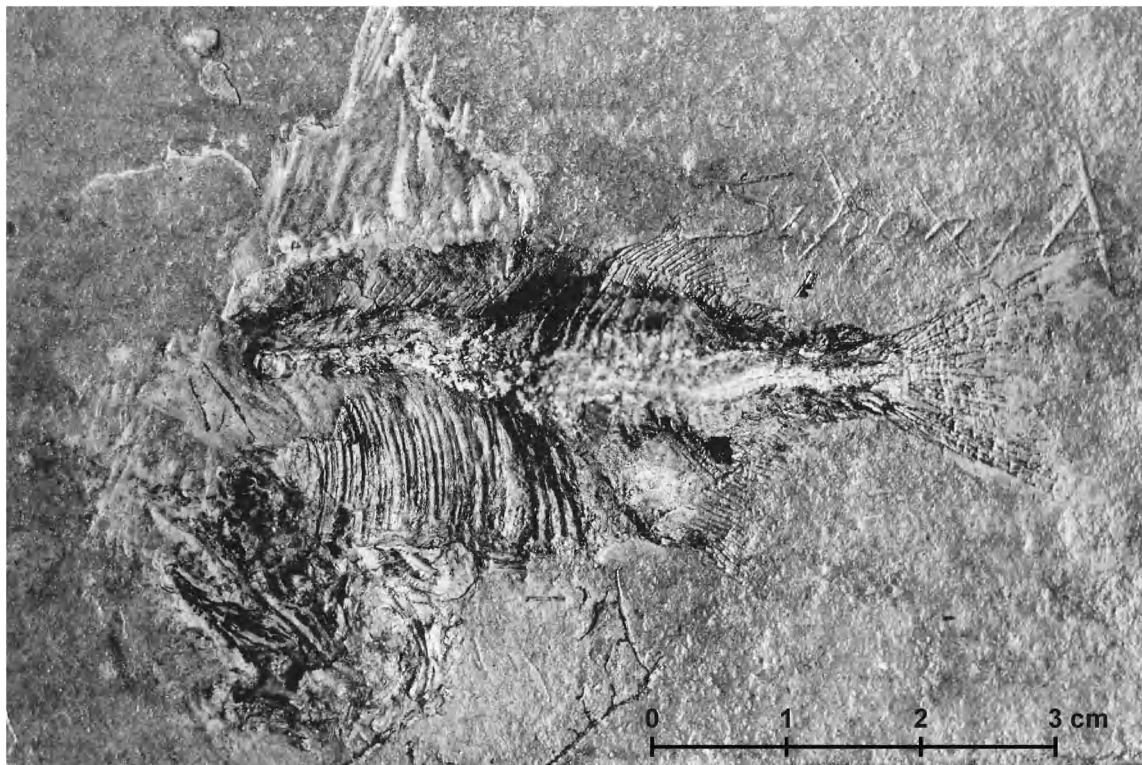


Fig. 11 – *Musperia radiata* (HEER, 1874). Specimen GSI (without number).

of the skull remained superficial and she wrote nothing on the caudal skeleton. TAVERNE (1978: 48-50) has reviewed the available information concerning the fish at that time.

Unfortunately, all the specimens used by SANDERS (1934) were destroyed during World War II. Two new very small specimens were discovered later, the largest without the head (TAVERNE, 1978: fig. 27), the other with a severely crushed and displaced head (Fig. 11). They are both the property of the Geological Survey of Indonesia in Bandung.

However, SANDERS' photograph of the skull of *M. radiata* (pl. 3, fig. a) is clear enough to show that it presents the same large teeth and the same lateral expansion of the frontal as in *Phareodus* and *Brychaetus*. The two long and wide nasals meet on the mid-line, without any bone between them, and are articulated posteriorly with the frontals (Fig. 12).

The dermethmoid is not visible but must inevitably be separated from the frontals by the nasals. Thus, the snout of *M. radiata* differs from the one of *Phareodus* and exhibits the same specialized pattern as *Brychaetus*, *Osteoglossum*, *Scleropages* and some other fossil Osteoglossidae.

An enlargement of a good photograph of the largest new specimen (TAVERNE, 1978: fig. 27) allows me to observe perfectly the well preserved caudal skeleton and to describe it for the first time (Fig. 13). The size of the last vertebrae decreases regularly up to ural centrum 2, which is a small compressed autogenous vertebra. The last neural arches are fused to their corresponding centra. The neural spines are thin and well separated from each other. Preural centrum 2 carries two neural spines. The first one is fully developed but the second is reduced. Both preural centrum 1 and ural centrum 1 bear a complete neural spine. The last haemal arches

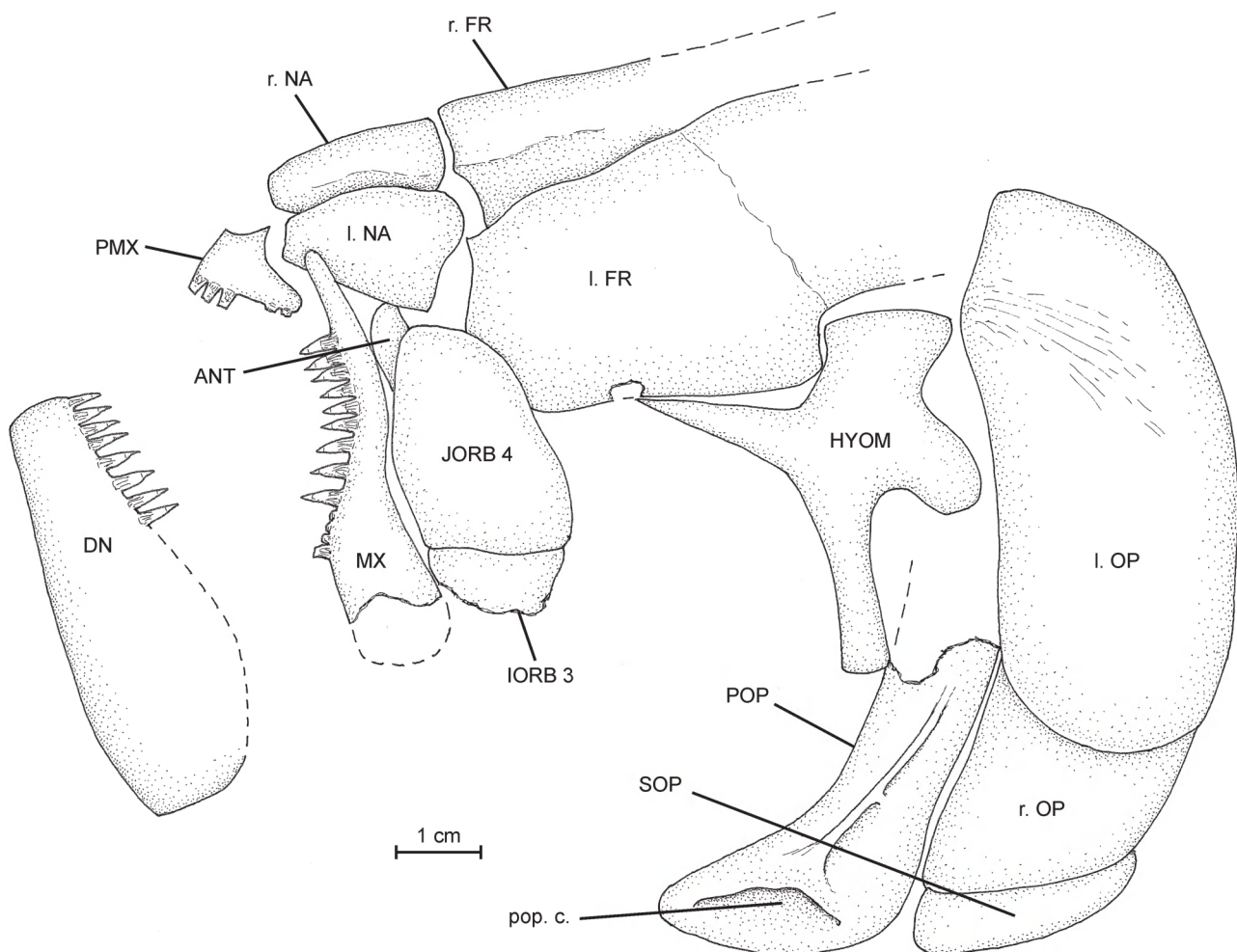


Fig. 12 – *Musperia radiata* (HEER, 1874). Schematic reconstruction of the skull from SANDERS, 1934: pl. 3, fig. a.

are autogenous. Their haemal spines and the parhypural are lengthened and enlarged. They meet each other all along their length. A supplementary haemal arch with a haemal spine is inserted between preural centrum 3 and preural centrum 4. That is very probably an individual variation rather than a specific character. Only five hypurals are visible, all autogenous. The two ventral hypurals are articulated on the ventral face of ural centrum 1. The first one is wide and the second narrower. The three dorsal hypurals are moderately wide. They rest on the posteroventral face of ural centrum 2. There is only one pair of uroneurals and no epural. The uroneural is located just behind ural centrum 2.

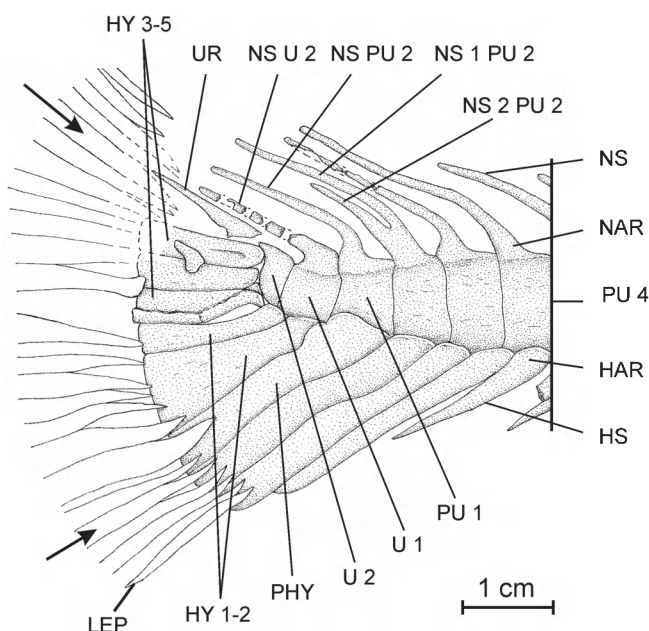


Fig. 13 – *Musperia radiata* (HEER, 1874). Caudal skeleton of specimen GSI (without number) shown in TAVERNE, 1978: fig. 27. The arrows point to the more external principal caudal rays.

The caudal fin is deeply forked. There are 17 principal caudal rays of which 15 are branched, like *Phareodus*. There are four procurent rays in each lobe.

The caudal skeleton of *M. radiata* differs from that of *P. encaustus* (LI *et al.*, 1997: fig. 5A) by the presence of only one neural spine on ural centrum 1, of two neural spines on preural centrum 2 and by the wideness of its last haemal spines. It contrasts with the one of *P. testis* (GREENWOOD, 1966: fig. 12; TAVERNE, 1978: fig. 13; LI *et al.*, 1997: fig. 5B) by the absence of the sixth hypural, the presence of only one neural

arch on preural centrum 1 and ural centrum 1 and, once again, by the wideness of its last haemal spines. On the other hand, the likeness with the caudal skeleton of *P. songziensis* (ZHANG, 2003: fig. 2) is striking. Both species possess five hypurals, only one neural spine on preural centrum 1 and ural centrum 1 and the large last haemal spine connected by its all length to the parhypural. It is quite possible that *P. songziensis* belongs to the genus *Musperia* and not to *Phareodus*. In this case, the Chinese fossil fish represents however another species than *M. radiata* because of its very short dorsal fin (only 12 principal rays *versus* 22–26 in the Indian species). The caudal skeleton of *M. radiata* is also clearly different from that of *Ridewoodichthys caheni* (TAVERNE, 2009a: fig. 4).

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List of institutional abbreviations

AMNH: American Museum of Natural History, New York, U.S.A.

GSI: Geological Survey of Indonesia, Bandung, Indonesia.
MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgique.

NHM: Natural History Museum, London, UK.

UQ: University of Queensland, Brisbane, Australia.

USNM: United States National Museum, Washington, U.S.A.

List of abbreviations used in the text-figures

ANT: antorbital

BO: basioccipital

DETH: dermethmoid (= rostral)

DN: dentary

DPAL: dermopalatine

DSPH: dermosphenotic

ENPT: entopterygoid

EPI: epiotic (= epioccipital)

FR: frontal

HAR: haemal arch

HETH: hypoethmoid

HS: haemal spine
 HY 1-5: hypurals
 HYOM: hyomandibula
 IORB 1+2, 3, 4: infraorbitals 1 to 4
 LEP: caudal fin rays
 MX: maxilla
 NA: nasal
 NAR: neural arch
 NS: neural spine
 NS PU 1: neural spine of the first preural centrum
 NS 1, 2 PU 2: first and second neural spines of the second preural centrum
 NS U 1: neural spine of the first ural centrum
 OP: opercle
 PA: parietal
 PHY: parhypural
 PMX: premaxilla
 POP: preopercle
 PS: parasphenoid
 PSPH: pleurosphenoid (= pterosphenoid)
 PT: posttemporal
 PTE: pterotic
 PU 1-4: first to fourth preural centra
 SETH: supraethmoid
 SOC: supraoccipital
 SOP: subopercle
 SPH: sphenotic
 U 1, 2: first and second ural centra
 UR: uroneural
 VO: vomer
 d. f.: *dilatator fossa*
 f. IV: foramen for the trochlear nerve (IV)
 iorb. c.: infraorbital sensory canal
 l.: left
 m. g.: mucous gutter
 o. c.: otic sensory canal
 o. d. f.: occipito-dorsal fossa
 pop. c.: preopercular sensory canal
 r.: right
 sorb. c.: supraorbital sensory canal
 t. f.: temporal fossa

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well preserved caudal skeleton (photo, see TAVERNE, 1978: fig. 27).

GSI (without number): a specimen with a badly preserved caudal skeleton and a crushed head ventrally displaced (photo, see Fig. 11).

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Appendix 1

Phareodus encaustus (COPE, 1871)

USNM 11.724: a complete specimen (photo)

AMNH P 4587: a braincase (photo)

Phareodus testis (COPE, 1877)

USNM 4014: the complete holotype specimen (photo)

USNM 4916: a braincase (cast and photo)

USNM 15608: a braincase (photo)

AMNH P 2799: a skull (cast)

Phareodus queenslandicus HILLS, 1934

UQ F 14960: a skull roof (latex peel)

Chanopsis lombardi CASIER, 1961

MRAC RG 13.608: a skull roof (holotype)

Brychaetus muelleri WOODWARD, 1901

NHM 3893: a skull (holotype).

NHM 638: a skull (paratype)

NHM 39699: a skull (paratype)

Musperia radiata (HEER, 1874)

GSI (without number): a specimen without head but with a