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Revision of the scombroid fishes from the Cenozoic of England

Kenneth A. Monsch

ABSTRACT: Since 1966, when the last major work on fossil scombroid fishes (Scombroidei, Perciformes) from England appeared, our knowledge of the taxonomy and systematics of Recent scombroids has been thoroughly updated, improved and studied in the context of cladistic methods. In comparison, our knowledge of the fossil taxa has lagged much behind. As part of a revision of all fossil and Recent scombroid fishes, the present paper describes an updated systematic palaeontology of the English fossil taxa. These are a subset of taxa subject to a cladistic analysis of Recent and fossil genera combined, the results of which will appear in future papers. Three new genera are erected, two species transferred to other, already existing, ones and a new species is described (in a new genus). The author follows the opinion that *Eothynnus* Woodward, 1901 is a carangid. Several individual specimens are re-identified. The systematic affinities of *Tamesichthys* Casier, 1966, *Eocoelopoma* Woodward, 1901, *Scombramphodon* Woodward, 1901, *Sphyraenodus* Agassiz, 1844, *Wetherellus* Casier, 1966 and *Woodwardella* Casier, 1966, and a few new taxa, are here considered unknown. *Aglyptorhynchus* Casier, 1966 is probably a billfish, and *Cylindracanthus* Leidy, 1856, is possibly one as well, even though there are serious objections to this.

KEY WORDS: fossils, London Clay Formation, Scombroidei, taxonomic revisions.

The scombroids, or the mackerel-like fishes (Scombroidei, Perciformes), are the most abundant fishes from the early Eocene London Clay Formation in England (Casier 1966), and are arguably amongst the nicest and most spectacular teleost fossils. It was felt that the English fossil scombroids were in need of a thorough revision, which is presented here.

Most of the radiation of the scombroid fossil record starts in the Early Eocene period of the Ypresian, although a few specimens were found in Late Palaeocene sediments (Patterson 1993). The present author must remark that so-called Blochiids such as *Cylindracanthus* Leidy, 1856, are known from the Late Cretaceous (Schultz 1987), but, as laid out further on in this paper, their status as scombroids is questionable. The 'real' scombroids have a cosmopolitan fossil record, with specimens found in North America (e.g. Jordan 1921), Europe (e.g. Leriche 1910; Casier 1966), Africa (e.g. White 1926), the Middle East (e.g. Arambourg 1967), the former Soviet Union (e.g. Danil'chenko 1960; Bannikov 1985), Japan (e.g. Uyeno *et al.* 1994) and Australasia (R. Rust, pers. comm., 2000). One of the largest collections of fossil scombroids is probably in the Natural History Museum of London (BMNH). The majority of those specimens are from the London Clay, but there are also a few from other, older or younger sediments.

Since Casier's (1966) thorough investigation of London Clay fossils, there has been no adequate update of the knowledge of London Clay scombroids. Surveys such as Dineley & Metcalf (1999) and Clouter *et al.* (2000) do not revise or update, but give overviews of what was already known. The problem is not restricted to the large group of London Clay scombroids; hardly any work has been done on fossil scombroids from other English sediments since their first publication. Most of these publications are older than Casier's (1966) monograph (e.g. Dixon 1850, Woodward 1901). D. J. Kemp and his co-authors (e.g. Kemp *et al.* 1979, 1990) mentioned specimens of fossil scombroids from the Eocene of Hampshire in their faunal lists, but did not provide descriptions or taxonomic revisions. Illustrations of these taxa appear in Kemp *et al.* (1990). The taxonomy applied by Kemp and co-authors is outdated (see e.g. Kemp *et al.* 1990) and the specimens (which the present author has not seen) sometimes cannot be identified based on their illustrations (see section 2.1., 'Systematic palaeontology' below).

Since Casier's (1966) work, scombroid systematics have moved considerably forward. Taxonomic revisions have appeared (e.g. Gibbs & Collette 1967; Collette & Chao 1975; Russo 1983; Collette & Russo 1984). The available data which contain systematic information of scombroids has risen dramatically in recent times, which prompted Collette (1999) and Collette *et al.* (2001) to attempt a synthesis of scombroid systematics and proposals for further research in that field. The late 1960s and early 1970s (Hennig 1966; Farris *et al.* 1970) saw the advent of phylogentic systematics, which is now the most widely applied taxonomic methodology. From the early 1980s on, cladistic analyses of either subgroups of scombroids, or the whole suborder, appeared (e.g. Russo 1983; Collette *et al.* 1984; Johnson 1986; Finnerty & Block 1995; Gago 1998). In comparison taxonomic knowledge of (English) fossil scombroids has, in comparison, barely changed and hardly any effort has been made to interpret their relationships in a cladistic framework (but see Fierstine & Monsch 2002). Hence, fossil scombroid taxonomy is to be considered outdated and existing theories about their phylogenetic relationships (e.g. Casier 1966; Bannikov 1985) should be regarded with scrutiny. In other words, there was a need for a taxonomic revision of these taxa in the context of the most recent developments in ichthyology, scombroid systematics, palaeontology and systematics in general.

Recently, the present author finished a thesis on a cladistic analysis of scombroids in which both Recent and fossil taxa were included (Monsch 2000b). This paper presents an updated version of the systematic palaeontology of the English scombroids, as described in that thesis. A new cladistic analysis that includes material described here is currently in preparation. The systematic framework of this paper is based on Monsch (2000b). Suborder Scombroidei is hence understood to consist of Families Trichiuridae (cutlassfishes)

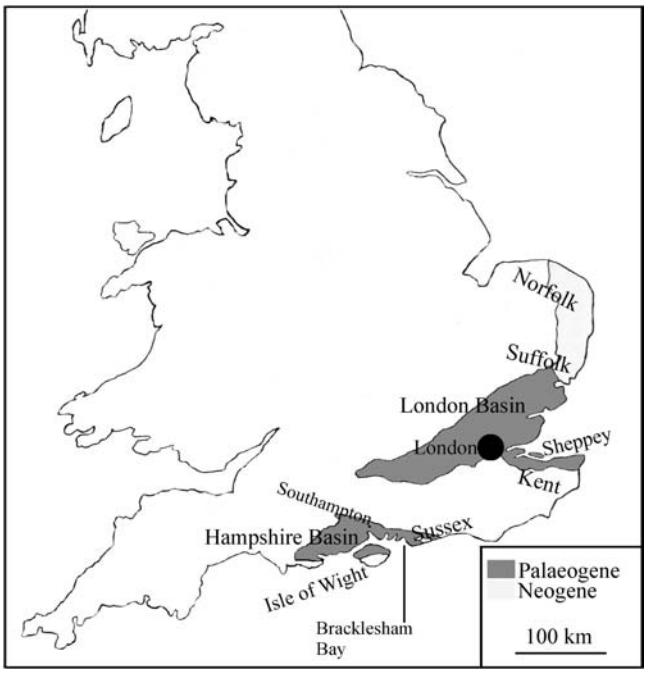

Figure 1 The Palaeogene and Neogene sediments of England. The London Clay Formation spans most of the Palaeogene basins (Casier 1966). Sediment outlines are based on Robson (1968).

and Scombridae (mackerels). The trichiurids consist of Subfamilies Trichiuridae and Gempylidae. Included with Family Scombridae is Subfamily Xiphiinae, which contains all Recent and fossil billfishes. This classification scheme resembles that of Johnson (1986), who also included the Sphyraenidae (barracudas) with the scombroids. An existing contrasting view of systematic affinity of billfishes is that they do not belong to Suborder Scombroidei (Collette *et al.* 2001).

1. Material

Most of the material described in the present paper is from the London Clay Formation in SE England. Most of the London Clay material is from the Isle of Sheppey. Casier (1966) stated that the London Clay Formation is dated as Ypresian (Early Eocene, 54–45·5 Ma, following the International Commission on Stratigraphy 2001). Other material described here is from the Thanetian, Late Palaeocene (Oldhaven Beds, Blackheath Beds, Reading and Woolwich Formation), Bartonian, Middle Eocene (Barton Clay), Piacenzian, Late Pliocene (Red Crag and Coralline Crag), Early Pleistocene (Lower Forest Bed Formation) and Middle Pleistocene (Pebble Gravel). All the relevant Formations and locations are situated in S England (Fig. 1). Much of the stratigraphic information presented here is drawn from sources such as Dineley & Metcalf (1999), Chatwin (1948) and Sherlock (1947).

Woodward (1901), Casier (1966) and Monsch (2000b) all included *Eothynnus* Woodward, 1901 amongst fossil scombrids from the London Clay. However, the present author now follows Bannikov (1979, 1985), who considered this genus a member of the Carangidae (Perciformes, Percoidei).

Repository abbreviations. BMNH: The Natural History Museum, London; GLAHM: Hunterian Museum, University of Glasgow; IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels; KAM: private collection of Kenneth A. Monsch, currently at the University of Wrocław, Poland; MNHN: Muséum National d'Histoire Naturelle, Paris; USNM: National Museum of Natural History, Smithsonian Institution, Washington DC.

2. Results

The osteological terminology applied here derives mostly from de Sylva (1955), which is, besides some modifications, the standard for descriptive osteology of scombroids (e.g. see Collette & Chao 1975; Monsch 2000b). The terminology of the external as well as internal features of billfish rostra is taken from Fierstine & Voigt (1996). The present author will not provide extensive descriptions of (scombroid) osteology and characters here. He refers those who are interested in more detailed explanations of these to the sources of osteological terminology as mentioned here, as well as to reviews of Recent scombroids, as mentioned in the 'Introduction' above. Most of the descriptions of previously known taxa are kept concise, and the present paper focuses mainly on the difference between previous descriptions and the author's own observations. Figure lettering is explained in section 4.

Although most of the taxa described here are included in Monsch's (2000b) systematic palaeontology, this work is not mentioned in the synonymies presented here, since it concerns an unpublished thesis.

Following Monsch (2003), taxonomic diagnoses consist strictly of apomorphies alone to equal a taxon definition of taxa under the 'Linnaean' system (as opposed to name definitions of the PhyloCode). Other distinguishing characters, useful for determination but which are not apomorphies, are mentioned here under a separate heading 'Comparisons'.

Although Dineley & Metcalf (1999) extensively enumerated and sometimes figured taxa which are described here, the present author does not include their work in the present synonymy lists. Their work did not contain anatomical (re-)descriptions since it mainly concerned descriptions of fossil fish sites. The faunal lists and all figures of taxa which they present are taken from previously published works.

2.1. Systematic palaeontology

Suborder Scombroidei Bleeker, 1859
Family Trichiuridae Rafinesque-Schmaltz, 1815
Subfamily Trichiurinae Rafinesque-Schmaltz, 1815
Genus *Trichiurus* Linnaeus, 1758

Type species. *Trichiurus lepturus* Linnaeus, 1758, p. 246, South Carolina, U.S.A (Recent).

Diagnosis. Fossil *Trichiurus* are known from teeth only. Typically, these are fangs which are curved like an 'S' (Fig. 2a), and whose tips may or may not be barbed, depending on the species.

Trichiurus sp.
(Fig. 2b)

1979 *Trichiurus gulincki* Cas. Kemp *et al.*, p. 101 (*nomen nudum*).
1984 *Trichiurus gulincki* Cas. Kemp, p. 162 (*nomen nudum*).
1985 *Trichiurus gulincki* Cas. Kemp, p. 43 (*nomen nudum*).
1990 *Trichiurus gulincki* Cas. Kemp *et al.*, p. 12, pl. 17, fig. 24.

Material. BMNH P26354 and P26357–9 (Fig. 2b), Bracklesham Bay, Sussex, Middle Eocene (Bracklesham Beds).

Diagnosis. As for genus.

Remarks. It is clear that these teeth belong to *Trichiurus*, but there are no diagnostic characters to identify to species

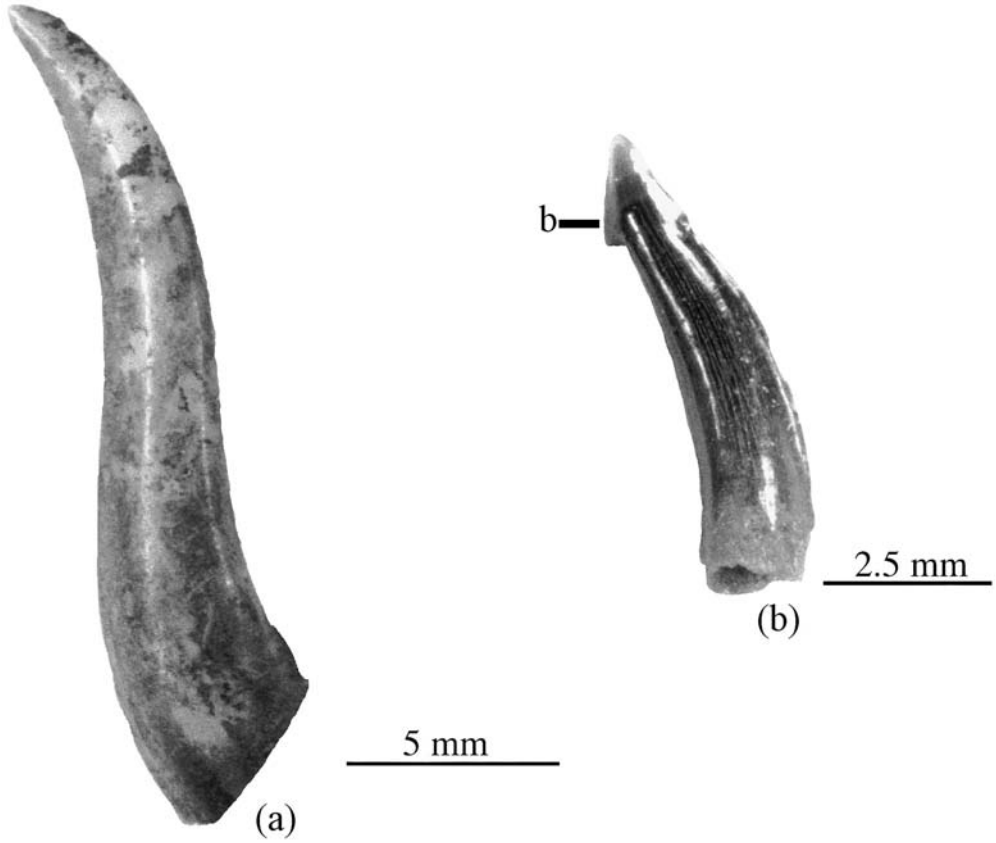

Figure 2 Teeth of *Trichiurus* sp. Each tooth is one of many stored under the same collection number. (a) complete fossil tooth displaying a typical S-shaped curve, not from English territories, BMNH P15599–601, Eocene, Noil Tobé, Timor, Indonesia; and (b) BMNH P26357–9, Eocene, Bracklesham Beds, Sussex.

level. Some of the specimens concerned here have a specific epithet attached to them, but the present author does not know on what basis these identifications were made. Since the *Trichiurus* teeth do not possess any specific characters which the author knows of, he has decided to categorise them all as *Trichiurus* sp. The author does not recognise the presence of *Trichiurus gulincki* Casier, 1967 from the Middle Eocene of England as mentioned and figured by Kemp *et al*. (1979, 1990, pl. 17, fig. 24). Their figure does not provide any characteristics which permit the present author to make a specific identification. Casier (1967) described his *T. gulincki* from the Palaeocene of Belgium. The present author thinks it better not to assign a species identification to these Middle Eocene *Trichiurus*.

Incertae subfamiliae
Genus *Eutrichiurides* Casier, 1944a

Type species. *Trichiurides delheidi* Leriche, 1908, p. 380, lower Oligocene, Belgium.

Diagnosis. Can readily be identified as a member of a Trichiurinae + Gempylinae clade by the following combination of characters: elongate skull, premaxilla–maxilla complex, tightly bound and non-protractile (a synapomorphy of scombroids); one or two large, curved premaxilla fang(s) (Fig. 3c), possessing small barbs; serial teeth straight (Fig. 3d). At the generic level, *Eutrichiurides* can be diagnosed by their comparatively large semiconical, elongate, stout erect teeth, slightly barbed at their apices.

Comparisons. Fangs and serial teeth of trichiurins are less clearly differentiated morphologically, they have fewer fangs and/or their fangs are closer together. In *Eutrichiurides*, the serial teeth seem to be less compressed than in trichiurins.

Species composition. Seven species are known (Casier 1966). *Eutrichiurides winkleri* Casier, 1946, is known from England.

Remarks. Casier (1944a) stated that *Eutrichiurides* is a trichiurin. Large barbed fangs, such as those of *Eutrichiurides*, are predominantly found in trichiurins, but some large specimens of gempylins also possess similar fangs. Because of this and a lack of other definite trichiurid apomorphies, the phylogenetic position of *Eutrichirides* is uncertain. *Eutrichiurides* is not a gempylin because it does not possess retrorse serial teeth, as seen in gempylids. *Eutrichiurides*' serial teeth are straight.

Eutrichiurides winkleri Casier, 1946
(Fig. 3).

non 1876 *Trichiurides sagittidens* Win. Winkler, p. 31 pl. 2, fig. 23.
1891b *Lepidosteus* sp. Woodward, p. 107.
1905 *Lophius sagittidens* (Win.) Leriche, p. 172.
1931 *Trichiurides* cf. *sagittidens* Win. White, p. 87, pl. fig. 3a, b.
non 1944a *Eutrichiurides* cf. *delheidi* Leriche, 1908 Casier, p. 8, pl. 2, figs 8–12.
1946 *Eutrichiurides winkleri* Casier, p. 144, pl. 6 fig. 19a, b.
1966 *Eutrichiurides winkleri* Cas. Casier, p. 244, text figs 55 & 56, pl. 23, figs 2–5.
1979 *Trichiurides winkleri* Cas. Kemp *et al*., p. 101 (*nomen nudum*).
1984 *Eutrichiurides winkleri* Cas. Kemp, p. 162 (*nomen nudum*).
1985 *Eutrichiurides winkleri* Cas. Kemp, p. 43 (*nomen nudum*).
1990 *Eutrichiurides winkleri* Cas. Kemp *et al*., p. 12, pl. 17, fig. 23.
?1990 *Eutrichiurides* sp. Kemp *et al*., p. 12, pl. 17, fig. 26.
?2000 *Eutrichiurides* sp. Clouter *et al*., p. 68, fig. 1.

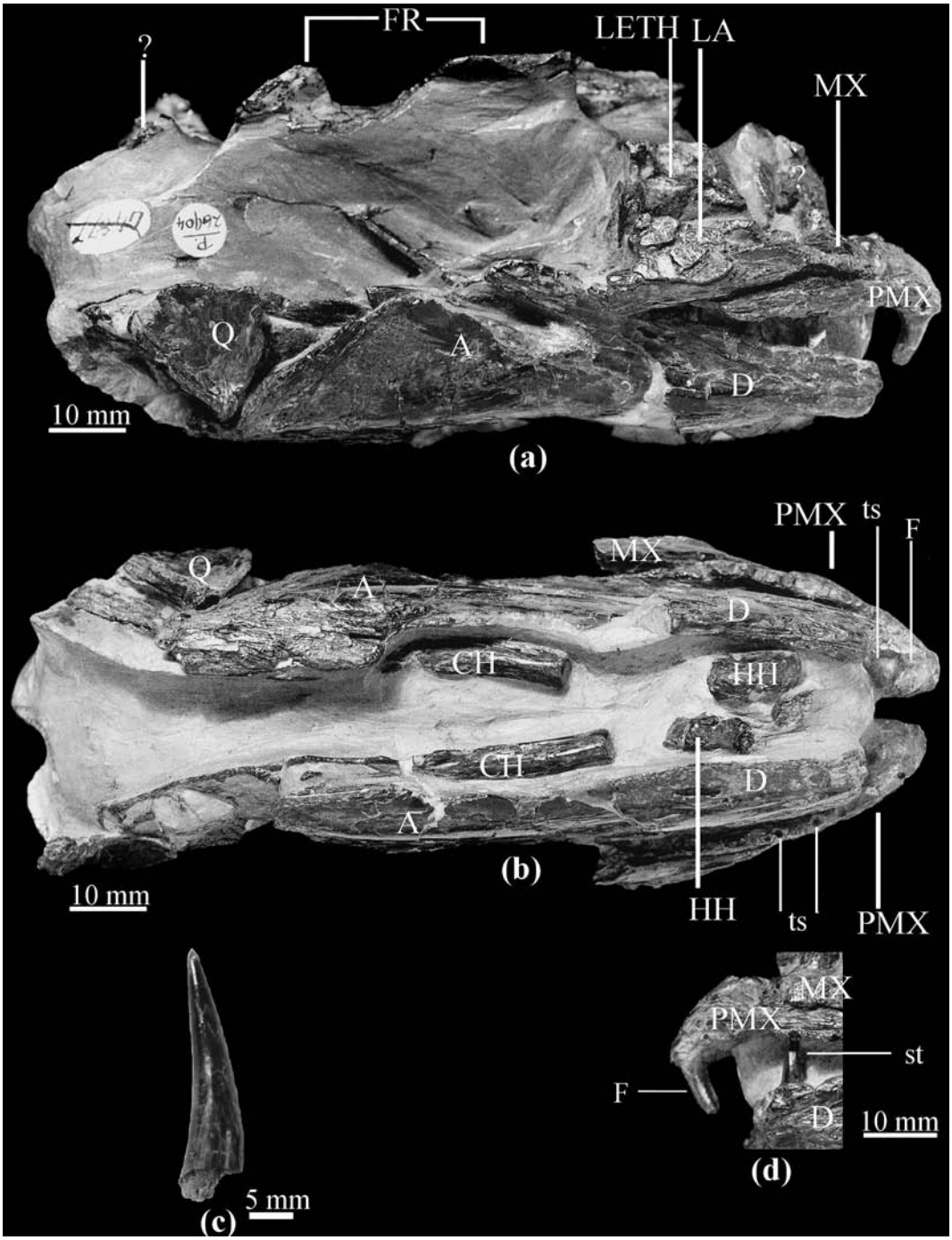

Figure 3 *Eutrichiurides winkleri* Eocene, London Clay, Sheppey, Kent: (a) BMNH P26904, right view; (b) BMNH P29604, ventral view; (c) fang, BMNH P65194; and (d) detail of BMNH P26904, left view, showing serial tooth.

Holotype. IRSNB 9219, lower Lutetian, Belgium (not seen).

Material. BMNH P26904 (Fig. 3a, b, d), P21321–9 (Warden Point) and P26097–107, Sheppey, Ypresian, London Clay; P49757, Abbey Wood, Thanetian (Blackheath Beds, Oldhaven Formation); P65194 S England, Middle Eocene (Upper Barton Beds, Bartonian).

Diagnosis. Seemingly one large premaxillary fang (possibly two) surrounded laterally, and followed, by smaller serial teeth with ovoid (semicircular) base.

Comparisons. Other *Eutrichiurides* with more circular tooth bases. The dentary of *E. winkleri* seems straight, while the dentary of *E. delheidi*, the type species, seemingly curves ventrad at symphysis.

Description. Casier (1966) described the species in detail. In that description, it is stated that *E. winkleri* has a solitary, isolated fang in the premaxilla. However, this large fang seems to have been followed immediately by one of the numerous small premaxilla teeth, and the fossil even suggests that the first fang preceded one other, most likely somewhat smaller (Fig. 3b). Furthermore, Casier (1966) stated that the dentary has a very blunt ending. The anterior tips of both dentaries are heavily damaged, so Casier's description is unfounded.

Remarks. Casier (1966) described differences between the dentaries of *E. winkleri* and *E. delheidi* in a confusing manner. He wrote that, in the Eocene species, the dentaries do not have to be as high as in the other one (Casier 1966, p. 245). The present author believes this puzzling description to mean that

the dentary of *E. delheidi* is deeper than that of *E. winkleri* (see also Leriche 1910, pl. 25, fig. 1). Casier (1966) also failed to mention that the dentary of *E. delheidi* seemingly curves ventrad at symphysis (Leriche 1910), whereas the dentary of *E. winkleri* seems straight (despite damage at symphysis).

Eutrichiurides winkleri and *E.* sp. are recorded from the Bracklesham Group in Hampshire (Kemp *et al.* 1979) and West Sussex (Dineley & Metcalf 1999).

Subfamily Gempylinae? Gill, 1862
Genus *Progempylus* Casier, 1966

Type species. *Progempylus edwardsi* Casier, 1966, p. 250 (by monotypy), Early Eocene, England.

Diagnosis. Dentary teeth curved strongly posteriorly, elongate slender skull, orbit almost circular.

Comparisons. Supraoccipital, parietals and epiotics considerably elevated (Fig. 4). In *Gempylus*, the skull roof is comparatively flat all over.

Species composition. Only the type species.

Remarks. Mainly because of the retrorse, slender and sharp teeth, the affinities of *Progempylus* seem to lie within the gempylins. In the provisional cladogram of scombroids presented in Monsch (2000b), however, its phylogenetic position remains uncertain.

Progempylus edwardsi Casier, 1966
(Fig. 4)

1901 Percidae? cf. *Planesox vorax* Woodward, p. 519.
1966 *Progempylus edwardsi*, Casier, p. 250, pl. 40, fig. 2.

Holotype. BMNH 32888, Sheppey, Early Eocene: Ypresian (London Clay).

Material. Holotype only.

Diagnosis. As for genus.

Description. See Casier (1966).

Remarks. Woodward (1901) described the holotype of this species as 'probably belonging to the Percidae', but being very close to *Planesox vorax* Owen, 1854. However, the specimen cannot possibly be assigned to *Planesox*. Although seemingly matching Owen's (1854) description, the skull of *Progempylus* is less complete than his original material, hence some of *Planesox*'s characters cannot be found in the holotype of *P. edwardsii*. The 'type' of Owen's (1854) description is missing. Thus, it cannot be verified whether the fossils in question are *Planesox vorax*. The present author follows here Casier's (1966) suggestion of adopting the generic name *Progempylus* for this specimen.

Gempylinae? *incertae sedis*.
(Fig. 5)

1966 cf. *Eutrichiurides* Casier, p. 249, text fig. 56, pl. 24, fig. 3.

Material. BMNH 41318, Sheppey, Early Eocene: Ypresian (London Clay) (Fig. 5).

Diagnosis. Cranium similar to that of a Scombrinae (*Scomber* Linnaeus, 1758; *Rastrelliger* Jordan & Starks, 1908, and probably *Scombrinus* Woodward, 1901; see below), but more elongated.

Comparisons. Pattern of cranial ridges similar to those in gempylins.

Description. Only briefly described in Casier (1966). More detailed description follows here. Elongated cranium, about 133 mm long. The most anterior parts of ethmoidal complex and vomer missing. Orbit somewhat ovoid, longer than deep, its dorsal ridge somewhat flattened. Frontals strongly constricted above middle of orbit. Suture between frontals slightly undulating. Frontal slightly depressed directly adjacent to suture. This depression broadens and deepens gradually posteriorly. Supratemporal groove short, extending just into frontal and anteriorly bordered by ridge, which slants posteriorly towards axis of cranium. Anterior borders of left and right supratemporal grooves meet above axis of cranium. Epiotic ridges almost straight, extending anteriorly as lateral borders of supratemporal groove. Temporal groove (next to supratemporal groove) also short. Postero-superior fossa (fossae for lateral muscles of the trunk-the term 'fossae postéro-supérieures' was first used by Casier 1966) well posterior of middle of orbit. This fossa is the anterior depression of the supratemporal groove (see also Allis 1903). Post-temporal region of skull relatively long: length of the part of supraoccipital crest distal to point where epiotics meet about 22% of total skull length.

Remarks. Casier (1966) was the first to describe this cranium and believed it could belong to genus *Eutrichiurides*, since it shows a combination of characters of Scombrinae and Trichiurinae (mainly *Lepidopus* Goüan, 1770). The above author believed that *Eutrichiurides winkleri* (described above) shows a mixture of trichiurin and scombrin characters, but the scombrin characters are not based on any clear apomorphies, but on superficial resemblances such as the shape of the articular. The cranium of *Eutrichiurides winkleri* is almost completely unknown. Considering all this, the present author feels that there is no basis to assign BMNH 41318 to *Eutrichiurides*. Furthermore, Casier (1966) contradicted himself when he stated that *Eutrichiurides* shows a combination of characters of both scombrins and trichiurids because he placed *Eutrichiurides* in the Trichiuridae. BMNH 41318 resembles a trichiurin cranium in that it resembles an elongate scombrid cranium with large orbits. However, most gempylin skulls can also be thus typified. The fossil does not possess any characters or apomorphies by which it could be assigned to either an existing trichiurin or gempylin genus. Cranium BMNH 41318 superfically resembles *Progempylus edwardsii*. However, *Progempylus* and this fossil do not share any unique character (combinations). The parietal, epiotics and supraoccipital are elevated much higher over the frontals in *Progempylus* than in this cranium (compare Figs 4c & 5c).

Family Scombridae Rafinesque-Schmaltz, 1815
Subfamily Scombrinae? Rafinesque-Schmaltz, 1815
Genus *Scombrinus* Woodward, 1901

Type species. *Scombrinus nuchalis* Woodward, 1901, p. 461, from the London Clay of England.

Diagnosis. Articulation between upper and lower jaw posterior to middle of orbit. Large circumorbital bones (a reversal – amongst scombroids, only Scombrinae and billfishes have fully developed circumorbital bones).

Comparisons. Resembles *Scomber* and *Rastrelliger*, but these are less coarsely scaled. *Scomber* has its frontals depressed anterior to the supraocciptal. This depression is absent in *Scombrinus*.

Species composition. Only the type species.

Remarks. Monsch (2000b) remarked on resemblances between the fossil genera *Scombrinus*, *Auxides* Jordan in Jordan & Gilbert, 1919, and *Scombrosarda* Danil'chenko, 1962, and lumped all three genera into *Scombrinus*. However, additional observations have revealed that the cranial morphology of *Scombrinus* differs from that of *Scombrosarda* and *Auxides*. The skull roof of the latter two is identical to that of *Scomber* (Bannikov 1985), i.e. an area of frontals anterior of the

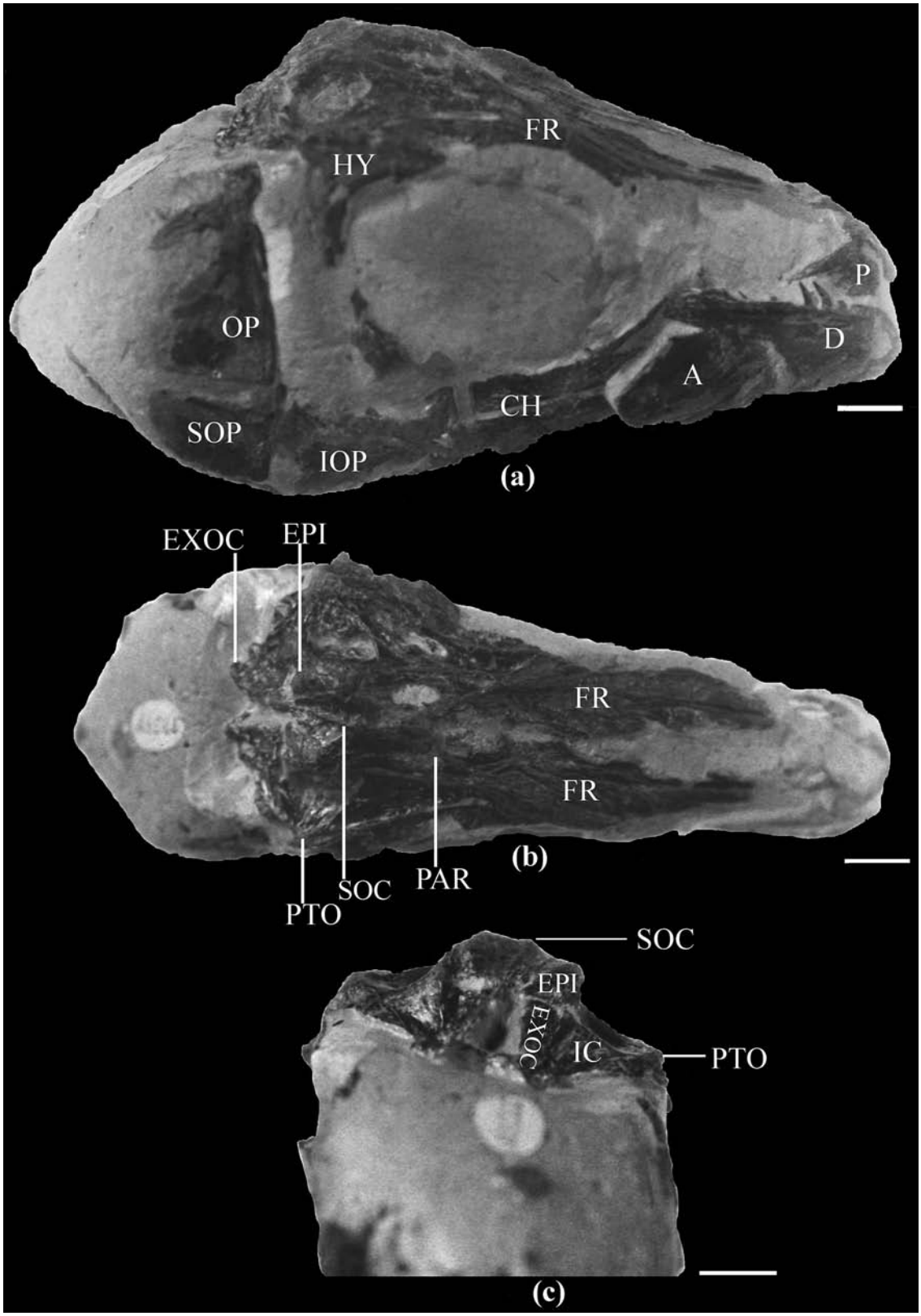

Figure 4 *Progempylus edwardsii*, BMNH 3288, Eocene, London Clay, Sheppey, Kent: (a) right view; (b) dorsal view; and (c) posterior view. Scale bars = 10 mm.

supraoccipital is depressed, while this is not the case in *Scombrinus*. The present author still does consider *Scombrosarda* and *Auxides* congeneric. The correct name for that genus, according to the Principle of Priority, is *Auxides*. It seems likely that *Scombrinus* is a primitive sister taxon of *Scomber* and *Rastrelliger*, even though a preliminary cladistic analysis (Monsch 2000b) leaves its phylogenetic position unresolved.

Woodward (1901, p. 461) circumscribed *Scombrinus* as 'essentially identical with *Scomber*, but with larger teeth'. However, as mentioned above, there are differences in skull morphology and squamation. Woodward's (1901) assertion that *Scombrinus* has larger teeth than *Scomber* is the result of misidentifications. The original hypodygm of *Scombrinus nuchalis* is heterogeneous. The holotype is a specimen with a few minute teeth, while specimens with large teeth belong to

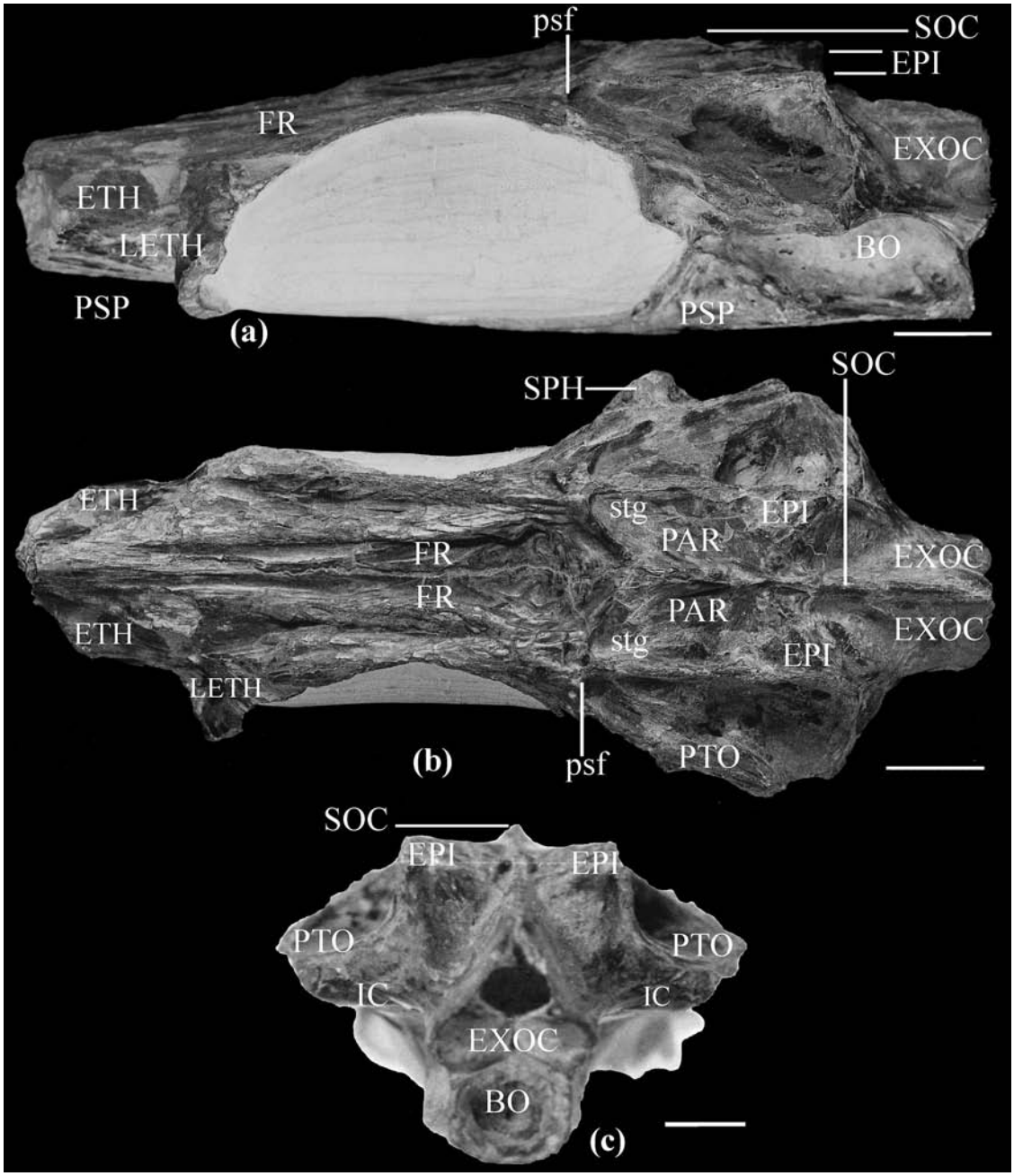

Figure 5 BMNH 41318 (a–c), possibly a gempylin, Eocene, London Clay, Sheppey, Kent: (a) left view; (b) dorsal view; and (c) posterior view. Scale bars = 10 mm.

other species (see also below). *Scombrinus macropomus* (Agassiz, 1844) is here described in a new genus.

Scombrinus nuchalis Woodward, 1901
(Fig. 6)

1845 *Scombrinus nuchalis* Agassiz, p. 308 (*nomen nudum*).
1901 *Scombrinus nuchalis* Woodward, p. 461.
non 1901 *Scombrinus nuchalis* Woodward, p. 462 (*partim*).
1966 *Scombrinus nuchalis* Wood. Casier, p. 277, text fig. 73, pl. 41.
non 1966 *Scombrinus nuchalis* Wood. Casier, p. 277 (*partim*).
non 2000 *Scombrinus nuchalis* Wood. Clouter *et al*., p. 59, fig. 'Top view' (*partim*).
2000 *Scombrinus nuchalis* Wood. Clouter *et al*., p. 59, fig. 'Side view' (*partim*).

Holotype. BMNH P4148, Sheppey, England, Ypresian (London Clay).

Material. The holotype, and two paratypes: BMNH 38919 and 43117, Sheppey, England, Ypresian (London Clay).

Diagnosis. As for genus.

Description and remarks. Descriptions are found in Woodward (1901) and Casier (1966). The present author regards the 'foramen' that Clouter *et al*. (2000) identified near the supraoccipital as an artefact of fossilisation. The hypodygm on which the present author bases his concept of the morphology of *S. nuchalis* differs from the ones recognised by previous authors. Woodward (1901) mentioned that the holotype of *S. nuchalis* contains no teeth, but the present author did observe a few minute teeth which are similar to those in *Scomber* (Fig. 6a). The paratypes BMNH P9455, P9456a and 40204 are described below under *Eocoelopoma curvatum* Woodward, 1901. Besides these and material included here, other paratypes have not been studied. These include BMNH 24614, which is amongst the specimens that Casier (1966) could not assign to this species with certainty. Other paratypes

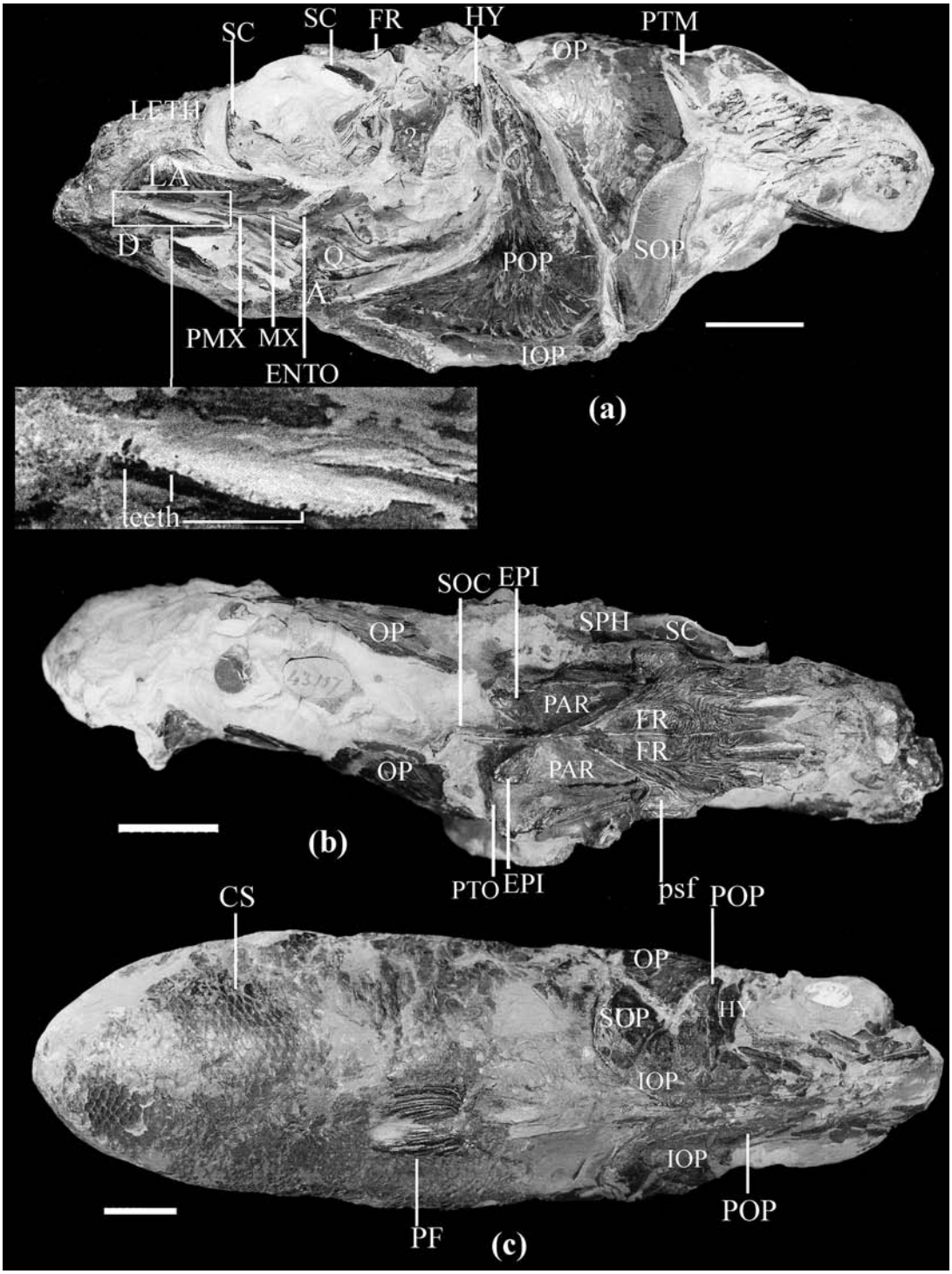

Figure 6 *Scombrinus nuchalis* Eocene, London Clay, Sheppey, Kent: (a) lateral view of holotype, BMNH P4148; (b) dorsal view of BMNH 43117; and (c) ventral view of BMNH 38919. Scale bars = 10 mm.

which Casier (1966) did include in his description of *S. nuchalis* are BMNH P2689–30 (previously P356a), P7524, P1742 and P4147a–c.

Subfamily Scomberomorinae Starks, 1910
Genus *Scomberomorus* Lacepède, 1802

Type species. *Scomber regalis* Bloch, 1793, p. 38, from Martinique (Recent).

Diagnosis. Caudal complex: fusion of urostyle and hypurals 1–5 (hypural 5 partially). Vertebrae 41–56 in number, anterior margin of vomer spatulate and strongly protruding, anterior margin of ethmoid emarginated, body covered by moderately sized scales.

Species composition. Eighteen Recent species are known, found in tropical and subtropical coastal seas (Collette & Russo, 1984). The present author recognises a total of 12 fossil species (Monsch 2000b), found from the Palaeocene to the Miocene, in sediments from W Europe, Congo-Kinshasa, SW Russia and Turkmenistan. Bannikov (1985) listed all fossil *Scomberomorus* known to that date except '*Scomberomorus tenuis*' (Agassiz, 1835a), which the present author does not recognise as a member of this genus (manuscript in preparation). The author assumes Bannikov's (1985) list of fossil

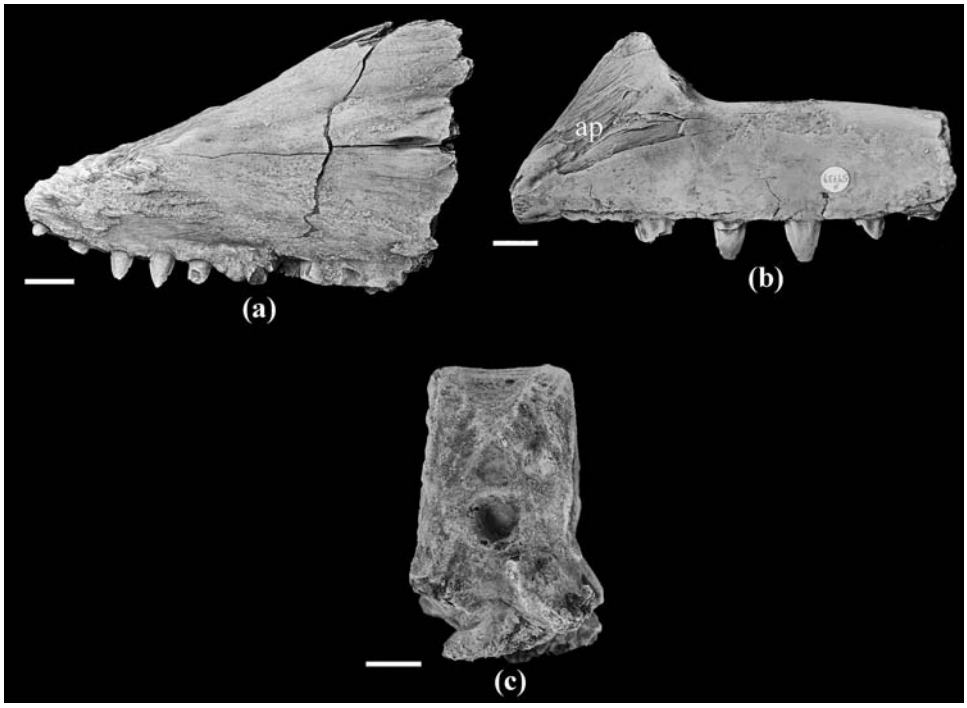

Figure 7 *Scomberomorus* sp. Eocene, Barton Clay, Hampshire: (a) part of BMNH P53 (holotype of '*C. bartonense*'): ascending process of premaxilla; (b) ascending process and part of posterior shank, BMNH P3958; and (c) lateral view of centrum of BMNH P53. Scale bars = 10 mm.

Scomberomorus to be valid save for the following points. He questions the validity of both *Scomberomorus bartonensis* (Woodward, 1901) and *Scomberomorus excelsus* (Woodward, 1901), does not recognise '*Scomberomorus speciosus*' (Agassiz, 1835a) as a member of this genus (see also Monsch 2000b), and reinstates the validity of *Scomberodon dumonti* Van Beneden, 1871 (see also, the description of gen et sp. indet. under subfamily Acanthocybiinae below) rather than considering it part of *Scomberomorus*. Supposed *S. excelsus*/*S. bartonensis* are described below and a few specimens of *Scomberomorus* whose specific identity could not be verified are mentioned. The present author is unable to confirm the validity of Kemp *et al.*'s (1990, pl. 17) '*Cybium stormsi*' Leriche, 1905.

Scomberomorus sp.
(Fig. 7)

1901 *Cybium excelsum* Woodward, p. 467, fig. 15.
1901 *Cybium bartonense* Woodward, p. 467, fig. 16.
?1976 *Cybium* spp. Kemp, p. 41 (*nomen nudum*).
1984 *Cybium excelsum* Wood. Kemp, p. 162 (*nomen nudum*)
1985 *Scomberomorus bartonensis* (Wood.) Bannikov, p. 34 (*nomen nudum*).
1985 *Scomberomorus excelsus* (Wood.) Bannikov, p. 34 (*nomen nudum*).
1985 *Cybium excelsum* Wood. Kemp, p. 43 (*nomen nudum*).
1990 *Cybium excelsum* Wood., Kemp *et al.*, p. 11, pl. 16, fig. 11.

Material. BMNH 1193, P14029 (some material of this number mentioned under *Acanthocybium* and Acanthocybiinae gen. et sp. indet.), Barton; P53, (holotype of *Cybium bartonense*, Fig. 7a, c), near Christchurch, Hampshire; P1528 (holotype of *Cybium excelsum*), P3958 (Fig. 7b), Barton Cliff, Hampshire. All fossils of Bartonian age (Barton Clay).

Diagnosis. Ascending process of premaxilla makes angle of approximately 40° with posterior shank.

Description. Short descriptions of both '*Cybium bartonense*' and '*Cybium excelsum*' were given by Woodward (1901). Some supplemental data follow here. Anterior ascending process of premaxilla makes an angle of approximately 40° with posterior shank. Vertebrae deeper than long, and in cross-section wider than deep, with deep lateral fossae.

Remarks. Woodward (1901) described the material discussed here under two different names: *Cybium bartonense* and *Cybium excelsum*. However, the present author considers both conspecific. The angle between the ascending process and shank of the premaxillae does not differ significantly between '*C. bartonense*' and '*C. excelsum*'. According to Woodward (1901), the most anterior premaxillary teeth of *C. excelsum* scarcely differ in size from those in the dentary, while the anterior premaxillary teeth in *C. bartonense* are clearly smaller than those of the dentary. However, the present author failed to see a significant difference between the two supposed species in this respect. The most anterior teeth in the premaxilla of *Scomberomorus* always seem smaller than the subsequent ones and smaller than the anterior mandibular teeth. This seems to be the case in both '*C. excelsum*' and '*C. bartonense*'. The author failed to discover differences in other characters, such as those of the dentition or the morphology of the dentary, which might account for specific differences. Woodward (1901) considered these '*Cybium*' as new species, based on comparison with other fossil species. However, he made no reference to Recent *Scomberomorus*. Collette & Russo (1984) measured the angle between the ascending process and the posterior shank of premaxillae in six of the 18 Recent species of *Scomberomorus*. Four of those [*Scomberomorus cavalla* (Cuvier, 1829), *Scomberomorus commerson* (Lacepède, 1800), *Scomberomorus maculatus* (Mitchill, 1815) and *Scomberomorus regalis* (Bloch, 1793)] have premaxillae with angles of 41–54° between the ascending process and the posterior shank. The fossils described as *C. bartonense* and *C. excelsum* fall into that category. On the basis of the fragmentary material, it is difficult to estimate the size that a complete specimen of these fossils would have had. Of

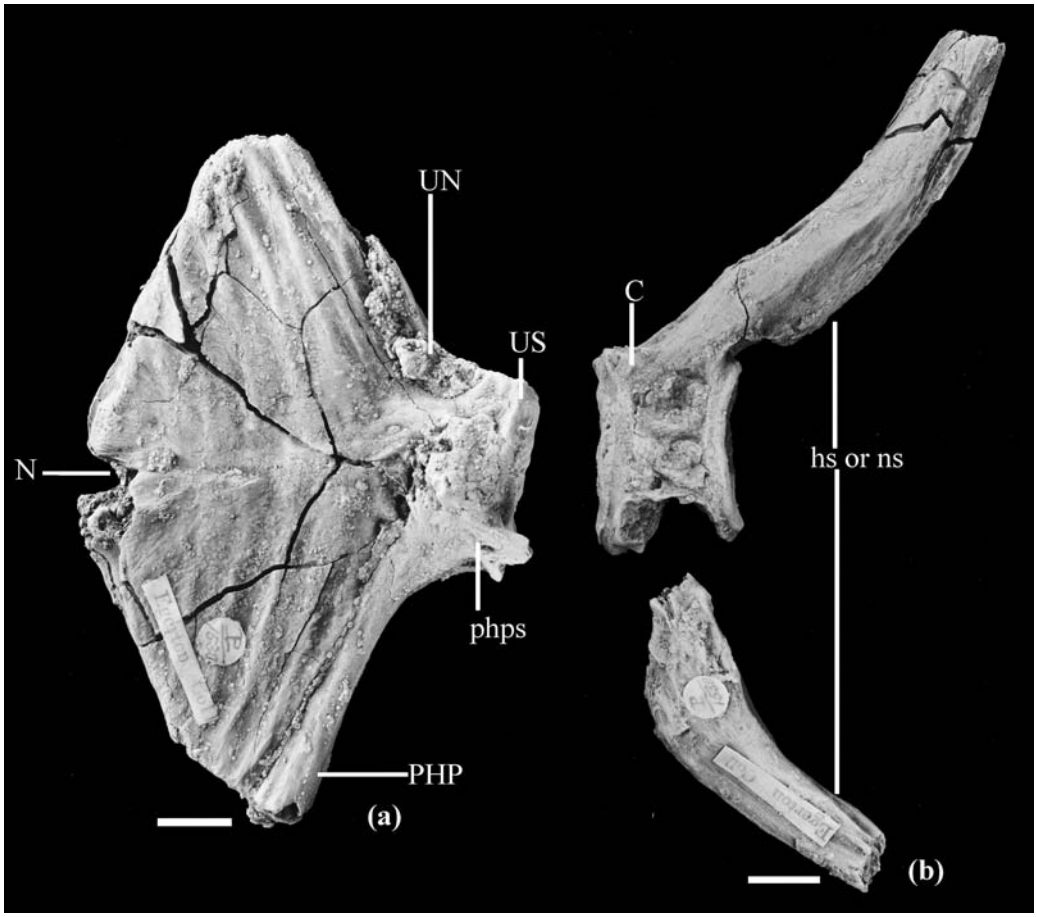

Figure 8 Scomberomorinae *incertae sedis*, BMNH P1530 Eocene, Isle of Wight: (a) right view of hypural plate; and (b) left view of preural vertebra. Scale bars = 10mm.

the Recent species of the '41–54° group', only two species could approach the possible size of the fossils. The largest specimen of *S. cavalla* that the present author knows of (USNM 110012) has a FL of 920 mm and of *S. commerson* (USNM 269674) of 1155 mm. However, he feels that, because of many uncertainties, the fossil specimens cannot be assigned to either an existing Recent or fossil species (if they are referable to Recent species, that would imply a considerable taxic longevity). The vertebrae do not possess characters which would justify a species assignment. The present author has included here all the specimens which can be referred to *Scomberomorus* from England. More fossils are needed in order to have definite taxonomic characters to work with. Another large species is *Scomberomorus sinensis* (Lacepède, 1800) (USNM 269706 has a FL of 1850 mm). If these specimens do belong to a species in their own right, their correct name is *Scomberomorus excelsus*. Both *Cybium excelsum* and *Cybium bartonense* appear on page 476 in Woodward (1901), with *C. excelsum* mentioned earlier on the page.

'*Scomberomorus* sp.' has been recorded before from Bognor Regis, West Sussex (see Dineley & Metcalf 1999) and teeth of *Cybium* sp. from London Clay deposits of Hampshire (Kemp & King 1995).

Scomberomorinae *incertae sedis* sp.
(Fig. 8)

Material. BMNH P1530 (Fig. 8), Isle of Wight, Lutetian (Bracklesham Beds).

Diagnosis. Hypurals 1–4 and urostyle fused into plate.

Description. Hypural plates and vertebral remains. Hypurals 1–4 and urostyle fused. Position of hypural 5 uncertain. Caudal notch present. Plate diamond-shaped, sides about equal in length and distal margins slightly swollen. Superficial grooves indicate that plate was (almost) completely covered by anteriorly extended bases of caudal fin lepidotrichia. Urostyle wider than deep. Uroneural and parhypural autogenous. Vertebrae short and robust, with stout neural and haemal spines. Much detail of centra obscured by matrix.

Remarks. The fusion of hypurals into one solid plate is a synapomorphy of Scomberomorinae and scombrids above them (Sardini, Thunnini, Acanthocybiinae and billfish). However, the caudal skeleton is more derived in those scombrids because their uroneural and parhypural may be fused into the hypural plate and the caudal notch may disappear. Within the Scomberomorinae, BMNH P1530 most resembles *Scomberomorus*, whose vertebrae are also short, as opposed to *Grammatorcynus* Gill, 1862, which has vertebrae which are longer than deep. However, it is not clear to the present author if within Scomberomorinae long vertebrae are plesiomorphous or apomorphous, hence he cannot, for the moment, determine a more exact systematic status of these fossils. Moreover, in *Scomberomorus*, the hypural plate tends to be more triangular rather than diamond-shaped.

Subfamily Sardinae Starks, 1910
Tribe Sardini Starks, 1910
Genus *Gymnosarda* Gill, 1862

Type species. *Thynnus unicolor* Rüppell, 1838, p. 40, from Jeddah, Red Sea (Recent).

Diagnosis. A genus of Sardini characterised by a parhypural that is fused to the hypural plate and a tendency of the caudal hypural notch to close.

Species composition. There is only one Recent species known: *G. unicolor*. Below, an unidentified *Gymnosarda* from the London Clay is mentioned, as well as *Gymnosarda prisca* Monsch, 2000a. The systematic palaeontology of *G. prisca* is taken from Monsch (2000a), with only slight modifications. *Gymnosarda* fossils are found in the Eocene and Oligocene of Europe (Bannikov 1985).

Gymnosarda prisca Monsch, 2000a
(Fig. 9)

1982 *Scomberomorus saevus* Bannikov, p. 135 (*partim*).
1985 *Scomberomorus saevus* Bann.; Bannikov, p. 37.
2000a *Gymnosarda prisca* Monsch, p. 75, figs 1A, B & 2A.

Holotype. BMNH P6485, Sheppey, Early Eocene: Ypresian (London Clay) (Fig. 9a).

Material. Holotype only.

Diagnosis. Hypural plate shorter than in the Recent species *G. unicolor*.

Comparisons. In *G. unicolor*, the caudal notch has almost closed (Fig. 9c), an apomorphic condition, while a large notch is still present in *G. prisca*.

Description. A description is given by Monsch (2000a) in which a specimen from Kazakhstan (PIN 1878–4) is included. Monsch (2000a) mistakenly reported that the specimen was from Turkmenistan.

Remarks. It seems unusual that fossils found so far apart should belong to the same species. However, the present author found that the specimens are identical in all respects (Monsch 2000a).

The only Recent species of *Gymnosarda* is characterised by only a vestigial caudal notch in its hypural plate. All other Sardini and all Thunnini are devoid of a caudal notch. This suggests that more primitive bonitos may once have had a large caudal notch. This notch is a primitive feature, which thus suggests that the ancestor of the bonitos came from within the Scomberomorinae. This is confirmed by *G. prisca*. This fossil *Gymnosarda* has a large notch. This discovery brings new insights into the evolution of the tail region of Sardinae. Monsch (2000a) hypothesised that the Sardinae evolved from the Scomberomorinae, which have a large caudal notch, and that this notch has the tendency to close within the Sardinae (only seen within *Gymnosarda*).

Although based on a hypural plate only, the present author does think that phylogenetic hypotheses can be made using *G. prisca*. Hypural plates provide strong characters, which are well indicative of genera (see Uyeno & Fuji 1975) .

Gymnosarda sp.
(Fig. 10)

Material. BMNH P1773b (Fig. 10), Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Hypurals 1–4 and parhypural fused, cross-section urostyle deeper than wide.

Description. Specific identity of specimen uncertain. BMNH P1773b has a clearly more acute outline than the hypural plates of *G. prisca* and the centrum of its hypural plate also has a more laterally compressed diameter. It is not clear whether there has been a caudal notch through damage to the specimen. If it was present, it must have been small. Height of plate uncertain because of damage to the specimen. Height of dorsal half 38 mm.

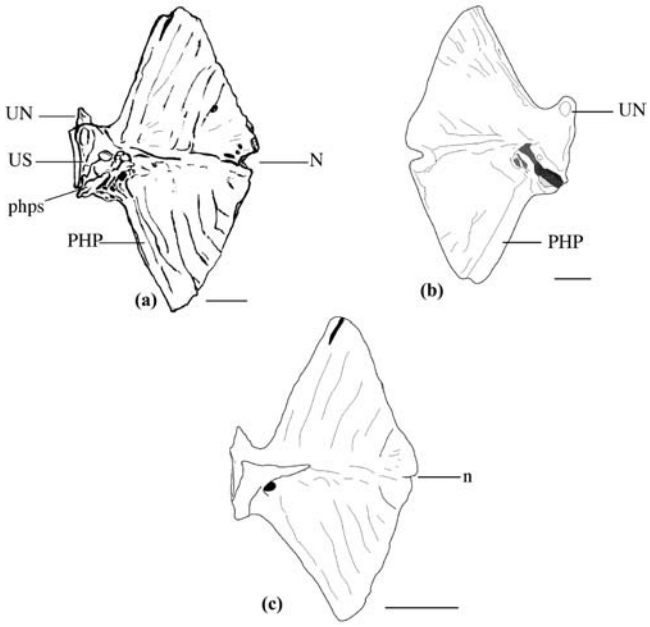

Figure 9 (In part taken from Monsch 2000a.) Caudal skeleton of *Gymnosarda prisca* compared to *Gymnosarda unicolor*: (a) left view of holotype of *Gymnosarda prisca*, BMNH P6485 Eocene, London Clay, Sheppey, Kent; (b) right view of *G. prisca*, PIN 1878–4, Eocene, Shorym Svita, Kazakhstan; and (c) left view of *G. unicolor*, after Collette & Russo (1984) and BMNH 1934.3.31. Scale bars = 10 mm.

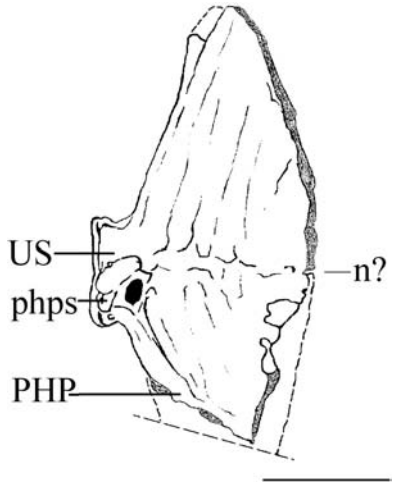

Figure 10 *Gymnosarda* sp., BMNH P1773b, Eocene, London Clay, Sheppey, Kent. Scale bar = 20 mm.

cf. *Gymnosarda* sp.
(Fig. 11)

Material. One damaged dentary, BMNH P4546 (Fig. 11), Sheppey, Early Eocene: Ypresian (London Clay); hypural plate BMNH 40278(a), Brooks, Hampshire, Late Palaeocene–Early Eocene: Thanetian–Ypresian (Reading and Woolwich Formations).

Diagnosis. Deep dentary with symphysial chin-like process, large, striated teeth with ovoid base. Hypural plate with hypurals 1–4 and parhypural fused and urostyle cross-section deeper than wide.

Description. Dentary: with large symphysial chin-like process. Deep, as dentary of *Sarda sarda* (Bloch, 1793). Dentigerous part of dentary seemingly almost complete. Dorsal and ventral branch separating at the tenth tooth. Teeth conical in lateral outline, but with ovoid base, straight or slightly curved inwards, slightly striated. All teeth damaged, but probably reached sizes of 6–6·5 mm, irregularly spaced. Distance between symphysis of dentary and fourteenth tooth, 108 mm.

Figure 11 cf. *Gymnosarda* sp., BMNH P4546, Eocene, London Clay, Sheppey, Kent. Scale bar = 10 mm.

Hypural plate: much damaged specimen. Hypurals 1–4 and urostyle fused. Parhypural fused to plate. Hypural 5 and uroneural not preserved.

Remarks. Scombroid taxa possessing a large symphysial chin-like process are Sardini (with the best developed process in *Sarda* Cuvier, 1829), *Eocoelopoma* Woodward, 1901, *Scomberomorus* and *Sphyraenodus* Agassiz, 1844. BMNH P4546 was catalogued as *Sphyraenodus*. However, the dentary of BMNH P4546 is clearly deeper than in *Scomberomorus* and *Sphyraenodus*. *Scomberomorus* teeth are laterally somewhat compressed, while the teeth of this specimen seem fully conical. BMNH P4546 perfectly fits the diagnosis of Sardini, especially *Sarda sarda* or *Gymnosarda* because of the large 'chin' and the deep dentary. The largest *Sarda* known today is *Sarda chiliensis chiliensis* (Cuvier in Cuvier & Valenciennes, 1832): $\leq$672 mm FL (Collette & Chao 1975). The length of the dentigerous part of BMNH P4546 (measured up to the fourteenth tooth), being almost complete, can be considered a good estimate of snout length. The length of the snout (without flesh) of *Sarda sarda* is about 8% of the FL (Collette & Chao 1975). Applying that ratio to the fossil dentary, the FL of the complete individual is estimated at about 1350 mm. Fossil *Sarda* of the former USSR are at most 800 mm long (Bannikov 1985). *Gymnosarda* is the largest Sardini known to date. A specimen of *G. uniclor* (BMNH 1934.3.31) has a FL of 860 mm, but the record length reported is 2060 mm (Collette & Nauen 1983). The present author feels that it is not possible to definitely state that BMNH P4546 is an (undescribed?) *Gymnosarda* (or possibly a new, large species of *Sarda*). Estimated lengths of complete individuals based on the size of one bony element cannot be used as a definite morphometric characteristic. Monsch (2000a) described a new species *G. prisca* based on remains from sediments in Kazakhstan and the London Clay. It is possible that the dentary described here and the hypural plate of *G. prisca* belong together. However, it is not known if both the jaw bone and the English specimen of *G. prisca* were found together or in association. Thus, at this point, BMNH P4546 cannot be identified more exactly than 'possibly *Gymnosarda*'.

Because of the fragmentary nature of the hypural plate, it cannot be said with certainty whether it belongs to a *Gymnosarda*, even though the preserved characters agree with the diagnosis of that genus.

Sardini *incertae sedis* 1
(Fig. 12)

Material. BMNH P9459, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Supratemporal groove extending to anterior apex of frontal, orbit low (expressed here by shallow basisphenoid) and dorsally not much arched.

Description. Skull wide (Fig. 12a): 197 mm long and widest preserved width 145 mm (maximum width not known through damage). Skull shallow: dorsal margin of orbit, skull roof and ventral outline of parasphenoid poorly arched (Fig. 12b). Basisphenoid broken, but presumably shallow: pedicel that connects alisphenoid to parasphenoid estimated at approximately 9 mm deep. In a specimen of *Auxis* Cuvier, 1829 (KAM 3) that has a cranium of 52 mm long, for comparison, this pedicel is 7 mm deep (*Auxis* is a Recent thunnin, and therefore, belongs to a tribe which can be considered derived compared to Sardini). Absence or presence of pineal window not clear from specimen, would have had a small slit at most. Pineal region around symphysis of frontals swollen. It can be inferred that the supratemporal groove was long and reached anteriorly up to the rostral apex of the frontal. Even though no lateral upturned ridges of this groove are visible (presumably damaged), there is no sharp anterior ridge that would mark the anterior margin of the groove (Fig. 12a). Postero-superior fossa clearly posterior of middle of orbit. Dorsal margin of orbit very poorly arched, almost straight. Frontoparietal window absent. Ethmoid damaged, but has tapered rostrad-pointing anterior margin. Pterotic and posteriormost portion of skull damaged. Anterior head of vomer bifurcated into two, short and blunt protuberances which are anteriorly widely spaced (Fig. 12c). Vomerine tooth plate not found, but presumed to have been present. Parasphenoid straight in lateral view. Because of the relative flatness of skull roof, straightness of dorsal margin of orbit, and parasphenoid, one can say that orbit was relatively shallow.

Remarks. Resembles a Sardini at first sight, based on the wideness of the skull and the length of the supratemporal grooves. However, these features could also be used to identify the specimen as a primitive tuna such as *Auxis*. However, the flatness of the dorsal margin of the orbit and the shallowness of the orbit as a whole are apomorphies which define Sardini.

Tuna orbits are much arched and deep. The specimen resembles most a *Gymnosarda*, considering the size and width of the skull. *G. unicolor* is the largest living sardin (see above). However, typical apomorphies of *Gymnosarda*, such as two tooth patches on the tongue and a fused parhypural, are not preserved in this fossil. Besides, the orbit of *Gymnosarda* is more arched than in this specimen.

This specimen was originally labelled as *Eocoelopoma colei* Woodward, 1901. However, this is no *Eocoelopoma*. In that genus, the ethmoid does not protrude beyond the frontals, the supratemporal groove is short, the postero-superior fossa are closer to the middle of the orbit and the morphology of the skull roof markedly differs from that in Sardini.

Sardini *incertae sedis* 2.

Material. BMNH P45150, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Wide skull, antero-lateral margins of frontals decorated with curved lines.

Comparison. Teeth comparatively large (small in Thunnini)

Description. Moderately large skull, 135 mm long, maximum width 90 mm. Antero-lateral margins of frontals rounded and decorated with fairly widely spaced curved lines. Anterior head of vomer short with slightly emarginated anterior margin, pronounced lateral articular processes (for articulation with maxilla and premaxilla), moderately narrow and ovoid tooth plate on anterior head, bearing minute teeth.

Remarks. Previously identified as *Eocoelopoma colei*. As in *Eocoelopoma* (see below), the antero-lateral margins of the frontals of this specimen are rounded and decorated with lines. However, some Thunnini or Sardini also possess frontals which can be thus described. The actual apomorphy that would identify this specimen as an *Eocoelopoma*, the anteriorly placed postero-superior fossa, are buried in the matrix. The size of the specimen is much larger than *E. colei* (the skulls of that species which the present author examined are at most 80 mm long). Furthermore, the vomerine tooth plate of *Eocoelopoma* normally protrudes, as the author has seen in *Eocoelopoma gigas* Casier, 1966 and *E. curvatum* Woodward, 1901 (see below). Judging by the general appearance and the comparatively large size of its teeth, the specimen is identified as a Sardini (Thunnini possess minute teeth). Based on skull shape and vomer, this specimen most resembles an *Orcynopsis* Gill, 1862. However, this identification cannot be certified for lack of definite characters. Because the specimen is of poor quality and could not be well identified it is not figured here.

Tribe Thunnini Starks, 1910
Genus *Thunnus* South, 1845

Type species. *Scomber thynnus* Linnaeus, 1758, p. 297, Recent.

Diagnosis. Frontoparietal fenestrae and pineal window present, first vertebra fused to basioccipital. FL up to 2700 mm.

Comparisons. Differs from other Thunnini by having shorter pterotic spines, denser scale covering and a less crescent-shaped preoperculum.

Species composition. Seven Recent species are normally recognised. Collette (1999) and Collette *et al*. (2001) recognised *Thunnus thynnus orientalis* (Temminck & Schlegel, 1844) as a species in its own right. This would make the number of Recent *Thunnus* species eight. Seven fossil species are known from across Europe and the former USSR, from the Eocene to the Miocene (Bannikov 1985).

Thunnus sp.
(Fig. 13)

non 1901 *Thynnus thynnus* (Linn.); Woodward, p. 455 (*partim*).
non 1901 *Thynnus scaldisi* Storms, 1889; Woodward, p. 455.

Material. BMNH 41989, Lea Valley, near Tottenham, Middle Pleistocene (Pebble Gravel); P5583, Suffolk, Piacenzian (Red Crag); P8737, E Runton, Norfolk, Early Pleistocene (Lower Forest Bed Formation); P9453, Aldborough, Suffolk, Piacenzian (Coralline Crag).

Diagnosis. Large vertebrae (35–42 mm long).

Description. The material is comprised of isolated centra (BMNH P5583, P8737, P9453) and three associated vertebrae (BMNH 41989, Fig. 13). BMNH P5583, a centrum from the caudal part of the vertebral column, is 35 mm long, 31 mm deep and 39 mm wide (including lateral keel). BMNH P9453 is a centrum that is 42 mm long, 36 mm deep and 45 mm wide (including keel). BMNH P8737 has similar dimensions, but is wider (50 mm), including lateral keel. BMNH P41989 consists of three articulated vertebrae, which originate from the caudalmost part of the vertebral column. The more caudally the centrum is situated in the vertebral column, the shorter it is. However, these centra are not as abruptly shortened as in the preural centra 2–4 of *Thunnus*. Centra deeply indented immediately dorsal and ventral of lateral midline.

Remarks. Woodward (1901) described BMNH 41989 and P8737 as *Thunnus thynnus* (Recent) and BMNH P9453 as '*Thynnus scaldisi*' (Pliocene, correct name *T. scaldisensis*) (Storms, 1889). The present author is confident, based on their dimensions, morphology and size, that these specimens do belong to *Thunnus*. Centra of Sardini are shorter and their lateral caudal keels less well developed. Individuals of other thunnin genera are considerably smaller than those of *Thunnus*. Storms (1889) described vertebrae which differ slightly from *Thunnus thynnus*. Initially, Storms seemed to consider the differences with *T. thynnus* insufficient to create a new species, after which he contradicted himself by doing exactly that: he established *Thynnus scaldisi* for these specimens because of their 'Tertiary' age. Judging from the size of Storms' specimens, complete individuals might have been as large as *T. thynnus* (whose maximum length is recorded at 3 m; see Collette & Nauen 1983). There are no synapomorphies which distinguish *T. scaldisensis* from any other *Thunnus*. The present author believes that, without other material than that available at present, *T. scaldisensis* is an invalid taxon. According to Woodward, *T. scaldisensis* is somewhat smaller than *T. thynnus*, but these specimens contradict this assertion (see also the dimensions in the description above).

Thunnini *incertae sedis* sp.

non 1901 cf. *Eothynnus salmoneus* Wood. 1901; Woodward, p. 458.

Material. BMNH P4300, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Preural vertebra 4 more than 1·5 times longer than preural vertebra 3.

Description. Fourth and third preural vertebrae. One long centrum (fourth), and one radically shortened (third). Fourth preural centrum 45 mm long, third preural centrum 12 mm. Vertebrae do not present many details. Cross-section of third preural: horizontal axis slightly longer than vertical axis. This cannot be measured in fourth preural. Bony median caudal keel preserved.

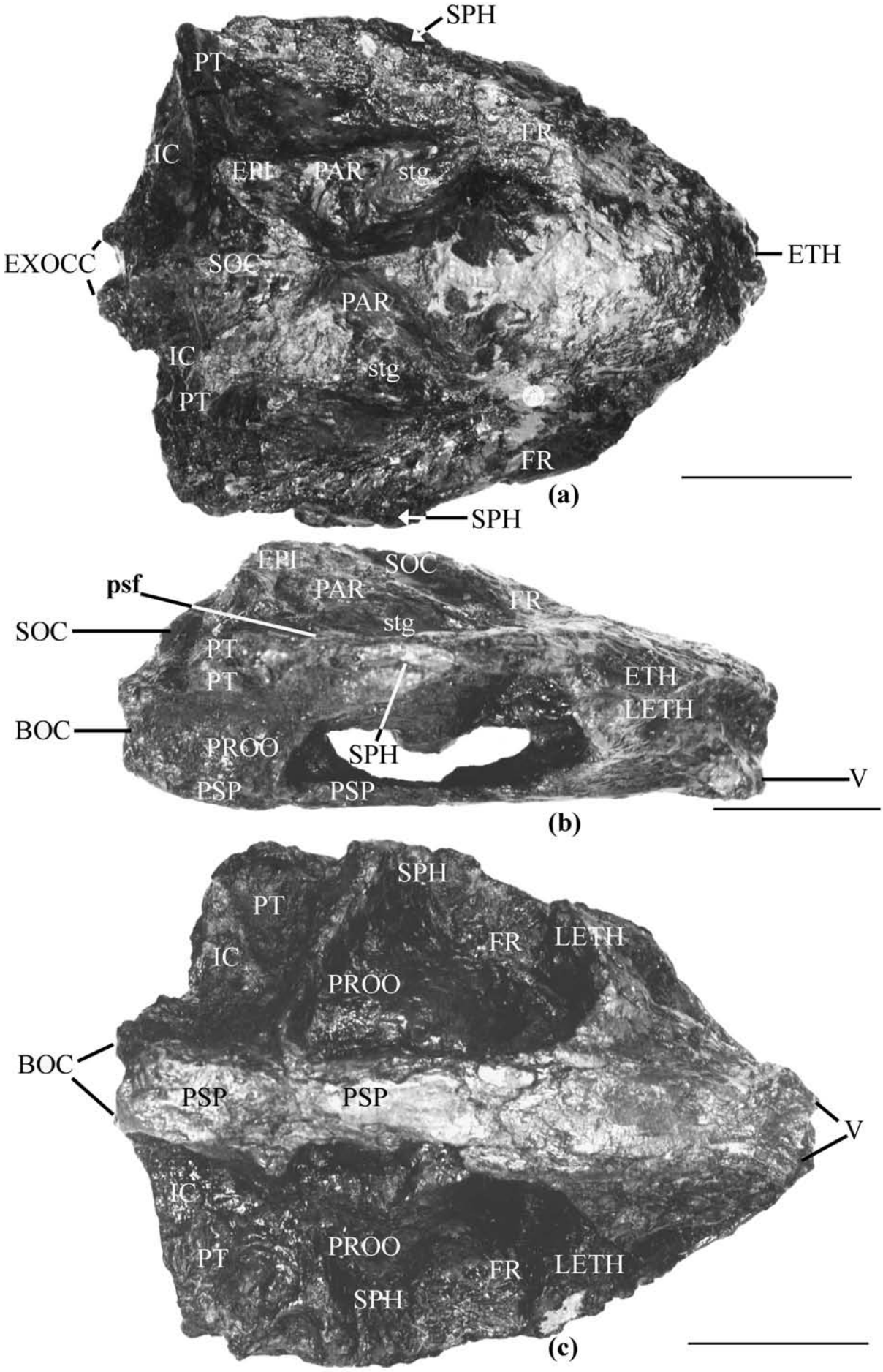

Figure 12 Sardini *incertae sedis* 1, skull, BMNH P9459, Eocene, London Clay, Sheppey, Kent: (a) dorsal view; (b) lateral view; and (c) ventral view. Scale bars = 50 mm.

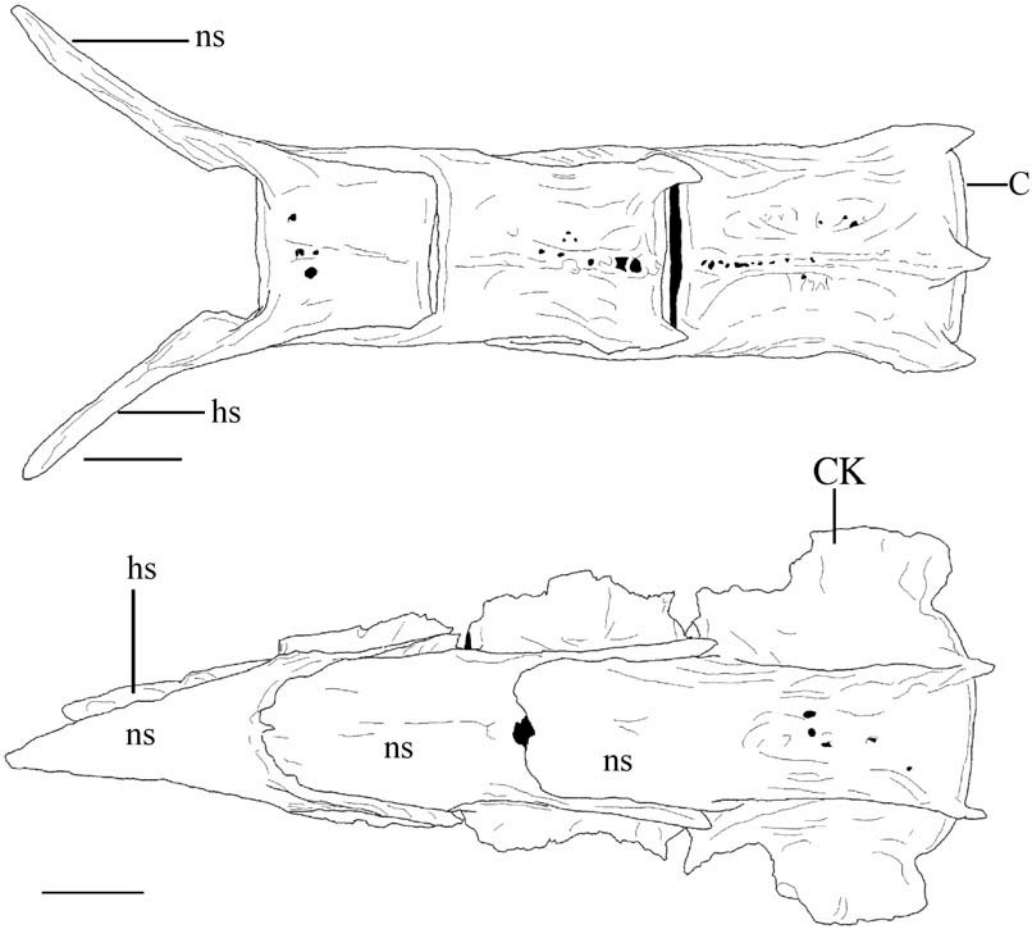

Figure 13 *Thunnus* sp., BMNH 41989, Pleistocene, Pebble Gravel, Lea Valley near Tottenham, vertebrae. Scale bars = 20 mm.

Remarks. Woodward (1901) described this specimen as being probably *Eothynnus* (a fossil carangid) without mentioning on which apomorphies this is based. However, based on the shortening of the vertebrae and the large lateral keel, the specimen is identified as a representative of the Thunnini. Based on only these few vertebrae, a more precise identification than to tribe level cannot be made. Because of the poor quality of the material and the inability to assign them to at least a certain genus, the specimen is not figured here.

Subfamily Acanthocybiinae Starks, 1910

This subfamily includes *Acanthocybium* Gill, 1862, and its fossil relatives. The fossils in question are thought to be related to *Acanthocybium*, based on their dental and vertebral morphology. The teeth are tightly packed and blunt-tipped, and the vertebrae have a mid-lateral fossa.

aff. Acanthocybium
(Fig. 14)

Material. BMNH P27010, Sheppey, Early Eocene: Ypresian (London Clay).

Description. Hypural plate, made up of the fusion of urostyle, hypurals 1–4 and parhypural. As in *Acanthocybium* and Scomberomorinae, this species might have had a rudimentary fifth hypural associated with the hypural plate, but not fused to it. However, the element labelled HYP5? in Fig. 14 could also be an epural. Plate diamond-shaped, sides almost equal in length. Height, as far as preserved (almost completely, see Fig. 14), 50 mm, length, as far as preserved (almost completely, see Fig. 14), 34 mm. Posterior outline of diamond not swollen outwardly; all sides more or less straight. Posteriorly, a clearly discernible notch. Extended bases of caudal fin lepidotrichia have left traces (diagonal grooves) in the surface of the plate. Ventral projection of parhypurapophysis makes an angle of about 45° with horizontal axis, while postero-dorsal process oriented horizontally. Uroneural not fused with urostyle. Cross-section of urostyle clearly ovoid with the long axis horizontal (as in *Scomberomorus* and *Acanthocybium*).

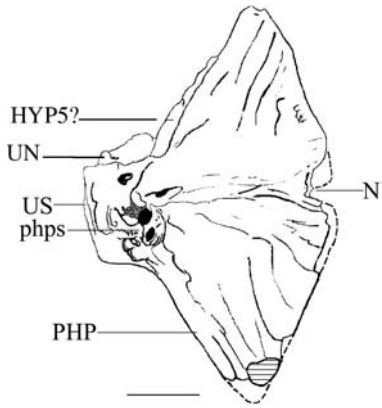

Figure 14 aff. *Acanthocybium*, left view of BMNH P270170, Eocene, London Clay, Sheppey, Kent.

Remarks. The fossil shows a striking resemblance to *Acanthocybium solandri* (Cuvier in Cuvier & Valenciennes, 1832). Hypural plates of Scomberomorinae and *Acanthocybium* consist of the fused hypurals1–4 and urostyle, and possess a caudal notch. Hypural 5 and the uroneural are not fused to the plate

and are autogenous in the caudal skeleton. In *Acanthocybium*, the parhypural is fused to the plate. However, this specimen cannot be assigned to *A. solandri*. Compared to that species, the fossil plate is slightly shorter, has a longer urostyle, a slightly larger caudal notch and its dorsal half does not protrude beyond the ventral half. The incomplete hypural plate is 50 mm high. This indicates that the individual was larger than *A. solandri* would have been. Two hypural plates of *A. solandri* have been measured at 34·5 mm (USNM 270396) and 41 mm (USNM 270393). The fossil specimen shares the following apomorphy with *A. solandri*: parhypural fused to a single plate that, in turn, consists of fused hypurals. However, it is clear based on its dimensions, that the fossil does not concern a specimen of *A. solandri*. It can even be argued that it may not belong to *Acanthocybium*. *Gasterochisma* Richardson, 1845, a supposed scombrid (for a discussion on its systematic status, see Johnson 1986) has a hypural plate consisting of hypurals 1–4 completely and hypural 5 partially fused, the uroneural, urostyle, and parhypural. Compared to *Acanthocybium*, *Gasterochisma* has a more advanced hypural plate because the uroneural is also fused into the complex. Hence, all that can be argued is that the fossil hypural plates discussed here are plesiomorphous compared to those in *Gasterochisma*. Moreover, other (fossil) representatives of the Acanthocybiinae such as *Scomberodon* Van Beneden, 1871 and a new genus (see below) have the uroneural fused to the plate. The fossil discussed here cannot be assigned to *Acanthocybium* based on the symplesiomorphy of an unfused uroneural.

Genus *Palaeocybium* Monsch gen. nov.

Type species. *Cybium proosti* Storms, 1895, p. 160, from the Eocene of Belgium and England.

Derivation of name. *Cybium* is a junior synonym of *Scomberomorus*, with whom this genus shares a similar dentition. *Palaeo* is Greek for 'old'.

Diagnosis. Teeth blunt-tipped and tightly packed in a double tooth row. Vertebrae with large midlateral fossa.

Species composition. The type species only.

Palaeocybium proosti (Storms, 1895) comb. nov. (Fig. 15)

1895 *Cybium proosti* Storms, 160.
1905 *Cybium proosti* Storms, Leriche, p. 79, pl. 10, fig. 2.
1906 *Cybium proosti* Storms, Leriche, p. 168, pl. 13, fig. 2.
1946 *Cybium proosti* Storms, Casier, p. 148, pl. 6, fig. 11.
1966 *Cybium* cf. *proosti* Storms, Casier, p. 298, pl. 47, fig. 2.
1979 *Cybium proosti* Storms, Kemp *et al.*, p. 101 (*nomen nudum*).
1984 *Cybium proosti* Storms, Kemp, p. 162 (*nomen nudum*).
1985 *Cybium proosti* Storms, Kemp, p. 43 (*nomen nudum*).
1990 *Cybium proosti* Storms, Kemp *et al.*, p. 11, pl. 17, fig. 16.
2000 *Cybium proosti* Storms, Clouter *et al.*, p. 68, fig. 1.

Holotype. In the IRSNB, Lutetian, Belgium (Casier 1966) (not seen).

Material. BMNH 36166, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus.

Description. Only jaw bones preserved in the studied specimen. Maxilla and premaxilla tightly interlocked, forming non-protractile complex. There are two rows of teeth. Outer tooth row consists of minute laterally flattened, blunt-tipped semiconical teeth. Interspace between outer row teeth approximately the width of one tooth. Inner row teeth much larger, similar in shape to outer teeth, tightly packed. Vertebrae are described by Storms (1895). These are amphicoelous, short, stout and possess a large midlateral fossa.

Remarks. The description of this specimen perfectly matches Storm's (1895) description of *Cybium proosti*. Casier (1966) identified the specimen as *Cybium* cf. *proosti* without mentioning the reasons for uncertainty regarding the specific identification. Before Casier's description, *C. proosti* was only known from the Lutetian of Belgium. *Cybium proosti* shows a peculiar apomorphy in that it has a double tooth row, which is unique for the Acanthocybiinae.

'*Cybium proosti*' is also mentioned from the Bracklesham Group of Hampshire (see Kemp *et al.* 1979, 1990).

Acanthocybiinae *incertae sedis* sp. (Fig. 16)

Diagnosis. Hypurals 1–4, uroneural and urostyle fused.

Material. BMNH 241686c and 38883, Sheppey, Early Eocene: Ypresian (London Clay); one specimen of P14029 (Fig. 16), Barton, Hampshire, Bartonian (Barton Clay).

Description. Hypural plates consisting of the following elements which are fused together: hypurals 1–4, uroneural and urostyle (Fig. 16a). Urostyle wider than deep (Fig. 16b), parhypural autogenous.

Remarks. These hypural plates are identical to those of the acanthocybiins *Scomberodon* and *Neocybium*. *Scomberodon* has been synonymised with *Scomberomorus* (see Leriche 1910). However, the presence of a midlateral fossa in the vertebrae and the fact that its uroneural is fused to the hypural plate clearly distinguish *Scomberodon* from *Scomberomorus*. *Neocybium* Leriche, 1908, is known from remains of the skull and the axial skeleton, which resemble those of *Scomberodon* (Leriche 1908). Apparently, there is nothing that separates hypural plates of *Scomberodon* and *Neocybium*. The difference between the two lies in their vertebral column. Neocybium has a large, fully developed midlateral depression in its vertebrae. In *Scomberodon*, this depression is small and partially developed (Leriche 1910). Similar hypural plates to these described here are known from the USA (Monsch 2000b).

Subfamily Xiphiinae Swainson, 1839
Tribe Xiphiorhynchini Regan, 1909

A fossil billfish family, known from rostra, skull parts and vertebrae. The most striking feature is the presence of four nutrient canals in the rostrum, while there are two in istiophorins and in the swordfish *Xiphias* Linnaeus, 1758. Schultz (1987) erected a new xiphiorhynchin genus *Thalattorhynchus*, based on a fossil rostrum. The assignment of this 'new' genus is primarily based on the eccentrically placed nutrient canal, an anomaly previously found in Istiophorins. In rostra of Recent *Tetrapturus* Rafinesque-Schmaltz, 1810, for example, often just one of the normally two lateral nutrient canals is observed in cross-sections close to the apex. The present author suspects that '*Thalattorhynchus*' is an unidentifiable istiophorin, hereby following Fierstine & Voigt's (1996) opinion. Hence, the Xiphiorhynchini are a monogeneric tribe, containing *Xiphiorhynchus*.

Genus *Xiphiorhynchus* Van Beneden, 1871

Type species. *Xiphiorhynchus elegans* Van Beneden, 1871, p. 499, from the Eocene of Belgium.

Diagnosis. Rostra ovoid in cross-section, with four nutrient canals (Figs 17 & 18). Central canal extends far anteriorly.

Species composition. Schultz (1987) mentioned a total of seven species, occurring from the Late Palaeocene to the

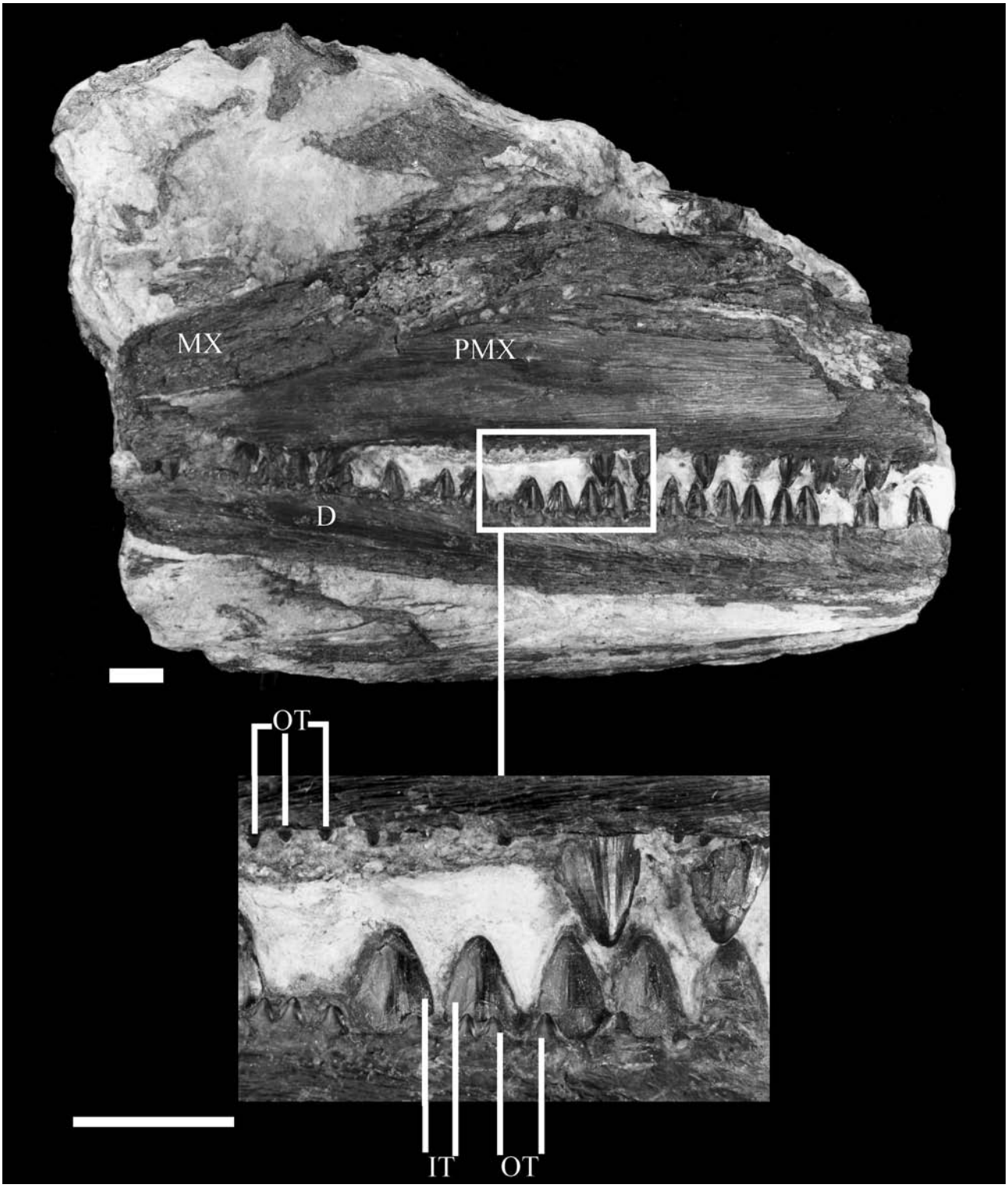

Figure 15 *Palaeocybium proosti*, BMNH 35166, Eocene, London Clay, Sheppey, Kent, complete specimen and enlarged detail of dentition. Scale bars = 10 mm.

Middle Eocene. *Xiphiorhynchus parvus* Casier, 1966, is here considered to be an unidentifiable istiophorin. *Xiphiorhynchus priscus* (Agassiz, 1844) and *X. eocaenicus* (Woodward, 1901) were originally described under genus *Histiophorus* Cuvier in Cuvier & Valenciennes, 1832. Monsch, Fierstine and Weems (in press) recognise *Histiophorus rotundus* Woodward, 1901 as a member of *Xiphiorhynchus*. Kemp *et al.*'s (1990, pl. 18) '*Xiphiorhynchus* sp.' is an ovoid rostrum, apparently without nutrient canals preserved, that cannot be identified. It is even doubtful whether it belongs to the genus in question.

Remarks. The identity of the various fossils which have been identified as *Xiphiorhynchus* is problematic because no articulated parts are known. Many specimens in the collection of the BMNH which are thus labelled are not *Xiphiorhynchus*. In the present paper, the author identifies many such remains as cf. *Gymnosarda* sp., Istiophorinae indet., *Scomberodon*, *Scomberomorus* and 'unidentifiable'. Woodward (1901) mentioned a few vertebral remains which he thought could be vertebrae of *Xiphiorhynchus*, probably because they are 'Xiphioid vertebral centra' found in sediments of the same age

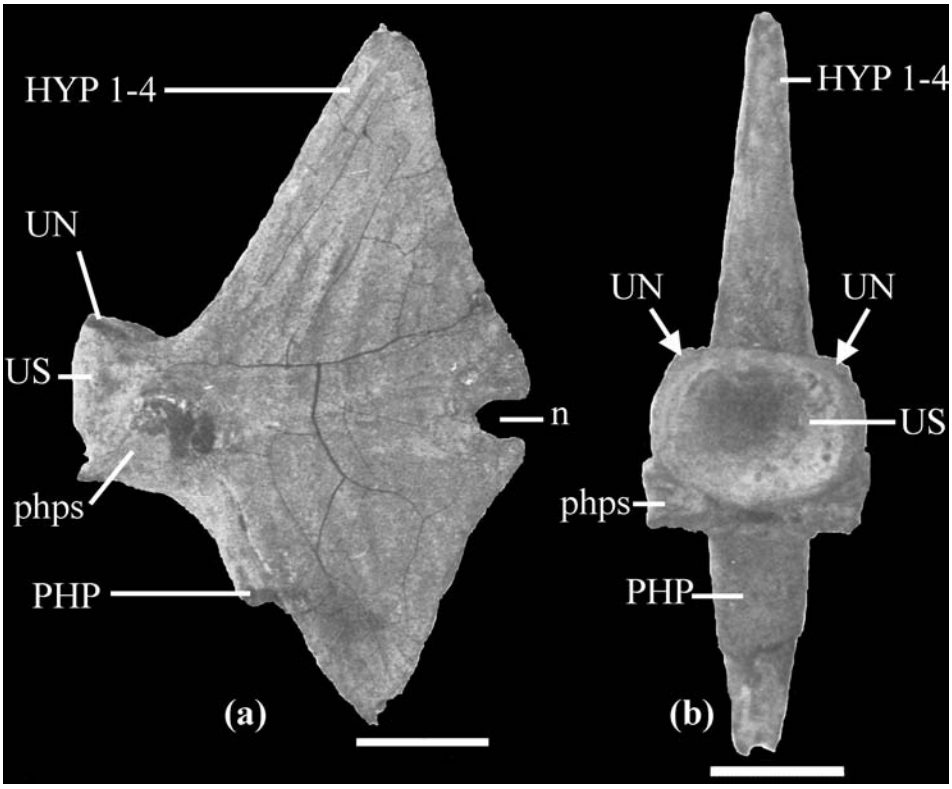

Figure 16 Acanthocybiinae *incertae sedis*, hypural plate, BMNH P14029, Eocene, Barton Clay, Barton, Hampshire: (a) lateral view; and (b) anterior view. Scale bar = 10 mm.

and the same place as *Xiphiorhynchus priscus*. Of the specimens mentioned by Woodward, the present author has seen BMNH 30530 and 38888, and BMNH 32570 (Fig. 19), which has not been described but is catalogued as *Xiphiorhynchus*. These resemble the vertebrae of *Xiphias*, in that they are stout, elongate and circular in cross-section. However, because these vertebrae are not known to be found associated with remains which are surely *X. priscus*, it is better to consider these vertebrae unidentified. None of the hypural plates labelled as *Xiphiorhynchus* in the collection of BMNH could the present author assign (with certainty) to that genus. A hypural plate similar to these is figured by Kemp *et al.* (1990, pl. 18). I here describe some of these here as taxa other than *Xiphiorhynchus* and others as unidentifiable fossils. A published figure of *Xiphiorhynchus* cranial remains (Kemp *et al.* 1990, pl. 16) is unclear and presents no characters for identification. *Xiphiorhynchus* are recorded from the Bracklesham beds and the Elmore Formation of the Middle Eocene (Kemp *et al.* 1979, 1990).

The name *Xiphiorhynchus* was first given to remains of billfish rostra with four nutrient canals (Figs 17 & 18a). Agassiz (1833–1844) was the first to associate the rostra with certain skull remains (which he supposed to be of *Tetrapturus*). However, the remains in question do not seem similar to *Tetrapturus* to the present author. It could be possible that the various bills, skulls and vertebrae have nothing to do with each other, and share only a superficial, accidental resemblance to *Tetrapturus*. It has been in doubt for some time whether the various remains do indeed belong together (see Fierstine 1974). However, the present author believes that at least a substantial portion of such fossils can indeed be assigned to *Xiphiorhynchus*. Two skulls, BMNH P26990 (Fig. 18b) and BMNH P13056 (Fig. 18c), have teeth preserved on their premaxillae. These teeth are small, almost villiform cones in multiple rows. Skull BMNH 28711 (Fig. 18d) has the posterior end of its rostrum preserved. In there, one can see a pair of premaxillae (nasals *sensu* Monsch 2000b) which are not fused along the midline of the bill. In *Xiphiorhynchus* bills, there is a pair of large unfused bones on the dorsal surface (Fig. 17a), which the present author interprets as the nasals. It looks as if these bills would fit perfectly on a skull such as the one pictured in Fig. 18c. The author believes there is enough evidence to support the proposition that the rostra and crania in question are indeed associated.

The rostrum of *Xiphiorhynchus* differs from both istiophorins and *Xiphias*. The rostra are ovoid in cross-section, often a little more circular than in istiophorins. *Xiphias* bills are dorsoventrally flattened. The configuration of elements which contribute to the structure of the bill (see Figs 17a & 18a) is similar to that of *Xiphias*, in which large paired bones on the dorsal surface are interpreted as ascending processes of premaxillae (Conrad 1937). The dorsal surface of the bill of an istiophorin is covered by three paired elements: nasals, prenasals and premaxillae (see Fig. 20).

Ommatolampes eichwaldi Fischer von Waldheim, 1851, shows great similarity with skulls identified as *Xiphiorhynchus priscus* (first remarked on by Woodward 1901). The holotype is reported by Fischer von Waldheim (1851) to be stored in the Museum of the Imperial Society of Naturalists of Moscow (during the era of the Tsars), but further information regarding the specimen is missing. The description and illustration of Fischer von Waldheim (1851) are not sufficient in themselves to certify the identity of the specimen.

The bill of '*Xiphiorhynchus* sp.' figured by Clouter *et al.* (2000, p. 66) belongs to an unidentifiable istiophorin. It does not possess a central canal and has only two nutrient canals. What Clouter *et al.* (2000) in their figure indicate as the 'top surface' is the ventral side that is covered by alveoli which once contained villiform teeth.

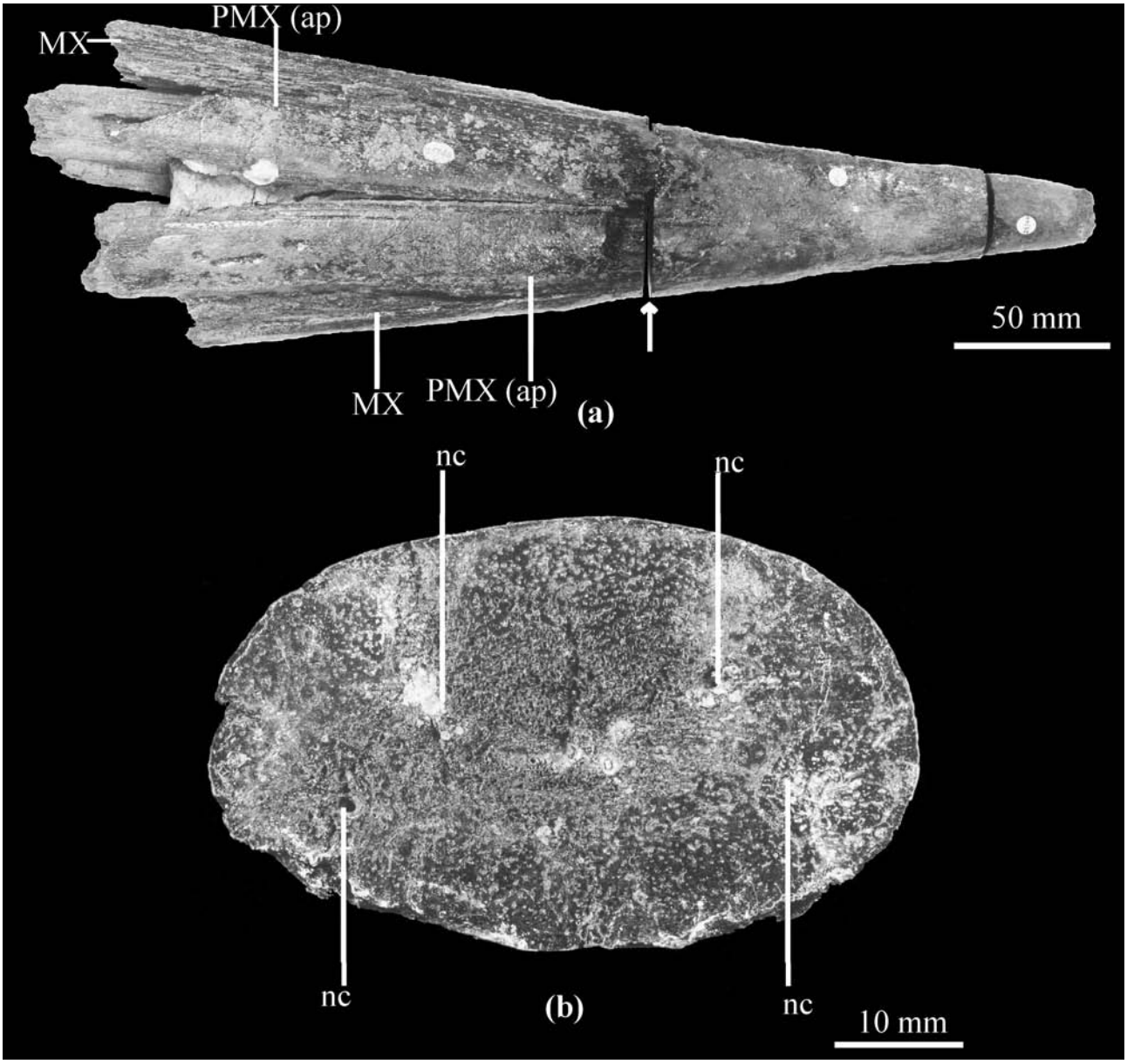

Figure 17 *Xiphiorhynchus eocaenicus*, BMNH P25744, Eocene, Bracklesham Beds, Bracklesham Bay, Sussex: (a) dorsal view of rostrum; and (b) cross-section of rostrum, taken at arrow in Figure 17.

Xiphiorhynchus eocaenicus (Woodward, 1901)
(Fig. 17)

1901 *Histiophorus eocaenicus* Woodward, p. 495, fig. 18 (2).
1987 *Xiphiorhynchus eocaenicus* Wood. Schultz, fig. 5, tab. 2.

Holotype. BMNH P25744 (holotype of *Histiophorus eocaenicus*, Fig. 17), Bracklesham, Early–Middle Eocene: Ypresian-Lutetian (Bracklesham Beds).

Material. Holotype only.

Comparisons. Four nutrient canals, small and difficult to distinguish. Rostrum dorsoventrally flattened, almost as in istiophorins. *Xiphiorhynchus priscus* has an almost circular rostrum in which canals are clearly visible (although this species can be determined by these characters, the present author is unsure whether these are apomorphies or plesiomorphies, and hence, whether to mention them in a list diagnostic characters).

Description. The first description was given by Woodward (1901). Monsch (2000b) recognised that the generic affinities of this species are in *Xiphiorhynchus*. An updated description of the holotype is not given there, but will be presented in a forthcoming paper by Fierstine & Starnes (in press).

Remarks. Woodward (1901) assigned certain fossil rostra to *Histiophorus* Cuvier, 1832 (an invalid emendation of *Istiophorus* Lacepède, 1801) 'for convenience of reference', implying uncertainty regarding their identity. The holotype of *X. eocaenicus* is amongst the specimens in question. The flatness of the rostrum of *X. eocaenicus* compared to that of X. priscus and superficial resemblances to *Istiophorus* might have led Woodward (1901) to believe that this could not concern a *Xiphiorhynchus*. However, four nutrient canals, as found in this specimen, are definitely an apomorphy of *Xiphiorhynchus*.

Schultz (1987) included '*Histiophorus eocaenicus*' in the species composition of *Xiphiorhynchus*, but still seemed to find the assignment of the species to genus *Xiphiorhynchus* questionable since he stated that he had only references without material to verify their validity.

The present author does not know on what basis the identification of Kemp *et al.*'s (1990, pl. 18) *Brachyrhynchus* sp.

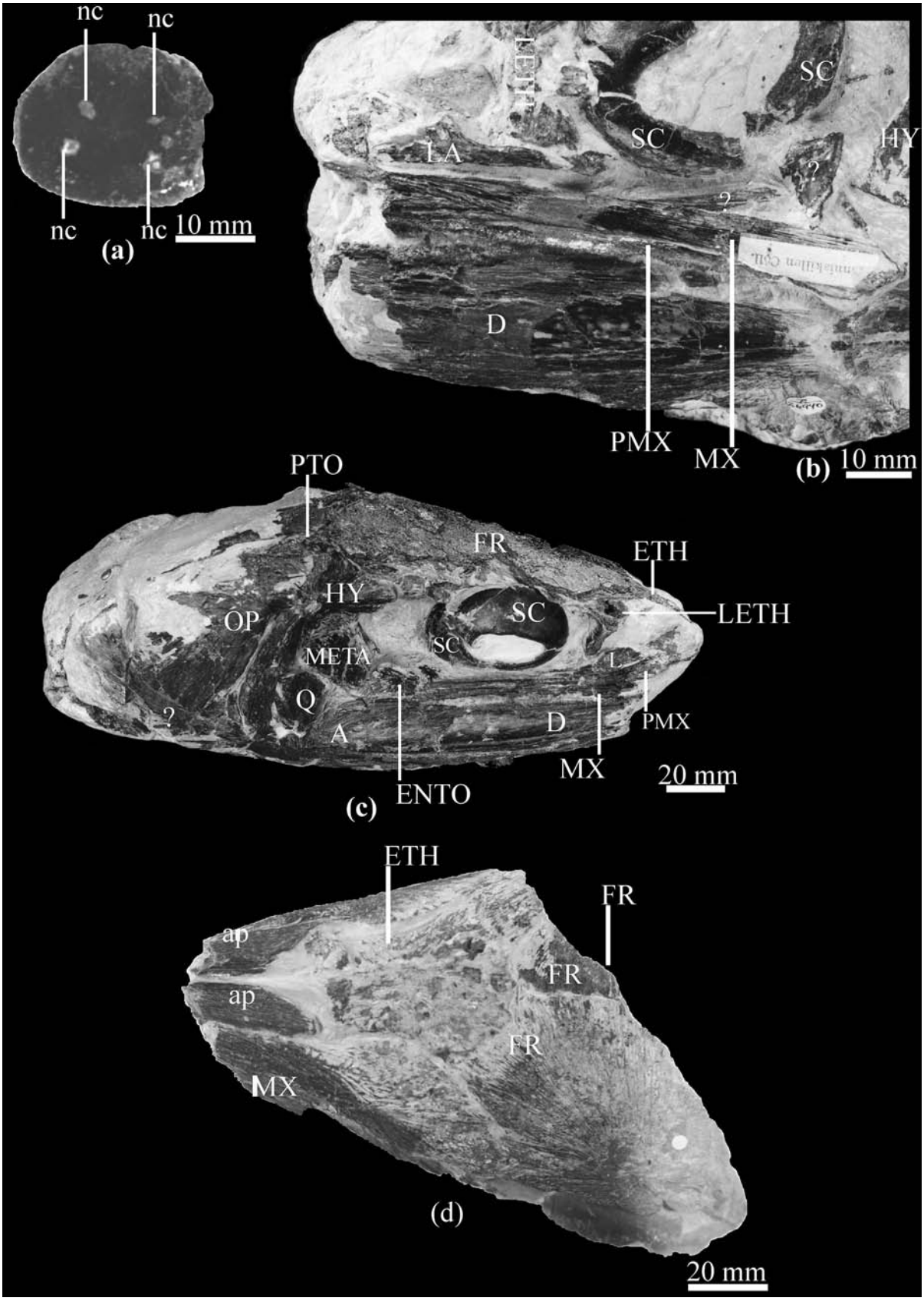

Figure 18 *Xiphiorhynchus priscus*, Eocene, London Clay, Sheppey, Kent: (a) cross-section of rostrum, BMNH 36133a; (b) left view of skull, BMNH P26990; (c) right view of skull, BMNH P13056; and (d) dorsal view of anterior part of skull, BMNH 28711.

was made. There is no description, and the illustration does not provide any diagnostic features of a damaged and ovoid rostrum. *Brachyrhynchus* Van Beneden, 1871, is an invalid heterogeneous taxon, the assignment of which is based on specimens of the Recent billfish *Makaira* Lacepède, 1802, and *Xiphiorhynchus* (Schultz 1987).

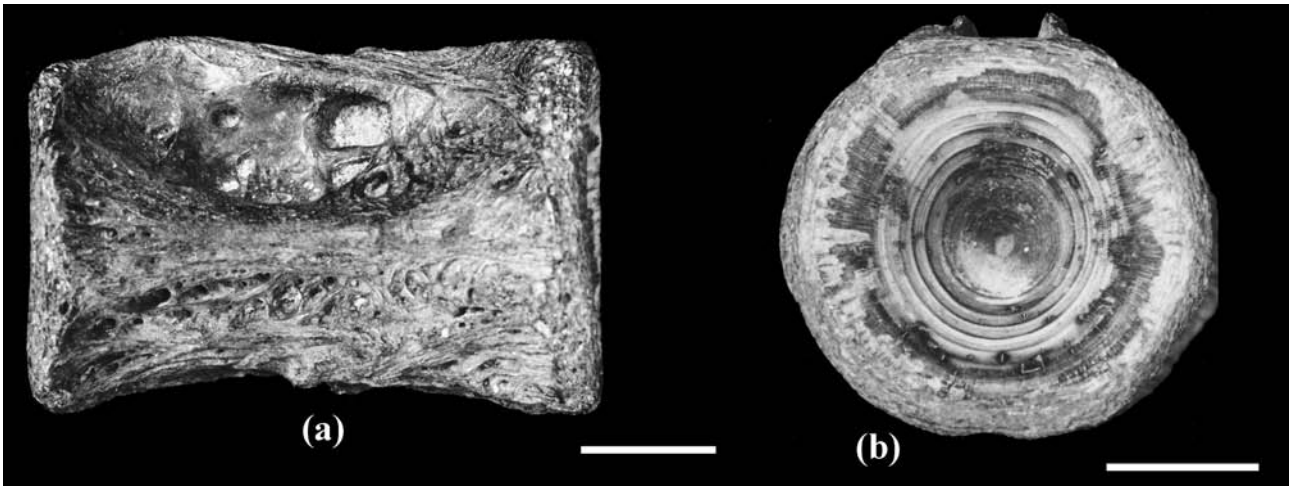

Figure 19 Vertebra, aff. *Xiphiorhynchus*, BMNH 32570, Eocene, London Clay, Sheppey, Kent: (a) lateral view; and (b) anterior or posterior view. Scale bars = 10 mm.

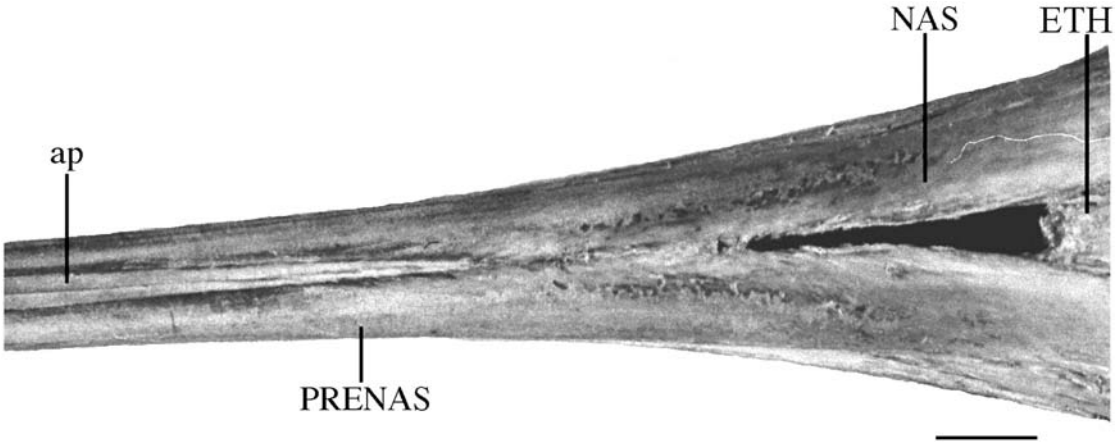

Figure 20 Prenasals and surrounding bone elements, as seen in a dorsal view of a part of a rostrum of *Tetrapturus albidus* Poey 1860, USNM 27066. Scale bar = 20 mm.

Xiphiorhynchus priscus (Agassiz, 1844)
(Fig. 18)

1835a *Tetrapturus* sp. Agassiz, p. 303.
1833–44 *Tetrapterus priscus* Agassiz, p. 91, pl. 31.
?1851 *Ommatolampes eichwaldi* Fischer von Waldheim, p. 3, fig. 1.
1869 *Histiophorus priscus* (Ag.) Cope, p. 310.
1901 *Xiphiorhynchus priscus* (Ag.) Woodward, p. 491, fig. 18 (1), pl. 19, figs 1 & 2.
1901 Xiphioid Woodward, 1901, p. 495.
1905 *Xihiorhynchus priscus* (Ag.) Leriche, p. 158, pl. 11, fig. 1.
1906 *Xiphiorhynchus priscus* (Ag.) Leriche, p. 251, pl. 14, fig. 1.
1966 *Xiphiorhynchus priscus* (Ag.) Casier, p. 309, text figs 72 & 73, pls 52 & 65.

Holotype. MNHN PTE 747 (formerly AC 11346).

Material. The holotype, and BMNH 3888, 28711 (Fig. 18d), 32387, P4300, P13056 (Fig. 18c), P26990 (Fig. 18b) and 36133a (Fig. 18a), Sheppey, England Early Eocene: Ypresian (London Clay); P12204, East shore, Selsey, Bartonian (Selsey Sands, Bracklesham Beds); P19492, Beltinge, Herne Bay, Kent, Early Eocene: Ypresian (London Clay).

Comparisons. Four nutrient canals comparatively large and clearly visible, cross-section of bill rather rounded. The present author is unsure whether these are apomorphies or plesiomorphies, and hence, considers it better not to mention them as diagnostic characters here.

Description. Woodward's (1901) descriptions of BMNH 28711, 32387 and 36133 (a specimen that the present author has not studied) are quite comprehensive and detailed. Woodward's (1901, pl. 19) nasals are interpreted here as ascending processes of premaxillae. Nasals are indeed visible at the base of the rostrum of istiophorins and are anteriorly bordered by the ascending processes of premaxillae (Fig. 20). In *Xiphiorhynchus*, however, the dorsal surface of the bill seems to be covered mainly by only one pair of bones (see also Fig. 17), which is interpreted as a pair of ascending processes of the premaxillae, as found in Recent *Xiphias*. Nasals are not found in *X. priscus*. In this genus, the situation may be similar to that in *Xiphias*, in which nasals are presumed by some (see Conrad 1937; Monsch 2000b) to be reduced to minute fragile bones which would probably not survive fossilisation.

Remarks. Woodward (1901) mentioned a xiphioid rostrum (BMNH P4300) that he described as flattened and showing two longitudinal canals. However, the present author considers that the bill is not flattened such that is not referable to *X. priscus*. A close examination of the specimen reveals that it possesses four nutrient canals, the ventral pair being smaller and more difficult to perceive.

Tribe Istiophorini Lütken, 1875
Genus *Makaira* Lacepède, 1802

Type species. *Makaira nigricans* Lacepède, 1802, p. 688, Bay of Biscay (Recent).

Figure 21 *Makaira* sp., vertebra, BMNH 30798, Eocene, London Clay, Sheppey, Kent: (a) right view; and (b) dorsal view. Anterior end on the right, scale bars = 10 mm.

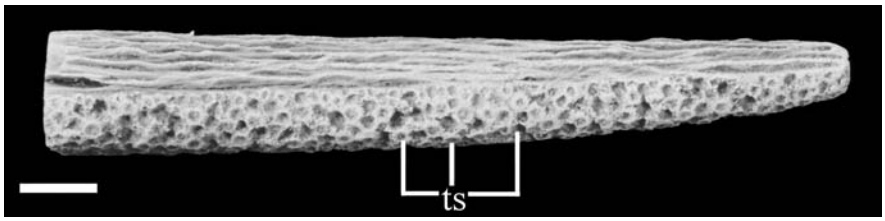

Figure 22 Rostrum of unidentified istiophorin (non *Xiphiorhynchus*), BMNH P21306, Eocene, London Clay, Sheppey, Kent. Scale bar = 2 mm.

Diagnosis. Nape (anterodorsal profile of head) elevated, makes angle of >45° with body axis, lateral apophyses of vertebrae developed into anterolateral transverse plate-like flanges, centrum strongly widened and deepened anteriorly.

Species composition. Three Recent species of *Makaira* occur world-wide (Nakamura 1985). A review of fossil species is in Fierstine (2001), who mentions four extinct species and fossil specimens of extant species.

Makaira sp.
(Fig. 21)

Material. BMNH 30798, Sheppey, Early Eocene: Ypresian (London Clay) (Fig. 21), 1086–8, Alum Bay, Isle of Wight, Bartonian (Lower Barton Clay).

Diagnosis. Centrum strongly widened anteriorly.

Description. Amphicoelous, elongate, narrow centra, strongly constricted medially: haemal arch excluded, centrum at narrowest point has diameter less than 30% of maximum depth. Anterior apex abruptly deepening, thus achieving a greater diameter and depth than posterior apex. Transverse section of anterior and posterior end of centrum almost circular in outline. Rib socket preserved.

Remarks. The present author interprets these centra as having been in the most anterior part of the vertebral column because of the presence of rib sockets. Moreover, more posterior vertebrae of *Makaira* have laterally expanded lateral apophyses.

Kemp *et al*. (1990, pl. 18) figured (but did not describe) a rostrum that they assigned to *Brachyrhynchus* Van Beneden, 1871 (an invalid heterogenous taxon based, amongst others, on *Makaira*, see Schultz 1987), from the middle Eocene of England. The present author was unable to identify the specimen on the basis of their illustration.

Incertae sedis sp. non *Xiphiorhynchus*
(Fig. 22)

1966 *Xiphiorhynchus parvus* Casier, p. 314, pl. 51, fig. 5.

Material. BMNH P21306 (Holotype of *Xiphiorhynchus parvus*, Fig. 22), Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Billfish rostra without preserved generic or specific apomorphies.

Description. *Xiphiorhynchus parvus* is based on a small rostrum that is almost circular in cross-section, striated dorsally, bears multiple rows of villiform teeth (no teeth are preserved, but empty alveoli are easily visible), and has one pair of large nutrient canals. *Xiphiorhynchus*, on the contrary, is characterised by four nutrient canals.

Incerti Tribus
Genus *Aglyptorhynchus* Casier, 1966

Type species. *Cylindracanthus denticulatus* Leriche, 1908, p. 381, from the Oligocene of Belgium.

Diagnosis. Known from rostra only (Fig. 23), which bear two dentigerous zones which are separated by a narrow median edentulous zone. Number of nutrient canals variable (Fierstine 2001).

Species composition. Nine species (Fierstine 2001) from the Early Eocene to Late Oligocene of England, Belgium and the USA. *Aglyptorhynchus venablesi* Casier, 1966, is the only English species.

Remarks. Leriche (1906) realised that the name *Coelorhynchus* for fossil billfish rostra was preoccupied by a Recent macrurid. Thus, he introduced the new generic name *Glyptorhynchus*, apparently unaware of an already existing valid generic name *Cylindracanthus*. Leriche (1908, 1910) subsequently regarded *Glyptorhynchus* as a subgenus of *Cylindracanthus*, a generic name he then apparently did recognise. However, the '*Glyptorhynchus*' that Leriche (1906) described concerns what is now known as a distinct genus, *Cylindracanthus* (see below), and the '*Cylindracanthus* subgen. *Glyptorhynchus*' he described later (Leriche 1910) is generically different from *Cylindracanthus*. Casier (1966) erected the new genus *Aglyptorhynchus* to replace Leriche's (1910) 'subgen. *Glyptorhynchus*'.

This genus is represented by fossils of rostra only. Judging by its four large nutrient canals and multiple tooth rows (Fig. 23d), it is likely that *Aglyptorhynchus* is a billfish, maybe one related to *Xiphiorhynchus*. A recently described species, *Aglyptorhynchus maxillaris* Fierstine, 2001, is preserved as a near-complete rostrum, together with maxillae and premaxillae. This is the most convincing evidence so far that *Aglyptorhynchus* is a billfish. A preliminary phylogenetic analysis of scombroids was carried out without *Aglyptorhynchus* (Monsch 2000b). It remains to be seen whether the new cladistic analysis

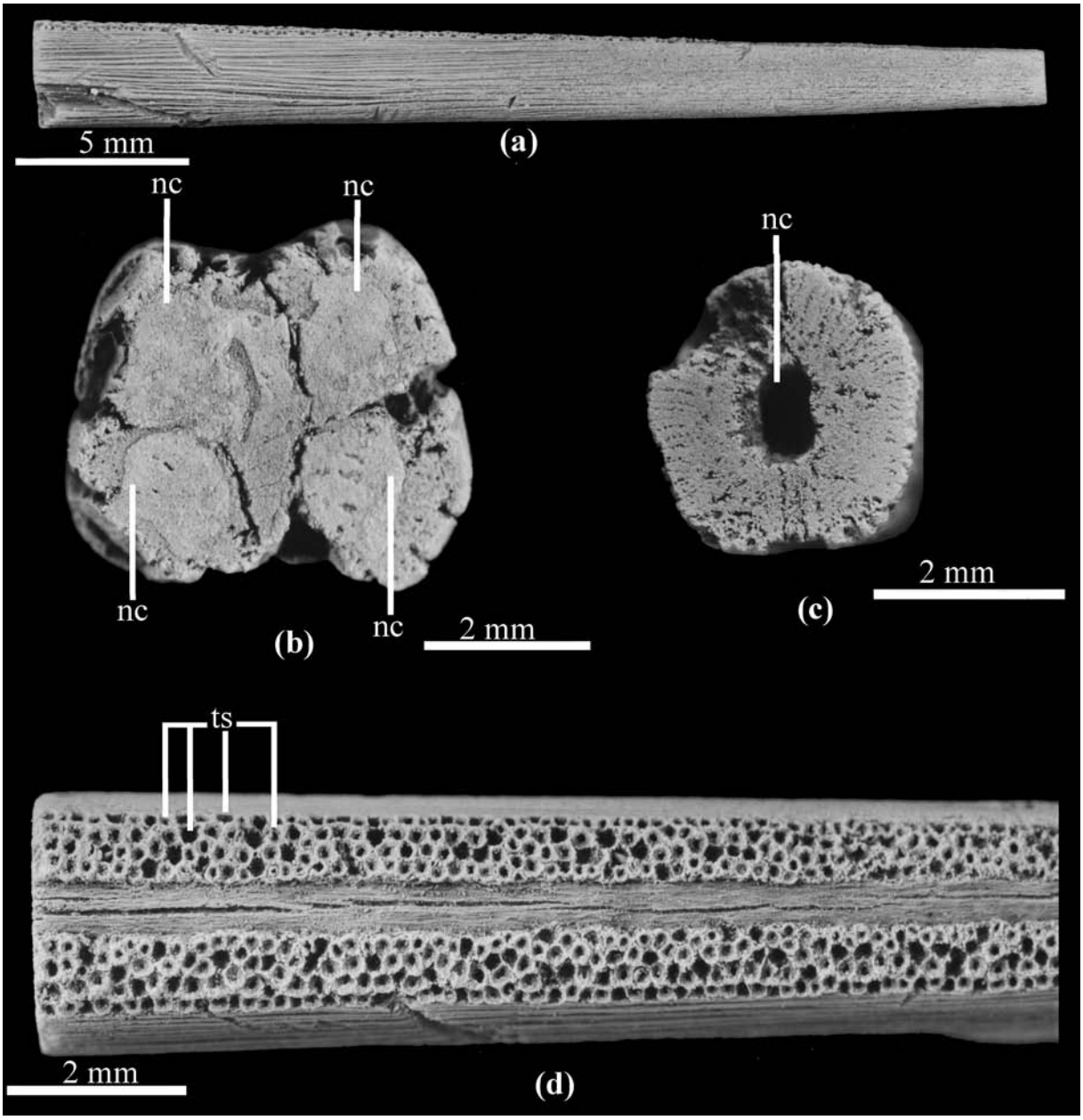

Figure 23 *Aglyptorhynchus venablesi*, Eocene, London Clay, Bognor Regis, Sussex: (a) dorsolateral view of almost complete? Rostrum, BMNH P21305; (b) transverse cross-section near base of rostrum, BMNH P27612; (c) transverse cross-section near anterior tip of rostrum, BMNH P21305; and (d) ventral view of part of BMNH P21305.

in preparation will resolve the position of *Aglyptorhynchus*, but with *A. maxillaris*, that now seems more hopeful than before. *Aglyptorhynchus maxillaris* possesses a large, downturned maxillary flange, as is found in the fossil billfish tribe Palaeorhynchini (e.g. see Bannikov 1993). Thus, it may be that the affinity of *Aglyptorhynchus* is with palaeorhynchins.

'*Aglyptorhynchus* sp.' is mentioned from the Bracklesham Group of Hampshire (see Kemp *et al.* 1990).

Aglyptorhynchus venablesi Casier, 1966
(Fig. 23)

1966 *Aglyptorhynchus venablesi* Casier, p. 305, text fig. 71, pl. 51, figs 1–3.
2000 *Aglyptorhynchus venablesi* Cas. Clouter *et al.*, p. 66, 4 figures.

Holotype. P26157 (Fig. 23b), Bognor Regis, Sussex, Ypresian (Fish tooth bed of London Clay).

Material. The holotype and the paratypes BMNH P21305 (Fig. 23a, c, d) and P27612–4, Bognor Regis, Sussex: Ypresian (fish tooth bed of London Clay).

Diagnosis. Cross-section at base of rostrum almost square (Fig. 23b), and more or less circular near anterior tip (Fig. 23c). Four nutrient canals at base of rostrum occupy almost the whole of the area in transverse cross-section (compare Fig. 23b, c) and coalesce into a single canal distally (Fig. 23c) A thin section of a proximal part of the rostrum also showed three minute additional dorsal (nutrient?) canals (Casier 1966, plate 61).

Description. See Casier (1966).

Genus *Enniskillenus* Casier, 1966

Type species. *Enniskillenus radiatus* Casier, 1966, p. 299, from the Early Eocene of England.

Diagnosis. Frontals dorsally convex (Fig. 24), provided with numerous minute perforations, postero-superior fossa posterior to orbit.

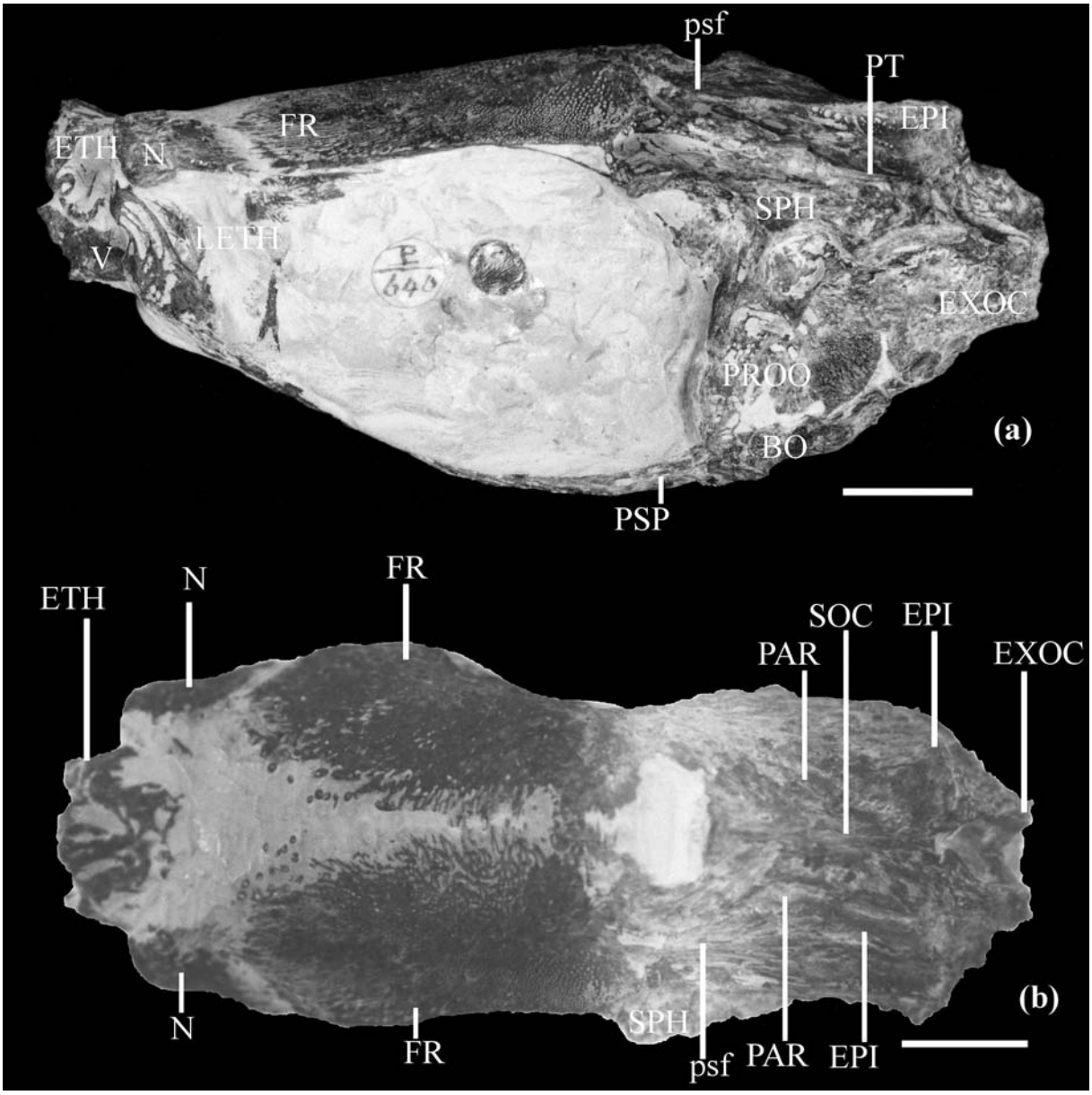

Figure 24 *Enniskillenus radiatus*, BMNH P646; Eocene, London Clay, Sheppey, Kent: (a) lateral view; and (b) dorsal view (some features which are obscured in the picture are better visible in Fig. 24a. Scale bars = 10 mm.

Species composition. Only the type species.

Remarks. Because of superficial resemblances, Woodward (1901) considered that BMNH P646 and P647 could belong to the fossil billfish *Palaeorhynchus* De Blainville, 1818. Casier (1966) concluded the specimens are not *Palaeorhynchus*, but erected a new palaeorhynchid genus, *Enniskillenus*, for them. Monsch (2000b) considered the characters chosen by Casier (1966) to identify these specimens palaeorhynchids superficial and was of the opinion that the skulls do not reveal any synapomorphies for palaeorhynchins, billfishes, or even scombroids. It is not known whether palaeorhynchins possess a similar cranial morphology as *Enniskillenus*. However, Clouter *et al*. (2000, p. 61) figured specimens of *Enniskillenus* with billfish rostra and elongated istiophorin-like vertebrae. Even though this confirms that the genus belongs to the Xiphiinae, the fossils contain no apomorphies which would assign them to one of the existing xiphiin tribes.

Enniskillenus radiatus Casier, 1966
(Fig. 24)

1833–44 *Ptychocephalus radiatus* Agassiz, p. 139 (*nomen nudum*).
1845 *Ptychocephalus radiatus* Agassiz, p. 307 (*nomen nudum*).
1901 *Palaeorhynchus*? Woodward, p. 497.
1966 *Enniskillenus radiatus* Casier, p. 299, text fig. 70, pl. 54.
?1985 *Enniskillenus* cf. *radiatus* Cas. Kemp, p. 43 (*nomen nudum*).
?1990 *Enniskillenus* cf. *radiatus* Cas. Kemp *et al*., p. 12, pl. 16, fig. 8.
2000 *Enniskillenus radiatus* Cas. Clouter *et al*., p. 61, 3 figures.

Holotype. P646, Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype and the following paratypes: BMNH 33136, P1741 and P26893, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus.

Description. A detailed description of the skull was given by Casier (1966). Specimens with broken rostra (provided with numerous rows of alveoli) and long, slender, istiophorin-like vertebrae were briefly described and illustrated by Clouter *et al*. (2000, p. 61).

Genus *Rotundorhynchus* Monsch gen. nov.

Type species. *Rotundorhynchus brittanicus* nov. sp. from the Eocene of the London Clay.

Derivation of name. The name *Rotundorhynchus* is composed of the Latin word *rotundus*, meaning round, and the Greek word *rhynchos*, meaning snout.

Diagnosis. One large central canal extending to almost anterior tip of rostrum, two lateral nutrient canals.

Comparisons. Transverse cross-section of bill almost circular, becoming slightly ovoid near the base, deeper than bill of *Xiphiorhynchus*.

Remarks. *Rotundorhynchus* shows an interesting mix of characters. A central canal that extends far anteriorly is known for *Xiphiorhynchus*. The possession of one pair of nutrient canals is a feature of istiophorins.

Rotundorhynchus brittanicus Monsch sp. nov.
(Fig. 25)

1901 Xiphioid Woodward, p. 493.

Holotype. BMNH P1765, Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype and BMNH P23838, Sheppey, Early Eocene: Ypresian (London Clay).

Derivation of name. Species named after country of origin of only known specimens.

Diagnosis. As for genus.

Description. Holotype has been cut in two halves, perhaps during original preparation of specimen (Fig. 25a). Sagittal cross-section reveals that central nutrient canal almost reaches anterior tip of bill (fig. 25b). Multiple rows of minute teeth, evidenced by empty alveoli (Fig. 25a). Dorsal surface rugose (Fig. 25c). Transverse cross-section of holotype (near the tip) almost circular, of paratype (near the base) more ovoid (Fig. 25d). One central canal, two rather large nutrient canals, one of which is preserved in paratype (Fig. 25d).

Incerti tribus
Genus *Eocoelopoma* Woodward, 1901

Type species. *Eocoelopoma colei* Woodward, 1901, p. 470, from the Early Eocene of England.

Diagnosis. Postero-superior fossa more anteriorly placed than in other scombrids: near middle of the of orbit (see description of species below). Part of frontal anterior of postero-superior fossa, thickened and ornamented with more or less fine lines.

Species composition. *Eocoelopoma curvatum* Woodward, 1901; *E. colei*, and *Eocoelopoma gigas* Casier, 1966, from England and *Eocoelopoma portentosa* Bannikov, 1985, from Turkmenistan. *Eocoelopoma* teeth of Equatorial Africa are known (Bannikov 1985), but the present author is not familiar with those taxa as such. Bannikov (1985) considered *E. curvatum* a synonym of *E. colei*. However, the present author thinks that there are significant differences between the specimens (see below) which justify a recognition of two different species here.

Remarks. *Eocoelopoma hopwoodi* Casier, 1966, is here assigned to a new genus (see below).

Eocoelopoma colei Woodward, 1901
(Fig. 26)

1833–44 *Coelopoma colei* Agassiz, p. 139 (*nomen nudum*).
1845 *Coelopoma colei* Ag. Agassiz, p. 307 (*nomen nudum*).
1901 *Eocoelopoma colei* Woodward, p. 470.
non 1901 *Eocoelopoma colei* Wood. Woodward, 1901: 471 (*partim*).
1966 *Eocoelopoma colei* Wood. Casier, p. 280, pl. 43, fig. 1.
non 1966 *Eocoelopoma colei* Wood. Casier, p. 280 (*partim*).
1985 *Eocoelopoma colei* Wood. Bannikov, p. 40 (*nomen nudum*, *partim*).
2000 *Eocoelopoma colei* Wood. Clouter *et al*., p. 61.

Holotype. BMNH P623a, Sheppey, England, Early Eocene: Ypresian (London Clay).

Material. BMNH P26702, P26805 and USNM 22388 (Fig. 26), Sheppey, England, Early Eocene: Ypresian (London Clay); P12945, Southend-on-Sea, Essex, Early Eocene: Ypresian (London Clay).

Diagnosis. Opercular bones, especially preoperculum, ornamented with clearly visible irregular wrinkles.

Comparisons. Other species have relatively smooth opercular bones and the ornamentation on the frontals consists of finer, more curved lines.

Description. A description is given by Casier (1966). Additional information and observations differing from that description given here. Small skulls, almost as long as wide. Neurocranium length 55–83 mm, maximum width 46·5–76 mm. Supratemporal groove short, not extending rostrad to snout. Temporal groove posteriorly strongly depressed, anterior part of groove shallower (Fig. 26b). Postero-superior fossa reaching middle of orbit, near lateral margin of frontal. Anterior apex of frontal pointed. Pterotic a short, narrow, triangular wing. Anterior margin of vomer slightly protruding, with patch of villiform teeth. Palatine with numerous, minute, elongate, retrorse teeth which are round in cross-section. Teeth in jaws relatively stout, conical, about equal in size (2 mm) and at most a few millimetres apart. Hyoidean window present.

Remarks. Casier (1966) excluded BMNH 39221 from Woodward's (1901) hypodygm of *E. colei* and made it the holotype of *E. gigas* Casier, 1966. Monsch (2000b) considered that another specimen of *E. colei*'s original hypodygm (BMNH 33305) is to be considered as *E. gigas*. This is maintained here.

Eocoelopoma curvatum Woodward, 1901
(Fig. 27)

1833–44 *Coelopoma laeve* Agassiz, p. 139 (*nomen nudum*).
1845 *Coelopoma laeve* Ag. Agassiz, p. 370 (*nomen nudum*).
1854 *Coelopoma curvatum* Owen, p. 162 (*nomen nudum*).
non 1901 *Scombrinus nuchalis*, Wood. Woodward, p. 462 (*partim*).
1901 *Eocoelopoma curvatum* Woodward, p. 472.
1966 *Eocoelopoma curvatum* Wood. Casier, p. 282, pl. 43, figs 2 & 3, pl. 44, figs 1 & 2.
non 1985 *Eocoelopoma colei* Wood. Bannikov, p. 81 (*partim*).
non 2000 *Scombrinus nuchalis* Wood. Clouter *et al*., p. 59, fig. 'Top view'.
2000 *Eocoelopoma curvatum* Wood. Clouter *et al*., p. 61, 3 figures.

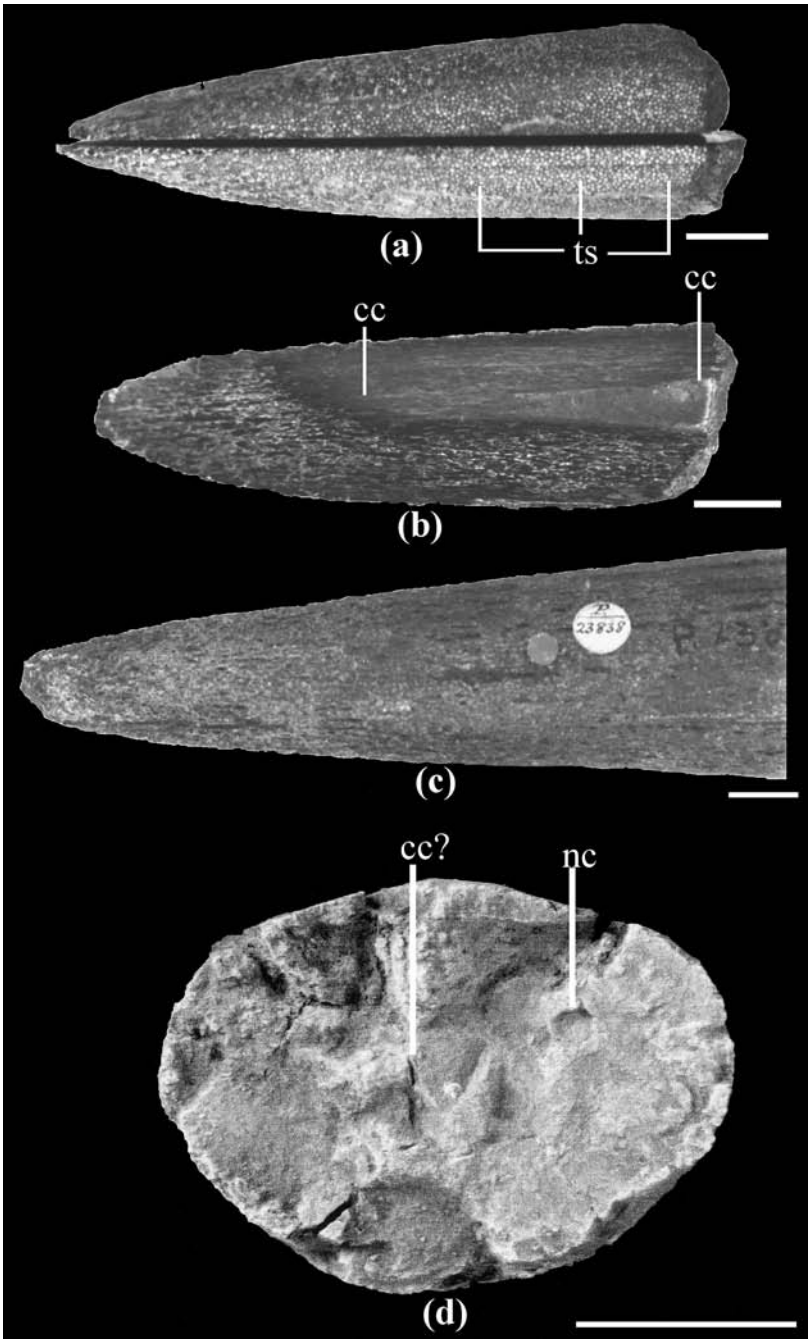

Figure 25 *Rotundorhynchus brittanicus*, Eocene, London Clay, Sheppey, Kent: (a) ventral view of BMNH P1765; (b) cross-section of BMNH P1765; (c) dorsal view of BMNH P23838; and (d) transverse cross-section of BMNH P23838. Scale bars = 10 mm.

Neotype (as established by Casier 1966). BMNH 44877a, Sheppey, Early Eocene Ypresian (London Clay).

Material. BMNH 24613 (Fig. 27b, c), P4151, P9455 (Fig. 27a), P9456a, P26714 (formerly P1698c) and USNM 22389, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Frontal anterior to postero-superior fossa densely ornamented with fine curved lines.

Description. Previous description given by Casier (1966). Different observations and additional information are given here. Sizes of cranial remains variable, but generally not very large. Crania about 1·7 times longer than wide. BMNH 24613, P4151 and USNM 22389: 80 mm long, BMNH P26714 more than 80 mm long, but unable to measure whole length. Maximum width frontals 29–71 mm. Anterior margin of frontal rather blunt and rounded. Postero-superior fossa somewhat posterior of middle of orbit (Fig. 27b). Anterior part of temporal groove shallow, posterior part strongly depressed, thus resembling a large fossa (Fig. 27b). Apex of epiotic with a flat, short projection pointing laterally. Pterotic a short wing. Palatine with minute sharp, curved teeth. Parasphenoid rather wide anteriorly, tapering posteriorly. Opercular bones rather smooth, only preoperculum with a slightly rugose ornamentation (Fig. 27a). Anterior ascending process of premaxilla rather large, but short. Teeth slender, elongate, sharply pointed, with ovoid base and smooth surface, almost all of them of same size (about 3·5 mm long). Right dentary of BMNH P9455 possesses at least 15 teeth which are a few millimetres apart. Eye sclerotics rather large (diameter 27 mm), clearly bulging laterally. Lachrymal large, longer than orbit diameter. Ventral margin of ceratohyal with ventral projections, as in Recent Thunnini. Opercular bones covered by scales with a maximum diameter of 3·5 mm. In BMNH P4151,

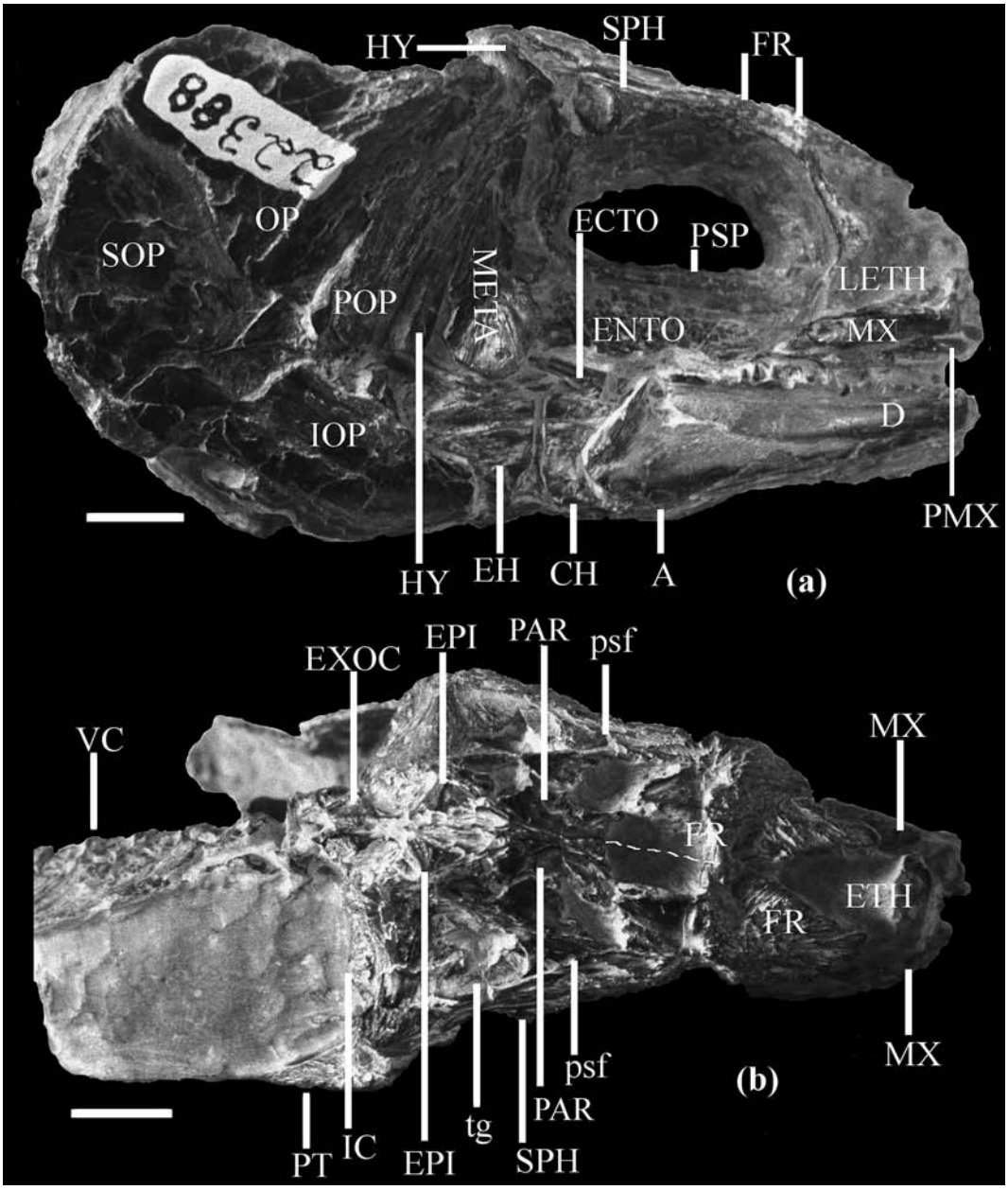

Figure 26 *Eocoelopoma colei*, USNM 22388, Eocene, London Clay, Sheppey, Kent: (a) right view; and (b) dorsal view. Scale bars = 10 mm.

first six vertebrae preserved. Centrum about as long as deep and wider than deep. Second centrum 6 mm long and deep.

Eocoelopoma gigas Casier, 1966
(Fig. 28)

non 1901 *Eocoelopoma colei* Wood. Woodward, p. 471 (*partim*).
1966 *Eocoelopoma gigas* Casier, p. 281, pl. 45.
1985 *Eocoelopoma gigas* Cas. Bannikov, p. 41 (*nomen nudum*).
?2000 *Eocoelopoma* sp. Clouter *et al.*, p. 68, 1 fig.

Holotype. BMNH 39221 (Fig. 28a). Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype and BMNH 33305 (Fig. 28b–d), Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. Significanty larger species than other species of this genus: length between hind margin of preoperculum and snout 220 mm (BMNH 39221). Crania of other species differ little in size within a length range of 55–135 mm. Small area of slight ornamentation anterior of postero-superior fossa.

Description. A description was given in Casier (1966). Different observations and additional information given here. Postero-superior fossa somewhat anterior of middle of orbit, close to lateral margin of frontal (Fig. 28b, c). Anterior of postero-superior fossa, frontal thickened. Hinder part of this thickened region slightly ornamented with fine curved lines (Fig. 28c). Apex of epiotic with a flat, short projection pointing laterally. Anterior margin of vomer diamond-shaped and strongly protruding anteriorly (Fig. 28d). Opercular bones rather smooth, only preoperculum with a slightly rugose ornamentation. Teeth slender, elongate and sharp-pointed, base ovoid, surface smooth (only slightly striated basally), almost all of the same size (about 6 mm long).

Eocoelopoma sp.

Material. BMNH P29983, Bognor, Sussex; BMNH P26706, Sheppey, Early Eocene: Ypresian (London Clay).

Description and remarks. BMNH P29983: clearly an *Eocoelopoma* tooth: slender, elongate, sharply pointed and

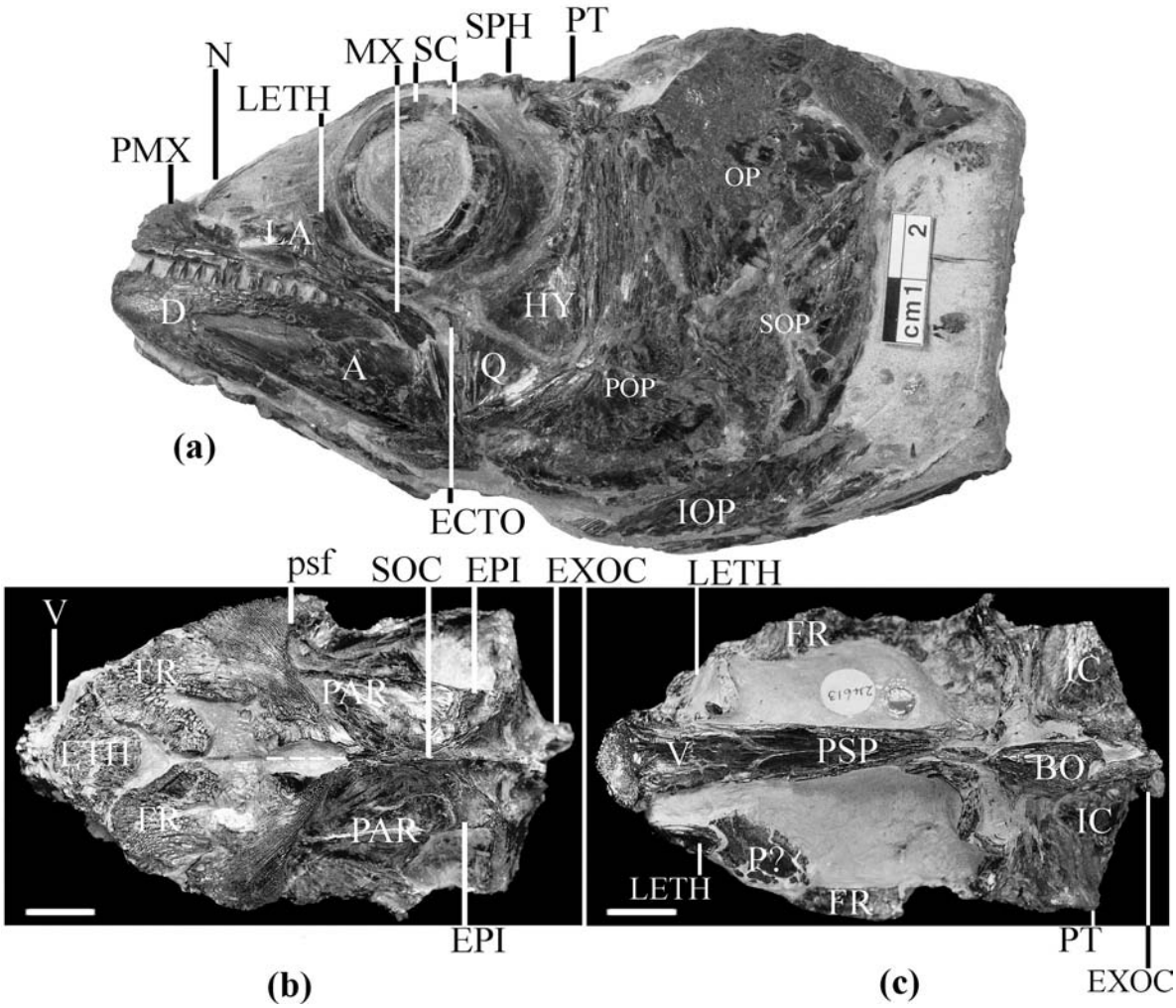

Figure 27 *Eocoelopoma curvatum*, Eocene, London Clay, Sheppey, Kent: (a) left view of BMNH P9455; (b) dorsal view of BMNH 24613; and (c) ventral view of BMNH 24613. Scale bars = 10 mm.

slightly bent (presumably towards the axial, lingual side), smooth (barely striated basally), ovoid in cross-section, about 4 mm long. Specific identity cannot be determined. If the specimen belongs to *E. gigas*, it is not a fully grown individual. BMNH P26706: damaged neurocranium, anterior part of frontals missing. Identified as *Eocoelopoma* through pattern of ridges and dents on skull roof, and anteriorly placed postero-superior fossa. Identity uncertain: could be juvenile *E. gigas*, adult *E. colei* or *E. curvatum*, but apomorphies which would identify to species level are missing. The specimen was labelled as *E. curvatum* in the collection.

Remark. Clouter *et al.* (2000, p. 65) figured a 'lower jaw' (which is really a premaxilla pictured upside down) and an upper palate of '*Eocoelopoma* sp.'

Genus *Tamesichthys* Casier, 1966

Type species. *Tamesichthys decipiens* Casier, 1966, p. 271, from the Early Eocene of England.

Diagnosis. Lower jaw protrudes upper jaw, large scales on opercular bones.

Species composition. Only the type species.

Tamesichthys decipiens Casier, 1966
(Fig. 29)

1966 *Tamesichthys decipiens* Casier, p. 271, pl. 40, fig. 1.
1985 *Scombrosarda decipiens* Cas. Bannikov, p. 13.

Holotype. BMNH 41319 (Fig. 29), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype only.

Diagnosis. As for genus.

Description. A detailed description was given by Casier (1966), to which the present author now adds an observation concerning the jaw apparatus. On the right side of the skull (not figured), the anterior portion of the premaxilla is preserved, which Casier (1966) mistook for the maxilla. The dentary protrudes beyond the upper jaw.

Remarks. It is not easy to assess the affinities of *Tamesichthys*. The protruding lower jaw is a characteristic of trichiurids, but *Tamesichthys* does not possess any trichiurid-like fangs. Superficially, *Tamesichthys* somewhat resembles a generalised gempylin, but when given a closer look, cannot be assigned to this subfamily after all for a lack of gempylin synapomorphies (for example, its teeth are straight, not retrorse as in gempylins). *Tamesichthys* may have affinities with advanced scombrids, if the large scales on its opercular apparatus are remnants of an anterior corselet. The anterior margin of the preoperculum forms a blunt angle, as in *Scomberomorus*, *Acanthocybium* and Sardinae. The operculum is deep and acutely tapered ventrally, as in the scombrins.

Bannikov (1985) considered *Tamesichthys* identical to the fossil mackerel-like genus *Auxides* (also known as *Scombrosarda*), whose skulls are, in most respects, the same as those of Recent mackerel. Bannikov (1985) based his assignment on

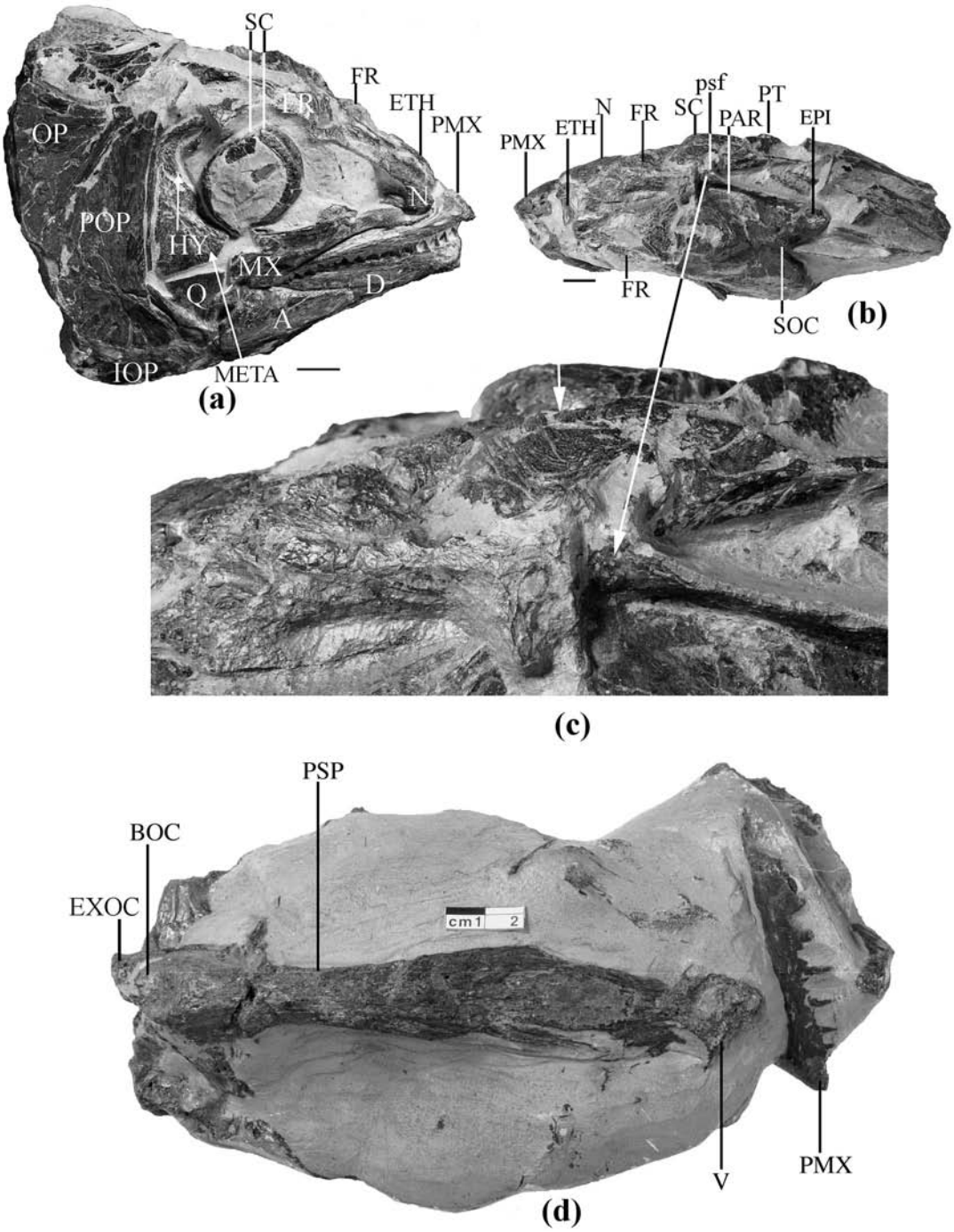

Figure 28 *Eocoelopoma gigas*, Eocene, London Clay, Sheppey, Kent: (a) left view of BMNH 39221; (b) dorsal view of BMNH 33305; (c) detail of Fig. 28b with frontal ornamentation indicated by short arrow; and (d) ventral view of BMNH 33305. Scale bars = 20 mm.

the small size of *Tamesichthys*' straight and conical teeth (preserved at the right side of the skull; not figured) and the shape of its operculum. However, when other characteristics of the London Clay cranium are taken into account, it is found that *Tamesichthys* is not identical to neither *Scomber* nor *Auxides*, and is to be considered a genus in its own right.

Scombroidei *incertae familiae*
Genus *Duplexdens* Monsch gen. nov.

Type species. *Cybium macropomum* Agassiz, 1844, p. 62, from the Early Eocene of England.

Derivation of name. *Duplexdens* is a free Latin translation of 'double tooth'. An apomorphy of this genus is the possession of (incomplete) double tooth rows.

Diagnosis. Genus known from skull only. Length of lachrymal greater than maximum diameter of orbit, anterior margin of ethmoid concave, jaw teeth represented by two incomplete tooth rows.

Species composition. Type species only.

Remarks. The only species of *Duplexdens* was previously known as *Scombrinus macropomus* (Agassiz, 1844). This species is not congeneric with *Scombrinus*, which has much smaller teeth arranged in only a single row, and the anterior margin of its ethmoid is not emarginate. Since *Scombrinus*

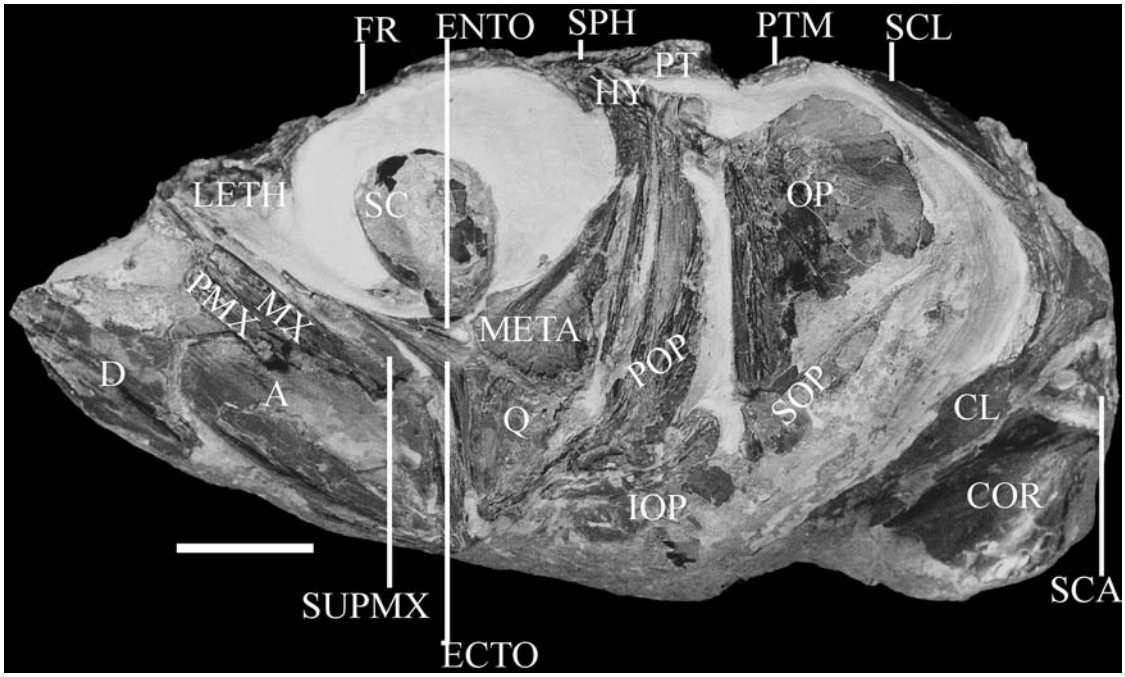

Figure 29 *Tamesichthys decipiens*, BMNH 41319, Eocene, London Clay, Sheppey, Kent. Scale bar = 10 mm.

nuchalis is the type species of its genus, a new genus *Duplexdens* has been created for '*Scombrinus macropomus*'.

Duplexdens macropomus (Agassiz, 1844) comb. nov.
(Fig. 30)

1835b *Cybium macropomum* Agassiz, p. 42 (*nomen nudum*).
1833–44 *Cybium macropomum* Agassiz, p. 62, pl. 26. figs 1–3.
1901 *Scombrinus macropomus* (Ag.) Woodward, p. 463.
non 1901 *Scombramphodon crassidens* Woodward, 1901, Woodward, p. 475 (*partim*).
1966 *Scombramphodon sheppeyensis* Casier, p. 276, pl. 40, fig. 4.
1966 *Acestrus elongatus* Casier, p. 316, pl. 40, fig. 3.

Holotype. MNHN PTE 10 (formerly MNHN 1872–557), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype and BMNH 28755, (holotype of *Scombramphodon sheppeyensis*), 28758, 38907, P158 (paratype of *Scombramphodon crassidens* Woodward, 1901), P166, P12954 (holotype of *Acestrus elongatus*) and P4145 (Fig. 30a, b); GLAHM V2017 and V3470; Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus.

Description. Neurocranium 122–140 mm long. Frontals coarsely ornamented with rugose lines, most of which are parallel to axis of skull. Pineal window and frontoparietal fenestra absent. In some specimens, through damage, a large pineal window seemingly present (Fig. 30a). Supratemporal groove present and short, not extending to anterior tip of frontal. Postero-superior fossa situated towards hind margin of orbit. Epiotic triangular, pointing postero-laterally. Lachrymal damaged, but length clearly greater than maximum diameter of orbit (Fig. 30b). The pterotic appears as a short spine. Upper jaw long, reaching hind margin of orbit. Presence or absence of supramaxilla not clear. Maxilla/premaxilla complex tightly bound, non-protrusible. Premaxilla long and stout, with a relatively short and small rostral ascending process, which ascends with angle of 40° with posterior shank of premaxilla. Ascending process dorso-caudally two-pronged (Fig. 30a), as in Scombrinae. Both upper and lower jaw slightly damaged, and with rugose horizontal striations, upper jaw seemingly protruding over lower jaw slightly. Two types of teeth: inner row of larger and outer row of smaller teeth (Fig. 30c). Outer tooth row not observed in anteriormost part of either dentary or premaxilla. Small, conical teeth, less than 1 mm long. Principal teeth stout but slender, all of about same length of 6 mm and a few millimetres apart. Teeth semiconical (ovoid in cross-section), and slightly striated basally. Rostral margin of ethmoid indented, semi-forked (Fig. 30a), as in Scomberomorinae and *Scombramphodon*. Eye sclerotics surrounding somewhat ovoid area, long side of oval vertical, about 33 mm long (BMNH P4145). Operculum deep, its ventral margin at same level as dorsal margin of dentary. Ventral margin of ceratohyal smooth, without projections. Vertebral centrum (only seen in holotype) short, amphicoelous and only very slightly medially constricted.

Duplexdens? sp.

Material. BMNH 38903, Sheppey, Ypresian, London Clay.

Description. One pair of damaged premaxillae. Ascending processes, small horizontal portion of premaxillae and anteriormost fragments of maxillae preserved. Ascending process of premaxilla stout, makes angle of 35° with posterior shank, two-pronged dorsally. Empty tooth alveoli are circular.

Remarks. Resembles *Duplexdens* by the stout and relatively long ascending process, which distally has two projections. However, the differentiation of those two processes is less pronounced than in *Duplexdens*. Furthermore, the ascending process of this specimen seems to be longer than in *Duplexdens*, resembling somewhat a premaxilla of a Scomberomorinae, although those have even longer ascending processes. Tooth alveoli are circular. Because of the lack of tooth themselves, it cannot be said whether the teeth are conical over their whole length or compressed towards the apex. *Duplexdens*' teeth are conical.

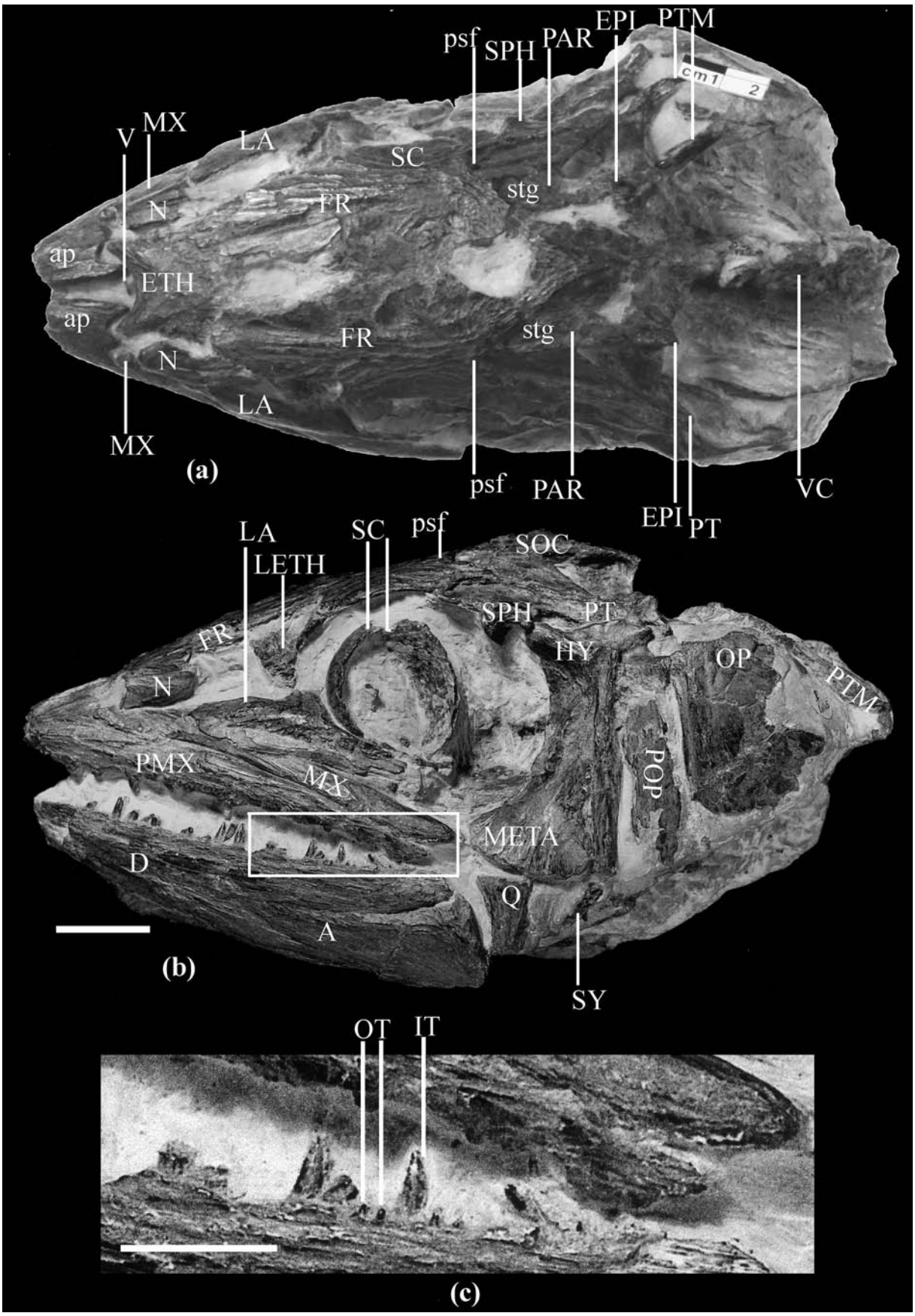

Figure 30 *Duplexdens macropomus*, BMNH 4145, Eocene, London Clay, Sheppey, Kent: (a) dorsal view; (b) left view, rectangle indicates selection for Fig. 30c; and (c) detail of Fig. 30b, showing inner and outer teeth. Scale bars = 10 mm.

Genus *Micrornatus* Monsch gen. nov.
(Fig. 31)

Type species. *Eocoelopoma hopwoodi* Casier, 1966, p. 284, from the Early Eocene of Sheppey.

Derivation of name. Skull is characterised by a few shallow lines of ornamentation (micro-ornatus), as opposed to the numerous, clearer lines which cover the anterior part of the frontals of the similar genus *Eocoelopoma*.

Diagnosis. Postero-superior fossa near middle of orbit, pineal window present, anterior margin of ethmoid emarginate, anterior part of frontal thickened and slightly ornamented with curved lines.

Species composition. Only the type species.

Remarks. *Micrornatus* superficially resembles *Eocoelopoma*, hence it was regarded as such by Casier (1966). However, close investigation revealed significant differences. The antero-dorsal margin of the ethmoid is not emarginate in *Eocolopoma*, but it is in *Micrornatus* (Fig. 31a). Some specimens of *Eocoelopoma* seemingly possess a large pineal window, but since the others do not, the present author considers all apparent pineal windows in *Eocoelopoma* specimens to be artefacts of fossilisation. In *Micrornatus*, however, the borders of the narrow pineal slit appear to be smooth and natural, because of which the author recognises this as a real pineal window. The frontals of *Micrornatus* are much less densely ornamented than those of *Eocoelopoma*. The teeth of *Micrornatus* (see Fig. 31b) are more slender and longer than those of *Eocoelopoma*.

Micrornatus hopwoodi (Casier, 1966) comb. nov.
(Fig. 31)

1966 *Eocoelopoma hopwoodi* Casier, p. 284, text fig. 65, pl. 44, fig. 3.

Holotype. BMNH 36136 (Fig. 31), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype only.

Diagnosis. As for genus.

Description. See description of *Eocoelopoma hopwoodi* (Casier 1966). Holotype is pictured in Fig. 31.

Genus *Scombramphodon* Woodward, 1901

Type species. *Amphodon benedeni* Storms, 1887, p. 265, pl. 4, from the Oligocene of Belgium.

Diagnosis. Anterior margin of ethmoid emarginate. Complete double tooth row with teeth of outer tooth row smaller than those of inner row.

Comparisons. Differs from similar genus *Duplexdens*, which has an incomplete outer tooth row and a wider skull.

Species composition. Three species are recognised: *S. benedeni* and *Scombramphodon curvidens* (Storms, 1887) from the type locality and *Scombramphodon crassidens* Woodward, 1901, from England.

Remarks. *Scombramphodon sheppeyensis* Casier, 1966, is here considered a junior synonym of *Duplexdens macropomus* because it has an incomplete rather than a complete double tooth row. *Scombramphodon* has two complete tooth rows, of which the outer tooth row contains teeth much smaller than those of the inner tooth row. The holotype of *Scombramphodon woodwardi* White, 1926 (BMNH P11853α, β), suggests that both its tooth rows contained teeth of approximately the same size. The present author feels that the fossil is too poorly preserved to attach any identification to it. *S. crassidens* is described below.

Scombramphodon crassidens Woodward, 1901
(Fig. 32)

1833–44 *Sphyraenodus crassidens* Agassiz, p. 99 (*nomen nudum*).
1890 *Dictyodus*? *crassidens* (Ag.) Woodward & Sherborn, p. 64 (*nomen nudum*).
1901 *Scombramphodon crassidens* Woodward, p. 475.
non 1901 *Scombranphodon crassidens* Wood. Woodward, p. 475 (*partim*).
1966 *Scombramphodon crassidens* Wood. Casier, p. 274, text fig. 63, pl. 39, figs 1 & 2.
non 1966 *Scombramphodon crassidens* Wood. Casier, p. 274, pl. 39, fig. 3.
?2000 *Scombramphodon* sp. Clouter *et al.*, p. 68, fig. '*Scombramphodon* sp.'

Holotype. BMNH P1779 and P1779a, Sheppey, Early Eocene (London Clay).

Material. The holotype and BMNH 38945, P1763 (Fig. 32), P1780 (paratype), and P65644; Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus. Other species of this genus have not been studied for comparison.

Description. A detailed description was given by Casier (1966). Recently, a new specimen has been discovered, which is more complete than any other *S. crassidens* specimen and well articulated (Fig. 32). The most significant new information contained in that specimen is found in the well-preserved premaxillae, which possess complete double tooth rows (Fig. 32c), as do the dentaries.

Remarks. Woodward (1901) did not clearly indicate that BMNH P1779 is the holotype of the species, but mentioned it first in the list of specimens of *S. crassidens*, and stated that the specimen was previously labelled as, and intended to be, the type by Louis Agassiz. Even though this is not explicit, Woodward (1901) established holotypes in a similar manner throughout the catalogue and always mentioned the holotype first in his lists of specimens. The same can be seen in his assignment of the holotype of *Scombrinus nuchalis*, which was indeed interpreted correctly by Casier (1966). However, Casier (1966) seemed to assume that Woodward (1901) did not establish a holotype, and represented Woodward's hypodygm as a series of syntypes. BMNH 38907 and P158, two specimens of Casier's (1966) 'syntypes', are considered part of *Duplexdens macropomus* here.

Genus *Sphyraenodus* Agassiz, 1844

Type species. *Sphyraenodus priscus* Agassiz, 1844, p. 98, from the Early Eocene of England.

Diagnosis. Teeth with basal striations, post-temporal fossae present (see description of *S. priscus*, below). Preserved precaudal part of trunk with large scales.

Species composition. Besides the type species, four other species are known (Casier 1966). *Sphyraenodus goniopleurus* (Casier 1966, p. 35 and index) is a misprint of *Myliobatis goniopleurus* Agassiz, 1834. Woodward (1901) noted that *Sphyraenodus conoideus* Von Meyer, 1851, resembled a *Stereodus* Owen, 1865. However, a specimen figured by Von Meyer (1851) does not really compare with *Stereodus*. The shape of its

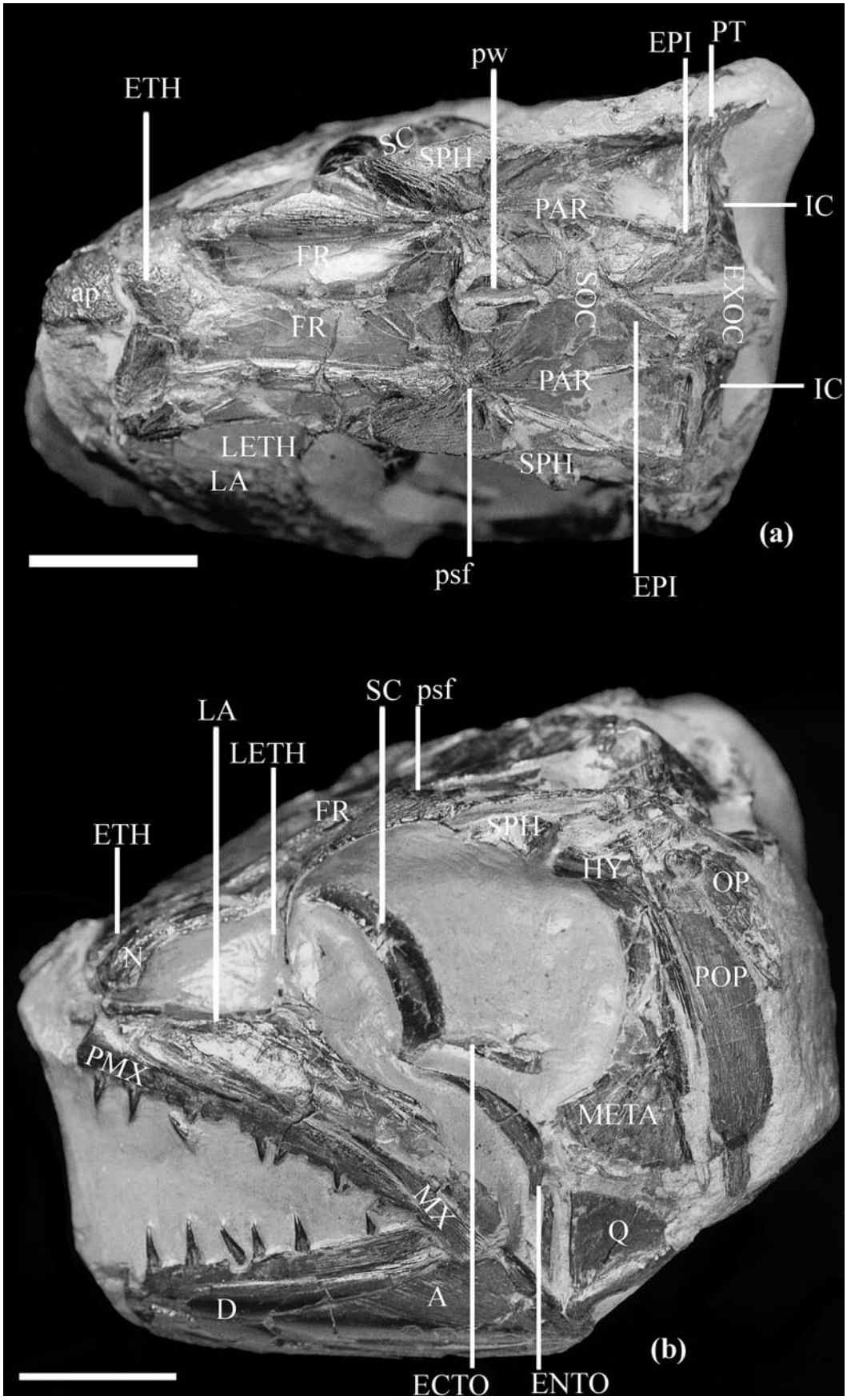

Figure 31 *Micrornatus hopwoodi*, BMNH 36136, Eocene, London Clay, Sheppey, Kent: (a) dorsal view; and (b) left view. Scale bars = 15 mm.

teeth at the base is different: *Stereodus* teeth are more circular and their density in the dentary is also less (Owen 1865). Besides that, the present author suspects that '*S. conoideus*' cannot be assigned to *Sphyraenodus* either. The base of a *Sphyraenodus* tooth is shaped differently and is striated, whereas the '*S. conoideus*' tooth is not. The author has not

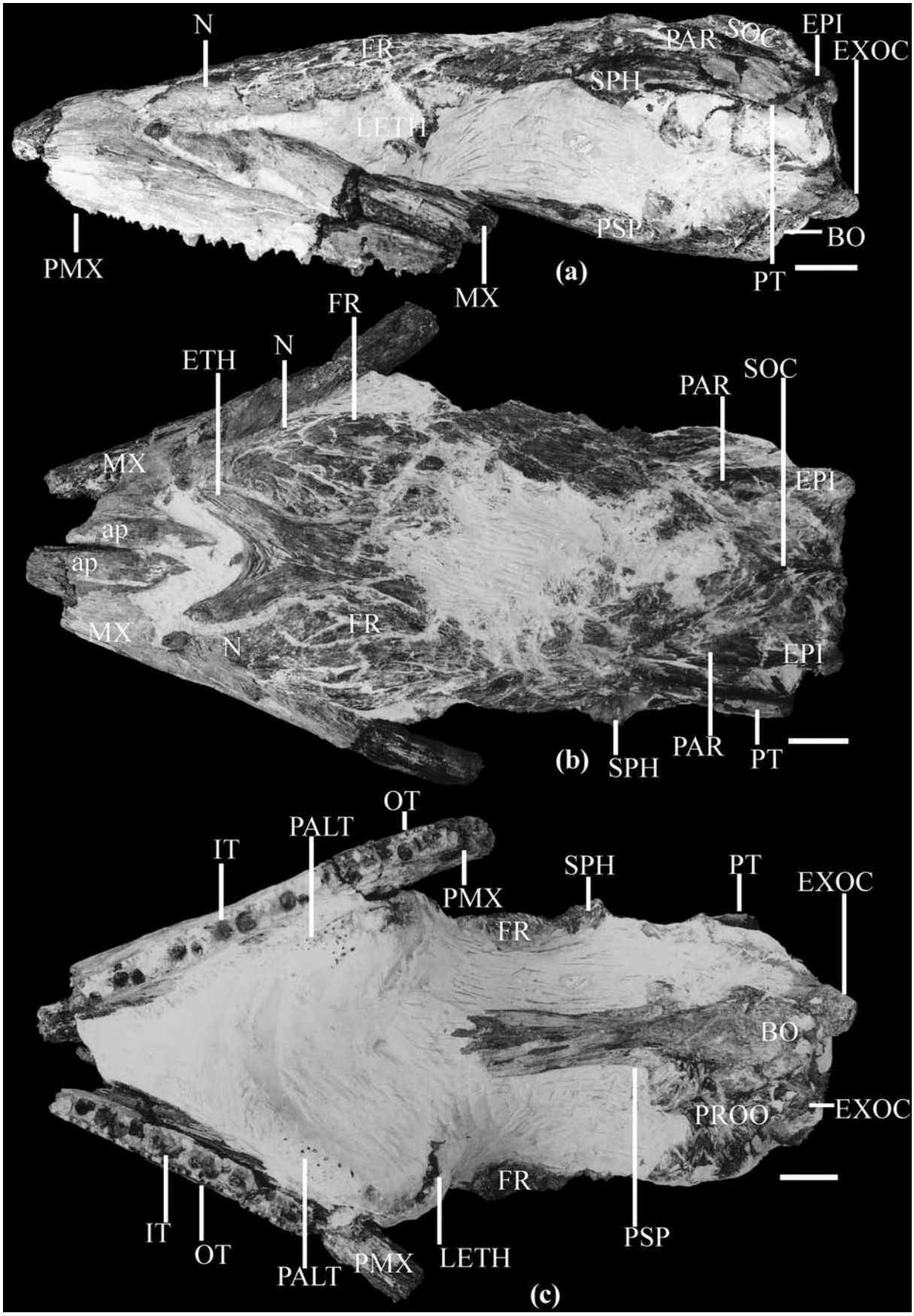

Figure 32 *Scombramphodon crassidens*, BMNH P1763, Eocene, London Clay, Sheppey, Kent: (a) left view; (b) dorsal view; and (c) ventral view. Scale bars = 20 mm.

been able to determine the identity of the fossils figured by Von Meyer (1851). A specimen of *Sphyraenodus* (USNM 265382) is known from Ypresian of Maryland, USA (Monsch 2000b). Unfortunately, its specific identity could not be established. It remains the only American specimen of *Sphyraenodus* known.

Remarks. Owen (1839) published the description of genus *Dictyodus*, based on fragmentary jaws. The name *Sphyraenodus* appeared for the first time in 1839, in a volume of plates of Agassiz' *Recherches sur les Poissons Fossiles* (Vol. 5). The text volume, with the description of *Sphyraenodus* did not appear until 1844 (Agassiz 1833–1844). Later, Owen (1840–1845; the section concerned here was published in 1841) stated that *Dictyodus* is a synonym of *Sphyraenodus*. However, the name *Dictyodus* should have had age preference over *Sphyraenodus*: that name was not validly published in 1839 (figure only) and is to be recognised as formal only at the appearance of the description in 1844. It seems that Owen's *Dictyodus* is based on some fragmentary jaws (now missing) in the Royal College of Surgeons. The specimens show a resemblance to *Sphyraenodus*, but they are too imperfect for a definite determination (Woodward 1901). Hence, it is not possible to employ the name *Dictyodus* and the next valid name *Sphyraenodus* is retained. *Sphyraenodus tenuis* Dixon, 1850, is based on an unidentifiable jaw fragment, which is described below as *Incertae sedis* sp. under *Incerti subordinis*.

Following Casier (1966), *S. priscus* and *Sphyraenodus lerichei* Casier, 1944b, are known from distinctly separated locations, i.e. SE England and Belgium, respectively. Kemp *et al*. (1979, 1990, pl. 17, fig. 12) mentioned S. lerichei teeth from Middle Eocene outcrops of S England. The figure they provided is not sufficient to base a generic and specific identification on, and the tooth pictured there is retrorse as opposed to the relatively straight teeth of *Sphyraenodus* of which the present author is aware (Casier 1944b, 1946, 1966).

Sphyraenodus priscus Agassiz, 1844
(Fig. 33)

1833–44 *Sphyraenodus priscus* Agassiz, p. 98, pl. 26, figs 4–6.
1890 *Dictyodus priscus* (Ag.) Woodward & Sherborn, p. 64.
1901 *Sphyraenodus priscus* Ag. Woodward, p. 473.
1966 *Sphyraenodus priscus* Ag. Casier, p. 286, text fig. 66, pl. 46, pl. 47, fig. 1.

Holotype. BMNH P3957 (Fig. 33c), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype and BMNH 35106 (Fig. 33a, b), P21651–54 (Fig. 33d), P21669 and P25386–46, Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus.

Description. Detailed description given by Casier (1966). Different observations and additional information given here. Teeth about equal in size. Eye sclerotics thick, with combined diameter about 25% of total length of neurocranium. Hyoid complex elongate. Hypohyal small, 17 mm long, ceratohyal (95 mm) long (measurements from holotype). Pelvic plate ('basipterygium') large, but not well preserved in specimens.

Remarks. Casier (1966, p. 287) figured a reconstruction of the neurocranium, with large posttemporal fossae (rounded depressions or openings at the junction of sphenotic, pterotic and parietal). The present author regards the presence of these fossae as an autapomorphy of *Sphyraenodus*. From the specimens (BMNH 35106, Fig. 33b), their exact size, shape and depth cannot be determined. However, it is still possible that these are not genuine fossae, but depressed parts of the temporal groove. The samples of isolated teeth mentioned here (BMNH P21651–54 and P25386–46) are in the collection labelled '*Sphyraenodus* sp.'. Casier (1966) described the differences in tooth morphology between the different species of *Sphyraenodus*, but did not describe the teeth of *Sphyraenodus rupeliensis* Dollo & Storms, 1888. The samples of isolated teeth in question here (Fig. 33d) seem to be identical to teeth of *S. priscus*. Only on the largest teeth, the striations seem a bit stronger than on teeth in crania such as BMNH P3957 and 35106. *Sphyraenodus rupeliensis* is only known from the Oligocene of Belgium (Leriche 1910), while *S. priscus* is known from the Ypresian of England only. Therefore, it is likely that these teeth belong to *S. priscus*.

Genus *Wetherellus* Casier, 1966

Type species. *Wetherellus cristatus* Casier, 1966, p. 263, from the Early Eocene of England.

Diagnosis. Double tooth row, both rows seemingly cover whole length of tooth bearing bone.

Comparisons. Other genera with double tooth row (*Scombramphodon* and *Duplexdens*) possess deeply emarginate, forked ethmoids. That of *Wetherellus* only slightly emarginate.

Species composition. Casier (1966) described three species of *Wetherellus*, all known from the London Clay. Bannikov (1985) expressed his suspicion that all three species of *Wetherellus* are identical. The present author can now confirm that this is indeed the case, and hence, describe the type (and only) species *W. cristatus* below, along with the reasons for recognising only one species.

Wetherellus cristatus Casier, 1966
(Fig. 34)

1833–44 *Pachycephalus cristatus* Agassiz, p. 139 (*nomen nudum*).
1845 *Pachycephalus cristatus* Agassiz, p. 308 (*nomen nudum*).
1901 Indeterminable Woodward, p. 612.
1966 *Wetherellus cristatus* Casier, p. 263, text figs. 60–62, 73A, pl. 36, pl. 37, figs 2 & 3.
1966 *Wetherellus brevior* Casier, p. 270, pl. 38.
1966 *Wetherellus longior* Casier, p. 270, pl. 37, fig. 1.

Holotype. BMNH 28498, (Fig. 34b), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype and BMNH 269891 (holotype of *Wetherellus brevior* Casier, 1966; Fig. 34a), P26719 (formerly P1698, paratype of *W. cristatus*), P45045 (previously P1758a, paratype of *W. cristatus*), P45047 (previously 30893, holotype of *Wetherellus longior* Casier, 1966; Fig. 34c), P45048 (previously 38093a, paratype of *W. cristatus*), Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus.

Description. Species described in detail under three different names, which are mentioned above in synonymy. Casier's (1966) *W. cristatus* is described in more detail than the other two 'species'. Differences with Casier's descriptions and additional information are noted here. Supratemporal groove short, ending posterior to middle of orbit. Postero-superior fossa posterior to middle of orbit. Pterotic is a short spine. Intercalar with short, inconspicuous posterior projection. Tooth rows double, teeth of inner and outer row almost of same size, inner teeth slightly larger. Ceratohyal with hyoidean window. Ethmoid slightly emarginate, but not fork-shaped as in Scomberomorinae, *Acanthocybium* and fossils such as *Scombramphodon*.

Remarks. The present author recognises here only one species, rather than three as Casier (1966) did on erection of the genus. Casier seemed to treat the presence of a double tooth row in '*W. brevior*' as a special feature, one of the characters he used to diagnose the species. The teeth are badly preserved in specimens of '*W. cristatus*' and '*W. longior*' in such a way that one cannot conclude that they have a single

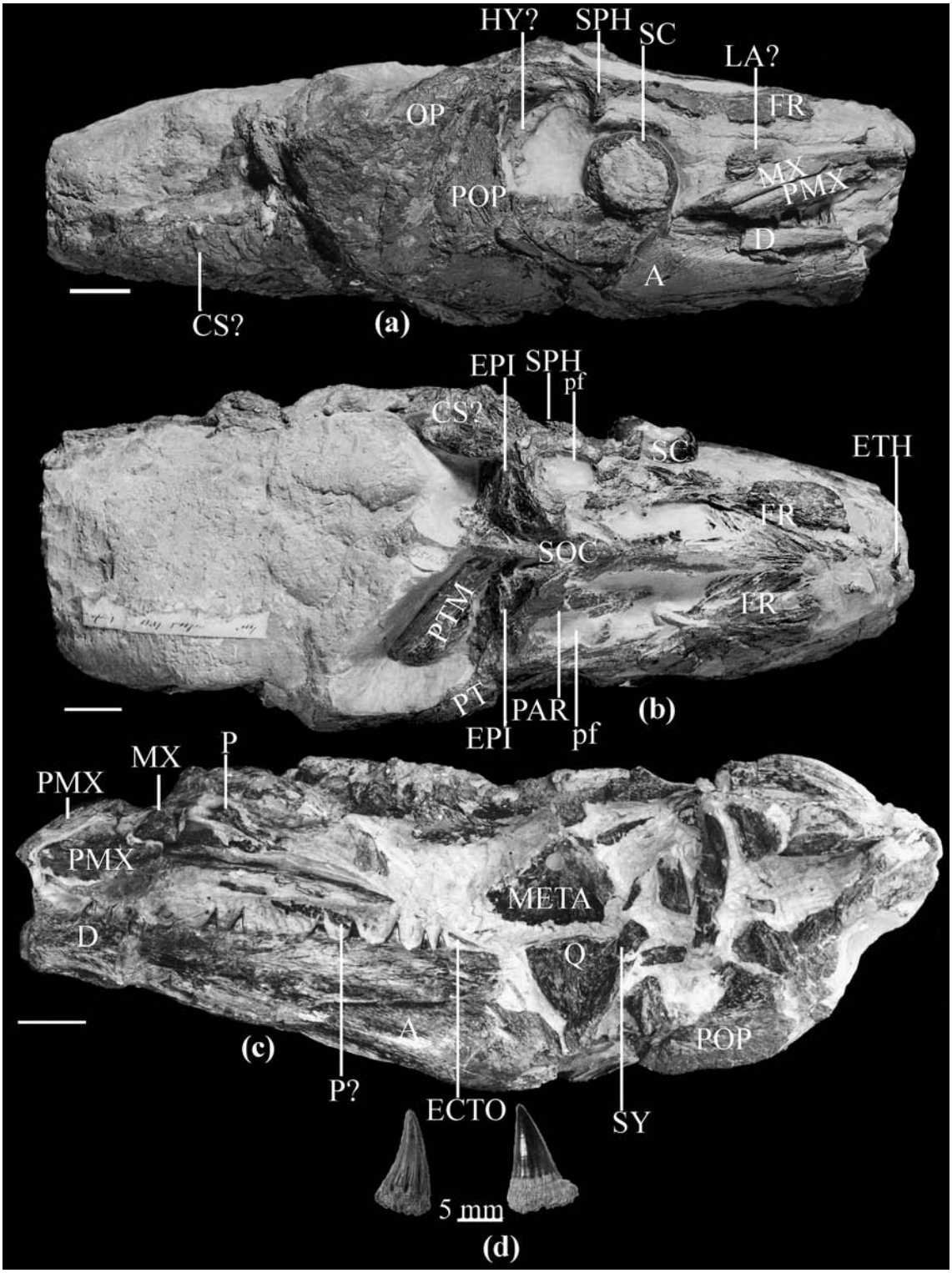

Figure 33 *Sphyraenodus priscus*, Eocene, London Clay, Sheppey, Kent: (a) right view of BMNH 35106; (b) dorsal view of BMNH 35106; (c) left view of BMNH P3957; and (d) two teeth from BMNH P21651–54. Scale bar = 20 mm, unless otherwise indicated.

tooth row, and that a multiplied tooth row is thus an apomorphy of '*W. brevior*'. Casier (1966) distinguished *W. longior* from other species of *Wetherellus* (amongst others) by the length of its exoccipital. He considered the exoccipital in *W. longior* longer than in other species. Although the exoccipital might have been longer in '*W. longior*', the difference does not seem significant. Moreover, in specimens of '*W. cristatus*' and '*W. brevior*', the exoccipitals cannot be properly investigated because they are obscured by the first vertebra. The exoccipital seems to be longer in '*W. longior*' because it is fully exposed. The present author has failed to see any significant differences between the different 'species' of *Wetherellus*. He considers them one and the same species, characterised by a double tooth row.

Genus *Woodwardella* Casier, 1966

Type species. *Woodwardella patellifrons* Casier, 1966, p. 290, from the Early Eocene of England.

Diagnosis. Postero-superior fossae near anterior margin of orbit.

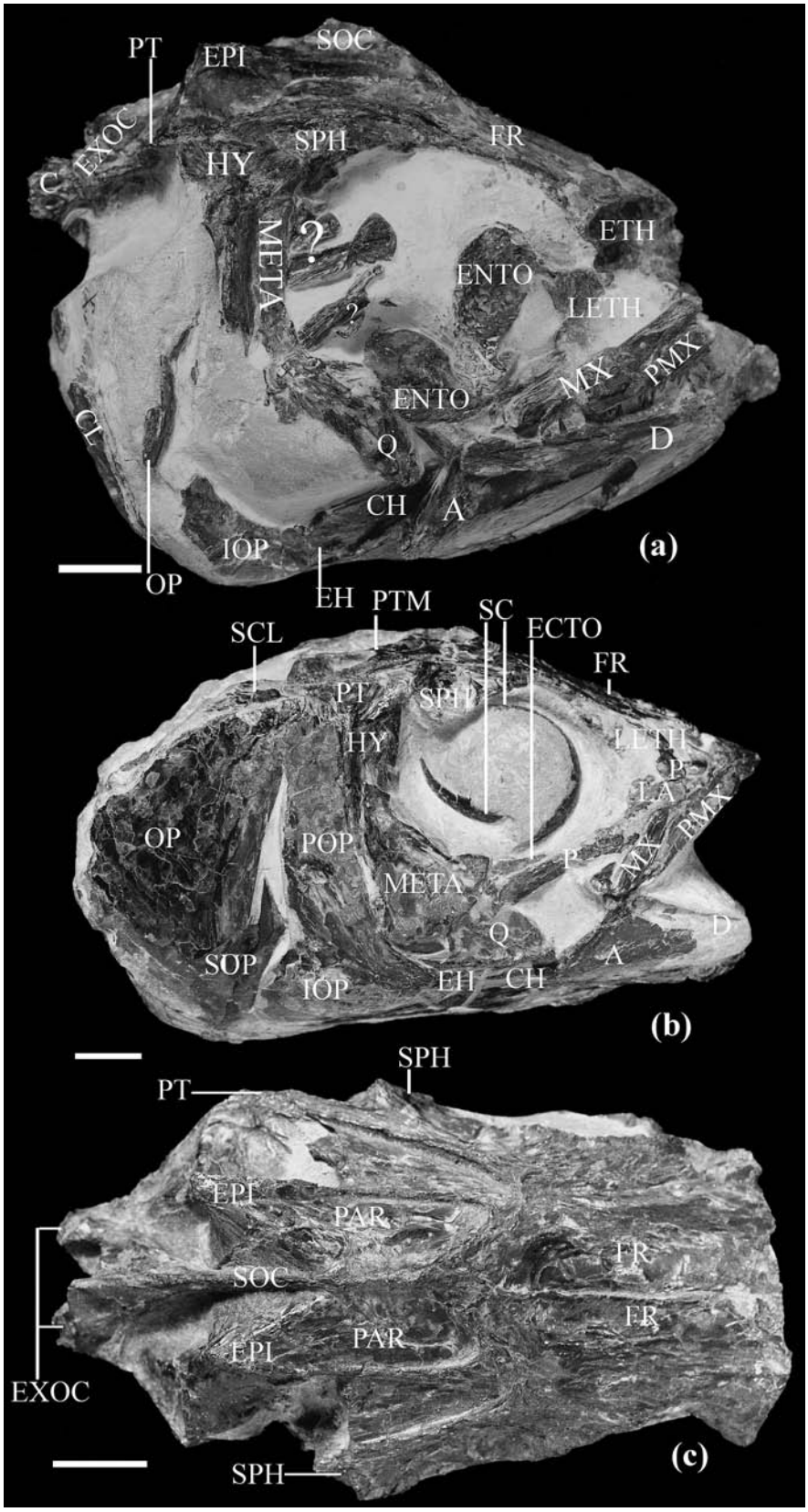

Figure 34 *Wetherellus cristatus*, Eocene, London Clay, Sheppey, Kent: (a) BMNH 269891 (holotype of '*Wetherellus brevior*'); (b) BMNH 28498 (holotype of *Wetherellus cristatus*); and (c) BMNH P45047 (holotype of '*Wetherellus longior*'). Question marks indicate branchial arch elements which cannot be identified further. Scale bar = 10 mm.

Species composition. Type species only.

Remarks. *Woodwardella* is probably a scombrid. It shares a vomerine character with Scomberomorinae and *Acanthocybium* (see below). However, in a provisional cladistic analysis of scombroids (Monsch 2000b), its place within the scombroids is unresolved through lack of other definite characters.

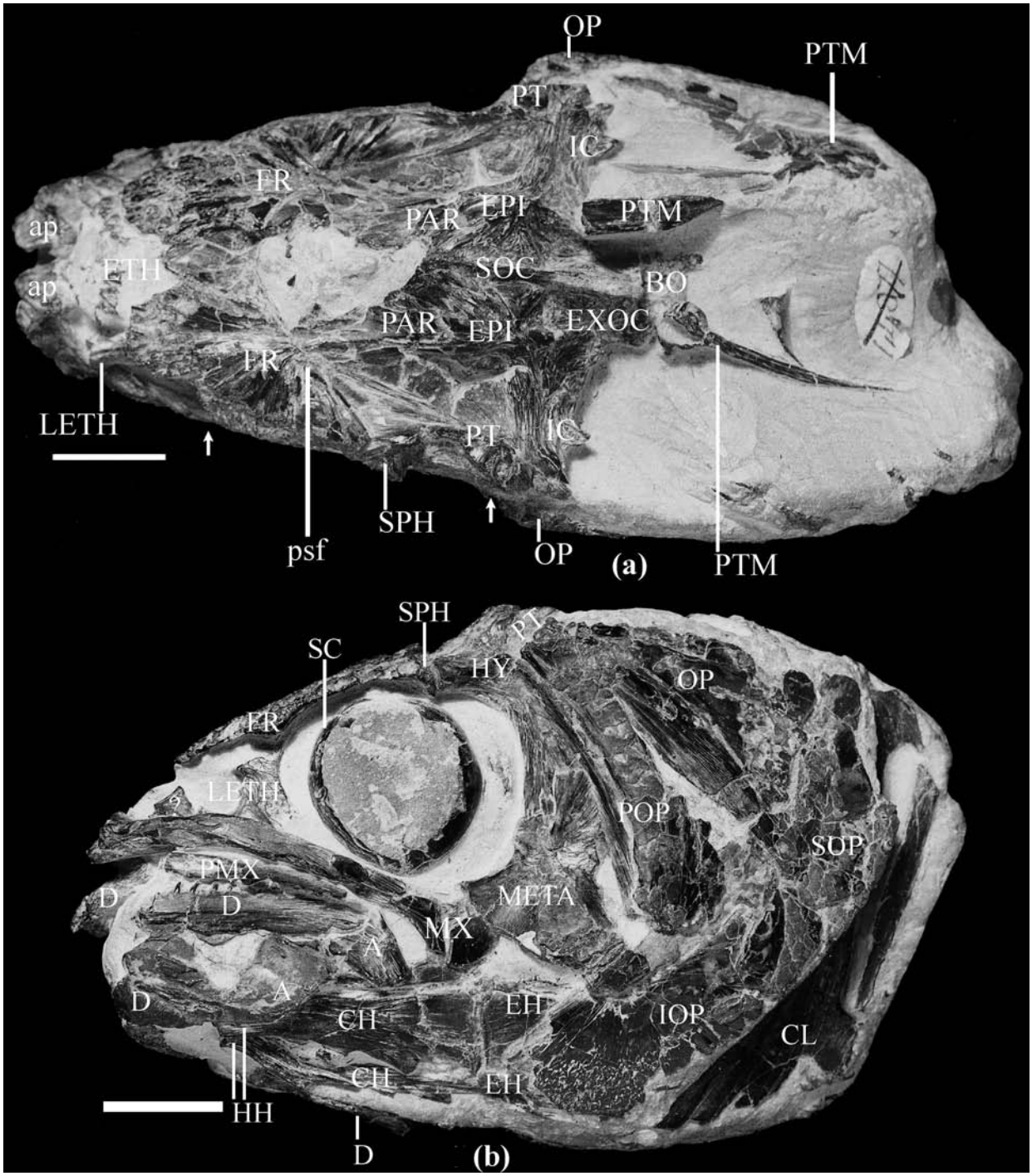

Figure 35 *Woodwardella patellifrons*, BMNH P26903, Eocene, London Clay, Sheppey, Kent: (a) dorsal view; and (b) left view. Arrows indicate anterior and posterior margin of orbit. Scale bars = 10 mm.

Woodwardella patellifrons Casier, 1966
(Fig. 35)

1966 *Woodwardella patellifrons* Casier, p. 290, text fig. 67, pl. 25, fig. 3.

Holotype. BMNH P26903, Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype only.

Diagnosis. As for genus.

Description. A description was given by Casier (1966). Additional information and differences are given here. Premaxilla forms non-protrusible complex with maxilla. Supratemporal groove relatively short, reaching up to anterior margin of orbit. Skull roof damaged at pineal region, through which presence or absence of pineal window cannot be assessed. Pterotic spine short, reaching up to base of exoccipital. Anterior margin of vomer spatulate, as in Scomberomorinae and *Acanthocybium*. Scales on opercular bones large.

Incerti subordinis
Genus *Ardiodus* White, 1931

Type species. *Ardiodus mariotti* White, 1931, p. 89, Late Palaeocene (Oldhaven Beds)-Early Eocene (Ypresian).

Diagnosis. Known from teeth which resemble the subconical, short, stout teeth of Scomberomorinae, but are more strongly curved.

Comparisons. Similarities between *Ardiodus* and *Eocoelopoma* are remarked first by Casier (1966). However, *Ardiodus*

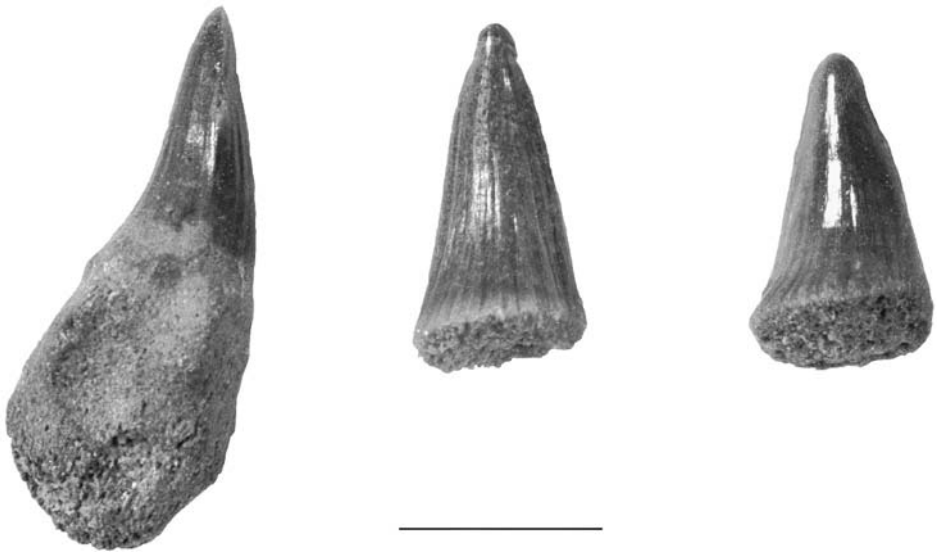

Figure 36 *Ardiodus mariotti*, three teeth from BMNH P14809, Palaeocene, Oldhaven Beds, Upnor, Kent. Scale bar = 5 mm.

teeth are larger than those of *Eocoelopoma*. The largest *Ardiodus* tooth that the present author has seen (amongst specimens listed in species description below) possesses a crown of 8 mm. The largest *Eocoelopoma gigas* teeth are 6 mm long. *Ardiodus* teeth have a lateral cutting edge, which is absent in *Eocoelopoma*. Another feature of *Ardiodus*' teeth, missing in *Eocoelopoma*, is the presence of barbed apices in most teeth (compare with trichiurins and gempylins).

Species composition. Only the type species.

Remarks. Although known from teeth only, *Ardiodus* is most likely to be a scombroid. There are resemblances to gempylins, trichiurins, *Eocoelopoma* and Scomberomorinae. Casier (1966) also remarked resemblances to *Eutrichiurides* and *Scombramphodon*. White (1931) and Danil'chenko (1960) placed *Ardiodus* in the Trichiurinae, most likely because of the barbed teeth. The present author does not recognise this as an apomorphy exclusive to the trichiurins. These dental remains do not provide sufficient characters to assess the phylogenetic position of *Ardiodus*.

Ardiodus mariotti White, 1931
(Fig. 36)

1931 *Ardiodus mariotti* White, p. 89, plate figs 4 & 5.
1966 ?*Ardiodus mariotti* Wh. Casier, p. 297.

Holotype. BMNH P14692, Upnor, Kent, Late Palaeocene (Oldhaven Beds).

Diagnosis. As for genus.

Material. The holotype and BMNH P14809 (Fig. 36), Upnor, Kent, Late Palaeocene (Oldhaven Beds); P26601–4, Sheppey, Early Eocene: Ypresian (London Clay); P42689, Bognor Regis, Sussex, Early Eocene: Ypresian (Lower Fish-tooth Bed, London Clay).

Description. Base of tooth circular (especially in the larger specimens) to semicircular. Crown gradually tapering labiolingually towards apex. Lateral edges sharp, without serrations. Apical barbs in most teeth. Largest tooth 8 mm (in sample BMNH P14809). Striations on surface of tooth variable: seemingly smooth (but under binoculars, faint striations visible), basally straited to completely and densely striated.

Remarks. The present author here identifies a sample of teeth, BMNH P38281–3 (Morocco, Phosphates, Late Palaeocene–Early Eocene: Thanetian-Ypresian) as of *A. mariotti*. This is the first report of Moroccan *Ardiodus*. The spatial distribution of this species as known so far (England and Morocco) does seem somewhat unlikely, but the author is confident of the specific identification. All Moroccan teeth seem smooth at first sight, although faint striations are visible under the microscope. The English teeth show a large variety, from hardly to densely striated. The degree of striations of the Moroccan sample does fit in with the variety as seen in the English specimens and there seem to be no other diagnostic characters. Hence, the Moroccan samples are also identified as *A. mariotti*.

Ardiodus mariotti fossils are known from the Thanetian (Thanet Formation) to the Ypresian (London Clay) of the Herne Bay locality in Kent (see Dineley & Metcalf 1999).

Incertae sedis sp. 1

1901 *aff. Planesox vorax* Ow. Woodward, p. 519.
1966 Unidentifiable percomorph, Casier, p. 317.

Material. BMNH P26709 (formerly P1998x), Sheppey, Early Eocene: Ypresian (London Clay).

Description and remarks. Woodward (1901) regarded the specimen in question as an unidentifiable percid, but similar to *Planesox vorax*. He also considered BMNH 32388 (later the holotype of *Progempylus edwardsi*, see above) to be similar to *P. vorax*. The name *Planesox* cannot be assigned to BMNH P26709, for reasons which the present author mentioned earlier in this paper. Viewed from dorsal, the cranium of P26709 does resemble that of a gempylin, but it lacks any clear generic and specific apomorphies. Only a few generalised comparisons with other taxa can be made. The operculum of this specimen seems much larger than in known gempylins. The skull as a whole is also shorter than expected from a Gempylinae. Viewed from lateral, it reminds more of a skull belonging to a Sardini or Thunnini. However, the cranium is clearly elevated, as opposed to the flat cranium of the tunnies and bonitos. Furthermore, the absence of the premaxillary–maxilla complex makes it unsure whether this specimen belongs to the scombroids at all. An apomorphy of scombroids is the non-protrusibility of the upper jaw.

Incertae sedis sp. 2

1850 *Sphyraenodus tenuis* Dixon, p. 112, pl. xi, fig. 24.
1850 *Sphyraenodus gracilis* Dixon, p. 205.
1901 *Cybium*? Woodward, p. 469.

Material. BMNH 25739, 25740, 25819 (Holotype of *Sphyraenodus tenuis*), 25819a, Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

Description. The holotype of *Sphyraenodus tenuis* is a badly preserved piece of teeth-bearing bone (either a dentary of premaxilla) in which the teeth are worn and damaged to such a degree that an identification seems impossible. Woodward (1901) thought it possible that the specimen may be a premaxilla of '*Cybium*' (*Scomberomorus*), for reasons he did not specify. The specimens BMNH 25739, 25740 and 25819a seem similar to the holotype of *S. tenuis*, but do not provide any further clarity.

Incertae subfamiliae *non* Xiphiinae

The taxa described in this section have previously been identified as billfish. The present author is particularly concerned about 'rostrum'-based taxa such as *Cylindracanthus*; he is uncertain if these can really be assigned to teleosts or even to fish at all.

Genus *Cylindracanthus* Leidy, 1856

Type species. *Cylindracanthus rectus* (Dixon, 1850), Bracklesham Bay, England: Eocene.

Diagnosis. 'Rostra' with almost circular cross-section, whole outer surface with parallel lengthwise grooves, two large and two small nutrient canals (sometimes the small canals are missing) and two narrow, widely separated tooth rows.

Species composition. Six species are known to occur from the Cenomanian (Late Cretaceous) to the Priabonian (Late Eocene), but possibly occurring in the Pliocene (Schultz 1987). *Cylindracanthus rectus* is described below.

Remarks. *Cylindracanthus* remains are often diagnosed as billfish because they superficially remind one of rostra, and possess what are interpreted as nutrient canals. There are lengthwise grooves over the whole of the surface. This character state is also found in the billfish *Blochius* Volta, 1796 (Fierstine & Monsch 2002). The probable billfish *Aglyptorhynchus* also possesses such shallow grooves (Fierstine 2001). *Cylindracanthus* is sometimes considered a relative of *Blochius* (see Casier 1966, Schultz 1987). However, the present author is sceptical of the assignment of *Cylindracantus* remains to billfish. *Cylindracathus* rostra appear much more conical through their whole length than any known billfish rostrum. In all billfishes, there is a degree of flattening near the anterior tip of the bill. The bulk of the scombroid fossils appear in the Ypresian (Early Eocene), but the oldest *Cylindracanthus* fossils date from the Late Cretaceous period of the Cenomanian (Schultz 1987). It has been suggested that the *Cylindracanthus* 'rostrum' is a chimaeroid spine (Woodward 1891a).

Cylindracanthus rectus (Dixon, 1850)
(Fig. 37)

1833–1844 *Coelorhynchus rectus* Agassiz, p. 92 (*nomen nudum*).
1850 *Coelorhynchus rectus* Dixon, p. 112, pl. 10, figs 14–17; pl. 11, fig. 26.
1856 *Cylindracanthus ornatus* Leidy, p. 12.
1871 *Coelorhynchus burtini* Le Hon, p. 14.
1871 *Coelorhynchus rectus* (Dixon) Van Beneden, p. 500.
1891a *Coelorhynchus rectus* (Dixon) Woodward, p. 107.
1891b *Coelorhynchus rectus* (Dixon) Woodward, p. 120.
1905 *Coelorhynchus rectus* (Dixon) Leriche, p. 79, pl. 11, figs 4–6.
1905 *Glyptorhynchus rectus* (Dixon) Leriche, p. 159.
1906 *Glyptorhynchus rectus* (Dixon) Leriche, p. 168, pl. 14, figs 4–6.
1910 *Cylindracanthus rectus* (Dixon) Leriche, p. 223 (*nomen nudum*).
1920 *Cylindracanthus rectus* (Dixon) Leriche, p. 82.
non 1926 *Cylindracanthus rectus* (Dixon) White, p. 67, pl. 17, figs 1–5, pl. 18, figs 1 & 5.
1966 *Cylindracanthus rectus* (Dixon) Casier, p. 174, pl. 22, figs 1–5.
1979 *Cylindracanthus rectus* (Dixon) Kemp *et al*., p. 101 (*nomen nudum*).
1984 *Cylindracanthus rectus* (Dixon) Kemp, p. 162 (*nomen nudum*).
1985 *Cylindracanthus rectus* (Dixon) Kemp, p. 43 (*nomen nudum*).
1990 *Cylindracatnus rectus* (Dixon) Kemp *et al*., p. 11, pl. 18, fig. 1.
2000 *Cylindracanthus rectus* (Dixon) Clouter *et al*., p. 66, 3 figures.

Lectotype (as established by Woodward 1891a). BMNH 25859, Bracklesham Bay, Sussex, Ypresian-Lutetian (Bracklesham Beds).

Material. The lectotype and BMNH 25729 (Fig. 37b) from the type locality; 38881, 38881a (Fig. 37a), Sheppey; P4304, Barton Cliff, Hampshire, Bartonian (Barton Clay); P6232, Sheppey; Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus. Besides material of this species the present author managed to study only one other member of this genus, namely *Cylindracanthus gigas* Woodward, 1888, (BMNH 893–5, from the Eocene of Egypt) which is larger ('rostrum' diameter of about 17·8 mm, *C. rectus* 7–11 mm). See also remarks.

Description. Long and slender spine-like structure, 7–11 mm in diameter, with numerous narrow lengthwise grooves. Transverse cross-section circular. In ventral grooves (which are about 1 mm wide), immediately next to midline of BMNH 38881, are badly preserved empty alveoli. In some specimens, there are two pairs of 'nutrient canals', a pair of larger and a pair of smaller canals (Fig. 37a). The large canals diminish in size anteriorly. There are also specimens that have one pair of large canals which coalesce into a single large canal anteriorly.

Remarks. The present author suspects that material of *C. rectus* is heterogenous. The different systems of 'nutrient canals', as described above, seem too variable to be ascribed to a single species, or maybe even to a single genus. At this point, the author cannot verify what the original *C. rectus* is like. He has not been able to trace all type specimens of Dixon (1850). Thus, *C. rectus*, rather than a valid specific name, seems to be an indication for different kinds of spines whose origins are uncertain.

White (1926) described vertebrae that he supposed to be *Cylindracanthus rectus*. The present author describes these vertebrae above under 'Xiphiinae indet'.

Genus *Acestrus* Woodward, 1901

Type species. *Acestrus ornatus* Woodward, 1901, p. 494, from the Early Eocene of England.

Diagnosis. Postero–superior fossae posterior of orbit.

Species composition. Only the type species. *Acestrus elongatus* Casier, 1966, is not recognised here. Its holotype, BMNH

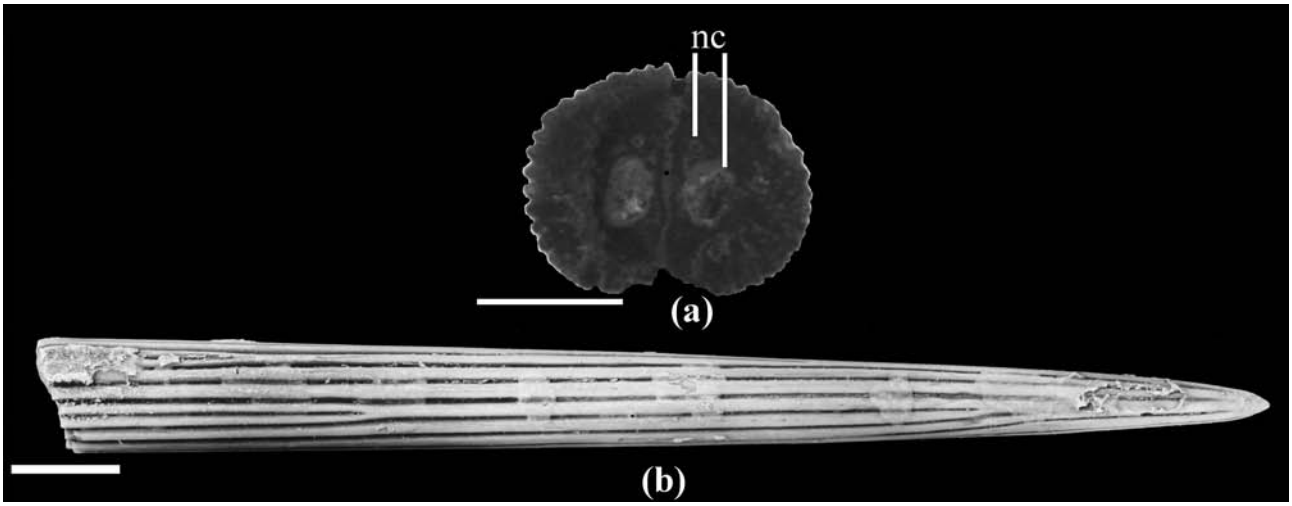

Figure 37 *Cylindracanthus rectus*, Eocene: (a) one of the spines from BMNH 25729, Bracklesham Beds, Bracklesham Bay, Sussex; and (b) transverse cross-section of BMNH 38881a, London Clay, Sheppey, Kent. Scale bars = 5 mm.

P12954, bears only a superficial resemblance to the type species of *Acestrus*, has longer supratemporal grooves and more anteriorly placed postero-superior fossae. Casier (1966) remarked that BMNH P12954 is similar to '*Scombrinus*'. The hypodygm of *Scombrinus* is revised here, and thus '*Scombrinus macropomus*' is assigned to a new genus *Duplexdens*. The holotype of '*A. elongatus*' is here included in the hypodygm of *D. macropomus*.

Remarks. This genus is known from its braincase only. It was considered a scombroid because of similarities with *Xiphias* (Casier 1966). However, these similarities come down to superficial resemblances, such as the shape of the cranium and the pattern of ridges on the skull roof. However, there are no diagnostic synapomorphies which permit an inclusion of *Acestrus* in Scombroidei. The maxilla and premaxilla are missing, and hence, there is no information on whether these form a non-protrusible complex. Neither can it be deduced from the specimens whether *Acestrus* possesses a billfish-like rostrum, through which affinities to *Xiphias* could be postulated with a good degree of certainty. The postero-superior fossa is situated posterior to the orbit. In billfish, the fossa in question is situated close to the vertical midline of the orbit (Monsch 2000b).

Acestrus ornatus Woodward, 1901
(Fig. 38)

1845 *Acestrus ornatus* Agassiz, p. 308 (*nomen nudum*).
1901 *Acestrus ornatus* Woodward, p. 494, pl. 19, fig. 3.
1966 *Acestrus ornatus* Wood. Casier, p. 315, fig. 73D.

Holotype. BMNH 627 (Fig. 38a), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype, and BMNH P1793, P60905 (Fig. 38b), Sheppey, Early Eocene: Ypresian (London Clay).

Diagnosis. As for genus.

Description. Adequate descriptions were given by Woodward (1901) and Casier (1966).

Genus *Congorhynchus*? Dartevelle & Casier, 1949

Diagnosis. 'Rostrum' with angular, longitudinal ridges and two single tooth rows.

Type species. *Congorhynchus trabeculatus* Dartevelle & Casier, 1949, p. 247, from the Late Cretaceous of Congo.

Species composition. Four species are known (Schultz 1987), ranging in age from the Maastrichtian to the Early Eocene. The only specimen that the present author has seen that might have an affinity with *Congorhynchus* is one of *Congorhynchus elliotti* (Casier, 1966).

Remarks. *Congorhynchus* is known from spine-like fossils only. They are thought to be billfish based on a superficial resemblance to billfish rostra. However, no synapomorphies with billfishes or even scombroids are preserved in the spines concerned. The present author doubts whether all so-called *Congorhynchus* species belong to one and the same genus. The variety between the different 'species' (Schultz 1987, fig. 5) looks too great in my opinion.

Congorhynchus? *elliotti* (Casier, 1966)
(Fig. 39)

1966 *Hemirhabdorhynchus elliotti* Casier, p. 175, text fig. 30, pl. 22, fig. 6.
1987 *Congorhynchus elliotti* Cas. Schultz, fig. 5.

Holotype. BMNH P21304 (Fig. 39), Sheppey, Early Eocene: Ypresian (London Clay).

Material. The holotype only.

Diagnosis. Four dorsal ridges, tooth rows widely separated, two pairs of nutrient canals, one large, one small.

Description. Description given by Casier (1966). In that description, two large nutrient canals are mentioned, while the present author believes there is a pair of dorsal small canals as well (Fig. 39a).

Remarks. The present author doubts whether the holotype of *C. elliotti* concerns a billfish. Rather than a rostrum, this minute fossil resembles more a hollow spine with two rows of 'ventral' denticles.

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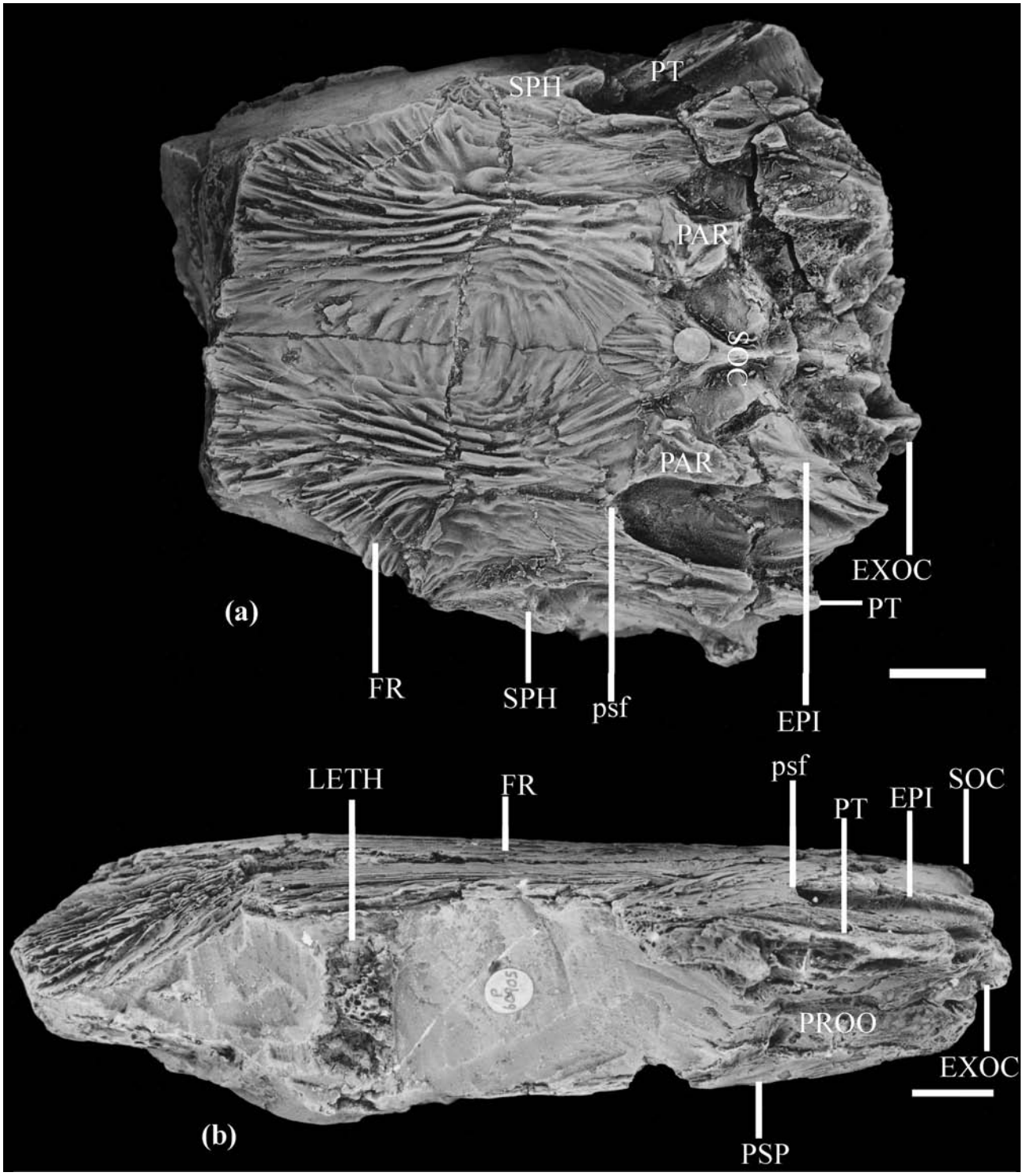

Figure 38 *Acestrus ornatus*, skulls, Eocene, London Clay, Sheppey, Kent: (a) BMNH 627 (dorsal view); and (b) BMNH P60905 (lateral view).

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4. Appendix 1. Explanation of anatomical and institutional abbreviations

A	angular
ap	ascending process of premaxilla
b	barb on premaxillary fang
BOC	basioccipital
C	centrum
cc	central canal
CH	ceratohyal
CK	caudal keel
COR	coracoid
CS	corselet scale
D	dentary
EH	epihyal
EPI	epiotic
ETH	ethmoid
F	fang

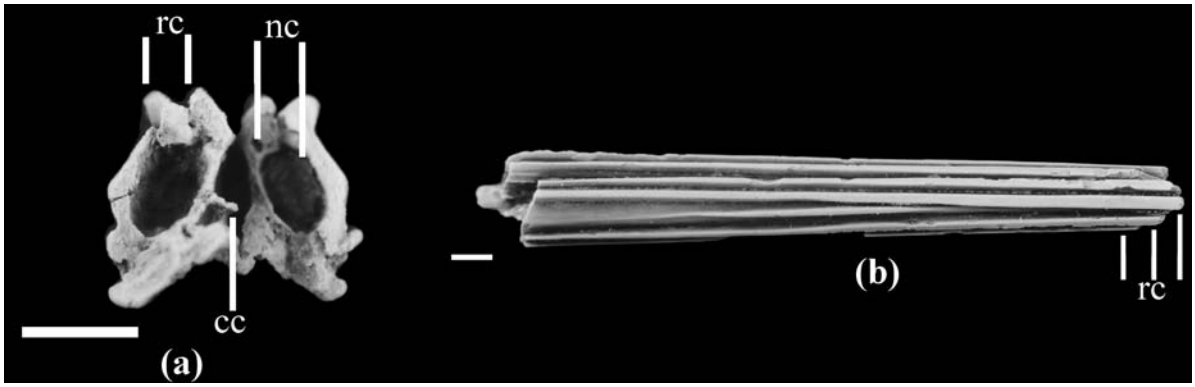

Figure 39 *Congorhynchus elliotti*, BMNH P21304, Eocene, London Clay, Sheppey, Kent: (a) basal transverse cross-section; and (b) dorsal view. Scale bars = 1 mm.

FL	fork length
HH	hypohyal
FR	frontal
HY	hyomandibula
HYP	hypural
IO	infraorbital
IOP	interoperculum
IT	inner tooth
LA	lachrymal
LETH	lateral ethmoid
META	metapterygoid
MX	maxilla
N	caudal notch (hypural plate)
n	remnant of caudal notch
NAS	nasal
nc	nutrient canal
OP	operculum
OT	outer tooth
P	palatine
PALT	palatine tooth
PAR	parietal
PF	pelvic fin
pf	posttemporal fossa
PHP	parhypural
phps	parhypurapophysis
PIN	Palaeontological Institute, Moscow
PMX	premaxilla
POP	preoperculum
psf	postero-superior fossa
PSP	parasphenoid
PT	pterotic
PTM	posttemporal
pw	pineal window
Q	quadrate
rc	rostral crest
rs	rib socket
SC	sclerotic
SCA	scapula
SCL	supracleithrum
SOC	supraoccipital crest
SOP	suboperculum
SPH	sphenotic
st	serial tooth
stg	supratemporal groove
tg	temporal groove
ts	tooth socket/alveolus
U	ural centrum
UN	uroneural
US	urostyle
V	vomer
VC	vertebral column

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KENNETH A. MONSCH, Department of Vertebrate Zoology, Institute of Zoology, University of Wrocław, ul. H. Sienkiewicza 21, 50–335 Wrocław, Poland.
e-mail: kmonsch@biol.uni.wroc.pl

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