

A REVISION OF SCOMBRID FISHES (SCOMBROIDEI, PERCIFORMES) FROM THE MIDDLE EOCENE OF MONTE BOLCA, ITALY

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Abstract: A taxonomic revision of mackerel-like fishes (Scombridae, Scombroidei, Perciformes) from the Monte Bolca localities in Italy is presented as part of continuing research into phylogenetic relationships of fossil and Recent scombroidei. Three new genera are proposed: †*Godsilia*, †*Pseudauxides* and †*Thunnoscomberoides*. In addition, species generally known as †*Thynnus bolcensis*, †*Thynnus lanceolatus*, †*Scombrosarda propterygia*, †*Scomberomorus speciosus* and †*Scomberomorus tenuis* are renamed †*Thunnoscomberoides bolcensis* comb. nov., †*Godsilia lanceolata* comb. nov., †*Auxides propterygius* comb. nov. and †*Pseudauxides*

speciosus comb. nov., respectively. †*S. tenuis*, a *nomen nudum*, is a junior synonym of †*P. speciosus*. Provisional phylogenetic hypotheses of these Monte Bolca scombroidei are as follows. †*Auxides* and †*Pseudauxides* are most likely primitive sister taxa of the mackerels *Scomber* and *Rastrelliger* with †*Pseudauxides* as the most primitive. †*Godsilia* may be placed between Scombrinae and Scomberomorinae. †*Thunnoscomberoides* seems to fit between Scombrinae and Thunnini.

Key words: Scombridae, fossil fish, Recent taxa, Monte Bolca, taxonomic revisions, phylogeny.

OUTCROPS of the middle Eocene of Monte Bolca, Italy, have long been known as a rich source of fish fossils from which a large number of taxa has been described (see e.g. Volta 1796; Agassiz 1833–44; Woodward 1901; Blot 1980; Bellwood 1996). The taxonomic scope of these fish is wide: it includes Chondrichthyes and a large number of families of Osteichthyes (Blot 1980), including the family Scombridae (Scombroidei, Perciformes) or the mackerel-like fishes. The systematic framework of this paper follows that of Monsch (2000b). ‘Scombridae’ are thus understood to include Recent subfamilies Scombrinae, Scomberomorinae, Sardinae (tribes Sardini and Thunnini), Acanthocybiinae and Xiphiinae (billfishes, tribes Xiphiini and Istiophorini). Johnson (1986) also included billfishes with the Scombridae, but there are hypotheses that billfishes are separate from suborder Scombroidei (Collette 1999; Collette *et al.* 2001). In the first post-Linnaean publication on fishes from Monte Bolca, Volta (1796) described ten scombrid species, but he misidentified many of them. In a revision of Monte Bolca fishes, Agassiz (1835) mentioned seven scombrid species: †*Orcynus lanceolatus* Agassiz, 1835, †*Orcynus latior* Agassiz, 1835, †*Cybiium speciosum* Agassiz, 1835, †*Cybiium tenue* Agassiz, 1835, †*Thynnus propterygius* Agassiz, 1835,

†*Thynnus bolcensis* Agassiz, 1835 and †*Blochius longirostris* Volta, 1796. Agassiz (1835) preserved only two of Volta’s specific epithets for scombroidei, namely *longirostris* and *speciosus*, and transferred the latter species to a different genus, renaming it †*Cybiium speciosum*. Among the seven species, Agassiz recognized four that Volta (1796) did not identify as scombroidei and rejected three of Volta’s scombrid species, transferring them to other, non-scombrid, families. He transferred the billfish †*Blochius* Volta, 1796 to the ‘Sclerodermi’.

In his systematic catalogue of the ichthyofauna of Monte Bolca, Blot (1980) included all scombrid species mentioned by Agassiz (1835) although he revised the generic status of some of them. †*B. longirostris* and †*Blochius moorheadi* Eastman, 1911 were placed in the family Blochiidae of the suborder Scombroidei. Blot also added two undescribed and unnamed new species to the Scombridae. In 1984, Bannikov and Sorbini revised †*T. propterygius* as †*Scombrosarda propterygia* (Agassiz, 1835). In the most recent study of scombroidei fishes from Monte Bolca, Fierstine and Monsch (2002) redescribed †*Blochius* and classified it in the monogeneric family †Blochiidae, which forms part of suborder Scombroidei.

I have been studying scombrids from Monte Bolca as part of a continuing research project on the phylogenetic relationships of Recent and fossil scombrids in which I have often found the taxonomy of the fossil taxa to be problematic. The aim of this paper is to present a revision of fossil scombrid taxa from Monte Bolca. †*Blochius* is not included in this paper because it was recently revised by Fierstine and Monsch (2002).

LOCALITY AND STRATIGRAPHY

The palaeobiology, geology and locality of the fish-bearing beds of Monte Bolca (mostly the Pesciara cave) have been extensively described (Medizza 1975; Landini and Sorbini 1996; Bellwood 1998; Tang 2002). The Monte Bolca outcrops are situated north of Verona in northern Italy, and their age is based on the presence of the nannoplankton *Discoaster subloidoensis*, which indicates the NP14 zone (Medizza 1975). The deposit is sometimes referred to the upper Ypresian, upper Lower Eocene (Blot 1980). However, Aubry (1983) defined zone NP14 as Lutetian (Middle Eocene), a standard now universally accepted (Patterson 1993; Fierstine and Monsch 2002). The palaeoenvironment of Bolca is interpreted as tropical marine coastline (Landini and Sorbini 1996; Bellwood 1998). A precise depth estimation of the coastal waters is not given, but it is hypothesized that they were relatively shallow and under fluvial influences (Landini and Sorbini 1996).

Institutional abbreviations. BMNH, Natural History Museum, London; CMNH, Carnegie Museum of Natural History, Pittsburgh; IGUP, Istituto di Geologia della Università di Padova; IPUM, Istituto di Palaeontologia della Università di Modena; MCSNM, Museo Civico di Storia Naturale di Milano; MCSNV, Museo Civico di Storia Naturale di Verona (specimen numbers with prefix IG are stored in the Museo dei Fossili di Bolca in Bolca); MNHN, Muséum National d'Histoire Naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC.

SYSTEMATIC PALAEOLOGY

Remarks. Taxon diagnoses consist only of synapomorphies, through which diagnosis equals taxon definition (Monsch 2003). Other distinguishing characters that are not apomorphies are mentioned in a separate header. The osteological terminology used here is drawn mostly from de Sylva (1955), which still forms the basis of most descriptions of the skeletal anatomy of Recent scombrids (Collette *et al.* 1984; Johnson 1986). The two latter papers also contain cladistic hypotheses, so they can be consulted to understand better the osteological evolution of scom-

broids, which is one of the cores of the present work. The systematic descriptions of Monte Bolca scombrids presented here also contain comparisons with other fossil taxa. For detailed descriptions of these, see Bannikov (1985) for scombrids of the former USSR and Monsch (2005) for London Clay taxa.

Division TELEOSTEI Müller, 1844

Order PERCIFORMES Bleeker, 1859

Suborder SCOMBROIDEI Bleeker, 1859

Family SCOMBRIDAE Rafinesque-Schmaltz, 1815

Genus †AUXIDES Jordan, 1919

[= †*Scombrostarda* Danil'chenko, 1962; †*Pinulothunnus* Ciobanu, 1970]

Type species. †*Thynnus propterygius* Agassiz, 1835, from the Lutetian of Monte Bolca, Italy.

Diagnosis. First haemal spine thickened and bent (Text-Fig. 1A–B), teeth small, lachrymal slightly longer than orbit.

Other distinguishing characters. Thirty-one vertebrae, two smaller hypural plates (one consists of a fusion of hypurals 1–2 and the other of hypurals 3–4), fifth hypural autogenous, dorsal fins close together, body covered by medium-sized scales (Text-fig. 1C), orbit partially covered by sclerotic bones.

Remarks. The generic name †*Scombrostarda* Danil'chenko, 1962 is employed for mackerel-like fishes found in the former USSR and Monte Bolca (Danil'chenko 1962; Bannikov and Sorbini 1984; Bannikov 1985). Monsch (2000b) believed that †*Scombrinus* Woodward, 1901 and †*Scombrostarda* refer to the same genus. However, they differ in the morphology of the dorsal region of the cranium (compare Monsch 2005 and Bannikov 1985). Bannikov and Sorbini (1984) correctly observed that †*Thynnus propterygius* is congeneric with †*Scombrostarda* and renamed the species †*S. propterygia*. However, they were unaware that Jordan (1919) had made †*T. propterygius* the type species of his new genus †*Auxides*, a name that has priority over †*Scombrostarda*. Bannikov and I together discovered the validity of †*Auxides* during our personal communications.

†*Auxides* is known from Palaeocene–Oligocene sediments of the Tethys Sea (Bannikov and Sorbini 1984; Bannikov 1985). Mackerel-like fishes from the Miocene of North America, once considered †*Auxides* (e.g. †*Auxides sanctae-monicae* Jordan, 1919) are now classified in other genera (David 1943; Bannikov 1985).

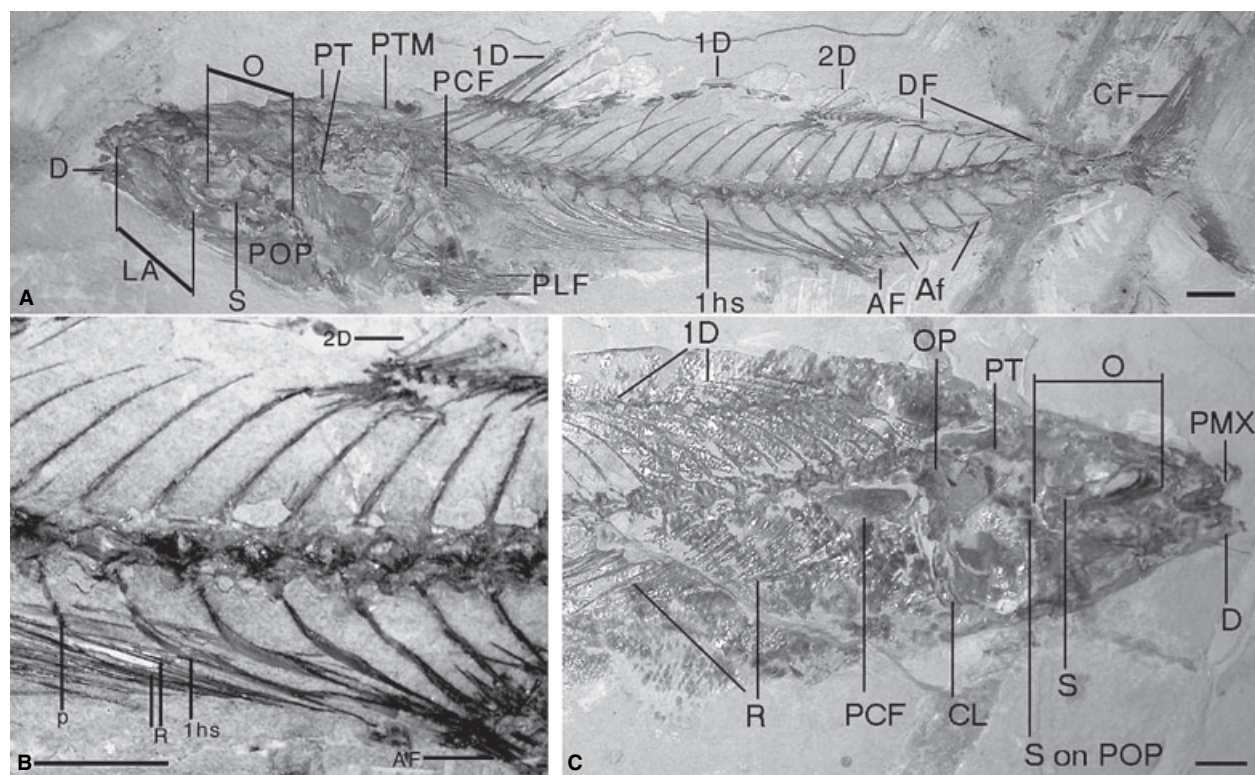
†*Auxides* is a primitive scombrid that shares an apomorphy (a moderate fusion of hypurals) with *Scomber* Linnaeus, 1758, which separates them from more primitive scombroids such as the gempylids. Furthermore, they have many traits of cranial morphology in common, such as apomorphic small teeth and an apomorphic large lachrymal, as well as a similar number of vertebrae (31 vertebrae is the plesiomorphic condition within scombrids) and a similar body shape. Within scombrids, a plesiomorphy of †*Auxides* and *Scomber* is the presence of large sclerotic elements that cover part of the orbit. †*Auxides* is more primitive than *Scomber* regarding its scale covering (the latter has smaller scales), the configuration of their dorsal fins (the first and second dorsal fin are clearly separated in *Scomber*) and the development of the fifth hypural (in *Scomber* this is fused to the uroneural). A remarkable synapomorphy of †*Auxides* and Recent Scombrini is their thickened and bent first haemal spine (Text-fig. 1A–B), a trait that is also found in †*Pseudauxides speciosus* (see description of that species, below). Although †*Auxides* appears to be more primitive than *Scomber* in all respects, a preliminary phylogenetic analysis (Monsch 2000b) did not resolve its phylogenetic position. In the cladogram in question, the fossil genus appears in an unresolved bush

together with a clade that consists of *Scomber* and *Rastreliger* Jordan and Starks, 1908.

†*Auxides propterygius* (Agassiz, 1835) comb. nov.

Text-figures 1–2

- .1796 *Scomber pelamis* Volta (*non* Linnaeus), p. 66, pl. 14, fig. 2.
 v.1796 *Scomber trachurus* Volta (*non* Linnaeus), p. 169, pl. 29, fig. 2.
 1796 *Ophicephalus striatus* Volta (*non* Bloch), p. 193, pl. 48, fig. 1.
 v.1796 *Labrus bifasciatus* Volta (*non* Bloch), p. 204, pl. 50, fig. 1.
 1818 *Scomber pelamis* Linnaeus?; de Blainville, p. 345.
 v.1818 *Labrus bifasciatus* Bloch?; de Blainville, p. 351.
 v*.1835 *Thynnus propterygius* Agassiz, p. 292.
 v.1833–44 *Thynnus propterygius* Agassiz; Agassiz, p. 55, pl. 27.
 v.1874 *Thynnus propterygius* Agassiz; de Zigno, p. 111.
 v.1876 *Thynnus propterygius* Agassiz; Bassani, p. 20.
 1882 *Thynnus? propterygius* Agassiz; Gorjanović-Kramberger, p. 118.
 v.1901 *Auxis? propterygius* (Agassiz); Woodward, p. 464.



TEXT-FIG. 1. †*Auxides propterygius* (Agassiz, 1835) comb. nov. A, holotype, MNHN 1084. B, detail of first haemal spine of MNHN 1084. C, head region of IPUM 30104. Abbreviations: 1D, first dorsal fin; 2D, second dorsal fin; Af, anal finlet; AF, anal fin; CF, caudal fin; D, dentary; DF, dorsal finlet; hs, haemal spine; LA, lachrymal; O, orbit; OP, operculum; p, parapophysis; PCF, pectoral fin; PLF, pelvic fin; POP, preoperculum; PP, pelvic plate; PT, pterotic; PTM, post-temporal; R, rib; S, sclerotic. Scale bars represent 10 mm.

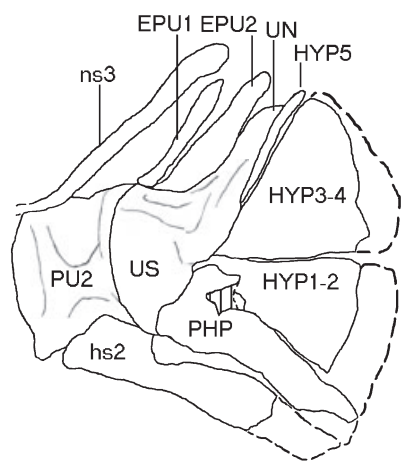
- ?1911 *Auxis? propterygia* (Agassiz); Eastman, p. 11.
 v.1919 *Thunnus propterygius* (Agassiz); Jordan, p. 11.
 v.1980 *Thynnus propterygius* (Agassiz 1833–44) [sic]; Blot, p. 381.
 vp.1984 *Scombrosarda propterygia* (Agassiz 1833–44) [sic]; Bannikov and Sorbini, p. 309, figs 1, 3, 6 [non MCSNM V202, V218 = †*Pseudauxides speciosus* Agassiz, 1835].
 vp.2000b *Scombrinus speciosus* Monsch (non Agassiz), p. 111 (BMNH P4137, P4480, P15091, P16302, P16303; USNM 1946).

Holotype. MNHN 1084 (Text-fig. 1A–B), from Monte Bolca, northern Italy.

Material. The holotype and BMNH P4137, P4480, P15091, P16302 P16303; MCSNM V89, V147 and V236 (counterparts), V1193; MCSNV 50, IG2449, ILD207, VI.N11 and VI.N12 (counterparts), VI.N13, T354; IGUP 8901, 26248, 8738 and 8739 (counterparts), 8939 and 8940 (counterparts), IPUM 30104, 30105; USNM (1946), from the type locality.

Diagnosis. First pair of dorsal and anal finlets clearly separated from second dorsal and anal fin, respectively. Seven or eight pairs of finlets.

Other distinguishing features. Other species of †*Auxides* have fewer finlets and a first haemal spine that is thickened and strongly bent into a sickle-like structure (Danil'chenko 1962; Bannikov and Sorbini 1984; Bannikov 1985). In †*A. propterygius* the first haemal spine is only slightly thickened and bent.



TEXT-FIG. 2. Caudal skeleton of †*Auxides propterygius* (Agassiz, 1835) comb. nov., IGUP 8901. Abbreviations: as in Text-figure 1 and: EPU, epural; HYP, hypural, ns, neural spine; PU, preural centrum; UN, uroneural; US, urostyle. Scale bar represents 1 mm.

Description. Bannikov and Sorbini (1984) published an extensive and detailed description of this species. However, †*Scombrosarda propterygia* as defined in that work is a heterogeneous taxon, since it includes two specimens of †*Pseudauxides speciosum* (see description below). Despite this, the observations of Bannikov and Sorbini (1984) are mostly correct and reference should be made to this work for more detailed information. I present here only corrections and additions where necessary. The body is slender and shallow, the skeleton is thin and seems rather fragile. The individuals vary in size: well-preserved complete specimens have a fork length of 69–317 mm. While Bannikov and Sorbini (1984) mentioned that the pterotic has a 'lengthened shape', this bony element is short for a scombroid because its caudal projection does not reach much further than the articulation with the hyomandibular or the anterior margin of the preoperculum (Text-fig. 1A–B). In some Thunnini, the length of this spiny projection by far exceeds that of the anterior part of the pterotic. On MCSNV IG24498 one can discern part of a palatine that bears a row of minute teeth. Although in general †*A. propterygius* has a vertebral formula of 13+18, there are specimens with 14 pre-caudal and 17 caudal vertebrae. One aberrant individual (IGUP 89439-40) was found to have a vertebral formula of 15+15. In most specimens the first dorsal fin consists of 13 spines, although there are individuals that have as few as ten. The longest spine of that fin (the first) is shorter than the maximum depth of the head. The second dorsal fin is composed of one rigid spine and 10–11 soft rays. The anal fin has 10–12 soft rays preceded by two rigid spines. There are seven or eight pairs of finlets. The pectoral fin has 14–19 rays. Three to four median lepidotrichia in the caudal fin are slightly widened and the empty spaces between them are somewhat larger than between other lepidotrichia in this fin. Bannikov and Sorbini (1984) misidentified two structures in the caudal skeleton. The fifth hypural as in Text-figure 2 is, according to Bannikov and Sorbini, the uroneural, which is an element that is situated on the urostyle (preural centrum 1). In some cases uroneural and urostyle are fused. Thus, I have labelled the element that Bannikov and Sorbini (1984) named 'stegural' as the uroneural, because it is fused to the urostyle. In IPUM 30105 the caudal fin is displaced and its distal tips are not preserved. Each individual hypural can be discerned in the caudal skeleton because the surface of this region is damaged, thus exposing sutures between individual hypurals that are not visible from the outside. Five hypurals can be clearly identified, leaving no doubt that Bannikov and Sorbini's (1984) uroneural is the fifth hypural. The caudal fin has no procurrent spur. It consists of more than 25 (in a damaged specimen) and certainly 30–33 lepidotrichia in total. The pelvic plate has a simple structure. It has the shape of a single lamellar bony wing.

Remarks. Jordan (1919) assigned †*T. propterygius* as the type species of genus †*Auxides*, but he referred to the species as †*Thunnus propterygius* throughout his paper. The combination †*Auxides propterygius* appears on collection labels (e.g. USNM 1946), but it has never been officially published hitherto.

It seems to be generally assumed (Blot 1980; Bannikov and Sorbini 1984) that the specific epithet *propterygius* was validly published in 1844 (Agassiz 1833–44) and that at first mention (Agassiz 1835) it was merely a *nomen nudum*. Although Agassiz (1835) did not provide a formal description of his new species †*Thynnus propterygius*, the name should be considered valid from then on. Agassiz (1835) erected †*T. propterygius* to rename four specimens that were misidentified by Volta (1796). In doing so, he referred to Volta's original descriptions and plates of these specimens. Hence, Agassiz (1835) is to be considered the publication in which the epithet *propterygius* became available, following the ICZN (1999, arts. 12.1, 12.2) provisions for names published before 1931.

On two of its labels, MNHN 1084 is identified as †*Programmatorcynus propterygius*, which is a generic name that Blot intended to publish (Goujet, pers. comm. 2003).

Blot (1980) mentioned unnamed and undescribed specimens of new scombrid species that he reported to be in IPUM and MCSNV. In the collections of IPUM I have found specimens of †*A. propterygium* as the only fossils of non-billfish scombroids present there, and hence I assume that Blot mistakenly supposed that (one of) these concerned a new taxon.

Genus †GODSILIA gen. nov.

Derivation of name. After the late H. C. Godsil, an expert of bonito- and tuna-like fishes.

Type species. †*Scomber orcynus* Volta, 1796, from the Lutetian of Monte Bolca, Italy.

Diagnosis. Dorsal and neural spines and pterygiophores wider than in other similar-sized scombrids (Pl. 1, figs 1–2), anterior corselet of enlarged and thickened scales medially reaching up to pectoral fins and ventrally up to the origin of the anal fin (Pl. 1, figs 1–5), 33–34 vertebrae, hypurals 1–4 and urostyle fused into hypural plate, pectoral fin long.

Other distinguishing features. Besides the anterior corselet, body covered by small scales, dorsal fins close together, teeth moderately large, conical and sharply pointed, pelvic plate simple.

Godsilia lanceolata (Agassiz, 1835) comb. nov.

Plate 1

- v.1796 *Scomber alatunga* Volta (*non* Gmelin), p. 123, pl. 29, fig. 1.
v.1796 *Scomber orcynus* Volta, p. 226, pl. 55, fig. 2.

- v.1796 *Salmo cyprinoides* Volta (*non* Linnaeus), p. 214, pl. 52.
v.1818 *Clupea cyprinoides* de Blainville (*non* Linnaeus), p. 343.
v.1818 *Scomber orcynus* de Blainville, p. 346.
v.*1835 *Orcynus lanceolatus* Agassiz, p. 293.
v.1835 *Orcynus latior* Agassiz, p. 294.
v.1833–44 *Orcynus lanceolatus* Agassiz; Agassiz, p. 59, pl. 23.
v.1833–44 *Orcynus latior* Agassiz; Agassiz, p. 60, p. 24.
v.1876 *Orcynus lanceolatus* Agassiz; Bassani, p. 138.
1889 *Thynnus lanceolatus* (Agassiz); Storms, p. 178.
v.1901 *Thynnus lanceolatus* (Agassiz); Woodward, p. 456.
v.1901 *Orcynus latior* Agassiz; Woodward, p. 456.
?1911 *Thynnus lanceolatus* (Agassiz); Eastman, p. 372.
?1911 *Thynnus latior* (Agassiz); Eastman, p. 373.
v.1980 *Thynnus lanceolatus* (Agassiz 1833–44) [*sic*]; Blot, p. 381.
v.2000b *Godsilia lanceolata* (Agassiz); Monsch, p. 113, fig. 7.24.

Syntypes. MNHN BOL72 and BOL73 (formerly 10827 and 10828, counterparts), BOL312 and BOL313 (counterparts, formerly 10828 [*sic*] and 10828a), from Monte Bolca, northern Italy.

Material. The syntypes, BMNH P3946, IGUP 8744 and 8745 (counterparts), MCSNV IG142532, M.VI10, S.VI2 and S.VI3 (counterparts), T89; MNHN BOL315 and BOL316 (counterparts, formerly 10824 and 1086), MNHN BOL74 and BOL75 (syntypes of †*Scomber orcynus*, counterparts, formerly 10829 and 10830), from the type locality.

Diagnosis and other distinguishing features. As for genus.

Description. Body fusiform, deep, 177–311 mm long. The lachrymal is shorter than the diameter of the orbit. The supratemporal groove is short; its anterior margin coincides more or less with that of the parietals. Premaxilla and maxilla are tightly bound in a non-protrusible complex. The ascending process of the premaxilla is split into two small prongs that point caudo-dorsad (not visible in Pl. 1, fig. 6). Teeth (Pl. 1, fig. 6) are in a single row and are not tightly packed (interspacing between teeth about 1 mm), the crown is about 0.7 mm long (measurements on medium-sized specimens), conical, gradually tapering apically, sharply pointed and straight. The ceratohyal does not possess ventral projections as seen in those of Thunnini. The branchiostegal rays are difficult to discern, but in MCSNV S.VI2 there are two of them caudal of the epihyal that are slender, semi-sickle-shaped structures. The total number of vertebrae is 33–34 (11–12+21–22). Vertebrae are slightly constricted medially and are short (about 1.4 times as long as deep). Preural vertebrae 2–4 are not remarkably shortened in comparison with preceding ones. Epurals two in number. Urostyle, uroneural and hypurals 1–4 are fused into one single plate with a small caudal notch. A fifth hypural has not been found. It is impossible to say whether it has become part of the hypural plate during ontogenetic

development or it was an autogenous element that was lost in the process of fossilization. The parhypural is autogenous. Most of the hypural plate is covered by the bases of caudal fin lepidotrichia (or caudal fin hypurostegic). Median caudal fin rays are enlarged and widely spaced. In total there are 40–45 lepidotrichia in this fin. Neural and haemal spines are thicker and pterygiophores of the unpaired fins are wider than in other similar-sized scombrid fishes. The pectoral fin is long, reaching up to about half-way from the base, or up to the hind margin of the anterior lobe of the second dorsal fin, and consists of 18–34 rays. The pelvic plate is a simple one-winged lamellar bone (as opposed to pelvic plates in certain other taxa that have a complex multi-winged structure). The pelvic fin as a whole is longer than the interpelvic process, and consists of one rigid spine and five soft rays. The dorsal fins are close together. The first pterygiophore of the first dorsal fin is inserted in the third interneural space. The first dorsal fin is depressible into a groove and consists of 8–12 spines. Its longest spine (the first) is shorter than the maximum depth of the head. There is no clear anterior lobe; subsequent spines gradually decrease in length. The second dorsal consists of a rigid spine followed by 13–17 soft rays. The 11–15 soft rays of the anal fin are preceded by two rigid spines, the first of which is much shortened and thickened and is often not preserved in specimens. There are eight or nine pairs (dorsal and ventral) of finlets. Sometimes there are nine dorsal and eight anal finlets. The first pair of finlets immediately follows the second dorsal and anal fin, respectively. A large corselet of thick, large scales is situated posterior to the head, and extends to a region ventral to the pectoral fins, and ventrally it reaches to the origin of the anal fin. Superficially, the corselet appears to be a large darkened spot on the specimens (Pl. 1, figs 1–2, 5), but the structure of individual corselet scales becomes visible (Pl. 1, figs 3–4) under high magnification. Some of the corselet scales are more or less round and display a pattern of concentric rings, especially in the anterior region of the corselet (Pl. 1, fig. 3). Other corselet scales, mostly in posterior parts of the corselet, are splint-like structures that strongly overlap each other (Pl. 1, fig. 4). The remainder of the body is covered by small cycloid scales.

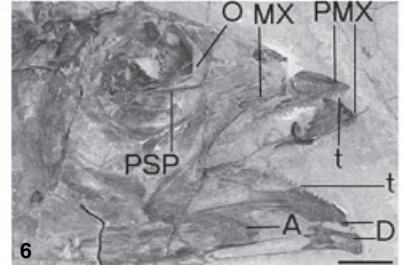
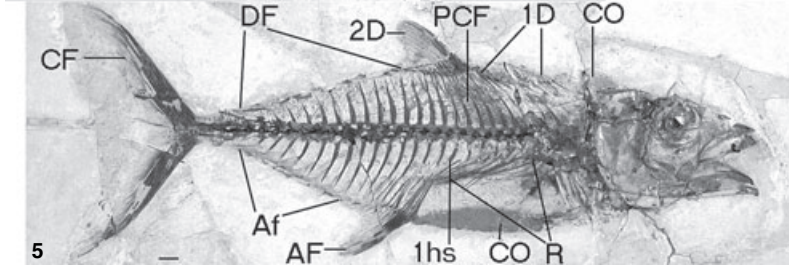
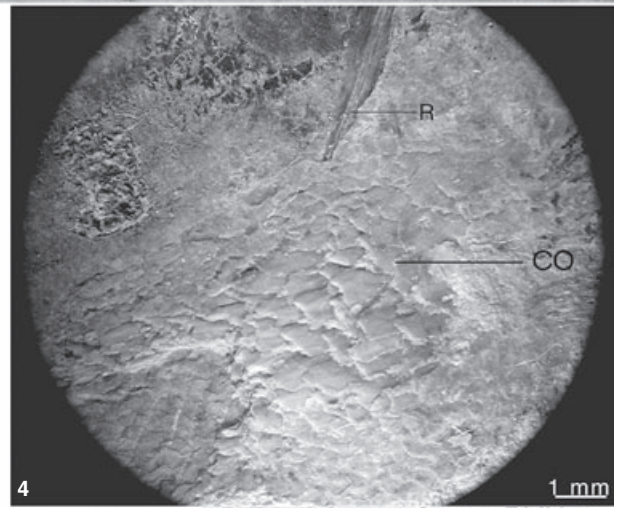
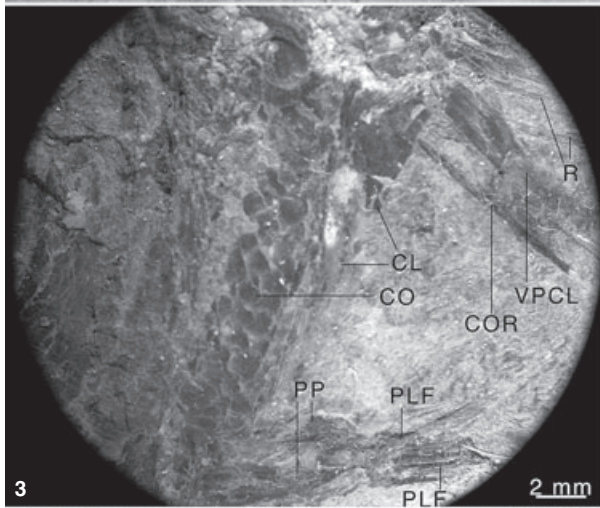
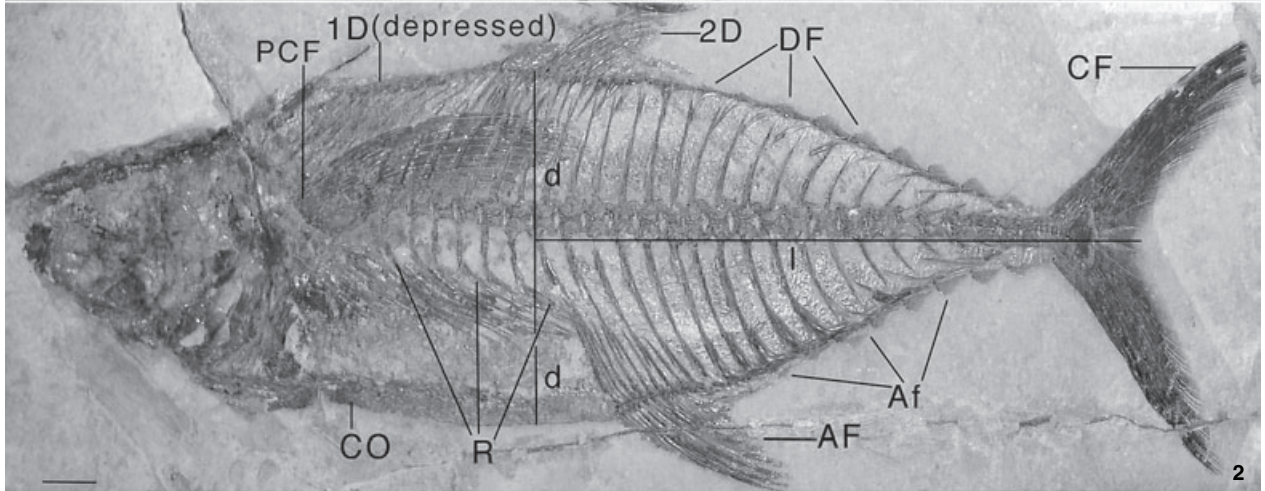
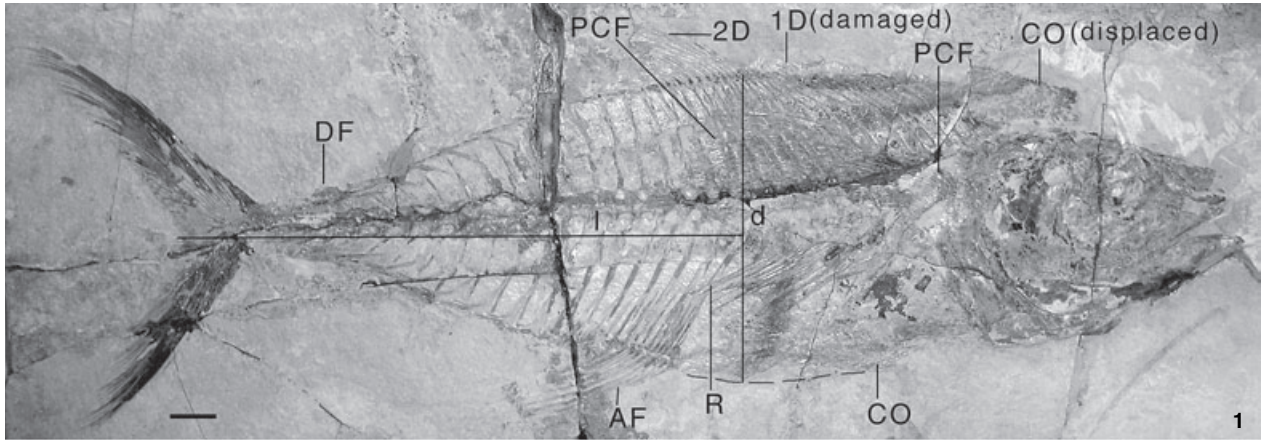
Remarks. In Blot (1980) the fossil described above appears as †*Thynnus lanceolatus* Agassiz (1844). Nowadays, *Thunnus* South, 1845 is accepted as the correct name for the genus in which Blot (1980) classified the species. However, these fossils do not belong to *Thunnus*,

for the following reasons. *Thunnus* possess 39 vertebrae. The corselet in †*Godsilia* and in tunas have a different shape. In tunas, the corselet reaches beyond the pectoral fin medially and only up to an area around the pelvic fins ventrally. I erect a new genus for the species because it possesses apomorphies not found in other known scombrid genera (the shape of the corselet, the thickness of neural and haemal spines and the pterygiophores) and because the combinations of features found in †*Godsilia* (see ‘Diagnosis’ and ‘Other distinguishing features’) does not occur in other genera.

Blot (1980) considered †*Thynnus latior* to be a junior synonym of †*Thynnus lanceolatus*, but did not provide any supporting evidence for this. A collection label on the syntypes of †*Scomber orcynus* (†*T. latior*) proves that he considered them to be part of the hypodygm of †*Prothynnus lanceolatus*, a name that he intended to publish. Agassiz (1833–44) stated that †*Orcynus latior* differs from †*O. lanceolatus* only by a stockier body outline. I have not observed any differences between specimens of †*T. latior* and †*T. lanceolatus* that warrant a specific distinction. I believe that the stockier outline of the type specimens of †*T. latior* is an artefact of fossilization, because the specimens that look more slender have their heads displaced, and as a consequence the body outline is damaged to make them look thinner. In the syntypes of †*Scomber orcynus* the head is firmly in place and the body appears to be more robust. I was able to calculate a depth/length ratio in one of the syntypes of †*T. latior* (BOL74) and in one of †*T. lanceolatus* (BOL 72), in which I took the depth of the body at the level of the origin of the second dorsal-fin spine (d in Pl. 1, figs 1–2) and the length from the origin of the first haemal spine to the caudal margin of the median lepidotrichia of the caudal fin (l in Pl. 1, figs 1–2). The d/l of 0.57 for BOL74 is slightly larger than that for BOL72 (0.54), a difference I do not consider sufficient for recognizing two separate species. The d/l ratio is in general about 0.5 in this species: in five specimens (types and non-types) it varies between 0.42 and 0.57. However, the body of this species can be much deeper, as in MCSNV IG142532, which has a d/l ratio of 0.65.

EXPLANATION OF PLATE 1

Figs 1–6. †*Godsilia lanceolata* (Agassiz, 1835) comb. nov. 1, MNHN BOL72 (syntype). 2, MNHN BOL74 (syntype of †*Scomber orcynus/Thynnus latior*). 3, light microscope photographs of corselet scales of MNHN BOL316; circular scales near head and pectoral girdle. 4, light microscope photographs of corselet scales of MNHN BOL313; posterior, ventral part of corselet with overlapping splint-like scales. 5, MCSNV S.V13.6. 6, anterior detail of 5. Abbreviations: as in Text-figure 1 and: CL, cleithrum; CO, corselet; COR, coracoid; d, body depth at origin of second dorsal fin; l, length from origin of first haemal spine to mid-region of tail; MX, maxilla; PMX, premaxilla; PSP, parasphenoid; t, teeth; VPCL, ventral postcleithrum. Dotted lines indicate possible ventral margin of trunk. Scale bars represent 10 mm except where indicated otherwise.



MONSCH, †*Godsilia*

The nomenclatorial history of this species is complex. The oldest epithet given for the species is *orcynus* (Volta 1796), which Agassiz (1835) rejected in favour of his own *latior* without indicating why the older name was invalid. In describing †*Scomber orcynus*, Volta clearly considered it a fossil specimen of a Recent tuna-like fish. From his description, it cannot be determined which tunny he had in mind, only that it was the size of a mackerel and that it is known in Italy as ‘Tarantello’. This vernacular name is now extinct, since it cannot be found in lists of common names (Palombi and Santarelli 1969; Collette and Nauen 1983). What is certain, however, is that the epithet has been employed for this fossil species only (see the entry *orcynus* in Eschmeyer 1998). It follows, therefore, that Agassiz’ (1835) nomenclatorial revision was unnecessary and illegitimate. Furthermore, neither of the later epithets *latior* or *lanceolatus* meets the conditions for maintenance because of prevailing usage. To be maintained, these epithets should have been employed by at least ten different authors in no less than 25 different works within the last 10–50 years (ICZN 1999, art. 23.9.1). However, the name to be adopted for this species still has to be *lanceolata*. Blot (1980) remarked that †*T. latior* and †*T. lanceolatus* are the same species, with *lanceolatus* being the valid name since it appears on an earlier page in the same work. My work confirms his conclusion and his revision validates the epithet *lanceolata* based on the Principle of the First Reviser (ICZN 1999, art. 24). Although Agassiz (1835) did not provide a formal description of his new species †*Orcynus lanceolatus*, he referred to Volta’s (1796) description and plate of *Scomber alatunga*. Hence, Agassiz (1835) is to be considered the publication in which *lanceolatus* became validly published, following the ICZN (1999) provisions for names published before 1931.

From Eastman’s (1911) brief description of †*Thynnus lanceolatus* and †*T. latior* it cannot be determined whether the author attached the correct name to the specimens.

One individual in two counterparts (IGUP 8742 and 8743) that is in a museum catalogue as †*Thynnus lanceolatus* belongs to a taxon that is currently unknown. The morphology of the axial skeleton, the arrangement of unpaired fins and the structure of the snout are uncharacteristic for scombroids.

The phylogenetic position of †*Godsilia* within scombrids is considered uncertain, pending a future cladistic

analysis. Monsch (2000b) concluded from a preliminary analysis that †*Godsilia* is more advanced than Scombrinae, but more primitive than Scomberomorinae, Sardinae and billfishes.

Genus †PSEUDAUXIDES gen. nov.

Derivation of name. After the superficial resemblance to †*Auxides* and Latin, *pseudo*, false or fake.

Type species. †*Cybium speciosum* Agassiz, 1835, from the Lutetian of Monte Bolca, Italy.

Diagnosis. Ornamentation of deep grooves on frontals, first haemal spine thickened and bent (Pl. 2, figs 1–3), median caudal fin lepdotrichia enlarged and widely spaced (Pl. 2, figs 4–5), vertebrae with dorsolateral and ventrolateral fossae, large anteroventral indentation in dentary.

Other distinguishing features. Thirty vertebrae, snout shorter than remainder of head (i.e. from anterior margin of orbit to distal margin of opercular apparatus), body covered by medium-sized scales without an anterior corselet, teeth conical and sharply pointed, not tightly packed, dorsal fins close together, hypurals 1–2 and 3–4, respectively, fused together

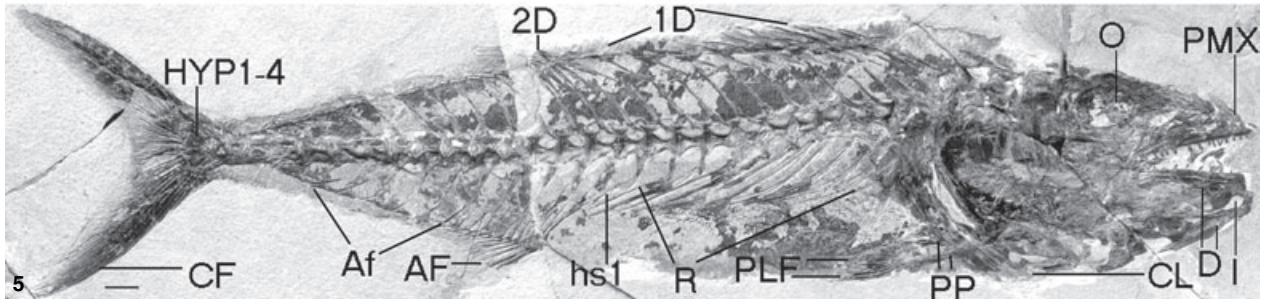
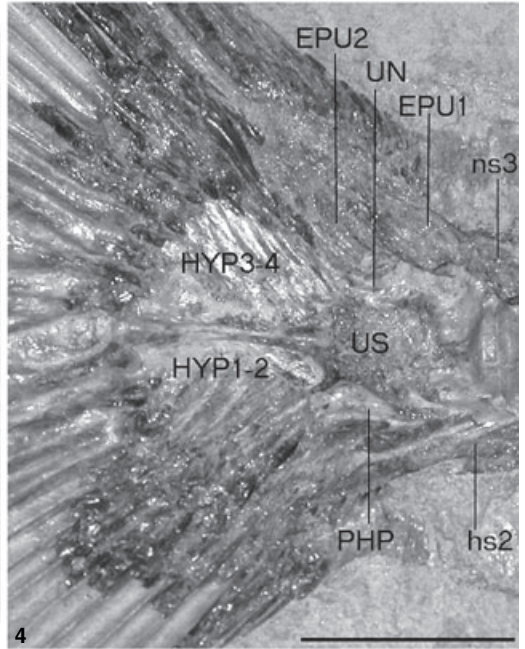
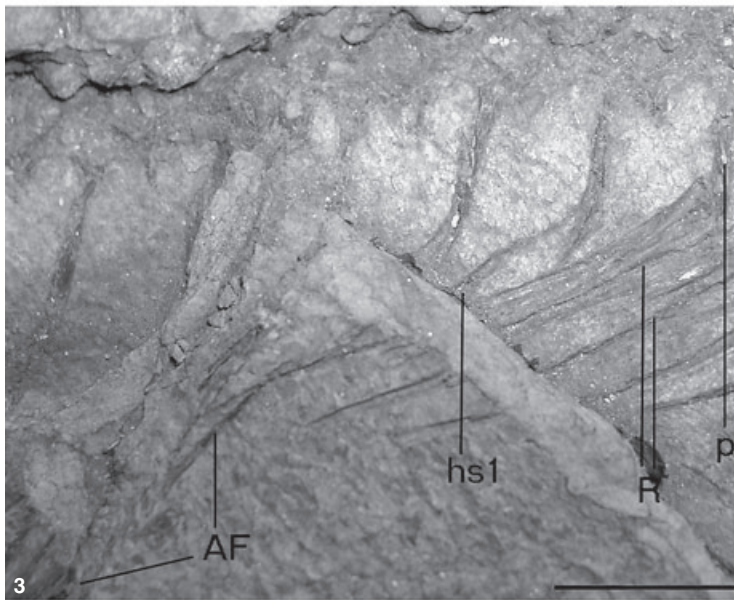
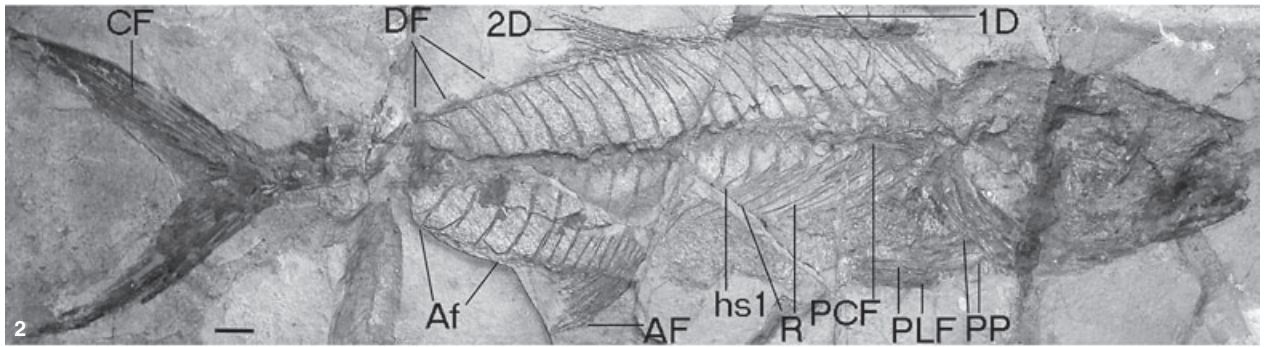
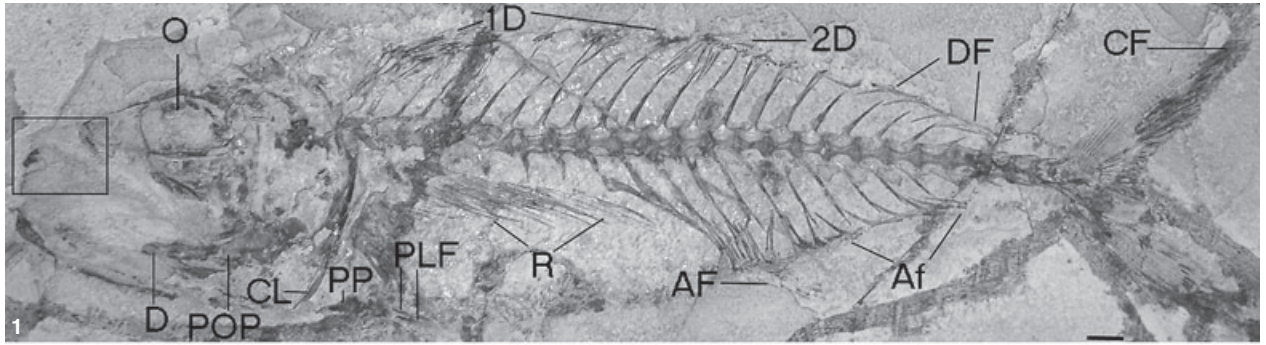
†*Pseudauxides speciosus* comb. nov.

Plate 2; Text-figure 3

- v.1796 *Scomber speciosus* Volta (*non* Forsskål), p. 169, pl. 14, fig. 2.
- v.1818 *Scomber? speciosus* Forsskål?; de Blainville, p. 346.
- v.*1835 *Cybium speciosum* Agassiz, p. 293.
- v.1835 *Cybium tenue* Agassiz, p. 305.
- v.1833–44 *Cybium speciosum* Agassiz; Agassiz, p. 61, pl. 25.
- v.1901 *Cybium speciosum* Agassiz; Woodward, p. 466.
- v.1901 *Cybium tenue* Agassiz; Woodward, p. 470.
- v?1967 *Scomberomorus speciosus* (Agassiz 1835–44) [*sic*]; Arambourg, p. 151, text fig. 55A, pl. 14, figs 1–3.
- v.1980 Nov. gen.-nov. sp.; Blot, p. 381.

EXPLANATION OF PLATE 2

Figs 1–5. †*Pseudauxides speciosus* (Agassiz, 1835) comb. nov. 1, syntype, MNHN BOL517. 2, MNHN BOL442 (syntype of †*Cybium tenue*); the rectangle delineates the area of detail presented in Text-figure 3. 3, close-up of 2, showing the first haemal spine in detail. 4, tail region of IGUP 11886. 5, BMNH P9942. Abbreviations: as in Text-figures 1–2, Plate 1 and: I, indentation in dentary. Scale bars represent 10 mm.



MONSCH, †*Pseudauxides*

- v.1980 *Scomberomorus speciosus* (Agassiz 1833–44) [sic]; Blot, p. 381.
 v.1980 *Scomberomorus tenuis* (Agassiz 1833–44) [sic]; Blot, p. 382.
 vp.1984 *Scombrosarda propterygia* (Agassiz 1833–44) [sic]; Bannikov and Sorbini, p. 309 [MCSNM V202, V218].
 vp.2000b *Scombrinus speciosus* (Agassiz); Monsch, p. 111, fig. 72.1 [non BMNH P4137, P4480, P15091, P16302, P16303; USNM 1946 = †*Auxides propterygius*].

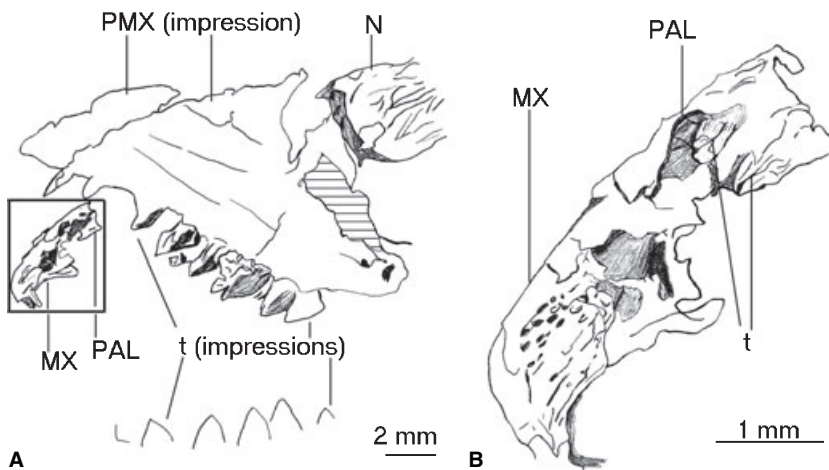
Syntypes. MNHN BOL102 and BOL517 (formerly 10848 and 10849, counterparts), from Monte Bolca, northern Italy. Blot (1980) mistakenly asserted that the types are not specified. However, hitherto only the two specimens in the collections of the MNHN were known as †*Scomberomorus speciosus*; hence, there is no doubt that these are the types.

Material. The syntypes, IGUP 3901 and 3902 (counterparts), 8740 and 8741 (counterparts), 8746 and 8747 (counterparts), 8748 and 8749 (counterparts), 8750 and 8751 (counterparts), 8752 and 8753 (counterparts), 11885 and 11886 (counterparts), 26252 and 26253 (counterparts), 26266 and 26267 (counterparts), 26289; MCSNM V202 and 218 (counterparts); MCSNV T271, T1019, VI.N4 and VI.N5 (counterparts), VI.N35, VI.N36; MNHN BOL441 and BOL442 (formerly 10850 and 10851, counterparts, syntypes of †*Cybius tenue*); BMNH P4136 and P1989 (counterparts), P9942; from the type locality.

Diagnosis and other distinguishing features. As for genus.

Description. The body is fusiform and robust in appearance: the skeleton is stout and bones appear to be thick. In general the fork length varies between 179 and 448 mm, but MCSNV T1019, which is mounted in a locked glass cabinet for public exhibition, has a fork length that I estimate to be somewhat under 800 mm. The head is relatively large. The snout (the region anterior to the eye) is acute in shape and shorter than the rest of head (i.e. from the anterior margin of the orbit to

the hind margin of the opercular apparatus). The supratemporal groove is short; its anterior margin more or less coincides with that of the parietal. The shape of the ethmoid in dorsal aspect is difficult to assess (MCSNV T271), but its anterior margin does not appear to be emarginate. Rather, there seems to be a median anteriorly protruding process. The jaw apparatus is strong and robust; the dentary is especially deep. It possesses a large antero-ventral indentation, through which there seems to be a ‘chin’ (Pl. 2, fig. 5). Maxilla and premaxilla are tightly bound in a non-protrusible complex. The presence or absence of a supra-maxilla is uncertain in the specimens. Small conical teeth can be observed on palatine of BOL517 (Text-fig. 3A–B). Palatine teeth are also preserved, albeit poorly, in MCSNV T1019. Dentary and premaxillary teeth (Text-fig. 3A) are in single rows, in which teeth are close together (about 1 mm apart in medium-sized specimens) but not tightly packed. The premaxillary teeth in Text-figure 3A appear to be closer together than they actually are because the premaxilla was preserved in an oblique position. The dentary teeth of other specimens are not tightly packed and are conical and comparatively large. In medium-sized specimens the crown is about 3 mm high, slightly striated at the base, straight, abruptly tapered, and has a sharp, unserrated cutting edge. There are about 15 teeth in the premaxilla. The sclerotic bones in the orbit are large. The frontals have an ornamentation of thick, deep grooves near the orbits. These grooves originate more or less from a single point near the axial margin of the frontal and diverge towards the outside margin. The ceratohyal lacks a ceratohyal window and ventral projections that shape sockets for branchiostegal rays as in the tribe Thunnini. Branchiostegal rays are slender and curved into an almost sickle-shaped structure. Their number is uncertain, but at least five can be discerned on MCSNV IV.N5. The opercular apparatus is poorly preserved, but there does not seem to be a dorso-caudal indentation in the operculum as found in *Scomber*. The post-temporal has two large anterior processes. The total number of vertebrae is 30 (12–13+17–18). Vertebrae are slightly constricted medially. Each centrum has one dorsolateral and one ventrolateral fossa. The first haemal spine is medially thickened and bent into an almost sickle-shaped projection (Pl. 2, figs 2–3). Preural vertebrae 2–4 are not radically shortened in comparison with those



TEXT-FIG. 3. Jaw apparatus of †*Pseudauxides speciosus* (Agassiz, 1835) comb. nov., MNHN BOL517. A, line drawing of rectangle in Plate 2, figure 1. B, line drawing of rectangle in A. Abbreviations: as in Plate 1 and: N, nasal; PAL, palatine.

preceding them. Two epurals are present. Hypurals 1–2 and 3–4, respectively, are fused to form two small hypural plates. The presence or absence of the fifth hypural could not be determined. The uroneural and parhypural are both autogenous. The caudal fin is hypurostegic, large, and its median lepidotrichia are enlarged and widely spaced. There are in total 25–41 lepidotrichia in this fin. The pectoral fin consists of 17–21 rays. The pelvic fin is small but longer than the interpelvic process and consists of one rigid spine and five soft rays. The first dorsal pterygiophore is inserted in the third interneural space. The first and second dorsal fins are adjoined. The first dorsal is spinous and contains 11–13 spines. It lacks a clear anterior lobe and is less deep than the maximum depth of the head. The second dorsal fin consists of one rigid spine and (8?) 9–11 soft rays. The 10–15 soft rays of the anal fin are preceded by two hard spines, the first of which is small, thickened and often not preserved in specimens. There are seven or eight pairs of dorsal and anal finlets, the former situated immediately caudal to the second dorsal, the latter immediately caudal to the anal fin. The pelvic plate is a simple, one-winged lamellar bone. The body is covered by medium-sized scales. There is a concentration of scales between the pelvic and the anal fins, but there is no anterior corselet as in †*Godsilia* or Thunnini.

Remarks. Agassiz (1835) was the first taxonomist to publish a combination of generic and specific name for this species. Even though he did not provide a formal description of †*Cybium speciosum*, a reference was made to Volta's (1796) description and plate of †*Scomber speciosus* (which is based on the same specimens). Hence, Agassiz (1835) is considered to be the publication in which the specific epithet *speciosus* was validly published (ICZN 1999).

Blot (1980) treated †*Scomberomorus speciosus* and †*Scomberomorus tenuis* as two distinct species. He apparently did not realize that †*S. tenuis* is a *nomen nudum* of Agassiz (1835) rather than a valid name of Agassiz (1833–44) in which the species was not mentioned. The undescribed specimens of †*S. tenuis* are conspecific with those of †*S. speciosus*, because they share the same diagnostic characters. There are several possible reasons why they were previously identified as two different species. The specimens of †*S. tenuis* are comparatively poorly preserved, so that it is difficult to assess the number of their vertebrae. Because of the poor preservation of their teeth they seem to be smaller and more compressed than in the type specimens of †*P. speciosus*. I believe these differences are an artefact of fossilization.

†*Pseudauxides* shows similarities to both †*Auxides* and *Scomberomorus*. Both †*Auxides* and †*Pseudauxides* are covered by medium-sized scales and have similar (for scombrids plesiomorphic) caudal skeletons. †*Pseudauxides* differs from †*Auxides* by being clearly more robust and by having a pelvic plate that is less advanced than in †*Auxides*, which has a plate consisting of more than one bony wing. †*P. speciosus* is similar to *Scomberomorus*

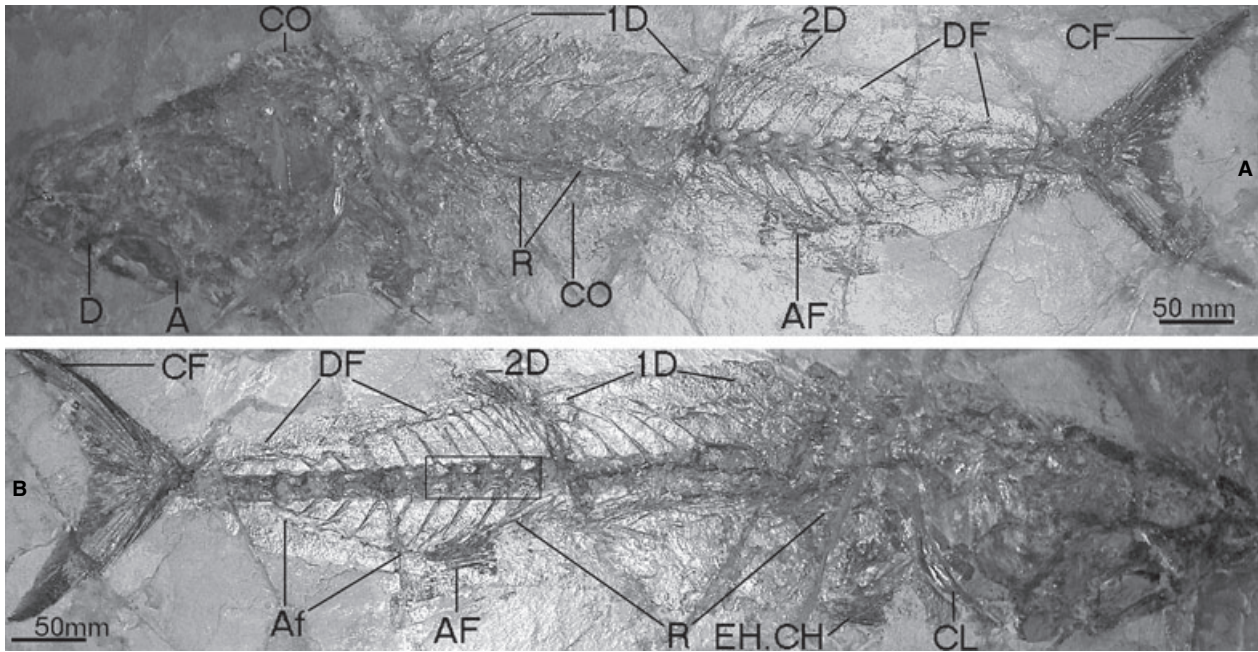
in the following characters: its short snout, and the apparent shape of the teeth of specimens of †*Scomberomorus tenuis*. The latter trait is, however, an artefact of fossilization. Moreover, †*Auxides* and †*Pseudauxides* possess far fewer vertebrae than any species of *Scomberomorus* (at least 41 vertebrae). *Scomberomorus* lacks a thickened first haemal spine. †*Pseudauxides* is in many ways similar to the scomberomorphine *Grammatorcynus* Gill, 1862. However, the following characters warrant a generic differentiation: †*P. speciosus* has a sickle-shaped first haemal spine, a pelvic plate consisting of one lamellar wing rather than many wings as in *Grammatorcynus*, and the caudal skeleton of †*Pseudauxides* is more primitive than that of *Grammatorcynus*. Besides the genera to which I have compared it above, †*Pseudauxides* cannot be referred to any other Recent scombrid genus. The deep grooves on the frontals are not found in Recent taxa and the ventral indentation in the dentary is a character that within scombrids occurs in the tribe Sardini. †*Pseudauxides* resembles †*Eocoelopoma* Woodward, 1901 regarding the morphology of the skull (see Monsch 2005) but cannot be compared to other London Clay taxa because these have teeth that are either gradually tapered, tightly packed or arranged in two rows. In addition, †*Eocoelopoma* has a more advanced caudal skeleton and lacks the strong curve in the first haemal spine (Bannikov 1985). Hence, a new genus and species are erected to name the specimens described here. Considering the plesiomorphic nature of many of the characters of †*Pseudauxides*, also in comparison to *Scomber* and †*Auxides*, I hypothesize that it is the primitive sister group of these two.

Arambourg (1967) identified specimen MNHN 1939-6-389 from the Oligocene of Istehbanât, Iran, as †*Scomberomorus speciosus*. This specimen lacks crucial synapomorphies. The caudal skeleton is missing and it is not clear whether the median caudal fin lepidotrichia are enlarged. Moreover, Monte Bolca taxa have not been found in sediments from other localities and ages. Specimens of †*Auxides* are also known from the Lower Oligocene in the Caucasus of Russia (Bannikov 1985). The affinities of this fossil cannot be determined with certainty, even though it does show superficial resemblances to both †*Auxides* and †*Pseudauxides*.

Genus †THUNNOSCOMBEROIDES gen. nov.

Derivation of name. After *Thunnus* and *Scomber* because the new genus shows morphological traits found in both of these scombrid genera.

Type species. †*Thunnus bolcensis* Agassiz, 1835, from the Lutetian of Monte Bolca, Italy.



TEXT-FIG. 4. †*Thunnoscomberoides bolcensis* (Agassiz, 1835) comb. nov. A, syntype, MNHN BOL537. B, syntype, MNHN BOL538. Rectangle delineates area of detail in Text-figure 5. Abbreviations: as in Text-figures 1–2, Plate 1 and CH: ceratohyal.

Diagnosis. Hypurals 1–4, uroneural and urostyle fused into single hypural plate; caudal fin hypurostegic, seven dorsal and anal finlets; anteriorly a well-developed corselet composed of enlarged and thickened scales, rest of body covered by small scales.

Other distinguishing features. Twenty-seven vertebrae preserved; I hypothesize that the total count may be 31. The preural vertebrae are not radically shortened. The hypural plate has a caudal notch.

†*Thunnoscomberoides bolcensis* (Agassiz, 1835) comb. nov.
Text-figures 4–6

- v.1796 *Scomber thynnus* Volta (*non* Linnaeus), p. 119, pl. 27.
- v.*1835 *Thynnus bolcensis* Agassiz, p. 305.
- v.1833–44 *Thynnus bolcensis* Agassiz; Agassiz, p. 57.
- v.1901 *Thynnus bolcensis* Agassiz; Woodward, p. 457.
- ?1911 *Thynnus bolcensis* Agassiz, 1844 [*sic*]; Eastman, p. 373.
- v.1980 *Thynnus bolcensis* Agassiz (1833–44) [*sic*]; Blot, p. 381.
- v.1985 *Thynnus bolcensis* Agassiz; Bannikov, p. 61.

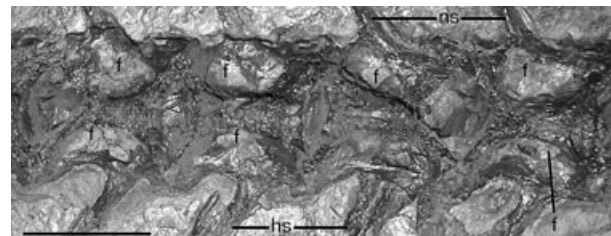
Syntypes. MNHN BOL537, BOL538 (formerly 11010, 11011; counterparts), from Monte Bolca, northern Italy.

Material. Syntypes only.

Diagnosis and other distinguishing features. As for genus.

Description. The syntypes (Text-fig. 4A–B) were difficult to study and photograph because they are mounted on top of a cabinet in the permanent exhibition of the MNHN. The following description and photographs are as accurate as can be expected in the circumstances.

The body is fusiform and has a fork-length of 786 mm. The preservation of the cranial region is poor. The premaxilla-maxilla complex is not modified into a rostrum, but no other characteristics of this complex are preserved (including teeth). BOL538 contains a fragment of the ceratohyal (Text-fig. 4B) that is devoid of ventral projections that shape sockets for branchiostegial rays as in Thunnini. Vertebrae and neural and haemal spines are stout. Centra are almost square when viewed laterally, and they possess both deep dorsolateral and ventrolateral fossae



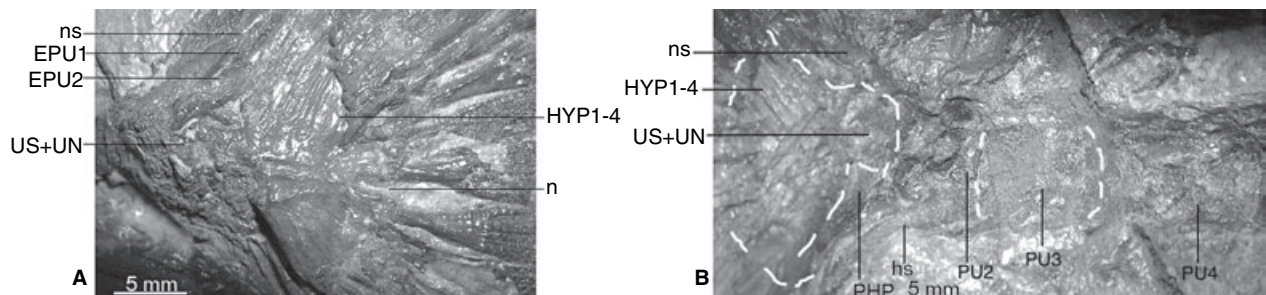
TEXT-FIG. 5. Detail of vertebral column (enlargement of rectangle in Text-fig. 4B). Scale bar represents 10 mm. Abbreviations: as in Text-figures 1–2 and: f, lateral fossa on centrum.

(Text-fig. 5). Although BOL538 appears to possess large inferior foramina as in some Thunnini, these are really patches of matrix covering parts of the vertebral column, mainly the lateral fossae of the centra. The vertebral column is incomplete. Twenty-seven vertebrae are preserved, although the total number was undoubtedly higher. Anteriorly, the vertebral column is obscured by cracks in the matrix, scales and possibly by other bones. I estimate that there may be four centra in the obscured vertebral region, for a total vertebral count of 31. Two epurals are present (Text-fig. 6A). Preural centra 2–4 are shorter than those preceding them, but are not as abruptly shortened as in Thunnini. This morphology is visible in the caudal skeleton of BOL537 (Text-fig. 6B), even though the preservation of the caudal region in that specimen is relatively poor. Hypurals 1–4, urostyle and uroneural are fused into a single hypural plate that contains a caudal notch (Text-fig. 6A). A fifth hypural was not found. The caudal fin is hypurostegic, with deep diagonal grooves in the surface of the hypural plate, formed by the overlapping lepidotrichia. The caudal fin is large and semilunate, with its median rays enlarged and widely spaced. The two dorsal fins are close together. The first dorsal fin is spinous, less deep than the head, and gradually declines in depth caudally. The exact number of spines in the fin is uncertain, with only 14 visible. The second dorsal and anal fins consist of 13 and eight elements, respectively, the first of which may be spinous, while the remainder are formed of soft rays. Both are followed by seven pairs of finlets. Anteriorly, there are traces of a corselet of enlarged, thickened scales (best seen in BOL537, Text-fig. 4A). The corselet scales are most easily discerned in an area dorsocaudal of the head. Less well-preserved areas of the corselet can be seen near the shoulder girdle and around the ribs. In the latter areas, the corselet appears as dark spots in the matrix, but closer inspection reveals that these marks are formed by large scales. The remainder of the body is covered by small scales whose exact shape could not be determined.

Remarks. Agassiz (1835) did not provide a formal description of his new species †*Thynnus bolcensis*, but referred to the description and plate of *Scomber thynnus* in Volta (1796), which is based on the same specimens. Hence, Agassiz (1835) is considered to be the publication in which the specific epithet *bolcensis* was validly published (ICZN 1999). I am not the first to remark that this species does not belong to the genus *Thynnus*. That hon-

our goes to Blot (1980), who unfortunately passed away before he could officially change the name.

†*Thunnoscomberoides* is a non-billfish member of family Scombridae, because its jaw apparatus is not modified into a rostrum. It is recognized as a valid genus based on postcranial characters. †*Palimphytes* Agassiz, 1844 has 32–39 vertebrae (Bannikov 1993). †*Thunnoscomberoides* is estimated to have possessed, at most, 31 vertebrae (as in *Scomber*) and has a higher degree of hypural fusion than †*Palimphytes*. The subfamily Scombrinae contains the genera *Scomber* and *Rastrelliger*, both of which possess 31 vertebrae. †*Turio* Jordan and Gilbert, 1920, a fossil scombrid from California, possesses only 28 vertebrae. Within the tribe Thunnini (tuna-like fishes), only members of the genus *Thunnus* have scales caudal of their anterior corselet. However, all species of *Thunnus* possess 39 vertebrae. While the Scombrinae possess only five pairs of finlets, other scombrids have up to ten pairs. †*Thunnoscomberoides* has seven dorsal and seven anal finlets. The caudal skeleton of Scombrinae has two hypural plates (hypurals 1–2 and 3–4 fused together, respectively) and an autogenous urostyle. In the Thunnini, the hypural plate is a fusion of five hypurals and the urostyle. In †*Thunnoscomberoides*, four hypurals and the urostyle are fused into one plate but the fifth hypural cannot be observed. The hypural plate of †*Thunnoscomberoides* possesses a caudal notch, a plesiomorphic state that can be found in Scomberomorinae. In Sardinini there is an evolutionary trend of closure and disappearance of this notch, while the Thunnini are characterized by its absence (Monsch 2000a). Non-billfish scombrids possess two epurals instead of three. Within the scombrids, however, Thunnini appear to possess only one epural, but their most anterior one is fused to a neural arch, to give the impression of a large neural spine (Collette *et al.* 1984). This apomorphy of Thunnini is not found in †*Thunnoscomberoides*, which does not have any character (state) that is not found in other scombrids. However, in no other genus do they appear in the combination found in the specimens described here. †*Thunnoscomberoides* possesses a peculiar mixture of apomorphic and plesiomorphic character



TEXT-FIG. 6. †*Thunnoscomberoides bolcensis* (Agassiz, 1835) comb. nov. A, detail of caudal region of MNHN BOL537. B, Detail of caudal region of †*T. bolcensis*, MNHN BOL538, with clarifying tracing marks. Abbreviations as in Text-figure 1.

states, and cannot possibly be assigned to any previously known taxon. Hence, my erection of a new genus and species for this fossil. I will not attempt here to establish the exact phylogenetic position of †*Thunnoscomberoides*, but I assume it can be placed somewhere between the primitive Scombrinae and the advanced Sardinae.

There are some non-billfish scombrids from the London Clay known only from cranial remains; however, the cranium of †*Thunnoscomberoides* is not well-enough preserved for comparison. It is possible that some London Clay scombrids and †*Thunnoscomberoides* are the same; future discoveries may confirm or refute this hypothesis. However, when I consider the British fossils in question, namely †*Tamesichthys* Casier, 1966, †*Sphyraenodus* Agassiz, 1844, †*Woodwardella* Casier, 1966, †*Wetherellus* Casier, 1966, and †*Scombramphodon* Woodward, 1901, I believe that there are still enough grounds to recognize †*Thunnoscomberoides* as a distinct genus. †*Tamesichthys* resembles a gempylid skull (Monsch 2005); hence, I think it unlikely to have belonged to an individual with a scombrid postcranial skeleton. †*Sphyraenodus* and *Scombramphodon* have elongated skulls that gradually taper anteriorly, while †*Thunnoscomberoides* possesses a relatively deep skull. †*Woodwardella* and †*Wetherellus* are only known from small crania, the largest of which is a specimen of †*Wetherellus* with a neurocranium about 80 mm long. The length of the neurocranium of †*Thunnoscomberoides* is estimated at 160 mm. †*Eocoelopoma* Woodward, 1901 was known only from fossil crania from the London Clay (Casier 1966), until Bannikov (1985) described †*Eocoelopoma portentosum* Bannikov, 1985 from the Eocene of Turkmenistan, a species estimated to have 40 vertebrae. †*Eothynnus* Woodward, 1901, originally described as a *Thunnus*-like scombrid (Woodward 1901; Casier 1966) is now considered to be a carangid (Bannikov 1979, 1985).

From the brief description of †*T. bolcensis* by Eastman (1911), I cannot determine whether he attached the correct name to the specimen in question. It measured 0.95 m (fork length?). A detailed description in a future paper was announced, but far as I know, this account never appeared.

DISCUSSION

Taxonomic knowledge of Monte Bolca scombrids is difficult to overlook. Ignorance, poor taxonomic practice and confusion over generic identification have caused chaos and misunderstanding. Here I have tackled many nomenclatural and identification issues and added to our understanding of the ichthyological fauna of Monte Bolca. All hypotheses regarding the phylogenetic position of the fishes described are speculative because they display a

mixture of apomorphic and plesiomorphic characters. Moreover, the total number of Recent and fossil scombrids and the number of diagnostic characters they possess do not permit a reliable phylogenetic estimate without a fundamentally new analysis. The improved understanding of the taxa in this paper will be taken into account in a new cladistic analysis of Recent and fossil scombrids. Provisional phylogenetic hypotheses of these Monte Bolca scombrids are as follows. †*Auxides* and †*Pseudauxides* are most likely to be related to Recent mackerels *Scomber* and *Rastrelliger*. Of all of these, †*Pseudauxides* seems to be the most primitive, and †*Auxides* may be the immediate sister group of *Scomber* and *Rastrelliger*. †*Godsilia* may be placed between Scombrinae and Scomberomorinae. †*Thunnoscomberoides* seems to fit between Scombrinae and Thunnini. I have not (yet) seen the Monte Bolca fossils in the CMNH collections, from which Eastman (1911) published poor taxonomic descriptions.

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