

A new fossil bonito (Sardini, Teleostei) from the Eocene of England and the Caucasus, and evolution of tail region characters of its Recent relatives

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Abstract. A new species of a fossil bonito, *Gymnosarda prisca* (Scombridae, Perciformes) from the Early Tertiary shows an interesting combination of characters not seen in other, Recent, bonitos. The new species is based on hypural bones from the caudal region. Although a bonito, the fossil hypural plates possess a caudal notch, a character not known in Recent bonitos. The discovery of this new taxon causes a redefinition of the synapomorphies of the caudal region that define bonitos and their relatives, the tunas and Spanish mackerels. The fossil species has previously been described as part of *Scomberomorus saevus*.

Key words: bonitos, evolution, fossil, new species, synapomorphies, tunas

Introduction

The discovery of a new fossil fish has changed concepts of the characters that define tunas, bonitos and the evolution of their characters. Tunas and bonitos (tribes Thunnini and Sardini, Scombridae) have been stably defined for sometime according to characteristics described in Collette and Chao (1975), Collette (1978) and Collette *et al.* (1984). A new fossil scombrid, described here, shows a remarkable combination of characters which changes current concepts. This fossil species has been studied in the context of a phylogenetic study of the suborder Scombroidei. The main hypotheses (Collette *et al.*, 1984; Johnson, 1986; Finnerty and Block, 1995) on phylogenetic relationships of scombroid fishes, based on data of Recent taxa, present highly conflicting results. In an attempt to solve this problem, I carry out a phylogenetic analysis, containing Recent as well as fossil taxa. Here I present part of my results.

Scomberomorus saevus Bannikov was described from the Eocene of Turkmenistan and Kazakhstan (Bannikov, 1982, 1985). This paper concerns amongst others a specimen of a hypural plate, originally assigned to *S. saevus*. Hypural elements are bones that provide the principal support for the lepidotrichia of the tail in fishes, and are normally separate from one another. In the Scombridae the hypural elements are fused to such a degree that they form one single hypural plate. This plate articulates directly with the vertebral column. Bannikov (1982) did not describe hypural plates in the original description of *S. saevus*, although the type material did include these plates (Bannikov pers. comm., 1998).

They are described in a later account (Bannikov, 1985). These hypural elements are part of a series of paratypes. The holotype of *S. saevus* is a premaxilla. Bannikov's (1982, 1985) material of *S. saevus* includes one specimen which I have identified as Sardini. One fossil specimen from England has been identified as identical to the aforementioned Sardini.

Materials

Except for RAN PIN 1878–8 (premaxilla), the fossil material consists of hypural plates.

BMNH: the Natural History Museum, London:

New species: P6485, Isle of Sheppey, England, Ypresian (London Clay Formation).

Gymnosarda unicolor (Rüppell): 1934.3.31, Red Sea (Recent).

Scomberomorus nipponius (Cuvier): 1874.1.16.9, no data; 1890.2.26.90, inland sea, Japan (Recent).

Sarda orientalis (Temminck and Schlegel): 1920.7.23.59, Durban, South Africa (Recent).

RAN PIN: Russian Academy of Sciences, Paleontological Institute, Moscow:

New species: 1878–2 Western extremities of Ustyurt, Kazakhstan, Upper Eocene (Shorym Svita); 1878–4, Turkmenistan, Upper Eocene (Shorym Svita); 1878–8 (holotype of *S. saevus*), Mangyshlak Peninsula, Karagiye basin, Kazakhstan, Upper Eocene (Shorym Svita).

USNM: Natural History Museum, Smithsonian Institution, Washington DC:

Scomberomorus plurilineatus (Fourmanoir): 64809 and 269760, Durban, South Africa (Recent).

Sarda sarda (Bloch): USNM 26953, 26954, no data (Recent); 270730, New Jersey, U.S.A. (Recent); 270731, Ponte Delgada Fish Market, San Miguel, Azores (Recent).

Systematic palaeontology

Order Perciformes sensu Johnson and Patterson, 1993
Suborder Scombroidei sensu Carpenter *et al.*, 1995

Family Scombridae Rafinesque, 1815
Genus *Gymnosarda* Gill, 1862

Gymnosarda prisca sp. nov.

Figure 1A, B

Scomberomorus saevus Bannikov, 1982, p. 135 (in part); Bannikov 1985, p. 37 (in part).

Holotype.—BMNH P6485, (previously labelled "unidenti-

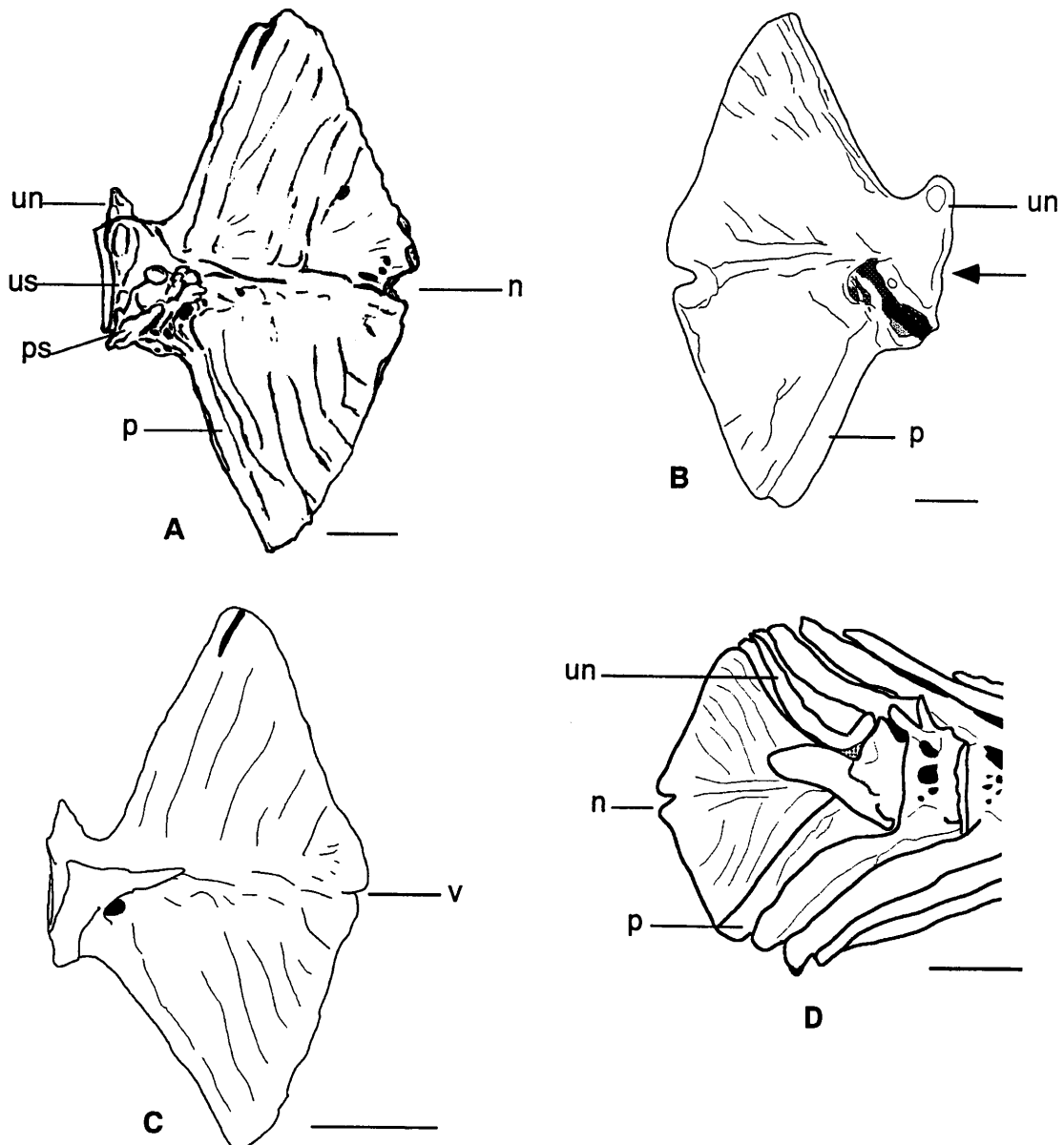


Figure 1. Hypural plates, lateral view. *Gymnosarda prisca* sp. nov. **A.** Holotype, BMNH P6485 (left view). **B.** RAN PIN 1878-4 (right view). Arrow indicates perspective of Figure 2A. **C.** *Gymnosarda unicolor* (Rüppell) (left view), after Collette and Russo (1984) and BMNH 1934.3.31. **D.** *Scomberomorus regalis* (Bloch): USNM 270053, (right view). Abbreviations: hyp5: fifth hypural, n: caudal notch, p: parhypural, ps: parhypurapophysis, un: uroneural, us: urostyle, v: remnant of caudal notch. Scale bars indicate 10 mm.

fied teleost") (Figure 1A).

Material.—Holotype, and RAN PIN 1878-4, (Figure 1B).

Etymology.—Priscus is Latin for "old", indicating it is an extinct ancient species of *Gymnosarda*. The only other species is the Recent *Gymnosarda unicolor*.

Diagnosis.—Species of a Sardini: uroneural and fifth hypural fused to hypural plate and urostyle cross-section with long axis horizontal. Differs from other Sardini by having parhypural fused to hypural plate and possession of caudal notch. Recent bonitos lack a conspicuous notch, and of Recent bonitos only *Gymnosarda unicolor* has a fused parhypural (see Figure 1).

Description.—Hypural plate, made up of fusion of urostyle, uroneural, hypurals 1-5 (hypural 5 not completely fused to plate) and parhypural. Plate diamond-shaped; sides equal in length. Height 75 mm (holotype, Figure 1A) or 79 mm (RAN PIN 1878-4, Figure 1B), which is twice the length without uroneural in both specimens (length: along axis of fish, height: along line perpendicular to axis). Posterior outline of diamond slightly swollen outwardly (more on dorsal side). Posteriorly, a clearly discernible notch. Markings made by fin rays crossing plate visible as shallow grooves, running parallel to rostral sides of diamond. Parhypurapophysis (damaged) making angle of about 41° with horizontal axis. Uroneural large, fused to urostyle [urostyle, according to definition of Potthoff (1975): fusion of preural centrum 1 and ural centrum]. Cross-section of urostyle round or slightly ovoid with the long axis vertical (as Thunnini, Figure 2).

Remarks.—The hypural plate-based taxon *G. prisca* is referable to the Sardini based on the diamond-shaped plate and the large anterior upturned end of the uroneural which is fused to the plate. With its proportions the hypural plate of *G. prisca* is almost identical to that of the Recent *G. unicolor* (Figure 1C). In *Gymnosarda*, the hypural plate is about twice as deep as long. In the other bonitos *Sarda*, *Orcynopsis* and *Cybiosarda* the hypural plate is less deep. *Allothunnus* was previously recognised as a bonito (Collette and Chao, 1975; Johnson, 1986). Collette *et al.* (1984) suggest that *Allothunnus* is better regarded as a primitive Thunnini, for which later convincing evidence has been found (Graham and Dickson, in press). *Gymnosarda unicolor* is unique among Recent bonitos in having a fused parhypural, just like *G. prisca*, and has a small vestige where *G. prisca* has a caudal notch (BMNH 1934.3.31 and Collette and Chao, 1975, p. 578 and fig. 56). No bonito with a caudal notch is known (Collette and Chao, 1975). I have not seen such notches in specimens of *Sarda* (BMNH 1920.7.23.59; USNM 26953, 26954, 270730 and 270731). Still, the *G. prisca* hypural plate possesses all other characteristics of a Sardini.

The specimen figured in Figure 2B (RAN PIN 1878-2) is an unknown scombrid, described and figured as *S. saevus* by Bannikov (1985, p. 37, figures 17 g, d) and is part of the *S. saevus* type series. The parhypural is fused to the plate and hence it is not a *Scomberomorus* (Table 1; see also Discussion), but no name as yet is assigned to that specimen. The systematic position of the taxon this plate represents is still under consideration.

Discussion

Previously, *G. prisca* was believed to belong to *Scomberomorus* because of apparent similarities with the latter (Figure 1D). It now seems that it is not a *Scomberomorus*. The most conspicuous character to identify a Sardini from a *Scomberomorini* is the cross-section of their urostyles (see their descriptions and Figure 2). *Gymnosarda prisca* has a hypural plate in which the cross-section of the urostyle is ovoid with the long axis vertical (Figure 2A), whereas in *Scomberomorini* the long axis is horizontal (Figure 2B). In *G. prisca* the parhypural is fused with the hypural plate, whereas in Recent *Scomberomorus* it is not. Collette and Russo (1984) mention that *Scomberomorus nipponius* and *Scomberomorus plurilineatus* have parhypurals partially fused to the hypural plate. In specimens of *S. plurilineatus* (USNM 264809 and 269760) and *Scomberomorus nipponius* (BMNH 1874.1.16.9 and 1890.2.26.90) the parhypural is not fused to the hypural plate. Possibly there is a light degree of fusion in specimens that I have not seen. Bannikov (1982) noted that the parhypural of *S. saevus* is separated from the hypural plate by a fissure. Although the parhypural can be clearly identified in the hypural plate of *G. prisca*, the division between the plate and the parhypural is not sharp enough to represent an autogenous parhypural.

The assignment of the name *S. saevus* to its whole type series is partially incorrect. Bannikov's (1982, 1985) holotype is RAN PIN 1878-8, which is a premaxilla that is identical to one of *Scomberomorus*. A *Scomberomorus* premax-

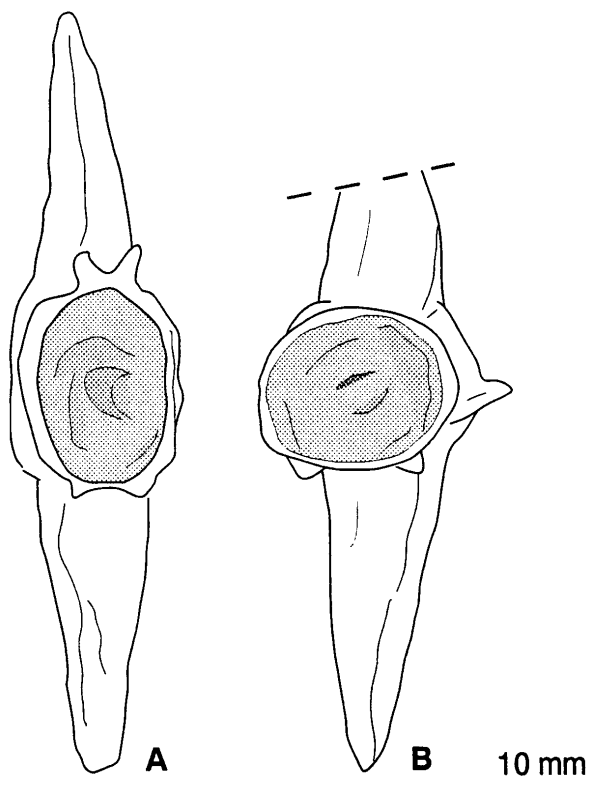


Figure 2. Hypural plates viewed to show the diameters of urostyles. **A.** *Gymnosarda prisca* sp. nov., RAN PIN 1878-4. **B.** *Scomberomorini* indet., RAN PIN 1878-2.

illa is recognised by a relatively long ascending process: 31–48% of the total premaxilla (Collette and Russo, 1984), and makes a sharp angle with the shank: 32°–61° (Collette and Russo, 1984). The holotype of *S. saevus* fits this description well. Being recognised as a *Scomberomorus* and being the holotype of the epithet *saevus*, the name *Scomberomorus saevus* is retained for this specimen.

Gymnosarda prisca shows a peculiar mix of characters. A noticeable caudal notch in the hypural plate is a primitive character, found in amongst others the Scomberomorini, where it can be large. I do not think that *G. prisca* can be anything but a Sardini and indeed, a *Gymnosarda*. According to Collette and Chao (1975) and Collette *et al.* (1984)

one of the synapomorphies of the scombrids above the Spanish mackerels (Scomberomorini) is the absence of the caudal notch (see Table 1). *Gymnosarda prisca* clearly possesses a large caudal notch. *Gymnosarda unicolor* is in fact not devoid of a caudal notch, it has a small, hard to spot vestigial one. It seems thus, that Sardini are not characterised by the absence of a caudal notch, but rather by a tendency of this notch to close down, and ultimately disappear in their evolution. Thunnini are characterised by a complete absence of the notch. The caudal notch in *G. prisca* is evidence that it is not a sharp divider above species level: the Scomberomorini have a notch; so do primitive Sardini and in advanced ones this notch has disappeared. Therefore, be-

Table 1. Overview of hypural plate characters of *Scomberomorus* and Sardini.

	Parhypural	Caudal notch	Uroneural	Hypural fusion pattern	Cross-section of urostyle
<i>Scomberomorus</i>	not fused	yes	not fused	1–4, 5	long axis vertical
<i>Gymnosarda prisca</i> sp. nov.	fused	yes	fused	1–5	long axis horizontal
<i>Gymnosarda unicolor</i> (Rüppell)	fused	remnant	fused	1–5	long axis horizontal
other Sardini	not fused	no	fused	1–5	long axis horizontal

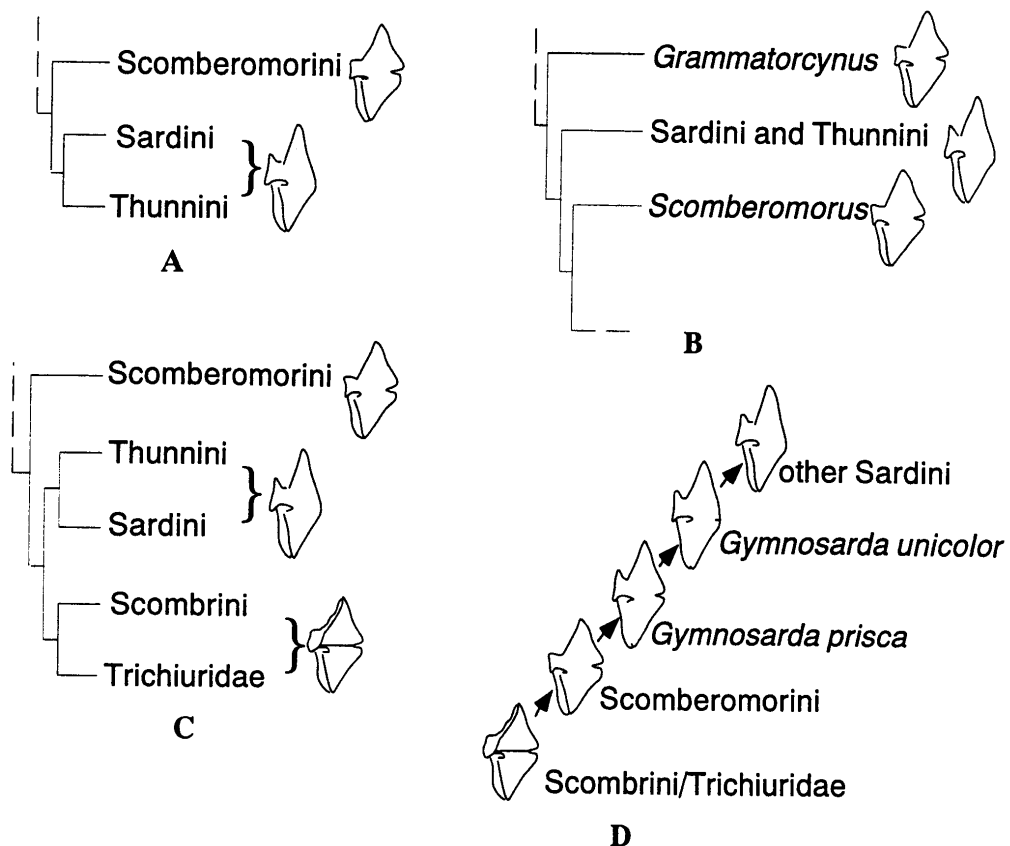


Figure 3. Phylogenetic relationships of Sardini, Thunnini and their closest relatives. **A.** After Collette *et al.* (1984). **B.** After Johnson (1986). **C.** After Finnerty and Block (1995). **D.** Proposed evolutionary sequence.

cause of the great similarities with *G. unicolor*, I describe this fossil taxon as a new species within this genus.

The small vestigial notch of *G. unicolor* suggests that more primitive bonitos have once had a large caudal notch. This is confirmed by *G. prisca*. This notch is a primitive feature, which thus suggests that the ancestor of the bonitos came from within the Scomberomorini (see Table 1).

Collette *et al.* (1984) and Johnson (1986) published phylogenies of Scombroidei based on morphological data (Figs. 3A and B). Finnerty and Block (1995) published a phylogeny based on DNA analyses (Figure 3C). In Collette *et al.* (1984), Sardini and Thunnini are the most advanced scombroids, with Scomberomorini as the sistergroup. According to Johnson (1986), Sardini+Thunnini are a specialised offshoot of a paraphyletic Scomberomorini. Finnerty and Block (1995) present a phylogenetic relationship in which the Sardini+Thunnini clade is sister-group to a Scombrini (mackerels)+Trichiuridae (cutlassfishes) clade. The clade containing these four taxa is in turn the advanced sistergroup to Scomberomorini. Keeping in mind the proposed evolutionary sequence (Figure 3D), all three hypotheses of relationships in Fig. 3A–C seem to be possible. Finnerty and Block's hypothesis is less parsimonious than the morphological ones, because it requires reversals. The caudal region of Scombrini and Trichiuridae is plesiomorphic compared to that of other Scombridae. Johnson's (1986) Scomberomorini are paraphyletic, caused by the offshoot of Sardini and Thunnini, but his phylogenetic hypothesis remains possible. However, this hypothesis is less parsimonious than that of Collette *et al.* (1984). If you map tail-region morphology on Johnson's (1986) phylogeny, there are character reversals (Figure 3B). Further research on the phylogeny of scombroids will hopefully contribute more to the solution of the controversy of these relationships.

Although based on a hypural plate only, I do think that phylogenetic hypotheses can be made using *G. prisca*. Hypural plates provide strong characters, which are well indicative of genera (see Uyeno and Fujii, 1975).

Conclusions

While studying the type series of *Scomberomorus saevus*, a new species has been found: *Gymnosarda prisca*. Sardini are to be characterised by a tendency of the hypural notch to close and disappear in their evolution. Thunnini are characterised by a complete absence of the notch. *Gymnosarda prisca* fits in with every one of the different scombroid cladograms, with respect to Recent Sardini-Scomberomorini relationships. Finnerty and Block's (1985) phylogeny seems to be less parsimonious than the morphological phylogenies. In Johnson's (1986) hypothesis, Scomberomorini are paraphyletic and the tail region evolution requires reversals.

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