

Discovery of the Recent genus *Trigonognathus* (Squaliformes: Etmopteridae) in the Lutetian of Landes (southwestern France). Remarks on the teeth of the Recent species *Trigonognathus kabeyai*.*

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with four figures

[An English translation of the abstract is provided in the original]

Introduction

The Squaliformes contains 24 modern genera, of which 12 are known from the fossil record (Compagno, 1984; and personal data), plus 17 known only as fossils (Cappetta, 1987 and personal data). This order, of which the phyletic relationships have been recently re-evaluated (Shirai, 1992, 1996; Carvalho, 1996), represents about 23% of sharks in terms of specific diversity. The Squaliformes frequent the bathyal zone and are characterized as a group by a strong dignathic heterodonty. Some genera are exceptions to the rule: genera with cutting-type dentitions s.s. (*Squalus* Linnaeus 1758, *Cirrigaleus* Tanaka 1912), clutching-type dentitions (*Centroscyllum* Muller and Henle 1841, *Aculeola* de Buen 1959), tearing-type (*Trigonognathus* Mochizuki and Ohe 1990), and even clutching-cutting type (*Miroscyllum* Shirai and Nakaya 1990), as far as can be determined for the latter from the inadequate figure of the dentition provided. The dentitions of some modern genera have been figured by Herman et al., (1989); the genera *Trigonognathus* and *Miroscyllum*, both described in 1990, were not studied by those authors.

The genus *Trigonognathus* has been described on the basis of three specimens caught off Japan. While its anatomy has been studied in detail, by Shirai and Okamura (1992), in particular, the same cannot be said for its dentition which has been figured only in a superficial manner. The goal of this note is to make known its precise dental morphology and describe a related fossil species.

The genus *Miroscyllum* was based on the species *sheikoi* Dolganov 1986, originally assigned to the genus *Centroscyllum*. The few specimens of this taxon were caught in the Kyushu-Palau Ridges Zone in the northwestern Pacific. The dentition of *Miroscyllum* is imperfectly known; it recalls that of *Etmopterus* according to Dolganov's figures (1986).

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The Dentition of the modern species *Trigonognathus kabeyai* Mochizuki and Ohe 1990

The studied dentition is from specimen No. BSKU 44653 (fig. 1), bought in the Mimase fish market by H. Endo. It was caught in Tosa Bay off Okitsu at a depth between 200 and 230 meters. It is a female 25.8cm in total length, studied and partially dissected by Shirai (1992). It is necessary to add that the specimen's preservative liquid partially damaged the teeth (weakening the enameloid and demineralizing the roots of the laterals, which left only incomplete samples of the latter.)

The anterior teeth of the lower and upper jaws possess a long and slender cusp (fig. 2.1 – 2.6). In profile the cusp is lingually inclined at an angle of about 45 degrees (fig. 2.2). Its labial contour is quite convex to its base. Its lingual contour is at first quite concave, then almost rectilinear. In labial view the narrow crown is blade-shaped; it is slightly broader at its midsection than at its base with the crown noticeably overhanging the root. The labial face is transversely convex and smooth. The lingual face is also quite convex transversely and some weak though broad enameloid folds are observable.

The root is mesiodistally compressed and lingually extended; its contour is elliptical and its basal surface is almost flat (fig. 2.6). The crown-root boundary is indistinct due to damage to the crown enameloid. Lingually, below the crown base two lobes branch out separated by a narrow depression (fig 2.5). The vascularization consists of numerous foramina on the labial, lingual, and basal faces. The marginal areas of the root are nearly devoid of foramina.

The anterolateral teeth* possess a lower, wider, and distally-inclined cusp. The crown is inclined lingually at about a 45 degree angle in relation to the root, the root being clearly more developed than in the anterior teeth. As in the latter, the lingual face of the cusp bears some broad yet inconspicuous enameloid folds. The root is reniform in contour with a flat basal surface dotted by just a few foramina (fig. 2.10). The labial face of the root is high, oblique in profile, and transversely convex (fig. 2.7). A first line of lower, rather large, and elliptical foramina are observable with another line of them limited to the mesial area of the root. Numerous foramina lie on the lingual face of the root with a principal median foramen.

The more lateral teeth feature a similar morphology with the cusp, however, being lower and root being less transversely spread out. (fig. 2.12). The mediolingual foramen is well-developed (fig. 2.14).

The lateralmost teeth (not figured) are of a very reduced size compared to the anterior files. The cusp is very low and triangular with a root that possesses a much more oblique basal face in relation to the outline of the cusp.

Discussion

* or laterals [JS]

Most of the modern and fossil Squaliformes are characterized by a strong dignathic heterodonty with labiolingually compressed lower teeth and generally more slender upper teeth. As exceptions to the rule, the modern genera *Squalus* and *Cirrigaleus* bear very similar teeth in both jaws with a cutting-type dentition in the strict sense. Within the Squaliformes these genera possess a dentition that can be considered as primitive in relation to the dignathic heterodonty typical in most of the other genera (Cappetta, 1986). Other genera have similar teeth in both jaws: *Centroscyllum*, *Aculeola*, and *Trigonognathus*, which is of interest to us in this article. Among the first two genera there is no monognathic heterodonty and the dentition is of a clutching-type, while the third is of a tearing-type with a strong monognathic heterodonty. For the genus *Miroscyllum* the dental type is difficult to establish unequivocally on the basis of the available figures (Dolganov, 1986; Shirai and Nakaya, 1990).

The dentition as a whole was summarily described and figured by Mochizuki and Ohe (1990: p. 388, fig. 3). The authors indicated that all the teeth were identical in both jaws and provided a dental formula (7-1-7/7-1-7 and 8-1-8/8-1-8) showing the presence of a symphyseal tooth in each jaw which does not agree with our own observations. The fact that the two individuals studied by Mochizuki and Ohe were males and the one that we have examined is a female cannot explain this discrepancy. In fact there is no unpaired symphyseal in either the lower or upper jaw.

Fig. 2. Teeth of the Recent species *Trigonognathus kabeyai* Mochizuki and Ohe 1990 (Specimen No. BSKU 44653). **1.** upper anterior tooth, labial view, x 11; **2.** same tooth, profile, x 11; **3.** same tooth, lingual view, x 11; **4.** same tooth detailed lingual view, x 25; **5.** same tooth, detailed lingual view of the base of the tooth, x 25; **6.** same tooth, basal view, x 25; **7.** lower anterolateral tooth, labial view, x 25; **8.** same tooth, profile, x 25; **9.** same tooth, lingual view, x 25; **10.** same tooth, basal view, x 40; **11.** same tooth, apical view, x 25; **12.** upper anterolateral tooth, labial view, x 25; **13.** same tooth, profile, x 25; **14.** same tooth, lingual view, x 25.

The dental formula of the specimen we have in hand is: 2A + 8L per upper or lower jaw quadrant. Mochizuki and Ohe noted the presence of folds on the labial and lingual faces of the crown of the anterior teeth in the two male individuals, though in the female that we have examined, there are only folds on the lingual face. This difference certainly shows sexual dimorphism.

In its dental design, this genus is very unusual and presents a striking hypertrophy of the anterior teeth; the two others of the group with dignathic heterodonty within the Etmopterinae possess a clutching-type dentition with numerous dental files and rows, however, with teeth of a very different morphology. *Aculeola* bears single-cusped teeth without lateral cusplets but of a small size; *Centroscyllum* has teeth of a scyliorhinoid morphology with one or two pairs of lateral cusplets.

The genus *Miroscyllium* Shirai and Nakaya 1990, considered as a sister group to *Etmopterus* by its authors, possesses labiolingually compressed, multicuspited lower teeth and upper teeth similar to those of *Etmopterus*, according to what was figured by Dolganov (1986: p. 150, fig. F-I). However, the precise dental morphology of *Miroscyllium* remains virtually unknown at the moment.

The genus *Trigonognathus* distinguishes itself by a series of unique characters, both at the level of the dentition as a whole and at the level of the dental morphology itself.

First of all, we must note the hypertrophy of the anterior teeth, which is the most striking feature of the specimen. According to anatomical studies led by Shirai and Okamura (1992), *Trigonognathus* was able to open its wide mouth and therefore seize large prey, this type of predation being facilitated by the quite sizable anterior teeth. Compared to the recorded proportions of other genera of the subfamily Etmopterinae, *Trigonognathus* possesses anterior teeth 5 to 10 times larger than either *Centroscyllium*, *Etmopterus*, or *Aculeola*.

Another striking feature of the dentition is the reduced number of tooth rows and files, the teeth being largely separated – each file spaced apart from its neighboring files. Generally, we indeed observe a more or less significant overlapping of the teeth or at least a close juxtaposition from one file to the other.

In terms of dental morphology the root exhibits a basal face virtually perpendicular to the plane of the cusp at least in the anteriors and anterolaterals. This last character is unique among the Squaliformes with a very derived dentition. It recalls in contrast what is observed in primitive forms, as in the fossil genera *Protosqualus* Cappetta 1977, *Megasqualus* Herman 1982, or even still in certain species of *Squalus* with a less advanced morphology.

The teeth of fossil *Trigonognathus*

Origin of the fossils

The fossil teeth referred to the genus *Trigonognathus* come from the Miretrain quarry in the Angoume district on the right bank of the Adour in Landes (fig. 3). The fossiliferous layer is situated in the northern part of the slope supporting the Miretrain farm. It is a thick layer of well-indurated, rusty-yellow marly limestone rich in planktonic foraminifera. Nearly a metric ton of this limestone has been washed and screened down to 300 micron mesh. The forams indicate a Middle to Late Lutetian age (Sztrakos et al., 1998).

The Miretrain quarry is already the study area for work devoted to foraminifera (Mancion, 1985; Sztrakos et al., 1998). More recently, a work on the rich and diverse shark fauna has been undertaken by one of us (Adnet, 1997 and in progress).

Fig. 3. Location of the deposit at Angoume. [see original]

Fig. 4. Teeth of *Trigonognathus virginiae* n. sp.: **1.** anterior tooth (ANG 1), labial view, x 12.5; **2.** same tooth, profile, x 12.5; **3.** same tooth, lingual view, x 12.5; **4.** anterolateral tooth (ANG 2), labial view Holotype, x 12.5; **5.** same tooth, profile x 12.5; **6.** same tooth, apical view, x 12.5; **7.** same tooth, basal view, x 12.5; **8.** same tooth, lingual view, x 12.5; **9.** anterolateral tooth (ANG 3), profile, x 11.

Order Squaliformes Goodrich 1909

Family Squalidae Bonaparte 1834

Genus *Trigonognathus* Mochizuki and Ohe 1990

Trigonognathus virginiae n. sp.

Fig. 4

Name derivation: species dedicated to Virginie Parra, thanks to whom we have been able to have access to the *Trigonognathus kabeyai* specimen.

Holotype: Fig. 4.4 to 4.8 (ANG 2).

Type Locality: Miretrain Farm, Angoume district, Landes.

Age: Middle to Late Lutetian (*G. subconglobata* zone; Sztrakos et al., 1998).

Diagnosis: species of *Trigonognathus* close to the one modern species but distinguished by its anterior teeth lacking enameloid folds and by its anterolateral teeth, which have a more mesiodistally-developed and labially less-high root.

Material: three teeth.

Description: The one anterior tooth is incomplete at the root level; either this root was subjected to stress within the sediment or it was incompletely mineralized. The crown is narrow and tapering in lingual view (fig. 4.1). In profile it is curved lingually to its base (fig. 4.2); it is quite bent near its base but almost rectilinear along its apical half. The cutting edges are well-developed and they reach the base of the lingually-directed tooth. The lingual face is clearly transversely convex to its base.

The root is incomplete but it can be stated that it is low and not very mesiodistally extended.

The holotype is a complete anterolateral tooth (fig. 4.4 – 4.8). In labial view the cusp is high and only slightly inclined distally. Its mesial cutting edge is sigmoid while the distal one is practically rectilinear. In profile the cusp is weakly inclined lingually and virtually perpendicular to the root. The labial face of the cusp is quite transversely convex, especially at its base. There are low, oblique, and well-developed cutting edges on the heels, which are clearly directed lingually in apical view.

The root consists of two lobes of unequal size, the mesial one being short and rounded in contour. The distal one is elongated and tapered to its end. In apical view the root overhangs the crown all along the perimeter of the tooth; its labial edge is convex as a whole. The vascularization consists of numerous small foramina dotting the labial face of the root, certain ones being more developed at the lobes. On the labial part of the basal face are two aligned foramina; on their axis a narrow but clearly marked notch is observed at the level of the cusp; just above in lingual view is a quite visible foramen.

Another anterolateral tooth is incomplete (fig. 4.9) and shows a similar morphology with however a higher and slightly more lingually-inclined cusp.

Discussion

The unique morphology of the anterolateral teeth of *T. virginiae* n. sp. did not permit a satisfactory identification at first. In their general morphology, they are reminiscent of the teeth of the genus *Sphenodus* Agassiz 1843. This genus, however, existed in the Jurassic and Cretaceous, becoming extinct in the Danian, where it is represented by a species of large size, *Sphenodus lundgreni* (Davis, 1890). Moreover, the anterior tooth was not interpretable. The examination of the *Trigonognathus kabeyai* dentition alone allowed us to resolve these determination problems and to report the presence of this genus in the fossil record.

Compared to the modern taxon, the fossil species shows a certain number of differences. In the anterolateral files the teeth of the fossil species are more spread out mesiodistally with the heels more developed. The labial face of the root is subvertical in profile (fig. 4.5 and 4.9) with irregularly-arranged foramina, while in the Recent species, it is more oblique with larger foramina aligned parallel to the basal edge of the root.

Conclusions

This work offers a detailed report on the dentition of the modern genus *Trigonognathus*, which had been previously only summarily described and figured. This study confirms the unique dental morphology of this genus as much in the dentition as a whole as in the morphology of the isolated teeth. *Trigonognathus* possesses hypertrophied teeth in the anterior files, a unique character within the Squaliformes.

The examination of the modern species allowed the identification of some fossil teeth from the Lutetian of southwestern France of which the determination was previously impossible.

Despite some morphological differences, the teeth of the fossil species compare well with those of the modern species. The presence of a genus with such a derived dentition in the Lutetian testifies to the quite ancient nature of the adaptations and dental specializations within the Squaliformes and attests to an early colonization of the bathyal environment

by this group. The range of distribution of the genus is very narrow today, confined to Tosa Bay, Japan. This distribution is perhaps more extensive than it seems. Indeed, we must remember that bathyal faunas living today are poorly known in many regions of the world and that their distribution is reflected by only the extent of commercial fishing. In view of the presence of the genus in the Early Pliocene of Venezuela (pers. obs. H. C., based on the collections of O. Aguilera) and in the Lutetian of Landes, one can expect to find it in other modern seas outside of Japan.

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