UNDERDEVELOPED AND UNUSUAL XENACANTH SHARK TEETH FROM THE LOWER PERMIAN OF TEXAS

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ABSTRACT

Xenacanth sharks from the Wichita and Clear Fork Groups in north-central Texas are represented by 51,400 isolated teeth, obtained by bulk-sampling sediments at 65 localities, of *Orthacanthus texensis* (50% of total), *O. platypternus* (12%), *Barbclabornia luedersensis* (38%), and *Xenacanthus slaughteri* (0.01%) in Early Permian (late Sakmarian-Artinskian) strata spanning some 5 million years (285-280 Ma). Discounting deformed teeth (0.06%), which could usually be identified to species, there remain much more common underdeveloped teeth (1-2%?) and unusual teeth that are rare (<<0.1%). Teeth not fully developed, and presumably still within the dental groove when a shark died, lack the outer hypermineralized pallial dentine on the cusps, which display open pulp cavities; tooth bases possess a poorly developed apical button. Most could be assigned to the species of *Orthacanthus*, the remainder to *B. luedersensis*. Based on histological development in modern shark teeth, in which the base is last to develop, it would seem the reverse occurred in xenacanth teeth, but this conclusion is uncertain. Unusual teeth were most closely affiliated with *Orthacanthus*, but they possess characters normally not associated with that genus, exceeding the presumed limits of variation that might be accepted for its heterodont dentition. Examples include teeth with cristated cusps, in which the distribution of cristae is highly asymmetrical; possession of a single cusp or of three equally developed principal cusps (two are normal in xenacanth teeth); and one tooth with a primary intermediate cusp that may have been larger than the principal cusps. *B. luedersensis*, which possessed a largely homodont dentition, is not represented by any of these "extreme variants."

Keywords

Xenacanthida, Chondrichthyes, Lower Permian, Texas

INTRODUCTION

Vertebrate microfossils representing the remains of Early Permian fishes and tetrapods obtained by bulk-sampling techniques (Johnson et al. 1994) of some 50 localities from the Wichita Group (Johnson 1979) and 15 localities from the overlying Clear Fork Group (Murry and Johnson 1987) in north-central Texas include various species of predominantly freshwater sharks. The sampled portion of the Wichita Group represents successively the upper Nocona Formation, upper Petrolia Formation, and all of the Waggoner Ranch Formation (including the Lueders Formation of the Albany Group, for present discussion; Johnson 1999:table 1, 2003:table 1). The Clear Fork Group is not formally divided (Johnson 1999:230). The ages of these strata are Sakmarian (Nocona Formation) and Artinskian (Johnson 1992, 2003), representing an estimated range of five million years, from 285 Ma to 280 Ma, based on Menning et al. (2002). The dominant group of sharks represented in these faunas were the xenacanths (Order Xenacanthida, Class Chondrichthyes). A total of 51,400 isolated teeth represent *Orthacanthus texensis* (50% of total), *O. platypternus* (12%), *Barbclabornia luedersensis* (38%), and *Xenacanthus slaughteri* (0.01%). All occur in the Wichita Group; in the Clear Fork Group, only *O. platypternus* is present, except *Barbclabornia* persisted only into the lowermost part as *B.* cf. *luedersensis*. The teeth of all of these species were described by Johnson (1999, 2003).

Xenacanth teeth bear a pair of principal conical cusps on the labial side of an enlarged base (Fig. 1). The cusps may be compressed, are smooth or variably bear cristae, carinae, or both. A variable number of smaller intermediate cusps may be present except in *Barbclabornia*. The base possesses a lingual apical (coronal) button on the oral surface and a labial basal tubercle on the aboral surface, which was in contact with the apical button in the next successive replacement tooth within a file, as in modern sharks.

The second-most common sharks, the hybodonts, were described by Johnson (1981), and the remaining much less common taxa (Johnson 1981:fig. 3) have not been described. About 0.06 percent of the xenacanth teeth were determined to be deformed (Johnson 1987). The purpose of this report is to document the occurrence of presumably underdeveloped and unusual xenacanth teeth.

All of the teeth described here are reposited in the Waggoner Ranch Collection, Shuler Museum of Paleontology at Southern Methodist University (SMU) in Dallas, Texas. The faunas and localities mentioned in this paper are listed in Johnson (1999:table 1, 2003:table 1).

Underdeveloped Xenacanth Teeth

Except for *Xenacanthus slaughteri*, all of the xenacanth species from the sampled Lower Permian show evidence of underdeveloped or "immature" teeth (Johnson 1979:216-217, 1999:232). They occur throughout the sampled stratigraphic section, but were not segregated from collections of normal teeth except those illustrated here (Fig. 2). They are relatively more common in *Orthacanthus* than *Barbclabornia*.

The apical button is often poorly developed, and the cusps lack cristae or carinae (and therefore serrations; Figs. 1, 2). The principal cusps are poorly developed, often exhibiting an opening to the pulp cavity at their tips (Fig. 2B, C, F). If an intermediate cusp is supposed to be present, it is even less developed. In *Barbclabornia luedersensis* teeth, which lack an intermediate cusp, a broad saddle is formed by the medial margins of the principal cusps (Fig. 2D).

DISCUSSION

Johnson (1979) initially thought these fossils may be merely functionless teeth that occurred at the commissural end of the jaws. However, this condition occurs in both the lateral and medial teeth of *Orthacanthus* (Johnson 1999), which strongly suggests that they represent replacement teeth (Zidek et al. 2003: fig. 3). If this is the case, then their morphology suggests a rather intriguing problem. It is well known (Romer 1962, Applegate 1965, Schaeffer 1977) that the initial part of a tooth to develop is the cusps, particularly the outer hypermin-

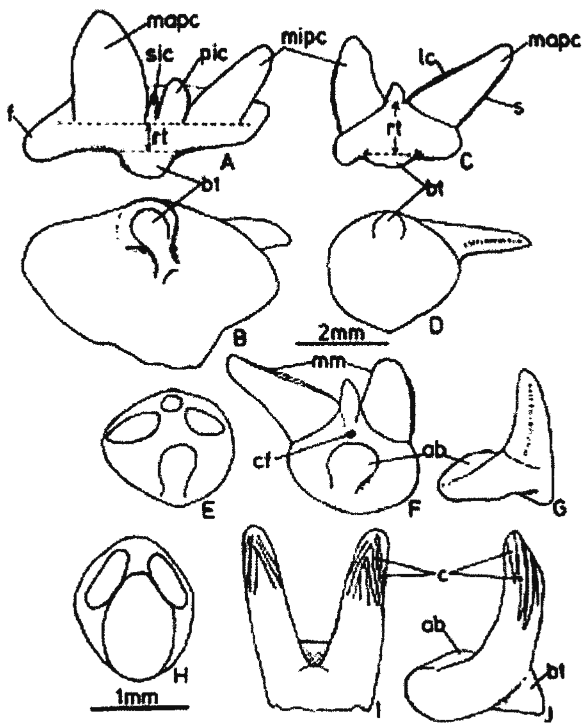

Figure 1. Tooth morphological nomenclature used in describing xenacanth teeth: A, labial, and B, aboral, views of* Orthacanthus platypternus*; C, labial, D, aboral, E, occlusal (oral, coronal), F, lingual-occlusal, and G, anteromedial, views of* O. texensis*; H, occlusal, I, labial, and J, anteromedial or posterolateral views of* Barbclabornia luedersensis*; the serrations and cristae are slightly exaggerated; upper scale bar for A-G; lower scale bar for H-J; ab = apical button; bt = basal tubercle; c = cristae; cf = central foramen; f = flange; lc = lateral carina; mapc = major principal cusp; mipc = minor principal cusp; mm = medial margin of cusp; pic = primary intermediate cusp; rt = thickness of tooth base ("root" thickness); s = serrations; sic = secondary intermediate cusp. Modified from Johnson (1999:fig. 1).

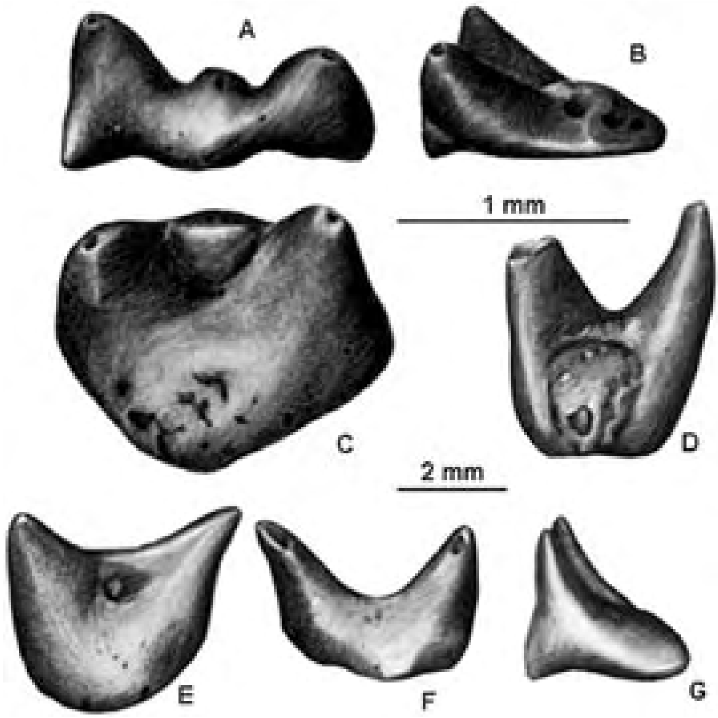

Figure 2. Underdeveloped xenacanth teeth from the upper Petrolia Formation: A-C,* Orthacanthus platypternus, *Brushy Creek K/ac locality (SMU 372), A, labial, B, anteromedial or posterolateral, and C, lingual-occlusal views of SMU 64300; D,* Barbclabornia luedersensis, *Wolf Creek B locality (SMU 285), lingual-occlusal view of SMU 64091; E-G,* O. texensis, *Wolf Creek/ac locality (also SMU 285), E, lingual-occlusal, F, labial, and G, anteromedial or posterolateral views of SMU 64236. Upper scale bar represents A-D and lower scale bar represents E-G. Modified from Johnson (1979:plate 42).

eralized pallial dentine (see discussion in Johnson 2003:134-137) followed by the other tissues. But this tissue, which especially comprises the cristae in *Barbclabornia* and serrated carinae in *O. texensis*, is absent. The base is the last part of the tooth to develop. Yet, in the xenacanth teeth described here, the cusps appear to be less developed than the base (Fig. 2), although the apical button remains undeveloped (but see the description of Fig. 4D below). Hampe (1997) noted comparable "tooth embryos" in *O. senkenbergianus*. Furthermore, he noted that the foramina in the tooth bases are poorly defined, so perhaps the base is at least as undeveloped as the cusps in this species. Hampe (1997:129) also described the abnormal absence of cristae in an otherwise normal *Triodus* tooth and suggested they may not have developed because of trauma.

In the various species of hybodont sharks described by Johnson (1981), based on nearly 4,000 isolated teeth, none appeared to be underdeveloped. It would seem unlikely that this phenomenon should be restricted to xenacanths. The differences in their histology is not so significant as to suggest that xenacanth tooth development is in some way aberrant, and would seem not to explain the observations noted above (compare Johnson 1981, 2003; Hampe 1991, 1997).

Unusual Xenacanth Teeth

Besides the variants of otherwise normal teeth described by Johnson (1999: figs. 5O, 6F, 7J, N, 12A-D, M-N, 13O, 14A-D; 2003:fig. 10L-M) and the underdeveloped and deformed teeth, there are some probable *Orthacanthus* (mostly *O. texensis*) teeth from the Wichita Group that are quite unusual. For example, a few *O. texensis* teeth have cristae in addition to the lateral carinae, despite *Orthacanthus* being defined as not possessing cristae (Johnson 1999). One (SMU 64194, Brushy Creek C fauna) has coarse cristae on the labial side of one of its principal cusps (distal ends of both cusps are missing). Only two teeth of *O platypternus* were found in the Wichita Group which possess cristae; they were described by Johnson (1999:243). Presumably this is an atavistic character, as presumed ancestors of these species possessed cristae (Johnson 1979:165; see other examples and further discussion in Johnson 1999:243, 250, 251-252).

Only one tooth (SMU 64191, Lake Kemp A fauna), probably from *Orthacanthus texensis*, might be considered symphysial, in the sense of *Barbclabornia* dentitions, with a highly compressed base (Johnson 2003:134). The cusps lack serrations, but the apical button is typical of *Orthacanthus* (Fig. 1F). *O. texensis* probably did not possess symphysial teeth (Johnson, 1979:200).

Another tooth, with an unusual base (Fig. 3), has a single serrated lateral carina on the posterior(?) margin of the larger cusp, but two on the medial margin, with the one nearer the apical button slightly serrated. The smaller principal cusp has three cristae on the anterior(?) margin, with serrations on the two nearest the labial margin; none occurs on the medial margin, but two shorter cristae occur on the medio-labial corner of the cusp. The base is thicker than normal (Fig. 1C), with the side lingual to the cusps highly abbreviated. The poorly developed apical button (Fig. 3A) barely extends between the cusps, which is unusual for *Orthacanthus* where it is normally isolated from the cusps (Fig. 1E, F; Johnson 1999). The basal tubercle is massive and protrudes labially (Fig. 3C). The identification of this tooth is questionable. Oliver Hampe (pers. comm., 8 June 2005) doubts it is an *Orthacanthus* tooth; but it more closely resembles that genus than any other shark genus.

A single tooth (Fig. 4A-C) has an anteromedial-posterolaterally elongated and somewhat distinctly separate base. The tooth may be an extreme variant of *Orthacanthus texensis*. It is less similar to the *Xenacanthus slaughteri* teeth described by Johnson (1999:254-259, see also Hampe 2003:221, verifying the generic assignment).

An underdeveloped(?) tooth possesses an enlarged and apparently fully developed primary intermediate cusp (Fig. 4D). The principal cusps and two secondary intermediate cusps appear to be largely undeveloped. It appears that even if all the cusps had been fully developed, the centrally positioned primary intermediate cusp would still be the largest. It is not a cladodont tooth, however, as the base is typically that of a medial *Orthacanthus* texensis tooth (Johnson, 1999:233).

One tooth (Fig. 4E-G) appears to lack a developed apical button despite possessing a normal basal tubercle. It is possible it was broken away during transport, as the tooth shows possible wear from water currents although it is largely

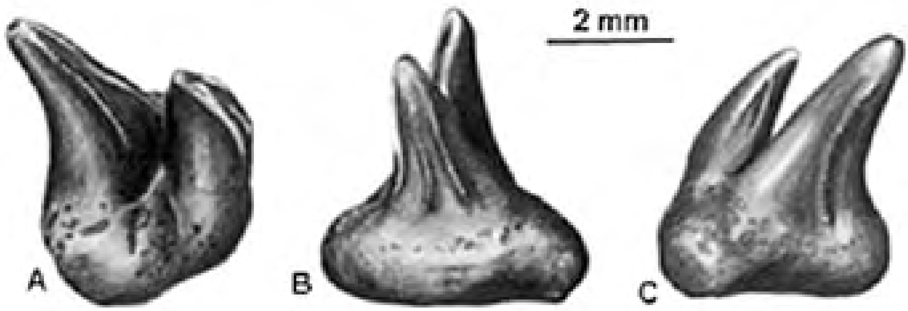

Figure 3. Unusual* Orthacanthus? *tooth, Brushy Creek C/ac locality (SMU 377), upper Petrolia Formation; A, oblique lingual-occlusal, B, anteromedial or posterolateral, and C, labio-anteromedial or -posterolateral views of SMU 64210. Modified from Johnson (1979:plate 30).

intact. It is probably a posterolateral tooth, as all three cusps are leaning in the same direction (Johnson 1999:233, fig. 7A-E). The intermediate cusp is unusually large (Johnson 1999:232), similar to an *Orthacanthus senkenbergianus* tooth described by Hampe (1997:125).

Teeth with only one or with three principal cusps are rare. One (SMU 64189, Bluff Creek A fauna) has only a single cusp that resembles the inverted blade of a guillotine; the base is normal. Teeth with three equal-size cusps were recovered from two faunas. One (SMU 64197, Brushy Creek C fauna) has a compressed but unserrated medial cusp. Two teeth (SMU 64238, Mitchell Creek B/ac fauna) have an anteromedial-posterolaterally elongated and slightly bifurcated apical button and basal tubercle; one also has secondary intermediate cusps between an enlarged primary intermediate cusp and the principal cusps (Fig. 4H, I). Both also have rather thin bases (as seen at the labial margin) and the cusps (broken) are not serrated, characters that are attributed to *Orthacanthus platypternus* (Fig. 1A; Johnson 1999:235). Their identification is therefore questionable. The structure of the apical button and basal tubercle in these two teeth suggests the possibility of lateral fusion of teeth (Johnson 1987), but the normal appearance of the cusps renders this unlikely. Also, the possibility that they are some sort of phoebodont tooth (Johnson 2005) is very doubtful because the cusps apparently lack cristae, among other reasons (Johnson 2005).

DISCUSSION

One or two (Figs. 3, 4A-C) of the unusual teeth may represent different species than those previously identified (Johnson 1999, 2003). If so, they would be new species. Because they are rare does not preclude this possibility. The presence of a single phoebodont-like tooth in the entire Waggoner Ranch Collection of more than 55,000 shark teeth is a good example (Johnson 2005).

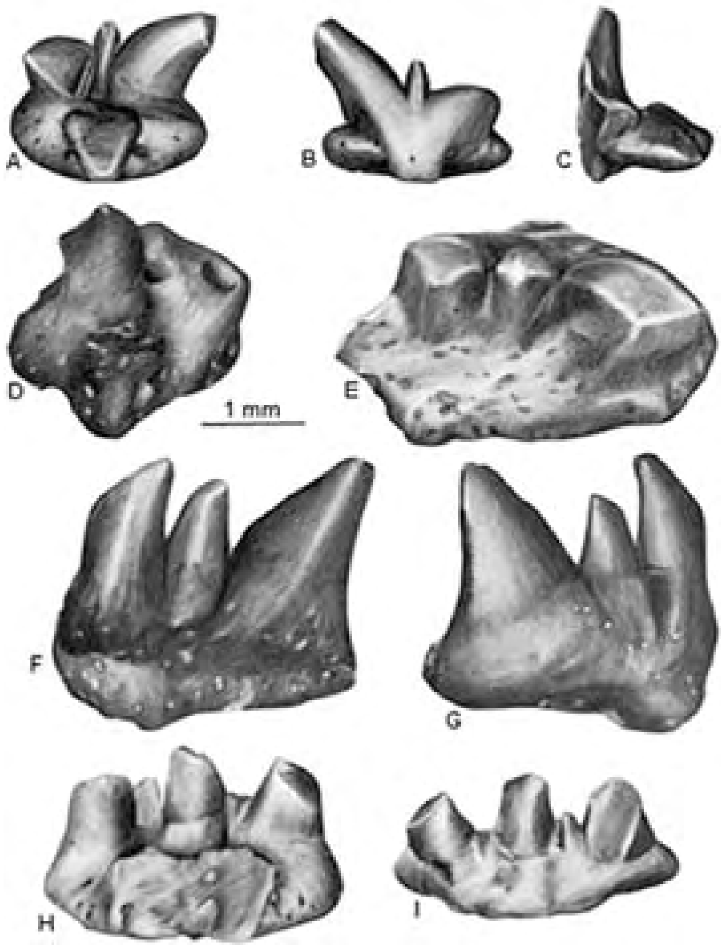

Figure 4. Examples of unusual* Orthacanthus *teeth: A-C,* O. texensis?, *Lake Kemp B/ac locality (SMU 345), lower upper Waggoner Ranch Formation, A, lingual-occlusal, B, labial, and C, anteromedial? views of SMU 64237; D,* O. texensis?, *Tit Butte/ac locality (SMU 344), lower upper Waggoner Ranch Formation, lingual-occlusal view of SMU 64208; E-G,* O. texensis, *Franklin Bend A locality (SMU 366), lower middle Waggoner Ranch Formation, E, occlusal, F, lingual, and G, labio-posterolateral views of SMU 64186; H-I,* O. platypternus?, *Mitchell Creek B/ac locality (SMU 160), middle Waggoner Ranch Formation, H, lingual, and I, labial views of SMU 64238 (one of two teeth). Modified from Johnson (1979:plate 30).

CONCLUSIONS

Underdeveloped xenacanth teeth were probably unerupted teeth in the dental groove. The cusps in these teeth appear to be less developed than the bases although the cusps are normally first to develop in other sharks. The absence of hypermineralized pallial dentine on the cusps could have resulted from trauma, but seems unlikely. The absence of underdeveloped hybodont teeth in the same faunas suggests tooth development may have been different in xenacanths. But this also seems unlikely, as there are no significant histological differences. The explanations for the relatively common occurrence of underdeveloped xenacanth teeth and their seemingly unusual development remain elusive.

Given the presence of underdeveloped and deformed teeth in the Wichita Group faunas, the presence of rare unusual teeth in a large population of *Orthacanthus* might be expected. But the underlying cause (trauma, developmental abnormality, etc.) for their occurrence can only be speculated at this time. In view of the general variability of *Orthacanthus* teeth and the heterodont dentitions in this genus (Johnson 1999), and the absence of similar teeth in other geographic and stratigraphic contexts, it would be difficult to demonstrate the existence of new species without the discovery of additional specimens. Perhaps significantly, "unusual" teeth were not observed in *Barbclabornia luedersensis*, which possessed a largely homodont dentition.

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