

RAPID COMMUNICATION

Dicentrodus (Chondrichthyes: Xenacanthida) from the Early Carboniferous (Visean: upper St Louis Formation) of Iowa, USA

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Abstract

Dicentrodus possessed bicuspid teeth with a flat base and nonserrated or finely serrated, labio-lingually compressed, highly unequal cusps. Originally known from the late Visean–early Serpukhovian of Scotland (*D. bicuspidatus*), it is now known also to occur in the middle Visean of North America. This is the earliest occurrence of a xenacanthid yet reported from North America; its presence is based on incomplete teeth, which are easily distinguished from other xenacanthid genera. The cross-continental distribution of *Dicentrodus*, like that of other xenacanthid genera, can be explained by an increasing body of data that intimate that xenacanthids were euryhaline sharks and not restricted to a freshwater habitat.

Keywords: Xenacanthida, Carboniferous, palaeogeography, Iowa, Scotland.

1. Introduction

Included in the amphibian and fish remains from Delta site in southeastern Iowa, USA, reported by Bolt *et al.* (1988), are isolated xenacanthid teeth and an associated crushed skull. The skull has not been prepared, and the presence of a dorsal spine characteristic of xenacanthids has not been found. Johnson (1990) provided an initial description of the teeth, but was then uncertain of their generic identity.

The Xenacanthida represent an impressive group of elasmobranchs with a wide stratigraphic range beginning in the Lower Carboniferous and terminating in the Upper Triassic. Their main characteristics are paired fins of archipterygium type, a single elongated dorsal fin, and a single dorsal spine of varied position at the anterior half of the body (e.g. Fritsch, 1889, 1890; Schneider & Zajíc, 1994; Heidtke, 2003; Heidtke & Schwind, 2004; Soler-Gijón, 2004). The mouth carries usually tricuspid teeth with two well-developed lateral cusps and an often weaker and smaller median cusp. The tooth base is lingually extended and has a coronal button on the upper side and a basal tubercle on its bottom side (e.g. Davis, 1892; Johnson, 1980, 1999; Hampe, 1988a, 1988b, 1989, 1993, 2003; Schneider, 1988,

1996; Turner, 1993). *Dicentrodus bicuspidatus*, erected by Traquair (1881) from the Pendleian Blackband Ironstone (lower Serpukhovian) of Scotland and initially recognized as a species of *Cladodus*, was discovered to be a xenacanthid just recently (Hampe, 2003). The teeth of *Dicentrodus* have a distinct morphology lacking a median cusp. The histology of the cusps resembles that of the oldest known representative of the xenacanthids, *Diplodoseleche woodi*, from the upper Arundian to Brigantian (Visean) in Scotland (Dick, 1981; Hampe, 2003). Dorsal spines assigned to the Scottish *Dicentrodus bicuspidatus* reveal a close relationship with the Early Permian *Lebachacanthus senckenbergianus* from SW Germany (Hampe, 2003).

2. Systematic palaeontology

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order XENACANTHIDA Glikman, 1964
Family ?DIPLODOSELACHIDAE Dick, 1981
Genus *Dicentrodus* Traquair, 1888

Dicentrodus sp. IA
Figures 1, 2

1990 *Orthacanthus?* Johnson, p. 31–32, 1 fig.

Material: Five incomplete teeth and tooth fragments, FMNH PS-14024, 14025, 14028.

Occurrence: Upper St Louis Formation, Holkerian, Lower Carboniferous, near Delta (Heimstra Quarry, Keokuk County; McKay, Witzke & McAdams, 1987), SE Iowa, USA.

Remarks: The teeth are deposited in the Field Museum of Natural History, Chicago, USA (FMNH).

Description: The crown of the teeth consists of two cusps of different size. Both major cusps and the minor cusp lean posteriorly (Figs 1a, c, 2a, b, d, h, j). The range of variation in cusp attitude, whether they may be divergent, for example, is not known. Intermediate cusps, as usual for xenacanthid elasmobranchs except *Dicentrodus*, are absent in all specimens. The cusps are compressed and bear lateral edges on the posterior, medial and anterior margins (Figs 1b, 2c, i). None of the preserved edges is serrated. The surface of

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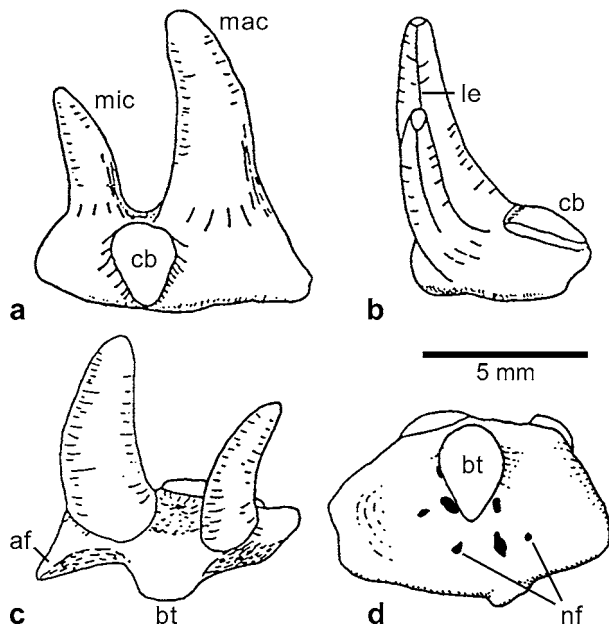


Figure 1. Composite illustration based on FMNH PS-14024 of *Dicentrodus* sp. IA in (a) lingual, (b) posterior, (c) labial, and (d) basal views. Abbreviations: af – anterior flange of the base, bt – basal tubercle, cb – coronal button, le – lateral edge, mac – major cusp, mic – minor cusp, nf – nutrient foramina.

the cusps is smooth, as cristae are absent. The most notable feature is the thinness (flatness) of the base. A conspicuous flange occurs on the anterior end of the base (Figs 1c, 2d, j); it is more deeply flexed in some teeth than in others. A distinct depression can occur between the principal cusps, but a median foramen is absent. The coronal button is isolated from the two cusps (Figs 1a, b, 2a, b, c, f, h, i, k). It projects lingually beyond the base margin in some teeth. The egg-shaped basal tubercle is prominent (Figs 1c, 2d, e) and has no basal depression. The number of nutrient foramina on the upper side of the base is uncertain because of its rugose surface. About five or six larger foramina appear to occur on the bottom side (Figs 1d, 2e). The tooth base is longer (anterior–posterior) than wide (labial–lingual) in all the teeth (Figs 1d, 2e, g, j). The observed sizes of the base range from slightly larger than 7×4 mm to slightly larger than 10×10 mm. The height of the teeth is estimated between 7 and 16 mm (Fig. 2).

3. Discussion

The teeth of *Dicentrodus* sp. IA represent the second oldest record of the Xenacanthida after *Diplodoselache woodi* from Scotland, which is known from the upper Arundian (Fig. 3). Earlier Tournaisian to early Visean records of yet undetermined xenacanthid teeth have been found in central Russia (Lebedev, 1996) and Queensland (Turner, 1982, 1993). There is yet no evidence of pre-Tournaisian representatives of that order.

The tooth morphology of *Dicentrodus* sp. IA resembles closely that of the Pennsylvanian *Dicentrodus bicuspidatus* from Scotland (known from Burghlee and Loanhead/Midlothian, and Cowdenbeath/Fife), so that the generic determination

is undoubted. Both have a bicuspid crown with cusps of markedly different size, labio-lingually compressed with lateral edges present. The base is flat in both forms and an anteriorly positioned, downward oriented flange is present as well, as is the egg-shaped, lingually pointed coronal button that is isolated from the cusps.

However, there are also significant differences between the North American and Scottish teeth. The size difference between the principal cusps is greater in *Dicentrodus bicuspidatus* than in *Dicentrodus* sp. IA. The anterior cusp is extremely dominant in the Scottish teeth (Woodward, 1889: pl. VI, fig. 7; Hampe, 2003: fig. 8a–d, k, l). The edges of the cusps are not serrated in the North American form whereas in *Dicentrodus bicuspidatus* they are finely serrated (Hampe, 2003: fig. 8c, d, i). The base of *Dicentrodus bicuspidatus* shows a stronger mesio-distal elongation (Hampe, 2003: fig. 8g, h). The basal tubercle is less developed than in teeth of *Dicentrodus* sp. IA and has a flat or open lingual margin (Hampe, 2003: fig. 8g, h, k–n). Teeth with uncommonly equal-sized cusps or multicuspoid crowns (Hampe, 2003: fig. 8e, f, m, n) are as yet unknown from the North American *Dicentrodus*.

Although *Dicentrodus* teeth have a distinct morphology and are usually not comparable with other xenacanthid species, there are similarities with a few other taxa. Teeth of *Orthacanthus platypternus* from the Upper Carboniferous (*O.* aff. *platypternus*) and Lower Permian of North America possess, as in *Dicentrodus*, crescent-shaped divergent cusps (Hotton, 1952: fig. 2A; Johnson, 1999: figs 11, 12I–N). The base of *Orthacanthus platypternus* is almost flat as in *Dicentrodus* (Johnson, 1999: Fig. 11G, J, M, P). However, *Orthacanthus platypternus* has a tricuspid crown with a median cusp always shorter and sometimes with accessory intermediate cuspules, but the anterior cusp is also clearly larger than the posterior cusp (Johnson, 1999: fig. 11) as in *Dicentrodus*. *Orthacanthus platypternus*, like all species of *Orthacanthus*, possesses a prominent median foramen behind the coronal button (Johnson, 1999: fig. 11I, Q; fig. 12D, F, I; fig. 13H, M, P). A median foramen is not present in *Dicentrodus*.

Thin bases can also be found in *Xenacanthus* species, for example in teeth of *Xenacanthus remigiusbergensis* from the lowermost Permian of the Saar–Nahe basin (Hampe, 1994: figs 8, 9) and in *Xenacanthus slaughteri* (Johnson, 1999: figs 21, 22). However, the remaining characters and the characters of the cusps differ clearly from those of *Dicentrodus*.

The taxonomy of '*Pleuracanthus*' *albuquerquei* from the Permo-Carboniferous of Estado do Maranhão, Brazil remains unclear. The Brazilian teeth show a prominent cusp as seen in *Dicentrodus* (Silva Santos, 1946: pl. II, figs 1, 2, 2b), and also a mesial flange (Silva Santos, 1946: pl. II, fig. 2). Numerous fine cristae on the cusps are described in '*Pleuracanthus*' *albuquerquei*, which is a characteristic for the genus *Triodus* (e.g. Hampe, 1989, Soler-Gijón & Hampe, 1998). The prominent coronal button supported by a lingual shaft is also different from *Dicentrodus*.

The poor and fragmentary preservation of the teeth of *Dicentrodus* sp. IA do not warrant the erection of a new species until more material becomes available.

4. Palaeogeographical distribution

Dicentrodus sp. IA from Iowa represents the oldest representative of the genus and is the oldest recorded evidence of a

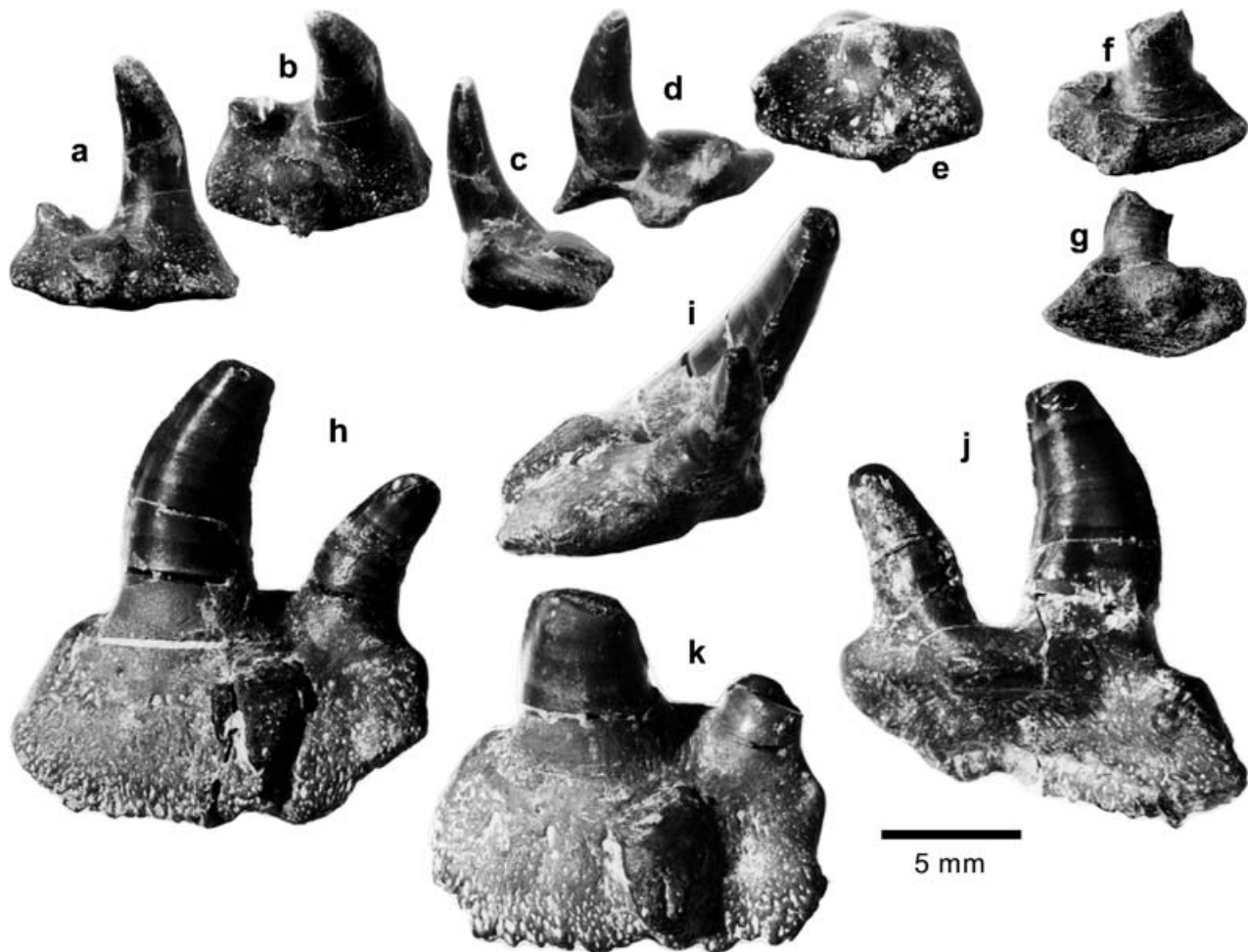


Figure 2. Teeth of *Dicentrodus* sp. IA from the Holkerian (Visean, upper St Louis Formation) of SE Iowa. FMNH PS-14024 in (a) lingual, (b) linguo-occlusal, (c) posterior, (d) labial, and (e) basal views; FMNH PS-14025 (1 of 2 specimens) in (f) linguo-occlusal, and (g) basal-labial views; FMNH PS-14028a in (h) lingual, (i) posterior, and (j) labial views; FMNH PS-14028b in (k) lingual view.

xenacanthid in North America. The younger *Dicentrodus bicuspidatus* is documented from the Midland Valley in Scotland, a shallow basin between the Southern Uplands High and the Highland Massif (see Hallsworth *et al.* 2000).

Prior to the Westphalian (Moscovian), the Iberian–Midcontinent Seaway connected the Panthalassan Ocean with the Palaeotethys Sea (Vai, 2003, García-Bellido & Rodríguez, 2005, R. Blakey, unpub. data, 2004: <http://jan.ucc.nau.edu/~rcb7/340Nat.jpg>), which allowed faunal exchange between North American and European basins independent of the uplift of the Appalachians. A similar fish fauna at generic level is shared between the Iowan Delta site and about seven Scottish localities of West Lothian, Edinburgh, and Midlothian, including the island of Inchkeith (Asbian to Pendleian), with the acanthodian *Gyracanthus* (pectoral and other fin spines), rhizodont sarcopterygians (bones, teeth and scales), and the organ genus *Cynopodius* (teeth) (Schultze & Bolt, 1996, Turner, Burrow & Warren, 2005).

Xenacanthids are interpreted today as euryhaline organisms (Schultze & Soler-Gijón, 2004), so that they were capable of migrating through marine nearshore waters around Palaeotethys. A northern exchange through the Palaeoarctic seems to be of less probability for a mainly tropical fauna.

5. Conclusions

The occurrence of *Dicentrodus* in the middle Visean of western Laurentia (Iowa, North America) precedes its occurrence in eastern Laurentia (late Visean–early Serpukhovian, Scotland). It is also the oldest xenacanthid yet reported from North America. Although these occurrences are likely represented by different species, the palaeogeographic implications are significant. Given the known time span of this genus and the euryhaline habitat of xenacanthid sharks in general, it is possible that speciation occurred as individuals migrated via a marine nearshore route. However, given the rarity of the taxon and the unusual asymmetry of its teeth, it might well have been a highly specialized xenacanthid.

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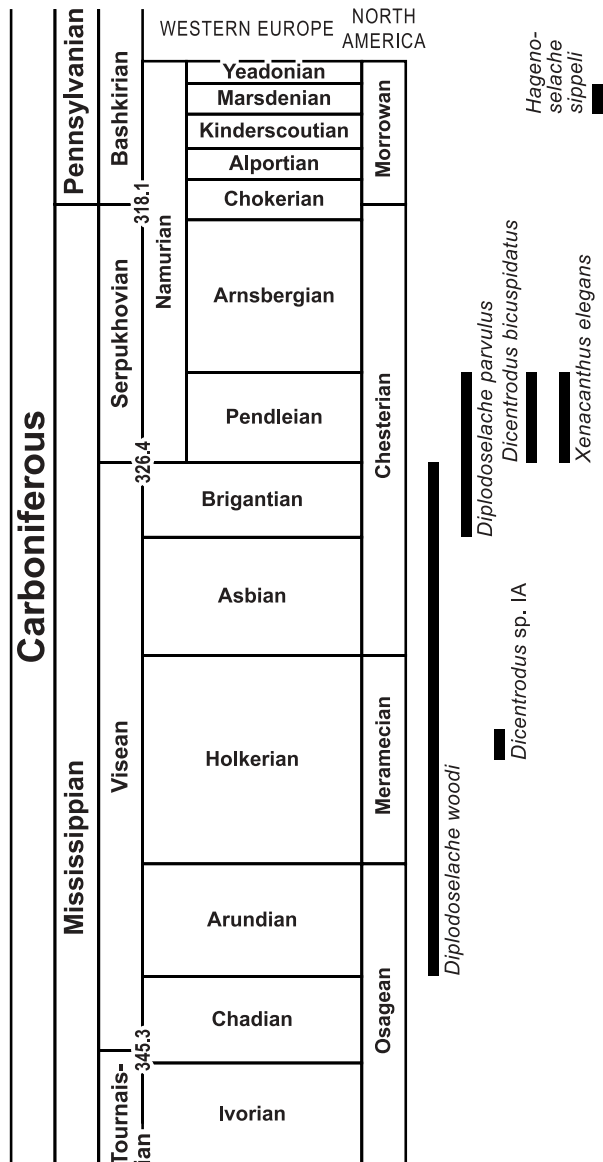


Figure 3. Vertical distribution of the oldest known xenacanthid species (stratigraphy based on Davydov, Wardlaw & Gradstein, 2004). *Diplodoselache woodi* Dick, 1981, *Diplodoselache parvulus* (Traquair, 1881), *Dicotrodus bicuspidatus* (Traquair, 1881), and *Xenacanthus elegans* (Traquair, 1881) are all known from sites in the Scottish Midland Valley. Whereas *Diplodoselache woodi* is documented by a complete skeleton, the others are known mainly from their hard parts: *Diplodoselache parvulus* only by teeth, *Xenacanthus elegans* by teeth and spines, and *Dicotrodus bicuspidatus* by teeth, spines and jaw fragments (see Hampe, 2003). *Hagenoselache sippeli* Hampe & Heidtke, 1997 came from a locality in the Sauerland/Germany and is also known by a nearly complete skeleton. *Dicotrodus* sp. IA (this paper) is based on incomplete teeth.

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