

Bransonelliformes — a new order of the Xenacanthimorpha (Chondrichthyes, Elasmobranchii)

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Abstract

The order Bransonelliformes is erected for the genera *Bransonella* Harlton, 1933 and *Barbclabornia* Johnson, 2003 based on the distinct characters of an inverted “V”-nested pattern of ornamentation preliminary on the labial aspect at the tooth cusps, the presence of labial foramina, and the occasional occurrence of a centrally positioned lingual opening of a main nutrient canal at the bases of the teeth. The Bransonelliformes comprises the primitive sister group to the Xenacanthiformes within the Xenacanthimorpha.

Schlüsselwörter: Xenacanthimorpha, *Bransonella*, *Barbclabornia*, Phylogenie.

Zusammenfassung

Für die Gattungen *Bransonella* Harlton, 1933 und *Barbclabornia* Johnson, 2003 wird die neue Ordnung Bransonelliformes eingeführt basierend auf den Merkmalen von bevorzugt auf der labialen Seite der Zahnschmelz auf tretenden, dachziegelartig ineinander geschachtelten Skulpturleisten, dem Vorhandensein labialer Foramina sowie dem häufigen Auftreten einer größeren lingualen Öffnung an der Zahnbasis, dem Durchtritt eines zentralen Nährkanals. Die Bransonelliformes stellen die ursprünglichere Schwestergruppe zu den Xenacanthiformes innerhalb der Xenacanthimorpha dar.

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Updated knowledge

Bransonella is an elasmobranch genus known only from teeth. It has a tricuspid crown and a lingually extended base with a coronal button on the upper side and a basal tubercle situated on the bottom side as is typical for xenacanthiform teeth. Three species are recognized to date: the early Pennsylvanian *B. tridentata* from Oklahoma (Harlton 1933, first identified as a conodont), *B. nebraskensis* from late Pennsylvanian deposits of Nebraska (Johnson 1984, as *Xenacanthus? nebraskensis*) and Kansas

(Tway & Zidek 1983, as “Subtype 173” in an ichthyolith catalogue) and from early Permian strata of Kansas (Schultze 1985, as *Xenacanthus luedersensis*), and *B. lingulata* from Viséan deposits of the Kuznetsk Basin (Rodina & Ivanov 2002) and Serpukhovian rocks of the Moscow syneclise (Ivanov & Ginter 1996). *B. nebraskensis* was identified also from Viséan sediments of the Nearpolar and South Urals (Ivanov & Ginter 1996), the Kuznetsk Basin (Rodina & Ivanov 2002) in Russia, the Holy Cross Mountains in Poland (Ivanov & Ginter 1996), and from the Dinant synclinorium in Belgium (Derycke

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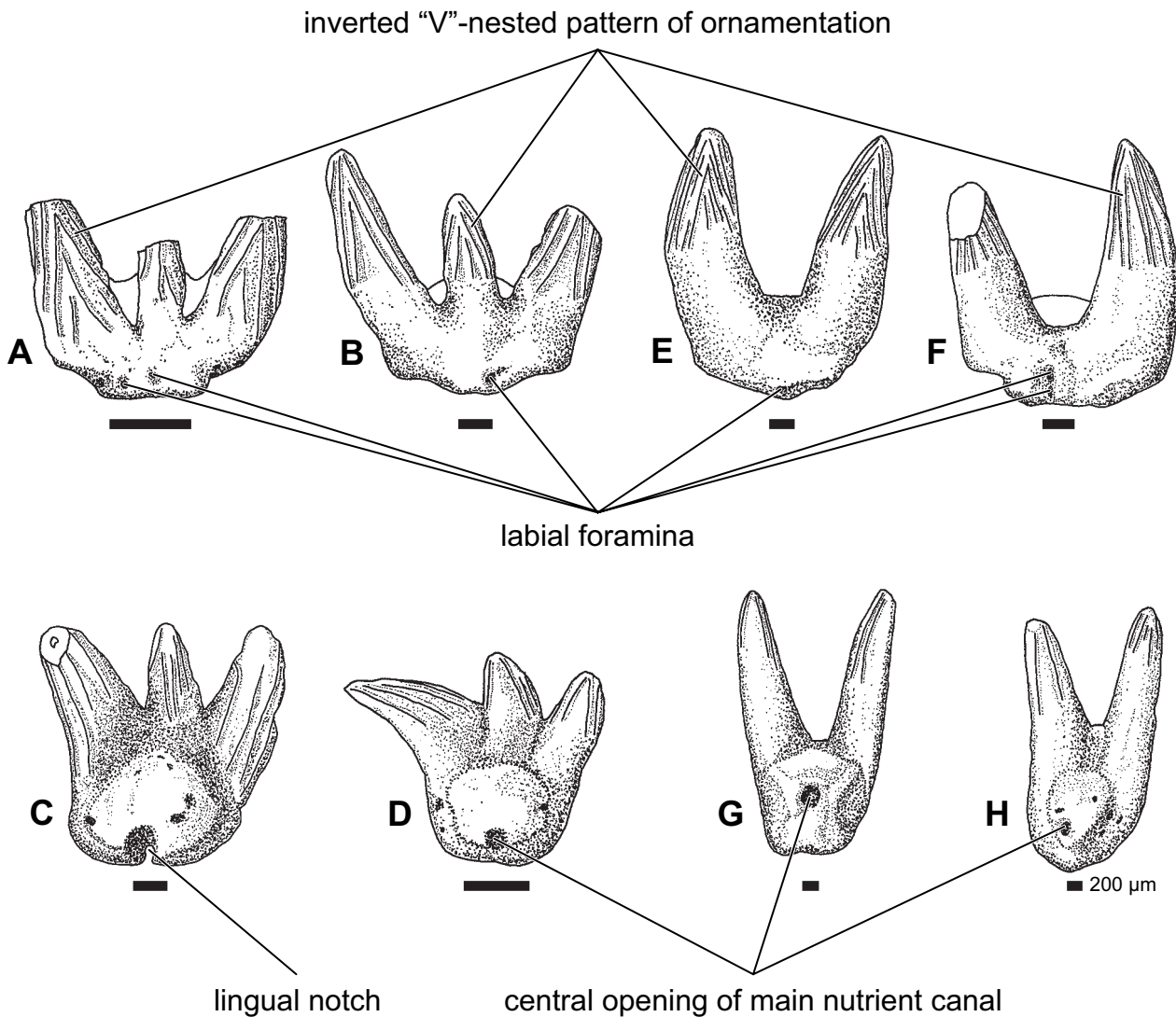


Fig. 1. Typical teeth of *Bransonella* (A–D) and *Barbclobornia* (E–H) and their characteristic features. **A** – *Bransonella linguata*, LP 16-3, from Kalinovskie Vyselki Quarry, Moscow Syncline, Russia (Serpukhovian, late Mississippian), in labial view; **B** – *Bransonella nebraskensis*, TMM 41648-139, in labial view; **C** – *Bransonella nebraskensis*, TMM 41647-20, in lingual view, both from Nemaha County, Nebraska, USA (Virgilian = Gzhelian, late Pennsylvanian); **D** – *Bransonella nebraskensis*, LP 16-2, from Kozhim River, Polar Urals, Russia (Visean, Mississippian), in lingual view; **E** – *Barbclobornia luedersensis*, SMU 64112, from Wolf Creek, Texas, USA (Artinskian, Cisuralian), in labial view; **F** – *Barbclobornia luedersensis*, SMNS 52067.1, from Jefferson County, Oklahoma, USA (Wolfcampian, Cisuralian), in labial view; **G** – *Barbclobornia luedersensis*, SMU 64101, from Spring Creek, Texas, USA (Artinskian, Cisuralian), in lingual view; **H** – *Barbclobornia luedersensis*, SMU 64056, from West Franklin Bend, Texas, USA (Artinskian, Cisuralian), in lingual view. Drawings based on figures from Ivanov & Ginter (1996: **A**, **D**), Johnson (1984; **B**, **C**; 2003: **E**, **G**, **H**) or are from the first author (**F**). Abbreviations: LP (Laboratory of Palaeontology, St. Petersburg University, Russia); SMNS (Staatliches Museum für Naturkunde, Stuttgart, Germany); SMU (Southern Methodist University, Dallas, Texas); TMM (Texas Memorial Museum, University of Texas, Austin).

et al. 2005), as well as from Moscovian deposits of the Moscow syncline, Russia (Lebedev 2001). Additional teeth and tooth fragments certainly belonging to *Bransonella* are reported from Mississippian sediments of North Qilian Mountain in China (Wang et al. 2004), from Pennsylvanian deposits of the Amazon Basin in Brazil (Duffin et al. 1996, as *?Triodus* sp.) and of the Bükk Mountains in Hungary (Kozur 1984, as *Xenacanthus* sp.).

The resemblance to *Bransonella*, due to poor or corroded preservation, is questionable in remains described by Ji & Ziegler (1992) from Guilin, South China (late Famennian), Xia (1997) from Xinjiang,

North China (middle Famennian), Ivanov (1999) from Timan-Pechora Province, Russia (early Tournaisian), Ginter (2001) from Utah, USA (late Famennian), and Ginter et al. (2002) from Dalmeh, Iran (late Famennian). Some of these may belong to the Jalodontidae (phoebodontiform sharks, known by teeth having an ornament of the cusps similar to that of *Bransonella*, but with a different morphology of the base; Ginter et al. 2002), while others might be an early form of *Bransonella*.

Species of *Bransonella* share some peculiar characters that never occur in sharks of the order Xenacanthiformes. These are the inverted “V”-nested

cus ornamentation reaching the base, the presence of labially positioned foramina on the base, and the lingual position of a large central opening of a main nutrient canal forming often a distinct notch at the lingual margin of the base.

The general tricuspid tooth morphology is the reason why *Bransonella* was often identified as a xenacanthid in the past. Chronologically, Zidek (1973) identified *B. tridentata* as belonging to the genus *Dittodus*. Zangerl (1981) grouped *Bransonella* under Xenacanthidae incertae sedis. Johnson (1984) assigned the Nebraskan teeth to the genus *Xenacanthus*, but pointed out similarities to *B. tridentata*. Zidek (1993) then characterised *Bransonella* as a true xenacanthiform. Schneider (1996) groups the 'crushing-type' teeth in the family Xenacanthidae. Ginter & Ivanov (1996) see in *Bransonella* a representative of the Xenacanthida. Ivanov & Ginter (1996) also followed this position and classify *Bransonella* as to be a xenacanthid belonging to the order Xenacanthida and Family indet. However, they mentioned that the characteristic ornamentation of *Bransonella* does not occur in any other representative of the Xenacanthida/Xenacanthiformes [Berg (1940) established the subclass Xenacanthi and order Xenacanthiformes. Glikman (1964) was the first author who suggested superordinal rank for the "Xenacanthi" and used dental characters to define the superorder and the order "Xenacanthida". The definition of Berg, however, has priority, even though he used no dental features in his diagnosis.]. Ginter et al. (2002) attributed *Bransonella* to Xenacanthiformes and Family indet. as did Wang et al. (2004: Xenacanthida and Family indet.). Hampe (2003) indicated that further information and investigation is needed to resolve the position

of *Bransonella*. Subsequently, Hampe et al. (2004) demonstrated a sister group relationship with the Xenacanthidae. *Bransonella* is defined in their analysis by the presence of an inverted "V"-nested pattern of the cusps and a large central opening of a main nutrient canal at the lingual margin of the base. Characters shared with representatives of the xenacanthids are regarded as parallel developments. Hampe et al. (2004) assume that *Bransonella* and xenacanthids probably shared the same ancestor, perhaps a phoebodont. Also Ginter (2004) discussed the possibility of a transition from a phoebodont (ancestor) to the xenacanth dentition, probably via *Bransonella* and/or *Jalodus*, a widespread tooth genus from the Late Devonian (middle Fammenian) to Tournaisian, which has a tricuspid crown of very strong cusps and the same ornamentation as *Bransonella*.

Another problematic taxon is the newly erected genus *Barbclabornia* (Johnson 2003), based on a species described first by Berman (1970: *Xenacanthus luedersensis*). The usually bicuspid teeth of *Barbclabornia luedersensis* are known from Late Carboniferous(?) and Early Permian sediments of Texas and Oklahoma also show, like teeth of *Bransonella*, an inverted "V"-nested pattern of ornamentation, here covering the upper half of the cusps concentrated on the labial aspect. Also labial foramina can be present at the base. A centrally positioned canal opening can be situated at the lingual margin of the base or on the surface of the coronal button (first author, pers. observ.). The teeth belong to an elasmobranch of estimated 4.5 to 5 m in total length based on the data of a preserved palatoquadrate (see Zidek et al. 2003). Combined with the small teeth (average of 2 mm height) Zidek

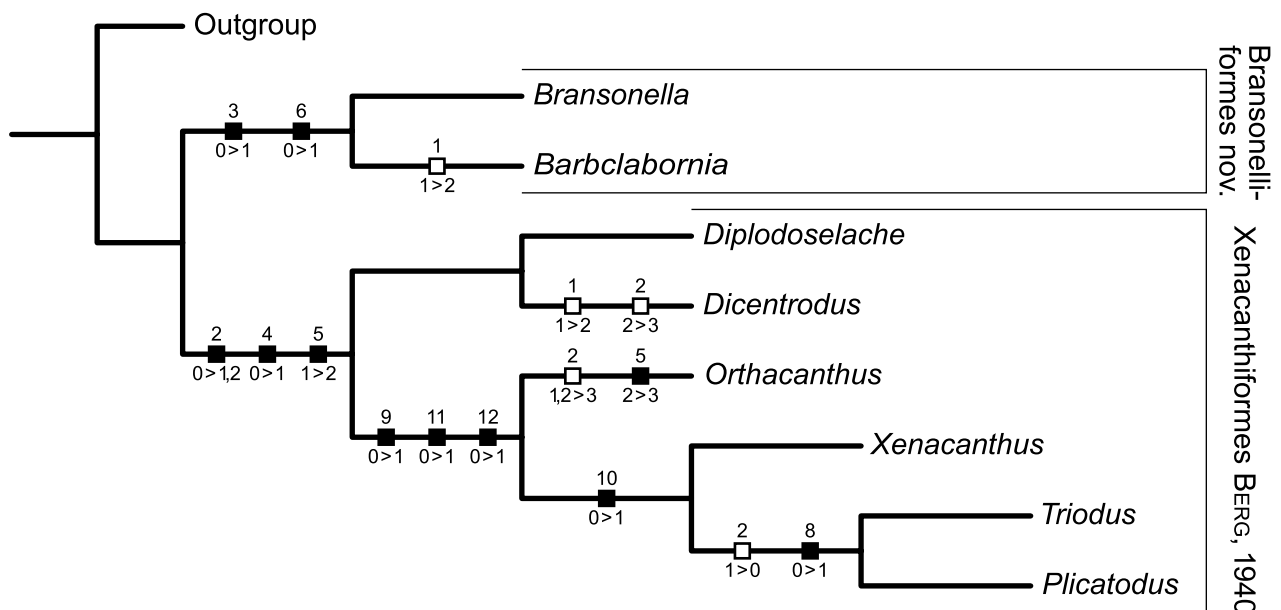


Fig. 2. Phylogenetic analysis of the Xenacanthimorpha with unambiguous character changes [heuristic search setting; tree length = 24; consistency index (CI) = 0.790; retention index (RI) = 0.780]. The character numbers are placed above the squares, the character states below.

Table 1
Character matrix

Character #	1	2	3	4	5	6	7	8	9	10	11	12	13
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodoselache</i>	1	2	0	1	2	0	1	0	0	0	0	0	0
<i>Dicentrodus</i>	2	3	0	1	2	0	1	0	0	0	0	?	?
<i>Orthacanthus</i>	1	3	0	1	3	0	2	0	1	0	1	1	?
<i>Xenacanthus</i>	1	1	0	1	2	0	1 & 2	0	1	1	1	1	1
<i>Triodus</i>	1	0	0	1	2	0	2	1	1	1	1	1	1
<i>Plicatodus</i>	1	0	0	1	2	0	2	1	1	1	1	?	?
<i>Bransonella</i>	1	0	1	0	1	1	2	0	?	?	?	?	?
<i>Barbclabornia</i>	2	0	1	0	1 & 2	1	2	0	?	?	?	?	?

et al. (2003: 143) assume that *Barbclabornia luedersensis* was a large filter feeder like the extant basking shark or whale shark.

A new systematic status

Based on the striking differences in tooth morphology (ornamentation of cusps, presence of labial foramina and a frequently occurring lingual nutrient canal opening), which do not correspond with those known from representatives of other xenacanthiforms, we propose the exclusion of *Bransonella* and *Barbclabornia* from the order Xenacanthiformes/Xenacanthida. A cladistic analysis of different xenacanthimorph genera based on the characters listed below confirms our suggestion (Fig. 2). A single tree resulted placing *Bransonella* and *Barbclabornia* as the most basal taxa in the analysis. The cladistic analysis was performed using the programs WINCLADA (Nixon 2002) and NONA (Goloboff 1999).

Character list:

- [1] Teeth multicuspid (0), tricuspid (1), bicuspid (2)
- [2] Cusps without lateral cutting edges (0), cusps lanceolate with always smooth lateral edges (1), edges muricated (2), edges serrated (3)
- [3] Simple or no vertical cristae at the cusps (0), ornamentation of inverted "V"-nested pattern (1)
- [4] Tooth base with labially positioned nutrient foramina (0), lack of labial foramina (1)
- [5] No basal tubercle developed on the bottom side of the base (0), bottom side of base with a prominent developed, halfmoon-shaped basal tubercle (1), closed and rounded with concave depression (2), rounded without depression (3)
- [6] General absence of a central canal opening at the lingual margin of the base (0), presence of a central canal opening common (1)
- [7] Crown of teeth (cusps) consisted of trabecular dentine (0), cusp with only basal cone-like trabecular dentine core – remaining tissue orthodentine (1), exclusively orthodentine (2)
- [8] Base of teeth consists of trabecular dentine (0), base consists of orthodentine (1)

- [9] Dorsal spine not cranial (0), dorsal spine cranial (1)
- [10] Dorsal spine with rounded cross-section and ventrad arranged double-row of denticles (0), spine dorso-ventrally compressed with clearly lateral positioned rows of denticles (1)
- [11] Dorsal spine with irregular, bark-like surface structure (0), relatively smooth surface including delicate striations (1)
- [12] Pectoral fins not of archipterygium type (0), biserial archipterygium (1)
- [13] Caudal fin heterocercal (0), caudal fin diphyrcercal (1)

We propose a systematic position for *Bransonella* and *Barbclabornia* within the superorder Xenacanthimorpha and erect a new order, Bransonelliformes n. ord., for these distinct genera.

Superorder **Xenacanthimorpha** Berg, 1940
Order **Bransonelliformes** n. ord.

Diagnosis. Xenacanthimorph teeth with an inverted "V"-nested pattern of ornamentation, the presence of labial foramina, and the frequent occurrence of a large central opening of a main nutrient canal at the base.

Included genera. *Bransonella* Harlton, 1933; *Barbclabornia* Johnson, 2003

Conclusion

The systematic situation of the genera *Bransonella* Harlton, 1933 and *Barbclabornia* Johnson, 2003, often labelled as xenacanthiform sharks (by, among others, Zangerl 1981; Schneider 1996; Ginter et al. 2002) is revised. A recent cladistic analysis of the Xenacanthimorpha confirmed the separation of *Bransonella* (including the recently erected *Barbclabornia*) from the order of Xenacanthiformes Berg, 1940 (= Xenacanthida Glikman, 1964) as suggested by Hampe et al. (2004).

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