Phylogenetic relationships of Lebachacanthidae Soler-Gijón 1997 (Xenacanthiformes; Elasmobranchii)

Rodrigo Soler-Gijón, Berlin

With 4 figures, 3 tables and 2 appendices

Kurzfassung: Die Familie Lebachacanthidae war für „*Orthacanthus*" *senkenbergianus*, einen Xenacanthiformen aus dem unteren Perm von Lebach (Deutschland), aufgestellt worden. Die Gültigkeit der Familie ist in Frage gestellt worden, und die Typart *Lebachacanthus senkenbergianus* wurde in die Gattung *Orthacanthus* Agassiz 1843, Untergattung *Lebachacanthus* Soler-Gijón 1997 eingegliedert. Argumente gegen ein solches Vorgehen werden hier vorgelegt. Eine neue phylogenetische Analyse wird durchgeführt, um die Verwandtschaftsbeziehungen der Lebachacanthidae zu den übrigen Xenacanthiformen zu untersuchen. *Hagenoselache*, ein vor kurzem beschriebener Xenacanthiforme aus dem Namur Deutschlands, und neue Daten zur Zahnhistologie werden in die Verwandschaftsanalyse einbezogen. Die neue Verwandtschaftanalyse bestätigt die Lebachacanthidae als eigenständige Familie der Xenacanthiformes. Die Lebachacanthidae sind die Schwestergruppe der Xenacanthidae, zu der der echte *Orthacanthus* gehört. *Hagenoselache* ist weiter abgeleitet als *Diplodoselache* (der primitivste Xenacanthiforme) und stellt die Schwestergruppe der Lebachacanthidae und Xenacanthidae dar. Die phylogenetische Stellung der Lebachacanthidae stimmt mit der Vorstellung des Wirkens von heterochronen Prozessen in der Evolution der xenacanthiden Haie überein. Heterochronie (peramorpher Typ) kann die morphologische Entwicklungsreihe des Dorsalstachels von basalen Xenacanthiformen (Diplodoselachidae) über die Lebachacanthidae zu den fortschrittlichen Xenacanthidae (diese umfassen die Gattungen *Orthacanthus*, *Xenacanthus*, *Triodus* und *Plicatodus*) erklären.

Abstract: The family Lebachacanthidae was erected for "*Orthacanthus*" *senkenbergianus*, a xenacanthiform from the Lower Permian of Lebach (Germany). Recently, the validity of the family has been questioned and the type species, *Lebachacanthus senkenbergianus*, has been included in the genus *Orthacanthus* Agassiz 1843, subgenus *Lebachacanthus* Soler-Gijón 1997. Arguments against such changes are presented here. A new phylogenetic analysis is performed in order to determine the relationships of Lebachacanthidae with the rest of xenacanthiforms. *Hagenoselache*, a xenacanthiform recently described from the Namurian of Germany, is included in the phylogenetic analysis together with new data on tooth histology. The new phylogenetic analysis confirms Lebachacanthidae as a distinct family within Xenacanthiformes. Lebachacanthidae is the sister group of Xenacanthidae which

includes true *Orthacanthus*. *Hagenoselache* is more derived than *Diplodoselache* (the most primitive xenacanthiform) and is the sister group of the clade formed by Lebachacanthidae and Xenacanthidae. The phylogenetic position of Lebachacanthidae is consistent with the idea of heterochronic processes in the evolution of the xenacanth sharks. Heterochrony (peramorphic type) can explain morphological clines in dorsal spine morphology from basal xenacanthiforms (Diplodoselachidae) through Lebachacanthidae to the derived Xenacanthidae (comprising *Orthacanthus*, *Xenacanthus*, *Triodus* and *Plicatodus*).

Introduction

The systematic position of the xenacanth *Orthacanthus* Agassiz 1843 has been unclear, because taxa with differing combinations of characters have been included in the same genus (Zidek 1993a). The type species, *O. cylindricus* Agassiz 1843, was founded on an isolated spine from the Upper Carboniferous of Manchester, Great Britain; articulated remains which can be referred to the type species have not yet been found. Species exhibiting different morphologies of the neurocranium and dorsal spine possess the general dental characters that were proposed by Fritsch (1889) as diagnostic for the genus (relatively short central cusp, lateral cusps with lanceolate cross section and serrated carinae). Such is the case in *Orthacanthus bohemicus* and "*Orthacanthus*" *senkenbergianus*. In *O. bohemicus* (Westphalian D of Bohemia, Czech Republic) the dorsal spine is occipital as in other members of Xenacanthidae (*Xenacanthus*, *Triodus* and *Plicatodus*) (Fritsch 1889; Schneider & Zajíc 1994; Hampe 1995), whereas in "*O.*" *senkenbergianus* (Lower Permian of the Saar-Nahe region, Germany) the dorsal spine is inserted in front of the dorsal fin at the level of the pectoral girdle (Fritsch 1889). In contrast to *O. bohemicus*, "*O.*" *senkenbergianus* is known from complete and articulated remains (Heidtke 1982), for which reason numerous authors have used this species as a model for *Orthacanthus*, emphasizing the use of dental characters for the generic diagnosis (see
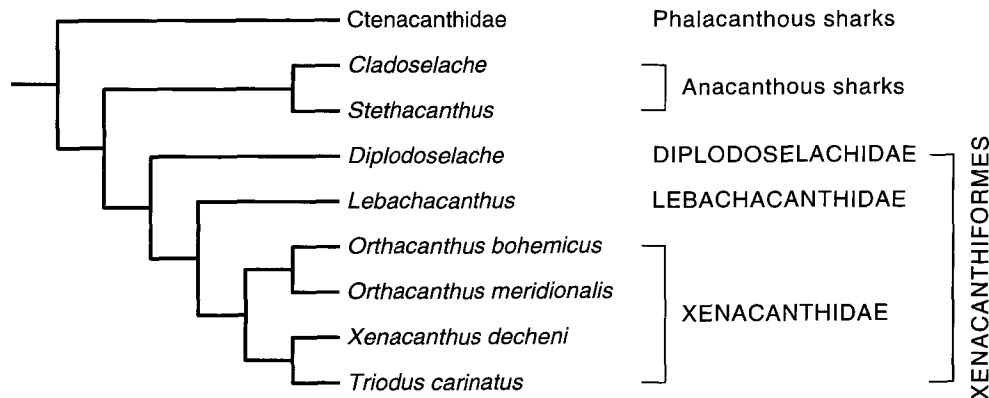
Fig. 1. Single most parsimonious tree generated by PAUP 3.1., representing a hypothesis of phylogenetic relationship of Paleozoic xenacanthiform and anacanthous sharks (after SOLER-GIJÓN 1997b).

SOLER-GIJÓN 1997b and references therein). However, ZIDEK (1993a) noted differences between *O. cylindricus* and *"O." senkenbergianus* and suggested that *"O." senkenbergianus* represented a new xenacanth genus. This idea has recently been supported by a cladistic analysis of nine taxa (one ctenacanthid, two anacanthous sharks, and four xenacanthiforms) and 48 characters comprising information on the neurocranium, teeth, dorsal spine, scales, axial skeleton, and fins (SOLER-GIJÓN 1997b). Based on that phylogenetic analysis, SOLER-GIJÓN (1997b) referred *"O." senkenbergianus* to a new genus, *Lebachacanthus*, and a new family, Lebachacanthidae. The Lebachacanthidae was proposed as the sister group of the Xenacanthidae, which includes the valid species of *Orthacanthus* (Fig. 1). SOLER-GIJÓN (1997b: 3) defined Lebachacanthidae as "Xenacanthiform sharks with neurocranium with unexpanded occipital segment; diplodont teeth with serrated crown; dermal denticles of *"Cladodus" pattersoni* type; dorsal spine type B located at the level of the pectoral girdle; mesopterygium and metapterygium participating equally in the pectoral articulation; superior lobe of the caudal fin two times longer than inferior lobe".

Recently, HEIDTKE (1998) rejected the results of SOLER-GIJÓN (1997b) and subdivided the genus *Orthacanthus* AGASSIZ 1843 into the subgenera *Orthacanthus* AGASSIZ 1843 and *Lebachacanthus* SOLER-GIJÓN 1997. However, several points raised by HEIDTKE require an urgent reply.

The objectives of this paper are:

(1) to discuss the arguments presented by HEIDTKE (1998: 142-143) regarding the diagnosis of Lebachacanthidae, dealing with the neurocranium, teeth, pectoral fin, dorsal spine, squamation and caudal fin.

(2) to analyse the phylogenetic position of Lebachacanthidae following the recent description of *Hagenoselache*, a xenacanthiform from the Namurian B of Germany (HAMPE & HEIDTKE 1997), and including new results of studies of tooth histology. A new

phylogentic analysis, supplemented by the recent data, enables testing of the stability of the phylogenetic hypothesis proposed by SOLER-GIJÓN (1997b), especially concerning the relationships of *Lebachacanthus* and *Orthacanthus*.

Discussion of diagnostic characters of Lebachacanthidae SOLER-GIJÓN 1997

Neurocranium

HEIDTKE (1998: 142) stated that "The occipital segment of the neurocranium [in *Lebachacanthus*] expands only very little postero-laterally (like in all other species of the genus *Orthacanthus*)". That is not correct. All known neurocrania of xenacanth sharks (except *Lebachacanthus*: specimen MB. f. 2813) possess a broadly expanded occipital segment which projects strongly posteriorly behind the lateral otic region and the occipital segment is massive and quadrangular in outline (MAISEY 1984; GAUDIN 1991: fig. 3). In addition, the lateral otic process appears to have been well developed (see BROILI 1904: pl. 24 for *O. platypternus*; SCHAEFFER 1981: fig. 2 for *"Xenacanthus"* sp.; HEYLER & POPLIN 1989: fig. 1 for *O. buxieri* and *O. commailli*; ZIDEK 1992: fig. 2 for *O. huberi*; SCHNEIDER & ZAJÍC 1994: fig. 1 for *Xenacanthus decheni*; and SOLER-GIJÓN & HAMPE 1998: fig. 3 for *Triodus ?frossardi*). The neurocranium of *Lebachacanthus* (specimen MB. f.2813) does not exhibit evidence of prominent posterolateral otic processes, and the occipital segment is unexpanded in a fashion similar to anacanthous sharks (e.g. *Cladoselache* [SCHAEFFER 1981: fig. 13A] and *Stethacanthus* [COATES & SEQUEIRA 1998: fig. 5 A, B]).

Teeth

HEIDTKE (1998: 142-143) wrote that "diplodont teeth with crenulated [serrated] lateral edges are typical of all
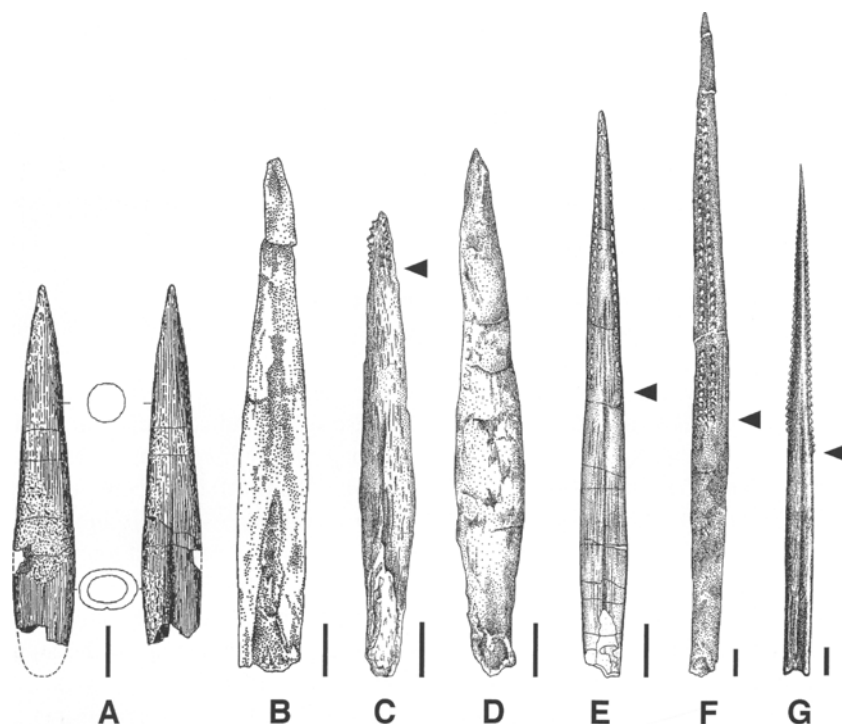
Fig. 2. Spines of xenacanth sharks. Arrowheads indicate proximal end of denticulated region. – **A**: *Anodontacanthus belemnoideus*, anterior and posterior views (after ZIDEK 1978); **B**: *Platyacanthus ventricosus*, posterior view (after HEIDTKE 1998); **C** and **D**: *Lebachacanthus senkenbergianus*, posterior view (after HEIDTKE 1998); **E**: *Orthacanthus meridionalis*, posterior view (after SOLER-GIJÓN 1999); **F**: *Orthacanthus kounoviensis*, posterior view (after HEIDTKE 1998); **G**: *"Pleuracanthus" erectus*, posterior view (after DAVIS 1892). – Scale bars = 1 cm. *Platyacanthus ventricosus*, *Lebachacanthus senkenbergianus*, *Orthacanthus meridionalis* and *Orthacanthus kounoviensis* are included in *Orthacanthus* by HEIDTKE (1998). *"Pleuracanthus" erectus* belongs to *Xenacanthus* (HAMPE in preparation) (see Tab. 1).

orthacanthid xenacanths [the author includes *Orthacanthus* in Orthacanthidae HEYLER & POPLIN 1989] ...". This statement is far from correct. The teeth of *Orthacanthus platypternus* (a species not included in HEIDTKE's revision) exhibit smooth lateral edges as in *Xenacanthus* teeth; only the largest teeth show wrinkles or incipient serration (JOHNSON 1979, 1999). Consideration of the character state "crown always showing serration" as diagnostic for *Orthacanthus* (e.g. HAMPE 1988; SCHNEIDER 1996) has led to the inclusion of *O. platypternus* in the genus *Xenacanthus*. However, detailed studies of the dental morphology of *O. platypternus* placed it in *Orthacanthus* because it shows close affinities with other North American species such as *O. texensis*, which possess serrations to varying degrees (JOHNSON 1979, 1995, 1996, 1999; ZIDEK 1993b). The recent discovery of numerous occipital spines of *Orthacanthus* type associated with *O. platypternus* teeth (and fragments of calcified cartilage) in the Lower Permian of Texas (DONELAN & JOHNSON 1997) has finally ended the controversies regarding *Orthacanthus platypternus*. In addition to interspecific differences, it is well known that the serration of *Orthacanthus* teeth varies in relation to ontogeny and heterodonty. The holotype of *O. bohemicus*, a juvenile individual, has only wrinkles in the lateral edges of

the cusps. Small medial and posterior teeth of *O. texensis* lack serrations, and the absence of serrations is common in *O. compressus* (JOHNSON 1979, 1999). On the other hand, both juvenile and adult specimens of *Lebachacanthus* possess serrations (HAMPE 1988: fig. 2) and consequently this feature appears to be significant in comparison with other xenacanths.

Pectoral fin

HEIDTKE (1998: 143) stated that "the participation of the mesopterygium in the pectoral articulation varies individually". This contention is not documented in the paper. HEIDTKE (1998: 142) indicated that information obtained from a collection of more than 50 specimens (some of them complete and articulated [see HEIDTKE 1982]) is the basis for his correction of the diagnostic characters proposed by SOLER-GIJÓN (1997b), but his paper contains only one pertinent illustration (fig. 7a), the anterior half of a single individual. The figure, which lacks labels, only permits speculation concerning the kind of pectoral articulation present in the specimen. More complete and detailed information was provided in an earlier paper (HEIDTKE 1982) and was included by SOLER-GIJÓN in his cladistic analysis (1997b: 19, character 36).

Dorsal spine

HEIDTKE (1998) agrees with SOLER-GIJÓN (1997b) on the diagnostic importance of the morphology and position of the dorsal spine. Indeed, he subdivides the genus *Orthacanthus* into two subgenera "on the basis of different development and insertion of the dorsal spine". However, the data shown by HEIDTKE indicate instead the separation of *Lebachacanthus senkenbergianus* from Xenacanthidae including true *Orthacanthus* [*Orthacanthus (Orthacanthus)* of HEIDTKE)]. The range of variability of the spine (e.g. length: maximum width ratio [robustness] and extent of denticulation) is extremely wide in *Orthacanthus* as defined by HEIDTKE, and the differences between the spines of *O. (Lebachacanthus)* and *O. (Orthacanthus)* are thus greater than those between *O. (Orthacanthus)* and *Triodus* or *Xenacanthus* (see Tab. 1, Fig. 2). Moreover, HEIDTKE (1998: 135) writes that the insertion of the dorsal spine of *O. (Orthacanthus)* is "similar to that of the genera *Triodus* and *Xenacanthus* but not to that of *Orthacanthus (Lebachacanthus)*". Con-

sequently, if HEIDTKE's results are to be accepted, then all three genera should be united (cf. DAVIS 1892).

HEIDTKE (1998: 140-141, fig. 5) described and illustrated a single spine of *O. pinguis* (n° 84 in the FRITSCH collection, National Museum, Prague; pl. 87, figs. 3 and 3i in FRITSCH 1889) and regarded the specimen as an aberrant spine similar in some aspects to *"O". senkenbergianus* and *O. kounoviensis*. HEIDTKE overlooked the existence of two other isolated spines of *O. pinguis* (n° 85 and 87 in the FRITSCH collection) described and figured by FRITSCH (1889: 109, pl. 87, figs. 4 and 6). Table 2 shows the catalogue numbers of these spines, still housed in the National Museum, Prague. A comparative analysis of these spines indicates that the species *O. pinguis* is not founded on aberrant spines. As shown in Table 1, *O. pinguis* is quite different from *"O". senkenbergianus* and *O. kounoviensis*, especially in respect of the robustness and extent of the denticulation.

HEIDTKE (1998: 143) assigned *Platyacanthus ventricosus* (Kounov Beds, Stephanian B, Kladno-Rakovník basin, central Bohemia, Czech Republic) to *Orthacan-*

Tab. 1. Variation of the length: maximum width (robustness) ratio and of the denticulation (% of the total length) for dorsal spines of xenacanth sharks. Numbers in brackets indicate sources of data: (1) HEIDTKE (1998), (2) ZIDEK (1992), (3) ZIDEK (1978), (4) SOLER-GIJÓN (1997a, 1999), (5) present report according to figures in DAVIS (1892) and personal observation. Specimens SMU 68801 (*Orthacanthus platypternus*) and MB. f. 3960 (*Triodus sessilis*) belong to the Shuler Museum of Paleontology (Southern Methodist University, Dallas, Texas) and Museum für Naturkunde (Berlin, Germany), respectively. Note the wide variation in *Orthacanthus* of HEIDTKE (1998) that includes *Platyacanthus ventricosus, Lebachacanthus senkenbergianus, Orthacanthus cylindricus, O. bohemicus, O. kounoviensis, O. pinguis, O. buxieri* and *O. meridionalis. "Pleuracanthus" laevissimus* and *"Pleuracanthus" erectus* (DAVIS collection) belong to *Xenacanthus* (HAMPE in preparation). *Xenacanthus* and *Triodus* can also be included in *Orthacanthus* sensu HEIDTKE on the basis of their robustness and denticulation (see Fig. 2).

(*) Subgenus *Lebachacanthus* SOLER-GIJÓN 1997

(+) Subgenus *Orthacanthus* AGASSIZ 1843

Taxon	Robustness	Denticulation
Anodontacanthus belemnoideus	6.2:1 (3)	absent
(*) *Platyacanthus ventricosus*	7.5:1 (1)	absent
Platyacanthus avirostratus	4.6:1 (3)	absent
(*) *Lebachacanthus senkenbergianus*	8:1 (1)	absent to less than 20 %
(+) *Orthacanthus cylindricus*	more than 15:1 (1) / 20:1 (2)	45 %
(+) *Orthacanthus bohemicus*	17:1 (1)	35 % to 45 %
(+) *Orthacanthus kounoviensis*	18:1 (1) / 20:1 (2)	over 50 %
(+) *Orthacanthus pinguis*	17:1 (1) / 15:1 (2)	ca. 33 %
(+) *Orthacanthus buxieri*	16:1 (1)	over 50 %
(+) *Orthacanthus meridionalis*	15:1 (4)	ca. 38 %
Orthacanthus huberi	26:1 (2)	50 %
Orthacanthus platypternus (SMU 68801)	more than 12:1 (5)	ca. 41 %
Xenacanthus spp.	12:1--20:1 (3)	50 %
"Pleuracanthus" laevissimus	15:1 (5)	54 %
"Pleuracanthus" erectus	18:1 (5)	56 %
Triodus sessilis (MB.f. 3960)	16:1 (5)	50 %

Tab. 2. Occipital spines of *Orthacanthus pinguis* housed in the National Museum, Prague. –**A:** actual catalogue number; **B:** catalogue number in FRITSCH collection; **C:** figure in FRITSCH (1889); **D:** figure in HEIDTKE (1998).

A	B	C	D
M 646	orig. no. 84	Pl. 87 fig. 3	Fig. 5
M 1142	orig. no. 85	Pl. 87 fig. 6	---
M 1148	orig. no. 87	Pl. 87 fig. 4	---

thus [subgenus *Lebachacanthus*] without discussion and suggested that the absence of denticulation was an indication of a senile stage. In a relevant paper, ZIDEK (1978, not cited by HEIDTKE) compared *Platyacanthus* with *Anodontacanthus* (a genus also based on isolated spines without denticles) and described the new species *Platyacanthus avirostratus* (Lower Permian, Garber Formation, southwestern Oklahoma). ZIDEK (1978: 1076) concluded that "neither *Anodontacanthus* nor *Platyacanthus* can be regarded as possibly synonymous with *Xenacanthus* and/or *Orthacanthus*. This is evidenced by the total lack of denticulation in both *Anodontacanthus* and *Platyacanthus* spines which show only a minor degree of abrasion; by the impossibility of comparing the (postero-) lateral ridges of *Platyacanthus* to worn-off denticle rows in *Xenacanthus* and/or *Orthacanthus* spines because the ridges show no separate denticle bases, and, moreover, are located in the wrong place – in the middle third of the spine's length instead of in the distal third or half; by the differing length : width ratios; and also by the different extent of curvature of the *Platyacanthus* and *Orthacanthus* spines".

Squamation and caudal fin

HEIDTKE (1998: 143) criticized the inclusion of data related to squamation and morphology of the caudal fin in the cladistic analysis of SOLER-GIJÓN (1997b) because they are known only for "*O.*" *senkenbergianus*. The author concluded that these kinds of features "not yet found in other species were judged to be not present in the species". Consequently, according to HEIDTKE (1998: 143) "pseudo-diagnostica are created which can be manipulated depending on the approach of the person working on it". Unfortunately, HEIDTKE misinterpreted the coding of characters in the data matrix presented by SOLER-GIJÓN (1997b). As clearly stated by SOLER-GIJÓN (1997b: 26), the symbol '?' was coded for those cases in which the character state is unkown (due either to poor preservation or absence of fossil remains) or not applicable. For example, in *O. meridionalis*, '?' was coded for characters 28 (presence of dermal denticles of "*Cladodus*" *pattersoni* type) and 47 (length of superior lobe of caudal fin), because only cranial remains are known and squamation is not associated. Coding '?' does not mean a subjective selection of the primitive or derived state. For example,

coding '?' for character 28 in *O. meridionalis* does not mean "absence of denticles of "*Cladodus*" *pattersoni* type", and coding '?' for character 47 does not mean "absence of caudal fin similar to that of *Lebachacanthus*". The coding '?' means that the primitive or derived state of characters 28 and 47 is unknown for *O. meridionalis*. The phylogenetic analysis, based on the principle of parsimony, enables prediction of the primitive or derived state for those characters initially coded as '?'. The predictions will be confirmed or rejected with future descriptions of new material.

The caudal region is only known for "*O.*" *senkenbergianus*, and HEIDTKE therefore criticized the use of characters of the postcranial region in the cladistic analysis. Nevertheless, HEIDTKE (1998: 137) included features of the pectoral and caudal fins in his emended diagnosis of *Orthacanthus* (and Orthacanthidae). In contrast to *Lebachacanthus*, the pectoral fin of *Orthacanthus* is to some extent known only in the holotype of *O. bohemicus* (specimen n° 56 in FRITSCH's collection, National Museum, Prague). The preserved elements do not show the pectoral articulation with the scapula, but the biaxial condition of the radials is clear. FRITSCH (1889: 104-106, pls. 81 and 81b) described and figured the positive of the holotype and the galvanoplastic copy of the negative prepared by him (see Tab. 3). Surprisingly, HEIDTKE (1998: figs. 3a, b) erroneously regarded the material illustrated by FRITSCH (a unique individual, the holotype) as two different individuals, and the pectoral fin is not shown in any of his figures.

Finally, the diagnosis of *Lebachacanthus* proposed by SOLER-GIJÓN (1997b) is based on the results of a cladistic analysis. In contrast, the emended diagnosis of Orthacanthidae (with *Orthacanthus* as the only included genus) proposed by HEIDTKE (1998: 137) for the tooth and caudal-fin morphology is a set of plesiomorphic characters widely distributed in the order Xenacanthiformes. Thus HEIDTKE indicates the following characters: (a) "...Tricuspid teeth with massive bases, lateral cusps dagger-like with lanceolate cross section..."; (b) "...massive base with a wide, saddle- or heart-like coronal tubercle..."; (c) "...a

Tab. 3. Material referred to the holotype of *Orthacanthus bohemicus* (original number 56 in the FRITSCH collection) housed in the National Museum, Prague. – **A:** actual catalogue number; **B:** characteristic of the material; **C:** figure in FRITSCH (1889); **D:** figure in HEIDTKE (1998).

A	B	C	D
M 1145	positive	Pl. 81	Fig. 3a
M 1146	negative (mostly impression)		
M 1147	galvanoplastic copy of the negative	Pl. 81b	Fig. 3b

large foramen lingual to the median cusp...”; (d) “...Basal tubercle in the labial part of the inferior face of the base...”; (e) “...Caudal fin (if known) diphycercal with reduced hypochordal lobe which is structurally similar to an anal”.

These characters are discredited by the following arguments:

(a) The tricuspid condition was considered earlier by HAMPE & HEIDTKE (1997: 35-38, fig. 12) as a synapomorphy for the order Xenacanthiformes. A lanceolate cross section of the cusps is exhibited by *Diplodoselache*, *Lebachacanthus*, *Orthacanthus* and *Xenacanthus*. The wide distribution of this character has also been cited by HAMPE & HEIDTKE (1997).

(b) The massive base of the teeth is not diagnostic, because it is not present in some species (e.g. *Orthacanthus platypternus*, see JOHNSON 1979) and in the teeth of juvenile *Orthacanthus* and *Lebachacanthus* (HAMPE 1988). The shape of the coronal tubercle is highly variable in xenacanths and some *Orthacanthus* teeth lack a heart-like shape (JOHNSON 1979: pl. 28, figs. 1, 7, pl. 37, fig. 11; HAMPE 1994: figs. 1a, 2b, e, g), but it is present in other genera (e.g. *Triodus*, HAMPE 1993: fig. 3a). The triangular shape of the coronal tubercle is related to the common development of a lingual shaft (HAMPE 1993: figs. 2a, d, 3a).

(c) The central foramen is known at least in the teeth of *Hagenoselache sippeli* (HAMPE & HEIDTKE 1997: fig. 4A), *Lebachacanthus senkenbergianus* (HAMPE 1993: figs. 2a, 4a), *Orthacanthus meridionalis* (SOLER-GIJÓN 1993: pl. 6, fig. 4b, pl. 7, fig. 2b, pl. 9, fig. 3c), *Xenacanthus remigiusbergensis* (HAMPE 1994: fig. 8a), and *Triodus kraetschmeri* (HAMPE 1993: fig. 4e).

(d) The labial basal tubercle is also primitive for xenacanth teeth, as indicated by HAMPE & HEIDTKE (1997: fig. 12).

(e) The character definition of the caudal fin is very broad and can be applied to all xenacanthiforms except *Diplodoselache* (see discussion on the caudal and anal fins of xenacanths in POPLIN & HEYLER [1989] and HEYLER & POPLIN [1989]). For example, SCHNEIDER (1996: 333) included the condition of the caudal fin his diagnosis of the Xenacanthidae (including *Xenacanthus*, *Triodus*, “*Bohemiacanthus*” and *Plicatodus*) and stated: “Caudal fin anatomically heterocercal, functionally diphycercal, i.e. the hypochordal lobe is reduced to the so-called “second anal fin” situated shortly behind the true anal fin”.

Analysis of the phylogenetic position of Lebachacanthidae SOLER-GIJÓN 1997

The recent description of *Hagenoselache*, a new xenacanthiform from the Namurian B of Germany (HAMPE & HEIDTKE 1997), and new data on dental histology

(HAMPE & HEIDTKE 1997; HAMPE & LONG 1999) enable a more complete analysis of the phylogenetic position of Lebachacanthidae. *Hagenoselache* is relevant to the discussion because of its geologic age and the presence of a mosaic of primitive and derived characters. *Hagenoselache* is close to the primitive *Lebachacanthus* in caudal-fin morphology, but is quite similar to the derived *Triodus* in dental features (see below for details). According to SOLER-GIJÓN (1997b), *Lebachacanthus* is the sister group of Xenacanthidae, in which *Triodus* is included as a derived genus. In order to test the impact of the new discoveries on the results of SOLER-GIJÓN (1997b), the results of a new cladistic analysis are presented here.

The new analysis comprises 10 taxa (the same as those of SOLER-GIJÓN 1997b plus *Hagenoselache*) and 48 characters (the same as those in SOLER-GIJÓN 1997b). The Ctenacanthidae has been chosen as the outgroup. The ingroup comprises *Cladoselache*, *Stethacanthus*, *Diplodoselache woodi*, *Lebachacanthus senkenbergianus*, *Orthacanthus bohemicus*, *Orthacanthus meridionalis*, *Xenacanthus decheni*, *Triodus carinatus* and *Hagenoselache sippeli*.

The data were analyzed using PAUP version 3.1 (SWOFFORD 1993) with DELTRAN option for character optimization. All characters have the same weight and are treated as unordered.

Character-transformation series

Characters and character states are given in Appendix I. The character-state matrix is shown in Appendix II.

Characters 8 and 10 to 15 could not be polarized by outgroup comparisons. The states of character 8 are unknown in the outgroup because of incomplete preservation; characters 10 to 15 are not logically applicable in the outgroup. Character 8 was then coded as ‘?’, while characters 10 to 15 were coded as ‘9’. Two or more derived unordered states were coded for the ingroup. Previously, SOLER-GIJÓN (1997b) coded characters 8 and 10 to 15 as ‘?’ and assigned the primitive state (‘0’) to the anacanthous sharks. The coding used here avoids the possibility of biases in the polarity of character states, which may appear after an *a priori* assignment of the plesiomorphic state to a determinate taxon in the ingroup. Moreover, the codings ‘?’ and ‘9’ permit distinction of two very different conditions (missing *vs.* inapplicable data) that enable a more detailed computerized analysis of the data.

A detailed description and discussion of the character states can be found in SOLER-GIJÓN (1997b). Some comments on *Hagenoselache* (the new taxon included in the phylogenetic analysis) and histological features of the teeth of *Diplodoselache woodi* are included here.

Hagenoselache was defined on a single specimen, which is nearly complete and partially articulated (HAMPE & HEIDTKE 1997: figs. 3A, 7-10), but lacks a dorsal spine. It is unclear whether the absence of a spine is due to taphonomic processes or is a true morphologi-
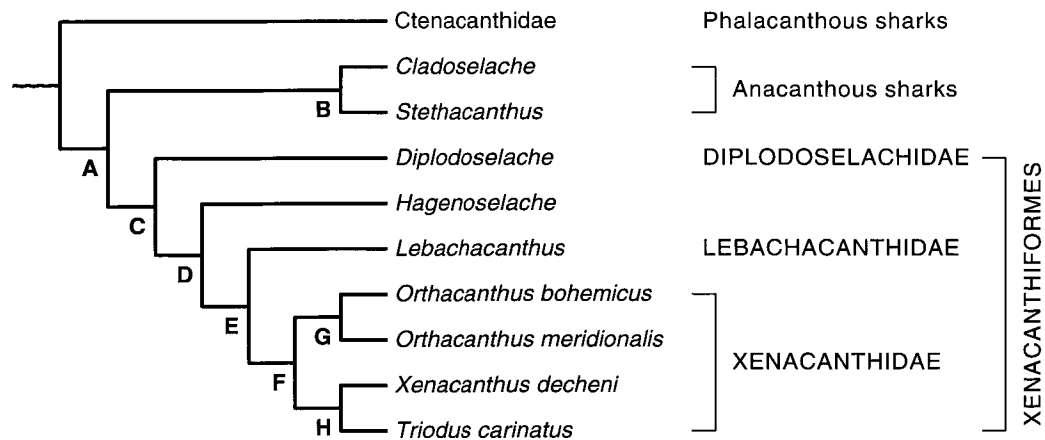
Fig. 3. Single most parsimonious tree generated by PAUP 3.1 after the addition of *Hagenoselache* to the analysis of SOLER-GIJÓN 1997b (Fig. 1). See appendices I and II for list of characters and character-state matrix, respectively. Character optimization used DELTRAN, CI (excluding uninformative characters) 0.768 and RI 0.813. The nodes are supported by the following characters [the asterisk (*) indicates unique derived characters]. Node A: 6[1]* 9[1]* 11[1]* 40[1]*. Node B (anacanthous sharks): 1[1] 2[1] 10[2] 12[1]* 15[1] 27[1] 35[1]* 45[1]*. Node C (Xenacanthiformes): 12[2]* 14[1]* 16[1]* 17[1]* 18[1]* 19[1]* 20[1]* 26[1] 33[1] 34[1]* 37[1]*. Node D (unnamed taxon): 24[1]* 27[1] 30[1]* 31[1]* 41[1]* 42[1]* 46[1]*. Node E (unnamed taxon): 3[1]* 5[1]* 13[1]* 15[2] 39[1]*. Node F (Xenacanthidae): 7[1]* 8[2]* 11[2]*. Node G (*Orthacanthus*): 4[1]* 21[1]. Node H (unnamed taxon): 13[3]* 14[2]* 15[3] 47[2]* 48[1]*. The taxa included in the analysis possess the following characters. *Cladoselache*: 26[1] 38[1]* 43[1]. *Stethacanthus*: 28[1] 29[1]* 33[1] 44[1]*. *Diplodoselache*: 10[1] 15[3] 23[1]. *Lebachacanthus*: 2[1] 10[2] 21[1] 28[1] 32[1] 36[1]* 47[1]*. *Orthacanthus meridionalis*: 13[1]*. *Xenacanthus decheni*: 23[1] 32[1] 35[3]* 36[2]* 37[2]* 43[1]. *Triodus carinatus*: 22[1] 25[1] 35[2]*. *Hagenoselache*: 1[1] 22[1] 25[1]. No character supports *Orthacanthus bohemicus* in this hypothesis.

cal feature of *Hagenoselache*. Therefore, characters 5 to 16, which concern the dorsal spine, were coded as unknown ('?').

The character state "absence of enameloid" for character 26 in *Diplodoselache woodi* is coded following recent histological studies of that taxon (HAMPE & HEIDTKE 1997; HAMPE & LONG 1999). SOLER-GIJÓN (1997b) coded "presence of enameloid" based on the original description of *Diplodoselache* by DICK (1981: 108).

Results and discussion

The phylogenetic analysis gives a single tree with a length of 77 steps, a CI (excluding uninformative characters) of 0.768, and an RI of 0.813. The addition of *Hagenoselache* does not change the relative position of *Lebachacanthus* in relation to *Diplodoselache* and the more advanced xenacanths such as *Orthacanthus*, *Xenacanthus* and *Triodus*. *Hagenoselache* appears more derived than *Diplodoselache* and represents the sister group of the clade formed by *Lebachacanthus* plus Xenacanthidae (Fig. 3).

Description of the tree (Fig. 3)

Node A, Paleozoic anacanthous sharks plus Xenacanthiformes, are characterized by four unique derived characters: presence of one dorsal spine (6[1]), presence of dorsal spine type B (9[1]), spine type B robust (11[1]) and

premetapterygial radials of the pectoral fin articulate with shoulder girdle or simple basals (40[1]).

Node B, the anacanthous-shark clade (*Cladoselache* + *Stethacanthus*), is defined by three unique derived-character states and five homoplasies. The unique characters refer to absence of denticulation on dorsal spine type B (12[1]), presence of multibasal articulation in the pectoral fin (35[1]) and absence of an anal fin (45[1]). The homoplasies are: neurocranium short, deep, with large orbits (1[1]) (also present in *Hagenoselache*), neurocranium with occipital segment unexpanded (2[1]) (shared with *Lebachacanthus*), spine type B at level of the pectoral girdle (10[2]) (also found in *Lebachacanthus*), spine type B with oval cross section (15[1]) and absence of scales of ctenacanthid type (27[1]) which also supports node D. *Cladoselache* is characterized by one unique derived character and two homoplasies. The unique character is pectoral metapterygial axis small or lost (38[1]), and the homoplasies are: absence of enameloid (26[1]) (also located as synapomorphy for the Xenacanthiformes at node C); and presence of ceratotrichia in the pectoral fin (43[1]), which is also found in *Xenacanthus decheni*. *Stethacanthus* presents two unique derived characters and two homoplasies. The unique characters are: notochordal canal constricted (29[1]); and posterior position of the pelvic girdle (44[1]). The homoplasies are: presence of dermal denticles of *"Cladodus" pattersoni* type (28[1]) (convergent with *Lebachacanthus*); and presence of one dorsal fin (33[1]), a condition also found in Xenacanthiformes (Node C).

Node C, Xenacanthiformes, is supported by 11 synapomorphies, nine unique derived characters and two homoplasies. The unique characters are: presence of denticulation in dorsal spine type B (12[2]); posterior or posterolateral position of denticles in spine type B (14[1]); absence of basal cartilage associated with the spine (16[1]); presence of diplodont teeth (17[1]); absence of labial foramina in the basal plate of the teeth (18[1]); presence of labial process (basal tubercle) in the teeth (19[1]); presence of coronal button on the upper side of the basal plate of the teeth (20[1]); dorsal fin low and elongated (34[1]); and pectoral propterygium and mesopterygium reduced (37[1]). The homoplasic characters are: absence of enameloid (26[1]) as in *Cladoselache*; and presence of one dorsal fin (33[1]) as in *Stethacanthus*. *Diplodoselache woodi* is defined by three homoplasies: presence of spine type B far behind the pectoral girdle (10[1]); spine type B with elliptical cross section (15[3]); and presence of diplodont teeth with smooth lateral carinae (23[1]), the two latter conditions being shared with *Xenacanthus*.

Node D (unnamed taxon): *Hagenoselache* branches off from the remaining xenacanthiforms (*Lebachacanthus* plus Xenacanthidae). This node is supported by six unique derived characters and one homoplasy. The unique characters are: whole tooth cusps formed of orthodentine (24[1]); presence of straight notochordal axis in caudal fin (30[1]); presence of calcified basiventrals anterior to caudal fin (31[1]); presence of postaxial radials (41[1]); pectoral fin biserial (42[1]); and caudal fin heterocercal inequilobate (asymmetrical) (46[1]). The homoplasy is absence of scales of ctenacanthid type (27[1]) (shared with anacanthous sharks). *Hagenoselache* is characterized by three homoplasies: neurocranium short, deep, with large orbits (1[1]) (also possessed by anacanthous sharks); diplodont teeth with vertical cristae on crown (22[1]); and presence of orthodentine in the tooth base (25[1]), the two latter conditions also occuring in *Triodus*.

Node E, *Lebachacanthus* plus Xenacanthidae, is supported by four unique derived characters and one homoplasy. The unique characters are: otico-occipital region of neurocranium longer than ethmo-orbital region (3[1]); absence of hyomandibula/neurocranium articulation (5[1]); denticulated to non-denticulated length ratio in spine type B of 1/4 to 1/3 (13[1]); and pectoral metapterygium segmented (39[1]). The homoplasy is a circular cross section of the spine type B (15[2]). *Lebachacanthus* is defined by two unique derived characters and five homoplasies. The unique characters are: mesopterygium and metapterygium both participating equally in the pectoral articulation (36[1]); and superior lobe of the caudal fin twice as long as the inferior lobe (47[1]). The five homoplasic characters are: neurocranium with unexpanded occipital segment (2[1]) (shared with anacanthous sharks); spine type B at the level of the pectoral girdle (10[2]); diplodont teeth showing serration and/or crenulation (21[1]) – a character state also found

in *Orthacanthus* (Node G); presence of denticles of "*Cladodus*" *pattersoni* type (28[1]); and presence of calcified ribs (32[1]), also found in *Xenacanthus*.

Node F, the clade Xenacanthidae, is supported by three unique derived characters: cranial spine (7[1]); spine longer than 2/3 of the total neurocranial length (8[1]); and spine slender (11[2]).

Node G, *Orthacanthus* is defined by one unique character, postorbital region of the neurocranium equal to or greater than 2/3 of the total skull length; and one homoplasy, presence of diplodont teeth with serration and/or crenulation (21[1]). *O. meridionalis* is supported by one unique derived character, denticulated to non-denticulated length ratio in spine type B of 3/8. There are no characters supporting the species *O. bohemicus* in this hypothesis.

Node H, *Xenacanthus* plus *Triodus*, is defined by four unique character states and one homoplasy. The unique characters are: denticulated to non-denticulated length ratio in spine type B of 1/2 (13[3]); lateral position of denticles in spine type B (14[2]); superior lobe of caudal fin more than twice the length of the inferior lobe (47[2]); and superior lobe of caudal fin with anguiliform shape (48[1]). The homoplasic character is, elliptical cross section of spine type B (15[3]), and is shared with *Diplodoselache*. *Xenacanthus* is defined by three unique characters and three homoplasies. The unique characters are: dibasal pectoral articulation (35[3]); mesopterygium forms the principal element in the pectoral articulation (36[2]); and presence of reduced propterygium of the pectoral fin (37[2]). The homoplasic features are: diplodont teeth always with smooth lateral carinae (23[1]); presence of calcified ribs (32[1]); and ceratotrichia in the pectoral fin (43[1]). *Triodus* is defined by one unique derived character, the monobasal pectoral articulation (35[2]); and two homoplasies, diplodont teeth with vertical cristae (22[1]) and orthodentine in the tooth base (25[1]).

Comparison between the analysis of SOLER-GIJÓN (1997b) and the analysis in this paper reveals the following differences:

(1) *Lebachacanthus* is better supported in this new analysis following the discovery of the homoplasic character "presence of spine type B at level of the pectoral girdle" (10[2]). *Orthacanthus* is supported by the same characters in both analyses.

(2) The clade Xenacanthidae (Node F in Fig. 3) is supported by one less synapomorphy (presence of biserial pectoral fin (42[1]) than in SOLER-GIJÓN (1997b).

(3) The clade Xenacanthiformes (Node C in Fig. 3) is supported by eight unique derived characters and two homoplasies, i.e. one more homoplasy than in SOLER-GIJÓN (1997b). The new homoplasic character is the absence of enameloid in *Diplodoselache woodi* (26[1]).

When the characters referring to the shape of the spine (characters 9 to 15, see SOLER-GIJÓN 1997b) are excluded

Fig. 4. **A:** Strict-consensus tree resulting from three equally parsimonious trees obtained after deletion of characters 9 to 15 from the phylogenetic analysis shown in Fig. 3. Consistency index for each hypothesis is 0.745 (excluding uninformative characters). **B:** Topologies resulting after deletion of characters 9 to 15: details of the relationships between *Lebachacanthus* and Xenacanthidae.
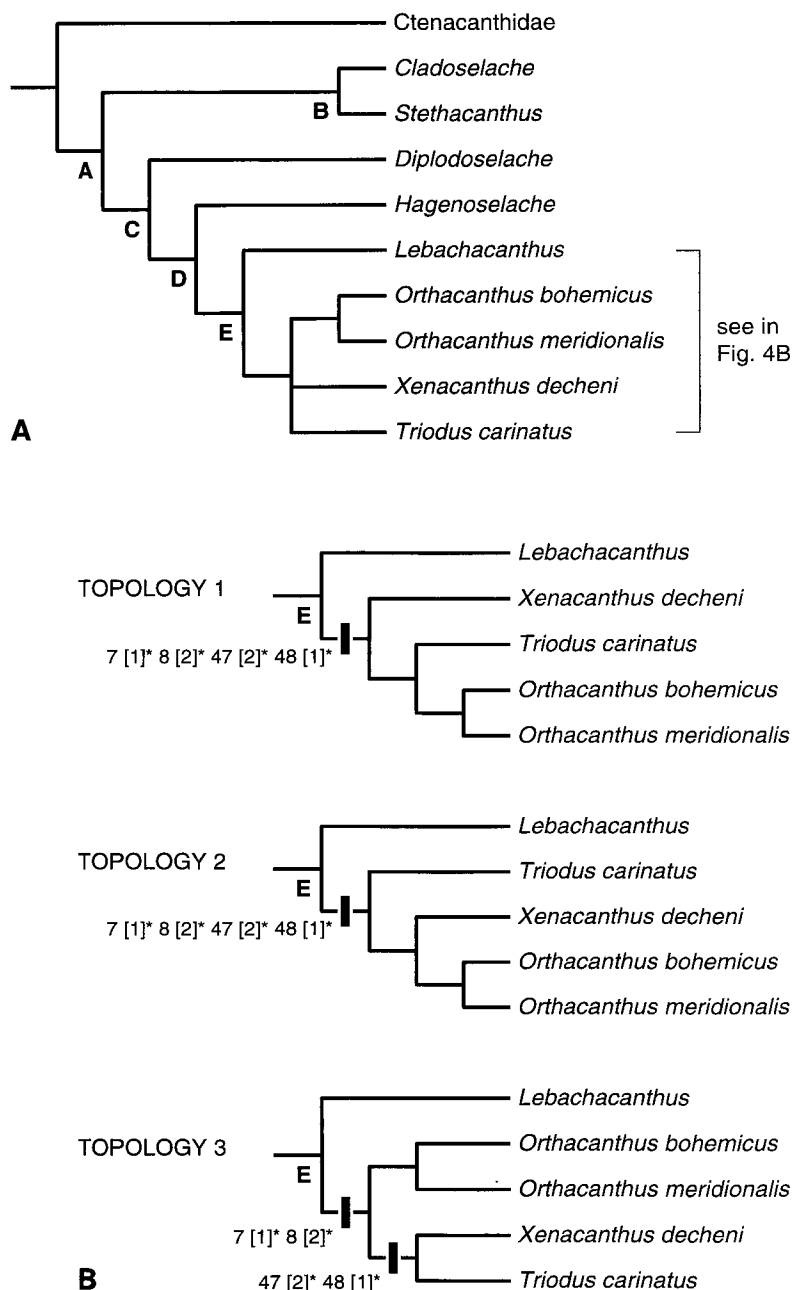
from the analysis, the taxa *Orthacanthus, Xenacanthus* and *Triodus* collapse into an unresolved trichotomy, but *Lebachacanthus* (and *Hagenoselache*) remain stable in the same topological position (Fig. 4). The analysis results in three equally parsimonious trees each of 59 steps, a CI (excluding uninformative characters) of 0.745 and an RI of 0.803. The strict consensus tree is presented in Fig. 4A. The three topologies differ only in the relative positions of *Orthacanthus, Xenacanthus* and *Triodus* (see Fig. 4B). *Lebachacanthus* is the sister group of the Xenacanthidae clade in each tree. Characters 47 and 48 (related to the caudal fin) plus characters 7 and 8 (related to the dorsal spine) support Xenacanthidae in two trees (*Orthacanthus* forms the sister group of *Xenacanthus* or *Triodus*). In the third tree, characters 7 and 8 support Xenacanthidae and characters 47 and 48 support the

clade [*Xenacanthus* + *Triodus*] (*Orthacanthus* is the sister group of [*Xenacanthus* + *Triodus*]). The absence of postcranial data for *Orthacanthus* leads to the unresolved trichotomy, because characters 47 and 48 have two possible distributions. The data concerning the spine (characters 9 to 15) resolve the trichotomy among *Orthacanthus, Xenacanthus* and *Triodus*: one of the trees is taken as more parsimonious (even though the postcranial skeleton of *Orthacanthus* is still unknown). This result suggests that the spine characters have a great effect in diagnosing the Xenacanthidae.

The strict consensus tree closely resembles the cladogram presented by HAMPE & HEIDTKE (1997: fig. 12). The authors analyzed (with the aid of PAUP) seven taxa (ctenacanthids [outgroup], *Diplodoselache, Hagenoselache, Orthacanthus* [including *"O." senkenber-*

gianus], *Xenacanthus*, *Triodus* and *Plicatodus*) and 25 characters that included information on the external morphology of teeth and spines, histology and postcranial anatomy. Their *Orthacanthus* (including *"O." senkenbergianus*) is located between *Hagenoselache* and the most derived xenacanths: *Xenacanthus*, *Triodus* and *Plicatodus* which form an unresolved trichotomy. Interestingly, the data used for *Orthacanthus* in this analysis are mainly based on *Lebachacanthus*. The characters 18 to 25, for example, concern the postcranial anatomy of *Lebachacanthus senkenbergianus*. Only two characters, 16 and 17, are related to the dorsal spine. Character 16 refers to the position of the spine, "dorsal spine articulates with the neurocranium", a derived state shared by *Orthacanthus (O. bohemicus)* and the unresolved clade that includes *Xenacanthus*, *Triodus* and *Plicatodus*. Character 17 refers to the shape of the spine, "dorsal spine dorso-ventrally compressed having laterally arranged denticles", a synapomorphy for the clade [*Xenacanthus* +*Triodus* +*Plicatodus*].

These results emphasise the importance of morphological analysis of the spine. Recently, SOLER-GIJÓN (1998) proposed the operation of heterochronic processes in the evolution of xenacanthiforms. These processes (peramorphic type) can explain clines in dorsal spine morphology from *Lebachacanthus* to the most derived xenacanths, *Xenacanthus/Triodus*. The clines consist, mainly, of an increase in the ratio between length of the denticulated region and the total length of the spine, and the increasing ratio between the total length and maximum width (robustness). According to SOLER-GIJÓN (1998), variation in the denticulation can be produced by increase in the rate of formation of denticles (which are derived from independent dermal papillae [SOLER-GIJÓN 1999]) on the spine proper, and an earlier onset of the denticulation (pre-displacement).

Ontogenetic studies allow us to make some predictions about phylogeny and can be very useful in systematics. The spine-genera *Anodontacanthus* and *Platyacanthus* (Westphalian) share the absence of denticulation with the first ontogenetic stages of *Orthacanthus* (SOLER-GIJÓN 1999) and some adult spines of the Permian *Lebachacanthus senkenbergianus* (HEIDTKE 1998: fig. 7d). This strongly supports the inclusion of these spine based genera in the Xenacanthiformes and the family Lebachacanthidae.

Lebachacanthus is known only from the Lower Permian, but some of the oldest xenacanthids come from the Westphalian D (e.g. *Orthacanthus bohemicus* from Nyrany). Sister taxa have the same time of origin, so Lebachacanthidae can be expected to be found in deposits of that age. Significantly, the assignment of *Anodontacanthus* and other isolated (denticulated) spines from the Westphalian of the British Isles (e.g. *"Pleuracanthus" robustus* and *"Pleuracanthus" alatus* from the DAVIS collection; see DAVIS 1892) to Lebachacanthidae (HAMPE, in preparation) confirms this prediction. The phylogenetic position of *Hagenoselache* and *Diplo-*

doselache is in total agreement with their stratigraphic positions (Namurian and Viséan, respectively).

Conclusions

The family Lebachacanthidae is supported by seven synapomorphies, two of which are unique derived characters: mesopterygium and metaptgerygium participating equally in the pectoral articulation and presence of superior lobe of the caudal fin twice as long as the inferior lobe. *Lebachacanthus* is more derived than *Hagenoselache*. However, *Lebachacanthus* is more primitive than *Orthacanthus* and retains some primitive characters of the anacanthous sharks and *Diplodoselache*, such as a neurocranium with unexpanded occipital region and a dorsal, noncephalic spine. In contrast, *Orthacanthus* shares with the rest of the Xenacanthidae (*Xenacanthus*, *Triodus* and *Plicatodus*) the presence of a slender occipital spine.

Acknowledgments

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Appendix I. List of characters and character states used in the phylogenetic analysis. [0] = primitive state; [1]-[3] = derived states; [?] = unknown due to preservation, [9] = not applicable.

1   Neurocranium: relatively long and flattened [0]; short, deep, with large orbits [1].

2   Occipital segment: broadly expanded [0]; unexpanded [1].

3   Otico-occipital region: equal to or shorter than length of orbito-ethmoidal region [0]; longer than orbito-ethmoidal region [1].

4   Postorbital region of neurocranium equal to or longer than 2/3 of total lenth: absent [0]; present [1].

5   Hyomandibula/neurocranium articulation: present [0]; absent [1].

6   Number of dorsal spines: two [0]; one [1].

7   Location of spine: non-cranial [0]; cranial [1].

8   Length of dorsal spine in relation to neurocranium: outgroup [?]; dorsal spine equal or shorter than 2/3 of total neurocranium length [1]; dorsal spine longer than 2/3 of total neurocranium length [2].

9   Type of dorsal spine: type A (dorsal spine of the phalacanthous sharks) [0]; type B [1].

10   Position of non-cranial non-phalacanthous spine in relation to pectoral girdle: outgroup [9]; far behind pectoral girdle [1]; at level of pectoral girdle [2].

11   Morphology of dorsal spine type B: outgroup [9]; spine robust with a maximum diameter to length ratio less than 1:12 [1]; slender spine (maximum diameter to length ratio equal or greater than 1:12) with the widest area displaced proximally [2].

12   Denticulation in dorsal spine type B: outgroup [9]; absent [1]; present [2].

13   Denticulated to non-denticulated region ratio in dorsal spine type B: outgroup [9]; 1/4 to 1/3 [1]; 3/8 [2]; 1/2 [3].

14   Position of denticles in dorsal spine type B: outgroup [9]; posterior or posterolateral [1]; lateral [2].

15   Cross section in dorsal spine type B: outgroup [9]; oval (laterally compressed) [1]; circular [2]; elliptical (anteroposteriorly compressed) [3].

16   Basal cartilage associated with dorsal spine: present [0]; absent [1].

17   Diplodont teeth: absent [0]; present [1].

18   Nutrient foramina in labial side of tooth base: present [0]; absent [1].

19   Labial process (basal tubercle): absent [0]; present [1].

20   Coronal button in upper side of tooth base: absent [0]; present [1].

21   Diplodont teeth with crown showing serration and/or crenulation: absent [0]; present [1].

22   Diplodont teeth with vertical cristae on crown: absent [0]; present [1].

23   Diplodont teeth with crown always showing smooth lateral carinae: absent [0]; present [1].

24   Whole cusp formed of orthodentine: absent [0]; present [1].

25   Orthodentine in base: absent [0]; present [1].

26   Enameloid on crown: present [0]; absent [1].

27   Scales of ctenacanthid type: present [0]; absent [1].

28   Dermal denticles of *"Cladodus" pattersoni* type: absent [0]; present [1].

29   Notochordal canal: unconstricted [0]; constricted [1].

30   Notochordal axis in caudal fin: upturned [0]; straight [1].

31   Basiventrals anterior to caudal fin: not calcified [0]; calcified [1].

32   Calcified ribs: absent [0]; present [1].

33   Number of dorsal fins: two [0]; one [1].

34   Dorsal fin: unexpanded [0]; expanded rostro-caudally [1].

35   Pectoral-fin articulation: tribasal [0]; multibasal [1]; monobasal [2]; dibasal [3].

36   Principal elements as support of pectoral articulation: several basal elements (the metapterygial is not the primary element in the shoulder articulation) [0]; mesopterygium and metapterygium both participate equally [1]; mesopterygium only [2].

37   Pectoral propterygium and mesopterygium: both unreduced [0]; both reduced [1]; only propterygium reduced [2].

38   Pectoral metapterygial axis: large [0]; small or lost [1].

39   Pectoral metaperygium: unsegmented [0]; segmented, distinguished from post-metapterygial elements by absence of post-axial radials [1].

40   Premetapterygial radials of pectoral fin: articulate with compound basal (i.e more than one radial per basal) [0]; articulate with shoulder girdle or simple basals [1].

41   Postaxial radials: absent [0]; present [1].

42   Pectoral fin: uniserial [0]; biserial [1].

43   Ceratotrichia in pectoral fin: absent [0]; present [1].

44   Relative position of pelvic girdle: distance from posterodorsal border of scapular process to border of pelvic girdle/ distance from posterodorsal border of scapular process to base of inferior lobe of caudal fin: less than 1/2 [0]; equal or more than 1/2 [1].

45   Anal fin: present [0]; absent [1].

46   Caudal fin: homocercal or heterocercal equilobate [0]; heterocercal inequilobate (asymmetrical) [1].

47   Length of superior lobe of caudal fin: superior lobe nearly similar to inferior lobe [0]; superior lobe twice as long as inferior lobe [1]; superior lobe more than twice the length of inferior lobe [2].

48   Shape and dimension of superior lobe of caudal fin: superior lobe with relatively long radials and/or separated by long gap from dorsal fin [0]; superior lobe with relatively short radials, no long gap between superior lobe of caudal fin and dorsal fin (anguilliform shape) [1].

Appendix II. Character-state matrix used to analyze phylogenetic relationships of xenacanthiform and anacanthous sharks. [0] = primitive state; [1]-[3] = derived states; [?] = unknown due to preservation; [9] = not applicable.

References for taxa employed in the phylogenetic analysis:

Ctenacanthidae: ZANGERL 1973, 1981; MAISEY 1975; HAMPE 1995. *Cladoselache*: DEAN 1909; HARRIS 1951; BENDIX-ALMGREEN 1975; MAISEY 1977; ZANGERL 1981. *Stethacanthus*: LUND 1974, 1984, 1985; ZANGERL 1981, 1984; WILLIAMS 1985. *Diplodoselache*: DICK 1981; HAMPE 1995. *Hagenoselache*: HAMPE & HEIDTKE 1997. *Lebachacanthus*: FRITSCH 1889; HEIDTKE 1982; KLAUSEWITZ 1986, 1987; HAMPE 1988a, 1991, 1995; ZIDEK 1993a; SOLER-GIJÓN 1997b. *Orthacanthus bohemicus*: FRITSCH 1889; ZIDEK 1993a. *Orthacanthus meridionalis*: SOLER-GIJÓN 1993, 1994, 1995, 1997a, 1999. *Xenacanthus decheni*: FRITSCH 1895; HAMPE 1988b, 1991, 1995; ZIDEK 1993a; SCHNEIDER & ZAJÍC 1994. *Triodus carinatus*: FRITSCH 1895; HAMPE 1989, 1991, 1995; SCHNEIDER & ZAJÍC 1994.

Taxon	1	2	3	4	5	6	7	8	9	10
Cladoselache	1	1	0	0	0	1	0	1	1	1&2
Stethacanthus	1	1	0	0	0	1	0	1	1	2
Diplodoselache	0	?	?	?	?	1	0	?	1	1
Lebachacanthus	0	1	1	0	1	1	0	1	1	2
O. bohemicus	0	0	1	1	?	?	1	2	1	?
O. meridionalis	0	0	1	1	?	?	1	?	1	?
X. decheni	0	0	1	0	1	1	1	2	1	9
Hagenoselache	1	?	0	0	?	?	?	?	?	?
Ctenacanthidae	0	0	0	0	0	0	0	?	0	9
T. carinatus	0	0	?	0	?	1	1	2	1	9

Taxon	11	12	13	14	15	16	17	18	19	20
Cladoselache	1	1	9	9	1	0	0	?	0	0
Stethacanthus	1	1	9	9	1	0	0	0	0	0
Diplodoselache	1	2	?	1	3	1	1	1	1	1
Lebachacanthus	1	2	1	1	2	1	1	1	1	1
O. bohemicus	2	2	1	1	2	1	1	1	1	1
O. meridionalis	2	2	2	1	2	1	1	1	1	1
X. decheni	2	2	3	2	3	1	1	1	1	1
Hagenoselache	?	?	?	?	?	?	1	1	1	1
Ctenacanthidae	9	9	9	9	9	0	0	0	0	0
T. carinatus	2	2	3	2	3	1	1	1	1	1

Taxon	21	22	23	24	25	26	27	28	29	30
Cladoselache	0	0	0	0	0	1	1	0	0	0
Stethacanthus	0	0	0	0	0	0	1	1	1	0
Diplodoselache	0	0	1	0	0	1	0	0	0	0
Lebachacanthus	1	0	0	1	0	1	1	1	0	1
O. bohemicus	1	0	0	1	0	1	?	0	?	?
O. meridionalis	1	0	0	1	0	1	?	?	?	?
X. decheni	0	0	1	1	0	1	1	0	0	1
Hagenoselache	0	1	0	1	1	1	1	0	?	1
Ctenacanthidae	0	0	0	0	0	0	0	0	0	0
T. carinatus	0	1	0	1	1	1	1	0	0	1

Taxon	31	32	33	34	35	36	37	38	39	40
Cladoselache	0	0	0	0	1	0	?	1	0	1
Stethacanthus	0	0	1	0	1	0	?	0	0	1
Diplodoselache	0	0	1	1	0	0	1	0	0	?
Lebachacanthus	1	1	1	1	0	1	1	0	1	1
O. bohemicus	?	?	?	?	?	?	?	0	1	?
O. meridionalis	?	?	?	?	?	?	?	?	?	?
X. decheni	1	1	1	1	3	2	2	0	1	1

Hagenoselache	1	0	1	1	?	?	?	0	?	1
Ctenacanthidae	0	0	0	0	0	0	0	0	0	0
T. carinatus	1	0	1	1	2	?	?	0	1	?

Taxon	41	42	43	44	45	46	47	48
Cladoselache	0	0	1	0	1	0	0	0
Stethacanthus	0	0	0	1	1	0	0	0
Diplodoselache	0	0	0	0	0	0	0	0
Lebachacanthus	1	0&1	0	0	0	1	1	0
O. bohemicus	1	1	?	?	?	?	?	?
O. meridionalis	?	?	?	?	?	?	?	?
X. decheni	1	1	1	0	0	1	2	1
Hagenoselache	1	1	0	0	0	1	0	0
Ctenacanthidae	0	0	0	0	0	0	0	0
T. carinatus	1	1	0	0	0	1	2	1