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Symmoriiform sharks from the Pennsylvanian of Nebraska

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ABSTRACT:

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The Indian Cave Sandstone (Upper Pennsylvanian, Gzhelian) from the area of Peru, Nebraska, USA, has yielded numerous isolated chondrichthyan remains and among them teeth and dermal denticles of the Symmoriiformes Zangerl, 1981. Two tooth-based taxa were identified: a falcatid *Denaea saltsmani* Ginter and Hansen, 2010, and a new species of *Stethacanthus* Newberry, 1889, *S. concavus* sp. nov. In addition, there occur a few long, monocuspid tooth-like denticles, similar to those observed in *Cobelodus* Zangerl, 1973, probably representing the head cover or the spine-brush complex. A review of the available information on the fossil record of Symmoriiformes has revealed that the group existed from the Late Devonian (Famennian) till the end of the Middle Permian (Capitanian).

Key words: Symmoriiformes; Microfossils; Carboniferous; Indian Cave Sandstone; USA Midcontinent.

INTRODUCTION

The Symmoriiformes (Symmoriida *sensu* Zangerl 1981) are a group of Palaeozoic cladodont sharks sharing several common characters: relatively short skulls, large eyes, terminal mouth, epicercal but externally symmetrical caudal fin, pectoral fins with a long metapterygial axis, posterior dorsal fin devoid of a fin-spine, anterior dorsal fin missing or transformed (at least in males) into a specific structure, such as a spine-brush complex in *Stethacanthus* Newberry, 1889 and *Orestiacanthus* Lund, 1984 or an anteriorly directed head spine in falcatids (see e.g., Zangerl 1981, 1984; Lund 1984, 1985, 1986; Williams 1985; Coates and Sequeira 2001; Maisey 2007, 2009). Their skin is generally naked, but specialised denticles usually occur on the head, on the spine, protecting the lateral line and there also occur very characteristic, complex, *Stemmatias*-type pharyngeal denticles.

The teeth of symmoriiforms are of cladodont design, i.e., with the central main cusp the highest, but they differ considerably within the group, as far as the size and shape is concerned [compare the thick median cusp, almost a centimetre long, in *Stethacanthus neilsoni* (Traquair, 1898), and the minute, 0.5 mm wide, multicuspid, comb-like tooth of *Denaea wangi* Wang, Jin and Wang, 2004; Ginter *et al.* 2010, figs 58A–C and 61, respectively]. However, again several important common dental features can be observed. First of all, the cusps are structurally separate (the feature first noted by Sequeira and Coates 2000, pp. 162, 167); only rarely, when the bases of cusps are very close to each other, a thin enameloid connection exists. Also, the cusps and base tissues are clearly separated and they react differently to diagenetic processes (see e.g., Ginter *et al.* 2010, fig. 58D). The cusps are rounded in cross section; the labio-lingual compression, if it occurs at all, is slight. The bases are usually flat, with a broad lingual extension, and in primitive members of the group (e.g., *Stethacanthus*) provided with pronounced articulation devices (single button + basolabial projection). In later taxa (e.g., *Stethacanthulus* Zangerl, 1990) such devices may be highly modified or are absent.

In 1974, Clair R. Ossian presented his Ph. D. dissertation, in which he described numerous fossils, mainly of vertebrate and botanic origin, from the locality at Peru, Nemaha County, Nebraska, USA (Ossian 1974). The fossils were found in the Indian Cave Sandstone, which is presumed to represent the Upper Pennsylvanian, Gzhelian (for the geological setting see Fischbein *et al.* 2009; Ginter 2016, pp. 300, 301, text-fig. 1). Among the very diverse vertebrate macro- and microfossils – counted in thousands – he reported about 20 chondrichthyan tooth-based taxa, together with chondrichthyan dermal denticles, spines, and putative calcified cartilage fragments. Although the fossils were found in sandstone matrix, it was possible for Ossian to recover them by chemical processing, using acetic acid. Many chondrichthyan teeth are beautifully preserved, displaying only a slight, superficial abrasion. Larger vertebrate skeletal fragments, however, are usually broken.

Among the Chondrichthyes, Ossian (1974) identified a few cladodontomorphs, at least two xenacanthiforms, euselachians (see Ginter 2016), various euchondrocephalans (orodonts?, petalodonts, eugeneodontiforms, and holocephalans), and iniopterygians. Unfortunately, the dissertation has never been published and the specimens, except the xenacanthiforms (Johnson 1984, 1999), have never been formally described. Based on our current knowledge it can be stated that only one tooth illustrated by Ossian (1974, pl. 3, figs 7–9), as *Cladodus gracilis* Newberry and Worthen, 1966, belongs to the Symmoriiformes. However, he also illustrated a few symmoriiform denticles, as teeth or tooth-whorls of *Styptobasis aculeata* Cope, 1894 (= *Cobelodus aculeatus*). The identity of these elements will be discussed below. It should be noted that Ossian (1974) reported 221 teeth of "*C. gracilis*" and 275 elements of "*S. aculeata*", but illustrated only single representatives of each form, so the diversity in his material can be much broader than that inferred from the photographs.

In the Carnegie Museum of Natural History in Pittsburgh, USA, there occurs a collection of chondrichthyan teeth, apparently from the same locality and horizon (SE of Peru, Nebraska, Indian Cave Sandstone) as that studied by Ossian. The teeth are perfectly prepared and, as in the case of Ossian's material, most of them are only slightly abraded. The quality and diversity of these teeth is so high that some of them were illustrated in the Handbook of Paleoichthyology, vol. 3D (Ginter *et al.* 2010, figs 3, 6) as examples of various tooth forms in Palaeozoic chondrichthyans. In the collection there occur teeth of two symmoriiform species (one of them new and rather unusual) and a few denticles similar to those referred by Ossian (1974) to *S. aculeata*. The description of these microfossils and the short review of post-Mississippian symmoriiforms are the main purposes of this paper.

Institutional abbreviation: CM, Carnegie Museum of Natural History, Pittsburgh, USA.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Symmoriiformes Zangerl, 1981
Family Falcatidae Zangerl, 1990
Genus *Denaea* Pruvost, 1922

TYPE SPECIES: *Denaea fournieri* Pruvost, 1922.

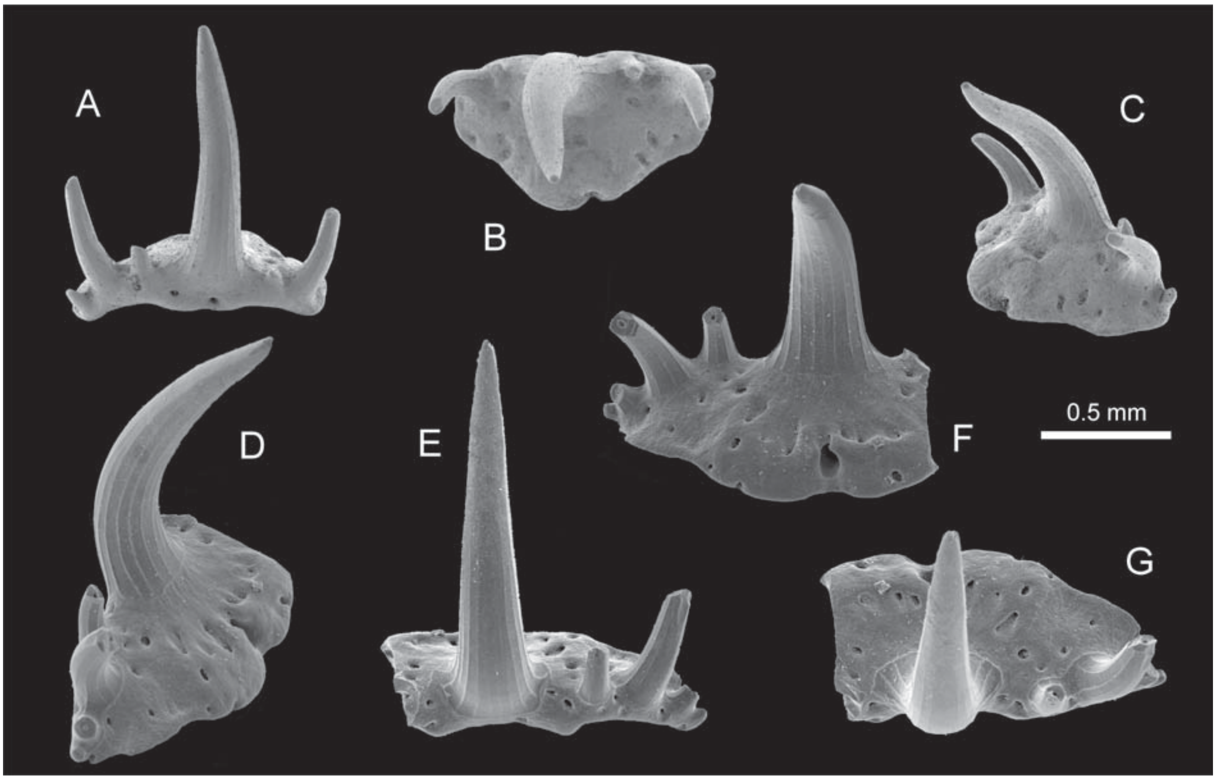
Denaea saltsmani Ginter and Hansen, 2010
(Text-fig. 1)

1983. Subtype 021; Tway and Zidek, p. 416, fig. 38.
2010. *Denaea saltsmani* sp. nov.; Ginter and Hansen, pp. 32–34, fig. 2.

MATERIAL: Two teeth with the same collection number, CM 44548 (a and b); Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

DESCRIPTION: The following description is based mostly on the two teeth illustrated herein, but also on the specimens from the other localities in the Pennsylvanian of the USA Midcontinent (Ginter and Hansen 2010). The tooth crown of *D. saltsmani* is characterised by the following combination of features: the crown comprises five to eight cusps; in seven-cuspid teeth, the second to the outermost pair of the lateral cusps is the highest; the central cusp is circular in cross section, and curves markedly linguad with only slight sigmoid flexure; the cristae on the cusps are delicate, subparallel, extend from the base to the tip and generally do not converge; the cristae are equally spaced both labially and lingually and the lateral carinae are absent.

The tooth base of *D. saltsmani* is triangular to trapezoidal. The base of the triangle forms a straight labial margin (this feature is particularly evident in smaller specimens of this species) and the distal part of the lingual extension forms the apex of the triangle (or a shorter edge of the trapezoid). The base does not



Text-fig. 1. *Denaea saltsmani* Ginter and Hansen, 2010, from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska. A-C – tooth CM 44548a, in labial, oral and oblique lateral views; D-G – tooth CM 44548b, in lateral, labial, lingual and oral views

have a distinct button, but only a vague thickening or hump on the oral-lingual side: the lingual edge of the central part of the base is developed into a raised, bulbous area, in the centre of which, on the lingual margin, is a prominent, circular lingual foramen. Another, slightly smaller foramen perforates the labial side of this thickening (Text-fig. 1B, C). Yet another large foramen is present in the centre, or slightly linguad of centre, on the aboral surface. On the labial margin of the aboral surface, beneath the central cusp, is an elongate (mesio-distally), slightly raised, weak, articular boss. The lateral edges of the tooth base are slightly downturned in some specimens.

It is notable that both teeth of *D. saltsmani* from Peru (Text-fig. 1) and the holotype from the Noble limestone in Ohio (Ginter and Hansen 2010, fig. 2A–D) are asymmetrical and have six cusps in the crown. Such a condition rarely occurs, if at all, in the other falcatids (compare e.g., *Denaea* cf. *fournieri* in Ginter *et al*. 2015, figs 10A–E, 12).

REMARKS: Of the Pennsylvanian Falcatidae, only the teeth of *D. saltsmani* appear to closely resemble those of the type species, *D. fournieri* from the Viséan of Belgium. The combination of such features as the presence of (however weak) articular devices (oral-lingual thickening and basolabial projection) and the faint, even, subparallel cristation of the cusps, distinguish *D. fournieri* and *D. saltsmani* from *Stethacanthulus meccaensis* (Williams, 1985) and *S. decorus* (Ivanov, 1999). Isolated teeth of *Denaea* cf. *fournieri* from the upper Viséan of Poland differ from *D. saltsmani* in having the outermost pair of the lateral cusps being the largest in seven-cuspid specimens (Ginter *et al.* 2015). Thus far, this condition has not been definitely recognised in the type material of *D. fournieri* from Belgium.

All the illustrated teeth of *Ozarcus mapesae* Pradel, Maisey, Tafforeau, Mapes and Mallatt, 2014 are pentacuspid and the orolingual region of their bases is hardly visible, so, although these teeth are definitely falcatid in character (Pradel *et al.* 2014), it is difficult to compare them to the forms mentioned in the previous paragraph. A similar problem concerns the falcatids from the upper Mississippian of Bear Gulch, Montana, USA (*Falcatus* Lund, 1985 and *Damocles* Lund, 1986); the complete morphology of their teeth is still unknown.

A very well preserved seven- or perhaps even eight-cuspid tooth of *D. saltsmani* (putatively one of 221 specimens) was described by Ossian (1974, pl. 3, figs 7–9). He referred to it as *Cladodus gracilis* Newberry and Worthen, 1866, and suggested that *C. springeri* St. John and Worthen, 1875 might have represented the lower jaw dentition of the same species. It seems, however, that both mentioned Mississippian species (*C. gracilis* and *C. springeri*) sufficiently differ from the Pennsylvanian *D. saltsmani* to keep the latter as a separate taxon.

OCCURRENCE: Carboniferous, Upper Pennsylvanian, Gzhelian, USA (SE Nebraska; this paper). *Denaea saltsmani* appears to range through much of the Pennsylvanian marine sequence in the Appalachian Basin (Kentucky, Ohio and Pennsylvania, USA; Pottsville through Conemaugh Formations; Hansen 1986; Ginter and Hansen 2010) and similar teeth were reported by Tway and Zidek (1983) from 16 localities in Virgilian (Upper Pennsylvanian) rocks of Iowa, Kansas, Missouri, Nebraska and Oklahoma, USA.

Family Symmoriidae Dean, 1909
Genus *Stethacanthus* Newberry, 1889

TYPE SPECIES: *Physonemus altonensis* St. John and Worthen, 1875.

Stethacanthus concavus sp. nov.
(Text-fig. 2)

2010. "undescribed symmoriiform"; Ginter *et al.*, fig. 3F, G.

ETYMOLOGY: From the concave appearance of the basolabial region of the tooth.

HOLOTYPE: Tooth, CM 44550b, from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

MATERIAL: Five teeth; Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

DIAGNOSIS: Symmoriiform shark with the following combination of dental features: five-cuspid crown composed of a long and slender median cusp, lingually convex and slightly flattened labially, covered with subdued, dense, subparallel cristae up to three-fourth of its height, and two pairs of small lateral cusplets, not higher than one-fourth of the median cusp; reniform to rectangular base with a short, crescentic button on the orolingual side, perforated in the middle by a foramen leading to the main basal canal, and a corresponding to it short, labially concave basolabial ridge.

DESCRIPTION: Among the small collection of teeth of *S. concavus* sp. nov. several secondary differences between the teeth can be observed. The mesio-distal dimension of the base varies from 3 to 5 mm. The median cusp can be longer and narrower, with almost parallel lateral sides (Text-fig. 2E), or shorter and triangular (Text-fig. 2B). The base outline can be reniform or rectangular with rounded angles. The basolabial articulation device forms a simple, curved ridge (Text-fig. 2A), or a complex horseshoe structure with two labial projections (Text-fig. 2D, E). However, in all the instances, the ornamentation of the cusps and their relative separation, as well as the concave basolabial region unify these teeth.

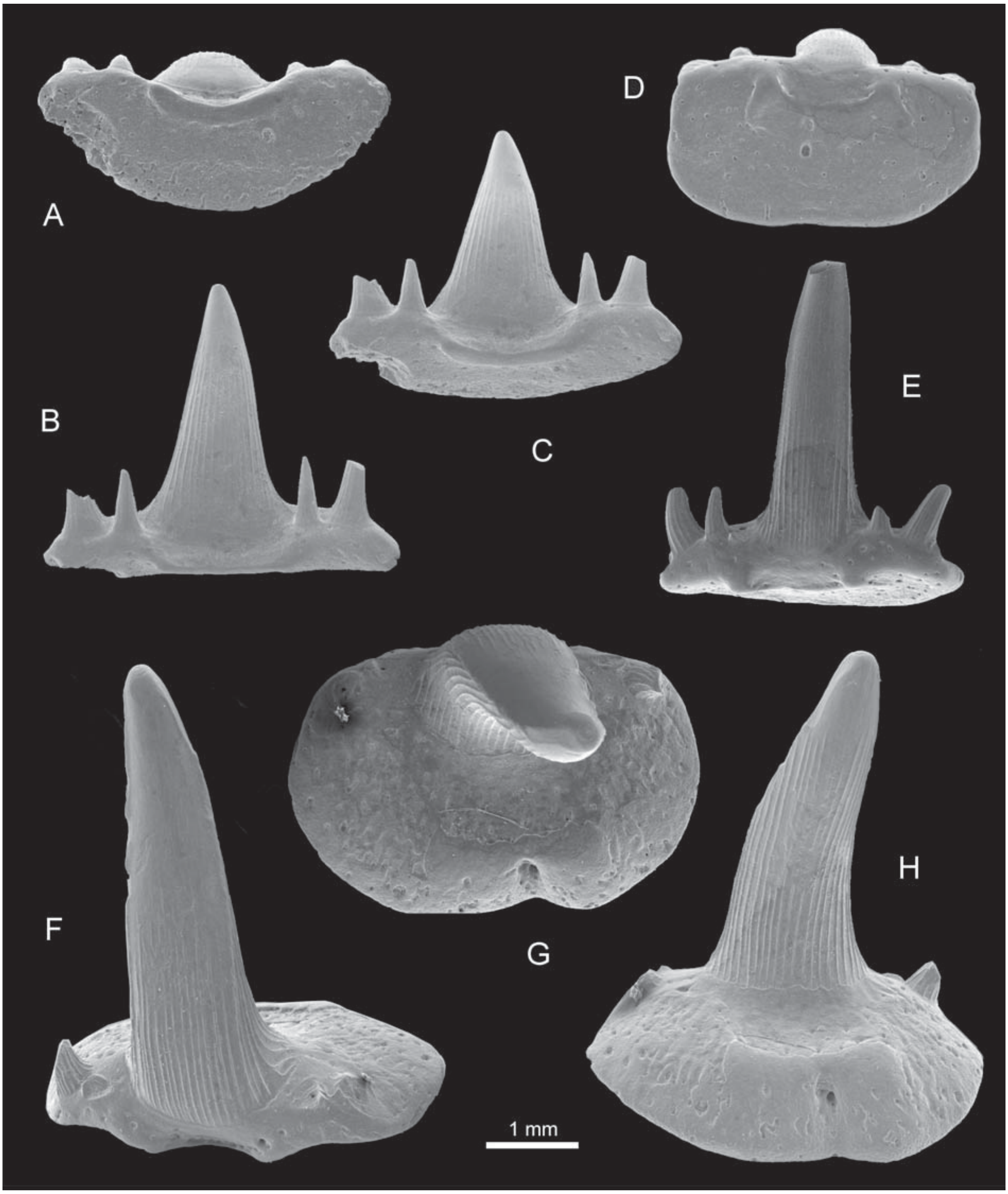
REMARKS: Of all the known symmoriiforms, the teeth of *S. concavus* sp. nov. are morphologically the closest to those of *Stethacanthus*: the size relation between the median and lateral cusps in the pentacuspid crown and the general outline of the base are the common features. However, the deep basolabial concavity and the curved button corresponding to it distinguish the new species from all hitherto described stethacanths. Thus, it is possible that in future, when more specimens of this type are studied, the taxon will be translated to a new genus.

OCCURRENCE: Carboniferous, Upper Pennsylvanian, Gzhelian, USA (SE Nebraska).

Stethacanthus sp.
(Text-fig. 3)

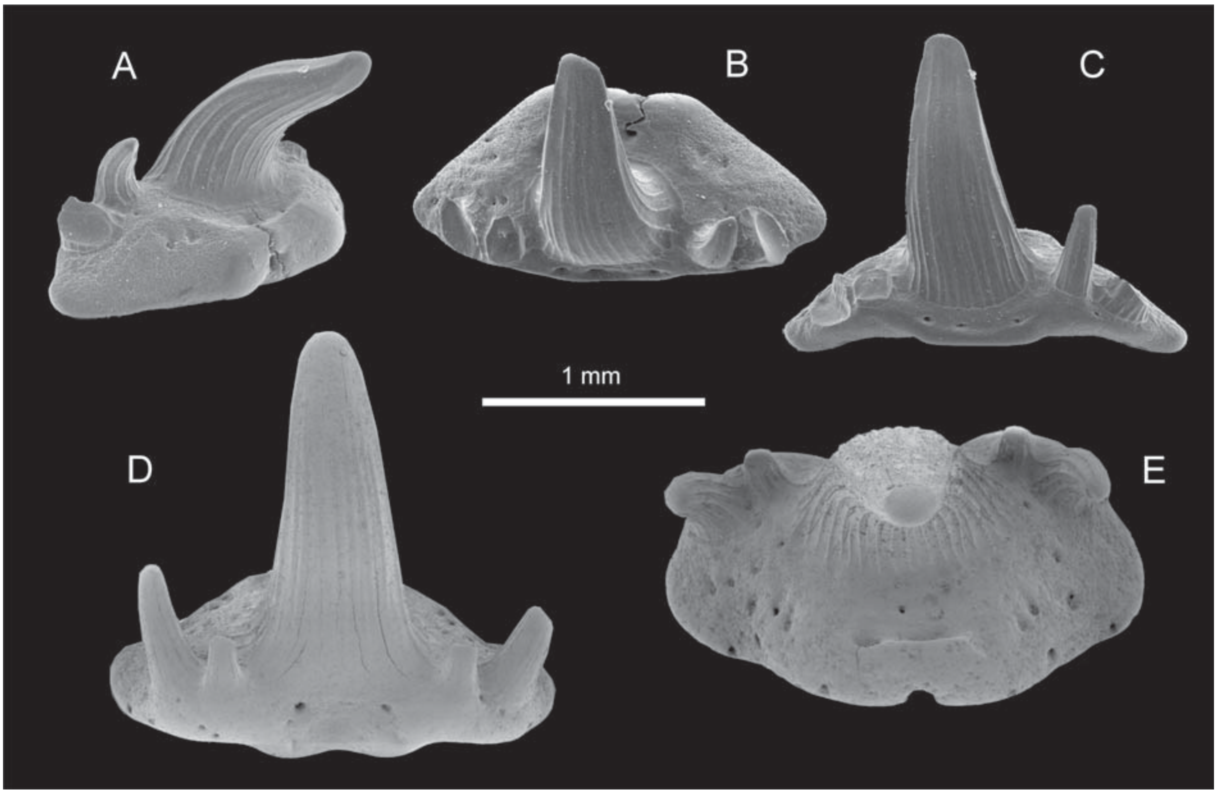
MATERIAL: Two teeth; Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

DESCRIPTION and REMARKS: The first tooth referred here to as *Stethacanthus* sp. is generally similar to *S. concavus* sp. nov. (Text fig. 3A–C). It does have a curved, weakly developed button, but the concavity in the basolabial region is much shallower than in the typical specimens. Moreover, the cristae appear to reach the apex of the median cusp, whereas in the typical teeth they disappear lower, leaving the tip of the cusp completely smooth.



Text-fig. 2. *Stethacanthus concavus* sp. nov. from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska. A-C – holotype, CM 44550b, in basal, labial and basal/labial views; D, E – tooth CM 44550c, in basal and labial views; F-H – large tooth, CM 44550a, in oblique labial, oral and lingual views

The second tooth, in addition to having the above mentioned characters, displays strong interconnection between the cusps. This latter feature is unusual for the symmoriids, but perhaps reflects some special position in the dentition. Otherwise, the tooth is definitely stethacanthid.



Text-fig. 3. Teeth of *Stethacanthus* sp. from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska. A-C – CM 44550d, in oblique lingual, oral and labial views; D, E – CM 44550e, in labial and oral views

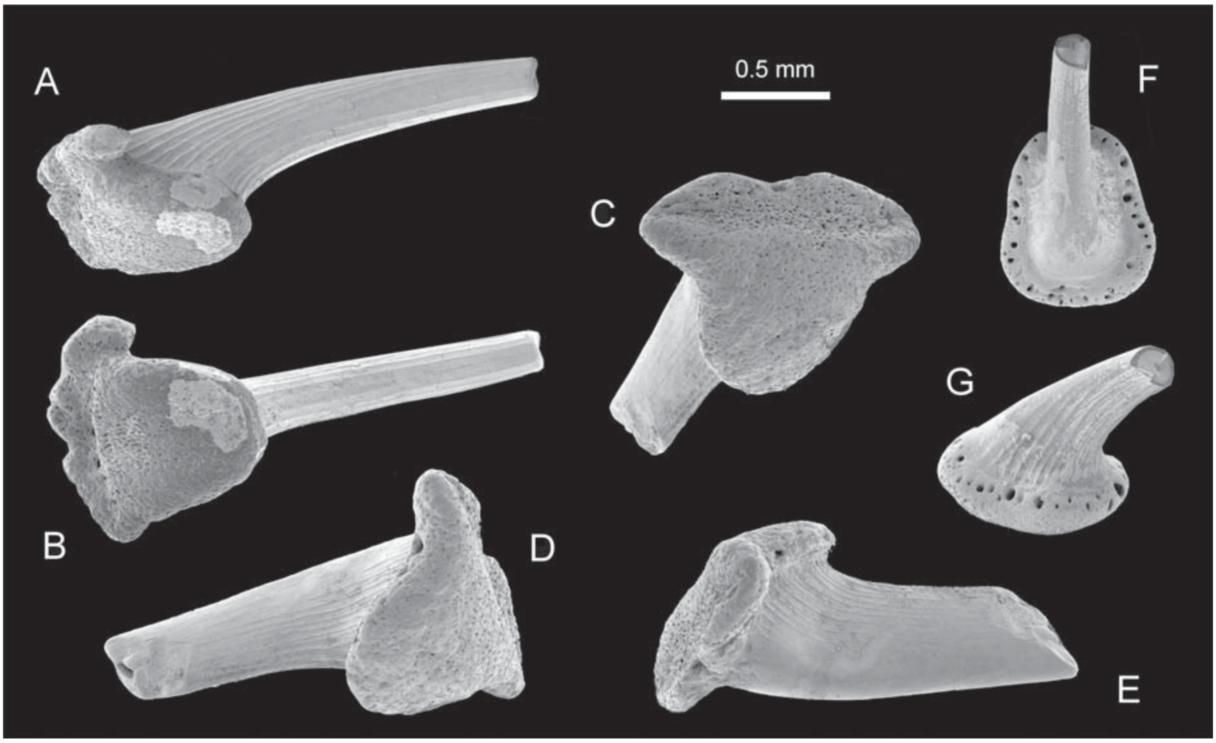
OCCURRENCE: Carboniferous, Upper Pennsylvanian, Gzhelian, USA (SE Nebraska).

SYMMORIIFORM HEAD DENTICLES

In the collection from Peru, Nebraska, housed at the Carnegie Museum, there occur three monocuspid denticles (Text-fig. 4) with interestingly shaped bases. In all cases the tips of the cusps are broken, but it can be approximated that the length of the largest denticle was greater than 3 mm. The cusps are curved (backwards?), elliptical in cross section, slightly laterally compressed. They are ornamented with subparallel cristae, sometimes bifurcating near the base. For the obvious reason, it is unknown whether the cristae reach the apex of a cusp.

The base in two of the denticles (Text-fig. 4A–E) has a three-fold appearance, with two small lateral lobes and one, larger, directed backwards. The base of the smallest denticle (Text-fig. 4F, G) has a simple, trapezoidal base with rounded angles. Numerous irregularly placed openings occur on the upper side of the base, around the basal part of the cusp; the lower side of the base is devoid of any foramina.

The size, form and ornamentation of the cusps are extremely similar to those of the denticles of *Cobelodus aculeatus* (Zangerl and Case 1976, fig. 16, upper row), a symmoriid from Pennsylvanian black shales in central USA. However, the bases of the denticles in the drawings provided by the mentioned authors do not have any specific features, they are simply rounded portions of spongeous tissue attached at the base of the cusps. They may have lost lost their form due to the unfavourable preservation (pyritisation). Zangerl and Case (1976), as well as Zangerl (1981, fig. 8E) suggested that such denticles are upper jaw dentition teeth because they were found near the palatoquadrate. M. Ginter and A. Ivanov independently suggested around 2003–2004 (unpublished communications) that the shape of these denticles, and especially the form of their bases, precludes their belonging to the dentition and that they are rather head denticles, similar to those called *Cladodus pattersoni* by Newberry (1875) and Williams (1985). This concept, that the denticles represent a cranial cap, was subsequently suggested by



Text-fig. 4. Symmoriiform head denticles? from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska. A, B – CM 44550f, in lateral and basal/posterior views. C-E. CM 44550g, in basal, posterior and lateral views; F, G – CM 44550h, in external and lateral views

Maisey (2007, p. 63), Ginter *et al.* (2010, pp. 60, 61) and Ivanov (2016, p. 720).

The typical, tricuspid dentition teeth of *Cobelodus* (Ginter *et al.* 2010, fig. 57; Ivanov 2016, figs 2H–J, 3A–C) have not been found in the material from Peru, despite the very large number of symmoriiform teeth occurring in Ossian's collection. Therefore it is likely that the monocuspid denticles are associated with the teeth of *S. concavus* sp. nov, the only larger symmoriid present at the Peru locality.

It is interesting that the morphology of these denticles resembles that of alleged monocuspid teeth of *Celtiberina maderi* Wang, 1993, an Early Devonian shark from Spain (Ginter *et al.* 2010, fig. 21). This is yet another argument supporting the idea expressed by Turner (2004, p. 88) and followed by Ginter *et al.* (2010, p. 28) that *Celtiberina* elements are actually modified dermal denticles, and not dentition teeth.

FOSSIL RECORD OF THE SYMMORIIFORMES

The Devonian record of symmoriiform sharks is sparse. Here and there falcatid-like delicate teeth have been reported from the Famennian (e.g., Ginter 2000, fig. 7B; 2001, fig. 2A–E) and the only partly articulated specimens (*Stethacanthus*) come from the upper Famennian Cleveland Shale of Ohio (Williams 1985). The situation is much better in the Mississippian, and particularly in the Viséan-Serpukhovian. In addition to the numerous isolated teeth, characteristic denticles (e.g., *Stemmatias* branchial denticles) and spines from spine-brush complexes, found all over the world (e.g., Zidek 1993; Ginter *et al.* 2015), quite a few fairly complete skeletons have been described. The major source of these are the Serpukhovian Bear Gulch Beds in Montana (*Falcatus*, *Damocles*, *Orestiacanthus*; Lund 1984, 1985, 1986), the Upper Mississippian of Scotland (*Stethacanthus*-like forms "*Akmonistion*" and "*Gutturensis*"; Sequeira and Coates 2000; Coates and Sequeira 2001), and the Viséan Black Marble in Belgium (*Denaea*; Fournier and Pruvost 1928; Maisey 2008). There is also a recently described, well preserved skull with associated teeth of a falcatid, *Ozarcus mapesae*, from the Upper Mississippian (Chesterian) of Arkansas (Pradel *et al.* 2014).

The known distribution of post-Mississippian symmoriiforms is restricted to the areas of USA,

Table 1. The Symmoriiformes from post-Mississippian rocks.

Current name	Original name	Important references	Age, occurrence	Articu-lated
Symmoriidae				
Symmorium reniforme Cope, 1893		Williams 1985; Ginter 2002	Pennsylvanian, USA	yes
Cobelodus aculeatus (Cope, 1894)	*Styptobasis aculeata*	Zangerl and Case 1976; Ivanov 2013a, 2016	Pennsylvanian, USA; Permian, Russia [?]	yes
Stethacanthus altonensis (St. John and Worthen, 1875)	*Physonemus altonensis*	Newberry 1889; Williams 1985; Zidek 1993	Pennsylvanian, USA	yes
Stethacanthus concavus sp. nov.		this paper	Pennsylvanian, USA	no
Stethacanthus rosanovi (Minikh, 1999)	*Ctenacanthus rosanovi* + *Pinegia grunti*	Minikh 2004, 2006; Ivanov and Lebedev 2014	Permian, Russia	no
Falcatidae				
Denaea saltsmani Ginter and Hansen, 2010		Tway and Zidek 1983; Hansen 1986	Pennsylvanian, USA	no
Stethacanthulus meccaensis (Williams, 1985)	*Denaea meccaensis* + *Stethacanthulus longipeniculus*	Zangerl 1990, 1995; Ginter and Hansen 2010; Ivanov 2013b, Ivanov *et al.* 2013, 2015	Lower Pennsylvanian, Uzbekistan; Pennsylvanian and Permian, USA	yes
Stethacanthulus decorus (Ivanov, 1999)	*Denaea decora*	Ivanov 2005, 2013b	Lower Pennsylvanian, Uzbekistan; Pennsylvanian, USA; Permian, Russia	no
Family indet.				
"*Cladodus*" *acuminatus* Newberry, 1856		Newberry 1875	Pennsylvanian, USA	no
"*Cladodus*" *fulleri* St. John and Worthen, 1875			Pennsylvanian, USA	no
"*Cladodus*" *pandatus* St. John and Worthen, 1875			Pennsylvanian, USA	no
Kawichthys moodiei Pradel, Tafforeau, Maisey and Janvier, 2011			Pennsylvanian, USA	yes
Kungurodus obliquus [?] (Ivanov, 2005)	*Cobelodus obliquus*	Lebedev 2009; Ivanov 2016	Permian, Russia and Kazakhstan	no

Russia, and Central Asia. However, their diversity is still high in the Pennsylvanian (see Table 1). The flourishing Serpukhovian falcatids were replaced with *Denaea saltsmani* and at least two species of *Stethacanthulus*. The most durable symmoriid genus, *Stethacanthus*, is well documented from the Pennsylvanian black shales of Indiana and adjacent states. The same formation yielded two new larger sharks, *Symmorium* Cope, 1893 and *Cobelodus*. Two interesting skulls with denticulated dorsal crests (but no associated teeth) were reported from the Upper Pennsylvanian (Virgilian) of Kansas, under the name of *Kawichthys* (Pradel *et al.* 2011). The newly described teeth of *Stethacanthus concavus* sp. nov. from Nebraska and a few forms incorrectly referred to *Cladodus* by 19th century writers, and still requiring revision, add to the picture.

The record of symmoriiforms decreases considerably at the Carboniferous–Permian boundary. Thus far almost only isolated teeth and dermal denticles have been recovered from Permian rocks. Among these, only three undoubtedly symmoriiform species have been identified: *Stethacanthulus meccaensis* (Williams, 1985) (Capitanian, Texas; Ivanov *et al.* 2013, fig. 4a, b; 2015, pl. 1, figs 1–9), *S. decorus* (Ivanov, 1999) (Asselian and Sakmarian, Urals; Ivanov 1999, pl. 7, fig. 12, pl. 8; 2005, fig. 3K–P) and *Pinegocaptus rosanovi* (Minikh, 1999) (Kazanian, mainly Roadian, northern European Russia; Minikh 2004, pl. 1, figs 1, 2; Ivanov and Lebedev 2014, pl. 9, figs 1–4). The latter species is represented by large, up to a few centimetres high *Stethacanthus*-like teeth with a very thick median cusp, covered with numerous dense cristae. Not all authors accept the validity of the generic name *Pinegocaptus* Minikh, 2006. For instance, Ivanov *et al.* (2009, p. 244) stated that it is a junior synonym of *Stethacanthus*. Even if so, the unusual size and ornamentation of the median cusp suggests that *S. rosanovi* is a separate species.

The only partly articulated fragment of a symmoriid skeleton found in the Permian thus far, is a skeleton of a pectoral fin recovered from Artinskian deposits of the Middle Urals. It was described by Ivanov (2013a) as belonging to *Cobelodus*.

Special attention should be given to the tooth-based genus *Kungurodus* Ivanov, 2016. The beautifully preserved teeth from the Lower Permian of South Urals and Cisurals (Russia and Kazakhstan; Ivanov 2005, 2016; Lebedev 2009) were originally described as *Cobelodus obliquus* by Ivanov (2005), but later, after Ivanov's study of the original specimens of *Cobelodus*, the species was transferred to a new genus (Ivanov 2016) within the Symmoriiformes. However, its symmoriid affinity is at least doubtful. The teeth of *K. obliquus* resemble such falcatids as *Denaea williamsi* Ginter and Hansen, 2010 (e.g., Ginter *et al.* 2015, fig. 13E) to some extent, but its cusps are divergent, compressed labio-lingually and, moreover, connected with a carina. Owing to such characters I put *Kungurodus* on the list of post-Mississippian symmoriiforms (Table 1), but only tentatively.

Judging from the available information, the Symmoriiformes did not persist into the Upper Permian. The latest occurrences (*S. meccaensis*) were reported from the Capitanian (uppermost Middle Permian) of the Apache Mountains (Ivanov *et al.* 2013) and Guadalupe Mountains (Ivanov *et al.* 2015), West Texas. However, it must be taken into account that a few teeth very similar to those of the falcatids, and designated as such by Guinot *et al.* (2013, fig. 2a–e) were found in the deep marine deposits of the Lower Cretaceous, Valanginian, of southern France.

CONCLUSIONS

In the last two decades information on the symmoriiform sharks has considerably grown. On the one hand, several old articulated specimens have been restudied (Coates and Sequeira 2001; Maisey 2007, 2008, 2009) and new ones, particularly neurocrania, were added to the data base (Pradel *et al.* 2011, 2014) thanks to the new techniques employed, such as computer tomography. On the other hand, intensive works on symmoriid microfossils, particularly teeth, has helped to solve taxonomic problems and misunderstandings from the past (e.g., Ginter 2002; Ginter *et al.* 2010; Ivanov 2016) and considerably broadened our knowledge on the distribution of symmoriiforms in time and space (numerous publications by A.O. Ivanov since 1999). Currently we know that this group has existed since the Famennian through to the Middle Permian. The studies on the Permian are so promising that perhaps they will show an increased upper range of these sharks, even if the report from the Valanginian (Guinot *et al.* 2013) is considered dubious.

The symmoriiform microfossils from the Indian Cave Sandstone body near Peru, Nebraska, described herein, are only a small contribution to that growing mass of knowledge. The sample is very small, only about ten elements altogether. Even so, this has permitted a new species to be erected (*Stethacanthus concavus* sp. nov.). However, the sample from the Carnegie Museum is only the tip of an iceberg. It is certain that a re-examination of the whole material collected by Ossian from the same locality and housed at the University of Texas at Austin would bring very interesting results, particularly as far as the intraspecific diversity is concerned.

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