The revision of “*Cladodus*” *occidentalis*, a late Palaeozoic ctenacanthiform shark

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The teeth of a well known late Palaeozoic cladodont chondrichthyan, “*Cladodus*” *occidentalis* from Russia, USA, and England are restudied and a new generic name, *Glikmanius* gen. nov., is proposed for this species. Yet another tooth-based species, formerly described as ?*Symmorium myachkovensis*, occurring on the Russian Platform and in Nebraska, is considered to belong to the newly erected genus. Although there is no direct evidence that *Glikmanius* possessed fin spines, the broad similarity between its teeth and those of *Ctenacanthus compressus* suggests it had a ctenacanthiform affinity. The possible relationships between *Glikmanius*, *Cladodus* sensu stricto, “*Ctenacanthus*” *costellatus*, and *Heslerodus*, are suggested. However, the proposition put forward by an earlier author that the teeth of *Heslerodus* might represent the lower jaw dentition of *G. myachkovensis*, is rejected. The overall resemblance of *Glikmanius* teeth and those of *Cladoselache* and *Squatinactis* is recognised as convergent.

Key words: Chondrichthyes, Ctenacanthiformes, teeth, Carboniferous, Permian.

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Introduction

Since the description of *Cladodus mirabilis* by Agassiz (1843), more than seventy nominal species attributed to the genus *Cladodus* have been erected, in most cases based only on isolated teeth. Many of these tooth forms, characterised by lingually expanded bases and “cladodont” crowns, i.e., with the median cusp longer and thicker than the others, are known today to represent taxa only remotely related to *Cladodus* sensu stricto, such as the Stethacanthidae or Cladoselachidae. However, several others are morphologically similar enough to *C. mirabilis* to be reckoned as belonging to *Cladodus* (e.g., *C. elegans* Newberry and Worthen, 1870; *C. bellifer* St. John and Worthen, 1875) or at least to genera closely related to it (for an updated definition of *Cladodus*, see Duffin and Ginter in press). Interestingly, all the species which belong to the latter group and of which the postcranial skeleton is known, possess ctenacanth-like, ornamented fin spines (e.g., *Ctenacanthus compressus* Newberry, 1889, see Dean 1909, Williams 2001; *Tamiobatis vetustus*, Eastman, 1897, see Williams 1998). This might suggest that *Cladodus* and its kin are all in fact ctenacanthiforms.

The most spectacular *Cladodus*-like tooth form, described several times and under different names, mainly from the Upper Carboniferous of USA and Russia, is “*Cladodus*” *occidentalis* Leidy, 1859. The holotype of this species, although incomplete, shows all of the important characters. It is housed at the Academy of Natural Sciences of Philadelphia, and was described in detail and illustrated by Leidy (1873: pl. 17: 4–6; see also Fig. 1A) a few years after the first publication of its name. It is easily distinguishable from other large cladodonts by its two, well developed, widely spaced buttons on the oral side of the lingual torus, and two corresponding, tubercle-like basolabial projections. We consider that these features are distinctive enough to establish a new genus, separate from *Cladodus*, and our paper is mostly dedicated to the description of this new genus, its probable components, range, diversity, and relationships.

Our study is based, in addition to the materials already published elsewhere, on the specimens collected from the Carboniferous (Serpukhovian through Kasimovian) in the vicinities of Moscow, and from the Pennsylvanian Onaga Formation of Peru, Nebraska.

Institutional abbreviations.—ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; BMNH, Natural History Museum, London; CM, Carnegie Museum, Pittsburgh, Pennsylvania; FMNH (collection acronym PF), Field Museum of Natural History, Chicago, Illinois; MB, Museum für Naturkunde, Humboldt Universität, Berlin; MP, Palaeontological Museum, Saint-Petersburg University, St. Petersburg; UWr, Institute of Geology, Wrocław University, Wrocław, Poland (collection acronym PCh); PIN, Palaeontological Institute, Moscow.

Systematic palaeontology

Class Chondrichthyes
Order Ctenacanthiformes Glikman, 1964a
Family indet.
Genus *Glikmanius* nov.

Type species: *Cladodus occidentalis* Leidy, 1859; upper Coal Measures of Manhattan, Kansas, Pennsylvanian.

Etymology: In honour of the late Russian palaeontologist, Dr. Leonid Glikman, who thoroughly studied this genus and was the first to propose its ctenacanthiform affinity; the suffix *-us* indicates the masculine gender of the name.

Referred species.—*Glikmanius occidentalis* (Leidy, 1859), *G. myachkovensis* (Lebedev, 2001).

Diagnosis.—Sharks with cladodont teeth having a robust, triangular median cusp, strongly convex lingually and slightly convex or flattened labially, with a well developed depression in the basolabial part. There are usually from two to four pairs of lateral cusps, the outermost the largest. At least one pair of intermediate cusplets is not in line with the others, but positioned labially. The base is reniform, with two rounded, compact basolabial projections flanking the labial depression, and two widely spaced buttons on the oral-lingual side.

Differential diagnosis.—Teeth of *Glikmanius* gen. nov. present a unique combination of features, most of them observed in other cladodont shark taxa. They share the shape of the tooth-crown with *Cladodus* Agassiz, 1843, and particularly with *Cladodus bellifer* St. John and Worthen, 1875, but differ clearly from the latter by a greater depth of the basolabial depression and the presence of two pairs of separate basal articulation devices (buttons and basolabial projections). Similar basal features are observed in the teeth of *Heslerodus* Ginter, 2002 (= *Phoebodus heslerorum* sensu Williams 1985) which, however, are characterised by a phoebodont-like crown with delicate, slender cusps. Prominent, labially flattened median cusp, typical of *Glikmanius*, occurs in *Ctenacanthus* Agassiz, 1838 (see Dean 1909) and *Symmorium* Cope, 1893, but in the latter two genera, as in the case of *Cladodus*, the articulation devices are in a form of an undivided orolingual ridge and a single basolabial shelf.

Remarks on tooth histology.—The observations on the internal morphology of *Glikmanius* teeth made by Mertiniene (1995) and a new study in transmitted light of a tooth immersed in aniseed oil (Fig. 1F–H) showed that the whole crown is covered by a thin, uniform layer of enameloid and pallial dentine (Fig. 1G, H). The internal part of the median cusp (Mertiniene 1995: fig. 2) and larger lateral cusps (Fig. 1H) is composed of osteodentine. The basal vascular system consists of a network of numerous, thin, and sinuous canals which occupy the whole interior of the base (Fig. 1F). Between the buttons, usually about 2–4 larger labio-lingual canals occur.

Stratigraphic range.— Carboniferous, Serpukhovian–Permian, Wordian (= Kazanian).

Glikmanius occidentalis (Leidy, 1859)

Figs. 1A, C–E, 2A, B.

Hybodus; Prestwich 1840, pl. 41: 12.
Cladodus occidentalis; Leidy 1859: 3.
cf. *Cladodus mortifer*; Newberry and Worthen 1866: 22, pl. 1: 5.
cf. *Cladodus gracilis*; Newberry and Worthen 1866: 30, pl. 1: 17.
Cladodus mortifer Newberry and Worthen, 1866; St. John 1870: 431–432.
Cladodus mortifer Newberry and Worthen, 1866; St. John 1872: 239–240, pl. 6: a, b, pl. 13: a–d.
Cladodus occidentalis; Leidy 1873: 311–312, pl. 17: 4–6 .
Cladodus lamnoides Newberry and Worthen, 1866; Trautschold 1874: 286–288, text-fig.; cf. pl. 28: 3c–e; non pl. 18: 3a, b.
Cladodus occidentalis; Woodward 1889: 24.
Cladodus mortifer Newberry and Worthen, 1866; Newberry 1897: 285, pl. 22: 2.
Cladodus girtyi sp. nov.; Hay 1900: 98–100, fig. 2.
Cladodus girtyi Hay; Hay 1902: 268.
Cladodus mortifer Newberry and Worthen, 1866; Hay 1902: 269.
Cladodus occidentalis Leidy; Hay 1902: 269.
Cladodus occidentalis Leidy; Eastman 1903: 168, pl. 2: 3, 8, 9.
Cladodus sp.; Stukenberg 1905: 110, pl. 13: 24.
Cladodus sp.; Pavlov 1914: 19, fig. 7.
Cladodus occidentalis Leidy; Branson 1916: 652–653, pl. 2: 23, 24.
Ctenacanthus occidentalis; Glikman 1964a: pl. 1: 5.
Ctenacanthus occidentalis (Leidy); Glikman 1964b: pl. 3: 10–12.
Cladodus occidentalis Leidy; Zidek 1973: fig. 2.
Cladodus sp.; Case 1973: figs. 13–18.
Symmorium reniforme Cope; Williams 1985: 107, pl. 7: 2–13.
Symmorium reniforme; Mapes and Hansen 1984: fig. 2.
cf. *Symmorium* sp. indet.; Goto et al. 1988: 292, fig. 2, pl. 1: 1.
Symmorium reniforme; Hansen and Mapes 1990: fig. 171.
Symmorium reniforme Cope; Zidek 1992: 152–153, fig. 7.
cf. *Symmorium reniforme* Cope; Mertiniene 1995: 148, figs. 1, 2.
Symmorium reniforme Cope; Hansen 1996: 291, fig. 21-5.1.
Symmorium occidentalis [sic] (Leidy); Lebedev 1996: 394, fig. 7A, B.
Ctenacanthus volgensis A. Minikh, sp. nov.; Minikh and Minikh 1996: 262, pl. 5.4-I: 1a, b.
?*Symmorium lamnoides* Newberry and Worthen, 1866; Lebedev 2001: pl. 41: 3.
cf. *Ctenacanthus artiensis* Kozlov, sp. nov.; Kozlov 2000: 152–153, pl. 3: 4 [non fig. 5].
Symmorium reniforme Cope; Lucas and Estep 2000: 22–23, fig. 6A–O.
"*Symmorium*" *occidentalis* (Leidy); Malysheva et al. 2000: fig. 2A–C.
"*Cladodus*" *occidentalis* Leidy; Ginter 2002: fig. 1D–F.
"*Cladodus*" *occidentalis*; Elliott et al. 2004: 275–276, fig. 4J–M.

Original diagnosis (from Leidy 1859: 3).—"Enameled crown, when perfect, about an inch in length, demi-conical; the outer convex side provided with narrow oblique folds. Lateral denticles two, the outer one the larger. Base of the tooth reniform, with a breadth of about an inch, and the short diameter about 5 lines; lateral extremities provided with a pair of large ovoid tubercles, one above the inner margin, the other below the outer margin."

Description of the holotype, specimen ANSP 8394, from the upper Coal Measures of Manhattan, Kansas, by Leidy (1873: 311; see Fig. 1A).—"The specimen has lost one-half of its base, a large portion of its principal cusp, and the points of the lateral cusps, but sufficient remains to give us a correct idea of the form of the perfect tooth.

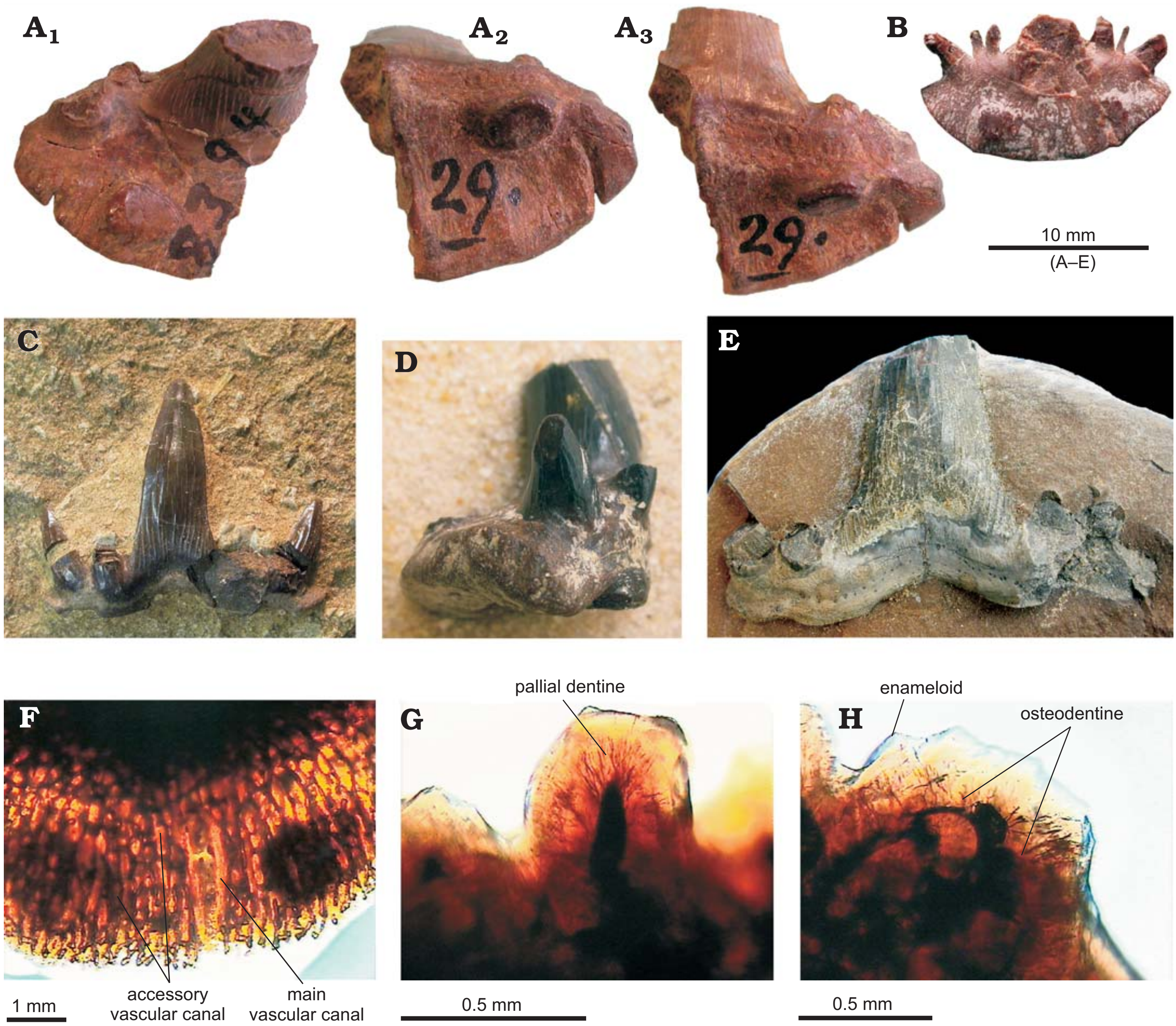


Fig. 1. **A**. *Glikmanius occidentalis* (Leidy, 1859), holotype, specimen ANSP 8394, from the upper Coal Measures (Pennsylvanian) of Manhattan, Kansas, in lingual (A_1), aboral (A_2), and labial/aboral (A_3) views. **B**. *Glikmanius* sp., specimen CM 44504B, from the Namurian E3, Bear Gulch, Montana, in lingual view. **C**–**E**. *G. occidentalis*. **C**. Specimen USNM 14107, from undetermined Carboniferous of Illinois, labial view. **D**. Specimen BMNH P.7043 (labelled as *Cladodus impressus* Woodward), from the Moscovian of Myachkovo, Moscow District, in lateral view. **E**. The first ever published specimen, BMNH P.7364, from the Chance Pennystone, Coal Measures of Donnington, Coalbrook Dale, Shropshire, UK, labial view. **F**, **G**. *Glikmanius* sp., photographs in aniseed oil, parts of occlusal view, specimen MP30-1, from the Serpukhovian of the Kalinovskie Vyselki Quarry, Moscow District. **F**. Lingual part of the base. **G**. Intermediate cusp. **H**. Lateral cusp.

The base of the tooth is oblong in outline, with the inner [= lingual] border somewhat angular and the outer [= labial] one concave. Its upper inner surface slopes from the cusps, and near its margin, a short distance from the extremities, supports a pair of oval tubercles. Similar protuberances occupy a position beneath the base externally.

The median or principal cusp of the tooth is elongated demiconical, with acute lateral edges. The inner convex surface of the cusp at its base exhibits sharp, oblique folds or striae. The outer less convex or nearly flat surface is smooth, except a few vertical wrinkles at its base.

The lateral denticles on each side of the principal cusp are two, of which the outer is the larger.

In its perfect condition the tooth has approximated 1 1/4 inches in length and about 1 inch in breadth at base.”

Description based on additional material.— As evident from the literature and museum collections, numerous teeth of *G. occidentalis* were studied in Russia, USA, and England before

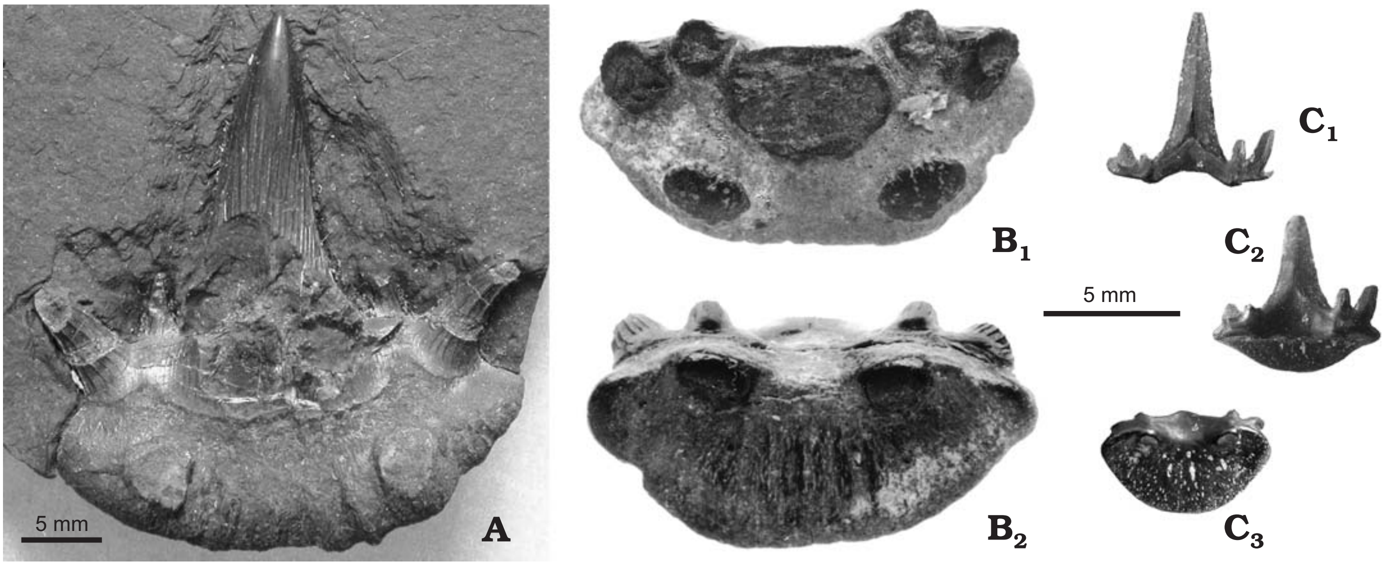


Fig. 2. **A**, **B**. *Glikmanius occidentalis* (Leidy, 1859). **A**. Specimen PF 8240, from the Pennsylvanian black shales of the Hesler Quarry, Indiana, in oral/lingual view (same as Williams 1985: pl. 7: 7). **B**. Specimen PCh/425a, from the Moscovian of Myachkovo, Moscow District, in oral (B_1) and aboral (B_2) views. **C**. *Glikmanius myachkovensis* (Lebedev, 2001), specimen MB.f.9452.1, from the Moscovian of Myachkovo, in labial (C_1), labial/aboral (C_2), and aboral (C_3) views.

and after the descriptions by Leidy (1859, 1873). Still more are yet unpublished. Based on all the material that was available to us, and especially, the specimens from the Moscovian of central Russia, from the Kazanian of the Uralian Foredeep, and from various Pennsylvanian formations of central and southwestern USA, we were able to add several details to the above characteristics of this species.

The lingual rim of the base seems to be "angular" in the holotype only because of partial abrasion. In most other specimens the lingual torus is trapezoidal indeed, but with the angles definitely rounded. In the type specimen, the basolabial projections differ in shape and size from the buttons. The former are smaller, with almost flat basal surfaces, whereas the surface of the buttons is more rounded. However, it was noted from several specimens that the buttons and projections can be almost equal in diameter. The buttons are not always circular, but they can be oval; usually they are situated rather close to the lingual rim (Fig. $2B_1$). On the aboral surface, a mesio-distal furrow occurs lingually to the basolabial projections.

The median cusp is relatively wide, with almost parallel lateral edges in the middle part (Fig. 1C). The lingual face of the median cusp is considerably convex, covered with moderate, subparallel, vertical, only slightly curved cristae (Fig. 2A). The labial face is deeply depressed basally, then becomes almost flat to slightly convex near the tip. The sculpture of the labial face is specific (see especially Glikman 1964b: pl. 3: 10): the cristae which begin at the basal depression, close to the midline, first turn slightly outwards, but at the midpoint of the cusp they become vertical and then turn back inward, parallel to the edges of the narrowing cusp, and gradually fade. The cristae which start at the base but in more outward position, are almost vertical and intersect the lateral edges of the median cusp rather soon. The uppermost part of the cusp on both labial and lingual sides is smooth (Figs. 1C, 2A).

The outer lateral cusps can be quite robust, but usually rather short. It appears that in all known specimens of this species, there is no more than one intermediate cusplet in the crown. A feature, characteristic of the whole genus, but particularly typical of *G. occidentalis*, must be emphasised here: because of the great depth of the basolabial indentation, framed by two projections, the intermediate cusplets are not in line with the median and outermost cusps, but are substantially displaced labially (Figs. 1D, $2B_1$).

Remarks.— The long synonymy list reflects the complex history of understanding this species, from the mid-19th century up to recent times. Probably the first specimen representing this species, from the Coal Measures of Coalbrook Dale in England, was illustrated by Prestwich (1840: pl. 41: 12), under the name of *Hybodus*. No description of the tooth is provided and the woodcut, although very good, is slightly simplified. The artist drew an undivided basolabial rim, without any sign of basolabial projections, therefore the tooth looks like *Cladodus bellifer*. However, the original which is available for investigation at The Natural History Museum, London (P.7364), clearly shows an outline of a basolabial projection, typical of *Glikmanius*, on the preserved side of the base (Fig. 1E).

In 1859, Leidy's brief, but clear description of the type specimen of *Cladodus* (now *Glikmanius*) *occidentalis*, was published in the Proceedings of the Academy of Natural Sciences of Philadelphia. However, because he did not illustrate his new species, Leidy's note apparently went unnoticed both by J. S. Newberry and O. H. St. John. Therefore, the latter used Newberry and Worthen's (1866) name, "*C.*" *mortifer*, for the specimens he presented in his reports on Carboniferous vertebrates from Nebraska (St. John 1870, 1872). To clarify the priority situation, Leidy (1873) gave a longer description and illustrated his type specimen, synonymising "*Cladodus*" *mortifer* sensu St. John with "*C.*" *occidentalis*. That does not necessarily mean that the holotype of "*C.*" *mortifer* sensu Newberry and Worthen belongs in *Glikmanius occidentalis*, because the tooth is apparently lost and its drawing (Newberry and Worthen 1866: pl. 1: 5) does not show diagnostic features.

Meanwhile, Trautschold (1874), evidently unaware of the discussion among American palaeontologists in the early 1870-s, described specimens of *G. occidentalis* from the vicinities of Moscow under another name from Newberry and Worthen's (1866) paper, this time, "*Cladodus*" *lamnoides* (for photographic illustrations of Trautschold's specimens, see Fig. 2A and Ginter 2002: fig. 1D–F). This mistake was noticed and corrected by Branson (1916: p. 653). From that time, until 1985, such forms were usually referred to as *Cladodus occidentalis*, with the exception of Glikman (1964a, b) who proposed the ctenacanth affinity of this species. Williams (1985) applied Cope's (1893) name *Symmorium reniforme* to such teeth from the Pennsylvanian Black Shales. This unfortunate decision influenced many later authors for more than a decade, but the revision of the type material of *S. reniforme* (Ginter 1998, 2002) definitely showed that teeth of the latter species are different in important aspects from those of *G. occidentalis*. They do have large median cusps and kidney-shaped bases, but such characters are insignificant, since they are typical of almost all cladodont sharks, with exception of *Heslerodus* and, perhaps, certain advanced stethacanthids.

It should be noted that one of the best collections of *G. occidentalis* teeth, from the Council Grove Group (Lower Permian) of Wabaunsee County, Kansas, is presented at Michael Everhart's web page, http://www.oceansofkansas.com/Leidy1859.html.

Distribution.—Pennsylvanian–Lower Permian marine deposits of USA (New Mexico, Arizona, Kansas, Indiana, Illinois, Ohio, Colorado); Pennsylvanian, Moscovian–Permian, Wordian (= Kazanian) of Russia (central and eastern Russian Platform, the Urals); Middle Permian of Japan (?).

Glikmanius myachkovensis (Lebedev, 2001)

Figs. 2C, 3.

?*Symmorium myachkovensis* [sic] Lebedev, sp. nov.; Lebedev 2001: 196–197, pl. 41: 4.
"*Cladodus*" sp.: Nekrylov 1997: 52.
"*Symmorium*" sp.: Keltsiyan 2002: 25.

Original material.—The original description was founded on about 50 teeth from the Moscovian and Kasimovian of the Moscow and Riazan Regions in Russia. The holotype, PIN 1704/180 (Lebedev 2001, pl. 41: 4a), comes from the vicinities of the village of Myachkovo, Moscow Region; its stratigraphic position is uncertain: either Myachkovian Regional Stage, Moskovian, or Krevyakinian Regional Stage, Kasimovian.

New material.—28 teeth, CM 44549, from Peru, Nebraska, Indian Cave Sandstone, Onaga Formation, Upper Pennsylvanian; generally well preserved, with only slight traces of overall abrasion. Two teeth partly embedded in white limestone, MB.f.9452.1-2, from the type locality at Myachkovo, probably Moscovian.

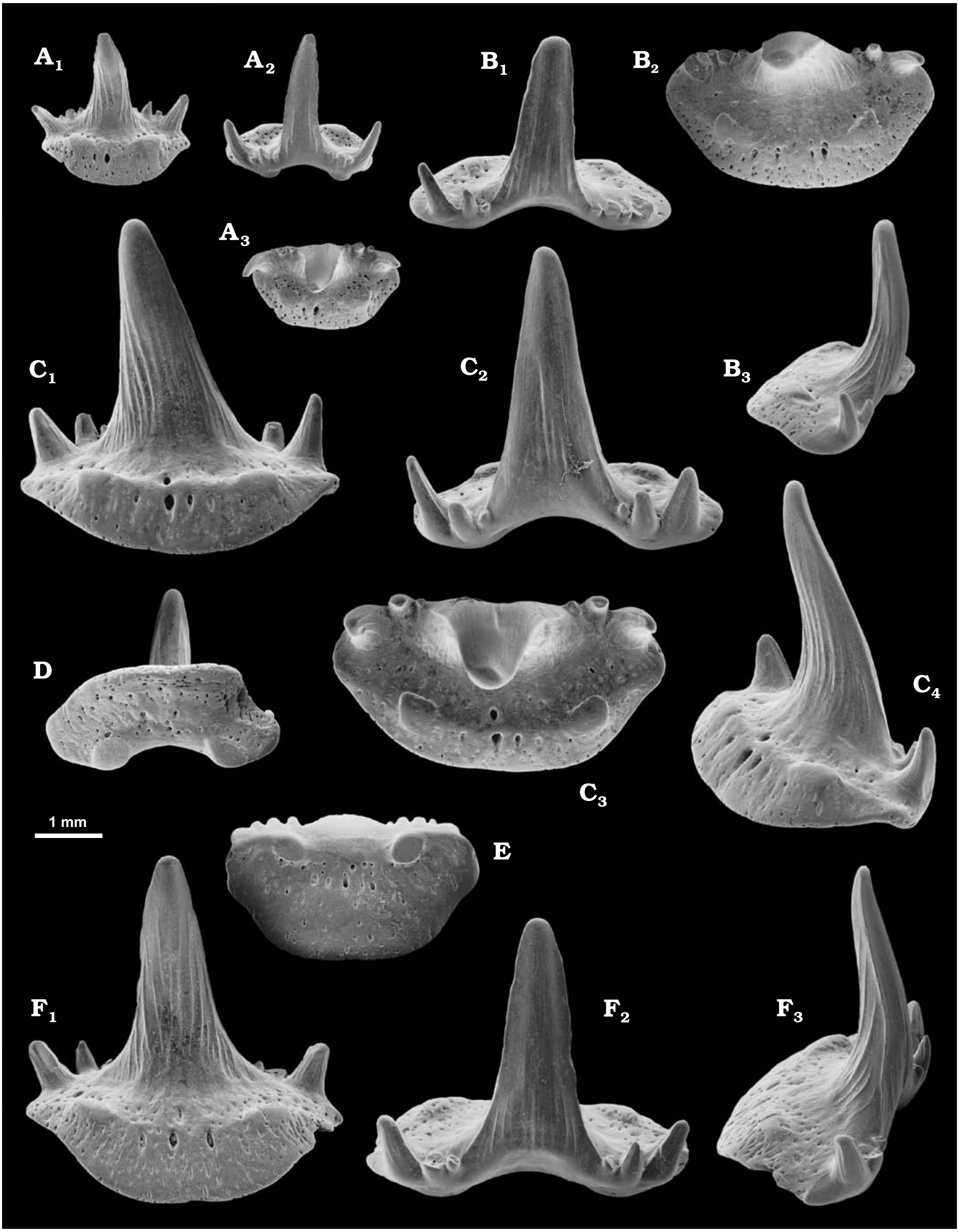
Specimens belonging to the same species were described by Nekrylov (1997) as "*Cladodus*" sp. and Keltsiyan (2002) as "*Symmorium*" sp. Material studied by these two authors includes about 200 unnumbered teeth in the collection of the Geography Department of the Lugansk Pedagogical University (Lugansk, Ukraine) from the Gurkovaya Ravine close to Kalinovo village, Popasnya District, Lugansk Region, Ukraine. The age of the fossil-bearing layer is regarded as limestone M_7^1, Formation C_2^7 according to the local Donetsk Basin stratigraphical scheme (corresponding to the Podolskian–Myachkovian Regional Stages of the Russian Platform General unified scheme), Moscovian, Middle Carboniferous (Nekrylov 1997; Keltsiyan 2002). Material from this collection was examined by one of the authors of the present paper (O. L.) and is currently under description by V. Keltsiyan (Lugansk, Ukraine).

Description.—This species of *Glikmanius* is characterised by small teeth with a relatively long and narrow median cusp and in most cases more than one, usually two to three, intermediate lateral cusplets on each side, smaller than the outermost ones. All the cusps in the crown are more in line than in *G. occidentalis*. The basolabial depression, projections, and rounded oral-lingual buttons are relatively weakly developed. The buttons are rather far from the lingual rim and can be connected by a thin and vague ridge. The part of the base lingual to the line connecting the buttons is folded downwards.

The level of heterodonty in this species is rather low. However, several differences, particularly between smaller and larger teeth in the collection, can be pointed out. The smaller teeth (2–4 mm in the mesio-distal dimension) often have more than two intermediate cusplets on each side (up to four; Fig. 3A); the larger ones (4–6 mm; Figs. 2C, 3C, F) have one or two such cusplets, and in the latter case the more lateral cusplet is the higher (Fig. 3C_2, C_3, F_2). There are specimens, usually of intermediate size (3–4 mm), which possess more cusplets on one side than on the other, e.g., two and three or three and four (Fig. 3B_2, E). Because the teeth are otherwise virtually symmetrical, it is impossible to say, whether the larger number of cusps is strictly side-related.

The ornamentation of the median cusp is typical of *Glikmanius*, with only a few vertical cristae in the lower half and a smooth upper part of the labial side, whereas the lingual side is covered with 12 and more cristae, almost reaching the tip (Fig. 3C_1, F_1).

There is a single specimen in the collection from the Peru site, in all aspects of form resembling typical teeth of *G. myachkovensis*, but much larger than the rest. It is broken, but when complete must have measured well above 1 cm across the base. We think that it belonged to a particularly large individual of the same species.


A1
A2
B1
B2
A3
C1
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D
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1 mm
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Comparisons.—The teeth of *G. myachkovensis* are considerably smaller than *G. occidentalis*, with a more slender, uniformly narrowing median cusp throughout its length, and usually with a larger number of intermediate cusplets which are more in line than in the other species. The basolabial depression is shallower in *G. myachkovensis*, the buttons are less prominent, situated further from the lingual rim, and often connected with a low ridge; the latter feature is rather rare in *G. occidentalis*. Also the sloping lingual part of the base is a diagnostic feature of *G. myachkovensis*.

Remarks.—This small form of *Glikmanius* was first noted by Ossian (1974) in the Peru site in Nebraska in his unpublished dissertation. He attributed an enormous number of such teeth (1325), which he found at Peru, to the upper dentition of *Cladodus occidentalis*. He also decided to include considerably different teeth (467), with three almost equal main cusps, in the same species, as representing its lower dentition. We consider the "upper teeth" to represent *G. myachkovensis* and the "lower teeth" as belonging to *Heslerodus divergens*. It is a tempting idea to treat *G. myachkovensis* and *H. divergens* teeth as coming from the same fish, because indeed there are several similarities, particularly in the structure of the base (two buttons and basolabial projections, and the median depression). However, there exist quite a few contradictory arguments. Firstly, the semi-articulated specimens of *H. divergens* described by Williams (1985, under the name of *Phoebodus heslerorum*) from the Pennsylvanian Black Shales of Indiana are associated with only one type of tooth. Secondly, teeth of *H. divergens* are, on average, smaller than those of *G. myachkovensis*. It is also notable that the number of *G. myachkovensis* teeth, collected by Ossian, is more than twice as large as that of *H. divergens*, and the numbers are so extreme, that this observation is evidently statistically significant. This ratio in the sample studied by us, housed at the Carnegie Museum, is less striking (28:19), but also in favour of *G. myachkovensis* teeth.

It is probable that a tooth from the Namurian of Bear Gulch in Montana, illustrated by Lund (1985: fig. 8A, B) as *Stethacanthus* sp., belongs to some species related to *G. myachkovensis* (see Fig. 1B for a similar tooth from the same locality). It has two intermediate cusplets on each side, and the other features are typical of *Glikmanius*. However, Lund's figure suggests that the more median cusplet is the larger, which is opposite to the situation observed in the teeth from Peru. The tooth from Montana is much larger than the average size of *G. myachkovensis* teeth (the width of the base reaches 1.5 cm), but does not exceed the size of the largest specimen from Peru. It also ought to be remembered that Lund's specimen was collected as a macrofossil and specimens from Peru come from processed conodont samples. The latter method usually reveals smaller teeth.

Some other teeth figured by Lund (1985: fig. 8) are also similar to *G. myachkovensis*, but their possible relationship is even less certain than in the case of that mentioned above. The large tooth in Lund (1985: fig. 8E) probably belongs to "*Cladodus*" *striatus* Agassiz, 1843.

Distribution.—Upper Carboniferous, Pennsylvanian of the Moscow Syneclise, Donetsk Basin, and Nebraska.

Discussion

There are several taxa, whose tooth morphology is close to *Glikmanius* gen. nov. Two of them, viz. *Heslerodus divergens* (Trautschold, 1879) (= *Phoebodus heslerorum* Williams, 1985) and "*Ctenacanthus*" *costellatus* Traquair, 1884, share general basal features with *Glikmanius*, such as the deep median depression, two pad-like basolabial projections and two prominent buttons, but their crowns are considerably different. *Heslerodus* has gentle, thin, phoebodont-like main cusps, with the central cusp only slightly larger than the laterals; that was the reason why Williams (1985) attributed it to the genus *Phoebodus*. In the holotype of "*C.*" *costellatus*, there is only one imperfect tooth (Traquair 1884: pl. 2: 6), but the second specimen, described by Moy-Thomas (1936; see Ginter 2002: figs. 4A, 5), provides much better material for comparison. Its teeth can have up to three pairs of lateral cusps, which can be observed in *Glikmanius myachkovensis*, but all the cusps are in line and very coarsely ornamented with cristae converging at various heights. Moreover, the teeth of "*C.*" *costellatus* and *Heslerodus* are much smaller, on average, than those of *Glikmanius*.

On the other hand, the size and the tooth-crown form are shared features of *Glikmanius occidentalis* and the Lower Carboniferous *Cladodus* sensu stricto (as noted above, the re-establishment of this genus is under way, Duffin and Ginter in press). In particular, the crown of *C. bellifer* (St. John and Worthen 1875: pl. 4: 10), with its large, gently striated central cusp, and intermediate cusplets moved labially off the line connecting the bases of the main cusps, resembles that of *Glikmanius*. However, in this case the basal articulation devices are different: in *Cladodus*, instead of two buttons there is a single, slightly curved ridge, and instead of two basolabial projections, there occurs a long, unbroken shelf or parapet.

There are two more cladodont genera which have a deep median basolabial depression in their teeth, two basolabial projections, and may or may not have two buttons. These are *Cladoselache* Dean, 1894, and *Squatinactis* Lund and Zangerl, 1974. Although their tooth-bases are superficially similar to those of *Glikmanius* teeth, examination reveals that the nature of the basolabial projections is different. The projections in *Cladoselache* (Ginter 2002: fig. 4B) and *Squatinactis*

← Fig. 3. *Glikmanius myachkovensis* (Lebedev, 2001) from the Onaga Formation, Pennsylvanian, of Peru, Nebraska, six of the specimens under common number CM 44549. **A**. CM 44549a in lingual (A_1), labial (A_2), and oral (A_3) views. **B**. CM 44549b in labial (B_1), oral (B_2), and lateral (B_3) views. **C**. CM 44549c in lingual (C_1), labial (C_2), oral (C_3), and lateral/lingual (C_4) views. **D**. CM 44549d in aboral/lingual view. **E**. CM 44549e in aboral view. **F**. CM 44549f in lingual (F_1), labial (F_2), and lateral (F_3) views.

(Lund 1988: fig. 1; MG, personal observations), as well as in "*Symmorium*" *glabrum* Ginter, 1999 (whose real generic assessment is yet undetermined), are simply specifically formed parts of the labial rim of the base; in contrast, such projections in *Glikmanius*, *Heslerodus*, and "*Ctenacanthus*" *costellatus* appear to be independent entities. This suggests that in the mentioned two groups of taxa the overall appearance of tooth-bases developed convergently.

Despite our belief that *Glikmanius* possessed ctenacanthiform spines, there is no direct evidence on that. Therefore, Glikman's (1964a, b) decision to assign *G. occidentalis* as *Ctenacanthus* appears to be premature. The type species of *Ctenacanthus*, *C. major* Agassiz, 1837, is based on a fin spine from the Lower Carboniferous Limestone of the British Isles. It is probable, considering the size of the spine, that one of the big tooth-based cladodont taxa from the same formation, such as *Cladodus mirabilis*, is conspecific with *C. major*. However, no such undoubted association, indicative of which particular tooth form it could be, has yet been found. Therefore, the only shark possessing true *Ctenacanthus* fin-spines (*sensu* Maisey 1981) and associated teeth is *C. compressus* Newberry, 1889 (= *C. clarki* Newberry, 1889; see Dean 1909, Williams 2001), from the late Famennian Cleveland Shale of Ohio. Its teeth, although definitely similar to those of *Cladodus* sensu stricto, are also distinctly different from those of *Glikmanius*, e.g., by lacking two buttons and two basolabial projections.

We temporarily refrain from defining a new family for *Glikmanius* sp. nov., because some more comparative work on presumably related genera must be done. However, the above discussion suggests that, of all mentioned taxa, such a family should also include *Heslerodus* and "*Ctenacanthus*" *costellatus*.

In this paper, we could confidently distinguish only two species of *Glikmanius* from the Permo-Carboniferous. However, future detailed studies, particularly on the material from the Serpukhovian of Montana and Moscow Syneclise, may show that more species deserve to be recognised. Several specimens, such as "*Cladodus girtyi*" (Hay 1900: fig. 2) and a part of "*Cladodus lamnoides*" teeth figured by Trautschold (1874: pl. 28: 3c–e), also differ in certain aspects from the classic model of *G. occidentalis*. It seems an irony that such a well known tooth form is known only from isolated teeth and never even a partial dentition was recorded. This makes an account of probable ontogenetic and position-related heterodonty, and distinguishing it from an inter-specific variation, virtually impossible.

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