Taxonomic notes on "*Phoebodus heslerorum*" and *Symmorium reniforme* (Chondrichthyes, Elasmobranchii).

MICHAŁ GINTER

Ginter, M. 2002. Taxonomic notes on "*Phoebodus heslerorum*" and *Symmorium reniforme* (Chondrichthyes, Elasmobranchii). *Acta Palaeontologica Polonica* 47 (3): 547–555.

The revision of shark teeth from the Pennsylvanian black shales of central USA, ascribed to "*Phoebodus heslerorum*" Williams, 1985 and *Symmorium reniforme* Cope, 1893, shows that "*Ph. heslerorum*" is a junior synonym of "*Cladodus*" *divergens* Trautschold, 1879. This species belongs neither to *Phoebodus* nor to *Cladodus*, so a new genus *Heslerodus* is proposed. Very common, robust cladodont teeth with a deep labio-basal depression and two buttons, often referred to as *S. reniforme*, do not belong to the latter species, but to "*Cladodus*" *occidentalis* Leidy, 1859. The generic affinity of "*C.*" *occidentalis* is yet undetermined, but it is possible that it represents ctenacanthoids.

Key words: Chondrichthyes, Palaeozoic, Carboniferous, teeth, taxonomy.

Michał Ginter [fiszbit@geo.uw.edu.pl], Instytut Geologii Podstawowej, Uniwersytet Warszawski, Żwirki i Wigury 93, PL-02-089 Warszawa, Poland.

Introduction

In his classic paper, Williams (1985) described or revised several species of cladodont sharks from the Pennsylvanian black shales of central USA, viz. *Symmorium reniforme*, *Stethacanthus altonensis*, *Denaea meccaensis*, and *Phoebodus heslerorum*. In all instances a certain tooth type was ascribed to a shark species, well defined by other features, such as skull and/or postcranial skeleton. For more than a decade Williams' assignments were used as a standard by palaeoichthyologists studying isolated shark remains. "*Symmorium*", "*Stethacanthus*" or "*Denaea*" were commonly identified in the shark teeth collections, and many used to refer *Phoebodus* to Ctenacanthoidea, because of Williams' decision, supported by Zangerl's (1981) Handbook.

My recent studies of original collections from USA and the information provided by Dr. A. Ivanov (St. Petersburg), showed that not all mentioned assignments are justified. The major taxonomic problems were presented in a poster at the IGCP 406 Meeting in Warsaw (Ginter 1998). Some of these problems, concerning "*Ph. heslerorum*" and *S. reniforme*, are discussed herein and a few solutions are proposed.

Repository institutions.—Field Museum of Natural History, Chicago, Illinois (collection acronyms PF and UF); Museum of Natural History, University of Kansas, Lawrence, Kansas (KUVP); Orton Museum, Ohio State University, Columbus, Ohio (OSU); Palaeontological Museum, Sankt-Petersburg University, St. Petersburg, Russia (LP, currently changed to MP); Natural History Museum, London, UK (NHM-P); Institute of Geology, Warsaw University, Warsaw, Poland (IGPUW); Institute of Zoology, Wrocław University, Wrocław, Poland (PCh).

Taxonomic status of *Phoebodus heslerorum* Williams, 1985

This species has one or two short, partially ornamented fin spines. Because of that, Williams (1985) decided to include his newly established species in Ctenacanthoidea. He referred to it as *Phoebodus* because of alleged resemblance between phoebodont and "*Ph. heslerorum*" teeth. This assignment resulted in including all the phoebodonts in the ctenacanthoids. However, the teeth of *Phoebodus* differ considerably from those of Williams' shark (see "Remarks" below). Thus, "*Ph. heslerorum*" may be a ctenacanthoid, but it is not a phoebodont, and the relationship between phoebodonts and ctenacanthoids is still open to speculation. Moreover, the specific epithet, *heslerorum*, appears to be a junior synonym of "*Cladodus*" *divergens* Trautschold, 1879. *Cladodus* is probably a *nomen dubium* (Zangerl 1973: 6; Chorn and Whetstone 1978), but even if it is a valid name, the teeth of *C. mirabilis* Agassiz, the type species of *Cladodus*, are strongly different (C. Duffin personal communication 1998). Thus, in any case, "*C.*" *divergens* needs a new generic name. The diagnosis of the new genus, *Heslerodus*, the review of records of *H. divergens* (= "*Ph. heslerorum*"), and the redescription of its teeth are presented below.

Cohort Euselachii Hay, 1902
Incertae ordinis
Superfamily Ctenacanthoidea Zangerl, 1981
Incertae familiae
Genus *Heslerodus* gen. nov.

Type species: *Cladodus divergens* Trautschold, 1879.

Etymology.—In order to retain the names of Mr. and Mrs. Bennie Hesler in the scientific nomenclature, in spite of the taxonomic revision of "*Phoebodus heslerorum*". Mr. and Mrs. Hesler "kindly permitted the Field Museum's fossil quarrying operation on their farm near Rockville, Indiana" (Williams 1985: 125).

Diagnosis.— As for the type and only species.

Heslerodus divergens (Trautschold, 1879)

Figs. 1A–C, 2A–G.

Cladodus divergens Trautschold; Trautschold 1879: 51, pl. 6: 11.
Phoebodus sp.; Case 1973: fig. 47.
Phoebodus n. sp.; Zangerl 1981: figs. 56–58.
"*Cladodus*" sp.; Schultze 1985: fig. 3.5.
Phoebodus heslerorum sp. n.; Williams 1985: 124–131, figs. 22–23, pls. 16, 17.
"*Cladodus*" *divergens* Trautschold; Ivanov 1999: 276–277, fig. 3, pl. 7: 1.

Holotype: The largest and most complete of three specimens (herein designated as a, b, c) catalogued under the same museum number PCh/617 at the Institute of Zoology, Wrocław University, Wrocław, Poland (Fig. 1A). The specimen was described and figured by Trautschold (1879: 51, pl. 6: 11).

Type locality and horizon: Moscow Region, Myachkovo, Upper Carboniferous, Upper Moscovian, Myachkovian Regional Stage.

Original diagnosis (translated from Trautschold 1879).—In the limestone from Mjatschkowo there occur small teeth of *Cladodus* which totally differ from the others; the median cusp is not as large as in usually found *Cladodus* teeth and the lateral cusps are curved sidewards. The figured specimen is a typical representative of this species. Both lateral cusps are almost as high as the median cusp and strongly diverge sidewards; the smaller intermediate cusplets are also divergent, but less than the lateral cusps, and the main median cusp runs straight upwards with a slight lingual bend.

Emended diagnosis.—Sharks bearing teeth whose crown is composed of three long, recurved main cusps, and usually two intermediate, smaller cusplets. The median cusp is slightly larger than the lateral main cusps or equal to them in size. The lateral cusps are sigmoidal and strongly divergent mesio-distally, at about 80–90 degrees between each other. The base is rounded, with a distinct labial concavity and usually two buttons on the apical side of the lingual torus.

Description.—Thus far *Heslerodus divergens* was found from seven regions in the world and these records will be mentioned here in a following order: the type material from Myachkovo, Moscow Region (Trautschold 1879); the type material of "*Phoebodus heslerorum*" from Indiana (Williams 1985); teeth from Peru, Nebraska (Case 1973; Ossian 1974); from Ohio and Pennsylvania (Hansen 1986); from Kansas (Schultze 1985) and from boreholes in Moscow Region and Pechora Sea (Ivanov 1999). A new specimen from Haystack Range in Wyoming (C. Sandberg's coll.) will also be described.

The type material of *H. divergens* from Myachkovo consists of three black, five-cusped teeth, embedded in small pieces of white limestone. Only labial views of the teeth are visible. The largest tooth (Fig. 1A; the holotype, illustrated and described by Trautschold 1879) has all five cusps preserved almost to the tips and covered with shiny enameloid. The lateral main cusps reach about 3/4 of the length of the median cusp which is also a little thicker. The lateral cusps curve mesio-distally: the angle between their proximal parts is about 80 degrees, but closer to the tips it almost reaches 90 degrees. The main cusps seem to have primary and secondary ornamentation. On each cusp there are two strong cristae joining distally, before reaching the tips, and a few (2–4) gentle, subparallel striae. The striae, however, can be only cracks on the enameloid. The intermediate cusplets are very thin and almost smooth. They reach about 2/3 of the length of the lateral cusps. There is a distinct depression in the labial side of the base, below the median cusp. The wavy outline of the base on each side of the depression suggests the presence of two symmetrically placed labio-basal projections. The width of the base is about 3.5 mm.

The second tooth (Fig. 1B) is slightly smaller, it lacks the intermediate cusplet on the left side and the tip of the median cusp is abraded stronger than in the holotype. Remains of two cristae are visible on the right intermediate cusplet. The angle between the lateral cusps is unusually small compared to the holotype (about 45–50 degrees). The median cusp of the third tooth (Fig. 1C) is also worn, so it looks as if it was of equal length to the lateral cusps. However, it is evidently thicker which suggests that it must have been longer as well. Both intermediate cusplets are partially preserved and the angle between the main lateral cusps is about 60 degrees. The primary cristation and the labio-basal depression are visible in both the second and the third tooth.

Locality and stratigraphic position: Myachkovo, Moscow Region; Upper Carboniferous, Upper Moscovian, Myachkovian Regional Stage.

The type material of "*Ph. heslerorum*" from Indiana consists of teeth, fin spines, scales, and partially articulated endoskeletons, including braincases and jaws. It was described in detail by Williams (1985), so only the teeth will be reviewed here. Four well prepared teeth were illustrated (PF 8180, 8322, 2440, 8242; Williams 1985: pl. 16: 1–4, 7, 8), in addition to several scattered around the palatoquadrate, hidden in the black shale and visible only on an X-ray photograph (PF 8212; Williams 1985: pl. 16: 10). Three teeth (PF 8180, 8322, 8242) are displayed in labial and/or basal views. All of them possess a distinct labio-basal depression, framed by two rounded projections of moderate size. The median cusp is slightly larger than the main lateral cusps, which form an angle of about 80 degrees between each other. The intermediate cusplets are relatively as long as in the holotype of *H. divergens*, and in PF 8242 they seem to be even longer. The ornamentation of the labial face of the main cusps consists of subparallel cristae (from 4 in PF 8242 up to 8 in PF 8322) and some of them apparently reach the tips. PF 2440 is figured in lingual view, and two lateral cusps and the occlusal side of the base are visible. The cusps are evidently

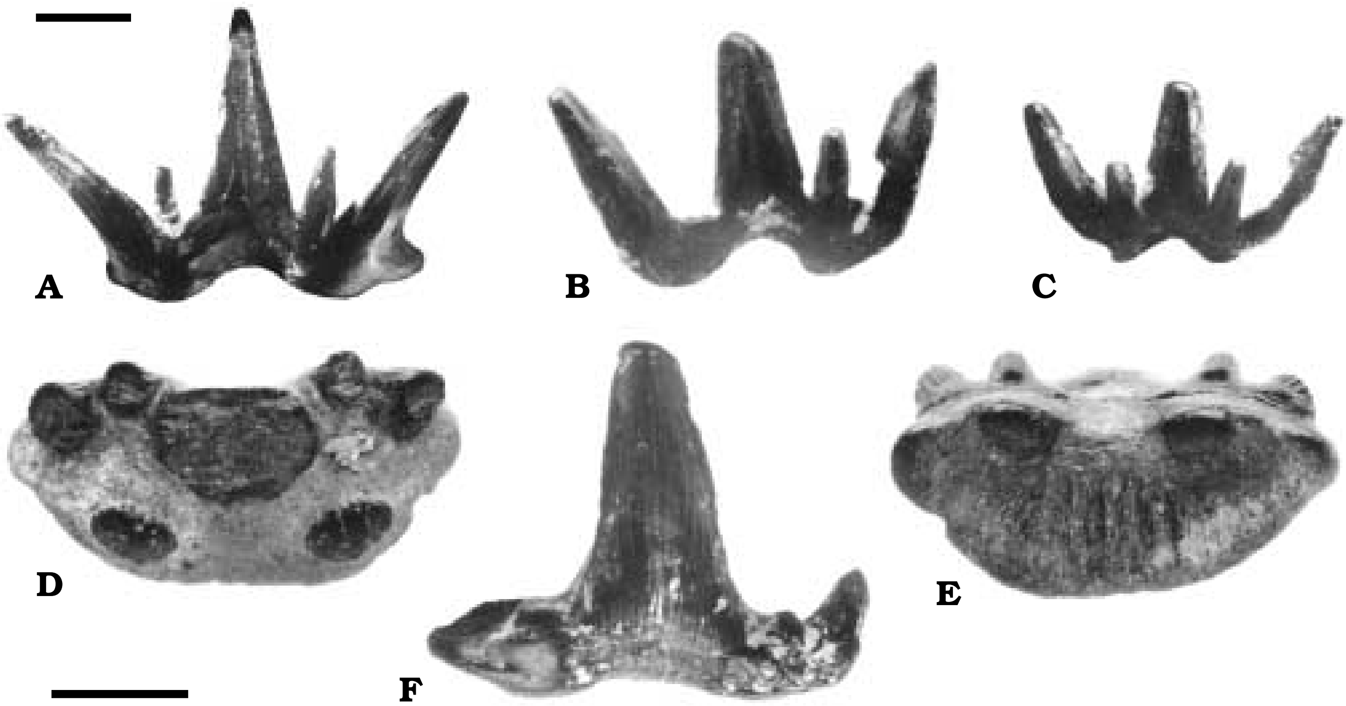

Fig. 1. Shark teeth from Myachkovo, Moscow Region, Russia, Upper Carboniferous, Upper Moscovian. **A**–**C**. *Heslerodus divergens* (Trautschold, 1879). **A**. Holotype PCh/617a. **B**, **C**. Associated specimens PCh/617b, c (respectively), all in labial views. Scale bar 1 mm. **D**–**F**. "*Cladodus*" *occidentalis* Leidy, 1859 (= "*C*." *lamnoides* sensu Trautschold 1874). **D**, **E**. PCh/425a, occlusal and basal views. **F**. PCh/425b, labial view. Scale bar 5 mm.

sigmoidal, their lingual faces seem to be almost smooth, and two separate buttons occur on the lingual torus, rather close to the lingual rim. Currently, after further preparation, it appeared that PF 2440 belongs to a tooth-file with two more teeth lying behind (M.G. personal observation 1997).

The X-rayed teeth (PF 8212) are characterised by approximately the same size ratio between the cusps as the above described specimens and by strongly divergent lateral cusps. It is possible that two symmetrically placed white spots in the basal area (Williams 1985: pl. 16: 10, central left) represent labio-basal projections.

There are also a few teeth of *H. divergens* on a slab with a spine (PF 8183). They stick out from the rock at different extent. The best visible tooth (Williams 1985: pl. 17: 2, upper left) probably shows its lingual side, but the lingual torus of the base is missing. The position and relative size of the cusps is typical of this species.

Locality and stratigraphic position of illustrated teeth: Hesler, Mecca, and Logan Quarries, Parke County, Indiana; Upper Carboniferous, Desmoinesian (Moscovian), Linton and Staunton Formations. For other details see Williams (1985).

Teeth from Peru, Nebraska, were illustrated by Case (1973: fig. 47, as *Phoebodus* sp.) and Ossian (1974: pl. 3: 4–6, a tooth from a collection of 476 specimens, as *Cladodus occidentalis*). The teeth are almost identical, fairly well preserved, only the tips of the main cusps and distal halves of intermediate cusplets are missing. The angle between the lateral cusps, which are slightly sigmoidal, exceeds 80 degrees, typical of the species. The median cusp is slightly thicker and probably was slightly higher than the lateral cusps before having lost the tip. Since only photocopies of photographs of these teeth are at my disposition, I cannot say much about the ornamentation of the cusps. However, on the labial face of the median cusp two strong cristae are visible, probably joining before the tip (Case 1973: fig. 47, labial view).

The base is semicircular to slightly triangular, the labio-basal depression and two rounded labio-basal projections are well developed. The buttons on the occlusal side are closely spaced.

Locality and stratigraphic position: Peru, Nebraska; Upper Carboniferous, Onaga Formation, Indian Cave Sandstone.

Teeth from Ohio and Pennsylvania (two five-cusped specimens, OSU 35438–35439) were recorded by Hansen (1986, as *Ph. heslerorum*). The teeth are strongly abraded and only basal parts of the cusps are preserved. However, two lingually placed buttons on a semicircular to triangular lingual torus, corresponding to them two rounded labio-basal projections, and a labio-basal depression ("median sulcus" sensu Hansen 1986) are clearly visible. The diameter of the subcircular proximal part of the median cusp is only slightly larger than those of the lateral main cusps. During my visit to Columbus, Ohio, in 1997, I managed to find two more, similar teeth in the unnumbered part of Hansen's collection (Fig. 2F, G, new numbers: OSU 50490 and 50491). Their overall appearance and state of preservation resemble those of the other *H. divergens* teeth from Ohio. It can be added to the

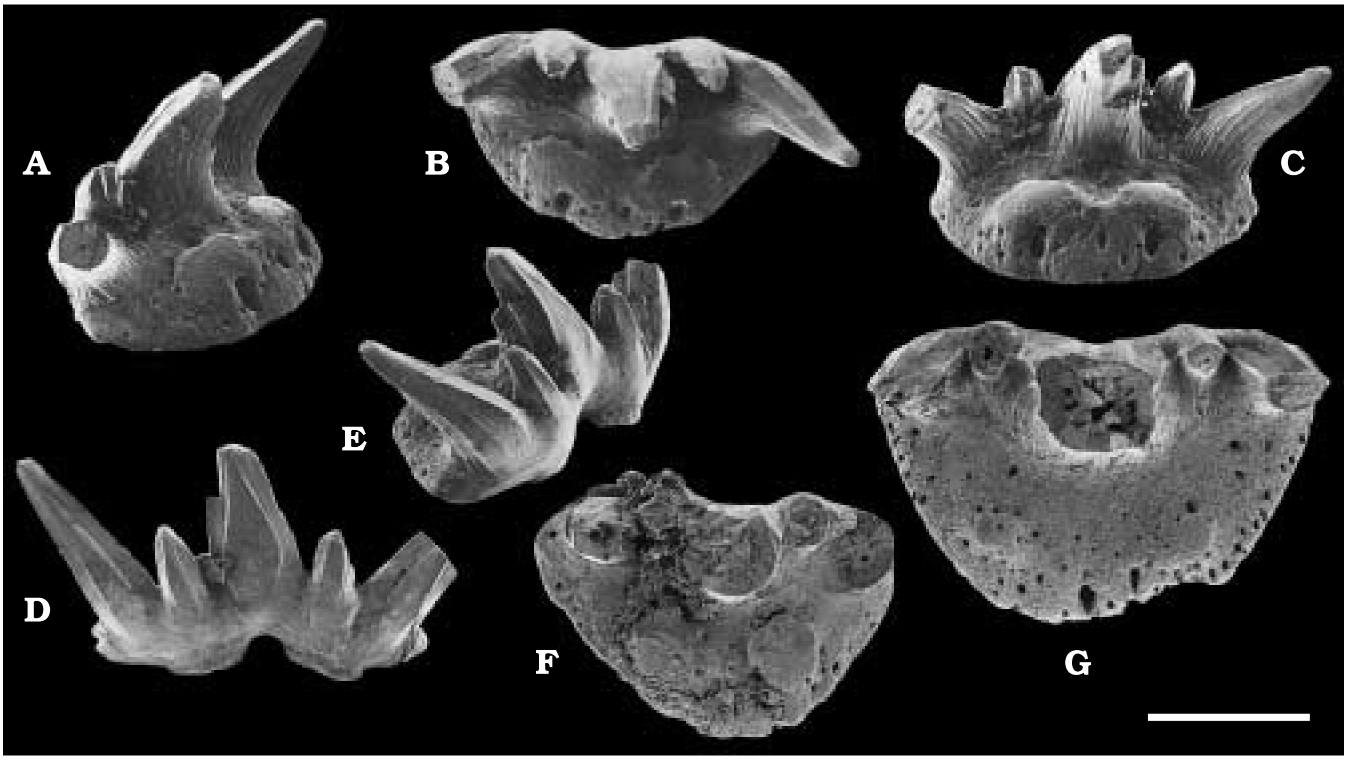

Fig. 2. *Heslerodus divergens* (Trautschold, 1879). **A**–**E**. Specimen IGPUW/Ps/6/1 from sample BAH-4, Steeple Pasture, Haystack Range, Wyoming, Upper Carboniferous, Morrowan, in lingual-lateral, occlusal, lingual, labial, and labial-lateral views. **F**–**G**. Specimens OSU 50490 and 50491 from Gwi-3 and At-64 localities, Ohio, Upper Carboniferous, Conemaugh Group, Ames Limestone, in occlusal views. Scale bar 1 mm.

characteristics given above that the ornamentation of the labial face of the cusps consists of only a few (3–4) strong cristae, whereas the lingual face is covered by numerous (up to 20? on the median cusp), very gentle cristae.

Localities and stratigraphic position: PA-1, rip-rap blocks (now removed) on east side of Pennsylvania Rte. 286, Allegheny County, Pennsylvania; Gwi-3, exposure on north side of Interstate 70, Guernsey County, Wills Township, Ohio; At-64, exposure along Trimble Township Road 345 to hill top at Athens-Morgan County line, Ohio; Ld-1, quarries of Marquette Cement Company, Lawrence County, Decatur Township, Ohio. Upper Carboniferous; PA-1, Gwi-3, and At-64, Conemaugh Group, Ames limestone; Ld-1, Allegheny Group, Vanport limestone. Hansen (1986) also notes one tooth of this type (OSU 35440) from the Wewoka Formation, Oklahoma. For details see Hansen (1986).

A tooth from the Permian of Kansas (KUVP 82667; Schultze 1985: fig. 3.5, "*Cladodus*" sp.) has the lingual part of the base damaged, but the two distinct, rounded, widely separated buttons are preserved. The crown is fairly complete. It consists of three large main cusps, almost equal in size, and two much thinner intermediate cusplets. All the cusps lack their tips. The lateral main cusps are strongly divergent. The ornamentation of the cusps is well preserved, it is composed (as in the case of the specimens from Ohio) of few strong cristae on the labial and numerous delicate cristae on the lingual face. One stronger crista runs along the lateral edges of each cusp. The cristae on the lingual face of the median cusp form a peculiar pattern. They start close to the midline and run laterally, leaving the middle part of the cusp unornamented.

Locality and stratigraphic position: KS Highway 13 roadcut, Pottawatomie County, Kansas; Lower Permian, uppermost Threemile Limestone. For details see Schultze (1985).

Teeth from boreholes in Moscow Region (Ivanov 1999: fig. 3D, E, "*Cladodus*" *divergens*) are largely damaged. Their state of preservation resembles that of the specimens from Ohio. Drawings of only two of five teeth are available. The presence of two buttons and labio-basal projections is evident, but the labio-basal depression is only slightly marked. One of the specimens (Ivanov 1999: fig. 3D) has the buttons, as well as the labio basal projections, widely separated, in the other (Ivanov 1999: fig. 3E) the buttons apparently touch each other and the labial projections are closely spaced.

Locality and stratigraphic position: Mytischi 15 and 17, Afonas'evo 9, and Vodniki V2/3 boreholes, Moscow Region; Upper Carboniferous, Kasimovian.

A tooth from Pechora Sea, figured by Ivanov (1999: fig. 3A, pl. 7: 1; LP 6-61, "*Cladodus*" *divergens*), differs from all the above mentioned teeth by the lack of intermediate cusplets in the crown, rounded labio-basal projections, and two separate buttons on the lingual torus. There is only one, rather flat button, surrounded by about seven foramina. However, the labio-basal depression is present, the cusps are almost equal to each other and the main lateral cusps diverge sidewards at about 40 degrees towards the median cusp. These characters show that the specific identification made by Ivanov (1999) was apparently correct.

Locality and stratigraphic position: borehole Gulyayevskaya, Pechora Sea (Russian Arctic); Upper Carboniferous, Gzhelian or Lower Permian, Lower Asselian.

A tooth from Wyoming, IGPUW/Ps/6/1, collected by C.A. Sandberg (US Geological Survey, Denver) is a typical representative of the species (Fig. 2A–E). The base seems to be almost complete, perhaps only slightly lingually abraded. One of the lateral main cusps is preserved from the base to the tip, the distal half of the other and about 1/3 of the median cusp is broken. The intermediate cusplets lack their tips. The angle between the proximal parts of the lateral cusps is about 80 degrees; the angle between the distal parts probably could reach 90 degrees. The median cusp is thicker, and probably originally it was longer than the lateral cusps. The completely preserved lateral main cusp is sigmoidal. All the cusps bear two strong cristae on their labial faces. The cristae apparently anastomose far below the tip of the median cusp, but on the lateral cusps they run separately almost to the tip. The lingual face of the crown is covered by numerous gentle cristae. In the proximal part of the cusps short intercalating cristae occur. As in the specimen from Kansas a smooth, unornamented area is left in the middle of the lingual face of the median cusp. A blade-like crista runs along the lateral edges of all the cusps. The labio-basal depression and two rounded projections are present. The buttons on the occlusal side of the lingual torus are separate, but rather close to each other. Two major lingual nutritive foramina open below each button. This feature was also noted from the Oklahoma specimen by Hansen (1986). Another, also lingually facing opening of moderate size is placed between the buttons.

Locality and stratigraphic position: sample BAH-4, Steeple Pasture, Haystack Range, Wyoming; Upper Carboniferous, Morrowan (Bashkirian), *Idiognathodus sinuosis* conodont Zone.

The above presented review shows that the morphology of hitherto found teeth of *Heslerodus divergens* is rather uniform, with only a few exceptions, and that they are characterised by the following features:

– *the base* outline is semicircular to triangular with rounded angles;
– a labio-basal depression ("median sulcus"), with a rounded labio-basal projection on each side, occurs below the median cusp;
– in most cases two distinct, rounded buttons (articular bosses), corresponding to the labio-basal projections, are present on the occlusal ("upper") side of the lingual torus; the buttons can be widely separated to closely spaced, very rarely they can be fused, forming a single boss;
– the main upper nutritive foramina can perforate the lingual side of the buttons and/or a single, medially placed lingual foramen can occur;
– the crown consists of three recurved main cusps and two intermediate cusplets; very rarely the intermediate cusplets can be absent;
– the median cusp is usually slightly larger than the main lateral cusps;
– the lateral main cusps are sigmoidal; the angle between their proximal (basal) parts is about 80 degrees, but the angle between their distal parts can reach 90 degrees;
– the cusps are rounded proximally and slightly labio-lingually compressed distally;
– the ornamentation of the labial side of the cusps is usually composed of only two strong cristae which, on the median cusp, join before reaching the tip; however, several secondary, less distinct cristae can also occur;
– the lingual face of the cusps is covered with numerous very gentle cristae; at the basal part additional, short, intercalating cristae can occur; the middle part of the median cusp is smooth;
– a low, blade-like crista, runs along the lateral edges of all the cusps.

Remarks.—The overall appearance of *H. divergens*, and especially the crown, is similar to that of Famennian phoebodonts, such as *Phoebodus politus* Newberry, 1899 or *Ph. turnerae* Ginter and Ivanov, 1992. That was the reason why Williams (1985) referred to his specimens from Indiana as *Phoebodus heslerorum*. However, all the species of *Phoebodus*, including the type species *Ph. sophiae* St. John and Worthen, 1875, are characterised by a single, arcuate labio-basal projection and a single button on the upper side of the lingual torus. No trace of a labio-basal depression has been recorded. Moreover, the median cusp in the phoebodonts is always equal to or lower than the lateral cusps, whereas in almost all known specimens of *H. divergens* the median cusp is slightly larger. The latter feature was pointed out independently by Trautschold (1879) and by Williams (1985: 127).

The presence of two buttons, two labio-basal projections and the "median sulcus" suggests the relationship between *H. divergens* and "*Cladodus*" *occidentalis* Leidy, 1859. Ossian (1974) proposed that these two tooth forms can occur in one individual as lower and upper jaw teeth, respectively. The discovery of partially articulated specimens of *H. divergens* in Pennsylvanian black shales (Williams 1985), with only *Heslerodus*-like teeth dispersed around the jaw cartilages, proved Ossian's idea improbable. Teeth of several other Late Devonian through Early Permian sharks, probably representing different groups, display similar features, particularly the occurrence of a labio-basal depression. Such teeth will be considered below, in the section dedicated to *Symmorium reniforme*.

Stratigraphic range.—Late Carboniferous (Bashkirian–Gzhelian), probably through the Lower Permian (Asselian).

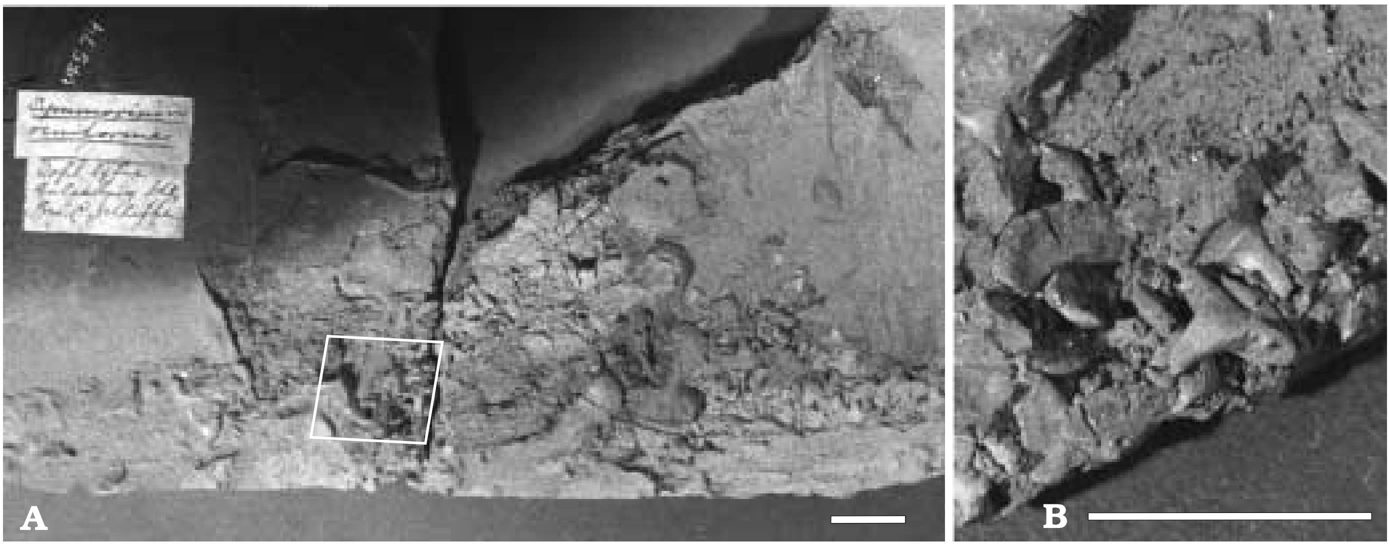

Fig. 3. *Symmorium reniforme* Cope, 1893, holotype, UF 574 (FMNH), from the vicinity of Galesburg, Knoxville County, Illinois, Upper Carboniferous, Desmoinesian. **A**. Anterior part of the specimen (corresponding to the right side in Williams 1985: text-fig. 16). **B**. Close-up of a group of teeth situated in the marked area. Scale bars 20 mm.

Taxonomic status of *Symmorium reniforme* Cope, 1893

The redescription of *S. reniforme* made by Williams (1985: 103–116) was based on three types of specimens, all from Pennsylvanian black shales:

1. The holotype of *S. reniforme* (UF 574), illustrated by Cope (1894, *fide* Williams 1985: text-fig. 16), comprising disarticulated fragments of the anterior part of the body, together with a few tens of well preserved teeth, grouped around the jaws (Fig. 3). The teeth are quite large, their base measures 1–1.2 mm mesio-distally. It is kidney-shaped with a shallow and wide labial depression. There is a long, low, crescentic ridge close to the lingual rim on the upper side of the base, and corresponding to it a shallow, curved basal concavity. No labio-basal projection is present. The crown is composed of five cusps, the median cusp much larger than the others. It occupies about 1/3 of the base width. As described by Cope (1894) "The principal cusp is about as high as the base is long. It is flattened anteriorly (= labially), and very convex posteriorly (= lingually), and is curved backward. The anterior surface is finely striate, and the posterior face is more strongly and sharply striate with close and fine ridges. The two faces are separated by a cutting edge."

2. Several partially articulated skeletons, most of which are available for observation only with the use of X-ray photography (Williams 1985: text-figs. 13–15, 17–20) or preserved as natural moulds and photographed from casts (Williams 1985: frontispiece illustration, pl. 6: 3, 4, pl. 7: 14–17). Sketches of a few small teeth scattered around the jaws are visible on several tracings from radiographs. In one of the casts (PF 2202) a few teeth are preserved almost *in situ*. Without the access to original radiographs it is difficult to determine the characters of the teeth from this group. However, all of them are apparently smaller than the teeth of the holotype (see Williams 1985: Appendix 5), and most have much narrower median cusps and relatively more prominent lateral cusps (except for PF 7366, Williams 1985, text-fig. 15B, the teeth of which are the closest to the type).

3. Large isolated teeth which Williams (1985: 107, pl. 7: 1–13) tentatively identified as representing "larger specimens of *Symmorium reniforme* or a new, as yet unrecognized species". The crown, and especially the form of the median cusp, is very similar to that of the holotype (compare Figs. 1F and 3B). The base is also broad and kidney-shaped, but instead of a low lingual ridge it possesses two distinct, rounded to oval, widely separated buttons (Fig. 1D). The labio-basal depression is deeper and it is framed by two rounded labio-basal projections (Fig. 1E). Because of such a form of the labio-basal rim, the intermediate cusplets are not in line with the median and outer lateral cusps (as is the case in the holotype), but are slightly displaced labially. Thus, "a line drawn connecting the centers of the cusps would describe a broad, low 'W'" (Williams 1985; compare Fig. 1D). These teeth are much larger than all the other ascribed to *S. reniforme*. The width of the base in all figured specimens exceeds 1 cm and often reaches 3 cm (PF 8248, 8232, 8201, 8252). The only smaller tooth (PF 2415, Williams 1985: pl. 7: 1) seems to be considerably different and probably belongs to a stethacanthid.

It is clear that these three groups of cladodont teeth differ from each other. Williams (1985) carefully noted the differences, but nevertheless he decided, with some reservations, that all the above mentioned specimens are conspecific and in figure captions he presented them simply as *Symmorium reniforme*. It is possible that the holotype is indeed a larger specimen, conspecific with the specimens known from casts and radiographs. This cannot be accepted or rejected without a thorough revision of all the available material. However, it is obvious that the differences between the isolated teeth and those of the type are sufficient for the distinction on the specific, or perhaps even, the generic level. Moreover, such teeth (large cladodonts with two buttons), were illustrated and named long before Cope described *S. reniforme*. Leidy (1859, figured in 1873: pl. 17: 4–6) introduced for them the name *Cladodus occidentalis*. The specific name *occidentalis* has priority, but the question about the generic name still remains unresolved. There are several possibilities:

– "*C.*" *occidentalis* retains the name *Cladodus*; this depends on the results of the revision of shark teeth from the type locality for *C. mirabilis*, the type species of *Cladodus*, which is currently in progress (C. Duffin personal communication 1998);
– "*C.*" *occidentalis* is a species of *Symmorium* and should be referred to as *S. occidentalis*; this concept was presented by Lebedev (1996: 394);
– "*C.*" *occidentalis* belongs to some other genus of cladodont sharks.

Because of its size, robustness, and very characteristic features, "*C.*" *occidentalis* is one of the best known Palaeozoic shark tooth forms. It was recorded, under several different names, from the Carboniferous and Lower Permian of various regions of USA (e.g., Newberry and Worthen 1866, as "*C.*" *mortifer*), Russia (e.g., Moscow Region, Trautschold 1874, as "*C.*" *lamnoides*; Glikman 1964: pl. 3: 10–12, as *Ctenacanthus occidentalis*), and elsewhere. More recently, after Williams' (1985) publication, such teeth were reckoned to belong to *Symmorium* (Zidek 1992, *S. reniforme*; Lebedev 1996, *S. occidentalis*). Mapes and Hansen (1984), in their paper on the shark-cephalopod predation, illustrated "*C.*" *occidentalis* teeth under the name of *S. reniforme*. Consequently, several other isolated Palaeozoic cladodont tooth types, different from "*C.*" *occidentalis*, but possessing a deep labio-basal depression and two buttons were also referred to as *Symmorium* (e.g., Long 1990, *Symmorium* sp. from the upper Famennian of Thailand; Ginter 1995, *S.* aff. *reniforme* from the upper Famennian of Poland; Ivanov 1996, *Symmorium* sp. from the Tournaisian of the South Urals). From the time I have seen the type material of *S. reniforme* in Chicago I decided for a temporary use of the name "*Symmorium*" (in inverted commas) for such teeth (e.g., "*S.*" *glabrum* Ginter, 1999), until the problem is finally solved.

However, it does not mean, even if the generic name of "*C.*" *occidentalis* is determined, that all similarly looking teeth belong to the same genus, or even to the same order. In a tooth-file, the deep labio-basal depression embraces the lingual-basal part of the median cusp of an older, more labially situated tooth. Thus, the presence of the depression seems to be an effect of a tendency to make a tooth family more compact and the connection between the teeth more tight. The development of two labio-basal projections and two buttons is a secondary result of this process. There are quite a few sharks

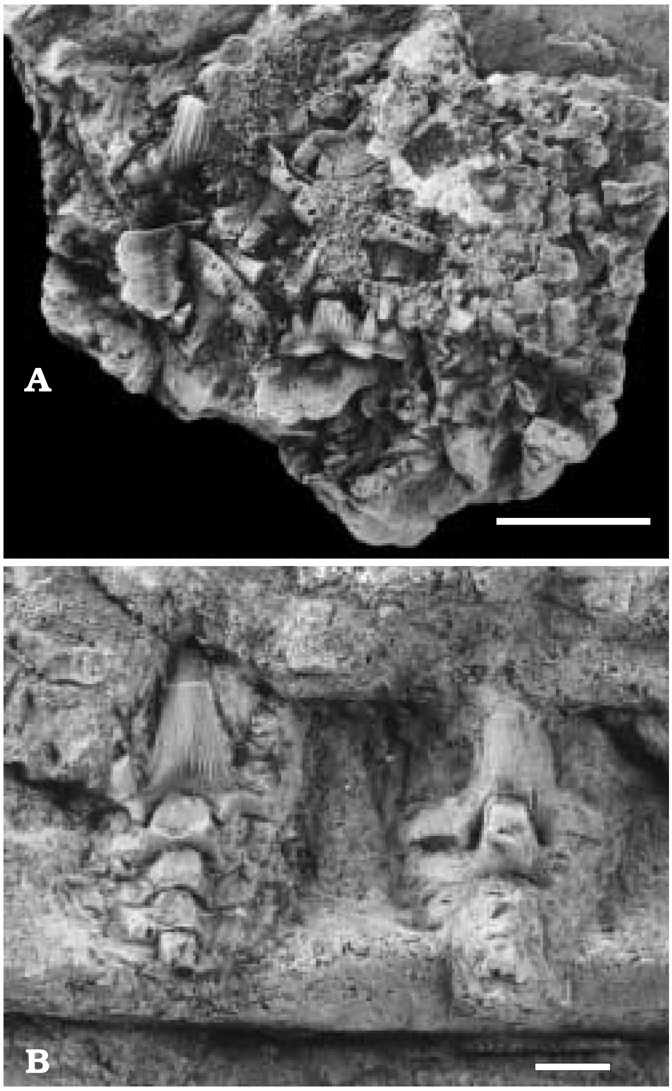

Fig. 4. **A**. "*Ctenacanthus*" *costellatus* Traquair, 1884, fragment of specimen NHM-P 20144-5 from Eskdale, Dumphrieshire, Scotland, Lower Carboniferous; a group of teeth. **B**. *Cladoselache clarki* (Claypole, 1893), fragment of specimen NHM-P 9272 from Berea, Ohio, late Famennian, Cleveland Shale; two tooth families in occlusal-labial views. Scale bars 5 mm. Coated with ammonium chloride for better contrast.

known to have teeth with a labio-basal depression and a single, undivided button of various shapes and distinctness (e.g., "*Cladodus*" *vanhornei*, St. John and Worthen 1875: pl. 4: 5; "*Symmorium*" sp. A, Ginter et al. 2002: pl. 7B). Moreover, teeth with a labio-basal depression occur in such different sharks like *Cladoselache* (Fig. 4B; Williams 2001: fig. 16, lower left), *Heslerodus* gen. nov., and "*Ctenacanthus*" *costellatus* (specimen NHM-P 20144-5; Figs. 4A, 5), so it seems that this feature was attained independently in different elasmobranch groups.

In spite of that, an attempt to distinguish different kinds of labio-basally depressed teeth, perhaps reflecting phylogenetic differences, can be made. The labio-basal projections in *Cladoselache* (Fig. 4B), "*Symmorium*" *glabrum* (e. g. Ginter

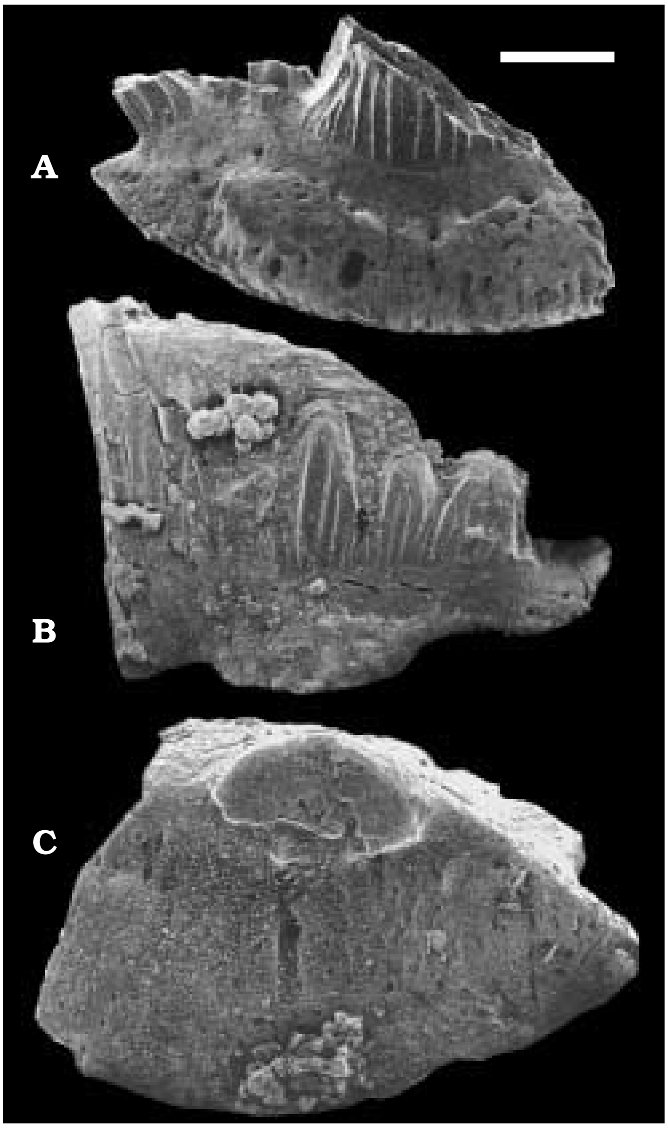

Fig. 5. "*Ctenacanthus*" *costellatus* Traquair, 1884, isolated, incomplete teeth from specimen NHM-P 20144-5 from Eskdale, Dumphrieshire, Scotland, Lower Carboniferous. **A**. Lingual view of a five-cusped tooth, the cusps and the right side of the base are missing. **B**, **C**. A half of a seven-cusped tooth in labial and basal views; the lingual side is embedded in rock. Scale bar 1 mm. SEM micrographs.

and Ivanov 1996: figs. 5E, G), and "*Symmorium*" sp. *sensu* Ivanov (1996: fig. 5A–C, E, G) are rather thin, more triangular than rounded, and sharply sticking labially, whereas in "*C.*" *occidentalis* (Fig. 1E; see especially Glikman 1964: pl. 3: 11) and "*Ct.*" *costellatus* (Fig. 5B, C) they are semi-oval to oval in basal view, and project basally. The cladoselachian-type projections are simply specifically formed parts of the labial rim of the base; in contrast, such projections in "*C.*" *occidentalis* appear to be independent entities.

It seems that teeth of *Heslerodus* gen. nov. would also represent the second type (see Case 1973: fig. 47; Ossian 1974: pl. 3: 6). Since both "*Ct.*" *costellatus* and *H. divergens* are supposed to belong to Ctenacanthoidea (Zangerl 1981), this can suggest that "*C.*" *occidentalis* is also related to this group. On the other hand, the superfamily Ctenacanthoidea lacks any unique apomorphic features. It includes those phalacanthous (fin spines-bearing) Palaeozoic sharks which have not been placed elsewhere (e.g., within hybodonts or neoselachians), and it is clear that nothing like a common "ctenacanthoid tooth morphotype" can currently be defined. Ctenacanthoid sharks with similar spines can have different teeth (although usually of a cladodont design, compare "*Ct.*" *costellatus*, Fig. 4A, and *Ct. compressus* sensu Williams 2001: figs. 6, 8, 10), so the possible ctenacanthoid relationship of "*C.*" *occidentalis* will not be proven based on teeth alone. Moreover, even if it should be shown to have fin spines, this would not resolve the phylogenetic position of the species, unless the spine has some derived features, suggesting a relationship with a particular group of phalacanths.

Conclusions

- *Phoebodus heslerorum* Williams, 1985 is a junior synonym of "*Cladodus*" *divergens* Trautschold, 1879. This species belongs neither to *Phoebodus* nor to *Cladodus*, even if the latter is a valid generic name, so a new genus, *Heslerodus* gen. nov., is proposed. The species should be referred to as *Heslerodus divergens* (Trautschold, 1879).
- Isolated cladodont teeth with two buttons, ascribed by Williams (1985) to *Symmorium reniforme* Cope, 1893, do not belong to the latter species, but to "*Cladodus*" *occidentalis* Leidy, 1859. The generic affinity of "*C.*" *occidentalis* is thus far undetermined. It is possible that it belongs to ctenacanthoids.
- The partly articulated specimens from the Pennsylvanian black shales allegedly belonging to *S. reniforme* need a re-study and a detailed comparison with the type specimen of this species.

Acknowledgments

I am greatly indebted to Dr. Alexander Ivanov (St. Petersburg, Russia) who was the first to discover the affinities between *Phoebodus heslerorum* and *Cladodus divergens*, but generously allowed me to continue investigation on this subject. I also want to thank Dr. Michael Hansen (Columbus, USA) and Dr. Charles A. Sandberg (Denver, USA) who allowed me to use their specimens for the study, and to Dr. Christopher Duffin (Sutton, UK) who provided the information on his yet unpublished work, and Dr. Sally V.T. Young (London, UK) who organised my studies at the Natural History Museum of London in 1996 and 1998; to Dale Gnidovec, the Curator of the Orton Geological Museum (Columbus, USA) who helped me during my work at the Museum in 1997 and sent the most important specimens to Poland for further investigation; and to Dr. Krzysztof Stefaniak (Wrocław, Poland) for his kind assistance during my examination of Trautschold's collection. Warm thanks are also due to Dr. John Maisey (New York, USA) and Dr. Alain Blieck (Lille, France), the reviewers, whose insightful comments helped to improve the final version of the manuscript. Photographs in Fig. 1 were taken by Bożena Malinowska (Warsaw, Poland), and those in Figs. 4 and 5 by the Natural History Museum of London photographers. The costs of my studies at the Field Museum of Natural History, Chicago, in 1997 were covered by the FMNH Visiting Scientist scholarship. Publication of this paper was financed from the Committee for Scientific Research (KBN) grant 6 P04D 053 18.

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