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Devonian filter-feeding sharks

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ABSTRACT:

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Upper Frasnian rocks of Utah and Nevada yielded several multicuspid, low-crowned shark teeth. It is proposed that they were used mainly for filtering food from water. Two new chondrichthyan species bearing such teeth were distinguished: a phoebodontid *Diademodus utahensis* sp. nov., with up to 17 very delicate cusps in the tooth-crown; and a cladodont of uncertain systematic position, *Lesnilomia sandbergi* gen. et sp. nov., also known from the upper Frasnian of Moravia.

Key words: Chondrichthyes, Teeth, Devonian, Frasnian, Utah, Nevada.

INTRODUCTION

Most of the teeth of known Devonian sharks function either as grasping or clutching cuspidate elements with relatively few cusps (diplo-, phoebo-, and cladodonts) or as parts of a crushing or grinding pavement dentition (protacrodonts and orodonts). There also exist, however, examples of multicuspid teeth with very delicate cusps which presumably could not have served to pierce the prey, but rather formed a kind of a sieve, preventing minute organisms from escaping from the buccal cavity before swallowing. Such teeth are elongated laterally and short labio-lingually, with only a rudimentary lingual torus. Basal articulation devices (buttons and basolabial projections) which commonly occur in primitive clutching teeth of Palaeozoic sharks, protecting a single tooth from being torn out of a tooth-family by a struggling prey, in such multicuspid teeth are virtually obsolete. Probably, for filter feeding such protection was unnecessary and the connection by soft tissues and simple overlapping of bases was sufficient to ensure the correct position and replacement of teeth.

The first teeth of this type were described from the partly articulated specimen of *Diademodus hydei* from the late Famennian Cleveland Shale of Ohio. HARRIS (1951, p. 685) noted that its teeth are minute, 1 mm in width at the base, and with ten conical cusps "of which the two outermost and the two central ones are considerably longer than the remaining six". He also provided a sketch drawing which shows two large median cusps. This description and illustration were adopted, apparently without personal observation of the material, by ZANGERL (1981, p. 68). He speculated that the symmetrical structure of the illustrated tooth and the presence of a double median cusp indicated that "the tooth may be the product of fusion of two adjacent teeth". However, the re-examination of the specimen (pers. obs. 2003) showed that the teeth of *Diademodus* are by no means unusual and display no trace of fusion. In fact, the single median cusp can be indicated. Generally, the crown is of a phoebodont type with a larger than usual number of intermediate cusplets; probably one of these cusplets, relatively long, was mistaken for the second median cusp. Similar, albeit not so extensive, multiplication of intermediate cusplets is known from *Phoebodus latus* GINTER & IVANOV, 1995, in which, rarely, more than one intermediate cusplet may occur on each side (see GINTER & IVANOV 1992, fig. 7A-B).

The other type of Devonian low-crowned multicuspid teeth was observed by GINTER (1991) in the collection from the upper Frasnian to lower Famennian of the Lesní Lom Quarry in Moravia. There, several teeth were identified as '*Cladodus*' spp., because the median cusp was larger than the others, as in cladodont crowns. Three of those, from the Late *rhenana* conodont Zone, show numerous lateral cusps (GINTER 1991, pl. 9, figs 1, 6; pl. 10, fig. 5). This kind of teeth is described below as a new genus and species, *Lesnilomia sandbergi*.

Both above mentioned types of multicuspid teeth, i.e. *Diademodus*-like and those of *Lesnilomia sandbergi* sp. nov., were found in several upper Frasnian samples belonging to a large collection of Devonian and Carboniferous ichthyoliths from western USA, mainly Utah and Nevada, loaned to me in 1997 by Dr. C. A. SANDBERG (USGS, Denver). The samples are precisely dated by conodonts: the Frasnian part served as a basis for the Standard Conodont Zonation (ZIEGLER & SANDBERG 1990). The richest sample, with *Diademodus utahensis* sp. nov. and a dental series of *L. sandbergi* sp. nov., comes from the upper Frasnian of Confusion Range (CON 3B; see SANDBERG & *al*. 1988). It also yielded three phoebodont teeth (*Phoebodus bifurcatus* GINTER & IVANOV, 1992 and *P. fastigatus* GINTER & IVANOV, 1992; Text-fig. 3A-D), as well as chondrichthyan scales of ctenacanth, protacrodont, and possibly hybodont type (sensu GROSS 1938, REIF 1978; Text-fig. 3H-J). The specimens are housed at the Institute of Geology, University of Warsaw, Poland (IGPUW).

SYSTEMATIC DESCRIPTIONS

Class Chondrichthyes
Subclass Elasmobranchii
Order Phoebodontiformes GINTER, HAIRAPETIAN & KLUG, 2002
Family Phoebodontidae WILLIAMS in ZANGERL 1981

Diademodus HARRIS, 1951

TYPE SPECIES: *Diademodus hydei* HARRIS 1951; Cleveland Shale, Upper Devonian (upper Famennian); Big Creek, SW of Cleveland, Ohio, USA.

Diademodus utahensis sp. nov.
(Text-fig. 1A-H)

HOLOTYPE: IGPUW/Ps/9/1, sample CON-3B, upper Frasnian, Late *rhenana* Zone, Pilot Shale, Little Mile-and-a-Half Canyon, Confusion Range, Millard Co., Utah, USA (for additional data see SANDBERG & *al*. 1988).

ETYMOLOGY: From the state of Utah.

DIAGNOSIS: Teeth with multicuspid crowns based on the phoebodont pattern, but with more numerous intermediate cusplets (three to seven on each side) than in typical phoebodonts. All the cusps very delicate, smooth, and rounded in cross section, as in *Phoebodus fastigatus*. The main cusps and the larger intermediate cusplets slightly sigmoidal, with a vague lateral carina. The base trapezoidal with rounded angles, short labio-lingually, similar to that of *Ph. latus*, but with only faint traces of articulation devices in a form of a weak basolabial shelf and a mesio-distally elongated orolingual hump.

MATERIAL AND OCCURRENCE: Four teeth from sample CON-3B, Late *rhenana* Zone, Little Mile-and-a-Half Canyon, Confusion Range, Millard Co., Utah; one tooth from sample DVG-14, Late *hassi* Zone, Devils Gate Pass, Eureka Co., Nevada (SANDBERG & *al*. 1988).

DESCRIPTION: The diagnosis and description are mostly based on two best preserved teeth from CON-3B, considered representative of the new species. The base width reaches 1.2 mm. In the holotype (Text-fig. 1A-D), there are altogether ten cusps in the crown. Nine of them are symmetrically placed, but the smallest, minute cusplet (third from the left in Text-fig. 1C) does not have a corresponding one on the other side. Among the symmetrically placed cusps, there are three main cusps (the median and two laterals) and six intermediate cusplets. The intermediate cusplets form triples consisting of the central, larger cusplet (about 3/4 of the height of the main cusps) flanked on each side by shorter and thinner ones (1/3 of the size of the main cusps). The smallest, single cusplet is probably the first of a new generation. In the other tooth (Text-fig. 1E-F) such minute cusplets occur in spaces between all the cusps, so the crown is composed of 17 cusps (seven intermediate cusplets on each side).

The base is very wide and short, with rounded linguolateral angles, gently compressed at the midline, so it may look like bi-lobed. The basolabial shelf, elongated but not reaching the lateral cusps, is only slightly marked. The orolingual hump is discernible only because its surface is smooth and it is surrounded by pores. Most of the aboral foramina are grouped in a mesio-distally elongated central area.

REMARKS: The labial view of teeth of *Diademodus utahensis* sp. nov. resembles that of the type species, *D. hydei*. However, as all the teeth in the holotype of *D. hydei* are embedded in rock, we do not know the form of their bases and several other features observable in *D. utahensis*, whose teeth were obtained by acid leaching. Moreover, the stratigraphic distance between the two findings is large (upper Frasnian vs. upper Famennian). These are the reasons why the new species was erected, perhaps temporally.

Diademodus is placed among the Phoebodontidae because of the similarity of its tooth-crowns to such forms as *Ph. fastigatus*, from which they differ mainly by the presence of additional generations of minute intermediate cusplets. Contrary to the idea of HARRIS (1951) who considered the teeth of *Diademodus* as primitive, from which both diplodont and cladodont pattern could have evolved, it appears to be a derived product of modification of phoebodont teeth. The tooth crown formula in phoebodontids could be presented as:

$$N = \left(\sum_{0}^{n} 2^{n}\right)^{-1},$$

where *N* is the total number of intermediate cusplets and *n* is the number of generations of such cusplets. In *Phoebodus* (except *Ph. latus*) we deal with generation 0 (no intermediate cusplets present) or 1 (two intermediates, one on each side); in *Diademodus*, with generation 1 and 2 (six intermediates) or 1, 2, and 3 (14 intermediates).

The lack of intermediate cusplets in *Phoebodus* is quite common (see, e.g., the holotype of *Ph. fastigatus*, GINTER & IVANOV 1992, fig. 3A, B), but the presence of one intermediate cusplet on each side is the most

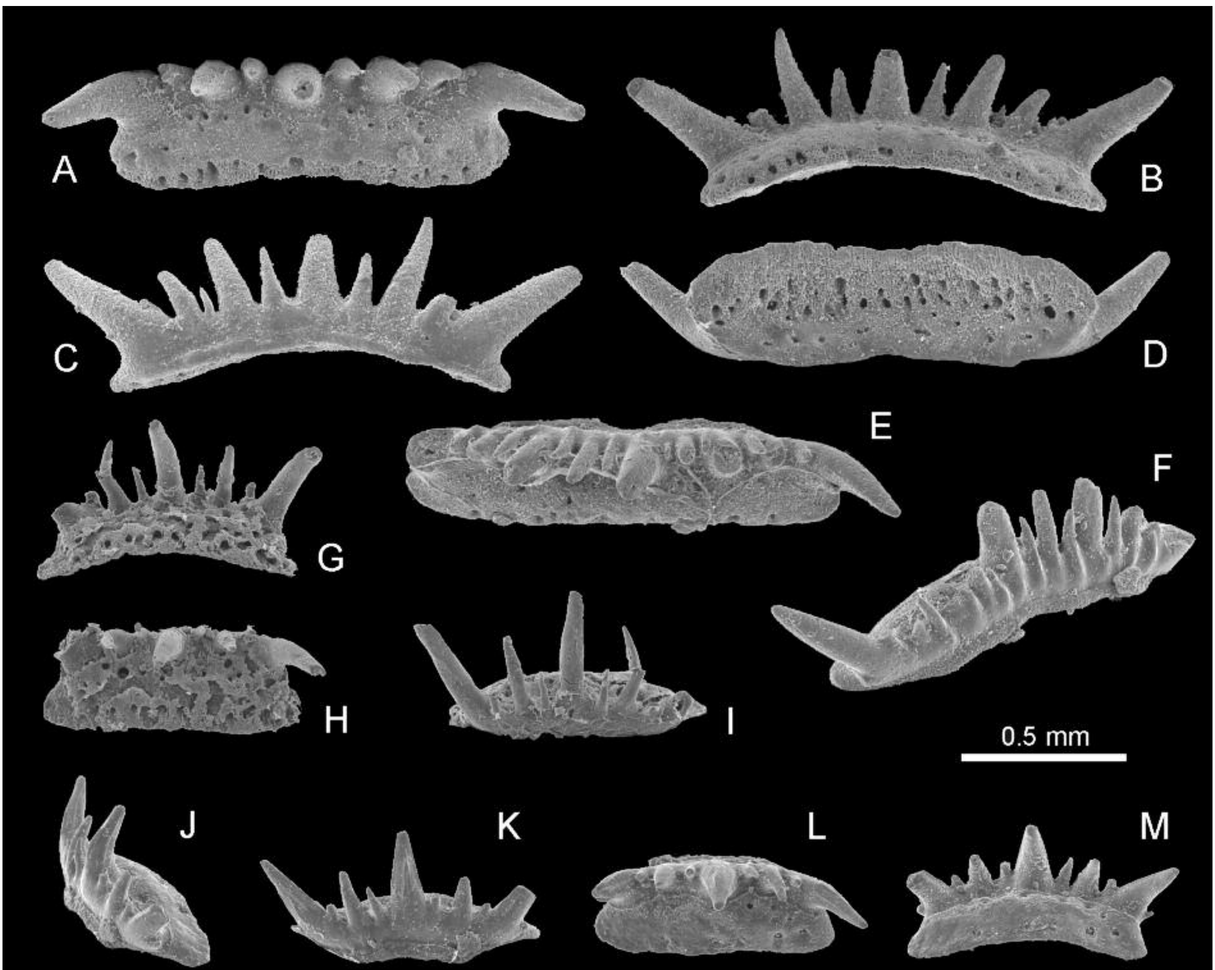

Fig. 1. A-H. Teeth of *Diademodus utahensis* sp. nov. A-D – Holotype (IGPUW/Ps/9/1) from sample CON-3B, in oral, lingual, labial, and aboral views. E, F – IGPUW/Ps/9/2 from sample CON-3B, in oral and oblique labial views. G-I – IGPUW/Ps/9/3 from sample DVG-14, in lingual, oral, and labial views. J-M – Small, symmetrical tooth of *Lesnilomia sandbergi* gen. et sp. nov. (IGPUW/Ps/9/4) from sample CON-3B, in oblique lateral, labial, oral, and lingual views

typical condition. Because the available number of *Diademodus* teeth is very low, it is uncertain whether the heterodonty is limited to generations 2 and 3. It can be speculated, that anterior teeth are narrower and more adapted for catching, and therefore phoebodont-like. If they were so, such teeth could look exactly like the one identified here tentatively as *Ph. fastigatus* (Text-fig. 3A-D). On the other hand, although it is hard to imagine a tooth with four generations of intermediate cusplets (i.e., 30 cusplets), it is not impossible in a larger individual. It is also yet unknown, to what extent the teeth of *Diademodus* could be asymmetrical. As shown above, there is a single, asymmetrically placed cusplet of the third generation in the holotype. Also, a single asymmetrical tooth with very delicate cusps was found in the material from CON-3B, but it is so abraded, that it is hard to say whether it represents *Diademodus* or rather *Lesnilomia* gen. nov.

Ctenacanthiformes? incertae sedis
Genus *Lesnilomia* gen. nov.

TYPE SPECIES: *Lesnilomia sandbergi* sp. nov.

ETYMOLOGY: From the Lesní Lom Quarry near

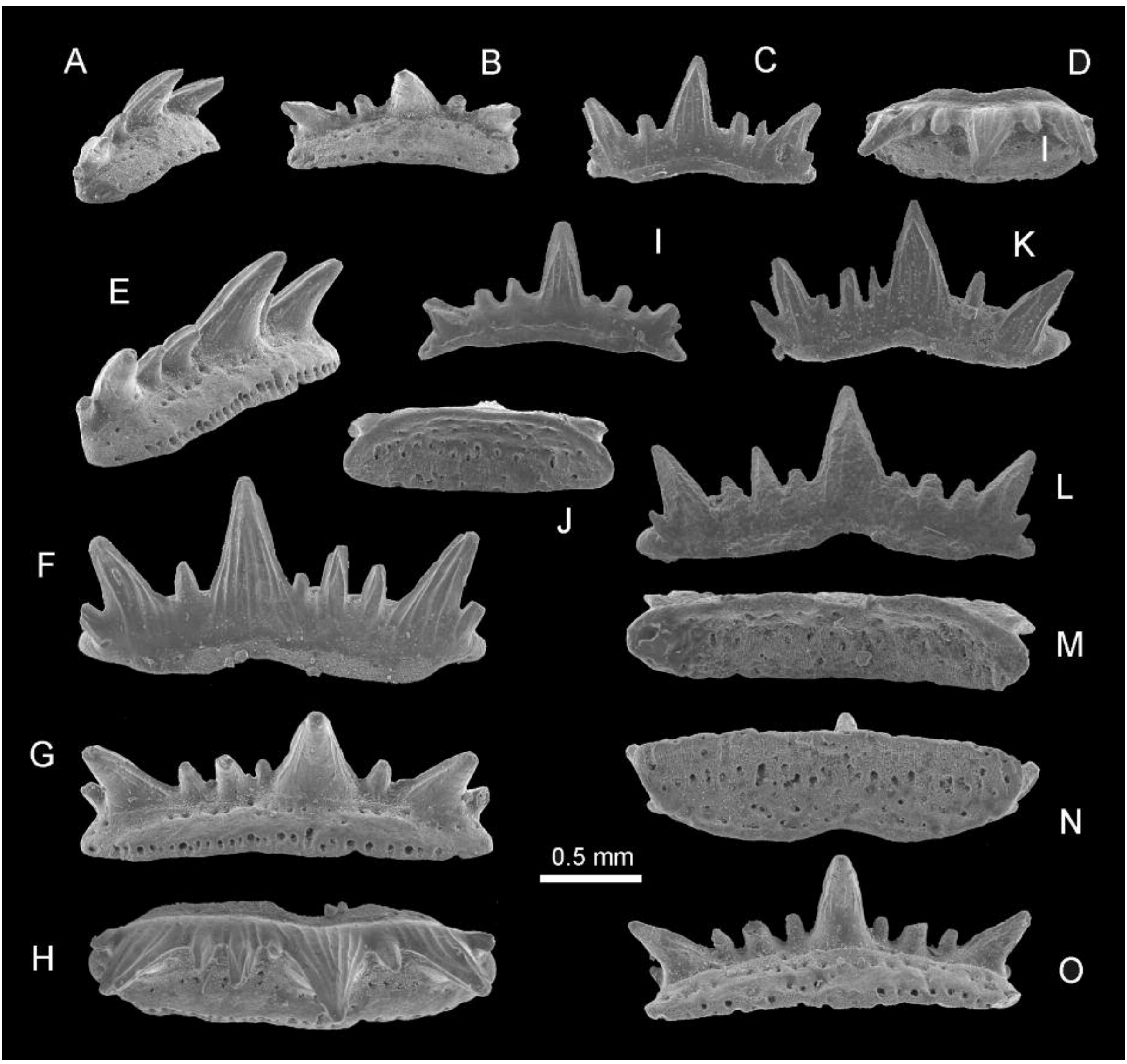

Fig. 2. Teeth of *Lesnilomia sandbergi* gen. et sp. nov. from sample CON-3B. A-D – IGPUW/Ps/9/5 in oblique lingual, lingual, labial, and oral views. E-H – Holotype (IGPUW/Ps/9/6), in oblique lingual, labial, lingual, and oral views. I-J – IGPUW/Ps/9/7 in labial and aboral views. K – IGPUW/Ps/9/8 in labial view. L, M. IGPUW/Ps/9/9 in labial and aboral views. N, O – IGPUW/Ps/9/10 in aboral and lingual views

Brno, where the first specimens of this genus were found.

DIAGNOSIS: Multicuspid teeth with symmetrical to asymmetrical crowns. The median cusp only slightly larger than the main lateral cusps. The main cusps and larger intermediate cusplets triangular, compressed labio-lingually, recurved but non-sigmoidal, ornamented on the labial faces with distinct cristae joining just below the tips. Lateral carina connecting all the cusps. A small accessory cusplet present on each lateral end of the crown. The base provided with a well developed basolabial rim, slightly depressed below the median cusp. Two mesio-distal rows of pores on the orolingual surface: one near the crown, another along the lingual rim.

Lesnilomia sandbergi sp. nov.
(Text-figs 1J-M, 2)

1991. '*Cladodus*' sp.; M. GINTER, p. 75, pl. 10, fig. 5 [cf. pl. 9, figs 1, 6; non pl. 9, figs 4, 5].

HOLOTYPE: IGPUW/Ps/9/6, sample CON-3B, upper Frasnian, Late *rhenana* Zone, Pilot Shale, Little Mile-and-a-Half Canyon, Confusion Range, Millard Co., Utah (for additional data see SANDBERG & *al*. 1988).

ETYMOLOGY: In honour of Dr CHARLES A. SANDBERG, the outstanding American stratigrapher.

DIAGNOSIS: As for genus.

MATERIAL AND OCCURRENCE: 16 teeth from sample CON-3B, Late *rhenana* Zone, Little Mile-and-a-Half Canyon, Confusion Range, Utah; one tooth from sample DVG-7G, *linguiformis* Zone, Devils Gate Pass, Nevada; two teeth from sample WCD-2, Early *rhenana* Zone, Water Canyon, Diamond Mts, Nevada (SANDBERG & *al*. 1988). One tooth from sample DMW-11, Early *rhenana* Zone, Deadman Wash, Burbank Hills, Utah; one tooth and two fragments from sample BPA-8, mixed fauna of the *linguiformis* and *triangularis* Zones, Black Point Area, North Pancake Range, Nevada (C. SANDBERG, pers. comm. 1997). Three teeth from samples 8E and 90/29, Late *rhenana* Zone, Lesni

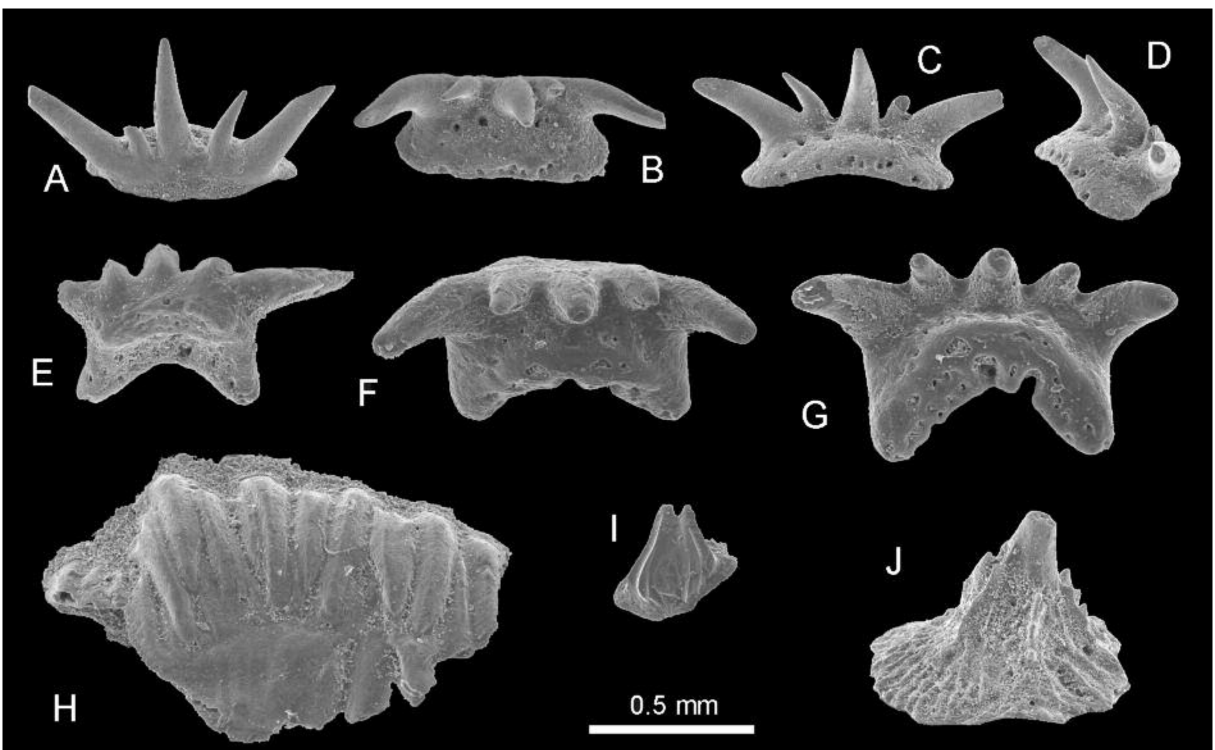

Fig. 3. Associated chondrichthyan microremains from sample CON-3B. A-D – *Phoebodus fastigatus* GINTER & IVANOV, 1992 (IGPUW/Ps/9/11) in labial, oral, lingual, and lateral views. E-G – *Ph. bifurcatus* GINTER & IVANOV, 1992. E – IGPUW/Ps/9/12 in aboral/labial view. F, G – IGPUW/Ps/9/13 in oral and lingual views. H – Ctenacanth-type scale (IGPUW/Ps/9/14) in coronal view. I – Protacrodont-type scale (IGPUW/Ps/9/15) in coronal view. J – Hybodont?-type scale (IGPUW/Ps/9/16) in lateral view

Lom Quarry NNE of Brno, Moravia (HLADIL & *al*. 1991).

DESCRIPTION: The most common teeth of *L. sandbergi* sp. nov. in the studied material are symmetrical, 11-cuspid, with the relatively low principal cusp, two lateral main cusps, two outermost accessory cusplets, and six intermediate cusplets (three on each side: one larger flanked by two smaller ones). However, there are also asymmetrical forms with different numbers of intermediate cusplets on each side: 2 to 1 (Text-fig. 2A-D), 3 to 1 (holotype, Text-fig. E-H), or 3 to 2; there are also fragments with four cusps on one side.

The base is intermediate between the primitive and euselachian types. The position of orolingual rows of foramina is similar to that in protacrodonts, but the presence of the well developed basolabial rim is reminiscent of a ctenacanthiform *Tamiobatis* sensu WILLIAMS (1998). The shallow basolabial depression and the labio-lingual compression of the cusps are typical of many cladodont sharks, especially the ctenacanths. Also the occurrence of outer accessory cusplets is known from *Tamiobatis*. Taken all this together, *Lesnilomia* appears to be situated, in the sense of tooth morphology, somewhere between the Ctenacanthiformes and Protacrodontoidea.

FINAL REMARKS

Diademodus and *Lesnilomia* are not the only Palaeozoic sharks with multicuspid teeth. However, most of them, such as *Squatinactis* LUND & ZANGERL, 1974, *Tamiobatis* sensu WILLIAMS 1998, *Saivodus* DUFFIN & GINTER, 2006, and a series of cladodont teeth from the lower Famennian of Coumiac section in Montagne Noire (RIEMANN & *al*. 2002, e.g., pl. 5, figs 10, 11), possess long median cusps which definitely served for grasping at first place. The size differences between the cusps in *Lesnilomia*, and especially in *Diademodus*, are much less conspicuous. It is interesting that teeth of these two genera reached similar appearance probably by convergence: the former by the secondary reduction of the median cusp of a cladodont crown, and the latter by the multiplication of the phoebodont model. The cusps of *Lesnilomia* look more robust and probably retained some capability for biting at soft prey (the ornamentation with vertical cristae confirms that), but those of *Diademodus* could be used apparently only for filtering (with exception of the hypothetical phoebodont-like front teeth).

The occurrence of small and large teeth of the same shape and the same number of cusps in *D. utahensis* and *L. sandbergi* (compare Text-fig. 1B and G; Text-figs 1M and 2O) suggests that the pattern and, therefore, function of the dentition was rather stable throughout the animal's life. However, this is probably not so in the case of small Carboniferous stethacanthids, also called falcatids. It was noted (GINTER 2005) that small articulated specimens of *Damocles serratus* LUND, 1986 have asymmetrical, multicuspid, very delicate teeth (similar to those illustrated by WANG & *al*. 2004 as *Denaea wangi*), whereas in the large specimens the teeth are pentacuspid, symmetrical, and typically cladodont with a long median cusp. If the large and small specimens attributed to *Damocles* indeed belong to the same species, it means that the mode of feeding was changing from filter-feeding to hunting during the ontogeny.

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