

A classic Late Frasnian chondrichthyan assemblage from southern Belgium

MICHAŁ GINTER¹, SOFIE GOUWY² and STIJN GOOLAERTS³

¹ Faculty of Geology, University of Warsaw, Żwirki i Wigury 93, 02-089 Warsaw, Poland.

E-mail: m.ginter@uw.edu.pl

² Paleontology Section, Geological Survey of Canada, 3303, 33str NW Calgary, T2L 2A7, Canada

E-mail: Sofie.Gouwy@canada.ca

³ Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium

E-mail: stijn.goolaerts@naturalsciences.be

ABSTRACT:

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Samples from the Upper Frasnian (Devonian) of Lompret Quarry and Nismes railway section in Dinant Synclinorium, southern Belgium, yielded several chondrichthyan teeth and scales. The teeth belong to three genera: *Phoebodus*, *Cladodoides* and *Protacrodus*. The comparison with selected Late Frasnian chondrichthyan assemblages from the seas between Laurussia and Gondwana revealed substantial local differences of taxonomic composition due to palaeoenvironmental conditions, such as depth, distance to submarine platforms, oxygenation of water, and possibly also temperature. The assemblage from Belgium, with its high frequency of phoebodonts, is the most similar to that from the Ryauryak section, South Urals, Russia, and the Horse Spring section, Canning Basin, Australia.

Key words: Late Devonian; Belgium; Dinant Synclinorium; Chondrichthyes; Microfossils.

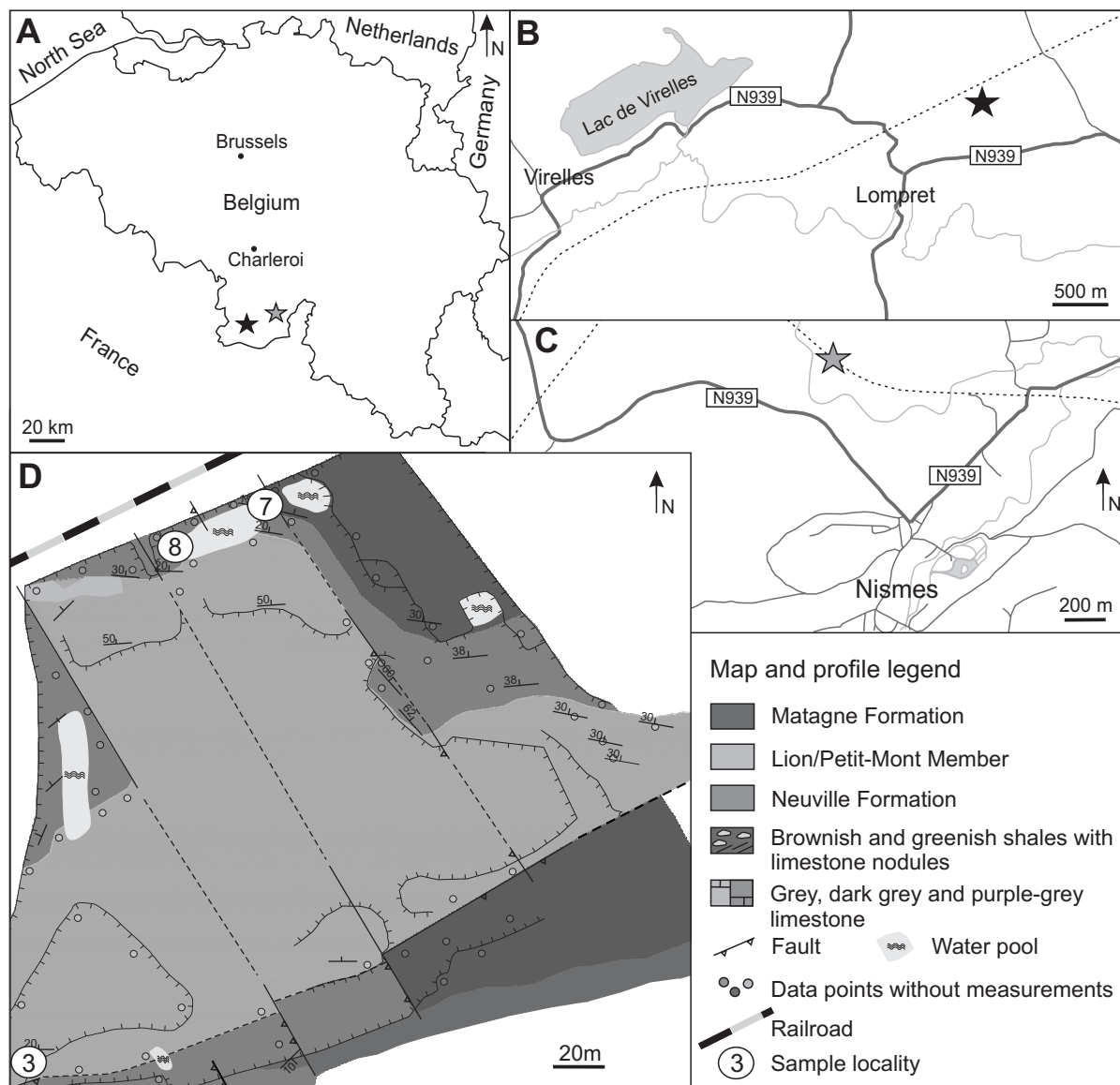
INTRODUCTION

Excavation in the Lompret Quarry expanded northward during the last four years, revealing Frasnian reefal limestone deposits close to the old railroad. The limestone lens and surrounding deposits are the subjects of an ongoing study on the sedimentology, stratigraphy, micro- and macropaleontology of the Middle to Upper Frasnian deposits (Goolaerts and Gouwy 2015a, b; Gouwy and Goolaerts 2015). Several of the conodont samples taken in these deposits contained micro fish remains (teeth and scales) as a by-product.

The Nismes railway section was studied for Upper Frasnian conodont biostratigraphy by Helsen and colleagues (Helsen and Bultynck 1992; Bultynck *et al.* 1998) and also contained micro fish remains

in several of the collection samples (Collections of the Royal Belgian Institute for Natural Sciences, Brussels, Belgium).

Altogether 23 identifiable chondrichthyan teeth were recovered from both sections. The taxonomic content of this small assemblage (almost only *Phoebodus bifurcatus* Ginter and Ivanov, 1992, *Cladodoides wildungensis* Jaekel, 1921, and *Protacrodus vetustus*, Jaekel, 1925), representing the *jamieae*/Lower *rhenana* Conodont zones is comparable to several other Upper Frasnian localities in the world. However, a few local differences can be observed, and they will be discussed at the end of the paper. In addition to chondrichthyan teeth, a few compound shark scales were found, as well as teeth, scales and bone fragments of actinopterygian and sarcopterygian origin,



Text-fig. 1. Location of the Nismes and Lompret outcrops and indication of the section locations in the Lompret quarry

including the teeth of an onychodont *Strunius rolandi* (Gross 1956).

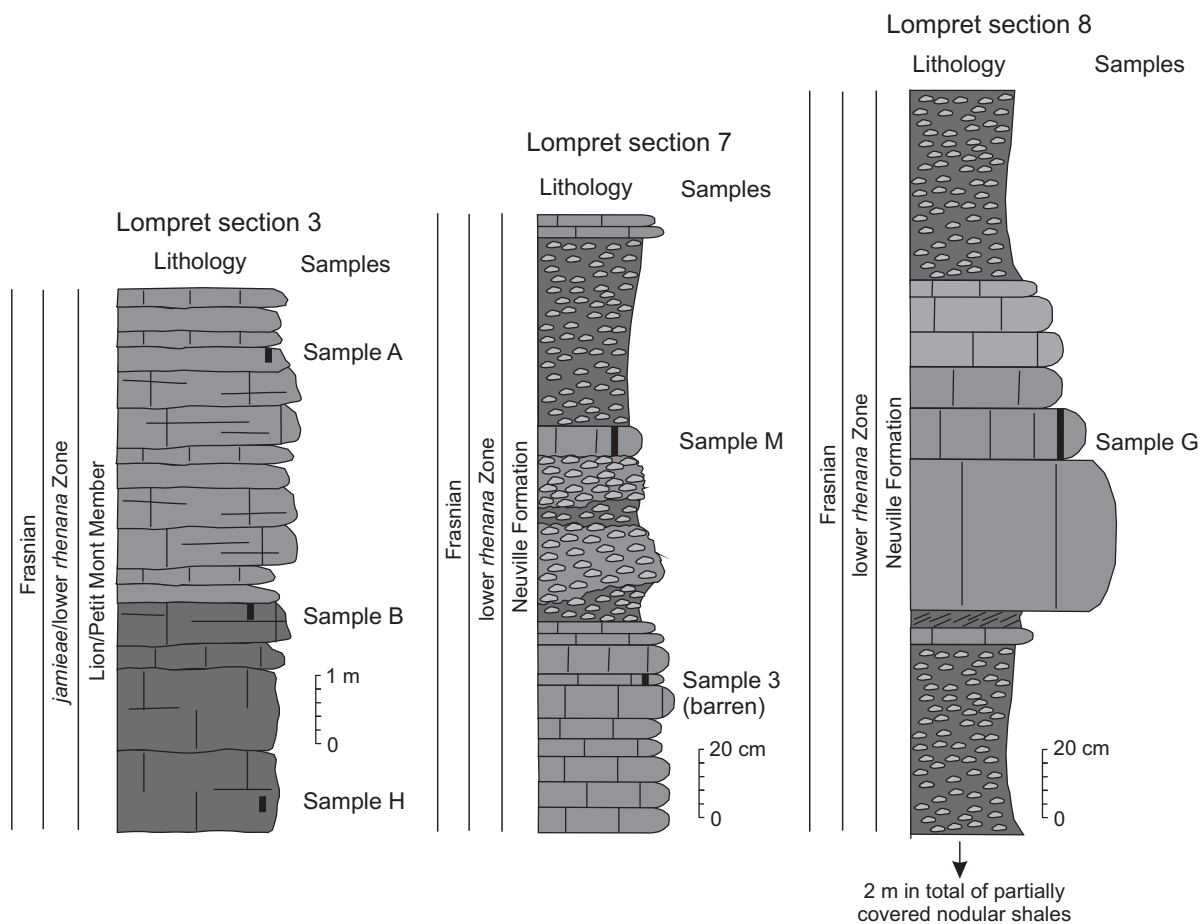
Institutional abbreviations: MB, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The studied outcrops are both located in southern Belgium (Text-fig. 1A). The Lompret outcrop

is exposed in a recently expanded limestone quarry situated to the northeast of Lompret village, about 10 km west of Frasnes. In this quarry, in the old, now ceased, pit Middle Frasnian limestones of the Bieumont Member (Grands Breux Formation) were quarried (Humblet and Boulvain 2000; Da Silva *et al.* 2013). In the new pit, active since 2011 and located somewhat to the northeast, a greyish limestone body is quarried, also exposing the overlying and fossiliferous Upper Frasnian deposits of the Neuville and Matagne formations.

The most recent geological map of the area (Marion and Barchy 1999), based on fieldwork prior



Text-fig. 2. Detailed profiles taken at different localities in the quarry (see also legend to Text-fig. 1)

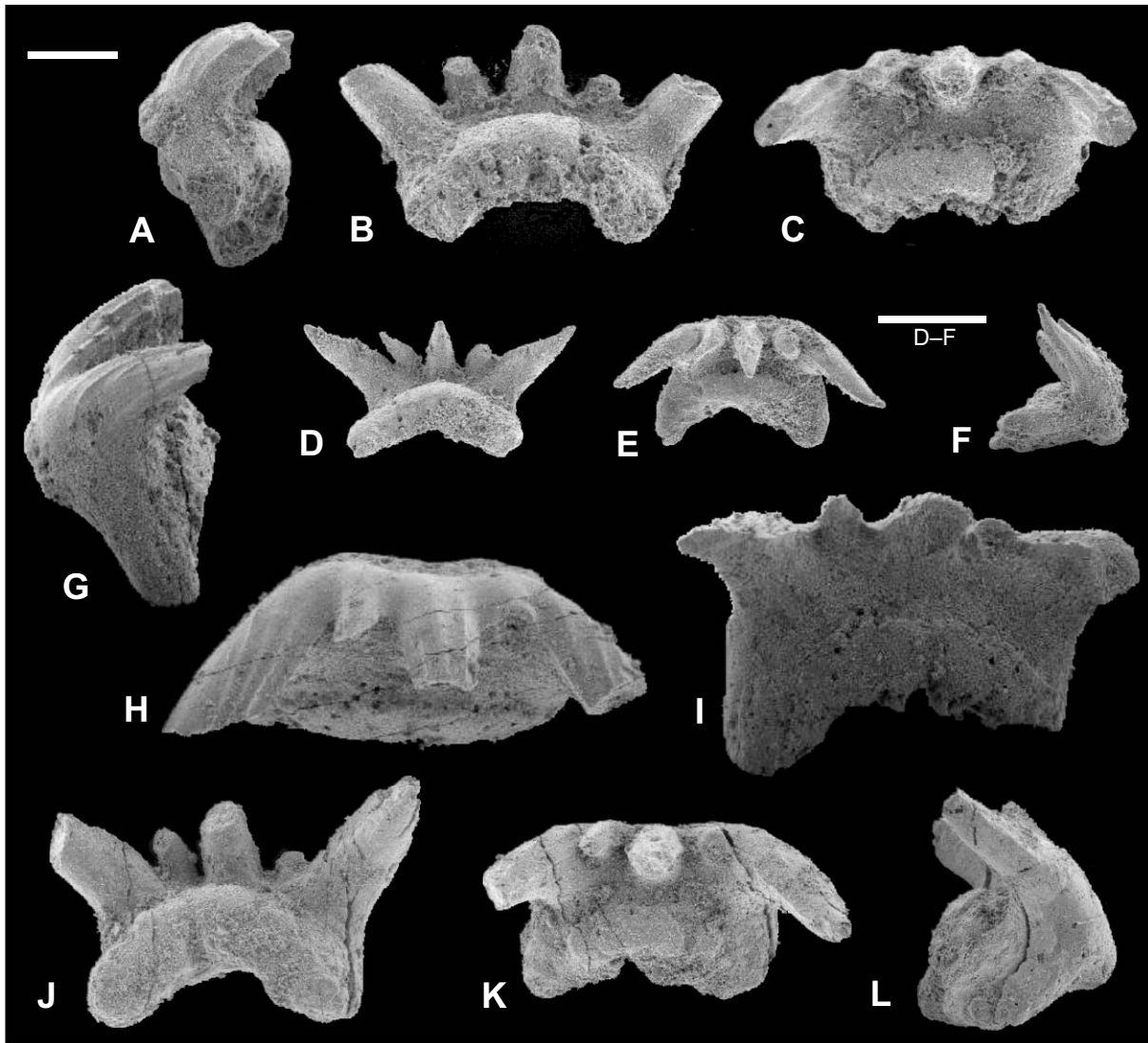
to the opening of the new pit, assigned the limestone body to the Upper Frasnian Petit Mont Member. This erroneous interpretation also misled Goolaerts and Gouwy (2015a), although they had serious doubts since the limestone strongly resembled the Middle Frasnian Lion Member limestone (Grands Breux Formation). Ongoing research by colleagues from the Université de Liège confirmed the quarried limestones do belong to the upper part of the Lion Member sequence (J. Denayer, pers. comm. 2015; F. Boulvain pers. comm. 2015). A high number of faults cutting through the limestone hinder an easy interpretation. The few conodont samples from this body processed so far lack zonal indexes, and only allow positioning in a conodont zones interval within the Middle–Upper Frasnian sequence. Most of the chondrichthyan bearing samples however, originate from the overlying Neuville Formation (Table 1). The Nismes outcrop (Helsen and Bultynck 1992; Bultynck *et al.* 1998) is situated along the railway from Mariembourg to Olloy-sur-Viroin (Text-fig. 1B–C). Geologically,

both sections are positioned on the southern flank of the Dinant Synclinorium, a synform structure consisting of a series of synclines and anticlines and part of the Variscan fold belt.

The Upper Frasnian in this area is represented by the Neuville, Valisettes and Matagne formations (Bultynck and Dejonghe 2001). The peri-reefal Neuville Formation typically consists of nodular shales with several nodular and argillaceous limestone beds and locally includes reefal limestone lenses (Petit-Mont Member). Recently, Coen-Aubert (2015) pro-

Locality	Lompret			Nismes		Total
	B	G	M	C''A''	C9	
<i>Phoebodus bifurcatus</i>		3	7	2		12
<i>Cladodoides wildungensis</i>	2					2
<i>Protacrodus vetustus</i>	2		1	1	4	8
<i>Phoebodus sp.</i>	1					1
Total	5	3	8	3	4	23

Table 1. Distribution of chondrichthyan teeth in the samples from the upper Frasnian of Lompret and Nismes, southern Belgium



Text-fig. 3. Teeth of *Phoebodus bifurcatus* Ginter and Ivanov, 1992, from the Upper Frasnian of Lompret and Nismes. **A-F** – From Lompret, sample G; **A-C** – RBINS P 9861, in lateral, lingual and oral views. **D-F** – RBINS P 9862, in lingual, oral and lateral views. **G-I** – RBINS P 9863, from Lompret, sample M, in lateral, oral and lingual views. **J-L** – RBINS P 9864, from Nismes, sample C'A', in lingual, oral and lateral views. Scale bars = 0.5 mm

posed a rearrangement of the lithostratigraphic subdivision, placing the Neuville and Valisettes formations, as well as the Petit-Mont unit, as three members of the new Champ Broquet Formation. The younger Matagne Formation overlying the Neuville Formation comprises thin dark greenish-brown to brownish-black shales with a few dark argillaceous limestone beds in the lowermost part of the Formation. The dark grey-green and violet shales of the Valisettes Formation are only locally found with reduced thickness (Nismes outcrop) in between the Neuville and Matagne formations in the southern part of the Dinant Synclinorium.

The studied samples in the Lompret outcrop

are taken from limestone levels within the Neuville Formation overlying the quarried reefal limestone lens (samples M and G, Table 1) and from the Middle Frasnian Lion Member (Bieumont Formation) reefal limestone in the deeper part of the quarry (Text-fig. 1D). The resulting conodont faunas position this limestone reefal lens and the Neuville shales covering the limestone body within the *jamieae*/Lower *rhenana* zones and the Lower *rhenana* Zone respectively (Text-fig. 2; Gouwy and Goolaerts 2015). The studied Nismes samples (microfossil collection of Helsen and Bultynck 1992) come from the lowermost part of the Neuville Formation and the upper part of a

small limestone lens found within this formation, and are stratigraphically positioned within the *jamieae*/Lower *rhenana* zones (Bultynck *et al.* 1998).

SYSTEMATIC PALAEOONTOLOGY

Chondrichthyan teeth

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Phoebodontiformes Ginter, Hairapetian and Klug, 2002

Family Phoebodontidae Williams in Zangerl (1981)

Genus *Phoebodus* St. John and Worthen, 1875

Phoebodus bifurcatus Ginter and Ivanov, 1992
(Text-fig. 3)

MATERIAL: Twelve teeth, ten from Lompret (samples G and M) and two from Nismes (sample C" A").

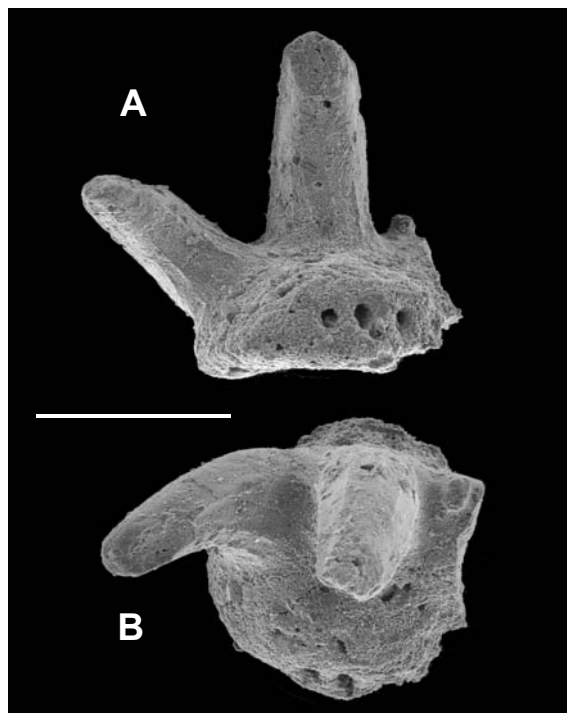
DESCRIPTION AND REMARKS: The teeth of this characteristic species have rather long lingual basal extensions, bifurcating at the lingual end. The material from Belgium is very similar to that described from Poland and Russia by Ginter and Ivanov (1992, fig. 4, 5D–G). It contains both morphotypes, i.e., large teeth with relatively short lingual ends of the base (Text-fig. 3A–C, G–L) and small teeth with a pronounced bifurcation (Text-fig. 3D–F; “juvenile” teeth sensu Ginter and Ivanov 1992; see also Turner and Youngquist 1995). The smaller teeth are generally better preserved than the larger ones which are usually broken and abraded.

OCCURRENCE: Most of the occurrences of *Ph. bifurcatus* are limited to the *rhenana* Conodont Zone, upper Frasnian. However, there are also rare reports of the existence of this species in uppermost Frasnian *linguiformis* Zone, e.g., in the Middle Urals, Russia (A. Ivanov, pers. comm. 2015) and possibly also at Płucki, Holy Cross Mts., Poland (MG pers. obs.).

Phoebodus sp.
(Text-fig. 4)

MATERIAL: One tooth from Lompret, sample B.

DESCRIPTION AND REMARKS: This tooth has a rather narrow base (0.6 mm mesio-distally) with



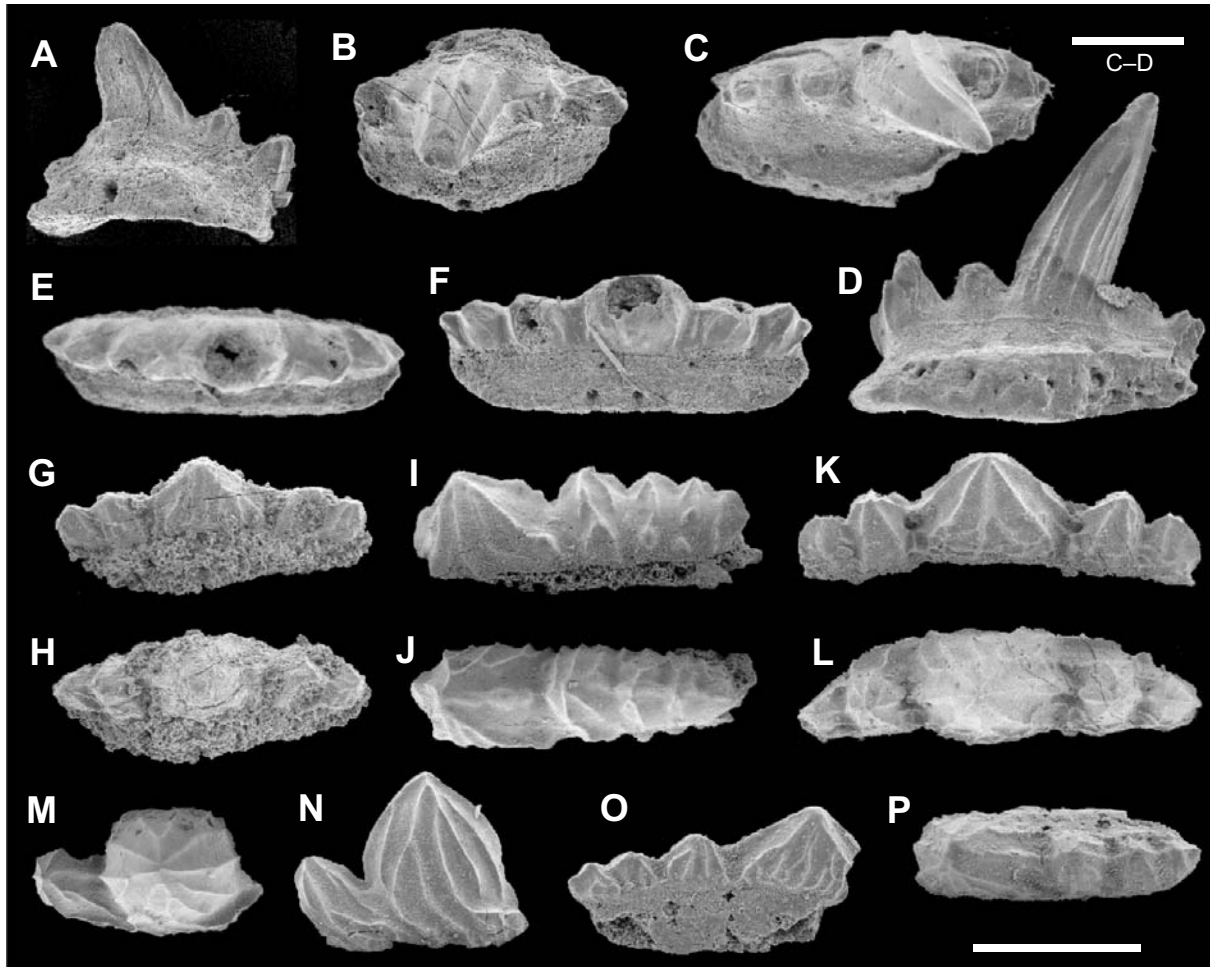
Text-fig. 4. Tooth of *Phoebodus* sp., RBINS P 9865, from the Upper Frasnian of Lompret, sample B, in lingual and oral views. Scale bar = 0.5 mm

a rounded lingual extension and a weakly marked orolingual button. The specimen is abraded and one lateral cusp and a piece of the base are missing. However, it is possible to assume that originally there were three rather long main cusps, rounded in cross-section, and only one minute intermediate cusp. There are remnants of subparallel cristae on the main cusps. The only similar phoebodont teeth from the Frasnian are those designated as *Phoebodus* sp. C by Ginter and Ivanov (1992, particularly fig. 5C).

OCCURRENCE: Such teeth are very rare in the Frasnian. According to Ginter and Ivanov (1992), Ginter (1994) and A. Ivanov (pers. comm.) all of them were found in the *rhenana* Zone: in the South Urals (Ryauzyak and Lemeza sections) and in Poland, Holy Cross Mountains (Wietrzna Quarry).

Order Ctenacanthiformes Glikman, 1964
Family Ctenacanthidae Dean, 1909
Genus *Cladodoides* Maisey, 2001

John Maisey, the author of the name of this genus, noted as follows: “It is important to note that the braincase described by Gross (1937) is not the ho-



Text-fig. 5. **A-D** – Teeth of *Cladodoides wildungensis* (Jaekel, 1921), from the Upper Frasnian of Lompret, sample B. **A, B** – RBINS P 9866 in lingual and oral views; **C, D** – RBINS P 9867 in oral and lingual views. **E-P** – Teeth of *Protacrodus vetustus* Jaekel, 1925. **E-F** – From the Upper Frasnian of Lompret, sample B, RBINS P 9868, in oral and lingual views; **G-N** – From the Upper Frasnian of Nismes, sample C9. **G, H** – RBINS P 9869, in lingual and oral views. **I, J** – RBINS P 9870, in labial and oral views; **K, L** – RBINS P 9871, in labial? and oral views; **M, N** – median cusp and a lateral cusplet, RBINS P 9872, in oral and labial views. **O, P** – From the Upper Frasnian of Nismes, sample C”A”, RBINS P 9873, in lingual and oral views. Scale bar = 0.5 mm

holotype of *C. wildungensis*. That taxon is founded on jaw elements associated with teeth (Jaekel 1921), and while Gross (1937) presented a circumstantial case for including the braincase in this species, no diagnostic characters can actually be compared. Thus, the precise identity of the braincase is problematic, despite its importance as a source of data concerning early elasmobranch cranial morphology.” (Maisey 2005 p. 4). Fortunately, the taxonomic problem holotype vs. alleged braincase of *Cladodoides wildungensis* has no influence on the identification of isolated teeth. The casts of teeth from the holotype of *C. wildungensis* (MB.f.198; Ginter *et al.* 2010, fig. 66I, J) are informative enough and the teeth found elsewhere can be easily compared to them.

Cladodoides wildungensis (Jaekel, 1921)
(Text-fig. 5A–D)

MATERIAL: Two teeth from Lompret, sample B.

DESCRIPTION AND REMARKS: The characteristics of the teeth from Belgium correspond very well to the description and illustrations of *C. wildungensis* provided by Ginter *et al.* (2010). The cladodont crown with a very long, cristated median cusp and two much smaller lateral cusps on each side, combined with the wide base bearing an elongated orolingual button almost split in two by a large median canal (compare Text-fig. 5A and Ginter *et al.* 2010, fig. 66F) are typical of this species.

OCCURRENCE: Articulated material of *C. wildungensis* (jaws with teeth) was described from the Kellwasserkalk of Bad Wildungen, Hessen, Germany, *linguiformis* Conodont Zone. Isolated teeth were reported from the upper Frasnian through to middle Famennian of many places in the world.

Cohort Euselachii Hay, 1902

Family Protacrodontidae Cappetta, Duffin and Zidek, 1993

Genus *Protacrodus* Jaekel, 1925

Protacrodus vetustus Jaekel, 1925

(Text-fig. 5E–P)

MATERIAL: Eight teeth; three from Lompret (samples B and M) and five from Nismes (samples C”A” and C9).

DESCRIPTION AND REMARKS: The specimens from Belgium generally conform to the early descriptions and illustrations of the type material (e.g., Gross 1938), they have protacrodont crowns with pyramidal, coarsely cristated cusps and typical, elongated, euselachian-type bases. However, the bifurcation of the cristae close to the crown-base interface appears here to be more intensive, in some cases there is more than one generation of splitting (Text-fig. 5O).

OCCURRENCE: Articulated material of *P. vetustus* was described from the Kellwasserkalk of Bad Wildungen, Hessen, Germany, *linguiformis* Conodont Zone. Isolated teeth most probably belonging to this species were found from the uppermost Frasnian and lower Famennian of the Holy Cross Mountains, Poland (Ginter 2002) and very similar teeth were reported from that interval of several places in the world, e.g., Morocco (Ginter *et al.* 2002), Moravia (Hladil *et al.* 1991) and the South Urals (Ginter and Ivanov 2000).

CHONDRICHTHYAN SCALES

Three types of chondrichthyan scales have been found. The first, with numerous, irregularly placed odontodes in the crown (Text-fig. 6A) and a delicate, cup-like base corresponds to the ctenacanthid-type body scales *sensu* Reif (1978). The second, with almost flat, diamond-shaped crowns composed of symmetrically situated odontodes (Text-fig. 6B–E) and bulbous, acanthodian-like bases is rather similar to Gross' (1938) protacrodont type. The third

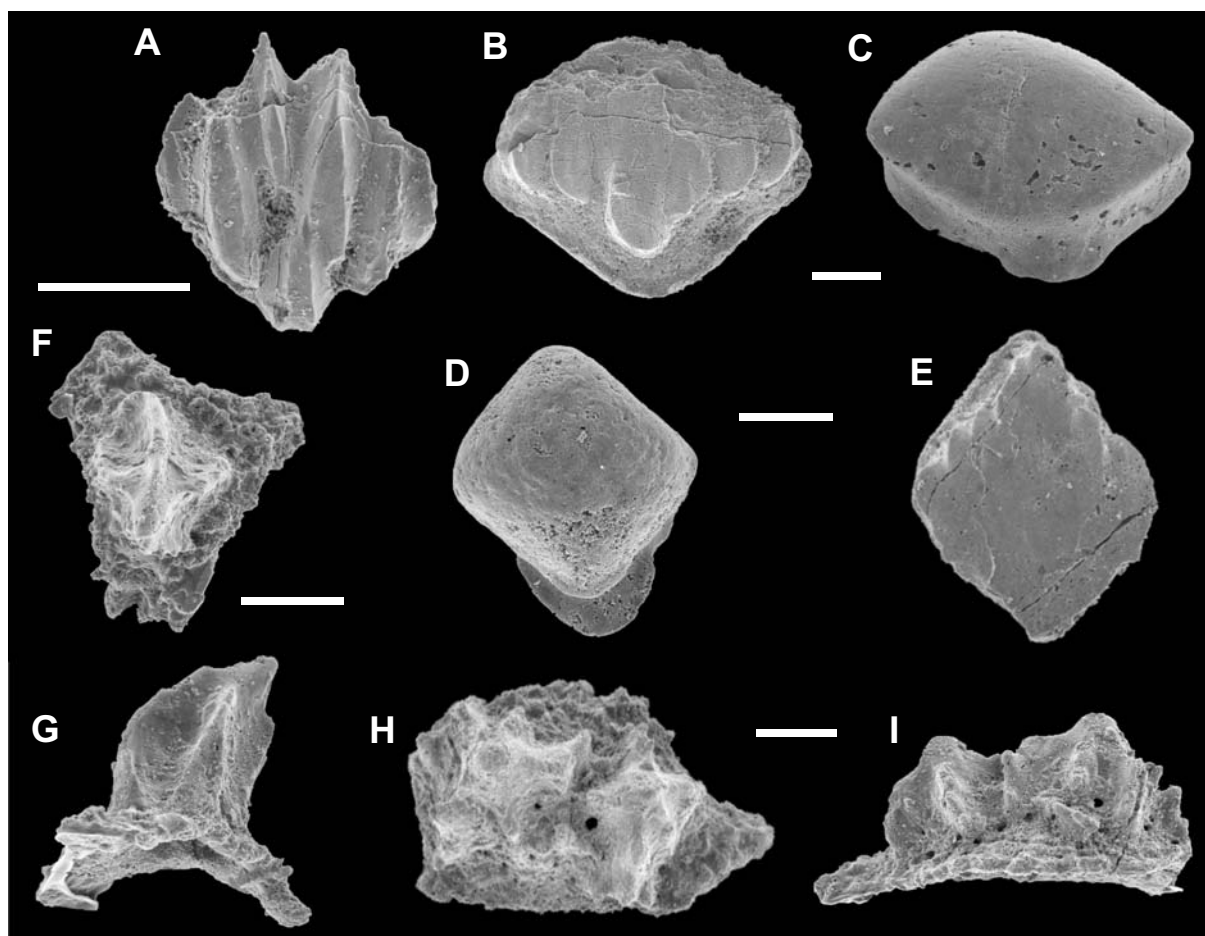
is characterised by vertically protruding, star-like crowns on flat, spongy bases, with multiple neck canals (Text-fig. 6F–I). Such elements look exactly like those illustrated by Reif (1978) in his figures 2–5 as hybodontid-type scales.

It is difficult to decide which of the mentioned type corresponds to which teeth present in the material. Ctenacanthid scales may occur both in the ctenacanthiforms (Reif 1978) and phoebodontiforms (e.g., Ginter and Turner 1999). The scales of the second type probably belong to *Protacrodus vetustus*, but they are not identical to those illustrated by Gross (1938) from the type specimen. The hybodontid type of scales may occur in any of the above described sharks, if we consider, for instance, that their form does not reflect the systematic position but some special place on the body (e.g., the snout).

DISCUSSION

The collection of chondrichthyan microfossils from Lompret and Nismes, although very small and unsuitable for statistical analysis, can be compared with assemblages from the other Upper Frasnian localities (Table 2). From the best documented sections, the most similar assemblage was recovered from the area of Ryauzyak River, South Urals (A. Ivanov, pers. comm.). The age of the analysed part of the section (samples 6391–6431, condensed, massive and thick-layered organogenic limestones) is Lower to Upper *rhenana* Conodont Zone (Artyushkova *et al.* 2011, fig. 21), i.e., partly coeval to Belgian samples. In both places there is a co-occurrence of *Ph. bifurcatus*, *C. wildungensis* and *P. vetustus* plus certain unnamed phoebodonts, similar to that referred to by Ginter and Ivanov (1992) as *Phoebodus* sp. C. A South Urals specialty is *Ph. latus* Ginter and Ivanov, 1995, which predominates in the lower part of the Upper Frasnian and then gradually gives way to *Ph. bifurcatus*. It should be noted that non-phoebodont sharks play a minor role here. Unfortunately, because this material is still unpublished, the precise data are not included in the tables and diagrams in this paper.

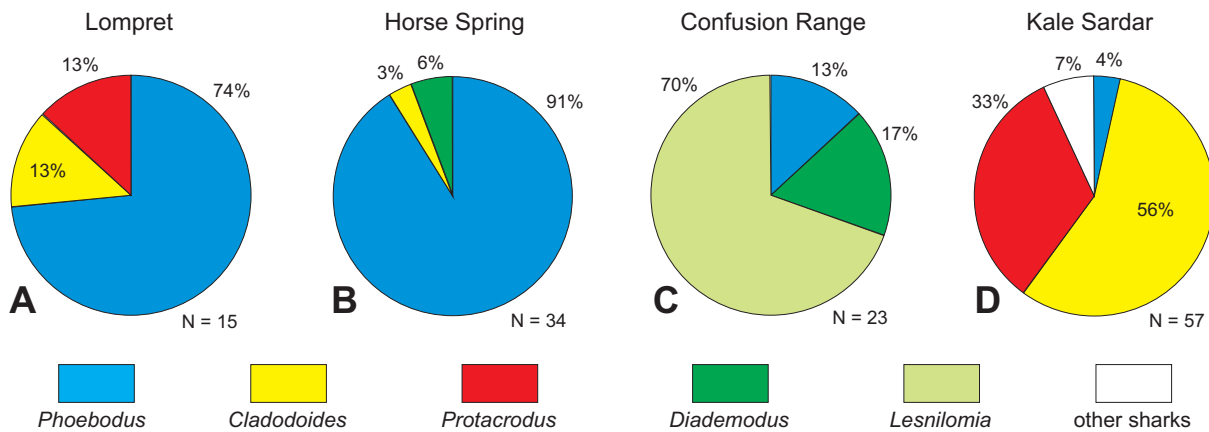
Very similar is the collection of specimens from Horse Spring in the Canning Basin area, north-western Australia, recently described by Roelofs *et al.* (2015). Here, among 34 shark teeth from five samples dated as *jamieae*–Lower *rhenana* Conodont zones (MN11 Montagne Noire zone), 31 belong to at least three species of *Phoebodus* (including strange, probably juvenile teeth of *Ph. bifurcatus* with very long bases), one to *Cladodooides* and two to *Diademodus*.



Text-fig. 6. Chondrichthyan scales from the Upper Frasnian of Lompret. **A** – Ctenacanthid body scale from sample C, RBINS P 9874, coronal view. **B-E** – Protacrodont scales from sample C; **B** – RBINS P 9875 in coronal view; **C** – RBINS P 9876 in basal view; **D** – RBINS P 9877 in basal view; **E** – RBINS P 9878 in coronal view (**D**, **E** may represent acanthodians). **F-I** – Hybodontid scales from sample B; **F**, **G** – Single-odontode scale, RBINS P 9879, in coronal and lateral views; **H**, **I** – Double-odontode scale, RBINS P 9880, in coronal and lateral views. Scale bars = 0.2 mm

Locality	Lompret	Horse Spring	Confusion Range	Kale Sardar	Kowala	Bad Wildungen
Age (CZ)	<i>jam.?-L. rhen.</i>	<i>jam.-L. rhen.</i>	<i>U. rhenana</i>	<i>U. rhen.-ling.</i>	<i>linguiformis</i>	<i>linguiformis</i>
<i>Phoebodus latus</i>		8				
<i>Phoebodus bifurcatus</i>	10	6	2	1		
<i>Cladodoides wildungensis</i>	2	1		32	3	1 (jaws with teeth)
<i>Protacrodus vetustus</i>	2			19	1	1 (jaws, teeth and scales)
<i>Diademodus</i> spp.		2	4			
<i>Lesnilomia sandbergi</i>			16			
<i>Phoebodus</i> spp.	1	17	1	1		
other sharks				4		
Total	15	34	23	57	4	2

Table 2. Occurrence of chondrichthyans in selected upper Frasnian sections: Lompret, southern Belgium (this paper); Horse Spring section, Canning Basin, Australia, samples VHS-308-315, (Roelofs et al. 2015); Confusion Range, Little Mile-and-a-half Canyon, Utah, USA, sample CON-3B (Ginter 2008); Kale Sardar, Shotori Range, eastern Iran, sample K5 (Hairapetian and Ginter 2010); Kowala-Wola Quarry, Holy Cross Mountains, Poland, samples Kx-12 and Ko-SF (Ginter 2002); Bad Wildungen, Hessen, Germany (Gross 1938). *U. rhen.-ling.*, Upper *rhenana-linguiformis* Conodont zones; *jam.-L. rhen.*, *jamieae*-Lower *rhenana* Conodont zones



Text-fig. 7. Pie-diagrams illustrating relative abundances of teeth representing chondrichthyan genera in Lompret and comparative Upper Frasnian sections. **A** – Lompret, southern Belgium, *jamieae?* – Lower *rhenana* CZ (this paper). **B** – Horse Spring section, Canning Basin, Australia, samples VHS-308-315, *jamieae* – Lower *rhenana* CZ (Roelofs *et al.* 2015). **C** – Confusion Range, Little Mile-and-a-half Canyon, Utah, sample CON-3B, Upper *rhenana* CZ (Ginter 2008). **D** – Kale Sardar, Shotori Range, eastern Iran, Upper *rhenana* – *linguiformis* CZ (Hairapetian and Ginter 2010)

Again, the predominance of phoebodonts is striking (Text-fig. 7). Roelofs *et al.* (2015, p. 75) describe the lithology in this section as “a lower slope succession dominated by platform derived skeletal to non-skeletal packstones and grainstones, slope derived rudstones and margin-derived megabreccias”.

A slightly younger sample (but still within the age span of the Ryauzyak section), placed in the Upper *rhenana* Zone, from the Confusion Range, Rocky Mountains, Utah (Ginter 2008) yielded a different assemblage. Teeth of *Ph. bifurcatus* are still present, but *C. wildungensis* and *P. vetustus* are absent. Instead of these two latter sharks, there occur rather special, multicuspid teeth of *Diademodus utahensis* and *Lesnilomia sandbergi*. This sample (CON-3B of Sandberg *et al.* 1988) represents basal facies of the edge of Pilot Basin, whereas all Upper Frasnian samples from Lompret sections were collected from the relatively shallow-water limestones. Therefore, the difference in taxonomic composition may reflect different environmental conditions. It still needs to be confirmed, but perhaps the putative plankton feeders *Lesnilomia* and *Diademodus* (see Ginter 2008) preferred the open-marine, basal areas and sharks with crushing teeth, like *Protacrodus*, lived on and near the shallower submarine platforms.

Because of the events at the Frasnian–Famennian boundary, the *linguiformis* Conodont Zone is often missing from the sections. It also sometimes goes unrecognised, because its index conodont species are rather rare. Therefore, the information about sharks from this zone is relatively poor. However, from what we know, the most common taxon is *Cladodooides*

wildungensis, sometimes associated by *Protacrodus vetustus*. In the thoroughly studied section at Kowala-Wola Quarry (Holy Cross Mountains, Poland; Ginter 2002) and in the classic Kellwasserkalk site at Bad Wildungen (Hessen, Germany) thus far only these two shark species were found (on the affinity of a dubious isolated fin spine from Bad Wildungen, described by Gross 1933 as *Ctenacanthus jaekeli*, see Maisey 2005, p. 92). There were also noted occurrences of *Ph. bifurcatus* (Middle Urals, A. Ivanov pers. comm. 2015) and *L. sandbergi* (Ginter 2008; Devils Gate Pass, Nevada, sample DVG-7G of Sandberg *et al.* 1988) in the confirmed *linguiformis* Zone, but such records are extremely rare.

A very interesting and rich upper Frasnian sample was studied by Hairapetian and Ginter (2010). This sample, K5 from the Kale Sardar section in the Shotori Range, eastern Iran, yielded 57 chondrichthyan teeth and 93 scales. Among the teeth, only one belonged to *Ph. bifurcatus*, one to another phoebodont, 32 to *C. wildungensis*, 19 to *P. vetustus*, three to a strange cladodont *Arduodens flammeus* Hairapetian and Ginter, 2009, and one to a protacrodont *Deiham mansureae* Ginter, Hairapetian and Klug, 2002. Unfortunately, despite the abundance of conodonts in the sample, its age could not be precisely defined, so it is unknown whether it represents the Upper *rhenana* or *linguiformis* zones. Nevertheless, it can be observed that the taxonomic composition of the assemblage from sample K5, with the absolute predominance of *C. wildungensis* and *P. vetustus*, only accessory occurrence of phoebodonts and other sharks, and the total lack of *Lesnilomia* and

Diademodus, is more similar to those from the Upper Kellwasserkalk (Kowala-Wola and Bad Wildungen), than to that from the Confusion Range. According to Gholamalalian (2007), the dominance of polygnathid conodont biofacies species in sample K5 suggests a distal shelf or slope palaeoenvironment. This confirms that these two pairs of late Frasnian sharks (*Lesnilomia–Diademodus* vs. *Cladodoidea–Protacrodus*) must have had different environmental preferences (basinal vs. shallower areas, respectively).

CONCLUSIONS

If we consider the late Frasnian interval covered by the Lower *rhenana* Zone through to the lower part of the *linguiformis* Conodont Zone (i.e., before the formation of the Upper Kellwasserkalk horizon), we can observe at least three chondrichthyan biofacies in the South Laurussian – North Gondwanan seas (Text-fig. 7). The first, which can be called the phoebodont biofacies, is characterised by the abundance of *Phoebodus* species, and particularly *Ph. latus* or *Ph. bifurcatus*, and the low input of *C. wildungensis* and *P. vetustus*. This biofacies developed in the subequatorial seas covering drowned carbonate platforms, in perfectly oxygenated, pelagic, but not very deep conditions. Lompret, Ryauzyak, and Horse Spring sections represent this biofacies. The typical taxa of the second, basinal biofacies, are *L. sandbergi* and *D. utahensis*, sharks with multicuspid teeth. The absence of *C. wildungensis* and *P. vetustus* and the low number of phoebodonts suggest either the great depth and/or distance from submarine platforms, or unfavourable conditions (low oxygen level?) lower in the water column.

The third, protacrodont biofacies, with the dominance of *C. wildungensis* and *P. vetustus*, observed at Kale Sardar, most probably represents relatively shallow water conditions, but not much shallower than in the case of Ryauzyak or Lompret. Some other factor than the water depth must have been the reason of the reduced number of phoebodonts. It has been suggested earlier that the phoebodonts of *Ph. latus* – *Ph. bifurcatus* lineage “were extremely stenothermic, warm water-dependent animals, which could not survive sudden cooling of subtropical areas” (Ginter 2002, p. 337). This was said in the context of their disappearance at the Frasnian–Famennian boundary, but also might be applied to the differences between the Late Frasnian faunas of the South Urals and eastern Iran. However, the postulated cooling in the pre-Kellwasser time is not reflected in the isotope

curves (Joachimski *et al.* 2004 *fide* Roelofs 2015) and nothing is observed to support the concept of significantly cooler conditions in Iranian waters. Therefore, although it is evident now that the reduction in diversity and abundance of phoebodonts in the seas between Laurussia and Gondwana started long before the final Frasnian–Famennian crisis, most probably in the Upper *rhenana* Zone, and that in some areas they began disappearing earlier than in the others, the reason of that process still remains unknown.

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