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The early Famennian recovery of phoebodont sharks

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ABSTRACT:

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Early Famennian microvertebrates from the Cape Fortune Member, Parry Islands Formation, of the Beverley Inlet area of Melville Island, Arctic Canada, comprise the teeth and possible scales of a new phoebodontid shark, *Phoebodus rayi* sp. n., of a protacrodont shark, *Protacrodus aequalis* IVANOV, and rare teeth of other sharks. The new phoebodont from the early Famennian *crepida* Zone is closely related to the Lazarus taxon, *Ph. typicus* GINTER & IVANOV. *Ph. typicus* emerges in the early Famennian Late *triangularis* Zone following the phoebodont shark hiatus subsequent to the Kellwasser Event which apparently caused the extinction of most earlier phoebodonts.

Key words: Chondrichthyes, microfossils, Devonian, Arctic Canada.

INTRODUCTION

Sample GSC C-128762, collected in early 1980s by Dr R. THORSTEINSSON from the Parry Islands Formation, Cape Fortune Member, in the Beverley Inlet Area (75°08’50”N, 107°32’W) of Melville Island (Text-fig. 1) yielded many fish microfossils of chondrichthyan, sarcopterygian, palaeoniscoid and possible acanthodian origin (non-chondrichthyan remains are available on CD-Rom held at the Geological Survey of Canada). The age of the material was determined, on the basis of icriodontid and palmatolepid conodonts, as the early Famennian, Early or Middle *crepida* conodont Zones.

Among the shark remains, the most common are over 200 specimens of teeth of a new species of *Phoebodus*, the third phoebodont species recorded thus far from the early Famennian. In addition there are protacrodont sharks represented by a few teeth and scales and rare shark teeth less certainly ascribed. The bulk of the shark scales, however, are not clearly of forms previously described and so we illustrate them here and tentatively suggest they might belong to *Ph. rayi*.

GEOLOGICAL BACKGROUND

Exploration and mapping of Melville Island for oil and gas led to the discovery of vertebrate bearing horizons in the Upper Devonian. HARRISON (1995) has fully described the geology and tectonic history of the Melville Island salt-based fold belt which is the western part of the lower Palaeozoic Franklinian mobile fold belt situated between flat-lying Cambrian to Devonian rocks of the Arctic Platform to the south and post-orogenic Carboniferous to Tertiary strata of the Sverdrup basin to the north.

Vertebrate remains have been found in both Middle and Upper Devonian rocks on Melville

Island. Middle Devonian bonebeds, some of which are housed at Drumheller Museum, near Calgary, Canada, have not yet been investigated (NORRIS *in* HARRISON 1995, p. 315; TURNER 1991, *personal observations*). Classic Old Red Sandstone facies in the Frasnian bears bothriolepid and holoptychiid remains (TURNER 1993). TOZER and THORSTEINSSON discovered "crossopterygian" remains in the Beverley Inlet Formation (NORRIS *in* HARRISON 1995, p. 318). The latter underlies the Parry Islands Formation which contains a limestone which has provided one sample from conodont-dated early Famennian rocks. This sample, GSC C-128762, yielded the marine microfauna rich in chondrichthyan remains which we describe here. This material was collected by C. HARRISON during mapping in the early 1980s and was forwarded to one of us (ST) by Dr. Ray THORSTEINSSON.

The Parry Islands Formation

Type section

The Parry Islands Formation is the upper of two marine and nonmarine siliciclastic formations that make up the "Griper Bay Subgroup" of EMBRY & KLOVAN (1976). The type section is situated 8 km north-northeast of the head of Beverley Inlet, southeastern Melville Island (HARRISON 1995, fig. 51). The Parry Islands Formation is exposed on Devon Island, Bathurst and adjacent small islands, and Prince Patrick Island. Five distinct units have been recognized and mapped (Text-fig. 2). The sample discussed here came from the second lowest unit, the Cape Fortune Member of EMBRY & KLOVAN (1976). The Cape Fortune Member consists of grey-green and medium green weathering, fine to very

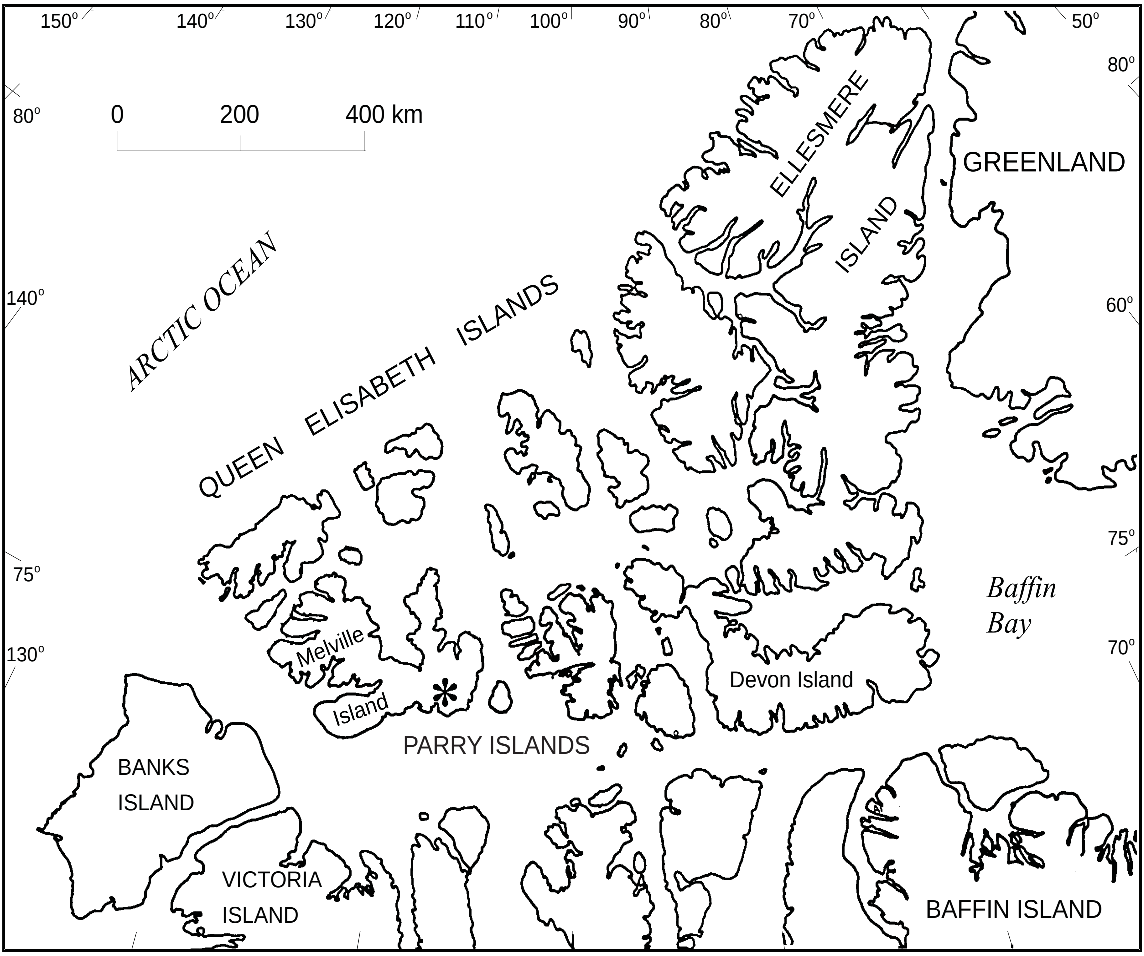

Fig. 1. Sketch map of a part of Arctic Canada, showing the position of Melville Island; the study area marked with an asterisk

fine grained fossiliferous sandstone, siltstone, silty micaceous mudrock, and minor, argillaceous limestone. Macrofauna found in this member includes brachiopods, bivalves, trilobites, crinoids and cephalopods (Harrison 1995). Besides fish and conodonts, other phosphatic microfauna include small hand-shaped phyllocarid remains which have been identified previously as shark mucous membrane denticles (Ivanov & Lukševičs 1994, fig. 1a, b). Excellent exposures of the Cape Fortune Member, which has a thickness of between 50-420 m, occur in the vicinity of the type section and in coastal cliffs along the east arm of Weatherall Bay. GSC C-128762 came from 7.8 km upstream and northeast of the head of Beverley Inlet on a small ridge; the fish-bearing horizon, being 60 m above the base of the member, was treated for conodonts (Higgins *in* Harrison 1995, p. 318).

Embry & Klovan (1976) interpreted the Parry Islands Formation as deposited in a variety of fluvial, deltaic and shallow-marine settings. The gradational transition from fluvial Burnett Point Member through marine Cape Formation marks a rise in relative sea level beginning at the base of the formation.

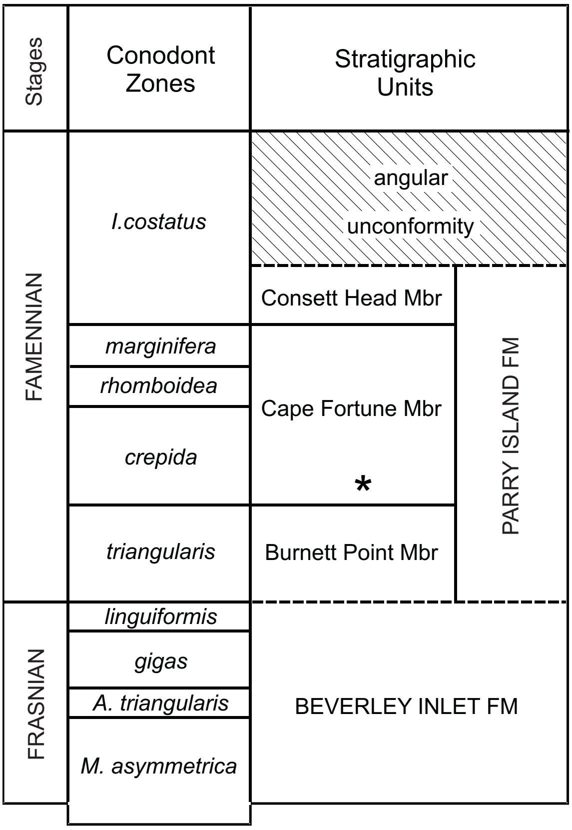

Fig. 2. Stratigraphic sequence of the Upper Devonian on Melville Island; asterisk marks the position of the studied fish fauna

Age and correlation

The Parry Islands Formation is dated on palynomorph assemblages as late Frasnian through middle Famennian or early late Famennian. Two conodont assemblages of early Famennian (Early-Middle *crepida*) and late Famennian (*Icriodus costatus* local conodont zone) ages occur in the type section of the Cape Fortune Member near Beverley Inlet (reports of Uyeno & Higgins *in* Harrison 1995). The studied fish fauna occurs together with the first of the mentioned conodont assemblages in the Early or Middle *crepida* zones.

MATERIAL

The *crepida* Zone fish fauna, which comes from a small amount of residue, comprises a diverse assemblage of chondrichthyan, sarcopterygian, palaeoniscoid and possible acanthodian teeth, scales and lepidotrichia. More than 500 specimens of chondrichthyan origin were recovered. Specimens are of bright amber colour, very well preserved, often showing details of the structure or ornamentation which cannot be seen elsewhere. The cusps, however, especially of larger teeth, are usually broken. Sometimes slight abrasion can be observed. Canadian specimens (GSC) are housed in the National Type Collection, Ottawa, and in the Geological Survey of Canada, Calgary. Comparative specimens are housed in the Geology and Mining Museum, Sydney (MMMC); Institute of Geology, University of Warsaw, Warsaw (IGPUW); and Laboratory of Palaeontology, St. Petersburg University, St. Petersburg (LP).

SYSTEMATIC ACCOUNT

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838

Order indeterminate
Family Phoebodontidae Williams, 1985
Genus *Phoebodus* St. John & Worthen, 1875

TYPE SPECIES: *Phoebodus sophiae* St. John & Worthen, 1875

Phoebodus rayi sp. n.
(Text-figs 3E-G, 4A-L, 5A-I, 6A-U, 8E-F)

HOLOTYPE: Specimen GSC 115385 (Text-fig. 3E-G) from sample C-128762, Famennian, Early or Middle *crepida* conodont Zones; Parry Islands Formation, Cape Fortune Member; Beverley Inlet Area (75°08'50"N, 107°32'W) of Melville Island, Arctic Canada.

ETYMOLOGY: In honour of Dr. Ray Thorsteinsson, OC, for his contributions to Palaeozoic geology of the Canadian Arctic.

STRATIGRAPHIC RANGE: Famennian, Early or Middle *crepida* conodont zones

OCCURRENCE: Famennian, Early or Middle *crepida* conodont zones; Parry Islands Formation, Cape Fortune Member; Melville Island, Canada.

MATERIAL: Over 200 specimens of teeth including co-types, figured specimens GSC 115385-115400. CD-Rom of image files held at the Geological Survey of Canada.

DIAGNOSIS: The teeth with three- to five-cuspid phoebodont-type crowns; the cusps rounded in cross section, gently striated on both labial and lingual sides. The tooth base roughly pentagonal, widening lingually and later narrowing to form an obtuse lingual angle; the button hemispherical to oval, situated at the lingual end of the base.

Teeth

DESCRIPTION : The range of size is about 1-2 mm. Teeth are mainly of two types, five-cusped and three-cusped. The cusps are long and slender and slightly sigmoidal. The angle between the median and the lateral cusp is about 45 degrees. Perfect preservation of the tooth surface often allows observation of the ornament on the cusps. The cusps are ornamented with numerous subparallel cristae on the labial and lingual sides (Text-figs 4G, I, K, L). The cristae are usually more prominent on the labial side. The number of cristae can vary from two to six, rarely more. The cusps have a lateral keel which unites the main and accessory cusps sometimes with a distinct web (Text-figs 4B, J, K, 5G). Cristae run parallel with the cusps but can make *Y*-shaped junctions at the proximal end of the cusps (Text-figs 3E, 4A), and can unite in the middle or towards the distal end of the cusps. The abrupt boundary between the crown and the base, probably the end of the enameloid layer, is clear in some specimens (Text-figs 4A, C). As usual for phoebodonts, number of intermediate cusplets may differ from specimen to specimen. Most commonly there are two cusplets, but many teeth lack cusplets at all (Text-figs 5B-C) or, rarely, only one cusplet is present (Text-figs 4A, J, K; compare *Ph. gothicus* in Ginter 1990).

Specimens of *Ph. rayi* sp. nov. display considerable variability, especially as far as the base outline is concerned. The lingual angle varies from 135 to almost 180 degrees; the length (labio-lingual) to width (mesio-distal) ratio may be from 0.5 to 0.8. The base is usually pentagonal in outline as in the holotype (Text-figs 3E, 4H). In some specimens the base is more laterally elongated forming a subelliptical outline (Text-figs 4C, J), and in the others it is narrower and longer, almost trapezoidal (Text-fig. 4A). Between these two extremes are gradations of basal shape. The base is slightly arched (Text-figs 5E, G). The labial surface of the base is low with the prominent median arcuate tubercle typical of *Phoebodus* (Text-figs 4D, G-I, L, 5D, E, I). On the apical side of the lingual extension of the base there is a well-developed button at the lingual rim which can be rounded (Text-figs 3E-G), more oval (Text-figs 4B, 5F-H) to strongly elongate (Text-fig. 4C). The lateral elongation of a button corresponds to the width of a base. The button is penetrated by a few nutritive foramina (usually four or less, Text-fig 4C). If the base is narrow the button appears to have only one large basal canal opening (Text-figs 3E, G, 4G, 5C, G). The button can be subdivided into two or three parts (Text-figs 4J-K). The basal surface is gently concave with the deepest depression close to the labial tubercle (Text-fig. 4D). There can be a large medial canal opening (Text-fig. 4H) or a series of smaller foramina (Text-figs 4D, 5D).

One possible pathological specimen (Text-figs 4E-F) has a skewed median, labially-directed cusp producing a larger angle between the basal and crown surfaces. Also the button is reduced to an elongate ridge-like thickening across the lingual rim.

A few specimens (Text-figs 4J-L), which we include here in *Phoebodus rayi* sp. n., have a

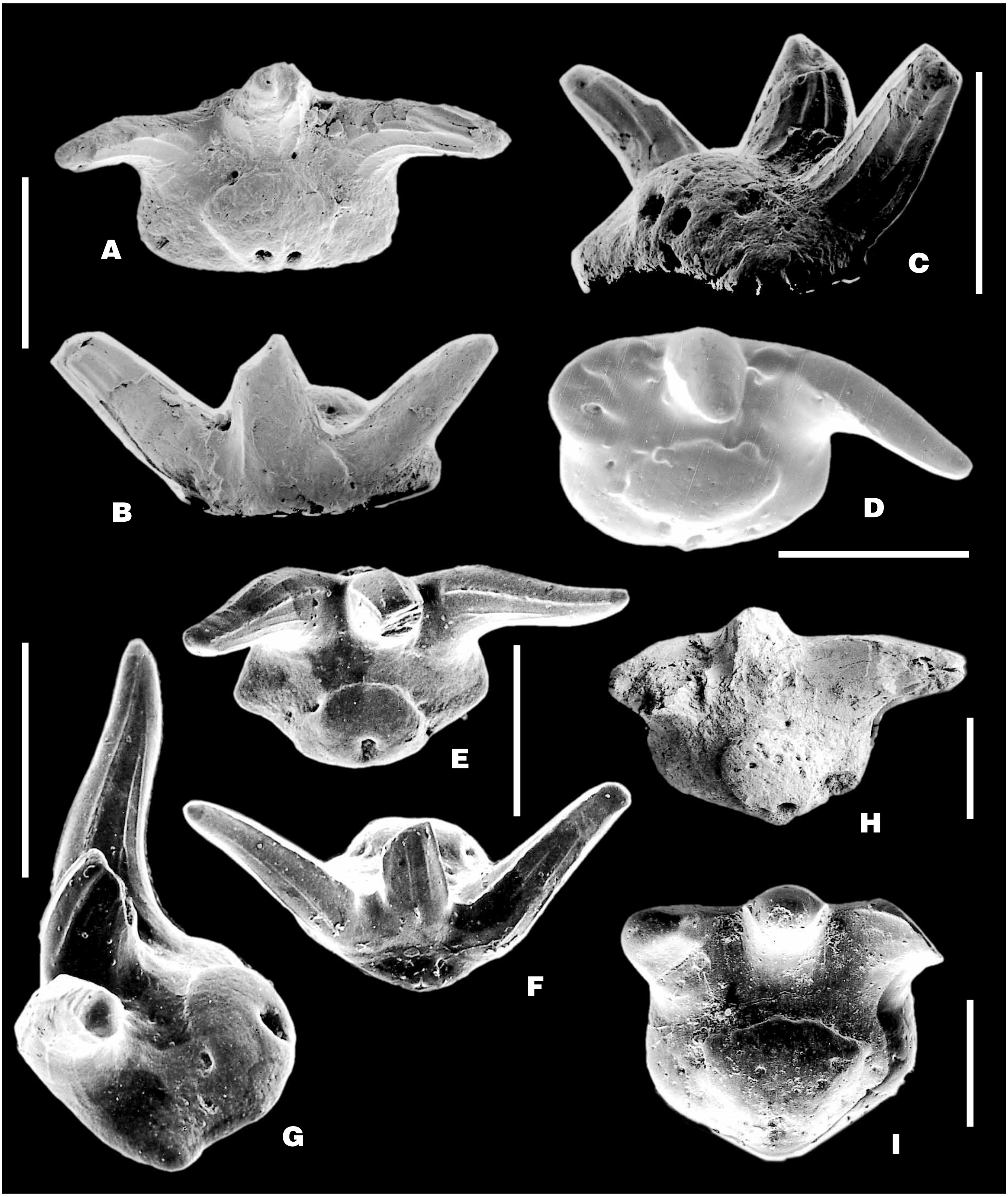

Fig. 3. **A-D** – *Phoebodus typicus* Ginter & Ivanov; A-C – MMMC 01629 from Australia, north Queensland, Myrtlevale Formation near the base of Topsy Hill Beds, sample C410, Early *marginifera* Zone; occlusal, labial and oblique lingual views; D – LP 7-25 from the South Urals, Ryauzyak River, sample 6483, Early *marginifera* Zone; occlusal view; A-B × 56, C × 68, D × 60; **E-G** – *Phoebodus rayi* sp. n.; GSC 115385, holotype, from Arctic Canada, Melville Island, Parry Island Fm., sample GSC C-128762, Early or Middle *crepida* Zone; occlusal, labial and oblique lateral views; E-F × 56, G × 75; **H-I** – *Phoebodus turnerae* Ginter & Ivanov; occlusal views; H – IGPUW Ps/1/102 from Poland, Holy Cross Mts, Miedzianka Hill, sample Md-6, *rhomboidea* or Early *marginifera* zones × 30; I – LP 7-24 from the South Urals, Ryauzyak River; sample 6478, Early or Late *rhomboidea* Zone; × 40; Scale bars = 0.5 mm

partially divided button more characteristic of stethacanthids, e.g. *Stethacanthus thomasi* (TURNER 1982). Probably the growth pattern of the nutritive canals determines the structure of the button. Because of the mixture of phoebodontid and stethacanthid characters observed in these specimens, there remains a small doubt about their systematic position. For now we regard them as falling within the variation of dentition morphology caused by slight differences in growth of the teeth and the position of the main basal canal in relation to the button.

REMARKS: The teeth of *Ph. rayi* sp. nov. are characterised by crowns typical of other early Famennian phoebodonts: *Ph. typicus* GINTER & IVANOV, 1995 and *Ph. turnerae* GINTER & IVANOV, 1992. However, the wide, pentagonal

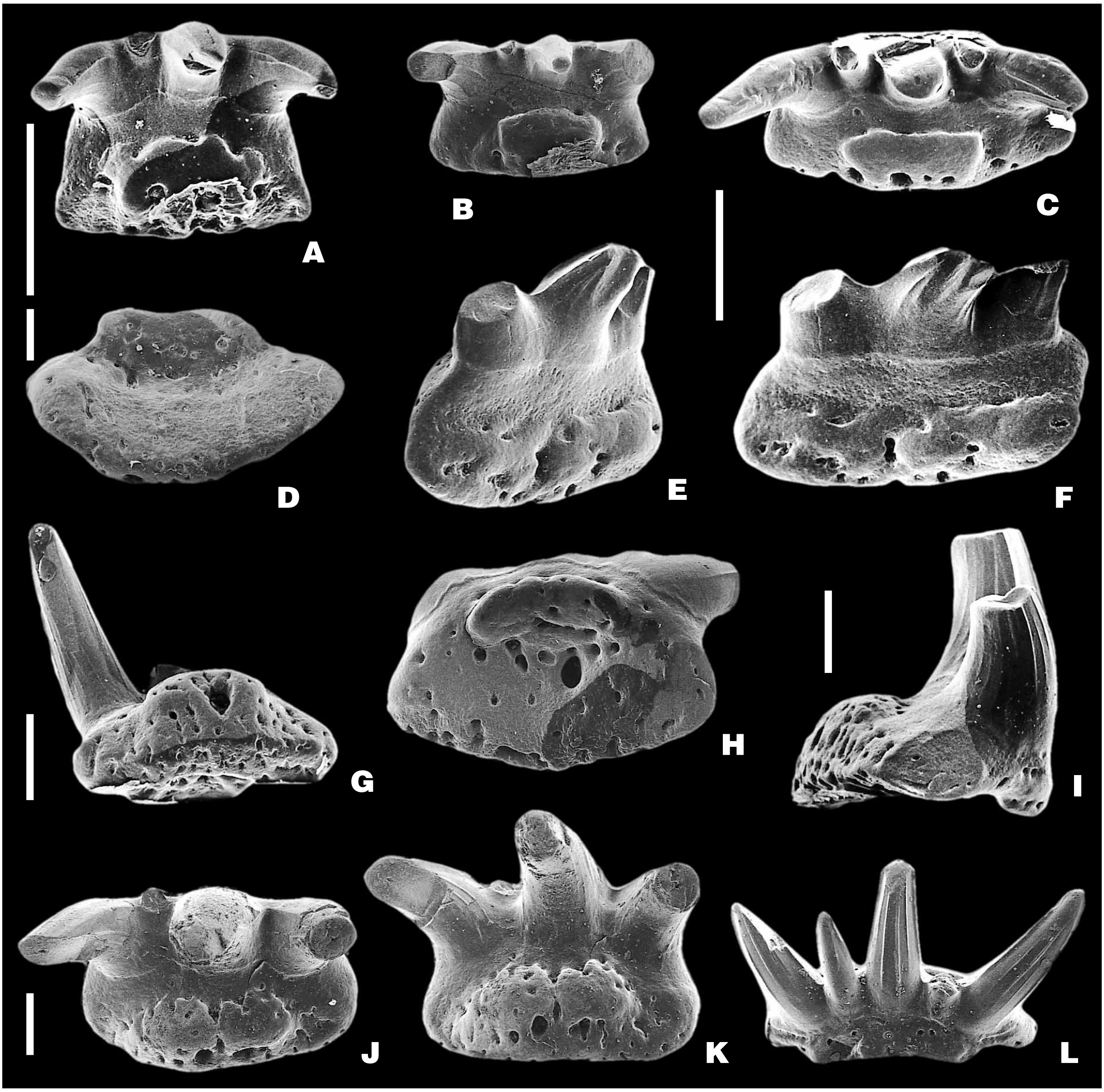

Fig. 4. Teeth of *Phoebodus rayi* sp. n.; Arctic Canada, Melville Island, Parry Island Fm.; sample GSC C-128762, Early or Middle *crepida* Zone; **A** – GSC 115386, × 50; **B** – GSC 115387, × 37; **C** – GSC 115388, × 37; **D** – 115389, × 22; **E-F** – GSC 115390, × 37; **G** – GSC 115391, × 25; **H** – GSC 115392, × 25; **I** – GSC 115393, × 25; **J-K** – GSC 115394, × 18; **L** – GSC 115395, × 18
A-C, J – occlusal; D, H – basal; F, G, K – lingual; E – oblique lingual; I – lateral; L – labial views; Scale bar = 0.5 mm

base, with a button on its lingual end, is unique for the new species. The base of *Ph. typicus* is clearly rectangular, with the button, in most cases, in the center of the base. The base of *Ph. turnerae* is much more similar to that of *Ph. rayi*: it is pentagonal and the button is at the lingual end, but while the width of the base in *Ph. turnerae* never exceeds the width at the crown region, the distance between the lateral angles of the *Ph. rayi* base is always longer than the width of base under the crown.

The above remarks concern characteristic and well preserved specimens of the three species. Since outlines of the base and of the button (especially the length to width ratio) vary from specimen to specimen, some forms of *Ph. rayi* may be mistakenly attributed to *Ph. turnerae* or *Ph. typicus*, or *vice versa*, especially when the bases are not in a perfect state.

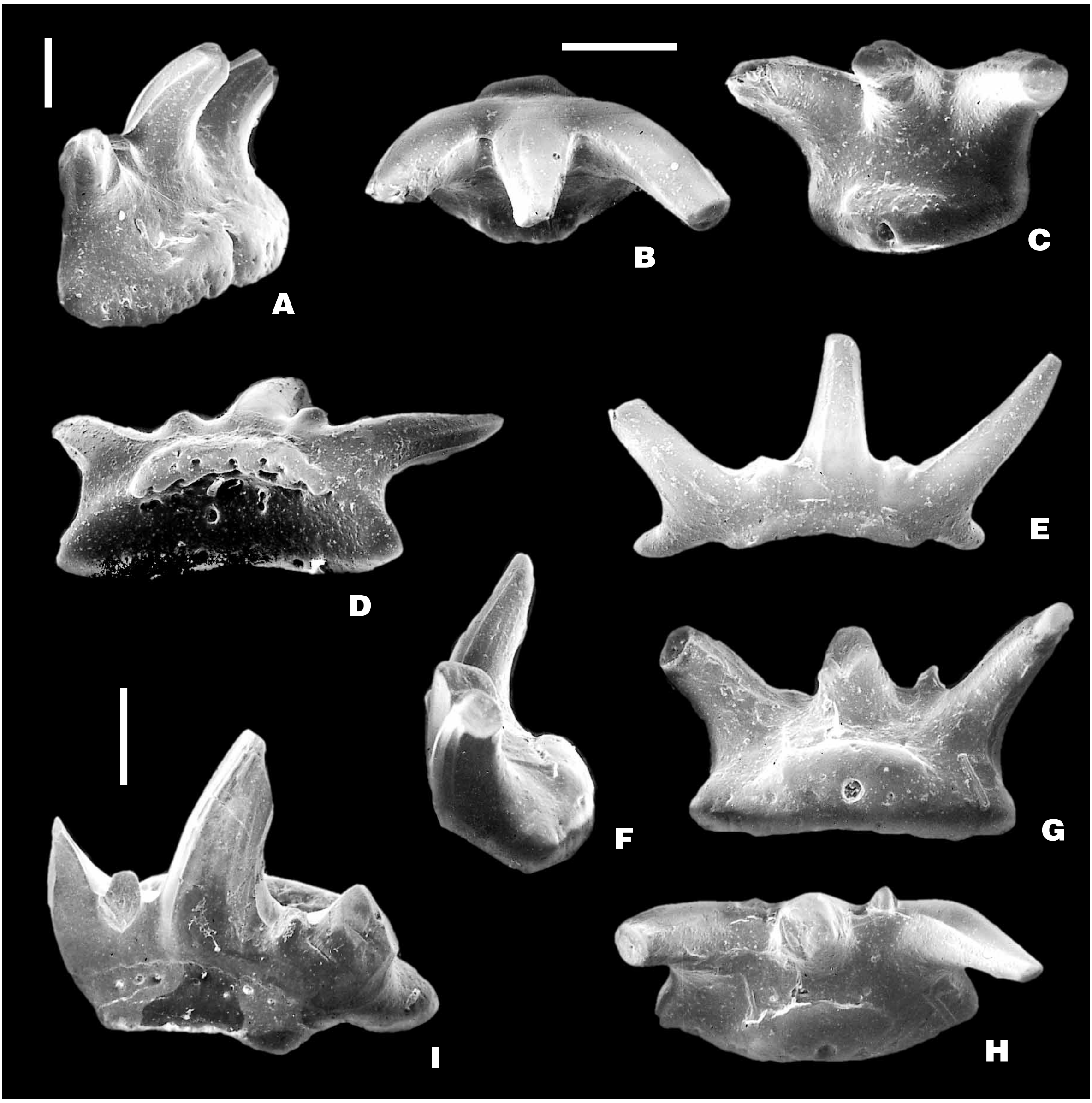

Fig. 5. Teeth of *Phoebodus rayi* sp. n.; Arctic Canada, Melville Island, Parry Island Fm.; sample GSC C-128762, Early or Middle *crepida* Zone; **A** – GSC 115396, oblique lingual view, × 20; **B-C** – GSC 115397, occlusal and lingual views, × 33; **D-E** – GSC 115398, baso-labial and labial views, × 27; **F-H** – GSC 115399, lateral, lingual and occlusal views, × 27; **I** – GSC 115400, oblique labial view, × 27; Scale bar = 0.5 mm

Scales

DESCRIPTION: Here we describe the numerous scales (at least 300 extracted) found in sample C-128762; figured specimens are numbered GSC 115406-115425. We consider them to represent one sequence of scale forms which grade into one another which we take to represent examples from the squamation of one taxon of shark.

The scales are typical aggregate dermal denticles, composed of many odontodes, originating generally from the median anterior rim, on a solid, bony base. They vary in size from just over 0.5 mm to around 1.5 mm, not greatly different from the size range of the teeth.

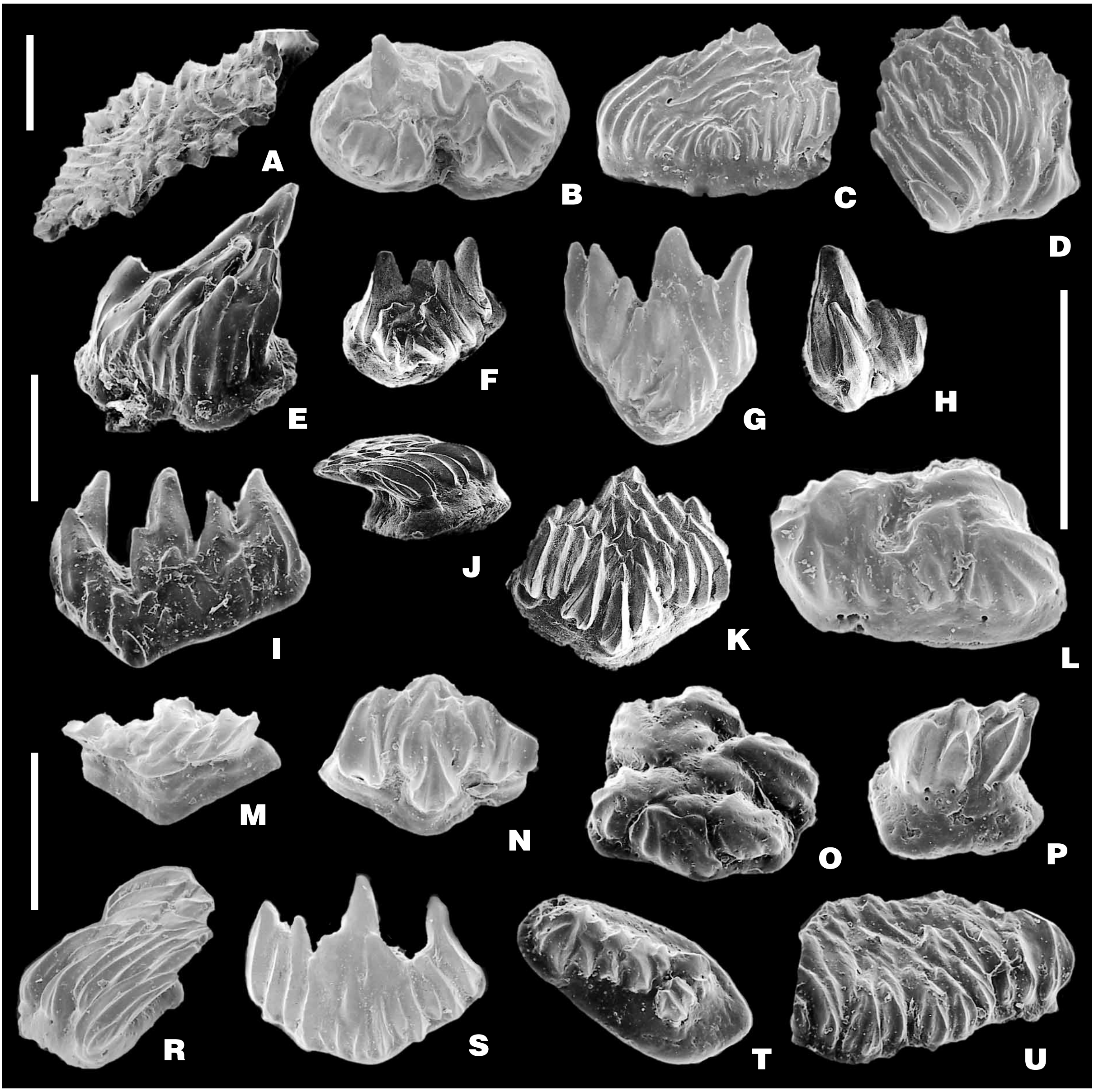

Fig. 6. Scales of *Phoebodus rayi* sp. n.; Arctic Canada, Melville Island, Parry Island Fm.; sample GSC C-128762, Early or Middle *crepida* Zone; **A** – GSC 115408, × 28; **B** – GSC 115409, × 28; **C** – GSC 115410, × 28; **D** – GSC 115411, × 28; **E** – GSC 115412, × 37; **F** – GSC 115413, × 37; **G** – GSC 115414, × 37; **H** – GSC 115415, × 37; **I** – GSC 115416, × 37; **J-K** – GSC 115417, × 37; **L** – GSC 115418, × 70; **M-N** – GSC 115419, × 45; **O** – GSC 115420, × 45; **P** – GSC 115421, × 45; **R** – GSC 115422, × 45; **S** – GSC 115423, × 45; **T** – GSC 115424, × 45; **U** – GSC 115425, × 45; Scale bar = 0.5 mm

The basal shapes are typical of Palaeozoic complex shark scales, varying from rhombic (Text-figs 6M-N, 8F) to sub-rhombic to sub ellipsoid (Text-figs 6T, 8E). The bases are also gently rounded and possess no clear or only one laterally placed small pulp depression. Ventrally the base of most scales is flat (Text-fig. 8E) to slightly convex (Text-figs 6J, 8F) but this might be a consequence of the individual shark's age and ontogeny of the scales.

The crown of most scales is composed of an initial anterior odontode, triangular in shape, sometimes with one or more pair of ridges. From this the crown expands with a series of rows of odontodes some of which curve gently towards a mid posterior point (Text-figs 6C, K, N). Although we have not as yet investigated internal structure, we presume these zones represent centrifugal growth within the dentine of scale crown. Distinct foramina can be seen especially at the crown/base interface (Text-figs 6D, L, P, R). Generally the scale crown is relatively flat (e.g. Text-fig. 6J) but occasionally the crown tubercles point upwards; these can be few in number (Text-fig. 6P) or several (Text-fig. 6T). Some scales appear to represent two convergent units (Text-fig. 6B). Whereas the former seem to be typical body scales these latter might be the snout or oral scales of the shark. Other rounded scales with a radiating pattern of odontodes (Text-fig. 6O) might also be head scales. Comparison of scale shapes in relation to position on the body is made here by reference to modern sharks as illustrated for example by REIF (1985) and for certain Palaeozoic sharks (*see* ZANGERL 1981).

The crown ornament mostly consists of simple ridges generally converging into the top of the triangular units. Occasionally the anterior ridges are split giving a double ridge (*e.g.* Text-figs 6C, K, N, R, U). There are even indications of the type of cusp ornament seen in some later phoebodonts, with a small ridge linking the stacked triangular segments. Some scales have a prominent notch (Text-figs 6B, E) which might mark the position of a sensory canal.

Some scales which are more laterally divergent can have several triangular segments stacked one close to another, ending in one or more prominent points (Text-figs 6G, I, S). These crowns are relatively low (Text-fig. 6M) to more angular (Text-fig. 6E). These scales resemble in style the stemmatodont branchial denticles of symmoriid and stethacanthid sharks and thus we consider that these might be similar (ST. JOHN & WORTHEN 1875, ZIDEK 1993). Similar scales have been illustrated by IVANOV & LUKŠEVIČS (1994, fig.2d, e) which they called *Cladolepis* type scales. We do not, however, think our scales resemble closely those called *Cladolepis* by GROSS (1973).

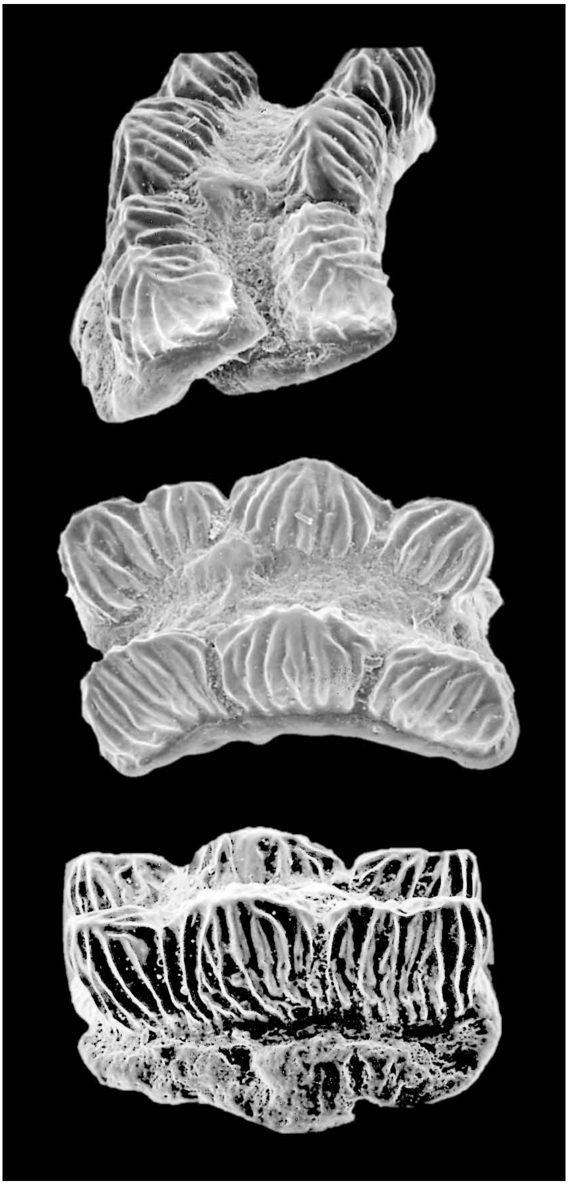

Fig. 7. **A-C** – *Protacrodus aequalis* IVANOV; GSC 115401 from Arctic Canada, Melville Island, Parry Island Fm.; sample GSC C-128762, Early or Middle *crepida* Zone; two imbricating teeth in lateral, labial and lingual views; × 56; Scale bar = 0.5 mm

Large flattened scales are made up of several anterior odontodes forming rows of ridges some curving inwards to the midpoint, while others end in further posterior points in parallel. Some of these scales have as many as 14 anterior cristae (Text-fig. 8A). We think these might be the flank scales.

REMARKS: Because the large majority of shark teeth found in the Melville Island sample belong to the new phoebodont species, *Phoebodus rayi,* it seems reasonable to us that the shark scales might be also considered as belonging to this phoebodont. If this is true, our report would be the first one presenting scales of any *Phoebodus*. No complete phoebodont shark has yet been found, all taxa being known from teeth only (*see* GINTER & IVANOV 1992 *and* GINTER 1998 for discussion of so-called "*Phoebodus*" *heslerorum*). However, we surmise that such a shark would possess a squamation of growing scales of the type illustrated here, with a range of scale forms including snout, head, flanks and mucous membrane denticles and branchial scales (e.g. REIF 1982). Needless to say, any future discovery of articulated phoebodont shark material may alter our conclusion regarding these scales and about their relative positions in the squamation.

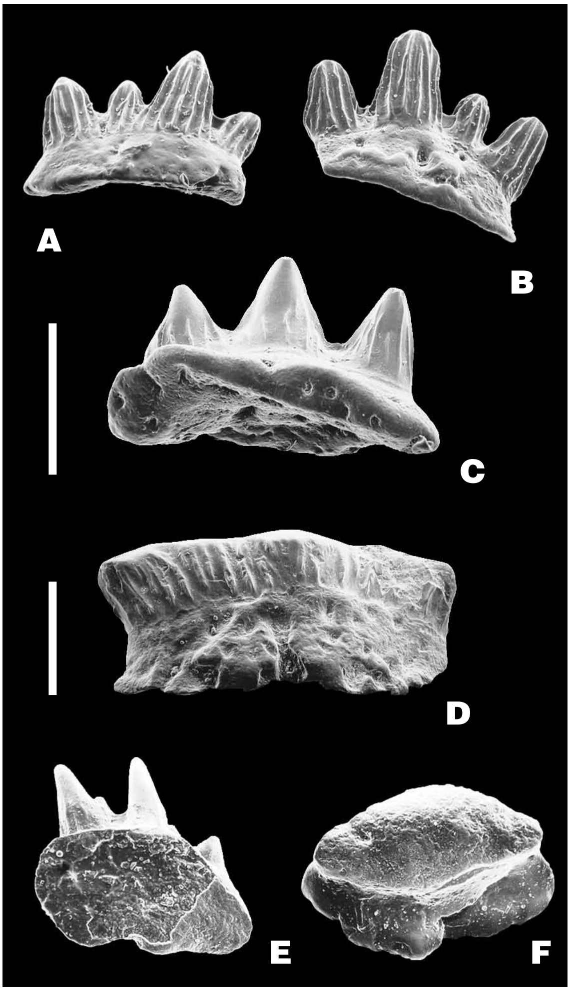

Fig. 8. Teeth and scales from Arctic Canada, Melville Island, Parry Island Fm.; sample GSC C-128762, Early or Middle *crepida* Zone; **A** – GSC 115402, protacrodontid or stethacanthid tooth, lingual view, × 40; **B** – GSC 115403, protacrodontid or stethacanthid tooth, lingual view, × 40; **C** – GSC 115404, tooth of Elasmobranchii indet, lingual view, × 40; **D** – *Protacrodus* sp., GSC 115405, lingual? view, × 30; **E** – *Phoebodus rayi* sp. n., scale, GSC 115406 basal view, × 30; **F** – *Phoebodus rayi* sp. n., scale, GSC 115407, basal view, × 30

Scale bar = 0.5 mm

Cohort Euselachii HAY, 1902
Superfamily Protacrodontoidea ZANGERL, 1981
Genus *Protacrodus* JAEKEL, 1921

Protacrodus aequalis IVANOV, 1996
(Text-figs 7A-C)

cf. 1982. *Protacrodus* sp. 'C' S. TURNER, pp. 125-126, fig. 7.

? 1994. *Protacrodus* sp. 'C'; A. IVANOV & E. LUKŠEVIČS, pp. 25, 26, fig. i, j.

1996. *Protacrodus aequalis* sp. nov.; A. IVANOV, pp. 420, fig. 6a-g.

MATERIAL: 3 or 4 teeth.

DESCRIPTION: Tooth-crown of *P. aequalis* is composed of three thick, broad and low cusps, slightly compressed labio-lingually. The cusps are almost equal in size, the median one may be the largest; the cusp bases are fused. All the cusps are ornamented with strong cristae; the ribs are wavy, sometimes dividing or anastomosing at various points; some join at the tips of the cusps, but all reach the apical crest of the crown separately. The base is convex, its short lingual extension forming a rounded triangle.

One specimen (Text-fig. 7A-C) is composed of two teeth with imbricating bases, probably showing the relative position of teeth in a tooth family. Such "double" protacrodont teeth are not unusual in the fossil record (GINTER 1995), whereas this phenomenon is unknown so far, for instance, in phoebodont and cladodont shark teeth. One of the lateral cusps of a tooth from this cluster is divided in two. A similar condition was observed on a tooth of *P. aequalis* from the Tournaisian of the South Urals (GINTER 1994, fig. 31D).

REMARKS: Teeth of *P. aequalis* from Melville Island differ slightly from those described from the type locality (Sikaza River, South Urals, IVANOV 1996), mainly by the ornamentation of the cusps. In the type specimens, the ribs are more regular and usually join at the tips of the cusps. However, other features, like shape of the cusps and the base, are so similar that our identification of Canadian specimens seems warranted.

OCCURRENCE: Famennian-Tournaisian, Early-Middle *crepida* – *sulcata* (? *typicus*) zones; Melville Island; elsewhere in Australia, Russia and Latvia.

Protacrodus sp.

One tooth in our sample (GSC 115405, Text-fig. 8D) has a low occlusal ridge rather than clearly separate cusps. It closely resembles one described by IVANOV & LUKŠEVIČS (1994, fig. 2f, g) from the early Famennian Kursa regional Stage of Latvia.

Elasmobranchii indet. teeth
(Text-figs 8A-C)

Two broken teeth (GSC 115402-115403, Text-figs 8A-B), apparently possessing five thick cusps covered with strong cristae might represent either protacrodonts or stethacanthids.

One tooth (GSC 115404, Text-fig. 8C) is a new form with three equal triangular cusps but an unusual torus-like base which is asymmetrical.

DISCUSSION

In general, phoebodonts from the early Famennian are very rarely found, in comparison to those from the late Frasnian or the late Famennian. The new taxon described here represents one of the oldest Famennian phoebodonts. Only two regions outside Arctic Canada are known today to have yielded specimens of *Phoebodus* from the Late *triangularis* or *crepida* conodont Zones: Ryauzyak river on the western slope of the South Urals, and the Kuznetsk Basin. In the other places (Australia, Poland) the first phoebodonts, after the early Famennian break, appear in the *rhomboidea* or Early *marginifera* Zones, although one or two teeth from a possible early to mid Famennian horizon of New South Wales, Australia, are recorded (JONES & *al.*, *in press*). Phoebodonts from the Early and Middle *triangularis* Zones have never been found.

As articulated skeletons of phoebodont sharks are unknown, only differences between their dentitions can lead to any conclusion on their interrelationships and evolution. Teeth of early Famennian phoebodonts considerably differ from those from the late Frasnian, as well as from later Famennian ones; however, in the latter the differences are less dramatic. On the other hand, distinction between the three known phoebodont species of the *triangularis* – *rhomboidea* Zones, *Ph. typicus*, *Ph. turnerae* and *Ph. rayi* sp. nov., is rather difficult and often arbitrary. The tooth crowns, as mentioned above, are generally identical in all the three species, and the bases differ only by secondary characters. Since teeth can vary in a tooth row, and from one row to another, the less characteristic forms often occur, and such forms, even originating from different species, may resemble each other. Thus, only the most characteristic tooth forms were used to decide that these three species can be distinguished.

It is important to add, that the overall appearance of the teeth of the three early Famennian species, especially of *Ph. typicus*, is very close to that of the type species, *Ph. sophiae* from the late Givetian. Unless the time gap and the difference in size (the average tooth of *Ph. sophiae* is 2-3 times larger than that of *Ph. typicus*), they could be considered conspecific. In fact, teeth of that type also were found in the late Frasnian, but those are isolated and very rare specimens.

Phoebodonts of the *sophiae*/*typicus* lineage probably were much less numerous and competitive than the highly specialised sharks from the *bifurcatus* group (*Ph. bifurcatus*, *Ph. latus*), which occupied the most favourable niches on the continental margins during the late Frasnian. The latter sharks, whose teeth are very characteristic of the late Frasnian, were extinct by the Frasnian-Famennian boundary (Text-fig. 9). Teeth of that type did not appear again in the history of *Phoebodus*. The *sophiae*/*typicus* group survived the unfavourable conditions of the Frasnian/Famennian boundary (WALLISER 1995), possibly in some peripheral refugia. After the return of pelagic conditions to the areas surrounding the Old Red Continent in the later *triangularis* time, sharks of that group began a slow adaptive radiation. However, during the early

Famennian the evolutionary changes were rather small, and significant differentiation started only in the *marginifera* Zone. From the Early *marginifera* Zone we know the most characteristic and undoubted forms of *Ph. typicus* and *Ph. turnerae*, and the first appearance of *Ph. gothicus*. Slightly later there appeared the immediate descendant of the latter, a species of *Thrinacodus*.

Thus, in the early Famennian there is a specific "grey zone" of coexisting, only slightly differentiated phoebodont species, derived from a presumed common ancestor, which survived the Kellwasser crisis (Lazarus species). The transgression of the Early *marginifera* Zone allowed further differentiation of the genus *Phoebodus*, even leading to the emergence of new genera. A similar situation was described by SANDBERG & ZIEGLER (1973) for conodonts from the *Palmatolepis glabra* group; that group was derived from a common ancestor, which emerged from *P. tenuipunctata*. The early forms of platform conodonts of that group, occurring from the Late *crepida* Zone to the base of the Early *marginifera* Zone, are sometimes so similar to each other, that the authors marked that interval on their diagram as a "field of transition between related forms". In the Early *marginifera* Zone the situation changed: typical, easily distinguished forms of older species have already developed, and quite new, very characteristic species (*P. distorta*, *P. duplicata*) appeared. Of course, any observation regarding the evolution of shark teeth probably gives much less information about the whole organism than is the case with platform conodonts, but the mechanism of evolutionary differentiation – first slow and then rapid afterwards, when the environmental conditions improved – seems to be very similar.

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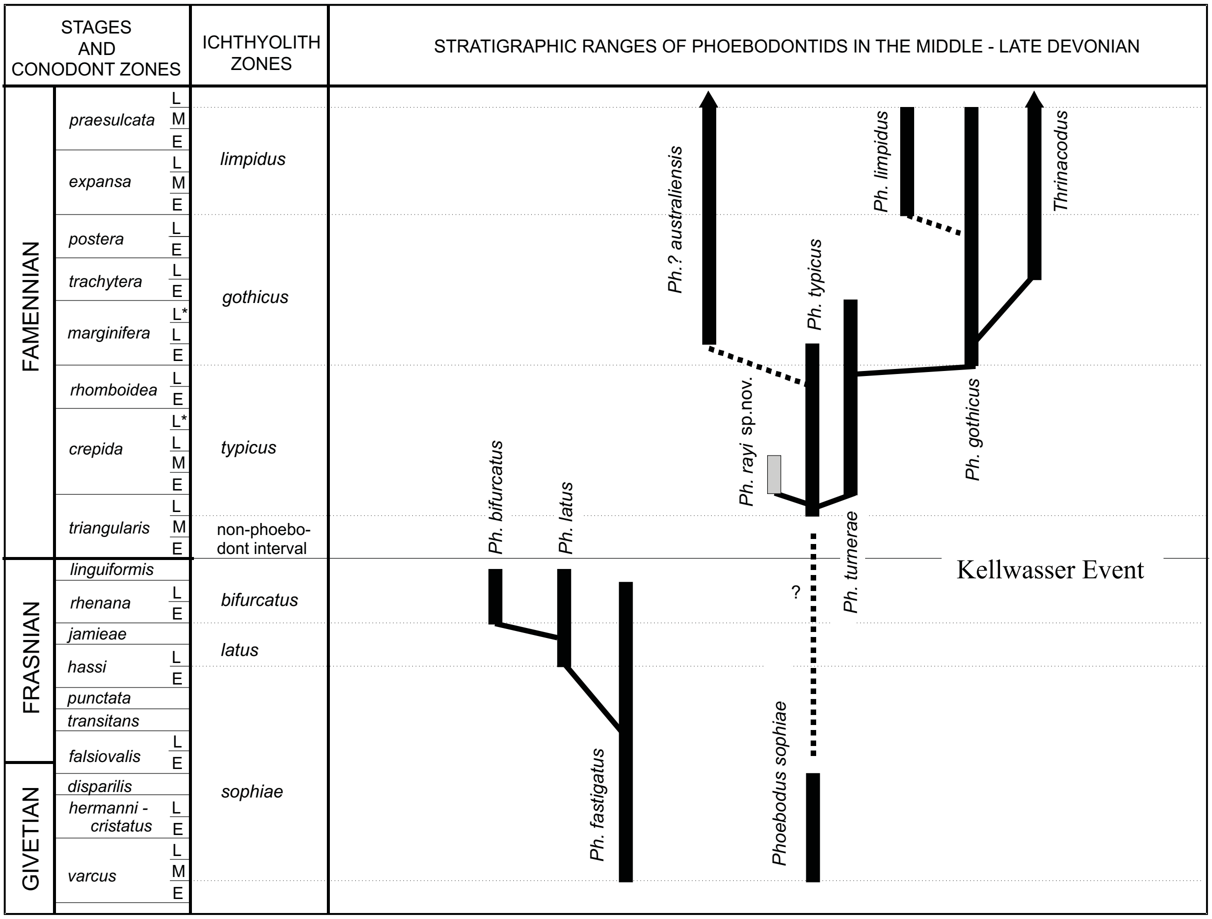

Fig. 9. Stratigraphic ranges and possible interrelationships of phoebodontids in the Middle and Late Devonian

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