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Late Devonian – Early Permian chondrichthyans of the Russian Arctic

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ABSTRACT:

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New chondrichthyan material is reported from the Upper Devonian – Lower Permian of the various regions of the Russian Arctic. Shark remains are recorded from the Novaya Zemlya Archipelago for the first time. Ten species are described, two of which are new, *Denaea? decora* sp.n. and *Adamantina foliacea* sp.n. Upper Devonian – Lower Permian shark assemblages are discussed.

Key words: Chondrichthyans, Devonian – Permian, Russian Arctic.

INTRODUCTION

Chondrichthyans from the Upper Devonian – Lower Permian of the Russian Arctic have not been adequately studied and there are only isolated references documenting their occurrences. *Cladodus*, *Helodus*, ?*Psephodus*, Cochliodontidae and a new genus of Bradyodonti were mentioned from the Upper Viséan of the Lower Carboniferous (Tulian and Mikhailovian Regional stages) of the North Urals (River Podcherem) and Nearpolar Urals (rivers Kozhim and Schugor) (KALASHNIKOV 1967). An edestid tooth whorl fragment was found in the Lower Permian (Artinskian) of Kozhim, Nearpolar Urals (CHUVASHOV 1989), and was determined as Helicoprion albeit with inadequate data. The remains of Early Carboniferous chondrichthyans from that area were cited and illustrated by LEBEDEV (1996). He reported *Deltodus*, *Psephodus* and '*Helodus*' from the Tulian Regional Stage of the North Urals (River Podcherem); *Deltodus*, *Psephodus*, '*Helodus*', *Copodus auriculatus* (DAVIS), Psammodontidae and Petalodontidae from the Mikhailovian Regional Stage of the North Urals (rivers Podcherem and Kozhva), Nearpolar Urals (rivers Kozhim and Schugor) and Polar Urals (River Vorkuta); and *Cochliodus contortus* AGASSIZ from the Upper Viséan (?) of the Chernyshev Ridge (River Vangyr). Teeth of *Phoebodus bifurcatus* GINTER & IVANOV and *Bransonella nebraskensis* (JOHNSON) were described from the Upper Devonian (Upper Frasnian) of South Timan and the Lower Carboniferous (Upper Viséan) of the Nearpolar Urals, respectively (*see* GINTER & IVANOV 1992, IVANOV & GINTER 1996). Chondrichthyan denticles were mentioned from the Middle Frasnian of South Timan (IVANOV 1995).

This paper is a first attempt to analyse the chondrichthyan distribution and diversity in the Upper Devonian – Lower Permian of the Russian Arctic.

MATERIAL

Various isolated remains of chondrichthyans (teeth, tooth plates, spines, scales and denticles)

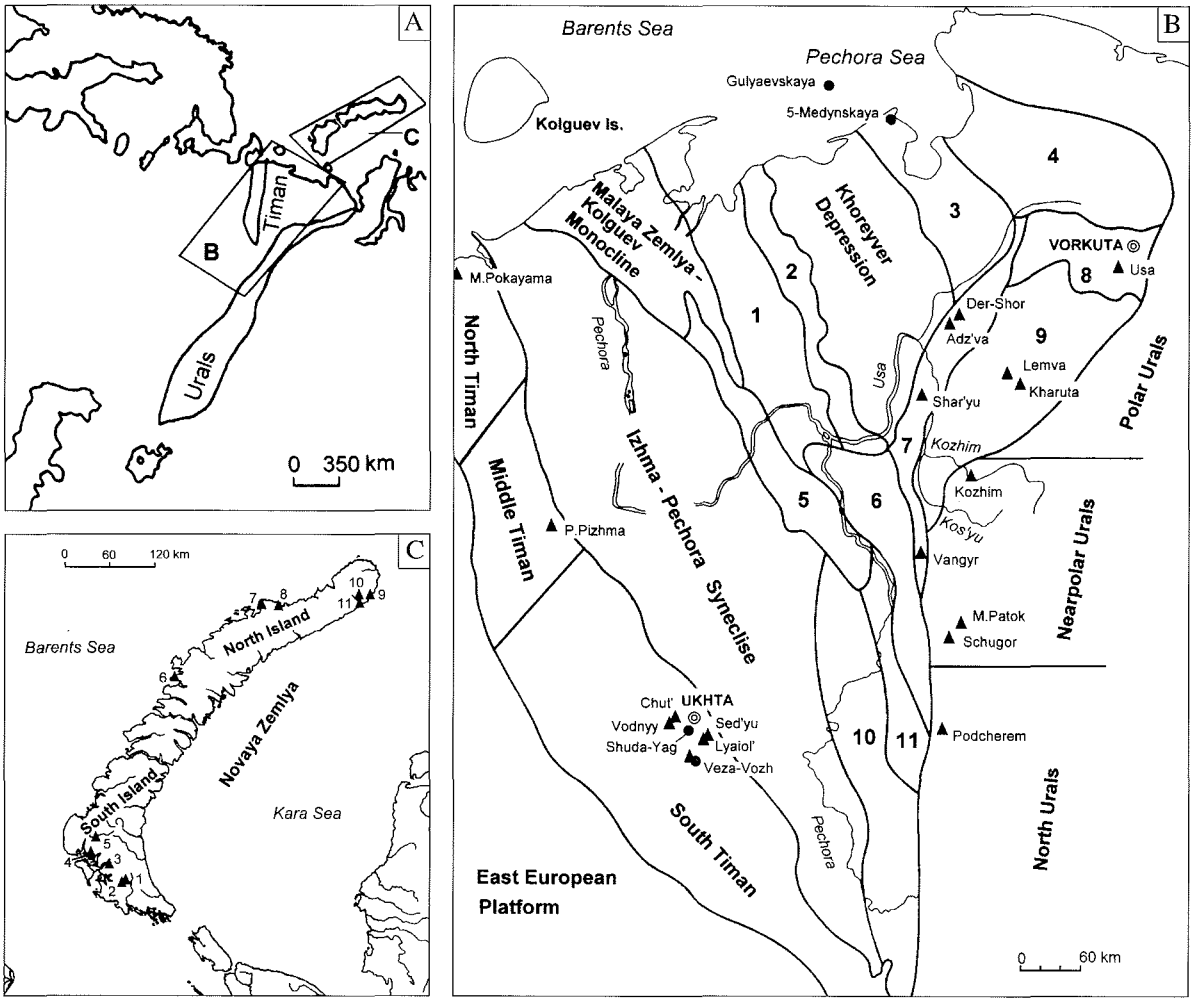


Fig. 1. **A** – Sketch map of the studied regions; **B** – Map of the Timan – Pechora Province and the Urals showing location of chondrichthyan sites (*after* MOSKALENKO 1997); 1 – Denisov Depression, 2 – Kolva Megaswell, 3 – Varandey – Adz'va structural zone, 4 – Korotaikha Depression, 5 – Pechora – Kozhva Megaswell, 6 – Bol'shaya Synya Depression, 7 – Chernyshev Ridge, 8 – Vorkuta Transverse Uplift, 9 – Kos'yu – Rogovaya Depression, 10 – Upper Pechora Depression, 11 – Middle Pechora Transverse Uplift; **C** – Map of Novaya Zemlya with chondrichthyan sites; 1-2 – Bol'shaya Yunau River, 3 – Nekhvatova River, Yastrebinyy Creek, 4 – Vypuklyy Peninsula, 5 – Rogachev River, 6 – Krasnyy Partizan Peninsula, 7 – Velikaya River, 8 – Russkaya Gavan' Bay, western bank, 9 – Eks Bay, 10 – Kan'onnaya River, 11 – Sporyy Navolok Cape; Chondrichthyan sites: black circles – boreholes, black triangles – outcrops

occur in the Timan – Pechora Province (South, Middle and North Timan, Varandey – Adz'va structural zone), Chernyshev Ridge, North, Nearpolar and Polar Urals, Pechora Sea, South and North islands of Novaya Zemlya (Text-fig. 1, Table 1). Detailed stratigraphical data are given in numerous publications, the most important of which are as follows: Upper Devonian of South Timan (MENNER & *al.* 1992, YUDINA & MOSKALENKO 1994, KUZMIN 1995, KUZMIN & YATSKOV 1997), Upper Devonian of Middle Timan (TSAPLIN & SOROKIN 1988), Carboniferous of North Timan (KASHIK 1997), Upper Devonian of the Chernyshev Ridge (TSYGANKO & *al.* 1985, YUDINA 1989), Carboniferous of the Chernyshev Ridge, North, Nearpolar and Polar Urals (CHERMNYKH 1976), Permian of the Nearpolar Urals (MURAV'EV 1972, CHUVASHOV & *al.* 1987), Carboniferous and Permian of Novaya Zemlya (SCHECOLDIN & *al.* 1994, SOBOLEV & NAKREM 1996). Chondrichthyan microremains were collected from chemically processed conodont and ostracod samples. The

Table 1. Collections used in the paper; chondrichthyan remains from the Arctic regions

Location	Stratigraphic dating
Timan:	
South Timan, Ukhta Region:	
Ukhta River, Vodnyy Village	L. Devonian, E. Frasnian; Timan Fm., U. Mb.
Chut' River	L. Devonian, E. Frasnian, *Pa. transitans* c.z.; Uste Yarega Fm., U. Mb.
Borehole 1003 (Shuda-Yag); 117.8-118.8 m	L. Devonian, M. Frasnian, *Pa. punctata* c.z.; Domanik Fm., M. Mb.
Borehole 2021 (Vezha-Vozh River); 292 m	L. Devonian, M. Frasnian, *Pa. punctata* c.z.; Domanik Fm., U. Mb.
275 m	L. Devonian, M. / L. Frasnian; boundary beds of Domanik and Lyaiol' Fm.
187 m	L. Devonian, L. Frasnian, L. *Pa. rhenana* c.z.; Lyaiol' Fm.
Borehole 2022; (Vezha-Vozh River); 25 m	L. Devonian, L. Frasnian, *Pa. rhenana* c.z.; Lyaiol' Fm., M. Mb.
32 m	L. Devonian, L. Frasnian, L. *Pa. rhenana* c.z.; Ukhta Fm., Lo. Mb.
Borehole 2023 (Vezha-Vozh River); 149 m	L. Devonian, L. Frasnian, *Pa. rhenana* c.z.; Lyaiol' Fm.
Borehole 2068 (Lyaiol' River); 11 m	L. Devonian, L. Frasnian, L. *Pa. rhenana* c.z.; Lyaiol' Fm., U. Mb.
Borehole 2013; 248 m	L. Devonian, L. Frasnian; Sirachoy – Lo. Ukhta interval
Lyaiol' River	L. Devonian, L. Frasnian, L. *Pa. rhenana* c.z.; Lyaiol' Fm., U. Mb.
Vezha-Vozh River	L. Devonian, L. Frasnian, *Pa. rhenana* c.z.; Lyaiol' Fm.
Sed'yu River	L. Devonian, L. Frasnian, *Pa. rhenana* c.z.; Sed'yu Fm.
Middle Timan:	
Pechorskaya Pizhma River, Yaranskiy Meg	L. Devonian, E. Frasnian; Uste Yarega Fm., Srednyaya Beds.
	L. Devonian, M. Frasnian; Kraipole Fm., U. Mb.
North Timan:	
Malaya Pokayama River	M. Carboniferous, Moskovian, *Idiognathodus medadultimus* c.z.; Volonga Fm., Lo. Mb.
Timan – Pechora Province, Varandey – Adz'va structural zone:	
Borehole Medynskaya-5; 2330.6-2344.4 m	Devonian/Carboniferous boundary beds (Tournaisian)
Chernyshev Ridge:	
Shar'yu River	L. Devonian, E. Famennian; Shar'yu Fm.
	L. Devonian, M. Famennian, *Pa. marginifera* c.z.; Sortomael' Fm.
	M. Carboniferous, L. Bashkirian
Der-Shor River	L. Devonian, M. Famennian, L. *Pa. marginifera* c.z.
Adz'va River	L. Devonian, M. Famennian, *Pa. marginifera* c.z.
Vangyr River	L. Carboniferous, Gzhelian – E. Permian, Asselian (boundary beds)

Table 1 – cont.

North Urals:	
Podcherem River	E. Carboniferous, L. Tournaisian, *Siphonodella crenulata – S. isosticha* c.z.
Borehole Vychegodskaya, 14031 m	M. Carboniferous, Bashkirian
Nearpolar Urals:	
Kozhim River	E. Carboniferous, L. Viséan; Tulian R.S.
	E. Carboniferous, L. Viséan, *Mestognathus beckmanni* c.z; Aleksian R.S.
	L. Carboniferous, Gzhelian – E. Permian, Asselian (boundary beds)
	E. Permian, Asselian
Schugor River and its affluent Malyy Patok River	E. Permian, Asselian Middle Urals, Sylva River, 2 km from village Platonovo to downstream
Polar Urals:	
Lemva River	L. Devonian, M. Famennian, *Pa. marginifera* c.z.
Kharuta River	E. Carboniferous, Serpukhovian - M. Carboniferous, E. Bashkirian
Vorkuta Region, Usa River	E. Permian, E. Asselian
Pechora Sea:	
Borehole Gulyaevskaya; 2710 m	L. Carboniferous, Gzhelian – E. Permian, E. Asselian, *Adetognathus lautus* c.z.
Novaya Zemlya:	
South Island:	
Bol'shaya Yunau River	E. Carboniferous, Serpukhovian; Mila Fm.
	M. Carboniferous, Moskovian; Kazarka Fm., Lo. Mb.
Vypuklyy Peninsula	M. Carboniferous, Bashkirian; Kazarka Fm.
Rogachev River	M. Carboniferous, Bashkirian; Kazarka Fm.
Nekhvatova River, Yastrebinyy Creek	E. Permian, E. Asselian; Kazarka Fm., U. Mb.
North Island:	
Eks Bay	E. Carboniferous, E. Tournaisian; Spokoynaya Fm.
Krasnyy Partizan Peninsula	E. Carboniferous, E. Viséan; Rogachev Fm.
Sporyy Navolok Cape	M. Carboniferous, L. Moskovian; Sporyy Navolok Fm.
Kan'onnaya River	M. Carboniferous, L. Moskovian; Sporyy Navolok Fm.
Velikaya River	M. Carboniferous, L. Moskovian; Barents Fm.
Russkaya Gavan' Bay, western bank	L. Carboniferous, Gzhelian – E. Permian, Asselian; Barents Fm.

Abbreviations: c.z. – conodont zone, E. – Early, Fm. – Fm., f.z. – foraminifer zone, L. – Late, Lo. – Lower, M. – Middle, Mb. – Member, Pa. – *Palmatolepis*, R.S. – Regional Stage, U. – Upper

descriptions of Carboniferous and Permian shark teeth from the Arctic region are supplemented by material from the Middle and South Urals. The described material is housed in the Laboratory of Palaeontology, St. Petersburg University, St. Petersburg, Russia (collection LP 6 and additionally specimens LP 2-1, 7-7, 16-2). The specimens of *Denaea meccaensis* from the Upper Pennsylvanian of Indiana, USA housed in the Swedish Museum of Natural History, Stockholm (SMNH) were used for comparison. The term 'zone' in this paper is used for the conodont zones of the Late Devonian – Carboniferous; in the case of other zonal schemes, the name of the relevant fossil group is added.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes HUXLEY, 1880
Subclass Elasmobranchii BONAPARTE, 1838
Cohort Euselachii HAY, 1902
Family Phoebodontidae WILLIAMS, 1985
Genus *Phoebodus* ST. JOHN & WORTHEN, 1875

Phoebodus bifurcatus GINTER & IVANOV, 1992 (Pl. 1, Figs 9-11)

1991. *Phoebodus* sp. nov.; M. GINTER, p. 74, Pl. 8, Figs 1-2.
1992. *Phoebodus bifurcatus* sp. n.; M. GINTER & A. IVANOV, pp. 65-66, Figs 4A-F, 5D-H, 6A.
1995a. *Phoebodus bifurcatus* GINTER & IVANOV; M. GINTER & A. IVANOV, Pl. 1, Figs 5-6.
1995. Phoebodus bifurcatus GINTER & IVANOV; S. TURNER & W. YOUNGQUIST, pp. 389-392, Figs 1-2.
1995. *Phoebodus bifurcatus* GINTER & IVANOV; M. GINTER, Fig. 1F-G.
1995. *Phoebodus bifurcatus* GINTER & IVANOV; S.-T. WANG & S. TURNER, p. 65, Pl. 7, Fig. 7.

MATERIAL: 16 teeth; Late Frasnian, *rhenana* conodont Zone; from boreholes in the Ukhta Region, rivers Lyaiol' and Vezha-Vozh, South Timan.

REMARKS: The so-called juvenile teeth (Pl. 1, Fig. 11) in the studied material are more common than larger specimens, which have a thick base with almost parallel lateral edges (Pl. 1, Fig. 9). In the juveniles the labial part of the base is considerably narrower than the lingual part, there is a rather small button and the cusps are either smooth or very slightly sculptured. Such a tooth type was found recently in the USA (TURNER & YOUNGQUIST 1995) and China (WANG & TURNER 1995). One abnormal tooth (Pl. 1, Fig. 10) has a depression in the middle part of the labial side and, accordingly, two separated buttons on the upper side of the base in place of the large single one. These features are not typical of phoebodont teeth but can be found in the teeth of some symmoriids. This tooth anomaly indicates a correlation between the central labial depression and the presence of two buttons, and suggests close relationships between phoebodontids and oldest symmoriids.

OCCURRENCE: Russia, Central Devonian Field, *rhenana* Zone, and South Urals, *rhenana* Zone – lower part of *linguiformis* Zone; Poland, Holy Cross Mountains, *rhenana* Zone; Czech Republic, Moravia, Late *rhenana* Zone (GINTER & IVANOV 1992); USA, Utah, *rhenana* Zone (TURNER & YOUNGQUIST 1995); China, *rhenana* – ?*linguiformis* zones (WANG & TURNER 1995).

Phoebodus latus GINTER & IVANOV, 1995a (Pl. 1, Figs 13, 17)

1992. *Phoebodus* sp. A; M. GINTER & A. IVANOV, p. 70, Fig. 7A-I.
1995a. *Phoebodus latus* nov. sp.; M. GINTER & A. IVANOV, p. 355, Pl. 1, Figs 3-4.
1995b. *Phoebodus latus* sp. nov.; M. GINTER & A. IVANOV, p. 19, Fig. 1.
1995. *Phoebodus latus* GINTER & IVANOV; M. GINTER, Fig. 1E.

MATERIAL: Six teeth; Late Frasnian (*rhenana* Zone – lower part of *linguiformis* Zone) of the boreholes in the Ukhta Region, River Lyaiol', South Timan.

REMARKS: GINTER & IVANOV (1995b) noted that the new, additional cusplets sometimes originated from between the lateral and intermediate cusps. Some teeth from a new collection (Pl. 1, Fig. 17) indicate that small additional cusplets can develop between any of the higher cusps, as well as on the inner side of the lateral cusp. The crown of such teeth consists of nine cusps and cusplets; in this case the central cusp is equal in height to the intermediate cusps.

OCCURRENCE: Russia, South Urals, Early *hassi* Zone – lower part of *linguiformis* Zone; Poland, Holy Cross Mountains, *rhenana* Zone (GINTER & IVANOV 1992).

Table 2. Collections used in the paper

A. Additional specimens of *"Denaea" decora* sp.n.

Location	Stratigraphic dating
South Urals, Aktyubinsk District, Sholak-Say	E. Carboniferous, Serpukhovian, *Lochrea nodosa - Gnathodus bilineatus bollandensis* c.z., Yuldybay R.S.
South Urals, Usolka River (affluent of the Belaya River)	E. Permian, E. Asselian, Kholodnyy Log R.S., *Daixina robusta* f.z.
South Urals, Chelyabinsk District, road cut of Sim – Min'yar, 1 km western of station Simskaya	E. Permian, Sakmarian, lower part of the Tastuba R.S., *Pseudofusulina moelleri* f.z.
South Urals, Sim River, right riverside, near Sim	E. Permian, Sakmarian, upper part of the Tastuba R.S., *Pseudofusulina verneuili – P. uralica* f.z.
South Urals, Bashkortorstan, road cut of Chulpan – Mesyagutovo, near Maloyaz	
South Urals, Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim in the direction of	E. Permian, Sakmarian, upper part of the Sterlitamak R.S., *Pseudofusulina urdalensis* f.z.
South Urals, Sterlitamak Districk, 300 m north from Tra-Tau Hill	E. Permian, L. Artinskian, Sarga R.S., *Parafusulina solidissima* f.z.
South Urals, Ay River, right riverside, 0,5 km from the entry of the Anzyak Creek to upstream	E. Permian, L. Artinskian, Sarga R.S., *Parafusulina solidissima* f.z.
Middle Urals, Barda River (right affluent of the Sylva River), near village Voskresentsy	E. Permian, L. Artinskian, Sarga R.S., *Parafusulina solidissima* f.z.
Middle Urals, Sylva River, 2 km from village Platonovo to downstream	

B. Additional specimens of *"Cladodus" divergens* TRAUTSCHOLD.

Location	Stratigraphic dating
Moscow Region, Mytischi, borehole 15.	L. Carboniferous, Kasimovian.
Moscow Region, Mytischi, borehole 17: 77,9–81,3 m	L. Carboniferous, Kasimovian, Dorogomilovskiy R.S.
106,3-108,1 m	L. Carboniferous, Kasimovian, Krevyakino R.S.
Moscow Region, Afonas'evo, borehole 9, 110 m	L. Carboniferous, Kasimovian, Dorogomilovskiy R.S.
Moscow Region, Vodniki, borehole V-2/3, 114 m	L. Carboniferous, Kasimovian, Krevyakino R.S.

C. Additional specimens of *Adamantina foliacea* sp.n.

Location	Stratigraphic dating
South Urals, Sikaza River	E. Carboniferous, L. Tournaisian, E. *Gnathodus typicus* c.z., Kizelian R.S.
Middle Urals, Sylva River, 2 km from village Platonovo to downstream	E. Permian, L. Artinskian, Sarga R.S., *Parafusulina solidissima* f.z.

Abbreviations see Table 1

Genus *Thrinacodus* ST. JOHN & WORTHEN, 1875

Thrinacodus sp.
(Pl. 4, Figs 2, 4)

MATERIAL: Four teeth; Devonian/Carboniferous boundary beds and Early Tournaisian of Medynskaya-5 Borehole, Varandey – Adz'va structural zone, Timan – Pechora Province, and Eks Bay, North Island, Novaya Zemlya.

REMARKS: The collection contains three asymmetrical teeth and one with a symmetrical crown and asymmetrical base. The lingual part of the base in the asymmetrical teeth varies from concave to convex. These teeth (Pl. 4, Figs 2, 4) bear only two cusps, the third cusp is absent. Three-cuspid teeth of *Thrinacodus* are usually cited in the references.

OCCURRENCE: Russia, South Urals, Late Famennian, *expansa* Zone – Late Viséan, *bilineatus* Zone (IVANOV 1996), central part of the Moscow Sineclise, Serpukhovian, *nodosus* Zone (GINTER & IVANOV 1996), as well as unpublished material from the Northern Caucasus, Late Famennian – Early Tournaisian (author's collection); Poland, Holy Cross Mountains, Middle Famennian, *trachytera* Zone – Viséan (GINTER 1995); Germany, Thuringia, Late Famennian, *praesulcata* Zone – Early Tournaisian (GINTER 1996); southern France, Early Tournaisian, *sulcata* and the *kockeli – dentilineatus* zones; and Belgium, Tournaisian (DERYCKE & *al.* 1995); England, Bristol District, ?Late Famennian – Tournaisian (DUFFIN 1993b) and Derbyshire, Late Viséan (DUFFIN 1993a); Morocco, Middle – Late Famennian, *marginifera – costatus* zones (DERYCKE 1992); South China, Late Famennian, ?*expansa* Zone – Early Tournaisian (WANG & TURNER 1995); Thailand, Late Famennian, *expansa* Zone (LONG 1990); Australia, ?Late Famennian – Viséan (TURNER 1993); USA, Illinois, Early Viséan, *texanus* Zone (NEWBERRY & WORTHEN 1866), Iowa, Tournaisian (Kinderhookian), *sulcata – isosticha* zones (ST. JOHN & WORTHEN 1875), New Mexico, ?Famennian (KIETZKE & LUCAS 1992).

Order Symmoriida ZANGERL, 1981
Family Symmoriidae DEAN, 1909
Genus *Symmorium* COPE, 1893

Symmorium sp.
(Pl. 3, Fig. 1)

MATERIAL: Seven teeth.

REMARKS: GINTER (1998) showed that the teeth of the holotype of the type species *Symmorium reniforme* COPE do not have the features that have long been accepted as characteristic of the genus: two separated apical buttons and two labio-basal projections on each side of the labial depression. This tooth morphology is characteristic of "*Symmorium*" *occidentalis* (LEIDY) and "*Symmorium*" *lamnoides* (NEWBERRY & WORTHEN). The name *Symmorium* is used here for the last tooth morphotype in the absence of a systematic revision of the genus.

OCCURRENCE: Late Devonian (Middle Famennian), *marginifera* Zone of the River Lemva, Polar Urals and River Shar'yu, Chernyshev Ridge.

Genus *Denaea* PRUVOST, 1922

"*Denaea*" *decora* sp.n.
(Text-fig. 2; Pl. 7, Fig. 12; Pl. 8)

1996. *Denaea* sp.; A. IVANOV, Figs H, I.
1996. *Denaea*? sp.; M. GINTER & A. IVANOV, Fig. 4E.

HOLOTYPE: LP 6-74, tooth (Pl. 8, Fig. 2).

TYPE LOCALITY: road cutting on the Ufa – Chelyabinsk road, 1 km from Sim in the direction of Chelyabinsk, South Urals.

TYPE HORIZON: Lower Permian (Sakmarian), upper part of the Sterlitamak Regional Stage, *Pseudofusulina urdalensis* foraminifer Zone.

ETYMOLOGY: Latin, *decorus* – adorned.

MATERIAL: 158 teeth (Tables 1, 2A).

DIAGNOSIS: Cladodont teeth with from three to seven rather thin cusps in the crown. The lateral cusps are slightly inclined from the central one. The main cusps in seven-cusp crowns are the central and intermediate ones, which are subequal to each other in height. Both sides of the cusp are sculptured. The labial sculpture consists of distinct ridges forming lanceolate ornament in the upper

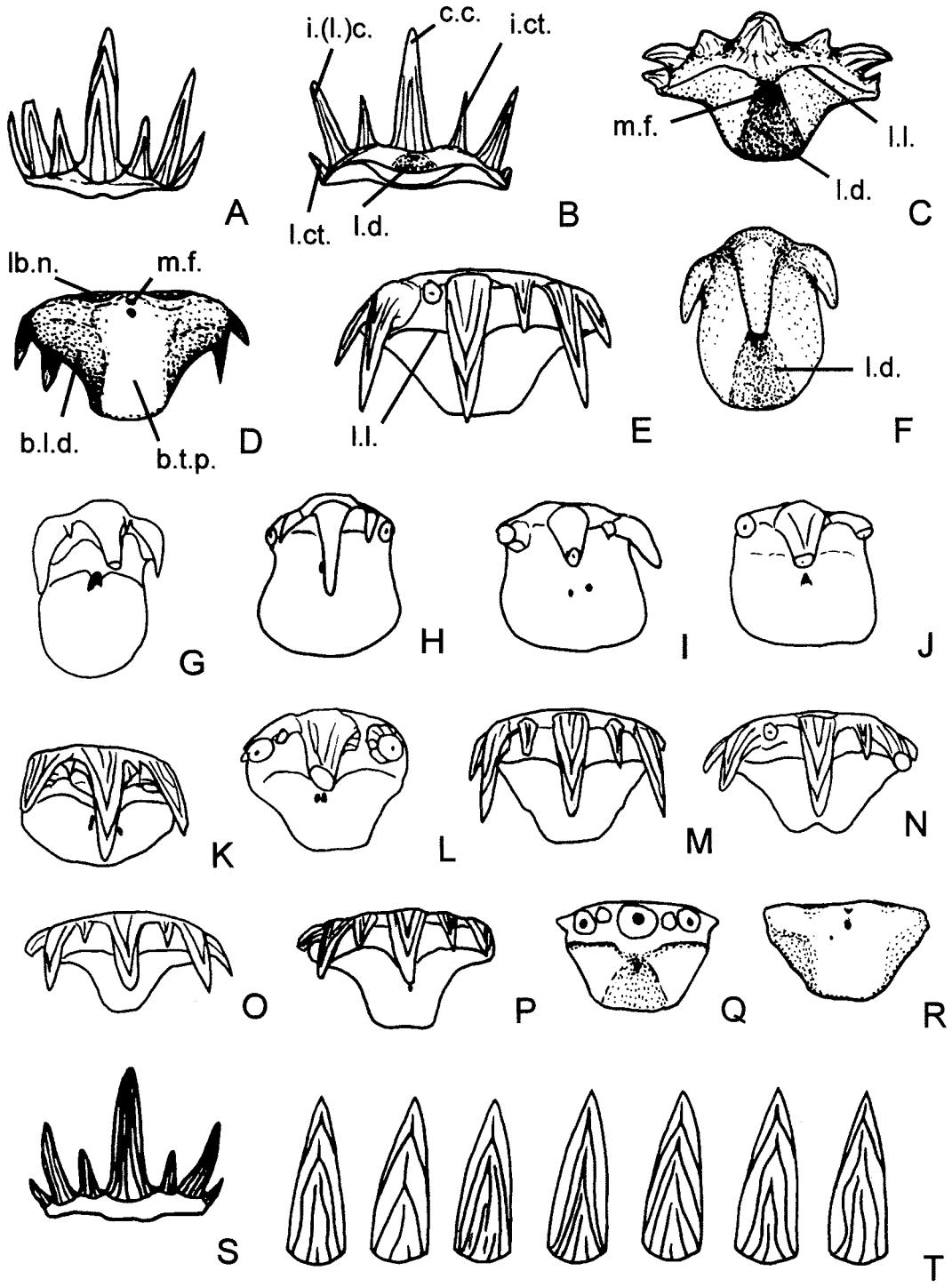


Fig. 2. **A-P** – *"Denaea" decora* sp.n., South and Middle Urals, Early Permian; A – labial, B – lingual, C – oblique occlusal, D – basal and E – occlusal views of multicuspid teeth, F – occlusal view of a "juvenile" tooth, G-P – variations of the base shape, T – variations of the labial sculpture of the central cusp; **Q-S** – *"Denaea" meccaensis* WILLIAMS, Indiana, Late Pennsylvanian; Q – occlusal, R – basal and S – labial views; abbreviations: b.l.d. – basal lateral depression, b.t.p. – basal transverse prominence, c.c. – central cusp, i.ct. – intermediate cusplet, i.(l.)c. – intermediate (or lateral) cusp, lb.n. – labio-basal notch, l.ct. – lateral cusplet, l.d. – lingual depression, l.l. – lingual ledge, m.f. – foramen of main canal

part of the cusp. The angle between the crown and the base is between 40° and 50°. The tooth base lacks a button but possesses a deep lingual depression on the upper side, and a distinct transverse prominence with lateral depressions on each side basally. The base of the multicuspid tooth is elongated lingually. Two foramina open on the base: in the top of lingual depression (m.f., Text-fig. 2c) and on the labio-basal edge.

DESCRIPTION: The teeth have a cladodont-type crown. The number of cusps in the crown varies from three to seven. There are three main cusps in a crown and from two to four cusplets. The central cusp in the three-cusped crown is thicker and higher for one third of its height than the lateral cusps. The central cusp in the teeth with five to seven cusps is slightly higher than the other main cusps. A pair of intermediate cusplets is intercalated between the central and lateral cusps in five-cusped teeth. In teeth with seven cusps the lateral accessory cusplets are located at the outer lateral corner of the crown, and the former main lateral cusps become intermediates. The cusplets in such crowns are almost equal in height (Pl. 8, Fig. 7a) or the intermediate cusplet is higher (Pl. 8, Fig. 8b). The intermediate or lateral cusps are gently inclined from the central one. All the cusps are relatively thin, slightly sigmoidal, only slightly separated from each other, and rounded in cross section. They have well developed sculpture on the labial side and gentle sculpture on the lingual side. The labial sculpture includes distinct ridges forming the very characteristic lanceolate or leaf-shaped ornament at the top part of the main cusp. Two ridges run from the base to the top of the cusp, meeting on the axial line, and continuing as a single central ridge. Isolated, slightly curved ridges are present beneath the leaf-shaped ornament, and the small ridges – in the centre of the cusp, near the base. The ridges on the lingual side of the cusp are thinner, do not meet and do not reach the top of the cusp. The boundary of the crown with the base is very distinct. They form an acute angle (40°– 50°).

The outline of the base varies, according to the number of the cusps and the width of the base, from an oval, elongated linguad, to subtriangular and "T"-shaped with an elongated lingual part. The deep triangular lingual depression is located in the central part of the base and extends to the lingual edge. The main foramen opens on the top of this depression, in its labal part. The distinct lingual ledges are located on each side of this foramen, some distance from the crown. The basal surface of the base has a central arched transverse prominence, with two lateral depressions on each side. The foramen of the main vascular canal opens in the centre of the labio-basal edge. Shallow labio-basal notches are located on either side of the foramen.

Tooth to tooth articulation in a single row (tooth file) is between the lingual depression on the upper side and the basal transverse prominence with the pair of the lateral depressions basally. The basal prominence of the younger tooth is inserted into the lingual depression of the older tooth, and the lateral depressions on the basal side contact both convex surfaces of the upper side of the older tooth. In this case, the lingual ledges articulate with the labio-basal notches. The lingual and labio-basal foramina lie adjacent to each other in a tooth file. A similar pattern of tooth articulation in the row is characteristic of the recent Frilled Shark *Chlamydoselachus* (PFEIL 1983). Variation in the tooth morphology of a new species can be explained by differing positions in the jaw or in the tooth files. Such slight heterodonty occurs in *Chlamydoselachus*.

REMARKS: The genus and species *Denaea fournieri* were established by PRUVOST (1922) and FOURNIER & PRUVOST (1928) based on disarticulated partial skeletons from the Lower Carboniferous (Viséan) of Belgium. The teeth of this species were described insufficiently and illustrated in labial view only (FOURNIER & PRUVOST 1928, Fig. 2). Study of the original collection, housed at the Maredsous Abbey (Belgium), has shown that the teeth have a small apical button, a slightly developed labio-basal projection, a convex occlusal and concave basal surfaces of the base. They differ from the taxon described here. These features are more characteristic of stethacanthid symmoriids.

WILLIAMS (1985) described the skeletons of a new species, *D. meccaensis*, from the Upper Pennsylvanian (Middle Carboniferous, Upper Moscovian) of Indiana, USA, giving a detailed description of their teeth. They differ completely from those of other symmoriids in the distinctive tooth to tooth articulation in the row. The tooth base lacks either buttons on the occlusal side and tubercles or projections on the basal side, but the lingual depression and basal prominence are present. Such teeth are very similar to those of species described here.

ZANGERL (1990) considered that the teeth of *Denaea meccaensis* WILLIAMS are indistinguishable from those of *Stethacanthulus longipeniculus* ZANGERL from the same locality and stratigraphic level. His arguments seem to be inconclusive and the suggestion that such teeth are dermal denticles (ZANGERL 1995) is even more doubtful.

The species described here is congeneric with *D. meccaensis*, on the basis of tooth morphology and articulation type, and is unlike the type-species of *Denaea*, *D. fournieri*. These two species need a new generic name. Some authors (MADER & SCHULTZE 1987; GINTER 1990, 1995; DUFFIN & *al.* 1996; LEBEDEV 1996) cited cladodont teeth under the name *Denaea* with varying degrees of confidence. These teeth, which belong to stethacanthid sharks and probably partly to the genus *Denaea*, differ greatly from the teeth of the "*D.*" *meccaensis – decora* group.

The teeth of "*Denaea*" *decora* differ from those of "*D.*" *meccaensis* in the labial sculpture of the cusps, and in the outline of the base and lingual depression. The labial surfaces of the cusps of "*D.*" *meccaensis* are covered by straight ridges reaching the top of the cusp (Pl. 9, Figs 1, 3, 4). The lingual depression on the occlusal side of the base, as well as the lateral depressions on the basal side, are not so deep and distinct in "*D.*" *meccaensis* as in "*D.*" *decora*. The base of the teeth with five or seven cusps in "*D.*" *meccaensis* is usually trapezoidal or polygonal, without the elongated lingual part (Pl. 9, Figs 5-8, 12) that is typical of the new species.

Occurrence: Early Carboniferous (Serpukhovian), *bilineatus bollandensis* Zone – *unicornis* Zone – Early Permian (Late Artinskian), *Parafusulina solidissima* foraminifer Zone of River Schugor, Nearpolar Urals; rivers Barda and Sylva, Middle Urals; rivers Ay, Sim and Usolka, road cuttings near Sim and Maloyaz, Sholokh-Say, South Urals (for details – *see* Table 2A).

'Cladodus' divergens TRAUTSCHOLD, 1879
(Text-fig. 3, Pl. 7, Fig. 1)

1879. *'Cladodus' divergens* TRAUTSCHOLD; H. TRAUTSCHOLD, p. 51, Pl. 6, Fig. 11.
1973. *Phoebodus* sp.; G. CASE, Fig. 47.
1985. *Phoebodus heslerorum* sp. n.; M. WILLIAMS, pp. 124-131, Figs 22, 23, Pl. 16, 17.

MATERIAL: Six isolated teeth (Tables 1, 2B); Late Carboniferous (Kasimovian)– Early Permian (Early Asselian), *Adetognathus lautus* Zone; Gulyaevskaya, Borehole Pechora Sea; boreholes, Moscow Region.

DESCRIPTION: The teeth have a cladodont-type crown with three large cusps and sometimes two intermediate ones. The central cusp is slightly higher than the lateral ones. The latter are sigmoidal, curved, strongly inclined linguad and directed away from the central cusp. The angle between the lateral cusps is almost 90°. They are covered with straight striae. A distinct lateral carina marks the boundary

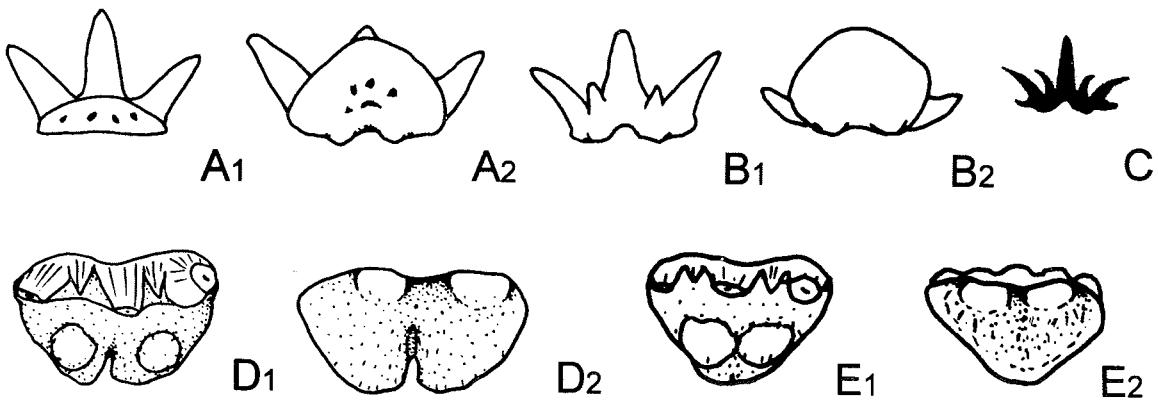


Fig. 3. *"Cladodus" divergens* TRAUTSCHOLD; teeth; A – Pechora Sea, borehole Gulyaevskaya, Late Carboniferous, Gzhelian – Early Permian, Early Asselian; A_1 – lingual and A_2 – basal views; B – *after* CASE (1973, Fig. 47), Nevada, Permian, B_1 – labial and B_2 – basal views; C – *after* TRAUTSCHOLD (1879, Pl. 6, Fig. 11), Moscow Region, Middle Carboniferous, Late Moskovian, labial view; D-E – Moscow Region, Late Carboniferous, Kasimovian, D_1-E_1 – occlusal and D_2, E2 – basal views

between the labial and lingual cusp faces. The base is rounded with a slightly subtriangular lingual part. The basal surface is almost flat. There is a gentle concavity in the middle part of the labial surface of the tooth with two small rounded labio-basal projections on each side. The upper surface of the base bears two distinct rounded apical buttons at varying distances from each other.

REMARKS: '*Cladodus*' *divergens* was described by TRAUTSCHOLD (1879) based on one isolated tooth from the Middle Carboniferous (Upper Moscovian, Myachkovian Regional Stage) of Myachkovo in the Moscow Region; he illustrated the specimen only in labial view. Study of TRAUTSCHOLD's collection, housed at the Institute of Zoology of Wrocław University, Wrocław, Poland, has shown that this species is represented by two isolated teeth from the type locality with the single museum catalogue number PCh/617.Both teeth are 3.5 mm wide along the labial part of the base and have three main and two additional cusps in the crown. The lateral cusps are slightly smaller than the central cusp. Most of the cusps are covered with two to three weak straight ridges. The middle labial concavity of the tooth bears two small labio-basal projections on either side. The upper side of the base in both specimens is obscured by matrix.

A similar tooth from the Permian of Nevada, USA, was illustrated by CASE (1973) under the name *Phoebodus* sp.

WILLIAMS (1985) described a new species, *Phoebodus heslerorum*, on the basis of complete specimens from the Upper Pennsylvanian (Upper Moscovian: the stratigraphic level is close to that of '*Cladodus*' *divergens*) of Indiana, USA, and gave its dentition in detail. He cited the presence of two apical buttons on the upper side of the base. These teeth differ from those of typical *Phoebodus* and do not belong to that genus (GINTER & IVANOV 1992, 1996); however, they are similar to TRAUTSCHOLD's specimens and the teeth described in this paper. As correctly noted by GINTER (1998), the specific name *heslerorum* could be a junior synonym of *divergens*, but their generic definition still remains undecided. Some of the specimens included in *Pristicladodus springeri* var. *armatus* ST. JOHN & WORTHEN probably belong to "*C.*" *divergens*, especially the specimen figured in Plate 1, Figure 11 (ST. JOHN & WORTHEN 1875).

All of the specimens cited above resemble the teeth of *Phoebodus*, especially those of *P. turnerae* GINTER & IVANOV, in the form and direction of the lateral cusps. However, they differ from the teeth of *Phoebodus* in the higher central cusp and the presence of the middle labial concavity and two associated small labio-basal projections, as well as in the presence of two apical buttons on the upper side of the base.

OCCURRENCE: Russia, Moscow District, Middle Carboniferous, Late Moscovian (TRAUTSCHOLD 1879); USA, Midcontinent, Indiana, Late Pennsylvanian (Middle Carboniferous), Late Moscovian (WILLIAMS 1985) and Nevada, Permian (CASE 1973).

Order Xenacanthiformes BERG, 1940
Family *incertae sedis*
Genus *Bransonella* HARLTON, 1933

Bransonella sp.
(Pl. 4, Fig. 1)

MATERIAL: One tooth.

DESCRIPTION AND REMARKS: The crown has three cusps of equal height, the central cusp is slightly narrower than the lateral ones. The lateral cusps are sub-parallel to the central cusp. The crown is at right angles to the base. The sculpture consists of straight ridges and is present on both sides of the cusps. The ridges reach the top of the cusp. Similar sculpture is present on the lingual face of the cusp in *Bransonella nebraskensis* (JOHNSON). The latter is smooth and rounded in cross section. The base is wider than the crown, and the lateral parts of the base project well beyond the crown. This tooth base has a large apical button surrounded by numerous foramina. The button is flat, and its border is indistinct in contrast to those of typical representatives of the genus. The large central foramen opens on the centre of the lingual rim, as in of *Bransonella nebraskensis*. The labio-basal tubercle is elongated laterally and its inner border is indistinct.

GINTER & IVANOV (1996) suggested that *Phoebodus*? *australiensis* LONG is related to xenacanthids, especially *Bransonella*. The occurrence of the tooth described above has verified this suggestion. It is characterized by some features of typical species of *Bransonella* (the presence of a rounded apical button, labio-basal tubercle and foramen on the labial rim, the position of the lateral cusps

near to the crown centre), as well as by features of *Phoebodus*? *australiensis* LONG (cusps of equal height, base wider than the crown, with lateral projections). In addition, there are unique characters of the taxon described above that link *Bransonella* with *P.*? *australiensis* same sculpture on both sides of the cusp, smooth cusp top, flat, indistinct apical button and labio-basal tubercle. The stratigraphic position and the presence of this combination of characters suggest that the taxon described above is the oldest representative of the genus *Bransonella*, occupying an intermediate position between *P.*? *australiensis* and typical *Bransonella* species.

OCCURRENCE: Devonian/Carboniferous boundary beds (rather Early Tournaisian) of Medynskaya-5 Borehole, Varandey – Adz'va structural zone, Timan – Pechora Province.

Superfamily Ctenacanthoidea ZANGERL, 1981
Family Sphenacanthidae MAISEY, 1982
Genus *Sphenacanthus* AGASSIZ, 1837

Sphenacanthus sp.
(Pl. 3, Fig. 5)

MATERIAL: One tooth.

DESCRIPTION: The teeth have an almost cladodont crown with a high, thick central cusp. The crown is pyramidal with cusp height decreasing laterally. The cusps are rather short, and their basal parts are fused. They are covered by straight ridges. There are three ridges on the labial side of the central cusp; a single ridge is present on both sides of the other cusps and on the lingual face of the central cusp. Tiny accessory cusplets are present in the lateral corner of the crown. The elongate apical button is central, and its border is perforated by numerous foramina. The base is almost rectangular with a straight lingual edge. The basal side is slightly concave and lacks a projection.

REMARKS: This tooth is very similar to that of *Sphenacanthus hybodoides* EGERTON from the Coal Measures (Late Carboniferous) of Staffordshire, England, but the teeth of *S. hybodoides* have a more triangular base and numerous tiny, curved ridges on the cusps.

OCCURRENCE: Late Devonian (Middle Famennian), *marginifera* Zone of the River Shar'yu, Chernyshev Ridge.

Cohort Neoselachii COMPAGNO, 1977
Family Anachronistidae DUFFIN & WARD, 1983
Genus *Cooleyella* GUNNELL, 1933

Cooleyella sp.
(Pl. 5, Figs 7, 8; Pl. 6, Fig. 11)

MATERIAL: Three teeth.

DESCRIPTION AND REMARKS: The material comprises three teeth in various states of preservation. The outline of the crown is oval to slightly triangular. It is shorter than the crown of the known species of *Cooleyella*. The central cusp is not so prominent in the crown as in *Cooleyella fordi* (DUFFIN & WARD) from the Late Viséan of England (DUFFIN & WARD 1983) and *C. amazonensis* DUFFIN, RICHTER & NEIS from the Late Pennsylvanian of Brazil (DUFFIN & *al.* 1996). The lateral blades are curved upward (Pl. 5, Fig. 8b; Pl. 6, Fig. 11c). The basal flange is poorly developed in comparison with that of *C. fordi*. The occlusal crest is smooth and imperceptible. The basal side is strongly concave. The labial buttress is wide, prominent and has a smooth transition with the base (Pl. 5, Fig. 8b). These teeth most closely resemble those of *Cooleyella* sp. from the Early Permian of Nevada (DUFFIN & WARD 1983).

OCCURRENCE: Early Carboniferous (Late Viséan), *Mestognathus beckmanni* Zone – Middle Carboniferous (Moscovian), *Idiognathodus medadultimus* Zone of the River Kozhim, Nearpolar Urals and River Malaya Pokayama, North Timan.

Elasmobranchii *incertae sedis*

Genus *Adamantina* BENDIX-ALMGREEN, 1993

TYPE SPECIES: *Adamantina benedictae* BENDIX-ALMGREEN, 1993

Adamantina foliacea sp.n.
(Text-fig. 4; Pl. 7, Fig. 11; Pl. 9, Figs 13-14)

1983. Subtype number 083; L. TWAY & J. ZIDEK, p. 430, Fig. 43.
1983. Subtype number 169; L. TWAY & J. ZIDEK, p. 431, Fig. 50.

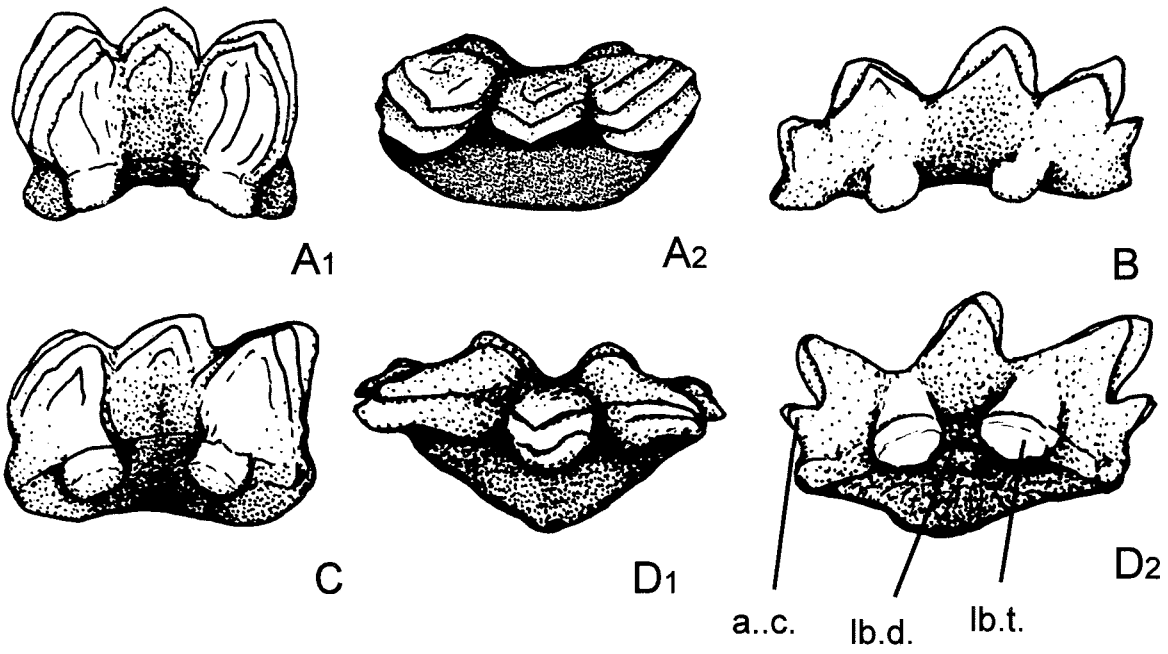


Fig. 4. *Adamantina foliacea* sp. n.; A – South Urals, Sikaza River, Early Carboniferous, Late Tournaisian; A_1 – labial and A_2 – occlusal views; B – Polar Urals, Vorkuta River; Early Permian, Early Asselian, labial view; C-D – after TWAY & ZIDEK (1983, Figs 43, 50); C, D_2 – oblique labial and D_1 – occlusal views; abbreviations: a.l.c. – additional lateral cusp, lb.d. – labio-basal depression, lb.t. – labio-basal tubercle

HOLOTYPE: LP 6-83, tooth (Pl. 9, Fig. 14).

TYPE LOCALITY: River Sikaza, South Urals.

TYPE HORIZON: Lower Carboniferous (Upper Tournaisian), Early *Gnathodus typicus* Zone, Kizel Regional Stage.

ETYMOLOGY: Latin *foliacea* – leaf-shaped.

MATERIAL: Four teeth (Tables 1, 2C); Early Carboniferous (Late Tournaisian), Early *typicus* Zone – Early Permian (Late Artinskian), *Parafusulina solidissima* foraminifer Zone; River Usa, Polar Urals, River Sylva, Middle Urals and River Sikaza, South Urals.

DIAGNOSIS: The crown has three or five cusps, which are labio-lingually flattened. The labial sculpture is lanceolate. The base is smooth and extended linguad. The labio-basal depression has prominent rounded tubercles.

DESCRIPTION: The crown is composed of three or five cusps. The cusps in the tricuspid teeth are sub-equal in height and width, and labio-lingually flattened (Pl. 9, Figs 13-14). Their axes are sub-parallel. Additional lateral cusplets are shorter than the inner ones in the five-cusped crowns (Pl. 7, Fig. 11), which are fan-shaped. The cusps of the tricuspid teeth are closely packed, and their bases are fused. By contrast, they are separated in the five-cusped crowns. The labial face is covered by strong lanceolate sculpture. The number of lanceolate ridges varies from two to five. The lingual face bears rare weak ridges or lacks sculpture altogether. The lateral carina separates the lingual and labial faces of the crown. The base is smooth, slightly arched, usually short and extended linguad. The numerous foramina in the five-cusped teeth open along the lingual rim on the upper side of the base (Pl. 7, Fig. 11c; TWAY & ZIDEK 1983, Fig. 43c). There is a moderate labio-basal depression in the middle of the teeth continued on the basal side. The lateral edge of the depression bears two distinct, rounded tubercles on each side (Pl. 7, Fig. 11b; Pl. 9, Fig. 14a).

REMARKS: TWAY & ZIDEK (1983) illustrated unnamed specimens from the Upper Pennsylvanian

(Upper Kasimovian) of Iowa, USA, which also belong to a new species. A specimen described from the Upper Pennsylvanian of Brazil (DUFFIN & *al.* 1996) probably belongs to the same species but the teeth are strongly labio-lingually compressed.

The teeth of *Adamantina benedictae* BENDIX-ALMGREEN from the Late Permian of Greenland (BENDIX-ALMGREEN 1993) differ from those of *A. foliacea* in the spirally curved sculpture, the linguo-basal direction of the base, the more widely separated lateral cusps, and in the fact that the central cusp is shorter than the lateral ones.

OCCURRENCE: Russia, South Urals, Late Tournaisian; Middle Urals, Early Permian (Late Artinskian); Polar Urals, Early Permian (Early Asselian); USA, Iowa, Late Pennsylvanian (Late Kasimovian).

Chondrichthyan assemblages

The Late Devonian – Early Permian chondrichthyan assemblages in the different regions of the Russian Arctic are reviewed from older to younger (see Table 3).

Late Devonian (Frasnian)

The earliest Late Devonian chondrichthyans are recorded in the Lower Frasnian of South Timan and represented by rare isolated protacrodont scales and symmoriid mucous membrane denticles ("*Stemmatias*"). Presumed hybodont scales (Pl. 1, Fig. 1) and scales of undetermined chondrichthyans are found in the shallow water deposits of the same age in Middle Timan. The Middle Frasnian Domanik Formation of South Timan (Ukhta region) contains stethacanthid (Pl. 1, Fig. 5) and *Protacrodus* (Pl. 1, Fig. 4) teeth, mucous membrane denticles, scales of *Protacrodus* (Pl. 1, Fig. 4), ctenacanths, hybodonts (Pl. 1, Figs 7, 8) and other chondrichthyans. The highly diverse assemblage of abundant chondrichthyan remains in the Upper Frasnian Lyaiol' Formation of South Timan contains numerous teeth of *Phoebodus bifurcatus* GINTER & IVANOV (Pl. 1, Figs 9-11), teeth of *P. latus* GINTER & IVANOV (Pl. 1, Fig. 13), teeth and scales of *Protacrodus* cf. *P. vetustus* JAEKEL (Pl. 1, Fig. 14), ctenacanthid and other scales (Pl. 1, Figs 12, 15, 16), and rare stethacanthid teeth. This assemblage includes two index-species for phoebodont zonation: *Phoebodus bifurcatus* and *P. latus* (GINTER & IVANOV 1995a). Chondrichthyans occur there in deep-water carbonate deposits dominated by the conodont genus *Palmatolepis* and ammonoids. *P. latus* (Pl. 1, Fig. 17) is also reported from the uppermost Frasnian Ukhta Formation of the same region.

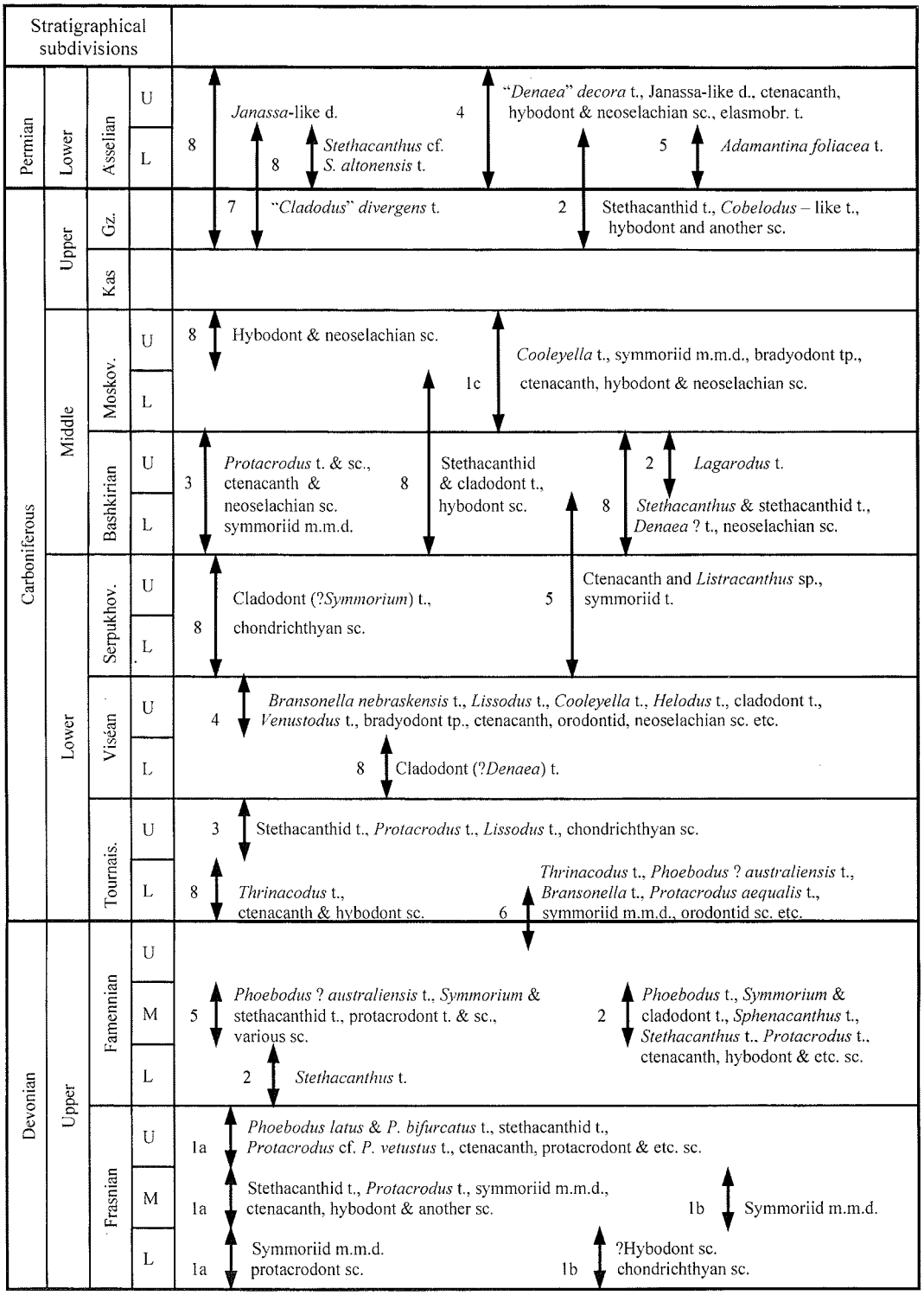
Late Devonian (Famennian)

Early Famennian fossil sharks are scarce in the Russian Arctic. Only two isolated teeth of *Stethacanthus* have been found in beds of this age in the *River Shar'yu of Chernyshev Ridge*. A rich Middle Famennian chondrichthyan assemblage occurs in the Chernyshev Ridge and the Polar Urals (see Table 3). The Chernyshev Ridge assemblage includes the teeth of *Phoebodus*, *Symmorium* (Pl. 3, Fig. 1), *Stethacanthus* (Pl. 3, Fig. 3), cladodont teeth with a short, strongly arched base lacking button or labio-basal projection, and with fused bases of the cusps (Pl. 3, Fig. 2); teeth of *Protacrodus* (Pl. 3, Fig. 4); ctenacanth (Pl. 2, Fig. 5), protacrodont (Pl. 2, Fig. 2), hybodont and various other scales and denticles, as well as the first record of a *Sphenacanthus* tooth (Pl. 2, Figs 1, 3). Shark remains of the same age from the Polar Urals are represented by the teeth of *Phoebodus? australiensis* LONG (Pl. 2, Figs 9, 12), *Symmorium* and stethacanthid teeth (Pl. 2, Fig. 10), protacrodont teeth and scales (Pl. 2, Figs 6, 11) and some chondrichthyan scales (Pl. 2, Figs 7, 8). *Phoebodus? australiensis* dominates the chondrichthyans in the Middle Famennian assemblage of the deep-water Lemva zone of the Polar Urals, which contains abundant palmatolepid conodonts. The fossil sharks are less diverse in the shallow water polygnathid biofacies in the Middle Famennian and represented by rare protacrodonts, ctenacanths and sporadic stethacanthids (Pl. 2, Fig. 4). Acanthodians and palaeoniscids dominate the vertebrate assemblage of this facies.

Devonian/Carboniferous boundary beds

A peculiar shark assemblage occurs in the Devonian/Carboniferous boundary beds (probably Early Tournaisian) of the Varandey – Adz'va structural zone of the northern part of the Timan – Pechora Province, Medynskaya-5 Borehole. These comprise an asymmetrical tooth of *Thrinacodus* with two cusps on the crown (Pl. 4, Fig. 2), teeth of *Phoebodus? australiensis*, *Protacrodus aequalis* IVANOV (Pl. 4, Fig. 3), and *Bransonella* (Pl. 4,

Table 3. Distribution of chondrichthyans in the Upper Devonian – Lower Permian of the Russian Arctic



Abbreviations: d. – denticles, m.m.d. – mucous membrane denticles, sc. – scales, sp. – spines, t. – teeth, tp. – toothplates; 1a – South Timan, 1b – Middle Timan, 1c – North Timan, 2– Chernyshev Ridge, 3 – Northern Urals, 4 – Nearpolar Urals, 5 – Polar Urals, 6 – Timan-Pechora Province, 7 – Pechora Sea, 8 – Novaya Zemlya. Gz. – Gzhelian, Kas – Kasimovian, Moskov. – Moskovian, Serpukhov. – Serpukhovian, Tournais. – Tournaisian

Fig. 1), symmoriid mucous membrane denticles, and orodontid and ctenacanth scales. *Protacrodus aequalis* is characteristic of the boundary beds, *praesulcata – sulcata* zones (IVANOV 1996). *Phoebodus*? *australiensis* crosses the boundary and occurs in the lowermost Tournaisian. The oldest occurrence of the genus *Bransonella* known so far is Late Viséan (IVANOV & GINTER 1996, LEBEDEV 1996). Thus, this tooth belongs to the oldest species of the genus mentioned above and is probably placed between *Phoebodus*? *australiensis* and the typical representative of *Bransonella*, *B. nebraskensis* (JOHNSON), on the basis of tooth morphology.

Early Carboniferous

Carboniferous chondrichthyans are common in the Russian Arctic regions. Early Carboniferous (Early Tournaisian) shark remains are recorded in the North Island of Novaya Zemlya and are represented by the teeth of *Thrinacodus* (completely asymmetrical teeth with two cusps on the crown (Pl. 4, Fig. 4), and one specimen with a symmetrical crown and an asymmetrical base); scales of hybodonts (Pl. 4, Fig. 5) and a scale of a presumed ctenacanth (Pl. 4, Fig. 6). Chondrichthyans from the Upper Tournaisian of the North Urals, River Podcherem, include a stethacanthid tooth (Pl. 4, Fig. 7), teeth of *Protacrodus*, tooth fragments of *Lissodus* (Pl. 4, Fig. 8) similar to the form described from the Lower Permian of Germany (HAMPE 1996), and scales of undetermined sharks. A single cladodont tooth, probably belonging to the genus *Denaea*, occurs in the Lower Viséan of the North Island of Novaya Zemlya. A rich chondrichthyan assemblage was found in the Lower Carboniferous (Upper Viséan) of the Nearpolar Urals, River Kozhim. It is represented by teeth of *Bransonella nebraskensis* (Pl. 5, Fig. 4; IVANOV & GINTER 1996), teeth of *Lissodus*, some of which resemble *L. wirksworthensis* DUFFIN (DUFFIN 1985), cladodont teeth, *Cooleyella* teeth (Pl. 5, Figs 7, 8), a *Helodus*-type tooth, a *Venustodus* tooth (Pl. 5, Fig. 2), orodontid (Pl. 5, Fig. 6), ctenacanthid and neoselachian scales, presumed cephalic (Pl. 5, Fig. 5) and other denticles, as well as an undetermined bradyodont tooth plate. Another Early Carboniferous (Serpukhovian) chondrichthyan locality, in the South Island of the Novaya Zemlya Archipelago, has yielded cladodont teeth probably belonging to *Symmorium* (Pl. 4, Fig. 9), as well as a scale (Pl. 4, Fig. 10) similar to that illustrated by BENDIX-ALMGREEN (1993, Figs 4 F-M) and referred by him to *Adamantina benedictae* BENDIX-ALMGREEN.

Shark spines are very rarely represented in the material from the Russian Arctic Region. Nevertheless, the spines of *Listracanthus* and some ctenacanth, as well as symmoriid teeth were found in the Serpukhovian – Early Bashkirian interval of the Polar Urals, River Kharuta (Table 3).

Middle Carboniferous

Middle Carboniferous (Bashkirian) chondrichthyan remains, such as *Protacrodus* teeth (Pl. 6, Fig. 1), symmoriid mucous membrane denticles (Pl. 6, Fig. 2), ctenacanth and neoselachian scales, are found in the borehole of the North Urals. An isolated toothplate of *Lagarodus* is reported from the Upper Bashkirian of the River Shar'yu of Chernyshev Ridge. In addition, a rich shark assemblage comprising numerous stethacanthid (Pl. 6, Figs 4-10) and *Denaea*-like (Pl. 6, Fig. 3) teeth, and neoselachian scales, occurs in the Bashkirian of the South Island of the Novaya Zemlya Archipelago. Moscovian deposits of North Timan contain teeth of *Cooleyella* (Pl. 6, Fig. 11), fragments of bradyodont toothplates, „*Stemmatias*"-like denticles, and ctenacanthid, hybodont and neoselachian scales.

Late Carboniferous

Scattered chondrichthyan remains are recorded from the Upper Carboniferous (Gzhelian) – Lower Permian (Asselian) boundary deposits: "*Cladodus*" *divergens* TRAUTSCHOLD from the Pechora Sea borehole (Pl. 7, Fig. 1), *Janassa*-like denticles from the North Island of Novaya Zemlya (Pl. 7, Fig. 2), stethacanthid teeth, *Cobelodus*-like teeth, hybodont, neoselachian (Pl. 7, Figs 3, 4), and other shark scales (Pl. 7, Fig. 5) from the Chernyshev Ridge.

Early Permian

Teeth of *Stethacanthus* cf. *S. altonensis* (ST. JOHN & WORTHEN) occur in the Lower Asselian of the North Island of the Novaya Zemlya Archipelago. *Adamantina foliacea* sp.n. (Pl. 7, Fig. 11) was found in the Lower Asselian at the same stratigraphic level in the Polar Urals. The Early Permian (Asselian) assemblage from the Nearpolar Urals contains various chondrichthyan

remains, such as the teeth of a new species, "*Denaea*" *decora* (Pl. 7, Fig. 12), an unusual tooth (Pl. 7, Fig. 1) slightly resembling *Thrinacodus* with a symmetrical crown and short base (TURNER 1982, DUFFIN 1993b, IVANOV 1996, Fig. 4E), as well as numerous neoselachian (Pl. 7, Figs 9-10), hybodont, a few ctenacanth and other (Pl. 7, Fig. 7) scales, and *Janassa*-like denticles.

Neoselachian scales are the dominant chondrichthyan scales in the Early Permian occurrences, while ctenacanth and hybodont scales are common in the late Devonian – Carboniferous, as well as protacrodont scales – in the Devonian.

The foregoing analysis of new material demonstrates the high taxonomic diversity of chondrichthyans in the Upper Devonian – Lower Permian interval of the Russian Arctic regions and documents their wide geographical and stratigraphical distribution.

Acknowledgements

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PLATE 1

Late Devonian (Frasnian) chondrichthyan remains of the Timan

1 – ? Hybodont scale, LP 6-1, × 80; a – lateral and b – oblique lateral views; Middle Timan, Pechorskaya Pizhma River; Early Frasnian, Uste Yarega Fm., Srednyaya Beds

2 – Symmoriid mucous membrane denticle, lateral view, LP 6-2, × 100; Middle Timan, Pechorskaya Pizhma River; Middle Frasnian; Kraipole Fm.

3 – Symmoriid mucous membrane denticle, anterior view, LP 6-3, × 80; South Timan, Ukhta Region, Chut' River; Early Frasnian, Uste Yarega Fm.

4, 6 – *Protacrodus* sp.; 4 – tooth, occlusal views, LP 6-4, × 60; 6 – scale, crown view, LP 6-6, × 70; South Timan, Ukhta Region, Borehole 2021, 292 m; Middle Frasnian, Domanik Fm., Upper Member

5 – Stethacanthid tooth, occlusal views, LP 6-5, × 40; South Timan, Ukhta Region, Borehole 2021, 292 m; Middle Frasnian, Domanik Fm., Upper Member

7 – ?Hybodont scale, oblique crown view, LP 6-7, × 90; South Timan, Ukhta Region, Borehole 2021, 292 m; Middle Frasnian, Domanik Fm., Upper Member

8 – ?Hybodont scale, lateral view, LP 2-1, × 40; South Timan, Ukhta Region, borehole 1003, 117,8-118,8 m; Domanik Fm., Middle Member

9 – *Phoebodus bifurcatus* GINTER & IVANOV, LP 6-8, × 15; a – occlusal and b – lingual views; South Timan, Ukhta Region, Lyaiol' River; Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

10 – *Phoebodus bifurcatus* GINTER & IVANOV, LP 6-10, × 40; a – occlusal and b – labial views; South Timan, Ukhta Region, borehole 2068, 11 m, Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

11 – *Phoebodus bifurcatus* GINTER & IVANOV, occlusal view, LP 7-7, × 30; South Timan, Ukhta Region, borehole 2023, 149 m; Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

12 – Ctenacanth scale, crown view, LP 6-9, × 70; South Timan, Ukhta Region, Lyaiol' River; Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

13 – *Phoebodus latus* GINTER & IVANOV, occlusal view, LP 6-11, × 40; South Timan, Ukhta Region, borehole 2022, 225 m; Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

14 – *Protacrodus* cf. *P. vetustus* JAEKEL, LP 6-12, × 30; a – occlusal and b – lingual views; South Timan, Ukhta Region, borehole 2021, 187 m, Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

15-16 – Chondrichthyan scales (15 – ?*Cladolepis*-type), crown views, 15 – LP 6-13, × 50, 16 – LP 6-14, × 60; South Timan, Ukhta Region, borehole 2022, 225 m; Late Frasnian, Lyaiol' Fm., the *rhenana* Zone

17 – *Phoebodus latus* GINTER & IVANOV, LP 6-15, × 35; a – occlusal and b – labial views; South Timan, Ukhta Region, borehole 2022, 32 m; Late Frasnian, Ukhta Fm., Lower Member

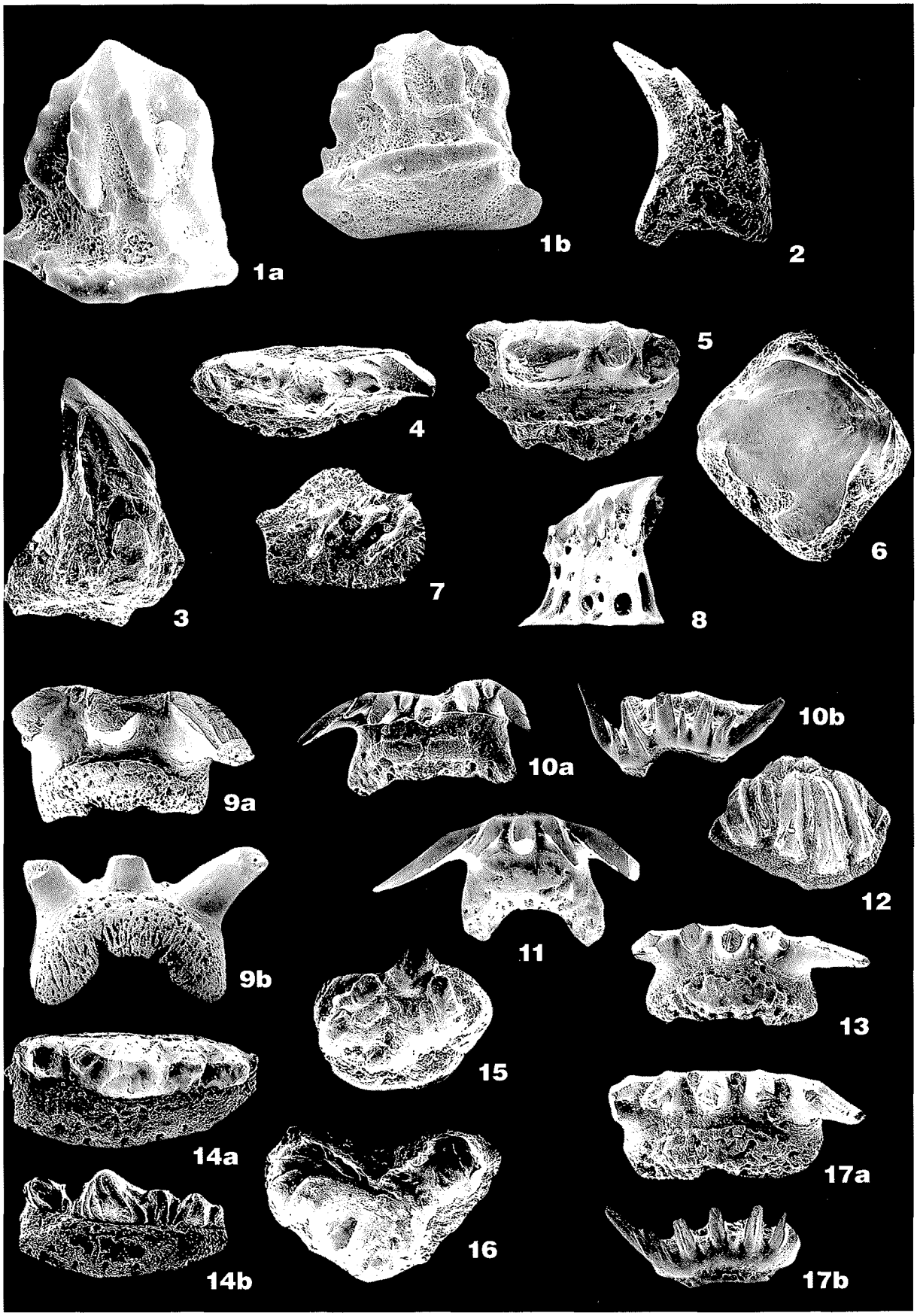
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PLATE 2

Late Devonian (Famennian) chondrichthyan remains

1 – ? Ctenacanth scale, crown view, LP 6-16, × 50; Chernyshev Ridge, Der-Shor River; Middle Famennian, the Late *marginifera* Zone

2 – Protacrodont scale, crown view, LP 6-17, × 65; Chernyshev Ridge, Der-Shor River; Middle Famennian, the Late *marginifera* Zone

3 – Chondrichthyan scale, crown view, LP 6-18, × 60; Chernyshev Ridge, Der-Shor River; Middle Famennian, the Late *marginifera* Zone

4 – Stethacanthid tooth, occlusal view, LP 619, × 40; Chernyshev Ridge, Adz'va River; Middle Famennian, the *marginifera* Zone

5 – ?Ctenacanth scale, crown view, LP 6-20, × 50; Chernyshev Ridge, Adz'va River; Middle Famennian, the *marginifera* Zone

6 – Protacrodont scale, crown view, LP 6-21, × 30; Polar Urals, Lemva River; Middle Famennian, the *marginifera* Zone

7-8 – Chondrichthyan scales, crown views; 7 – LP 6-22, × 70; 8 – LP 6-23, × 65; Polar Urals, Lemva River; Middle Famennian, the *marginifera* Zone

9, 12 – *Phoebodus? australiensis* LONG, teeth; 9 – labial view, LP 6-24, × 60; 12 – occlusal view, LP 6-25, × 75; Polar Urals, Lemva River; Middle Famennian, the *marginifera* Zone

10 – Stethacanthid tooth, LP 6-26; a – labial and b – lateral views, × 35; Polar Urals, Lemva River; Middle Famennian, the *marginifera* Zone

11 – Protacrodont tooth, occlusal view, LP 6-27, × 40; Polar Urals, Lemva River; Middle Famennian, the *marginifera* Zone

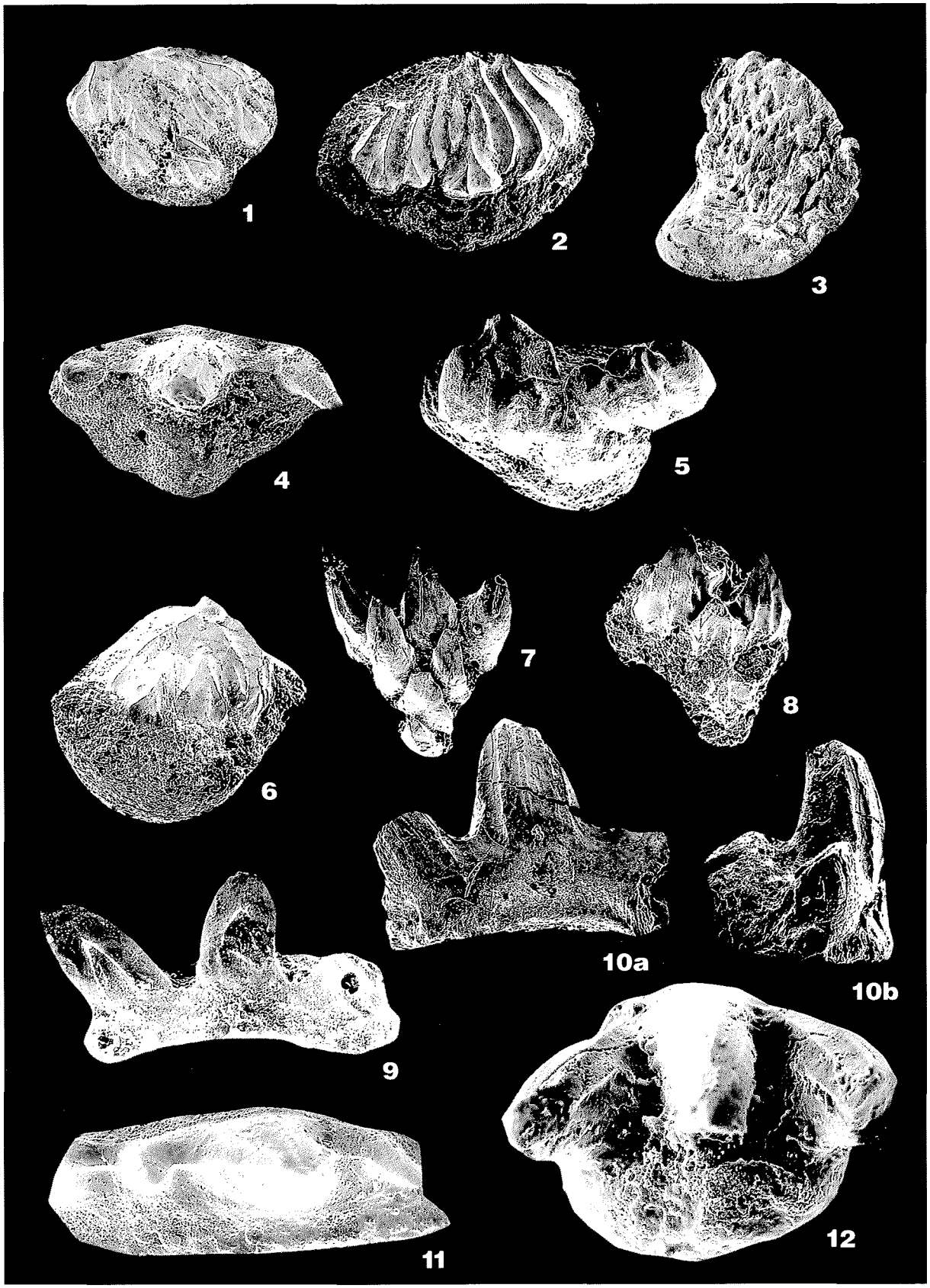
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PLATE 3

Late Devonian (Middle Famennian, the *marginifera* Zone) chondrichthyan remains of the Chernyshev Ridge, Shar'yu River

1 – *Symmorium* sp., tooth, LP 6-28, × 40; a – labial and b – oblique basal views
2 – Cladodont tooth, LP 6-29, × 30; a – labial and b – occlusal views
3 – *Stethacanthus* sp., tooth, LP 6-30, × 35; a – occlusal, b – labial and c – basal views
4 – *Protacrodus* sp., tooth, LP 6-31, × 50; a – occlusal and b – labial views
5 – *Sphenacanthus* sp., tooth, LP 6-32, × 60; a – occlusal, b – lateral, c – labial and d – lingual views

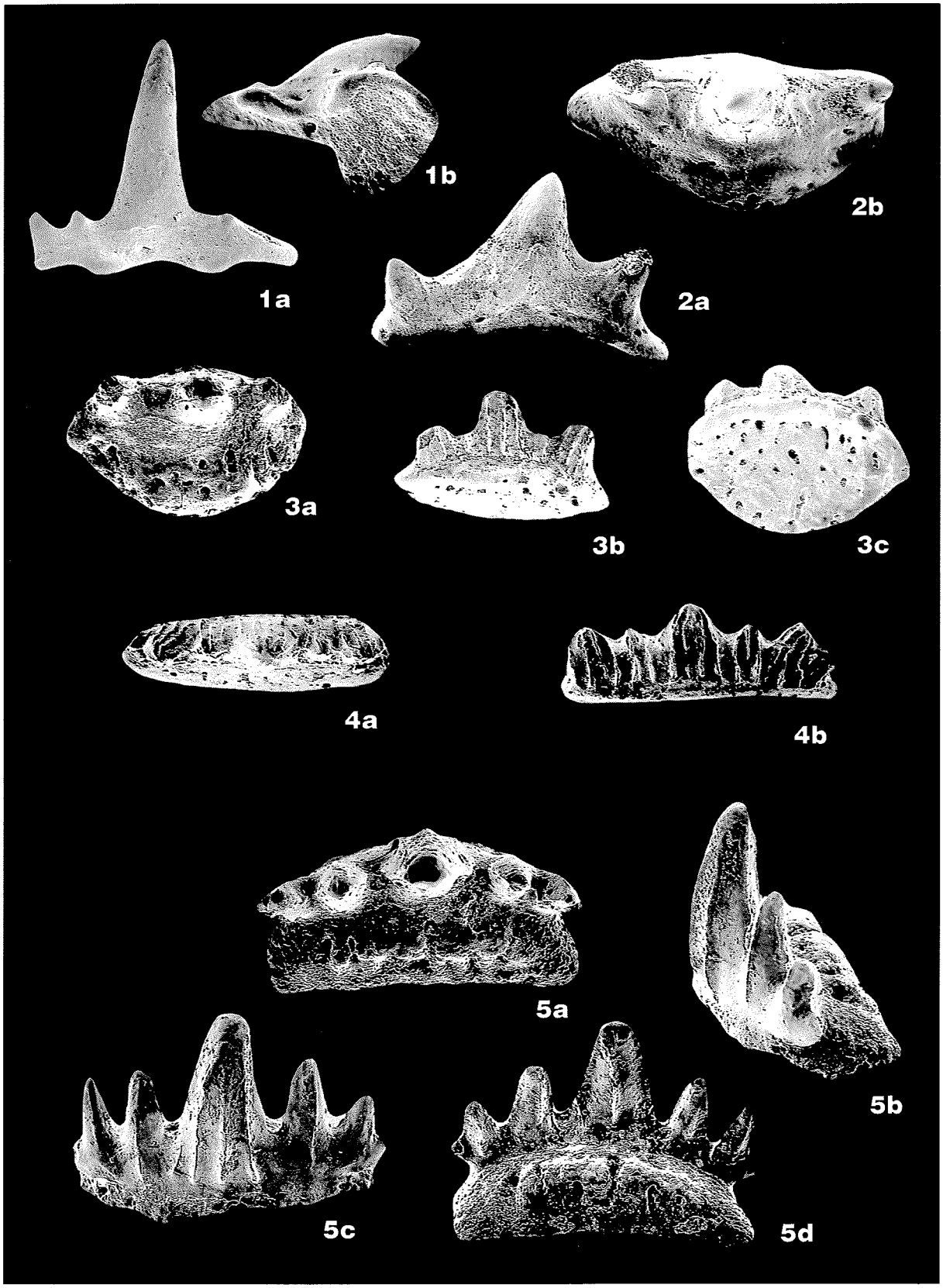
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PLATE 4

Early Carboniferous chondrichthyan remains

1 – *Bransonella* sp., tooth, LP 6-33, × 55; a – labial and b – basal views; Timan – Pechora Province, borehole Medynskaya-5, 2330,6-2344,4 m; Devonian/Carboniferous boundary beds (Tournaisian)

2 – *Thrinacodus* sp., tooth, occlusal view, LP 6-34, × 40; Timan – Pechora Province, borehole Medynskaya-5, 2330,6-2344,4 m; Devonian/Carboniferous boundary beds (Tournaisian)

3 – *Protacrodus aequalis* IVANOV, tooth, LP 6-35, × 40; a – labial, b – lateral and c – occlusal views; Timan – Pechora Province, borehole Medynskaya-5, 2330,6-2344,4 m; Devonian/Carboniferous boundary beds (Tournaisian)

4 – *Thrinacodus* sp., tooth, lateral view, LP 6-36, × 50; Novaya Zemlya, North Island, Eks Bay; Early Tournaisian

5 – Hybodont scale, oblique crown view, LP 6-37, × 60; Novaya Zemlya, North Island, Eks Bay; Early Tournaisian

6 – ?Ctenacanth scale, anterior view, LP 6-38, × 80; Novaya Zemlya, North Island, Eks Bay; Early Tournaisian

7 – Stethacanthid tooth, LP 6-39, × 45; a – occlusal and b – labial views; North Urals, Podcherem River; Late Tournaisian

8 – *Lissodus* sp., tooth crown, LP 6-40, × 50; North Urals, Podcherem River; Late Tournaisian

9 – Cladodont (?*Symmorium*) tooth, LP 6-41, × 35; a – labial and b – occlusal views; Novaya Zemlya, South Island, Bol'shaya Yunau River; Serpukhovian

10 – Chondrichthyan scale, crown view, LP 6-42, × 60; Novaya Zemlya, South Island, Bol'shaya Yunau River; Serpukhovian

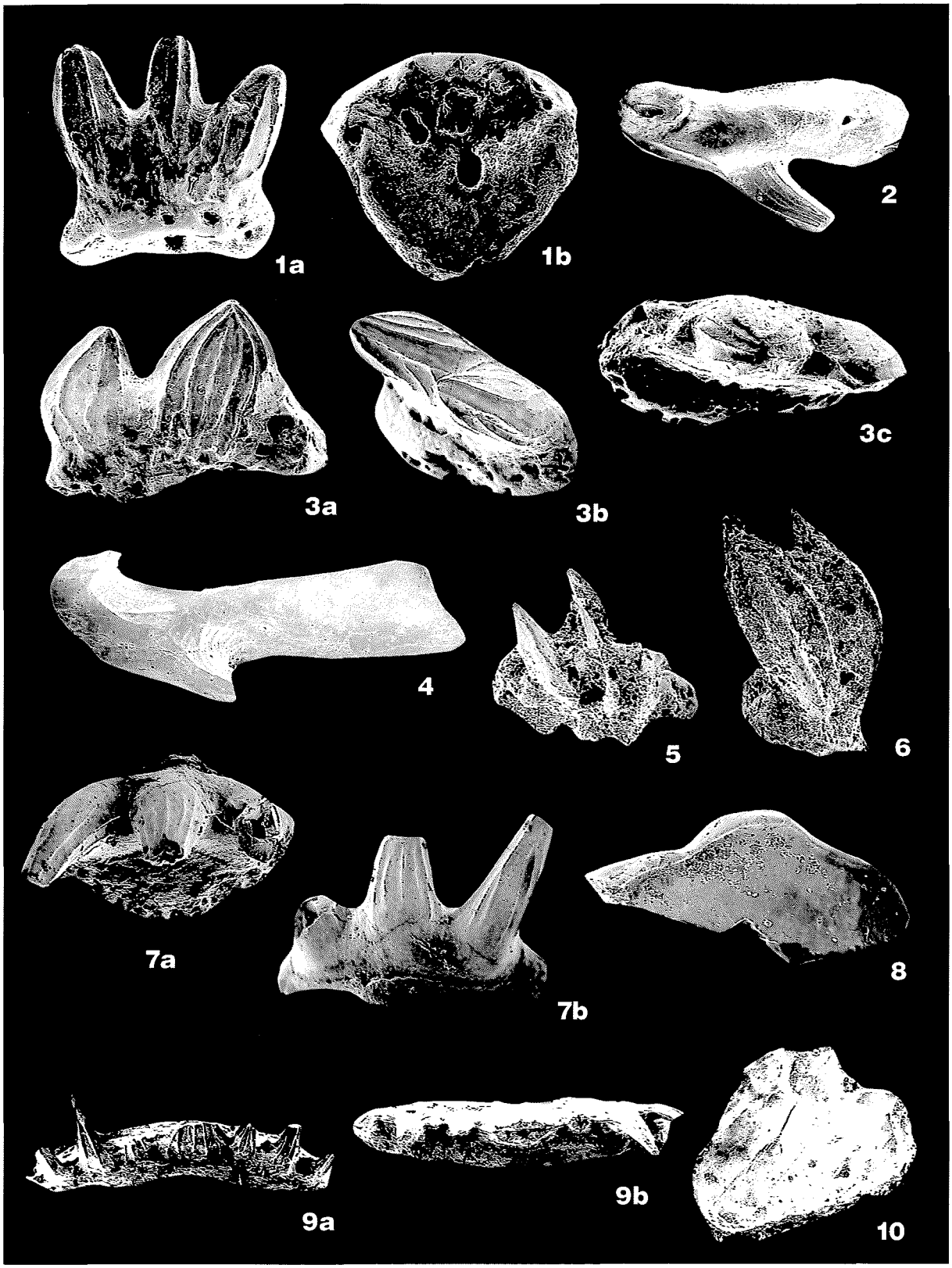
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PLATE 5

Early Carboniferous (Late Viséan) chondrichthyan remains of the Nearpolar Urals, Kozhim River

1, 3 – *Lissodus* sp., teeth, 1 – LP 6-43, × 50; a – occlusal and b – lingual views; 3 – LP 6-45, × 55, a – occlusal, b – labial and c – lingual views

2 – *Venustodus* sp., tooth, LP 6-44, × 70; a – labial and b – occlusal views

4 – *Bransonella nebraskensis* (JOHNSON), tooth, occlusal view, LP 16-2, × 60

5 – Chondrichthyan (?cephalic) denticle, LP 6-46, × 75; a – oblique lateral and b – crown views;

6 – Orodontid scale, crown view, LP 6-47, × 60

7-8 – *Cooleyella* sp.; 7 – LP 6-48, a – oblique occlusal, b – lateral and c -occlusal views, × 40; 8 – LP 6-49, × 55, a – labial and b – oblique basal views

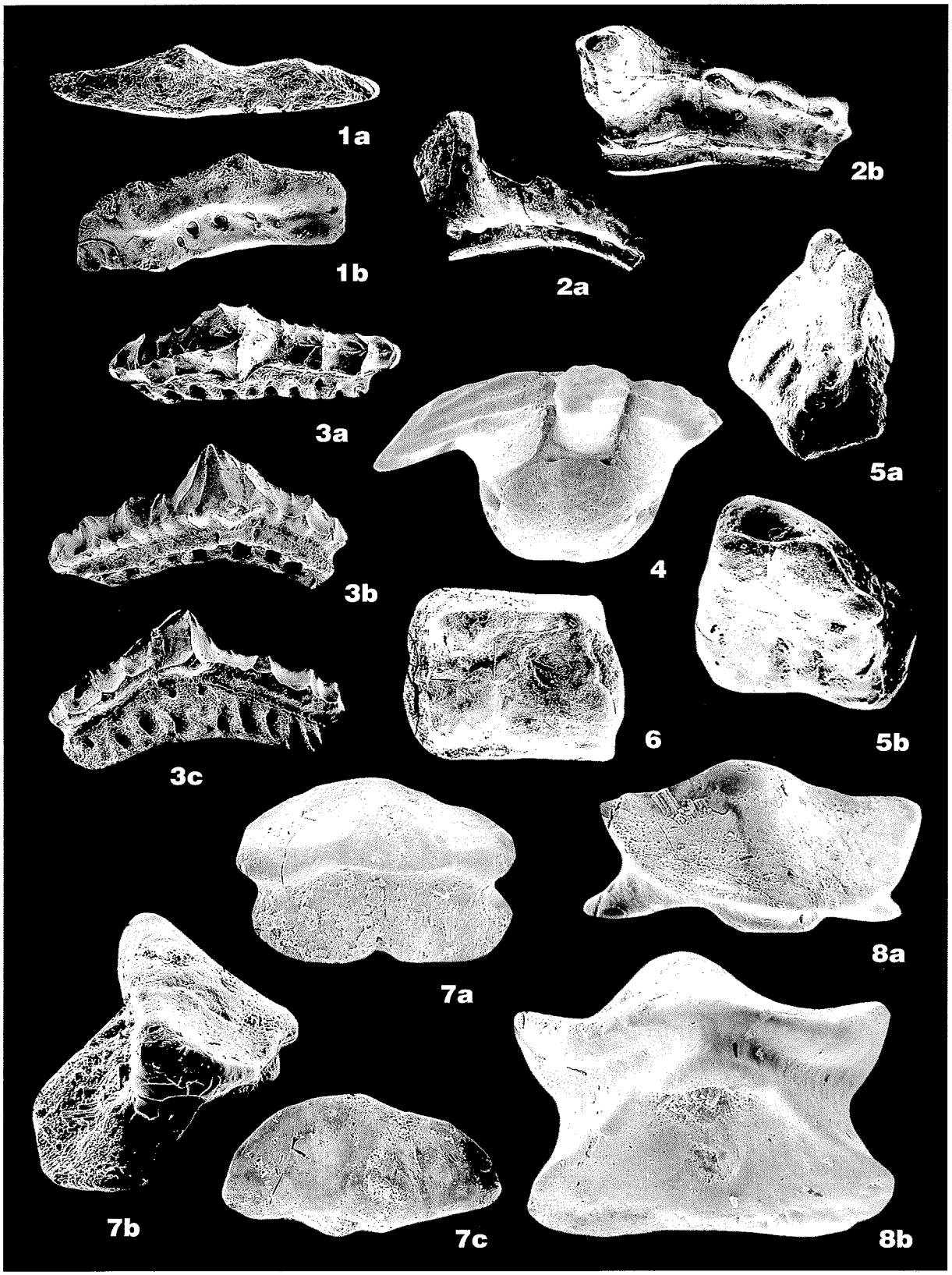
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PLATE 6

Middle Carboniferous chondrichthyan remains

1 – *Protacrodus* sp., tooth, LP 6-50, × 40; a – occlusal and b – lingual views; North Urals, Borehole Vychegodskaya, 14031 m; Bashkirian

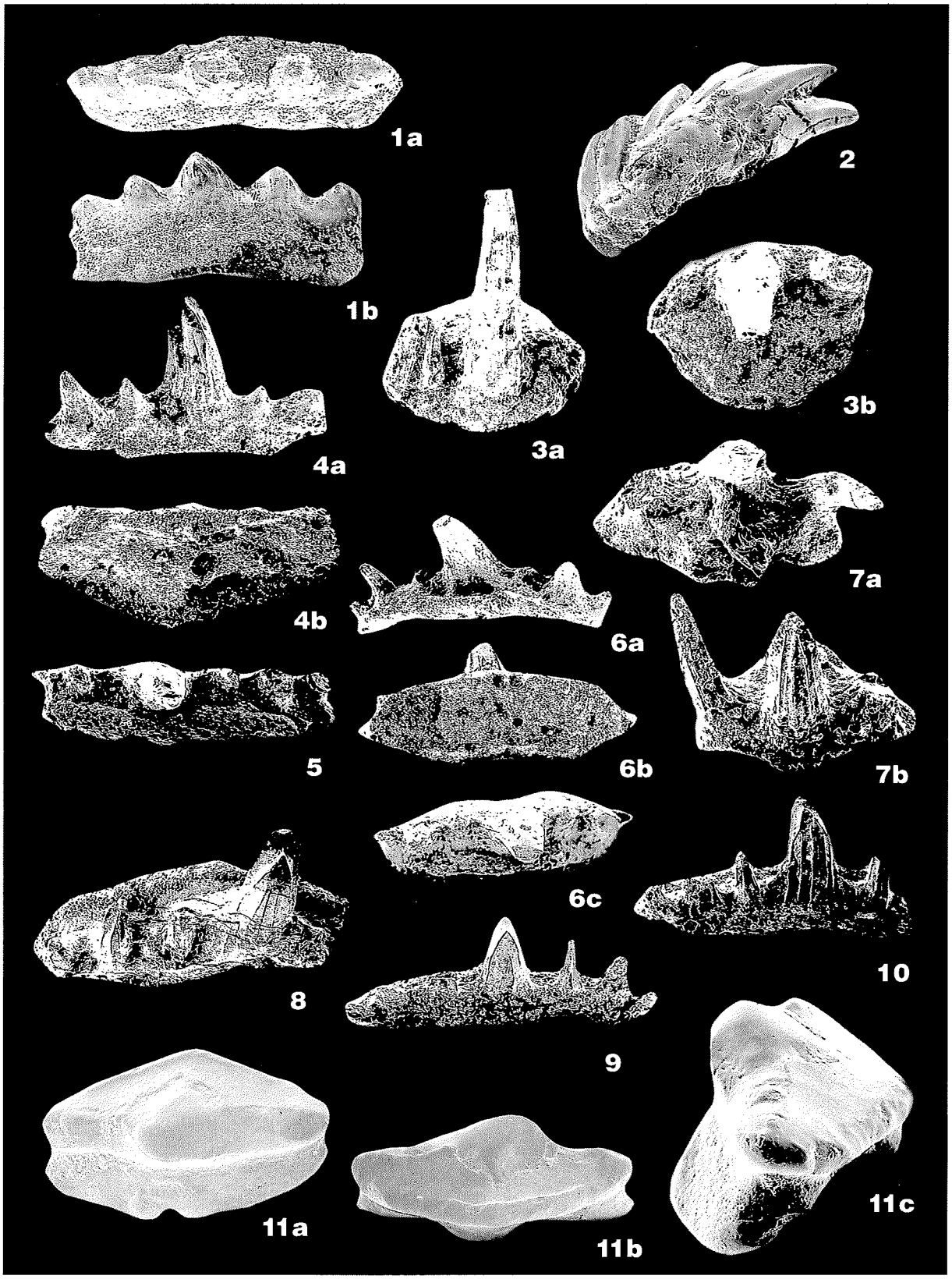
2 – Symmoriid mucous membrane denticle, lateral view, LP 6-51, × 60; North Urals, Borehole Vychegodskaya, 14031 m, Bashkirian

3 – ?Stethacanthid tooth, LP 6-52, × 35, a- labial and b – occlusal views; Novaya Zemlya, South Island, Rogachev River; Bashkirian

4-6, 8-10 – Stethacanthid teeth; 4 – LP 6-53, × 50, a- labial and b – basal views; 5 – occlusal view, LP 6-54, × 50; 6 – LP 6-55, a- lingual, b – basal and c – occlusal views; 8 – oblique occlusal view, LP 6-56, × 45; 9 – labial view, LP 6-57, × 40; 10 – labial view, LP 6-58, × 40; Novaya Zemlya, South Island, Vypuklyy Peninsula; Bashkirian

7 – *Stethacanthus* sp., tooth, LP 6-59, × 50; a – occlusal and b – labial views; Novaya Zemlya, South Island, Vypuklyy Peninsula; Bashkirian

11 – *Cooleyella* sp., tooth, LP 6-60, a, b × 40, c × 45; a – linguo-occlusal, b – labial and c – lateral views; North Timan, Malaya Pokayama River; Moskovian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7b
6c
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11a
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11c

PLATE 7

Carboniferous/Permian and Early Permian (Asselian) chondrichthyan remains

1 – "*Cladodus*" *divergens* TRAUTSCHOLD, tooth, LP 6-61, × 45; a –occlusal, b – lingual, c – lateral, d – basal and e – labial views; Pechora Sea, borehole Gulyaevskaya, 2710 m; L. Carboniferous, Gzhelian – E. Permian, E. Asselian

2 – *Janassa*-like denticle, oblique lateral view, LP 6-62, × 60; Novaya Zemlya, Russkaya Gavan' Bay; Gzhelian – Asselian

3-4 – Neoselachian scales, crown views; 3 – LP 6-63, × 70; 4 – LP 6-64, × 60; Nearpolar Urals, Kozhim River; Carboniferous/Permian boundary beds

5 – Chondrichthyan scale, oblique lateral view, LP 6-65, × 55; Nearpolar Urals, Kozhim River; Carboniferous/Permian boundary beds

6 – Undetermined elasmobranch tooth, LP 6-66, × 30; a – lingual and b – occlusal views; Nearpolar Urals, Malyy Patok River; Asselian

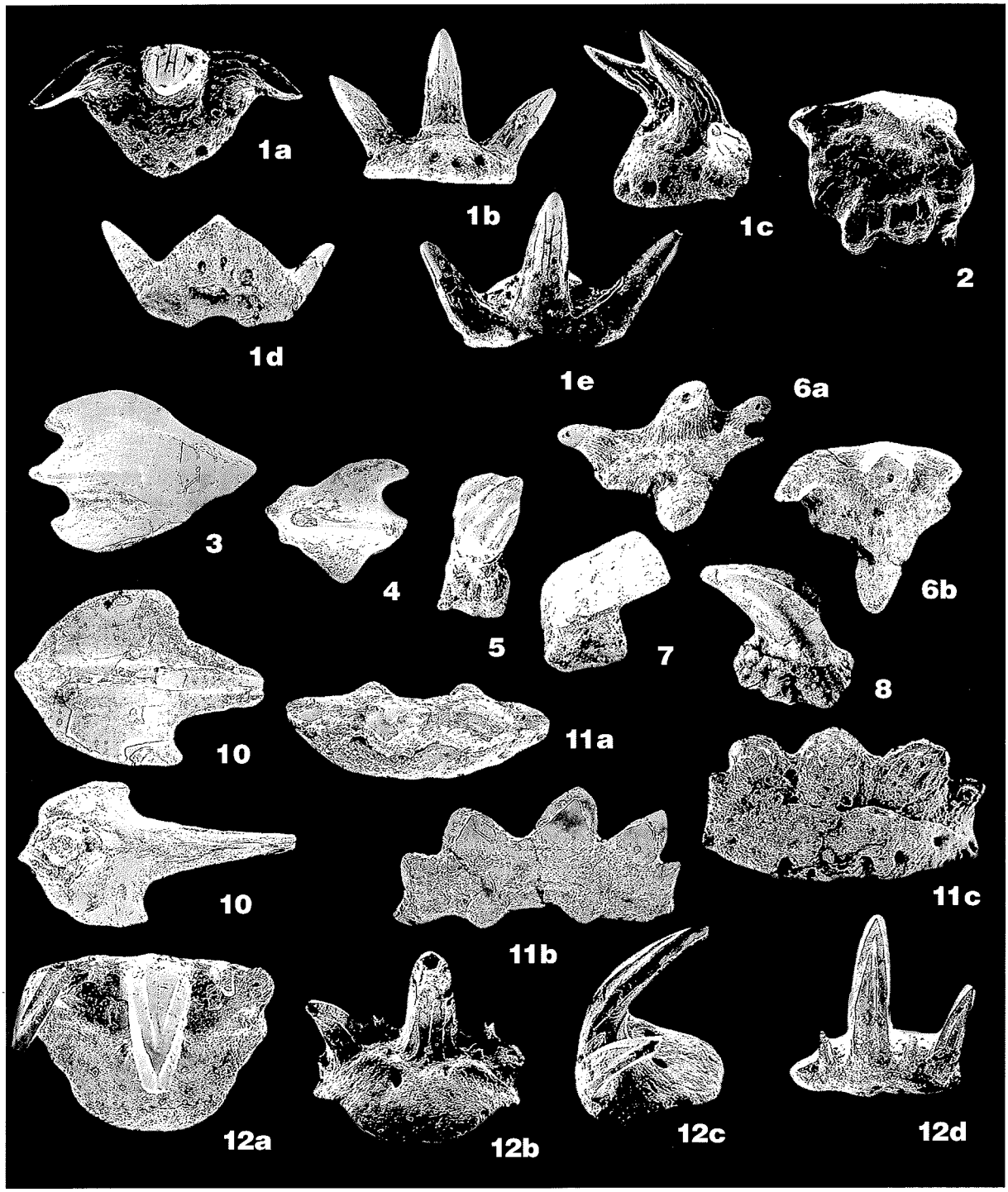
7 – Chondrichthyan scale, oblique lateral view, LP 6-67, × 75; Nearpolar Urals, Malyy Patok River; Asselian

8 – ?Hybodont scale, lateral view, LP 6-68, × 60; Nearpolar Urals, Malyy Patok River; Asselian

9-10 – Neoselachian scales, 9 – crown view, LP 6-69, × 80; 10 – basal view, LP 6-70, × 75; Nearpolar Urals, Malyy Patok River; Asselian

11 – *Adamantina foliacea* sp.n., tooth, LP 6-71, × 60, a – occlusal, b – labial and c – lingual views; Polar Urals, Vorkuta Region, Usa River; Early Asselian

12 – "*Denaea*" *decora* sp.n., tooth, LP 6-72; a × 50, b-d × 45, a – occlusal, b – lingual, c – lateral and d – labial views; Nearpolar Urals, Schugor River; Asselian.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12a
12b
12c
12d

PLATE 8

"Denaea" decora sp.n., teeth; South Urals; E. Permian, Sakmarian

1 – LP 6-73; a – occlusal view, × 45, b – detail in oblique occlusal view, × 120; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

2 – Holotype, LP 6-74; a – occlusal view, × 50, b – detail, × 130; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

3 – Occlusal view, LP 6-75, × 60; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

4 – LP 6-76; a – occlusal view, × 35; b – detail in oblique labial view, × 90; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

5 – Occlusal view, LP 6-77, × 55; Sim River, right riverside, near Sim

6 – LP 6-78, × 60; a – labial and b – oblique lateral views; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

7 – LP 6-79; a – labial view, × 40, b – detail, × 120; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

8 – LP 6-80, × 45; a – linguo-occlusal and b – lingual views; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

9 – Basal view, LP 6-81, × 50; Chelyabinsk District, road cut of Ufa – Chelyabinsk, 1 km from Sim

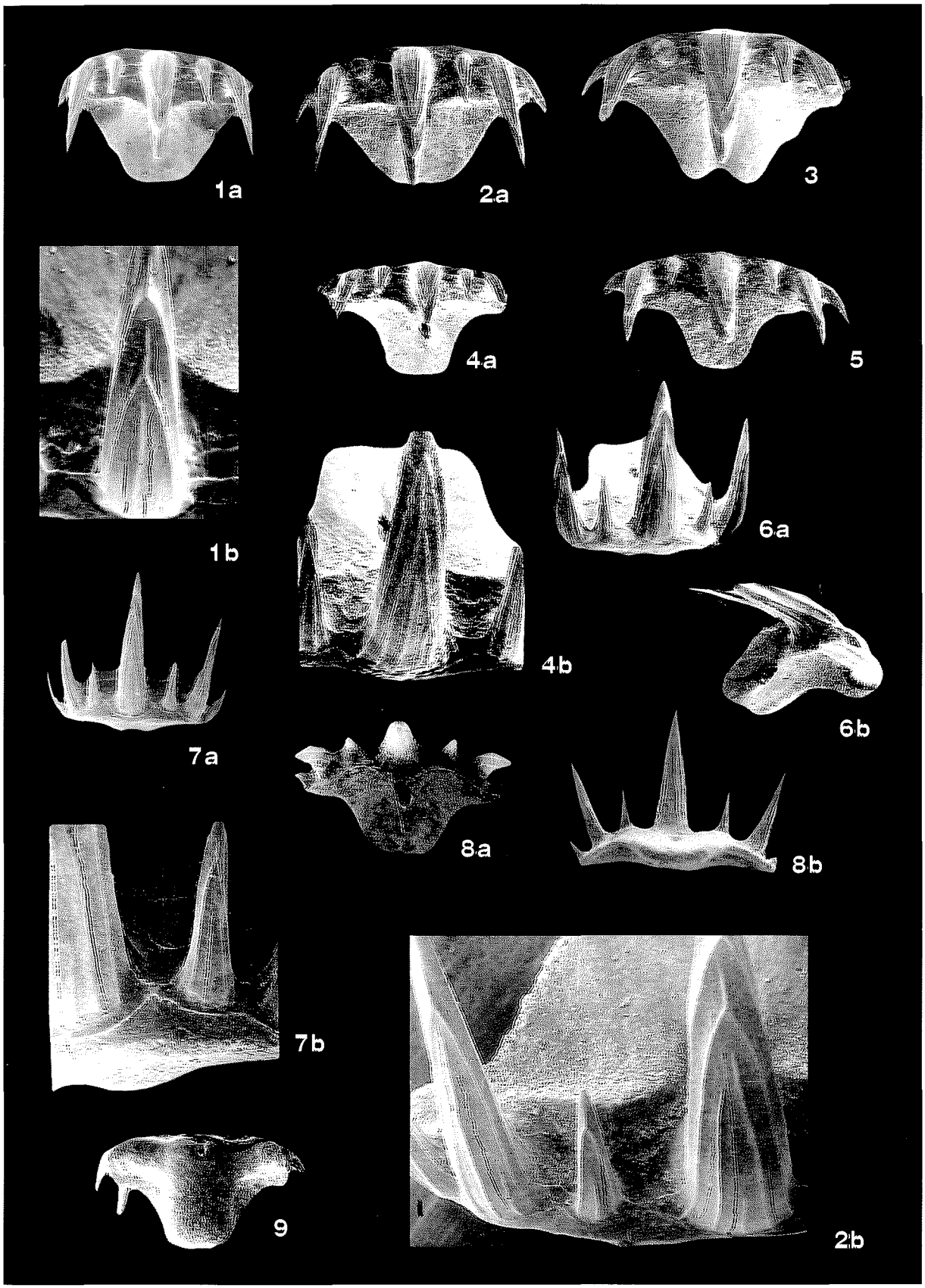
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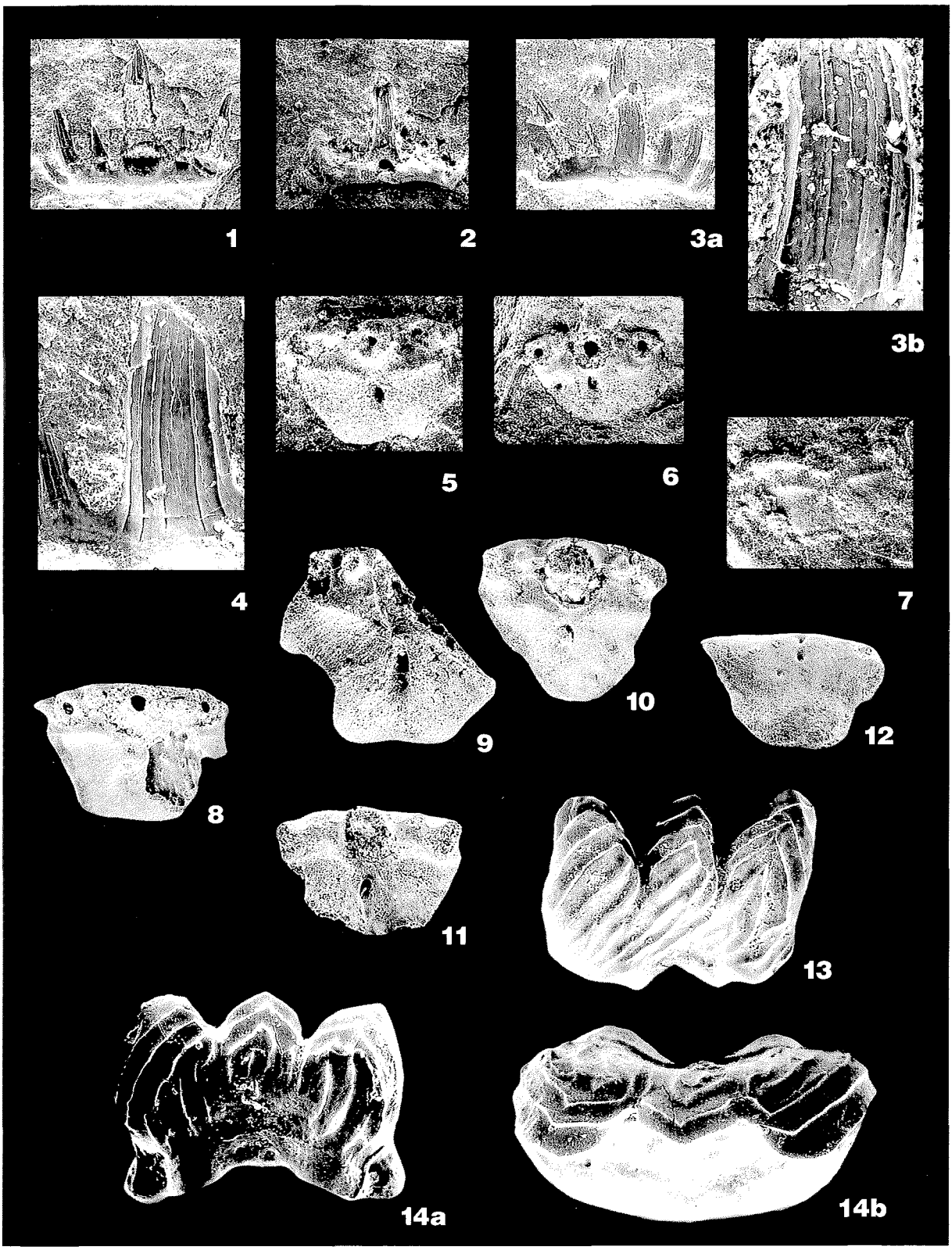
PLATE 9

1-12 – *"Denaea" meccaensis* WILLIAMS, teeth; USA, Indiana, Bethel quarry; Late Pennsylvanian, Excello Shale; 1 – imprint of labial surface, SMNH, × 50; 2 – lingual view, SMNH, × 35; 3 – SMNH, a – imprint of labial surface, × 50, b – sculpture of central cusp, × 200; 4 – sculpture of central cusp, SMNH, × 120; 5-11 – occlusal view; 5 – SMNH, × 50; 6 – SMNH, × 45; 7 – SMNH, × 50; 8 – SMNH, × 50; 9 – SMNH, × 75; 10 – SMNH, × 75; 11 – SMNH, × 60; 12 – basal view, SMNH, × 60

13-14 – *Adamantina foliacea* sp. n., teeth; 13 – labial view, LP 6-82, × 70; Middle Urals, Sylva River, near village Platonovo; Early Permian, Late Artinskian; 14 – holotype, LP 6-83, a – × 50, b – × 55, a – labial & b – occlusal views; South Urals, Sikaza River, Early Carboniferous, Late Tournaisian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