Conodont micropalaeontology of mid-Ordovician aged limestone clasts from Lower Old Red Sandstone conglomerates, Lanark and Strathmore basins, Midland Valley, Scotland

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ABSTRACT - Mid-Ordovician limestone clasts in the Lower Old Red Sandstone conglomerates of the Lanark and Strathmore basins of the Midland Valley, Scotland, were derived from a cryptic carbonate platform, now hidden beneath the Southern Uplands Allochthon. These have yielded 17 multi-element species of conodonts, which are systematically described herein and include the eponymous biozonal species *Pygodus serra* and *Pygodus anserinus*. The fauna represents an outer shelf-ocean margin biofacies, found only in Upper Ordovician conglomerates in the Southern Uplands and the Malopolska Terrane, Poland. *J. Micropalaeontol.* **19**(1): 45–59, May 2000

INTRODUCTION

The Midland Valley of Scotland is bounded by the Highland Boundary and Southern Upland faults, both major tectonic boundaries within the northern British Caledonides (Bluck *et al.*, 1992; Fig. 1). Pre-Devonian rocks are only poorly exposed and much of the basement geology has been inferred from studies of clast suites in Ludlow to Devonian age, Lower Old Red Sandstone (LORS) conglomerates. Clasts in conglomerates not only provide indirect evidence of the complex geological history

of the Midland Valley (Bluck, 1978, 1983, 1985; Haughton, 1988; Haughton & Bluck, 1988; Haughton *et al.*, 1990; Bluck *et al.*, 1992) but also the temporal and spatial history of adjacent terranes (Armstrong & Owen in press).

Smith (1995), Phillips *et al.*, (1997) and Armstrong & Owen (in press) have revised and reviewed the lithostratigraphy (Fig. 2), macropalaeontology and tectono-stratigraphic setting of the Midland Valley during the Ordovician to Devonian. New finds of conodont-bearing limestone clasts in southerly derived LORS
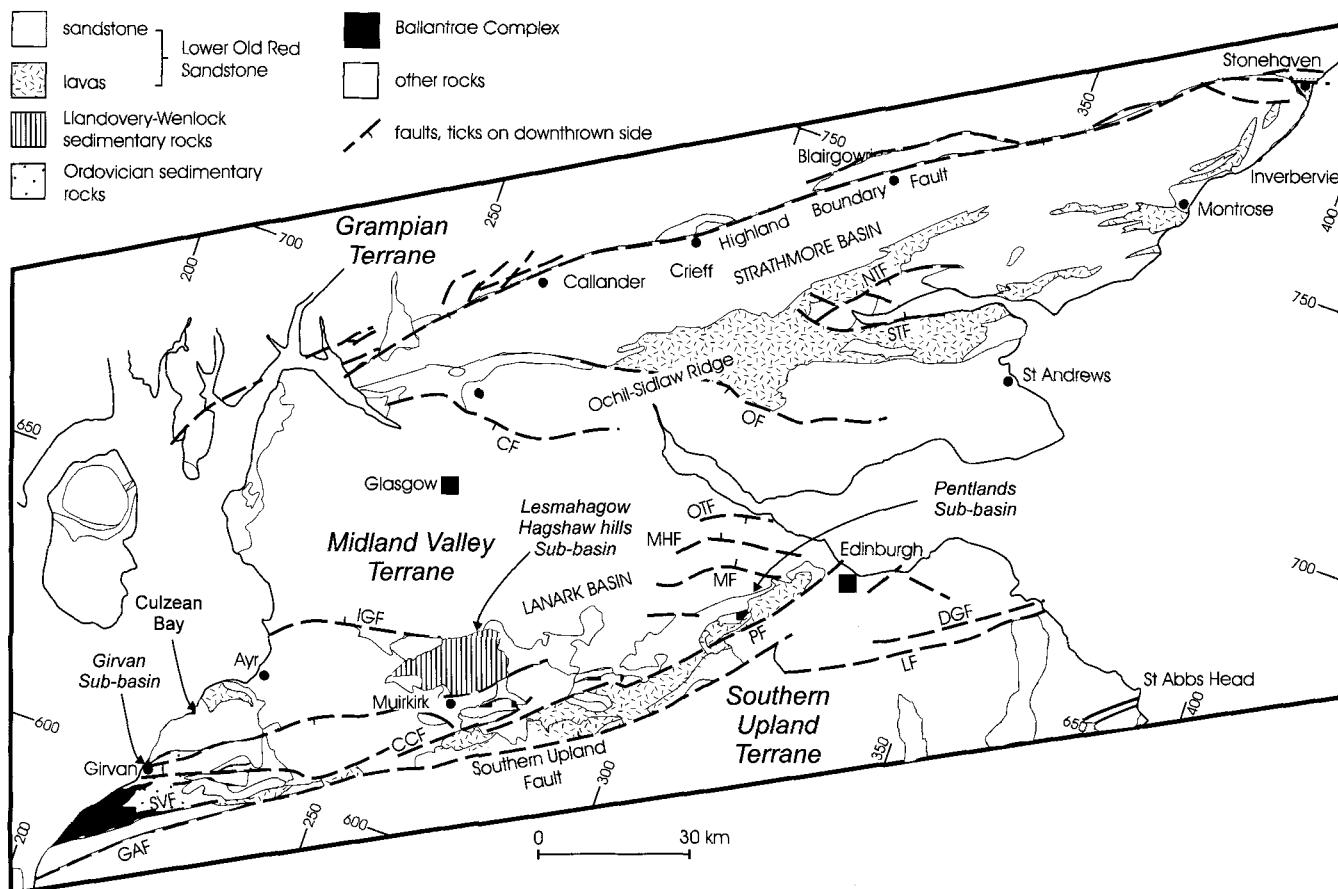

Fig. 1. General geological map of the Midland Valley of Scotland showing the distribution of the Ordovician, Silurian and Lower Old Red Sandstone sedimentary successions. Lower Old Red Sandstone volcanics and the two principal sedimentary basins and sub-basins are marked (redrawn after Phillips *et al.*, 1997). CCF, Carmacoup Fault; CF, Campsie Fault; DGF, Dunbar Gifford fault; GAF, Glen App Fault; IGF, Inchgotrid Fault; KLF, Kerse Loch Fault; LF, Lammemuir Fault; MF, Murieston Fault; MHF, Middleton Fault; NTF, North Tay Fault; OF, Ochil Fault; OTF, Ochiltree Fault; PF, Pentland Fault; STF, South Tay Fault; SVF, Stinchar Valley Fault (redrawn from Armstrong & Owen in press).
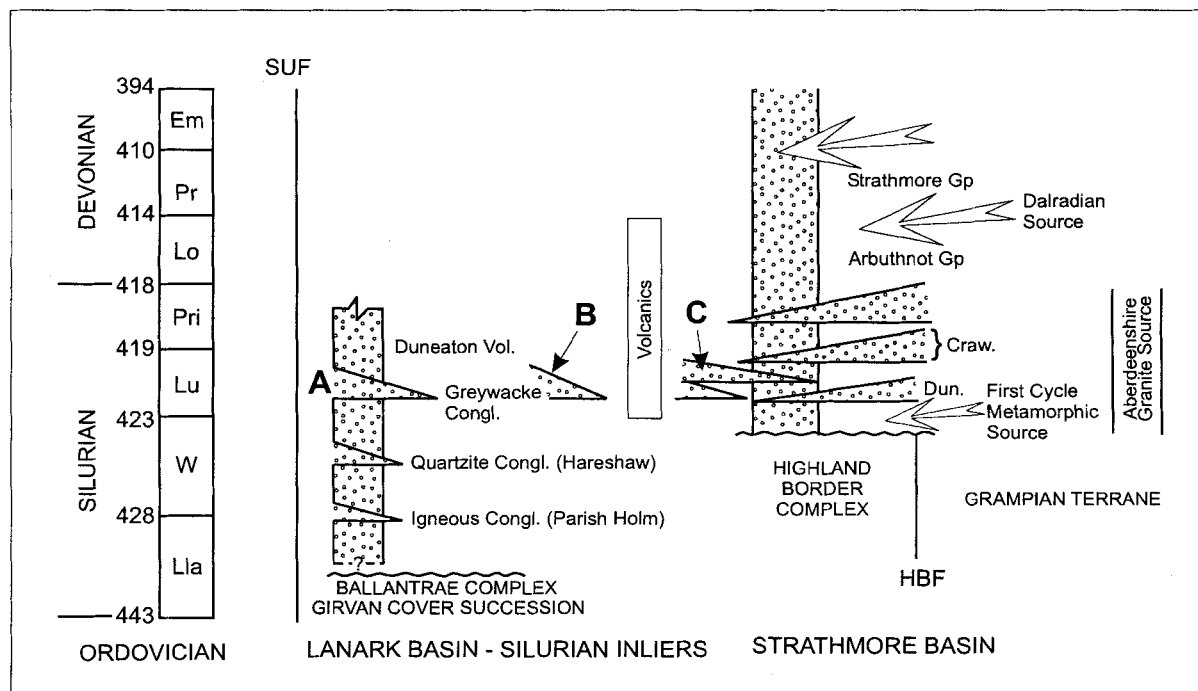
Fig. 2. Chrono- and lithostratigraphy of Ordovician to Devonian successions in the Southern Uplands (composite section), Midland Valley and Grampian terranes, data synthesised from various sources cited in the text. Levels yielding fossiliferous limestone-bearing conglomerates are labelled: A, Greywacke Conglomerate, Culzean Bay; B, Greywacke Conglomerate, Bavelaw Inlier, Pentland Hills; C, Crawton Group, Inverbervie. Lavas above the Greywacke Conglomerate Formation in the Midland Valley are dated at 412.65.7Ma (Thirlwall 1988) suggesting that the Greywacke Conglomerate may be late Silurian to earliest Devonian in age, the base of the Devonian system now being dated at about 418 Ma (Tucker *et al.*, 1998). Ordovician and Lower Silurian timescale based on Harland *et al.*, (1990), Upper Silurian and Devonian timescale based on Tucker *et al.*, (1998). SUF, Southern Upland Fault; HBF, Highland Boundary Fault; C, V Chert and volcanics; Craw., Crawton Group; Dun., Dunnottar Group; K, Kirkcolm Formation; Kirk Kirkland Conglomerate; M, Marchburn Formation; P, Portpatrick Formation; Sh, Shinnel Formation; Tw, Tweeddale Member.

conglomerates in the Lanark and Strathmore Basins and the Pentland Hills Inlier, Midland Valley, Scotland (Fig. 2), were reported by Armstrong *et al.* (2000) and Armstrong & Owen (in press).

Conodonts indicate that the source for the limestone clasts was a cryptic carbonate platform of mid-Ordovician, *Pygodus serra – P. anserinus* Biozone age, now hidden beneath the allochthonous Southern Uplands (Armstrong & Owen in press). The fauna from the limestone clasts is more closely similar to coeval faunas in Upper Ordovician limestone-bearing conglomerates from Ordovician conglomerates in the Southern Uplands and the Mójcza Limestone, Malopolska Terrane, Poland, than to those from the Laurentian margin including Girvan (Armstrong & Owen in press). To reconcile this distribution, Armstrong & Owen (in press) conclude that it is most likely that the taxa present in the clasts represent an outer shelf – ocean margin biofacies. The aim of this paper is to describe 'systematically' conodonts from the southerly derived limestone-bearing conglomerates within the Midland Valley succession.

CONODONT BIOSTRATIGRAPHY
The presence of the eponymous biozonal species *Pygodus serra* and *Pygodus anserinus* in the clast faunas indicate a late Llanvirn–early Caradoc, Llandeilian to Aurelucian age (*sensu* Fortey *et al.*, 1995) for the limestone clasts in the LORS of the

Midland Valley (Armstrong & Owen in press). Bergström (1990) documented the stratigraphical distribution of conodont species in the Barr Group at Girvan. *Pygodus serra* first appears in the lower Stinchar Limestone (Bergström, 1990, fig. 3) and the *P. serra–P. anserinus* Biozone boundary lies at a level in the middle of the Stinchar Limestone. Bergström (1973, 1986) placed the base of the *P. serra* Biozone within the mid- *D. murchisoni* graptolite biozone (Abereiddian) and the top of the *P. anserinus* Biozone at a level within the mid- *N. gracilis* graptolite biozone (Aurelucian). Consequently the *P. serra* Biozone lies within the Llanvirn and much of the *P. anserinus* Biozone lies within the Caradoc (*sensu* Fortey *et al.*, 1995). Armstrong *et al.*, (1996) reviewed the biostratigraphy of mid-Ordovician conodont faunas in southern Scotland, indicating that correlations could be made across the Southern Upland Fault.

METHODS
Samples of limestone up to 2 kg were processed using standard preparation techniques of acid dissolution in buffered 10% acetic acid and bromoform separation. Clasts were processed separately and processed weights and specimen abundances are recorded in Table 1. Conodonts are most abundant in the sparry limestone clasts from Culzean Bay. In general the preservation is moderate to poor with conodont colour alteration index (CAI) values ranging from 5 to 6 indicating heating to in excess of

Table 1. Sample localities and specimen abundances.

Sample	D017	D029	D045	D030	D041	D042	D043	D039	D038	D048
Grid reference	NO84507300	NO84507300	NO84407290	NS245130	NS245130	NS245130	NS245130	NS246130	NS245131-	NX255951
Locality	King's Step	King's Step	Rich Madam	Culzean Bay	Culzean Bay	Culzean Bay	Culzean Bay	Culzean Bay	Culzean Bay	Brodvick Farm
Beltoniodus cf. *variabilis*										
Pa						1				
Belodina confluens										
rastrate				1		4	1			
Cornuodus cf. *C. longibasis*										
unassigned q						3				
unassigned p						2				
Dapsilodus mutatus										
?ae				1	1	1				
?qg				2	1					
?qt				1		2				
Drepanodus arcualus										
pt						4				
pf						10	2			
qa						19				
qg						11	3			
qt						14				
Drepanodus robustus										
qa				4		25				
qg				2	4	28				
qt				4	8	12				
pf				1	8	20				
pf						26				
?ae				1	1	5				
Eoplacognathus lindstroemi										
Pa						2				
Pb						2				
?Pc						1				
Panderodus sulcatus										
qa						5				
qg					8	1				1
qt						1				
pf						1				1
Periodon aculeatus										
Pa	1			32	9	136	40			
Pb				10	5	64	15			
M				48	15	162	53			
Sa				5		30	9			
Sb1				11	4	71	11			
Sb2				19	13	128	39			
Sc1				7		34	20			
Sc2				3		14	10			
Protopanderodus graeai										
qa						19				
qg asym						18				
qg sym						104				
qt						17				
pf					1	25				
pt						13				
ae						4				
Protopanderodus varicostatus										
qa							1			
qg				3	6	8	3			
qt				1	1					
pf						5				
pf				1	2	2				
ae				15	6	3	6			
Pygodus anserinus										
Pa						9				
Pb						11	1			
Pc						14				
M						4				
Pygodus serra										
Pa						1				
Pb						1				
Pc						5				
M						1				
?Sb						1				
Sc						3				
Spinodus spinatus										
Pa				2	4	32				
Pb					10	60				
M						13				
Sa					3	23				
Sb					4	11				
Sc				2	2	9				
Strachanognathus parvus										
qa						38	5			
qg						38	26			
qt						169				
pt				5		18	5			
pf				10	113	19				
ae						47				
Walliserodus costatus										
qa						23				
qg/?ae						23				
pt						22				
pf						26				
Walliserodus nakholmensis										
ae						1				
Total identifiable elements (excl. fragments)	1	frags	frags	199	267	1632	256	frags	frags	2
Weight Processed (kg/g)	4.3	44g	55g	1.2	0.3	1.4	0.18	55g	0.3	1.5
Conodonts per kg	0.23			166	890	1166	1422			1.33

300°C (Rejebian *et al.*, 1987). The majority of specimens show mineral overgrowth and surface recrystallization.

SYSTEMATIC PALAEONTOLOGY

The species recorded from the limestone clasts are generally well known and full descriptions of elements can be found in cited publications, particularly Dzik (1994) and Armstrong (1997). Abbreviated synonymies include the holotype (*), first multi-element reconstruction and the most recent reference to embrace the concept favoured herein. Figured specimens (prefix GLAHM) are housed in the Hunterian Museum, Glasgow. The remainder of the collection is stored in the micropalaeontological collections at the University of Durham.
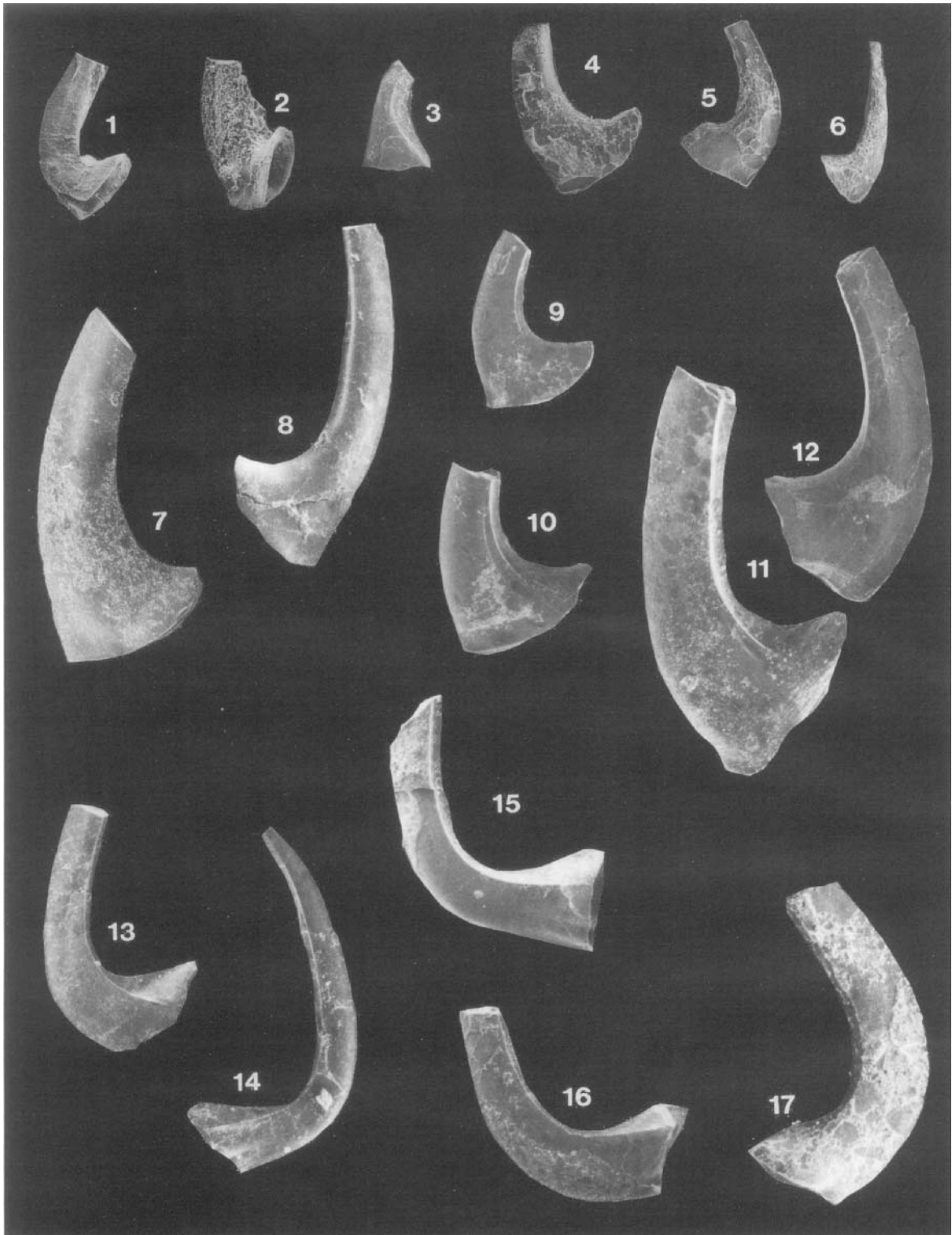
The notational scheme proposed by Sweet & Schönlaub (1975) and modified by Cooper (1975) for ramiform taxa is adopted here as it remains the most widely used amongst conodont workers. The major shape categories and morphological terminology for ramiform taxa are as employed by Sweet (1981). The major shape categories and morphological terminology are used to describe coniform elements follow Sweet (1988) as modified by Sansom *et al.*, (1994).

The application of element location schemes to coniform taxa depends largely upon inference, rather than homology, as few bedding plane assemblages exist. Purists would argue that until such assemblages are found it would be prudent to delay the use of element location terminology. Sansom *et al.*, (1994) developed an element location scheme and functional paradigm for panderodontid conodonts based upon a bedding plane assemblage and diagenetic clusters of *Panderodus unicostatus* that appears to be more widely applicable to other coniform taxa. Of particular use is the recognition that coniform apparatuses comprised three morphologically and functionally distinct domains. In the panderodontids the perfectly symmetrical ae element must have lain on the mid-line of the animal and of all the elements could be homologous to the Sa element of ramiform bearing apparatuses. The anterior domain of multiple pairs of grasping q elements is homologous to the S elements in ramiform bearing apparatuses. The posterior domain of two pairs of food processing, p elements is probably homologous to the P elements in ramiform-bearing apparatuses. A functional homologue of the M element in ramiform taxa is not obvious and if the ae element may have fulfilled the role of an opposing grasping element it would, therefore, not be homologous to the Sa element.

In the absence of direct evidence from bedding plane assemblages it is difficult to homologize element locations between the panderodontids and other coniform taxa. The inferred locational nomenclature applied to non-panderodontid coniform taxa herein should therefore be regarded as preliminary. The application of P, M and particularly S element terminology to coniform apparatuses is considered highly speculative.

The fauna contains the following taxa for which little new taxonomic information is provided:

Belodina confluens Sweet, 1979, Pl. 5, fig. 3.
Panderodus sulcatus (Fåhræus, 1966), Pl. 4, figs 16–20; Pl. 5, figs 1, 2.
Cornuodus cf. *C. longibasis* (Lindström, 1955), Pl. 1, figs 1, 2.
Dapsilodus mutatus (Branson & Mehl, 1933), Pl. 1, figs 3-6; Pl. 2, figs 14–15.
Walliserodus nakholmensis (Hamar, 1966), Pl. 1, fig. 15.
Strachanognathus parvus Rhodes, 1955 *sensu* Armstrong, 1997, Pl. 5, figs 6–16.

Baltoniodus cf. *variabilis* (Bergström, 1962). A single broken specimen of a pastinate Pa element was found in sample D841, this was unsuitable for illustration.

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Phylum *Chordata*
Class *Conodonta*
Order **Protopanderodintida** Sweet, 1988.

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Remarks. The Protopanderodontida includes conodonts from a number of families (Aldridge & Smith, 1993) bearing apparatuses comprising longitudinally costate and striated, coniform elements. Members of the Protopanderodontida appear to have a panderodontid apparatus plan but lack the furrow typical of panderodontids. A homologous structure appears to be formed from the longitudinal costae (Armstrong, 1997).

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Family **Protopanderodontidae** (Lindström, 1970)
Genus *Drepanodus* Pander, 1856

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Type species. *Drepanodus arcuatus* Pander, 1856.
Remarks. Lindström (in Ziegler, 1973, p. 65) recognized 'drepanodontiform' and 'oistodontiform' elements in his emended diagnosis of *Drepanodus*. These equate with the q and p elements respectively and subsequent additions to the apparatus can be considered as subcategories of these main types (van Wamel, 1974; Löfgren, 1978; Dzik, 1990, 1994). *Drepanodus arcutatus* has a panderodontid apparatus comprising an anterior domain of laterally compressed, commonly smooth, q elements and a posterior domain with a falciform pf and tortiform pt. Both p elements have laterally flared bases, the inner margin of which bear a prominent basal notch. The ae element more closely resembles the morphology of the p elements. Contrary to Dzik (1994, p. 68) species are best distinguished on the basis of p element morphology.
Drepanodus shares a similar apparatus plan with *Protopanderodus* and there is a marked convergence (or parallelism) in the morphology of the q elements in these taxa. The fused cluster of elements figured by McCracken (1989, pl. 2, figs 1–5), as *Protopanderodus* sp. A, contains a falciform pf element with a prominent basal notch and thus falls into the concept of *Drepanodus* advocated herein. There seems to be little substantive evidence to support a continued separation of the two genera at family level.

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Drepanodus arcuatus Pander, 1856
(Pl. 3, figs 1–18)

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* 1856 *Drepanodus arcuatus* Pander: 20, pl. 1 figs 2, 4, 5, 17, ?pl. 1, figs 6–8.
1974 *Drepanodus arcuatus* Pander; van Wamel: 61, pl. 1 Figs 10–13.
1978 *Drepanodus arcuatus* Pander; Löfgren: 51, pl. 2 figs 1–8.
1994 *Drepanodus arcuatus* Pander; Dzik, 6: pl. 15 figs 2–6.

Holotype. *Drepanodus arcuatus* Pander, 1856, p. 20.
Emended diagnosis. A species of *Drepanodus* in which the falciform pf and tortiform pt elements bear a single, upwardly pointing, carina or costa on either side of the upper edge keel.
Remarks. The pf and pt elements of this species are of similar morphology and costate; the q elements are essentially acostate, only the qa element bears an indistinct inwardly directed lower edge keel. The falciform pf has prominent upper and lower edge keels and a single, upwardly pointing, costa flanks the upper

keel. The pt has a broader basal flare and the cusp is twisted towards the outer face, away from the basal notch. The costae on the p elements become less prominent in younger examples of this species. Dzik (1994, pl. 15, fig. 5) illustrated the pt element and homologized this with the Pb ('oz' *sensu* Dzik) element of the ozarkodinid apparatus; this implies a location in the apparatus just to the posterior of the q elements. The fused cluster illustrated by McCracken (1989, pl. 2, fig. 1) has a falciform pf and not a tortiform pt element fused to the q elements. In *Panderodus unicostatus* the falciform pf element is located posterior of the q elements (Sansom *et al.*, 1994) with the pt element the most posterior element in the apparatus. If these elements can be considered homologous with those in ozarkodinid conodonts then the pt and the pf elements would be homologous with the Pa and Pb elements respectively. The aequaliform ae element of *D. arcuatus* resembles the pf element but is smaller and is more markedly recurved.

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Drepanodus robustus Hadding, 1913
(Pl. 1, figs 7–12; Pl. 2, figs 12, 13)

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* 1913 *Drepanodus robustus* Hadding: 31, pl. 1, fig. 5
1971 *Drepanodus robustus* Hadding; Lindström: 41.
1978 *Protopanderodus robustus* Hadding; Löfgren: 94, pl. 3, figs 32–35, fig. 31G-J.
1994 *Drepanodus robustus* Hadding; Dzik: 70, pl. 14, figs 10–14

Holotype. *Drepanodus robustus* Hadding, 1913, p. 31, from the lower *Dicellograptus* Shale, base of section E14a of Fågelsång near Lund, Skåne, Sweden.
Diagnosis. Refer to Dzik (1994, p. 70).
Remarks. Löfgren (1978) considered the holotype of *D. robustus* to be a member of *Protopanderodus*. *Drepanodus robustus* has p elements that have up to four prominent costae on their lateral faces.

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Genus *Protopanderodus* Lindström, 1971

</div>

Type species. *Acontiodus rectus* Lindström, 1955.
Remarks. Armstrong (1997) noted the panderodontid nature of the *Protopanderodus* apparatus. Both p and q elements are costate and species can be distinguished on the number of lateral face costae on the pf element and by the ae element which varies with respect to the degree of upward flaring of the basal cavity.

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Protopanderodus graeai (Hamar, 1966)
(Pl. 1, figs 13–17; Pl. 2, figs 6–11, 16)

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* 1966 *Acodus graeai* Hamar: 47, pl. 3, figs 11–14, text-fig. 3:5
1978 *Protopanderodus graeai* (Hamar); Löfgren: 93, pl. 3, figs 19–25 text-fig. 3I, K–M.
1994 *Protopanderodus graeai* (Hamar); Dzik: 72, pl. 13, figs 14–22, text-fig. 10b–c.

Holotype. *Acodus graeai* Hamar, 1966, p. 47, from sample 187 within the upper 10m of the *Ampyx* Limestone at Rødeløkken, Bygdøy Penninsula, Oslo, Norway.
**Diagnosis.** Refer to Dzik (1994, 72).
Remarks. *P. graeai* elements have flatter bases than other species; pf element is markedly recurved, has a lower edge keel and upper edge costa. Specimens tentatively designated pt elements have two costae merging to form the upper edge of the

Explanation of Plate 2

figs 1–5 *Protopanderodus varicostatus* (Sweet & Bergström, 1962). **fig. 1**, pf element specimen GLAHM 109156, sample D843, ×50; **fig. 2**, pf element, specimen GLAHM 109157, sample D843, ×50; **fig. 3**, costate qg element, specimen GLAHM 109158, sample D842, ×50; **fig. 4**, ae element, specimen GLAHM 109159, ×50; **fig. 5**, inner view pt element, specimen GLAHM 109160, sample D843, ×50. figs 6–11, 16 *Protopanderodus graeai* (Hamar, 1966). Specimens from D842. **fig. 6**, qa element, specimen GLAHM 109161, ×50; **fig. 7**, qa element, specimen GLAHM 109162, ×50; **fig. 8**, asymmetrical qg element inner, specimen GLAHM 109163, ×40; **fig. 9**, asymmetrical ?p element outer, specimen GLAHM 109164, ×40; **fig. 10**, asymmetrical ?p element inner, specimen GLAHM 109165, ×40; **fig. 11**, ?pf element outer, specimen GLAHM 109166, ×40; **fig. 16**, pf element inner, specimen GLAHM 109171, ×40. figs 12, 13 *Drepanodus robustus* Hadding, 1913. Specimens from sample D842. **fig. 12**, pf element outer, specimen GLAHM 109167, ×40; **fig. 13**, pf element inner, specimen GLAHM 109168, ×40; figs 14, 15 *Dapsilodus mutatus* (Branson & Mehl, 1933). Specimens from D842. **fig. 14**, q element outer, specimen GLAHM 109169, ×40; **fig. 15**, ae element, specimen GLAHM 109170, ×40.
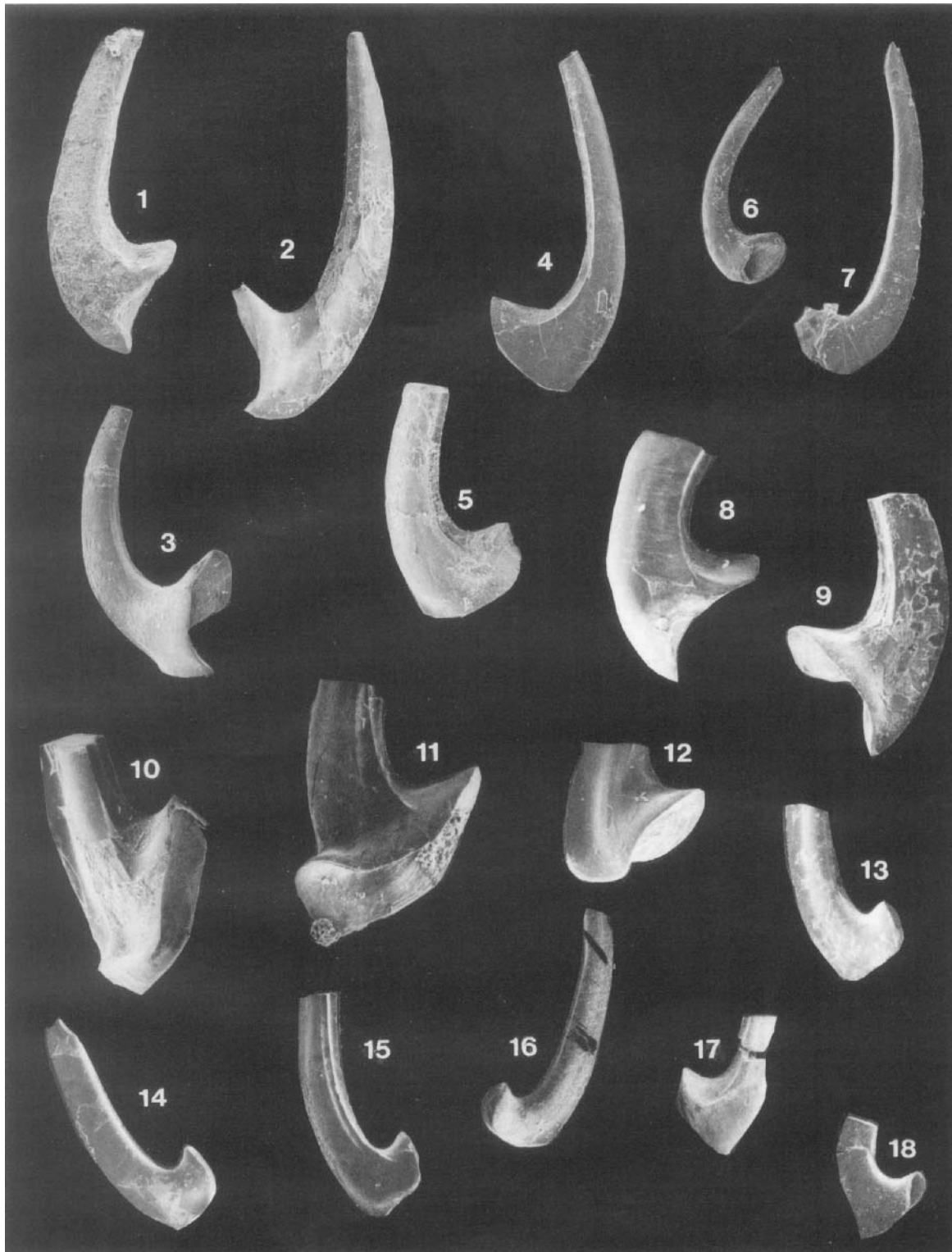
Explanation of Plate 3

figs 1–18 *Drepanodus arcuatus* Pander, 1856. Specimens from sample D842. **fig. 1**, pf element outer, specimen GLAHM 109172, ×50; **fig. 2**, pf element inner, specimen GLAHM 109173, D842, ×50; **fig. 3**, pt element, specimen GLAHM 109174, ×50; **fig. 4**, large qt element outer, specimen GLAHM 109175, ×50; **fig. 5**, qg element inner, specimen GLAHM 109176, ×50; **fig. 6**, ?qg element, specimen GLAHM 109177, ×50; **fig. 7**, ?qg element, specimen GLAHM 109178, ×50; **fig. 8**, pf element outer, specimen GLAHM 109179, ×50; **fig. 9**, pf element inner, specimen GLAHM 109180, ×50; **fig. 10**, pt element oblique inner, specimen GLAHM 109181, ×50; **fig. 11**, pt element outer, specimen GLAHM 109182, ×50; **fig. 12**, ?ae element, specimen GLAHM 109183, ×50; **fig.13**, qa element inner, specimen GLAHM 109184, ×40; **fig. 14**, qg element outer, specimen GLAHM 109185, ×40; **fig. 15**, qq element outer, specimen GLAHM 109186, ×40; **fig. 16**, qa element inner, specimen GLAHM 109187, ×40; **fig. 17**, qt element outer, specimen GLAHM 109188, ×40; **fig. 18**, qt element inner, specimen GLAHM 109189, ×40.

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lateral faces and the base is more upwardly flared than in other elements. q elements have smooth faces and a costa close to the upper edge. qg elements dominate this collection with low (Pl. 1, fig. 13) and high-based (Pl. 1, fig. 14; Pl. 2, fig. 8) forms present. The qa element is larger than the other elements and bears a weakly developed inwardly directed keel; the outer face has a single costa close to the upper edge. An unequivocal qt element cannot be distinguished in this collection. The ae element is similar to the high-based qg but has a flat base.

Protopanderodus varicostatus (Sweet & Bergström, 1962)
(Pl. 2, figs 1–5; Pl. 4, figs 1–5)

* 1962 *Scolopodus varicostatus* Sweet & Bergström: 1247, pl. 168, figs 4–9; text-fig. 1A, C, K.
1974 *Protopanderodus varicostatus* (Sweet & Bergström); Bergström *et al.*: pl. 1, figs 9–10.
1994 *Protopanderodus varicostatus* (Sweet & Bergström); Dzik: 74, pl. 14, figs 1–5, text-fig. 11b.

Holotype. *Scolopodus varicostatus* Sweet & Bergström, 1962, p. 1247: from the Pratt Ferry Formation (Middle Ordovician), Alabama.
Diagnosis. Refer to Armstrong (1997).
Remarks. Atypically, elements from this collection are small and slender and may represent juveniles. In this species the pf and qg elements each bear a pair well developed longitudinal costae on the inner and outer faces. The pt element only has a single costa on the inner face. The upward flare of the basal cavity of the ae element is not as well developed as in larger specimens.

Genus Walliserodus Serpagli, 1967

Type species. *Acodus curvatus* Branson & Branson, 1947, by subsequent designation of Cooper (1975, p. 995).
Remarks. Armstrong (1990) reconstructed the apparatus of Silurian *Walliserodus*, demonstrating that it possessed a fully developed panderodontid apparatus plan. At that time it was not clear whether Ordovician and Silurian *Walliserodus* were congeneric. *W. costatus* in this collection appears to lack a qt element and the qg/?ae element (Pl. 4, figs 12, 13) is difficult to homologize. In *W. curvatus* the latter and closely comparable element is symmetrical and was considered by Armstrong (1990) to be an ae element. In *W. costatus* this element is inwardly bowed (Pl. 4, fig. 13), suggesting it could not have occupied a location on the mid-line of the animal and is more likely to have occupied the qg location. These observations indicate either there have been considerable changes in the apparatus of *Walliserodus* through evolution or that Ordovician and Silurian *Walliserodus* are not congeneric.

Walliserodus costatus Dzik, 1976
(Pl. 4, figs 6–14)

* 1976 *Walliserodus costatus* Dzik: 421, pl. 41, fig. 2, text-fig. 14m,n.
1994 *Walliserodus costatus* Dzik: Dzik: 56, pl. 12, figs 1–6, text-fig. 2a.
1997 *Walliserodus* aff. *W. sancticlairi* Cooper; Armstrong: 784, pl. 5, figs 6–9.

Holotype. *Walliserodus costatus* Dzik, specimen ZPAL CV1/307 from sample MA-14 Mojcza Limestone, Holy Cross Mountains, Poland.
Diagnosis. Refer to Dzik (1994, p. 56).
Remarks. The ?qg/?ae element of *W. costatus* closely resembles that of the Silurian species *W. curvatus*, but differs in being inwardly bowed. The ?qg/?ae element of *W. nakholmensis* is laterally compressed and bears multiple costae on the lateral faces; the lower edge costa is also less prominent.

Order **Prioniodinida** Sweet, 1981
Family **Periodontidae** Lindström, 1970
Genus *Periodon* Hadding, 1913
Periodon aculeatus (Hadding, 1913)
(Pl. 6, figs 14–18; Pl. 7, figs 1–6)

* 1913 *Periodon aculeatus* Hadding: p. 33, pl. 1, fig. 14.
1966 *Periodon aculeatus* (Hadding); Sweet & Bergström: pl. 18, figs 1, 3–4, text-figs 1C, E.
1974 *Periodon aculeatus* (Hadding); Bergström *et al.*: pl. 1, figs 4–6.
1976 *Periodon aculeatus* (Hadding); Dzik: figs 34i–r.
1997 *Periodon aculeatus* (Hadding); Armstrong: 774, pl. 2, figs 13–21; text-fig. 3

Holotype. Hadding (1913, pl. 1, fig. 14) specimen LO 2353 T (mouldic preservation); *Climacograptus haddingi* Biozone (= *Climacograptus putillus* in Hadding, 1913), from the upper part of section E15 of Fågelsång near Lund, Skåne, Sweden
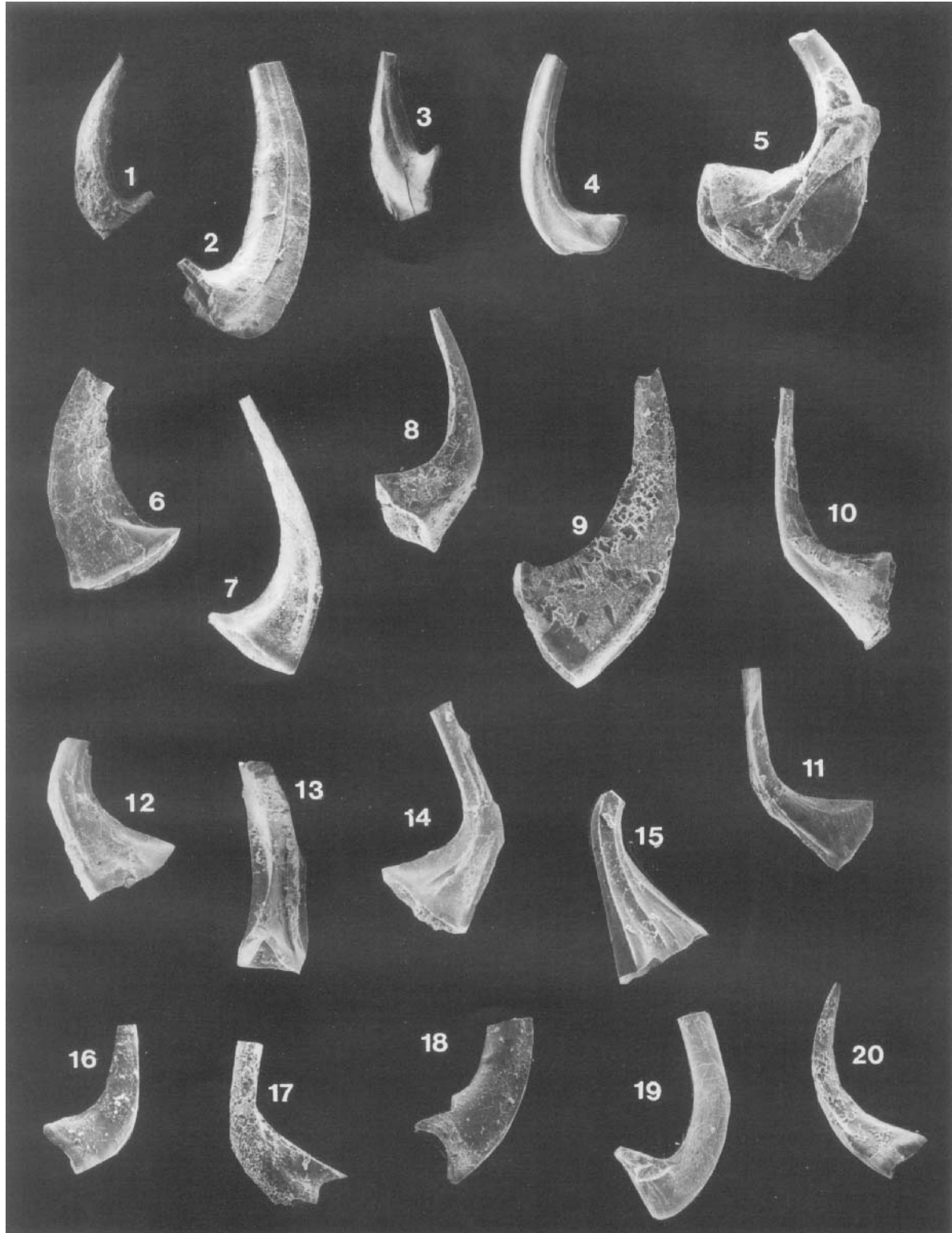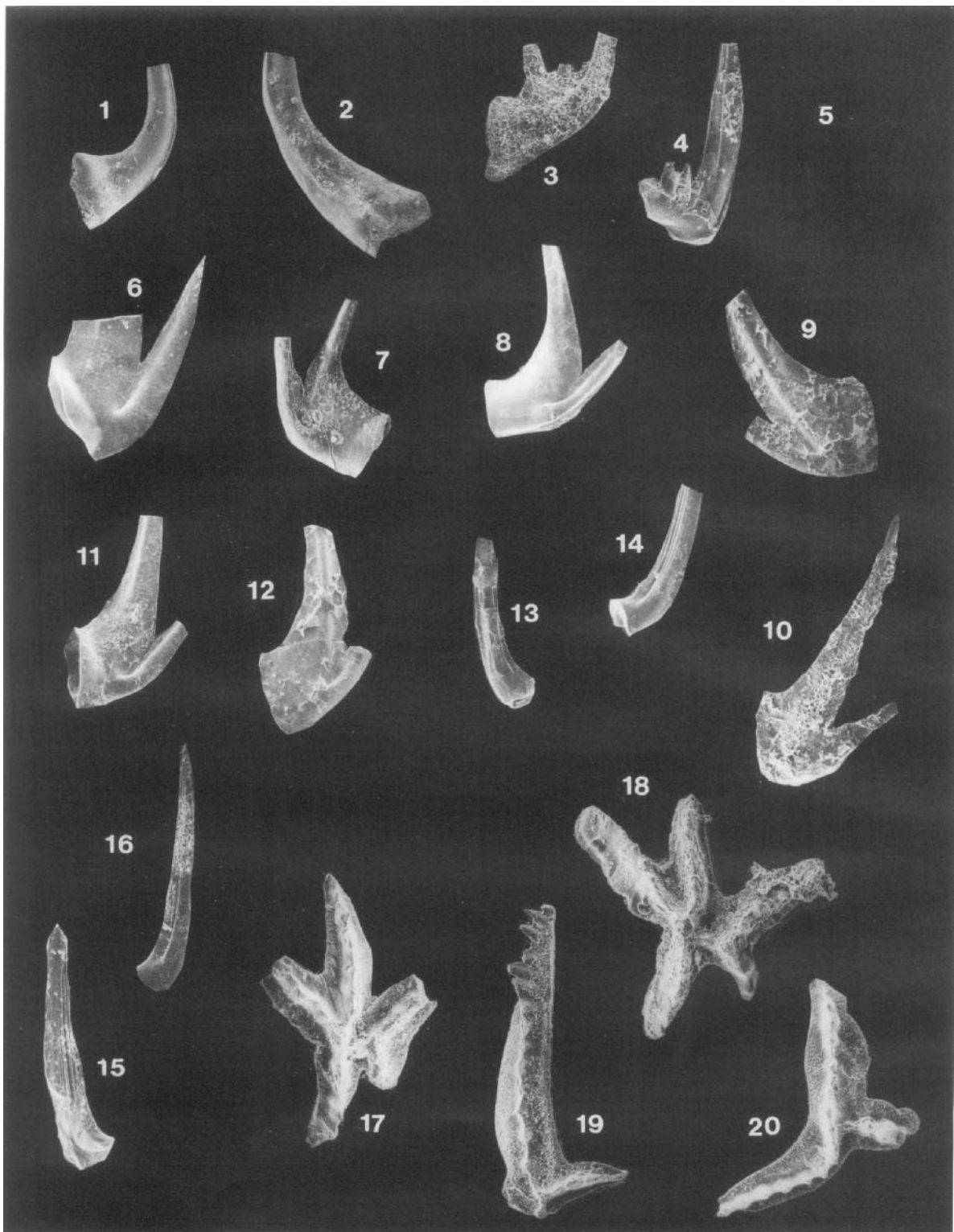**Diagnosis.** Refer to Armstrong (1997, p. 774).
Remarks. The supra-generic classification of *Periodon* is somewhat confused. Aldridge & Smith (1993) followed Sweet (1981) and classified *Periodon* in the Family Periodontidae, Order Prioniodontida. Dzik (1994) moved the Periodontidae to the Order Ozarkodinida. Armstrong (1997) placed *Periodon* in the Prioniodontida but transferred the genus to the Prioniodontidae.

Periodon aculeatus has an extensiform digyrate (or angulate) Pa, a breviform digyrate Pb and a dolabrate M element,
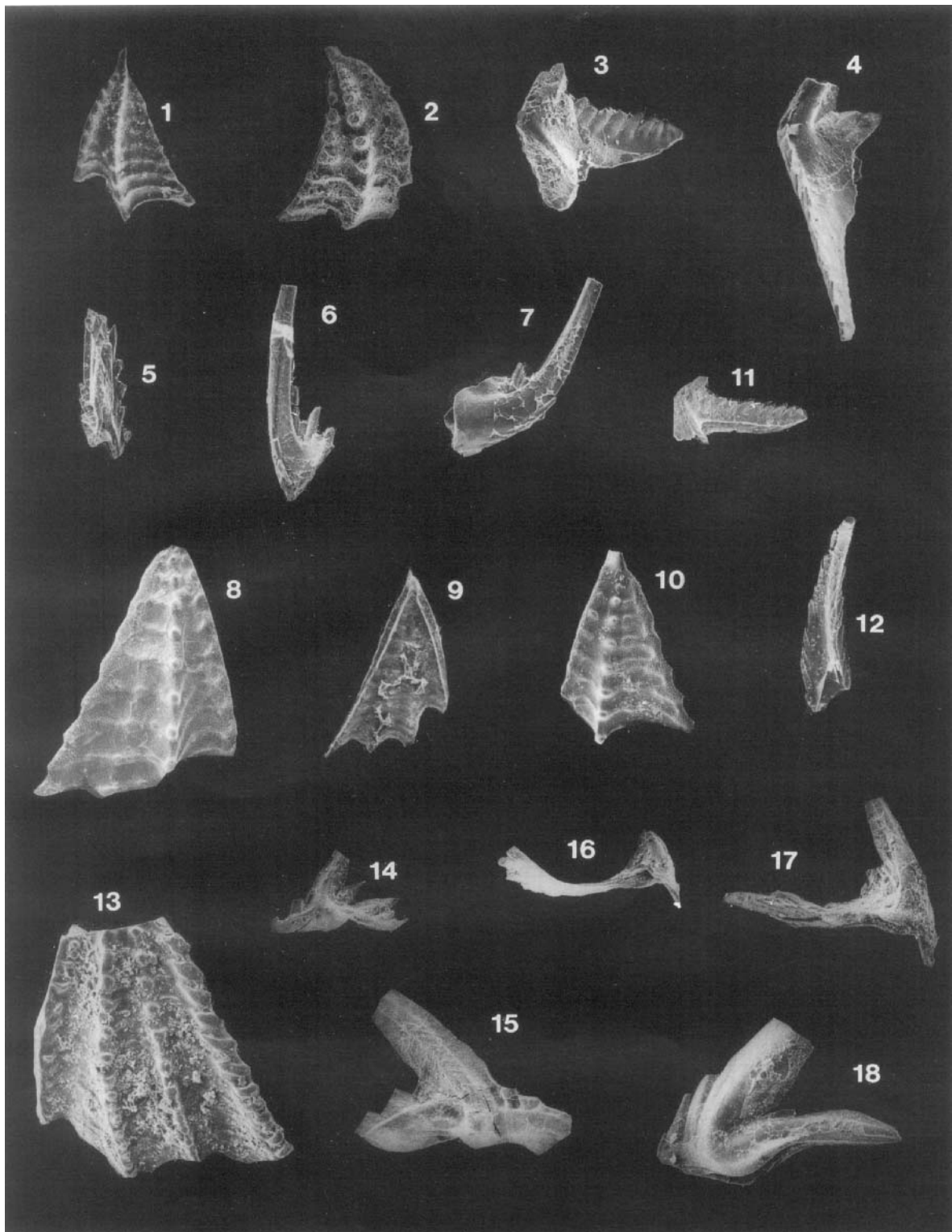

Explanation of Plate 4
figs 1–5. *Protopanderodus* cf. *P. varicostatus.* Specimens from D842. **fig. 1**, pf element, specimen GLAHM 109190, ×40; **fig. 2**, pf element, specimen GLAHM 109191, ×50; **fig. 3**, pt element, specimen GLAHM 109192, ×40; **fig. 4**,*Protopanderodus varicostatus* (Sweet & Bergström, 1962), qg element, specimen GLAHM 109193, ×50; **fig. 5**,?qt element specimen GLAHM 109194, ×50. **figs 6–14**. *Walliserodus costatus* (Dzik, 1976). Specimens from D842. **fig. 6**, pt element inner, specimen GLAHM 109195, ×50; **fig. 7**, pt element inner, specimen GLAHM 109196, ×50; **fig. 8**, pt element outer, specimen GLAHM 109197, ×50; **fig. 9**, pf element, specimen GLAHM 109198, ×50; **fig. 10**, qa element outer, specimen GLAHM 109199, ×50; **fig. 11**, qa element inner, specimen GLAHM 109200, ×50; **fig. 12**, qg/?ae element, specimen GLAHM 109201, ×50; **fig. 13**, qg/?ae element, GLAHM 109202, ×50; **fig. 14**, *Walliserodus costatus* (Dzik, 1976), qa element inner, specimen GLAHM 109203, ×50. **fig. 15** *Walliserodus nakholmensis* (Hamar, 1966), ae element, specimen GLAHM 109204, sample D841, ×70. **figs 16–20** *Panderodus sulcatus* (Fåhræus, 1966). Specimens from D842. **fig. 16**, pf element, specimen GLAHM 109205, ×70; **fig. 17**, qa element outer, specimen GLAHM 109206, ×70; **fig. 18**, qa element inner, specimen GLAHM 109207, ×70; **fig. 19**, qt element outer, specimen GLAHM 109208, ×70; **fig. 20**, qg element inner, specimen GLAHM 109209, ×70.

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Explanation of Plate 6

figs 1–7 *Pygodus serra* (Hadding, 1913). Specimens from D842. **fig. 1**, Pa element, specimen GLAHM 109230, ×50; **fig. 2**, Pb element, specimen GLAHM 109231, ×50; **fig. 3**, Pc element lateral view, specimen GLAHM 109232, ×70; **fig. 4**, ?Pd element oblique lateral view, specimen GLAHM 109233, ×70; **fig. 5**, M element posterior view, specimen GLAHM 109234, ×70; **fig. 6**, ?Sc element, specimen GLAHM 109235, ×70; **fig. 7**, Sc element, specimen GLAHM 109236, ×70. **figs 8–13** *Pygodus anserinus* (Lamont & Lindström, 1957). Specimens from sample D841. **fig. 8**, Pa element oral view, specimen GLAHM 109237, ×70; **fig. 9**, Pa element aboral view, specimen GLAHM 109238, ×70; **fig. 10**, Pb element oral view, specimen GLAHM 109239, ×70; **fig. 11**, Pc element lateral view, specimen GLAHM 109240, ×70; **fig. 12**, M element posterior view, specimen GLAHM 109241, ×70; **fig. 13**, Pa element oral view, specimen GLAHM 109242, ×50. **figs 14–18** *Periodon aculeatus* (Hadding, 1913). Specimens from D842. **fig. 14**, Pa element, specimen GLAHM 109243, ×50; **fig. 15**, Pa element, specimen GLAHM 109244, ×50; **fig. 16**, Pb element, specimen GLAHM 109245, ×50; **fig. 17**, Pb element, specimen GLAHM 109246, ×50; **fig. 18**, M element, specimen GLAHM 109247, ×50.

characters shared with members of the Prioniodinidae (see also generic discussion of *Spinodus*). However, the denticles on all elements of *Periodon* are fused almost to their tips. Based on these criteria it would appear logical to retain the family Periodontidae for *Periodon* and *Microzarkodina* (Sweet, 1981) but place the family in the order Prioniodinida. The absence of a posterior process in the Sb elements and the dolabrate M element suggests a common ancestry with *Erismodus* Branson & Mehl, 1933.

Family ?Prioniodinidae Bassler 1925
Genus *Spinodus* Dzik, 1976

Type species. *Polygnathus spinatus* Hadding, 1913.
Remarks. Lindström (1964) recognised a symmetry transition series including three elements previously described as *C. ramosus* Hadding and *C. spinatus* (Hadding). Uyeno & Barnes (1969) added a fourth element to *C. spinatus*. Barnes & Poplawski (1973) described a quadrimembrate apparatus for *C. ramosus*. The affinities of *Spinodus* are, however, problematic.

The gross morphology of the elements suggests two competing phylogenetic hypotheses. One is that *Spinodus* be assigned to the Chirognathidae with a possible ancestor in *Erraticodon*, the oldest known chirognathid (Dzik, 1994). Members of this family have an apparatus characterized by a pastinate Pa element, a digyrate Pb and modified digyrate M or, as in *Chirognathus*, an alate M element (Sweet, 1981). Alternatively, members of the Prioniodinidae, for example *Oulodus*, have an extensiform digyrate elements in both P locations or, extensiform digyrate Pa, a breviform digyrate Pb and a denticulate bipennate or dolabrate M element (Sweet, 1981; Armstrong, 1990).

In his reconstruction of *S. spinatus,* Dzik (1994) designated the digyrate element as the M, consistent with a chirognathid affinity. However, this reconstruction left the P locations to be filled by dolabrate elements, a feature not seen in either chirognathids or prioniodinids. The apparatus reconstruction favoured herein contains a breviform digyrate Pa (Pl. 7, fig. 11), breviform digyrate Pb (Pl. 7, fig. 12) and dolabrate M element (Pl. 7, figs 7, 14); the Pa element is distinguished in possessing a short anticusp. The ramiform elements include an alate Sa (symmetrical with a long posterior process), a modified tertiopedate Sb (in which the inner lateral process is reduced to a prominent costa) and a bipennate Sc element. This interpretation places *Spinodus* as the oldest member of the Prioniodinidae.

Spinodus spinatus (Hadding, 1913)
(Pl. 7, figs 7–14)

* 1913 *Polygnathus spinatus* Hadding: 32, pl. 1, fig. 8.
1913 *Corylodus ramosus* Hadding: 31, pl. 1, fig. 6.
1976 *Cordylodus spinatus* (Hadding); Dzik: 424, text-fig. 21c.
1981 *Spinodus ramosus* (Hadding); Nowlan: 15–16, pl. 4, figs 18–19.
1994 *Spinodus spinatus* (Hadding); Dzik: 113, pl. 24, figs 22–25, text-fig. 32.

Holotype. *Polygnathus spinatus* Hadding, 1913, p. 32, pl. 1, fig. 8. Specimen LO 2347 T (mouldic preservation), from the *Climacograptus haddingi* Biozone (= *Climacograptus putillus* in Hadding, 1913) of Fågelsång, near Lund (upper part of section E15).

Diagnosis. Refer to Dzik (1994, p. 113).
Remarks. Refer to those for the genus.

Order Prinoiodontida Dzik, 1976

Remarks. The Prioniodontida (*sensu* Aldridge & Smith 1993) contains at least two major clades, one represented by the coniform Oistodontidae and a non-coniform clade in which taxa bear up to four pairs of P elements. The latter includes the Balognathidae comprising taxa with at least two P elements and fully differentiated S elements (e.g., *Rhodesgnathus* and *Baltoniodus*). The Polyplacognathidae bear at least three P elements and lack S elements (e.g., *Eoplacognathus*) and the Pygodontidae contains taxa which bear at least three P elements and a reduced number of S elements (e.g., *Pygodus*). Dzik (1994) included members of each of these families within the Balognathidae.

Family Polyplacognathidae Bergström, 1981b
Genus *Eoplacognathus* Hamar, 1966

Type species. *Ambalodus lindstroemi* Hamar, 1964, p. 258.

Eoplacognathus lindstroemi (Hamar, 1964)
(Pl. 5, figs 17–20)

* 1964 *Ambalodus lindstroemi* Hamar: 258, pl. 5, figs 1, 4, 7–8, 10–11; text-fig. 5, nos. 1a–b, 3a–b, 4a–b.
1971 *Eoplacognathus lindstroemi* (Hamar); Bergström: 139, pl. 2, figs 15–18.
1994 *Eoplacognathus lindstroemi* (Hamar); Dzik: 98, pl. 21 figs 6–9, text-fig. 23.

Holotype. *Ambalodus lindstroemi* Hamar, 1964, p. 258, pl. 5, figs 8, 11. Specimen PMO 69791, *Ampyx* Limestone, Ringerike, Norway.
**Diagnosis.** Refer to Dzik (1994, p. 98).
Remarks. Bergström (1971) and Dzik (1994) reconstructed the apparatus of this species as bimembrate, herein regarded as the Pa and Pb elements. An additional Pc element is distinguished in this small collection. The trimembrate apparatus contains a stelliscaphate Pa (Pl. 5, figs 17, 18), in which the single outer and bifurcate inner processes are directed anteriorly at an angle of 45° to the main carina. The Pb (Pl. 5, fig. 20) is pastinate, in which the posterior process is inwardly deflected inwards at an angle of 100°, the short outer lateral process diverges from the main carina at 90°. The Pc element is also pastinate but the posterior process is reduced to a single denticle; the anterior process is approximately twice as long as that of the Pb element and distally, discrete denticles are developed. Element homologies follow those proposed for *Amorhognathus ordovicicus* Branson & Mehl *sensu* Armstrong *et al.*, (1996). All elements have a ledge-like platform beneath the denticles.

Family Pygodontidae Bergström, 1981a
Genus *Pygodus* Lamont & Lindström, 1957

Type species. *Pygodus anserinus* Lamont & Lindström, 1957, p. 68.
Remarks. Armstrong (1997) reconstructed the apparatus of the type species *P. anserinus* with a modified prioniodontid plan distinguishing a stelliscaphate Pa, pastiniscaphate Pb, bipennate Pc, tertiopedate M and an Sc element using the apparatus plan of the Silurian genus *Astropentagnathus* as a template.
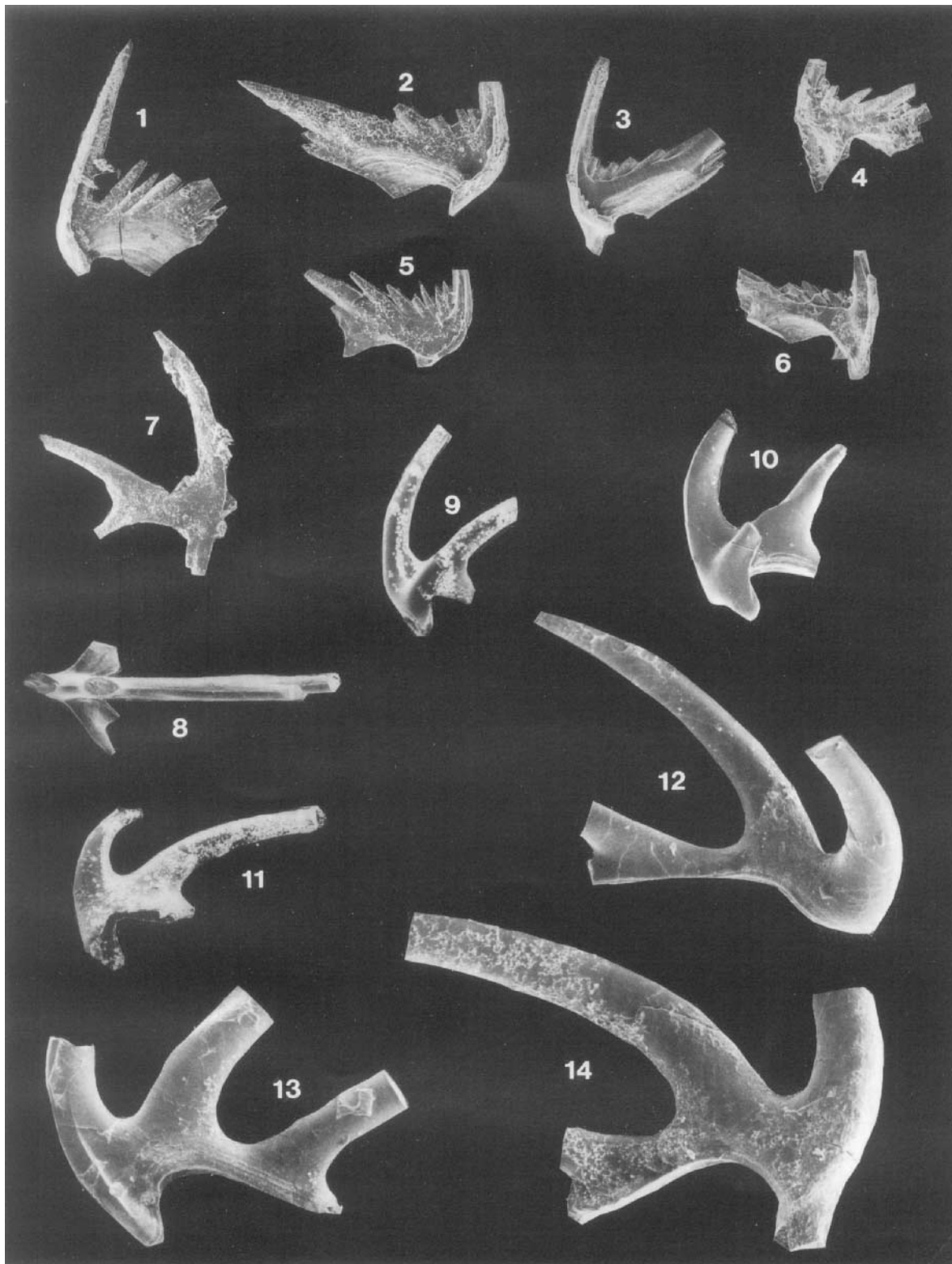
Explanation of Plate 7

figs 1–6 *Periodon aculeatus* (Hadding, 1913). Specimens from D842. **fig. 1**, Sa element, specimen GLAHM 109248, ×50; **fig. 2**, Sa element, specimen GLAHM 109249, ×50; **fig. 3**, Sc element, specimen GLAHM 109250, ×50; **fig. 4**, Sb1 element (with lateral process), specimen GLAHM 109251, ×50; **fig. 5**, Sc (lacking lateral process), specimen GLAHM 109252, ×50; **fig. 6**, Sb2 (bears lateral process), specimen GLAHM 109253, ×50. figs 7–14 *Spinodus spinatus* (Hadding, 1913). Specimens from D842. **Fig. 7**, M element, specimen GLAHM 109254, ×50; **fig. 8**, Sa element oral view, specimen GLAHM 109255, ×50; **fig. 9**, Sa element lateral view, specimen GLAHM 109256, ×50; **fig. 10**, Sc element (bears inner lateral process), specimen GLAHM 109257, ×50; **fig. 11**, Pa element, specimen GLAHM 109258, ×50; **fig. 12**, Pb element, specimen GLAHM 109259, ×70; **fig. 13**, Sb element, specimen GLAHM 109260, ×70; **fig. 14**, M element, specimen GLAHM 109261, ×70.

Pygodus anserinus Lamont & Lindström, 1957
(Pl. 6, figs 8–13)

* 1957 *Pygodus anserinus* Lamont & Lindström: 68, fig 1a, b.
1957 *Pygodus anserinus* Lamont & Lindström: 68, pl. 5, figs 12, 13.
1976 *Pygodus anserinus* Lamont & Lindström; Dzik: 440, fig. 29f.
1997 *Pygodus anserinus* Lamont & Lindström; Armstrong: 777, pl. 4, figs 1–7, text-fig. 4.

Holotype. *Pygodus anserinus* Lamont & Lindström 1957, p. 68, fig 1a, b. Specimen LO 3871 T, from grey trilobite-bearing limestone, Gärdslösa Bodar, Öland, Sweden.
Diagnosis. Refer to Armstrong (1997, p. 778).
Remarks. *P. anserinus* is distinguished by the Pa element which bears four rows of nodes. When viewed orally both Pa and Pb elements have a much straighter sided, triangular outline than *P. serra*.

Pygodus serra (Hadding, 1913)
(Pl. 5, figs 4, 5; Pl. 6, figs 1–7)

* 1913 *Arabellites serra* Hadding: 33, pl. 1 figs 12, 13.
1971 *Pygodus serrus* (Hadding); Bergström: 149, pl. 2, figs 22–23.
1978 *Pygodus serra* (Hadding); Löfgren: 98, fig. 32D–F.
1991 *Pygodus serra* (Hadding); McCracken: 51, pl. 2, figs 1–3, 5, 8, 10, 13, 19.

Holotype. *Arabellites serra* Hadding, 1913, p. 33, from upper part of the Lower *Dicellograptus* Shale, section E15 of Fågelsång near Lund, Skåne, Sweden.
Emended diagnosis. A species of *Pygodus* in which the Pa and Pb elements bear three rows of nodes.
Remarks. Specimens of this species are only found in sample D842. The apparatus reconstruction proposed here follows that for *P. anserinus* (*sensu* Armstrong, 1997). The Pb element of *P. serra* has a central row of discrete nodes and in oral view the entire platform is more inwardly bowed than the Pa element. The Pc element exhibits variability in the length of the down-turned anterior process.

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