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 serru* and *Pygodus unserinus*. 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), micropalaeontology 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).
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...
Mid-Ordovician conodonts

Table 1. Sample localities and specimen abundances.

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Abbreviated synonomies 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 confuens Sweet, 1979, Pl. 5, fig. 3.
Panderodus sulcatus (Fähreus, 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.

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 synonomies 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.
figs 1, 2 Cornuodus cf. C. longibasis. Specimens from sample D842. fig. 1, specimen GLAHM 109139, ×70; fig. 2, specimen GLAHM 109140, ×70.
figs 3-6 Dapsilodus mutatus (Branson & Mehl, 1933). Specimens from sample D830. fig. 3, symmetrical costate element (?ae) outer view, specimen GLAHM 109141, ×70; fig. 4, outer view of falciform acostate (?qg) element, specimen GLAHM 109142, ×50; fig. 5, inner outer view of falciform acostate (?qg) element, specimen GLAHM 109143, ×50; fig. 6, outer view of acostate truncatiform element (?qt), specimen GLAHM 109144, ×70.
figs 7-12 Drepanodus robustus Hadding, 1913. Specimens from sample D842. fig. 7, inner view of ?qg element, specimen GLAHM 109145, ×50; fig. 8, inner view of ?qg element, specimen GLAHM 109146, ×40; fig. 9, outer view of ?qg element, specimen GLAHM 109147, ×80; fig. 10, inner view of ?qg element, specimen GLAHM 109148, ×80; fig. 11, inner view of ?qg element, specimen GLAHM 109149, ×80; fig. 12, outer view of ?qg element, specimen GLAHM 109150, ×80.
figs 13-17 Protopanderodus graeai (Hamar, 1966). Specimens from sample D842. fig. 13, inner view of symmetrical ?qg element, specimen GLAHM 109151, ×80; fig. 14, outer view of symmetrical ?qg element, specimen GLAHM 109152, ×80; fig. 15, ?ae element, specimen GLAHM 109153, ×40; fig. 16, symmetrical ?qg/?qg element, specimen GLAHM 109154, ×80; fig. 17, symmetrical ?qg/?qg element, specimen GLAHM 109155, ×80.
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*Balaniodus* cf. *variabilis* (Bergström, 1962). A single broken specimen of a pastinate *Pa* element was found in sample D841, this was unsuitable for illustration.

**Phylum Chordata**  
**Class Conodontata**  
**Order Protopanderodontida** Sweet, 1988.

**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).

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

**Type species.** *Drepanodus arcuatus* Pander, 1856.

**Remarks.** Lindström (in Ziegler, 1973, p. 65) recognized 'drepanodontiform' and 'ostodontiform' 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 arcuatus* 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* element. 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.

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

* 1856 *Drepanodus arcuatus* Pander: 20, pl. 1 figs 2, 4, 5, 17, ?pl. 1, figs 6–8.
  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 *p* 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 unicusstatus* 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.

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

* 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.

**Genus Protopanderodus** Lindström, 1971

**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.

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

* 1966 *Acontiodus 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. 31, K–M.  
  1994 *Protopanderodus graeai* (Hamar); Dzik: 72, pl. 13, figs 14–22, text-fig. 10b–c.

**Holotype.** *Acontiodus graeai* Hamar, 1966, p. 47, from sample 187 within the upper 10m of the *Amphix* Limestone at Rødelskken, 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, x50; fig. 2, pf element, specimen GLAHM 109157, sample D843, x50; fig. 3, costate qg element, specimen GLAHM 109158, sample D842, x50; fig. 4, ae element, specimen GLAHM 109159, x50; fig. 5, inner view pt element, specimen GLAHM 109160, sample D843, x50. figs 6–11, 16 Protopanderodus graeai (Hamar, 1966). Specimens from D842. fig. 6, qa element, specimen GLAHM 109161, x50; fig. 7, qa element, specimen GLAHM 109162, x50; fig. 8, asymmetrical qg element inner, specimen GLAHM 109163, x40; fig. 9, asymmetrical ?p element outer, specimen GLAHM 109164, x40; fig. 10, asymmetrical ?p element inner, specimen GLAHM 109165, x40; fig. 11, ?p element outer, specimen GLAHM 109166, x40; fig. 16, pf element outer, specimen GLAHM 109167, x40. figs 12, 13 Drepanodus robustus Hadding, 1913. Specimens from sample D842. fig. 12, pf element outer, specimen GLAHM 109167, x40; fig. 13, pf element inner, specimen GLAHM 109168, x40. figs 14, 15 Dapsilodus mutatus (Branson & Mehl, 1933). Specimens from D842. fig. 14, q element outer, specimen GLAHM 109169, x40; fig. 15, ae element, specimen GLAHM 109170, x40.
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, ×9; 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, qa 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, qg 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.
lateral faces and the base is more upwardly flared than in other elements. qg elements have smooth faces and a costa close to the upper edge. qg elements dominate this collection with low (P1, fig. 13) and high-based (P1, fig. 14; P2, 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)

* 1994 *Walliserodus costatus* Dzik: 56, pl. 12, figs 1–6, text-fig. 2a.
* 1997 *Walliserodus aff. W. sancticlairei* Cooper; Armstrong: 784, pl. 5, figs 6–9.

**Holotype.** *Walliserodus costatus* Dzik, specimen ZPAL CV1/307 from sample MA-14 Mojca 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) and *Periodon curvatus* (Hadding, 1913), pl. 1, figs 3–4, text-figs 1C, E.
* 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 Fågelsäng near Lund, Skåne, Sweden

**Diagnosis.** Refer to Armstrong (1997, p. 774).


*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), ug element, specimen GLAHM 109193, ×50; fig. 5, qg 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 element, specimen GLAHM 109201, ×50; fig. 13, qg element, specimen GLAHM 109202, ×50; fig. 14, *Walliserodus costatus* (Dzik, 1976), qa element inner, specimen GLAHM 109203, ×50; fig. 15, *Walliserodus nakholmensis* (Hamarin, 1966), ae element, specimen GLAHM 109204, sample D841, ×70. Figs 16–20 *Panderodus sulcatus* (Fürhauers, 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, ug element inner, specimen GLAHM 109209, ×70.

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Explanation of Plate 5

figs 1, 2 Panderodus sulcatus (Fähraeus, 1966). Fig. 1, pf element, specimen GLAHM 109210, sample D848, ×70; fig. 2, qg element, specimen GLAHM 109211, sample D848, ×70. fig. 3 Belodina confluenta Sweet 1979, rastrate element, specimen GLAHM 109212, sample D842, ×70. figs 4–5 Pygodus serros (Hadding, 1913). fig. 4, Sc element, specimen GLAHM 109213, sample D842, ×70; fig. 5, Sc element, specimen GLAHM 109214, sample D842, ×70. figs 6–16 Strachanognathus parvus (Rhodes, 1955). Specimens from sample D842. fig. 6, qg element inner specimen GLAHM 109215, ×70; fig. 7, qf element inner, specimen GLAHM 109216, ×70; fig. 8, specimen GLAHM 109217, qf element inner, ×70; fig. 9, qf element, specimen GLAHM 109218, ×70; fig. 10, af element, specimen GLAHM 109219, ×70; fig. 11, qa element inner, specimen GLAHM 109220, ×70; fig. 12, qa element outer, specimen GLAHM 109221, D842, ×70; fig. 13, pt element outer, specimen GLAHM 109222, ×70; fig. 14, pt element inner, specimen GLAHM 109223, ×70; fig. 15, pf element outer, specimen GLAHM 109224, ×70; fig. 16, pf element inner, specimen GLAHM 109225, ×70. figs 17–20 Eoplacognathus indescuoensis (Hamar, 1966). Specimens from sample D842. fig. 17, Pa element, specimen GLAHM 109226, sample D842, ×70; fig. 18, Pa element, specimen GLAHM 109227, ×70; fig. 19, Pq element specimen GLAHM 109228, ×70; fig. 20, Pb element, specimen GLAHM 109229, ×70.
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
Periododontidae 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 compet-
ing 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
chirognathid or prioniodinid. The apparatus reconstruction
favoured herein contains a breviform digyrate Pa (Pl. 7, fig.
17, 18), in which the single outer and
inner lateral process is reduced to a single denticle; the anterior
and distal processes are developed. Element homo-

P. anserinus

* 1913 Polygnathus spinatus Hadding: 32, pl. 1, fig. 8.

1913 Corylodus ramosus Hadding: 31, pl. 1, fig. 6.

1976 Cordyloius 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 Prioniodontida Dzik, 1976

Remarks. The Prioniodontida (sensu Aldridge & Smith 1993)
contains at least two major clades, one represented by the
conform Oistodontidae and a non-conform 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 Balto-
niodus). 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, 1981

Genus Eoplacognathus Hamar, 1966

Type species. Eoplacognathus lidstroemi Hamar, 1964

Eoplacognathus lidstroemi (Hamar, 1964)

(Pl. 5, figs 17–20)

* 1964 Ambalodus lidstroemi Hamar: 258, pl. 5, figs 1, 4, 7–8,
10–11; text-fig. 5, nos. 1a–b, 3a–b, 4a–b.

1971 Eoplacognathus lidstroemi (Hamar); Bergström: 139, pl. 2,
figs 15–18.

1994 Eoplacognathus lidstroemi (Hamar); Dzik: 98, pl. 21 figs
6–9, text-fig. 23.

Holotype. Ambalodus lidstroemi Hamar, 1964, p. 258, pl. 5, figs
8, 11. Specimen PMO 69791, Amopyx 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 trinemembrate apparatus contains a
stelliscaphate Pa (Pl. 5, figs 17, 18), in which the single outer and
difaricate inner processes are directed anteriorly at an angle of
45° to the main carina. The Pb (Pl. 5, fig. 20) is a modified
stelliscaphate Pa, 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 a modified
stelliscaphate Pa, in which 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 homo-

Polyplacognathidae Bergström, 1981

Genus Pygodus Lamont & Lindström, 1957

68.

Remarks. Armstrong (1997) reconstructed the apparatus of the
type species P. anserinus with a modified prioniodontid plan
distinguishing a stelliscaphate Pa, pastinsiscaphate Pb, bifaricate
Pc, tertiopedate M and an Sc element using the apparatus plan
of the Silurian genus Astropentagnosthus 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.
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