CONODONTS FROM THE ORDOVICIAN SHINNEL FORMATION, SOUTHERN UPLANDS, SCOTLAND

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ABSTRACT. The Shinnel Formation is dominated by over 2 km of quartzose sandstones. It crops out between the Fardingmullach and Orlock Bridge faults, Northern Belt of the Southern Uplands, and is of mid Ashgill age. The interbedded and distinctive Tweeddale Member (previously the Wrae Limestone and Tweeddale lavas) comprises debris flow deposits with clasts of limestone which yield a diverse and abundant conodont fauna, including *Pygodus anserinus*, *Baltoniodus variabilis*, *Periodon aculeatus*, *Protopanderodus varicostatus*, *Spinodus spinatus*, *Eoplacognathus lindstroemi*, *Strachanognathus parvus* and coniform species; an assemblage considered to be of *P. anserinus* Biozone (late Llanvirn (Llandeilian) to early Caradoc (Aurelucian)) age. These conodont faunas are similar to those from the upper Stinchar Limestone from Girvan to the north-west. The deep or cool water, predominantly prioniodontid and panderodontid, conodont fauna is described systematically for the first time. Emended apparatus plans are proposed for *Pygodus anserinus*, *Protopanderodus varicostatus* and *Strachanognathus parvus*.

FLOYD (1996) redefined many of the lithostratigraphical units within the Southern Uplands. The Shinnel Formation (Floyd 1982) is up to 2 km thick and is dominated by quartzose sandstones. Floyd and Rushton (1993) reviewed the biostratigraphy of the formation, referring an interbedded graptolite fauna to the Rawtheyan to Cautleyan, *D. anceps* graptolite Biozone (GBZ). In the Tweeddale area, the Wrae Limestone and Tweeddale lavas (Thirwall 1981) have been included within the Tweeddale Member (Hughes and Boland 1995; Floyd 1996) and are interbedded within the Shinnel Formation. The Tweeddale Member extends for over 20 km along strike to the south-west of Peebles. In its type section at Wrae (NT 1175 3240) it is *c.* 35 m thick but appears to thicken markedly to the north-east of Peebles (Hughes and Boland 1995). The apparently restricted nature of the original depositional environment and re-forestation now mean the Tweeddale Member only crops out sporadically (Text-fig. 1). Limestone occurs as variable sized blocks in a clast-supported debris flow deposit. Clasts range in size from grains to large boulders, which were individually quarried during the late nineteenth century.

James Hutton first discovered fossils in the limestone on Wrae Hill, and this led him to conclude (Hutton 1795, p. 334) that the greywackes of the Southern Uplands were marine in origin. Subsequently the geology of the Tweeddale Member (Wrae Limestone) was described in detail by Peach and Horne (1899), Eckford and Ritchie (1931) and Leggett (1980). Peach and Horne (1899, p. 53) reported a shelly fauna in both the limestone clasts, grit and tuffaceous beds at Wrae Hill, Glencotho, Winkston and Hamilton Hill, and concluded that the deposit was late Caradoc in age. The limestone clasts contain a marine macrofauna of trilobites attributable to the Illaenid-Cheirurid community, (A. W. Owen, pers. comm.), brachiopods, gastropods and crinoids which Clarkson (*in* Leggett 1980, p. 101) attributed to reefal biofacies.

Following the work of Leggett (1980) it has been widely accepted that the clasts within the Tweeddale Member were derived from a volcanic palaeo-high or seamount, accreted to the Laurentian margin from the south. The seamount interpretation relies heavily upon the field observations made by Peach and Horne (1899) who reported a lava flow in association with the limestone conglomerate on Wrae Hill; these field relationships are now obscure. This interpretation conflicts with limited palaeocurrent data from the adjacent greywackes, which suggest a derivation from the north-west, and is further undermined by the absence of limestone deposits in the vicinity

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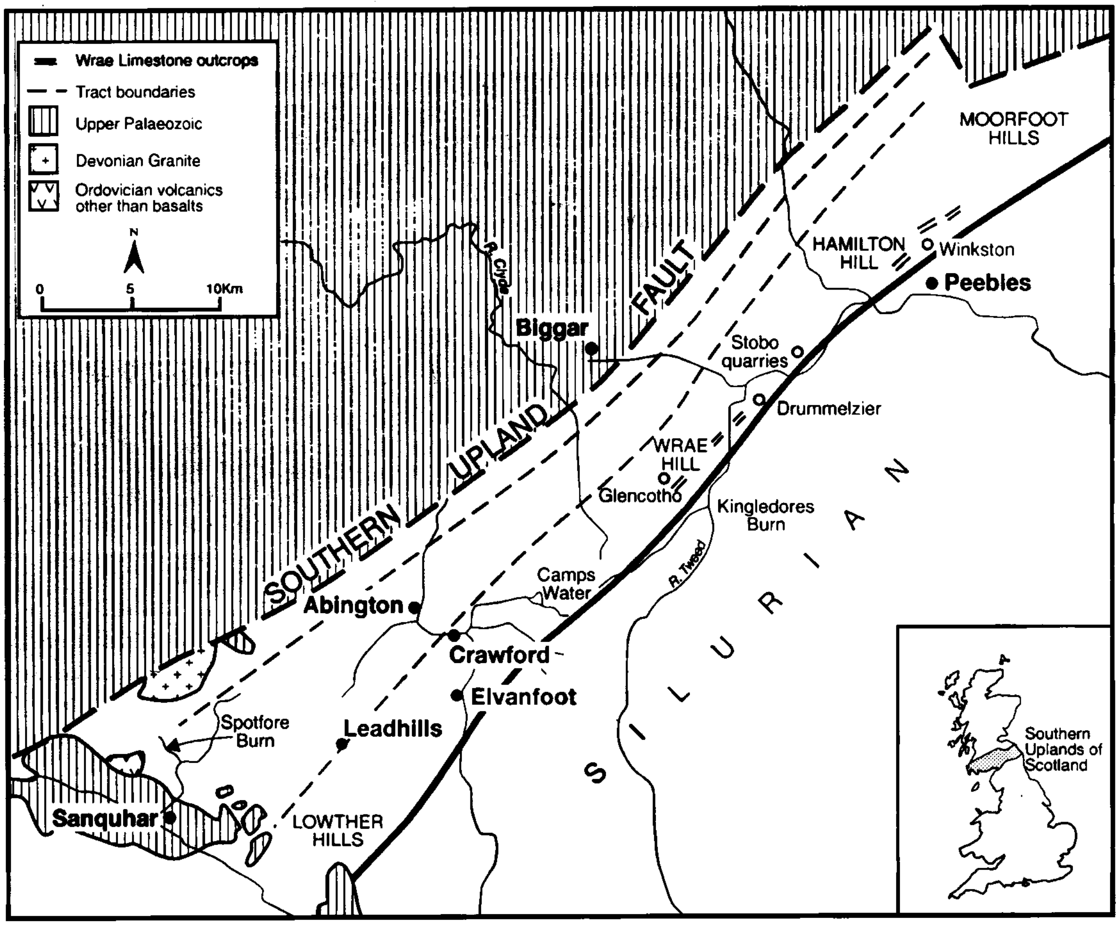


TEXT-FIG. 1. Locality and general geology of the Northern Belt of the Southern Uplands (redrawn from Leggett 1980).

of Bail Hill, the proposed location of the seamount. Regardless of these considerations, the 'Wrae seamount' has often been cited as part of the evidence that the geology of the Southern Uplands is best explained in terms of an accretionary prism (refer to Armstrong *et al.* 1996 for an alternative view). The aim of this paper is to present the first systematic description of conodonts from the limestone clasts. The associated shelly fauna is typical of the northern margin of the Iapetus Ocean and correlations with the shelf succession to the north-west are the most appropriate.

CONODONT STUDIES

Mid Ordovician conodont faunas from the British Isles are relatively poorly known and there is a major difference, at generic level, between the faunas from the series type areas in Wales and the Welsh Borderland, and those from Scotland. Late Llanvirn faunas from Wales are dominated by *Plectodina*, *Icriodella*, *Amorphognathus*, *Panderodus*, *Drepanoistodus* and *Baltoniodus* (Bergström and Orchard 1985) and cannot be correlated directly with Scottish faunas. However, a mid Caradoc, *A. tvaerensis* CBZ (*B. variabilis* Sub-biozone) conodont fauna has been recorded from limestone clasts within the Garn Formation, of the Anglesey terrane, and this includes many species in common with the Tweeddale Member, together with *Complexodus* and *Plectodina* (Bergström 1981*a*).

Ordovician conodonts from the Southern Uplands are known only from the Northern Belt, and have been documented mainly from cherts and shales of mid Arenig, Llanvirn (Llandeilian of Fortey *et al.* 1995) and Caradoc age (see Bergström and Orchard 1985, for a review). Llandeilian (*P. anserinus* CBZ) faunas were first described from red cherts and shales within the Marchburn Formation. Lindström (1957) recorded *P. anserinus* Lamont and Lindström, *P. serra* (Hadding), *Periodon aculeatus* (Hadding) and *Spinodus spinatus* Dzik in association with graptolites. At Ruddenleys [NT 2025 5067] near Leadburn, red cherty mudstones have yielded conodonts (*P. anserinus* CBZ) in close association with dark shales yielding *N. gracilis* GBZ graptolites (Lamont 1975).

Armstrong *et al.* (1990) reported a *Periodon-Protopanderodus* fauna from red shales (Crawford Group, Kirkton Formation *sensu* Floyd 1996) in the Hawkwood Burn [NS 976 254] and, based upon the absence of *Pygodus* and regional considerations, suggested a Llanvirn age. Ethington and Austin (1993) have since extracted four specimens of *Pygodus* sp. from loose blocks of red cherts along strike from Hawkwood Burn, close to Raven Gill. The latter contains exposures of brown and grey cherts and fossiliferous green mudstones of mid Arenig, *O. evae* CBZ age (Lamont and Lindström 1957; Bergström and Orchard 1985). These cherts comprise olistostromes within the Leadhills melange (Hepworth *et al.* 1982; Armstrong *et al.* 1996) and are lithologically, temporally and spatially distinct from the red cherts of the Kirkton Formation. It is therefore likely that the blocks collected by Ethington and Austin (1993) were derived from nearby Kirkton Formation chert outcrops. The red cherts and mudstones of the Marchburn and Kirkton formations are almost certainly correlatives (Armstrong *et al.* 1996).

Smith (1907) and Lamont and Lindström (1957) have recorded probable Llandeilian faunas, including *Periodon aculeatus* and *Spinodus spinatus*, from red shales (Crawford Group, Kirkton Formation) in Morroch Bay [NX 017 252]. Lindström (1957) reported *Periodon* n. sp. aff. *P. aculeatus* (= *P. grandis*, see Löfgren 1978), *Protopanderodus* sp., *Drepanoistodus* sp. and *Dapsilodus* sp. from the Moffat Shale Group, higher in the succession at the same locality. These were associated with *Climacograptus wilsoni* Lapworth, suggesting a Burrellian (mid Caradoc) age.

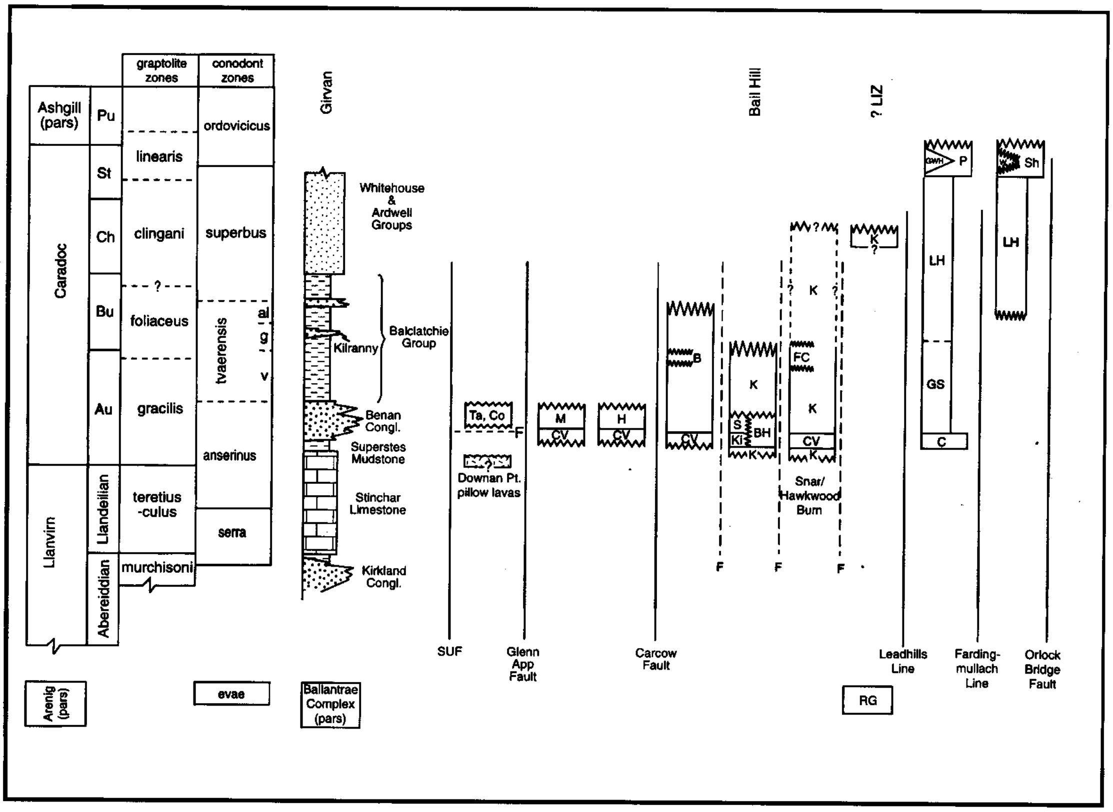
Lindström (*in* Walton 1965) reported ten species of conodont from the Tweeddale Member (Wrae Limestone) at Winkston that Bergström (1981*a*) considered to be the same as those from the Tweed Valley. Bergström *et al.* (1974) listed conodont species from the Tweeddale Member in the Tweed Valley area, from Glencotho Quarry, Wrae Hill and Drumelzier Quarry. They showed that the limestone contains a diverse fauna including *Pygodus serrus* (Hadding), *Periodon aculeatus* (Hadding), *Protopanderodus varicostatus* (Sweet and Bergström), *Spinodus spinatus* (Hadding), *Eoplacognathus* sp., *Strachanognathus parvus* Rhodes and *Prioniodus prevariabilis* (Fåhræus), an association they considered to be of late Llanvirn or slightly younger age. Bergström and Orchard (1985) reported *Polonodus* sp. from the Tweeddale Member. Bergström (1990, table 1) listed additional coniform taxa including *Dapsilodus mutatus* (Branson and Mehl) *Cornuodus*, *Drepanoistodus*, *Walliserodus ethingtoni* (Fåhræus) and *Panderodus*. He also updated his earlier faunal list, omitting *Eoplacognathus* sp. and transferring *Prioniodus prevariabilis* to *Baltoniodus*. From these collections, it has been accepted that the limestone clasts were of late Llanvirn–early Caradoc *Pygodus anserinus* CBZ age (Lamont and Lindström 1957).

Based upon conodont biostratigraphy, the red chert and shales of the Marchburn Formation, Kirkton Formation and limestone clasts within the Shinnel Formation, Tweeddale Member, are all *P. anserinus* CBZ age (see Armstrong *et al.* 1996 for the regional implications of this correlation).

Conodont biozonation

Two main conodont faunal provinces existed throughout the Ordovician, the North American Midcontinent and the North Atlantic provinces (Barnes and Fåhræus 1975). The former was characterized by warm-water, low latitude faunas, the latter by cold-water, high latitude or deeper water faunas. Marked endemicity has resulted in the establishment of separate zonations for each province (see Bergström 1971, 1983; Lindström 1971; Löfgren 1978 for details of the North Atlantic

Province). Conodont faunas from the Southern Uplands are dominated by species considered to be characteristic of the North Atlantic Province and have traditionally been correlated with the standard North Atlantic zonal scheme (Text-fig. 2). In this, the Llanvirn to Ashgill biozones are



TEXT-FIG. 2. Simplified chronostratigraphy, biostratigraphy and lithostratigraphy of the Girvan and Northern Belt areas. The succession between the Leadhills Line and the Fardingmullach Line is a composite of sections to the north-east of Sanquar and at Morroch Bay. Lithostratigraphical terminology for the Southern Uplands succession is that proposed by Floyd (1996). Chronostratigraphy and biostratigraphy are from Fortey *et al.* (1995). Abbreviations: Au = Aurelucian, Bu = Burrellian, Ch = Cheneyan, St = Streffordian, al = *alobatus*, g = *gerdae* and v = *variabilis* Sub-biozones, Ta = Tappins Group, Co = Corsewall Formation, CV and C = Kirkton Formation, chert and volcanics, M = Marchburn Formation, H = Hartree Formation, B = Blackcraig Formation, K = Kirkcolm Formation, S = Spothfore Member, Ki = Kiln Formation of Hepworth *et al.* (1982), now considered a local facies variation of the Kirkcolm Formation, BH = Bail Hill Volcanic Group, FC = fossiliferous conglomerate, LIZ = Leadhills Imbricate Zone, RG = Raven Gill Formation (considered to lie within the Leadhills Imbricate Zone), GS = Glenkiln Shale Formation, LH = Lower Hartfell Shale Formation, P = Portpatrick Formation, GWH = Glenwhargen Formation, Sh = Shinnel Formation, W = Tweeddale Member, SUF = Southern Upland Fault. Snar/Hawkwood Burn section generalized from sections exposed in Snar Water [NS 9085 1685] and the Hawkwood Burn [NS 9770 2540]. The top of the *P. anserinus* CBZ is poorly constrained in the Girvan sequence and most, if not all, the Benan Conglomerate may lie within this biozone.

based on the phylogeny of the rapidly evolving lineages of *Pygodus*, *Eoplacognathus*, *Baltoniodus* and *Amorphognathus*.

Bergström (1983) has reviewed middle and upper Ordovician biozonal units. The base of the *P. anserinus* CBZ was originally defined at the first appearance of the nominate species (Bergström

TABLE 1. Abundances of conodont elements found in the Shinnel Formation, Southern Upland, Scotland.

	D153	D156	D159	D160	D208	D209
Baltoniodus variabilis						
Pa		3				
Pb				1		
Pm				2		
Pc				3		
M				5		
Sa		1		1		
Sb				1		
Sc				1		
Belodina sp. indet.						
rastrate						1
Cornuodus longibasis						
ae						1
qa						3
qg						3
qt						3
pf						2
pt						1
Dapsilodus mutatus						
ae		2				
qg		3	1			
pf		9				
Dapsilodus aff. D. obliquicostatus						
ae		2		1		
qg		2		4		
pf		2				
Drepanoistodus suberectus						
ae						2
qg		1		6		4
qt				2		1
qa		4	1	1		2
pf		2		3		1
pt		1	1	2		
Eoplacognathus lindestroemi						
Pa		1		1		
Panderodus sp. indet.						
qa				1		
qg			2	3		2
?qt			1	1	1	
pf		1	1			
Periodon aculeatus						
Pa		43	3	15	1	20
Pb		20	1			2
M		51	1	34	2	51
Sa		17	1	3		7
Sb	1	63	8	25	4	21
Sc		7		7		5
Protopanderodus varicostatus						
ae		8		15		3
qa				3		4
qg		8		27		1
qt		6		5		
pf		4		4		3
pt		9		13		
Pseudooneotodus sp. indet.						1
Pygodus anserinus						
Pa		8	5	39		
Pb		2		8		
Pc		20	2	49		
M		1		17		
Sc		6		1		
Spinodus spinatus		64	5	102		
Strachanognathus parvus						
?ae		32	6	4		1
qa		63	15	2		2
qg		13	2	2		1
qt		18		3		2
?pf		17	1	3	2	3
Walliserodus ethingtoni						
ae				1		1
qg				2		2
Walliserodus aff. W. sancticlairi						
ae		7				
qa		3				
qg		6		3		
?pf		3		1		
Genus and sp. indet.						
Pa				2		9
pb						2
M						1
Sa						2
Sb						11
Total identifiable fragments	1	235	21	123	8	132
Indeterminate fragments	1	180	45	241	12	157
Elements per Kg	2	1942	455	1010	118	400

1971, p. 97). This species is thought to be a direct descendant of *P. serra* and first appeared in the upper Llandeilian (Bergström 1971, p. 150; Fåhræus 1982; Fortey *et al.* 1995, fig. 1). Bergström (1971) subdivided the *P. anserinus* CBZ based upon the evolution of *Baltoniodus variabilis* from *B. prevariabilis*. Dzik (1978) and Bergström (1983) also considered that the transition from *Amorphognathus kielcensis* Dzik to *A. inaequalis* Rhodes occurred at this level, and suggested that an *A. inaequalis* Sub-biozone can be defined on the co-occurrence of *P. anserinus* and *A. inaequalis*. The precise position of the Llanvirn-Caradoc boundary in the North Atlantic conodont zonation remains uncertain. Fortey *et al.* (1995) placed the base of the Caradoc Series (Aurelucian Stage) at the base of the *N. gracilis* GBZ (see Finney and Bergström 1986 for a discussion of this biozone). The base of the Aurelucian evidently falls within the lower part of the *P. anserinus* CBZ (Bergström 1986, 1990; Fortey *et al.* 1995). Bergström (1986, fig. 3) tied the top of the *P. anserinus* CBZ to a level within the mid *N. gracilis* GBZ; consequently, much of the *P. anserinus* CBZ lies within the Caradoc (Fortey *et al.* 1995, fig. 1).

CORRELATION AND PROVINCIALITY

Species from the *P. anserinus* CBZ in southern Scotland are identical to those from coeval strata in eastern North America, such as the Cobbs Arm Limestone, Newfoundland (Bergström *et al.* 1974), the Lenoir Limestone of eastern Tennessee (Bergström 1990), Norway (Hamar 1964, 1966) and Sweden (Bergström 1971; Dzik 1976). The species present in these areas have been categorized as the *Periodon-Pygodus* RSA (Restricted Species Association, *sensu* Bergström and Carnes 1976), characteristic of deeper, cool water, shelf and slope environments, and thought to have contained mainly nektonic taxa. An exception occurs in the Cobbs Arm Limestone of north-eastern Newfoundland, where strata containing this RSA have been interpreted as being of shallow water origin, laid down in a volcanic island setting (Fåhræus and Hunter 1981).

In Scotland north of the Southern Upland Fault, the affinities of all but the deepest water shelly biofacies are Laurentian, even to the end of the Caradoc. Lower Ordovician conodont (Ethington and Austin 1991), brachiopod (Williams 1962; Higgins 1967; Ingham 1978; Bergström and Orchard 1985; Ingham *et al.* 1985; Ingham and Tripp 1991) faunas are characteristic of the American Midcontinent Province centred on Laurentia. Bergström (1971) recorded conodonts from the middle and upper Ordovician of Girvan and later (Bergström 1990) presented a detailed biostratigraphical, palaeoecological and palaeobiogeographical analysis of these faunas. The base of the *P. anserinus* CBZ lies within the upper part of the Stinchar Limestone. The upper part of the biozone (*A. inaequalis* Sub-biozone *sensu* Bergström 1983) is recorded in the overlying Superstes Mudstone (in association with upper *N. gracilis* GBZ graptolites), though the index species is absent. A slightly younger, *Baltoniodus gerdae* Sub-biozone fauna, is known from the Balclatchie Group, near Laggan Burn, Girvan, and occurs in association with *Diplograptus multidens* GBZ graptolites of early Caradoc age (Bergström and Orchard 1985; Bergström 1990). This fauna contains *Periodon aculeatus* and *Spinodus spinatus*, in common with the *P. anserinus* CBZ, but the younger species *Protopanderodus liripipus* Kennedy, Barnes and Uyeno and *Amorphognathus tvaerensis* Bergström are also present (Bergström 1990, fig. 5).

Early Caradoc conodont species from the Scottish deep water sequences to the south of the Southern Upland Fault were cosmopolitan, and are known from similar facies rimming Laurentia, across Baltica and the palaeo-Pacific (Bergström 1990, p. 21). Recent palaeomagnetic data have confirmed the tropical and subtropical location of the Laurentian margin at that time (Trench and Torsvik 1992). The *Periodon-Pygodus* RSA is therefore best considered as an outer shelf and slope, cool water biofacies containing cosmopolitan species, rather than being indicative of a particular faunal province.

EXPLANATION OF PLATE 1

Fig. 1. *Belodina*? sp. indet.; GLAHM Y 357; sample D209, Glencotho Farm; rastrate pf element.

Fig. 2. *Baltoniodus variabilis* (Lindström, 1959); GLAHM Y 358; sample D156, Winkston: Pa element.

Figs 3–8. *Dapsilodus mutatus* (Branson and Mehl, 1933*c*); sample D156, Winkston. 3–4, GLAHM Y 359; anterior and posterior sides of ae element. 5–6, GLAHM Y 360; anterior and posterior sides of qg element. 7–8, GLAHM Y 361; anterior and posterior sides of pf element.

Figs 9–11. *Dapsilodus* aff. *D. obliquicostatus* (Branson and Mehl, 1933*a*); sample D156, Winkston. 9, GLAHM Y 362; ae element. 10, GLAHM Y 363; qg element. 11, GLAHM Y 364; pf element.

Figs 12–23. *Drepanoistodus suberectus* (Branson and Mehl, 1933*b*). 12–16, sample D209, Glencotho Farm. 12–13, GLAHM Y 365; anterior and posterior views of ae element. 14–15, GLAHM Y 437; anterior and posterior views of qg element. 16, GLAHM Y 367; qt element. 17–18, 20–23, sample D160, Winkston. 17–18, GLAHM Y 368; anterior and posterior views of qa element. 20–21, GLAHM Y 370; anterior and posterior views of pf element. 22–23, GLAHM Y 371; anterior and posterior views of pt element. 19, GLAHM Y 369; sample D156, Winkston; qa element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.

ARMSTRONG, Ordovician conodonts

LOCALITIES

Localities at Glencotho and Winkston provide the best exposures of limestone. At Glencotho, grey recrystallized limestone boulders up to 3 m across are exposed in a small quarry in the hillside above Glencotho farm (NC 090 294, samples D208–D209). Here they are associated with a matrix of pebbly and tuffaceous breccia. The pebbles are composed predominantly of red chert, basalt and, rarely, mudstone. Limestone boulders are now only exposed for some 10 m along strike to the north-east of the quarry. Leggett (1980) reported limestone clasts up to 30 mm long in a brecciated grit exposed to the south-west of the quarry (in the north bank of a tributary of Glencotho Burn, NC 089 293) but these could not be re-located.

At Winkston, 3 km north of Peebles, several abandoned roadside quarries (NC 2425 4350, samples D156, 159, 160) contain limited exposures and talus screes of breccia, containing limestone clasts up to 0·2 m long. Here the clast-supported matrix is coarse grained and forms more than 50 per cent. of the rock; mudstone, red and grey chert and basalt predominate. Various outcrops on Winkston Hill were described by Peach and Horne (1899, pp. 260–262), including a small outcrop of porphyritic lava. Field relations are not now visible. Leggett (1980, p. 99) noted an apparent fining and diminution of limestone clasts up the hill.

A single sample of calcareous breccia (D153), collected from the Spotfore Burn [NS 789 149], may represent an outcrop of the Tweeddale Member interbedded with the Kirkcolm Formation, between the Carcow and Leadhills faults. This clast-supported breccia has a fine grained matrix; the clasts are predominantly sub-rounded, calcareous mudstone up to 5 mm in diameter. The thin breccia bed crops out in the west bank of the burn, approximately 5 m downstream from a small waterfall. Associated with the breccia, but not in direct contact, are radiolarian cherts and black shales (on the east bank) from which Peach and Horne (1899, pp. 314, 315) reported a graptolite fauna including abundant *Didymograptus superstes* (Lapworth), *Dicranograptus ramosus* (Hall), *Dicellograptus sextans* (Hall) and *Climacograptus scharenbergi* (Lapworth) indicating a probable upper *N. gracilis* GBZ age. The waterfall at this locality is formed from a volcanic agglomerate.

CONODONT FAUNA

Samples up to 2 kg in weight were processed for conodonts using standard techniques, buffering with calcium carbonate and using a 63 μm mesh bottom sieve. Acid resistant, heavy residues were large and underwent magnetic separation prior to picking. Conodonts are abundant and diverse, although generally poorly preserved. Specimens are black with a CAI of 5, indicating they have been subjected to temperatures in excess of 300 °C (Epstein *et al.* 1977). This is consistent with the illite crystallinity data in Oliver *et al.* (1984). The majority of specimens exhibit surficial alteration, best seen as a thin recrystallized mineral film under the SEM. Consequently, specimens are easier to identify and look better preserved under the light microscope. Illustrated specimens are housed in the collections of the Hunterian Museum, with the specimen numbers prefixed by GLAHM Y. The remaining collection is housed in the micropalaeontological collections of the Department of Geological Sciences, University of Durham. Specimen abundances are recorded in Table 1.

SYSTEMATIC PALAEONTOLOGY

The widespread application of multi-element taxonomy has led to the erection of a number of element notational schemes. The scheme proposed by Sweet and Schönlaub (1975), and modified by Cooper (1975), Männik and Aldridge (1989) and Aldridge *et al.* (1995), for platform-ramiform taxa is adopted here as it remains the most widely used amongst conodont workers. The major shape categories and morphological terminology are as detailed by Sweet (1981). Coniform taxa have received less taxonomic treatment and there is no widely accepted terminology for homologous elements within multi-element apparatuses. Sansom *et al.* (1995) have developed a scheme based upon bedding plane and diagenetically fused assemblages of *Panderodus* that appears to be widely applicable to other coniform genera and is employed herein. The major shape categories and morphological terminology used to describe coniform elements follow Sweet (1988) and Sansom *et al.* (1995). Suprageneric classification of conodonts is currently in a state of flux. The scheme proposed by Sweet (1988) and modified by Aldridge and Smith (1993) is employed herein. Synonomy lists are annotated as recommended by Matthews (1973, after Richter 1948). Complete synonomies are given only for emended taxa; shortened synonomies include the original species designation, subsequent important taxonomic changes, British material and the most recent full synonomy lists.

Phylum CHORDATA
Class CONODONTA
Order PRIONIODONTIDA Dzik, 1976
Family BALOGNATHIDAE Hass, 1959

Genus BALTONIODUS Lindström, 1971

Type. Prioniodus navis Lindström 1955*a*, p. 590.

Remarks. Löfgren (1978) argued that *Baltoniodus* should be considered a subgenus of *Prioniodus*. Lindström *et al.* (1974) and Stouge (1984) considered that *Baltoniodus* was well-founded and should be maintained as a separate genus.

Baltoniodus variabilis (Lindström, 1959)

Plate 1, figure 2; Plate 2, figures 2–9

1959 *Prioniodus variabilis* Bergström; Lindström, p. 444, pl. 3, figs 17–19.
1961 *Prioniodus* cf. *Prioniodus variabilis* Bergström; Wolska, p. 56, pl. 5, fig. 2*a–b*.
*1962 *Prioniodus variabilis* Bergström, p. 51, pl. 12, figs 1–7.
1966 *Prioniodus variabilis* Bergström; Hamar, p. 279, pl. 5, figs 2–3, 6.
1971 *Keislognathus gracilis* Rhodes; Bednarczyk, pl. 4, fig. 1.
1976 *Prioniodus variabilis* Bergström; Dzik, text-fig. 24h-1.
1981 *Baltoniodus variabilis* (Bergström); Nowlan, p. 12, pl. 14, figs 10–12, 14–17.
1984 ?*Baltoniodus variabilis* (Bergström); Chen and Zhang, pl. 2, figs 8–15.
1985 *Baltoniodus variabilis* (Bergström); Bergström and Orchard, pl. 2.3, fig. 2.
1994 *Baltoniodus variabilis* (Bergström); Dzik, p. 84, pl. 19, figs 1–9; text-figs 14c, 15.

Holotype. Prioniodus variabilis Bergström, 1962, p. 51.

Diagnosis. Refer to Bergström and Orchard (1985, p. 58).

Description. A single, complete pastinate Pa element was found in sample D156 (Pl. 1, fig. 2). The inner margin is extended to form a markedly triangular platform when viewed orally. Pb element arched and bipennate, with the anterior process deeper and longer than the posterior; both bear a prominent ledge beneath the denticles (Pl. 2, fig. 2). A short, adenticulate inner lateral process projects beneath and extends up the cusp as a prominent costa. Pc element similar to the Pb element but much more strongly arched; anterior and posterior processes form an acute angle beneath the cusp (Pl. 2, figs 4–5). Pd element arched, bipennate and bowed to the inner side (Pl. 2, fig. 6). Short lateral processes bearing prominent inflation beneath the denticles; anterior process is sharply down-turned, the posterior subhorizontal. Prominent cusp, slightly inclined towards the posterior.

M element tertiopedate, similar to the Sb; the inner lateral process is more sharply directed towards the posterior.

Sa element alate with short posterior process (Pl. 2, fig. 7). Lateral processes sharply down-turned and bear three or four peglike denticles. Sb element tertiopedate, similar to Sa element; inner lateral process much shorter, commonly only bears a single denticle (Pl. 2, fig. 8). Sd element laterally compressed and pyramidal quadriramate, with the processes reduced to rows of denticles.

Remarks. Lindström (1959) first illustrated and recorded this species as *Prioniodus variabilis*, referring the authorship to a manuscript not published until 1962 (Bergström 1962). An apparatus interpretation was provided by Bergström (1971) and all the elements were illustrated by Dzik (1976). This species is distinguished from the older *B. prevariabilis* (Dzik) by the prominent development of the inner margin, and ledges along the process (Dzik 1994).

Family POLYPLACOGNATHIDAE Bergström, 1981*b*

Genus EOPLACOGNATHUS Hamar, 1966

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

Eoplacognathus lindstroemi (Hamar, 1964)

Plate 2, figure 1

*1964 *Ambalodus lindstroemi* Hamar, p. 258, pl. 5, figs 1, 4, 7–8, 10–11; text-fig. 5, figs 1a–b, 3a–b, 4a–b.
1971 *Eoplacognathus lindstroemi* (Hamar); Bergström, p. 139, pl. 2, figs 15–18.
1985 *Eoplacognathus lindstroemi* (Hamar); Bergström and Orchard, pl. 2.2, figs 11, 13.

Holotype. Hamar (1964, pl. 5, figs 8, 11); specimen PMO 69791; *Ampyx* Limestone; Ringerike, Norway.

Diagnosis. Refer to that of Dzik (1994, p. 98).

Description. A single fragmentary Pa element bears the characteristic ledge beneath the denticles and an outer lateral process which diverges at a right angle to the anterior process.

Remarks. No ramiform elements have been described for *Eoplacognathus*. The platform elements develop a distinctive ledge beneath the denticles, a convergent feature with members of the Pterospathodontidae. Pb, Pc, Pd and ramiform elements with a prominent ledge are present in sample D160 (Pl. 2, figs 2–9), in association with an *E. lindstroemi* Pa element, but closely resemble elements traditionally included in *Baltoniodus variabilis*.

EXPLANATION OF PLATE 2

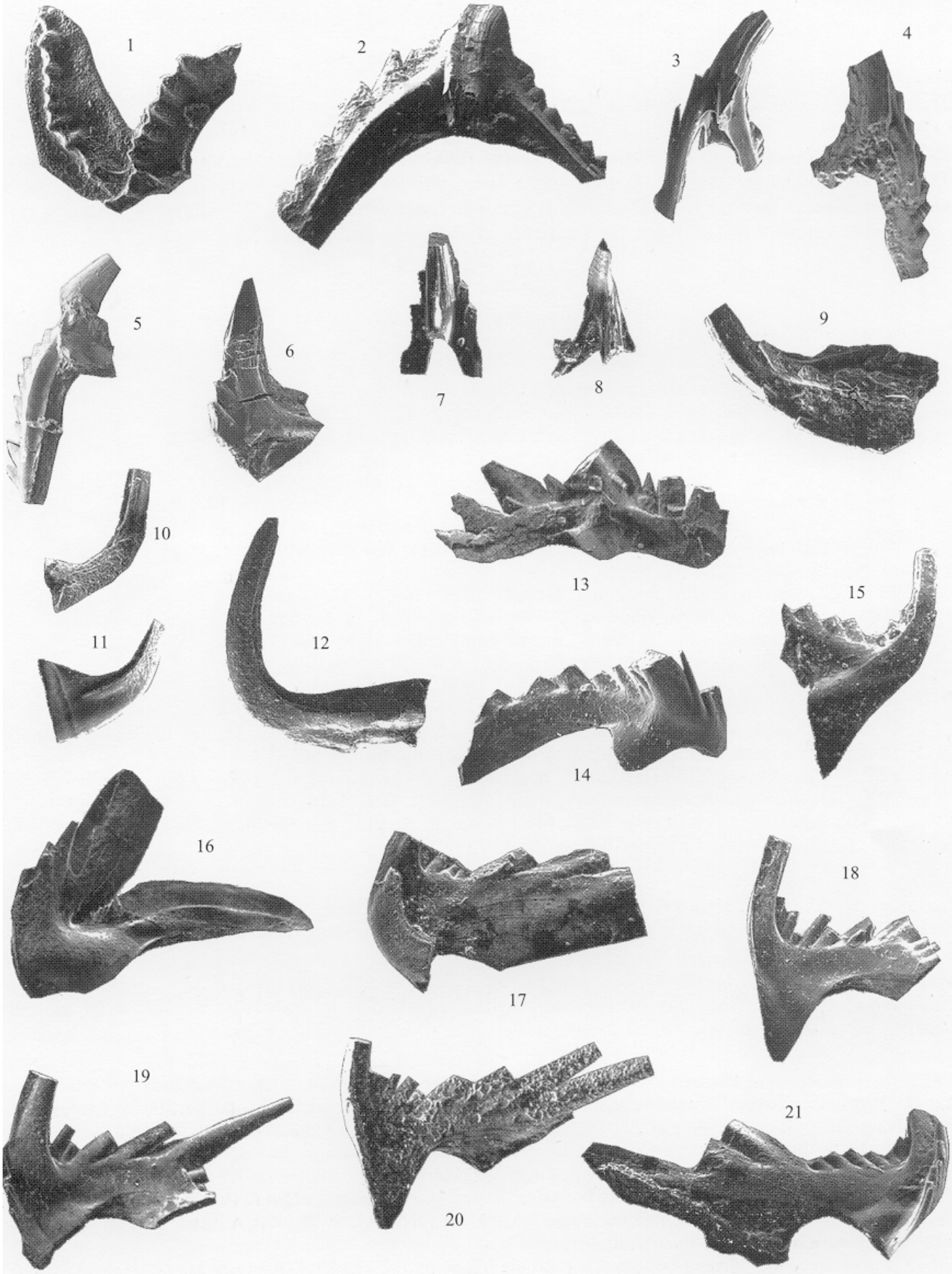
Fig. 1. *Eoplacognathus lindstroemi* (Hamar, 1964); GLAHM Y 372; sample D156, Winkston; Pa fragment.

Figs 2–9. *Baltoniodus variabilis* (Lindström, 1959); Winkston. 2–6, 8–9, sample D160. 2, GLAHM Y 373; Pb element. 3, GLAHM Y 374; Sb element. 4–5, Pc elements; 4, GLAHM Y 375; 5, GLAHM Y 376. 6, GLAHM Y 377; Pd element. 8, GLAHM Y 379; Sb element. 9, GLAHM Y 380; Sc element. 7, GLAHM Y 378; sample D156; Sa element.

Figs 10–12. *Panderodus* aff. *P. recurvatus* Rhodes, 1953. 10, GLAHM Y 381; sample D209, Glencotho Farm; qg element. 11, GLAHM Y 382; sample D156, Winkston; pf element. 12, GLAHM Y 383; sample D160, Winkston; ?pt element.

Figs 13–21. *Periodon aculeatus* Hadding, 1913; sample D156, Winkston. 13, GLAHM Y 384; Pa element. 14, GLAHM Y 385; Pb element. 15, GLAHM Y 386; Sb element. 16, GLAHM Y 387; M element. 17, GLAHM Y 388; Sa element. 18–20, Sb elements; 18, GLAHM Y 389; 19, GLAHM Y 390; 20, GLAHM Y 391. 21, GLAHM Y 392; Sc element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.



ARMSTRONG, Ordovician conodonts

Family PRIONIODONTIDAE Bassler, 1925

Genus PERIODON Hadding, 1913

Type species. *Periodon aculeatus* Hadding, 1913, p. 33.

Remarks. *Periodon* shares a common apparatus plan with other members of the Prioniodontidae. This is typically septimembrate containing a bipennate Pa, digyrate Pb, dolabrate M, alate Sa, Sb and Sc elements. Two pairs of Sb elements occur in most genera. Dzik (1994) and Armstrong *et al.* (1996) noted homology between the elements of *Periodon* and *Hamarodus* Viira.

Periodon aculeatus (Hadding, 1913)

Plate 2 figures 13–21; Text-figure 3

*1913 *Periodon aculeatus* Hadding, p. 33, pl. 1, fig. 14.
1941 *Loxognathus flabellata* Graves and Ellison, p. 12, pl. 2, figs 29, 32.
1941 *Oistodus prodentatus* Graves and Ellison, p. 13, pl. 12, figs 8, 22–23, 28.
1941 *Ozarkodina macrodentata* Graves and Ellison, p. 14, pl. 2, figs 33, 35–36.
1941 *Loxognathus flabellata* Graves and Ellison, p. 12, pl. 2, figs 29, 32.
1955*b* *Periodon aculeatus* Hadding; Lindström, p. 110, pl. 22, figs 10–11, 14–16, 35.
1957 *Periodon aculeatus* Hadding; Lamont and Lindström, p. 61, pl. 5, fig. 15.
1962 *Falodus prodentatus* (Graves and Ellison); Sweet and Bergström, p. 1227, pl. 170, figs 2–3, text-fig. 2B.
1962 *Ligonodina tortilis* Sweet and Bergström, p. 1240, pl. 171, figs 7–8.
1966 *Periodon aculeatus* Hadding; Sweet and Bergström, pl. 18, figs 1, 3–4; text-fig. 1C, E.
1973 *Periodon aculeatus* Hadding; Barnes and Poplawski, p. 780, pl. 5, figs 15–18a.
1974 *Periodon aculeatus* Hadding; Bergström *et al.*, pl. 1, figs 4–6.
1976 *Periodon aculeatus aculeatus* Hadding; Dzik, fig. 34i–r.
1976 *Periodon aculeatus zgierensis* Dzik, p. 424, pl. 44, figs 5–6; fig. 34e–k.
1978 *Periodon aculeatus* Hadding; Löfgren, p. 74, pl. 10, fig. 1A–B; pl. 11, figs 12–26; fig. 29 (*pars*).
1984 *Periodon aculeatus* (Hadding); Chen and Zhang, pl. 2, figs 1–7.
1985 *Periodon aculeatus* (Hadding); Bergström and Orchard, pl. 2.2, figs 6–7.
1990 *Periodon aculeatus* (Hadding); Bergström, pl. 1, figs 15–16.
1991 *Periodon aculeatus* (Hadding); McCracken, p. 50, pl. 1, figs 13, 20, 22, 25–28; pl. 2, figs 24–27, 31, 34–35.
1994 *Periodon aculeatus* (Hadding); Dzik, p. 111, pl. 24, figs 10–13; text-fig. 31b.

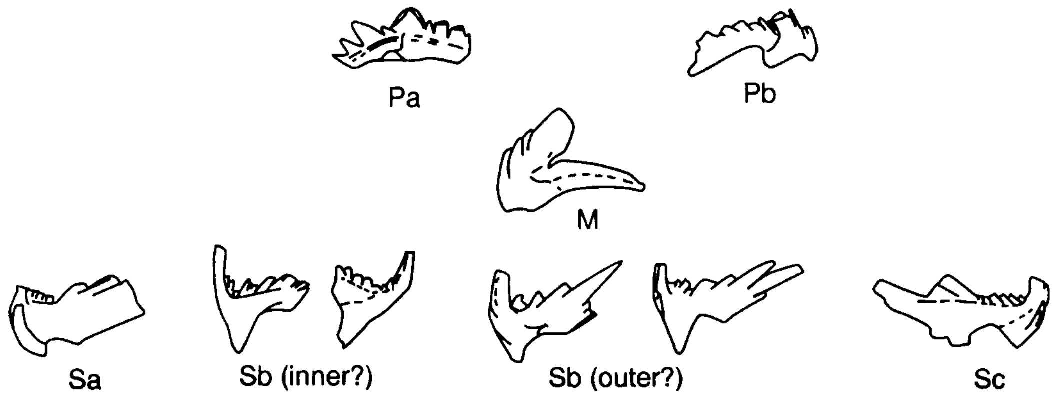
Holotype. Hadding (1913, pl. 1, fig. 14); specimen LO 2353 T (mouldic preservation); *Climacograptus haddingi* GBZ (= *Climacograptus putillus* in Hadding 1913) of Fågelsång, near Lund (upper part of section E15).

Emended diagnosis. A species of *Periodon* with a markedly digyrate Pb; dolabrate M element bearing three to six anterior edge denticles.

Description. Pa element inwardly bowed and angulate; cusp and denticles inclined towards posterior (Pl. 2, fig. 13). Processes of approximately equal length, bearing four to six denticles. Moderate inward flare of basal cavity, directed posteriorly. Pb element digyrate with short anterior process, commonly bearing three or four denticles (Pl. 2, fig. 14). Posterior process longer than anterior, variably bowed downwards and inwards. Pronounced basal cavity flare beneath cusp, directed posteriorly.

M element dolabrate, slightly inwardly bowed (Pl. 2, fig. 16). Anterior margin of the reclined cusp commonly bears three and rarely up to six denticles. Posterior process adenticulate. Weak development of an anticusp on large specimens. Narrow, symmetrically disposed basal cavity flare beneath cusp.

Sa element alate with deep, denticulate processes (Pl. 2, fig. 17). Lateral processes bear two or three short denticles and continue up the cusp as faint costae. Sb element variable in morphology from flat (dolabrate) to inwardly bowed, tertiopedate (Pl. 2, figs 18–20). Posterior process bears up to eight posteriorly inclined denticles; may be outwardly twisted. Inner lateral process developed as two or three, tall denticles, up the edge of the cusp. Outer lateral process reduced to a costa along upper edge of the cusp. Basal cavity flare beneath cusp variably developed, may extend as a ridge along lower margin of the posterior process in large specimens. Sc element similar to Sa but outer lateral process reduced to a costa, rarely a denticulate ridge (Pl. 2, fig. 21). Posterior process has a pronounced downward curvature.



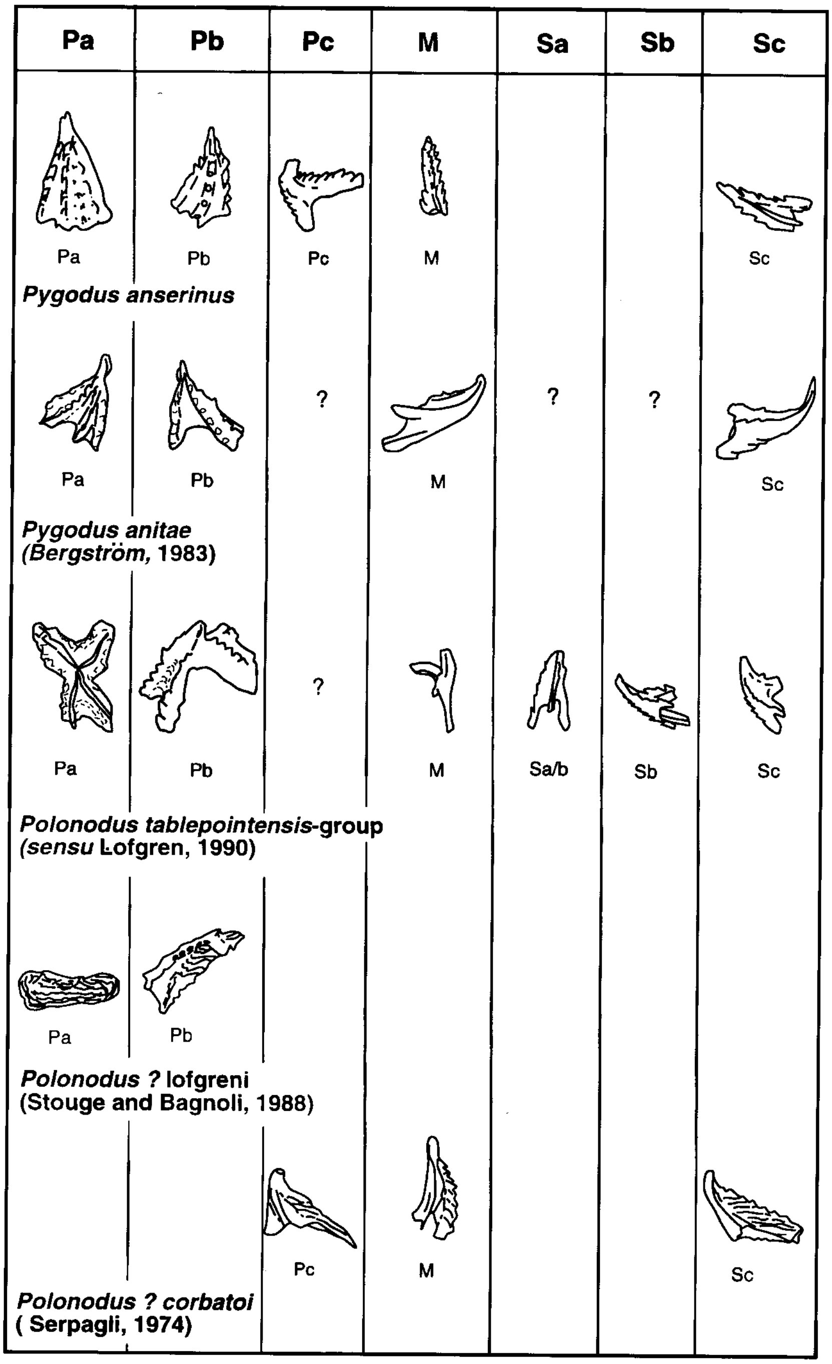
TEXT-FIG. 3. Line drawings of elements placed in the apparatus of *Periodon aculeatus* (Hadding, 1913). Specimens are as figured in Plate 2.

Remarks. Sweet and Bergström (1966) proposed a partial multi-element reconstruction, Bergström *et al.* (1974) included the Pb element and Dzik (1976) proposed the first complete apparatus. Flat and inwardly curved sinistral and dextral morphotypes of the Sb element suggest inner and outer pairs within the apparatus.

Family PYGODONTIDAE Bergström, 1981*b*

Remarks. Pygodus appears to have a modified prioniodontid apparatus plan. The family Pygodontidae is retained for conodonts bearing scaphate Pa, pastiniscaphate Pb and bipennate Pc elements. *Polonodus* Dzik also belongs to this family. *Amorphognathus* is not included as it contains a Pd element (Armstrong *et al.* 1996).

The earliest species of *Polonodus* and *Pygodus* have a stelliscaphate Pa and a pastiniscaphate Pb (Text-fig. 4). Historically, phylogenies for this group have been based upon morphological transitions in the Pa element. Löfgren (1990) summarized the current thinking on the evolution of this group. According to Bergström (1983, p. 44) an ancestral, Tremadoc platform conodont, such as *Nericodus* Dzik, 1983, evolved into *Polonodus* and *Pygodus* in the Llanvirn. Löfgren (1990, p. 256), however, considered the ancestry of *Polonodus* to be much more complex. She noted differences in the ramiform elements between the earliest Arenig species, *Polonodus*? *corbatoi* (Serpagli) (equivalent to *Polonodus*? sp. Löfgren, 1985) and the later *P. tablepointensis* Stouge-group (*sensu* Löfgren 1990), which possess ramiforms more similar to those of *Baltoniodus*. No records exist of *Polonodus* between the *O. evae* and *A. variabilis* CBZ and Löfgren (1990, p. 256) concluded that, to derive the later species of *Polonodus* from the early Arenig forms, one must invoke parallel evolution of the ramiforms in the (*Acodus*)-*Baltoniodus* and *Polonodus* lineages. She considered it to be more parsimonious for the *Polonodus*-type platforms to have evolved twice, firstly



TEXT-FIG. 4. Proposed homologies between the elements of *Pygodus* and *Polonodus*. Elements are redrawn: *Pygodus anserinus* (Pl. 4). *Pygodus anitae* Bergström (1983; elements illustrated from Löfgren 1978, pl. 16, figs 5–6, 3 and 4 are from the *E. suecicus* Biozone). Bergström (1983, fig. 6z) figured a possible Pc element but this has well-spaced, peg-like denticles on the posterior process. *P. tablepointensis*-group (*sensu* Löfgren 1978, pl. 16, figs 10 and 9; Löfgren 1990, fig. 1k, 1b, 1f and 1h) from the *A. variabilis* Biozone: *Polonodus*? *lofgreni* in the early Arenig and secondly from *Baltoniodus* in the late Arenig. Members of the *tablepointensis* group have an oistodontiform (M) element (Löfgren 1990, fig. 1K) which is not recognized in *Pygodus anserinus*. It appears more likely that *Pygodus* is directly descended from the *P.*? *corbatoi* group. Until the apparatus of early Arenig *Polonodus* is fully diagnosed, the ancestry of *Pygodus* must remain in doubt.

If iterative appearances of homeomorphic platform elements and relatively conservative ramiform elements are common features of the evolution in prioniodontid clades, then traditional phylogenies must be reconsidered in light of new multi-element reconstructions. The M and ramiform elements gain a new importance in diagnosis and in tracing cladogenesis.

Genus PYGODUS Lamont and Lindström, 1957

Type species. *Pygodus anserinus* Lamont and Lindström, 1957, p. 68.

Pygodus anserinus Lamont and Lindström, 1957

Plate 4, figures 1–7; Text-figure 4

*1957 *Pygodus anserinus* Lamont and Lindström, p. 68, pl. 5, figs 12–13; text-fig. 1a–d.
1958 *Phragmodus* spp. Ethington *et al*., p. 764, text-fig. 1A–D.
1958 *Falodus*? sp. Ethington *et al*., p. 764, text-fig. 1E.
?1958 *Oistodus* cf. *O. parallelus* Pander; Ethington *et al*., p. 764, text-fig. 1F.
1960 *Pygodus anserinus* Lamont and Lindström; Lindström, p. 91, figs 7.1, 7.3.
?1960 '*Arabellites*' *serra* Lindström, p. 95, fig. 7, no. 6.
?1961 *Pygodus anserinus* Lamont and Lindström; Wolska, p. 337, pl. 5, figs 4–5.
1962 *Tetraprioniodus lindstroemi* Sweet and Bergström, p. 1248, pl. 170, figs 5–6.
1962 *Roundya pyramidalis* Sweet and Bergström, p. 1243, pl. 170, figs 7–9.
1962 *Pygodus anserinus* Lamont and Lindström; Sweet and Bergström, p. 1241, pl. 171, figs 11–12; text-fig. 4.
1962 *Haddingodus serra* (Hadding); Sweet and Bergström, p. 1229, pl. 170, figs 1, 4.
1964 *Pygodus anserinus* Lamont and Lindström; Hamar, p. 279, pl. 4, figs 1–4, 11.
1964 *Pygodus* sp. Lindström; Hamar, p. 280, pl. 4, figs 5–8.
1964 *Haddingodus serra* (Hadding); Hamar, p. 266, pl. 4, figs 13, 16.
1964 *Roundya pyramidalis* Sweet and Bergström; Hamar, p. 280, pl. 5, figs 15–16, 20–21; text-fig 4, no. 12.
1964 *Tetraprioniodus lindstroemi* Sweet and Bergström; Hamar, p. 285, pl. 6, figs 4–5.
1966 *Pygodus anserinus* Lamont and Lindström; Hamar, pl. 7, fig. 1.
1974 *Pygodus anserinus* Lamont and Lindström; Bergström *et al*., pl. 1, figs 16–17.
1974 *Pygodus anserinus* Lamont and Lindström; Viira, p. 115, pl. 11, figs 26–27.
1974 *Roundya pyramidalis* Sweet and Bergström; Viira, p. 115, pl. 11, figs 7–8, 11.
1974 *Tetraprioniodus lindstroemi* Sweet and Bergström; Viira, p. 126, pl. 11, figs 9–10, 12.
1974 *Haddingodus serra* (Hadding); Viira, p. 86, pl. 11, fig. 25.
1976 *Pygodus anserinus* Lamont and Lindström; Dzik, p. 440, fig. 29f.
1978 *Pygodus anserinus* Lamont and Lindström; Bergström, pl. 79, figs 1–2.
1979 *Pygodus anserinus* Lamont and Lindström; Harris *et al*., pl. 4, fig. 17.
1983 *Pygodus serra* (Hadding); Ni *in* Zeng *et al*., pl. 12, figs 3–5.
1983 *Pygodus anserinus* Lamont and Lindström; Ni *in* Zeng *et al*., pl. 12, figs 4, 22.
1984 *Pygodus anserinus* Lamont and Lindström; Chen and Zhang, pl. 2, figs 18–21.
1985 *Pygodus anserinus* Lamont and Lindström; Bergström and Orchard, pl. 2.3, fig. 3.
1990 *Pygodus anserinus* Lamont and Lindström; Pohler and Orchard pl. 2, fig. 20.
1994 *Pygodus anserinus* Lamont and Lindström; Dzik, p. 105, pl. 17, figs 7–8; text-figs 26–27.

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elements are from the *P. elegans* Biozone (Stouge and Bagnoli 1988, pl. 11, figs 4 and 1) and *P.*? *corbatoi* (Serpagli) from the *O. evae* Biozone (illustrated from Stouge and Bagnoli 1988, pl. 10, figs 2, 5, 3) are considered together as the *P.*? *corbatoi*-group.

Holotype. Lamont and Lindström (1957, text-fig. 1a–b); specimen LO 3871 T. From grey trilobite-bearing limestone, Gärdslösa Bodar, Öland, Sweden.

Emended diagnosis. A species of *Pygodus* in which the quinquimembrate apparatus comprises stelliscaphate Pa, pastiniscaphate Pb, bipennate Pc element and tertiopedate M element. The ramiform complex is apparently reduced to an Sc element.

Description. Pa element stelliscaphate and triangular in oral view (Pl. 4, figs 1–3). Short, triangular, posterior cusp, markedly inclined towards posterior. Anterior platform bears three prominent, inwardly curved rows of nodes, which lie along the margins and just off-centre. A fourth, incipient row of nodes lies between the outer and inner row. Low ridges may join the nodes across the platform. The inter-ridge areas bear a micro-ornament of small nodes and pock-marks which in a very few specimens are arranged in small circles. The aboral surface is entirely excavated.

Pb element is similar to the Pa element, but lacks the fourth incipient row of nodes (Pl. 4, fig. 4). Platform more inwardly curved; central row of nodes most prominent. Specimens from the Tweeddale Member lack the transverse ridges which join the nodes.

Pc element arched and bipennate, with prominent, posteriorly inclined cusp, deep inwardly directed anterior lateral process and horizontal posterior process (Pl. 4, fig. 5). Base of cusp inwardly inflated, extending to basal margin, bisecting angle between processes. Processes bear eight to ten denticles, fused almost to their tips.

M element tertiopedate, narrow and triangular in posterior view (Pl. 4, fig. 6). Cusp short, posteriorly inclined and often difficult to distinguish from the other denticles. Processes comprise denticulate ridges which run the height of the element. Denticles are as in the Pc element. Posterior process commonly slightly, offset laterally.

Sc element similar in morphology to M element, but strongly, latero-obliquely compressed, posterior process becoming more prominent and sub-horizontal (Pl. 4, fig. 7). Outer lateral process reduced to adenticulate ridge and inner process only slightly bowed inwardly.

Remarks. Lamont and Lindström (1957, p. 68) diagnosed *P. anserinus* as comprising 'a very small cusp and three rows of small, irregular denticles and in big specimens a fourth row', which implies that they considered specimens with three rows of nodes to be juvenile. In the new collections there is no significant size difference between three- and four-rowed specimens, and a range from small to large specimens is present. The incipient fourth row of nodes in *P. anserinus* has since been considered to be a phylogenetic (Bergström 1971, pp. 97, 147) or ecophenotypic (Fåhræus 1982, pp. 4–6) characteristic. Dzik (1994, p. 26) illustrated three- and four-rowed Pa elements from samples 57, 59 and 60 in the Mójcka Limestone at the base of range of *P. anserinus*. Lamont and Lindström (1957, p. 64) and Lamont (1975) recorded both *P. anserinus* and *P. serra sensu formae* from Noblehouse and Ruddenleys from a level high in the *N. gracilis* GBZ and therefore high in the *P. anserinus* CBZ (Fortey *et al*. 1995). The three- and four-rowed *Pygodus* morphotypes would thus appear to co-occur throughout the *P. anserinus* CBZ. Nowlan (1981) and McCracken (1991) applied conferred species status to similar co-occuring elements from the Yukon.

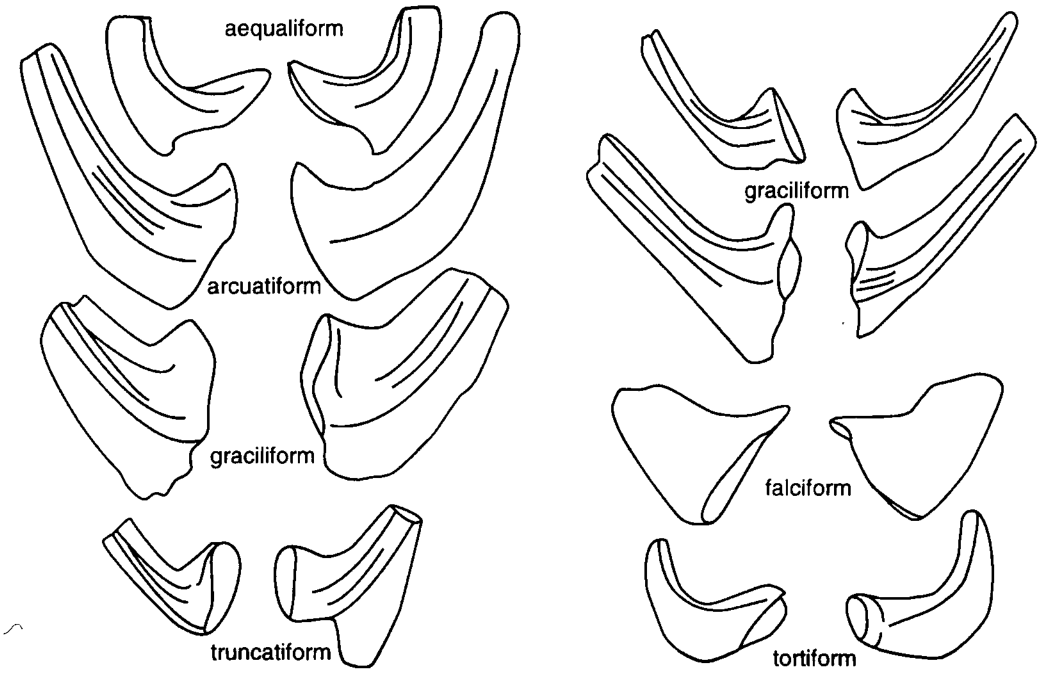
EXPLANATION OF PLATE 3

Figs 1–15, 17–18. *Protopanderodus varicostatus* (Sweet and Bergström, 1962); Winkston. 1–2, 9–15, 17–18, sample D156. 1–2, GLAHM Y 393; ae element. 9–12, anterior and posterior views of qg elements; 9–10, GLAHM Y 397; 11–12, GLAHM Y 398. 13–14, GLAHM Y 399; anterior and posterior views of pf element. 15, GLAHM Y 400; qt element. 17–18, GLAHM Y 402; pt element. 3–8, sample D160. 3–4, GLAHM Y 394; anterior and posterior views of qa element. 5–6, GLAHM Y 395; anterior and posterior views of qg element. 7–8, GLAHM Y 396; anterior and posterior views of qt element, 7 taken before large anticusp was lost.

Fig. 16. *Pseudooneodotus* sp. indet.; GLAHM Y 401; sample D209, Glencotho Farm.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.

ARMSTRONG, *Protopanderodus*, *Pseudooneotodus*



TEXT-FIG. 5. Line drawings of elements placed in *Protopanderodus varicostatus* (Sweet and Bergström, 1962) and figured in Plate 3. Homologies are suggested with the apparatus plan of *Panderodus* (Sansom *et al.* 1995): graciliform (qg element), truncatiform (qt), arcuatiform (qa) falciform (pf), tortiform (pt) and aequaliform (ae).

Order PROTOPANDERODONTIDA Sweet, 1988

Remarks. Protopanderodontida includes conodonts from a number of clades (Aldridge and Smith 1993) bearing apparatuses comprising longitudinally costate and striated, coniform elements. Most of the members of Protopanderodontida appear to have a panderodontid apparatus plan but lack the incised and torted furrow typical of panderodontids. The homologous structure appears to be formed from well-developed costae.

Family PROTOPANDERODONTIDAE Lindström, 1970

Genus PROTOPANDERODUS Lindström, 1971

Type species. Acontiodus rectus Lindström, 1955*a*.

Protopanderodus varicostatus (Sweet and Bergström, 1962)

Plate 3, figures 1–15, 17–18; Text-figure 5

*1962 *Scolopodus varicostatus* Sweet and Bergström, p. 1247, pl. 168, figs 4–9; text-fig. 1A, C, K.
1962 *Scandodus unistriatus* Sweet and Bergström, p. 1245, pl. 168, fig. 12; text-fig. 1E.

1964 *Scolopodus varicostatus* Sweet and Bergström; Hamar, p. 284, pl. 1, figs 1–2; text-fig. 4, 7a–b.
1964 *Scandodus lunatus* Hamar, p. 281, pl. 2, figs 16–17.
?1966 *Scandodus unistriatus* Sweet and Bergström, Hamar, p. 74, pl. 3, figs 1, 7.
?1966 *Scolopodus insculptus* (Branson and Mehl); Hamar, p. 75, pl. 1, fig. 18; text-fig. 2, 1.
1969 *Scolopodus varicostatus* Sweet and Bergström; Bradshaw, p. 1163, pl. 132, fig. 10; pl. 134, figs 12–13.
1969 *Scandodus unistriatus* Sweet and Bergström, Bradshaw, p. 1161, pl. 135, figs 5–6.
1971 '*Scandodus*' *unistriatus* Sweet and Bergström, Bergström, p. 92, figs 4–5.
1973 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström, p. 272, figs 5–9.
1974 *Scolopodus varicostatus* Sweet and Bergström; Viira, p. 123, pl. 5, figs 23–24; text-fig. 160.
1974 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström *et al.*, pl. 1, figs 9–10.
1978 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström, pl. 79, figs 6–7.
1978? *Protopanderodus* cf. *varicostatus* (Sweet and Bergström); Löfgren, p. 91, pl. 3, figs 26–31.
1978 *Protopanderodus varicostatus* (Sweet and Bergström); Tipnis *et al.*, pl. 8, figs 8, 12.
1980 *Protopanderodus varicostatus* (Sweet and Bergström); Simes, pl. 1. fig. 6.
1981 *Protopanderodus varicostatus* (Sweet and Bergström); Gastil and Miller, fig 2j–k.
1983 *Protopanderodus varicostatus* (Sweet and Bergström); An *et al.*, p. 132, pl. 16, figs 9–12.
1983 *Protopanderodus varicostatus* (Sweet and Bergström); Burrett *et al.*, p. 184, figs C–D.
1983 *Protopanderodus varicostatus* (Sweet and Bergström); Dzik, figs 3–29.
1984 *Protopanderodus varicostatus* (Sweet and Bergström); Nowlan and Thurlow, p. 293, pl. 2, figs 1–3, 8.
1984 *Protopanderodus varicostatus* (Sweet and Bergström); Chen and Zhang, pl. 3, figs 36–38.
1985 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström and Orchard, pl. 2.3, fig. 5.
1987 *Protopanderodus varicostatus* (Sweet and Bergström); Bauer, p. 27, pl. 3, figs 19, 21–23.
1990 *Protopanderodus varicostatus* (Sweet and Bergström); Pohler and Orchard, pl. 2, figs 16–17.
?1990 *Protopanderodus giganteus* (Sweet and Bergström); Pohler and Orchard, pl. 2, fig. 15.
1991 *Protopanderodus varicostatus* (Sweet and Bergström); Marquis and Nowlan, pl. 1, figs 24–25.
1994 *Protopanderodus varicostatus* (Sweet and Bergström); Dzik, p. 74, pl. 14, figs 1–5; text-fig. 11b.

Holotype. *Scolopodus varicostatus* Sweet and Bergström, 1962 from the Pratt Ferry Formation (middle Ordovician), Alabama.

Emended diagnosis. A species of *Protopanderodus* comprising robust, strongly costate q elements with moderately flared bases; acostate pf and costate and strongly curved pt elements.

Description. Symmetrical, aequaliform, continuously upwardly recurved ae element bearing a single costa and deep groove on upper part of each face (Pl. 3, figs 1–2). Upper edge flat. Short base extended upwards as a long heel and downwards as a short anticusp.

Broad, erect, arcuatiform qa element with smooth outer face and multicostate inner (bowed) face (Pl. 3, figs 3–4). Upper and lower edges sharp, the latter extended as an apically narrowing keel. Up to four costae situated in upper half of inner face; outer two most prominent; all costae separated by narrow grooves. Costae terminate short of basal margin. Base extended upwards as a short heel.

Short, recurved, sub-symmetrical, tortiform qt element; upper edge shallowly concave with lateral margins extended as costae; lower edge bears a broad keel which extends downwards as a very prominent anticusp (Pl. 3, figs 7–8). Lateral faces bear two lower and a single upper costa, all separated by deep V-shaped grooves. Costae terminate short of basal margin. Base short and inflated, may bear weakly developed basal wrinkles.

Sub-symmetrical, graciliform qg elements; straight, erect or continuously upwardly curved, with two costae on inner face and three on outer (Pl. 3, figs 5–6, 9–12). Additional minor costae may be present at base of cusp. Major costae extend almost to basal margin. Lower edge with a narrow keel and short anticusp, upper edge shallowly concave and extended upwards as a short heel in straight and erect specimens. The range of morphologies exhibited by these elements suggests that they may have occupied more than one position in the apparatus.

Acostate, falciform pf element; slightly bowed towards inner face (Pl. 3, figs 13–14). Short base; broad cusp with prominent keel on upper edge. Base extended upwards as a sinuously curved heel.

Narrow pt element, laterally compressed, sub-symmetrical, tortiform, continuously upwardly curved (Pl. 3, figs 17–18). Base narrow and twisted inwards. Cusp broadens to midheight before tapering apically. Two costae, close to upper margin on both lateral faces, sub-symmetrically arranged.

Remarks. The pf and ae elements have not been previously included in the apparatus. The specimen figured by Hamar (1966, pl. 1, fig. 18) appears to be an ae element with three major costae crossing the base. *P. varicostatus* ae elements from the Tweeddale Member have only two major costae. Dzik (1994, p. 75) noted that *P. varicostatus* can be distinguished from the younger *P. liripipus*, which has a more broadly flaring base. As reconstructed, *P. varicostatus* has an apparatus plan similar to that proposed for *Drepanodus* by Dzik (1994, fig. 9). The qg elements of *D. robustus* (Dzik 1994, p. 70) have prominent multiple costae on the upper margins, a convergent feature shared with species of *Protopanderodus*.

Genus WALLISERODUS Serpagli, 1967

Type species. Acodus curvatus Branson and Branson, 1947, by subsequent designation of Cooper (1975, p. 995).

Diagnosis. Refer to Cooper (1975, p. 995).

Remarks. Armstrong (1990) reconstructed the apparatus of Silurian *Walliserodus* demonstrating that it possessed a panderodontid plan. It is not clear whether Ordovician and Silurian *Walliserodus* are congeneric.

Walliserodus ethingtoni (Fåhræus, 1966)

Plate 5, figures 10–12.

*1966 *Panderodus ethingtoni* Fåhræus, p. 26, pl. 3, fig. 5a–5b.
1974 *Walliserodus ethingtoni* (Fåhræus); Bergström *et al.*, pl. 1, fig. 12.
1981 *Walliserodus ethingtoni* (Fåhræus); Fåhræus and Hunter, p. 1180, pl. 3, figs 11–16; text-fig. 6A–H.
1994 *Walliserodus ethingtoni* (Fåhræus); Dzik, p. 56, pl. 12, figs 7–10, 15–19; text-fig. 2b.

Holotype. Fåhræus (1966, pl. 3, fig. 5a–5b); specimen LO 4122 T; middle Ordovician; Gullhögen Quarry, Sweden.

Diagnosis. Refer to that of Dzik (1994, p. 56).

Remarks. An incomplete apparatus comprising geniculate ae and sub-symmetrical, recurved qg elements is recognized. These bear the characteristic, paired longitudinal costae of the holotype. Löfgren (1978, p. 114) and Stouge (1984, p. 64) recorded symmetrical and asymmetrical elements.

EXPLANATION OF PLATE 4

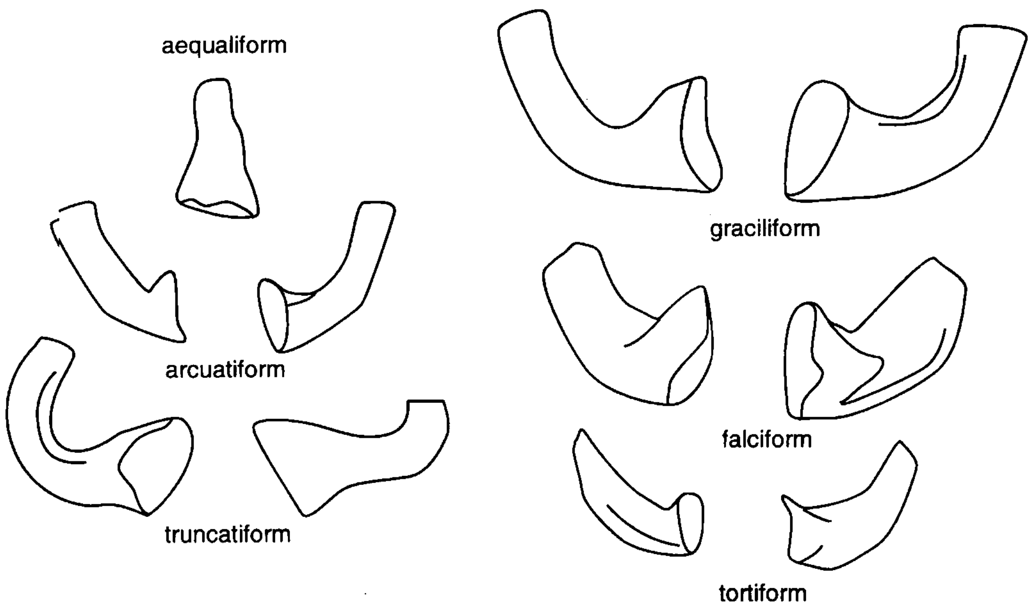
Figs 1–7. *Pygodus anserinus* Lamont and Lindström, 1957; sample D156, Winkston. 1–3, Pa elements; 1, GLAHM Y 403; 2, GLAHM Y 404; 3, GLAHM Y 405. 4, GLAHM Y 406; Pb element. 5, GLAHM Y 407; Pc element. 6, GLAHM Y 408; M element. 7, GLAHM Y 409; Sc element.

Figs 8–11. *Spinodus spinatus* (Hadding, 1913); Winkston. 8–10, sample D160; 8, GLAHM Y 410; 9–10, GLAHM Y 411. 11, GLAHM Y 412; sample D156.

Figs 12–22. *Cornuodus longibasis* (Lindström, 1955*a*); sample 209, Glencotho Farm. 12, GLAHM Y 413; ae element. 13–14, GLAHM Y 414; anterior and posterior views of qa element. 15–16, GLAHM Y 415; anterior and posterior views of qg element. 17–18, GLAHM Y 416; anterior and posterior views of qt element. 19–20, GLAHM Y 417; anterior and posterior views of pf element. 21–22, GLAHM Y 418; anterior and posterior views of pt element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.

ARMSTRONG, *Pygodus*, *Spinodus*, *Cornuodus*



TEXT-FIG. 6. Line drawings of elements placed in *Cornuodus longibasis* (Lindström, 1955*a*) and figured in Plate 4. Homologies are suggested with the apparatus plan of *Panderodus* (Sansom *et al.* 1995): graciliform (qg element), truncatiform (qt), arcuatiform (qa) falciform (pf), tortiform (pt) and aequaliform (ae).

Walliserodus aff. *W. sancticlairi* Cooper, 1976

Plate 5, figures 6–9

Remarks. Elements referred to this species comprise thin-walled, deeply excavated cones. The characteristic ae element bears two lateral costae along the lower edge, making it triangular in cross section. A similar element was described as *W.* cf. *W. sancticlairi* Cooper from the Lower Silurian of North Greenland (Armstrong 1990). The arcuatiform and ae elements in the Ordovician species have more prominent upper edge keels. *W. sancticlairi* Cooper consists of slender cones with a similar basal outline but more prominent costae on the ae and arcuatiform elements. Dzik (1994, p. 57) noted that during evolution *W. ethingtoni* elements became more prominently ornamented and thinner walled. The presence of only weakly developed costae in *W.* aff. *W. sancticlairi* appears to distinguish this form.

Family CORNUODONTIDAE Stouge, 1984

Remarks. Cornuodus is currently retained in the Cornuodontidae, but *C. longibasis* appears to have a panderodontid apparatus plan. If this can be confirmed for other species, then this feature and the absence of an incised and torted longitudinal furrow would warrant the transfer of this genus to the Protopanderodontidae Lindström, 1970.

Genus CORNUODUS Fåhræus, 1966

Type species. Cornuodus erectus Fåhræus, 1966, p. 20.

Emended diagnosis. A protopanderodontid with acostate, short, recurved, sub-circular, conical q elements and laterally compressed, keeled pf and pt elements. The q elements have a faint groove along the upper edge. All elements are both faintly microstriate and deeply excavated.

Remarks. Löfgren (1978, p. 49) considered *Drepanodus longibasis* Lindström and *Cornuodus erectus* Fåhræus to be conspecific, and included symmetrical and asymmetrical elements in the apparatus of *Cornuodus longibasis*. *Cornuodus* can be distinguished from *Scalpellodus* Dzik by the less prominent microstriations. Both genera appear to have a panderodontid apparatus plan and are probably closely related. Dzik (1994, p. 61) suggested a close similarity between the apparatus organization of *Cornuodus* and *Dapsilodus*. The panderodontid apparatus plan, and qt and qg elements with a rounded rather than oval cross section would suggest a closer relationship between *Cornuodus* and *Drepanodus*.

Cornuodus longibasis (Lindström, 1955*a*)

Plate 4, figures 12–22; Text-figure 6

*1955*a* *Drepanodus longibasis* Lindström, p. 564, pl. 3, fig. 31.
1966 *Cornuodus erectus* Fåhræus, p. 20, pl. 2, fig. 8a–b; text-fig. 2B.
1967 *Cornuodus erectus* Fåhræus; Serpagli, p. 57, pl. 12, figs 5a–8b.
1967 *Scandodus*? *lanzaensis* Serpagli, p. 95, pl. 26, figs 4a–7d.
1967 *Cornuodus bergstroemi* Serpagli, p. 57, pl. 12, figs 1a–2c.
?1969 *Drepanodus longibasis* Lindström; Bednarczyk, pl. 2, fig. 2.
1970 '*Cornuodus*' *longibasis* (Lindström); Serpagli, p. 43, pl. 7, fig. 2a–b; pl. 20, fig. 12.
1974 '*Cornuodus*' *longibasis* (Lindström); Serpagli, p. 43, pl. 7, fig. 2a–b; pl. 20, fig. 12.
1974 *Protopanderodus longibasis* (Lindström); van Wamel, p. 92, pl. 4, figs 4–6.
1976 *Cornuodus longibasis* (Lindström); Landing, p. 631, pl. 1, figs 12–13, 15.
1976 *Scalpellodus* (?*Cornuodus*) *laevis* Dzik, p. 421, pl. 41, fig. 1; text-fig. 13a–c.
1978 *Cornuodus longibasis* (Lindström); Löfgren, pl. 4, figs 36, 38–42; text-fig. 25A–C.
1978 *Cornuodus bergstroemi*; Löfgren, pl. 2, fig. 37; text-fig. 25D.
1984 *Cornuodus longibasis* (Lindström); Stouge, p. 62, pl. 8, figs 1–8.
1988 *Cornuodus longibasis* (Lindström); Stouge and Bagnoli, p. 114, pl. 1, figs 20–21.
1991 *Cornuodus longibasis* (Lindström); Stouge and Bagnoli, p. 14, pl. 3, figs 3–7.
p1994 *Cornuodus longibasis* (Lindström); Dzik, p. 61, pl. 11, figs 9–13; text-fig. 4a (*non* sp element).

Holotype. Lindström (1955*a*, pl. 3, fig. 31); Upper Planilimbata Limestone (Arenig); Lanna near Orebo, Sweden.

Diagnosis. Refer to Dzik (1994, p. 62).

Description. Conical, entirely excavated ae element approximately twice as long as wide (Pl. 4, fig. 12).

Sub-symmetrical, arcuatiform qa element with short sub-circular base extended upwards as a short heel (Pl. 4, figs 13–14). Cusp circular in cross section, recurved and flexed at midheight. The qt element is similar to qa; truncatiform, strongly recurved particularly above midheight (Pl. 4, figs 17–18). Base more prominently flared and extends downwards as a short anticusp. A shallow groove runs along upper edge. The qg element is difficult to distinguish from qa element (Pl. 4, figs 15–16). Graciliform, basal heel absent, base more circular in cross section and cusp lacking midheight flexure. Faint groove along upper edge.

Falciform pf element with upper and lower edge keels (Pl. 4, figs 19–20). Slightly inwardly bowed, with base inflated on inner side. The pt element is similar to the pf, smaller, with keel only on the lower edge (Pl. 4, figs 21–22). Base more markedly twisted towards inner face.

Remarks. Löfgren (1978) first identified the main element types in *Cornuodus* and the distinction between the species. The qt and qg elements have a very generalized morphology. Dzik (1994, p. 61; fig. 4) included a geniculate 'sp' element in his reconstruction. This type of element has not been found. The pf and pt elements are laterally compressed.

Family DAPSILODONTIDAE Sweet, 1988

Genus DAPSILODUS Cooper, 1976

Type species. Distacodus obliquicostatus Branson and Mehl, 1933*a*, p. 41.

Remarks. The type species has an apparatus which comprises multiple pairs of qg elements, a pair of pf elements and a single ae element (see Armstrong 1990, for a review). Two species of *Dapsilodus* are distinguished, both with the typical apparatus plan.

Dapsilodus mutatus (Branson and Mehl, 1933*c*)

Plate 1, figures 3–8

*1933*c* *Belodus* (?) *mutatus* Branson and Mehl, p. 126, pl. 10, fig. 17.
1976 *Panderodus* (*Dapsilodus*) *mutatus* (Branson and Mehl); Dzik, fig. 15g–i.
1994 *Dapsilodus mutatus* (Branson and Mehl); Dzik, p. 64, pl. 11, figs 24–26, 31–35; pl. 14, figs 8–9; text-fig. 6d.

Holotype. Branson and Mehl (1933*c*, pl. 10, fig. 17). From the upper Ordovician, Thebes Sandstone, Ozora, Missouri.

Remarks. An apparatus comprising a laterally compressed ae element, qg elements with a large upper edge keel and pf elements which are keeled, small and geniculate. The Silurian species *Dapsilodus obliquicostatus* (Branson and Mehl, 1933*a*) has a similar trimembrate apparatus (Armstrong 1990), including a recurved pf element.

Dapsilodus aff. *D. obliquicostatus* (Branson and Mehl, 1933*a*)

Plate 1, figures 9–11

Remarks. Element morphologies are similar to those in *Dapsilodus mutatus* (Branson and Mehl). The qg lacks the well-developed upper edge keel (Pl. 1, fig. 10). The pf element is recurved and the base is extended upwards as a short heel and downwards as a short anticusp (Pl. 1, fig. 11). These are characters found in the Silurian species *D. obliquicostatus* (Branson and Mehl, 1933*a*). Hamar

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EXPLANATION OF PLATE 5

Figs 1–5. *Strachanognathus parvus* Rhodes, 1955; sample D156, Winkston. 1, GLAHM Y 419; qt element. 2, GLAHM Y 420; ?ae element. 3, GLAHM Y 421; ?pf element. 4, GLAHM Y 422; qg element. 5, GLAHM Y 423; qa element.

Figs 6–9. *Walliserodus* aff. *W. santiclairi* Cooper, 1976; sample D156, Winkston. 6, GLAHM Y 424; ?pf element. 7, specimen 619/30; qa element. 8, GLAHM Y 425; qg element. 9, GLAHM Y 426; ae element.

Figs 10–12. *Walliserodus ethingtoni* (Fåræhus, 1966); sample D209, Glencotho Farm. 10, GLAHM Y 429; ae element. 11–12, GLAHM Y 428; qg element.

Figs 13–18. Gen. et sp. indet.; sample D209, Glencotho Farm. 13, GLAHM Y 430; Pa element. 14, GLAHM Y 431; Pb element. 15, GLAHM Y 432; M element. 16, GLAHM Y 433; Sa element. 17, GLAHM Y 434; Sb1 element. 18, GLAHM Y 435; Sb2 element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.

ARMSTRONG, Ordovician conodonts

(1966, pl. 2, figs 3–9, 13) illustrated identical specimens as *Acodus similaris* Rhodes, from the middle Ordovician of the Oslo region, Norway.

Family DREPANOISTODONTIDAE Sweet, 1988

Genus DREPANOISTODUS Lindström, 1971

Type species. Oistodus forceps Lindström, 1955*a*.

Drepanoistodus suberectus (Branson and Mehl, 1933*b*)

Plate 1, figures 12–23; Text-figure 7

*1933*b* *Oistodus suberectus* Branson and Mehl, p. 111, pl. 9, fig. 7.
1933*b* *Oistodus curvatus* Branson and Mehl, p. 110, pl. 9, figs 4, 10, 12.
1933*b* *Oistodus inclinatus* Branson and Mehl, p. 110, pl. 9, fig. 8.
1933*c* *Drepanodus incurvus* (Hinde); Branson and Mehl, p. 154, pl. 12, fig. 11.
1955*a* *Drepanodus homocurvatus* Lindström, p. 563, pl. 2, figs 23–24, 39.
1955*a* *Drepanodus suberectus* (Branson and Mehl); Lindström, p. 568, pl. 2, figs 21–22.
1966 *Drepanodus suberectus* Branson and Mehl; Bergström and Sweet, p. 330, pl. 35, figs 22–27.
1988 *Drepanoistodus suberectus* (Branson and Mehl); Nowlan *et al.*, p. 16, pl. 3, figs 19–22.
1990 *Drepanoistodus suberectus* (Branson and Mehl); Armstrong, p. 130, pl. 22, figs 7–10.
1994 *Drepanoistodus suberectus* (Branson and Mehl); Dzik, p. 78, pl. 17, figs 2–6; text-fig. 12b.

Holotype. Branson and Mehl (1933*b*, pl. 9, fig. 7). From the middle Ordovician, Plattin Formation, Jefferson County, Missouri.

Diagnosis. Refer to Armstrong (1990, p. 130).

Description. All elements have been described previously (see synonomy). In general, specimens from the Tweeddale Member are smaller than at equivalent levels in the Appalachians. The ae element has a broader basal margin than upper Ordovician examples.

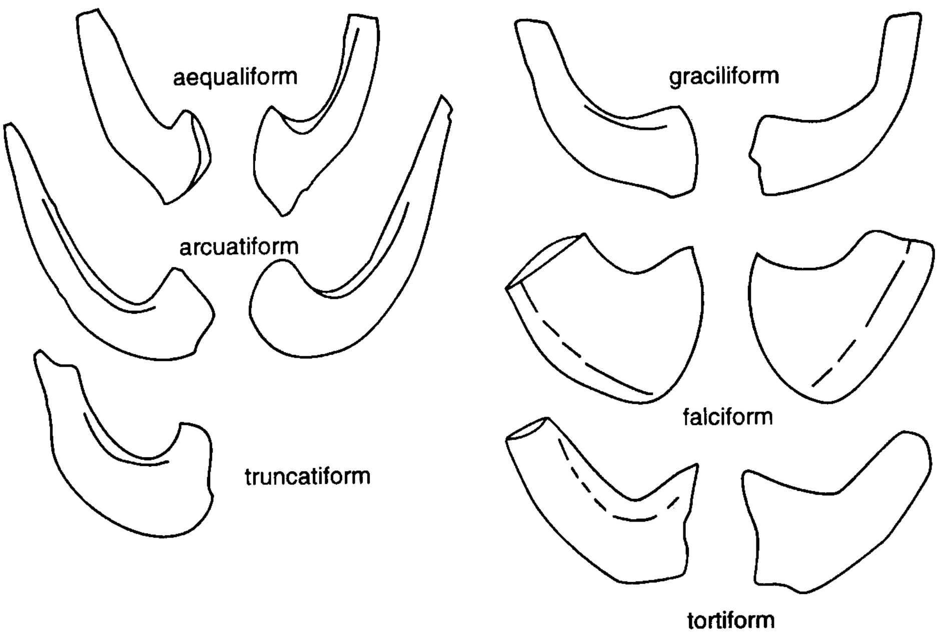
Remarks. A widely known species from the North Atlantic and American Midcontinent Provinces in mid and late Ordovician strata. Considerable variation occurs in the basal outline of the qg, qt and qa elements which Carnes (1975, pp. 129–132), and Bauer (1987, p. 16) divided into three (homocurvatiform) integrading morphotypes.

Family STRACHANOGNATHIDAE Bergström, 1981*b*

Genus STRACHANOGNATHUS Rhodes, 1955

Type species. Strachanognathus parvus Rhodes, 1955, p. 132.

Remarks. Striate coniform elements have commonly been attributed to species of *Scolopodus* Pander, *Staufferella* Sweet *et al.* and *Parapanderodus* Stouge. *Parapanderodus* species appear to have a trimembrate apparatus (Smith 1991, p. 48). The gross similarity in the proposed plans of *Parapanderodus* and *Strachanognathus* suggests that they are members of the same family. Protopanderodontidae contains taxa in which elements in the anterior and posterior domains of the apparatus are morphologically similar. Strachanognathidae is retained for coniform taxa with markedly distinct elements in the anterior and posterior domains. The qt element in these taxa is



TEXT-FIG. 7. Line drawings of elements placed in *Drepanoistodus suberectus* (Branson and Mehl, 1933*b*) and figured in Plate 1. Homologies are suggested with the apparatus plan of *Panderodus* (Sansom *et al.* 1995): graciliform (qg element), truncatiform (qt), arcuatiform (qa), falciform (pf), tortiform (pt) and aequaliform (ae).

closer morphologically to the elements in the posterior domain. In the absence of recognized posterior domain elements *Parapanderodus* is transferred tentatively to the Strachanognathidae.

Strachanognathus parvus Rhodes, 1955

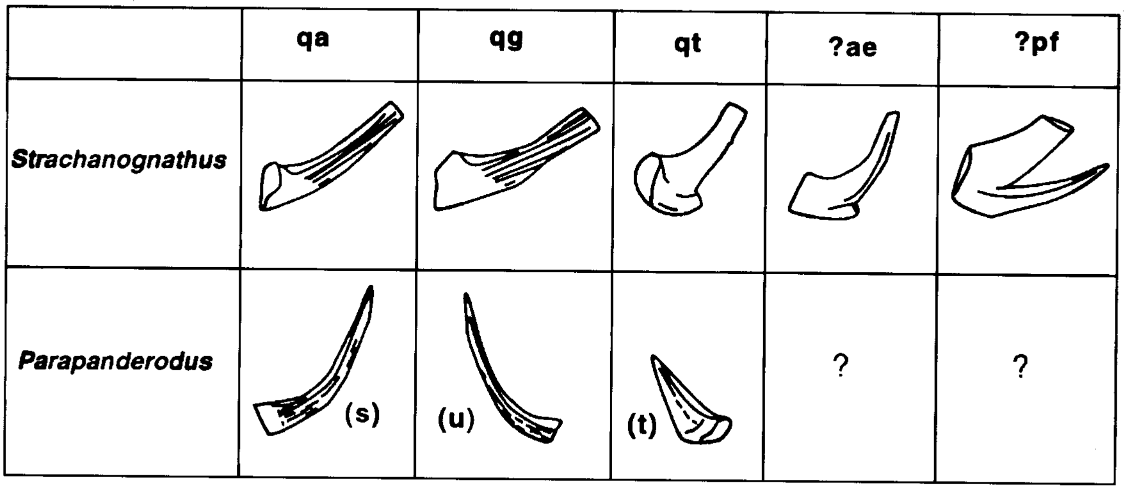
Plate 5, figures 1–5; Text-figure 8

*1955 *Strachanognathus parvus* Rhodes, p. 132, pl. 7, fig. 16; pl. 8, figs 1–4.
1962 *Strachanognathus parvus* Rhodes; Bergström, p. 54, pl. 3, figs 1–6; text-figs 2B, 3H–I.
1964 *Strachanognathus parva* Rhodes; Lindström, p. 140, text-fig. 48K.
1974 *Strachanognathus parvus* Rhodes; Bergström *et al.*, pl. 1, fig. 7.
1976 *Strachanognathus parvus* Rhodes; Dzik, p. 444, text-fig. 14j–k.
1978 *Strachanognathus parvus* Rhodes; Löfgren, p. 112, pl. 1, fig. 29.
1978 *Strachanognathus parvus* Rhodes; Palmeri, p. 27, pl. 6, figs 27–28.
1979 *Strachanognathus parvus* Rhodes; Rhodes; Kennedy *et al.*, p. 550, pl. 1 fig. 24.
1980 *Strachanognathus parvus* Rhodes; Orchard, p. 26, pl. 4, figs 34–35.
1981 *Strachanognathus parvus* Rhodes; Nowlan, p. 13, pl. 3, fig. 18; pl. 5, fig. 5.
1982 *Strachanognathus parvus* Rhodes; Lenz and McCracken, pl. 2, fig. 21.
1984 *Strachanognathus parvus* Rhodes; Stouge, p. 57, pl. 5, fig. 9.
1985 *Strachanognathus parvus* Rhodes; Bergström and Orchard, pl. 2.3, fig. 1.
1990 *Strachanognathus parvus* Rhodes; Bergström, pl. 1, fig. 10.
1990 *Strachanognathus parvus* Rhodes; Pohler and Orchard, pl. 1, fig. 6.
1991 *Strachanognathus parvus* Rhodes; McCracken, p. 52, pl. 2, fig. 36.
1994 *Strachanognathus parvus* Rhodes; Dzik, p. 62, pl. 13, figs 1–6; text-fig. 5.

Holotype. Rhodes (1955, pl. 8, figs 1–4). From the Keisley Limestone, Westmoorland.

Emended diagnosis. Quinquimembrate, comprising short based, laterally compressed elements with prominent cusps show varying degrees of upward and inward curvature. These include an inwardly twisted qa element, recurved ?ae element and bowed ?pf element; all bear a single, keeled and microstriate denticle. Erect qa and qg elements are densely striate.

Description. The ?ae element is similar to qt element, laterally compressed rather than bowed and with recurved cusp (Pl. 5, fig. 2). The qa element is similar to the qg element, base twisted inwards relative to cusp (Pl. 5, fig. 5). Basal cavity with a slight, inwardly and upwardly oblique flare. The qg element is laterally compressed, short based; cusp erect, striate, with upper edge extended as a low keel (Pl. 5, fig. 4). Basal cavity outline symmetrical and lacking flare. The qt element is inwardly bowed; cusp inwardly flexed with faint longitudinal striations (Pl. 5, fig. 1). Prominent groove runs close to and parallels lower edge of cusp. A single large, microstriate denticle fused to lower edge of cusp, with parallel curvature. Upper edge of denticle extended as a narrow keel. Basal cavity narrow with moderate inward flare. The ?pf element is similar to the ?ae element, cusp erect rather than recurved, inwardly bowed (Pl. 5, fig. 3).



TEXT-FIG. 8. Comparison of homologous elements in *Strachanognathus* (proposed herein) and *Parapanderodus* (*sensu* Smith 1991, text-fig. 8). Locations are designated in comparison with *Panderodus* (Sansom *et al.* 1995). The locational terminology applied by Smith (1991) is placed in brackets.

Remarks. The decision of Armstrong *et al.* (1996) to include striate elements in the apparatus of *S. parvus* was based upon comparison with other coniform apparatus plans; co-occurrence and the morphological similarities in the denticles of the qa-qg elements and in the cusps of the pf-pt elements. Both groups of elements bear striations, although these are less obvious in the qa-qg elements. Lenz and McCracken (1982, pl. 2, fig. 21) illustrated an Ashgill q element of *S. parvus* with oblique striations on the denticle. All the elements in the new apparatus reconstruction have been recognized in samples from the Tweeddale Member, the Stinchar Limestone (Bergström 1990) and Ashgill samples from the Dent Group, English Lake District (Orchard 1980; Armstrong *et al.* 1996). Dzik (1994, p. 60) recorded the striate coniform species *Scolopodus peselephantis* Lindström co-occurring with *S. parvus* in samples from the *A. tvaerensis* Biozone, Mójcza Limestone, Poland.

Element location has been assigned *a priori* and is based upon the *Parapanderodus* plan (*sensu* Smith 1991; Text-fig. 9). The diagenetically fused cluster illustrated by Smith (1991, fig. 29c–d) contains in order, a single large 'qa' element, a pair of 'qg' elements, a single, compressed and twisted 'qt' element and a further pair of 'qg' elements. Homology is suggested with the anterior domain of the *Panderodus* apparatus. The posterior domain (pf and pt elements) and ae element are not preserved in the cluster. In the discrete collections of the Tweeddale Member, two additional elements are present. These have been assigned questionably as the ae element and pf element. A pt element has not been recognized.

Order PANDERODONTIDA Sweet, 1988
Family PANDERODONTIDAE Lindström, 1970
Genus PANDERODUS Ethington, 1959

Type species. Paltodus unicostatus Branson and Mehl, 1933*a*, p. 42.

Panderodus aff. *P. recurvatus* Rhodes, 1953

Plate 2, figures 10–12

Remarks. Rare elements attributable to *Panderodus* species are present in all samples, except D153. In the absence of a complete apparatus it is difficult to speciate these, but the general morphology suggests that they belong to a single species. The qg (Pl. 2, fig. 10) and pf (Pl. 2, fig. 11) elements suggest an affinity with *Panderodus recurvatus* Rhodes.

Order and Family Unknown
Genus SPINODUS Dzik, 1976

Type species. Cordylodus spinatus Hadding, 1913.

Remarks. Lindström (1964) recognized a symmetry transition series including three elements previously described as *C. ramosus* Hadding and *C. spinatus* (Hadding). Uyeno and Barnes (1969) added a fourth element to *C. spinatus*. Barnes and Poplawski (1973) described a quadrimembrate apparatus for *C. ramosus*.

Spinodus spinatus (Hadding, 1913)

Plate 4, figures 8–11

*1913 *Polygnathus spinatus* Hadding, p. 32, pl. 1, fig. 8.
1913 *Cordylodus ramosus* Hadding, p. 31, pl. 1, fig. 6.
1976 *Cordylodus spinatus* (Hadding); Dzik, 424, text-fig. 21c.
1981 *Spinodus ramosus* (Hadding); Nowlan, p. 15, pl. 4, figs 18–19.
1985 *Spinodus spinatus* (Hadding); Bergström and Orchard, pl. 2.2, figs 1–4.
1991 *Spinodus spinatus* (Hadding); McCracken, p. 52, pl. 1, fig. 2.
1994 *Spinodus spinatus* (Hadding); Dzik, p. 113, pl. 24, figs 22–25; text-fig. 32.

Holotype. Hadding (1913, pl. 1, fig. 8); specimen LO 2347 t (mouldic preservation); *Climacograptus haddingi* GBZ (= *Climacograptus putillus* in Hadding, 1913) of Fågelsång, near Lund (upper part of section E15).

Remarks. The fragmentary nature of the specimens attributed to *S. spinatus* does not allow an apparatus to be reconstructed. Two categories of elements can be distinguished. 'Coniforms' (Pl. 4, figs 8–10) have long curved cusps and inflated bases; the latter may be extended as a short posterior process. 'Ramiforms' (Pl. 4, fig. 11) develop processes with widely spaced sub-circular denticles and a recessive basal margin. Specimen abundances in Table 1 include all fragments and are thus overestimates.

Genus PSEUDOONEOTODUS Drygant, 1974

Type species. Oneotodus (?) *beckmanni* Bischoff and Sannemann 1958, p. 98.

Diagnosis. Refer to Barrick (1977, p. 57).

Pseudooneotodus sp. indet.

Plate 3, figure 16

Remarks. A single uni-denticulate element was recovered from sample D209. Silurian species of *Pseudooneotodus* have an apparatus which comprises sinistral, dextral and symmetrical uni-denticulate and bi-denticulate or tri-denticulate elements (Armstrong 1990). It is not possible to distinguish species without the full apparatus.

Gen et sp. indet.

Plate 5, figures 13–18

Remarks. Elements attributable to a species of oulodontid-type are present in sample D209. The Pa element (Pl. 5, fig. 13) is similar to that found in *Periodon aculeatus*, although a single denticle on the anterior process is separated from the cusp. The poorly preserved Pb element appears to be bipennate (Pl. 5, fig. 14). The M element is dolabrate (Pl. 5, fig. 15) and two Sb elements are distinguished (Pl. 5, figs 17–18). These are separated on the style of the basal cavity flare beneath the cusp. In the Sb1 this is rounded and in the Sb2 extended as a narrow, short process.

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