

CARADOC-ASHGILL CONODONT FAUNAS FROM WALES AND THE WELSH BORDERLAND

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ABSTRACT. Twenty-two multi-element conodont species are described from Caradoc-Ashgill (Ordovician) strata sampled throughout Wales and the Welsh Borderland. *Plectodina bullhillensis*, *P. bergstroemi*, and *Prioniodus deani* are described as new species. Strata from the Costonian to Soudleyan stages appear to lie within the *tvaerensis* conodont Biozone, with Longvillian to ?Onnian strata in the *superbus* Biozone, and Pusgillian to Hirnantian strata in the *ordovicicus* Biozone, although in no sections are the zonal boundaries sharply defined. Contrasts in Colour Alteration Index suggest that the Caradoc-Ashgill rocks of the Welsh trough have been subjected to much higher geothermal temperatures than those on the Welsh Borderland platform.

THE starting point for modern work on conodonts of all ages in the British Isles was the description by Rhodes (1953) of four Lower Palaeozoic faunas from Wales and the Welsh Borderland, three from Ordovician rocks and one from Silurian. Given this initial impetus in Ordovician studies, and the fact that numerous faunas of this age have been described subsequently from virtually all parts of the world, it is somewhat surprising at first sight that very few further investigations have been made in the historical type areas of the Ordovician System within the Welsh region. In fact only three additional publications (Lindström 1959; Bergström 1964; Orchard 1980) contain systematic accounts of Ordovician conodont faunas from this area, covering seven discrete stratigraphical units over and above those described by Rhodes. To these should also be added Bergström's (1971*a*) wider biostratigraphical review, which does contain comments on undescribed faunas from other horizons and localities, plus brief mention of the correlative significance of a late Llandeilo (*Nemagraptus gracilis* Biozone) fauna from limestone blocks in the Garn Formation of Anglesey (Bergström 1981*b*) and other Llandeilo elements from the type area (Bergström *et al.* 1984). Some elements from South Wales and Shropshire were also noted and illustrated by Bergström (1983, pp. 50, 51, fig. 6A-H) in a discussion of Llandeilo-Caradoc correlations.

This somewhat limited systematic coverage has inevitably restricted the interpretation in the Welsh area of various aspects of Ordovician history based on conodonts, such as biostratigraphy, palaeobiogeography, and palaeotemperatures (e.g. see Bergström 1973, 1977, 1981*a* for summaries). However, the relative paucity of data is certainly not a reflection of lack of interest in the area but is a result of one dominant factor—the absence of stratigraphically and geographically widespread carbonate units suitable for the techniques of acid digestion that are now standard practice in conodont studies. Throughout both the platform and trough areas of the Wales-Welsh Borderland depositional basin, Ordovician sediments are developed mainly in clastic facies ranging from boulder down to clay grade, with a predominance of fine sands and silts; the relatively few, locally developed carbonate units in the sequence were naturally those first subjected to study for conodonts in the investigations referred to above. This has resulted in a somewhat piecemeal and restricted analysis of the faunas.

Notwithstanding the problems of extraction and stratigraphical/geographical coverage, our studies suggest that the potential for collecting further data on Ordovician conodont faunas in Wales and the Welsh Borderland is far from exhausted. Apart from the carbonate units already investigated, there are a number of other thin, lensoid limestone levels that have not been analysed, and there are also units of calcareous-cemented clastic strata in thin macro-shelly partings that can be broken down by standard techniques. This paper represents an attempt to expand our knowledge of

Ordovician conodont faunas from the region, first by concentrating on a limited part of the sequence (Caradoc and Ashgill) throughout the whole area, and secondly by systematic collecting through vertical sequences rather than from spot samples.

STRATIGRAPHY, LOCALITIES, COLLECTIONS

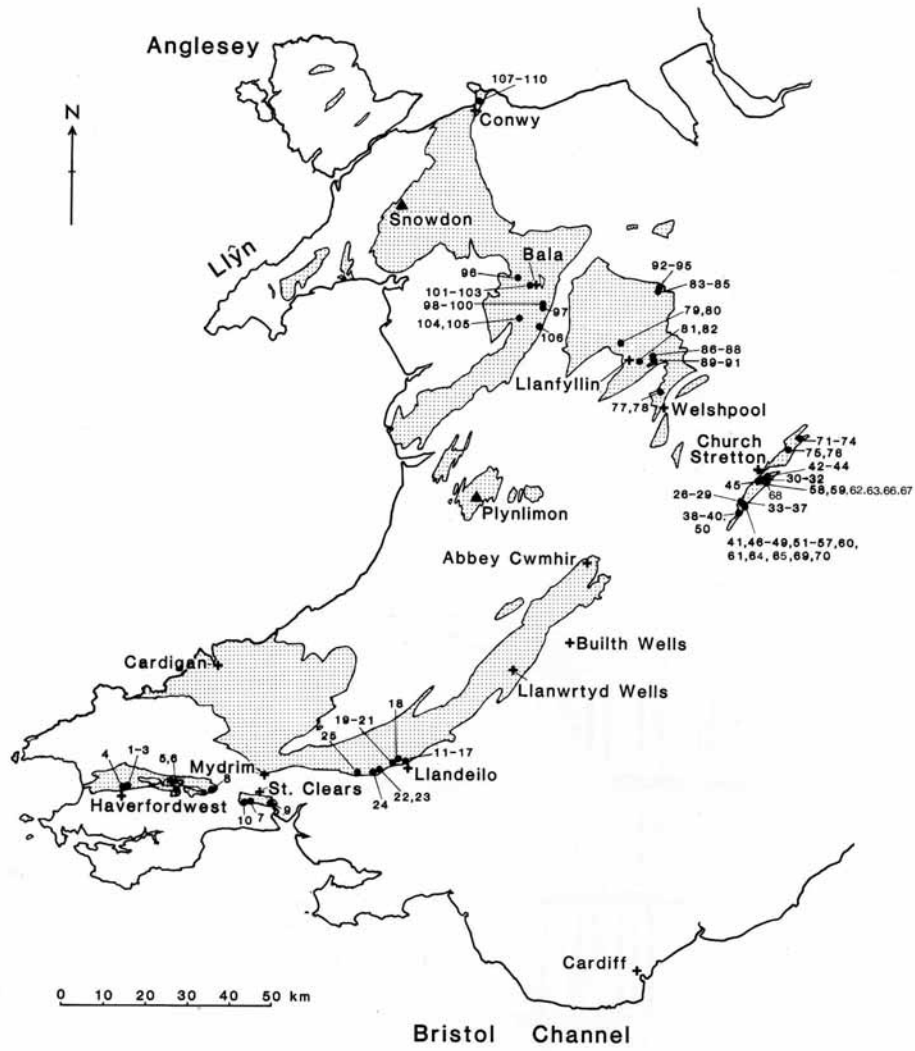
The geographical and stratigraphical coverage of our collections from Caradoc and Ashgill strata throughout Wales and the Welsh Borderland is shown in text-figs. 1–3. Within this coverage we collected 110 samples, ranging in weight from 1.5 kg up to about 4.0 kg, and of these there were forty-eight that yielded no conodont faunas. Text-fig. 4 shows the stratigraphical ranges of species from the forty more productive horizons represented in the collections, and Table 1 gives the yields of all elements in the same samples. Yields from all sixty-two productive samples are plotted in Table 2. As a means of reviewing and interpreting data from previous publications, these samples include new collections of those Caradoc–Ashgill faunas already known from the area. It must be admitted that the results of intensive collecting are still disappointing, and that there is still far from adequate knowledge of conodonts in the region, but our new faunas do represent a substantial increase in data and provide a further base for additional investigations. We believe it likely that many of the seemingly intractable sediments will produce biostratigraphically significant faunas if very large samples are collected in the future.

Williams *et al.* (1972) summarized the distribution of Caradoc–Ashgill sequences in Wales and the Welsh Borderland, and our sampling programme was based initially on this review. In the light of our conodont studies, any departures from this correlation scheme are shown in text-fig. 2 and discussed below. Full details of the stratigraphy and locality of all our 110 samples have been deposited with the British Library, Boston Spa, Yorks UK, as Supplementary Publication No. SUP 14024 (21 pages). They may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorks L23 7BQ. In addition, they are available from the Department of Geology, National Museum of Wales (NMW Geology Open File No. 2). For immediate reference, a summary of the data is given in the Appendix (p. 710). All collections referred to in this paper are housed in the National Museum of Wales (NMW) under Accession Numbers 81.4G, 81.5G, and 81.6G. In the text below, numbers in brackets refer to the sample numbers indicated in text-figs. 1–4 and Tables 1 and 2.

Stratigraphy and correlation (text-fig. 2)

South Wales. Our oldest productive samples (5, 6) from the south-western areas of the Caradoc–Ashgill outcrop (text-fig. 1) were from the Robeston Wathen Limestone in its type development to the west of St Clears (see Price 1973, pp. 231–234, figs. 2 and 3). On the basis of its apparent stratigraphical conformity below calcareous siltstones equivalent to the Sholeshook Limestone that bear a rich shelly fauna, the Robeston Wathen Limestone is dated firmly as early mid Ashgill in age, within Cautleyan zones 1–3 (Price 1973, fig. 6). From these beds we have recovered *Amorphognathus ordovicicus*, which accords well with the general acceptance of this species as an indicator of the Ashgill (e.g. Bergström 1983, fig. 1). Samples (1–4) in the type development of the Sholeshook Limestone further to the west near Haverfordwest were unproductive. Older beds in this region are mostly in graptolitic shales, but a report by Addison (*in* Williams *et al.* 1972, p. 36) suggests that some limestones previously thought to be of Llandeilo age include basal Caradoc (Costonian) shelly faunas; the same report mentions a conodont fauna from this horizon indicative of a *gracilis* graptolite Biozone age, but details are as yet unpublished and we have not collected further samples.

In the Llandeilo region, Price (1973, p. 244; 1984, p. 103) has summarized the shelly faunal evidence for assigning a late Purgillian to early Cautleyan age to the Birdshill and Crûg limestones (see also Owens 1973, p. 48). Correlation of these levels based on conodonts has been the subject of considerable discussion (cf. Bergström 1971a; Orchard 1980) but they have been placed consistently by all authors within the *superbus* Biozone, although Orchard (1980, p. 13) suggested that the Crûg may be the slightly younger of the two and close to the *superbus/ordovicicus* boundary. Our samples from both these horizons (11–17, Crûg Limestone; 19–25, Birdshill Limestone) contain similar faunas



TEXT-FIG. 1. Outcrop of Caradoc-Ashgill strata in Wales and the Welsh Borderland showing the geographical distribution of conodont samples 1-110.

(Table 1) suggesting a closely similar age, and include what we identify as abundant specimens of *A. ordovicicus* (see discussion below); there are no specimens identified as *A. superbus*. On this basis we see no evidence for a *superbus* age in either the Crûg or Birdshill limestones; their assignment to the *ordovicicus* Biozone is consistent with the early Ashgill age suggested by the shelly faunas and removes this otherwise anomalous extension of the *superbus* Biozone well above the top of the Caradoc. Fragmentary specimens illustrated by Orchard (1980, pl. 4, figs. 23, 26) as *A. cf. A. superbus* from the type Ashgill area of northern England (Cautleyan) are inadequate to show the characteristic features of the species.

An isolated limestone lenticle at Pen-y-banc (sample 18) to the north-west of Llandeilo, generally included previously in the Birdshill outcrop (e.g. see Pringle and George 1948, fig. 11), contains an anomalous fauna; here we identify *A. superbus* but no *A. ordovicicus*. We consider that these beds are probably of mid Caradoc age (text-fig. 2) and are unrelated to the Birdshill-Crûg limestones.

Welsh Borderland and eastern Wales. Most of the stages and lithostratigraphical divisions of the Caradoc Series in the south Shropshire type area (samples 26–76) have yielded conodonts (text-figs. 2 and 3), but they are rarely abundant in the dominantly clastic sediments. No diagnostic zonal forms have been recovered, and correlation with the conodont zonal scheme continues to be based on broader shelly faunal and graptolitic evidence in various areas of Europe (e.g. Bergström 1971a, b, 1977, 1978, 1983). Our collections in the upper part of the succession are based on the revised stratigraphy of Hurst (1979).

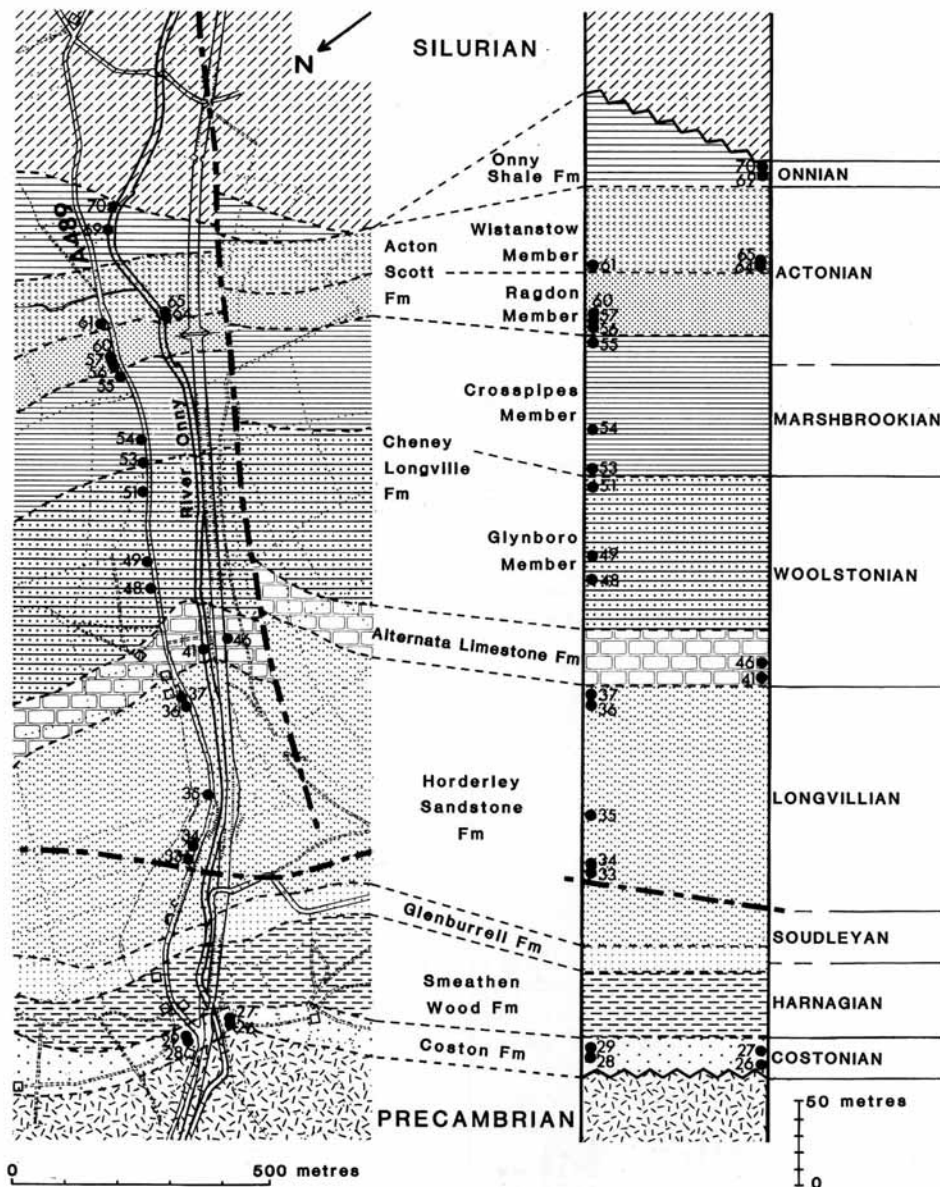
In the Gwern-y-Brain section near Welshpool (Cave 1965), two samples (77, 78) from the Nod Glas Formation have yielded fairly common faunas whose age interpretations are problematical. The uppermost Nod Glas beds here contain the trilobite *Onnia gracilis* indicative of the Onnian, while the unconformably underlying Gaerfawr Formation contains a Woolstonian shelly fauna (Cave 1965), so that the limits of the Nod Glas Formation are fairly well circumscribed by comparison with the Shropshire succession (text-fig. 2). However, conodonts from the basal 50 cm (sample 77) of the phosphoritic limestones making up the Nod Glas here contain fairly common *Plectrodina bullhillensis* sp. nov., which in Shropshire occurs only in samples from the Costonian to the Woolstonian. In addition the same sample contains *Amorphognathus* aff. *A. tvaerensis* (see p. 694), which again might support an earlier Caradoc age (?pre-mid Soudleyan—text-fig. 2). The full stratigraphical range of *P. bullhillensis* is not yet known from continuous, productive sections, but it cannot be ruled out that the base of the Nod Glas at Gwern-y-Brain is older than has been supposed previously, although the limit may be dictated by the Gaerfawr shelly fauna; it is also possible that the lowest Nod Glas conodonts are reworked although the specimens themselves show no sign of this, and further studies will be necessary to resolve the problem. The top 30 cm of the Nod Glas phosphoritic limestones (sample 78) below the nodular beds (Cave 1965, fig. 1) yielded abundant specimens of *A. ordovicicus*. If the trilobite evidence from here is definitive of the Onnian, then it could be that the *superbus-ordovicicus* Biozone boundary is as low as this below the Ashgill (see discussion above) as we propose tentatively in text-fig. 2, although further investigations are again required to test these relationships.

North Wales. In the Berwyn Hills (79–82) and Bala district (97–100), well-dated Longvillian–Woolstonian formations contain *superbus* Biozone faunas, including *P. bullhillensis* that gives further weight to correlations with the Shropshire succession. Various discontinuous limestone units of Cautleyan–Rawtheyan ages (83–95, 97–105) (text-fig. 2) generally yielded sparse faunas, but all are indicative of the *ordovicicus* Biozone.

None of our samples of Hirnantian age has yielded conodonts. Large samples from the type Hirnant Limestone of Bala (106) and from calcareous-cemented arenites of the Conway Castle Grits at Deganwy (107–110) were processed in the hope of isolating post-*ordovicicus* Biozone faunas to compare with the *Gamachignathus* faunas described from North America and northern England (e.g. McCracken and Barnes 1981a, b; McCracken *et al.* 1980; Orchard 1980; Uyeno and Barnes 1983); the potential of the latter for wider correlation is still unknown as the diagnostic forms have not yet been identified in other regions. *Gamachignathus* is a subjective synonym, apparently junior, of

[Text continues on page 689]

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TEXT-FIG. 3. Geological map and stratigraphical section of the Caradoc Series in the Onny valley, Shropshire, showing detail of the distribution of conodont samples; stratigraphical thicknesses are based mainly on measurements made along the section on the north side of the A489 road. Samples plotted on the left of the vertical column are from the A489 road section, those on the right are from the Onny river and old railway section. Details of strike/dip are omitted from the map for clarity, but the dip is fairly constant throughout the section from 8° to 15° (maximum observed 22°) along a bearing of 150° .

Pen-y-banc (18) in the probable Marshbrookian. Both ends of its range in Britain are much lower than presently recorded in North America where Sweet (1981*b*) shows it from the late Kirkfieldian to late Richmondian.

P. bullhillensis sp. nov. is the most abundant species in our collections with almost 700 elements, mostly from the Hoar Edge Grit (71–74) in the Costonian to early Harnagian but with a range extending up to the Cymerig Limestone (97–99) in the probable Longvillian–Woolstonian. It is characterized by a very small Pb element which has a high anterior blade and by a Pa element which is usually large but rather delicate just behind the main cusp and therefore usually broken at that point. In some samples the Pa element is smaller but is still recognizable by its three anterior denticles, backwardly inclined main cusp, and the frequent breakage just behind that cusp. The species is not known from elsewhere but may be a useful indicator of early–mid Caradoc age deposits in Britain.

P. bergstroemi sp. nov. is known mainly from the Smeathen Wood Formation (31, 32) in the Harnagian but also from a few specimens from the lower Cheney Longville Formation (47) in the probable Woolstonian. The complete apparatus is still not known, partly because of the relatively few elements available and partly because most of the known specimens are broken. Nevertheless, it is quite distinctive. *Icriodella superba* Rhodes is a variable species and therefore difficult to subdivide in a meaningful way. It appears to range throughout the upper Caradoc and most of the Ashgill. *A.* aff. *A. tvaerensis* Bergström is known only from nineteen elements from the lower part of the Nod Glas Formation (77). It has some of the characteristics of *A. inaequalis* (the Pa element) and some of *A. tvaerensis* (the M and Pb elements). As discussed above, the occurrence of this form along with *P. bullhillensis* in this fauna suggests that the lower part of the Nod Glas Formation might be much older than the upper beds which include *A. ordovicicus*.

The type locality of *Rhodesognathus elegans* (Rhodes) is at Rhodes's Locality 3, Pen-y-garnedd, Wales (Rhodes 1953) (our samples 79, 80). According to Lindström (1977) and Sweet *et al.* (1971) the species ranges from the low Caradoc to the end of the Ashgill. In our collections it ranges from the Woolstonian Cheney Longville Formation (47) to the Pusgillian as represented in the Crûg and Birdshill samples (11–17, 19, 20). Thus we seem to be in approximate agreement with Lindström and others.

The type locality of *A. superbus* is Rhodes's Locality 2 (Rhodes 1953, p. 264) in the Cymerig Limestone (our samples 93–100). The holotype is an M element and these are rare and may vary more than earlier suspected. Difficulties in distinguishing *A. superbus* from *A. ordovicicus* may be reduced by noting the differences between the respective Pb elements, as described in the systematic section below. It appears that *A. ordovicicus* is present in the Glyn Formation (92–95), the Crûg Limestone (11–17), the Birdshill Limestone (8–10), the limestones at Dryslwyn (23) and Llanegwad (25), the Robeston Wathen Limestone (5, 6), and the upper part of the Nod Glas Formation (78), whilst *A. superbus* is present in the limestone at Pen-y-banc (18) and the Cymerig Limestone (97, 98).

?*Ozarkodina pseudofissilis* (Lindström) probably does not belong to *Ozarkodina* but is referred to that genus until its affinities can be clarified. The apparatus is currently known only from Pa and Pb elements. The species is characteristic of the Crûg Limestone at Crûg (11–17), which is the type locality, and also of the Birdshill Limestone (19, 20), and the limestones at Dryslwyn (22, 23) and Llanegwad (25). It appears to be an indicator of early Ashgill age. *Aphelognathus rhodesi* (Lindström) occurs in our samples only from the Crûg Limestone (11–17) and may be a useful Pusgillian indicator.

GEOTHERMAL HISTORY OF THE CONODONTS

The colour of conodonts indicates the thermal history of the deposits and largely reflects the thickness and duration of the overburden, although igneous and hydrothermal activity also may be factors. Dynamic (regional) metamorphism should not influence the colour of conodonts. In general the colour, measured as the Colour Alteration Index (CAI) of Epstein *et al.* (1977), will be the same for conodonts of the same age in the same area. Where distances of several tens of kilometres are involved the overburden thickness may have varied sufficiently for conodont colour differences to result (Savage 1983).

The Caradoc age conodonts from Shropshire all exhibit a Colour Alteration Index of 1 to 2 (Table 2), suggesting low geothermal temperatures. The Caradoc conodonts of Central and North Wales, and the Ashgill conodonts from South Wales, all have a CAI of 4.5 or more (Table 2), suggesting much higher geothermal temperatures. Bergström (1981a, p. 385) noted the CAI contrast in the region and suggested that volcanism or heat flow associated with tectonism is a more likely explanation for the high Welsh indices than overburden. If one accepts the calculations of Epstein *et al.* (1977), the overburden on the deposits of the Welsh trough necessary to produce the thermal changes would need to have been several kilometres greater than that on the Borderland platform deposits.

SYSTEMATIC DESCRIPTIONS

In this study we use the element notation of Sweet (1981a) adopted in the recent conodont volume of the *Treatise on Invertebrate Paleontology*. We have attempted to identify dextral and sinistral elements in the descriptions and plate explanations, assuming laterally organized pairs with the elements pointed away from the observer. Illustrations on the plates are arranged in stratigraphical and geographical order, with the older faunas from the Caradoc area on Plates 80–82, and the younger late Caradoc and Ashgill faunas on Plates 83–86. This arrangement is made to emphasize associations in the different areas and to assist in facies comparisons.

Order CONODONTOPHORIDA Eichenberg, 1930
 Family BALOGNATHIDAE Hass, 1959
 Genus AMORPHOGNATHUS Branson and Mehl, 1933c

Type species. Amorphognathus ordovicica Branson and Mehl, 1933c, p. 127.

Remarks. The orientation of the dextral and sinistral Pa elements used here is that used by Bergström (1978, pl. 80, figs. 1–3) but the reverse of that used by Lindström (1977) and by Orchard (1980). Many workers state that dextral elements are distinguished by high anterior blades (Schopf 1966; Lindström 1977; Orchard 1980). In our material both sinistral (Pl. 85, figs. 25 and 26; Pl. 86, figs 25 and 26) and dextral (Pl. 83, figs. 1 and 2; Pl. 84, figs. 1 and 3) elements may have high or low blades.

Amorphognathus ordovicicus Branson and Mehl, 1933c

Plate 84, figs. 1–21; Plate 85, figs. 1–26; Plate 86, figs. 1–13

- 1933c *Amorphognathus ordovicica* n. sp. Branson and Mehl, p. 127, pl. 10, fig. 38 [holotype] [Pa element].
 1933c *Ambalodus triangularis* n. sp. Branson and Mehl, p. 128, pl. 10, figs. 35–37 [Pb element].
 1959 *Goniodontus superbus* n. sp. Ethington, p. 278, pl. 40, figs. 1 and 2 [M element].
 1959 *Trichonodella inclinata* Rhodes; Ethington, p. 290, pl. 41, fig. 6 [Sa element].
 1959 *Tetraprioniodus parvus* n. sp. Ethington, p. 288, pl. 40, fig. 8 [Sb element].
 1959 *Eoligonodina elongata* (Rhodes); Ethington, p. 277, pl. 40, fig. 5 [Sc element].
 1959 *Keislognathus simplex* n. sp. Ethington, p. 280, pl. 40, figs. 9 and 10 [Sd element].
 1978 *Amorphognathus ordovicicus* Branson and Mehl; Bergström, pl. 80, figs. 1–11 [multielement apparatus].

Remarks. *Amorphognathus ordovicicus* is most easily distinguished from earlier species of the genus by its smaller and more robust Pb elements (Pl. 84, figs. 4–10) as well illustrated in Bergström and Sweet 1966, pl. 28, figs. 7 and 8. The M element is also characteristic (Pl. 84, figs. 15 and 16), and is well illustrated in Bergström 1971a, p. 93, fig. 4(5), but this element is infrequently recovered and is not generally convenient for diagnosis.

Amorphognathus superbus (Rhodes, 1953)

Plate 83, figs. 1-19

- 1953 *Holodontus superbus* n. sp. Rhodes, p. 304, pl. 21, figs. 125-127 [holotype] [M element].
 1953 *Amorphognathus ordovicicus* Branson and Mehl; Rhodes, p. 283, pl. 20, figs. 47-49 [Pa element].
 1953 *Ambolodus triangularis* var. *indentatus* n. var. Rhodes, p. 280, pl. 20, figs. 35-37 [Pb element].
 1953 *Ligonodina elongata* n. sp. Rhodes, p. 305, pl. 21, figs. 130 and 131 [Sc element].
 1953 *Ligonodina extensa* n. sp. Rhodes, p. 306, pl. 21, figs. 128 and 129 [Sc element].
 1953 *Trichonodella gracilis* n. sp. Rhodes, p. 314, pl. 21, figs. 144, 147-150 [Sa element].

Remarks. In this species of *Amorphognathus* the sinistral Pb element is large, deeply excavated, thin-walled, and has a deeply indented and strongly sinuous aboral inner margin (Pl. 83, fig. 8). The dextral Pb element has an aboral inner margin which is deeply indented but non-sinuous (Pl. 83, fig. 6). The M element has an arched aboral margin and bears a low cusp and from one to three subequal denticles (Pl. 83, figs. 11-14).

Confusion about the distinctions between this species and *A. ordovicicus* may have added to the difficulty in correlating the Caradoc and Ashgill in Britain and elsewhere. The type species of *A. superbus* is from the Cymerig Limestone at Locality 2 of Rhodes (1953) in 'the shallow quarry 1750 ft due north of Plas Rhiwaldog and 600 ft east of Y-Garnedd, Merioneth' (our samples 98-100), and the holotype is a M element. M elements of *Amorphognathus* are usually very rare and seem to vary enough within a single fauna to make several specimens desirable for species

EXPLANATION OF PLATE 80

All figs. $\times 40$.

- Figs. 1-5. *Plectodina tenuis* (Branson and Mehl, 1933). 1, inner lateral view of sinistral Pa element, NMW 81.6G.1; 2 and 3, inner lateral and outer lateral views of sinistral M element, NMW 81.6G.2; 4 and 5, outer lateral and inner lateral views of dextral Sc element, NMW 81.6G.3; all from sample 58.
 Figs. 6 and 7. *Pseudooneotodus* sp. A. Lateral and upper views, NMW 81.6G.4, from sample 58.
 Figs. 8-14. *Icriodella superba* Rhodes, 1953. 8-10, outer lateral, upper, and lower views of dextral Pa element, NMW 81.6G.5; 11 and 12, outer lateral and inner lateral views of dextral Pb element, NMW 81.6G.6; 13 and 14, anterolateral and posterolateral views of inner side of dextral M element, NMW 81.6G.7; all from sample 58.
 Figs. 15-22. *Plectodina bullhillensis* sp. nov. 15, inner lateral view of sinistral Pa element, NMW 81.6G.8; 16, outer lateral view of dextral Pb element, NMW 81.6G.9; 17, inner lateral view of dextral Sb element, NMW 81.6G.10; 18, outer lateral view of sinistral Sc element, NMW 81.6G.11; 19, inner lateral view of dextral M element, NMW 81.6G.12; 20, posterior view of Sa element, NMW 81.6G.13; 21, outer lateral view of dextral Pa element, NMW 81.6G.14; 22, outer lateral view of sinistral Sc element, NMW 81.5G.1. Figs. 15-17 from sample 74; figs. 18-21 from sample 73; fig. 22 from sample 74.
 Figs. 23-39. *Prioniodus deani* sp. nov. 23 and 24, outer lateral and inner lateral views of sinistral Pa element, NMW 81.5G.2 (holotype); 25 and 26, inner lateral and outer lateral views of dextral Pa element, NMW 81.5G.3; 27-29, outer lateral, lower, and inner lateral views of dextral Pb element, NMW 81.5G.4; 30-32, lower, outer lateral, and inner lateral views of sinistral Pb element, NMW 81.6G.15; 33 and 34, inner lateral and outer lateral views of sinistral Pb element, NMW 81.6G.16; 35-37, inner lateral, outer lateral, and upper views of sinistral Pb element, NMW 81.6G.17; 38 and 39, lower and upper views of S element, NMW 81.5G.48. Figs. 23-29, 38 and 39 from sample 26; figs. 30-32 from sample 73; figs. 33-37 from sample 71.
 Figs. 40, 41. ?*Plectodina* sp. Inner lateral and outer lateral views of dextral M(?) element, NMW 81.6G.18, from sample 31.
 Figs. 42-47. *Panderodus* cf. *P. gracilis* (Branson and Mehl, 1933). 42, outer view of sinistral compressiform element, NMW 81.6G.19; 43, inner view of dextral compressiform element, NMW 81.5G.5; 44 and 45, outer and inner views of dextral graciliform element, NMW 81.6G.20; 46 and 47, outer and inner views of dextral graciliform element, NMW 81.6G.21. Fig. 42 from sample 74; fig. 43 from sample 26; figs. 44-47 from sample 71.



SAVAGE and BASSETT, Caradoc conodonts

identification. The Pb elements recovered from the type locality were named by Rhodes *Ambolodus triangularis* var. *indentatus* n. var. In our collections from Y Garnedd the M and Pb elements look the same as the Rhodes specimens (Rhodes 1953, figs. 35–37, 125–127). The Pb element is thin-walled, deeply excavated, and deeply indented, with a strongly sinuous inner margin. In contrast, the Pb element of *Amorphognathus ordovicicus* is small and stout. The illustration by Rhodes of Pb elements of *A. superbus* (Rhodes 1953, pl. 20, figs. 30–37), from his Locality 2, with Pb elements from his Locality 3 (Rhodes 1953, pl. 20, figs. 28–31), which is 'a disused quarry about 900 ft east of the Powis Arms at Pen-y-garnedd, Montgomeryshire' (our samples 79, 80) appears to have led to some confusion. These Pb elements from Pen-y-garnedd are the small, stout kind, very similar to those of *A. ordovicicus* but in this case most likely belonging to *A. complicatus* Rhodes, the holotype of which also comes from Rhodes's Locality 3. *A. complicatus* is thought by Bergström (1971a, 1983) to have a range corresponding with the upper half of that of *A. superbus*. This distinction between the Pb elements of *A. superbus* and *A. complicatus* does not seem to have been recognized sufficiently hitherto and it has become common to show the forms, named by Rhodes as *Ambolodus triangularis* var. *indentatus* n. var. and *A. triangularis* Branson and Mehl, as synonyms (Bergström 1964, p. 56; Lindström 1977, p. 44; Orchard 1980, p. 16). Any confusion is probably compounded by the inclusion by Lindström of a small, stout Pb element as part of the illustration of the *Amorphognathus superbus* apparatus in the *Catalogue of Conodonts* (Lindström 1977, pp. 40, 41). The material used in this illustration is not from the type area in Wales but is from Banklick Creek in Kentucky (Bergström and Sweet 1966, pp. 273, 296, 426, pl. 28, figs. 7 and 8) and probably does not belong to *A. superbus*. Orchard assigned material from the Crûg and Birdshill limestones to *A. superbus* and *A. aff. A. superbus* but illustrated only single views of four broken elements (Orchard 1980, pl. 4, figs. 19–21, and 24). These specimens inadequately support his determination and probably belong variously to *A. ordovicicus* and *Prioniodus* sp.

Amorphognathus aff. *A. tvaerensis* Bergström, 1962

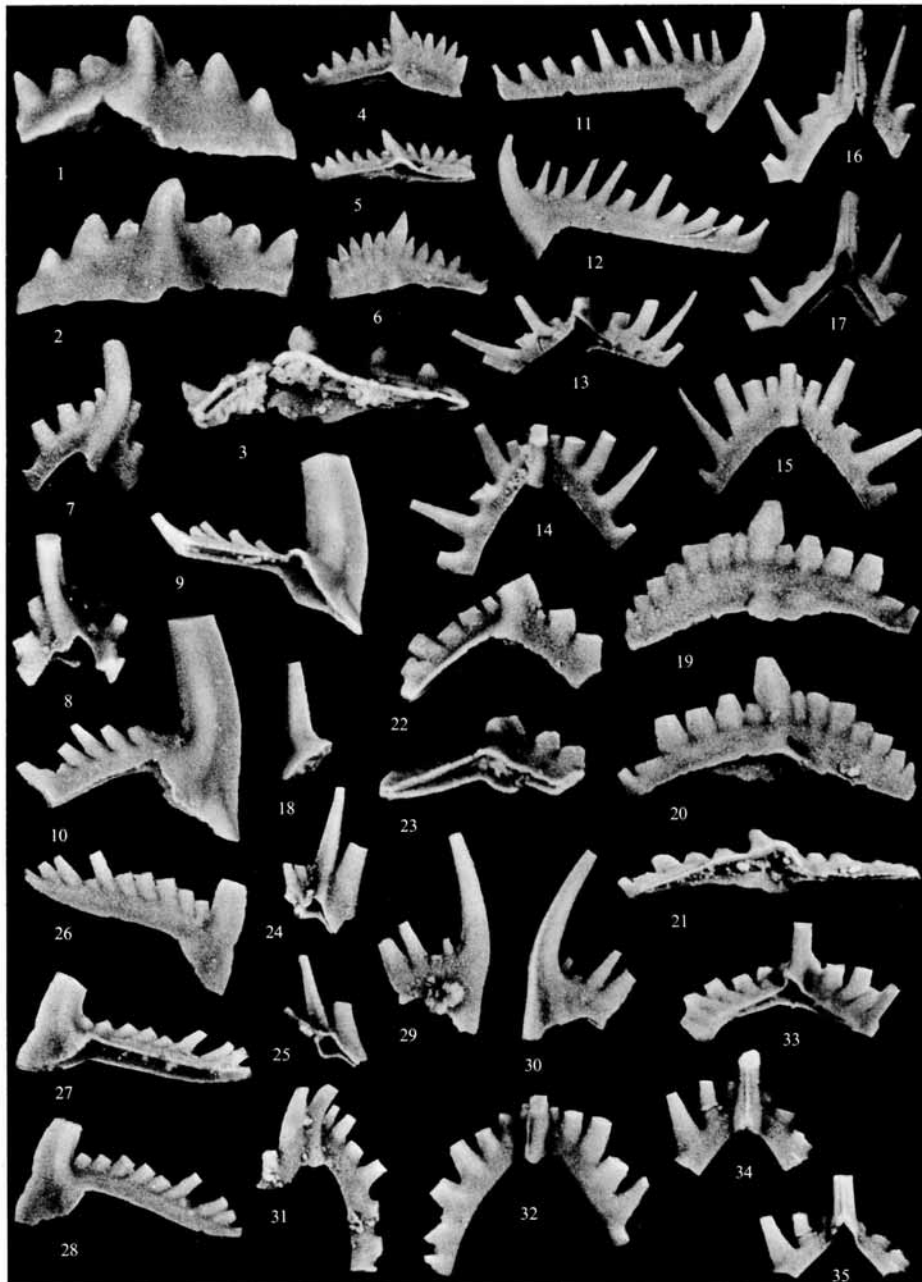
Plate 86, figs. 25–33

- aff. 1962 *Amorphognathus tvaerensis* n. sp. Bergström, p. 36, pl. 4, figs. 7 and 8 [holotype], 9 and 10 [Pa element].
 aff. 1962 *Tvaerognathus ordovicica* n. gen. et sp. Bergström, p. 57, pl. 1, figs. 1–5 [M element].
 aff. 1962 *Ambalodus triangularis erraticus* n. ssp. Bergström, p. 26, pl. 3, figs. 15–17 [Pb element].

EXPLANATION OF PLATE 81

All figs. × 40.

- Figs. 1–17. *Plectodina bullhillensis* sp. nov. 1–3, inner lateral, outer lateral, and lower views of sinistral Pa element, NMW 81.6G.22 (holotype); 4–6, inner lateral, lower, and outer lateral views of sinistral Pb element, NMW 81.6G.23; 7 and 8, outer lateral and inner lateral views of dextral Sb element, NMW 81.6G.24; 9 and 10, lower and inner lateral views of sinistral M element, NMW 81.6G.25; 11 and 12, inner lateral and outer lateral views of sinistral Sc element, NMW 81.6G.26; 13–15, lower, inner lateral, and outer lateral views of asymmetric sinistral Sa element, NMW 81.6G.27; 16 and 17, posterior and postero-lower views of Sa element, NMW 81.6G.28; all from sample 72.
- Fig. 18. *Drepanoistodus suberectus* (Branson and Mehl, 1933). Inner lateral view of NMW 81.6G.29, from sample 72.
- Figs. 19–35. *Plectodina tenuis* (Branson and Mehl, 1933). 19–21, inner lateral, outer lateral, and lower views of Pa element, NMW 81.5G.6; 22 and 23, lateral and lower views of sinistral Pb element, NMW 81.5G.7; 24 and 25, inner lateral and lower views of sinistral Sb element, NMW 81.5G.8; 26–28, outer lateral, lower, and inner lateral views of dextral M element, NMW 81.5G.9; 29 and 30, outer lateral and inner lateral views of dextral Sc element, NMW 81.5G.10; 31, inner lateral view of dextral Sb element, NMW 81.5G.11; 32 and 33, inner lateral and lower views of asymmetric sinistral Sa element, NMW 81.5G.12; 34 and 35, posterior and lower views of Sa element, NMW 81.5G.13; all from sample 26.



SAVAGE and BASSETT, *Plectodina, Drepanoistodus*

- aff. 1962 *Ambolodus triangularis suecicus* n. ssp. Bergström, p. 28, pl. 3, figs. 11–14 [Pb element].
 aff. 1983 *Amorphognathus tvaerensis* Bergström; Bergström, p. 47, fig. 4H–P [multielement apparatus].

Remarks. A few specimens of *Amorphognathus* from sample 77 comprise what is probably a new species of the genus. The Pa, M, and Pb elements resemble those of the early to middle Caradoc species *A. tvaerensis*. As discussed above (p. 715), the age of sample 77 in the lower Nod Glas Formation was earlier thought to lie within the range of *A. superbus* but the absence of that species from our fauna and the presence of *A. aff. A. tvaerensis* suggests that it may be older.

Genus RHODESOGNATHUS Bergström and Sweet, 1966

Type species. *Ambolodus elegans* Rhodes, 1953, p. 278.

Rhodesognathus elegans (Rhodes, 1953)

Plate 82, figs. 34–37; Plate 83, figs. 26 and 27; Plate 84, figs. 28 and 29; Plate 85, figs. 36–39; Plate 86, figs. 23 and 24

- 1953 *Ambolodus elegans* n. sp. Rhodes, p. 278, pl. 20, figs. 22 and 24 [holotype], 21, 23, and 25 [Pa element].
 1953 *Ambolodus pulcher* n. sp. Rhodes, p. 279, pl. 20, figs. 38–41 [Pb element].
 1953 *Ambolodus robustus* n. sp. Rhodes, p. 279, pl. 20, figs. 26, 27, 32, and 33 [Pa element].
 1977 *Rhodesognathus elegans* (Rhodes); Lindström, p. 535 [multielement apparatus].

Remarks. Sweet (1979a, p. G21) and Orchard (1980, p. 25) have commented on the apparatus of *Rhodesognathus*, and particularly on the possibility that *R. elegans* may have possessed ramiform elements like those of *Amorphognathus*. Orchard (1980) found no evidence of these ramiform elements but considers (pers. comm. 1985) such an apparatus quite likely. We have no ramiform elements with our Pa and Pb elements and we are particularly conscious that the twelve Pa and nine Pb elements recovered from our Cheney Longville Formation sample 50 have no ramiform elements associated with them. In this fauna the absence of *Amorphognathus* and its ramiform elements is helpful in reducing the number of possible associations.

EXPLANATION OF PLATE 82

All figs. $\times 30$.

- Figs. 1–16. *Plectodina bergstroemi* sp. nov. 1 and 2, outer lateral and inner lateral views of dextral Sb element, NMW 81.6G.30; 3 and 4, outer lateral and inner lateral views of dextral Pb element, NMW 81.6G.31; 5–7, inner, lower, and outer views of sinistral Sb element, NMW 81.6G.55; 8 and 9, inner lateral and outer lateral views of dextral Sc element, NMW 81.6G.56; 10–12, inner lateral, outer lateral, and lower views of dextral Pb element, NMW 81.6G.32 (holotype); 13–15, inner lateral, outer lateral, and lower views of dextral Pa element, NMW 81.6G.33; 16, inner lateral view of broken M element, NMW 81.6G.34; all from sample 32.
 Figs. 17–27. *Plectodina bullhillensis* sp. nov. 17–19, inner lateral, outer lateral, and lower views of dextral Pa element, NMW 81.5G.14; 20–22, outer lateral, lower, and inner lateral views of dextral Pb element, NMW 81.5G.15; 23 and 24, inner lateral and outer lateral views of dextral Sc element, NMW 81.5G.16; 25, inner lateral view of dextral M element, NMW 81.5G.17; 26 and 27, posterior and anterior views of Sa element, NMW 81.5G.18; all from sample 45.
 Figs. 28–33. *Icriodella superba* Rhodes, 1953. 28 and 29, inner lateral and outer lateral views of dextral M element, NMW 81.5G.19; 30–32, upper, outer lateral, and lower views of sinistral Pa element, NMW 81.5G.20; 33, outer view of sinistral Pb element, NMW 81.5G.21. Figs. 28–32 from sample 46; fig. 33 from sample 50.
 Figs. 34–37. *Rhodesognathus elegans* (Rhodes, 1953). 34, outer lateral view of dextral Pa element, NMW 81.5G.22; 35 and 36, outer lateral and inner lateral views of dextral Pb element, NMW 81.5G.23; 37, outer lateral view of sinistral Pb element, NMW 81.5G.24; all from sample 50.
 Fig. 38. *Drepanoistodus suberectus* (Branson and Mehl, 1933). Inner lateral view of NMW 81.5G.25, from sample 50.
 Figs. 39–41. ?*Staufferella* sp. Lower, inner lateral, and outer lateral views of NMW 81.5G.26, from sample 45.



SAVAGE and BASSETT, Caradoc conodonts

Family CYRTONIODONTIDAE Hass, 1959
Genus APHELOGNATHUS Branson, Mehl and Branson, 1951

Type species. Aphelognathus grandis Branson, Mehl and Branson, 1951, p. 9.

Aphelognathus rhodesi (Lindström, 1959)

Plate 84, figs. 34–46

- 1959 *Ozarkodina rhodesi* n. sp. Lindström, p. 441, pl. 1, figs. 1 and 2 [holotype], 3–9 [Pb element].
1959 *Prioniodus pulcherrima* n. sp. Lindström, p. 442, pl. 3, figs. 28–30 [Pa element].
1959 *Cordylodus* cf. *spurius* Branson and Mehl; Lindström, pl. 4; figs. 19 and 20 [Sc element], 21 [M element].
1959 *Zygognathus crugensis* n. sp. Lindström, p. 451, figs. 11–27 [Sb element].
1959 *Trichonodella parabolica* n. sp. Lindström, p. 450, figs. 18–22 [Sa element].
1980 *Aphelognathus nudus* sp. nov. Orchard, p. 18, pl. 2, figs. 1 and 2 [Sc element], 3 [Sb element], 4 [Pb element], 8 and 11 [M element].
1981b *Aphelognathus rhodesi* (Lindström); Sweet, p. 49, figs. 1–6, p. 51, 52 [multielement apparatus].

Remarks. Lindström (1959) described and figured as form species all the elements of this species from the Crûg Limestone of South Wales (our samples 11–17). The first of these form species is *Ozarkodina rhodesi* on p. 441 and this should thus determine the multielement name. Orchard (1980) believed that the Pa and Pb elements are indistinguishable from those described by Hinde (1879) from Ontario, Canada, and tentatively named the apparatus *Aphelognathus furcatus* (Hinde) based on the Pa element. Sweet (1979b, p. 66) has presented evidence to show that *Prioniodus furcatus* Hinde is part of an *Oulodus* apparatus, and it now seems best to assign the Crûg material to *A. rhodesi*. *A. rhodesi* is easily distinguished from other species of *Aphelognathus* by its short Sb element, lack of denticles anterior of the cusp on the M and Sc elements, and more reclined denticles on the Pa element.

Genus PLECTODINA Stauffer, 1935

Type species. Plectodina dilata Stauffer, 1935, p. 152.

EXPLANATION OF PLATE 83

All figs. $\times 40$; all from sample 97.

- Figs. 1–19. *Amorphognathus superbus* (Rhodes, 1953). 1–3, upper, outer lateral, and lower views of dextral Pa element, NMW 81.5G.27; 4–7, outer lateral, upper, inner lateral, and lower views of dextral Pb element, NMW 81.5G.28; 8–10, inner lateral, lower outer lateral, and upper views of sinistral Pb element, NMW 81.5G.29; 11 and 12, inner lateral and outer lateral views of sinistral M element, NMW 81.5G.30; 13 and 14, outer lateral and inner lateral views of dextral M element, NMW 81.5G.31; 15, inner lateral views of dextral Sc element, NMW 81.5G.32; 16, inner lateral view of Sa element, NMW 81.5G.33; 17 and 18, inner lateral and outer lateral views of dextral Sc element, NMW 81.5G.34; 19, lateral view of Sd element, NMW 81.5G.35.
- Figs. 20–25. *Iciodella superba* Rhodes, 1953. 20 and 21, outer lateral and inner lateral views of sinistral M element, NMW 81.5G.36; 22–24, upper, lower, and inner lateral views of sinistral Pa element, NMW 81.5G.37; 25, outer lateral view of sinistral Pb element, NMW 81.5G.38.
- Figs. 26 and 27. *Rhodesognathus elegans* (Rhodes, 1953). 26, outer lateral view of dextral Pb element, NMW 81.5G.39; 27, outer lateral view of dextral Pa element, NMW 81.5G.40.
- Figs. 28–35. *Plectodina bullhillensis* sp. nov. 28, outer lateral view of sinistral Pa element, NMW 81.5G.41; 29 and 30, inner lateral and outer lateral views of sinistral Sc element, NMW 81.5G.42; 31 and 32, inner lateral and outer lateral views of dextral M element, NMW 81.5G.43; 33 and 34, inner lateral and outer lateral views of dextral Sb element, NMW 81.5G.44; 35, anterior view of Sa element, NMW 81.5G.45.
- Figs. 36 and 37. *Pseudooneotodus* sp. B. Lateral and upper views of NMW 81.5G.46.
- Fig. 38. Gen. et sp. indet. B. Lateral view of element, NMW 81.5G.47.



SAVAGE and BASSETT, Caradoc and Ashgill conodonts

Plectodina bergstroemi sp. nov.

Plate 82, figs. 1-16

Diagnosis. A species of *Plectodina* in which all the elements have broad bases containing conspicuous white matter. The denticles are typically discrete and widely spaced.

Holotype. Pb element NMW 81.6G.32, sample 31 (Smeathen Wood Formation, Ragleth, Shropshire); Plate 82, figs. 10-12.

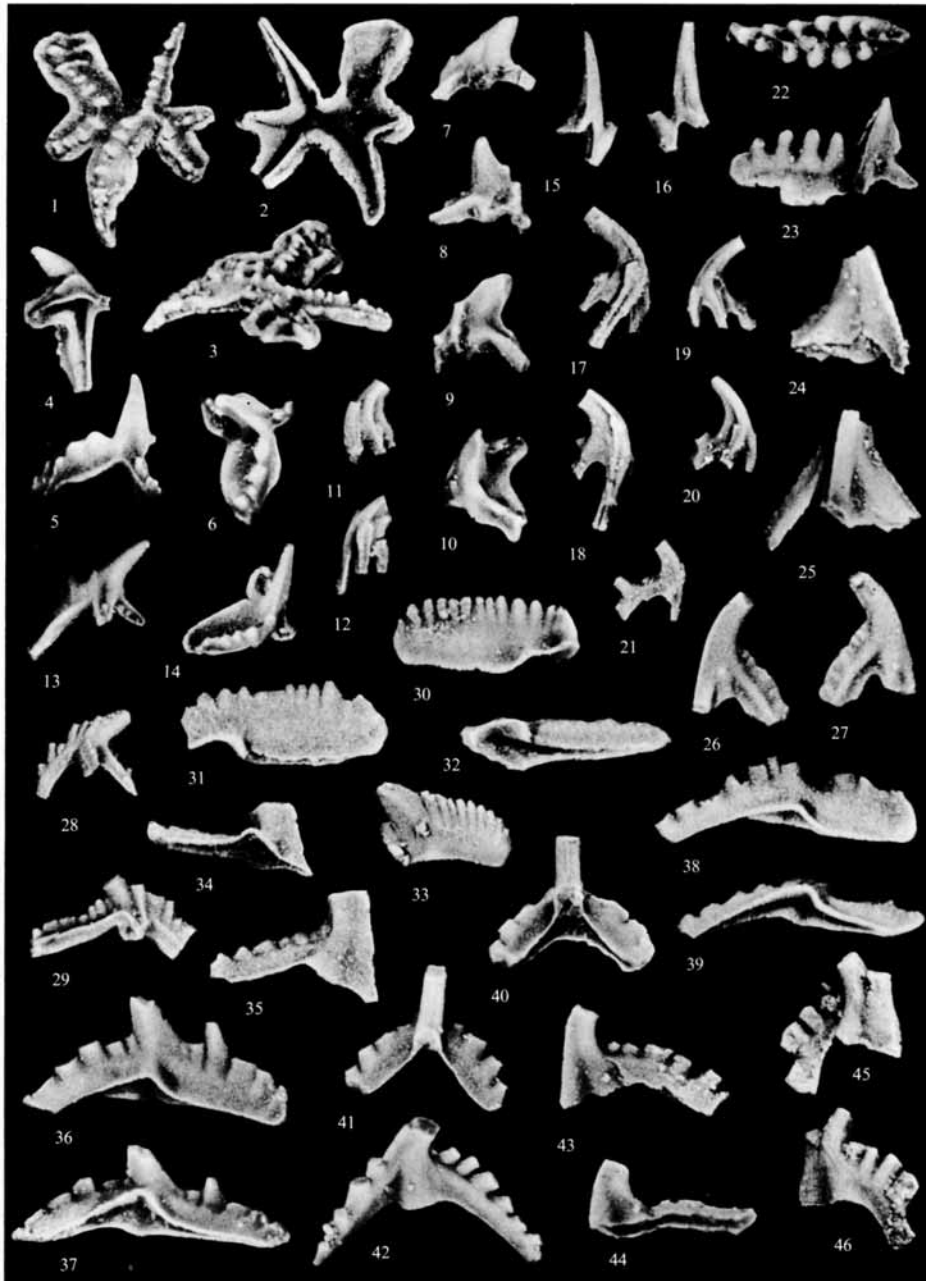
Description. The Pa element bears stout, nodular denticles and a main cusp which is inwardly curved with a distinct ridge up its inner face (Pl. 82, figs. 13-15). The Pb element has large, strongly inclined denticles and an inwardly curved main cusp below which the basal cavity is deeply cupped (Pl. 82, figs. 3, 4, 10-12). A narrow ridge runs up the inner face of the main cusp from the basal margin (Pl. 82, figs. 4, 10). The M element is strongly curved and has sharp anterior and posterior edges; its basal cavity is widely expanded inward (Pl. 82, fig. 16). The Sc element has a gently recurved main cusp and long, discrete denticles along its posterior bar (Pl. 82, figs. 8, 9). The Sb element consists of a large median cusp curving posteriorly and extending below its junction with the anterior and posterior bars. These bars slope sharply downward to enclose an angle of about 90° and bear widely spaced denticles (Pl. 82, figs. 1, 2, 5-7). The Sa element has not been recovered. All the elements have thick, conspicuous white matter in their broadly excavated aboral surfaces. This material does not grade into the darker material comprising the remainder of the element (Pl. 82, figs. 3, 6, 11).

Remarks. This species is named after Stig Bergström in recognition of his contributions to knowledge of Ordovician conodonts.

EXPLANATION OF PLATE 84

All figs. ×40.

- Figs. 1-21. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1-3, upper, lower, and upper outer lateral views of dextral Pa element, NMW 81.4G.1; 4-6, lower, outer lateral, and upper views of sinistral Pb element, NMW 81.4G.2; 7 and 8, outer lateral and inner lateral views of sinistral Pb element, NMW 81.4G.3; 9 and 10, inner lateral and upper views of dextral Pb element, NMW 81.4G.4; 11, lateral view of Sd element, NMW 81.4G.5; 12, lateral view of Sd element, NMW 81.4G.6; 13 and 14, outer lateral and upper views of sinistral Pb element, NMW 81.4G.7; 15 and 16, outer lateral and inner lateral views of dextral M element, NMW 81.4G.8; 17, lateral view of Sd element, NMW 81.4G.9; 18, lateral view of sinistral Sb element, NMW 81.4G.10; 19 and 20, lateral view of Sd element, NMW 81.4G.11; 21, outer lateral view of dextral Sc element, NMW 81.4G.12. Figs. 1-12, 17, and 18 from sample 14; figs. 13, 14, and 19-21 from sample 11; figs. 15 and 16 from sample 17.
- Figs. 22-25. *Icriodella superba* Rhodes, 1953. 22, upper view of anterior fragment of sinistral Pa element, NMW 81.4G.13; 23, outer lateral view of sinistral Pa element, NMW 81.4G.14; 24 and 25, inner lateral and outer lateral views of sinistral M element, NMW 81.4G.15; all from sample 14.
- Figs. 26 and 27. *Prioniodus* sp. Inner lateral and outer lateral views of dextral Sc element, NMW 81.4G.16, from sample 14.
- Figs. 28 and 29. *Rhodesognathus elegans* (Rhodes, 1953). 28, outer lateral view of sinistral Pb element, NMW 81.4G.17, from sample 11; 29, outer lateral view of dextral Pa element, NMW 81.4G.57, from sample 14.
- Figs. 30-33. *?Ozarkodina pseudofissilis* (Lindström, 1959). 30, inner lateral view of dextral Pa element, NMW 81.4G.18; 31 and 32, inner lateral and lower views of sinistral Pa element, NMW 81.4G.19; 33, outer lateral view of dextral Pb element, NMW 81.4G.20. Figs. 30 and 33, from sample 11; figs. 31 and 32, from sample 14.
- Figs. 34-46. *Aphelognathus rhodesi* (Lindström, 1959). 34 and 35, lower and inner lateral views of sinistral M element, NMW 81.4G.21; 36 and 37, inner lateral and lower views of sinistral Pb element, NMW 81.4G.22; 38 and 39, inner lateral and lower views of sinistral Pb element, NMW 81.4G.23; 40 and 41, lower and posterior views of Sa element, NMW 81.4G.24; 42, inner lateral view of dextral Pa element, NMW 81.4G.25; 43 and 44, inner lateral and lower views of dextral Sc element, NMW 81.4G.26; 45 and 46, inner lateral and outer lateral views of sinistral Sb element, NMW 81.4G.27. Figs. 34, 35, 38-46 from sample 14; figs. 36 and 37 from sample 11.



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Plectodina bullhillensis sp. nov.

Plate 80, figs. 15–22; Plate 81, figs. 1–17; Plate 82, figs. 17–27; Plate 83, figs. 28–35

Diagnosis. A species of *Plectodina* in which the Pa element bears discrete, stout denticles, a main cusp more posteriorly inclined than the anterior denticles, and a basal cavity which is widely expanded along the posterior two-thirds of the element. The Pb element is relatively small with an anterior blade twice the height of the posterior blade.

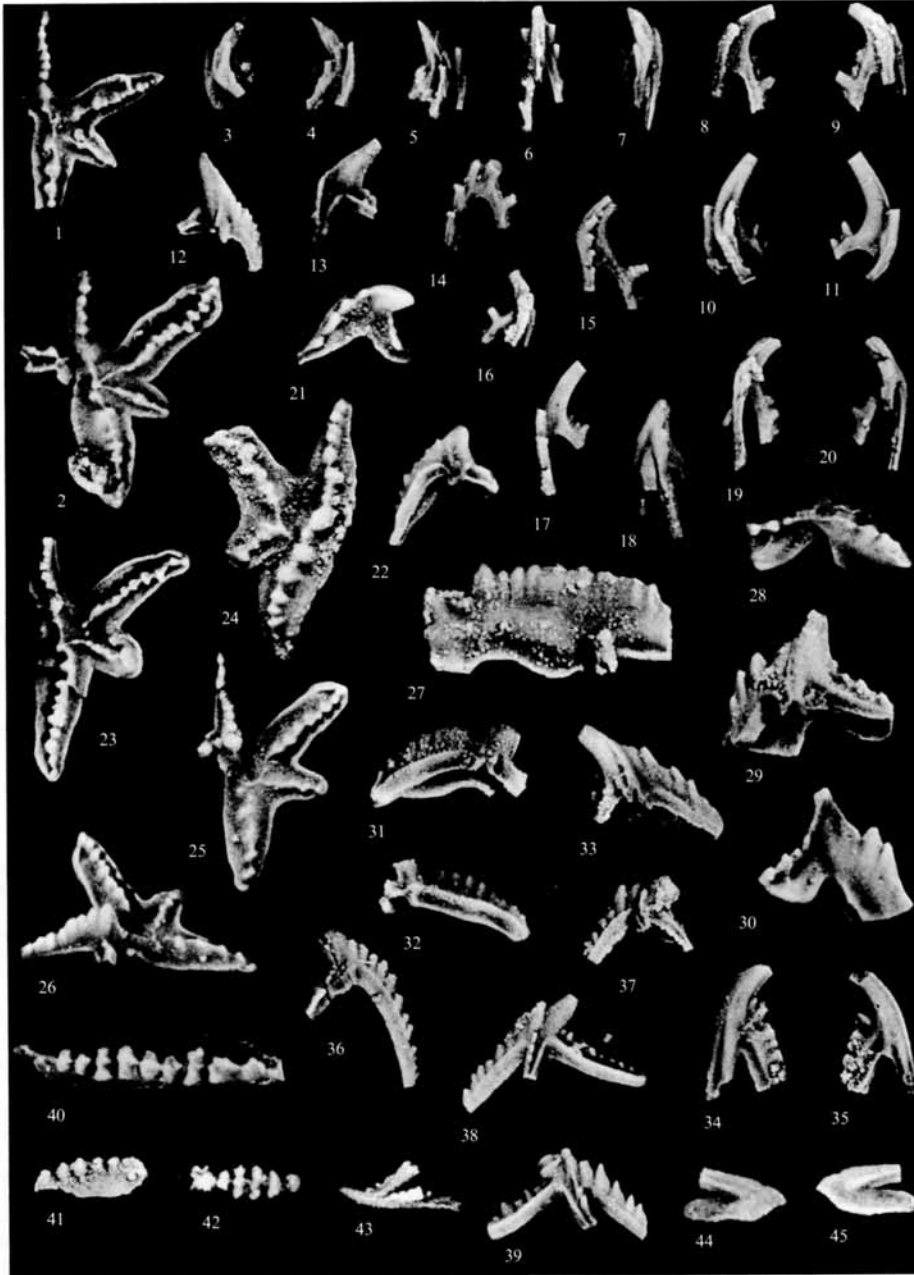
Holotype. Pa element NMW 81.6G.22, sample 72 (Hoar Edge Grit, Bullhill Gutter, Shropshire); Pl. 81, figs. 1–3.

Description. The Pa element shows some ontogenetic range. It may be large and broad, in which case it bears about three short, stout anterior denticles and four to six fairly stout posterior denticles. In these large specimens the entire basal cavity is widely expanded, and particularly so along the posterior two-thirds of the element (Pl. 81, figs. 1–3). In smaller specimens the cusp and denticles are less thickened and the posterior part of the element usually is broken off (Pl. 80, fig. 15; Pl. 82, figs. 17–19). The Pb element is consistently small and delicate. It has an anterior blade twice the height of the posterior blade and a basal cavity expanded beneath the fairly upright main cusp (Pl. 81, figs. 4–6). The M element has a long blade-like main cusp which is sharply twisted inward and backward near its base. There are no anterior denticles. The basal margin of the cusp is quite sharply inclined at an angle of about 110° relative to the basal margin of the posterior bar (Pl. 81, fig. 10). The posterior bar is thin, particularly where it attaches to the cusp, so that in many specimens it is broken from the cusp. It is straight or slightly recurved, tapers posteriorly, and bears seven or more posteriorly inclined denticles which are in contact at their bases but are otherwise discrete. A posteriorly expanded basal cavity is present below the cusp. It is sharply constricted where it extends to the posterior bar but then continues along the bar as a pronounced groove (Pl. 81, figs. 9 and 10). The Sc element has a gently reclined main cusp and a long, straight posterior bar which bears eight or more well-spaced denticles (Pl. 81, figs. 11 and 12). The cusp is laterally compressed apart

EXPLANATION OF PLATE 85

All figs. × 40.

- Figs. 1–26. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1, upper view of sinistral Pa element, NMW 81.4G.28; 2, upper view of sinistral Pa element, NMW 81.4G.29; 3–5, outer lateral and inner lateral views of Sd element, NMW 81.4G.30; 6 and 7, posterior and anterolateral views of Sa element, NMW 81.4G.31; 8 and 9, inner lateral and outer lateral views of dextral Sb element, NMW 81.4G.32; 10 and 11, outer lateral and inner lateral views of sinistral Sb element, NMW 81.4G.33; 12 and 13, outer lateral and inner lateral views of dextral Pb element, NMW 81.4G.58; 14, inner lateral view of dextral Sc element, NMW 81.4G.34; 15, inner lateral view of dextral Sc element, NMW 81.4G.35; 16, outer lateral view of dextral Sb element, NMW 81.4G.36; 17, inner lateral view of dextral Sc element, NMW 81.4G.37; 18–20, anterior and lateral views of Sa element, NMW 81.4G.38; 21, upper view of sinistral Pb element, NMW 81.4G.39; 22, inner lateral view of sinistral Pb element, NMW 81.4G.40; 23, upper view of sinistral Pa element, NMW 81.4G.41; 24, upper view of dextral Pa element, NMW 81.4G.42; 25 and 26, upper and upper lateral views of sinistral Pa element, NMW 81.4G.43. Figs. 1–11 and 22 from sample 19; figs. 12–20 from sample 21; figs. 21 and 23–26 from sample 20.
- Fig. 27. *Ozarkodina pseudofissilis* (Lindström, 1959). Inner lateral view of sinistral Pa element, NMW 81.4G.44, from sample 21.
- Figs. 28–35, 44, and 45. *Prioniodus* sp. 28–30, upper, outer lateral, and inner lateral views of sinistral Pa element, NMW 81.4G.45; 31 and 32, outer lateral and inner lateral views of sinistral Pb element, NMW 81.4G.46; 33, outer lateral view of dextral Pb element, NMW 81.4G.47; 34 and 35, outer lateral and inner lateral views of sinistral Sc element, NMW 81.4G.48; 44 and 45, lateral views of M element, NMW 81.4G.49. Figs. 28–32, 34, and 35 from sample 21; figs. 33, 34, and 45 from sample 19.
- Figs. 36–39. *Rhodesognathus elegans* (Rhodes, 1953). 36, inner lateral view of dextral Pb element, NMW 81.4G.50; 37, outer lateral view of sinistral Pb element, NMW 81.4G.51; 38, outer lateral view of sinistral Pa element, NMW 81.4G.52; 39, outer lateral view of dextral Pa element, NMW 81.4G.53. Figs. 36 and 37 from sample 21; fig. 38 from sample 20; fig. 39 from sample 19.
- Figs. 40–43. *Icriodella superba* Rhodes, 1953. 40, upper view of fragmentary Pa element, NMW 81.4G.54; 41 and 42, lateral and upper views of fragmentary Pa element, NMW 81.4G.55; 43, lateral view of Pb element, NMW 81.4G.56. Figs. 40 and 43 from sample 20; figs. 41 and 42 from sample 19.



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from a gentle expansion extending down its inner side (Pl. 81, fig. 11). There are no anterior denticles. The basal cavity beneath the cusp is narrow and continues back along the posterior bar with only minor decrease in width. The Sb element has a weakly sinuous and posteriorly recurved main cusp with basal lips projecting downward on both the anterior and posterior sides (Pl. 81, figs. 7 and 8). The lateral bars are of unequal length and diverge at an angle of 75° to 80°. The shorter lateral bar, which is flexed slightly posteriorly and arched, bears three or four compressed denticles. The longer lateral bar is straighter and bears three or four more widely spaced denticles. The Sa element is usually symmetrical with lateral processes enclosing an angle of about 65°. The posterior face of the cusp bears a median ridge which is cleft where it runs into the basal cavity (Pl. 81, fig. 16). Occasionally the Sa element is slightly asymmetrical and then has the lateral processes more open, to enclose an angle of about 85°, and the cusp ridge twisted sideways (Pl. 81, figs. 13-15).

Remarks. This species is characterized by its broad Pa element, bearing only three or four anterior denticles, and its contrastingly small, delicate Pb element. At present it is known from the lower part of the Costonian to the upper part of the Woolstonian.

Plectodina tenuis (Branson and Mehl, 1933c)

Plate 80, figs. 1-5; Plate 81, figs. 19-35

- 1933c *Ozarkodina tenuis* n. sp. Branson and Mehl, p. 128, pl. 10, figs. 19 [syntype], 20, 21, and 23 [Pa element].
 1933c *Prioniodus(?) flexuosus* n. sp. Branson and Mehl, p. 130, pl. 10, fig. 16 [M element].
 1933c *Cordylodus? delicatus* n. sp. Branson and Mehl, p. 129, pl. 10, figs. 14 and 15 [Sc element].
 1933c *Phragmodus mirus* n. sp. Branson and Mehl, p. 123, pl. 10, fig. 12 [Sb element].
 1933c *Trichognathus tenuis* n. sp. Branson and Mehl, p. 131, pl. 10, fig. 18 [Sa element].
 1966 *Plectodina furcata* (Hinde); Bergström and Sweet, p. 377, pl. 32, figs. 17-19; pl. 33, figs. 1-4; pl. 34, figs. 9-12 [part of multielement apparatus].
 ?1981b *Plectodina tenuis* (Branson and Mehl); Sweet, p. 274, figs. 10-18, pp. 287-290 [multielement apparatus: but note reversal of Pa and Pb notation compared with that used herein and in Sweet 1979b, 1981a].

Remarks. This species has been referred frequently to *Plectodina furcata* (Hinde) but it now appears that the holotype of *furcata* is part of an *Oulodus* apparatus as discussed above in the remarks on

EXPLANATION OF PLATE 86

All figs. ×40.

- Figs. 1-13. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1, upper view of sinistral Pa element, NMW 81.6G.35; 2, upper view of sinistral Pa element, NMW 81.6G.36; 3, upper view of sinistral Pa element, NMW 81.6G.37; 4 and 5, upper and lower views of sinistral Pa element, NMW 81.6G.38; 6, upper view of sinistral Pb element, NMW 81.6G.39; 7, upper view of sinistral Pb element, NMW 81.6G.40; 8 and 9, upper and outer lateral views of sinistral Pb element, NMW 81.6G.41; 10, upper view of dextral Pb element, NMW 81.6G.42; 11-13, anterior and posterior views of Sa element, NMW 81.6G.43; all from sample 95.
 Fig. 14. Gen. et sp. indet. A. Lateral view of element, NMW 81.6G.44, from sample 95.
 Fig. 15. *Protopanderodus liripipus* Kennedy, Barnes and Uyeno, 1979. Lateral view of NMW 81.6G.45, from sample 95.
 Figs. 16 and 17. *Phragmodus* cf. *P. undatus* Branson and Mehl, 1933. 16, inner lateral view of dextral S element, NMW 81.6G.46; 17, inner lateral view of sinistral M element, MNW 81.6G.47; both from sample 95.
 Figs. 18-22. *Icriodella superba* Rhodes, 1953. 18-21, upper, lower, inner lateral, and outer lateral views of dextral Pa element, NMW 81.6G.48; 22, inner lateral view of sinistral M element, NMW 81.6G.49; all from sample 77.
 Figs. 23 and 24. *Rhodesognathus elegans* (Rhodes, 1953). Inner lateral and outer lateral views of dextral Pa element, NMW 81.6G.50, from sample 77.
 Figs. 25-33. *Amorphognathus* aff. *A. tvaerensis* Bergström, 1962. 25-27, inner lateral, upper, and lower views of sinistral Pa element, NMW 81.6G.51; 28 and 29, posterior and anterior views of sinistral M element, NMW 81.6G.52; 30, lateral view of Sa element, NMW 81.6G.53; 31-33, outer lateral, inner lateral, and lower views of sinistral Pb element, NMW 81.6G.54; all from sample 77.



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Aphelognathus rhodesi. The elements of *Plectodina* in the Branson and Mehl fauna now take the name *P. tenuis* (Branson and Mehl, 1933c). These Shropshire occurrences of this species are from the Costonian to Woolstonian or possibly lowest Marshbrookian. The Costonian occurrences appear to extend the lower range of the species, previously thought to commence in the late Kirkfieldian (Sweet 1981b).

The type material of this species is from the Maquoketa Formation, Clarksville, Missouri. Our material is very similar to the specimens illustrated from that formation by Branson and Mehl (1933c). The multielement apparatus assigned to *P. tenuis* and figured by Sweet (1981b, p. 274) in the *Catalogue of Conodonts* is from several localities in Kentucky and one in Ohio. The M element is different from the Branson and Mehl specimen (1933c, pl. 10, fig. 16) in having smaller and more upright denticles. The Sa element illustrated by Sweet (1981b, p. 275, figs. 11 and 12) also appears to be more slender and sinuous than the Branson and Mehl specimen (1933c, pl. 10, fig. 12), although the latter is incomplete and difficult to compare.

?*Plectodina* sp.

Plate 80, figs. 40 and 41

Remarks. This M(?) element is relatively short, with closely set inclined denticles along the bar. It cannot be assigned to any known species but is probably part of a *Plectodina* apparatus.

Family ICRIODONTIDAE Müller and Müller, 1957

Genus ICRIODELLA Rhodes, 1953

Type species. *Icriodella superba* Rhodes, 1953, p. 288.

Icriodella superba Rhodes, 1953

Plate 80, figs. 8-14; Plate 82, figs. 28-33; Plate 83, figs. 20-25; Plate 84, figs. 22-25; Plate 85, figs. 40-43

- 1953 *Icriodella superba* n. sp. Rhodes, p. 288, pl. 20, figs. 62, 63, 78 [holotype], 54, 58, and 65 [Pa element].
 1953 *Sagittodontus robustus* n. sp. Rhodes, p. 311, pl. 21, figs. 141 and 142 [M element].
 1953 *Sagittodontus robustus* var. *erectus* n. var. Rhodes, p. 311, pl. 21, figs. 143, 151, and 152 [M element].
 1953 *Sagittodontus robustus* var. *distaflexus* n. var. Rhodes, p. 312, pl. 21, figs. 137 and 138 [M element].
 1953 *Trichonodella divaricata* n. sp. Rhodes, p. 313, pl. 21, figs. 140, 145, and 146 [Pb element].
 1953 *Icriodella superba* var. *acuta* n. var. Rhodes, p. 288, pl. 20, figs. 59, 60, 64, 65, 71-73, and 77 [Pa element].
 1953 *Icriodella plana* n. sp. Rhodes, p. 287, pl. 20, figs. 67, 74, and 76 [Pa element].
 1953 *Icriodella* n. sp. Rhodes, p. 288, pl. 20, fig. 61 [Pa element].
 1953 *Icriodella deforma* n. sp. Rhodes, p. 286, pl. 20, figs. 67-70 [Pa element].
 1953 *Icriodella elongata* n. sp. Rhodes, p. 287, pl. 20, figs. 79-81 [Pa element].
 1981 *Icriodella superba* Rhodes; Klapper and Bergström, pp. W125, W126, fig. 74(1a-j) [multielement apparatus: but note that this figured material is not from the type locality and is quadrimembrate compared with our trimembrate apparatus].

Remarks. Although specimens of *Icriodella* occur at several horizons in Shropshire and Wales, no consistent differences are evident by which the genus can be subdivided. All the specimens are referred to *I. superba* Rhodes, originally described from the Cymerig Limestone of North Wales. Orchard (1980) recognized *I. superba superba* Rhodes and *I. superba deforma* Rhodes from the Cymerig Limestone, the latter being diagnosed by uneven development of the anterior denticles of the Pa elements. Although some specimens in the collections described herein have an uneven development, we are not able to recognize consistent differences. The Pa elements from any particular locality show sufficient range of variation of anterior denticle development, asymmetry of anterior

platform, inclination of denticles and main cusp, and total length of the unit, that the taxonomic subdivisions of Rhodes (1953) commonly have been synonymized by later workers (Bergström 1964; Schopf 1966; Orchard 1980).

Family PHRAGMODONTIDAE Bergström, 1981c
Genus PHRAGMODUS Branson and Mehl, 1933b

Type species. *Phragmodus primus* Branson and Mehl, 1933b, p. 98

Phragmodus cf. *P. undatus* Branson and Mehl, 1933b

Plate 86, figs. 16 and 17

cf. 1933b *Phragmodus undatus* n. sp. Branson and Mehl, p. 115, pl. 8, figs. 22–24 [S element].

cf. 1966 *Phragmodus undatus* Branson and Mehl; Bergström and Sweet, p. 369, pl. 28, figs. 13–20 [Pa, Pb, M, and S elements = multielement apparatus].

Remarks. Only a few specimens of each of the S and M elements have been recovered and these are broken. Nevertheless, the S element is sufficiently diagnostic to make tentative assignment to *Phragmodus undatus* possible.

Family PRIONIODONTIDAE Bassler, 1925
Genus PRIONIODUS Pander, 1856

Type species. *Prioniodus elegans* Pander, 1856, p. 29.

Prioniodus deani sp. nov.

Plate 80, figs. 23–39

Diagnosis. A species of *Prioniodus* in which the Pa elements are strongly arched and relatively short. The dextral Pb element has straight lower margins and a prominent lateral process. The sinistral Pb element has arched lower margins and a weak lateral process.

Holotype. Pa element NMW 81.5G.2, sample 26 (Coston Formation, Shropshire); Plate 80, figs. 23 and 24.

Description. The dextral Pa element is short and strongly arched with a small, posteriorly inclined main cusp (Pl. 80, figs. 25 and 26). At least seven small denticles are present on the anterior process and four on the posterior process. The outer lateral process arises from the base of the main cusp. The sinistral Pa element is more strongly arched but otherwise very like the dextral element (Pl. 80, figs. 23 and 24). The dextral Pb element has straight lower margins, a large, slightly inclined main cusp, and a prominent lateral process (Pl. 80, figs. 27–29). The sinistral Pb element has arched lower margins, a relatively small main cusp which is inclined posteriorly and inwards, and a very weak lateral process which arises just anterior of the cusp (Pl. 80, figs. 29–37). The S element has a very weak cusp, one edentulate process, and two denticulate process (Pl. 80, figs. 38 and 39). The M element has not been recovered.

Remarks. This species is known at present only from the Costonian and may be a useful indicator of a pre-Harnagian age. The specific name recognizes W. T. Dean's contributions to the Ordovician geology of Shropshire.

Prioniodus sp.

Plate 84, figs. 26 and 27; Plate 85, figs. 28–35, 44, and 45

1980 *Prioniodus* sp. nov. A, Orchard, p. 24, pl. 6, figs. 5, 9, 11, and 12

Remarks. This species is represented by specimens from the Birdshill Limestone and Crûg Limestone. Unfortunately, all the Pa and Pb elements in the collection are broken. Orchard (1980, p. 24) discussed specimens from the Birdshill Limestone which are probably conspecific with this material.

Family PANDERODONTIDAE Lindström, 1970
Genus PANDERODUS Ethington, 1959

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

Panderodus cf. *P. gracilis* (Branson and Mehl, 1933b)

Plate 80, figs. 42-47

cf. 1933b *Paltodus gracilis* n. sp. Branson and Mehl, p. 108, pl. 8, figs. 20 and 21 [graciliform element].
cf. 1933b *Paltodus compressus* n. sp. Branson and Mehl, p. 109, pl. 8, fig. 19 [compressiform element].
cf. 1976 *Panderodus gracilis* (Branson and Mehl); Dzik, p. 428, fig. 15a, b, e, f [multielement apparatus].

Remarks. Workers who have attempted to distinguish multielement apparatuses of *Panderodus* include Barrick (1977), Cooper (1975), Dzik (1976), and Barnes *et al.* (1979). We have chosen to adopt a simple distinction in dealing with our specimens and to separate only the more flattened 'compressiform' elements from the narrower 'graciliform' elements.

Family SCOLOPODONTIDAE Bergström, 1981c
Genus STAUFFERELLA Sweet, Thompson and Satterfield, 1975

Type species. Distacodus falcatus Stauffer, 1935, p. 142.

?*Staufferella* sp.

Plate 82, figs. 39-41

Remarks. This species is represented in our collections by a single specimen. It is rounded in cross-section and has a weak carina on one side. It may be a unicarinate element of *Staufferella*.

Family DREPANOISTODONTIDAE Bergström, 1981c
Genus DREPANOISTODUS Lindström, 1971

Type species. Oistodus forceps Lindström, 1955, p. 574.

Drepanoistodus suberectus (Branson and Mehl, 1933b)

Plate 81, fig. 18; Plate 82, fig. 38

1933b *Oistodus suberectus* n. sp. Branson and Mehl, p. 111, pl. 35, figs. 22-27.
1979b *Drepanoistodus suberectus* (Branson and Mehl); Sweet, p. 79, figs. 7-21, 23, and 30 [multielement apparatus].

Remarks. Only non-geniculate elements of this species have been recovered. They range throughout the full stratigraphical coverage of our samples.

Family PROTOPANDERODONTIDAE Lindström, 1970
Genus PROTOPANDERODUS Lindström, 1971

Type species. Acontiodus rectus Lindström, 1955, p. 549.

Protopanderodus liripipus Kennedy, Barnes and Uyeno, 1979

Plate 86, fig. 15

1979 *Protopanderodus liripipus* n. sp. Kennedy, Barnes and Uyeno, p. 546, pl. 1, figs. 9-19 [multielement apparatus].

Remarks. The sixteen specimens in the sample 78 collection include symmetrical and asymmetrical protopanderodiform elements and a single scandodiform element. The elements are very similar to the type material from the early Caradoc age Tetaugouche Group, New Brunswick.

Family POLYGNATHIDAE Bassler, 1925
Genus OZARKODINA Branson and Mehl, 1933a

Type species. *Ozarkodina typica* Branson and Mehl, 1933a, p. 51.

?*Ozarkodina pseudofissilis* (Lindström, 1959)

Plate 84, figs. 30–33; Plate 85, fig. 27

1959 *Ctenognathus pseudofissilis* n. sp. Lindström, p. 439, pl. 4, figs. 1–9 [Pa element].

1959 *Ozarkodina pseudotypica* n. sp. Lindström, p. 441, pl. 4, figs. 17 and 18 [Pb element].

Remarks. Numerous well-preserved Pa elements of this species have been recovered by us from the Crûg quarry (11–17), which is the type locality, and also farther west along the Towy Anticline. The Pb elements are rare. No other elements of a possible apparatus have been recovered and the species is referred only tentatively to *Ozarkodina*. In these South Wales localities this species is commonly associated with *Amorphognathus ordovicicus* and appears to indicate an Ashgill age.

Orchard (1980) reconstructed this species to include the Pa and Pb elements and, as a possible Sc element, the single *Hindeodella?* sp. specimen recovered from the Crûg Limestone by Lindström (1959, pl. 1, fig. 10). It is surprising that other parts of the apparatus have failed to show up in any of our thirteen samples that yield the Pa or Pb elements, and that Lindström and Orchard had much the same result. There remains the possibility that the species is bimembrate.

Family UNKNOWN
Genus PSEUDOONEOTODUS Drygant, 1974

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

Pseudooneotodus sp. A

Plate 80, figs. 6 and 7

1967 Genus et species ind. B Serpagli, p. 107, pl. 29, figs. 1a, b.

Remarks. This material appears to be identical to that figured by Serpagli (1967) from the Ashgill of the Carnic Alps. The form described as *Pseudooneotodus* aff. *P. beckmanni* by Orchard (1980), from the Ashgill of the English Lake District, appears to have a more acutely angled cone.

Pseudooneotodus sp. B

Plate 83, figs. 36 and 37

Remarks. This single element differs from *Pseudooneotodus* sp. A in having a subrectangular outline, a difference which additional specimens might show to be of no taxonomic significance if a range of variation can be demonstrated. The specimen illustrated by Branson and Mehl (1933b, pl. 9, fig. 3) from the Ordovician Plattin Formation of Missouri is even more angular.

Gen. et sp. indet. A

Plate 86, fig. 14

Remarks. This element has a sharply angled triangular cross-section near the base and in this respect is similar to some of the specimens assigned to *Walliserodus debolti* (Rexroad) by Serpagli

(1967, pl. 31). However, the element figured herein is more flared posteriorly and bears some small denticles on this posterior edge.

Gen. et sp. indet. B

Plate 83, fig. 38

Remarks. This element is flattened on its inner side and is convex, with a weak carina on its outer side. The outer base is flared.

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APPENDIX

Summary of stratigraphical horizon (Formation/Member) and locality of samples 1-110 for immediate reference to data plotted in text-figs. 1-4 and Tables 1 and 2. Locality details are given here as a generalized field name plus an eight figure National Grid Reference. Full topographical descriptions and stratigraphical plots of individual samples within sections are given in the Supplementary Publication deposited in the British Library (see p. 680).

SOUTH WALES

Sample No.(s)

- 1-3 Sholeshook Limestone, Sholeshook railway cutting, SM 9681 1705.
- 4 Sholeshook Limestone, Prendergast quarry, SM 9564 1662.
- 5, 6 Robeston Wathen Limestone, Robeston Wathen quarry, SN 0841 1615.
- 7 Sholeshook Limestone, Llanddowror quarry, SN 2538 1429.
- 8 Sholeshook Limestone, Fron quarry, SN 1711 1711.
- 9 Sholeshook Limestone, Trefenty quarry (Foxhole), SN 2962 1355.
- 10 Sholeshook Limestone, Parke trackside, SN 2392 1335.
- 11-17 Crûg Limestone, Crûg quarry and farm, SN 6270 2306.
- 18 Un-named limestone, Pen-y-banc quarry, SN 6081 2385.
- 19-21 Birdshill Limestone, Birdshill quarry, SN 6014 2312.
- 22, 23 Birdshill Limestone, Dryslwyn Castle, SN 5545 2034.
- 24 Birdshill Limestone, Tŷ-picca quarry, SN 5395 2064.
- 25 Birdshill Limestone, Llanegwad quarry, SN 5151 2130.

WELSH BORDERLAND AND EASTERN WALES

Sample No.(s)

- 26, 27 Coston Formation, Onny section quarry, SO 4118 8624.
- 28, 29 Coston Formation, A489 quarry, SO 4119 8623.
- 30-32 Smeathen Wood Formation, Ragleth quarry, SO 4456 9135.
- 33, 34 Horderley Sandstone Formation, A489 road section, SO 4151 8599.
- 35 Horderley Sandstone Formation, A489 road section, SO 4153 8595.
- 36, 37 Horderley Sandstone Formation, A489 road section, SO 4175 8583.
- 38 Horderley Sandstone Formation, Longlane quarry, SO 4129 8422.
- 39, 40 Horderley Sandstone Formation, High Wood quarry, SO 4119 8522.
- 41 Alternata Limestone, Onny river, SO 4179 8575.
- 42-44 Alternata Limestone, Soudley quarry, SO 4772 9182.
- 45 Alternata Limestone, Marshbrook railway cutting, SO 4403 9049.
- 46 Alternata Limestone, Onny railway, SO 4175 8570.
- 47 Cheney Longville Formation, Glynboro Member, Soudley quarry, SO 4772 9182.
- 48, 49 Cheney Longville Formation, Glynboro Member, A489 road section, SO 4193 8575.
- 50 Cheney Longville Formation, Glynboro Member, Cheney Longville roadside, SO 4185 8501.

- 51 Cheney Longville Formation, Glynboro Member, A489 road section, SO 4201 8571.
 52 Cheney Longville Formation, Crosspipes Member, Cheney Longville roadside, SO 4191 8495.
 53, 54 Cheney Longville Formation, Crosspipes Member, A489 road section SO 4209 8566.
 55 Cheney Longville Formation, Crosspipes Member, A489 road section, SO 4219 8559.
 56, 57 Acton Scott Formation, Ragdon Member, A489 road section, SO 4232 8552.
 58 Acton Scott Formation, Ragdon Member, Hatton stream SO 4645 9013.
 59 Acton Scott Formation, Ragdon Member, Hatton stream SO 4642 9018.
 60 Acton Scott Formation, Ragdon Member, A489 road section, SO 4239 8551.
 61 Acton Scott Formation, Wistanstow Member, A489 road section, SO 4241 8550.
 62, 63 Acton Scott Formation, Wistanstow Member, Ragdon stream, SO 4507 9061.
 64, 65 Acton Scott Formation, Wistanstow Member, Onny river, SO 4236 8539.
 66, 67 Acton Scott Formation, Wistanstow Member, Ragdon stream, SO 4505 9054.
 68 Acton Scott Formation, Henley Member, Acton Scott church quarry, SO 4496 8955.
 69, 70 Onny Shale Formation, Onny river, SO 4259 8535.
 71, 72 Hoar Edge Grits, Bullhill Gutter stream, SO 5122 9825.
 73, 74 Hoar Edge Grits, Black Dicks Coppice quarry, SO 5092 9787.
 75, 76 Alternata Limestone, Chatwall farmyard, SO 5135 9741.
 77, 78 Nod Glas Formation, Gwern-y-Brain stream, SJ 2181 1268.

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Sample No.(s)

- 79, 80 Pen-y-garnedd Formation, Pen-y-garnedd quarry, SJ 1090 2375.
 81, 82 Pen-y-garnedd Formation, Greenhall Park quarry, SJ 1572 1888.
 83-85 Dolhir Formation, Dolhir Limestone Member, Ddöl-hir quarry, SJ 2029 3675.
 86, 87 Dolhir Formation, Dolhir Limestone Member, Gelli Farm quarry, SJ 2360 1939.
 88 Dolhir Formation, Dolhir Limestone Member, Gelli Farm yard, SJ 2368 1924.
 89-91 Dolhir Formation, Dolhir Limestone Member, Cefngoed quarry, SJ 2127 3643.
 92-95 Glyn Formation, Glyn Limestone Member, Ty-draw hill quarry, SJ 2062 3704.
 96 Nant Hir Mudstones, Derfel Limestones Member, Aberderfel stream, SH 8508 3920.
 97 Gelli Grin Ashes, Cymerig Limestone Member, Gelli Grin quarry, SH 9449 3401.
 98-100 Gelli Grin Ashes, Cymerig Limestone Member, Y Garnedd quarries, SH 9451 3537.
 101 Moelfryn Mudstones, Rhiwlas Limestone Member, Rhiwlas river section, SH 9231 3690.
 102-105 Moelfryn Mudstones, Rhiwlas Limestone Member, Creigiau Bychan crags, SH 9200 3150.
 106 Foely Ddinas Mudstones, Hirnant Limestone Member, Cwm Hirnant quarry, SH 9510 2963.
 107-110 Conway Castle Grits, Deganwy quarry, SH 7853 7908.

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