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Middle-Upper Ordovician conodonts from the Ffairfach and Golden Grove groups in South Wales, United Kingdom

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ABSTRACT

The conodont fauna of the reference succession of the regional British Llandeilian Stage of the Llanvirn Series was first described in a classical study by Rhodes more than 65 years ago using single element (form) taxonomy. Although several subsequent authors have recorded a substantial number of conodont taxa from the Llandeilo area, the present study is the first to present a modern taxonomic review of these late Darriwilian-early Sandbian faunas that include approximately 20 multielement species. Most prominent are representatives of *Amorphognathus*, *Baltoniodus*, *Eoplacognathus*, and *Plectodina*. The study faunas have their own biogeographical character. The distinctive genera *Complexodus*, *Protopanderodus*, and *Pygodus*, which are common in coeval Baltoscandic faunas, are not present, but the occurrence of *Amorphognathus*, *Baltoniodus*, and *Eoplacognathus* provides a link to age equivalent Baltoscandic faunas. The presence of abundant specimens of *Plectodina* and less common representatives of *Erismodus* and *Icriodella* are reminiscent of North American Midcontinent faunas. This type of faunal assemblage is in some respects similar to those of the early Caradoc Series of the Welsh Borderland. Biostratigraphically diagnostic species indicate that the Llandeilo study succession ranges from the *Eoplacognathus lindstroemi* Subzone of the *Pygodus serra* Zone to the *Baltoniodus variabilis* Subzone of the *Amorphognathus tvaerensis* Zone.

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Introduction

There is no doubt that the beginning of the post-pioneer period of research on Lower Palaeozoic conodonts in not only the United Kingdom but also in the entire Europe is marked by the publication of Rhodes' (1953) monograph on the Ordovician and Silurian conodonts from Wales and the Welsh Borderland. One important portion of this classical work is the description of a conodont fauna from the Llandeilo Limestone. This unit, which is well known in British Lower Palaeozoic geology, was named (Murchison 1839) for the small town of Llandeilo in South Wales (Figure 1), where there are many outcrops of the unit. The term Llandeilo became internationally known as a standard series unit in the British regional series classification of the Ordovician System (e.g., Williams et al. 1972). What Rhodes (1953) referred to as the Llandeilo Limestone is now known as the Llandeilo Group, which is subdivided into three formations, the Lower, Middle, and Upper Llandeilo Flags (Figure 2).

As was the practice at that time, Rhodes (1953) used single element (form) taxonomy in his description of this conodont fauna. He recognised 16 species, among which five were new and one not identified at the species level. A restudy of the Rhodes collection along with additional samples led Bergström (1964) to identify 23 form species from the Llandeilo Group, three of which were not identified at the species level. Some further observations on the Llandeilo Group conodonts were published by Bergström (1971). Part of this fauna was reported in terms of multielement taxonomy by Bergström and Orchard (1985) but a more comprehensive account was published by Bergström et al. (1987). Their

account was based on many additional samples not only from the Llandeilo area but also from coeval strata in the Narberth area some 60 km west-southwest of Llandeilo. The study of Bergström et al. (1987) was mainly of biostratigraphical nature and did not include any formal taxonomic descriptions. Whereas a considerable amount of taxonomic work has been carried out on slightly younger conodont faunas in Wales and the Welsh Borderland (e.g., Lindström 1959; Orchard 1980; Savage and Bassett 1985; Ferretti et al. 2014a; Bergström and Ferretti 2018), the conodont faunas of the Llandeilo Group and the slightly older Ffairfach Group have never been formally described in terms of modern conodont taxonomy. The purpose of the present study is to present an illustrated taxonomic description of these important conodont faunas and assess their significance in terms of also biostratigraphy, biogeography and evolution of some taxa.

Current stratigraphical classification of the study interval and conodont sample levels

During the more than half a century since the publication of the Rhodes (1953) classic paper, there have been very significant changes in the stratigraphical classification of his study unit (Figure 2), and a brief review of this reclassification is needed for placing these faunas in a modern stratigraphical framework. What was formerly known as the Llandeilo Limestone is now classified as three formations, the Lower, Middle, and Upper Llandeilo Flags, which constitute the Golden Grove Group (cf. Sutton et al. 1999; Fortey et al. 2000). This group rests on strata of the Ffairfach Group, which is subdivided into five formations (Figure 2).

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Everyone stands alone at the heart of the world pierced by a ray of sunlight and suddenly it's evening. Salvatore Quasimodo (1930)
The present study is dedicated to the memory of our recently deceased friend F. H. T. Rhodes.

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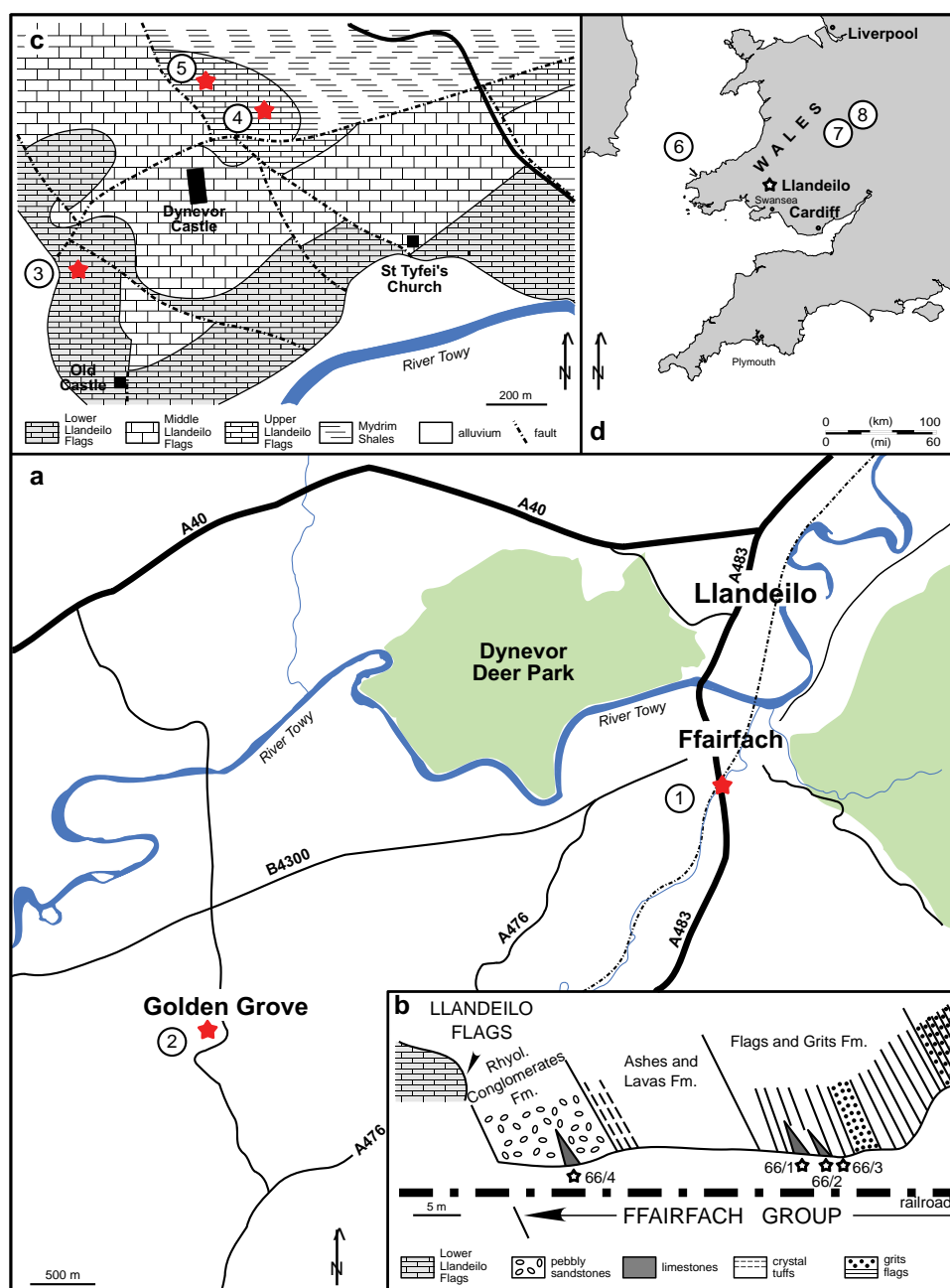


Figure 1. Geographic location of principal outcrops dealt with in the present study. **a**, location of selected sites in the Llandeilo type area. 1, Ffairfach. This is the type section of the Ffairfach Group along the railway near Ffairfach (SN 628212); 2, Golden Grove. Disused quarry in the lower Llandeilo Flags at Llanfihangel Aberthythch (SN 592198). This is Locality 1 of Rhodes (1953). **b**, detail of Site 1 showing conodont sample levels; modified after Williams (1952) and Bergström et al. (1987). **c**, location of Sites 3–5 in the Dynevor Park. Site 3 is along dirt road 0.5 km west south–west of Dynevor Castle (SN 608223). This is Stop II–10 of Bassett et al. (1974). Site 4 is disused quarry in the Upper Llandeilo Flags 0.25 km north–east of Dynevor Castle (SN 616227). This is Stop II–8 of Bassett et al. (1974). Site 5 is the disused quarry in the Upper Llandeilo Flags 0.3 km north north–east of Dynevor Castle (SN 615229). Note that Sites 1–5 correspond to homologous sites in Bergström et al. (1987). **d**, sketch map of Wales showing location of the Llandeilo District (black star, Collecting Sites 1–5) and Abereiddi Bay (Collecting Site 6), Onny Valley (Collecting Site 7), and Evenwood (Collecting Site 8).

For a long time, the Llandeilo Series was taken to correspond to the *Glyptograptus* (now *Hustedograptus*) *teretiusculus* graptolite Zone (e.g., Fortey et al. 1995) but studies of conodonts (Bergström 1971; Bergström et al. 1987) and shelly fossils (Addison in Williams et al. 1972) showed that only part of the Lower Llandeilo Flags corresponds to that graptolite zone, the Middle and Upper Llandeilo Flags formations being coeval to the lower part of the *Nemagraptus gracilis* graptolite Zone, which by definition marks the lower part of the regional Caradoc Series.

Furthermore, the regional British Llandeilo Series, which has its reference area at Llandeilo, has been reduced to the Llandeilian Stage of the Llanvirn Series (Fortey et al. 1995, 2000). The top of the revised Llanvirn Series is now defined as the base of the *Nemagraptus gracilis* graptolite Zone, and the base of the current Llandeilian Stage as the base of the *Hustedograptus teretiusculus* graptolite Zone. Unfortunately, because biostratigraphically diagnostic graptolites are absent in this stratigraphical interval in the Llandeilo region, neither the precise level of the top, nor that of the

base of the Llandeilian Stage can be identified based on graptolites in the Llandeilian reference sections. Based on the ranges of a few brachiopods and trilobites, Rushton et al. (2000, fig. 8.16) suggested with question that the base of the Llandeilian Stage corresponded to a level in the upper Pebbly Sands unit of the Ffairfach Group. In the absence of diagnostic graptolites, conodonts have been used to locate the approximate level of the top of the Llandeilian Stage, which Bergström et al. (1987) assumed to be somewhere in the middle of the Lower Llandeilo Flags.

Added to the uncertain range of the Llandelian Stage in its reference section is the fact that both the name and precise range of the *H. teretiusculus* Zone have been the subject of discussion in recent years. Because the zone index ranges from well below the base of the *H. teretiusculus* Zone to some distance into the overlying *N. gracilis* Zone, the range of the zone index does not coincide with what has generally been taken to be the interval of the *H. teretiusculus* Zone. Because of this confusing situation, some recent authors have redefined the graptolite zone classification of this interval (e.g., Goldman et al. 2015; Chen et al. 2016) and proposed the use of the designation of the *Jiangtzeograptus* (formerly *Dicellograptus*) *vagus* Zone for the stratigraphical interval just below the base of the *N. gracilis* Zone.

The Ffairfach Grits and Llandeilo Limestone sequence, which has an estimated total thickness of more than 700 m, consists of a lithologically diverse succession of limestone, sandstone, grit, conglomerate, and shale deposited in intertidal to sublittoral open shelf environments. Virtually all our samples were collected before 1980 from limestone intervals and are the same as those dealt with by Bergström et al. (1987). The most productive samples are from interbeds and lenses of limestone in the Ashes and Lavas and Rhyolitic Conglomerates formations of the Ffairfach Group at the well-known railway cut at Ffairfach (Loc. 1 in Figure 1a–b). Some samples from the Golden Grove Group were collected from outcrops of the Llandeilo Flags at Golden Grove (Loc. 2 in Figure 1a) and Dynevor Park (for details, see Bergström et al. 1987). Important collection sites in this latter area are shown in Figure 1c (Loc. 3–5). For further information about localities and sample levels, see the Appendix. We have also had full access to the conodont collections from the Narberth area recorded by Bergström et al. (1987) as well as Bergström's samples from the Castell Limestone at its type locality near the quarry entrance at the northern end of Aberiddi Bay in Pembrokeshire (Nat. Grid Reference SM 795301; Loc. 6 in Figure 1d). For comparative purposes we have also investigated Bergström's (1971) Sandbian (early Caradoc) conodont collections from the Caradoc type area in the Onny Valley (Loc. 7 in Figure 1d) and at Evenwood Quarry (Loc. 8 in Figure 1d) 13 km south-east of Shrewsbury in South Shropshire (cf. Dean 1958) as well as numerous other collections, especially from Sweden.

Summary of the conodont biostratigraphy of the Ffairfach and Golden Grove groups and associated strata

As noted in Bergström et al. (1987), relatively numerous samples from calcareous beds in the Upper Ffairfach and the Golden Grove groups have yielded a fair number of biostratigraphically diagnostic conodonts although the frequency of conodonts in individual samples varies greatly from zero to relatively abundant. Whereas the conodont element yield from the relatively impure limestones in the Llandeilo Flags formations as a rule is not great, several of the limestone interbeds and calcareous lenses in the Upper Ffairfach Group produced rich and well-preserved conodont faunas. The elements exhibit a Colour Alteration Index (CAI; cf. Epstein et al. 1977) of about 5 (Bergström et al. 1987). The species identified and their frequency in the investigated samples are listed in Table 1.

The biostratigraphical evidence provided by the conodont collections studied herein has been discussed in some detail by Bergström et al. (1987) and their conclusions are still valid. Therefore, we here restrict our biostratigraphical comments to some major points.

The conodont species association in the samples from the Upper Ffairfach Group includes the biostratigraphically important species *Eoplacognathus lindstroemi* and *Baltoniodus prevariabilis* that suggest correlation respectively with the *Eoplacognathus lindstroemi* Subzone of the *Pygodus serra* Zone and the *Sagittodontina? kielcensis* Subzone of the *Pygodus anserinus* Zone. In terms of standard graptolite zones, these subzones correspond to the upper part of the *J. vagus* Zone. The presence of the Subzone index species *Amorphognathus inaequalis* in the Flags and Grits Formation and in a sample from the Rhyolitic Conglomerates Formation in the uppermost Ffairfach Group, as well as in the Llandeilo Limestone at Golden Grove and at Dynevor Park, indicates the presence of the *A. inaequalis* Subzone of the *Pygodus anserinus* Zone. In Baltoscandia, the base of the *Nemagraptus gracilis* Zone, which coincides with the base of the Sandbian Global Stage, corresponds to a level in the lower to middle part of the *A. inaequalis* Subzone (Bergström 1983). In view of the fact that the Upper Llandeilo Flags Formation is overlain by the *Dicranograptus* Shales, which contain graptolites of the upper *N. gracilis* Zone but from which no conodonts have been recorded, the biostratigraphical evidence at hand indicates that virtually the entire Llandeilo Group corresponds to the *N. gracilis* Zone and is of Caradoc age in terms of the regional British series classification. The Llandeilian Stage, in its type area, would include only the very lowermost part of the Lower Llandeilo Flags Formation and possibly, a probably undeterminable part of the Ffairfach Group.

In an attempt to clarify the biostratigraphy around the base of the Caradoc Series, a level defined as the base of the *N. gracilis* Zone in South Wales, Bergström et al. (1987) reviewed the ranges of conodont taxa in samples from the calcareous succession in the Narberth area approximately 60 km west-southwest of Llandeilo. Although the faunas proved to have a relatively low diversity of conodonts, the presence of *Amorphognathus tvaerensis*, *Baltoniodus variabilis*, and *Eoplacognathus elongatus* in the upper portion of the Bryn-banc Limestone of the Narberth Group was interpreted by Bergström et al. (1987) as indicating the presence of strata corresponding to the *Baltoniodus variabilis* Subzone of the *Amorphognathus tvaerensis* Zone, hence an interval a little above the base of the *N. gracilis* Zone, and by implication, a little above the base of the Caradoc Series. This dating is consistent with the fact that the same interval of the Bryn-banc Limestone has yielded a few shelly fossils of early Caradoc affinity. However, more detailed investigations are needed to clarify if the successions in these quarries could serve as a standard reference for the base of the Caradoc Series. As is well known, in its typical development in the Welsh Borderland, the base of the Caradoc Series is at a major unconformity of regionally variable magnitude. Unfortunately, at Narberth, as well as elsewhere, the base of the Caradoc succession does not appear to coincide with a conodont zone or subzone boundary, being located biostratigraphically somewhat above the base of the *Pygodus anserinus* Zone. Our interpretation of the stratigraphy of the study interval in South Wales is illustrated in Figure 2.

Systematic Palaeontology

Most of the species listed in Table 1 are well known taxa that have already been adequately described in the conodont literature. Accordingly, there is no need to describe and comment on

Table 1. Conodont species occurrence in selected samples used in the present investigation.

LOCALITY	Site 1		Site 2		Sites 3-5				Site 6	Site 7	Site 8	number of elements			
	FFAIRFACH		GOLDEN GROVE		DYNEVOR PARK				ABEREIDDI BAY	ONNY VALLEY	EVEN- WOOD				
	FLAGS AND GRITS FORMATION			'LLANDEILO LMST.'											
	RHYOL. CONGLOMERATES FM.		RHYOL. LOCALITY 1 RHODES 1953 62/ 62/												
	RHODES' SAMPLES	SMB SAMPLES	FFAIRFACH 66/ 1-3	Rhodes 1-3	Ffairfach Stig	66/4	62/26 55' below top of section	62/ 27 top of section	Dynevor Castle 70/1 lower Llandeilo	Dynevor Park 70/2 lower Llandeilo	Dynevor Llandeilo 50 m below top Dynevor Park O. Llandeilo	62/17B	75/1	66/13	
Conodont taxa	lens 1 & 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	lens 2	
<i>Amorphognathus</i>															
<i>inaequalis</i>															
Pa	1	1	6	16	1	16	4	16	5		4	18	75/1	66/13	55
Pb	3	4	4	16		19	4	16	4		7	15			55
M						1					3	1			1
Sa											2	8			0
Sb	1										3	1			2
Sc	1				1						3	3			3
Sd		2			2						3	4			2
<i>Amorphognathus</i>															
<i>tvaverensis</i>															
Pa			24				4				4	18			50
Pb			7				4				4	15			31
M			3				3				3	1			7
Sa			2				2				2	8			10
Sb			3				3				3	3			6
Sc			3				3				4	4			8
Sd			3				3				1	1			1
<i>Amorphognathus</i>															
<i>sp.</i>															
Pa													4	27	31
Pb													8	13	21
Sc													1		1
<i>Baltoniodus</i>															
<i>prevariabilis</i>															
Pa	1	3	15												20
Pb	6	15	26												54
M		6	10	4											19
Sa	1	4	2	9											36
Sb	1	1	13	1			1								20
Sc		8	18	2			1								32
Sd	1	7	17	5											33
<i>Baltoniodus</i> sp.															
Pa			6						1						16
Pb			9						1						11
M			3				2		1						6
Sa			10				3		1						13
Sb			2				2		1						3
Sc			15				4		1						17
Sd			4				4		1						4
<i>?Baltoniodus</i> sp.															
Drepanoistodus	2	13	13	45	5	26	8	43	7	3	10	12	8	39	254
<i>subrectus</i>															
		3		3						1	1	19	1	19	6
		13		45						3	10	12	8	39	254
		3		45						1	1	19	1	19	6
		13		45						3	10	12	8	39	254

(Continued)

the taxonomy of these taxa although we provide illustrations of representative specimens of most of these species, which include *Baltoniodus prevariabilis* (Fåhræus, 1966) (Figures 8M–U and Z–B', 9O–P), *Drepanoistodus suberectus* (Branson and Mehl, 1933) (Figures 10I, N and 12A–I), *Pseudooneotodus mitratus* (Moskalenko, 1973) (Figure 9N), and *Venoistodus venustus* (Stauffer, 1935) (Figure 10M, O). The illustrated conodont elements are kept in the Type Collection of the Department of Chemical and Geological Sciences, University of Modena and Reggio Emilia, Modena, Italy under the Repository Numbers IPUM 28846–28982.

Remarks on the early evolution of the genus *Amorphognathus* (Branson and Mehl, 1933)

Amorphognathus is a genus globally distributed and the short stratigraphical range of several of its species makes it one of the biostratigraphically most useful conodont genera in the Middle and Upper Ordovician. In the standard and widely used North Atlantic Upper Ordovician conodont zonation proposed by Bergström (1971), several zones were based on species of this genus. As shown by Bergström (1983, fig. 1), the oldest typical species of *Amorphognathus*, *A. inaequalis*, forms the beginning of an evolutionary lineage of a series of conodont species in which taxa grade into each other in stratigraphical order. These taxa include *A. tvaerensis* Bergström, 1962, *A. superbus* (Rhodes, 1953), and *A. ordovicicus* Branson and Mehl, 1933, and the evolution of these taxa in the *Amorphognathus* lineage is well documented (see Ferretti et al. 2014a; Bergström and Ferretti 2017).

However, the evolutionary origin of this lineage remains enigmatic. Lindström (1977a, p. 22) interpreted *Amorphognathus* as derived from *Baltoniodus* but his concept of *Amorphognathus* was much wider than that favoured by conodont specialists today. The suggestion by Bergström (1983) that *A. inaequalis* might have evolved from *Amorphognathus* (now *Sagittodontina*?) *kielcensis* (Dzik, 1976) seems less likely now than 35 years ago but a true ancestor of *Amorphognathus* is not yet firmly established. For instance, the poorly known 'Polyplacognathus' *angarene* Moskalenko, 1984 (cf. Sennikov et al. 2015, fig. 5:12) from the middle Darriwilian Mukteian horizon in Siberia has a P element that exhibits a superficial similarity to a species of *Amorphognathus* but its apparatus remains unknown.

Our collections of topotype material of *A. inaequalis* and well-preserved specimens of *A. tvaerensis* also include a few different ontogenetic stages. Study of these revealed that during the ontogeny, there were significant morphological changes both in the amorphognathiform (Pa) (Figures 3–4) and holodontiform (M) (Figure 5) elements. When dealing with other faunas, recognition and illustration of such growth stages may assist in making correct identification of particularly more or less fragmentary elements of different growth stages of these taxa.

Genus *Amorphognathus* Branson and Mehl, 1933

Type species. *Amorphognathus ordovicicus* Branson and Mehl, 1933.

Remarks. For a description and discussion of this species based on new collections from its type locality, see Leslie and Bergström (2005).

Amorphognathus inaequalis Rhodes, 1953

(Figures 3G–J, 4I–K, 5J–L, 9A–M)

1953 *Ambolodus* sp. Rhodes: 281, pl. 22, figs 171, 203.

1953 *Amorphognathus inaequalis* n. sp. Rhodes: 283–284, pl. 22, fig. 204.

1953 *Ligonodina valma* n. sp. Rhodes: 307–308, pl. 22, figs 184–185.

1953 *Trichonodella inclinata* n. sp. Rhodes: 315, pl. 22, figs 176–177, 186.

1964 *Hibbardella? inclinata* (Rhodes); Bergström: text-fig. 10.

1964 *Ligonodina valma* Rhodes; Bergström: text-fig. 13.

1974 *Amorphognathus inaequalis* Rhodes; Lindström et al.: 16–17, pl. 1, figs 8–11, pl. 2, figs 1–2, 7.

1977a *Amorphognathus inaequalis* Rhodes; Lindström: 33–34, pl. 1, figs 6–12.

1985 *Amorphognathus inaequalis* Rhodes; Bergström and Orchard: 58, pl. 2.2, fig. 14.

1987 *Amorphognathus inaequalis* Rhodes; Bergström et al.: pl. 18.1, figs 8–10.

Material. 118 specimens.

Description. For a concise diagnosis and description of this species, see Lindström (1977a). Both blade and non blade amorphognathiform (Pa) elements are present in our investigated collections. Our material includes elements that closely match the single Pa blade element (Figure 3H) that was selected by Rhodes (1953) as the holotype of the species. An almost complete Pa blade element (Figures 3G and 9C–D) has a slender blade-like anterior process and a longer platform-like posterior process, which has proximally a distinct, but low, cusp. The posterior process has a single row of denticles, which runs in the middle of the platform from the cusp to the end of the element. From the cusp diverges a short bi-lobed postero-lateral process that is less than half as long as the posterior process. The bifid postero-lateral process has a posterior lobe with a single row of denticles running almost parallel to the posterior process denticulation. An incipient anterior lobe is developed as well, with a central ridge (our material, Figures 3G and 9C–D and the specimen illustrated in Bergström and Orchard 1985, pl. 2.2:14, Figure 3I and in Bergström et al. 1987, pl. 18.1:9) or a denticle (holotype, Rhodes 1953, pl. 22:204, Figure 3H). The amorphognathiform element illustrated by Lindström et al. (1974, pl. 2:1) lacks this lobe, representing probably a less evolute form (Figure 3J). All specimens document an incipient foreword bulge in the posterior process on the opposite side of the postero-lateral process. The antero-lateral process is not completely preserved but appears diverging. Otherwise, the upper surface of the entire Pa element is smooth.

Homologous elements of *A. tvaerensis* possess a double-branched postero-lateral process, having all branches distinctly denticulated. The anterior lobe of the postero-lateral process is of equal size of the posterior lobe (our material, Figures 3E–F and 11B, E) or longer (e.g. Bednarczyk 1971, pl. 6:6a, Figure 3B; Viira 2008, fig 5:O, Figure 3A). The postero-lateral process appears to migrate from a posterior position in *A. inaequalis* to a more anterior position in *A. tvaerensis*, in the latter developing at about mid-length of the element main axis.

Non blade Pa elements of *A. inaequalis* are preserved in our material with incomplete specimens documenting an anterior and posterior process of similar size and with a straight alignment (Figures 4I–J and 9A–B). The posterior process possesses a single incipient adenticulated bulge, located at mid-length on the outer side, diverging with a step-like 90° angle from the posterior process. The same feature is documented also in the material described by Lindström et al. (1974, pl. 1, fig. 9) (Figure 4K). This bulge will give rise in *A. tvaerensis* to the diagnostic second posterior process (Figure 4E), possibly through intermediate forms where this process is present but not denticulated (Figures 4F and 11C). An additional lobe is common in *A. tvaerensis* on the anterior side of the second posterior process (Figures 4A, C–H and 11C, J).

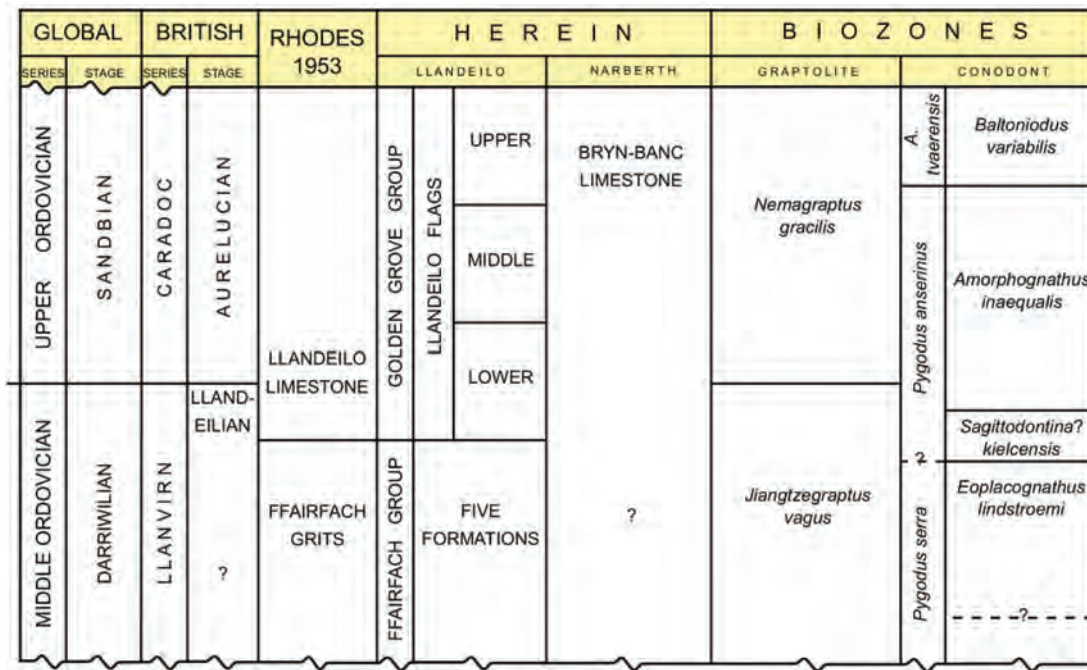


Figure 2. Diagram showing the stratigraphical classification of the study successions at Llandeilo and Narberth. Note that the precise relations between the graptolite and conodont biostratigraphy are still not precisely known in the Welsh study successions due to the lack of records of biostratigraphically important graptolites in these successions. Also note that the stage classification of the study successions follows Williams et al. (1972).

It should be noted that the non blade Pa element is not present in the Rhodes (1953) collection but it is represented in the material described by Lindström et al. (1974).

The unpaired Pb elements are relatively abundant in our collections. Sinistral Pb elements (Figure 9E-F) have a more rounded basal margin compared with the straighter basal margin of the dextral elements (cf. Figure 9G-I). The same difference has been illustrated in Pb elements of other species of *Amorphognathus* (e.g., Bergström 1962; Ferretti and Serpagli 1991, 1999; Bagnoli et al. 1998; Ferretti et al. 2014a, 2014b, 2014c; Bergström and Ferretti 2015). The Pb elements have a short, denticulated lateral process whose edge extends up to the cusp (Figure 9H) sometimes revealing a small rudimental expansion located on the outer edge of the cusp (Figure 9E, G). The anterior surface of both the anterior and posterior processes has a well-developed ledge.

A single holodontiform (M) element was recovered in a sample from the Ffairfach Group (Figures 5J, 9J-K). It has three processes with many subequal-sized denticles and a cusp of similar size as the denticles. The long anterior process is uniformly denticulated along its entire length with small, fused, and upwards-directed denticles. In outer-lateral view, the upper denticles are oriented posteriorly and the whole element is strongly arched (Figure 9K). There is also a rather long and denticulated posterior process in the M element. Lindström et al. (1974) remarked that the holodontiform elements of *A. inaequalis* have a more equant denticulation and a smaller cusp than those of *A. tvaerensis*. However, the specimen of *A. inaequalis* from the French material is photographed in lateral view (pl. 2:7, Figure 5L), and therefore hardly informative to illustrate denticle size. The specimen illustrated by Bergström et al. (1987, pl. 18.1:10) (Figure 5K) shows an anterior process lacking a distinct denticulation, but denticles on the oral side appear to have similar size.

There are only a few S elements (Figure 9L-M) in our Llandeilo collection. These clearly correspond to the homologous elements in

other species of *Amorphognathus*. We have nothing to add to the descriptions of these elements published by previous authors.

Remarks. Compared with other species of *Amorphognathus*, *A. inaequalis* has been rather poorly known. This is undoubtedly due to the fact that only a comparatively limited number of elements of this species has been recorded. The holotype of the species, collected from the Llandeilo Limestone at Golden Grove (Site 2 in Figure 1), is a blade Pa element (Rhodes 1953, pl. 22: 204; Figure 3H) that is almost complete, possibly missing only a minor part of the antero-lateral process. Rhodes (1953) also described a single Pb element from the same locality that undoubtedly belongs to the same species. Lindström et al. (1974) were the first to propose a multielement reconstruction of the apparatus of *A. inaequalis* based on collections from the Postolonnec Formation of the Armorican Massif in Brittany and they described and illustrated all element types in the apparatus. We agree that their specimens, although they come from quite a different region than that of the holotype, represent *A. inaequalis*.

Bergström (1964, 1971), Bergström and Orchard (1985) and Bergström et al. (1987) recorded the species from several localities in South Wales. Lindström (1977a) gave a succinct description of the species and discussed its relations to *A. tvaerensis*.

Dzik (1984) regarded the Welsh and French specimens as belonging to *Rhodesognathus* Bergström and Sweet, 1966. However, his few and very fragmentary specimens come from the *B. variabilis* Subzone of the Mójca Limestone in Poland, hence from a younger interval than the type stratum in Wales, and the Polish species record clearly needs to be confirmed by better specimens. The Pb elements of *A. inaequalis* documented in this paper show a rudimental expansion on the lateral surface of the cusp, that cannot be confused with the separate denticle located on the anterior process of *Rhodesognathus* to which the lateral process connects in that genus. The lateral process of *A. inaequalis* is clearly

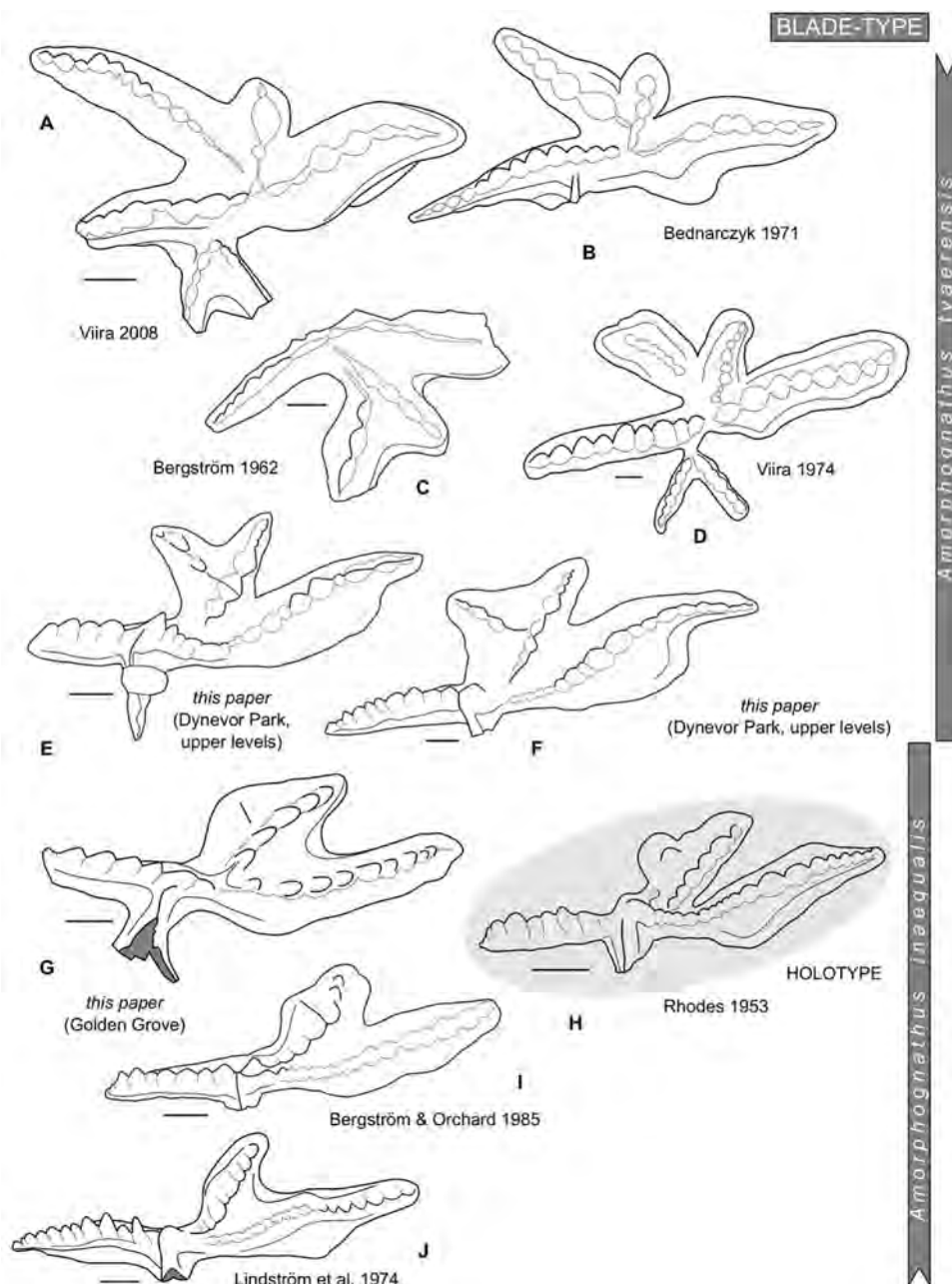


Figure 3. Outline drawings of amorphognathiform (Pa; blade-type) elements of *Amorphognathus tvaerensis* (A–F) and *A. inaequalis* (G–J) recovered in the present project or illustrated in the literature. Scale bars at figures correspond to 100 μm . Note that no magnification was provided by Bednarczyk (1971). **A**, *Amorphognathus tvaerensis*, specimen from Viira (2008, fig. 50); **B**, specimen from Bednarczyk (1971, pl. 6, fig. 6a); **C**, specimen from Bergström (1962, pl. 4, fig. 4); **D**, specimen from Viira (1974, pl. VII, fig. 24); **E–F**, previously unfigured specimens from a high level in the Dynevor Park succession; **G**, *Amorphognathus inaequalis*, previously unfigured specimen recovered from Golden Grove; **H**, the holotype of *A. inaequalis* Rhodes, 1953 from the Golden Grove succession. From Rhodes (1953, pl. 22, fig. 204); **I**, *A. inaequalis*, specimen from the Fairfach Group at the railway crossing. Previously figured by Bergström and Orchard (1985, pl. 2.2, fig. 14); **J**, specimen from Lindström et al. (1974, pl. 2, fig. 1).

connected directly with the cusp (Figure 9H). In addition, the M element does not present the diagnostic reclined cusp. However, we cannot exclude that *A. inaequalis* might have represented the ancestral form of both lineages. Specimens of *A. inaequalis* have also been recorded, but as far as we know not illustrated, from an interval just below the appearance level of *A. tvaerensis* in Estonia (Männik 2003; Männik and Viira 2005; Viira 2008) and even an *A. inaequalis* Zone between the *Pygodus anserinus* Zone and the *A. tvaerensis* Zone has been introduced in the Estonian conodont zone succession (Viira 2008).

The species has not yet been firmly identified in Sweden although it has been used as a designation for an *A. inaequalis*

Subzone in the upper part of the *P. anserinus* Zone in the standard conodont succession in central Sweden (cf. Bergström 2007).

***Amorphognathus tvaerensis* Bergström, 1962**

(Figures 3A–F, 4A–H, 5A–I, 11A–W)

1962 *Ambalodus triangularis* Branson & Mehl ssp. *erraticus* n. ssp.; Bergström: 26–27, pl. 3, figs 15–17.

1962 *Ambalodus triangularis* Branson & Mehl ssp. *suecicus* n. ssp.; Bergström: 28–29, pl. 3, figs 11–14.

1962 *Amorphognathus tvaerensis* n. sp.; Bergström: 36–37, pl. 4, figs 7–10.

1962 *Amorphognathus ordovicica* Branson & Mehl ssp. *simplicior* n. spp.; Bergström: 34–35, pl. 4, figs 2, 5–6.

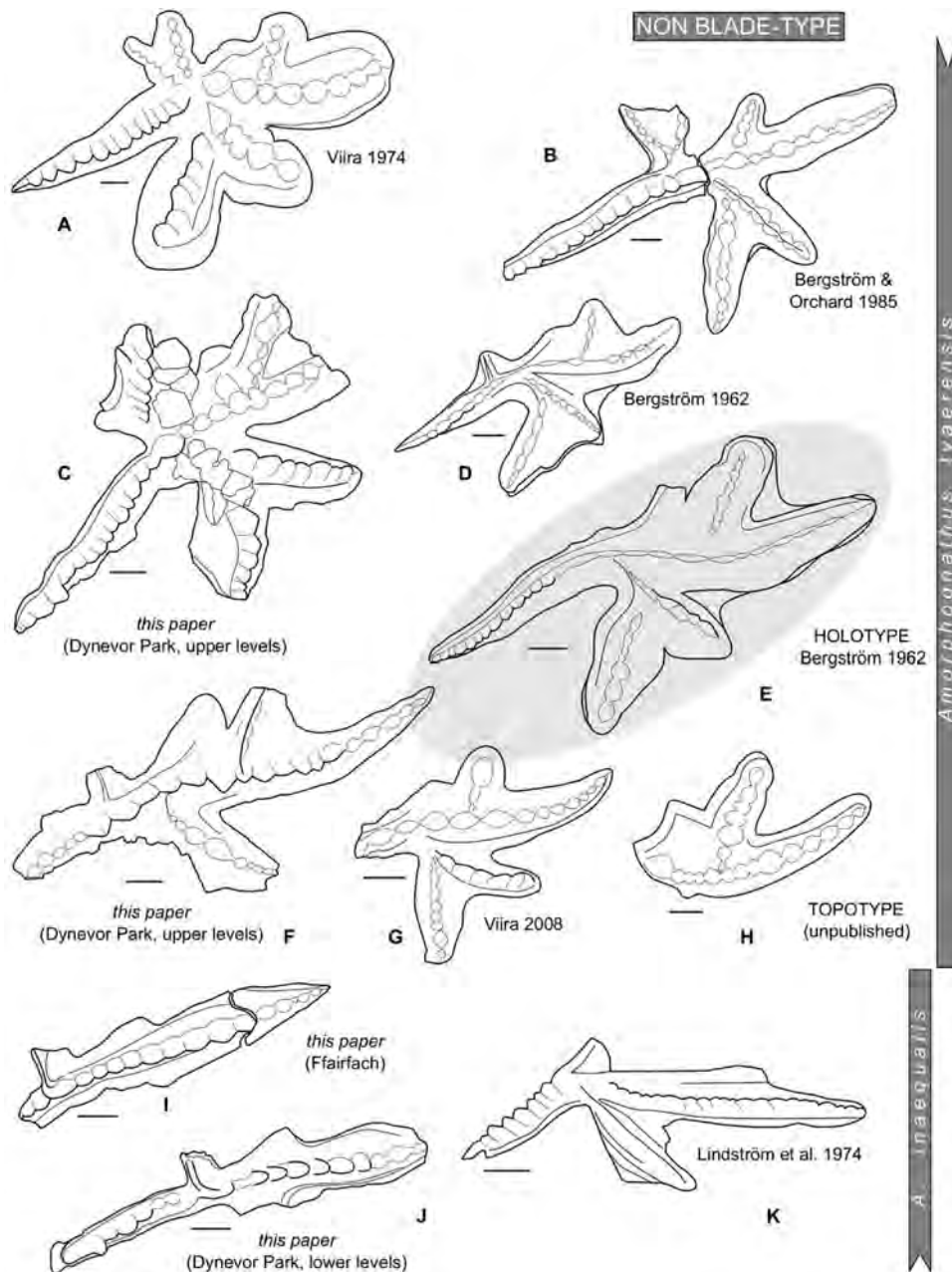


Figure 4. Outline drawings of amorphognathiform (Pa; non blade-type) elements of *Amorphognathus tvaerensis* (A–H) and *A. inaequalis* (I–K) recovered in the present project or illustrated in the literature. Scale bars at figures correspond to 100 μm . **A**, *Amorphognathus tvaerensis*, from Viira (1974, pl. VII, fig. 23); **B**, from Bergström and Orchard (1985, pl. 2.3, fig. 11); **C**, previously unfigured specimen from a high level in the succession at Dynevör Park; **D**, from Bergström (1962, pl. 4, fig. 9); **E**, holotype of *A. tvaerensis* Bergström, 1962. From Bergström (1962, pl. 4, fig. 7); **F**, previously unfigured specimen from a high level in the succession at Dynevör Park; **G**, from Viira (2008, fig. 6E); **H**, previously unfigured topotype; **I**, *Amorphognathus inaequalis*, previously unfigured specimen from the Ffairfach railroad section; **J**, previously unfigured specimen from a lower level in the Dynevör Park succession; **K**, from Lindström et al. (1974, pl. 1, fig. 9).

1962 *Amorphognathus ordovicica* Branson & Mehl sp. *simplicior* n. ssp.; Bergström: 35, pl. 4, figs 1, 3–4.

1962 *Ligonodina elongata* Rhodes; Bergström: 43–44, pl. 5, figs 14–15, 17–18.

1962 *Roundya inclinata* (Rhodes); Bergström: 53–54, pl. 5, figs 10–13.

1962 *Tvaerognathus ordovicica* n. sp.; Bergström: 57–58, pl. 1, figs 1–5; text-fig. 2F.

1963 *Prioniodus moiczansis* sp. nov. Spassov and Teller: 81, 85, pl. 1, fig. 12a–b.

1966 *Amorphognathus tvaerensis* Bergström; Schopf: 41, pl. 3, figs 8–9.

1967 *Amorphognathus tvaerensis* Bergström; Viira: text-fig 3: 20a–b.

1971 *Ambalodus triangularis* Branson and Mehl; Bednarczyk: pl. 4, fig. 1.

1971 *Holodontus superbus* Rhodes; Bednarczyk: pl. 6, fig. 1a–b.

1971 *Ambalodus frognoeyensis* Hamar; Bednarczyk: pl. 6, fig. 3.

1971 *Amorphognathus ordovicica* Branson & Mehl; Bednarczyk: pl. 6, fig. 6a–b.

1971 *Amorphognathus tvaerensis* Bergström: 135–137, pl. 2, figs 10–11.

1971 *Amorphognathus tvaerensis* Bergström; Sweet et al.: pl. 1, figs 2–5, 24.

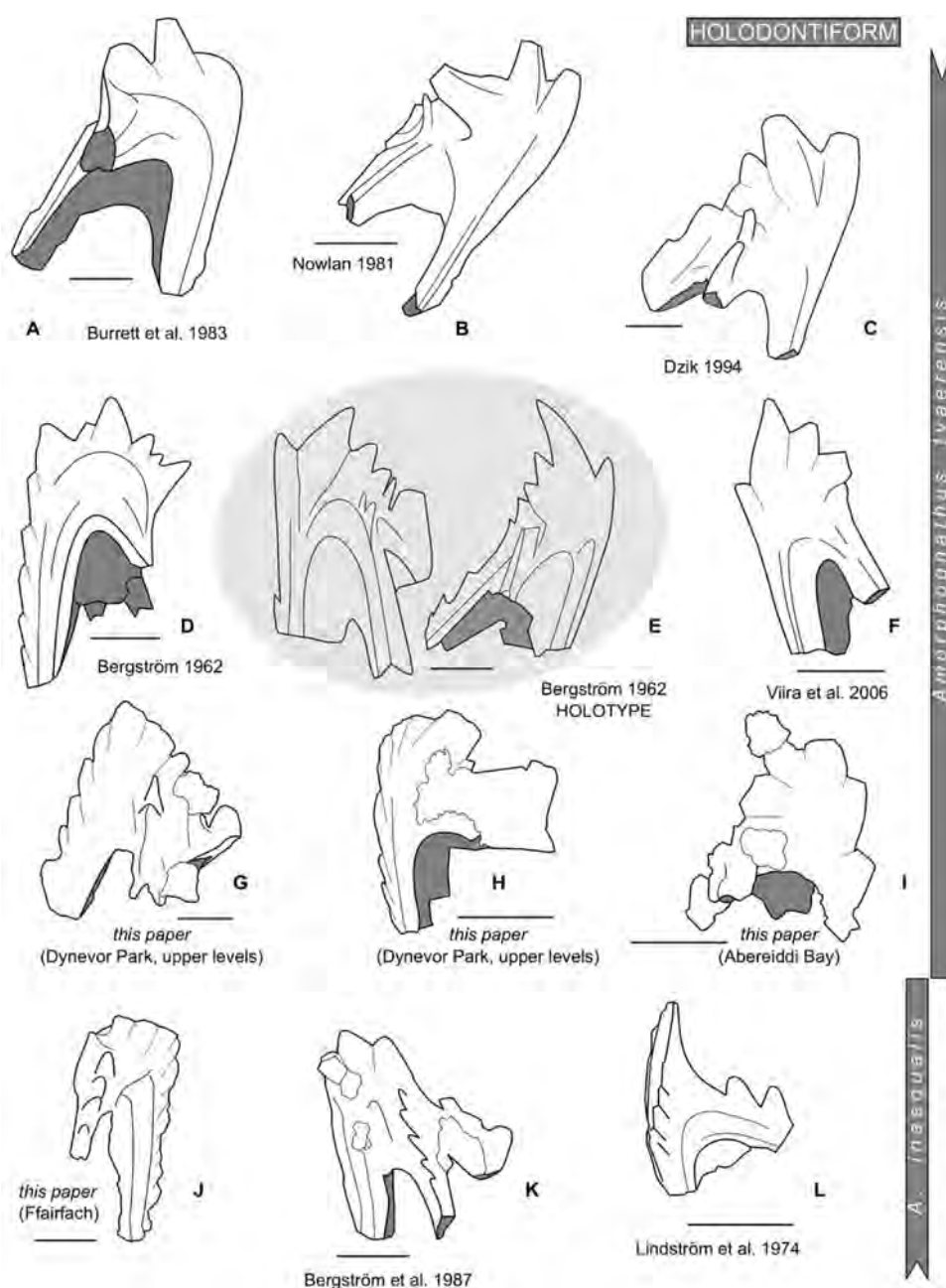


Figure 5. Outline drawings of holodontiform (M) elements of *Amorphognathus tvaerensis* (A–I) and *A. inaequalis* (J–L). Scale bars at figures correspond to 100 μ m. **A**, *Amorphognathus tvaerensis*, from Burrett et al. (1983, fig. 4B); **B**, from Nowlan (1981, pl. 5, fig. 16); **C**, from Dzik (1994, pl. 22, fig. 16); **D**, from Bergström (1962, pl. 1, fig. 1); **E**, holotype of *A. tvaerensis* Bergström, 1962. From Bergström (1962, pl. 1, figs 3–4); **F**, from Viira et al. (2006, pl. 1, fig. 4); **G**, previously unfigured specimen from a high level in the Dynevor Park succession; **H**, previously unfigured specimen from a high level in the Dynevor Park succession; **I**, previously unfigured specimen from Abereiddi Bay; **J**, *Amorphognathus inaequalis*, previously unfigured specimen from the Ffairfach railway section; **K**, from Bergström et al. (1987, pl. 18.1, fig. 10); **L**, from Lindström et al. (1974, pl. 2, fig. 7).

1974 *Amorphognathus ordovicica* ssp. n. 2; Viira: pl. VII, figs 17, 20–22.

1976 *Amorphognathus inaequalis* Rhodes; Dzik: text-fig. 27a–f.

?1976 *Amorphognathus tvaerensis* Bergström; Dzik: text-fig. 27g–q.

1977a *Amorphognathus tvaerensis* Bergström; Lindström: 47–49, pl. 2, figs 1–12.

1977c ‘*Tvaerognathus*’ sp.; Repetski and Ethington: tab. 2.

1981 *Amorphognathus tvaerensis* Bergström; Nowlan: 11, pl. 5, figs 13–14, 16.

1983 *Amorphognathus tvaerensis* Bergström; Burrett et al.: 181–182, text-fig. 4.

1983 *Amorphognathus tvaerensis* Bergström; Bergström: 40, text-fig. 4H–P.

1994 *Amorphognathus tvaerensis* Bergström; Dzik: 91–93, text-figs 19–20, 21a, 22, pl. 22, figs 8–22.

2000 *Amorphognathus tvaerensis* Bergström; Bednarczyk and Stupnicka: figs 10B, O, V, 11W–ZZ.

2000 *Amorphognathus tvaerensis* Bergström; Leslie, fig. 7:14–19.

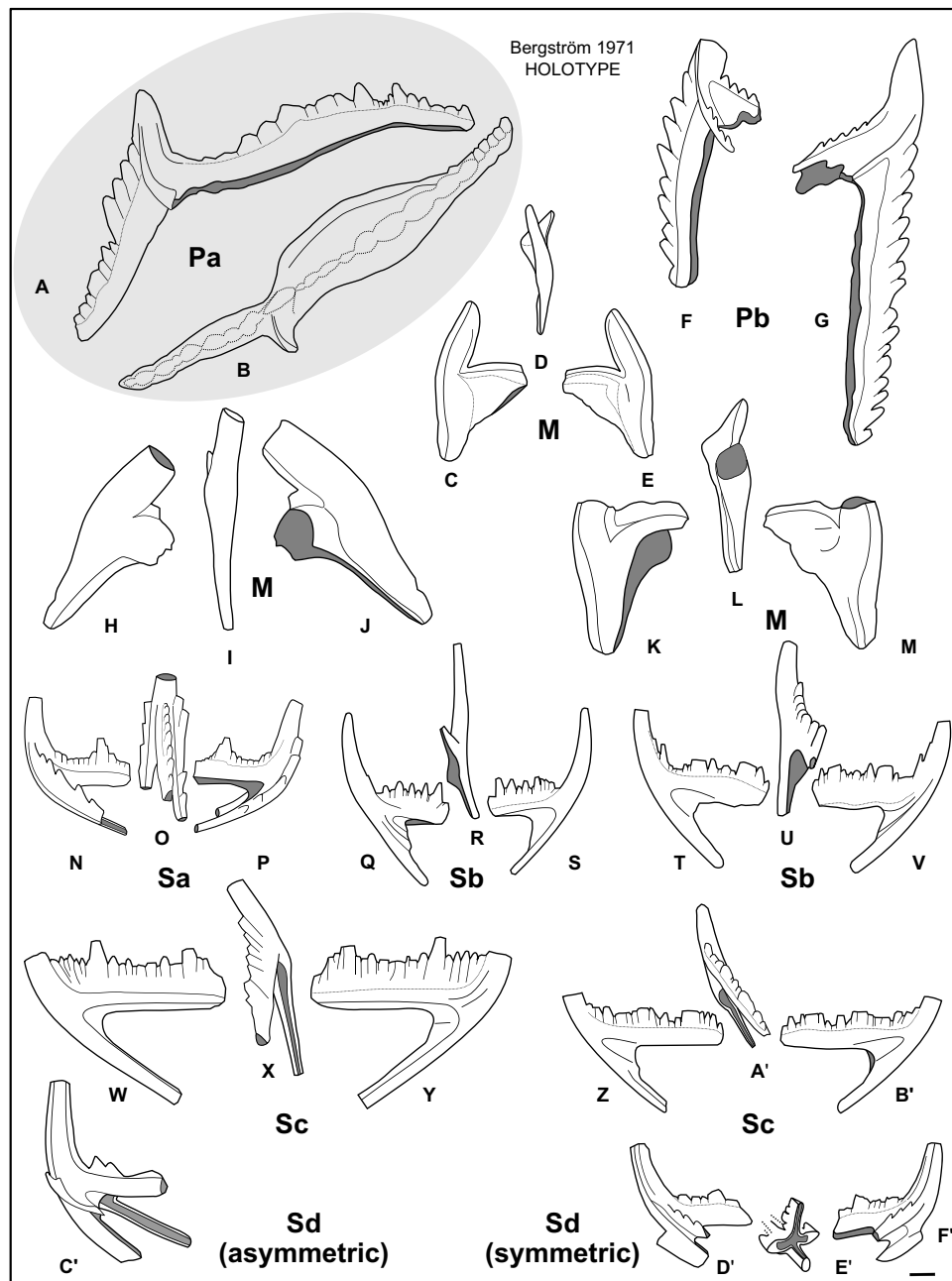


Figure 6. Outline drawings of elements of *Baltoniodus alobatus* (Bergström, 1971). Material comes from the upper part of the middle *B. alobatus* Subzone of the Dalby Limestone in the Fjäckå section, Sweden (Bergström 2007). **A–B**, lateral and upper views of Pa element LO 4333T (holotype), Dalby Limestone, Fjäckå, Dalarna, Sweden (sample D60–160). From Bergström (1971, pl. 2, figs 4–5); **C–E**, lateral and upper views of M element; **F**, lateral view of Pb element; **G**, lateral view of Pb element; **H–J**, lateral and upper-lateral views of M element; **K–M**, lateral and upper views of M element; **N–P**, lateral and postero-lateral views of Sa element; **Q–S**, lateral and posterior views of Sb element; **T–V**, lateral and postero-lateral views of Sb element; **W–Y**, lateral and postero-lateral views of Sc element; **Z–B'**, lateral and posterior views of Sc element; **C'**, postero-lateral view of asymmetric Sd element; **D'–F'**, lateral and lower-lateral views of symmetric Sd element.

2006 *Amorphognathus tvaerensis* Bergström; Viira et al.: 223–227, pl. 1, figs 1–9, 11, 13–15.

2008 *Amorphognathus tvaerensis* Bergström; Viira: pl. 1, figs 5A–R, 6A–I, 8A–S.

2015 *Amorphognathus tvaerensis* Bergström; Männik et al.: fig. 8A–B.

Material. 113 specimens.

Description. This species was introduced by Bergström (1962) based on specimens from the Ludibundus (now Dalby) Limestone at a locality in southeastern Sweden. According to the original description, the non blade-type amorphognathiform (Pa) element

consists of five processes: one anterior, one posterior, and three lateral processes. Among the latter, one bilobate antero-lateral process branches from the anterior process, another bilobate process branches from the anterior part of the posterior process (creating the '1st posterior lateral process') on the opposite side of the antero-lateral process, and one unilobate postero-lateral process ('2nd posterior lateral process') diverges from a middle point of the posterior process on the same side of the bifid postero-lateral process. All lateral processes are shorter than the anterior and posterior processes and carry a single row of denticles (Figures 4A–E, G–H, 11J) or in immature specimens, a thin undenticulate

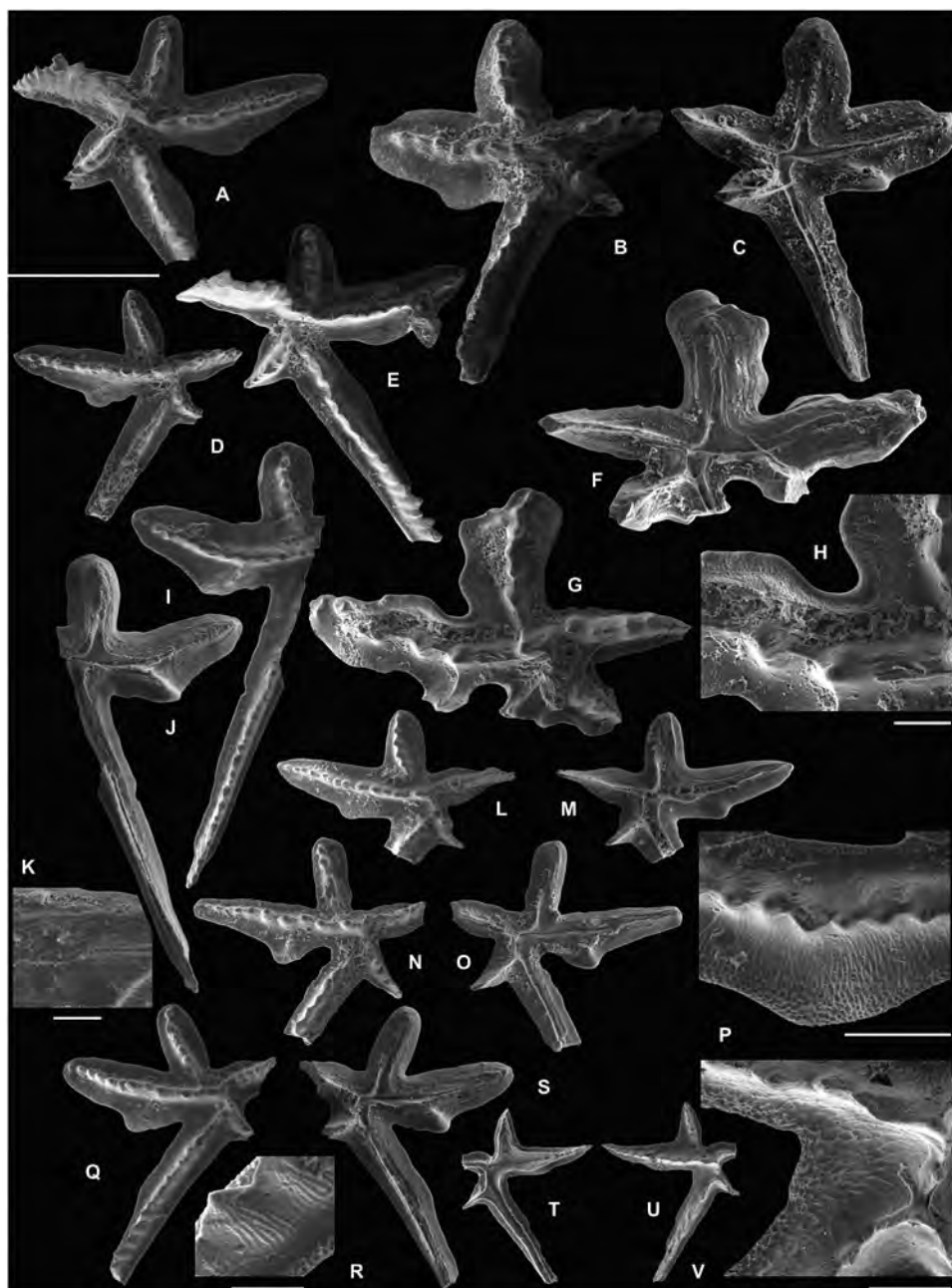


Figure 7. Conodonts from the Middle-Upper Ordovician of South Wales investigated in the present project. **A–V**, *Eoplacognathus lindstroemi* (Hamar, 1964), all figured specimens Pa elements. Note that all specimens are illustrated at the same scale and represent different growth stages. Scale bars correspond to 500 μm except in Figs H, K, and P, where the scale bar is 100 μm , and in Figs R and V where it is 50 μm . **A**, upper view of IPUM 28846, an adult sinistral element from sample Ffairfach; **B–C**, upper and lower views of IPUM 28847, an adult dextral element from sample lens 1 & 2; **D**, upper view of IPUM 28848, a medium-sized dextral element from sample 66–2; **E**, upper view of IPUM 28849, a sinistral adult element from sample lens 2; **F–G**, lower and upper views of IPUM 28850, a dextral adult element from sample Ffairfach; **H**, detail of the upper surface ornamentation of the same specimen; **I–J**, upper and lower views of IPUM 28851, a dextral element from sample 66–2; **K**, detailed view of lower surface of IPUM 28852, a dextral element from sample Ffairfach, showing the almost closed basal cavity; **L–M**, upper and lower views of IPUM 28853, a small dextral element from sample 66–2; **N–O**, upper and lower views of IPUM 28854, a medium-sized dextral element from sample 66–2; **P**, detail of the upper surface of IPUM 28855, a medium-sized sinistral element from sample 66–2; **Q, S**, upper and lower views of IPUM 28856, a medium-sized dextral element from sample lens 1 & 2; **R**, detail of ornamentation of the outer-lateral process of the same specimen in upper view; **T–U**, lower and upper views of IPUM 28857, a dextral small-medium-sized specimen from sample 66–2; **V**, detail of the ornamentation of the same specimen in upper view.

ridge (Figures 4F and 11C). Importantly, in this type of Pa element, there is a single uni-lobe postero-lateral process, not a double one as in *A. inaequalis*.

The blade-type Pa element is similar to the non blade-type Pa element except it lacks the uni-lobe postero-lateral process. Apparently almost complete blade Pa elements of different growth stages occur in our study collections. In blade Pa

elements, the anterior process is shorter than the posterior one and is strongly laterally compressed. The antero-lateral process, which branches from the anterior process, is as a rule broken off in the Welsh specimens but in a single immature specimen (Figures 3E and 11B) it appears to be unilobate. The posterior process may be twice as long as the anterior one and carries a central row of nod-like denticles

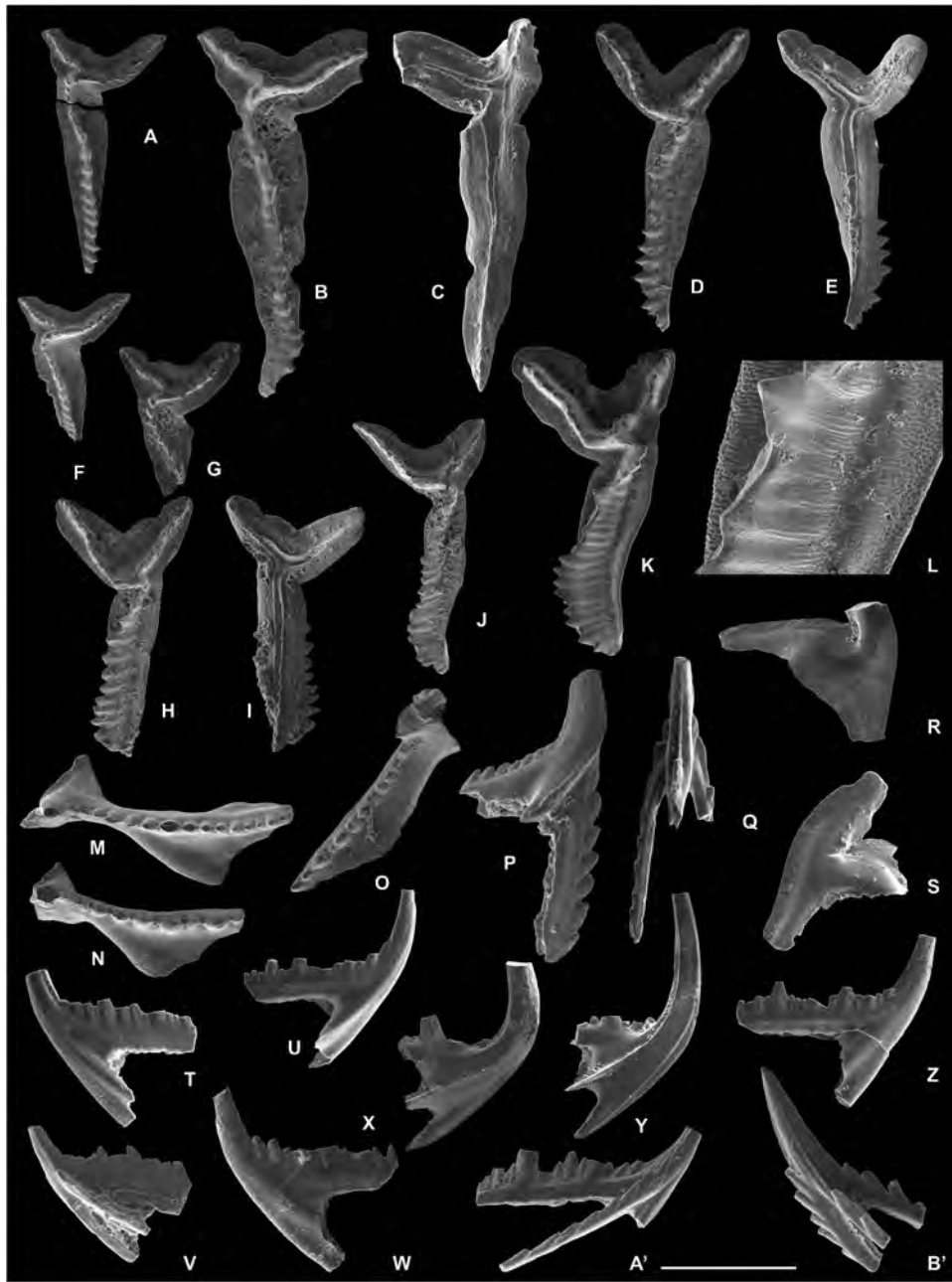


Figure 8. Conodonts from the Middle–Upper Ordovician of Wales investigated in the present project. All specimens are from the Ffairfach railway outcrop. Scale bar corresponds to 500 μm in Figs A–K, 300 μm in Figs M–B', and 150 μm for L. **A–L**, *Eoplacognathus lindstroemi* (Hamar, 1964). **A–L**, Pb elements; **A**, upper view of IPUM 28858, a sinistral medium-sized element from sample lens 1 & 2; **B–C**, upper and lower views of IPUM 28859, an adult sinistral element from sample lens 1 & 2; **D–E**, upper and lower views of IPUM 28860, an adult dextral element from sample lens 2; **F**, upper view of IPUM 28861, a small sinistral element from sample 66–2; **G**, upper view of IPUM 28862, a small sinistral element from sample 66–2; **H–I**, upper and lower views of IPUM 28863, a medium-sized dextral element from sample lens 1 & 2; **J**, upper view of IPUM 28864, an adult dextral element from sample FF gr. Stig; **K**, upper view of IPUM 28865, an adult dextral element from sample lens 2; **L**, a detail of the anterior process in the same specimen; **V**, Sb element, lateral view of IPUM 28875 from sample lens 2; **W**, ?Sc element, lateral view of IPUM 28876 from sample lens 2. **M–U** and **Z–B'**, *Baltoniodus prevariabilis* (Fähræus, 1966). **M**, Pa element, upper view of IPUM 28866 from sample 66–2; **N**, Pa element, upper view of IPUM 28867 from sample 66–2. **O**, Pa element, upper-lateral view of IPUM 28868 from sample lens 2; **P**, Pb element, lateral view of IPUM 28869, sample 66–2; **Q**, Sa element, posterior view of IPUM 28870 from sample 66–2; **R–S**, M elements, lateral views of IPUM 28871 and IPUM 28872 from sample 66–2; **T–U**, Sb elements, lateral views of specimens IPUM 28873 and IPUM 28874 from sample 66–2; **Z**, Sc element, lateral view of IPUM 28879 from sample 66–2; **A'–B'**, Sd elements, lateral views of IPUM 28880 and IPUM 28881 from sample 66–2. **X–Y**, ?*Baltoniodus* sp. Sd non-denticulated elements, lateral views of specimens IPUM 28877 and IPUM 28878, both from sample 66–2.

that continue to the end of the posterior process. In some specimens, the surface of the posterior process opposite and posterior to the postero-lateral process is widened (Figures 3E–F and 11E). The postero-lateral process is bifid with single central rows of denticles on each lobe. A prominent ledge runs along the margin of the processes.

The unpaired Pb elements resemble those in *A. inaequalis*.

The holodontiform (M) elements are represented by only a few specimens (Figure 5G–I), which have three denticulated processes. The anterior process is long and straight and carries a row of basally fused denticles which are continuous with the apical denticulation. The upper margin of the M element has a row of denticles of somewhat large size which is flexed postero-laterally. Among these denticles, the cusp can be distinguished although it is not

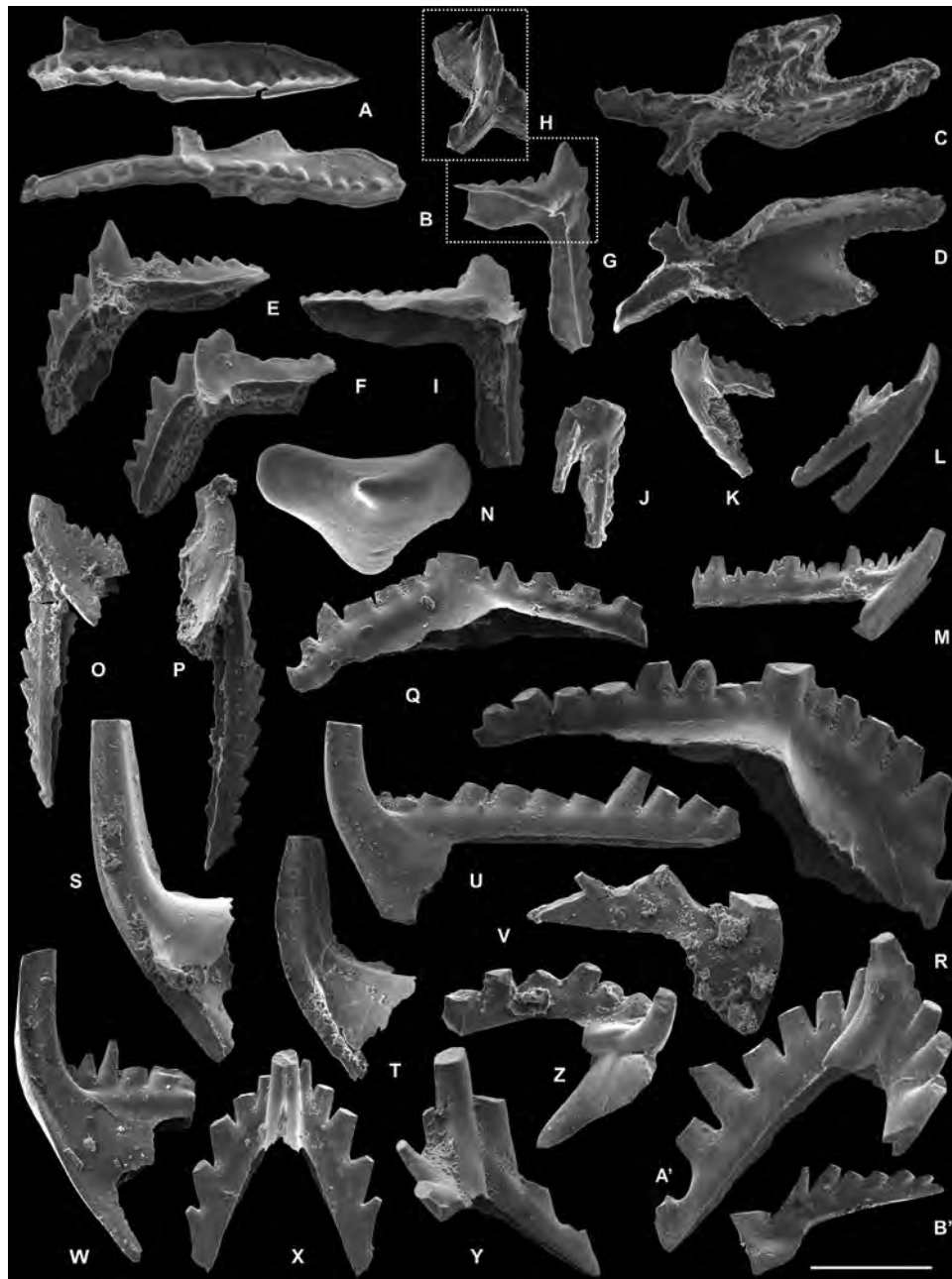


Figure 9. Conodonts from the Middle-Upper Ordovician of Wales investigated in the present project. Scale bar corresponds to 300 μ m. **A–M**, *Amorhognathus inaequalis* Rhodes, 1953. **A**, Pa element, upper view of IPUM 28882 from sample lens 2; **B**, Pa element, upper view of IPUM 28883 from sample DC–LL; **C–D**, Pa element, upper and lower views of IPUM 28884 from sample topotypes Llandeilo; **E–F**, sinistral Pb elements, lateral views of IPUM 28885 and IPUM 28886 from samples GG62–27 and DC–LL, respectively; **G–I**, dextral Pb elements, lateral views of IPUM 28887 (G–H) and IPUM 28888 (I) from samples 66–2 and lens 2, respectively; **J–K**, M element, postero-lateral and antero-lateral views of IPUM 28889 from sample 66–4; **L**, Sb element, lower-lateral view of IPUM 28890 from sample lens 2; **M**, Sc element, lateral view of IPUM 28891 from sample lens 2. **N**, *Pseudooneotodus mitratus* (Moskalenko, 1973), upper view of IPUM 28892 from sample 66–2. **O–P**, *Baltoniodus prevariabilis* (Fähræus, 1966), Pb elements, lateral views of IPUM 28893 and IPUM 28894, both from sample GG62–27. **Q–B'**, *Plectodina flexa* (Rhodes, 1953). **Q–R**, Pa elements, lateral views of IPUM 28895 and IPUM 28896 from sample lens 1 & 2 and lens 2, respectively; **S–T**, Pb elements, lateral views of IPUM 28897 and IPUM 28898 from samples FF gr. Stig and 66–2, respectively; **U**, Sc element, inner-lateral view of IPUM 28899 from samples lens 2; **V**, M element, lateral view of IPUM 28900 from sample GG62–26; **W**, Sc element, inner-lateral view of IPUM 28901 from sample lens 1 & 2; **X**, **A'**, Sa elements, posterior and postero-lateral views of IPUM 28902 and IPUM 28905 from samples FF Rhodes and lens 1 & 2, respectively; **Y–Z**, Sb elements, postero-lateral and posterior views of IPUM 28903 and IPUM 28904 from samples 66–2 and lens 2, respectively; **B'**, M element, lateral view of IPUM 28906 from sample D61–1.

very prominent. Some specimens from Aberiddi Bay have a reclined marginal apical denticle (Figure 5I) as was noted by Bergström et al. (1987).

Remarks. The relations to *A. inaequalis*, the apparent ancestor of *A. tvaerensis*, have been discussed above. Leslie (2000) noted that the M element of *A. tvaerensis* has at least two relatively large denticles adjacent to the cusp whereas *A. superbis* has a single

such denticle and *A. ordovicicus* lacks such denticles adjacent to the cusp.

Genus *Eoplacognathus* Hamar, 1966

Type species. *Ambalodus lindstroemi* Hamar, 1964.

Remarks. *Eoplacognathus* includes species with short stratigraphical ranges and some of these taxa are used as index species for upper Darrwilian and lower Sandbian subzones in the Baltoscandic

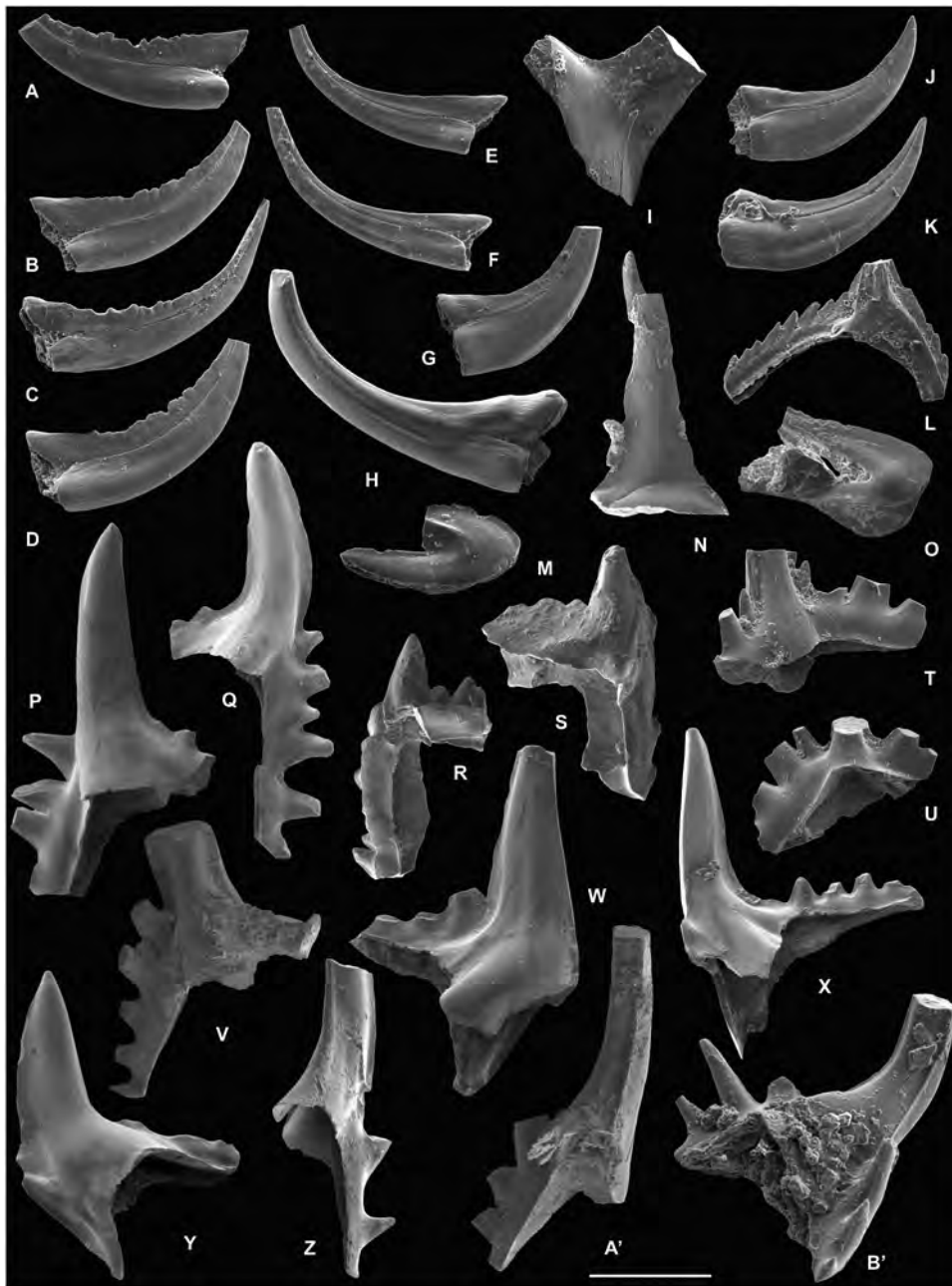


Figure 10. Conodonts from the Middle-Upper Ordovician of Wales investigated in the present project. Scale bar corresponds to 300 μm , M–O, where it is 230 μm , and P, V, Y, A'–B' where it is 370 μm , and Q, W–X, where it is 500 μm . **A–D**, *Panderodus alabamensis* (Sweet and Bergström, 1962). **A**, lateral view of IPUM 28907 from sample 66–2; **B**, lateral view of IPUM 28908 from sample 66–2; **C**, lateral view of IPUM 28909 from sample 66–2; **D**, lateral view of IPUM 28910 from sample 66–2. **E–F**, **H**, *Panderodus gracilis* (Branson and Mehl, 1933). Lateral views of IPUM 28911, IPUM 28912 and IPUM 28914 from sample 66–2 (E–F) and 66–13 (H). **G**, *Panderodus gracilis*, lateral view of IPUM 28913 from sample lens 2. **I**, *Drepanoistodus suberectus* (Branson and Mehl, 1933), IPUM 28915 from sample 66–2. **J–K**, *Panderodus gracilis*, lateral views of IPUM 28916 and IPUM 28917 from samples lens 2 and lens 1 & 2, respectively. **L**, unidentified IPUM 28918 from sample 66–2. **M**, **O**, *Venoistodus venustus* (Stauffer, 1935). Lateral views of IPUM 28919 and IPUM 28921 from samples 66–4 and lens 1 & 2, respectively. **N**, *Drepanoistodus suberectus*, IPUM 28920 from sample 66–13. **P–Q** and **T–B'**, *Erismodus cf. E. bergstroemi* Savage and Bassett, 1985. **P**, Sa element, IPUM 28922 from sample 66–13; **Q**, Sa element, IPUM 28923 from sample 66–13; **T–U**, IPUM 28926 and IPUM 28927 from samples DC–LL and DP–LL respectively; **V**, IPUM 28928 from sample DP–LL; **W–X**, Pb? elements, IPUM 28929 and IPUM 28930, both from sample 66–13; **Y**, M element, IPUM 28931 from sample 66–13; **Z**, M element, IPUM 28932 from sample 66–13; **A'**, IPUM 28933 from sample DP–LL; **B'**, IPUM 28934 from sample GG62–26. **R–S**, *Amorphognathus* sp., Pb elements, lateral views of IPUM 28924 and IPUM 28925, both from sample 66–13.

conodont biostratigraphical scheme (e.g., Bergström 1971; Bergström and Ferretti 2017). The genus was originally proposed in single element taxonomy by Hamar (1966) but Bergström (1971), using multielement taxonomy, revised the genus to include both polyplacognathiform (Pa) and ambalodiform (Pb) elements, both types being morphologically unpaired, which particularly applies to

the Pb elements. Lindström (1974) and subsequent authors have followed this revision of the genus.

Amorphognathiform (Pa) elements are symmetrical, having sinistral and dextral elements as mirror images, bearing an anterior, posterior, and at least two lateral processes, one of which is bilobate. Ambalodiform (Pb) elements, on the contrary, have Y-shaped

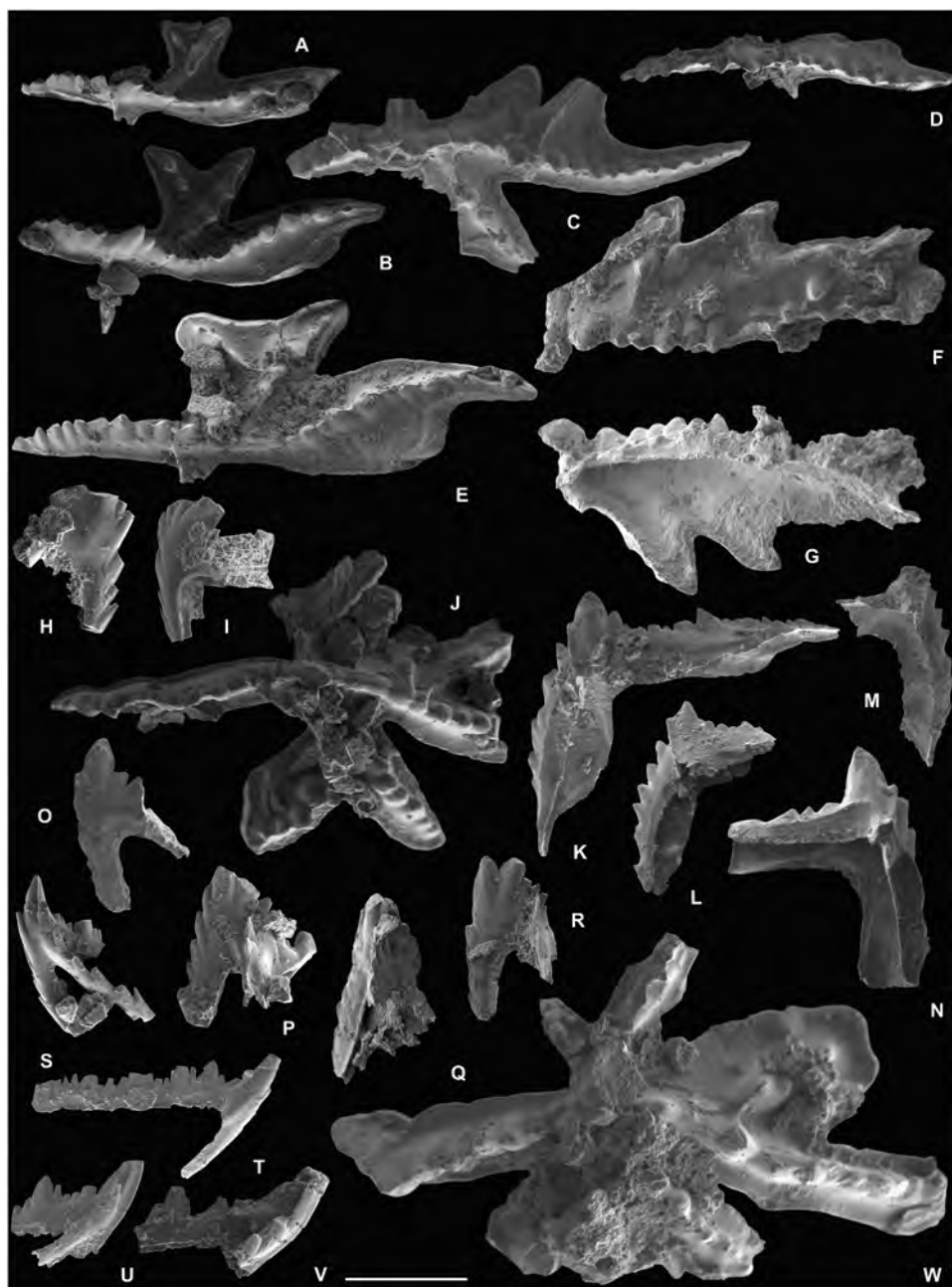


Figure 11. Conodonts from the Middle–Upper Ordovician of Wales investigated in the present project. **A–W**, *Amorphognathus tvaerensis* Bergström, 1962. Scale bar corresponds to 300 μm except for H–I and U–V where it corresponds to 200 μm . Note that the Pa elements are illustrated in the same scale and the size differences reflect different ontogenetic stages. **A–B**, Pa (blade-type) elements, upper views of IPUM 28935 and IPUM 28936 from sample D61–1; **C**, Pa (non blade-type) element, upper view of IPUM 28937 from sample D61–1; **D**, Pa element (non blade-type), upper view of IPUM 28938 from sample D61–1; **E**, Pa (blade-type) element, upper view of IPUM 28939 from sample D62–1; **F–G**, Pa element (non blade-type), upper and lower views of IPUM 28940 from sample AB; **H–I**, M element, postero-lateral and antero-lateral views of IPUM 28941 from sample D61–1; **J**, Pa (non blade-type) element, upper view of IPUM 28942 from sample D61–1; **K–L**, sinistral Pb elements, lateral views of IPUM 28943 and IPUM 28944 from samples D61–1 and AB, respectively; **M–N**, dextral Pb elements, lateral views of IPUM 28945 and IPUM 28946, from sample AB and Ö–LL–DP, respectively; **O**, M element, outer-lateral view of IPUM 28947 from sample D61–1; **P**, M element, postero-lateral view of IPUM 28948 from sample D61–1; **Q**, M element, outer-lateral view of IPUM 28949 from sample D62–1; **R**, M element, postero-lateral view of IPUM 28950 from sample D62–1; **S**, Sb element, lateral view of IPUM 28951 from sample D61–1; **T**, Sc element, lateral view of IPUM 28952 from sample D61–1; **U–V**, Sa elements, lateral views of IPUM 28953 and IPUM 28954, both from sample AB; **W**, Pa (non blade-type) element, upper view of IPUM 28955 from sample D61–1.

sinistral and dextral elements, not specular images each other, bearing three processes, with the anterior process as the longest. Lindström (1977b, p. 128) remarked how ‘its main distinguishing features with respect to *Amorphognathus* Branson & Mehl, 1933f, are the great thickening of the platform ledges and the narrowness of the basal cavity, as well as the development of a strongly outwards pointing

lobe of the anterior lateral process in the amorphognathiform elements, and a very long anterior process in the ambalodiform elements.’

The evolution of the genus, and its relations to several other platform genera, such as *Polyplacognathus* Stauffer, 1935 and *Cahabagnathus* Bergström, 1983 have been discussed



Figure 12. Significant conodonts from the Middle–Upper Ordovician of Wales investigated in this paper. Scale bar corresponds to 300 μm except for T–U, A' where it corresponds to 200 μm and V–W, Y where it corresponds to 500 μm . **A–I**, *Drepanoistodus suberectus* (Branson and Mehl, 1933). **A**, lateral view of IPUM 28956 from sample GG62–27; **B**, lateral view of IPUM 28957 from sample lens 2; **C**, lateral view of IPUM 28958 from sample GG62–26; **D**, lateral view of IPUM 28959 from sample 66–13; **E**, lateral view of IPUM 28960 from sample 66–2; **F**, lateral view of IPUM 28961 from sample GG62–26; **G**, lateral view of IPUM 28962 from sample 66–2; **H**, lateral view of IPUM 28963 from sample 66–2; **I**, lateral view of IPUM 28964 from sample 66–2. **J–R**, *Plectodina flexa* (Rhodes, 1953). **J**, Pa element, lateral view of IPUM 28965 from sample OV; **K**, Pa element, inner–lateral view of IPUM 28966 from sample OV; **L**, Pb element, outer–lateral view of IPUM 28967 from sample OV; **M**, Pb element, inner–lateral view of IPUM 28968 from sample OV; **N**, M element, inner–lateral view of IPUM 28969 from sample OV; **O**, M element, inner–lateral view of IPUM 28970 from sample OV; **P**, Sa element, posterior view of IPUM 28971 from sample OV; **Q**, Sb element, posterior view of IPUM 28972 from sample OV; **R**, ?M element, inner–lateral view of IPUM 28973 from sample OV. **S, U–X**, *Icriodella* cf. *I. praecox* Lindström, Racheboeuf and Henry, 1974. **S**, Pb element, lateral view of IPUM 28974 from sample 66–13; **U, X**, Pa elements, upper views of IPUM 28976 and IPUM 28978 from sample 66–13; **V–W**, Pa element, upper lateral and upper views of IPUM 28977 from sample 66–13. **T**, *Icriodella* cf. *I. superba* Rhodes, 1953. Pa element, upper view of IPUM 28975 from sample AB. **Y**, *Icriodella* sp., Pb element, lateral view of IPUM 28979 from sample Ö–LL–DP. **Z–A'**, *Phragmodus* cf. *P. inflexus* Stauffer, 1935, lateral views of IPUM 28980 and IPUM 28981 from sample AB.

by several authors, including, among others, Bergström (1971, 1973, 1983), Dzik (1976, 1978, 1984, 1994) and Zhang (1998).

Based on collections from China and Sweden, Zhang (1998) gave *Eoplacognathus* a more restricted scope in recognising two species previously referred to *Eoplacognathus* (*E. reclinator* (Fåhræus, 1966) and *E. robustus* Bergström, 1971) as representing

a separate lineage, for which she proposed the generic designation *Baltoplacognathus*. For another lineage, which includes mainly Chinese taxa and which was recognised as a side branch of *Eoplacognathus* by Bergström (1983, fig. 2), she introduced the designation *Yangtzeplacognathus*. The species *E. lindstroemi*, and

E. elongatus remained in *Eoplacognathus* following Zhang's (1998) classification, which has been adopted by some, but not all, subsequent authors. Because the species present in our Welsh collections, *E. lindstroemi*, is the type species of *Eoplacognathus*, its generic classification is obvious whether or not Zhang's (1998) revised classification is accepted.

In some respects, *Eoplacognathus* is reminiscent of *Amorphognathus* Branson & Mehl, 1933, but, as noted by Lindström (1977b), the main distinguishing features from *Amorphognathus* are the great thickening of the platform ledges, the much narrower basal cavity, the conspicuous development of a laterally pointing lobe in the Pa element, and the presence of a very long anterior process in the Pb element.

For many years, *Eoplacognathus* was interpreted to lack ramiform elements in the apparatus (e.g., Bergström 1983). However, in recent years, some authors have proposed that the apparatus of at least some species of this genus included also ramiform and geniculate elements. For instance, Dzik (1994) reconstructed the apparatus of the species *E. zgierzensis* Dzik, 1976 to include, apart from Pa and Pb elements, an M element with three denticulated processes, and a set of four types of S elements. Stouge and Bagnoli (1990) identified S and M elements in *Lenodus* (herein *Eoplacognathus*) *pseudoplanus*.

Viira et al. (2001), in a study of conodonts from the Middle Ordovician Mäekalda section in Estonia, illustrated the apparatus of *Eoplacognathus pseudoplanus* as having ramiform elements (referred to as Sb, Sc1, and Sc2 elements) and a geniculate M element.

In another study, based on a large conodont collection from south-central China and Sweden, Löfgren and Zhang (2003) recognised seven morphologically distinct element types, and possibly a total of 17 elements, in the apparatuses of *Lenodus variabilis*, *Yangtzeplacognathus crassus* and *Eoplacognathus pseudoplanus*. Separation of the non-platform elements of these genera from the homologous ones in the co-occurring *Baltoniodus* specimens was possible based on the presence in the former genera of wart-like extensions at the top of the cusp (cf. Löfgren 1990). Heredia et al. (2014) reported the presence of S and M elements in *E. suecicus*, *E. robustus*, and *E. lindstroemi* and Heredia and Mestre (2019) described full apparatuses of *E. robustus* and *E. lindstroemi*.

Several authors (e.g., Dzik 1994; Löfgren and Zhang 2003; Heredia and Mestre 2019) have discussed the suprageneric classification of these Darriwilian platform genera but at the present time, there is little agreement. The species *E. lindstroemi* clearly evolves into *E. elongatus* and several authors (e.g., Barnes and Fähræus 1975) have suggested that the latter species is the ancestor of *Polyplacognathus ramosus* Stauffer, 1935 although transitional forms between the two latter taxa have not yet been recorded.

The latter species has generally been interpreted to have a bimembrate apparatus but its platform elements are commonly associated with ramiform elements originally described as *Trichonodella? tricurva* Schopf, 1966 and *Tetraprioniodus breviconus* Webers, 1966. Both these taxa look like S elements and they were later referred to a new genus, *Schopfodus* Leslie, 1996. Although Leslie (1996) expressed the opinion that these elements might not be a part of the apparatus of *P. ramosus*, we feel that at the current state of knowledge, this possibility cannot be dismissed. If this idea proves to be correct, the S elements of this taxon differ conspicuously from those assigned to early species of *Eoplacognathus*. This obviously would support the current generic separation of these two genera.

Eoplacognathus lindstroemi (Hamar, 1964)

(Figures 7A-V, 8A-L)

1964 *Ambalodus lindstroemi* n. sp. Hamar: 258-259, pl. 5, figs 1, 4, 7-8, 10-11, text-fig. 5: 1a-b, 3a-b, 4a-b.

1964 *Ambalodus* aff. *lindstroemi* n. sp. Hamar: 259-260, pl. 5, figs 5, 12, text-fig. 5: 2a-b.

1964 *Polyplacognathus elongata* (Bergström); Hamar: 275-276, pl. 6, figs 3, 6-10, text-fig. 5: 7a-b, 9a-c.

1967 *Eoplacognathus lindstroemi* (Hamar); Viira: fig. 4: 5a-b.

1971 *Eoplacognathus lindstroemi* (Hamar); Bergström: 139, pl. 2, figs 15-18, text-fig. 4-5: 9.

1977b *Eoplacognathus lindstroemi* (Hamar); Lindström: 135-136, pl. 1, figs 7-9 (contains additional synonyms from the 1970s).

1985 *Eoplacognathus lindstroemi* (Hamar); Bergström and Orchard: 58, pl. 2.2, figs 11, 13.

1998 *Eoplacognathus lindstroemi* (Hamar); Zhang: text-fig. 8A-K.

1990 *Eoplacognathus lindstroemi* (Hamar); Stouge and Bagnoli: pl. 2, figs 5-8.

2006 *Eoplacognathus lindstroemi* (Hamar); Heredia and Rosales: fig. 3: 7, 11.

2008 *Eoplacognathus lindstroemi* (Hamar); Viira: fig. 6P.

2011 *Eoplacognathus lindstroemi* (Hamar); Viira: fig. 9G.

2012 *Eoplacognathus lindstroemi* (Hamar); Hints et al.: fig. 5G-I.

2019 *Eoplacognathus lindstroemi* (Hamar); Heredia and Mestre: fig. 4.

Description. The Ffairfach conodont collection contains a surprisingly large number of well-preserved elements of this geographically widespread species. Many of the elements are complete and the presence of growth stages illustrates the ontogeny of both the Pa and Pb elements. Both the Pa and Pb elements of this species are easily recognisable also in fragments by their thick and robust platform ledges and the narrow, slit-like basal cavity. Even the smaller specimens revealed to have yet the diagnostic features well delineated, both in Pa and Pb elements.

Because elements of this species have been described repeatedly in the literature, we restrict ourselves to offer only some specific comments. The Pa elements have a straight antero-posterior axis and a well-developed postero-lateral process which is almost as long as the posterior process. The posterior process is expanded laterally (Figure 7B, D) with a bifurcating terminal denticulation in many mature specimens (Figure 7E). According to Lindström (1977b) the Pb elements have posterior and lateral processes of approximately equal length, diverging from one another at an angle 'Y-shaped.' In our collection, this applies only to the dextral Pb elements, which have two processes of similar size that represent the upper 'arms' of the Y. Sinistral elements have lateral processes that are always shorter than the posterior one. The posterior process of sinistral elements lacks lateral expansion of the posterior part of its distal corner also in mature specimens. In both sinistral and dextral elements, the antero-posterior axis is lightly sinuous.

Despite the large number of platform elements in our collections, there are only a few M and S elements that may possibly be a part of the *E. lindstroemi* apparatus based on previous descriptions of such elements. Hence, a single broken M element recovered in sample 66-2 has a distinct anterior margin denticulation, a proclined cusp and a typical continuity in the curve of the anterior process and cusp that serve to separate this element from the M element in *Baltoniodus*.

No Sa element was recovered but a single Sb element (Figure 8V) from the same sample has three denticulated processes, which are connected by a basal sheet. These elements are distinguished from the corresponding element in *Baltoniodus* by the presence of a denticulated lateral process. A possible Sc element (Figure 8W) was recovered from the same sample.

A polygonal micropattern has been observed on the platform ledges of the Pa and Pb elements but not in the M and S elements. It should be noted that Löfgren and Zhang (2003) observed such micro-ornamentation in S elements of *Lenodus antivariabilis*. There are also thin parallel striae running from the platform ledges to and along the denticles in both the Pa and Pb elements.

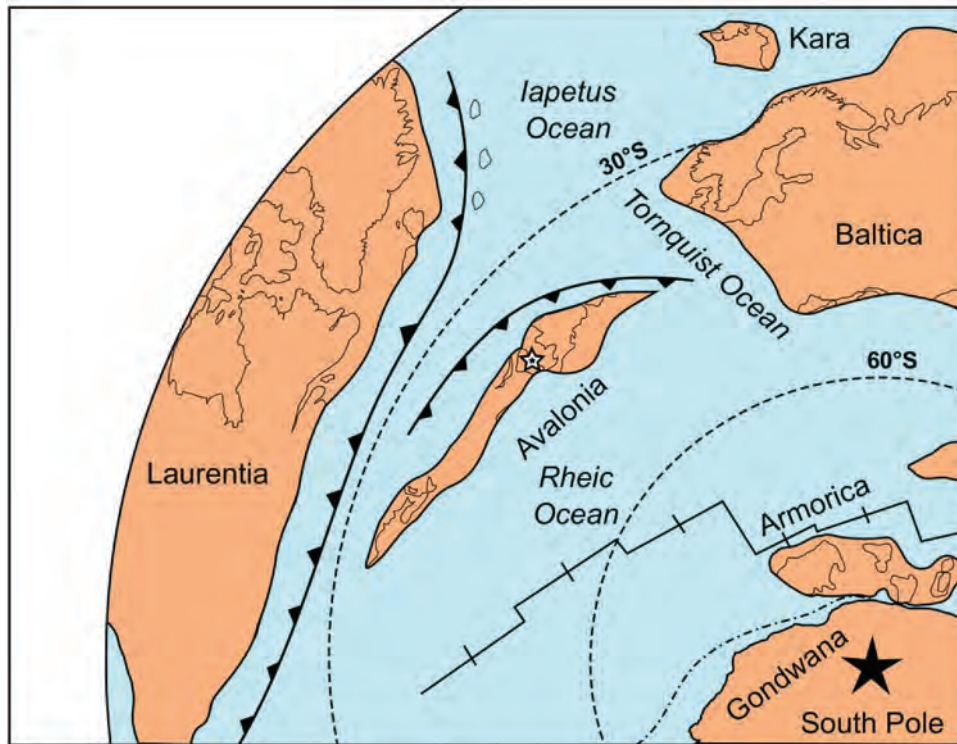


Figure 13. Hypothetical palaeogeographical sketch map of the Iapetus-Rheic region during Sandbian-early Katian time (slightly modified after Bergström and Ferretti 2018) showing the geographical location of the microcontinent Avalonia between Baltica and Laurentia. Open star marks the location of the Llandeilo region in Avalonia.

Remarks. In an attempt to better define the differences between the M and S elements of *E. lindstroemi* and corresponding elements of *Baltoniodus*, which are superficially closely similar, we examined large collections of *Baltoniodus* from the Dalby Limestone at Fjäska, in south-central Sweden (Bergström 2007). In the latter genus, the Pa and Pb elements are quite different from the homologous elements in *E. lindstroemi*. In *Baltoniodus*, the M elements have a long, generally adenticulated, anterior process (Figure 6C–E, H–M) that in some elements may have a distal crenulation. These elements have a flat inner face and a strongly convex outer face due to the presence of a conspicuous lateral bulge on the base. In inner view, both the inner and outer basal margin are visible. In some specimens, the cusp is twisted with respect to the base.

The Sa elements of *Baltoniodus* are symmetrically alate (Figure 6N–P) with three denticulated processes. In many specimens, the posterior process has a hindeodellid type of denticulation.

The Sb elements (corresponding to Sc2 elements of Löfgren; Figure 6Q–V) are asymmetrical, strongly compressed laterally, and have a more or less undenticulated lateral rib near the anterior margin.

The Sc elements (corresponding to the Sc1 elements of Löfgren; Figure 6W–B') are similar to the Sb elements but differ from the Sb elements in lacking the outer lateral rib. In some cases it is difficult to separate Sb and Sc elements.

Sd elements (corresponding to Sb elements of Löfgren; Fig. 6C'–F') are tetracostate, having four denticulated processes that may be symmetrically or asymmetrically arranged in relation to the posterior process. In this type of element, the posterior process in some elements has a hindeodellid type of denticulation.

Genus *Erismodus* Branson and Mehl, 1933

Type species. *Erismodus typus* Branson and Mehl, 1933.

Erismodus cf. *E. bergstroemi* (Savage and Bassett, 1985)

(Figure 10P–Q, T–B')

1964 *Erismodus* cf. *E. typus* Branson and Mehl; Bergström: 42–43, text-fig. 21G–H.

1964 *Chirognathus* sp. Bergström: 42, text-fig. 21D.

cf. 1985 *Plectodina bergstroemi* sp. nov. Savage and Bassett: 700, pl. 82, figs 1–16.

Material. 141 elements.

Remarks. One of the more notable taxa in our collections from the Llandeilo region includes frequently very large but uncommon elements that are currently difficult to classify. Bergström (1964) first described these elements and interpreted them as representatives of the North American genus *Erismodus* based on the similarity of some of these elements to *E. typus*, the type species of *Erismodus*. Bergström (1964) also illustrated another type of element that he referred to another North American genus, namely *Chirognathus* Branson & Mehl, 1933. We now believe that these types of elements are likely to belong to the same multielement apparatus but the currently available Welsh collections are insufficient to reconstruct the composition of this apparatus. Added to this problem is the fact that the apparatus of *E. typus* is not well known. Interestingly, Savage and Bassett (1985) described very similar conodonts from the Caradocian of South Shropshire which they named *Plectodina bergstroemi*. Our collections from the lower Caradocian of that region includes some representatives of this taxon but the collections at hand are insufficient to determine if the Caradocian species is the same as the Llandeilo one. However, we believe that these distinctive conodonts are not representatives of *Plectodina* but are more likely to belong to *Erismodus*. Pending the availability of more informative collections, we prefer to tentatively classify the Llandeilo specimens as *Erismodus* cf. *E. bergstroemi*.

Genus *Icriodella* Rhodes, 1953

Type species. *Icriodella superba* Rhodes, 1953.

Icriodella cf. *I. praecox* Lindström, Racheboeuf and Henry, 1974

(Figure 12S, U-X)

cf. 1974 *Icriodella praecox* n. sp. Lindström et al.: 18, pl. 1, fig. 7, pl. 2, figs 5-6, 8-9.

1985 *Icriodella* cf. *praecox* Lindström et al.; Bergström and Orchard: 58, pl. 2.3, figs 7, 10, 12-14.

1987 *Icriodella* sp. cf. *I. praecox* Lindström et al.; Bergström et al.: pl. 18.1, figs 1, 3.

Material. One specimen from the Narberth succession and eight from Evenwood, Welsh Borderland (Bergström 1971) for a total of nine elements.

Description. Lindström et al. (1974) proposed their new species of *Icriodella* based on specimens with a single row of denticles running in the centre of the anterior and posterior processes of a Pa element. They also recorded a Pb element and a Sa element associated with the Pa element. Our collections from the Narberth sections (Bergström et al. 1987) include Pa elements with a distinct cusp, equal-sized anterior and posterior processes, and a short undenticulated lateral process. The denticles in the single central denticle row are well developed and more massive than in the French holotype described by Lindström et al. (1974, pl. 2: 5-6) in which the raised central ridge of the upper platform surface is crenulated. The Pb and S elements are more similar than the Sa element to those of *I. superba* and the S elements have well developed denticulation.

Remarks. The holotype (Pa) and Pb element illustrated by Lindström et al. (1974) are relatively small and possibly juvenile specimens. However, in the Narberth collections, the denticulated ramiform elements are of similar size as the Pa element. Hence, the weak denticulation in the Pa element is unlikely to reflect just an early ontogenetic stage.

Genus *Panderodus* Ethington, 1959

Type species. *Paltodus unicosatus* Branson and Mehl, 1933.

Remarks. Despite the study by, among others, Sansom et al. (1994), the multielement taxonomy of species of *Panderodus* is currently not well understood and this particularly applies to Ordovician taxa. As shown by Fähræus and Hunter (1985) there is a great deal of variation in the morphology of the coniform elements in the apparatus of *P. gracilis* (Branson & Mehl) and the discovery of an apparent apparatus in the Waukesha Lagerstätte in the lower Silurian Brandon Bridge Formation in Wisconsin (Smith et al. 1987; Sansom et al. 1994) has not helped greatly in clarifying which morphological characteristics are of particular importance to separate *Panderodus* taxa at the species level. Our study collection contains both graciliform (Figure 10E-F) and sulcatiform (Figure 10G, J-K) elements. Furthermore, there are weakly denticulated elements (Figure 10A-D). Provisionally, we distinguish two species in our collections from the Llandeilo region, namely *P. alabamensis* (Sweet and Bergström, 1962) and *P. gracilis* (Branson and Mehl, 1933).

Panderodus alabamensis (Sweet and Bergström, 1962)

(Figure 10A-D)

1962 *Belodina alabamensis* Sweet & Bergström: 1223-1224, pl. 170, figs 10-11.

1969 *Panderodus?* *alabamensis* (Sweet & Bergström); Ethington and Schumacher: 469, pl. 69, fig. 8.

cf. 1981 *Panderodus* aff. *P. serratus* Rexroad; Nowlan: 12, pl. 1, figs 16, 19.

Material. 96 specimens.

Remarks. The present species was described in detail by Sweet and Bergström (1962) based on a small number of elements from the latest Darriwilian Pratt Ferry Beds in Alabama. They interpreted it as

a primitive species of *Belodina* that was transitional between coniform taxa and typical representatives of *Belodina*. Ethington and Schumacher (1969) recognised that apart from the denticulated upper margin, this species is closely similar to species of *Panderodus* and they questionably referred this taxon to the latter genus, an opinion we now share. The precise composition of its apparatus is still not firmly established but in the Pratt Ferry collections, typical denticulated elements are associated with closely similar elements lacking denticles. This is also the case in our collections from the Llandeilo region.

We have had the opportunity to carry out side-by-side comparisons between the Welsh elements and Pratt Ferry topotypes and found no obvious difference. Also the specimen illustrated by Ethington and Schumacher (1969, pl. 69, fig. 8) appears to belong to the same taxon. The specimens illustrated by Nowlan (1981, pl. 1, figs 16, 19) are less well preserved but in overall morphology, they are similar to *P. alabamensis*. It is noteworthy that all these occurrences are of about the same age, being from a narrow stratigraphical interval in the latest Darriwilian to the earliest Sandbian. On the other hand, the relatively recently described Swedish species *P. serratus hallekisensis* Mellgren, 2010 comes from a stratigraphical older part of the Darriwilian, namely the *Lenodus variabilis* Zone. This taxon is distinguished from *P. alabamensis* by being more slender and having proclined, rather than straight, denticles (cf. Mellgren 2010, fig. 5). Also, the denticulated *P. serratus* (Rexroad, 1967) from the lower Silurian Brassfield Limestone of southern Ohio (Rexroad 1967; Cooper 1975) differs from *P. alabamensis* in that the elements are more slender and have a differently shaped base.

Panderodus gracilis (Branson and Mehl, 1933)

(Figure 10E-H, J-K)

1933 *Paltodus gracilis* Branson and Mehl: 108, pl. 8, figs 20-21.

1953 *Paltodus equicostatus* n. sp. Rhodes: 297, pl. 21, figs 106-109, pl. 22, figs 162, 165.

1964 *Panderodus gracilis* (Branson & Mehl); Bergström: 32, text-fig. 16.

For many additional synonyms, see Bergström and Sweet (1966, p. 355-359); Del Moral and Sarmiento (2008, p. 200, 202); Voldman and Toyos (2019, p. 470).

Material. 433 specimens.

Remarks. As noted by Bergström (1964, p. 31), Rhodes (1953) described three species of *Panderodus* (= *Paltodus* in Rhodes) from the Llandeilo Limestone, namely *P. acostatus* (Branson and Branson, 1947), *P. equicostatus* n. sp., and *P. unicosatus* (Branson and Mehl, 1933). Bergström (1964) suggested that *P. equicostatus* was a junior synonym of *P. gracilis*. The latter is a stratigraphically long-ranging taxon that has been adequately described by several authors and our investigation of our collections from South Wales adds nothing to the knowledge of the species. Sansom et al. (1994, text-fig. 7) illustrated seven types of elements in the apparatus of *P. gracilis* based on collections from Washington Land, North Greenland but we have experienced difficulty in sorting up our Welsh collections into their shape categories.

Genus *Phragmodus* Branson and Mehl, 1933

Type species. *Phragmodus primus* Branson and Mehl, 1933 (= *P. undatus* Branson and Mehl, 1933).

Remarks. Based on new collections from the type stratum of *P. primus*, Leslie and Bergström (1995) showed that there is no obvious morphological difference between this species and the much more widely distributed and better known species *P. undatus* Branson and Mehl, 1933. These two species were proposed in the same publication so neither name has priority, but Leslie and Bergström (1995) suggested that in view of the far more widespread use of the species name *P. undatus*, it would be appropriate to use that species name for this taxon. It is of interest to note that *P. undatus* has

been found, although rarely, in a few British faunas. Such occurrences include the Shoeshook Limestone of South Wales (Ferretti et al. 2014a), the Alternata Limestone in the Welsh Borderland, Shropshire (Savage and Bassett 1985), the Glyn Formation in north-central Wales (Savage and Bassett 1985), and the Whitehouse Group at Girvan, South Scotland (Bergström 1990).

Phragmodus* cf. *P. inflexus Stauffer, 1935 (Figure 12Z-A')

Material. Four specimens.

Remarks. In Bergström's (1964) collections from the Castell Limestone at Aberiddi (formerly Aberiddy) Bay, there are four S elements that closely resemble those of the North American species *P. inflexus* Stauffer, 1935. It should also be noted that our Castell Limestone elements exhibit some similarity to the tr (S) elements of *Phragmodus polonicus* Dzik, 1978 (cf. Dzik 1994, fig. 25b-c). To confirm the identification, additional collecting is needed to recover the other elements of the apparatus. Because this is the only potential record of this species in Europe, it has considerable biogeographical interest. This species has not been recovered in the Llandeilo region.

Genus *Plectodina* Stauffer, 1935

Type species. *Plectodina dilatata* Stauffer, 1935.

Plectodina flexa (Rhodes, 1953) (Figure 9P-A')

1953 *Cordylodus rectilineatus* (Stauffer); Rhodes: 300-301, pl. 22, figs 172-175.

1953 *Cyrtoniodus complicatus* Stauffer; Rhodes: 302, pl. 22, figs 193-196.

1953 *Trichonodella flexa* n. sp. Rhodes: 313-314, pl. 22, figs 181-183, 188-189, 191-192.

1953 *Trichonodella* sp. Rhodes: pl. 22, fig. 190.

1953 *Dichognathus* cf. *D. typicus* Branson & Mehl; Rhodes: 317-318, pl. 22, figs 178-180.

1953 *Gyrogathus elongatus* n. sp. Rhodes: 318-319, pl. 22, figs 201-202, 205-206.

1953 *Ozarkodina tenuis* Branson & Mehl; Rhodes: 320, pl. 22, figs 187, 197-200.

1964 *Trichonodella flexa* Rhodes; Bergström: 39-40, text-fig. 20.

Material. 2267 elements.

Description. This species is the most abundant taxon in our Llandeilo region collections and all components of the apparatus are present. The blade-like Pa elements (Figure 9Q-R) have a somewhat expanded basal cavity that extends, especially in mature specimens, along the under side of the anterior and posterior processes. These processes are of about equal length and form an angle of 130-140 degrees with each other in lateral view. In most cases, the anterior process is slightly wider (higher) than the posterior one. Both processes carry about half a dozen short and erect denticles that tend to be less densely spaced in the posterior process. The Pb elements in our collection are broken but appear to be of dichognathiform type (Figure 9S-T). The M element has a well-developed, more or less straight posterior process with about half a dozen very strongly reclined, densely spaced, denticles of about half the length of the cusp (Figure 9V, B'). One face of the base of the cusp is expanded laterally to form a bulge, the pointed basal corner of which forms an angle of slightly less than 50 degrees with the anterior margin of the cusp. The S elements form a transition series of four types of elements. The Sa element (Figure 9X) is alate but lacking posterior process. Its two lateral processes have a small number of stout and straight denticles of about half the length of the cusp. It should be noted that the specimen illustrated in Figure 9X is essentially identical in morphology to Rhodes' holotype of *Trichonodella flexa* (cf. Bergström 1964, text-fig. 20). The Sb element (Figure 9Y-Z) is conspicuously digyrate with two asymmetrically located lateral processes and no posterior process. The Sc element (Figure 9U-W) is

dolabrate with a series of slightly reclined denticles along the posterior process. There is no distinct Sd element but slightly asymmetrical elements that are morphologically intermediate between the Sb and Sa elements (Figure 9A') are present.

Remarks. In general organisation, the apparatus of *P. flexa* agrees with that of several species of *Plectodina* best known in the North American Midcontinent faunas, such as *P. tenuis* Branson and Mehl, 1933. Components of the apparatus of these taxa have been described in a multitude of form taxonomic names (cf. Bergström and Sweet 1966) but the multielement taxonomy of species of this genus has not yet been fully established. Especially in the appearance of the Pa element, *P. flexa* is clearly different from, for instance, *P. tenuis*, *P. aculeata* Stauffer, *P. florida* Sweet, *P. aculeatoides* Sweet and *P. bullhillensis* Savage and Bassett but in some characteristics, it is similar to specimens from the Welsh Borderland identified as *P. tenuis* by Savage and Bassett (1985). Pending a needed revision of the genus, we herein use the species name introduced by Rhodes (1953) for the late Darriwilian-early Sandbian species from the Llandeilo region.

***Plectodina* sp.**

(Figure 12J-R)

Material. 59 elements.

Remarks. A complete set of elements of the *Plectodina* apparatus was documented in the material from Onny Valley and a single element was recovered from the Evenwood Quarry. Pa elements do not reveal the expanded basal cavity that typifies *P. flexa* (compare Figures 9Q-R and 12J-K). Furthermore, Pb elements are typical arched dichognathiform elements that preserve a denticulate anterior and posterior processes but are lacking the plica observed in the corresponding element of *P. flexa* (compare Figures 9S-T and 12L-M). On the contrary, a ridge is visible in outer-lateral view. M and S elements are indistinguishable from the homologous elements of *P. flexa*. This species from Onny Valley might be new, but it is insufficiently known at present.

Conclusions

The principal results of the present study may be summarised as follows:

1. The examination of all available conodont collections from the reference sections of the British Llandeilian Stage confirms the biostratigraphical conclusions presented by Bergström et al. (1987), namely that in its classical development in the Llandeilo region, the age of the Llandeilo Flags corresponds to an interval ranging from the *Sagittodontina?* *kielcensis* Subzone of the *Pygodus anserinus* Zone to the *Baltoniodus variabilis* Subzone of the *A. tvaerensis* Zone. The underlying Ffairfach Group yields diverse conodont faunas of the *Eoplacognathus lindstroemi* Subzone of the *Pygodus serra* Zone and its upper part is of late Darriwilian age. Following the common practice of defining the base of the regional Caradoc Series as the base of the *Nemagraptus gracilis* Zone, most of the type Llandeilian succession corresponds to the lower Caradoc, only the lowermost part of the Llandeilian being of pre-Caradoc age.

2. The conodont faunas of the upper Ffairfach Group and the overlying Llandeilo Flags of the Golden Grove Group include about 20 multielement species. Apart from the presence of a few widespread coniform species, these faunas are characterised by the presence of stratigraphically important platform taxa of *Amorphognathus*, *Eoplacognathus*, and *Icriodella* along with representatives of the widespread genus *Baltoniodus*. Because these genera exhibited rapid evolution and the development of short-ranging species, they are very useful for precise biostratigraphical dating, especially as these taxa commonly are quite widespread geographically.

3. The investigated conodont faunas from Wales have their own provincial character. The biostratigraphically broadly equivalent Sandbian conodont fauna recently described from the Garn Formation of Anglesey (Bergström and Ferretti 2018) includes representatives of *Amorphognathus*, *Eoplacognathus*, and *Baltoniodus* but the presence of *Periodon*, *Protopanderodus*, *Pygodus*, and *Spinodus* gives the Garn conodont fauna a rather different appearance than those from the Llandeilo area. In view of its presumed geographical location off the microcontinent Avalonia between Baltica and Laurentia during Sandbian-early Katian time (Figure 13) it is not surprising that the Avalonian conodont faunas dealt with herein share quite a few species with coeval Baltoscandic faunas (cf. Männik and Viira 2005; Bergström 2007) but most of the latter differ by the absence of, for instance, representatives of *Plectodina* and the common occurrence of *Protopanderodus*, *Periodon* and *Pygodus*. Equivalent faunas from the eastern Appalachian thrust belts in North America (e.g., Sweet and Bergström 1962; Bergström 1971) share quite a few species with the Welsh faunas dealt with herein but they also contain a variety of different species. On the other hand, equivalent faunas from the North American Midcontinent, for instance the Tulip Creek Formation of Oklahoma (Bauer 1987), have very little in common with the Darriwilian-Sandbian faunas of Wales. For further discussion of the global conodont biogeography of this stratigraphical interval, see Bergström (1973, 1983), Dzik (1993), and Sweet and Bergström (1974).

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APPENDIX. LIST OF COLLECTING LOCALITIES

- 66-2: Ffairfach Flags. Collected by SMB in 1966.
- 66-4: Ffairfach Conglomerate. Collected by SMB in 1966.
- lens 1 & 2: the original collection by Rhodes (1953).
- lens 2: the original collection by Rhodes (1953).
- Ffairfach: the original collection by Rhodes (1953).
- FF Rhodes: the original collection by Rhodes (1953).
- FF gr. Stig: Ffairfach Flags.
- DC-LL: lower Llandeilo, Dynevor Castle. 74B70-1.
- DP-LL: lower Llandeilo, Dynevor Park. 74B70-2.
- D61-1: upper Llandeilo, Dynevor Park. 85B61-1.
- D62-1: upper Llandeilo, ~50 m below top Dynevor Park. 85B62-1.
- AB: Abereiddi Bay, type locality of Castell Limestone W62-17B.
- 66-13: Costonian, Evenwood.
- Ö-LL-DP: upper Llandeilo, Dynevor Park.
- OV: Onny Valley, basal Costonian. 74B75-1.
- topotypes Llandeilo: Golden Grove, lower Llandeilo. Locality 1 of Rhodes (1953).
- GG62-26: Golden Grove, lower Llandeilo. Locality 1 of Rhodes (1953). 55 feet below top of succession.
- GG62-27: Golden Grove, lower Llandeilo, top of succession.