

Original Article

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Chitinozoan biostratigraphy of the regional Arenig Series in Wales and correlation with the global Lower–Middle Ordovician series and stages

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Abstract

The Arenig Fawr area of North Wales constitutes the type area for the British Lower to Middle Ordovician Arenig Series and is complemented by sections in the Carmarthen and Whitland areas of South Wales. We describe chitinozoan assemblages from both areas in order to aid correlation of the Arenig Series in its type region with the global Ordovician series and stages. Chitinozoans recorded from Arenig Fawr provide permissive rather than conclusive evidence but suggest that the Henllan Ash Member correlates with the upper Floian Stage Slice Fl3 or lower Dapingian Stage Slice Dp1. Better results were obtained from South Wales where six chitinozoan assemblages are distinguished, ranging in age from late Tremadocian to middle Darriwilian (early Llanvirn). Most species are known from South China, Gondwana and/or Baltica where there are controls on ranges. They show that much of the lower Arenig (Moridunian) succession in South Wales correlates with the upper Floian Stage (Fl3). Correlatives of the lower and middle Floian Stage (Fl1, Fl2), if present, must be represented by the Ogof Hên Formation and lowest Carmarthen Formation. Chitinozoan assemblages from the upper Arenig Series (Fennian Stage) are more readily correlated with Gondwanan biozones and indicate correlation of the Fennian Stage with the Dapingian and lower Darriwilian (Dw1) stages. The middle Arenig Whitlandian Stage is constrained in South Wales to an interval from the uppermost Floian Stage to the basal Dapingian Stage, resulting in an inferred increased rate of sediment accumulation.

1. Introduction

Following establishment of the Ordovician System in England and Wales by Lapworth (1879), the Anglo-Welsh Ordovician succession and its constituent series (Tremadoc, Arenig, Llanvirn, Caradoc, Ashgill; Fortey *et al.* 2000) served as a standard reference for Ordovician correlation for more than a century (e.g. Williams *et al.* 1972, fig. 2; Fortey *et al.* 1991). Nevertheless, as a type area for the system, the Anglo-Welsh region has its limitations. Structural complexity is common and much of the succession, particularly in the Welsh Basin and NW England, has been subjected to low-grade metamorphism. In addition, there is a lack of long continuous sections and a predominance of clastic sedimentary rocks that hampers the recovery of some stratigraphically useful fossil groups, notably conodonts (Fortey *et al.* 1991). Despite efforts to redefine the Anglo-Welsh series in accordance with modern stratigraphic practice and more appropriate stratotypes (Fortey *et al.* 1995, 2000), the global Ordovician series (Lower, Middle and Upper) and stages (Tremadocian, Floian, Dapingian, Darriwilian, Sandbian, Katian and Hirnantian; Bergström *et al.* 2009) are now all defined outside the British Isles (Cooper & Sadler, 2012). Nevertheless, as the historic type region for the system, England and Wales remain a key reference area for Ordovician stratigraphy.

Graptolites and conodonts are the quintessential tools of Ordovician biostratigraphy, although trilobites and other shelly fossils have also been used (e.g. Fortey & Owens, 1987). Chitinozoans have the potential for global Ordovician biostratigraphic correlation, and chitinozoan biozonations have been developed for Baltica (Nölvak, 1999; Nölvak *et al.* 2006), different parts of Gondwana (Paris, 1990; Paris *et al.* 1995, 2007; Grahn, 2006; Quintavalle & Playford, 2006; Videt *et al.* 2010; de la Puente & Rubinstein, 2013; Nowak *et al.* 2016), South China (X Wang *et al.* 2005, 2009; Chen *et al.* 2009; W Wang *et al.* 2013; Liang *et al.* 2017) and Laurentia (Achab, 1989; Vandenbroucke *et al.* 2003). However, a comparable biozonation

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covering the entire Ordovician succession for Avalonia, including England and Wales, has yet to be established. Data are available from Belgium (J Vanmeirhaeghe, unpub. PhD thesis, Univ. Ghent, 2006; Vanmeirhaeghe, 2007) and the upper Middle and Upper Ordovician of England and Wales (Jenkins, 1967; Vandenbroucke, 2008a, b; Vandenbroucke *et al.* 2005, 2008, 2009a; Challands *et al.* 2014), but the Lower Ordovician and the lower part of the Middle Ordovician in England and Wales have remained largely unstudied until now.

The aims of this paper are (i) to describe chitinozoan assemblages from the upper Tremadoc, Arenig and lowermost Llanvirn series in Wales, including the historical type area of the Arenig Series in North Wales and complementary sections in South Wales; (ii) to establish a biostratigraphical framework; and (iii) to assess biostratigraphic ages of sampled successions based on species ranges in Gondwana, Baltica and Laurentia, and therefore to correlate the British regional series with the equivalent global Tremadocian, Floian, Dapingian and lower Darriwilian stages. The new data are also expected to contribute towards tracking biogeographical affinities with Gondwana, Baltica, South China and Laurentia, and to help constrain the stratigraphy of a time interval that is becoming increasingly pivotal in understanding the evolution of Ordovician climate (e.g. Trotter *et al.* 2008; Vandenbroucke *et al.* 2009b; Turner *et al.* 2011; Dabard *et al.* 2015; Amberg *et al.* 2016, Pohl *et al.* 2016a, b; Rasmussen *et al.* 2016; Elrick, 2022).

2. Geological setting

The term ‘Arenig’ was first used by Sedgwick (1852) for rocks that crop out on Arenig Fawr Mountain in North Wales, where the Ordovician System extends around the Cambrian Harlech Dome from the Llŷn Peninsula in the west to the Bala area in the east and the Arenig Mountains in central Wales (Fig. 1). The Arenig Fawr section is stratigraphically incomplete (Zalasiewicz, 1984), however, and more complete sections are to be found in South Wales, where lower and upper Arenig successions are well developed in the Carmarthen area (Fortey & Owens, 1978) and around Whitland (Fortey & Owens, 1987) respectively. The Ordovician System in South Wales extends over 160 km from SW Wales to east central Wales (Fig. 1), following the Tywi lineament (Fortey *et al.* 2000). The Arenig Series is at the centre of this Ordovician tract and extends from Ramsey Island, off the westernmost point of the Pembrokeshire coast, towards Llandeilo, east of Carmarthen.

The Arenig Series in South Wales has a relatively rich and diverse macrofauna comprising trilobites, brachiopods, other shelly fossils and graptolites (Fortey & Owens, 1978, 1987; Cope, 1996, 2005; Cocks & Popov, 2019) and has also yielded acritarchs and chitinozoans (Molyneux, 1987). Fortey and Owens (1987) proposed a subdivision of the Arenig Series in South Wales into the Moridunian, Whitlandian and Fennian stages, although the base of the series itself was not defined there (Fortey *et al.* 1995). Wider correlations have been hindered, however, by the provincialism of many of the macrofossil species present (Cocks & Fortey, 1982), the generally poorly preserved and sparse acritarchs with low species richness, and the preliminary nature of the published chitinozoan record. Graptolites are poorly represented in the Moridunian and Whitlandian stages, but become more numerous, diverse and stratigraphically useful in the Fennian Stage. The lithostratigraphy and biostratigraphy of the areas sampled are summarized below.

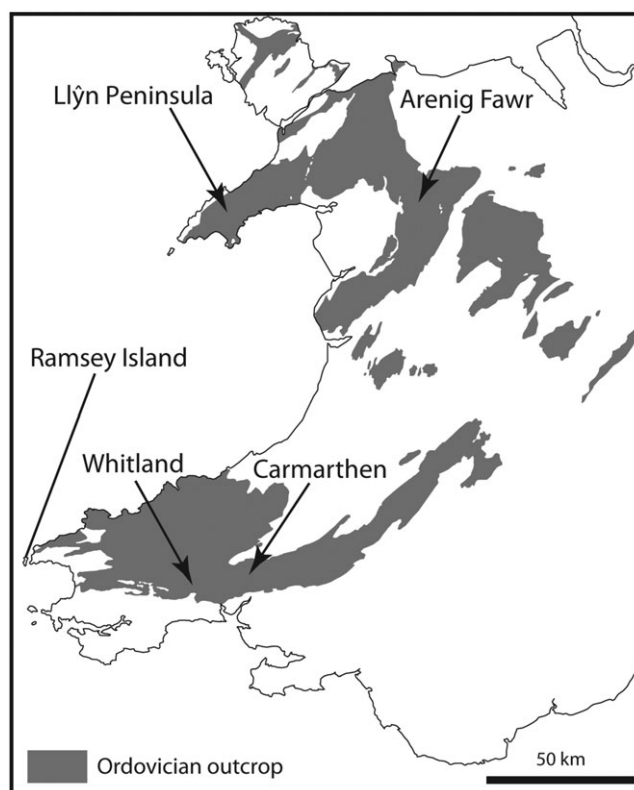


Fig. 1. Ordovician outcrop in Wales indicating sampled areas at Arenig Fawr in North Wales and the Carmarthen and Whitland areas in South Wales.

2.a. Carmarthen area

2.a.1. Stratigraphy

Fortey and Owens (1978) provided a modern account of the stratigraphy of the Carmarthen area where the lower Arenig Moridunian Stage is best exposed (Figs 2, 3). The ‘Login beds’, consisting of siltstone, shale and sandstone, comprise the lowest exposed unit in the succession and were dated by acritarchs as latest Tremadoc to earliest Arenig (Molyneux & Dorning, 1989; Molyneux *et al.* 2007).

The Login beds are overlain by the Moridunian Ogorf Hên Formation, although the contact between the two units is not exposed (Fortey & Owens, 1978). The Ogorf Hên Formation includes conglomerate, sandstone and siltstone of the Allt Cystanog Member overlain by micaceous mudstone and shale of the Bolahaul Member. The overlying Carmarthen Formation comprises, in upwards succession, black mudstone of the Pibwr Member, turbidite beds and shale of the Cwmffrŵd Member, and grey mudstone of the Cwm yr Abbey Member. The Carmarthen Formation passes up into the Afon Ffynnant Formation, consisting of turbidite deposits. The base of the middle Arenig Whitlandian Stage is placed 40 m above the base of the Afon Ffynnant Formation (Fortey & Owens, 1987, p. 87). Traynor (1988) assigned the Ogorf Hên Formation to his facies 3, comprising fluviodeltaic deposits. The mudstones of the Pibwr and Cwm yr Abbey members are placed in facies 6 (deep water mudstone), and the Cwmffrŵd Member and Afon Ffynnant Formation are placed in facies 5, representing deep water sediment-gravity flows in which turbidites are interbedded with facies 6 mudstone (Traynor, 1988).

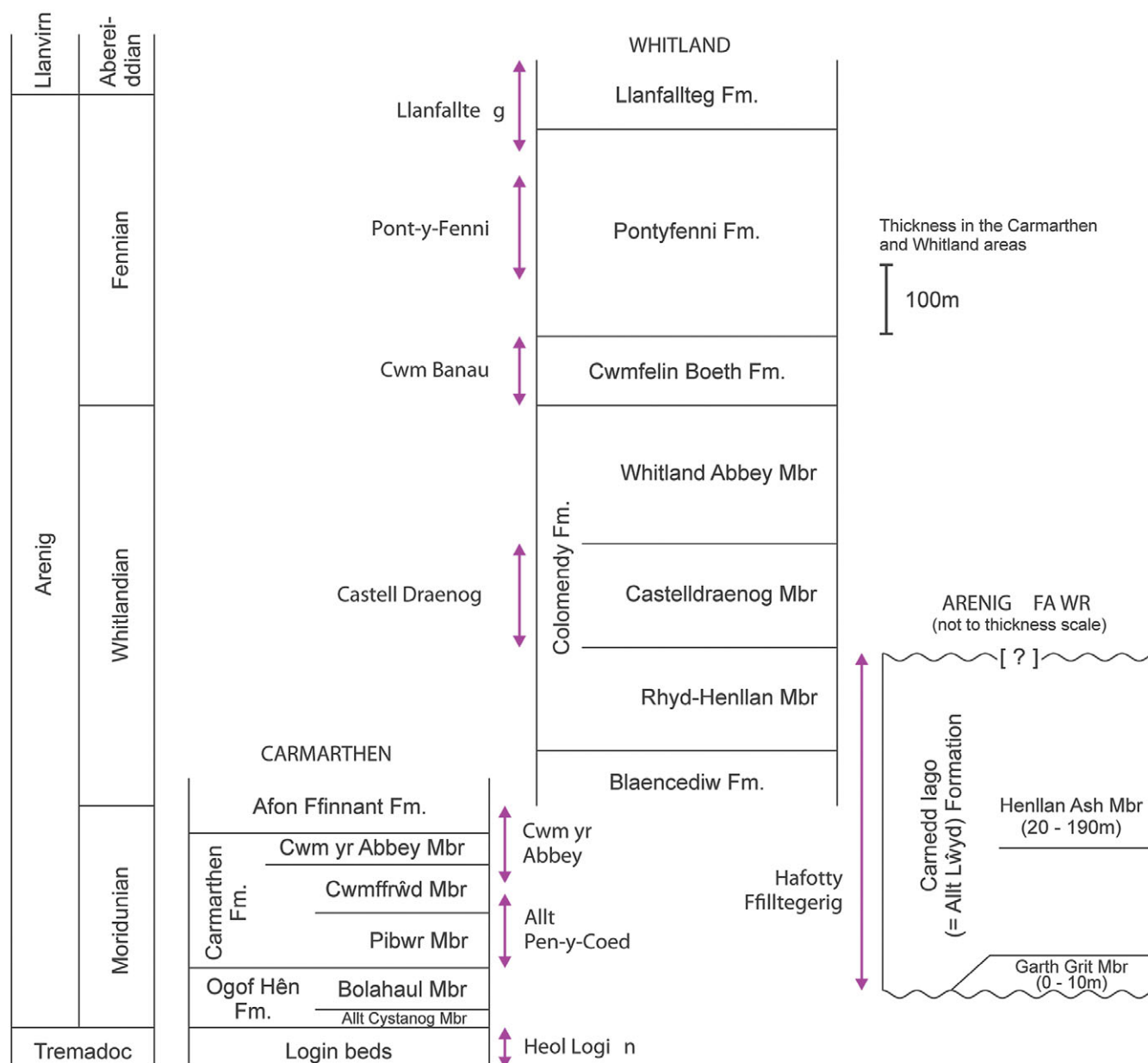


Fig. 2. (Colour online) Generalized vertical sections for the Arenig successions in the Carmarthen, Whitland and Arenig Fawr areas. Arrowed lines indicate the stratigraphical extent of sampled sections.

2.a.2. Fauna and microflora

The acritarch assemblage from the Login beds (Molyneux & Dorning, 1989) is similar to the *messauoudensis-trifidum* acritarch assemblage from the English Lake District and has been recorded as an occurrence of that assemblage in South Wales (Molyneux et al. 2007). Molyneux and Dorning (1989) concluded that the Login assemblage was from the uppermost Tremadoc or lowest Arenig series. Fortey et al. (2000, fig. 7), however, considered the acritarchs to indicate the upper Tremadoc Migneintian Stage and suggested correlation with the *Araneograptus murrayi* graptolite Biozone.

Above the Login beds, much of the Arenig succession in the Carmarthen area has yielded shelly faunas, rare graptolites and acritarchs (Fortey & Owens, 1978, 1987; Molyneux, 1987; Cope, 1996, 2005; Cocks & Popov, 2019; Ebbestad & Cope, 2021). No

shelly fossils or graptolites have been recorded from the Allt Cystanog Member, but shelly faunas from the rest of the succession are varied. Echinoderm fragments, brachiopods and gastropods occur in the Bolahaul Member, bivalves in the Bolahaul, Pibwr and Cwmffrwd members, orthoconic nautiloids in the Cwm yr Abbey Member, and trilobites throughout. Fortey and Owens (1987) established a succession of seven trilobite biozones in the Arenig succession of South Wales, of which the lower three occur in the Carmarthen area: the *Merlinia selwynii* Biozone in the upper Ogof Hên and lower Carmarthen formations (Bolahaul and Pibwr members), the *Merlinia rhyakos* Biozone in the upper part of the Carmarthen Formation (Cwmffrwd and Cwm yr Abbey members), and the *Furcalithus radix* Biozone in the lower Afon Ffynnant Formation.

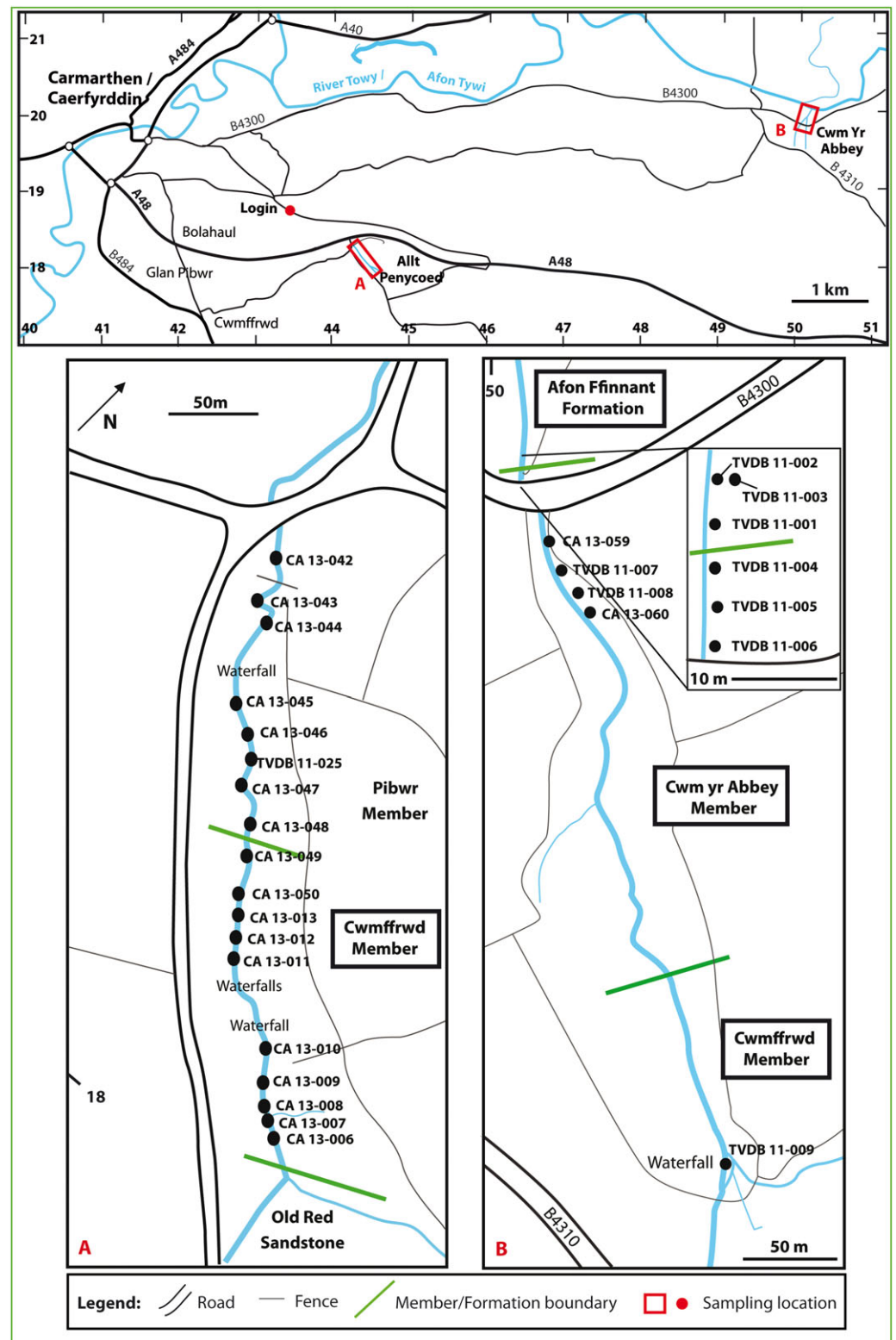


Fig. 3. (Colour online) Sample localities in the Carmarthen area, South Wales.

Graptolites recorded from the Carmarthen area include *Phyllograptus cf. densus* and *Pseudophyllograptus aff. angustifolius* from the Pibwr Member, dendroid graptolites from the the Cwm yr Abbey Member, including *Callograptus cf. tenuis*, *Callograptus salteri* and *Palaeodictyota sp.*, and *Azygograptus eivionicus* and

A. hicksii from the Whitlandian part of the Afon Ffynnant Formation (Fortey & Owens, 1978, 1987).

Molyneux (1987) described four acritarch assemblages from the Moridunian Stage in the Carmarthen area, informally designated Assemblage I to Assemblage IV in upwards succession. All

comprise relatively sparse and poorly preserved specimens in assemblages of generally low diversity, however, and do not currently provide enough evidence to assist correlation.

2.b. Whitland area

2.b.1. Stratigraphy

The Whitlandian and Fennian stages are better exposed in the Whitland area (Fig. 2), where the succession was described by Fortey and Owens (1987). The Whitlandian Blaencediw Formation at the base of the succession consists of turbidite deposits, shale and siltstone, and is correlated with the upper part of the Afon Ffynnant Formation in the Carmarthen area (Fig. 2). The overlying Colomendy Formation, also Whitlandian, is divided into the sandy shale of the Rhyd-Henllan Member, the grey shale of the Castelldraenog Member and the black shale of the Whitland Abbey Member. The base of the Fennian Stage is placed at the base of the Cwmfelin Boeth Formation, which consists of turbidite beds and black shale. The overlying Pontyfenni Formation comprises black to dark grey shale and mudstone, and the Llanfallteg Formation at the top of the Arenig succession, passing up into the Llanvirn Series, comprises light grey mudstone and shale. The Colomendy, Pontyfenni and Llanfallteg formations were classed as facies 6 deep water mudstone units by Traynor (1988), interbedded with two coarse facies 5 deep water turbidite units represented by the Blaencediw and Cwmfelin Boeth formations.

2.b.2. Fauna and microflora

Trilobites have been collected from all lithostratigraphical units in the Whitland area except the Castelldraenog Member of the Colomendy Formation, graptolites from all except the Rhyd-Henllan Member, and brachiopods, chordates and ostracods are known from some levels (Fortey & Owens, 1987; Cocks & Popov, 2019). The Rhyd-Henllan and Whitland Abbey members contain the typical Whitlandian trilobite *Bohemopyge scutarix*. The latter also contains the graptolite *Expansograptus simulans* (recorded as *Didymograptus simulans*), which is present throughout the Whitlandian Stage (Fortey *et al.* 2000; Cooper *et al.* 2004; Zalasiewicz *et al.* 2009). Fossils are numerous in the upper part of the Cwmfelin Boeth Formation and include brachiopods and the trilobite *Asaphellus*. Fortey and Owens (1987) considered them likely to be derived from a relatively shallow source.

The Pontyfenni Formation yielded a rich fauna of graptolites, trilobites, chordates and ostracods (Fortey & Owens, 1987; Jefferies in Fortey & Owens, 1987). A diverse graptolite fauna includes *Expansograptus? uniformis lepidus*, *Expansograptus hirundo* and *Undulograptus cumbrensis* (= '*Glyptograptus? dentatus*' of Fortey & Owens, 1987; Owens, 1999). Fortey and Owens (in Fortey *et al.* 2000) placed the Pontyfenni Formation of the Whitland area in the *Isograptus gibberulus* graptolite Biozone. Trilobites are nowhere common but comprise diverse cyclopygid and atheloptic assemblages with *Pricyclopyge binodosa eurycephalathe*, *Placoparia cambriensis* and *Selenopeltis buchii macrophthalma*, the last two species being typical of the Fennian Stage (Fortey & Owens, 1987).

Fortey *et al.* (2000, fig. 7) depicted the Llanfallteg Formation as straddling the Arenig–Llanvirn boundary, corresponding to the upper Fennian *Didymograptus hirundo* graptolite Biozone (since replaced by the *Aulograptus cucullus* graptolite Biozone: Rushton in Cooper *et al.* 2004; Zalasiewicz *et al.* 2009) and the lower Aberiddian (lowest Llanvirn) *Didymograptus artus* graptolite Biozone. Graptolites include *Undulograptus cumbrensis*

(recorded in part as '*Glyptograptus? dentatus*' by Fortey & Owens, 1987; see Owens, 1999), found only in the uppermost Arenig section at Llanfallteg but spanning the Arenig–Llanvirn boundary elsewhere (Zalasiewicz *et al.* 2009, fig. 4), and *Acrograptus acutidens* and *U. austrodentatus*, which range across the Arenig–Llanvirn boundary at Llanfallteg. A diverse trilobite fauna is also present, with *Dionide levigena*, the eponymous species of the uppermost Arenig trilobite biozone, although it also ranges into the Llanvirn Series, and *Ectillaenus perovalis*, *Barrandia homfrayi*, *Stapeleyella inconstans*, *Amphyx linleyensis* and *P. cambriensis*, all of which have ranges that span the Arenig–Llanvirn boundary at Llanfallteg (Fortey & Owens, 1987).

Trilobite biozones established by Fortey and Owens (1987) in the Whitland area comprise, in upwards succession, the *Gymnostomix gibbsii* Biozone, *Stapeleyella abyfrons* Biozone, *Bergamia rushtoni* Biozone and *Dionide levigena* Biozone. *Gymnostomix gibbsii* occurs in the Rhyd-Henllan and Whitland Abbey members of the Whitland area, meaning that the *gibbsii* Biozone coincides with most of the upper part of the Whitlandian Stage. The other three zones all occur in the Fennian Stage, the *Stapeleyella abyfrons* Biozone in the basal Pontyfenni Formation immediately overlying the Cwmfelin Boeth Formation, the *Bergamia rushtoni* Biozone through an estimated two-thirds of the Pontyfenni Formation, and the *Dionide levigena* Biozone in the upper Fennian part of the Llanfallteg Formation.

Molyneux (1987) described one Whitlandian acritarch assemblage, Assemblage V from the Whitland Abbey Member. The assemblage, like those from the Moridunian succession in the Carmarthen area, is of low diversity and comprises mainly small acanthomorph acritarchs (*Micrhystridium* spp.) that do not assist correlation. More diverse acritarch assemblages of Fennian age, with stratigraphically useful forms, were described from the Pontyfenni Formation (Molyneux, 1987). Assemblage VI, from just above the base of the formation, is distinguished by the presence of *Coryphidium bohemicum* Vavrdová, *?Frankea hamata* Burmann, *Orthosphaeridium* sp., *Stellechinatum uncinatum* (Downie) Molyneux, *?Striatotheca mutua* Burmann, *S. rarirrugulata* (Cramer *et al.*) Eisenack *et al.* and species of *Uncinisphaera*. Assemblage VII, from higher in the formation at Pont-y-Fenni, includes *Coryphidium bohemicum* Vavrdová, *Dasydorus cirritus?* Playford & Martin, *Orthosphaeridium ternatum* (Burmann) Eisenack *et al.*, *Stellechinatum papulessum* Molyneux, and species of *Solisphaeridium*, *Stelliferidium* and *Uncinisphaera*. Chitinozoans assigned to species of *Belonechitina*, *Conochitina* and *Lagenochitina* were recorded from the Pontyfenni Formation at Pont-y-Fenni (Molyneux, 1987).

2.c. Arenig Fawr

2.c.1. Stratigraphy

The Arenig Series is represented in the Arenig Fawr area by a single formation, previously referred to as the Carnedd Iago Formation, with unconformities at the base and top (Fig. 2; Fortey *et al.* 2000). The Carnedd Iago Formation is now considered to be equivalent to and has been superseded by the Allt Lwŷd Formation throughout North Wales (Rushton & Howells, 1998), but the older terminology is retained here for better comparison with work reported in the literature.

The Carnedd Iago Formation was established by Lynas (1973) and described by Zalasiewicz (1984) as extending throughout the Arenig with three members: the Garth Grit Member, consisting of

quartzo-feldspathic sandstone, the Llyfnant Member, consisting of laminated dark siltstone and pale sandstone, and the Henllan Ash Member, comprising variably bioturbated feldspathic sandstone and sandy mudstone. Fortey *et al.* (2000) revised the stratigraphy of the Carnedd Iago Formation, restricting it to the lower Moridunian to middle Whitlandian stages and including only the Garth Grit and the Henllan Ash as separate members.

2.c.2. Fauna

The Llyfnant Member contains common *Expansograptus* aff. *simulans*, which suggests correlation with the *E. simulans* Biozone, the *Isograptus victoriae victoriae* Biozone, or possibly the *Isograptus gibberulus* Biozone of the English Lake District (Zalasiewicz, 1984; Zalasiewicz *et al.* 2009). Specimens of *Corymbograptus* aff. *deflexus* and *Azygograptus* cf. *eivionicus* have also been recorded. The ranges in England and Wales of the three nominal species, *A. eivionicus*, *C. deflexus* and *E. simulans*, overlap in the *simulans* Biozone, which is correlated with the lower Whitlandian Stage (Zalasiewicz *et al.* 2009).

Fortey and Owens (1978, 1987) suggested correlation of the Henllan Ash Member with the Bolahaul Member or the Pibwr Member, or both, based on its abundant trilobite fauna (Whittington, 1966), and therefore with the middle Moridunian Stage. Graptolites from the uppermost Henllan Ash Member were re-examined by Zalasiewicz (1984), who identified a fauna characterized by *Expansograptus* cf. *praenuntius* and *Tetragraptus reclinatus*. Fortey *et al.* (2000) placed the Henllan Ash in the upper Moridunian Stage, but Zalasiewicz *et al.* (2009) depicted *E. cf. praenuntius* as present in the *simulans*, *victoriae* and *gibberulus* graptolite biozones, the last with some doubt. This suggests a possible slightly younger, Whitlandian age than that indicated by Fortey *et al.* (2000), albeit still Floian.

3. Sample localities

3.a. Carmarthen area

Samples were collected from the Login beds, Carmarthen Formation and Afon Ffynnant Formation in the Carmarthen area (Fig. 3). No samples were collected from the Ogof Hên Formation.

3.a.1. Heol Login

Ten samples from the Login beds, originally collected by SGM (Molyneux & Dorning, 1989) and curated in the British Geological Survey's collections at Keyworth, Nottingham, UK (BGS sample registration numbers MPA 26829 to MPA 26838), were resampled. The samples are from a section along Heol Login ('Login road'), about 2 km SE of Carmarthen (British National Grid References SN 4352 1873–SN 4364 1870; 'Login' in Fig. 3; Molyneux & Dorning, 1989, figs 1, 2).

3.a.2. Allt Pen-y-Coed

Allt Pen-y-Coed [SN 4425 1823–SN 4446 1803] (Fig. 3a) is a steep-sided, wooded stream section, oriented NW–SE, about 3 km SE of Carmarthen. It exposes the Pibwr and Cwmffrwd members of the Carmarthen Formation. The succession dips steeply to the south or SE so that the older beds are to the north. At the southern end of the section, the Cwmffrwd Member is unconformably overlain by upper Silurian (Pridoli) beds of Old Red Sandstone facies (<https://mapapps2.bgs.ac.uk/geoindex/home.html>, accessed 26

March 2020; see also *Bedrock map of Wales and adjacent area* in Howells, 2007).

Eight samples (CA 13-042 to CA 13-048 and TVDB 11-025) were collected from the Pibwr Member and ten samples (CA 13-006 to CA 13-013, CA 13-049, CA 13-050) from the Cwmffrwd Member, upstream from the point at which the stream passes under a bridge on a minor road (Fig. 3a).

3.a.3. Cwm yr Abbey

The upper Cwmffrwd Member, the Cym yr Abbey Member and the lower Afon Ffynnant Formation are exposed in the stream section of Cwm yr Abbey [SN 5002 1988–SN 5013 1943], about 9 km east of Carmarthen (Fig. 3). The section is oriented approximately N–S with the succession generally dipping northwards, although there is much minor folding and faulting (Owens, 1999, fig. 8.7).

One sample (TVDB 11-009) was collected from the upper Cwmffrwd Member, seven samples (TVDB 11-004 to TVDB 11-008, CA 13-059, CA 13-060) from the Cwm yr Abbey Member, and three samples (TVDB 11-001 to TVDB 11-003) from the base of the Afon Ffynnant Formation, downstream from the bridge crossing the stream on the minor B4300 road [SN 5002 1978] (Fig. 3b).

3.b. Whitland area

Samples were collected from the Castelldraenog Member of the Colomendy Formation and from the Cwmfelin Boeth, Pontyfenni and Llanfallteg formations in the Whitland area (Fig. 4). No samples were taken from the Blaencediw Formation or the Rhyd-Henllan and Whitland Abbey members of the Colomendy Formation.

3.b.1. Castell Draenog

Four samples (CA 13-055 to CA 13-058; Fig. 4a) were collected from the Castelldraenog Member south of Castell Draenog [SN 2077 2139]. Other samples collected in the vicinity of Castell Draenog are CA 13-053, collected about 750 m SE of Castell Draenog in the vicinity of Pantygroes, about 50 m west of the minor road from Whitland Abbey to Llanboidy on the east side of Nant Colomendy, and CA 13-054, collected from the track approximately 260 m north of Castell Draenog. CA 13-053 is from beds mapped as Pontyfenni Formation by Fortey and Owens (1987, fig. 2), and CA 13-054 from beds now placed in the Abergwilli Formation of Aberiddian (early Llanvirn) age (British Geological Survey, 2010; Burt *et al.* 2012).

3.b.2. Cwm Banau

Six samples (CA 13-040, CA 13-041, CA 13-051, CA 13-052, TVDB 11-019, TVDB 11-020) were collected from the Cwmfelin Boeth Formation at Cwm Banau [SN 2123 1862] (Fig. 4), NE of Whitland Abbey.

3.b.3. Pont-y-Fenni

Eight samples (CA 13-036 to CA 13-039, TVDB 11-021 to TVDB 11-024) were collected from the Pontyfenni Formation in a disused quarry at Pont-y-Fenni [SN 2379 1690–SN 2381 1693], the formation's effective type locality, on the east bank of the Afon Fenni (Fig. 4b). The beds at Pont-y-Fenni comprise black to dark grey shale and blocky mudstone dipping northwards at about 60°, either on the northern limb of a fold that

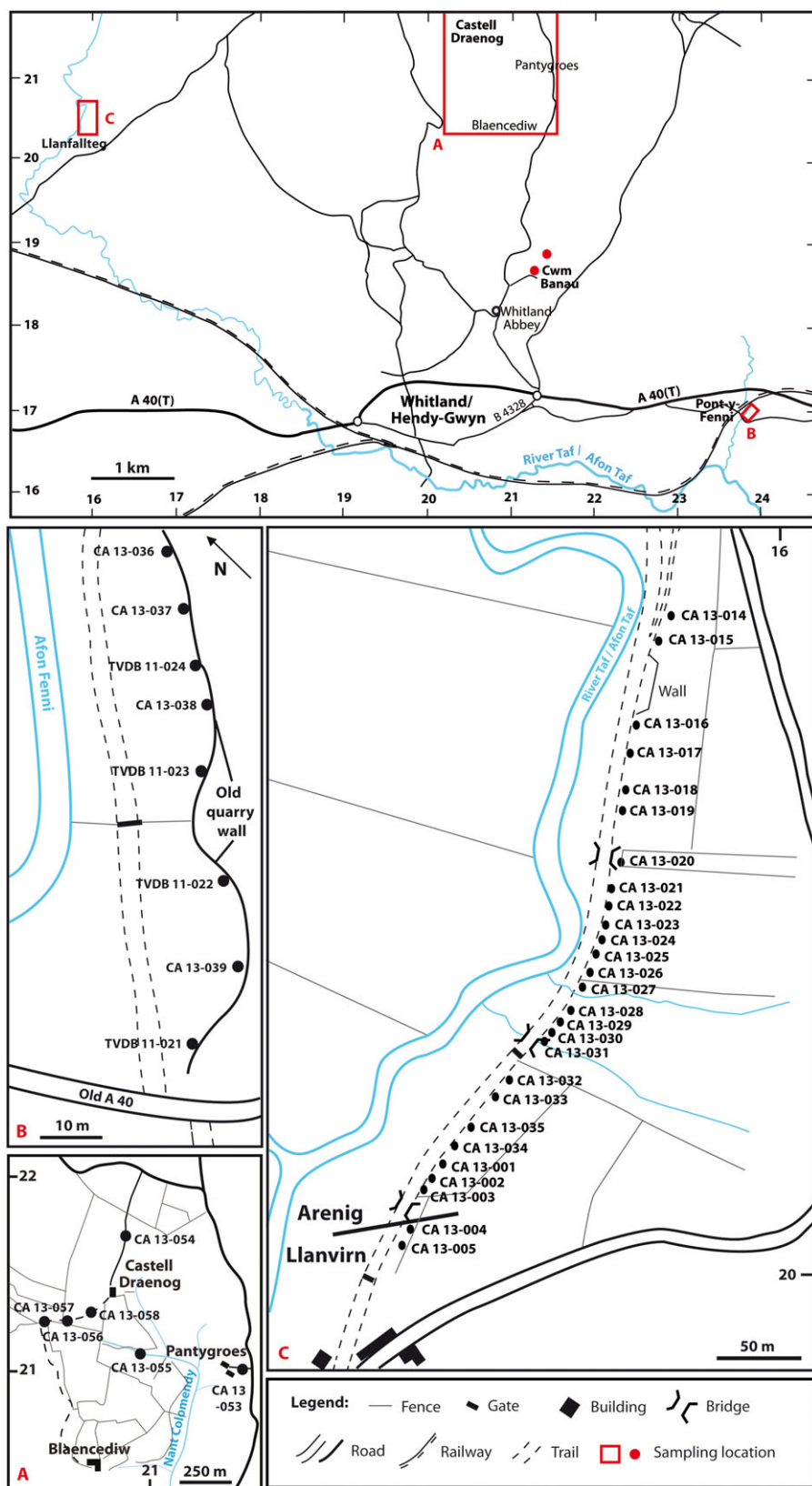


Fig. 4. (Colour online) Sample localities in the Whitland area, South Wales.

is subsidiary to an anticlinal area to the north, or on the overturned southern limb of the latter (Owens, 1999). The latter interpretation accords with the British Geological Survey's

(1975) map of the area and is adopted here. The southernmost sample, TVDB 11-021, is therefore placed highest in the succession.

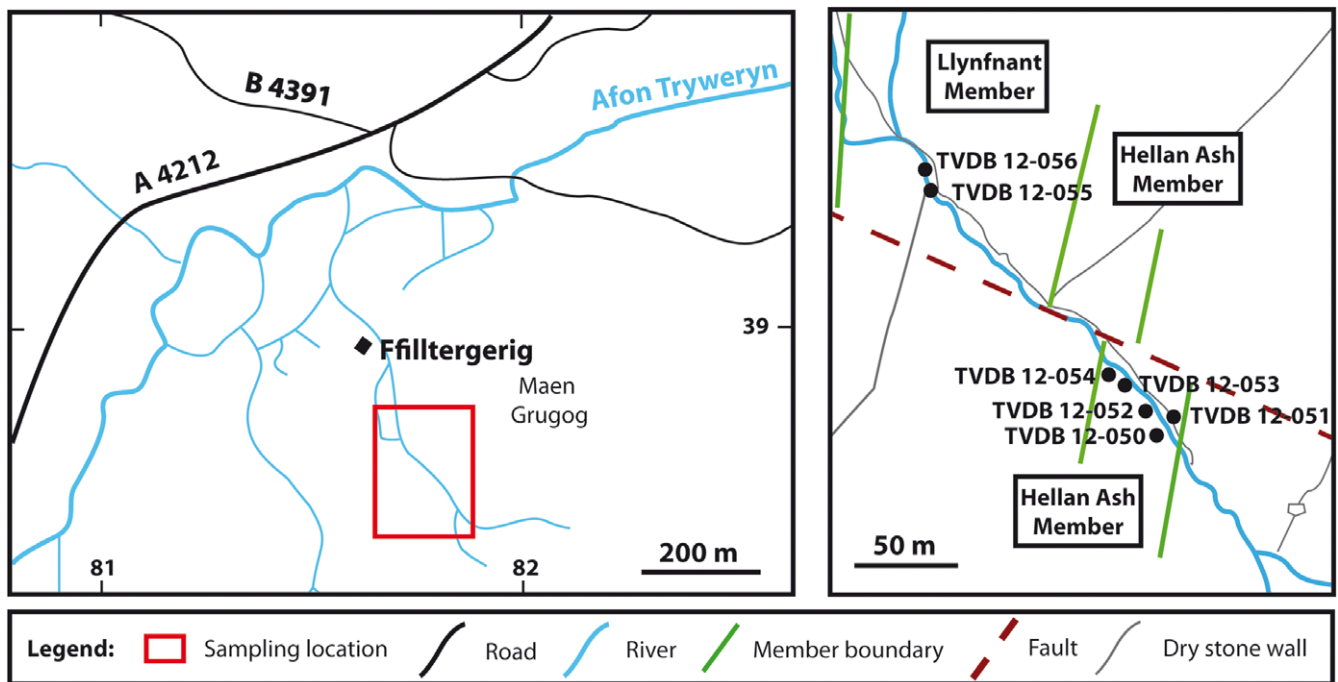


Fig. 5. (Colour online) Sample locality at Arenig Fawr, North Wales.

3.b.4. Llanfallteg

The Llanfallteg section is along a disused and dismantled railway line, oriented NNE–SSW on the east bank of the Afon Taf (Fig. 4c). Beds at the northern end of the section are placed in the Pontyfenni Formation (locality 52Z of Fortey and Owens, 1987) but pass southwards into light grey mudstone and shale of the Llanfallteg Formation. The contact between the two formations is mapped as a fault north of locality 52Y of Fortey and Owens (1987, figs 2, 8; British Geological Survey, 1976). The Arenig–Llanvirn series boundary is placed towards the southern end of the section, within the Llanfallteg Formation, and is marked by pendent didymograptid graptolites that include *Didymograptus artus*, the eponymous index of the lowest Llanvirn graptolite biozone.

Twenty-seven samples (CA 13-001–CA 13-005, CA 13-014–CA 13-035) were collected from the Llanfallteg section over a distance of about 530 m [SN 1592 2058–SN 1567 2012] (Fig. 4c). Two samples at the northern end of the section (CA 13-014, CA 13-015) are from the Pontyfenni Formation. Twenty samples are from the Llanfallteg Formation, the most northerly of which, CA 13-021 (Fig. 4c), is from around locality 52Y of Fortey & Owens (1987). Of these, 18 are from the Arenig part of the formation (CA 13-001–CA 13-003, CA 13-021–CA 13-035) and two from the Llanvirn (CA 13-004, CA 13-005). The remaining five samples (CA 13-016–CA 13-020) were collected between localities 52Y and 52Z of Fortey and Owens (1987) and are therefore from either the upper Pontyfenni Formation or lower Llanfallteg Formation, most likely the former.

3.c. Arenig Fawr

Seven samples (TVDB 12-050 to TVDB 12-056; Fig. 5) were collected along a stream section southeast from Hafotty Ffilltirgerig [SH 8184 3857], corresponding to the Llynfnant and Henllan Ash members of Zalasiewicz (1984).

4. Methods

4.a. Sample preparation and analysis

Ninety-three samples were prepared using standard palynological techniques. Between 40 and 60 g of rock were dissolved per sample. See Amberg *et al.* (2016) for the full procedure. The organic residues were sieved at 51 μm , and the top fraction was hand-picked under a stereomicroscope at $\times 50$ magnification. More than 4400 specimens were obtained, and identifications are based on images taken with a FEI Scanning Electron Microscope (SEM) and a ZEISS LEO SEM. All figured material is stored and available for consultation in the collections of the UMR 8198 at the University of Lille. Ten genera and 44 species were identified from the sections and localities studied. Occurrences and ranges are shown in Figure 6.

4.b. Data analysis

R version 3.6.2 (R Core Team, 2019) was used for data analysis and visualization. Stratigraphically constrained hierarchical cluster analysis was carried out on a distance matrix using the ‘rioja’ package (Juggins, 2017) and the CONISS method. The distance matrix was computed from presence–absence data of species occurrences per sample using the Jaccard index for binary data in the ‘vegan’ package (Oksanen *et al.* 2019). Ranges, stratigraphic columns and the dendrogram were plotted using the ‘ggplot2’ and ‘gridExtra’ packages (Wickham, 2016; Auguie, 2017). A broken-stick model (Bennett, 1996) was applied to the cluster analysis to determine the significance of each cluster. Clusters identified as significant using this method form the basis of assemblages identified in the succession.

5. Preservation, abundance and species richness

Preservation is variable between localities and sections, depending on the degree of metamorphism. Robinson and Bevins (1986,

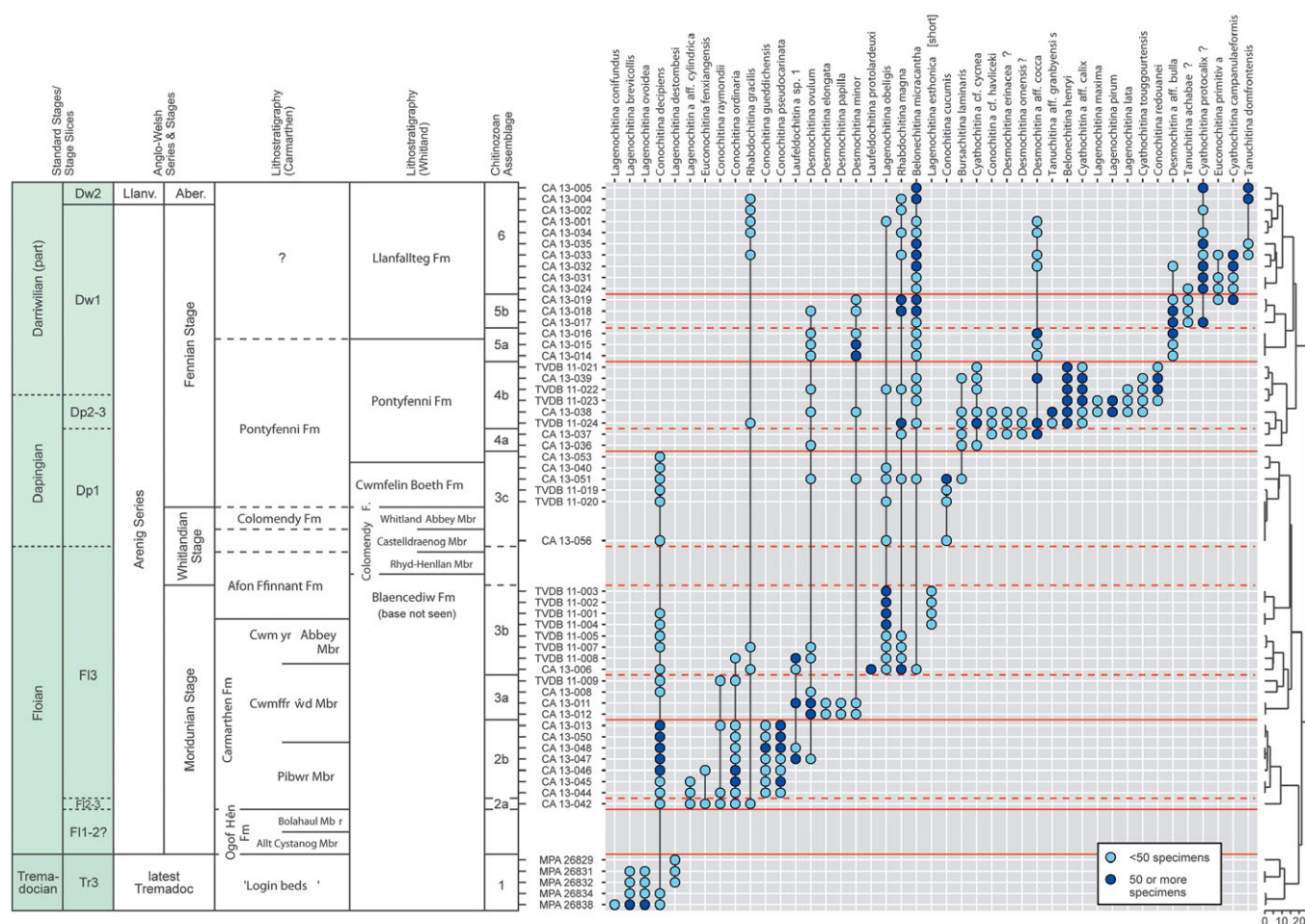


Fig. 6. (Colour online) Chitinozoan occurrences and ranges in the highest Tremadoc – lowest Llanvirn (Tremadocian–Darrivilian) succession of South Wales, plotted against lithostratigraphy in the Carmarthen and Whitland areas, Anglo-Welsh series and stages and global stages and stage slices. Sampled lithostratigraphical units are indicated by bold typeface; unsampled or unproductive units are in italics. The dendrogram is from constrained hierarchical cluster analysis of binary (presence/absence) data (Jaccard dissimilarity index, rioja and vegan packages, R) and distinguishes the six assemblages identified in this paper (indicated by solid lines across the range chart). Sub-assemblages are based on successive lowest occurrences of chitinozoan species (indicated by dashed lines).

fig. 2) and Merriman (2006) delineated zones of incipient metamorphism in the Welsh Basin based on clay mineral assemblages and illite crystallinity, with the Carmarthen–Whitland area in the diagenetic zone to low anchizone and Arenig Fawr at a higher grade in the epizone. Intense small-scale folding affects the shale and mudstone units in the Carmarthen area (Fortey & Owens, 1978), and small-scale reverse faults occur in the Whitland area (Fortey & Owens, 1987), especially around Castelldraenog, where a NNE–SSW fault along Nant Colomendy pushes a block of the Colomendy Formation up in contact with the Pontyfenni Formation, and around Llanfallteg. The deformation results in generally only slight distortion of the macrofauna and mineralization (Fortey & Owens, 1987).

Abundance and species richness also vary between sections and within sections themselves. For this study, we consider a number of 1 to 50 specimens per sample of dissolved rock (about 40 g) to be low abundance, 51 to 150 specimens to be moderate abundance and over 150 specimens to be high abundance.

Five of the 10 samples from the Login beds yielded chitinozoans, mainly large lagenochitinids, belonging to between one and four species in a maximum of two genera. They are not abundant, but are relatively well preserved, although flattened.

Six of the 18 samples from the Carmarthen Formation at Allt Pen-y-Coed were unproductive, two from the Pibwr Member and four from the Cwmffrwd Member. The remainder, six each from the Pibwr and Cwmffrwd members, yielded abundant and diverse chitinozoans. Productive samples from the Pibwr Member consistently yielded five to six species belonging to two to four genera. Most of the productive samples from the Cwmffrwd Member were similar, with four or five species belonging to one or two genera, mostly conochitinids in the lower part, but desmochitinids higher in the succession. There is a marked increase in species richness in the uppermost sample from the Cwmffrwd Member, CA 13-006, however, with seven species of five genera. Both three-dimensional and flattened specimens were found, some being pyritized. Except for the largest specimens, chitinozoans are generally complete.

The samples from the upper Carmarthen Formation (Cwmffrwd and Cwm yr Abbey members) and lower Afon Ffynnant Formation in the Cwm yr Abbey section produced moderately abundant and diverse faunas dominated by small lagenochitinids and a few conochitinids. Three of the 11 samples were barren. The rest yielded between two and five species belonging to between one and five genera, the most diverse assemblages being from the Cwm yr Abbey Member. All specimens are relatively

poorly preserved, however, the majority being flattened, although a few specimens of *Conochitina* are preserved in 3D.

The samples from the Castelldraenog Member at Castell Draenog and the Cwmfelin Boeth Formation at Cwm Banau were less productive. Five out of the 12 samples were barren and the rest yielded very sparse faunas, although large rock samples were dissolved (about 100 g). Most productive samples contained two or three species belonging to one or two genera. The exception is sample CA 13-051 from the Cwmfelin Boeth Formation, which yielded eight species of six genera.

The most diverse and abundant faunas are from the samples of the Pontyfenni Formation collected at Pont-y-Fenni. All eight samples yielded chitinozoans, and the specimens are well preserved, although often flattened. Yields are variable, from a minimum of three species in three genera, to a maximum for the area of 14 species belonging to seven genera in sample CA 13-038. Assemblages are dominated by large cyathochitinids with lagenochitinids and desmochitinids.

Abundance and species richness are variable throughout the Llanfallteg section. The six samples (CA 13-014 to CA 13-019) from the northern part of the section, and therefore definitely or probably from the Pontyfenni Formation, yielded assemblages of moderate abundance and diversity, with five to seven species and two to six genera. In contrast, the middle part of the section (11 samples, CA 13-020 to CA 13-030) is almost barren, despite some samples being re-processed twice to enhance recovery (totaling up to about 150 g of dissolved rock for these samples). Only one sample from this part of the section (CA 13-024) yielded chitinozoans, albeit moderately diverse with five species and four genera. Nine of the ten samples from the southern part of the section, however, including those from the lowermost Llanvirn Series, yielded assemblages of moderate abundance and diversity, with between three and eight species in two to six genera. The faunas from the Llanfallteg section are dominated by desmochitinids, belonechitinids and cyathochitinids. The specimens are often pyritized or broken, and both 3D and flattened specimens were found.

The samples from the Arenig Fawr section yielded the poorest assemblages with low abundance and diversity. Only two of the seven samples, both from the Henllan Ash, yielded chitinozoans and the specimens are severely broken. Three species belonging to three genera were determined, with most specimens being lagenochitinids.

6. Chitinozoan assemblages from South Wales

The broken-stick model applied to the constrained hierarchical cluster dendrogram distinguished six significant chitinozoan assemblages, here numbered 1–6 from the base of the succession upwards (Fig. 6). Assemblages 2–5 are further subdivided, based on stratigraphic changes in the composition of their faunas. Correlation of the assemblages and sub-assemblages with global series and stages, Anglo-Welsh series and stages, and graptolite, chitinozoan and conodont biozones, is shown in Fig. 7.

6.a. Assemblage 1

Assemblage 1 is restricted to the Login beds and comprises *Conochitina decipiens*, *Lagenochitina brevicollis* (Fig. 8s, t), *L. conifundus* (Fig. 9, o), *L. destombesi* (Fig. 8a, b) and *L. ovoidea* (Fig. 9a, b). The species of *Lagenochitina* have only been recorded from the Login beds in South Wales, whereas *C. decipiens* ranges at least as high as the basal Pontyfenni Formation (Fig. 6).

The species of *Lagenochitina* all have Tremadocian records or affinities with Tremadocian species. *Lagenochitina ovoidea*, described from the Ordovician of the Sahara by Benoit and Taugourdeau (1961), has perhaps the longest range, with records from the Dapingian and Darriwilian stages of Baltica (Nölvak *et al.* 2019) as well as the Tremadocian of South China (Liang *et al.* 2017). The other three *Lagenochitina* spp. are all zonal indicators for Tremadocian biozones in Gondwana.

Lagenochitina destombesi has its lowest occurrence in the middle Tremadocian of Morocco (Elaouad-Debbaj, 1988; Paris, 1990) and South China (Chen *et al.* 2008; Wang *et al.* 2013), and ranges into the upper Tremadocian *Araneograptus murrayi* graptolite Biozone in Morocco (Nowak *et al.* 2016), South China (Wang *et al.* 2013) and NW England (Amberg *et al.* 2017). It gives its name to the *Lagenochitina destombesi* chitinozoan Biozone of high palaeolatitude Gondwana (Fig. 7), stated in its original description as having a likely late early Tremadoc – early late Tremadoc age (Paris, 1990, p. 188).

The *destombesi* Biozone is succeeded in Paris's (1990) Gondwanan scheme by the *L. conifundus* chitinozoan Biozone (previously known as the *Amphorachitina conifundus* Biozone). *Lagenochitina conifundus* was depicted as having an upper Tremadocian to lower Floian range by Paris (1990), but the lower Floian record was based on the occurrence of abundant specimens, recorded as *Amphorachitina conifundus*, in sample 2 of Paris and Mergl (1984; Paris, 1990) from the lowermost Klabava Formation of the Prague Basin. The locality was reported by Paris and Mergl (1984) to be from 'the lowermost part of the *Corymbograptus v. similis* Zone; assemblage with *Clonograptus*' and was correlated with the *Tetragraptus approximatus* Graptolite Zone. Fatka (1993) reported *L. conifundus* from the same locality (his sample KL-7) but pointed out that an absence of graptolites at the level of his sample precluded direct correlation with the graptolite zonation.

In revisions of the Gondwanan biozonation scheme, the *conifundus* Biozone has been replaced either wholly (Paris *et al.* 2007; Videt *et al.* 2010) or in part (Cooper & Sadler, 2012) by the *brevicollis* Biozone. Where it replaces the *conifundus* Biozone entirely, the *brevicollis* Biozone is correlated with the upper Tremadocian *Araneograptus murrayi* and *Hunnegraptus copiosus* graptolite biozones (Paris *et al.* 2007; Videt *et al.* 2010). In other instances (Cooper & Sadler, 2012, fig. 20.1), the *brevicollis* Biozone is correlated with the uppermost Tremadocian *Hunnegraptus copiosus* Biozone and the *conifundus* Biozone with the *Araneograptus murrayi* Biozone (Fig. 7). In both instances, the *brevicollis* Biozone is overlain by the *symmetrica* Biozone. Recent revision of the *symmetrica* Biozone has placed its base below instead of at the base of the Floian Stage (i.e. below the base of the Arenig Series; Nowak *et al.* 2016; Amberg *et al.* 2017; Liang *et al.* 2017; Achab & Maletz, 2021) so that the *conifundus* and *brevicollis* biozones now lie entirely within the upper Tremadocian Stage (Webby *et al.* 2004; Paris *et al.* 2007; Videt *et al.* 2010; Cooper & Sadler, 2012).

The lowest occurrence of *Lagenochitina brevicollis* in South China is in the *Araneograptus murrayi* graptolite Biozone of the Jiangnan Slope (Wang *et al.* 2013) and the upper Tremadocian part of the *Paroistodus proteus* conodont Biozone on the Yangtze Platform (Liang *et al.* 2017). In both cases, correlation of the lowest occurrence with a level in the upper Tremadocian Stage Slice Tr3 is indicated (Fig. 7). The species' highest occurrence there is in the *Acrograptus filiformis* graptolite Biozone of the Yangtze Platform (Liang *et al.* 2018), which correlates with a level in the

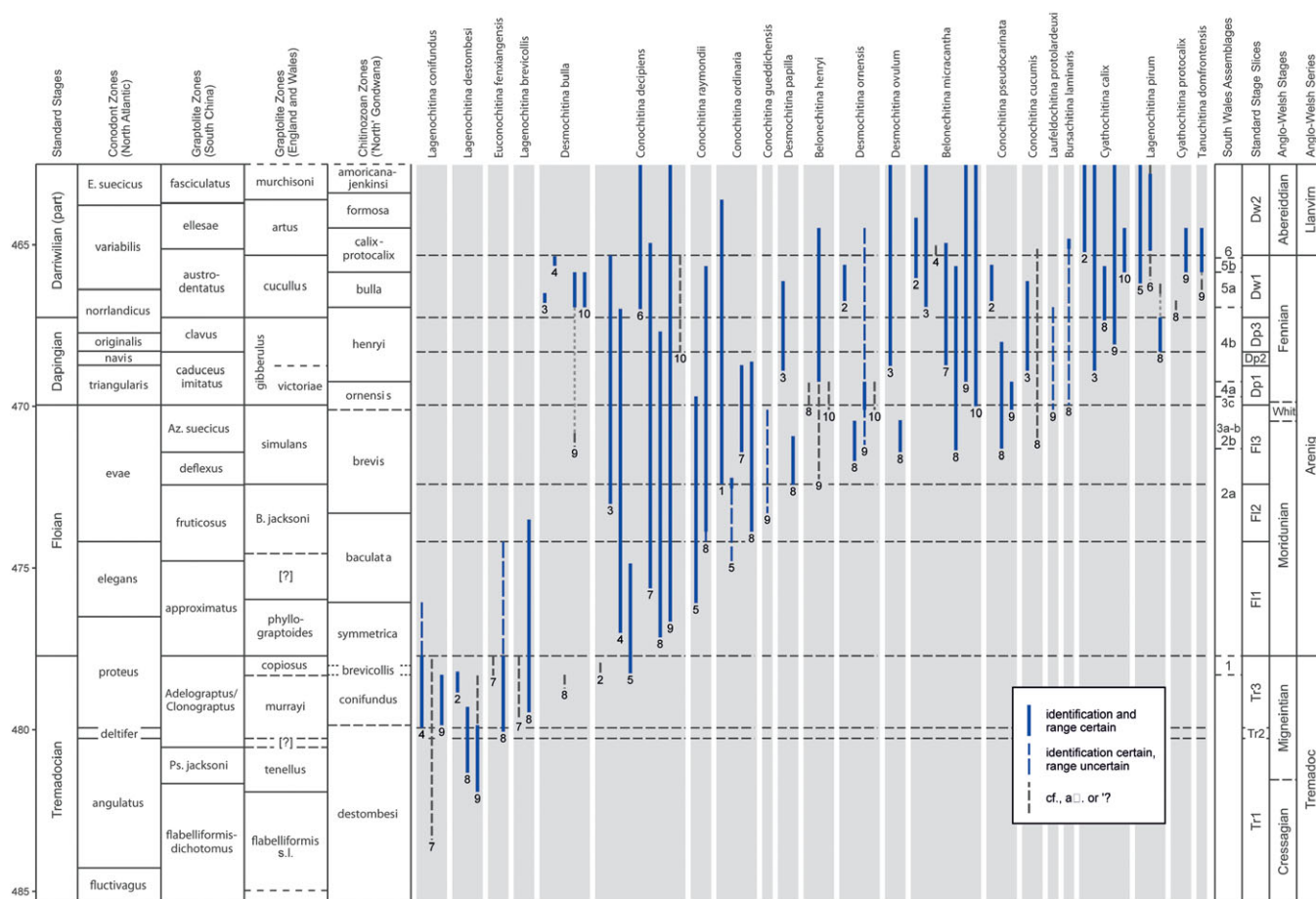


Fig. 7. (Colour online) Ranges of selected species from South Wales recorded elsewhere in (1) low palaeolatitude Gondwana (Australia): Quintavalle & Playford (2006); (2) Perigondwana (Megumia, Avalonia or Ganderia: UK, Belgium): Jenkins (1967); Samuelsson & Verniers (2000); Herbosch & Verniers (2014); Amberg *et al.* (2017); (3) Baltica: Grahn (1984); Nölvak & Grahn (1993); Grahn *et al.* (1996); Hints & Nölvak (2006); Grahn & Nölvak (2007); Tammekand *et al.* (2010); Nölvak *et al.* (2019); (4) Bohemia: Paris & Mergl (1984); Fatka (1993, 2003); (5) Laurentia: Achab (1980, 1989); Achab & Maletz (2021); (6) Qaidam: W Wang *et al.* (2018); (7) South America (Gondwana): Heuse *et al.* (1999); Achab *et al.* (2006); Grahn (2006); de la Puente & Rubinstein (2009, 2013); Toro *et al.* (2010); (8) South China: Brocke *et al.* (2000); X Wang, *et al.* (2005); Tang *et al.* (2007); Chen *et al.* (2008, 2009); Liang *et al.* (2017, 2018, 2009); W Wang *et al.* (2013); (9) high southern palaeolatitude Gondwana (North Africa, southern Europe; North Gondwana of Paris, 1990): Paris (1981, 1990); Elaouad-Debbaj (1984, 1988); Soufiane & Achab (1993); Oulebsir & Paris (1995); Nowak *et al.* (2016); (10) middle palaeolatitude western Gondwana (Iran, Oman, Saudi Arabia, Pakistan): Al-Hajri (1995); Quintavalle *et al.* (2000); Le Herisse *et al.* (2007); Sansom *et al.* (2009); Rickards *et al.* (2010); Ghavidel-syooki *et al.* (2014). Left-hand columns are from TimeScale Creator v. 7.4 (<https://timescalecreator.org/index/index.php>) and are calibrated to the age model in Ogg *et al.* (2016). Right-hand columns: chitinozoan assemblages (this paper) correlated with standard stage slices and Anglo-Welsh series and stages, based on chitinozoan ranges depicted in this figure and discussed in the text.

middle Floian, either in the upper part of Stage Slice F11 (Zhang *et al.* 2007, 2010; Wang *et al.* 2013) or in F12 (Zhang *et al.* 2010).

Lagenochitina brevicollis is possibly also present in the upper Tremadocian of South America (Fig. 7). De la Puente and Rubinstein (2009) recorded a single specimen from the Tremadocian *A. murrayi* graptolite Biozone of the Parcha Formation, NW Argentina. They also noted that the holotype of *Lagenochitina brevicollis* Taugourdeau and de Jekhowsky (1960) was likely to be a specimen of *Lagenochitina* with a broken neck whereas the paratype displayed characteristics of *Desmochitina*. Consequently, they referred to their specimen as *Desmochitina* sp. cf. *L. brevicollis*. Furthermore, de la Puente and Rubinstein (2009, 2013) regarded specimens recorded by Heuse *et al.* (1999) as *Desmochitina* sp. gr. *minor* from the upper Tremadocian *A. murrayi* and *H. copiosus* biozones of south Bolivia to be conspecific with the paratype of *L. brevicollis* and with their *Desmochitina* sp. cf. *L. brevicollis*.

The specimen of *Desmochitina* sp. cf. *L. brevicollis* from the Parcha Formation is accompanied by *Euconochitina*

paschaensis, *Lagenochitina confundus* and *L. cf. longiformis*. Wang *et al.* (2013) suggested that the last species might be equivalent to *L. destombesi*. Specimens referred to *Lagenochitina* cf. *longiformis* also occur in an assemblage from the Leetse Formation, in the *proteus* conodont Biozone of the Hunneberg Stage of Estonia, close to the Tremadocian–Floian stage boundary (Hints & Nölvak, 2006). The specimens of *L. cf. longiformis* from the Leetse Formation are similar to the specimens of *L. aff. destombesi* from Assemblage 1 and are suggested here to be conspecific.

Conochitina decipiens has widespread lowest occurrences in the Floian Stage (Fig. 7), perhaps as low as the basal Floian *approximatus* graptolite Biozone in Bolivia (Heuse *et al.* 1999) and Bohemia (Paris & Mergl, 1984). Achab & Maletz (2021), however, recorded its lowest occurrence in Québec at a level in the *symmetrica* chitinozoan Biozone that is now placed in the highest Tremadocian. Amberg *et al.* (2017) recorded a similar form as *Conochitina* aff. *decipiens* from the *murrayi* graptolite Biozone in the Tremadocian of NW England (Fig. 7).

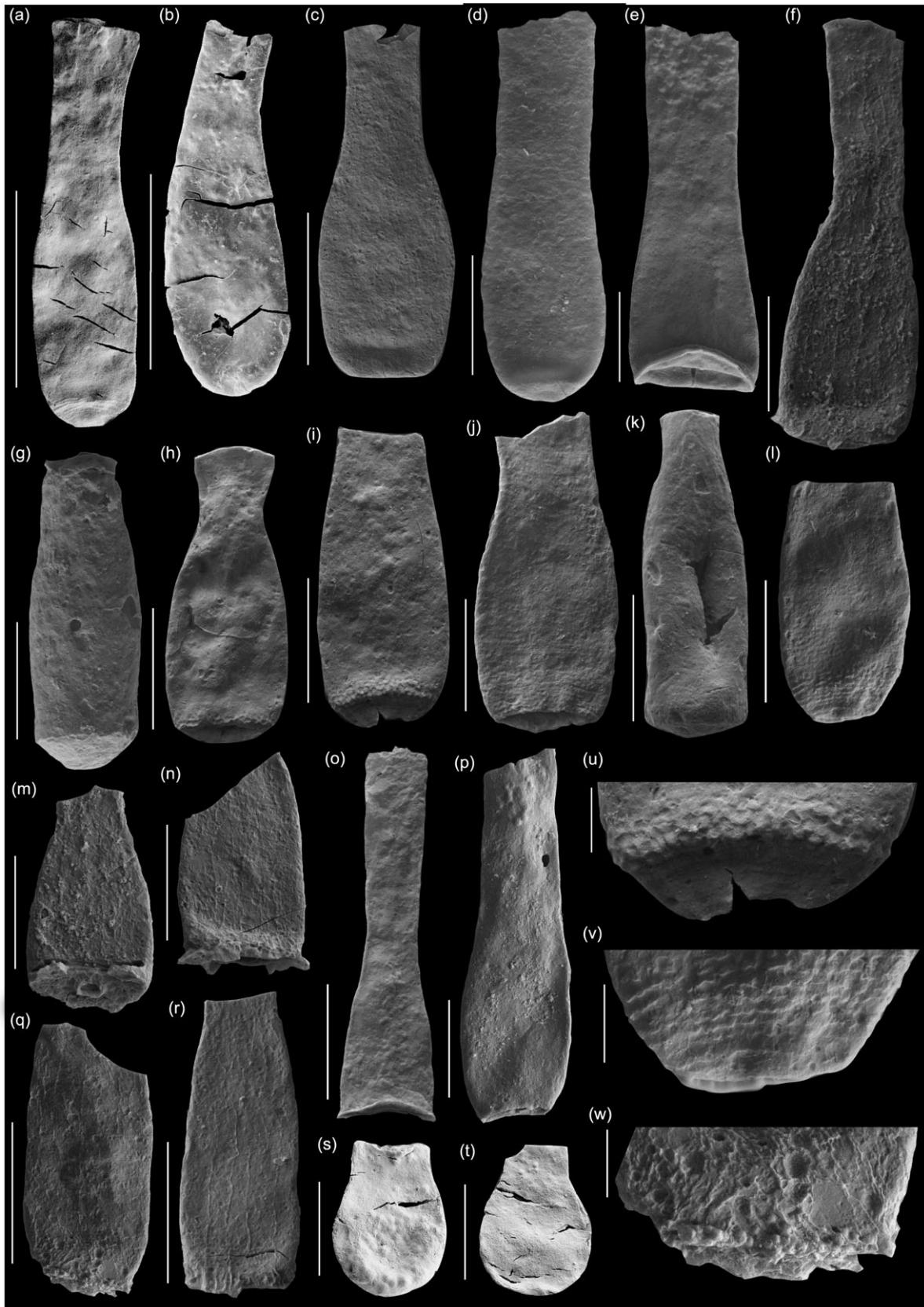


Fig. 8. Scanning electron micrographs of selected chitinozoans with location, formation and sample number. (a, b) *Lagenochitina destombesi* Elaouad-Debbaj (Heol Login, 'Login Beds', MPA 26829/ MPA 26831); (c) *Lagenochitina pirum* Achab (Pont-y-Fenni Old Quarry, Pont-y-Fenni Fm., TVDB 11-023); (d) *Conochitina raymondii* (Achab) (Cwm Yr Abbey, Afont Ffynnant Fm., TVDB 11-009); (e) *Cyathochitina* cf. *cycnea* (Vandenbroucke, Hennissen & Servais) (Pont Y Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-023); (f, m, n, q, r, w) *Laufeldochitina* sp. 1 (Cwm Yr Abbey, Carmarthen Fm., TVDB 11-008); (g) *Conochitina pseudocarinata* Paris (Allt Pen-y-Coed, Carmarthen Fm., TVDB 11-007); (h-j), l, u, v) *Conochitina queddichensis* Oulebsir & Paris (Allt Pen-y-Coed, Carmarthen Fm., TVDB 11-007), where (u) is an enlargement of (i), (v) is an enlargement of (l) and (w) is an enlargement of (q); (k) *Lagenochitina* aff. *cylindrica* Eisenack (Allt Pen-y-Coed, Carmarthen Fm., CA 13-044); (o) *Cyathochitina* aff. *calix* (Eisenack) (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-022); (p) *Laufeldochitina protolardeuxi* Soufiane & Achab (Allt Pen-y-Coed, Carmarthen Fm., CA 13-006); (s, t) *Lagenochitina brevicollis* Taugourdeau & de Jehkowsky (Heol Login, 'Login Beds', MPA 26838). Scale bars = 100 μ m except for (a), (b), (c), (o), (r) = 200 μ m and (u) (v) (w) = 20 μ m.

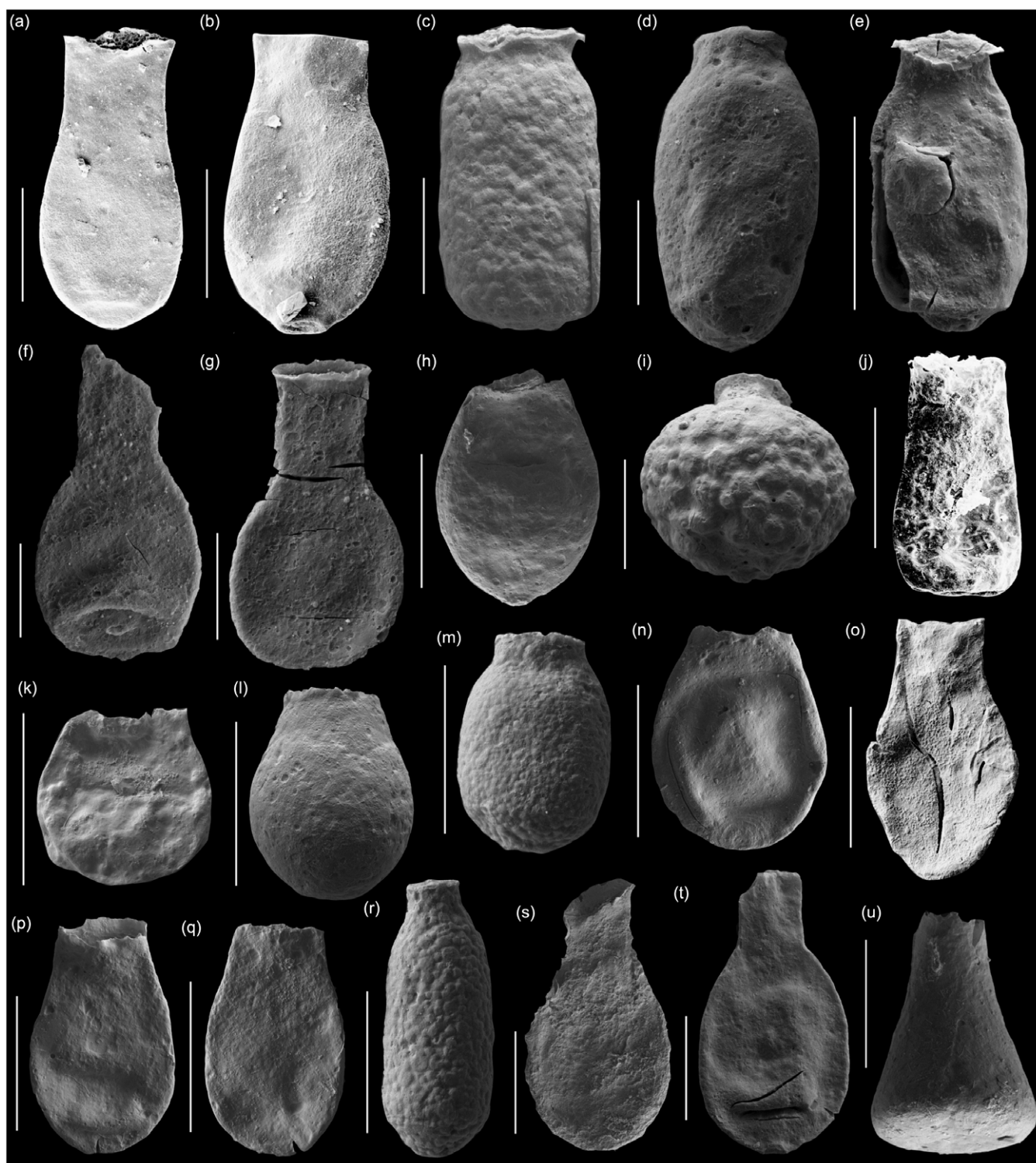


Fig. 9. Scanning electron micrographs of selected chitinozoans with location, formation and sample number. (a, b) *Lagenochitina ovoidea* Benoit & Taugourdeau (Heol Login, 'Login Beds', MPA 26838); (c, m) *Desmochitina minor* Paris (Allt Pen-y-Coed, Carmarthen Fm., CA 13-014); (d) *Desmochitina ovulum* (Eisenack) (Allt Pen-y-Coed, Carmarthen Fm., CA 13-012); (e) *Desmochitina papilla* Grahn (Allt Pen-y-Coed, Carmarthen Fm., CA 13-012); (f, g) *Lagenochitina esthonica* Eisenack (short forms, Cwm yr Abbey, Afont Ffynnant Fm., TVDB 11-002); (h, i) *Desmochitina* aff. *bullata* Taugourdeau & de Jehowsky (Llanfallteg Old Railway, Llanfallteg Fm., CA 13-015/13-018); (j) *Euconochitina fenxiangensis* Chen, Paris & Zhang (Allt Pen-y-Coed, Carmarthen Fm., CA 13-042); (k) *Desmochitina erinacea?* Eisenack (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., CA 13-037); (l) *Desmochitina ornensis?* Paris (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., CA 13-037); (n) *Desmochitina* aff. *cocca* (Eisenack) (Llanfallteg Old Railway, Llanfallteg Fm., CA 13-014); (o) *Lagenochitina conifundus* (Poumot) (Heol Login, 'Login Beds', MPA 26838); (p, q) *Bursachitina laminaris* Tang, Paris, Geng & Zhu (Pont-Y-Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-024); (r) *Desmochitina elongata* Eisenack (Allt Pen-y-Coed, Carmarthen Fm., CA 13-008); (s, t) *Lagenochitina obelgis* Paris (19, Arenig Fawr, Carned Iago Fm., TVDB 12-052; 20, Cwm yr Abbey, Afont Ffynnant Fm., TVDB 11-002); (u) ?*Conochitina primitiva* Eisenack (Llanfallteg Old Railway, Llanfallteg Fm., CA 13-019). All scale bars = 100 μ m.

The co-occurrences of *Conochitina decipiens* and *Lagenochitina destombesi* suggest a latest Tremadocian, Tr3 age for Assemblage 1 (Figs 6, 7), confirming and perhaps further restricting the latest Tremadocian or earliest Floian age indicated for the same beds by acritarchs (Molyneux & Dorning, 1989; Molyneux et al. 2007).

6.b. Assemblage 2

Assemblage 2 occurs in Allt Pen-y-Coed, where it extends from sample CA 13-042 in the Pibwr Member to CA 13-013 in the lower part of the Cwmffrwd Member (Fig. 6). Species of *Conochitina* dominate the faunas. *Conochitina decipiens* and *C. ordinaria* are present throughout, and *C. gueddichensis* (Fig. 8h–j, l, u, v) and *C. pseudocarinata* (Fig. 8g) occur in all except the lowest sample. *Conochitina raymondii* (Fig. 8d) occurs more sporadically.

The assemblage is subdivided into a lower Assemblage 2a, comprising the fauna from the lowest sample of the Pibwr Member in Allt Pen-y-Coed (CA 13-042), and a higher Assemblage 2b comprising chitinozoans from the rest of the samples from the Pibwr Member and the lower Cwmffrwd Member in the section (Fig. 6). Neither subdivision contains index species of Gondwanan chitinozoan biozones, which precludes direct correlation and introduces some uncertainty regarding their ages.

Assemblage 2a is characterized by the association of *Euconochitina fenxiangensis* (Fig. 9j) with *Conochitina decipiens*, *C. ordinaria*, *C. raymondii* (Fig. 8d), *Lagenochitina* aff. *cylindrica* (Fig. 8k) and *Rhabdochitina gracilis*. All range into Assemblage 2b, although *E. fenxiangensis* and *L.* aff. *cylindrica* are restricted to its lower part.

Euconochitina fenxiangensis was described by Chen et al. (2008) from the upper Fenxiang and lower Honghuayuan formations on the Yangtze Platform of South China. Chen et al. (2008) indicated that it ranged from the upper *Lagenochitina destombesi* Biozone into the *Euconochitina symmetrica* Biozone and therefore, based on correlations accepted at the time, from upper Tremadocian into lower Floian strata. Liang et al. (2017), however, recalibrated the *symmetrica* Biozone on the Yangtze Platform, placing it entirely within the uppermost Tremadocian Stage (Fig. 7). This might be taken to indicate that *Euconochitina fenxiangensis* is restricted to the Tremadocian Stage in South China, but Chen et al. (2008) also noted its coexistence with conodonts of the *Paroistodus proteus* and *Prioniodus elegans* biozones, which supports its occurrence in the lower Floian Stage. Subsequent records, however, have been from the upper Tremadocian of South China (Wang et al. 2013; Liang et al. 2017, 2018), including beds of the *murrayi* graptolite Biozone, and from the upper Tremadocian *copiosus* graptolite Biozone of NW Argentina (Toro et al. 2010; E. cf. *fenxiangensis*).

The species of *Conochitina* in Assemblage 2a all have lower Floian or upper Tremadocian lowest occurrences. That of *Conochitina decipiens* is noted under discussion of Assemblage 1 above. *Conochitina raymondii* was described by Achab (1980) from the Lévis Formation of Québec, where its lowest occurrence is in zone A of Raymond (1914) with *Tetragraptus approximatus* (Achab & Maletz, 2021, fig. 2). Chen et al. (2009) designated a *Conochitina raymondii* Biozone in the Yichang area of South China at a level that correlates with the *Oepikodus communis* conodont Biozone. This in turn equates with the lower Floian Stage Slice Fl1 (pre-*evae* Biozone; Wang et al. 2005, 2009). Chen et al. (2009) further noted that the lowest occurrence of *C. raymondii* was in Floian strata older than their sampled level, indicating an earlier Floian age.

Conochitina ordinaria was also described by Achab (1980) from the Lévis Formation, Québec, but its lowest occurrence there is a little higher than that of *C. raymondii*, in Zone B of Raymond (1914) with the graptolites *Phyllograptus typus*, *Tetragraptus quadribrahiatus* and *Dichograptus octobrahiatus*. Raymond's (1914) Zone B has been correlated with the *Tshallograptus fruticosus* graptolite Biozone (Achab & Maletz, 2021, fig. 2) in the middle Floian Stage. The lowest occurrence of *Conochitina ordinaria* in the Yichang area of South China is at about the base of the *Lagenochitina lata* Sub-biozone of the *Clavachitina langei* chitinozoan Biozone. Conodonts of the lower *Oepikodus evae* Biozone and graptolites of the *Didymograptus* [*Didymograptellus*] *bifidus* Biozone provide independent evidence for a middle to late Floian age (Chen et al. 2009; Fig. 7. See Toro & Herrera Sánchez (2019), for correlation of the *D. bifidus* Biozone with Stage Slice Fl3 and with the *eobifidus*, *deflexus* and probably the lower part of the *suecicus* biozones in South China).

Of the other two forms included in Assemblage 2a, *Lagenochitina* aff. *cylindrica* has affinities with a species that ranges in South China from the *Euconochitina symmetrica* chitinozoan Biozone (Liang et al. 2017) into the *Sagenachitina dapingensis* chitinozoan Biozone (Chen et al. 2009), respectively of latest Tremadocian and Dapingian age. *Rhabdochitina gracilis* is a long-ranging and widespread Ordovician species that has lowest occurrences in the upper Tremadocian of Morocco (Nowak et al. 2016) and close to the Tremadocian–Floian boundary in the *Paraistodus proteus* conodont Biozone and Hunneberg Regional Stage of Estonia (Hints & Nölvak, 2006), but ranges into the Upper Ordovician (e.g. Grahn & Nölvak, 2007).

The base of Assemblage 2b is marked by the lowest occurrences of *Conochitina gueddichensis* and *C. pseudocarinata* (Fig. 6). *Desmochitina ovulum* and *Laufeldochitina* sp. 1 (Fig. 8f, m, n, q, r, w) have lowest occurrences midway through the interval (Fig. 6). Paris (1981) described *Conochitina pseudocarinata* from the Armorican Massif, where it occurs in the same samples as *Desmochitina ornensis* and is one of the index species of his middle Arenig *Desmochitina ornensis* – *Conochitina pseudocarinata* Biozone. The latter biozone was not included in Paris's (1990) scheme, but *C. pseudocarinata* is listed as one of the associated species of his *Desmochitina ornensis* Biozone (Fig. 7).

In South China, *Conochitina pseudocarinata* gives its name to the *Conochitina pseudocarinata* Biozone of Wang et al. (2005, 2009) and the *Conochitina pseudocarinata* Sub-biozone of Chen et al. (2009). In both instances, the base of the unit, defined by the lowest occurrence of *C. pseudocarinata*, is in the upper part of the *Oepikodus evae* conodont Biozone and the lower part of the *Azygograptus suecicus* graptolite Biozone. These correlations indicate that the lowest occurrence of *C. pseudocarinata* in South China is in the upper part of the Floian Stage (Stage Slice Fl3; Fig. 7). Zhang et al. (2010, Fig. 2) correlated the base of the *suecicus* Biozone with the base of the Australian Castlemainian Stage, which in turn lies in the upper part of Stage Slice Fl3 (Bergström et al. 2009; Cooper & Sadler, 2012, fig. 20.9). Records of the species from Belgium (Samuelsson & Verniers, 2000; Herbosch & Verniers, 2014) and NW France (Paris, 1981, 1990) are also from the 'middle' Arenig or higher.

Conochitina gueddichensis and *Desmochitina ovulum* support a later Floian age for Assemblage 2b. *Conochitina gueddichensis* was described by Oulebsir and Paris (1993) from the *Eremochitina brevis* chitinozoan Biozone of Algeria, which is correlated with the upper Floian Stage, equivalent to the upper part of Stage Slice Fl2 and most of Fl3 (Cooper & Sadler, 2012, figs 20.1,

20.9) (Fig. 7). *Desmochitina ovulum* is generally found in deposits of Darriwilian and younger age (Paris, 1981; Nölvak & Grahn, 1993; Oulebsir & Paris, 1995; Tammekand *et al.* 2010; Nölvak *et al.* 2019), but was recorded by Liang *et al.* (2018) from the lower *Azygograptus suecicus* graptolite Biozone in the upper Floian Stage (Stage Slice Fl3) of South China.

It seems unlikely that Assemblage 2b is much older than Fl3 given the First Appearance Datums (FADs) of *Conochitina gueddichensis*, *C. pseudocarinata* and *Desmochitina ovulum* (Fig. 7). The possibility then is that Assemblage 2a is not much older than Assemblage 2b, either Fl3 or possibly Fl2. This suggestion is supported by the continuity of lithostratigraphy and lithofacies between assemblages 2a and 2b and records of the graptolites *Phyllograptus cf. densus* and *Pseudophyllograptus aff. angustifolius* from lower in the Pibwr Member at Glan Pibwr (Fortey & Owens, 1978; Owens, 1999). *Pseudophyllograptus angustifolius* has been reported in England and Wales from the middle Floian *jacksoni* graptolite Biozone to the middle Darriwilian *artus* graptolite Biozone, and *Phyllograptus densus* only from the Dapingian *victoriae* graptolite Biozone (Zalasiewicz *et al.* 2009). Webby *et al.* (2004) correlated the *Phyllograptus densus* and *Pseudophyllograptus angustifolius elongatus* biozones of Baltoscandia with their Time Slice 2c, which correlates in turn with the upper Floian Stage. Against this, the occurrence of *Euconochitina fenxiangensis* in Assemblage 2a and its co-occurrence with *C. pseudocarinata* and *C. gueddichensis* in the lower part of Assemblage 2b introduces some uncertainty, given that *E. fenxiangensis* has not been recorded with confidence from such a high level in the Floian Stage. Nevertheless, a middle to late Floian, Fl2–Fl3 age is suggested here for Assemblage 2a, albeit with a degree of uncertainty, and an Fl3 age for Assemblage 2b (Figs 6, 7). The suggestion of a middle to late Floian age for Assemblage 2a implies the possibility of significant hiatuses lower in the succession. Either the Ogof Hên Formation covers a significant amount of time (Fl1–Fl2?), or there are breaks at the base, top and/or within that formation.

6.c. Assemblage 3

Assemblage 3 covers much of the middle Arenig succession in South Wales, from the upper Moridunian Stage to the basal Fennian Stage, and is subdivided into assemblages 3a, 3b and 3c by successive lowest occurrences of chitinozoan species (Fig. 6). Assemblages 3a and 3b are found in the Carmarthen area and Assemblage 3c in the Whitland area.

Assemblage 3a is restricted to four samples from the upper part of the Cwmffrŵd Member in Allt Pen-y-Coed and Cwm yr Abbey (Fig. 6). It is characterized by a change from conochitinid to desmochitinid-dominated faunas, with the lowest occurrences of *Desmochitina elongata* (Fig. 9r), *D. minor* (Fig. 9c, m) and *D. papilla* (Fig. 9e) at its base. *Desmochitina ovulum* ranges up from Assemblage 2b and is relatively common in the lowest two samples. *Conochitina decipiens*, *C. ordinaria*, *C. raymondii* and *Laufeldochitina* sp. 1 also range up into Assemblage 3a, but the species of *Conochitina* only occur in the highest two samples and are the only forms recorded in those samples.

The records of *Desmochitina ovulum* documented above indicate an Fl3 age or younger for Assemblage 3a. There is nothing in the assemblage to limit it to the upper Floian, but it is most likely to correlate with the Fl3 Stage Slice (Figs 6, 7) given the ages suggested below for assemblages higher in the South Wales succession. Of the other desmochitinids in the assemblage, records of *D. elongata* are from the Darriwilian and Sandbian stages (Nölvak & Grahn, 1993;

Tammekand *et al.* 2010; Nölvak *et al.* 2019), and *Desmochitina papilla* was described by Grahn (1984) from Estonia where its lowest occurrence is at the base of the Vaana Substage in the middle of the regional Volkhov Stage. This in turn suggests correlation with a level in the lower Dapingian Stage (Cooper & Sadler, 2012, fig. 20.9). In South China, the lowest occurrence of *D. papilla* is in the *Didymograptellus bifidus* graptolite Biozone and the lower part of the *Oepikidus evae* conodont Biozone (Wang *et al.* 2005), and therefore in the upper Floian Stage (Cooper & Sadler, 2012).

Assemblage 3b covers the rest of the sampled succession in the Carmarthen district, from the upper Cwmffrŵd Member into the basal Afon Ffynnant Formation in Allt Pen-y-Coed and Cwm yr Abbey (Fig. 6). Its base is marked by the lowest occurrences of *Belonechitina micracantha*, *Lagenochitina obeligeris* (Fig. 9s, t), *Laufeldochitina protolardeuxi* (Fig. 8p) and *Rhabdochitina magna* (Fig. 10l). *Conochitina decipiens* (Fig. 10g, h), *C. ordinaria*, *Desmochitina ovulum*, *Laufeldochitina* sp. 1 and *Rhabdochitina gracilis* are also present in the lower part of the assemblage, some ranging through. Short forms of *Lagenochitina esthonica* (Fig. 9f, g) are consistently present at the top of the succession in samples collected across the contact of the Carmarthen and Afon Ffynnant formations.

Of the four species with lowest occurrences at the base of Assemblage 3b, *Lagenochitina obeligeris* occurs in all samples and is particularly common in those from the upper part of the Cwm yr Abbey Member and the Afon Ffynnant Formation in Cwm yr Abbey. It is a characteristic species of Assemblage 3b but is nevertheless long-ranging. It was described by Paris (1981) from Brittany and depicted by Paris (1990) as ranging from the middle Arenig *Eremochitina brevis* Biozone into the Llanvirn Series in southern Gondwanan terranes. Other records are from the Tremadocian Stage of South China (Wang *et al.* 2013; Liang *et al.* 2017, 2018) and the Darriwilian Stage in South America (Grahn 2006), Belgium (Herbosch & Verniers, 2014) and Oman (Sansouret *et al.* 2009; Heward *et al.* 2018), with similar forms (*L. cf. obeligeris*) recorded from the upper Tremadocian of Morocco (Nowak *et al.* 2016) and NW England (Amberg *et al.* 2017) and the Darriwilian Stage in Iran (Ghavidel-syooki *et al.* 2014).

Laufeldochitina protolardeuxi, only recorded from the lowest sample of Assemblage 3b, was originally described from the middle Arenig of Morocco (Soufiane & Achab, 1993), and *Rhabdochitina magna* was reported as an associated species of the lower–middle Arenig *Eremochitina baculata* Biozone (Fl1–Fl2; Fig. 7) of Gondwana (Paris, 1990). Other records of *R. magna*, however, are from the Dapingian (Liang *et al.* 2018), Darriwilian (Jenkins, 1967; Grahn *et al.* 1996; Rickards *et al.* 2010; Tammekand *et al.* 2010; Wang *et al.* 2018; Nölvak *et al.* 2019) and higher stages (Paris, 1990; Oulebsir & Paris, 1995; Vandenbroucke, 2008a, b). Similar forms have been reported as *Rhabdochitina cf. magna* from the middle Floian of Argentina (de la Puente & Rubinstein, 2013) and the Tremadocian of Morocco (Nowak *et al.* 2016).

Other species from Assemblage 3b are long-ranging, but *Belonechitina micracantha* corroborates the evidence of *Desmochitina ovulum* to indicate that this part of the succession is not older than late Floian. *Belonechitina micracantha* is only present in the lowest sample from Assemblage 3b but reoccurs higher in the South Wales succession. Elsewhere, its lowest occurrence is in the lower *Azygograptus suecicus* graptolite Biozone of the upper Floian Stage (upper Fl3) in South China (Wang, X. *et al.* 2005; Liang *et al.* 2018; Fig. 7). As with Assemblage 3a, there is nothing to limit the assemblage to the late Floian, but the base of

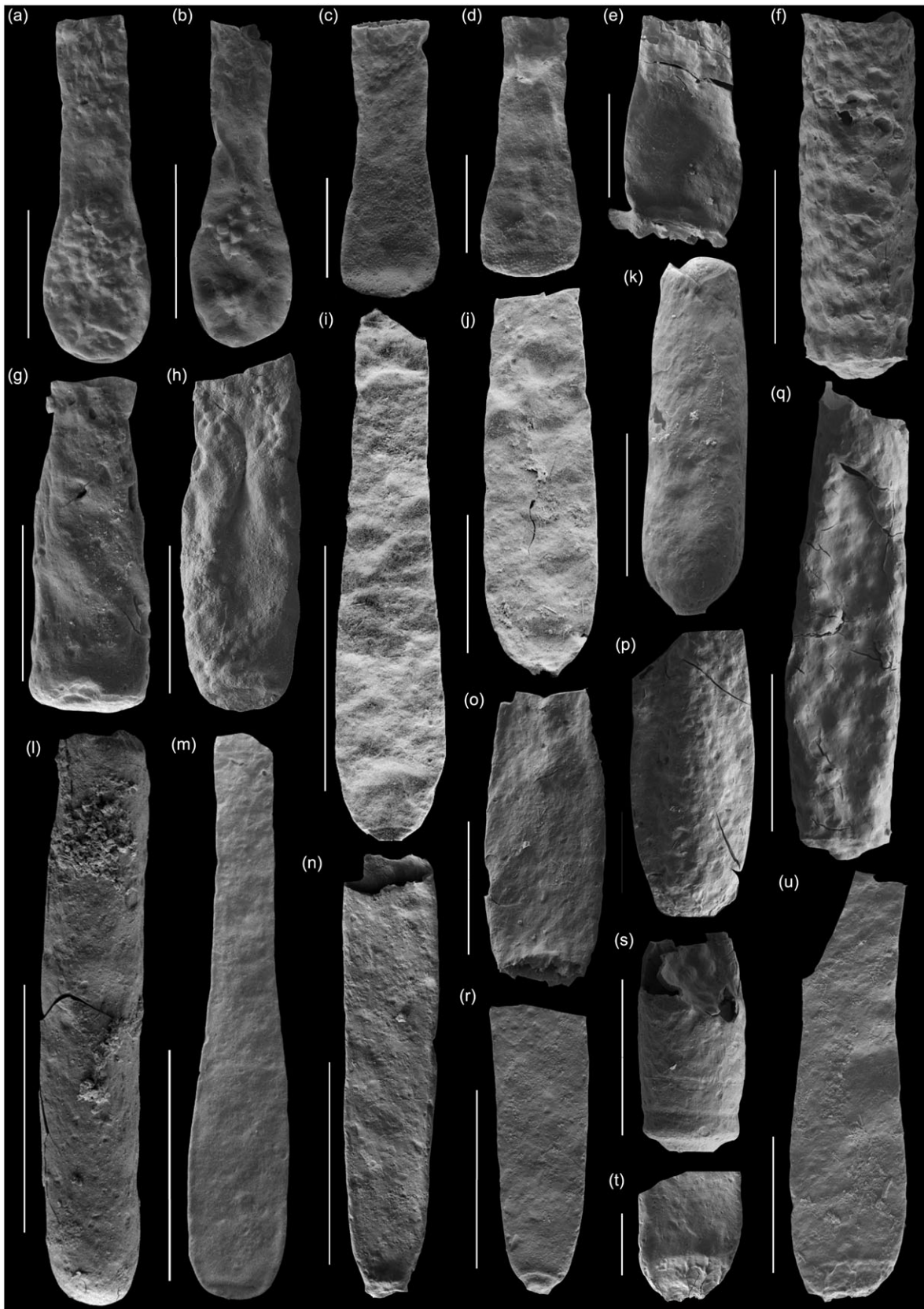


Fig. 10. Scanning electron micrographs of selected chitinozoans with location, formation and sample number. (a, b) *Conochitina* cf. *redouanei* Oulebsir & Paris (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-022); (c, d) *Belonechitina henryi* Paris (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-022); (e) *Cyathochitina touggourtensis* Oulebsir & Paris (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., CA 13-038); (f, q, s) *Cyathochitina protocolix?* Paris (Llanfallteg Old Railway, Llanfallteg Fm., CA 13-017, (s) CA 13-031); (g, h) *Conochitina decipiens* Taugourdeau & de Jekhowsky, (g) Allt Pen-y-Coed, Carmarthen Fm., CA 13-045, (h) Arenig Fawr, Carned Igo Fm., TVDB 12-052); (i, j) *Conochitina* cf. *havliceki* Paris & Mergl (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., CA 13-038); (k) *Conochitina cucumis* Grahn (Cwm Banau, Cwmfelin Boeth Fm., CA 13-051); (l) *Rhabdochitina magna* Eisenack (Cwm Yr Abbey, Carmarthen Fm., CA 13-006); (m) *Lagenochitina maxima* Taugourdeau & de Jekhowsky (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-023); (n, r) *Tanuchitina granbyensis* Grahn, Nölvak & Paris (Pont-y-Fenni Old Quarry, Pont-Y-Fenni Fm., TVDB 11-024); (o, p) *Tanuchitina achabae?* Paris (Llanfallteg Old Railway, Llanfallteg Fm., CA 13-018); (t, u) *Tanuchitina domfrontensis* Paris (Llanfallteg Old Railway, Llanfallteg Fm., CA 13-004). Scale bars = 100 μ m except (i), (j), (l) = 200 μ m and (m) = 300 μ m.

the Dapingian Stage is placed at a higher level in the Whitland area. Assemblage 3b is correlated accordingly with the Fl3 Stage Slice (Figs 6, 7).

Assemblage 3c comprises chitinozoans from the Castelldraenog Member of the Colomendy Formation, the Cwmfelin Boeth Formation and the basal Pontyfenni Formation in the Whitland area, and therefore spans the Whitlandian–Fennian stage boundary (Fig. 6). The lowest sample, from the Castelldraenog Member, yielded only three species, *Conochitina cucumis* (Fig. 10k), *Conochitina decipiens* and *Lagenochitina obeligeris*, and the base of the assemblage is marked by the lowest occurrence of *C. cucumis*.

Conochitina cucumis is the eponymous species of the *cucumis* Biozone of Baltoscandia (Nölvak & Grahn, 1993). The base of the biozone was originally placed in the upper Volkhov Stage of Baltoscandia, at a level that correlates approximately with the basal Darriwilian Stage (Nölvak & Grahn, 1993; Webby *et al.* 2004). Nölvak *et al.* (2019), however, repositioned its base to a lower level, within the Dapingian Stage. Furthermore, a form from the lower unit of the Dawan Formation in the Huanghuachang section of South China, designated as *Conochitina cf. cucumis* by Chen *et al.* (2009), has its lowest occurrence in the upper Floian, Stage Slice Fl3, in the lower *Azygograptus suecicus* graptolite Biozone and upper *Oepikodus evae* conodont Biozone (cf. sample positions in Wang *et al.* 2005, fig. 8; 2009, fig. 5).

Assemblage 3c is a low-diversity assemblage. *Conochitina decipiens* occurs in all samples but was not recorded from any of the overlying assemblages. *Belonechitina micracantha*, *Desmochitina ovulum*, *Rhabdochitina magna* and *Lagenochitina obeligeris* range through Assemblage 3c, occurring in one or more samples, but the most diverse microfauna with all five of these species plus *Bursachitina laminaris*, relatively common *Conochitina cucumis* and *Desmochitina minor* is from the Cwmfelin Boeth Formation (sample CA 13-051). The lowest occurrence of *Bursachitina laminaris* (Fig. 9p, q) is at this level.

Bursachitina laminaris was described by Tang *et al.* (2007) from South China and is shown as occurring in only one sample from the lower Darriwilian Stage on their range charts (*austrodentatus* Biozone, Dianbatou section: Tang *et al.* 2007, fig. 5). It was reported in the text of their paper, however, as occurring in the '3rd Stage' (i.e. Dapingian) and lower Darriwilian Stage, and as ranging from the *Azygograptus suecicus* graptolite Biozone to the *Undulograptus austrodentatus* graptolite Biozone. As the *suecicus* Biozone spans the Floian–Dapingian boundary in South China (Zhang *et al.* 2007, 2010), it follows that the lowest occurrence of *Bursachitina laminaris* there is likely to be close to the base of the Dapingian Stage (Fig. 7).

Based on their previous records, the occurrences of *Bursachitina laminaris* and *Conochitina cucumis* in Assemblage 3c are taken here to indicate a level close to the Floian–Dapingian stage boundary. Possible positions for the base of the Dapingian Stage are at (1) the lowest occurrence of *C. cucumis* and therefore correlating with a level in the Whitlandian Stage (Fig. 6); (2) the lowest occurrence of *B. laminaris* and therefore within the lowest Fennian Stage; or (3) within the assemblage, somewhat arbitrarily at a level that coincides with the base of the Fennian Stage. There is no conclusive evidence to favour one of these options over the others, but the lowest occurrence of *C. cucumis* and the base of Assemblage 3c is adopted here. Assemblage 3c is thus provisionally interpreted as being early Dapingian in age (Figs 6, 7). This position also suggests correlation of Assemblage 3c, at least in part, with the Gondwanan

Desmochitina ornensis Biozone (Fig. 7), following the correlations depicted by Webby *et al.* (2004) and Cooper and Sadler (2012), although the index species is not present at this level in South Wales.

6.d. Assemblage 4

There is a significant change in the upper part of the succession that distinguishes assemblages 4–6 from assemblages 2 to 3. It coincides with division of the dendrogram into two high-level clusters (Fig. 6), the change taking place within the Pontyfenni Formation. Chitinozoan faunas from assemblages 4–6 contain Gondwanan index species, and these are accompanied by graptolites to aid correlation. The dating and the correlation of assemblages 4–6 are consequently more secure.

Assemblage 4 corresponds to the chitinozoan fauna from the Pontyfenni Formation at Pont-y-Fenni. Its base is marked by the lowest occurrence of *Cyathochitina cf. cycnea* (Fig. 8e) Vandenbroucke *et al.* (2013), which ranges through but is restricted to the assemblage. It also contains *Desmochitina ornensis?* (Fig. 9l) and *Belonechitina henryi* (Fig. 10c, d), both of which are Gondwanan index species, and is subdivided into assemblages 4a and 4b at the lowest occurrence of the latter. *Cyathochitina cycnea* is a replacement name in Vandenbroucke *et al.* (2013) for *Cyathochitina giraffa* Hennissen *et al.* (2010), described from the Darriwilian–Sandbian section at Dawangou in the Tarim Basin of NW China, but a junior homonym of *Cyathochitina giraffa* Grahn and Nölvak (2010) from the Upper Ordovician (Sandbian) of Sweden.

Assemblage 4a is based on the two samples considered to be the lowest from the section at Pont-y-Fenni (CA 13-036, CA 13-037). Sample CA 13-036 yielded only *Bursachitina laminaris*, *Cyathochitina cf. cycnea* and *Desmochitina ovulum* (Fig. 9d). The second sample also has *Bursachitina laminaris*, accompanied by *Conochitina cf. havliceki* (Fig. 10i, j), *Desmochitina erinacea?* (Fig. 9k), *D. ornensis?* (Fig. 9l), relatively common *D. aff. cocca* (Fig. 9n) and *Rhabdochitina magna*.

The characteristic rugged, scaly wall of *D. ornensis* was rarely observed on specimens from South Wales, hence the question over the identification. Nevertheless, the specimens from South Wales are similar to *D. ornensis* in size and morphology, and the difference in wall ornamentation could be the effect of alteration. Despite the uncertain identification, the occurrence of *D. ornensis?* suggests correlation of Assemblage 4a with the Gondwanan *Desmochitina ornensis* Biozone (Paris, 1990; Fig. 7). This biozone is correlated in turn with the highest Floian and lower Dapingian stages in some schemes (Webby *et al.* 2004); Cooper & Sadler, 2012), although Videt *et al.* (2010) showed a higher correlation with stage slices Dp2 and Dp3. Interpretation of the age of Assemblage 3c as early Dapingian places Assemblage 4a within the Dapingian Stage, and in Stage Slice Dp1 following the correlations of Cooper & Sadler (2012) and Webby *et al.* (2004), or possibly Dp2 after Videt *et al.* (2010).

Associated species from the *ornensis* Biozone of Gondwana are *Conochitina pseudocarinata*, *Lagenochitina obeligeris*, *Sagenachitina oblonga*, *Tanuchitina achabae* and *Velatachitina veligera*. None of these occur in Assemblage 4a, although *C. pseudocarinata*, *L. obeligeris* and *T. achabae* are all present at other levels in South Wales.

Of the other chitinozoan species present in Assemblage 4a, *Bursachitina laminaris* and *Rhabdochitina magna* range through. *Conochitina havliceki* was described by Paris & Mergl (1984) from the upper Arenig *Tetragraptus cf. pseudobigsbyi* graptolite Biozone

of the Prague Basin, Bohemia. Specimens from South Wales do not have a foveolated surface, as originally described by Paris and Mergl (1984) and are here designated *C. cf. havliceki*. Specimens similarly designated as *Conochitina cf. havliceki* from South America, but not necessarily the same as those from South Wales, range from the lower Floian *Tetraraptus phyllograptoides* graptolite Biozone (Heuse *et al.* 1999) into the lower–middle Floian *Conochitina decipiens* Interval Zone of Grahn (2006) and possibly into the lower Darriwilian *dentatus* graptolite Biozone (Grahn, 2006, fig. 2). *Desmochitina erinacea* has Darriwilian and Sandbian records from Baltoscandia (Nölvak & Grahn, 1993; Tammekand *et al.* 2010; Nölvak *et al.* 2019) and South China (Tang *et al.* 2007). The other species of *Desmochitina* are long-ranging, from at least the Floian Stage to the Darriwilian Stage, and higher in the case of *D. cocca* (Paris *et al.* 2007; Rickards *et al.* 2010; Tammekand *et al.* 2010; Liang *et al.* 2018).

Assemblage 4b is defined by the total range of *Belonechitina henryi* and is the most diverse chitinozoan assemblage recorded from the Arenig Series of South Wales. In South China, the base of the Dapingian Stage was correlated with the base of the *Belonechitina cf. henryi* Biozone by Wang *et al.* (2009), but the FAD of the species is usually taken to be above the base of the stage. The *Belonechitina henryi* chitinozoan Biozone of Gondwana (Paris, 1990) thus succeeds the *ornensis* Biozone in the Dapingian Stage (Fig. 7), but there are differences of correlation between different schemes. The base of the *henryi* Biozone was placed in Stage Slice Dp1 by Cooper and Sadler (2012) and its top in Stage Slice Dp3. In contrast, Videt *et al.* (2010) placed the base of the *henryi* Biozone in Stage Slice Dp3 and its top in the lower Darriwilian Dw1 Stage Slice.

Other species restricted to Assemblage 4b include *Conochitina redouanei* (Fig. 10a, b), *Cyathochitina aff. calix* (Fig. 8o), *Cy. tougourtensis* (Fig. 10e), *Lagenochitina lata*, *L. maxima* (Fig. 10m), *L. pirum* (Fig. 8c) and *Tanuchitina aff. granbyensis* (Fig. 10n, r). *Cyathochitina calix* and *Lagenochitina pirum* have lowest occurrences in the Dapingian Stage elsewhere. *Cyathochitina calix*, for example, has lowest occurrences in the Dapingian Stage of Baltoscandia and South China (Grahn, 1984; Liang *et al.* 2018; Nölvak *et al.* 2019) and has been recorded from the Darriwilian Stage of Baltoscandia, Avalonia and South China (Jenkins, 1967; Grahn, 1984; Nölvak & Grahn, 1993; Grahn & Nölvak, 2007; Tammekand *et al.* 2010; Herbosch & Verniers, 2014; Liang *et al.* 2018; Nölvak *et al.* 2019). It is the index species for the early Darriwilian *Cyathochitina calix* Biozone (Paris, 1990; Webby *et al.* 2004; Cooper & Sadler, 2012). *Lagenochitina pirum* has its lowest occurrence in the upper Dapingian Stage of South China (Brocke *et al.* 2000; Chen *et al.* 2009), and has been recorded from the Darriwilian Stage of South China (Chen *et al.* 2009), Qaidam (Wang *et al.* 2018, including forms recorded as ‘cf.’), Australia (Quintavalle & Playford, 2006) and eastern Laurentia (Achab, 1989). In the last of these, *Lagenochitina pirum* is the index species of the Darriwilian *C. pirum* Biozone (Achab, 1989). *L. maxima* is very similar to *Conochitina ulsti* sp. nov. described by Nölvak *et al.* (2022) from the Kunda Stage (lower Darriwillian) in central Latvia.

The other forms restricted to Assemblage 4b have so far only been recorded lower or higher in the Ordovician succession. *Conochitina redouanei* and *Cyathochitina tougourtensis* were both described by Oulebsir and Paris (1993) from the *Eremochitina brevis* Biozone (upper Floian) of Algeria; *Lagenochitina lata* has been recorded from the Tremadocian of Baltoscandia (Liang *et al.* 2017; Nölvak *et al.* 2019), and the Tremadocian and Floian of South China (Wang *et al.* 2005;

Chen *et al.* 2009; Liang *et al.* 2018); and *Tanuchitina granbyensis* has been described and recorded from the Darriwilian Stage of Sweden (Grahn *et al.* 1996) and Latvia (Nölvak *et al.* 2021). There are no complete specimens of *T. granbyensis* in the Welsh assemblage, but the largest specimen measures more than 600 µm and the specimens have the typical ovoid apex with a carina that corresponds to the description given by Grahn *et al.* (1996). *Conochitina cucumis* and *Tanuchitina granbyensis* highlight increasing affinities between the Welsh and Baltoscandian assemblages during the Dapingian and early Darriwilian, in addition to *Cyathochitina calix*, although the latter was not found in association with the others in central Latvia (Nölvak *et al.* 2021).

Belonechitina micracantha, *Desmochitina aff. cocca*, *D. minor*, *D. ovulum*, *Lagenochitina obeligeris*, *Rhabdochitina gracilis* and *R. magna* all range through the assemblage. *Bursachitina laminaris*, *Conochitina cf. havliceki*, *Cyathochitina cf. cycnea*, *Desmochitina erinacea?* and *D. ornensis?* range into and have their local highest occurrences in Assemblage 4b.

The relatively common occurrence of *Belonechitina henryi* throughout the Pont-y-Fenni section is taken to indicate correlation of Assemblage 4b with the *henryi* Biozone and therefore with a level that is probably in the upper part of the Dapingian Stage, perhaps Dp2–Dp3, or the basal Darriwilian Stage (Dw1). This correlation is corroborated and perhaps further restricted by graptolites from the Pontyfenni Formation at Pont-y-Fenni, which are reported to indicate the *Undulograptus sinicus* Subzone of the basal Darriwilian *U. austrodentatus* Biozone (Owens, 1999).

6.e. Assemblage 5

Assemblage 5 straddles the Pontyfenni–Llanfallteg formation boundary in the lower part of the Llanfallteg section and comprises samples CA 13-014 to CA 13-019 (Fig. 6). Its base is marked by the lowest occurrence of *Desmochitina aff. bulla* (Fig. 9h, i), which is present in all samples and relatively common in three (CA 13-016 to CA 13-018). The lowest occurrences of *Cyathochitina protocalix?* (Fig. 10f, q, s) and *Tanuchitina achabae?* (Fig. 10o, p) in sample CA 13-017, midway through Assemblage 5 and low in the Llanfallteg Formation, are used to subdivide the assemblage into 5a and 5b.

Assemblage 5a is a low-diversity assemblage in the lower three samples (CA 13-014–CA 13-016). It consists mainly of *Desmochitina* spp., with *D. aff. cocca*, *D. minor* and *D. ovulum* in addition to *D. aff. bulla*. *Belonechitina micracantha* is the only other species present. All occur in all three samples.

Desmochitina bulla is the index species of the *bulla* Biozone (Paris, 1990), which succeeds the *henryi* Biozone in the Gondwanan Arenig biozonal scheme and is placed in the lower Darriwilian Stage Slice Dw1 (Videt *et al.* 2010; Cooper & Sadler, 2012; Fig. 7). *Desmochitina aff. bulla* differs from *D. bulla* in having a wider opening and a less sub-spherical shape. Nevertheless, correlation of Assemblage 5a with Stage Slice Dw1 is consistent with previous correlations of the highest part of the Anglo-Welsh Arenig Series with the lower Darriwilian Stage.

Cyathochitina protocalix was described by Paris (1981) from the Armorican Massif, where it was shown as ranging across the Arenig–Llanvirn series boundary and was described as a good marker for the boundary interval between the two series. It is the marker species for the *protocalix* Biozone of Paris (1990), which was regarded as the lowest Llanvirn biozone. More recently published schemes, however, have placed the *protocalix* Biozone in the upper Arenig (Webby *et al.* 2004) or have shown it spanning the

Arenig–Llanvirn series boundary (Videt *et al.* 2010; Cooper & Sadler, 2012). As the base of the Llanvirn Series is placed higher in the succession, a Dw1 age is indicated here for Assemblage 5b.

Cyathochitina protocalix was not positively identified in Assemblage 5b due to preservation, but specimens referred to as *Cyathochitina protocalix?* nevertheless display the restriction just above the base of the vesicle that is typical of the species (Fig. 10f, q, s). Tang *et al.* (2007) described a similar form from the lower Darrivilian (Dw1) of South China, but as there were only three poorly preserved specimens and they were significantly smaller than those from the Armorican Massif (France), they were kept in open nomenclature as *Hyalochitina cf. protocalix*.

Tanuchitina achabae was described by Paris (1981) from the base of the Pissot Formation in the Armorican Massif as an accessory species of the lower Dapingian *Desmochitina ornensis* Biozone, to which it was restricted (Paris, 1990, fig. 3). Higher in the Pissot Formation, however, Paris (1981) described a second form as *Tanuchitina* sp. aff. *achabae*, with a longer carina and ranging from the *Belonechitina henryi* Biozone into the *Cyathochitina protocalix* Biozone. As no entire specimen was found in the Welsh material, we cannot determine which form is the closest.

6.f. Assemblage 6

Assemblage 6 was identified as one of the significant clusters on the dendrogram (Fig. 6), but its base is not marked by any lowest occurrences. It comprises ten samples in the upper part of the Llanfallteg Formation, from CA 13-024 at the base to CA 13-005 at the top. Most species range up from underlying assemblages. *Belonechitina micracantha*, *Cyathochitina protocalix?*, *Desmochitina* aff. *cocca*, *Rhabdochitina gracilis* and *R. magna* range through all or most of the assemblage; *Conochitina primitiva* (Fig. 9u), *Cyathochitina campanulaeformis*, *Desmochitina* aff. *bullae* and *Tanuchitina achabae?* have highest occurrences in the lower part of the assemblage; and *Lagenochitina obeligitis* returns in sample CA 13-001, above its absence from Assemblage 5. The only lowest occurrence within Assemblage 6 is that of *Tanuchitina domfrontensis* (Fig. 10t, u), which is present in samples CA 13-033 and CA 13-035 in the lower half of the assemblage and again in the top two samples (CA 13-004, CA 13-005) where it is relatively common.

Tanuchitina domfrontensis was described by Paris (1981) from the Pissot Formation of the Armorican Massif, where its lowest occurrence is in the *protocalix* Biozone at a level that coincides with the lowest occurrence of pendant graptoloids (Paris, 1981, fig. 7). This led Paris (1981) to observe that the FAD of *Tanuchitina domfrontensis* might provide a useful criterion for the position of the Arenig–Llanvirn boundary in other successions, notably in the Cacemes Group of Portugal, from which it was also recorded. The successive lowest occurrences of *Cyathochitina protocalix* and *Tanuchitina domfrontensis* in the Pissot Formation further led Paris (1981) to propose a subdivision of the *Cyathochitina protocalix* Biozone into a lower subzone of *Rhabdochitina ?gracilis* – *Cyathochitina protocalix* and an upper subzone of *Cyathochitina protocalix* – *Tanuchitina domfrontensis*.

Tanuchitina domfrontensis is more bulbous than *T. achabae* and smaller. Very few complete specimens were recovered from Wales, but based on measurement and morphology, both *T. achabae?* and *T. domfrontensis* are present in Assemblage 6, albeit not continuously and their ranges do not overlap. *Tanuchitina achabae?* occurs in one sample at the base of Assemblage 6 (Fig. 6).

Tanuchitina domfrontensis occurs higher in the Llanfallteg Formation, from a few metres below the Arenig–Llanvirn boundary as defined by Fortey and Owens (1987) on graptolite evidence. Consequently, either the base of the Llanvirn Series is slightly lower than previously located in the section, or the range of *T. domfrontensis* straddles the Arenig–Llanvirn boundary rather than its FAD pinpointing the boundary. Either way, Assemblage 6 spans the boundary between the Arenig and Llanvirn series and between stage slices Dw1 and Dw2 (Figs 6, 7).

6.g. Sample CA 13-054

Sample CA 13-054 was collected north of Castell Draenog [c. SN 208 217] at a locality mapped as the Abergwilli Formation of Abereiddian (early Llanvirn) age (British Geological Survey, 2010; Burt *et al.* 2012). It yielded *Bursachitina laminaris*, *Conochitina decipiens*, *Desmochitina ornensis?*, *D.* aff. *cocca*, *D. minor* and *Lagenochitina obeligitis*. Other samples in which *Bursachitina laminaris* and *Desmochitina ornensis?* occur together are from the top of Assemblage 4a and the base of Assemblage 4b in the Pontyfenni Formation (Fig. 6). Most of the other species range through that interval. If the beds at the locality are from the Llanvirn Series, it implies a recurrence at a higher stratigraphic level of a chitinozoan assemblage associated with the Pontyfenni Formation. An alternative explanation is that the sample is from an outcrop of the Pontyfenni Formation north of and overlying or in faulted contact with the Whitland Shale Member (see Fortey & Owens, 1987, Fig. 2).

7. Chitinozoan assemblage from Arenig Fawr

Three species were identified from the two productive samples of the Henllan Ash Member: *Conochitina decipiens*, *Lagenochitina obeligitis* (Fig. 9s) and *Rhabdochitina magna* from sample TVDB 12-052, and *L. obeligitis* and *R. magna* from sample TVDB 12-054. All three species range through long intervals in the South Wales succession, but their ranges overlap in assemblages 3b and 3c (Fig. 6). Applying the same ranges to the sections around Arenig Fawr would indicate a late Moridunian to early Fennian age and correlation with the late Floian Stage Slice Fl3 or early Dapingian Stage Slice Dp1. This is consistent with the late Moridunian age shown for the Henllan Ash by Fortey *et al.* (2000), or with the Whitlandian age supported by the graptolite fauna (Zalasiewicz, 1984, 1986; Zalasiewicz *et al.* 2009). But although they support previous interpretations of the age of the Henllan Ash, all three species have longer stratigraphic ranges elsewhere so their evidence must be considered permissive rather than conclusive.

8. Discussion

The chitinozoans recorded from Arenig sections in the Carmarthen and Whitland areas of South Wales indicate correlation with stage slices from the upper Tremadocian through the Floian and Dapingian stages to the middle Darrivilian Stage, but with a degree of certainty that varies through the succession. Assemblage 1 is certainly close to the Tremadocian–Floian boundary and probably late Tremadocian (Stage Slice Tr3). The age and correlation of Assemblage 2a has the greatest uncertainty, but it is suggested to correlate with the middle to upper Floian Stage (Fl2–Fl3). There is more certainty over correlation of assemblages 2b, 3a, 3b and 3c. The occurrences of *Conochitina gueddichensis*,

Conochitina pseudocarinata and *Desmochitina ovulum* in Assemblage 2b all suggest that the assemblage is not older than the late Floian Fl3 Stage Slice. Correlation of the overlying assemblages is constrained by their observed or, in the case of Assemblage 3c, inferred superpositional relationships and by the occurrence of species that support a late Floian or younger age. The certainty of correlation increases upwards, with that of assemblages 4, 5 and 6 and their sub-assemblages supported by the presence of index species, or related forms, and by the occurrence of graptolites to corroborate the chitinozoan evidence, particularly in the Pontyfenni and Llanfallteg formations.

Chitinozoan zonal schemes covering the same stratigraphic interval (Fig. 7) have been developed for South Gondwana (Paris, 1990), based on successions in North Africa, SW and Central Europe, with a separate scheme for the upper Tremadocian of Morocco published by Nowak *et al.* (2016); South America (Grahn, 2006), with a separate scheme for NW Argentina (de la Puente & Rubinstein, 2013); Baltoscandia (Nölvak & Grahn, 1993; Grahn *et al.* 1996), Estonia (Nölvak *et al.* 2019) and Sweden (Grahn & Nölvak, 2007); South China (X Wang *et al.* 2005, 2009; Chen *et al.* 2009; W Wang *et al.* 2013; Liang *et al.* 2017); and Laurentia (Achab, 1989). Each of these regions and zonal schemes has species in common with South Wales, but the regions with the highest numbers in common are South China, South Gondwana and Baltica. South China has the most in common overall. For assemblages 2 and 3, 16 of the 19 named species from South Wales (84 %) are also known from South China, 10 (53 %) are known from South Gondwana, and another 10 are known from Baltica. For assemblages 4–6, 18 of the 24 named species (75 %) are known from South China, 18 from South Gondwana and 13 (54 %) from Baltica.

The lack of Gondwanan index species in assemblages 2 and 3 is notable. The absence of *Conochitina symmetrica* and *Eremochitina baculata*, the index fossils of the lowest two biozones in the Floian Stage of Gondwana, might be explained by an absence of strata or a lack of samples (Figs 6, 7), but this does not explain the absence of *Eremochitina brevis*. This species is the eponymous index of Paris's (1990) upper Floian *brevis* Biozone with which assemblages 2 and 3 are mainly correlated (Fig. 7). Furthermore, *Eremochitina brevis* has been widely reported from North Africa (Paris, 1990; Oulebsir & Paris, 1995; Videt *et al.* 2010; Nowak *et al.* 2016), South China (Liang *et al.* 2017, 2018) and NW Argentina (de la Puente & Rubinstein, 2013). Avalonia rifted away from Gondwana at around the beginning of the Ordovician Period (Domeier, 2016), but there is no indication of increased faunal provincialism following rifting to explain the absence of the species from South Wales. Moreover, Avalonia's trajectory only served to increase the distance from Gondwana during the Fennian Stage, whereas Gondwanan index species are present at that level.

The *Eremochitina brevis* Biozone is itself in need of revision. It was originally defined as a total range biozone (Paris, 1990), but Nowak *et al.* (2016) recorded *Eremochitina brevis* from the upper Tremadocian of Morocco and furthermore introduced an *Eremochitina brevis* Biozone (Fig. 7) at a much lower level than the *brevis* Biozone of other schemes (Paris, 1990; Grahn, 2006; de la Puente & Rubinstein, 2013). The occurrence of *Eremochitina brevis* in Morocco is accompanied by graptolites of the *Araneograptus murrayi* Biozone, acritarchs of the *mesaoudensis-trifidum* microflora, and other chitinozoans that are consistent with a late Tremadocian age such as *Lagenochitina* cf. *destombesi* and the *Euconochitina paschaensis-symmetrica* group. Nor is this Tremadocian record of *E. brevis* the only one to come to

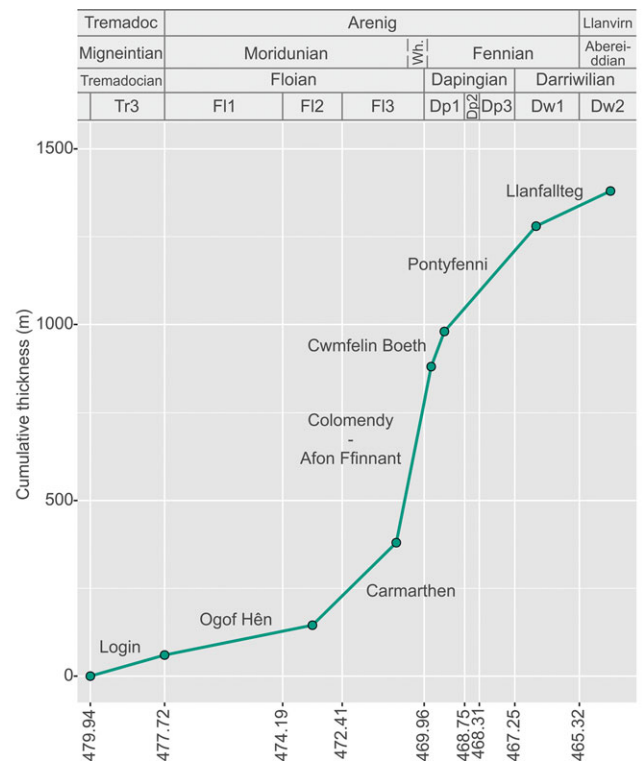


Fig. 11. (Colour online) Cumulative thickness curve for the upper Tremadocian to middle Darriwilian succession in South Wales based on thicknesses in Table 1.

light recently, as Liang *et al.* (2017, 2018) recorded the species from the upper Tremadocian Tungtzu Formation of South China. This indicates a downward extension of the species range in both areas and necessitates a redefinition of Paris's (1990) *brevis* Biozone from a total range to a partial range biozone. It is nevertheless unfortunate that Nowak *et al.* (2016) chose to use the same species as the index of a Tremadocian biozone, bringing with it the potential for confusion.

The absence of Gondwanan index species from the Moridunian succession in South Wales perhaps has a parallel with graptolite faunas in South Wales. In their synoptic history of the Arenig Series in South Wales, Fortey and Owens (1987) noted that ongoing transgression in the early Arenig resulted in soft, muddy sea-floor conditions represented by the Pibwr Member, but while oceanic connections were sufficiently developed for the appearance of a few graptolites at one level, a fully oceanic suite of species is not known. Fortey and Owens (1987) postulated that the subsequent development of a probable barrier to circulation further west, during deposition of the Cwmffrŵd and Cwm yr Abbey members, then produced a stagnant basin with restricted circulation in the Carmarthen region. This interpretation was augmented by Traynor's (1988) investigation of sedimentary processes during deposition of the Arenig Series in South Wales, which concluded that the Arenig deposits across South Wales were ponded in small interconnected marine sub-basins with facies and facies distributions controlled by intra-Arenig tectonic activity during an overall sea-level rise. Graptolites first become locally numerous in the Afon Ffynnant, Blaencediw and Colomendy formations, with species of *Azygograptus* and *Expansograptus*, and together with cyclopygid trilobites bring the first indications of oceanic conditions. Graptolites from the Pontyfenni and Llanfallteg formations are yet more cosmopolitan and oceanic, the Pontyfenni Formation

Table 1. Thicknesses of formations and members from the Arenig Series of South Wales used to compile the cumulative thickness curve in Figure 11

Formation	Member	Thickness	Comment	Source
Login		60 m	minimum	Fortey & Owens (1978)
Ogof Hên	Allt Cystanog	25 m	minimum	Fortey & Owens (1978)
Ogof Hên	Bolahaul	60 m	minimum	Fortey & Owens (1978)
Carmarthen	Pibwr	80 m	minimum	Fortey & Owens (1978)
Carmarthen	Cwmffrŵd	70 m	minimum	Fortey & Owens (1978)
Carmarthen	Cwm yr Abbey	45 m	minimum	Fortey & Owens (1978)
Afon Ffynnant		40 m	minimum	Fortey & Owens (1987)
Blaencediw		80 m	minimum	Fortey & Owens (1987)
Colomendy	Rhyd Henllan	150 m	approximate	Fortey & Owens (1987)
Colomendy	Castelltraenog	150 m	approximate	Fortey & Owens (1987)
Colomendy	Whitland Abbey	200 m	minimum	Fortey & Owens (1987)
Cwmfelin Boeth		100 m	minimum	Fortey & Owens (1987)
Pontyfenni		300 m	minimum	Fortey & Owens (1987)
Llanfallteg		100 m	minimum	Fortey & Owens (1987)

perhaps representing the most oceanic conditions (Fortey & Owens, 1987, p. 104). It is very likely that the change from a restricted marine basin to the more oceanic setting documented by Fortey and Owens (1987) affected chitinozoans as much as the graptolites, and offers an explanation for the presence of Gondwanan index species in the higher parts of the succession, in contrast to their absence from the lower part.

The results from this study have implications for the extent of the regional Whitlandian Stage. The chitinozoan assemblages from the Carmarthen and Afon Ffynnant formations suggest correlation of much of the Moridunian Stage succession in the Carmarthen area with the Fl3 Stage Slice (Figs 6, 7). As the base of the regional Fennian Stage is placed at a level low in the Dapingian Stage, based on recognition of the *ornensis* and *henryi* biozones higher in the succession, the interval available for correlation with the Whitlandian Stage is restricted to the upper part of the Fl3 Stage Slice and the lower part of the Dp1 Stage Slice (Figs 6, 7).

A consequence of re-correlating the Whitlandian Stage with the upper part of the Fl3 Stage Slice and the lower part of Dp1 is that Whitlandian strata in South Wales would have been deposited in a relatively short period of time. A cumulative thickness curve (Fig. 11) shows trends from the Tremadocian Stage to the mid Darriwilian Stage that take account of the revised correlation. Although the curve is not corrected for compaction or tectonic thickening, it steepens in the upper Floian and lowest Dapingian stages, represented by the 500 m minimum thickness of the Colomendy Formation (Table 1). Similarly, cumulative thickness curves published by Verniers *et al.* (2002, fig. 3) and Linnemann *et al.* (2012, fig. 6) for the Lower Palaeozoic of the Brabant Massif, also part of Avalonia, show increases in cumulative thickness around 470 Ma. The Brabant formation associated with this, however, is the Tribotte Formation (Linnemann *et al.* 2012, fig. 6), which is dated biostratigraphically as early Darriwilian (Herbosch & Verniers, 2014).

An assessment of global chitinozoan distribution patterns in the Lower and Middle Ordovician is not an aim of this paper, but it has been shown that such patterns respond to large-scale environmental changes related to palaeoclimate (Vandenbroucke *et al.* 2010a, b). Several studies using proxy data, sequence stratigraphy

and Global Circulation Models have suggested important global cooling during the Early–Middle Ordovician (Trotter *et al.* 2008), with ice caps present from the Darriwilian if not earlier (Turner *et al.* 2011, 2012; Dabard *et al.* 2015; Pohl *et al.* 2016a, b; Rasmussen *et al.* 2016). The data presented here has the potential to contribute to a better understand of chitinozoan distribution patterns and migrations during this period in the development of Earth's climate system, as well as augmenting stratigraphic correlations.

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