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An Early Silurian 'Herefordshire' myodocope ostracod from Greenland and its palaeoecological and palaeobiogeographical significance

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Abstract – Here we record the occurrence of a new species of the Herefordshire Lagerstätte ostracod genus *Pauline* from the Lower Silurian (upper Telychian) of North Greenland. *Pauline nivisis* sp. nov. was recovered from a limestone boulder (Pentamerus Bjerge Formation) collected south of Kap Schuchert, Washington Land. It is reasonable to transpose the palaeobiology known from the Herefordshire *Pauline avibella* – body, limbs including swimming antennae, lateral eyes, gills and alimentary system – into the carapace of the Greenland species, which represents the oldest cylindroleberidid myodocopid and almost the oldest known myodocope, and is the first record of a Herefordshire Lagerstätte genus from outside the Welsh Borderland locality. Morphological, sedimentological and faunal evidence suggest that the Greenland species was nektobenthic. This is compatible with the notion that ostracods (specifically myodocopids) did not invade the water column until later in the Silurian, in the Wenlock and Ludlow epochs. *Pauline* is an Early Silurian link between 'Baltic-British' and North Laurentian ostracod faunas, endorsing the idea that the UK and Greenland were in close geographical proximity, near a remnant Iapetus Ocean, during late Llandovery time.

Keywords: Telychian, Franklinian Basin, Cylindroleberididae, palaeobiology, lifestyle.

1. Introduction

The Silurian has relatively few exceptionally preserved biotas compared to most other periods of Earth history. The Early Silurian (Wenlock Epoch) Herefordshire Lagerstätte (Briggs, Siveter & Siveter, 1996), UK, known from a single locality in the Welsh Borderland, has yielded unrivalled anatomical data in a diversity of three-dimensionally preserved invertebrates, including brachiopods, a polychaete worm, molluscs, an asterozoan and a range of arthropods including four (myodocope) ostracod species (Briggs *et al.* 2008, 2012; Siveter *et al.* 2010, 2013; Sutton *et al.* 2011, 2012). This material has provided unparalleled information about the palaeobiology of Early Palaeozoic ostracods. None of the mostly soft-bodied invertebrate taxa of the Herefordshire Lagerstätte were known outside the type locality in the Welsh Borderland until now. The exceptional preservation in this Lagerstätte results from rare geochemical conditions prevailing locally after an ash fall, producing three-dimensional infill fossils preserved in calcite (Orr *et al.* 2000).

Here we record the occurrence of a new, second species of the Herefordshire myodocope ostracod genus *Pauline* (Siveter *et al.* 2013) from the Lower Silurian (Telychian Stage) of North Greenland and assess its morphology, likely ecology and palaeobiogeographical significance. The new record demonstrates that the evolving corpus of functional anatomical evidence gleaned from the Herefordshire Lagerstätte fossils has potentially wide-ranging application for interpreting the biology of related taxa and the ecology of Silurian fossil assemblages elsewhere.

2. Material and methods

The ostracods described herein were recovered from a single boulder (GGU 216856) collected in August 1976 by J. M. Hurst during an expedition of the Geological Survey of Greenland (GGU), which is now part of the Geological Survey of Denmark and Greenland. The ostracod-bearing rock comes from the Lower Silurian section at Kap Schuchert, Washington Land, western North Greenland (Fig. 1), at approximately 80° 78′ N, 64° 87′ W.

The ostracods consist of 3D-preserved specimens that are housed in the Geological Museum, Copenhagen University, a part of the Natural History Museum of Denmark (MGUH), with the numbers MGUH 30487–30495. The morphological terminology for the myodocope carapace follows that of Siveter, Vannier & Palmer (1987). Rock matrix was removed from the specimens mechanically using a vibrotool. The photographs were taken using a Leitz Aristophot mounted with a Canon EOS 5D camera, following the methods outlined in Siveter (1990).

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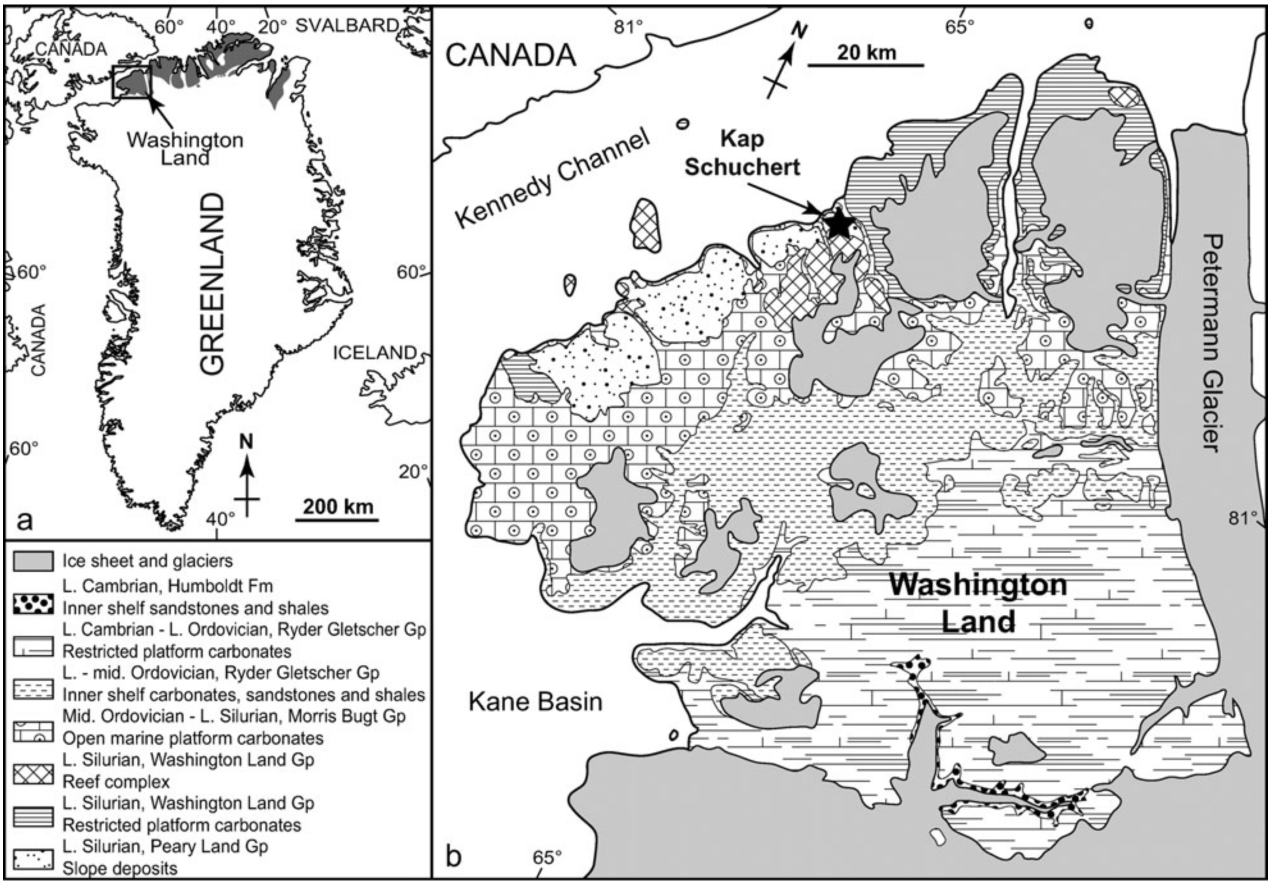

Figure 1. Geological setting of the locality for *Pauline nivisis*. (a) Location and extension of the Greenland segment of the Franklinian Basin (grey filling) and Washington Land. (b) Geological map of Washington Land and location of the Kap Schuchert outcrop (star): maps after Peel & Sønderholm (1991).

3. Geological setting

The Lower Palaeozoic succession of the Franklinian Basin extends over almost 2000 km across the Canadian Arctic Islands to eastern North Greenland and is well exposed over 1000 km in North Greenland (Fig. 1a; Peel & Sønderholm, 1991). The ostracod-bearing rock documented here is from an extended reef belt that formed an important component of the Greenland carbonate shelf margin in Early Silurian times and which survived until the late Llandovery Epoch. The reef formed a patchwork barrier across the region and was limited seawards by a steep shelf margin to the north while a flat carbonate platform was maintained between and behind the reef mounds (Fig. 1b; Sønderholm & Harland, 1989). The fossil material was collected immediately south of Kap Schuchert (Fig. 1b). In this region, marine shelf sedimentary deposits are represented by the Pentamerus Bjerge Formation of the Washington Land Group; the marine slope sedimentary deposits are referred to the Lafayette Bugt and Cape Schuchert formations, Peary Land Group (Peel & Sønderholm, 1991).

The new myodocope species was recovered from a pale grey biosparite boulder collected from near the top of the section (Hurst, 1980, fig. 24, section A; Fig. 1b). Thin-section petrological analysis shows fragmented brachiopods, articulated trilobites and possible algae but no corals or coralline algae. Such biosparites occur as blocks in the breccia of the Lafayette Bugt Formation and are considered to be derived from the partly coeval Pentamerus Bjerge Formation (Hurst, 1980). Hughes & Thomas (2011) considered these sedimentary deposits to represent high-energy environments within the euphotic zone. Graptolites indicative of the *Monograptus spiralis* Biozone *sensu lato*, conodonts of the *Pterospathodus amorphognathoides* Biozone and trilobites (*Meroperix aquilonaris*) indicate a late Telychian, Llandovery age (see discussion in Lane & Owens, 1982).

4. Palaeobiogeographical significance

There is one previous record of a myodocope ostracod from the Silurian of North Greenland, that of the Telychian *Entomozoe* aff. *E. tuberosa*, from Centrum Sø, Kronprins Christian Land, eastern North Greenland (Siveter & Lane, 1999). *Entomozoe* is also known from several other locations in the Early Silurian, in Scotland, Arctic Russia and South China (Siveter & Vannier, 1990; Siveter & Bogolepova, 2006) and possibly the Middle Silurian of Australia (Siveter, Vannier & Palmer, 1991). All currently identified Llandovery myodocope ostracods are referred to either *Pauline* or *Entomozoe*. The only known older myodocope is

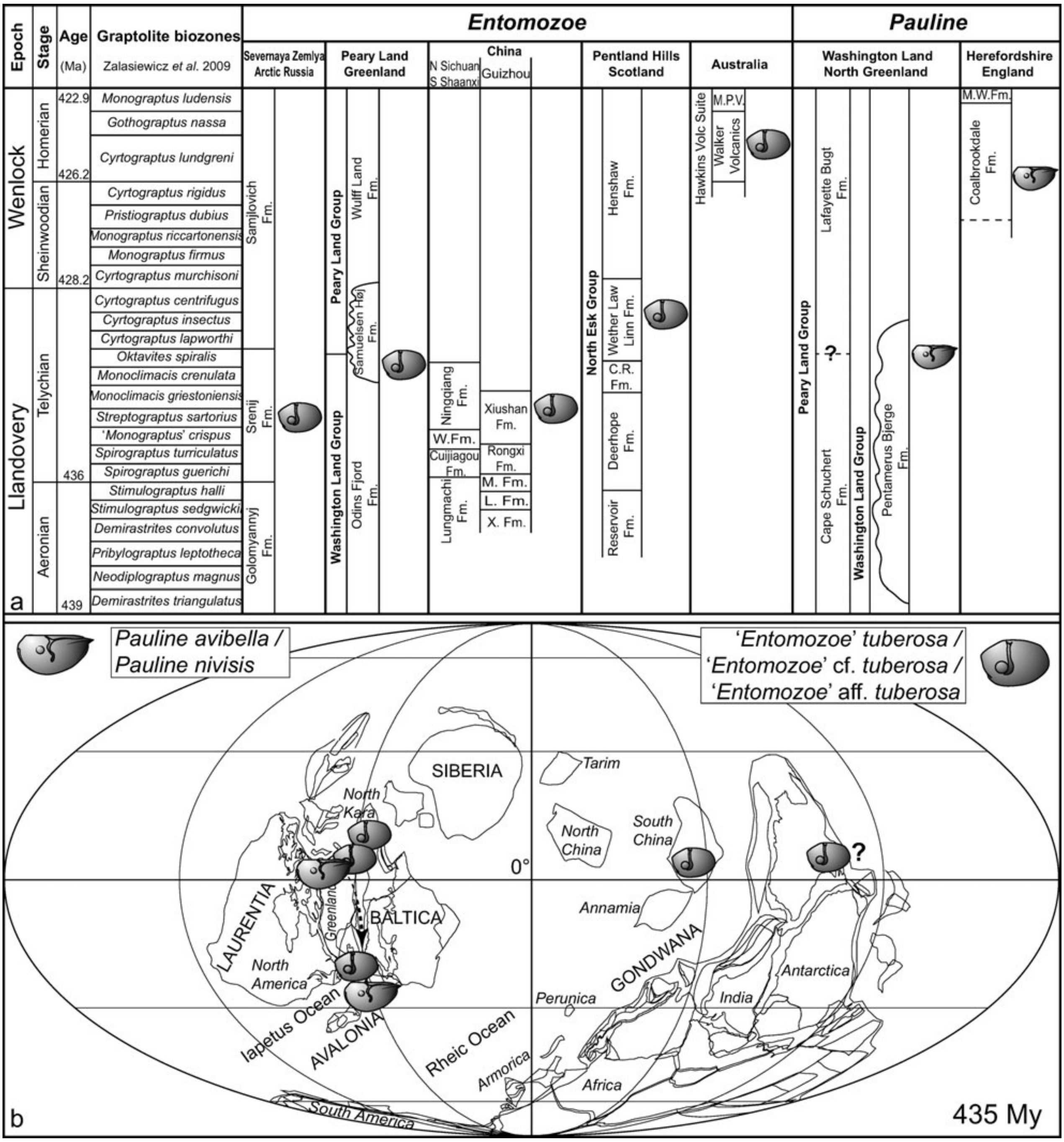

Figure 2. Stratigraphic and palaeogeographic distribution of *Entomozoe* and *Pauline*. (a) Stratigraphic position, which is approximate within each formation. (b) Palaeogeographic distribution and possible migration pathways (dashed arrows). Stratigraphy for Greenland after Peel & Sønderholm (1991); Scotland and England after Siveter & Vannier (1990); Arctic Russia after Siveter & Bogolepova (2006); China after Rong, Wang & Zhang (2012); Australia after Strusz (1984); palaeogeographic map after Torsvik (2009). C. R. Fm. – Cock Rig Formation; L. Fm. – Leijiatun Formation; M. Fm. – Majiaochong Formation; M.P.V. – Mount Painter Volcanics; M.W. Fm. – Much Wenlock Formation; W. Fm. – Wangjiawan Formation; X. Fm. – Xiangshuyuan Formation.

Myodoprimigenia fistuca from the Upper Ordovician, Ashgill Series, Soom Shale of South Africa (Gabbott *et al*. 2003). There is probably a minimum of 2 million years of time difference between the occurrence of the new Greenland species of *Pauline* (late Llandovery) and the Herefordshire *Pauline avibella*, which comes from approximately the Homerian–Sheinwoodian Stage boundary within the Wenlock (unpublished evidence from chitinozoan associates; G. Mullins, pers. comm.; see Zalasiewicz *et al*. 2009, fig. 2 for an approximate estimate of the time difference between these horizons).

At present, *Pauline* is known only from two localities, both at a low palaeolatitude. During Early Silurian times, North Greenland was situated close to the equator on the northern margin of the Laurentia palaeocontinent while England and Wales were in the southerly subtropics (~ 30° S) on the Avalonia microplate (Cocks & Torsvik, 2002, 2011; Fig. 2). During the late Llandovery, these regions were separated by a vestige of the Iapetus Ocean. *Pauline*, a supposed nektobenthic ostracod, is an Early Silurian link between 'Baltic-British' and North Laurentian ostracod faunas (for which see Siveter, 1989; Perrier & Siveter, in press) and, as pelagic larvae are unknown in ostracods, this endorses the idea that southern Britain and Greenland were in close geographical proximity at that time. The shelf margins of the remnant Iapetus Ocean could have acted as a channel for the migration of *Pauline* species.

The Late Ordovician – Early Silurian (*c*. 455–425 Ma) 'Early Palaeozoic Icehouse' (see Page *et al*. 2007) is an interval characterized by the waxing and waning of a major Gondwanan ice-sheet. The presence of *Pauline* within tropical latitudes (Fig. 2) in late Telychian time may be consistent with the recovery patterns of ostracod faunas post-dating glacial advances of the Early Palaeozoic Icehouse. Whilst diverse podocope ostracod assemblages are known from the Lower Silurian (Rhuddanian) of low latitude Laurentia (Copeland, 1974) and Baltica (Sarv, 1968; Truuver *et al*. 2012), no ostracods are known from the Rhuddanian strata of Avalonia, and only a few from the Aeronian (Siveter, 2009). In part this reflects the availability of suitable lithofacies to preserve the fauna, with much of the Rhuddanian succession in southern Britain represented by deep-water facies of the Welsh Basin and northern England. The appearance of *Pauline* farther south (~ 30° S; Fig. 2) in the Wenlock Epoch is consistent with the hypothesis that low latitude faunas spread out to higher latitudes in the Wenlock, both as the high latitude climate ameliorated and as seas advanced into shelf areas as the Gondwanan ice-sheet decayed. Thus, Hairapetian *et al*. (2011) documented the essentially Laurentian aspect of the earliest podocope ostracod faunas in the Llandovery of peri-Gondwanan Iran. The temporal and geographic distribution of *Entomozoe tuberosa* and related forms also supports this notion (see Siveter & Vannier, 1990; Siveter & Lane, 1999; Siveter & Bogolepova, 2006). *Entomozoe* is known only from low latitudes (~ 0–10° N) in the early Telychian (Greenland, Arctic Russia and South China) and then apparently spread farther south in the latest Telychian (Scotland, ~ 20° S; Fig. 2).

Pauline is known from only two localities, but *Entomozoe* is more geographically widespread (Fig. 2), with *E. tuberosa sensu stricto* and *sensu lato* forms present in tropical regions from Laurentia to Gondwana (Australia). To explain at least a part of this wide distributional pattern, Siveter & Lane (1999) suggested that *Entomozoe* may have spread by 'island hopping' (e.g. see Cocks & Fortey, 1982); for example, using the Siberia and North China plates to reach South China and possibly Australia (Siveter, Vannier & Palmer, 1991; Fig. 2). To do so it seems that *Entomozoe* probably had greater dispersal capacity than *Pauline*. Such a pattern of distribution is not replicated, for example, in podocopid ostracods (their dispersal capacity is generally regarded as more limited than that of some myodocopes; see Perrier & Siveter, in press; but see Hairapetian *et al*. 2011). Another possible explanation for the wide biogeographical occurrence of *Entomozoe* is that they were distributed by ocean currents, as is the case for some Recent myodocopes. For example, the Japan Current is probably responsible for the extensive distribution of the nektobenthic myodocope *Vargula hilgendorfii*, which has rapidly (< 10,000 years) dispersed over 3000 km northward along the Japanese coastline (Ogoh & Ohmiya, 2005). Nektobenthic myodocopes live at the water–sediment interface and move into the water column typically at night (e.g. Recent cylindroleberidids; see L. Corbari, unpub. Ph.D. thesis, Univ. Bordeaux 1, 2004, Corbari, Carbonel & Massabuau, 2005). Although their active movement in the water column is limited to a few metres above the sea bed, such buoyant organisms may be transported by bottom currents. This may be one mechanism that nektobenthic myodocope ostracods use to colonize coastal environments over long distances (e.g. *Vargula* in Japan). If *E. tuberosa* (*sensu stricto*/*sensu lato*) was pelagic this would also explain its global distribution. However, such a conclusion requires vigorous testing of its faunal associates, range of lithofacies and functional morphology.

5. Palaeoecology

5.a. Environmental setting

Within the North Greenland Telychian reef environments (Fig. 2) the myodocope faunal associates include abundant stromatoporoids and pelmatozoan debris, together with rugose and tabulate corals, trilobites, gastropods, cephalopods, rostroconchs, graptolites, brachiopods, bivalves and other, undescribed, mostly non-palaeocope ostracods (Hughes & Thomas, 2011). The other ostracods include *Euprimitia*? sp. and *Ceratocypris symmetrica* (Poulsen, 1934) from the Kap Schuchert Formation and *Monoceratella mazos*, which was recovered from a boulder about 1 m stratigraphically from the *Pauline* material (block GGU 216855; Lane, 1980). This essentially epibenthic fauna, along with the reef lithofacies, indicates a relatively shallow shelf setting (see Hurst, 1980; Peel & Sønderholm, 1991). By comparison, the Herefordshire Lagerstätte biota comprises a diverse 'shelly' fauna (see Section 1) and four large nektobenthic myodocope species (Siveter *et al*. 2003, 2007, 2010, 2013), in an environmental setting that is estimated to reflect a water depth of 100–200 m (Briggs, Siveter & Siveter, 1996).

5.b. Functional anatomy

Pauline nivisis sp. nov. has such a similar carapace morphology to that of *P. avibella* that it is reasonable to transpose the palaeobiology known from the Herefordshire fossil – body, limbs including swimming antennae, lateral eyes, gills and alimentary system – into the carapace of the Greenland species (reconstruction in Fig. 3b). The preadductorial node of *P. nivisis* most likely housed a well-developed lateral eye and this also suggests that its carapace was thin and translucent, at

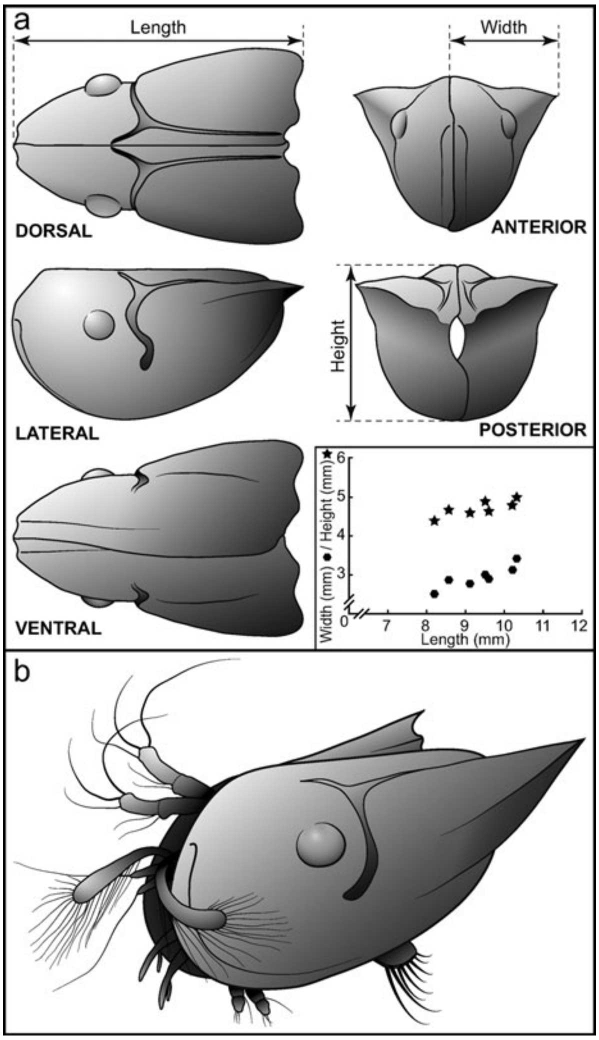

Figure 3. *Pauline nivisis* sp. nov. (a) Reconstruction and measurements of the carapace. (b) Idealized reconstruction in life position.

least at the position of the eye, as in most Recent myodocopes (see Land & Nilsson, 1990, fig. 1; Vannier, Abe & Ikuta, 1998, fig. 4). The large basipod and setate exopod of the second antenna of *P. avibella* suggests that it was an efficient swimmer (Siveter *et al.* 2013) and the same can be assumed for *P. nivisis*. A swimming lifestyle would have been supported by the presence of gills and paired epipods, as present in *P. avibella* and a supposed well-developed cardiovascular system including a heart (see Vannier & Abe, 1992; Williams *et al.* 2011). The morphology of the mandible and first maxilla of *P. avibella*, with well-developed endites, and its clawed furca is similar to that in Recent nektobenthic myodocopids (see Vannier, Abe & Ikuta, 1998) and suggests a similar feeding strategy for *Pauline* species (Siveter *et al.* 2013), which are presumed to have scavenged, preyed or were detritovores on or near the substrate. Appendages and the furca would cut and tear the food held by the mandible. Both male (see *Colymbosathon*, Siveter *et al.* 2003) and female (see *Nymphatelina*, Siveter *et al.* 2007) myodocopes were identified from the Herefordshire Lagerstätte, but it was not possible to determine the gender of *P. avibella*. The presence of carapace dimorphism in *P. nivisis* is uncertain, but like living myodocopids *P. nivisis* presumably reproduced sexually and brooded its young.

6. The origin of pelagic ostracods

The limited known palaeogeographical distribution, facies occurrence, faunal associates and morphology of *P. nivisis* sp. nov. suggest that like most Recent myodocopids it had a nektobenthic rather than pelagic lifestyle. This is consistent with the idea that known prelate Wenlock myodocopes were probably epibenthic (Siveter & Vannier, 1990; Siveter & Lane, 1999; Gabbott *et al.* 2003; Siveter & Bogolepova, 2006), and supports the notion of a Late Silurian ecological shift for the origin of pelagic (myodocope) ostracods (Siveter, Vannier & Palmer, 1987, 1991; Siveter & Vannier, 1990; Perrier, Vannier & Siveter, 2011). Early Silurian, Llandovery–Wenlock myodocopes were nektobenthic, with most living with dominantly benthic associates on well-oxygenated marine shelves (e.g. reef environments). Myodocope ostracods appear to have undergone an ecological shift by the latest Wenlock or earliest Ludlow (see Siveter, 1984; Siveter, Vannier & Palmer, 1987, 1991; Siveter & Vannier, 1990; Vannier & Abe, 1992; Perrier, Vannier & Siveter, 2007, 2011) an event that may be associated with the recovery interval post-dating the middle Homerian biotic extinction (see Porebska, Kozłowska-Dawidziuk & Masiak, 2004). However, the precise environmental trigger and anatomical pre-adaptations that facilitated this transition remain to be elucidated in detail.

The only exception in this scenario is the long-lived *Entomozoe tuberosa*. If the Australian material belongs to the same species (Perrier *et al.* in prep.) then it would occur from the Telychian to the Homerian with an almost global tropical distribution. This suggests that *Entomozoe* might not have been strictly nektobenthic as suggested by Siveter & Vannier (1990), Siveter & Lane (1999) and Siveter & Bogolepova (2006), and that its ability to widely disperse may have been fundamental to its long-lived survival.

7. Systematic palaeontology

Class OSTRACODA Latreille, 1802 (*nom. correct.*
Latreille, 1806).
Subclass MYODOCOPA Sars, 1866.
Order MYODOCOPIDA Sars, 1866.
Family CYLINDROLEBERIDIDAE Müller, 1906.
Genus *Pauline* Siveter, Briggs, Siveter,
Sutton & Joomun, 2013

Diagnosis. Large cylindroleberidid. Carapace elongate with an adductorial sulcus, an anterior lobal complex, a prominent wing-like posterolateral lobal structure and a simple anterior gape (after Siveter *et al.* 2013).

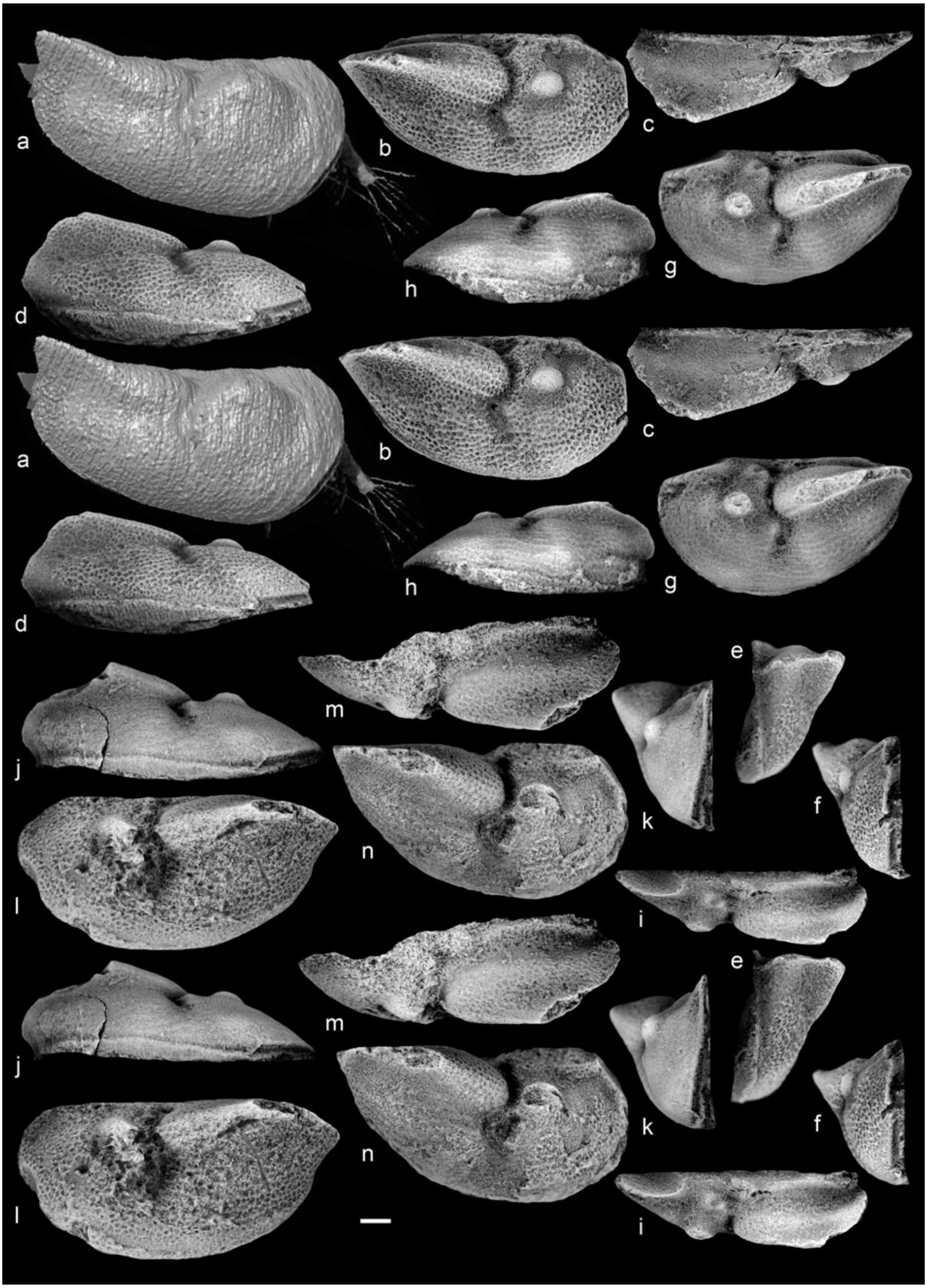

Figure 4. *Pauline avibella*, Herefordshire Lagerstätte, UK; Wenlock, Silurian (a) and *Pauline nivisis* sp. nov. Kap Schuchert, Washington Land, North Greenland; upper Telychian, upper Llandovery, Silurian (b–n). (a) Carapace with soft parts (Oxford University Museum of Natural History C.29613), lateral view. (b–f) Right valve (holotype; MGUH 30487), (b) right lateral view, (c) dorsal view, (d) ventral view, (e) posterior view, (f) anterior view. (g–i) Left valve (MGUH 30488), (g) lateral view, (h) ventral view, (i) dorsal view. (j, k) Right valve (MGUH 30489), (j) ventral view, (k) anterior view. (l, m) Left valve (MGUH 30490), (l) lateral view, (m) dorsal view. (n) Right valve (MGUH 30491), lateral view. All pictures are stereo-pairs, (a) digital reconstruction ('virtual fossil'), (b–n) photographs. Scale bar is 1 mm across.

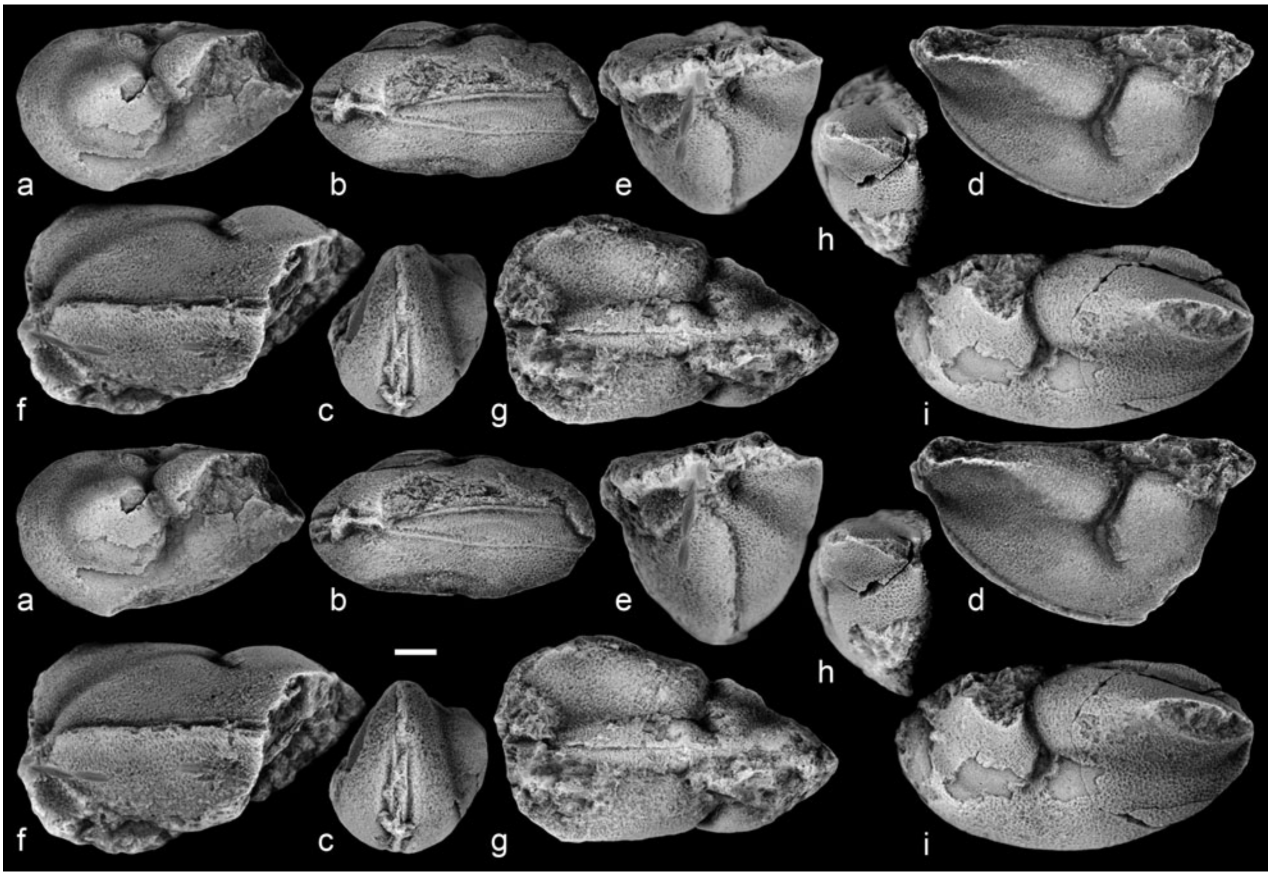

Figure 5. *Pauline* cf. *nivisis* sp. nov. Kap Schuchert, Washington Land, North Greenland; upper Telychian, upper Llandovery, Silurian. (a–c) Incomplete carapace (MGUH 30492), (a) left lateral view, (b) ventral view, (c) anterior view. (d–g) Incomplete carapace (MGUH 30493), (d) right lateral view, (e) posterior view, (f) ventral view, (g) dorsal view. (h) Left valve (MGUH 30494), posterior view. (i) Left valve (MGUH 30495), lateral view. All are stereo-pair photographs. Scale bar is 1 mm across.

Type species. Pauline avibella Siveter *et al*. 2013.

Pauline nivisis sp. nov.
Figures 3a, b, 4b–n

Derivation of name. Latin *nivis*, snow + *avis*, bird; alluding to the northerly locality and the ala.

Holotype. Geological Museum, Copenhagen University, specimen MGUH 30487 (Fig. 4b–f), almost complete right valve.

Diagnosis. Pauline with a well-developed preadductorial node and a posteriorly projecting posterolateral wing-like lobal projection (ala).

Material. Two carapaces and seven valves.

Measurements. Maximum valve length – valve height of largest and smallest well-preserved specimens: 10.3–5.0 mm (MGUH 30490; Fig. 4l, m), 8.2–4.4 mm (MGUH 30488; Figs 3a, 4g–i).

Locality and stratigraphy. Kap Schuchert, Washington Land, North Greenland; upper Telychian, upper Llandovery, *Monograptus spiralis* graptolite Biozone *sensu lato*, Silurian.

Description. Valves elongate, tapering posteriorly; maximum length and width at the tip of the ala, maximum height half way between mid-length and anterior end of the valve. Lateral valve outline strongly curved ventrally, almost straight dorsally, pointed posterodorsally and rounded anteriorly. The valve is bordered by a fine marginal ridge that is weaker posteriorly. A wide, thin, striated, lamella-like feature extends adaxially from the ventral to posterior regions of the marginal ridge of the right valve, giving left over right valve overlap. A small indistinct posterior gape is apparent in one specimen (Fig. 5h). A large anterior lobe is gently rounded dorsally. A small (diameter about 1 mm), distinct preadductorial node occurs just above mid-height. An adductorial sulcus occurs at mid-length, is widest dorsally, weakly z-shaped, extends to just below valve mid-height and has a simple muscle spot ventrally. The ventral two-thirds of the valve posterior of the adductorial sulcus is gently inflated; above is a prominent posterolaterally projecting wing-like ala that has two posterodorsal projections and curves gently above the hinge line. The external surface of the valves is finely reticulate, with fossae about 140 μm wide and muri about 80 μm wide.

Remarks. That *P. nivisis* is considered to be a cylindroleberidid myodocopid follows the assignment of *Pauline* to that family based on soft-part evidence (see Siveter *et al*. 2013). *P. nivisis* thereby represents the earliest known cylindroleberidid. *P. nivisis* differs from

P. avibella by its more subdued anterior lobe, the presence of a distinct preadductorial node, and its more posterolaterally projected ala. All of the *P. nivisis* specimens are supposed adults and large instars, which may reflect 'small sample' bias or size sorting. Four *Pauline* specimens (MGUH 30492–30495, Fig. 5) from the single block differ from the other material in having a more prominent anterior lobe, a weaker preadductorial node and ornament consisting of very gentle and fine reticulation in which the fossae and muri are about 50 μm wide (Fig. 5). These differences could represent simple intraspecific variation or reflect dimorphism or a separate species, but the limited nature of the material precludes further attribution. Herein, these specimens are referred to *P. nivisis* with *confer*.

8. Conclusions

Pauline nivisis sp. nov. from Greenland is the first 'Herefordshire' Lagerstätte genus found outside the type locality and is the oldest known cylindroleberidid myodocopid ostracod. It provides an Early Silurian link between 'Baltic-British' and North Laurentian ostracod faunas along a remnant Iapetus Ocean. Its stratigraphic occurrence and supposed lifestyle endorse the notion that pre-Late Silurian myodocopes are nektobenthic. The palaeogeographic and stratigraphic distribution of *Pauline* and *Entomozoe* support the hypothesis that low latitude faunas spread out to higher latitudes post-dating the Early Palaeozoic Icehouse.

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References

BRIGGS, D. E. G., SIVETER, D. J. & SIVETER, D. J. 1996. Soft-bodied fossils from a Silurian volcaniclastic deposit. *Nature* **382**, 248–50.

BRIGGS, D. E. G., SIVETER, D. J., SIVETER, D. J. & SUTTON, M. D. 2008. Virtual fossils from 425 million-year-old volcanic ash. *American Scientist* **96**, 474–81.

BRIGGS, D. E. G., SIVETER, D. J., SIVETER, D. J., SUTTON, M. D., GARWOOD, R. J. & LEGG, D. 2012. A Silurian horseshoe crab illuminates the evolution of chelicerate limbs. *Proceedings of the National Academy of Science* **109**, 15702–5.

COCKS, L. R. M. & FORTEY, R. A. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. *Journal of the Geological Society, London* **139**, 465–78.

COCKS, L. R. M. & TORSVIK, T. H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society, London* **159**, 631–44.

COCKS, L. R. M. & TORSVIK, T. H. 2011. The Palaeozoic geography of Laurentia and western Laurussia: a stable craton with mobile margins. *Earth-Science Reviews* **201**, 1–51.

COPELAND, M. J. 1974. *Silurian Ostracoda from Anticosti Island, Quebec*. Ottawa: Geological Survey of Canada Bulletin no. 241, 133 pp.

CORBARI, L., CARBONEL, P. & MASSABUAU, J. C. 2005. The early life history of tissue oxygenation in crustaceans: the strategy of the myodocopid ostracod *Cylindroleberis mariae*. *Journal of Experimental Biology* **208**, 661–70.

GABBOTT, S. E., SIVETER, D. J., ALDRIDGE, R. J. & THERON, J. N. 2003. The earliest myodocopes: ostracods from the late Ordovician Soon Shale Lagerstätte of South Africa. *Lethaia* **36**, 151–60.

HAIRAPETIAN, V., MOHIBULLAH, M., TILLEY, L. J., WILLIAMS, M., MILLER, C. G., AFZAL, J., GHOBADI POUR, M. & HEJAZI, H. S. 2011. Early Silurian carbonate platform ostracods from Iran: a peri-Gondwanan fauna with strong Laurentian affinities. *Gondwana Research* **20**, 645–53.

HUGHES, H. E. & THOMAS, A. T. 2011. Trilobite associations, taphonomy, lithofacies and environments of the Silurian reefs of North Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* **302**, 142–55.

HURST, J. M. 1980. Palaeogeographic and stratigraphic differentiation of Silurian carbonate buildups and biostromes of North Greenland. *American Association of Petroleum Geologists Bulletin* **64**, 527–48.

LAND, M. F. & NILSSON, D. E. 1990. Observations on the compound eyes of the deep-sea ostracod *Macrocypridina castanea*. *Journal of Experimental Biology* **148**, 221–33.

LANE, P. D. 1980. *Monoceratella* (Ostracoda) from the Silurian of Washington Land, North Greenland. In *Palaeontology of Greenland: Short Contributions* (ed. J. S. Peel). *Rapport Grønlands Geologiske Undersøgelse* **101**, 37–43.

LANE, P. D. & OWENS, R. M. 1982. Silurian trilobites from Kap Schuchert, Washington Land, western North Greenland. In *Palaeontology of Greenland: Short Contributions* (ed. J. S. Peel). *Rapport Grønlands Geologiske Undersøgelse* **108**, 41–69.

LATREILLE, P. A. 1802. *Histoire Naturelle Générale et Particulière des Crustacés et des Insectes. Tome 3. Familles Naturelles des Genres*. Paris, 467 pp.

LATREILLE, P. A. 1806. *Genera Crustaceorum et Insectorum, Tome 1*. Paris & Strasbourg, 302 pp.

MÜLLER, G. W. 1906. Ostracoda. Die Ostracoden der Siboga-Expedition. In *Siboga-Expeditie* (ed. H. M. Siboga), pp. 1–40. Uitkomsten op Zoologisch, Botanisch, Oceanographisch Monographien no. 30.

OGOH, K. & OHMIYA, Y. 2005. Biogeography of luminous marine ostracod driven irreversibly by the Japan Current. *Molecular Biology and Evolution* **22**, 1543–5.

ORR, P. J., BRIGGS,, D. E. G., SIVETER, D. J. & SIVETER, D. J. 2000. Three-dimensional preservation of a non-biomineralised arthropod in concretions in Silurian volcaniclastics from Herefordshire, England. *Journal of the Geological Society, London* **157**, 173–86.

PAGE, A., ZALASIEWICZ, J. A., WILLIAMS, M. & POPOV, L. E. 2007. Were transgressive black shales a negative feedback modulating glacioeustasy in the Early Palaeozoic Icehouse? In *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies* (eds M. Williams, A. M. Haywood, F. J. Gregory, & D. N. Schmidt), pp. 123–56. The Micropalaeontological Society, Special Publications no. 2.

PEEL, J. S. & SØNDERHOLM, M. (eds). 1991. *Sedimentary Basins of North Greenland*. Bulletin Grønlands Geologiske Undersøgelse no. 160, 164 pp.

PERRIER, V. & SIVETER, D. J. In press. The use of 'European' ostracode faunas in testing Silurian stratigraphy and palaeogeography. *Geological Society of London, Memoirs*.

PERRIER, V., VANNIER,, J. & SIVETER, D. J. 2007. The Silurian pelagic myodocope ostracod *Richteria migrans*. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **98**, 151–63.

PERRIER, V., VANNIER, J. & SIVETER, D. J. 2011. Silurian bolbozoids and cypridinids (Myodocopa) from Europe: pioneer pelagic ostracods. *Palaeontology* **54**, 1361–91.

PORĘBSKA, E., KOZŁOWSKA-DAWIDZIUK, A. & MASIAK, M. 2004. The *lundgreni* event in the Silurian of the East European Platform, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* **213**, 271–94.

POULSEN, C. 1934. The Silurian faunas of North Greenland. The fauna of the Cape Schuchert Formation. *Meddelelser om Grønland* **72** 2(1), 1–46.

RONG, J. Y., WANG, Y. & ZHANG, X. L. 2012. Tracking shallow marine red beds through geological time as exemplified by the lower Telychian (Silurian) in the Upper Yangtze Region, South China. *Science in China Series D: Earth Sciences* **55**, 699–713.

SARS, G. O. 1866. *Oversigt af Norges marine Ostracoder*. Norske Videnskaps-Akademien Forhandlingar 1865, 130 pp.

SARV, L. 1968. *Ostracode Families Craspedobolbinidae, Beyrichiidae and Primitiopsidae in the Silurian of Estonia*. Eesti NSV Teaduste Akadeemia Toimetised, Geologia Institut, Tallinn, 134 pp (in Russian).

SIVETER, D. J. 1984. Habitats and modes of life of Silurian ostracods. In *The Autecology of Silurian Organisms* (eds M. G. Bassett & J. D. Lawson), pp. 71–85. Special Papers in Palaeontology no. 32.

SIVETER, D. J. 1989. Ostracodes. In *A Global Standard for the Silurian System* (eds C. H. Holland & M. G. Bassett), pp. 252–64. National Museum of Wales Geological Series no. 9.

SIVETER, D. J. 1990. Photography. In *Palaeobiology: A Synthesis* (eds D. E. G. Briggs & P. R. Crowther), pp. 505–8. Oxford: Blackwell.

SIVETER, D. J. 2009. The Silurian. In *Ostracods in British Stratigraphy* (eds J. E. W. Whittaker & M. B. Hart), pp. 45–90. The Micropalaeontological Society, Special Publications no. 3.

SIVETER, D. J. & BOGOLEPOVA, O. K. 2006. The myodocope ostracod *Entomozoe* from the early Silurian of Severnaya Zemlya, Russian Arctic. *Norwegian Journal of Geology* **86**, 51–8.

SIVETER, D. J., BRIGGS, D. E. G., SIVETER, D. J. & SUTTON, M. D. 2010. An exceptionally preserved myodocopid ostracod from the Silurian of Herefordshire, UK. *Proceedings of the Royal Society of London, Series B* **277**, 1539–44.

SIVETER, D. J., BRIGGS, D. E. G., SIVETER, D. J., SUTTON, M. D. & JOOMUN, S. C. 2013. A Silurian myodocope with preserved soft-parts: cautioning the interpretation of the shell-based ostracod record. *Proceedings of the Royal Society of London, Series B* **280** (1752), doi: 10.1098/rspb.2012.2664.

SIVETER, D. J. & LANE, P. D. 1999. The myodocope ostracode *Entomozoe* from an early Silurian (Telychian, Llandovery) carbonate mound of the Samuelson Høj Formation of North Greenland. *Bulletin of the Geological Survey of Denmark & Greenland* **184**, 5–13.

SIVETER, D. J., SIVETER, D. J., BRIGGS, D. E. G. & SUTTON, M. D. 2007. Brood care in a Silurian ostracod. *Proceedings of the Royal Society of London, Series B* **274**, 465–9.

SIVETER, D. J., SUTTON, M. D., BRIGGS, D. E. G. & SIVETER, D. J. 2003. An ostracode crustacean with soft-parts from the Lower Silurian. *Science* **302**, 1749–51.

SIVETER, D. J. & VANNIER, J. 1990. The Silurian myodocope ostracode *Entomozoe* from the Pentland Hills, Scotland: its taxonomic, ecological and phylogenetic significance and the affinity of bolbozoid myodocopes. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **81**, 71–6.

SIVETER, D. J., VANNIER, J. & PALMER, D. 1987. Silurian myodocopid ostracodes: their depositional environment and the origin of their shell microstructures. *Palaeontology* **30**, 783–813.

SIVETER, D. J., VANNIER, J. & PALMER, D. 1991. Silurian myodocopes: pioneer pelagic ostracods and the chronology of an ecological shift. *Journal of Micropalaeontology*, **10**, 157–73.

SØNDERHOLM, M. & HARLAND, T. L. 1989. Franklinian reef belt, Silurian, North Greenland. In *Reefs – Canada and Adjacent Area* (eds H. H. J. Geldsetzer, N. P. James & G. E. Tebbutt), pp. 263–70. Canadian Society of Petroleum Geologists Memoir no. 13.

STRUSZ, D. L. 1984. Brachiopods of the Yarralumla Formation (Ludlovian), Canberra, Australia. *Alcheringa* **8**, 123–50.

SUTTON, M. D., BRIGGS, D. E. G., SIVETER, D. J. & SIVETER, D. J. 2011. A soft-bodied lophophorate from the Silurian of England. *Biology Letters* **7**, 146–9.

SUTTON, M. D., BRIGGS, D. E. G., SIVETER, D. J., SIVETER, D. J. & SIGWART, J. D. 2012. A Silurian armoured aplacophoran: implications for molluscan phylogeny. *Nature* **490**, 94–7.

TORSVIK, T. H. 2009. BugPlates software (IGCP 503). With reconstructions of Torsvik, T. H. and Cocks, L. R. M. (2002–2009). Statoil Hydro.

TRUUVER, K., MEIDLA, T., AAINSAAR, L., BERGSTRÖM, J. & TINN, O. 2012. Stratigraphy of the Ordovician-Silurian boundary interval in Östergötland, Sweden, based on ostracod distribution and stable carbon isotopic data. *Geologiska Föreningens i Stockholm Förhandlingar (GFF)* **134**, 295–308.

VANNIER, J. & ABE, K. 1992. Recent and early Palaeozoic myodocope ostracodes: functional morphology, phylogeny, distribution and lifestyles. *Palaeontology* **3**, 485–517.

VANNIER, J., ABE, K. & IKUTA, K. 1998. Feeding in myodocopid ostracods: functional morphology and laboratory observations from videos. *Marine Biology* **132**, 391–408.

WILLIAMS, M., VANNIER, J., CORBARI, L. & MASSABUAU, J.-C. 2011. Oxygen as a driver of early arthropod micro-benthos evolution. *PLoS One* **6** (12), e28183, doi: 10.1371/journal.pone.0028183.

ZALASIEWICZ, J. A, TAYLOR, L., RUSHTON, A. W. A., LOYDELL, D. K., RICKARDS, R. B. & WILLIAMS, M. 2009. Graptolites in British stratigraphy. *Geological Magazine* **146**, 785–850.