

## Spontaneous Article

# *Ametrobeyrichia schizopyge*: a non-dimorphic beyrichioidean Silurian ostracod?

David J. SIVETER<sup>1\*</sup>  and Derek J. SIVETER<sup>2,3</sup> 

<sup>1</sup> School of Geography, Geology and the Environment, University of Leicester, Leicester LE1 7RH, UK.

<sup>2</sup> Earth Collections, University Museum of Natural History, Oxford OX1 3PW, UK.

<sup>3</sup> Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, UK.

\*Corresponding author. Email: [djs@leicester.ac.uk](mailto:djs@leicester.ac.uk)

**ABSTRACT:** Sexual dimorphism of the mineralised part (shell, carapace) of invertebrate animals is recognised in many fossil groups; for example, in ammonoids, trilobites and especially in ostracod crustaceans, arguably the most species-rich and specimen-abundant group of arthropods in the fossil record. Shell dimorphism in ostracods is most stark in several major Palaeozoic groups. Beyrichioidean ostracods are known abundantly worldwide from hundreds of genera in Ordovician to Carboniferous deposits and are characterised by a distinctive well-defined shell dimorphism in which the presumed female of the species develops a so-called brood pouch (crumina) on each valve. However, *Ametrobeyrichia schizopyge*, a Silurian ostracod species from the UK, challenges the definition of the group: it is, ostensibly, a non-dimorphic beyrichioidean. Reasons for its seemingly non-dimorphic nature include heterochronic mechanisms. Apparently not all beyrichioideans had cruminal brood care strategy.



**KEY WORDS:** dimorphism, heterochrony, Ostracoda, Palaeocopida, Welsh basin

Sexual dimorphism is known in fossils of many invertebrate groups (Westerman 1969, 1979). It is recognised almost exclusively in their preserved mineralised hard parts (shell, carapace), in overall size differences and/or a range of other, group-specific morphological features. For example, in molluscs it has been extensively reported from Mesozoic cephalopods (e.g., Calloman 1963, 1980; Lehmann 1981), and it is also recognised in Miocene gastropods (Halder & Paira 2019) and a Jurassic bivalve (Karapınar *et al.* 2021). Additionally, the tests of a few Cretaceous and Cenozoic echinoids display dimorphism (Philip & Foster 1971; Néaudeau 1993).

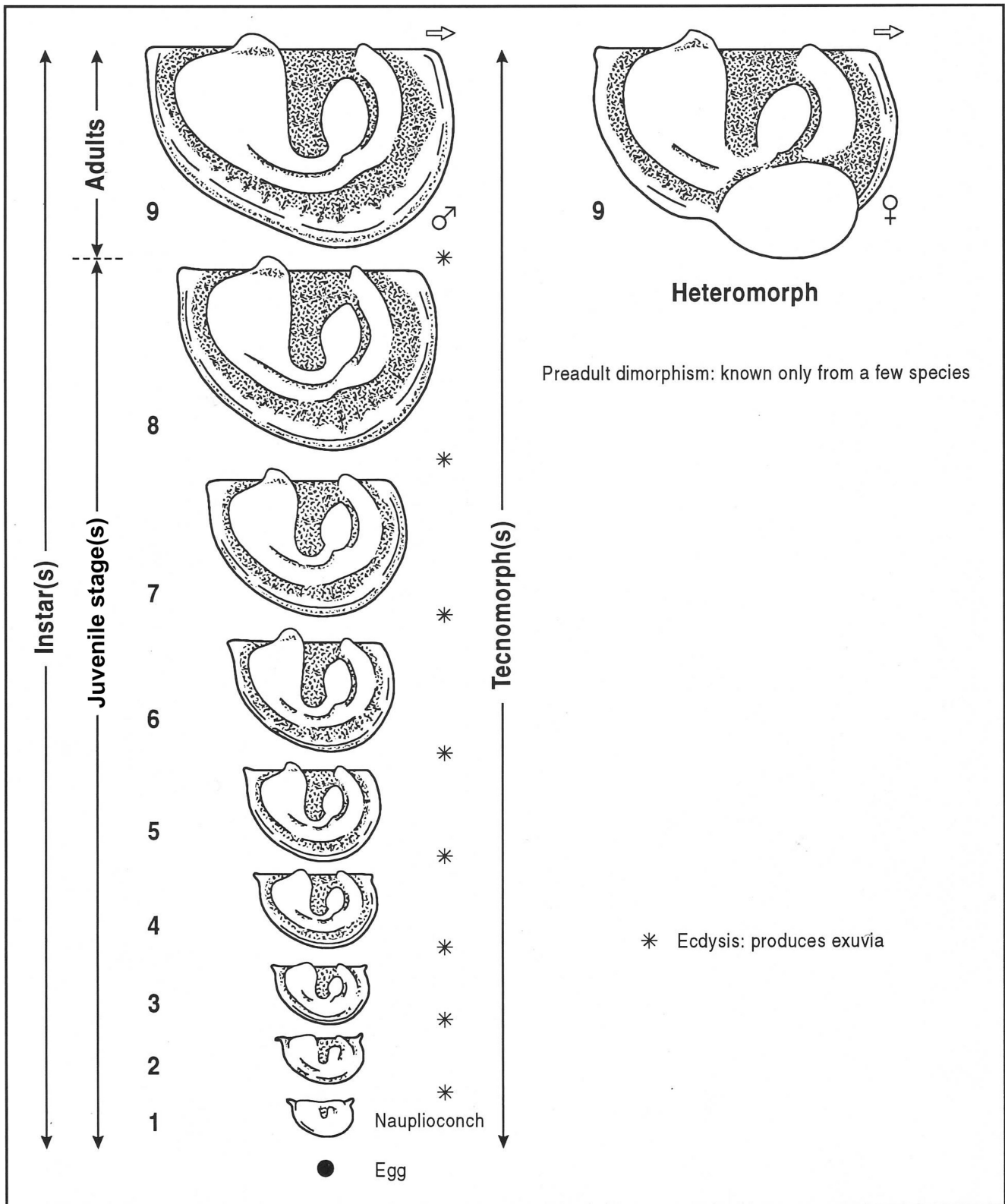
There are many examples of sexual dimorphism within fossil arthropods. Various trilobite species have been claimed to be sexually dimorphic, based for example on differences in size or the eye (Clarkson 1969; Hu 1971), but most such examples have been regarded as unrigorously supported (Hughes & Fortey 1995; Fortey & Hughes 1998). However, more likely instances include those which show the presence/lack of a preglabellar brood pouch in Cambrian and Ordovician species (Fortey & Hughes 1998; see also Cederström *et al.* 2011) or of an anterior median spine in raphiophorids (Knell & Fortey 2005) or of a long trident-like anterior cephalic projection in the asteropygine *Walliserops* (Gishlick & Fortey 2023). In chelicerates sexual dimorphism has been proposed in a Silurian pycnogonid (Siveter *et al.* 2023), where the female form displays a thickened trunk and coxa (related to the possession of ovaries and egg development); male eurypterids have been identified on the grounds of supposed sperm-carrying parts (Kamenz *et al.* 2011); and a Xiphosuran specimen has been designated as male based on its anterior scalloped carapace margin (Lamsdell &

McKenzie 2015). Instances of sexual dimorphism in non-ostracod crustaceans include Jurassic lobsters (Chény *et al.* 2023) and insects, for example in a Cretaceous beetle (Jiang *et al.* 2019).

Ostracod crustaceans are known from at least 33,000 living and fossil species (Horne *et al.* 2002) and arguably are by far the most specimen abundant group of arthropods in the fossil record. Shell dimorphism is common in all the major ostracod taxa but is most glaring in several major Palaeozoic groups. Beyrichioidean (Palaeocopida) ostracods, known abundantly worldwide from hundreds of genera, from the Ordovician to the Carboniferous, are characterised by well-defined shell dimorphism. Herein we report a commonly occurring Silurian beyrichioidean ostracod species from the UK that is unique in seemingly being non-dimorphic, thereby challenging the definition of the group. Reasons for its possible non-dimorphic nature include heterochronic mechanisms. Seemingly not all beyrichioideans had the same brood care strategy.

## 1. Ontogeny and dimorphism in ostracods

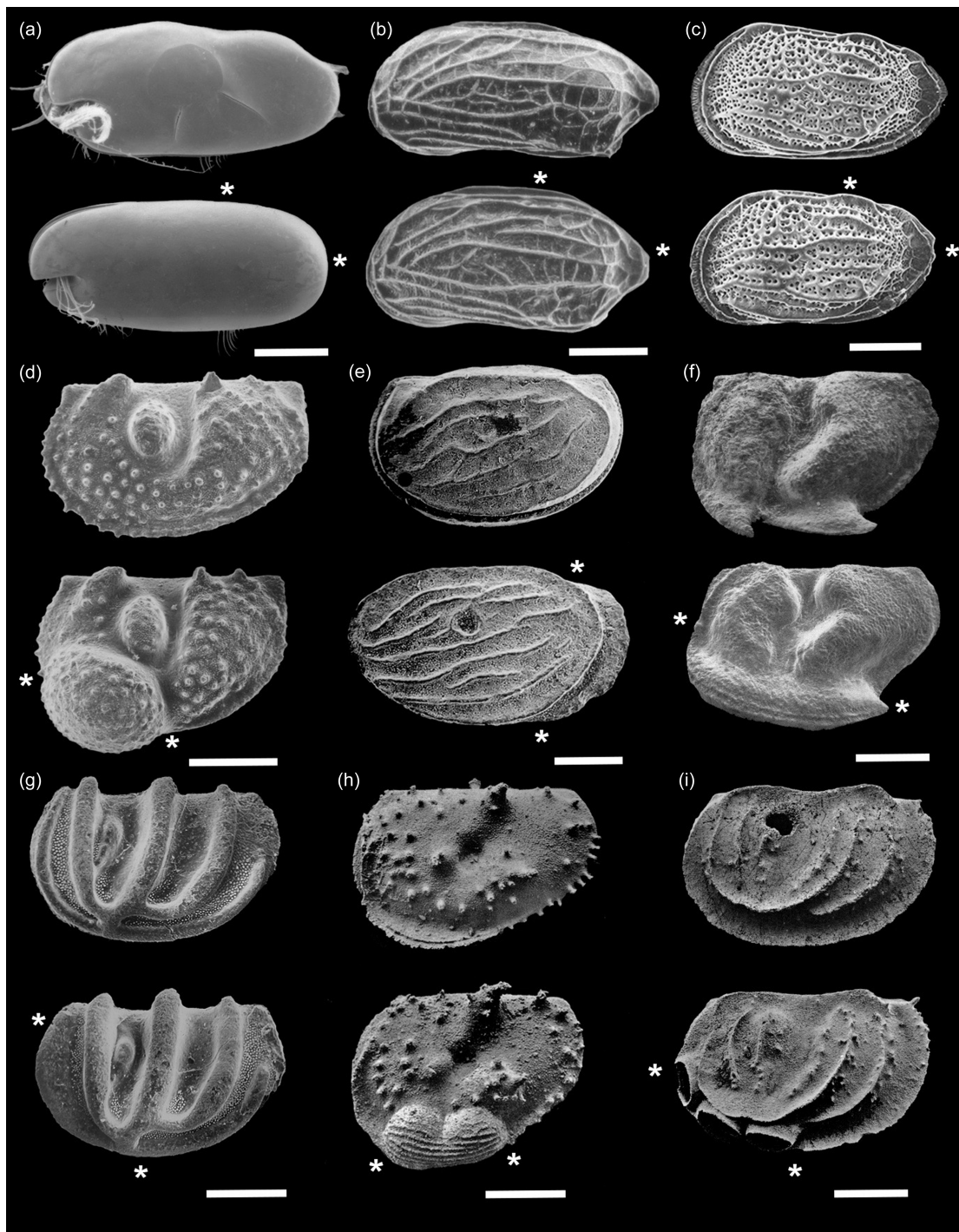
Ostracods grow by ecdysis (Fig. 1), when the cuticle is shed and a new, larger one is secreted by the epidermis. Each growth stage (instar) is designated as either first, second, third, etc. in ascending order of size, or alternatively as A (= Adult), A-I, A-2 etc in descending order. The number of instars is species-specific, from four to nine (Martinsson 1962; Horne *et al.* 2002; Smith 2025). Ontogenetic development involves, *inter alia*, the sequential acquisition of appendages and addition and maturation of the sex organs. Embryonic development occurs



**Figure 1** Ontogeny of the beyrichioidean *Craspedobolbina clavata* (Kolmodin, 1869), based on Martinsson 1962, fig. 21. Mulde Brick-clay Member, Halla Formation, Wenlock Series, Silurian, Mulde, Gotland, Sweden.

within what are remarkably hardy eggs. Most ostracods expel their eggs directly into water to develop, but embryo/brood care within the domicilium is known from several major living and fossil taxa (see Horne *et al.* 2002; Siveter *et al.* 2007, 2014, 2015). The first post-embryonic growth stage (nauplius) and subsequent sexually immature juvenile growth stages are succeeded by the last growth stage (adult) which is normally the first and only stage to be fully sexually mature.

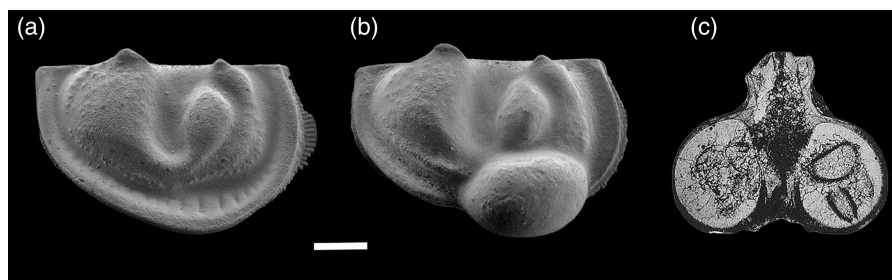
Sex-related dimorphism of the shell is common in living and fossil ostracods (e.g., Henningsmoen 1965; Vannier *et al.* 1989; Horne *et al.* 2002; Ozawa 2013; Hunt *et al.* 2017). Some adult and, very rarely, in some species, late juvenile stage specimens (collectively termed heteromorphs) differ morphologically from juvenile and other adult specimens (collectively termed tecnomorphs) of the same species by the development of dimorphic characters of the shell (Fig. 1) involving, for



**Figure 2** Shell dimorphism in some major groups of ostracods. In each dimorphic pair the upper figure is the (assumed) male and the lower figure is the (assumed) female. All lateral views are of left valves except for the images of the female of *Xystista graffhami* (f, lower) and of the male and female of *Tetradella? trilocolata* (i) which are right valves reversed. An asterisk (\*) indicates the approximate limit of the dimorphic region/structure in each female; (a–d) examples of domiciliar dimorphism; (e–i) examples of extradomiciliar dimorphism. (a) Cythrodoleberidoidean myodocopid *Xenoleberis yamadai* (Hiruta, 1979); Recent, Japan Sea, Oshoro, Hokkaido, Japan. (b) Cytheroidean podocopid *Semicytherura sella* (Sars, 1866); Recent, Oslo Fjord, Norway (after Whittaker 1974). (c) Cytheroidean podocopid *Kuiperiana bathymarina* Ayress, Coles & Whatley, 1994; Pleistocene, Tasman Sea (after Ayress *et al.* 1994). (d) Beyrichioidean palaeocopid *Beyrichia clausa* Jones & Holl, 1886; Much Wenlock Limestone Formation, Wenlock Series, Silurian, Lincoln Hill, Shropshire, England (after Siveter 2009). (e) Primitiopsioidean palaeocopid *Venzavella costata* (Neckaja, 1960); Kaugatuma Regional Stage, Pridoli Series, Silurian, Saaremaa, Estonia (after Siveter & Sarv 1991). (f) Triemilomatelline hollinoidean palaeocopid *Xystista graffhami* (Lundin, 1965); Henryhouse Formation, Ludlow, Series, Silurian, Pontotoc County, Oklahoma, USA (after Lundin & Siveter 1985). (g) Tetradellid hollinoidean palaeocopid *Harperopsis scripta* (Harper, 1947); Harnage Shales, Sandbian Stage, Cwms Cottage, near Caer Caradoc, Shropshire, England (after Jones & Siveter 1983). (h) Euychilinoidean palaeocopid *Distobolbina bispinata* Schallreuter, 1977; Öjlemyrflint erratic boulder, Lummellunds Bruk, Gotland, Sweden, Ordovician (after Schallreuter 1977). (i) Tetradellid hollinoidean palaeocopid *Tetradella? trilocolata* Schallreuter, 1978; Öjlemyrflint erratic boulder, Ordovician, Gnisvårds, Gotland (after Schallreuter 1978). All scale bars represent  $\mu\text{m}$ : a, 500; b, 100; c, 100; d, 800; e, 300; f, 400; g, 1000; h, 200; i, 300.

example, carapace size, shape, ornament and/or particular morphological structures. Precocious sexual dimorphism of the carapace and/or some soft parts (e.g., hemipenes, antennae) involving A-1, A-2, A-3 and even A-4 juvenile stages is

relatively rare, but is known from both fossil and living species of ostracods; for example, in Myodocopa, Palaeocopida, Platycopida and Podocopida (e.g., see Shaver 1953; Schallreuter 1976; Whatley & Stevens 1977; Hart *et al.* 1985;



**Figure 3** Dimorphism in the beyrichioidean *Craspedobolbina clavata* (Kolmodin, 1869). Mulde Brick-clay Member, Halla Formation, Wenlock Series, Silurian, Mulde, Gotland, Sweden. (a) Male right valve, lateral view (OUMNH PAL-CZ.1021). (b) Female right valve, lateral view (OUMNH PAL-CZ.1022). (c) Transverse section through a female carapace, showing juveniles in the cruminae (from Spjeldaes 1951, pl. 103, fig. 1). Scale bar (a–c): 400  $\mu$ m. Repository: Oxford University Museum of Natural History (OUMNH).

Jones 1987; Cohen & Morin 1990; Kamiya 1992; Tinn & Meidla 2003). Some ostracods reproduce asexually: female parthenogenetic populations are known from living species, especially in the freshwater group Darwinulidae (see, e.g., Martens 1998; Smith *et al.* 2006). Parthenogenesis has also been proposed for a few Palaeozoic palaeocopid species (see Section 3).

## 2. Dimorphism of the shell in major groups of ostracods

Sex-related shell dimorphism in ostracods has been reviewed or featured in many papers, including Ozawa (2013) for post-Palaeozoic taxa and Henningsmoen (1965), Jaanusson (1957, 1985), Vannier *et al.* (1989), Adamczak (1991) and Meidla (1996) for Palaeozoic species. Dimorphism in ostracods is manifest by spaces of different volumes/configurations in the carapace that in some cases are bounded by dimorphic morphological structures. Dimorphism is essentially either ‘domiciliar’, in which the space that is dimorphic lies within the domicilium, or ‘extradomiciliar’, in which the space in question lies outside the domicilium. Minor ornamental features such as spines may also be dimorphic.

Of the major ostracod taxa, Podocopa and Myodocopa, both of which range from the Ordovician to Recent, display domiciliar shell dimorphism that manifests itself externally in differences in size and shape of the carapace (Fig. 2a–c). In contrast, most Palaeocopida, which are almost exclusively Palaeozoic (e.g., Euychilinoidea, Primitiopsioidea and Hollinoidea), are characterised by extradomiciliar shell dimorphism which involves the addition or modification in one adult of prominent adventral linear ornamental projections and associated spaces external to the domicilium (Fig. 2e–i). Beyrichioidean palaeocopids prominently display domiciliar shell dimorphism, whereby each valve of one of the adults (the presumed female) has extra domiciliary space provided by a special pouch-like structure (crumina) on each valve that opens internally to within the domicilium (Figs 1, 2d, 3, 4c, d, h–k).

## 3. *Ametrobeyrichia schizopyge*: a non-dimorphic beyrichioidean ostracod?

Beyrichioidean ostracods are a major, ubiquitous group of shallow water biostratigraphically important palaeocopids documented from some 180 genera and thousands of species. Most are Silurian or Devonian in age, with just one species known from the Ordovician (Schallreuter 1989a, 1989b) and a few in the Carboniferous (e.g., Jones 1989). Angelin (1838) was the first not only to recognise that a Silurian form that he named ‘*Battus kloedeni* n. sp.’ (= *Craspedobolbina clavata*; Figs 1, 3) is

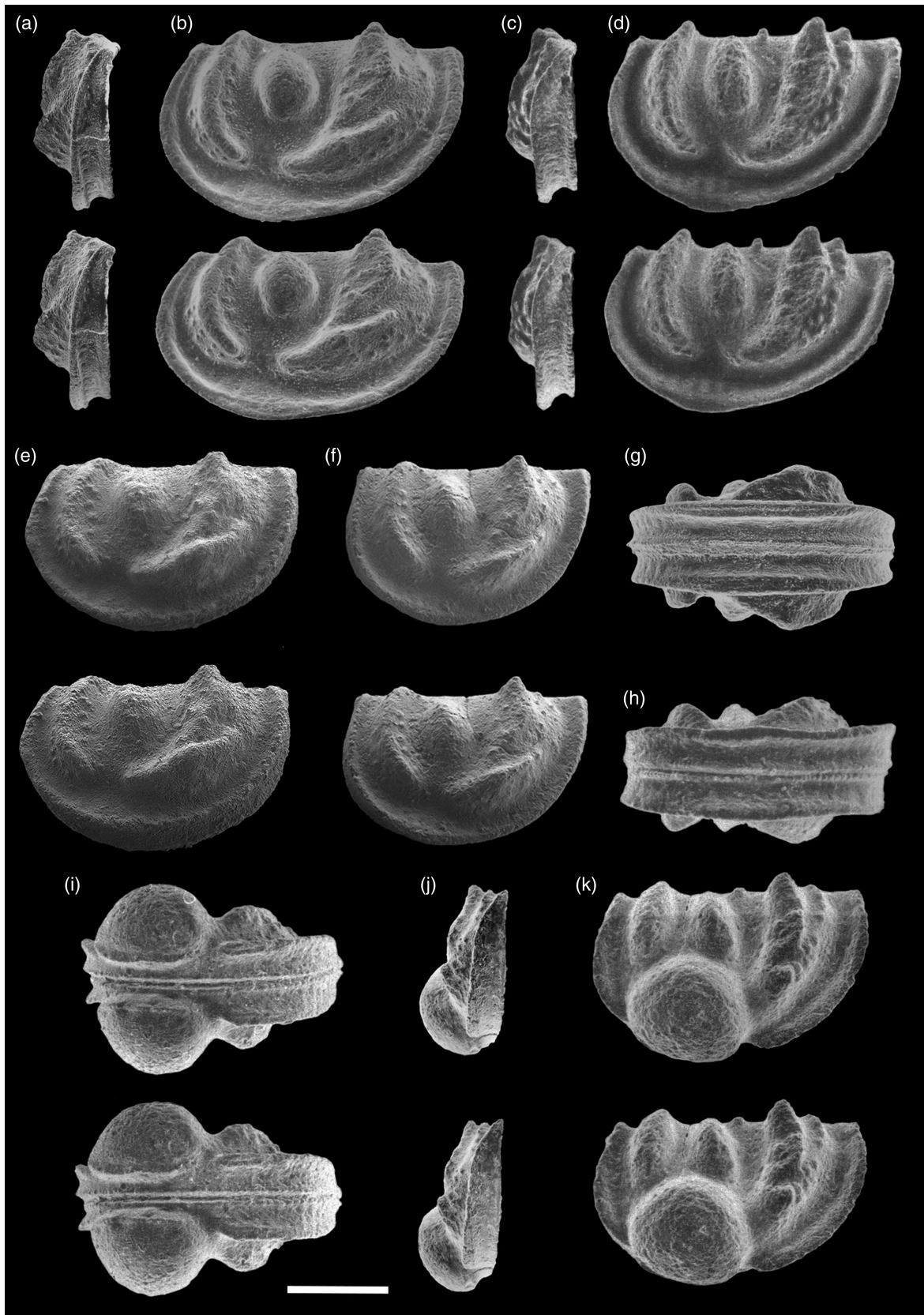
an ostracod but also that it displayed dimorphism of the shell (Spjeldaes 1966). Beyrichioidean species are characterised by cruminal domiciliar dimorphism in adults (see, e.g., Hessland 1949; Martinsson 1962; Siveter 1980, 2022; Adamczak 1990). The cruminate adult housed juveniles (Fig. 3c) and is presumed to be the female dimorph (Spjeldaes 1951). Against this background the apparent beyrichioidean *Ametrobeyrichia schizopyge* Siveter, 2022 (Fig. 4a, b, e–g) from the Silurian of the Welsh basin challenges all records of previously documented beyrichioidean species in seemingly being non-dimorphic by lacking cruminate adults.

Detailed ontogenetic studies of superbly preserved palaeocopid faunas from the Silurian of Gotland, Sweden (Jaanusson & Martinsson 1956; Martinsson 1956) record final growth stage adult sex ratios of 50:50 for four of the species studied (the beyrichioidean *C. clavata* and two primitiopsioidean and a hollinoidean species) and 30:70 (supposed male:female) for another (primitiopsioidean) species. *A. schizopyge* is ubiquitous and abundant in the British Silurian. It is known from over 4,100 mostly adult and late growth stage juvenile specimens (Figs 4a, b, e, f, 5) from some 25 localities in mostly the Wenlock (Homerian Coalbrookdale and Much Wenlock Limestone formations) and also Ludlow (Gorstian Lower Elton Formation) series across the Welsh Borderland and English West Midlands (Siveter 2022). In practice, sampling localised marl horizons, weathered debris or shaley bands proved the most successful (and often the only method) to process and obtain abundant and relatively well-preserved ostracods. *A. schizopyge* is the most common palaeocopid recovered from those localities, but it is represented uniquely and unexpectedly for a supposed beyrichioidean only by non-cruminate specimens. There are other beyrichioidean species also known only from tecnomorphs, but in such cases the total number of specimens recovered is small. Supposed parthenogenesis has also been documented or suggested for a few palaeocopid taxa, including the beyrichioideans *Huntonella bransoni* Lundin, 1968, *Kloedenia leptosoma* Martinsson, 1963 and *Kloedenia wilckensiana* (Jones, 1855) (see Martinsson 1963) and the primitiopsioidean *Clavofabella reticristata* (Jones, 1888) (see Martinsson 1956).

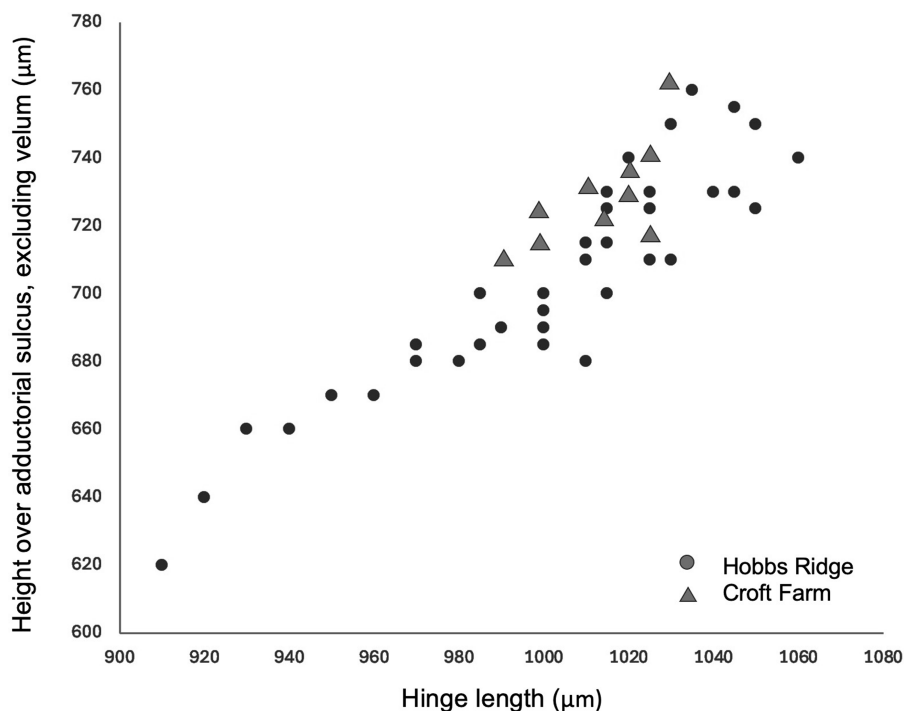
## 4. Possible reasons for the non-dimorphic nature of *A. schizopyge*

### 4.1. Sexes misinterpreted?

Could the non-cruminate adult of beyrichioidean species be the female and the cruminate forms be the males? As the cruminae of beyrichioideans contain juveniles (Fig. 3c) this interpretation is considered very unlikely, but it nevertheless remains a possibility. Male brood care is known, but only very rarely, from other arthropods; for example, in pycnogonids (King 1973).



**Figure 4** Beyrichioideans from the Much Wenlock Limestone Formation, Wenlock Series, Silurian, UK. (a, b, e–g) *Ametrobeyrichia schizopyge* Siveter, 2022, from Hobbs Ridge, May Hill inlier, Gloucestershire (locality 15b of Siveter 1980). (a, b) Posterior and lateral view stereo-pairs of adult left valve (NHMUK OS6630). (e) Lateral view stereo-pair of probable A-1 left valve of carapace (OUMNH PAL-C.36705). (f) Lateral view stereo-pair of probable A-2 left valve (OUMNH PAL-C.36706). (g) Ventral view of carapace, anterior to the left (NHMUK OS6633). (c, d, h–k) *Sleia pauperata* (Jones, 1869), from Lincoln Hill, near Ironbridge, Shropshire (locality 49c of Siveter 1980). (c, d) Posterior and lateral view stereo-pairs of male left valve (NHMUK OS6400). (h) Ventral view of male carapace, anterior to the left (NHMUK OS6405). (i) Ventral view stereo-pair of female carapace, anterior to the left (NHMUK OS6404). (j, k) Posterior and lateral view stereo-pairs of female left valve (NHMUK OS6401). Repositories: Natural History Museum, London (NHMUK) and Oxford University Museum of Natural History (OUMNH). Scale bar (a–k): 400  $\mu$ m.



**Figure 5** Size dispersion of valves of *Ametrobeyrichia schizopyge* Siveter, 2022 from the Much Wenlock Limestone Formation, Wenlock Series, at Hobbs Ridge, May Hill inlier and Croft Farm, near Malvern (localities 15b and 18 of Siveter 1980).

#### 4.2. Collecting/sampling failure?

From the at least 25 Silurian localities from which *A. schizopyge* was recovered, many tens of kilograms of material were sampled, processed and manually picked under a binocular microscope (by David J. S.). It is highly unlikely that sampling, processing or picking issues resulted in a failure to recover cruminate specimens of the species.

#### 4.3. Ecological separation of dimorphs?

Could the dimorphs have lived in separate geographical regions or distinct ecological environments? An analogous case is that of the myodocope ostracod *Philomedes globosa* in which the females and males inhabit separate water depths and meet only to reproduce. Both Triebel (1941, p. 362) and Kesling (1952, p. 266) suggested that some palaeocypid dimorphs may be adapted for life in separate biotopes. That notion found some acceptance with Henningsmoen (1965, p. 356) but Hessland (1949, p. 128) considered it doubtful. Moreover, in his comprehensive monographic study of some 120 beyrichioidean species from the Silurian of Gotland Martinsson (1962, p. 121) concluded that both sexes and their juvenile stages ‘generally lived together in the same environment’.

Specimens of *A. schizopyge* are from relatively shallow water shelf facies (Siveter 2022). Perhaps the missing dimorphs lived in the more scarcely sampled deeper basinal environments that existed to the west of the shelf/slope facies in the Welsh Basin in mid-Silurian times? This is considered unlikely, as within the thousands of specimens recovered it might be expected that at least some dimorphs would be preserved together in the same environment.

#### 4.4. Questionable taxonomic assignment?

The notion that the morphology of *A. schizopyge* is compatible (belongs) with another, non-beyrichioidean palaeocypid group is not sustainable. All valves recovered display the characteristic features of lobate beyrichioidean tecnomorphs (velum, anterior lobe, preadductor node, syllobium and prenatal and adductor sulci) and have no morphological feature

incompatible with the Beyrichioidea. Plots of the size of specimens of *A. schizopyge* (e.g., Fig. 5) have not yielded clearly defined growth stages (for possible reasons for this when sampling for Palaeozoic ostracods, such as unsuspectedly collecting across minute chronodemes and/or ecodemes, see Martinsson 1962, pp. 122, 123), but nevertheless offer no reason to suppose that dimorphism might be reflected merely by size differences. In theory it is possible that *A. schizopyge* represents a remarkable instance of homeomorphy within Palaeocypida. However, it is the presence and nature of dimorphism that is the key to true affinity of palaeocypid taxa (Swartz 1936; Henningsmoen 1953; Jaanusson 1957, 1966; Kesling 1969). On balance the evidence strongly suggests that *A. schizopyge* represents a unique beyrichioidean species, one that has not developed cruminae and cruminal brood care strategy.

#### 4.5. Origin by heterochrony?

Various genetically controlled mechanisms involving the timing and rate of development are normally precisely linked to the eventual size and morphology of an animal, but heterochronic decoupling of mechanisms may result in ‘changes through time in the appearance or rate of development of ancestral characters’ (Gould 1977; McNamara 1990; McKinney & McNamara 1991). Heterochronic changes are by nature ‘instantaneous’ and help in understanding the origin of macroevolutionary novelties (Clarkson 1998). Heterochrony has been suggested to explain morphological aspects of the ontogeny of a few living (e.g., Abe 1988; Kamiya 1992; Tsukagoshi & Kamiya 1996) and fossil (e.g., Schweitzer *et al.* 1986; Olempska 1989) ostracod species. Some type of paedomorphosis, whereby the complete ‘juvenile’ morphology (or only certain juvenile characters) of the ancestor is retained into the adult of the descendant, resulting in a descendant adult that resembles a juvenile of the ancestral form, may have resulted in the non-dimorphic nature of *A. schizopyge*. The valve morphology of *A. schizopyge* bears general similarity to tecnomorphs of European Silurian dimorphic beyrichioideans such as species of *Plicibeyrichia*, *Gannibeyrichia* and *Navibeyrichia* (all Martinsson 1962) and *Pseudobeyrichia*

*cristata* Copeland, 1989 from Canada. *A. schizopyge* especially resembles tecnomorphs of the amphitoxotidine beyrichioidean *Sleia* Martinsson 1962 from which it differs only in minor details of syllibial morphology and by the lack of a characteristic tubercle dorsally on the adductor sulcus (Fig. 4a, b, e–g; cf. Fig. 4a, d, h). Of six species of *Sleia* in the Silurian of Britain four occur at Wenlock Series localities with *A. schizopyge* (Siveter 2022), including the morphologically closely similar *Sleia pauperata* (Jones, 1869) whose adults are of similar size to those of *A. schizopyge* (Fig. 4c, d, h–k). Some form of paedomorphosis acting in a beyrichioidean morphologically similar to a *Sleia* species may be the evolutionary origin of *A. schizopyge*.

## 5. Conclusions

Beyrichioidean ostracods are known abundantly worldwide from hundreds of Palaeozoic genera. Each is characterised by a distinctive well-defined shell dimorphism in which the supposed female of the species develops a pronounced brood pouch (crumina) on each valve. *A. schizopyge*, a ubiquitous Silurian ostracod species from the UK, fundamentally challenges the definition of the group. Known only from juveniles and supposed adults of like morphology it is, ostensibly, a unique, non-dimorphic beyrichioidean species. Its apparent non-dimorphic nature may have resulted from a heterochronic mechanism. Seemingly not all beyrichioideans had cruminal brood care strategy.

## Acknowledgements

We thank Dr Leon Hicks and Professor Mark Williams (University of Leicester) for scanning electron microscope work. We are grateful to Dr Vincent Perrier (University of Lyon) and one other referee for comments on the manuscript.

## Competing interests

The authors declare no competing interests.

## References

- Abe, K. 1988. Speciation completed? In *Keijella bisanensis* species group. In Hanai, T., Ikeya, N. & Ishizaki, K. (eds) *Evolutionary biology of Ostracoda*, Vol. 11, 919–25. Tokyo and Amsterdam: Kodansha and Elsevier.
- Adamczak, F. J. 1990. The crumina in *Craspedobolbina* Kummerow 1924 (Palaeocopa, Ostracoda). *Courier Forschungsinstitut Senckenberg* **123**, 303–14.
- Adamczak, F. J. 1991. Kloedenellids: morphology and relation to non-myodocopide ostracodes. *Journal of Paleontology* **65**, 255–67.
- Angelin, N. P. 1838. Museum Palaeontologicum svecicum. *Naturhistorisk Tidsskrift*, Vol. 2.
- Ayress, M. A., Coles, G. P. & Whatley, R. C. 1994. On *Kuiperiana bathymarina* Ayress sp. nov. *A Stereo-Atlas of Ostracod Shells* **21**, 27–30.
- Callomon, J. H. 1963. Sexual dimorphism in Jurassic ammonites. *Transactions of the Leicester Literary and Philosophical Society* **57**, 36.
- Callomon, J. H. 1980. Dimorphism in ammonoids. In House, M. R. & Senior, J. R. (eds) *The Ammonoidea* Vol. 18, 257–73. London and New York: Systematics Association and Academic Press.
- Cederström, P., Ahlberg, P., Nilsson, C. H., Ahlgrens, J. & Eriksson, M. T. 2011. Moulting, ontogeny and sexual dimorphism in the Cambrian ptychopariid trilobite *Strenuaeva inflata* from the northern Caledonides. *Palaeontology* **54**, 685–703.
- Chény C., Charbonnier S. & Audouin D. 2023. Middle Jurassic lobsters (Crustacea, Decapoda) from Normandy, France. *Geodiversitas* **45**, 139–61.
- Clarkson, E. N. K. 1969. Dimorphism of the eye in *Weberides shumnerensis* (King) [Trilobita]. In Westerman, G. E. G. (ed.) *Sexual dimorphism in fossil metazoa and taxonomic implications*, 185–195. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.
- Clarkson, E. N. K. 1998. *Invertebrate palaeontology and evolution*. 4th edn. Oxford: Blackwell Science.
- Cohen, A. C. & Morin, J. G. 1990. Patterns of reproduction in ostracodes: a review. *Journal of Crustacean Biology* **10**, 184–212.
- Copeland, M. J. 1989. Silicified Upper Ordovician–Lower Silurian ostracodes from the Avalanche Lake Area, Southwestern District of Mackenzie. *Bulletin of the Geological Survey of Canada* **341**, 1–100.
- Fortey, R. A. & Hughes, N. 1998. Brood pouches in trilobites. *Journal of Paleontology* **72**, 638–749.
- Gishlick, A. D. & Fortey, R. A. 2023. Trilobite tridents demonstrate sexual combat at 400 Mya. *Proceedings of the National Academy of Sciences USA* **120**, e2119970120.
- Gould, S. J. 1977. *Ontogeny & phylogeny*. Cambridge, MA: Harvard University Press.
- Halder, K. & Paira, S. 2019. First record of sexual size dimorphism in fossil Strombidae (Mollusca, Gastropoda) from the Miocene of Kutch, western India and its evolutionary implications. *Royal Society Open Science* **6**, 181320.
- Harper, J. C. 1947. *Tetradella complicata* (Salter) and some Caradoc species of the genus. *Geological Magazine* **84**, 345–53.
- Hart, C. W. Jr., Hayek, L. C., Clark, J. & Clark, J. W. 1985. The life history and ecology of the entocytherid ostracod *Ucinocythera occidentalis* (Kozloff and Whitman) in Idaho. *Smithsonian Contributions to Zoology* **419**, 22 pp.
- Henningsmoen, G. 1953. Classification of Paleozoic straight-hinged ostracodes. *Norsk Geologisk Tidsskrift* **31**, 185–288.
- Henningsmoen, G. 1965. On certain features of palaeocene ostracodes. *Geologiska Föreningens i Stockholm Förhandlingar* **86**, 329–39.
- Hessland, I. 1949. Investigations of the Lower Ordovician of the Siljan District, Sweden. I. Lower Ordovician ostracods of the Siljan District, Sweden. *Bulletin of the Geological Institutions of the University of Uppsala* **33**, 397–408.
- Hiruta, S. 1979. A new species of the genus *Bathyleberis* Kornicker from Hokkaido, with reference to the larval stages (Ostracoda, Myodocopina). *Journal of the Faculty of Science Hokkaido University, Series VI Zoology* **22**, 99–121.
- Horne, D. J., Cohen, A. & Martens, K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. In Holmes, J. A. & Chivas, A. (eds), *The Ostracoda: applications in Quaternary research*, Vol. 131, 5–36.
- Hu, C. H. 1971. Ontogeny and sexual dimorphism of Lower Paleozoic Trilobita. *Palaeontographica Americana* **44**, 1–155.
- Hughes, N. & Fortey, R. A. 1995. Sexual dimorphism in trilobites with an Ordovician case study. In Cooper, J. C., Droser, L. M. & Finney, S. C. (eds), *Ordovician odyssey*, 419–21. Los Angeles: Society of Economic Paleontologists and Mineralogists.
- Hunt, G., Martins, M. J. F., Puckett, T. M., Lockwood, R., Swaddle, J. P., Hall, C. M. S. & Stedman, J. 2017. Sexual dimorphism and sexual selection in cytheroidean ostracodes from the Late Cretaceous of the US Coastal Plain. *Paleobiology* **43**, 620–41.
- Jaanusson, V. 1957. Middle Ordovician ostracodes of central and southern Sweden. *Bulletin of the Geological Institutions of the University of Uppsala* **37**, 173–442.
- Jaanusson, V. 1966. Ordovician ostracodes with supravelar antra. *Bulletin of the Geological Institutions of the University of Uppsala* **43**, 1–30.
- Jaanusson, V. 1985. Functional morphology of the shell in platycope ostracodes – a study of arrested evolution. *Lethaia* **18**, 73–84.
- Jaanusson, V. & Martinsson, A. 1956. Two hollinid ostracodes from the Silurian Mulde marl of Gotland. *Bulletin of the Geological Institutions of the University of Uppsala* **36**, 401–10.
- Jiang, R., Liu, Z. & Wang, S. 2019. Fossil evidence for sexual dimorphism in Monotomidae beetles from mid-Cretaceous Burmese amber. *Cretaceous Research* **102**, 7–11.
- Jones, C. R. & Siveter, D. J. 1983. On *Harperopsis scripta* (Harper, 1947). *A Stereo-Atlas of Ostracod Shells* **10**, 5–12.
- Jones, P. J. 1987. *Rhytiobeyrichia*, a new beyrichioidean ostracod from the late Devonian of Western Australia. *Bureau of Mineral Resources, Australian Geology and Geophysics* **10**, 287–300.
- Jones, P. J. 1989. Lower Carboniferous Ostracoda (Beyrichiocopida and Kirkbyocopa) from the Bonaparte Basin, northwestern Australia. *Bulletin-Australia, Bureau of Mineral Resources, Geology and Geophysics* **228**, 1–97.
- Jones, T. R. 1855. Notes on the Palaeozoic bivalved Entomostraca, no. 1. Some species of *Beyrichia* from Upper Silurian limestones of Scandinavia. *Annals and Magazine of Natural History* **16**, 80–92.
- Jones, T. R. 1869. On the Palaeozoic bivalved Entomostraca. [Paper read before the Geologists' Association, May, 1869], 15 pp., 23 text-figs, Hertford.

- Jones, T. R. 1888. Notes on the Palaeozoic bivalved Entomostraca, no. XXV. On some Silurian Ostracoda from Gothland. *Annals and Magazine of Natural History* **1**, 395–411.
- Jones, T. R. & Holl, H. B. 1886. Notes on the Palaeozoic bivalved Entomostraca, no. XX. On the genus *Beyrichia* and some new species. *Annals and Magazine of Natural History* **17**, 337–63.
- Kamenz, C., Staude, A. & Dunlop, J. A. 2011. Sperm carriers in Silurian sea scorpions. *Naturwissenschaften* **98**, 889–96.
- Kamiya, T. 1992. Heterochronic dimorphism of *Loxocochoa uranouchiensis* (Ostracoda) and its implication for speciation. *Paleobiology* **18**, 221–36.
- Karapınar, B., Werner, W., Fürsich, F. T. & Nützel, A. 2021. The earliest example of sexual dimorphism in bivalves – evidence from the astartid *Nicaniella* (Lower Jurassic, southern Germany). *Journal of Paleontology* **95**, 1216–25.
- Kesling, R. V. 1952. A study of *Ctenolocolina cicatricosa* (Warthin). *Contributions from the Museum of Paleontology, University of Michigan* **9**, 247–90.
- Kesling, R. V. 1969. Copulatory adaptations in ostracods. Part III. Adaptations in some extinct ostracods. *Contributions from the Museum of Paleontology, University of Michigan* **22**, 273–312.
- King, P. E. 1973. *Pycnogonids*. London: Hutchinson, 144 pp.
- Kolmodin, L. 1869. *Bidrag till kannedomen om Sveriges siluriska ostracoder*. Uppsala: Edquist et Berglund, 22 pp.
- Knell, R. & Fortey, R. A. 2005. Trilobite spines and beetle horns: sexual selection in the Palaeozoic?. *Biology Letters* **1**, 196–99.
- Lamsdell, J. C. & McKenzie, S. C. 2015. *Tachypleus syriacus* (Woodward) – a sexually dimorphic Cretaceous crown limulid reveals underestimated horseshoe crab divergence times. *Organisms Diversity and Evolution* **15**, 681–93.
- Lehmann, U. 1981. *The ammonites: their life and their world*. Cambridge: Cambridge University Press.
- Lundin, R. F. 1965. Ostracodes of the Henryhouse Formation (Silurian) in Oklahoma. *Oklahoma Geological Survey, Bulletin* **108**, 104.
- Lundin, R. F. 1968. Ostracodes of the Haragan Formation (Devonian) in Oklahoma. *Oklahoma Geological Survey, Bulletin* **116**, 121.
- Lundin, R. F. & Siveter, D. J. 1985. On *Xystista graffhami* (Lundin). *A Stereo-Atlas of Ostracod Shells* **12**, 81–84.
- Martens, K. (ed). 1998. *Sex and parthenogenesis: evolutionary ecology of reproductive modes in non-marine ostracod*. Leiden: Backhuys Publishers, 335 pp.
- Martinsson, A. 1956. Ontogeny and development of dimorphism in some Silurian ostracodes. A study on the Mulde Marl fauna of Gotland. *Bulletin of the Geological Institutions of the University of Uppsala* **37**, 1–42.
- Martinsson, A. 1962. Ostracodes of the family Beyrichiidae from the Silurian of Gotland. *Bulletin of the Geological Institution of the University of Uppsala* **41**, 1–369.
- Martinsson, A. 1963. *Kloedenia* and related ostracode genera in the Silurian and Devonian of the Baltic area and Britain. *Bulletin of the Geological Institutions of the University of Uppsala* **42**, 1–63.
- McKinney, M. L. & McNamara, K. J. 1991. *Heterochrony – the evolution of Ontogeny*. 1–437. New York: Plenum.
- McNamara, K. J. 1990. Heterochrony. In Briggs, D. E. G. & Crowther, P. R. (eds), *Palaebiology – a synthesis*, 111–18. Oxford: Blackwell.
- Meidla, T. 1996. *Late Ordovician ostracodes of Estonia. Fossilia Baltica 2*. Tartu: Institute of Geology, University of Tartu, 222 pp.
- Neckaja, A. I. 1960. New Paleozoic ostracods from the Russian and Siberian platforms, the Urals and the Pechora Plateau. In Abushik, A. F., Ivanova, V. A., Kochetkova, N. M., Martinova, G. P., Netskaya, A. I. & Rozhdestvenskaya, A. A. (eds) *New species of prehistoric plants and invertebrates of the USSR* **2**, 280–366. Moscow: Vsesoyuznyi Nauchno-Issledovatel' Geologorazvedochnyi Institut (VSEGEI).
- Néraudeau, D. 1993. Sexual dimorphism in mid-Cretaceous hemi-asterid echinoids. *Palaebontology* **36**, 311–17.
- Olempska, E. 1989. Gradual evolutionary transformations of ontogeny in an Ordovician ostracod lineage. *Lethaia* **22**, 159–68.
- Ozawa, H. 2013. The history of sexual dimorphism in Ostracoda (Arthropoda, Crustacea) since the Palaeozoic. In Moriyama, H. (ed.) *Sexual dimorphism*. InTech, 152 pp. <https://doi.org/10.5772/55329>
- Philip, G. M. & Foster, R. J. 1971. Marsupiate Tertiary echinoids from south-eastern Australia and their zoogeographic significance. *Palaebontology* **14**, 666–95.
- Sars, G. O. 1866. Oversigt af Norges marine ostracoder. *Forhandlinger i Videnskabs-Selskabet i Christiania* **1**, 1–130.
- Schallreuter, R. E. L. 1976. Ctenontellidae (Ostracoda, Palaeocopina) aus Backsteinkalk-Geschieben (Mittelordoviz) Norddeutschlands. *Palaebontographica A* **153**, 161–215.
- Schallreuter, R. E. L. 1977. On *Distobolbina bispinata* Schallreuter sp. nov. *A Stereo-Atlas of Ostracod Shells* **4**, 17–24.
- Schallreuter, R. E. L. 1978. On *Tetradella? trilocolata* Schallreuter sp. nov. *A Stereo-Atlas of Ostracod Shells* **5**, 73–78.
- Schallreuter, R. E. L. 1989a. Die älteste bekannte 'Beyrichie' (The oldest known Beyrichian ostracode). *Geschiebekunde aktuell* **5**, 17–20.
- Schallreuter, R. E. L. 1989b. On *Fallaticella schaeferi* Schallreuter. *A Stereo-Atlas of Ostracod Shells* **16**, 25–28.
- Schweitzer, P. N., Kaesler, R. L. & Lohmann, G. P. 1986. Ontogeny and heterochrony in the ostracode *Cavellina coryell* from Lower Permian rocks in Kansas. *Paleobiology* **12**, 290–301.
- Shaver, R. H. 1953. Ontogeny and sexual dimorphism in *Cytherella bullata*. *Journal of Paleontology* **21**, 471–80.
- Siveter, D. J. 1980. British Silurian Beyrichiacea (Ostracoda). Part 1. *Monograph of the Palaeontographical Society* **133**, 1–76.
- Siveter, D. J. 2009. The Silurian. In Whittaker, J. E. W. & Hart, M. B. (eds) *Ostracods in British stratigraphy. the micropalaebontological society special publications*, 45–90. London: Geological Society.
- Siveter, D. J. 2022. British Silurian Beyrichiacea (Ostracoda). Part 2. *Monograph of the Palaeontographical Society* **176**, 77–157.
- Siveter, David J., Briggs, D. E. G., Siveter, Derek J. & Sutton, M. D. 2015. A 425-million-year-old Silurian pentastomid parasitic on ostracods. *Current Biology* **25**, 1632–37.
- Siveter, D. J. & Sarv, L. 1991. On *Venzavella costata* (Neckaja). *A Stereo-Atlas of Ostracod Shells* **18**, 9–12.
- Siveter, David J., Siveter, Derek J., Sutton, M. D. & Briggs, D. E. G. 2007. Brood care in a Silurian ostracod. *Proceedings of the Royal Society London B* **274**, 465–69.
- Siveter, David J., Tanaka, G., Farrell, C. Ú., Martin, M. J., Siveter, Derek J. & Briggs, D. E. G. 2014. Exceptionally preserved 450 million-year-old Ordovician ostracods with brood care. *Current Biology* **24**, 801–06.
- Siveter, Derek J., Sabroux, R., Briggs, D. E. G., Siveter, David J. & Sutton, M. D. 2023. Newly discovered morphology of the Silurian sea spider *Haliestes* and its implications. *Papers in Palaeontology* **9**, e1528.
- Smith, R. J. 2025. Development and morphology of podocopan ostracod limbs (Crustacea) – a review. *Arthropod Structure & Development* **85**, 101402.
- Smith, R. J., Kamiya, T. & Horne, D. J. 2006. Living males of the 'ancient' asexual Darwinulidae (Ostracoda, Crustacea). *Proceedings of the Royal Society B*, **273**, 1569–78.
- Spjeldnæs, N. 1951. Ontogeny of *Beyrichia jonesi* Boll. *Journal of Paleontology* **25**, 745–55.
- Spjeldnæs, N. 1966. N. P. Angelin's work on fossil ostracodes. *Geologiska Föreningens i Stockholm Förhandlingar* **88**, 407–09.
- Swartz, F. M. 1936. Revision of the Primitiidae and Beyrichiidae, with new Ostracoda from the Lower Devonian of Pennsylvania. *Journal of Paleontology* **10**, 541–86.
- Tinn, O. & Meidla, T. 2003. Ontogeny and thanatocoenoses of early middle Ordovician Palaeocope ostraode species *Brezelina palmata* (Krause, 1889) and *Ogmoopsis bocki* (Opik, 1935). *Journal of Paleontology* **77**, 64–72.
- Triebel, E. 1941. Zur Morphologie und Ökologie der fossilen Ostracoden: mit Beschreibung einiger neuer Gattungen und Arten. *Senckenbergiana* **23**, 294–400.
- Tsukagoshi, A. & Kamiya, T. 1996. Heterochrony of the ostracod hingement and its significance for taxonomy. *Biological Journal of the Linnean Society* **57**, 343–370.
- Vannier, J. M. C., Siveter, D. J. & Schallreuter, R. E. L. 1989. The composition and palaeogeographical significance of the Ordovician ostracode faunas of southern Britain, Baltoscandia and Ibero-America. *Palaebontology* **32**, 163–222.
- Westerman, G. E. G. (ed). 1969. *Sexual dimorphism in fossil Metazoa and taxonomic implications*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, 251 pp.
- Westermann, G. E. G. 1979. Sexual dimorphism. In *Palaebontology: encyclopedia of earth science*. Berlin, Heidelberg: Springer.
- Whatley, R. C. & Stephens, J. M. 1977. Precocious sexual dimorphism in fossil and recent Ostracoda. In Löffler, H. & Danielopol, D. (eds), *Aspects of ecology and zoogeography of recent and fossil ostracoda*, 69–91. The Hague: W. Junk.
- Whittaker, J. E. 1974. On *Semicytherura sella* (Sars). *A Stereo-Atlas of Ostracod Shells* **2**, 85–92.