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Silurian myodocope ostracods from Poland

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Newly collected material reveals that the Silurian myodocope ostracods from the Holy Cross Mountains, Poland comprise ten species (one new to science) belonging to four families: Bolbozoidae, Entomozoidae, Rhomboentomozoidae, and Cypridinidae. Biostratigraphic control using graptolites indicates that all three Polish outcrops investigated are of about the same chronostratigraphical level: middle Gorstian, lower Ludlow. The new occurrences in Poland extend the known distribution of several species and reinforce data that show many Silurian myodocope species with wide dispersal. Our new observations on the Holy Cross Mountains material confirm that the occurrences of Silurian myodocopes are mostly associated with pelagic animals and with rocks ranging from mudstone, siltstone or shale deposited in open- or deep-shelf marine settings. The cosmopolitan distribution of these ostracods, coupled with their facies and faunal associations, supports the notion of an ostracod (myodocope) ecological shift from benthic to planktonic habitats during the late Wenlock and Ludlow.

Key words: Ostracoda, Myodocopa, Silurian, Ludlow, Poland, Holy Cross Mountains.

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Introduction

This paper is part of series of works, initiated during the 1980s, that focuses on the (Silurian) origin of zooplanktonic ostracods. The idea that some Silurian ostracods represented pioneer zooplankton was developed when taxonomic, distributional and facies studies of British and other European myodocope faunas demonstrated that some had undergone a benthic to pelagic ecological shift during Silurian times (Siveter 1984; Siveter et al. 1987, 1991; Siveter and Vannier 1990; Vannier and Abe 1992; Perrier et al. 2015). More recent studies have endorsed the idea regarding the shift in the mode of life of some Silurian myodocopes and have strengthened and expanded knowledge of their systematics, habitats, lifestyles, and their biostratigraphical and palaeogeographical utility (Perrier et al. 2007, 2011, 2014a–c, 2019; Perrier 2012; Perrier and Siveter 2013). These studies are underpinned by the discovery of five exceptionally preserved myodocope ostracod species from the Silurian Herefordshire Lagerstätte (Welsh Borderland, UK), which

provide unrivalled data on the soft-anatomy and palaeobiology of ancient representatives of the group (Siveter et al. 2003, 2007, 2010, 2013, 2015, 2018).

Research on Silurian myodocope ostracods from Poland began at the end of the 19th century, when Gürich (1896) recorded two species of “*Entomis*” and *Bolbozoe* in the Silurian of the Holy Cross Mountains, Poland, from the so-called “*Interrupta-Schiefern*”. For more than 100 years, these faunas remained essentially unstudied. They were only mentioned briefly by Stupnicka et al. (1991), who identified four different species of bolbozoids and entomozoids at a new locality. The material studied for the present paper was collected over the last 30 years by Polish scientists and by our new field work that yielded additional material from the localities of Gürich (1896) and Stupnicka et al. (1991); see Geological Setting. Ten myodocope species are identified herein from the Silurian of Poland.

Institutional abbreviations.—FSL, Université Claude Bernard Lyon 1, Lyon, France; GSM, British Geological Survey, Keyworth, UK; I, Museo de Storia Natural e del Territo-

rio, Calci, Italy; LPB, University of Brest, Brest, France; NM, Národní Museum, Prague, Czech Republic; OUMNH, Oxford University Museum of Natural History, Oxford, UK; UMC-IP-VP, University of Montpellier, Montpellier, France; ZPAL, The Polish Academy of Science, Warsaw, Poland.

Other abbreviations.—H, height; L, length.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:act:01C7B8C0-33F5-4067-939B-1568F17AB8C9

Material and methods

The Polish myodocopes occur as internal and external moulds in laminated brownish-grey shaly limestone beds. Rock matrix was removed from the specimens mechanically using fine needles. Casts of external moulds of the ostracods recovered were made with silicone rubber (Silicoset 105) using the techniques of Siveter (1982). Specimens and casts were coated with a thin layer of ammonium chloride and photographed using a Leitz Aristophot mounted with a Canon EOS 5D camera following the methods of Siveter (1990). Stereopairs were used for the description of a new species *Nudator elegantulus* sp. nov. and for the revision of *Rhombentomozoe rhomboidea*. For scanning electron microscopy, specimens were mounted on aluminum stubs and coated with gold/aluminum alloy using an “Emitech K500X” and photographed with a HITACHI S-3600N scanning electron microscope at Leicester University. Specimens were measured using a micrometer under a Leica M80 binocular microscope.

Silurian myodocopes possess a bivalved carapace that is typically presumed to have been lightly calcified, with a probable ligamentous dorsal connection (see Perrier 2012). The moulds of each valve in many specimens preserves an adductor muscle scar/spot sub-centrally, corresponding to the site of internal attachment of the adductor muscle. The surface of the carapace, preserved via the external mould, may be smooth or have a range of types of ornament, including reticulation, corrugation and punctuation. The carapace surface shows, in some cases, post-mortem diagenetic features (“rosettes” of Siveter et al. 1987). The morphological terminology and measurements (including the adductor muscle position) follow Siveter et al. (1987) and Perrier et al. (2019).

Geological settings

Silurian myodocopes from Poland were originally documented by Gürich (1896) from “*Interrupta*-Schiefern” layers at several sites in the Holy Cross Mountains, central Poland, such as Niestachów, Kleczanów, Zalesie, and Brzezinki. Most of these localities are now lost or inaccessible and the material has been lost during World War II. We had access

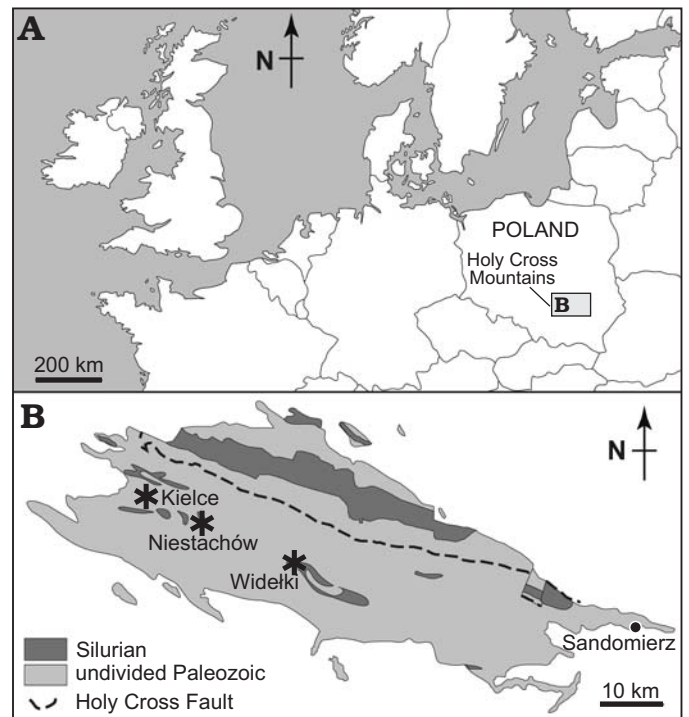


Fig. 1. Distribution of Silurian myodocope-bearing localities in the Holy Cross Mountains, Poland. **A.** Location of the Holy Cross Mountains. **B.** Myodocope-bearing localities (asterisks) sampled in the Holy Cross Mountains (geological map modified from Kozłowski et al. 2014).

to recently collected material and made new collections (2014) of Silurian myodocopes from three localities in the Holy Cross Mountains (Fig. 1).

Widelki.—Two exposures, 10 m apart, along a small track about 400 m from the road at Widelki village, 20 km SE of Kielce, Holy Cross Mountains. Together with material obtained in 2014, we studied specimens collected from Widelki by Barbara Żbikowska (Polish Geological Institute; 1991) and from a trench by Jan Malec (Holy Cross Division of the Geological Institute; 2005). Fossiliferous, laminated brownish-grey shaly limestone; Niewachłów Beds, lower part of the Ludlow Series based on graptolites (Stupnicka et al. 1991). Ostracods occur as flattened and disarticulated valves. The myodocope fauna includes *Bolbozoe anomala*, *Bolbozoe psittaca*, *Nudator angiportatus*, *Nudator elegantulus* sp. nov., *Parabolbozoe bohemica*, *Richteria migrans*, *Rhombentomozoe rhomboidea*, and *Silurocypridina calva*. Associates include graptolites, cephalopods, and bivalves.

Niestachów.—Four field-side exposures several 10s of metres apart, about 500 m from the road at Niestachów Village, c. 1.5 km SE of Kielce, Holy Cross Mountains. Together with material collected in 2014, we studied specimens obtained from Niestachów by EO in 2014. Fossiliferous, laminated brownish-grey shaly limestone; Niewachłów Beds, lower part of the Ludlow Series based on graptolites (probably *Cucullograptus* (*Lobograptus*) *scanicus* Biozone; see Tomczyk 1956: fig. 7 upper). Ostracods are dominant and occur as flattened and disarticulated valves. The myodo-

cope fauna includes *Bolbozoe anomala*, *Bolbozoe psittaca*, *Nudator angiportatus*, *Nudator elegantulus* sp. nov., *Nudator inflatus*, *Richteria migrans*, *Rhomboentomozoe rhomboidea*, *Silurocypridina calva*, and *Silurocypridina retroreticulata*. Associates include graptolites, cephalopods and bivalves. Part of Gurich's (1896) material is from Niestachów, but precise localities are unknown.

Kielce.—Material collected by Jan Malec in 2014 (Malec 1993: fig. 2) during road work in Skrajna Street, Kielce, Holy Cross Mountains. Fossiliferous, laminated brownish-grey shaly limestone; Niewachlów Beds, lower part of the Ludlow Series based on graptolites (*Cucullograptus* [*Lobograptus*] *scanicus* Biozone; see Malec 1993: fig. 4 upper, locality A). Ostracods are abundant and occur as flattened and disarticulated valves. The myodocope fauna includes *Bolbozoe anomala* and *Parabolbozoe bohémica*. Associates include graptolites and cephalopods.

Systematic palaeontology

Class Ostracoda Latreille, 1802

Subclass Myodocopa Sars, 1866

Order Myodocopida Sars, 1866

Suborder Myodocopina Sars, 1866

Remarks.—The overwhelming majority of Myodocopa are Recent species that are defined on soft-part morphology. All known fossil myodocopes are assigned to the order Myodocopida; halocyprid myodocopes are unknown from the fossil record. The suborder Paleomyodocopina Kornicker and Sohn, 2000 was established for those fossil myodocopids that were known only from their carapaces in which a sub-central to anterodorsal node/bulb was present: namely, the Cypridinelliformacea, Nodophilomedacea, and Swainellacea. The Bolbozoidea (Silurian–Devonian) also have an anterodorsal bulb and therefore qualify for inclusion within that suborder. However, new knowledge of the appendages and other soft-parts of fossil myodocopids from the Ordovician and Silurian (Siveter et al. 2003, 2007, 2010, 2013, 2014, 2015, 2018) has fundamentally questioned the utility of carapace-based taxonomy alone and therefore the suborder Paleomyodocopina is not used here.

Stratigraphic and geographic range.—Ordovician to Recent; worldwide.

Superfamily Bolbozooidea Bouček, 1936

(sensu Bolbozoacea Bouček, 1936)

Family Bolbozoidae Bouček, 1936

1936 Bolbozoidae n.f.; Bouček 1936: 62.

1951 Entomozoidae nov. nom.; Přibyl 1951: 4 (= Entomidae Jones, 1873).

1990 Bolbozoidae Bouček, 1936; Siveter and Vannier 1990: 48.

2019 Bolbozoidae Bouček, 1936; Perrier et al. 2019: 27.

Included genera: *Bolbozoe* Barrande, 1872; *Entomozoe* Přibyl, 1951 (pro *Entomis* Jones, 1861; not Herrich-Schaffer, 1856); *Oculparva* Perrier et al. 2019; *Parabolbozoe* Přibyl, 1988.

Stratigraphic and geographic range.—Lower Silurian (*Entomozoe tuberosa*, Llandovery Series, Scotland; Siveter and Vannier 1990) to Lower Devonian (*Bolbozoe largiglobosa*, Emsian Stage, China; Wang and Zhang 1983).

Genus *Bolbozoe* Barrande, 1872

Type species: *Bolbozoe anomala* Barrande, 1872; subsequent designation by Bassler and Kellett, 1934. Ludlow Series, Silurian, Prague, Czech Republic.

Species included: Type species and *Bolbozoe acuta* Perrier, Vannier, and Siveter, 2011, *Bolbozoe beccata* Perrier, Siveter, Williams, Strusz, Steeman, Verniers, and Vandembroucke, 2014c, *Bolbozoe largiglobosa* Wang and Zhang, 1983, *Bolbozoe parvafraga* Perrier, Vannier, and Siveter, 2011, *Bolbozoe psittaca* Perrier, Siveter, Williams, and Palmer, 2019, *Bolbozoe rugosa* Perrier, Vannier, and Siveter, 2011, *Bolbozoe* sp. nov. A of Perrier et al. 2019, *Bolbozoe* sp. nov. B of Perrier et al. 2019, and possibly *Bolbozoe jonesi* Barrande, 1872.

Stratigraphic and geographic range.—Upper part of the Wenlock Series, Silurian, to Emsian Stage, Devonian; Czech Republic (Perrier et al. 2011), France (Perrier et al. 2011), Sardinia (Gnoli et al. 2009), China (Wang 2009), Australia (Perrier et al. 2014c), Wales and England (Perrier et al. 2019) and Poland.

Bolbozoe anomala Barrande, 1872

Fig. 2A, B.

1861 *E. divisa* MSS.; Jones (in Salter) in Howell and Geikie 1861: 137 (GSM 36876).

1868 *Entomis divisa* Jones; Bigsby 1868: 74.

1868 *Bolbozoe anomala* Barr.; Bigsby 1868: 200.

1870 *Entomis divisa* Jones; Jones 1870: pl. 61: 12 (GSM 36876).

1872 *Bolboz. anomala* Barr.; Barrande 1872: 501, pl. 24: 27, 28 (NM-L 13993), 29, 30 (NM-L 23572).

1872 *Bolboz. Jonesi* Barr.; Barrande 1872: 503, pl. 27: 8 (NM-L 23650 [ex. NM-1600]); pl. 31: 4–6 (NM-CF 1242).

1873 *Entomidella divisa* Jones; Jones 1873: 416 (GSM 36876).

1878 *Entomis divisa* Jones; Salter 1878: 130 (GSM 36876).

1884 *Bolbozoe divisa* Jones; Jones 1884: 401, pl. 15: 4 (GSM 36876).

1900 *Bolbozoe* (?) *italica* n. f.; Canavari 1900: 208, pl. 26: 16 (I 97a), 17 (I 97b), 18 (I 98).

1900 *Bolbozoe* (?) *capellinii* n. f.; Canavari 1900: 208, pl. 26: 19.

1900 *Bolbozoe* (?) *lanceolata* n. f.; Canavari 1900: pl. 26: 20 (I 99).

1934 *Bolbozoe anomala* Barrande; Bassler and Kellett 1934: 215.

1934 *Bolbozoe* (?) *lanceolata* Canavari; Bassler and Kellett 1934: 215.

1934 *Bolbozoe* (?) *capellinii* Canavari; Bassler and Kellett 1934: 215.

1934 *Bolbozoe* (?) *italica* Canavari; Bassler and Kellett 1934: 215.

1936 *Bolbozoe anomala* Barrande; Bouček 1936: 62.

1937 *Bolbozoe* (?) *lanceolata* Canavari; Chaubet 1937: pl. 7: 19 (UMC-IP-VP 7).

1954 *Bolbozoe anomala* Barrande; Hughes 1954: 42.

1958 *Bolbozoe anomala* Barrande; Pokorný 1958: 315.

1961 *Bolbozoe anomala* Barrande; Sylvester-Bradley 1961: 395, text-fig. 316.1c–f.

1985 gen. nov. A sp. nov. 1; Lethiers et al. 1985: 57, pl. 5: 1.

1985 gen. nov. A sp. nov. 2; Lethiers et al. 1985: 57, pl. 5: 3.

1985 gen. nov. C sp. nov. 1; Lethiers et al. 1985: 57, pl. 5: 4.

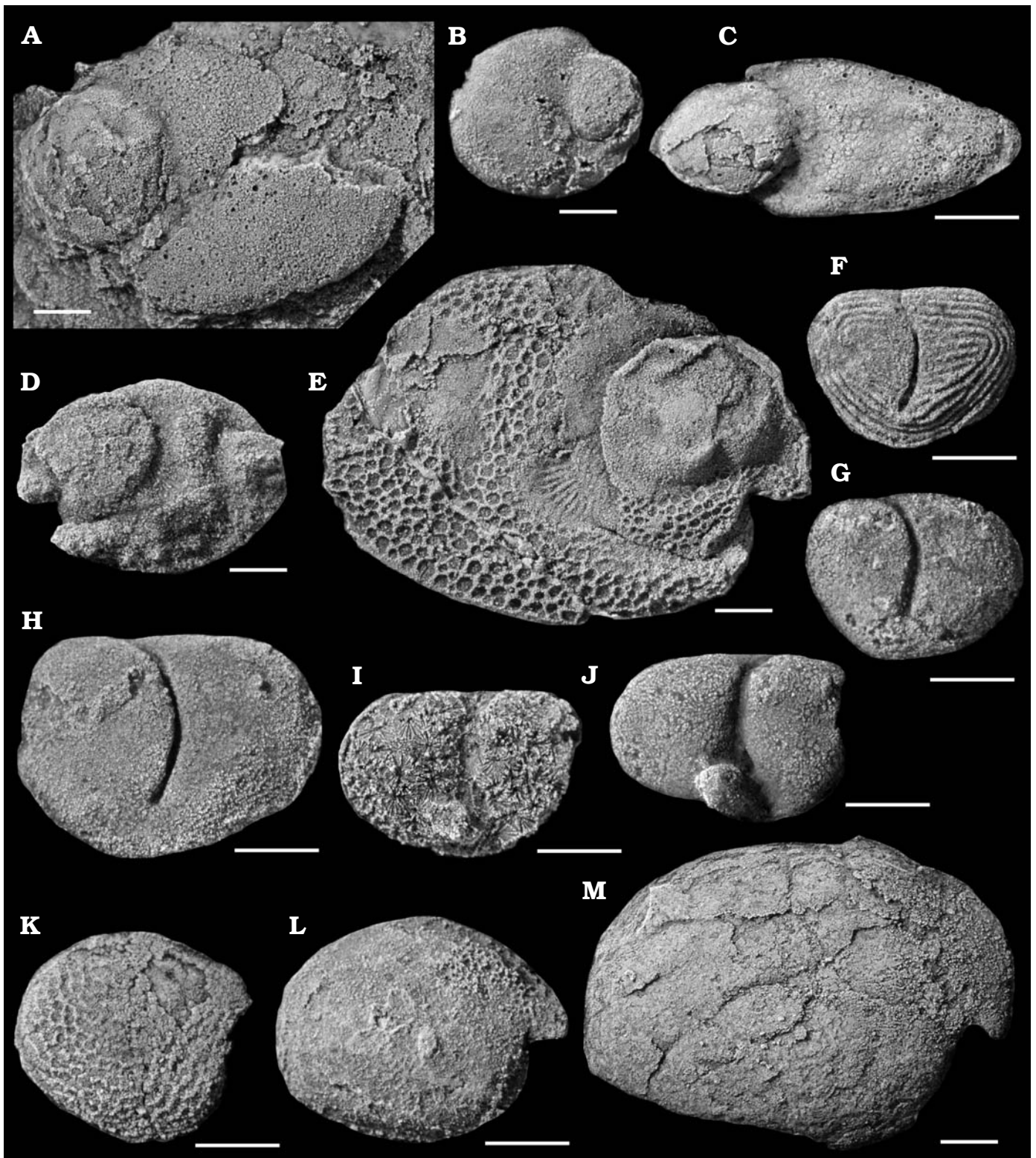


Fig. 2. Selected Silurian myodocope species, Holy Cross Mountains, Poland; Ludlow Series, Silurian. **A, B.** *Bolbozoe anomala* Barrande, 1872. **A.** ZPAL O.63/1, incomplete left valve. **B.** ZPAL O.63/2, juvenile right valve. **C.** *Bolbozoe psittaca* Perrier, Siveter, Williams, and Palmer, 2019, ZPAL O.63/3, left valve. **D, E.** *Parabolbozoe bohémica* (Barrande, 1872). **D.** ZPAL O.63/4, juvenile left valve. **E.** ZPAL O.63/5, right valve. **F.** *Richteria migrans* (Barrande, 1872), ZPAL O.63/6, left valve. **G, H.** *Nudator angiportatus* Perrier, Siveter, Williams, and Palmer, 2019. **G.** ZPAL O.63/7, juvenile left valve. **H.** ZPAL O.63/8, left valve. **I, J.** *Nudator inflatus* Perrier, Siveter, Williams, and Palmer, 2019. **I.** ZPAL O.63/9, right valve showing post-mortem diagenetic structures. **J.** ZPAL O.63/9, right valve. **K.** *Silurocypridina retroreticulata* Perrier, Vannier, and Siveter, 2011, ZPAL O.63/10, incomplete right valve. **L.** *Silurocypridina calva* Perrier, Vannier, and Siveter, 2011, ZPAL O.63/11, right valve. **M.** Cyprididid?, ZPAL O.63/12, right valve. All light photographs in lateral view. A–H, J, M, silicone casts of external moulds; I, K, L, internal moulds. Scale bars 1 mm, except M 2 mm.

- 1987 *Bolbozoe* cf. *anomala* Barrande; Siveter et al. 1987: pl. 85: 3, 8–11; pl. 86: 1–6, pl. 87: 8, text-fig. 7.
 1988 *Bolbozoe* (*Bolbozoe*) *anomala* Barrande; Přibyl 1988: 119.
 1988 *Bolbozoe* (*Bolbozoe*) *jonesi* Barrande; Přibyl 1988: 118.
 1990 *Bolbozoe* cf. *anomala* Barrande, 1872; Siveter and Vannier 1990: text-fig. 7c–d.
 1990 “*Bolbozoe*” cf. *anomala* Barrande; Siveter and Vannier 1990: text-figs. 13C, 13F, 23.
 1991 *Bolbozoe* cf. *anomala* Barrande; Siveter et al. 1991: pl. 1: 1; pl. 2: 2, 5.
 1992 “*Bolbozoe*” cf. *anomala* Barrande; Vannier and Abe 1992: pl. 2: 1; text-fig. 1A.
 2009 *Bolbozoe anomala* Barrande, 1872; Gnoli et al. 2009: pl. 2: 1–15.
 2011 *Bolbozoe anomala* Barrande, 1872; Perrier et al. 2011: pl. 1: 1–20; text-figs. 6, 7H, 8, 9B, 10.
 2012 *Bolbozoe anomala* Barrande, 1872; Perrier 2012: text-fig. 7C, D.
 2013 *Bolbozoe anomala* Barrande, 1872; Perrier and Siveter 2013: text-fig. 22.6C.
 2019 *Bolbozoe anomala* Barrande, 1872; Perrier et al. 2019: pl. 3: 1–18.

Type material: Lectotype: a right valve, NM-L 23572 (ex. CE1194); Barrande (1872: pl. 24: 29, 30); Perrier et al. (2011: pl. 1: 1); designated by Přibyl (1988: 119). Paralectotype: a left valve, NM-L 13993; Barrande (1872: pl. 24: 27, 28); Perrier et al. (2011: pl. 1: 2); designated by Přibyl 1988: 119. All from type locality.

Type locality: Lochkov suburb of Prague, Czech Republic.

Type horizon: Požáry Formation, Pridoli Series, stratigraphical division e2 of Barrande 1872 (Kříž 1992).

Material.—Tens of valves, from three localities (Wieleki, Niestachów, and Kielce), Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 1.8, H = 1.25 (ZPAL O.63/24) to L = 8.25, H = 6 (ZPAL O.63/25). Lectotype: L = 8.50, H = 5.95 (NM-L 23572). Paralectotype: L = 7.10, H = 4.95 (NM-L 13993). L/H ratio and adductor muscle position for four specimens from two localities (Fig. 3).

Description.—Adult valve sub-ovoid, slightly tapering posteriorly. Anterior third of valve mostly occupied by a large hemispherical bulb forming c. 20–25% of valve area; bulb-centre lies just above valve mid-height and well above other surface areas of valve. Maximum valve length is just above bulb mid-height; maximum valve height is at mid-length and maximum valve width is at central part of bulb. Right valve overlaps left valve along ventral margin. A deep, narrow sulcus surrounds the bulb posteriorly and ventrally. An adductor muscle scar consisting of a single series of 7–8 inclined, almost parallel individual scars including about seven furrows, occurs at mid-length in the sulcus. Rostrum is very small, in some cases beak-like or absent. Rostral incisure slit-like, as seen in 3D preserved carapaces in anterior view. Early growth stages are more rounded in valve outline and the bulb is relatively larger than in adults.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains. Also known from the upper part of the Wenlock to at least the middle part of the Pridoli Series; the Czech Republic, France, Sardinia (Perrier et al. 2011), Wales and England (Perrier et al. 2019). If *Bolbozoe jonesi* is conspecific with *Bolbozoe anomala* the range of the species

would extend into the Lochovian Series, Lower Devonian (see Perrier et al. 2011).

Bolbozoe psittaca Perrier, Siveter, Williams, and Palmer, 2019

Fig. 2C.

2019 *Bolbozoe psittaca* sp. nov.; Perrier et al. 2019: pl. 4: 1–13.

Holotype: A laterally compressed left valve (OUMNH 35080); Perrier et al. 2019: pl. 4: 1–4.

Type locality: Radnorshire (loc. 12 of Perrier et al. 2019), Powys, Wales, UK.

Type horizon: “Striped Flags” of Kirk 1947, *Cucullograptus* (*Lo-bograptus*) *scanicus* Biozone, Gorstian Stage, Ludlow Series (Perrier et al. 2019).

Material.—Five valves from two localities (Wieleki and Niestachów), Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 4.5, H = 2 (ZPAL O.63/3). *Holotype*: L = 5.15, H = 2.5 (OUMNH 35080). L/H ratio and adductor muscle position for one complete specimen (Fig. 3).

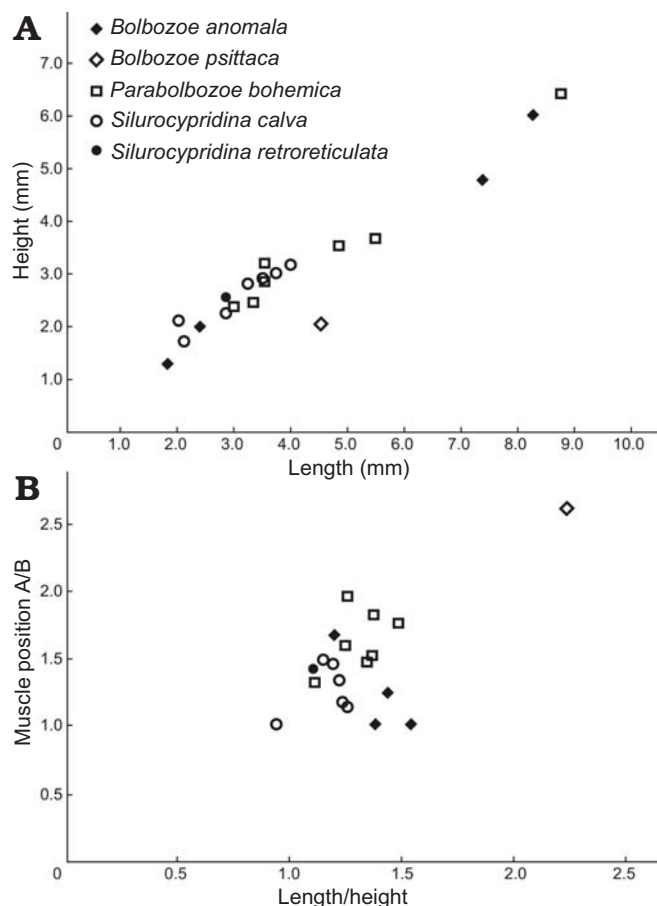


Fig. 3. Valve length/height plot (A) and position of the adductor muscle scar (A/B, where A and B are the distances between the muscle scar and the posterior end of the valve and the ventral margin, respectively) against length/height (B) of complete specimens of bolbozoid and cypridinid species from the Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Description.—Lateral outline of adult valve is elongate ovoid, strongly tapered posteriorly. Anterior third of valve mostly occupied by large hemispherical bulb that forms the most prominent feature of valve; its diameter in adults is about one-third of valve length and its center is at valve mid-height. Maximum valve length is at about mid-height; maximum valve height is at about mid-length; maximum valve width is at the central part of bulb. A narrow sulcus surrounds the bulb almost entirely except anteriorly where bulb merges into rostrum without clear demarcation. Sulcus is widest at and above presumed site of (unknown) adductor muscle scar. Valve surface smooth.

Stratigraphic and geographic range.—Ludlow Series of the Holy Cross Mountains, Poland, England, and Wales (Perrier et al. 2019).

Genus *Parabolbozoe* Přibyl, 1988

Type species: *Bolbozoe bohémica* Barrande, 1872; by monotypy. Ludlow Series, Silurian, Prague, Czech Republic.

Species included: Type species and *Parabolbozoe armoricana* Perrier, Vannier, and Siveter, 2011 and *Parabolbozoe britannica* Perrier, Siveter, Williams, and Palmer, 2019.

Stratigraphic and geographic range.—Upper part of the Wenlock to Ludlow or Pridoli Series; Czech Republic (Perrier et al. 2011), France (Perrier et al. 2011), Sardinia (Gnoli et al. 2009), Wales and England (Perrier et al. 2019), and Poland.

Parabolbozoe bohémica (Barrande, 1872)

Fig. 2D, E.

1868 *Bolbozoe Bohémica* Barr.; Bigsby 1868: 200.

1872 *Bolbozoe Bohémica* Barr.; Barrande 1872: 502, pl. 27: 14 (= same specimen as fig. 17 upper) and 17 lower (= 2 specimens on slab NM-CE1192), 15, 16, 18, 20 (= NM original specimen numbers 1608, 1609, 1611, 1613), 19 (holotype, specimen NM-L 23658 [ex. CE1193]).

1896 *Bolbozoe polonica* nov. sp.; Gürich 1896: 378, pl. 15: 12a–c.

1898 *Cypridina? polonica* (Bolbozoe, Gürich); Jones 1898: 339, pl. 17: 16.

1900 *Bolbozoe (?) bohémica* Barr.; Canavari 1900: 205, text-fig. 15a–c (specimen I 96).

1934 *Bolbozoe bohémica* Barrande; Bassler and Kellett 1934: 215.

1936 *Bolbozoe bohémica* Barrande; Bouček 1936: 63, text-fig. 4.

1937 *Bolbozoe (?) bohémica* Barr.; Chaubert 1937: 188, pl. 7: 18 a, 18b (specimens UMC-IP-VP 1, UMC-IP-VP 6).

1954 *Bolbozoe bohémica* Barrande; Hughes 1954: 42.

1958 *Bolbozoe bohémica* Barrande; Pokorný 1958: 315, text-fig. 1044.

1961 *Bolbozoe bohémica* Barrande; Sylvester-Bradley 1961: 396, text-figs. 316.1a, 18b; ?316.1g–i.

1984 *Bolbozoe bohémica* Barrande; Siveter 1984: pl. 2: 7–11; text-figs. 2, 3.

1987 “*Bolbozoe*” cf. *bohémica* Barrande; Siveter et al. 1987: pl. 84: 6–8, pl. 87: 6, 7; text-fig. 5E, F.

1988 *Bolbozoe (Parabolbozoe) bohémica* Barrande; Přibyl 1988: 120.

1990 “*Bolbozoe*” *bohémica* Barrande; Siveter and Vannier 1990: text-fig. 7g–i, 17, 23.

1991 *Parabolbozoe* cf. *bohémica* Barrande; Siveter et al. 1991: pl. 2: 9, 11, pl. 3: 2, 6.

1992 “*Bolbozoe*” cf. *bohémica* Barrande; Vannier and Abe 1992: text-fig. 1B.

2009 *Parabolbozoe bohémica* (Barrande, 1872); Gnoli et al. 2009: pl. 2: 18, 22–27, ?16, ?17, ?19–21.

2009 *Parabolbozoe bohémica* (Barrande, 1872); Siveter 2009: 54, pl. 8: 9.

2011 *Parabolbozoe bohémica* (Barrande, 1872); Perrier et al. 2011: pl. 3: 1–9, 18, 19, text-figs. 6, 7F, 8A.

2013 *Parabolbozoe bohémica* Barrande, 1872; Perrier and Siveter 2013: text-fig. 22.6B.

2015 *Parabolbozoe bohémica?* Barrande, 1872; Williams et al. 2015: text-fig. 2k–l.

2019 *Parabolbozoe bohémica* (Barrande, 1872); Perrier et al. 2019: pl. 6: 1–13; pl. 7: 1–10.

Lectotype: A left valve, NM-L 23658 (ex. CE1193); Barrande (1872: pl. 27: 19, in reverse); Perrier et al. (2011: pl. 3: 1); designated by Bouček (1936: 63).

Type locality: Praha-Malá Chuchle, Vyskočilka, Czech Republic.

Type horizon: Kopanina Formation, Ludlow Series (stratigraphical division e2 of Barrande 1872; horizon with the trilobite “*Cromus*” *beaumonti*).

Material.—Tens of valves from two localities (Niestachów and Kielce), Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 2.95, H = 2.35 (ZPAL O.63/26) to L = 8.75, H = 6.35 (ZPAL O.63/5; Fig. 2E). Lectotype: L = 11.25, H = 8.10 (NM-L 23658). L/H ratio and adductor muscle position for seven specimens from one locality (Fig. 3).

Description.—Adult valve is sub-ovoid in lateral outline, gently curved dorsally and ventrally, posteriorly tapering slightly. Bulb is large, anterodorsal, has centre above valve mid-height, extends posteriorly to almost line of maximum valve height and ventrally to below valve mid-height; outline is sub-circular, with a slight indentation opposite the rostrum. Rostrum is large, hook-like, generally with a pointed end. Rostral incisure is well developed, below which the valve has a forward pointing projection. Caudal process well developed, pointed in early instars, subdued and rounded in late instars. Maximum valve length is at about the level of end of rostrum; maximum valve height is at about valve mid-length; maximum valve width is at the crest of bulb. A narrow, fairly deep sulcus flanks the bulb posteriorly and ventrally, is widest dorsally and at its mid-length site of adductor muscle scar. In posterior one-third of valve a narrow S-shaped sulcus skirts around dorsal and anterior base of caudal process and projects forward near valve ventral margin. Adductor muscle scar prominent, consisting of about 18–24 sub-parallel, radiating and alternating ridges and furrows arranged in a double series feather-like pattern. Reticulation covers external valve surface, including ventral part of bulb; consists of elongate polygons (muri 80–200 μm wide; fossae 100–500 μm wide), many hexagonal. Posteriorly and centrally in some large valves some polygons are extremely elongate, almost resembling corrugation. Centrodorsally in some valves 3–5 pore-bearing tubercles (diameter about 100 μm) occur atop the muri. In other valves 8–10 pore-bearing tubercles (diam-

eter about 100 µm) occur atop the muri arranged in two rows ventrally. During ontogeny, size of bulb becomes relatively smaller and valve shape changes from almost circular to ovoid and density of reticulations decreases.

Remarks.—*Bolbozoe polonica* Gürich, 1896 was established on a single specimen, assumed lost during World War II. Gürich's (1896) description and drawings indicate that the species had two sulci, a feather-like adductor muscle scar and reticulated ornament like that of *P. bohemica* and it is probably its junior synonym.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the upper part of the Wenlock and lower part of the Ludlow series of the Czech Republic, France, Sardinia (Perrier et al. 2011), England and Wales (Perrier et al. 2019).

Suborder Entomozocopina Gründel, 1969

Superfamily Entomozoidea sensu Entomozoacea Příbyl, 1951

1951 Entomozoacea nov. nom.; Příbyl 1951: 103.
2019 Entomozoidea; Perrier et al. 2019: 51.

Remarks.—“Entomozoaceans” (= Entomozoacea sensu Příbyl, 1951) have long been regarded as myodocopes (e.g., Sylvester-Bradley 1961), but by their signature “finger-print” ornament and in generally lacking a rostrum and rostral incisure they are considered to be the most atypical of all of the ostracod groups that have traditionally been assigned to the Myodocopa (see discussion in Siveter and Vannier 1990; Kornicker and Sohn 2000). However, the discovery of a Palaeozoic myodocope with preserved soft-parts, *Colymbosathon eplecticos* Siveter Sutton, Briggs, and Siveter, 2003 from the Silurian of England, has yielded new evidence to support a myodocope affinity for “entomozoaceans”. *Colymbosathon eplecticos* has a very similar valve outline and lobal/sulcal morphology to that of *Richteria migrans* and both taxa lack a rostrum and rostral incisure.

Herein the concept of the “Entomozoacea” is used in its widespread and traditional sense, even though the type species of the type genus of the “Entomozoidae”, namely *Entomozoe tuberosa* (Jones, 1861) from the Silurian of Scotland, is known to be an entirely different form of ostracod (assigned to the myodocope superfamily Bolbozoidea Bouček, 1936; see Siveter and Vannier 1990 for discussion and recommendations).

Family Entomozoidae Příbyl, 1951

Emended diagnosis.—“Entomozoaceans” with bean-shaped or symmetrically to asymmetrically ovoid lateral outline, rarely with a weak anteroventral indentation; dorsal margin curved or straight, shorter than carapace length. Adductor sulcus concave toward anterior end or straight; posteroventral sulcus present (subfamily Bouciinae) or absent. Adductor muscle scar characteristically a smooth patch (in some cases composed of many tiny scars), a pit or absent. Ornament

usually present, consisting of transverse, longitudinal, spiral, concentric or irregular pattern of ribs, in some cases reduced to minute spines and reticulations (modified after Perrier et al. 2019).

Genus *Richteria* Jones, 1874

Type species: *Cypridina serrate-striata* Sandberger, 1845; by subsequent designation by Kegel 1934: 413. Lower Famennian, Upper Devonian of Germany.

Stratigraphic and geographic range.—*Richteria* is known from the Silurian and Devonian. Supposed records of its occurrence in younger and older strata (all the unrevised “*Entomis*” species, see Bassler and Kellett 1934) have not been confirmed by the present authors. The genus is known from Europe (Czech Republic, Germany, Poland, Belgium, France, Italy, UK; Perrier et al. 2007), Arctic Russia (Perrier et al. 2014a), Central Asia, and China (Perrier et al. 2007).

Richteria migrans (Barrande, 1872)

Fig. 2F.

- 1872 *Entomis migrans* Barr.; Barrande 1872: 514, pl. 24: 10–14, pl. 27: 22.
- 1873 *Entomis migrans* Barr., 1872; Jones 1873: 416.
- 1896 *Entomis migratoria* n. sp.; Gürich 1896: 374.
- 1899 *Entomis migrans* Barr.; Canavari 1899: 151.
- 1900 *Entomis migrans* Barr.; Canavari 1900: 193, pl. 25: 1, 2.
- 1900 *Entomis Lamarmorai* n. f.; Canavari 1900: 195, pl. 25: 3–5.
- 1900 *Entomis* n. f.?; Canavari 1900: 196, pl. 25: 6.
- 1900 *Entomis Meneghinii* n. f.; Canavari 1900: 196, pl. 25: 7–11.
- 1934 *Entomis (Richteria) migrans* Barr.; Kegel 1934: 413.
- 1934 *Entomis migrans* Barrande; Bassler and Kellett 1934: 304 (pars).
- 1936 *Entomis (Richteria) migrans* Barrande, 1872; Bouček 1936: 57, pl. 6: 5, 6; text-fig. 2a, 2b.
- 1937 *Entomis (Richteria) migrans* Barrande; Chaubet 1937: 186, pl. 4: 8a–c.
- 1951 *Entomozoe (Richteria) migrans* (Barrande); Příbyl 1951: 11, pl. 1: 4.
- 1952 *Entomozoe migrans* Barrande, 1872; Kupfahl 1952: 178.
- 1958 *Entomozoe (Richteria) migrans* (Barrande); Pokorný 1958: 311, text-fig. 1032.
- 1961 *Entomozoe meneghinii* Canavari; Sylvester-Bradley 1961: 389, text-fig. 312.2g–j.
- 1961 *Richteria lamarmorai* Canavari; Sylvester-Bradley 1961: 390, text-fig. 313.1a–e.
- 1984 “*Entomis*” *migrans* Barrande; Siveter 1984: 78, pl. 2: 12, 13, text-fig. 3.
- 1988 *Richteria migrans* (Barrande, 1872); Příbyl 1988: 113, text-fig. 5.1.
- 1990 “*Entomis*” *migrans*; Siveter and Vannier 1990: 64, text-fig. 23.
- 1995 “*Entomis*” aff. *lamarmorai* Canavari, 1900; Kříž and Bogolepova 1995: 580, pl. 70: 12.
- 2000 *E. migrans* Barrande, 1872; Groos-Uffenorde et al. 2000: text-fig. 2.
- 2003 *Richteria migrans taimyrica* Abushik, subsp. nov.; Abushik et al. 2003: 122, pl. 27: 1, 2.
- 2007 *Richteria migrans* (Barrande, 1872); Perrier et al. 2007: 156, text-figs. 6–10.
- 2009 “*Entomis*” *migrans* Barrande, 1872; Siveter 2009: pl. 9: 14.
- 2009 *Richteria migrans* (Barrande, 1872); Gnoli et al. 2009: pl. 1: 1–11.
- 2012 *Richteria migrans* (Barrande, 1872); Perrier 2012: text-fig. 7G, H.
- 2013 *Richteria migrans*; Perrier and Siveter 2013: text-fig. 22.6D.

2014a *Richteria migrans* (Barrande, 1872); Perrier et al. 2014a: 56, pl. 1: A–N., text-figs. 2, 3.

2019 *Richteria migrans* (Barrande, 1872); Perrier et al. 2019: pl. 12: 1–3, 11, 12.

Lectotype: An incomplete right valve; on slab NM-L 22944; subsequently designated by Pribyl (1951: 111); figured by Barrande (1872: pl. 24: 12–14); Bouček (1936: text-fig. 2a); Perrier et al. (2007: text-fig. 6a, b).

Type locality: Former Dvorce quarry (today Podolí swimming pool), Podolí district of Prague, Czech Republic.

Type horizon: Kopanina Formation, Ludlow Series.

Material.—Tens of valves, from two localities (Wielki and Niestachów), Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 1.4, H = 1.1 (ZPAL O.63/27) to L = 3.05, H = 2 (ZPAL O.63/28). *Lectotype*: L = 2.25, H = 1.50 (NM-L 22944). L/H ratio and adductor muscle position for seven specimens from two localities (Fig. 4).

Description.—Valve large, bean-shaped in lateral outline. Greatest length is slightly above mid height; greatest height is at the adductor sulcus. Dorsal margin shorter than valve length. Preadductorial and postadductorial areas very slightly curved dorsally; ventral, anterior and posterior margins convex. Right valve slightly larger and overlaps left valve along entire free margin. Contact list in left valve is narrow, ornamented by very fine striation. Anterior valve margin shows a faint notch in some large specimens. Adductor sulcus long, deep, crescent shaped, extends two-thirds of valve height from in front of mid length near dorsal margin to below the preadductorial node. A simple elliptical adductor muscle scar is present at the slightly widened ventral extremity of the sulcus. Dorsal part of sulcus is deeper and narrower, ending at a small “bridge” (height about 50 μ m) connecting preadductorial and postadductorial areas. Preadductorial node is generally unornamented but can be weakly ribbed, and is less developed in some specimens. External valve surface has up to 25 longitudinal ribs, including in some specimens short, intercalated and bifurcated ribs. The alignment of ribs is not disturbed by the adductor sulcus. Ribs merge posteriorly, converge on a triangular smooth area anteriorly and curve slightly away from the valve margin ventrally. Some specimens show what seems to be very weak secondary reticulate ornament between the ribs. No evidence for presence of hinge structure; conjoined open valves are consistently connected along dorsal margin.

Remarks.—From its description and occurrence *Entomis migratoria* Gürich, 1896 (nomen nudum), is likely to be conspecific with *Richteria migrans*.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the upper part of the Ludlow Series in the Czech Republic, France, Sardinia, Poland, Central Asia, Arctic Russia, England, Wales, and possibly Germany and Sweden (see Perrier et al. 2007, 2014a, 2019).

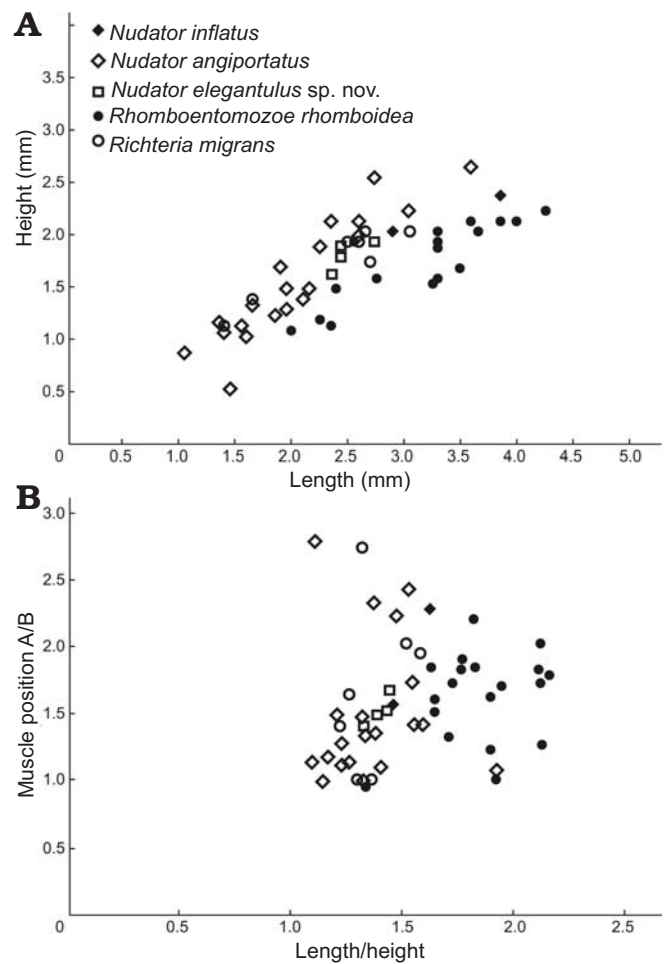


Fig. 4. Valve length/height plot (A) and position of the adductor muscle scar (A/B, where A and B are the distance between the muscle scar and the posterior end of the valve and the ventral margin, respectively) against length/height (B) of complete specimens of entomozoid species from the Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Genus *Nudator* Perrier, Siveter, Williams, and Palmer, 2019

Type species: *Nudator inflatus* Perrier, Siveter, Williams, and Palmer, 2019. Ludlow Series, Silurian, Powys, Wales, UK.

Species included: Type species and *Nudator angiportatus* Perrier, Siveter, Williams, and Palmer, 2019, *Nudator artumatus* Perrier, Siveter, Williams, and Palmer, 2019, *N. elegantulus* sp. nov. and *Nudator* sp. nov. A of Perrier et al. 2019.

Emended diagnosis.—Entomozoidae with bean-shaped to ovoid lateral outline, dorsal margin slightly rounded. Adductor sulcus narrow, well developed, extending up to 3/4 of valve height. Prominent postadductorial node present in type species only. Faint notch in anterior valve margin. Valve smooth or bearing minute ornament (modified after Perrier et al. 2019).

Remarks.—*Nudator* differs from other entomozoid genera in having unornamented or very faintly ornamented valves. *Sineruga* Perrier, 2012 and *Nudator* differ mainly in valve outline in lateral view.

Stratigraphic and geographic range.—Wenlock and Ludlow Series, Silurian of England, Wales (Perrier et al. 2019), Poland, and possibly France (Perrier et al. 2019).

Nudator inflatus Perrier, Siveter, Williams, and Palmer, 2019

Fig. 2I, J.

2019 *Nudator inflatus* sp. nov.; Perrier et al. 2019: 43, pl. 13: 1–14.

Holotype: A laterally compressed right valve (OUMNH 35000); Perrier et al. (2019: pl. 13: 4, 5).

Type locality: Radnorshire (loc. 10 of Perrier et al. 2019), Powys, Wales, UK.

Type horizon: “*nilssoni-scenicus* blue Mudstones” of Kirk (1947), *Cucullograptus (Lobograptus) scanicus* Biozone, Gorstian Stage, Ludlow Series.

Material.—Tens of valves, from two localities (Wielki and Niestachów), Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 2.9, H = 2 (ZPAL O.63/9, Fig. 2I, J) to L = 3.85, H = 2.35 (ZPAL O.63/29). Holotype: L = 2.00/H = 1.70 (OUMNH 35000). L/H ratio and adductor muscle position for two specimens from two localities (Fig. 4).

Description.—Valve large, bean-shaped in lateral outline. Greatest length is just above mid height; greatest height is at the adductor sulcus. Valve outline in lateral view is almost straight dorsally, gently curved ventrally, posteriorly and anteriorly is evenly rounded. Valve surfaces gently inflated overall, lacking distinct or discrete lobes. Anterior valve margin in some cases has a faint indentation. Adductor sulcus narrow, occurs just in front of mid-length, extends almost vertically from dorsal margin to just below mid-height ending with the adductor muscle spot. Prominent postadductor tubercle variable in shape and size, diameter 15–25% of valve length. Adductor sulcus generally curves around the front of the tubercle, in some specimens the sulcus appears to bifurcate and border both sides of tubercle. A simple elliptical adductor muscle scar occurs at the slightly widened ventral extremity of the sulcus. Valves smooth. No evidence for presence of hinge structure, but open valves in “butterfly position” are consistently to be connected along dorsal margin.

Remarks.—*Nudator inflatus* is distinguished from all other *Nudator* species by the presence of its large postadductor node.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the Gorstian Stage, Ludlow Series of England and Wales (Perrier et al. 2019).

Nudator angiportatus Perrier, Siveter, Williams, and Palmer, 2019

Fig. 2G, H.

2019 *Nudator angiportatus* sp. nov.; Perrier et al. 2019: 44, pl. 14: 1–15.

Holotype: A laterally compressed left valve (OUMNH 35267); Perrier et al. (2019: pl. 14: 5–8, 14, 15).

Type locality: Loc. 56 of Perrier et al. (2019), Long Mountain, Wales, UK.

Type horizon: Lower part of the Irfon Formation, *Cucullograptus (Lobograptus) scanicus* Biozone, Gorstian Stage, Ludlow Series.

Material.—Tens of valves, from two localities (Wielki and Niestachów), Holy Cross Mountains, Poland; Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 1.05, H = 0.85 (ZPAL O.63/30) to L = 3.6, H = 2.6 (ZPAL O.63/8, Fig. 2H). Holotype: L = 2.70, H = 2.35 (OUMNH 35267). L/H ratio and adductor muscle position for 19 specimens from two localities (Fig. 4).

Description.—Valve large, bean-shaped in lateral outline. Greatest length is just above mid height; greatest height just in front of the adductor sulcus at the site a small anterodorsal inflation of the carapace. Valve outline in lateral view is slightly concave dorsally, gently curved ventrally, posteriorly is evenly rounded, anteriorly above mid-height is more sharply rounded, and anteriorly has a weak indentation. Valve surfaces gently inflated overall, lacking distinct or discrete lobes. Adductor sulcus narrow, occurs just in front of mid-length, originates just posteriorly of the small anterodorsal protuberance and curves forward from dorsal margin to just below mid-height ending with the adductor muscle spot. Anterior-anteroventral valve margin appears slightly concavely indented in lateral view in some specimens and has an apparent incisure (gape). A simple elliptical adductor muscle scar occurs at the slightly widened ventral extremity of the sulcus. Valves smooth. No evidence for presence of hinge structure, but conjoined open valves but open valves in “butterfly position” are connected along dorsal margin. During ontogeny valve shape changes from sub-triangular to more rounded/ovoid.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the Wenlock and Ludlow series of England and Wales (Perrier et al. 2019).

Nudator elegantulus sp. nov.

Figs. 5–7.

ZooBank LSID: urn:lsid:zoobank.org:act:01C7B8C0-33F5-4067-939B-1568F17AB8C9

Etymology: From Latin *elegantulus*, fine, elegant.

Holotype: A laterally compressed left valve (ZPAL O.63/15); Fig. 5C.

Type locality: Niestachów, Holy Cross Mountain, Poland.

Type horizon: Niewachłów Beds, Lower part of the Ludlow Series, based on graptolites, *Cucullograptus (Lobograptus) scanicus* Biozone.

Material.—Four valves from two localities (Wielki and Niestachów), Holy Cross Mountain, Poland, Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 2.35, H = 1.6 (ZPAL O.63/13, Fig. 5A) to L = 2.75, H = 1.9 (holotype,

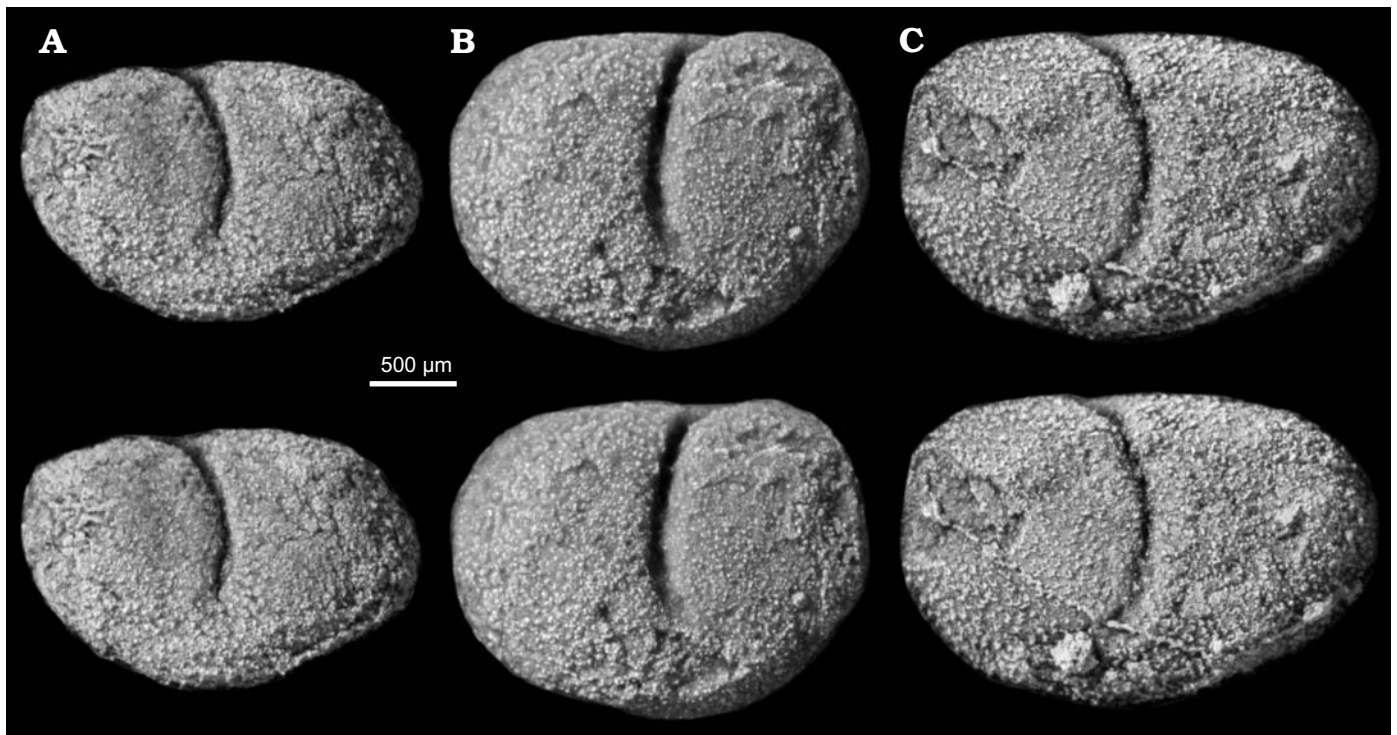


Fig. 5. Myodocope ostracod *Nudator elegantulus* sp. nov., Holy Cross Mountains, Poland; Ludlow Series, Silurian. **A.** ZPAL O.63/13, left valve. **B.** ZPAL O.63/14, right valve. **C.** Holotype ZPAL O.63/15, left valve. Light stereo-pair photographs in lateral view (of silicone casts of external moulds).

ZPAL O.63/15, Fig. 5C). L/H ratio and adductor muscle position for four specimens from two localities (Fig. 4).

Diagnosis.—*Nudator* with ornament consisting of very delicate reticulation to backward oriented “chevrons”, excluding the triangular smooth area in front of carapace.

Description.—Valve large, bean-shaped in lateral outline. Greatest length at mid height; greatest height at the level of the adductor sulcus. Valve outline in lateral view is straight dorsally, gently curved ventrally and rounded posteriorly and anteriorly. Valve surfaces gently inflated overall, lacking distinct or discrete lobes. Adductor sulcus narrow, occurs just in front of mid-length, originates in the first third of the dorsal margin to just below mid-height ending with the adductor muscle spot. A simple elliptical adductor muscle scar occurs at the slightly widened ventral extremity of the sulcus. The triangular smooth area in front of the carapace has a slightly negative relief and covers an area representing 1/4 of the maximum length and 1/3 of the maximum height. The valve surface is ornamented apart from the anterior triangular smooth area. This ornament consists mainly of small backward oriented “chevrons” that are possibly the remains of a delicate reticulation (Fig. 6). There are about 200–250 chevrons per mm², each about 20–50 μm across. During ontogeny, valve lateral outline changes from rounded to more ovoid.

Remarks.—*Nudator elegantulus* differs from *N. angiportatus* by its more distinct triangular smooth anterior area and by its ornament.

Stratigraphic and geographic range.—Known only from the type locality.

Family Rhomboentomozoidae Gründel, 1962

Type genus: *Rhomboentomozoe* Přibyl, 1951.

Emended diagnosis.—Left and right valves of apparently equal size. Lateral outline “triangular” to subquadrate, sometimes broadly egg-shaped. Straight dorsal margin usually well developed, sometimes corresponding to greatest carapace length; cardinal angles distinct or rounded. Sulcus always present, usually strongly developed, often extending across more than half of valve surface. Muscle attachment area absent or represented by a simple elliptical area at the ventral end of the sulcus. Spines may be developed near margin. Valve ornament absent or consisting of longitudinal ribs arranged parallel to dorsal margin; some outer ribs may be parallel to ends of valve (modified after Gooday 1983).

Remarks.—In addition to the type genus, conventionally the family includes *Franklinella* Stewart and Hendrix, 1945, *Pseudoentomozoe* Přibyl, 1951, *Paraungerella* Wang, 1986, *Yulinentomozoe* Wang, 1989, and possibly *Vltavina* Bouček, 1936. It is distinguished from the Entomozoidae by the generally triangular to subquadrate lateral outline and long, straight dorsal margin of the valves.

Subfamily Rhomboentomozoinae Gründel, 1962

Genus *Rhomboentomozoe* Přibyl, 1951

Type species: *Rhomboentomozoe rhomboidea* (Barrande, 1872), des-

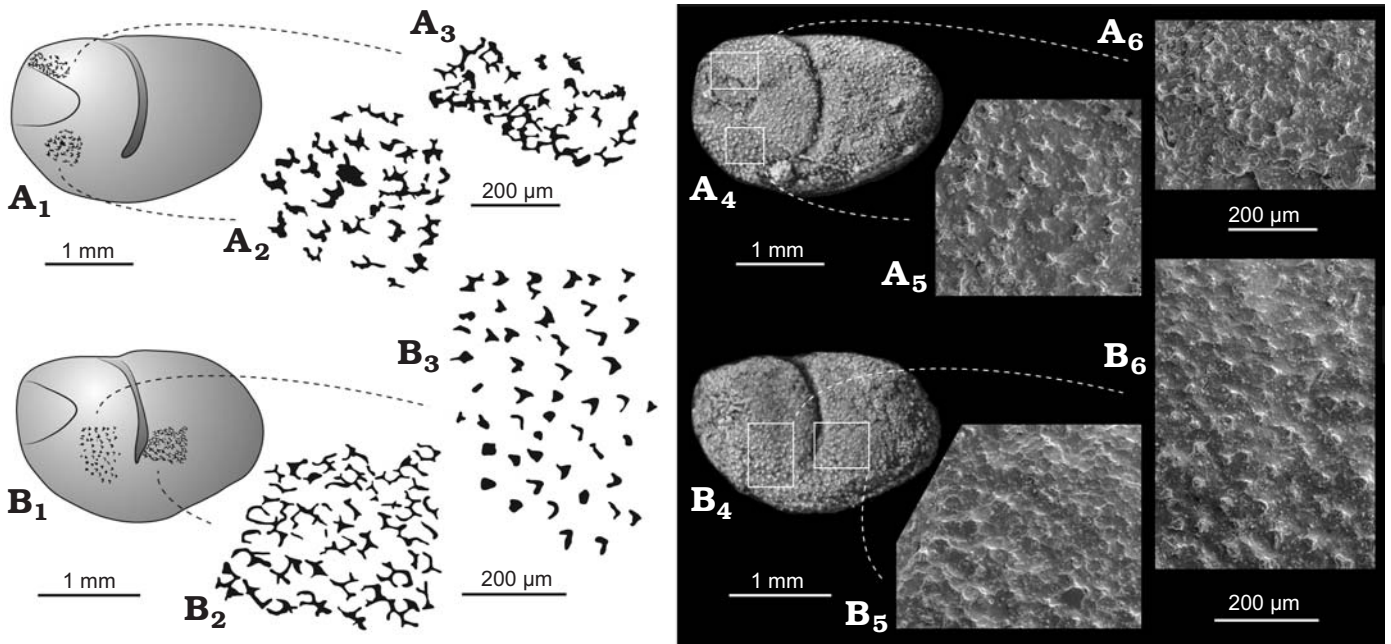


Fig. 6. Myodocope ostracod *Nudator elegantulus* sp. nov., details of the ornament, Holy Cross Mountains, Poland; Ludlow Series, Silurian. **A.** Holotype ZPAL O.63/15. Left valve (A₁): detail of the ornament anterodorsally (A₃, A₆); detail of the ornament anteroventrally (A₂, A₅). **B.** ZPAL O.63/13. Left valve (B₁): detail of the ornament anteriorly (B₃, B₆); detail of the ornament posterior to the adductor sulcus (B₂, B₅). A₄, B₄, light photographs; A₅, A₆, B₅, B₆, SEM photographs; A₁–A₃, B₁–B₃, explanatory drawings; all lateral views of silicone casts of external moulds.

ignated by Přibyl (1951: 111). Upper Silurian of Kozel near Beroun, Bohemia, Czech Republic.

Species included: Type species and possibly *Rhombentomozoe?* sp. of Wang 2009.

Emended diagnosis.—Same as species.

Remarks.—Přibyl (1951: 115) assigned *Isochilina armata pygmaea* Ruedemann, 1901, from the Upper Ordovician Mohawkian of New York State, USA, to *Rhombentomozoe*. Following Přibyl’s (1951) opinion, the Treatise on Invertebrate Paleontology (Sylvester-Bradley 1961: Q390) lists one “myodocopid” genus from the Ordovician, namely *Rhombentomozoe* Přibyl, 1951. This supposed Ordovician record of *Rhombentomozoe* is not accepted herein. *Isochilina armata pygmaea* is clearly very different from the Bohemian Silurian type-species of *Rhombentomozoe*, namely *Cryptocaris rhomboidea* Barrande, 1872. The specimen from China of *Rhombentomozoe?* sp. of Wang 2009 (15: pl. 1: 9) is incomplete and cannot be assigned to *Rhombentomozoe* with certainty. If it is a *Rhombentomozoe* species it would extend the range of the genus into the Lower Devonian (Pragian).

Siveter and Vannier (1990) considered that the genus *Rhombentomozoe* is, “at best, a very atypical myodocope and most likely belongs to another group”. However, evidence from new material (e.g., muscle scar, rostrum) indicates its myodocope affinities. The species from Sardinia described by Canavari (1900: 201, pl. 26: 3–5) as *Entomozoe preriodes* shows marked resemblance to *R. rhomboidea*.

Stratigraphic and geographic range.—Ludlow Series, Silurian of the Czech Republic (Barrande 1872) and Poland,

and possibly Sardinia (Canavari 1900). Also possibly Pragian, Lower Devonian of China (Wang 2009).

Rhombentomozoe rhomboidea (Barrande, 1872)

Figs. 7, 8.

1872 *Cryptoc. ? rhomboidea* Barr.; Barrande 1872: 464, pl. 31: 14, 15.
1936 *Entomis (Richteria) rhomboidea* (Barrande, 1872); Bouček 1936: 58, pl. 6: 3, 4.

1951 *Rhombentomozoe rhomboidea* (Barrande); Přibyl 1951: 15, pl. 1: 2, pl. 2: 5.

1954 *Rhombentomozoe rhomboidea* (Barrande); Pokorný 1954: 462, text-fig. 680.

1958 *Rhombentomozoe rhomboidea* (Barrande); Pokorný 1958: 311, text-fig. 1035.

1960 *Rhombentomozoe rhomboidea* (Barrande); Zanina and Polenova 1960: 331, text-fig. 834.

1961 *Rhombentomozoe rhomboidea* (Barrande); Sylvester-Bradley 1961: 390, text-fig. 315.2.

1962 *Rhombentomozoe*; Gründel 1962: 1193, 1198, text-fig. 9.

1988 *Rhombentomozoe rhomboidea* (Barrande); Přibyl 1988: 114, text-fig. 5.2.

1991 *Rhombentomozoe rhomboidea* (Barrande); Stupnicka et al. 1991: 391.

1994 *Rhombentomozoe rhomboidea* (Barrande, 1872); Whatley et al. 1994: 351.

Holotype: A carapace in butterfly position (NM-L 23322; CE 1222, Inv. No. 1648); Barrande (1872: pl. 31: 14, 15) and Bouček (1936: pl. 6: 4); herein Fig. 8G.

Type locality: Kozel, 3 km east of Beroun, Bohemia, Czech Republic.

Type horizon: Lower part of the Kopanina Formation, Ludlow Series, Silurian, horizon with the trilobite “*Cromus*” *beaumonti*.

Material.—Type specimens plus tens of valves from two

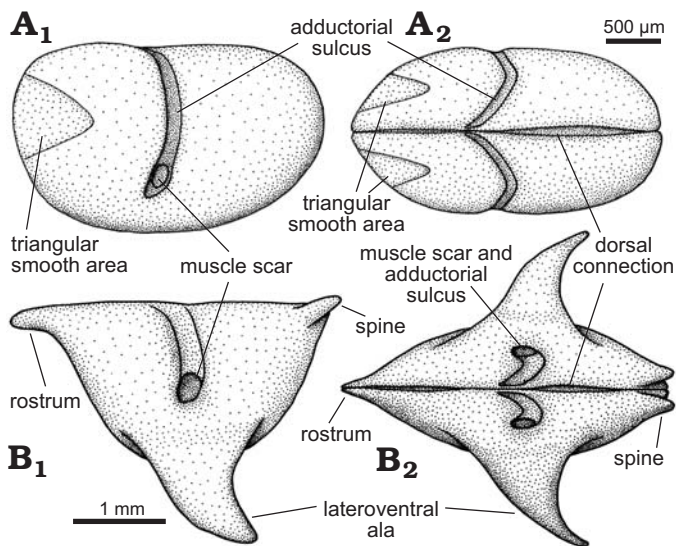


Fig. 7. Idealized reconstructions and terminology of *Nudator elegantulus* sp. nov. (A) and *Rhomboentomozeo rhomboidea* (B) from the Holy Cross Mountains, Poland; Ludlow Series, Silurian. In left lateral (A₁, B₁) and dorsal (A₂, B₂) views.

localities (Widełki and Niestachów), Holy Cross Mountain, Poland, Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 2, H = 1.05 (ZPAL O.63/16, Fig. 8A) to L = 4.25, H = 2.2 (ZPAL O.63/31). Holotype: L = 2.07, H = 1.67 (NM-L 23322; CE 1222, Inv. No. 1648). L/H ratio and adductor muscle position for 19 specimens from two localities (Fig. 4).

Emended diagnosis.—Entomozoidae with a triangular lateral valve outline, and a large, posterolaterally projecting ventral ala. Dorsal margin straight or slightly concave, ventral margin gently curved. Anterior and posterior cardinal corners pointed. Adductor sulcus narrow, well developed, extending up to 1/2 of valve height, ending ventrally at a simple muscle spot. Faint notch in anterior valve margin. Valves smooth or weakly ribbed (modified after Gooday 1983).

Description.—Valve large, having an inverted triangular lateral outline. Maximum length at the dorsal margin; maximum height at the level of the lateroventral ala. Valve lateral outline is straight to weakly concave dorsally, gently curved posteriorly and anteriorly and more strongly curved ventrally. Valve surface is gently inflated overall. Adductor sulcus narrow, concave forward, occurs just in front of mid-length and extends from the dorsal margin to just below mid-height ending with a simple adductor muscle

spot. The anterodorsal frontal projection resembles the straight rostrum of Recent halocyprid ostracods, and bears a well-developed notch on its valve margin and very weakly developed rostral incisure. Immediately adjacent to the posterodorsal cardinal corner a short posterodorsally projecting spine extends just above valve margin. Lateroventral ala is large, projects posteroventrally from the ventral part of the valve; in lateral view its anterior margin is convex anteriorly, its posterior margin is concave. During ontogeny, the ala becomes larger and projects more posteroventrally, and the rostrum and posterodorsal spine become more distinct.

Remarks.—The type specimen from Bohemia (Fig. 8G) was originally described as a phyllopod by Barrande (1872: 464, pl. 31: 14, 15). The Polish material is very similar to this type specimen, differing only by its seemingly flatter ala. The unique ribbed specimen figured by Bouček (1936: pl. 6: 3) and redrawn by Přibyl (1951: pl. 1: 2) is one of a kind: it has ribs that are absent in both the type specimen and the Polish material. More material would be needed to determine if it belongs to a separate species.

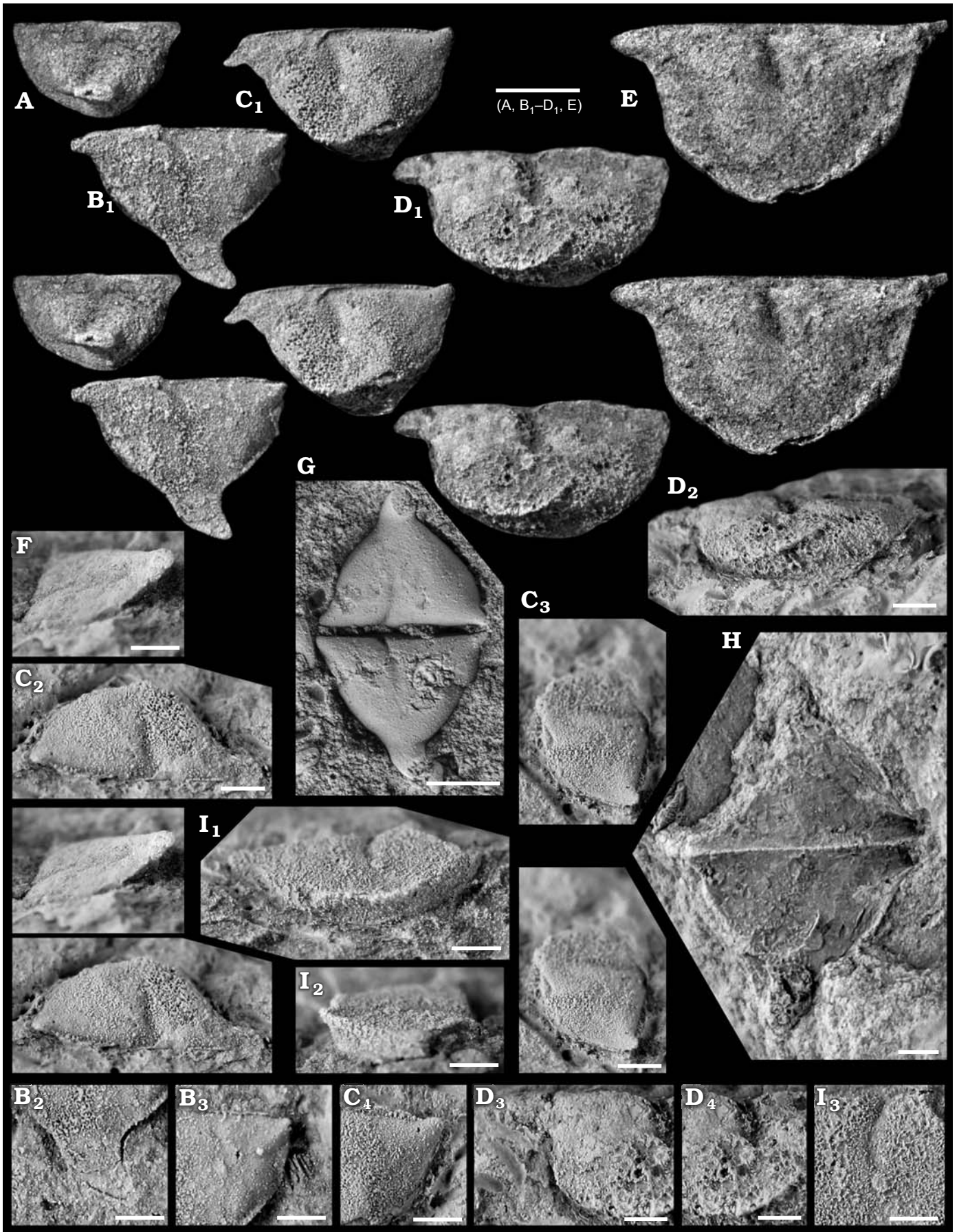
Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the Ludlow Series, Silurian of the Czech Republic: rarely in the lower part of the Kopanina Formation, “*Cromus*” *beaumonti* horizon, together with *Richteria migrans*, *Vltavina perneri* and other ostracodes and trilobites. Praha-Podolí (old quarry Dvorce, now the swimming pool) and Kozel (below Listice) near Beroun (Barrande 1872).

Superfamily Cypridinoidea sensu Cypridinacea Baird, 1850

Family Cypridinidae Baird, 1850

Remarks.—The Silurian genera *Calocaria* Vannier, 1987 and *Silurocypridina* Perrier, Vannier, and Siveter, 2011 are more similar in carapace morphology to typical Recent cypridinids than to typical living cylindroleberidid or sarsiellid myodocopids (see e.g., Kornicker 1975, 1981; Horne et al. 2002). The Silurian genera differ from typical cylindroleberidids in their less elongate shape. They are like sarsiellids in general shape but lack the caudal process characteristic of that family. Moreover, typically, the females of sarsiellids lack a well-developed rostrum and rostral incisure, thus contrasting with all known specimens of the two Silurian genera, in which those features are prominently developed. Verification of the familial assignment of the two Silurian genera depends on knowledge of their soft-part morphology.

Fig. 8. Myodocope ostracod *Rhomboentomozeo rhomboidea* (Barrande, 1872), Holy Cross Mountains and Bohemia; Ludlow Series, Silurian. **A.** ZPAL O.63/16, left valve with incomplete ala, in lateral view. **B.** ZPAL O.63/17, left valve, in lateral view (B₁), detail of the ala (B₂), detail of the posterodorsal part of the valve (B₃). **C.** ZPAL O.63/18, left valve with incomplete ala, in lateral (C₁), dorsal (C₂), and posterior (C₃) views, detail of the posterodorsal part of the valve (C₄). **D.** ZPAL O.63/19, left valve with incomplete ala, in lateral (D₁), ventral (D₂), and anterior (D₃) views, detail of the rostrum (D₄), detail of the adductor muscle scar (D₅). **E.** ZPAL O.63/20, left valve with incomplete ala, in lateral view. **F.** ZPAL O.63/21, right valve, in anterior view showing the ala. **G.** Holotype, L23322, open carapace in “butterfly” position. **H.** ZPAL O.63/22, open carapace in “butterfly” position. **I.** ZPAL O.63/23, right valve, in ventral view showing the proximal part of the ala on the ventrolateral part of the valve (I₁), frontal view (I₂), detail of the muscle scar (I₃) view. All light photographs; A, B₁, C₁, C₃, D₁, E, F, stereo-pairs. A, E, F, silicone casts of external moulds; B–D, G–I, internal moulds. Scale bars: A, B₁, C₁, D₁, E, G, 1 mm; B₂, B₃, C₂–C₄, D₂–D₄, F, H, I, 500 μm.



Stratigraphic and geographic range.—Silurian to Recent; possibly also Ordovician (*Myodoprimgenia fistuca* from the Ashgill of South Africa; Gabbott et al. 2003).

Genus *Silurocypridina* Perrier, Vannier, and Siveter, 2011

Type species: *Silurocypridina retroreticulata* Perrier, Vannier, and Siveter, 2011. Upper Silurian of France.

Species included: *Silurocypridina variostrata* Perrier, Vannier, and Siveter, 2011 and *Silurocypridina calva* Perrier, Vannier, and Siveter, 2011.

Remarks.—Some of the Silurian myodocopid material from Europe that was provisionally referred to as “Cypridinid” and “cypridinid-like” by Siveter et al. (1987, 1991), an assignment supported by Kornicker and Sohn (2000), was subsequently assigned to *Silurocypridina* (Perrier et al. 2011). The tiny crescent-shaped adductor muscle scar of *Silurocypridina* is similar to that of the Silurian myodocope *Calocaria* but has no counterpart in other fossil or extant cypridinids. The simple dome-like valve morphology of *Silurocypridina* is similar to that of several late Palaeozoic and Mesozoic myodocopid genera (see Kornicker and Sohn 2000; e.g., *Eocypridina* Kesling and Ploch, 1960, see Wilkinson et al. 2004). Without information about their soft-anatomy, the classification of such relatively featureless cypridinaceans will remain unresolved.

Stratigraphic and geographic range.—Upper part of the Silurian; France, Czech Republic, England, Wales, Poland, and possibly Sardinia (see Perrier et al. 2011, 2019).

Silurocypridina retroreticulata Perrier, Vannier, and Siveter, 2011

Fig. 2K.

- 1987 “Cypridinid” gen. et sp. nov. A; Siveter et al. 1987: pl. 84: 1, 3, 5, pl. 87: 1, 5.
 1991 “Cypridinid” gen. et. sp. nov. A of Siveter et al. 1987; Siveter et al. 1991: pl. 1: 4, pl. 2: 10.
 1992 “Cypridinid” sp. nov. A of Siveter et al. 1987; Vannier and Abe 1992: text-fig. 2B.
 1995 “Cypridinid” sp. nov. A of Siveter et al. 1987; Vannier and Abe 1995: text-fig. 16A, B.
 2000 “Cypridinid” Genus A, sp. A, Siveter et al. 1987; Kornicker and Sohn 2000: 21.
 2011 *Silurocypridina retroreticulata* sp. nov.; Perrier et al. 2011: pl. 4: 1–7, text-figs. 6, 8A, 9H.
 2012 *Silurocypridina retroreticulata* Perrier, Vannier and Siveter, 2011; Perrier 2012: text-fig. 7E.
 2019 *Silurocypridina retroreticulata* Perrier, Vannier and Siveter, 2011; Perrier et al. 2019: pl. 17: 6, 7, 12, 13.

Holotype: A laterally compressed right valve (FSL 710505); Perrier et al. (2011: pl. 4: 4, text-fig. 9H).

Type locality: Les Buardières, Mayenne, France (Perrier et al. 2011).

Type horizon: La Lande Murée Formation; the type horizon is within the range of the upper part of the Wenlock Series to middle part of the Ludlow Series, and currently cannot be further resolved.

Material.—Three valves, all from locality Niestachów, Holy Cross Mountain, Poland, Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 2.85, H = 2.55 (ZPAL O.63/10, Fig. 2K). Holotype: L = 3.46, H = 2.53 (FSL 710505). L/H ratio and adductor muscle position for one specimen (Fig. 3).

Description.—Valve dome-like, with nearly ovoid lateral outline; hinge short, located dorsally. Rostrum well developed, is about 15% of valve length, protrudes distinctly forward beyond the anteroventral margin of the valve. Rostral incisure well developed, rounded or angular in lateral outline. Adductor muscle scar is small, sited subcentrally, crescent-shaped convex anteriorly. Behind the adductor muscle scar and ventrally valves are reticulate, consisting of polygons with muri 50–100 µm wide and sola 100–250 µm wide. Anterodorsal part of valve (some 25% of lateral valve area) lacks ornament. A fine, narrow ridge occurs along ventral margin of the valve.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the Silurian of France, England and Wales (see Perrier et al. 2011, 2019).

Silurocypridina calva Perrier, Vannier, and Siveter, 2011

Fig. 2L.

- 1899 *Cypridina* sp. aff. *C. Tosterupi* Mob; Canavari 1899: 152.
 1900 *Cypridina tyrrhenica* n.f.; Canavari 1900: 204, pl. 26: 10–12 (specimens I91, I92).
 1987 “Cypridinid” sp.; Siveter et al. 1987: 801, pl. 85: 1, 2, 4, 5.
 1987 “Cypridinid” sp. nov. B; Siveter et al. 1987: 805, pl. 87: 2–4.
 1990 “Cypridinid” sp. nov.; Siveter and Vannier 1990: 64, text-fig. 23 (number 6).
 1991 “Cypridinid” sp.; Siveter et al. 1991: 157, pl. 1: 3.
 1992 “Cypridinid”-like myodocopes; Vannier and Abe 1992: 489, 509, pl. 2: 2, text-fig. 1.
 1992 “Cypridinid” sp.; Vannier and Abe 1992: 494, text-fig. 6I, J.
 2000 “Cypridinid” Genus B, sp. B of Siveter et al. 1987; Kornicker and Sohn 2000: 21.
 2003 “Cypridinid” sp. nov. B of Siveter et al.; Gabbott et al. 2003: 157, text-fig. 4B.
 2009 “*Cypridinid*” gen. and sp. nov.; Gnoli et al. 2009: 1, text-figs. 12–22.
 2011 *Silurocypridina calva* sp. nov.; Perrier et al. 2011: pl. 5: 1–9, 12–14, text-figs. 6, 8A, 10.
 2012 *Silurocypridina calva* Perrier, Vannier and Siveter, 2011; Perrier 2012: text-fig. 7F.
 2019 *Silurocypridina calva* Perrier et al., 2011; Perrier et al. 2019: pl. 17: 1–5, 8–11.

Holotype: A three-dimensionally preserved left valve (LPB 18926); Perrier et al. (2011: pl. 5: 8, 9).

Type locality: Les Chevrolières, near St Denis-d’Orques, Sarthe, France (Perrier et al. 2011).

Type horizon: Le Val Formation; the type horizon is within the upper part of the Ludlow Series or lower part of the Pridoli Series, and currently cannot be further resolved.

Material.—Tens of valves, from two localities (Widełki and

Niestachów), Holy Cross Mountain, Poland, Ludlow Series, Silurian.

Measurements (in mm).—Size range: L = 2, H = 2.1 (ZPAL O.63/32) to L = 4, H = 3.15 (ZPAL O.63/33). Holotype: L = 2.38, H = 1.48 (LPB 18926). L/H ratio and adductor muscle position for seven specimens from two localities (Fig. 3).

Description.—Valve dome-like, with sub-ovoid lateral outline; hinge short. Rostrum well developed, is about 10–15% of valve length, protrudes distinctly forward beyond anteroventral margin of valve. Rostral incisure well developed, rounded to angular in lateral outline. Adductor muscle scar is small, subcentral, crescent-shaped convex anteriorly. Valves smooth. During ontogeny valve shape changes from almost circular to sub-ovoid.

Remarks.—*Silurocypridina calva* displays considerable variation in valve outline and shape of the rostrum. Besides material from France and the Czech Republic other, less well preserved and limited material from Sardinia (*Cypridina tyrrhenica* Canavari, 1900; types in Museo de Storia Natural e del Territorio, Calci) is possibly conspecific. One very large incomplete specimen from Wieleki (ZPAL O.63/12, Fig. 2M) shares some characteristics with “cypridinid” ostracods (i.e., valve outline and rostrum); however, its size (L = 15.25, H = 10.75 mm) and the absence of a crescent shape muscle scar are not consistent with the genus *Silurocypridina*. Either this specimen represents a deformed fossil belonging to a completely different group or it may belong to a new group of fossil “cypridinids”.

Stratigraphic and geographic range.—Ludlow Series, Holy Cross Mountains, Poland. Also known from the Silurian of the Czech Republic, France, England, Wales, and possibly Sardinia (see Perrier et al. 2011, 2019).

Discussion

Biostratigraphy.—Biostratigraphic control using graptolites and the uniformity of the myodocope assemblage of the Holy Cross Mountains succession indicates that, although they might not be exactly synchronous (Stupnicka et al. 1991), all Polish outcrops investigated herein are of about the same chronostratigraphical level (see Fig. 9): that is, middle Gorstian (lower part of the Ludlow) and more precisely within the *Cucullograptus (Lobograptus) scanicus* graptolite biozone sensu Zalasiewicz et al. (2009) or early part of the *Angochitina elongata* chitinozoan biozone sensu Steeman et al. (2016). This is consistent with the results of Perrier et al. (2019) who also identified *Bolbozoe anomala*, *Bolbozoe psittaca*, *Parabolbozoe bohemia*, *Nudator angiportatus*, *Nudator inflatus*, *Silurocypridina calva*, and *Silurocypridina retroreticulata* in the *Cucullograptus (Lobograptus) scanicus* Biozone of the UK (Fig. 9). The Polish myodocope assemblage corresponds to the assemblage present in the *S. retroreticulata* myodocope biozone of the UK (Perrier et al. 2019), with the exception of the presence of *Richteria migrans*. The *S. retroreticulata* Biozone is also recognized in France (Armorican Massif; Perrier et al. 2011). The new

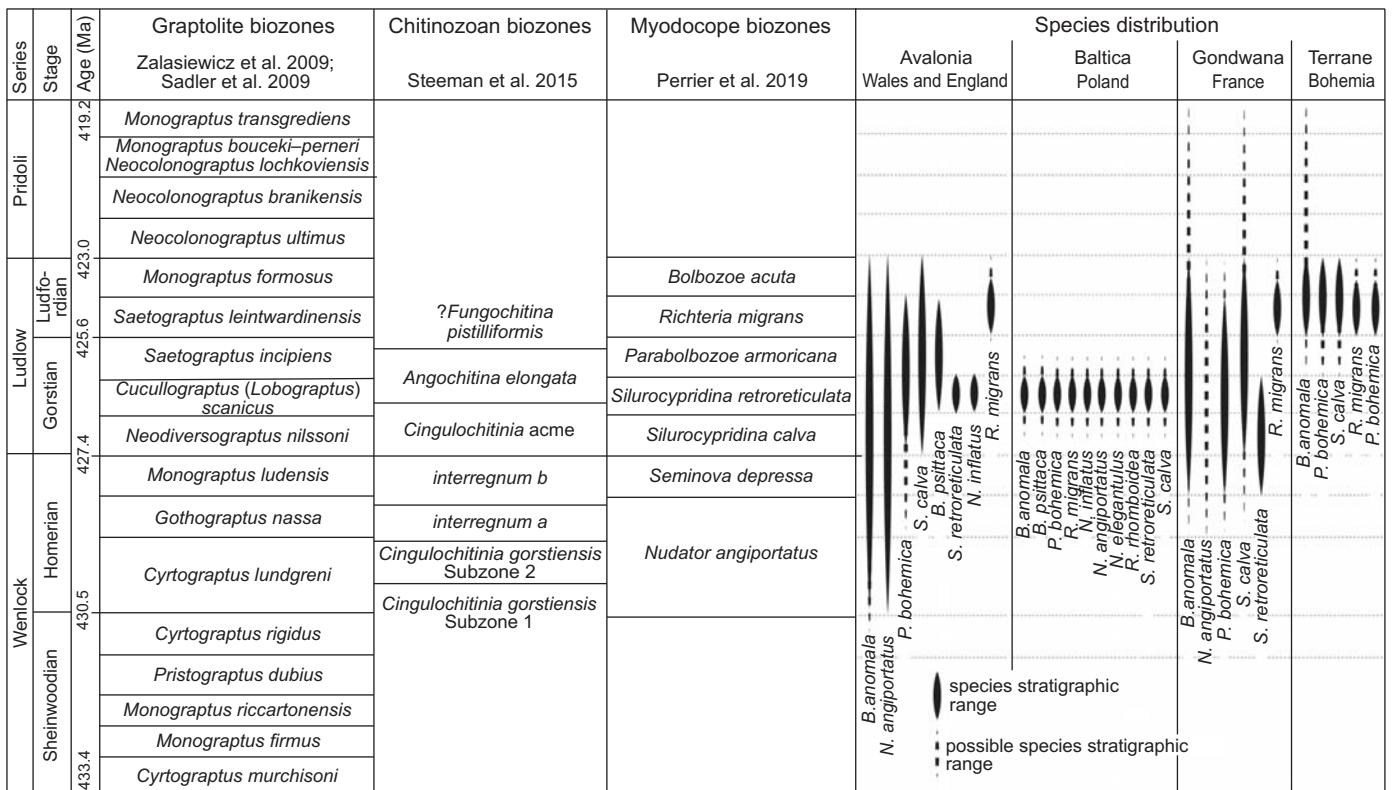


Fig. 9. Stratigraphical distribution of myodocope species in the Silurian of Poland compared to England, Wales, France, and Bohemia.

Polish occurrences of species restricted to the *S. retroreticulata* myodocope Biozone, that is *N. inflatus* and *S. retroreticulata*, endorses their position as widespread biostratigraphical markers of the middle Gorstian.

The Polish occurrence of *Richteria migrans* is the first record of that species at stratigraphical levels seemingly below the Ludfordian Stage (below the interval of the *Saetograptus leintwardinensis* and *Monograptus formosus* graptolite biozones). *Richteria migrans* is restricted to strata of the Ludfordian Stage in the UK (Long Mountain, Montgomery area and Ludlow area; Perrier et al. 2019), France (Armorican Massif and Montagne Noire; Perrier et al. 2007), the Czech Republic (Prague Basin; Perrier et al. 2007), Sardinia (Gnoli et al. 2009), Arctic Russia (Kotel'ny Island and Taimyr Peninsula; Perrier et al. 2014a), Uzbekistan (Nura-Tau Range; Perrier et al. 2014a) and possibly Germany and Gotland (Perrier et al. 2014a).

Biogeography, lifestyle, and the origin of ostracod zooplankton.—The widespread palaeogeographical distribution of several myodocope species at tropical to mid palaeo-latitudes in both hemispheres during the Silurian has been noted extensively (e.g., Siveter et al. 1991; Perrier et al. 2007, 2011, 2014a, c, 2019; Fig. 10). The new occurrences in Poland extend the known distribution of several species and reinforce data that show many Silurian myodocope species with wide dispersal. According to current knowledge, the northern part of the Tornquist Ocean, which separated Avalonia from Baltica, closed in the latest Ordovician Hirnantian (Torsvik and Rehnström 2003) and during the late Silurian the south part of the Holy Cross Mountains was situated along the Trans-European Suture Zone margin of Baltica (Nawrocki et al. 2007; Kozłowski et al. 2014). This region was located in southerly subtropical palaeolatitudes (15–20°; Fig. 10). Torsvik and Cocks (2011, 2013) placed Baltica east of the amalgamated Laurentia and Avalonia continents. The closest upper Silurian myodocope-bearing regions are Gotland (south Baltica), Germany, Wales and the Welsh Borderland (Avalonia). South Baltica shows strong myodocope faunal links with the Welsh Basin (eight species in common; Perrier et al. 2019). Other regions show similar assemblages, with the following number of myodocope species in common with the Holy Cross Mountains: Bohemia (terrane situated in the Rheic Ocean, Fig. 10; five species), the Armorican Massif (North Gondwana; six species), the Montagne Noire (North Gondwana; five species), Sardinia (North Gondwana; five species) and Uzbekistan (probably situated between North and South China terranes; four species; VP, DJS, and MW unpublished material). Both localities from Arctic Russia, Taimyr, and New Siberian Islands have been little studied and bear only one myodocope species namely the highly cosmopolitan *R. migrans* (Perrier et al. 2014a), a species also present in Poland.

Our new observations on the Holy Cross Mountains confirm that the occurrences of Silurian myodocopes are mostly associated with mudstone, siltstone or shale beds

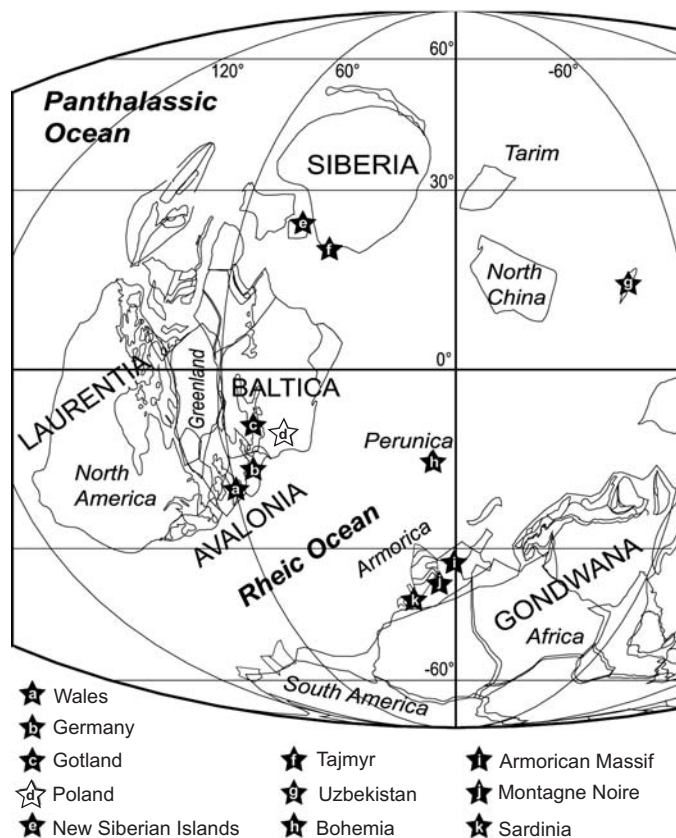


Fig. 10. Palaeogeographical distribution of Silurian myodocope bearing regions; map for Ludow (420 Ma, after Torsvik and Cocks 2013), but species span from late Wenlock to Pridoli. The position of the occurrence in Uzbekistan is poorly constrained palaeogeographically.

deposited in open- or deep-shelf marine settings. In addition to ostracods, these assemblages are dominated by other pelagic animals, namely cephalopods and graptolites, and rare bivalves, preserved in laminated sediments that lack bioturbation (Siveter et al. 1991; Perrier et al. 2011). The cosmopolitan distribution of the ostracods, coupled with their facies and faunal associations, supports the notion of an ostracod (myodocope) ecological shift from benthic to planktonic habitats during the late Wenlock and Ludlow (Siveter 1984; Siveter et al. 1987, 1991; Siveter and Vannier 1990; Vannier and Abe 1992; Perrier et al. 2007, 2011, 2014a, c, 2019).

Conclusions

Silurian myodocope ostracods from the Holy Cross Mountains, Poland comprise ten species (including one new, *Nudator elegantulus* sp. nov.) that belong to four families: Bolbozoidae, Entomozoidae, Rhomboentomozoidae, and Cypridinidae. Biostratigraphic control, *Cucullograptus (Lobograptus) scanicus* graptolite Biozone, *Angochitina elongata* chitinozoan Biozone and *Silurocypridina retroreticulata* myodocope Biozone, indicates that the three Polish outcrops investigated are of mid-Gorstian age. The new

occurrences in Poland extend the known distribution of several species and reinforce data that show many Silurian myodocope species with wide dispersal. Poland shows links at the species level with other regions on Baltica, Avalonia, Siberia, Gondwana, and two Rheic Ocean terranes. Our observations on the Holy Cross Mountains confirm that the occurrences of Silurian myodocopes are mostly associated with pelagic animals and with depositional environments ranging from open- to deep-shelf. The cosmopolitan distribution of these ostracods, coupled with their facies and faunal associations, supports the notion of an ostracod (myodocope) ecological shift from benthic to planktonic habitats during the late part of the Wenlock and continuing into the Ludlow.

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