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The Silurian pelagic myodocope ostracod *Richteria migrans*

Vincent Perrier[1], Jean Vannier[1] and David J. Siveter[2]

[1] Université Lyon 1, Lyon, F-69003, France; UFR Sciences de la Terre, CNRS, UMR 5125 PEPS 'Paléoenvironnements et Paléobiosphère', Bâtiment Géode, 2 rue Raphäel Dubois, 69622 Villeurbanne, France.
E-mail: vincent.perrier@univ-lyon1.fr
[2] Department of Geology, Bennett Building, University of Leicester, University Road, Leicester LE1 7RH, UK.

ABSTRACT: A study of type and newly collected material of the Silurian ostracod *Richteria migrans* (Barrande, 1872) demonstrates that it had wide distribution, occurring in at least the Czech Republic, France, Sardinia, Wales, central Asia and probably Poland. *R. migrans* has biostratigraphic value, as an indicator for the mid to late part of the Ludlow Series. It was almost certainly pelagic, living predominantly in probable shelf topographic lows to marginal/off-shelf environments, characteristically with cephalopod-graptolite-bivalve-dominant associates. It had at least five to six growth stages, exhibits polymorphic variation, and its morphology provides evidence to endorse the notion that 'entomozoaceans' are myodocopes.

KEY WORDS: Ecology, entomozoid, Ludlow series, Myodocopa, polymorphism

The Late Silurian species *Richteria migrans* (Barrande, 1872) is the oldest known representative of an important group of cosmopolitan Silurian-Carboniferous myodocope ostracods, the 'entomozoaceans', otherwise known as 'finger-print' ostracods because of their characteristic pattern of ribbed ornament. 'Entomozoaceans' have particularly wide geographical distribution and biostratigraphical value in the Devonian and the Carboniferous, occurring for example in Europe, North Africa, North America and China (see, e.g., Gooday 1983; Groos-Uffenorde & Wang 1989; Olempska 2002a, b). *R. migrans* was originally erected as *Entomis migrans* from the Lower Palaeozoic Prague Basin of Bohemia in the Czech Republic. It is a large 'entomozoacean', ubiquitous in the Late Silurian Ludlow Series of Europe and elsewhere. Supposedly conspecific material was later recorded from Sardinia (Canavari 1900) and from the Montagne Noire in southern France (Chaubet 1937).

The 'entomozoaceans' have traditionally been presumed to be myodocopes, the group that contains essentially all of the Recent pelagic ostracod fauna, but given the lack of soft-part evidence such an assignment could only be tentative. The recent discovery of the Silurian myodocope *Colymbosathon ecplecticos* with preserved soft-parts (Siveter *et al.* 2003), to which the shell of *R. migrans* bears marked similarity, gives firmer support to the idea that at least some 'entomozoaceans' may be myodocopes.

Opinions differ regarding the lifestyle of the 'entomozoaceans'. Some authors consider that 'entomozoaceans' were benthic, possibly living in oxygen-depleted environments (Warshauer & Duffield 1983; Casier 1987). However, it is generally thought that most members of the group occupied pelagic, perhaps midwater niches (e.g. see Gooday 1983 and Olempska 1992 and references therein).

The biostratigraphic value and palaeoecological significance of *R. migrans* is evaluated in the present paper based on revision of relevant type material and in the light of new collections obtained principally from the Armorican Massif and Montagne Noire regions of France and from Bohemia. This material, together with other newly recognised occurrences of the species facilitates testing of the model of the colonisation of the water column by pioneer pelagic (myodocope) ostracods during the Silurian (Siveter 1984; Siveter & Vannier 1990; Siveter *et al.* 1991; Vannier & Abe 1992).

1. Material and methods

R. migrans was originally documented from Barrande's (1872) 'E' limestone layer from many sites in the Prague Basin such as Braník, Lochkov, Beroun and Praha Podolí. Most of these localities are now lost or inaccessible, but some of Barrande's specimens are extant in the Národní Museum, Prague. With the assistance of J. Kříž (Czech Geological Survey) we have made new collections of *R. migrans* from several sites in Bohemia (Fig. 1a–b). We have also recovered the species from localities in France (Fig. 1a, c–d) and have identified the species in the Welsh depositional basin, UK. Details of these localities are as follows.

Lounín (Fig. 1b). Roadside exposure in the western slope of Holy Hill, northwest of Lounín village, Prague Basin (see Kříž 1999). Highly fossiliferous, laminated brownish-grey shaly limestones; Kopanina Formation. Ostracods are dominant; *R. migrans* occurs as flattened and disarticulated valves. The myodocopes *Parabolbozoe bohemica* and cypridinids are also present. The presence of the graptolites *Bohemograptus bohemicus*, *Monograptus dubius* and *Monograptus* (*Saetograptus*) *linearis* indicate an assignment to the mid Ludlow *Monograptus fritschi linearis* Biozone (Kříž 1999). Other associates include cephalopods (*Parakionoceras originale*), bivalves (*Cardiola docens*), phyllocarids (*Ceratiocaris*), trilobites (*Cromus beaumonti*) and crinoids.

Koukolova Hora (Fig. 1b). Several exposures along a forest road on the southeast slope of Koukolova Hora Hill, northeast of Slavíky village, Prague Basin. Fossiliferous, laminated brownish-grey shaly limestones; Kopanina Formation. The occurrence of the graptolite *Bohemograptus bohemicus* indicates an assignment to the mid Ludlow *B. bohemicus* s.l. Biozone. Ostracodes are abundant; *R. migrans* occurs as slightly deformed, flattened and disarticulated valves.

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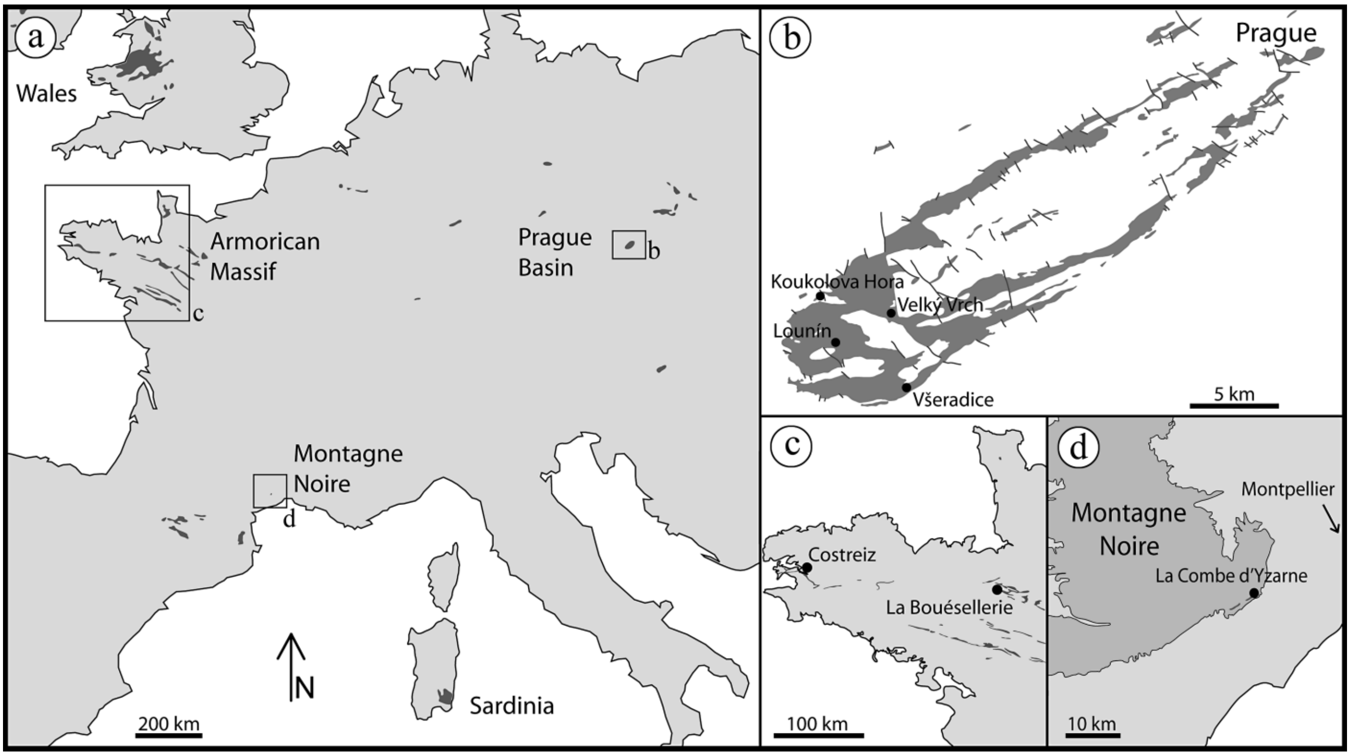

Figure 1 (a) Silurian outcrops in Europe, including localities in France, the Czech Republic and Sardinia that have yielded *Richteria migrans*; (b) localities sampled in the Prague Basin, Bohemia (Silurian outcrop distribution after Kříž 1992); (c–d) localities sampled in the Silurian of the Armorican Massif (c), and Montagne Noire (d).

Parabolbozoe bohemica is also common. Cephalopods (*Parakionoceras*), bivalves (*Cardiola*), phyllocarids (*Ceratiocaris*) and indeterminate conodonts are also present.

Všeradice (Fig. 1b). Roadside exposure northwest of Všeradice Village, south of Beroun, Prague Basin (locality 2.3 of Kříž 1992). Fossiliferous black limestones; Kopanina Formation. Graptolites indicate the presence of the mid Ludlow *M. fritschi linearis* Biozone. *R. migrans* occurs as isolated three-dimensionally preserved valves. This locality also yielded the bivalve *Cardiola*, the phyllocarid *Ceratiocaris* and indeterminate cephalopods.

Velký Vrch (Fig. 1b). Outcrops in the east of Koněprusy, south of Beroun, Prague Basin. Highly fossiliferous black limestones; Kopanina Formation. Graptolites indicate an assignment to the mid Ludlow; *Bohemograptus bohemicus s.l.* Interzone. *R. migrans* occurs as isolated three-dimensionally preserved valves. The abundant associated faunas include bivalves, brachiopods and cephalopods.

La Bouésellerie (Fig. 1c). Outcrop on the motorway side of the intersection of the N12 and A83(E3) south of St Aubin Du Cormier, Ille-et-Vilaine, Menez-Belair synclinorium, Brittany, France. Finely laminated, fossiliferous black shales; La Lande-Murée Formation. A palynomorph flora indicates a Ludlow age (F. Paris, pers. comm. 2004). *R. migrans* occurs as flattened and disarticulated valves. The myodocope *Bolbozoe anomala* is also present. Indeterminate associates include graptolites and cephalopods.

Costreiz (Fig. 1c). Exposure along the River Aulne, 1 km south of Rosnoën village, Finistère, Châteaulin synclinorium, Brittany. Siltstones and mudstones; La Tavelle Formation. Unpublished graptolite data indicates a mid-Ludlow age (Y. Plusquelec pers. comm. 2005). *R. migrans* occurs as flattened moulds of carapaces. Cypridinid ostracods and *B. anomala* are also present, as are phyllocarids (*Ceratiocaris*), bivalves and orthoconic nautiloids.

La Combe d'Yzarne (Fig. 1d). Outcrop near La Rouquette farm, between Cabrières and Neffiès, Montagne Noire, France. Black bioclastic limestones; La Rouquette Formation. Well-preserved, 3-D specimens of *R. migrans* were previously collected from calcareous nodules in vineyards near La Rouquette (Chaubet 1937). All the nodules in this vicinity seem to be of mid to late Ludlow (R. Feist, pers. comm. 2004). *P. bohemica*, *B. anomala* and other, palaeocope ostracods are also present. Associates include bivalves (*Cardiola*), phyllocarids (*Ceratiocaris*), indeterminate graptolites and numerous *Orthoceras* nautiloids.

Powys. Outcrop in the Long Mountain Siltstone Formation just E of Brunant, Long Mountain, Wales, UK. 3-D specimens of *R. migrans*. Graptolites indicate the presence of the Ludfordian Stage either the *S. leintwardinensis* Biozone or the *Bohemograptus* Biozone (Siveter, in press).

The ostracods in limestones were prepared manually, by using a 'Vibrotool' and small needles. The external moulds of ostracods preserved in shale were casted using latex. Carapace morphology was studied by scanning electron microscopy ('Hitachi S800' SEM). The lateral outline of the ostracods was evaluated by using 'Optimas 6–5.1', and the data transformed and reduced with 'Systat 10'. The significance of resultant differences was tested using discriminant analyses and 'Multivariate Analysis of Variance' (MANOVA) with 'PAST 1.34' (Hammer *et al.* 2001). The new collections from France and Czech Republic are deposited at the Faculty of Sciences (FSL numbers), Université Claude Bernard Lyon 1. The specimen from Wales is deposited in the Natural History Museum, London (NHM numbers).

2. Biostratigraphical significance of *R. migrans*

R. migrans can be used as a marker fossil for the mid to late Ludlow Series across Europe (Fig. 2) and even into central

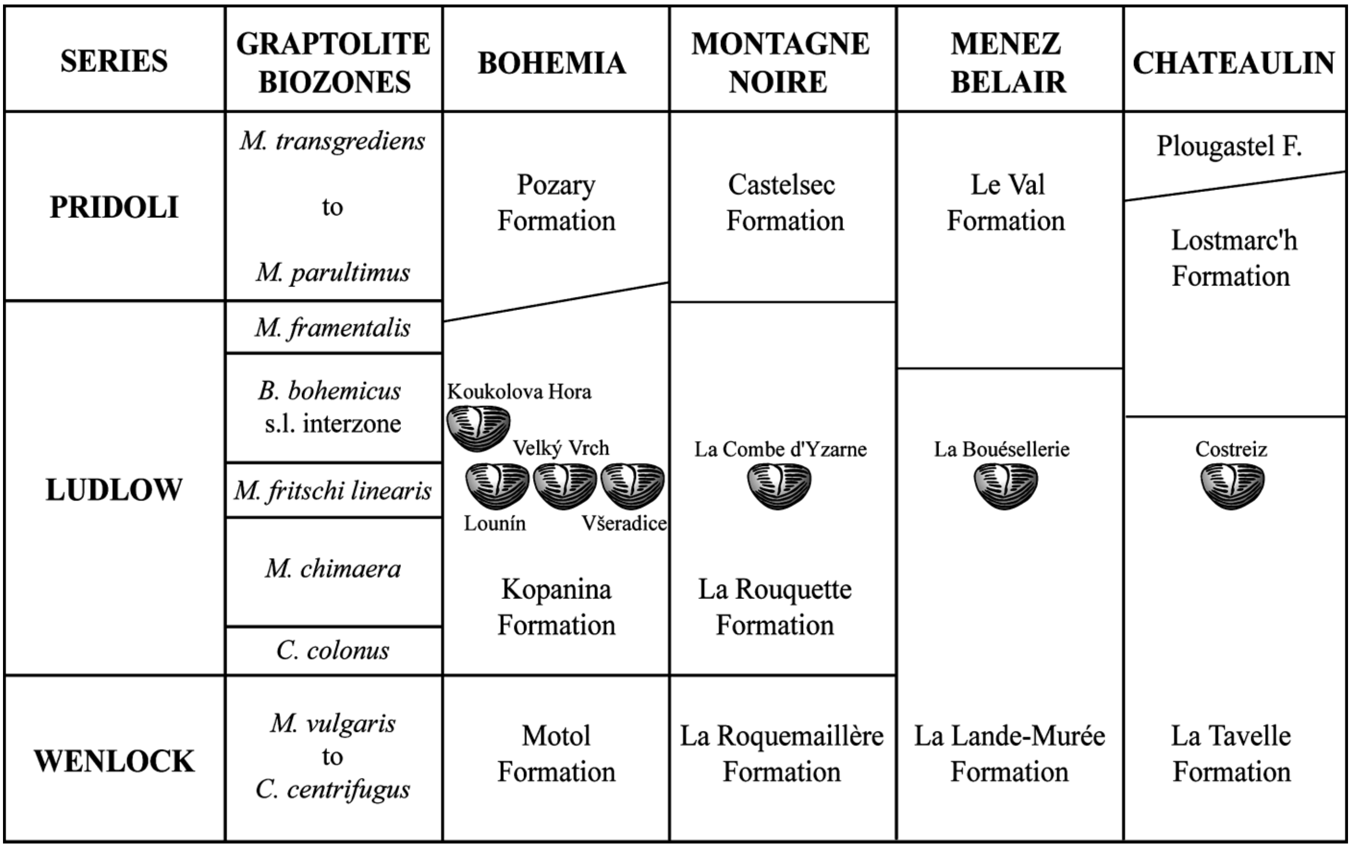

Figure 2 Approximate stratigraphic position of the localities sampled for *Richteria migrans*. Successions after the following: Menez-Belair (Paris 1981); Châteaulin (Y. Plusquelec pers. comm. 2005); Bohemia (Kříž 1999); Montagne Noire (Feist 2002).

Asia. The species occurs in the Kopanina Formation, Bohemia, Czech Republic (e.g., Bouček 1936 and herein); the La Lande-Murée and La Tavelle formations of the Armorican Massif and La Rouquette Formation of the Montagne Noire, France (herein); the Fluminimaggiore Formation ('*Orthoceras*' Limestones facies), Sardinia (mid to late Ludlow; Canavari 1900; see also Siveter *et al.* 1991, pp. 164–5); the Long Mountain Siltstone Formation, Welsh basin, U.K., Wales (D. Palmer collections; see Siveter, in press); the North Nura-Tau Range, central Asia (Mikhailova & Siveter unpublished data); and probably the *Cardiola interrupta* Shales (Niewachlow greywacke; Early/Late Ludlow boundary), Poland (Gürich 1896).

The occurrence of *R. migrans* in the Czech Republic ranges from the *Monograptus fritschi linearis* to *Bohemograptus bohemicus* s.l. Interzone graptolite biozones (Fig. 2; J. Kříž, pers. comm. 2004). In Britain it occurs in the *Bohemograptus bohemicus* and probably the *Saetograptus leintwardinensis* graptolite biozones. In central Asia it is known from the Ludlow Series. The graptolites associated with some of the French and Sardinian occurrences of *R. migrans* are insufficiently studied or too ill-preserved to provide precise independent stratigraphic control; however, based on its consistent stratigraphic range in the Czech Republic and Britain it seems highly likely that such localities yielding *R. migrans* are also of mid to late Ludlow age.

3. Lifestyle of *R. migrans*: palaeoecological significance

In interpreting the lifestyle of any vagile organism, especially a long extinct fossil species, morphological ('design') considerations should be assessed alongside independent geological evidence relating to the nature of the faunal associates and the palaeogeographical and facies distribution patterns (e.g., see Fortey 1985 for trilobites; Siveter *et al.* 1991, Vannier & Abe 1992, Siveter & Lane 1999, Siveter & Bogolepova 2006 for Silurian ostracods). Siveter (1984) suggested a pelagic lifestyle for *R. migrans*, a conclusion endorsed in the studies of Siveter *et al.* (1991), Vannier & Abe (1992) and herein.

3.1. Morphological evidence

The overall valve shape and morphology of *R. migrans* is closely similar to the recently discovered cylindroleberidid myodocopid ostracod with preserved soft-parts, *Colymbosathon ecplecticos* from the Silurian (Wenlock) Herefordshire Lagerstätte, England (Siveter *et al.* 2003). In *C. ecplecticos* the first and second antennae simply protrude from the gaping carapace, thus, in theory, playing a major role in swimming. A similar disposition and extension of soft parts, and hence function, could possibly pertain in *R. migrans*. Indeed, in many Recent myodocopes the carapace is normally held slightly agape during swimming (Angel 1993). In addition, the ribbed type of ornament across almost the entire valve surface in *R. migrans* may have functioned to increase the area of the carapace in order to aid buoyancy (Siveter 1984). Palaeobiologically it should also be noted that the preadductorial node of *R. migrans* may have housed the lateral eye, as is known from *C. ecplecticos*.

In spite of the fact that *R. migrans* does not show valve features definitive of a swimming mode of life, it does not exclude the possibility that it could swim. Many Recent myodocope swimmers lack a rostral incisure. In these forms a simple anterior gap between the valves allows the protrusion of the first and especially the second antennae for use in locomotion (Fig. 3a, c; see also Angel 1993). Similarly, *R. migrans* has neither a rostrum nor an incisure. The valves overlap each other along the entire free margin, but this overlap is moderate and has no interlocking feature. A smooth, triangular area is present on each valve and lies in the same position as the rostral incisure of other myodocopes. The absence of ornament in this particular area of the carapace might be related to the protrusion of swimming appendages. In conclusion, nothing excludes the possibility that *R. migrans* was a swimmer.

3.2. External ornament

The external ornament of entomozoids is distinguished by its longitudinal, concentric so-called 'finger-print' or spiral ribs. This ribbing pattern is rare among Recent and fossil ostracods, which are more commonly reticulated or smooth. A noticeable exception, however, are the halocypridid myodocope ostracods (e.g. Thaumatocypridacea and Halocypridacea) whose carapace is non-calcified, flexible and displays a unique variety of longitudinal, oblique and concentric striated patterns (e.g. Angel 1993). For example, fossil Thaumatocypridacea like *Pokornyopsis feifeli* (see Kornicker & Sohn 1976) bear longitudinal ribs in the central part of the valves. However, these ribs tend to reticulation in juvenile instars and the outline of the valves (rounded) differs markedly from that of *R. migrans*. In the pelagic halocyprid *Conchoecia imbricata*, the carapace is more elongated and deeply sculptured with rectangular cells that mimic reticulation (Fig. 3a; Vannier *et al*. 2003). The fine concentric pattern of *Conchoecia lophura*, centred on the adductorial spot, is of particular interest here because of its close resemblance to the 'finger-print' ornament of numerous entomozoids such as *Maternella* (compare ornament on Fig. 3f and g). SEM observations reveal that the concentric striae of *C. lophura* are actually terrace-lines associated with pores of possible sensory function (Fig. 3d–e). The present authors have no knowledge that *R. migrans* (and other entomozoid) had surface pores as observed in *C. lophura*. Terrace-lines occur on the exoskeleton of a great variety of invertebrates, typically in burrowers (e.g. trilobites, crustaceans) in which they interact mechanically with the substratum and play a major role in burrowing and anchoring mechanisms (see Vannier *et al.* 1997). The terrace-line pattern of *C. lophura* obviously has a different function, as this ostracod lives permanently in the water column and does not interact with sediment at any time during its life cycle. This ostracod, as with most other Recent halocypridids, performs rhythmic vertical migrations through the water column, alternating swimming ascent (ca. 40 m/hr) and free-sinking descent (Angel 1993). The immediate environment of small pelagic animals such as halocypridids (0·5–3 mm long) is dominated by viscosity (Reynolds 1997, 2001). In other words, these ostracods are constantly 'embedded' within a bubble of sticky water. Although no detailed experimental work or modelling has been attempted so far to understand the physical constraints experienced by pelagic ostracods, it is almost certain that any external microstructures such as striae or ribs that may increase or decrease the effect of viscosity, have direct effects on locomotion (for example, to retard sinking, or improve swimming efficiency). This might explain why pelagic ostracods are provided with this unique type of ornament. The ribbing pattern of entomozoids may have had a similar functional significance in relation to a pelagic lifestyle and possible migratory habits through the water column. Thus, the longitudinal ribs of *R. migrans* may have had a double function: that of improving the hydrodynamics of the animal during upward migration (swimming) and to retard sinking during vertical descent. This interpretation is supported by the more pronounced ribbing pattern of Devonian entomozoids ('flanges' in Olempska 1992, fig. 1; see also Groos-Uffenorde 1993, fig. 2).

3.3. Depositional environment: facies and faunal associates

The nature of the associated facies and faunas indicates that *R. migrans* probably lived off the sea bottom. In the Czech Republic *R. migrans* occurs in fossiliferous dark, platy, laminated, fine-grained mudstones ('micrites'; e.g., at Holy Hill near Lounín) and also in more carbonate-rich, black limestones (e.g., at Vseradice and Velký Vrch) of the classic so-called 'Cephalopod' or '*Orthoceras*' limestone facies. As noted by Siveter *et al.* 1991 (pp. 165–6), such cephalopod-graptolite-bivalve-dominant myodocope-bearing assemblages typify possible marginal to off-shelf environments and 'quiet-water' topographic lows on the shelf of the Prague Basin. Characterised by the lack of bioturbation, the presence of lamination and by a low-diversity, mostly pelagic fauna, these areas of fine-grained mud and silt deposition are often associated with lowered oxygen levels, both in the lower part of the water column and at the sediment/water interface. The locality at La Combe d'Yzarne in the Montagne Noire is of a broadly similar 'Cephalopod Limestone' facies.

The Silurian myodocopes of Sardinia occur in a complex sedimentary and tectonic setting, being found within displaced blocks of different ages, especially in an '*Orthoceras*' limestone (*siluricus* conodont Biozone; Ludlow Series) and a micrite (Přídolí Series) microfacies (see Siveter *et al*. 1991, pp. 164–5). *R. migrans* was originally obtained from near Flumminimaggiore (Canavari 1900), by calcining *ex situ* '*Orthoceras*' limestone blocks found in dry-stone walls. Ferretti (1990, fig. 4) reported that ostracodes can form up to 60% of the skeletal clasts in some of the limestone blocks. Sardinian myodocopes are generally associated with a recurring orthoconic nautiloid-graptolite-dominated pelagic fauna, with bivalves typically the only sign of a benthic epifauna; the implication (the occurrence of anoxic bottom conditions) is, clearly, important with respect to notions of the habitat of *R. migrans*. The facies of the orthoceratid-dominated assemblage in Sardinia has been considered to represent shallow shelf conditions, albeit with anoxic bottom waters (Gnoli *et al.* 1979), or a deep water environment (Jaeger 1976).

Within the Welsh depositional basin, the vast majority of myodocopes are known only from the off-shelf and more axial part of the basin of the Ludlow series (Siveter *et al.* 1991, pp. 163–4). The myodocopes generally show a close association with hemipelagic and low oxygen levels and comprise a minority element of a dominantly pelagic graptolite-nautiloid-bivalve fauna. Such palaeogeographical and facies distributions bring strong evidence for a pelagic habit for Welsh Basin myodocopes such as *R. migrans*.

Silurian myodocope-bearing localities in Armorica (e.g., La Bouésellerie and Costreiz) differ from all other known such strata in consisting predominantly of unbioturbated black graptolitic shales that, with their high organic content and positive anomalies of certain trace elements, have been characterised as typically euxinic deposits (see Siveter *et al.* 1991, pp. 166–7). These black shales contain a low-diversity, essentially pelagic fauna (in essence the *Schugurocaris* Community of Racheboeuf 1999) of myodocopes, graptolites, cephalopods, phyllocarids and bivalves and a rich microbiota including acritarchs, chitinozoa and spores. Their palaeogeographical setting, between two relatively shallow shelf facies of the northern Gondwanan epicontinental shelf, and the condensed nature of the hemipelagic mud facies with terrestrial detritus no larger than silt size suggested (Siveter *et al.* 1991) that these

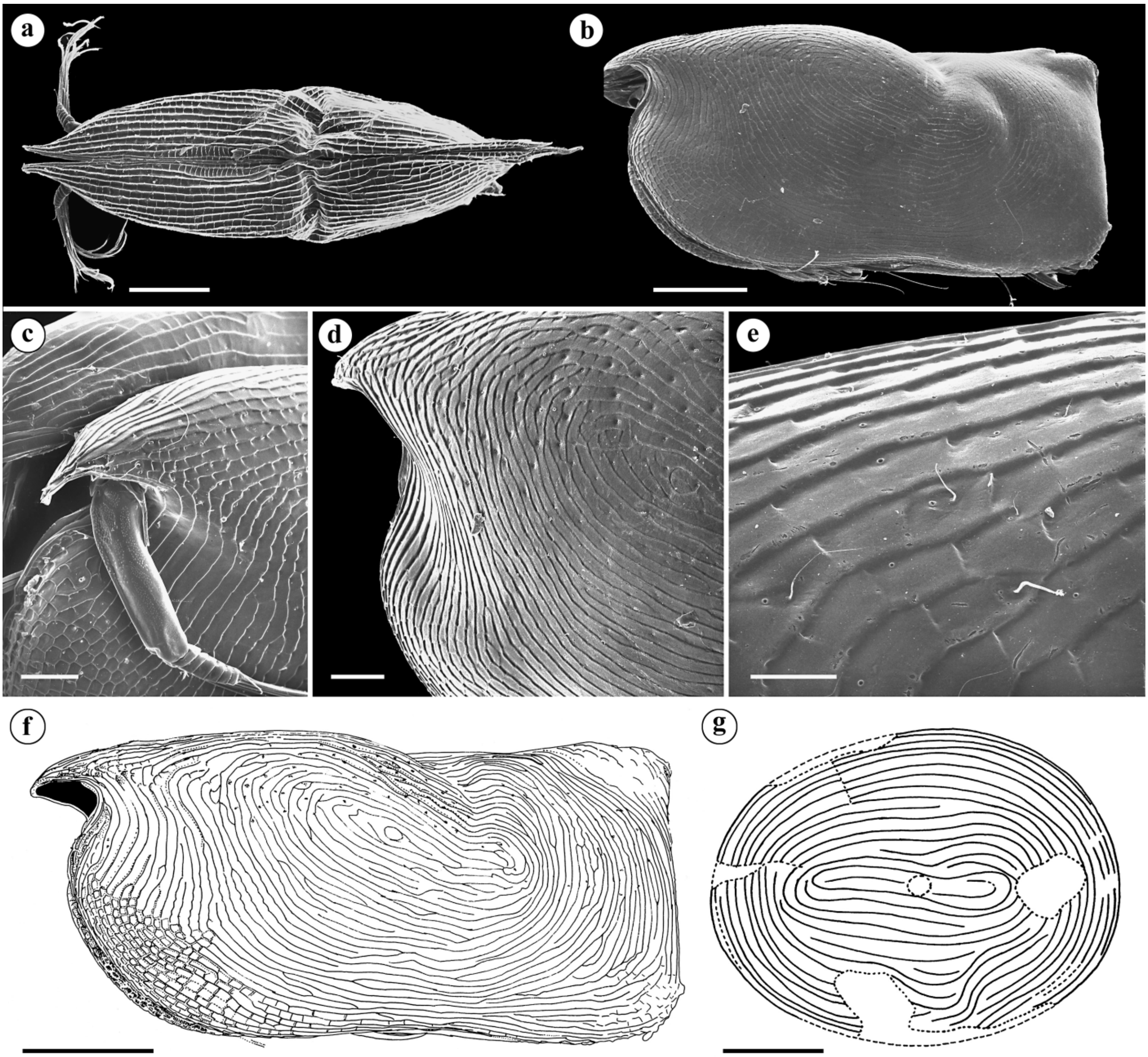

Figure 3 External ornament of Recent pelagic ostracods and Palaeozoic entomozoids: (a–f): *Conchoecia* (Halocyprididae) from Japan, Pacific Ocean. (a) *Conchoecia imbricata*, dorsal view showing linear ornament parallel to dorsal line and symmetrical swimming antennae (A2). (b–f) *Conchoecia lophura*, lateral view, detail of rostrum with protruding A2, details of 'finger-print' ornament near rostrum, and line-drawing showing pattern of ornament on the left valve. (g) *Maternella* (*Maternella*) *clathrata* from the Early Carboniferous (Mississippian) of Whiteway Slate, UK, line-drawing showing fine concentric striae ('finger-print' ornament) on the left valve (after Gooday 1983). All scanning electron micrographs. Scale bar = 500 μm for (a), (b), (f), (g); = 200 μm for (c), (d); = 50 μm for (e).

black shales possibly accumulated within a starved (stagnant/anoxic?) basin on the shelf.

3.4. Palaeogeographical distribution

The widespread palaeogeographical distribution of *R. migrans* suggests that it had good dispersal capacity consistent with a possible pelagic lifestyle. The species is known from both the high latitude southern margin (Bohemia, Montagne Noire, Armorican Massif, Sardinia) and the subtropical northern margin (Wales and probably Poland) of the Rheic Ocean (Fig. 4).

3.5. Palaeoecological significance

Certain Upper Silurian myodocopes are good candidates for pioneer pelagic ostracodes (Siveter, 1984; Siveter *et al.* 1987, 1991; Siveter & Vannier 1990, Vannier & Abe 1992). Evidence from Britain, France, Czech Republic, Sardinia, Australia, China and elsewhere underpins the idea that myodocope ostracodes may have undergone a benthic to pelagic ecological shift in mid Silurian times (Siveter *et al.* 1991; Vannier & Abe 1992). Lower Silurian Llandovery and Wenlock myodocopes lived with dominantly benthic associates on well oxygenated shelves. By contrast, Upper Silurian Ludlow and Přídolí myodocopes lived with low diversity pelagic faunas, in outer shelf topographic lows or off-shelf basin slopes, and are often associated with deposits which imply anoxic or lowered oxygen conditions. Thus, the habitats, assumed pelagic lifestyle, and Ludlow Series stratigraphical distribution of *R. migrans* are consistent with the model and timing of an ecological shift affecting myodocopes during the Silurian.

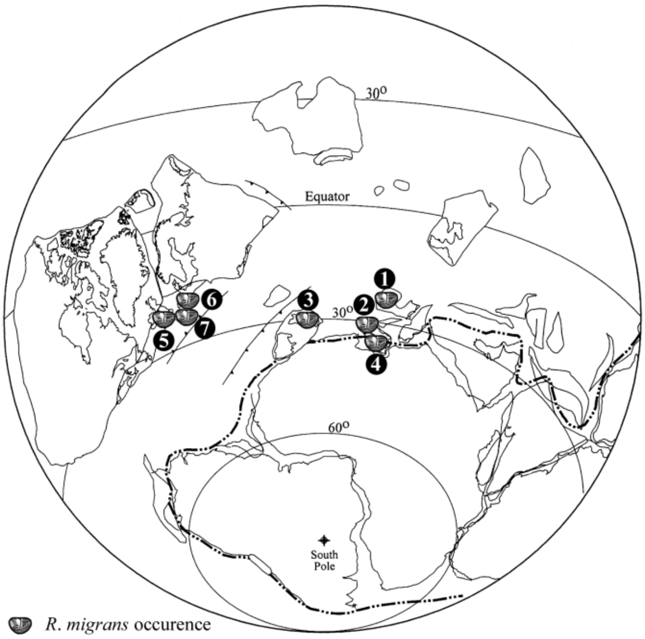

Figure 4 Distribution of *Richteria migrans* on a mid-Silurian palaeogeography (420 Ma; map after Cocks & Trosvik 2002), 1, Bohemia; 2, Montagne Noire; 3, Armorican Massif; 4, Sardinia; 5, Wales, UK; 6, Poland; 7, Germany.

4. Systematic palaeontology

Class Ostracoda Latreille, 1802 (nom. correct. Latreille, 1806)
Subclass Myodocopa Sars, 1866
Order Myodocopida Sars, 1866 (nom. correct. Pokorný, 1953)
Suborder 'Entomozocopina' Gründel, 1969
(=Entomozocopina Gründel, 1969)
Superfamily 'Entomozoacea' Přibyl, 1950
(=Entomozoacea Přibyl, 1950)

Diagnosis. Valves generally thin, weakly calcified, adults >1 mm long, characteristically ornamented with longitudinal, concentric or spirally arranged ribs. Lacking a rostrum and rostral incisure. Adductorial sulcus well developed to absent.

Remarks. 'Entomozoaceans' (= Entomozoacea *sensu* Přibyl, 1950) have long been regarded as myodocopes (e.g., Sylvester-Bradley 1961), but by their signature 'finger-print' ornament and in lacking generally a rostrum and rostral incisure they are considered the most atypical of all of the ostracode groups that have traditionally been assigned to the Myodocopa (see discussion in Siveter & Vannier 1990, Kornicker and Sohn 2000). However, the recent discovery of a Palaeozoic myodocope with preserved soft-parts, *Colymbosathon ecplecticos* from the Silurian of England (Siveter *et al.* 2003), has yielded new evidence to support a myodocope affinity for 'entomozoaceans'. *R. migrans* has a very similar valve outline and lobal/sulcal morphology to that of *C. ecplecticos* and both taxa lack a rostrum and rostral incisure.

In the present paper, 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 Bolbozoacea Bouček, 1936; see Siveter & Vannier 1990 for discussion and recommendations).

The classification used for the higher taxa of Ostracoda is that of Horne *et al.* 2002.

Family 'Entomozoidae' Přibyl, 1950
(=Entomidae Jones, 1873)

Diagnosis. 'Entomozoaceans' with bean-shaped or symmetrically to asymmetrically ovoid lateral outline, rarely with a weak anteroventral indentation; dorsal margin shorter than carapace length. Adductorial sulcus concave toward anterior end or straight; muscle scar as a smooth patch (but sometime 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 (modified after Gooday 1983).

Subfamily 'Entomozoinae' Přibyl, 1950

Diagnosis. 'Entomozoidae' generally with a symmetrical lateral outline; dorsal margin mainly curved. Ornament longitudinal with concentric ribs at anterior and posterior ends, or concentric or spiral around the muscle scar (modified after Gooday 1983).

Genus *Richteria* Jones, 1874

1874 *Richteria neues* Genus; Jones, p. 180.
1879 *Richteria*; Jones, p. 183.
1934 *Entomis* (*Richteria*) Jones (1874); Kegel, p. 413.
1954 *Entomozoe* (*Richteria*) Jones, 1874; Rabien, p. 87.

Type species. *Cypridina serrate-striata* Sandberger, 1845; by subsequent designation, Kegel, 1934, p. 413. From the Lower Famennian, Late Devonian of Germany.

Diagnosis. 'Entomozoinae' with bean-shaped lateral outline. Adductorial sulcus well developed, extending up to $\frac{3}{4}$ of carapace height. Dorsal margin slightly rounded, curved at the level of the adductorial sulcus. Longitudinal or concentric ribbing pattern; small preadductorial node present or lacking.

Remarks. The genus *Richteria* was established in a published letter (Jones 1874). Jones later reconsidered his ideas when he stated that he could not find 'any reason for the establishment of my proposed genus' (Jones, 1879, p. 183). Kegel (1934) subsequently designated *R. serratostriata* as type species. *Richteria* differs from *Nehdentomis* in the absence of a distinct muscle pit.

Distribution. *Richteria* is known from at least the Silurian and Devonian. Supposed records of its occurrence in younger and older strata have not been confirmed by the present authors. The genus is known from at least Europe (Czech Republic; Germany; Poland; Belgium; France; Italy; U.K.), central Asia and China.

Richteria migrans (Barrande, 1872)
(Figs 5–10)

v. 1872 *Entomis migrans* Barr.; Barrande, p. 514, pl. 24, figs 10–14; pl. 27, fig. 22.
1873 *Entomis migrans* Barr, 1872; Jones, p. 416.
? 1896 *Entomis migratoria* n. sp.; Gürich, p. 374.
1899 *Entomis migrans* Barr.; Canavari, p. 151.
v. 1900 *Entomis migrans* Barr.; Canavari, p. 193, pl. 25, figs 1, 2.
v. 1900 *Entomis Lamarmorai* n. f.; Canavari, p. 195, pl. 25, figs 3–5.
v. 1900 *Entomis* n. f. ?; Canavari p. 196, pl. 25, fig. 6.
v.? 1900 *Entomis meneghinii* n. f.; Canavari, p. 196, pl. 25, figs 7–11.
1934 *Entomis* (*Richteria*) *migrans* Barr.; Kegel, p. 413.

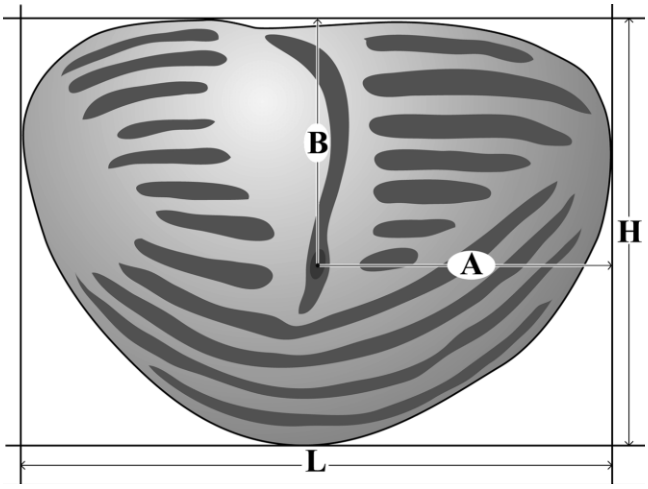

Figure 5 Parameters used for measurements of *Richteria migrans*. L=Length; H=height of the valve; the intersection of lines A and B marks the centre of the adductor muscle scar.

1934 *Entomis migrans* Barrande; Bassler & Kellett, p. 304 (*pars*).

1936 *Entomis* (*Richteria*) *migrans* Barrande 1872; Bouček, p. 57, pl. 6, figs 5, 6; text-fig. 2a, b.

v. 1937 *Entomis* (*Richteria*) *migrans* Barrande; Chaubet, p. 186, pl. 4, figs 8a–c.

1950 *Entomozoe* (*Richteria*) *migrans* (Barrande); Přibyl, p. 11, pl. 1, fig. 4.

? 1952 *Entomozoe migrans* Barrande 1872; Kupfahl, p. 178.

1958 *Entomozoe* (*Richteria*) *migrans* (Barrande); Pokorný, p. 311, fig. 1032.

? 1961 *Entomozoe meneghinii* Canavari; Sylvester-Bradley, p. 389, figs 312, 2g–j.

1961 *Richteria lamarmorai* Canavari; Sylvester-Bradley, p. 390, figs 313, 1a–e.

1984 *'Entomis' migrans* Barrande; Siveter, p. 78, pl. 2, figs 12–13, text-fig. 3.

1988 *Richteria migrans* (Barrande, 1872); Přibyl, p. 113, text-fig. 5.1.

1990 *'Entomis' migrans*; Siveter & Vannier, p. 64, text-fig. 23.

2000 *E. migrans* Barrande, 1872; Groos-Uffenorde, Lethiers & Blumenstengel, fig. 2.

v. In press *'Entomis' migrans* Barrande, 1872; Siveter, pl. 9, fig. 4.

Lectotype. Incomplete right valve; Národní Museum, Prague, on slab NM-L 22944; subsequently designated by Přibyl, 1950, p. 111. Figured Barrande 1872, pl. 24, figs 12–14; Bouček 1936, text-fig. 2a; figs 6a–b.

Type locality and horizon. Kopanina Formation, Ludlow Series, the former Dvorce quarry (today Podolí swimming pool), Podolí district of Prague.

Material. Hundreds of valves from localities in the Czech Republic, France and Sardinia. About 100 specimens were measured and studied in detail, including valves preserved in 3-D in limestones (from Velký Vrch, Všeradice and la Combe d'Yzarne) and flattened valves in shales (from Lounín, Koukolova Hora Hill, La Bouésellerie and Costreiz). Several valves from Wales, UK.

Measurements. The length:height (L:H) of 50 undistorted, 3-D preserved specimens from Všeradice, Velký Vrch, and La Combe d'Yzarne were measured and L:H ratios were calculated (Figs 5, 11). The largest and smallest specimens at La Combe d'Yzarne are 1·98–1·39 mm and 0·53–0·39 mm (Figs 7i, n; 11); at Velký Vrch, they are 1·69–1·00 mm and 0·56–0·42 mm respectively (Figs 7a, g; 11).

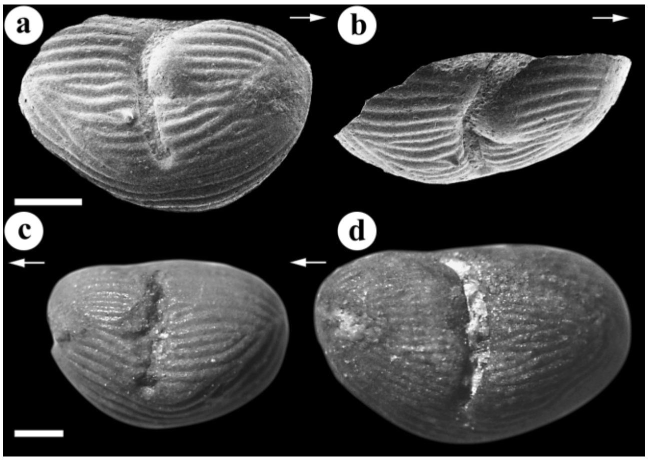

Figure 6 *Richteria migrans* (Barrande, 1872), three-dimensionally preserved material from Praha-Podolí, Bohemia (a–b) and Xea San Antonio, Sardinia (c–d): (a–b) plastic cast made from a latex cast, incomplete right valve (NM-L 22944), Lectotype, lateral and dorsal views, courtesy H. Groos-Uffenorde; (c) carapace (I 71) left lateral view, (d) carapace (I 73), left lateral view. Arrow points to anterior in each case. Scale bars=500 µm.

Diagnosis. Species of *Richteria* with lateral longitudinal ribs that merge posteriorly, converge on a triangular smooth area anteriorly and diverge slightly from the valve margin ventrally. Preadductorial node generally smooth, can be slightly ribbed.

Description. Carapace large, bean-shaped in lateral outline. Greatest length is slightly above mid height; greatest height is at the adductorial sulcus (Fig. 5). 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 vale is narrow, ornamented by very fine striation.

Adductorial 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 muscle scar is present at the slightly widened ventral extremity of the sulcus. The dorsal part of the sulcus is deeper and narrower, ending at a small 'bridge' (height about 50 µm) connecting preadductorial and postadductorial areas. The preadductorial node is generally unornamented but can be weakly ribbed, and is less developed in some specimens (material from France).

The external surface of each valve has up to 25 longitudinal ribs, including in some specimens short, intercalated and bifurcated ribs. The alignment of ribs is not disturbed by the adductorial sulcus. The ribs merge posteriorly, converge on a triangular smooth area anteriorly and curve slightly away from the valve margin ventrally.

Ontogeny. *R. migrans* is represented by juveniles and adults in all of the French and Czech localities sampled, but the instars do not plot as discrete size clusters (Figs 7, 11). This possibly reflects taphonomic processes or sampling of populations of different ecotypes and/or chronotypes. Based on growth factors (1·26) known from the palaeocope *Craspedobolbina clavata* (see Martinsson 1962; see also the entomozoacean *Franklinella lysogorensis* Olempska 2002b), it is estimated that *R. migrans* had at least five (possibly six) ontogenetic growth stages (Fig. 11). The number of ontogenetic stages of *R. migrans* is very close to that of Recent myodocopes (four to six pre-adult instars; see Cohen and Morin 1990).

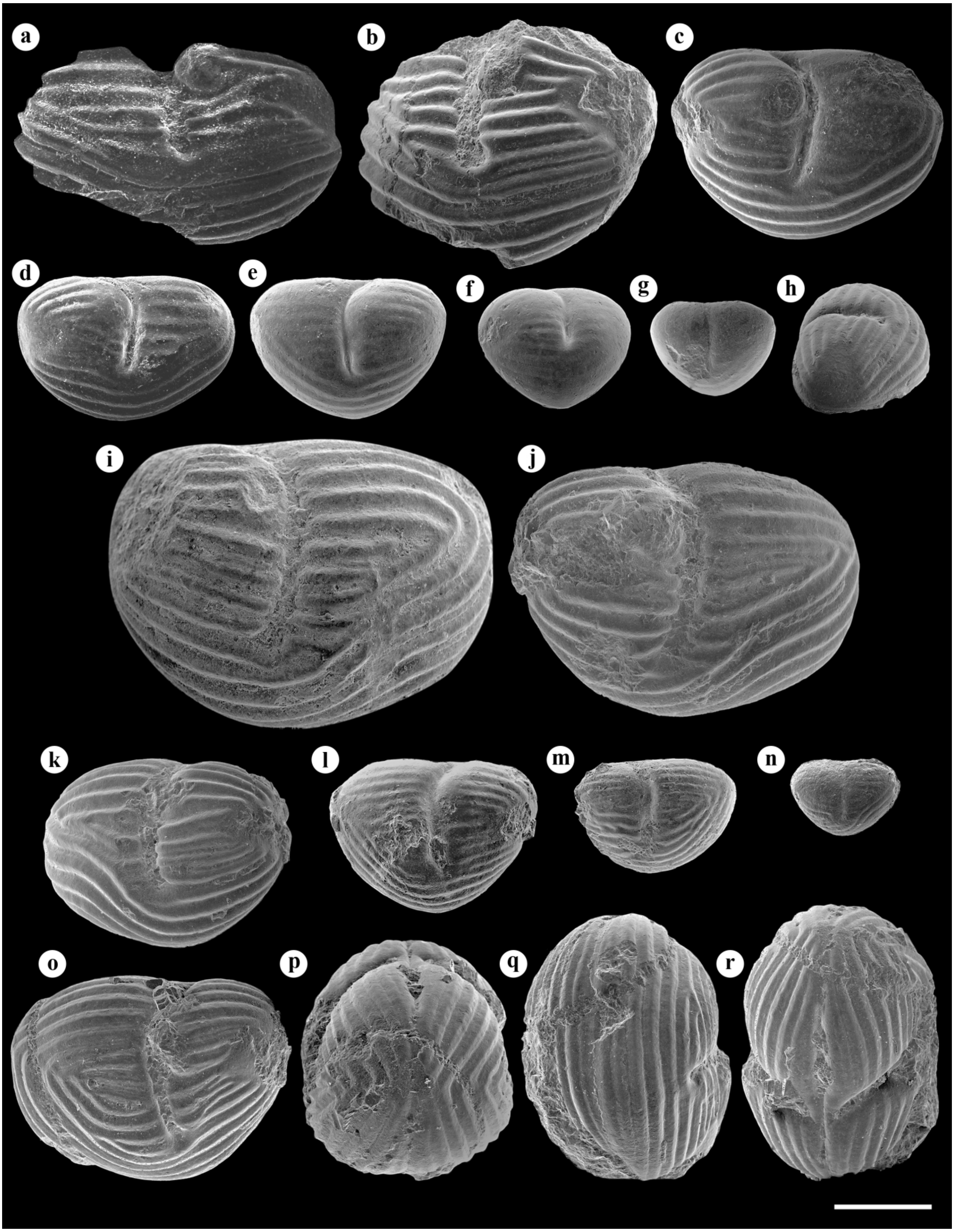

Figure 7 *Richteria migrans* (Barrande, 1872), three-dimensionally preserved material from Velký Vrch, Bohemia (a–h) and La Combe d'Yzarne, France (i–r): (a) latex cast of an incomplete right valve (FSL 705003a), lateral view; (b) incomplete right valve (FSL 705007b), lateral view; (c) left valve (FSL 705002a), lateral view; (d), (h) left valve (FSL 705009a), lateral and anterior views; (e) right valve (FSL 705001a), lateral view; (f) left valve (FSL 705004a), lateral view; (g) left valve (FSL 705001b), lateral view; (i) left valve (FSL 705029a), lateral view; (j) left valve (FSL 705034a), lateral view; (k) right valve (FSL 705033a), lateral view; (l) right valve (FSL 705031b), lateral view; (m) left valve (FSL 705031a), lateral view; (n) left valve (FSL 705030a), lateral view; (o–r) complete carapace (FSL 705032a), right lateral, posterior, ventral and dorsal views. Scale bars = 500 µm.

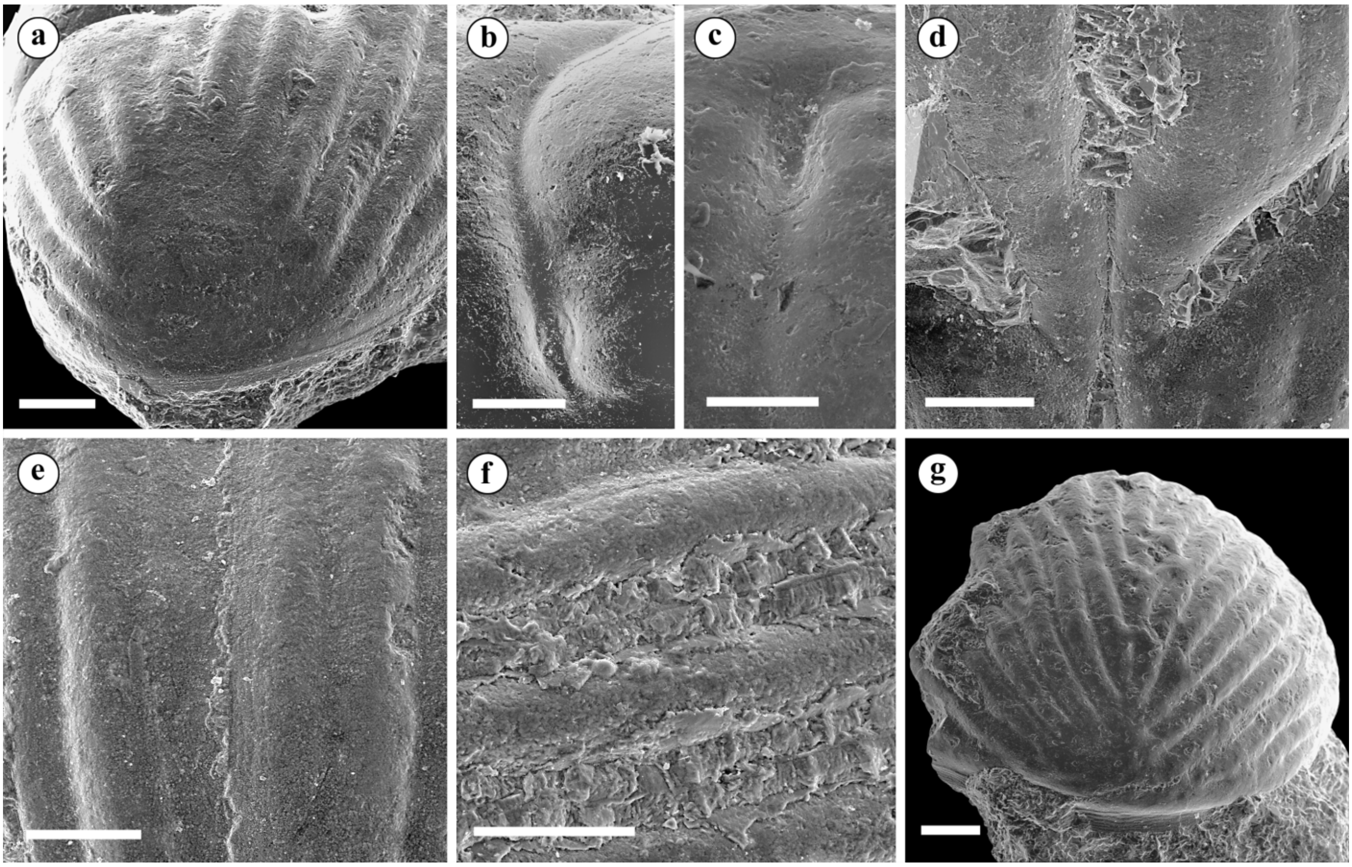

Figure 8 *Richteria migrans* (Barrande, 1872), three-dimensionally preserved material from Velký Vrch, Bohemia (a–c) and La Combe d'Yzarne, France (d–g): (a) left valve (FSL 705009a), detail of triangular smooth area, anterolateral view; (b) right valve (FSL 705001a), detail of adductorial sulcus and muscle scar, lateral view; (c) right valve (FSL 705004a), detail of adductorial sulcus and muscle scar, dorsolateral view; (d–e), carapace (FSL 705032a), details of central part of dorsal margin, dorsal view, and ventral overlap, ventral view; (f) right valve (FSL 705035a), detail of ornament, lateral view; (g) right valve (FSL 705037a), detail of ornament, posterior view. Scale bars = 100 µm (a–f); 200 µm (g).

During ontogeny valve shape becomes more elongate and most of the morphological features of the carapace, such as the adductorial sulcus and ornament, develop gradually (compare Fig. 7c–g). The smallest specimens are about 0·5 mm long and 0·4 mm high (=instar A–6?). They have weak longitudinal ribs, a triangular smooth area anteriorly, a muscle scar and a similar-shaped but less deep sulcus than in adults, but lack a well-defined preadductorial node. The first instars have numerous (10–12) and well marked ribs in the French specimens, whereas they are smoother in Bohemian ones. The preadductorial node strengthens in the third or fourth instar and in adults is well developed and appears to slighty deflect the course of the local ribs.

Remarks. Of Barrande's (1872) original material of *R. migrans*, the following specimens have been recognised in the Národní Museum, Prague: Barrande 1872, pl. 24, figs 10, 11 (a left valve not identified with certainty; possibilities exist on slabs L22944 and L22945); pl. 24, figs 12–14 (Lectotype); pl. 27, fig. 22 (right valve; on slab L8944). The three other '*Entomis*' species that Barrande erected, namely *E. dimidiata* (1872, pl. 24, figs 7–9; five rock pieces, NM1490), *E. pelagica* (1872, pl. 24, figs 1–6; six rock pieces, NM CF 535) and *E. rara* (1872, pl. 25, figs 23–24; NM L8843), do not appear to be conspecific with *R. migrans*. From the description and its occurrence Gürich's (1896) *Entomis migratoria* (=*nomen nudum*), from the Ludlow Series (*Cardiola*) '*Interrupta*-Schiefern' of the Holy Cross mountains of Poland, is likely to be conspecific with *R. migrans*. Kupfahl (1952) also described eight specimens of *Entomozoe migrans* from the (middle ?) Ludlow of Germany (Kellerwald/Rhein Schiefergebirge) which may be conspecific with *R. migrans*.

Of the new forms of *Entomis* that Canavari described (1900) from the Ludlow of Sardinia, based on examination (VP) of the original material (Calci Museum, University of Pisa, Italy)

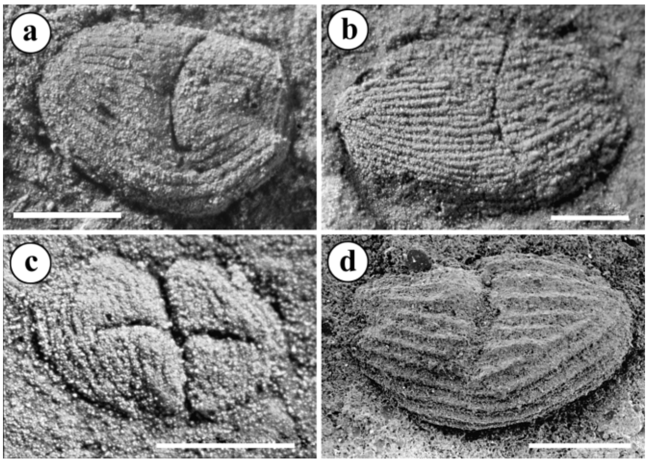

Figure 9 *Richteria migrans* (Barrande, 1872). Flattened specimens from Lounín (a) and Koukolova Hora Hill (b–c), Bohemia and three-dimensionally preserved specimen from Powys, Wales (d): (a) right valve (FSL 705026a), lateral view; (b) right valve (FSL 705027a), lateral view; (c) carapace (FSL 705028a), open in 'butterfly position', lateral view; (d) left valve (NHM OS15729), lateral view. Scale bars = 1000 µm.

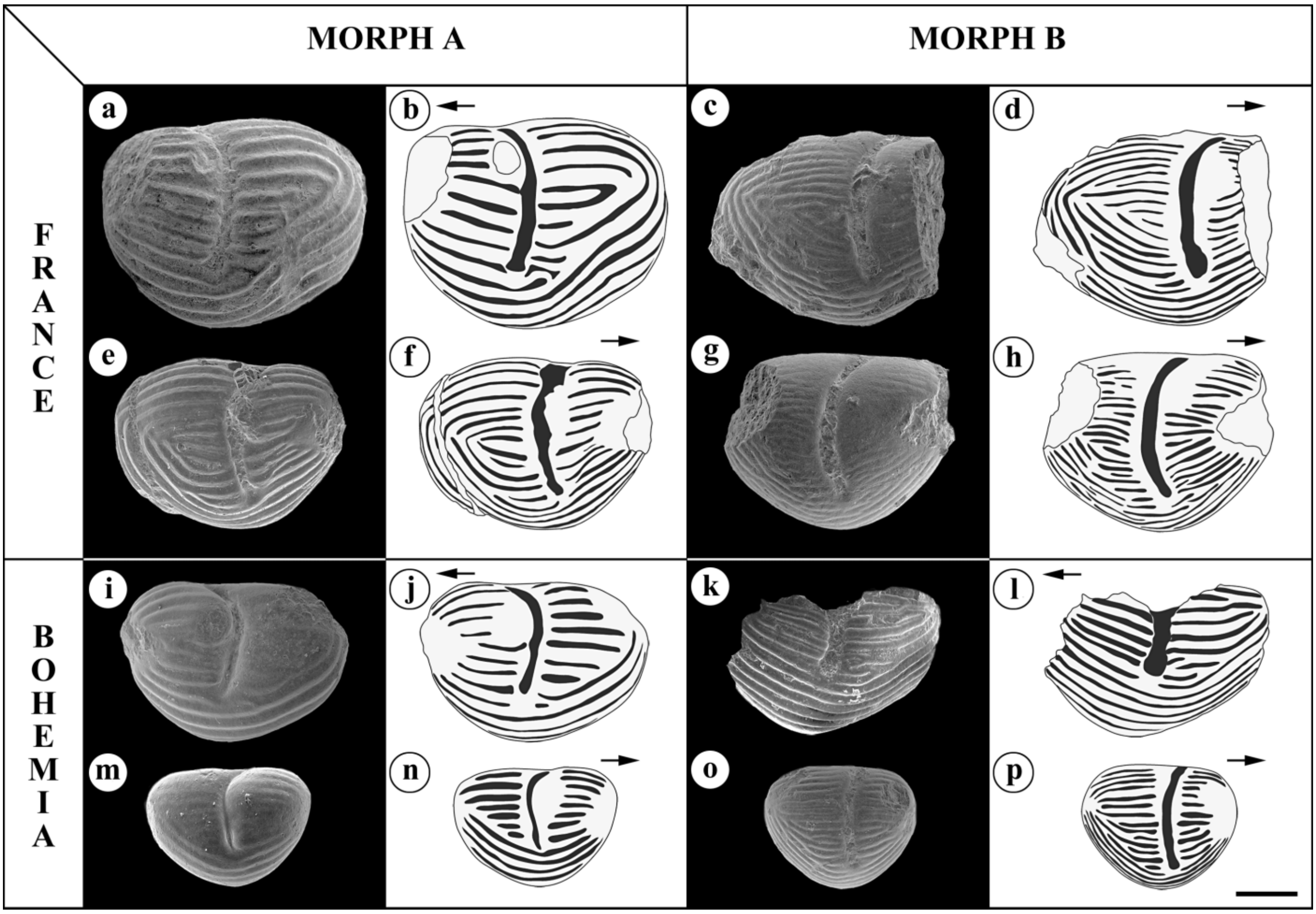

Figure 10 Sequence of specimens and camera lucida drawings, in lateral view, that illustrate polymorphism in *Richteria migrans* (Barrande, 1872). Specimens from La Combe d'Yzarne, France (morph A (a–b, e–f); morph B (c–d, g–h)) and Vseradice, Bohemia (morph A, (i–j, m–n); morph B, (k–l, o–p)): (a–b), left valve (FSL 705029a); (c–d) carapace (FSL 705038b), right lateral view; (e–f) right valve (FSL 705032a); (g–h) right valve (FSL 705036a); (i–j) left valve (FSL 705002a); (k–l) incomplete left valve (FSL 705008a); (m–n) right valve (FSL 705001a); (o–p) right valve (FSL 705005a). Arrow points to anterior in each case. Scale bars = 500 µm.

the present authors consider that his *Entomis migrans* (Fig. 6c), *Entomis lamarmorai* (Fig. 6d), *Entomis* n. f. ? and possibly *Entomis meneghinii* are conspecific with *R. migrans*. The non-ribbed taxa that he documented as *Entomis ichnusae* Canavari, 1899, *Entomis zoppii* Canavari, 1899, *Entomis* (?) *pteroides* Canavari, 1899, *Entomis subreniformis* n. f., *Entomis* (?) *amygdaloides* n. f., *Entomis* (?) *parvula* n. f. and *Entomis* (?) f. ind. belong outside *Richteria*.

Distribution. Known from the Ludlow Series of the Czech Republic, France, Sardinia, UK (Fig. 9d), Germany, central Asia, probably Poland and possibly Germany (see section 2. 'Biostratigraphic significance' above).

5. Polymorphism

Canavari (1900) distinguished his *Entomis migrans* and *Entomis lamarmorai* on the basis of different ribbing patterns, and Chaubet (1937) interpreted similar variation in French material as polymorphism within a single species, *Entomis migrans*. For most of the specimens examined, two morphs can be distinguished, based on ornament, in a range of ontogenetic stages of *R. migrans* from both France and the Czech Republic (Fig. 10): Morph A (Fig. 10a–b, e–f, i–j, m–n) with typically 10–12 somewhat regularly arranged, coarse ribs, and Morph B (Fig. 10c–d, g–h, k–l, o–p) characteristically with 15 to at least 18 narrower, finer and in some cases more irregularly arranged or discontinuous ribs. However, some specimens of both the coarser and more delicately ribbed forms appear to have 13 or 14 ribs. The two morphs occur as associates on rock pieces, in both flattened and 3-D material (Figs 9a–b; 10), and are otherwise alike in shape and morphology (e.g. adductorial sulcus, preadductorial node and anterior triangular smooth area). Supposed sexual dimorphism reflected in pattern of ornament is known in the Devonian rhomboentomozoid

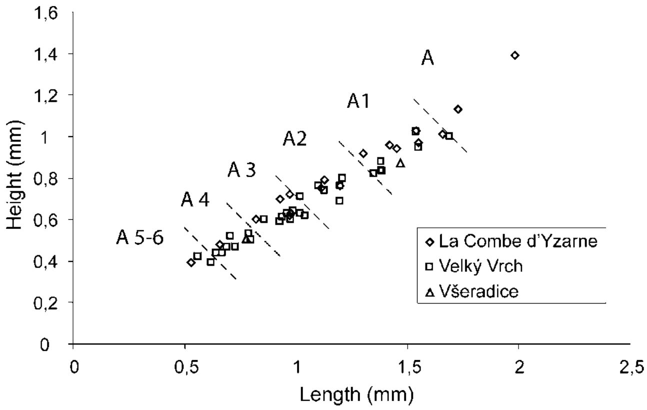

Figure 11 Measurements of fifty complete specimens of *Richteria migrans*; specimens comprise both latex casts from external moulds and 3-D preserved specimens, from La Combe d'Yzarne, France and Velký Vrch and Vseradice, Bohemia. Length and height of the valves is as given in Figure 5; A to A5–6 = instars (see text).

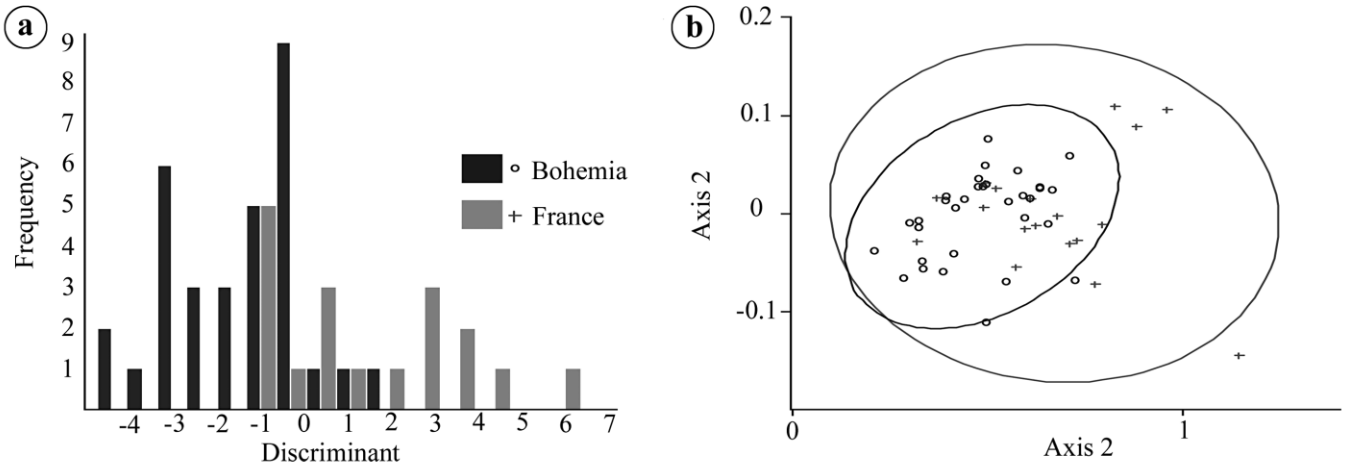

Figure 12 Discriminant analysis and MANOVA analysis (on four measurements) of fifty complete specimens (as in Fig. 12) of *Richteria migrans*: (a) discriminant analysis realised using length, height, A and B (as given in Fig. 5); (b) MANOVA analysis realised using length, height, A and B (as given in Fig. 5).

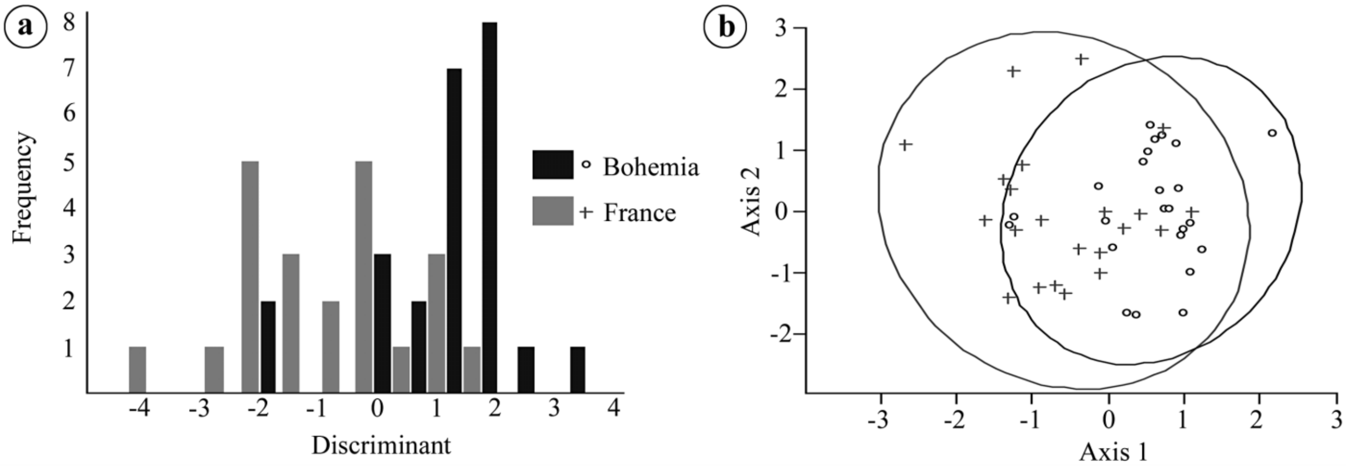

Figure 13 Discriminant analysis and MANOVA (on valve outline) of fifty complete specimens (as in Fig. 12) of *Richteria migrans*, (a) discriminant analysis realised using valve outline; (b) MANOVA analysis realised using valve outline.

'entomozoacean' *Franklinella lysogorensis* Olempska, 2002b, but only in the adult stage, where tecnomorphs have 20–22 ribs and heteromorphs have 35–38 ribs. The morphs of *R. migrans* occur over a size range that must represent at least five instars (Figs 10–11) and may, therefore, be a case of precocious sexual dimorphism. While Whatley & Stephens (1977) demonstrated that precocious sexual dimorphism is present in some myodocope ostracodes, from documented evidence it is a rare phenomenon in the Ostracoda as a whole (Whatley & Stephens 1977). For example, *Thaumatoconcha radiata* (Thaumatocypridacea, Halocyprida) show size differences between male and female in the two first juvenile instars, but other characters of the carapace (e.g. ornament) are similar (see Kornicker and Sohn 1976 p. 16 and fig. 3). In addition to the possibility that the polymorphic variation in *R. migrans* represents intraspecific variation due to ontogenetic or perhaps environmental factors, it may simply reflect the occurrence of two separated species. The later notion is discounted because of the presence of continuous variation in the number and pattern of ribbing in both of the French and Czech material. Moreover, the two 'morphs' always occur together (France, Czech Republic and Sardinia) and not as isolated morphs. On balance, the present authors prefer to consider that the two morphs are conspecific. Some Devonian 'Entomozoacea' (e.g. *Maternella dichotoma* Rabien, 1954 (pl. 2, fig. 14; pl. 4, figs 33–34) and *Richterina zimmermanni* Rabien, 1954 (fig. 6; pl. 1, figs 8–9; pl. 5, fig. 41)) show a similar pattern of two morphs with different number of ribs taken as conspecific (Rabien 1954). In addition there has been a discussion to determine if the different ribbing pattern within one species may be caused by different preservations (Groos-Uffenorde 1985). For example, the number of ribs of *Entomoprimitia variostriata* Rabien, 1954 may vary within separate layers of the shell (see Groos-Uffenorde 1985, p. 213, pl. 2, figs 2–3).

There is a good, though not complete, degree of overlap in valve size range and also valve shape (outline) between the French and Czech material. Discriminate size analysis (Fig. 12) and discriminate shape analysis (Fig. 13) do not reveal any major differences between the specimens from these two areas. The minor differences could be the result of a variety of factors including sampling across a range of 'populations'.

6. Conclusions

The Silurian ostracod *R. migrans*:

- occurs in the Czech Republic, France, Sardinia, Wales, central Asia and probably Poland;
- has biostratigraphic value as an indicator for the middle part of the Ludlow Series;
- was almost certainly pelagic, living predominantly in probable shelf topographic lows to marginal/off-shelf

environments, characteristically with cephalopod-graptolite-bivalve-myodocope dominant associates;

- furnishes morphological evidence to support the notion that 'entomozoaceans' are myodocopes;
- endorses the model that pioneer pelagic ostracods were upper Silurian myodocopes;
- had at least five (maybe six) growth stages and exhibits polymorphic variation.

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