Silurian Myodocopes: Pioneer pelagic ostracods and the chronology of an ecological shift

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ABSTRACT - Analysis of all relevant palaeontological and global geological data strongly supports the notion that representatives of Silurian myodocope ostracods had pelagic lifestyles and habitats and that they may well be, within the Ostracoda, pioneer colonisers of such environments. Morphological evidence (from fossil and Recent myodocopes) combined with facies distributional and concomitant faunal evidence (from the Silurian of, for example, Britain, France, Czechoslovakia, Sardinia, Australia and China) endorses the idea that myodocope ostracods may have undergone a benthic to pelagic ecological shift during mid Silurian times.

Lower Silurian myodocopes lived, with benthic associates, on well oxygenated shelves. Upper Silurian ostracods lived, typically with low diversity, largely pelagic faunas in outer shelf topographic lows or off-shelf basin slopes, and are characteristically associated with deposits which are in part suggestive of lowered oxygen levels or even anoxic conditions. A pre-adaptation for swimming may have allowed Silurian myodocopes to respond to environmental forcing (negative oxygen levels; positive trophic and nutrient incentives; rises in sea levels) by migrating, through time, up the water column.

INTRODUCTION

Until relatively recently the documentation and interpretation of Silurian representatives of the ostracod Superorder Myodocopa was a neglected field of study. These ostracods received scant attention for several reasons, including their relatively scarce geological occurrence and their often 'unattractive' state of preservation (they typically occur as moulds). Moreover, they can be easily overlooked in the field, being normally associated with facies (characteristically mud-silt laminites) which at first sight appear unpromising as possible ostracod yielding deposits. Such drawbacks should not, however, hinder the realisation of the potential and importance of the group. They demonstrate that pelagic Ostracoda were probably present by the Silurian, that such lifestyles may have originated at that time, and that there is the prospect of establishing (especially in the Upper Silurian) an ostracod biostratigraphy which can integrate with coeval graptolite zonal schemes.

The ecological, stratigraphical and phylogenetic significance of Silurian myodocope ostracods are currently being assessed by the present authors in a series of papers which have hitherto concentrated on European faunas of the group. The present paper aims to marshall and categorise the various lines of evidence which collectively corroborate the notion that certain typical Silurian myodocopes may possibly be regarded as pioneer pelagic ostracods (Siveter 1984). Moreover, in order to appropriately place such myodocopes within the established context of ostracod studies we compare them herein with another group of Silurian ostracods that have been well studied and are regarded as benthic, namely the ubiquitous palaeocopes and in particular the superfamily Beyrichiacea. Furthermore, in reviewing the worldwide spatial and chronological occurrence of Silurian myodocopes we also support the idea (Siveter & Vannier 1990) that there is evidence for a possible ecological shift of myodocope stock actually during that time period - a shift which is charted in a change from a benthic to pelagic mode of life and from relatively shallow nearshore/shelf habitats to somewhat deeper and relatively more outer/off-shelf environments.

'Typical Silurian myodocopes' are herein taken to include representatives of two families, the Cypridinidae and Bolbozoidae, and to exclude members of what traditionally have been regarded (but see Siveter & Vannier 1990) as 'Entomozoacea'. Bolbozoids and cypridinids are relatively large ostracods (adults 1-15mm long) with very distinctive morphological features, such as the presence of a rostrum and associated rostral incisure at the anterior margin of the valve and (in the case of bolbozoids) a prominent anterodorsal valve bulb (Siveter 1984; Siveter, Vannier & Palmer 1987; Siveter & Vannier 1990). The 'Entomozoacea' of traditional usage have a Silurian to Carboniferous, world-wide distribution, are characteristically associated with hemipelagic sediments, and are generally regarded as embracing mostly pelagic forms (*e.g.* Gooday 1983). However, in spite of a few various and taxonomically inconsistent morphological similarities between 'entomozoaceans' and obvious myodocopes such as polycopids, cylindroleberidids, philomedids, cypridinids and bolbozoids, the 'Entomozoacea' are judged "clearly the most atypical of all of the ostracode groups which have traditionally been assigned to the Myodocopa and their true taxonomic position may well lie elsewhere" (Siveter & Vannier 1990, p.19).

That some Silurian myodocopes probably had pelagic lifestyles was proposed in a paper interpreting the habitats and modes of life of Silurian ostracods in general (Siveter 1984). Of all Silurian ostracods, the myodocopes were judged to be the prime candidates for forms which lived off the bottom. In a paper fundamental to subsequent taxonomic studies of the group, Siveter, Vannier & Palmer (1987) described enigmatic polygonal and associated radiate shell microstructures from a wide variety of Silurian myodocopes, and considered them to be the surface expression of calcium carbonate platelets and possibly the result of *in vivo* shell calcification processes

and post-mortem 'diagenetic' changes. In contrast, reticulation, corrugation and tuberculation are recognised in the same paper as the true, genetically controlled external shell ornament in Silurian bolbozoid and cypridinid myodocopes and as such can be employed as diagnostic features in taxonomy.

It is also now clear that most European Silurian myodocope ostracod faunas form part of an almost exclusively pelagic, recurring faunal association (Siveter, Vannier & Palmer 1987). Their facial and palaeogeographical distributional patterns suggested to Siveter, Vannier & Palmer (1987) an ecology that was perhaps in some way depth controlled. They are typically found in laminated, fine grained clastic or carbonate successions representing probable quiet, low energy, outer shelf/slope environments and are essentially unknown from thorough-going platform carbonate (e.g. reef-bearing) sequences in the Silurian of Europe.

The earliest true myodocope recognised in modern studies is the bolbozoid *Entomozoe* s.s. from the Lower Silurian Llandovery Series in Scotland, where it forms part of a low diversity, shallow water, nearshore assemblage (Siveter & Vannier 1990). The latter authors concluded that, in contrast to the certain other, younger, Upper Silurian myodocopes, this currently monotypic genus is probably a benthic form; that a benthic to pelagic transition of the myoodocopes could, therefore, have occurred early in the Silurian; and that this event is possibly reflected in changes to the shell (and perhaps appendage) morphology within the group. However, similar large *Entomozoe* ostracods have recently been discovered from Upper Llandovery sediments in South Central China and, in the light of these finds, the total evidence (see below) as to whether the genus really was benthic throughout its entire range is somewhat equivocal. Notwithstanding the latter, a Silurian benthic to pelagic transition for the myodocopes as a whole is endorsed herein based on an analysis of their overall distributional patterns in time and space.

ECOLOGY OF RECENT MYODOCOPES

Recent ostracods have proved to be opportunistic in colonising a wide variety of environments. They live in brackish, marine and freshwater habitats and have adapted to many lifestyles. In addition to salinity barriers, depth and/or depth related factors clearly have a marked influence over the distribution of present day marine ostracod faunas. Most Recent marine ostracods are benthic crawlers and swimmers, living in the shallow, relatively warm thermospheric waters from the littoral zone down to some 500m depth. Burrowing and other cryptic lifestyles are also known but are comparatively uncommon. Benthic ostracods are also found at greater depths, off the continental shelves. There, in the deeper, colder and dark conditions of the psychrospheric realm, diversity is generally much reduced.

Pelagic free swimmers and planktonic forms constitute a numerically relatively small but nevertheless important part of modern marine osrtracod faunas. Most present day pelagic Ostracoda belong to the Superorder Myodocopa. Their systematics rely in most part on the morphology of appendage and other soft part features and on the nature of the adductor muscle scars (e.g. Kornicker & Sohn 1976). Myodocopes are often comparatively large sized ostracods (1-30mm long) and, in fact, the group embraces a wide variety of habitats and modes of life (reviewed in Siveter & Vannier 1990). Indeed, of the some 650 Recent species assigned to the Superorder most are benthic crawlers or nektobenthic forms. For example, within the Order Myodocopida the geographically widespread rutidermatids have

benthic, shelf living forms (1-560m depth); both sarsiellids and philomedids are benthic/nektobenthic from intertidal to abyssal environments; and cypridinids and cylindroleberidids are good swimmers and include both bottom dwelling and pelagic forms. Within the other myodocope Order, the Halocyprida, species living on or close to the bottom are also common; for example, some thaumatocypridids and most polycopids.

Of the Recent pelagic myodocopes most belong to the Halocyprida. The Halocyprididae are mostly pelagic and they comprise the majority of the living truly oceanic pelagic ostracods. The family has global distribution and, although its taxa commonly occur deeper than 200m, they can be found at depths up to 4000m. Some halocyprid species are also capable of substantial vertical migration, possibly associated with particular feeding strategies (Angel 1983a, 1983b). Vertical migration is also known from philomedids, where it is related to mating behaviour. Depth control is clearly important in influencing the distributional patterns of many modern pelagic myodocopes.

COMPARATIVE ECOLOGY OF SILURIAN OSTRACODS

The balance of evidence suggests that, like the majority of modern ostracod species, most Silurian ostracods were benthic, living at relatively shallow depths on the shelf and shelf slope of marine basins (Siveter 1984). By applying design principles and evidence from modern analogues (Henningsmoen 1965, Benson 1981), it is thought that most Silurian palaeocope (e.g. beyrichiacean) and leperditiid ostracods were probably primarily benthic with crawling abilities and that it would be reasonable to assume that many could also swim on or near the bottom (Siveter 1984). Though less obviously so, the characteristically smooth-shelled podocope, metacope and platycope ostracods in the Silurian also embrace benthic forms, both crawlers-swimmers and possibly infaunal burrowers (Siveter 1984).

Some, relatively uncommon and morphologically specialised Silurian ostracods possibly inhabited pelagic environments (Siveter 1984). These include many, although not all myodocopes (for example, *Entomozoe tuberosa* may be an exception; Siveter & Vannier 1990), especially representatives of the myodocopid Cypridinidae and (the entirely fossil groups) Bolbozoidae and 'Entomozoacea', all of which are rare/unknown from normal shelf environments but which typically occur in unusual shelf (troughs) and/or more offshore deposits such as shelf - basin slopes (Siveter, Vannier & Palmer 1987). Thus, the geographical (facies) distribution of typical Silurian myodocope ostracods generally appears to be separate from that of the dominant benthic ostracod (palaeocope-podocope-metacope-platycope) associations of the coeval normal shelf areas (Siveter 1984), a point exemplified by the distributional patterns of the Silurian ostracods of the Welsh Basin (Fig.1). Although there are some records of benthic ostracods within the myodocopid 'off-shelf' realm their presence can be attributed to transport (see below).

The 'Entomozoacea' have traditiohally been regarded as Myodocopa largely as a matter of convenience rather than being an assignment based on any firm morphological or other evidence; they may well be unrelated to 'typical' myodocopes (Siveter & Vannier 1990). Notwithstanding this possibility, the 'entomozoaceans' are widely distributed in fine grained, offshore clastic deposits, especially in the Devonian of Europe, the majority have been interpreted as pelagic by most researchers (Gooday 1983). Their possible adaptation to a life in the water column may have included the often present external ornament of longitudinal ribbing, a strategy designed to
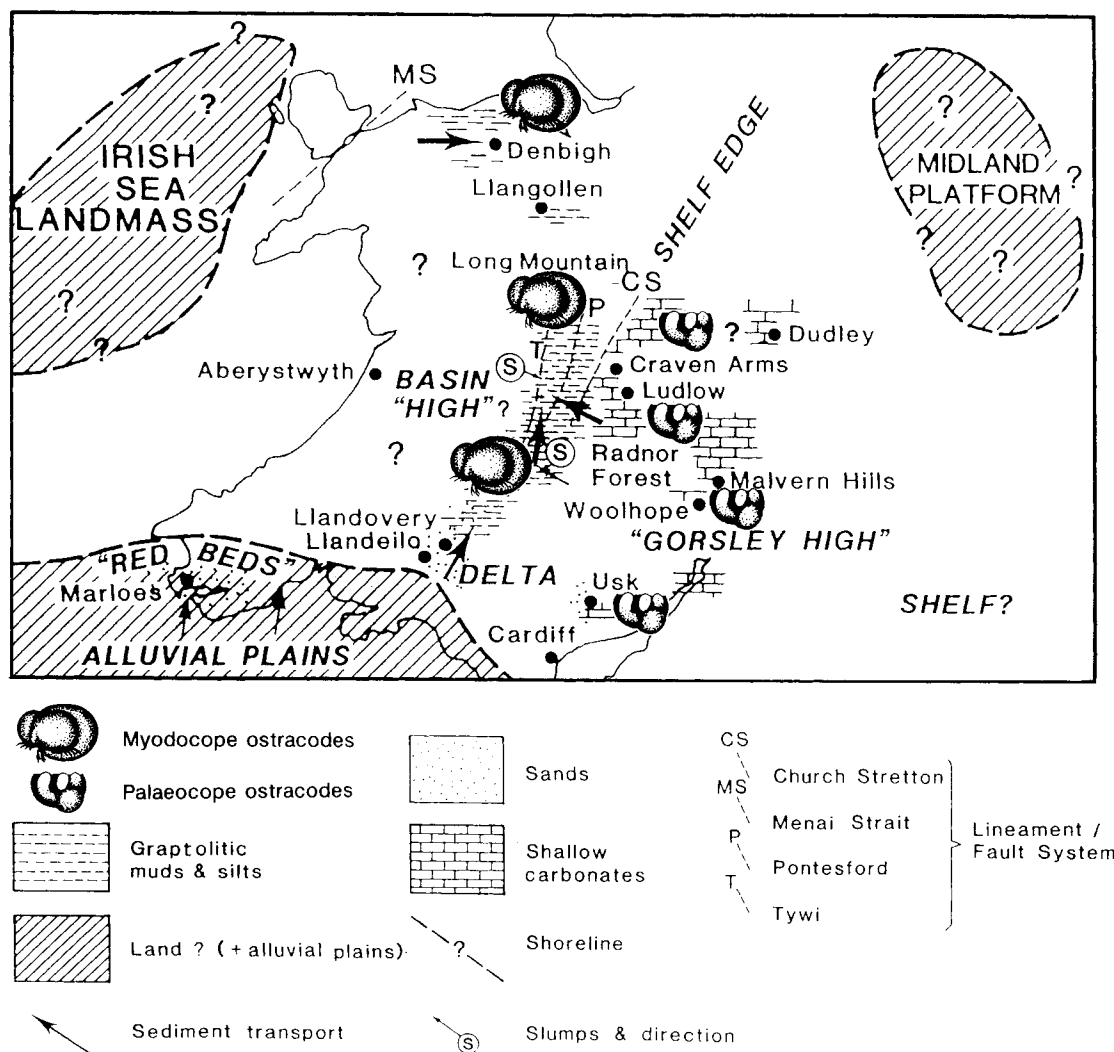
Fig. 1 Generalised distribution of myudocopes and characteristic palaeocopes relative to lithofacies in the Silurian of the Welsh Basin. Base map (after Siveter *et al.* 1989) is for late Gorstian (Lower Ludlow) times.

increase valve surface area in order to aid buoyancy.

Other possible pelagic ostracods in the Silurian included the morphologically bizarre Aechminidae (Siveter 1984). With their single elongate, tapering spines, projecting from near the dorsal margin of each valve to well above the valve itself, some members of this family represent very rare potential candidates for the occurrence of (epi- ?) planktonic lifestyles in Silurian ostracods. The hollow spines may have aided buoyancy or have been used for some form of attachment.

SILURIAN MYODOCOPES: TYPES OF EVIDENCE FOR A (PELAGIC ?) LIFESTYLE

The interpretation of the mode of life of fossil animals relies on evidence from animal 'design' and associated paradigm principles and functional morphology and from facies and palaeogeographical distribution patterns. The process of deduction would appear to benefit if there are Recent, taxonomically close representatives of the group or other analogues for comparison. However, as Fortey (1985) has clearly highlighted in a critique of methods used to deduce life habits

in trilobites, arguments based on (Recent) analogues in particular, easily become circular. Also, although commendable in providing an independent test for life habits, types of geological evidence such as patterns of distribution may themselves be open to several possible interpretations.

The interpretation of the mode of life of Silurian ostracods is partially hindered because they lack generic or species level representatives today and because of the relevant problems particular to vagile animals; denied specimens in life position, the demonstration of types of vagile habits rests solely on assessing all available circumstantial evidence (Siveter 1984). Moreover, lifestyles supposed for Silurian ostracods could, if indiscriminately applied, impose notions on where they lived in the water column and vice versa; such secondary interpretation is fraught with potential circular argument and misinterpretation (Siveter 1984). For example, possible swimming ability does not automatically denote a life off the bottom, unequivocal proof of which can never be established. If all the lines of evidence tested concur, the truest verdict for the palaeontologist is to regard it as a 'best bet' interpretation of lifestyle.
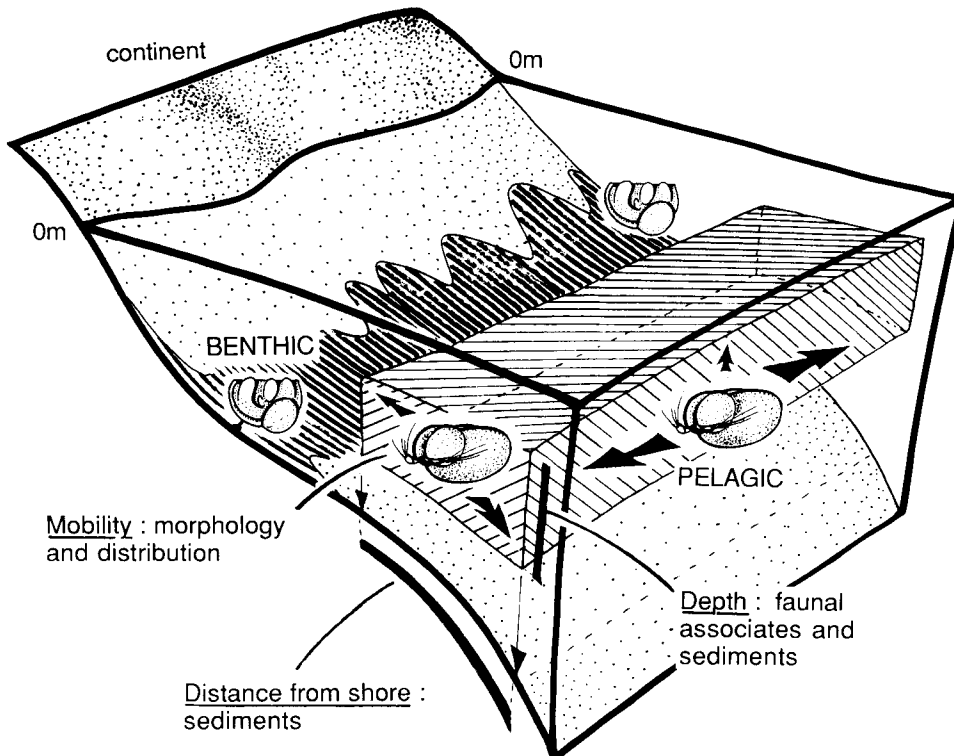
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Fig. 2 Schematic diagram of criteria used to determine lifestyles and habitats of a vagile group such as ostracods, both benthic (*e.g.* Beyrichiacean palaeocopes) and pelagic (*e.g.* myodocopes) forms.

**Abbreviations for morphological features illustrated in plates 1-3:**

al	1st antenna;	l	ligament;
a2	2nd antenna;	le	lateral eye;
am	adductor muscles;	lv	left valve;
as	adductor muscle scars;	m	mandible
b	bulb;	mu	murum;
bc	body cavity;	pr	protodite;
br	bristles;	ps	posterior sulcus
es	external surface;	r	rostrum;
f	furca;	rd	ridge;
fo	fossa;	ri	rostral incisure;
g	groove;	rv	right valve;
is	internal surface;	s	sulcus (adductorial);
		se	chemo-mechanoreceptor seta;
		t	tubercle

Explanation of Plate 1

Comparative morphology of Silurian (Figs 1-4) and Recent (Figs 5, 6) myodocope ostracods.

1. *Bolbozoe* cf. *anomala* Barrande, 1872. Left valve, external lateral view, x19; IGR. Chernire-en-Charnie, Sarthe, Armorican Massif, France; from siliceous nodules, Ludlow (or Pridoli) Series.

2. *Parabolbozoe* sp. nov. A (='*Bolbozoe*' sp. nov. A of Siveter *et al.* 1987). Right valve (reversed to appear as a 'left valve' for comparison), external lateral view, x19; BM OS 13060. Cause Castle Farm, Long Mountain, Powys, Wales; Long Mountain Siltstone Formation, Ludlow Series.

3. *Entomozoe tuberosa* (Jones, 1861). Left valve, external lateral view, x19; GSE 10812. Right bank of River North Esk above junction with Wetherlaw Linn. North Esk Inlier, Pentland Hills, near Edinburgh, Scotland; probably from the Wetherlaw Linn Formation, Llandovery Series.

4. 'Cypridinid' gen. et sp. nov. A (of Siveter *et al.* 1987). External lateral view, x17; IGR 33035. Les Buhardieres, Andouille, Mayenne, Armorican Massif, France; La Lande-Muree Formation, Ludlow Series.

5. *Vargula contragula* Cohen & Morin, 1986. Adult male left valve, external lateral view showing protruding appendages, x46, USNM 193230. Coral reef, San Blas, Panama; Recent. After Cohen & Morin 1986, Fig. 3D.

6. *Cycloleberis squamiger* (Scott, 1894). Adult female, left valve removed to show appendages and other soft parts, x21; USNM 149378A. Lagoon at Sao Tome Island, Gulf of Guinea; Recent. After Kornicker 1975, Fig.2.

Figs 1-4 are silicone rubber casts from external moulds. All scanning electron micrographs except Fig.3. For abbreviations denoting morphological features (see Explanation of Plate 3). Repositories: BM, British Museum (Nat. Hist.), London; IGR, Institut de Geologie, Universite de Rennes, France; GSE, British Geological Survey, Edinburgh, Scotland; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
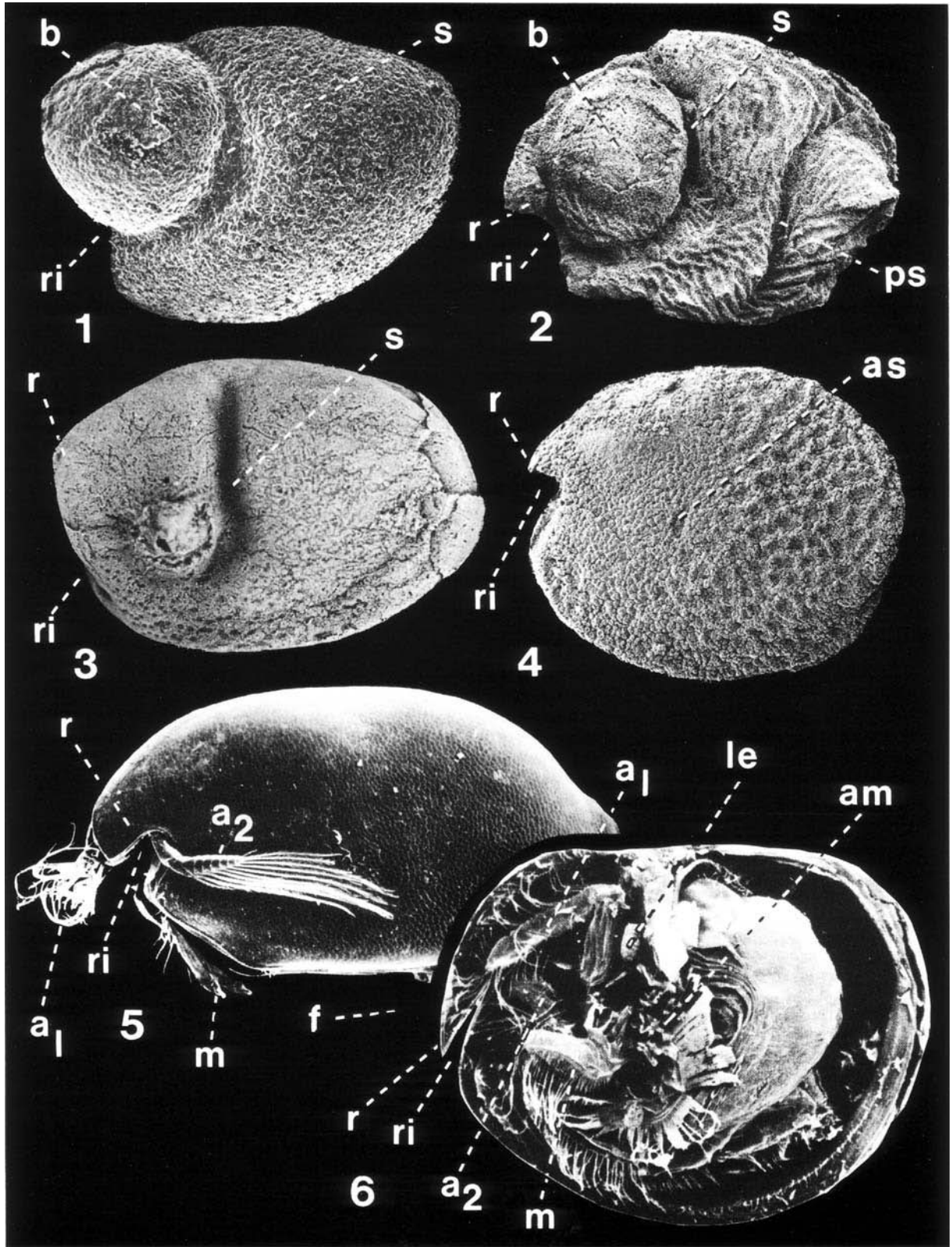
Nevertheless, although there are such problems of interpretation for fossil groups there is substantial evidence that morphological differences between animals reflect real differences in life habits and that these in turn are recorded in particular (sedimentary facies) distributional patterns of those organisms. Moreover, by also, where appropriate, contrasting the Silurian myodocopes in question with their (presumed benthic) contemporaries (*e.g.* the Beyrichiacea), serves to highlight what we recognise as a significant number of differences between the two groups that require explanation.

Deducing the lifestyle and living environment of Silurian ostracods such as myodocopes demands an assessment of their potential mobility, of the distance they lived from the shore and of their possible depth range in the marine realm (Fig. 2). Deducing their relative vagility involves assessing morphological and geological (distributional) evidence; deducing the distance from the shore and the depth in which they lived demands an assessment of chiefly geological evidence such as an analysis of associated litho-(sediments) and biofacies (faunal associates) (Fig. 2).

EVIDENCE FROM MORPHOLOGICAL 'DESIGN'

That the (bolbozoid and cypridinid) Silurian ostracods under consideration belong to the Myodocopa and that they probably had a swimming capability and, therefore, the potential for enhanced mobility can be deduced from several lines of morphological evidence (1-8 below) involving particularly a comparison between Silurian and Recent myodocopes (Pls 1-3).

1. Valve shape.

The overall, generally ovoid valve shape of typical bolbozoid and cypridinid ostracods from the Silurian (Pl.1, figs 1-4) closely accords with that of many Recent myodocopes (Pl.1, figs 5, 6), both Myodocopida and Halocyprida. From the point of view of design analysis, ostracods with smooth or ornamentally simple dome-shaped shells (*e.g.* polycopids) often live away from the benthic zone, in habitats of uniform mechanical stress, and are likely to be swimmers or even burrowers (Benson 1981). In considering the functional morphology of the shell of Palaeozoic ostracods Henningsmoen (1965) concluded that a ventrally convex (rather than flat; see also Siveter 1984) carapace most likely signifies a swimmer. By comparison an analysis of the form and function of typical, straight-hinged (beyrichiacean) palaeocopes led Siveter (1984) to conclude that their shell was designed for benthic (crawling-swimming?) modes of life.

2. Rostral incisure.

The rostral incisure, an anterior marginal opening to the carapace (and present even in closed valves), is common to most Silurian bolbozoid and cypridinid myodocopes (Pl.1, figs 1-4; Pl.2, figs 2, 3, 5, 7-10). It is protected by an overhanging beak-like feature, the rostrum. The earliest known, (Lower) Silurian myodocope has (in lateral view) a poorly differentiated rostrum and a more elongate slit-like incisure

Explanation of Plate 2

Main morphological features and functional interpretations of Silurian (Figs 2, 3, 5, 7-11, 15 right, 16) myodocope ostracods by comparison with Recent myodocopes (Figs 1, 4, 6, 12-14, 15 left).

1, 4. *Harbansus bradmyersi* Kornicker, 1978. Adult female, left valve, external lateral (1) and dorsal (4) view, x70; USNM 156688. Continental shelf off Oxnard, California; Recent. After Kornicker 1978, Pl.3, fig.a, Pl.5, fig.a.
2, 5. *Bolbozoe* cf. *anomala* Barrande, 1872. Left valve, external lateral view of anterodorsal bulb (2) and external ventral view of same area of valve (5), x20; IGR. Chemire-en-Charnie, Sarthe, Armorican Massif, France; from siliceous nodules, Ludlow (or Pridoli) Series.
3. 'Cypridinid' sp. Carapace, anterior view showing rostrum and rostral incisure, x3; IGR. Same locality and horizon as figs. 2, 5.
6. *Anarthron dithrix* Kornicker, 1975. Female carapace, anterior view showing rostral incisure; x34. Station V-18-16 (Kornicker 1975a), Vema Cruise 18, Continental Shelf of South Atlantic Antarctic region, east of Argentina; Recent. After Kornicker 1975a, Fig.228F.
7. Reconstruction of internal view of a right valve of a Silurian bolbozoid myodocope to show the possible function (accommodation of 1st and 2nd antennae, especially 2nd antenna protopodite) of the anterodorsal bulb.
8. Reconstruction of a carapace of a Silurian bolbozoid myodocope to show probable life attitude, with appendages protruding.
9. *Parabolbozoe* cf. *bohemica* (Barrande, 1872). Carapace, external lateral view of dorsally cojoined, open valves, x12; NMW 91.4G.1A.B. Friends Meeting House Quarry, near Llandegley, Powys, Wales; 'Striped Flags', *C. scanicus* Zone, Ludlow Series.
10. 'Cypridinid' gen. et sp. nov. A (of Siveter *et al.* 1987). Carapace, external lateral view of cojoined, open valves, x14; IGR 33016. Les Buhadieres, Andouille, Mayenne, Armorican Massif, France; ; La Lande-Muree Formation, Ludlow Series.
11. *Parabolbozoe* cf. *bohemica* (Barrande, 1872). Right valve, dorsal oblique view of adductor muscle scar, x105; IGR 33067. La Cultais, Vieux-Vy-sur-Couesnon, Ille-et-Vilaine, Armorican Massif, France; La Lande-Muree Formation, Ludlow (or Pridoli) Series.
12. *Thaumatoconcha radiata* Kornicker & Sohn, 1976. Adult, adductor muscle attachment scar on right valve (outer layer of shell not present), x285; USNM 143753 WW. Station 245A (Kornicker & Sohn 1976), South Atlantic, east of Argentina; Recent, depth 2707m. After Kornicker & Sohn 1976, Fig.23e.
13. *Sarsiella neapolis* Kornicker, 1974. Adult male, adductor muscle bundle attached to left valve, x125; USNM 153928. Gulf of Naples, Italy; Recent. After Kornicker & Caraion 1978, Pl.7a.
14. *Sarsiella gomoiui* Kornicker & Caraion, 1978. Adult male, adductor muscle endings, x415; USNM 156652. Station X048, Continental Shelf off Noadhibou, Mauritania; Recent. After Kornicker & Caraion 1978, Pl.24c.
15. Schematic cross sections to show the dorsal valve connection of myodocope ostracods. Left: Recent species (after Kornicker 1969). Right: possible mode of carapace opening in Silurian species (see explanation in text).
16. Schematic reconstruction of the adductor muscle and its attachment to the shell in Silurian myodocopes such as bolbozoids.

Figs 2, 3, 5, 9-11 are silicone rubber casts from external moulds. All scanning electron micrographs. For abbreviations denoting morphological features see Explanation of Plate 3.

Repositories: IGR, Institute de Geologie, Universite de Rennes, France; USNM, National Museum of Natural History, Smithsonian Institution, Washington; NMW, National Museum Wales, Cardiff.
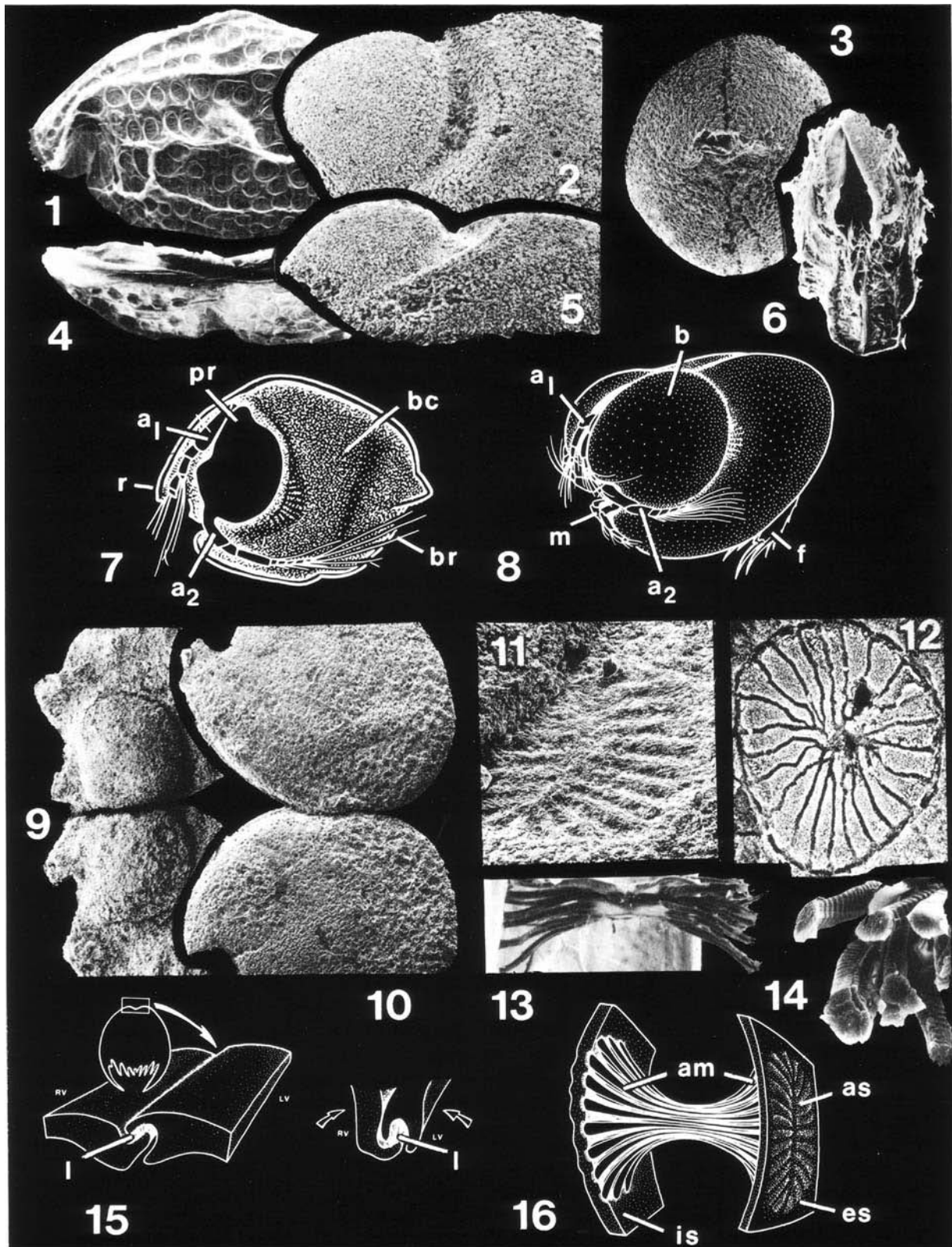
(Pl.1, fig.3). The thaumatocypridid and polycopid halocyprids lack a rostral incisure and have (polycopids only), if developed at all, only a weak rostrum. However, in most Recent myodocopids (*e.g.* philomedids, cypridinids, cylindroleberidids) and halocyprid halocyprids a rostrum and associated incisure are developed to a greater or lesser extent (Pl.1, figs 5, 6; Pl.2, figs 1, 6). The rostrum sometimes forms a prominent beak-like projection as, for example, in the active swimming Recent cypridinids, or is more indistinct along the anterior lateral margin, as in many Recent cylindroleberidids. The rostral incisure accommodates the protrusion, from within the carapace, of the long first and second appendages in order to facilitate activities of locomotion such as swimming (Pl.1, fig.5). The same activity would be possible in typical Silurian myodocopes (Pl.2, figs 7, 8) which, uniquely for Silurian ostracods, have such morphological features as a rostrum and associated incisure.

3. External sculpture: bulb.

Valves of typical Silurian byodocopes are, in essence, overall dome-like, either of simple form (cypridinids; Pl.1, fig.4; Pl.2, fig.10) or distinctive in having a prominent anterodorsal bulb and associated posteriorly adjacent adductorial sulcus (bolbozoids; Pl.1, figs 1-3; Pl.2, figs 2, 5, 9). Relatively simple, dome-like carapaces represent the most common 'architectural type' amongst Recent myodocopes (Benson 1975, 1981), as in the cypridinids (Pl.1, fig.5). Although there is a weak anterior/anterodorsal swelling and adjacent, demarcating depression in some Recent myodocope species (Pl.2, figs 1, 4), the often huge and well demarcated anterior bulb and associated sulcus of the typical Silurian myodocopes has no obvious Recent homologue or, indeed, analogue in other Silurian ostracode groups.

The function of the bulb is speculative. In Recent myodocopes the first and second antennae (swimming appendages) are well developed, often with long natatory setae and massive 2nd antennae protopodites. In Recent philomedids such appendages are accommodated in the area of the anterior valve swelling (in front of the eye and area of adductor muscle attachment), even when completely retracted to within the valve. A similar function may be postulated for the prominent bulb cavity of Silurian bolbozoids (Siveter & Vannier 1990) and, if correct, again suggests the presence of possibly similarly large and perhaps powerful appendages adapted for swimming (Pl.2, figs 7, 8).

Alternatively, bearing in mind its anterodorsal position on the valve, the fact that it often shows plastic deformation which possibly indicates a thin shell (see below), and that except for its ventralmost region it is consistently the only part of the lobal surface to lack ornament in several taxa, it is possible that the bulb on each valve was the site of some form of visual organ in Silurian bolbozoids (Siveter 1984; Siveter, Vannier & Palmer 1989). In Recent myodocopes the Myodocopida have either a median eye or a pair of visual organs ('parabolic reflectors'). The Halocyprida lack a median eye.

4. Carapace Hinge.

Unusually for ostracods Silurian myodocopes are frequently preserved in the rock in the form of open-flat carapaces, in so-called 'butterfly position' (Pl.2, figs 9, 10). The internal hingement structure of these fossils are still unknown, although from preserved open carapaces it appears that valves are hinged relatively simply but clearly effectively, either anterodorsally, above and behind the bulb (bolbozoids; Pl.2, fig.9), or mediodorsally ('cypridinids'; Pl.2, fig.10). Recent myodocopes also have a simple hinge (*e.g.* Kornicker 1969), consisting of a chitinous ligament forming a relatively short, mediodorsally to/or posterodorsally located connection between overlapping valves (Pl.2, fig.15 (left)). Hingement may be of a similar nature in Silurian myodocopes, with ligament and dorsal valve overlap arrangements permitting the occurrence of butterfly arranged carapaces on the substrate and hindering the dislocation of cojoined valves (Fig.3 and Pl. 2, fig.15 (right)).

The valves of the Silurian myodocopes in question occur on rock slabs either as separate valves or in the completely open butterfly position and still attached by the hinge, each valve having rotated through 90° since death (Fig. 3). Very rarely (*e.g.* in Brittany) they are found with both valves in the closed carapace position; they are virtually never found in any intermediate angular relationship, as may be found in bivalve molluscs. This would seem to indicate that with post-mortem decay of the adductor muscle the valves automatically open fully in that each rotates through 90°. This can only be achieved by the consequent release of tension in the hingeing ligament which must therefore be quite strong. The principle is basically the same as in bivalved molluscs but in detail shows interesting differences since there does not appear to be to be any separation into internal (resilifer)
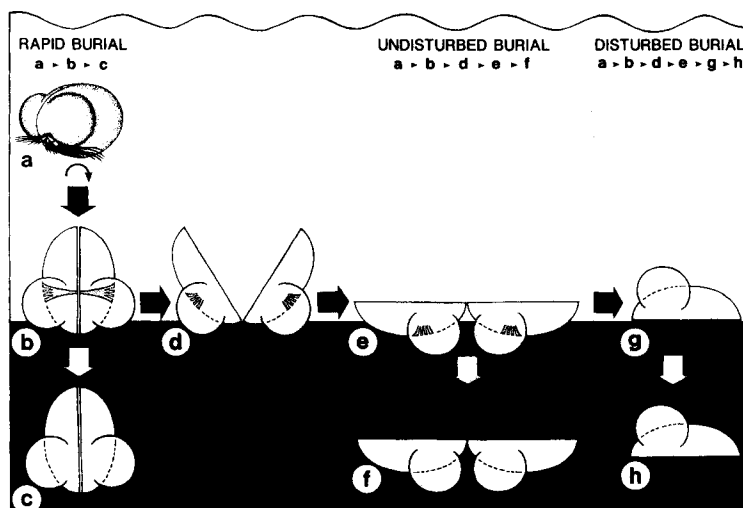

Fig. 3 Taphonomic processes affecting myodocopes in different substrate settings. **Stippled area**: adductor muscle.
Rapid burial: a, pelagic life position; b, inverted life position post-mortem, but before decay of the adductor muscle; c, burial with two valves (single carapace) in inverted life position.
Undisturbed burial: a, b, as above; d, partially open carapace (position not yet found); e, decay of adductor muscle, valves still attached by ligament (= the open 'butterfly' position); f, decay of ligament and burial without physical or biological disturbance.
Disturbed burial: a, b, d, e, all as above; g, ligament decay, separation of valves, reorientation into stable position; h, burial in hydrodynamically stable position.
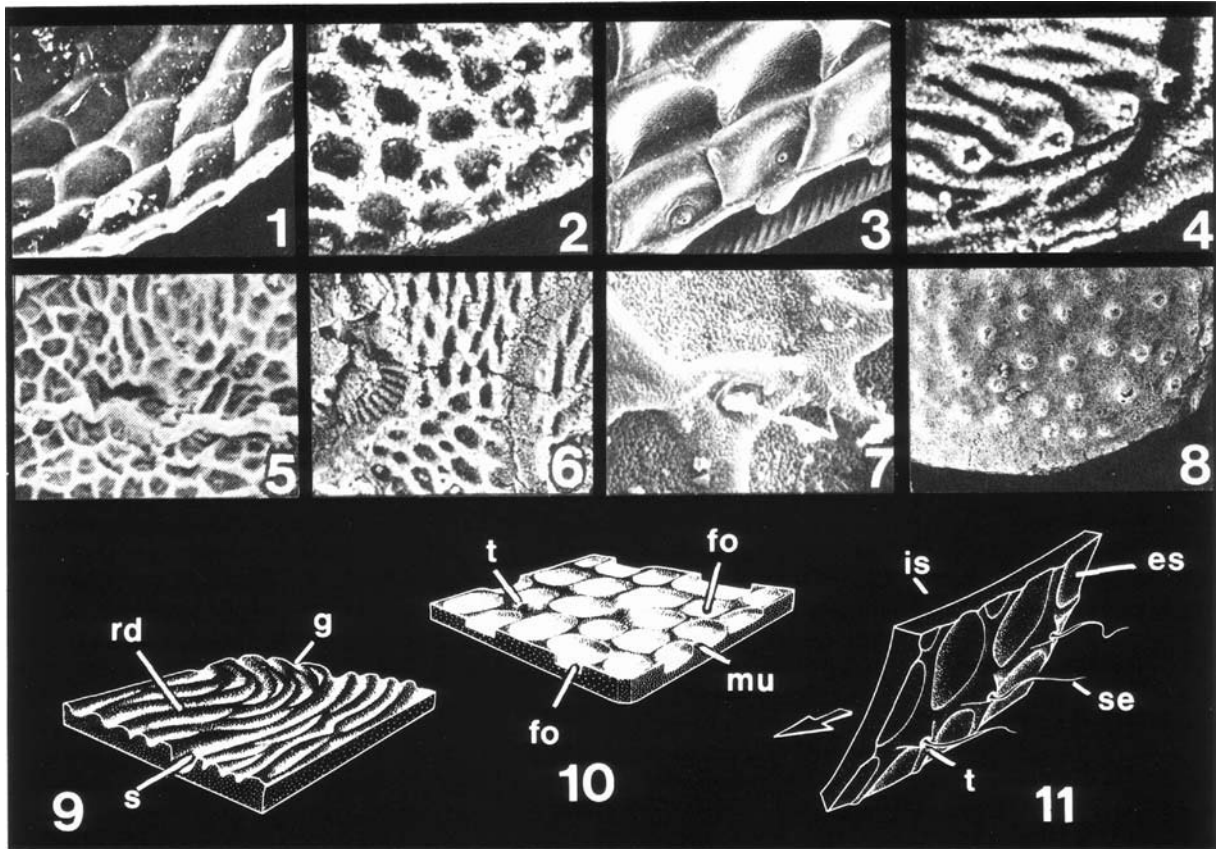
Explanation of Plate 3

Comparison of ornament (and its possible function) in Silurian (Figs 2, 4, 8-11) and Recent (Figs 1, 3, 5, 7) myodocope ostracods.

1.   *Metapolycope* sp. Anteroventral margin, showing reticulation, x350; unnumbered specimen (Kornicker & Van Morkhoven 1976, Fig.23). Denmark Strait between Greenland and Iceland; Recent, depth 1068m.

2.   *Parabolbozoe* cf. *bohemica* (Barrande, 1872). Carapace, anteroventral margin of right valve showing reticulation, x100; IGR 33057. La Cultais, Vieux-Vy-sur-Couesnon, Ille-et-Vilaine, Armorican Massif, France; La Lande-Muree Formation, Ludlow (or Pridoli) Series.

3.   *Metapolycope hartmanni* Kornicker & Van Morkhoven, 1976. Adult male, anteroventral margin showing tubercles with pores, x 830; USNM 152857. Off Recife, Brazil; Recent, depth 587m. After Kornicker & Van Morkhoven 1976, Fig.9a.

4.   *Parabolbozoe* sp.nov. A (= '*Bolbozoe*' sp.nov. A of Siveter *et al.* 1987). Left valve, ventral margin showing four tubercles with pores, x 80. IGR 33048. Same locality and horizon as Fig.2.

5.   *Scleroconcha frons* Kornicker, 1975. Male carapace, anteroventral area showing reticulation, x100; USNM 128504. Southwest Pacific, off Chile; Recent, depth c.1200m. After Kornicker 1975a, Pl.209a.

6.   *Parabolbozoe* cf. *bohemica* (Barrande,1872). Left valve, reticulation and corrugation in region behind the adductor muscle scar, x10; IGR 33069. Same locality and horizon as Fig.2.

7.   *Anarthron chilensis* (Hartmann, 1965). Female, reticulation and seta, x650; HZM K22280. Continental shelf, off Chile; Recent, depth c.110m. After Kornicker 1975a, Fig.224a.

8.   Bolbozoid gen. et sp. nov. A (of Siveter *et al.* 1987). Right valve, ventral region showing tubercles, x25; IGR 33040. Les Buhardieres, Andouille, Mayenne, Armorican Massif, France; La Lande-Muree Formation, Ludlow Series.

9.   Schematic reconstruction of corrugation, external ornament in Silurian myodocope ostracods.

10.   Schematic reconstruction of reticulation, external ornament in Silurian myodocope ostracods.

11.   Schematic reconstruction and possible (setal) function of perforate tubercles in Silurian (bolbozoid) myodocope ostracods.

Figs 1, 3, 5, 7 are shell. Figs 2, 4, 6, 8 are silicone rubber casts from external moulds. All scanning electron micrographs except Figs 2, 4, 6. Repositories: IGR, Institute de Geologie, Universite de Rennes, France; HZM, Hamburg Zoological Museum, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.

and external (C-spring) elements of the ligament as in many bivalved molluscs. It is an aspect on which further research is required. What is undoubtedly the case is that the high prevelance of butterfly-valve preservation is a phenomenon known amongst Silurian ostracods only from the myodocopes. Occasionally, straight-hinged palaeocopes (*e.g.* some Beyrichiacea in the pridoli of the Welsh Basin) are similarly preserved, but, by comparison to the myodocopes, such specimens represent very rare occurrences.

Whatever the exact nature of the hingement in the Silurian myodocopes in question it would seem to be reasonably secure in that it must be a major factor responsible for often keeping the valves cojoined post-mortem. Silurian myodocopes are commonly found in what were once oxygen deficient muds (Siveter, Vannier & Palmer 1987) and this may also have helped to prevent rapid soft part decay and carapace dislocation. The absence of benthic scavengers would also obviously help in this respect, as would the low energy environmental conditions of deposition supposed for most Silurian myodocope-bearing facies (see below).

5. Adductor Muscle Scars.

Somewhat atypically for Palaeozoic ostracods, the scars marking the attachment areas of the adductor muscles are commonly large and well developed in Silurian myodocopes, both internally and on the external surface of the valves (Siveter 1984; Siveter, Vannier & Palmer 1987). The muscle scars are characteristically radiate in Silurian bolbozoids (Pl.1, fig.2; Pl.2, fig.11) and reniform in cypridinids (Pl.1, fig. 4). In Recent myodocopes the adductor muscle scar also consists of a fairly densely packed agglomeration of tiny pinprick-like to more elongate scars, variously arranged in random fashion or often forming radiate ('rosette')-like patterns (Siveter & Vannier, 1990, fig. 17; herein Pl.2, fig. 12). Most Recent myodocope species have a powerful adductor muscle bundle consisting of many individual strands which diverge before embedding themselves in each calcified valve (Pl.2, figs 13, 14). It is reasonable to assume that Silurian myodocopes had similarly arranged strong adductor muscle fibres (Pl.2, fig.16). Well developed adductor muscles, together with a possible relatively thin shell (an adaptation for a pelagic lifestyle; see below), would help account for the fact that the associated scars are visible on the external surface of the valve in Silurian myodocopes. Possession of strong, efficient adductor muscles would be an obvious advantage in keeping the valves closed when necessary and would counteract the tendency for the carapace to open during any possible swimming activities. In contrast to the situation in Silurian myodocopes the adductor muscle scar of Silurian palaeocopes is only manifest externally (or internally) in extremely rare cases.

6. External Ornament and Sensory System.

Silurian myodocopes are characterised by three main types of external ornament (Siveter, Vannier & Palmer 1987), reticulation, corrugation and tuberculation (Pl.3, figs 2 & 10, 4 & 9, 8 & 11 respectively), which sometimes occur together on the same valve (Pl.3, figs 4, 6). Similar types of ornament occur in Recent myodocopes (Pl.3, figs 1, 3, 5, 7). Such types of ornament develop gradually and to a consistent pattern throughout the ontogeny of both Recent and Silurian myodocopes and in the case of those Silurian species studied in detail their patterns of reticulation, corrugation and tuberculation seem to be homologous (Siveter, Vannier & Palmer 1987). It seems reasonable to regard as similar both the design and possible function of 'ornament' in both the Silurian and Recent taxa. The perforate tubercles, often found aligned all over the valve surface (Pl.3, fig.8) or just ventrally (Pl.3, fig. 4) in Silurian myodocope and other coeval species (see also Siveter 1982), very likely housed sensory setae. Such setae are particularly abundant along the ventral and frontal (around the rostral incisure) margins of the valves in Recent myodocopes (Pl.3, fig. 7) and presumably act as chemo- and/or mechanoreceptors (Pl.3, fig.11), as is the case in other types of Recent Ostracoda (*e.g.* Kamiya 1989).

7. Shell Structure.

The shells of Silurian bolbozoids and cypridinids contain discrete and/or coalesced platelet microstructures of various sizes, many of which are characterised by a possibly post-mortem produced, radiate ('rosette') pattern (Siveter, Vannier & Palmer 1987). Calcium carbonate discs and spherulites (Bate & Sheppard 1982) and more irregular calcium carbonate 'nodules' (Sohn & Kornicker 1969) have been observed as forming the "shell" (*i.e.* the calcified part of the cuticle) in some Recent myodocopes. There is some conflicting evidence as to whether the calcium carbonate discs were, like the nodules, post-mortem diagenetic products or whether in fact they represent true, *in vivo*, shell calcification. Notwithstanding this doubt, the 'shell' structures observed in both Silurian and Recent myodocopes are closely alike in many fundamental respects and may well be a reflection of both the fact that similar calcite depositional processes have been operative in, and of the affinity of, the fossil and Recent forms. No such platelet or associated rosette patterns have ever been documented in the thousands of recorded palaeocope taxa.

8. Shell thickness and strength.

Since the vast majority of Silurian myodocopes are preserved as moulds there is little direct evidence of their shell thickness. However, indirect evidence suggests that Silurian myodocopes were (especially for such large ostracods) thin shelled, a feature in contrast to the thick shells of the typically lobate palaeocopes (Siveter 1984) and consistent with a pelagic lifestyle.

That most Silurian myodocopes are preserved as moulds is in itself (weak) evidence of valve thinness, particularly since associated shelled invertebrates may occasionally retain some of their carbonate. However, this may be the result of compositional differences. Firmer evidence for valve thinness comes from the plasticity of the carapaces which commonly (*e.g.* in Welsh Basin specimens) and obviously deform rather than fracture during sediment compaction (see Siveter 1984, Pl.2, fig.7; Siveter, Vannier & Palmer 1987, p.792, Pl.84, figs 2, 6). By comparison, associated shelly invertebrates with crystalline carbonate shells preserve their post-mortem compactional fracture patterns. The only Silurian myodocopes that show shell fractures are those relatively rare specimens whose valves have crystallised into a pavement or tessera of polygonal platelets and thus become more rigid (see Siveter, Vannier & Palmer 1987, Pl.86, figs 2, 5, text-fig.7). Furthermore, the fact that the muscle scar is so often prominently expressed externally may indicate, in addition to a probable strong adductor muscle, a relatively thin shell, as does the fact that fossil myodocopes are rarely found as bioclastic fragments.

It has been shown by Sohn (1977) that in modern myodocopes the initial form of carbonate in the valves is an amorphous gel evenly distributed throughout the cuticle. This non-crystalline state allows for flexibility of the shell and we have previously argued (Siveter, Vannier

& Palmer 1987) that the fossil representatives of the group may well have had a similar valve chemistry, and, consequently, physical properties such as valve strength.

From the various lines of evidence discussed above it is reasonable to conclude that Silurian bolbozoids and cypridinids show close affinities to various Recent myodocopes and, moreover, that they probably had swimming abilities. However, the ability to swim does not necessarily denote a pelagic existence off the substrate, corroboratory evidence for which must be sought in the geological nature of Silurian myodocope-bearing deposits.

GEOLOGICAL EVIDENCE

Analysis of the geological distributions of Silurian myodocopes, especially across Europe (Siveter, Vannier & Palmer 1987), endorses the notion (Siveter 1984) that some, typical myodocopes (cypridinids and bolbozoids) were probably pelagic. By and large the Silurian myodocope-bearing deposits exhibit a recurring pattern of a relatively restricted range of lithofacies and faunal associates which focus on particular environments and, taken together with broader scale palaeogeographical evidence, point to an enhanced dispersal (mobility) capability and non-benthic lifestyle for some of the myodocope ostracods.

Siveter, Vannier & Palmer (1987) discussed the main European areas of occurrence of Silurian myodocopes (e.g. the Welsh depositional basin, France, Czechoslovakia, Sardinia) and also noted their presence as far afield as Australia and China. The following data analyses the facies distribution and faunal associates of all known major Silurian myodocope faunas; the nature of their geological context in Australia (material kindly sent to D.J.S. for study by Dr L. Strusz) and China (material collected by D.P.) are detailed for the first time.

1. Environments of deposition: Sedimentary facies and faunal associates.

Scotland, China and Australia have all yielded myodocopes of Lower Silurian (Llandovery Series, Wenlock Series) age. In the Welsh Basin, France, Czechoslovakia and Sardinia the myodocopes occur in Upper Silurian (ludlow Series, Pridoli Series) rocks.

a) Scotland. i) Facies: The oldest recorded true myodocope, *Entomozoe tuberosa*, occurs in upper Llandovery Telychian Stage rocks of the Pentland Hills in the Midland Valley of Scotland (Siveter & Vannier 1990). The Pentland Hills is the most easterly of several small Silurian inliers along the southern margin of the Midland Valley graben, a complex structure some 90km wide that extends across Scotland and 500km beyond to the west coast of Ireland (see Palmer *et al.* 1989). The inliers represent part of a progressively shallowing and perhaps nearly enclosed linear Silurian marine basin (or interconnected basins) that gradually became debarred from normal marine waters and stenohaline faunas (of the Iapetus Ocean) to the south by a positive topographic barrier (plutonic-volcanic arc of Bluck 1983).

In the Pentlands *Entomozoe* occurs only rarely (and then with very particular associates; see below) in the open marine, possibly sub-littoral, silty mudstones of the Lower Member of the Wether Law Linn Formation. It is mostly found through the silty mudstones of the Upper Member of the Formation (Robertson 1985, Siveter & Vannier 1990), which underlie the continental red beds and conglomerates of the Henshaw Formation at the top of the Pentlands Silurian regressive sequence. Sedimentological and faunal evidence indicates that the

Upper Member of the Wether Law Linn Formation reflects a quiet water, nearshore, possibly restricted marine (other than normal salinities?) environment, representing a lagoon or possibly a coastal embayment (Robertson 1985, 1989).

ii) Faunal associates: Of the four, brachiopod-taxa dominated faunal associations recognised from the Lower Member of the Wether Law Linn Formation *E. tuberosa* is recorded only from the *Liospira ? simulens*-Synek association, a diverse fauna (32 genera, 32 spp.) dominated taxonomically by brachiopod and molluscan (gastropods, bivalves, cephalopods) species (Robertson 1989). Detailed analysis reveals that *E. tuberosa* in fact occurs only as a very minor constituent of this association (less than 1% of specimens), together with only a few members of the association, and at only a few levels within the Lower Member. Analysis of Robertson's data shows that the most common co-occurring associates of *E. tuberosa* in the Lower Member are, in descending order of abundance, the benthic beyrichiacean ostracod *Craspedobolbina impendens*, cephalopods, the phyllocarid arthropod *Dictyocaris* sp., the brachiopod *Trimerella* cf. *wisbyensis* and the gastropods *Spirina antiquata*, *Liospira? simulens* and *Holopea*. Moreover, *E. tuberosa* is rarely found associated with the very commonly occurring brachiopod *Eoplectodonta*, bryozoans or crinoids, all of which are sessile epibenthic animals.

The predominant occurrence of *E. tuberosa* is through the relatively low diversity, Upper Member of the Wether Law Linn Formation (Robertson 1985, 1989; Siveter & Vannier 1990, figs 14,15), where it again has virtually the same associates as in the Lower Member. The ostracods *C. impendens* and *E. tuberosa* display an inverse correlation of abundance through the Upper Member (Siveter & Vannier 1990), highest abundances of *E. tuberosa* coinciding with marked reductions in numbers of *C. impendens*. The above analysis shows that the co-occurring associates of *E. tuberosa* are predominantly vagile forms and are to a greater extent substrate independent.

iii) Conclusion: The fact that here in Scotland *Entomozoe* appears to have preferentially inhabited shallow, nearshore, possibly stressful environments, and with no records from the more open water, offshore (deeper) coeval facies elsewhere (*e.g.* the other Midland Valley Silurian inliers), combined with evidence from shell morphology, to lead Siveter & Vannier (1990) to consider these particular myodocopes as habitually vagile (swimming?) benthos (as are most of their associates: see above) and not pelagic forms.

b) China. i) Facies: Recent fieldwork (D.P.) has yielded myodocope ostracods, including material close to *Entomozoe tuberosa*, from the upper Llandovery Telychian Stage of the South China plate, in the Yangtze Platform area of South Central China., These Telychian sediments are dominantly fine-grained siliciclastics (mud-silts), but also include red beds and interbedded bioclastic limestones; they are extensively developed, being over 7km thick and occurring over some 250,000sq. km. They represent a major, rapidly subsiding, shallow marine shelf area which experienced voluminous and rapid sediment supply, but with regular interruptions of sediment input or stasis in subsidence that periodically allowed coraliferous carbonates to develop.

There is very little evidence of bottom traction currents and most of the non-carbonate sediments appear to be suspension deposits that may well have given rise to cohesionless substrates. Supporting evidence for this interpretation comes largely from the composition of the shelly fauna and particularly the shell form of many of the dominant epibenthic brachiopods (see below). Intermittent interruptions in sediment supply would have led to somewhat more cohesive

substrates colonised by a rapid succession of epibenthic forms leading to the climax coral communities. The myodocopes have been found in the siliciclastics but not in the carbonates.

ii) Faunal associates: The Chinese myodocopes are rare, with only about 20 specimens found so far from three sections within otherwise abundant faunas distributed throughout the Telychian. In the Leijatun to Jiguling road section in the Shiqian area of north-eastern Guizhou Province, south-west China, the 450m thick middle to upper Telychian (*M. greistoniensis* zone) Xuishan Formation consists of yellow-olive mudstones and bioclastic limestones. Some of the mudstones are quite fossiliferous; brachiopod species (*Nucleospira calypta, Aegiria* sp., *Nalivkinia* sp.) dominate an otherwise moderately diverse fauna of cephalopods (*Sichuanoceras cylindricum, Sichuanoceras "parcum", Sichuanoceras quadratum, Sichuanoceras stenosiphanonatum, Sichuanoceras submarginale*), trilobites (*Coronocephalus* spp., *Kailaia intersulcata, Parakailia* sp.) and rare bivalves (*Nuculoides* sp., *Technophorus* sp., rostroconchs) and graptolites. One horizon (TT 742) near the middle of the formation yielded a single myodocope from amongst the usual, abundant dominants.

The hillside section in the valley of the Jia Lin River and road from Chaotian (north-east Sichuan Province) to Ningqiang (south-west Shaanxi Province) is also a very thick succession (about 2km) of the *M. greistoniensis* Zone, upper Telychian Ningqiang (414m) and Shenxuanyi (1386m) formations. The lower part has coraliferous mud-mounds and passes up into dominantly grey-green mudstones containing four substantial (up to 30m thick) bedded carbonate horizons. The latter are coral dominated and have subordinate bioclastic limestones with mixed coral, trilobite, brachiopod and cephalopod faunas broadly similar to those of the coeval Xuishan Formation. About 165m above the base of the Shenzuanyi Formation (locality TT 604) grey-green mudstones, with interbedded limestones, yield the ubiquitous, relatively low diversity brachiopod-trilobite fauna (*Spinochonetes* spp., *Aegiria* sp.; *Coronocephalus* spp.), graptolites (*Dictyonema* sp., *Monograptus* sp., *Octovites* cf. *spiralis*) and a myodocope specimen.

The Ningqiang and Shenzuanyi formations are also exposed 30km to the north-east, in the Yushitan-Shizuizigon section near Ningqiang. About 500m below the top of the 1500m thick Ningqiang Formation (localities TT 174, 175) myodocopes were collected from, again, green-grey shales within similar and yet more diverse brachiopod (14 spp.) - trilobite (6 spp.) faunas: *Aegiria* cf. *greyi, Aegiria* sp., *Atrypa* sp., *Cryptatrypa ovalis, Cryptatrypa* sp., *Leptostrophia* sp., *Megaspinochonetes* sp., *Mesopholidostrophia minor, Nalivkinia* sp., *Quangyuania ovalia, Salopinella minuta, Spinochonetes notata, Spinochonetes* sp., *Striispirifer* cf. *hsiehi; Chuanqianoproteus constrictus, Chuanqianoproteus affluens, Coronocephalus qianjiangensis, Encrinuroides enshiensis, Kalia* sp. and *Scharyia* sp. Some 800m further down the sequence green-grey shales (occurring with small bioherm mud-mounds and thin interbedded limestones) of broadly similar faunal composition also yield myodocopes (locality TT 277).

These and other new myodocope-bearing Chinese faunas are at an early stage of investigation (Siveter & Wang in prep.). Inevitably with such thick successions, the preliminary faunal lists for individual localities represent 'lumped' data from perhaps a metre or more thickness of rock. Nevertheless, it is clear that these mudstones faunas are dominated numerically by brachiopod specimens, although more

trilobite or cephalopod taxa may be recorded at some localities. The common brachiopods are mainly small, thin-shelled species, many of which have flat or concave-convex valve forms (e.g. *Aegiria*) and/or are spinose (e.g. *Spinochonetes*). Even some species with more inflated valves are highly spinose (e.g. *Nucleospira*). Such adaptations to these adult, non-pedunculate brachiopods allowed the colonisation of soft cohesionless mud substrates by increasing the surface area of support. Even if the physical nature of the substrate was unsuitable for some animals, the fact that it was often colonised by numerous epibenthic, free-living brachiopods and vagile trilobites, cephalopods etc., that were largely independent of substrate conditions, indicates that the bottom waters were well oxygenated. This picture is supported by the presence of numerous bioclastic carbonate-rich intervals with quite diverse coral faunas, presumably reflecting relatively shallow, shelf waters and also periods of clearer, less turbid waters in which the (unprotected) suspension feeding corals settled to establish colonies of up to 20cm in diameter. The Chinese brachiopod genera are largely cosmopolitan but the trilobites, although showing some affinities with Australia (encrinurids; P.D. Lane pers. comm.) are largely endemic.

iii) Conclusion: With regard to the life habits of these Chinese myodocopes, the evidence from the sediments and associated (shelf) fauna is equivocal.

c) Australia. i) Facies: The Wenlock 'gap' in the known stratigraphic range of Silurian myodocopes can to some extent be filled by a recently rediscovered myodocope-bearing fauna (D.L. Strusz pers. comm.; see Siveter, Vannier & Palmer 1987, p.784) from the Canberra district, Australia. Currently being investigated (Siveter *et al.*), its taxonomic identity and affinities with the other known (and rare) Wenlock myodocopes, from Wales, Britain, have yet to be established.

Australian '*Entomis*' were found by Strzelecki (Jones 1884), presumably in the 1840's when the Polish geologist was exploring south-east Australia with Joseph Beete-Jukes and discovered Palaeozoic strata in New South Wales. If so, they represent probably the first ever finds of Silurian myodocopes. At the locality in question, now believed with some certainty to be Coppins Crossing (not far downstream on the Molongo River from Yarralumla House: Strusz 1982, fig.1), both the lithology and fauna correspond closely with Jones' (1884) account for the myodocopes, being internal 'casts' in shelly mudstones. Unfortunately, the actual specimens referred to by Jones cannot currently be traced (in prep.).

The myodocope-bearing sediments are brown, lenticular, fine-grained, blocky mudstones, some 5m thick, interbedded with halysitid coraliferous limestones within the Walker Volcanics. The latter are presumed shallow water (Strusz 1982) dacitic ignimbrites of probable late Wenlock age, although an earliest Ludlow age cannot be excluded (see Jell & Talent 1989). The mudstones are thought to be volcanogenic and possibly represent a submarine slump or slurry deposit, in which a prolific, shallow shelf brachiopod-trilobite dominated shelly fauna was transported (Strusz 1982).

ii) Faunal associates: The mudstones at Coppins Crossing have bedding poorly defined by somewhat irregular shell layers. Strusz (1980, 1982) records small trilobite excuvae (e.g. *Calymene, Cheirurus, Cromus, Encrinurus* and *Proteus*; mostly smaller than 1cm rarely larger than 3cm size), small brachiopods (24 spp.) and rare corals, gastropods, cephalopods, bryozoa, sponges and myodocopes (we have noted some 50 specimens = 2% of the fauna). The fossils are broken, disarticulated and characteristically randomly orientated,

with mud matrix generally separating individual specimens. Although not noticeably abraided, fossils are concentrated to some extent in bedding parallel lags and are clearly transported, perhaps within a mud flow (Strusz 1982) rather than by a traction current.

The shallow water assignation for the fauna (Strusz 1982) is largely based on interpretations of the general stratigraphic context of the mudstones and their associated ignimbrites. Nearly all of the brachiopod genera in fact span Boucot's (1975) benthic assemblages 3-5 (and thus possibly represent mixed assemblages) and are cosmopolitan. The trilobites are equally cosmopolitan and have particular affinities with Asia and Europe.

iii) Conclusion: There are no purely sedimentological and/or palaeoecological criteria which would, in themselves, argue for a pelagic habit for these particular myodocopes of presumed shelf provenance.

d) The Welsh depositional basin. i) Facies: Much of the myodocope material under consideration in this paper comes from Upper Silurian strata and especially from the lower Ludlow of the Welsh depositional basin (Siveter, Vannier & Palmer 1987). In fact, the Long Mountain (Palmer 1970) in the Welsh Borderland has provided more myodocope-bearing localities and horizons than any other area in the world: over 200 of some 1500 fossiliferous localities within its 40 sq km of Ludlow Series outcrop. Within the Welsh Basin myodocopes occur in 'Denbigh', Clwyd; the Long Mountain, Powys and Shropshire; and the Montgomery and Radnor areas of Powys. Thus, myodocopes have been found only from the off-shelf slope/axial regions of the basin (Fig.1).

The basin itself is a relatively restricted early Palaeozoic trough of rapid sedimentation, occurring between the Midland Platform to the east/south-east and the Irish Sea Platform to the west/north-west. The whole region is generally regarded (e.g. Pickering et al. 1988) to have its origins as part of the (originally Gondwanan, southerly latitudinal) microcontinent of Eastern Avalonia. Woodcock (1990, p.544) assigns the Silurian sequence of the basin to "a dominantly non-volcanic setting either on an active margin or in a collision zone". The earlier tectonic setting of the basin was extensional but by Silurian times is thought to have become transpressional.

The Ludlow deposits of the off-shelf slope/axial (deeper) parts of the basin are genetically disparate within a broadly siliciclastic framework. They include allochthonous sand turbidites, mud turbidites and silt storm deposits, all of which have been transported from adjacent shelf areas into the topographic 'lows' of the basin. Such deposits are interbedded with the more autochthonous, background hemipelagic, myodocope-bearing laminated muddy silts, which are characterised by alternating silt and organic carbon enriched laminae (3-4 per mm; Dimberline et al. 1990). This is the so-called 'Striped Flag' or 'Ribbon Banded' lithology (Kirk 1947, Warren et al. 1984; see Siveter, Vannier & Palmer 1987). The silt layers have a mottled appearance due to the presence of silt-clay aggregates of up to 2mm diameter. Essentially unbioturbated, the muddy silts are usually found interbedded with turbiditic deposits (Cave 1979, Cave & Hains 1986) but also extend laterally beyond the basin lows with their turbiditic infills, lapping on to the slopes of the basin and even draping over basin highs such as the Berwyn Ridge. Thus, in addition to vertical repeat sequences, geographical distributions emphasise a close horizontal association of the two facies.

The laminated muddy silts have been interpreted as hemipelagic sediment that accumulated by slow rain through the water column, and

was intermittently interrupted by incursions of turbidite flows. Where the turbidity currents were at their most energetic their erosive power removed much of the hemipelagic sediment. Consequently, laminated hemipelagite is best preserved where thin mud turbidites of low erosive power occur. Dimberline et al. (1990, p. 694) have also discussed the possibility that such laminated hemipelagites 'could have resulted from the re-establishment of water stratification and oxygen depletion of bottom waters between storm events". This type of laminated lithology can only have formed and been preserved where the bottom waters, and/or interstitial waters immediately below the water-sediment interface, were sufficiently low in oxygen to have prevented the oxidation of organic matter and the establishment of a (bioturbating) infauna.

Furthermore, it is clear that the geographical distribution, axial within the basin, of these Silurian myodocopes is generally separate from that of the dominant benthic (e.g. palaeocope) ostracod associations of the contiguous shelf areas (see Siveter 1984, 1989; above and Fig.1 herein). There are some records of such benthic forms from offshelf and more axial, basinal sequences. However, these rare occurrences are largely restricted to either the bases or tops of calcareous (carbonate cemented) clean silt beds within the laminated muddy silts. Such calcareous silts show many characteristics of distal turbidite or tempestite storm deposits. Whatever their genesis, both interpretations involve derivation from shelf areas and their high energy sources empowered transport of the biogenic material into the more offshelf parts of the basin. Large bioclasts, in the form of generally disarticulated and current-orientated shells of typical shelf dwelling macro-invertebrates such as brachiopods and trilobites, are confined to the soles of such beds as a graded fraction. The smaller meiofauna (e.g. palaeocope ostracods) or less dense skeletons (e.g. graptolites, crinoid columnals) are generally found in the uppermost laminated interval (Bouma D division). Again, any linear elements (e.g. graptolites) may be current-orientated. In these situations the benthic ostracods are essentially bioclasts transported as part of the sediment load of the turbidite, originating from the shelf. Such fine distinctions, between the lithological context of various (transported as opposed to in situ) faunal components of a sequence, are not recorded in faunal lists for the Welsh Basin Ludlow, where fossils from different beds within a single collecting locality tend to be lumped together.

ii) Faunal associates: In the Welsh Basin myodocopes generally comprise a minor element of a very particular and recurring faunal association, a picture demonstrated below by detailed examination of two Welsh Borderland localities.

From Friends Meeting House Quarry (SO 138 641; see Siveter, Vannier & Palmer 1987, p. 786), Llandegley, Powys, some 50km south of the Long Mountain, the first 100 fossiliferous samples we collected (D.J.S. & D.P.) were analysed for specimen frequency. They produced 120 graptolite colonies (12 P. dubius, 33 C. scanicus, 56 S. chimaera semispinosus, 15 S. varians, 4 B. bohemicus); 111 separate and 27 pairs of myodocope valves (= 75+ individuals; mostly P. bohemica, but including at least 3 other species); 20 orthoconic nautiloids; 6 brachiopods (A. grayi); and 9 bivalve specimens (2 S. fibrosa, 2 Cardiola sp., 5 bivalve sp. indet.). Graptolite individuals dominate, although their species frequency may be matched by myodocopes. Orthoconic nautiloids (rarely with small epifaunal pisocrinids attached; presumably post-mortem, but needs further investigation), brachiopods and bivalves are minor associates of this

essentially rather low diversity fauna. Apart from localities in the Armorican Massif (see below), this is the only other known locality where myodocopes are close to being a dominant faunal element.

Secondly, from Garbett's Hall Mill, beside Cwm y Sul (SJ 082 259), Buttington, Powys, in the Long Mountain, two 30cm samples from horizons 2.5m stratigraphically apart were broken down until in excess of 100 fossils were obtained (D.J.S. & D.P.). Horizon A yielded 142 fossils representing some 95 individual organisms. Except for some fragmented, large, thin-shelled cardiolid bivalves, crowded on a bedding plane with parallel orientated orthocones, other bivalves and a few myodocopes (clearly representing a current-transported assemblage), the fossils are mostly entire. Small pterineid bivalves (up to 1cm long; two species, total 38 individuals) and graptolites (mostly *S. varians*; 33 individuals) dominate the assemblage. Minor associates include orthoconic nautiloids (indet. spp.; 13 specimens), cardiolid bivalves (two individuals) and myodocopes (*P. bohemica* and at least two other species; 12 individuals). Horizon B was collected twice, once in as unbiased a way as possible for comparison with Horizon A, and again specifically for myodocopes. The unbiased collection yielded 174 fossils with the same taxonomic and abundance characteristics as Horizon A samples. Recollection produced 77 myodocope valves, 62 of which were unequivocally *P. bohemica* with 26 of these preserved as dorsally joined, butterfly position specimens.

The same sort of taxonomic abundance of the myodocope-associated fauna can be demonstrated from a quite independent source. Kirk (1947), the first person to describe this faunal association from Wales, recorded 19 myodocope-bearing localities, of which 17 yielded both orthoconic nautiloids and graptolites. 13 had pterineid bivalves and 9 had cardiolid bivalves. A minority of localities yielded several species of brachiopods and other bivalves, most of which are transported shelf benthos (see above). Thus, in the Welsh Basin myodocopes generally comprise a minority element of a graptolite-orthoconic nautiloid-bivalve fauna, an association (Watkins & Berry 1977; Palmer 1989, 1991) of mostly pelagic animals and of which the bivalves are the only autochthonous, epibenthic element. At Garbett's Hall Mill a notable percentage of pterineid valves (10 out of 67) were preserved cojoined in the open butterfly position. Both the planktonic graptolites and the nektonic orthoconic nautiloids are, of course, not strictly autochthonous and both may be found current orientated, by bottom currents at velocities within the lower flow regime (parallel grain orientation). In marginal and off-shelf environments it appears that environmental stresses (?low oxygen - dysaerobic conditions, unsuitable substrates) prevented benthic brachiopods from becoming established. Certain bivalves, such as pterineids and cardiolids, were either especially adapted for such conditions or were more tolerant and opportunistic than the brachiopods and able to flourish there in a similar way to that in which they colonised stressful shallow water environments that were equally unsuitable for brachiopods.

iii) **Conclusion:** In summary, pertinent palaeogeographical (off-shelf) and facies (close association with laminated hemipelagites and low oxygen levels) distributions, when taken together with other, palaeontological criteria (faunal associates and taphonomic data), are in themselves strong evidence for a pelgic habit for these Welsh Basin myodocopes. This notion is further supported by other geological evidence, namely the wider palaeogeographical distribution of particular taxa (see below).

e) **Sardinia. i) Facies:** Silurian myodocopes occur in south-west Sardinia and have recently been collected (D.P.). They occur in a complex sedimentary and tectonic context, being found mostly within displaced limestone blocks (Palmer & Gnoli 1985), which themselves represent a variety of microfacies (Ferratti 1989) of different ages (conodont evidence; Serpagli 1971). In this part of Sardinia four such carbonate microfacies occur in the Wenlock to Pridoli interval; a further two microfacies occur in the Lochkov. Myodocopes are mainly found in two of these microfacies, an '*Orthoceras* limestone' (Ludlow) and a micrite (Pridoli).

In the 45m thick Fluminimaggiore Formation at Fluminimaggiore village (Gnoli *et al.* 1990), the displaced blocks represent three carbonate microfacies. Stratigraphically these blocks occur above Llandovery black graptolitic shales and below Pridoli micritic limestones and lower Devonian nodular limestones of the Mason Porcus Formation (Gnoli *et al.* 1988). The sediments of the limestone blocks show no tectonic deformation and very little compaction, flattening or crushing. Nor is there any evidence of post-depositional, pre-lithification substrate disturbance, as aligned (bedding parallel) geopetal infills, mainly of orthconic nautiloid shells, are common. The break-up of these bedded limestones into separate blocks is therefore post-lithification and of pre-late Pridoli age. The exact timing and nature of the event is unknown but it seems to have involved some major submarine disturbance (faulting?) of normally stratified and massive limestones (up to 2m thick) and their transport and subsequent accumulation down slope. The blocks occur neither as rounded boulders, brecciated small pieces, nor sheared or tectonically deformed pieces. Unfortunately exposures are small, and it is difficult to determine detailed relationships of individual blocks and their matrix. At Fluminimaggiore myodocopes occur in a poorly washed, Ludlow biosparite carbonate microfacies (peloid-cephalopod-ostracod packstone-wackestone), the presence in which of fragmented shells (ostracods), bimodaly orientated orthocone shells, shelter porosity and micrite have indicated (to Ferratti 1989) high energy, shallow water deposition, perhaps within wave base (Gnoli *et al.* 1979).

Myodocopes have also been found (see Palmer & Gnoli 1985) in the younger (upper Ludlow - Pridoli), bioturbated micritic limestones (dark laminated mudstone to wackestone) of the Mason Porcus Section. Here the carbonates form a more normally stratified succession and are less fossiliferous than the older limestones. Shell laminae and lags in the micrite are thought to represent phases of high energy (storm events?) in otherwise quieter water deposition with some bioturbation.

The four other carbonate microfacies in south-west Sardinia only very rarely contain myodocopes. They include graptolitic packstones (generally current orientated); 'coated grain' biomicrite, either representing high energy wave base sediments or secondarily derived from such an environment; pre-nodular mudstones, often iron oxide enriched with shell lags; and crinoid bioclastic packstone (confined to the latest Silurian-early Devonian). In the latter the crinoids are completely disarticulated but include complete scyphocrinitid loboliths (floats).

Thus it can be seen from the above data that most of the carbonate microfacies of Sardinia show some features of possible shallow water origin. However, palaeontological evidence (see below) indicates that they should not be considered as typical shelf carbonates.

Silurian deposits in south-east Sardinia are characteristically euxinic black graptolitic shales. They form a condensed sequence (less than 40m) for the whole of the Llandovery to Wenlock and lower Ludlow, before passing up into upper Ludlow and Pridoli carbonates (over

30m) similar to those of south-west Sardinia (Barca & Jaeger 1990). The Wenlock to lower Ludlow (shale) part of this sequence (less than 30m thick) closely compares in almost all aspects with the coeval black graptolitic shale sequence of Thuringia and neighbouring Saxony, Germany. Moreover, it is clearly in marked contrast to the facies of the limestone blocks of Fluminimaggiore. The latter occur some 90km to the west, across a major tectonic feature (north-west, Oristano to south-east, Cagliari) separating the so-called 'external zone' of the south-west from the central 'nappe zone'. Interestingly, Sardinian myodocopes have been found only in the 'atypical shelf' carbonates and not from these black shale sequences, a factor which in itself might argue against a pelagic habit for these particular ostracods.

ii) Faunal associates: The myodocopes of south-west Sardinia are part of an unusual and interesting shelly fauna, from a few localities near Fluminimaggiore, that has been known for nearly 150 years (Meneghini 1857). A rich orthoceratid nautiloid assemblage was originally described (Meneghini 1880; see Gnoli & Serpagli 1977) from some 'cephalopod limestones'. Canavari (1900) monographed the associated myodocopes; however, only one of his three *Bolbozoe* species and three of his '*Entomis*' species were based on any more than a few specimens. Canavari obtained the whole fauna by calcining *ex situ* limestone blocks found in dry-stone walls around the Xea Sant'Antonio area of Fluminimaggiore (Palmer & Gnoli 1985).

Just as the ages of these various allochthonous blocks of '*Orthoceras*' limestone differ within a certain range (Wenlock - Ludlow), so do their microfacies and macrofauna. Within this part of the south-west Sardinian Silurian succession the four different carbonate microfacies (Ferratti 1989) contain two main faunal assemblages. There is an orthoceratid dominated assemblage and a virtually monotypic graptolite dominated assemblage; admixtures of the two are rare. Within the orthoceratid-rich assemblage the pelagic nautiloids are by far the dominant taxonomic group, both numerically and in diversity (39 taxa), with bivalves (mainly juvenile cardiolids), gastropods and myodocopes as minor constituents (less than 5% of specimens). However, the myodocope (?) '*Entomis*' *migrans* can form up to 60% of the skeletal clasts in some blocks (Ferratti 1989, text-fig. 4). As in the Bohemian '*Orthoceras*' limestones, the abundant orthoconic shells are invariably current orientated (Gnoli *et al.* 1979 and below). Gnoli *et al.* (1979) considered that the facies of the orthoceratid dominated assemblage represents shallow shelf conditions, albeit with anoxic bottom waters, whilst Jaeger (1976) suggests that it reflects deep water within Palaeotethys.

Although the Mason Porcus carbonates are less fossiliferous than the older limestones, they have a greater diversity of higher taxa. Thus, the sparse macrofauna consists mainly of orthoconic nautiloids (10 species), graptolites (*Monograptus* sp.), and bivalves (*Cheiopteria bridgei*, *Lunulacardium* sp., *Dualina* sp.), with rare phyllocarids (*Ceratiocaris* cf. *bohemica*), myodocopes and a single rhaphiophorid trilobite (*Ampyx* cf. *roualti*; see Palmer & Gnoli 1985). The conodont assemblage is typical of the Pridoli *Ozarkadina remscheidensis eosteinhornensis* Zone (Gnoli *et al.* 1988). Some 2-3 metres above the level of this fauna crinoidal limestones yield scyphocrinitid loboliths and a Lochkov conodont fauna.

Thus, the Sardinian myodocopes are associated with a recurring fauna basically similar to that found with, for example, the Welsh Basin Ludlow myodocopes. It is the pelagic, orthoconic nautiloid - graptolite association, with large nektonic phyllocarids. Indeed, Ferratti *et al.* (in Press) conclude that in Sardinia there was a regionally continuous sedimentation involving almost exclusively "pelagic environments" (albeit, in their opinion, relatively shallow ones) during the Silurian and into the Devonian. The small, spinose and blind rhaphiophorid trilobite may well also have been pelagic. Again, as with the Welsh Basin fauna, bivalves are the only significant sign of a benthic epifauna, the typical brachiopod dominated, epifaunal, shelf shelly invertebrate fauna being conspicuously absent. In this respect, clearly the possible occurrence of anoxic bottom conditions is significant and, not least, for the implications this has for the lifestyles of the concomitant myodocopes.

iii) Conclusions: Overall, the combined palaeontological and sedimentological data indicates that the Sardinian myodocopes are probably part of a non-benthic faunal association.

f) Czechoslovakia. i) Facies: In the early Palaeozoic Prague basin, Silurian myodocopes were first found by Barrande (1872) and his collectors in the mid 19th Century. Unfortunately Barrande's cited localities and horizons are often vague and unreliable or lost and mostly cannot be recollected. Boucek (1936) determined an *Encrinurus-Calymene* level (= within the Ludlow Series Kopanina Formation) of occurrence for some finds of *Parabolbozoe bohemica*, based on the associated occurrence of the trilobite *Encrinurus* (-*Cromus*) *beaumonti*. Recently Pribyl (1988), although also generally vague regarding the geological occurrence of the ostracods he discusses, does again indicate that *P. bohemica* is found in the *Cromus beaumonti* 'horizon'. Although this use of the term horizon in the sense of a biostratigraphical marker is inappropriate (*E. beaumonti* occurs at several horizons in the Kipanina Formation, Snajdr 1985; this fauna was recognised as an *E. beaumonti* - smooth atrypid community by Havlicek & Storch (in Press)), it does provide another example (and therefore palaeoecological link) of the association of myodocopes with encrinurids, as in Australia and to a lesser extent in China and Scotland. Pribyl also comments that *Bolbozoe* aff. *anomala* occurs in the *Scyphocrinites* horizon at the base of the Devonian Lochkov Series; interestingly, myodocopes have been collected (D.P.) from a similar, high horizon in Sardinia (in prep.).

With the aid of Czechoslovakian colleagues, new myodocope faunas have recently been recollected (D.J.S.) from Czechoslovakia. They occur predominantly as mould faunas in the Ludlow (Siveter, Vannier & Palmer 1987); for example, *P. bohemica* (and '*Entomis*' *migrans*) from the middle part of the Ludlow, in the *Monograptus fritschi linearis* Zone, at Holy Vrch Hill near Lounin. These myodocopes occur in fossiliferous micrites (dark, platy, laminated, fine-grained, carbonate mudstones) similar to one of the Sardinian myodocope-bearing carbonate microfacies except for the lack of bioturbation. '*Entomis*' *migrans* (myodocope?) also occurs in Czechoslovakia in more carbonate rich horizons.

The essentially low terriginous, biogenic myodocope-bearing Silurian deposits of Sardinia and (sometimes) Czechoslovakia are the classic so-called 'Cephalopod' or '*Orthoceras*' limestone related facies for which it is obviously difficult to separate palaeontological from sedimentological criteria. The terrigenously derived clastic component of these Bohemian sediments is low (less than 15%; volcanogenic origin), as it is in the Sardinian carbonates (less than 5%). Although the Ludlow sequence is relatively thin and condensed, again, as in south-west Sardinia, there is ample indication of traction currents. Many fossils, especially the orthoconic nautiloids and graptolites are parallel orientated and often consistently so through many centimetres; bottom currents of fairly consistent velocity and

direction persisted over a considerable time span. Thus, there is evidence from Czechoslovakia and Sardinia of broadly similar depositional regimes. Each contains bioclastic carbonate components (*e.g.* ostracods) but are seemingly debarred from types of shallow shelf clastic and deeper water turbiditic depositional processes. Moreover, the carbonates present in both areas show no reefal structures; however, certainly in the case of the Sardinian carbonates, there is some evidence of possibly shallow water (shelf) depositional features. As in Sardinia, the sedimentary and palaeontological (see below) context of the myodocope-bearing deposits of Czechoslovakia may be best interpreted in terms of atypical shelf environments, perhaps topographic lows (troughs) within (on the outer part of ?) the shelf itself. Indeed, Horny (1962) regarded the 'Cephalopod' limestones and the calcareous shales as the most offshore tongues of the Ludlow carbonate development in Czechoslovakia (see Chlupac 1987). However, it is fair to say that other authors (*e.g.* Kriz 1979) regarded some of the cephalopod associated carbonates in Czechoslovakia (and in Sardinia; see above) as rather shallow water deposits.

ii) Faunal associates: The Silurian faunas of Bohemia are, overall, dominated by a great diversity and abundance of shelly, shelf, benthic invertebrates, especially brachiopods, trilobites, bivalves and cephalopods etc. From time to time, small coral-stromatoporoid build-ups occurred. Overall, myodocopes are very rare elements of this fauna. From amongst the several thousand Czechoslovakian species which Barrande described, there were only three myodocope species, based on a few specimens.

Within the new but still rare sites (*e.g.* Holy Vrch Hill; see above) yielding myodocopes in the Kopanina Formation the ostracods are reasonably common on certain bedding planes. Much work is now needed on their taxonomy and ecology. In the platy carbonate mudstones (chiefly bolbozoid) myodocopes occur as moulds or as degraded carbonate; in more pure limestones *E. migrans* is preserved as calcium carbonate shells, sometimes in large numbers (Siveter 1984, Pl.2, figs 12, 13). The myodocopes are accompanied by orthoconic nautiloids, graptolites and occasional bivalves and plyllocarids. They represent, by general standards of fossil abundances in Bohemia, a numerically insignificant component of the Silurian fauna; recent reviews of relevant communities (*e.g.* Havlicek & Storch, in Press) fail even to mention the myodocopes. These community schemata reflect a complex division of shelf benthos of the area (Havlicek & Storch recognise 24 Silurian - Lochkov communities), resulting from an original diversity of topography and facies. Synsedimentary faults dissected the shelf into linear basins of differing rates of subsidence; fault-controlled volcanoes provided much of the clastic input into the area.

Because of these complex local facies and faunal changes, correlation within the basin has sometimes been difficult. Successful international correlation is achieved at some horizons, notably at the level of the Siluro-Devonian boundary; however, considering graptolites are usually present, correlation from the Prague Basin is sometimes still difficult. A degree of endemism seems to have developed amongst, for example, the graptolites, especially in the Ludlow. Thus, the Upper Silurian myodocopes have a potential biostratigraphical significance beyond their impoverished numerical and taxonomic abundance in the area.

The cephalopod-graptolite-bivalve myodocope-related assemblage typifies possible marginal to off-shelf environments and 'quiet water', topographic lows on the shelf in the Prague Basin. These areas of fine-grained mud and silt deposition are often associated with lowered oxygen levels (lack of bioturbation; presence of lamination; low diversity, mostly pelagic fauna), both in the lower part of the water column and in deposits near the sediment/water interface. There is an obvious lack of benthic fauna, except for the occasional presence of bivalves, which seem to have adapted to this chemically stressful environment away from competition from the dominant shelf brachiopods. The abundance in the other, non myodocope-bearing, Silurian beds of shelf shelly benthos suggests that, in contrast, most of the Silurian basin was well oxygenated; moreover, nutrient-rich waters may have emanated from the local volcanic centres. Nevertheless, throughout especially the Ludlow there were these areas of fine-grained mud deposition, less well ventilated, bottom waters/substrates and (now) containing myodocope associated assemblages; such areas are found especially in the eastern part of the southern segment of the Silurian outcrop. Havlicek & Storch (in Press) characterise this 'community' as consisting mainly of epibyssate bivalves (*Cardiola, Mila, Tenka* and *Dualina*), that used vacant orthoconic nautiloid shells as substrates for attachment; some rare trilobites (e.g. *Cromus, Cerauroides, Deckmannites*); and a few pedunculate brachiopods (e.g. *Stenorhynchia, Lissatrypa*).

iii) Conclusion: Combined sedimentological and palaeontological evidence suggests that the typical Ludlow myodocopes of Czechoslovakia were non-benthic forms.

g) Armorican Massif, France. i) Facies: Sedimentologically the Armorican localities differ from all other myodocope-bearing strata in that they are predominantly black graptolitic shales (muds to muddy silts) of upper Ludlow to lower Pridoli age (Siveter, Vannier & Palmer 1987). World-wide, of the known Silurian myodocope localities only the Mason Porcus section of south-west Sardinia and possibly some of the post-*Bohemograptus bohemicus* Zone (see Holland & Palmer 1974) localities of the Long Mountain in the Welsh Basin are as young. Because of the tectonic complexity of the Armorican Massif, outcrops tend to be isolated and their exact stratigraphic context is often obscured. The Silurian is estimated to be 100-200m thick (*e.g.* Paris *et al.* 1986). Thin Llandovery transgressive sequences pass up into Wenlock-Ludlow black shales (ampelites) which have a high organic carbon content (5-15% and, rarely, up to 30% and, at some localities, subordinate black carbonate horizons. This lithology continues up into the Pridoli Series in the Cherbourg peninsula, but in the Brest-Rennes central outcrop it passes into coarser siliciclastics at about the Ludlow/ Pridoli boundary.

The black shales of Armorica, with their high organic carbon content and positive anomalies of certain trace elements (Sr, Cr, Va, Ru, Yt), have been characterised as typically euxinic deposits. However, as is often the case with such deposits, it is difficult to accurately assess their original depth of deposition. Nevertheless, both their lithostratigraphical setting, between two relatively shallow shelf facies, and their regional setting, as part of the northern Gondwanan epicontinental shelf, strongly implies that they too are to be seen within the overall context of shelf environments. The lack of terrestrial detritus larger than silt size and the generally condensed nature of the hemipelagic mud facies suggests that they could have been deposited within a starved (stagnant/anoxic?) basin on the shelf, perhaps during a transgressive phase.

Robardet *et al.* (1990) place these Armorican outcrops in their Medio-North Armorican domain, the most northerly of several microplates that they recognise in present day southern Europe. If the relative latitudinal relationships of these different, originally

Gondwanan terranes has been retained in their present geographical position, then the Medio-North Armorican domain and the Cherbourg peninsula were nearest to the (southern side of the) Rheic Ocean proper in Silurian times. This might explain the greater preponderance of black shales there, compared with the more carbonate-rich sequences of Bohemia and Sardinia that presumably lay further south and therefore more adjacent to the actual continental margin of Gondwana.

ii) Faunal associates: These black shales contain a low diversity, high abundance fauna of varying admixtures of myodocope ostracods, graptolites, cephalopods, phyllocarids, rare eurypterids, crinoids and bivalves and a rich microbiota of chitinozoa, acritarchs, spores and conodonts. Overall, this is a pelagic fauna with very little normal shelly benthos and no discernible bioturbation. The reasons for the occasional presence of a few thin-shelled bivalves in such facies has often been discussed; were they epifaunal (epiplanktonic), nektonic or adapted to oxygen deficient waters? The relative abundance of the faunal elements varies between localities. For example, in the Ludlow Series de la Lande Muree Formation of the Menez-Belair and Laval areas (Paris 1981), the black shales often have myodocope dominated assemblages (some of the highest myodocope abundances known; up to 2000 individuals per sq.metre), with a few graptolites, bivalves, orthoconic nautiloid fragments and very rare phyllocarid and eurypterid remains. By comparison, the more silty laminated mudstones of the Sarthe area of Loire-Atlantique have relatively fewer ostracods and more phyllocarids and nautiloids, together with rare graptolites and the rhombiferan echinoderm *Lophotocystis*.

The latter fauna occurs as three-dimensional moulds, mainly within small, silt-mud, somewhat pyritous and originally calcareous nodules. It is uncertain whether the nodules were early diagenetic products, with only those organisms enclosed by them being preserved, or whether they only developed from bacterial activity around cadavers. What is certain is that they are pre-compaction growths, and that many of the associated larger fossils (*e.g.* phyllocarids) show decay on one side (Racheboeuf in Press), a preservational aspect analogous to specimens from the Posidonienschiefer (Kauffman 1981) in the Jurassic of Germany. There it was argued that the degraded surface was exposed to a more oxygenated environment above the sediment/water interface, whilst the lower surface was buried, in the sediment, in an anoxic environment. However, if this was true for our French material why, if bottom waters were sufficiently oxygenated to permit the degradation of the organic matter, did it not allow the development of a pioneering shelly benthos? These nodules have most of the rare known occurrences of Silurian myodocopes with both valves still closed, a mode of preservation suggestive of very rapid post-mortem burial (Fig.3).

This black shale fauna is effectively Racheboeuf's (in Press) *Shugurocaris* Community, one of several communities recognised in the Wenlock-Lochkov interval of the Armorican Massif and Artois. It consists of the phyllocarids *Sugurocaris* and *Ceratiocaris*, myodocopes, orthoconic nautiloids, monograptids, cariolids, complete crinoids, chitinozoa, acritarchs and spores. The type locality for the community is one yielding a nodule fauna. Racheboeuf says the fauna occurs exclusively in the nodules but this is clearly not the case, as it is virtually indistinguishable from the fauna of the shales themselves elsewhere in the Armorican Massif and, furthermore, it is not fundamentally different from the Ludlow myodocope-related fauna in the Welsh Basin, Bohemia and Sardinia. It is mainly relative abundances of the various faunal elements that differ.

A general trophic analysis of this association identifies abundant primary producers (acritarchs) and primary consumers (? chitinozoa), perhaps indicating an oxygen and nutrient-rich upper part to the water column. Microplankton abundance was presumably the main reason why the myodocopes and, to a lesser extent, the filter-feeding graptolites and crinoids flourished. The next preserved trophic level was provided by the, nektonic, orthoconic, nautiloids and phyllocarids, larger carnivorous and detritivores which might have fed on the ostracods. The phyllocarids certainly had powerful mandibles and, although their grasping appendages are not generally regarded as being powerful enough for an active preditor, they may have been adequate to capture the relatively large, slow swimming, thin-shelled myodocopes.

iii) Conclusion: The data implies a highly stratified water column in which the vagile myodocopes lived as part of a pelagic fauna within the oxygenated ('upper') layers. The absence of virtually any (either epi-or infaunal) benthos, and the ubiquitous occurrence of laminated muds enriched with organic carbon and early diagenetic pyrite indicate bottom anoxia. Periodic oxygenation of the bottom may have occurred; there are degraded, exposed shell surfaces and, occasionally, current orientation of fossils indicating intermittent bottom current activity. However, such periodic oxygenation was not sufficient or long enough to establish pioneer benthic communities.

2. Palaeogeographical distribution.

As myodocope faunas of Lower Silurian age are rare, it is difficult to defend any possible interpretation of their lifestyle that may be inferred by pertinent palaeogeographical distributions alone (Fig.4). Nevertheless, it should be noted that although there is good reason to regard the Scottish myodocopes as benthic (Siveter & Vannier 1990), as revealed above taxonomically similar and coeval (Telychian) *Entomozoe* material is now known to occur also in China. this wide distribution suggests that as a group they were either much better established temporally and distributed geographically than previously envisaged and/or that previous ideas that the genus had a totally benthic lifestyle should be questioned. Perhaps some myodocopes had already acquired a pelagic habit? If so, then predictably they should be found elsewhere in coeval rocks.

Palaeogeographic evidence for the Upper Silurian clearly endorses the idea that some myodocopes were pelagic (Fig.4). As outlined above, Silurian cypridinid and bolbozoid myodocopes have a widespread distribution across present day Europe. In addition to the records from Britain, France, Sardinia and Czechoslovakia (and Australia and China) discussed above, myodocopes are also known to occur in Portugal, Spain, Poland and North Africa (see Siveter, Vannier & Palmer 1987, p.784; Vannier 1987). Although taxonomic revision still has to be completed for much of the European fauna it is clear that several key Upper Silurian myodocope species have relatively extensive distributional patterns. For example, *Parabolbozoe bohemica* is known from Ludlow Series deposits in Wales, France, Czechoslovakia and Poland. *'Entomis' migrans* is known from Wales, Czechoslovakia and Sardinia (Siveter, Vannier & Palmer 1987) and has recently also been identified from Upper Silurian deposits of Soviet Central Asia (Siveter, unpublished information).

It is apparent that when relevant European, Upper Silurian Ludlow Series occurrences are plotted on palaeogeographic maps (Fig.4) the widespread geographic distribution for myodocopes contrasts with a generally more restricted distribution known for certain other and often typical 'N Atlantic' (see Siveter 1989) Silurian ostracod

associations. Reconstructions of global palaeogeography for Silurian times have North Africa, Ibero-Armorica and Czechoslovakia as part of the continent of Gondwana on the southern side of an (The Rheic) Ocean (interestingly most of the world's known Silurian myodocope-bearing strata, including those from the Lower Silurian of China and Australia, were originally part of the terranes of northern Gondwana). Britain and Baltoscandia were sited on the microcontinent Avalonia and continent of Baltica respectively; both formed part of the northern flanks of the Rheic Ocean and, northwards, both faced North America (Laurentian continent; positioned equatorially) which was on the opposite side of the remnant Iapetus Ocean (Cocks & Fortey 1982; Pickering *et al.* 1988; Vannier *et al.* 1989). The Silurian ostracod faunas of Czechoslovakia (Boucek 1936, Pribyl 1988) are essentially non-palaeocope dominated and are thus different in overall taxonomic composition from the coeval and similarly benthic, beyrichiacean rich, British-Baltic (-N American) ostracod faunas (Siveter 1989). Although apparently providing an efficient barrier to the dispersal of such supposedly benthic ostracod faunas between, for example, Czechoslovakia and Britain, the Rheic Ocean did not prevent the transoceanic migration of pertinent (presumably pelagic) myodocope faunas and species.

However, if these particular Ludlow age myodocopes were truly pelagic an explanation is needed to account for their lack of occurrence in, for example, Baltoscandia and North America. One possible answer is that their undoubted relatively restricted facies range (see above) in their main region of occurrence (Welsh Basin, France, Czechoslovakia, Sardinia) may simply imply some vertical depth control on the distribution of the Silurian myodocodes in question(Siveter, Vannier & Palmer). The carbonat rig Midd to Late platforms of, for example, the Welsh Borderland and Baltoscandia (*e.g.* Gotland-Estonia) may possibly represent environments which were just too shallow (energetic?) for myodocopes to flourish there (or survive to be fossilized?). After all, by the Upper Silurian it appears that in general myodocope stock had made an ecological shift down-slope (see below). If myodocopes are to be found in the Silurian of North America, we predict that they might occur in the Ludlow age fine-grained clastic sediments of that part of Avalonia which is now found in Maine and New Brunswick, New England, where the orthoconic nautiloid-bivalve-graptolite association occurs in its characteristic setting of laminated mud-silts.

3. Geological evidence: conclusions.

The Silurian myodocope-yielding outcrops thus reflect a range of sedimentary regimes, depositional environments and palaeogeographical positions. Nethertheless, regarding the geological ranges and lifestyle of Silurian myodocopes, certain patterns of distribution and other factors common between particular areas do emerge from the above analyses. In particular, the geological aspect of the myodocope-bearing rocks in Scotland, China and Australia appears to display factors in common and yet differs from that shared by relevant deposits in the Welsh Basin, France, Czechoslovakia and Sardinia (Fig.5).

(i) Scotland, China and Australia:

a) Although the character of the rocks in these areas differs in detail, all may be categorised as shelf deposits. Their sedimentary structures, in themselves, betray few diagnostic characters directly related to depth of deposition. Indirect evidence clearly suggests deposition on epicontinental shelves, associated presumably with

relatively shallow waters. The Scottish deposits may represent quite nearshore environments (lagoonal?). The fine-grained mud-silt siliciclastics, characteristic of relevant deposits in all three areas, reflect generally quiet water, low energy conditions.

b) The myodocope-associated faunas are generally abundant, quite diverse, dominantly brachiopod-rich benthic assemblages, presumably reflecting well oxygenated bottom conditions. Detailed bedding plane analysis demonstrates a generally low diversity, vagile epibenthos for the myodocope associated Scottish fauna, within a typically diverse benthic marine faunal sequence. The characteristic occurrence, at possibly the same specific levels as myodocopes (China, Australia) or within the myodocope-bearing sequence (Scotland) of resuspinate and spinose brachiopods, presumably also reflects originally soft, cohesionless (mud laden) substrates.

c) Geological evidence (a and b above) from facies and faunas does not, in itself, clearly indicate a particular lifestyle for myodocopes from China and Australia. Geological evidence (faunas: environmental context) is clearly more supportive in regarding the Scottish myodocopes as benthic (Siveter & Vannier 1990). If the ostracods in all three areas were benthic then they must have been tolerant of the sort of stresses (*e.g.* turbid waters, soft cohesionless substrates) that prevailed. Alternatively, if the ostracods were 'allochthonous' and recruited only on death, in such low energy conditions they can only have been secured from the water column above the substrate itself.

d) The rarity of Lower Silurian myodocope faunas does not, based on evidence from their palaeogeographical distribution alone, allow any clear judgement to be made regarding their lifestyle.

(ii) Welsh Basin, France, Czechoslovakia and Sardinia:

a) These European myodocope-bearing deposits, generally in laminated mud-silt to more carbonate-rich sequences, were probably formed in outer-shelf (France, Czechoslovakia, Sardinia) to off-shelf/shelf slope (Welsh Basin) environments. Within a broadly outer shelf setting, the French and Czechoslovakian (and Sardinian?) sequences may have accumulated in topographic lows (shelf basins). None of the areas is associated with high energy (tidal) clastic depositional processes or carbonate reef facies, typical of a shallow shelf environment, nor with the large scale terrigenous input of the turbidite systems of the deep oceans. In the areas of fine-grained deposition in question quiet, low energy conditions generally prevailed, often with lowered oxygen levels in the bottom waters. The black shales of northern France reflect probable, static, anoxic conditions.

b) The myodocope associates are relatively low diversity orthoconic nautiloid-graptolite-bivalve (and phyllocarid etc.) faunas. This is a dominantly substrate independent, pelagic group; only the bivalves may have been adapted for the dysaerobic conditions characteristically prevailing at the bottom. The relative abundance of the different faunal elements varies in time and space. In parts of the Ludlow of Sardinia and Bohemia, where the supply of clastic terrigenous sediment was very low, orthoconic nautiloids accumulated in sufficient numbers to form the famous cephalopod ('*Orthoceras*') limestones, in which the other faunal components are all minor associates. In the laminated muddy silts of the Welsh Basin bivalves often dominate, whilst in the black shales of Armorica the myodocopes themselves are sufficiently abundant to be the dominant member of the association.

c) That, as a generalisation, the myodocopes of these areas were pelagic is strongly indicated by the geological evidence from pertinent facies and faunas (a and b above). For example, the characteristic occurrence of oxygen deficient bottom conditions and a predominantly
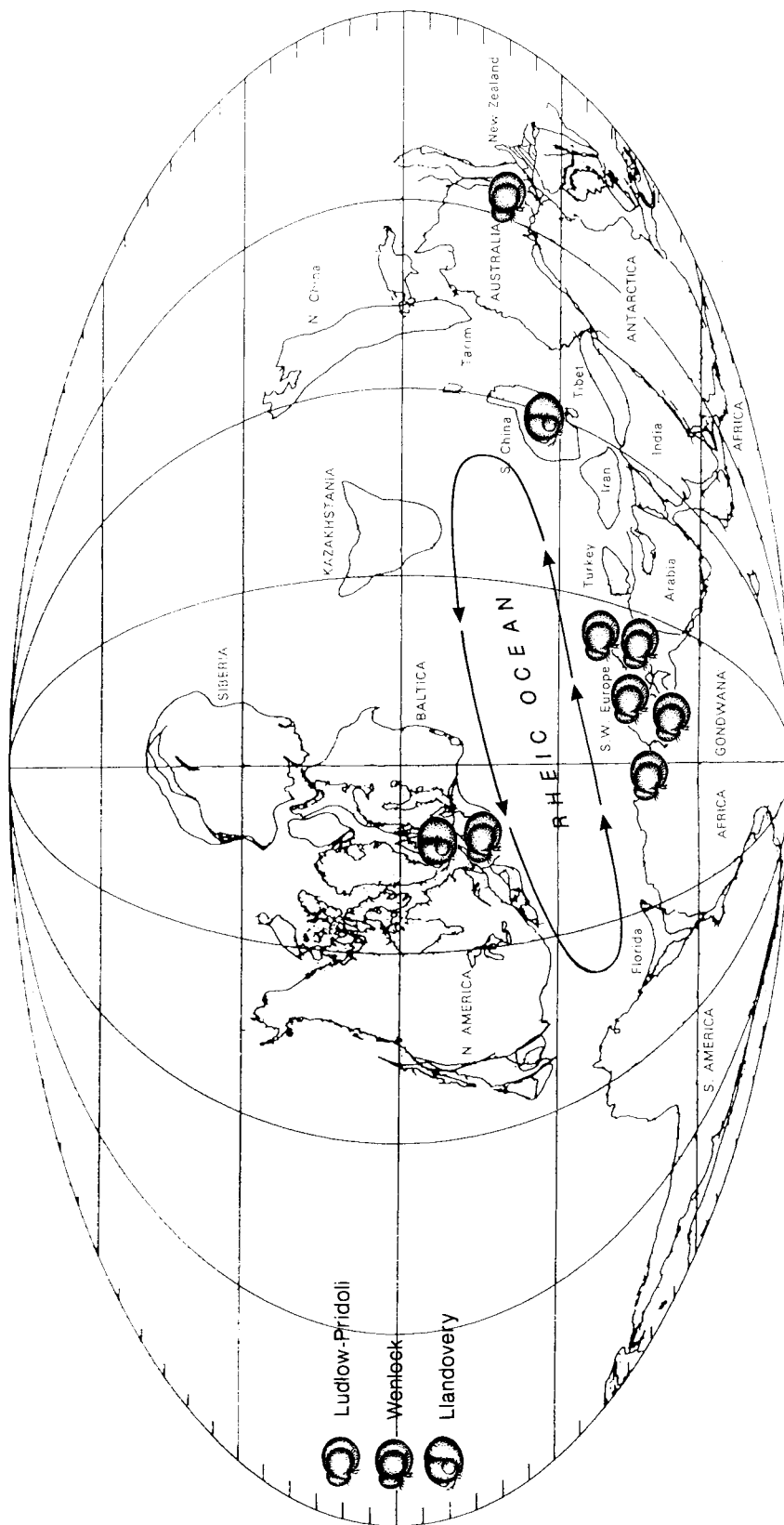
Fig. 4 Global distribution of Llandovery (Scotland, China), Wenlock (Australia) and Ludlow/Pridoli (Welsh Basin, France, Czechoslovakia, Sardinia, North Africa, Spain) series Silurian myodocopes. Base map (after Bergstrom 1990) for mid Silurian (Wenlock) times. Arrows indicate possible circulation within the Rheic Ocean.

pelagic faunal association.

d) Palaeogeographical distributions of certain Upper Silurian (Ludlow) myodocopes from Europe (across the Rheic Ocean) clearly support the idea that, at the very least, some members of the group were pelagic.

MYODOCOPES; AN ECOLOGICAL SHIFT IN THE SILURIAN

It is apparent from the geological conclusions above that Silurian myodocopes are found in two, broadly drawn categories of depositional environments, which are duly reflected in the pertinent facies and faunas (Fig.5). Moreover, the stratigraphical distribution of these categories of environment implies a fundamental ecological shift for Silurian myodocopes, at about the Lower - Upper Silurian (= Wenlock - Ludlow series) boundary, involving a change in their depositional environment (habitat) and a (corollary?) change in their lifestyle. This idea of an ecological shift was first proposed by Siveter & Vannier (1990) when they documented the Scottish myodocopes, and is endorsed by our detailed overall analysis herein. In particular, we add new information on the Chinese and Australian occurrences of Silurian myodocopes.

Evidence indicates that the Llandovery (Scotland, China) and Wenlock (Australia) myodocopes lived in relatively shallow, oxygenated waters, on the shelf and perhaps (Scotland; ? China, Australia) as part of the benthos. In post-Wenlock times Silurian myodocopes are still associated with fine-grained, quiet water deposits, but ones which are characteristically suggestive in part of lowered oxygen levels or even anoxic conditions. This occurred in either what were perhaps outer shelf topographic troughs (France, Czechoslovakia; ? Sardinia) or off-shelf basin slopes (Welsh Basin), both of which harboured a largely pelagic fauna. This postulated ecological shift (Fig.5) of course implies the origin, at around the Wenlock-Ludlow boundary, of pelagic lifestyles for myodocopes. Possible reasons for this shift are outlined below.

Significantly, no Llandovery myodocopes have yet been found in any off-shelf, deeper water deposits. Sedimentation during the late Llandovery Telychian in many mainland European areas, such as the Prague Basin, was dominated by graptolitic shales and there is no equivalent there to the shallow water clastics of the Pentlands, Scotland, or even to the deeper shelf shelly mudstones of the Yangtse platform, China; thus, it is no surprise that Telychian myodocope ostracods have not been found in, for example, Czechoslovakia. Furthermore, the only known locality, besides Australia, to have yielded Wenlock myodocopes is the Long Mountain area of the Welsh Basin, where a very few poorly preserved specimens occur in bioturbated shelly mudstones of the Glyn Member of the Trewern Brook Mudstone Formation (Palmer 1979), deposits which probably represent the shallowest water phase in the Wenlock to Ludlow sedimentation of this basin margin area.

PIONEER PELAGIC OSTRACODS; WHEN AND WHY?

Accepting the idea, as outlined above, that some Silurian myodocopes were possibly pelagic, how correct is it to dub them 'pioneer' pelagic ostracods? What evidence is there for pre-Silurian myodocopes or pre-Silurian possible pelagic ostracods of any other taxonomic group?

Records of Ordovician myodocopes are considered spurious (Siveter 1984; see also Siveter & Vannier 1990, Fig.23). In the Treatise on Invertebrate Paleontology Sylvester-Bradley (1961, Q 391) lists

only one 'myodocopid' genus from the Ordovician, *Rhomboentomozoe* Pribyl, 1951. This record appears to have been based on Pribyl's (1951) opinion that the middle Ordovician taxon *Isochilina armata pygmaea* Ruedemann, 1901, from the Mohawkian of New York State, U.S.A., should be assigned to his genus *Rhomboentomozoe*. This supposed Ordovician record of a myodocope can be viewed as false because *I. pygmaea* (Ruedemann 1901, Pl.7 figs 19-25) is clearly very different from the Bohemian Silurian type-species of *Rhomboentomozoe*, namely *Cryptocaris rhomboidea* Barrande, 1872. Furthermore, even if Pribyl's generic reassignment of *I. pygmaea* is regarded as 'correct', it can be firmly argued (Siveter & Vannier 1990) that the genus *Rhomboentomozoe* is, at best, a very atypical myodocope and most likely belongs to another group.

Evidence for the existence of pelagic lifestyles in pre-Silurian ostracods is circumstantial and more so because one is then considering entirely non-myodocope groups. Although, however, it is virutally inconceivable that pre-Silurian ostracods could not swim (even Cambrian ostracods are considered nektobenthic, on or near to the bottom *e.g.* see Müller 1979, 1983, p.94), the evidence (from morphological design and geology) for Ordovician pelagic ostracods has not yet been documented nor, indeed, systematically addressed. The shape, centre of gravity and ventral structures of typical Ordovician palaeocope and binodicope ostracods suggests that they were mostly benthic crawlers or maybe bottom swimmers (Schallreuter & Siveter 1985; Vannier *et al.* 1989). A cursory investigation would probably identify forms such as certain leiocopes (see Vannier 1990) to be amongst possible contenders for the title of pelagic ostracods in the Ordovician, but even then the evidence would not be as clear cut as if it had the added bonus of involving myodocope-like morphology.

Whether it occurred in the Silurian or even in the Ordovician, there is still the intriguing question of why (myodocope) ostracods adopted non-benthic lifestyles. Siveter & Vannier (1990) postulated that the origin of pelagic modes of life for Silurian myodocopes might be associated with enhanced swimming capabilities related to modification of appendages, evidence of which they ventured was present in the enlarged anterodorsal bulb and rostral incisure in Upper (as compared to certain Lower) Silurian myodocopes. Alternatively to, and/or together with such morphological changes (myodocope) ostracods may have been driven from the substrate/bottom waters by some factor such as a change in physical (*e.g.* water chemistry) conditions or competition. Furthermore, perhaps the relatively virgin, yet plankton-rich waters held persuasive attractions. We consider significant the fact that in the Ludlow myodocope-bearing sequences there is good evidence for both oxygen deficiency in the bottom waters/substrates and plankton-rich upper waters (organic rich sediments). With primitive fish, cephalopods and rare trilobites forming most of what there was of an early Palaeozoic macro-pelagic fauna, there was also perhaps a niche in the trophic structure of marine environments which could be exploited to advantage by relatively tiny, omnivorous animals; perhaps ostracods did just that (Siveter 1984).

A further point to consider is the fact that the 'off-shelf' ecological shift and the acquisition of a pelagic lifestyle evidenced herein for Silurian myodocopes might also be a result of a rise in sea-level (and the consequent flooding of shelf areas) in addition to an actual down-slope migration, through time, of myodocope faunas. In this respect it is pertinent that McKerrow (1979) noted that the Welsh Basin (Welsh Borderland) and several other areas (*e.g.* Nova Scotia) of the continents of the southern flank of the Iapetus Ocean all record a drop in sea level
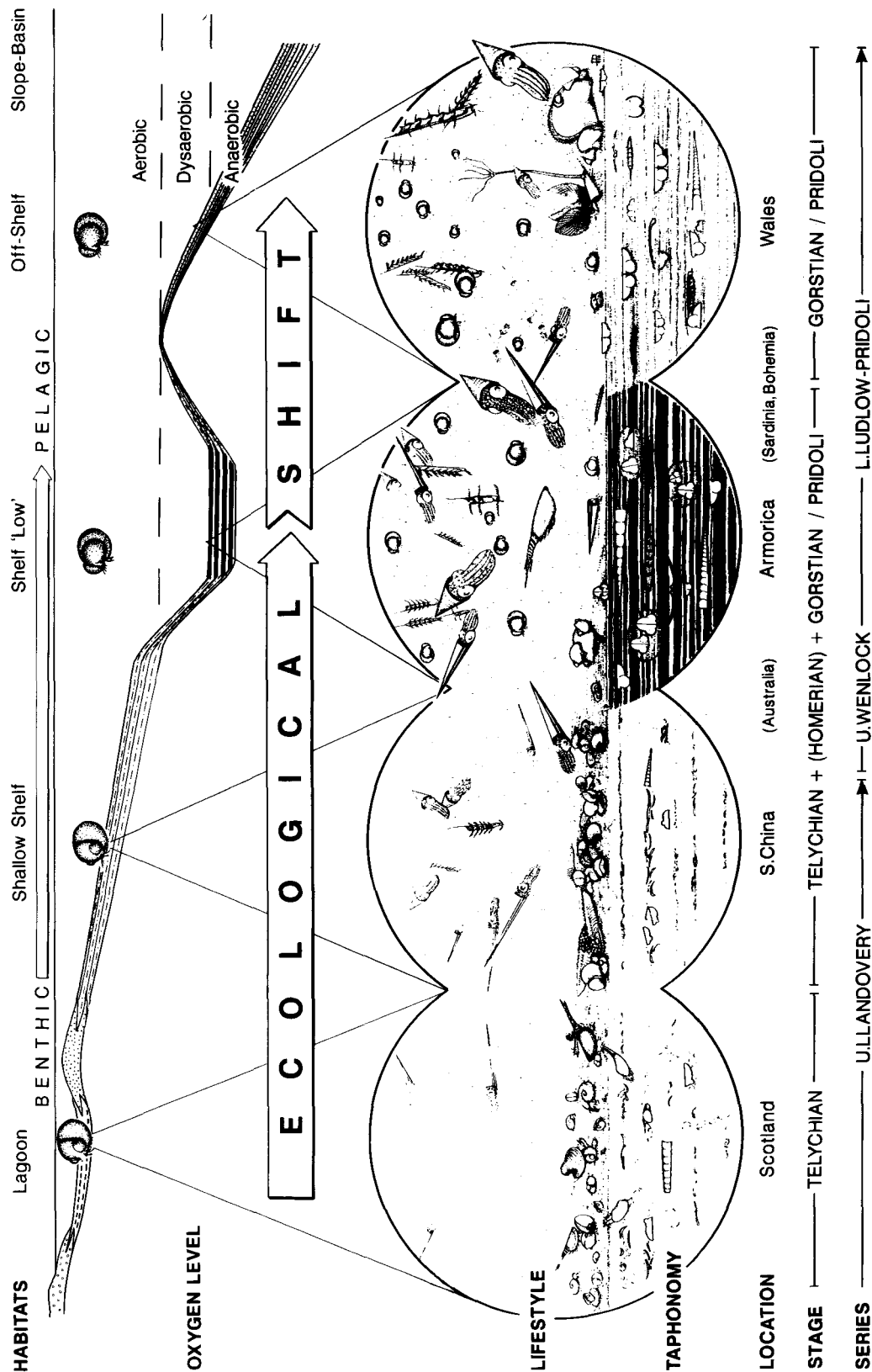
Fig. 5 Diagram showing the postulated temporal, benthic to pelagic shift in the lifestyle of myodocopes, in relation to their characteristic associated facies and faunas, during the Silurian. The ecological shift is illustrated by reconstructions of the habitats, lifestyle and taphonomy of myodocope-bearing fossil assemblages from Scotland (Pentland Hills; Telychian), China (Yangtse Platform; Telychian), France (Armorica; Gorstian to Pridoli), Wales (Powys; Gorstian to Pridoli) and other areas described in the text but not illustrated here (Canberra, Australia - Homerian; Sardinia and Bohemia, Gondwanan plate fragments - Gorstian to Pridoli).

In general order of abundance the fossil taxa illustrated are: **Scotland**: the palaeocope ostracod *Craspedobolbina impendens*; orthoconic nautiloids; gastropods *Liospira simulans*, *Spirina antiquata*; brachiopod *Trimerella* sp.; bivalve *Synek* sp.; phyllocarid arthropod *Dictyocaris* sp.; myodocope ostracod *Entomozoe tuberosa* **South China**: brachiopods *Nalivkinia* sp., *Nucleospira* sp., *Spinochonetes* sp., *Aegiria* sp., lissatrypids; orthoconic nautiloids; trilobite *Coronocephalus* sp.; monograptids; myodocope ostracod *Entomozoe* aff. *tuberosa*. **Armorica, France**: myodocope ostracods '*Bolbozoe*' sp; orthoconic nautiloids; monograptids; phyllocarid arthropods. **Wales**: orthoconic nautiloids; monograptids; myodocope ostracods *Parabolbozoe* sp.; pisocrinid crinoids. These four assemblages are shown located in their relative positions on a shelf to basin transect model. The older (Telychian) Scottish and south China assemblages are typical shelf benthos dominated by shelly invertebrate epifaunas, as is the Australian (Wenlock) fauna (not illustrated, see text). The younger French (and Sardinian and Czechoslovakian; not illustrated, see text) and Welsh assemblages represent outer shelf topographic lows and off-shelf slope facies respectively, with organic carbon-rich black shales and laminated hemipelagites respectively; their poorly aerated (dysaerobic) bottom conditions and waters were inhabited dominantly by pelagic organisms. From the associated faunas and facies myodocope ostracods can be seen to have shifted their habitats and lifestyles from benthic to pelagic during upper Llandovery to lower Ludlow times.

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in the late Wenlock and a subsequent rise in sea level in the early Ludlow. However, in the discussion to that paper Bassett argued that the rise in sea level in the early Ludlow was of much more local geographical extent than McKerrow had supposed. More recently (Johnson et al. 1989), data from North America, Britain, parts of the Baltic (Gotland, Estonia) and Australia have in some measure supported McKerrow by indicating that high sea level stands are typical in these areas in the early Ludlow. This idea needs to be tested with further analysis.

Thus, perhaps, it was their preadaptation for swimming that allowed the myodocopes to respond to an environmental forcing which stemmed from several possible factors; negative oxygen levels; positive trophic and nutrient incentives; and sea level rises? Rather than migrate up-slope (shore-wards) together with their original benthic associates, their response was to migrate up the water column.

ACKNOWLEDGEMENTS

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