RECENT AND EARLY PALAEOZOIC MYODOCOPE OSTRACODES: FUNCTIONAL MORPHOLOGY, PHYLOGENY, DISTRIBUTION AND LIFESTYLES

by JEAN VANNIER *and* KATSUMI ABE

ABSTRACT. Myodocope ostracodes are represented worldwide in a variety of modern environments as benthic, nektobenthic or exclusively planktonic organisms. Their Silurian ancestors form one component of the early Palaeozoic marine crustacean fauna. Aspects of biology (body plan, functional morphology, behaviour relevant to the interpretation of the fossil record) newly investigated by, for example, video-recordings are described. A high degree of specialization of appendages and paired visual organs known in modern (this paper) and Mesozoic myodocopes presumably occurred very early (Silurian) in the evolution of the group. External bulbs of typical Upper Silurian bolbozoid myodocopes are interpreted as having housed possible visual receptors comparable to modern analogues (e.g. planktonic forms). A phylogeny of Myodocopa (Lower Silurian to Recent), based on cladistic analysis, is proposed for higher taxa. The two major components of the Recent myodocope fauna, Myodocopida and Halocyprida, were probably already differentiated during the Silurian. The modern myodocopids may have originated from late Palaeozoic forms (Superfamily nov. A) via the cypridinacean lineage (Lower Triassic to Recent). This analysis of the distribution, morphology and lifestyles of Recent myodocopes supports the hypothesis previously presented by Siveter and Vannier that representatives of Silurian myodocopes were truly pelagic. Upper Silurian myodocopes are considered as active swimmers, capable of vertical migrations and feeding on detrital organic material sinking out from the photic zone. Their vertical distribution may have preferentially ranged from 100–200 m down to 400–500 m. They probably lived in relatively dark environments with possibly highly sensitive visual organs as an adaptive response to dim conditions. They may have been one of the pioneer crustacean faunas to fill vacant mid-water niches during the early Palaeozoic.

OSTRACODES form one of the most diverse groups of living crustaceans, ranging worldwide in marine environments since the Cambrian (Müller 1979, 1982*a*; Jones and McKenzie 1980; Zhang 1987; Zhao 1989*a*, 1989*b*). Over more than 500 million years, these organisms have acquired a variety of lifestyles and colonized the shallowest coastal as well as the deepest bathyal and abyssal environments. Major structural and functional transformations, among them the modification of appendages in relation to new lifestyles (e.g. planktonic), probably contributed largely to the diversification of the group. A significant phase of profound changes in the body plan and carapace structure seems to have occurred relatively early in the evolution of Ostracoda, by Silurian times, leading to the emergence of a new group, the myodocopes (for definition of Superorder Myodocopa and Order Myodocopida, see Text-fig. 3). Their very distinctive morphology (carapace architecture, shell calcification, size), distribution pattern, associated faunas and sediments suggest ecological preferences, lifestyles and appendage structure different from all other known lower Palaeozoic ostracodes (e.g. Bradoriina, Phosphatocopina, Palaeocopa, Leperditiocopa, Podocopa: see Table 1). Inferred models proposed in a series of palaeontological papers (Siveter 1984; Siveter *et al.* 1987, 1988; Siveter and Vannier 1990; Siveter *et al.* 1991) favour a possible pelagic lifestyle for most Upper Silurian myodocopes which therefore might represent (with other groups such as the phyllocarids) a significant component of the mid-water crustacean fauna in the early Palaeozoic.

Myodocope ostracodes (Text-fig. 3) are still abundantly represented in modern environments, from tropical reefs and marine caves to higher latitude deep seas, as nektobenthic or exclusively

[Palaeontology, Vol. 35, Part 3, 1992, pp. 485–517, 2 pls.]

planktonic organisms. This provides an exceptional and partly unexploited source of data for testing current interpretations of the functional morphology, palaeoautecology and distribution of their Palaeozoic ancestors. We describe newly investigated aspects of the morphology, physiology, behaviour and ecology of both benthic and planktonic living myodocopes, relevant to the study of the fossil record. The significance of the Silurian representatives of the group is discussed within a broader phylogenetic, faunal, sedimentological and geodynamic framework.

MATERIAL AND METHODS

Living material

Vargula Skogsberg, 1920 (Order Myodocopida, Family Cypridinidae; Text-fig. 3) was chosen as a representative example of a widespread living myodocope ostracode, sharing obvious morphological similarities (carapace shape) with typical Silurian (Text-fig. 2B), later Palaeozoic (Kesling and Ploch 1960; Becker and Bless 1987) and Mesozoic (Dzik 1978; Weitschat 1983*a*, 1983*b*) myodocope species. *Vargula* (see Cohen and Morin 1989, 1990*a*, 1990*b*; Moguilevski 1990) has an almost worldwide distribution from shallow water tropical and temperate (e.g. Pacific Coast of Honshu, Japan) to high latitude deep-sea environments (e.g. Antarctica: see Kornicker 1975*a*). Most species (about thirty) have a complex benthic/nektobenthic mode of life (Cohen and Morin 1986). *Vargula hilgendorfii* (G. W. Müller, 1890) (Pl. 1) is abundantly distributed along the coast of Japan (Pacific Ocean, Japan Sea, Seto Inland Sea: Okada and Kato 1949; Nakamura 1954; Hanai *et al.* 1977) and present in the Celebes Sea and the South China Sea off Singapore, Thailand and Vietnam (Hanai *et al.* 1980), within a depth range of 1 to 25 m. Its habitat is typically a fine-grained sand with good water circulation. Epibenthic collections of *Vargula hilgendorfii* were made using fish carcasses (as bait) enclosed within a thick-walled glass container covered with a piece of cloth, sufficiently small (1–5 mm in diameter) to keep out crustaceans other than ostracodes. Several thousands specimens of *Vargula hilgendorfii* and other associated myodocopids were collected at night in August and November 1989 and in March and August 1990 from the shallow-water (3–5 m deep) sand bottom of Aburatsubo Bay (Pacific Coast, Honshu, Japan, 139° 37′ long. E, 35° 9′ 40″ lat. N: see Abe 1983; Abe and Hiruta 1985; Abe and Vannier 1990; Vannier and Abe 1991) near the Misaki Marine Biological Station (University of Tokyo).

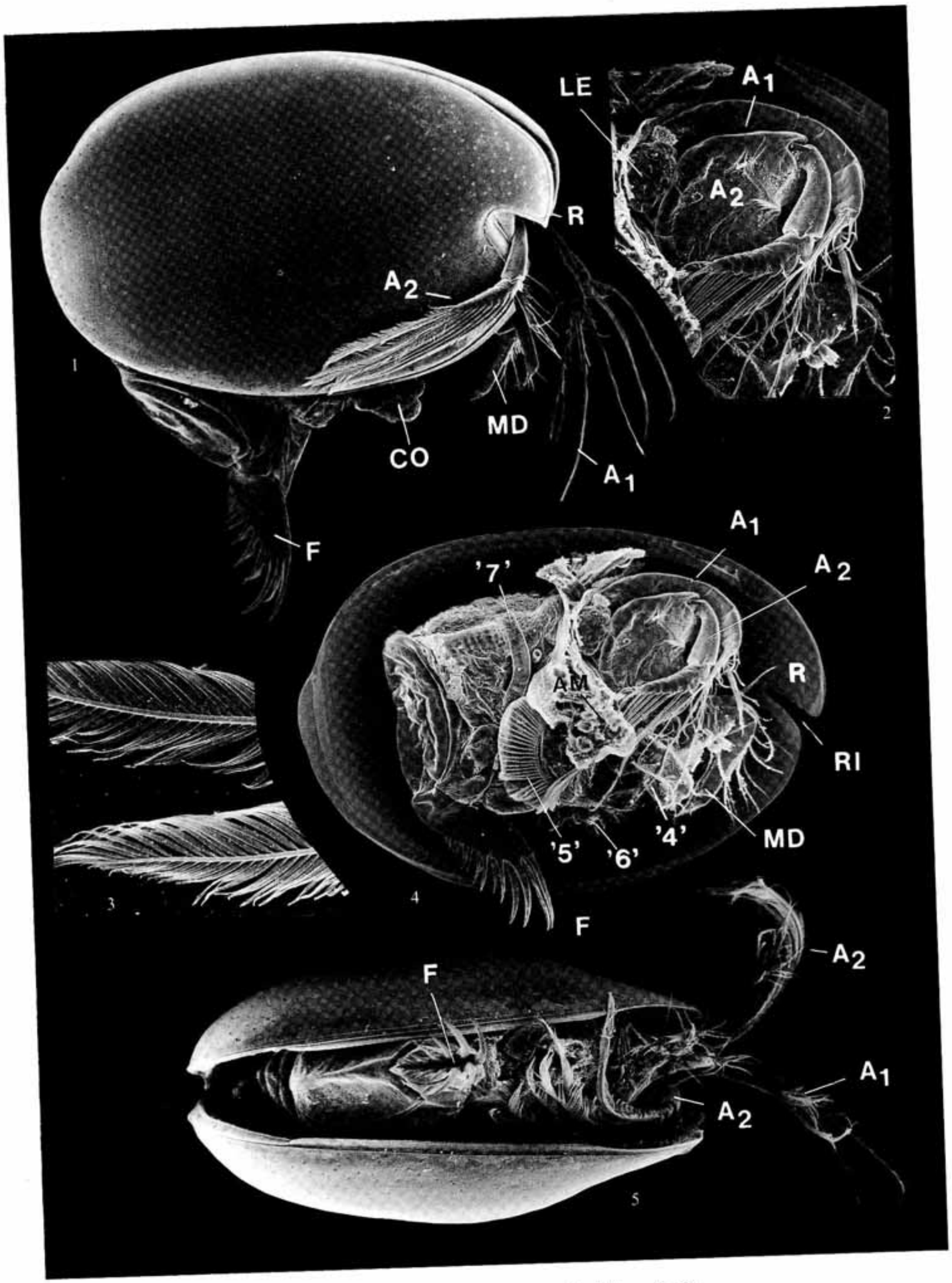
Species of *Euphilomedes* Poulsen, 1962 were also studied as an example of strongly calcified myodocope ostracodes with reduced swimming abilities; living material (e.g. *Euphilomedes sordida* (G. W. Müller, 1890): Hiruta 1976) was collected at Misaki from tidal pools (calcareous algae *Corallina pilulifera* and *Amphiroa dilatata*).

Data on the behaviour of living ostracodes were obtained by macro/microscopic observations and video-recordings (video-camera VK-C 350 and image-printer EP-P1, Hitachi: see Abe and Vannier (1991) and Vannier and Abe (in press)) within two weeks of collection; material was kept at a constant temperature of approx. 14 °C. Specimens for SEM observations were fixed with 5 per cent formaldehyde, kept in 70 per cent ethanol and then processed through the 'Critical Point' drying method (carbon dioxide).

EXPLANATION OF PLATE 1

Figs 1–5. *Vargula hilgendorfii* Skogsberg. Recent shallow-marine nektobenthic myodocopid ostracode. All specimens from Aburatsubo Bay near Misaki, Pacific Coast of Honshu, Japan. 1, 3, FSL 575010; adult male; 1, carapace with protruding appendages, seen from right, lateral view, ×28; 3, detail of natatory bristles, right second antenna, ×200. 2, 4, FSL 575011; juvenile; 2, internal morphology, first and second right antennae, ×65; 4, internal morphology, lateral view, carapace seen from right, ×45. 5, FSL 575012; adult male, carapace with protruding appendages seen from right, ventral view, ×30. A1, first antenna; A2, second antenna; CO, copulatory organ; F, furca; LE, lateral eye; MD, mandible; R, rostrum; RI, rostral incisure; '4' to '7', fourth to seventh limbs respectively. All scanning electron micrographs.

PLATE 1



VANNIER and ABE, *Vargula hilgendorfii*

Fossil specimens

Our Silurian faunas refer to abundant newly collected (J. Vannier, D. J. Siveter, D. Palmer) material from the Armorican Massif, France; the Welsh Basin, Britain (see localities in Siveter *et al.* 1987); the North Esk Inlier, Scotland (Siveter and Vannier 1990); and the High Atlas, Morocco (Vannier 1987) in typically laminated, fine-grained sediments. Associated graptolites from the numerous ostracode localities of France and Wales indicate an Upper Wenlock to lower Pridoli age, the myodocope fauna increasing markedly in abundance and diversity during the Ludlow. The earliest known myodocope in the fossil record is from the Llandovery Series of Scotland (*Entomozoe tuberosa* (Jones, 1861): Siveter and Vannier 1990). Silurian myodocopes are usually preserved as moulds; casts of external moulds were prepared with silicone rubber (method described by Siveter 1982).

Specimens figured in this paper are deposited in the collections of the Department of Geology, Université Claude Bernard-Lyon I, (FSL), France.

FUNCTIONAL MORPHOLOGY

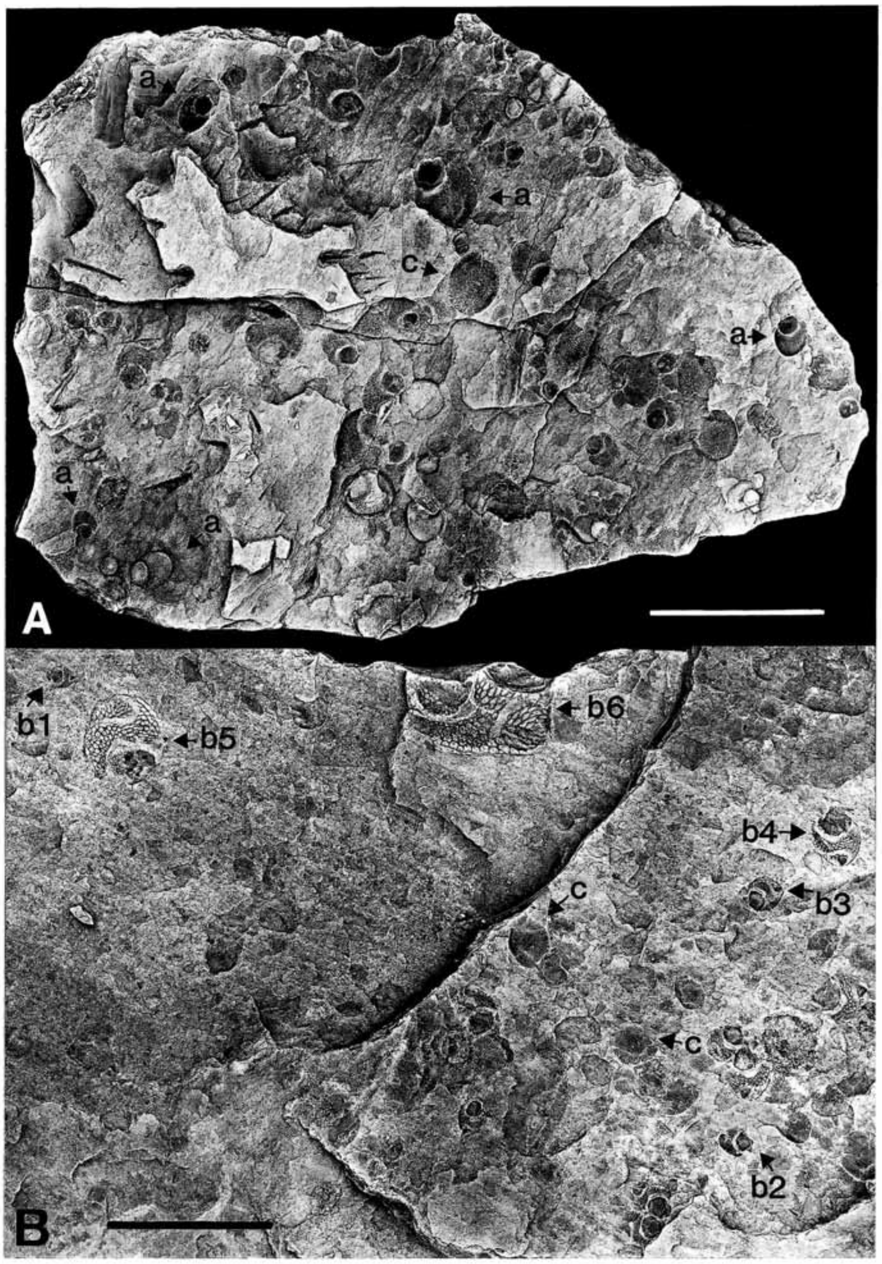
This section mainly focuses on specific aspects of functional morphology related to vision and locomotion. Many Silurian myodocopes are characterized by a pair of prominent hemisphaerical bulbs (Pl. 2, fig. 1; Text-fig. 2C) in the anterodorsal region of the carapace. This enigmatic feature has no apparent homologue in other fossil or Recent ostracodes. The only ostracode features of like shape/size but located elsewhere on the valve are the posterior marsupium-related bulge of living female sarsiellid myodocopes (Kornicker 1975*b*, 1986; Hall 1985, 1987) and the inferred ventral brood-care pouch (crumina: see Martinsson 1962) of typical Palaeozoic beyrichiaceans. In most Recent myodocope ostracodes the internal anterodorsal space of the carapace is exclusively occupied by the first and second antennae (Text-fig. 5) and complex visual (lateral eyes and 'nauplius' or medial eye according to the authors' terminology) or/and sensory organs (e.g. Bellonci organ: see Hartmann 1966; Andersson 1977). Sensory tubes attached to the first antenna and acting as probable chemoreceptors (Heimann 1979) are also known in the frontal part of the carapace. If we exclude the halocyprids (e.g. planktonic forms, Text-fig. 5G) in which both lateral and medial eyes are absent and most 'blind' deep-sea benthic species (Kornicker 1975*a*), vision, through a variety of optical mechanisms, is remarkably developed in myodocope ostracodes.

The bulb as a vision-related organ?

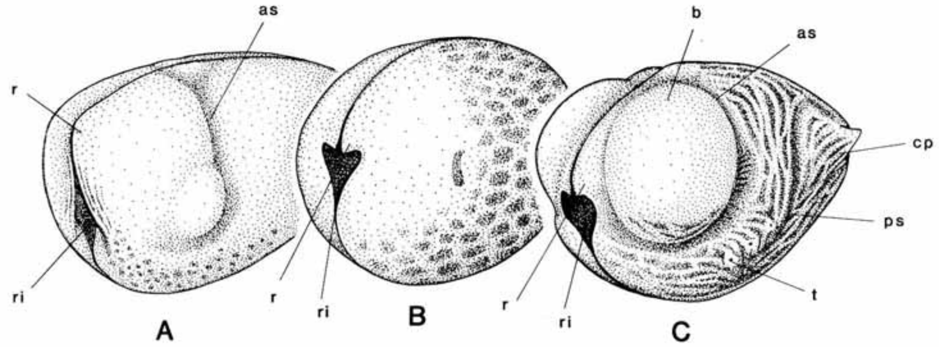
Lateral compound eyes of typical myodocopids contain a variable number of more or less closely packed ommatidia (up to 80: Kornicker 1975*a*) and perform their visual function through a relatively simple optical process (Text-fig. 4). In *Vargula hilgendorfii* light passes through the evenly transparent carapace, penetrates the crystalline cones of individual ommatidia (Text-fig. 4A, F, K) and is finally received by underlying retinula cells. As in many other myodocopid species (Land and Nilsson 1990), lateral eyes have spontaneous movements such as slow rotations and a low frequency tremor.

The so-called 'nauplius' or medial eye (Hartmann 1966) is common to the vast majority of crustaceans including myodocopid ostracodes and basically consists of a cluster of small eye cups containing receptors but no optical arrangements (Land 1984, fig. 1). In *Vargula hilgendorfii* (Text-figs 4A, 6D) this organ is located anteriorly to the strongly pigmented lateral eyes and reflects light

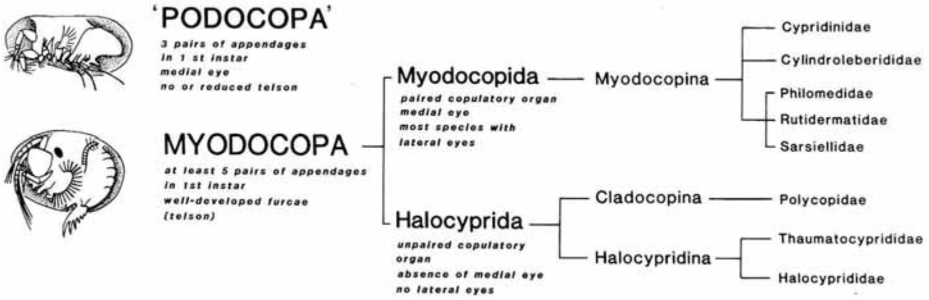
TEXT-FIG. 1. Typical Silurian myodocope ostracodes on two slabs. A, FSL 575001; bolbozoids (mainly '*Bolbozoe*' cf. *anomala*) and 'cypridinid'-like myodocopes; Les Buhardières near Andouillé, France; La Lande-Murée Formation, Ludlow Series, Silurian. B, FSL 575002; reticulated bolbozoids (mainly '*Bolbozoe*' cf. *bohemica*) and 'cypridinid'-like myodocopes; La Cultais, Vieux-Vy-sur-Couesnon, Ille-et-Vilaine, Armorican Massif, France. a, '*Bolbozoe*' cf. *anomala*; b1–b6, several successive ontogenetic stages of '*Bolbozoe*' cf. *bohemica*; c, indet. 'cypridinid'-like forms. Scale bar represents 1 cm. FSL, Faculty of Science, Université Claude-Bernard, Lyon I, France.



TEXT-FIG. 1. For legend see opposite.



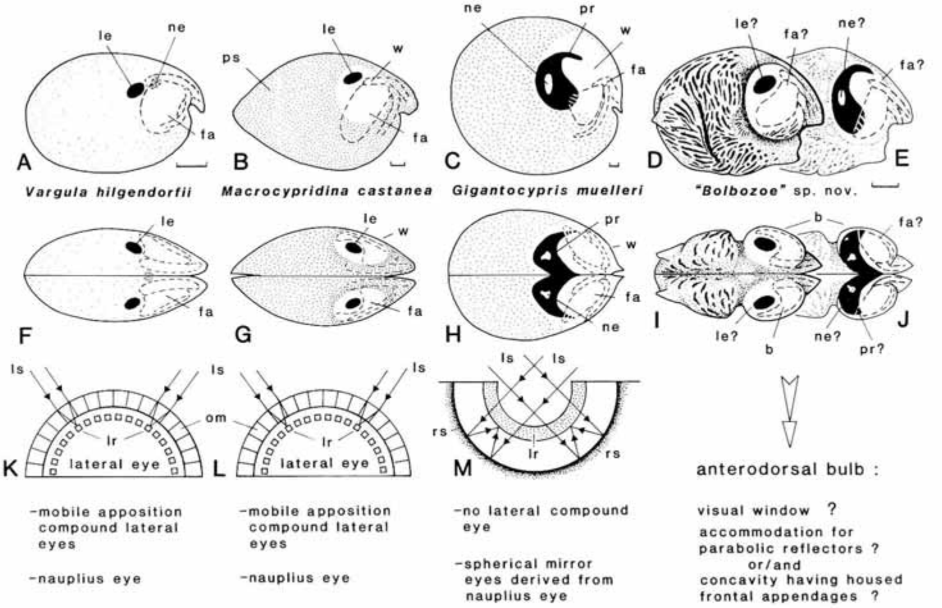
TEXT-FIG. 2. Reconstruction of typical Silurian myodocope species showing the frontal part of the carapace. A, *Entomozoe tuberosa*; Llandovery Series of Scotland (see Vannier and Siveter 1990). B, reticulated 'cypridinid'-like myodocope (= 'cypridinid' gen. et sp. nov. A *in* Siveter *et al.* 1987); Ludlow Series; Armorican Massif, France. C, '*Bolbozoe*' sp. nov. A (see Siveter *et al.* 1987). A, B, C, approx. 9·5, 1·2, 3·5 mm long, respectively. am, adductor muscle scars; as, adductorial sulcus; b, anterodorsal bulb; cp, caudal process; r, rostrum; ri, rostral incisure; t, tubercles.



TEXT-FIG. 3. Systematic position of Recent myodocope and podocope ostracodes. Main internal diagnostic features given for the Superorder Myodocopa, the Orders Myodocopida and Halocyprida and also for 'Podocopa' (= Orders Podocopida and Platycopida). No consideration on the ranking of 'Podocopa' (Superorder? or Subclass as *in* Bowman and Abele 1982; Maddocks 1982) is given here. Comparative internal morphology of typical podocopid and myodocopid ostracodes figured on left (open carapaces from left). Mainly after Kornicker 1975*a*, 1975*b*, 1981, 1983, 1986, 1989; Kornicker and Sohn 1976; Kornicker and Illife 1989*a*, 1989*b*.

with a metallic appearance, as also observed in copepod crustaceans (multilayered mirror structure: Vaissière 1961; Land 1984).

Discussing the extraordinary variety and degree of sophistication of optical systems in crustaceans, Land (1978, 1984) and Land and Nilsson (1990) show that deep-sea myodocopid ostracodes have developed either mirror optics (*Gigantocypris*: Text-fig. 4C, H, M) or high sensitivity compound eyes (*Macrocypridina*: Text-fig. 4B, G, L) as a possible adaptive response to dark environments and dim conditions. The brown-pigmented carapace of *Macrocypridina castanea* has a clear visual window above and in front of each lateral eye (see Land and Nilsson 1990, fig. 1, and the beautiful colour illustrations of Müller 1908). This transparent incurved surface undoubtedly



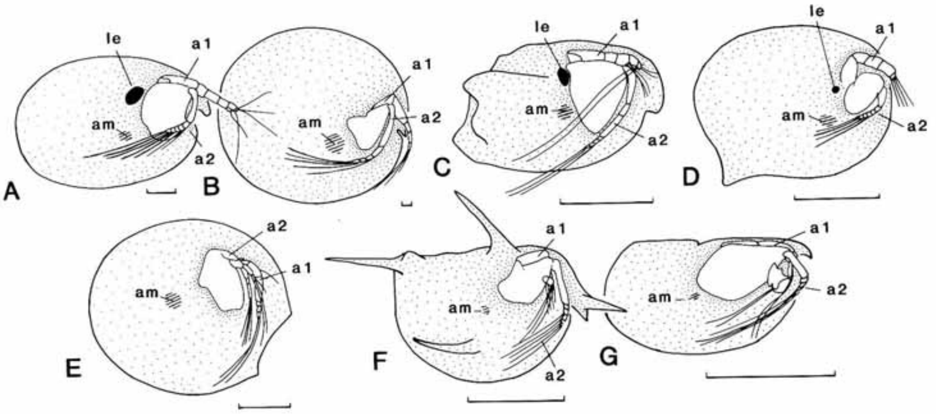
TEXT-FIG. 4. Visual systems of Recent shallow-water benthic/nektobenthic (A, F, K) and deep-sea planktonic (B, G, L; C, H, M) myodocope ostracodes with possible homologous features in Silurian representatives (two interpretations given in D–E, I–J). The occurrence and position of ocular features and appendages in Silurian myodocopes are hypothetical. From top to bottom, lateral and dorsal views of carapaces seen from right, and schematic cross-sections showing optical systems. Explanation in the text. b, anterodorsal bulb; fa, frontal appendages (first and second antennae); le, lateral eye; lr, light receptor; ls, light source; ne, 'nauplius eye' (medial eye); on, ommatidia; pr, parabolic reflector; ps, pigmented surface; re, reticulated/corrugated surface; rf, reflecting surface; w, non-pigmented window. B–C, H, K–M based on Land (1978, 1984) and Land and Nilsson (1990); D, on Siveter *et al.* 1987. Scale bar represents 500 μm.

plays the role of directing light to the underlying highly sensitive eyes (large ommatidia with large aperture diameter and wide retinula cell with rhabdoms). *Gigantocypris muelleri* (Text-fig. 4C, H, M), the biggest living ostracode species (adults up to 30 mm long) is also equipped with large, frontal non-pigmented windows (Land 1978) but receives light through a very distinctive mechanism (Text-fig. 4M). This species has a pair of relatively huge, symmetrical metallic-looking parabolic reflectors, focusing light on massive photoreceptor cells (retina) lying dorsoventrally near the centre of each mirror (Land 1984, fig. 4). Although the resolution abilities of such eyes are probably very poor, the optical design itself increases light sensitivity substantially. Interestingly, the visual windows of Recent myodocopes have almost the same rounded outline, frontal position and relative size (about 1:5 of total valve area) as the bulb of Silurian species (Pl. 2; Text-figs 2, 4D–E, I–J, 6). Moreover, reticulated or corrugated Silurian myodocopes (e.g. *Bolbozoe*, Text-fig. 2C: see also Siveter *et al.* 1987) lack any ornamented pattern on the bulb except along the edge of its ventral margin. This complete absence of ornamentation, comparable to the non-pigmentation of visual windows in *Macrocypridina* or *Gigantocypris* supports the idea (Siveter *et al.* 1987) that the bulb may have had a visual or a vision-related function (Land, pers. comm.). Three-dimensional well-preserved specimens from Silurian siliceous nodules (Armorican Massif, France: Pl. 2) show the hemispherical nature of the bulbs. On the other hand, individuals from laminated black shales (Text-fig. 1) show frequent apparent plastic deformations of the bulb and also indicate that most Silurian myodocopes (bolbozoids, 'cypridinid'-like species) were probably thin-shelled poorly calcified ostracodes (Siveter *et al.* 1987). Moreover, the central part of the bulb is very often damaged and depressed even in the best preserved individuals, suggesting an especially reduced shell thickness in this particular region of the carapace. The bulbs of Silurian myodocopes which represent voluminous internal cavities may have housed either well-developed lateral eyes (Text-fig. 4D, I) or optical devices comparable to the parabolic reflectors and the medial-eye-derived receptors of *Gigantocypris* (Text-fig. 4E, J). The nature of the main visual receptor (lateral eye? medial eye?) in Palaeozoic myodocopes is speculative. However, lateral eyes are likely to be present in the Palaeozoic. Exceptionally preserved phosphatized specimens from Spitzbergen (Weitschat 1983*a*, 1983*b*) show evidence of well-differentiated lateral compound (ommatidia) eyes in lower Triassic myodocopids (*Triadocypris*, Cypridinidae). Paired sessile compound eyes of similar basic design are also widespread in early arthropods such as trilobites. Concerning ostracodes, the reconstructions given in Text-figure 4D, I show hypothetical lateral eyes comparable in size and position to those of the most common Recent myodocopes (e.g. *Vargula*), but it is clear that various alternatives could be envisaged, such as huge compound eyes occupying most of the cavity of bulbs. Some Ordovician trilobites (Fortey and Owens 1987) are characterized by hypertrophied lateral compound eyes, probably related to their pelagic mode of life. Another point that one might argue concerns the possible optical properties of the bulb itself. According to Land (1978), the carapace of *Gigantocypris* is thin and parallel-sided with water on both faces. Although transparent and spherical (e.g. over the eyes) is has no optical properties. Similar conclusions seem to apply to most living myodocopes (especially planktonic species with typical thin chitinous laminate endocuticle: see Sohn and Kornicker 1988) and also probably to the Palaeozoic myodocopes, including bolbozoids.

The bulb as an accommodation for frontal appendages?

All Recent myodocope ostracodes have two pairs of well-developed appendages, both located in the anterodorsal part of the domiciliar concavity (Pl. 1, figs 2, 4; Text-fig. 5) and able to protrude outwards partly through the rostral opening in relation to locomotory activities. Generally speaking, the second antenna of nektobenthic active swimmers (e.g. *Vargula*) and truly planktonic species consist of a massive protopodite with associated musculature and long exopodial bristles (Text-fig. 6D, H). The length of the protopodite in exclusively planktonic *Conchoecia* species (Text-fig. 5G) is about half the carapace length. Relatively smaller protopodites occur in myodocopes with reduced swimming abilities. Behavioural differences between males and females of the same species, in many cases, are related to significant differences in the appendage structure. For example, adult females of *Vargula hilgendorfii*, by contrast with conspecific adult males, have shorter exopodial bristles with less natatory setae and are therefore much less active swimmers. A greatly enlarged muscular prodopodite enables the adult males of *Rutiderma hartmanni* (Kornicker 1985; Text-fig. 5C) to swim more actively than the adult females.

Generally, frontal appendages of living myodocopes are not known to produce major deformation or swelling visible on the external surface of the carapace. The only exception occurs in the widespread planktonic halocyprids. In these thin-shelled, poorly calcified ostracodes, the trace of frontal appendages is often clearly expressed externally as an anterodorsal hump-like projection (shoulder vault: see Hartmann 1966) and/or as a well-marked constriction of the carapace posterior to the insertion of the massive protopodite of the second antenna (e.g. *Conchoecia kyrtophora* in Angel 1981; Text-fig. 5G). These features may possibly be considered as homologous with the bulb and adductorial sulcus of typical Silurian bolbozoids (Text-figs 2C, 6F–G). However, the hypothesis of bulbs fully occupied by inferred powerful appendages (Siveter and Vannier 1990, fig. 22) is neither consistent with the usual laterally compressed designs of protopodites (e.g. *Vargula*: Pl. 1; Text-fig. 4A, F) nor with the basic functional constraints of frontal appendages.



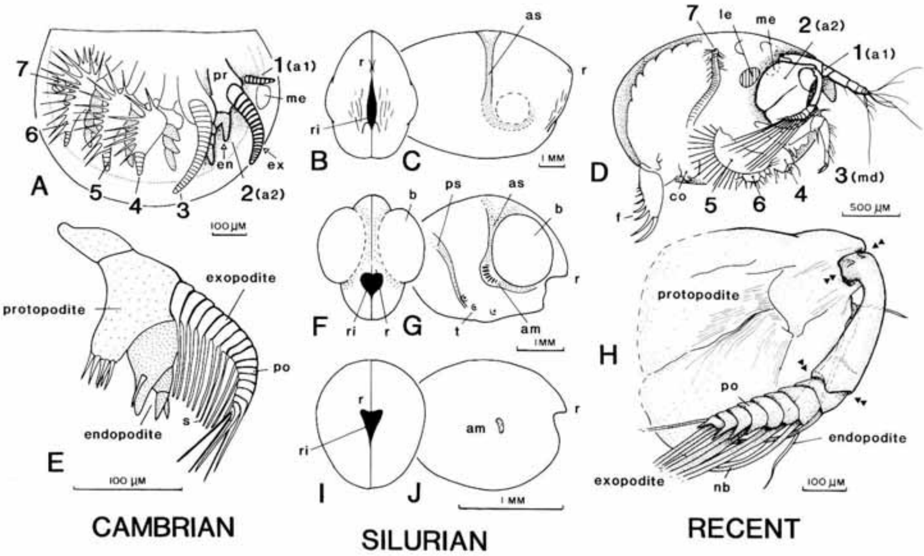
TEXT-FIG. 5. Shape, position and relative size of the first and second antennae in representative Recent myodocope ostracodes. A–D, Order Myodocopida (see classification *in* Text-fig. 3). E–G, Order Halocyprida. A, *Vargula hilgendorfii* (shallow water benthic/demersal cypridinid). B, *Gigantocypris muelleri* (pelagic cypridinid). C, *Rutiderma hartmanni* (shallow water benthic/demersal rutidermatid, after Kornicker 1985). D, *Eusarsiella texana* (shallow water nektobenthic sarsiellid, after Kornicker 1986). E, *Thaumatoconcha radiata* (abyssal benthic thaumatocyprididid, after Kornicker and Sohn 1976). F, *Bathyconchoecia septemspinosa* (ornamented pelagic halocypridid, after Kornicker and Angel 1975). G, *Conchoecia kyrtophora* (pelagic halocyprid, after Angel 1981). Location of lateral eye and adductor muscle attachment also represented. a1, first antenna; a2, second antenna; le, lateral eye; am, adductor muscles. All schematic lateral views of carapaces seen from right. Scale bar represents 500 μm.

In the present state of research, it seems more reasonable to consider the bulb of Silurian myodocopes as a feature resulting from the development of visual organs (lateral eyes? medial eye?). However, this interpretation does not exclude the possibility that a part of the cavity of the bulb may have housed frontal appendages (first and second antennae: see reconstruction in Text-fig. 4D–E, I–J).

Preliminary observations (unpublished) from abundant material collected in the Silurian of the Armorican Massif, France (Text-fig. 1) indicate that some myodocope species (e.g. bolbozoid '*Bolbozoe*' cf. *bohemica*: Text-fig. 1B) probably developed through at least six successive ontogenetic stages. This growth pattern is strikingly similar to that of Recent cypridinid myodocopes, which have five (e.g. *Vargula hilgendorfii*; see Hiruta 1980, 1983*a*) or six free-living juvenile instars (Cohen and Morin 1990*a*). The bulb of Silurian bolbozoids shows a gradual development (in size and volume) throughout its ontogeny. However, young instars seem to have a more voluminous bulb relative to the carapace size than that of adult (Siveter and Vannier 1990, figs 7, 13). Comparable observations can be made concerning the visual organs of some Recent myodocopids. For example, the relative size of the lateral eyes and the medial eye of *Vargula hilgendorfii* is slightly larger in early juveniles than in adults (e.g. ratio eye diameter: carapace length). This does not apply to the frontal appendages (first and second antennae). Therefore ontogenetic data would favour the 'visual' hypothesis proposed to explain the bulb-like structures of the Silurian bolbozoids.

Silurian myodocopes: key-step in the evolution of carapace and appendage structure?

Exceptional preservation of soft parts in the Upper Cambrian of Sweden (Müller 1979, 1982*a*, 1990) provides extremely valuable information about the appendage structure in an early stage of ostracode evolution. The typical Cambrian phosphatocopine *Hesslandona* (reconstruction of a complete preadult specimen, Müller 1982*a*; Text-fig. 6A) has at least seven pairs of basically



TEXT-FIG. 6. Three steps in the evolution of Ostracoda. A, E, primitive appendage structure and carapace design exemplified by Upper Cambrian Phosphatocopida; A, *Hesslandona*; internal view from right, pairs of appendages numbered 1 to 7, exopodial setae not represented; E, *Vestrogothia*; second antenna from right in inferred life position; simplified after Müller's (1979, 1982*a*) reconstructions. B–C, F–G, I–J, major transformation of carapace design and probably internal features (explanation in text) as illustrated by Silurian myodocopes; B–C, *Entomozoe tuberosa* (Llandovery Series); F–G, '*Bolbozoe*' sp. nov. (Ludlow Series); I, J, 'cypridinid' *sp.* (Ludlow Series; Siveter *et al.* 1987); simplified outline of carapace from front and right. D, H, achieved high specialization of appendages and internal organs in Recent myodocopes, exemplified by *Vargula hilgendorfii*; D, internal view of a male carapace from right (pairs of appendages numbered 1 to 7); H, structure of the second antenna (outline of endopodite indicated in dotted line; arrows indicate main articulated joints; natatory exopodial setae not represented). a1, first antenna; a2, second antenna; am, adductor muscle scars; as, adductorial sulcus; b, anterodorsal bulb; co, copulatory organ; en, endopodite; ex, exopodite; f, furca; le, lateral eye; md, mandible; me, medial eye; nb, natatory bristle; po, podomere; pr, protopodite; ps, posterior sulcus; r, rostrum; ri, rostral incisure; s, seta; t, tubercle.

biramous and segmented appendages; their uniform structure suggests a relatively low degree of specialization. The first and second pairs of appendages are accommodated in the frontal part of the carapace together with a tripartite 'medial eye'. For example, the second antennae (Text-fig. 6E) have strong exopodites, segmented into numerous podomeres each bearing a long bristle (natatory function?: see Müller 1979). It is not unreasonable to suppose that the vast majority of lower Palaeozoic ostracodes (e.g. Palaeocopa) had a similar type of appendage structure; their overall external morphology (elongated shape, straight dorsal margin, lobal/sulcal sculpture) remains close to that of most Cambrian Phosphatocopina or Bradoriina. They also probably shared the same ecological preferences (relatively shallow shelf environments) and lifestyles (benthic to occasionally nektobenthic; see Siveter 1984).

There is a morphological gap between these ostracodes (the non-myodocopes listed in Table 1) considered as a whole and the Silurian myodocopes (Table 1; Text-fig. 6). Even the earliest known Lower Silurian myodocopes (*Entomozoe*, Llandovery Series: see Siveter and Vannier 1990) already exhibit very distinctive characteristics (rostrum and slit-like frontal opening, large size, radiated

TABLE 1. Comparative overall morphology and inferred lifestyles of the Silurian myodocopes (right column) and other major groups of ostracodes (Phosphatocopina, Bradoriina, Leperditiocopa, Palaeocopa and 'Podocopa'; consideration on the ranking of these taxa not given here) represented in the Lower Palaeozoic (Cambrian-Ordovician-Silurian). Complete time range indicated below. AD, anterodorsal; Add., adductorial; A1, first antenna; A2, second antenna; calc., calcified; D, dorsal; incl., including; L, Lower; LV, left valve; MD, mediodorsal; Md, Middle; Ord., Ordovician Rec., Recent; RV, right valve; U, Upper. Mainly after Martinsson (1962); Müller 1979, 1982*a*, 1990; Jones and McKenzie 1980; Vannier *et al.* 1989; Siveter and Vannier 1990.

Morphology/taxa	Phosphatocopina	Bradoriina	Leperditiocopa	Palaeocopa	'Podocopa'	Silurian Myodocopa
Lateral outline	Hemicircular/ hemielliptical	Hemielliptical	Hemielliptical	Hemielliptical/ hemicircular	Semi-elliptical	Circular/ elliptical
External sculpture	Lobe(s), sulci	Sinuous lobes or ridges	Dorsal sulcus, tubercle	Complex lobal/ sulcal sculpture	Often absent	Absent or 1/2 sulci + AD lobe
Dorsal margin	Straight	Straight	Straight	Straight	Convex	Convex
Ventral area	Convex	Convex (possible marginal rim)	Convex	Flat/concave complex ridges	Convex	Convex
Frontal area	Convex	Convex	Convex	Convex	Convex	Rostrum, rostral incisure
Valve connection	Complex attachment (D)	Hinge groove (LV)	Long	Usually long (D)	Long (D)	Short (AD or MD)
Ventral overlap	No	No	Overlapping RV, stop-pegs	Marginal	Overlapping LV, stop-pegs	No
Duplicature	Present	Non-documented	Unknown	Unknown	Present	Unknown
Add. muscle scars	No	Unknown	Numerous	Muscle spot?	Unknown	Radiated/reniform
External surface	Smooth	Often reticulated/ punctuated	Smooth	Smooth/ reticulated/ punctuated	Smooth	Smooth/reticulated corrugated tuberculated
Dimorphism	Non-documented	Unknown	Unknown	Common, incl. possible brood-care	Unknown	Probable size/ shape dimorphism
Appendages	● less than 8 pairs ● poorly differentiated ● A1: reduced ● A2: strong exopodite numerous podomeres	Structure unknown (at least 4 thoracic segments)	Unknown	Unknown	Unknown	Unknown probably already specialized frontal appendages
Ocular system	Tripartite medial eye	Unknown	Unknown	Unknown	Unknown	Possible lateral eyes or medial eye
Shell thickness/ calcification	Thin, primarily phosphatic	Thin chitino-calc.-phosphatic	Thick calcified	Thick calcified	Thick	Poorly calcified flimsy (?) shell
Lifestyles	Probable abilities for swimming (nektobenthic)	Unknown	Unknown	Probably benthic	Probably benthic	Probable good swimmers (pelagic fauna?)
Range	Mid-Upper Cambrian	Cambrian	Ord.-U. Dev.	L. Ord.-Perm.	L. Ord.-Rec.	From Llandovery

muscle scars) totally unknown in any other Ordovician or lowermost Silurian ostracode group (Table 1). Judging from living ostracodes in general, important differences in carapace architecture most commonly also imply major differences in the basic arrangement and structure of appendages (e.g. compare podocopes and myodocopes: Text-fig. 3). Although no evidence from soft parts has been obtained so far, a radical transformation of internal structure (body, appendages, vision-related organs) may have happened in ostracodes during the early Silurian. This transformation may have mainly affected the frontal appendages and especially the second pair of antennae through: (1) a sharp reduction of the endopodite; (2) a substantial increase in size of the protopodite; and (3) the development of a flexible articulated exopodite able to protrude outwards through the frontal opening of the carapace (Pl. 1; Text-fig. 6). There is no difficulty for this new design to have been derived from a primitive type of appendage similar to that reconstructed by Müller (1979, 1982*a*) from Upper Cambrian ostracodes (Text-fig. 6E).

Another significant morphological change and differentiation process may have concerned the posterior end of the body. Most Silurian myodocopes (e.g. 'cypridinid'-like forms; Text-figs 2B, 6I–J) have an evenly rounded or elliptical outline. In living representatives (e.g. *Vargula hilgendorfii*: Pl. 1; Text-fig. 6D) the mediodorsal to medioventral curvature of the carapace coincides internally with the posterior part of the body which is strongly arched, wrapped with a complex muscular network (Cannon 1940; Hartmann 1966), terminated by a pair of particularly developed articulated furcae (Pl. 1; Text-fig. 6D) and longer and more flexible than in any other ostracodes. Observations from videos (Vannier and Abe, in press) show that these features are important in relation to the increased mobility of the animals on the bottom (crawling activities, rotation), in the sediment (digging) or off the substratum (swimming). That Palaeozoic myodocopes were provided with a comparable musculature and furcae is speculative but still a serious hypothesis to consider.

Lower Triassic representatives (phosphatic preservation; Weitschat 1983*a*, 1983*b*) have compound lateral eyes, antennae, basal furcal attachments, highly specialized organs (e.g. seventh limb: Text-fig. 6D) almost identical to their Recent homologues.

Current investigations by Vannier, Müller and Walossek on Upper Devonian ostracodes with preserved appendages (Müller 1982*b*) are expected to provide essential data on the body plan of Palaeozoic species.

PHYLOGENY

Few attempts have been made to derive a phylogeny both for extant and extinct higher taxa of Myodocopa. There have been substantial contributions by Kornicker and Sohn (1976) through a detailed study of the thaumatocypridid lineage (see classification, Text-fig. 3) and by Neale (1983) who mainly focused on the Carboniferous and later development of polycopid ostracodes. Hessler *et al.* (1982) reviewed current interpretations of the origin and evolution of Ostracoda. Although fragmentary, the present knowledge of Silurian myodocope faunas (Siveter and Vannier 1990) allows us to reconsider the problem of the phylogenetical relationships between the Palaeozoic, post-Palaeozoic and Recent representatives of the group.

Silurian myodocopes

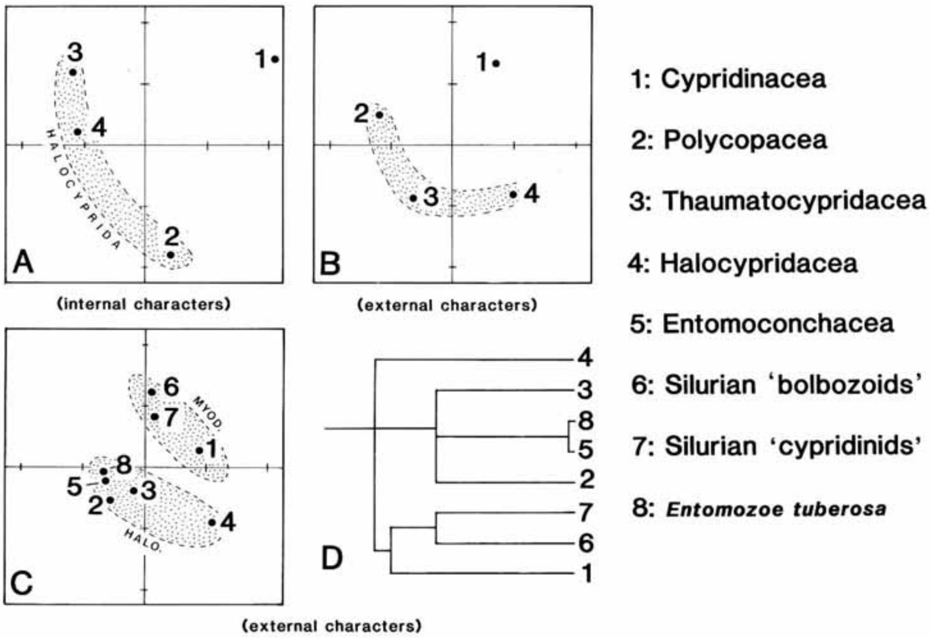
Major groups of Silurian myodocopes can be distinguished on the basis of external carapace morphology: the 'cypridinid'-like myodocopes (so-called because of the overall resemblances with modern cypridinaceans), the 'bolbozoids', and forms like the early Silurian *Entomozoe tuberosa* (Text-fig. 2A). Multivariate and cluster analysis were used to assess the degree of similarity between these three groups and the following established superfamilies (Text-fig. 3): Cypridinacea, Polycopacea, Thaumatocypridacea, Halocypridacea and extinct Entomoconchacea (see Kornicker and Sohn 1976). The Siluro-Devonian 'entomozoids' (Gooday 1983; Siveter and Vannier 1990), whose myodocope affinities are controversial, are not considered in this analysis. Other myodocope superfamilies such as Cylindroleberidacea and Sarsiellacea probably derive from a cypridinacean stock (Kornicker 1986) and are therefore beyond the scope of our study.

Degree of similarity between extinct and extant myodocopes

The selected morphological characters used in the analysis are designated in Table 2 and numbered from 1 to 17 and 18 to 26 for external and internal features, respectively. External characters have been chosen according to their functional and structural significance (e.g. the rostral incisure is related to the function of frontal appendages). Internal characters are those used by Kornicker and Sohn (1976) to distinguish major taxonomic catagories among living myodocopes. A range of (mostly) qualitative values (coded 1 to 4) was attributed to each character (e.g. the adductor muscle scars are known to be either radiated (1), reniform (2) or composite (3). The classification of Recent myodocopes is mainly based on complex anatomical differences (e.g. appendages, copulatory organs). However, for the purpose of comparing extinct and extant taxa we considered the external characters only (1 to 17, Table 2). An important point prior to interpretation was to test the reliability of similarities obtained from the external morphology only. Text-figure 7A shows the affinities of four superfamilies of Recent ostracodes based on nine internal characters (18 to 26, Table 2). A comparable pattern of similarities (Text-fig. 7B) is obtained using the selection of external characters listed in Table 2. In both cases (Text-fig. 7A–B), myodocopids (1) and halocyprids (2, 3, 4) appear as clearly separated groups. Results illustrated on a similarity diagram and a dendrogram (Text-fig. 7C–D) are as follows:

TABLE 2. Morphological characters (1 to 26) with corresponding actual range (coded 1 to 4) used for comparative analysis (Text-fig. 7) of Recent and fossil myodocopes (see explanation in text).

Morphology	Code 1	Code 2	Code 3	Code 4
External				
1 Size range	Less than 1 mm	Between 1 and 3 mm	More than 3 mm	
2 Outline	Circular	Elliptical	Hemielliptical	
3 Rostrum	Present	Absent	Reduced	
4 Rostral incisure	Present	Absent		
5 Frontal opening	Cardioid	Slit-like	Absent	
6 Anteroventral margin	Convex	Flat to concave		
7 Ventral margin	Convex	Flat		
8 Posterior margin	Convex	Flat		
9 Dorsal margin	Convex	Straight		
10 Rostral margin	Straight	Curved	Strongly curved	
11 Adductorial sulcus	Present	Absent	Occasionally present	
12 Posterior sulcus	Present	Absent	Occasionally present	
13 Adductorial muscle scars	Radiated	Reniform	Composite	
14 Caudal process	Present	Absent	Occasionally present	
15 Length of valve connection	Less than L/2	More than L/2		
16 Location of valve connection	Anterodorsal	Mediodorsal	Posterodorsal	Dorsal
17 Number of growth stages	5 or less	6 or more	Unknown	
Internal				
18 Furcae	Present	Absent		
19 Copulatory organ	Paired	Unpaired		
20 Complexity of copulatory organ	High	Low		
21 Medial eye	Present	Absent		
22 Lateral eyes	Present	Absent		
23 6th limb	Long	Absent	Reduced	
24 Maxilla	Uniramous	Biramous		
25 7th limb	Present	Absent		
26 1st antenna	Long	Short	Very reduced	



TEXT-FIG. 7. Degree of similarity between Recent and fossil myodocopes (1 to 8) deduced from multivariate (A–C) and cluster (D) analysis. Internal and external characters are those designated in Table 2. Halo, Halocyprida; Myod., Myodocopida (see classification, Text-fig. 3). Silurian 'cypridinids' encompasses the cypridinid-like species figured in Siveter *et al.* (1987).

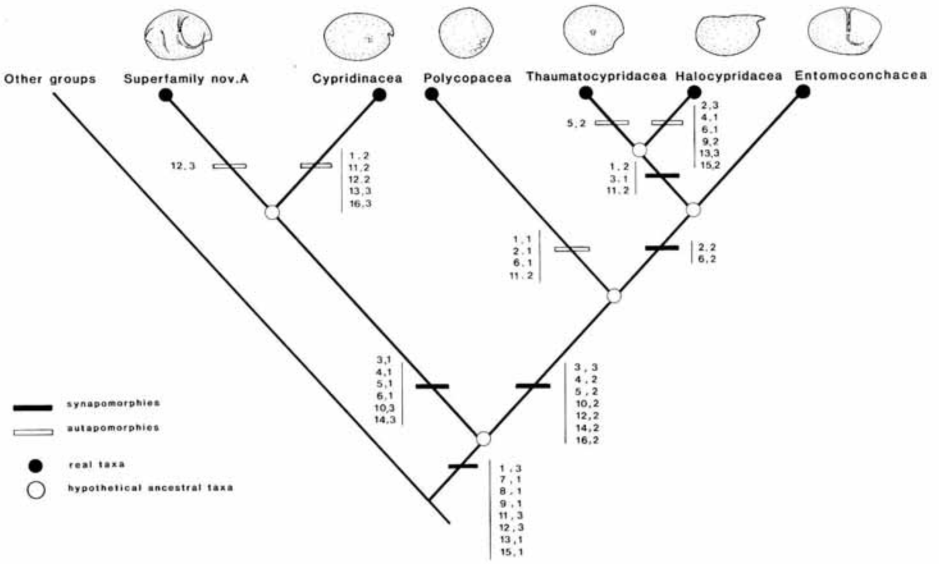
a. Silurian 'bolbozoids' (6) and 'cypridinids' (7) show strong similarities to each other, are probably closely related to Recent cypridinaceans (1) and therefore belong to the Order Myodocopida. Their exact taxonomic assignment (tentatively Bolbozoidae (6) and Family nov. A (7) within a Superfamily nov. A) has to be defined on the bases of ongoing detailed systematic studies of the British, French, Bohemian and Sardinian faunas by D. J. Siveter and J. Vannier.

b. Entomozoe tuberosa (8) probably belongs to the Entomoconchacea (5), an extinct superfamily known up to the Lower Carboniferous and from which the Mesozoic and Recent thaumatocypridaceans (3) may have derived (Kornicker and Sohn 1976).

We conclude that the two major components of the Recent myodocope fauna, Myodocopida and Halocyprida (Text-fig. 3) were probably already differentiated during the Silurian.

Cladistic analysis

A cladistic method (Hennig 1979; Eldredge and Cracraft 1980; Forey 1990) is used to present the distribution of sixteen external characters (numbered 1 to 16, Table 2) between six superfamilies (Superfamily nov. A, Cypridinacea, Polycopacea, Thaumatocypridacea, Halocypridacea, Entomoconchacea) and consequently to express a possible sister-group hierarchy within the myodocope ostracodes (Text-fig. 8). In the present cladistic analysis, a character is defined by two numbers referring to the list given in Table 2. For example, the character coded '13, 1' on the cladogram (Text-fig. 8) refers to adductorial muscle scars ('13') which are radiated ('1'). Shared derived characters (synapomorphies) and retained primitive characters (symplesiomorphies) are recognized. Autapomorphies define the terminal taxa on the cladogram. A phyletic tree is proposed (Text-fig. 9) derived from phylogenetical relationships (cladogram) and stratigraphic distribution.



TEXT-FIG. 8. Cladogram of relationships of six Superfamilies included within the Order of Myodocopa. Superfamily nov. A and Entomoconchacea are extinct taxa. Each synapomorphic or autapomorphic character is identified by two numbers according to Table 2 (see also text). 'Other groups' used to designate Lower Palaeozoic (Cambrian, Ordovician, Silurian) ostracodes other than myodocopes (see explanation in text).

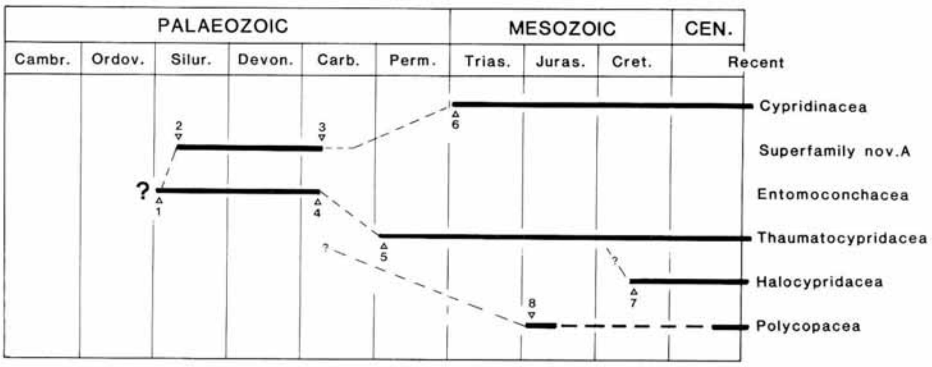
Origin of myodocopes

The original, Silurian groups of the Myodocopa (Superfamily nov. A and Entomoconchacea) share numerous synapomorphic characters (elliptical shape with neither straight dorsal margin nor flat ventral margin, severe reduction of lobation/sulcation, general increase in size). They most probably diverge from one of the ostracode groups present in the Upper Ordovician/Lower Silurian but there is still no evidence for their exact origin (Beyrichiocopa? see Vannier *et al.* 1989). Representatives of Superfamily nov. A, already widespread by Upper Silurian times, presumably derived from Lower Silurian entomoconchaceans such as *Entomozoe tuberosa* (Siveter and Vannier 1990; Text-fig. 2A) through further major transformations of the frontal part of the carapace (e.g. development of the rostrum). However, they retain ancestral characters (bolbozoids have radiate muscle scars and an adductorial sulcus); they became extinct by the Late Devonian (Text-fig. 9C) or possibly Carboniferous times (Bless and Sanchez de Posada 1973). Entomoconchaceans are known to occur up to the Lower Carboniferous (Text-fig. 9D).

The existence of myodocopes (Text-fig. 9; Siveter and Vannier 1990, fig. 23) in the Carboniferous and the Permian is attested by several authors (e.g. Jones *et al.* 1884; Kornicker and Sohn 1976; Neale 1983) but is relatively poorly illustrated and documented. This almost unexploited field has to be investigated in order to establish phylogenetic links between Palaeozoic and post-Palaeozoic myodocope taxa.

Origin of modern myodocopids

Modern myodocopids probably originated from Upper Palaeozoic forms (Superfamily nov. A) via the cypridinacean lineage (lower Triassic to Recent: Text-fig. 9). The total loss of lobation/sulcation



TEXT-FIG. 9. Phyletic tree of the six myodocope Superfamilies discussed in the present paper, derived from phylogenetical relationships (cladogram, Text-fig. 8) and stratigraphic distribution. Lowermost and uppermost stratigraphic occurrence of each Superfamily defined by species 1 to 8. 1, *Entomozoe tuberosa*, Llandovery Series, Silurian (Siveter and Vannier 1990); 2, '*Bolbozoe*' cf. *anomala*, Ludlow Series, Silurian (Siveter *et al.* 1987); 3, *Sulcuna rabieni*, Upper Devonian (Becker and Bless 1987); 4, *Entomoconchus scouleri*, Lower Carboniferous (Kornicker and Sohn 1976); 5, *Thaumatomma piscifrons*, Permian (Kornicker and Sohn 1976); 6, *Triadocypris spitzbergensis*, Lower Trias (Weitschat 1983*a*, 1983*b*); 7, *Conchoecia*? *cretacea* Cretaceous (Pokorny 1964) and Cretaceous halocyprid species studied by Colin and Andreu (1990); 8, *Polycope plumhoffi*, Lower Jurassic (Bate and Coleman 1975). Camb., Cambrian; Carb., Carboniferous; Cen., Cenozoic; Cret., Cretaceous; Devon., Devonian; Juras., Jurassic; Ordov., Ordovician; Perm., Permian; Silur., Silurian; Trias., Triassic.

is one of the most significant autapomorphic character of cyrpidinaceans. The retention of a prominent rostrum in cypridinaceans and most living myodocopids is symplesiomorphic.

DISTRIBUTION PATTERN OF RECENT MYODOCOPE FAUNAS

The bathymetric distribution of the eight families of Recent myodocopes is represented in Text-figure 10, along a marine profile from littoral to oceanic trench. None of these broad taxonomic groups shows any apparent specificity to a particular depth zone. For example, benthic/nektobenthic cypridinids (Text-fig. 10G) and also sarsiellids, philomedids and cylindroleberidids cover an extremely wide bathymetrical range from the shallowest to abyssal environments (Siveter *et al.* 1991). Similarly, planktonic cypridinids, although more common in the mesopelagic and abyssal zones, are also known from shallower neritic water layers (Angel 1983*a*). In ostracodes and many other major groups of living crustaceans (Abele 1982) species diversity generally increases from higher to lower latitudes and decreases from shallower to deeper environments. These very general characteristics apply to benthic, nektobenthic and planktonic myodocopes (Poulsen 1962, 1969, 1972, 1973, 1977; Kornicker 1975*a*, 1975*b*, 1977; Angel and Fasham 1975), and probably also to their Palaeozoic early representatives. The latitudinal effect on the diversity of benthic myodocope faunas living deeper than 1000 m is negligible (see Kornicker 1977) and attributed to greater uniformity in environment at increasing depths. Although biogeographic regions and subregions can be recognized for benthic/nektobenthic faunas (e.g. Kornicker 1975*a*), oceanic planktonic myodocopes (e.g. halocypridids) are widely distributed (Angel 1972; Poulsen 1977). Referring to Poulsen's zoogeography, Abele (1982) notes that 'of 74 species found in at least 3 samples, 91 per cent are found in all major 3 oceans'. Similarly, Hartmann and Hartmann-Schröder (1988) conclude that twenty three of the deep-sea planktonic halocypridine species have a circumtropical distribution while fifteen occur worldwide. Truly planktonic halocyprids show vertical stratification (Angel 1983*a*, 1983*b*) throughout the water column from the uppermost surface layers (neuston: see Text-fig. 10) to the deepest abyssopelagic water masses (see Angel 1983*b* for north-east Atlantic). Their species richness reaches a maximum at depths of about 1000–1500 m whereas their numerical abundance generally culminates at about 200–400 m (Angel 1983*a*; Text-fig. 11). Seasonal and diel (related to the day-night light cycle, *sensu* Angel 1983*a*) vertical migrations are one of the most striking phenomena to occur in halocyprids but also in planktonic myodocopids (e.g. *Cypridina*: Text-fig. 10G). In the case of diel migrations, it consists of an upward vertical movement (e.g. nocturnal: Arashkevich 1977) followed by a downward passive sinking, probably associated with feeding activities (Angel 1983*a*). To a certain extent, this type of migration is comparable to the sexually-related migrations of nektobenthic myodocopids (Text-fig. 10). Both imply strongly developed frontal appendages for active swimming.

The environment range of Lower Palaeozoic ostracodes was probably much narrower than that of living representatives. In the Ordovician, ostracodes are mainly benthic, strongly endemic organisms living in shallow shelf environments (Siveter 1984). If the widespread Silurian myodocopes really represent a successful attempt by crustaceans to colonize (off bottom) the epipelagic (and upper mesopelagic?) zone, then their distribution must have reflected some of the fundamental biological and distributional aspects of Recent myodocopes: vertical stratification, swimming abilities and migrations, latitudinal effect, etc. However, it might be excessive to consider the Silurian myodocopes as the earliest mid-water crustacean fauna. Another group of partly described crustaceans, the phyllocarids, are widespread in exterior sites around Gondwana from the Tremadoc onward, if not from the Middle Cambrian (R. Fortey, pers. comm.).

DISTRIBUTION PATTERN AND MODE OF LIFE OF EARLY PALAEOZOIC MYODOCOPES

Spatial distribution

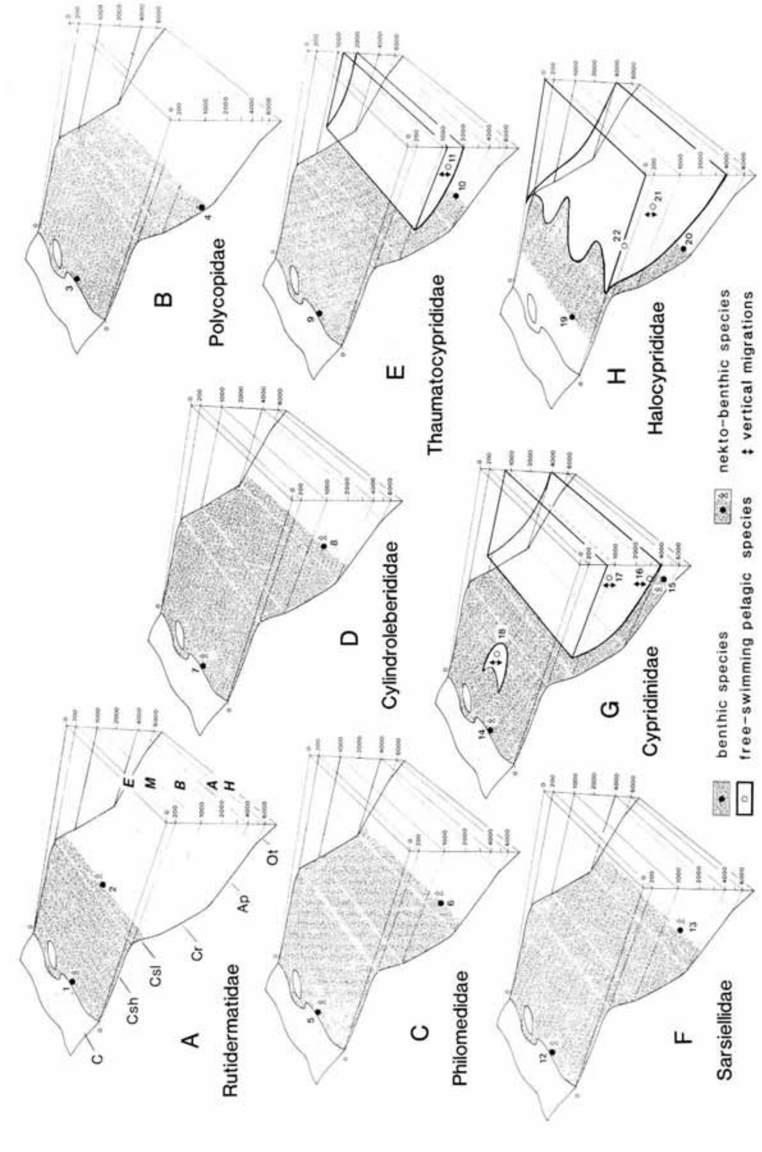
Although their presence is recorded as early as the Lower Silurian (Llandovery Series of Scotland: Siveter and Vannier 1990), myodocopes become a substantial component of the marine fauna only in late Silurian times. Most myodocopes so far recovered (Siveter *et al.* 1987; Vannier 1987) are predominantly of Ludlow and or Pridoli age (dated by associated graptolites). During this fifteen million year time interval, they show a pattern of spatial distribution fundamentally different from that of contemporaneous shallow marine benthic ostracode faunas (compare A with B, Text-fig. 12). Evidence for benthic lifestyles in Palaeozoic ostracodes derive from thorough analysis of carapace design, calcification and comparison with modern analogues (Siveter 1984; Vannier *et al.* 1989).

1. Myodocopes are known from numerous sites (Text-fig. 12B; Siveter *et al.* 1987; Siveter *et al.* 1991) located on both sides of the Rheic Ocean which has been recognized as a major widening marine separation between North Gondwanan and North European regions by early Silurian times (evidence from the distribution of brachiopods and phytoplankton: Cocks and Fortey 1982, 1989) and probably even earlier in the Upper Ordovician (evidence from benthic ostracodes: Vannier *et al.* 1989). Their considerable distributional area includes the perigondwanan margins from the High-Atlas of Morocco (Vannier 1987) to Bohemia, and even as far as China and New South Wales (Australia) and Avalonia-Baltica (Welsh Basin of Britain and Poland).

2. Upper Silurian myodocopes have a remarkable uniformity of composition. Ornamented/smooth bolbozoids (Text-figs 1–2) and associated 'cypridinid'-like taxa form the exclusive and taxonomically closely related (Text-figs 2, 7–9) components of the fauna. Judging from the number of taxa identified so far, they seem relatively poorly diversified.

3. Several widespread key species (e.g. '*Bolbozoe*' *bohemica* from the Ludlow Series; Text-fig. 12B) have been recognized on the opposing margins of North Gondwana (Armorican Massif, Bohemia) and Avalonia-Baltica (Welsh Basin, Poland).

By contrast (Siveter 1984, p. 78) contemporaneous shelf benthic ostracodes show strong provincial differentiation (Text-fig. 12A). As their modern representatives (Cohen and Morin 1990*a*) they most probably belong to the category of inner shelf cratonic faunas (*sensu* Cocks and Fortey



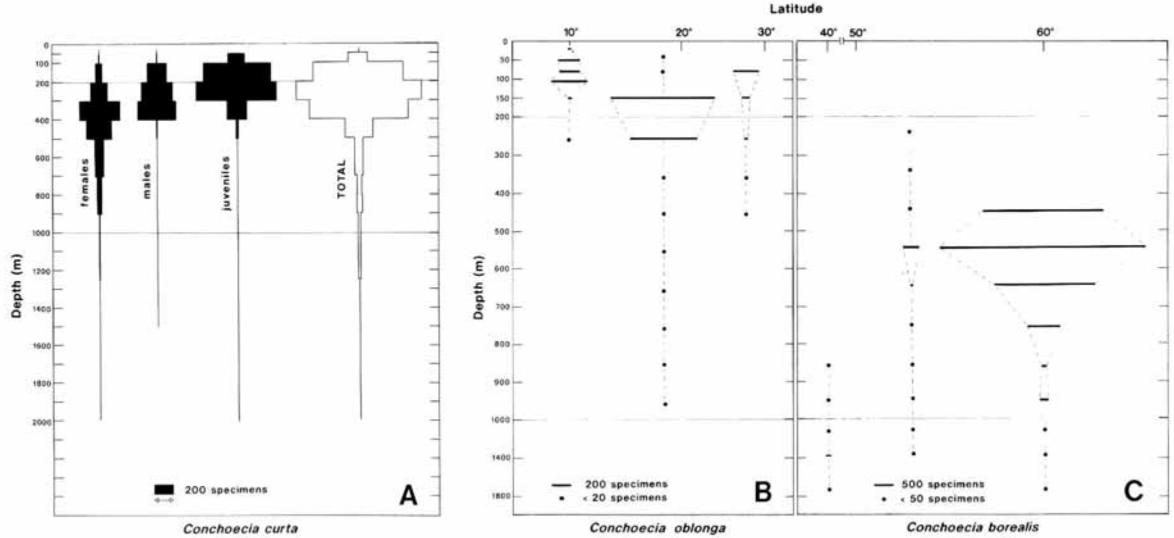
TEXT-FIG. 10. For legend see opposite.

1989, p. 185) with no pelagic larval stage (Siveter 1984) and, therefore, have low potential for transoceanic dispersal. This distributional pattern is applicable to the Lower Palaeozoic benthic ostracodes in general (see Schallreuter and Siveter 1985; Vannier *et al.* 1989). Even reduced to a narrow oceanic stretch from late Ordovician times (Pickering *et al.* 1988), the 'Remnant Iapetus' still sharply restricted ostracode interchanges until the late Silurian (Berdan 1990): Avalonia and Baltica form one broad biogeographical entity (e.g. identical Pridolian *Frostiella* and *Londinia* species from Maine to Podolia; Siveter 1989), distinct from the north American regions (Copeland and Berdan 1977; Berdan 1990). The widening Rheic Ocean (see Cocks and Fortey, 1982, 1990; Vannier *et al.* 1989), between Avalonia-Baltica and the higher latitude north Gondwanan domain (Text-fig. 12A), creates an obvious, increasing oceanic and latitudinal barrier to inner shelf organisms such as benthic ostracodes. For example, Bohemian faunas have very distinctive characteristics and no apparent faunal links with northern Europe and north America. The faunal list proposed by Pribyl (1988) for the Ludlow-Pridoli of Bohemia contains an 'unusual' low proportion of beyrichiids, a family which is abundantly represented in the lower latitude (shallower?) carbonate deposits of the Appalachian (e.g. Anticosti) or in the Avalono-Baltic (south Britain, Gotland) regions. A similar scarcity in beyrichiids also applies to the Ludlow/Pridoli deposits of the Armorican Massif (J. Vannier, unpublished material) and of the French Pyrenees (Degardin 1988). The distribution of myodocopes as plotted in reconstructed maps for the Upper Silurian (Text-fig. 12B) is obviously not controlled by the same chief factors (climatic/latitudinal effect, oceanic separations, etc.). As they also never occur together with any of the typical shelf faunas (e.g. 'shelly' assemblages of benthic ostracodes, brachiopods, trilobites, etc.: Siveter *et al.* 1987), they most probably belong to another category in terms of biofacies, including the two possible alternatives of a deeper outer-shelf benthic fauna or of planktonic fauna.

Deeper-benthic or planktonic fauna?

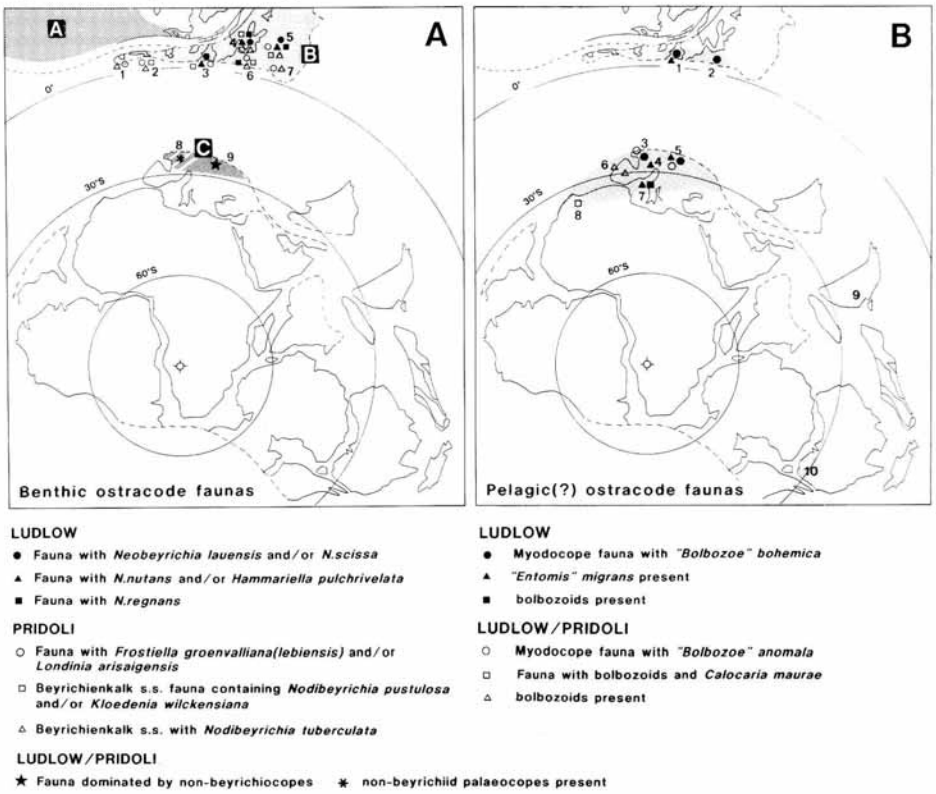
According to Cocks and Fortey (1989), deeper-shelf faunas can be recognized in the lower Palaeozoic (e.g. Ordovician trilobite cyclopygid biofacies around Gondwana). The extremely wide distribution of some of the taxa, including intercontinental links at generic level, is interpreted as resulting from more uniform environmental conditions at greater depth. To some extent, this view is consistent with the cosmopolitan character of numerous Quaternary deep-sea podocopid and platycopid ostracode species (deep-bathybenthic to abyssobenthic faunas: Whatley and Ayress 1988). Although a succession of depth-related shelf assemblages can be identified in the Silurian

TEXT-FIG. 10. Depth range of Recent myodocopid (A, C–D, F–G) and halocyprid (B, E, H) ostracodes. Shallowest and deepest occurrence indicated (black spots) on the profile for benthic/nektobenthic representatives of each family. 1, *Rutiderma cohenae* (subtidal to 4 m: Kornicker 1983); 2, *Alternochelata neali* (52–560 m; Kornicker 1983); 3, *Polycope japonica* (0–0·3 m: Hiruta 1983*b*); 4, *Polycope ovalis* (335–3105 m: Bonaduce *et al.* 1983*a*); 5, *Euphilomedes agilis* (rock pool; Kornicker 1975*a*); 6, *Igene walleni* (4303 m; Kornicker 1975*a*); 7, *Microasteropteron youngi* (0·3–0·6 m: Kornicker 1981); 8, *Bathyleberis grossmani* (3431–4303 m; Kornicker 1975*b*); 9, *Danielopolina orghidani* (shallow marine caves: Kornicker and Sohn 1976); 10, *Thaumatoconcha elongata* (4758 m: Kornicker and Sohn 1976); 11, *Thaumatocypris echinata* (1100–2000 m: Kornicker and Sohn 1976); 12, *Sarsiella misakiensis* (tide pool: Hiruta 1978); 13, *Spinacopia octo* (3495–4758 m: Kornicker 1975*b*); 14, *Vargula hilgendorfii* (1–7 m: Nakamura 1954; Kornicker 1975*a*); 15, *Hadacypridina brunii* (5340–6000 m: Kornicker 1975*a*); 16, *Gigantocypris dracontovalis* (2100–3900 m: Angel 1983*b*); 17, *Gigantocypris muelleri* (700–1500 m: Moguilevski and Whatley 1988); 18, *Cypridina* and *Metavargula* species (plankton of neritic seas: Angel 1983*a*); 19, non spinous *Bathyconchoecia* (130–3165 m: Kornicker and Angel 1975); 20, *Bathyconchoecia septemspinosa* (271–3600 m: Kornicker and Angel 1975); 21, planktonic halocyprids (max. abundance, 200–400 m; max. diversity, 1000–1500 m: max. depth, 3900 m: Angel 1983*a*, 1983*b*); 22, neustonic halocyprids (= the surface 10 cm of the water column: Moguilevski and Angel 1975, Angel 1983*a*, 1983*b*; exact horizontal distribution unknown). E, epipelagic zone (0–200 m); M, mesopelagic zone (200–1000 m); B, bathypelagic zone (1000–4000 m); A, abyssopelagic zone (4000–6000 m); H, hadopelagic zone (deeper than 6000 m). C, continent; Csh, continental shelf; Csl, continental slope; Cr, continental rise; Ap, abyssal plain; Ot, ocean trench.



TEXT-FIG. 11. Vertical distribution and numerical abundance of planktonic halocyprid ostracodes exemplified by three *Conchoecia* species from the North-East Atlantic. A, depth range of *Conchoecia curta* at 30° lat. N; sexual difference in distribution appears. B–C, spatial distribution of *Conchoecia oblonga* (form A) and *Conchoecia borealis*; note latitudinal effect on bathymetrical range and abundance. All data from Fasham and Angel (1975, table 1; figs 10–11).

Upper Silurian (Ludlow-Pridoli) = 424-410 Ma



TEXT-FIG. 12. Distribution of selected peri-Gondwanan, North-European and North-East American ostracode faunas in late Silurian (Ludlow-Pridoli) times. A, benthic shelf faunas. A, Appalachian province; B, Avalono-Baltic province; C, North Gondwanan province. 1, Maine; 2, Nova Scotia; 3, Welsh Basin and South-east England; 4, Scania and Gotland; 5, North-east, Central and South-east Baltic; 6, Poland; 7, Podolia; 8, Armorican Massif; 9, Bohemia. B, inferred planktonic faunas. 1, Welsh Basin 2, Poland; 3, Armorican Massif; 4, Montagne-Noire; 5, Montagne-Noire; 6, Portugal and Central Spain; 7, Sardinia; 8, High-Atlas, Morocco; 9, China; 10, New South Wales. Palaeogeographical setting mainly after Pickering *et al.* (1988), Cocks and Fortey (1982, 1989), Vannier *et al.* (1989) modified. Faunal data from de Koninck (1876), Canavari (1900), Chaubet (1937), Copeland and Berdan (1977), Siveter (1978, 1989), Siveter *et al.* (1987), Vannier (1987).

(Siveter 1984) and the Ordovician (Vannier *et al.* 1989), there is no evidence for the existence of deep-sea benthic ostracodes in the lower Palaeozoic. The vast majority of living deep-sea benthic/nektobenthic myodocope ostracodes show much stronger tendency to endemicity than to pandemicity (Kornicker 1975*a*; Hartmann and Hartmann-Schröder 1988).

Concerning the Upper Silurian myodocopes, associated sediments (typically organic-rich laminated mud-silt or carbonate sequences; Siveter *et al.* 1987, 1989) strongly suggest a depositional environment different and most probably deeper (at least locally; e.g. in the Welsh Basin) than the inner shelf.

1. Myodocopes are found in association with organisms generally considered either as phytoplanktonic or planktonic passive drifters (e.g. graptolites: Berry 1987; acritarchs, chitinozoans; scyphocrinitid crinoids: Haude 1972; Ubaghs 1978*a*, 1978*b*) or as active nektonic swimmers (e.g. phyllocarid crustaceans: Abele 1982; Schram 1982; eurypterids, orthoconic nautiloids, entomozoid ostracodes such as '*Entomis*' *migrans*: Gooday 1983; Siveter and Vannier 1990). The only significant and possible epi/infaunal dwellers are precardiacean and small pterineid bivalves (Kriz 1984; Pojeta 1987; Siveter *et al.* 1987) although their benthic mode of life is not fully understood.

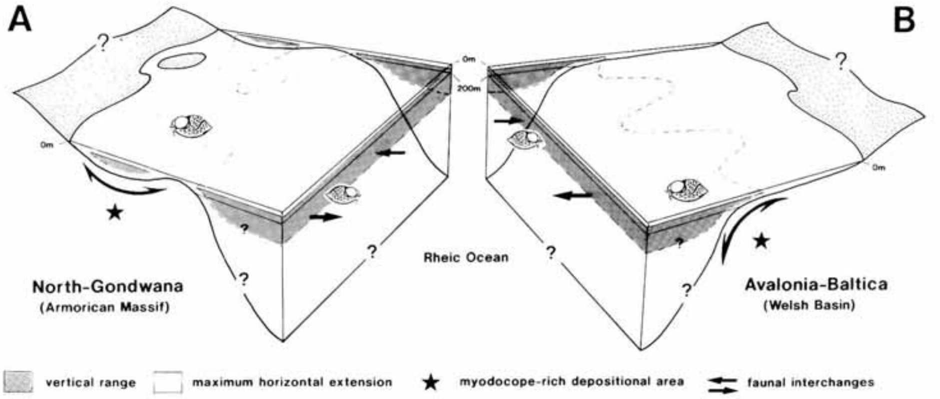
2. The scarcity or even total absence of benthic fauna and bioturbation in myodocope-bearing sediments (Text-fig. 1) suggests that anoxic conditions prevailed in the lowermost layers of the water column, including the sediment-water interface (Text-fig. 13). This is supported at least in the north Gondwanan domain (e.g. Armorican Massif) by the composition and geochemistry (Dabard and Paris 1986; Paris *et al.* 1986) of the sediments. They typically contain 'abnormal' high percentages of organic carbon (from 5 to exceptionally 40 per cent), trace-elements (Sr, Y, Rb, Cr; VD, up to 5600 ppm), and disseminated fine-grained framboidal pyrite, associated with reducing conditions and depletion of oxygen on/in the substrate. Together with a relatively quiet environment, such conditions probably largely contributed to the preservation of the thin and presumably organic-rich ('chitinous'?: see Sohn and Kornicker 1988 for Recent) carapace of myodocopes.

For these reasons and thus following the interpretations of Siveter (1984), Siveter *et al.* (1987), Siveter and Vannier (1990), and Siveter *et al.* (1991), we conclude that the vast majority of Upper Silurian myodocopes lived off-bottom. Their distribution (Text-fig. 12B) and uniformity of composition reproduces that of modern planktonic myodocopes (e.g. halocyprids). All other Recent benthic and nektobenthic myodocopes, including the deep-sea species, show an overwhelming tendency to endemicity (Hartmann and Hartmann-Schröder 1988). The ability of numerous nektobenthic species to swim in the water column (mostly vertical migrations in the vicinity of sea-bottom) does not apparently lead to a greater geographical distribution. For example the typical nektobenthic active swimmer *Vargula hilgendorfii* (Pl. 1; Text-fig. 6D–H) is distributed along the Pacific Coast of Japan and in adjacent seas according to the same overall pattern as numerous truly benthic non-myodocope species. Such considerations do not apply to planktonic species. Although Palaeozoic myodocopes may have adopted various lifestyles (e.g. shallow-water benthic/nektobenthic, as in the earliest representative of the group *Entomozoe tuberosa*: Siveter and Vannier 1990), it is most probable that the Upper Silurian myodocope fauna was truly planktonic.

Neritic or oceanic fauna?

At what distance from shore such planktonic organisms may have lived is a more difficult question to answer. If we consider that the accumulation of myodocopes in sediments resulted from a continuous, almost *in situ*, sinking of dead carapaces and exuviae (as organic pellets in modern oceans: Angel 1984; Text-fig. 14), then their horizontal extension within the water masses can be deduced from their facies occurrence in the depositional environment (see schematical profile, Text-fig. 14A–B). The actual horizontal range of myodocopes probably included outer-shelf to slope (e.g. Welsh Basin, Bohemia: Siveter *et al.* 1987, 1991) and also more proximal environments judging from the locally (e.g. Sardinia: Gnoli *et al.* 1979) higher proportion of bioclastic material in some myodocope-bearing sediments. The distribution of lithofacies in the Silurian of the Welsh Basin is given by Siveter *et al.* (1989).

The hemipelagic muds of the Armorican Massif, extremely rich in myodocopes (e.g. Ludlow Series, Text-fig. 1), are regarded as deposited in a stagnant anoxic basin (for geological evidence see Paris *et al.* 1986) along the northern margin of Gondwana. Faunal and sedimentological data would favour the hypothesis of a depositional environment probably shallower and more proximal than in the Welsh Basin (Siveter *et al.* 1989 and reconstruction, Text-fig. 13). For example, disarticulated eurypterids, a group of arthropods common in Silurian marginal-marine and freshwater facies (Hanken and Størmer 1973; Robison, 1987), occur in Armorican black shales. Frequent intercalated



TEXT-FIG. 13. Reconstructed depositional environments and possible distributional pattern of myodocope ostracodes by Upper Silurian times: A, in the Armorican Massif (anoxic basinal conditions); B, in the Welsh Basin (outer-shelf to slope environments). Myodocope ostracodes are considered as oceanic to neritic planktonic organisms (a tentative spatial and bathymetrical distribution is indicated). In each case, the relative position and morphology of land masses and deep oceanic domains are hypothetical. After Paris (1977, 1981), Paris *et al.* (1986), Siveter *et al.* (1987, 1989).

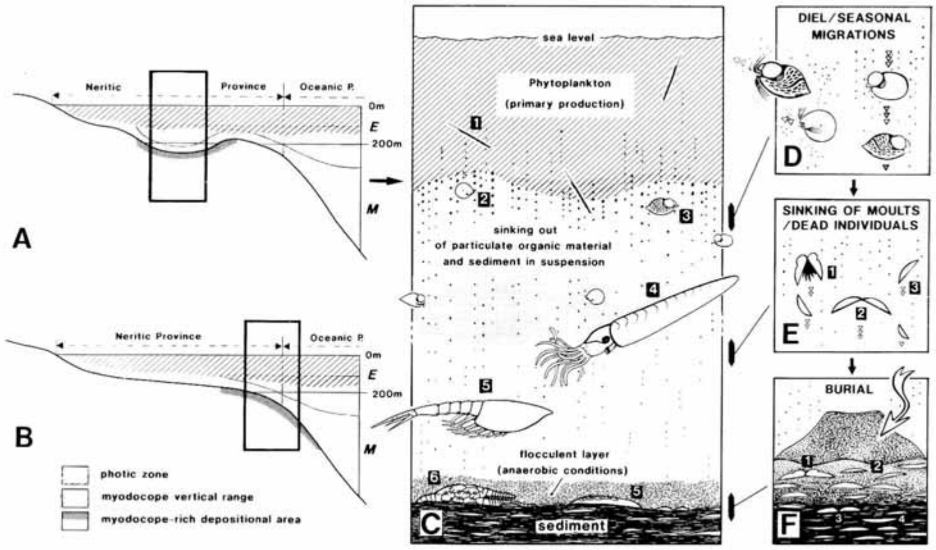
sandstones (Paris 1977, 1981; Paris *et al.* 1986) would also indicate the vicinity of land masses (continental blocks bordering the Rheic Ocean?: Robardet *et al.* 1990).

Similar to the Recent planktonic communities (Text-fig. 10), the Upper Silurian myodocopes probably mainly inhabited the oceanic province (e.g. Welsh Basin, Text-fig. 14B) and also the distal part of the neritic province (e.g. Armorican Massif, Text-fig. 14A).

Vertical range

The spatial distribution and vertical structure of modern planktonic communities is partly controlled by the available food supply from the photic zone (mainly phytoplanktonic primary production). The sinking detrital organic-rich material generated by phytoplankton and zooplankton (faecal pellets, marine snow, etc..) is an important source of nutrients for mid-water organisms and deep-benthic faunas (Angel and Baker 1982; Angel 1984). According to Angel (1984), snow particles occur at particularly high concentration at 250–340 m and in 10–20 m layers at 850 and 1500 m. Concerning the upper layers of the water column, these figures seem to coincide with the maximum abundance of many halocyprid species (Angel 1983*a*, 1983*b*; see example at 30° lat., Text-fig. 11) within the 200–400 m depth range. Although direct predatorial feeding is reported (large size meso/bathypelagic *Gigantocypris muelleri*: Moguilevsky and Gooday 1978), the huge mass of sinking particles at various stages of microbial degradation constitutes a potential and probably largely exploited source of energy for the most common small size planktonic ostracodes (e.g. halocyprids, Angel 1983*a*). Studies of the gut contents of planktonic cypridinid ostracodes (Arashkevich 1977; Angel 1983*a*) reveal major diet components such as crustacean copepods, diatoms, flagellates, radiolarians, foraminiferans with the proportion of radiolarians and flagellates increasing for animals living below 100 m (Angel 1983*a*).

Although involving different marine micro/macro-organisms, a comparable stratification of the water masses and organic flux (Text-fig. 14) is likely to have regulated the Lower Palaeozoic planktonic ecosystems. The Upper Silurian widespread organic-rich sediments (e.g. Armorican Massif) strongly suggest a relatively high productivity from the phyto/zooplankton (mainly algae,



TEXT-FIG. 14. Interpretation for the depositional environments (A–B), autecology and taphonomy (C–F) of myodocope ostracodes by Upper Silurian times. A, basinal conditions (e.g. North Gondwana, Armorican Massif). B, outer-shelf/slope conditions (e.g. Avalonia-Baltica, distal part of Welsh Basin). C, reconstructed life style and ecological range of myodocopes and their faunal associates within the water column (example from the Ludlow/Pridoli of the Armorican Massif; conditions indicated in A) 1, graptolites; 2,3, typical myodocope ostracodes (see Text-fig. 2); 4, orthoconic nautiloid; 5, phyllocarid (in life attitude and disarticulated carapace lying on the substratum); 6, partly disarticulated scyphocrinitid crinoid. D, upward (active swimming, left) and downward (passive or controlled sinking, right) movement through the water column, related to possible diel (related to the day-night light cycle; *sensu* Angel 1983*a*) and/or seasonal migrations. E, post-mortem sinking of individuals (1); complete exuviae (2) or disarticulated valves (3). F, burial conditions (possible flocculent layer under anaerobic conditions and sediment); 1, open carapace with remaining dorsal attachment; 2, 3, scattered isolated valves; 4, carapace in 'butterfly' position (see explanation in text).

EXPLANATION OF PLATE 2

Upper Silurian myodocope ostracodes and their associated fauna (see Text-fig. 14C).

Fig. 1. '*Bolbozoe*' cf. *anomala* Barrande, 1872. FSL 575003; right valve, lateral view, stereo-pair, × 20.

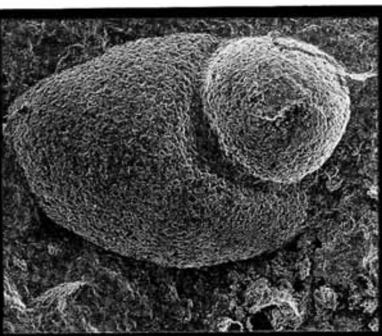
Fig. 2. 'Cypridinid'-like myodocopid (systematic position discussed in text). FSL 575004; right valve, lateral view, stereo-pair, × 21.

Figs 3, 5–6. Fragments of undetermined phyllocarid crustaceans. 3, FSL 575005; carapace seen from right with numerous incrustated coiled tubes of calcareous polychaetes '*Spirorbis*' (see Racheboeuf 1992, in press); lateral view, × 1.4. 5, FSL 575006; furca seen from left, lateral view, × 2.6. 6, FSL 575007; telson and furca seen from left, lateral view, × 2.4.

Figs 4, 7. Scyphocrinitid (*Scyphocrinites*?) crinoids. 4, FSL 575009; fragment of calyx, × 1.2. 7, FSL 575008; branching arms, × 2.4.

All from Chemiré-en-Charnie, Sarthe, Armorican Massif, France; Upper Silurian (Ludlow/Pridoli); all silicone rubber casts from external undeformed moulds (siliceous nodules from the Guillier's collections, Museum d'Histoire Naturelle, Nantes, Loire-Atlantique, France). Figures 1–2 are scanning electron micrographs. FSL, Faculty of Science, Université Claude-Bernard, Lyon I, France.

PLATE 2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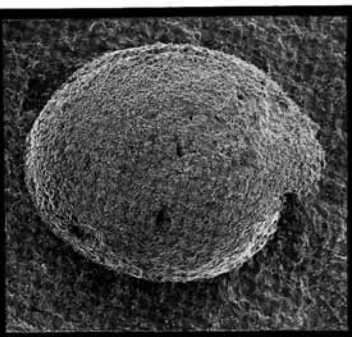
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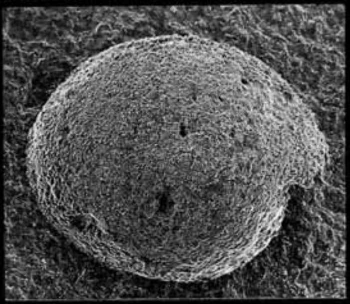
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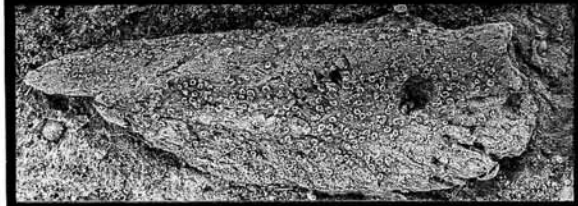
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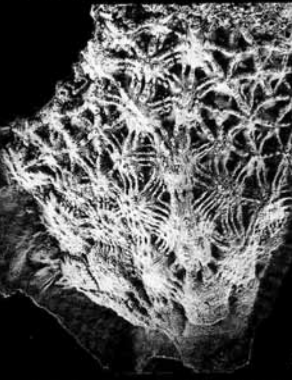
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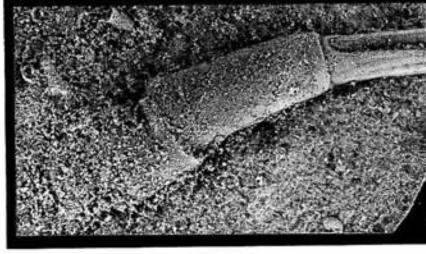
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7

VANNIER and ABE, Upper Silurian fauna

chitinozoans, acritarchs, graptolites, etc.) proliferating in the overlying water strata. Silurian planktonic myodocope ostracodes may have preferentially fed on some of the detrital material continuously sinking out of the photic zone (Text-fig. 14). Thus, and similarly to the modern mid-water myodocope fauna, they may have played an important role in recycling the detrital organic matter of ancient oceans.

An interpretation for the distribution and lifestyle of Lower Palaeozoic myodocopes

According to the zonation of water masses proposed in Text-figure 14, myodocopes may have preferentially occurred in strata underlying and probably slightly overlapping the photic zone. In modern marine environments, the photic zone extends deeper in the clear waters of the oceanic province, down to 100–200 m. It is probable that Silurian myodocopes had ranged from such depth zones down to 400–500 m (?) or deeper. This vertical distributional pattern might have been mainly controlled by the abundance in sinking detrital organic material, marine snows, faecal pellets which ostracodes are supposed to exploit (Text-fig. 14C). The depth range is expected to have varied from one species to another and possibly according to latitude for some particular taxa (see data from Recent, Text-fig. 11).

1. Myodocopes were probably detritivore active swimmers capable of feeding-related diel and/or seasonal migrations (Text-fig. 14D) consisting of alternating active upward movements and passive downward sinking with possible buoyancy control (flimsy, poorly calcified carapace). This interpretation is supported by morphofunctional analysis of fossil carapaces (this paper, Siveter 1984, Siveter *et al.* 1987, 1991) and by the general behaviour of living planktonic ostracodes (estimated vertical climb and sinking rates are 30–50 and 15–100 m per h, respectively: data from Angel 1983*a*).

2. They probably lived in dark environments where effective light penetration was negligible. Even in these dim conditions, vision remains a major sense for many marine animals (Land 1990). Therefore our interpretation of high-sensitivity optical/visual systems in some Silurian myodocopes (this paper) remains plausible. A tempting interpretation is that such eyes could have mainly been used to assist the detection of luminescent organisms (including the ostracodes themselves; e.g. searching for mates) or fluorescent particles within the water column. Luminescence in neritic and oceanic myodocope ostracodes is a well-documented phenomenon (Angel 1984; Cohen and Morin 1986, 1989, 1990*b*: Morin and Cohen 1988). Less known but probably widespread is the luminescence of faecal pellets (e.g. from mid-water fish) due to the presence of bacteria (Robinson and Bailey 1981; Angel 1984).

3. Macrofaunal associates represented in Text-figure 14C are mainly planktonic or nektobenthic organisms. *Scyphocrinites* (Pl. 2, figs 4, 7) was a crinoid with bulbous holdfasts interpreted as floating organs (Haude 1972; Ubaghs 1978*a*, 1978*b*). Phyllocarids (Pl. 2, figs 3, 5–6) were nektonic crustaceans; their modern representatives are distributed from 0–3500 m deep, but are apparently more commonly found at intermediate depth range (e.g. 200–400 m: Abele 1982). Coiled tubes of calcareous polychaetes ('*Spirorbis*': see Bordeaux and Brett 1990) have been found attached to disarticulated carapaces of Silurian phyllocarids (Pl. 2, fig. 3; Racheboeuf, in press).

4. Myodocope exuviae and dead carapaces (Text-fig. 14E) are expected to have sunk down from mid-water to the sea bottom and then to have been buried in a possible anaerobic flocculent layer overlying sediments (Text-fig. 14C) or in the muddy sediment itself, thus providing optimal conditions for preservation. Low turbidity both in the water column and on the substratum would have increased the probability for non-disarticulated dead carapaces and exuviae to reach the substratum and to be preserved within the sediment. Silurian myodocopes are commonly found (e.g. Armorican Massif, Welsh Basin) in a so-called 'butterfly' position (Siveter *et al.* 1987) indicating a remaining post-mortem/post-moulting dorsal valve attachment (chitinous ligament; see Kornicker 1969 for structure in living myodocopes). The sinking rate of exuviae and dead carapaces is likely to have approximated that of organic pellets (50–100 m per day), crustacean moults (300–800 m per day) or sinking living myodocopes (360–2400 m per day) (see Angel 1984). In this case and according to the depth range proposed for the main Silurian myodocope-rich

depositional areas, the sinking process was probably too short to allow any substantial pre-burial microbial degradation within the water column. The remarkable numerical abundance of myodocopes (Text-fig. 1) in certain depositional areas (e.g. Armorican Massif, Text-fig. 14A) may partly result from sinking through a relatively short distance.

Upper Silurian myodocopes as indicators of the post-glacial restoration of oceanic structure?

If we agree with the interpretation proposed in Text-figure 14, there is still the unanswered and intriguing question as to why ostracodes had adopted non-benthic lifestyles by Upper Silurian times. According to Fortey (1989), the glaciation/deglaciation-related extinctions at the Ordovician-Silurian boundaries more severely affected the outer-shelf and planktonic organisms (e.g. graptolites), or those having planktonic larvae (e.g. some asaphine trilobites) than the inhabitants of shallower in-shore sites (brachiopods, trilobites, etc.). Although affected by numerous generic extinctions (Vannier *et al.* 1989; Vannier, work in progress) many higher taxonomic groups of benthic ostracodes (Palaeocopa, Binodicopa, Podocopa) living in relatively shallow environments survived the end Ordovician crisis. One of the most significant faunal changes is a dramatic impoverishment of mid-water communities, probably due to the disruption of oceanic stratified structure (long period of anoxia?). Fortey (1989) notes that the effects of the glaciation might have spread long after the late Ordovician, as indicated by the complete absence of replacements for pelagic trilobites during the Silurian. This strongly suggests that the inferred planktonic myodocopes (Text-fig. 14) may have simply filled the vacant niche after the oceanic structure had been restored during the Silurian (R. Fortey, pers. comm.). The probable vision-related bulbs of Upper Silurian bolbozoid myodocopes (Text-figs 2, 4) are interestingly similar to the very peculiar, huge, compound lateral eyes of epipelagic and mesopelagic trilobites (e.g. cyclopygids: see Fortey and Owens 1987, p. 106; Fortey 1989, p. 345) which became extinct at the Ordovician-Silurian boundary. These apparent homologous features would indicate that 'preglacial' Ordovician pelagic trilobites and 'post-glacial' Silurian myodocope ostracodes provided the same adaptive response to the dim conditions that prevailed in their respective upper-water niches. Since the Lower Silurian myodocopes are regarded as benthic inhabitants of shallow water environments (evidence from faunal associates and sediment; Siveter and Vannier 1990), it is probable that myodocope ostracodes have undergone a benthic to planktonic ecological shift during the Silurian (Siveter *et al.* 1991). The origin and the chronology of this significant event is fully discussed in the latter paper.

Acknowledgments. We thank Dr M. F. Land (University of Sussex, Brighton) for valuable information concerning the visual systems of crustaceans, Professor I. Hayami, Drs K. Tanabe and T. Oji (University of Tokyo) and Professor K. Müller (Bonn), Drs R. A. Fortey (Natural History Museum, London), D. Horne (Thames Polytechnic, London), P. R. Racheboeuf (Lyon), H. Groos-Uffenorde (Göttingen) and J. L. Henry (Rennes) for critical reading of the manuscript. J. V. is very grateful to Professor I. Hayami for allowing him to study at the Geological Institute of the University of Tokyo, to the Japan Society for the Promotion of Science (JSPS, Tokyo), the Japanese Ministry of Education (Monbusho) and the CNRS; INSU 91, DBT 2-25-337 for financial support, and to Drs K. Tanabe and T. Oji (Tokyo) for their advice and help.

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JEAN VANNIER

Université Claude Bernard-Lyon I
Centre des Sciences de la Terre
URA 11 du CNRS
17–43, bd du 11 Novembre 1918
69622 Villeurbanne-cedex, France

KATSUMI ABE

University of Tokyo
Geological Institute
Section of Palaeobiology
7-3-1 Hongo, Tokyo 113, Japan

Typescript received 22 October 1990
Revised typescript received 29 May 1991