SIZE, BODY PLAN AND RESPIRATION IN THE OSTRACODA

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ABSTRACT. Ostracodes are small (0·3–32 mm) bivalved crustaceans with an exceptional fossil record covering the last 540 million years of aquatic life; the group is still represented by nearly 8000 species (Podocopa and Myodocopa). Only two major body plans prevail in the modern fauna if we except the enigmatic punciids. 'Body plan 1' corresponds to ostracodes (Myodocopida, Halocyprida) with a bilateral symmetry, a frontal polarity, a high activity level, an ellipsoidal shape, well designed for moving through water or soft muddy sediment, and (primarily) a circulatory system. 'Body plan 2' corresponds to ostracodes with a ventral or lateral polarity (left/right valve asymmetry). Such organisms (Podocopa) are mostly crawlers (on thoracic legs) on a substratum or within flocculent material, and occasionally remain motionless, simply resting on one valve. The carapace is heavily calcified, bearing strengthening features, and no circulatory features (e.g. a dorsal heart) are present. The living ostracode fauna as a whole has a high diversity at low taxonomic level and conversely a low disparity of body plans. The respiratory and circulatory processes with relation to animal size have been investigated using a scanning electron microscope, microtomized sections, and high-resolution video observations of live specimens. Small ostracodes (0·3 to less than 3 mm) rely exclusively on integumental gaseous diffusion. Larger ones (up to 32 mm) have a dorsal heart, with haemolymph circulation supplementing diffusion. Fewer (e.g. cylindroleberidids) develop additional paired gill-like features, also present in the Triassic. Integumental circulation, evidence for which is preserved as anastomozing features in fossils, is shown to have occurred early in the evolution of Ostracoda, among Ordovician to Devonian leperditicopes, through the myodocope lineage (Silurian to Recent) and also possibly in bivalved arthropods such as the Bradoriida. The post-Cambrian evolution of Ostracoda is believed to have been influenced strongly by either the loss or the conservation of the circulatory system, leading (respectively) to minute organisms confined within a narrow size range (e.g. all living podocope ostracodes) and to larger crustaceans (e.g. living myodocope ostracodes) capable of higher metabolism and free swimming life styles.

THE nearly 8000 described species of living Ostracoda are confined within a surprisingly narrow size range compared with other crustacean groups of comparable diversity (e.g. Copepoda, Isopoda, Cirripedia and Decapoda; Table 1). Thus, the largest known mesopelagic ostracode (*Gigantocypris*; Cannon 1940) is only 60 times bigger in adult size than the smallest deep sea pelagic (e.g. *Archiconchoecia*) and interstitial (see Hartmann 1973) representatives of the group. Comparatively, malacostracan decapods exhibit a much higher size ratio; the Japanese spider-crab (*Macrocheira kaempferi*; Sakai 1970), with thoracic legs spanning over three meters, is about 1000 times larger than the smallest decapods, such as *Pinnotheres laquei*, a commensal pinnotherid crab living within the mantle cavity of brachiopods (Feldman *et al.* in press). If variations of the same amplitude occurred in ostracodes, then a maximum size of at least a metre would be expected.

Exceptionally abundant data from the fossil record show that a comparable size pattern also applies to the 40000–50000 ostracode species (Schram 1986; Maddocks 1992) known from the Lower Cambrian to the present and whose adult size rarely exceeds 1–2 mm (see Benson *et al.* 1961; Scott 1961; issues of the *Stereo-Atlas of Ostracod Shells* from 1973–1994). Noticeable exceptions do exist, however, and relatively larger forms, which may attain several tens of millimetres in carapace length, are common among the Ordovician to Devonian leperditicopes (Berdan 1984; Text-fig. 13), throughout the myodocope lineage from the Silurian (Vannier and Abe 1992) to the Recent, and may be found in very early ancestors of ostracodes such as Lower Cambrian cambriids (see Text-fig. 17; Siveter *et al.* 1994, in press; Williams *et al.* 1994). In this paper, we analyse the

TABLE 1. Size range (in mm), size ratio and approximate number of species in the main groups (subclasses) of living crustaceans. Classification after Bowman and Abele (1982) and Barnes and Harrison (1992a). a = minimum adult length; b = maximum adult length. In the classification proposed by Barnes and Harrison (1992a), the Subclass Sarcostraca comprises the Order Anostraca, the Subclass Calmanostraca the Order Notostraca and the Subclass Diplostraca the Orders Conchostraca and Cladocera (see Fryer 1987; Martin 1992). (*): tantulocarids are minute ectoparasites known from two genera (see Boxshall and Lincoln 1983). Eumalacostracan data is given for three major orders only: Amphipoda (1), Isopoda (2) and Decapoda (3).

Class	Subclass	a	b	$b:a$	Number of species	References
Cephalocarida		2	3·7	~2	9+	Hessler and Elofsson (1992); Hessler (pers. comm. 1994)
Branchiopoda	Sarcostraca	15	100	6·7	190	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
	Calmanostraca	30	100	3·3	10	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
	Diplostraca	0·3	18	60	600	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
Remipedia		15	40	2·7	~12	Felgenhauer et al. (1992)
Maxillopoda	Branchiura	3	30	10	200	Overstreet et al. (1992)
	Mystacocarida	0·5	1	2	9	Schram (1986)
	Copepoda	1	250	250	8400	Boxshall (1992)
	Cirripedia	~1	300	300	1240	Walker (1992); Høeg (1992); both pers. comm. (1994)
Ostracoda	Myodocopa	~0·5	32	64	650	Maddocks (1992); Morin and Cohen (1991)
	Podocopa	~0·3	~2·5	9	7000	Maddocks (1992); Benson et al. (1961)
Tantulocarida		?	<0·3	?	(*)	Boxshall and Lincoln (1983)
Malacostraca	Phyllocarida	4	12	3	15+	Schram (pers. comm. 1994)
	Hoplocarida	10	600	60	500	Schram (pers. comm. 1994)
	Eumalacostraca (1) = Amphipoda	5	280	56	6000	Schmitz (1992 and pers. comm. 1994)
	Eumalacostraca (2) = Isopoda	0·6	400	660	9000	Wägele (1992 and pers. comm. 1994)
	Eumalacostraca (3) = Decapoda	~4?	4000	1000	10000	Barnes and Harrison (1992b)

relation of size to the body plan, the carapace design and to the respiratory processes of Ostracoda, throughout the last 500 million years of evolution of the group.

MATERIALS AND METHODS

Living material. A nektobenthic myodocopid species, *Vargula hilgendorfii* (Müller, 1890), was used extensively for documenting the internal (functioning organs, circulatory system) and external (carapace design) features of myodocopid ostracodes (Text-figs 1c–d, 2). Live material was collected at night in December 1993 and March 1994 from shallow water environments (water depth < 5 m) at Tateyama (Boso Peninsula, 35° 00′ N, 139° 51′ E) along the Pacific Coast of central Japan, and kept in aquaria at the University of Tokyo and Shizuoka University. Repeated observations of live (video recordings, optical binocular microscope) and fixed (SEM) specimens were made through the year. Morphofunctional and behavioural aspects of *Vargula hilgendorfii* were described in Vannier and Abe (1992, 1993). Respiratory features (haemolymph sinuses, circulation, heart) of *Vargula hilgendorfii* and Caribbean congenerics have been recently investigated by Abe (1994) and Abe and Vannier (in press). Other species were used for comparative studies:

1. *Conchoecia atlantica* Lubbock, 1856 (Halocyprida; Text-figs 1a–b, 3), *Archiconchoecia striata* Müller, 1894 and *Bathyconchoecia* sp. (both Halocyprida), collected by K. Tachibana from the mesopelagic waters of Sagami Bay (Pacific Ocean; 35° 00′ N, 139° 20′ E).

2. Undetermined *Conchoecia* species collected (JV) in May 1994 during the sampling cruise of the research vessel Tanseimaru (operation KT 94-07, Ocean Research Institute, University of Tokyo), S of Atsumi Peninsula (loc. EN-03, 34° 13′ 86″ N, 137° 21′ 71″ E at about 300 m depth) and at Shima Spur (loc. KN-26, 33° 59′ 43″ N, 136° 52′ 76″ E at about 500 m depth) using a 1·5 m diameter conical plankton net (mesh size 0·69 mm).

3. *Leuroleberis surugaensis* Hiruta, 1982. (Myodocopida; Text-fig. 7; Vannier *et al.* in press) recovered from benthic collections off Shimoda, Izu Peninsula, Pacific Coast, Japan (34° 37′ 00″ to 34° 38′ 64″ N, 138° 57′ 30″ to 138° 56′ 55″ E at depths of 35 to nearly 100 m).

4. *Bicornucythere bisanensis* (Okubo, 1975) (Podocopida; Text-figs 1e–f, 4) from the flocculent muddy bottom sediments (depth approx. 4 m) of Aburatsubo Cove (Pacific Coast of the central part of Japan; 35° 09′ 40″ N, 139° 37′ E, see Abe and Vannier 1991; Abe 1983).

Technical aspects of fixation, observation and microtome sectioning and staining are in Abe and Vannier (in press).

Fossil specimens. Ordovician and Silurian leperditicope (see Swartz 1949; Berdan 1984) ostracodes were reviewed, especially those bearing well-preserved anastomozing or radiating features. Among them were:

1. *Bivia tumidula* (Ulrich, 1891), *B. linneyi* (Ulrich, 1891), *B. frankfortensis* (Ulrich, 1891), *Teichochilina jonesi* (Wetherby, 1881; Text-figs 13a, 15e), all from the Middle to Upper Ordovician Lexington Limestone, Kentucky.

2. *Ceratoleperditia kentuckyensis* (Ulrich, 1891) from the Tyrone Limestone, Middle Ordovician, Kentucky; *Kenodontochilina pustulosa* Berdan, 1984 and *Saffordellina striatella* Berdan, 1984, both from the Ashlock and Bull Fork Formations, Upper Ordovician, Kentucky; *Eoleperditia fabulites* (Conrad, 1843; Text-fig. 14b) from the Platteville Formation, Wisconsin, the Tyrone Limestone and Glade Limestones, Kentucky, and the Lebanon Limestone, Tennessee, all of which are Ordovician in age.

3. *Saffordellina muralis* (Ulrich and Bassler, 1923; Text-figs 13b, 15c) from the Upper Trenton (Middle Ordovician; see Berdan 1984, p. 33) of Nashville, Tennessee.

4. *Isochilina venosculptis* Swartz, 1949 (Text-fig. 15a) from the Pamelia Limestone (Middle Ordovician) of Aylmer, Quebec, Canada.

5. *Dihigmochilina straitcreekensis* Swartz, 1949 from the late Silurian Tonoloway Limestone, Virginia.
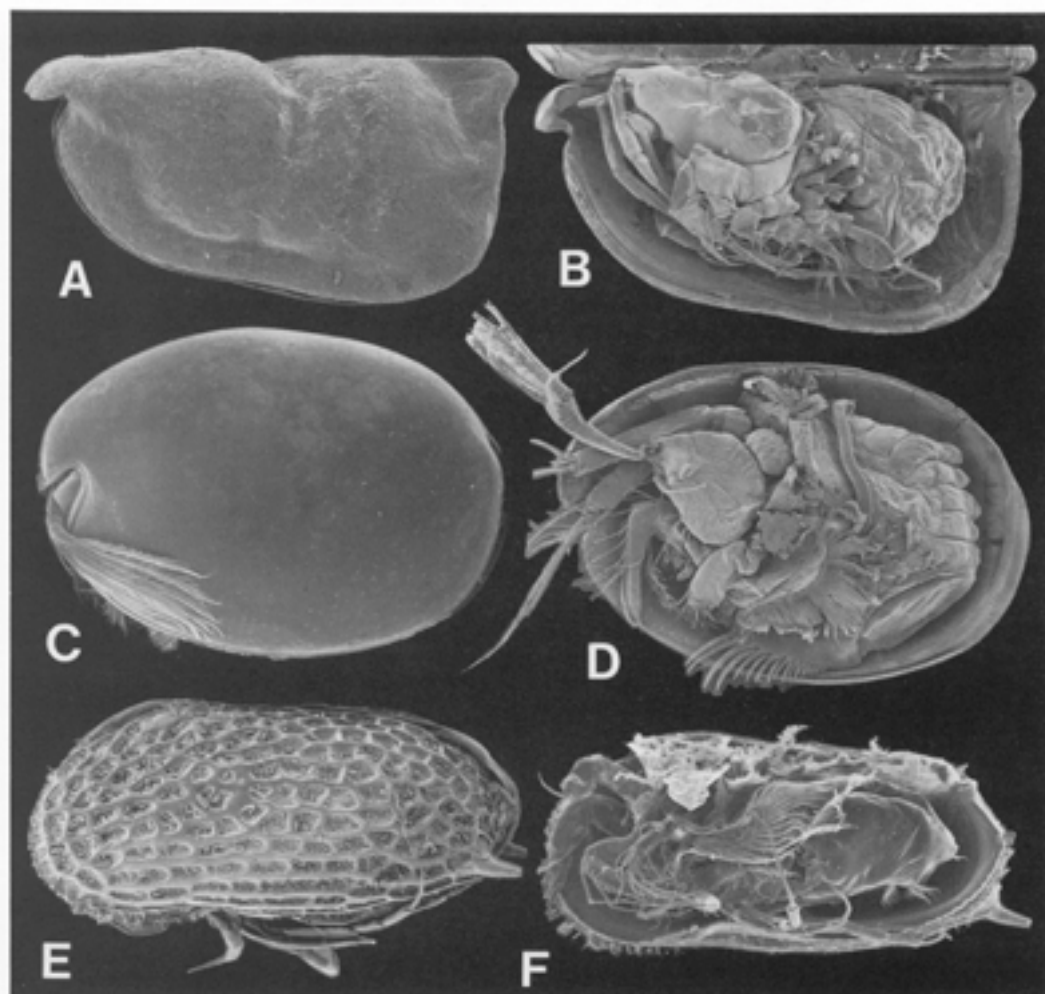
TEXT-FIG 1. Internal and external ostracode morphology as exemplified by typical representatives of the orders Halocyprida (A–B), Myodocopida (C–D) and Podocopida (E–F) from the NW Pacific region, Japan. All are scanning electron micrographs of external lateral, and internal (left valve removed) views. A–B, *Conchoecia atlantica* (Lubbock, 1856); FSL 575087; a mesopelagic species from Sagami Bay; adult specimen; ×19. C–D, *Vargula hilgendorfii* (G. W. Müller, 1890); a nektobenthic species from shallow water environments; C, FSL 575090; Aburatsubo Cove, Misaki; male specimen; ×23. D, FSL 575088; Tateyama; male specimen; ×23. E–F, *Bicornucythere bisanensis* (Okubo, 1975); FSL 575089; benthic species from shallow water environments (flocculent layer); Aburatsubo Cove, Misaki; male specimen; ×78.

None of this material, mostly kept in the collections of the Smithsonian Institution, Washington DC and too fragile (R. Benson, pers. comm.) for transport through the mail, could be obtained for new SEM studies. Our observations are based on the original descriptions and the light photographic illustrations of Swartz (1949) and Berdan (1984).

Type specimens of Devonian leperditicopes from Russia (see Abushik 1990) were borrowed through a loan arranged by Derek J. Siveter, A. Abushik and L. Melnikova (Derek J. Siveter, pers. comm. to JV). Among them, *Leperditia marinae* Abushik, 1980 (Text-fig. 13C–E) from the Lower

Devonian (lower Lochkovian) of Novaya Zemlya (A. Abushik, pers. comm. to JV) and *Moelleritia moelleri* (Schmidt 1883; Text-fig. 13F–H), from the Upper Emsian of Central Ural (A. Abushik, pers. comm. to JV) have been chosen to illustrate the overall morphology (e.g. carapace shape, overlap features) and the size range of leperditicopes.

The Upper Silurian myodocope ostracodes figured here (Text-fig. 16) were collected (JV) in September 1992 from several exposures along the D104 road at Les Buhardières between Andouillé and Saint-Germain-le-Fouilloux, 15 km N of Laval, Mayenne, France. We also refer to the myodocope material described by Siveter *et al.* (1987, 1991), Siveter and Vannier (1990) and Vannier and Abe (1992). Latex casts were made from external moulds of all this Silurian material.

Gibba kandarensis Vannier *in* Galle *et al.* 1995, a beyrichiacean palaeocope ostracode from the Lower Devonian of Immouzer of Kandar, 40 km S of Fes, Morocco (see Galle *et al.* 1995), was examined as an example of an exceptionally large palaeocope (Text-fig. 11).

Anabarochilina primordialis (Linnarsson, 1869; see Text-fig 17B and Siveter *et al.* 1993), from the late Middle Cambrian of northern Europe, and a cambriid species (Text-fig. 17A; Siveter *et al.* in press) from the Lower Cambrian Buen Formation of North Greenland are selected examples of early ostracodes of centimetric size and bearing radiating markings.

Light photographs of large specimens coated with ammonium chloride, were taken with an Aristophot camera. A Hitachi S2400S SEM was used for electron microscopy. Figured specimens are deposited in the collections of the Université Claude Bernard-Lyon 1, Centre des Sciences de la Terre (FSL), France, the United States Smithsonian Institution, Washington DC (USNM), the Palaeontological Institute, Moscow, Russia (N) and the Sveriges Geologiska Undersökning (GSU), Uppsala, Sweden.

BODY PLANS OF LIVING OSTRACODA

Ostracodes are minute crustaceans characterized by a reduction in the number of trunk segments (Swanson 1990); the body (five to seven pairs of appendages) is laterally compressed and entirely enclosed within a bivalved carapace impregnated with calcium carbonate. As in many other crustaceans (see Brusca and Brusca 1990; Gruner 1993), the ostracode carapace is a cuticular fold which originates embryologically from a cephalic segment. It is already well developed as an expansive protective structure in the earliest free-living embryos (Weygoldt 1960, 1993) and forms a bilateral extension of the body (Maddocks 1992; Text-figs 2B, 3B, 4B) that accommodates important cellular compounds and functional systems (e.g. hepatopancreas in podocopes; haemolymph sinuses in myodocopes; Text-fig 8). It is, therefore, neither a shell (e.g. molluscan shell; Crenshaw 1990) nor a simple covering shield-like carapace such as that of notostracan branchiopods (Martin 1992). The uncalcified inner lamella is a continuation of the body integument (see Abe and Vannier in press). Rhythmic and synchronized beatings of specialized appendages (e.g. epipodial ventilatory plates) and appendage movements induce water circulation within the domiciliar cavity as seen clearly from videos of nektobenthic (*Vargula*) and planktonic (*Conchoecia*) species (unpublished data).

Recent ostracodes are commonly subdivided (Barnes and Harrison 1992a) into two subclasses: the Podocopa (about 7000 living species; Orders Podocopida and Platycopida) and the Myodocopa (about 650 living species; Orders Myodocopida and Halocyprida). Using combined electron microscopy, microtomized serial sections, and live video recordings, we analysed the three-dimensional aspects of the anatomy of typical representatives of Myodocopida, Halocyprida and Podocopida as well as the functional anatomy of these organisms. Minor groups (Platycopida, Polycopidae, Thaumatocyprididae, Punciidae) represented by only a few taxa were not investigated in the present study.

Myodocopida (Vargula: Text-figs 1C–D, 2; Leuroleberis: Text-fig. 17). Two pairs of trunk appendages are present, the second one being modified into a pair of multifunctional serpentiform appendages (= 7th limb; see Vannier and Abe 1993). The carapace is ellipsoidal, valves being provided with a rostrum and a rostral incisure allowing well-developed frontal appendages to
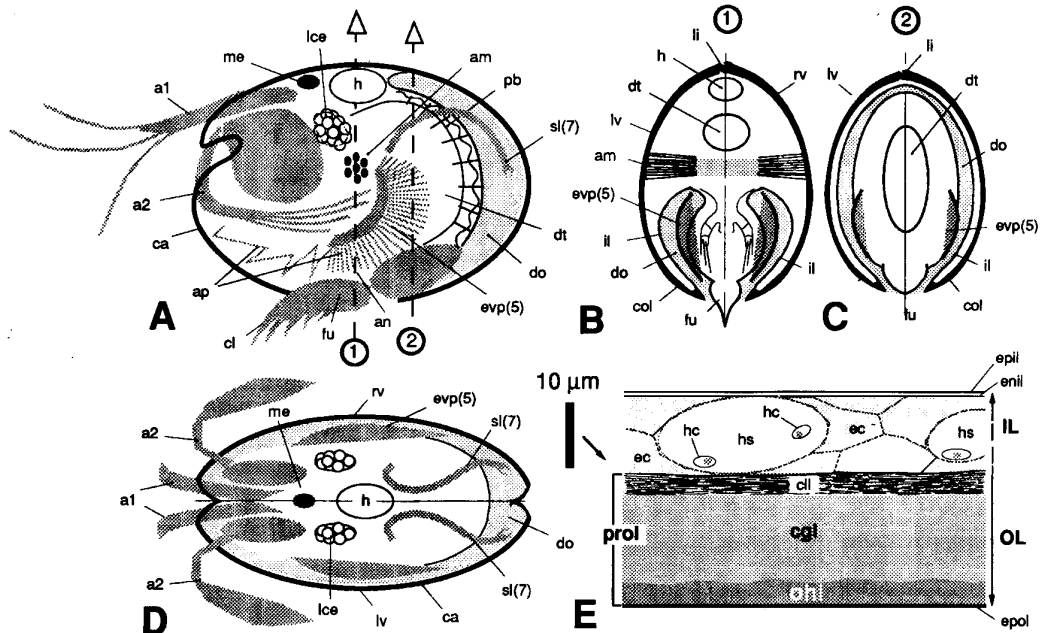
TEXT-FIG 2. Anatomy, carapace design and carapace ultrastructure of Recent myodocopid ostracodes, exemplified by *Vargula hilgendorfii* (G. W. Müller, 1890) (Myodocopida, Cypridinidae) from Japan. A, lateral view from left, left valve removed; B–C, simplified transverse sections as indicated in A (① and ②); D, simplified horizontal section; E, schematic cross section through carapace. Animal length approx. 3 mm. Outline of anatomical features simplified from SEM observations and microtomized sections. a1 = 1st antenna; a2 = 2nd antenna; am = adductor muscles; an = anus; ap = 3rd to 6th pair of appendages (not represented); ca = carapace; cel = calcified inner lamella; cgl = coarse granular calcified layer; cl = claw of furca; cll = chitinous-rich laminated layer; col = calcified outer lamella; do = domiciliar cavity; dt = digestive tract; ec = epidermal cells; enil = endocuticle of inner lamella; epil = epicuticle of inner lamella; epol = epicuticle of outer lamella; evp(5) = epipodial ventilatory plate (5th limb); fu = furcal lamella; h = heart; hc = haemolymph corpuscle (haemocyte); hs = haemolymph sinus; il and IL = inner lamella; lce = lateral compound eye; li = ligament; lv = left valve; me = medial eye; ohl = outer calcified homogeneous layer; OL = outer lamella; pb = posterior wall of body; prol = procuticle of outer lamella; rv = right valve; sl(7) = serpentiform limb (7th limb).

protrude from the carapace forward and laterally; it is an important functional feature (Vannier and Abe 1992, 1993) involved in swimming and digging activities. A pair of sclerotized furcal lamellae terminates the body posteriorly. Light receptors consist of a medial eye and may include a pair of compound lateral eyes (Huvard 1990). A circulatory system (heart, arteries, haemolymph sinuses; Abe and Vannier 1993*b*; Text-figs 8, 15) is present. Book gills, usually seven pairs, occur in one particular family, the Cylindroleberididae (e.g. *Leuroleberis*; Text-fig. 7) and are interpreted (Vannier *et al.* in press) as the possible remains of lost appendages. The same overall morphology can be recognized in most living myodocopid species and also in the lowermost Mesozoic (Weitschat 1983*a*, 1983*b*; Weitschat and Guhl 1994) and Lower Palaeozoic (Vannier and Abe 1992) ancestors of the group.

Halocyprida (Conchoecia: *Text-figs 1A–B, 3*). The most distinctive features of halocypridid ostracodes such as *Conchoecia* are 1), the lobation of the carapace expressed as a major constriction
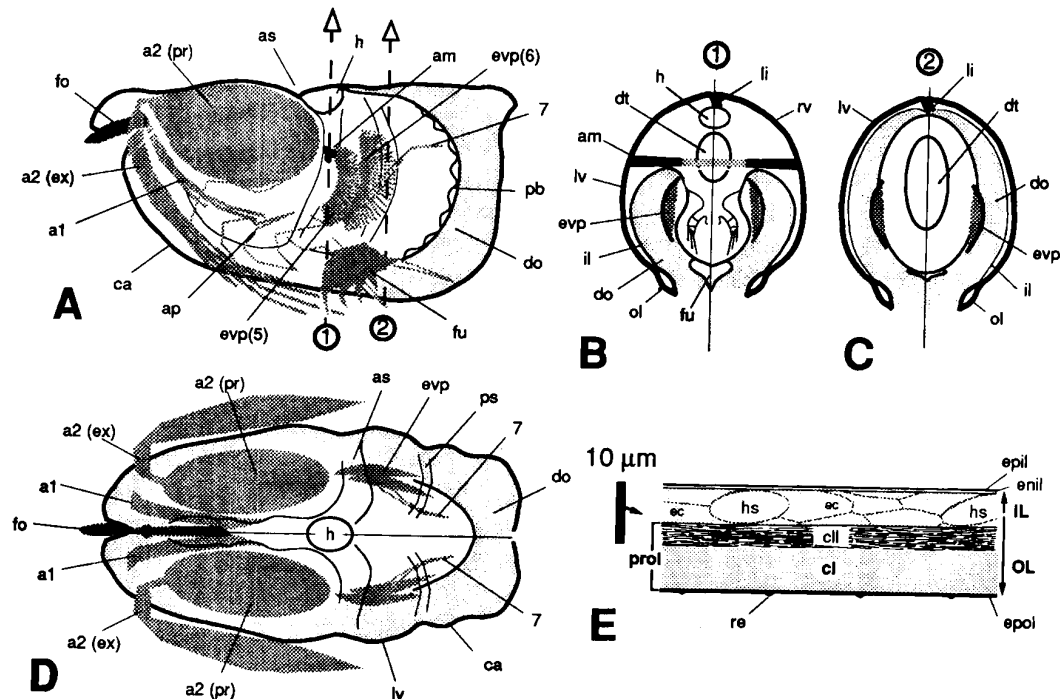
TEXT-FIG 3. Anatomy, carapace design and carapace ultrastructure of Recent halocyprid ostracodes, exemplified by *Conchoecia atlantica* (Lubbock, 1856) (Halocyprida, Halocyprididae) from Japan. A, lateral view from left, left valve removed; B–C, simplified transverse sections as indicated in A (① and ②); D, simplified horizontal section; E, schematic cross section through carapace. Animal length, approx. 3·5 mm. Outline of anatomical features simplified from SEM observations and microtomized sections. Abbreviations (additional to those used in Text-figure 2): a2 (ex) = 2nd antenna (exopodite); a2 (pr) = 2nd antenna (protopodite); ap = appendages (3rd and 4th pair; not represented); as = adductorial sulcus; cl = calcified layer; evp = epipodial ventilatory plate; evp(6) = epipodial ventilatory plate (6th limb); fo = frontal organ; ol and OL = outer lamella; ps = posterior sulcus; re = reticulation; 7 = 7th limb.

posterior to the 2nd antenna, and 2), the exceptionally long and straight dorsal attachment of the valves. These two features are unknown in other ostracodes except Palaeozoic archaeocopes, palaeocopes and some myodocopes. The muscular protopodite of the 2nd antenna (Text-fig. 1B) is developed in relation to the free-swimming lifestyle of the animals. The second pair of trunk appendages (= 7th limb) is directed backwards and oscillates along the posterior part of the body (e.g. *Conchoecia*; Text-figs 1, 3; unpublished data from video recordings). These appendages may have the same function as the 7th limbs of myodocopids although they are not serpentiform. Integumental anastomozing channels and a dorsal heart are present, although the integument is much thinner than that of myodocopids (compare Text-figs 2E and 3E). Eyes are missing; the frontal organ protruding from the carapace below the rostrum is assumed to be the main (chemo?) sensory receptor.

Podocopida (Bicornucythere *Text-figs 1E–F, 4*). The lack of anterior rostral features and frontal openings is a distinctive characteristic of podocopid ostracodes. Appendages mainly protrude ventrally through the narrow gape of the valves to accommodate the benthic lifestyle of these animals. The maxillules are derived from head segments and the two pairs of trunk appendages are
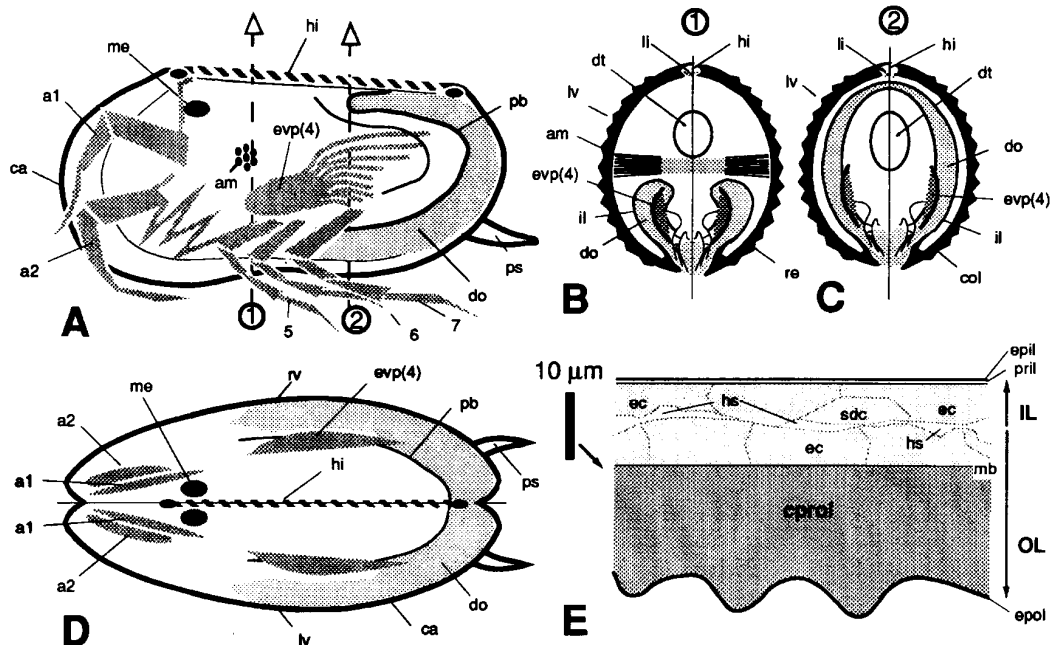
TEXT-FIG 4. Anatomy, carapace design and carapace structure of Recent podocope ostracodes, exemplified by *Bicornucythere bisanensis* (Okubo, 1975) (Podocopida, Cytheracea) from Japan. A, lateral view from left, left valve removed; B–C, simplified transverse sections as indicated in A (① and ②); D, simplified horizontal section; E, schematic cross section through carapace. Animal length, approx. 0·9 mm. Outline of anatomical features simplified from SEM observations and microtomized sections. Abbreviations (additional to those used in Text-figure 2): cprol = calcified procuticle of outer lamella; evp(4) = epipodial ventilatory plate (4th limb); hi = hinge; hs = haemocoelic space; mb = membrane; pril = procuticle of inner lamella; ps = posterior spine; re = reticulated ornament; sdc = subdermal cell; 5–7 = 5th to 7th pair of appendages.

transformed into legs for locomotion and sometimes for precopulatory activities (see Abe and Vannier 1991, 1993a). The visual organs derived from the medial eye complex are the only photoreceptors. The epidermal layers of the cuticle lack any differentiated vascular system (see Okada 1981, 1982, 1983; Keyser 1982, 1990) or heart. Furcae are generally poorly developed in comparison with those of myodocopes. The carapace integument is comparatively more heavily calcified in podocopes than it is in myodocopes (see Dalingwater and Mutvei 1990).

Other groups. The overall body plan of platycopine ostracodes (Howe *et al.* 1961; Whatley 1991), represented by only two cytherellid genera in the Recent, remains comparable with that of most podocopids. The only distinctive characteristics include a brood chamber defined anteriorly by a vertical ridge, strong clustered adductor muscle scars, a lamelliform furca and the reduction of the two last thoracic appendages. The peculiar appendage morphology of the platycopines may be closely related to the filter feeding (Cannon 1933) and the burrowing mode of life of these animals. A similar adaptation to filter feeding also occurs within the Myodocopa as, for instance, in the cylindroleberidids (Kornicker 1981; Vannier *et al.* in press; JV, unpublished data from scanning electron microscopy and video recordings).

The thaumatocypridid (three genera; Kornicker and Sohn 1976), and the polycopid ostracodes (four genera; Kornicker and Morkhoven 1976) are typically small (1–2·5 mm) myodocopes enclosed within an ellipsoidal, often nearly circular carapace. In spite of a distinctive carapace

design (e.g. no rostrum), these animals have basically the same internal anatomy as that of most myodocopes (Cohen 1982) except that they lack a heart and visual organs. The absence of the 6th and 7th pairs of appendages in polycopids is probably related strongly to the miniaturization of these animals in interstitial habitats (see Hartmann 1973).

The living punciids, represented by *Manawa*, are unique in terms of soft anatomy, carapace design and ontogeny (Swanson 1989a, 1989b, 1990). The carapace of adults has a flattened horizontal life position with appendages extending laterally. The hinge line is long and straight, similar to that of extinct Palaeocopa. Another peculiar feature is the univalved-bivalved transition during the ontogeny, unknown in ostracodes other than in the early Cambrian ancestors of the group (Zhang and Pratt 1993). The affinities of punciids within the Ostracoda (Podocopida or Platycopida?) are still unclear (Swanson 1989b). New collections and video observations of live specimens by one of us (KA, Dec. 1994) are expected to shed new light upon these enigmatic organisms.

The body plans of Recent Ostracoda. The term 'body plan' or 'Bauplan' encompasses here the notion of symmetry, architecture and structural range, as well as the functional aspect of the design. Although the internal and external anatomy of the living representatives of Ostracoda may vary greatly in detail, making generalizations difficult, it seems that only two body plans prevail within the modern fauna.

'Body plan 1' corresponds to bivalved crustaceans with a bilateral symmetry and a strong frontal polarity. The anterior part of such animals (e.g. rostrum, antennae) confronts the environment first either when swimming or digging. Nektobenthic or planktonic organisms have a high activity-level and an ellipsoidal shape well suited for moving through water or soft muddy sediment. Internal and integumental circulation occurs primarily, allowing a larger body size (see below). Most myodocopes (Myodocopida, Halocyprida) fall into this category.

'Body plan 2' corresponds to bivalved crustaceans with a ventral polarity (left/right valve symmetry) or a lateral polarity (left/right valve asymmetry). Such organisms (e.g. Podocopa) are mostly crawlers (on the thoracic legs) on a substratum or within flocculent material, and occasionally remain motionless, simply resting on one valve. The carapace is heavily calcified usually bearing strengthening features. A circulatory system is absent. The physical constraints of gaseous diffusion confine these animals to a small size (see below).

The living ostracode fauna as a whole has a high diversity at low taxonomic level (Table 1) and conversely a low disparity (Gould 1991; Willis *et al.* 1994) in terms of high-level body plans. Judging from the great variety of carapace designs known from the fossil record, one might easily speculate that the diversity of body plans was much higher in the early history of the group, especially in the Ordovician (see Vannier *et al.* 1989). The Cambrian fauna produced unique carapace designs, unknown in present day faunas, e.g. the extinct archaeocopids with interdorsal features (Hinz 1993). However, the lack of information on the soft anatomy of Palaeozoic ostracodes makes it difficult to evaluate the actual magnitude of differences between higher taxa. Whether the disparity among ostracodes was greater in the early Palaeozoic than in the present day has not been clearly determined yet.

RESPIRATORY FEATURES

Molecular diffusion. Most ostracodes (e.g. all podocopes) lack any specialized respiratory organs such as gills, or a heart and circulatory system. Similarly with other minute invertebrates, gas exchange is assumed (McMahon and Wilkens 1983) to take place through the integument of the carapace inner lamella and across the general surface of the body integument (Text-fig. 5A–B, D–E). Ultrastructural studies (Keyser 1990) showed that the uncalcified inner lamella of podocopid ostracodes is not only a respiratory site of exchange but also a preferential area for osmoregulation. The epipodal respiratory plates (Text-figs 1–4) which are well developed in ostracodes, are in no way true respiratory organs comparable with the thin-walled and well vascularized gills of, for instance, malacostracans (Taylor and Taylor 1992); their actual and major function is to ventilate

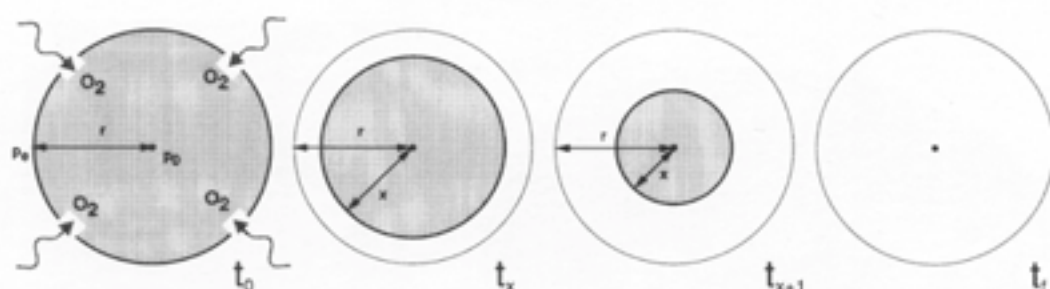ventilation   integumental diffusion   gaseous transport to metabolizing tissues
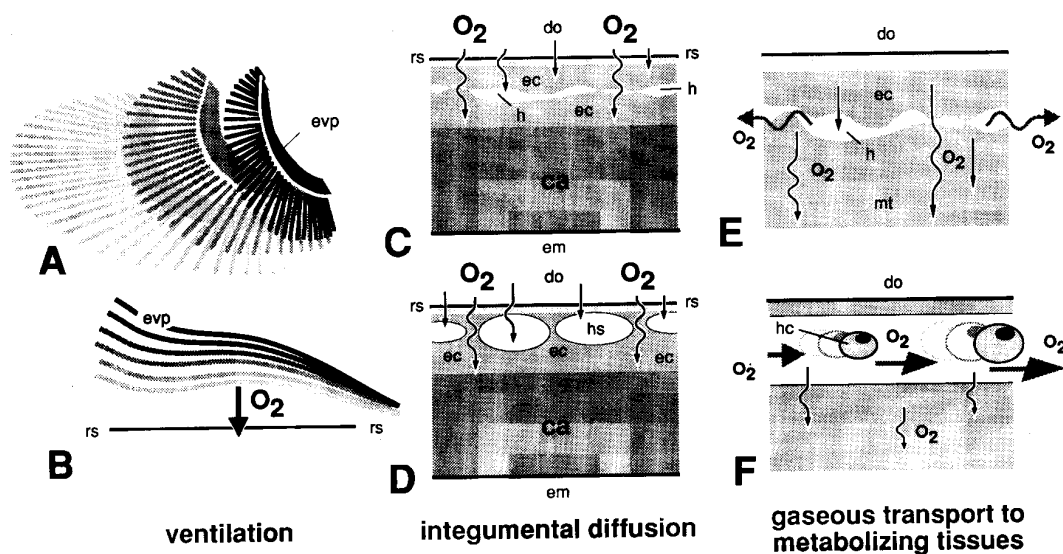
TEXT-FIG 5. Successive steps in the respiratory processes of Ostracoda. A–B rhythmic ventilation (epipodial ventilatory plate) over the surface of integument. C–D, integumental diffusion through the inner lamella (see Text-figs 2–4B–C, E); C, podocopes; D, myodocopes with a circulatory system. E–F, gaseous transport to metabolizing tissues; E, mainly by diffusion in podocopes; F, by fluid convection in myodocopes. ca = calcified part of outer lamella; do = domicilium; ec = epidermal cells; em = external medium; evp = epipodial ventilatory plate; h = haemocoelic space; hc = haemolymph corpuscle (haemocyte); hs = haemolymph sinus; mt = metabolizing tissues; O_2 = oxygen; rs = respiratory surface; vs = ventilatory surface.

the domiciliar cavity (Abe and Vannier in press), thus creating and maintaining partial pressure gradients between the medium and the respiratory surface. The integument of the inner lamella of the podocopid *Bicornucythere bisanensis* (Text-fig. 4) and the myodocopid *Vargula hilgendorfii* (Text-fig. 2) is uncalcified and consists of an epicuticle (Okada 1982) and a procuticle overlying epidermal cell layers. In *Vargula hilgendorfii*, the integument is as thin as 3–5 μm on the muscular protopodite of the swimming appendages or on the posterior surface of the body and ten times thicker and heavily sclerotized on the furcal lamellae. Gaseous diffusion is obviously facilitated in areas with a thinner integument, in relation to metabolic and functional requirements.

Fluids are present within the carapace of ostracodes even in those lacking a circulatory system (Hartmann 1966). Transmission electron microscope sections of *Cyprideis torosa* (Podocopida; Keyser 1990, fig. 12) and *Hirschmannia viridis* (Podocopida; Keyser 1982, fig. 4) show irregular haemocoelic spaces between the inner and outer layers of epidermal cells (see Text-fig. 4E); similar features are widespread among small crustaceans, for instance in branchiopods (*Daphnia magna*; see Martin 1992, fig. 7). Although their function has not been examined, it is clear that such haemocoelic fluids may increase the effectiveness of diffusion in transferring respiratory gases over short distances.

Specialized respiratory surfaces. External integumental folds attached to the dorsal part of the body and usually interpreted (e.g. Kornicker 1981, 1991a, 1991b, 1992, 1994) as gill-like features involved in respiration processes (see Hartmann 1967) are found in cylindroleberidid myodocopid ostracodes. However, no illustrations, using modern techniques, have been published so far. We observed these features in *Leuroleberis surugaensis* from Japan (Text-fig. 7). They consist of a right and a left series

TEXT-FIG 6. Gaseous diffusion of oxygen through the living tissues of a spherical animal (see explanation in text) from the integumental respiratory surface (initial time t_0) to the centre of the animal body (final time t_f). p_r = partial pressure of oxygen in the external medium; p_0 = partial pressure of oxygen in centre of animal body; r = body radius; t_0, t_x, t_{x+1} and t_f = time for each step.
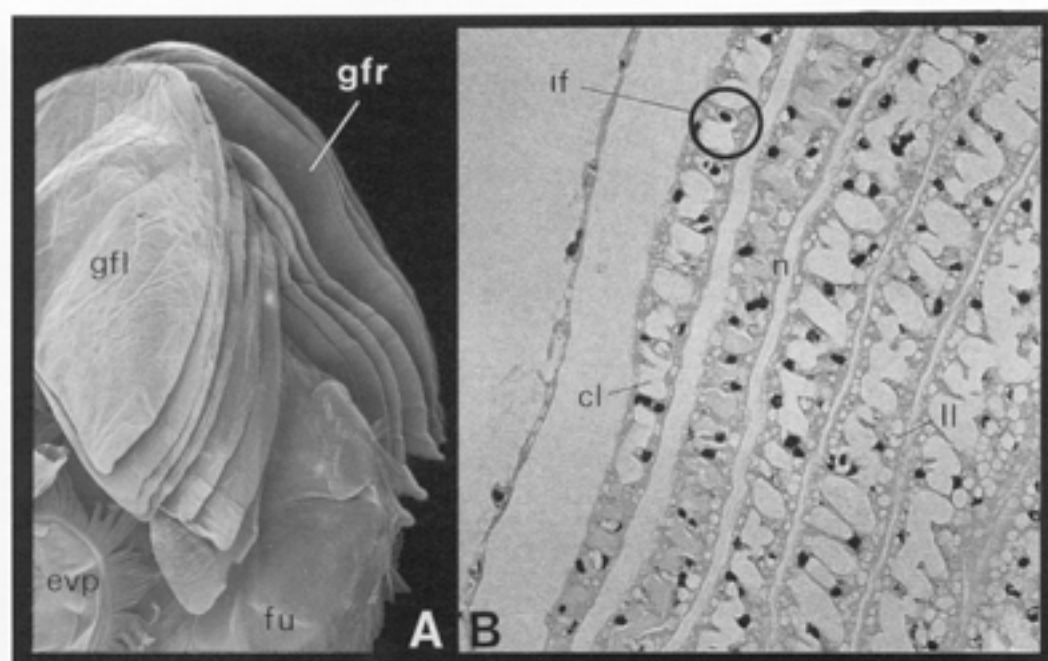
TEXT-FIG 7. Specialized respiratory features in myodocopid ostracodes exemplified by *Leuroleberis surugaensis* Hiruta, 1982, from Shimoda, Japan. A, FSL 575091; scanning electron micrograph showing 7 pairs of book gills on both sides of the posterior part of the body; carapace removed; ×24. B, stained (haematoxylin-eosin) microtomized paraffin horizontal section through the gills; ×215. cl = central lacunae; evp = epipodial ventilatory plate; fu = furcae (basal part); gf(l) and gf(r) = left and right gills; if = individual fold; ll = lateral lacunae; n = nucleus.

of seven lamellar fold-like extensions of the body integument, each individual lamella representing a large double-sided surface in contact with sea water. In section (Text-fig. 7B), these lamellae show a complex system of central and smaller lateral lacunae surrounded by connective cells, both characteristics suggesting that these are sites for respiratory exchanges. The vascular nature of this
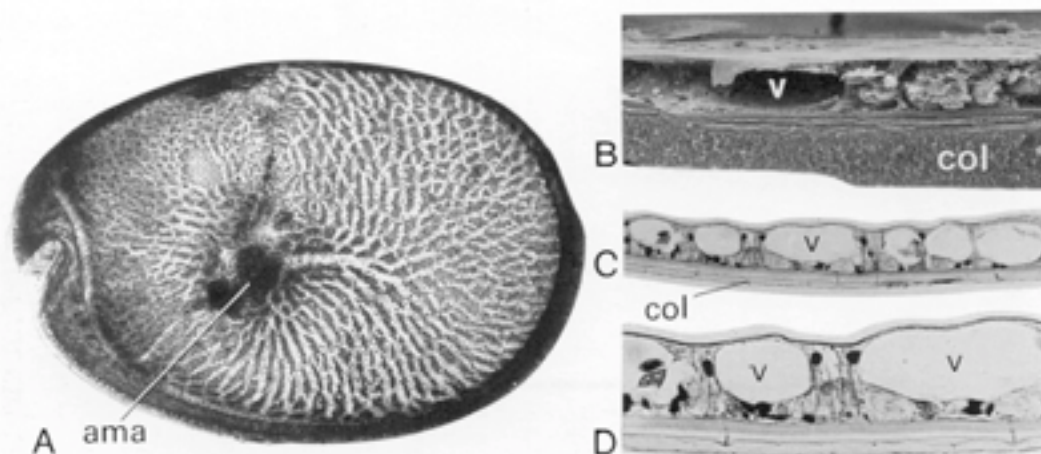
TEXT-FIG 8. Integumental circulatory system of *Vargula hilgendorfii* (Mydocopida, Cypridinidae) from Tateyama, Japan. A, FSL 575092; anastomozing pattern of a left valve (adult female) in transmitted light; ×24. B, transverse section through carapace showing vascular features (sinuses); scanning electron micrograph; ×450. C–D, stained (haematoxylin-eosin) microtomized paraffin section through carapace (see Text-fig. 2); ×145 and ×330, respectively. ama = adductorial muscle attachment; col = calcified outer lamella; v = vascular space (haemolymph sinus).

lacunar network and the flow route of haemolymph through it, have been examined in a separate study (Vannier *et al.* in press). Possible homologues of the paired book gills of Recent cylindroleberidids can be found in lowermost Mesozoic myodocopid ostracodes (Weitschat 1983*a, b*).

Circulation. In larger ostracodes, both Myodocopida and Halocyprida, diffusion obviously remains the basis of gaseous exchanges but is supplemented by internal fluid convection. A fluid (haemolymph) conveying cellular components (haemocytes) was observable both on video recordings and in stained paraffin sections (Text-fig. 5F; Abe and Vannier in press) within the integument of *Vargula hilgendorfii* (Myodocopida) and of *Conchoecia atlantica* (Halocyprida). The anastomozing vascular network present within the carapace of such ostracodes (Text-fig. 8) is part of an integrated circulatory system including a propulsive organ (dorsal heart; Text-figs 9, 12), efferrent (aorta) and afferent vessels (e.g. dorsal channel). In *Vargula hilgendorfii* and other myodocopids, the vascular network is always best developed in the posterior half of the carapace (Text-fig. 8A) and this particular area of the domiciliar cavity is assumed to be a preferential site for oxygen uptake, similar to that in other bivalved crustaceans (e.g. Branchiopoda; see Martin 1992, fig. 68). Haemolymph enters the anastomozing network of each valve around the adductor muscle attachment (Text-fig. 8A), through an isthmus which connects the body wall to the inner lamella and then flows radially through the sinuses back to the pericardial cavity of the heart. It is not understood yet how oxygen is transported to the metabolizing tissues, whether it is dissolved in plasma, bound to extracellular pigments such as haemoglobin (Goodwin 1960; Martin 1992) or, less probably, conveyed by the haemocytes. In other crustaceans closely related to Ostracoda, such as Branchiopoda, the extracellular respiratory pigments are not present in haemocytes (Martin 1992).

The living leptostracan phyllocarids possess a comparable circulatory system (Rolfe 1969). The carapace integument is pervaded by a dense network of arched sinuses and marginal channels through which haemolymph flows (video observations; JV unpublished) before returning to the dorsal pericardial cavity. *Nebalia bipes* (see Cannon 1960) from Japan and *Dahlella caldarensis* (see

Hessler 1984) from the East Pacific region are currently being studied for comparison with ostracodes.
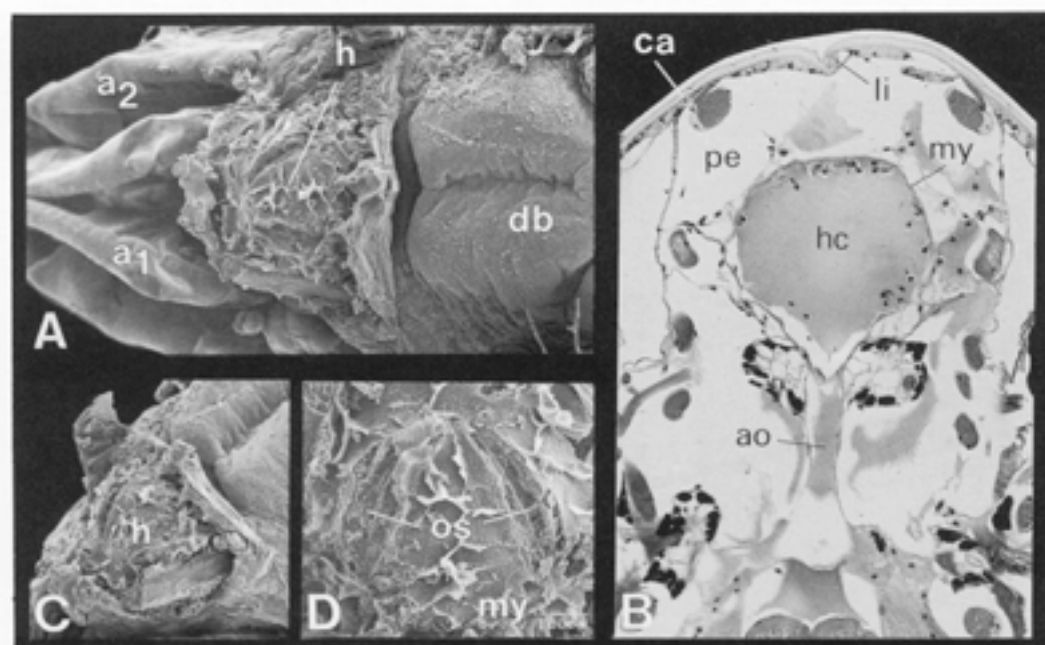
TEXT-FIG 9. Heart morphology of *Vargula hilgendorfii* (Mydocopida, Cypridinidae) from Tateyama, Japan. A, C–D, FSL 575093; male specimen, carapace removed; dorsal view ($\times 60$), intermediate anterior view ($\times 60$) and dorsal close-up ($\times 100$) of heart. B, female specimen; stained (haematoxylin-eosin) microtomized paraffin section through carapace; transversal section through heart; $\times 95$. a1 = first antenna; a2 = second antenna; ao = aorta; ca = carapace; db = dorsal part of body; h = heart; hc = heart cavity with haemolymph and haemolymph corpuscles (haemocytes); li = ligament; my = myocardium; os = ostium; pe = pericardium.
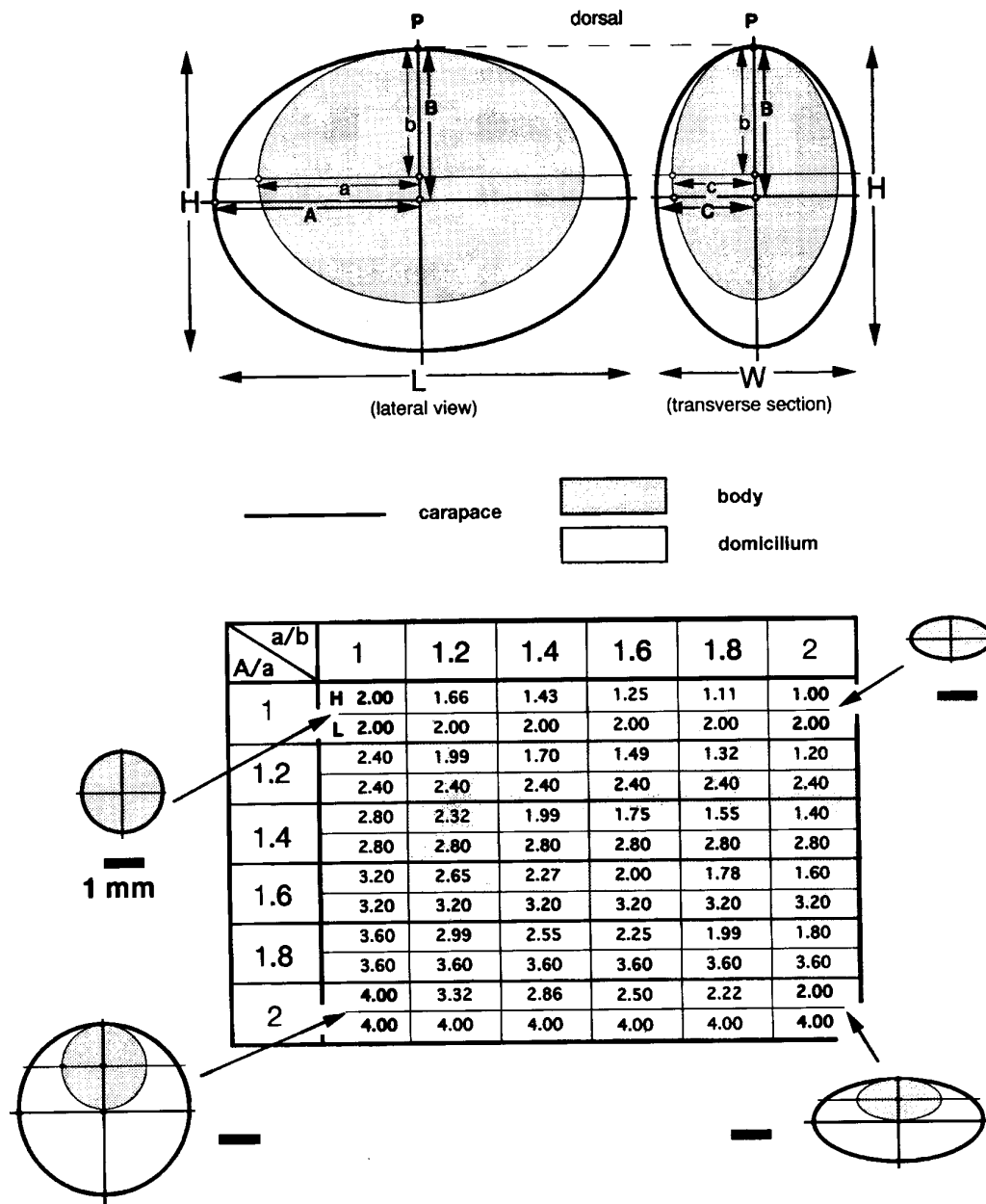
CRITICAL SIZE OF OSTRACODES

Ostracodes with no circulatory system. We considered the theoretical case of an ostracode having an ellipsoidal body (parameters *a–c* in Text-figure 10) enclosed within an ellipsoidal carapace (parameters A–C in Text-figure 10) attached to the body by a single point (P). Although this assumption obviously ignores the actual complexity of ostracodes (e.g. external ornament and appendage morphology), it remains fairly consistent with the average shape of living ostracodes (see Text-figs 2–4). Gaseous diffusion is assumed to occur evenly over the entire surface of the body and at a constant rate through the integument to the metabolizing tissues (Text-fig. 6). Gases such as oxygen diffuse (McMahon and Wilkens 1983) along partial pressure gradients from the outer (integument) to the innermost regions of the body at a rate J (mm³ s⁻¹) given by the equations

$$J = -SK\, dp/du \tag{1}$$

and

$$J = mV, \tag{2}$$

where S (mm²) is the area across which the diffusion occurs, K, a permeability constant (mm² atm⁻¹ sec⁻¹), p, the partial pressure (atm) of O_2, u, the distance (mm) over which O_2 is having to diffuse, dp/du, the partial pressure gradient, m, the rate at which O_2 is used per unit volume of tissue (mm³ O_2. mm³ sec⁻¹) and V, the volume of tissues (mm³). These relations apply to many other

dorsal

P   P

B   B
b   b
a   c
A   C

H   H

L   W
(lateral view)   (transverse section)

carapace   body
domicilium

1 mm

A/a \ a/b	1	1.2	1.4	1.6	1.8	2
1 — H	2.00	1.66	1.43	1.25	1.11	1.00
1 — L	2.00	2.00	2.00	2.00	2.00	2.00
1.2	2.40	1.99	1.70	1.49	1.32	1.20
1.2	2.40	2.40	2.40	2.40	2.40	2.40
1.4	2.80	2.32	1.99	1.75	1.55	1.40
1.4	2.80	2.80	2.80	2.80	2.80	2.80
1.6	3.20	2.65	2.27	2.00	1.78	1.60
1.6	3.20	3.20	3.20	3.20	3.20	3.20
1.8	3.60	2.99	2.55	2.25	1.99	1.80
1.8	3.60	3.60	3.60	3.60	3.60	3.60
2	4.00	3.32	2.86	2.50	2.22	2.00
2	4.00	4.00	4.00	4.00	4.00	4.00

TEXT-FIG 10. Maximum carapace size (length L and height H in mm) of ostracodes relying on gaseous diffusion only, assuming that 1 mm is the critical distance from integument surface to body centre (see equations and explanation in text). The ostracode carapace and body are considered herein as simple ellipsoidal volumes defined by three parameters: A, B, C and a, b, c, respectively, with $A/a = B/b = C/c$, $a = 1, a > b > c$. Figures in table are given for a/b and A/a varying from 1 to 2. Lateral outlines of ostracodes are given for extreme values of a/b and A/a. The shaded area in the table corresponds to the expected maximum size for most ostracodes (a/b and A/a ranging from 1·2 to 2 and 1·2 to 1·6, respectively).
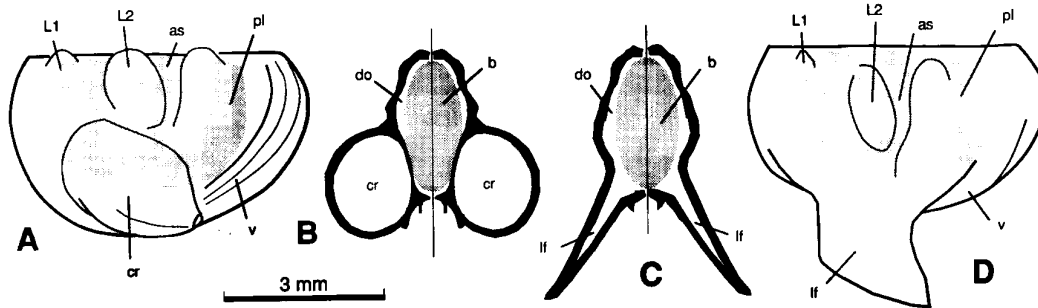
TEXT-FIG 11. Carapace and estimated body size in large beyrichiacean (Palaeocopa) ostracodes, exemplified by *Gibba kandarensis* (see Galle *et al.* 1995) from the Lower Devonian of Morocco. A, D, lateral external views of an adult male and female (left valves), respectively. B–C, simplified transversal section through a male and female carapace. Estimated body volume represented by a shaded area. as = adductorial sulcus; b = body; cr = crumina (brood pouch); do = domicilium; lf = lateroventral flange; L1 = anterior lobe; L2 = preadductorial lobe; pl = posterior lobe; v = velum.

invertebrate animals and have been used often by biologists (Alexander 1979; Schmidt-Nielsen 1990; Motokawa 1992) to tackle the problem of maximum body size. If we consider the simplest case where $a = b = c = r$ (spherical body of radius r), then, $u = r - x$ (radius) at a time t_x (see Text-fig. 6), $S = 4\pi x^2$ and $V = 4/3\pi x^3$. Equating (1) and (2) we have

$$mV/A\,dx = K\,dp.$$

In the present case, O_2 diffuses through the whole body of an ostracode from the integument (partial pressure p_e) to the centre (p_0).

$$m\int_0^r V/A\,dx = k(p_e - p_0),$$

$$m\int_0^r x/3K\,dx = k(p_e - p_0),$$

that is,
$$p_e - p_0 = mr^2/6K.$$

Because $p_e - p_0$ must be positive (oxygen goes from the periphery to the inside of the body),

$$p_e \geqslant mr^2/6K$$

that is
$$r \leqslant \sqrt{(6Kp_e/m)}. \tag{3}$$

The partial pressure of O_2 in well aerated water is $p_e = 0.21$ atm; K and m are about $2\ 10^{-5}$ mm^2 atm^{-1} sec^{-1} and $2.8\ 10^{-5}$ mm^3 O_2.mm^{-3} sec^{-1}, respectively (Alexander 1979; Motokawa 1992). The final calculation (3) indicates a critical radius of 1 mm, over which diffusion does not suffice to supply a spherical organism with O_2. If we suppose that ostracodes have an overall ellipsoidal body shape with $c < b < a$, then 'a' should not exceed 1 mm. We estimated (Text-fig. 10) the critical maximum size of ostracodes assuming gaseous diffusion only, for a body ratio a/b, and for body:carapace ratios B/b and A/a varying from 1 to 2. For instance, $A/a = B/b = 1$ and $a/b = 2$ (top right figure, Text-fig. 10) corresponds to an elongated carapace of 2 mm length and 1 mm height, entirely occupied by the body mass; $A/a = B/b = 2$ and $a/b = 1$ (bottom left figures, Text-fig. 10) give an ostracode of 4 mm in both length and height. These two extreme examples are not expected to be found in nature, nor in the fossil record, and the actual range of critical sizes is likely to be narrower than that envisaged in the whole table (Text-fig. 10). The vast majority of living ostracodes has A/a, B/b or C/c ratios ranging from 1.2 to 1.6 with a body ratio of about 1.2 to 2. For such organisms the maximum size would approach 3.2 mm long (Text-fig. 10). Our

calculations are consistent with the fact that living podocopes and small myodocopes with no vascular system (e.g. Polycopidae) are all smaller than 3 mm in adult carapace size. The same predictions seem to be applicable to the entire fossil record of the podocope ostracodes (Ordovician to Recent) and to numerous extinct ostracode groups such as Palaeocopa and Binodicopa (Vannier *et al.* 1989) and to many Cambrian archaeocopes as well. A few exceptions apparently exist. Some beyrichiacean ostracodes (Palaeocopa) are known to exceed 5 mm in adult carapace length (Groos and Jahnke 1970; Galle *et al.* 1995; Text-fig. 11). However, this unusually large size is mainly a result of calcified extensions of the carapace such as the inferred brood pouch of females and the large lateroventral flanges of adult males; the body of these ostracodes was obviously much smaller, confined within a relatively narrow ellipsoidal domiciliar space (Text-fig. 11B–C). In such a case, diffusion may have been sufficient to provide the animal with oxygen.

Ostracodes with a circulatory system. Simple calculations for invertebrate organisms such as marine worms bearing a simple peripheral circulatory vessel have been attempted by Alexander (1979) and Motokawa (1992), and can be tentatively applied to ostracodes if we consider, again, a theoretical animal with a spherical shape (Text-fig. 12A). This is a relatively close approximation of the actual circulatory system of myodocopid ostracodes in which the anastomozing channels develop over almost the entire surface of the carapace (Text-fig. 12B). Equations (1) and (2) above are used again with $S = 4\pi r^2$ and $V = 4/3\pi r^3$ and $dp/ds = (p_e - p_b)/d$ (see Text-fig. 12A). We have

$$r = 3K(p_e - p_b)/md. \tag{4}$$

The partial pressure of O_2 in the peripheral haemolymph channel (p_b) of diameter (d) is estimated to be about $5\ 10^{-2}$ atm by comparison with figures obtained from other small invertebrates (Motokawa 1992); $d = 3\ 10^{-2}$ mm is consistent with the average diameter of the integumental haemolymph sinuses in *Vargula hilgendorfii* (Abe and Vannier in press). We assume, as before, that the partial pressure of $O_2(p_e)$, K and m are about 0·21 atm, $2\ 10^{-5}$ mm^2.atm^{-1} sec^{-1} and $2·8\ 10^{-5}$ mm^3 O_2.mm^{-3} sec^{-1}, respectively. Calculations indicate that the maximum possible radius would be 11·4 mm. Consequently, the maximum length of a spherical ostracode having such a peripheral circulatory system is estimated to reach 22·8 mm. This estimation fits surprisingly the actual size range of *Gigantocypris*, the largest known living ostracode with an almost spherical soft carapace about 32 mm long and a circulatory system (Cannon 1940).
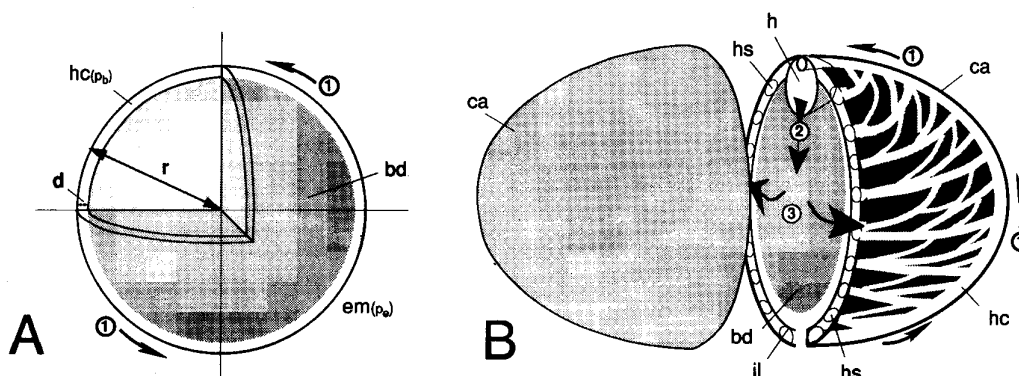
TEXT-FIG 12. Peripheral fluid convection in a spherical animal (A) and as observed in *Vargula hilgendorfii* (B), simplified. bd = body; ca = carapace; d = diameter of channel; em (p_e) = partial pressure of $O_2(p_e)$ in external medium (em); h = heart; hc = haemolymph channel; hc (p_b) = partial pressure of $O_2(p_b)$ in haemolymph channel; hs = haemolymph sinus; il = inner lamella of cuticle; r = radius; ① = peripheral circulation; ② = circulation from heart to organs; ③ = circulation from organs to anastomozing vascular system.

However, a major criticism can be made against such simplistic models and their subsequent predictions of a maximum size. The peripheral circulatory system of myodocopid ostracodes runs between the outer and the inner cuticular lamellae of the carapace and therefore does not supply oxygen directly to adjacent metabolizing tissues other than epidermal cells. It is the efferent system (aorta and secondary vessels and lacunae), well developed in large cypridinid species (e.g. Cannon 1931) which actually delivers oxygen from the heart to the organs (see Text-fig. 12B②, 12B③). If such a system, even though partly lacunar, is dense and efficient enough to bring down the diffusion distances to optimal values, then no maximum critical size exists and ostracodes reaching greater than 32 mm are possible, at least in theory. In fact, the increase of body size in ostracodes with a circulatory system is most probably limited by other constraints such as design (strength of internal and external skeleton) or functional (cardiac pulse· and vascular pressure). Leaving apart speculations on ostracode size, fluid convection appears as one of the key features (Abe and Vannier 1993b) which, by augmenting the diffusion processes, most probably allowed ostracodes to range beyond 3·2 mm (see calculations for diffusion only) and to attain a centimetric body size.

The minimum size of ostracodes. The smallest known living adult representatives of the group can be found among the interstitial fauna (Hartmann 1973), the deep-marine benthos (Peypouquet 1977; Coles *et al.* 1994 for *Krithe*) and the deep-sea pelagic fauna. Interstitial species (e.g. mesopsammitic organisms with a reduced mobility) belong either to podocopids or myodocopes (Cladocopina, Polycopidae); their body sizes rarely exceed 0·5 mm, usually ranging between 0·1 mm and 0·3 mm (Hartmann 1973). Reduction in the number of appendages, genital and visual organs is a common feature of these microcrustaceans that lack any circulatory system. Extremely small adult sizes also occur in free-living bathyal halocyprid ostracodes such as *Bathyconchoecia* sp. (0·50 mm in adult length) from Sagami Bay, Japan (unpublished data).

Critical size and depth. Since the critical body size of an ostracode is proportional to the partial pressure of oxygen in the surrounding medium (equation (3)), we may expect to observe variations of this critical size according to depth. The vertical distribution of oxygen dissolved in sea water, illustrated by profiles (Kester 1975) in the major oceanic basins (NE Atlantic, Indian and NE Pacific Oceans), shows a relatively constant pattern with an oxygen minimum layer (OML) between 750 m and 1100 m and relatively higher O_2 concentrations in deeper waters. For example, in the NE Atlantic (Kester 1975) surface and deep (from 1500 m to 5000 m) waters have comparable values of O_2 concentration (about 250 μmol kg^{-1}) and consequently of O_2 partial pressure. In this case and according to our model, no significant variation of the critical size is likely to occur between shallow water and deep-sea ostracodes relying on gaseous diffusion. Only those living near or within the oxygen minimum layer may have a smaller critical body size. This prediction, which may have some implications in palaeobathymetry, has to be tested by thorough investigations of the size range of the deep-sea OML species.

## SIZE, CIRCULATORY AND RESPIRATORY FEATURES IN EARLY OSTRACODA

Leperditicopes. The extinct Order Leperditicopida (early Ordovician–Upper Devonian; Text-figs 13–14) contains the biggest ostracodes known from the palaeontological and Recent records and is particularly relevant to the problem of size in fossil Ostracoda. Leperditicopes have been reviewed extensively by Berdan (1976, 1984) and Abushik (1990). Apart from the size (adult length from several mm up to 80 mm in *Moelleritia*), the main ordinal characters include (Berdan 1984, p. 4) large adductorial muscle scars composed of numerous individual attachment stigmata, a ventral overlap of the right valve over the left, including stop-features, and an inferred eye tubercle (Text-fig. 14A). The postplete lateral outline present in many leperditicopes is most probably a primitive character related to the retral swing of the animal's body within the carapace (Hinz 1993). Although their assignment to Ostracoda was denied by several authors (Swartz 1949; Heidrich 1977), we agree with Berdan (1984), Schallreuter (1978) and Langer (1973), that leperditicopes are true ostracodes.
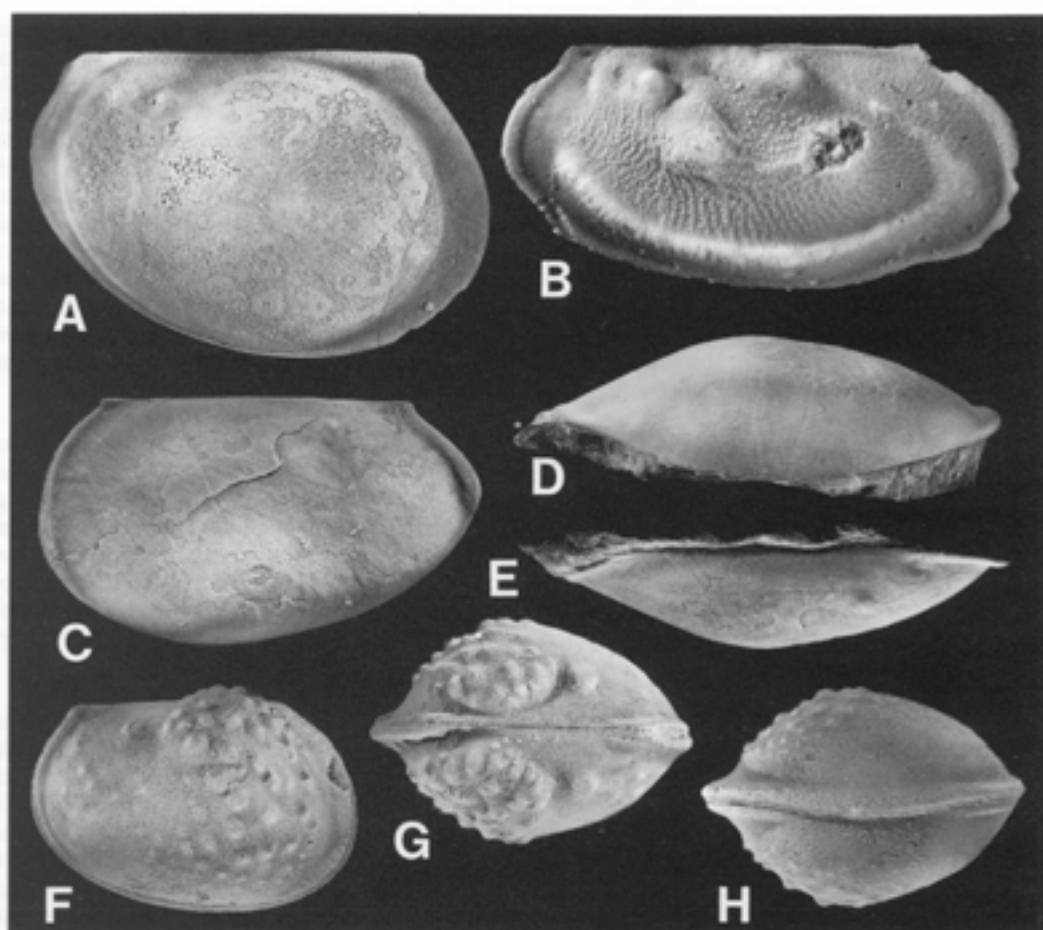
TEXT-FIG 13. Palaeozoic leperditicope ostracodes. A, *Teichochilina jonesi* (Wetherby, 1881); USNM 338709; Lexington Limestone, Middle Ordovician; Kentucky, USA; left valve (silicified), lateral view; ×4·7. B, *Saffordellina muralis* (Ulrich and Bassler, 1923); USNM 41561B, paralectotype; Cathey Formation, Middle Ordovician; West Nashville, Tennessee, USA; left valve, lateral view; ×9. C–E, *Leperditia marinae* Abushik, 1980; N 7837-2; Lower Devonian (Lochkovian) of Novaya Zemlya, Russia; right valve in lateral ventral and dorsal views, respectively; ×1·6. F–H, *Moelleritia moelleri* (Schmidt, 1883); neotype (housed in the collections of the VSEGEI Geological Institute, Saint-Petersburg, Russia; the material is being revised by A. Abushik); Devonian (Upper Emsian) of the Belaya River, Central Urals, Russia; lateral view of carapace from left, dorsal and ventral views, respectively; ×2·7. All are light photographs. A and B reprinted from J. Berdan's negatives.

Leperditicopes share many morphological features with coeval non-lobate ostracodes such as leiocopes (Williams and Vannier 1995), for instance the overlap pattern (Text-fig. 14), the outline of transverse sections and even the shell thickness relatively to the carapace size. The only, but significant difference is size (compare Text-fig. 14B and D–F) and to a lesser extent the shell ultrastructure (see Langer 1973).

Peculiar anastomozing features frequently occur in leperditicopes, most commonly expressed as ridges on the steinkerns or negative markings on the inner surface of silicified valves (e.g. Berdan 1984, pl. 8, fig. 5), more rarely on the external surfaces (Text-fig. 13B). Whether these markings represent former vascular features, with the implication that leperditicopes may have possessed a
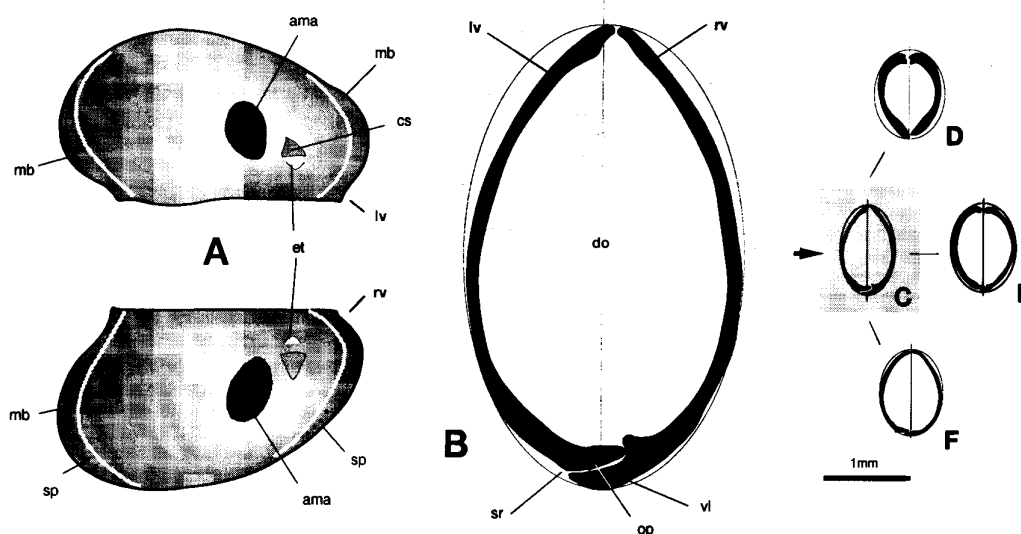
TEXT-FIG 14. Overall morphology (A), size, shell thickness and overlap features of Ordovician leperditiid (B–C) and leiocope ostracodes (D–F). B–C, *Eoleperditia fabulites*, (Conrad, 1843) from the Ordovician of Wisconsin, USA; D–F, *Baltonotella paraspinosa* (Kraft, 1962), *Hyperchilarina nodosimarginata* Harris, 1957 and schmidtellid gen. nov. from the Middle Ordovician of Oklahoma, USA, respectively. B, D–F, all represented at the same scale (after Williams and Vannier 1995) for comparison of size. C = B but reduced to the same height as D–F for comparison of shell thickness. A–B, after Berdan (1984), modified. ama = adductor muscle area; as = adductorial sulcus; cs = chevron scar; do = domiciliar cavity; et = eye tubercle; lv = left valve; mb = marginal brim; op = overlap platform; rv = right valve; sp = stop pits; sr = stop ridge; vl = ventral lappet.

heart, has long been argued (Schmidt 1873; Triebel 1941; Adamczak and Weyant 1973; Langer 1973; Sohn 1974). We provide herein new evidence from detailed comparisons with living ostracodes (Text-fig. 15).

1. The anastomozing markings of leperditicopes radiate from the adductor muscle area toward the periphery of the valve, similar to the integumental sinuses of Recent myodocopes. In living myodocopes, this pattern is a result of the fact that haemolymph enters the vascular spaces of the valve integument in that particular area surrounding the bundles of adductor muscles, then flows radially all the way down to the peripheral channels (Abe and Vannier in press).

2. The radiate network of leperditicopes and living myodocopes (Text-fig. 15A–B) has a similar average density with individual channels comparable in diameter.

3. In leperditicopes, the narrow area situated above the muscle scars lacks any markings and is, therefore, similar to that in living ostracodes. In living animals, this area, which runs between the heart region and the adductor muscle spots, is an attachment area (see Kornicker 1969).

4. Anastomozing markings, as commonly expressed in leperditicopes, are unknown in other groups of non-myodocope fossil Ostracoda, and seem to occur exclusively in specimens reaching over 3 mm in adult carapace length. It is important to note that the same relation of vascularization to large size is observed in living ostracodes. The so-called vascular markings of *Rishona tumida* (Middle Devonian; maximum carapace size 1·8 mm; see Adamczak and Weyant 1973, fig. 2) form a much more intricate network which probably belongs to a different type of shell microstructure. The ramose imprints present on the internal mould of the Ordovician *Cochoprimitia socialis* (c. 4 mm long; Henningsmoen 1954) occur in only some specimens and are thicker than those observed in leperditicopes.

We conclude that Palaeozoic leperditicopes already possessed a vascular system comparable in design and function (for fluid convection) with that of modern ostracodes. Since no information is available on the soft anatomy of these fossil organisms, the presence of a heart (see Sohn 1974) cannot be demonstrated directly. However, almost all crustaceans in which circulatory convection occurs do have a heart. Although the general body movements may, in certain cases, assist haemolymph flow, the heart plays an essential role as the propulsive organ of the circulatory system. Exceptions may be found in some copepods lacking a heart and using valve movements to regulate the direction of haemolymph flow (Maynard 1960). We believe that leperditicopes bearing inferred haemolymph sinuses were also provided with a heart. This organ is likely to have been accommodated dorsally in the upper part of the adductorial sulcus (Text-figs 15A–B, 18F).
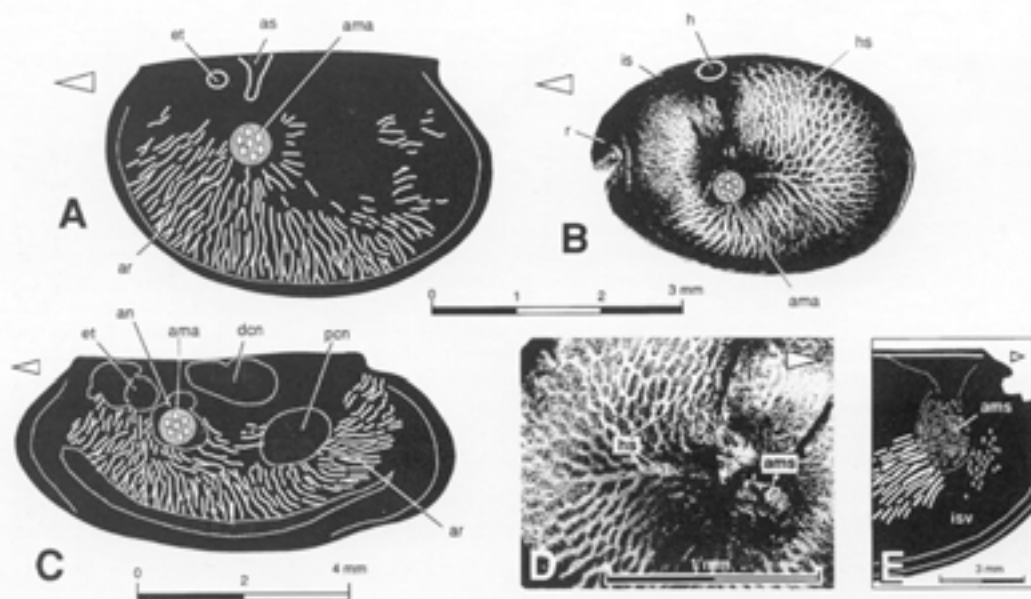
TEXT-FIG 15. Anastomozing patterns of some Ordovician leperditicope ostracodes compared with the integumental vascular pattern of Recent myodocopids. A, lateral view of a left valve of *Isochilina venosculptis* from the Ordovician of Quebec, Canada; B, D, anastomozing haemolymph sinuses of *Vargula hilgendorfii*, Pacific Ocean, Japan, seen in transmitted light; C, lateral view of the external surface of *Saffordellina muralis* (see Text-Fig. 14B) from the Ordovician of Tennessee (grey shading indicates elevations on the valve); E, inner surface of a silicified valve of *Teichochilina jonesi* (see Text-Fig. 14A) from the Ordovician of Kentucky, showing the relationships of the radiated markings to the adductorial area. White arrows indicate anterior part of the animal. Adductorial morphology simplified. A, C and E drawn from the original photographic illustrations of Swartz (1949, pl. 66, fig. 13) and Berdan (1984, pl. 11, fig. 2; pl. 8, fig. 5), respectively. ama = adductorial muscle attachment; ams = adductor muscle scars; ar = anastomozing ridges; as = adductorial sulcus; dcn = dorsocentral node; et = eye tubercle; h = heart; hs = haemolymph sinuses; is = isthmus; isv = internal surface of the valve; pcn = posterocentral node; r = rostrum.

Silurian myodocopes. Morphological and ecological aspects of the early representatives of Myodocopa have been examined recently in a series of papers (see Vannier and Abe 1992 for complete references). These widespread ostracodes are characterized by a relatively large size (from 3–4 mm up to more than 10 mm in *Entomozoe tuberosa*; see Siveter and Vannier 1990), far exceeding that of all other non-leperditicope Ordovician to Devonian ostracodes. No radial or

anastomozing markings, as typically expressed in numerous Ordovician leperditicopes (Text-figs 14–15), are found in Silurian myodocopes. However, the ornamented pattern of, for instance, the late Silurian bolbozoids shares intriguing resemblances with the anastomozing circulatory pattern of Recent myodocopids such as *Vargula*. The species figured by Siveter *et al.* (1987, pl. 84, fig. 2) as *Bolbozoe* sp. nov. A, has sinuous and bifurcating lines throughout the carapace except on the sulci, the rostrum and the upper part of the bulb. In *Vargula*, circulatory sinuses are similarly much attenuated or absent in the anterodorsal part of the valves. Moreover, the ornament of many bolbozoid species, either retriculated or corrugated, shows clear tendencies to radiate and to bifurcate from the adductorial area (large composite scars) toward the ventral, the dorsal and the posterior part of the valve, which corresponds to the main routes of the circulating haemolymph in *Vargula*. The peripheral convergence of the reticulated/corrugated pattern of bolbozoids (e.g. Siveter *et al.* 1987, pl. 84, figs 2, 7) may correspond, in Recent myodocopids, to the afferent channels, which collect haemolymph before it returns to heart. In this case, the discrete bulbous or triangular features which dorsally terminate the adductor sulcus of *Bolbozoe* or *Entomozoe* (Siveter and Vannier 1990; Vannier and Abe 1992, fig. 2) may indicate the presence of a heart, possibly housed in these small cavities.
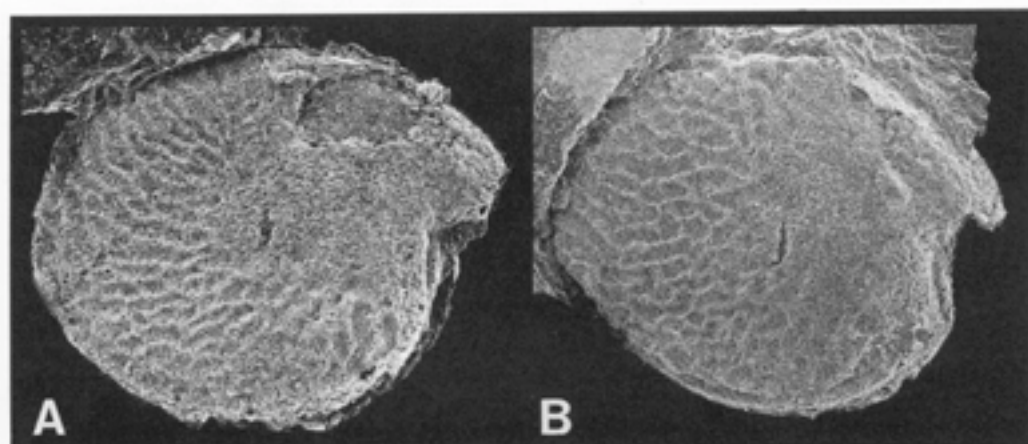

TEXT-FIG 16. Late Silurian myodocopid ostracode (gen. et sp. nov. *in* Siveter *et al.* 1987) showing external ornament interpreted here as the possible traces of a vascular system (see text for explanation); Lande-Murée Formation; Andouillé, Mayenne, France. A, FSL 575094; B, FSL 575095; both right valves, external lateral views; SEM micrographs of latex casts from external moulds; × 16.

Some late Silurian cypridinid-like ostracodes (Text-fig. 16), sharing more obvious similarities (outline, rostrum) with modern myodocopids, also bear an anastomozing 'ornament' which strongly resembles the integumental circulatory network of modern ostracodes. However, the 'ornament' of Silurian myodocopes always appears as positive features on the surface of both casts and steinkerns. This is a major difference from the integumental sinuses of living myodocopids which always run below the calcified layers of the carapace (Text-fig. 8) and are never expressed externally either as grooves or ridges. If the reticulated or corrugated patterns (*sensu* Siveter *et al.* 1987) of early myodocopids represent the trace of a circulatory system, then this system must have had original characteristics in relation to integument. Silurian myodocopids, often preserved as flattened organic-rich imprints in sediments, were probably extremely thin-shelled and poorly calcified ostracodes comparable with living pelagic halocyprids (Text-figs 1A–B, 3). Although very speculative, based on this early stage of our research (thin sections of Palaeozoic specimens are obviously needed), we might envisage that the ornamented network of these ostracodes, if produced

by epidermal layers (see Okada 1981, 1982), also housed circulatory sinuses within the positive features of the polygons. If so, the question still remains as to how such discrete and fragile features may have been preserved in sediment (e.g. Ordovician leperditicopes and Silurian myodocopids). Experimental fossilization of shrimps in the laboratory (Briggs and Kear 1993) indicated that even minute details of soft tissues (e.g. muscles) become mineralized in amorphous calcium phosphate within the first two to eight weeks of the decay processes. The same type of process may account for the '3-D stabilization' of the integumental microstructures of fossil ostracodes, prior to their complete fossilization. In *Vargula* (Text-figs 2E, 9) both internal vessels (e.g. pericardium, aorta) and integumental sinuses are filled with haemolymph. The composition of this fluid is not documented in ostracodes. In larger crustaceans (see Florkin 1960) chemical substances such as inorganic ions, glucids, plasma proteins, coagulable proteins and enzymes have been recognized. If also present in ostracodes, such organic components, still confined in vessels after the animal's death, may be the source for some of the key components of the early mineralization process.

Mesozoic myodocopes. Exceptionally preserved phosphatized ostracodes (*Triadocypris*) from the lower Triassic of Spitzbergen (Weitschat 1983a, 1983b; Weitschat and Guhl 1993) reveal a fascinating internal anatomy (e.g. appendages, lateral eyes, 7th limb) surprisingly similar to that of modern myodocopids. However, the shell microstructures (Weitschat, pers. comm.) have not been investigated so far and no evidence is available for the presence or absence of integumental circulatory vessels in these medium-sized ostracodes (carapace length up to 3·1 mm). A recent reconstruction (Weitschat and Guhl 1993) features ciliate protozoans attached to various parts of the integument of the same Triassic species. It is worthwhile noting here that five of these ciliates are found in the dorsal part of the domicilium, which in living myodocopids (e.g. *Vargula*; Text-fig. 9) correspond exactly to the location of heart; they seem to be distributed radially as if they were attached to the outer wall of the pericardium. Continuing scanning electron microscope investigations of this exceptional fossil material may shed light upon this particular problem.

Inferred gill-like features are also found in *Triadocypris* (Weitschat 1983a). They consist of bag-like flattened infolds equally distributed on each side of the body. The quality of preservation of these organs is again good enough to attempt detailed comparisons with Recent homologues. They are most probably similar in morphology and function to the external (intradomiciliar) integumental folds, resembling book gills (Maddocks 1992; Text-fig. 7; Vannier *et al.* in press) in modern cylindroleberidids (Kornicker 1981). These Triassic gills attest to the existence of additional respiratory features implementing diffusion since at least 225 million years ago.
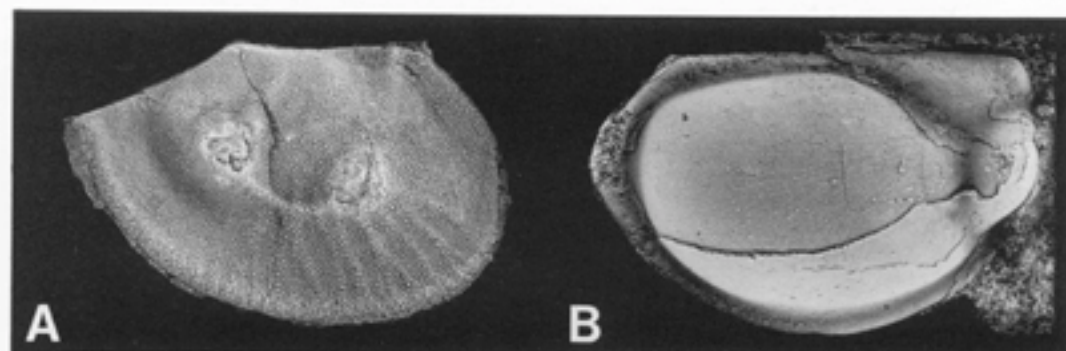
TEXT-FIG 17. Radiating markings interpreted as possible vascular features in Cambrian bivalved arthropods (see text for explanation). A, cambriid bradoriid (Siveter *et al.* in press); Buen Formation, Lower Cambrian; N Greenland; left valve, lateral view; ×5·5. B, *Anabarochilina primordialis* (Linnarson, 1869); GSU 8662, holotype; Middle Cambrian *Lejopyge laevigata* Zone; Djopadalen, Västergötland, Sweden; partly exfoliated right valve showing radiating features on internal mould (see Siveter *et al.* 1993), lateral view; ×6·8.

Ancestry of circulatory systems in ostracodes and other bivalved arthropods. If our interpretations are correct, circulatory features have existed in ostracodes since at least the Ordovician (Leperditicopa) and occur in the Silurian (Myodocopa); they may be also present in Cambrian bivalved arthropods. *Anabarochilina primordialis* (Linnarsson, 1869; see Siveter *et al*. 1993; Text-fig. 17B) from the late middle Cambrian of southern Britain, Scandinavia and Australia and the early late Cambrian of Russia reaches a centimetric size and clearly shows on the surface of exfoliated specimens fine anastomozing lines radiating from the adductor muscle scar region. These features are likely to represent the traces of former circulatory sinuses comparable to those of leperditicope ostracodes (Text-fig. 15). However, *Anabarochilina* shares more morphological traits with phyllocarids than with any other group of bivalve crustaceans or non-crustacean arthropods. For example, the peculiar orientation and design of its inferred circulatory sinuses and the morphology of its nodes have close homologues in Palaeozoic phyllocarid crustaceans (see Rolfe 1969) such as *Carnarvonia venosa* Walcott, 1912 (Middle Cambrian, Burgess Shale, Canada), *Rhinocaris* (Devonian; see Clarke 1893; Rolfe 1969), *Tropidocaris* (Devonian; see Rolfe 1969 and pers. comm.), *Aristozoe* (Devonian; see Barrande 1872; Chlupac 1992, 1994) and, to some extent, *Canadaspis* (also from the Burgess Shale; see Briggs 1978; Whittington 1985). These possible phyllocarid affinities would support the idea (Text-fig. 18E) that the abdomen of *Anabarochilina* and related genera protruded from the carapace posteriorly or posteroventraly similarly to that of *Aristozoe* or *Canadaspis*. Whether *Anabarochilina* should be placed within the Phyllocarida, the Ostracoda (Leperditicopa) or the Bradoriida (Williams and Siveter, pers. comm.) is debatable and outside the scope of the present paper.

The oldest record of possible circulatory features comes from several unpublished (M. Williams, pers. comm.; Siveter *et al*. in press) bradoriid arthropods (Cambriidae) from the Lower Cambrian of North Greenland. This material (Text-fig. 17A), of centimetric size, exhibits bifurcating lineations best developed in the posteroventral area of both valves and radiating from central nodes. Comparable features are observed also in Ordovician leperditicopes, especially *Saffordellina* (compare Text-figures 13B and 17A). It seems that integumental circulation can be traced back to the early Cambrian and developed in different lineages of bivalved arthropods, such as the crustaceans, throughout the Lower Palaeozoic.

EVOLUTIONARY CHANGES IN CARAPACE DESIGN, BODY PLAN AND RESPIRATORY FEATURES

The earliest Palaeozoic ancestors of Ostracoda were probably small crustaceans with a univalved or a bivalved carapace unable to enclose the body completely, thus differing markedly from all the post-Cambrian representatives of the group. Evidence for this ancestral body plan (Hinz 1993) comes from: 1) the posterodorsal gape of some bradoriid species, suggesting that the abdominal segments of the animal protruded from the domiciliar cavity (e.g. *Aristaluta*, Middle Cambrian; see Hinz 1993); and 2) interdorsal features (a flattened central area demarcated by integumental bends; Müller 1979, 1982), preventing the ventral closure of the valves (Hinz 1993; Hinz-Schallreuter 1993). Hinz (1993) suggested that the gradual reduction of thoracic and abdominal regions of these arthropods, added to the lateral compression of the body and to the increasing biomineralization of the shell, may have set the basis of the body plan of modern ostracodes. The idea that some early lower Cambrian ancestors of Ostracoda were univalved crustaceans bearing a shield-like carapace, is supported by Zhang and Pratt (1993), who demonstrated the univalved-bivalved transition during the early ontogeny of lower Cambrian bradoriids. To some extent, the larval stages of *Manawa* (Recent; Swanson 1989*a*, 1989*b*) give a relatively good image of what univalved ostracodes may have looked like.

The profound anatomical changes that are supposed to have taken place in the early stages (Cambrian) of the evolution of Ostracoda have most probably also affected the respiratory features of these organisms. According to Hinz (1993), ancestors of Ostracoda were crustaceans with an elongate and fully segmented body (with head, thorax, and abdomen) protected by a shield-like

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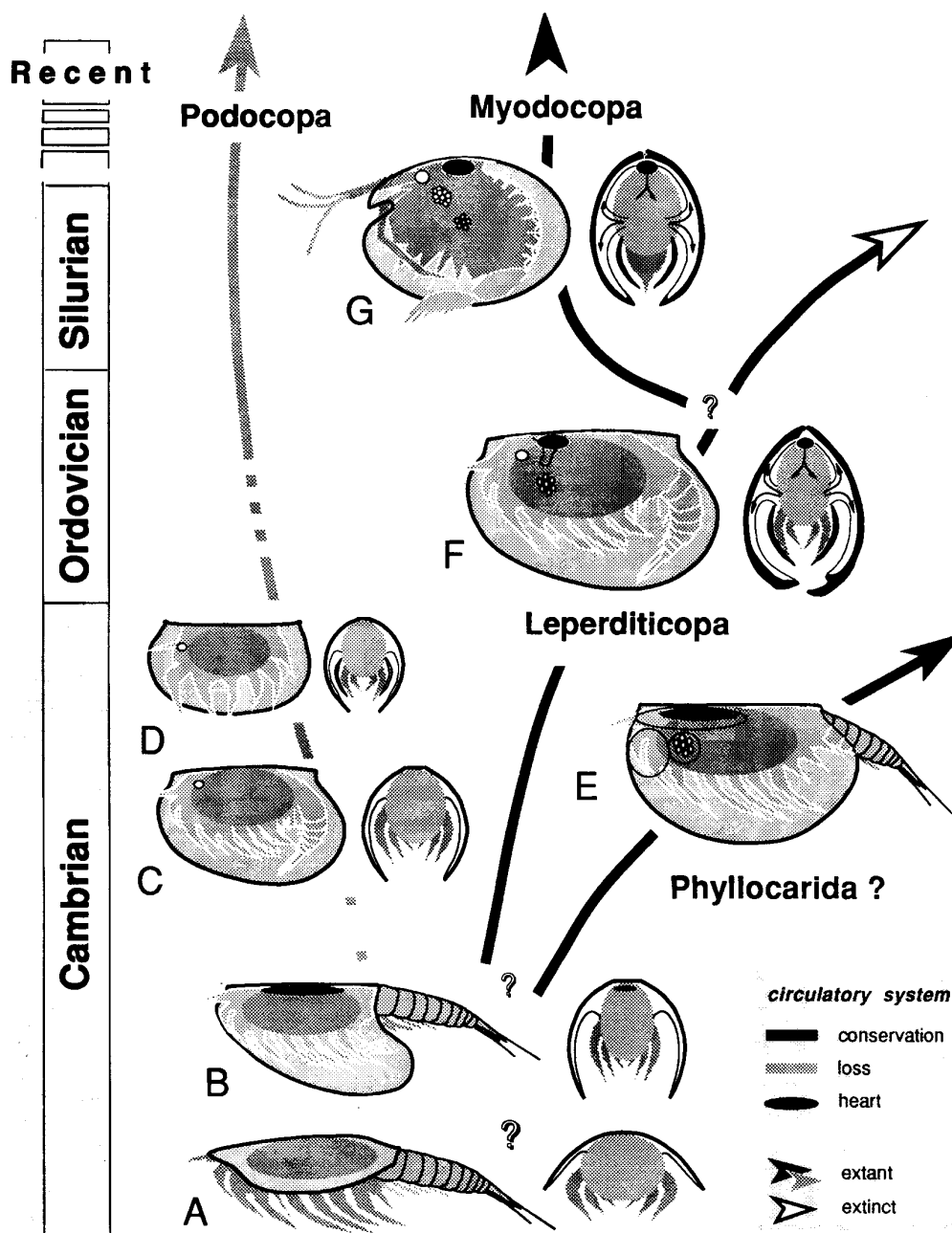
TEXT-FIG 18. Main evolutionary changes in the body plan, carapace design and respiratory features of early
Palaeozoic (Cambrian to Silurian) Ostracoda and possibly related groups. Simplified lateral views from left and
transverse sections through animals; main characteristics of anatomy and respiratory features are indicated for
each design (A–G). Lateral views of A–D from Hinz (1993), modified. Arrows in F and G (sections) indicate

carapace of obviously cephalic origin (Text-fig. 18A–B). From a strictly morphofunctional point of view, excluding phylogenetic considerations, this body plan recalls, for example, that of the leptostracan phyllocarids such as *Nebalia*. In *Nebalia geoffroyi* (see Cannon 1960; Schram 1986), the circulatory system has an elongated dorsal heart with series of ostia and a haemolymph sinus extending into the carapace. According to Schram (1986, p. 8), the heart is segmentally derived and the ostia are the remnants of the intersegmental spaces. We suggest in our model (Text-fig. 18) that a comparable system including integumental diffusion and fluid convection (haemolymph) may have existed in Cambrian ancestors of Ostracoda as well. The later reduction of the body, both in terms of size and segmentation (to thorax and abdomen), led to the gradual enclosure of the soft parts within the mineralized carapace. An implication of this new design is the achievement of a closed space, the domiciliar cavity. In such a confined space, ventilation is crucial. Ventilatory plates (e.g. on exopodites or epipodites of thoracic segments) may have developed markedly at that stage, creating and maintaining higher and constant partial pressure gradients over respiratory surfaces (carapace inner lamella and body integument), thus making oxygen uptake more efficient. Müller (1979, 1982) described 'vibratory plates' on the thoracic appendages of *Hesslandona* from the Upper Cambrian of Sweden; this ostracode had a carapace 1–1·5 mm long and a segmented body entirely enclosed within the domiciliar cavity. None of these excellently preserved (by secondary phosphatization of soft anatomy) specimens of *Hesslandona* and related taxa exhibit circulatory or cardiac features. The subsequent reduction of body and carapace size probably brought ostracodes down to the critical size below which gaseous diffusion is sufficient to supply enough O_2, leading to the partial or total loss of the ancestral circulatory system. The haemocoelic lacunae (Text-fig. 4) still present within the integument of modern podocopes (D. Keyser, pers. comm.) are probably vestigial features and are interpreted tentatively here as the remains of ancient circulatory features.

In our interpretation (Text-fig. 18), some ostracodes, for example the leperditicopes, did not undergo such drastic changes and retained many ancestral characters such as a circulatory system (heart, vessels, sinuses), the postplete shape of the carapace in relation to the abdominal morphology (Text-fig. 18F), and also, possibly, compound visual organs (eye tubercles; Berdan 1984). Circulatory features allowed these organisms to reach an exceptionally large (up to centimetric) size during the Lower Palaeozoic (Cambrian? to Devonian). Silurian myodocopes belong to the same category of ostracodes. In contrast with the leperditicopes, which became extinct by the Devonian, the myodocope lineage (Vannier and Abe 1992) persists through to the present day. The living myodocopids (Text-fig. 2) still have anatomical features, for example the dorsal heart, the strongly arched and well developed curvature of the posterior part of the body, the furcal lamellae, and the compound lateral eyes directly inherited from lower Mesozoic (Weitschat

possible haemolymph circulation, based on observations of Recent ostracodes (Abe and Vannier in press) and phyllocarids (JV, unpublished). A–B, hypothetical crustacean ancestors (Cambrian) of Ostracoda and possibly related groups. A, shield-like univalved soft carapace; long segmented body; integumental gaseous diffusion only. B, bivalved carapace bearing possible interdorsal features (see Hinz 1993); domiciliar cavity open widely; long segmented body protruding from the carapace through a posterior gape; integumental diffusion; possible circulatory system including an elongated dorsal heart. C, Cambrian bradoriid with reduced body segmentation; bivalved carapace; body accommodated within domiciliar cavity; integumental diffusion; sharp reduction or loss of circulatory system. D, late Cambrian ostracode with more reduced body segmentation; reduction or absence of interdorsum; semi-closed domiciliar cavity with ventilation creating partial pressure gradients of O_2; integumental gaseous diffusion only. E, Middle Cambrian phyllocarid crustacean(?) based on *Anabarochilina* (Siveter *et al.* 1993); centimetric size; abdomen protruding from the carapace; inferred dorsal heart and integumental circulation expressed as anastomozing features on valves. Abdomen reconstructed from phyllocarid morphology (Rolfe 1969). F, Ordovician leperditicope; large size up to centimetric; calcified bivalved carapace; ventral overlap features; body accommodated in domiciliar cavity; adductor muscles; intradomiciliar ventilation; inferred dorsal heart and integumental circulation expressed as anastomozing features. G, Silurian myodocopes; large size up to centimetric; calcified, or soft bivalved carapace; body accomodated in domiciliar cavity; adductor muscles; intradomiciliar ventilation; inferred dorsal heart and integumental circulation expressed as anastomozing features.

1983*a*, 1983*b*) and probably Lower Palaeozoic ancestors. Circulation may also have allowed myodocope ostracodes to acquire higher metabolic rates, a condition of importance for ostracodes adapted to free-swimming life styles by Silurian times (Siveter *et al.* 1991; Vannier and Abe 1992). The fact that leperditicopes and myodocopes apparently share ancestral characters (Text-fig. 18E–F) brings new information relevant to the pre-Silurian origin and history of myodocopes, considered by many authors (see *Entomozoe in* Siveter and Vannier 1990; Vannier and Abe 1993) to be enigmatic.

CONCLUSIONS

The early achievement (mid or late Cambrian) of the bivalved design and the probable loss of the circulatory system, implying sharp physical constraints related to respiration, may have confined many representatives of the Ostracoda to within a relatively low and narrow size range, inducing remarkably conservative features among the group up to the present time. The 7000 species of Recent podocopes belong to that category of organisms. In contrast, size constraints were partly overcome by those conserving a circulatory system probably inherited from the early Cambrian arthropodan stock. Thus, large size could develop in several lineages of ostracodes, successively in the archaeocopes (Text-fig. 17A), the leperditicopes and the myodocopes (Text-fig. 18) from the early Palaeozoic through to the Recent (e.g. *Gigantocypris*).

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