THE OSTRACOD *PARAPARCHITES MINAX* IVANOV, SP. NOV. FROM THE PERMIAN OF THE U.S.S.R., AND ITS MUSCLE-SCAR FIELD

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ABSTRACT. The ostracod *Paraparchites minax* sp. nov., from the early Permian of the Pre-Donetz Depression of the Rostov area of the Soviet Union, is described and figured. Particular attention is paid to the muscle scars, to mandibular and frontal scars and especially to the adductor muscle scars, which are in the form of a cluster of up to 190 spots. An outline of the ontogenetic development of the scars is given. The systematic position of the Paraparchitacea is discussed in the light of outline, inner lamella, dimorphism, and central muscle-scar pattern, with the conclusion that the superfamily is related neither to the Platycopa, nor the Kloedenellidae, and in consequence, a new suborder of the Podocopida, the Paraparchitocopa, is proposed.

IN the early Permian strata of the Donetz, amongst the commonest ostracods are members of the Paraparchitacea, a preliminary account of which has been given by Ivanov (1964). Particularly well-preserved specimens, including large numbers of the form *Paraparchites minax* sp. nov., were recovered from a depth of 474–475 m in Asselian stage beds in drillings in the Rostov region (Tatzin district, Skosyr area). Such was the preservation that some thirty specimens showed details of adductor, mandibular, and frontal scars, improving our hitherto scanty knowledge of the muscle-scar patterns of Palaeozoic ostracods. Thus, the main purpose of this paper is to describe and analyse these structures and to discuss the systematic position of the Paraparchitacea. In most earlier works the central muscle-scar field has been studied from internal moulds, or from the inner surface of valves. In the specimens described here the details have been obtained by treating translucent or semi-transparent carapaces with castor oil or sugar solutions and photographing the specimens in reflected light.

All specimens referred to in the text under No. 146 have been deposited in the Ukrainian Scientific Research Institute for natural gas (UkrNIIGas), Kharkov.

SYSTEMATIC DESCRIPTION

Order PODOCOPIDA Müller, 1894
Suborder PARAPARCHITOCOPA Gramm, n. suborder

Diagnosis. Dorsal margin straight, ventral margin generally convex. Surface smooth, one or two postero-dorsal spines may be present. Calcified inner lamella narrow. Adductor muscle scar in the form of a cluster, which may contain a large number of spots. Mandibular scar elongate; frontal scar complex. Dimorphism of non-kloedenellid type. One superfamily—Paraparchitacea Scott, 1959. Range: Devonian to Permian.

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Superfamily PARAPARCHITACEA Scott, 1959
Family PARAPARCHITIDAE Scott, 1959
Genus PARAPARCHITES Ulrich and Bassler, 1906
Paraparchites minax Ivanov, sp. nov.

Plate 64, figs. 1–9

1964 *Paraparchites humerosus* Ulrich and Bassler, 1906, morpha *magna* Ivanov, 1964, p. 110, pl. 2, fig. 1*a–c*.

Derivation of name. 'Minax' = prominent (Latin).

Holotype. Complete carapace, 146/1.

Paratypes. Thirteen complete carapaces (146/2, 3, 4, 5, 146/9–3, 146/10–1, 146/10–2, 146/11–1, 146/11–2, 146/11–4, 146/12–3, 146/13, and one right valve, 146/6). All types are from Borehole 2323, from the Asselian Stage, at 474/475 m, Tatzin district, Skosyr area, Rostov.

Material. Eighty carapaces, and over 100 valves.

Diagnosis. Carapace large, up to 2800 μm, elongate and sub-oval; left valve slightly overlaps right valve along the entire free margin, with reversal of overlap along the hinge margin.

In lateral view, anterior and posterior margins evenly rounded, although the former is more fully curved; dorsal margin short, straight, and somewhat inclined posteriorly; cardinal angles weakly developed; ventral margin convex, merging smoothly with anterior and posterior margins. Shell surface smooth, with a few scattered pits corresponding to normal pore canals. Parallel to the free margin, and close to it, thin elevated ridges sometimes observed. No internal features other than the central muscle-scar field are known, these consisting of the adductor field located centrally within the valve and made up of up to 190 spots, an elongate mandibular scar, and a frontal scar.

Dimensions. Details of type specimens given in Table 1.

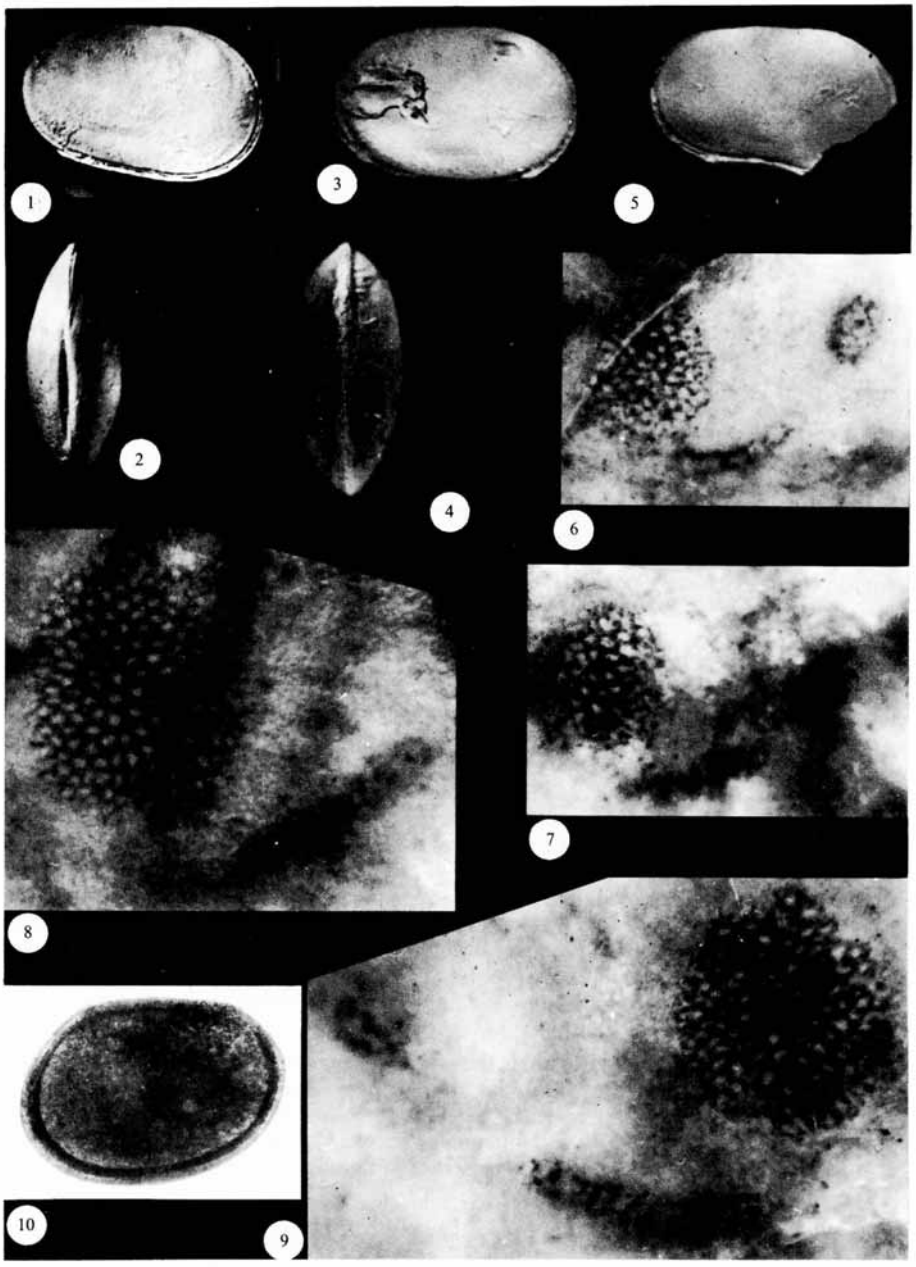
Ontogeny. The smallest specimens, 725 μm long, possibly Instar III, differ little morphologically from the holotype (an adult carapace). Changes during growth follow a pattern of regular increase in all basic dimensions relating to shape. There is size increase in the adductor scar field, as well as an increase in number and size of

EXPLANATION OF PLATE 64

Figs. 1–5. *Paraparchites minax* Invanov, sp. nov. 1, 2, carapace, holotype, no. 146/1. 1, right view; 2, dorsal view. 3, 4, carapace, no. 146/3; 3, right view. 4, dorsal view. 5, carapace, no. 146/4, right view. Rostov region, Skosyr area; Lower Permian. All × 15.

Figs. 6–9. Central muscle-scar field of *Paraparchites minax* Ivanov. 6, 7, larval stages. 6, right side of carapace, VI? instar, L = 1400 μm, no. 146/10–1; adductor muscle spots, mandibular spot, and frontal spot are seen. 7, right side of carapace, VI? instar, L = 1500 μm, no. 146/9–3; adductor muscle spots, mandibular spot, and frontal spot are seen. 8, 9, adults. 8, right side of carapace, L = 2525 μm, holotype, no. 146/1; adductor muscle spots and mandibular spot are seen. 9, left side of carapace, L = 2550 μm, no. 146/4; adductor muscle spots, mandibular spot, and frontal spot are seen. Photographs were taken from the outer side in reflected light. L—length of carapace. Rostov region, Skosyr area; Lower Permian. All × 150.

Fig. 10. *Paraparchites* sp., right valve, no. 1116/76–1, internal view in transmitted light; the inner lamella is seen. Leningrad region; Lower Carboniferous. × 30.



GRAMM and IVANOV, *Paraparchites*

the spots. There is limited variation in the adult stage, rare specimens showing greater inflation, or concave ventral margins. Other than the inflation mentioned above, no clearly dimorphic features have been observed.

Remarks. The new species differs from *Paraparchites scotoburdigalensis* (Hibbert) from the British Carboniferous in its greater dimensions, and length:height ratio. Some of our specimens are morphologically close to those figured as *P. humerosus* Ulrich and Bassler by Scott (1959), but these are of much smaller dimensions (length 2000 μm).

Ecology. The early Permian paraparchitaceans from the Donetz area appear to have lived in conditions of varied salinity, leading Ivanov (1964) to conclude that they were euryhaline. A similar conclusion was reached by Robinson (1969) and Sohn (1971) who both thought that, although essentially a marine genus, *Paraparchites* may have tolerated brackish and hypersaline conditions at times. In the Donetz region *P. minax* sp. nov. occurs in grey and dark-grey argillaceous limestones, accompanied by an abundance of darwinulaceans and carbonitids (*Darwinula* sp. and *Carbonita* sp.). Other fauna includes micro-gastropods and bivalves, calcareous worm tubes, stick bryozoan fragments, fish scales, and denticles. Particularly the abundance of darwinulids, and the paucity of marine invertebrates, suggest abnormal salinity conditions, verging upon fresh water.

THE MORPHOLOGY OF THE CENTRAL MUSCLE-SCAR FIELD OF *PARAPARCHITES MINAX*

Adductor scar field. On the surface of adult carapaces, 2450–2800 μm long, the adductor scar field is sometimes evident as a shallow, circular depression located in the centre of the valve. In the adult, the adductor scar field is a circular to elliptical cluster of small spots, the long axis of the cluster aligned dorso-ventrally. The cluster can be 270 μm in length and 300 μm in height. The number of spots within the cluster varies from 128 to 190, and may differ in the two valves of a single carapace. As can be seen from Table 1, there is no close correlation between spot number and size of carapace, indeed, in the right valve of one of the largest specimens examined (2800 μm length), one of the lowest spot counts, 128, was recorded. The shape of the spots varies from circular or oval to angular, the packing being usually close-set. Any kind of consistent pattern of spots within the scar is difficult to detect. While details of the ontogenetic development of the scar is scanty, the present material suggests a general increase both in size and number of spots with growth. Thus, in specimens *c.* 1100 μm long, spot counts range from 25 to 35; for specimens *c.* 1400 μm long, the count is 40–60; for carapaces greater than 1500 μm, the count is 46-plus.

Mandibular scar. Antero-ventral to the adductor-scar field, there lies an elongate scar which is best interpreted as a mandibular scar. Sometimes visible on the outer surface of the valves, the scar may be horizontal but sometimes slightly bowed. Although the scar might suggest the coalescence of spots, there is no evidence to support this idea. There is a gradual increase in size through ontogeny.

Frontal scar. Dorsal to the adductor-scar field, there is an oval frontal scar, 75–90 μm high in carapaces 1400–1500 μm long, increasing to 100 μm in adults.

TABLE 1. Dimensions of *Paraparchites minax* sp. nov. and details of the central muscle-scar field.

Collection no.		Length (μm)	Adductor muscle scar: Number of spots	Adductor muscle scar: Length (μm)	Adductor muscle scar: Height (μm)	Mandibular scar: Length (μm)	Frontal scar: Height (μm)
146/12–3	C left view	1100	16				
146/11–1	C right view	1200	25				60
146/11–2	C right view	1400	35–40				
146/10–1	C right view	1400	60	125	140	175	75
	C left view			125	140	170	90
146/9–2	C left view	1500	46				
146/9–3	C right view	1500	40	125	150	200	80
	C left view		40	140	160	200	
146/10–2	C right view	1650		170	170	210	50?
	C left view			150	160	200	
146/10–3	C right view	2050		200			
146/7	C right view	2250		250	250	250	
146/6	RV	2450	151	225	240	325	
146/1	C right view	2525	190	250	290	250	
	C left view		184	250	300		
146/4	C right view	2550	132	225	250	250	100
	C left view		138	225	250	250	
146/3	C right view	2650	131	250	250	300	
	C left view			270	300	325	
146/5	C right view	2800	128	225	250	350	
	C left view			250	250	335	

The central muscle field of *Paraparchites minax* can be homologized with this structure in bairdids, cyprids, and cytherids, the scar representing the points of attachment of muscle and chitin elements of the soft-part anatomy. Its mandibular scar was presumably the attachment point of the chitinous rods springing from the dorsal apex of the basal podomere of the mandible protopodite (Triebel 1960). The presence of two mandibular scars reported by Ivanov (1964) and Robinson (1969), and to be seen in Sohn's plates (1971), may prompt the idea that these have become fused to form the single scar of *P. minax*. As Smith (1971) has demonstrated that the dorsal anterior scar in Recent cytherids and cyprids has no direct relationship to the antennae, the term frontal scar is employed for the scars here described. The relative disposition of the scars described by Ivanov (1964), Robinson (1969), and Sohn (1971), together with the present evidence from *P. minax*, removes any doubt as to the orientation of *Paraparchites*. Orientation in fact, is as described by Scott (1959).

The Paraparchitacean central muscle-scar field. Data as to the central muscle-scar field of *Paraparchites* is limited, and usually refers to a smooth muscle scar in the centre of the valve (Tschigova 1960), or a central muscle scar with faint marks (Kummerow 1953). The first detailed description appears to be that of Ivanov (1964, p. 110, pl. 2, fig. 4) for *P. humerosus* morpha *oblima*. Later, in 1967, Bless described and illustrated fifty discrete spots as the muscle pattern for *P. cantelii* Bless, 1967, from the Upper Carboniferous of Spain. Robinson (1969) noted that the central muscle-scar field of *Paraparchites* is essentially the same as that for *Bernix*, a large

patch area covered with clusters of small pits, with one or two linear scars obliquely below. Such scars were figured for *Paraparchites* sp. from Tournaisian, and for *Paraparchites* cf. *inornatus* (M'Coy) from the Viséan (Robinson 1969, pl. 3, figs. 3 and 4).

The fullest documentation of paraparchitid muscle-scar patterns is to be found in the monographs of Sohn (1971, 1972), in which he specifically mentions the presence of a 'cyprid adductor muscle scar pattern in some of the genera' (Sohn 1971, A1, Abstract). According to Sohn's schematic illustration, the most complete cypridid pattern is that of *Shishaella marathonensis* (Hamilton, 1942) in which there are some six elongate obliquely arranged adductor scars, and two closely adjoined mandibular scars (Sohn 1971, A5, fig. 2). At the same time the scar pattern in the genus *Chamishaella* Sohn, 1971 is described as follows, 'The subcentral adductor scar consists of a circle of small individual scars' (Sohn 1971, A11).

Available data indicate three types of paraparchitid adductor muscle-scar patterns:

1. The pattern of *P. minax*, characterized by a circular cluster of many spots (up to 190). Close to this type are the patterns of *P.* sp. and *P.* cf. *inornatus* from the Lower Carboniferous (Robinson 1969) and of *Chamishaella* (Sohn 1971). *P. cantelii* Bless, 1967 also has this type of adductor muscle scar, as does *Bernix*; and Robinson (1969) has argued persuasively that *Bernix* belongs to the Family Paraparchitidae. The presence of one or two mandibular scars is also typical, but a frontal scar is, at present, known in *P. minax* only.
2. The pattern of *P. humerosus* morpha *oblima*, consisting of a circular group of a few scars (up to ten?) associated with two mandibular scars (Ivanov 1964).
3. The pattern of *Shishaella marathonensis*, with six large scars associated with two elongate mandibular scars. This pattern was regarded as being of cyprid type by Sohn (1971).

It is difficult to envisage three such strongly dissimilar adductor muscle-scar patterns forming a morphological series within the paraparchitid group. At the moment, the available data, especially for the second and third adductor muscle-scar types, are very limited and any final assessment of the taxonomic significance of the second and third types mentioned above must await further information.

(Latest observations on some well-preserved Viséan paraparchitids from Novgorod region revealed that in some old individuals on the adductor muscle-scar area an intense calcification took place, due to which the structure acquired a form of a coarse, uneven elevation. May this be the cause of scars which give the impression of a cyprid-like adductor muscle-scar pattern?)

THE SYSTEMATIC POSITION OF THE PARAPARCHITACEA

In the past, three general views have been widely held:

1. Assigning the genus *Paraparchites* to the Family Kloedenellidae Ulrich and Bassler, 1923, which in turn would place it within the Order Palaeocopa (Henningsmoen 1953; Mertens 1958), or alternatively within the Platycopa, Podocopida (Pokorný 1958).
2. That of the 1961 *Treatise of Invertebrate Paleontology*, placing the Superfamily Paraparchitacea Scott, 1959, within the Suborder Kloedenellocopina Scott, 1961, which in turn belongs to the Order Palaeocopida (Scott, 1961).
3. Amalgamating the Paraparchitacea with the Kloedenellacea and the Cytherellacea within a Suborder Platycopina (opinion of Schallreuter 1968).

Other views to record are those expressed in *Osnovy*, placing *Paraparchites* within

the Family Aparchitidae Jones, 1910 (Orlov 1960) and more recently, Sohn's definition of the Paraparchitacea as Podocopida *incertae subordinis* (Sohn 1971). In all these opinions, there appear to have been judgements based upon the following criteria. First, the presence of a form of kloedenellid dimorphism. Second, carapace outline. Third, the presence of what is judged a calcified inner lamella. Fourth, the type of central muscle-scar pattern.

Taking these in turn, a presumed kloedenellid dimorphism in *Paraparchites* has been taken as evidence of affinity to the Kloedenellidae (Pokorný 1958 and Schallreuter 1968). On the other hand, evidence of dimorphism was regarded as inconclusive by Scott (1961, p. Q86), and of limited value by Gründel (1967, p. 323). Because their possible dimorphic features are so weak, Knüpfer has rejected any relationship of Paraparchitacea to the Platycopina, preferring to regard them as a discrete branch of the Podocopida, equal in status with the Platycopina and Metacopina (Knüpfer 1968). A kloedenellid-type dimorphism in paraparchitids has been completely rejected by some, including Tschigova (1967). The same author has noted a ventral inflation in possible female carapaces (Tschigova 1960; Buschmina 1968), a view repeated by Robinson for *Paraparchites* and *Bernix* (1969) and by Sohn (1971, p. A5). In *P. minax* some forms are 'inflated' with obtuse extremities, whereas others are 'thin or uninflated' with acute extremities, but no traces of kloedenellid dimorphism have been revealed. All this leads to the conclusion that any sexual dimorphism in paraparchitids would seem to be of non-kloedenellid type, and no basis for allocation of the group within either the Kloedenellidae, or the Platycopa.

Carapace outlines do not provide a reliable basis for placing the paraparchitids within the Kloedenellacea or the Platycopa, groups which normally possess a rectilinear or slightly concave ventral margin in contrast to the strongly convex venter of Paraparchites. In *P. minax* the ventral margin is convex with the exception of a few rare specimens with obvious concave ventral margins.

Published information concerning the calcified inner lamella is scanty, and even contradictory. Scott notes that a duplicature is generally absent in the Kloedenellicopina, but present in the Geisinidae (Scott 1961, p. Q90; Sohn *in* Scott 1961, p. Q182). Such observations have been extended more recently by Pollard (1966) and Knüpfer (1968) to include the genera *Glyptopleura* Girty, 1910, *Electia* Tschigova, 1960, *Hypotetragona* Morey, 1935, *Knoxites* Egorov, 1950, *Mennerella* Egorov, 1950, ?*Marginia* Polenova, 1952, and others. Data are scarce for the Paraparchitecea. Scott has written of a 'vestibule' in *P. humerosus* Ulrich and Bassler, 1959. Once again Sohn (1971) is our main source of information, recording a narrow inner lamella in the genera *Shivaella* Sohn, *Shamishaella* Sohn, *Shishaella* Sohn, and *Shemonaella* Sohn. Working with the complete carapaces of *P. minax*, it has been impossible to confirm such structures, but in well-preserved single valves of *Paraparchites* from the Lower Carboniferous of the Leningrad region, a clearly visible inner lamella has been found (Pl. 64, fig. 10). Thus it can be said that the possession of a calcified inner lamella is a characteristic of paraparchitaceans as well as of some kloedenellaceans, separating both from Platycopa *sensu stricto*, the latter possessing only rudimentary traces at best (Van Morkhoven 1962).

Our total knowledge of the central muscle-scar field of *P. minax* confirms the opinion of Sohn that, 'the lateral outline, hingement, calcified inner lamella and

adductor muscle scar pattern negates this assignment' (of the Paraparchitacea to the Platycopina: Sohn 1971, p. A5). For the Platycopa, the pattern and its evolution could be said to be well established, changing from the multiserial scar of the Cavellinidae (six rows of from 7 to 10 spots, totalling between 40 and 56 spots, Triebel 1941 and Scott 1944), to the biserial scar of the Cytherellidae (Gramm 1972). In contrast, relatively little is known of the adductor muscle scar of the Kloedenellidae. *Nyhamnella* from the Lower Silurian, has an oval group of spots (23) somewhat drawn out in a dorsal direction (Adamczak 1966, fig. 1). The Lower Carboniferous genera *Geisina* and *Kloedenellitina* have biserially arranged adductor scars with up to 11 spots (Knüpfer 1968, also Pollard 1966). With so little evidence, it is impossible to discuss any morphological evolution of the kloedenellid scar, except to observe that the scar type differs considerably from that of the Platycopa, that of the paraparchitids described by Sohn (1971), and that described herein for *P. minax*. Table 2 summarizes our knowledge of muscle-scar patterns for Ostracoda,

TABLE 2. Central muscle-field elements of various ostracod groups.

+ known, − unknown.

From data published by the following authors: Sars 1922–1928; Triebel 1941, 1960; Scott 1944, 1951; Schweyer 1949; Swartz 1949; Schneider 1956; Kashevarova 1958; Abushik 1960; authors in *Osnovy Paleontologii*, 1960; authors in *Treatise on Invertebrate Paleontology*, Pt. Q, 1961; Morkhoven 1962, 1963; Sandberg 1964; Darby 1965; Smith 1965, 1971; Gramm 1970; Gramm *et al.* 1972; Gramm and Posner 1972; Hartmann 1966; Adamczak 1966, 1968; Benson 1967; McKenzie 1967; Knüpfer 1968; Maddocks 1969; Gründel 1970; Bolz 1971; Malz 1971; Ishizaki 1973; Shornikov and Gramm 1974.

	Central muscle field		
	Adductor muscle scar	Mandibular scar	Frontal scar
Leperditiida	+	−	−
Palaeocopida–Beyrichicopa:			
Scrobicula (possibly Podocopida)	+	−	?
Placidea	+	−	−
Sulcicuneus, Svislinella, Kielciella	+	−	−
Puncia, Manawa	+	−	−
Kloedenellacea:			
Nyhamnella	+	−	−
Geisina	+	−	−
Kloedenellitina	+	−	−
Myodocopida:			
Myodocopa	+	−	−
Cladocopa	+	−	−
Podocopida–Platycopa:			
Cavellinidae	+	−	−
Cytherellidae	+	−	−
Metacopa:			
Healdiidae	+	+	+
Podocopa:			
Darwinulacea	+	+	−
Bairdiacea	+	+	+
Cypridacea	+	+	+
Cytheracea	+	+	+
—			
Sigilliidae	+	−	+

requiring it to be said that data relating to several important Palaeozoic groups are very limited.

CONCLUSIONS

On the basis of the absence of kloedenellid dimorphism, aspects of outline, the nature of the central muscle-scar field and its pattern, it is apparent that the Paraparchitacea cannot be united with either the Kloedenellacea or the Platycopa. The presence of a calcified inner lamella moves the superfamily still further from a relationship to the Platycopa, while the development of the same structure in some kloedenellids may be regarded as instances of evolution in parallel. On the possible criteria for a more refined taxonomic judgement upon the Paraparchitacea, that which appeals most is consideration of the central muscle-scar field. Such structures are, we believe, important, because the scars are intimately associated with the soft-body anatomy of the Ostracod, and in fossil carapaces provide as Smith said, 'one of the common meeting grounds between the palaeontologic and zoologic systems of classification' (Smith 1965, p. 1). Of course, it is necessary to take other criteria into consideration, but many internal structures in Palaeozoic ostracods are very poorly known and ideas and opinions are frequently based on insufficient evidence. As a result, the importance attached to certain features for taxonomic purposes varies, and the same features may have varying significance in different groups' ability to recognize homologous structures of independent origin, which is crucial for phylogenetic systematics. As our discussion has shown, the central muscle-scar field of the Paraparchitacea can best be compared with that of the Podocopa—a view strengthened by the record of the elongate mandibular scar. Thus in taxonomy, serious attention should be given to the close relationship with the Podocopida postulated by Sohn (1971). As, however, aspects of shape and outline, the absence of radial pore canals coupled with the rudimentary nature of the duplicature, and special features of the scar pattern, do not allow the assignment of the Paraparchitacea to any of the recognized Suborders of the Podocopida, we feel that it is necessary and appropriate to propose a new Suborder Paraparchitocopa to accommodate this group.

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