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Parvancorina — an arthropod from the Late Precambrian (Ediacarian) of South Australia

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(With 1 textfigure and 3 plates)

Abstract

After consideration of the preservation of the remains of the flexible integuments of some 60 specimens of *Parvancorina minchami* GLAESSNER, 1958, from Ediacara, available details of their morphology are reviewed and interpreted in terms of growth, feeding and locomotion. Insufficient detail of their limbs is preserved to define unequivocally the systematic position and phylogenetic significance of *Parvancorina*. Resemblances with other fossils support assignment to the Arthropoda. The genus is believed to be related to Marrellomorpha which appear to be phylogenetically close to ancestral Trilobitomorpha. These are considered to have diversified into divergent lines of descent leading to Crustacea and Chelicerata, but *Parvancorina* is unlikely to have direct descendants among the living arthropods.

Zusammenfassung

Etwa 60 Exemplare von *Parvancorina minchami* GLAESSNER, 1958, von der Fundstelle Ediacara wurden untersucht. Die Fossilisation ihrer oft deformierten und ursprünglich biegsamen Körperhülle wird beschrieben und Wachstum, Nahrungsaufnahme und Bewegung werden dargestellt. Der Bau der Gliedmaßen ist nicht in Einzelheiten erkennbar, so daß die systematische und phylogenetische Einordnung der Gattung nicht präzisiert werden kann. Auf Grund der beobachteten Merkmale von *Parvancorina* und Ähnlichkeiten mit anderen Fossilien ist der Schluß berechtigt , daß sie zu den Arthropoden gehört. *Parvancorina* zeigt Verwandtschaftsbeziehungen zu Marrellomorpha und steht primitiven Trilobitomorpha nahe, aus denen nach heutigen Ansichten die Crustacea und Chelicerata hervorgegangen sind. Sie ist jedoch nicht als Ahnenform von rezenten Arthropoden anzusehen.

1. Material and preservation

The re-examination of the enigmatic fossil *Parvancorina* from the Ediacara fauna is based on about 60 specimens. They were collected at the original locality by my colleagues and students and myself and their study was carried out, with long interruptions, in the course of the past 20 years. Further specimens from correlated strata in the Flinders Ranges are not included in the present detailed study. The material represents various stages of growth, from about 2 mm to about 30 mm in length (GLAESSNER 1979, Fig. 18, p. A106). The

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shield-like fossils are preserved on the lower surfaces of layers of sandstone or quartzite which are separated by thin clay or silt layers. The convex elements of their sculpture are invariably directed upward. Distortions of the outlines occurring in many specimens are caused not by tectonic movements but by pushes in various directions from moving water or sediment. This and particularly the folding-over of some specimens indicates that the integument was soft and pliable, probably like thin leather. The matrix consists mostly of sand grains with diameters of about 0.1 to 0.5 mm, so that preservation of fine detail cannot be expected. However, fine, thread-like structures about 0.5 mm wide are not infrequently seen, apparently imprinted in the surface shield. Unfortunately, the pronounced convex ridges on the surface of the carapace were so stiff that they prevented the preservation of imprints of the underlying proximal parts of the appendages. No organic matter is preserved in the matrix of the Ediacara fossils. They are generally seen as external moulds. It is essential to study together with the natural moulds also latex casts of these fossils and the following descriptions are based on such casts (positive).

The preservation of essentially soft-bodied fossils in the coarse sediments of the Pound Quartzite at Ediacara can be explained as follows. The bodies settled during short periods of quiet sedimentation on smooth or gently wavy surfaces of sediment in muddy pools between sand ridges. The recurrence of the dominant higher-energy regime moved sand waves over the clay pans. Their sediments were subsequently reduced by compaction to thin partings between thicker lenses of sand. The sand was of the right size and composition to act like a form sand in metal casting technology. It produced on its lower bedding surfaces replicas of the upper surfaces of the clay pans, with their mechanical current lineations, locomotion traces, sessile organisms, impressions left by bodies which had decayed, and resistant bodies resting on the clay or silt surface, such as clay pellets or organisms. *Tribrachidium*, *Spriggina*, *Parvancorina* and others are invariably found as impressions on the lower surfaces of sandstone slabs. During the deposition of the fossiliferous strata at Ediacara the movement of the sand waves was gentle enough not to obliterate the fossils or their traces, yet fast enough to cover and replicate them before they were destroyed by decay or removed by stronger water currents. There were no macrophagous predators or animals feeding on dead bodies, but bacterial action must have affected their organic matter. Decay products were apparently totally removed after their migration from the compacting clay and silt lenses by water flushing the porous sand deposits.

2. Morphology

The shield-shaped area is described as a carapace. It apparently incorporates the tergites of all body somites rather than being a backward extension of the head as in the Crustacea. It is unsegmented but appendages emerge in regular series from its median zone, indicating metameric composition

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of its underlying body. DALLE CAVE & SIMONETTA (1975) proposed the alternative view that *Parvancorina* represents not a carapace but a compressed three-dimensional body. The presence of appendages under it supports the original assumption. The smooth, anchor-shaped marking on the shield is a convex surface configuration which resists compression, not an infilled gut with caeca. It could have covered these internal organs. It is very rarely eliminated by compaction but tends to retain its essential shape even where the margins of the shield are distorted. Where the anterior or posterior portion of the shield is folded over (no sagittally folded specimens are known), the inside of the shield is visible rather than the underside of the animal. In one instance (Pl. 3, Fig. 14) it includes a U-shaped section of the median ridge where it was torn from the lateral ridges. The peripheral margins are strengthened by a faint raised rim and the areas between the ridges are thin, contrary to what would be expected if they were the integument of the body. The broadly convex margin of the shield is considered as anterior; the posterior end is pointed and lacks a telson or appendages. The raised anchor-shaped mark consists of one median and two anterolateral ridges which are joined without external separation. Several specimens show 4—5 narrow elevated structures, separated by grooves, in the areas between the anterolateral ridges and the median ridge. One or two of them tend to bisect the angle formed by the ridges and others are more or less parallel to it. In most specimens in which they are preserved, they are gently convex toward the median ridge but in one or two they trend in different directions. They are provisionally named anterolateral appendages. Suggestions that they might represent the maxillary glands which are visible through the carapace in living and fossil Crustacea Notostraca have been considered but found unacceptable because there are no loops between them. They may be comparable with the larger, anterior appendages of *Marrella*, *Mimetaster* and *Vachonisia* (see below). Behind them are 15—20 thread-like posterior appendages arising from the edge of the median ridge. They trend obliquely or transversely toward the posterolateral margin or are slightly sinuous, and they overlap each other in some specimens and some places. The appendages are 0.3—0.6 mm wide. They have not been seen to cross the peripheral margin of the shield. The anterolateral and posterior appendages may cross over each other in one or two specimens but this is uncertain. Altogether, about 12 specimens with appendages were found, 5 with both kinds and 3—4 each with either one or the other kind. The probably largest number counted was 5 anterolateral and 15—20 posterior appendages. These are generally weaker and become very faint posteriorly. They exhibit no segmentation and their curvature, where observed, is sinuous. In a few specimens (particularly P 12901/1, Pl. 1, Fig. 2, 3, Pl. 3, Fig. 15) the bases of the anterolateral appendages appear as projections on the posterior margins of the ridges, separated by indentations, and posterior appendages show a similar relation to the edges of the median ridge in one or two specimens. This appearance is interpreted as the result of compression which causes the resistant ap-

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pendages to raise the edges of the normally overlying ridges while the spaces between them are indented. In the numerous small specimens the appendages would be so small that they could not be moulded in the coarse matrix but the flanks of a considerable number of large, well preserved carapaces are also perfectly smooth. It is probable that in these individuals the appendages decayed before fossilisation, or alternatively they may be moults. Where preserved, the appendages vary in position relative to each other as well as to the outlines of undisturbed carpaces. There is no doubt about their motility. Although the relatively coarse matrix does not permit observation of their fine structure or segmentation, they are considered as organs of locomotion (and/or respiration). An alternative interpretation would consider them as intestinal coeca but lack of branching and positional and configurational evidence for their motility tends to oppose this interpretation. Concerning the anterolateral appendages, their relation to the ridge margins and their general similarity to the posterior appendages point in the same direction for both kinds.

There are no traces of any other organs, either within or outside the carapaces. There are no antennae but it is probable that they would have been too thin to be preserved. There are no traces of sessile or stalked eyes and there is no caudal furca and no tail spine. The posterior spine figured by H. and G. TERMIER (1968a, p. 188, fig. 387b, see Pl. 2, Fig. 8) is an accidental groove behind one particular specimen. Such grooves occur commonly on bedding planes. A few specimens show evidence of shifting after deposition, resulting in partially double impressions. There are also bedding plane lineations within the areas of the fossil specimens and accidental longitudinal or transverse wrinkling of anterior ridges. The median ridge is never segmented.

An attempt was made to examine biometrically the effect of growth of *Parvancorina* on the length/width ratio of the carapace. This proved inconclusive because of postmortal distortion of the outline which can vary from almost circular to transversely or longitudinally elliptical (Pl. 3, Fig. 13). It may also show irregular indentations. Although no reliable numerical data can be presented, several observers agree that small (young) specimens (including the holotype) tend to have a greater length/width ratio than larger specimens, indicating allometric growth. There are also indications of at least three moulting stages in the grouping of these ratios but this remains to be confirmed by more measurements of undistorted specimens.

The available morphological data can be tentatively interpreted in functional terms. The organism was probably able to feed on small detritus particles when the mud of the sea floor was stirred up by its locomotory movements. It was capable of nectobenthic locomotion by swimming or crawling with its stronger anterolateral and weaker posterior appendages. The latter probably moved like the limbs of branchiopod crustaceans but the body to which they were attached was fused with the carapace. An additional function for the anterolateral limbs is suggested by their different position relative to the axis of the body and the proximity of their bases to the assumed position

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of the mouth below the junction of the median and anterolateral ridges. These limbs may have had small gnathobasic processes acting as jaws for the grasping of food particles. The locomotive appendages would have filled the space under the carapace between the anterolateral and median ridges, with the internal organs confined mainly to the space under the ridges, with possible extensions in the narrow spaces under the flanks.

3. Systematic position

When *Parvancorina* was first described, the affinities of this fossil were stated to be "entirely unknown" (Glaessner 1958, p. 187) and this remained unchanged when possible traces of appendages were first observed (Glaessner 1959, p. 380). A resemblance to Notostraca (Crustacea Branchiopoda) was noted later (Glaessner 1962, p. 484) but the genus remained unassigned to any phylum (Glaessner & Wade, 1966). H. and G. Termier (1966, 1968a, b) considered that *Parvancorina* "semble un Arthropode incontestable. Il suggère étonnamment une jeune larve de Trilobite (Protaspis), mais d'une taille gigantesque" (1968b, p. 75, 1966, p. 1684, also 1968a, 1976). On this and very few other questionable examples they built their "Nymphoid" hypothesis. It maintains that mature animals in the form of gigantic larvae, known today only as early ontogenetic stages, precede the explosive evolution of the first coelomates. No further factual evidence in favour of this generalisation is available. It advances our understanding no more than the oversimplified and much criticised version of Haeckel's biogenetic law which considered existing larval stages as representatives of adult organisms of the past. *Parvancorina* is not a gigantic crustacean nauplius nor a trilobite protaspis as it lacks many distinctive characters of these larval stages, nor is it an overgrown larva of a chelicerate though it has vague resemblances with early ontogenetic stages of these arthropods. Without entering into far-reaching speculations it can be added that the broadly oval and almost flat dorsal shield of the metanauplius of the branchiopod crustacean *Lynceus* (Linder 1946) resembles the carapace of *Parvancorina,* while the cruciform head of this larva resembles the spiny head of *Marrella.* A thin, flat, rounded shield together with indications of a small number of somites is present also in *Onega* Fedonkin (in Keller & Fedonkin 1976). It was found in the Vendian of Northern Russia and was placed in the family Vendomiidae Keller, of uncertain position within the Arthropoda. Appendages are unknown, unless the asymmetrically displayed metameric structures along a sagittal groove are interpreted as limb gnathobases. At present, possible resemblances in the body morphology to Trilobitomorpha and Chelicerata cannot be properly evaluated. This applies also to *Parvancorina* which shares with the Chelicerata the fusion of the carapace with the thoracic somites.

Delle Cave & Simonetta (1975, p. 77—79) indicated that the Middle Cambrian (Burgess Shale) *Skania fragilis* Walcott, 1911 is "comparable only

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to *Parvancorina minchami* Glaessner, 1958". Their Italian summary uses the words "appare essere sostanzialmente affine" with reference to this comparison. Unfortunately, only hypotheses which "appear far fetched" resulted from it, due to poor preservation of all known specimens of *Skania*. In the absence of detailed knowledge of the limb structure, the systematic position of such fossils as *Parvancorina* or *Skania* must remain questionable. The fact that the small appendages of *Parvancorina* cannot have their segments (podomeres) preserved in a coarse, sandy matrix becomes obvious when the limbs of fossils from the Burgess Shale are compared with what is visible in specimens from the Pound Quartzite. The assigment of *Parvancorina* to the Arthropoda rests not only on the presence of a carapace but also on certain similarities with *Marrella* Walcott, *Mimetaster* Gürich, and *Vachonisia* Lehmann. The latter two genera are of Lower Devonian age. The resemblance of the anterolateral ridges of *Parvancorina* to the lateral cephalic spines of *Marrella splendens* Walcott, 1912, has been noted. The resemblance of the carapace of *Parvancorina* to that of *Vachonisia* and of the differentiation of the limbs into four or five anterior (oblique) and numerous (20—80) undifferentiated posterior (transverse) appendages in the two genera is remarkable (Text fig. 1). In both

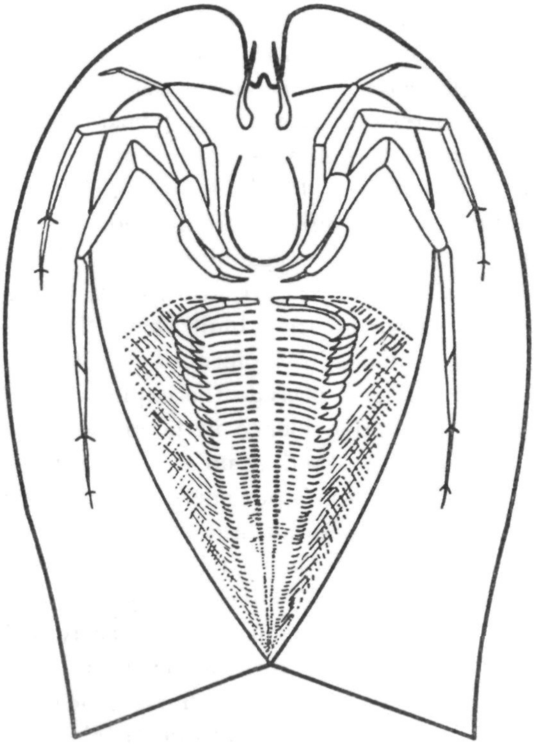

Fig. 1. *Vachonisia rogeri* (Lehmann). Tentative reconstruction in ventral view. About × 2. (Reproduced from Stürmer & Bergström, Paläont. Z., **50**: 92, Fig. 10, 1976, by permission)

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the carapace is fused with the body somites. The ventral "marginal flat shelf" surrounding the heart-shaped central area in which the posterior "appendages are sheltered" (STÜRMER & BERGSTRÖM 1977, p. 92) is not a distinctive character of *Limulus* or other Merostomata but occurs convergently also in Malacostraca (Crustacea Decapoda) such as the Eryonidae and Scyllaridae. The appendages in the three Palaeozoic genera of the Marrellomorpha are biramous and unlike those of the Branchiopoda Notostraca. Exites resembling those of *Vachonisia* could not be preserved in the matrix of *Parvancorina* in which the appendages are known only incompletely and approximately. Their presence is in general agreement with what is known of the structure of the Marrellomorpha. The presence of different kinds of major spines in *Marrella* and *Mimetaster* and of a shield-like carapace in *Vachonisia* indicates a closer relation of *Parvancorina* (and possibly *Skania*) with the latter genus but their joint placement in family-group or higher taxa would be premature. The Order Acercostraca (LEHMANN 1955) is formally available for *Vachonisia* but after STÜRMER & BERGSTRÖM's (1977) revision, little of its diagnosis (TASCH 1969) remained valid. The assignment of the family Parvancorinidae GLAESSNER (1979, p. A105) to the Crustacea Branchiopoda had to be corrected in proof when this revision appeared after completion of the Treatise manuscript in 1976.

The question of the phylogenetic relations of *Parvancorina* should be considered in a wider framework of a discussion on the early diversification of the Arthropoda. In the context of the present revision of this genus it is, however, relevant to refer to the widely held view that the Marrellomorpha represent a branch of very primitive Arthropoda and that they had affinities with Trilobitomorpha, Crustacea, and possibly also the ancestors of the Chelicerata. Phylogenetic trees (CISNE 1974; HESSLER & NEWMAN 1975) summarise modern views on principal lines of arthropod evolution. A precise place for *Parvancorina* has yet to be found but available data tend to place the two Late Precambrian arthropod families, the Vendomiidae (see KELLER & FEDONKIN 1976, GLAESSNER 1979) and the probably marrellomorph Parvancorinidae near the point of branching of the ancestral Trilobitomorpha into Crustacea and Chelicerata though not among the direct ancestry of either.

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Explanation of Plates

Plates 1—3. *Parvancorina minchami* GLAESSNER, Late Precambrian, Pound Quartzite, Ediacara, South Australia.

Plate 1

Fig. 1. External mould showing some anterolateral and (on left) some posterior appendages. (P 14190, × 5).

Fig. 2. Latex cast showing appendages (P 12901/1, × 2).

Fig. 3. Same, with visible structures outlined.

Plate 2

Fig. 4. External mould, showing appendages (F 17027, × 5).

Figs. 5—12. Adult specimens. 5: External mould (P 14190), 6—12: Latex casts (F 17027, P 14248, P 12887, P 14243, P 14244, 531, P 12091/2. Photos by Dr. M. WADE. × 1).

Plate 3

Figs. 13—14. Latex casts of deformed specimens (493, P 14251; × 2.8).

Figs. 15—16. External moulds of specimens with traces of appendages. (P 12901/1, × 3; 542, × 3.8).

(Note: Specimens with numbers prefixed F in the collections of the South Australian Museum; others in the collection of the Department of Geology, University of Adelaide).

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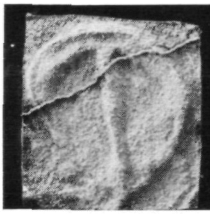

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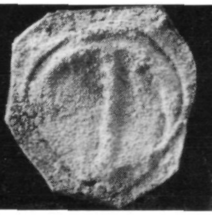

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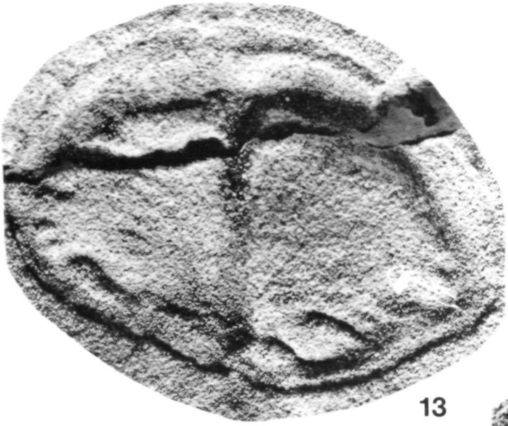

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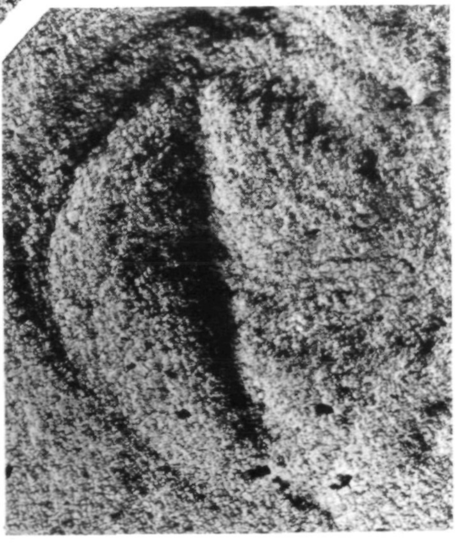

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