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FIRST RECORD OF A PARANACYSTID MITRATE FROM THE BOKKEVELD GROUP OF SOUTH AFRICA

by

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ABSTRACT

The Upper Eifelian paranacystid mitrate *Paranacystis simoneae* sp. nov. from the Waboomberg Formation (Bokkeveld Group, Western Cape Province, South Africa) is described, and a revised diagnosis of the Family Paranacystidae is presented. *Paranacystis simoneae* differs from *Paranacystis petrii*, the type species of the genus, in possessing a remarkably well-developed right subcentral plate; the latter extends distally with respect to the distal margins of the left and right intermediate lateral marginal plates, and bears a robust, distal triangular process. Other features of *Paranacystis simoneae* are: the presence of knobs on the proximal three-quarters of the lateral margins of the two proximal lateral marginal plates; the presence of two latero-distal pits, probably associated with the main orifice of the body; and a well-developed styloid process. *Paranacystis simoneae* extends both the geographical and the stratigraphical range of the genus, and strengthens the links between Malvinokaffric fossil faunas from the central and western parts of Gondwana in the Devonian.

KEYWORDS: *Paranacystis*, Waboomberg Formation, Middle Devonian, Bokkeveld Group, South Africa.

INTRODUCTION

The paranacystids are a small group of poorly known mitrates originally recorded from the Lower Devonian of South America (Caster 1954; Haude 1995). The Suborder Paranacystida, which includes the single Family Paranacystidae, was erected by Caster (1954) to accommodate *Paranacystis petrii* from the Ponta Grossa Formation in the State of Paraná, Brazil (Figure 1A-B). Caster's assignment of *Paranacystis* to a distinct suborder of the Mitrata (Jaekel 1918) was mainly based on the fact that this genus lacks several morphological characters found in representatives of other mitrate suborders, such as Lagynocystida, Mitrocystitida and Anomalocystitida (Caster 1952; Ubaghs 1968; see Jefferies 1973, 1986, Derstler 1979, Kolata & Guensburg 1979, Kolata, Frest & Mapes 1991 and Parsley 1991 for revised classifications of the mitrates). According to Caster (1954), the paranacystids may be derived from Ordovician mitrocystitid taxa, as these two groups share the presence of similar 'soft' anatomical structures pertaining to the body. However, most of the 'soft' characters considered by Caster (1954) to be typical of both the mitrocystitids and the paranacystids are in fact generalized features, as shown by the natural internal moulds of other mitrate taxa (Ubaghs 1968; Jefferies 1973, 1986; Jefferies & Lewis 1978; Kolata & Jollie 1982; Parsley 1991; Ruta & Theron 1997).

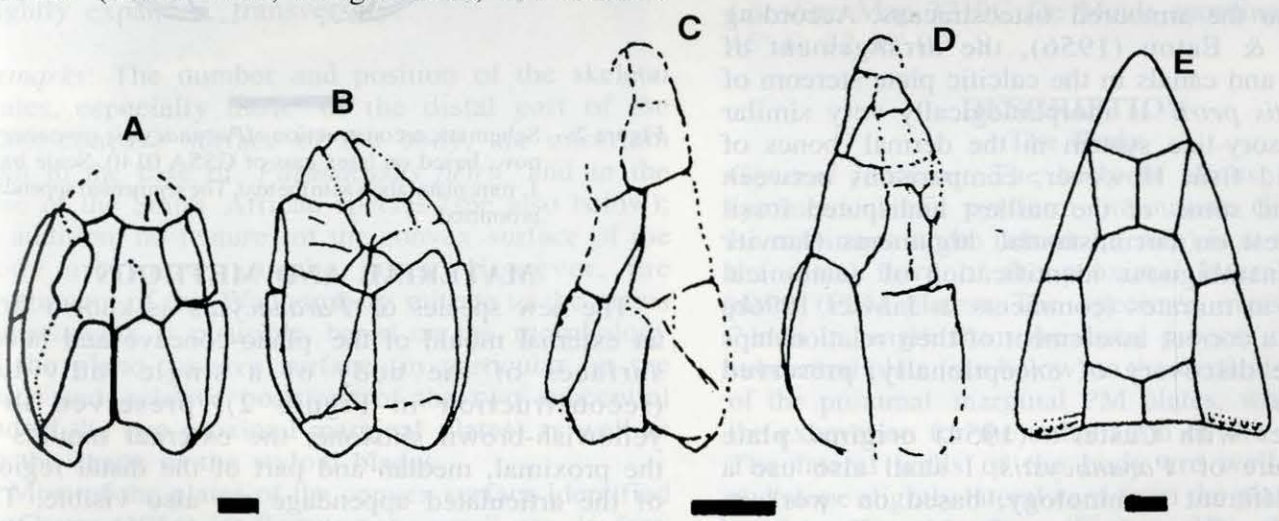

Figure 1: A, B, *Paranacystis* petrii (modified from Caster 1954); C, D, *Yachalicystis triangularis* (modified from Haude 1995); E, *Dalejocystis casteri* (modified from Prokop 1963). Scale bar = 1 mm. In all figures, the segmented appendage is omitted.

Ubaghs (1968) retained *Paranacystis* in the monotypic Family Paranacystidae, but placed the latter in the Suborder Mitrocystitida. As originally defined (Caster 1952), the Mitrocystitida is a paraphyletic assemblage (Jefferies 1986, 1991; Craske & Jefferies 1989; Cripps 1990; Beisswenger 1994; Ruta 1997; Ruta & Theron 1997); as such, it cannot be characterized on the basis of synapomorphies (but see Ubaghs 1968, 1979, 1994 and Parsley 1991, 1994).

Yachalicystis triangularis from the Lower Devonian Talacasto Formation of Argentina (Figure 1C-D), assigned by Haude (1995) to the Paranacystidae on the basis of the plating pattern of the convex surface of the body, is known from poorly preserved material, and a correct assessment of its relationships with *Paranacystis* and other mitrate genera is still premature.

A third and stratigraphically younger mitrate, *Dalejocystis casteri* from the Middle Devonian Daleje Shales in the Barrandian basin of Bohemia (Figure 1E), was regarded as a representative of the Lagynocystida by Prokop (1963), and as a mitrate of uncertain affinities by Ubaghs (1968). The general shape and plate arrangement of *Dalejocystis* in the reconstruction provided by Prokop (1963) are similar to those of *Yachalicystis*, and suggest that these two genera may be related to one another. As in the case of *Yachalicystis*, the resolution of the affinities of *Dalejocystis* awaits the discovery of additional, better preserved material.

The controversial nature of mitrates, variously regarded as echinoderms (Ubaghs 1968) or as chordates (Jefferies 1986) is still extensively debated (e. g. Peterson 1995; Jefferies 1997), and the reader is referred to the literature for a detailed account of the subject (see in particular Gee's (1996) recent synthesis). After Gregory (1935), Caster & Eaton (1956) were the first authors to address in some detail the question of the possible chordate affinities of mitrates (Jefferies & Lewis 1978; Jefferies 1986) by comparing them directly with extinct craniates, in particular the armoured osteostracans. According to Caster & Eaton (1956), the arrangement of trabeculae and canals in the calcitic plate stereom of *Paranacystis petrii* is morphologically very similar to the sensory-line system in the dermal bones of cephalaspid fish. However, comparisons between mitrates and some of the earliest undisputed fossil craniates rest on circumstantial arguments (Janvier 1996a). Unambiguous identification of anatomical characters in mitrates (comments in Janvier 1996b) as well as a correct assessment of their relationships awaits the discovery of exceptionally preserved specimens.

Together with Caster's (1954) original plate nomenclature of *Paranacystis*, I shall also use a slightly different terminology, based on work in progress by the author on the identification of homologous skeletal elements in various mitrate groups (see also Ruta & Theron 1997).

In January 1993, Dr J. N. Theron of the Geological Survey at Bellville (near Cape Town, South Africa), Dr R. P. S. Jefferies of the Palaeontology Department of the Natural History Museum (London, UK) and Mr J. J. Savill of Airton, Skipton (North Yorkshire, UK) collected several mitrate specimens from different localities in the Bokkeveld beds (Western Cape Province, South Africa). The fossil material includes at least three species. Two of these, the anomalocystitids *Placocystella africana* (Reed 1925) from the Gydo and Voorstehoek Formation (see also Rennie 1936) and *Bokkeveldia oosthuizeni* Ruta & Theron, 1997 from the Gydo Formation, were discussed elsewhere (Ruta & Theron 1997). The third mitrate, herein identified as a new species of *Paranacystis*, was collected from the Waboomberg Shale, and represents the first record of this genus from South Africa.

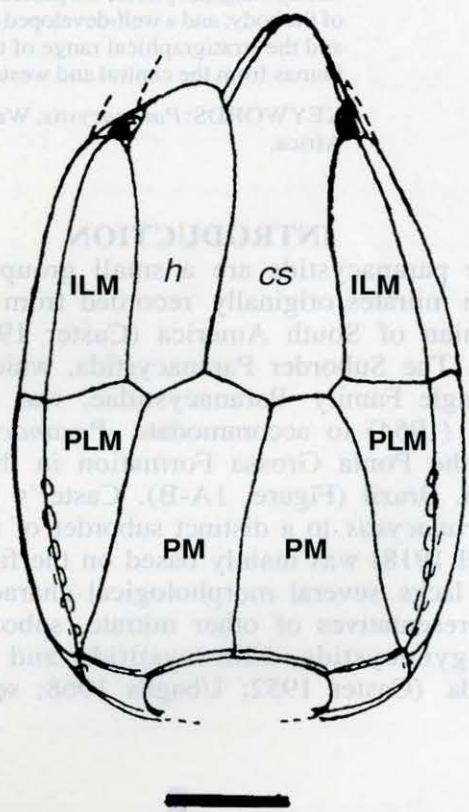

Figure 2: Schematic reconstruction of *Paranacystis simoneae* sp. nov., based on latex cast of GSSA 0140. Scale bar = 1 mm; plate labels as in the text. The segmented appendage is omitted.

MATERIAL AND METHODS

The new species of *Paranacystis* is known from an external mould of the plano-concave and lateral surfaces of the body of a single individual (reconstruction in Figure 2), preserved in a yellowish-brown siltstone; the external moulds of the proximal, median and part of the distal regions of the articulated appendage are also visible. The specimen was cleaned in ethanolamine thioglycollate and serially cast using latex. Serial casting removed

small lumps and thin layers of iron oxide (see Caster 1983). The latex casts were coated with ammonium chloride to accentuate relief before being photographed. Various features of the external anatomy of the body and the appendage were drawn with the aid of a camera lucida.

SYSTEMATIC PALAEONTOLOGY

Superphylum Deuterostomia
Phylum *incertae sedis*
Class Stylophora
Order Mitrata
Suborder *incertae sedis*
Family Paranacystidae

Diagnosis: Presence of two proximo-distally elongate, subcentral plates of different size on the plano-concave surface of the body; right subcentral plate separated from the left marginal plates of the plano-concave surface by the interposition of the left subcentral plate; proximal marginal plates of the plano-concave surface asymmetrical, the left plate being slightly larger than the right plate and with a comparatively longer, chevron-shaped distal margin; suture between the proximal marginal plates bending slightly rightward; downward projections of the lateral marginal plates well-developed and forming two almost vertical lateral walls; insertion for the articulation of the segmented appendage framed by the downward projections of the proximal marginal plates of the plano-concave surface; presence of two large, shield-like proximal plates occupying more than half of the length of the convex surface of the body, showing gently convex lateral margins, and sutured with a small subquadrangular plate inserted between their distal margins; distal part of the convex surface consisting of two polygonal elements with concave lateral and distal margins and slightly protruding latero-distal angles; styloid with flared, non-recumbent blades and a large, stout articulation process; proximal ossicles much more robust than the remaining ossicles and slightly expanded transversely.

Remarks: The number and position of the skeletal plates, especially those of the distal part of the plano-concave surface of the body, are uncertain both in the case of *Paranacystis petrii* and in the case of the South African species (see also below); in addition, no features of the convex surface of the body are known in the latter. However, the assignment of the Waboomberg mitrate to the genus *Paranacystis* is plausible, based on the morphology of the plano-concave surface (in particular on the shape and relative positions of the two subcentral and of the two proximal marginal plates) as well as on the shape of the styloid blades.

Most of the plates of the convex surface identified by Caster (1954) in *Paranacystis petrii* are, in fact, fragments of two subpentagonal plates lying distal to the central, subquadrangular plate. The plating pattern of the convex surface of *Paranacystis petrii* recalls in part that of *Peltocystis cornuta* Thoral, 1935 (see also Ubaghs 1969), in which two large, shield-like elements comprise the proximal half of this surface (see also description below).

Genus *Paranacystis*

Diagnosis: As for the family.

Type species: *Paranacystis petrii*; Lower Devonian, Ponta Grossa Formation; Paraná, Brazil.

Paranacystis simoneae sp. nov.

Diagnosis: A species of *Paranacystis* characterized by the remarkable length of the right subcentral plate, the distal third of which is a robust triangular process extending distally with respect to the intermediate lateral marginal plates.

Etymology: The species is named after Miss Simone Wells, Enquiries Co-ordinator at the Palaeontology Department of the Natural History Museum, London, for her unceasing support and enthusiasm.

Holotype: GSSA 0140. Almost complete external mould of the plano-concave and lateral surfaces of the body, only slightly disrupted distally; complete external mould of the proximal, median, and of the terminal part of the distal region of the articulated appendage. The specimen is in the palaeontological collections of the Geological Survey of South Africa at Bellville.

Geological horizon and age: Waboomberg Formation, Bidouw Subgroup, Bokkeveld Group; presumably Upper Eifelian in age (Hiller & Theron 1988).

Locality: Map 3219C De Meul; coordinates: 19 21' 45" E; 32 59' 00" S.

DESCRIPTION

The Body

General features: The body is almost bilaterally symmetrical and pyriform in outline (Figure 3A). Its maximum width (about 4.1 mm) is at the level of the distal third of the proximal lateral marginal plates (PLM plates). The specimen measures about 7 mm in length from the distal process of the right subcentral plate (see below) to the vertical projections of the proximal marginal PM plates, which delimit the excavation for the articulation of the appendage. The lateral walls of the body are well-developed and slope slightly lateralward from the plano-concave to the convex surface (Figure 3B). The lateral margins of the plano-concave surface are gently

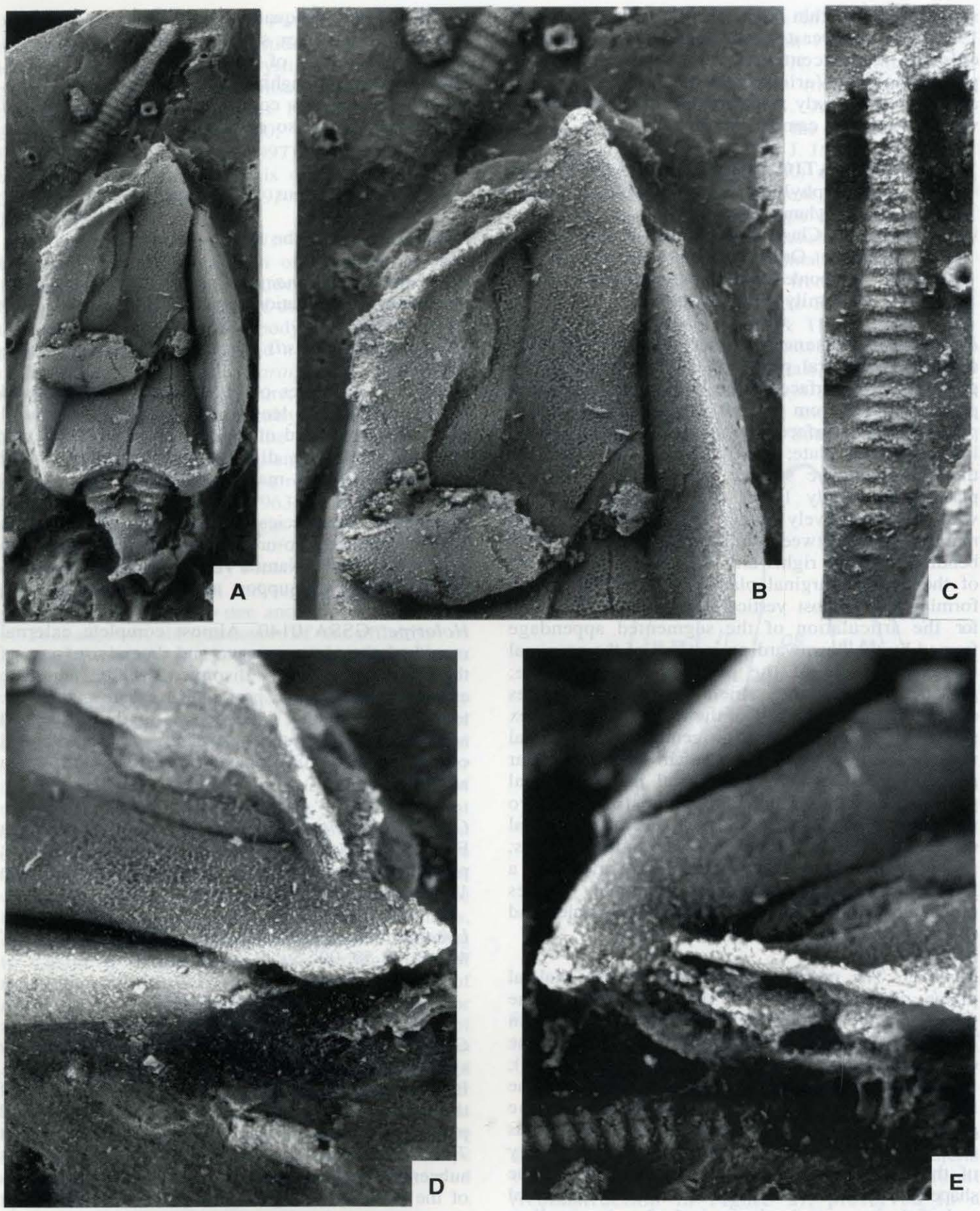

Figure 3: *Paranacystis simoneae* sp. nov.; holotype GSSA 0140; Waboomberg Formation, Bidouw Subgroup, Bokkeveld Group; Western Cape Province, South Africa. A, general external aspect of the plano-concave surface of the body; x 10; B, close-up of the distal two-thirds of the plano-concave surface; x 20; C, terminal segments of the distal region of the appendage; x 25; D, close-up of the right lateral pit, framed by the proximal part of the lateral margin of the triangular process on plate *cs* and by the distal margin of the right plate ILM; x 25; E, close-up of the left lateral pit, framed by plate *h* and by the distal margin of the left plate ILM; x 25.

rounded in cross-section (Figure 3D). From these, the subhorizontal projections of the lateral marginal plates extend slightly downward and medially. The specimen is only partly disrupted; therefore, the shallower aspect of the central part of the plano-concave surface is likely to represent a genuine feature and not an artifact of preservation. Only the central part of the right proximal marginal plate and the right, proximal angle of the right subcentral plate show signs of breakage. The skeletal plates can be divided into marginal and subcentral elements.

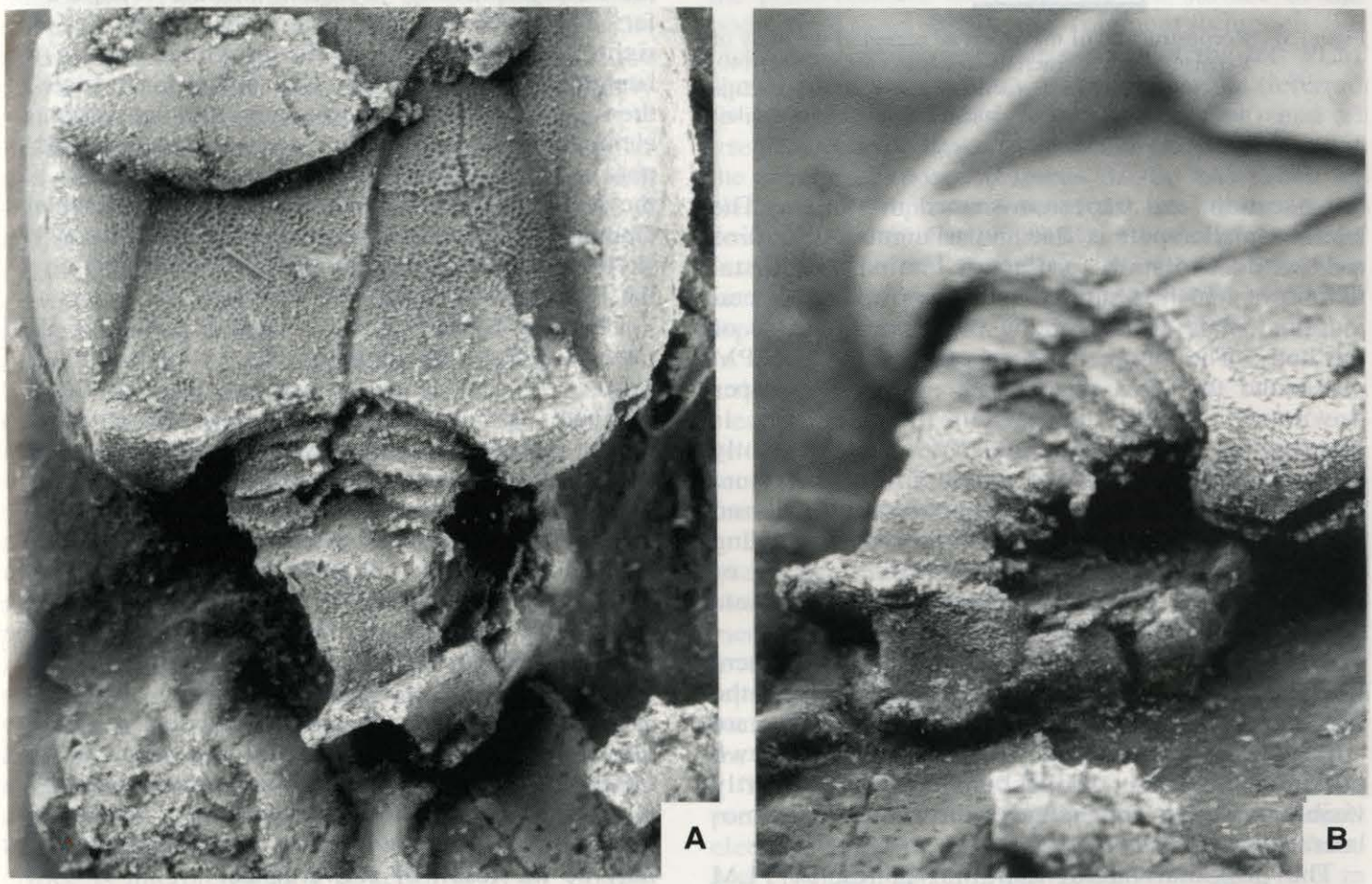

Figure 4: *Paranacystis simoneae* sp. nov.; holotype GSSA 0140; Waboomberg Formation, Bidouw Subgroup, Bokkeveld Group; Western Cape Province, South Africa. A, close-up of the proximal third of the plano-concave surface and of the proximal and intermediate regions of the appendage; x 20; B, details of the right proximo-lateral angle of the body, excavation for the insertion of the appendage, tetramerous rings and styloid; x 25.

The proximal marginal plates, or PM plates (basal medians, or plates *bm* of Caster 1952, 1954) (Figure 2), are markedly asymmetrical and the suture between them bends slightly rightward (Figure 4A). Most of the distal third of the left PM is covered by a skeletal fragment, presumably belonging to the same individual, but of difficult interpretation (see below) (Figures 3A-B, 4A). The distal margin of the right PM is distally convex and much shorter than the proximal margin. The distal margin of the left PM, visible immediately distal to the skeletal fragment mentioned above, is chevron-shaped and forms a triple junction with the two subcentral plates. The right arm of the chevron is slightly longer than the left arm (Figure 4A). The lateral margins of both the left and the right PM are sinuous, the distal two-thirds of them being slightly convex laterally. The different shape and size of the two PM plates in both *Paranacystis petrii* and *Paranacystis simoneae* recalls the similar morphological condition found in several Ordovician mitrates, especially lagynocystids and some of the least derived mitrocystitids (Ubaghs 1961, 1968, 1969; Jefferies 1973, 1986; Ruta 1997); at present, it is impossible to ascertain whether this feature is also a primitive condition for the paranacystids.

The two PM plates contribute to most of the insertion of the articulated appendage by sending vertically projected extensions, the median margins of which show a broad excavation (Figures 3A, 4A-B). These extensions are shaped like two subquadrangular walls and are partly visible when the plano-concave surface of the specimen is oriented towards the observer (reconstruction in Figure 5). The external surface of each of the two subquadrangular walls is divided into two parts of unequal size by a low keel, bearing three or four small, poorly defined knobs. The medial, larger part of each of the two walls is gently convex externally both in a vertical and in a horizontal

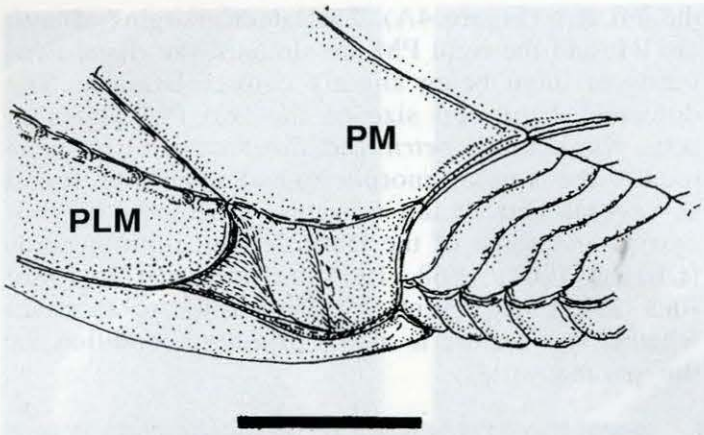

Figure 5: Reconstruction of the proximal region of the body of Paranacystis simoneae, based on latex cast of SAM 0140, showing the excavation for the insertion of the appendage and the suture between plates PLM and PM of the left side. Scale bar = 1 mm.

cross-section, and trapezium-shaped in outline. The lateral, smaller part is flat and triangular in outline and sends a distally projected lamina, the distal margin of which is sutured with the proximal lateral marginal plate (PLM) of the corresponding side of the body. The suture between each of the two PM plates and the PLM plate of the same side slopes downward and distally when the specimen is observed in lateral view, and runs along a gently curved line (Figure 5). The upper third of the suture is strongly convex in a proximal direction, and might have acted as a hinge in life, perhaps providing this part of the skeleton with some degree of flexibility (see also Beisswenger 1994 and Ruta 1997).

That the proximo-lateral angles of the body were flexible to some extent in life is also shown by the fact that the lower margins of the two PM plates are articulated with the trough-like margins of the two proximal elements of the convex surface, partly visible near the appendage insertion in proximo-lateral view (Figure 4B).

The proximal lateral marginal plates, or PLM plates (posterior lateral marginals, or plates *plm* of Caster 1952, 1954) (Figure 2), occupy the proximal half of the left and right sides of the body. Morphologically, they consist of a subhorizontal, approximately triangular projection and an almost vertical projection. Six or seven small, subelliptical knobs are visible along the proximal three-quarters of the lateral margins of the two PLM plates (Figure 2). The knobs of the left side are more clearly distinguishable than those of the right side, which appear as an irregular fringe, probably as a result of preservation. The presence of knobs is obvious when the original specimen is observed. The parts of the external mould corresponding to the lateral margins of the PLM plates show small, proximo-distally elongate, shallow pits. Caster (1954) did not report proximo-lateral knobs in *Paranacystis petrii*, but this may be due to preservation. The presence of knobs in *Paranacystis simoneae* is interesting, in that a sculpture confined to the proximal part of the lateral margins of the plano-concave surface is observed in some of the earliest known mitrates (e.g. *Chinianocarpos thorali*, *Mitrocystites mitra* and *Peltocystis cornuta*), although in these forms such sculpture consists mainly of denticulations or short ridges (Thoral 1935; Ubaghs 1961, 1968, 1969; Jefferies 1986). Well-developed, serrated lateral flanges are present in *Jaekelocarpus oklahomensis* from the Upper Carboniferous of Oklahoma (Kolata, Frest & Mapes 1991), which is the stratigraphically youngest mitrate recorded so far. The subhorizontal projections of the left and right PLM contribute to the proximal half of the lateral walls of the body. The medio-distal angle of the two plates forms a short suture with the subcentral element of the same side. Most of the left PLM is not visible in GSSA 0140, since it is covered, like the left ILM (see below), by an elongate skeletal element of uncertain interpretation as well as by the skeletal fragment mentioned in the description of the PM plates (Figures 3A-B, 4A).

The intermediate lateral marginal plates, or ILM plates (median lateral marginals, or plates mlm of Caster 1952, 1954) possess narrow, proximo-distally elongate subhorizontal projections whose sinuous medial margins are sutured with the subcentral plates (Figure 2). The vertical projections of the left and right ILM form the distal half of the lateral walls.

The two subcentral plates occupy half of the length of the body (Figure 2). At present, it is difficult to homologize these plates with the subcentral elements of the plano-concave surface in the mitrocystitid and anomalocystitid mitrates. The arrangement and relative positions of the two subcentral plates of *Paranacystis* with respect to the lateral marginal elements is similar to that observed in most allanicytidiid anomalocystitids (Caster & Gill 1968; Philip 1981; Caster 1983; Haude 1995; Ruta & Theron 1997), although this may be the result of convergence.

The left subcentral plate (plate *h*, or *hypocentral* of Caster 1952, 1954) shows a gently sinuous medial margin in contact with the right subcentral plate (Figure 3A-B). Its lateral half is partly covered by the distal portion of the elongate skeletal element mentioned previously. Its lateral margin was presumably in contact with the left ILM in life. Its distal margin is not well-preserved, but seems to have been approximately semicircular. As far as the preserved parts of plate *h* reveal, this element reaches its maximum width near its distal third, and becomes progressively narrower in a proximal direction; its minimum width corresponds to that part of the plate which is inserted between the left PLM and the left PM.

The right subcentral plate (plate *cs*, *hypocentral epibasal* or *central somatic* of Caster 1952, 1954) (Figure 2) is larger than *h* both proximally and

distally; its central third is approximately as wide as the distal third of *h*. Plate *cs* is likely to correspond to the largest subcentral element of both the mitrocystitids and the anomalocystitids, since in all mitrates the position of this element with respect to the surrounding plates is rather conservative (Ubaghs 1968; Jefferies 1986; Craske & Jefferies 1989; Parsley 1991; Ruta 1997; Ruta & Theron 1997). Proximally, *cs* is sutured with: the medial arm of the chevron-shaped, distal margin of the left PM (see above); the right PM along a short, proximally concave suture; and the medio-distal angle of the right PLM. The lateral margin of *cs*, sutured with the right ILM, is the almost exact mirror image of its medial margin. The proximal two-thirds of both the lateral and the medial margins of *cs* diverge slightly externally in a distal-proximal direction.

The proximal third of *cs* forms a robust, triangular process (Figure 3A-B, D-E) extending distally with respect to the distal parts of the left and right ILM and of *h*. The process possesses flat lateral sides and a blunt, rounded distal tip, and thickens in a distal-proximal direction. A small, proximo-distally elongate pit is visible near the distal end of the suture between *cs* and the right ILM (Figure 3D). The pit is delimited by a notch present on the underside of the right proximal angle of the triangular process of *cs* and by a thin subhorizontal wall projecting from the distalmost edge of the right ILM; three or four small knobs are observed along the free margin of this wall. It is impossible to say whether the pit was delimited in life by *cs* and the right ILM only, since no details of the convex surface of the specimen are visible. It is also impossible to ascertain whether the pit was merely a shallow excavation on the surface of the skeleton or whether it represented the external opening of a duct. Its position, close to the transversely elongate, main orifice of the body (only partly visible along the distal margin of the latter), suggests that it may have communicated in part with the orifice (the orifice is interpreted as a posterior anus by Ubaghs (1968) and as an anterior mouth by Jefferies (1986)). Distally, the pit sends a narrow groove running for a short distance along the right lateral margin of the triangular process of *cs* and disappearing medially. A second pit is visible near the distalmost part of the left margin of *h* and the distalmost edge of the left ILM (Figure 3E). Its spatial relationships with respect to the surrounding body plates are more difficult to reconstruct than those of the right pit. The left pit seems to be roofed over by the plano-concave surface of the body and is surrounded by the partially exposed, distal edge of a plate of the convex surface, although the identification of the latter is problematic.

Some features of the plano-concave surface of GSSA 0140 deserve further comments. The number and arrangement of plates in *Paranacystis* is, at present, still unclear. In some of the diagrammatic sketches of *Paranacystis petrii* given by Caster (1954), the distal part of the body shows a poorly defined arrangement of plates. Whether these represent genuine elements of the skeleton or simply broken fragments is difficult to ascertain. Caster (1954) expressed uncertainty as to the number and shape of the distal elements in *Paranacystis petrii*. However, in his diagnosis of the species he highlighted the presence of a distal 'ostial cover'. Such a structure, as reconstructed by Caster (1954), would have consisted of two leaf-like, partly imbricated plates. It is not clear whether these plates belong to the plano-concave or to the convex surface of the body. In GSSA 0140, the fragment lying on the distal third of the external surface of the left PLM shows a slightly convex proximal margin (referred to its orientation with respect to the animal) and an irregular, partly broken distal margin, with part of the stereom exposed (Figures 3A-B, 4A). Such an element may represent one of the two distal 'ostial cover' plates of Caster (1954). However, the distal margins of the two ILM plates do not seem to show an articulation surface; rather, their blunt, rounded aspect suggests that they were probably free margins in life. Alternatively, the fragment may have articulated with the distal process of plate *cs*, but no clear indication of the modalities of articulation can be detected. It is likewise difficult to interpret a second skeletal fragment which occupies most of the distal, lateral part of the plano-concave surface in GSSA 0140 (Figure 3A-B, D-E). The fragment in question is smooth-surfaced, proximo-distally elongate and with an irregular, presumably broken median margin and a slightly upturned (with respect to the observer) lateral margin. This fragment may represent part of the internal mould of the convex surface, or a displaced element of the distal part of the body.

The surface of the slab in which GSSA 0140 is preserved reveals the presence of scattered, small elements lying in proximity to the specimen. These are elongate and subtriangular to tongue-like in shape, measure about 1-1.5 mm in length, and show traces of stereomic structure in the form of minute pits. Despite their small size, it is possible to recognize a rounded margin at one end and a straight to irregularly sinuous margin at the opposite end. I suggest tentatively that these scattered elements are orifice-framing plates. These plates have been observed in several mitrates, where they appear as a row of spike-shaped, wedge-like or spatulate elements (Ubaghs 1968, 1979; Jefferies 1973, 1986; Jefferies & Lewis 1978; Kolata & Guensburg 1979; Kolata & Jollie 1982; Craske & Jefferies 1989; Beisswenger 1994; Ruta 1997). No orifice plates were recorded by Caster (1954) in the type material of *Paranacystis petrii*, but this may be the result of a preservational accident. Orifice plates are present in recently discovered specimens of a new, *Paranacystis*-like mitrate from Australia which will

be described by the author elsewhere (Dr Peter Jell, pers. comm. 1996). This Australian form is also noteworthy in that it shows a complete set of plates framing the distal part of the plano-concave surface, and may provide clues to the arrangement of the skeletal body plates in *Paranacystis*.

Stereom: The stereomic fabric on the external surface of the body plates varies. The lateral walls as well as the lateral parts of the vertical projections of the two PM plates show a compact stereom (Figures 3A-B, D, 4A). The external surface of the median parts of the vertical projections of the two PM plates is likewise compact. A sudden change in the stereomic fabric is observed at the level of the lateral margins of the plano-concave surface. These show an irregular arrangement of small pits (0.02-0.04 mm indiameter). Slightly larger (about 0.06 mm in diameter) subcircular pits are found on the subhorizontal projections of the lateral marginal plates, on the distal two-thirds of the two PM plates and on the subcentral plates. The proximal third of the subhorizontal projections of the two PM plates shows slightly elongate pits separated by narrow, sinuous trabeculae; the greater axis of these pits is oriented mainly proximo-distally. Near the proximal margins of the two PM plates, the stereom shows a more compact aspect. Along the sutures between adjacent plates on the plano-concave surface, as well as on the distal third of plate *cs*, the stereom consists of minute, subcircular pores.

Caster & Eaton (1956) discussed at length the plate microstructure in *Paranacystis petrii*. Their detailed morphological analysis of the stereomic system of trabeculae and canals led them to postulate that the stereom might have originally functioned in respiration and would have eventually acquired sensory functions. I emphasize that such hypothesized changes in the function of the stereom presupposes a relationship between carpoids and extinct armoured fish in Caster & Eaton's (1956) argument. Leaving aside problems of functional interpretation, the plate microstructure in *Paranacystis petrii* is remarkable, as it constitutes one of the rare examples of three-dimensional preservation of stereom in mitrates. It is difficult to say whether the arrangement of trabeculae of *Paranacystis petrii*, described by Caster & Eaton (1956) as a 'labyrinth of curved, branched and interlacing white strands or rods', occurred also in *Paranacystis simoneae*. However, this is likely to have been the case, as the external plate surface in *Paranacystis simoneae* resembles the 'external pitted and tuberculate surface' reported by Caster & Eaton (1956) in *Paranacystis petrii*.

The Appendage

Proximal region: As in almost all mitrates (Ubaghs 1961, 1969; Jefferies 1973), the proximal region of the appendage consists of tetramerous rings, approximately circular in cross-section and decreasing in size proximo-distally (Figures 3A, 4A-B, 5). Four rings are visible just distal to the excavation for the insertion of the appendage, but one or possibly two other rings are present immediately proximal to the first ring, although these are only partly visible. The rings overlap each other to a small extent in a proximo-distal direction and the degree of overlap decreases rapidly in the same direction. The stereomic sculpture of the external surface of the rings consists of minute, irregular pits. The 'low-relief ornament of bosses or broad spines' reported by Caster (1954) in *Paranacystis petrii* has not been observed in *Paranacystis simoneae*. The 'broad spines' of *Paranacystis petrii* are likely to be displaced ring plates. In *Paranacystis simoneae*, the distal margins of the rings are convex and shaped like a fringe, although such irregular aspect may be accidental, resulting from deformation of the latex peel. The left and right plates showing the same orientation as the plano-concave surface of the body contact each other along a vertical, flat suture (partly visible as a result of disruption). The suture between each of these plates and the plate of the corresponding side in the same ring (i. e. the plate with the same orientation as the convex surface of the body) is gently curved in lateral view.

Intermediate region: A prominent styloid (reconstruction in Figure 6) is present in the intermediate region of the appendage, but I could not observe plates articulated with it, presumably as a result of preservation. The styloid can be divided morphologically into two parts: a proximal process and a distal bladed region (Figures 3A, 4A-B). The proximal process is unusually large in comparison

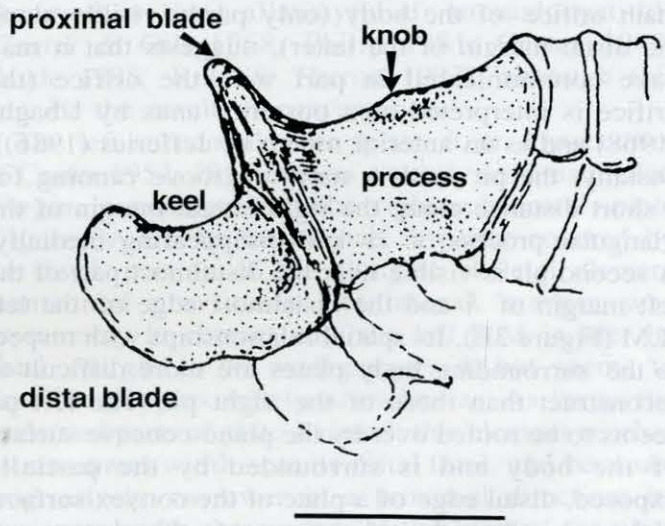

Figure 6: Reconstruction of the styloid of *Paranacystis simoneae*, based on latex cast of GSSA 0140, showing in right lateral view the stout articulation process with the median knob, the proximal and distal blades and the sharp keel between the two blades. Scale bar = 1 mm.

with that of other mitrates, a feature noted by Caster (1954) in *Paranacystis petrii*. In *Paranacystis simoneae*, the styloid process is approximately hemicylindrical. Its proximal end is roughly semicircular in outline and slightly wider than the rest of the process, and is surrounded by the most distal ring. It is difficult to ascertain whether the process was completely inserted into the lumen of the proximal region of the appendage or whether part of it was exposed in life. A median, proximo-distally elongate knob is visible half-way between the proximal end of the process and the bladed region. The part of the external surface of the process situated between the knob and its proximal end is slightly concave in lateral view. Distally, the knob merges into a sharp, median longitudinal keel which terminates against the proximal styloid blade. The external surface of the styloid process, like that of the rings of the proximal part of the appendage, shows minute, irregular pits.

The distal bladed region of the styloid is slightly shorter than the proximal process and saddle-like, and bears a median longitudinal keel. The keel extends from the lower third of the distal surface of the proximal blade to the proximal surface of the distal blade. The two styloid blades are flared and smooth-surfaced, but only the proximal blade can be reconstructed in some detail.

The proximal blade is slightly higher than wide, and bears a flattened proximal surface and gently concave distal surface. Its free margin does not seem to have been sharp. Two small, lateral notches are visible along this margin but these may not represent a genuine feature of the proximal blade.

The distal blade is poorly preserved, but the visible part of the proximal surface of the latter suggests that the blade was fan-shaped in life, although perhaps less expanded transversely than the proximal blade. The free lateral margins of both the proximal and the distal blade merge gradually into the lateral surfaces of the styloid.

Distal region: About 25 terminal segments of the distal region of the articulated appendage are visible in left lateral aspect just anterior to the body (Figure 3A, C). As in all mitrates, each segment consists of an ossicle and a pair of plates articulated with it. In the preserved part of the distal region of the appendage, the ossicles decrease uniformly in size in a proximo-distal direction. The most proximal ossicles are at least twice as high as long and possess a rectangular outline and a blunt apex. The most distal ossicles are as high as long and approximately hemicylindrical in shape. The preserved plates are slightly longer than high. The external surface of both the ossicles and the plates shows a compact stereom. The appendage seems to have ended in a small, rounded segment, but the latter is poorly preserved and not easily discernible.

DISCUSSION

The presence of *Paranacystis* in the Bokkeveld Group strengthens the similarities between fossil shelly faunas from various regions of the Southern Hemisphere in Siluro-Devonian times (Reed 1925; Rennie 1936; Caster 1954, 1983; Caster & Gill 1968; Boucot 1971; Derstler 1979; Philip 1981; Hiller & Theron 1988; Theron & Loock 1988; Haude 1995; Ruta & Theron 1997). It also extends the stratigraphical distribution of the genus, as the Waboomberg Formation is presumably Upper Eifelian in age (Hiller & Theron 1988) and younger than the Ponta Grossa Formation of Brazil (Caster & Petri 1947).

The Waboomberg Formation consists of a 200-m thick sequence of siltstone, quartz arenite and shale, with a progressive darkening of the latter near the top. Like other shaly sequences of the Bokkeveld Group, this formation represents the lower part of an upward-coarsening, wave-dominated deltaic complex (Hiller & Theron 1988; Theron & Loock 1988; Ruta & Theron 1997). According to Hiller & Theron (1988), the much smaller number of brachiopods in the Waboomberg Formation with respect to other shaly formations (especially the Gydo and Voorstehoek Formaiton) may result from a local increase in sedimentation rates despite the fundamentally similar environmental settings which characterize the lowermost deltaic sequences in the Bokkeveld Group.

Together with *Jaekelocarpus oklahomensis* (Upper Carboniferous of Oklahoma; Kolata, Frest & Mapes 1991) and *Dalejocystis casteri* (Middle Devonian of Bohemia; Prokop 1963), *Paranacystis simoneae* is one of the youngest mitrates known to date, although precise data on the age of the Waboomberg Formation are not available. It has long been recognized that the Bokkeveld fossil faunas are very similar to those of other basins of the Malvinokaffric Realm, for which an Early Emsian age has been proposed (e. g. the Paraná basin; Caster & Petri 1947). Recent studies encompassing the entire Devonian System in South Africa, namely the upper Table Mountain Group, the Bokkeveld Group and the lower two-thirds of the Witteberg Group, suggest an almost continuous sedimentation of the Bokkeveld beds from the Upper Emsian to the late Middle Givetian (Plumstead 1967; Boucot, Brunton & Theron 1983; Cooper 1982, 1986; Hiller & Theron 1988). A recent summary on the geological and stratigraphical settings of the Bokkeveld Group can be found in Ruta & Theron (1997).

As in the case of the anomalocystitid Family Allanicytidiidae (Caster & Gill 1968), current knowledge of the Paranacystidae shows that this family has a palaeogeographical distribution 'restricted' to the Southern Hemisphere. Although it would be premature to interpret such a distribution in terms of endemism (given the scanty fossil record

of mitrates), it is noteworthy that both the Allanicytidiidae and the Paranacystidae appear to show several derived skeletal features with respect to other mitrates.

The presence of a *Paranacystis*-like mitrate in Australia (Dr Peter Jell, pers. comm. 1996) corroborates the hypothesis that the origin and evolutionary history of the Paranacystidae may have been confined to Gondwana. Work in progress by the author on the interrelationships of the Anomalocystitida shows that the Allanicytidiidae (as defined by Haude, 1995) is the sister group of at least one boreal taxon, the genus *Enoploura* from North America. However, while the monophyletic status of the Allanicytidiidae is well-corroborated (Caster 1983; Haude 1995; Ruta & Theron 1997), the status and relationships of the Paranacystidae need assessing properly on the basis of a character analysis.

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