

A new genus of Protasteridae (Ophiuridea) from the Lower Devonian Bokkeveld Group of South Africa

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Received 17 October 2018. Accepted 20 December 2018

Gamiroaster tempestatis, a new genus and species of Palaeozoic ophiuroid, is described from four specimens identified in the Lower Devonian Voorstehoek Formation (Ceres Subgroup, Bokkeveld Group) of South Africa. This ophiuroid belongs to the family Protasteridae, a Middle–Late Ordovician taxon that continued into the late Palaeozoic. This new ophiuroid forms part of a much wider fauna of the Malvinokaffric Realm, a biogeographical term used to denote the cool- to cold-water, high-latitude endemic, benthic marine, Devonian faunas of southwestern Gondwana, which also includes the invertebrate fossil assemblages of the Argentine Precordillera and the Fox Bay Formation of the Falkland Islands. The specimens were collected from an obrution deposit excavated on Karbonaatjies farm, ~145 km northeast of Cape Town in the Western Cape. The excavated rock samples contain >700 articulated specimens of *Gamiroaster tempestatis* that are closely associated with two types of less common mitrate stylophorans. Silicone casts and high-resolution three-dimensional digital models obtained via micro-CT scanning of these mould fossils provided detailed morphological proxies for this taxonomic description.

Keywords: Asterozoans, Ophiuroids, Malvinokaffric Realm, Emsian, *Gamiroaster tempestatis*.

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INTRODUCTION

The Bokkeveld Group of South Africa has yielded abundant invertebrate fossil assemblages that belong to the cool- to cold-water, high-latitude Malvinokaffric Realm, a term introduced by Richter (1941) and originally used to denote the endemic, marine benthos from the Devonian of southwestern Gondwana. The high-level provincialism was initially based on the restricted distribution of certain Devonian brachiopod and trilobite genera that are only present in the Bokkeveld Group of South Africa and similar aged successions in Argentina, Bolivia, Brazil and the Falkland Islands (Clarke 1913; Richter 1941; Richter & Richter 1942; Boucot *et al.* 1969; Eldredge & Ormiston 1979; Boucot 1985, 1988; Melo 1988). Penn-Clarke *et al.* (2018a) provides a recent comprehensive review of the history of the Malvinokaffric realm in South Africa. Generally, the Malvinokaffric Realm is characterised by a low-diversity fauna with high endemism of certain taxa and abundant conulariids, tentaculitids and hyolithids, as well as rare thermophilic reef-building corals and bryozoans (Oliver 1977; Boucot 1985, 1988; Pedder & Oliver 1990; Oliver & Pedder 1994; Meyerhoff *et al.* 1996). The absence of certain major groups such as stromatoporoid sponges, conodonts, goniatite ammonoids, and graptolites make inter- and intra-basinal biostratigraphic correlations difficult (Boucot 1985, 1988; Meyerhoff *et al.* 1996a).

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The Malvinokaffric biota of the Bokkeveld Group consists of characteristic species of brachiopods (e.g. *Australospirifer* sp.; *Australocoelia* sp.), trilobites (e.g. *Burmeisteria* sp.; *Homalonotus* sp.) and gastropods (Caster 1939; Richter & Richter 1942; Eldredge & Ormiston 1979; Boucot & Gill 1956; Boucot *et al.* 1969; Meyerhoff *et al.* 1996). Many of these genera also occur in the Devonian of the Falkland Islands (Clarke 1913a,b; Hunter *et al.* 2016) and in the southern parts of South America, including the Ponta Grossa Formation in the Parana Basin, Brazil, and the lower part of the Lolén Formation Sierra de la Ventana, Argentina (Limarino *et al.* 1999; Alessandretti *et al.* 2013).

The first asterozoan in the Lower Devonian Bokkeveld Group was recorded by Reed (1925), and subsequently ophiuroids were mentioned by Rossouw (1933) and Spencer (1930). Work by Spencer (1950) provided the first description of the ophiuroid *Hexuraster weitzi* (Spencer). This was followed by work done by Rilett (1971) who described two new ophiuroid taxa, *Haughtonaster reedi* (Rilett) and *Taeniaster stuckenbergi* (Rilett). The first extensive account of South African ophiuroids including crinoids, blastoids and asteroids was by Jell & Theron (1999), who revised the previously reported echinoderms from the Bokkeveld Group and described two new ophiuroid species, *Marginura hilleri* and *Eugasterella africana*. In this study, we systematically describe a new addition to the Malvinokaffric asterozoan fauna of South

Palaeontologia africana 53: 66–74 — ISSN 2410-4418 [Palaeontol. afr.] Online only

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Africa. The specimens described herein were collected from an echinoderm-rich obrution bed on farm Karbonaatjies in the Western Cape of South Africa (Fig. 1). The sampled rock specimens contained >700 articulated ophiuroids that are dominated by the proposed new genus and species. Other echinoderms found within the Karbonaatjies bed include >145 articulated mitrate stylophorans *Paranacystis* cf. *petrii* Caster 1954, eight *Placocystella africana* (Reed 1925) and unidentifiable crinoid ossicles.

GEOLOGICAL SETTING

The Early to middle Devonian (Emsian-Givetian) Bokkeveld Group is a metasiliciclastic succession of the Cape Supergroup comprising repetitive and laterally continuous sandstones and mudstones that are exposed in the Cape Fold Belt (Western and Eastern Cape Provinces) of South Africa (Fig. 1) (Theron & Johnson 1991; Penn-Clarke *et al.* 2018b). The lowermost six formations in the Bokkeveld Group, collectively referred to as the

Ceres Subgroup, consist of three continuous, upward-coarsening successions of mudstones, siltstones and sandstones that have been recently interpreted as an array of depositional systems in a marginal- to shallow-marine setting (Penn-Clarke *et al.* 2018b). Located within the Ceres Subgroup, the mudstone-rich Voorstehoek Formation conformably overlies the Gamka Formation and is overlain by the Hex River Formation. The lower part of the Voorstehoek Formation is made up of dark grey mudstones with thin calcareous lenses, which give way up-sequence to siltstone and thin sandstone lenses. The sedimentary features in these heterolithic tempestite-dominated successions suggest that the Voorstehoek Formation was deposited in a predominantly shallow marine, inner shelf setting with deltas and tidal flats to the north. In the south, close to the location of the studied outcrop, mud to fine-grained sand sedimentation occurred in a deeper water setting closer to the outer shelf (Theron 1972, 2003; Reid *et al.* 2015).

The obrution bed was excavated from a road cutting

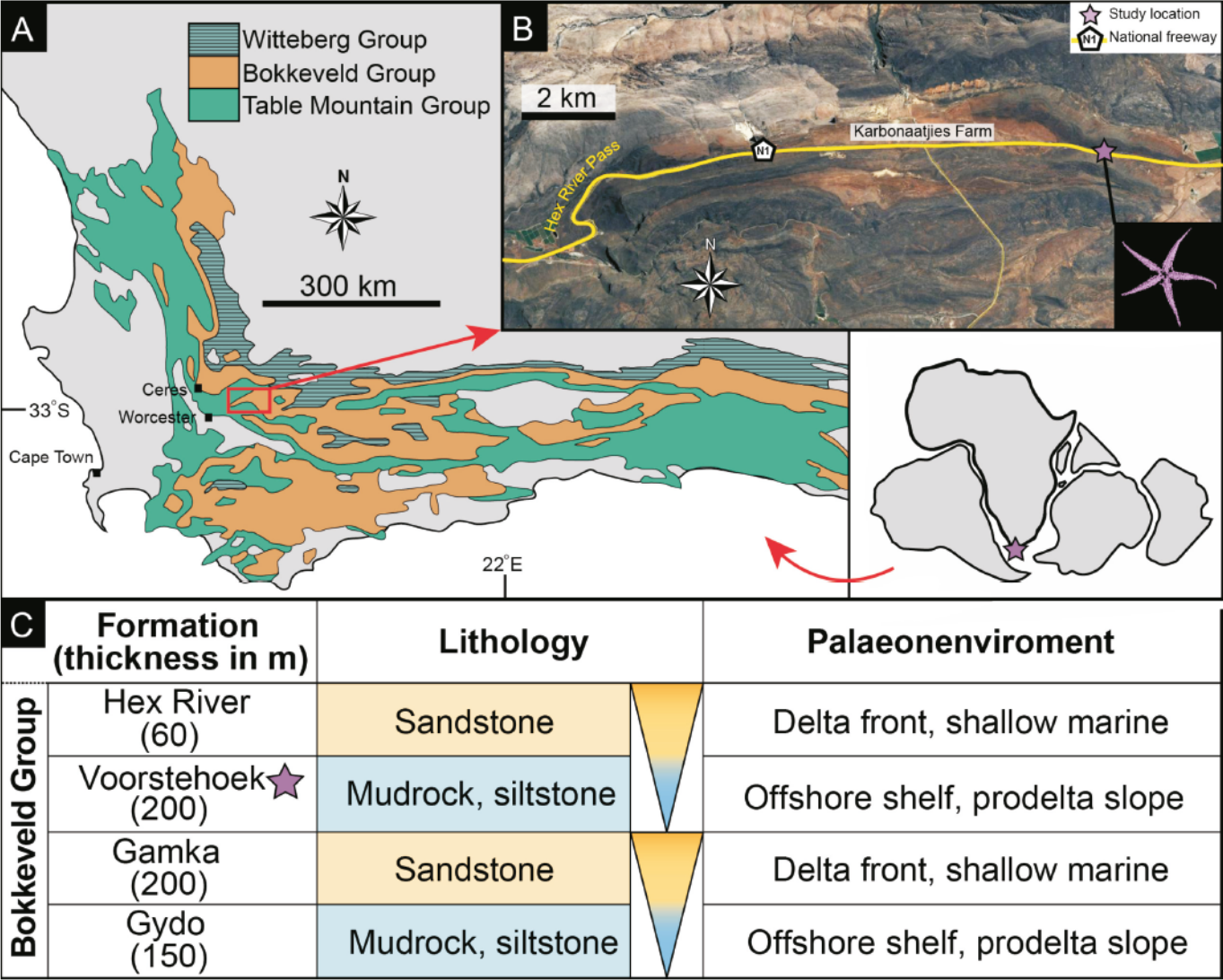


Figure 1. Locality maps and stratigraphic context of the study site: A, Simplified geological map of the Cape Supergroup in South Africa. The fossil locality (red square) is within the Cape Fold Belt, ~145 km NE of Cape Town (modified after Theron & Looock, 1988 and Reid *et al.* 2015). Insert on right shows Africa’s position within Gondwana. B, Aerial photograph of the study area near the Karbonaatjies obrution bed (star) along the N1 national road in the Western Cape (GPS coordinates: 33°24003.600S, 19°52042.700E). C, Stratigraphic context of the Karbonaatjies obrution bed (star), which belongs to the Voorstehoek Formation of the middle Ceres Subgroup in the lower Bokkeveld Group (see Penn-Clarke *et al.* 2018b for details).

on the Karbonaatjies Farm, ~80 km E of Ceres near the Hex River Pass in the Western Cape Province (GPS: 33°24003.600S; 19°52042.700E) (Fig. 1). In a preliminary report conducted by Reid *et al.* (2015), the sedimentary successions in the study area were identified as proximal storm deposits or event beds as they displayed a characteristic facies succession ranging from massive conglomerate beds with reworked brachiopod shell fragments at the base, to amalgamated beds of fine-grained sandstone with hummocky cross-stratification. It was concluded, based on these sedimentary features, that the Karbonaatjies obrution bed formed in a shallow marine environment, within the storm-influenced, proximal part of an offshore transition zone (Reid *et al.* 2015).

MATERIALS AND METHODS

All material studied has been deposited in the collections of the Iziko Museum of South Africa (SAM) in Cape Town under the accession number SAM-PB-022501. The mould fossil specimens were described from blackened silicone rubber casts made at the University of Cape Town. These casts were then dusted with a white coat of ammonium chloride sublimate and photographed at the Western Australian Museum in Perth (Australia). The morphological terminology used is that of Glass & Blake (2004), Shackleton (2005), Glass (2006) and Hunter *et al.* (2016). Micro-CT scanning of ophiuroid specimens was performed at the Stellenbosch University Central Analytical Facility (South Africa) in a walk-in microfocus X-ray CT scanner; the General Electric Phoenix V|Tome|X L24 model with additional NF180 option. The tomographic reconstruction dataset obtained from scanning was visualized and analysed using VGStudioMax 3.1 software package to create a three-dimensional (3D) view of individual fossils within each sample.

SYSTEMATIC PALAEONTOLOGY

Class Ophiuroidea Gray 1840

Order Oegophiuroidea Matsumoto 1915

Suborder Lysophiurina Gregory 1897

Family Protasteridae Miller 1889

Diagnosis

Hunter *et al.* (2016) revised the diagnosis as follows: Ambulacral ossicles not fused across the midline; periradial suture distinct, either straight or zigzag; opposing or alternating ambulacrals; adambulacral groove spines broadened towards the tip (i.e. paddle-shaped); longitudinal ridge for groove spines raised and curved; adambulacral vertical spines of greater length than adambulacrals.

Remarks

This diagnosis follows that of Shackleton (2005) emended by Hunter *et al.* (2016), which emphasises characteristics of the periradial suture (straight or zigzag/sinuuous) and paired or offset ambulacrals. Glass & Blake (2004) established that the shape of the ambulacra 'boots' and the adambulacral 'sickles' are taxonomically significant and genus level and we follow this opinion herein.

Subfamily Protasterinae Hunter, Rushton & Stone 2016

Diagnosis

'Ambulacrals alternating by up to half an ossicle length; periradial suture distinct, either straight or zigzag. Ambulacrals boot-shaped. Adambulacrals elongated with a bulbous nose or sickle-shaped. Mouth angle plates stout, crossed by oblique ridge in lateral section.' (Hunter *et al.* 2016: 6).

Remarks

This new subfamily was recently proposed by Hunter *et al.* (2016) to accommodate genera that possess alternating ambulacrals (as opposed to paired ambulacrals, e.g. *Furcaster* Stürtz 1886, *Hypohiura* Jaekel 1923 and *Lapworthura* Gregory 1897) and places emphasis on the variation in boot-shaped ambulacra as a morphological classification between Protasteridae (Glass & Blake 2004).

Gamiroaster gen. nov.

Etymology

'Gamiro' derived from the Khoikhoi word for star, was chosen to honor the first peoples of the Western Cape in South Africa.

Type species

Gamiroaster tempestatis sp. nov., by original designation.

Diagnosis

Protasterid ophiuroid with periradial suture tight, narrow and zigzag, both aborally and orally. Oral ambulacral boots: width of foot (WF) is equal to the length of the leg (LL); width of distal fitting (WDF) greater than length of the foot (LF) and equal in width of the central leg (WCL). Distal end of WDF is slightly concave, abradial edges curved. Toe (WT) is shorter than width of distal fitting (WDF). The abradial edge of the toe is straight to convex. Width of toe (WT) is approximately half the width of foot (WF). Podial basins large, sub-rounded and deep.

Remarks

The comparison here serves to differentiate *Gamiroaster* from other protasterids, with emphasis on the described protasterids by Jell & Theron (1999) of the Lower Devonian Bokkeveld Group in South Africa. Variations in boot-shaped ambulacral will be used here to differentiate between the various protasterid genera, as used in Glass & Blake (2004), Glass (2006) and Hunter *et al.* (2016) (Fig. 2).

Spencer (1950a) originally described several specimens from the Lower Devonian Bokkeveld Group as a new species *Hexura weitzi* assigned to the family Euzonosomatidae Spencer 1930. This material was subsequently re-studied by Jell & Theron (1999) who assigned these specimens to three different taxa: (1) Spencer's holotype specimen SAM11055 (figs 1, 2, p. 301, unknown formation) was reassigned to *Hexuraster weitzi* (Spencer 1950a) (figs 38, 39 in Jell & Theron 1999, pp. 162–163) but placed into the family Cheiropterasteridae Spencer 1934; (2)

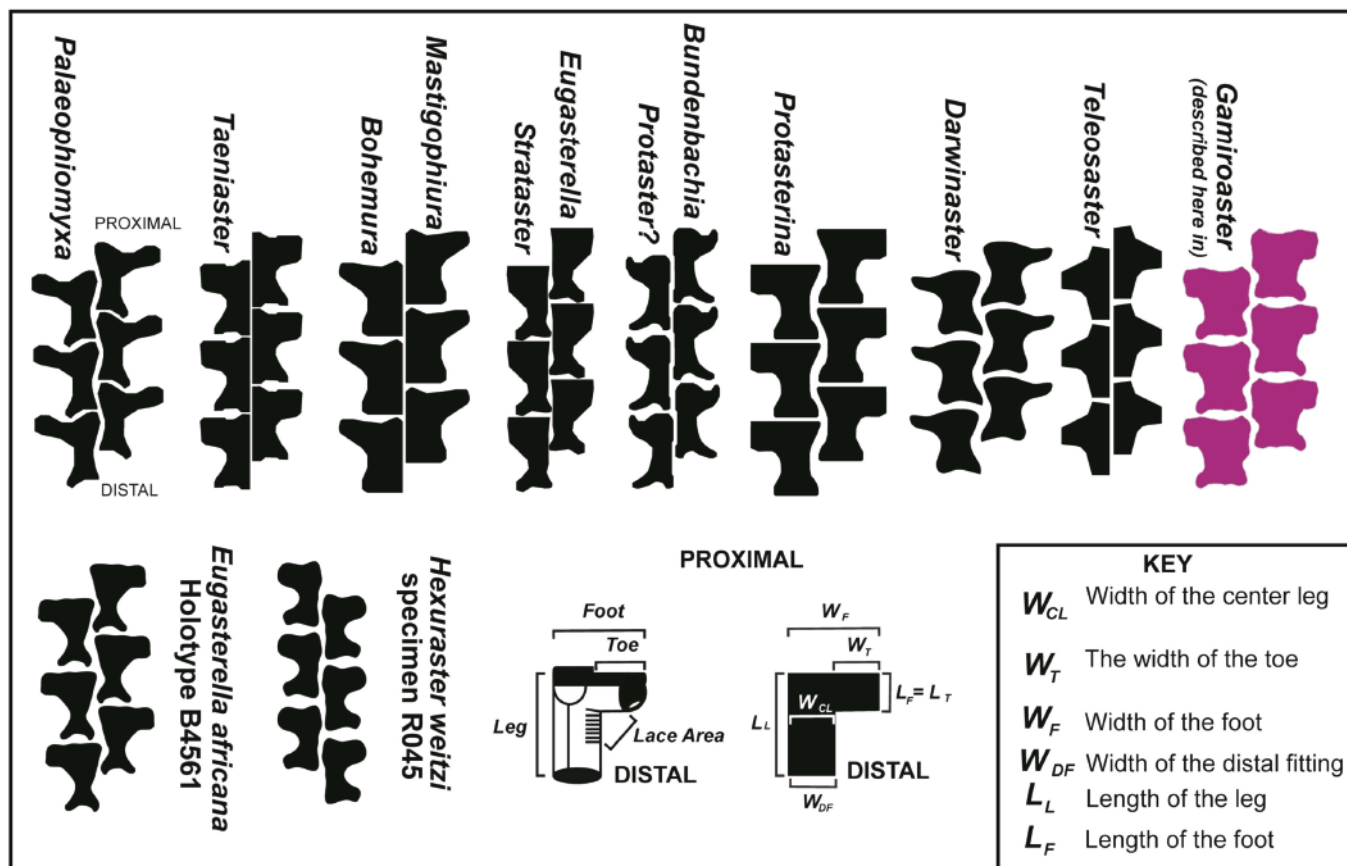


Figure 2. Ventral outlines of protasterid ophiuroid ambulacrals, and common terminology used for describing the boot-shaped ambulacrals (modified from Glass & Blake 2004 and Hunter *et al.* 2016).

Spencer's specimens, which he illustrates in figures 4 and 5, were re-identified as *Encrinaster tischbeinianus* (Roemer 1863) (figs 40–43 in Jell & Theron 1999, pp. 165–170); and (3) Spencer's specimen shown in figure 3 (p. 301) as the new species *Eugasterella africana* Jell & Theron 1999 (figs 46–48, pp. 174–178). Spencer (1934: 439) erected the family Cheiropterasteridae for ophiuroids with alternating cylindrical ambulacrals, adambulacrals lacking vertical spines, and an extremely swollen disk. Subsequently Spencer & Wright (1966) synonymized Cheiropterasteridae and Euzonosomatidae with Encrinasteridae. However, Jell (1997: 162) maintained the family on the basis of a very unique feature: 'an unplated skin to the dorsal disk and extent of the disk to, or very close to the tips of the arms.' This unique feature is apparent in Jell & Theron (1999) figure 38 of *Hexuraster weitzii* (lectotype SAM11055); however, this is not the case for the specimen R045 (fig. 39, p. 163 in Jell & Theron 1999, Gydo Formation) of the same taxa, nor are the cylindrical ambulacrals, T-shaped adambulacrals and lateral spines apparent. Whether Cheiropterasteridae should be re-erected as a family or synonymized with Encrinasteridae is beyond the scope of this paper. The discussion here serves to point out that only specimen R045 (fig. 39; p. 163 in Jell & Theron 1999) resembles *Gamiroaster tempestatis* and not the lectotype specimen (SAM11055 – fig. 38, p. 162 in Jell & Theron 1999) on the basis of having a small thin web-like disk; arms are slightly petaloid; the mouth frame ossicles are similar in appearance; the ambulacrals are boot-shaped; and disk, groove or lateral spines are absent.

However, *Gamiroaster* is distinctive from *Hexuraster* (R045 fig. 39; p. 163 in Jell & Theron 1999) in that its boot-shaped ambulacrals have a much wider (LF) and shorter (WF) foot and distal fitting (WDF). The adambulacrals in *H. weitzii* (R045 fig. 39) also differ in that the adradial nose is narrow, short and rectangular and the abradial head is large and flat (large distal facet?) that along with the nose region give a more L-shaped appearance rather than a sickle or crescent shape seen in *Gamiroaster*. Finally, due to the shape and size of the ambulacrals and adambulacrals in *H. weitzii*, the podial basins are wide and sub-circular compared to narrow and circular basin in *Gamiroaster*. It is possible then that specimen R045 (fig. 39; p. 163 in Jell & Theron 1999) belongs to the family Protasteridae, but further revision to assess this is needed.

The blocky appearance of the ambulacra in *Gamiroaster* bears some resemblance to those of *Eugasterella africana* Jell & Theron 1999 (Holotype B4561, Voorstehoek Formation, fig. 46, p. 175) and *Strataster stuckenbergi* (Rilett 1971) (Holotype NM 831, Gydo or Voorstehoek Formations, fig. 54–56, p. 183) in that the width of the foot (WF) and length of the leg (LL) are roughly equal, the length of the toe (LT) is relatively wide with a straight to convex abradial edge, the width of the toe (WT) is relatively short and a slightly sinuous ambulacral groove (Fig. 2). This is not the same for the type species *Eugasterella logani* (Hall 1868) and *Strataster ohioensis* Kesling & Le Vasseur 1971, where the width of the toe (WT) and consequently the width of the foot, is much shorter and only slightly wider than the central leg (for a comprehensive review of

E. logani, see Harper & Morris 1978). However, *Gamiroaster* has a notably wider width of the centre leg than the above-mentioned genera. The ambulacrals of *Gamiroaster* differ greatly from the overall sinuous shape seen in *Palaeophiomyxa* (Stürtz 1886) and *Bundenbachia* Stürtz 1886, in particular the prominent curvature of the toes, sinuously concave distal and proximal settings and the relatively narrow width of the central leg (Glass & Blake 2004) (Fig. 2). The foot being as wide (WF) as the length of the leg (LL), *Gamiroaster* shares a wide central leg and blocky appearance with *Darwinaster* Hunter, Rushton & Stone 2016, *Mastigophiura* Lehmann 1957 and *Bohemura* Jaekel 1903 and *Teleosaster* Hunter & McNamara 2017. However, *Gamiroaster* differs in that the distal position of the toe is almost at right angles to the adradial edge of the leg (i.e. lace area) making the toe wide and blocky as opposed to tapering to a narrow tip (see comparison in Glass & Blake 2004; Glass 2006; Hunter *et al.* 2016). This is also evident in *Taeniaster* Billings 1858 and *Protasterina* (Glass & Blake 2004) in that the length of the toe (LT) is relatively wide with a straight to convex abradial edge, but *Taeniaster* has a characteristically straight periradial suture and *Protasterina* has straight distal and proximal settings and a unique hourglass-shaped leg (Glass 2006; Hunter *et al.* 2007) (Fig. 2). *Gamiroaster* has a slight heel on the WF similar to *Taeniaster*, *Mastigophiura* and *Bohemura* and unlike the proximal platform heel characteristic of *Teleosaster*. Although *Gamiroaster* does not have a highly distinctive ventral shape to the ambulacrals, the differences given above set it apart from other protasterid genera. Lastly, *Gamiroaster* has very distinct heart-shaped mouth angle ossicles (mao) (Fig. 3C).

Gamiroaster tempestatis sp. nov., Figs 3 & 4

Type material

Holotype by monotypy SAM-PB-022501, due to general poor preservation a number of paratype material was selected: SAM-PB-022502, SAM-PB-022503, SAM-PB-022504.

Etymology

Named after the storm (tempest) that consequently smothered the ophiuroids.

Occurrence

Lower Devonian Voorstehoek Formation, lower Ceres Subgroup, Bokkeveld Group, Cape Supergroup, Karbonaatjies Farm, near the Hex River Pass, Western Cape, South Africa.

Diagnosis

Disk web-like; no apparent marginal ridge between interradii; thin skin stretched over disk. Disk spines absent. Medium length, gradually tapering arms; pointed and enclosed at the distal end. Aboral surface of the arm smooth with quadrate plates. Ambulacral ossicles alternate over midline, periradial suture tight, narrow and zigzag, both aborally and orally. Oral ambulacral

surface with prominent boot-shaped ambulacral plates. Groove crosses distal surfaces from podial region to periradius. Oral ambulacral boots have blocky ambulacrals with concave distal and proximal fittings. Width of foot (WF) is equal to the length of the leg (LL); width of distal fitting (WDF) greater than length of the foot (LF) and equal in width of the central leg (WCL). Toe (WT) is shorter than width of distal fitting (WDF). The abradial edge of the toe is straight to convex.

Description

Small protasterid with diameter of 8 mm. Disk web-like or slightly concave, extending to the fourth ambulacral (Fig. 3A,B). Both aboral and oral disk are preserved, but this is not wholly apparent from the silicone molds; thin skin stretched over disk and proximal arms is, however, apparent in CT scans (Fig. 3); disk appears naked with no patches of granules and lacks marginal ossicles. Disk spines appear to be absent. Arms 18 mm from the mouth angle plates; slightly bowed from mouth frame to about the margin of the disk and gradually tapering; pointed and enclosed at distal end (possibly due to post-mortem contraction) (Fig. 3). Madreporite not seen. Ventral oral surface consists of visible mouth angle ossicles (mao). Abradially the circumoral ossicle surface curved and bears a distal facet, which adjoins first arm ambulacral and a proximal facet that articulates to the corresponding facet on the mouth angle plate. Mao are distinctive in that they are curved inwards towards the buccal region abutting with the opposite mao creating a triangular heart shape with the accompanying circumoral ossicles (Fig. 3C). In aboral view, the mouth frame ossicles are slender and slightly bowed to form a petaloid or heart shape. There appears to be no apparent buccal slit. The furrow is open to the end portion of the arms; this is seen in the CT scans and derived 3D models (Fig. 3). The distalmost ends of the arms are either missing or poorly preserved in the silicone casts, but clearly visible in the CT scans; arms remain flattened in form, becoming slightly enclosed towards the tip where the adambulacrals close over the furrow (Fig. 3). The aboral surface of the arm smooth with quadrate plates (Fig 3B,E). Ambulacral ossicles alternate over the midline, periradial suture tight and slightly sinuous along oral surface and more strongly zigzag along aboral surface of the arm. Number of ambulacrals in disk varies between four and five on oral surface (Fig. 3A). Aboral ambulacral sub-cylindrical, with slight ridge-bound indentations. Ventral surface of ambulacral boot-shape is blocky; width of foot (WF) is as wide as the length of the leg (LL). Width of the distal fitting (WDF) is larger than the length of the foot (LF) and equal in width to the central leg (WCL). Distal end of WDF is slightly concave to straight, abradial edge slightly curved. Toe (WT) is shorter than width of distal fitting (WDF). Abradial edge of toe straight to slightly convex. Width of toe (WT) is approximately half the width of foot (WF). Proximal end of foot is straight to concave with a slight bulbous heel. Lace area is weakly concave. Podial basins large, sub-rounded and deep (Fig. 3D). Oral view of adambulacrals in CT scans shows adradial nose that thins

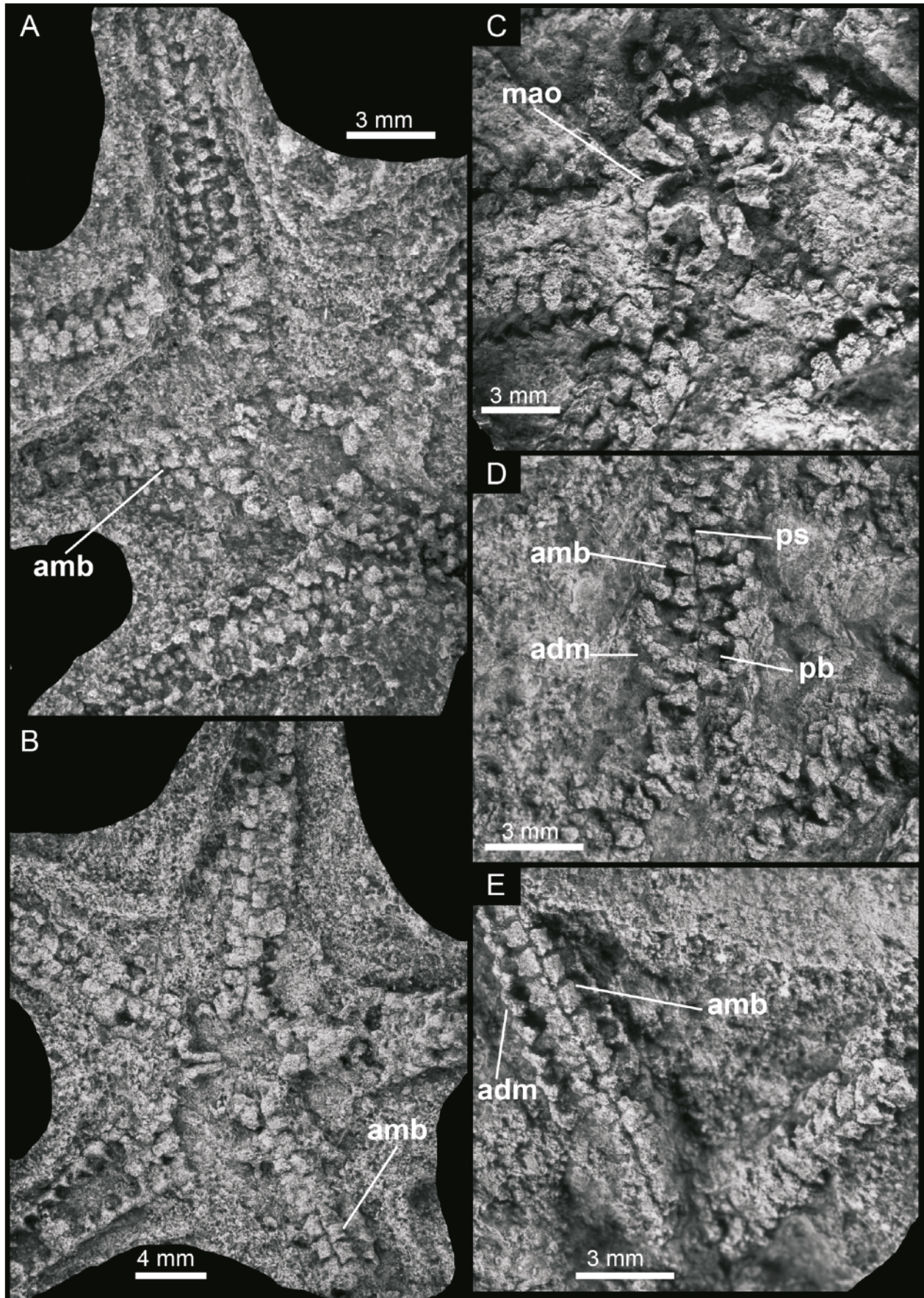


Figure 3. *Gamiroaster tempestatis* from the Karbonaatjies obrution bed in the Lower Devonian Voorstehoek Formation, Western Cape, South Africa. **A**, Holotype SAM-PB-022501, general view of a nearly complete specimen in ventral view. **B**, Paratype SAM-PB-022502, general view of a nearly complete specimen in aboral (dorsal) view. **C**, Paratype SAM-PB-022504, detail of mouth angle ossicles. **D**, Paratype SAM-PB-022503, arm in ventral view showing boot-shaped ambulacra and slightly zig-zag periradial suture. **E**, Paratype SAM-PB-022503, arm in aboral (dorsal) view showing quadrate adambulacra. Abbreviations adm = adambulacra or laterals; amb = ambulacra; mao = mouth angle ossicles; pb = podial basin; ps = periradial suture. Photographs taken of ammonium-whitened silicone casts of the mould fossils.

to a point and abradial distal square head, ventral outline sickle-shaped (Fig. 4). Laterals abutting laterals begin to overlap distally over the ambulacra. No evidence of articulation sites or grooved spines. Vertical spines not preserved.

Remarks

Nearly all ophiuroids found within the obrution bed were revealed through CT scanning of a section of the entire bed. This posed a challenge in exposing specimens for taxonomic descriptions, as such mechanical preparation was used to expose the largest and most articulated ophiuroids within the bed. Disk diameter was measured for >700 specimens and ranges from 1.45 mm to 10 mm. *Gamiroaster* belongs to the same group as the basal ophiuroid genus *Protaster* (Blake & Guensburg 2015). This distinct clade of asterozoan echinoderms, the protasterids, includes Middle–Upper Ordovician taxa from the famous Lady Burn Starfish Beds in Scotland and localities in Bohemia, Czech Republic (Shackleton 2005; Hunter *et al.* 2016).

DISCUSSION

We have demonstrated that the Karbonaatjies obrution bed is dominated by a single ophiuroid taxon *Gamiroaster tempestatis*, which is part of the basal ophiuroid family *Protasteridae* that first appear in the middle–late Ordovician and continue into the late Palaeozoic with little change in morphology (Shackleton 2005; Hunter *et al.* 2016). With >700 specimens observed within the obrution bed, preservation was generally good in comparison to other echinoderms found within the Bokkeveld Group and the age equivalent Fox Bay Formation in the Falkland Islands (Jell & Theron 1999; Hunter *et al.* 2016). Using both silicone casts and 3D models of these mould fossils, a rather unique perspective of the adambulacra or laterals can be seen, greatly aiding in not only the description of *Gamiroaster* specimens, but also their orientations within in the bed. In a recent study on the Karbonaatjies obrution bed by Reid (2017) taphonomic analysis of this ophiuroid–stylophoran assemblage indicates that this benthic community was preserved due to rapid and deep smothering during a single storm event. The ophiuroids

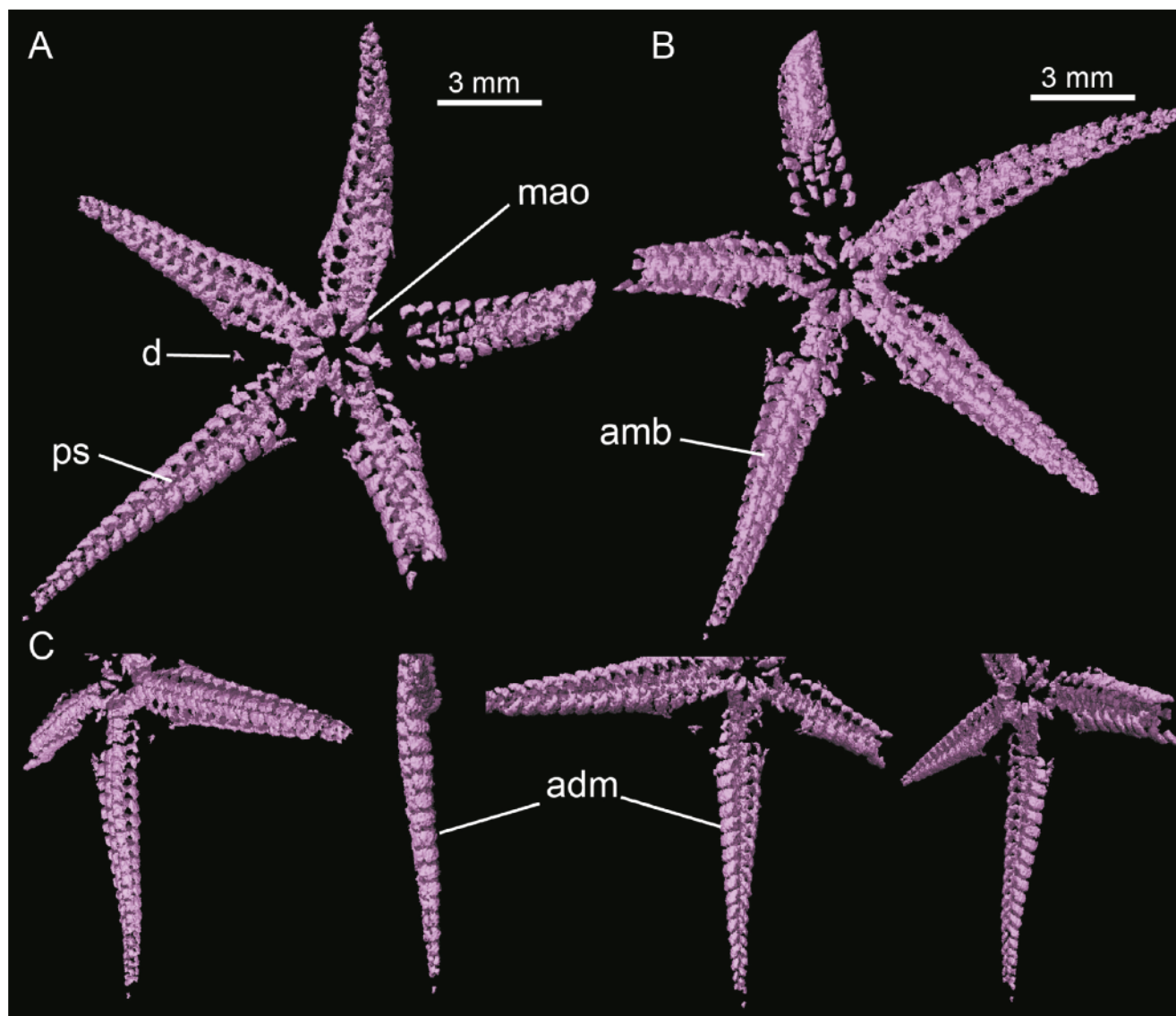


Figure 4. Three-dimensional (3D) reconstruction of *Gamiroaster tempestatis* specimen (sample UU2) taken from the Karbonaatjies obrution bed. A, Oral view of specimen. B, Aboral view of specimen. C, 360° rotation of the arm, showing shape of adambulacra. Abbreviations adm = adambulacra or laterals; amb = ambulacra; mao = mouth angle ossicles; ps = periradial suture; d = disk.

Table 1. Ophiuroid occurrences across the Malvinokaffric faunal province.

	Argentine Precordillera (Haude 2004)	South African Bokkeveld (Jell & Theron 1999)	Falkland Islands (Hunter <i>et al.</i> 2016)
Eophiuridae	<i>Haughtonaster</i> sp. <i>Eophiura</i> sp.	<i>Haughtonaster reedi</i>	
Cheiropterasteridae	<i>Hexuraster</i> sp.	<i>Hexuraster weitzii</i>	
Encrinasteridae	<i>Magura yach</i> <i>Magura</i> sp.	<i>Ecrinaster tischbeinianus</i> <i>Marginura hilleri</i>	
Protasteridae	<i>Eugasterella</i> sp.	<i>Eugasterella africana</i> <i>Startaster ohoiensis</i> <i>Startaster stuckenbergi</i> <i>Gamiroaster</i> sp. nov.	<i>Darwinaster coleenbiggsae</i>
Ophiurinae	<i>Argentinaster bodenbenderi</i> <i>Argentinaster</i> sp.	<i>Argentinaster</i> sp.	
Furcasteridae	<i>Furcaster separatus</i>		
Eospondylidae	<i>Eospondylus</i> sp.		

formed a dense population or ‘meadow’ with the co-occurring small stylophoran *Paranacystis* cf. *petrii* and the larger mitrate *Placocystella africana*. Preservation of Bokkeveld Group asterozoan assemblages are commonly associated with obrution events caused by a rapid influx of fine-grained sediments (Hiller & Theron 1988). Such beds often contain crinoid calyces, arms, stems, as well as exquisitely preserved bryozoans, complete trilobites, and fully articulated ophiuroids (Hiller & Theron 1988; Jell & Theron 1999). Similar preservation is seen strata of the Argentine Precordillera where ophiuroids often occur in obrution *lagerstätte* and have been attributed to the same palaeoenvironmental conditions as in the Bokkeveld Group (Haude 2010).

The most diverse Lower Devonian echinoderm assemblage is in the extensively documented Hunsrück Slate (Rhineland-Palatinate) in Germany and is consequently the best source of data on Early Devonian ophiuroids (e.g. Glass & Blake 2002; Blake 2003, 2009; Glass 2004, 2008; Glass & Poschmann 2006). Following this, ophiuroids from the Lower Devonian Bokkeveld Group show a high taxonomic diversity similar to that known from the Talacasto Formation of the Argentine Precordillera (Table 1). Thirteen ophiuroid taxa are reported in Jell & Theron (1988) with a significant proportion of genera belonging to the same protasterid group as *Gamiroaster*. In the Argentinean Precordillera seven distinct genera are recognized, with *Ophiurinae* and *Furcasteridae* making up significant components, in contrast to the higher proportion of *Protasteridae* in South Africa and the Falkland Islands (Jell & Theron 1999; Haude 2004, 2010; Hunter *et al.* 2016). The faunal differences between these two assemblages reflect aspects of the depositional environments that are specific to areas within the Precordillera and Bokkeveld basins (Hunter *et al.* 2016). To better understand and compare these assemblages further study is needed in these areas, as well as a major revision of all ophiuroids found within the Bokkeveld Group. Important echinoderm-dominated assemblages from the early Devonian are recognized from the Bokkeveld Group of South Africa, the Lolên Formation of Argentina and the Fox Bay Formation of the Falkland Islands. These assemblages preserve snapshots of benthic communities that

were rapidly buried in similar shallow marine, storm-dominated depositional settings.

This project was supported by grants to W.L.T. and E.M.B. as well as Honours and Masters bursaries to M.R. from the DST-NRF Centre of Excellence in Palaeosciences (CoE PAL). We gratefully acknowledge these financial contributions. Opinions expressed and conclusions arrived at are those of the authors and are not necessarily to be attributed to CoE PAL. We also gratefully acknowledge the reviewers and the editor, Jonah Choiniere, for meaningfully contributing with their insightful comments to the overall quality of this study. The dataset was acquired and compiled during the course of M.R.’s postgraduate studies at University of Cape Town supervised by E.M.B. and W.L.T.; M.R., E.M.B. and W.L.T. conceived and designed the project. M.R. wrote most of the final paper, and coordinated with co-authors, who performed critical revision of the manuscript.

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