*Journal of Paleontology*, 90(6), 2016, p. 1017–1026
Copyright © 2016, The Paleontological Society
0022-3360/16/0088-0906
doi: 10.1017/jpa.2016.94

Journal of PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

# *Ernietta* from the late Edicaran Nama Group, Namibia

David A. Elliott,[1] Peter W. Trusler,[1] Guy M. Narbonne,[1,2] Patricia Vickers-Rich,[1] Nicole Morton,[1] Mike Hall,[1] Karl H. Hoffmann,[3] and Gabi I.C. Schneider[3]

[1]School of Geosciences, Monash University, Clayton, Victoria 3800, Australia, ⟨david.alexanderus@gmail.com⟩ ⟨peter@petertrusler.com.au⟩ ⟨pat.rich@monash.edu.au⟩ ⟨nicole.d.morton@gmail.com⟩
[2]Department of Geological Sciences and Geological Engineering, Queen's University, Kingston, ON K7L 3N6, Canada, ⟨narbonne@queensu.ca⟩
[3]Namibian Geological Survey, Ministry of Mines and Energy, Windhoek, Namibia, ⟨mkh.hoffmann@iway.na⟩ ⟨gschneider@mme.gov.na⟩

**Abstract.**—*Ernietta plateauensis* Pflug, 1966 is the type species of the Erniettomorpha, an extinct clade of Ediacaran life. It was likely a gregarious, partially infaunal organism. Despite its ecological and taxonomic significance, there has not been an in-depth systematic description in the literature since the original description fell out of use. A newly discovered field site on Farm Aar in southern Namibia has yielded dozens of specimens buried in original life position. Mudstone and sandstone features associated with the fossils indicate that organisms were buried while still exposed to the water column rather than deposited in a flow event. *Ernietta plateauensis* was a sac-shaped erniettomorph with a body wall constructed from a double layer of tubes. It possessed an equatorial seam lying perpendicular to the tubes. The body is asymmetrical on either side of this seam. The tubes change direction along the body length and appear to be constricted together in the dorsal part of the organism.

## Introduction

*Ernietta* is a distinctive Ediacaran megafossil that is typically preserved as three-dimensional impressions within beds of sandstone. It had a gregarious habit, and unlike most Ediacara-type fossils was neither a recliner nor a frond. It is one of the best candidates for a semi-infaunal Ediacaran organism. Thousands of specimens have been collected in Namibia where it is among the most common megascopic Ediacaran taxa, along with the related form *Pteridinium* Gürich, 1933. In marked contrast to its abundance there, the only other report of *Ernietta* worldwide is from a single site in the western USA (Horodyski, 1991), and these specimens have not yet been figured or described.

*Ernietta* is the type-genus for the Erniettomorpha, a late Ediacaran clade of soft-bodied organisms characterized by modular construction of cm-scale tubular elements (Narbonne, 2011; Laflamme et al., 2013). *Ernietta* has been featured in most Ediacaran dioramas (e.g., Erwin et al., 1997; Monastersky, 1998) and has been discussed and figured in most global overviews of Ediacaran paleobiology (e.g., Glaessner, 1984; Seilacher, 1989, 1992; Jenkins, 1992; Narbonne, 2005; Xiao and Laflamme, 2009; Erwin et al., 2011). However, the diagnosis and description of *Ernietta* remain inadequate. The original diagnosis of the type species, *E. plateauensis* Pflug, 1966, placed emphasis on the presence of a thick, but flexible, 'dorsal' exoskeleton, which was referred to as a shell (*Schale*)—a feature that has not been observed by any subsequent worker. Pflug (1966) originally defined *Ernietta* as a monospecific genus, but later Pflug (1972) split this single species into 29 species grouped into 13 genera. Glaessner and Walter (1975) and Jenkins et al. (1981) expressed doubt about the validity of these new taxa, and they were subsequently recognized as synonymous with *E. plateauensis* by Runnegar (1992), Pickford (1995), and Vickers-Rich (2007). All references to *Ernietta* since 1972 are from authors who accepted that all of the new taxa defined by Pflug (1972) are junior synonyms of *E. plateauensis*.

Although the boundaries of the clade Erniettomorpha originally excluded forms such as *Pteridinium*, the term has come to encompass members of the Ediacaran macrobiota bearing parallel, unbranched tubular elements that meet along a 'suture' or 'mid-line' with an offset symmetry on either side of this suture (Laflamme et al., 2009; Hofmann and Mountjoy, 2010; Erwin et al., 2011). In practice it refers to those taxa morphologically more similar to *Ernietta* than to rangeomorphs within the Ediacaran megascopic biota. As well as *Pteridinium* and *Ernietta*, this has been taken to include *Swartpuntia germsi* Narbonne, Saylor, and Grotzinger, 1997, *Miettia salientensis* Hofmann and Mountjoy, 2010, and *Phyllozoon hanseni* Jenkins and Gehling, 1978.

*Ernietta* has been considered in discussions focusing on other fossils or sedimentary features (Jenkins et al., 1981; Jenkins, 1985, Jenkins, 1992; Seilacher, 1992), and as part of broader sedimentologic and stratigraphic studies (Bouougri et al., 2011). However, with the exception of Dzik (1999), *Ernietta* has not been the focus of published research since 1972.

This study is based on examination of hundreds of specimens of *Ernietta* from Farm Aar in Namibia, including a newly discovered locality (Fig. 1, locality 1). The size, number, and



https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

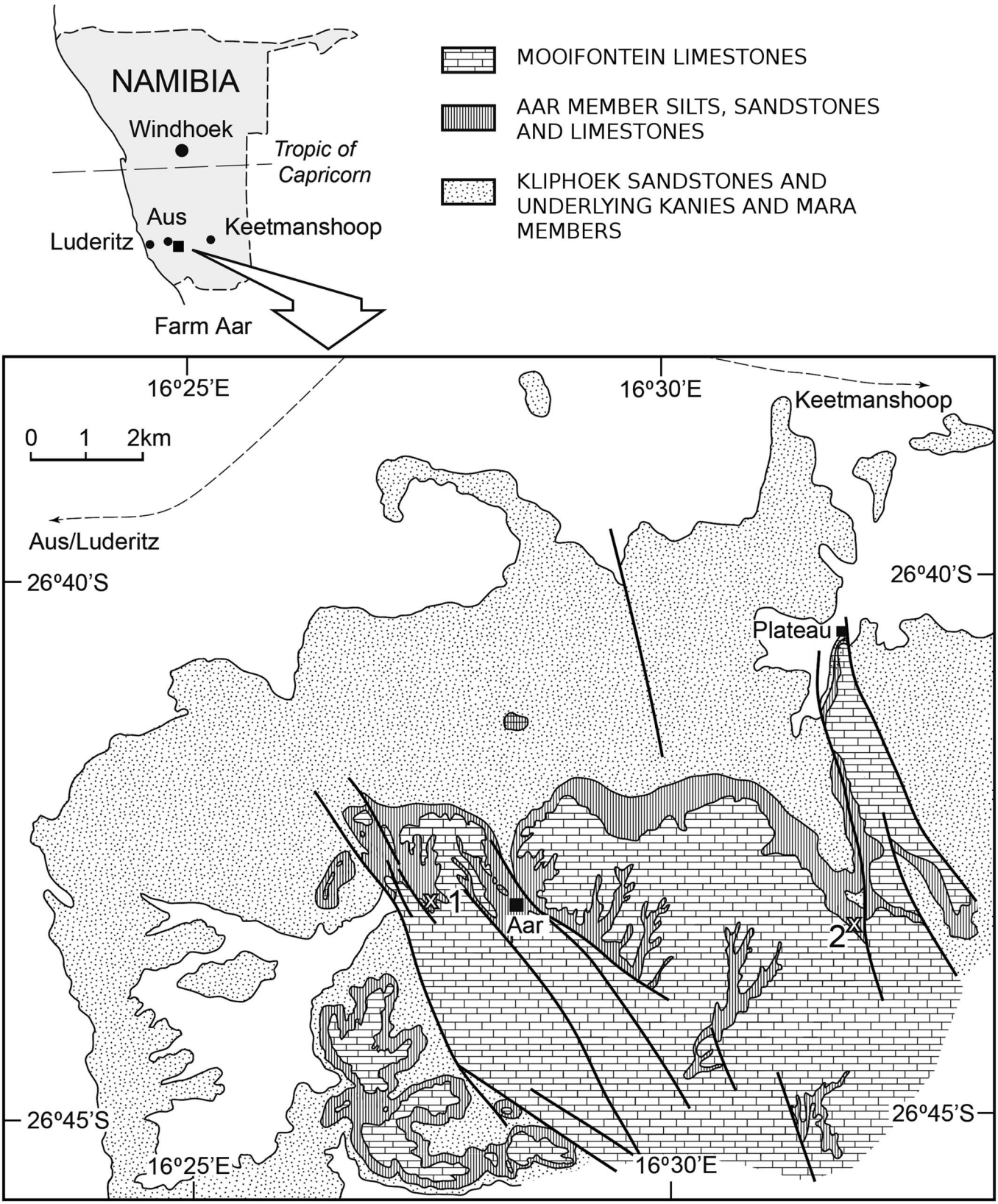



**Figure 1.** Location of the two newly discovered sites in the Nama Group exposed at Farm Aar. Both are to the west of the *Ernietta* type locality reported by Pflug (1966, fig. 1b C). (**1**) New locality containing *Ernietta* fossils in likely life position ('Teapot' locality of Hall et al., 2013). (**2**) Location of bag-like structure presented in Fig. 5.1; after Vickers-Rich et al., 2013.

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

completeness of these specimens, along with their probable occurrence in life position, presents an opportunity to revisit the details of morphology and possible life habits of this organism.

## Geological setting

Most specimens of *Ernietta* have been recovered from the Kuibis Subgroup in southwestern Namibia, which consists of sediments deposited on the edge of the Kalahari Craton in a foreland basin associated with the Damara Orogen to the north (Germs, 1974; Saylor et al., 1995, 1998; Grotzinger and Miller, 2008). The Kuibis Subgroup represents a regional transgression onto the Kalahari Craton, characterized by sandstones giving way to limestones towards the west and up-section (Gresse and Germs, 1993), deposited in two sub-basins separated by a topographic high in the region of Osis.

The lowermost, unfossiliferous Kanies Member (Kuibis Subgroup, Dabis Formation) consists of immature, poorly sorted, pebbly to conglomeratic sandstones, interpreted as fluvial plain deposits that overlie crystalline basement (Germs, 1983). In the region of Farm Aar (Fig. 1), this member is overlain by a thin sequence of interbedded siltstones and limestones of the Mara Member. Above this, the Kliphoek Member represents the progradation of thick-bedded sandstones. The Kliphoek is characterized by channelization and abundant scour surfaces, implying a deltaic environment, but the absence of unconformities and exposure surfaces suggests continuous submersion (Grotzinger and Miller, 2008). The top meter of this member contains transported beds of *Pteridinium* associated with scours and overlying dish structures, likely representing material washed into a shallow-marine deltaic setting during storm events (Elliott et al., 2011). Above this lies the Aar Member, a 31- to 38-m sequence of interbedded siltstones and carbonates with sporadic sandstone beds (Hall et al., 2013). The Aar Member contains the new material reported below. It represents a transitional sequence between the siliciclastic shallow-marine Kliphoek, and the overlying subtidal carbonates of the Mooifontein Member of the Zaris Formation (Fig. 2).

## Occurrence

More than 100 specimens of *E. plateauensis* were recovered both as float and in situ within a bedding layer during the 2009 and 2011 field expeditions of IGCP 493/587 on Farm Aar in southwestern Namibia (Fig. 1). The newly discovered *Ernietta* fossils were recovered from sandstone beds within the Aar Member, which consists primarily of thin interbedded sands, muds and carbonates (Fig. 2).

*Depositional Setting*.—The Aar Member represents subtidal muds with occasional influxes of sand from storm-induced events (Hall et al., 2013). Limestones are increasingly common towards the upper part of the Aar Member, indicative of clearer water. These were interrupted by periods of clastic mud deposition and sandy event beds. At least one of these sandy beds preserves closely packed *Ernietta* specimens. Mud layers of the overlying bed surround upper parts of some specimens, but the tops of the organisms were not preserved—a feature typical of all known specimens of *Ernietta*.

*New* Ernietta *fossils*.—The 'Teapot' locality of Hall et al. (2013; Fig. 1, locality 1 in the present paper) contains specimens ranging from 3 cm up to 10 cm in their maximum dimension preserved in mud and fine-grained sand. Float specimens and float blocks with multiple specimens have been scattered by erosion tens of meters downslope from the layer containing in-situ material. The in-situ section represents only the edge of a fossiliferous deposit, the bulk of which has eroded and is scattered a short distance downslope as float. Despite being removed by erosion from their original layer, these float specimens are well preserved, with evidence of their context. The base of the bed and the fill of the fossils is fine-grained sand with no sedimentary structures. Mica flakes are present, as well as occasional pyrite pseudomorphs. This material characterizes most of the specimens. More complete fragments of the original bed preserve a sharp contact at the top of the sandstone with a layered mudstone containing mica. This mudstone does not fill the fossils, but surrounds the tops of some of them. It breaks away readily from sandstone fossils and beds when the rock is vibrated by sectioning with a rock saw or splitting with a geological hammer.

## Materials and methods

*Repositories and institutional abbreviations*.—Specimens (NESM prefix) are housed in the Namibian Geological Survey/Geological Survey of Namibia, Windhoek, which also contains Pflug's collection (Pf prefix). One specimen (Fig. 4.2) is in private hands.

## Systematic paleontology

Morphological terminology is shown in Figure 3.1–3.2

Group Erniettomorpha Pflug, 1972

*Remarks*.—Many fossils of Ediacaran age are difficult to relate to defined higher-level taxa of modern organisms and all such classification schemes are controversial. Grouping of these fossils into morphological clades (Xiao and Laflamme, 2009; Erwin et al., 2011; Laflamme et al., 2013; Narbonne et al., 2014) provides a more objective system to group similar Ediacara-type taxa without the assumptions necessary to relate these Ediacaran groupings to living groups of organisms.

Genus *Ernietta* Pflug, 1966

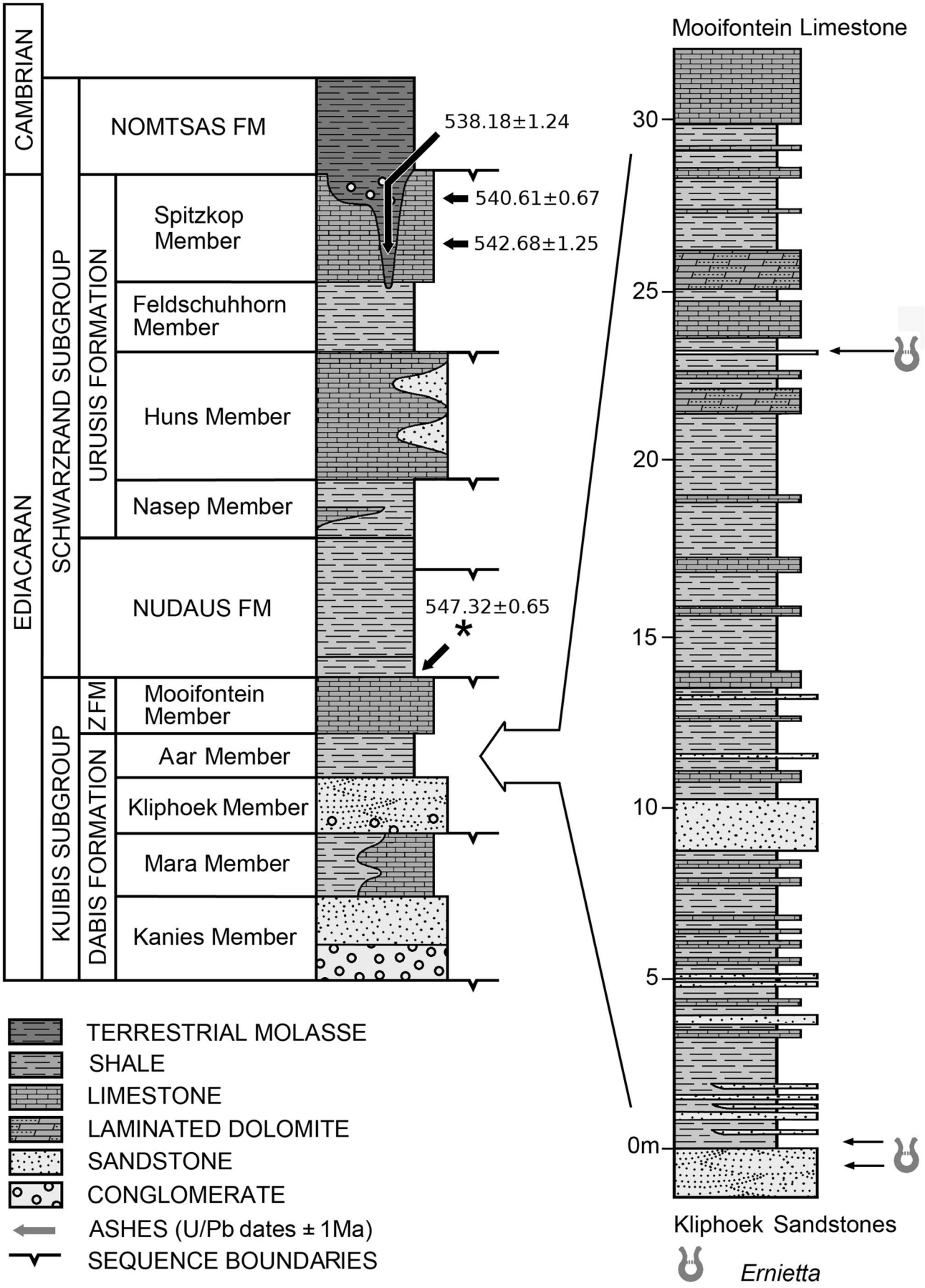
*Type species*.—*Ernietta plateauensis* Pflug, 1966, by original monotypy.

*Ernietta plateauensis* Pflug, 1966

Figures 3.1, 4.1–4.4, 5.1–5.4

1966 *Ernietta plateauensis* Pflug, p. 19, pl. 1, figs. 1–6, pl. 2, figs. 3–6.
1972 *Erniodiscus rutilis* Pflug, p. 158, pl. 27, fig. 3.
1972 *Erniodiscus clipeus* Pflug, p. 158, pl. 27, fig. 1.
1972 *Erniaster apertus* Pflug, p. 159, pl. 28, figs. 1–3, 5–7.
1972 *Erniaster patellus* Pflug, p. 159, pl. 29, figs. 1, 4, 8.

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press




https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

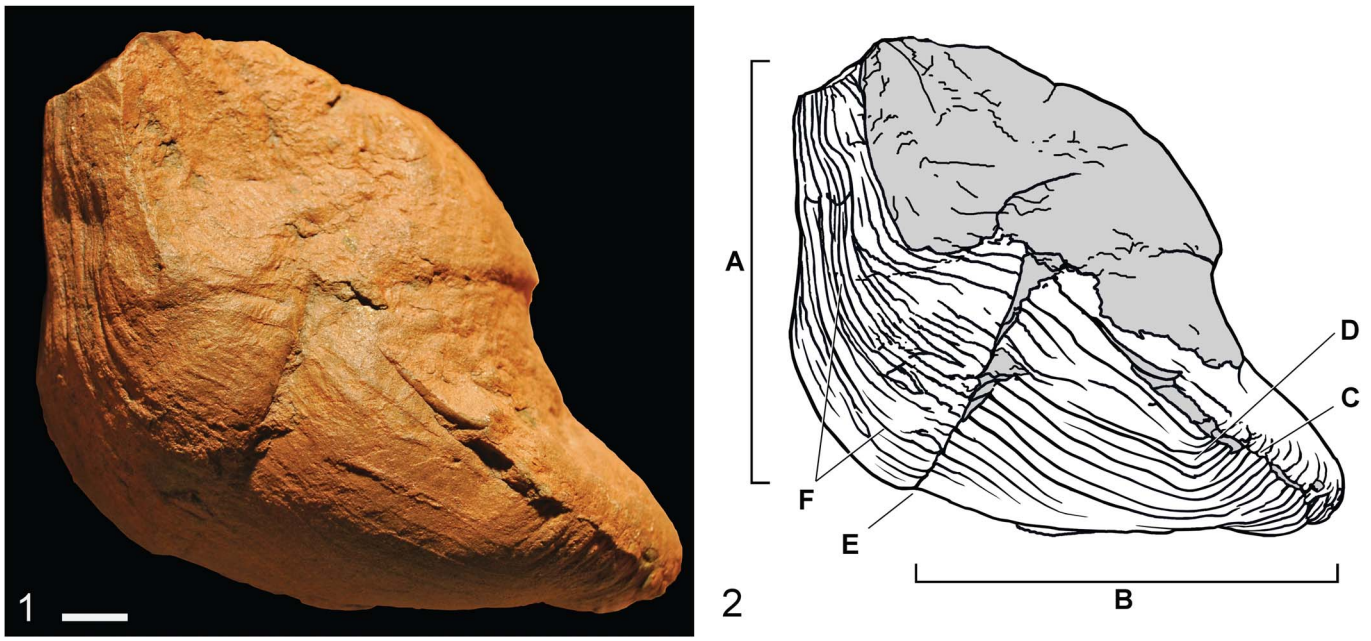



**Figure 3.** (**1**) NESM-F-389, the holotype for *Erniograndis sandalix* Pflug, 1972. This specimen is one of the most complete *Ernietta* fossils, bearing nearly all of the diagnostic features referred to in the text. Scale bar represents 1cm. (**2**) Outline of Fig. 3.1 showing diagnostic features. A: 'upper part' of the organism, relative to the stratigraphy; B: 'lower part' of the organism; C: 'suture' located along a surface that is shorter than the perpendicular axis of the fossil, displaying characteristic erniettomorph 'zigzag' symmetry; D: zone on the lower (ventral) half of the fossil in which segments can be deflected by an angle of up to 80 degrees (Fig. 4.1); E: 'equatorial seam' lying perpendicular to the longitudinal segments, and morphologically distinct from the suture (C); F: 'constricted' zone, where segments are less regular than on the lower part of the fossils, are upturned toward the top of the sediment, and often restricted to form a 'neck' (Fig. 4.3). Shading delimits unrelated sediment and the negative impressions of adjacent specimens now absent from the specimen block.

1972 *Erniocentris centriformis* Pflug, p. 159, pl. 28, figs. 4, 8, 9.
1972 *Erniofossa prognatha* Pflug, p. 159, pl. 27, figs. 2, 6, 7.
1972 *Ernionorma abyssoides* Pflug, p. 160, pl. 29, figs. 6, 12.
1972 *Ernionorma peltis* Pflug, p. 160, pl. 29, figs. 2, 5, tab. 30; figs. 1, 7.
1972 *Ernionorma clausula* Pflug, p. 160, pl. 31, figs. 2, 3.
1972 *Ernionorma rector* Pflug, p. 161, pl. 32, figs. 7–9.
1972 *Ernionorma corrector* Pflug, p. 161, pl. 32, figs. 1, 2.
1972 *Ernionorma tribunalis* Pflug, p. 161, pl. 31, figs. 4–8.
1972 *Erniobaris baroides* Pflug, p. 162, pl. 32, fig. 11.
1972 *Erniobaris gula* Pflug, p. 162, pl. 33, figs. 1, 2, 4.
1972 *Erniobaris epistula* Pflug, p. 162, pl. 31, figs. 9, 10.
1972 *Erniobaris parietalis* Pflug, p. 162, pl. 33, fig. 5.
1972 *Erniopelta scrupula* Pflug, p. 163, pl. 33, figs. 7, 10.
1972 *Ernietta aarensis* Pflug, p. 163, pl. 34, figs. 5, 7, 8.
1972 *Ernietta tsachanabis* Pflug, p. 164, pl. 34, fig. 12.
1972 *Erniocarpus carpoides* Pflug, p. 164, pl. 35, figs. 5–9.
1972 *Erniograndis sandalix* Pflug, p. 165, pl. 38, figs. 1, 2, 4.
1972 *Erniograndis paraglossa* Pflug, p. 166, pl. 39, figs. 7, 8.
1972 *Erniobeta scapulosa* Pflug, p. 166, pl. 39, fig. 6.
1972 *Erniobeta forensis* Pflug, p. 166, pl. 39, figs. 2–4, 10.
1972 *Ernietta plateauensis* Pflug; Pflug, pl. 34, figs. 1–4, 6, p. 163.
1979 "*Erniograndis* sp." Glaessner, p. A101, fig. 13 1a, b.
1979 "*Ernionorma* sp." Glaessner, p. A101, fig. 13 3a, b.
1979 "*Erniobeta* sp." Glaessner, p. A101, fig. 13 4a, b.
1979 "*Ernietta* sp." Glaessner, p. A101, fig. 13 2a, b.
1981 *Ernietta plateauensis*; Jenkins et al., p. 74, fig. 5A–E.
1984 *Ernietta plateauensis*; Glaessner, p. 82, fig. 2.15 A–D.
1985 "*Ernietta* sp." Jenkins, fig. 1.
1992 *Ernietta plateauensis*; Jenkins, p. 152, fig. 7.
1994 "*Ernietta* sp." Buss and Seilacher, p. 3, fig. 4 (pars).
1999 *Ernietta plateauensis*; Dzik, p. 519, figs. 1, 2, 3.
2003 "*Ernietta* sp." Seilacher et al., p. 51, fig. 10 (partim), fig. 11 (partim).
2005 "*Ernietta* sp." Narbonne, p. 429, fig. 4b.
2006 "*Ernietta* sp." McCall, p. 44, figs. 33, 36.
2007 "*Ernietta* sp." Vickers-Rich, p. 77, figs. 114 (partim), 117, 123, 125–129.
2007 *Ernietta plateauensis*; Vickers-Rich et al., p. 77, fig. 124; p. 271.
2007 *Erniaster apertus*; Vickers-Rich et al., p. 270.
2007 *Erniaster patellus*; Vickers-Rich et al., p. 270.
2007 *Ernietta aarensis*; Vickers-Rich et al., p. 271.
2007 *Erniobaris baroides*; Vickers-Rich et al., p. 271.
2007 *Erniobaris parietalis*; Vickers-Rich et al., p. 271.
2007 *Erniobeta forensis*; Vickers-Rich et al., p. 271.
2007 *Erniocarpus carpoides*; Vickers-Rich et al., p. 271.
2007 *Erniocentris centriformis*; Vickers-Rich et al., p. 271.
2007 *Erniodiscus rutilis*; Vickers-Rich et al., p. 271.
2007 *Erniograndis paraglossa*; Vickers-Rich et al., p. 272.

**Figure 2.** Generalized stratigraphic section of the Nama Group south of Osis (left) and the Aar Member (right). The longer arrow on the right hand side indicates the sandstone layer preserving newly recovered *Ernietta* specimens. The two shorter arrows indicate previously reported *Ernietta* discoveries (Vickers-Rich et al., 2013). Ages are in Ma and refer to revised U-Pb zircon dates of ash beds after Schmitz in Schmitz et al., 2012. Asterisk refers to a stratigraphically correlated date from the Hoogland Member of the Zaris Sub-basin, which crops out north of Osis (Grotzinger et al., 1995). ZFM = Zaris Formation; after Vickers-Rich et al., 2013.

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

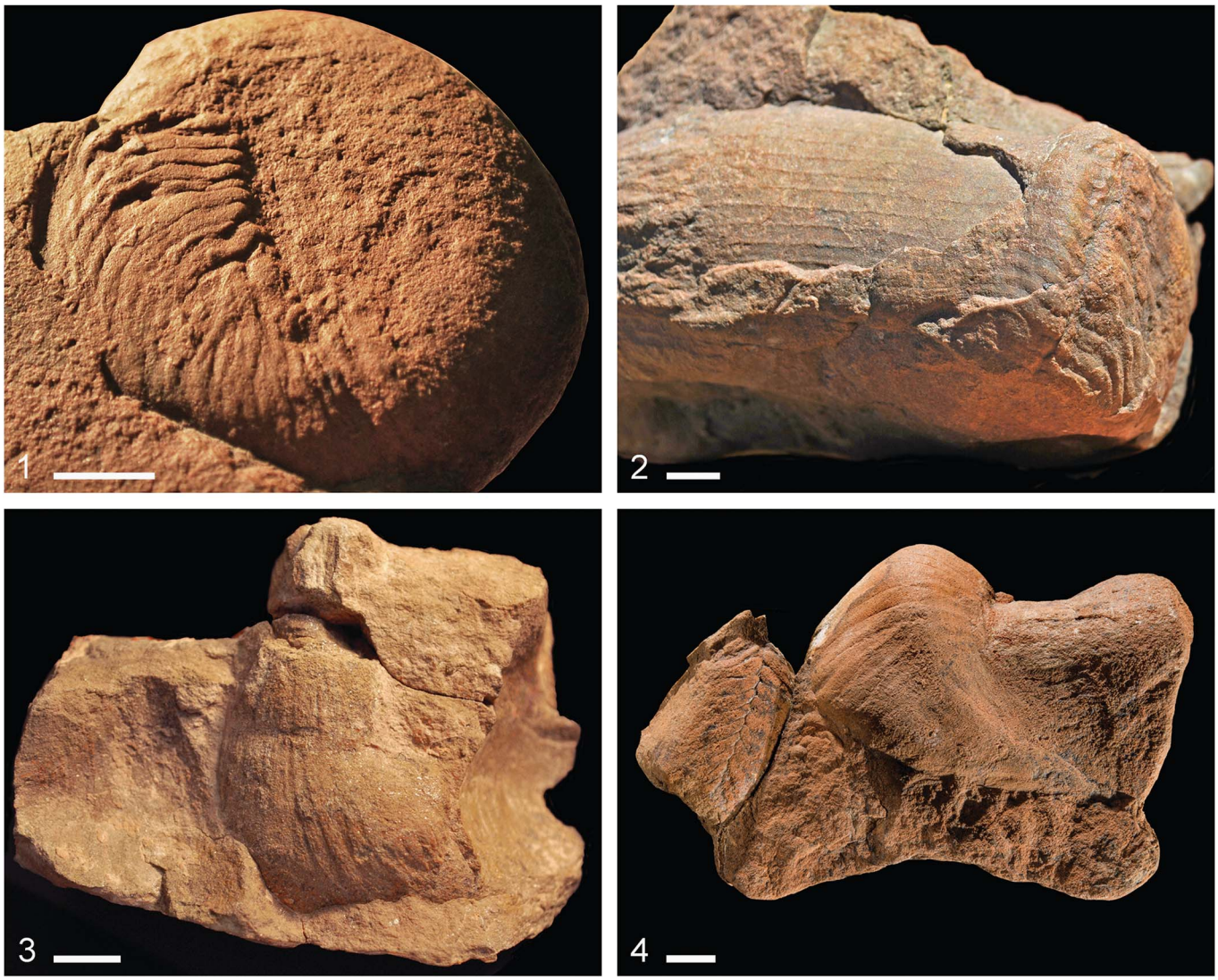


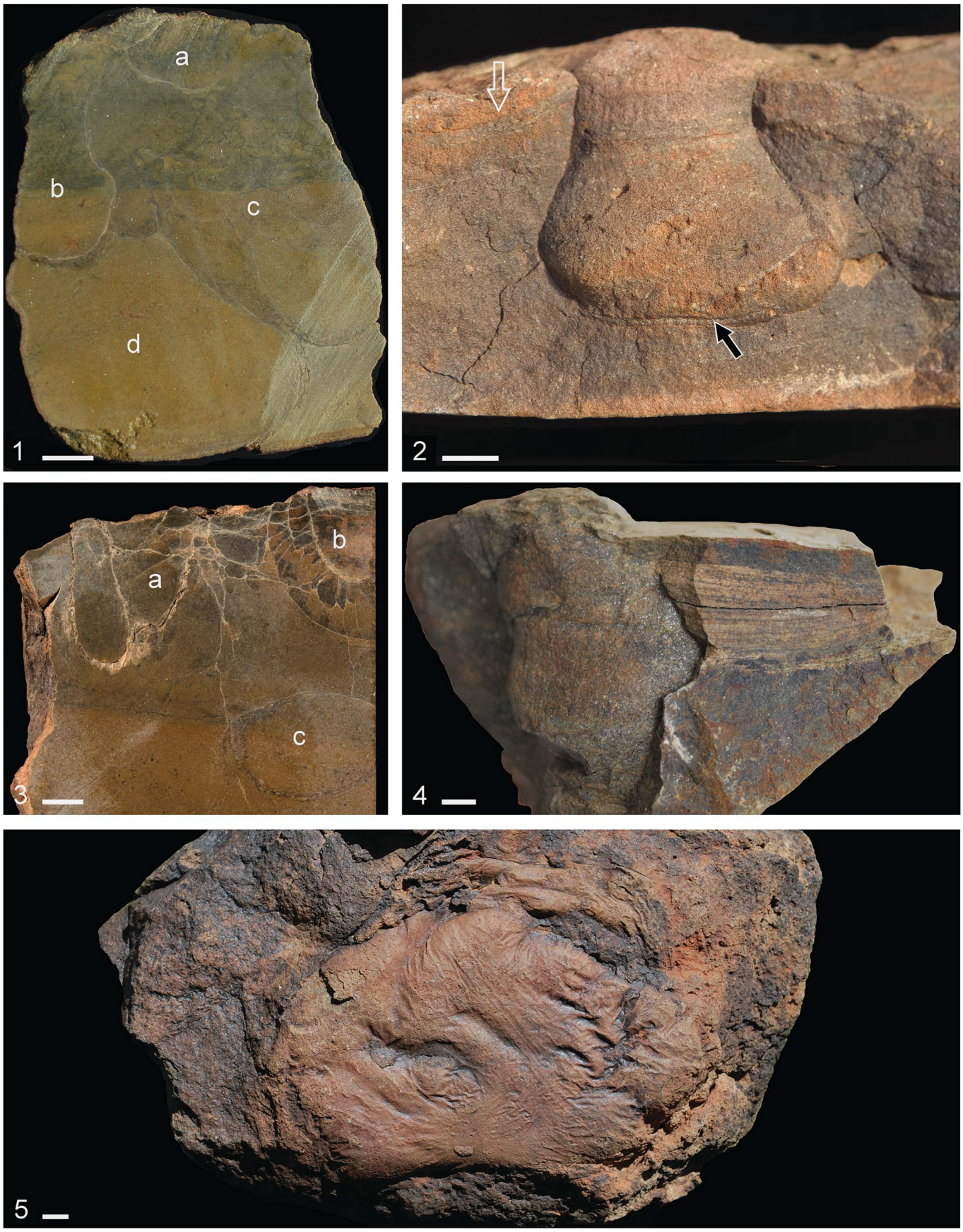

**Figure 4.** (**1**) NESM-F-435, holotype for *Erniobeta forensis* Pflug, 1972, demonstrating segments (left) deflected at an angle of 80°; (**2**) specimen of *Ernietta plateauensis* kept at Farm Plateau. The exterior surface of the outer layer of tubular elements (visible in the lower right-hand corner), which includes the zigzag suture. Above, there is a step down to the inner layer of tubular elements. The exterior surface of the inner layer records both the offset impressions made by the outer layer upon the tubular elements of the inner layer and the zigzag suture of the inner layer beneath the outer layer suture. A further step down to the center of the specimen shows that the sediment-filled internal cavity has cast the internal surface of the inner layer of tubular elements in negative relief. (**3**) NESM-F-1239, *E. plateauensis* excavated from Pflug's original stratigraphic level. Specimen is oriented relative to original position within the strata. Segments converge at the restricted upper part of the fossil. (**4**) NESM-F-1240, showing two specimens of *E. plateauensis*. On smaller specimen at left, the zigzag suture is visible, displaying the characteristic alternating symmetry. The right-hand side the larger specimen shows the level of deformation observed in some specimens. Scale bars represent 1cm.

2007 *Erniopelta scrupula*; Vickers-Rich et al., p. 272.
2007 *Ernionorma corrector*; Vickers-Rich et al., p. 272.
2007 *Ernionorma rector*; Vickers-Rich et al., p. 272.
2007 *Ernionorma abyssoides*; Vickers-Rich et al., p. 272.
2007 *Erniofossa prognatha*; Vickers-Rich et al., p. 272.
2008 *Ernietta plateauensis*; Grotzinger and Miller, fig. 13.207G.
2011 "*Ernietta* sp." Bouougri et al., p. 475, figs. 5c, d, e, f, g, h, 7b, 10a, b, c, d.

*Diagnosis*.—(Emended from Pflug, 1972) Sac-shaped fossil with body wall consisting of two sheet-like layers of parallel tubular elements. Tubular elements meeting with offset symmetry at a suture located along the short-axis of the fossil.

**Figure 5.** Taphonomic aspects of the new *Ernietta* localities. (**1**) NESM-F-1241, float specimen from the Teapot locality on Farm Aar, containing multiple individual *E. plateauensis* fossils (a–d), sectioned to demonstrate that the entire rock is comprised of fossil specimens such that each boundary is common between two organisms. (**2**) NESM-F-1242, float block from the Teapot locality on Farm Aar. Compressed mudstone laminae are visible in cross-section on the left (white arrow). The outer layer of tubular elements has been exfoliated except along the zigzag suture on underside of the specimen (black arrow). (**3**) NESM-F-1243, sectioned *E. plateauensis* specimens (a–c), from the Teapot locality on Farm Aar. In specimen b, weathering delineates the shapes of the tubes in cross-section, clearly demonstrating a double-layer as in Fig. 4.2. (**4**) NESM-F-1244, float block from the Teapot locality on Farm Aar, showing mudstone laminae terminating abruptly at the fossil. This indicates that the organism was in place while mudstone was being deposited. (**5**) NESM-F-1245, bag-like structures found associated with *E. plateauensis* 8 km west of Teapot locality (Fig. 1). Scale bars represent 1 cm.

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press




https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

An indented equatorial seam lying perpendicular to the tubular elements commonly divides specimens into two unequal parts.

*Description*.—Sac-shaped body (Figs. 3, 4, 5.2, 5.4), commonly 2–15 centimeters in length. Tubular elements and central body cavity are typically sand-filled. Its surface bears parallel lines formed by the tubular elements that may be expressed as furrows or ridges following the long-axis of the body. The linear relief represents a double-layered, longitudinal array of tubular elements that constitute the body wall (Fig. 4.2). Two sheets of the double array meet along a 'suture' with an offset, 'zigzag' symmetry on either side of this suture. The zigzag suture lies perpendicular to the tubular elements and is located along the short axis, at one end of the fossil (Figs. 3.2C, 4.2, 4.4). As the zigzag suture curves towards the long axis of the body, the tubular elements bend abruptly to align longitudinally to form the body circumference (Figs. 3.2D, 4.1). An 'equatorial seam' lies perpendicular to the tubular elements, encircling the fossil and dividing it in two asymmetrical parts (Fig. 3.2A, B). The equatorial seam does not have a zigzag appearance, differing from the suture, and it forms a sharp indentation of the specimen (Fig. 3.2E). The seam does not replicate the alternating symmetry of the zigzag suture.

The zigzag suture consistently appears on only one side of the equatorial seam, and this is invariably the downward-facing side. On some specimens the tubes near the suture are deflected by an angle of up to 80 degrees (Figs. 3.2D, 4.1, 4.2), which distinguishes *Ernietta* from fragmentary *Pteridinium*.

The tubular elements range from 1–6 mm in width and can vary in width within a single specimen (Figs. 4.3, 5.3). Tubular elements making up the body wall on the non-sutured side of the equatorial seam can appear quite different. They become more variable in width, are bound by less regular lines, and in some cases appear to form a 'constricted zone' where segments converge toward each other (Figs. 3.2F, 4.3, 5.2). In such cases, the tubular elements continue upward and slightly outward, towards the overlying sediment.

*Remarks*.—As listed by Pickford (1995), Runnegar (1992), and Vickers-Rich (2007), most of the multitude of genera and species established by Pflug (1972) represent junior synonyms of *E. plateauensis*, following the urging of Glaessner and Walter (1975) and Jenkins et al. (1981). However, as a result of this study, three of Pflug's (1972) species were inappropriately placed within *E. plateauensis*. These three species are herein excluded from synonymy: *Erniotaxis segmentrix* appears to be a part of the midline of a fragmentary *Pteridinium* fossil. *Erniocarpus sermo* and *E. orbiformis* are enigmatic features with no visible characteristics in common with *Ernietta plateauensis* or other erniettomorphs. *Namalia villersiensis* Germs, 1968 may also be a junior synonym of *E. plateauensis* (Runnegar, 1992), but this was disputed by Grazhdankin and Seilacher (2002).

The top of *Ernietta* is not preserved. Jenkins et al. (1981, p. 73) suggested that the living *Ernietta* had an open end that faced upwards in life and bore a "crenellate margin." Crimes and Fedonkin (1996), conversely, suggested that both ends of *E. plateauensis* were closed. The 'open end' is shown in more than one reconstruction of the living organism (Jenkins et al., 1981, fig. 6; Seilacher, 1992, fig. 1; Monastersky, 1998; Schneider and Marais, 2004), and according to Jenkins et al. (1981, p. 73) the open end is found "collapsed and deformed", preserved only in "rare instances." Some specimens show a few expanded, lappet-like segments beyond the restricted zone, but there remains no conclusive termination of their structure.

Jenkins et al. (1981, p. 76) referred to a "caul-like" outer membrane in *E. plateauensis*, "only faintly showing underlying longitudinal structure," which is a feature reminiscent of membranous structures associated with both *Rangea* Gürich, 1930 and *Pteridinium* from Namibia (Germs, 1973; Elliott et al., 2011). This feature is not visible in any of the *E. plateauensis* specimens of this study. Rare structures associated with *E. plateauensis* resemble highly wrinkled large plastic bags filled with sand (Fig. 5.5), but their relationship to *Ernietta* is uncertain.

## Lifestyle and taphonomy

Two interpretations of *Ernietta* burial have been proposed: Seilacher (1992) regarded it as a semi-infaunal organism, while Dzik (1999) argued that most specimens were emplaced as sand-filled bodies sinking through fluidized sands and muds. Many of the new specimens reported here are from beds containing a high density of fossils and in many cases, the contours of each individual are constrained by adjacent individuals (Fig. 5.1, 5.3), leaving no room for either surrounding sand or mud in the scenario suggested by Dzik (1999). The surface on which the mudstone layers were deposited changes angle around the fossils (Fig. 5.2, 5.4), suggesting either draping of the mudstone over a surface with some relief, or differential compaction above the sand-filled organism. The fossils themselves do not show signs of compaction. Specimens are invariably oriented with their distal end facing upwards, and many specimens show mudstone laminations that terminate at the body wall of an individual *E. plateauensis* fossil (Fig. 5.2, 5.4). These features imply that the organisms were living in place before and/or during mudstone deposition, and that these fossils represent an in situ rather than transported community (Fig. 6). This evidence supports the semi-infaunal habit illustrated by Seilacher (1992).

One specimen of *E. plateauensis* (Pf 308) figured by both Jenkins et al. (1981) and Dzik (1999) contains four different layers of fill and shows that the interface between the layers changes angle along the fossil (Jenkins et al., 1981, fig. 5C). The specimen demonstrates that the orientation of the organism changed between each of the four successive events that filled the interior. The change in orientation may be due to the growth of the organism, implying that *E. plateauensis* was filled with sediment during life and remained growing, supporting a partly buried life habit, or at the least a basally sediment-filled interior. At the Teapot locality, the sandy fill of specimens is not significantly different from surrounding sand, and is massive without any layering, unlike in Pf 308 (Fig. 5.1, 5.3).

## Discussion

*Community structure in* Ernietta.—The discoveries on Farm Aar allow for some limited interpretation of the original

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

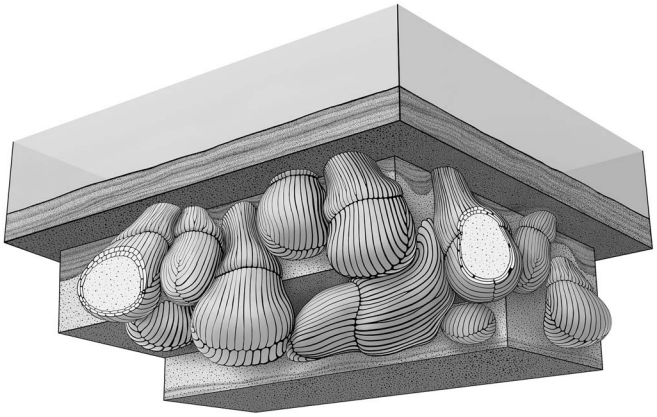


**Figure 6.** Reconstruction of the community at the Teapot site after some burial (artwork by Peter Trusler). Nama-style preservation is distinct from other forms of preservation known for the Ediacaran fauna in that it retains features beneath the sediment-water interface, rather than preserving features of bed soles (Narbonne, 2005) or tops of beds. Features that cannot be seen in this manner of preservation are excluded from reconstruction. The primary diagnostic features for *E. plateauensis* are visible, as is the range of forms observed in the fossils.

community structure of *Ernietta*. The high density of some *Ernietta* fossil assemblages, in which the shape of individual organisms is tightly controlled by other individuals surrounding them, implies a great deal of competition for space in life, rather than a closely packed death assemblage to the exclusion of burying sediments (Fig. 6).

*Variation in form.—Ernietta plateauensis* exhibits a wide variation in size and form. Pflug's (1972) 'erniobetines', which included the largest specimens, represent the more complete specimens. Jenkins et al. (1981) noted that syndepositional erosional processes truncated the upper parts of many specimens. These were the first *E. plateauensis* specimens reported (Pflug, 1966, 1972), and this truncation is characteristic of the population of fossils Pflug (1972) named ernionormines. These are mainly half-dome shaped, showing only the suture along which segments meet, as they are apparently truncated along a plane below the equatorial seam. Numerous such truncated *E. plateauensis* individuals are present at other sites on Farm Aar. The process leading to their truncation, whether syn- or post-depositional, removed all trace of the equatorial seam and any structure above it.

Based on the more complete forms known before the new site was uncovered, Dzik (1999) considered that variation in morphology within *E. plateauensis* was due to the original organism sinking through hydrated mud during transport, producing a range of shapes. Many of the float specimens discussed here were found in dense concentrations, in which there is little-to-no sediment between one fossil and another to permit the settling scenario proposed by Dzik (1999). Cross-sections show shared boundaries between fossils, and some blocks have been excavated to demonstrate clearly that specimens of *E. plateauensis* abut one another. The shape of the body wall of any one fossil within the denser concentrations is strongly constrained by the surrounding fossils.

## Conclusions

The initial naming of *Ernietta* came at a time when newly discovered Precambrian organisms were interpreted as precursors to modern clades. This influenced the description of *E. plateauensis*, which focused on the potential connection between the fragmentary type specimen and modern mollusks (Pflug, 1966), so that a soft dorsal shell became a key part of the diagnosis. Further work on Ediacaran fossils led to a consensus that at least some of the large, soft-bodied biota, including *Ernietta*, represent organisms with no living descendants, but the particular anatomical characteristics of *Ernietta* were never systematically codified after the initial interpretations of Pflug (1966, 1972). Recent work on Ediacaran paleobiology has resulted in a preliminary taxonomy (Erwin et al., 2011), raising the need for a clear diagnosis for many fossil taxa. Based both on re-examination of existing collections and a large number of new specimens, we present a revised diagnosis for *Ernietta* and show that it contains just the type species, *E. plateauensis*. Interpretation of its biology and taphonomy is hampered by the fact that no specimens preserve the distal parts of the organism, those parts that were originally highest in the water column. However, it is clear that *Ernietta* exhibited a wide range in size and shape and lived in dense, semi-infaunal clusters.

## Acknowledgments

This work was made possible by grants from UNESCO through the International Geosciences Program (IGCP projects 493 & 587), from the National Geographic Society grants 9208-12 and 8467-08, and assistance from Monash University. GMN acknowledges support from the Natural Sciences and Engineering Council of Canada (NSERC) and a Queen's Research Chair. PVR appreciates support from the vice-Chancellor's Emerita Grant for Research. The support of the Geological Survey of Namibia and the landowners B. Boehm-Erni and the late B. Boehm (who have provided both hospitality and material assistance to enable fieldwork to take place at Farm Aar) has been crucial. We thank the owners of Farm Plateau for permission to examine a specimen in their possession. A.Y. Ivanstov provided invaluable expertise in the field and laboratory. Work was carried out under permits from the National Heritage Council of Namibia (Permit 13 of 2009 and Permit 6 of 2011). C. Greentree provided helpful assistance in editing images for publication. We would also like to thank B. Runnegar, B. MacGabhann, and B. Pratt for their constructive comments on the manuscript.

## References

Bouougri, E.H., Porada, H., Weber, K., and Reitner, J., 2011, Sedimentology and palaeoecology of *Ernietta*-bearing Ediacaran deposits in southern Namibia: Implications for infaunal vendobiont communities: Advances in Stromatolite Geobiology, v. 131, p. 473–506.

Buss, L.W., and Seilacher, A., 1994, The phylum Vendobionta: a sister group of the Eumetazoa?: Paleobiology, v. 20, p. 1–4.

Crimes, T.P., and Fedonkin, M.A., 1996, Biotic changes in platform communities across the Precambrian-Phanerozoic boundary: Rivista Italiana di Paleontologia e Stratigrafia, v. 102, p. 317–332.

Dzik, J., 1999, Organic membranous skeleton of the Precambrian metazoans from Namibia: Geology, v. 27, p. 519–522.

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press

Elliott, D.A., Vickers-Rich, P., Trusler, P., and Hall, M., 2011, New evidence on the taphonomic context of the Ediacaran *Pteridinium*: Acta Palaeontologica Polonica, v. 56, p. 641–650.
Erwin, D.H., Valentine, J.W., and Jablonski, D., 1997, The origin of animal body plans: American Scientist, v. 85, p. 126–137.
Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J., 2011, The Cambrian Conundrum: early divergence and later eecological success in the early history of animals: Science, v. 334, p. 1091–1097.
Germs, G.J.B., 1968, Discovery of a new fossil in the Nama Group, South West Africa: Nature, v. 219, p. 53–54.
Germs, G.J.B., 1973, A reinterpretation of *Rangea schneiderhoehni* and the discovery of a related new fossil from the Nama Group, South-West Africa: Lethaia, v. 6, p. 1–9.
Germs, G.J.B., 1974, The Nama Group in South-West Africa and its relationship to the pan-African geosyncline: The Journal of Geology, v. 82, p. 301–317.
Germs, G.J.B., 1983, Implications of a sedimentary facies and depositional environment analysis of the Nama Group in South-West Africa/Namibia: Special Publications of the Geological Society of South Africa, v. 11, p. 89–114.
Glaessner, M.F., 1979, Precambrian, *in* Robinson, R.A., and Teichert, C., eds., Treatise on Invertebrate Palaeontology Part A Introduction Fossilization (Taphonomy) Biogeography and Biostratigraphy, Lawrence, Kansas, The Geological Society of America and the University of Kansas, p. A79–A118.
Glaessner, M.F., 1984, The Dawn of Animal Life, Cambridge, Cambridge University Press, 256 p.
Glaessner, M.F., and Walter, M.R., 1975, New Precambrian fossils from the Arumbera Sandstone, Northern Territory, Australia: Alcheringa, v. 1, p. 59–69.
Grazhdankin, D.V., and Seilacher, A., 2002, Underground Vendobionta from Namibia: Palaeontology, v. 45, p. 57–78.
Gresse, P.G., and Germs, G.J.B., 1993, The Nama foreland basin: sedimentation, major unconformity-bounded sequences and multisided active margin advance: Precambrian Research, v. 63, p. 247–272.
Grotzinger, J.P., and Miller, R., 2008, The Nama Group, *in* R. Miller, ed., The Geology of Namibia: Geological Society of Namibia Special Publication 2, p. 13-229–13-272.
Grotzinger, J.P., Bowring, S.A., Saylor, B.Z., and Kaufman, A.J., 1995, Biostratigraphic and geochronologic constraints on early animal evolution: Science, v. 270, p. 598–604.
Gürich, G., 1930, Die bislang altesten Spuren von Organismen in Sudafrika: International Geological Congress (XV), Pretoria, Union of South Africa, Die altesten Fossilien Sud-Afrikas, v. 2, p. 670–680.
Gürich, G., 1933, Die Kuibis-Fossilien der Nama-Formation von Sudwestafrika: Paläontologische Zeitschrift, v. 15, p. 137–154.
Hall, M., Kaufman, A.J., Vickers-Rich, P., Ivantsov, A., Trusler, P., Linnemann, U., Hofmann, M., Elliott, D.A., Cui, H., Fedonkin, M., Hoffmann, K.-H., Wilson, S.A., Schneider, G., and Smith, J., 2013, Stratigraphy, Palaeontology and Geochemistry of the late Neoproterozoic Aar Member, southwest Namibia; Reflecting environmental controls on Ediacara fossil preservation during the terminal Proterozoic in African Gondwana: Precambrian Research, v. 238, p. 214–232.
Hofmann, H.J., and Mountjoy, E.W., 2010, Ediacaran body and trace fossils in Miette Group (Windermere Supergroup) near Salient Mountain, British Columbia Canada: Canadian Journal of Earth Sciences, v. 47, p. 1305–1325.
Horodyski, R.J., 1991, Late Proterozoic megafossils from Southern Nevada: Geological Society of America Abstracts with Programs, v. 23, no. 5, p. A163.
Jenkins, R.J.F., 1985, The enigmatic Ediacaran (Late Precambrian) genus *Rangea* and related forms: Paleobiology, v. 11, p. 336–355.
Jenkins, R.J.F., 1992, Functional and ecological aspects of Ediacaran assemblages, *in* Lipps, J.H., and Signor, P.W., eds., Origin and Early Evolution of the Metazoa, New York, Plenum Press, p. 131–176.
Jenkins, R.J.F., and Gehling, J.G., 1978, A review of the frond-like fossils of the Ediacara assemblage: Records of the South Australian Museum, v. 17, p. 347–359.
Jenkins, R.J.F., Plummer, P.S., and Moriarty, K.C., 1981, Late Precambrian pseudofossils from the Flinders Ranges, South Australia: Transactions of the Royal Society of South Australia, v. 105, p. 67–183.
Laflamme, M., Xiao, S., and Kowalewski, M., 2009, Osmotrophy in modular Ediacaran organisms: Proceedings of the National Academy of Sciences, v. 106, p. 14438–14443.
Laflamme, M., Darroch, S.A.F., Tweedt, S.M., Peterson, K.J., and Erwin, D.H., 2013, The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat?: Gondwana Research, v. 23, p. 558–573.
McCall, G.J.H., 2006, The Vendian (Ediacaran) in the geological record: Enigmas in geology's prelude to the Cambrian explosion: Earth-Science Reviews, v. 77, p. 1–229.
Monastersky, R., 1998, Life grows up: National Geographic Magazine, no. 4 (April), p. 100–115.
Narbonne, G.M., 2005, The Ediacara biota: Neoproterozoic origin of animals and their ecosystems: Annual Review of Earth and Planetary Sciences, v. 33, p. 421–442.
Narbonne, G.M., 2011, When life got big: Nature, v. 470, p. 339–340.
Narbonne, G.M., Saylor, B.Z., and Grotzinger, J.P., 1997, The youngest Ediacaran fossils from southern Africa: Journal of Paleontology, v. 71, p. 953–969.
Narbonne, G.M., Laflamme, M., Trusler, P.W., Dalrymple, R.W., and Greentree, C., 2014, Deep-water Ediacaran fossils from northwestern Canada: Taphonomy, ecology and evolution: Journal of Paleontology, v. 88, p. 207–223.
Pflug, H.D., 1966, Neue Fossilreste aus den Nama-Schichten in Südwest-Afrika: Paläontologische Zeitschrift, v. 40, p. 14–25.
Pflug, H.D., 1972, Zur fauna der Nama-Schichten in Südwest-Afrika; III. Erniettomorpha, bau und systematik: Palaeontographica Abteilung A, v. 139, p. 134–170.
Pickford, M.H.L., 1995, Review of the Riphean, Vendian and Early Cambrian palaeontology of the Otavi and Nama Groups, Namibia: Communications of the Geological Survey of Namibia, v. 10, p. 57–81.
Runnegar, B.N., 1992, Proterozoic fossils of soft-bodied metazoans (Ediacaran faunas), *in* Schopf J.W., and Klein, C., eds., The Proterozoic Biosphere: A multidisciplinary study, Cambridge, Cambridge University Press, p. 999–1007.
Saylor, B.Z., Grotzinger, J.P., and Germs, G.J.B., 1995, Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand Subgroups (Nama Group), southwestern Namibia: Precambrian Research, v. 73, p. 153–171.
Saylor, B.Z., Kaufman, A.J., Grotzinger, J.P., and Urban, F., 1998, A composite reference section for terminal Proterozoic strata of southern Namibia: Journal of Sedimentary Research, v. 68, p. 1223–1235.
Schmitz, M.D., 2012, Appendix 2—Radiometric ages used in GTS2012, *in* Gradstein, F., Ogg, J., Schmitz, M.D., and Ogg, G., eds., The Geologic Time Scale 2012, Boston, Elsevier, p. 1045–1082.
Schneider, G., and Marais, C., 2004, Passage Through Time: The Fossils of Namibia, Windhoek, Namibia, Gamsberg MacMillan, 158 p.
Seilacher, A., 1989, Vendozoa: Organismic construction in the Proterozoic biosphere: Lethaia, v. 22, p. 229–239.
Seilacher, A., 1992, Vendobionta and Psammocorallia: lost constructions of Precambrian evolution: Journal of the Geological Society, London, v. 149, p. 607–613.
Seilacher, A., 2003, Ediacaran biota: The dawn of animal life in the shadow of giant protists: Paleontological Research, v. 7, p. 43–54 DOI: http://dx.doi.org/10.2517/prpsj.7.43
Vickers-Rich, P., 2007, The Nama fauna of southern Africa, *in* Fedonkin, M.A., Gehling, J.G., Grey, K., Narbonne, G.M., and Vickers-Rich, P., eds., The Rise of Animals: Evolution and Diversification of the Kingdom Animalia, Baltimore, Johns Hopkins University Press, p. 69–88.
Vickers-Rich, P., Fedonkin, M.A., Gehling, J.G., Leonov, M.V., Ivantsov, A.Yu., Komarower, P., and Fuller, M., 2007, Atlas of Precambrian Metazoans, *in* Fedonkin, M.A., Gehling, J.G., Grey, K., Narbonne, G.M., and Vickers-Rich, P., eds., The Rise of Animals: Evolution and Diversification of the Kingdom Animalia, Baltimore, Johns Hopkins University Press, p. 260–292.
Vickers-Rich, P., Ivantsov, A.Y., Trusler, P., Narbonne, G.M., Hall, M., Wilson, S.A., Greentree, C., Fedonkin, M.A., Elliott, D.A., Hoffmann, K. H., and Schneider, G.I.C., 2013, Reconstructing *Rangea*: New discoveries from the Ediacaran of Southern Namibia: Journal of Paleontology, v. 87, p. 1–15.
Xiao, S., and Laflamme, M., 2009, On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota: Trends in Ecology & Evolution, v. 24, p. 31–40.

Accepted 13 December 2014

https://doi.org/10.1017/jpa.2016.94 Published online by Cambridge University Press