Organic membranous skeleton of the Precambrian metazoans from Namibia

Jerzy Dzik

Instytut Paleobiologii PAN, Twarda 51/55, 00-818 Warszawa, Poland

ABSTRACT

Unlike the celebrated Ediacara fossils, those from the roughly coeval localities of the Kuibis Quarzite of Namibia are preserved not as imprints on the sandstone bedding plane, but three-dimensionally, within the rock matrix. The pattern of deformation and the presence of sand in lower parts of the bodies of *Ernietta*, the most common and typical of those organisms, indicate that their three-dimensional preservation is a result of a density-controlled sinking of sand-filled organic skeletons within hydrated mud layers. Specimens of *Ernietta* have preserved various stages of migration across the mud beds. Their wall material, as documented by the mode of deformation, was not only flexible, but also elastic, which makes it unlike chitin. The walls thus seem to be proteinaceous, built probably of a collagenous fabric. The *Ernietta* skeleton was built of series of parallel chambers, which excludes the possibility that these were external body covers. The chambers apparently represent walls of hydraulic skeleton units, resembling the basement membrane of chaetognaths or the notochord sheath of primitive chordates. Such chambers are widespread among the earliest fossil animals represented by fossils preserved in sandstone. The rise and fall of the Ediacaran faunas thus seem to be partially preservational artifacts. The range of its occurrence is a result of two successive evolutionary events: the origin of an internal hydraulic skeleton enclosed by a strong basement membrane, and the appearance of decomposers with abilities to disintegrate such collagenous sheaths.

INTRODUCTION

The fossiliferous horizons of the Kuibis Quarzite in Namibia are classic fossil localities of highly organized latest Precambrian metazoans (Gürich, 1930, 1933; Richter, 1955; Pflug, 1966, 1972; Glaessner 1979; Hahn and Pflug, 1985; Seilacher, 1994; Geyer and Uchman, 1995). These fossils may range into the Cambrian in Namibia (Grotzinger et al., 1995; Narbonne et al., 1997; Jensen et al., 1998). Radiometric dating of their last occurrences is 545 Ma, the same as the age of the Vendian-Cambrian boundary in northern Siberia (Bowring et al., 1993). This concurs with reports on other Cambrian occurrences of related fossil organisms (Conway Morris, 1993).

The original soft tissue is not preserved in the Kuibis Quarzite fossils; they usually are within unstratified sandstone or mudstone beds that apparently originated instantaneously as a result of a mass flow or storm events (Jenkins, 1985), and their morphology is represented only by sandstone casts of internal body cavities or collapsed bodies (Jenkins, 1992; Buss and Seilacher, 1994). The three most common Namibian fossils, *Ernietta*, *Pteridinium*, and *Rangea*, are rarely found together. Current-oriented specimens of *Rangea*, with sand-filled basal discs and collapsed fronds, occur within beds of sandstone presumably produced by local mass flows (Jenkins, 1985). *Pteridinium* specimens are restricted to storm sand layers, without any preferred horizontal orientation (Jenkins, 1992; Seilacher, 1994). Their basally strongly convex shapes suggest that they were deposited together with the suspended sediment,

and were gradually loaded with sand while sinking. Specimens of *Ernietta* occur in a dark reddish mudstone with an admixture of coarser sand grains of variable size. Their preservation history was apparently complex but informative, revealing the taphonomic mechanisms involved in the origin of the Namibian-type fossils.

THREE-DIMENSIONAL PRESERVATION OF *ERNIETTA*

The oval bodies of *Ernietta* vary greatly in size; the width of the largest specimen, GU Pf 308, is 80.5 mm, and the smallest well-preserved specimen, GU Pf 488, is 29.5 mm wide. Only one block, GU Pf 536, has specimens of *Ernietta* preserved in situ (Jenkins, 1992). It shows how the numerous drop-like bodies of *Ernietta* penetrate the mudstone bed from the surface, their blunt ends oriented downward (Fig. 1D). The muddy matrix dominates the space between the specimens, and their interior, exposed in several broken apices, is filled with a harder sandstone of a slightly lighter coloration. The rock matrix between specimens in the block is more or less homogeneous, although there is an indistinct lamination (probably a result of compaction) and a lot of mica near the top of the bed. A distinct stratification of the sediment fill can be seen within particular fossil specimens. The lower parts of several loose sectioned specimens invariably have a pure quartz sand filling, which gradually changes upward into a less-homogenous sand or mud. The longitudinally cut specimen GU Pf 308 exhibits a thin cap of white pure sand at its

tip (Birkenmajer, 1958); in its middle there is a mix of a darker mud with white sand that forms small aggregates, and the upper part is filled with homogenous mud, apparently of the same kind as that around the specimens (Fig. 1C). The gradation suggests that the fill developed in one depositional event, but this does not explain the difference between the composition of the fill and the surrounding sediment matrix.

The disparity between the sediment filling the bodies and that surrounding them is remarkable and requires a special explanation. A possibility that empty cavities left by decaying *Ernietta* bodies were gradually filled by the sediment coming from above can be rejected, because sand pressure would result in their immediate collapse (Jenkins, 1992), and there is no evidence of especially early diagenetic cementation of the surrounding rock matrix. The other interpretation, that the organisms of *Ernietta* lived immersed in the sediment with margins growing upward (Buss and Seilacher, 1994), is contradicted by similar proportions between particular morphologic structures in specimens of different size. They apparently grew in their whole volume, not marginally. Growth increments on the specimens surface are also lacking.

TAPHONOMIC INTERPRETATION OF *ERNIETTA* SHAPE VARIABILITY

Although spatial relationships between particular structures in the bodies remain constant, and only a single species is represented in the fauna (Jenkins, 1992), the shapes of particular speci-

Figure 1. *Ernietta plateauensis* Pflug, 1966 specimens from sandstone intercalations in dark mudstone and shale of Kliphoek Member of Dabis Formation, Nama Group, Namibia (under care of Hans Pflug, Lich, Germany); scale bars = 1 cm. A, B: Profile and lateral views of drop-like specimen GU Pf 182 with wall chambers filled with fine sandstone, collected in southern part of farm Aar (site E-F of Pflug, 1972), showing damaged left junction with displacement of membranes and remnants of chambers and external membrane preserved close to tip. C: Sectioned specimen GU Pf 308 showing internal fill with gradation from pure white sandstone at tip, through darker fine sandstone with patches of larger white grains, to pure mudstone above (also in Jenkins et al., 1981, Fig. 5C). When body became elongated and reached drop-like appearance, sand fill was probably compressed from sides and its originally flat upper surface deformed into concave cup shape (U shape in vertical section); this affected slightly even topmost mudstone layer within specimen, which indicates that migration of objects started after they were completely filled with sediment. D: Profile view of block GU Pf 536, muddy sandstone collected at farm Plateau (probably site C6) west of Schakalkuppe, with several three-dimensionally preserved bodies showing drop-like appearance of sinking specimen (basal view in Jenkins, 1992, Fig. 7).
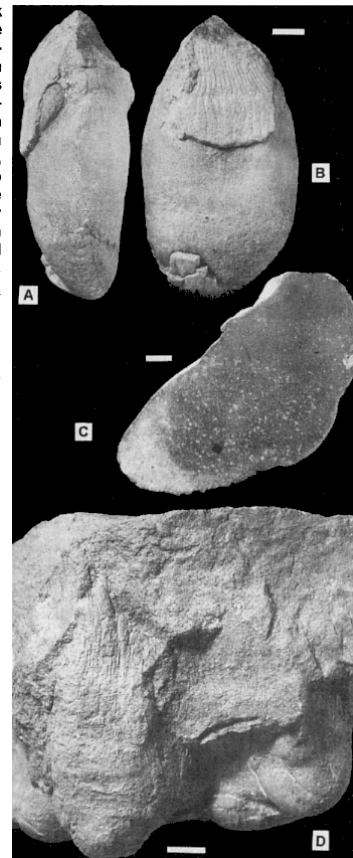
mens of *Ernietta* show great variation (Fig. 2). The shape transformations resemble consecutive stages of sinking of denser bodies in a lighter fluid. Such a causal interpretation is strongly supported by the presence of an internal fill of sand in the fossils (Fig. 3). They were obviously objects of a higher density than the surrounding hydrated muddy sediment. It is thus proposed that the *Ernietta* sand-filled bodies traveled across the hydrated mud from its surface (hemispheric load distribution), through its interior (parabolic or spatulate tip), to the boundary with the underlying, already dehydrated bed (at which the tip flattens). This taphonomic sequence closely approaches the phenomenon of a density-controlled movement within soft sediments with reversed density gradients, responsible for load casts (Birkenmajer, 1958; Allen, 1984), a phenomenon that is common in flysch sediments and has been experimentally proven (Cegła and Dżułyński, 1970; Anketell et al., 1970). Some artificially produced drop structures (Cegła and Dżułyński, 1970) exactly match the shapes observed in the population of *Ernietta*. A similar interpretation has been proposed for the Early Cambrian "sand corals" by Jensen (1997, p. 23): according to him, those structures "formed by sediment that foundered into mud similar to the formation of pseudonodules."

The origin of the sand load cannot be directly inferred from the limited available evidence, but this does not significantly interfere with the proposed interpretation of the nature of the bodies. It is possible that the organic membrane of *Ernietta* was loaded with sediment while sinking within a storm-suspended cloud of sediment, in a way similar to that proposed for *Pteridinium*. Originally, the chambered body wall of *Ernietta* could have been completely flat. The loaded bodies reached the base of the bed faster than the suspended grains, their gradation corresponding to the order of deposition. Those specimens that accumulated their sand load in the center penetrated the underlying hydrated mud layer. This requires that there was a gradation from coarse sand to increasingly fine sediment above the bed with preserved *Ernietta* bodies. This cannot be

confirmed because the block was collected from rock debris. Abiotically produced sand tongues should also be present between the *Ernietta* bodies, which is not the case, and this seems to be the main weakness of this interpretation. The alternative is that the organic wall of *Ernietta* had been initially completely filled with sand, and subsequently transported within a mass flow down the slope to a deeper region dominated by muddy sediment. In this interpretation, the fossilizing structure should be at least cup-like if not spherical; otherwise the sand load would be lost in transport. On its way to the muddy bottom, the fluidized mud completely or partially replaced the sand fill. The patches of sand grains in the middle part of their sediment fill may represent floating clasts within the fluidized mud (Nichols et al., 1994), which requires some cohesion between the quartz grains within the original sand fill, perhaps by organic material derived from the decomposition of soft tissues of the animal. Only those specimens that preserved their sand fill at least partially were involved in subsequent events.

According to J. P. Grotzinger and P. Myrow (1999, personal commun.), immediately above and below the bed that produced the *Ernietta* specimens are many beds with well-developed ball and pillow structures. The succession, which is exclusively in shallow-shelf facies, is dominated by storm-emplaced beds, many of which show signs of soft-sediment deformation. This makes the first interpretation of the origin of *Ernietta* fossils much more plausible.

Metazoans with nonmineralized organic walls are known to fossilize in sandstones of not only Vendian, but also Cambrian ages (e.g., exuvia of *Xenusion* [Dzik and Krumbiegel, 1989], and skeletons of the eldonioids [Dzik, 1991; Dzik et al., 1997]), indicating a persistence of taphonomically similar conditions. The conditions of fossilization in post-Cambrian time must have been different from today's, presumably because of the lack of efficient decomposers which would have led to the destruction of all organic skeletons. During late diagenetic stages, the organic membranes of Ediacaran metazoans must have decomposed relatively easily, and did not leave

behind a carbonaceous film, which distinguishes them from the associated multicellular plants whose protective tissues are impregnated with resistant polymers (Waggoner, 1995). Only less-resistant building materials, such as polysaccharides (cellulose, chitin) or polypeptides (collagen, elastin and its analogues), can be considered for the walls of the Ediacaran fossils.

BIOLOGICAL NATURE OF *ERNIETTA*

The deformation of the membranous walls of *Ernietta* involved not only bending and folding, but also significant expansion of its regions by the internal sand load and shrinking of its upper ends. The material that composed the wall was thus not only flexible, but also elastic. This makes *Ernietta* different from the flexible but not-so-elastic body covers of *Xenusion* or the eldonioids. The *Ernietta* wall was thus not chitinous. The most likely biological material that can be as elastic as that in the Namibian organisms is collagen (perhaps with a contribution from elastin or its invertebrate analogues; McConnell et al., 1996). It is the main
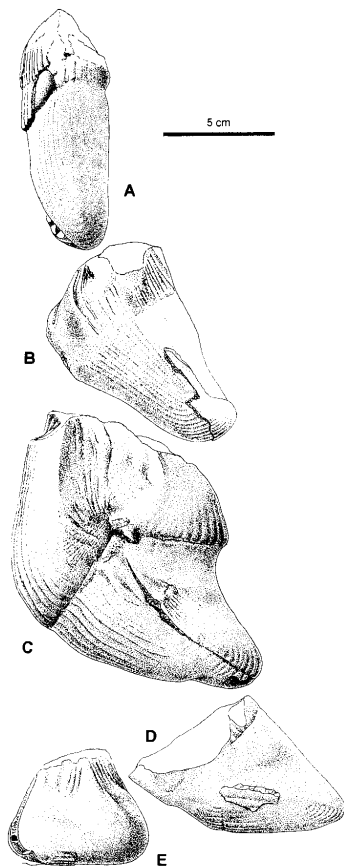
Figure 2. *Ernietta plateauensis* Pflug, 1966 from Kliphoek Member, Namibia; drawings of series of specimens in profile views show gradation of shapes, which range from vertically elongated (A, specimen GU Pf 182) through asymmetric conical (B, GU Pf 178), asymmetric with slightly flattened base (C, GU Pf 192), and asymmetric with strongly flattened base (D, GU Pf 183) to reversed conical specimen (E, GU Pf 287).

Figure 3. Interpretation of observed variety of shapes of *Ernietta plateauensis* Pflug, 1966 from Kliphoek Member, Namibia, as result of successive stages of sinking of sand-loaded membranous sacs in hydrated mud. Restorations are based on actual specimens; from left to right, GU Pf 287, GU Pf 192, GU Pf 182 (not to scale; see Fig. 1, A and B), and GU Pf 488. Subspherical shape corresponds to initial stage of sinking, body being only partially submerged in mud (part of specimen above mudstone bed is not preserved). Drop-like shape corresponds to later stage of penetration of mud; final frontal body flattening corresponds to moment of reaching boundary with underlying firm bed. Bulbous appearance of some regions of body is effect of pressure from internal sediment load. Note that all specimens are restored with three transverse zones of junction of wall chambers, which are recognizable in all well-preserved specimens. Third wall (Jenkins et al., 1981) is tentatively restored as free membrane, usually forced to parallel external wall of chambers while sinking; its margin is visible at base of mudstone bed in specimen GU Pf 287.

component of membranes underlying epithelial and muscular tissues in the metazoan body, and it enables contractile cells and tissues to perform their functions (Pedersen, 1991).

For example, the basement membrane in the Chaetognatha, which consists of the basal laminae of the epidermis and muscle cells and a layer of collagenous fibers that are obliquely oriented in alternating directions, forms a sort of exoskeleton that is both firm and flexible (Kapp, 1991; Duvert, 1991; Shinn, 1997). The coelomic cavities of the chaetognaths develop as muscula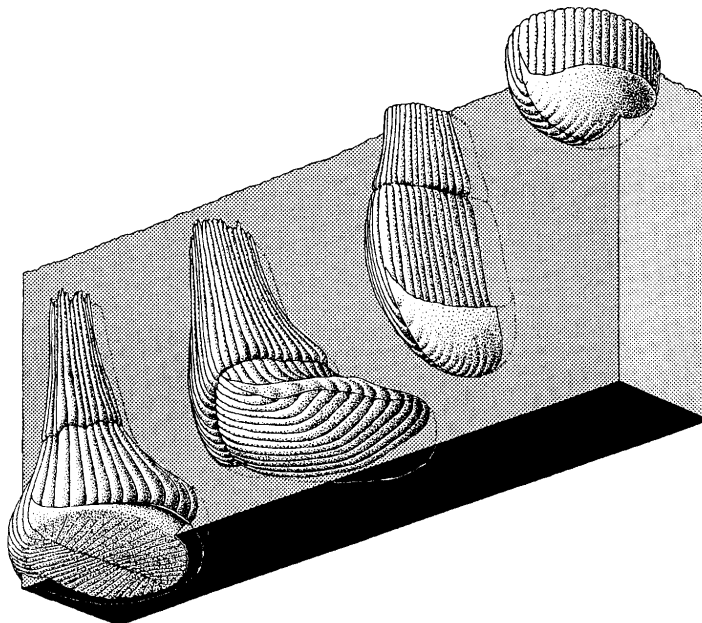r units, their walls composed of myoepithelial cells. Similarly organized is the fibrous layer of the dermis and the notochord sheath in *Branchiostoma* (Briggs and Kear, 1994; Ruppert, 1997). These collagenous sheaths are much more resistant to decay than other soft tissues and, remarkably, as a result of decay of the muscle blocks in *Branchiostoma*, the myosepta together with the connective tissue of the dermis create three-dimensional "boxes" within which the muscles shrink and collapse (Briggs and Kear, 1994). The *Branchiostoma* myomeres alternate at their dorsal contact (Simonetta and Insom, 1993), probably to attain the most geometrically and mechanically stable positions. This is exactly the situation observed in *Ernietta*, except for its much larger size and, consequently, a proportionally greater thickness of the sheath.

The most reasonable interpretation of *Ernietta* wall chambers thus seems to be that the membrane was collagenous and that it enclosed some muscular units. Such an extensive and resistant basal membrane implies a connection with a strong muscular system, as those structures are functionally connected in recent metazoans (Pedersen, 1991). If so, *Ernietta* chambers formed a sheath of serial myomeres or perhaps empty muscular vesicles, resembling those in the embryo of *Branchiostoma*. A comparable chambered organization also characterizes other Ediacaran organisms (Seilacher, 1989; Narbonne et al., 1997; Fedonkin, 1985; Ivantsov and Grazhdankin, 1997), suggesting that they represent fossilized collagenous basement membranes of muscular units of an internal hydraulic skeleton. They do not provide enough anatomical information to restore the complete anatomy of those organisms. Such evidence is available for other chambered Ediacaran organisms (especially *Dickinsonia*; reviewed by Jenkins, 1992; Dzik, 1999), but they are not necessarily closely related to *Ernietta*.

CONCLUSIONS

The absence of decomposing agents may have played a crucial role in the preservation of the

Ediacaran fauna. I suggest that the appearance of collagen-consuming decomposers led to the loss of preservation typical of those peculiar kind of fossils. The rise of the Ediacaran faunas thus seems to be mostly a result of the evolutionary development of an internal hydraulic skeleton with metameric muscular chambers enclosed by a collagenous basement membrane. Many of the Ediacaran fossils apparently represent only such an internal collagenous skeleton, not truly soft bodies. Organic membranes and cuticles were relatively resistant to decay in the Precambrian and Early Cambrian taphonomic conditions. The appearance and gradual diversification of decomposers with abilities to disintegrate collagenous and polysaccharide sheaths made this kind of preservation less and less likely. Today arthropods are the main benthic marine decomposers and their Early Cambrian evolutionary radiation seems to parallel the decrease in abundance of the Ediacaran-like fossils.

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