PROCEEDINGS B

Research

Check for updates

Author for correspondence:
E. F. Smith
e-mail: esmit163@jhu.edu

THE ROYAL SOCIETY
PUBLISHING

A cosmopolitan late Ediacaran biotic assemblage: new fossils from Nevada and Namibia support a global biostratigraphic link

E. F. Smith[1,2], L. L. Nelson[2,3], S. M. Tweedt[1,4], H. Zeng[1,5] and J. B. Workman[6]

[1]Smithsonian Institution, PO Box 37012, MRC 121, Washington, DC 20013-7012, USA
[2]Department of Earth and Planetary Sciences, Johns Hopkins University, 3400 N. Charles Street, Olin Hall, Baltimore, MD 21218, USA
[3]Department of Earth and Planetary Sciences, Harvard University, 20 Oxford Street, Cambridge, MA 02138, USA
[4]The Department of Geology and Geophysics, Yale University, 210 Whitney Ave, New Haven, CT 06511-8902, USA
[5]State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, No. 39 East Beijing Road, Nanjing 210008, People's Republic of China
[6]US Geological Survey, Geosciences and Environmental Change Science Center, Southwest Region PO Box 25046, MS 980, Denver, CO 80225-0046, USA

(iD) EFS, 0000-0001-9260-9355; SMT, 0000-0003-2114-4997

Owing to the lack of temporally well-constrained Ediacaran fossil localities containing overlapping biotic assemblages, it has remained uncertain if the latest Ediacaran (*ca* 550–541 Ma) assemblages reflect systematic biological turnover or environmental, taphonomic or biogeographic biases. Here, we report new latest Ediacaran fossil discoveries from the lower member of the Wood Canyon Formation in Nye County, Nevada, including the first figured reports of erniettomorphs, *Gaojiashania*, *Conotubus* and other problematic fossils. The fossils are spectacularly preserved in three taphonomic windows and occur in greater than 11 stratigraphic horizons, all of which are below the first appearance of *Treptichnus pedum* and the nadir of a large negative $\delta^{13}C$ excursion that is a chemostratigraphic marker of the Ediacaran–Cambrian boundary. The co-occurrence of morphologically diverse tubular fossils and erniettomorphs in Nevada provides a biostratigraphic link among latest Ediacaran fossil localities globally. Integrated with a new report of *Gaojiashania* from Namibia, previous fossil reports and existing age constraints, these finds demonstrate a distinctive late Ediacaran fossil assemblage comprising at least two groups of macroscopic organisms with dissimilar body plans that ecologically and temporally overlapped for at least 6 Myr at the close of the Ediacaran Period. This cosmopolitan biotic assemblage disappeared from the fossil record at the end of the Ediacaran Period, prior to the Cambrian radiation.

1. Introduction

Three distinctive Ediacaran assemblages have been proposed based on temporal and biostratigraphic distributions of Ediacaran fossils: the Avalon assemblage (*ca* 570–560 Ma), the White Sea assemblage (*ca* 560–550 Ma) and the Nama assemblage (*ca* 550–541 Ma) [1–3]. However, the significance of these three fossil assemblages has remained controversial, and it has been argued that they are artefacts of provinciality [4], palaeoecology [5,6] or taphonomy [7]. By contrast, others have suggested that perceived changes in diversity and disparity between the different Ediacaran assemblages represent true biotic turnover within the Ediacaran Period [8].

Disentangling provincial, palaeoecological and taphonomic biases from biotic turnover is necessary to address the causes and tempo of both evolution within the Ediacaran Period and the disappearance of the diverse array of large, macroscopic Ediacaran organisms that preceded the Cambrian radiation

of animals. This has been difficult due to the scarcity of Ediacaran fossil localities that contain overlapping biotas and temporal constraints. Strata from the few localities containing latest Ediacaran soft-bodied fossils are chronologically constrained by a combination of radioisotopic ages, chemostratigraphic correlations and overlying early Cambrian fossiliferous strata.

Fossils described from terminal Ediacaran strata include enigmatic, soft-bodied macroscopic organisms categorized in the collectively termed 'Ediacara biota' and a variety of calcifying and soft-bodied tubular fossils of uncertain taxonomic affinities. Similar to modern polyphyletic vermiform organism diversity, it is likely that Ediacaran vermiform fossils represent multiple phyla and possibly multiple kingdoms. Because anatomical details within the tubes are often poorly preserved or absent, the taxonomic affinities and phylogenetic relationships of these fossils remain problematic. The biological affinities of erniettomorphs have also been the subject of taxonomic debate, with suggestions that they should be classified as osmotrophs [2,9], chordates [10], cnidarians [11,12] or vendobionts [13,14]. Largely as a result of these taxonomic uncertainties, recent classification schemes for the enigmatic, soft-bodied Ediacara biota have focused on characterizing the morphological disparity of these Ediacaran organisms [2,8,15] rather than attempting to force them into a phylogenetic framework.

The temporal distribution of clades of Ediacara biota suggests that there is a loss in diversity between the White Sea and Nama assemblages [8]. Globally, the only two morphoclades of Ediacara biota found in latest Ediacaran strata are Erniettomorpha and Rangeomorpha. The latest Ediacaran successions with figured reports of these classic Ediacara biota are the Nama Group in Namibia [16−18] and the Dengying Formation (Fm) in South China [19]. Latest Ediacaran soft-bodied tubular body fossils have been reported from the Nama Group in Namibia [20,21], the Khatyspyt and Aim Fms in Siberia [22,23], the Dengying Fm in South China [19,24−26], the Krol and Tal Groups in India [27], the Itapucumi Group in Paraguay [28], the Tamengo Fm in Brazil [29], the Blueflower Fm of Northwest Canada [30], the Deep Spring Fm in Nevada [31−33] and the Wood Canyon Fm in Nevada [34,35]. The late Ediacaran calcifying fossils *Cloudina* and *Namacalathus* have been reported from a number of localities globally and subsequently recognized as potential late Ediacaran index fossils [36]. Despite the similar ages of the stratigraphic sequences listed above, there is little overlap in the soft-bodied fossil assemblages at these localities; specifically, the classic Ediacaran fossils reported from the Nama Group are markedly different from the range of tubular fossils found in temporally correlative strata in South China. Here, we provide the first reports of *Gaojiashania* in the Nama Group and new fossils from terminal Ediacaran strata of the Wood Canyon Fm that include erniettomorphs and a variety of tubular body fossils that support a biostratigraphic link between latest Ediacaran biotic assemblages globally.

2. Background and previous work

(a) Southern Nevada stratigraphy

The late ediacaran to early Cambrian Stirling Quartzite and Wood Canyon Fm are exposed across southern Nevada and southeastern California, and comprise up to 1 km mixed carbonate and siliciclastic succession that thickens to the northwest [37]. This study focuses on exposures of these units in the Montgomery Mountains, Nevada (figure 1a,b). The upper Stirling Quartzite is a well-sorted and crossbedded medium- to very coarse-grained quartz arenite that records deposition in a shoreface environment [40]. In the Montgomery Mountains, the Stirling Quartzite interfingers with siltstone and sandstone of the lowermost Wood Canyon Fm. The lower member of the Wood Canyon Fm has three shallowing-up parasequences of siltstone and sandstone capped by tan dolomite marker beds, and each parasequence has been interpreted to record deposition in a subtidal, shallow marine environment [41−43]. The overlying middle member of the Wood Canyon Fm incises into the lower member and is a poorly sorted, cross-stratified sandstone to conglomerate that records a fluvial environment and a prominent sequence boundary [43,44].

The first appearance datum (FAD) of the trace fossil *Treptichnus pedum* is stratigraphically located just above the second dolomite marker bed in the lower member of the Wood Canyon Fm, which contains the nadir of the basal Cambrian negative $\delta^{13}C$ excursion (BACE; figure 1b) [45]. Because the Global Boundary Stratotype Section and Point (GSSP) of the Cambrian in Newfoundland is intended to coincide with the FAD of *T. pedum* [46], the Ediacaran−Cambrian boundary in the Death Valley region has been placed at the top of the second parasequence in the lower member of the Wood Canyon Fm (figure 1b), which is consistent with chemostratigraphic age models for the Ediacaran−Cambrian boundary [45].

The only fossils previously reported from the Stirling Quartzite are poorly preserved calcareous conical fossils from carbonates in member D of the Stirling Quartzite in the northern Funeral Mountains [47] and problematic ring-shaped fossils from the upper Stirling Quartzite in the Montgomery Mountains [35]. Others have suggested that the calcareous conical fossils are abraded specimens of the late Ediacaran index fossil *Cloudina* [35], which is consistent with stratigraphic correlation to the *Cloudina*-bearing Reed Dolomite in the White−Inyo Mountains [41]. The ring-shaped structures have been tentatively identified as *Nimbia* medusoid specimens; however, they are on the surface of a single slab and could alternatively be abiotic sedimentary structures [35].

Ediacaran fossils that have been previously described from the lowermost Wood Canyon Fm include casts and moulds of tubular fossils [35]. A single external tube with weak transverse annulations was assigned to *Archaeichnium*, but, as the authors noted, the taxonomic assignment is tentative due to poor preservation and lack of additional specimens [35]. External casts and moulds of narrow annulated and smooth-walled tubes of variable sizes were identified as possible *Cloudina* [35]; however, the poor preservation and the morphology of the fossils have led others to criticize this identification [48]. A paired cast and mould specimen of a different annulated tubular fossil was identified as *Corumbella* due to the presence of a helical, tetraradial twist along the main axis of one specimen, and a single specimen of a smooth-walled tubular fossil preserved by an external layer of agglutinated mica was identified as *Onuphionella*. Additionally, fragments of sandstone with parallel structural elements were identified as *Swartpuntia*, but this is a problematic classification with no complete specimens or specimens preserving a basal stalk [35]. The
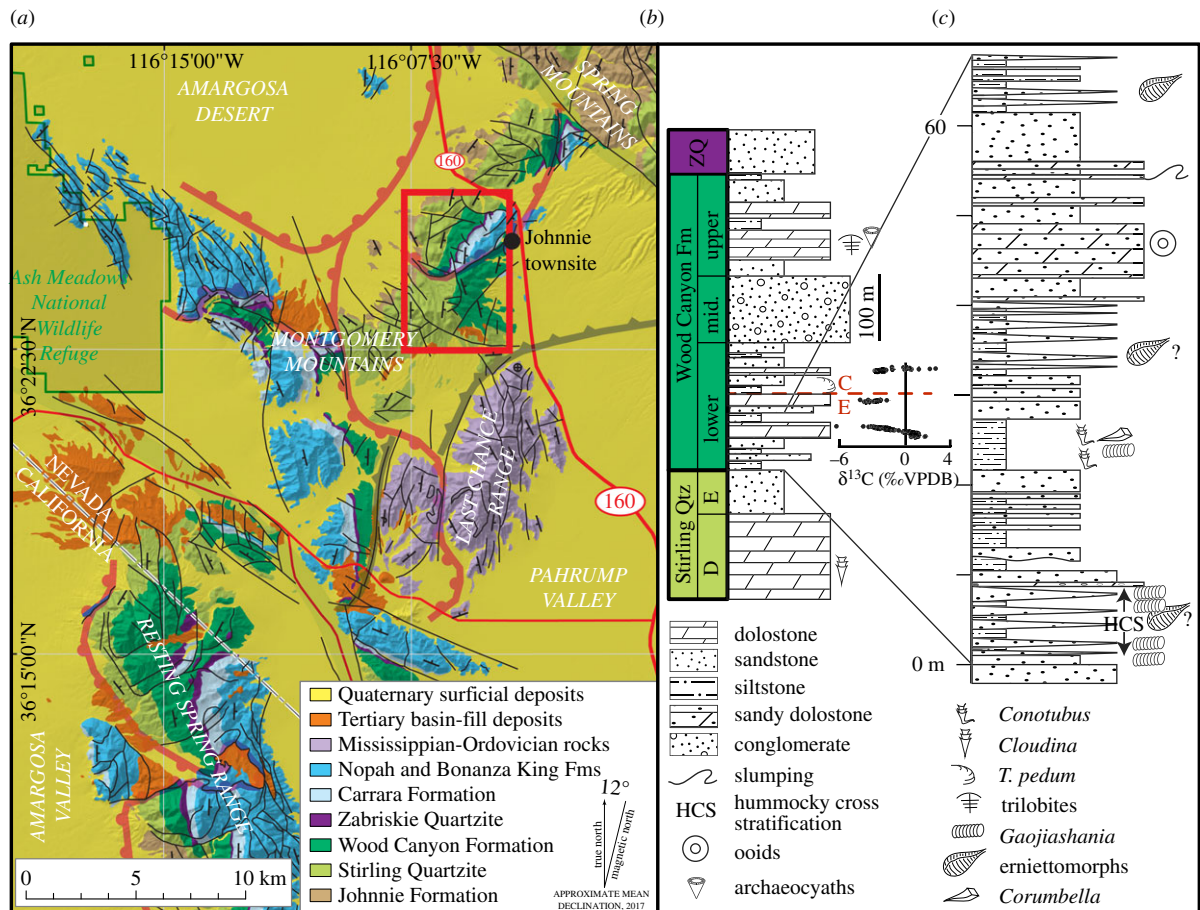
Figure 1. (a) Geologic map of the Montgomery Mountains, Nevada [38,39]. The fossils and measured sections included in this report are from within the red box near the Johnnie townsite. (b) Generalized regional stratigraphy and biostratigraphy [37], and carbon isotope chemostratigraphy. Dashed red line marks the Ediacaran–Cambrian boundary. (c) Composite detailed measured section of fossiliferous latest Ediacaran strata of the lower member of the Wood Canyon Fm. New fossil horizons are marked on the right-hand side of stratigraphic column.

ribbed, sac-like fossil *Ernietta* has also been reported from the lowest parasequence of the Wood Canyon Fm in the Montgomery Mountains, Nevada, and in the Salt Spring Hills, California [49], but has never been figured in a publication.

More recently, a number of new Ediacaran fossils—many of which are similar in morphology and preservation to the fossils in this report—were discovered in latest Ediacaran strata approximately 150 km to the northwest in the Deep Spring Fm at Mount Dunfee, Nevada [32,33]. The fossils were found below and within the large negative $\delta^{13}C$ excursion that is considered to be the BACE, and therefore, correlative with the excursion in the lower member of the Wood Canyon Fm [50]. These fossils include carbonaceous compressions of a multicellular algal fossil *Elainabella* [33], pyritized *Conotubus*, casts and moulds of *Gaojiashania* and possible *Wutubus*, and lightly pyritized compressions of vermicular fossils reported from two stratigraphic intervals of the Deep Spring Fm [32].

(b) Nama Group stratigraphy

There are multiple stratigraphic intervals in the Nama basin of Namibia containing latest Ediacaran fossils. The fossils reported here are from Donkergange Farm in the Zaris subbasin, the northern of the two subbasins that compose the Nama foreland basin [51]. In the Donkergange area, the lower part of the Kuibis Subgroup of the Nama Group is composed of the Zaris Fm, which is divided into three

formal members. The Dabis Member (Mb), a sandstone to conglomerate which sits unconformably on basement, is overlain by the Omkyk Mb, which is composed primarily of grey to black limestone grainstone (figure 2) [51,53]. The top of the Omkyk Mb is capped by stromatolitic patch reefs, which are overlain by shale, siltstone, fine sandstone, and minor calcarenite and limestone beds of the basal Hoogland Mb [54,55]. A volcanic ash bed within the lower Hoogland Mb has been dated with U–Pb zircon geochronology at 547.32 ± 0.65 Ma (figure 2) [16,52]. Above the Kuibis Subgroup, mixed sandstone and siltstone beds of the Schwarzrand Subgroup contain casts and moulds of tubular fossils with transverse annulations that were recently reported and identified as *Shaanxilithes ningqiangensis* [20].

South of the Zaris subbasin, in the Witputz subbasin of the Nama foreland, equivalent late Ediacaran strata with additional age constraints and fossils have been described [51]. At Swartpunt Farm, Namibia's youngest erniettomorphs from the Spitskopf Mb of the Schwarzrand Subgroup are temporally constrained by U–Pb zircon ash ages of 540.61 ± 0.88 Ma and 538.18 ± 1.24 Ma [52,56]. Combined U–Pb zircon geochronology and $\delta^{13}C$ chemostratigraphy suggest that the Kuibis and Schwarzrand Subgroups were deposited approximately between 548 and 538 Ma [16,52,56]. The Witputz subbasin is well known for its assemblage of soft-bodied Ediacaran biota that have been described from beds as low as the Kliphoek Mb, correlative to the Dabis Mb of the Zaris subbasin, to beds that are just below the top
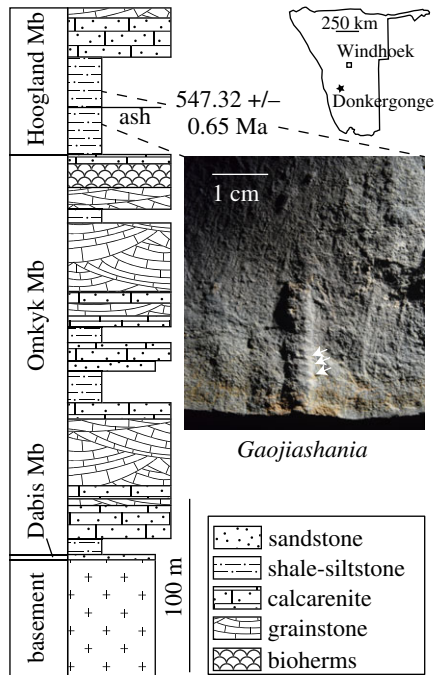
Figure 2. Generalized stratigraphic column [9], U−Pb zircon ash age [16,52] and newly discovered tubular body fossil *Gaojiashania* from the Hoogland Mb in the Zaris subbasin in Namibia. Inset map shows field locality at Donkergange Farm. White arrows point to transverse annulations on *Gaojiashania*.

of the Spitskop Mb [16]. These fossils include the frond-like *Rangea*, *Swartpuntia* and *Pteridinium*, and the sac-like *Ernietta* and *Namalia* [57−60].

3. Material and methods

In the Montgomery Mountains, Nevada, hundreds of fossils were collected, both in float and *in situ*, from the lower member of the Wood Canyon Fm. Fossils were collected from five separate fault blocks, and five detailed stratigraphic sections of the upper Stirling Quartzite through lower Wood Canyon Fm were measured within four of these fault blocks. Distinctive marker beds were used to construct a composite stratigraphic section and to place fossiliferous beds into a detailed stratigraphic framework within the lower Wood Canyon Fm (figure 1c). Detailed photographs were taken of well-preserved fossil specimens, some after whitening with ammonium chloride. The fossils are reposited at the Smithsonian Institution (catalogue numbers USNM 642300−642311). Carbonate carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopic measurements were measured from dolomite samples of the lower member of the Wood Canyon Fm (see electronic supplementary material for more details and data).

Gaojiashania specimens were discovered on Donkergange Farm in the Zaris subbasin in southern Namibia while measuring a stratigraphic section of the Hoogland Mb of the Kuibis Subgroup (figure 2).

4. New Ediacaran body fossil reports

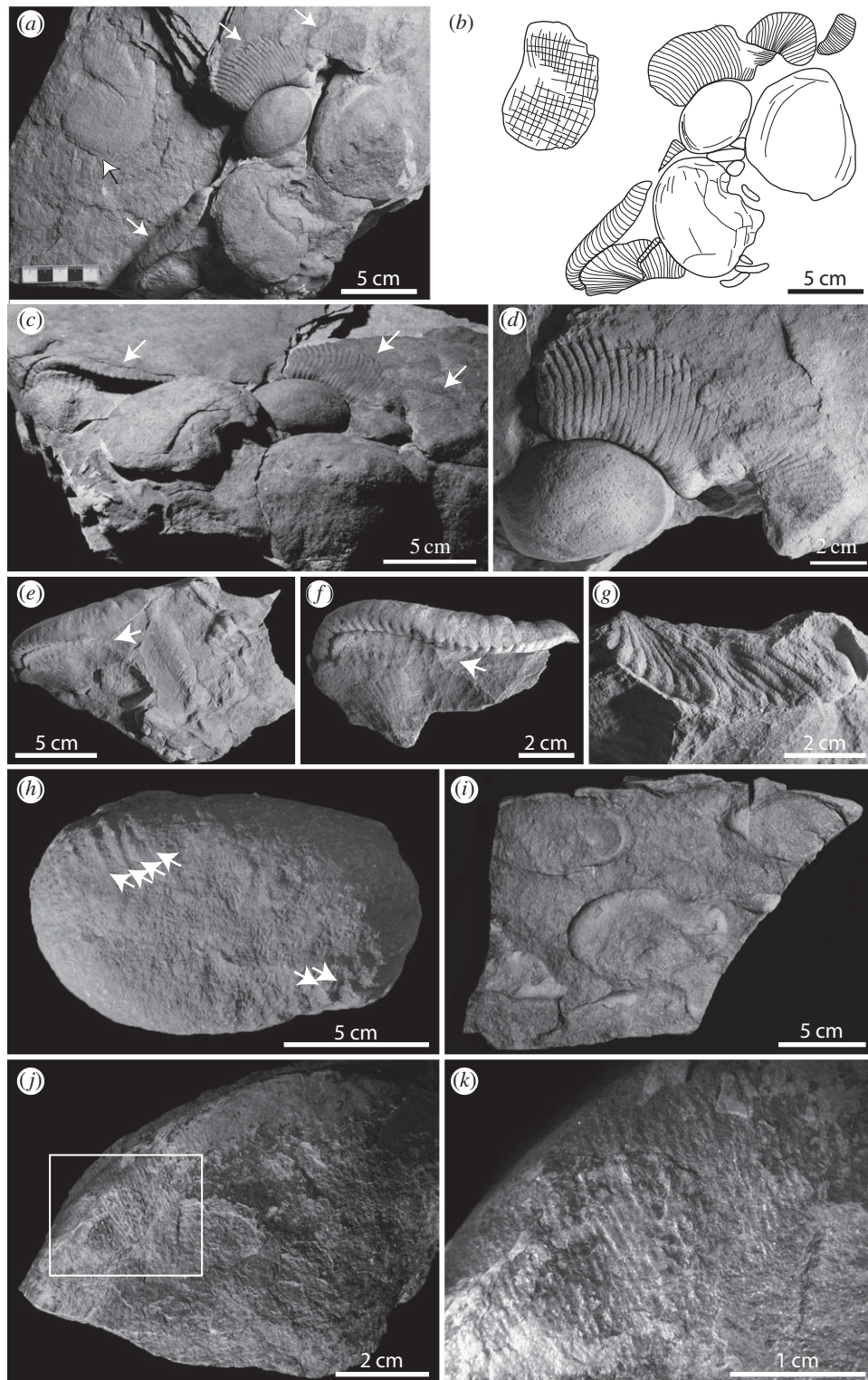## (a) *Ernietta* and problematic cross-hatched body fossil from Montgomery Mountains, Nevada

Over 10 three-dimensionally preserved *Ernietta* were discovered in the strata just below and above the first dolomite marker bed of the lower member of the Wood Canyon Fm. Like the *Ernietta* from the Nama assemblage in Namibia

[11,61,62], the Nevada specimens are preserved three-dimensionally as ribbed sacs of sandstone, surrounded by a sandstone or siltstone matrix.

Exceptionally preserved specimens occur within a 35 × 30 × 6 cm slab of tan to green micaceous fine to medium sandstone that was found in float. This slab preserves at least five *Ernietta*, a problematic cross-hatched fossil described below and three smooth cobble-sized clasts (figure 3a−g). The largest of these fossils is greater than 10 cm in length, and the complete fossils have an irregular sac-like three-dimensional morphology. The infill of each *Ernietta* is medium-grained arenitic sandstone, similar to the surrounding matrix. The outer wall has cast preservation of 1−4 mm parallel to subparallel ridges or ribs. Moulds of these ribs are also preserved in the surrounding matrix (e.g. figure 3g). In one *Ernietta*, a suture line is present and exhibits branching towards the thicker end of the organism (figure 3c,e,f). This *Ernietta* opens towards the flat rounded clast adjacent to it (figure 3a−c). Additional photographs are provided in the electronic supplementary material.

Although the *Ernietta* from the single slab described above are exceptionally preserved, many other probable *Ernietta* fossils from the Montgomery Mountains are poorly preserved. Channels are common in the lower member of the Wood Canyon Fm, and loading structures and redeposited siliciclastic cobble clasts within these channels can be easily confused with poorly preserved *Ernietta*; in some cases, it was not possible to distinguish between the two. However, the uniformity in shape, the occasional well-defined ridges visible along outer walls, and the morphological similarities to specimens from the single slab with exceptionally preserved fossils provide confidence that some of these poorly preserved specimens can be classified as *Ernietta* (figure 3h−k). On most specimens, the ridges on the outer walls are raised and spaced 0.7−1 cm apart (figure 3h), but one sac-shaped fossil preserves very fine-scale (submillimetre) ridges (figure 3j−k). We tentatively classify this specimen as an erniettomorph, but acknowledge it could be a different Ediacaran organism entirely. The *Ernietta* fossils range in length from 1.5 to 19.0 cm and in width from 1.0 to 11.0 cm. Most of the fossils are preserved three dimensionally in sandstone, giving them a ribbed, ovoid appearance (figure 3h), while others are partially filled with sediment, similar to deflated sacs (figure 3i).

Possible *Ernietta* were recovered *in situ* from sandstone channels in three distinct stratigraphic horizons: within the basal 10 m of the Wood Canyon Fm, approximately 35 m below the base of the first dolomite marker bed of the lower member of the Wood Canyon Fm and approximately 10 m above the top of this dolomite marker bed (figure 1c). We emphasize that nearly all of the specimens found in place are poorly preserved. Similar to specimens reported from Namibia [63], some of the *Ernietta* found *in situ* in Nevada were preserved clustered together within sandstone channels. Other single fossils found *in situ* were preserved in fine- to medium-grained sandstone, weathering out of siltstone or finer-grained sandstone. Because these fossils are preserved within laterally discontinuous sand channels that are common throughout the lower member of the Wood Canyon Fm, their preservation is localized along a bed. The concentration of *Ernietta* within these discontinuous sand channels suggests they could have been transported prior to burial.

Figure 3. Erniettomorphs and a problematic fossil from the lower member of the Wood Canyon Fm. (a) *Ernietta* (marked with white arrows) and problematic cross-hatched body fossil (marked with outlined white arrow). (b) Line drawing of figure 3a. (c) *Ernietta* (marked with white arrows) preserved on slab of sandstone. (d) Close-up photographs of *Ernietta* adjacent to smooth cobble. (e,f) Close-up photographs of individual *Ernietta*. White arrow marks a suture line. (g) A mould of a single *Ernietta* (specimen in (e,f)) displaying impressions of a fan-like array of subparallel ridges. (h) Weathered *Ernietta* specimen. White arrows point to parallel high-relief ridges along the edges of the fossil. (i) Slab with at least four flattened *Ernietta* preserved on it. (j) Erniettomorph with fine-scale ridges preserved on one side of the fossil. White box indicates area shown in (k). (k) Fine-scale (millimetre-size) annulations preserved on a single erniettomorph.

Inside the same slab with the well-preserved *Ernietta* fossils is a single problematic finely cross-hatched body fossil (figure 3a,b). Unlike the *Ernietta* from this slab that are three dimensionally infilled with sand, this fossil is preserved as a cast and mould in micaceous sandstone. One end of the fossil has well-preserved small- and larger-scale cross-hatching with a minimum spacing of approximately 1 mm, and the other end has faint cross-hatching with a minimum spacing of approximately 3 mm (see electronic supplementary material for more photographs). Several long parallel lines with spacing of approximately 1 cm are continuous between the ends. The fossil is subrectangular in shape, with a length of 8.4 cm and a width of 5.6 cm. The perpendicular cross-hatching is suggestive of the quadrate spicular skeletons

common in fossils of early Palaeozoic poriferans [64]. Based on the limited morphological features of this fossil, other taxonomic possibilities include a taphomorph of an erniettomorph and a cnidarian.

(b) Diversity of tubular fossils from Montgomery Mountains, Nevada

There is a diverse assemblage of tubular fossils within the lower member of the Wood Canyon Fm (figure 4a–h), some of which are similar in morphology and preservation to those reported from the Gaojiashan assemblage in South China [25,65,66] and the Deep Spring assemblage in Nevada [32]. These tubular fossils are preserved as casts and moulds in siltstone and fine sandstone, and as three-dimensional pyrite pseudomorphs. The cast and mould specimens are found on at least five bedding surfaces within the basal 10 m of the Wood Canyon Fm, and the pyritized fossils are on at least four bedding planes of green siltstone approximately 22–27 m above the base of the Wood Canyon Fm (figure 1c). This is the first report of pyritization of Ediacaran body fossils in the Wood Canyon Fm. Similar to the assemblage of tubular fossils from the Dengying and Deep Spring Fms, the tubular fossils in the Wood Canyon Fm range in size and morphology. Some are comparable to previously identified late Ediacaran taxa, while others remain difficult to classify.

(i) Conotubus

At least two specimens of Conotubus (figure 4a) were collected from a 2 m interval of micaceous green siltstone and shale in the first parasequence of the Wood Canyon Fm (figure 1c). In addition, hundreds of poorly preserved specimens of similar shape and size were collected, and likely many of these fossils are also Conotubus, despite lacking the diagnostic funnel-in-funnel morphology. The fossils range from 1 to 2 mm in diameter and from 1.0 to 2.7 cm in length and are similar in size, morphology and preservation to the Conotubus from the Dengying [65,67,68] and Deep Spring Fms [32]. The well-preserved specimens exhibit the diagnostic funnel-in-funnel structure of cloudiniids and non-uniform bends that are used to distinguish Conotubus from Cloudina [67]. All of the fossils collected are red to brown in colour, reflecting oxidation of a pyrite pseudomorph; in some specimens, the pyritized wall has been partially weathered, leaving behind a cast.

(ii) Corumbella

At least two specimens of Corumbella (figure 4d) were found in the same stratigraphic interval as the Conotubus specimens (figure 1c) and are also preserved as pyrite pseudomorphs within green siltstone. We identify these specimens as Corumbella due to a helical, tetra-radial twist down the main axis and to their morphological similarity to the paired cast and mould specimen classified by Hagadorn & Waggoner [35], which was found at a nearby locality in a similar stratigraphic position. One of the specimens exhibits faint transverse annulations (figure 4d), a feature reported on Corumbella specimens from Paraguay and Brazil [28,29,69].

(iii) Gaojiashania

Approximately 30 specimens of transversely annulated tubular fossils were collected from micaceous siltstone and fine sandstone in between coarse arenitic sandstone channels within the basal 10 m of the Wood Canyon Fm (figures 1c and 4c). These fossils are preserved as casts and moulds and range from 0.2 to 1.0 cm in diameter and from 2.7 to 6.5 cm in length, although the complete length is never preserved. The body fossils do not taper and do not have terminal ends, and they are identified as specimens of Gaojiashania due to their similarity in size and morphology to Gaojiashania specimens from the Dengying [70] and Deep Spring Fms [32]. In addition to the specimens preserved as casts and moulds, at least eight pyritized Gaojiashania (figure 4b) were found in the same stratigraphic interval as Conotubus and Corumbella (figure 1c). Two of these specimens are folded or twisted (figure 4b), which demonstrates that the walls of this organism were flexible. The pyritized specimens are also identified as Gaojiashania due to the size and morphology of these annulated tubes, and to the absence of tapering or terminals.

Owing to the similarities between the previously described single specimens of Onuphionella and Archaeichnium [35], and the Gaojiashania fossils described here, we suggest that these few former fossils are also poorly preserved, and are instead poorly preserved casts and moulds of Gaojiashania. Additionally, we dispute previous reports of casts and moulds of Cloudina [35] because the morphology and size ranges of these specimens differ from cloudiniids and more closely resemble fossils that we identify as Gaojiashania, or enigmatic smooth-walled specimens.

(iv) Other enigmatic tubular fossils

Dozens of other enigmatic pyritized tubular fossils were found in the same stratigraphic interval as the pyritized Conotubus, Corumbella and Gaojiashania (figure 4e–h), many of which remain problematic. These smooth-walled fossils range in diameter from 1 to 5 mm and in length from 0.3 to 7.0 cm, and also vary in morphology. One specimen has a narrow 1 mm-wide tube wall with non-uniform curvature (figure 4g). Its length to width ratio is much greater than that of any other smooth-walled tube from this stratigraphic interval. Another tubular specimen has continuous longitudinal ridges (figure 4h) that could represent original ridges on the tube walls or possibly differential pyritization of the original wall. Although all of these specimens are smooth-walled tubular fossils, it is likely that multiple taxa are present due to the diversity of sizes and morphologies.

(c) Gaojiashania specimen from Donkergange, Namibia

Late Ediacaran strata of the Nama Group in Namibia have yielded many well-preserved specimens of classic Ediacara biota from a number of different localities in the Witputz subbasin of southern Namibia; however, with the exception of recently discovered specimens of Shaanxilithes in the Zaris subbasin [20], no soft-bodied tubular body fossils have been reported from these strata. Here, we report new transversally annulated tubular body fossils from fine micaceous sandstone near the base of the Hoogland Mb at Donkergange Farm that are identified as Gaojiashania due to morphological similarities to those from China and the Southwest USA (figure 2). We acknowledge that the Gaojiashania fossils
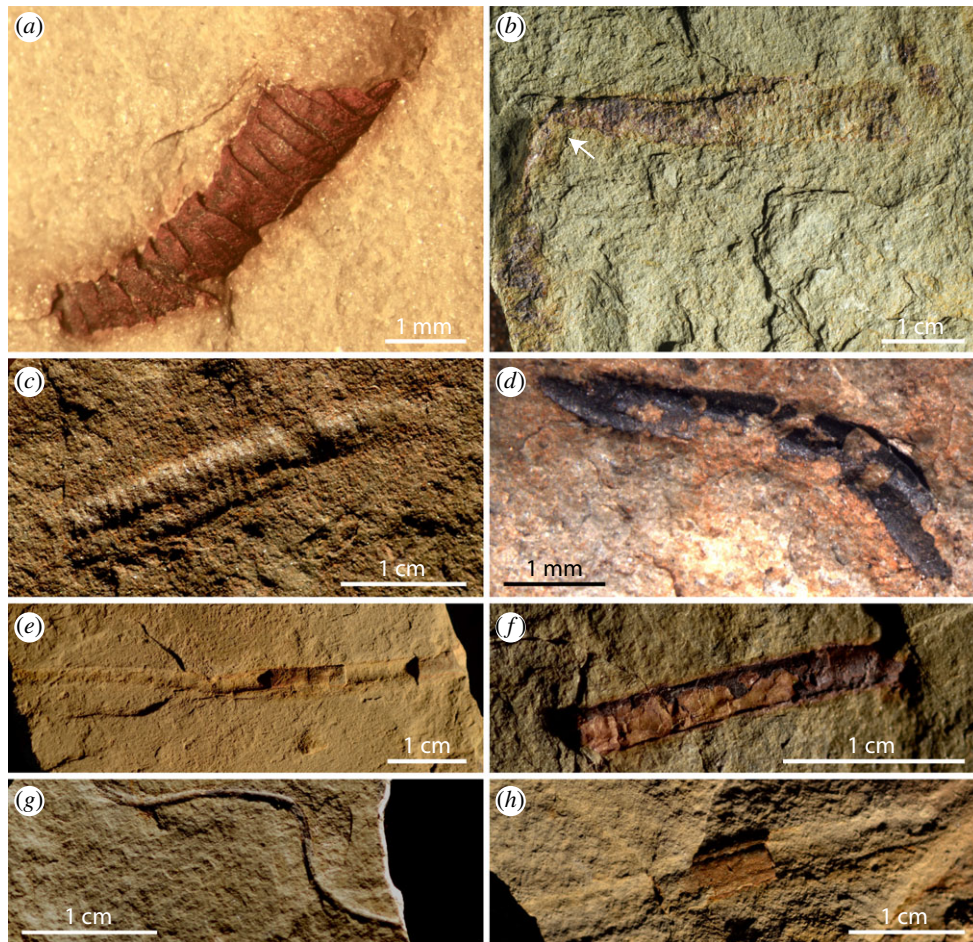
Figure 4. Diverse assemblage of Ediacaran tubular body fossils from the lower member of the Wood Canyon Fm. (*a*) Pyritized *Conotubus* specimen. (*b*) Partially pyritized *Gaojiashania* specimen. White arrow marks a fold in the fossil. (*c*) Mould of a *Gaojiashania* specimen. (*d*) Pyritized *Corumbella* specimen. (*e,f*) Pyritized smooth-walled tubular fossils. (*g*) Pyritized narrow, tubular fossil that exhibits non-uniform bends. (*h*) Partially pyritized smooth-walled tubular fossil with possible transverse ridges.

reported here could be synonymous with the *Shaanxilithes* fossils that were previously discovered at a higher stratigraphic position within the same subbasin [20]. The new fossils were found within 5 m of the Hoogland Mb ash bed that has a U–Pb zircon age of 547.32 ± 0.65 Ma [16,52], establishing them as the oldest annulated tubular body fossils globally and providing an upper radiometric limit on the FAD of *Gaojiashania*, potentially an important late Ediacaran index fossil.

5. Discussion

Although the taxonomic affinities of the tubular body fossils, erniettomorphs and other problematic body fossils are not well understood, the data presented herein and in other recent fossil reports [21,32,65,71–73] from late Ediacaran strata in a range of taphonomic modes (e.g. pyritization, carbonaceous compressions, casts and moulds) have made it increasingly apparent that a morphologically diverse assemblage of macroscopic organisms comprising at least two disparate phyla existed at the end of the Ediacaran Period. Specifically, the co-occurrences of *Ernietta*, *Conotubus*, *Corumbella*, and *Gaojiashania* in terminal Ediacaran strata in Nevada biostratigraphically link a number of late Ediacaran fossil localities globally to validate the existence of a distinctive cosmopolitan biotic assemblage at the close of the Proterozoic,

providing support that the Nama assemblage represents true biological turnover within the Ediacaran Period rather than reflecting provincial, palaeoecological or taphonomic biases.

The fossils reported from Nevada and Namibia are also globally significant because, combined with previous age constraints and fossil reports, they help temporally constrain the biostratigraphic duration of this end-Ediacaran biotic assemblage. In Namibia, the new report of *Gaojiashania* is broadly correlative to strata in the Witputz subbasin that contain *Ernietta* [51]; the stratigraphic context of these fossils combined with a previous U–Pb zircon ash age radiometrically constrains the upper limit of the FAD of both of these fossils globally to *ca* 547 Ma. In Nevada, the last appearance datum (LAD) of *Ernietta* is stratigraphically above the first dolomite marker bed of the lower Wood Canyon Fm, a bed that preserves the initial downturn of the BACE (figure 1*b,c*), establishing these *Ernietta* as the youngest definitive occurrence of classic Ediacara biota in the fossil record. Furthermore, *Gaojiashania* and *Conotubus* occur in the sediments just below this marker bed and regionally within the downturn of the BACE [32]. Therefore, the LAD of each of these fossils is within the onset of a chronostratigraphic marker of the Ediacaran–Cambrian boundary, the nadir of which is thought to be *ca* 541 Ma [52,74], or possibly as young as *ca* 539 Ma [75]. These fossil assemblages from Nevada and Namibia, combined with the existing

radiometric age constraints, demonstrate that erniettomorphs and a diversity of tubular fossils coexisted and ecologically overlapped in shallow marine environments for at least 6 Myr at the end of the Ediacaran Period.

In addition, these data provide new constraints for understanding coeval environmental and biotic change across the Ediacaran–Cambrian boundary. Currently, the three leading hypotheses for the end-Ediacaran extinction are: (i) a gradual, ecologically driven extinction, (ii) an environmentally driven extinction, similar to Phanerozoic mass extinctions, and (iii) a combined scenario in which extinction is both ecologically and environmentally driven [8]. The biotic replacement model suggests that Phanerozoic-like metazoans displaced Ediacara biota through predation and ecological engineering [8,76]. Although there is no direct evidence for predation upon the soft-bodied Ediacara biota, diversity metrics among fossils in the Nama Group compared to older assemblages have been used as evidence to support an intra-Ediacaran biotic replacement model [76]. This argument is problematic due to the pervasive preservational and geological biases in these datasets and the lack of taxonomic understanding of these biotic assemblages. Still, documentation of a greater diversity of late Ediacaran trace fossils [20,77,78] has suggested an increase in ecosystem engineering during the last few million years of the Ediacaran Period. In addition, recent reports have found a co-occurrence of cloudiniids and Cambrian small shelly fossils in a single bed, demonstrating some degree of biostratigraphic overlap between distinctive Ediacaran and Cambrian organisms [23,79,80]. However, cloudiniids are not widely reported from Cambrian strata and are still considered an end-Ediacaran index fossil, and holdover taxa are found across every Phanerozoic extinction event.

The biostratigraphic data presented herein support the notion that a distinctive Nama assemblage, compositionally different from earlier Ediacara biota assemblages, was the result of true biotic turnover within the Ediacaran Period prior to 547 Ma. This dataset demonstrates that a range of tubular organisms were coexisting with erniettomorphs for at least the last 6 Myr of the Ediacaran Period. Instead of tubular organisms gradually replacing Ediacara biota, tubular organisms and erniettomorphs are found stratigraphically overlapping from *ca* 547 Ma until the nadir of the BACE. Both at Mt. Dunfee [32] and in the Montgomery Mountains, all Ediacaran body fossil horizons, which total greater than 11 stratigraphic horizons, have been found below the nadir of the BACE. It is notable that, between these two localities in Nevada, there are four taphonomic windows [32,33] and, despite the presence of similar facies in the earliest Cambrian strata above the BACE, no body fossils have been discovered in these beds. Therefore, the disappearance of a morphologically diverse, cosmopolitan biotic assemblage of tubular fossils and erniettomorphs from the fossil record at the Ediacaran–Cambrian boundary appears to have coincided with a major geochemical perturbation, perhaps representing the first Phanerozoic-style mass extinction event.

References

1. Waggoner B. 2003 The Ediacaran biotas in space and time. *Integr. Comp. Biol.* **43**, 104–113. (doi:10.1093/icb/43.1.104)

2. Xiao S, Laflamme M. 2009 On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends Ecol. Evol.* **24**, 31–40. (doi:10.1016/j.tree.2008.07.015)

3. Xiao S, Narbonne GM, Zhou C, Laflamme M, Grazhdankin DV, Moczydłowska-Vidal M, Cui H. 2016 Toward an Ediacaran time scale: problems, protocols, and prospects. *Episodes* **39**, 540–555. (doi:10.18814/epiiugs/2016/v39i4/103886)

4. Meert JG, Lieberman BS. 2008 The Neoproterozoic assembly of Gondwana and its relationship to the Ediacaran–Cambrian radiation. *Gondwana Res.* **14**, 5–21. (doi:10.1016/j.gr.2007.06.007)

5. Grazhdankin D. 2004 Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology* **30**, 203–221. (doi:10.1666/0094-8373(2004)030<0203:PODITE>2.0.CO;2)

6. Zhuravlev AY, Vintaned JAG, Ivantsov AY. 2009 First finds of problematic Ediacaran fossil *Gaojiashania* in Siberia and its origin. *Geol. Mag.* **146**, 775–780. (doi:10.1017/S0016756809990185)

7. Narbonne GM. 2005 The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annu. Rev. Earth Planet Sci.* **33**, 421–442. (doi:10.1146/annurev.earth.33.092203.122519)

8. Laflamme M, Darroch SAF, Tweedt SM, Peterson KJ, Erwin DH. 2013 The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat? *Gondwana Res.* **23**, 558–573. (doi:10.1016/j.gr.2012.11.004)

9. Laflamme M, Xiao S, Kowalewski M. 2009 Osmotrophy in modular Ediacara organisms. *Proc. Natl Acad. Sci. USA* **106**, 14 438–14 443. (doi:10.1073/pnas.0904836106)

10. Dzik J. 1999 Organic membranous skeleton of the Precambrian metazoans from Namibia. *Geology* **27**, 519–522. (doi:10.1130/0091-7613(1999)027<0519:OMSOTP>2.3.CO;2)

11. Glaessner MF. 1979 An echiurid worm from the Late Precambrian. *Lethaia* **12**, 121–124. (doi:10.1111/j.1502-3931.1979.tb00991.x)

12. Richter R. 1955 Die ältesten Fossilien Süd-Afrikas. *Senckenbergiana Lethae.*

13. Seilacher A. 1989 Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia* **22**, 229–239. (doi:10.1111/j.1502-3931.1989.tb01332.x)

14. Bouougri EH, Porada H, Weber K, Reitner J. 2011 Sedimentology and palaeoecology of *Ernietta*-bearing Ediacaran deposits in southern Namibia: implications for infaunal vendobiont communities.

9

rspb.royalsocietypublishing.org   Proc. R. Soc. B 284: 20170934

In *Advances in stromatolite geobiology* (eds J Reitner, N-V Queric, G Arp), pp. 473 – 506. Berlin, Germany: Springer.

15. Erwin DH, Laflamme M, Tweedt SM, Sperling EA, Pisani D, Peterson KJ. 2011 The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091 – 1097. (doi:10.1126/science.1206375)

16. Grotzinger JP, Bowring SA, Saylor BZ, Kaufman AJ. 1995 Biostratigraphic and geochronologic constraints on early animal evolution. *Science* **270**, 598 – 604. (doi:10.1126/science.270.5236.598)

17. Narbonne GM, Saylor BZ, Grotzinger JP. 1997 The youngest Ediacaran fossils from southern Africa. *J. Paleontol.* **71**, 953 – 967. (doi:10.1017/S0022336000035940)

18. Elliott DA, Vickers-Rich P, Trusler P, Hall M. 2011 New evidence on the taphonomic context of the Ediacaran *Pteridinium*. *Acta Palaeontol. Pol.* **56**, 641 – 650. (doi:10.4202/app.2010.0060)

19. Chen Z, Zhou C, Xiao S, Wang W, Guan C, Hua H, Yuan X. 2014 New Ediacara fossils preserved in marine limestone and their ecological implications. *Sci. Rep.* **4**, 4180. (doi:10.1038/srep04180)

20. Darroch SAF, Boag TH, Racicot RA, Tweedt S, Mason SJ, Erwin DH, Laflamme M. 2016 A mixed Ediacaran-metazoan assemblage from the Zaris Sub-basin, Namibia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **459**, 198 – 208. (doi:10.1016/j.palaeo.2016.07.003)

21. Cohen PA et al. 2009 Tubular compression fossils from the Ediacaran Nama Group, Namibia. *J. Paleontol.* **83**, 110 – 122. (doi:10.1017/S0022336000058169)

22. Grazhdankin DV, Balthasar U, Nagovitsin KE, Kochnev BB. 2008 Carbonate-hosted Avalon-type fossils in arctic Siberia. *Geology* **36**, 803 – 806. (doi:10.1130/G24946A.1)

23. Zhu M, Zhuravlev AY, Wood RA, Zhao F, Sukhov SS. 2017 A deep root for the Cambrian explosion: implications of new bio-and chemostratigraphy from the Siberian Platform. *Geology* **45**, G38865.

24. Weber B, Steiner M, Zhu MY. 2007 Precambrian – Cambrian trace fossils from the Yangtze Platform (South China) and the early evolution of bilaterian lifestyles. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **254**, 328 – 349. (doi:10.1016/j.palaeo.2007.03.021)

25. Chen Z, Bengtson S, Zhou CM, Hua H, Yue Z. 2008 Tube structure and original composition of Sinotubulites: shelly fossils from the late Neoproterozoic in southern Shaanxi, China. *Lethaia* **41**, 37 – 45. (doi:10.1111/j.1502-3931.2007.00040.x)

26. Cai Y, Hua H, Xiao S, Schiffbauer JD, Li P. 2010 Biostratinomy of the late Ediacaran pyritized Gaojiashan Lagerstätte from southern Shaanxi, South China: importance of event deposits. *Palaios* **25**, 487 – 506. (doi:10.2110/palo.2009.p09-133r)

27. Tarhan LG, Hughes NC, Myrow PM, Bhargava ON, Ahluwalia AD, Kudryavtsev AB. 2014 Precambrian – Cambrian boundary interval occurrence and form of the enigmatic tubular body fossil *Shaanxilithes ningqiangensis* from the Lesser Himalaya of India.

Palaeontology **57**, 283 – 298. (doi:10.1111/pala.12066)

28. Warren LV, Fairchild TR, Gaucher C, Boggiani PC, Poire DG, Anelli LE, Inchausti JCG. 2011 *Corumbella* and *in situ Cloudina* in association with thrombolites in the Ediacaran Itapucumi Group, Paraguay. *Terra Nova.* **23**, 382 – 389. (doi:10.1111/j.1365-3121.2011.01023.x)

29. Babcock LE, Grunow AM, Sadowski GR, Leslie SA. 2005 Corumbella, an Ediacaran-grade organism from the Late Neoproterozoic of Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **220**, 7 – 18. (doi:10.1016/j.palaeo.2003.01.001)

30. Carbone CA, Narbonne GM, Macdonald FA, Boag TH. 2015 New Ediacaran fossils from the uppermost Blueflower Formation, northwest Canada: disentangling biostratigraphy and paleoecology. *J. Paleontol.* **89**, 281 – 291. (doi:10.1017/jpa.2014.25)

31. Signor PW, Mount JF, Onken BR. 1987 A pre-trilobite shelly fauna from the White-Inyo region of eastern California and western Nevada. *J. Paleontol.* **61**, 425 – 438. (doi:10.1017/S0022336000028614)

32. Smith EF, Nelson LL, Strange MA, Eyster AE, Rowland SM, Schrag DP, Macdonald FA. 2016 The end of the Ediacaran: two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA. *Geology* **44**, 911 – 914. (doi:10.1130/G38157.1)

33. Rowland SM, Rodriguez MG. 2014 A multicellular alga with exceptional preservation from the Ediacaran of Nevada. *J. Paleontol.* **88**, 263 – 268. (doi:10.1666/13-075)

34. Hagadorn JW, Fedo CM, Waggoner BM. 2000 Early Cambrian Ediacaran-type fossils from California. *J. Paleontol.* **74**, 731 – 740. (doi:10.1666/0022-3360(2000)074<0731:ECETFF>2.0.CO;2)

35. Hagadorn JW, Waggoner B. 2000 Ediacaran fossils from the southwestern Great Basin, United States. *J. Paleontol.* **74**, 349 – 359. (doi:10.1017/S0022336000031553)

36. Grant SW. 1990 Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *Am. J. Sci.* **290**, 261 – 294. (doi:10.2475/ajs.290.4.425)

37. Prave AR, Fedo CM, Cooper JD. 1991 Lower Cambrian depositional and sequence stratigraphic framework of the Death Valley and eastern Mojave Desert regions. In *Geological excursions in southern California and Mexico* (eds MJ Walawender, BB Banan), pp. 147 – 170. San Diego, CA: San Diego State University.

38. Burchfiel BC, Hamill GS, Wilhelms DE. 1982 Stratigraphy of the Montgomery Mountains and the northern half of the Nopah and Resting Spring Ranges, Nevada and California. Map and Chart Series MC-44. Geological Society of America, Boulder, Colorado. (doi:10.1130/0016-7606(1983)94<1359:SGOTMM>2.0.CO;2)

39. Workman JB, Menges C, Fridrich CJ, Thmpson RA. 2016 Geologic map of Death Valley National Park, Nevada and California. In *GSA Annual Meeting in Denver, Colorado.* Paper No. 245-10. See https://gsa.

confex.com/gsa/2016AM/webprogram/Paper286651.html.

40. Wertz WE. 1982 Stratigraphy and sedimentology of the Stirling Quartzite, Death Valley area, California and Nevada. In *Geology of selected areas in the San Bernardino Mountains, Western Mojave Desert, and southern Great Basin, California: volume and guidebook for field trip* (eds JD Cooper, LA Wright, BW Troxel), pp. 165 – 170. Shoshone, CA: Death Valley Publishing.

41. Stewart JH. 1970 *Upper Precambrian and lower Cambrian strata in the southern Great Basin, California and Nevada*, pp. 2330 – 7102. Washington, DC: US Govt. Print. Off.

42. Diehl PE. 1974 Stratigraphy and sedimentology of the Wood Canyon Formation, Death Valley area, California. In *Death Valley region, California and Nevada, Geol. Soc. Am., Cordilleran section guidebook*, pp. 38 – 48. See http://irmafiles.nps.gov/reference/holding/462571?accessType=DOWNLOAD.

43. Fedo CM, Prave AR. 1991 Extensive Cambrian braidplain sedimentation: insights from the southwestern USA Cordillera. In *AAPG-SEPM-SEG-SPWLA Pacific Section Annual Meeting, Bakersfield, California, March 6 – 8*. See http://www.searchanddiscovery.com/abstracts/html/1991/pacific/abstracts/0362a.htm.

44. Diehl PE. 1979 *Stratigraphy, depositional environments, and quantitative petrography of the pre-Cambrian – Cambrian wood canyon formation, death valley*. University Park, PA: Pennsylvania State University.

45. Corsetti FA, Hagadorn JW. 2000 Precambrian – Cambrian transition: Death Valley, United States. *Geology* **28**, 299 – 302. (doi:10.1130/0091-7613(2000)28<299:PTDVUS>2.0.CO;2)

46. Narbonne GM, Myrow PM, Landing E, Anderson MM. 1987 A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Can. J. Earth Sci.* **24**, 1277 – 1293. (doi:10.1139/e87-124)

47. Langille GB. 1974a Problematic calcareous fossils from the Stirling Quartzite, Funeral Mountains, Inyo County, California. *Geological Society of America Abstracts with Programs* **6**, 204 – 205.

48. Zhuravlev AY, Liñán E, Vintaned JAG, Debrenne F, Fedorov AB. 2012 New finds of skeletal fossils in the terminal Neoproterozoic of the Siberian Platform and Spain. *Acta Palaeontol. Pol.* **57**, 205 – 224. (doi:10.4202/app.2010.0074)

49. Horodyski RJ. 1991 Late Proterozoic megafossils from southern Nevada. *Geological Society of America Abstracts with Programs* **26**, 163.

50. Corsetti FA, Awramik SM, Pierce D, Kaufman AJ. 2000 Using chemostratigraphy to correlate and calibrate unconformities in Neoproterozoic strata from the southern Great Basin of the United States. *Int. Geol. Rev.* **42**, 516 – 533. (doi:10.1080/00206810009465096)

51. Germs GJB. 1983 Implications of a sedimentary facies and depositional environmental analysis of

the Nama Group in South West Africa/Namibia. *Geol. Soc. South Afr. Spec. Publ.* **11**, 89–114.

52. Schmitz MD, Gradstein F, Ogg J, Schmitz MD, Ogg G. 2012 Appendix 2-Radiometric ages used in GTS2012. *Geol. Time Scale* 1045–1082. (doi:10.1016/B978-0-444-59425-9.15002-4)

53. Smith OA. 1999 *Terminal proterozoic carbonate platform development: stratigraphy and sedimentology of the Kuibis subgroup (ca. 550–548 Ma), Northern Nama Basin.* Namibia, Southern Africa: Massachusetts Institute of Technology.

54. DiBenedetto S, Grotzinger J. 2005 Geomorphic evolution of a storm-dominated carbonate ramp (c. 549 Ma), Nama Group, Namibia. *Geol. Mag.* **142**, 583–604. (doi:10.1017/S0016756805000890)

55. Grotzinger JP, Watters WA, Knoll AH. 2000 Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. *Paleobiology* **26**, 334–359. (doi:10.1666/0094-8373(2000)026<0334:CMITSR>2.0.CO;2)

56. Saylor BZ, Kaufman AJ, Grotzinger JP, Urban F. 1998 A composite reference section for terminal Proterozoic strata of southern Namibia. *J. Sediment. Res.* **68**, 1223–1235. (doi:10.2110/jsr.68.1223)

57. Gürich G. 1929 Die bislang ältesten Spuren von Organismen in Südafrika. *Int. Geol. Congr. South Afr.* **2**, 670–680.

58. Germs GJB. 1972 *The stratigraphy and paleontology of the lower Nama Group.* Cape Town, South Africa: University of Cape Town, Dept. of Geology.

59. Saylor BZ, Grotzinger JP, Germs GJB. 1995 Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand subgroups (Nama Group), southwestern Namibia. *Precambrian Res.* **73**, 153–171. (doi:10.1016/0301-9268(94)00076-4)

60. Germs GJB. 1968 Discovery of a new fossil in the Nama System, South West Africa. *Nature* **219**, 53–54. (doi:10.1038/219053a0)

61. Pflug H-D. 1972 Systematik der jung-präkambrischen PetalonamaePflug 1970. *Paläontologische Zeitschrift* **46**, 56–67. (doi:10.1007/BF02989552)

62. Pflug HD. 1972 Zur fauna der Nama-Schichten in Sudwest Afrika. I. Pteridinia, Bau und systematische Zugehorikeit. *Palaeontographica Abteilung A* **143**, 226–262.

63. Ivantsov AY, Narbonne GM, Trusler PW, Greentree C, Vickers-Rich P. 2015 Elucidating *Ernietta*: new insights from exceptional specimens in the Ediacaran of Namibia. *Lethaia* **49**, 540–554. (doi:10.1111/let.12164)

64. Finks RM, Rigby JK. 2004 Palaeozoic hexactinellid sponges. In *Treatise on invertebrate paleontology, Part E* (*revised*), vol. 3 (eds RM Finks, REH Reid, JK Rigby), pp. 320–448. Lawrence, KS: Geological Society of America and the University of Kansas Press.

65. Cai Y, Schiffbauer JD, Hua H, Xiao S. 2011 Morphology and paleoecology of the late Ediacaran tubular fossil *Conotubus hemiannulatus* from the Gaojiashan Lagerstätte of southern Shaanxi Province, South China. *Precambrian Res.* **191**, 46–57. (doi:10.1016/j.precamres.2011.09.002)

66. Chen Z, Sun W, Hua H. 2001 Preservation and morphologic interpretation of late Sinian Gaojiashania from southern Shaanxi. *Acta Palaeontol. Sin.* **41**, 448–454.

67. Hua H, Chen Z, Yuan X. 2007 The advent of mineralized skeletons in Neoproterozoic Metazoa— new fossil evidence from the Gaojiashan Fauna. *Geol. J.* **42**, 263–279. (doi:10.1002/gj.1077)

68. Schiffbauer JD, Xiao S, Cai Y, Wallace AF, Hua H, Hunter J, Xu H, Peng Y, Kaufman AJ. 2014 A unifying model for Neoproterozoic–Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. *Nat. Commun.* **5**, 5754. (doi:10.1038/ncomms6754)

69. Hahn G, Hahn R, Leonardos OH, Pflug HD, Walde DHG. 1982 Körperlich erhaltene Scyphozoen-Reste aus dem Jungpräkambrium Brasiliens. *Geol. et Palaeontol.* **16**, 1–18.

70. Cai Y, Hua H, Zhang X. 2013 Tube construction and life mode of the late Ediacaran tubular fossil *Gaojiashania cyclus* from the Gaojiashan Lagerstätte. *Precambrian Res.* **224**, 255–267. (doi:10.1016/j.precamres.2012.09.022)

71. Schiffbauer JD, Huntley JW, O'Neil GR, Darroch SAF, Laflamme M, Cai Y. 2016 The latest Ediacaran Wormworld fauna: setting the ecological stage for the Cambrian Explosion. *GSA Today* **26**, 4–11. (doi:10.1130/GSATG265A.1)

72. Amthor JE, Grotzinger JP, Schröder S, Bowring SA, Ramezani J, Martin MW, Matter A. 2003 Extinction of *Cloudina* and *Namacalathus* at the Precambrian-Cambrian boundary in Oman. *Geology* **31**, 431–434. (doi:10.1130/0091-7613(2003)031<0431:EOCANA>2.0.CO;2)

73. Xiao S, Yuan X, Steiner M, Knoll AH. 2002 Macroscopic carbonaceous compressions in a terminal Proterozoic shale: a systematic reassessment of the Miaohe biota, South China. *J. Paleontol.* **76**, 347–376. (doi:10.1017/S0022336000041743)

74. Bowring S, Myrow P, Landing E, Ramezani J, Grotzinger J. 2003 Geochronological constraints on terminal Neoproterozoic events and the rise of Metazoan. In *EGS - AGU - EUG Joint Assembly, Nice, France, 6–11 April.* Abstract 13219.

75. Tsukui K, Ramezani J, Zhu MY, Maloof AC, Porter SM, Moore J et al. 2016 High-precision temporal calibration of the early Cambrian biotic and paleoenvironmental records: new U-Pb geochronology from eastern Yunnan, China. In *American Geophysical Union Annual Meeting,* San Francisco, CA.

76. Darroch SAF et al. 2015 Biotic replacement and mass extinction of the Ediacara biota. *Proc. R. Soc. B* **282**, 20151003. (doi:10.1098/rspb.2015.1003)

77. Jensen S, Saylor BZ, Gehling JG, Germs GJB. 2000 Complex trace fossils from the terminal Proterozoic of Namibia. *Geology* **28**, 143–146. (doi:10.1130/0091-7613(2000)28<143:CTFFTT>2.0.CO;2)

78. Macdonald FA, Pruss SB, Strauss JV. 2014 Trace fossils with spreiten from the late Ediacaran Nama Group, Namibia: complex feeding patterns five million years before the Precambrian–Cambrian boundary. *J. Paleontol.* **88**, 299–308. (doi:10.1666/13-042)

79. Yang B, Steiner M, Zhu M, Li G, Liu J, Liu P. 2016 Transitional Ediacaran–Cambrian small skeletal fossil assemblages from South China and Kazakhstan: implications for chronostratigraphy and metazoan evolution. *Precambrian Res.* **285**, 202–215. (doi:10.1016/j.precamres.2016.09.016)

80. Han J, Cai Y, Schiffbauer JD, Hua H, Wang X, Yang X, Uesugi K, Komiya T, Sun J. 2017 A *Cloudina*-like fossil with evidence of asexual reproduction from the lowest Cambrian, South China. *Geol. Mag.* 1–12. (doi:10.1017/S0016756816001187)