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GR Letter

Dickinsonia discovered in India and late Ediacaran biogeography

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ABSTRACT

The discovery of *Dickinsonia* in India allows assessment of biogeographic provinces and plate tectonic reconstructions for the late Ediacaran. The fossils were found in the roof of Auditorium Cave at Bhimbetka Rock Shelters, a UNESCO World Heritage Site for Paleolithic and Mesolithic cave art, near Bhopal, Madhya Pradesh. The fossils are identical with *Dickinsonia tenuis* from the Ediacara Member of the Rawnsley Quartzite in South Australia, and like them also show deformation due to lateral impingement, arcuate pieces missing, and alignment. They are within the late Ediacaran, Maihar Sandstone of the Bhander Group, in red sandstones formed in coastal plain paleoenvironments, including eolian, tsunamite, and intertidal bedforms. This new occurrence confirms assembly of Gondwanaland by 550 Ma, but not reconstructions adjusted for true polar wander. *Cloudina* and other small shelly marine fossils were low latitude, but vendobionts such as *Dickinsonia* were at temperate to subtropical latitudes.

1. Introduction

Dickinsonia remains the most iconic and controversial of the dazzling array of Ediacaran fossils now known worldwide (Bobrovskiy et al., 2018; Muscente et al., 2019; Retallack, 2020; Retallack and Broz, 2020). Here we report three newly discovered fossils as the first record of the genus from India, with the same proportions and segment spacing as *Dickinsonia tenuis* from South Australia (Retallack, 2007), as further evidence for the distribution and paleoenvironments of *Dickinsonia*. Revised distribution of fossils and facies allows reevaluation of a problem that has long plagued continental reconstructions for the Late Ediacaran. Ediacaran-Cambrian plate motions of 10 to 20 cm yr^{-1} (Schmidt and Williams, 2010) exceed the post-Cambrian speed limit of 10 cm yr^{-1} (Meert et al., 1993), and have been explained by true polar wander (Evans, 2003; Mitchell et al., 2011). Plate reconstructions with and without true polar wander show very different continental paleolatitudes (Torsvik and Cocks, 2013), but can be evaluated with biogeographic data (Warren et al., 2014).

2. Material and methods

Dickinsonia fossils were hiding in plain sight, on the roof of the Auditorium Cave (N22.938402° E77.613504°), the first of several Paleolithic and Mesolithic cave painting and petroglyph sites on the path into Bhimbetka Rock Shelters (Fig. 1), a UNESCO World Heritage Site, 40 km southeast of Bhopal, Madhya Pradesh (Dubey-Pathak, 2014; Bednarik, 2019). The specimens remain in place there, fully accessible, but out of reach. The delicate tracery of segments as negative reliefs on the roof 3.5 m above ground level contrasts with the crude cupule and meandering groove petroglyphs in rock near the floor of the Auditorium Cave, and also with red ochre cave paintings there (Dubey-Pathak, 2014; Bednarik, 2019). Parts of the fossils are obscured by soot, and other parts have a tracery of white waxy material (Fig. 2b), perhaps alkanes and polycyclic aromatic hydrocarbons produced by wood cooking fires (Reddy et al., 2003). These spectacular fossils are directly above an excavated early to middle Paleolithic occupation site (Bednarik, 2019).

Photogrammetric processing of multiple digital images was conducted in Agisoft Metashape Professional Edition, Version 1.5.5 Build 9097 (64 bit), an image-based 3D modeling/photogrammetric software package. Images were taken with a Nikon D90, Nikon D3100 digital SLR, and an iPhone 6 Plus at 3.5 m distance (Fig. 2). Scale for the subject was derived from a 10 cm scale card and 1 m rod with 5 cm graduations. The scales were held at arm's length toward the ceiling. All images of the subject were aligned together, appropriate error reduction perimeters were applied given the low light available in the ceiling area of the rock shelter, and constraints of movement in relation to the subject. At the conclusion of the error reduction and optimization phase a root mean square error of 0.157 pixels was reached. Factoring in an average image resolution of 0.34 mm per pixel and a scale bar error of 0.309 mm, a total photogrammetric project error of 1.1 cm was achieved. Dense

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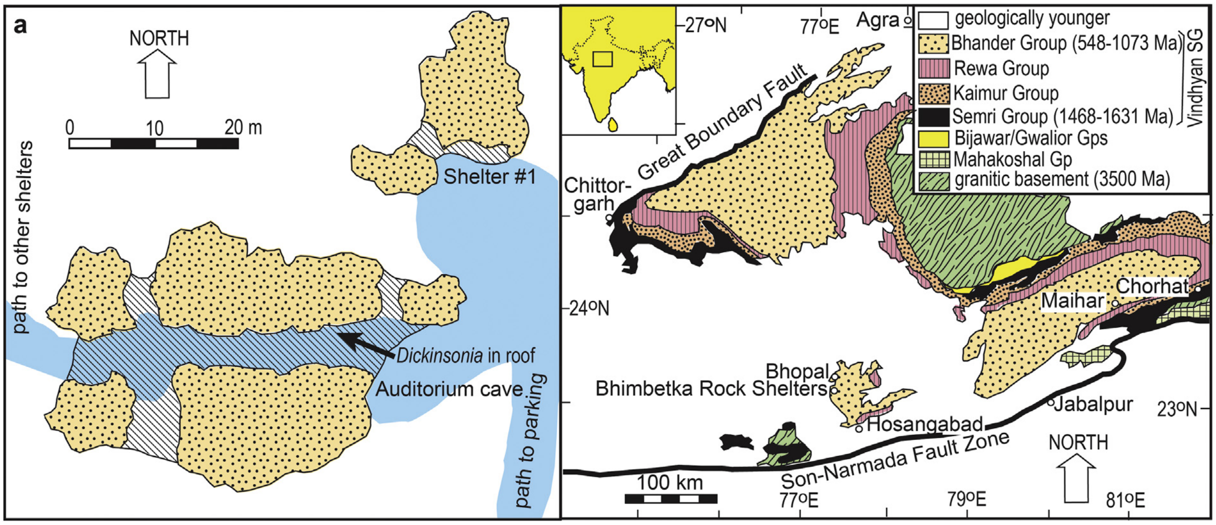

Fig. 1. Locality of newly discovered specimens of the Ediacaran fossil *Dickinsonia tenuis* from the Maihar Sandstone at Bhimbetka, India: a, site map after Bednarik (2019); b, geological map after Bose et al. (2015). Age ranges are after Gopalan et al. (2013) and Lan et al. (2020).

point clouds, meshes, digital elevation models (DEM), and digital orthorectified image mosaics (orthomosaics) were generated for the fossil-bearing surface (Matthews et al., 2016).

3. Geological setting

Indian *Dickinsonia* fossils described here are within Maihar Sandstone of the Bhander Group of the Vindhyan Supergroup (Fig. 1) near Bhopal, Madhya Pradesh (Kumar, 2012). The Maihar Sandstone has been regarded as possibly Ediacaran, based on the presence of *Arumberia* (now considered a vendobiont: Retallack and Broz, 2020) and other megafossils (Kumar and Pandey, 2008). The youngest detrital zircon date for the Maihar Sandstone is 548 Ma, which is Late Ediacaran (Lan et al., 2020). Limestones of the lower Bhander Group in the Son and Chambal Valleys are Tonian, with Pb-Pb isochron ages of 908 ± 72 Ma, 866 ± 180 Ma and 1073 ± 210 Ma, respectively (Gopalan et al., 2013). Other supposed Ediacaran megafossils have been reported stratigraphically in the Maihar Sandstone (De, 2003, 2006) and in the Lower Vindhyan (Kathal et al., 2000). Two rhyolites of the Lower Vindhyan Supergroup have yielded U-Pb zircon ages of 1631 ± 5 Ma and 1631 ± 1 Ma, resolving the Mesoproterozoic age of fossils at those stratigraphic levels (Ray et al., 2002).

Our new specimens now confirm an Ediacaran age for the Maihar Sandstone, because an age of 555.3 ± 0.3 Ma of *Dickinsonia tenuis* has been determined by U-Pb on zircons from the White Sea region of Russia (Martin et al., 2000). Poorly constrained age models for comparable *Dickinsonia tenuis* and *D. costata* in South Australia (Fig. 3) also suggest an age of ca. 550 Ma (Retallack, 2019).

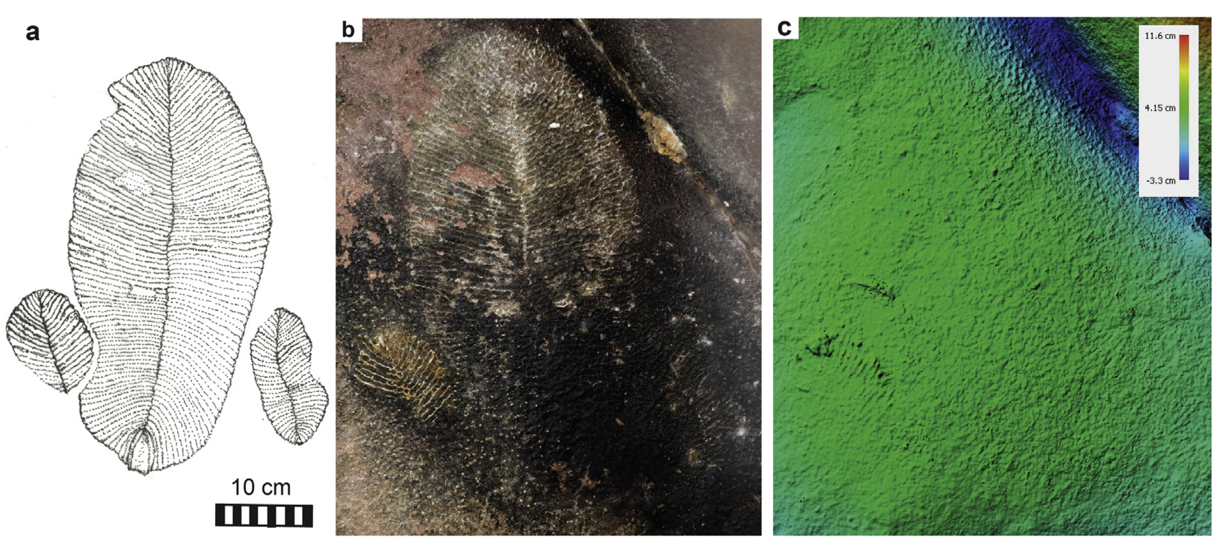

Fig. 2. Newly discovered specimens of the Ediacaran fossil *Dickinsonia tenuis* from the Maihar Sandstone at Bhimbetka, India: a, interpretive sketch; b, photograph; c, false color digital elevation model from photogrammetry.

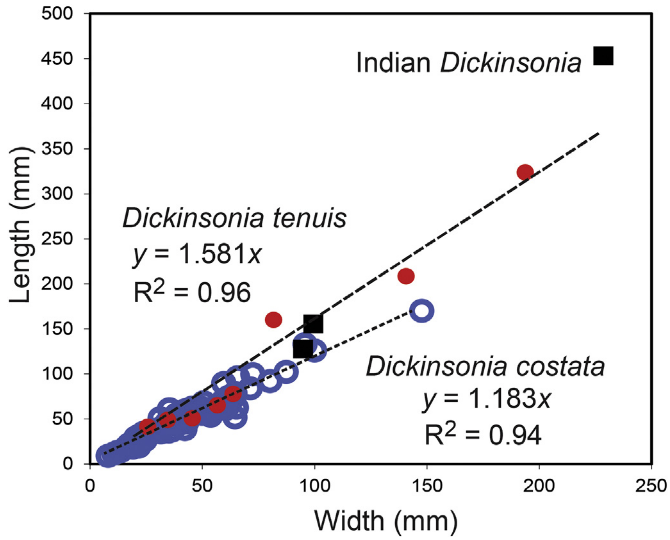

Fig. 3. Length and width of Indian *Dickinsonia* (black squares) compared with growth trajectories for *Dickinsonia tenuis* and *D. costata* from South Australia (Retallack, 2007).

The Indian fossils are within rocks previously studied nearby for granulometry (Mohammadi, 2015), comprising a succession of red medium-grained sandstones (2.2 ± 0.5 Φ of 44 measurements), interbedded with yellow fine-grained sandstones (3.5 ± 0.5 Φ of 5 measurements). These bimodal grain sizes are comparable with flagstones (2.2 ± 0.9 Φ) and interflag siltstones (4.1 ± 1.3 Φ) of an interbedded, sandstone and siltstone facies, preserving *Dickinsonia* in South Australia (Retallack, 2019). Sandstones at Bhimbetka were tested in the field with dilute acid, and were non-calcareous throughout. Most of the outcrop is "interbedded siltstone and fossil-bearing sandstone", a facies recognized in the Ediacara Member of Australia (Retallack, 2019). At the top and bottom of 3 m of that facies is channelized sandstone facies with trough cross-bedding (Fig. 4a,d), another facies common in South Australian *Dickinsonia* localities (Retallack, 2019). Three other facies, (1) red siltstone, (2) white concretionary sandstone, and (3) massive sandstone facies of the South Australian Ediacaran (Retallack, 2019) were not seen at Bhimbetka, but are recorded from the Maihar Sandstone at Maihar (Fig. 1b), 350 km to the northeast (Sarkar et al., 2011a, 2011b). An additional similarity with South Australian rocks containing *Dickinsonia* is thin, drab-haloed filament-traces branching downward from the drab upper part to the red lower part of the beds (arrows in Fig. 4C). These drab filaments are a trace fossil called *Prasinema gracile* (Retallack, 2011). *Prasinema* is a thread-like reduction halo, without grain size change, lateral continuity, or orientation orthogonal to bedding of mud cracks. Another similarity with South Australia is textured surfaces widely known as "old elephant skin", or *Rivularites repertus*, which were found in loose flagstones around Auditorium Cave (Fig. 4d; Retallack, 2019).

Comparable interbedded sandstone and siltstone facies in the Maihar Sandstone at Maihar (Fig. 1b) are interpreted (by Sarkar et al., 2011a, 2011b) as flood or shoreface traction deposits (medium-grained sandstones) alternating with eolian reworking (fine sandstones and siltstones), and this is also the most recent interpretation of the comparable South Australian facies (Retallack, 2019). The ferruginized sandstones with *Prasinema* and *Rivularites* and drab tops (Fig. 4d) are thus interpreted as paleosols on which *Dickinsonia* lived, similar to Wadni pedotype profiles (Retallack, 2013, 2016). Alternatively, this same facies in South Australia has also been interpreted as marine, or more specifically subtidal wave-base sands (Gehling et al., 2005; Evans et al., 2019). By either interpretation, the high ratio of quartz to feldspar and rock fragments in the Maihar Sandstone suggests a granitic continental

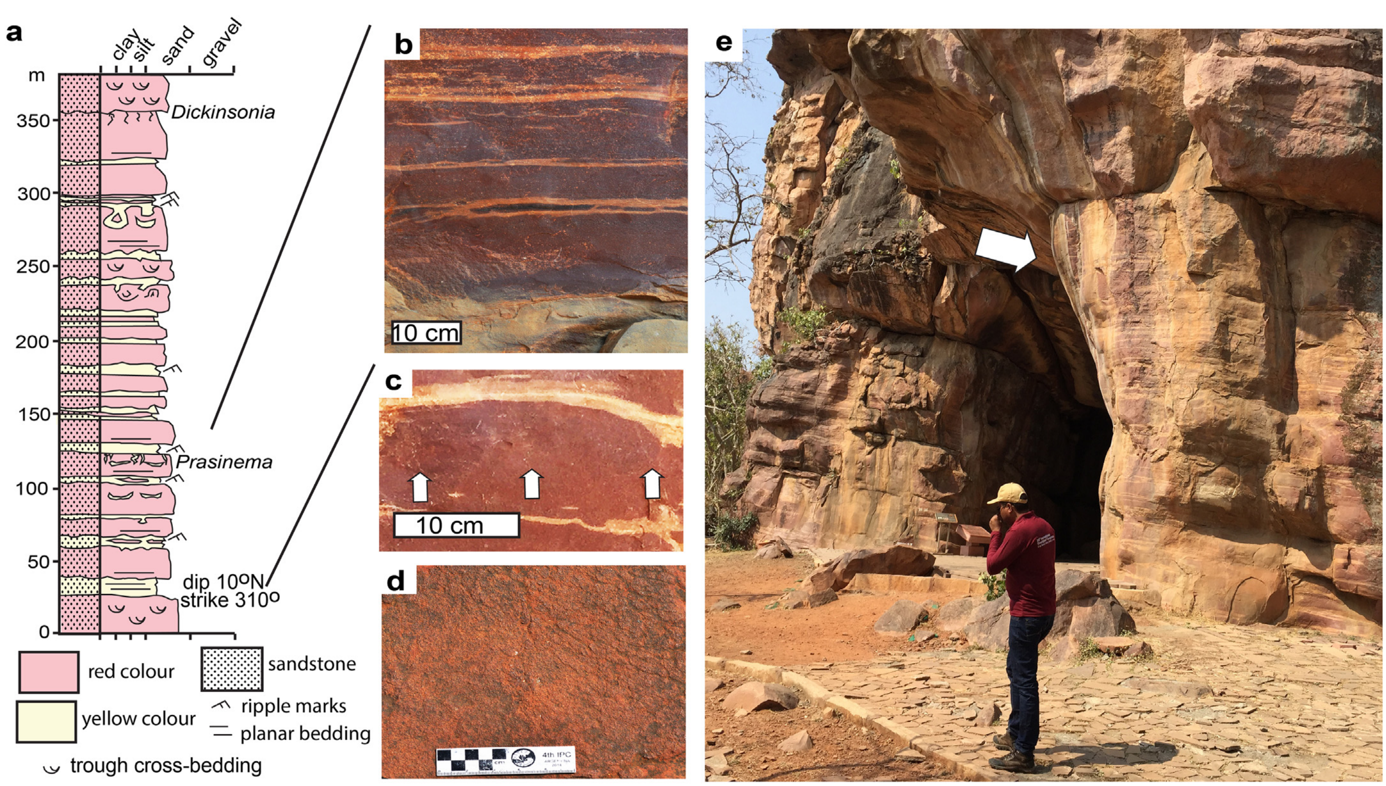

Fig. 4. Geological setting of *Dickinsonia* from Bhimbetka Rock Shelters, India: a, stratigraphic section with level of *Dickinsonia* and *Prasinema* labelled: b, detail of 40–140 cm with arrow indicating *Prasinema* drab-haloed filaments: c, "old elephant skin" (*Rivularites repertus*) trace of microbial earth crust in a loose paving slab; d, Auditorium Cave with measured section and arrow indicating level of *Dickinsonia*.

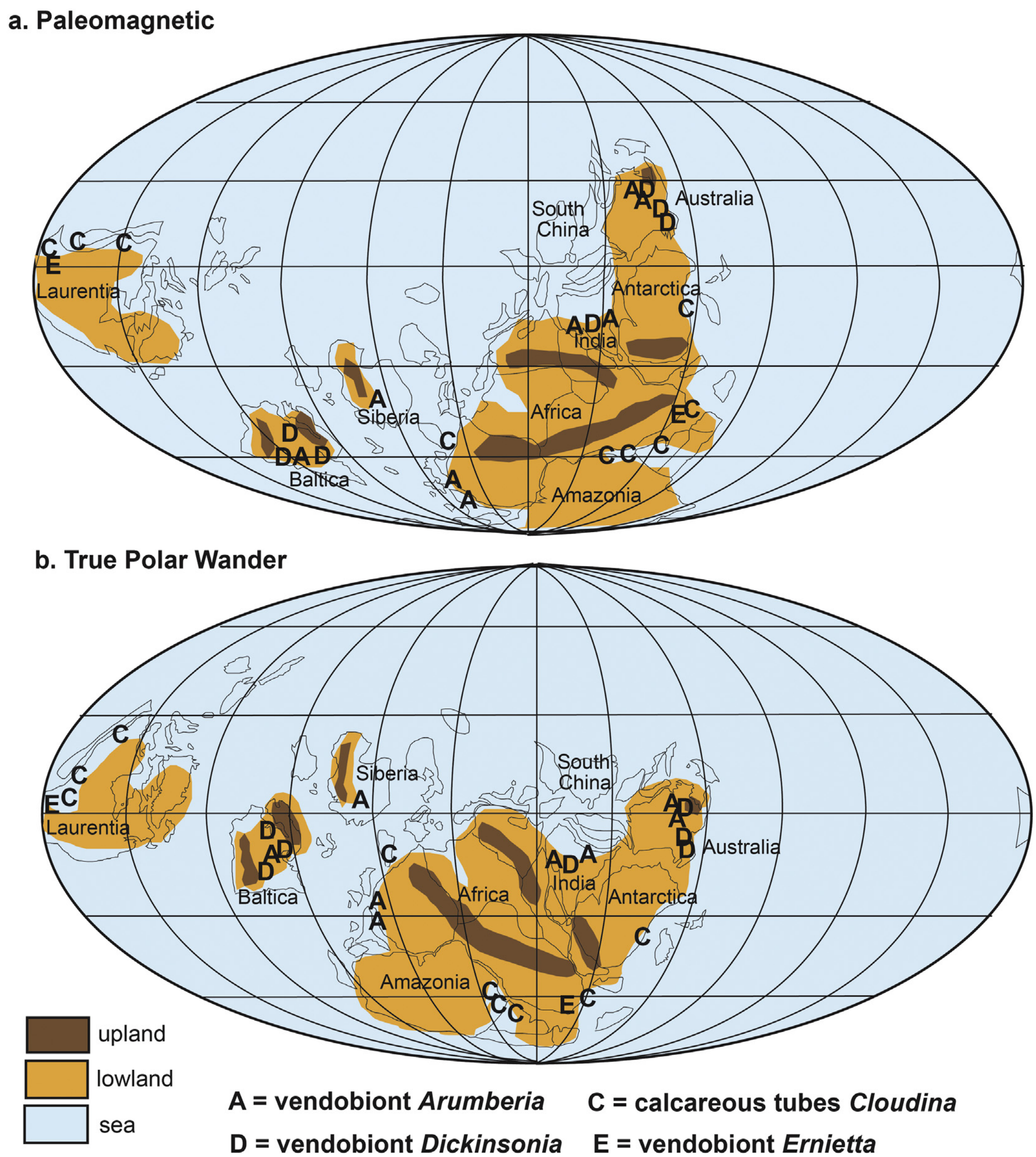

Fig. 5. Alternative plate reconstructions for the Ediacaran-Cambrian boundary ca. 540 Ma, with (a) and without (b) true polar wander (Torsvik and Cocks, 2013), showing land masses (Scotese, 2009), and fossil distributions (Muscente et al., 2019; Retallack and Broz, 2020).

provenance of low relief (Mohammadi, 2015). Paleosols and petrography at Bhimbetka are not diagnostic of climate, but eolian bedforms elsewhere in the Maihar Sandstone are evidence of semiarid paleoclimate (Sarkar et al., 2011a, 2011b).

4. Description of the fossils

The Indian fossils are up to 453 mm long and show glide symmetry along a midline of alternating lateral segmentation characteristic of the Ediacaran genus *Dickinsonia* (Retallack, 2007). They also show a subtriangular terminal segment (deltoid) at one end, but converging segments (antideltoid) at the other end, characteristic of *Dickinsonia* (Hoekzema et al., 2017). The segments also are rounded at the margin, where they are shingled as in that genus (Retallack, 2007). The Indian specimens have narrow segments and high length to width ratio like *Dickinsonia tenuis* from South Australia, and distinct from *D. costata* (Fig. 3). Russian *Dickinsonia ovata* has been proposed to be a juvenile form of *D. tenuis* (Zakrevskaya and Ivantsov, 2017), but large *D. ovata* missing in Russia are present in Australia (Fig. 3). *Dickinsonia lissa* is much more elongate than the present material and also has distinctive lateral bulges to the undulating midline, and *D. menneri* is a small form with proportionally larger and flaring terminal deltoid (Ivantsov, 2007). Our photogrammetric mapping of the fossils confirms that they are concave upwards into the overlying cover (Fig. 2c), and thus preserved as negative hyporeliefs as is common for *Dickinsonia* in South Australia (Retallack, 2007). These features, and the regular elliptical outline of the specimens, rule out interpretation of these features as parts of corrugated microbial mats, such as the ichnotaxon *Rugalichnus* (Stimson et al., 2017).

Four peculiarities of the Indian specimens are also found in South Australian Ediacaran *Dickinsonia*: impingement, missing pieces, alignment, and pustulation. Impingement of a smaller specimen to the left on the largest specimen to the right (Fig. 2a), also is known for *Dickinsonia costata* in South Australia, and has been interpreted as allelopathic reaction of encroaching sessile individuals (Retallack, 2007). Another interpretation is a double shrinkage, or piled up loose individuals (Gehling et al., 2005), but then the high relief of this structure is puzzling for unskeletonized organisms. Missing arcuate chunks of the large *Dickinsonia* from India also are known from South Australia, and have been interpreted as marginal lift-off in preparation for movement (Evans et al., 2019). But there is no seam from the portion supposedly upturned, so missing portions are more likely from current flows strong enough to overcome internal cohesion of a creature firmly attached to the substrate (Retallack, 2017). Finally, the Indian fossils are roughly aligned in the same direction, which is occasionally found in South Australian *Dickinsonia* as well, although random orientations are more common (Evans et al., 2019). In each of the Indian fossils, the deltoid end is toward the north, which is the direction of paleocurrents in the Maihar Sandstone (Bose et al., 2015). Such alignment of *Dickinsonia* has been interpreted as rheotaxis of fellow travelers, or of successive "footprints", moving in the same direction (Evans et al., 2019), like other examples of Ediacaran fossil alignment (Paterson et al., 2017). Impingement noted in the Indian specimens is evidence against rheotaxis. Alternatively, these creatures may have been sessile and grew toward a directional stimulus, such as moisture influx or maximal solar radiation during a growing season, as for oriented plants (Ehleringer et al., 1980). The appearance of oval to circular pustules on our largest specimen (Fig. 2b), is also known in *Dickinsonia* in Russia (Ivantsov et al., 2019). The biological interpretation of these pustules is uncertain: they may be reproductive structures or parasites.

Not only the paleoenvironments, but also the biological affinities of *Dickinsonia*, remain controversial. The deltoid end has been interpreted as a head by those who consider *Dickinsonia* an animal (Hoekzema et al., 2017), and as a holdfast by those preferring comparison with other sessile Ediacaran fossils (Retallack, 2016). The animal interpretation of *Dickinsonia* has been considered supported by recent isolation of steranes likely from C^{27} cholesterol in Russian specimens (Bobrovskiy et al., 2018), but such cholesterol is widespread in red algae and most fungi other than higher Ascomycota and Basidiomycota (Weete et al., 2010). Furthermore, doubt has been cast about marine habitats from low boron assay of *Dickinsonia* fossils from South Australia, Estonia, and Russian White Sea and Ural localities (Retallack, 2020). A widespread marine submergence inferred from gray Vendian shales of the Baltica continent (Scotese, 2009), may instead have been lakes (Retallack, 2020).

5. Ediacaran biogeography

New fossils from the Maihar Sandstone now allow re-evaluation of Late Ediacaran continental reconstructions, and confirm close proximity of Australia and India supported by detrital zircon age spectra (Lan et al., 2020). Unusually high plate velocities between 550 and 540 Ma have prompted suspicion that true polar wander should be added to paleomagnetically determined continental drift (Evans, 2003; Mitchell et al., 2011). Others, however, argue for drift without true polar wander (Schmidt and Williams, 2010). Both options for plate reconstruction have been visualized by Torsvik and Cocks (2013) and are shown in Fig. 5. Calcareous tubes of *Cloudina* in marine limestones with stromatolites and thrombolites (Warren et al., 2014) show a broadly equatorial distribution, but extend unrealistically into the Antarctic Circle in the true polar wander reconstruction.

There remains controversy about whether vendobionts of siliciclastic facies, *Ernietta*, *Dickinsonia*, and *Arumberia* are shallow-marine or non-marine (Retallack, 2016), but either way, there are deep ocean separations of *Ernietta* in Namibia and Nevada (Smith et al., 2017), and of *Dickinsonia* in Australian-India compared with Baltica (Fig. 5). Strong clustering of Baltic and Australian Ediacaran assemblages, which share *Dickinsonia* (Retallack, 2007; Ivantsov, 2007; Retallack and Broz, 2020), may thus reflect similar paleoenvironments rather than a single biogeographic province (Muscente et al., 2019). Thus siliciclastic vendobionts such as *Dickinsonia* and *Arumberia* were in temperate biomes in the purely paleomagnetic reconstruction (Fig. 5a). They were in non-calcareous, desert paleosols in the case of Bhimbetka (Sarkar et al., 2011a, 2011b), and in semiarid paleosols with pedogenic carbonate and gypsum in the case of Australia (Retallack, 2019; Retallack and Broz, 2020), but humid in the case of Baltica (Retallack, 2016, 2020). *Ernietta* in Namibia and Nevada were in coastal sandstones near tropical to subtropical marine carbonates with *Cloudina* (Smith et al., 2017). Although controversy remains, the Ediacaran world is coming into focus.

Authors statement

This is to declare that we, Gregory Retallack, Sharad Master, Rangit Khangar and Merajuddin Khan, all shared equally in fieldwork for this study of Ediacaran *Dickinsonia* in India. Neffra Matthews provided photogrammetric analysis. Sharad Master and Gregory Retallack provided images. Ranjit Khangar and Merajuddin Khan aided in local scientific literature and manuscript preparation.

Declaration of Competing Interest

This is to declare that we, Gregory Retallack, Neffra Matthews, Sharad Master, Rangit Khangar and Merajuddin Khan, have no conflict of interest in publication of this article on Ediacaran *Dickinsonia* in India.

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Advice and discussion came from Subir Sarkar, Ian Raine, Pamela Dexter, David Nickerson, and Mukund Sharma, and two helpful and detailed reviews from Santosh K. Pandey and Zhongwu Lan. We also thank the International Geological Congress for allowing our preconference excursion to proceed despite cancellation of the congress due to the pandemic.

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