

A new species of the iconic triradial Ediacaran genus *Tribrachidium* from Nilpena Ediacara National Park, Flinders Ranges (South Australia)

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Non-technical Summary.—The Ediacara Biota is a suite of globally distributed, exceptionally-preserved, soft-bodied organisms appearing in the fossil record from 575 million years ago to the base of the Cambrian. Nilpena Ediacara National Park (NENP) in the Flinders Ranges of South Australia preserves one of the most morphologically and taxonomically diverse assemblages of this period. *Tribrachidium heraldicum* is one of the more abundant taxa at this site (> 200 specimens) and is described as a circular organism, ~3–50 mm in diameter, showing triradial symmetry. Here we describe a new species from NENP within the *Tribrachidium* genus: *Tribrachidium gehlingi* new species. This new species has three main arm-like structures that are slightly curved and do not reach the outer margin. There are three secondary arm-like structures that are approximately half of the length of the main arms and it is, overall, lower in relief. The process of burial and deformation are unlikely to be the cause of these morphological differences because both species co-occur within the same bedding horizon.

Abstract.—*Tribrachidium heraldicum* Glaessner in Glaessner and Daily, 1959 is a triradial Ediacaran organism found in abundance within the Ediacara Member of the Flinders Ranges, South Australia. Here we report and describe a new species within the genus *Tribrachidium* Glaessner in Glaessner and Daily, 1959: *Tribrachidium gehlingi* new species from Nilpena Ediacara National Park (NENP), South Australia. *Tribrachidium gehlingi* n. sp. has low relief and three slightly curved, main arm-like structures that leave a conspicuous gap between the end of the arm-like structures and rim. In place of the ‘bulla’ found on *T. heraldicum*, there are three secondary arm-like structures approximately half of the length of the main arm-like structures. Key morphological differences between the two species are statistically significantly different. Additionally, the species occur together within the same fossiliferous event horizons, indicating that the observed morphological differences are unlikely a result of taphonomy.

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Introduction

The Ediacara Biota is a suite of exceptionally preserved soft-bodied organisms that span the last ~36 million years of the Ediacaran period (Linnemann et al., 2019). The biota is grouped into three assemblages (Waggoner, 2003): the Avalon (~575–565 Ma), White Sea (~558–555 Ma), and Nama (~549–539 Ma), of which the White Sea assemblage is the most morphologically and taxonomically diverse with 70 described genera (Droser and Gehling, 2015; Evans et al., 2022). The Ediacara Member of the Rawnsley Quartzite in the Flinders Ranges of South Australia is host to 37 of these genera (Evans et al., 2022).

Tribrachidium heraldicum Glaessner in Glaessner and Daily, 1959 is an enigmatic soft-bodied Ediacaran organism described as circular in shape with triradial symmetry (Glaessner

and Daily, 1959). The arm-like structures radiate from the center and spiral to the outer margin in a counterclockwise direction in the fossil (clockwise in life). Predominantly found in South Australia and Russia, its diameter can range from 3–50 mm, with well-preserved specimens displaying fine ridges (originally termed ‘tentacular fringe’) extending from the arms to the outer rim (Glaessner and Daily, 1959; Hall et al., 2015). Fluid dynamics conducted on a *T. heraldicum* model by Rahman et al. (2015) found that this body plan slowed water flow over the specimen and passively directed food particles to its apex, consistent with a passive suspension-feeding mode of life. The species has been found to live in populations of similar-sized individuals that are not restricted to specific paleoenvironments suggesting that they reproduced seasonally or opportunistically and that they were ecological generalists (Hall et al., 2015).

Here we describe a new species within the genus *Tribrachidium* Glaessner in Glaessner and Daily, 1959: *Tribrachidium gehlingi* new species, from Nilpena Ediacara National Park

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(NENP) in South Australia (Fig. 1.1). The occurrence of the type species and *T. gehlingi* n. sp. within the same beds is regarded as evidence that the distinct morphological features are not a product of taphonomic overprint but rather constitute original structural differences.

Geological setting

The coarse feldspathic Rawnsley Quartzite of the Adelaide Geosyncline in South Australia includes in its upper part the Ediacara Member that is uniquely characterized by the presence of exceptionally preserved Ediacara Biota. The Ediacara Member cuts deep channel and canyon incisions into underlying units from meter- to kilometer-scales (Gehling, 2000; Fig. 1.2), and the resulting accommodation space provided by this enabled the development of different facies. At NENP, fossils of the Ediacara Biota predominantly occur in four facies: Flat-Laminated to Linguoid-Rippled Sandstone (FLLRS), Oscillation-Rippled Sandstone (ORS), Planar-Laminated and Rip-Up Sandstone (PLRUS), and Channelized Sandstone and Sand-Breccia (CSSB) (Gehling and Droser, 2013; Droser et al., 2017; Tarhan et al., 2017; Reid et al., 2018).

Tribrachidium gehlingi n. sp. was found on various float pieces in an area 150 m long by 30 m wide on the southern end of Boomerang Hill, ~1.5 km NE of the original Tennis Courts (Droser et al., 2019), and probable presence on a single, continuous, excavated bedding plane (fossil bed) ('1 Tree Tribe', 1T-T) at One Tree Hill, 300 m N of the Tennis Courts, in all cases as negative hyporelief external molds. *Tribrachidium gehlingi* n. sp. occurs within the ORS Facies, which is interpreted to have been deposited between fair weather and storm wave base under oscillatory flow, characterized by thin-bedded, rippled, fine-to-coarse grained, feldspathic quartz sandstone (Tarhan et al., 2017). The float pieces on Boomerang Hill range from brown to red-brown, medium-grained sandstone with bed thickness ranging from 30–90 mm. Presence of relatively clear ripples, no adherence with underlying beds, and visible textured organic surface (TOS) in the form of micropucker indicates Mat Maturity Index 3 (MMI3, Droser et al., 2022). Despite beds with an MMI3 generally displaying a higher number of taxa, there are only two instances of other taxa co-occurring with *T. heraldicum* and *T. gehlingi* n. sp. on these pieces: *Parvancorina minchami* Glaessner, 1958 and *Dickinsonia costata* Sprigg, 1947. 1T-T on the other hand, has an MMI4, with nine taxa coexisting at a density of 40.6 individuals per m² (Droser et al., 2022).

Materials and methods

We have identified 95 specimens of *Tribrachidium gehlingi* n. sp. from 78 float pieces on Boomerang Hill, and two probable specimens on 1T-T bed, all at NENP, South Australia. Specimens were documented through photographs using a Canon EOS 50D SLR camera with a Canon Compact Macro Lens EF 50 mm, replica casts made with Splash! dental putty, and three-dimensional (3D) surfaces using a HDI Compact C506 laser scanner (accuracy reported to 12µm). The morphologies of *T. heraldicum* and *T. gehlingi* n. sp. were primarily compared using the 3D surface models in the MeshLab software v.2022.02 (Cignoni et al., 2008).

To quantitatively capture differences in morphology between *Tribrachidium heraldicum* and *T. gehlingi* n. sp., linear measurements were taken of various features (see Supplementary material). Of the 95 specimens, only 46 *T. gehlingi* n. sp. were complete enough to measure. Similarly, only 57 *T. heraldicum* were available to be measured. First, maximum diameter and height was measured for each specimen. Height was transformed into a ratio by dividing by diameter. Accordingly, mean arm width and secondary arm/bulla width (per specimen) measurements were taken from valley to valley. Linear measurements were taken of the mean arm length and width, and the mean secondary arm/bulla length and width per specimen. The mean distance of the arm per specimen was measured from the furthest point of the arm from the center perpendicular to the outer rim. Finally, the mean arm curvature was quantified by creating a straight line connecting each end of the arm and measuring from the center of said line to the peak of the arms' curve. Raw measurements were natural logarithm-transformed to normalize the data.

To determine whether the measurements were statistically significantly different, unpaired Welch's t-tests were performed in the R Statistical Environment v.4.0.3 (R Core Team, 2020) using 't.test' function in car v.3.0.11 (Fox and Weisberg, 2019) on the natural logarithm-transformed data. Diameter, ratio of height, arm distance from outer margin, arm length, secondary arm/bulla width, and secondary arm/bulla length were subjected to the t-test. Differences between the species for arm length, arm distance, and curvature were also compared directly with diameter. The null hypothesis of no difference was rejected if the significance level (P-value) was equal to or less than 0.05.

Repositories and institutional abbreviations.—Types examined during this study are deposited in the South Australian Museum—Paleontological Collections (SAMA P); nontype, figured material has been left in situ at NENP.

Systematic paleontology

Class, Order, and Family unassigned

Genus *Tribrachidium* Glaessner in Glaessner and Daily, 1959

Type species.—*Tribrachidium heraldicum* Glaessner in Glaessner and Daily, 1959.

Emended diagnosis.—Disc-shaped, hyporelief fossil molds, ~3–50 mm in diameter, of a slightly convex organism. Dorsal side with three raised arms radiating from the center and curving clockwise (in life), tapering to their extremities. A small, central, Y-shaped groove is occasionally recognizable between the arms. Additional, smaller raised structures occupy part of each interbrachial space. Raised fine lines sometimes evident radiating from the center to the perimeter, occasionally only preserved just inside the perimeter (modified from Glaessner and Wade, 1966, p. 626).

Tribrachidium gehlingi new species
Figures 2, 4–6

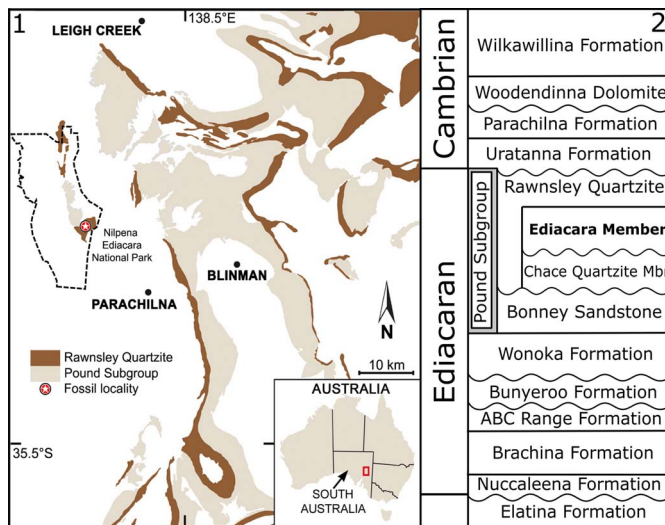


Figure 1. (1) Map indicating the location of Nilpena Ediacara National Park (NENP), Flinders Ranges, South Australia, the Pound Subgroup (part of geosyncline), and Rawnsley Quartzite, which contains the fossiliferous members. (2) Schematic sequence illustrating the occurrence of the Ediacara Member. Both modified from Gehling and Droser (2009).

Type specimens.—Holotype: SAMA P59794; Paratypes: SAMA P59795, P59796, P59798, P59800–P59806.

Diagnosis.—Circular triradial fossil, ranging from 10–50 mm in diameter. Low relief dome-shaped in life. Three arms radiating from the central area but do not touch in the center. Arms curved clockwise in life and extending ~50% from the center to the outer margin of the organism, leaving a conspicuous flat rim of ~50% around the perimeter. Raised, shorter, slightly curved, secondary arms between each main arm. Very faint outer margin. Occasional presence of numerous fine, raised lines just inside the perimeter.

Occurrence.—The new species is present at two sites at Nilpena Ediacara National Park, Flinders Ranges, South Australia: Ediacara Member, upper Rawnsley Quartzite at Boomerang Hill, where specimens appear to be from the same event horizon, because the float pieces display similar lithologies and follow the same horizon along the ridge. Additionally, two very small, probable specimens from One Tree Tribe bed (1T-T).

Description.—Fossils found preserved on the undersides of beds as a negative, shallow hyporelief (Figs. 2.2–2.9, 4). Diameter ranging from 10–50 mm with the main arms ranging in length from 3 mm long and 0.6 mm wide in the smallest specimens to 25 mm long and 4 mm wide in the largest. The arms do not join at the center (Figs. 2.5, 2.7, 5.1), tapering distally and extending approximately half of the diameter, leaving a distinct rim between the end of the arms and the outer margin. Between the three main arms are three secondary arms, 2.6 mm long and 0.7 mm wide in the smallest specimens to 19.5 mm long and 4.2 mm wide in the largest. The three secondary arms start farther out from the center, and do not curve as much as the main arms. Each secondary arm appears to be associated with a main arm,

nested in the strong curvature of the main arm immediately to its left in the fossil (Figs. 2.2, 2.7, 5.1), or to its right in life.

Fine ridges are each up to 3 mm long and ~0.8 mm wide and are found around the perimeter of at least six specimens of *Tribrachidium gehlingi* n. sp. (arrows in Fig. 2.3, 2.5, 2.6, Fig. 5.4). These fine ridges are angled in approximately the same direction as the main arms' rotation. Where best preserved, there are ~20 ridges per 10 mm of perimeter, which extrapolates to some 300 around the largest specimens.

In 20 instances, convex structures are found overlapping or next to *Tribrachidium gehlingi* n. sp. specimens and display a similar diameter (Fig. 5).

Etymology.—*Tribrachidium gehlingi* n. sp. is named in honor of Jim Gehling for his decades of dedicated research to the geology of the Flinders Ranges and the Ediacaran fossils, and mentor to both of the authors.

Materials.—Ninety-five specimens located on float pieces along a single ridge (Boomerang Hill) and two specimens at One Tree Hill, all within Nilpena Ediacara National Park, Flinders Ranges, South Australia.

Remarks.—Several morphological similarities place *Tribrachidium gehlingi* n. sp. within the *Tribrachidium* genus, e.g., triradial symmetry of three main arms curving from the center, fine periphery fringe preserved, and occasional associated convex hyporelief structures (as described here and by Hall et al., 2015). The main differences that place *T. gehlingi* n. sp. as a new species are the three main arms being consistently shorter and less curved, leaving a gap between the end and outer margin, extended secondary arms that reach approximately half the length of the main arms, and a low relief independent of size. All morphological differences are present across all size classes for both species.

The presence of the described morphological differences on specimens of the same size of both *Tribrachidium heraldicum* and *T. gehlingi* n. sp. supports the distinction of different species. Furthermore, the presence of both species together in not only the same event horizon, but the same float pieces (Fig. 4) support that *T. gehlingi* n. sp. is not simply a taphomorph of *T. heraldicum*.

Results

On Boomerang Hill, there were 95 specimens of *Tribrachidium gehlingi* n. sp. and 80 specimens of *T. heraldicum*, the latter displaying a narrow size range of 5–10 mm in diameter at this locality. Overall, 46 *T. gehlingi* n. sp. and 57 *T. heraldicum* from across NENP were complete enough to study in detail to obtain information on overall size and the proportions of different morphological features for both species. Visual assessment of scan cross sections determined a wavelength pattern of the arms and secondary arms as independent structures for *T. gehlingi* n. sp. In comparison, for *T. heraldicum*, each 'bulla' (which is the slightly convex structure near the bend of each arm) was found to be attached to its corresponding arm. However, a slight wavelength pattern of the arm and its related 'bulla' was still observed (see Appendix 1). Unpaired Welch's t-test indicated

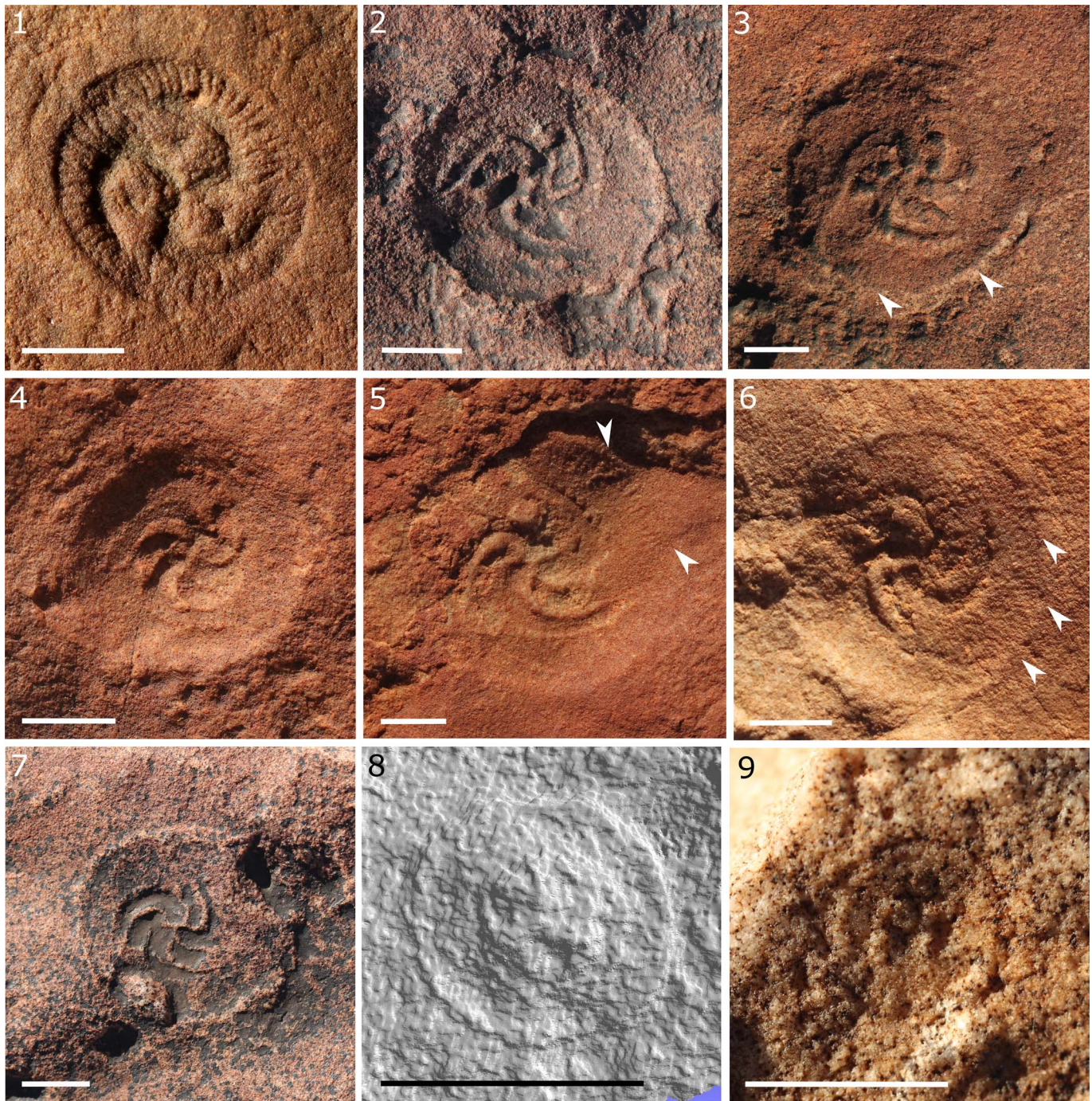


Figure 2. (1) *Tribrachidium heraldicum* Glaessner in Glaessner and Daily, 1959, SAMA P12898 (holotype). (2–9) *Tribrachidium gehlingi* n. sp. from Nilpena Ediacara National Park (NENP), Flinders Ranges, South Australia: (2) SAMA P59794 (holotype); (3) SAMA P59803 (paratype); (4) SAMA P59796 (paratype); (5) F18; (6) F42; (7) SAMA P59802 (paratype); (8) IT-T Bed Specimen; (9) SAMA P59800 (paratype). White arrowheads indicate preserved fine ridges on *T. gehlingi* n. sp. Scale bars = 10 mm.

that the mean diameters of *T. heraldicum* (across NENP) (3.1–39 mm) and *T. gehlingi* n. sp. (10–50 mm) and height ratios (0.0123–0.267 and 0.010–0.136, respectively) are statistically significantly different from each other (Table 1).

Distance from the furthest point of each arm to the outer rim had a range of 0.4–4.6 mm for *Tribrachidium heraldicum* (mean 2.1 mm), which was 12% of the diameter, whereas *T. gehlingi* n. sp. had a range of 3–10 mm (mean 6.5 mm) at 20% of the diameter. The log-transformed means were suggested to be

statistically significantly different in a Welch's t-test (Table 1), with each species displaying linear relationships (Fig. 3.1). When viewing the fossils, the arms of *T. heraldicum* tended to reach most of, if not all, the way to the outer margin of the organism, whereas a discernable gap is present for *T. gehlingi* n. sp.

Arm length for *Tribrachidium heraldicum* ranges from 1.9–30 mm (mean 12.3 mm) which is ~75% of the diameter. *Tribrachidium gehlingi* n. sp. has a range of 3–25 mm (mean 15.1 mm) which is only 48% of the diameter. When plotted, they form two

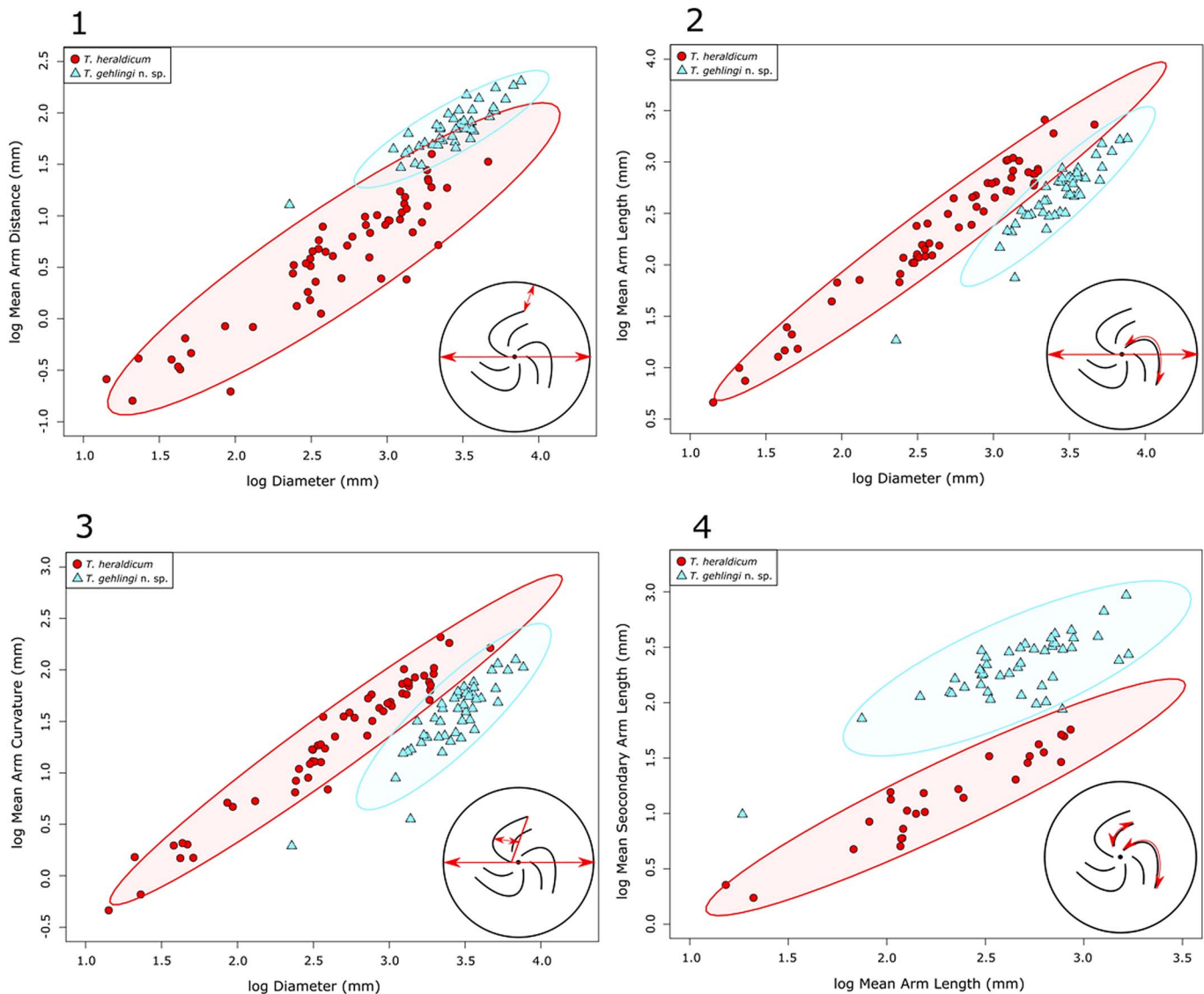


Figure 3. Linear measurements of *Tribrachidium gehlingi* n. sp. and *T. heraldicum* Glaessner in Glaessner and Daily, 1959: (1) Diameter vs Mean Arm Distance (from outer margin); (2) Diameter vs Mean Arm Length; (3) Diameter vs Mean Arm Curvature; (4) Mean Arm Length vs Mean Secondary Arm Length. Colored ellipses represent 95% confidence intervals of the fitted linear models. All measurements taken in millimeters and all values natural logarithm-transformed. Schematic depictions of the measured traits illustrated in bottom right corner of each plot.

distinct groups with only slight overlap (Fig. 3.2) and unpaired Welch's t-test suggested that they are statistically significantly different (Table 1). Overall, *T. gehlingi* n. sp. has wider arms with a mean of 2.55 mm (range 0.6–4.03 mm) compared to a mean of 1.82 mm for *T. heraldicum* (range 0.3–4.3 mm). The relative curvature of the arms had similar means for *T. heraldicum* and *T. gehlingi* n. sp.: mean 4.43 mm (range 0.7–10.2 mm) and mean 4.99 mm (range 1.7–8.2 mm), respectively. However, when compared to diameter, the species are distinct (Fig. 3.3). The arms of *T. heraldicum* appear to join in the center of the organism, whereas the arms of *T. gehlingi* n. sp. do not join in the center (Figs. 2.2–2.9, 4.2–4.4, 4.6, 4.7).

Unpaired Welch's t-test indicated that the secondary arm/bulla length of each species were statistically significantly different from each other (Table 1) and displayed independent linear trends when plotted (Fig. 3.4). *Tribrachidium heraldicum* bulla

measured 1.2–5.8 mm in length (mean 3.3 mm) at 27% of the arm length. Comparatively, *T. gehlingi* n. sp. secondary arms measured 2.6–19.5 mm (mean 10.5 mm) at 69% of arm length. Similar to arm width, *T. gehlingi* n. sp. had wider secondary arms overall than *T. heraldicum* bulla width, at a mean of 2.71 mm (range 0.7–4.21 mm) compared to a mean of 1.88 mm (range 0.6–3.13 mm) for *T. heraldicum*. Unpaired Welch's t-tests revealed that arm and secondary arm/bulla widths were not statistically significantly different within each species, however the main arm and secondary arm/bulla widths between species were statistically significantly different (Table 1).

Both species within the fossil beds appear to present little deformation, displaying consistent morphologies across bedding planes. Fine ridges are preserved in most instances for *Tribrachidium heraldicum* on the periphery of the organism and

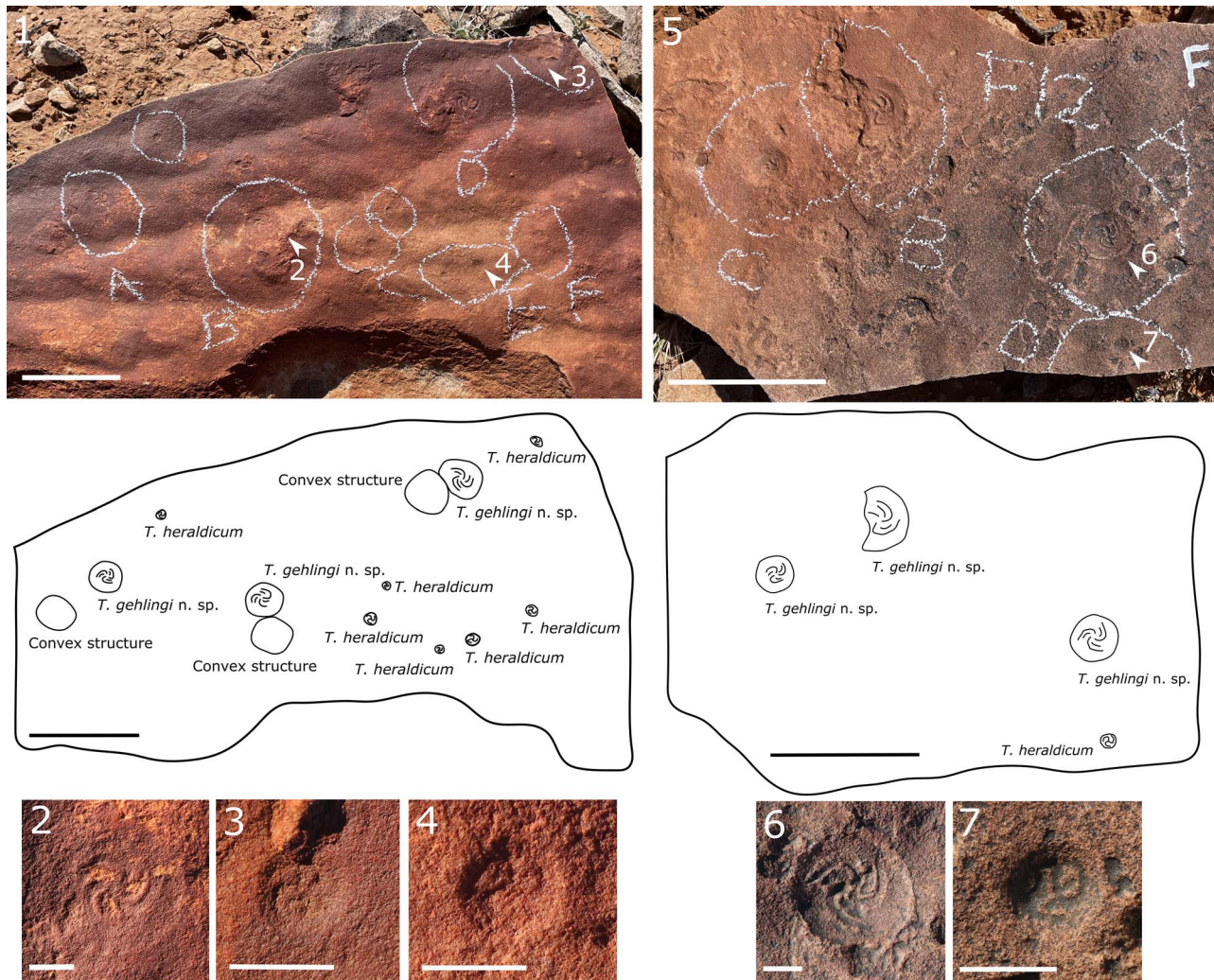


Figure 4. Float pieces illustrating co-occurring examples of the two *Tribrachidium* species. (1) Slab (overall image and schematic) with three specimens of *T. gehlingi* n. sp. and six small specimens of *T. heraldicum* Glaessner in Glaessner and Daily, 1959; (2) *T. gehlingi* n. sp., SAMA P59804; (3) *T. heraldicum*, SAMA P59807; (4) *T. heraldicum*, SAMA P59808. (5) Slab (overall image and schematic) with three *T. gehlingi* n. sp. and one small *T. heraldicum*: (6) *T. gehlingi* n. sp., SAMA P59794; (7) *T. heraldicum*, SAMA P59797. White arrowheads and numbers indicate which individual specimens are viewed in more detail below the slab images. Scale bars = 100 mm (1, 5); 10 mm (2–4, 6, 7).

this was also observed faintly in a few specimens of *T. gehlingi* n. sp. (Figs. 2.3, 2.5, 2.6, 5.4), albeit much finer and shorter, never reaching the arms.

Convex structures were found associated with 20 specimens of *Tribrachidium gehlingi* n. sp. and display similar diameters (Figs. 4.1, 5). For half of these instances, the convex structure (concave in life, originally a depression into the microbial mat covering the sea floor) appears to overlap with *T. gehlingi* n. sp. by varying degrees, up to a third of the body fossil (Fig. 5.4). When they were not found overlapping, the convex structures were usually within a couple centimeters distance of the body fossil (Fig. 5.2). Relief of the convex structures also varied, with some being relatively flat (Fig. 5.2) and others having quite high relief (Fig. 5.3, 5.4).

Observations of all 3D scans of both species indicate that *Tribrachidium gehlingi* n. sp. has a consistently flat relief, whereas *T. heraldicum* has a comparatively higher relief in relation to diameter, supported by the t-test result for height ratios of the two species.

Discussion

Morphology.—Overall, in life, *Tribrachidium gehlingi* n. sp. had a low relief, three short main arms that did not join in the center nor reach the organism's margin, and three secondary arms between each main arm extending over half their length (Fig. 6). In comparison, *T. heraldicum* had a higher relief, longer, more curved main arms, with a small bulla attached to the bend of each main arm. The fine ridges preserved on the periphery of *T. heraldicum* are particularly conspicuous in the *T. heraldicum* specimens from the White Sea (Ivanstov and Zakrevskaya, 2021, figs. 2C, 2, pl. 3, pl. 4, 9a), in which these ridges are preserved from the outer margin of the organism to the center, possibly due to the much finer-grained sediment and the ensuing greater resolution in the fossils. It is therefore reasonable to suggest that these would have extended across the entire upper surface in life for the South Australian specimens of the type species, but grain size precludes their preservation. However, the fine ridges in *T. gehlingi* n. sp.

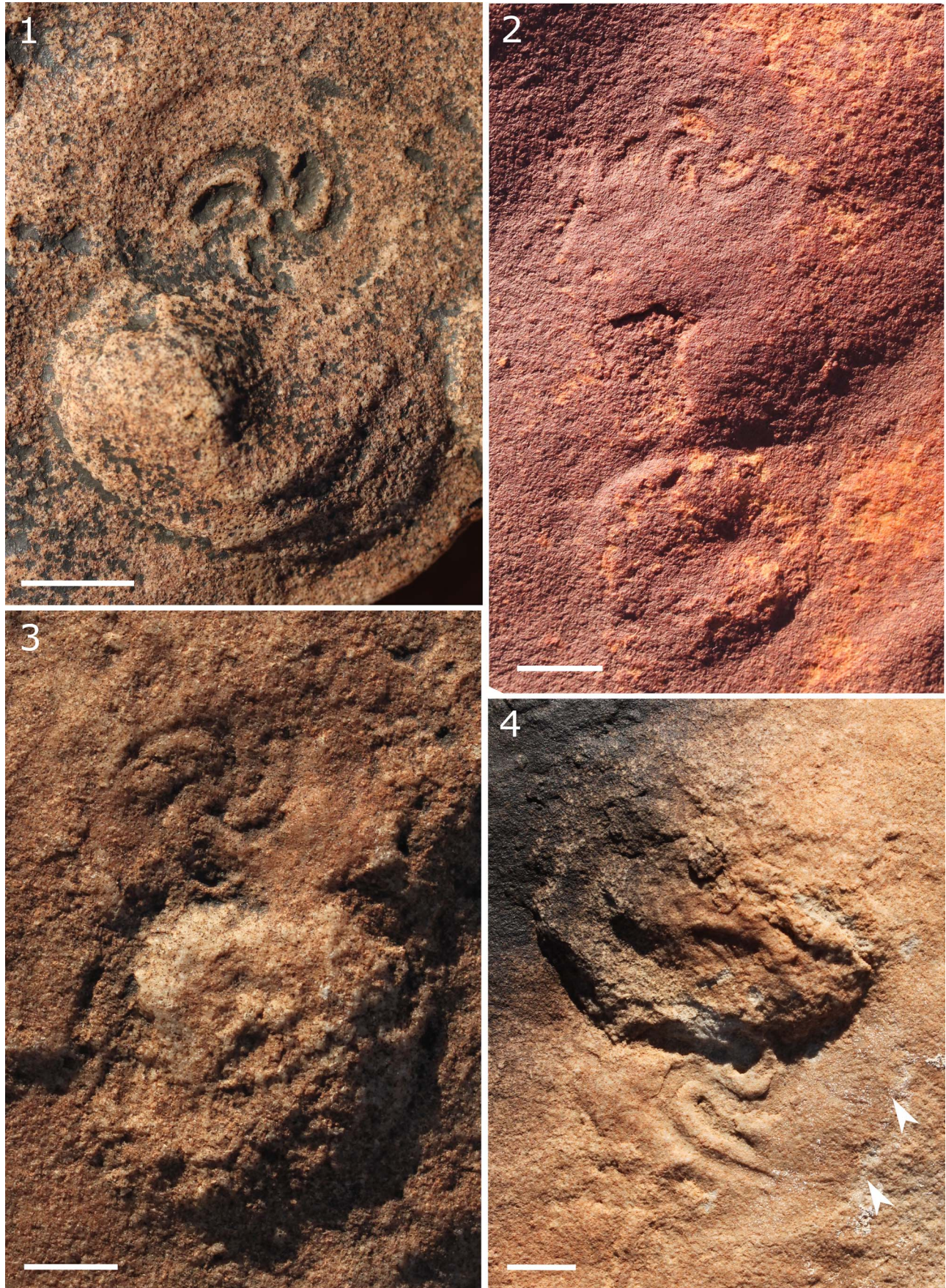


Figure 5. Convex structures associated with *Tribrachidium gehlingi* n. sp.: (1) SAMA P59798 (paratype); (2) SAMA P59804 (paratype); (3) F65A; (4) F70A. White arrowheads point to peripheral areas with preserved fine ridges. Scale bars = 10 mm.

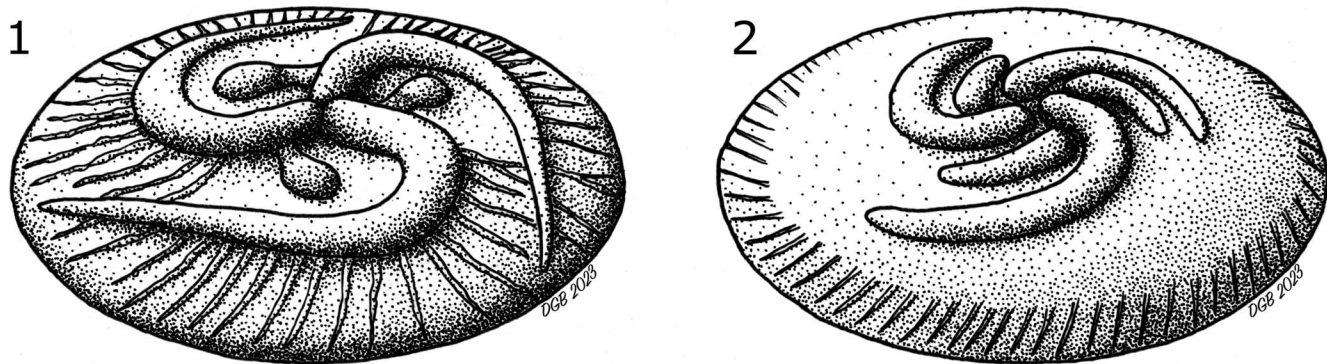


Figure 6. Reconstruction of (1) *Tribrachidium heraldicum* Glaessner in Glaessner and Daily, 1959 and (2) *Tribrachidium gehlingi* n. sp.

Table 1. Welch's t-test results comparing the means of various natural logarithm-transformed linear measurements taken from *Tribrachidium heraldicum* Glaessner in Glaessner and Daily, 1959 and *T. gehlingi* n. sp.

	t-value	degrees of freedom	p-value
Diameters (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	−8.9215	79.179	1.36E-13
Height ratios (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	11.241	87.344	2.20E-16
Arm Distance (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	−14.555	74.267	2.20E-16
Arm Length (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	−3.361	88.242	0.001149
Secondary Arm/Bulla Length (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	−12.493	41.852	1.04E-15
Arm Width (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	−4.9599	87.083	3.46E-06
Secondary Arm/Bulla Width (<i>T. heraldicum</i> vs <i>T. gehlingi</i> n. sp.)	−4.3842	41.308	7.83E-05
Arm vs Bulla Width (within <i>T. heraldicum</i>)	0.97163	68.295	3.35E-01
Main Arm vs Secondary Arm Width (within <i>T. gehlingi</i> n. sp.)	0.97492	88.966	3.32E-01

have no evidence of reaching the arms, let alone extending farther to the center.

The morphological similarity to *Tribrachidium heraldicum* warrants this new species' inclusion within the *Tribrachidium* genus rather than in other triradial genera in the Ediacaran (Hall et al., 2018; Ivanstov and Zakrevskaya, 2021). Unlike *Alburnares* Keller and Fedonkin, 1977, *Anfesta* Fedonkin, 1984, *Rugoconites* Glaessner and Wade, 1966, *Hallidaya* Wade, 1969, and *Skinnera* Wade, 1969, the new species described here does not demonstrate any branching morphology (the periphery ridges remain parallel). Although *Alburnares* and *Anfesta* do have three 'rays' radiating from the center, these do not spiral/curve as is seen in *T. gehlingi* n. sp. Additionally, *Hallidaya* and *Skinnera* have three main disc-shaped 'nuclei' depressions rather than distinct, elongate ridges. Finally, *Coronacollina* Clites, Droser, and Gehling, 2012 is a truncated cone with three narrow, straight spicules, the most morphologically disparate from *T. gehlingi* n. sp.

If no *Tribrachidium heraldicum* were found within this event horizon, the argument could be made that the morphological differences of *T. gehlingi* n. sp. are simply a result of taphonomy. However, the appearance of both species together on the several float pieces (Fig. 4) and a fossil bed (1T-T) indicates that they were exposed to the same burial conditions, and thus the morphological differences observed are likely not a result of different taphonomic processes at the time of burial, but are rather biological (Tarhan et al., 2010; Droser et al., 2017, 2019). Although decay can occur both pre- and postburial, the assessment of only complete, well-preserved specimens

provides the clearest view into their shape during life, limiting the overprint that decay could have on morphological trends. In addition to the apparent lack of deformation observed across fossil beds, the species falling apart within the measured traits (Fig. 3) likely represents morphological differences in life, with limited taphonomic overprint.

Ecophenotypism refers to nongenetic, phenotypic change in response to different environmental conditions (Whelan et al., 2012). This has been proposed to have occurred in at least one lineage of Rangeomorpha, with the possibility of occurring in many more Ediacaran taxa (Hoyal Cuthill and Conway Morris, 2017). However, the co-occurrence of both proposed species in two different paleoenvironments (1T-T and Boomerang Hill), with specimens of similar sizes in both localities, indicates that they were exposed to the same environmental conditions in life. Thus, ecophenotypic variation driving the morphological differences is not supported in this instance (Dececchi et al., 2018).

Ecology.—A passive suspension-feeding mode was hypothesized by Rahman et al. (2015) for *Tribrachidium heraldicum*, illustrating through fluid dynamics that its body plan passively directs water flow toward the apex, generating low-velocity eddies above specific areas of the body where particles are found to passively fall out of suspension. Given the somewhat similar morphology of *T. gehlingi* n. sp., it is not unreasonable to suggest that a similar feeding mode was possibly utilized in life. The longer secondary arms observed for *T. gehlingi* n. sp. could compensate for the shorter,

less-curved main arms and flatter relief when it comes to directing water flow.

Although there is a probability of similar feeding modes for the two species, given their morphological similarities, their ecologies appear to have been slightly disparate. *Tribrachidium heraldicum* was found in higher diversity across numerous facies at NENP, whereas *T. gehlingi* n. sp. has only been found in two localities of similar paleoenvironmental conditions. This suggests that whereas *T. heraldicum* was most likely an ecological generalist (Hall et al., 2015), *T. gehlingi* n. sp. might have required specific conditions to survive. Additionally, the occurrence of similar-sized cohorts of *T. heraldicum* on bedding surfaces indicates opportunistic/seasonal reproduction (Hall et al., 2015). Across Boomerang Hill, *T. heraldicum* still maintains a very narrow size range, whereas *T. gehlingi* n. sp. has a broader size range, suggesting a possible divergence in reproductive mode, which is typically predicted to promote species coexistence (Blackford et al., 2020). However, due to the specimens not occurring on a contiguous bedding plane, hypotheses regarding reproduction cannot be made for *T. gehlingi* n. sp. without this ecological context.

The convex structures found associated with *Tribrachidium heraldicum* (see Hall et al., 2015, fig. 10) were interpreted as the impression of their basal surface in the microbial mat, filled with sand after the specimens were displaced by current. The overlapping nature and similar diameters of the convex structures to the associated body fossils of *T. gehlingi* n. sp. could also be explained by this hypothesis. The overlap of these structures suggests that the organisms were only slightly moved out of place prior to burial, whereas the instances in which there is distance between the structure and specimen (typically a couple of centimeters) suggests a full displacement (or removal) (Fig. 4.2) of the organism, which is consistent with the model proposed by Hall et al. (2015).

Additionally, the convex structures associated with *Tribrachidium gehlingi* n. sp. have a somewhat proportional frequency to those observed for *T. heraldicum*. The positive relief, concentric-ring morphology is associated with larger specimens of *T. heraldicum* on WS-TBEW (Hall et al., 2015), and whereas the convex structures of *T. gehlingi* n. sp. do not display concentric ring morphology, they are also only associated with larger specimens. Given that the microbial mat on the *T. gehlingi* n. sp. float pieces is relatively thin, and larger specimens would have been sitting on the sea floor for a long time, hollows would have been more likely to form than smaller specimens on a thicker mat (Hall et al., 2015), suggesting a passive feature. Due to the lack of ecological context of the float pieces, it is unknown whether these structures occurred in a particular orientation.

On the other hand, a motile mode of life has been suggested previously through the presence of a curved wide trace extending from *T. heraldicum* (Ivanstov et al., 2019, fig. 3C, D). However, this feature was only found associated with a single specimen from the White Sea locality and no such feature has been found associated with the hundreds of specimens from South Australian localities. Moreover, known motile taxa, e.g., *Dickinsonia* Sprigg, 1947, *Kimberella* Glaessner and Wade, 1966, and *Ikaria* Evans et al., 2020, leave consistent, frequent traces, directly related to their feeding mode, across the sea floor, independent of size (Ivanstov, 2013; Evans et al., 2019,

2020). Therefore, it is more likely, given the hypothesized passive suspension-feeding mode of *Tribrachidium*, that they were sessile, and that the convex structures are a result of passive transport rather than active movement because they are only associated with specific size ranges.

Implications.—The identification of this new species represents another instance of speciation within a monospecific genus, an occurrence that is not very common in the Ediacaran, with majority of described genera being monospecific (Narbonne, 2005). This further illustrates the level of taxonomic complexity that was already present in the Ediacaran. The identification of a new species within *Tribrachidium*, and the abundance of *T. heraldicum* in various fossil assemblages throughout the Flinders Ranges, also highlights the success of this genus. A spiraling triradial body plan could be the contributing factor of this observed success. The functional nature of this morphology—to direct water flow to localized regions without having to orient themselves with current direction—enables effective passive suspension feeding. This efficient ability of *Tribrachidium* to manipulate the environment for resources could also explain why triradial body plans in general have a high diversity during the Ediacaran. However, the lack of this body plan in the Phanerozoic could point to the microbial mat being more of a contributing factor to their success, creating a high nutrient concentration at the sediment-water interface where the triradials inhabited. Overall, the identification of a new species within a widespread genus increases the overall known diversity of the Ediacaran, enriching our understanding of Earth's earliest complex ecosystems.

Conclusion

A new species of *Tribrachidium* has been identified at Nilpena Ediacara National Park, Flinders Ranges, South Australia. *Tribrachidium gehlingi* n. sp., although shown to display features typical of *Tribrachidium*, e.g., triradial symmetry and fine peripheral ridges, statistically differs from the type species through shorter, less-curved main arms and three shorter secondary arms in place of the 'bullae' of the type species. Additionally, *T. gehlingi* n. sp. has a flatter relief overall than *T. heraldicum*, which presents a higher relief. The appearance of both species within the same paleoenvironment indicates that one of these species is most likely not simply a taphomorph of the other. Overall, the identification and description of this new species further illustrates and adds to the complexity and diversity of the Ediacara Biota and emphasizes how successful Ediacaran body plans often present multispecific genera, e.g., *Dickinsonia*.

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Declaration of completing interests

The authors declare none.

Data availability statement

Data for this study are available in the Figshare Digital Repository: <https://doi.org/10.25909/25341625>.

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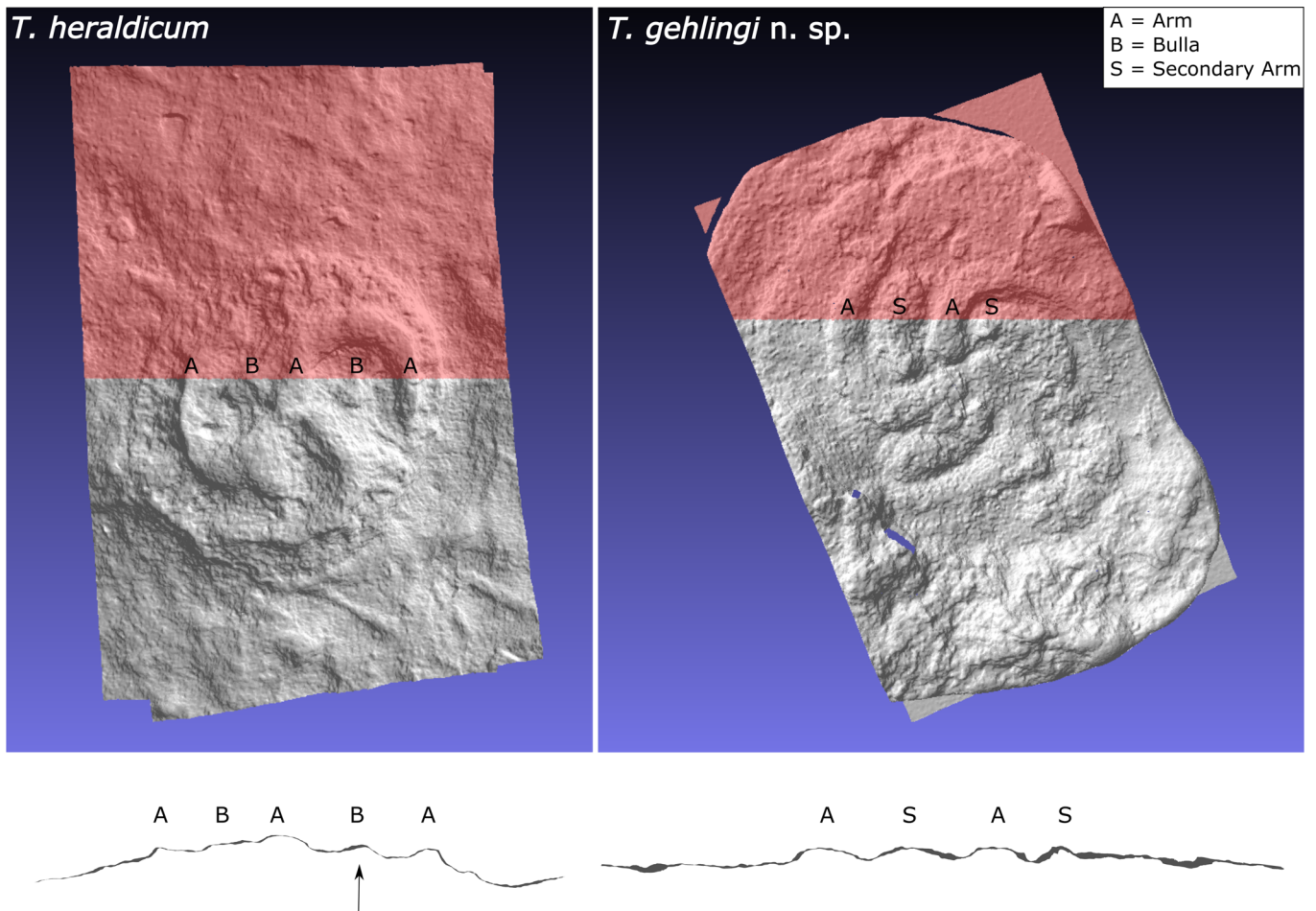
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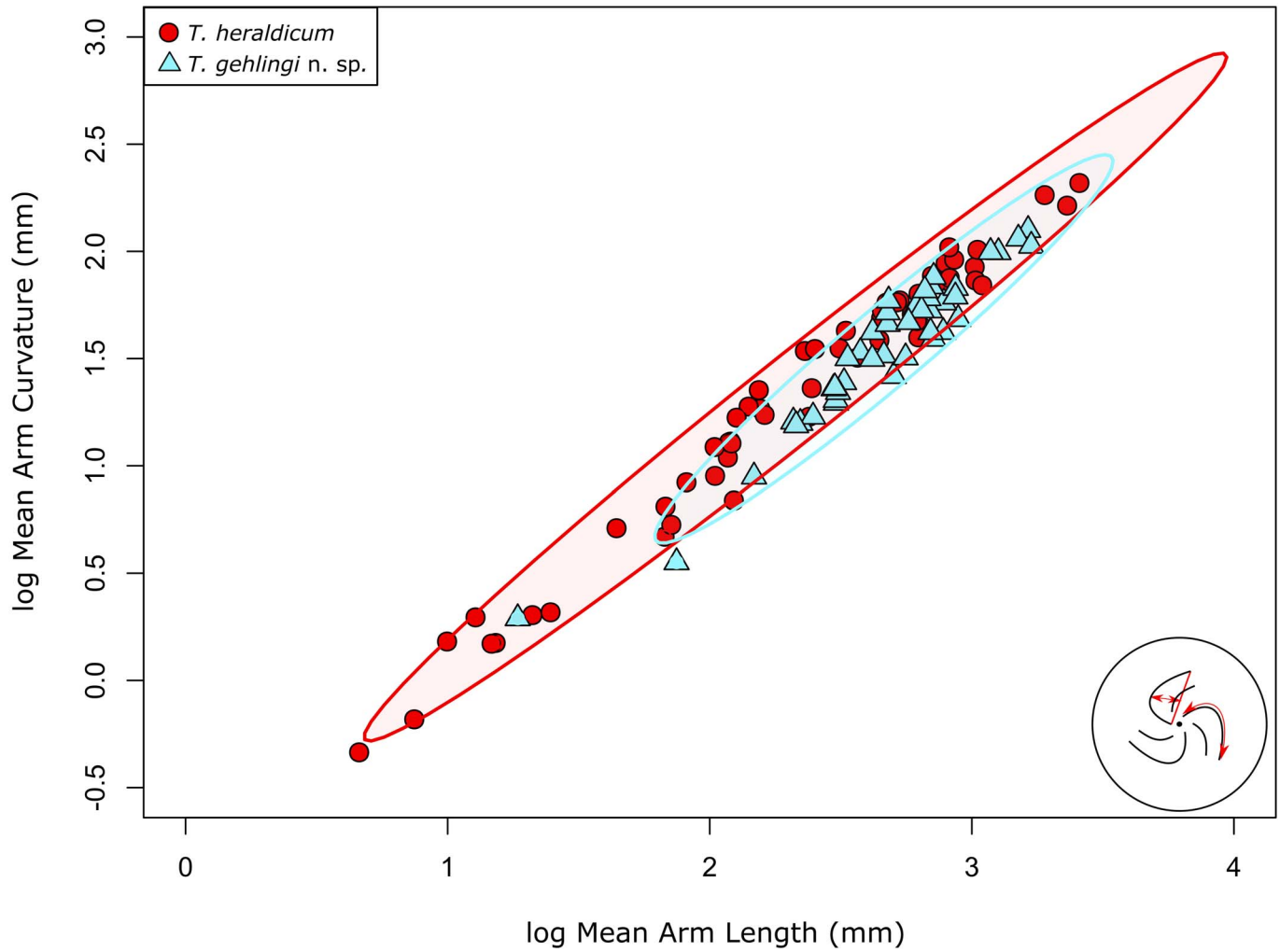
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Appendix



Appendix 1. Arm width analysis of *Tribrachidium heraldicum* Glaessner in Glaessner and Daily, 1959 (SAMA P49372) and *T. gehlingi* n. sp. (SAMA P59801). Red area indicates where scans were cut in half to assess the arms in cross section. Each arm in the cross section is indicated by 'A,' bulla 'B,' and secondary arm 'S.' Arrow points to a bulla associated with an arm not captured in the cross section.



Appendix 2. Linear measurements of *Tribrachidium gehlingi* n. sp. and *T. heraldicum* Glaessner in Glaessner and Daily, 1959, comparing Mean Arm Length with Mean Arm Curvature. Colored ellipses represent 95% confidence interval of the fitted linear models. Measurements taken in millimeters and natural logarithm-transformed. Schematic depictions of the measured traits illustrated in bottom right corner of each plot.