



Does “form follow function” in the rotiferan genus *Keratella*?

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Abstract Most species of *Keratella* possess dome-shaped, dorsal plates comprising a network of polyhedral units (facets), delineated by slightly raised ridges. The arrangement of facets define a species’ facet pattern (FP), with the resulting structure resembling a geodesic dome. Researchers have sorted species into categories based on their FPs, but those have not been analyzed. Additionally, while a strong lorica has been suggested to protect *Keratella* from predatory attack or other actions causing blunt force trauma (BFT), we know little of how that occurs. Thus, in our study

we tested two hypotheses. (1) There is support for categorizing *Keratella* species into unique groupings based on their FPs. (2) FPs provide resistance to physical stresses. To test that hypothesis we used the structural analysis software SkyCiv®. Our results indicate support for four FP categories. Additionally, the SkyCiv analysis provided preliminary ‘proof-of-concept’ that *Keratella* FPs have a functional significance: i.e., adding or subtracting facets in our model was followed by a change in predicted structural reliability. We posit that FPs are adaptations protecting *Keratella* from fractures to the lorica that may result from BFT incurred during predatory attack by copepods or while caught within the branchial chambers of daphnids.

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The analysis of biological form must emphasize the concept of adaptation—the fitness of a structure to perform functions beneficial to an organism. Gould (1971).

Introduction

Genus *Keratella* Bory de St. Vincent, 1822 warrants study for several reasons, both practical and theoretical. It is distributed world-wide (Segers & De Smet, 2008) with species being present in fresh and marine waters and at temperatures ranging from cold arctic

waters to warm equatorial regions (Ahlstrom, 1943). Moreover, *Keratella* is among the top 10 specious genera of monogonont rotifers (Segers, 2002) and can be an important component of planktonic rotifer biomass (Dokulil & Herzig, 2009); its presence informs us of a waterbody's trophic state (Haberman & Haldna, 2014). Actually, quite a bit is known about the biology of the genus, including (1) aspects of life history (Cieplinski et al., 2018), (2) population dynamics (Gutkowska et al., 2018), (3) diapausing egg banks (Eskinazi-Sant'Anna & Pace 2018), (4) diel and seasonal changes in their morphology and distribution (Galkovskaya & Mityanina, 1989; Fussmann, 1993; Bielańska-Grajner, 1995; Galkovskaya, 1998), (5) endemism (Segers & De Smet, 2008), and (6) variability of easily assessable morphological features such as the body width and length, number of anterior spines, and presence of posterior spines, as well as their length, symmetry, and inducibility (Stemberger, 1979; Green, 1980; Cieplinski et al., 2017; Zhang et al., 2017; García-Morales et al., 2021).

Yet, of the many planktonic rotiferan genera typically found in freshwaters (e.g., *Asplanchna*, *Brachionus*, *Filinia*, *Notholca*, *Synchaeta*), species of *Keratella* exhibit a striking morphology that is iconic for the phylum (Ahlstrom, 1943; Stemberger, 1979). Most *Keratella* species possess a roughly rectangular lorica with a dome-shaped dorsal plate and a thinner, flattened ventral plate; all lack a foot. Nearly all *Keratella* possess six anterior spines (one species has four). Their morphology is complicated by the fact that the number of posterior spines may vary within a species: e.g., Bartoš (1946) reported *Keratella testudo* (Ehrenberg, 1832) possesses 0, 1, or 2 spines. Likewise, the length of posterior spines may vary (e.g., *Keratella americana* Carlin, 1943). Also solitary spines may be located asymmetrically with respect to the body axis [e.g., *Keratella mixta* (Oparina-Charitonova, 1924)] and paired spines may be unequal in length and shape [e.g., *Keratella tropica* (Apstein, 1907)].

However, perhaps the most striking feature of *Keratella* is the presence of thick struts (ridges) on the dorsal plate (Fig. 1). These ridges form a pattern of symmetrical and/or asymmetrical polygons termed facets, plaques, or panels that are composed of from three to eight sides (García-Morales et al., 2021). These ridges are not monohedral tessellations nor are they random motifs. The facets are curved plates (Ahlstrom, 1943; Ruttner-Kolisko, 1974; Koste,

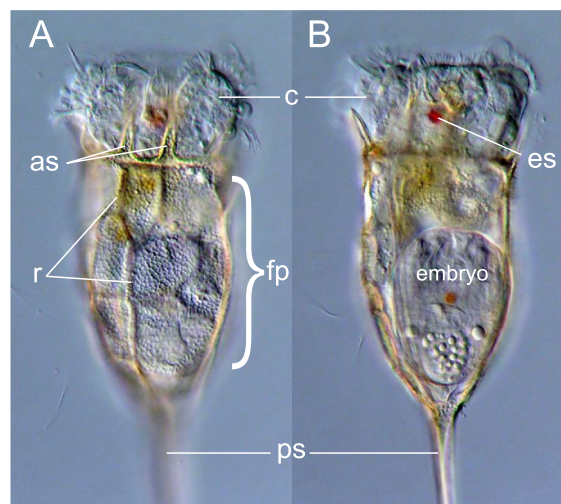


Fig. 1 Photomicrograph of *Keratella cochlearis*. **A** Three-quarter dorsal view. The dorsal plate is characterized by a series of ridges that delineate several polyhedrals, which form the species' Facet Pattern (FP). **B** Three quarter ventral view with an embryo that is partly out of focus. *as* anterior spines, *c* corona, *es* eyespot, *fp* facet pattern, *ps* posterior spine, *r* ridges. The embryo is held outside the body along the ventral side (photomicrograph by RH)

1978; Modenutti et al., 1998), thus they are properly designated as polyhedrals. As a result, faceted *Keratella* resemble elongated versions of R. Buckminster Fuller's geodesic dome (Chu, 2018), Hadrian's Pantheon (Mark & Hutchinson, 1986), the ceiling of a Gothic ribbed vault (Leedy Jr., 1978; Webb & Buchanan, 2019), or the carbon-60 compound, Fullerene (Kroto et al., 1985). It is important to note that geodesic dome-like structures are common in the natural world: obvious examples include viruses, Radiolaria (Protista), Hexactinellida (Porifera), Crinoidea (Echinodermata), Ostraciidae (Arthropoda), and Testudines (Reptilia).

The arrangement of facets in *Keratella* species is useful in developing keys for taxonomic identification (Ahlstrom, 1943; Ruttner-Kolisko, 1974; Koste, 1978), although positioning of the ridges alone is inadequate for complete species identification. Yet within this diversity of topological patterns, there is sufficient unity for workers to separate species into categories. Indeed, Ahlstrom (1943) stated that the arrangement of facets in species varied so little among some species that they could be grouped (categorized) based on their "foundation patterns."

Stemberger (1990) refers to ridge assembly as “facet patterns” (hereafter FP). While the ventral plate often is reported as being smooth (Zhuge & Huang, 1998), it also may have a distinct FP (Hendelberg et al., 1979). Furthermore, both the dorsal and ventral sides of the lorica may possess embellishments including minute, raised projections (hispid), alveoli, areolations, granulations, pustules, spines, spinules, star-shaped, and spot-like structures (Chengaleth & Fernando, 1973; Ruttner-Kolisko, 1974; Boltovskoy & Urrejola, 1977; Hendelberg et al., 1979; Garza-Mouriño et al., 2005; Cieplinski et al., 2017; García-Morales et al., 2021). While several researchers have assigned *Keratella* species to specific categories, the taxa comprising those groupings varies slightly among authors (Ahlstrom, 1943; Sudzuki, 1964; Ruttner-Kolisko, 1974; Koste, 1978). Since those publications, a few new species have been described, but to our knowledge there has been no study that has explored these groupings, variations among FPs, or the role they might play in *Keratella* fitness.

Fitness in *Keratella* may be affected by several factors, but a critical one is that they can experience substantial interference from microcrustaceans in four ways. (1) Allelochemicals released from *Daphnia* have been shown to lower fecundity of *Keratella cochlearis* (Gosse, 1851) (Conde-Porcuna, 1998). (2) *Keratella cochlearis* also suffers from competition for resources from *Daphnia pulex* Leydig, 1860 (Gilbert, 1985a). (3) *Keratella* are prey for copepods (Meyer et al., 2017). (4) Because *Keratella* are small enough to become caught within the filtering chamber of cladocerans, they may be eaten or at least be subject to mechanical interference competition (Burns & Gilbert, 1986a, b; Diéguez & Gilbert, 2011). In this case, if not consumed, *Keratella* face significant damage and death, with larger sized daphnids causing higher mortality (Burns & Gilbert, 1986a). However, Gilbert & MacIsaac (1989) have shown that spined morphs of *K. cochlearis* are less susceptible to damage from *Daphnia*. Thus, whether through predatory attack by copepods or being entrained within the filtering chamber of a cladoceran, *Keratella* may suffer serious damage by blunt force trauma (BFT).

Although the functional significance of the FPs of *Keratella* have not been studied, lorica thickness has been proposed as a feature that reduces predatory losses. For example, both Gilbert & Williamson (1978) and Williamson (1993) suggested that

Mesocyclops edax (Forbes, 1891) was not an important predator of *K. cochlearis* because its hard lorica made it difficult for the copepod to attack successfully. Also Williamson (1987) noted that when *Skistodiaptomus* (*Diaptomus*) *pallidus* (Herrick, 1879) ingested *K. americana* or *K. cochlearis* the rotifers were “often mangled [but] more often rejected unharmed.” In predation experiments using the predatory copepod *Cyclops bicuspidatus thomasi* (Forbes 1882), Stemberger (1982) reported ingestion rates for *Keratella* that were 10× lower than for the illoricate rotifer *Synchaeta pectinata* Ehrenberg, 1832. He also noted that in experiments in which the copepod had been starved, “many *Keratella* were injured or dead but not eaten.” Injured *Keratella* had puncture wounds while those “that had been eaten had their ventral plate torn away, puncture wounds through the lorica, or had large chunks of the lorica bitten off from the anterior margin.” He argued that this demonstrated “the effectiveness of the lorica as a defense against *Cyclops* predation.” Apparently, *K. cochlearis* is also resistant to predation by similar crustaceans such as *Epischura lacustris* Forbes, 1882 and *Leptodora kindtii* (Focke, 1844) (Stemberger & Evans, 1984), as well as *Acanthocyclops robustus* (Sars, 1863) (Roche, 1990). On the other hand, *Hesperodiaptomus arcticus* (Marsh, 1920) selectively preys upon *Keratella* to the point where this calanoid significantly reduced prey biomass in a small Alpine lake (McNaught et al., 1999). Regardless of the importance of lorica thickness in thwarting predation, it does not protect *Keratella* against predators that engulf their prey; these include the testate amoeba *Diffugia* spp. (H. Dumont, pers. commun.), the heliozoan *Actinosphaerium* (S.S.S. Sarma & S. Nandini, pers. commun.), the predatory rotifer *Asplanchna* [see Fig. 13.38c in Wallace et al. (2015)], the calanoid copepod *Boeckella major* Searle, 1938 (Green & Shiel, 1992), the ostracod *Cypris pubera* Müller, 1776 (Gilbert, 2012), and larvae of the midge *Chaoborus* (Lewis Jr., 1977).

Accordingly, our study aimed to address the potential structural significance of *Keratella* FPs, with four key goals. (1) Based on published literature, we sought to compile a database of *Keratella* taxa that detailed their FPs, as well as other characteristics routinely used in describing species in the genus (Ahlstrom, 1943; Ruttner-Kolisko, 1974). (2) Using that information, we hypothesized that *Keratella* species could be systematically categorized

into groups by their FPs (Ahlstrom, 1943; Ruttner-Kolisko, 1974). (3) We evaluated the concept that these groups occupy distinctive regions within a larger potential morphospace (Pie & Weitz, 2005). However, we did not attempt to resolve issues of species descriptions, changes in form due to exogenous induction (e.g., temperature or food), cryptic speciation (including evolutionary significant units), or ecotypic and phenotypic plasticity described as seasonal and/or habitat variations in morphology (Ahlstrom, 1943; Hofmann, 1980; Koste & Shiel, 1989; Ruttner-Kolisko, 1993; Derry et al., 2003; Gómez, 2005; Giri & José de Paggi, 2006; Cieplinski et al., 2017). (4) Finally, with Gould's (1971) statement in mind, we tested the hypothesis that *Keratella* FPs represent an adaptation that resists fractures to the lorica that may be incurred when caught within the branchial chambers of daphnids: i.e., BFT. That is, we posed the question: Does FP form follow function in *Keratella* (Thompson, 1942)? To the best of our knowledge, there have been no previous tests of this hypothesis.

For convenience we provide definitions of the initialisms we use in this paper in Table 1.

Methods

Assembling the database

We assembled a comprehensive dataset of all *Keratella* taxa from those recorded in the Rotifer World Catalog (RWC) as of the 14th of July, 2022 (Jersabek & Leitner, 2013). To that list we added other taxa that came to our attention during our analysis (García-Morales et al., 2021). All taxa were evaluated to determine whether they were 'valid' according to rules established by the International Code of Zoological Nomenclature (ICZN) (Segers et al., 2012): i.e., those enumerated in the List of Available names (LAN) for phylum Rotifera (Segers et al., 2016; Jersabek et al., 2018). Differences in our list from that of Segers & De Smet (2008) were cross-checked with the LAN and RWC. The data we assembled included both taxonomic information and published images of *Keratella* taxa. However, we also included data on taxa where published information disagreed on their status. All taxonomic information is documented in the Supplemental Document. To ascertain the scope of previous research on *Keratella*, we searched Web

Table 1 Definitions of initialisms used in this paper

Term	Definition
BFT	Blunt Force Trauma: the stress that may be incurred by individual <i>Keratella</i> when attached by a predatory copepod or caught within the filtering chamber of a daphnid
DI	Displacement Index: $DI = \log_{10}$ of the Global Governing Displacement (GGD) value; the GGD is calculated by the SkyCiv© program to determine whether the structure being tested would meet or fail according to architectural code
FP	Facet Pattern: The pattern of ridges on the dorsal plate of <i>Keratella</i> spp.
cFP	The Facet Pattern exhibited by <i>Keratella</i> spp. that resemble that of <i>K. cochlearis</i>
qFP	The Facet Pattern exhibited by <i>Keratella</i> spp. that resemble that of <i>K. quadrata</i>
sFP	The Facet Pattern exhibited by <i>Keratella</i> spp. that resemble that of <i>K. serrulata</i>
nFP	The absence of the discernable Facet Pattern
GD	Structural tests (Fig. 6A): The model of a Geodesic Dome provided in the SkyCiv program that was used test its structural integrity
GD-1	Structural tests (Fig. 6A): The SkyCiv model of a Geodesic Dome in which one side ridge was removed
GD-2	Structural tests (Fig. 6A): The SkyCiv model of a Geodesic Dome in which two side ridges were removed
GD-T	Structural tests (Fig. 6A): The SkyCiv model of a Geodesic Dome in which one ridge on the top was removed
cFP	Structural tests (Fig. 6B): The model created using the SkyCiv© program to test the structural integrity of <i>K. cochlearis</i>
cFP-1	Structural tests (Fig. 6B): A modification of the <i>K. cochlearis</i> model used in SkyCiv© program in which one dorsal ridge was removed
cFP-2	Structural tests (Fig. 6B): A modification of the <i>K. cochlearis</i> model used in SkyCiv© program in which two dorsal ridges were removed
cFP+1	Structural tests (Fig. 6B): A modification of the <i>K. cochlearis</i> model used in SkyCiv© program in which one dorsal ridge was added and one another dorsal ridge was repositioned

of Science® (<https://www.webofscience.com/wos/woscc/basic-search>) using three search strategies: (i) Rotifer* + *Keratella*; (ii) Rotifer* + *Keratella* + facet; (iii) Rotifer* + *Keratella* + fundamental. (NB: where ‘*’ indicates any value.).

Categorizing *Keratella* FPs

To categorize species according to their FP, we collected line drawings from the literature. However, we were cognizant that they may not have been accurately portrayed in the publications we used; that is, they were not made using a camera lucida, as was done by Chengaleth & Fernando (1973) or by tracing from photomicrographs. Our strategy was to use images that were easily available to researchers regardless of their potential inadequacies. Because certain elements of morphology (e.g., body length and width,) are known to vary within *Keratella* populations, we did not use that information in assembling the morphological data (Carlin, 1943; Pejler, 1957, 1962; Chengaleth & Fernando, 1973; Green, 2005). Nevertheless, we did record presence or absence of posterior spines.

However, another factor further complicated our study of *Keratella* FPs. Illustrations of the FPs in a single morphospecies have been reported to vary seasonally and among lakes: i.e., illustrations may depict different configurations of FPs or even FPs with incomplete ridges. Three examples serve to demonstrate this point. (1) Pejler (1957) noted this phenomenon in populations of *K. cochlearis* in some Lapland waters. A population from an alpine tarn had a single, mid-dorsal ridge, while the FPs from specimens of a subalpine tarn had four complete mid-dorsal polyhedrons, but those differed slightly on two sampling dates (June 12, 1951 and July 31, 1951): i.e., compare Pejler’s figures 2, 5, and 9. (2) The ridges

illustrated in the original description of *Keratella reducta* (Huber-Pestalozzi, 1929) from Lake Cakedon (South Africa) begin, but do not form complete polyhedrons, while a population from a pan near Lake Chrissie (South Africa) is shown with complete polyhedrons: i.e., compare plate 39, figures 15 and 16 in Ahlstrom (1943). (3) Ahlstrom (1943) shows radically different FPs for *Keratella taurocephala* Myers, 1938 [compare plate 37, figures 11 and 14; bog in Wisconsin and a lake in Pennsylvania, respectively]. We addressed this by selecting representative figures that we evaluated (see also below). Thus, while the images we assembled are easily accessible, we do not affirm that our compilation is exhaustive, but we believe that it is representative of the scope of the variation reported in the literature.

To sort *Keratella* by their FP arrangements we inspected the FPs of species that are considered to be valid and arrived at a consensus judgement as to whether each taxon could be clearly assigned to a species group established by Ruttner-Kolisko (1974). Namely, we placed them into the following categories: *cochlearis* FP (cFP), *quadrata* FP (qFP), and *serrulata* FP (sFP). We also assigned some taxa that possessed variations from their nominotypical taxon into an appropriate FP category (see below).

Analyzing *Keratella* morphospace

Our analysis of *Keratella* morphospace had two parts. We began by doing a geometric morphometric analysis of four species, two in the cFP category [*K. cochlearis* and *Keratella tecta* (Gosse, 1851)] and two in the qFP category [*Keratella quadrata* (Müller, 1786) and *Keratella hiemalis* Carlin, 1943]. The landmarks used in this part of our analysis are illustrated in the Supplemental Document [Sheet #2 (FP examples)]. The species we used each had at least six illustrations

Table 2 Geometric morphometric analysis of the four species of *Keratella* examined in this study

Species	Authority	Sources of the illustration used
<i>Keratella cochlearis</i>	Gosse, 1851	Pejler (1957, Figs. 5, 9, 27, 30, 33, & 34)
<i>Keratella hiemalis</i>	Carlin, 1943	Pejler (1957, Figs. 50, 51, 52, 53, 54, 55)
<i>Keratella quadrata</i>	Müller, 1786	Ahlstrom (1943, Figs. 1, 2, 6, & 7), Bartoš (1946, Fig. 2A–C & E), Carlin (1943, Figs. F, G, H, & I), Chengalath et al. (1971, Figs. 21, 22, 23, & 24), Klement (1957, Figs. 2a–c)
<i>Keratella tecta</i>	Gosse, 1851	Pejler (1957, Figs. 23, 32, 35, 37, 38, & 40)

(Table 2). As noted above we selected these images to be representative of available works, but we did not consider them to provide complete coverage. Also we did not account for animal size because in rotifers size varies based on factors such as individual nutritional regimen and maternal age: e.g., (Robertson & Salt, 1981; Snell & Carrillo, 1984; Stelzer, 2001). For each image we used the *Point Picker* plugin in *ImageJ* to acquire configurations of landmark coordinates (points) (Ferreira & Rasband, 2012) for these species (Supplemental Document). Landmarks for species in both species in each group (cFP and qFP) were digitized by the same person. The coordinates were imported into *MorphoJ* (Klingenberg, 2011) for analysis: i.e., to create wireframe diagrams and transformation grids to visualize the location of variation among the FPs of these species. We analyzed landmark coordinates using Canonical Variate Analysis with significance determined using Procrustes ANOVA in *MorphoJ* (Klingenberg, 2011). A Principal Component Analysis was run to summarize differences in the landmark coordinates.

We extended our analysis by investigating *Keratella* morphospace in species deemed valid plus some taxa that possessed variations from their nominotypical taxon (see above). Unfortunately, illustrations of *Keratella* species do not always show the lateral view as was done by Chittapun et al. (2009). Thus, because illustrations from only the dorsal side provide incomplete information on lateral facets, we chose not to extrapolate the shape of those facets. Accordingly, to avoid adding bias to our dataset we evaluated the FPs only along the mid-sagittal region: i.e., the facets lying with the boundary defined by two parallel lines running from the two central, anterior spines toward the posterior. Also while illustrations of the ridges of mid-sagittal facets are curved, other illustrations depict them as straight lines; to simplify our analysis we simply treated all ridges as straight lines. Thus, using images from the literature we collated data on the 56 valid species plus the 14 taxa possessing variations from their nominotypical taxon. This analysis was done in two ways. (1) We counted the number of ridges in facets present in the mid-sagittal region of the FPs of these 70 taxa. (2) We recorded the number of their facets with 3, 4, 5, 6, and 7 or more sides. Also we recorded two other characteristics, the number of anterior spines (i.e., 4 or 6) and asymmetry within polyhedrons of the FPs, but did not use that

information in this study. All data, whether used in this analysis or not, are presented in the Supplemental Document.

Does FP form follow function in *Keratella*?

Currently there is no readily available and direct way to test the hypothesis that FPs provide *Keratella* resistance to fractures of the lorica caused by physical stress. Yet we know that for structures to be architecturally sound they must be able to withstand both dead and live loads. A dead (permanent) or Static Load refers to stresses on a structure due to its own mass; a live or Area Load refers to variable stresses due to all other forces: e.g., addition of stresses due to wind or the overburden of snow. Thus, using the built world as an analog, we adopted an indirect approach to examine the importance of *Keratella* FP structure. To do this, we employed the on-line, cloud-based, structural analysis and design software, SkyCiv© (skyciv.com). SkyCiv reports whether the structural elements of the building being tested meets standard architectural code when subject to its Static Load, with or without addition of an Area Load. Our assumption was that this approach can be used examine how well the arrangement of ridges comprising the *Keratella* FP withstand Static and Live Loads. We believe that our study is sufficient to provide a 'proof-of-concept' that *Keratella* FPs offer a degree of protection from extra loads (stresses) that may be manifest due to BFT. To do this, we evaluated two different, 3-dimensional systems: (1) the Geodesic Dome provided in the SkyCiv program and (2) a model of the ridges as seen in a common FP of *K. cochlearis*, as we created using the SkyCiv program. We began modeling *K. cochlearis* by constructing an approximation of a common FP of the species (i.e., figure 5 in Ahlstrom, 1943). Our methodology was to compare unmodified versions of these two models to several modifications where ridges were either removed or added (see below). Note while we used only one image to construct the *K. cochlearis* model, we document additional ones that could be explored in our database (Supplemental Document).

The Geodesic Dome (GD) model provided by SkyCiv is composed entirely of triangular facets; we used the unmodified structure and we also altered it in three ways: i.e., removal of one ridge from one side (GD-1); removal of two side ridges simultaneously

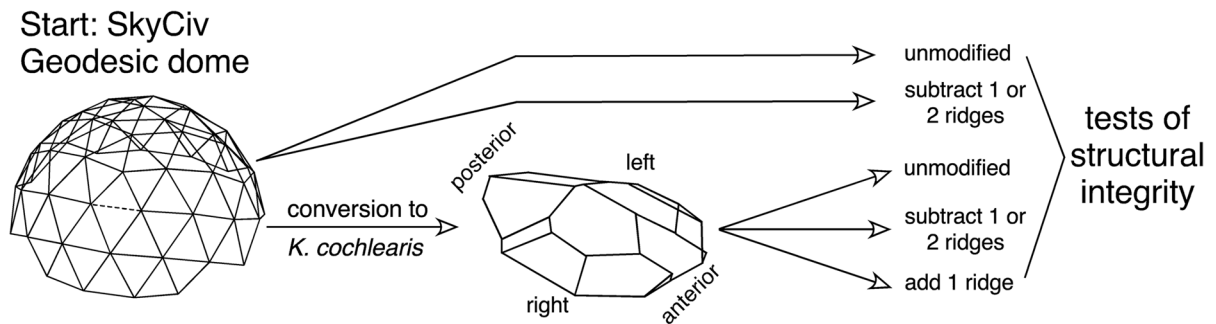


Fig. 2 Workflow for creating and subjecting test models of a geodesic dome (GD) and *Keratella cochlearis* to stresses using SkyCiv©. Tests of structural integrity were run on wireframe models of both systems without changes to the number or location of ridges (unmodified) and with several modifications in which ridges were removed or added. For the GD model we removed one or two ridges: the dashed line illustrates one

of the ridges that was removed. In *K. cochlearis* model we removed one or two ridges or added one and realigned the ridges. SkyCiv reports whether the structure being tested meets standard architectural code when subject to its static load, with or without addition of an area load (see text and Supplemental Document for additional details)

(GD-2); removal of a ridge from the top (GD-T) (Fig. 2). These changes created a GD either one or two, four-sided elements, rather than just three-sided ones. We followed the same general methods for the *K. cochlearis* model: i.e., the unmodified version (cFP) was compared to models in which we removed one (cFP-1) or two ridges (cFP-2), or by adding a ridge to the dorsal side and rearranging the FP (cFP+1) (Fig. 2). These alterations did not change the dorsal margin of the *Keratella* model, but they did alter the number and shape of the central facets. The starting structures and the modifications are shown in the Supplemental Document (sheet entitled Modifications GD & KC).

The SkyCiv application allows the use of various parameters to test whether a structure will fail according to specific architectural standards. For the construction material in all trials we used oakwood (i.e., not the other SkyCiv options of steel or reinforced concrete). We also applied two different stress conditions. (1) The first is an increase in the force of the Static Load: (i.e., 1, 2, 3, or 4×the mass of the system is applied to each ridge in the structure). (2) The second test applies those four Static Loads, but adds an additional, standard Area Load of 0.1 MPa to all ridges simultaneously. In that case, the structure is stressed by its own gravitational force plus an additional load of 0.1 MPa. SkyCiv determines whether a structure tolerates these stresses without failing. Naturally, we recognize that the SkyCiv program is

designed to test structures at least 5 orders of magnitude larger than *Keratella*: e.g., 100 μm vs. ≥ 10 m. However, our goal was to provide a proof of concept that structures with the KC configurations could withstand simulated stresses. From the SkyCiv report of each model run we evaluated the Global Governing Displacement value, a measure of how the structure's shape is displaced and because of that, whether the structure would meet or fail according to the architectural code applied by SkyCiv. We reported these values as the Displacement Index: $\text{DI} = \log_{10}$ of the Global Governing Displacement value.

Results

Assembling the *Keratella* database

Our literature review yielded 156 taxa; these included bi- and trinomial species names, variations, forms, and one unnamed taxon. Of those, only 56 qualified as valid species names according to criteria established by the ICZN (Segers et al., 2012): i.e., registered in the LAN and RWC.

Categorizing *Keratella* FPs

By inspecting the images of the valid 56 taxa we arrived at our own consensus judgement as to whether the species could be assigned to one of the three categories established by Ruttner-Kolisko (1974). We

placed ~30% ($n=17$) of these species in the *cochlearis* group (cFP), ~50% ($n=28$) in the *quadrata* group (qFP), and ~16% ($n=9$) in the *serrulata* group (sFP). However, two species (~4%), *Keratella kostei* Paggi, 1981 and *Keratella sinensis* Segers & Wang, 1997, lack ridges and therefore do not have a distinct FP; we categorized those as possessing no FP (nFP) (Fig. 3). Some species in each of these groups possessed one or more asymmetrical facets, but these are not evenly distributed among the groups; asymmetry in these three categories was as follows: cFP ~82% ($n=15$), qFP ~7% ($n=2$), and sFP ~11% ($n=1$).

Analyzing *Keratella* FP morphospace

In the first part of our morphospace analysis, we limited our exploration to images from four species in two of the FPs: (1) cFP, *K. cochlearis* and *K. tecta* and (2) qFP, *K. quadrata* and *K. hiemalis*. Transformation grids from the Canonical Variate Analysis of the four species showed variation in images of specific species from the published illustrations (Fig. 4A, B). Procrustes ANOVA indicated substantial variation

among coordinate points of the images ($F_{112}=2.00$, $P<0.001$).

The Procrustes ANOVA indicated substantial variation among coordinate points within species of the two groups. That is, comparisons of the two species in the cFP group (*K. cochlearis* vs. *K. tecta*) and the two species in qFP group (*K. quadrata* vs. *K. hiemalis*), both showed significant differences ($F_{28}=2.22$, $P<0.001$ and $F_{28}=10.56$, $P<0.001$, respectively). The Principal Component Analysis plots for those comparisons are shown in Fig. 4C, D, respectively. Because our study of FP variation was based on published images and not on samples and because the research was exploratory, we felt that these results were sufficient to demonstrate differences within and among species. Thus, we chose not to do additional analyses on published images.

In the second part of our FP morphospace analysis, we extended the taxa examined from the 56 species to include 14 other forms that displayed FPs distinct from their nominotypical taxon (see above). The remaining 87 forms recorded in our database were not analyzed. Results examining the morphospace of the 70 taxa showed that *Keratella* does not exploit all possible morphospace; i.e., there are unoccupied regions, where based on the criteria we used, one might expect to find *Keratella* FPs. We demonstrated this in two ways. (1) We noted that there is a wide range in the number of ridges comprising polyhedrons of the 70 taxa (Fig. 5 upper panel). These varied from zero in *K. kostei* and *K. sinensis* to 34 in *Keratella earlinae* Ahlstrom, 1943. The mean (± 1 SD) number of ridges of taxa with FPs was $16.1 (\pm 6.4)$. However, the distribution of the number of ridges was uneven among taxa: cFP had the widest range of ridges (1–34), qFP had an intermediate range (2–22), and sFP had the narrowest range (11–19). The number of polyhedrons in these taxa varied from 0 to 10, with two taxa having no polyhedrons, and 10 taxa having ≥ 6 . (2) A morphospace cube showed that the number of polyhedrons in the 70 taxa (as 3+4; 5+6; and 7 or more sides) had a wide variability. Yet in the *Keratella* FP morphospace there was a sizeable region that is unoccupied (Fig. 5 lower panel).

Does FP form follow function in *Keratella*?

As noted above, the SkyCiv program predicts whether a structural design will pass or fail the stressful

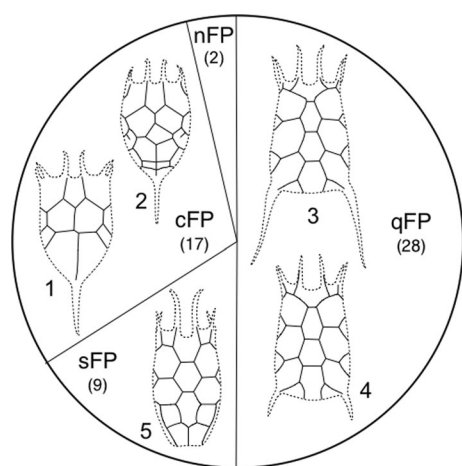


Fig. 3 Grouping of the 56 *Keratella* species by their dorsal facet pattern (FP) as defined by Ruttner-Kolisko (1974). Numbers in parentheses are the number of species assigned to each group. The FPs are as follows: *K. cochlearis* FP=cFP (~30%); *K. quadrata* FP=qFP (~50%); *K. serrulata* FP=sFP (~16%); no FP=nFP (~4%). Species illustrated: 1=*K. cochlearis*; 2=*K. irregularis*; 3=*K. quadrata*; 4=*K. testudo*; 5=*K. serrulata*. (Images are not to scale.) Ahlstrom (1943), among others, have enumerated the facets, but to avoid confusion this was not illustrated here. Thick lines=ridges; dashed lines=outlines of the body. Note the two different types of asymmetries in the two illustrations of *Keratella* spp. in cFP

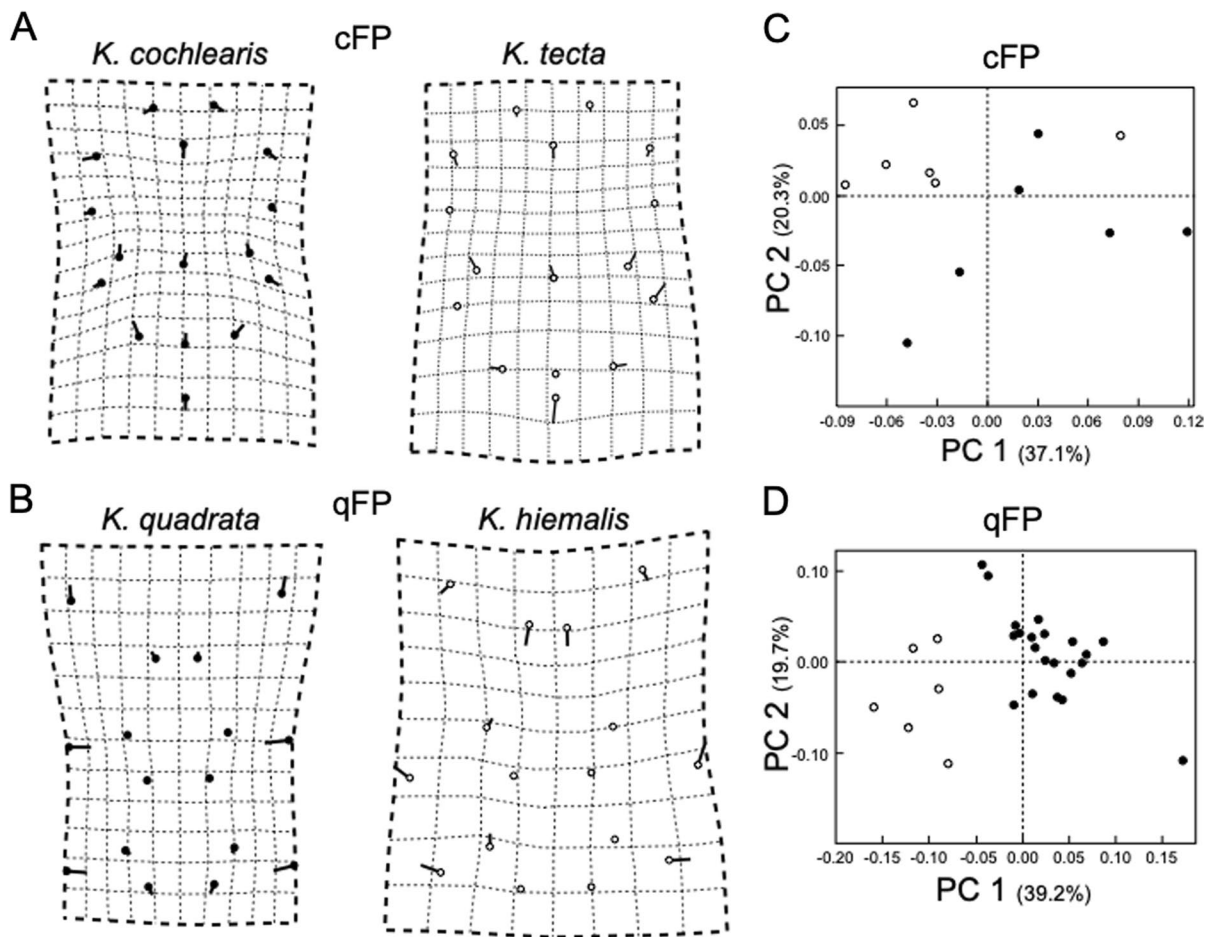


Fig. 4 Geometric morphometric analyses of four species of *Keratella*. Results of the analyses of two facet patterns (FP) are shown. **A** cFP (*K. cochlearis* and *K. tecta*); **B** qFP (*K. quadrata* and *K. hiemalis*). Transformation grids (dashed gridwork) are overlain by wireframe diagrams. The vertices and the line extensions indicate variation as indicated by the 1st principal

component. **C, D** Principal Component Analysis comparing each of the two species in their respective FP group. In both cases the 1st two principal components accounted for >50% of the variance. Open circles: *K. cochlearis* and *K. quadrata*; closed circles *K. tecta* and *K. hiemalis*

conditions imposed on it based on predetermined architectural standards. It is not surprising that all GD models passed the stress challenges we imposed (i.e., both Static and Area Loads), including those tests where one or two ridges were removed. Those had slightly lower Displacement Index (DI) values than the unmodified GD, but no model had a DI predicting failure (Fig. 6A).

On the other hand, results of tests of the *K. cochlearis* models varied depending on the modifications (Fig. 6B). The standard model of *K. cochlearis* (cFP) passed at all four levels of the Static

Load, but then failed at all levels when the Area Load was added. When one ridge was removed (cFP-1) the model failed at the Static Load of 3 and 4, while adding the Area Load did not change that outcome. Surprisingly, when two ridges were removed (cFP-2) the model did not fail at all Static Load levels, nor did it fail with the addition of the Area Load. Indeed, predicted DI values were higher in cFP-2 than in the cFP model at both stress levels. However, when one ridge was added and the FP slightly modified to accommodate the additional ridge (cFP+1), which created a slightly different FP (see Methods), the structure failed at both the Static

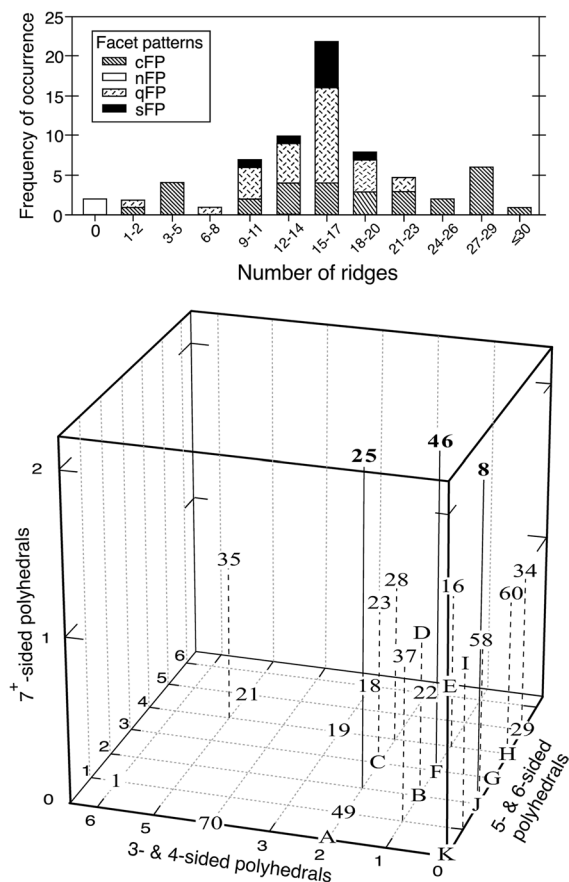


Fig. 5 Variation of facet patterns (FPs) in *Keratella*. This plot is of the 56 valid species and 14 selected forms that displayed FPs distinct from their nominotypical taxon. Upper panel: Bar plot of the number of ridges in each of the four *Keratella* FPs. Boxed insert: FP by groups = cFP, *cochlearis* pattern; nFP, no pattern; qFP, *quadrata* pattern; sFP, *serrulata* pattern. Lower panel: Morphospace cube of FP variability in *Keratella*. Numbers and letters refer to species and groups of species, respectively, as described in the Supplemental Document; the K indicates two species that lack a FP. Bold numbers with solid lines identify species with two polyhedrals with ≥ 7 ridges; numbers/letters with dashed lines identify species with one polyhedron with ≥ 7 ridges; numbers/letters without connecting lines have no polyhedrals with ≥ 7 ridges (see text and the Supplemental Document for additional details.)

and Area Loads. While all of the *K. cochlearis* models did not perform as well as the GD models, we believe that they did remarkably well, given that they have many fewer ridges than the GD.

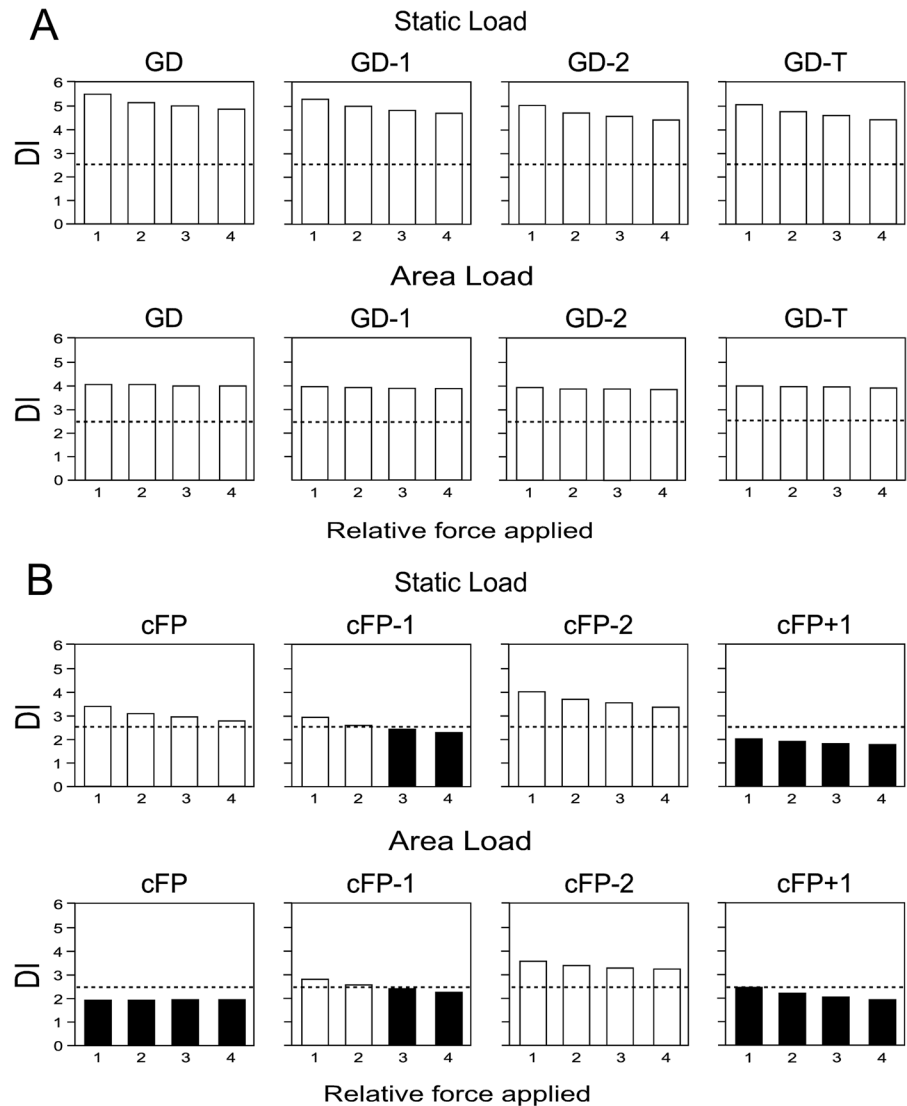
Discussion

With 56 species, *Keratella* is one of the most speciose and also widely distributed genera of Rotifera (Segers, 2002; Segers & De Smet, 2008). Presence of ridges on their lorica permits categorization of the species into three distinctive groups of FPs (cFP, qFP, and sFP), with a fourth group lacking ridges (nFP). Nevertheless, substantial variation within each of the FPs has been noted: e.g., see above and Pejler (1957, 1962). Thus, it is curious that with all the variations that have been documented, much of the available morphospace remains unoccupied. Because rotifers live in a precarious environment in which they are subjected to BFT from a variety of sources, we posited that their FPs offer a means of protection. Because there is no way of testing that concept directly, we employed the architectural program SkyCiv to test two model representations of dome structures: Geodesic Dome and a simulation of *K. cochlearis*. That is, we used this modeling system as a proxy for the physical stresses that may be imposed on *Keratella* when subjected to BFT.

It is not surprising that all Geodesic Dome models met the criteria of the architectural code used in SkyCiv. Geodesic domes distribute stress among all members of the structure allowing them to carry heavy loads; indeed they have been used successfully for nearly 100 years (Anon, 1926) and well before that in various domed buildings since construction of Hadrian's Pantheon (~126 CE) and probably even earlier (Mark & Hutchinson, 1986).

On the other hand, tests of the *K. cochlearis* models gave mixed results. The unmodified *K. cochlearis* model (cFP) passed the stress tests, but at higher stress levels the model with one ridge removed (cFP-1) failed, but curiously when two ridges were removed (cFP-2) the model passed all stress levels. Then when we added a ridge (cFP+1), the model failed at all stress levels. Indeed the prediction of that failure was indicated with the lowest DI levels of all the model runs. We recognize that our analysis does not provide apodictic proof that any of the FPs in *Keratella* are structural adaptations performing the beneficial function of reducing effects of BFT. Yet results from modeling indicate that if the *K. cochlearis* models were constructed buildings, they would pass or fail the SkyCiv architectural standards depending on the arrangements of the ridges.

Fig. 6 Results of structural integrity tests of wire-frame two models using SkyCiv®. (A) geodesic dome; (B) *Keratella cochlearis*. DI (Displacement Index) = Log_{10} of the Global Governing Displacement value. GD standard geodesic dome, GD-1 with one side ridge removed, GD-2 with two side ridges removed, GD-T with a ridge on the top removed, cFP standard *K. cochlearis* model, cFP-1 with one dorsal ridge removed, cFP-2 with two dorsal ridges removed, cFP+1 with one dorsal ridge added and one ridge realigned. Dotted lines indicate the DI value below which structural failure is predicted by SkyCiv (see text and the Supplemental Document for additional details)



Regardless of what we know about *Keratella*, it is remarkable that Stemberger's (1990) insightful observation that—"the morphology of *Keratella* is fundamental to understanding basic ecological interactions that promote coexistence with other, potentially harmful, zooplankton predators and competitors"—has not inspired greater study. Specifically we need to know why the facets are not all monohedral units or arbitrarily arranged polyhedrons, and why there are so few basic FPs ($n=4$). Because the 56 species possess a variable number of facets (0–15), each with 3 to 7+ edges, with nearly half exhibiting some form of asymmetry, the theoretical number of FPs arrangements in the genus is extremely large. The result is

that a substantial portion of the theoretical *Keratella* facet morphospace is unoccupied. However, it is also remarkable that there is variation within morphospecies as we have noted above.

There are at least two possible explanations for why there are gaps in the adaptive landscape of the genus. (1) Intermediate FPs are unavailable because of developmental bottlenecks: i.e., the genomic hypothesis (Pie & Weitz 2005). (2) Phenotypes differ in their ability to withstand substantial physical stress. The first idea would be testable, but requires extensive genetic analysis. The second may be testable with more sophisticated architectural analysis and/or Atomic Force Microscopy (Krieg et al., 2018).

However, if the genes involved in development of FPs could be identified, molecular knockout or knock-down (e.g., interference RNA) techniques to inhibit FP formation may allow more direct tests of the importance of FP arrangement in surviving traumatic physical stress.

The extensive variation within the FPs seen among species and forms remains an enigma, even to the point that the FP is so indistinct that species cannot be distinguished based on their FP alone (Chengalath & Koste, 1987). The illustration of *K. taurocephala* by Ahlstrom (1943) supports that view; in plate 37, compare the figure 9, 11, and 14. These variations in FP could reflect the existence of cryptic species or they could indicate phenotypic plasticity. Regardless, the fact that *K. kostei* and *K. sinensis* lack FPs argues that the facets are not essential under all circumstances. Ignoring the logical error of survivorship bias, we may assume that *Keratella* FPs provide a practical solution to BFT. We suggest restriction of *Keratella* facet morphospace represents an evolutionary tradeoff corresponding to the best possible solution to three important drivers of facet innovation: (1) survival from BFT; (2) minimizing energy costs to producing a thick lorica or even a FP with more ridges than needed; (3) developmental constraints of constructing the FP. That is, *Keratella* FPs function within the concept of Pareto optimality; i.e., evolutionary pressures do not work on one trait, but on the entire animal within its environment (Szekely et al., 2015; Tendler et al., 2015). Thus, within the context of form, adaptation, and fitness of the FP trait, we must be careful in positing that a character results from one evolutionary adaptation. Such suppositions are subject to the critique of epiphenomenal adaptationism. In this case, *Keratella* FPs would simply be a biological spandrel (Gould & Lewontin, 1979); that is, rather than arising as a unique adaptive trait, FPs evolved as a consequence of the evolution of another unrelated characteristic. For example, FPs may function to permit flexing of the lorica when the corona is withdrawn; however, given the loose articulation between the dorsal and ventral plates, this seems to be an unneeded adaptation. Regardless of how *Keratella* FPs evolved, we have provided proof-of-concept that they could operate in reducing effects of BFT.

Unfortunately, we do not know how *Keratella* FPs fail when subjected to a sufficient BFT. For example, in the built world, geodesic domes can fail by

snap-through bucking (Xu et al., 2017). In *Keratella* similar failures may occur resulting in fracturing of the lorica, but information on exactly how death occurs is lacking. We suggest that the FP architecture in *Keratella* acts as if they were a semi-compliant grid mechanism. That is, the complete FP is a flexible structure with nanomechanical properties that exhibit elastic rebound: e.g., external forces may be transmitted throughout the entire body (Schikore et al., 2021). This would mean that there is certain flexibility inherent in the FP. Of course, it is possible that BFT may initiate a resonance within the FP structure, which magnifies the stress causing greater damage. Because the lorica of *Keratella* comprises both the ridges demarking the FP boundaries and all the surfaces of the polyhedrals, a detailed analysis must consider how the entire system will flex when subjected to a BFT. That is, as is seen in Chladni plate harmonics or in the flexing of wings such in Odonata (Hoffmann et al., 2018). By necessity that analysis has to consider the whole structure: i.e., the materials forming the lorica and architectural properties inherent in the entire FPs. This will include both the thickness of the lorica within the polyhedral surfaces and the thickness and placement of the FP ridges.

While other researchers have suggested that firm body walls of loricate rotifers are protected from certain types of predators, to our knowledge the current study is the first to suggest that the FPs in *Keratella* are adaptive strategies to survive BFT. However, we do not suggest that we have conclusively solved the question of why *Keratella* possess their iconic FPs or, more curiously, in two species its absence. Our goal was to provide a proof-of-the-concept that FPs could be affective in providing resistance to BFT without considering lorica thickness.

Interestingly, evolution of FPs in rotifers (facetization) is not limited to *Keratella*; it is seen in some species of *Brachionus*, *Platytas quadricornis* (Ehrenberg, 1832) (Brachionidae), and in some species of *Trichotria* (Trichotriidae). This opens the question of whether FPs evolved independently in these families. Certainly, other organisms possess structures with polyhedral constructions including wings of dragonflies, the carapaces of *Ceriodaphnia*, and the armored plates of *Ceratium*. Other loricate rotifers also possess interesting morphological features that deserve study. These include longitudinal folds in *Notholca*,

textures and ridges in *Ploesoma*, arches in *Euchlanis*, and the double lateral fold in *Tripleuchlanis*.

The inchoate, conceptual model we propose here is that the ridges forming FPs in *Keratella* provide a flexible encasement that reduces effects of BFT. Thus, we posit a tradeoff in evolution of FPs and posterior spines (Marinone, 1995) against the cost of those elaborations and the occurrence of BFT (Stemberger, 1982). Following this logic, species with no FPs (*K. kostei*, *K. sinensis*) may survive well in habitats in which BFT is absent or rare. On the other hand, species with FPs may predominantly live in places where BFT is more common. But even in those habitats, evolution of a lorica with more ridges or a thicker lorica without ridges may not always be cost effective in terms of evolutionary tradeoffs. Evidence to test this model may be gathered using information theory to examine the relationship between variation of FPs and variation of BFT in habitats over seasons.

There are four other possible explanations for *Keratella* FPs that are not mutually exclusive. (1) As we previously discussed, FPs may be a spandrel. (2) FPs may reduce turbulent flow during swimming. However, most rotifers swim slowly ($\sim 0.2\text{--}2.0$ mm/s), as a result their Reynolds number will be low (< 0.5) indicating they move within a laminar flow field (Gilbert & Kirk, 1988; Santos-Medrano et al., 2001). Even species that can make rapid jumps such as *Polyarthra* have Reynolds numbers of ≤ 5 (Gilbert, 1985b). Thus, reducing turbulent flow would probably be inconsequential. Moreover, many rotifers lack FP, including two species of *Keratella*. (3) In the absence of a soft glycoprotein “extracellular layer” (Clément, 1977; Clément & Wurdak, 1991), FPs may provide a surface that disrupts colonization by smaller organisms (e.g., epizotic protists). Impeding colonization of protists in this way is an interesting suggestion that should be examined. (4) FP development may be influenced by the abiotic conditions of the habitat alone: e.g., temperature in *K. cochlearis* (Pejler, 1962). This idea may be tested by culturing different species under a variety of conditions.

Besides the four alternative hypotheses presented above, we note that our study has several limitations. (1) For practical reasons and to establish a protocol for advanced studies we used a small set of published figures. Of course, the accuracy of those images and accompanying descriptions of the species is unknown. A logical step would be to expand this

research using images from more published works and when possible, deposited type specimens. Nevertheless, it would be best to use images of fresh specimens collected from a wide variety of locations and through several seasons. Also few publications depict lateral views of the animals; that sort of information is certainly needed. (2) The size of dome-like structures ranges from < 100 μm in radiolarians and *Keratella* to ~ 200 μm in the Jeddah Superdome (Kingdom of Saudi Arabia). Thus, our assumption is that their dynamic, mechanical behavior is essentially constant over more than 6 orders of magnitude; this assumption needs to be examined. (3) We realize that using wireframe models for our SkyCiv analysis is an oversimplification of the *Keratella* lorica (e.g., as noted above, material between the ridges must be considered) and we have run the simulations using a sustained load, not a trauma caused by a sudden impact. (4) Finally, we have not accounted for lorica thickness and we do not know the physical influence of being surrounded by water on the structural integrity of FPs.

Evaluation of potential evolutionary transformations among *Keratella* FPs using the Cartesian coordinate, deformation system presented by D’Arcy Thompson (1942) and expanded by others (Abzhinov, 2017) is beyond the scope of our study. In those systems the fabric establishing Cartesian coordinates is distorted in various ways to illustrate transforms among basic forms. To illustrate transformation among *Keratella* species the vertices (points) of the Cartesian coordinates must be distorted and also the connections among the ridges must be broken and then reformed in new patterns. For example, consider *K. hiemalis* as illustrated in figures 7 and 9 by Chengeleth & Fernando (1973).

Future directions

We posit that the FP of *Keratella* is a Geodesic Dome that withstands BFT while using a minimal amount of biological material. If this hypothesis is correct, much remains to be done to achieve a comprehensive understanding of *Keratella* FP morphology. We recommend that studies be undertaken to include the following. (1) A thorough analysis of all *Keratella* species should be undertaken that includes a geometric morphometric analysis in which all polyhedrons

comprising the FP are documented and are plotted in 3-dimensional Euclidean space. Also lorica thickness should be surveyed across the genus. (2) Detailed genetic analysis of species should be undertaken across a wide geographic area: e.g., (Derry et al., 2003; Garcia-Morales & Elias-Gutierrez, 2013). That analysis should be combined with morphological information, including information on *Keratella* trophi and lorica structure, as well as ecological data. (3) Existing published data could be surveyed to compile data on geographical and seasonal distributions of *Keratella* species v. potential predators and cladocerans, both of which could cause BFT: e.g., (Diéguez & Gilbert, 2011). (4) Using cultures, research could be done to systematically vary factors to determine how FPs, as well as anterior and posterior spines develop: e.g., with and without predators or daphnids (Gilbert & MacIsaac, 1989). This could be extended to study ridge thickness. (5) Other methods of evaluating the structural integrity of the FPs should be used. These might include physical models, other software applications, and rigorous mathematical analyses (Barbieri et al., 2016; Lanzoni & Tarantino, 2020), particularly with models in which the facet elements are curved. Estimates of Young's modulus (structural elasticity; E) of the loricas of several *Keratella* species should be determined (Vogel, 1988). (6) Because little is known of the arrangement of proteins comprising the intracytoplasmic lamina (ICL) of rotiferan loricas (Bender & Kleinow, 1988; Kleinow, 1993), we posit that the micro-organization of the ICL may influence stiffness and flexibility thus resulting in better tolerance to BFT. (7) As part of an expanded study, FPs need to be evaluated in detail to determine whether certain configurations of facets are more critical than others to withstand BFT. (8) Being subjected to "leg kicks" while within the filtering chamber of daphnids is a likely mode whereby *Keratella* suffer BFT. Thus, we need to estimate the maximum force applied to the animals at the point of impact with a daphnid leg. (9) By using the principles of image recognition, algorithms could be developed that use artificial intelligence to identify species by their FPs (Stelzer, 2009). (10) Finally, we suggest that *Keratella* FPs may serve as biomimetic models for architectural systems that must endure unusual physical stresses (Hwang et al., 2015; Pohl & Nachtigall, 2015).

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Data availability Data are available in the Supplemental Document that accompanies the paper.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflicts of interest/competing interests. The sponsors had no role in the design, execution, interpretation, or writing of the study.

Ethical approval No collecting permits were required for this study. None of the specimens that we collected are endangered or threatened. Sampling and processing protocols followed appropriate guidelines established by the local municipalities.

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