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Tales of the crown: An integrative approach to the testate amoeba *Galeripora dentata* (Ehrenberg, 1830) Siemensma, 2021 (Amoebozoa, Arcellinida, Arcellidae)

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ABSTRACT

Species delimitation in unicellular organisms remains a significant challenge, primarily due to the limited number of taxonomically informative traits and their often adaptive nature. Moreover, most original descriptions of testate amoebae, dating from the late 19th to mid-20th century, relied solely on light microscopy, were often accompanied by inadequate diagnoses, and lacked illustrative drawings. To address the limitations of the historic phenetic classification, modern approaches are needed to resolve fundamental questions concerning true biodiversity and phylogenetic relationships. In this study, I employed an integrative framework that combines ecological data, morphological data (light and scanning electron microscopy), and biometric measurements to investigate the testate amoeba *Galeripora dentata* (Ehrenberg, 1830) Siemensma, 2021 from Bulgaria. I provide an improved diagnosis of the species, along with a synthesis of its global geographical distribution and ecological preferences.

1. Introduction

The genus *Arcella* comprises lobose testate amoebae characterized by more or less campanulate, proteinaceous shells composed of minute hexagonal units known as alveoli, and notably lacking incorporated exogenous particles. First described by Ehrenberg (1830), the genus initially included three species: *A. vulgaris*, *A. dentata*, and *A. aculeata* (the basionym of *Centropyxis aculeata*). Today, the number of recognized taxa exceeds 130 (Deflandre, 1928; González-Miguéns et al., 2021; Meisterfeld, 2002). A recent integrative approach—combining ecological, morphological, and genetic data—has refined the systematics of the group and led to the establishment of a new genus, *Galeripora* (González-Miguéns et al., 2021). According to the latest taxonomic frameworks, both genera are classified within the class Elardia, order Arcellinida, suborder Glutinoconcha, infraorder Sphaerothecina, and family Arcellidae (González-Miguéns et al., 2021; Kang et al., 2017; Kosakyan et al., 2016; Lahr et al., 2019). These amoebae are most abundant in aquatic habitats and exhibit a global distribution, occupying environments ranging from oligotrophic peatlands to eutrophic freshwater pools, and, less frequently, soil litter (Chardez, 1989; Deflandre, 1928). Several species are considered cosmopolitan, having broad ecological tolerance.

One such species is *Arcella dentata* Ehrenberg, 1830. The initial mention of this taxon was not accompanied by a formal description or diagnosis, rendering it a *nomen nudum*. Although referenced as early as 1830, the first brief description appeared in 1838, in which Ehrenberg provided only a vague diagnosis and comparative notes distinguishing *A. dentata* from *A. vulgaris*. Ehrenberg (1838) suggested that specimens of *A. vulgaris* with a concave depression and larger crystalline facets across the hemispherical shell surface should be considered a new species, *A. dentata*. Thus, the key distinction lies in the larger, crystalline facets of *A. dentata* compared to the finer, more regular facets of *A. vulgaris*. Ehrenberg (1838) further noted three intermediate forms within *A. dentata*, characterized by 10 to 12 spines, differing in length and angle. One of these forms was described as square-shaped, with a truncated apex and sharp but less prominent angles, and lacking spines. This ambiguous classification was later refined by Perty (1852), who divided Ehrenberg's forms into three new taxa: *A. dentata*, *A. okeni* (both spined), and the spineless *A. angulosa* (now recognized as *A. costata* var. *angulosa* (Perty, 1852) Playfair, 1918) (Claparède and Lachmann, 1858). Notably, three years earlier, Perty (1849) had already described *A. stellaris* from peat waters near Bern, Switzerland. He observed specimens bearing 8 to 12 spines of a varying degree of development, from small protuberances to elongated projections. In his diagnosis, Perty (1849) emphasized that *A. stellaris* should not be confused with

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A. dentata, noting that both *A. vulgaris* and *A. stellaris* from the Bern region exhibited a much finer texture than depicted by Ehrenberg (1838), consisting of numerous concentric lines radiating from the center. This texture is particularly visible in empty shells. The taxonomic status of *A. dentata* became further entangled when Ehrenberg (1854) described *A. stellata*, which corresponds to his earlier spined variety of *A. dentata*. Later, Ehrenberg (1871) attempted to summarize and categorize taxa within the genus *Arcella*, introducing additional names without formal diagnoses, including *A. homocochlamys dentata*, *A. sticholepis stellaris*, and *A. heterocosmia stellata*. Despite the distinctive morphology of *A. dentata*, a comprehensive description of its general appearance and cellular features was not provided until nearly half a century later by Leidy (1879), who also reviewed its taxonomic status and treated the subsequently described taxa as junior synonyms. In contrast, Penard (1902) advocated for the use of the name *A. stellaris* Perty, 1849 to avoid confusion stemming from Ehrenberg's (1838) spineless form. Leidy (1879) interpretation was later adopted in several monographs (Cash and Hopkinson, 1905; Deflandre, 1928; Todorov and Bankov, 2019). Based on observed variation in test morphology, Deflandre (1928) described two varieties: the starfish-like *A. dentata* var. *trapezica* (based on Leidy's (1879) illustration) and the more rounded *A. dentata* var. *cashiana*, with abruptly arising spines (based on Cash and Hopkinson's (1905) drawing).

Despite its distinctive morphology and global distribution, the phenotypic plasticity and distribution pattern of *A. dentata* remain poorly understood. Its infrequent occurrence—typically represented by single specimens—has resulted in limited data on its morphology, biometric variation, and ecological preferences. Broadly speaking, advancing our understanding of most testate amoebae is essential for transitioning from basic research to applied ecological studies. A more comprehensive understanding of their biology, ecology, and taxonomy, achieved through an integrative approach, will support the development of more reliable and precise bioindicator tools for monitoring both current and historical (palaeoecological) environmental changes.

An abundant population of *Arcella* (= *Galeripora*) *dentata* was found during a survey of *Sphagnum*-dwelling testate amoebae in Bulgaria (Bankov, 2022). I conducted detailed analyses using both light and scanning electron microscopy, complemented by morphometric examination of shells. The primary objectives of this study were to: (1) assess the degree of phenotypic plasticity and biometric variability within the examined population; (2) compare the findings with previous studies to identify hidden (pseudo)cryptic biodiversity; and (3) clarify the species' geographical distribution and ecological preferences.

2. Material and methods

The material was collected and processed in situ on 25 August 2017 from submerged hollows of *Sphagnum subsecundum* Nees, 1819, located in the Popovi Livadi area of the Pirin Mts., Bulgaria (41.54888° N, 23.64004° E, 1386 m a.s.l., Fig. 1). The peat mosses occurred in an open meadow bordered by coniferous forest, primarily dominated by *Pinus sylvestris* L. Concurrent with sampling, the following environmental parameters were recorded: air temperature 24.1 °C, water temperature 21.6 °C, pH 4.97, electrical conductivity 121.2 μS/cm, dissolved oxygen concentration 4.8 mg/L, oxygen saturation 63 %, and water table depth 2 cm. Laboratory analyses were conducted to identify testate amoebae, with a particular focus on specimens of *Galeripora dentata*. Isolation was performed under a stereomicroscope at 100× magnification.

Fig. 1. (**A**) Locality of the examined population. Map boundaries delineate the study area and do not necessarily reflect officially recognized national borders. (**B**) Habitat. (**C**) *Sphagnum subsecundum*.

Morphometric characteristics of 210 shells were examined using an "Amplival" optical microscope (Zeiss-Jena) equipped with 40× objective and 10× ocular lenses. Light micrographs were captured using an Axio Imager M2 (Carl Zeiss) compound microscope equipped with a ProgRes C7 digital camera and CapturePro software ver. 2.8. The following morphometric parameters and ratios were measured: shell diameter including dentate projections (D), aperture diameter (A), shell height (H), aperture/diameter ratio (A/D), and height/diameter ratio (H/D). For each variable, the following statistics were calculated: arithmetic mean (Mean), median (M), standard deviation (SD), standard error of the mean (SE), coefficient of variation in % (CV), and minimum (Min) and maximum (Max) values.

For scanning electron microscopy (SEM), selected specimens were extracted using a glass micropipette, washed several times in distilled water, mounted on a coverslip, and air-dried. The shells were then gold-coated in a vacuum sputter coater. Micrographs were obtained using a JEOL JSM-5510 SEM operating at 10 kV.

Statistical analyses were conducted using STATISTICA software ver. 10.0 (StatSoft, 2011). Normality tests (Shapiro–Wilk, Anderson–Darling, Lilliefors, and Jarque–Bera) were conducted using PAST software ver. 5.2.2 (Hammer et al., 2001). Topographic maps were created using QGIS.

To avoid ambiguous terminology, the term "dentate projections" is used instead of "spines", which traditionally refers to elongated, rigid, and sharply pointed structures, such as those found in *Euglypha*. In contrast, dentate projections encompass a broader morphological range, from small, bud-like protuberances to well-developed, prominent structures. For consistency and brevity, these structures are hereafter referred to as "projections," except in the diagnosis section, where the full term "dentate projections" is retained to preserve taxonomic precision.

3. Results

3.1. Biometry

Morphometric traits were measured for 210 specimens, with descriptive statistics summarized in Table 1. Shell diameter ranged from 96 to 161 µm, aperture diameter from 35 to 58 µm, and shell height from 32 to 50 µm (see Bankov, 2025a for the full dataset of biometrical measurements). The coefficients of variation (CV) ranged from 5.38 % to 9.79 %, indicating that the population was relatively homogeneous and that shell traits exhibited low to moderate variability. Among the measured traits, shell diameter was the most stable, while height showed the greatest variability. Aperture diameter displayed intermediate variability, with a CV of 7.38 %. The A/D (aperture/diameter) and H/D (height/diameter) ratios had CVs of 7.91 % and 10.00 %, respectively.

Analysis of size frequency distributions revealed that the population was size-monomorphic, with well-defined primary size classes for all major morphometric traits (Fig. 2). For example, 89 % of specimens had shell diameters between 130 and 150 µm, while only 5 % fell outside this range (Fig. 2A). Histograms for aperture diameter, shell height, and the A/D and H/D ratios showed similar patterns, with most values concentrated within narrow ranges: aperture diameter 40–50 µm (91 %), height 32–46 (86 %), A/D ratio 0.28–0.38 (97 %) and H/D ratio 0.22–0.32 (94 %) (Fig. 2B–E). Regarding the number of projections, over 93 % of specimens exhibited 11 to 13 projections, while 10, 14, and 15 projections were observed in 3, 5, and 1 specimens, respectively (Fig. 2F). The presence of clearly defined size classes and the absence of subsidiary peaks (i.e., bell-shaped curves) suggest a normal distribution of the measured traits.

The average values (Mean ± SD) of the measured shell traits were as follows: diameter 140.2 ± 7.5 µm ($n = 210$), aperture diameter 46.1 ± 3.6 µm ($n = 210$), and height 38.8 ± 3.8 µm ($n = 50$). These values align with the main size classes and support the conclusion that the examined population is size-monomorphic. The close agreement between mean and median values suggests a symmetrical distribution, with no significant skewing due to extreme values or outliers. This pattern indicates that the dataset likely follows, or closely approximates, a normal distribution. However, despite this visual symmetry, normality tests rejected the assumption of normality for both the shell diameter and aperture diameter datasets, while the height data met the criteria for normality (Table 2). After removing outliers, the shell diameter data approximated a normal distribution. In contrast, the aperture diameter data remained non-normal, even after outlier removal and log-transformation. This persistent deviation may reflect underlying structural asymmetry, the presence of subgroups, or intrinsic non-Gaussian characteristics that cannot be corrected through standard data cleaning or transformation techniques. One possible explanation lies in the large sample size: with 210 observations (206 after outlier removal), normality tests become highly sensitive and capable of detecting even minor deviations that may not be visually apparent.

These findings were further supported by scatter plots of shell diameter versus aperture diameter and shell diameter versus height (Fig. 3A, B), which revealed moderate, positive linear relationships. Additionally, boxplots (Fig. 4) indicated a symmetric distribution for shell diameter, consistent with normality, while aperture diameter and shell height exhibited positive skewness, suggesting deviation from a normal distribution.

The summarized biometric data from previous studies are provided in Table 3. The results of the present study are consistent with those reported by other authors (Bartoš, 1965; Cash and Hopkinson, 1905; Deflandre, 1928; Ehrenberg, 1838; Grospietsch, 1958; Leidy, 1879; Netzel and Grunewald, 1977; O'Donoghue, 2010; Penard, 1902; Perty, 1849, 1852; Playfair, 1918; Sigala et al., 2016; Silva et al., 2016; Snegovaya and Alekperov, 2010; Todorov and Bankov, 2019; Velho et al., 1996; Vikol, 1992; Vucetich, 1973a; Wenninger, 1934; Whitelegge, 1887), and fall within the biometric framework established by these studies. Variations observed among datasets likely reflect population-specific morphological differences, environmental influences, differences in measurement techniques, or a combination of these factors.

3.2. Description and diagnosis

Early studies of *Galeripora dentata* were based on light microscopy and focused primarily on the general appearance and shell structure (Leidy, 1879; Plate XXX, Figs. 10–19) (Fig. 5). Subsequent analyses incorporated live observations captured on microcinematographic film, as well as combined scanning and transmission electron microscopy

Table 1
Biometric characterization of *Galeripora dentata*.

Character	Mean	M	SD	SE	CV	Min	Max	*n*
Shell diameter (D)	140.2	140.4	7.54	0.52	5.38	96	161	210
Aperture diameter (A)	46.1	46	3.61	0.25	7.83	35	58	210
Shell height (H)	38.8	38	3.80	0.54	9.79	32	50	50
A/D ratio	0.33	0.33	0.03	0.002	7.91	0.25	0.43	210
H/D ratio	0.27	0.27	0.03	0.004	10	0.22	0.36	50

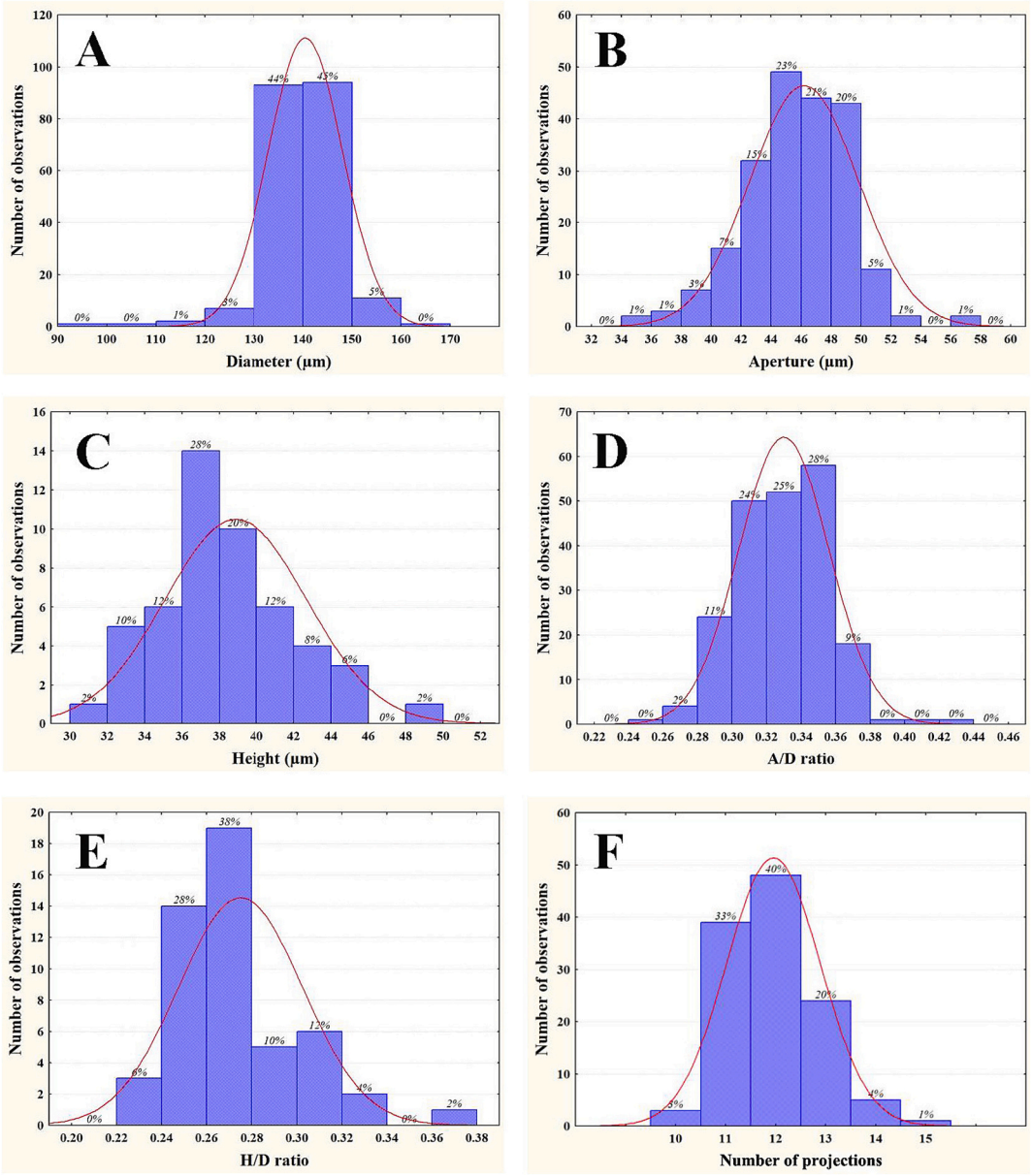

Fig. 2. Histograms showing the size-frequency distribution of key morphometric traits in the examined population of *G. dentata*. (**A**) Shell diameter. (**B**) Aperture diameter. (**C**) Shell height. (**D**) Aperture/diameter ratio. (**E**) Height/diameter ratio. (**F**) Number of projections.

Table 2
Results of normality tests for shell diameter (D), aperture diameter (A), and shell height (H).

	D	D (outliers removed)	A	A (outliers removed)	A (log10(x))	H
n	210	202	210	206	206	50
Shapiro–Wilk	0.8996	0.9921	0.9819	0.9777	9.71E–01	0.972
p (normal)	1.15E–10	0.3478	0.008296	0.002326	0.000258	0.2795
Anderson–Darling	2.895	0.3766	1.257	1.439	1.792	0.4051
p (normal)	2.67E–07	0.4078	0.0028	0.000996	0.000134	0.3407
p (Monte Carlo)	0.0001	0.4185	0.0045	0.0005	0.0003	0.3509
Lilliefors	0.09638	0.04826	0.0861	0.1011	0.1064	0.1051
p (normal)	0.0001	0.2922	0.0001	0.0001	1.00E–04	0.176
p (Monte Carlo)	0.0002	0.3072	0.0011	0.0001	0.0001	0.174
Jarque–Bera	518.8	0.7692	3.247	4.351	7.645	2.372
p (normal)	2.18E–113	0.6807	0.1972	0.1135	0.02187	0.3055
p (Monte Carlo)	0.0001	0.6592	0.158	0.0852	0.0253	0.1694

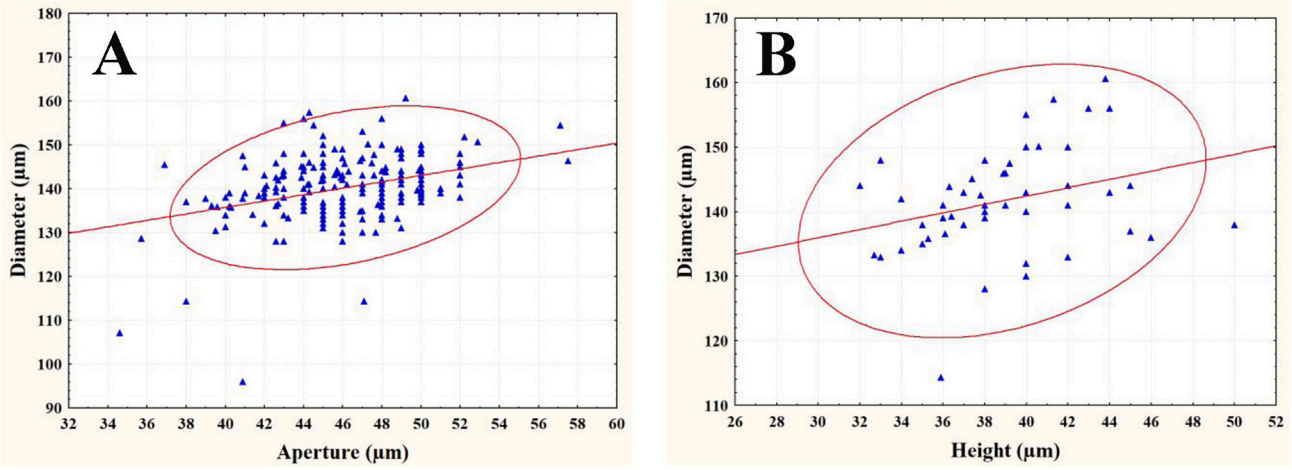

Fig. 3. Scatter plots. (**A**) Shell diameter and aperture. (**B**) Shell diameter and height.

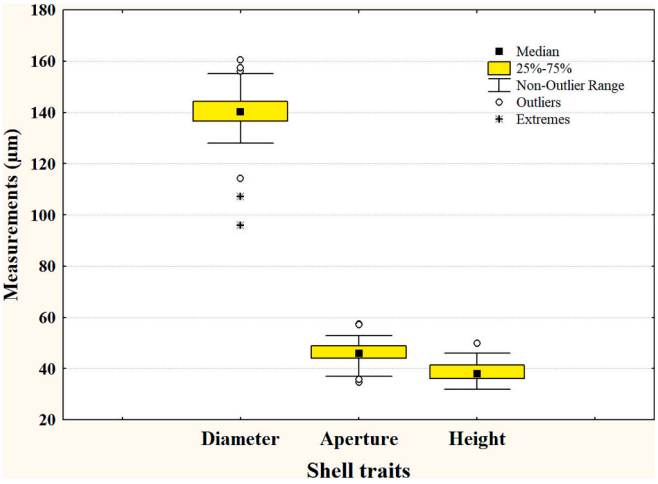

Fig. 4. Box plots showing variability of shell diameter, aperture, and height.

(Netzel, 1970, 1972a; Netzel and Grunewald, 1977). These investigations provided the first insights into the species' ultrastructure and yielded new information on its morphology, morphogenesis, locomotion, cell division, and gas vacuole formation. The results of the present study support and refine the earlier taxonomic diagnoses.

3.2.1. *Improved diagnosis*

Shell autogenous and proteinaceous, initially colorless and transparent, gradually darkening to various shades of yellow and brown due to iron ion accumulation over time (Fig. 6). Shell circular in both ventral and dorsal views, bearing 7 to 17 (occasionally up to 20) dentate projections, which may be bud-like or well-developed (Figs. 6, 7, 8A, B, 9A, B). Shell crown-like in lateral view, with an evenly rounded apex and a turned-up rim edged by a series of radiating ridges of variable length, curving toward projection tips (Fig. 7F). Dome of aboral region depressed at summit and broadly fluted along sides (Figs. 7, 8C). Apertural surface usually smooth, with numerous small pores, forming an inverted concave funnel. Apertural opening surrounded by a ring of approximately 50 large (0.5–1.0 µm), irregularly spaced pores (Fig. 9). Shell composed of hollow alveoli approximately 1 µm in diameter, rectangular in vertical section and hexagonal, or occasionally pentagonal, in horizontal section (Fig. 8D). Cytoplasmic amoeboid body occupies central shell cavity and attached by small epipodia to inner wall. Typically, a single granular, cylindrical, digitiform pseudopodium. Two vesicular nuclei, each with a large central nucleolus located opposite the aperture (Fig. 6E).

3.2.2. *Measurements*

Shell diameter: (68?) 95–188 µm (occasionally exceeding 200 µm); shell height: 30–60 µm; aperture diameter: 24–58 µm; aperture height: 10–22 µm; aperture/diameter ratio: 0.25–0.43; height/diameter ratio: 0.22–0.36.

3.3. *Geographic distribution*

The aim of this chapter is not to definitively establish the distribution pattern of *Galeripora dentata*, but rather to summarize the current state of knowledge (Fig. 10). The following data are interpreted under the assumption that the recorded morphological units (metapopulation lineages) are capable of interbreeding—a plausible scenario given that sexual reproduction has been observed in *Arcella* (Mignot and Raikov, 1992)—and that they share similar phenotypes and biometric characteristics, in line with the general lineage species concept (De Queiroz, 2005). However, due to the absence of molecular data, it is not possible to determine whether these morphological units represent a single biological species or multiple distinct lineages. To avoid taxonomic ambiguity, all previously reported specimens are here referred to as *Galeripora dentata* sensu lato (s.l.).

Specimens of *G. dentata* s.l. have been reported from numerous localities across Europe, including Austria (Aescht and Foissner, 1989), Bulgaria (Bankov, 2022; Golemansky, 1967; Golemansky et al., 2003, 2006; Pateff, 1924), Croatia (Lordan, 2018), the Czech Republic (Bartoš, 1965), the British Isles (Cash and Hopkinson, 1905; Curds and Cockburn, 1970; Deflandre, 1928 – reported as *Arcella dentata* var. *cashiana*), France (Deflandre, 1928 – reported as *A. dentata* and as *A. dentata* var. *trapezica*), Hungary (Daday, 1904; Grospietsch, 1982; Török, 1998), Moldova (Vikol, 1992), Poland (Lamentowicz et al., 2008, 2011; Moraczewski, 1961), Romania (Godeanu, 1972, 1977; Neagu-Godeanu et al., 1968), Russia (Kurina and Hongkai, 2018; Pavelko and Plotnikov, 2016; Tsyganov et al., 2012), Sweden (Bérzinš and Stensdotter, 1990), and Switzerland (Penard, 1902; Perty, 1849).

In Asia, populations have been recorded in Azerbaijan (Alekperov and Snegovaya, 1999; Snegovaya and Alekperov, 2010; Tahirova, 2023), China (Song et al., 2014), India (Prajapati et al., 2019), Iran (Sabkara, 2019), Japan (Tanaka et al., 2006), and Kazakhstan (Troshina, 2012; Troshina and Matmuratov, 2003). African records include Burundi, Rwanda, and Tanzania (Daday, 1910a), Egypt (Khalifa et al., 2015), and South Sudan (Daday, 1910b; Chardez, 1974).

In the Americas, *G. dentata* s.l. has been reported from North America (Bailey, 1851; Deflandre, 1928 – reported as *A. dentata* var. *trapezica*; Hegner, 1919b; Hempel, 1898; Landacre, 1903; Leidy, 1879; Wailes,

Table 3
Measurements of *G. dentata* based on previous biometric records and the present study. The number of specimens examined is indicated in parentheses.

Reference	Country	Shell diameter (μm)	Shell height (μm)	Aperture diameter (μm)	Aperture height (μm)	Projections (μm)	Projections (number)
Ehrenberg (1838)[a]	Germany	up to 106/127					10.12
Perty (1849) (reported as *A. stellaris*)	Germany?	113–161					8–14, mostly 10
Perty (1852) (reported as *A. okeni*)	Germany?	161					
Leidy (1879)	USA	132–184	44–48	40–44	10.16		
Whitelegge (1887)	Australia						10.15
Penard (1902)	Switzerland	150					8–12 or even more
Cash and Hopkinson (1905)	England	95		30		15–17	
Playfair (1918)	Australia	over 200 (1)					
Hegner (1919b)	USA	73–150 (100)					7–17 (up to 20) (100)
Deflandre (1928) (reported as *A. dentata* and *A. dentata* var. *trapezica*)	France, USA	123–168	38–40	32–40	17–22		
Deflandre (1928) (reported as *A. dentata* var. *cashiana*)	England	95		30		15–17	
Wenninger (1934)	USA	130–185					
Grospietsch (1958)	Germany?	123–168	38–40				
Bartoš (1965)	Czech Republic	120–150					
Bartoš (1965)	Germany?	107–229–133 (25)	41–48–58 (25)				
Vucetich (1973a)	Argentina	132–143	30–60	34–40			
Netzel and Grunewald (1977)	Germany	107–133 (25)	41–58 (25)				
Vikol (1992)	Moldova	150					
Velho et al. (1996)	Brazil	113–138 (8)	32–43 (8)	35–49 (8)	13–21 (8)		
O'Donoghue (2010)	Australia	200					
Snegovaya and Alekperov (2010)	Azerbaijan	100–110 (10)		30–35 (10)	15–20 (10)	8–10 (10)	
Sigala et al. (2016)	Mexico	68–176 (mean 144.3) (6)		24–42 (mean 32.3) (6)			
Silva et al. (2016)	Brazil	130–132.2 (5)		40.3–46 (5)			
Silva et al. (2016) (reported as *A. dentata* var. *trapezica*)	Brazil	125.4–149.9 (5)		34.6–40.5 (5)			
Todorov and Bankov (2019)	Bulgaria	96–161 (mean 140) (73)	33–44 (mean 37.8) (13)	35–58 (mean 44.9) (72)			
Present study	Bulgaria	96–161 (mean 140.2) (210)	32–50 (mean 38.8) (50)	35–58 (mean 46.1) (210)			10–15 (120)

[a] Ehrenberg's (1838) original measurements are reported in *linie* (1/10 or 1/12 of an inch); approximate maximum values are provided where applicable.

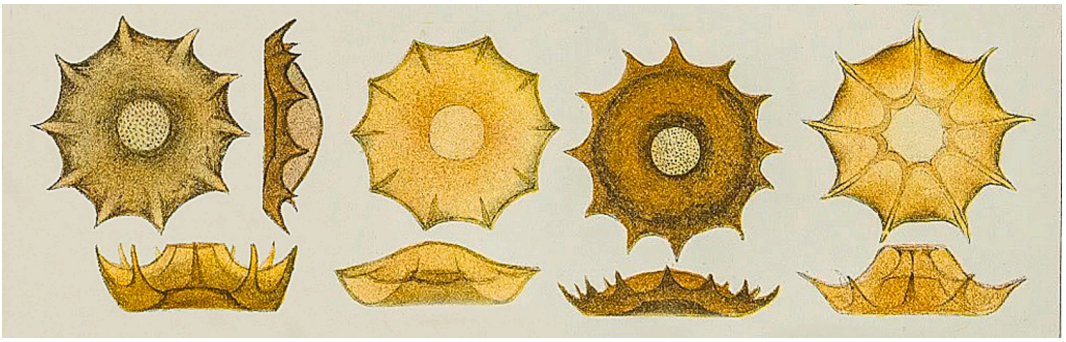

Fig. 5. Original drawings of Leidy (1879), modified.

1912; Welch, 1936; Wenninger, 1934), Central America (Mexico: Sigala et al., 2016, 2018), and South America, including Argentina (Claps et al., 2009; Vucetich, 1973a, 1973b), Brazil (Araujo et al., 2023; Arrieira et al., 2015; Bini et al., 2007; Dabés, 1995; Hardoim and Heckman, 1996; Neumann-Leitão et al., 1999; Pereira et al., 2011; Picapedra et al., 2019; Silva et al., 2016 – reported as *A. dentata* and as *A. dentata* var. *trapezica*; Velho et al., 1996, 2003; Vieira et al., 2015), Paraguay (Daday, 1905), and Venezuela (Grospietsch, 1975; Rivas et al., 2022).

The species has also been recorded in Australia (O'Donoghue, 2010; Playfair, 1918; Shiel and Tan, 2013; Whitelegge, 1887), and its presence on remote islands such as Tahiti (Decloitre, 1960) and the Azores (Barrois, 1888) highlights its high dispersal potential.

Applying the general lineage species concept to the global distribution and high dispersal capacity of *G. dentata* s.l. would suggest a high degree of genetic homogeneity due to extensive gene flow. However, this interpretation must be approached with caution. The limited number of morphological traits and the lack of molecular data in most protist studies likely result in an underestimation of true biodiversity. Morphology-based species delimitation is inherently constrained by phenotypic plasticity and short life cycles, which obscure differentiation

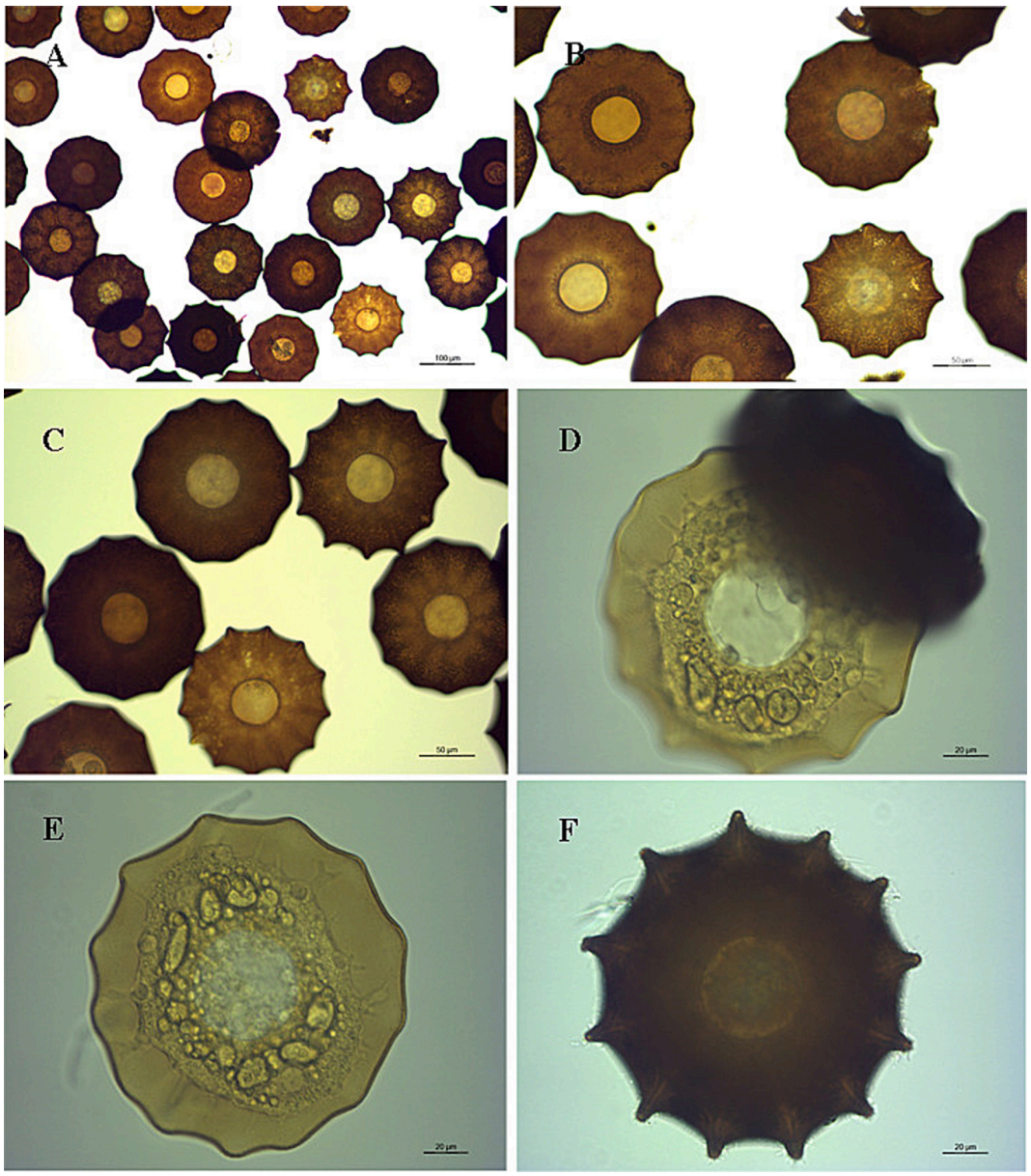

Fig. 6. Light photographs of the examined population of *G. dentata*. (**A–C**) Group photos. (**D**) Cell division. (**E**) A specimen with 13 bud-like projections. (**F**) A specimen with 12 well-developed projections. Scale bars: 20 μm (D–F), 50 μm (B, C), and 100 μm (A).

and speciation processes, as well as the mechanisms of dispersal. While summarizing distribution data is valuable, it must be interpreted carefully in light of recent findings that reveal species complexes with hidden (pseudo)cryptic diversity and distinct biogeographic patterns (González-Miguéns et al., 2021; Heger et al., 2013; Kosakyan et al., 2012, 2013; Singer et al., 2015; Soler-Zamora et al., 2023; Useros et al., 2023).

3.4. Ecology

Galeripora dentata s.l. has been recorded primarily in lentic freshwater environments, including lakes, ponds, reservoirs, and even temporary pools (Aescht and Foissner, 1989; Alekperov and Snegovaya, 1999; Bini et al., 2007; Cash and Hopkinson, 1905; Dabés, 1995; Daday, 1904, 1905, 1910a; Deflandre, 1928; Golemansky et al., 2006; Grospietsch, 1975, 1982; Hegner, 1919b; Khalifa et al., 2015; Moraczewski, 1961; Neagu-Godeanu et al., 1968; Pavelko and Plotnikov, 2016; Prajapati et al., 2019; Shiel and Tan, 2013; Sigala et al., 2016; Sigala Regalado et al., 2018; Silva et al., 2016; Snegovaya and Alekperov, 2010; Troshina, 2012; Vieira et al., 2015; Wailes, 1912; Wenninger, 1934). However, it has also been found in lotic systems such as rivers (Araujo et al., 2023; Arrieira et al., 2015; Chardez, 1974; Claps et al., 2009; Daday, 1910a, 1910b; Hempel, 1898; Lordan, 2018; Neumann-Leitão et al., 1999; Pereira et al., 2011; Picapedra et al., 2019; Sabkara, 2019; Snegovaya and Alekperov, 2010; Troshina and Matmuratov, 2003; Velho et al., 2003), as well as in artificial environments such as sewage treatment plants and drainage channels (Curds and Cockburn, 1970; Shiel and Tan, 2013).

This species has been reported from planktonic, periphytic, and benthic communities. Leidy (1879) noted that the undersides of floating leaves provide a favorable microhabitat. Its planktonic behavior is attributed to the production of gas bubbles within the cytoplasm, a buoyancy mechanism also observed in *Difflugia hydrostatica* Zacharias, 1897 (Meisterfeld, 1991). The small size of the organism and the

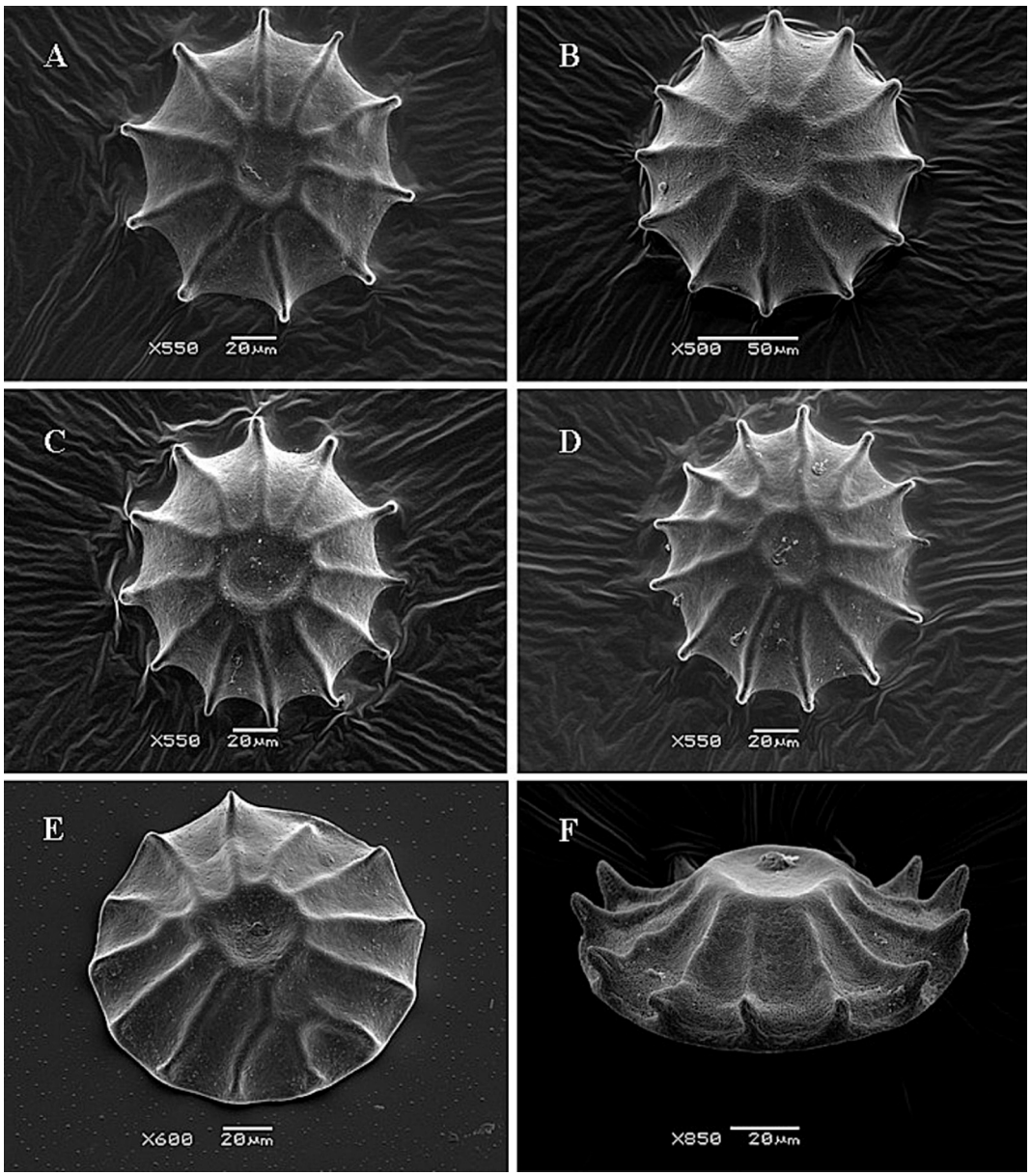

Fig. 7. Scanning electron photographs of dorsal side (A–E) and semilateral side (F). (**A**) A specimen with 10 well-developed projections. (**B, C**) Specimens with 12 well-developed projections. (**D**) A specimen with 13 well-developed projections. (**E**) A specimen with 13 bud-like projections. (**F**) A specimen with 13 well-developed projections. Scale bars: 20 µm (A, C–F) and 50 µm (B).

presence of shell projections are additional adaptations that facilitate passive drift within the water column.

It is not surprising that *G. dentata* has also been found in transitional zones between aquatic and terrestrial ecosystems, such as *Sphagnum* peatlands (Bankov, 2022; Lamentowicz et al., 2008, 2011; Pateff, 1924; Song et al., 2014; Welch, 1936), swamps (Daday, 1910a; Golemansky et al., 2003; Pateff, 1924), marshes (Payne et al., 2010; Penard, 1902; Tsyganov et al., 2012 – reported as *A. dentata* var. *trapezica*), minerotrophic mires (Kurina and Hongkai, 2018), and epiphytic mosses with high moisture content (Vucetich, 1973b). Occasional findings in terrestrial habitats, such as hydrophilic soil mosses in Bulgaria (Golemansky, 1967), are likely attributable to fluctuations in water levels in nearby aquatic systems and the proximity of sampling sites (see Bankov, 2025b for a complete list of occurrence records and references).

4. Discussion

4.1. Inconsistency between modern and classical studies

It is important to highlight key methodological limitations when comparing contemporary data with classical studies. Most foundational works (e.g., Cash and Hopkinson, 1905, 1909; Cash et al., 1915, 1919; Leidy, 1879; Penard, 1902) either do not report the number of measured specimens or are based on observations of only a few individuals. The absence of sample size reporting hinders the assessment of measurement robustness and reliability. Moreover, small sample sizes increase sampling error, reduce statistical accuracy, and amplify variability—particularly when outliers or extreme values are present—ultimately leading to less reliable conclusions in phenetic characterization.

Although basic statistical methods were available in the late 19th century (e.g., Davenport, 1899; Galton, 1877; Pearson, 1894), they were

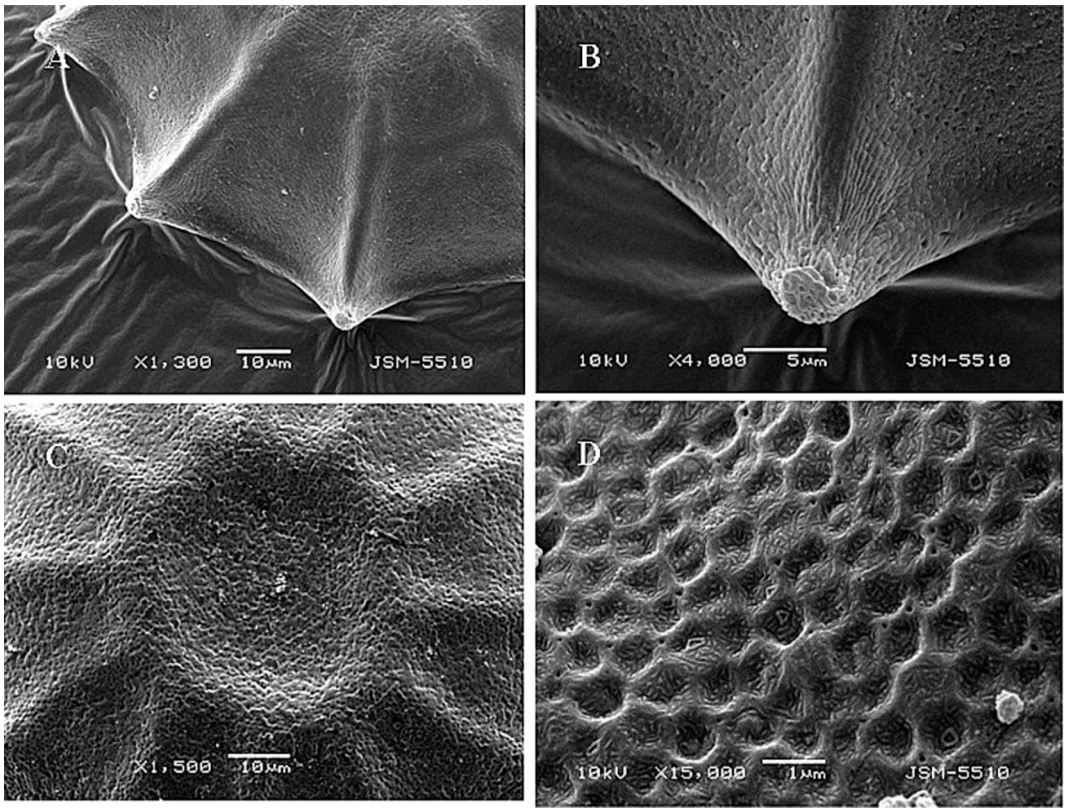

Fig. 8. Scanning electron photographs of dorsal ultrastructure. Scale bars: 1 µm (D), 5 µm (B), and 10 µm (A, C).

not formally introduced or widely adopted in testacean studies until the 1980s (e.g., Bonnet, 1984a, 1984b; Bonnet and Gomez-Sanchez, 1984; Lüftenegger et al., 1988; Ogden and Meisterfeld, 1989, 1991; Schönborn et al., 1983, 1987; Wanner, 1988). Consequently, a second major limitation in comparing modern data with earlier literature is the frequent absence of reported means or medians, with many older studies providing only ranges or extreme values. Without clear measures of central tendency, meaningful comparisons across studies become difficult.

The present study builds upon the biometric data of Todorov and Bankov (2019), derived from the same Bulgarian population. To date, the only other study reporting measures of central tendency for *Galeripora dentata* is that of Sigala et al. (2016), which analyzed six specimens from Mexico. Unfortunately, the small sample size in that study limits the statistical power of comparisons with the Bulgarian population. Mean shell diameter values are relatively consistent across regions, with Mexican specimens averaging 144.3 µm and the Bulgarian population averaging 140.2 µm (based on 210 specimens). Shell height has been measured only in the Bulgarian population, showing a slight increase in mean height from 37.8 µm (13 specimens, year 2019) to 38.8 µm (50 specimens in the current dataset), with the median height rising from 37.4 µm to 38.0 µm. Aperture size differs more noticeably between regions, with Mexican specimens averaging 32.3 µm compared to 46.1 µm in the Bulgarian population. While these findings suggest a degree of biometric uniformity, they should be interpreted with caution due to the limited sample size from Mexico. Additional data are needed to evaluate the potential influence of shared environmental pressures and the role of stabilizing selection.

4.2. The number of dentate projections: A species delimitation trait or phenotypic variation?

The taxonomy of testate amoebae has traditionally relied on light-microscopic observations of traits with limited taxonomic resolution, such as pseudopodial types and general test morphology. However, the adaptive nature of these phenotypic traits and their responsiveness to environmental conditions raise questions about whether observed morphotypes represent intraspecific variation or distinct species. This phenetic approach often depends on the researcher's subjective or numerical interpretation of morphological differences and provides limited insight into phylogenetic relationships or evolutionary history (Medioli and Scott, 1983). To address these limitations, new methodologies have been introduced. Scanning electron microscopy (SEM), in particular, has enabled high-resolution imaging of test ultrastructure and surface topography, revealing previously undetected morphological details (Ogden and Hedley, 1980). These advances have contributed to the discovery of hidden biodiversity. More recently, molecular techniques have profoundly influenced taxonomy by providing independent lines of evidence for species delimitation. However, discrepancies have emerged between traditional trait-based taxonomy and molecular data. The combined use of SEM and molecular analyses has revealed the existence of cryptic species—genetically distinct lineages with identical morphology—and pseudocryptic species, which are genetically distinct but exhibit subtle morphological differences detectable only through SEM (Heger et al., 2013; González-Miguéns et al., 2021; Kosakyan et al., 2012, 2013; Oliverio et al., 2014; Todorov et al., 2009). An integrative taxonomic approach, which incorporates biogeographical, ecological, morphological (including ultrastructural), biometrical, and molecular data, is essential for identifying traits of true taxonomic significance. Continued accumulation of data on (pseudo)cryptic diversity is crucial for addressing broader theoretical questions related to speciation in testate amoebae, phylogenetic relationships among taxa, and their biogeographic patterns, particularly in the context of the cosmopolitanism versus endemism debate.

In *G. dentata* s.l., the presence of dentate projections, along with variation in their number and size both within and among populations, raises important questions about their taxonomic significance. Whether the number of projections constitutes a reliable taxonomic character can

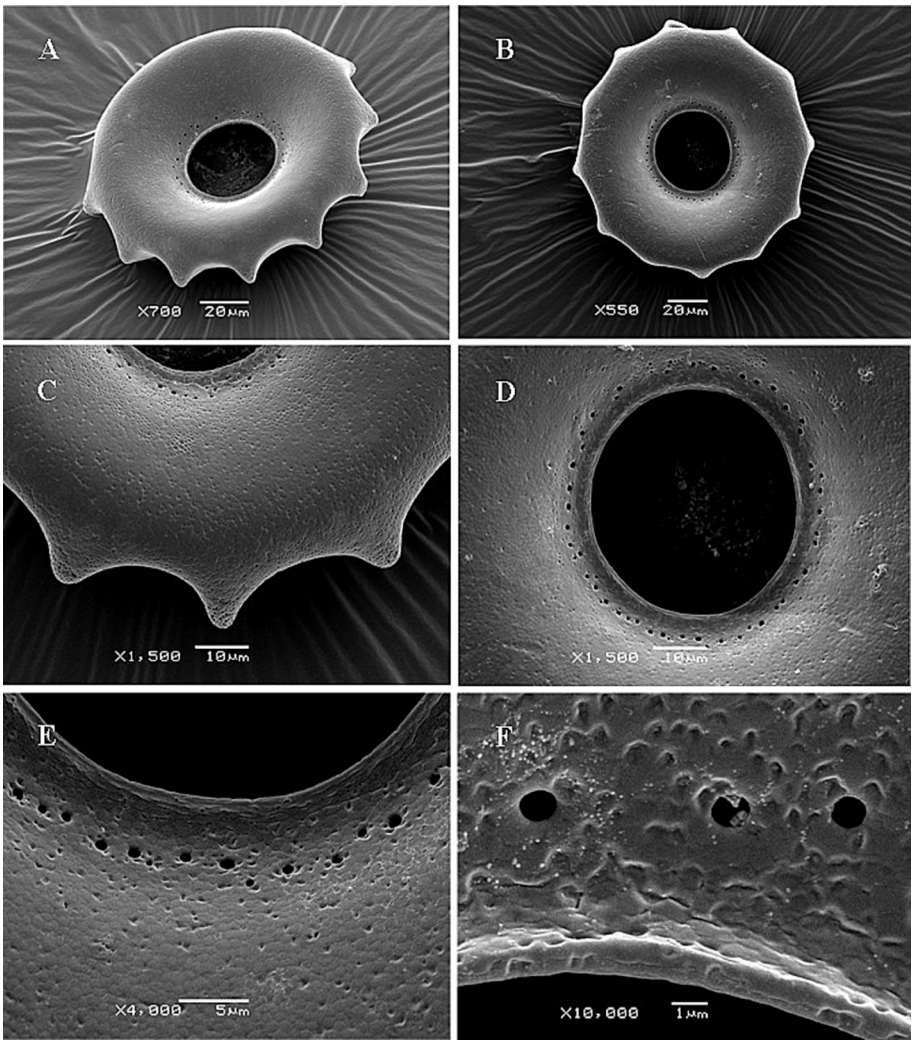

Fig. 9. Scanning electron photographs of ventral side (A, B) and ventral ultrastructure (C, D). (**A**) A specimen with 12 well-developed projections. (**B**) A specimen with 12 bud-like projections. (**C–F**) Ventral ultrastructure. Scale bars: 1 µm (F), 5 µm (E), 10 µm (C, D), and 20 µm (A, B).

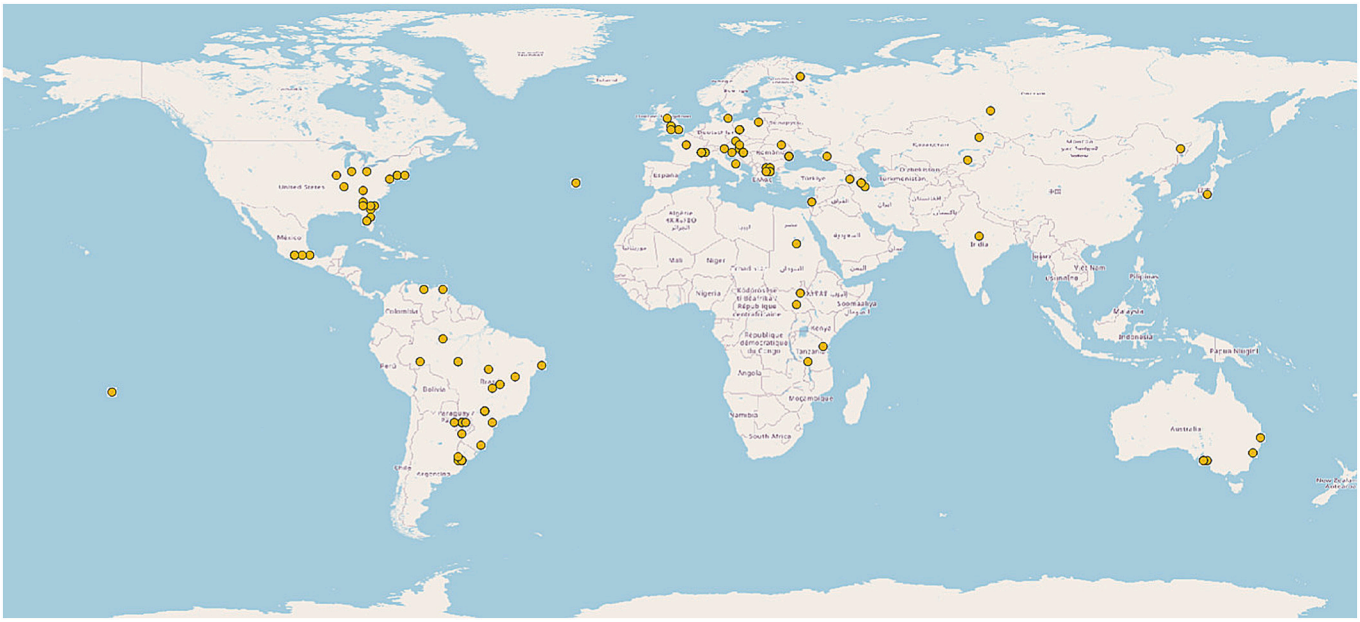

Fig. 10. Distribution of *G. dentata* records.

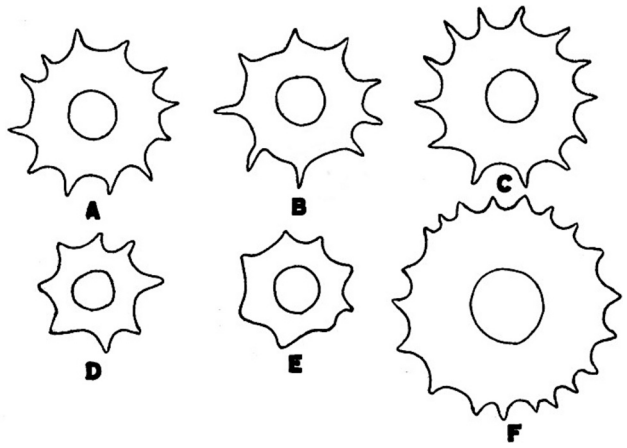

Fig. 11. Outline drawings of specimens of *G. dentata* (from Hegner, 1918). (**A**) Progenitor. (**B–F**) Descendants of a single progenitor.

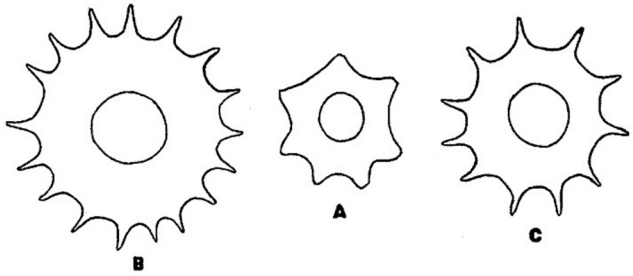

Fig. 12. Three specimens from a "wild" population of *G. dentata* (×207). Adapted from Hegner (1919a). (**A**) A specimen with a diameter of 73 μm and possessing 7 projections. (**B**) A specimen with a diameter of 150 μm and possessing 17 projections. (**C**) A specimen with a diameter of 116 μm and possessing 11 projections.

be partially assessed through the work of Hegner (1918, 1919a, 1919b), who conducted detailed studies on *G. dentata* sensu stricto under controlled laboratory conditions. Hegner's research focused on in vitro cultures and the inheritance of morphological traits through binary fission, assuming that the studied population represented a single, narrowly defined lineage. He examined both wild specimens collected from a pond near Johns Hopkins University (Homewood, Baltimore, USA) and their laboratory-cultured descendants. His findings revealed a positive correlation between shell diameter and the number of projections in both wild and cultured populations (Hegner, 1918, 1919a) (Fig. 11). Shell diameters ranged from 73 to 150 μm, while the number of projections varied from 7 to 17 (Fig. 12). Through selective breeding, Hegner (1918, 1919a, 1919b) demonstrated that descendants of a single individual could exhibit variation in these measurable traits, a conclusion later supported by Netzel and Grunewald (1977). Additionally, Hegner (1919a) documented differences in the overall size and shape of the projections, which ranged from indistinct ridges to well-defined structures (Fig. 13). He also showed that mechanical environmental factors, such as the presence of fine sand grains, could influence shell morphology during its plastic developmental phase, leading to a reduction in the number of projections. Notably, however, no increase in projection number was observed under such conditions. These findings suggest that while projection number and morphology are variable and environmentally influenced, they may not serve as reliable taxonomic markers on their own. Instead, they should be interpreted within a broader integrative framework that includes genetic, ecological, and ultrastructural data.

Fig. 13. Variations in projection size and shape in *G. dentata* (×420). Adapted from Hegner (1919a).

The size and number of projections in *G. dentata* s.l. are influenced by environmental conditions, particularly food availability and temperature. Hegner (1919b) demonstrated that underfed offspring consistently exhibited smaller shell sizes compared to their parents. However, when these offspring were subsequently provided with abundant food, their progeny developed larger shells and a higher number of projections. This suggests that nutritional status can influence not only individual morphology but also transgenerational phenotypic expression. Temperature also plays a role in shaping projection morphology. Under otherwise identical conditions, offspring cultivated at approximately 10 °C developed shorter projections than their parents, which were maintained at room temperature. This indicates that lower temperatures may inhibit the elongation of projections during shell formation. In another experiment, Hegner (1919b) introduced sodium silicate into the culture medium, hypothesizing that the presence of excess silicate might accelerate shell production and promote the formation of longer projections. Contrary to expectations, this treatment resulted in a reduction in projection size and, in some cases, near-complete loss of projections. However, this outcome should be interpreted with caution, as the reduction in projection number may have been a secondary effect of decreased shell diameter (Netzel and Grunewald, 1977). In natural environments, sodium silicate minerals can form through the evaporation of highly alkaline interstitial brines in near-surface horizons (Mees, 2018). These findings suggest that a combination of mechanical environmental factors, food supply, temperature, and subtle changes in mineral concentrations can induce a high degree of phenotypic plasticity. As such, these environmentally induced variations likely have limited taxonomic significance and should be interpreted within a broader integrative framework.

4.3. Ultrastructure

Examining the ultrastructure of testate amoebae offers an additional approach for species delimitation and can aid in identifying potential cryptic diversity. Ultrastructural analyses conducted by Netzel and Grunewald (1977) revealed that thecagenous granules are the sole type of organic building blocks used in the genera *Arcella* and *Galeripora* (the latter established following the taxonomic division of the original genus *Arcella*). Similar granules have also been observed in *Centropyxis discoides* (Penard, 1890) Deflandre, 1929 and *Netzelia oviformis* (Cash, 1909) Ogden, 1979, supporting the monotypy of building units within lobose testate amoebae, and consistent with the process described by Netzel as the 'one granum–one alveolus' hypothesis (Netzel, 1971a, 1971b, 1972b, 1975). These prefabricated granules are compressed into hexagonal structures arranged in a single layer, with small pores visible between them. Consequently, the presence of a different ultrastructural pattern may indicate a distinct taxon. Current observations align closely with the description provided by Netzel and Grunewald (1977). On the dorsal side of the examined specimens, a hexagonal, honeycomb-like pattern was observed, with numerous small pores between the units.

These structures form a single layer and are of a similar size (approximately 1 μm) to those described in the original study. To date, the only other study providing ultrastructural data for this species is that of Sigala et al. (2016); however, the micrographs presented in that work are not sufficiently detailed to support further conclusions.

4.4. Taxonomy

The application of an integrative approach, combining single-cell barcoding with morphological and ecological data, enabled González-Miguéns et al. (2021) to reassess the systematics of the family Arcellidae. Their phylogenetic analyses demonstrated that the phenotypic plasticity of the overall test outline is largely an adaptive response to environmental conditions and, therefore, is not a reliable character for inferring deep phylogenetic relationships within the group. In contrast, the presence of a ring of pores surrounding the aperture was identified as a valid and phylogenetically informative trait. Based on this criterion, the authors established the genus *Galeripora* (from Latin *galerus* = helmet and *porus* = pore), with the following diagnosis: "Tests built exclusively from proteinaceous organic material. Shape more or less campanulate, with a central, circular aperture and radial symmetry. The aperture is surrounded by pores. The ultrastructure of the test is composed of hexagonal units, at least partially covered by an organic matrix layer. Typically, two or more nuclei are present, located on opposite sides of the cytoplasm."

Eleven species were assigned to the newly described genus: *G. arenaria*, *G. balari*, *G. bathystoma*, *G. bufonipellita*, *G. catinus*, *G. discoides*, *G. galeriformis*, *G. naiadis*, *G. polypora*, *G. sitiens*, and *G. succelli*. However, somewhat unexpectedly, *A. dentata* was not included despite possessing the genus' most distinctive feature: a ring of pores surrounding the aperture.

In light of the genus diagnosis, I concur with the taxonomic revisions proposed by Siemensma (2021), including the new combination of *A. dentata* with *Galeripora* and the proposed synonymy:

***Galeripora dentata* (Ehrenberg, 1830) Siemensma, 2021**
Basionym: *Arcella dentata* Ehrenberg, 1830
Synonyms: *Arcellina dentata* Carter, 1856
Arcella stellaris Perty, 1849
Arcella okeni Perty, 1852
Arcella stellata Ehrenberg, 1854
Arcella heterocosmia stellata Ehrenberg, 1871
Arcella homoeochlamys dentata Ehrenberg, 1871
Arcella sticholepis stellaris Ehrenberg, 1871
Arcella dentata var. *cashiana* Deflandre, 1928
Arcella dentata var. *trapezica* Deflandre, 1928

5. Conclusions

Current evidence suggests that *Galeripora dentata* s.l. is a size-monomorphic species exhibiting consistent morphological characteristics across its geographic range. The observed variation in projection number appears to be a case of phenotypic plasticity, likely reflecting adaptation to local environmental conditions, and does not carry taxonomic significance. Ultrastructural analyses of two geographically distinct populations from Germany and Bulgaria supported the species' morphological uniformity across distant regions.

Galeripora dentata s.l. inhabits a wide range of freshwater environments, including both lentic (still water) and lotic (flowing water) systems, as well as transitional zones between aquatic and terrestrial ecosystems. It has been documented in planktonic, periphytic, and benthic communities. Its minute size, capacity to form desiccation-resistant cysts, and association with freshwater habitats facilitate effective long-distance dispersal, which likely accounts for its cosmopolitan distribution. The establishment of populations on remote oceanic islands such as Tahiti and the Azores further illustrates its high dispersal capability.

The species' ability to disperse via various physical and biological vectors likely promotes gene flow among populations, contributing to genetic homogeneity. However, further genetic and molecular investigations are necessary to clarify its taxonomic status and to assess the potential presence of (pseudo)cryptic diversity within *G. dentata* s.l.

CRediT authorship contribution statement

Nikola Bankov: Visualization, Validation, Supervision, Software.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The biometric measurement dataset supporting the findings of this study (including shell diameter, aperture diameter, shell height, and the number of projections observed in the Bulgarian population) has been deposited in the Zenodo repository and is publicly accessible at: doi:10.5281/zenodo.15291305. The geographic and ecological dataset underpinning this study has also been deposited in the Zenodo repository and is publicly available at: doi:10.5281/zenodo.15291478. Both datasets are provided in CSV format and cited in the reference list as Bankov (2025a, 2025b). Additional information is available upon reasonable request.

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