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ENTOGONIA BRIGGERI N. SP., A NEW DIATOM SPECIES FROM THE MIDDLE MIOCENE OF ROMANIA AND NEW INSIGHTS ON THE FOSSIL MARINE DIATOM GENUS *ENTOGONIA* GREVILLE

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Abstract A new diatom species, *Entogonia briggeri* n. sp. is described from Middle Miocene sediments of Romania. Detailed morphological investigations are presented using scanning electron microscopy with particular attention for internal coil system. This new species is compared with two related taxa *E. formosa* (Truan & Witt) Bergon described from the Middle Eocene sediments from Conset, Barbados and *E. hungarica* Holmes & Brigger 1979 from the Miocene sediments from Szurdokpüspöki, Hungary. This new species allows extending occurrences area of the genus and its time span distribution, as well as some remarks on some morphological elements of the genus.

Keywords: Diatoms; *Entogonia*; new species; morphology; Middle Miocene; Romania

INTRODUCTION

The fossil genus *Entogonia* Greville, 1863, which is distinguished from all other diatoms by the presence of the internal coil, was initially proposed (Greville, 1863a, 1863b) to include some tripolar species with frustules formed of a central triangular part and a peripheral border divided by transverse costae into punctate or cellulate compartments. The genus was later reviewed in detail by Bergon (1892a, 1892b) who emphasized its external and internal morphological features, including the internal coil system, and reconsidered its systematics. The revelation by Bergon of this surprising structure that is the internal coil system provoked at the time much sensation as Peragallo noticed in 1913: "les détails de structure qu'il révélait chez ces formes compliquées parurent si surprenants et si extraordinaires que de bons esprits doutèrent de leur exactitude ("structural details that he revealed in these complicated species seemed so surprising and so extraordinary that normal people doubted their accuracy"). Although some new species have been since described, Bergon's monograph remained the only thorough study of the genus until Holmes & Brigger (1977, 1979) revived the interest in *Entogonia*. These two remarkable papers improved our understanding of *Entogonia*'s stratigraphic range, morphology using both the light and scanning electron microscope. Holmes & Brigger (1977, 1979) also described a number of new species and varieties and reviewed most of the taxa described by previous workers.

It would seem, therefore, that very little could still be added to the knowledge of this interesting genus. However, as Holmes & Brigger (l. cit.) emphasized, *Entogonia* is far from well known. According to their data the oldest occurrences of the genus are as old as early Middle Eocene and the youngest are as young as Upper Miocene without no reliable record from the Oligocene. Later, Gombos & Ciesielski (1983) reported the genus in Deep Sea Drilling Project (DSDP) Site 511 from Southwest Atlantic; the authors observed fragments of *Entogonia* in the upper Eocene and lower Oligocene sediments of Hole 511 and attributed their presence to reworking. Unfortunately the auhors did not present any illustrations. Fenner & Mikkelsen (1990) found *Entogonia* in the Eocene sediments from the Indian Ocean (Mascarene Plateau, Chagos Ridge) cored during DSDP Leg 115. The authors presented an illustration of *Entogonia* sp. in plate 3, fig. 3 and mentioned that "most of the benthic, shallow-water diatom species found in the sites from the Indian Ocean were described originally from the Eocene island-arc-environments around Barbados (Greville,1860 ff.)".

Considering all these data, with a single exception, the *Entogonia* species mentioned in the literature come from the Caribbean, Pacific, Indian and Southwest Atlantic areas. The age of these occurrences varies from early Middle Eocene to early Middle Miocene. The exception refers to the single occurrence near Szurdokpüspöki (Hungary) signaled by Chenevière (1934), which represented until now the only occurrence of this genus in Europe and in the upper Miocene.

Since the works of Holmes & Brigger (1977, 1979), no exhaustive literature dedicated to *Entogonia* Greville, 1863 was published. Only recently, Witkowski et al. (2015) performed an extensive examination of several internally costate pseudocellate multipolar diatoms including *Entogonia* Greville, 1863. The authors summarized purported synapomorphies providing new evidence for the relationships between *Triceratium* Ehrenberg, 1839, *Sheshukovia* Gleser, 1975, *Medlinia* Sims, *1998* and *Entogonia* Greville, 1863 and also the two newly proposed sister genera: *Entogoniopsis* Sims, Strelnikova, Witkowski & Williams, 2015 and *Trilamina* Sims, Witkowski, Strelnikova & Williams, 2015. The proposed cladogram suggests that *Entogonia*, *Medlinia*, *Entogoniopsis* and *Trilamina* form a group of closely related taxa, while *Triceratium* and *Sheshukovia* are placed in a basal position since at present there are no characters allowing a more detailed interpretation of their relationship to the

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other mentioned genera. The picture of the phylogenetic relationship of *Entogonia* was very recently enriched with the description by Witkowski (2018) of the new genus *Fenneria* Witkowski 2018 that, according to the author, is closely related to *Medlinia* sensu Sims (1998).

The lack of continuous stratigraphic sequences bearing *Entogonia* makes it impossible to establish the precise range of individual species and to provide a closer insight into their evolution. The same thing makes it difficult to specify with certainty whether some of the morphological varieties observed in some taxa are the result of genetic change over time or of the plasticity of the genome in response to environmental or biotic changes. Finally, due also to the low numbers of specimens available for study, the range of morphological variability of most *Entogonia* spp. is not well known.

The present paper, based on the investigation of numerous specimens found in the Middle Miocene (Badenian and Sarmatian) of Romania (Fig. 1), aims to answer some of these questions.

MATERIAL AND METHODS

Geological setting

All specimens studied come from samples collected from Middle Miocene sediments of the Paratethys realm in Romania. The Paratethyan basin covered a large part of Central and Eastern Europe and communicated with the Mediterranean and the World Ocean by variable passageways determined by the evolution of various structural domains (Rogl, 1998; Palcu et al., 2018). This paleogeographic situation has led to the definition of Miocene regional stages and their equivalence with Mediterranean stages, discussed during a long time, was recently better precised (Steininger & Wessely, 2000; Harzhauser & Piller, 2007; Kovac et al., 2007; Piller et al., 2007; Hilgen et al., 2012; Pezelj et al., 2013; Hohenegger et al., 2014; Palcu et al., 2015). Consequently, the Middle Miocene in the Central Paratethys area (Fig. 2) comprises Badenian (= Langhian + lower part of Serravallian) and Sarmatian (= upper part of Serravallian) regional stages. The Badenian stage is subdivised in three substages : the Moravian corresponding pratically to the Langhian Mediterranean stage, the Wielician and the Kossovian corresponding to the lower and middle parts of the Serravalian. The lower part of the Sarmatian (Volhynian substage) corresponds to the upper part of the Serravalian.

As well as in other cases, the occurrences of the specimens of *Entogonia* are episodical. Three such episodes, highlighted by centimetric or decimetric layers (Fig. 2) have been recorded so far: one in the Upper Badenian (lower Kossovian) and two in the lower Sarmatian (Upper Volhynian).

Upper Badenian (middle Miocene) occurrence

The oldest occurrence level of *Entogonia* in Romania lies in the upper third of the so-called Radiolarian Shale Formation, a 20-100 m thick formation of grey to brown or shaly clay, commonly with thin intercalations of andesitic tuffs. The formation is wide-spread in the Getic Depression, Transylvania Basin and Carpathian Foredeep up to Poland (Barwicz-Pieskorz, 1978, 1981, 1999; Dumitrică, 1978b; Oszczypko, 1997; Rogl, 1998; Śliwiski, 2012; Palcu et al., 2015). It overlies the Badenian salt or gypsum deposits (the so-called salt breccia with salt massifs in Romanian literature), interpreted as deposits of a giant and shallow salina basin developed in the Central Paratethys during the middle Badenian (Wielician substage) salinity crisis (Bąbel, 2004). The Radiolarian Shale Formation is overlain by the *Spiratella* Marls Formation that close up the Middle Miocene marine series in the Central Paratethys. Both formations represent the Kossovian substage. The Radiolarian Shale Formation contains rich assemblages of radiolarians, silicoflagellates, ebridians, diatoms, siliceous endoskeletal dinoflagellates, calcareous nannoplankton, and planktonic foraminifers that enable correlation with nannoplankton zone NN6 (Martini, 1971), foraminifer eco/biozone *Bulimina-Bolivina* (Rögl, 1998), *Diartus laticonus* radiolarian zone or *Distephanopsis stauracanthus* silicoflagellate zone (Dumitrică et al., 1975; Dumitrică, 1978a, 1978b, 2016).

The *Entogonia*-bearing layer was encountered in two localities only, both of them in the Getic Depression, west of Olt river: on the Tilvici valley, Păuşeşti Otăsău village (sample 1315), and on the Sărata valley, Ocnele Mari village (sample OM 54), respectively (Fig. 1). In the former locality the layer was sampled in 1963 but a year later, when the senior author revisited the site it was already completely covered by an landslide. The outcrop from where the sample OM 54 was well exposed on the right flank of the Sărata valley in 1989 when the sample was collected, but 10 years ago when the section was revisited the outcrop was completely covered by soil and unrecognizable. Such situations occur commonly in unconsolidated deposits. The *Entogonia*-bearing level is represented by a bed, some 5 cm thick, of yellowish marly limestone contrasting with the dark-grey or brown colour of the argillaceous sequence of the Radiolarian Shale in which it is intercalated.

Diatom microflora containing the specimens of Entogonia consists mainly of marine planktic taxa such as: *Actinocyclus ehrenbergii* Ralfs in Pritchard, 1861, *Asterolampra gradiata* Gombos in Gombos & Ciesielski, 1983, *A. grevillei* (Wallich) Greville, 1860, *A. marylandica* Ehrenberg, 1844, *A. schmidtii* Hajós, 1968, *Asteromphalus parvulus* Karsten, 1905, *A. robustus* Castracane, 1875, *Biddulphia mobiliensis* (Bailey) Grunow in Van Heurck, 1882, *B. thuomeyi* (Bailey) Roper, 1859, *Climacosphenia moniligera* Ehrenberg, 1843, *Coscinodiscus lewisianus* Greville, 1866, *C. oculus-iridis* (Ehrenberg) Ehrenberg, 1840, *Cymatosira biharensis* Pantocsek, 1889, *Denticulopsis lauta* (Bailey) Simonsen, 1979, *Ethmodiscus* cf. *gazellae* (Janisch ex Grunow) Hustedt, 1928, *Grammatophora stricta* Ehrenberg, 1843, *Macrora stella* (Azpeitia) Hanna, 1932, *Paralia sulcata* (Ehrenberg) Cleve f. *radiata* Grunow, 1884, *Rhizosolenia* sp., *Thalassionema nitzschioides* (Grunow), Mereschkowsky, 1902, *Thalassiosira decipiens* (Grunow) Jorgersen, 1905, *Thalassiosira leptopus* (Grunow ex Van Heurck) Hasle & G.Fryxell 1977, etc. Lower percentages of benthic marine taxa represented by: *Cocconeis dirupta* Gregory, 1857, *C. scutellum* Ehrenberg, 1838, *Diploneis aestiva* var. *delicata* (A.Schmidt) R.Ross, 1986, *D. major* Cleve, 1894, *D. vacillans* (A.Schmidt) Cleve, 1894, *Mastogloia pusilla* Grunow, 1878, *M. splendida* (Gregory) Peragallo, 1888,

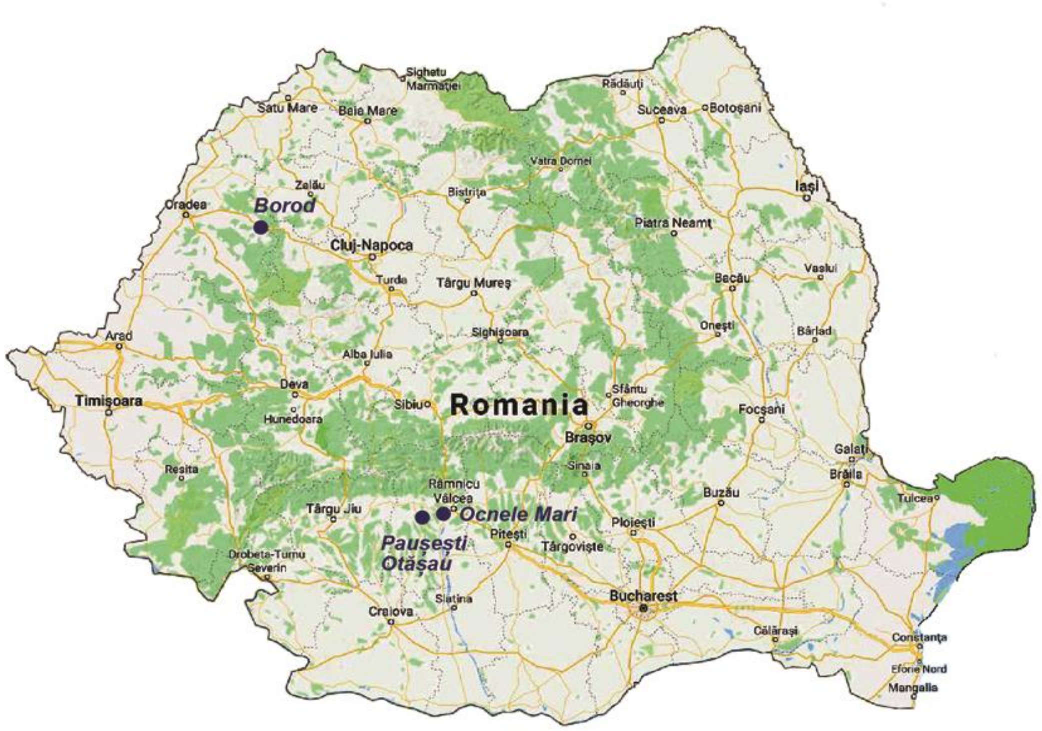


Fig. 1 Location of studied samples with *Entogonia briggeri* n. sp.

Navicula viridula (Kützing) Ehrenberg, 1836, *Rhabdonema diminutum* Pantocsek, 1892, *Rhaphoneis amphiceros* (Ehrenberg) Ehrenberg, 1844, *R. rhombica* (Grunow) (Andrews), 1975 also occur. Beside them the assemblage contains rare marine-brackish benthic taxa such as: *M. smithii* Thwaites ex Smith, 1856, *Nitzschia triblionella* Hantzsch in Rabenhost, 1860, *Surirella biharensis* Pantocsek, 1886, *S. neumeyeri* Janisch, 1877. The dominant marine planktic taxa argue for a true marine sequence suggesting connections between the Getic Basin and other paleocenographic domains. Indeed, some species were designed by Dumitrică (*in* Dumitrică et al., 1975) and Pestrea (1999) as stratigraphic marker species for the early Late Badenian (early Kossovian): *Coscinodsicus lewisianus* Greville, 1866 and *Denticulopsis lauta* (Bailey) Simonsen, 1979 allowing correlations with diatom biozones from North Pacific (Scharder, 1973; Barron, 1985b) and Indian and equatorial Pacific (Barron, 1985a).

The *Entogonia*-bearing level from Badenian represents a peculiar episode not only from lithological point of view but also from micropaleontological point of view, as it contains also numerous specimens of larger radiolarians such as *Centrocubus cladostylus* Haeckel, 1887, *Diplospongus dendrophorus* Mast, 1910 and *Lychnosphaera regina* Haeckel, 1887, all of them absent at other levels of the Radiolarian Shale and, in fact, in all the other sections of the Radiolarian Shale Formation from Subcarpathians, Getic Depression, and Transylvanian Basin studied by the senior author. *Entogonia* specimens are generally sparse in this layer but more than 50 well preserved specimens of *Entogonia briggeri* n. sp. were found.

Lower Sarmatian (late Middle Miocene) occurrences

The other two Entogonia occurrences were recorded in borehole 36 Subpiatră, a locality situated in the Borod Basin (Fig. 1). This basin, which represents an eastern fossil gulf of the Pannonian Basin, is filled up with Sarmatian and Pannonian deposits, many of them containing more or less abundant diatoms (Filipescu et al., 2014). Many of these diatoms have been described by Pantocsek (1886-1905) in his monographs on the diatoms of Hungary. It must be mentioned that many of the localities listed by him as located in Hungary are, since 1918, on the territory of Romania. The Romanian names are as follows: Borostelek=Borşa, Elesd=Aleşd, Izsopallaga=Hotar, Serges=Serghiş, Nyermegy=Nermiş, Karand=Cărand.

The borehole 36 Subpiatră penetrated and cored Lower Sarmatian (Volhynian) deposits consisting generally of white laminated marls showing a dense alternation of grey and white laminae (Papaianopol & Macaleţ, 1998; Popa, 2000). The latter are formed of elongate crystals of calcium carbonate belonging probably to ascidians, whereas the former are rich in organic matter and clay, all of them representing probably a system of varves.

Specimens of *Entogonia* occur at two levels of this borehole: at 88.5 m, and at 102 m, respectively. In both levels they are frequent but not as well preserved as in the Radiolarian Shale Formation, their internal coil system being in almost all specimens broken off. Diatom microflora contains a mixture of marine planktonic taxa: *Actinocyclus ehrenbergii* Ralfs in Pritchard, 1861, *Actinoptychus senarius* (Ehrenberg) Ehrenberg, 1843, *A. undulatus* Kützing (Ralfs in Pritchard 1861), *Biddulphia biddulphiana* (J.E.Smith) Boyer, 1900, *Biddulphia thuomeyi* (Bailey) Roper, 1859, *Coscinodiscus* cf. *obscurus* A. Schmidt, 1878, *Synedra cristalina* (Agardh) Kützing, 1844), marine benthic taxa (*Rhaphoneis rhombica* (Grunow) (Andrews, 1975, *Triceratium balearicum* Cleve f. *biquadrata* (Janisch in Schmidt et al.) Hustedt, 1930), benthic marine-brackish taxa: *Rhaphoneis boryana* Pantocsek, 1889, *Rhopalodia gibberula* (Ehrenberg) Otto Műller, 1895),

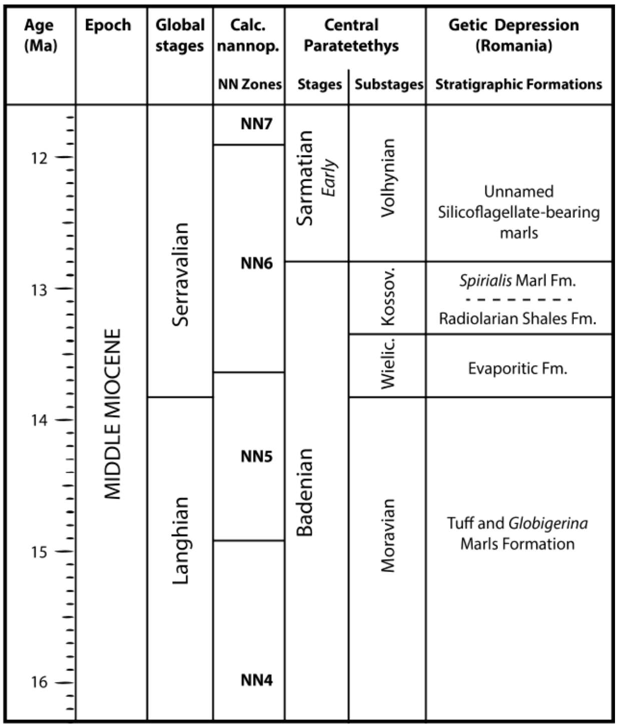


Fig. 2 Correlation table between global stages, Central Paratethys regional stages and substages (simplified after Pezelj et al., 2013; Hohenegger et al., 2014,) and the stratigraphic formations of Getic Depression (Romania).

and rare freshwater elements of which we mention: *Staurosirella leptostauron* (Ehrenberg) D.M. Williams, 1988, *Ellerbeckia arenaria* (Moore ex Ralf) R.M. Crawford, 1988. The diatom assemblage suggests a context of changing paleosalinity and paleobatimetric conditions due to complex communications between Borod and Panonian basins.

Rare specimens of phytoliths, ebridians (*Hermesinum adriaticum* var. *longispinosum* Hovasse, 1932), silicoflagellates (*Distephanopsis* cf. *crux* (Ehrenberg) Dumitrică, 1978), and chrysomonad cysts occur in addition to diatoms.

Approximately at the same levels occurs also a mollusc fauna consisting of species belonging to the genera *Calliostoma*, *Mohrensternia*, *Valvata* and *Pseudoamnicola* (Papaianopol et al., unpublished data) indicating a late Volhynian age.

Preparation and study of samples

Samples were first treated with 10% hydrochloric acid to remove the carbonates. When the reaction ceased, water was added and the disintegrated sediment was decanted several times to remove the remains of acid and the resultant $CaCl_2$. After that, the sediment was boiled for several minutes in water with a little hydrogen peroxide and calgon to remove the organic matter and clay from the sediment. Then all was sieved through a sieve of 63 µm meshes and the residue was dried and studied under the binocular. The best preserved specimens of *Entogonia* were picked up, mounted onto an aluminum stub, coated with gold, and examined with a SEM Zeiss EVO MA 10 at the Hochschule der Künste Bern (High School of Arts, Berne) of the University of Berne, Switzerland. The portion that passed through the sieve and that represents the small fraction, was successively decanted until the liquid was clean. The clean residue was pipetted onto glass coverslip, dried and mounted in Canada balsam on glass slides to study the microfossils smaller than 63 µm (diatoms, silicoflagellates, endoskeletal dinoflagellates, and other small siliceous microfossils) and studied under Zeiss Axioscope 40 microscope.

The processed residues of the studied samples are in the private collection of the senior author.

Terminology

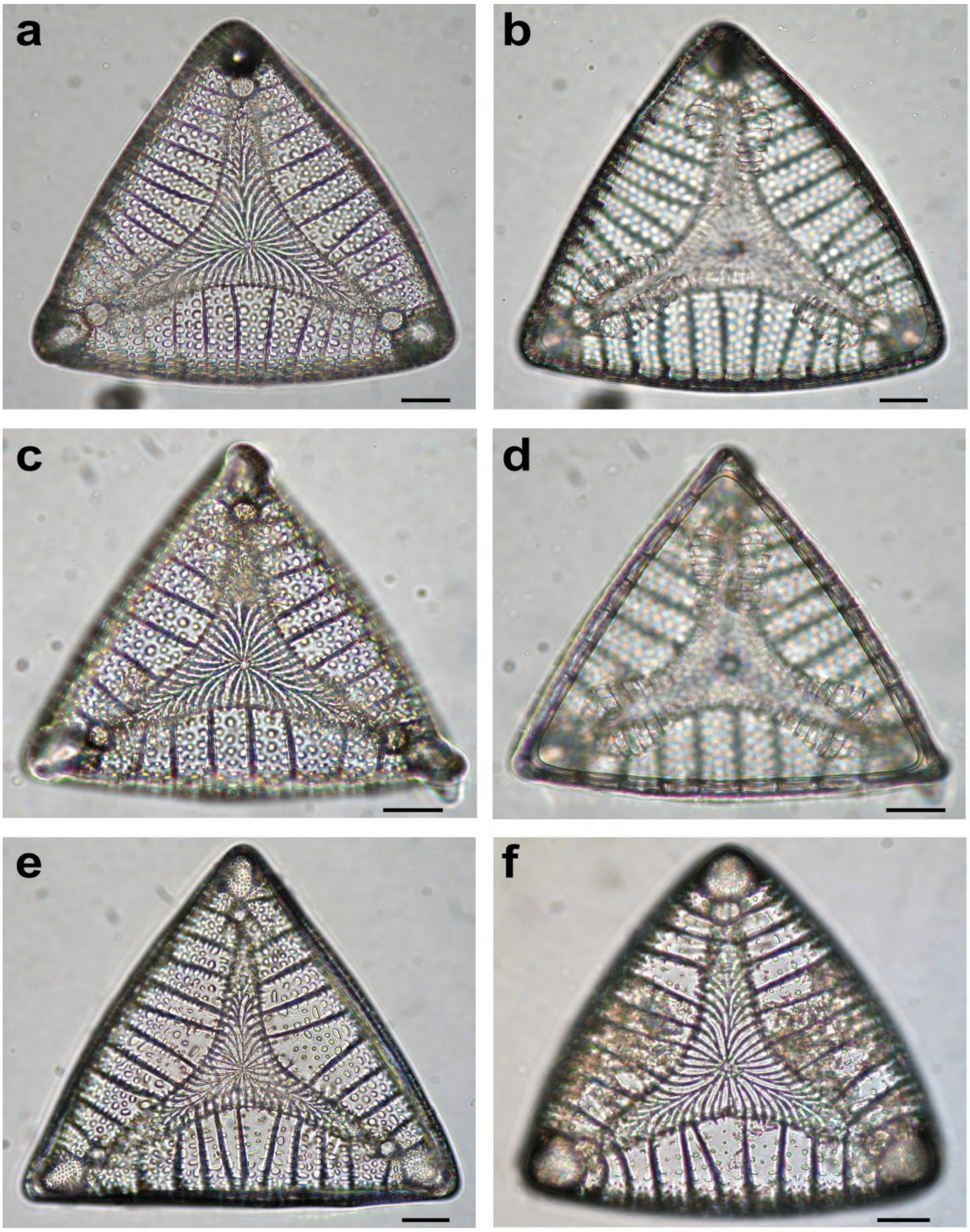
The terminology used in the description of taxa is that suggested by Anonymous (1975), Ross et al. (1979), Ross & Sims (1985), Round et al. (1990) and, more particularly for *Entogonia*, the terms used by Holmes & Brigger (1977, 1979) and Witkowski et al. (2015). *Entogonia* presents a unique morphologic feature that is an internal system of ducts named ‘internal duct” by Homes & Brigger (1977;1979) and “internal coil” by Witkowski et al. (2015). In our description we use the term of internal coil. The internal coil has an external opening situated at the base of each elevation; this opening is named “orifice” by Homes & Brigger (1977; 1979) and “exit pore” by Witkowski et al. (2015). In our description we employ the term exit pore. Another morphological feature of the genus is the presence on the inner side of the valve of siliceous thickenings that were considered “transverse costae” in Greville’s description of the genus (Greville 1861, 1863a), “fauses côtes” by Bergon (1892a), pseudosepta by Homes & Brigger (1977;1979) and finally “internal costae” by Witkowski et al. (2015). In our description we will employ the term of internal costae.

TAXONOMY

We followed here the classification indicated in WoRMS Editorial Board (2018). World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2018-02-20. doi 10.14284/170

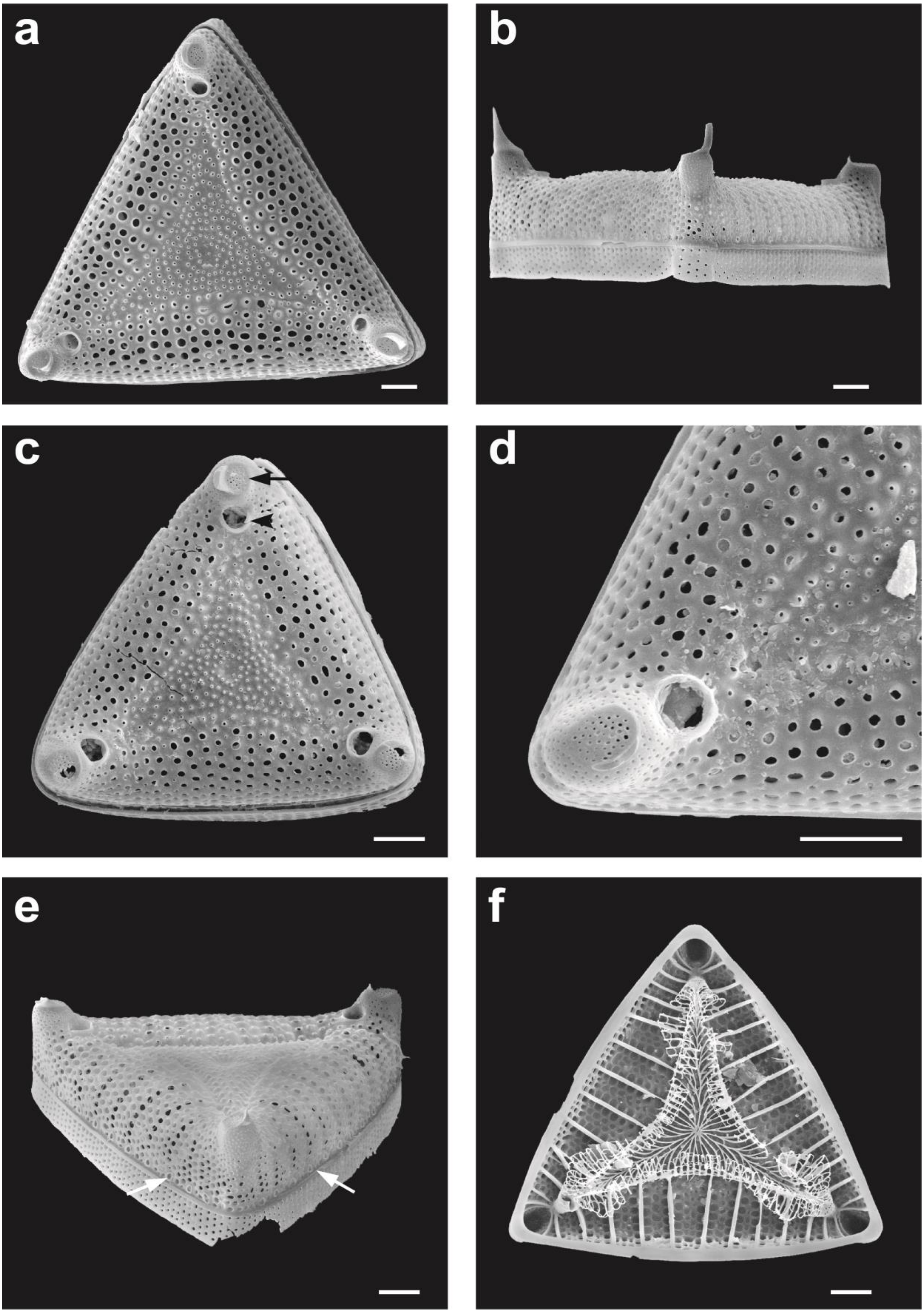
Class Bacillariophyceae
Subclass Bacillariophyceae incertae sedis
Genus *Entogonia* Greville, 1863
Entogonia briggeri Dumitrică and Saint Martin nov. sp.
Figs. 3-7

Description. The valves are tripolar with straight to slightly convex sides in valve view and round poles (Figs. 3a-f, 4a, 4c, 4f, 5a-b, 7a). Each pole bears an elevation circular to oval in outline and slightly raised above the surface of valve, with a height of about 17.5 µm. They are perforated by irregularly scattered areolae that are smaller than the valve areolae (Figs. 3a-f, 4b, 4c, 4e). Apices of the elevations are flat, finely punctate (perforate) with no particular arrangement of puncta as it can be seen in external valve view (Figs. 3e, 4d) and also in internal valve view (Fig. 5f). The diameter of apices is of circa 17 µm. On each apex there is a flat, triangular, claw-like linking spine on one lateral border (Figs. 4b, 6b). The length of spines is variable between 24-25 µm. Exit pores arise gently from the valve face close to



Figs. 3a-f *Entogonia briggeri* n. sp., sample 1315. LM views; **a** Holotype, valve view; **b** Same specimen figured in 3a focused on internal coil; **c** Isotype 1, valve view; **d** Same specimen figured in 3c focused on internal coil; **e** Isotype 2, valve view; **f** Isotype 3, valve view. Scale bars: 20 µm.

elevations; they are circular to oval in outline, with a diameter smaller than that of the elevations, of about 8.7-10.5 µm. (Figs. 3a, 3c, 3e, 4a, 4c, 7a). They have a protruding hyaline lip which does not surround the entire circumference of the exit pores as they are missing towards the projections (Fig. 4d). The valve face is perforated by poroid areolae exhibiting different dimensions and distribution patterns that delimit an outer triangle and an inner triangle (Figs. 3a-e, 4a, 4c, 4f, 7a). In external oblique view the outer triangle is gently elevated relative to inner triangle (Fig. 4e). The outer triangle is broad, convex in girdle view, with areolae arranged in 2-3 transverse rows between two internal costae as follows: the rows adjacent to internal costae comprise larger and closely spaced areolae (4-5 within a row); the rows located away from internal costae comprise smaller and more distantly spaced areolae (2-4 within a row); sometimes the rows of these smaller areolae are incomplete. The row of larger areolae which lie next to and parallel to each internal costae of the outer triangle are also much larger than those of the inner triangle (Figs. 3a, 3b, 3e, 4a, 4c - d). Rows are generally perpendicular to the valve face margins. Internal costae vary in number from 10 to 12 depending, but not compulsorily, on the size of the valve



Figs. 4a-f *Entogonia briggeri* n. sp., sample 1315; SEM external views (a-e) and SEM internal view (f). **a** Valve face exhibiting specific morphological features; **b** Girdle view showing elevations and one triangular spine on each elevation; **c** Valve face showing valve shape, round apices, elevations to poles (arrow) and exit pores (head arrow), areolae pattern on inner and outer triangles; **d** Detail showing the finely punctuated apices of elevation and exit pore close to elevation with a protruding hyaline lip; **e** Oblique valve view showing raised outer triangle, depressed central part of inner triangle, vertical mantle with one ring of enlarged pores (arrows); **f** Internal view showing the outer and inner triangles, internal costae, internal coil system. Scale bars: 20 µm.

and continue down the mantle until they fuse with the margin of the mantle (Figs. 4f, 5a-b, 7b). The internal costae of the outer triangle define sectors for areolae both on the valve face and on the mantle. The inner triangle presents straight or concave sides of circa 90-110 µm outlined on the valve surface by a deep constriction corresponding on the inner face to a costa (Figs. 4f, 5a-b). The central part of this triangle is depressed as seen in external oblique view (Fig. 4e) and sometimes hyaline (Fig. 3c). In internal view, from this center radiate a large number of dense costae which reach the boundary between the inner and outer triangles and which can be simple or bifurcate (Figs. 5a-b, 7b). Three such costae extend along the bisectors of the three corners and continuously ramify on both sides forming a dense network of costae. These three bisecting costae are never straight as in other species or more prominent than the resulted branches (Figs. 5c-e). The fine areolae of the inner triangle are dense, small and arranged in radial, circular or spiral rows, neither of them perfect (Figs. 4a, 4c, 7a). Inner coils very delicate, with annular costae joined to one another by curved and more delicate bars (Figs. 5a-f). There is no clear distinction between valve face and valve mantle since valve areolae pattern is continuous on the mantle. Mantle vertical of about 29-35 µm height. There is also a basal ring of enlarged pores with protruding lips, which occur between internal costae on the valve mantle (Figs. 4b, 4e, 6a, and especially 6c). A thin hyaline ridge is placed on the mantle edge, bordering this latter with the valvocopula (Figs. 4b, 4e). In internal view, it can be observed inwardly expanded hyaline mantle margin (Figs. 4f, 5a-b).

Cingulum composed of a closed valvocopula and one or two closed copulae. All are ornamented by areolae, but areolae of valvocopula are slightly smaller than those of copulae and of mantle. Valvocopula, with a pars exterior varying between 12.6-20 µm high, bears areolae arranged in almost vertical rows (Figs. 6a-b). There is a more conspicuous row of coarser and regularly arranged areolae of 2 µm diameter adjacent to the valve mantle (Figs. 6a-b). The copulae, with a pars exterior varying between 24-30 µm heigh, bear areolae arranged in diagonal rows (Figs. 6a-b). Sometimes, at the corners of copulae the pattern of the areolae seems slightly disturbed (Figs. 6a-b). All girdle elements observed (valvocopula and copulae) have a hyaline abvalvar margin 3-4 µm deep.

In girdle and oblique views the mantle margin appears slightly undulate (Figs. 4e, 6a).

Holotype: Figs. 3a,b, MNHN.F. F62406 (Muséum National d'Histoire Naturelle, Paris, France)

Isotype 1 : Figs. 3c,d, MNHN.F. F62407 (Muséum National d'Histoire Naturelle, Paris, France)

Isotype 2 : Fig. 3e, MNHN.F. F62408 (Muséum National d'Histoire Naturelle, Paris, France)

Isotype 3 : Fig 3f, MNHN.F. F62409 (Muséum National d'Histoire Naturelle, Paris, France)

Dimensions. Length of sides of the outer triangle 150-200 µm.

Remarks. Study of *Entogonia* specimens recorded in the three stratigraphic levels mentioned above has proven that all of them belong to a single species, *Entogonia briggeri* n. sp., that has many characters in common with both *Entogonia hungarica* Holmes & Brigger, 1979 (Holmes & Brigger, 1979, p. 182, figs. 66-72) and *Entogonia formosa* (Truan & Witt) Bergon 1892 (Holmes & Brigger, 1977, fig. 55-57; 1979, p. 179, figs 54-57, 58-59).

Entogonia briggeri n. sp. resembles very much *E. hungarica* Holmes & Brigger, 1979 in the morphology of the outer triangle, shape of the inner triangle and sometimes the ratio between the diameter of the exit pores and of the elevations. However, the diameter of the exit pores is generally smaller in this species than in *E. hungarica*. The most evident difference from the latter species regards the costae of the inner triangle, which are here and there absent or interrupted in *E. hungarica*, leaving areas without costae. Also, in *E. hungarica* there is no hyaline central area onto the inner triangle, at the origin of the internal costae, as we observed in *E. briggeri* n. sp. Another evident difference concerns a row of enlarged pores which occur between the internal costae on the valve mantle. This character is present in *E. briggeri* and absent in *E. hungarica.*

Entogonia briggeri n. sp. is wholly comparable with the early Middle Eocene specimens from Conset, Barbados, assigned to *E. formosa* (Truan & Witt) Bergon by Holmes & Brigger (1977, fig. 55-57), from which it differs especially in the greater number of costae in the inner triangle, denser areolae in the outer triangle, and in the presence of enlarged pores which occur between to the internal costae on the valve mantle. These pores, as observed by Holmes & Brigger (1979), are characteristic in some species as for instance: *Entogonia amabilis* Greville, 1863, *E. marginata* (Bright.) Greville, 1863, *E. pulcherrima* (Greville) Greville, 1863, *E. reinholdii* Holmes & Brigger, 1979, *E. robinsonii* Holmes & Brigger, 1979.

Range and occurrence. Upper Middle Miocene, (lower part of Upper Badenian = Kossovian substage): Radiolarian Shale Formation from Getic Depression: Tilvici Valley, Păuşeşti Otăsău village, and Valea Sărată (Salted Valley), Ocnele Mari village, both in Râmnicu Vâlcea district, Romania; also lower Sarmatian (late Vohynian) from Borod Basin, Romania.

Type locality. Tilvici valley, Păuşeşti Otăsău village, Râmnicu Vâlcea district, Romania

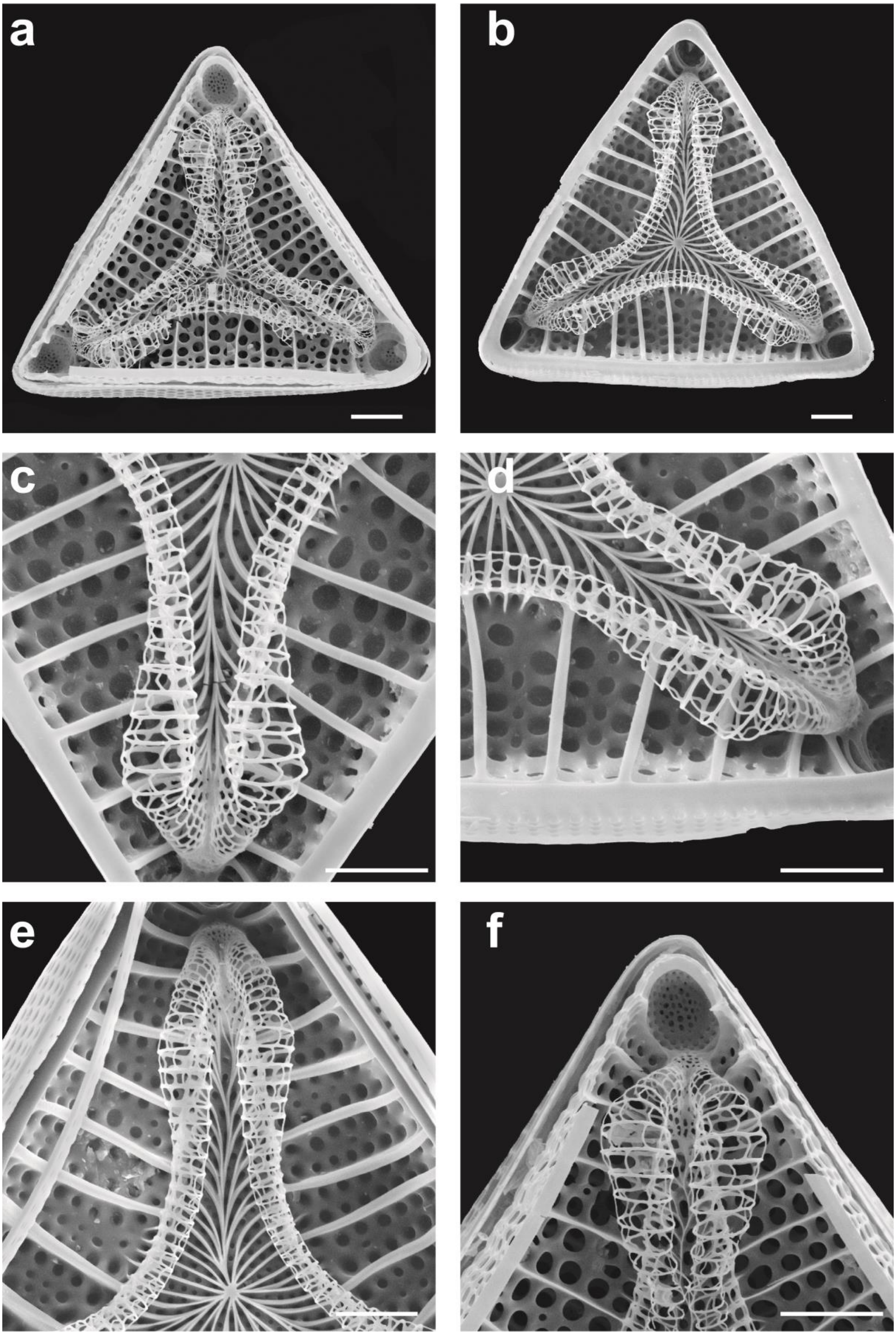
Etymology. The species is dedicated to A. L. Brigger to honor his contribution to the knowledge of the genus *Entogonia.*

DISCUSSION AND CONCLUSION

Remarks on some morphological elements

The large number of specimens and their very good preservation have permitted to study in detail some of the morphological elements of the valve of *Entogonia* less investigated so far.

Linking spines



Figs. 5 a-f *Entogonia briggeri* n. sp. sample 1315; SEM internal views; **a-b** Internal view illustrating the outer and inner triangles, internal costae, and internal coil system; **c-d** Details of poles of the specimen figured in **b** showing the ramifying of some costae to form a dense network, hyaline center of the inner triangle, inner coil with costae joined to one another by curved bars; **e** Detail of a pole showing the apices of the coil fusing to a siliceous punctate membrane within the exit pore on the side of the orifice touching the elevation; **f** Detail of a pole of the specimen figured in **a** showing the internal view of the elevation with delicate puncta. Scale bars: 20 µm.

Almost all specimens of *Entogonia briggeri* n. sp. possess on the three polar elevations a straight claw-like linking spine of variable length. This spine, "mucron" in Bergon's terminology, is flat and triangular, with bucket-like base. The linking spines have a well-established position on polar elevations, namely on a lateral side, which is always the same on all the three elevations and all specimens. This gives a symmetry of rotation to the projections.

As supposed by Holmes & Brigger (1977, p. 222) the linking spines "assist the joining of cells together in chains". In such a chain the valves of two specimens come in touch with the flat apices of the polar elevation, whereas the linking spines of a valve touch the lateral side of the polar elevation of the sibling valve. The imprint of this touch along the elevations is rather well marked by a slightly flattened area (Fig. 4d) situated on the side opposite to that in which the linking spine is originated. In such a way the sense of the symmetry of rotation is always preserved.

The connection effected by these linking spines is very weak as compared with the one effected by the interlocking linking spines specific to some genera such as *Briggera* Ross & Sims, 1985. After the death of the colony and the decomposition of the organic matter the individuals separates from one another. This weak link explains why *Entogonia* was never found with valves of two individuals connected in colony as is frequently the case in *Hemiaulus* or other genera.

Internal coil system

The internal coil system, so characteristic of *Entogonia*, was not discussed and illustrated in sufficient detail by the previous authors due especially to its poor preservation in many species as a result of its fragility.

Bergon (1892a, p. 86) was the first who mentioned that coils are reticulate and costate inside the valve. Annular costae were clearly illustrated in transmitted light by Chenevière (1934, pl. 3, fig. 2) with *Entogonia amabilis* Greville, 1863 that was later described as *Entogonia hungarica* by Holmes & Brigger (1979). Most details of the structure of the coils were illustrated by Holmes & Brigger (1977, figs. 12-14) in an Eocene *Entogonia* sp.

What is so far known regarding the coils of this genus is that they underlie and follow the border between the inner and outer triangles to which they are attached. In rare cases they are also attached to the internal costae (Holmes & Brigger, 1977). Towards their ends, in the region where they bend outside toward the outer valve surface, the coils generally fuse into a single coil to form the exit pore. The place of this fusion may be deep, inside the valve cavity, or at the surface. In the former case the fusion is complete, forming a single exit pore, whereas in the latter case the exit pore is divided into two by the median wall between the two coalescing coils.

The perfect preservation of *Entogonia briggeri* n. sp. in the Radiolarian Shale from Romania has permitted a very detailed investigation and knowledge of the coils and their relation to the inner and outer triangles. In all specimens of this species the coil diameter is smaller in the middle part, increases towards the ends, reaching its maximum diameter (16 µm) approximately at the corners of the inner triangle which practically correspond to the zone where the coils bend towards the valve face, and decreases rapidly towards the distal ends, where they coalesce. The apices of the coil cross the exit pores and fuse to form a punctate membrane within the exit pore on the side of the exit pore touching the elevation (Figs. 5a-f, 7b).

In *E. briggeri* each coil consists of 40-45 transverse rings made up of cylindric rods. The number of rings is equal with the number of internal costae of the inner triangle. The coils seem therefore to be, at least in this species, a continuation of these internal costae and of the wall between the inner and the outer triangles. They are therefore on all of their length connected to this border, and there is no reason to consider that it may be otherwise in other species of the genus. The attachment is more visible in the middle part of the coil system; on each side of the inner triangle, there are 3-5 short costae that extend and are attached on the outer triangle surface close to the limit with the inner triangle (Figs. 5b-e). The transverse rings are connected to one another by a system of bars. In this species these bars are much thinner than those of the rings and are always curved in the same direction (Figs. 5a-f).

We do not know yet how variable the morphology of the coils is and to what extent it has a systematic value at the species level. What can be remarked by comparing the coils of the very few species, where this structure was preserved, is that *E. briggeri* n. sp. and *E. hungarica* as illustrated by Chenevière under the name of *E. amabilis* (1934, Pl. 3, Fig. 2) seem to have similar coils. On the other hand, the coils of the Eocene specimens of *Entogonia* spp. illustrated by Holmes & Brigger (1977, figs. 9-14) are different enough from those of *E. briggeri* n. sp.; *Entogonia* sp. of Holmes & Brigger (1977) exibit a perforated tubular coil while the coil of *Entogonia briggeri* n. sp. described in this paper consists of a series of transverse rings linked to one another by curved and more delicate bars.

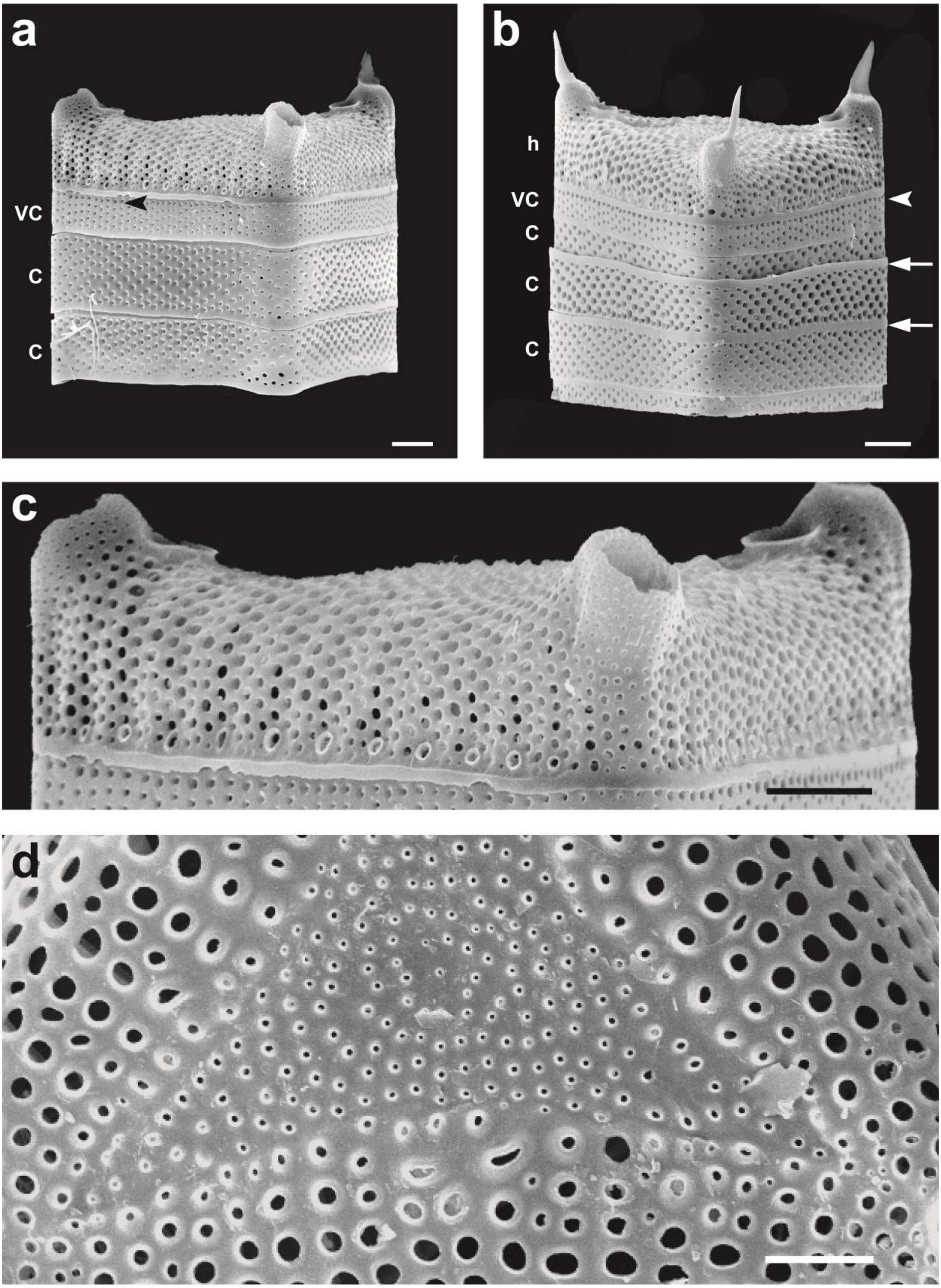
The function/purpose of this specialized structure still remains unknown and no similar morphological feature was found in any other diatom.

Cingulum

Little is known about the cingulum of *Entogonia* since there are only few illustrations and observations of previous authors. Holmes and Brigger (1977) note (p. 223 and figs. 10, 11) that the few cingula they observed “contain circular puncta in a predominately linear pattern. The diameter of the cingulum is slightly smaller than the valve to which it is attached and in at least one species fits into a groove in the valve flange”. Later, Holmes & Brigger (1979, p. 161 and figs. 120-121) refers to the cingulum structure as follows: “our limited observations indicate that the cingulum consists of one closed band of rather simple structure”.

Our observations on *Entogonia briggeri* n. sp. allow a better knowledge of the cingulum structure of the genus and its attachment to the mantle.

In the specimen figured in Fig. 4a we observed one valve with the closed valvocopula and two closed copulae.



Figs. 6a-d Cingulum of *Entogonia briggeri* n. sp., sample 1315; **a** Girdle view showing a valve with part of a cingulum composed of the valvocopula (vc) and two copulae (c). Note on valvocopula the vertical pattern of areolae and single row of coarser areolae regularly arranged adjacent to the valve mantle (head arrow). Areolae arranged in diagonal rows on copulae; **b** Girdle view of an incomplete frustule showing the hypovalve (h) with its valvocopula (vc) and one partly visible copulae (c) and a part of the epicingulum consiting of two copulae (c). Note on the valvocopula and also on the copulae a hyaline abvalvar margin (arrows); **c** Detail of specimen figured in **a** exhibiting the ring of enlarged pores occurring between internal costae on the valve mantle; **d** Detail of specimen figured in Fig. 4a showing the areolae size and pattern into the outer and inner triangle. Scale bars: 20 µm.

The specimen from sample 1315 (Badenian, Tilvici Valley, Păuşeşti Otăsău village), shows a broken frustule composed of the hypovalve with its hypocingulum consisting of the valvocopula and one partly visible copula (Fig. 6b-upper part) and two copulae of broken epicingulum (Fig. 6b- lower part). As explained in the description, the girdle elements are closed and perforated by areolae that are smaller on valvocopula. The arrangement of areolae varies between girdle elements: in vertical rows on valvocopula and in diagonal rows on copulae. On each element of cingulum either on valvocopula or copulae, there is a hyaline abvalvar margin. The copulae of the epicingulum and those of the hypocingulum have a similar morphology. Unfortuntaely we could not observe a complete frustule, so we are not able to precise the total number of copulae, but we may attribute to the hypocingulum the valvocopula and at least one copula and, and to the epicingulum at least two copulae.

Our observations of the interior of valves allow us to bring data about the attachment of valvocopula to the mantle. This is one of the characters evoked by Witkowki et al. (2015) in order to compare related internally costate pseudocellate multipolar diatoms including *Entogonia*. Concerning *Entogonia*, the authors marked (in table 1) “underlapping?” for valvocopula attachment. In our material, indeed the valvocopula underlaps the mantle (Fig. 6a). Moreover, thanks to a specimen showing a broken margin of valve mantle (Fig. 5e,f, 7b) we argue that internal costae do not present any specialized structure that could be implied in the attachment for the valvocopula, as is the case for *Entogoniopsis* and *Trilamina* in which the internal costae are part of the girdle attachment mechanism.

Remarks on the age of *Entogonia* occurrences in Paratethys

The *Entogonia* specimens found in Volhynian sediments from Romania likely represent the youngest occurrences of the genus. Therefore it is necessary to discuss the age of the *Entogonia* occurrence near Szurdokpüspöki (Hungary) considered as upper Miocene by Chenevière (1934) and Holmes & Brigger (1979).

Since the Upper Volhynian from Romania (Paratethys realm) corresponds to the upper Serravalian from the Mediterranean realm (Dumitrică et al., 1975; Motaş et al., 1976; Steininger & Wessely, 2000), it follows that the age of the occurrences of *Entogonia* in the borehole 36 Subpiatră (Borod Basin) are late middle Miocene in age. In such a way it would appear that the specimens of Chenevière (1934) near Szurdokpüspöki, considered as Upper Miocene in age, represent the youngest occurrences of this genus.

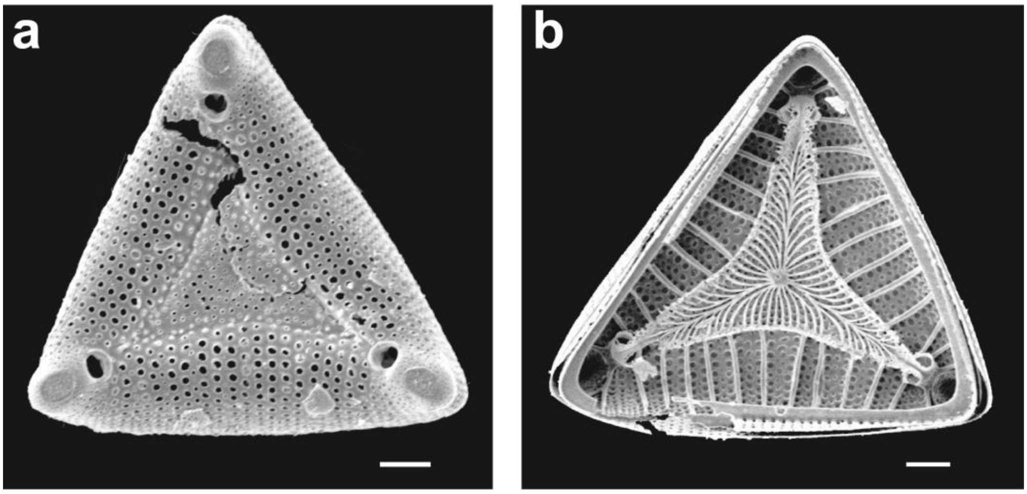
To solve this problem it is necessary to specify that the attribution to late Miocene age of the *Entogonia*-bearing deposits near Szurdokpüspöki by Chenevière (1934) and Holmes & Brigger (1979) results from a time span misinterpretation of the ancient age “Torton” from Paratethys with the current Tortonian age in Mediterranean realm.

Being established that the ancient Tortonian in Paratethys is not the chronostratigraphic equivalent of the Mediterranean Tortonian stage but corresponds to the Badenian stage (Dumitrică et al., 1975; Motaş et al., 1976; Dumitrică, 2016), which represents the Langhian and Lower Serravalian in Paratethys, it results that the *Entogonia*-bearing sample near Szurdokpüspöki is Badenian, that is Middle Miocene in age.

Holmes & Brigger (1979, p. 157) mentioned Castel, Hungary as location of Chenevière's sample. The locality, as Chenevière (l. cit.) mentioned, is Szurdokpüspöki and, according to him (text and map), the *Entogonia*-bearing material came from a very small exposure east of the castle ("chateau" in the French text) situated south of the locality of Szurdokpüspöki. The correct location of the sample should therefore be: some 400 m ESE of the castle south of Szurdokpüspöki, Hungary).

As regards the stratigraphic position of this sample, Chenevière's map is clear enough: it is located within the extension area of the andesitic rocks. Hajos (1968), in her monograph on the Miocene diatoms from the southern foothills of the Matra Mountains, figured also the castle ("Kastel" in the German text) on the map accompanying the paper. On that map Chenevière's sample would be placed within the extension area of the pyroxenite-andesite complex, considered early Tortonian, that is in fact early Badenian in age. The same Badenian age was assigned by Hajos (1977, 1986) to the whole brackish-water to marine diatomaceous complex from Szurdokpüspöki. A similar age was also indicated by the silicoflagellate assemblage (Dumitrică, 1978). There is also a possibility to date the sample of Chenevière based on the diatom assemblage. Chenevière (1934) listed about 102 marine species; some of them may support stratigraphic information: *Actinoptychus amblyoceros* (Ehr) A. Schm., 1874, *Actinoptychus stella* A. Schm., 1886, *Actinoptychus stella* var. *thumii* A. Schm., 1886, *Aulacodiscus grunowii* Cleve, 1885, *Biddulphia elegantula* Greville, 1865, *Clavicula polimorpha* Grunow & Pantocsek, 1886, *Coscinodiscus lewisianus* Greville, 1886, *Triceratium condecorum* Ehrenberg, 1844, *Zygoceros circinus* Bailey, 1854. These species were recorded in *Rhaphoneis paralis* diatom zone defined by Hajos (1986) in Karpatian (upper early Miocene) deposits from marine facies of Garáb Schlier Formation. The author noted that some of these species characterizing the Karpatian occur also in Badenian and extinct from the end of Middle Miocene: *Actinoptychus amblyoceros* (Ehr) A. Schm., *Actinoptychus stella* var; *thumii* A. Schm and *Coscinodiscus lewisianus* Greville. Since then, Horvat (2004) rewied the age of the diatom biozones proposed by Hajos (1986) and conclude that the biozone *Rhaphoneis paralis* (Hajos, 1986) should be considered within the lower Badenian eustatic maximum HSTB2.3, based on first occurrences of index diatom species and the sequence stratigraphy realized by Haq et al. (1987), Vandenberghe & Hardenbol (1998). Considering all these stratigraphic and calibrations information, we appreciate that the diatom microflora listed by Chenevière (1934) from “Castel” near Surdokpuspoki may be assigned to the early Badenian.

A special questioning about the age and source of Chenevière’s sample from Castel was raised by Ross (1995). The author presumed that the source area of Chenevière’s sample could be diatomaceous deposits situated north Szurdokpűspőki higher in the valley of river Győngyős dated by Hajos (1986) as lower Miocene and middle Miocene (Badenian). Considering the floristic content, Ross



Figs. 7 a, b *Entogonia briggeri* n. sp., sample 102m; SEM external view (**a**) and SEM internal view (**b**); **a** Valve face showing valve shape, round apices, elevations to poles and orifices, areolae pattern on inner and outer triangles; **b** Internal view showing the outer and inner triangles, internal costae of outer triangle, dense network of costae of the inner triangle, hyaline center of the inner triangle, the apices of the internal coil fusing to a siliceous punctate membrane within the orifice. Scale bars: 20 µm.

(1995) remarked that the species mentioned by Chenevière do not occur in any other locality. He concluded (1995, page 4): "there can thus be no certainly about either where it came from or its precise age. It cannot, however, be younger than the middle Miocene, and specimens from it are listed of being of that age, although they may be older".

Our conclusion is consistent with Ross (1995) conclusion about a middle Miocene (Badenian) age for the sample of Chenevière (1934).

It results that the age of the *Entogonia* specimens at Szurdokpüspöki is older than that of the oldest specimens in Romania so far known. It is however strange that this interesting genus was not mentioned in any of Hajos' papers.

Entogonia briggeri n. sp. from Romanian Middle Miocene - last survivor of the genus?

In light of these data, the stratigraphic occurrence known to date for the fossil genus *Entogonia* is early Middle Eocene to late Middle Miocene. It is interesting to note that *Entogonia* follows probably the same evolutionary history as other multipolar centrics characterized by heavily siliceous frustule. Sims et al. (2006) noticed that the marine floras that were dominating during the Paleocene and Eocene by relatively robust centric genera (e. g. *Trinacria*, *Sheshukovia*, *Triceratium*, *Hemiaulus*) were replaced by smaller and more delicate centric genera (e. g. *Coscinodiscus*, *Thalassiosira*). Moreover, some genera such as *Hemiaulus* that experienced a large species diversity in Eocene are represented by a lower number of species after Eocene. It seems also that the same is the case of *Entogonia* that records many species in Eocene and only a few species in Miocene. It is generally known that macroevolutionary changes in diatom frustule morphology correspond to changes in nutrient availability, predation and viral pressure, associated with climate change and ocean biology and dynamics over the geological time (Barron & Baldauf, 1989; Finkel & Kotrc, 2010; Lazarus et al., 2014). For instance, the global decrease in oceanic silicic acid concentrations especially over the Cenozoic impacted the diatom with heavily silicified frustule and so involved changes in silicification strategies (Finkel & Kotric, 2010). In the case of *Entogonia*, we may speculate that the unusual and unique morphological feature which is the internal coil system that allowed the survival of the genus in Eocene was little adapted to the newly environmental conditions specific to Middle Miocene and not at all after Middle Miocene. The occurrence of *Entogonia hungarica* described by Holmes & Brigger (1979) in the Middle Miocene deposits from Hungary appears to be restricted to Central Paratethys realm and *Entogonia briggeri* n. sp., described in this paper, is most probably in the same case. Despite carefully bibliographic investigations, the authors of the present paper found only one reference for the genus after Middle Miocene. Wu et al (2012) mention *Entogonia davyana* in the uppermost 1-cm sediment of the South China Sea and present a girdle view image (plate 2, fig.b). In our opinion this tripolar diatom is not *Entogonia* because it lacks one of the specific features of this genus: the presence of internal costae. In girdle view, the genus *Entogonia* exhibits internal costae down on the mantle, defining sectors in which areolae are arranged in vertical rows between internal costae. Moreover, in *Entogonia*, the elevations are perforated by areolae that are smaller than the valve areolae. All these morphologic features specific for *Entogonia* are missing in specimen illustrated by Wu et al. (2012).

It results that *Entogonia briggeri* n. sp. from the early Sarmatian from Romania seems to be the last occurrence of the genus known until present and probably its last survivor.

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