Meloneis Gen. Nov., a New Epipsammic Genus of Rhaphoneidaceae (Bacillariophyceae)

Ioanna Louvrou, Daniel B. Danielidis, Athena Economou-Amilli*

Department of Ecology and Systematics, University of Athens, Athens, Greece

Abstract
The diatom family Rhaphoneidaceae is characterized by high generic diversity and low species diversity with most genera known to have long stratigraphic ranges. The genera within this family are neritic marine, and mostly epipsammic. A new modern and epipsammic genus, Meloneis gen. nov., is described herein and is compared to all genera within Rhaphoneidaceae and especially to Rhaphonies Ehrenberg s.l. Within Meloneis three new species and one variety are distinguished and described herein: M. mimallis sp. nov., M. mimallis var. zephyria var. nov., M. akytos sp. nov., and M. gorgis sp. nov.

Introduction
The marine order Rhaphoneidales Round consists of two families, Psammodesidaceae Round & Mann in Round et al. 1990 [1] and Rhaphoneidaceae Forti 1912 [2]. The former includes only one living taxon: Psammodesidus nitidus (Gregory) Round & Mann. The latter includes the following thirteen genera: Adoneis G.W.Andrews & P.Rivera 1987 [3] with one living species and also one fossil species [4]; Delphinea G.W.Andrews 1977 [5] emend. G.W.Andrews 1981 [6] with many both living and fossil taxa; Detonia Frenguelli 1949 [7] with one living and one fossil species, recently transferred to Neodetonia S.Blanco 2011 [8] (see however [9]); Dickensoiniaformis R.P.Scherer 1997 [10] with two fossil species; Diplomenora K.L.Blaze 1984 [11] with one species both fossil and living; Drosandria P.A.Sims & R.Ross 1996 [12] with one fossil species; Insisia Højás, in Højás & Stradner 1975 [13] with three fossil species; Lancinea G.W.Andrews 1990 [14] with seven fossil species; Neodetonia Takano 1982 [15] with two living species; Perissonee G.W.Andrews & Stoezel 1984 [16] with two living, and few mainly living species; Rhaphonies Ehrenberg 1844 [17] (see also [18,19]) with many fossil and living species; Septonies Ehrenberg 1844 [17] with more than 10 mainly fossil species requiring reinvestigation (see [1,20]). Another genus (Polygoneis) of Rhaphoneidaceae was unofficially proposed as new in 2008 [21].

In this paper, a new genus of Rhaphoneidaceae, named Meloneis, is established, with four infraspecific taxa. Genus Meloneis is taxonomically distinct from the related genera Rhaphonies, Neodetoniae and Perissonee, or the superficially similar genera Adoneis and Dickensoiniaformis. The new taxa of Meloneis were found as epipsammic around submarine hydrothermal vents of Milos Island (Greece). Another genus of Rhaphoneidaceae, i.e. Detonia Frenguelli, was taxonomically rearranged from epipsammic material of the same area ([22]). A catalogue of epilithic diatoms found distant of the vents is also available [23], together with euendolithic chlorophytes and cyanobacteria (see also [24]).

Materials and Methods
Milos is an island in the middle of the Hellenic Volcanic Arc with some 35 km² of geothermally active seabed [25], and Paleochori Bay (24°31.00'E; 36°40.11'N) on the southeastern Milos is one of the most active geothermal submarine areas of the Aegean Sea [26]. The hydrothermal fluids of the submarine vents in Paleochori are warm (max. 115°C), acidic (min. pH 3.54), highly saline, generally enriched over seawater in chloride, calcium, strontium, baryum, sodium, potassium, lithium, silicon, iron, manganese, zinc, cobalt, lead, nickel, yttrium, vanadium but depleted in magnesium and sulphate [27]. The gases in these fluids contain mainly carbon dioxide up to 91.9%; methane, hydrogen, and hydrogen sulphide are also released at concentrations of up to 9.7%, 3.0%, and 8.1% respectively [25].

Sediment samples were collected from submarine hydrothermal vents in Paleochori Bay during two multidisciplinary field trips of some European institutions in June 1996 and June 1997 in the framework of EU-funded programmes. The study area is open to the public and is not under any protection act, therefore, no specific permits were required for visiting the area, working in the field and collecting samples. Furthermore, the collection did not involve in any way endangered or protected species of any kind. Each vent is surrounded by three characteristic concentric zones of distinctive color precipitates [25–26,28–29]: yellow (Y), white (W), and brown (B). The yellow color of the innermost zone results from sulfur condensing on sand grains; the nature of the white precipitates of the intermediate zone is a mixture of amorphous silica, Si nodules and hollow tubes containing elemental sulfur on the outer surfaces; the outermost brownish zone of the vent system consists of Mn-oxides which predominately precipitate at increasing distances from the vent outlet. Material was studied from all incoming distances from the vent outlet. Material was studied from all three color precipitates in both collections (in 1996 at a depth of 7 m; and in 1997 at a depth of 4 m and 7 m), and additionally from a control site (C) outside of the vents (in 1997, at a depth of
4 m and 7 m). The collected samples were preserved in formaldehyde solution. Material was oxidized and slides were prepared for diatom analyses according to standard procedures [30]. Observations were made using Zeiss Axiolab microscope equipped with a Sony DSC-S85 digital camera and Jeol JSM-35 Scanning Electron Microscope equipped with Adda 3 Olympus Soft Imaging Solutions and Scandium Universal SEM Imaging Platform.

Results

**Meloneis Louvrou, Danielidis & Econ.-Amilli gen. nov.**

Latin Diagnosis. Genus novum Rhaphoneidacearum. Valvae planes facie, substrictis limbis, late lanceolatae usque lateribus laeviter convexis et apicibus leniter productis. Area axialis hyalina, distincta, angusta, recta adusque mediocriter lanceolata. Areolae circulares adusque ovatae velis rotoidibus dispositae in striis radialibus curvatis axialis areae. Magna rimoportula unica locata inter areolas ultimae transversae striae. Una continua series areolarum transversae striae ad ambo apices valvae. Ambo apices valvae pseudocellulorum duobus adusque nonnullis porellis minutis forma magis rotundatis. Margo valvae facies decorata irregulari serie demissarum silicearum papillarum sinilium cupolae forma.

**GENUS TYPE:** *Meloneis mimallis* Louvrou, Danielidis & Econ.-Amilli, sp. nov.

DERIVATION OF NAME: Me.lo.ne’.is. femin., N.G. fem. Melos = the name of the greek island Μήλος (also written Milos) and the greek suff. neis, from N.G. ναύς (gen. νησί = boat.

**Meloneis mimallis** Louvrou, Danielidis & Econ.-Amilli spec. nov. var. mimallis

Figures 1A–E, 2A–E, 3A–B

**Latin Diagnosis.** Valvae planes facie, substrictis limbis, late lanceolatae usque lateribus laeviter convexis et apicibus minime productis et rotundatis; 21.5–29 μm longitudine, 14.5–18.5 μm latitudine. Area axialis hyalina, distincta, angusta, recta adusque mediocriter lanceolata. Areolae circulares adusque ovatae velis rotoidibus dispositae in striis radialibus curvatis axialis areae. Magna rimoportula unica locata inter areolas ultimae transversae striae ad ambo apices valvae. Magna rimoportula unica locata inter areolas ultimae transversae striae ad ambo apices valvae. Una continua series areolarum super limbum observata; areolae limbi continuae transversis striis. Magna rimoportula unica locata inter areolas ultimae transversae striae ad ambo apices valvae. Una continua series areolarum super limbum observata; areolae limbi continuae transversis striis.

**Description.** New genus in Rhaphoneidaceae described herein. Valves with flat surface, shallow mantles, broadly lanceolate outline, smoothly convex sides and slightly produced apices. Axial area hyaline, distinct, narrow, linear to slightly lanceolate. Valve surface covered with round to ovate rota-type areolae, radiating in curved transverse striae from the axial area. Transverse striae not aligned across the axial area. A single continuous row of areolae runs along the mantle; mantle areolae aligned with the transverse striae. A single large rimoportula placed in-between the areolae of the last transversal stria at each valve end. A pseudocell consisting of 2 to several fine pores in a rather circular pattern at each valve end. Edge of the valve face ornamented by an irregular row of low siliceous dome-like papillae.

GENUS TYPE: *Meloneis mimallis* Louvrou, Danielidis & Econ.-Amilli, sp. nov.

**Figure 1. Species of Meloneis gen. nov. under LM.** Figure 1A. *Meloneis mimallis* sp. nov., type of the genus. Figures 1B–E. Morphological variation of *M. mimallis* in the type locality. Figure 1F. *M. mimallis* var. zephyria var. nov.; the type. Figure 1G. The type of *M. akytos*, with two pseudocelli consisting of 3 & 4 pores respectively; note the robust areolae, and the distant striae. Magnified valve apices in Figs. 1Ga and 1Gb. Figure 1H. A valve of *M. akytos* with 2 pores per each pseudocellus, otherwise morphologically similar to the type. Magnified valve apices in Figs. 1Ha and 1Hb. Figures 1I–K. Morphological variation of *M. gorgis* sp. nov.; figure 1I represents the type. [Scale bars = 10 μm; the grey bar only for Figs. 1Ga, 1Gb, 1Ha, 1Hb.]

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**Description.** Valves with flat surface, shallow mantles, broadly lanceolate outline, smoothly convex sides, and rounded slightly produced ends; length 21.5 to 29 mm, width 14.5 to 18.5 mm. Axial area hyaline, distinct, narrow, linear to slightly lanceolate. Valve surface covered with large circular to ovate rota-type areolae radiating in curved transverse striae from the axial area. Transverse striae radial, in the middle (7.5) 8–8.5 (9)/10 mm, at the margin 6–7 (7.5)/10 mm, not aligned across the axial area. Areolae arranged also in slightly curved longitudinal rows, 6–7.5–(8)/10 mm at the middle. Few short marginal striae rarely present between complete striae. A single continuous row of areolae runs along the valve mantle; mantle areolae aligned with the transverse striae. Rimoportulae one at each pole, positioned diagonally or on the same side of the apical axis. Rimoportulae with a round external pore, and an elongate slit-like internal opening. A reduced pseudocellus consisting of 3–7 fine pores at each valve end. Edge of the valve face ornamented by an irregular row of low siliceous dome-like papillae; presence of an extra row of finer papillae at the poles.

**DERIVATION OF NAME:** mi.mallīs. femin., N.G. fem. Μίμαλλης = a nymph, also another ancient name of Milos Island cited by Callimachus (310/305-240 BC).

**HOLOTYPE:** Botanical Museum of the Athens University, Greece; ADH slide 1317, England Finder Ref. L21/3; Figure 1A in this paper.

**TYPE LOCALITY:** Palaeochori Bay, Milos Island, Greece; marine, neritic, epipsammic.

**SAMPLES EXAMINED:** depth-zone-year = 4m–U–1997, 4m–W–1997, 7m–W–1996, 7m–W–1997, 7m–B–1997, 7m–C–1997.

**Meloneis mimallis var. zephyria** Louvrou & Econ.-Amilli var. nov. Figure 1F

**Latin Diagnosis.** Valvae forma simillimae speciei *M. mimallis*, sed apicibus magis productis latitudine et rariora ordine linearum areolarum, in medio 4–4.5/10 μm.

**Description.** Valves morphologically identical to the species *M. mimallis* but with broader produced apices and with loosely spaced longitudinal rows of areolae, 4–4.5/10 μm at the middle.

**DERIVATION OF NAME:** zeph.rī.‘a. femin., N.G. femin. Ζέφυρια, previous name of Milos island (according to Aristotle) possibly from the prevailing there western winds, Zephyros.

**HOLOTYPE:** Botanical Museum of the Athens University, Greece; ADH slide 1314, England Finder Ref. N47/0; Figure 1F in this paper.

**TYPE LOCALITY:** Palaeochori Bay, Milos Island, Greece; marine, neritic, epipsammic.

**SAMPLES EXAMINED:** depth-zone-year = 7m–W–1996.

**Meloneis akytos** Louvrou & Econ.-Amilli spec. nov. Figures 1G–H, 3C–E
**Latin Diagnosis.** Valvae planes facie, substrictis limbis, late lanceolatae, usque lateribus laevis velis rotoidibus dispositae in stris radialibus curvatis axialis areae. Areolae magnae circulares adusque ovatae velis rotoidibus dispositae in striis radialibus curvatis axialis areae. Transverse striae composed of very large circular to ovate areolae with rota-type vela, not aligned across the axial area. Transverse striae radial, in the middle 4.5–6/10 μm (mainly 5/10 μm), at the margin 5–6.5/10 μm (mainly 6/10 μm), non frontales trans aream axialem. Areolae etiam dispositae in lineis minime curvatis in longitudinem, 5–6/10 μm in medio. Breves striae marginales praesentes inter perfectas striae. Una continua series areolarum transcurrit limbus valvae; areolae limbi continuae transversis stris. Rimoportulae, una in singulam apicem, locatae in diagnoio vel in utram partem axis apicis. Rimoportulae rotundo externali porelo, et parte interna longa unica caesa. Valvae pseudocellos extenuato ambobus apicibus. Pseudocelli se constant tribus et tribus an tribus et quattor (raris duobus et duobus) porellis minutis per valvam. Margo valvae facies decorata irregulari serie demissarum silicearum papillarum sinilium cupolae forma.

**Description.** Valves with flat surface, shallow mantles, broadly lanceolate outline smoothly convex sides and acutely produced apices; length 21.5 to 32 μm, width 14 to 19.5 μm. Axial area hyaline, distinct, narrow, linear to slightly lanceolate. Transverse striae composed of very large circular to oval areolae with rota-type vela, not aligned across the axial area. Transverse striae radial in the middle 4.5–6/10 μm (mainly 5/10 μm), at the margin 5–6.5/10 μm (mainly 6/10 μm). Areolae arranged also in slightly curved longitudinal rows, 5–6/10 μm at the middle. Short marginal striae present between complete striae. A single continuous row of areolae runs along the mantle of the valve; mantle areolae aligned with the transverse striae. Rimoportulae one at each pole, positioned diagonally or on the same side of the apical axis. Rimoportulae with a round external pore, and an elongate slit-like internal opening. A reduced pseudocellus at each valve end consisting either of 3 and 3 or 3 and 4 (rarely 2 and 2) fine pores. Edge of the valve face ornamented by an irregular row of low siliceous dome-like papillae.

**DERIVATION OF NAME:** Α’κυτος, femin., N.G. fem. Α’κυτος = unlivable, unsuitable for residence; also, old name of Milos island.

**HOLOTYPE:** Botanical Museum of the Athens University, Greece; ADH slide 1318, England Finder Ref. T31/1; Figure 1G in this paper.

**TYPE LOCALITY:** Palaeochori Bay, Milos Island, Greece; marine, neritic, epipsammic.
**Samples Examined:** Depth-zone-year = 4m-Y-1997, 7m-W-1996, 7m-W-1997, 7m-B-1997.

**Meloneis gorgis** Louvrou & Econ.-Amilli sp. nov. Figures 11 K

**Latin Diagnosis.** Valvae planes facie, substrictis limbis, late lanceolatæe, usque lateribus laeviter convexi et apicibus acriter productiis; 17–25 μm longitudinalis, 11–14 μm latitudine. Area axialis hyalina, distincta, recta et angusta ad polos valvae, et clariter latior in medio. Areolae circulares adsequae ovatae velis rotoidibus dispositae in striis radialibus curvatis axialis areae. Areolae in striis radialibus, in medio 10–12/10 μm, in margini (8) 8.5–10/10 μm, non frontales trans aream axialem. Areolae etiam dispositae in lineis minime curvatis in longitudinem, (8.5) 9–10.5 (11)/10 μm in medio. Absentia brevium striarum marginalium inter perfectas strias. Una continua series areolarum transcurrit limbum valvae; areolae limbis continuæ transversi striis. Rimoportulae, una in singulum apicem, locatae in diagonio vel in utram partem axis apicalis. Rimoportulae rotundæ externe porcelli, et parte interna longa unica caesa. Valvae pseudocellus extenuato ambobus apicibus. Pseudocelli se constant nonnullis porcellis minutis per valvam. Margo valvae facies decorata irregulari serie demissarum silicearum papillarum sinilium cupolae forma.

**Description.** Valves with flat surface, shallow mantles, broadly lanceolate outline, smoothly convex sides and acutely produced apices; length 17 to 25 μm, with 11 to 14 μm. Axial area hyaline, distinct, linear and narrow at the valve ends and slightly widened at the middle. Transverse striae composed of circular to ovate areolae with rota-type vela, not aligned across the area axială. Transverse striae radial, in the middle 10–12/10 μm, at the margin (8) 8.5–10/10 μm. Areolae arranged also in slightly curved longitudinal rows, (8.5) 9–10.5 (11)/10 μm at the middle. Absence of short marginal striae between complete striae. A single continuous row of areolae runs along the mantle of the valve; mantle areolae aligned with the transverse striae. Rimoportulae one at each pole, positioned diagonally or on the same side of the apical axis. Rimoportulae with a round external pore, and an elongate slit-like internal opening. A reduced pseudocellus consisting of several fine pores at each valve end. Edge of the valve face ornamented by an irregular row of low siliceous dome-like papillae.

**Derivation of Name:** Gor. gi’s. fem., N.G. fem. Gorijs = old name of Milos island.

**Holotype:** Botanical Museum of the Athens University, Greece; ADH slide 1315, England Finder Ref. Q27/3; Figure 11 in this paper.

**Type Locality:** Palaeochori Bay, Milos Island, Greece; marine, neritic, epipsammic.

**samples Examined:** Depth-zone-year = 4m-Y-1997, 7m-W-1996, 7m-W-1997, 7m-B-1997, 7m-C-1997.

**Discussion**

Taxa of the order Rhaphoneidales are generally characterized by bipolar, multipolar or circular valves, areolae occluded by rotae, and rimoportulae usually present at the apices. The established genera of the family Rhaphoneidaceae, already mentioned in the introduction chapter, are distinguished by the type of valvar outline, type of areolae, number and position of rimoportulae, position and form of pseudocellus (apical pore field), alignment/nonalignment of the transverse rows of areolae across the axial area, presence/lack of spines or papillae, and presence/lack of surface furrows along the transapical striae [3,5–7,10–18,20].

The detailed morphology of the new genus *Meloneis* is characterized by (i) valves broadly lanceolate with smoothly convex sides and slightly produced ends, forming an outline similar to that of *Adoneis*, some *Rhaphonis*, and the fossil *Dickensoniaforma*, (ii) areolae circular or ovate, containing solid, simple rotae connected to the valve by two or scarcely three struts aligned parallel to the margin of the valve closest to the areola, a feature reminiscent of *Adoneis*, *Neodelphineis*, *Neodelphineis*, *Diplomenora*, areolae externally showing central pits like those of *Adoneis* and *Perissonoe¨*, (iii) transverse rows of areolae fully nonaligned across the axial area, as found in *Neodelphineis*, *Adoneis*, *Dickensoniaforma*, *Diplomenora*, *Detonia*, and some *Rhaphonis*, (iv) a single row of areolae at the mantle below the marginal ridge in alignment with the transverse rows of areolae, a common feature of many genera such as *Delphineis*, *Neodelphineis*, *Perissonoe¨*, *Adoneis*, *Diplomenora*, and *Rhaphonis* (at least sensu Round et al. 1990 [1]), (v) rimoportulae one at each pole, diagonally or laterally positioned in relation to the longitudinal axis and lying at the last transverse row of areolae, as observed in *Neodelphineis*, *Perissonoe¨* (with 1–4 rimoportulae per valve), *Rhaphonis* (?), and *Lancinis* (?), (vi) pseudocelli one at each pole, consisting of two to seven fine pores in a rather circular pattern between the last transverse row of areolae and the marginal ring of papillae, a feature unique for *Meloneis* and vaguely similar to those of *Neodelphineis* (with one pore), *Perissonoe¨* (with pores in a rather radiating pattern), and *Rhaphonis* and *Lancinis* (with many pores in a rather disorganised pattern), (vii) lack of surface furrows along the transapical striae, similar to the genera *Adoneis*, *Detonia*, *Dickensoniaforma*, *Diplomenora*, *Lancinis*, *Perissonoe¨*, *Scoptroneis* and most possibly *Rhaphonis*, in contrast to the genera *Desmasto¨*, *Neodelphineis* and most *Delphineis* having grooved external valve face (the valves of the *Delphineis variella* group are usually smooth or very slightly grooved [6,31]); (viii) presence of a ring of papillae at the valve margin, a feature also found in *Perissonoe¨*, some *Delphineis*, and partly in *Adoneis* (*Neodelphineis* bears short spines).

The above descriptive comparison shows a closer similarity of *Meloneis* to the genera *Rhaphonis*, *Neodelphineis*, and *Perissonoe¨* especially concerning the fine structure of the apex (Table 1).

Concerning genus *Rhaphonis sensu lato* (see [32]) there is a lack of knowledge about the fine structure of some taxonomic features in several species. Therefore, comparison can be made to *Rhaphonis amphiceros* (Ehrenberg) Ehrenberg [18,19], the type species of the genus in which certain rhombic or broadly lanceolate forms were attributed as synonyms (i.e. *R. rhombica* (Ehrenberg) Peragallo & Peragallo). Besides, some drawings of *R. amphiceros* var. *amazonica* (Grunow in Van Heurck) *R. amphiceros* var. *rhomboidea* Grunow in Van Heurck, *R. amphiceros* var. *minor* Grunow in Van Heurck or remained as valid taxa [i.e. *R. amphiceros* var. *amazonica* (Grunow in Pantoce¨) M.Pera¨gallo, *R. amphiceros* var. *gymnifera* (Ehrenberg) Pera¨gallo & Pera¨gallo]. Besides, some drawings of *R. amphiceros* var. *rhomboidea* depicted later by several authors (e.g. [33] p. 29, fig. 10/17–19; [34] p. 329, fig. 83/22–23; and [35] p. 100, fig. 5/7 as *R. rhombica* Andrews), as well as the variety *R. amphiceros* var. *intermedia* (Pantoce¨) M.Pera¨gallo and the species *R. debyi* Pantoce¨ and *R. subtilissima* Pantoce¨, are reminiscent in general appearance of *Meloneis*. Generally, in *R. amphiceros* the areolae are occluded by perforated rotae, the pseudocellus is composed by many pores in a rather non-oriented pattern and there is absence of papillae or spines [1]; additionally, it seems that the single row of marginal areolae on the mantle of the valve is not continuous around the apices. However, within *R. amphiceros* there were also classified some discrepant individuals clearly having some valve structure
characteristics of *Meloneis* (e.g. [36] p. 51, fig. 9/2; [37] p. 101, fig. 8/5; [38] figs 16 & 47).

– Although *Neodelphineis* and *Perissonoe* have a different outline (elongate to elliptical valves, and quadrate or triangular respectively) from that of *Meloneis*, the three genera show similarities in the position of both pseudocelli and rimoportulae. However, in *Perissonoe* there are many pores in an almost radiating pattern, in *Neodelphineis* there is a reduction of the number of fine pores to one, whereas *Meloneis* with a rather circular pattern of 2 to several pores keeps an intermediate position between them concerning this particular feature.

– Similarities of *Meloneis* to other genera such as *Adoneis* and *Dickensoniaforma* are considered as rather superficial since they are restricted mainly to the general valve appearance and outline. Specifically, genus *Adoneis* bears an apical rimoportula at each pole positioned among the pores of pseudocellus, and additional rimoportulae at each lateral valve margin; genus *Dickensoniaforma* lacks pseudocelli and the apical pore fields, ocelli, appear to be consisting of vestigial (?) areolae i.e. fine areolae.

Therefore, the unique combination of features cited above and especially the morphology of pseudocellus and papillae suggest a new taxon deserving a distinct taxonomic status, i.e. *Meloneis* gen. nov. Within genus *Meloneis*, three species and one variety (i.e. *M. mimallis*, *M. mimallis var. zephyria*, *M. akytos*, *M. gorgis*) are discernible (see Table 2) mainly differing in size and polar outline of the valves, size of areolae, pore number in pseudocellus, and densities of transapical striae and areolae.

### Table 1. Valve morphology - according to the available literature and photodocumentation cited in this paper - differentiating *Meloneis* from the related genera of the family Rhaphoneidaceae (for the genus *Rhaphoneis s.s.* characters of the type species *Rhaphoneis amphiceros* were considered).

| Related Genera of Rhaphoneidaceae | *Meloneis* | *Neodelphineis* | *Perissonoe* | *Rhaphoneis s.s.* |
|----------------------------------|------------|----------------|--------------|--------------------|
| Specimen Status<sup>1</sup>       | Re         | Re             | Re, Fo       | Re, Fo             |
| Valve Outline<sup>2</sup>        | La         | Li, Elo-El    | Mu           | Rh                 |
| Rota of the areolae<sup>3</sup>  | So         | So             | Pe           | Co                 |
| Mantle areolae<sup>4</sup>       | SrA        | SrA            | SrA          | SrA                |
| Number of Rimoportulae           | 2          | 2              | 1–4          | 2                  |
| Types of Apical Pore Field<sup>5</sup> | Ps        | RP,           | Ps           | Ps                 |
| Number of pores in Apical Pore Field<sup>6</sup> | F         | 1              | M            | M                  |
| Pattern of pores in Apical Pore Field<sup>7</sup> |            |                |              |                    |
| Position of Apical Rimoportula and Apical Pore Field<sup>8</sup> | vE→Ps→(R-Lr) | vE→RP→(R-Lr)  | vE→Ps→(R-Lr)  | vE→Ps→?R→?Lr |
| External furrows along the transapical striae<sup>9</sup> | A          | P              | P, A         | A                  |
| Protrusions<sup>10</sup>         | Pa         | Sp             | Pa           | A                  |

<sup>1</sup>Fo = fossil, R = recent.
<sup>2</sup>Mu = multipolar, La = lanceolate, Rh = rhomboid, Ell = elliptic, Li = linear, Elo = elongate.
<sup>3</sup>So = solid, Pe = perforate, Co = concentric.
<sup>4</sup>SrA = presence of a single row of areolae even around the apices, SrNa = presence of a single row of areolae but not around the apices.
<sup>5</sup>Ps = pseudocellus, RP = apical pore field reduced to 1 pore.
<sup>6</sup>x = number, M = many, F = few.
<sup>7</sup>Ci = rather circular, Di = rather disorganised, Rd = rather radiating.
<sup>8</sup>Rimoportula (R) and Apical Pore Field (Ps, RP, ) in relation to vE = valve edge, and in relation to Lr = last transverse row of areolae. For instance: (R-Lr) = rimoportula positioned between the areole of the last transverse row, vE→Ps = pseudocellus positioned next to the valve edge. The question marks indicate unclear position of the rimoportula in relation to pseudocellus and to the last transverse row.
<sup>9</sup>P = presence, A = absence.
<sup>10</sup>Sp = spines, Pa = papillae, A = absence of protrusions.

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### Table 2. Characters of valve morphology differentiating the four taxa of *Meloneis*.

| Taxon         | Valve length (μm) | Valve width (μm) | Valve apices         | Transverse striae | Striae density (in 10 μm) | Areolae | Areolae density (in 10 μm) | Pores of pseudocellus |
|---------------|-------------------|------------------|----------------------|-------------------|---------------------------|---------|---------------------------|----------------------|
| *Meloneis mimallis* var. *mimallis* | 21.5–29 | 14.5–18.5 | rounded, slightly produced | radial            | (7.5) 8–8.5 (9) | large | 6–7.5 (8) | 3–7                  |
| *Meloneis mimallis* var. *zephyria* | 26.5–27 | 17.5–18 | rounded, broadly produced | noticeably radial | 7.5 | large, loosely spaced | 4–4.5 | not seen |
| *Meloneis akytos* | 21.5–32 | 14–19.5 | acutely produced | noticeably radial | 4.5–6 | very large, loosely spaced | 5–6 | 2–4               |
| *Meloneis gorgis* | 17–25 | 11–14 | acutely produced | radial            | 10–12 | small | (8.5) 9–10.5 (11) | not seen |

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Author Contributions

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