MORPHOLOGY OF THE DIATOM GENUS *CAMPYLONEIS* (BACILLARIOPHYCEAE, BACILLARIOPHYTA), WITH A DESCRIPTION OF *CAMPYLONEIS JULIAE* SP. NOV. AND AN EVALUATION OF THE FUNCTION OF THE VALVOCOPULAE[1]

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A revision of the monoraphid pennate diatom genus *Campyloneis* Grunow was carried out based on LM and EM observations. The material examined originated from various herbarium collections and from extant epiphytic diatom communities on leaves of *Posidonia* spp. We also examined the generitype *C. grevillei* (Smith) Grunow and the fossil material of *C. gheyselinchi* Reinhold from which the author extracted the type. Our results clarified the fine structure of *C. grevillei* and *C. gheyselinchi*. Of the various varieties of *C. grevillei*, only the variety *argus* (Grunow) Cleve was retained. This differs from the nominate variety in the arrangement and shape of the areolae adjacent to the sternum of the araphid valve. The newly described taxon *Campyloneis juliae* De Stefano differs from all *Campyloneis* species in areolae ultrastructure and morphology of the valvocopulae. As for the fossil species *C. gheyselinchi*, the sternum valve areolae are similar to those of *C. grevillei*, but scarcity of frustules in the type material prohibited evaluation of its variability. For this reason we provisionally maintained its rank of species. The elaborate linking systems among the valvocopulae and valves in *Campyloneis* species appear to provide structural reinforcement against pressure from neighboring epiphytic diatoms and scouring of seagrass leaves.

Key index words: *Campyloneis*; epiphytic diatoms; functional morphology; *Posidonia*; EM ultrastructure; valvocopula

Abbreviations: **AA,** apical axis; **RSV,** raphe-sternum valve; **SV,** sternum valve; **TA,** transapical axis

Campyloneis Grunow (Cocconeidaceae, Achnanthales) is one of the most architecturally elaborate raphid pennate diatoms because its two valves differ morphologically and its valvocopulae possess an elaborate *pars interior*. The two valves of *Campyloneis* differ in that only one of them, called the raphe-sternum valve (RSV), possesses a slit in its axial sternum called raphe. The other has only a sternum and is called the sternum valve (SV). For this reason, the genus is considered a member of the monoraphid pennates. In most raphid pennate diatoms the valves are, for all practical purposes, mirror images of one another. Both valves possess a raphe and therefore are functionally identical. In monoraphid pennates, however, the RSV always faces the substrate, whereas the SV is exposed to the environment (Cleve 1895, Hustedt 1959, Round et al. 1990). This functional differentiation has lead to morphological differentiation between the two valves (Holmes et al. 1982, Round et al. 1990).
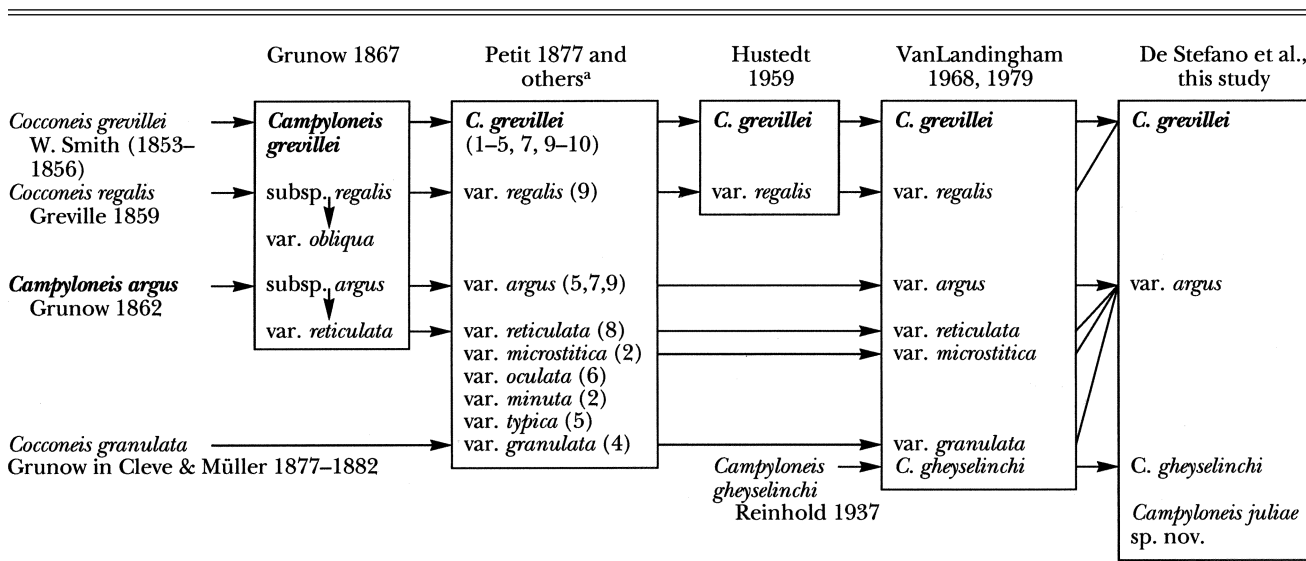
The complex girdle with its internal development constitutes the other reason for the high morphological complexity of *Campyloneis*. In all diatoms, the girdle is composed of a series of silica bands, called copulae, connecting the two valves (Anonymous 1975). In many diatoms these bands are open (horseshoe shaped), whereas in others, among them *Campyloneis*, the bands are closed (ring shaped). The girdle bands adjacent to the valves are often more complex than the other bands and are called valvocopulae (Round et al. 1990). In some species these bands possess inward projections called fimbriae (Holmes et al. 1982, Round et al. 1990). In *Campyloneis* the fimbriae of each valvocopula extend throughout the cell lumen and connect with one another to form a *pars interior* consisting of flat ribs (Round et al. 1990). The two *partes interiores* come into contact with one another and with the inside of their adjacent valves at several intricately designed points along their surfaces (Round et al. 1990).

Grunow (1862) erected the genus *Campyloneis*, distinguishing the type species *Campyloneis argus* (see Fig. 2, a–c) from *Cocconeis* Ehrenberg by its markedly costate RSV (Table 1). At that time, however, he was not able to ascribe this feature to the *pars interior* of the valvocopula. Subsequently, Grunow (1867) transferred *Cocconeis grevilli* W. Smith (1853–56) to the genus *Campyloneis* and made it the new type species (Table 1, Fig. 1, a–c). He also transferred *C. argus* and *Cocconeis regalis* Greville (Fig. 1, n and o) as subspecies of the new type (Table 1) and, in addition, introduced a variety for each of these two subspecies (Table 1). Subsequent authors (Petit 1877 and others in Table 1) retained most of Grunow's taxa but attributed different ranks to them. In addition, they described four new varieties and transferred *Cocconeis granulata* (Cleve & Muller 1877–1882) to a variety of *Campyloneis grevillei*. Reinhold (1937) described *Campyloneis gheyselinchi* from fossil material based on the arrangement of areolae (beads in Reinhold's terminology) in the SV (see Fig. 7a), but he did not encounter an RSV in his material. Hustedt (1959) ac-

TABLE 1. Historical overview of the taxonomic treatment of *Campyloneis*.

	Grunow 1867	Petit 1877 and others[a]	Hustedt 1959	VanLandingham 1968, 1979	De Stefano et al., this study
Cocconeis grevillei W. Smith (1853–1856)	***Campyloneis grevillei***	*C. grevillei* (1–5, 7, 9–10)	*C. grevillei*	*C. grevillei*	***C. grevillei***
Cocconeis regalis Greville 1859	subsp. *regalis* → var. *obliqua*	var. *regalis* (9)	var. *regalis*	var. *regalis*	
Campyloneis argus Grunow 1862	subsp. *argus* → var. *reticulata*	var. *argus* (5,7,9) var. *reticulata* (8) var. *microstitica* (2) var. *oculata* (6) var. *minuta* (2) var. *typica* (5)		var. *argus* var. *reticulata* var. *microstitica*	var. *argus*
Cocconeis granulata Grunow in Cleve & Müller 1877–1882		var. *granulata* (4)	*Campyloneis gheyselinchi* Reinhold 1937	var. *granulata* *C. gheyselinchi*	*C. gheyselinchi* *Campyloneis juliae* sp. nov.

Type species are indicated in bold type.

[a]Petit 1877 (1), Van Heurck 1880–1885 (2), Wolle 1890 (3), De Toni 1891 (4), Cleve 1895 (5), Brun 1896 (6), Van Heurck 1896 (7), M. Peragallo 1897–1903 (8), Peragallo and Peragallo 1897–1908 (9), and Boyer 1926–1927 (10).

cepted *C. grevillei* and the variety *regalis* and rejected all other varieties because he considered characters used to define these intraspecific taxa to be highly variable (Table 1). He did not mention *C. gheyselinchi* and may have been unaware of it (Table 1). VanLandingham (1968, 1979) recognized *C. gheyselinchi,* as well as *C. grevillei* and five of its varieties (Table 1).

Grunow (1867) and Hustedt (1959) observed complex internal structures but were unable to ascribe them to the valvocopulae because they had no access to EM. Round et al. (1990), studying *Campyloneis* using SEM, demonstrated that the internal stratum or skeleton (sensu Grunow and Hustedt, respectively) in fact constituted *partes interiores* of the valvocopulae. Until now, most taxa have only been described with LM. Moreover, several original descriptions (Smith 1853–1856, Cleve and Müller 1877–1882, De Toni 1891) lacked a detailed diagnosis or information on the locations of the type material.

In the present revision of the genus, we describe ultrastructural features of *Campyloneis* taxa in as far as material is available (Table 2). We propose a merge of most varieties of *C. grevillei* recognized by VanLandingham (1968, 1979) into two taxa, the nominate variety and var. *argus*. We maintain *C. gheyselinchi* and describe a new species, *C. juliae* (Table 1). The peculiar structure of the two valvocopulae gives rise to hypotheses about their function.

MATERIALS AND METHODS

Table 2 lists information on type material and additional samples examined in this study. Plates published here have been obtained from this material. Additional observations on seagrass samples from a range of localities across the world (De Stefano 2001, tables 3 and 4) were screened for the occurrence of *Campyloneis*. To collect frustules of living material, seagrass leaves of various ages were scraped with a scalpel. Frustules were cleaned with 70% nitric acid at 60° C for 1 h, washed in distilled water, and then treated with concentrated sulfuric acid, washed again, and mounted in Hyrax (Round et al. 1990). Slides from both our preparations and from historical collections were observed with a Zeiss Axiophot microscope (Carl Zeiss, Oberkochen, Germany). Cleaned material was also mounted on stubs and sputter coated with gold or platinum for SEM (Philips 505, Philips Electron Optics BV, Eindhoven, The Netherlands) or mounted on grids for TEM (Philips 400, Philips Electron Optics BV).

Terminology recommended in Anonymous (1975), Ross et al. (1979), Holmes et al. (1982), and Round et al. (1990) was used for the description of species. The classification proposed by Round et al. (1990) for suprageneric taxa was adopted.

RESULTS

Species descriptions.
Order: Achnanthales Silva
Family: Cocconeidaceae Kützing
Genus: *Campyloneis* Grunow

Campyloneis grevillei* var. *grevillei (W. Smith) Grunow
Fig. 1

Material: Holotype (slide 72, Natural History Museum, London, BM 25633).

Additional material: Slide BRM M1/16 and cleaned material Am 119a (Hustedt Diatom Collection, Bremerhaven); cleaned material 46, 47 (Tempere & Peragallo Diatom Collection, Museum National d'Histoire Naturelle, Paris, France).

Grunow 1867, p. 11; Petit 1877, p. 171, pl. 4, fig. 5; Wolle 1890, pl. 33, figs. 28–30 ; De Toni 1891, p. 439; Cleve 1895, p. 167; Schütt 1896, p. 121, fig. 223; Tempère & Peragallo (1889–95), slides 46, 47. Peragallo & Peragallo 1897–1908, p. 23, pl. 4, figs. 18–21; Boyer 1926–27, p. 242; Karsten 1928, p. 270, fig. 359;
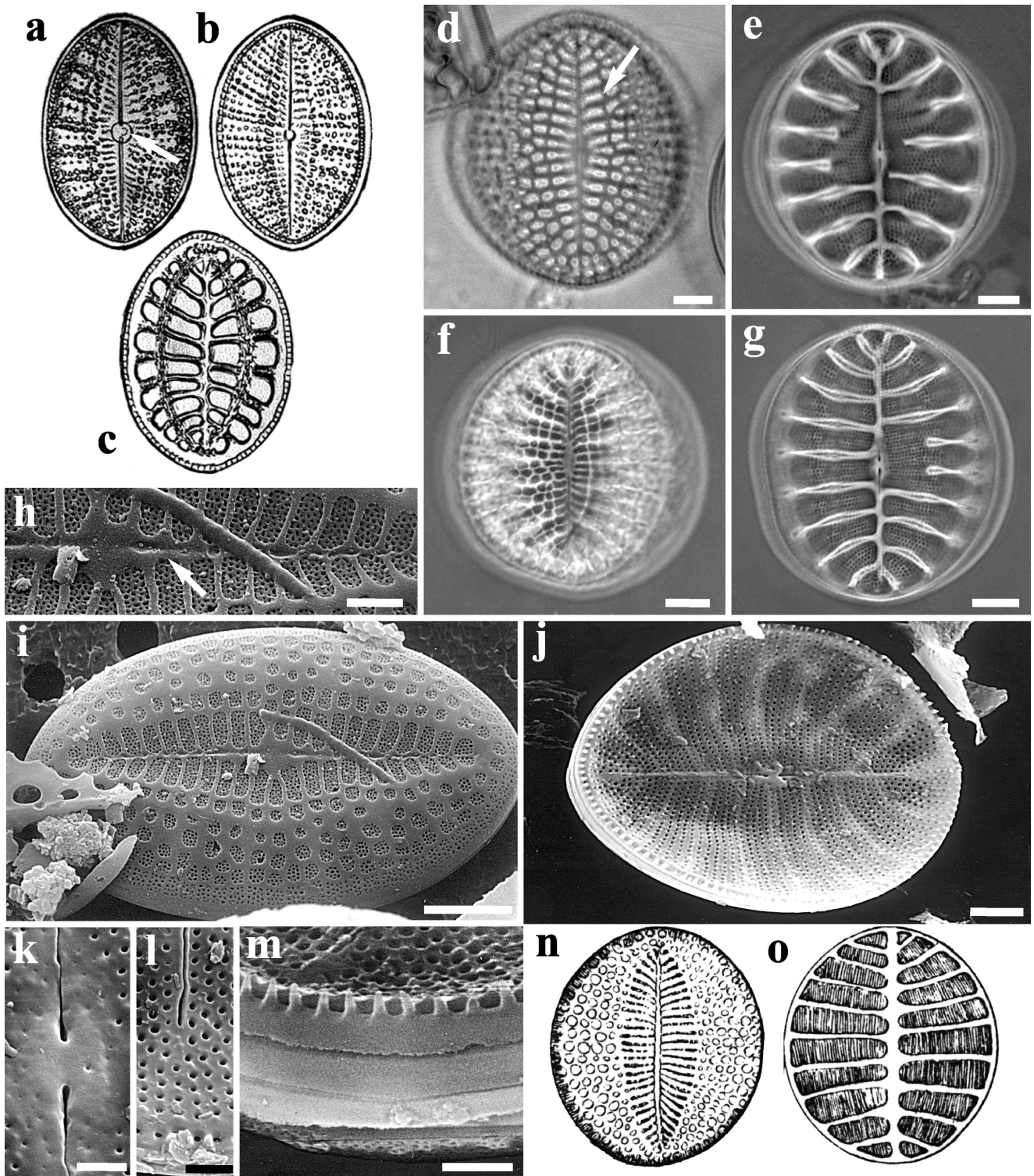
FIG. 1. *Campyloneis grevillei* (W. Smith) Grunow from various collection sources. (a–c) Smith's drawings of *Cocconeis grevilli* W. Smith (Basionym of *Campyloneis grevillei*) (1853–1856, plate 3 fig. 35a*) showing entire frustule with its pierced araphid valvocopula (a, arrow), the raphid valve (b), and its valvocopula (c). (d and e) Type material of *Cocconeis grevilli* (slide 72, BM 25633); arrow indicates transapically elongated areolae adjacent to the axial area in SV (d). Scale, 10 μm. RSV valvocopula with its transverse costae and a reduced longitudinal network of ribs (e). Scale, 10 μm. (f and g) *Campyloneis grevillei* from slide M1/16 (Hustedt Diatom Collection). (h–m) *Campyloneis grevillei* from cleaned material Am 119a (Hustedt Diatom Collection). Detail of vestigial raphe of SV (h, arrow). Scale, 2 μm. External surface of SV (i). Scale, 5 μm. External surface of RSV (j). Scale, 5 μm. External central raphe endings of RSV (k). Scale, 1 μm. External terminal raphe ending of RSV. (l). Scale, 1 μm. Detail of the entire frustule showing the girdle (m). Scale, 2 μm. (n and o) Greville's drawings of *Campyloneis grevillei* var. *regalis* valves.

TABLE 2. List of types, samples, and drawings of the *Campyloneis* taxa observed.

Species/variety	Material	Locality	Source[a]	Reference	Figures
Cocconeis grevilli	Type material slide 72 (BM 25633)	Sidmouth, UK	NHM	Smith (1853)	1, a–e
Campyloneis grevillei	Slide M1/16 Cleaned material Am 119a	Long Island Sound, USA	HDC	Hustedt (1959)	1, f–m
Campyloneis grevillei	Cleaned material 46, 47	Redondo Beach, CA, USA	T and P	Tempere and Peragallo (1889–1895)	
Campyloneis grevillei var. *argus*	Cleaned material from *Posidonia* leaves	Nancy Cove, Philip Rock, Rottnest I., W. Australia	SZN	De Stefano et al. (this paper)	3–6
Campyloneis grevillei var. *granulata*	Slide 276	California, USA	JBVG and NHM	Cleve and Müller (1877–1882)	2, i and j
Campyloneis grevillei var. *microstitica*	Drawings (pl. 28, figs. 8, 9) Grunow in Van Huerck			Grunow in Van Heurck (1880–1885)	2, g and h
Campyloneis grevillei var. *reticulata*	Description			Grunow (1867)	Description only
Campyloneis grevillei var. *regalis*	Drawing (pl. 7, fig. 1) in Greville			Greville (1859)	1, n and o
Campyloneis gheyselinchi	Fossil, cleaned material 611651	Goenoeng Gamping, Java, Indonesia	CAS	Reinhold (1937)	7, a–d and f
Campyloneis gheyselinchi	Fossil, cleaned material 611637	Mgambak-Sadang, Java, Indonesia	CAS	Reinhold (1937)	7, e and g
Campyloneis juliae	Type material Slide MDS 5	Philip Rock, Rottnest I., W. Australia	ZSN	De Stefano et al. (this paper)	8, a and 9g
Campyloneis juliae	Cleaned material from *Posidonia coriacea* leaves	Philip Rock, Rottnest I., W. Australia	ZSN	De Stefano et al. (this paper)	8–9

[a]NHM, Natural History Museum, London, UK; HDC, Hustedt Diatom Collection, Bremerhaven, Germany; T&P, Tempere and Peragallo Diatom Collection, Museum National d'Histoire Naturelle, Paris, France; SZN, Diatom Collection of the Stazione Zoologica "A. Dohrn", Naples, Italy; JbVG, Jardin Botaniques de la Ville de Genève, Switzerland; CAS, California Academy of Sciences.

Hustedt 1959, pp. 320–323, fig. 781; Hendey 1964, p. 184, pl. 27, figs. 9–11.

Basionym: Cocconeis grevilli Wm. Smith 1853–1856, p. 22, pl. 3, fig. 35

Synonyms: Cocconeis regalis Greville 1859, p. 156, pl. 7, fig. 1

Campyloneis argus sensu Round et al. (1990), p. 506–509, figs. a–x

Campyloneis grevillei var. *obliqua* Grunow 1867, p. 11, pl. 1, fig. 5

Campyloneis grevillei subsp. *regalis* Grunow 1867, p. 11

Campyloneis grevillei var. *regalis* Cleve 1895, p. 167

Campyloneis grevillei var. *regalis* Hustedt 1959, p. 323, fig. 782

Campyloneis grevillei var. *typica* Cleve 1895, p.167

Campyloneis notabilis Brun 1891, p.174, pl. 24, fig. 11

Campyloneis regalis var. *minuta* Grunow in Van Heurck 1880–1885, pl. 28, figs. 13,14

The valve shape varies from elliptic to ovoid (Fig. 1, d–g, i and j). Apical axis (AA): 20–100 μm; transapical axis (TA): 15–90 μm.

SV and valvocopula. Externally the valve face is slightly convex except for the area adjacent to the sternum, which is depressed. The shallow mantle is undifferentiated (Fig. 1i). The linear narrow axial area does not reach the valve apices (Fig. 1i) and exhibits marked raphe vestiges (Fig. 1h, arrow). Striae density ranges from 4 to 5 in 10 μm. Each stria consists of transapically elongated and partially fused areolae adjacent to the sternum and polygonal areolae at the perimeter of the valve face and on the mantle (Fig. 1i). Areolae are loculate, externally occluded by cribra (Fig. 1h), and open internally through small circular foramina. The closed valvocopula exhibits the same fine structure as the one shown in Round et al. (1990, p. 509, figs. t–w).

RSV and valvocopula. The valve face is concave (Fig. 1j), whereas the shallow and undifferentiated mantle is slightly convex and terminates in a crenulate marginal area (Fig. 1m). The raphe is straight and does not reach the valve apices (Fig. 1, j and l). External central (Fig. 1k) and polar raphe endings (Fig. 1l) are narrow and coaxial. Internal central raphe endings are deflexed in opposite directions, whereas the polar endings terminate in small coaxial helictoglossae. The uniseriate striae (13–18 in 10 μm) consist of small circular poroids, which are occluded by hymenes with linear, radially arranged, alternately shorter and longer perforations (see, e.g., Fig. 5h). The closed valvocopula is similar to the one in Round et al. (1990, pp. 508–9, figs. n and x).

Campyloneis grevillei var. argus (Grunow) Cleve Figs. 2–6

Material: Specimens scraped from Australian *Posidonia* spp.; slide 276, Natural History Museum, London.

Cleve 1895, p. 167; Van Heurck 1896, p. 285, pl. 8, fig. 345; Peragallo & Peragallo 1897–1908, p. 23, pl. 4, figs. 22–24.

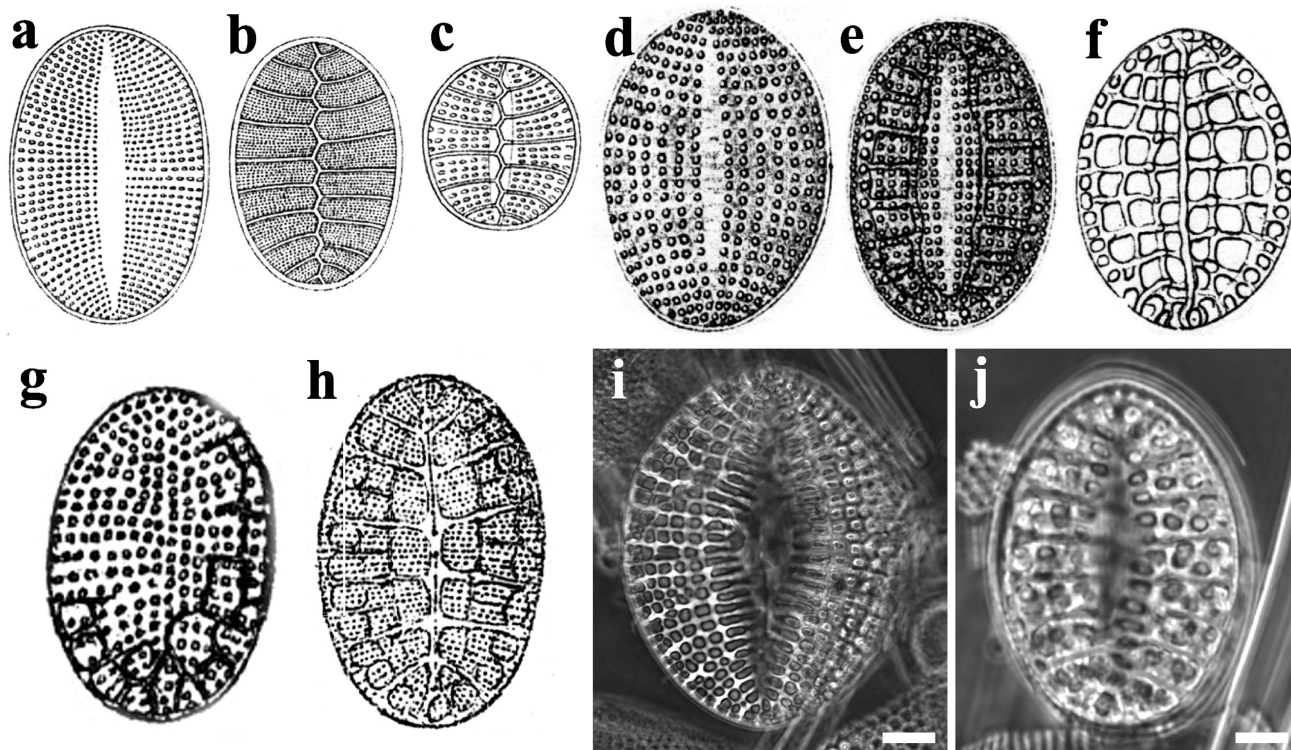*Basionym: Campyloneis argus* Grunow 1862, p. 429, pl. 7, figs. 9, a–f.

FIG. 2. *Campyloneis grevillei* var. *argus* (Grunow) Cleve from various collection sources. (a–c) Grunow's drawings of *C. argus* Grunow showing sternum valve (a), raphe-sternum valve with its valvocopula (b) and whole frustule (c). (d–f) Petit's drawings of *C. grevillei* var. *grevillei* showing a sternum valve with (d) and without valvocopula (e) and a raphe-sternum valvocopula (f). (g and h) Grunow's drawing of *Campyloneis grevillei* var. *microstitica* Grunow in van Heurck valves. (i and j) Type material of *Campyloneis grevillei* var. *granulata* Grunow in Cleve & Müller (slide 276, Natural History Museum, London). Scale, 10 μm.

Synonyms: Cocconeis granulata Grunow in Cleve & Müller 1877–1882, slide 276

    Campyloneis argus Wolle 1890, pl. 33, figs. 24, 25

    Campyloneis argus De Toni 1891, p. 441

    Campyloneis grevillei Petit 1877, pl. 4, fig. 5, a–d

    Campyloneis grevillei Van Heurck 1880–1885, p. 134, figs. 10–12

    Campyloneis grevillei Van Heurck 1896, p. 285, fig. 64

    Campyloneis grevillei subsp. *argus* Grunow 1867, p. 10

    Campyloneis grevillei subsp. *argus* var. *reticulata* Grunow 1867, p. 11

    Campyloneis grevillei var. *granulata?* Grunow in Cleve & Müller 1877–1882, slide 276

    Campyloneis grevillei var. *microstitica* Grunow in Van Heurck 1880–1885, p. 134, figs. 8–9

    Campyloneis grevillei var. *reticulata* (Grunow 1867) M. Peragallo 1897–1903

Valves vary in outline from elliptic-ovoid to ovoid (Figs. 2, 3a and 5a). AA: 39–50 μm; TA: 30–40 μm.

SV and valvocopula. Externally, the valve surface varies from flat to slightly convex except for the area adjacent to the sternum, which is depressed (Fig. 3b). The shallow and structurally undifferentiated mantle ends in a reduced marginal area where striae density increases. The narrow linear axial area reaches the valve apices (Fig. 3, a, b, and f) and shows a zigzag profile when observed at low magnification, due to the alternate arrangement of interstriae (Fig. 3a). The striae (6–8 in 10 μm) are uniseriate on both the valve face and mantle and reveal a radiate arrangement only close to the apices (Fig. 3b). Groups of three to five striae are separated from each other through irregular thickenings on the external surface (Fig. 3, a, b, arrows, and c, arrow).

Each stria consists of a row of large, circular, or polygonal loculate areolae (6–7 in 10 μm), which are occluded externally by cribra (Fig. 3e) and open internally by foramina of variable size (Fig. 3, h and k). The sieve pores of the cribra possess linear perforations of different length that are distributed radially along the margins. The marginal areolae are smaller (Fig. 3d). Because of the irregular distribution of longitudinal ribs between the interstriae, the areolae of adjacent striae are not aligned (Fig. 3g). The internal valve surface has the same structure as the external one (Fig. 3f), with thickened interstriae in both the valve face (Fig. 3i) and mantle. The linking points between the SV valvocopula and the valve are clearly visible on the internal valve surface (Fig. 3f, arrows). These structures correspond to the external irregular thickenings (Fig. 3, a, b, arrows, and c, arrow).

The closed valvocopula consists of a narrow *pars exterior* and a *pars interior* extending as a web of anastomosing flat ribs over most of the internal valve surface
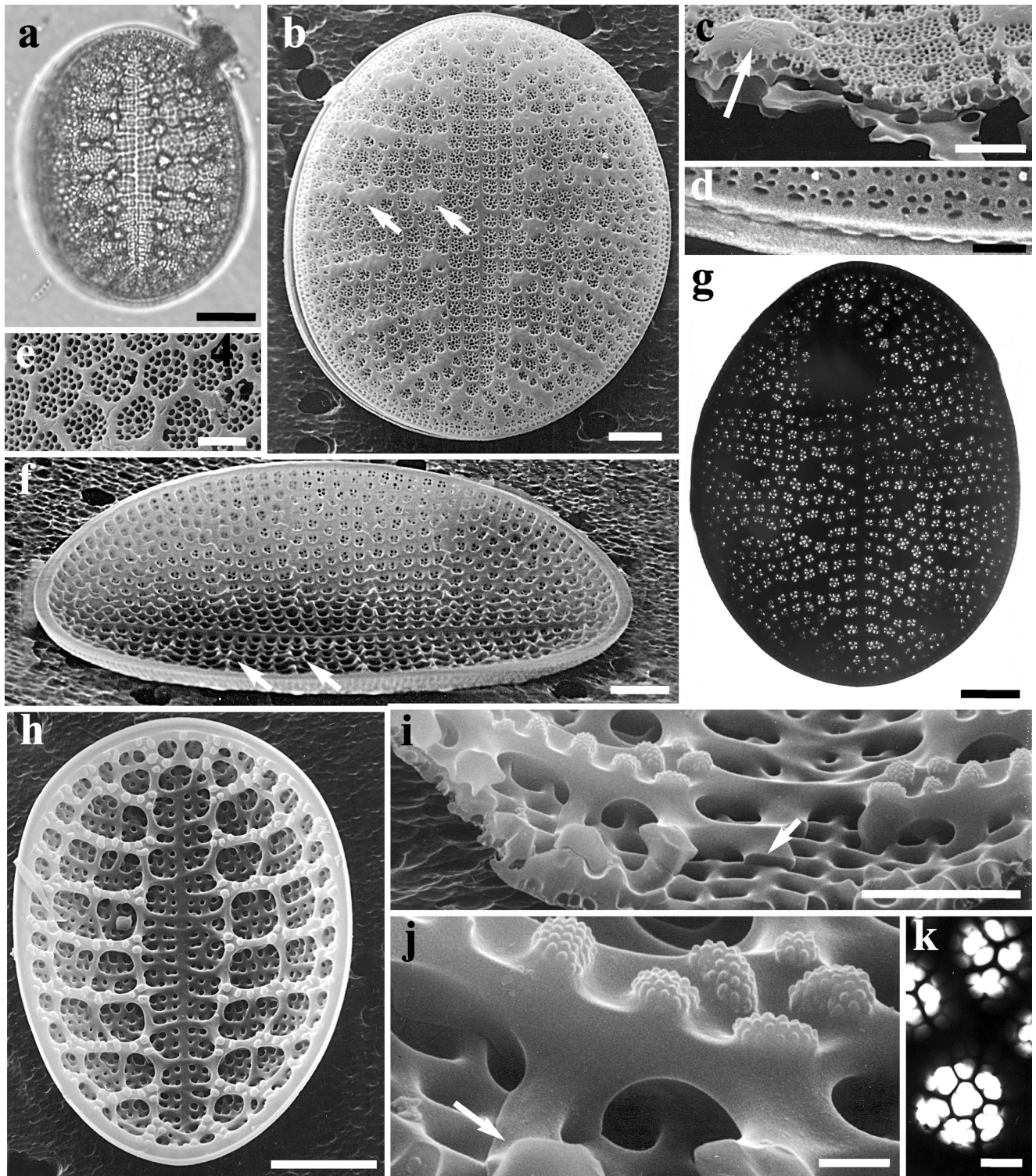
Fig. 3. Sternum valve of *Campyloneis grevillei* var. *argus* (Grunow) Cleve. (a) LM image of the valve. Scale, 10 μm. (b) External view of the valve. Irregular thickenings on the external surface (arrows) are indicated. Scale, 5 μm. (c) Detail of external valve surface with a thickening (arrow) and the underlying valvocopula. Scale, 2 μm. (d) Detail of the mantle areolae. Scale, 1 μm. (e) Fine structure of areolae cribra. Scale, 2 μm. (f) Internal view of SV showing linking points between valve surface and araphid valvocopula (arrows). Scale, 5 μm. (g) TEM image of whole valve. Scale, 5 μm. (h) Internal view of valve with its valvocopula *in situ*. Scale, 10 μm. (i) Sixty-degree tilted image of internal valve surface showing linkage between valvocopula and valve (arrow). Scale, 5 μm. (j) Detail of a cluster of raspberry-shaped papillae on abvalvar surface of araphid valvocopula. Small convexities on the opposite side of the *pars interior* fit into internal areolar openings of the valve face (arrow). Scale, 1 μm. (k) TEM image of internal surface of cribra. Scale, 1 μm.
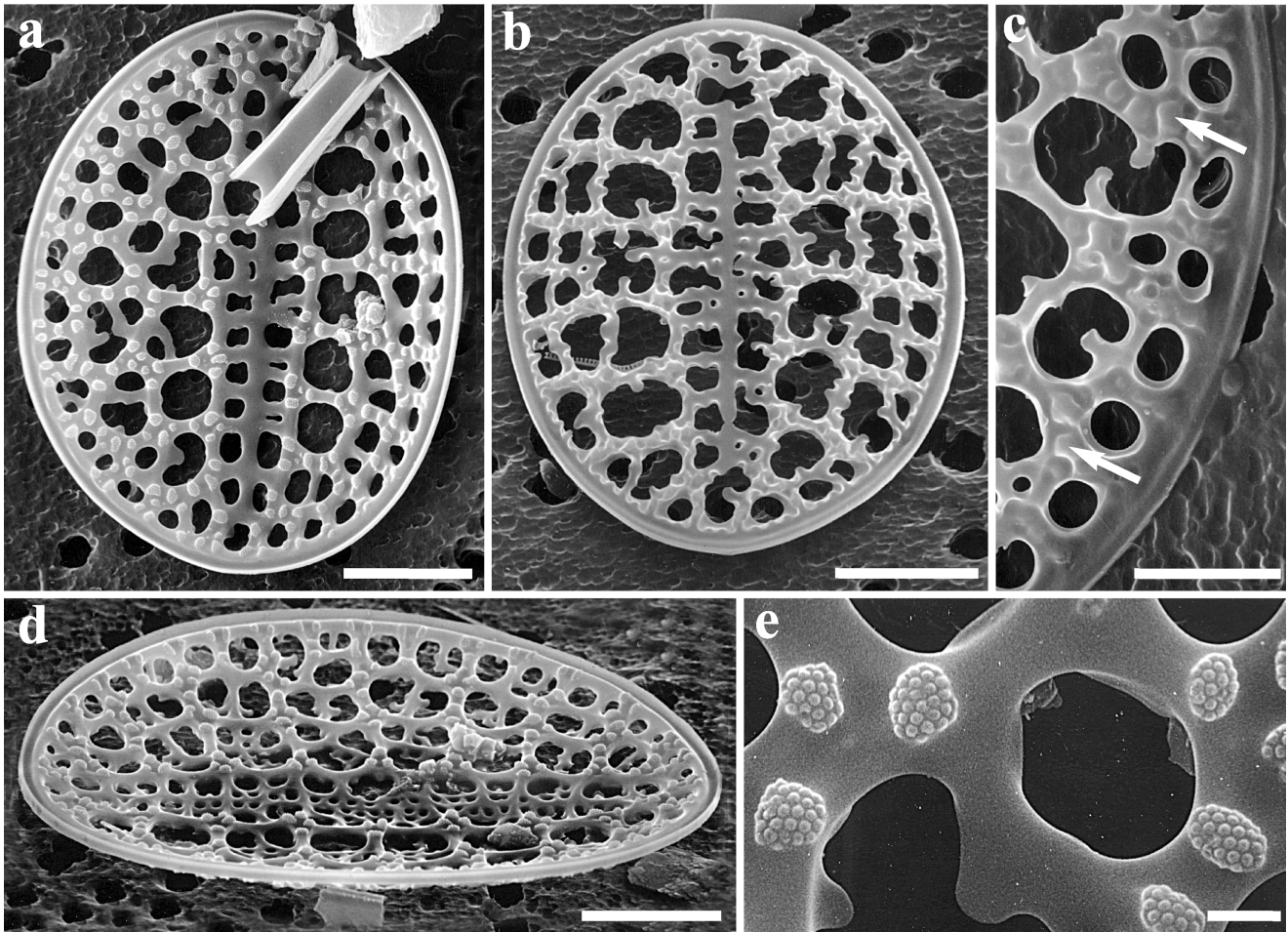
FIG. 4. Araphid valvocopula of *Campyloneis grevillei* var. *argus* (Grunow) Cleve. (a) Abvalvar surface. Scale, 10 μm. (b) Advalvar surface. Scale, 10 μm. (c) Detail of previous image. Arrows indicate small convexities distributed all over the surface. Scale, 5 μm. (d) Sixty-degree tilted image of abvalvar surface of valvocopula showing the slight concave central area. Scale, 10 μm. (e) Detail of papillae clusters on abvalvar surface of valvocopula.

(Fig. 3h). Both the advalvar and abvalvar surface of the *pars exterior* are smooth (Fig. 4, a and b). The advalvar surface of the *pars interior* (Fig. 4b) shows small convexities (Fig. 4c, arrows) that correspond to clusters of papillae on the abvalvar surface (Fig. 4, a and e). The shape of each papilla (about 1 μm in diameter) varies from more or less circular to polygonal and consists of several small spherical bosses (Figs. 3j and 4e).

RSV and valvocopula. Externally, the valve face is concave except for the area adjacent to the raphe that varies from convex, near the central nodule, to flat, close to the valve apices (Fig. 5, b and i). A shallow and undifferentiated mantle ends in a crenulate narrow marginal area (Fig. 5i, arrow). The raphe is straight with simple, coaxial, proximal endings situated on a subcircular central area (Fig. 5d). The distal raphe endings are narrow, coaxial, apically elongated, and terminate far from the valve margin (Fig. 5e). The density of the uniseriate radiate striae ranges from 15 to 17 in 10 μm. They consist of rounded poroids (13–15 in 10 μm) occluded by external hymenes.

The latter bear radially arranged linear perforations that are alternately longer and shorter (Fig. 5h). The internal pattern of the striae is similar to the external one. The internal proximal endings of the raphe deflect in opposite directions and converge near the subrhomboidal central nodule (Fig. 5g). The distal raphe endings are coaxial or slightly deflected, apically elongated, and terminate as prominent helictoglossae (Fig. 5f).

The advalvar surface of the RSV valvocopula (Fig. 6a) reveals concavities at the nodes of the network (Fig. 6g, arrow) and a regular pattern of small bosses unique for this structure (Fig. 6, a and b). The abvalvar surface of the RSV valvocopula (Figs. 5c, arrow, and 6e) shows clusters of distinctively shaped papillae on the transapical ribs.

Campyloneis gheyselinchi Reinhold Fig. 7

Material: Original cleaned material 611651 and 611637 (California Academy of Sciences). Reinhold 1937, p. 88, pl. 7, fig. 3.
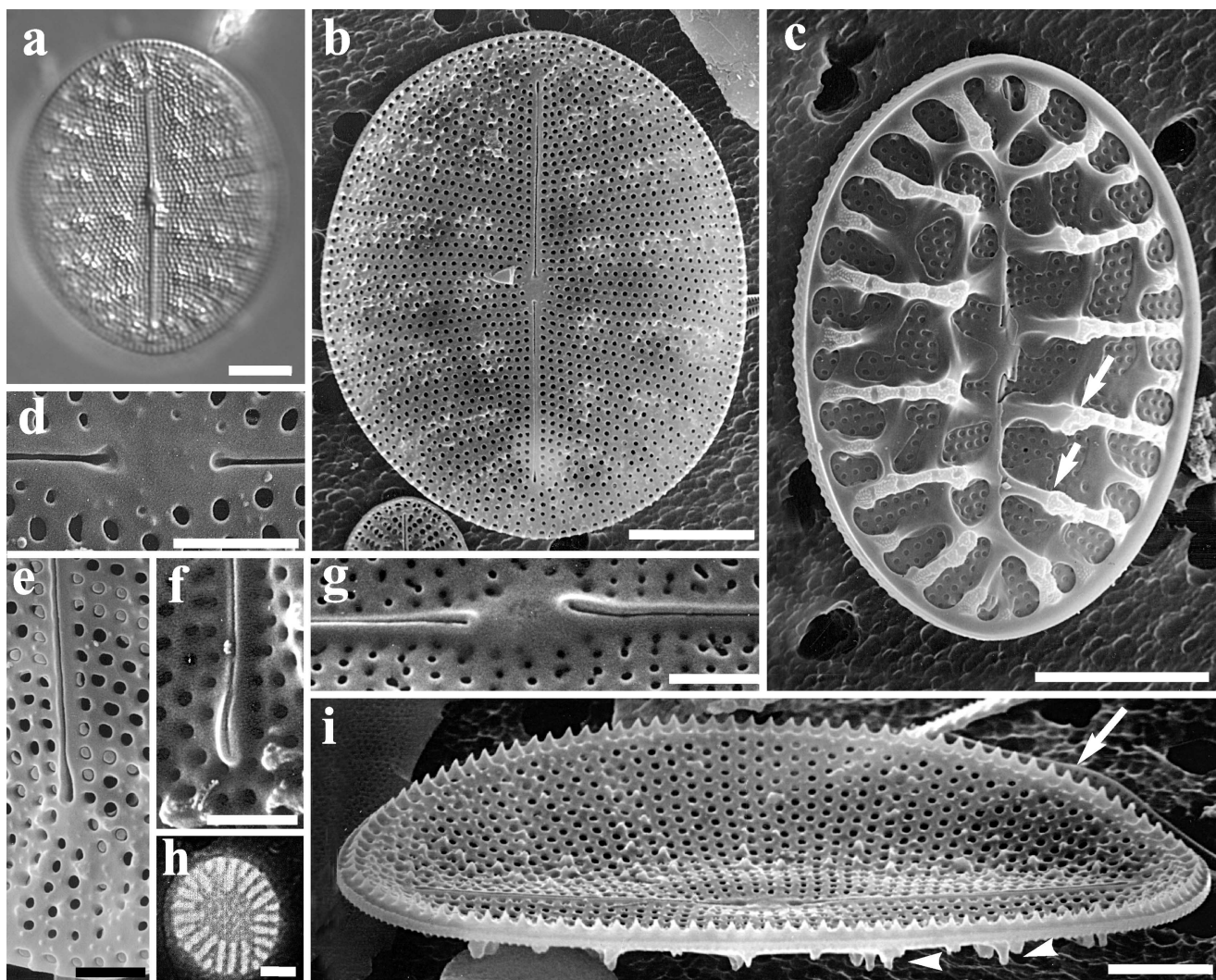
FIG. 5. Raphe-sternum valve of *Campyloneis grevillei* var. *argus* (Grunow) Cleve. (a) LM image of valve. Scale, 10 μm. (b) External view of valve. Scale, 10 μm. (c) Internal view of valve with raphid valvocopula *in situ*. Arrows indicates papillae clusters restricted to transapical ribs of valvocopula. Scale, 10 μm. (d) Detail of central area in external view, showing proximal raphe endings. Scale, 2 μm. (e) Detail of a distal raphe ending in external view. Scale, 2 μm. (f) Detail of an internal polar raphe ending. Scale, 2 μm. (g) Internal detail of the central nodule. Scale, 2 μm. (h) Fine structure of hymenes. Scale, 0.1 μm. (i) Sixty-degree tilted image of external valve surface. Arrow indicates the crenulated valve margin, whereas arrowheads show linking points between valvocopula and valve. Scale, 5 μm.

This fossil species was recorded as very rare by Reinhold (1937), who described it based solely on a single observation of a SV in external view in LM (Fig. 7a). In the original cleaned material we were able to find only three entire valves, all of them SVs (Fig. 7, b–d). One of them had a valvocopula attached to it (Fig. 7, e and g). The species description, therefore, must remain incomplete because information is lacking on its RSV and valvocopula.

Valves vary from elliptic to ovoid (Fig. 7, a–d). AA: 60–70 μm; TA, 40–55 μm.

SV and valvocopula. In external view the valve surface is convex (Fig. 7c). The narrow linear axial area does not reach the valve apices and has a zigzag profile when observed at low magnification, due to the al-ternate arrangement of the interstriae (Fig. 7, a–c). The uniseriate striae (about 5 in 10 μm) consist of rows of large loculate areolae (about 4 in 10 μm), which are rectangular adjacent to the sternum and polygonal in the remaining part of the valve (Fig. 7c). All areolae are occluded externally by cribra (Fig. 7c) and internally by foramina (Fig. 7f) of equal size (Fig. 7d). Internally, the axial area is characterized by a slightly lanceolate profile (Fig. 7d).

The closed valvocopula consists of a narrow *pars exterior* and a *pars interior*. The latter is composed of an anastomosing web of transverse and longitudinal flatted ribs that do not reach the axial area (Fig. 7b, arrows). The transverse ribs bear numerous clusters of papillae distributed over their abvalvar surface (Fig.
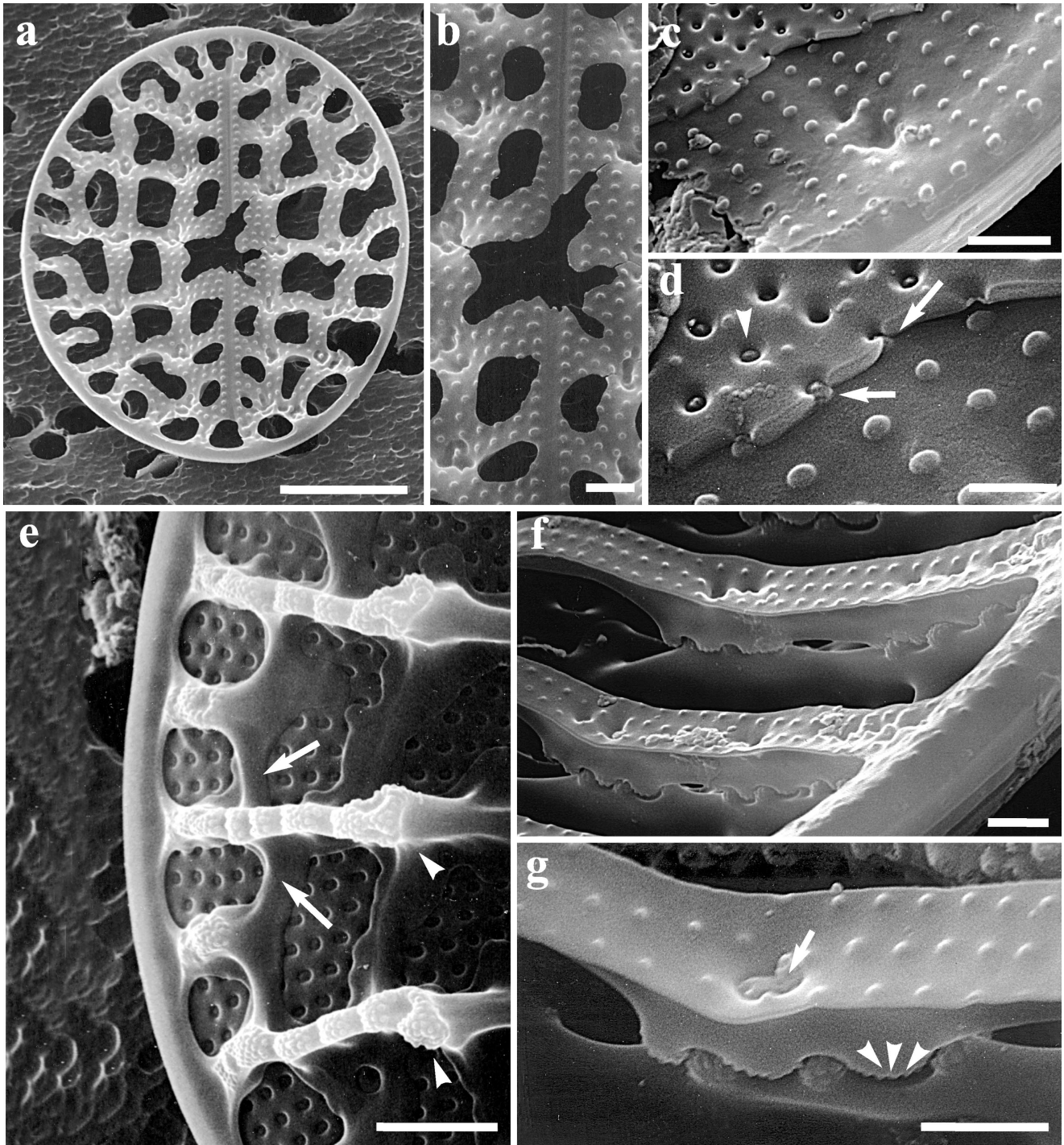
Fig. 6. Raphid valvocopula of *Campyloneis grevillei* var. *argus* (Grunow) Cleve. (a) Advalvar surface. Scale, 10 μm. (b) Detail of previous image. The raphe profile is recognizable in the central area. Scale, 2 μm. (c) Detail of valvocopula margin showing radiate rows of small bosses widely distributed on the advalvar surface. Scale, 2 μm. (d) Peg-and-hole fit of bosses (arrows). The poroids accommodating the bosses (arrowheads) do not differ from those that do not accommodate such structures. Scale, 1 μm. (e) Detail of abvalvar surface of valvocopula showing flat and smooth longitudinal ribs (arrows) and transapical ribs with several clusters of papillae (arrowheads). Scale, 5 μm. (f) Papillae and concavities of each corresponding cluster are complementary arranged when valvocopulae are *in situ*, thus forming structures similar to zippers. Scale, 2 μm. (g) Detail of a zipper. Arrowheads point to small bosses of each papilla, whereas arrow indicates the linking structure on advalvar side of valvocopula, which in turn connects to prominent thickenings of the internal raphid valve. Scale, 2 μm.
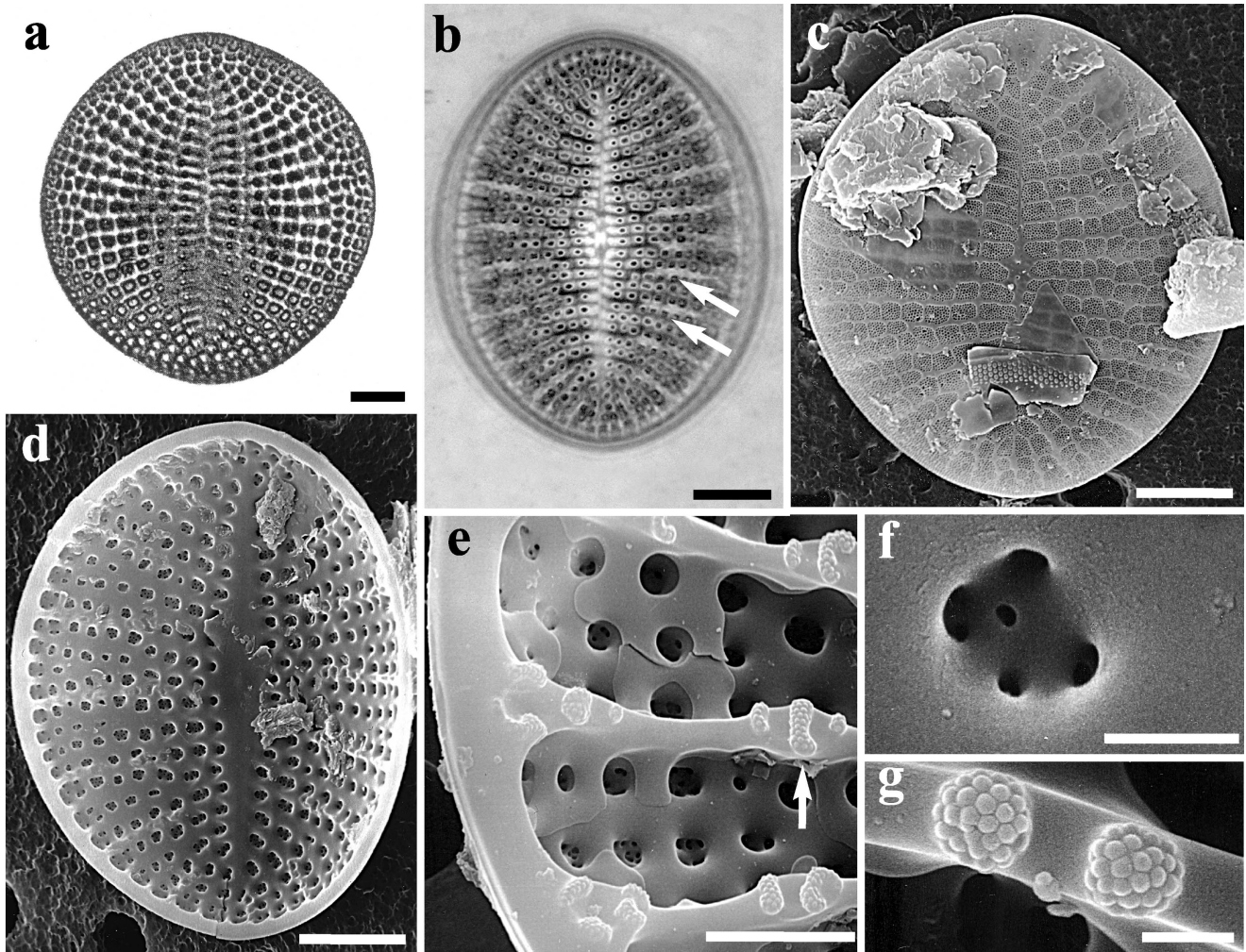
FIG. 7. *Campyloneis gheyselinchi* Reinhold from various collection sources. (a) Reinhold's picture of *C. gheyselinchi* showing sternum valve. Scale, 10 μm. (b–g) *C. gheyselinchi* from fossil material 611651 and 611637 (California Academy of Sciences). (b) LM image. Arrows indicate transverse costae of valvocopula, which do not reach the central region of the valve. Scale, 10 μm. (c) External view of sternum valve. Scale, 10 μm. (d) Internal view of sternum valve. Scale, 10 μm. (e) Detail of transverse costae of araphid valvocopula. Arrow indicates a cluster of papillae. Scale, 5 μm. (f) Internal view of an areola cribrum. Scale, 1 μm. (g) Detail of two papillae clusters showing numerous small bosses. Scale, 1 μm.

7e). Each papilla (about 1 μm in diameter) is circular to irregular in shape (Fig. 7, e, arrow, and g) and consists of a cluster of small spherical bosses (Fig. 7g).

Campyloneis juliae De Stefano sp. nov. Figs. 8 and 9

Material: Specimens scraped from leaves of Australian *Posidonia* spp.

Holotype: Slide MDS 5–Herbarium of the Stazione Zoologica of Naples.

Type locality: Nancy Cove, Rottnest Island (Perth), western Australia.

Possible synonym: C. grevillei sensu Tempere and Peragallo diatom collection, slides 46, 47.

Valvae lanceolatae-ellipticae, 24–38 μm longae, 11–17 μm latae. Areovalva concava in area axiali et convexa in area marginali. Sternum lineare aut leviter lanceolatum. Areovalvae habent structuram striis cum monoseriatis (9–10 in

10 μm) quae constant ex areolis inaequabili figura (4–6 in 10 μm). Implicatae volae partes exteriores areolarum occludunt. Areovalvae valvocopula anuli forma clauditur et constat e solidis costis radiatis quae in aream yalinam, in media parte perforatam, vergunt. Abvalvaris superficies costarum habet non nullas papillas quae aequaliter compositae sunt. Raphovalva convexa in area axiali et concava in area marginali. Raphovalva habet raphem rectam cum nodulo centrali elliptico. Striae (18 in 10 μm) constitutae sunt poroidis (16 in 10 μm) qui occlusi sunt hymenibus rimis cum inaequalibus. Raphovalvae valvocopula anuli forma clauditur.

Valves are lanceolate-elliptic, 24–38 μm long, 11–17 μm wide. The SV is concave in the region adjacent to the axial area and convex toward the mantle. The axial area is straight or slightly lanceolate. The uniseriate striae of the SV (9–10 in 10 μm) consist of irregu-
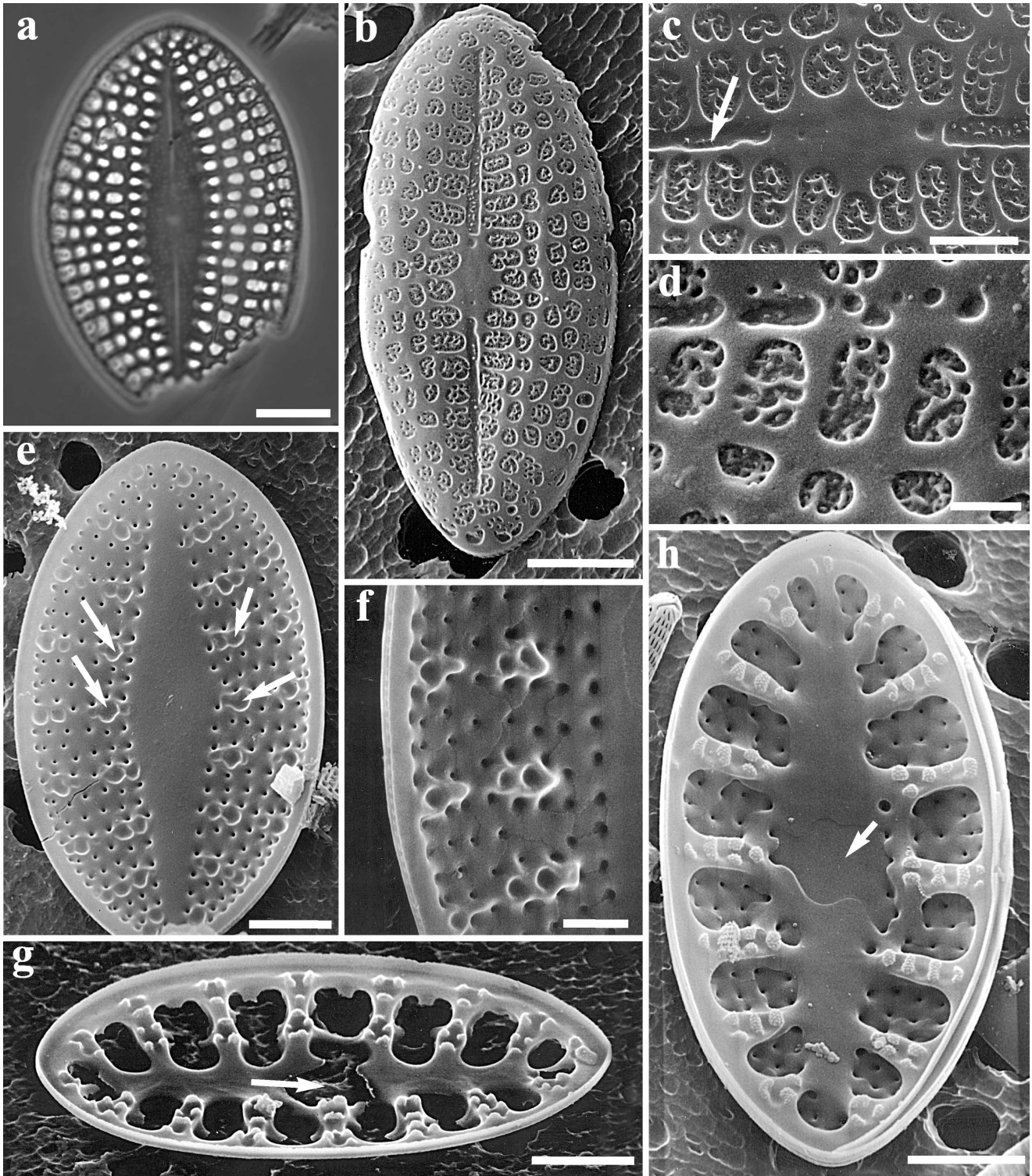
FIG. 8. Sternum valve of *Campyloneis juliae* De Stefano sp. nov. (a) LM image of a valve from Holotype, slide SZN MDS 5. Scale, 10 μm. (b) External view of the valve. Scale, 5 μm. (c) Central area of the valve. Raphe vestiges present (arrow). Scale, 2 μm. (d) Fine structure of irregularly shaped volae. Scale, 1 μm. (e) Internal view of valve; arrows indicate linking points between valve surface and araphid valvocopula. Scale, 5 μm. (f) Detail of linking points shown in previous image. Scale, 2 μm. (g) Sixty-degree tilted image of araphid valvocopula in abvalvar view; arrow indicates central foramen. Scale, 5 μm. (h) Internal view of valve with its valvocopula in situ. The center of the *pars interior* is perforated by a subcircular foramen through which the sternum is visible (arrow). Scale, 5 μm.
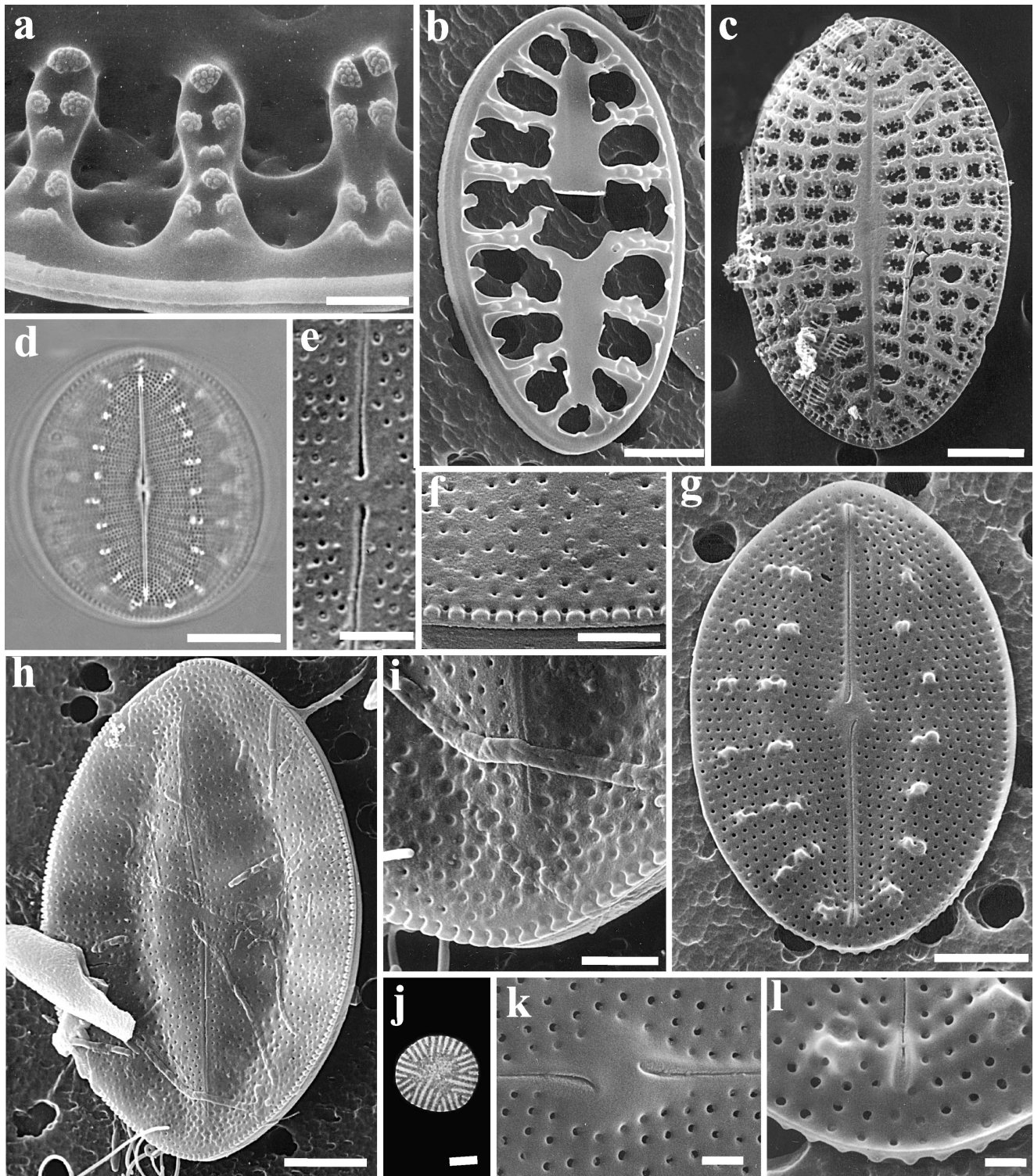
FIG. 9. *Campyloneis juliae* De Stefano sp. nov. (a) Transverse costae of the araphid valvocopula bearing regularly arranged clusters of papillae. Scale, 2 μm. (b) Advalvar surface of the araphid valvocopula. Scale, 5 μm. (c) SV of putative *C. juliae* from Tempere & Peragallo diatom collection (cleaned material 46, Redondo Beach, CA, USA). Scale, 5 μm. (d–k) Raphe-sternum valve of *C. juliae*. (d) LM image of a valve from Holotype slide SZN MDS 5. Scale, 10 μm. (e) Detail of central area in external view, showing proximal raphe endings. Scale, 2 μm. (f) Detail of valve mantle with its crenulated margin. Scale, 2 μm. (g) Internal view of valve. Irregularly shaped thickenings are transapically distributed on both sides of the raphe. Scale, 5 μm. (h) External view of the valve. Scale, 5 μm. (i) Detail of a distal raphe ending in external view. Scale, 2 μm. (j) Fine structure of hymenes. Scale, 0.1 μm. (k) Internal detail of rhombic central nodule and deflected internal proximal raphe endings. Scale, 1 μm. (l) Internal distal raphe ending with its apically elongated helictoglossa. Scale, 1 μm.

larly shaped areolae (4–6 in 10 μm). Complex volae occlude the areolae externally. The SV valvocopula is closed and exhibits transverse thickened costae that converge in a hyaline area; its central area is perforated. On the abvalvar surface of these costae, several papillae are present exhibiting a regular pattern of arrangement. The RSV is convex in the region adjacent to the axial area and concave toward the mantle. The RSV has a linear raphe and an elliptic central nodule. Striae (18 in 10 μm) consist of circular poroids (16 in 10 μm) occluded by hymenes with perforations of different length. The RSV valvocopula is closed.

The name of the species is dedicated to Giulia Carrada, whose love for nature gave joy to her short life.

Valve lanceolate to elliptic-lanceolate (Figs. 8a and 9d). AA: 24–38 μm; TA: 11–17 μm.

SV and valvocopula. In external view the valve surface is concave along the axial area and convex elsewhere. The shallow undifferentiated mantle terminates in a thin hyaline marginal area (Fig. 8b). The linear to slightly lanceolate axial area terminates close to the valve apices. Raphe vestiges are sometimes evident (Fig. 8c, arrow). Striae are uniseriate (9–10 in 10 μm) and consist of irregularly shaped areolae (4–6 in 10 μm) that are arranged in a more or less radiate pattern (Fig. 8b). The loculate areolae are externally occluded by a complex vola (Fig. 8d) and open internally by a small circular foramen (Fig. 8f). The volate hymenes have linear perforations of different size, which are radially distributed on the margins. In internal view, the valve face possesses a broad axial area with a lanceolate profile (Fig. 8e). Consequently, areolae adjacent to the axial area lack internal foramina. Irregularly shaped elevations and depressions (Fig. 8f) are radially distributed on both sides of the axial area (Fig. 8e, arrows).

The closed valvocopula is composed of a narrow *pars exterior* and a *pars interior* (Fig. 8g) consisting of thick transapical costae (Fig. 9a). The latter anastomose distally and converge in a hyaline central lanceolate area (Fig. 8, g and h). An irregularly shaped hole perforates the central area of the *pars interior* through which the central part of the valve surface can be seen (Fig. 8h, arrow). The smooth advalvar surface reveals some elevations and depressions (Fig. 9b). The abvalvar surface of the radiate costae bears several subrhomboidal clusters of papillae (Fig. 9a). The papillae are about 1 μm in diameter and consist of several small spherical bosses (Fig. 9a).

RSV and valvocopula. Externally, the valve face is convex along the axial area and is separated from the flat mantle by a slight depression (Fig. 9h). The valve margin is crenulated (Fig. 9f). The raphe is filiform and straight to slightly sigmoid (Fig. 9, d and h). Its proximal endings are simple, coaxial, and terminate in a reduced central area (Fig. 9e), whereas its distal endings are coaxial, narrow, and do not reach the valve apex (Fig. 9i). The uniseriate radiate striae (18 in 10 μm) consist of rounded poroids (16 in 10 μm), which are occluded by external hymenes with alter-

nately shorter and longer radially arranged perforations (Fig. 9j). The internal pattern of striae resembles the external one (Fig. 9g). The internal proximal endings of the raphe lie on a thickened rhombic central nodule and deflect in opposite directions (Fig. 9k), whereas the distal endings are coaxial and terminate in prominent helictoglossae (Fig. 9l). As in the SV, irregularly shaped thickenings are radially distributed on both sides of the axial area (Fig. 9g). These structures constitute the linking points for the valvocopula. We only observed the *pars exterior* of RSV valvocopula that showed the same structure as the SV valvocopula.

Under LM, *Campyloneis juliae* can be distinguished easily from the other three taxa of *Campyloneis* by its broader and more strongly lanceolate axial area on the SV (see Table 3).

Geographical distribution of Campyloneis *taxa.* We encountered *Campyloneis grevillei* var. *grevillei* in samples from the northwestern side of the Mediterranean Sea, Hawaii, and Beaufort, North Carolina, USA (for sample sites see De Stefano 2001, tables 3 and 4). The type and other material we studied (Table 2) originated from Sidmouth (UK), Long Island Sound (USA), and Redondo Beach, California (USA). We encountered *C. grevillei* var. *argus* only in Australian material (Table 2). The fossil species C. *gheyselinchi* has been recorded only from Java (Reinhold 1937). We observed *C. juliae* at sample sites around Rottnest Island (Perth, W. Australia) and at sites along the Turkish coast (De Stefano 2001, table 3). However, incomplete frustules in materials 46 and 47, Tempere & Peragallo diatom collection (Fig. 9c) collected from Redondo Beach, California (USA) and reported as *C. grevillei* var. *grevillei* appear better identified as the new species *C. juliae*.

DISCUSSION

Ultrastructural studies of *Campyloneis* taxa conducted by Round et al. (1990) and in the present study clearly reveal the main distinctive character of the genus, the elaborate girdle. In *Campyloneis,* this structure is composed of only two closed valvocopulae, with a small *pars exterior* and a reticulate *pars interior* extending across the entire valve surface. As in other diatoms, the *partes exteriores* link with one another and with the internal surfaces of the adjacent valve mantle; however, what renders *Campyloneis* unique is that the *partes interiores* also touch one another and the inner valve faces. The *partes interiores* contact one another by means of a system of papillae adorned with small spherical bosses. The connection between the SV valvocopula and its valve is provided by convexities and concavities on the nodes in the network of the valvocopula, fitting in their mirror images on the valve. The RSV valvocopula links to the RSV through a system of bosses that fit into poroids of the valve in a peg-and-hole arrangement. Large valvocopulae, extending over a large part or the entire internal

TABLE 3. Comparative morphology of the *Campyloneis* species studied.

Feature	*C. grevillei* var. *grevillei*	*C. grevillei* var. *argus*	*C. gheyselinchi*	*C. juliae*
Valve outline	Elliptic to ovoid	Elliptic to ovoid	Elliptic to ovoid	Lanceolate to elliptic
Apical axis (μm)	20–100	39–50	60–70	24–38
Transapical axis (μm)	15–90	30–40	40–55	11–17
Sternum valve				
Curvature	Convex	Flat to slightly convex	Slightly convex	Convex
External sternum profile	Linear, narrow	Linear, narrow	Linear, narrow	Linear, narrow
Internal sternum profile	Linear, narrow	Linear, narrow	Linear, slightly lanceolate	Lanceolate
Striae				
Density in 10 μm	4–5	6–8	∼5	9–10
Uni- or multiseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate
Areolae				
Density in 10 μm	∼6	6–7	∼4	—
Shape in area adjacent to the sternum	Transapically elongated	Polygonal	Transapically elongated	Polygonal
Shape in rest of valve	Polygonal	Polygonal	Polygonal	Polygonal
External opening	Cribrate	Cribrate	Cribrate	Volate
Internal foramen	Small, circular	Large, variable shape	Large, quadrangular	Small, circular
SV valvocopula				
Opened or closed	Closed[a]	Closed	Closed	Closed
Central foramen	Present	Absent	Absent	Present
Pattern of longitudinal ribs	Well developed	Well developed	Reduced	Well developed
Pars exterior: advalvar face	Rough[a]	Smooth	—	Smooth
Pars exterior: abvalvar face	Smooth[a]	Smooth	Smooth	Smooth
Pars interior: advalvar face	Bosses with a central hole	With small convexities	—	With small convexities
Pars interior: abvalvar face	With clusters of papillae[a]	With clusters of papillae	With clusters of papillae	With clusters of papillae
Raphe-sternum valve				
Curvature	Concave	Concave	—	Concave
Striae				
Density in 10 μm	13–18	15–17	—	18
Uni- or multiseriate	Uniseriate	Uniseriate	—	
Areolae	Circular poroids	Circular poroids	—	Circular poroids
Density in 10 μm	15	13–15	—	16
RSV valvocopula				
Opened or closed	Closed[a]	Closed	—	Closed
Pattern of longitudinal ribs	Reduced[a]	Well developed	—	—
Pars exterior: advalvar face	Smooth[a]	Rough	—	—
Pars exterior: abvalvar face	Smooth[a]	Smooth	—	—
Pars interior: advalvar face	Smooth[a]	Rough	—	—
Pars interior: abvalvar face	With clusters of papillae[a]	With clusters of papillae	—	—

[a]Data from Round et al. 1990. —, unknown.

valve surface, are also present in the recently described genus *Psammococconeis* (Garcia 2001). However, the *pars interior* of these structures only touches the adjacent valves, not one another.

Species and varieties within the genus. We used the ultrastructure of the areolae to delimit species within the genus *Campyloneis* because this was the character that showed distinct and discrete differences in the material we studied. We used shape of areolae and their arrangement in the striae as well as the pattern of ribs in the valvocopulae to delimit varieties in *C. grevillei*. Notably, Hustedt (1959) also used these traits to distinguish among intraspecific taxa for the same reason. Although these features showed considerable variation and although transitional forms were encountered, the specimens we observed grouped into two clusters conforming to the nominate variety and the variety *argus*. Based on the morphological data alone, we cannot clearly distinguish these entities as distinct species and therefore treat them as varieties. Table 3 shows the character states for the morphological features of the four taxa we recognized in this study.

Campyloneis gheyselinchi is strictly a fossil species of Miocene age and therefore at least 5.3 million years old, which in its own right would appear to render it distinct from the extant diversity of the genus. Nonetheless, it differs from the generitype only in the internal shape of the areolae and in the pattern of ribs in the SV valvocopula. Its internal foramina are more or less quadrangular, although they also appear to be larger than those in the type (Round et al. 1990, fig.

s). The ribs of its SV valvocopula do not reach the central region of the valve. These are, however, only features that would render it a variety of *C. grevillei*, not a distinct species (Table 3). Yet the areolae are occluded by external cribra similar to those in the generitype and the variety *argus*. Reinhold (1937) described *C. gheyselinchi* as a distinct species because of the presence of "two rows of smaller beads (areolae) border[ing] the pseudoraphe" but we could not confirm these biseriate areolae in our EM observations. Accordingly, this species could be considered a variety of *C. grevillei*. However, we provisionally maintained the rank of species because we lack information on the structure of the RSV and its valvocopula. Moreover, few specimens are available so that morphological variation in this fossil species and possible overlaps with the generitype cannot be addressed properly.

The discussion below refers only to the three extant taxa in *Campyloneis*: *C. grevillei*, *C. grevillei* var. *argus*, and *C. juliae*. Comparisons are made only among these taxa, excluding *C. gheyselinchi* (see Table 3).

The characters of the nominate variety of *Campyloneis grevillei* are as follows:

1. Loculate SV areolae are polygonal on most of the valve face and mantle but are transapically elongated adjacent to the sternum (Grunow 1867);
2. SV areolae possess external cribra and internal foramina (Round et al. 1990, p. 507, figs. g and i);
3. RSV valvocopula have transverse costae and a reduced longitudinal network (Round et al. 1990, p. 506, figs. d and x). This feature was reported in Smith (1853–1856) but misinterpreted as "upper valve from within;"
4. Prominent bosses with a small hole in the center (see Round et al. 1990, p. 509, fig. w) are found on the advalvar side of the *pars interior* of the SV valvocopula;
5. A central foramen is present in the SV valvocopula (Round et al. 1990, p. 509, fig. u) shown in drawings but not discussed in the text by Smith (1853–1856). This feature is not always present in all specimens.

We identified these characters in the type material and in material from the Hustedt collection both in LM and SEM. The five above-mentioned characters are also present in specimens of *Campyloneis* depicted in Round et al. (1990), although their specimens were reported as *Campyloneis argus*. Our EM pictures demonstrate that the depressed sternum of the SV (Grunow 1867, Van Heurck 1880–1885, Brun 1891, De Toni 1891) corresponds to a vestigial raphe (Round et al. 1990, pp. 506–507, figs. f and g). Apparently, a raphe is laid down early in the ontogeny of the SV and only filled in secondarily.

We consider the varieties *obliqua*, *typica*, and *regalis* synonyms of *C. grevillei* var. *grevillei*. The original descriptions of the varieties *obliqua* (Grunow 1867) and *typica* (Cleve 1895) are in accord with that of the nominate variety. In fact, VanLandingham (1968, 1979)

considered these taxa synonyms of *C. grevillei* var. *grevillei*, yet he retained the variety *regalis*, as did Hustedt (1959). We also consider the variety *regalis* to be a synonym because all its diagnostic features do not differ from those of the nominate variety. The larger size of its valves (AA: 70–100 μm; TA: 50–90 μm) (Cleve 1895) is within the range for the nominate variety reported by Hustedt (1959) (AA: 20–100 μm; TA: 15–90 μm). The length of the transapically elongated areolae adjacent to the sternum inferred from the drawings of variety *regalis* (Greville 1859, Wolle 1890, Hustedt 1959) is the same as that found for the nominal variety in the present study and in that of Round et al. (1990, p. 506, fig. f). The lanceolate sternum, reported as distinctive for the variety *regalis* (Greville 1859, Grunow 1867), appears in some drawings of this variety (Greville 1859, Grunow 1867) to be linear as in the nominal variety and, to add to the confusion, a lanceolate sternum sometimes appears in illustrations of the nominate variety (Peragallo and Peragallo 1897–1908, Hendey 1964). De Toni (1891) and Boyer (1926–1927) reported that the reduced density of striae found in variety *regalis* (Hustedt 1959) also occurs in the nominal variety. Finally, a drawing of the RSV valvocopula of the variety *regalis* with strong transverse costae and a reduced longitudinal network in Greville (1859) resembles the RSV valvocopula of the nominate variety (Round et al. 1990, p. 506, fig. d).

Campyloneis grevillei var. *argus* differs from the nominate variety in the following features:

1. Polygonal areolae over the entire SV, including the area facing the sternum;
2. Large areolar foramina, variable in shape;
3. SV valvocopula with a hyaline central area lacking a circular foramen;
4. RSV valvocopula consisting of a well-developed irregular network of flat ribs in a more or less parallel arrangement;
5. Regularly distributed bosses on the advalvar surface of the RSV valvocopula fitting into the valve poroids of the RSV.

Cell size and densities of striae and areola are similar for the two varieties (Grunow 1862, Van Heurck 1896, Cleve 1895).

The ultrastructure of the loculate areolae is the same in variety *argus* and the nominate variety. Grunow (1862, 1867) in his original description pointed out differences in areolar shape between the two varieties. This difference leads us to include specimens illustrated and erroneously ascribed to the nominate variety by Petit (1877) and Van Heurck (1880–1885, pl. 28, fig. 10) in variety *argus*. Petit and Van Heurck also drew the SV valvocopula (Van Heurck 1880–1885, pl. 28, fig. 10), which exhibits the same morphology as that observed in our specimens. The reticulate structure of the RSV valvocopula of variety *argus* was neither described as a valvocopula nor shown in the original drawings by Grunow (1862). He only depicted

transverse costae and believed them to be part of the valve. Petit (1877) first observed the RSV valvocopula detached from the valve and drew it as a separate element of the RSV with both a longitudinal and transverse pattern of ribs. The longitudinal ribs of this valvocopula are not visible in LM when valvocopula is attached to the RSV because the ribs are flat and fit close to the internal valve face. This is why Grunow (1862) could not observe them.

Cleve (1895) described the variety *microstitica*, introduced by Van Heurck (1880–1885) on the basis of drawings of the two valves with their attached valvocopulae. He recorded values for both striae density in the SV (7 in 10 μm) and cell size (AA: 40–50 μm; TA: 32–35 μm) that are within the ranges given for variety *argus* (AA: 16–60 μm; TA: 19–50 μm; SV striae 6–10 in 10 μm) by Grunow (1862), Van Heurck (1880–1885), and Cleve (1895). Moreover, the circular areolae adjacent to the sternum and the irregular network of flat ribs of the valvocopula show that variety *microstitica* is indistinguishable from variety *argus*.

Grunow (1867) introduced variety *reticulata* as the subspecies *argus* var. *reticulata*. Unfortunately, the type material apparently does not exist, so we have to rely solely on the original description, which focuses only on the RSV and its valvocopula. Grunow (1867) mentions one or two longitudinal lines on each half of the valve as diagnostic trait giving it a reticulate appearance. The lines can be interpreted as longitudinal ribs that join with the transverse costae of the RSV valvocopula in *C. grevillei* var. *argus*. Therefore, we merged this taxon in variety *argus*.

De Toni (1891) transferred *Cocconeis granulata* Grunow in Cleve & Müller (1877–1882) into *Campyloneis* as *C. grevillei* var. *granulata*. We found several araphid valves and valvocopulae of this variety on Cleve & Müller slide 276. Of the two, distinct forms were present, one of which we identified as *C. grevillei* var. *argus*. Cleve and Müller probably refer to the second form. This specimen differs from variety *argus* only in that it possesses a slightly lanceolate sternum and larger areolae. However, its valvocopula structure and areolar shape closely resemble those of variety *argus*. We therefore merged this taxon into variety *argus*.

The fact that a number of workers recognized a large number of infraspecific taxa within the morphological variation we interpret here as *Campyloneis grevillei* illustrates the problems encountered in delineating clear nonoverlapping categories within this species. These problems are partly due to the fact that electron microscopes were not readily available until the 1960s and therefore taxonomists had to rely solely on LM. Moreover, pre-1960 diatom taxonomists generally were concerned with entire floras and hence did not have the time to exhaustively study a small group of species, as one can do in a monograph. The different treatments also illustrate the change of views on the treatment of morphological variation. Forms within *C. grevillei* were originally perceived as discrete subspecies and varieties below the species level

(Grunow 1867). Later, these taxa were merely considered points along a continuum of variability characterizing a species (e.g. Hustedt 1959). At present, many taxonomically recognized diatom species appear to consist of series of biologically and genetically distinct taxa that are morphologically difficult to distinguish (Medlin et al. 1991, Sarno et al. unpublished results).

Campyloneis juliae differs from all other *Campyloneis* taxa in that it possesses the following:

1. A lanceolate valve profile;
2. Reduced valve size;
3. Higher SV striae density compared with that of the other species;
4. Irregularly shaped SV areolae externally occluded by complex volae;
5. Subrhomboidal clusters of papillae on the abvalvar surface of radiate costae of the SV valvocopula.

The SV areolae are similar to those observed in some *Cocconeis* species (e.g. *C. stauroneiformis* (Rabenhorst) Okuno, *C. pseudocostata* Romero, *C. fasciolata* (Ehrenberg) N. E. Brown). In all other *Campyloneis* taxa the areolae possess external cribra. Transverse costae with a reduced longitudinal network can also be found in the SV valvocopula of *C. grevillei* var. *grevillei*; however, the thickening of the costae and the more or less rhomboidal arrangement of clusters of papillae are unique for *C. juliae*.

Taxa described as *Campyloneis coelata* Walker-Arnott in Greville, *Campyloneis costata* (Gregory) Lagerstedt, and *Campyloneis notabilis* Brun do not belong to *Campyloneis* but instead to either *Diploneis* or *Cocconeis* (VanLandingham 1968, 1979).

Biogeography. Our findings of *Campyloneis grevillei* var. *grevillei* in the northwestern Mediterranean, Hawaii, Beaufort (NC, USA), Long Island Sound (USA), and Redondo Beach (CA, USA) (De Stefano 2001, table 3) suggest a warm temperate to subtropical distribution. We have never encountered this species in strictly tropical localities. Previous records suggest a wider distribution in Paleo- and Neoarctic regions in cold (Smith 1853–1856, Cleve-Euler 1949, 1953, Hendey 1964), temperate (Greville 1859, Peragallo and Peragallo 1897–1908, Hustedt 1959, Archibald 1983), and tropical seas (Smith 1853–1856, Grunow 1867, Petit 1877, Cleve 1895, De Toni and Forti 1922, Boyer 1926–1927, Foged 1987). However, some of these reports simply mention the species without any further proof, so its actual occurrence is in doubt. We observed *C. grevillei* var. *argus* only in Australian samples from Rottnest Island (Perth, W. Australia). Previous authors report this variety as pantropical (Grunow 1867, Petit 1877, Van Heurck 1880–1885, Cleve 1895, Peragallo and Peragallo 1897–1908, De Toni and Forti 1922). Although observations are limited, the variety appears to be limited to the tropics. *Campyloneis juliae* has been recorded from Rottnest Island (Perth, W. Australia) and from two sites along the Mediterranean coast of Turkey. However, incomplete frustules

observed in samples 46 and 47 of Tempere and Peragallo diatom collection, collected from Redondo Beach, California (USA) and reported as C. *grevillei* var. *grevillei*, appear to be *C. juliae* and thus suggest a wider distribution for this species.

Functional morphology of valvocopulae. We hypothesize that the elaborate valvocopulae and their linkage to the valves as observed in *Campyloneis* represent structural innovations to counteract various external deforming forces. *Campyloneis* species are flattened epiphytic diatoms that may often be abundant on seagrass leaves and large stiff seaweeds. In such habitats they are exposed to scouring, grazing, and to lateral pressure from neighboring competitors for space. Scouring by neighboring seagrass leaves might push valves inward or sideways, whereas lateral pressure by neighboring organisms focuses on narrow regions along the mantle and valvocopulae. Without any structural reinforcement to counteract such pressures, these elements might crack (Hamm et al. 2003).

Forces associated with the propensity of membranes to assume a spherical shape (Thompson 1917) do not explain the need for the elaborate *partes interiores*. The diatom cell assumes such a spherical shape only during zygote formation and the properizonial and perizonial bands later force the auxospore to deviate from such a shape. *Campyloneis* is obviously more disk-shaped than spherical so one would expect the protoplast to push the central parts of the valves outward and the valve mantle and *partes exteriores* of the valvocopulae inward. Nonetheless, this force is relatively weak because *Papiliocellulus* Hasle, von Stosch & Syvertsen, *Arcocellulus* Hasle, von Stosch & Syvertsen, *Phaeodactylum* Bohlin, and *Streptotheca* Shrubsole deviate considerably from a sphere while possessing only the flimsiest of siliceous cell walls, if any.

In all diatoms, valvocopulae connect the margin of one valve mantle via other girdle bands with the valve margin of the opposing valve mantle. These valvocopulae are generally open bands. Yet some diatoms (e.g. several *Cocconeis* species, *Campyloneis*) possess closed bands (von Stosch 1975, Holmes et al. 1982, Round et al. 1990). Closed valvocopulae permit less deformation than open ones of comparable construction (Hamm et al. 2003). Yet a ring can still fold or deform elliptically (Hamm et al. 2003). Once the valvocopula is closed, the structure can be adorned with a rigid *pars interior* as well, like the rigid network of crossbeams in *Campyloneis*. Such a structure provides further reinforcement because a disk prohibits elliptical deformation, although it still permits folding. The disk can, of course, be filled in only partially for the obvious reason that protoplasmic contact must be maintained throughout the cell. We believe that the closed valvocopulae with their *pars interior* in *Campyloneis* counteract vertical and lateral pressures more efficiently because instead of only the two valve faces serving to counteract deforming forces, this role has been transferred in four layers: two valve faces *and* two *partes interiores* of the valvocopulae.

The *partes interiores* of the valvocopulae and their connections with the valves strengthen the structure as a whole against deformation in a fashion similar to the way spandrels brace a dome and trusses reinforce a bridge. The valves and valvocopulae are linked to one another not only along the margins but also through connections between the *pars interior* of each valvocopula and the adjacent interior valve faces. On the advalvar side of the *pars interior* of the SV valvocopulae, small convexities (as in *C. grevillei* var. *argus* and *C. juliae*) or prominent bosses with a small hole in the center (as in *C. grevillei* var. *grevillei*; Round et al. 1990, p. 509, fig. w) can be seen. When the valvocopulae are *in situ*, these structures fit into concavities of the valve face and the internal openings of areolae (Round et al. 1990, p. 509, fig. s). The advalvar surface of the RSV valvocopula in *C. grevillei* var. *argus* is ornamented with small spherical bosses that fit into the poroids of the RSV. In addition, there are more prominent connections between the transapically aligned convexities on the internal surface of the RSV (Round et al. 1990, p. 507, figs. h and k) that fit into the concavities at the intersection points on the RSV valvocopular network (Round et al. 1990, p. 509, fig. x).

The *partes interiores* of the valvocopulae also link with one another, unlike the case in all other diatom genera. Transapically aligned clusters of papillae and concavities on the abvalvar surface of the SV valvocopula connect with similar clusters on the RSV valvocopula. Papillae and concavities of each corresponding cluster are complementarily arranged when the valvocopulae are *in situ*. Such connections prohibit major lateral sliding and compression. The raspberry-shaped papillae on the abvalvar surface of the valvocopulae probably provide a better grip than smooth papillae. The small bosses on the papillae permit distribution of point forces over many bosses on their neighbors. In addition, these bosses may permit minor sliding without loss of grip; strong lateral strain could be relieved through minuscule movement of the valvocopulae in any direction. The bosses could provide many alternative positions of attachment, each deviating slightly from the one when the system is at rest. This linking system is similar in all *Campyloneis* species observed.

The connections among the four frustule elements consist of compression members rather than tension members because the elements disconnect readily from one another in cleaned material. Tension connections between the two valvocopulae cannot exist in diatoms because these valvocopulae have to separate during the formation of new hypothecae of daughter cells. The linking structures between the valvocopulae align with linking structures on the advalvar side of the valvocopulae, which connect in turn with the prominent thickenings on the internal valve face. Such alignments form a series of compression elements (internal columns) connecting the two valvocopulae (internal floors) with the RSV (ground floor) attached to the substratum and the SV (roof) of the diatom. We assume that the vertical component of

pressure applied on the SV is thus directed to the surface on which the diatom has settled, whereas the horizontal component is dissipated completely over the valves and valvocopulae (Hamm et al. 2003). We also hypothesize that the strain is dissipated through the curved beams of the *pars interior*. The curvature may function as a spring, allowing minor deformation in the horizontal and vertical plane. Glass is not well known for its flexibility. However, thin layers of glass show at least some flexibility, and diatom frustules are extremely thin. Moreover, diatom silica is made of inorganic particles associated with an organic matrix, which gives the diatom frustule higher tensile and compressive strengths than a frustule made of plain glass (Hamm et al. 2003).

An alternative way of understanding the function of the *partes interiores* is through comparison with morphological structures found in unrelated diatom genera under comparable environmental pressures. Although valvocopulae with connecting *partes interiores* as in *Campyloneis* are uncommon, they occur in several unrelated pennate genera (e.g. *Diatomella* Greville, *Climaconeis* Grunow, *Climacosphenia* Ehrenberg, *Tabellaria* Ehrenberg). In all these relatively elongated taxa, the *partes interiores* form internal cross beams that prohibit the valvocopulae from deforming. However, they do not interconnect with one another and with the internal valve faces as seen in *Campyloneis.*

One reason for the rarity of valvocopular *partes interiores* could be that many alternative reinforcement modes are available (Hamm et al. 2003). Large diatoms generally possess double-layered valves or a system of struts, buttresses, or spandrels in the valve itself (e.g. *Surirella* Turpin, *Pinnularia* Ehrenberg, *Ardissonea* De Notaris, and *Tetracyclus* Ralfs; Round et al. 1990), whereas the valvocopulae remain simple bands without internal projections. Reinforced valves are encountered in many diatom genera, suggesting that such designs have evolved many times. Structural reinforcements may develop readily from structures (e.g. interstriae, fascia, stauros) already present in the architecturally elaborate valves, whereas the valvocopulae possess little such architectural complexity available for reinforcement.

For whatever reasons, *Campyloneis* has not evolved in the direction of valve reinforcement. A major disadvantage of a structurally reinforced valve is that compression forces perpendicular upon the valve face cannot be easily dissipated via simple valvocopulae to the other valve, whereas the interconnections between the valves and partes *interiores* of the valvocopulae of *Campyloneis* dissipate these forces throughout the diatom frustule.

Alternatively, structures inherited from its ancestors may have permitted development of the elaborate *partes interiores* in *Campyloneis* and not in other genera. *Campyloneis* appears to be a structurally advanced genus in comparison with *Cocconeis* Ehrenberg and might even represent a derived group therein. Some *Cocconeis* species possess open valvocopulae either with or without fimbriae (Holmes et al. 1982, De Stefano et al. 2000). Such fimbriae project under the valve mantle from the advalvar edge of valvocopulae, but they never connect with one another to form a network. Other *Cocconeis* species possess closed valvocopulae, either with or without fimbriae. If fimbriae are present, however, they are either disconnected from one another as in the *Cocconeis* species with open valvocopulae (De Stefano and Marino 2001) or are laterally connected to form an internal ring as in *C. britannica* Naegeli *in* Kützing, *C. scutellum* var. *posidoniae* De Stefano, Marino & Mazzella, and *C. maxima* (Grunow) H. Peragallo & M. Peragallo (De Stefano et al. 2000). Such a ring could be viewed as a structure from which the *pars interior* of the valvocopula in *Campyloneis* is derived.

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