

Eunophora gen. nov. (Bacillariophyta) from Tasmania and New Zealand: description and comparison with *Eunotia* and amphoroid diatoms

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A new raphid pennate diatom genus, *Eunophora*, and three new species are described from highland lakes and streams in Tasmania and New Zealand. *Eunophora tasmanica* and *E. indistincta* are only found in Tasmania; *E. oberonica* and a fourth species (*Eunophora* sp. 1) also occur in New Zealand. The presence of polar rimoportulae in *E. tasmanica* and *E. oberonica*, the relatively simple structure and arrangement of the raphe system and the stria pattern indicate that *Eunophora* belongs to the subclass Eunotiophycidae. However, it differs from the other genera in this subclass in the amphoroid symmetry of the cells, the length of the raphe slits and the non-coaxial internal central raphe endings; also unusual are the position of the raphe on the valve face instead of on the ventral mantle and the presence of many small discoid or band-like chloroplasts. *Eunophora* may represent a link between the Eunotiophycidae and the amphoroid genera of the Bacillariophycidae. *Eunophora* is characteristic of dystrophic to (ultra-)oligotrophic lakes and appears to be restricted to the Southern Hemisphere. The four species display a characteristic distribution in Tasmania: *Eunophora tasmanica* is common and widespread in all highland lakes, *E. oberonica* occurs mainly in the dystrophic western lakes, while *E. indistincta* and *Eunophora* sp. 1 were found mainly in intermediate lakes along the limnological corridor between the western dystrophic lakes and the eastern oligotrophic lakes.

Key words: biogeography, Bacillariophyta, phylogeny, Tasmania, taxonomy

Introduction

Amphoroid diatoms (strongly dorsiventral raphid diatoms, with bilaterally asymmetrical valves that lie at an acute or even obtuse angle to each other) have traditionally been classified in the genus *Amphora* Ehrenberg ex Kützing. However, this genus probably represents a polyphyletic group, consisting of members of several unrelated families (e.g. Cleve, 1895; Mereschkowsky, 1903; Mann, 1994). Whereas the generic status of many amphoroid diatoms is still unclear, there has hitherto been general agreement that all of them belong to the subclass Bacillariophycidae D. G. Mann (equivalent to the Monoraphideae and Biraphideae of Karsten, 1928 and Hustedt, 1927–66), and not to the Eunotiophycidae D. G. Mann (equivalent to the Raphidiodeae).

During recent studies of the diatom communities in lake sediments from the highlands of Tasmania (Hodgson *et al.*, 1997; Vyverman *et al.*, 1995, 1996) and New Zealand several unidentifiable amphoroid taxa were discovered. Light and electron microscopical analysis revealed that

four of these taxa have a unique combination of characters found in no known diatom genus. One of the most significant findings is that two of the taxa possess rimoportulae. Among raphid diatoms, rimoportulae are known only from the Eunotiophycidae, comprised of the genera *Eunotia* Ehrenberg, *Actinella* Lewis, *Semiorbis* Patrick, *Desmogonium* Ehrenberg and *Peronia* Brébisson & Arnott (Round *et al.*, 1990).

In this paper, we formally propose the establishment of a new diatom genus, *Eunophora*, and three new species. We provide information on the morphology, distribution and autecology of *Eunophora*, and discuss the taxonomic position of the genus within the current classification of the raphid diatoms (Bacillariophyceae). Since our first report of these diatoms in Tasmania (where *Eunophora* was introduced as a *nomen nudum*, Vyverman *et al.*, 1995), we have discovered that a fourth species of *Eunophora* (also present in Tasmania) had already been described from New Zealand by Cleve (1883), as *Amphora berggrenii* Cleve. This species will be dealt with in more detail in a forthcoming paper, but some aspects are described and illustrated here under the name used for the species by Vyverman *et al.* (1995), *Eunophora* sp. 1.

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Materials and methods

Surface sediment samples from central and south-western Tasmanian highland lakes were collected on several occasions between February 1994 and February 1995. Details of sampling and water analytical procedures are given elsewhere (Vyverman *et al.*, 1996, 1997). A limnological description of the Tasmanian lakeland is given by Tyler (1992). The New Zealand samples were collected in March 1997 (alpine acid-water tarns in Kelly Pass, Arthur's Pass National Park, South Island) and October 1997 (acid-water tarns and streams in alpine vegetation on Stewart Island).

For studies of valve morphology, samples were digested with hydrogen peroxide and glacial acetic acid and washed with distilled water by successive centrifugations. Permanent mounts were made using Naphrax. Light microscopy used a Zeiss Universal microscope equipped with phase contrast and Nomarski interference contrast illumination. Scanning electron microscopy was done using a Jeol JSM-840 electron microscope operated at 15 kV. On a number of occasions, live material was collected for the study of plastid and nucleus organization. Sediment samples were transported on ice and were examined within 3 days of collection.

Observations

Eunophora gen. nov. W. Vyverman, K. Sabbe et D. G. Mann

Cellulae solitariae, valde dorsiventrals. Chromatophora parietalia taeniata vel parva disciformes, quatuor ad numerosa. Cellulae aspectu cincturae plerumque visae, tum late ellipticae vel rectangulares angulis rotundatis; respectu axis apicalis semper asymmetricae. Valvae isopolares vel aliquantum heteropolares, fere lineares ad semiellipticae, margine ventrali recto vel ad centrum plusminusve constricto, limbo dorsali profundo a fronte valvae modice ad valde distincto, limbo ventrali non profundo vel fere nullo. Sternum ad instar areae angustae hyalinae longitudinalis respectu raphis dorsaliter positum a raphe ipsa distinctum. Striae plerumque simplices uniseriatae, poroidibus parvis circularibus nonnunquam a velis oclusis interdum in sulcum inter costas (interstriae) intus aperientibus (striis fere quasi alveolatis). Raphe biarcuata vel fere recta, in fronte valvae excentrice disposita. Fissurae raphis ad centrum valvae versus marginem ventralem plerumque flexae, extremis centralibus internis asymmetricis non coaxialibus. Fissurae terminales praesentes, in limbum dorsalem extensae. Rimoportulae aut nullae aut duae ad polos singulae positae; apertura interna rimoportulae grandis elongata sessilis, foramen externum circulare interdum margine incrassato circumcinctum interdum simplex. Cingulum ex copulis 5–7 apertis porosis curvatis constans, lateribus dorsalibus quam ventralibus multo latioribus. Species omnes benthicae aquam dulcem habitantes detrito sedimentoque consociatae.

Typus: *Eunophora tasmanica*.

Cells solitary, strongly dorsiventral. Four to numerous small, disc-shaped or band-like, parietal chloroplasts per cell. Cells usually lying in girdle view and then broadly elliptical or rectangular with rounded corners, always asymmetrical about the apical plane. Valves linear to semi-elliptical. Ventral margin more or less constricted centrally. Dorsal mantle deep, moderately to sharply differentiated from the valve face. Ventral mantle shallow or almost absent. Sternum taking the form of a narrow longitudinal hyaline area, positioned dorsally with respect to the raphe and separate from the raphe itself. Striae usually simple, uniseriate, containing small circular poroids, which are sometimes occluded by vela; poroids sometimes opening internally into a groove between adjacent interstriae, making the striae almost alveolate. Raphe biarcuata or nearly straight, eccentrically placed on the valve face. Towards the centre of the valve, raphe slits usually bent towards the ventral margin, central internal raphe fissures asymmetrical, non-coaxial. Terminal fissures present, extending onto the dorsal mantle. Rimoportulae sometimes present and then 2 per valve, located at the poles. Internal opening of rimoportula large, elongate, sessile; external opening circular, rimmed or simple. Cingulum composed of 5 to 7 open, curved, porous copulae, broad on the dorsal side, narrow on the ventral side.

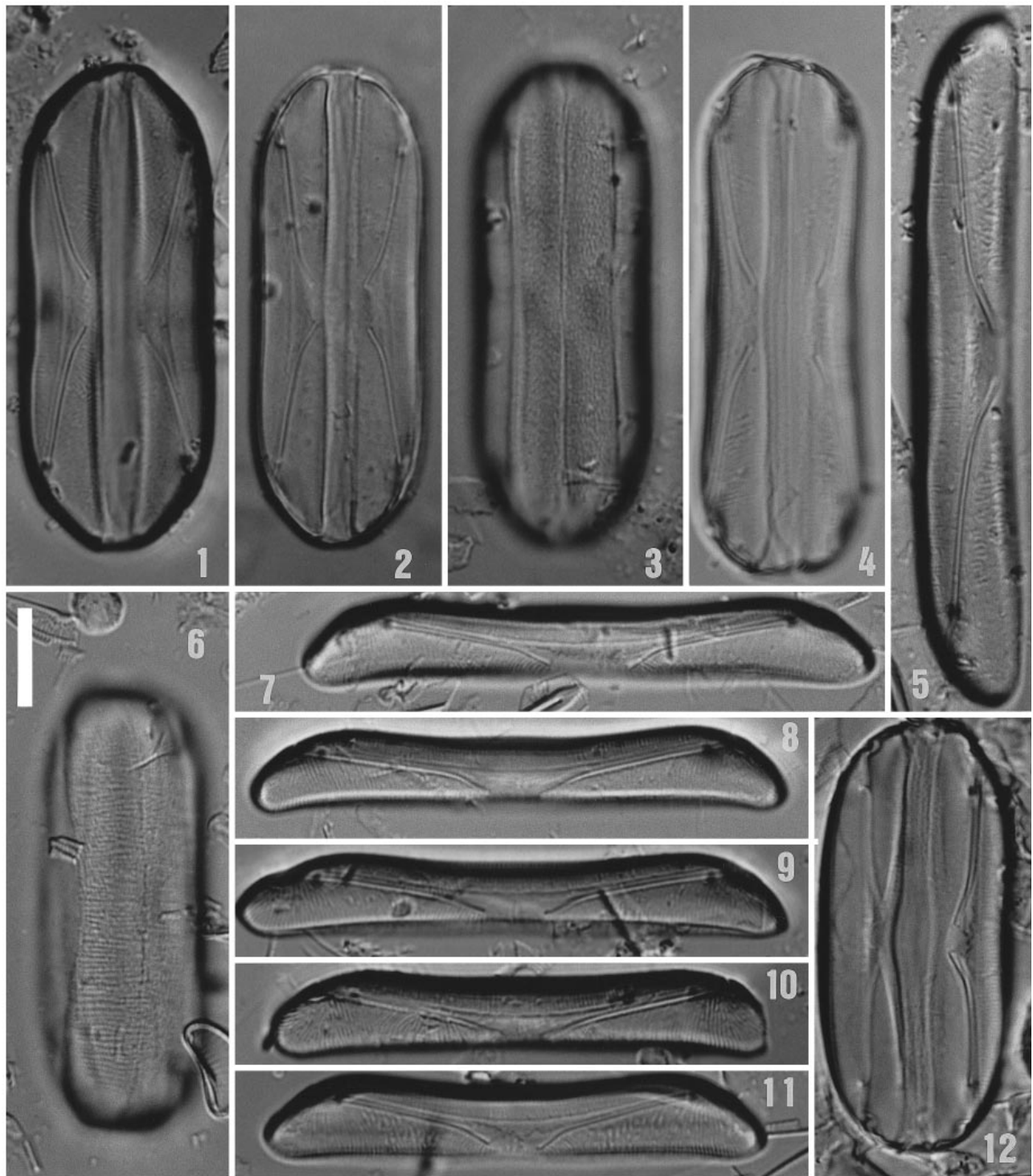
All species freshwater, benthic, probably living in close association with sediment and detritus.

Type species: *E. tasmanica*.

Eunophora tasmanica R. Vyverman et K. Sabbe, sp. nov. (Figs 1–18, 28)

Cellulae solitariae valde dorsiventrals, aspectu cincturae late ellipticae ad lineares-ellipticae, 29–74 μm longae, 13–18 μm latae. Valvae lineares ad fere semiellipticae, extra laeves vel minute granulosae, aspectu cincturae visae marginibus dorsalibus rectis vel leviter concavis marginibus ventralibus rectis ad centrum (secundum aspectum) saepe constrictis, apicibus late rotundatis ad oblique cuneatis, 5–10 μm latae. Sternum manifestum. Striae per microscopium usitatum saepe non facile detectae, 20–34 in 10 μm , densitate inter frontem valvae et limbum dorsalem vix mutandi, inter extrema centralia raphis area hyalina plerumque interruptae; in latere dorsali raphis striae ad centrum parallelae, apices versus leviter convergentes; in latere ventrali striae ad centrum valde radiatae, apices versus valde convergentes. Raphe biarcuata. Helictoglossae in latere ventrali valvae positae semper manifestae. Rimoportulae praesentes respectu raphis ventrales igitur in cellulis valvisve aspectu cincturae visis manifestae.

Cells solitary, strongly dorsiventral, broadly elliptical to linear-elliptical in girdle view, 29–74 μm long, 13–18 μm wide. Valves linear to almost semi-elliptical; when seen in girdle view, with straight or slightly concave dorsal margins; apices broadly rounded to obliquely cuneate; ventral margins straight, often constricted centrally (de-

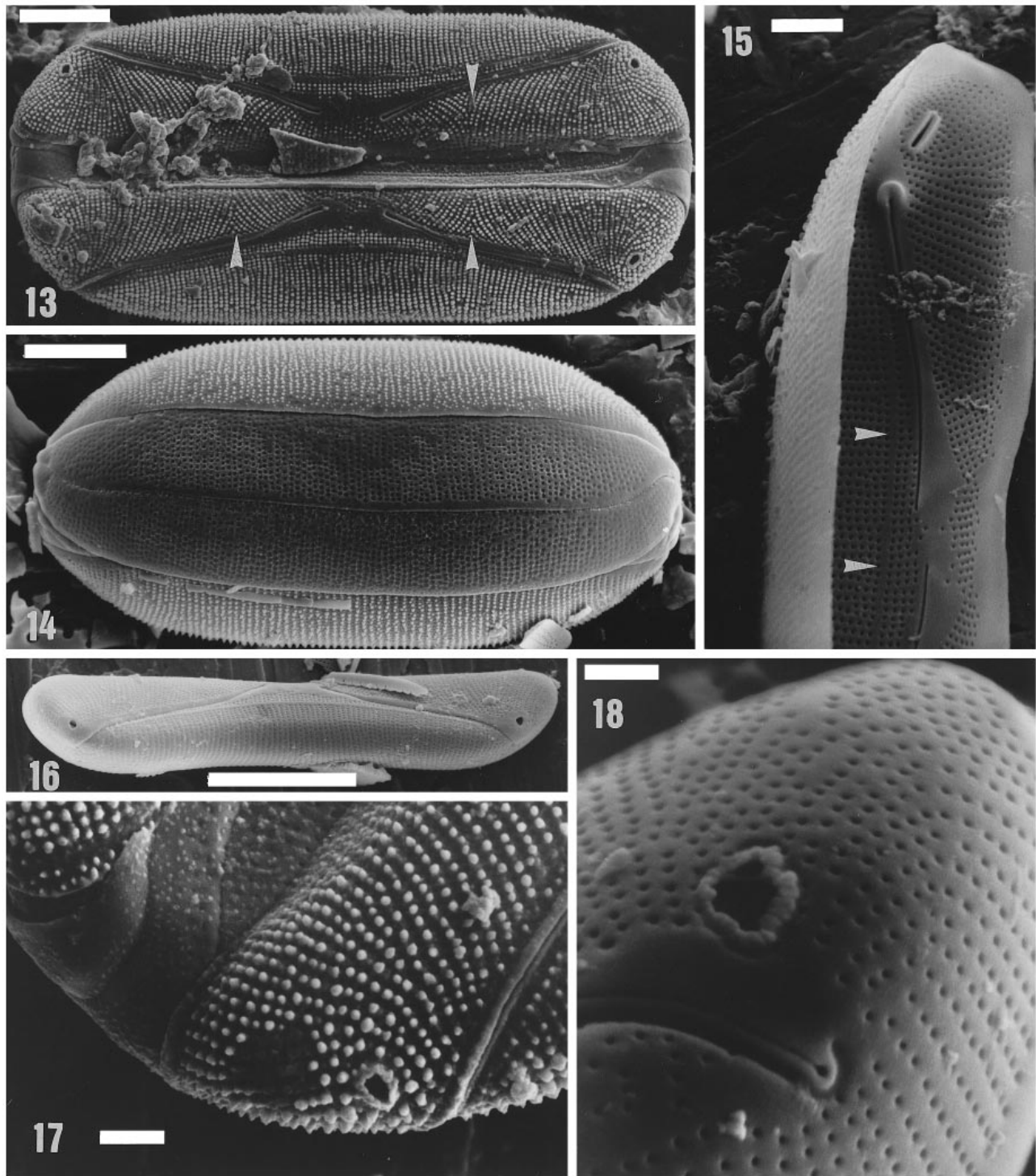


Figs 1–12. Light micrographs of *Eunophora tasmanica* gen. et sp. nov. Figs 1, 2, 4, 12. Ventral views. Figs 3, 6. Dorsal views. Figs 5, 7–11. Valve views. Scale bar represents 10 μm for all figures.

pending on the orientation of the valve); 5–10 μm wide. Exterior of valve smooth or covered in small granules. Sternum distinct. Striae often difficult to resolve with the light microscope, 20–34 in 10 μm , not differing greatly in density between the valve face and dorsal mantle, usually interrupted by a hyaline area between the central raphe endings; on the dorsal side of the raphe, striae parallel in the centre to slightly convergent towards the apices; on the ventral side, striae strongly radiate near the centre and

strongly convergent towards the apices. Raphe biarcuate. Helictoglossae always clearly visible on the ventral side of the valve. Rimoportulae distinct, one at each pole of each valve, ventral to the raphe and hence visible in cells or valves seen in girdle view.

Holotype: TASDIAT slide 18 (Lake Wurrawena, Tasmania), Tasmanian Herbarium, GPO Box 252c, Hobart 7001, Tasmania, Australia.



Figs 13–18. Scanning electron micrographs of *Eunophora tasmanica* gen. et sp. nov. Fig. 13. Ventral view. Note the fault lines (arrowheads) between the radial and convergent ventral striae. Fig. 14. Dorsal view. Fig. 15. Internal valve view; arrowheads indicate the sternum. Fig. 16. External valve view. Fig. 17. Detail of apical valve region, seen ventrally. Fig. 18. External view of terminal raphe fissure and rimoportula opening. Scale bars represent 5 μm in Figs 13 and 14; 2 μm in Fig. 15; 10 μm in Fig. 16; and 1 μm in Figs 17 and 18.

Isotypes: BM slide 99751, The Natural History Museum, Department of Botany, London; BRM slide Zu4/92, Friedrich Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven; TASDIAT slide 18, The Herbarium, University of Gent (GENT).

Type locality: Lake Wurrawena, Denison Range (Universal Grid Reference DN-407901).

The valve face and dorsal mantle are at right angles to

each other but are not sharply differentiated and there is no difference in stria density between them (Fig. 16). In some specimens, the whole exterior of the valves is covered with small, spine-like granules, which form rows between the poroids (Figs 13, 14, 17). Other specimens, however, are smooth (Figs 16, 18). A distinct longitudinal hyaline band is visible near the central raphe endings, dorsal to the raphe, towards the poles. It subtends striae on both sides and seems to be equivalent to the sternum

Table 1. Occurrence of *Eunophora tasmanica*, *E. oberonica*, *E. indistincta* and *Eunophora* sp. 1 in Tasmanian highland lakes and their physico-chemical characteristics

TWINSPAN group ^a	W	W-C	E-C	E
Number of lakes	26	14	11	24
<i>Eunophora tasmanica</i>	24	13	9	7
<i>Eunophora oberonica</i>	21	11	5	6
<i>Eunophora indistincta</i>	4	4	4	2
<i>Eunophora</i> sp. 1	2	11	5	6
Elevation (m.a.s.)	490–1135	725–1185	590–1195	829–1202
Surface area (km ²)	0.001–0.91	0.001–24.4	0.001–2.35	0.001–2.23
Catchment area (km ²)	0.01–7.8	0.01–275.9	0.01–10.1	0.01–33.6
Conductivity (µS cm ⁻¹)	15.5–47.0	11.8–40.0	15.1–42.5	16.1–59.2
pH	3.8–5.9	4.6–6.8	4.3–6.2	5.0–6.6
g ₁₄₀ (m ⁻¹)	1.09–15.20	0.17–3.11	0.17–6.79	0.04–1.87
Sodium (µeq l ⁻¹)	69.6–243.0	48.0–243.5	69.5–287.1	45.5–163.1
Potassium (µeq l ⁻¹)	2.0–23.7	3.0–26.0	1.6–9.6	2.7–23.8
Calcium (µeq l ⁻¹)	5.5–60.7	25.0–90.0	25.0–61.0	20.8–162.3
Magnesium (µeq l ⁻¹)	4.0–115.0	16.0–66.0	16.0–90.5	16.0–177.0
Chloride (µeq l ⁻¹)	51.0–398.0	28.0–304.8	57.5–336.7	38.0–190.4
Alkalinity (µeq l ⁻¹)	0.0–130.0	12.0–143.0	0.0–144.0	0.0–350.0
Sulphate (µeq l ⁻¹)	0.0–32.0	2.0–70.0	0.0–38.5	0.0–31.3

^a Western, Western corridor, Eastern corridor and Eastern lake groups were defined using a TWINSPAN analysis of diatom species composition data of 76 lakes (for a full explanation see Vyverman *et al.*, 1996).

present in *Eunotia* (Mann, 1984), where it usually lies near the junction between ventral mantle and valve face. Towards the poles, the sternum approaches the raphe slits very closely but they are still separated by a single row of poroids (Fig. 15).

The striae consist of small round poroids (Figs 15, 18). On the dorsal side of the valve most striae run unbroken from sternum to margin (Fig. 16). These striae and the shorter striae interposed between sternum and raphe are parallel or slightly convergent (Figs 13, 14, 16); the ventral striae, on the other hand, are strongly radial near the centre and strongly convergent near the poles, with a 'fault line' between opposing series (Figs 13, 15).

The external raphe slits are simple and bordered by narrow hyaline areas, which are more strongly developed on the ventral side. Towards the apices, this ventral part appears to fold over the raphe slits (Fig. 16). A simple sternum continues beyond each helictoglossa and rimoportula opening (Fig. 15). This sternum lies internal to the external terminal fissure, which continues a short distance onto the dorsal mantle (Figs 16–18). Its end is slightly expanded and surrounded by a hooked groove (Fig. 18). Internally, a zone devoid of areolae, corresponding to the terminal fissure, continues towards the dorsal valve margin from the helictoglossa, ending close to the rimoportula (Fig. 15). The external central raphe endings are slightly expanded (Fig. 13). Internally, the asymmetry of the internal central fissures is obvious (Fig. 15). Both internally and externally, the area between the central raphe endings is usually devoid of areolae (Figs 13, 15), although in some specimens isolated puncta or even short rows of puncta are visible.

The external rimoportula openings are circular (Figs 13, 16) and sometimes surrounded by a slightly elevated silica ring (Figs 17, 18). Internally, the rimoportulae are conspicuous, narrow and slit-like (Fig. 15); they lie on the valve face, to the ventral side of the raphe and are therefore more easily seen than the rimoportulae of *E. oberonica* (see below and compare Figs 1 and 5 with Figs 19–25).

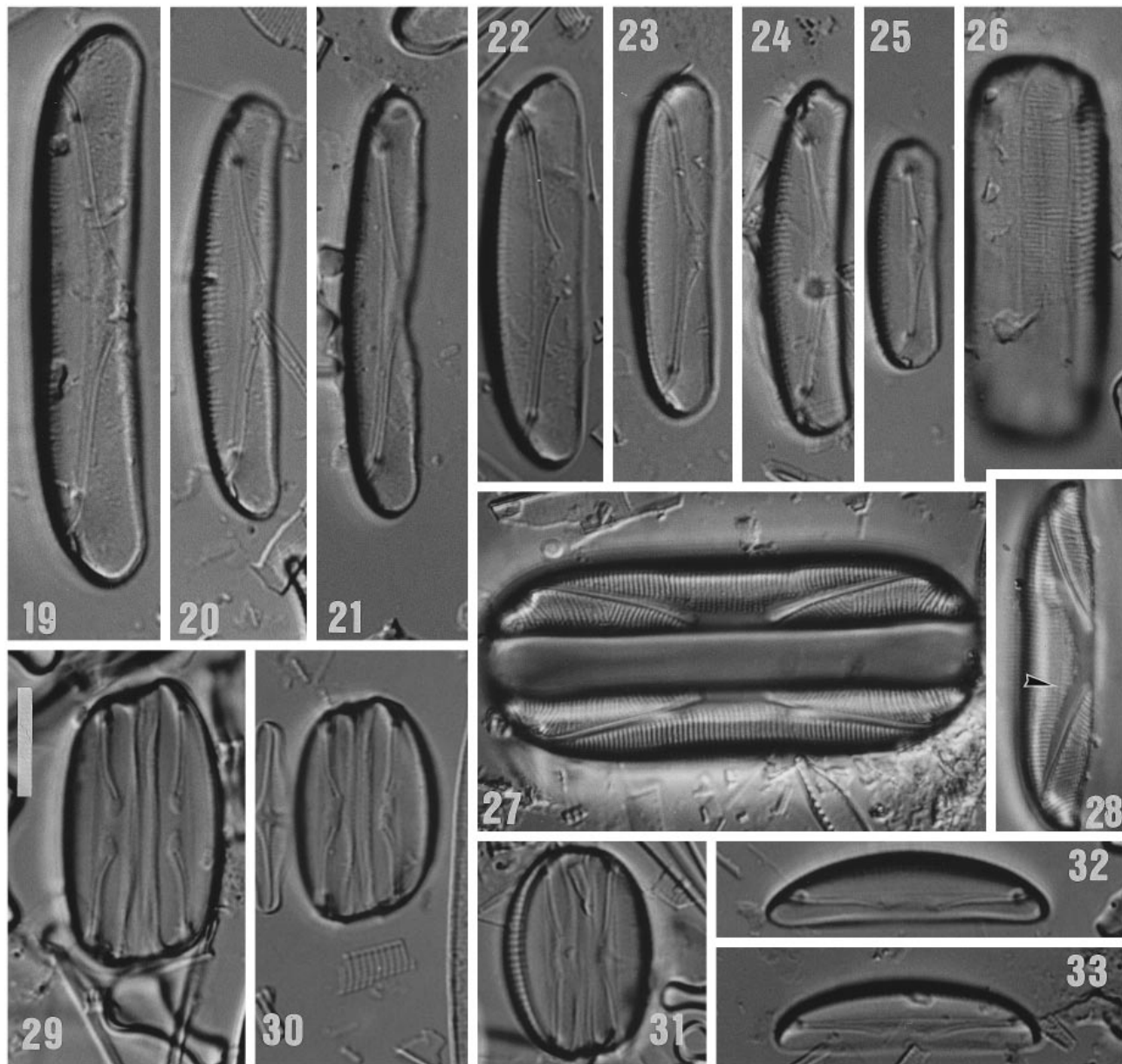
The cingulum consists of at least 5 open, porous copulae (Figs 14, 17), which may bear fine granules externally, resembling those of the valve but smaller (Fig. 17). These are wide on the dorsal side and narrow on the ventral side of the frustules (compare Figs 13 and 14).

Distribution: *Eunophora tasmanica* is the most widespread *Eunophora* species in Tasmania and was found in lakes covering the entire gradient from dystrophic to oligotrophic lakes although it was rare in the easternmost ultra-oligotrophic lakes. It occurred in 63 of the 76 lakes of the TASDIAT training set (Vyverman *et al.*, 1995, 1996) but only rarely in considerable numbers (Table 1, Fig. 50). *E. tasmanica* was not found in the New Zealand material.

Eunophora oberonica R. Vyverman *et* D. Hodgson, sp. nov. (Figs 19–27, 34–40)

Cellulae solitariae valde dorsiventrals, aspectu cincturae late ellipticae ad lineares-ellipticae, 24–56 µm longae, 12–18 µm latae. Structura chromatophorum incognita. Valvae lineares ad fere semiellipticae vel reniformes, extra plerumque rugulosae-reticulatae (appime dorsaliter), aspectu cincturae visae marginibus dorsalibus convexis, marginibus ventralibus aut rectis ad centrum constrictis aut manifeste concavis; 5.3–10.0 µm latae. Striae ventraliter et prope raphem regulares sed per microscopium usitatum non facile detectae, inter extrema centralia raphis non interruptae, 30–34 in 10 µm; in limbo dorsali irregulariores distantiores, circa 13–21 in 10 µm. Sternum manifestum. Raphe biarcuata, fissuris in utroque latere cristis angustis extra limitatis. Helictoglossae in fronte valvae positae semper manifestae. Rimoportulae praesentes, non in fronte sed submarginales in junctura frontis cum limbo dorsali positae, igitur quam in *E. tasmanica* per microscopium usitatum minus manifestae.

Cells solitary, strongly dorsiventral, broadly elliptical to linear elliptical in girdle view, 24–56 µm long, 12–18 µm wide. Plastid structure unknown. Valves linear to almost semi-elliptical or reniform; when seen in girdle view, with concave dorsal margins and broadly rounded apices; ventral margins either straight with a central constriction or distinctly concave; 5.3–10.0 µm wide. Valve exterior usually rugulose-reticulate, especially dorsally. Striae on the ventral side and near the raphe regular but difficult to resolve with the light microscope, not interrupted between the central raphe endings, 30–34 in 10 µm; more irregularly and widely spaced on the dorsal mantle, about 13–21 in 10 µm. Sternum distinct. Raphe biarcuate, the fissures bordered on each side externally by narrow ridges. Helictoglossae always clearly visible on the valve



Figs 19–33. Light micrographs of *Eunophora oberonica*, *E. indistincta* and *Eunophora* sp. 1, gen. et spp. nov. Figs 19–25. *Eunophora oberonica*, valve views. Fig. 26. *E. oberonica*, dorsal view. Figs 27, 28. *Eunophora* sp. 1, complete frustule and valve. Arrowhead in Fig. 28 indicates the narrow dorsal sternum. Figs 29–31. *E. indistincta*, ventral views. Figs 32, 33. *E. indistincta*, valve views. Scale bar represents 10 μm for all figures.

face. Rimoportulae present, located not on the valve face but submarginally, at the junction between valve face and dorsal mantle; they are therefore less distinct with the light microscope than in *E. tasmanica*.

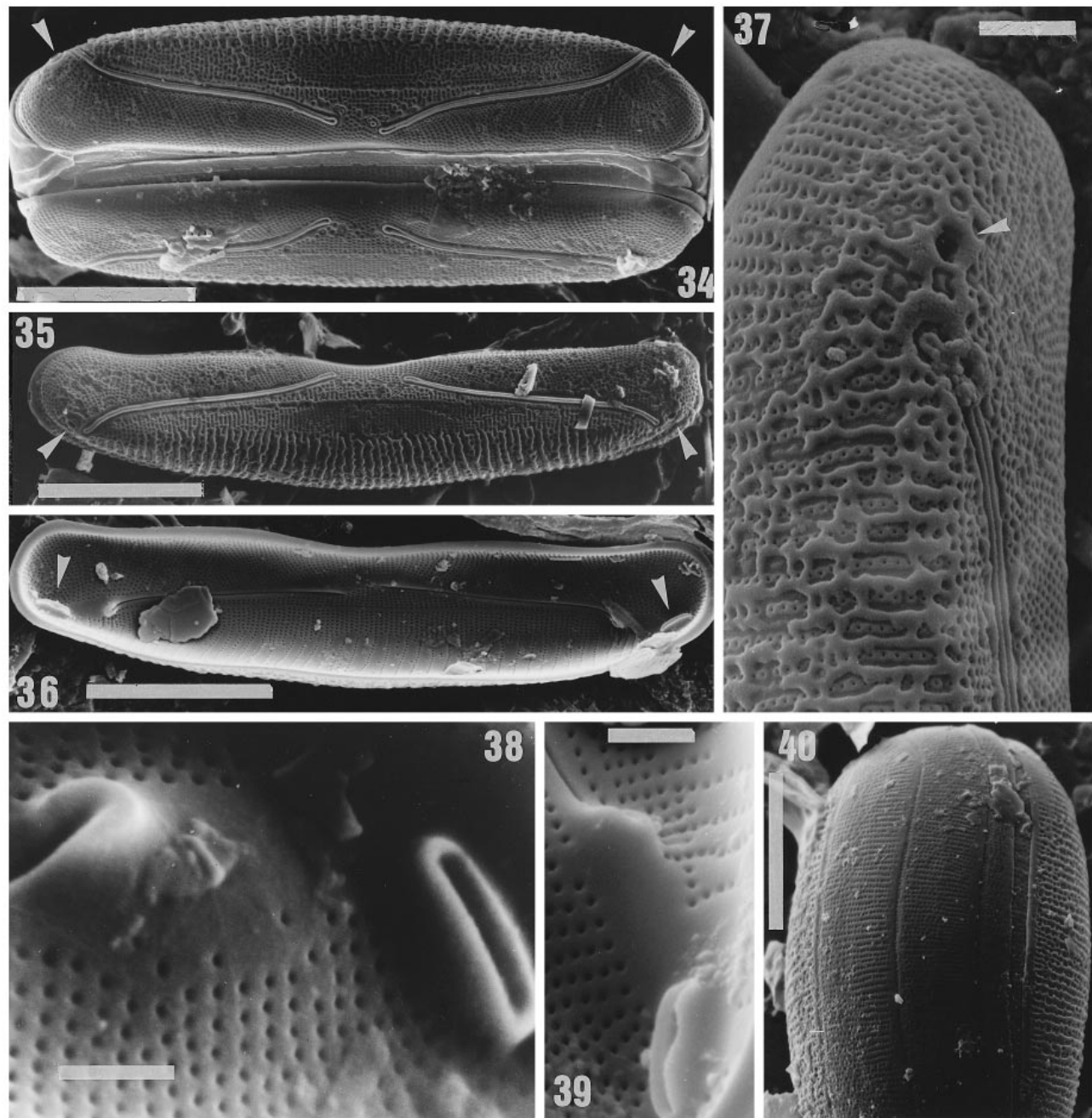
Holotype: TASDIAT slide 9 (Lake Oberon, Tasmania), Tasmanian Herbarium, GPO Box 252c, Hobart 7001, Tasmania, Australia.

Isotypes: BM slide 99752, The Natural History Museum, Department of Botany, London; BRM slide Zu4/93, Friedrich Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven; TASDIAT slide 9, The Herbarium, University of Gent (GENT).

Type locality: Lake Oberon, Western Arthur Range (Universal Grid Reference DN-406223),

The most striking features of this species are the abrupt

change in stria density between the dorsal valve face and mantle (Figs 19–25, 34–36) and the external ornamentation of the valve (Figs 34, 35, 37). Externally, most striae on the dorsal mantle are separated by siliceous ridges (Figs 34, 35, 37, 40), which often extend onto the dorsal part of the valve face. Around the external apertures of the poroids, narrow rings are sometimes present (Fig. 37). On the valve face, fine ridges are present, which anastomose to form a reticulum around the poroids (Figs 34, 35, 37). However, the degree of silicification varies between specimens and ornamentation may be only local on a valve. The sternum is always clearly visible (Figs 34, 35). Towards the poles it is very close to the raphe slits, but they are still separated by striae containing 1 or 2 poroids (Fig. 36 and unpublished observations). The striae contain small round poroids (Figs 38, 39). Areas of radial and



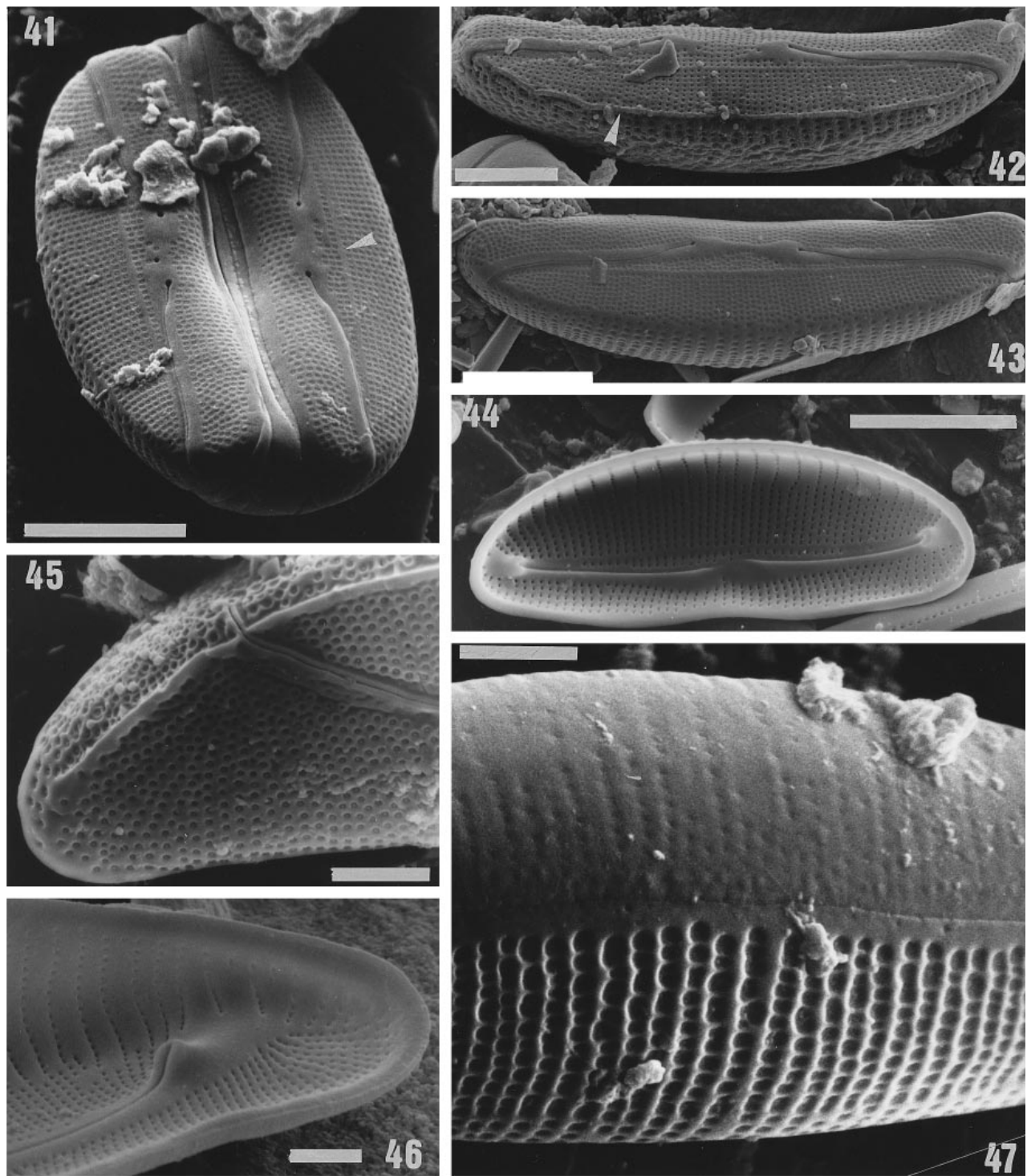
Figs 34–40. Scanning electron micrographs of *Eunophora oberonica* gen. et sp. nov. Fig. 34. Ventral view. Fig. 35. External valve view. Fig. 36. Internal valve view. Fig. 37. Detail of valve apex, seen externally. Fig. 38. Detail of internal valve apex, showing helictoglossa and rimoportula. Fig. 39. As Fig. 38 but in a different orientation. Fig. 40. Dorsal view showing girdle. Arrowheads in Figs 34–37 indicate the rimoportulae. Scale bars represent 10 μm in Figs 34–36, 40; 2 μm in Fig. 37; and 1 μm in Figs 38 and 39.

convergent striae are present as in *E. tasmanica* (Figs 34, 35, 36).

The raphe slit is bordered externally by distinct ribs (Figs 34, 35, 37). The external central raphe endings are slightly expanded (Figs 34, 25). The helictoglossae are clearly visible on the ventral side of the valve (Figs 19–25); beyond the helictoglossa is a straight terminal fissure (Fig. 37), which extends for a shorter distance onto the dorsal mantle than in *E. tasmanica*. Internally the central fissures are simple and non-coaxial, as in other species (Fig. 36). Between the helictoglossa (Fig. 38) and the rimoportula there is a plain area internally, corresponding to the position of the terminal fissure ex-

ternally (Fig. 39). The rimoportulae are similar to those of *E. tasmanica*, but are located somewhat more dorsally and more in line with the raphe (Figs 36, 39); the external apertures are smaller and more difficult to detect than in *E. tasmanica*. Unlike in *E. tasmanica*, striae are present between the central raphe endings (Figs 34, 35, 36). The cingulum consists of 5 open, curved and porous copulae (Fig. 40), which are much wider dorsally than ventrally, as in other *Eunophora* species.

Eunophora oberonica differs from the other species with rimoportulae, *E. tasmanica*, in the shape of the apices, which are always broadly rounded; the presence of anastomosing siliceous ridges and ringed poroids ex-

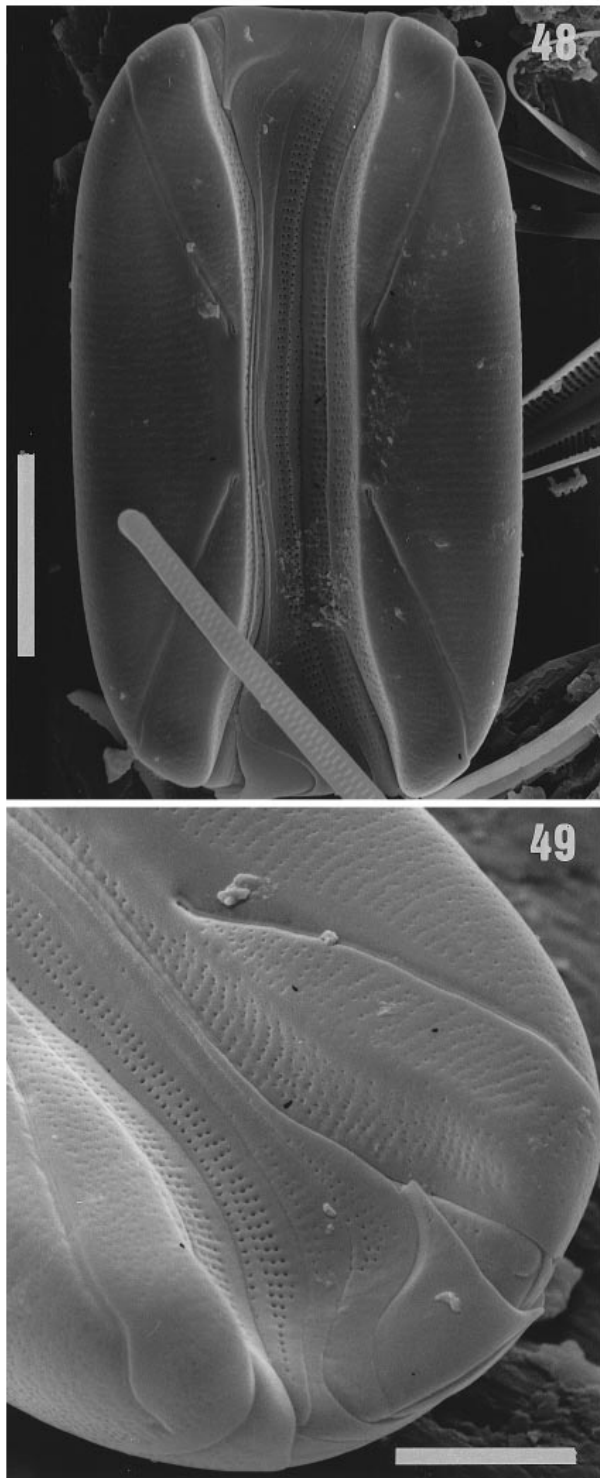


Figs 41–47. Scanning electron micrographs of *Eumophora indistincta* gen. et sp. nov. Fig. 41. Oblique ventral view (arrowhead indicates the narrow sternum). Figs 42, 43. External valve views. Fig. 42 shows a specimen with a marginal ridge (arrowhead) and with striae continuous between the proximal raphe fissures, Fig. 43 is a specimen without marginal ridge and with striae interrupted between the proximal raphe fissures. Fig. 44. Internal valve view showing striation pattern, sternum and raphe structure. Fig. 45. Detail of apical region and position of terminal raphe fissure. Fig. 46. Detail of internal valve apex showing stria structure and helictoglossum. Fig. 47. Detail of dorsal region (mid-valve) showing girdle and dorsal striae. Scale bars represent 5 μm in Figs 41–44, and 2 μm in Figs 45–47.

ternally; the position of the rimoportula; the length of the terminal fissures; and the constant presence of striae between the central raphe endings.

Distribution: In Tasmania, *Eumophora oberonica* has a much narrower distribution than *E. tasmanica* and is mainly restricted to the dystrophic western lakes and the lakes

along the limnological corridor (Vyverman *et al.*, 1995, 1996). It never occurred in high relative abundances in the less acid lakes; in humic lakes, however, it was more abundant. In Lake Oberon, one of the typical highly humic lakes in the south-west of Tasmania, it was one of the most important species (11.3%) in a low-diversity diatom assemblage dominated by *Eumotia* spp. and *Actinella* spp. In



Figs 48, 49. Scanning electron micrographs of *Eunophora* sp. 1. Fig. 48. Ventral view. Fig. 49. Detail of apical region, seen in ventral view. Scale bars represent 10 μm in Fig. 48, and 5 μm in Fig. 49.

New Zealand only empty valves were found in Table Hill Stream, a small acid-water stream (conductivity ca. 70 $\mu\text{S cm}^{-1}$) on Stewart Island. A single frustule was present in a sample from a small tarn located in alpine bogs on Kelly Pass (Arthur's Pass National Park, South Island).

Eunophora indistincta R. Vyverman *et* D. G. Mann, sp. nov. (Figs 29–33, 41–47, 54)

Cellulae solitariae, valde dorsiventrals, aspectu cincturae late ellipticae saepe asymmetrcae vel aliquantum heteropolares, 17–21 μm longae, 14–17 μm latae. Chromatophora breve taeniata, probabiliter quatuor. Valvae semiellipticae limbo dorsali extra laeves vel parum rugulosae-reticulatae, apicibus oblique cuneatis, marginibus ventralibus rectis vel ad centrum leviter constrictis. Striae per microscopium usitatum non facile detectae, 40–43 in 10 μm , praeter in limbo dorsali ubi distantiores, circa 27–32 in 10 μm . Raphe ad marginem ventralem fere parallela. Helictoglossae in parte ventrali frontis valvae prope polos manifestae. Rimoportulae nullae.

Cells solitary, strongly dorsiventral, broadly elliptical and often asymmetrical or heteropolar in girdle view, 17–21 μm long, 14–17 μm wide. Plastids short, band-like, probably 4. Valves semi-elliptical, with obliquely cuneate apices, 5.2–6.0 μm wide; the ventral margins straight or slightly constricted at the centre. Exterior of valve smooth or with the dorsal mantle slightly rugulose-reticulate. Striae difficult to resolve with the light microscope, 40–43 in 10 μm , except on the dorsal mantle, where they are more widely spaced, about 27–32 in 10 μm . Raphe almost parallel to the ventral margin. Helictoglossae visible close to the pole on the ventral part of the valve face. Rimoportulae absent.

Holotype: TASDIAT slide 24 (Lake Rodway, Tasmania), Tasmanian Herbarium, GPO Box 252c, Hobart 7001, Tasmania, Australia.

Isotypes: BM slide 99753, The Natural History Museum, Department of Botany, London; BRM slide Zu4/94, Friedrich Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven; TASDIAT slide 24, The Herbarium, University of Gent (GENT).

Type locality: Lake Rodway (Universal Grid Reference DP-135883).

This is the smallest and most delicately structured of the *Eunophora* species known so far. The valves are frequently asymmetrical about the median transapical plane and the girdle is sometimes oblique to the apical axis. As in *E. tasmanica* and *E. oberonica*, the valve face and mantle are at right angles; the transition between them is usually gentle, but in some valves there is a marginal ridge (Figs 42, 45). The valve exterior is smooth on the valve face (Figs 41, 43) and either smooth or slightly ridged or reticulate on the dorsal mantle (Figs 42, 45, 47). A narrow but distinct sternum is present (Fig. 41), becoming closer to the raphe slits near the apices and finally combining with them (Figs 41–44). The striae change in density at the junction of valve face and dorsal mantle (Figs 42–44, 46), as in *E. oberonica*; the poroids also become more widely spaced (Figs 42, 43, 46). The stria pattern on the ventral side of the raphe is more regular and parallel than in other *Eunophora* species (Figs 41, 43, 44). The poroids are circular and are occluded by vela close to their external apertures (Figs 41, 43, 45).

At the centre, the raphe slits curve towards the ventral

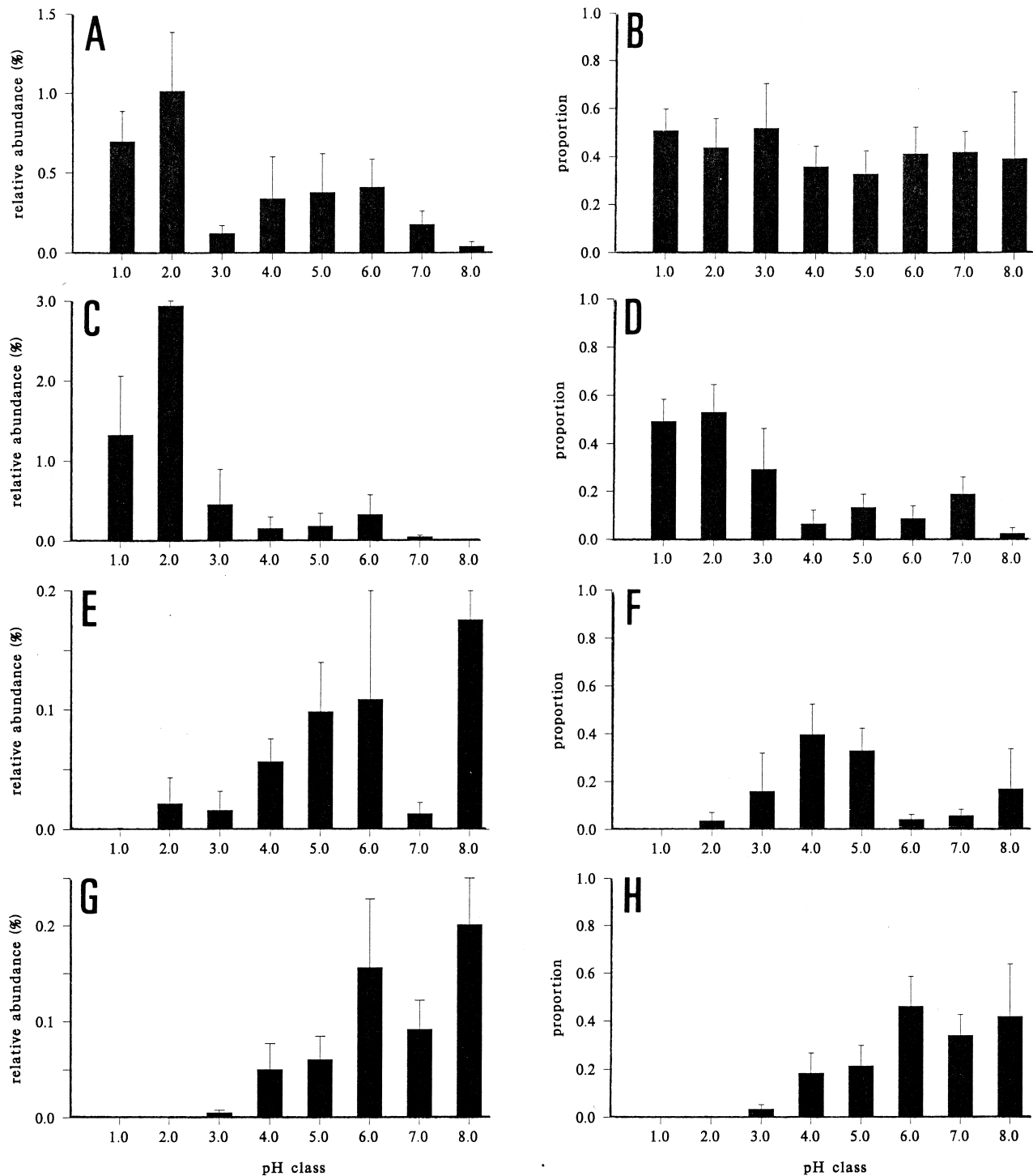
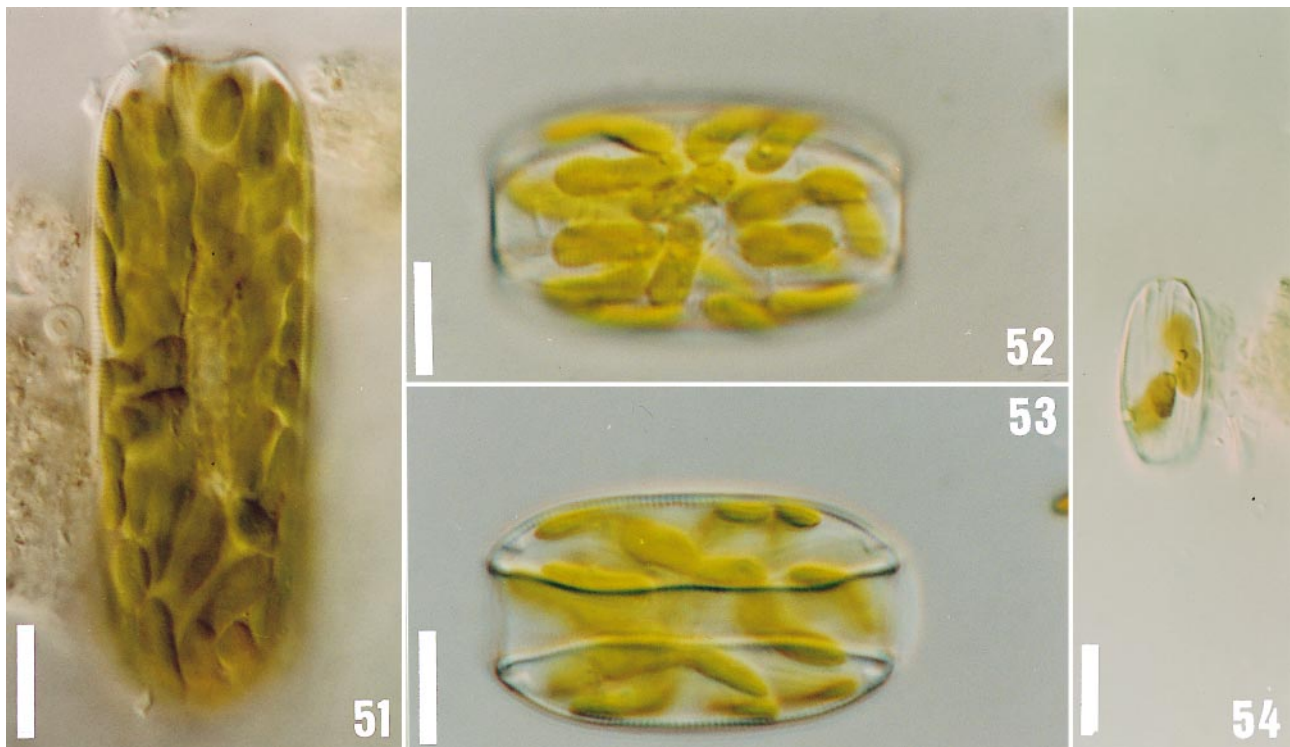


Fig. 50. Distribution of *Eunophora tasmanica* (A, B), *E. oberonica* (C, D), *E. indistincta* (E, F) and *Eunophora* sp. 1 (G, H) in relation to lakewater pH in the TASDIAT training set of Tasmanian highland lakes (Vyverman *et al.*, 1995, 1996). Figs A, C, E, G: mean relative abundance (with one-sided error bars) of *Eunophora* spp. in the total diatom assemblage of the lakes; Figs B, D, F, H: mean proportion of the *Eunophora* spp. expressed as their respective relative abundance based on a separate count of 30–50 specimens of all *Eunophora* spp. occurring in a particular lake. pH classes are: 1, 4.0–4.40; 2, 4.41–4.8; 3, 4.81–5.2; 4, 5.21–5.6; 5, 5.61–6.0; 6, 6.01–6.4; 7, 6.41–6.8; 8, 6.81–7.2.

margin, whereas near the poles they curve towards the dorsal margin and end on the dorsal mantle (Figs 42, 43, 45). Externally, the central raphe endings are always distinctly expanded and pore-like (Figs 41–43). Internally, the central fissures are simple and non-coaxial, as in the other species (Fig. 44). The internal raphe fissures end at the poles in a distinct helictoglossa (Fig. 46), beyond which there is a plain strip of silica, marking the external

course of the terminal fissure (Figs 44, 46). The raphe slits are flanked by hyaline areas, which are mainly developed on the ventral side. Towards the poles, these hyaline areas fold over the raphe slit as in *E. tasmanica*. The central raphe endings usually lie in a more or less apically expanded and often externally thickened hyaline area (Figs 42, 43). In some specimens these two areas merge and interrupt the striae in between the central raphe endings (Figs 41, 43).



Figs 51–54. Light micrographs of living cells of *Eunophora* sp. 1 and *E. indistincta*. Fig. 51. *Eunophora* sp. 1, Tasmania. Figs 52, 53. *Eunophora* sp. 1, dorsal and ventral views of the frustule, Stewart Island, New Zealand. Fig. 54. *E. indistincta*, Tasmania. Scale bars represent 10 μm for all figs.

The areolae are occluded by vela, which lie close to the valve exterior. None of the specimens that we observed possessed rimoportulae. The cingulum consists of at least 4 open, curved copulae. These are perforated by indistinct transverse rows of puncta (Fig. 47); in one specimen, only randomly placed puncta were visible on the inner side of the copulae (not illustrated). Plastids were only observed in some specimens (Fig. 54); they are less numerous than in *Eunophora* sp. 1 (cf. below).

Distribution: *E. indistincta* is less common than the other species. It occurred along most of the dystrophic-oligotrophic gradient except for the most dystrophic lake types. Its highest relative abundances were found in lakes along the limnological corridor (Table 1, Fig. 50). *E. indistincta* was not found in the New Zealand material.

Eunophora sp. 1 (Figs 27, 28, 48, 49, 51–53)

Eunophora sp. 1 (Vyverman *et al.*, 1995) is the largest, most heavily silicified and most coarsely structured of *Eunophora* species. Frustules and a valve are shown in Figs 27 and 28 and also in Figs 48 and 49 (cf. also Vyverman *et al.*, 1995, pl. 35, figs 5–7); a full description will be given in a forthcoming paper.

In most respects, valve, raphe and girdle structure are like those of the other three species. Two differences, however, are the presence of a very distinct ventral mantle (Fig. 49) and the fact that a sternum is very difficult to detect (Figs 48, 49), although one is present (it is just visible in Fig. 28 and in Vyverman *et al.*, 1995, pl. 35, fig. 7). As in *E. indistincta* rimoportulae are absent, but there is

little other similarity between these species: the raphe system of *Eunophora* sp. 1 is strongly biarcuate (Fig. 48), the central raphe endings are always linked by a heavily silicified hyaline area (even in long, post-initial cells, where the raphe slits are separated by about a third of the valve length), and the ventral striae are not parallel but either irregular (Fig. 49) or organized into opposing series of radial and convergent striae (Vyverman *et al.*, 1995, pl. 35, fig. 7), as in *E. tasmanica* (Figs 13, 15) or *E. oberonica* (Figs 34, 36). The poroids are small relative to the ribs separating the striae (Figs 48, 49) and in the centre of the valve and near the helictoglossae they open internally into deep grooves between the transapical ribs (interstriae). The girdle bands are open and porous, as in other *Eunophora* species (Figs 48, 49). *Eunophora* sp. 1 has numerous band-like to discoid, parietal plastids, most of which are positioned against the dorsal girdle (Figs 51–53). Note that the exact number of plastids can be quite variable.

Distribution: This species occurs in New Zealand and is common in eastern lakes and in lakes along the limnological corridor, where it often occurred together with another undescribed amphoroid diatom, *Amphora* sp. 1 (Vyverman *et al.*, 1995). *Eunophora* sp. 1 was absent in highly dystrophic lakes (Table 1, Fig. 50).

Discussion

Within the raphid pennate diatoms, which constitute the class Bacillariophyceae, two subclasses are currently recognized: the Eunotiophycidae and the Bacillariophycidae.

The main diagnostic difference between them is the absolute absence of rimoportulae in the Bacillariophycidae and the simple structure of the raphe in the Eunotiophycidae (Round *et al.*, 1990). In addition, the raphe is fully integrated into the pattern centre in the Bacillariophycidae, but not in the Eunotiophycidae. In *Eunotia* the short raphe slits are clearly separate from the sternum (pseudoraphe) and subtend their own set of striae, which are usually more closely spaced than the striae subtended by the sternum (for example, see the illustrations of Kobayasi *et al.*, 1981; Mann, 1984; Krammer & Lange-Bertalot, 1991; Lange-Bertalot, 1993; Round *et al.*, 1990). *Actinella* is similar (Hasle, 1973; Round *et al.*, 1990). In *Peronia*, the raphe slits lie along the midline of the valve, like the sternum, but integration between raphe and sternum is apparently incomplete, since the raphe slits still subtend their own, separate set of more closely or irregularly spaced striae (for *P. fibula* (Brébisson *ex* Kützing) R. Ross, see Hasle, 1973; Round *et al.*, 1990; Simonsen's 1987 micrographs of type material show this to be true also of *P. brasiliensis* Hustedt, although Hustedt's original 1952 drawings do not) (Table 2).

The presence of rimoportulae in some *Eunophora* species (*E. tasmanica* and *E. oberonica*), the generally simple structure of the raphe and the lack of integration between raphe and sternum (the sternum is difficult to discern in *Eunophora* sp. 1, but light micrographs show that its relation to the raphe slits is as in other *Eunophora* species, cf. Figs 27, 28) indicate clearly that *Eunophora* belongs in the Eunotiophycidae. Within this group it is most similar to *Eunotia* and *Desmogonium* (if this is kept separate from *Eunotia*), with which it shares isovalvy, symmetry of valve outline about the median transapical plane, and raphe slits that are clearly separate from the sternum (Krammer & Lange-Bertalot (1991) refer to this as the axial area), at least towards the centre of the valve. By contrast, *Actinella* and *Peronia* are heteropolar: their frustules are wider and deeper at one end, and there can also be differences between the poles in shape or structure (Hasle, 1973; Round *et al.*, 1990). In addition, *P. fibula* exhibits heterovalvy: one valve has two well-developed raphe slits and two rimoportulae, while the other has a very short raphe slit and a rimoportula at one pole (the narrower pole) and nothing at the other (Hasle, 1973; Round *et al.*, 1990). In *Semiorbis*, which is sometimes combined with *Eunotia* (by Morrow *et al.*, 1981; Krammer & Lange-Bertalot, 1991), the raphe slits are very short and the position of the sternum is unclear (Moss *et al.*, 1978). We will now concentrate our discussion on the relationship between *Eunophora* and *Eunotia*.

Eunophora indistincta has 4 plastids per cell, while *Eunophora* sp. 1 is polyplastidic. In the latter species the plastids are apparently distributed around the cell periphery, but mainly against the dorsal girdle. In *Eunotia* there are usually 2 chloroplasts per cell, 1 against each valve, with their margins extending well beneath the girdle on the ventral side, but much less far on the dorsal side (early literature summarized by Heinzerling, 1908;

Geitler, 1951a–c). *Eunotia pectinalis* var. *polyplastidica* Geitler, *E. multiplastidica* Mayama and *E. robusta* var. *tetraodon* (Ehrenberg) Ralfs (= *E. serra* var. *tetraodon* (Ehrenberg) Nörpel according to Krammer & Lange-Bertalot, 1991) are exceptions, however, all normally possessing at least 8 chloroplasts per cell during interphase (see Geitler, 1959; Geitler, 1973a; Mayama, 1992). However, the first two of these are more aptly described as oligoplastidic (Mann, 1996), since the chloroplast number is relatively small and determinate. *E. robusta* var. *tetraodon*, on the other hand, is polyplastidic like *Eunophora*, with 40–50 small discoid chloroplasts distributed around the whole of the cell periphery (Geitler, 1959). No other features of *Eunotia robusta* var. *tetraodon* suggest a link with *Eunophora*, however, and we believe that this is an instance of parallel evolution.

All *Eunophora* species have a deep dorsal mantle and either no ventral mantle (*E. indistincta*) or a very shallow one (most strongly developed in *Eunophora* sp. 1). The girdle is likewise much wider on the dorsal side. These features cause the cells to resemble *Amphora* species and towards the end of the cell cycle, when the cells are fully expanded, the valve faces lie almost in the same plane (Figs 13, 34, 41). In *Eunotia*, on the other hand, although the frustules are strongly dorsiventral, the girdle and valve mantles are almost equally developed on either side and the valve faces are therefore parallel (e.g. Round *et al.*, 1990; Mayama & Kobayasi, 1991). The valve faces are at a slight angle to each other in *E. catillifera* Morrow, but apparently only in smaller cells, produced towards the end of size reduction (Morrow *et al.*, 1981).

The raphe slits are longer in *Eunophora* than in most *Eunotia* species and are scarcely shorter than in many Bacillariophycidae. Indeed, the solid areas of silica surrounding the raphe slits fuse at the centre of the valve to form a 'central nodule' in some valves of *E. indistincta* and *E. tasmanica* and in all valves of *Eunophora* sp. 1. Only in *E. oberonica* are the raphe slits consistently separated by striae as in *Eunotia*. A further curious feature of the *Eunophora* raphe is the arrangement of the central internal raphe endings, which are non-coaxial and deflected in opposite directions. There is no equivalent deflection in *Eunotia*. The deflection of the internal raphe endings is accompanied by a less obvious but constant asymmetry of the raphe slits themselves – one is consistently slightly closer to the ventral margin than the other. Again, published micrographs give no indication that anything similar occurs in *Eunotia* (e.g. Lange-Bertalot, 1993, pls 17, 21). Non-coaxial internal raphe endings are known outside the Eunotiophycidae in *Hantzschia* Grunow (Mann, 1977, 1981) and most genera of the Achnanthes (including *Achnantheidium* Kützing, *Cocconeis* Ehrenberg, *Anorthoneis* Grunow and *Campyloneis* Grunow), but not in the Achnanthesaceae Kützing (i.e. in *Achnanthes* Bory *sensu stricto*: see Lange-Bertalot & Krammer, 1989; Round *et al.*, 1990). In all these taxa the deflection is in the same direction. Viewed from the inside of the valve, the raphe endings are displaced in an anticlockwise direction. In the

Table 2. Morphological and cytological characteristics of the genera of the Eunotiophycidae and some amphoroid taxa belonging to the Bacillariophycidae

Character	Eunotiophycidae				Bacillariophycidae	
	<i>Peronia</i>	<i>Semiorbis</i>	<i>Actinella</i>	<i>Eunotia</i>	<i>Amphora</i> s.s.	<i>Psammamphora</i> / <i>Anthlyamphora</i>
Valve outline	Asymmetric about median apical and transapical plane	Symmetric about median transapical plane	Asymmetric about median apical and transapical plane	Symmetric about median transapical plane	Symmetric about median transapical plane	Symmetric about median transapical plane
Mantle	Dorsal and ventral mantle of equal width	Dorsal and ventral mantle of equal width	Dorsal and ventral mantle of equal width	Deep dorsal mantle, very shallow or no ventral mantle	Deep dorsal mantle, very shallow or no ventral mantle	Deep dorsal mantle, very shallow or no ventral mantle
Marginal spines	Present	Present	Present	Absent	Absent	Absent
Rimoportulae	R-valve: at each pole, between the helictoglossa and apex; P-valve: lying at the base pole	Absent	Present, 2 per valve in <i>A. punctata</i> ; absent in <i>Actinella</i> sp. (Tasmania)	Present (2 species). 1 at each pole; absent in <i>E. indistincta</i> and <i>Eunophora</i> sp. 1	Absent	Absent
Number of plastids	2	Unknown	2 (<i>A. tasmanica</i>)	Polyplastidic	1, ventral, with lobes extending dorsally	1 or 2 large, plate-like
Position of raphe	± central	At the poles on the ventral (concave) side, terminal fissures turning across the valve face and ending on the convex side	At the poles on the ventral side, terminal fissures on the valve face	On the valve face, biarcuate and extending onto the dorsal mantle	On the valve face, biarcuate and extending onto the dorsal mantle	On the valve face, biarcuate and extending onto the dorsal mantle
Integration of raphe	Raphe incompletely separate from sternum	Position of sternum unclear	Raphe separate from sternum	Raphe largely separate from sternum	Raphe fully integrated in the primary pattern-centre (raphe-sternum)	Raphe fully integrated in the primary pattern-centre (raphe-sternum)
Raphe slits	R-valve: long, occupying two-thirds of the valve length; P-valve: very short, often missing at the head pole	Very short	Short	Usually long, sometimes forming a 'central nodule', shorter in <i>E. oberonica</i>	Long, forming a central nodule	Long, forming a central nodule
External raphe fissures	Simple, terminal fissures lacking; central endings expanded and curved slightly to one end	Bordered by rims of silica	A simple groove	A simple groove or bordered by rims of silica	A simple groove	A simple groove
Central internal raphe endings	Coaxial, not deflected(?)	Coaxial, not deflected(?)	Coaxial, not deflected	Non-coaxial, deflected in opposite directions	Coaxial, not deflected	Coaxial, not deflected

green algae, such dissymmetries have been found to be significant (e.g. in basal components of flagella), being constant within major lineages. Thus, a clockwise (1 o'clock to 7 o'clock) displacement of the basal bodies is characteristic of the Chlorophyceae *sensu stricto* (Sluiman, 1992). Whether the displacement of the raphe endings in *Eunophora*, *Hantzschia* and the Achnanthes has any phylogenetic significance, reflecting true homology, seems unlikely but cannot yet be ruled out. There are many other examples of dissymmetry and chirality in diatoms, such as the placing of the single rimoportula in many *Eunotia* species (see below), the pattern of segregation of the volutin granules in *Sellaphora* Mereschkowsky (Mann, 1985) and the clockwise rotation of the chloroplast pair in recently divided cells of *Navicula radiosa* Kützing (Rudzki, 1964).

The four known *Eunophora* species have either 2 rimoportulae per valve (*E. tasmanica*, *E. oberonica*) or none (*E. indistincta*, *Eunophora* sp. 1). Where present, the rimoportulae are like those in other Eunotiophycidae, lacking stalks internally and opening to the exterior by a simple pore. However, the external pores are larger and more obvious than in *Eunotia* and more similar to those of *Peronia fibula* (Hasle, 1973; Round *et al.*, 1990).

Most *Eunotia* species have only 1 rimoportula per valve, which occupies the same position as 1 of the 2 rimoportulae of *Eunophora*, lying just beyond the helictoglossa or near the dorsal margin near one of the poles (Hasle, 1973; Kobayasi *et al.*, 1981; Round *et al.*, 1990; Krammer & Lange-Bertalot, 1991). The single rimoportula always lies at the same end of the valve (except perhaps in *Eunotia exigua* (Brébisson *ex* Kützing) Rabenhorst: see below). Thus, if the valve is seen from the inside, with the dorsal side to the left, the rimoportula will be found towards the top (see, for example, Krammer & Lange-Bertalot, 1991, pl. 139, figs 4, 7, pl. 145, fig. 4; Alles *et al.*, 1991, taf. IV, fig. 36, taf. V, fig. 11; Mayama, 1992, figs 22, 25–28). This means that in a complete frustule the rimoportulae of the 2 valves lie at opposite poles (Moss *et al.*, 1978; Mayama & Kobayasi, 1991). According to Krammer & Lange-Bertalot (1991), however, the rimoportulae always lie at the broader pole of the valve in heteropolar frustules of *E. exigua*; this needs to be checked, since if it is so the rimoportulae would both lie at the same pole and the frustules would show mirror symmetry with respect to the median valvar plane, instead of diagonal symmetry.

Eunotia triodon Ehrenberg and *Eunotia catillifera* Morrow lack rimoportulae altogether (Hustedt, 1926; Krammer & Lange-Bertalot, 1991; Morrow *et al.*, 1981), as does *Semiorbis hemicyclus* (Ehrenberg) Patrick (Moss *et al.*, 1978), which Morrow *et al.* (1981) believe on other grounds to be closely related to *E. catillifera*. *Eunotia triodon* does not resemble *Eunophora indistincta* or *Eunophora* sp. 1 in any other respect and it seems most likely that the absence of rimoportulae in some *Eunotia* and some *Eunophora* species represents parallel losses on at least two occasions. In any case, the absence of rimoportulae is probably a derived character state within the Eunotiophycidae, given their

presence in araphid pennate and centric diatoms and most Eunotiophycidae.

According to Lange-Bertalot (1993, p. 202: legend to figs 6–8), there are 2 rimoportulae per valve in '*Eunotia* sect. *Desmogonium*', as in *Eunophora tasmanica* and *E. oberonica*. Unfortunately, Lange-Bertalot gives no description of sect. *Desmogonium*, which is often treated as a separate genus (most recently by Patrick & Reimer (1966) and Round *et al.* (1990, p. 128)), nor does he list the species that belong to it. Hustedt (1926) found that there are two rimoportulae ('Gallertporen') per valve in *Desmogonium guianense* Ehrenberg and this has also been established for *D. rabenhorstianum* Grunow (Hustedt in Schmidt *et al.*, 1874–1959) and *D. femoriforme* Patrick (Patrick, 1940). *Desmogonium* is also supposed to be characterized by the possession of small spines along both margins of the valve and by the ability to form zig-zag filaments (Patrick & Reimer, 1966). Among species that have only ever been classified in *Eunotia*, not *Desmogonium*, there are some in which there are 2 rimoportulae per valve. These include *E. pseudoflexuosa* Hustedt (Hustedt, 1949), *E. theronii* Cholnoky (Cholnoky, 1959, fig. 151) and *E. nipponica* Skvortzow (Kobayasi *et al.*, 1981). *E. nipponica* and *E. theronii* also resemble *Desmogonium* species in having a row of spines around the valve face (Kobayasi *et al.*, 1981; Cholnoky, 1954, 1959), but whether they form zig-zag filaments is unknown. Two other taxa with 2 rimoportulae per valve, *Actinella punctata* Lewis and *Peronia fibula* (Hasle, 1973; Round *et al.*, 1990; in *Peronia*, 2 rimoportulae occur only in the R valve), also have spines like those found in *Desmogonium* species and *Eunotia nipponica*. At present, we cannot identify a likely outgroup for the Eunotiophycidae (presumably among the many lineages of araphid pennate diatoms, as suggested by Simonsen, 1979) and so it is impossible to judge whether the primitive (plesiomorphic) character state is 2 rimoportulae per valve, as in *Eunophora*, or only 1, nor whether spininess is ancestral or derived.

The external raphe fissures of *Eunophora oberonica*, and to a lesser extent those of *E. tasmanica*, are bordered by distinct rims of silica. This is rare in the Eunotiophycidae. A hint of a rim is present in *Eunotia praerupta* Ehrenberg (Lange-Bertalot, 1993, pl. 26, fig. 4), but in other *Eunotia* species the external fissure is a simple groove (e.g. Kobayasi *et al.*, 1981; Round *et al.*, 1990; Krammer & Lange-Bertalot, 1991; Mayama & Kobayasi, 1991; Lange-Bertalot, 1993).

Eunophora bears a striking resemblance in the light microscope to the biraphid genus *Amphora* Ehrenberg *ex* Kützing *sensu lato*, which is in need of revision as it comprises several amphoroid but not closely interrelated genera (Mann, 1994). *Eunophora* most closely resembles species of Cleve's subgenera *Psammamphora* and *Amblyamphora*, which are characterized by their fine striae, unbroken by longitudinal ridges or areas, biarcuate raphe and \pm rectangular shape in girdle view (Table 2). We have examined the following species belonging to these subgenera: the marine species *A. obtusa* Gregory, *A. arenaria* Donkin, *A. spectabilis* Gregory, *A. cingulata* Cleve

and *A. latecingulata* M. Peragallo and the freshwater taxa *A. delphinea* Bailey and *Amphora* sp. 1 of Vyverman *et al.* (1995), an apparently new species from Tasmania and New Zealand (W. Vyverman & C. Kilroy, unpublished observations). All lack rimoportulae (e.g. Round *et al.*, 1990, p. 603, fig. s) and have a raphe that is fully integrated into the primary pattern-centre, in a raphe-sternum (for definitions see Mann, 1984). The dorsal striae are not interrupted by a longitudinal hyaline area (Round *et al.*, 1990, p. 602, fig. r), unlike some *Amphora sensu stricto* (such as *A. ovalis* (Kützing) Kützing and its relatives; cf. Table 2 and Krammer, 1980). At first sight, the presence of a dorsal sternum in *Eunophora* and *Amphora s.s.* suggests that their valves might be formed in the same way and that, consequently, these genera could be phylogenetically close. However, we think it is unlikely that the dorsal sterna are homologous in *Eunophora* and *Amphora s.s.* In *Eunophora* and other representatives of the Eunotiophycidae, the striae on opposite sides of the sternum can have slightly different densities and may be out of phase (cf. our Figs. 16, 41 and Round *et al.*, 1990, p. 459, fig. i), while this is never the case in *Amphora s.s.* (e.g. Krammer, 1980; Round & Lee, 1989). In this respect the sternum in the Eunotiophycidae is reminiscent of that in araphid diatoms (e.g. Round *et al.*, 1990, p. 351, fig. g and p. 361, fig. k), acting as a true pattern-centre. Externally, the raphe slits approach each other symmetrically (Round *et al.*, 1990, p. 361, figs o, p) in the *Psammamphora*/*Amblyamphora* group, while internally the central raphe endings are hidden in some species by an overgrowth of silica extending across from the ventral side (Round *et al.*, 1990, p. 361, figs q, r). We have been unable to detect any hint of offset, non-coaxial structure within the raphe in this group; the illustrations of *A. delphinea*, *A. obtusa*, *A. arenaria* and *A. ocellata* by Schoeman & Archibald (1984, 1986, 1987) confirm this. Furthermore, marine *Psammamphora* and *Amblyamphora* species usually possess 1 or 2 large, plate-like chloroplasts per cell, which lie against the dorsal side of the girdle, with the nucleus nearer the ventral side (Mereschkowsky, 1903; D. G. Mann, unpublished observations). The same arrangement is found in the freshwater species we have found in Tasmania and New Zealand and in *Amphora delphinea* (D. G. Mann, unpublished observations).

In all these respects the *Psammamphora*/*Amblyamphora* groups differs from *Eunophora*, where rimoportulae are present in two species, the raphe slits are not fully integrated into the pattern-centre, the internal raphe endings are exposed and non-coaxial, and there are many small chloroplasts distributed around the periphery of the cell. Schrader (1973) suggested that *Eunotia* and its allies might be transitional between the araphid pennate diatoms and asymmetrical biraphid genera, such as *Amphora* and *Cymbella* Agardh. Simonsen (1979) rejected this idea, finding nothing in common between the Eunotiaceae and *Amphora* beyond the ventral position of the raphe. However, the overall layout and symmetry of the frustule are so similar in *Eunophora* and *Psammamphora*/*Amblyamphora*

that it is best not to reject the possibility of a close relationship between them, with all that this would imply for the evolution of raphid diatoms. In this connection, it would be particularly interesting to know how *Eunophora* reproduces sexually. *Psammamphora* has a type of sexual reproduction that is unusual among raphid diatoms, involving *cis*-type physiological anisogamy (one gametangium produces 2 active gametes while the other produces 2 passive gametes; Mann, 1993). Thus if *Eunophora* were to prove to have the same pattern of behaviour, this would strengthen the case for a link between these genera. On the other hand, if *Eunophora* proves to be isogamous and produces only 1 gamete per gametangium, then this would merely confirm its links with *Eunotia* and *Actinella brasiliensis* Grunow (Geitler, 1973b; Mayama & Idei in Hori, 1993) where a single zygote is produced within a copulation tube formed by the fusion of 2 apical papillae. It is also noteworthy that *cis*-type anisogamy is characteristic of most araphid pennate diatoms (Geitler, 1973b; Mann, 1982; Roshchin, 1994), from which the raphid diatoms are presumably derived (Simonsen, 1979; this is consistent with recent molecular evidence, e.g. Medlin *et al.*, 1996). Thus, *cis*-type anisogamy is probably primitive within raphid diatoms and its occurrence in a member of the Eunotiophycidae would be especially significant.

Eunophora has been confirmed to be present only in recent and fossil samples from Tasmania and New Zealand. However, it is possible that the diatom described from Lake Baikal by Jasnitskij (1936) as *Amphora obtusa* var. *baicalensis* Jasnitskij and the similar diatom described by Skvortzow (1937) as *A. obtusa* var. *baicalensis* Skvortzow may belong in *Eunophora*. These diatoms have amphoroid symmetry and delicate punctate striation as in both *Psammamphora* and *Eunophora* and share the characteristic that the central raphe endings are distant from each other, with an elongate central nodule. No other species of *Psammamphora* (or *Amblyamphora*) has distant central raphe endings, whereas all *Eunophora* species do. Unfortunately, we have been unable to trace either Jasnitskij's or Skvortzow's material.

Nevertheless, even though we cannot reject the possibility that *Eunophora* occurs in the Northern Hemisphere, in Lake Baikal, it is very unlikely that the genus is cosmopolitan. Indeed, it is striking there seem to be no other reports of similar diatoms from the much more intensively studied lakes in the Northern Hemisphere, where in recent years a large number of studies on the benthic diatom flora of similar oligo- and dystrophic lakes have been conducted (e.g. Camburn *et al.*, 1984–1986; Stevenson *et al.*, 1991).

Eunophora seems to have ecological requirements similar to those of other members of the Eunotiophycidae. It is confined to dilute lowland and high-altitude lakes and tarns of low to very low alkalinity. Along the gradient from acid dystrophic western lakes to (ultra-)oligotrophic eastern lakes of the Tasmanian highlands (Tyler, 1992; Vyverman *et al.*, 1996), each of the described *Eunophora*

species displays a different distribution (Table 1, Fig. 50). In this respect *E. oberonica* and *Eunophora* sp. 1 are most interesting as they seem to have a distinct optimum in humic or oligotrophic waters, respectively. This makes them excellent potential indicators of the degree of dystrophy of the Tasmanian lakes. *E. tasmanica* has a much broader distribution but was found in highest relative abundances in slightly to moderately dystrophic waters. The distribution of *E. indistincta* is unclear but it seems to be mainly confined to corridor and eastern lakes.

We know very little of the life history of the species of the genus *Eunophora* and this certainly needs to be addressed in future research of members of this genus. Although lakes were sampled on various occasions during late spring and summer, we have never found thriving populations of *E. oberonica*, *E. tasmanica* or *E. indistincta*. Live cells of *Eunophora* sp. 1 were a little more abundant, but as for the other species most cells were dead or empty.

The discovery of the genus *Eunophora* provides further evidence that there is a distinct and unique biogeographic element in the algal flora of Australia and the south-west Pacific (Tyler, 1992; Moser *et al.*, 1995). Several new taxa, such as the new genera *Thecadiniopsis* (Croome *et al.*, 1987) and *Chrysonephele* (Pipes *et al.*, 1989), and numerous new species have been described from this region (Hustedt, 1955; Haworth & Tyler, 1993); several other species await formal description (P. Tyler, personal communication, Vyverman *et al.*, unpublished). Interestingly a number of these potentially endemic species have their closest affinities with marine taxa, e.g. *Thecadiniopsis*, five recently discovered *Biremis* species (Vyverman *et al.*, 1997) and the above-mentioned *Amphora* sp. 1 (Vyverman *et al.*, unpublished).

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