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Fossil species of the diatom genus *Tetracyclus* (Bacillariophyta, 'ellipticus' species group): morphology, interrelationships and the relevance of ontogeny

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SUMMARY

The diatom genus *Tetracyclus* Ralfs (Bacillariophyta) is composed largely of extinct, freshwater species many of which have been used as stratigraphic markers across several continents under the assumption that they are relatively widespread and confined to precise geological epochs. Until recently the taxonomy of the genus relied almost exclusively on the shape and dimensions of the preserved siliceous valves. This study forms part of a revision of the entire genus. In this paper the morphology of fossils from the 'ellipticus' species group is discussed. Significant to this study is the relative usefulness of diatom valve dimensions and overall shape, seen here in the context of siliceous morphogenesis and the appearance of particular valve 'shapes' at particular stages in their life cycles. In addition, alternative ways of representing character data have been applied to establish whether the 'ellipticus' species group is monophyletic with respect to the genus. Results suggest that the 'ellipticus' species group is not monophyletic and that the elliptical shape of valves is better viewed as a variable property of ontogeny.

1. INTRODUCTION

The diatom genus *Tetracyclus* Ralfs is composed largely of extinct, freshwater species many of which have been used as stratigraphic markers for several continents under the assumption that they are relatively widespread and confined to precise geological epochs.

The taxonomy of the genus has to a greater extent relied almost exclusively on the shape and dimensions of the siliceous valves and the frequency of particular valve characters such as striae and rib density (Hustedt 1914; Li 1982*a*, *b*, 1984). However, such features appear highly variable among species and warrant critical reappraisal. In previous studies (Williams 1987, 1989, 1990, 1995; Williams & Li 1990) it has been established that the genus has around 30+ species of which only four have been reported living and at least 27 reported exclusively as fossils (table 1). Williams (1995) divided the genus into five informal groups based upon the more typical identifying feature(s) of the valve, such as its overall shape, in line with previous work, of which one was the 'ellipticus' species group. No phylogenetic significance was attached to these groups.

Hustedt's (1914) monograph of the genus *Tetracyclus* was primarily undertaken for the illustrations he contributed to Schmidt's *Atlas der Diatomaceenkunde* (Schmidt *et al*. 1874–1959). Hustedt (1914) presented a particularly detailed study of the species *T. ellipticus* (Ehrenb.) Grunow and its relatives concluding that they were all closely related among themselves. Hustedt's views have remained largely intact since their publication and the assumption that all 'ellipticus' species are closely related has prevailed in discussions of their distribution both spatially and temporally (Williams 1995). The significance of these spatial and temporal distributions has yet to be examined in any detail, but continue to be utilized in assessing the origin of past micro-algal floras (Bradbury & Krebs 1982; Bradbury *et al*. 1985; VanLandingham 1991).

This study forms part of a revision of the entire genus with a view to future interpretation of their stratigraphic and biogeographical distribution with respect to other groups of organisms. In this paper, I discuss the morphology of the fossils from the 'ellipticus' species group and discuss their possible monophyly in the context of the entire genus. Significant to this study is the relative usefulness of diatom valve dimensions and overall shape, seen here in the context of siliceous morphogenesis and the appearance of particular valve 'shapes' at specific stages in their life cycles. Recent species discussed below have been published elsewhere (Williams 1987, 1989) or are in preparation.

2. METHODS

(*a*) *Material*

This study is based on approximately 500 slides (with an average of 50 relevant specimens to each slide). The majority of material examined is housed in The Natural History Museum, London (BM). Additional material has been studied from the following herbaria: BP (Botanical Department of the National Natural History Museum, Budapest, Hungary), CAS (California Academy of Sciences, San Francisco), FH-

Bail. (Farlow Herbarium of Cryptogamic Plants, Harvard University) and IGC-Beijing (Institute of Geology, Chinese Academy of Geological Sciences, Beijing).

Source of material is appended to the species descriptions below. Herbaria are listed by the acronym in *Index Herbariorum* (Holmgren *et al.* 1990). For herbaria not yet listed by Holmgren *et al.* (1990), an acronym has been created that does not conflict with those in the current edition or the listing created especially for diatomists by Fryxell (1975).

Significant to the study of *Tetracyclus* is material collected by C. G. Ehrenberg and F. Hustedt who both described new taxa of *Tetracyclus* from a fossil deposit in Columbia River, Oregon, USA.

Ehrenberg gave '…Brakisher Tripel von Columbia River [Oregon]' as the full locality details (Ehrenberg 1845). The material originated from the Wilkes Expedition (Tyler 1968) and sent to Ehrenberg by J. W. Bailey who was to undertake identification of the algae (Bailey 1854; Edgar 1979). Some of this material, housed in the Farlow Herbarium, Harvard (FH-Bail. 854), was examined by Edgar (1979) and myself but unfortunately contains no diatoms. Material that once belonged to Frederick Kitton may be from the original Wilkes sample and housed at BM (BM 56028, BM 56029).

There is some evidence to suggest that Hustedt's Columbia River material is from the same source as that which Ehrenberg used. Hustedt's material was provided by Reichelt, who may have mounted, or at least had access to, Ehrenberg's material. From the legend to the illustrations published by Hustedt in 1912 (in Schmidt 1874–1959) and Hustedt (1914), he states: 'The illustrations are prepared for the genus *Tetracyclus* in Schmidt's Atlas of Diatoms from the preparations of Herr. H. Reichelt, Leipzig, placed at my disposal' (my translation, see also Simonsen 1987, p. 25). In addition, Reichelt (in Hermann & Reichelt 1893, p. 75) observed: 'Von dieser in der Form der Schalenseiten höchst veränderlichen Art finden sich die von *Ehrenberg* aus einem Tripel von Oregon als *Biblarium compressum*, *B. ellipticum*, *B. lamina*, *B. Lancea*, *B. Rhombus* vor, aber auch andere Formveränderungen sind häufig.' I have used the material housed at BM under the assumption that it is from the same deposit that both Ehrenberg and Hustedt used for their accounts.

According to VanLandingham, the Columbia River deposit is from Southern Washington ('…"Columbia River" diatomites of Southern Washington… probably include the Quincy Diatomite…', VanLandingham 1991, p. 362, plate legend). This deposit is located in south-central Washington as part of the Columbia Plateau and is estimated to be between 11 and 12 million years ago.

Ehrenberg's material is not yet available for study but the prospects for its accessibility in the future seem promising. Hustedt's material is in BRM (Bremerhaven), his types have been catalogued by Simonsen (1987) and I have drawn on his study for illustrations.

In many instances material is sparse and limited to a single locality. I have chosen to include descriptions of these taxa as many fossil diatoms are poorly represented in certain deposits and it appears better to document these rather than wait for further material that may never be discovered.

Where possible, specimens have been studied using both the light (LM) and scanning electron microscope (SEM). The material has been stored as both processed and unprocessed samples as well as permanent mounts as glass slides. The material was processed for SEM work and specimens selected according to the method outlined in Paddock (1988, pp. 11–12). To retain complete cingula, acid treatment is sometimes too destructive. In these cases material was either washed in distilled water only or gently heated in hydrogen peroxide. In some cases a single frustule could be placed in a cavity slide and prepared as above. Where possible, girdle band counts were made this way to ensure that a complete cingulum was observed.

Throughout the text, abbreviations concerning the number and kind of specimens examined are as follows: *n* = number of valves observed, *po* = a population in excess of 30 individual valves (where appropriate a more specific number has been indicated, in some cases followed by a + sign to indicate 'in excess of') and *av* = average number. In the species descriptions, for the structural elements of the frustule where no specific statement is made, the observations refer to valves, otherwise *g* is used for 'girdle bands'; *f* indicates a fragment, where no statement of this sort is made, the observation refers to a complete feature, valve or girdle. For instance, *n = 3g* indicates that three complete specimens were examined all from girdle elements. Calculation of total numbers of specimens examined has been made by the addition of all individuals.

For species where no material was available, data have been determined from published accounts and illustrations. The primary source of published data (as references to previously published micrographs) is taken from Gaul *et al.* (1993).

Locality details follow a broadly political geography for ease of representation and do not imply natural biogeographical regions. Notes on some of the material used are discussed below because in some cases the origin and actual identity may be uncertain. For instance, many early diatomists exchanged specimens that later found their way by various circuitous routes into modern collections. Annotations on early (*ca.* 1800s) slides are sometimes vague, perhaps indicating only the country of origin. In some instances it has been important to establish precisely the origin of the material, particularly in the case of fossil deposits.

Author abbreviations follow Brummitt & Powell (1992) and exiccata diatom collections are abbreviated according to Stafleu & Cowan (1976–1993).

(*b*) *Morphological terminology*

A number of papers dealing with diatom valve terminology have been published in the last 15 years. For the siliceous parts of the diatom valve and girdle, Anonymous (1975) and its updated version, Ross *et al.* (1979), are the standard references and have been followed in this study. These have been expanded for certain siliceous features by Cox & Ross (1981) and all terminological nomenclature has been reviewed in Round *et al.* (1990). Stosch (1975) presented the first detailed discussion on girdle band morphology and nomenclature. However, since his pioneering effort much has been discovered and some of the conclusions reached in his paper are subject to debate and modification with certain aspects discussed in detail by Mann (1982), Williams (1985) and Round *et al.* (1990). I have indicated below where I depart from or expand on accepted usage.

(*c*) *Source of character data*

The diatom protoplast is encased in silica, which is divided into a number of distinctive units: the 'box'-like valves are separated by thinner strips of silica, the girdle. As the valves (and accompanying girdle) are made of silica, they are not capable of independent growth once they are fully formed, and as cell division takes place the valves become progressively smaller. After each cell division a new valve is formed along with a new set of girdle bands, collectively called the cingulum. The cingulum is divided into several elements, abbreviated as follows: v = valvocopula, p = primary copulae, s = secondary copulae, pl = pleura. The older valve (the larger one) is called the epivalve, its girdle elements, the epicingulum, and both together are referred to as the epitheca; the valve that results from the most recent cell division (the smaller valve) is the hypovalve, its girdle elements, the hypocingulum, and both together are referred to as the hypotheca. The epitheca and hypotheca together make up a complete frustule. The valve and girdle elements form the bulk of the source of data for this study.

Plasmogamy produces a binucleate cell which on fusion of the nuclei becomes a zygote. The cell that arises from this binucleate phase is the auxospore. In pennate diatoms, the expansion is largely bipolar. As the auxospore develops, a series of transverse silica bands is laid down. In addition there may be a series of longitudinal bands that underlay the set of transverse bands. The entire 'valve', encased in transverse and longitudinal bands, is referred to as the perizonium and, in pennate diatoms, is usually cigar-shaped (Stosch 1962, 1982; Pickett-Heaps *et al.* 1990).

After expansion, the initial epivalve is laid down followed by the initial hypotheca. These valves are formed beneath the auxospore wall and frequently have an atypical structure when compared to the more 'normal' vegetative valves. Thus, the initial cells are immediately post-auxospore and usually of a special morphology. Cells that are pre-auxospore are the smallest size of vegetative valve and occur immediately prior to auxospore production. The terms pre- and post-auxospore valves are used below to express the relations that particular valves occupy in the life cycle of the individual species. Taxonomic characters derived from the siliceous parts of the valve, girdle and auxospore are compared on the basis of their structure and position. However, the awareness that characters develop from precursor elements during the life cycle as well as during the silicification process of valve formation is now apparent, hence consideration of the mode of development (ontogeny) is vital and leads to a greater understanding of the relationship between different characters and their 'states' (Mann 1982, 1984; Pickett-Heaps *et al.* 1990). Examination of the life cycle, the structure and ontogeny of the frustules and its parts are discussed below.

3. INTRODUCTION TO THE GENUS *TETRACYCLUS*

Tetracyclus Ralfs (1843, p. 105) *nom. cons.* (Williams 1986).

Type species: *Tetracyclus glans* (Ehrenb.) Mills (1935, p. 1602) = *Tetracyclus lacustris* Ralfs (1843, p. 105, pl. 2, fig. 2).

Synonymy: *Biblarium* Ehrenb. (1843, p. 47), *nom. rej.*
Stylobiblium Ehrenb. (1845, p. 72).
Salacia Pant. (1889, p. 68), *non Salacia* L. (1771, p. 159).
Gomphogramma A. Braun in Rabenh. (1853, p. 33).
Castracania De Toni (1892, p. 750).
? *Prae-epithemia* Jousé (1952, p. 243).

Type localities: 'Nur fossil im Bergmehl von Kymmene Gård in Finnland bei Helsingfors beobachtet' (Ehrenberg 1838*b*, p. 185).

(*a*) *History*

In 1843, Ehrenberg described the genus *Biblarium* from a fossil deposit of Asian origin: 'Infusorien-Lager van Bargusina in Gouvernment Irkutzk in Sibirien' (Ehrenberg 1843, p. 47). He listed, but did not describe, nine species belonging to the new genus: *B. stella* Ehrenb., *B. rhombus* Ehrenb., *B. castellum* Ehrenb., *B. compressum* Ehrenb., *B. lineare* Ehrenb., *B. emarginatum* Ehrenb., *B. clypeus* Ehrenb. beginning his listing with *B. glans* (Ehrenb.) Ehrenb. which he previously described as *Navicula*? *glans* Ehrenb. (Ehrenberg 1838*a*). *Navicula glans* was first mentioned by Ehrenberg in 1838 in connection with his study of three Scandinavian fossil samples (Ehrenberg 1838*a*) but was not described until the publication of the *Infusionsthierchen* later that year (Ehrenberg 1838*b*).

Later, Ehrenberg received material from J. W. Bailey from Columbia River, Oregon (Bailey 1845; Ehrenberg 1845; Edgar 1979). The two samples came from James Dwight Dana who collected them on the Wilkes Expedition and forwarded them to Bailey for examination (Tyler 1968; Edgar 1979). One of the samples was a fossil diatomite collected near Astoria, Fort George on the Columbia River (Dana 1849), while the other was a Recent sample also collected from Fort George. Bailey sent sub-samples of each to Ehrenberg for his determinations. In his account of the fossil material from Columbia River, Ehrenberg published descriptions of the *Biblarium* species whose names had appeared as *nomina nuda* in 1843 (Ehrenberg 1843; Bailey 1845). Bailey also published on these samples but made only a cursory attempt at identification by including illustrations of a few valves appended by a cautious note saying that they were a 'new genus? allied to *Terpsinoe*?' (Bailey 1845, p. 321, pl. 4, figs 1–5).

Coincidentally, in August 1843 Ralfs described a new genus he called *Tetracyclus* based on a single living species *T. lacustris* Ralfs collected from Europe. Ralfs appeared unaware of Ehrenberg's fossil genus *Biblarium*. Later, W. Smith (1856) suggested synonymy with *Biblarium*, as the only differences he saw between the two genera were that the Recent species formed chains while the fossil species did not. This, Smith reasoned, was due to the fossil state of the *Biblarium* species and they would, when living, form chains. Smith made a new combination for *Biblarium emarginatum*, a species he discovered in his own non-fossil material, transferring it to the genus *Tetracyclus*. Smith also took the step of uniting with Ralfs' *T. lacustris* several species that appeared in Ehrenberg's fossil deposits: *B. stella*, *B. glans* and *B. speciosum* Ehrenb. Thus, many of Ehrenberg's fossil taxa were seen as identical to representatives still living.

From the same Oregon fossil material, noted above, Ehrenberg described another new genus, *Stylobiblium* Ehrenb. (Ehrenberg 1845). Ehrenberg (1845) described the genus *Stylobiblium* to distinguish those species with a circular outline from those with an elliptical outline, to remain in *Biblarium*. In the original generic description, Ehrenberg provided diagnoses for three species that were distinguished from each other by the arrangement and number of the transapical ribs. *S. clypeus* Ehrenb., based on the *nomen. nudum Biblarium clypeus* Ehrenb. (Ehrenberg 1843), was figured with few valve ribs extending from the valve margin to all parts of the valve face; *S. divisium* Ehrenb. was figured with many ribs, situated more or less parallel to each other but lying perpendicular to a central sternum; and *S. excentricum* Ehrenb. was illustrated with a few ribs extending transapically across the valve face, those at the centre lying parallel, those at the poles radially aligned.

A Japanese deposit at Sentenai was the source of a further six fossil species of *Stylobiblium* described by Pantocsek (1892, 1905) of which two, *Stylobiblium japonicum* Pant. (*non* Temp. & Perag., see later) and *Stylobiblium haradaae* Pant., were figured with distinctively circular valves, whilst the remaining four had valves which were more or less elliptical.

Petit (1890) proposed a further distinction between *Stylobiblium* and *Tetracyclus* due to the apparent lack of a septum on the girdle bands in the former genus. Hustedt (1914) demonstrated that this was not the case, further suggested that shape could no longer serve to distinguish the two genera, and made *Stylobiblium* a synonym of *Tetracyclus*. More recently, Li (1982*b*) transferred a further two species from *Stylobiblium* to *Tetracyclus*.

Species of *Stylobiblium* have been examined in detail by Williams (1989) and Williams & Li (1990). All possess the characters (synapomorphies) of *Tetracyclus*, with the possible exception of *T. divisium* of which no SEM observations are yet available (Williams 1989), supporting their inclusion in *Tetracyclus*.

Three other generic names have been used in connection with *Tetracyclus*: *Gomphogramma* A. Braun in Rabenh., *Salacia* Pant. and *Prae-epithemia* Jousé.

The genus *Gomphogramma* was established by Braun in 1853 to accommodate a small, extant elliptical species, *G. rupestris* A. Braun in Rabenh., characterized by 'direct and complete costae' (Braun in Rabenhorst 1853, p. 33). W. Smith (1857) noted, however, that the characters of *G. rupestris* given by Braun properly referred to specific rather than generic characters and considered that it should be transferred to *Tetracyclus*, but did not do so. Later, Grunow (in Van Heurck 1881, pl. 52, figs 13, 14) acknowledged the similarities between *G. rupestris* and *Tetracyclus* and transferred the species appropriately. Together with *T. emarginatus* and *T. glans*, *T. rupestris* was the third species of the genus discovered still living.

The genus *Salacia* was erected by Pantocsek (1889) for a single fossil species, *Salacia boryana* Pant. Pantocsek indicated in his protologue a possible relationship with *Stylobiblium* (a name he continued to use) as both genera lacked septa on the girdle bands. *Salacia* was not circular but lanceolate. However, studies by Hustedt (1914), and others, demonstrated the presence of septa on the girdle bands of *S. boryana* and that it was also a species correctly belonging to *Tetracyclus*.

Finally, Jousé (1952) described a new genus *Prae-epithemia* from a fossil deposit in Lake Khanka. It is difficult to determine exactly what species Jousé was describing, as material has not been available for study. There are a number of possibilities. It could be the septum from a species of *Epithemia* Brébisson (hence the name) or it could be a species of *Tetracyclus* that is partially eroded (as other specimens of *Tetracyclus* are evident in her illustrations of the Lake Khanka deposit). I have considered it a synonym for *Tetracyclus*, but only examination of relevant material will confirm its proper identity.

Tetracyclus is, therefore, a well-characterized genus with unique features of the valve and girdle (Williams 1987, 1989) and composed of both living and fossil representatives. However, interrelationships among the species have never been studied and the origin, diversification and extinction of species in the genus remain conjectural.

(*b*) *Description*

Frustules rectangular in girdle view, the pervalvar axis exceeding the apical axis. Valves isopolar, their surface flat, the mantle vertical, the margin a sharply stepped outward hyaline lip. Primary internal transapical ribs present, sometimes with secondary and tertiary ribs. Axial area longitudinal with indefinite margins, sometimes internally thickened to form a sternum. Striae parallel to slightly radiate, extending across the mantle as far as the projecting hyaline valve margin. Virgae much coarser than the small vimines and raised above the valve surface close to the margin, becoming less so towards the axial area. Areolae close to the axial area, more widely spaced than elsewhere and somewhat irregularly distributed. Apical pore fields present in some species, consisting of an area where the striae are as closely spaced as the areolae within them. Rimoportulae usually present, varying in number and position. Cingulum consisting of several open bands, their openings at alternate poles. The bands of four kinds: valvocopula bearing a septum; primary copulae each with a ligula and a septum; secondary copulae without septa their ligulae larger than those of the primary copulae; a single pleura. Septa arising from the abvalvar part of the pars exterior of the valvocopula and the primary copulae, extending variable distances into the frustule, with a pore close to the base on the abvalvar face connecting with the group of pores on the outer face of the band.

4. TAXONOMY OF THE 'ELLIPTICUS' GROUP

(*a*) *History*

Tetracyclus ellipticus was first recognized and described by Ehrenberg as a species of *Biblarium* (Ehrenberg 1843, 1845). Of the nine species described by Ehrenberg, five, *Biblarium lancea*, *B. lineare*, *B. lamina*, *B. compressus* and *B. ellipticum*, were placed in the *Tetracyclus ellipticus* species complex by Hustedt and others (Hustedt 1914; Li 1982*b*, 1984). Hustedt's evidence (1914) was based primarily on minor variations in valve shape and size, factors that have served to confuse ever since. A more detailed examination of the morphology of most of these taxa has been undertaken and is described below prior to the analyses.

(i) Tetracyclus boryanus (*Figure 1*a, b)

Tetracyclus boryanus (Pant.) Van Heurck (1896, p. 359).

Basionym: *Salacia boryana* Pant. (1889, pl. 23, fig. 341; 1905, p. 68).

Synonym: *Castracania boryanus* (Pant.) De Toni (1892, p. 750).

Type locality: 'Bory', [Hungary]. Pantocsek (1905, p. 68).

Type slides: BP 326/2542 ('Bacillariae fossiles Hungariae, Dr. J. Pantocsek, Tavarnok, Dg. Ort, no. 27-395', fragments only), holotype (Krenner 1979, p. 23), illustrated in Pantocsek (1889, pl. 23, fig. 341); BM 8096, BM 60461, BM 68440, BM 68441, BM C 500, BM J 3418, 3419, isotypes.

Description

Valve strongly lanceolate, 40–120 μm long, 30–45 μm wide ($n = 25+$). Striae parallel but uneven, *ca.* 25 in 10 μm; transapical ribs robust, 4–5 in 10 μm; primary, with very few secondary or tertiary ribs. Sternum central, linear. Rimoportulae present on valve face or near valve/mantle junction, 1–2 (3) (*av* = 1 per valve, $n = 10$) (figure 1*a*, *b*). Cingulum unknown.

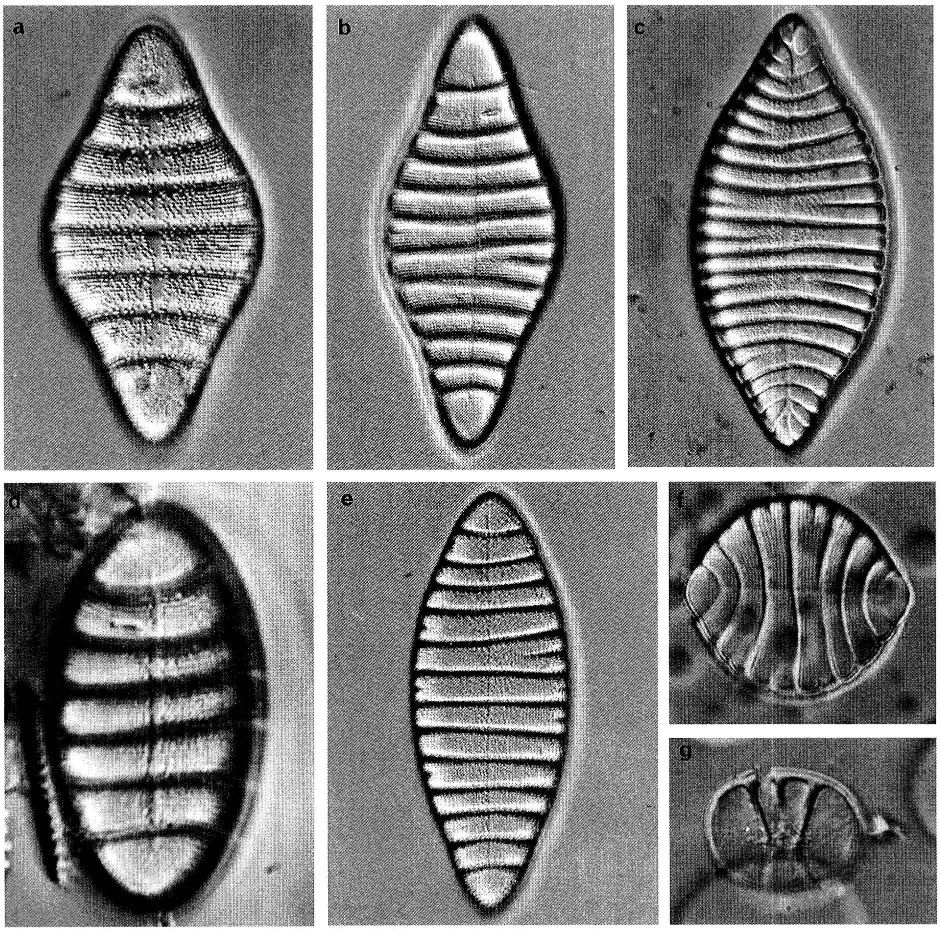

Figure 1. (*a*) and (*b*) *Tetracyclus boryanus*, Bory, Hungary, (*a*) BM Adams C500, length = 65 μm; (*b*) BM Adams J 3419, length = 75 μm; (*c*) *Tetracyclus maxima*, Swan Lake, Oregon, USA, BM GC 3113, length = 85 μm; (*d*) *Tetracyclus polygibbum*, Baikatsu, Hokkaido, Japan, BM 82313, length = 30 μm; (*e*) *Tetracyclus rhombus*, Oregon, USA, length = 40 μm; (*f*) *Tetracyclus ovalifolius*, Inner Mongolia, BM 81618, length = 65 μm; (*g*) *Tetracyclus shangduensis*, Inner Mongolia, BM 81618, length = 30 μm.

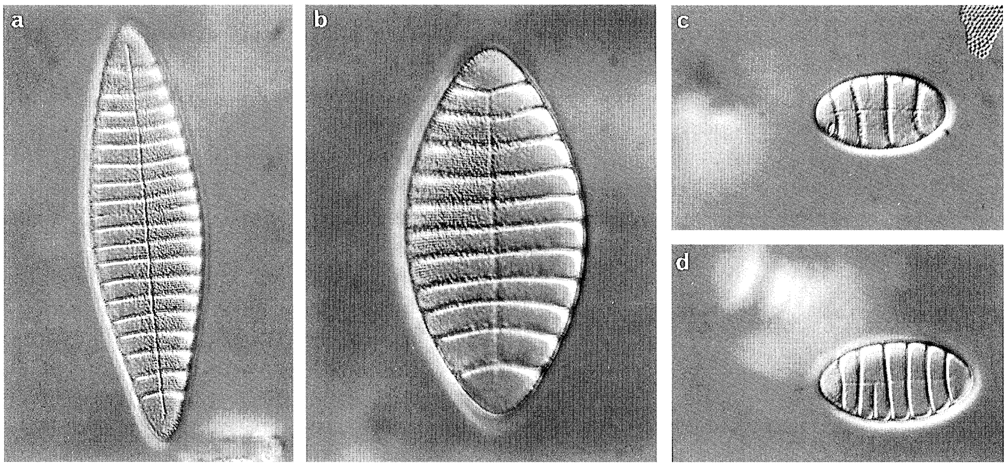

Figure 2 (*a*) *Tetracyclus lancea*, Oregon, Columbia River, USA, BM 56029, length = 120 μm; (*b*) *Tetracyclus lata*, Breite Busch bei Hainspach, BM 54725, length = 50 μm; (*c*) and (*d*) *Tetracyclus ellipticus*, Columbia River, USA, BM 56029, length = 20 μm.

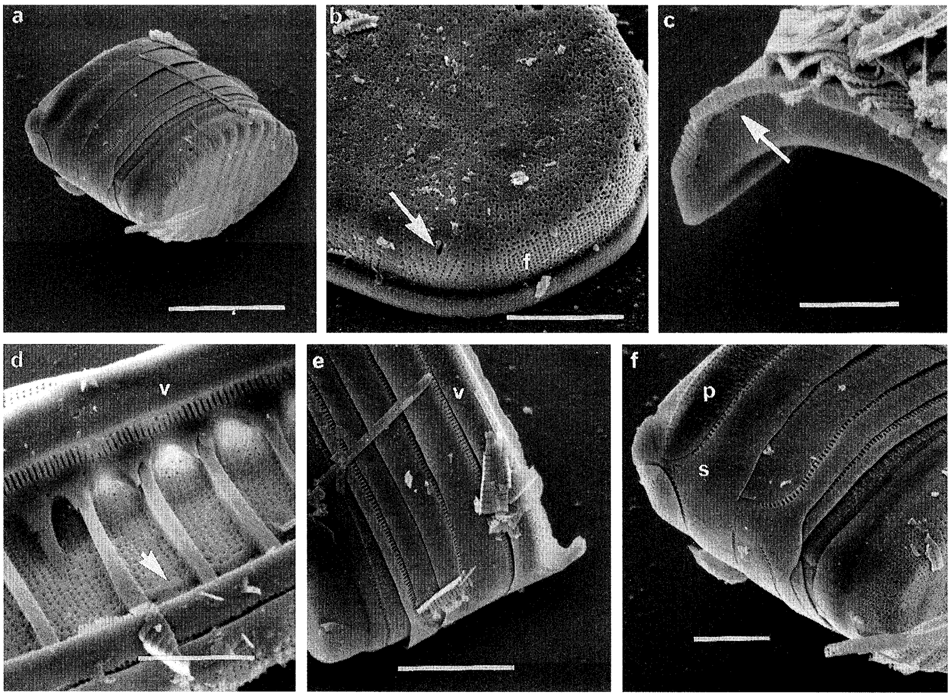

Figure 3. *Tetracyclus ellipticus*, Harper Region, Oregon, USA. (*a*) Valve with some girdle bands *in situ* (detail in (*f*), bar = 15 μm; (*b*) detail of external view of valve, arrow indicating *rp*, *f* as area of more closely packed striae, bar = 6.60 μm; (*c*) section through broken valve, arrow indicating the row of striae external to the transapical rib, bar = 4.0 μm; (*d*) internal view of valve with *v* in place, bar = 6.0 μm; (*e*) external view of valve with *v* separated, bar = 10 μm; (*f*) detail from figure 1, with *p* and *s* in place, bar = 7.5 μm.

Notes

All slides examined from Bory, Hungary are from the same deposit. Pantocsek figured a specimen with two very large 'pores' that are clearly rimoportulae (Pantocsek 1889, pl. 23, fig. 341; this particular specimen was not found on BP 326/2542, the holotype slide, which contained only fragments of valve and girdle). Pantocsek (1889) erected the new genus *Salacia* for this species in which the ribs are very prominent and on several slides specimens have plus or minus two extremely prominent and large rimoportulae, both situated within the same pole. Tempère took issue with Pantocsek's generic determination and suggested that his species was instead '…un *Rhabdonema* nouveau, mais ne saurait constituer un genre' (Tempère 1893, p. 50). Tempère went on to point out that he had frequently seen identical specimens in Carson City fossil material and that they were probably the same species. While Tempère seems to have been mistaken in his generic identification, he did appreciate the similarity between the Bory specimens and those in the USA, especially Carson City. However, while extremely similar, they are not the same species (see *T. lancea*).

T. boryanus is known from the type locality only. From other diatom species present on the holotype slide, it is clearly a brackish (possibly marine) water deposit. The only other brackish water fossil deposit

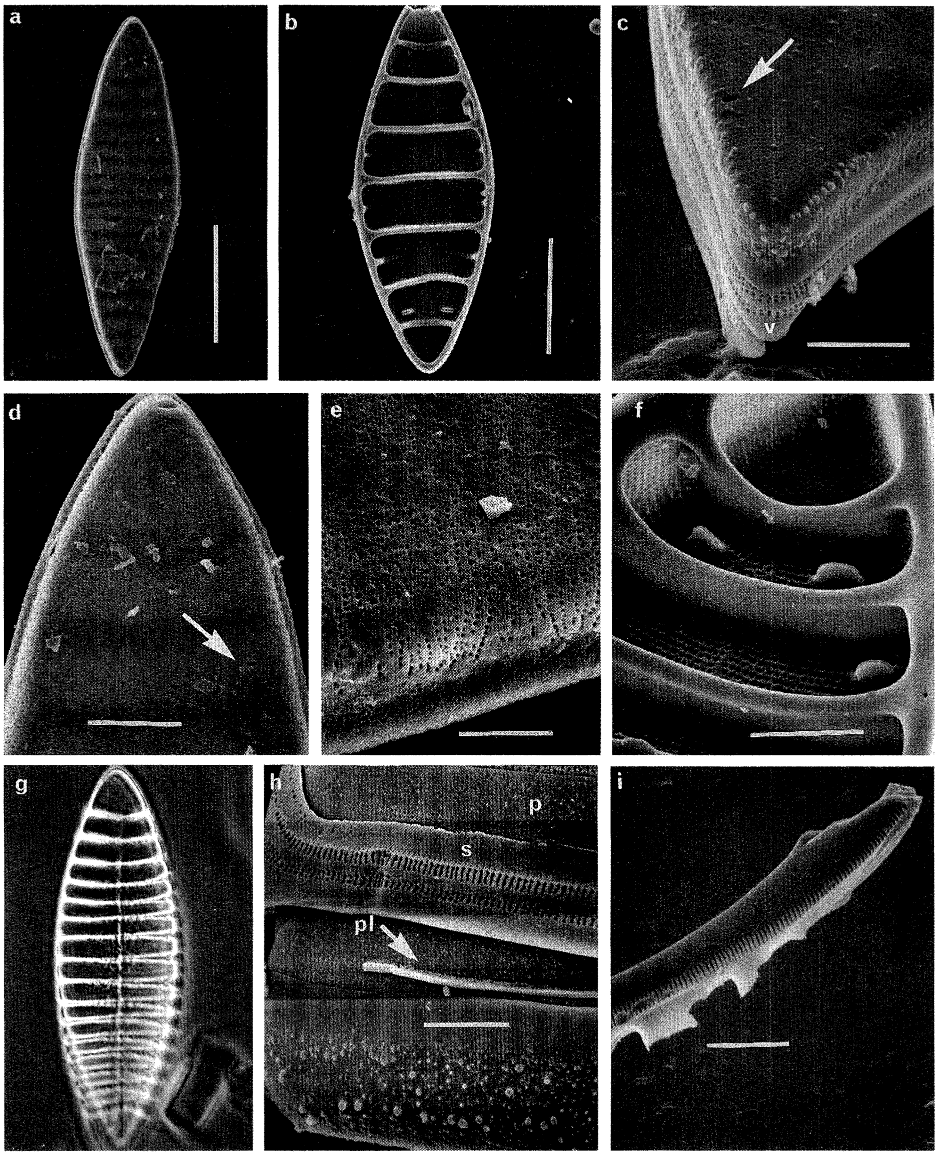

Figure 4. *Tetracyclus lancea*, Quesnel, British Columbia. (*a*) External view of entire valve, face view, bar = 30 μm; (*b*) internal view of entire valve, face view, two rimoportulae at the base of the valve, bar = 15 μm; (*c*) detail of external view of valve, arrow indicates *r*, note lack of differentiated *f*, bar = 6.0 μm; (*d*) detail of external view of valve pole, arrow indicates *r*, bar = 7.5 μm; (*e*) detail of external view of valve at the middle margin, note stepped lip at edge, undifferentiated by striae, bar = 4.0 μm; (*f*) detail of internal view of valve, with three *r*, bar = 5.0 μm; (*g*) LM, whole specimen from Oregon, Columbia River, USA, BM 56029, length = 120 μm; (*h*) detail of partial girdle, illustrating detached *s* and *pl* surrounding attached *p*, bar = 7.5 μm; (i), detail of *v*, bar = 9.0 μm.

with species of *Tetracyclus* is from San Clemente Is., China Point (CAS 307008, with specimens of *T. stella* (Ehrenb.) Hérib. and *T. constrictus* M. Perag. in Temp. & M. Perag.).

Material

HUNGARY: Bory, BP 326/2542, holotype, *n* = 4(*f*); BM 8096, *n* = 1; BM 60461, *n* = 1; BM 68440–1 (Tempère & Peragallo, *Diat. monde entier*, 2nd edition, slide nos 94, 95), *n* = *po*; BM C 500, *n* = 3; BM J 3418, 3419, *n* = 1, 1, respectively.

(ii) Tetracyclus *ellipticus* (*Figure* 2c–d, *Figure* 3a–f)

Tetracyclus ellipticus (Ehrenb.) Grunow (1862, p. 411).

Basionym: *Biblarium ellipticum* Ehrenb. (1845, p. 74).

Synonyms: *Biblarium compressum* Ehrenb. (1845, p. 74). *Tetracyclus compressus* (Ehrenb.) M. Perag. in Hérib. (1893, p. 159, pl. 3, fig. 26 excl. figs & desc.). *Tetracyclus ellipticus* f. *minor* Hust. in A. W. F. Schmidt (1912, pl. 281, fig. 16; see Simonsen 1987, p. 26).

Type localities: 'Sibiria. Oregon Fossile' Ehrenberg (1845, p. 74).

Type slides: Columbia River, Oregon, FH-Bail. 854, BM 56028, BM 56029, isotypes. Illustrated in Ehrenberg (1854, pl. 33/12, fig. 2); *Biblarium compressum* illustrated in Ehrenberg (1854, pl. 33/12, fig. 1). Type material from Siberia not available, illustrations in Ehrenberg (1854, pl. 33/2, fig. 5) and for *B. compressum*, Ehrenberg (1854, pl. 33/2, fig. 2). *Tetracyclus ellipticus* f. *minor* illustrated in Hust. in A. W. F. Schmidt (1912, pl. 281, fig. 16) and Simonsen (1987, pl. 12, figs 5–7).

Description

Valves gently elliptical (almost circular in some valves) with broadly rounded poles; 30–45 µm long and 25–40 µm wide (figure 2*c–d*, figure 3*a*). Transapical ribs robust, primary, rarely secondary or tertiary; (2)3–4 in 10 µm (figure 2*c–d*, figure 3*a*, *d*). Striae more or less parallel, 5–10 between ribs (figure 3*c*, arrow, 3*d*). Sternum central, linear, slightly raised (figure 3*d*, arrow). Pore fields greatly reduced at polar mantle, but evident (figures 3*b* (*f*), and 3*f*). Rimoportulae (*rp*) present 1–2 (maximum 3; *n* = *po*), located either on valve face or (less frequently) at mantle/face junction (figure 2*c*, figure 3*b*, arrow).

Cingulum consisting of three distinct components: all bands open, ligulate (figure 3*a*, *d–f*). Valvocopula attaching by crenelated lip overlaying ribs; pars interior consisting of 2–4 (5) distinct rows of poroids (which coalesce internally), ligula absent (figure 3*d*). Septum extending from pars interior with small pore penetrating pole of band. Primary copulae number no more than *ca.* 10 elements (*n* = *po*), each having pronounced advalvar ligula (figure 3*f*, (*p*)). Secondary copulae of four elements; pore area and septum absent, but pars interior consisting of 1–3 rows of poroids (figure 3*e*, *f* (*s*)). Pleura not observed.

Notes

Although Peragallo (in Héribaud 1893, p. 159) made the combination *Tetracyclus compressus*, his specimens are not the same as those of Ehrenberg and I suspect that they are the pre-auxospore valves of another yet undescribed species. Thus, the geographical distribution of this species is restricted to the west coast of the USA and the east coast of the former Soviet Union.

Material

USA: *Oregon*, Columbia River, FH-Bail. 854, BM 56028, BM 56029, *n* = *po*; Pit River, *Lt. R. S. Williamson*, BM 2342, BM 26181 = *H. L. Smith*, *Diat. spec. typ.* no. 620, *n* = *po* (see Bailey 1854); Falls River, BM 8822, *n* = *po*; Klamath Co., Poe Valley, CAS 359045–46, (USGS 1017), *n* = *f*; Baker Co., Baker, CAS 359061–2, (USGS 1036), *n* = *po*.

Washington, Adams Co., 100 NW of Spouante, Latah form, CAS 360020, (USGS 1209), *n* = *po*; Grant Co., Grennel Deposit, CAS 361086, (USGS 2058), *n* = *po*; Grant Co., Webley Principal Deposit, CAS 363005, (USGS 2314), *n* = *po*; Kittatas, BM s.n., *n* = *po*.

Idaho, Power Co., Upper Starlight formation, CAS 378039, (USGS 4992), *n* = *po*; Poison Creek Formation (Miocene), BM s.n., *n* = *po*.

(iii) Tetracyclus lancea (*Figure 2*a, *Figure 4*a–i)

Tetracyclus lancea (Ehrenb.) M. Perag. in Hérib. (1893, p. 159, pl. 3, fig. 25).

Basionym: *Biblarium lancea* Ehrenb. (1845, p. 74).

Synonym: *Tetracyclus ellipticus* var. *lancea* f. *elongata* Hust. in A. W. F. Schmidt (1912, pl. 281, figs 13, 14); Simonsen (1987, pl. 12, figs 1–2).

Type locality: 'In Oregonia fossile' Ehrenberg (1845, p. 74).

Type slides: FH-Bail. 854, BM 56028, BM 56029, isotypes. Illustrated in Ehrenberg (1854, pl. 33/12, fig. 5). *Tetracyclus ellipticus* var. *lancea* f. *elongata* illustrated in Hust. in A. W. F. Schmidt (1912, pl. 281, figs 13, 14) and Simonsen (1987, pl. 12, figs 1–2).

Description

Valve linear to lanceolate, large 60–140 µm long, 15–25 µm wide (figure 2*a*, figure 4*a*, *b*, *g*). Transapical ribs robust, 3–4 in 10 µm; mostly primary, few tertiary, rarely secondary (figure 2*a*, figure 4*b*, *g*). Striae parallel, 5–8 in 10 µm (figure 2*a*, figure 4*b*, *g*); Sternum central, linear (figure 2*a*, figure 4*a*, *b*, *g*). Valve mantle with external ridge (figure 4*c–e*, *h*); occasionally small stubble spines at mantle/face border (figure 4*c*, *h*). Polar pore fields absent or greatly reduced (figure 4*c*). Rimoportulae present on valve face, 1–3 (4) (figure 4*c*, arrow, and 4*f*). Cingulum consisting of four components, all bands open and ligulate (figure 4*c*, *h*, *i*). Valvocopula pars interior consisting of 2–4 rows of poroids coalescing as a bar internally (figure 4*i*). Septum extending from pars interior with a series of small pores penetrating the band; pars exterior plain. Primary copulae consisting of 10–12 elements, with advalvar ligula (figure 4*h* (*p*)). Secondary copulae consisting of *ca.* 4 bands (figure 4*h* (*s*), one in position), without a ligula pore; single pleural band present (figure 4*h* (*pl*)).

Notes

This species is known only from west coast North American and Canadian fossil deposits; possibly the same taxon has been observed in Kamchatka (Lupikina 1984).

Material

USA: Oregon, FH-Bail. 854, BM 56028, BM 56029, isotypes, *n* = *p*; *Oregon*, Pit River, *Lt. R. S. Williamson*, BM 1293, BM 2342, *n* = *p*; 'Fossil, Oregon', BM 13426, BM 25619 (*H. L. Smith*, *Diat. spec. typ.* no. 58), BM 50189, BM 50197, BM 55682, *n* = *po*; Falls River, BM 8822, BM 26181 (*H. L. Smith*, *Diat. spec. typ.* no. 620), BM 56399, *n* = *po*.

Nevada, Carson City, BM 60460 (as *Tetracyclus lancea* Ehr. 'Ehr. Mikrog. 12/5', Tempère, *Diatomées*), *n* = *po*; Virgin Valley, BM 92689, *n* = *po*.

Washington, Grant County, BM 77802, BM 77803, *n* = *po*, Maryland deposit, BM 31549, *n* = *po*; Kittatas, BM s.n., *n* = *po*.

CANADA: Quesnel, British Columbia, BM s.n., *n* = *po*.

(iv) Tetracyclus lata (*Figure 2*b)

Tetracyclus lata (Hust.) D. M. Williams, *nov. stat.*

Basionym: *Tetracyclus ellipticus* var. *lancea* f. *lata* Hust. in A. W. F. Schmidt (1912, pl. 281, fig. 11; see Simonsen 1987, p. 26).

Synonym: *T. ellipticus* var. *constrictus* Hust. in A. W. F. Schmidt (1912, pl. 281, fig. 9; see Simonsen 1987, p. 25).

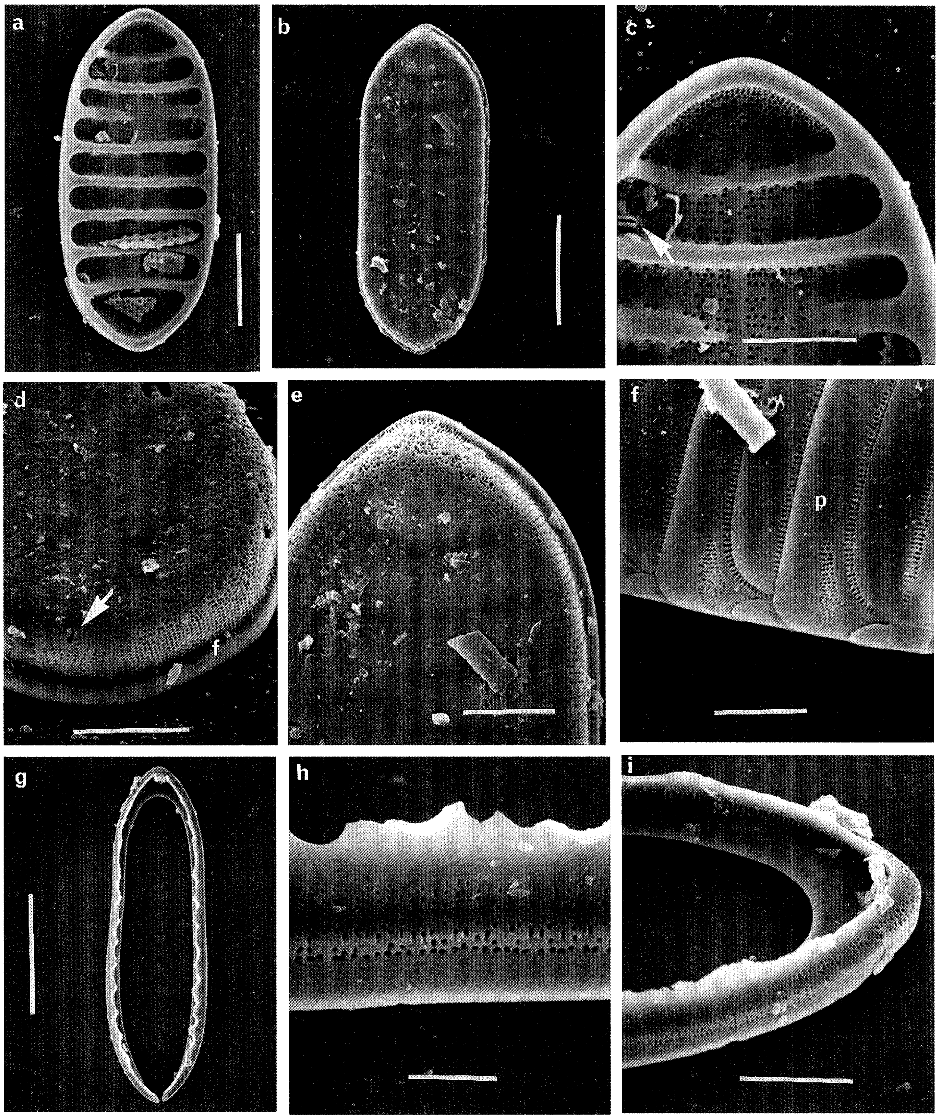

Figure 5. *Tetracyclus linearis*, Kittatas, Washington, USA. (*a*) Internal view of valve, bar = 10.0 μm; (*b*) external view of valve, bar = 20 μm; (*c*) detail of pole from (*a*) illustrating marginal *r*, arrowed, bar = 5.0 μm; (*d*) external detail of pole, illustrating marginal *r*, arrowed, and *f*, bar = 6.0 μm; (*e*) external detail of pole, illustrating *f*, bar = 6.0 μm; (*f*) detail of a portion of cingulum, one *p* indicated from a series of 5, bar = 7 μm; (*g*) whole *v*, bar = 25 μm; (*h*) detail of *p*, bar = 3.0 μm; (*i*) polar view of *v* with septum, bar = 6.0 μm.

Type locality: 'Breite Busch bei Hainspach' Hust. in A. W. F. Schmidt (1912, pl. 281, fig. 11).

Type slide: BRM J/53. Illustrated by Hustedt in A. W. F. Schmidt (1912, pl. 281, fig. 11) and Simonsen (1987, pl. 11, figs 1–3). Illustrations in Hustedt (1914, p. 102, taf. 1, fig. 8), Simonsen (1987, pl. 11, figs 1–3, *non* Hust. in A. W. F. Schmidt 1912, pl. 281, fig. 15; illustrated in Simonsen 1987, pl. 11, figs 4–5 = *Tetracyclus rhombus*).

Description

Valve linear to lanceolate, large 40–75 μm long, 2–25 μm wide ($n = 6$; fig. 2*b*). Transapical ribs robust, 2–4 in 10 μm; mostly primary, very occasionally secondary and/or tertiary. Striae parallel, 8–10 between ribs; sternum central, linear but faint (fig. 2*b*); rimoportulae present on valve face and mantle, 1–3 ($av = 2$, maximum = 6? [Simonsen 1987, pl. 11, fig. 4). Cingulum unknown.

Notes

Hustedt figured two specimens of *T. ellipticus* var. *lancea* f. *lata* in the illustrations for Schmidt's *Atlas der Diatomaceenkunde* (Hustedt 1912 in Schmidt 1874–1959, pl. 281, figs 11, 15): figure 11 was from Breiten Busch and figure 15 from Columbia River, Oregon. As Hustedt's description (1914, p. 102) was only accompanied with the illustration from figure 11 (= Hustedt 1914, taf. 1, fig. 8), Simonsen (1987) concluded that the Breite Busch material should be regarded as type. The material from Breite Busch was also the source material for *T. ellipticus* var. *constrictus* Hust.

It is clear from Simonsen's illustrations (1987, pl. 11, figs 1–5), as well as examination of material from both localities (Breite Busch bei Hainspach, BM 54725; Columbia River USA, BM 56028, BM 56029), that there are a number of distinguishing features of the striae and ribs, as well as their relative density and dimensions, between the specimens of Hainspach and

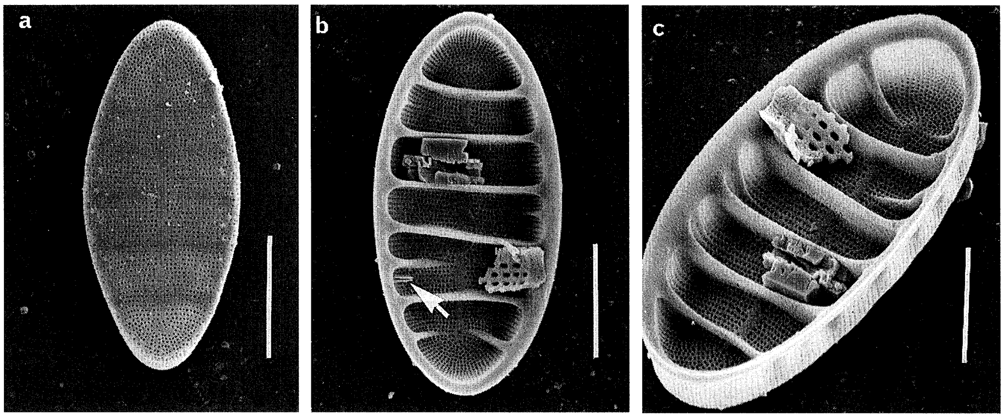

Figure 6. *Tetracyclus polgibbum*, Baikatsu, Hokkaido, Japan. (*a*) External view of valve, bar = 10 µm; (*b*) internal view of valve, illustrating marginal *r*, arrowed, bar = 10 µm; (*c*) internal view of valve, illustrating lack of *f*, bar = 7.5 µm.

Columbia River. The only specimens of *Tetracyclus* observed in the type material belong to *T. lata* (figure 2*b*; see Simonsen 1987, pl. 11, figs 1–3 for illustrations of type specimens). All five specimens illustrated by Simonsen have a similar outline. However, those from Columbia River (Simonsen 1987, pl. 11, figs 4, 5) possess very distinct rimoportulae, six in Simonsen's figure 4 and possibly three in his figure 5. They also have a somewhat more regular striation pattern meeting the sternum, as well as the number of ribs per valve being greater. *T. lata* (from Hainspach) is a different taxon to that described from Columbia River, that is *T. rhombus* (see below and Williams 1990 for a fuller discussion).

In summary, Hustedt confused matters by placing too much importance on valve outline and failing to consider the sometimes profound changes these species may go through during their ontogeny. In this instance, it is probably ontogeny that confounded him. Two separate species can be determined from material relevant to *T. ellipticus* var. *lancea* f. *lata*: *T. lata sensu stricto* and *T. rhombus* (see below). The taxon described as *T. ellipticus* var. *constricta* (also from 'Breite Busch bei Hainspach') is most probably a precursor (post-auxospore) valve for *T. lata*. Rubina illustrated a specimen from the 'Turtasskaya suite' of West-Siberian lowland that she named *Tetracyclus celatom* (Rubina 1968, taf. 1, fig. 10). This may possibly be an auxospore of *T. lata* but without examination of the material it is impossible to confirm, but remains an intriguing possibility. Rubina does cite the occurrence of specimens she refers to as *T.* aff. *ellipticus* in the same deposit, although these are not illustrated (Rubina 1968, p. 63).

Material

GERMANY: Brieten Busch bei Hainspach in Bohmen, BM 54725 (*Reichelt*, type material).

(v) Tetracyclus linearis (*Figure* 5a–i)

Tetracyclus linearis (Ehrenb.) Grunow (1862, p. 411).

Basionym: *Biblarium lineare* Ehrenb. (1845, p. 74).

Synonyms: *Biblarium lamina* Ehrenb. (1845, p. 74).
Tetracyclus lamina (Ehrenb.) Hérib. (1893, p. 159, pl. 4, fig. 20, [excl. figs & desc.]).
Tetracyclus ellipticus var. *lamina* (Ehrenb.) M. Perag. (1903 in M. Perag. 1897–1903, p. 921).
Tetracyclus lamina f. *lata* Temp. et H. Perag. (1909 in Tempère & Peragallo 1907–1915, p. 165, no. 301).
Tetracyclus ellipticus var. *linearis* (Ehrenb.) Hust. in A. W. F. Schmidt (1912, pl. 281, pl. 12).
Tetracyclus ellipticus var. *lamina* f. *lata* (Temp. et H. Perag.) Mills (1935, p. 1601).

Type localities: 'Fossile ad Bargus. Sibiriae et in Oregonia.' Ehrenberg (1845, p. 74).

Type slides: Columbia River, Oregon, FH-Bail. 854, BM 56028, BM 56029, isotypes. Illustrated in Ehrenberg (1854, pl. 33/12, fig. 6); Type material from Siberia not available, illustrated in Ehrenberg (1854, pl. 33/2 fig. 8); *Biblarium lamina* illustrated in Ehrenberg (1854, pl. 33/12, fig. 4).

Description

Valves linear with more or less parallel sides, 50–85 µm long, 25–30 µm wide (figure 5*a*, *b*). Transapical ribs robust 1–3 in 10 µm; mostly primary, very rarely secondary (figure 5*a*, *c*). Striae parallel but moderately unevenly spaced, 15–25 in 10 µm, *ca.* 5–8 between ribs (figure 5*a*, *c*). Sternum central, linear, slightly raised (figure 5*c*). Pore fields (*f*) situated on mantle, distinguished by definite area of closely packed striae (figure 5*d*, *e*). Single rimoportula, located either on valve face or, more usually, the mantle/face junction sub-terminally (figure 5*c*). Mantle extended, hyaline (figure 5*d*, *e*).

Cingulum consisting of open, ligulate bands (figure 5*f*–*i*). Valvocopula (figure 5*g*–*i*) and primary copulae only observed (figure 5*f* (*p*)); secondary copulae and pleurae not evident. Valvocopula attaching by shallow crenelated lip (figure 5*g*–*i*); pars interior consisting of 2–4 indistinct rows of poroids, ligula absent (figure 5*g*–*i*). Septum shallow, extending from pars interior with small pore penetrating the band (figure 5*g*, *i*). Primary copulae as valvocopula but each with an advalvar ligula (figure 5*f* (*p*)); probably number *ca.* 10 ($n = 15$).

Notes

This species occurs only in fossil deposits on the west coast of North America and the fossil deposit at 'Yezo,

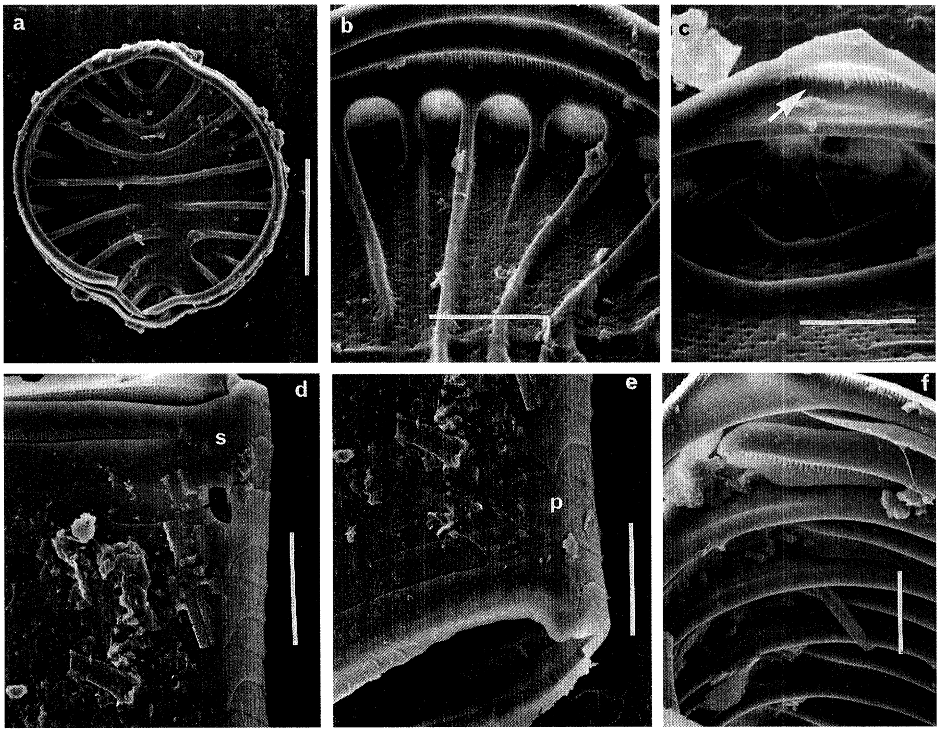

Figure 7. *Tetracyclus ovalifolius*, Poison Creek, USA. (*a*) Internal view of valve, bar = 15.0 μm; (*b*) detail of internal view of valve, illustrating valvocopulae attachment, bar = 5.0 μm; (*c*) detail of internal polar view of valve, illustrating valvocopulae septum, arrowed, bar = 5.0 μm; (*d*) and (*e*), section of cingulum, (*d*) with *s*, (*e*) with *p*, bar = 10 μm; (*f*) internal detailed view of cingulum illustrating attachments between successive bands, bar = 5.0 μm.

Hokkaido' in Japan. Tempère and Peragallo described their fossil deposit as 'Yeso (Japon) Dépot fossile d'eau douce' (Tempère & Peragallo 1909, p.164). According to Tsumura (1967) this spelling represents an old name for Hokkaido and should be correctly spelt 'Yezo'. This is often confused with an alternative locality, 'Yedo', which is an old name for Tokyo and describes a marine deposit (Brun & Tempère 1889). Yezo may be part of the Sentana deposit in Japan and may be from the same material as that studied by Pantocsek (1889) and Okuno (1958, 1959). In which case the distribution of this species, along with others from Japanese deposits, become somewhat clearer as circum-Pacific (see *T. polygibbum*).

Héribaud's combination for *T. lamina* (1893, p. 159, pl. 4, fig. 20) appears to be another yet to be described European species.

Material

USA: Columbia River, *Oregon*, FH-Bail. 854, BM 56028, BM 56029, isotypes.

Washington, Kittatas, BM s.n.; Kittatas, Diatomite, CAS 362079, (USGS 2301), *n* = *po*; E. of Wencellthiger, CAS 362080, (USGS 2302), *n* = *po*; Grant Co. Grennel Deposit, CAS 361086, (USGS 2058), *n* = *po*.

Japan: 'Yezo, Hokkaido', BM 68647, *n* = *po*.

(vi) Tetracyclus maxima (*Figure 1*c)

Tetracyclus maxima D. M. Williams, *nov. sp.*

Basionym: *Tetracyclus rhombus* var. *maxima* Temp. et Perag. (1912, p. 195, nos 365, 366), *nom. nud.*

Type locality: 'Swan Lake Klamath City, Oregon (Etats-Unis)' (Tempère & Peragallo 1912, p. 193).

Type slides: BM GC 3113, holotype, BM 68711–12 (Tempère & Peragallo 1912, *Diat. monde entier*, 2nd edn slide nos 366–7). Tempère & Peragallo (1912) used the name *Tetracyclus rhombus* var. *maxima* for specimens that were present in their Swan Lake, Klamath City, Oregon material. They provide no discussion or annotations for the name, hence it is a *nom. nud.* The specimens should belong to a new taxon and the name *maxima* adopted and validated. From the three slides held in BM, the holotype is designated from the Adams collection, BM GC 3113, as this has the best preserved specimen.

Description

Valve linear to lanceolate, large 50–140 μm long, 10–20 μm wide. Striae parallel, 5–10 in 10 μm; transapical ribs robust, 2–4 in 10 μm; most primary, few secondary and tertiary ribs. Sternum central, linear, rimoportulae not observed (absent?) (figure 1*c*). Girdle not observed.

Material

USA: *Oregon*, Swan Lake, Klamath City, BM GC 3113 (holotype), BM 68711–2, (Tempère & Peragallo, *Diat. monde entier*, 2nd edn nos 365, 366), *n* = *po*.

(vii) Tetracyclus ovalifolius (*Figure 1*f, *Figure 7*a–f)

Tetracyclus ovalifolius (J. Y. Li) D. M. Williams, *nov. stat.*

Basionym: *Tetracyclus ellipticus* var. *ovalifolius* J. Y. Li (1984, p. 232, pl. 1, figs 10, 11).

Type locality: Late Miocene flora of Inner Mongolia, China. (Li 1984, p. 236).

Type slides: BM 81618, 'No: SZ_{11}-1 (9) IM, China', specimen marked number 3, holotype. IGC-Beijing SZ_{11}-1-01 IMS, isotype.

Description

Valves broadly elliptical to circular, elongated at tips of poles, length 60–80 µm, breadth 30–50 µm (figure 1*f*, figure 7*a*). Transapical ribs robust, radiating towards the poles, 2–4 in 10 µm; primary, secondary and tertiary ribs all present, primary predominating (figure 1*f*, figure 7*a–c*). Striae radiate from sternum, parallel to each other at the margin and mantle, 20–30 in 10 µm, 10–15 between (primary) ribs (figure 7*a–c*). Sternum central, linear, slightly raised; pore fields absent (figure 7*a–c*). Rimoportulae not observed (absent?).

Cingulum consisting of open, ligulate bands (figure 7*d–f*). Valvocopula attaching by smooth lip, pars interior rarely extends over ribs, consisting of 2–4 distinct rows of poroids, 28–32 in 10 µm ($n = 4$), ligula absent (figure 7*b*, *c*). Septum extending no more than 1/8 into valve; emanates from pars interior with small pore penetrating to the exterior of the band (figure 7*b*, *c*, arrow). Copulae differ by having advalvar ligulae and mid-band pores; number uncertain, probably 8–10 ($n = 4$) (figure 7*d*, *e* (*p*), *f*). Secondary copulae at least four elements; lacks pore area at the ligula, pars interior consisting of a single row of poroids, band largely hyaline (figure 7*d*, *s*). Pleurae not observed.

Notes

The distribution of this species is limited to fossil deposits on the west coast of the United States and the east coast of China.

Material

USA: *Nevada*, Poison Creek formation, BM s.n. (*Barber* ex *J. P. Bradbury*), *n* = *po*.

CHINA: Den Hua Jiling Province and Shangdu County of Inner Mongolia, BM 81618, 'No: SZ_{11}-1 (9) IM, China', *n* = *po*.

(viii) Tetracyclus polygibbum (*Figure 1*d, *Figure 6*a–c)

Tetracyclus polygibbum (Pant.) Jousé (1952, p. 242, taf. 1, figs 2, 3).

Basionym: *Stylobiblium polygibbum* Pant. (1892, pl. 1, fig. 15; pl. 2, fig. 19); Pant. (1905, p. 99).

Synonyms: *Stylobiblium ovale* Pant. (1892, pl.1, fig. 13); Pant. (1905, p. 99).
Stylobiblium haradae Pant. (1892, pl. 2, fig. 20); Pant. (1905, p. 98).

Tetracyclus jimboi Jousé (1952, p. 242, taf. 1, figs 4–6), *non Stylobiblium jimboi* Pant. = *Tetracyclus stella* (Ehrenb.) Hérib.
Tetracyclus rhombus var. *producta* Temp. et H. Perag. (1909 in Tempère & Peragallo 1907–1915, p. 165, no. 301).

Type locality: 'In stratis tertiariis aquae dulcis ad Sentenaï in insula Jesso' (Pantocsek 1905, p. 99).

Type slides: Not available (Krenner 1979).

Description

Valves gently elliptical (almost circular in some valves) with broadly rounded poles; 20–45 µm long and 7.5–10 µm wide (figure 1*d*, 6*a–c*). Transapical ribs robust, primary, rarely secondary or tertiary; 1–3 in 10 µm (figure 1*c*, figure 6*b*, *c*). Striae more or less parallel, 15–25 in 10 µm, 8–10 between ribs (figure 6*b*, *c*). Sternum central, linear slightly raised; pore fields absent (figure 6*a*). Rimoportulae present 1–2 (maximum 3; *n* = *po*), located either on valve face or (less frequently) at mantle/face junction (figure 6*b*, arrow). Cingulum unknown.

Notes

Pantocsek (1892) described and figured a number of new species from the Sentenai deposit, all of which were eventually synonymized with known species of *Tetracyclus*. Brun (1893) pointed out soon after publication that, in his understanding, the many species described by Pantocsek were, in fact, already published (Brun 1893, p. 53: 'Pl. 2, figs 18–20, Deja nommees ainsi par M. P. Petit'). Such a suggestion has proved counter productive, as fresh inspection of Japanese material has allowed Pantocsek's species to be characterized. An exception is *Stylobiblium jimboi* that appears to be a specimen of *T. stella* (Williams 1995). Jousé (1952) was probably mistaken in synonymizing *S. jimboi* with the other elliptical specimens she examined from the Lake Khanka deposit (Jousé 1952, taf. 1, figs 4–6).

In its present delimitation, *T. polygibbum* is known only from fossils in Japan and Lake Khanka in Russia (although that material has not been available for study). Although it superficially resembles specimens observed from Miocene fossil deposits in the west coast of USA, distinguishing features are evident, such as rimoportulae distribution and the presence or absence of pore fields.

Material

JAPAN: Yezo, Hokkaido, BM 68647, (Tempère & Peragallo, *Diat. monde entier*, 2nd ed. no. 301), *n* = *po*. Baikatsu, Hokkaido, BM 82313–4, *n* = *po*.

(ix) Tetracyclus rhombus (*Figure 1*e, *Figure 8*a–d)

Tetracyclus rhombus (Ehrenb.) Ralfs in A. Pritch. (1861, p. 807).

Basionym: *Biblarium rhombus* Ehrenb. (1845, p. 75)

Synonyms: *Biddulphia woolmanii* Kain et Schultze (1889, p. 74, pl. 89, fig. 3). *Tetracyclus ellipticus* var. *lancea* f. *lata* Hust. in A. W. F. Schmidt (1912, pl. 281, fig. 15 *non* fig. 11); Simonsen (1987, pl. 11, figs 4–5 [excl. desc.]).
Tetracyclus ellipticus var. *lancea* f. *subrostrata* Hust. in A. W. F. Schmidt (1912, pl. 281, figs 17, 18); Simonsen (1987, pl. 12, figs 3–4).

Type localities: 'Fossile in Sibiria et Oregonia' (Ehrenberg 1845, p. 75).

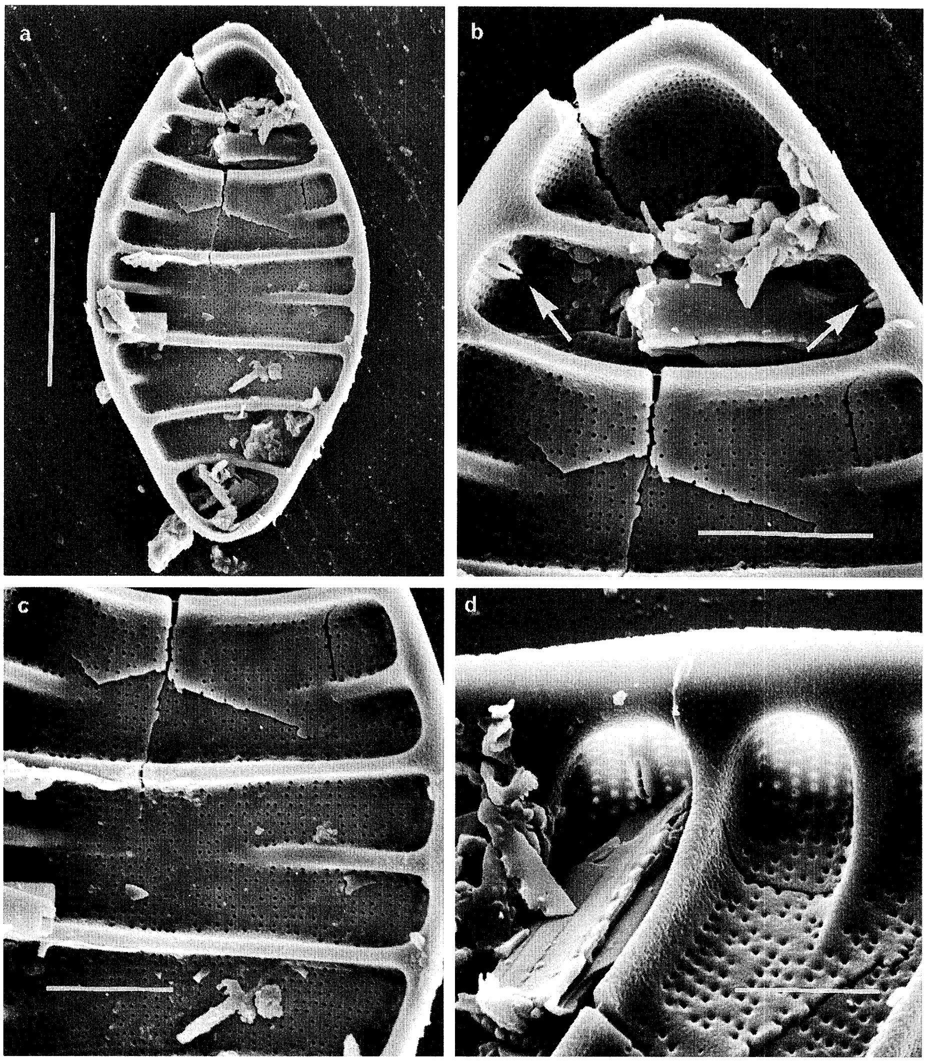

Figure 8. *Tetracyclus rhombus*, Oregon, USA. (*a*) Internal view of whole valve, bar = 15 μm; (*b*) detail of pole from (*a*), arrows indicate *r*, bar = 6.0 μm; (*c*) internal view of valve, illustrating relative positions of transapical ribs, striae and central sternum, bar = 7.5 μm. (*d*) internal view of valve, illustrating marginal *r*, bar = 4.0 μm.

Type slides: Columbia River, Oregon, FH-Bail. 854, BM 56028, BM 56029, isotypes. Illustrated in Ehrenberg (1854, pl. 33/12, figs 7, 8 *non* pl. 33/2, figs 9, 9*, 10 = possibly *T. glans*).

Description

Valve linear to lanceolate, large 30–65 μm long, 30–40 μm wide (figure 1*e*, figure 8*a*). Transapical ribs robust, 2–3 in 10 μm; mostly primary, with occasional secondary and tertiary (figure 1*e*, figure 8*a*–*d*). Striae parallel, 15–20 in 10 μm, 8–10 between ribs (figure 1*e*, figure 8*a*–*d*); Sternum central, linear but faint (figure 1*e*, figure 8*a*–*c*). Valve mantle with prominent external ridge (figure 8*d*). Polar pore fields possibly absent (figure 8*b*). Rimoportulae present on valve face and mantle, 1–3 (av = 2, maximum = 6(?) (figure 8*b*, arrows, see Simonsen 1987, pl. 11, fig. 4).

Notes

In Ehrenberg's original illustrations, he included drawings of specimens from both Siberia and Columbia River, Oregon. From these illustrations, it appears that the specimens from Siberia may really be examples of *T. glans* or a closely related species (e.g. *T. pagesi* or *T. stella*; cf. Hustedt 1914, p. 101, 105: Williams in prep.). Until the Siberian material has been examined these conclusions must be considered unsubstantiated. For further detail of this species see under *T. lata*.

Material

USA: *Oregon*, Columbia River, (FH-Bail. 854, BM 56028, BM 56029), *n* = *po*; Pit River, *Lt. R. S. Williamson*, BM 2342, BM 26181 = *H. L. Smith*, *Diat. spec. typ.* no. 620, (see Bailey 1854), *n* = *po*; Falls River, BM 8822, *n* = *po*; Grant Co., Rustler Peak Quad… Butte Falls-Prospect Hwy, CAS 434007–8; Rustler Peak Quad… Butte Falls-Prospect Hwy, CAS 434012, *n* = *f*(*g*); Harney Co., Trout Creek-Willow Creek Valley: close to NE corner of section 17, CAS 434095–6, *n* = *po*.

Idaho, Twin falls Co., Twin Falls, CAS 383001, (USGS 5585), *n* = *g*3.

Washington, Spokane Co., Mount Spokane, Quadrangle – Latah formation, CAS 383039, (USGS 5680) = auxospore [ribs merge with striae], *n* = *po*; Atlantic

City, artesian well, BM 8019, BM 32663, BM 32741, BM 68491–3, (Tempère & Peragallo, *Diat. monde entier*, 2nd ed. no. 145–47, isotype material of *Biddulphia woolmanii* Kain & Schultz), $n = po$.

Nevada, Esmeralda Co., SW of Loric Mountain + west of Tonopato Esmeralda formation, CAS 382005, (USGS 5078), $n = po$; Nye Co., Cedar Mountain Section Esmeralda formation, CAS 366051, (USGS 3405, Andrews 1970), $n = po$.

Wyoming, Teton Co., Colter Formation, CAS 377016, (USGS 4697), *T.* cf. *rhombus*, $n = f(g)$.

(x) Tetracyclus shangduensis (*Figure 1g*)

Tetracyclus shangduensis Li (1984, p. 235, pl. 2, figs 1–9)

Type locality: Late Miocene flora of Inner Mongolia, China (Li 1984, p. 236).

Type slides: BM 81618, 'No: SZ_{11}-1 (9) IM, China', specimen marked number 5, holotype. IGC-Beijing SZ_{11}-1–01 IMS, isotype.

Description

Valves almost square with rounded, 20–30 µm length, 10–25 µm breadth (fig. 1*g*). Transapical ribs robust, radiating towards the poles, 2–4 in 10 µm; primary, occasional secondary and tertiary ribs present, usually no more than 4–5 ribs per valve (fig. 1*g*). Striae radiate from sternum, parallel to each other at the margin and mantle, 20–30 in 10 µm, 10–15 between (primary) ribs (fig. 1*g*; Li 1984, pl. 2, figs 1–9; Li & Qi 1984, pl. 3, figs 10–11, 16–17). Sternum central, linear, slightly raised; pore fields possibly present (fig. 1*g*; Li 1984, pl. 2, figs 1–9, pore-field pl. 2, fig. 6); rimoportulae, at least two (Li 1984, pl. 2, figs 5–9; Li & Qi 1984, pl. 3, fig. 17). Cingulum consisting of open, ligulate, septate bands (Li 1984, pl. 2, fig. 3).

Notes

This is another distinct species recorded from the Chinese deposits. Although Li (1984) presented a few SEM images, detailed observations on the girdle structure have yet to be made.

Material

CHINA: Den Hua Jiling Province and Shangdu County of Inner Mongolia, BM 81618, 'No: SZ_{11}-1 (9) IM, China', $n = po$.

5. CHARACTER ANALYSIS

(*a*) *Are the 'ellipticus' species monophyletic?*

Data for these analyses have been drawn from a revision of all species currently understood to belong in the genus *Tetracyclus* (table 1, after Williams 1995 and in prep.). Morphological data for the 'ellipticus' species are presented in this paper; for other species see Williams (1987, 1989, 1995; Williams & Li 1990). The limiting factor is availability of specimens for examination. Fossils are usually considered notorious for their poor abundance. However, additional problems occur with diatoms in that often only fragmentary material from rare extant collections is available and many useful characters are not preserved. Hence, not all taxa from table 1 are included in the analyses. Character determination derived from material studied above should be understood as tentative. However, I view having working hypotheses of interrelationships open to testing with further specimens more productive than no hypothesis at all. I present the following discussion and analyses with this aim.

The goal of this analysis is to ascertain whether the 'ellipticus' species are monophyletic within the genus. Below I discuss in detail the morphological features pertinent to the analysis, followed by a cladistic analysis of the data with a discussion of the implications behind the various schemes of interrelationships.

The assessment of relative apomorphy is rendered problematical as outgroup taxa are somewhat difficult to identify. While an examination of the interrelationships of freshwater 'araphid' genera is in preparation, a somewhat different tactic has been used in this study. The derived state is considered to be the presence of a character (represented by a 1+ in the matrix), the primitive state its absence (represented by a 0, zero, in the matrix). Ontogeny (valve development) is used to relate states of the same character, ontogeny being the only empirical evidence of character transformation (Nelson 1978; Kociolek & Williams 1987). Where the plesiomorphic state of a character cannot be established (no ontogenetic evidence available), character states begin from 1 and the relationship among states is considered as unknown (see analysis).

(*b*) ***Characters***

(i) *Origin and transformation of valve shape* (*Figures 9 and 10*)

Character 0: Post-auxospore valve, with central constriction (1) linear (2) central inflation (3)

Character 1: Vegetative valves, with central constriction (1) linear (2) central inflation (3)

Character 2: Pre-auxospore valve, with central constriction (1) linear (2) central inflation (3)

Species in the genus *Tetracyclus* have differently shaped valves at different stages in their life cycles. These shapes may coincide among taxa as well as within a single taxon if different stages of the life cycle are compared. Such observations can cause considerable confusion, not least when the identity of specimens is known from fossils only. However, it is worth emphasizing that considerations of ontogenetic changes have not been as prominent in diatom studies as they have been for some other fossilized groups (e.g. coccoliths, see Young & Bown 1991). A notable recent diatom exception is a study presented by Yanagisawa (1994) on the occurrence of fossil initial (post-auxospore) valves of the raphid diatom *Denticulopsis* that were at first given the generic name *Katahiraia* (Komura 1976) and considered as an independent taxon.

Traditionally, observing a new shape, or a variation on a previously recognized shape in species of *Tetracyclus*, has prompted erection of new taxa, especially at subspecific level (Hustedt 1914). While this may not have any detrimental effect on the identification of specimens, consideration of the po-

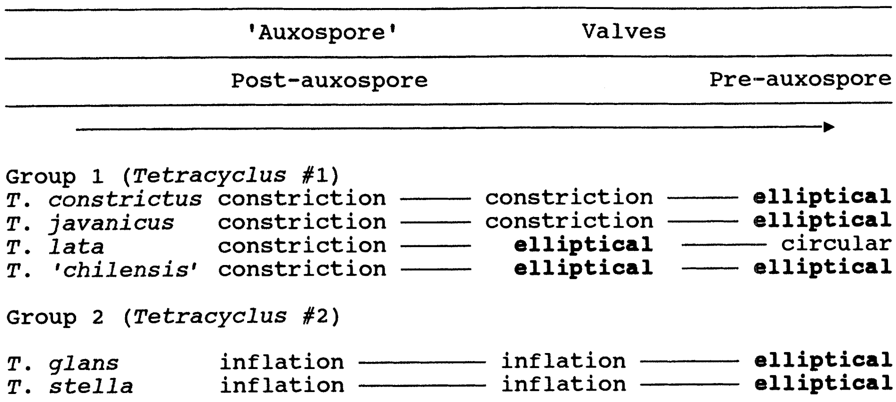

Figure 9. Diagram of valve shape change in a number of species from the genus *Tetracyclus*. The designations post- and pre- auxospore follow the usage in text (arrow for reference to directional change).

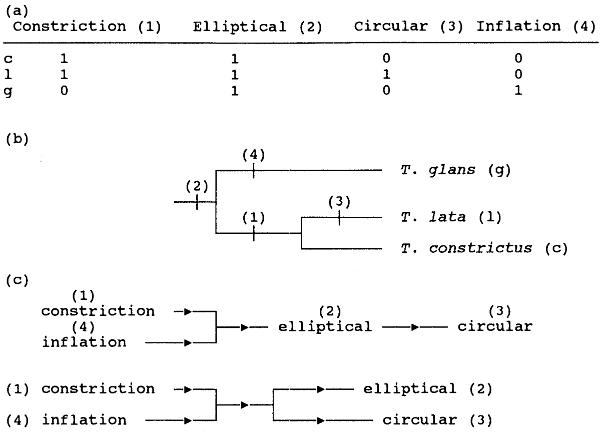

Figure 10*a–c*. (*a*) Matrix of characters against taxa as binary variables; (*b*) character state tree constructed from these data. c = *T. constrictus*, l = *T. lata* and g = *T. glans*. The figure in brackets above each shape designation is the coding number; (*c*) upper diagram is a representation of valve shape change with direction of change indicated by the arrow; lower diagram is the character state tree constructed from these data. The figure in brackets above each shape designation is the coding number. Arrows on lines indicate direction of change (ontogenetically).

tential intergrading of shapes has prompted complex representations of taxon interrelationships (Hustedt 1914; comments in Williams 1994) along with explicit suggestions that subspecific taxa are somehow 'closely related'.

The particular shape that the valves of *Tetracyclus* exhibit range from elliptical, lanceolate, elliptical with a centrally constricted 'waist', along with various 'star'- and 'box'-like shapes. Notwithstanding the difficulty in pigeon-holing a particular shape observed (see, for instance, Mou & Stoermer 1992 study on shape interpretation in the genus *Tabellaria* Ehrenb.), it is important to establish at which stage particular shapes occur in any one life cycle; that is, where and how does shape change occur and what factors may be responsible. It is plausible that the various valve shapes may be explained by the presence of transverse perizonial bands such that constraint is apparent only on certain parts of the valve: transverse bands that occur at the centre would cause a central constriction; polar transverse bands would cause a central inflation. Perizonial data are unavailable for species of *Tetracyclus* (but see Williams 1990).

Broadly speaking, species in the genus *Tetracyclus* can be divided into two distinct valve outline-types: those with a central inflation and those with a central constriction (shapes that occur somewhere in the life cycle; figures 9 and 10). Group 2 consists of those species that typically possess a central inflation, such as *T. glans* and *T. stella* (Williams 1990); and Group 1 typically consists of those that possess a central constriction, such as *T. constrictus*, *T. javanicus*, *T. lata* and *T. ellipticus* var. *lancea* f. *chilensis* Krasske (Williams 1990, 1995). The elliptical shape appears in all of these taxa at some stage in the life cycle.

If the auxospore is considered as the beginning of the life cycle, three alternatives occur: valves can have a central inflation, a central constriction or are linear (figure 10). As the cells divide and become smaller, these three alternatives pass through the elliptical stage (linear); only one species (*T. lata*) continues to a circular stage. The sequence of change may be considered as a continuum because of the dynamic nature of ontogenetic change.

Alternative character state trees do not reflect the temporal sequence constructed from ontogeny (compare figure 10*b* with 10*c*). The conflict appears in the distinction between auxospores with inflated as opposed to constricted valves and the shape of pre-auxospore valve. This suggests that one auxospore type may be derived relative to the other.

(ii) *Striae*

Character 3: Valve striae and sternum meet (1), do not meet directly except for an area of further silicification at the sternum (2)

Character 4: Striae diverge at poles (1), parallel (2)

Tetracyclus has a unique striae arrangement different from that of other freshwater 'araphid' diatoms where the vimines are considerably smaller relative to the virgae (Williams 1987). While this is a putative synapomorphy for the genus, differences among species are restricted to how 'completely' the striae meet the sternum (by meet, I refer to their appearance; clearly the striae develop from the sternum and this area, if coalesced, probably indicates additional silicification of the sternum rather than incompletely silicified striae). The striae vary also in the way they may or may not diverge at the poles. Characters derived from these observations are extremely tenuous and depend to a certain extent upon how well they can be discriminated. This is an area for further study from the perspective of valve morphogenesis rather than 'static' specimens – clearly impossible when dealing with fossils. For instance, *T. rupestris* (Williams 1987, figs 45 and 46) clearly has a sternum that coalesces with the striae. But is this due simply to its size? (*T. rupestris* is considerably smaller than other species in the genus.) In one respect this must be true, reinforcing a general point constantly re-emerging, that characters are truly understood by ontogeny (Mann 1984).

(iii) *Transapical ribs*

Character 5: Secondary ribs absent (0) present (1)

Character 6: Tertiary ribs absent (0) present (1)

Character 7: Ribs absent at the poles (0) present at the poles (1)

Williams (1985, p. 25–26) distinguished among three types of siliceous rib, primary, secondary and tertiary. The definitions were originally offered with the genera *Diatoma* Bory and *Meridion* C. A. Agardh in mind. However, it is possible to extend their meaning and application, with slight modification, to all 'araphid' diatoms that possess ribs, and the variation affords further characters. Primary ribs '... extend completely across the valve face from mantle to mantle, without any ... interruption ...' Williams (1985, p. 25); secondary ribs '... extend from the sternum to the mantle, only in a single half of the valve' (Williams 1985, p. 26; half is here understood as to one side of the sternum); and tertiary ribs '... extend from the sternum to the valve mantle but not noticeably raised above the surface of the valve until closer to the valve mantle' (Williams 1985, p. 26). Once again, ontogeny may assist in ascertaining the relationships these ribs have with each other (as in *Diatoma* and *Meridion*, Williams 1985). Are primary ribs complete secondary ribs, and, in turn, are secondary ribs complete tertiary ribs? Is there a connection between the various aspects of rib development? In this instance, while extremely likely that the ribs do progressively modify, there is as yet no available evidence and hence the features are treated as individual characters. No redundancy is introduced, as all types of ribs can co-exist and the presence of one type of rib need not force acceptance of other types. The development of ribs is a worthwhile area for further examination. Preliminary study suggests that, unlike *Diatoma* and *Meridion*, the ribs arise very early in valve morphogenesis (Williams 1987).

(iv) *Valve mantle*

Character 8: Mantle edge shallow (0), mantle edge deep (1)

T. clypeus (Williams 1989, figs 8–11) and *T. ovaliformis* (figure 7*a–c*) possess an extremely deep external valve lip giving them a 'bowl'-like appearance. All other species have a shallow or absent valve lip.

(v) *Rimoportulae*

Character 9: Rimoportulae 1 per valve (0) absent (1), more than 2 per valve (2)

Character 10: Rimoportulae situated on valve mantle/face border (1), on valve face (2), on valve mantle (3) both mantle and face (4)

The number of rimoportulae is significant in this genus and ranges from complete absence (in *T. glans*) to several (in *T. lata*). Occurrence of rimoportulae throughout 'araphid' diatoms suggests that their absence is a derived feature (Williams 1995). Indeed, one entire group of 'araphid' diatoms can be characterized by their absence, among other features (Williams 1995): *Ardissonea* De Notaris (Poulin *et al.* 1987; Round *et al.* 1990), *Climacosphenia* Ehrenb. (Round 1982; Round *et al.* 1990), *Synedrosphenia* Azpeitia (Round *et al.* 1990), *Entopyla* Ehrenb. (Prasad & Fryxell 1991) and *Gephyria* Arnott (John 1986; Round *et al.* 1990). This observation is taken into account for coding.

The position of rimoportulae may be either on the valve face or mantle. At present there seems to be no obvious pattern to their distribution.

(vi) *Pore fields*

Character 11: Pore fields absent (0) present (1)

Distinguishing pore fields may be problematic. In this study I have chosen to recognize pore fields if the striae at the polar portions become noticeably more compact. In this sense a pore field is demarcated and distinct from 'normal' valve structure. It may be argued that such a distinction simply characterizes the converging striae at the polar tips and has no bearing on whether the 'structure' functions as a pore field or not. While this may be true, in the sense that commonality of a structure implies commonality of function, it is not a pre-requisite and pore fields may indeed have originated (ontogenetically) from coalesced valve striation.

(vii) *Spines and surface notches*

Character 12: Spines or surface notches (= granules, Ross *et al.* 1979, p. 522) absent (0) present (1)

The term 'granule' has not received a great deal of attention and its usage has been limited. Ross *et al.* (1979, p. 522) defined a granule as a 'small rounded projection on the surface of the valve' and included it as a subdivision of terms appropriate for different kinds of valve surface spines. However, they gave no examples. Following their definition, the 'spines' observed on the valves of some species of *Tetracyclus* are properly interpreted as granules and I adopt their term here to avoid the introduction of a perhaps new and unnecessary term. Granules are present on the marginal surface of some species of *Tetracyclus*. They appear as small spine-like projections but probably play no part in colony formation.

(viii) *Girdle*

Character 13: Girdle with all open bands (0) with closed bands (1)

The girdle structure for *Tetracyclus* is extremely conservative and appears to be similar in all species examined. Examination is limited when fossil specimens are considered but a remarkable number have been discovered with complete sets of cingula. Some features, such as the amount and kind of band ornamentation, distinguish different species. A crucial difference is, however, emerging with the discovery of two species possessing completely closed bands: *T. cruciformis* and *T. lacustris* var. *parvula* Forti (as *T.* '*parvula*' below, Williams in prep.). The typical condition among 'araphid' diatoms is the open ligulate band (Williams in prep.). Hence the observation of closed bands is considered a derived condition.

(ix) *Valvocopula*

Character 14: Valvocopula attaches by extensions to the pars interior (1) by smooth flap (2)

Table 1. *Species of* Tetracyclus *currently recognized* (*Williams 1995*) *: 32 species listed, four extant, 28 known from fossils only*

(Available data are appended as either valve and/or girdle. In some instances data are only partially known (p). Species considered in this study are indicated with [a]; species with sufficient data to be considered in the character analysis are indicated with [b]. The taxon referred to as *T. parvula* is currently known as *Tetracyclus lacustris* var. *parvula*.

species	valve	girdle
extant		
T. emarginatus[b]	+	+
T. glans[a]	+	+
T. javanicus[b]	+	+ (p)
T. rupestris[a]	+	+
extinct		
T. boryanus[a]	+	−
T. castellum	+	+ (p)
T. clypeus[b]	+	+
T. constrictus[b]	+	+
T. cruciformis[b]	+	− (p)
T. divisium	+	−
T. ellipticus[a,b]	+	+ (p)
T. excentricum[b]	+	+
T. inflata	+	−
T. japonicus[b]	+	+
T. lancea[a,b]	+	+
T. lata[a]	+	−
T. liensis	+	−
T. linearis[a,b]	+	+
T. maxima[a]	+ (p)	−
T. ovalifolius[a,b]	+	+
T. pagesi	+ (p)	−
T. parvula[b]	+ (p)	+ (p)
T. peragalli	+	+ (p)
T. polygibbum[a]	+ (p)	−
T. pseudocastellum	+	+ (p)
T. quadriformis[b]	+	− (p)
T. rhombus[a,b]	+	−
T. shangduensis	+ (p)	+ (p)
T. stella[b]	+	+ (p)
T. subclypeus	+	−
T. subdivisium	+	−

The valvocopula can attach in various ways to the valve. Mann (1982) noted that the pars interior of the valvocopula may simply reflect the structure of the valve, use of its mode of attachment as an independent character may be suspect. Undoubtedly this is true, yet instances of dissimilar valvocopulae with similar valves have been observed in species of *Tetracyclus*. As such, this character is given some consideration with respect as to whether the internal part of the band is fragmented or not.

(x) *Copulae and pleurae*

There is great uniformity among the girdles of species in *Tetracyclus* and no differential characters have been discovered that suggest relationships among taxa. Data do suggest certain unique features (such as the multiple rows of pores in *T. clypeus*, see Williams 1989) but the overall composition of cingula is confined to *Tetracyclus* and *Tabellaria* (Williams 1995). Nevertheless, girdle characters are worth further exploration.

(xi) *Data matrix*

Data have been obtained for all species marked with [b] in table 1. Inclusion of all taxa in table 1 results in a completely collapsed tree, resolution obscured by the abundance of missing values. Therefore taxa have been selected to maximize information.

The matrix in table 2 consists of 17 taxa (four extant taxa, the remaining 13 known from fossils only) and a total of 15 characters (numbered 0–14) of which eight are coded as multistate characters and seven as binary characters. This matrix was used for (a) the standard analysis, (b) the successive weighting analysis and (c) 'implied weights' analyses.

The matrix in table 2 was used as the basis for a three-item statement matrix using the suite of programs TAX (Nelson & Ladiges 1995). With respect to three-item representation, two binary characters of the original matrix are considered uninformative (characters 2 and 7) while only one of the seven multistate characters of the original matrix is considered informative (character 9). Thus, characters 3, 5, 6, 8, 9, 11, 12, and 13 are used for three-item representation (three-item matrix available on request). This matrix yielded 838 three-item statements of which 704 were unique (84% of the total), and was used for the (d) three-item uniformly and (e) fractionally weighted analysis.

(xii) *Analyses*

Parsimony analysis was undertaken on all matrices produced as above, using the computer program Hennig86 (Farris 1988) and NONA (Goloboff 1996) with an all-zero outgroup and the non-additive option (unordered or 'Fitch' optimization, Fitch 1971). Matrices were analyzed using the *implicit enumeration* (*ie*) option wherever possible to find all most parsimonious trees (Farris 1988). In cases where excessive time prohibited the use of the *ie* option (in this case *ca.* 48 hours with no result), the *mhennig* (*mh*) and *bb* (extended branch-swapping) options were used in combination as

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Table 2. *Data matrix*

(Characters numbered 0–14 following the convention in Hennig86. Missing data are indicated by '?' for unknown and 'NA' for not applicable. Partitions of taxa correspond to informal groups recognized in Williams (1995).)

	characters														
taxa	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
extant															
T. glans	3	3	2	1	1	0	1	1	0	1	NA	1	1	0	2
T. javanicus	1	1	2	1	2	0	1	1	0	1	NA	1	0	0	2
T. rupestris	2	2	2	2	2	0	0	1	0	0	2	1	0	0	2
T. emarginatus	?	3	?	1	2	1	1	1	0	2	4	1	1	0	2
extinct															
T. cruciformis	3	3	?	2	1	1	1	1	?	1	2	?	?	1	?
T. parvula	?	3	?	1	1	0	1	1	?	1	NA	?	?	1	?
T. quadriformis	3	3	?	1	1	1	1	1	0	1	1	1	0	0	2
T. stella	3	3	2	1	1	0	1	1	0	0	1	1	0	0	2
T. constrictus	1	1	2	2	2	0	1	1	0	0	1	1	0	0	2
T. clypeus	2	2	2	2	1	1	1	1	1	1	3	0	1	0	2
T. excentricum	?	2	?	1	2	0	1	1	0	1	3	1	0	0	2
T. ellipticus	2	2	2	1	2	0	1	1	0	2	3	1	0	0	2
T. lancea	?	2	2	2	2	0	1	1	0	2	3	0	1	0	1
T. linearis	?	2	2	1	2	1	1	1	0	2	2	1	0	0	2
T. rhombus	?	2	?	1	2	1	1	1	0	2	3	1	0	0	?
T. ovalifolius	?	2	2	2	1	1	1	1	1	1	NA	0	0	0	2
T. japonicus	?	2	2	2	1	1	1	1	0	0	3	0	0	0	2

they have been reported to be as good as the *ie* option on many test data sets (Platnick 1989). The order of taxon input was varied to assist in obtaining the optimal result. The fit of data to the tree is measured by the consistency (*ci*, Kluge & Farris 1969) and retention (*ri*, Farris 1989) indices as well as tree length.

For the standard analysis, all characters were assigned equal weights. Character weighting, when applied *a posteriori*, should favour those that 'best fit' the initial topology; 'best fit' is judged by the shortest tree (Farris *et al.* 1970), shortest for the weighted data in terms of tree length (Farris 1969), or heaviest when considered as a function of the weights (Goloboff 1993). Trees yielded from equal weighting were the basis for application of successive weighting (Farris 1969, as implemented by the *xs w* option in Hennig86). The matrix in table 2 was used for the 'implied weighting' analysis of Goloboff (1993, as implemented in the MS-DOS program PIWE, Goloboff 1996). Successive weighting utilizes the rescaled consistency (*rc*) index (Farris 1989), calculated as the product of *ri* times *ci*, scaled between 0 and 10, as the active weighting functions of each character. Goloboff's (1993, 1996) implied weighting utilizes the number of extra steps per character such that the weight $= K/(K+ESi)$, where ESi is extra steps per character and K is a constant of concavity. The value K can be varied from 1 to 6 where higher values of K weight less strongly against homoplastic characters (Goloboff 1993).

Three-item matrices were analyzed using Hennig86. Tree length also measures how well the data fit a particular tree, the 'best-fitting' tree being the shortest. The rationale is that statements that fit a particular tree at a node count as one step towards the total tree length. Statements that fit the tree twice (at two nodes) have a value of two steps. As each statement has only two entries (taxa excluded from consideration receive a ?), the best possible fit is one step, the 'worst' possible fit is two steps (Nelson & Platnick 1991). Tree length can be calculated as the product of the number of statements that fit the tree plus twice the number of statements that do not (Nelson 1992, Nelson & Ladiges 1994).

For binary characters the number of possible three-taxon statements is given by the general formula: $(t-n)n(n-1)/2$, where $t =$ the number of taxa and $n =$ taxa with the informative (apomorphic) state. When $n > 2$ there is redundancy among the statements. The number of independent three-item statements is $(n-1)(t-n)$ and the absolute value is the ratio of independent statements to total statements, $2/n$ (Nelson & Ladiges 1992). Use of absolute values can eliminate redundancy. Absolute values have been used for the fractionally weighted matrix, total values have been used for the uniformly weighted matrix (as implemented by TAX, Nelson & Ladiges 1995).

For each three-item matrix processed, all trees were retained as tree files (using the *tsave* option of Hennig86). There is potential for conflict between a suite of most parsimonious trees and minimal trees when nodes may be resolved spuriously in the former. A strict consensus tree (*nelsen* option) from the suite of most parsimonious trees was recovered and its length noted. If the consensus tree was of identical length to the most parsimonious trees it was considered the minimal tree and 'best' for the particular matrix. This minimal tree should have all nodes supported by data; the most parsimonious trees, in these instances, would be over-resolved in having nodes not supported by data (Nelson 1992).

6. RESULTS AND DISCUSSION

(*a*) *Standard analysis* (*Figure 11*)

Analysis of the matrix in table 2 yielded 128 equally parsimonious trees (*ie**, length = 42, *ci* 61, *ri* 68). The strict consensus tree retains five nodes (length = 61) (figure 11*a*). The 128 equally parsimonious trees differ in their resolution: eight trees of 15 nodes, 29 trees of 14 nodes, 43 trees of 13 nodes, 33 trees of 12 nodes, 13 trees of 11 nodes and two trees of ten nodes.

Comparison with the use of NONA (Goloboff 1996) reveals some differences. With ambiguous optimization excluded, NONA yielded six trees (length = 42, 15 nodes, *ci* 61, *ri* 68; and length = 38, *ci* 57, with uninformative characters excluded). With the inclusion of ambiguous optimization, NONA yielded 119 trees (length = 42, *ci* 61, *ri* 68; and length = 38, *ci* 57, with uninformative characters excluded). This result implies that the majority of trees have support from ambiguous character optimizations. Recent discussion concerning over-resolution of trees caused by missing data (Platnick *et al.* 1991) and ambiguous optimizations (Wilkinson 1994) requires examination of each node on each tree to ascertain actual support in the data. This can be established by collapsing branches of particular trees and noting if the tree length changes. In such cases, when nodes can be collapsed and tree length remains the same, the final tree can be regarded as minimal, in the sense that all nodes are supported by actual data (Nelson & Ladiges 1996). Of the six trees resulting from exclusion of ambiguous optimizations, each can be reduced to a tree with fewer nodes and no increase in tree length. Of the six, two trees reduce to the same ten node tree, the remaining four trees reduce to trees of 11, 12, 13 and 14 nodes. The ten node tree is considered the minimal tree for these data (fig. 11*b*).

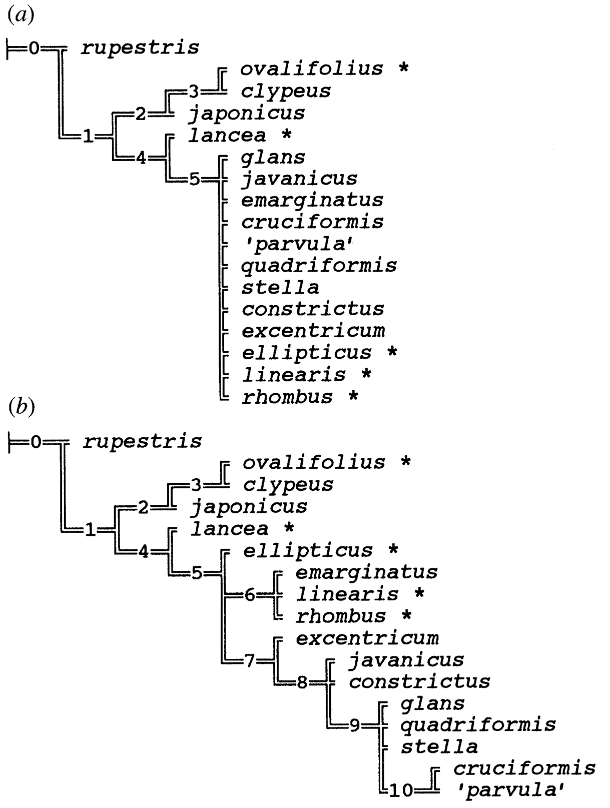

Figure 11*a*–*b*. (*a*) Strict consensus tree (consensus tree length = 61 from 128 trees, *ie**; length = 42, *ci* 61, *ri* 68). Of the 128 trees, eight have 15 nodes, 29 have 14 nodes, 41 have 13 nodes, 33 have 12 nodes, 13 have 11 nodes and two have ten nodes. (*b*). The ten node minimal tree from one of six found by NONA (length = 42; *hold* 100; *hold*/20; *mult**50, all replication founds trees of length = 42).

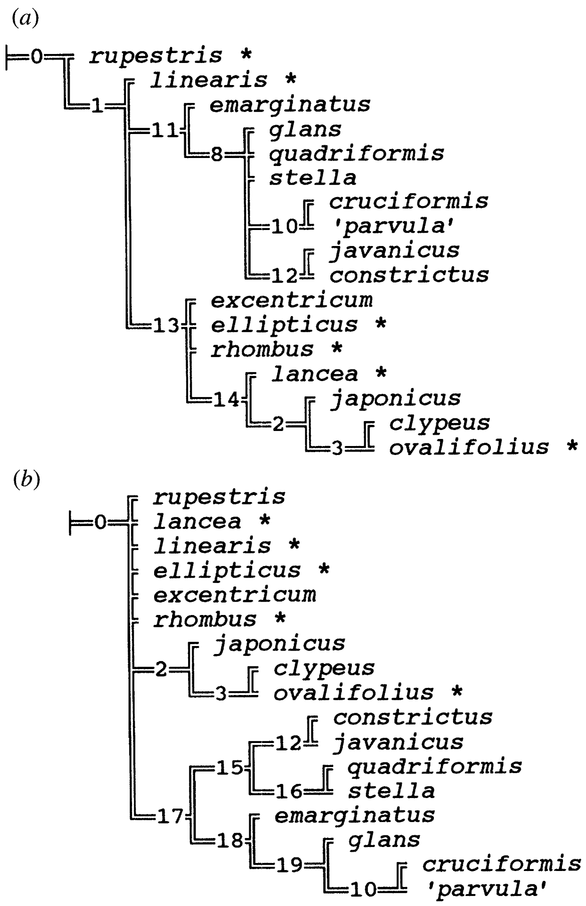

Figure 12*a*–*b*. (*a*) Strict consensus tree (length = 215, nine nodes) from successive weighting of the original 128 trees. Strict consensus tree derived from 40 trees (*ie**, length = 205, *ci* 90, *ri* 90). Original 128 trees on weighted data result in lengths = 212–238; weighted data on original trees are length = 45. (*b*) Strict consensus of two best-fitting trees from PIWE (length = 51, total fit = 91.5, nine nodes). PIWE yields two best-fitting trees (total fit = 91.9; 15 nodes; *hold* 100; *hold*/20; *mult**50; 11 of the replications found trees of fit = 91.5) but of greater length (length = 44) than those from equal weighting (length = 42). All 128 trees from the standard analysis (equal weighting) have a poorer total fit but are shorter.

(*b*) *Successive weighting* (*Figure 12*a)

Successive weighting (after six iterations) produces 40 cladograms (length = 205, *ie**; *ci* 90, *ri* 90) of which the strict consensus yielded a tree with nine nodes of length = 215 (figure 12*a*). None of the 128 equally weighted trees are included among these 40 (the original trees are of length = 212–238 for the weighted matrix). The 40 trees are of length = 45 when optimized on to the original unweighted matrix

Table 3. *Weights assigned to characters as implemented in* PIWE (*Goloboff 1996*)

(Constant (*K*) varied from 1–6 (first column), default $K = 3$. In each case PIWE recovered two trees. S, weights assigned from the *rc* (see text) as implemented in Hennig86 (last row).)

characters															
K	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	10.0	10.0	–	2.5	3.3	1.6	5.0	–	10.0	1.4	10.0	10.0	3.3	10.0	–
1	10.0	10.0	–	2.5	3.3	1.6	10.0	–	10.0	1.4	10.0	5.0	3.3	10.0	–
2	10.0	10.0	–	4.0	5.0	2.8	6.6	–	10.0	2.5	10.0	10.0	5.0	10.0	–
2	10.0	10.0	–	4.0	5.0	2.8	10.0	–	10.0	2.5	10.0	6.6	5.0	10.0	–
3	10.0	10.0	–	5.0	6.0	3.7	7.5	–	10.0	3.3	10.0	10.0	6.0	10.0	–
3	10.0	7.5	–	6.0	7.5	5.0	10.0	–	10.0	4.2	6.0	7.5	5.0	10.0	–
4	10.0	10.0	–	6.6	6.6	5.7	10.0	–	10.0	5.0	8.0	8.0	5.7	10.0	–
4	10.0	10.0	–	6.6	8.0	5.7	10.0	–	10.0	5.0	6.6	8.0	5.7	10.0	–
5	10.0	10.0	–	7.1	7.1	6.2	10.0	–	10.0	5.5	8.3	8.3	6.2	10.0	–
5	10.0	10.0	–	7.1	8.3	6.2	10.0	–	10.0	5.5	7.1	8.3	6.2	10.0	–
6	10.0	10.0	–	7.5	7.5	6.6	10.0	–	10.0	6.0	8.5	8.5	6.6	10.0	–
6	10.0	10.0	–	7.5	8.5	6.6	10.0	–	10.0	6.0	7.5	8.5	6.6	10.0	–
S	10	10	10	2	3	0	10	10	10	1	10	3	0	10	10

Table 4. *Numbers of best-fitting trees for* $K = 1$*–6*

(*K*, constant of concavity; *Tr*, number of trees; *L*, length of tree; Fit, best-fitting value (sum of character weights); s1, trees from Hennig86 (equal weighting); s2, trees from Hennig86 (weighted), fit statistics for $K = 3$ (PIWE default).)

K	Tr	*L*	Fit
1	2	45	77.1
2	2	45	85.9
3	2	45	91.5
4	2	42	95.6
5	2	42	98.7
6	2	42	101.2
s1	128	42	88.0–91.2
s2	40	45	90.9

(character's weights given in table 3, row s). Best fitting characters are 0, 1, 2, 7, 8, 10, 13 and 14; characters 2, 7 and 14 are uninformative, thus five characters provide maximum information (characters 0, 1, 8, 10 and 13).

(*c*) *Implied weighting* (*Figure 12*b)

PIWE yielded two best-fitting trees (total fit = 91.5, 56%; 15 nodes) both of greater lengths (length = 45) than those produced using equal weighting (length = 42). All 128 trees from the standard analysis (equal weighting) have a poorer total fit of 88.0–91.2 but are shorter (lengths = 42) (table 4). A strict consensus of the two best-fitting trees produces a tree of nine nodes with length = 51 and total fit = 91.9 (figure 12*b*). As with the equally weighting analyses, if ambiguous optimizations are allowed the number of trees produced is 31, again implying many of these trees are resolved by such optimizations.

When *K* is increased the overall value of the best fit also increases, as expected (77.1–101.2, see table 4). When $K =$ 5 characters 0, 1, 8 and 13 all have the highest values and are consistent across all trees. Characters 6 and 10 receive alternative weights between the maximum and 5.0 or 7.5 among the two equally best-fitting trees depending upon the *K* value (tables 3 and 4). When $K = 5$ and 6 both trees are of length = 42; the best characters (0, 1, 8 and 13) retain highest values (character weights given in table 3).

Experimentation needs to be undertaken to establish how strongly characters should be weighted in terms of *K*. Goloboff (1995, p. 45) suggests that if tree searches are performed under a variety of functions ($K = < 0 > 7$), the groups which appear throughout these available ranges should be retained. Turner, however, suggests caution in that 'different values of *k* corresponds to different weighting schemes, not all values are expected to result in the same trees' (Turner 1995, p. 43). This appears the case here when high values ($K = 5$ or 6) are used giving trees equivalent to equally weighted trees (length = 42 rather than 45 for the unweighted data).

(*d*) *Three-item analyses* (*Figure 13*)

For the uniformly weighted three-item matrix, 3264+ (overflow) trees results (length = 1057, *mh**, *bb**, *ci* 79, *ri* 73) with the strict consensus tree of length = 1113 (figure 13*a*; not a minimal tree, five nodes). However, if sample trees are examined from the suite of 3264, trees of equal length but with 11 nodes can be recovered by collapsing nodes unsupported by data. Because the tree file is large only a sample ($n = 50$) was examined in this way. Processing the matrix with NONA and excluding ambiguous optimizations results in 24 trees, with the implications that the majority of the 3264 trees have spurious resolution.

With fractional weighting (with a factor of × 50, total weight = 11264) nine trees were recovered (figure 13*b*, *mh**, *bb**, length = 13816, *ci* 81, *ri* 77) of which the strict consensus tree was also of length = 13816 and thus is the minimal tree (13 nodes). Results were identical using NONA.

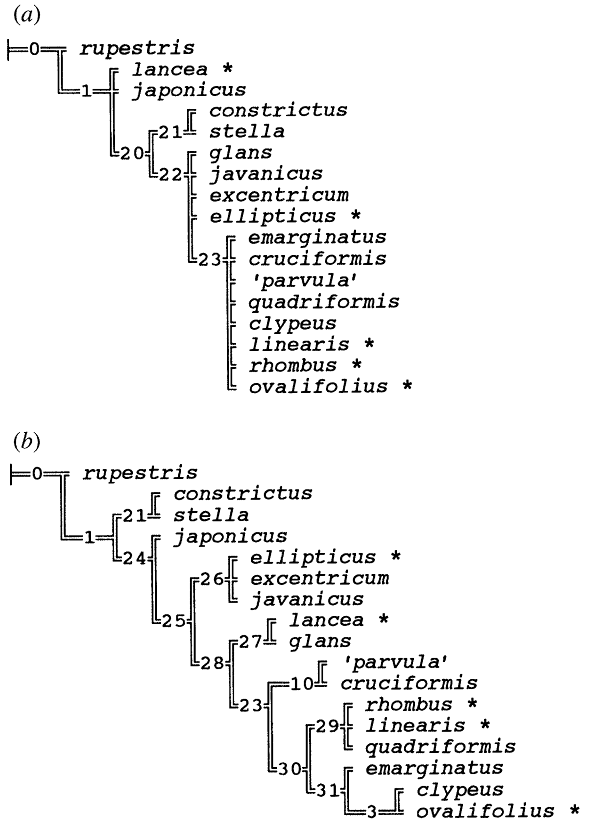

Figure 13*a–b*. (*a*) Uniformly weighted three-item matrix yields 3264+ (overflow) trees (*mh**, *bb**; length = 1057, *ci* 79, *ri* 73). Strict consensus tree illustrated with five nodes (length = 1113, not a minimal tree). (*b*) Fractionally weighted (×50) matrix yields nine trees (*mh**, *bb**; length = 13816, *ci* 81, *ri* 77). Strict consensus tree illustrated with 13 nodes (length = 13816, the minimal tree).

(*e*) *Assessment of trees, characters and taxa*

Trees yielded from each analysis differ in certain aspects of their topology. For a fully resolved tree of 17 taxa, 16 nodes are required to be fully informative. All trees presented are less than fully resolved: the best tree for the standard equally weighted analysis (figure 11*b*) having ten nodes, the successively weighted tree (figure 12*a*) having nine nodes (shared among the original 40 trees, with 10–15 nodes), the implied weighting tree (figure 12*b*) having nine nodes (shared among the original two trees, with 15 nodes), the three-item uniformly weighted tree (figure 13*a*) having five nodes (shared among the original 3264+, with 15 nodes) and the three-item fractionally weighted tree (figure 13*b*) having 13 nodes shared among the original (the strict consensus being a minimal tree).

Overall, solutions offer 31 different nodes (excluding basal node 0) of which none are common to all trees. Excluding the strict consensus tree for the standard analysis (figure 11*a*, all nodes from this tree are included in the minimal tree of figure 11*b*), for the five trees presented here, nodes 1, 3 and 10 are common to four trees, node 2 is common to three trees, nodes 8, 12, 21 and 23 are common to two trees, the remaining 23 nodes unique to a particular tree. None of these nodes group the 'ellipticus' species together.

Characters 2 (pre-auxospore valve structure) and 7 (transapical ribs absent or present at the poles) are uninformative; character 2 lacks an informative alternate state value and character 7 is autapomorphic for all taxa. Character 14 (valvocopula attachments) is seen as uninformative when using implied weights or three-item statement representation (see below).

In various analyses, characters 0 (post-auxospore valve structure), 1 (vegetative valve structure), 6 (tertiary transapical ribs absent or present), 8 (mantle edge), 10 (rimoportulae position) and 13 (girdle with open or closed bands) perform best receiving a maximum weight of 10. Maximum weight is assigned by both successive and implied weighting except for character 10 (table 3). Although successive weighting gives maximum weight to characters 2, 7 and 14, they are all uninformative (table 3).

Character 0, when analyzed alone, yields 3268+ (overflow) trees and seems ambiguous with respect to possible solutions, as does character 10 which yields 3266+ (overflow) trees; character 1 yields nine trees which jointly represents node 12 (*javanicus* plus *constrictus*), character 6 yields one tree representing basal node 1 (all taxa excluding *rupestris*), character 8 yields three trees which are ambiguous with respect to possible solutions among *clypeus*, *ovalifolius*, *cruciformis* and '*parvula*' as well as presenting possible conflict with character 13 which yields one tree representing node 10 (*cruciformis* plus '*parvula*').

The remaining characters vary in their performance with characters 5 (secondary ribs absent or present, weight of 0 for successive weighting; 1.6–6.6 for implied weighting) and 9 (rimoportulae number; weight of 1 for successive weighting; 1.4–6.0 for implied weighting) performing the worse. Parsimony analysis with the omission of character 5 yields six trees (length = 37, *ie**, *ci* 67, *ri* 73) of which the strict consensus is one of the six. However, parsimony analysis with the omission of character 9 yields 243 trees (length = 36, *ie**, *ci* 66, *ri* 72) of which the strict consensus tree has only three nodes and is of length = 56; character 9 is highly variable and establishing numbers of rimoportulae per valve is extremely difficult. It is worth noting that, in the past, such features as the number of rimoportulae has figured heavily in the classification of 'araphid' diatoms (e.g. Simonsen 1979). This may now seem premature. However, the position of rimoportulae on the valves (character 10) may have potential value.

From the perspective of three-item statement representation, different characters are seen as informative. Of the seven binary characters (table 2; 5–8, 11–13), 2 and 7 are likewise seen as uninformative. Of the eight multistate characters (table 2; characters 0–4, 9, 10 and 14) only character 9 is seen as informative, in contrast to the above. Removal of the uninformative characters leaves a matrix of just seven standard characters, when analyzed yields 3268+ (overflow) trees (length = 15, *mh**, *bb**, *ci* 53, *ri* 72) of which the strict consensus tree is a bush (length = 33). Application of successive weighting reduces this number to 1742 trees (length = 59, *mh**, *bb**, *ci* 89, *ri* 95) of which the strict consensus tree is still a bush. Again, because of the abundance of question marks, some of the original trees may be reduced to minimal trees. Of the original suite, 191 have 13 nodes, 505 have 12 nodes, 715 have 11 nodes, 789 have ten nodes, 621 have nine nodes, 328 have eight nodes, 101 have seven nodes, 17 have six nodes, and one has five nodes. NONA (with ambiguous optimizations suppressed) reduces the number of trees to 927, but it is not certain that this is the optimal solution under the criteria specified. Whatever, these data, as represented by standard characters, are uninformative, yet rendered into three-item format yield resolved solutions (figure 13*a*, *b*).

Nevertheless, these data, however represented, are ambiguous with respect to the interrelationships of the fossil species of the 'ellipticus' group as represented in the various matrices. Different representations see different observations as significant. Nevertheless, it seems clear that the 'ellipticus' species group does not form a monophyletic group. Characters referring to the post-auxospore and vegetative valve structure appear maximally informative. Significant to this analysis is that the 'nature' of the valves, however judged, appears primitive. *T. rupestris*, the basal species, is elliptical throughout its entire life cycle while many of the remaining species appear to have an elliptical stage as part of their life cycle.

Further consideration of the ontogeny of valves should illuminate these results, as it appears that post-auxospore valves are usually elliptical with ontogeny and phylogeny coinciding (Williams 1990, 1995). In short, diatom ontogeny is crucial to the understanding of their morphological characters.

With the revised species definitions above, a few of the fossil taxa have restricted distributions that (broadly) coincide with the circum-Pacific area. Clearly the relationship between fossil floras from the east coast of Japan and China and those from the west coast of USA and Canada share a number of species in common. This general biogeographical pattern was recognized as early as 1849 by Ehrenberg (1849, 1850) but comment on his analysis from diatomists has been limited. The relevance of diatom distribution to the broader question of Pacific biogeography will have to wait until more robust trees are available. However, one factor seems inescapable: endemism is significantly higher in diatoms than has previously been considered, leaving the possibility open that micro-algae may reflect ancient continental distributions.

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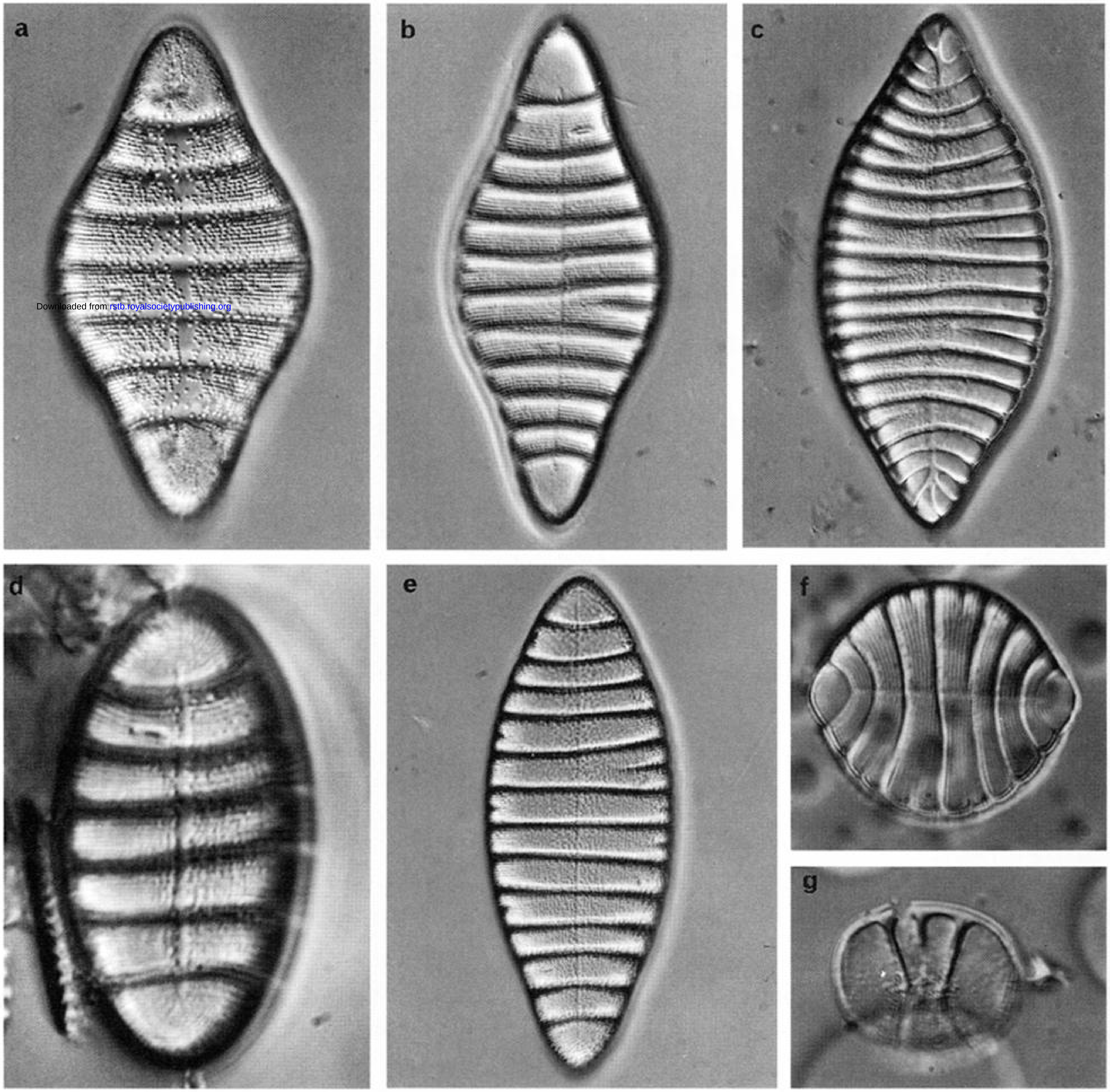
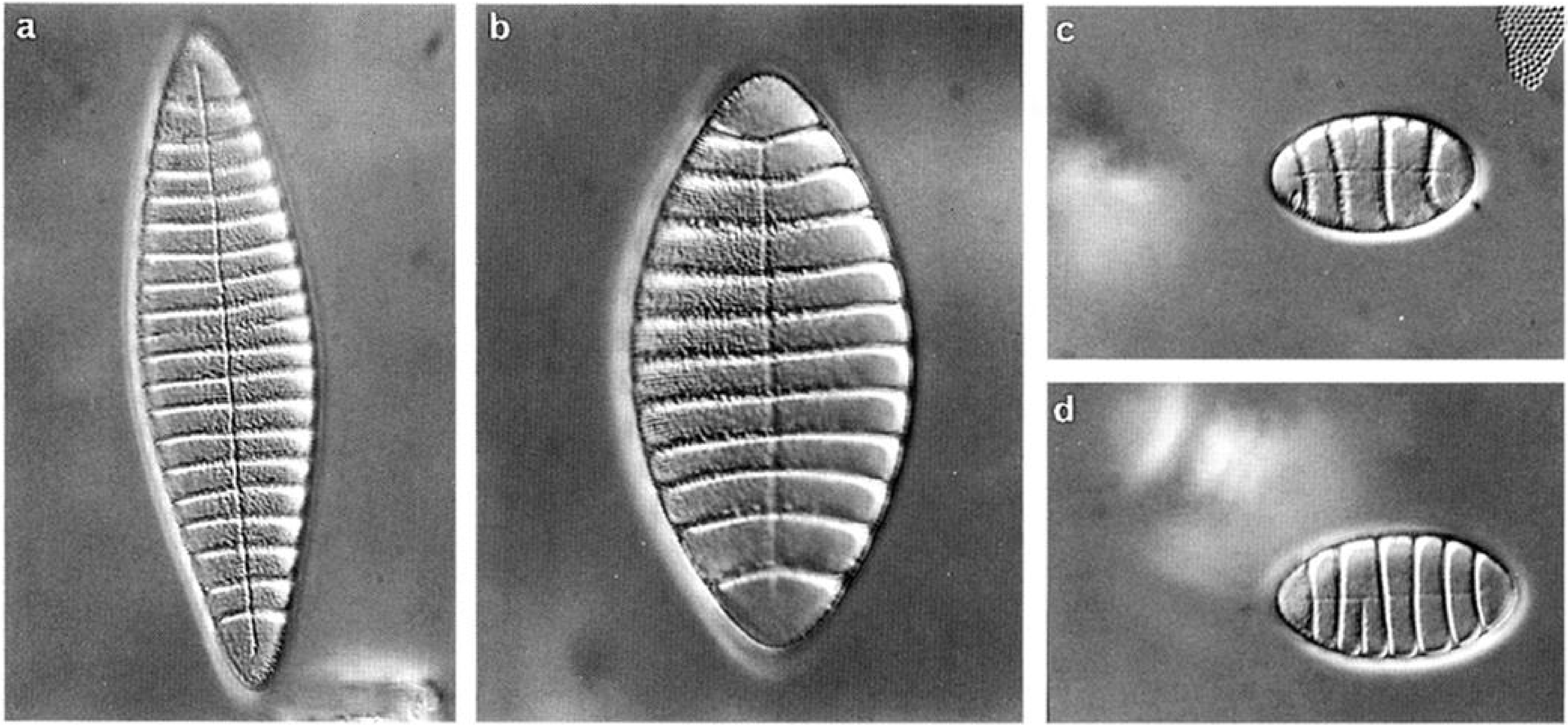
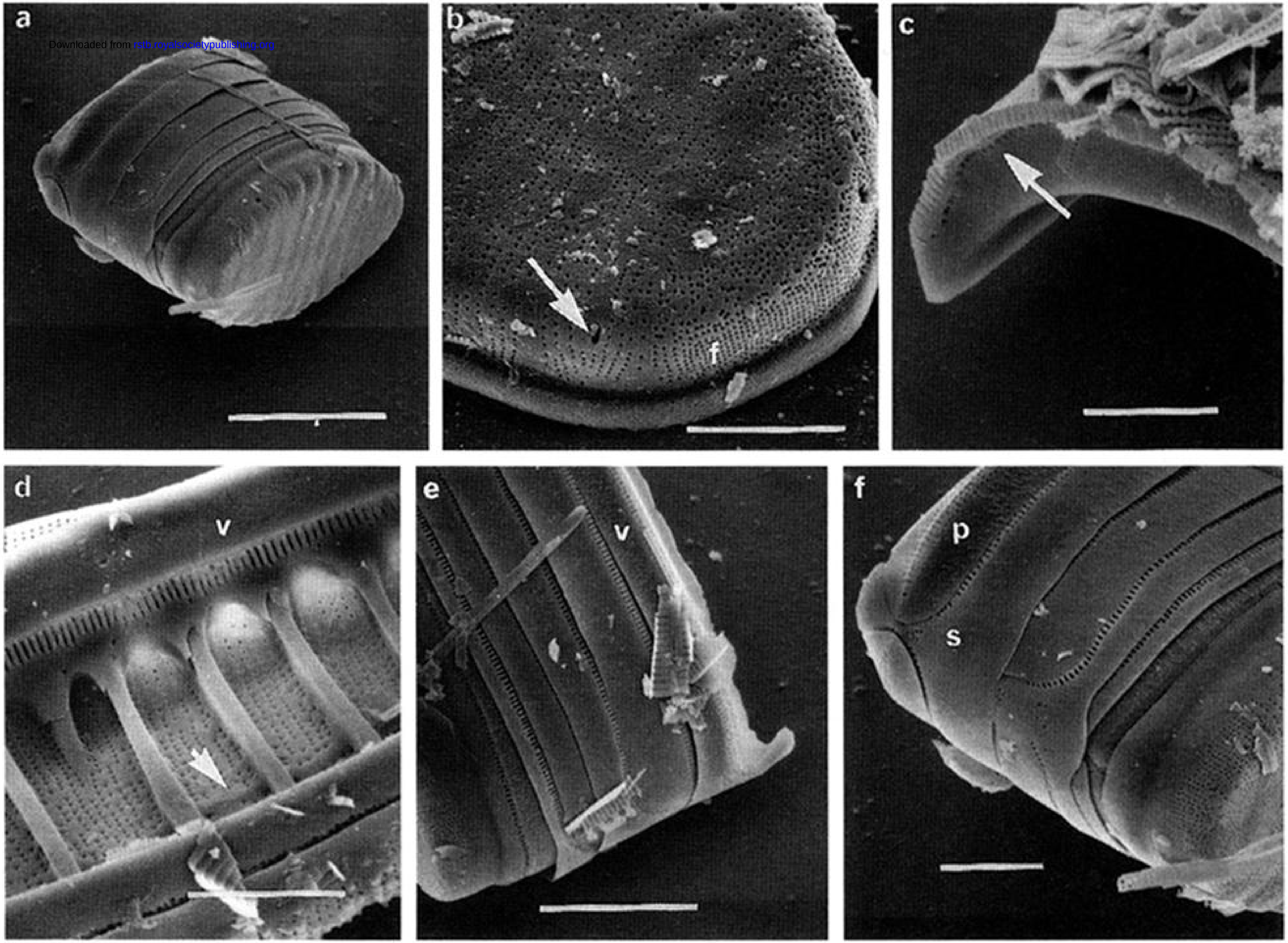


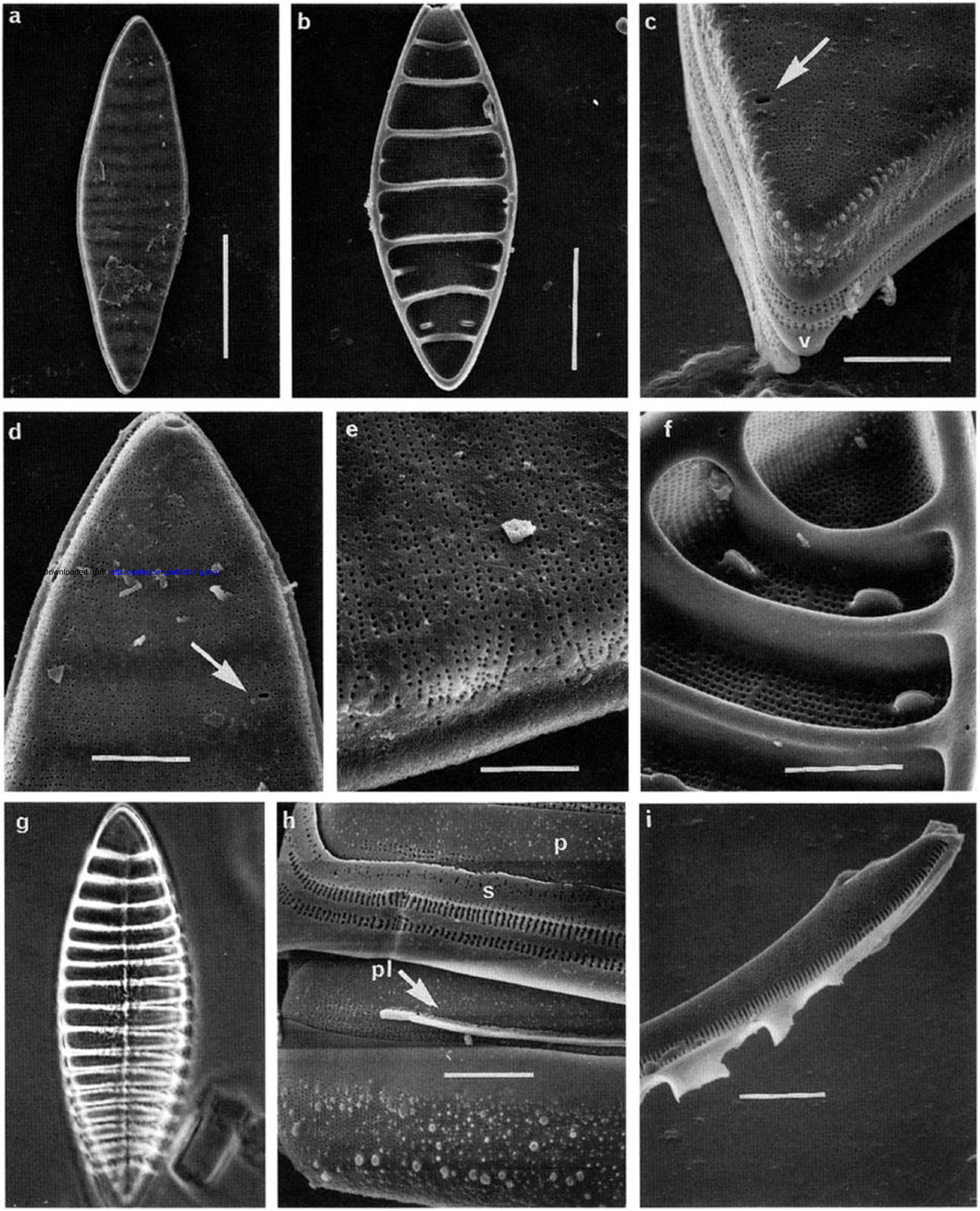
gure 1. (*a*) and (*b*) *Tetracyclus boryanus*, Bory, Hungary, (*a*) BM Adams C500, length = 65 μm; (*b*) BM Adams J 19, length = 75 μm; (*c*) *Tetracyclus maxima*, Swan Lake, Oregon, USA, BM GC 3113, length = 85 μm; (*d*) *etracyclus polygibbum*, Baikatsu, Hokkaido, Japan, BM 82313, length = 30 μm; (*e*) *Tetracyclus rhombus*, Oregon, USA, ngth = 40 μm; (*f*) *Tetracyclus ovalifolius*, Inner Mongolia, BM 81618, length = 65 μm; (*g*) *Tetracyclus shangduensis*, ner Mongolia, BM 81618, length = 30 μm.



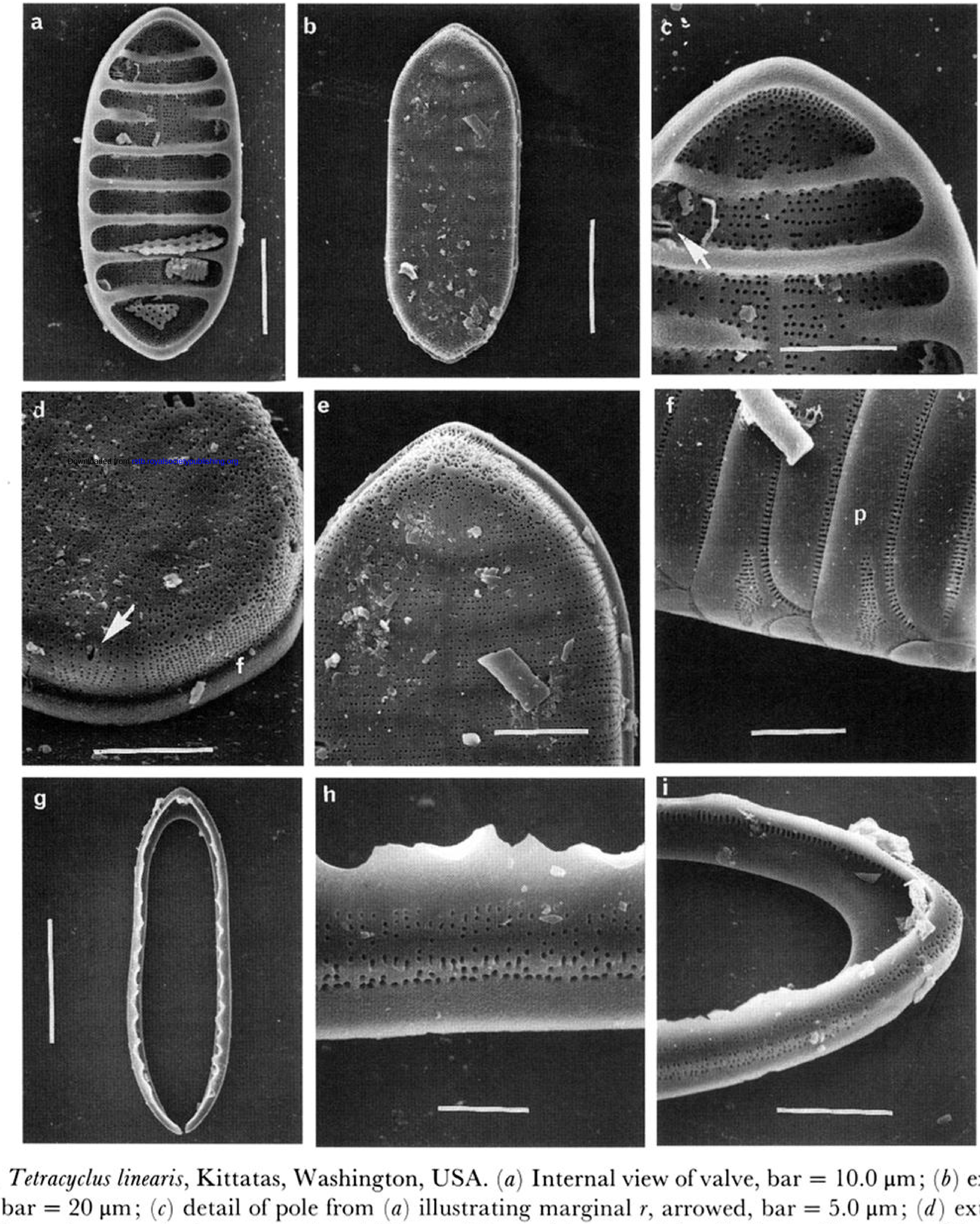
igure 2 (*a*) *Tetracyclus lancea*, Oregon, Columbia River, USA, BM 56029, length = 120 µm; (*b*) *Tetracyclus lata*, Breite usch bei Hainspach, BM 54725, length = 50 µm; (*c*) and (*d*) *Tetracyclus ellipticus*, Columbia River, USA, BM 56029, ngth = 20 µm.



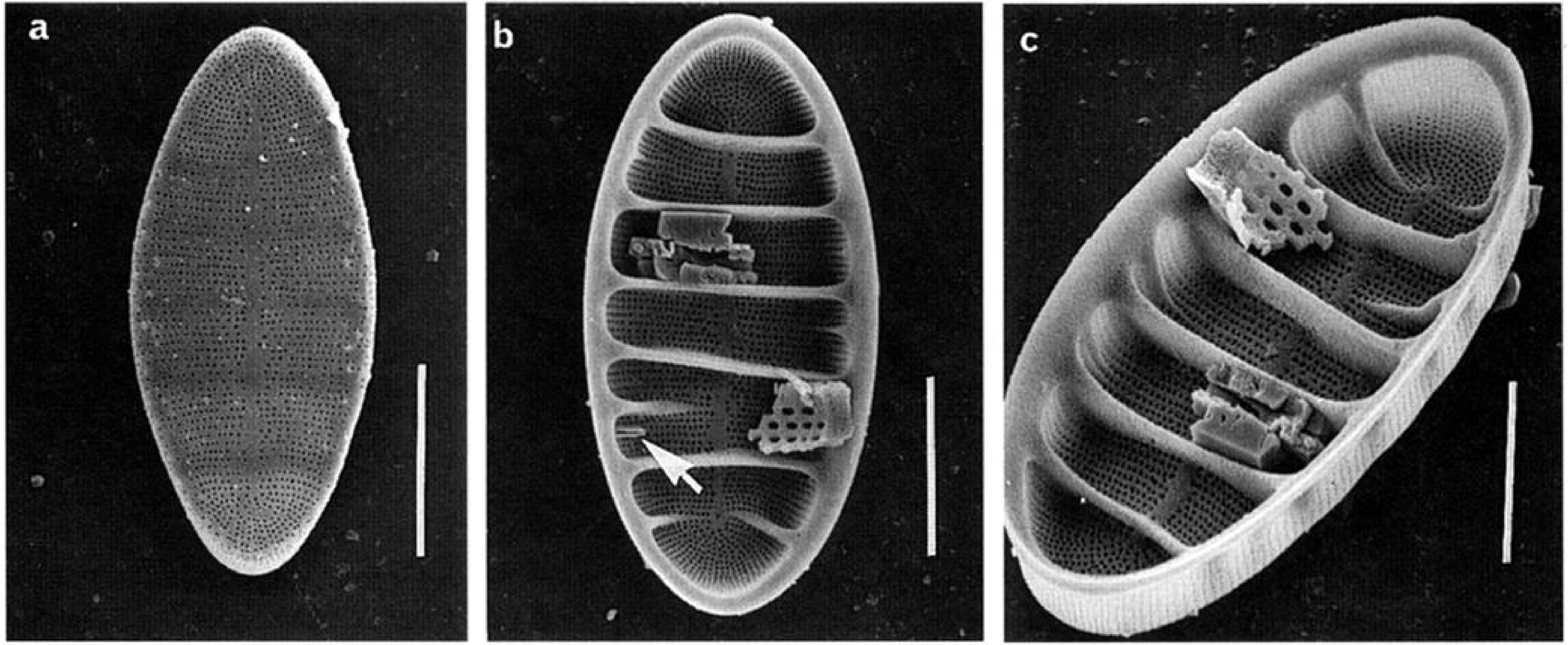
igure 3. *Tetracyclus ellipticus*, Harper Region, Oregon, USA. (*a*) Valve with some girdle bands *in situ* (detail in *f*), bar = 15 μm; (*b*) detail of external view of valve, arrow indicating *rp*, *f* as area of more closely packed striae, ar = 6.60 μm; (*c*) section through broken valve, arrow indicating the row of striae external to the transapical rib, ar = 4.0 μm; (*d*) internal view of valve with *v* in place, bar = 6.0 μm; (*e*) external view of valve with *v* separated, ar = 10 μm; (*f*) detail from figure 1, with *p* and *s* in place, bar = 7.5 μm.



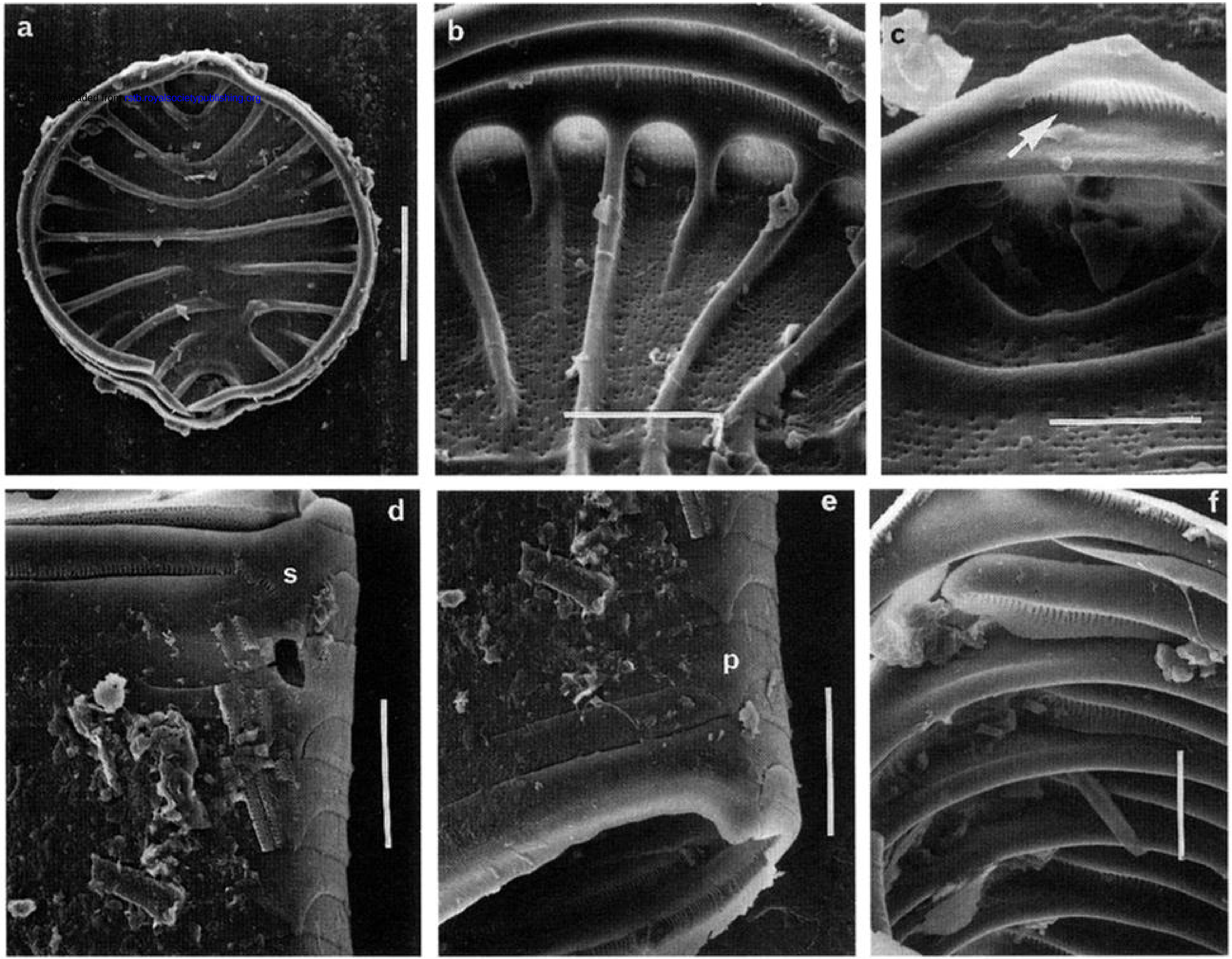
gure 4. *Tetracyclus lancea*, Quesnel, British Columbia. (*a*) External view of entire valve, face view, bar = 30 µm; (*b*) ternal view of entire valve, face view, two rimoportulae at the base of the valve, bar = 15 µm; (*c*) detail of external ew of valve, arrow indicates *r*, note lack of differentiated *f*, bar = 6.0 µm; (*d*) detail of external view of valve pole, row indicates *r*, bar = 7.5 µm; (*e*) detail of external view of valve at the middle margin, note stepped lip at edge, differentiated by striae, bar = 4.0 µm; (*f*) detail of internal view of valve, with three *r*, bar = 5.0 µm; (*g*) LM, hole specimen from Oregon, Columbia River, USA, BM 56029, length = 120 µm; (*h*) detail of partial girdle, ustrating detached *s* and *pl* surrounding attached *p*, bar = 7.5 µm; (i), detail of *v*, bar = 9.0 µm.



gure 5. *Tetracyclus linearis*, Kittatas, Washington, USA. (*a*) Internal view of valve, bar = 10.0 μm; (*b*) external view valve, bar = 20 μm; (*c*) detail of pole from (*a*) illustrating marginal *r*, arrowed, bar = 5.0 μm; (*d*) external detail pole, illustrating marginal *r*, arrowed, and *f*, bar = 6.0 μm; (*e*) external detail of pole, illustrating *f*, bar = 6.0 μm;) detail of a portion of cingulum, one *p* indicated from a series of 5, bar = 7 μm; (*g*) whole *v*, bar = 25 μm; (*h*) tail of *p*, bar = 3.0 μm; (*i*) polar view of *v* with septum, bar = 6.0 μm.



gure 6. *Tetracyclus polgibbum*, Baikatsu, Hokkaido, Japan. (*a*) External view of valve, bar = 10 μm; (*b*) internal view valve, illustrating marginal *r*, arrowed, bar = 10 μm; (*c*) internal view of valve, illustrating lack of *f*, bar = 7.5 μm.



igure 7. *Tetracyclus ovalifolius*, Poison Creek, USA. (*a*) Internal view of valve, bar = 15.0 µm; (*b*) detail of internal ew of valve, illustrating valvocopulae attachment, bar = 5.0 µm; (*c*) detail of internal polar view of valve, lustrating valvocopulae septum, arrowed, bar = 5.0 µm; (*d*) and (*e*), section of cingulum, (*d*) with *s*, (*e*) with *p*, ar = 10 µm; (*f*) internal detailed view of cingulum illustrating attachments between successive bands, bar = 0 µm.

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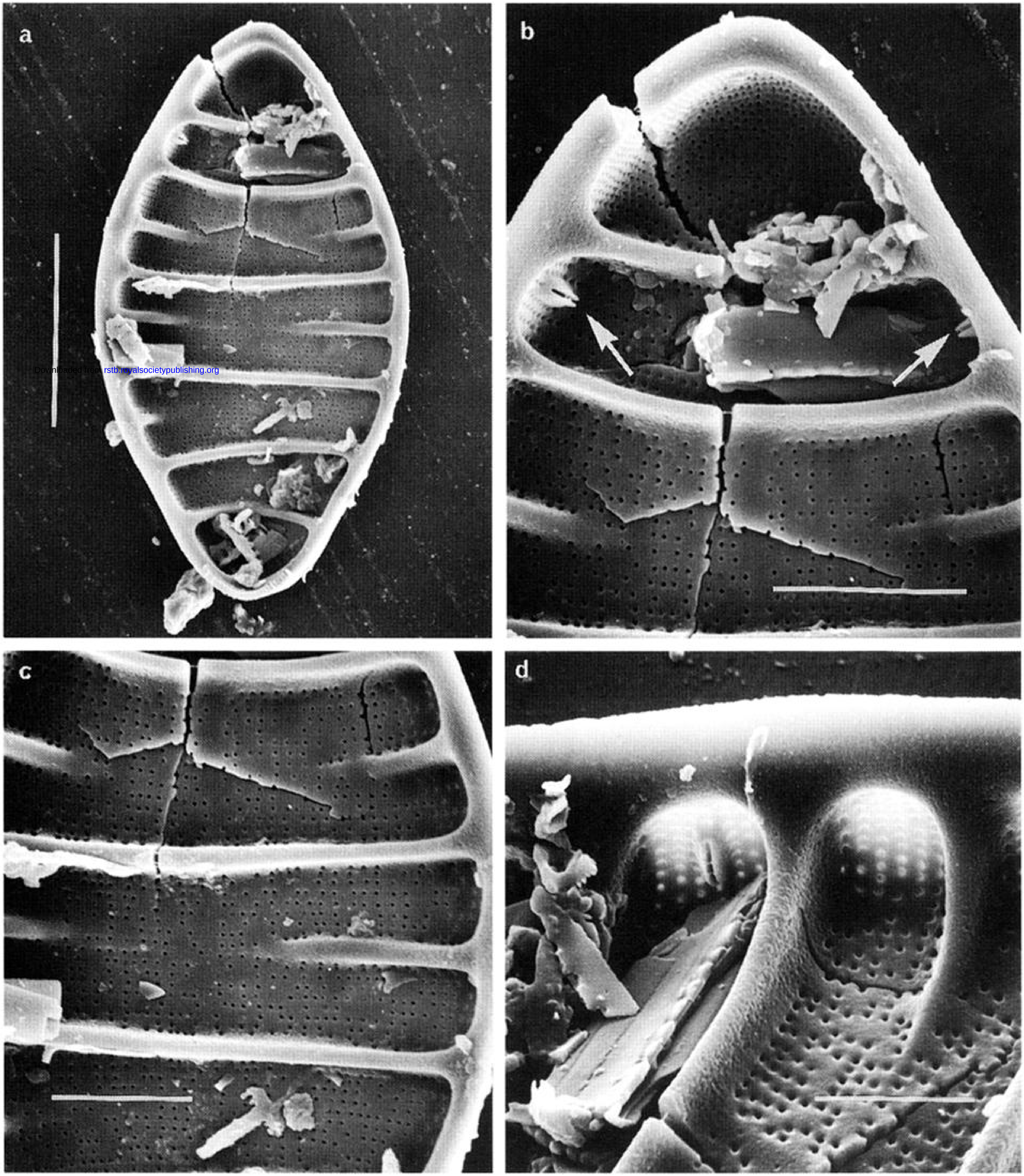

gure 8. *Tetracyclus rhombus*, Oregon, USA. (*a*) Internal view of whole valve, bar = 15 µm; (*b*) detail of pole from), arrows indicate *r*, bar = 6.0 µm; (*c*) internal view of valve, illustrating relative positions of transapical ribs, striae d central sternum, bar = 7.5 µm. (*d*) internal view of valve, illustrating marginal *r*, bar = 4.0 µm.