

Observations on valve morphology and the systematic position of *Rouxia californica* M. PERAGALLO (Bacillariophyceae)

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Valve morphology of the fossil diatom *Rouxia californica* is investigated with light and scanning electron microscopy. The valves are heteropolar due to differences in puncta pattern and structure between the two apices. Structural differences also exist between the valve interior and exterior. The exterior of *R. californica* is dominated by large elliptical puncta and coarse interstriae, while a broad axial area occupies the majority of the interior. The short raphe branches have recurved ends both internally and externally, and the internal distal ends do not terminate in helictoglossae. The relationship of *Rouxia* and its purported allies (*Amphipleura*, raphidioid taxa, *Gomphopleura*) is discussed.

Key Index Words: Bacillariophyceae—diatom—*Rouxia*—systematics—ultrastructure.

Since its original description from fossil deposits in Japan (BRUN and HÉRIBAUD in HÉRIBAUD 1893), the systematic position of the genus *Rouxia* has been debated. The genus was originally (HÉRIBAUD 1893) considered to be closely allied to *Eunotia*, *Peronia* and *Actinella* (then considered part of the araphid diatoms). VAN HEURCK (1896), and later KARSTEN (1928) and TAYLOR (1929), suggested *Rouxia* was related to raphid genera such as *Amphipleura*, *Frustulia* and *Gomphopleura* which have raphe systems shorter than most other biraphid diatoms. Although most reports of the genus have come from fossil localities, HEIDEN and KOLBE (1928) described an extant species from the Antarctic. A review of the early literature as well as described species of *Rouxia* can be found in HANNA (1930).

More recently BERG (1942) and SHESHUKOVA-PORETSKAJA (1956) have defined more explicitly their ideas regarding the systematic position of *Rouxia*. They suggest the genus is part of a primitive group of raphid diatoms, clearly allied with *Peronia* and

other raphidioid forms, but intermediate between them and naviculoid diatoms. The first electron microscopical observations of *Rouxia* were made on the valve exterior of *R. californica* by SCHRADER (1973). Based on his observations, SCHRADER (1973, p. 200) suggested the alignment of *Rouxia* near *Amphipleura* "...cannot be followed according to the submicroscopical structure." Instead he offered the view that *Rouxia* may represent a "...more degenerated" genus related to *Gomphopleura*.

The objective of the present report is to detail valve ultrastructure of *Rouxia californica* with a view to comparing its morphology with supposed allies.

Materials and Methods

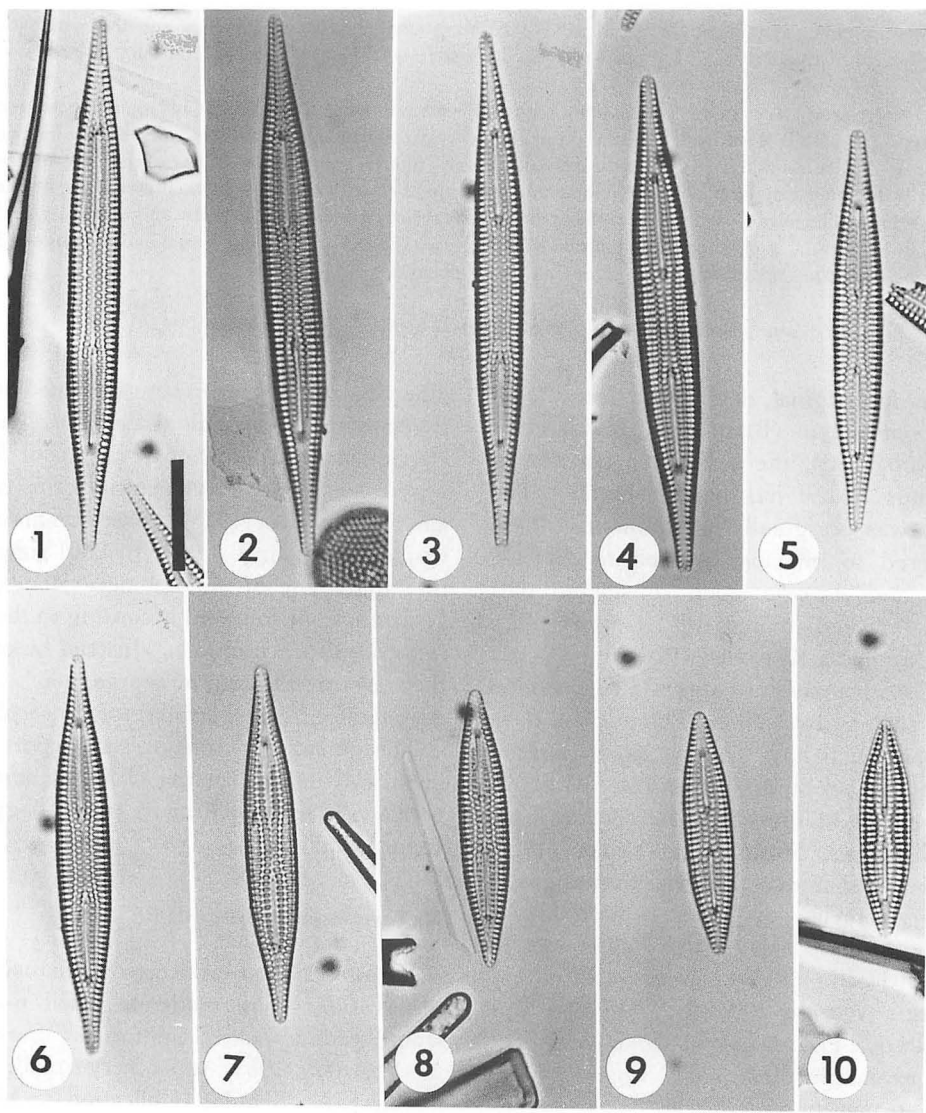
Light and scanning electron microscopical observations were made on fossil material from Redondo Beach, California ("Lump #1, 17 February 1983, some very small, Mat. #648, J. A. Schulze Collection," ANSP). Material was rinsed in distilled water and air-dried onto cover glasses. For light

microscopy dried material was mounted onto glass slides with Hyrax[®] and viewed with a Leitz Ortholux microscope. Additional light microscopic observations were made on isotype slides (TEMPÈRE and PERAGALLO 1910, 2nd edition, #648, 649, ANSP). For SEM, cover glasses bearing the dried material were mounted on aluminum stubs and sputter-coated with 20 nm of gold-palladium. Specimens were viewed on a JEOL T100 SEM at an operating voltage of 15 kV, and a

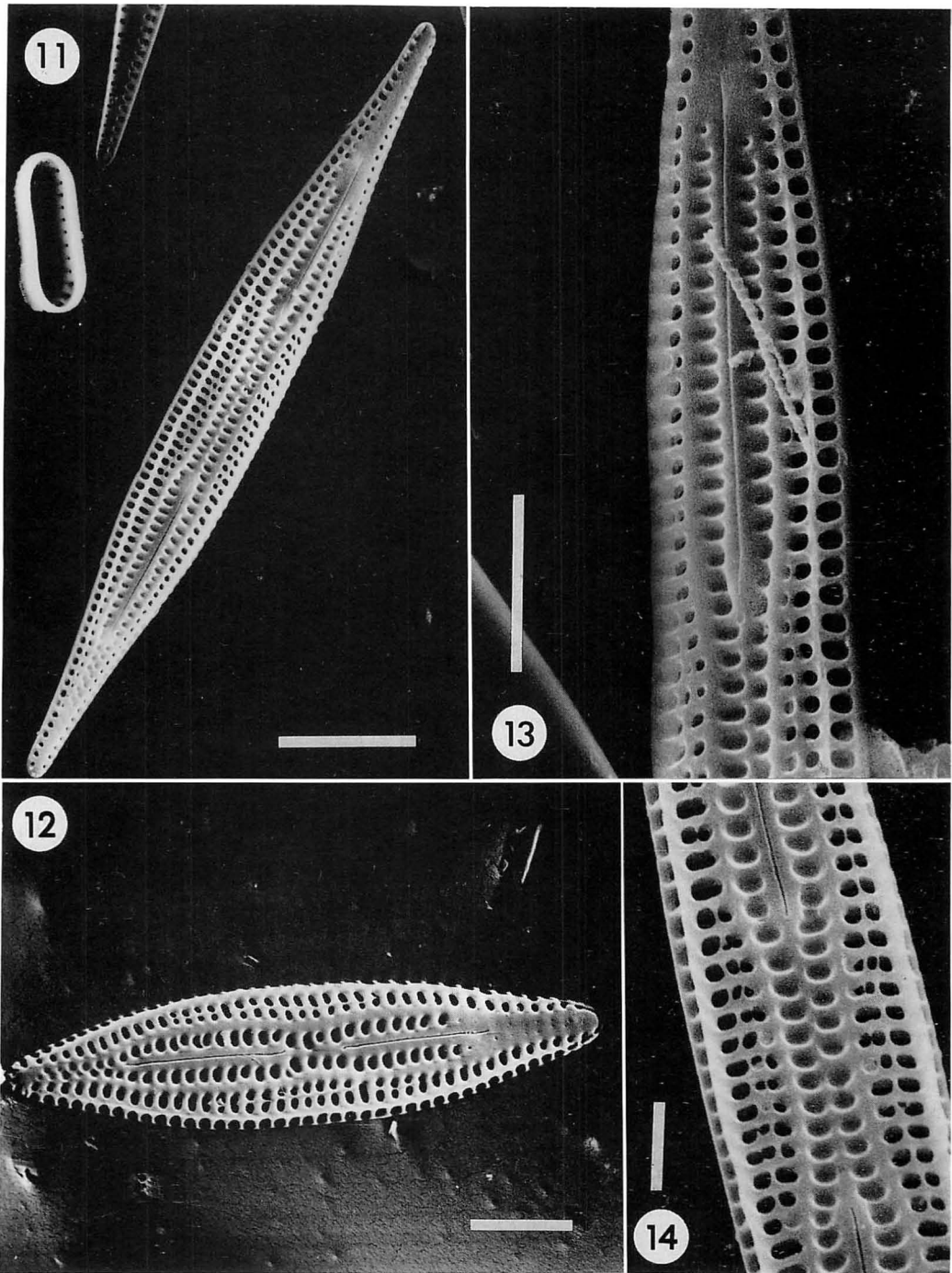
Cambridge S200 SEM operating at voltages ranging from 8 to 20 kV. Terminology of valve features follows that prescribed in Ross *et al.* (1979)

Results

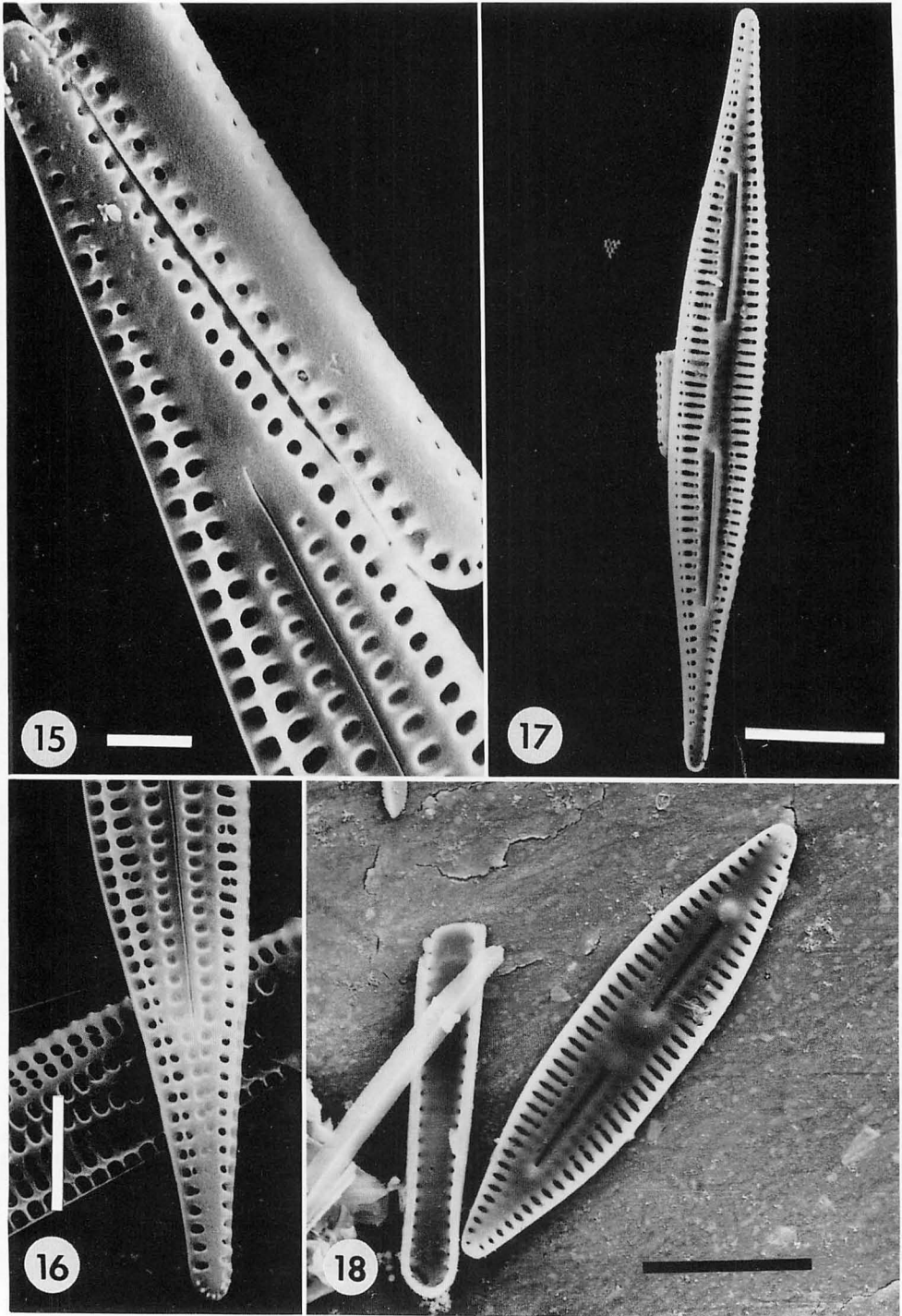
Light microscopic observations of *Rouxia californica* are presented in Figures 1-10. Valves are fusiform and angular with the poles blunt. Valves range from 30-82 μm in



Figs. 1-10. Light Microscopy. Size diminution series of *Rouxia californica*. Fig. 3 shows specimen with curved apex. Scale in Fig. 1 = 15 μm for Figs. 1-10.



Figs. 11–14. SEM, valve exterior. Figs. 11 and 12 show general valve features of a large and small valve, respectively. Scale in Fig. 11 = $10\ \mu\text{m}$, scale in Fig. 12 = $5\ \mu\text{m}$. Fig. 13. Complete raphe branch with ends curved in the same direction. Scale = $5\ \mu\text{m}$. Fig. 14. Central area showing proximal raphe ends recurved in the same direction. Note puncta between raphe ends appear occluded relative to other puncta. Scale = $2.5\ \mu\text{m}$.



Figs. 15-18. SEM. Figs. 15 and 16. Exterior of apices showing differences in ornamentation. Scale in Fig. 15=2.5 μm , scale in Fig. 16=5 μm . Figs. 17 and 18. Interior of whole valves showing axial area extending length of the valve with raphe system embedded within. Scales=10 μm .

length, and 6–8 μm in breadth. Through size diminution there is a great reduction in length with little corresponding reduction in breadth. Parallel striae extend up to raphe branches and across the central area between raphe branches. Striae densities range from 10–14 in 10 μm . Valves are isopolar with regard to outline but heteropolar with regard to ornamentation. Puncta extend along the axial area to one pole yet are much less distinct at the other. Lengths of the raphe branches are the same on a valve but vary with size. Although raphe branch length appears to be positively correlated with valve length, valves of similar length may have raphe branches of differing lengths. Some valves appear to be bent slightly at the poles (e.g. Fig. 3).

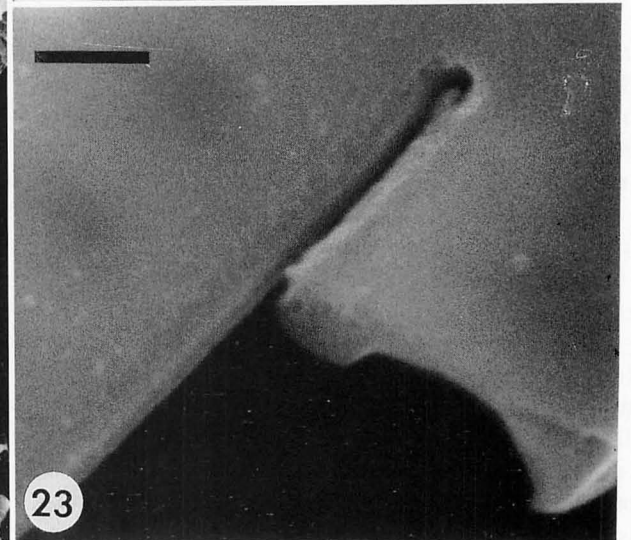
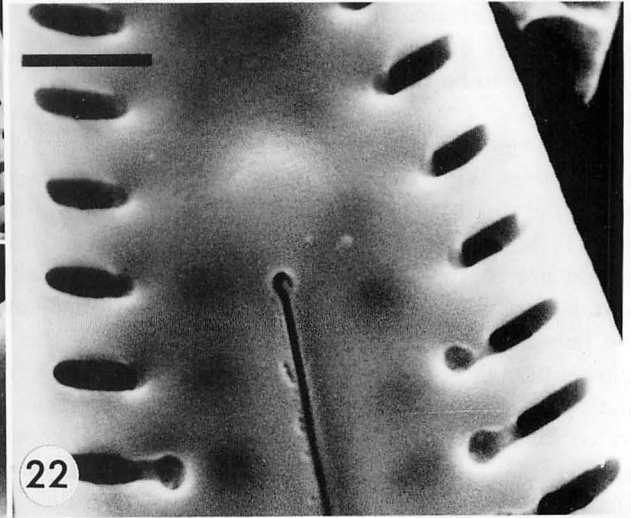
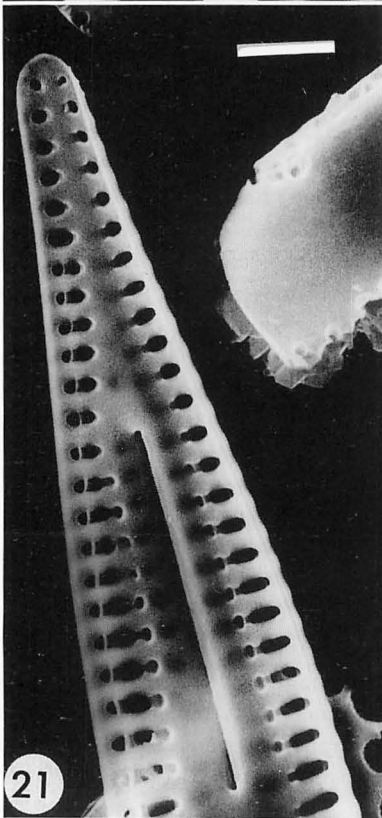
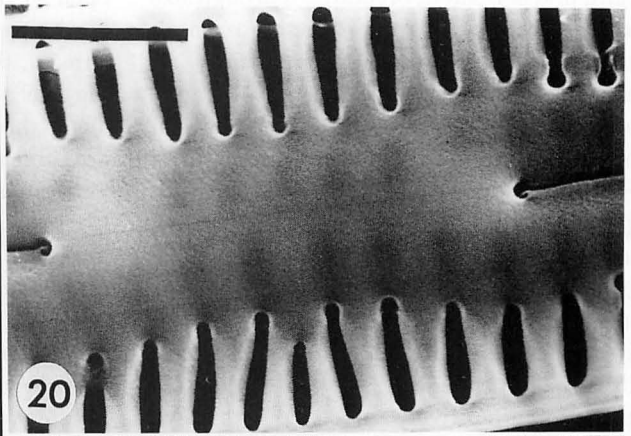
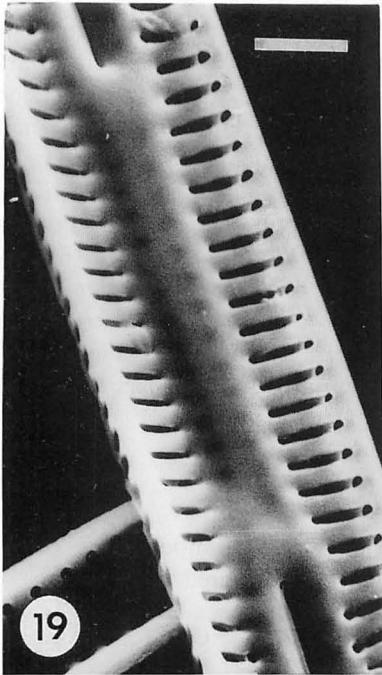
External views with SEM show the needle-shaped valves with unequal ornamentation between the distal raphe ends and the apices (Figs. 11, 12, 15, 16). The puncta in these areas do not completely penetrate the basal siliceous layer, with puncta at one end of the valve being smaller in diameter and much shallower than those at the other end. Puncta of the striae are interrupted by thick, slightly elevated siliceous ribs that run longitudinally (Figs. 11–14). Puncta are elliptical near the margin but smaller and more rounded near the axial and central areas (Figs. 11–16). Puncta appear occluded near the axial area and across the central area (Figs. 13, 14). Proximal and distal raphe ends are curved slightly in the same direction (Figs. 11, 14). In most specimens, the proximal raphe ends on a valve are curved in the same direction (Fig. 14), however specimens with ends curved in opposite directions (Fig. 12) have been encountered. Small spines may be present at the poles (Fig. 16).

Internal morphology of *R. californica* is dominated by a broad axial area which, unlike the valve exterior, extends the length of the valve (Figs. 17, 18). The axial area protrudes inward toward the middle of the frustule and has the raphe system embedded in it (Figs. 17–21). An elongated central nodule is bordered by elliptical puncta which

open to the mantle and valve face. Puncta bordering the raphe system become constricted, then expanded and rounded towards the axial area (Figs. 21, 22). Puncta positioned along the axial and central areas externally are subtended and apparently occluded by the axial area (Figs. 20, 21). External siliceous ribs are visible through the puncta. Both the proximal (Figs. 19, 20) and distal internal raphe ends are recurved in the same direction, while the distal raphe end terminates next to an internally raised area (Fig. 22). In transverse view the raphe appears to be of the plicate type (Fig. 23).

Discussion

Specimens from Redondo Beach correspond with the original description of PERAGALLO (in TEMPÈRE and PERAGALLO 1910) for *R. californica*. Size and striae densities of the specimens are in general agreement with values presented by CLEVE-EULER (1953) and SHESHUKOVA-PORETZKAJA (1956) for this species. Observations made on isotype material failed to yield specimens suitable for comparison. SHESHUKOVA-PORETZKAJA (1956) has previously illustrated bent valves of *R. californica* similar to Redondo Beach specimens. *Rouxia californica* is said to differ from *R. peragalli* BRUN & HÉRIBAUD "in that the entire surface [of *R. californica*] is covered with indistinctly punctate striae" (PERAGALLO in TEMPÈRE and PERAGALLO 1910, translated in HANNA 1930, p. 186). The original illustration of *R. peragalli* (HÉRIBAUD 1893) shows striae interrupted by broad longitudinal fasciae, although this is different from the interpretation of this taxon published by BRUN later in that same year. If distinction between the two species is based on striae pattern, then BRUN's (1893) illustration in *Le Diatomiste* may be that of *R. californica*. Striae pattern differences between *R. peragalli* and *R. californica* appear distinct enough to argue against SHESHUKOVA-PORETZKAJA's (1956) transfer of *R. californica* to *R. peragalli* f. *californica*, which is not followed by VANLANDINGHAM (1978).



Observations on the ultrastructure of *R. californica* allows comparison with other groups to which *Rouxia* has been aligned. *Rouxia californica* shares similarities with the genera *Berkeleya* and *Amphipleura*, particularly *B. rutilans* (LYNGB.) GRUN. and *A. pellucida* (KÜTZ.) KÜTZ., with regard to relative size and position of the raphe system. In *B. rutilans* external raphe ends are curved in the same direction (COX 1975), a feature also observed in *R. californica*. Interruption of striae by longitudinal ribs is found in *A. lindheimeri* GRUN. (COX 1975). *Rouxia* differs from these groups (and most other raphid diatoms) by lacking typical helictoglossae.

Although *Rouxia* is structurally heteropolar, there appears to be little evidence to support the suggestion of SCHRADER (1973) that the genus may be closely related to *Gomphopleura*. Unlike *Gomphopleura*, *Rouxia* is not asymmetrical to the transapical axis with regard to outline, and although the raphe systems are small in both genera, a number of raphe characteristics distinguish the two. In *Gomphopleura* the raphe extends to the poles and the external distal ends run onto the valve mantle (SCHRADER 1973, MAHONEY and REIMER in press), while in *R. californica* the raphe does not approach the poles. Also, the raphe in *Gomphopleura* is of the key and slot type (*sensu* KRAMMER 1982, SCHRADER 1973, MAHONEY and REIMER in press) whereas a plicate raphe is found in *Rouxia*. Presence of septa, pseudosepta, marginal laminae and apical pore fields in *Gomphopleura* (MAHONEY and REIMER in press) suggest a close relationship between this genus and *Gomphoneis*.

Another view (e.g. BERG 1942) suggests *Rouxia* may be related to the raphidoid diatoms, especially *Peronia*. Although both *Rouxia* and *Peronia* share the feature of structural heteropolarity, *Rouxia* lacks asymmetry in outline about the transapical axis. Both

genera have spines and external raphe ends that are curved in the same direction (HASLE 1973). Differences between these genera include presence of labiate processes and helictoglossae in *Peronia*, which are lacking in *Rouxia*. Construction of the raphe, particularly the external distal openings, also differs between the two genera.

Considering differences in ultrastructure between *R. californica* and genera previously held to share a close genealogical relationship, it might be best not to consider *Rouxia* as a form intermediate between raphidoids and naviculoids (as suggested by SHESHUKOVA-PORETZKAJA 1956), but as comprising a separate lineage within the raphid diatoms. HANNA (1930, p. 187) considers the possibility that, due to its association with pelagic species in fossil material, "the entire genus may have been pelagic." This observation leaves open the possibility that the small raphe system of *Rouxia* may be due to secondary reduction (as suggested for other groups such as the monoraphid diatoms, e.g. MANN 1983, KOCIOLEK and STOERMER 1986) rather than primitive development.

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Figs. 19–23. SEM, valve interior. Figs. 19 and 20. Large central nodule and proximal raphe ends recurved in the same direction. Scales = 2.5 μm . Fig. 21. Entire raphe branch with ends recurved in the same direction. Scale = 2.5 μm . Fig. 22. Recurved distal raphe end located at base of internally raised area. Scale = 1.25 μm . Fig. 23. Transverse section near proximal raphe end showing raphe to be of the plicate type. Scale = 0.5 μm .

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John P. KOCIOLEK* · Ronald K. MAHONEY** : 珪藻 *Rouxia californica*

M. PERAGALLO の殻形態の観察および系統的位

化石珪藻 *Rouxia californica* の殻の形態を光学顕微鏡と走査型電子顕微鏡で観察した。殻は、両端の点紋配列と構造の差異により、異極である。構造上の差異は、殻の内面と外面の間にも認められる。本種の殻の外面には大きな楕円形の点紋と粗い間条線が多数あり、内面の大部分は広い軸域によって占められている。短い縦溝枝は内部でも外部でも反曲した末端をもち、内部の殻端側末端は蝸牛舌に終わっていない。*Rouxia* とその類似の分類群 (*Amphipleura*, 原始縦溝類の種類, および *Gomphopleura*) との関係について論議した。 (*Great Lake Research Division, 2200 Bonisteel Boulevard, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.; **Diatom Herbarium, Academy of Natural Sciences of Philadelphia, 19th & The Parkway, Philadelphia, Pennsylvania 19103, U.S.A.)