

6: AMPHIPRORA

Amphiprora, which is a genus of medium size containing 40 species (teste Van Landingham 1967), has only recently been reconsidered as a possible close relative of the Nitzschiaceae or Epithemiaceae. This new view of the genus was prompted by the brief electron microscopic examination of some Amphiprora species by Hargraves & Levandowsky (1971) and Paddock & Sims (1977). Amphiprora has traditionally been classified in the Naviculaceae, near Tropidoneis (e.g. by Cleve 1894-5, Schutt 1896, Karsten 1928, Hustedt 1930, Hendey 1937, etc.), although a few (e.g. Mereschkowsky 1903a) have claimed this to be unsatisfactory. In order to explain the morphology and anatomy of an Amphiprora cell, A. alata (obtained from the salt-marsh at Sandbay, Co. Avon) will be taken as an example and described in some detail.

The frustule of A. alata, like that of any Amphiprora species, is oddly twisted (F.516, 992, 994), a fact which causes many problems in the drawing of these diatoms and the interpretation of their structure. It is as if a Navicula frustule were to be taken, each raphe-split raised on a high keel (see chapter 3), and then the frustule held by the poles and given a sharp twist: the raphe system is therefore sigmoid in valve view (F.992). The keels diminish in height towards the centre of the valve, and also towards the poles (F.514, 994). The raphe is quite central.

The valve is composed of transapical costae, each of which is separated from the next by two rows of small, round poroids (F.992-3): there are no sterna apart from the raphe-sternum. The marginal strip, which is striated externally, bears a small ridge at its junction with the remainder of the valve (F.996)

The poroids seem to be closed by hymena, although this has not yet been proved for this species: there is no sign of the slits which

would indicate the presence of a volate closing membrane such as that present in Epithemia or Rhopalodia. Three other Amphiprora species have been shown to possess hymena, though these are of a different type from that present in Nitzschia and Hantzschia (F.580, and see below).

The external surface of the valve is covered with tiny warts, and it is difficult to distinguish these from the domed structures presumed to be hymena: the latter, however, are slightly larger, and arranged in paired transapical rows (F.995-6). On some parts of the valve, especially where it is sharply folded, there are, in addition to the warts, small bars of silica which lie along the outside of the valve, orientated with their long axes at right angles to the transapical costae (F.955, arrows). The function of the warts and bars is unknown.

The raphe-sternum is not very broad, and is striated like the valve margin, with several tiny ridges running along it parallel to the raphe-slit (F.995-6). The raphe-slit itself opens onto the very apex of the keel and is difficult to distinguish. The raphe is interrupted centrally, the internal and external endings being coaxial-symmetrical (F.515, 993, 997). At the poles the raphe seems to end internally in helictoglossae (unpublished LM observations), while externally the terminal portion of each fissure is hidden by the 'marginal ridge' (F.996).

The raphe is subtended by numerous short, costate fibulae, each of which is borne on a transapical valve costa: they occur only in the keel (F.514-5, 993, 997). Each transapical costa may bear many fibulae, the number borne being dependent mostly on the height of the keel at that point (viz. few near the centre or poles, but up to 7 or 8 where the keel is deepest - F.514). There is, then, a resemblance in subraphe structure between A. alata and certain species of Nitzschia (N. ocellata and part of Nitzschia sect. Perrya).

There is also a resemblance between A. alata and Nitzschia in the form and arrangement of the chromatophores. In A. alata there are two broad, flattened chromatophores disposed one on each side of the median transapical plane. The only difference from Nitzschia is that the chromatophores do not lie in the same plane, but are set at an angle to one another, this reflecting the torsion of the cell (F.516-517). The nucleus lies centrally, in the cleft between the chromatophores (unpubl. obs.).

The cincture is as yet unknown.

The twisted frustule, keeled valves and bilobate shape are common to all Amphiprora species. There is some variation, however, in the valve construction, since A. hyalina and some of the other small, 'hyaline' species do not have rows of poroids as in A. alata: instead, the spaces between the transapical costae are occupied by long strips of thin, perforate silica (see Hargraves & Levandowsky 1971, Pl.1 f.4-5). This strip can probably be regarded as an extremely elongate hymen, since its pores are each approx. 5 nm. in diameter (calculated from Hargraves & Levandowsky 1971, f.5). The hymen pores are grouped into linear triplets, each triplet being orientated at right angles to the costae. There are two rows of triplets between each pair of adjacent costae; the thin strip of silica separating these rows also bears a few scattered pores, especially where the costae are more widely spaced - e.g. near the fibula bases (see Hargraves & Levandowsky).

Helmcke & Krieger's (1953- ) illustration of A. paludosa (T.179) shows that its construction is like that of A. alata. Hymena are present, and it seems that the hymen pores are arranged in short rows, as in A. hyalina, each row being orientated at right angles to the poroid margin. As in A. alata, warts are present on the valve surface. N.B. Helmcke & Krieger's identification must be held in some doubt in view of the scales given on their micrographs, which would give

their specimens less than 10 transapical costae in 10  $\mu\text{m.}$ , whereas Hustedt (1930) gives 20 for A. paludosa.

With regard to subraphe structure, A. paludosa, A. pulchra, A. gigantea and A. sulcata would all seem to have fibulae at many levels, as in A. alata (see the illustrations of Peragallo & Peragallo 1897-1908, Cleve 1894-5). A. hyalina, on the other hand, seems to have only one row of fibulae, just as in most Nitzschiae (unpubl. obs.; Hargraves & Levandowsky 1971, Pl.1 f.4). Perhaps this genus may be divisible into two sections, the first including the more heavily silicified forms with many rows of fibulae, the second including the 'hyaline' species, e.g. A. medulica and A. ornata (see Peragallo & Peragallo 1897-1908, Pl.38): the chromatophore arrangement would support this, since the smaller forms have only one chromatophore per cell, not two as in A. alata (unpubl. obs.; Mereschkowsky 1903a).

Amphiprora, then, has a fibulate raphe system, and this suggests that it belongs closer to the Nitzschiaceae/Epithemiaceae/Surirellaceae than to the Naviculaceae. The similarity of Amphiprora and Auricula (which has recently been shown to possess fibulae, by Paddock & Sims 1977) to Nitzschia was noted long ago by Cleve (1894-5). This author also claimed that 'the genera Tropidoneis and Amphiprora are very closely allied to several forms of Nitzschia. We meet in that genus with the carinated asymmetrical valves and the wing of Tropidoneis, also the complex zone and carinal puncta of Amphiprora' (at this time the nature of the 'carinal puncta' was not understood). But Tropidoneis, which has often been linked with Amphiprora, by various authors, has a valve, raphe and subraphe structure completely unlike that of the latter genus, except that the raphe is again borne on a keel. The chromatophore structure and arrangement also argue against their close kinship: Mereschkowsky (1903a) stated 'la structure intérieure montre clairement qu'il n'y a rien de commun entre ces deux genres.'

Peragallo & Peragallo (1897-1908) also noted similarities between Amphiprora, Auricula, Tropidoneis and Nitzschia, and considered that the first three genera, which they placed in the family 'Amphitropidées', ought, in a truly natural classification, to be placed near the Epithemiaceae/Surirellaceae/Nitzschiaceae. In view of the similarities between Amphiprora and Nitzschia in subraphe structure and chromatophore arrangement, it seems that the Peragallos' contention is worth careful consideration (except that Tropidoneis should be left in the Naviculaceae).

The twist of the frustule and the valve structure, taken together, set Amphiprora apart from other forms with fibulate raphe systems, but it is interesting that other twisted forms (Cylindrotheca and Surirella spiralis) do exist, in the Nitzschiaceae and Surirellaceae. There is little so far to suggest that Amphiprora should be transferred into the Nitzschiaceae (in spite of similarities in subraphe structure and chromatophore arrangement), although it will be necessary to examine N. ocellata (Nitzschia sect. Pseudoamphiprora) and some members of the sect. Perrya before this possibility is discounted. The little known about the hymen structure would argue against a close link with Nitzschia, the hymena of Amphiprora being more reminiscent of Cocconeis (compare F.579 with 580) than of the Nitzschiaceae.