

A discussion of *Caloneis* and related genera

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Abstract

The history and nature of *Caloneis* are discussed. The genus appears to possess no morphological synapomorphies and cannot be satisfactorily diagnosed versus *Pinnularia*. Thus, although molecular genetic data could yet show that *Caloneis* is strictly monophyletic, there is currently no evidence for this view. I suggest that *Caloneis* has been maintained largely because of historical precedent: diatoms with alveolate striae have been identified to the level of species or species complex directly, without reference to supposed generic characteristics; only once the species or species complex has been recognized is the diatom assigned to *Caloneis*, which is done using received knowledge, based on convention.

Key index words

alveolate striae, *Caloneis*, *Pinnularia*, taxonomy

In their account of diatom genera, Round *et al.* (1990) included *Pinnularia* Ehrenberg but omitted *Caloneis* Cleve. This was not because we had not examined material of *Caloneis* species (e. g. see Mann 1981, 1983, 1988, 1989a, b, Mann & Stickle 1988), but because we were 'unable to find a satisfactory basis for the traditional separation of *Pinnularia* from *Caloneis*.' Cox (1988) noted earlier that 'many consider it is no longer possible to make a clear distinction between the two genera.' Round *et al.* continued that 'we have investigated many species, including the type of *Caloneis*, *C. amphibaena*, and conclude that if *Pinnularia* is ever split, it will not be along the traditional boundary between these genera.' Again, Cox (1988) also stated: 'what is very apparent is that there is as much or as little similarity between *Pinnularia* and *Caloneis* as they presently stand, as between species within each' and she noted a similarity between the plastids of *C. silicula* (Ehrenberg) Cleve, *C. bacillum* (Grunow) Cleve and *Pinnularia isostauron* (Grunow) Cleve, which might indicate a close relationship between them, although we cannot get sure whether the plastid characteristics they share are symplesiomorphies or homoplasies (in which case the similarity tells us little), or synapomorphies. The omission of *Caloneis* from Round *et al.*'s account clearly surprised some diatomists (see below) and no-one,

as far as I know, even if they agreed with us, has pursued our logic any further, e. g. by transferring most or all *Caloneis* species into *Pinnularia*. By contrast, most of the other taxonomic changes to raphid diatom genera that we suggested (in Round *et al.* 1990) have now been accepted (e. g. see Metzeltin & Lange-Bertalot 1998, Witkowski *et al.* 2000).

Recently, Krammer (2000) has published a revision of the *Pinnularia* species 'of the temperate zone with some remarks to taxa from the tropics'. In this large and valuable work, he says (p. 8) 'in the succession of Round *et al.* (1990) a lot of new genera were produced and the splitting of genera is a frequent practice. In contrast Round *et al.* considered the large genera *Caloneis* and *Pinnularia* as synonyms. But the habitus (the correlation of the characters) of both is so different that any experienced diatomist can recognise it at once as a *Pinnularia* or a *Caloneis*.' And again (*op. cit.*, p. 18): 'when one studies the two genera closely, it is immediately obvious even in LM whether the genus is *Pinnularia* or *Caloneis*'. On the other hand, Krammer also states that both genera 'are very inhomogeneous' (p. 8) and in principle 'should be split in many small units so as to be certain that the groups are monophyletic' (p. 18): a single genus including both genera would be a 'single polyphyletic genus containing well in excess of a 1000 taxa'. The aim of my paper is to examine these claims.

First, what is the traditional distinction between *Caloneis* and *Pinnularia*? According to Cleve (1894, p. 46) - and this has been discussed also by Krammer & Lange-Bertalot (1985, p. 15) - the principal characteristics of his new genus *Caloneis* were that the striae were 'usually parallel, and divergent in the ends (rarely convergent), not distinctly (rarely finely) punctate, crossed by one or several longitudinal lines, which in some species increase to broad, lateral areas'. The essential point, therefore, was the combination of smooth, non-punctate, parallel striae and longitudinal lines. Cleve also noted that 'smaller forms of *Caloneis* with indistinct longitudinal lines closely resemble small *Pinnulariae*, and certain of the panduriform species seem to be very closely connected with some marine, panduriform *Pinnulariae*.' However, in *Pinnularia* species too, there are longitudinal lines crossing the striae (see for instance the illustrations of Hustedt 1930 and Hustedt in Schmidt 1874-1959, pls 385-390), which, as was shown by Flögel (1884; see also Lauterborn 1896), reflects the fact that the striae are chambered (alveolate: see below). Cleve seems to have regarded the lines present in *Caloneis* as qualitatively different from those in *Pinnularia*.

During most of the twentieth century, diatom classification and identification were strongly influenced by Hustedt. In his freshwater diatom flora of 1930, a standard text for identification for over 50 years, Hustedt characterized both *Pinnularia* and *Caloneis* by the presence of longitudinal lines: 'Transpikalstreifen jederseits von einer oder mehreren (oft schwer erkennbaren) Längslinien gekreuzt' (*op. cit.*, p. 213), thus contradicting Cleve's original diagnosis. In a later work (1956, p. 60), Hustedt resorted to a quantitative distinction: if 'Struktur meistens sehr grob, Schalen flach, vorwiegend Süßwasserformen', then the diatoms were identified as *Pinnularia*; but if 'Struktur zarter, Schalen mehr oder weniger gewölbt, vorwiegend Meeresformen', *Caloneis* was indicated. This separation is difficult. We are given no guidance as to how coarse a diatom has to be to qualify to be a *Pinnularia*. Although species traditionally classified in *Caloneis* are generally more densely striated than species of *Pinnularia*, the ranges overlap (see the accounts by Hustedt 1930 or Krammer & Lange-

Bertalot 1986). And whether the valve face is flat or vaulted is highly correlated with salinity in a variety of diatom lineages and appears to have little independent value in phylogenetic analysis (Mann 1984, 1994); a transition from flattened to curved valve faces is a phenotypic response to environmental salinity in *Skeletonema subsalsum* (A. Cleve) Bethge (Paasche *et al.* 1975). Hustedt's (1956) diagnosis is therefore inadequate; it is remarkable that, after *c.* 50 years of taxonomic research on diatoms, he was apparently unable to produce anything better to separate *Pinnularia* from *Caloneis*, which might suggest that the separation itself is unjustifiable.

In the 'Süßwasserflora von Mitteleuropa', Krammer & Lange-Bertalot (1986) offered a quite different differential diagnosis, which depends on the structure of the striae. Electron microscopy, especially from the early 1970s onwards (e. g. Schrader 1971), has demonstrated that not only *Pinnularia* but *Caloneis* possesses alveolate striae. In both genera, each stria consists of a transparently elongate chamber, which opens to the exterior via several rows of small round pores (each closed by a hymen: Mann 1981) and to the interior by one or more unoccluded foramina (e. g. see Montgomery 1978, Round *et al.* 1990, Stidolph 1995, Krammer 2000, and many illustrations listed by Gaul *et al.* 1993), which can be small and pore-like, or broad and slit-like; in extreme cases, the stria may lack an internal wall, so that it is not strictly alveolate but is essentially a simple multiserial stria (e. g. in *Pinnularia borealis* var. *islandica*: Krammer 2000, pl. 6, fig. 5). The foramina are generally tightly aligned along the valve. Comparisons between light and electron micrographs show that the 'longitudinal lines' detected by light microscopists in *Pinnularia* and *Caloneis* are produced in different ways in different species. In some cases, where the foramina are small, the lines are produced by the foramina themselves. Elsewhere, where the foramina are larger, the lines represent the proximal and distal edges of the foramina (as was known already to Cleve 1895, pp. 71, 72). The position and size of the foramina can often be detected with care in LM and Krammer & Lange-Bertalot (1986, p. 84) use this information to distinguish *Caloneis* from *Pinnularia*: in *Caloneis*, the alveoli, at least in the cen-

tral part of the valve, are said to be always closed (i.e. roofed over internally), with 1-2 narrow foramina that are marginal or lie in the mantle region; in *Pinnularia*, the alveoli are open or closed, with more or less wide foramina openings on the valve face ('Alveolen zumindest im mittleren Schalenbereich stets geschlossen, mit 1-2 schmalen Öffnungen marginal oder im Mantelbereich' versus 'Alveolen offen oder geschlossen mit mehr oder minder breiten inneren Öffnungen im Schalenbereich'). This is fairly similar to the distinction made by Patrick & Reimer (1966, p. 296): 'striae apparently crossed by one or more narrow longitudinal bands near the margin of the valve' (*Caloneis*) versus 'striae not apparently crossed by bands or if so, the bands are fairly broad' (*Pinnularia*).

Let us now return to Krammer's (2000) recent analysis. The first question is whether it is truly 'obvious' in LM whether or not a particular species belongs to *Pinnularia* or *Caloneis*. Assuming that the distinction is to be made primarily on the basis of foramen position and size, Krammer's claim resolves into two issues. One is the implicit claim that there is a discontinuity between *Pinnularia* and *Caloneis* in relation to the size and positions of the foramina; the other is the more obvious one that the foramina can be detected in LM, so that the discontinuity in the variation pattern can be used in practice to diagnose the genera. Cleve's own comment, that small species of *Caloneis* closely resemble *Pinnularia* suggests that the distinction is not always clear, and my own experience supports this: it is not always easy in practice to decide whether a species belongs in *Caloneis* or *Pinnularia*, especially if one lacks experience or visual acuity. If the distinction were really so 'obvious' as Krammer says, then it would be highly unlikely - even in the absence of a full understanding of what the longitudinal lines mean in terms of stria structure - that any species would be misclassified. Yet there are several examples of taxa that have been transferred between *Caloneis* and *Pinnularia*. *Caloneis tenuis* (Gregory) Krammer and *C. undulata* (Gregory) Krammer were originally placed in *Pinnularia*, not *Navicula* Bory, as might have been expected in 1854, when Gregory described them. *Caloneis sublinearis* (Grunow) Cleve, *C. molaris* (Grunow) Krammer,

C. budensis (Grunow) Krammer and *C. leptosoma* (Grunow) Krammer were all placed in *Pinnularia* by Cleve (1895). Transfers in the opposite direction are rare, but do exist: e. g. *Caloneis simplex* Skvortzow, transferred to *Pinnularia* by Skabichevski (VanLandingham 1968). *Caloneis butantanum* Krasske is also a *Pinnularia* according to Metzeltin & Lange-Bertalot (1998: their transfer on p. 628 is invalid, since there is no reference to the protologue of *C. butantanum*).

Too much should not be made of these taxonomic changes, however, since the vast majority of *Pinnularia* and *Caloneis* species have never been assigned to the other genus. More problematic is the fact that a simple differentiation between *Caloneis* and *Pinnularia* on the basis of foramen characteristics is impossible: there is apparently every intergradation between the genera in terms of the size and positions of the foramina. This is simply demonstrated by comparing Krammer's (2000, p. 297) illustrations of *Pinnularia acrosphaeria* W. Smith with those of *Caloneis crassa* (Gregory) R. Ross or *C. africana* (Giffen) Stidolph provided by Stidolph (1995). In all three, the foramina are small and positioned near the junction of valve face and mantle. *Pinnularia altiplanensis* Lange-Bertalot, Krammer & Rumrich also has small foramina, especially if considered relative to the transapical extent of the striae (Rumrich *et al.* 2000, pl. 145, figs 20-26). *Caloneis westii* (*sensu* Schrader 1971, pl. 4, fig. 1: plates 4 and 5 were transposed in this paper) possesses foramina that are as wide as or wider than those of *Pinnularia neomajor* Krammer (Krammer 2000, pl. 173, figs 1, 3). Hence, in order to classify on the basis of foramen size and position, it would be necessary to pick an arbitrary point along a continuum of variation.

Thus, if the genera intergrade with respect to the principal character used for diagnosis, and if this character is difficult to use in particular cases (e. g. small-celled species), why is it that there has been almost unanimous support for *Caloneis* in the last 100 years? The two main possibilities are (1) that *Pinnularia* and *Caloneis* are natural, monophyletic groups that are difficult to define because their synapomorphies are cryptic or difficult to describe in words; or (2) that diatomists have deluded themselves. No-one has the evidence to say whether (1) is true. The ob-

vious way to test this idea is via molecular genetic data, but there are as yet few sequences for members of the Pinnulariaceae: Medlin *et al.* (2000) include one *Pinnularia* 18S rDNA sequence, and we have an *rbcl* sequence for a *Caloneis* (D. G. Mann & G.E. Simpson, unpublished). Searches through available literature do not yield any unique morphological character states for either *Pinnularia* or *Caloneis*. The stria structure is similar in both and, although *Caloneis* species are generally more finely striate, there appears to be a continuum of variation, as with foramen morphology. The raphe system is similar in both genera: the central raphe endings are expanded externally and generally slightly deflected towards the primary side of the valve, and the terminal fissures are hooked towards the secondary side (as in most raphid diatoms). In both genera, the central raphe endings may be visible internally and abruptly turned towards the primary side (for *Pinnularia*, see e.g. Krammer 2000, pl. 6, fig. 2, pl. 35, fig. 4; for *Caloneis*, e.g. Stidolph 1995, fig. 38), or they may be hidden by an overgrowth of silica from the primary side (for *Pinnularia*, see e.g. Krammer 2000, pl. 19, fig. 6, pl. 82, fig. 8, pl. 117, fig. 5; for *Caloneis*: D. G. Mann, unpublished data for a large linear marine species). The girdle is apparently similar throughout, containing open bands, including a wide first band that bears a single row of areolae in the pars exterior (Round *et al.* 1990, D. G. Mann, unpublished). In both genera there is either a single H-shaped plastid or two girdle appressed plastids (e.g. Heinzerling 1908, Tschermak-Woess 1953, Cox 1988), and in both genera some species have invaginated pyrenoids (Tschermak-Woess 1953, Thaler 1972). I have found no significant difference between *Caloneis* and *Pinnularia* species in their sexual reproduction or perizonium structure (Mann 1989a and unpublished).

Hence there is as yet no evidence supporting the view that either *Pinnularia* or *Caloneis* is a monophyletic group. Either or both may be monophyletic, but if so, it is unlikely that any morphological or cytological autapomorphies exist that will enable each genus to be identified simply; if there were, they would almost certainly have been detected and used, e.g. by Hustedt. On the other hand, the consistency of stria, ra-

phe, girdle and plastid structure within the larger grouping of *Pinnularia* and *Caloneis* and related genera, such as *Oestrupia* Heiden (for which, see Schrader 1971 and Hein & Winsborough 2001), *Pinnunavis* Okuno (not *Pinnuavis*, as is sometimes written), and perhaps also *Diatomella* Greville and *Dimidiata* Hajós (Round *et al.* 1990), suggests that this larger grouping is monophyletic. It appears to have evolved well before the Upper Eocene, since in the Oamaru assemblages there are representatives of several different lineages of Pinnulariaceae, including *Pinnunavis*-like taxa (cf. *Navicula yarrensii* Grunow in Schmidt: Okuno 1950), *Pinnularia* spp. and *Oestrupia* spp. (Schrader 1969, Desikachary & Sreelatha 1989). Round *et al.* (1990) placed most of the genera mentioned above in the Pinnulariaceae: the combination of multiseriate, generally alveolate striae and raphe morphology is unique and there is no indication whatsoever from incongruent data sets that the alveolate striae of *Pinnularia*, *Caloneis* and *Oestrupia* are homoplasies (in 1990, I would have phrased this conclusion differently, without cladistic terminology, but the claim is unchanged); *Pinnunavis* has almost completely open alveoli, i.e. multiseriate striae (e.g. John 1988), but in all other respects it conforms to the *Pinnularia-Caloneis-Oestrupia* group. Thus, Krammer (2000) is quite wrong, in my view, to suggest that a larger grouping would necessarily be polyphyletic; indeed, the easiest way to achieve monophyly at the generic level would be to combine all taxa with the *Pinnularia* type of alveolus into a single large genus. Indeed Krammer hints at the logic of this himself in his comment that 'in the Naviculaceae [Krammer does not use this in the sense of Round *et al.* 1990] there are primarily two important construction plans: the *Navicula* plan and the *Pinnularia* plan.'

However, combining the genera is only one possibility. Another is to treat the alveolate diatoms related to *Pinnularia* as a family, the Pinnulariaceae, and (as indeed was suggested by Krammer) to split either or both of *Pinnularia* and *Caloneis* into smaller genera that can be arranged, formally (via sections, subgenera etc) or informally, into a system that reflects evolutionary relationships. Krammer (2000) has recently separated two new genera from *Pinnularia*: *Hy-*

gropetra Krammer & Lange-Bertalot, which he has established for the former *P. balfouriana* Grunow, together with a new species, *H. elongata* Krammer & Lange-Bertalot; and *Alveovalium* Lange-Bertalot & Krammer, which at present includes just one species - *A. beyensii* Lange-Bertalot & Krammer. It is unclear whether Krammer intends that these taxa should be regarded as only distantly related to the species he has left in *Pinnularia*, or whether they are simply the first of many new genera to be split off. *Hygropetra* is distinguished from *Pinnularia* 'by the septated copulae, not honeycomb-like arranged areolae and the arrangement of the vela, not on the exterior of the areolae'. *Alveovalium* has foramina that are surrounded by ridges. In both cases the morphology is distinctive and there are so few species in the genus that monophyly is extremely likely. However, if such small groups as these are to be regarded as genera, it is likely that many tens of other genera will need to be split from *Pinnularia* and *Caloneis*, if strict monophyly (holophyly) is to be achieved at the generic level. It is easy to split off small peripheral groups with particularly distinctive autapomorphies, like *Alveovalium*, but the consequence will often be to create a large paraphyletic 'rump' genus. The same danger is present in other groups, such as the Naviculaceae, where the separation of *Seminavis* D. G. Mann in Round *et al.*, *Pseudogomphonema* Medlin in Medlin & Round, *Hippodonta* Lange-Bertalot, Witkowski & Metzeltin and *Fogedia* Witkowski, Lange-Bertalot & Metzeltin makes it almost certain that *Navicula* itself, even as redefined to include only the lineolate species (e. g. in Round *et al.* 1990), is paraphyletic: it is highly unlikely that all of the other genera listed above diverged from each other before the evolution of *Navicula sensu* Round *et al.* (1990), which can currently be distinguished from these other genera principally through the absence of likely autapomorphies, such as amphoroid symmetry (*Seminavis*), heteropolarity (*Pseudogomphonema*) or lateral sterna (areas) (*Fogedia*).

Earlier, Lange-Bertalot & Metzeltin (1996) established a new genus, *Chamaepinnularia*, for a number of species previously classified in *Navicula sensu lato* or *Pinnularia*. The principal characteristic differentiating *Chamaepinnularia*

from *Pinnularia* appears to be the structure of the striae, which are said to be uniseriate but alveolate. After examining the SEM micrographs presented by Krammer & Lange-Bertalot (1985, pl. 26, figs 22-26), Lange-Bertalot & Metzeltin (1996, pl. 118, figs 6, 7) and Witkowski *et al.* (2000, pl. 69, figs 6, 8), and the original description of the genus (Lange-Bertalot & Metzeltin 1996, p. 32), I still do not understand the structure of the striae. In the published micrographs I cannot see several of the features that are apparently important for differentiation, e. g. the transapical, slit-like apertures to the alveoli; sieve membranes (hymenes); and fine pores with a density of 16-20 in 10 μm . This genus remains *incertae sedis*.

If I am correct and there is no adequate basis for the traditional *Pinnularia-Caloneis* distinction, we are forced towards the conclusion that diatomists have been deluded for 100 years. How could this be so? One explanation for the persistence of *Caloneis sensu* Hustedt (1930) or *sensu* Krammer & Lange-Bertalot (1986) is that people learn to recognize not the genus itself, but individual species and species complexes, which they then learn to associate with a particular genus name. Thus, they may become familiar with *bacillum*, *silicula*, *schumanniana*, *liber*, or *amphisbaena* morphologies and they may know, from floras or checklists, that these are supposed to belong together in *Caloneis*, for reasons that they cannot explain and which may not exist. My own identification of flowering plant families is exactly like this. I can recognize temperate oaks (*Quercus*), beeches (*Fagus*) and chestnuts (*Castanea*), and I know that these belong to the Fagaceae, but I have only the vaguest idea of what characterizes the Fagaceae; the family may or may not be natural and I do not know how I would determine whether other genera also belong to the Fagaceae, except by asking an expert. I have similar 'abilities' concerning the Betulaceae, which the books tell me contains birches (*Betula*), alders (*Alnus*) and hornbeams (*Carpinus*), all of which I can recognize. Hence identification is not always a matter of logic and identification via a hierarchical decision tree. *Caloneis* may exist in our floras, not because it is a natural grouping and not because its species have particular characteristics in common, but

simply by virtue of received knowledge. Within *Caloneis*, there are several groups that may well be natural, like the two that, respectively, include *C. amphibaena* (Bory) Cleve and *C. silicula* (Ehrenberg) Cleve (these groups are mentioned also by Krammer & Lange-Bertalot 1985, p. 16, who suggested that they might be appropriately recognized as subgenera); however, there is no evidence that these or other groups within '*Caloneis*' are more closely allied to each other than to groups within '*Pinnularia*' or *Oestrupia* or *Pinnunavis*.

Perhaps the best question to ask is: if we were setting out today to classify the diatoms of the Pinnulariaceae into genera, using modern technology and methods of analysis, and if we had no knowledge of previous classifications, would we re-invent *Caloneis*? I doubt it. However, until we have a clearer idea of relationships within the Pinnulariaceae, especially from gene sequence data, it may be best to accept the unsatisfactory classification that we have, rather than attempt to produce a new one that might be worse.

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