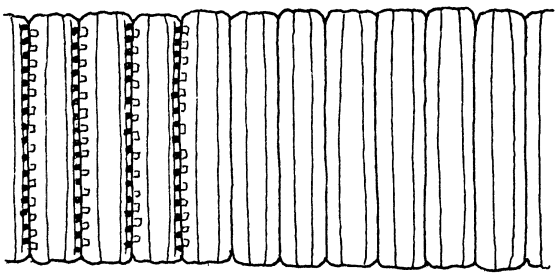
4.4 Colonial organization in the Nitzschiaceae

The majority of the Nitzschiaceae are solitary forms, united only for the short period after cytokinesis when the daughter cells remain connected by the parental cincture. Certain genera consist entirely of such forms, e.g. Hantzschia and Cylindrotheca; Bacillaria and Gomphonitzschia, however, are colonial, while Nitzschia encompasses species of both types.

Within the Nitzschiaceae it is possible to distinguish seven different kinds of colony:

4.4.1 Band-like colonies, formed by the persistent association of cells after cytokinesis



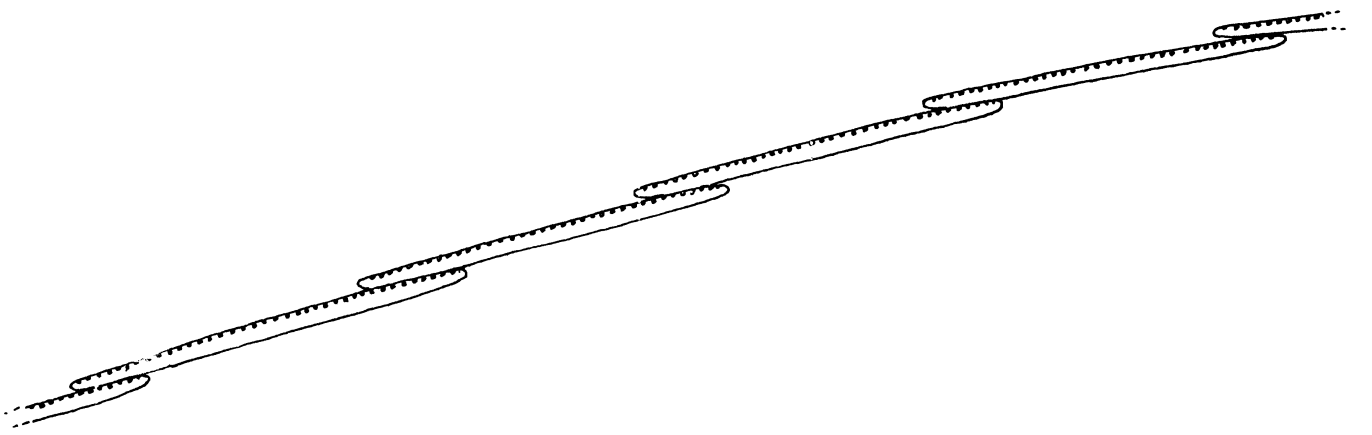
Well-developed colonies of this type are found in the genus Pseudoeunotia (q.v.) and in Nitzschia sect. Fragilariopsis (Hustedt 1958), both of whose members are marine and planktonic. Before the presence of a raphe was suspected, several of these species were classified as marine Fragilaria species, e.g. Nitzschia castracanei Hasle (= Fragilaria linearis Castracane 1886), N. cylindrus (Grun.) Hasle (= Fragilaria cylindrus Grun. in Cleve 1883). The region of contact between adjacent cells is over the whole valve face (Cupp 1943, p.191; Hasle 1965b; Paasche 1961, Pl.1b).

Similar, band-like colonies, but of only a few cells, are also

found occasionally in benthic Nitzscnia species. N. sinuata and N. denticula sometimes form short chains of cells, and W.Smith (1856) classified these two in Denticula for this reason. He noted that, whereas 'Odontidium' (now in Diatoma) was often in 'filaments of considerable length, and in some cases of no little tenacity', Denticula occurred 'invariably in fragmentary portions rarely presenting more than two or four in union and that union apparently of the feeblest kind.' He illustrated a chain of four cells for N. denticula (his 'Denticula obtusa') and one of six for N. sinuata (his 'Denticula sinuata'): both these species are now in Nitzschia sect. Grunowia.

In the Afon Bran samples, no chains of more than two N. sinuata cells were observed, in spite of the fact that the site, the underside of a bridge, is subject to minimal water flow and little shear stress, and thus would seem not unfavourable to colony formation. In a similar habitat at Carreg Cennen Castle, Dyfed, on an exposed limestone wall, conditions allowed the formation of short chains (4 or more cells) in N. hantzschiana (sect. Lanceolatae), although single cells were also present in this sample. Grunow (in Cleve & Grunow 1880) also recorded colony formation in this species, and in N. frauenfeldii and N. perpusilla.

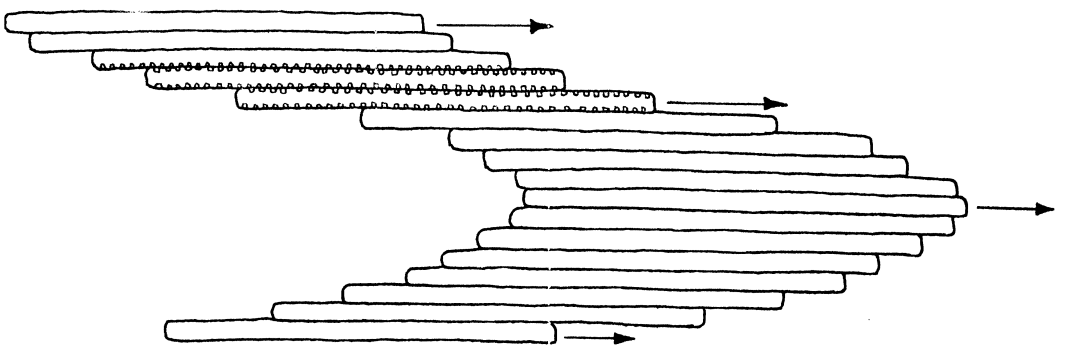
4.4.2 Stepped chains of non-motile cells



Whereas among the species exemplifying the first type there are a few benthic forms, colonies of the second type are found only in the marine, planktonic group, Nitzschia sect. Pseudonitzschia. Cells are in contact only over a short, but more or less constant, distance near their ends, and the chain is stepped. For the chain to increase in length it is clear that newly formed daughter cells must move relative to one another (otherwise end to end contact will not be achieved), but this process does not appear to have ever been observed. No other active movement of cells seems to occur, and it is this, coupled with the nature of the connection between cells, that separates these forms from Bacillaria.

There appears to be no special adaptation of the valve to facilitate colony formation. Cell to cell contact is via the valve face (F.969), and fragmentation of chains seems to take place quite easily, an inference drawn from Smayda & Boleyn's (1965) studies on sedimentation in N. seriata, where the mean colony size decreased during the course of the experiments.

4.4.3 Motile colonies of variable shape



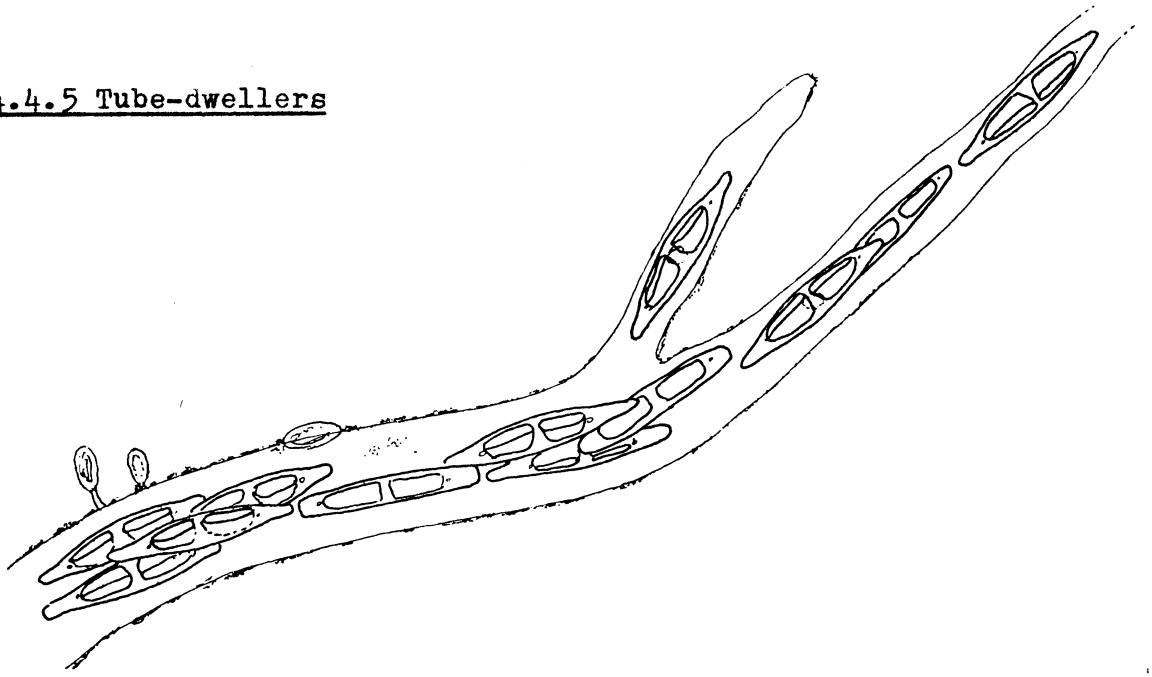
In this type, characteristic of the genus Bacillaria, each cell is fully motile; thus, the configuration of the colony can change

quickly from a band (as in the sect. Fragilariopsis) to an extended, stepped chain (as in the sect. Pseudonitzschia). The method of interlocking of the cells will be discussed more fully elsewhere ('Minor genera - Bacillaria'), but in this group the cells are obviously structurally adapted to their unique colonial existence; in the preceding groups structural adaptation is not immediately obvious, although there must be some factor which determines the degree of overlap of the cells in the sect. Pseudonitzschia.

4.4.4 Cells united in groups within mucilage

Nitzschia fasciculata forms small bundles of cells in a sheath of mucilage (Van Heurck 1880-5); hence the specific epithet. It must be noted that this colony type, apparently unknown in any other species, is distinct from the tubes formed by other Nitzschia species (see below) - 'cette espèce vit en petits faisceaux mais non en tubes' (Peragallo & Peragallo 1897-1908). It has not been observed in the course of this study.

4.4.5 Tube-dwellers



Diatoms belonging to several genera - Cymbella, Navicula, Berkeleya, Frustulia, Gyrosigma and Nitzschia - are known to form mucilage

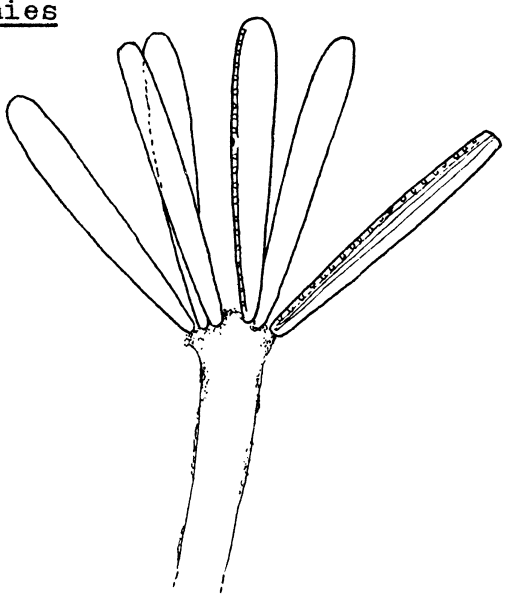
tubes in which they live and multiply (Cox 1975c). Originally these tube-dwelling taxa were classified in separate genera from their free-living counterparts: some tube-dwelling Navicula species were included in the form genus Schizonema, Nitzschia species in Homoeocladia, etc.

Within the Nitzschiaceae the tube-dwelling habit appears to be restricted to Nitzschia: Cylindrotheca closterium has also been recorded in tubes, but only as an invader - the tubes are formed either by Berkeleya rutilans or by Navicula ramosissima (Cox 1975c). Representatives of several sections of Nitzschia form tubes, with most coming from the sect. Nitzschia, more particularly that group which was formerly called the 'Obtusae'. Thus, Hustedt (1930) said of the sect. Obtusae 'Zellen häufig (vielleicht bei allen Arten) in Gallertschläuchen lebend.' Certainly N. filiformis is well known as a tube-dweller (Cox 1975c, Van der Werff & Huls 1957- , Pankow 1976), and N. obtusa was noted to be present in tubes in salt-marsh mud by Williams (1965). N. vidovichii is another tube-dweller belonging to this section; it was originally described as Homoeocladia vidovichii by Grunow (1862). Besides these, N. angularis, of the sect. Spathulatae, forms tubes (Karsten 1899, Cox 1975c, and my unpubl. obs.), as does N. recta, of the sect. Lineares (Cox 1975c). Various Homoeocladia species have been described which are apparently not synonymous with any of the above taxa, but in many of these the illustrations and descriptions given are inadequate for confident identification; it will be necessary here to go back to the original material, if this still exists, in order to establish their identities.

Several other Nitzschia species are to be found in tubes but, like Cylindrotheca closterium, only as invaders. Cox (1975c) noted that N. dissipata is often a symbiont of Cymbella prostrata or N. filiformis tubes, while N. lanceolata and N. frustulum may occur

separately or together within the tubes of a variety of marine taxa - Berkeleya rutilans, Navicula grevillei, N. ramosissima etc. Thus, it can happen that three Nitzschia species may inhabit the same tube, viz. the tube builder, N. angularis, with the two symbionts N. lanceolata and N. frustulum! Grunow (in Cleve & Grunow 1880) observed N. tubicola to be a symbiont of Schizonema grevillei (= Navicula grevillei): this Nitzschia ,a member of the sect. Lanceolatae, is imperfectly known - Lange-Bertalot (1977) supplies an illustration, but no analysis beyond Grunow's original remarks.

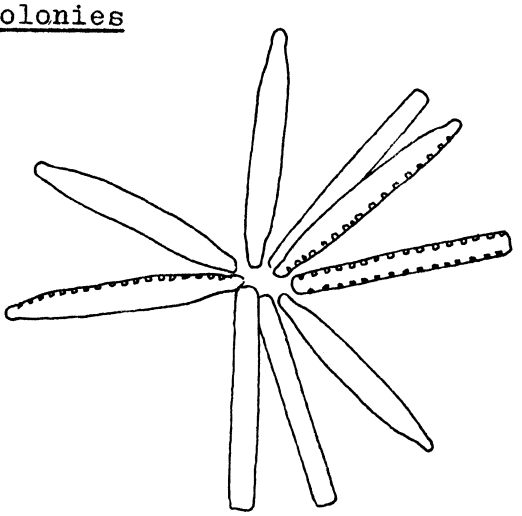
4.4.6 Stipitate colonies



The genus Gomphonitzschia comprises a few heteropolar species which are analogous in form and habit to species of Gomphonema or Licmophora. Grunow (1870) founded the genus for Gomphonitzschia ungeriana which he discovered attached to Cladophora macrogynia. His illustrations (1870, T.1 f.1) show that several frustules radiate from the end of a substantial stipe, consisting presumably of mucilage, by which attachment to the substratum is effected. When material of this species (or of G. clevei etc.) again becomes available, it will be interesting to see whether there is any structural adaptation facilitating stipe formation; in various other diatoms which form

mucilage pads or stalks (Striatella, Gomphonema, Cymbella etc.) there are ± well-defined areas of unoccluded pores (areas which are classifiable as ocelli or pseudocelli, Anon. 1975) through which the mucilage is extruded (Hufford & Collins 1972).

4.4.7 Stellate colonies



Among the freshwater planktonic species of Nitzschia there is at least one, N. actinastroides (= N. holsatica Hust.), which forms colonies of 4-16 cells, all radiating from a central point. This species was originally included in Synedra, but was transferred to Nitzschia by Van Goor (1925). Two other Synedra species, S. berolinensis and S. limnetica, may also belong in Nitzschia (Van Goor 1925), but confirmation of this must await examination of type material.

Only in one case, Bacillaria (which is either planktonic or benthic), are the colonies actively motile: in the others there is a greater or lesser loss of motility of the individual cells, save in the tube-dwelling forms where individual cells may be very active although the tube itself moves only passively. Hence colonial Nitzschiaceae are usually found attached to a substratum (types 4?, 5, 6), or in the plankton (types 1, 2, 7). It is interesting to note that within

this one family there are parallels to several other colony-forming taxa. Thus, Gomphonitzschia may be compared with Gomphonema, Rhoicosphenia or Licmophora; N. actinastroides with Asterionella; Nitzschia sect. Fragilariopsis with Fragilaria or Phaeodactylum (Borowitzka et al. 1977); sect. Pseudonitzschia with Nanoneis hasleae (Norris 1973); and'Homoeocladia' species with the tube-dwelling Naviculae, Berkeleyae, Cymbellae, etc. There appear to be no parallels to Bacillaria, however, and there are further colony types within the Bacillariophyta which find no parallel within the Nitzschiaceae, e.g. those exemplified in Pinnularia debesii (Hustedt 1930, f.612), Diatoma vulgare (Hustedt 1930, f.103a), Planktoniella muriformis (Round 1972b, f.9-11), etc.

It is difficult to explain why the tube forming habit should occur in such a variety of genera unless it is a general reaction of raphid diatoms to particular environmental conditions; if so, however, it is strange that more species do not form tubes. It may be relevant that tube-dwelling diatoms often occur in localities subject to burial under fine sediments; thus, tube floras are particularly well-developed along estuaries such as that of the Severn, where thick deposits of silt often cover most of the intertidal rock surfaces. Tube-dwelling diatoms also occur in salt-marshes (e.g. Gyrosigma eximium, unpubl. obs.) and sand-flats (e.g. Navicula sp., unpubl. obs. of intertidal sand from St.Martin's, Isles of Scilly), and the habit may in part be a protection against burial. In such situations the tubes will also stabilize the sediment, just as do the filaments of Vaucheria spp.