J. mar. biol. Ass. India, 1972, 14 (1) : 315-327

ORIENTATION OF SETAE IN THE GENUS *CHAETOCEROS*, IN REGARD TO THE APICAL AXIS*

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ABSTRACT

The taxonomy of the diatom genus *Chaetoceros* has largely been based, up to now, on the appearance of the chains in front view, the lateral apical views having often been neglected and only occasionally observed and illustrated by most authors. To partly remedy this situation, the author has photographed as many species as possible in apical view, and has collected from the literature all available illustrations in such view. He has then proceeded to establish six groups of species based on the divergence and orientation of setae in apical view. A key to those six groups, based on that character, is given, the author pointing out that the new system he proposes is not meant to replace the present one but to be complementary to it.

INTRODUCTION

WHILE preparing a monographic study on the phytoplankton of a part of the Gulf of St. Lawrence, published in 1962 under the title 'LE PHYTOPLANCTON DE LA BAIE DES CHALEURS' (Brunel, 1962), I have had the opportunity of working out in a rather extensive manner the genus *Chaetoceros*, which under our latitudes is the main constituent of the spring diatom plankton, and also the most diversified genus, as to number of species blooming up all at once.

Some species of *Chaetoceros* are represented by solitary cells, but most produce chains of cells held together by their lateral setae, i.e. pairs of heterocytic setae that I have proposed to call 'sister setae' in a recent paper (Brunel, 1966). Many of these chains, when placed on a slide under a cover-glass, fall flat on their backs, presenting, as we say, a front view or sagittal view of the chains, then considered as a single organism (Plate I).

Most, if not all, taxonomic treatments of the genus are based mainly on the appearance of the chains as viewed in such a position,—admittedly the more common one under the microscope,—and little attention is usually given to lateral view, still less to apical view, both often being all but impossible to see, on account either of the long lateral setae or of the long chains of cells, which obviously prevent the specimens from turning sidewise or standing on end in the thin film of water between slide and cover-glass. And yet, the divergence and orientation of setae in those positions are often very characteristic and of course different from the better known divergence and orientation in front view, so much so that, were they as well and as generally known, they would represent highly valuable criteria for the rapid or critical identification of many species.

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* Presented at the 'Symposium on Indian Ocean and Adjacent Seas—Their Origin, Science and Resources' held by the Marine Biological Association of India at Cochin from January 12 to 18, 1971.

The easier to tackle of the two neglected views is no doubt the *apical view* (also called *valvar view*). Some published figures of *Chaetoceros* cells in apical view show only one straight or variously curved seta right and left of an elliptical cell, either in the case of solitary cells of species that do not form chains (e.g. Section *Simplicia*) or of cells of normally catenate species that have become separated from the rest of the chain. It is to be noted that in both cases not one but a pair of setae should show right and left of the cell,—unless of course they are perfectly superimposed,—both the upper and the lower valves bearing one seta at each end (Fig. 1). Thus the diver-

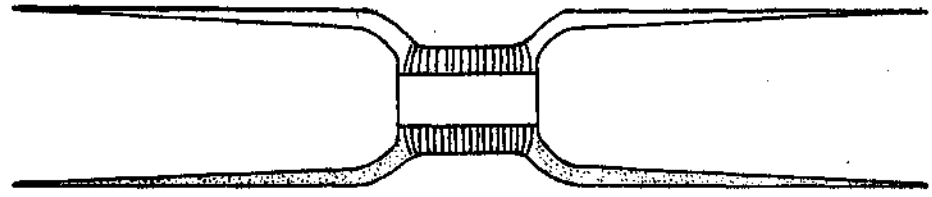

Fig. 1. Solitary cell of a hypothetical *Chaetoceros*, in wide girdle view, showing that the four setae are two autocytic and autovalvar pairs. The pair above is white, the pair below is stippled. Each lateral pair (*not sister setae*), seen from above in apical view, can look as one seta if both setae do not diverge at all from apical plane.

gence of these autocytic but heterovalvar lateral setae, with respect to the apical plane, can be measured and compared with the divergence in other species. There are only two exceptional cases that may warrant illustration of a valve with a single seta on each side. The first, of course, is when a single valve becomes detached from the rest of an already single cell. The second is when the cell in apical view is a *terminal* one bearing specialized terminal setae : inasmuch as these terminal setae often differ markedly from lateral ones in regard to size, structure, ornamentation and/or divergence, it is better to show them alone rather than in combination with those of the penultimate valve.

Now, it happens fairly frequently that chains become accidentally broken or dislocated in another way, i.e. not at the crossing point of the sister setae but at the junction of mantle and girdle, leaving pairs of consecutive heterocytic valves (Fig. 2). When such chain fragments rest on edge of a valve mantle, are visible in apical view, have on both valves intact setae that do not diverge too strongly from the valvar plane, then it is possible to analyse divergence in regard to *apical axis* (or its related *apical plane*) of the cell.

This is precisely what I have tried to do in this paper, firstly with some oceanic and neritic Atlantic species that I have myself observed and photographed, secondly with species that I have not personally observed in apical view but are so illustrated in such classical monographs as those of Gran (1905), Meunier (1910 and 1913), Hustedt (1930), Cleve-Euler (1951), Proschkina-Lavrenko (1955 and 1963), Hendey (1964). Species that have lately been studied under the electron microscope to determine the ultrastructure of the cell-wall or of setae, in works by Helmcke and Krieger 1953-1954, Okuno (1956), Desikachary (1954) and Desikachary and Bakadur (1954), and others, seldom yield information on divergence and orientation of setae, the very high magnification being in this case a hindrance rather than a boon.

My next step was to compile a comprehensive, though not exhaustive, list of illustrations of *Chaetoceros* in apical view, and to read the various authors' corresponding descriptions, making sure that the wording fitted the illustrations (which it

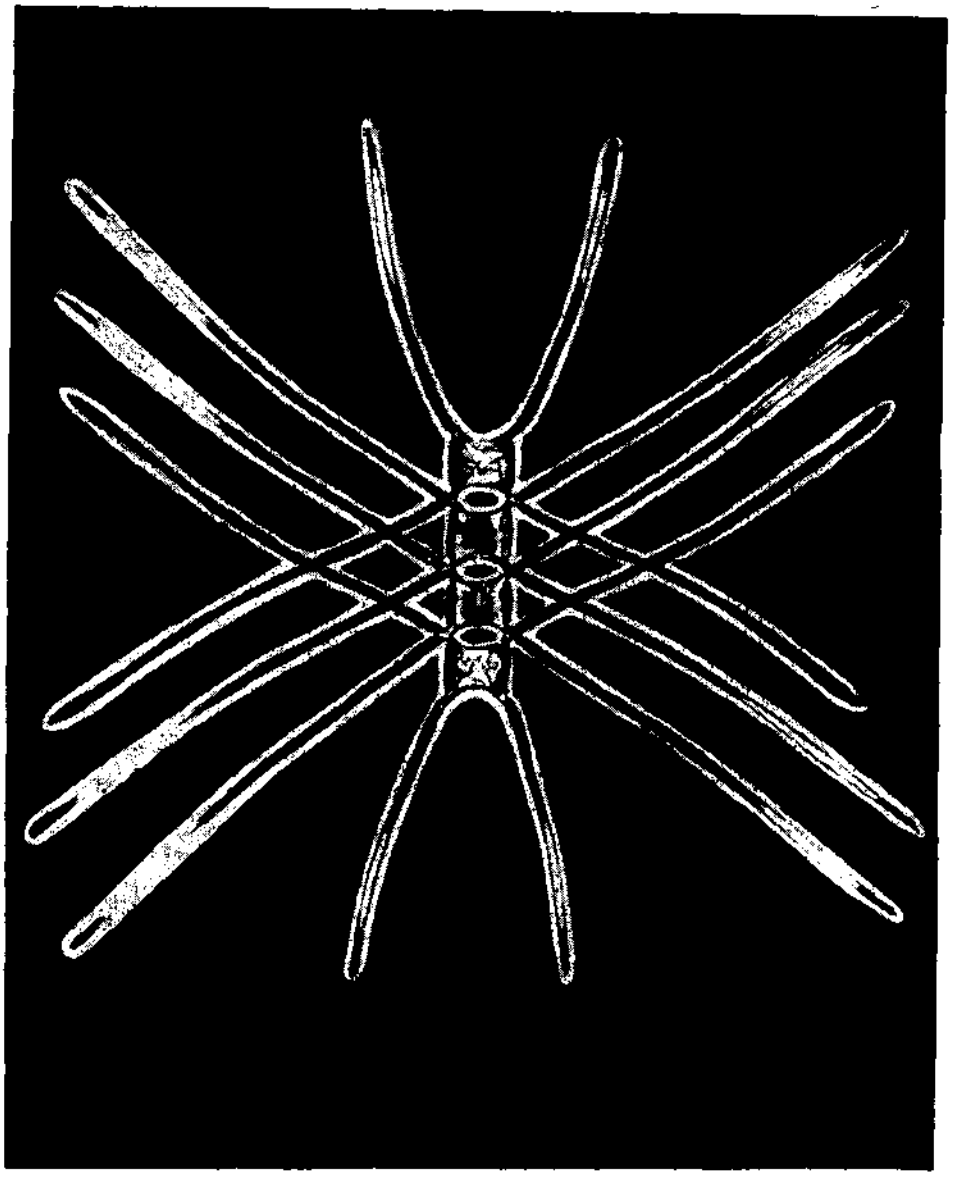

PLATE I. *Chaetoceros atlanticus*. A four-celled chain in front view. All setae, lateral and terminal, are visible from base to end, because they are all in the apical plane.

sometimes did not). Divergence of setae on all available illustrations was measured, and to facilitate comparison the originals were reproduced on tracing paper, and grouped according to that divergence criterion. All drawings were oriented in the same way, with apical axes always horizontal.

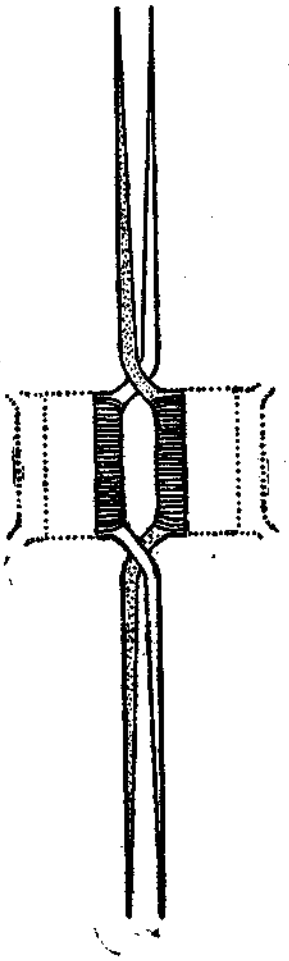

Fig. 2. Pair of contiguous heterocytic valves from two cells of a chain, in wide girdle view, showing that pair of setae above (white) and pair below (stippled) are both autovalvar but heterocytic. Each lateral pair are sister setae that can look as one when seen from above, in apical view, just as can those in figure 1.

Having thus listed, tabulated and compared all relevant pictures available to me, I came to the conclusion that most species of *Chaetoceros* as seen in apical view can be classified in six groups, the first four being pretty definite, the last two being perhaps provisional and susceptible eventually to fall into Group II or Group III.

As a first try-out I have prepared a key to these six groups. Later on, when all species are well known in apical view, I think they all could be included in one or the other of these groups.

KEY TO PROPOSED GROUPS OF *CHAETOCEROS*

BASED ON APICAL VIEW

1.	Sister setae parallel to apical plane (Fig. 3)	GROUP I
1.	Sister setae diverging more or less from apical plane ..	2
2.	Sister setae diverging 30° to 80° from each other at base, then either straight or curved ..	3
2.	Sister setae diverging 90° or more from each other at base, then either straight or curved ..	4
3.	Chains colonial, included in a mucilaginous matrix ..	GROUP VI
3.	Chains free, not included in mucus	5
4.	Sister setae diverging 90° or more but never attaining 180° (Fig. 5)	GROUP III
4.	Sister setae diverging 180°, i.e. perpendicular to apical axis (Fig. 6)	GROUP IV
5.	Sister setae symmetrically oriented on both sides of apical plane (Fig. 4)	GROUP II
5.	Sister setae all curved towards same side of apical plane (Fig. 7)..	GROUP V

I am fully aware that the key I propose is open to criticism, considering the large proportion of ill-known species, the several cases of erroneous graphic interpretations, and the frequent difficulty of determining the appurtenance of this or that seta to this or that pair, to this or that level, especially when medium-sized or very thin setae are involved. However, I am confident that the key, and the diagrams, should draw attention of phytoplanktologists on a morphological character that has been all too neglected up to now and that could be used with advantage much more frequently in the future to help unravel taxonomical problems in that complex genus.

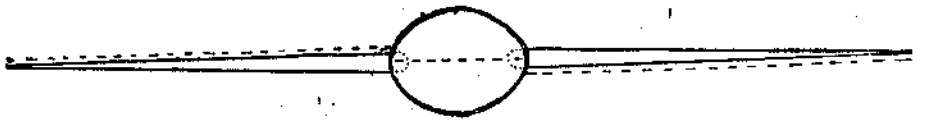

Fig. 3. Cell of a *Chaetoceros* in apical view, with a pair of superimposed setae right and left of contiguous valves, and strictly parallel to the apical plane. Upper setae : full line. Lower setae : broken line. All species with such an orientation of setae make up Group I, typified by *Ch. atlanticus*.

I cannot say that it was always easy to decide what group some species would fall into, on the sole basis of published figures, because, as I said before, discrepancies between authors do happen. The most glaring examples that I found concern *Chaetoceros holsaticus* and *Ch. similis* : they are worth a short description and comparative illustrations.

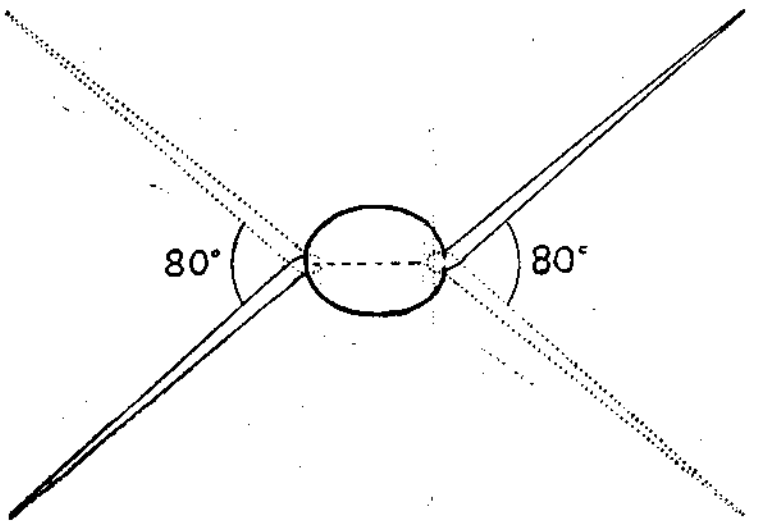

Fig. 4. Cell of a *Chaetoceros* in apical view, with a pair of sister setae right and left of contiguous valves, diverging from apical plane between about 30° and 80°. Upper setae : full line. Lower setae : broken line. All species with such an orientation of setae make up Group II, typified by *Ch. danicus*.

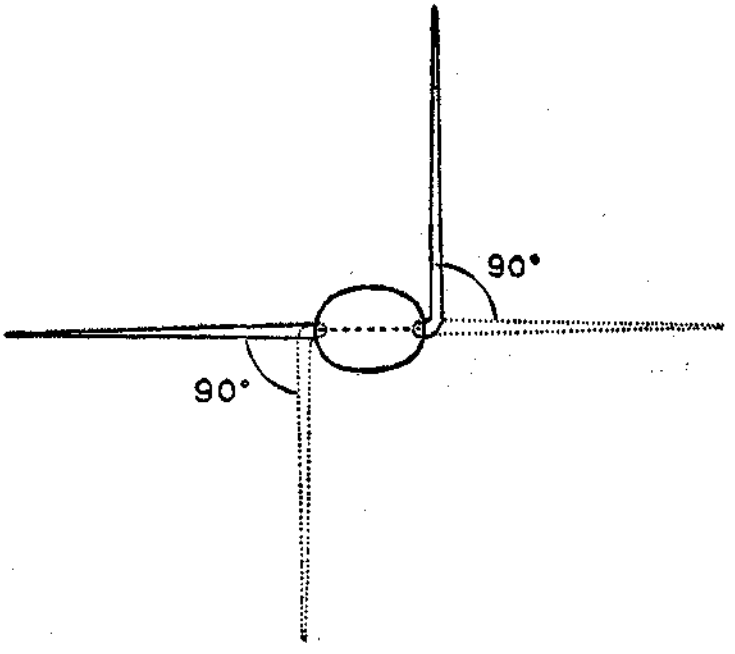

Fig. 5. Cell of a *Chaetoceros* in apical view, with a pair of sister setae right and left of contiguous valves, diverging 90° (or a little more) from each other. Upper setae : full line. Lower setae : broken line. All species with such an orientation of setae make up Group III, typified by *Ch. teres*.

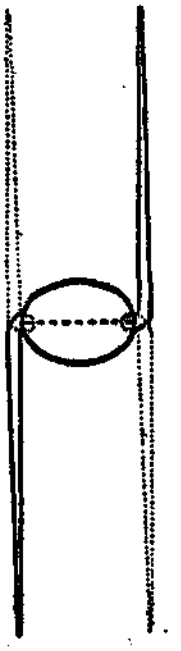

Fig. 6. Cell of a *Chaetoceros* in apical view, with a pair of sister setae right and left of contiguous valves, diverging 180° from each other, i.e. all four perpendicular to apical axis. Upper setae : full line. Lower setae : broken line. All species with such an orientation of setae make up Group IV, typified by *Ch. radicans*.

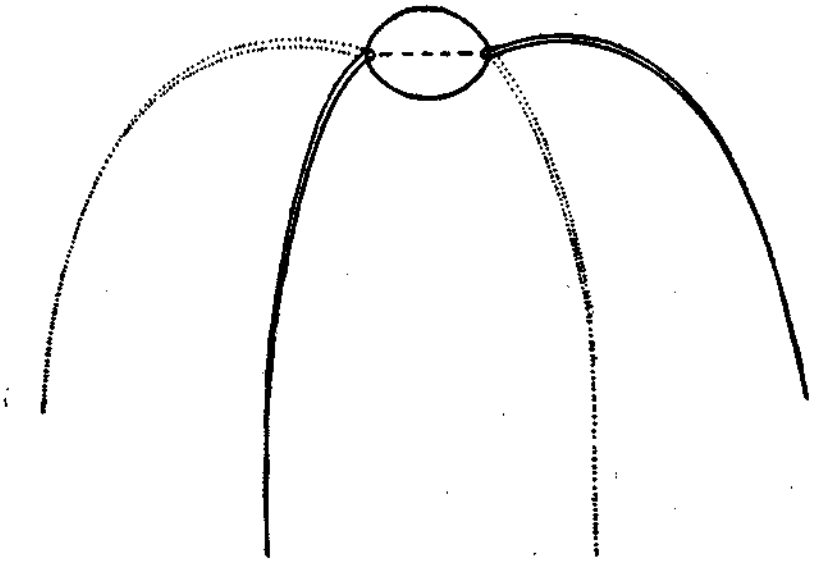

Fig. 7. Cell of a *Chaetoceros* in apical view, with a pair of sister setae right and left of contiguous valves, diverging approximately 40° to 50° at base, but all curved toward same side of apical axis. Upper setae : full black line. Lower setae : dotted black line. All species with such an orientation of setae make up Group V, typified by *Ch. debilis*.

If we look at three figures of *Ch. holsaticus* (Fig. 9 a-c), a species from NW Europe that I never have seen myself, we can see that it could be placed in three different groups : I, II or V,

(a) After Hendey (8, pl. 15, fig. 4a)
Divergence 0°. Falls into .. .. .. GROUP I

(b) After Proschkina-Lavrenko (14, fig. 32.4).
Divergence 90°+. Falls into.. .. .. GROUP III

(c) After Helmcke and Krieger (7, pl. 31σ).
All setae turned to one side and becoming parallel to transapical axis. Falls into .. .. .. GROUP V

I am not ready to throw blame, *a priori*, on any of the authors mentioned above, because seasonal and environmental conditions may be responsible for some of those variations, but in the present case I would be inclined to adopt Proschkina-Lavrenko's view, which corresponds best to Hustedt's written description, unaccompanied however by an illustration.

Another case of discrepancy is that of *Ch. similis* (Fig. 9, d-f) :

(d) After Proschkina-Lavrenk ° (13, fig 33.4).
Divergence 0°. Falls into .. .. .. GROUP I

(e) After Hendey (8, pl. 15, fig. 2a).
Divergence at base, ca. 50°. Falls into .. .. GROUP II

(f) After Meunier (11, pl. 6, fig. 13)
Divergence, near 0°. Falls into .. .. GROUP I

In this case I have a first-hand knowledge of the species, and though I do not have photographs in apical view, I have several in front view and they all show that lateral setae are in the apical plane throughout, therefore placing *Ch. similis* in Group I and confirming most authors' observations.

It must be said, however, that Hendey is not the only author to illustrate that species with diverging setae in apical view. Gran in 1905 (' nach Cleve '), Cleve-Euler in 1951 (' nach Cleve '), also published figures showing widely diverging lateral setae which became almost perpendicular to the apical axis. Is it possible that P.T. Cleve erred in drawing the initial figure in 1896 when describing *Ch. similis* for the first time? And is it possible that subsequent authors reproduced ' as is ' Cleve's figure time and again without checking if it fitted their written description? Hendey (1964) for instance writes : ' Setae....directed outwards obliquely in *stiff straight lines*.' A correct description for appparently erroneous figures, the setae in his illustrations being neither straight nor stiff.

I shall now proceed with the description of the six groups mentioned above in the key. For each group, I shall give at least one example of a species that I have personally observed and photographed in apical view, followed by a list of species that certainly or possibly belong to that group, ending with some ' Remarks ' concerning the group.

GROUP I

All sister setae, right and left of contiguous valves in apical view, parallel to apical plane, i.e. divergence 0° (Fig. 3). Example : *Chaetoceros atlanticus* (Plate I)

List of species

Chaetoceros	*atlanticus*
,,	*borealis f. solitaria*
,,	*ceratosporum*
,,	*decipiens*
,,	*dubius*
,,	*filiformis*
,,	*glandazii*
,,	*rigidus*
,,	*septentrionalis*
Chaetoceros	*gracilis*
,,	*heterovalvatus*
,,	*holsaticus* ***
,,	*lorenzianus*
,,	*lorenzianus v. forceps*
,,	*muelleri*
,,	*peruvianus*
,,	*similis*
,,	*vistulae*

*** See also Groups III and V

Remarks : When seen in sagittal view, the chains in group I show lateral setae that are in focus from base to end (Plate I) on both sides of the chain, due to the fact that they are parallel to apical plane (though usually not parallel to apical axis). Those species, of course, yield good photomicrographs consistently, especially in phase contrast microscopy.

GROUP II

All sister setae, right and left of contiguous valves in apical view, diverging 30° to 80° from each other, and about 15° to 40° from apical plane (Fig. 4). Example : *Chaetoceros danicus*.

List of species

Chaetoceros	*abnormis*
,,	*affinis****
,,	*affinis* v. *circinalis*
,,	*affinis* v. *willei*
,,	*borealis****
,,	*brevis*
,,	*concavicornis*
,,	*constrictus* v. *ambiguus*
,,	*convolutus*
,,	*orientalis*
,,	*perpusillus*
,,	*rigidus*
Chaetoceros	*costatus*
,,	*danicus*
,,	*exospermum*
,,	*fallax****
,,	*imbricatus*
,,	*karianus*
,,	*laciniosus*
,,	*lorenzianus**
,,	*mitra*
,,	*vixvisibilis*
,,	*wighamii*

* See also Group I.
*** See also Group III.

Remarks : Divergence, in this group and the next, is measured at the base of the sister setae, and no account is taken of the curvature farther out, which is often very pronounced. A special difficulty in these two groups arises with representatives of the Section *Borealia* where setae may have some or all of these peculiar characters : general bending towards one end of the chain, dissimilarity of insertion on ' upper ' and ' lower ' valves of each cell, sometimes twisting around each other at base on ' upper ' valve, though not on ' lower ' one, etc. Admittedly, placing of these species is provisional, pending further study.

GROUP III

All sister setae, right and left of contiguous valves in apical view, diverging by 90° (or a little more) from each other, and each seta by 90° also from the corresponding autovalvar seta, one of the sister setae being more or less parallel with apical plane, the other more or less perpendicular to it (Fig. 5). Example : *Chaetoceros teres.*

List of species

*Chaetoceros affinis***
,, *anastomosans*
,, *armatus***
,, *borealis*
,, *constrictus*
,, *coronatus*
,, *crinitus*
,, *densus*†
,, *diadema*
,, *didymus*
,, *dipyrenops*
,, *elbenii*
,, *fallax***
,, *furcellatus*

Chaetoceros cinctus
,, *compressus*
,, *concavicornis***
,, *holsaticus**
,, *lauderi*
,, *oppositisetaceus*
,, *pseudocrinitus*
,, *seiracanthus*
,, *subtilis* ††
,, *subtortilis*
,, *teres*
,, *tetrastichon*

** See also Group II.

Remarks : With regard to representatives of Section *Borealia*, see Remarks under Group II. Some species, belonging to various sections, have been placed in Groups II and III because of differences of opinion between illustrators, differences that we are not now ready to reconcile.

GROUP IV

All sister setae, right and left of contiguous valves in apical view, diverging 180° from each other, all four being perpendicular to apical axis (Fig. 6). Example : *Chaetoceros radicans.*

List of species

Chaetoceros karianus *Chaetoceros paulsenii*
,, *radicans*

* See also Groups I and V.
** See also Group II.
† Meunier : 90° or less ; Hustedt : 105° ; Proschkina-Lavrenko : 70-80°.
†† This species is provisionally placed in Group III, the illustration in Proschkina-Lavrenko showing a three-cell chain apically, where it is impossible to determine the divergence of each of the four pairs of setae.

Remarks : This is a small and very characteristic group, numbering only a few species. Furthermore, in the example chosen, all setae are densely hairy, an uncommon character in *Chaetoceros*.

Group V

All sister setae, right and left of contiguous valves in apical view, diverging approximately 40° to 50° from each other at base, but all curved toward same side of apical axis and becoming more or less perpendicular to it (Fig. 7). Example : *Chaetoceros debilis*.

List of species

Chaetoceros curvisetus *Chaetoceros holsaticus**
,, *debilis* ,, *pseudocurvisetus*

* See also Groups I and III.

Remarks : This small group, perhaps a temporary one, corresponds to Section *Curviseta*, and includes all three species of those *Chaetoceros* forming helicoidal chains with all setae bent outwards from the convex side of the helix. One should perhaps add to the group a form of *Ch. holsaticus* (Fig. 9c) illustrated in Helmcke and Krieger (1953-1954).

Group VI

Sister setae, right and left of contiguous valves in apical view, diverging approximately 30° to 50°, those of inside pair taking opposite directions, one completely reversing direction to parallel the outside pair toward periphery of mucilaginous colony, the other growing straight toward center of colony where it twists with similar long setae produced by other cells (Fig. 8). Example : *Chaetoceros socialis*.

List of species

Chaetoceros radians *Chaetoceros socialis*

Remarks : Here again, as in Group V, we have a possibly temporary group corresponding to Section *Socialia*, with two species. These are the only colonial

species of *Chaetoceros*, where chains of cells are held together in a common mucilage. Apparently, according to season, that mucilage may disappear, chains may become more or less independent and even break down into individual cells, leading to a

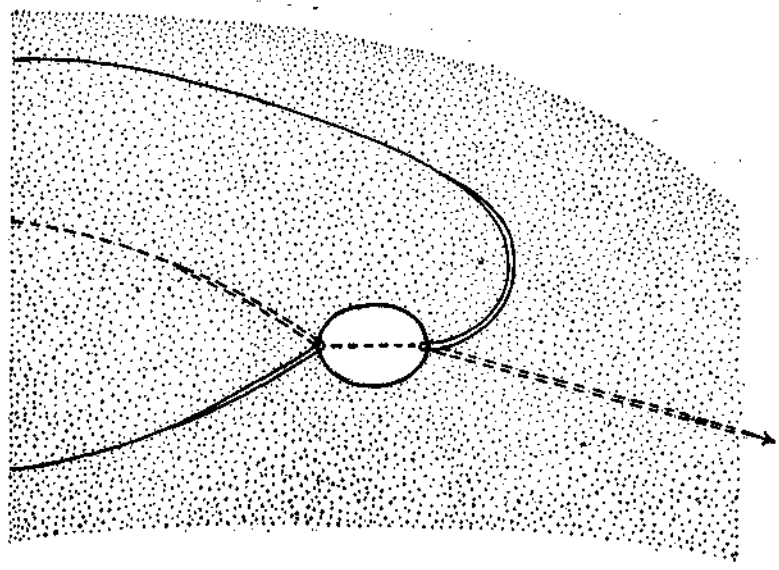

Fig. 8. Cell of a colonial *Chaetoceros* in apical view, with a pair of sister setae right and left of valve, diverging approximately 30° to 50° at base. Inside pair (right of valve) with one seta making a U turn toward, and ending at, the periphery of the colony, the other seta growing straight toward center of colony, becoming several times longer than the three others, and ending twisted with similar long setae from other cells. Upper setae: full line. Lower setae: broken line. Shaded zone represent colonial mucilage. All species with such an orientation of setae make up Group VI, typified by *Ch. socialis*.

reorientation of setae which may then look like those in Group V. But most published illustrations show that all setae then tend to become parallel with apical axis, whereas in Group V all setae become parallel with transapical axis.

Species of *Chaetoceros* Never Illustrated in Apical View

Chaetoceros

baculites	*ingolfianus*
coarctatus	*myriapodus*
dadayi	*pelagicus*
delicatulus	*pseudocurvisetus*
dichaeta	*rostratus*
difficilis	*saltans*
diversus	*tortissimus*
fragilis	*vanheurckii*

Conclusions

Is it possible to use divergence of lateral setae in apical view as a criterion in the classification of the genus *Chaetoceros*? I think so, and I have tried to prove it in the present paper. Of course, I do not mean that a system based on that criterion

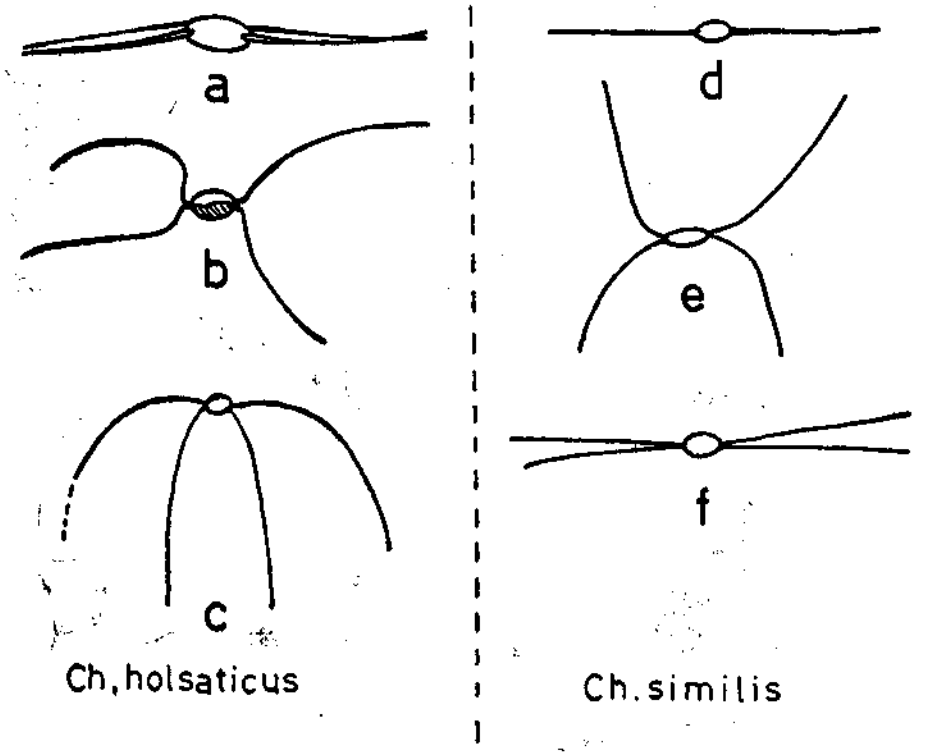

Fig. 9. Two sets of illustrations of *Chaetoceros* in apical view, from various authors, to show some striking discrepancies. *Ch. holsaticus*: (a) after Hendey 1964, (b) after Proschkina-Lavrenko 1963, (c) after Helmcke & Krieger 1953.—*Ch. similis*: (d) after Proschkina-Lavrenko 1955, (e) after Hendey 1964, (f) after Meunier 1913. (See text.)

alone could ever replace the present system on which have been rightly established the seventeen recognized sections of the genus in Hustedt's or Cleve-Euler's treatises. The observation of a chain fragment in apical view is too improbable an event to warrant erection of a new system on such a prerequisite. Furthermore, such a new system would certainly not be better than the present one. But I maintain that setae divergence in regard to apical axis could and should be used more and more frequently and carefully as a *complementary criterion* to better define the specific limits of all species of *Chaetoceros*, particularly those species that are difficult to identify in the usual manner. It is not meaningless that even now, about sixteen species out of approximately eighty, or 1 in 5, have not yet been illustrated in apical view. And should I recall that a species was named *Chaetoceros difficilis* by P. T. Cleve in 1900, a situation confirmed in 1910 by the Belgian master Alphonse Meunier when he wrote: ' Ce petit monde des *Chaetoceros* est plein d'embûches . . . Leur étude restera un problème difficile. Elle demande de la part de ceux qui s'y livrent une

sorte de flair acquis par la connaissance devenue familière d'un grand nombre d'espèces.'

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