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Chaetoceros phuketensis sp. nov. (Bacillariophyceae): a new species from the Andaman Sea

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SUMMARY

Over 400 species of *Chaetoceros* Ehrenberg have been described since the genus was created in 1844, making this one of the most species-rich genera of marine planktonic diatoms. Although *Chaetoceros* is cosmopolitan in distribution, the temperate north Atlantic taxa are best known. Examination of material from tropical seas suggests that there are numerous *Chaetoceros* endemic to these biogeographic regions, which await formal description. *Chaetoceros phuketensis* sp. nov. is described from the Andaman Sea, in the tropical Indian Ocean. It possesses several unusual morphological characteristics not found in temperate taxa, including multiple central processes on terminal valves, vermiform chloroplasts and large size. It is most similar to *Chaetoceros buceros* Karsten and *Chaetoceros bermejensis* Hernández-Becerril, which also inhabit tropical seas. These taxa are not easily accommodated in the traditional classification scheme, which was based on turn-of-the-century knowledge of north Atlantic taxa. Approaches for classifying these unusual species include modifications of the extant scheme and creation of a new scheme based on phylogenetic principles.

Key words: Andaman Sea, *Chaetoceros*, marine diatoms, phytoplankton, tropical diatoms.

INTRODUCTION

Chaetoceros was described by Ehrenberg over one and a half centuries ago, in the year 1844. In the course of the years which have followed, nearly 400 species have been described (VanLandingham 1968). Approximately half of these are considered valid (Rines and Hargraves 1988), making this one of the most species-rich genera of marine planktonic diatoms. *Chaetoceros* is cosmopolitan in distribution, but the temperate north Atlantic taxa have been best documented, for the simple reason that the majority of turn-of-the-century diatomists were Northern Europeans. The presently accepted classification scheme for *Chaetoceros* was developed by Gran (1897) and Ostenfeld (1903), and is strongly biased toward temperate north Atlantic taxa (Rines 1994), Rines and Theriot (unpublished data). Although *Chaetoceros* are often extremely abundant in the tropical latitudes, there are only a small number of classical papers describing the flora of these regions (e.g. Lauder 1864; Cleve 1873; Ikari 1926, 1928; Steemann Nielsen 1931). Several recent studies have begun to examine the *Chaetoceros* of Mexican and Caribbean waters (Hernández-Becerril 1991a; 1991b; 1992a; 1992b; 1993a; 1993b, 1996, 1998, 1999; Hernández-Becerril *et al.* 1993; Rines and Boonruang 1995). Their major findings have been that: (i) taxa originally known only from the Indo-West Pacific may also be found in the American tropics; (ii) there are numerous tropical taxa presently unknown to science; and (iii) tropical taxa have a variety of ultrastructural features unknown in temperate taxa, and thus they are poorly accommodated in Gran and Ostenfeld's traditional classification scheme (Gran 1897; Ostenfeld 1903). Virtually no contemporary studies of *Chaetoceros* have been conducted in the Indo-West Pacific region. In this paper we describe a new species from the Andaman Sea (Indian Ocean), which possesses an unusual terminal valve structure.

MATERIALS AND METHODS

Material was collected from locations in the vicinity of the Phuket Marine Biological Center (Thailand), in the Andaman Sea, during June 1992. Samples were observed live, and net tows were desalinated and stored in methanol for subsequent work. Two clonal cultures (P-9 and P-18) were initiated, in order to provide unambiguous material for electron microscopy. They were maintained according to the methods outlined in Rines (1994), and material for study was harvested within 2 months of isolation. Live material was photographed on a Zeiss Photomicroscope II (Carl Zeiss Inc., Thornwood, NY, USA). Material for permanent slides was desalinated, rinsed in deionized water,

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dried on coverslips and mounted in Hyrax. Material for transmission electron microscopy (TEM) was dried on formvar-coated grids and examined on a scanning transmission electron microscope (STEM; JEOL, Peabody, MA, USA). The grids were subsequently coated with Au/Pd and examined on the same instrument in scanning mode (SEM). *Chaetoceros buceros* Karsten is illustrated from Indian Ocean material (north-west Australian shelf, approximately 20°S, 1982). Terminology follows Rines and Hargraves (1988; also available on the World Wide Web at HTTP://thalassa.gso.uri.edu/rines/taxonomy/glossary.htm). Subgeneric nomenclature employs the nominal epithet subgenus *Phaeoceros* Gran, because of present uncertainty regarding the taxonomic diagnosis, and hence the subgeneric affiliation of the nomenclatural type of the genus, *Chaetoceros tetrachaeta* Ehrenberg (1844).

RESULTS

Diagnosis

Chaetoceros phuketensis sp. nov.
Cellulae in catenas rectas. Cellula aspectu cincturae, rectangularis, angulis extensis. Limbus brevissimus. Cellula aspectu valve, angustus et compressus, axe apicali 45–65 µm longo, axe transapicali 14–21 µm longo. Omnes setae, longae, tenues, ad basim plus minusve incrassatae, aspectu transapicale perpendiculares ad axem catenae, divergentes ab axe apicale. Foramina late ellipticala. Valvae terminales area centrali incrassata et elevata, habentes circa centrum processus. Multi chloroplasti granulati ad vermiformes in corpori cellulae, sed chloroplasti ab setis absentes.

Locus typicus: Phuket, Thailand, ~ 7°48′N, 98°24′E, June 1992.

Cells in straight chains. Cell in girdle view, rectangular, with drawn-out corners. Mantle very shallow. Cell in valve view, narrow and compressed, with an apical axis 45–65 µm long, transapical axis 14–21 µm long. All setae, long, thin, more or less thickened at the base, perpendicular to axis of chain in transapical view, diverging from apical axis. Foramina broadly elliptical. Terminal valves with a thickened, elevated central area, having about 100 central processes. Many granular to vermiform chloroplasts in the body of the cell, but chloroplasts absent from the setae.

Holotype: Deposited in the collection of the Academy of Natural Sciences of Philadelphia, USA.

Iconotype: (Figs 1–3).

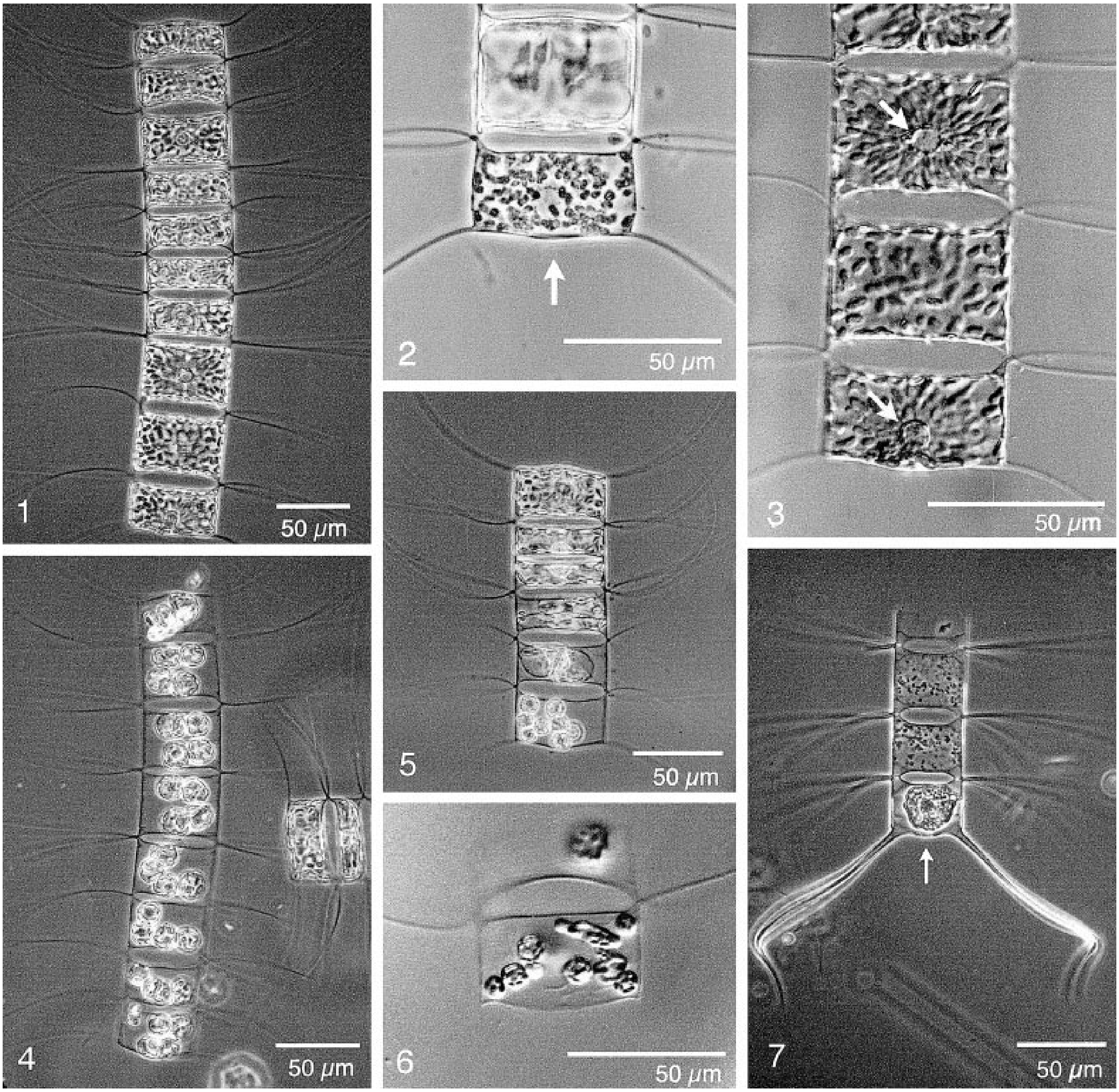
Etymology: The specific epithet refers to the type locale, near Phuket, Thailand.

Light microscope observations

Cells are united to form straight colonies (Fig. 1). In culture, chains have been comprised of about 10 cells. In wild and cultured material, the apical axis ranged from 45 to 65 µm, and the transapical axis from 14 to 21 µm. Thus, valves are narrow, compressed ellipses. In all observed specimens, dimensions of the apical axis have exceeded those of the pervalvar axis. Valves are flat, to concave (Figs 1–3). The valve corners are drawn up, and setae originate at the chain margin, without, or with a very short basal part (Figs 1–3). The resulting foramina are variable in shape and width, but in general are linear to lanceolate and quite distinct (Figs 1–3). The valve mantle is very shallow. The suture is distinct in cleaned frustules, but not in live cells unless the cytoplasm is retracted, as in spermatogenesis (compare Fig. 1 with Fig. 5). When observed in girdle view, the central region of terminal valves appears slightly thickened and elevated (Fig. 2). The setae of intercalary and terminal valves are similar in diameter, and are differentiated only by their orientation to the colony (Figs 1–5). All setae are thin and smooth. Intercalary setae are more or less perpendicular to the chain axis (Fig. 1). Terminal setae are initially almost perpendicular to the chain axis, and sweep in a widely divergent curve, becoming parallel to the chain axis. Intercalary setae slightly diverge from the apical plane (Brunel Group II). Each cell contains numerous small, vermiform chloroplasts, which are found only in the body of the cell and not in the setae (Figs 1–3). There is a very obvious and large nucleus in each cell (Fig. 3, arrows). Resting spores were not observed in our material.

Transmission electron microscope observations

There are two kinds of valves, intercalary and terminal, which are narrowly elliptical in shape (Fig. 8). Intercalary valves have numerous small pattern centres (Fig. 8), from which the costae radiate generally outward, extending all of the way to the base of the setae (Figs 8–11). Transverse connections between the costae are lacking. A marginal ridge appears to be absent, and the valve mantle is almost non-existent (Fig. 9). There are numerous simple pores on the valve face (Figs 10,11). Intercalary valves lack both processes and spines. Setae are thin and smooth. They are round in cross-section, and are composed of straight, non-spiralling longitudinal ribs connected by fine transverse elements (Fig. 11). Setae may possess a few minute spinules along the longitudinal ribs, but are generally smooth. Girdle bands are open Fig. 12), and possess striations running in the pervalvar direction (Fig. 13). There does not appear to be a differentiated valvocopula. Connecting bands were not observed in this material. Terminal valves are elliptical in shape. They possess a large, circular central area in which are clustered approximately 100 simple, round processes (Figs 14–17). The central region is surrounded by an irregular, electron-dense band (Figs 14–16). Under the

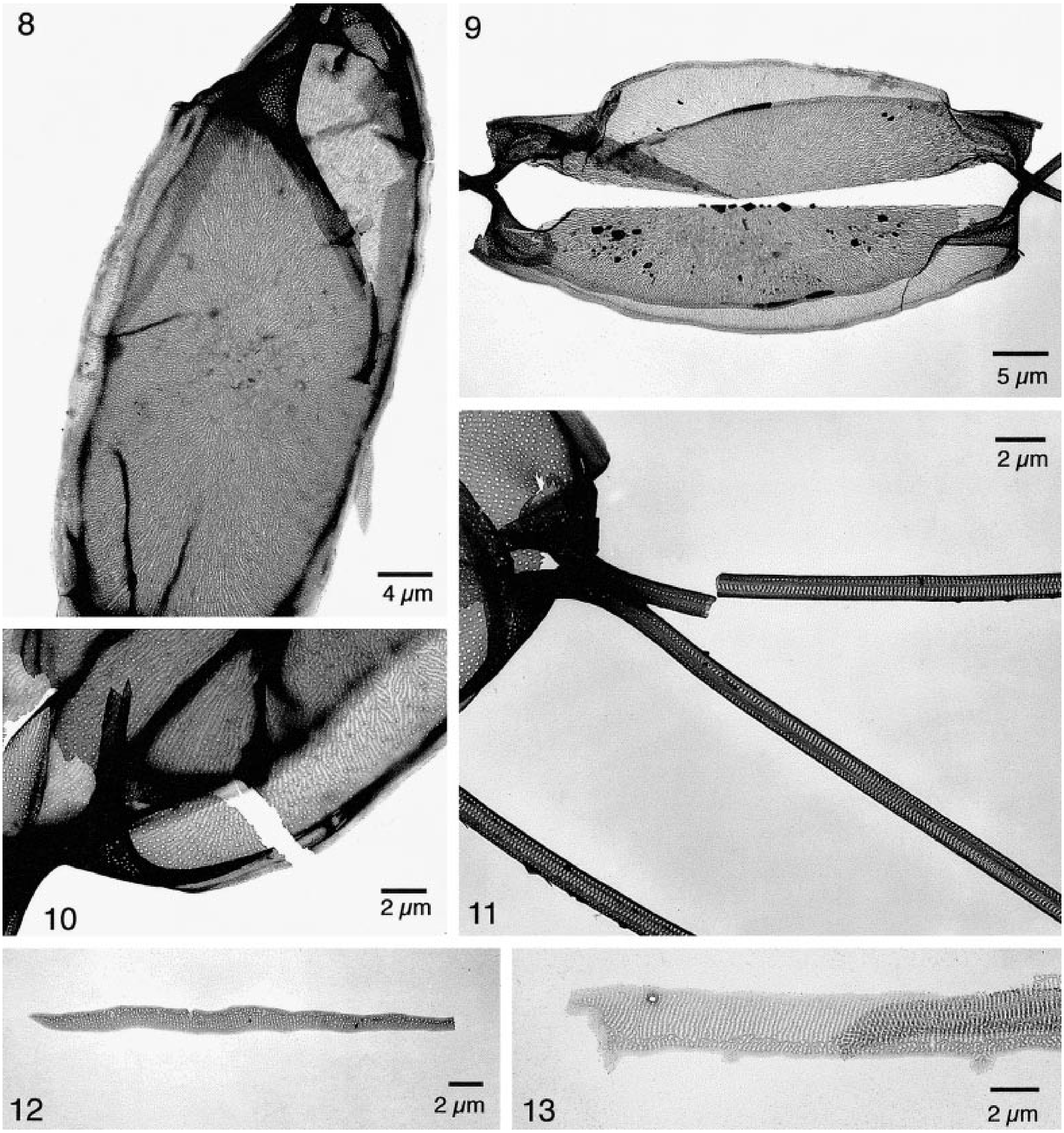


Figs 1–7. *Chaetoceros phuketensis* sp. nov. and *Chaetoceros buceros* Karsten. Light micrographs. 1–3. Iconotype. 1. Vegetative colony, phase contrast. 2. Terminal cell of a colony. Arrow denotes the thickened region which contains the numerous central processes. Phase contrast. 3. End of a colony. Arrows denote cell nucleus. Nomarski differential interference contrast. 4. Colony undergoing spermatogenesis. Spermatocytes, four-cell stage. 5. Colony undergoing spermatogenesis. Spermatocytes, two-cell and eight-cell stages. 6. Spermatogonangium with motile sperm cells. Note flagellum. 7. *Chaetoceros buceros*, partial colony. Note distinctive terminal setae, thickened region which contains the numberous central processes (arrow), and fused valve face near the point of setae origin. Phase contrast.

scanning electron microscope, it appears to consist of a hyaline siliceous sheath, which projects towards the interior of the cell (s in Fig. 17). Costae are lacking within the central region (Figs 15,16). Outside the central region, costae radiate towards the edge of the valve in a pattern similar to that of intercalary valves (Figs 15,16). There are numerous simple pores through the valve face both within and distal to the central region (Figs 15,16).

Sexual reproduction

Male gamete formation was observed in our cultures on several occasions (Figs 4–6). Vegetative cells undergoing spermatogenesis had an apical axis of approximately 45–50 µm. However, auxospores, and thus the formation of cells of the maximum dimensions for this taxon, were not observed.

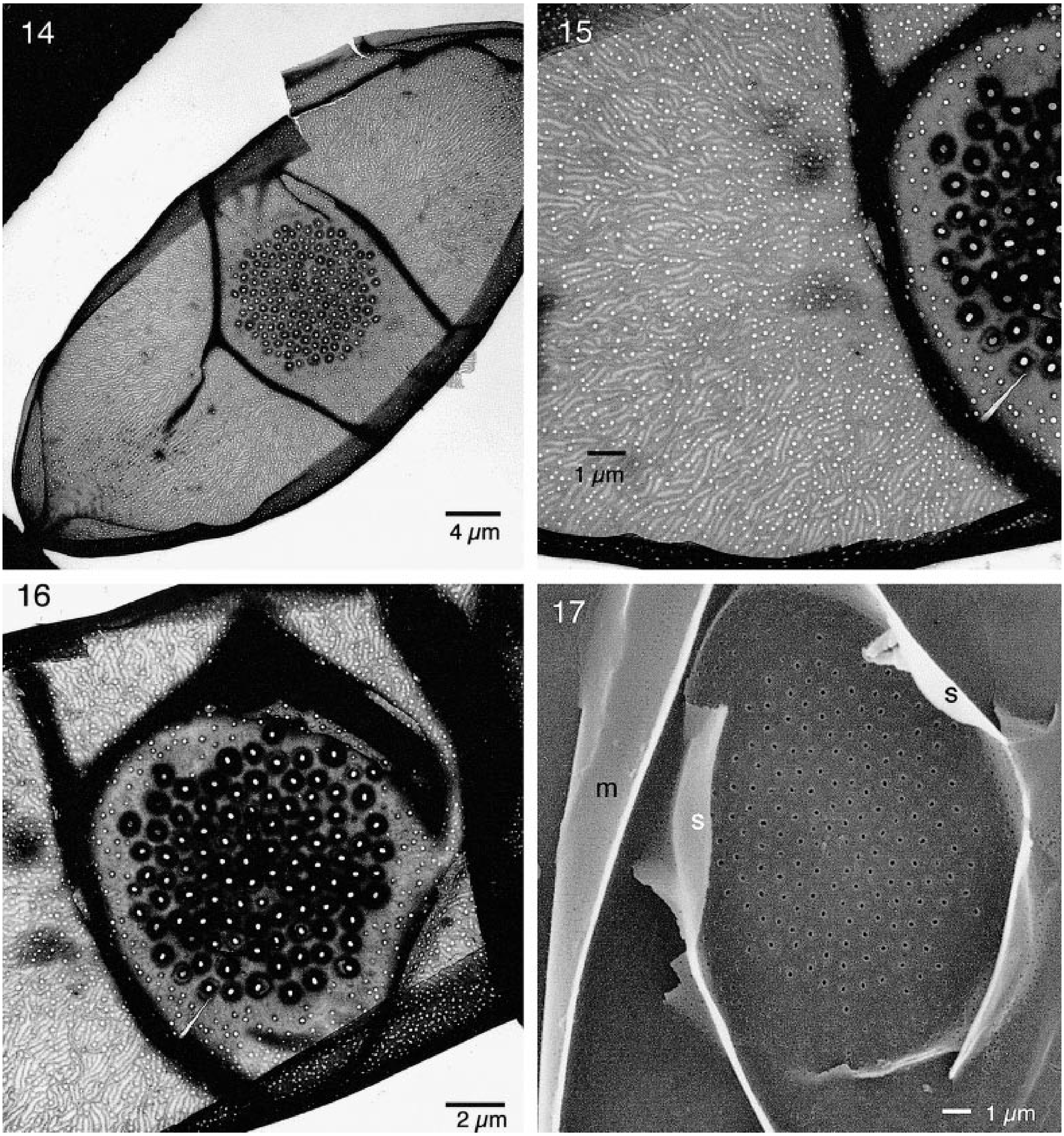


Figs 8–13. *Chaetoceros phuketensis* sp. nov. Transmission electron micrographs. 8. Pair of intercalary valves, valve view. 9. Pair of intercalary valves, girdle view. Note very shallow mantle. 10. Apical region of valve. Note pores. 11. Intercalary setae. 12. Nearly complete intercalary band. 13 Detail of intercalary band. Note striations running in the pervalvar direction.

DISCUSSION

Morphology of *Chaetoceros phuketensis*

Chaetoceros phuketensis possesses several distinctive characters, which include its size, vermiform chloroplasts, and multiple central processes on terminal valves. With an observed apical axis of 65 µm, this is a very large *Chaetoceros*, but it is possible that even larger specimens may exist in the oceans. In culture, male gamete formation was documented in cells with an apical axis of approximately 45–50 µm. Since gametes are usually formed in cells near the lower end of the size range, it suggests that this taxon may be capable of forming cells with an apical axis exceeding 100 µm. Vermiform chloroplasts are very unusual in *Chaetoceros*. The numerous chloroplasts found in *Chaetoceros* subgenus *Phaeoceros* are usually round or granular. Within subgenus *Hyalochaete* Gran, cells may have one, two, or a small number (e.g. four to 10) of plate- or disc-like chloroplasts. In addition to *Ch. phuketensis*, vermiform



Figs 14–17. *Chaetoceros phuketensis* sp. nov. Transmission and scanning electron micrographs. 14. Terminal valve. Note numerous central processes and electron-dense region around the central area. 15. Detail of terminal valve distal to the central region. Note costae and pores. 16. Detail of central region of terminal valve. Note the numerous processes and small pores. 17. Scanning electron micrograph of the inside of a terminal valve. Note the interior openings of the processes. m, valve mantle; s, sheath.

chloroplasts occur only in *Chaetoceros coarctatus* Lauder (personal observation), *Ch. buceros* (Karsten 1907; Hendey 1937), and possibly *Chaetoceros bacteriastroides* Karsten (Karsten 1907). However, the most unusual feature of *Ch. phuketensis* is the structure of the terminal valves, which have a cluster of approximately 100 processes located in a central, elevated and thickened region.

In a pioneering study, Evensen and Hasle (1975) examined four representatives of subgenus *Phaeoceros* and eight of subgenus *Hyalochaete* under electron microscopes. They found the *Phaeoceros* taxa to have one process on every valve in a colony, whereas the *Hyalochaete* had a process only on terminal (i.e. colony separation) valves. This pattern has held for nearly all species subsequently examined in the electron microscopes; multiple processes on either terminal or intercalary valves are rare. Rines and Hargraves (1990) noted the occurrence of two to five processes on the terminal valves of *Chaetoceros compressus* var. *hirtisetus* Rines and Hargraves, and two or three are occasionally found in the closely related *Chaetoceros contortus* Schütt (Rines 1999). Large numbers of processes were first documented by Hernández-Becerril (1991a, 1991b) in *Chaetoceros bermejensis* Hernández-Becerril (s.g. *Hyalochaete*) and *Ch. coarctatus* (s.g. *Phaeoceros*), and by Hernández-Becerril *et al.* (1993) in *Ch. buceros*. In *Ch. coaractatus* (s.g. *Phaeoceros*) they occur on every valve in a colony, whereas in *Ch. buceros* and *Ch. bermejensis* (s.g. *Hyalochaete*) processes are found only on terminal valves.

The only other taxon in which a thickened central plate is known is *Ch. buceros* (Fig. 7, and Hernández-Becerril *et al.* 1993). We were unable to fully interpret this structure. The refractive, raised valve centre observed with light microscopy (Fig. 2) suggests that in the central region, the valve is either composed of much thicker silicon, or is two-layered with tubular processes projecting through both layers. This impression is reinforced by the thick ring around each opening (Figs 15,16), which might suggest a loculate structure. Scanning electron microscopy revealed a simple interior opening for each process (Fig. 17), but since we were unable to find a valve broken through the centre, it provided no further information regarding possible three-dimensional structure of the central region. It did reveal, however, that the irregular, electron-dense area surrounding the central region seems to be a hyaline siliceous sheath which hangs down into the interior of the cell. A possible function of this structure is unknown.

Comparison to similar species

Although there are several hundred described species within this genus, *Ch. phuketensis* is so unusual that it can only be compared to *Ch. coarctatus*, *Ch. buceros*, and *Ch. bermejensis,* all of which are reported only from tropical seas. Characters of special interest include the vermiform chloroplasts, and multiple processes on terminal valves. *Chaetoceros coarctatus* possesses multiple processes on its valves, but in this case they occur on all valves rather than only on terminal valves (Hernández-Becerril 1991b). This character places it in the subgenus *Phaeoceros*, and thus, at least theoretically, it is not closely related to *Ch. phuketensis*. The delineating characters of *Ch. phuketensis*, *Ch. bermejensis* and *Ch. buceros* are compared in Table 1. *Chaetoceros phuketensis* appears most similar to *Ch. buceros*. These taxa share a narrow valve outline, chloroplast type and elevated cluster of processes on terminal valves, but differ in that the latter has markedly differentiated terminal setae, and cells which are connected not only by their setae, but also by fusion of part of the mantle near the poles of the apical axis.

Classification

Two different approaches can be taken to classifying *Chaetoceros* whose unusual morphological characters are not accommodated by the traditional classification scheme: either the scheme can be modified, or a *de novo* classification can be created based on other principles, such as evidence of evolutionary relationship. Hernández-Becerril has modified the extant scheme, creating one new subgenus and several sections for a variety of tropical taxa. Sub-genus *Bacteriastroidea* (Hernández-Becerril 1993a) contains a singular taxon, *Ch. bacteriastroides*, which appears intermediate between the genera *Chaetoceros* and *Bacteriastrum*. Within subgenus *Phaeoceros*, he created new sections *Coarctati*, to accommodate the multiple processes found on all valves in *Ch. coarctatus* and *Chaetoceros sumatranus* (Hernández-Becerril 1991b, 1999) and *Peruviana* to contain heterovalvate taxa (Hernández-Becerril 1996). In 1993 Hernández-Becerril *et al.* created section *Conspicua* (s.g. *Hyalochaete*) for a single, unusual taxon: *Ch. buceros*. Delineating characters of the section include multiple small chloroplasts, multiple processes on terminal valves, and terminal setae which are strongly curved, coarser and longer than the intercalary setae (i.e. differentiated terminal setae).

Chaetoceros phuketensis possesses chloroplasts only in the body of the cell, and processes only on terminal valves. These characters place it within subgenus *Hyalochaete*. It shares many characters with *Ch. buceros*, and would therefore logically be placed, along with it, in section *Conspicua*. However, as currently circumscribed, taxa assigned to *Conspicua* must have strongly differentiated terminal setae, which are lacking in *Ch. phuketensis*. This illustrates a significant problem with a scheme based on what is essentially a typological philosophy. The only way to accommodate variation is to create a new taxonomic category: ultimately, there would be a separate section for nearly every species.

At the turn of the century, new *Chaetoceros* were being described at an astonishing rate. Gran and Ostenfeld's (Gran 1897; Ostenfeld 1903) goal was simply to organize the rapidly increasing members of an exceedingly species-rich genus into a more convenient form for ease of identification. As early as 1910, it was noted (Meunier 1910) that Gran and Ostenfeld's scheme was 'artificial', because it lacked a basic underlying principle. An alternative to modifying a scheme which is inherently problematical is to create a new one, which does have an underlying principle. The premise that evolution has produced the myriad kinds

Table 1 Comparison of the characteristics of the *Chaetoceros phuketensis* sp. nov., *Chaetoceros bermejensis* Hernández-Becerril and *Chaetoceros buceros* Karsten

	Chaetoceros phuketensis	*Chaetoceros bermejensis* [a]	*Chaetoceros buceros* [b,c,d]
Light Microscope Structure			
Valve shape	Narrow, compressed elliptical	Subcircular to elliptical	Rectangular elliptical (Hendey 1937)
Apical axis (µm)	45–65	37–40	35–40 (Karsten 1907) 46–76 (Hernández–Becerril *et al* 1993) 40 (Hendey 1937)
Colony torsion	Not twisted	Straight to slightly twisted	Not twisted
Chloroplast number	Numerous	Numerous	Numerous
Chloroplast type	Small, elongate granules, vermiform	Small, round	Vermiform (Hendey 1937)
Cell corners	Drawn up	Rounded	Drawn up, apical part of sister valves in contact
Setae origin	Edge of chain	Within chain margin	Edge of chain
Depression at base of setae (apical areas)	No	Yes	No
Basal part	None, or very short	Short	None
Intercalary setae orientation to chain axis	Mostly perpendicular	Mostly perpendicular	Mostly perpendicular, and gently directed toward end
Brunel Group	II	Varied angles	Probably II
Valve mantle	Shallow	Shallow	Fairly shallow
Valve face	Intercalary = concave Terminal = convex	Flat	Intercalary = concave Terminal = convex
Sister cells with valve face connection	No	No	Yes
Suture	Distinct	Indistinct	Indistinct, except distinct on terminal valve
Foramina	Wide, elliptical	Narrow, linear	Wide, elliptical, shorter than length of the apical axis
Terminal setae differentiated	No	No	Yes
Transmission Electron Microscope Structure			
Intercalary valves			
Pores	Yes	Yes	Yes
Pattern centres	Multiple, but annuli indistinct	ND	Multiple annuli
Costae	Radiate, pattern like *Ch. buceros*	Radiate?	Radiate
Processes	No	No	No
Terminal Valves			
Pores	Yes	Yes	Yes
Costae	Yes	ND	No?
Process location	Grouped in centre	Grouped in centre	Grouped in centre
Process number	~ 100	30–40	21–30
Process shape	Round	Slit-shaped	Slit-shaped
Setae cross section	Polygonal	Circular	Polygonal

[a]Hernández-Becerril 1991a, [b]Karsten 1907, [c]Hendey 1937, [d]Hernández-Becerril *et al*. 1993. ND, not determined.

of organisms on earth can be used as the theoretical basis of a ‘natural’ classification. We believe that the classification of *Chaetoceros* should reflect its evolutionary history, and for this reason refrain from assigning *Ch. phuketensis* to a section, or modifying section *Conspicua* to accommodate it.

The principles of phylogenetic systematics, and cladistic analysis can be used to create hypotheses of evolutionary relationship among *Chaetoceros*, which in turn can be used to build a classification. In this case, subgeneric ‘units’ are based on evidence of common ancestry. In practice, they may be very similar to those created by Gran and Ostenfeld. A phylogenetic analysis of the family *Chaetocerotaceae* has been initiated by Rines (1994), and Rines and Theriot (unpublished data). It supports the close relationship of *Ch. phuketensis* and *Ch. buceros*. Our work, and that of Hernández-Becerril and colleagues has demonstrated that there are many unusual *Chaetoceros* living in tropical seas. In order to understand the diversity, ecology, systematics and evolutionary history of this large, species-rich lineage of diatoms, it is critical that future efforts concentrate on investigation of the *Chaetoceros* of the tropics.

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