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NEW OBSERVATIONS ON *PROBOSCIA* AUXOSPORES AND VALIDATION OF THE FAMILY PROBOSCIACEAE FAM. NOV.

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AUXOSPORES
PROBOSCIA ALATA
PROBOSCIA INDICA
PROBOSCIACEAE

ABSTRACT. – The re-examination of old water samples from the Southern Ocean has revealed the presence of *Proboscia alata* auxospores in various stages of development. Whilst previous studies have reported that *Proboscia* auxospores possess multiple columns of copulae, it is proposed here that they are actually scales, as they differ from the copulae of the developing initial cell inside the auxospore. The initial cell bears all the features characteristic of the vegetative cell, although some crease-like ridges have been observed running longitudinally along the proboscis of the initial valve. The diameter of the initial cell (40.0-45.0 µm) is generally 3-4 times that of the gametangial cell (16.3-17.6 µm). These dimensions suggest that we are dealing with a large form of *P. alata*. Somewhat bizarrely, the auxospores from the Southern Ocean are occasionally bifurcate at the opposite end to the gametangial cell. It has been shown here that the bifurcation represents two well-developed probosces (with crease-like features similar to those on the initial valve), each bearing a ring of spinulae and a longitudinal slit. However, there are no claspers and the probosces do not appear to be joined to a valve, i.e. there is no apparent distinction between valve and auxospore wall. Why some auxospores produce a bifurcate end rather than an initial cell is not known at present. One specimen from the Sulu Sea appears to be an auxospore of *Proboscia indica* due to its large size (almost 100 µm in diameter). Given the confusion surrounding the identification of this taxon, we have reviewed the literature and provided a more detailed species description. *Proboscia indica* exhibits a number of characters that together may be used to distinguish it from *P. alata* and related taxa: its frustule and valve dimensions are greater than other species, like *P. alata* the chain arrangement is asymmetric due to the possession of "displaced claspers", the long proboscis is more strongly sloped than *P. alata*, each "interlocular pore" is surrounded by four not six loculi, the auxospore does not develop a bifurcate end, and it occurs in tropical to temperate seas not polar waters. Lastly, the family Probosciaceae is re-erected here as a new taxon, accompanied with a Latin diagnosis in accordance with the rules of botanical nomenclature.

AUXOSPORES
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RÉSUMÉ. – Le ré-examen d'anciens échantillons d'eau en provenance de l'Océan Austral a révélé la présence d'auxospores de *Proboscia alata* à différents stades de développement. Alors que les études précédentes avaient décrit les auxospores de *Proboscia* comme possédant de multiples colonnes ou rangées de copulae, il est ici proposé que ce sont des écailles, et qu'elles diffèrent des copulae provenant du développement de la cellule initiale dans l'auxospore. La cellule initiale comporte toutes les caractéristiques distinctives de la cellule végétative, bien que des arêtes en forme de pli aient été observées longitudinalement le long du proboscis de la valve initiale. Le diamètre de la cellule initiale (40.0-45.0 µm) est généralement 3-4 fois plus grand que celui de la cellule gamétangiale (16.3-17.6 µm). Ces dimensions suggèrent qu'il s'agit d'une grande forme de *P. alata*. De manière un peu surprenante, les auxospores provenant de l'Océan Austral sont occasionnellement bifides à l'extrémité opposée à la cellule gamétangiale. On montre ici que cette bifurcation correspond à deux proboscis bien individualisés (avec une structure en forme de pli, similaire à celles de la valve initiale), chacun portant un anneau de spinules et une fissure longitudinale. Cependant, il n'y a pas de point d'ancrage et les proboscis n'apparaissent pas connectés à une valve, de telle sorte qu'il n'y a pas de distinction apparente entre la paroi de la valve et celle de l'auxospore. La raison pour laquelle certaines auxospores produisent une terminaison bifide plutôt qu'une cellule initiale demeure inconnue. Un spécimen provenant de la mer de Sulu apparaît comme étant une auxospore de *Proboscia indica* au vu de sa grande dimension (au moins 100 µm de diamètre). Etant donnée la confusion liée à l'identification de ce taxon, nous avons passé en revue la littérature et nous fournissons une description plus détaillée de cette espèce. *Proboscia indica* montre des caractéristiques qui peuvent permettre de distinguer cette espèce de *P. alata* et des taxons voisins: les dimensions du frustule et de la valve sont plus grandes que pour les autres espèces, comme chez *P. alata* l'agencement de la chaîne est asymétrique dû à l'existence de « points d'ancrage décalés », le long proboscis est plus fortement incliné que chez *P. alata*, chaque « pore interloculaire » est encadré par 4 et non 6 loculi, l'auxospore ne développe pas d'extrémité bifide, et ce taxon se rencontre dans les mers tropicales à tempérées et non dans les eaux polaires. Enfin, la famille des Probosciaceae est ici re-érigée comme nouveau taxon, avec une diagnose en latin en accord avec les règles de la nomenclature botanique.

INTRODUCTION

In the original description, *Rhizosolenia alata* Brightwell was said to differ "from the others by its blunt, turned-up nose, and its small but conspicuous appendages to the terminal process" (Brightwell 1858). Subsequent authors accepted this distinction and classified *R. alata* in its own section of *Rhizosolenia* Brightwell either under the name Alatae (Gran 1908, Hustedt 1930) or Inermes (Pavillard 1925). Okuno (1952, 1960, 1968), one of the early pioneers of diatom studies by TEM, showed that *R. alata* and its formae *gracillima* Cleve and *indica* Gran, as well as *R. inermis* Castracane, all possessed a "sieve membrane" (= velum) perforated by one or more round "sieve pores" (= pores). In his monograph of British coastal diatoms, Hendey (1964) placed *R. alata* (and its formae *curvirostris* Gran, *gracillima* and *indica*) and *R. obtusa* Hensen in the Section Inermes. Hasle (1975) noted that the terminal auxospore of *R. alata* "may indicate a taxonomic position distinct from true *Rhizosolenia* spp.", but she hesitated to erect a new genus, preferring to wait until further observations could be made. So, it was not until Sundström (1986) published his Ph.D. thesis that it was finally separated from *Rhizosolenia* sensu stricto and placed in a new genus, *Proboscia* Sundström. Like Sundström (1986), Priddle *et al*. (1990) were aware that other proboscis-bearing taxa needed to be transferred to *Proboscia*, but felt that it was "beyond the scope of" the "Polar Marine Diatoms" – a book of review chapters. Species of *Rhizosolenia*, both living and fossil, with similar morphology were later transferred by Jordan & colleagues (Jordan *et al*. 1991, Jordan & Priddle 1991, Takahashi *et al*. 1994, Jordan & Saito 1999, Jordan & Ito 2002) and Hernández-Becerril (1995). At present, all of the old formae and varieties of *R. alata* have either been made synonymous with the type (e.g. *R. alata* f. *gracillima*, *R. alata* f. *genuina* (Brightwell) Gran) or *Proboscia indica* (H. Peragallo) Hernández-Becerril (e.g. *R. alata* var. *corpulenta* Cleve), or been elevated to specific rank (e.g. *P. subarctica* Takahashi, Jordan et Priddle = ex *R. alata* f. *curvirostris* Gran). In the case of *R. obtusa* Hensen sensu Ostenfeld it is now known as *P. eumorpha* Takahashi, Jordan et Priddle, although the true *R. obtusa* remains an enigmatic species of *Rhizosolenia* (Takahashi *et al*. 1994).

Some of the fossil species of *Rhizosolenia* (regarded as species of *Proboscia* by Jordan & Priddle 1991 and many subsequent authors) were transferred to a new genus *Simonseniella* Fenner (Fenner 1991a, Gladenkov & Barron 1995). *Simonseniella* species were considered to be closely related to the extant species *Rhizosolenia alata* due to their morphological similarity. Although Fenner (1991a) made no mention of *Proboscia* in her paper, Gladenkov & Barron (1995) noted that if Sundström's (1986) thesis was validly published then the combinations made by Jordan & Priddle (1991) would take priority. However, this situation was exacerbated when Zielinski & Gersonde (1997) transferred *R. alata* (the type species of *Proboscia*) to *Simonseniella*. It should be strongly pointed out that, as Sundström's (1986) published thesis was widely distributed (and to our knowledge it is still available from Lund University), the thesis constitutes a valid publication according to the rulings of the ICBN (Article 29.1 of Greuter *et al*. 2000). Thus, if one accepts the emended generic diagnosis of *Proboscia* given by Jordan & Priddle (1991: 59-60), *Simonseniella* must be regarded as a superfluous and junior synonym of *Proboscia*.

Since Brightwell (1858) described both *Rhizosolenia* and *R. alata* there have been few reports on sexual reproduction or subsequent auxospore/initial cell development within *Rhizosolenia* or *Proboscia*. Here a brief summary is given of what is currently known. *Rhizosolenia* produces biflagellate sperm (sometimes referred to as microspores; Gran 1902, Wimpenny 1946, Ramsfjell 1959, Seaton 1970, Drebes 1977, Mann 1993) and so reproduces oogamously, and subsequently forms an isometric auxospore possessing a dilatable cell wall covered by multiple rows of scales (Peragallo & Peragallo 1897-1908, Kaczmarska *et al.* 2001). One may presume that *Proboscia* does likewise. *Proboscia* auxospores are supposedly covered by multiple columns of copulae (Jordan *et al.* 1991), although these may prove to be scales, as found in other genera. In the case of *Rhizosolenia* the auxospore is produced laterally, while in *Proboscia* it is terminal (Sundström 1986). In both genera the increase in size from the gametangial cell to the initial cell is of the order of 2: 1 or 4: 1 (e.g. Wimpenny 1946, 1966, Robinson 1957, Ramsfjell 1959, Robinson & Waller 1966). The steps in post-auxospore development in *Proboscia alata* have been documented in reasonable detail (Wimpenny 1936, Cupp 1943), whereas perhaps less is known about those of *Rhizosolenia* species. In this paper we provide further observations on the auxospores and initial cells of *Proboscia alata*, and new observations on an auxospore and initial valve of *P. indica*.

Within the last decade, two additional problems have arisen concerning the genus *Proboscia*. Firstly, the transfer of *Rhizosolenia indica* H. Peragallo to *Proboscia* (Hernández-Becerril 1995, p.254), though valid, has caused some confusion due to the nature of the accompanying illustrations and description. The specimen shown by Hernández-Becerril (1995) bore a deep groove in the contiguous area but not claspers, and a tip (seemingly broken) that possessed an open end rather than the characteristic ring of spinulae. His specimen appears to belong to a different diatom, perhaps a *Rhizosolenia* sp. with a broken spine, as *P. indica* has a longer, more tapered proboscis. In contrast, Takano (1990) clearly showed that claspers are present on the vegetative valve of *P. indica*. It was also suggested by Hernández-Becerril (1995) that observations on the girdle bands were necessary in the future, but Desikachary (1954), Okuno (1960, 1968), Hasle (1975) and Ferreyra & Ferrario (1983) had already documented their structure in several earlier papers. In order to undo some of this confusion, a more complete description and synonymy list are given below.

The second problem concerns the invalidity of the family Probosciaceae, which was erected but not described (Nikolaev & Harwood 2000). Here, we have attempted to address both of the above issues in order to alleviate the problems.

METHODS

Samples from two stations, 26 (59° 56'S, 19° 56'E) and 27 (61° 57'S, 19° 52'E), were collected from the Southern Ocean by Polish participants (K Opalinski & S Rakusa-Suszczewski) of the XIV Soviet Antarctic Expedition on 19th and 20th December 1968, respectively, during a cruise of the R/V Professor Zubov. Vertical net hauls to collect zooplankton were carried out with a Copenhagen-type net (opening diameter 30 cm, mesh size 25 = approx. 55 µm) through depths of 200 m (Station 27) or 600 m (Station 26). The net samples were fixed in 4% formalin. The specimens illustrated in Plate I Fig. 1-6 and Plate II Fig. 12 were prepared as water mounts, whereas those in Plate I Fig. 7 and Plate II Fig. 1-11 were cleaned using chromic acid and mounted in Naphrax on glass slides. Light micrographs were taken with a video camera attached to a Nikon Optiphot microscope using a ×10 (N.A. = 0.45), ×40 (N.A. = 0.95), or ×60 (N.A. = 1.40) planapochromatic objective lens. For electron microscopy, a subsample from each station was filtered (over 30 years after collection) and prepared for scanning electron microscopy using standard techniques employed in RWJ's laboratory (e.g. see Tanimoto *et al.* 2003).

The auxospore featured in Plate IV Fig. 5-7 was collected by RWJ from a depth of 40 m using the CTD rosette sampler at Station PA1 in the Sulu Sea (8° 50-.08'N, 121° 48.33'E) on 25th December 1996 during the KH96-5 cruise of the R/V Hakuho Maru. The water sample was filtered and prepared for the SEM using the same methods as noted above.

The physical and chemical data for these cruises can be found in Gamo (1997) and Grigoryev & Kornilov (1971), respectively.

RESULTS

The terminology used in describing our auxospore specimens mainly follows that of Ross *et al.* (1979) and Kaczmarska *et al.* (2001), in which the **auxospore** is a cell destined to restore large individuals to the population, and the **initial frustule** is the first two valves (**initial valves**) produced within the auxospore. However, the term **initial cell** is considered here to refer to the point in post-auxospore development when new copulae are produced and attached to the first initial valve whilst still inside the auxospore, not merely to the cell's liberation from the auxospore and its ability to undergo mitotic division (*cf.* Kaczmarska *et al.* 2001). This removes the need for a new term relating to the time between the production of the first initial valve (which by definition does not include copulae) and the completion or semi-completion of the initial frustule (bearing either two valves or retaining the remnant of the gametangial cell). Although Kaczmarska *et al.* (2001) defined initial valves as numbering 2-5 inside the auxospore depending on the species, the development of the initial cell in *Proboscia* inevitably starts with the formation of the first initial valve (no attempt has been made here to determine whether the first initial valve is the epivalve or the hypovalve) fol-

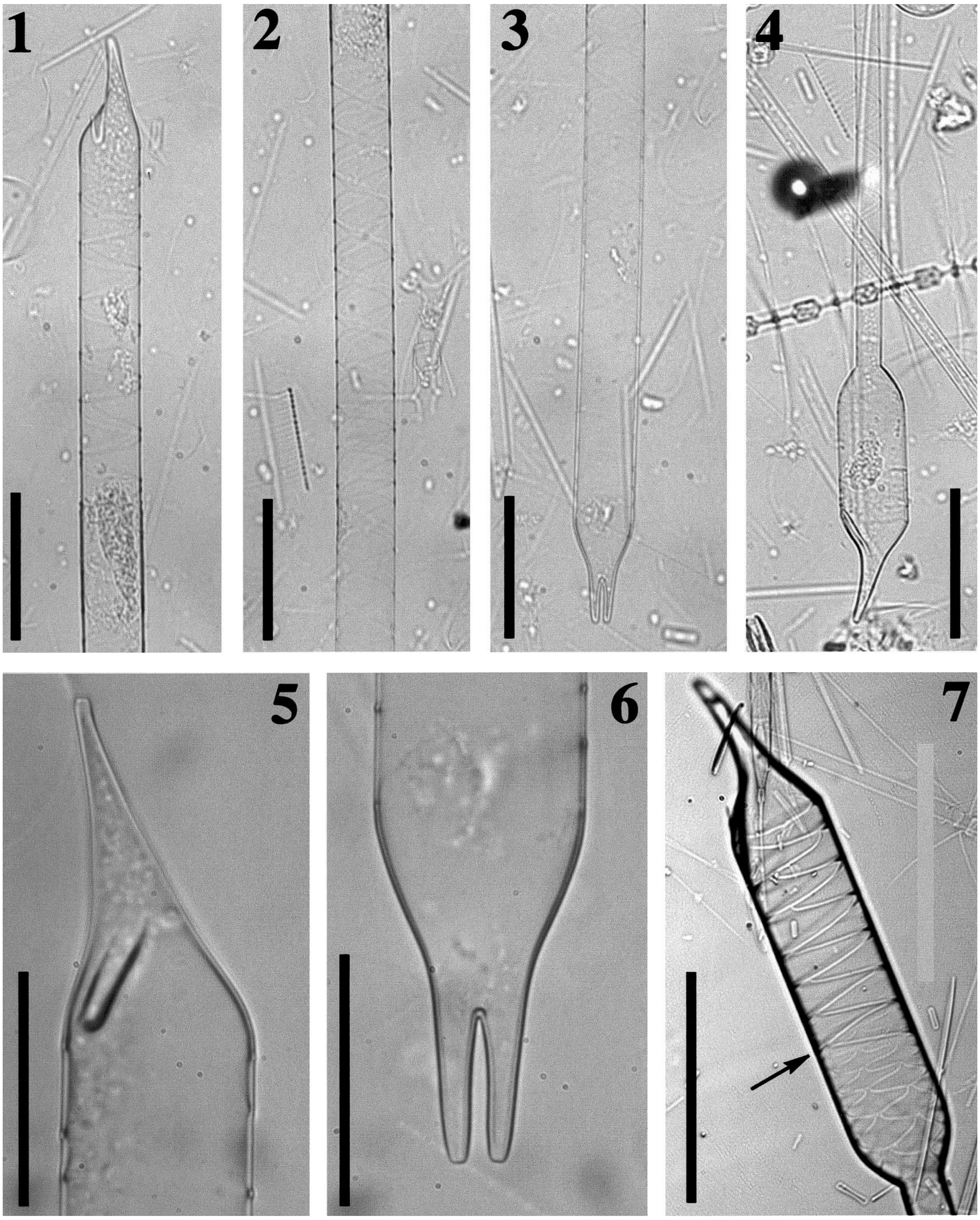

Plate I. Fig. 1-6. Auxospores of *Proboscia alata*, Station 26, Southern Ocean. Fig. 1-3. An extremely long specimen showing an initial cell with claspers, a proboscis and copulae in two dorsi-ventral columns (Fig. 1). Note, the connection to the auxospore can be clearly seen as a thickening of the wall (approximately level with the scale bar in Fig. 1) and a change in the pattern of the girdle region (Fig. 2). The auxospore possesses a bifurcate proboscis (Fig. 3). Scale bars = 100 µm. Fig. 4. An auxospore with a newly developing initial cell at one end and the narrower gametangial cell at the other. The initial valve bears claspers and a non-bifurcate proboscis. Note, this specimen represents an earlier stage in post-auxospore development than the specimen in Figures 1-3, which has become more elongate. Scale bar = 100 µm. Fig. 5-6. Close ups of the same specimen illustrated in Fig. 1-3, showing the initial valve (Fig. 4) and the bifurcate end of the auxospore (Fig. 5). Scale bars = 50 µm. Fig. 7. An auxospore with a developing initial cell at one end and a narrower gametangial cell at the other. The initial valve bears claspers and a non-bifurcate proboscis. Note, this specimen represents an intermediate stage in post-auxospore development as compared to the specimens in Fig. 1-3 and Figure 4. The black arrow indicates the position of the developing initial cell inside the auxospore and the change in the number of columns of scales/copulae. Scale bar = 100 µm.

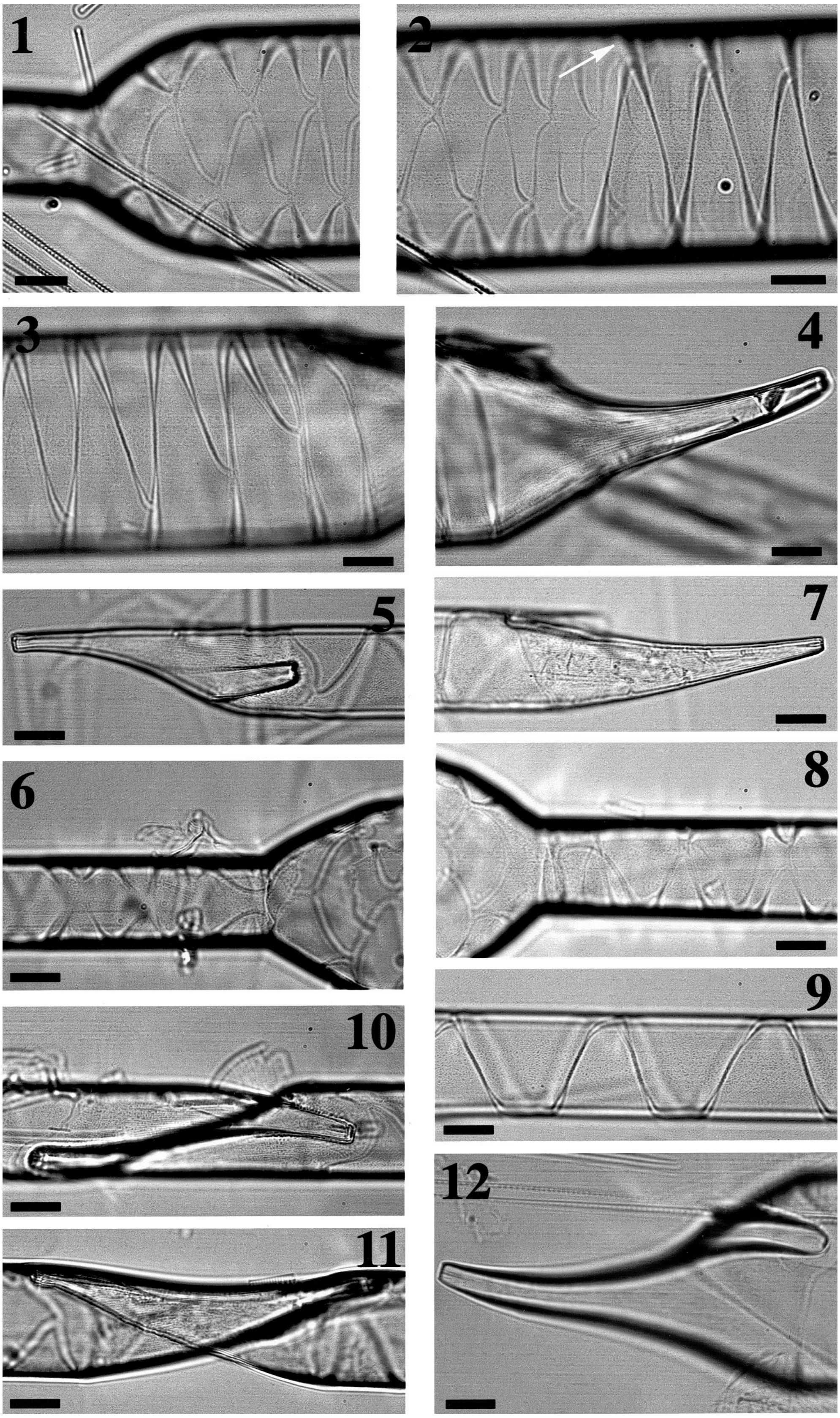

Plate II. Fig. 1-6. Auxospores of *Proboscia alata*, Station 26, Southern Ocean. All scale bars = 10 µm. Fig. 1-4. Close-ups of the specimen illustrated in Plate I Fig. 7, showing the junction between the gametangial cell and the auxospore with its multiple columns of scales (Fig. 1), the increased thickness of the wall and change in pattern (white arrow) representing the extent of the developing initial cell inside the auxospore (Fig. 2), the two dorsi-ventral columns of copulae belonging to the initial cell (Fig. 3), and the initial valve with claspers, longitudinal rows of pores along the proboscis, and the longitudinal slit at the tip (Fig. 4). Fig. 5-6. A gametangial valve bearing distinct claspers (Fig. 5) connected to an auxospore with multiple columns of scales (Fig. 6). Fig. 7-9. A gametangial valve bearing distinct claspers (Fig. 7) connected to an auxospore with multiple columns of scales (Fig. 8). Note that the girdle region of the gametangial cell possesses two dorsi-ventral columns of copulae (Fig. 9). Fig. 10-11. Two specimens showing the linking mechanism involved in chain formation, whereby the proboscis of one valve fits inside the claspers of an adjacent valve. As the claspers are situated ventro-laterally, the appearance is asymmetrical. Fig. 12. An initial valve with claspers and a longitudinal slit just visible at the tip.

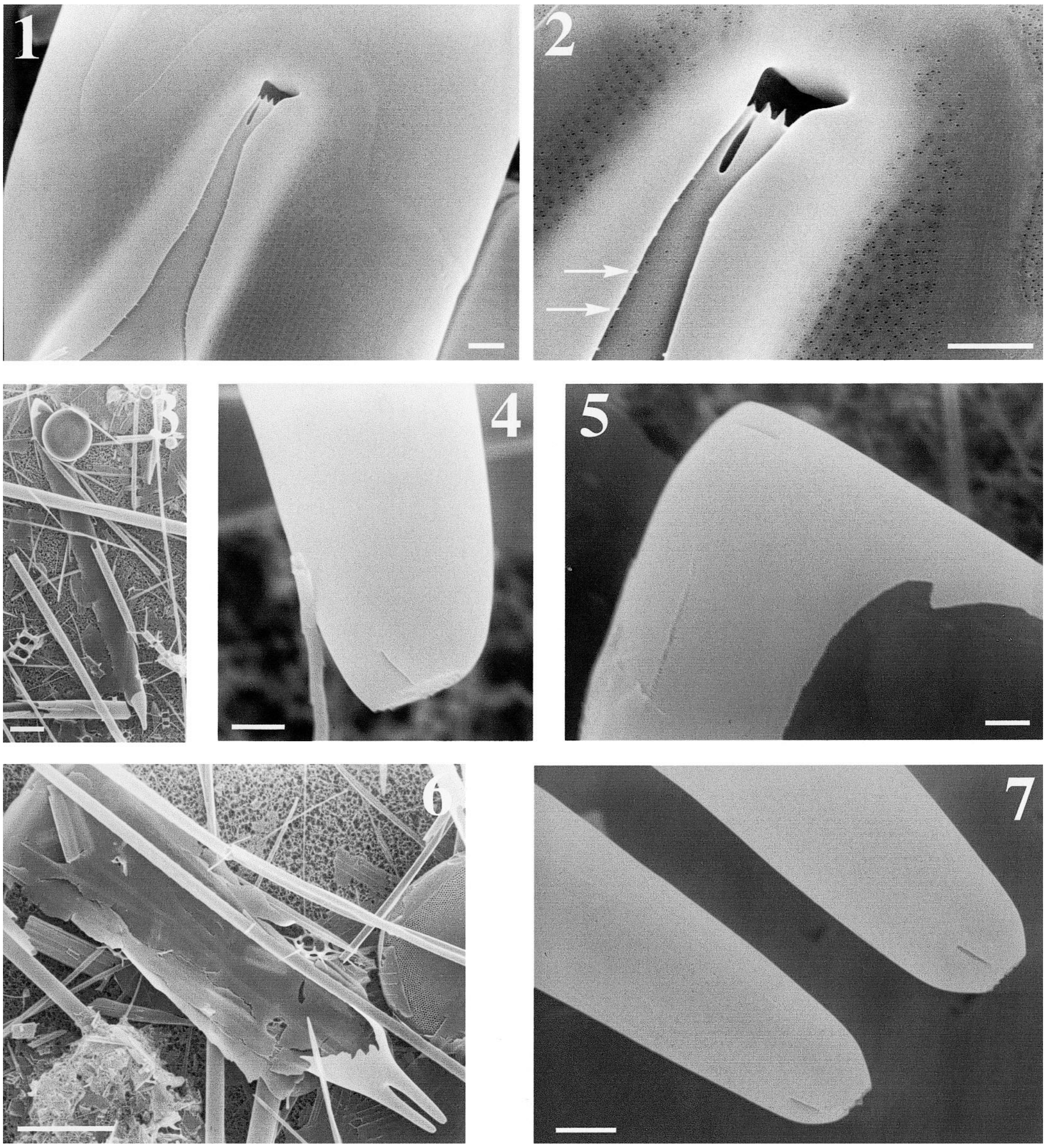

Plate III. Fig. 1-7. Specimens of *Proboscia alata*, Station 27, Southern Ocean. Fig. 1-2. Adjacent cells in a chain showing the nature of the linking mechanism, whereby the proboscis of one valve fits into the claspers of another valve. Note that the dorsal side of the inserted proboscis (determined by the presence of the longitudinal slit) faces outwards. Also there are no pores in the region of the valve bordering the valvocopula or the outer rim of the claspers. The white arrows in Figure 2 (a higher magnification of Fig. 1) indicate examples of where there appears to be threads of mucilage. Scale bars = 2 µm. Fig. 3-5. A gametangial cell bearing an auxospore in an early stage of development. Fig. 6-7. An auxospore with a bifurcate proboscis (Fig. 6), each one bearing a ring of spinulae and a longitudinal slit at the tip (Fig. 7). Scale bars = 50 µm (Fig. 6) or 2 µm (Fig. 7).

lowed by the girdle region. In fact, the second initial valve may not be produced before the cell divides (Fig. 10e in Wimpenny 1936). The order in which auxospore and post-auxospore steps are thought to occur in *Proboscia* follows that of Wimpenny (1936). These include i) the formation of a large globular structure ("capitulum" in Wimpenny 1936) at the broken end of a small vegetative cell (**gametangial cell**), ii) the elongation of this structure into a round-ended cylinder, iii) the formation of a new, large-sized valve (initial valve) and girdle region inside the auxospore wall, eventually resulting in the breaking of the end of the cylindrical structure, iv) subsequent elongation of the girdle portion of the new cell (initial cell), and v) first division of the new cell, which may occur while one end of the new cell is still attached to the remnant of the old gametangial cell (Wimpenny 1936; i.e. the initial frustule is never completed as defined by Kaczmarska *et al.* 2001).

In the literature the auxospore of *Proboscia* has been described or illustrated as bearing multiple

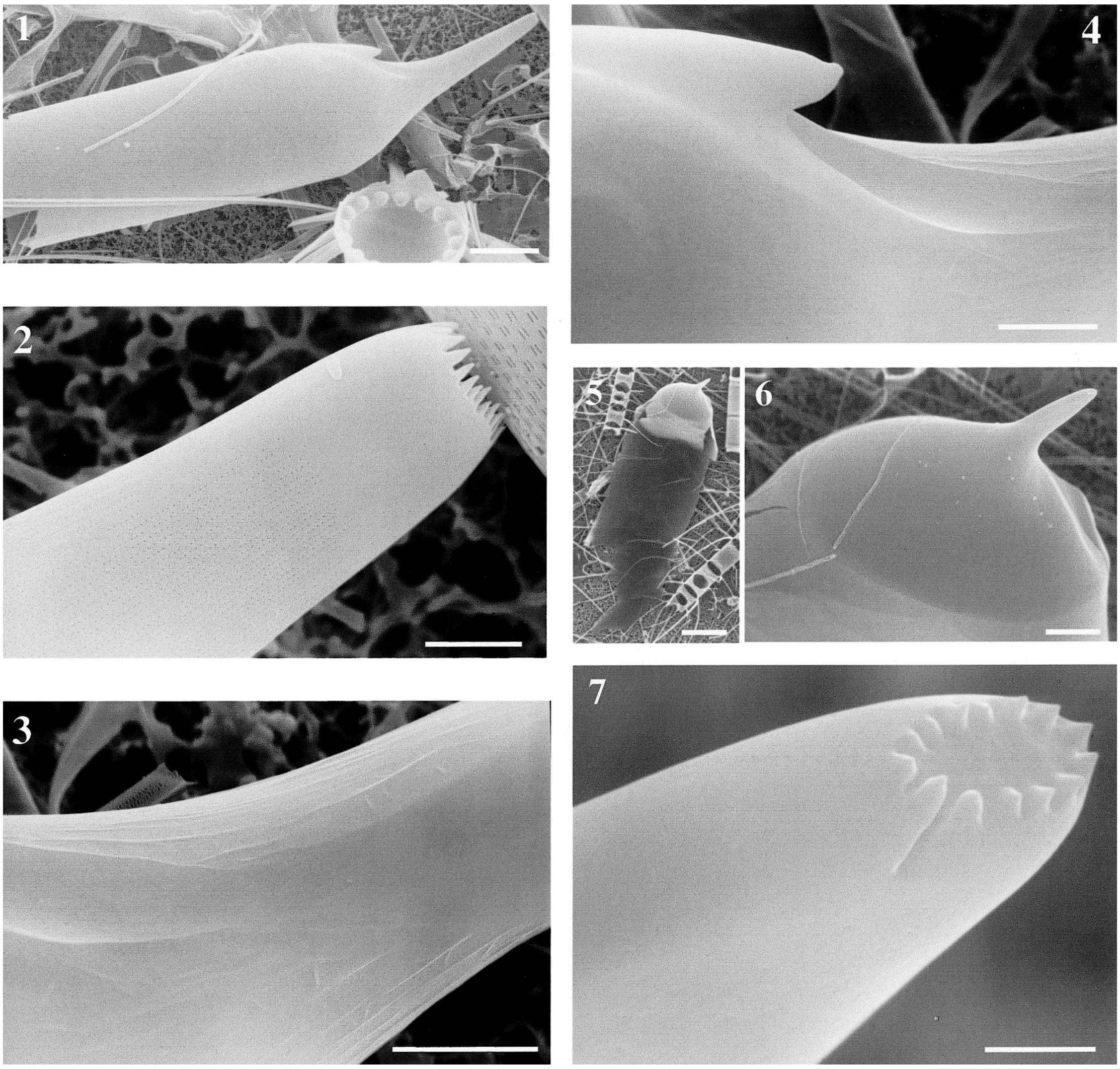

Plate IV. Fig. 1-4. Initial cell of *Proboscia alata*, Station 26, Southern Ocean. Fig. 1. Broken specimen. Scale bar = 20 µm. Fig. 2. Close-up of the claspers and fine crease-like ridges. Scale bar = 5 µm. Fig. 3. The fine crease-like ridges further along the proboscis. Scale bar = 5 µm. Fig. 4. Close-up of the proboscis tip bearing spinulae. Scale bar = 2 µm. Fig. 5-7. Auxospore of *Proboscia indica*, Sulu Sea. Fig. 5. Collapsed specimen. Scale bar = 50 µm. Fig. 6. Close-up of initial valve, showing claspers (right) and short proboscis. Scale bar = 10 µm. Fig. 7. Close-up of proboscis tip, showing ring of spinulae and longitudinal slit. Scale bar = 1 µm.

columns or rows of copulae (e.g. Mangin 1915, Jordan *et al.* 1991), however, these structures will be referred to hereafter as scales in line with the auxospore terminology used for other genera. This distinction then alleviates the confusion between the "multiple columns of copulae" reported for both the auxospores (but not the winter cells) of *Proboscia* and the spring or winter cells ("resting spores") of some *Rhizosolenia* species (e.g. Priddle *et al.* 1990, Jordan *et al.* 1991). As a consequence it is therefore unwise to continue using scales in the same context as copulae when describing the girdle segments of vegetative cells (*cf.* Round *et al.* 1990).

Observations on **Proboscia alata** *auxospores* (Plates I-III, Plate IV Fig. 1-4)

Our specimens from Stations 26 and 27 are in post-auxospore development, whereby the initial cell has already begun developing inside the auxospore. The specimens from Station 26 clearly show the difference in size between the gametangial (or parent) cell and the developing initial cell, and the number of columns of copulae in the girdle region (Plate I Fig. 4 & 7, Plate II Fig. 1-4). The size of the gametangial cells and auxospores in our samples ranged from 16.3-17.6 µm and 40.0-45.0 µm in diameter, respectively. This gives a two-fold to three-fold increase in cell diameter following auxosporulation. The gametangial cell and the initial cell, being essentially a small and large vegetative cell respectively, both have two dorsi-ventral columns of copulae. The auxospore, on the other hand, has about 6 columns of scales (Plate 2 Fig. 1). Occasionally, when viewing auxospore specimens, the multiple columns of scales on the auxospore are seen surrounding the growing half of an initial cell with its two columns of copulae (Plate II Fig.2).

SEM observations on a bifurcate auxospore from Station 27 shows that both probosces bear a longitudinal slit and a ring of spinulae at the tip (Plate III Fig. 7). A close-up of two adjoining valves clearly shows (as expected) that the slit of one proboscis faces outwards from the claspers of the other valve (Plate III Fig. 2). Another specimen from Station 27 shows a gametangial cell bearing an elongate, non-bifurcate auxospore (Plate III Fig. 3), at the pointed base of which is a prominent slit presumably homologous to the longitudinal slit/rimoportula (Plate III Fig. 5). A specimen from Station 26 appears to show an initial valve attached to a girdle section, about 40 µm in diameter and composed of two dorsi-ventral columns of copulae (Plate IV Fig. 1). The proboscis bears longitudinal crease-like structures, claspers, a contiguous area, and a ring of spinulae at the tip (Plate IV Fig. 2). The presence of the claspers and the contiguous area on an initial valve contradicts the statements made by Sundström (1986) and Jordan *et al.* (1991). On the other hand, Sundström's Fig. 261 could represent the side view of a bifurcate proboscis, which we have now shown is devoid of claspers and a contiguous area. The presence of fine crease-like structures at the base of the proboscis near the claspers are reported for the first time in *P. alata*, previously ridge-like features have only been seen in fossil forms (Jordan & Ito 2002, Jordan unpubl obs), *P. subarctica* (Takahashi *et al.* 1994) and an undescribed subarctic taxon (Jordan & Takahashi, unpubl obs).

Observations on a **Proboscia indica** *auxospore* (Plate IV Fig. 5-7)

Although our specimen from the Sulu Sea is broken, it measures almost 100 µm in diameter, which together with the presence of multiple rows of scales (visible on the negative, but not in our figure) confirms that we are dealing with an auxospore. An apparent initial valve is visible at the other end of the auxospore (Plate IV Fig. 5). The proboscis appears to be quite small in relation to the auxospore, but the valve is large. The presence of spinulae and a longitudinal slit at the proboscis tip (Pl. IV Fig. 7), and seemingly "displaced" claspers on the valve (Plate IV Fig. 6), suggest that this specimen is assignable to *Proboscia indica*.

DISCUSSION

Proboscia indica: *an emended description based on new observations*

As mentioned above, there has been some confusion over the true identity of this taxon. To address this problem we have compiled a synonymy of references which we have personally checked and which contain illustrations which we believe to represent *P. indica*. Our new observations on an auxospore of this taxon have been combined with previously published accounts of its general frustule morphology, most of which have been corroborated by us during this study, in order to compose a more detailed and accurate species description. The only point we have not been able to corroborate has been the girdle band features reported by various authors using transmission electron microscopy. Despite this, the known features clearly confirm this taxon's assignment to the genus *Proboscia*.

***Proboscia indica* (H. Peragallo) Hernández-Becerril emend. Jordan & Ligowski**

Basionym: *Rhizosolenia indica* H. Peragallo 1892, p.116, pl.18, fig.16.

Synonyms:

Rhizosolenia alata var. *corpulenta* Cleve 1897, p. 24, pl. 2, fig. 11; Hustedt 1920, pl. 317, figs 11-13 (accompanied by "= *R. indica*").

Rhizosolenia alata var. *indica* (H. Peragallo) Ostenfeld & Schmidt 1901, p. 160.

Rhizosolenia alata f. *indica* (H. Peragallo) Gran 1908, p.56; Hustedt 1930, p. 602, fig. 346; Lebour 1930, p. 90-91, fig. 60; Okuno 1960, p. 310, text-fig. 1a, pl. I, fig. 1; Hendey 1964, p. 147, pl. II, fig. 4; Hasle 1975, p. 111-112, figs 55, 59.

Rhizosolenia alata f. *corpulenta* (Cleve) H. Peragallo & M. Peragallo 1897-1908, p. 466.

Rhizosolenia corpulenta (Cleve) Cleve 1901, p. 22; Mills 1934, p. 1402.

Rhizosolenia alata f. *indica* (H. Peragallo) Ostenfeld <incorrect authority> – Allen & Cupp 1935, p. 131, figs 45, 45a; Cupp 1943, p. 93, fig. 52-C (a-c).

Rhizosolenia indica H. Peragallo – Drebes 1974, p. 57, fig. 42 – Takano 1990, p. 266-267, figs A-E.

Rhizosolenia alata f. *indica* (H. Peragallo) Hustedt <incorrect authority> – VanLandingham 1978, p.3482.

Pseudosolenia calcar-avis (Schultze) Sundström – sensu Desikachary 1989, pl. 695, fig.6.

Proboscia alata (Brightwell) Sundström – Desikachary 1989, pl.696, figs 1-3, 5.

Description: Cells solitary or in short chains, broadly cylindrical, valves calyptroform, generally 40-73 µm in diameter[1]. Girdle bands (copulae), scale-like, in two longitudinal columns. Valve and girdle bands with loculate areolae. Vela[2] on the outside of loculi perforated peripherally by six round pores[3] and sometimes one in the centre. "Interlocular pore" surrounded by four loculi[4]. Each valve bearing claspers[5] and terminating in a long, asymmetrically curved proboscis. Chain formation similar to *P. alata*, with claspers situated ventro-laterally[6] so that the chain appears asymmetrical in both dorsi-ventral and lateral views[7]. Proboscis tip bearing spinulae and a longitudinal slit[8]. Auxospore terminal, with multiple columns of scales, 100 µm or more in diameter[9]. Auxospore initial valve bearing claspers, a proboscis with spinulae and a short longitudinal slit at the tip[10].

Comments: It has been mentioned on several occasions that *R. indica* and *R. alata* are forms of the same species, because a valve of each form has been seen at opposite ends of the same cell (Lebour 1930, Hendey 1964) or one form has reverted to the other in culture (Boalch pers comm in Hasle 1975). However, it is more likely that this is an example of cryptic speciation. *P. indica* is easily distinguished from the other species in the genus, except *P. alata*, from which it differs by having a wider frustule and valve (vegetative cells of *P. alata* rarely exceed 40 µm), and a valve with a more strongly sloped profile when seen in lateral view. In addition, Hasle (1975) showed that the "interlocular pore" pattern differed between f. *indica* (a pore surrounded by four loculi) and other formae of *Rhizosolenia alata* (a pore surrounded by six loculi). Furthermore, the auxospores of *P. indica* may be different as the initial valves do not appear to be bifurcate and they are very large (up to 100 µm or more in diameter), in contrast to those of *P. alata* recorded from Station 26 (this study; Plate I Fig. 1-3, 5-6) or other locations in the Southern Ocean (Jordan *et al*. 1991, their Fig. 8-9), and a single specimen (as *Rhizosolenia alata* fo. *indica* "*bidens*") from the Persian Gulf (Simonsen 1974, his plate 22 Fig. 8), which rarely exceed 40 µm. A seemingly non-bifurcate auxospore from Station 26 (Plate I Fig. 4) is also assignable to *P. alata* (compare with Jordan *et al.* 1991, their Fig. 6-7) as the auxospore has a diameter of about 45 µm from which a gametangial valve 15 µm in diameter is still attached. *Proboscia indica* may also differ from other species in its ecological preference because it has never been reported with certainty from polar waters. Thus, it seems reasonable to retain this taxon as a separate entity at the species level.

Okuno (1960) illustrated a cell from the Seto Sea (southern Japan) with multiple columns of "girdle bands", and mentioned in the text of cells up to 300 µm in length and 110 µm in diameter. Takano (1990) was perhaps suspicious of this identification when he commented on *Rhizosolenia indica* (mentioned in the Japanese, but not the English text) in the book "Red tide organisms in Japan". However, a similar-looking specimen collected from the Sulu Sea clearly belongs to *Proboscia*, bearing spinulae and a longitudinal slit on the proboscis of the initial valve (Plate IV Fig. 7). In addition, on the negative it appears to possess multiple rows of scales (a characteristic of all *Proboscia* auxospores; Jordan *et al*. 1991) and the collapsed specimen measures almost 100 µm in diameter (Plate IV Fig. 5). It is quite possible that the two specimens from the literature noted above were auxospores of *P. indica*. Another enigmatic species, *Rhizosolenia arafurensis* Castracane (Castracane 1886, Fig. 12; Peragallo 1892, plate 3 Fig. 6; Gran 1908, Fig. 62; Allen & Cupp 1935, Fig. 33), may also be an auxospore of *P. indica* or a related taxon as it possesses multiple columns of "copulae", has a diameter of 65-120 µm, and is endemic to warm seas (Gran 1908, Allen & Cupp 1935). Due to the lack of distinction between process and valve, it was previously considered to be closely related to *Rhizosolenia alata* (Hasle 1975). Similarly, *Rhizosolenia quadriiuncta* (*quadrijuncta*) H. Peragallo (Peragallo 1892: 116, plate 5 Fig. 17; Hustedt 1920, plate 317, Fig. 14-16) also possesses the characteristics of a *Proboscia* auxospore and was synonymized with *R. alata* f. *indica* by VanLandingham (1978). Hustedt's (1920) specimen was collected off the French Atlantic coast near Arcachon.

A specimen identified as *Pseudosolenia calcar-avis* (Schultze) Sundström and others identified as *P. alata* from the Arafura Sea and Bay of Bengal have wide frustules with proboscis-bearing valves (Desikachary 1989). The shape of the valve and the lack of curvature of the process suggests that the one identified as *P. calcar-avis* was misidentified. A similar-looking specimen from the Southern Ocean, identified as an initial cell and assigned here to *Proboscia alata*, clearly has claspers and a proboscis tip bearing spinulae (Plate IV Fig. 1-4).

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[1] end range measurements taken from Lebour (1930) and Allen & Cupp (1935), respectively.
[2] = sieve membranes *in* Okuno (1960).
[3] = sieve pores *in* Okuno (1960), porelli *in* Hasle (1975).
[4] from Hasle (1975).
[5] from Takano (1990) and the present study.
[6] sometimes referred to as "displaced and unequal claspers" (e.g. Takahashi *et al.* 1994).
[7] as illustrated by Hustedt (1920), Hendey (1964), Desikachary (1989) and Takano (1990).
[8] from the present study.
[9] from Okuno (1960), Drebes (1974) and the present study. According to Drebes (1974), Osorio-Tafall (1936) studied phytoplankton off NW Spain and reported that *R. indica* produced a terminal auxospore.
[10] from the present study.

However, given the geographic location of Desikachary's samples his specimens may belong to *Proboscia indica*.

Distribution and ecology: *Proboscia indica* is generally found in subtropical to tropical waters, but may be present in temperate waters. Thus, its absence from polar waters clearly separates it from most other *Proboscia* species, however, *P. alata* is known to be cosmopolitan and can be found in the same samples as *P. indica*.

Although Simonsen (1974) noted that f. *indica* often outnumbered or completely replaced the type forma in the Persian Gulf waters, the two taxa (now regarded as separate species) are still closely related, as cultures of both *P. indica* and *P. alata* were recently shown to produce distinct organic compounds, which are often present in significant quantities in sediment traps and sediments. It was calculated that these compounds may be responsible for as much as 20-35% of the total lipid flux in the Arabian Sea, due to the productivity of *Proboscia* spp. during the start of the upwelling season (Sinninghe Damsté *et al.* 2003).

Auxospores of **Proboscia alata**

According to Robinson (1957), the gametangial cell and auxospore diameters of *R. alata* f. *alata* (including f. *gracillima* and f. *genuina*) are much smaller (2.5-4.9 µm and 12.1-18.2 µm respectively) than those of *R. alata* f. *indica* (10.9-18.2 µm and 32.8-47.3 µm respectively), but with both taxa exhibiting a 3:1 or 4:1 increase in cell diameter following auxosporulation. In comparison, our specimens would appear to belong to the latter rather than the former taxon. However, some of our auxospore specimens are clearly bifurcate at one end, a character previously assumed to be either unique to Antarctic *P. alata* or possibly shared with *P. truncata* (Jordan *et al*. 1991). Furthermore, other authors (Okuno 1960, Drebes 1974) have stated that the auxospore diameter of *R. indica* is much larger (i.e. over 100 µm), suggesting that our Southern Ocean specimens (and the observations by Robinson 1957) belong to a larger form of *P. alata* whilst our Sulu Sea specimen belongs to *P. indica*. Sundström (1986) based his description of *P. alata* on North Atlantic specimens (where the smaller form is seemingly dominant; Robinson 1957) when transferring it to the new genus *Proboscia*. However, some confusion has now crept in regarding the size range of this geographically-restricted *Proboscia alata*. Sundström (1986) reported dimensions of the mother cell (= gametangial cell) and auxospore of *P. alata* as 3-4.5 µm and 10-12.5 µm respectively. These dimensions clearly assign the specimens to the smaller form. However, the diameter of vegetative cells of *P. alata* on one of the slides used by Brightwell (and designated as the lectotype slide by Sundström 1986) are 8.5-11.5 µm, suggesting that it was the large form that Brightwell (1858) saw when describing *Rhizosolenia alata*. These specimens, according to Sundström (1986) came from off the coast of Hull (U.K.). Obviously there is a need to study the worldwide distribution and dimensions of *Proboscia alata*, before two (or more) forms can be distinguished as separate, but closely related taxa. Interestingly, a similar case involving different size populations of *Rhizosolenia styliformis* was reported from the same area of North Atlantic by Robinson & Colbourn (1970), but has yet to be re-investigated.

The need for a separate family, the Probosciaceae

As *Proboscia* was only described in 1986, it is necessary to consider historically the taxonomic position of *Rhizosolenia* when thinking about *Proboscia alata* and higher taxonomy. Hendey (1964) included the families Bacteriastraceae (= Chaetoceraceae), Leptocylindraceae, Corethronaceae (= Corethraceae) and Rhizosoleniaceae in the suborder Rhizosoleniineae. Simonsen (1972) added the fossil family Pyxillaceae, but excluded *Corethron* Castracane and *Leptocylindrus* Cleve, which did not appear in his classification scheme. In his later paper (Simonsen 1979), the suborder contained only two families, the Rhizosoleniaceae and the Pyxillaceae, with the Chaetoceraceae removed to the suborder Biddulphiineae. Round *et al*. (1990) included the two families used by Simonsen (1979) when they emended the order Rhizosoleniales (Silva 1962) and upgraded it to subclass rank, the Rhizosoleniophycidae. The family Rhizosoleniaceae of Round *et al.* (1990) contained *Dactyliosolen* Castracane, *Guinardia* H. Peragallo, *Proboscia*, *Pseudosolenia* Sundström, *Rhizosolenia* and *Urosolenia* Round & Crawford. However, Nikolaev & Harwood (2000) removed *Proboscia* from the Rhizosoleniaceae and created a new family, Probosciaceae, presumably (as no description was given) on the basis of morphological criteria, but kept it within the order Rhizosoleniales. In a later paper they placed two orders within the subclass, the Rhizosoleniales and the Corethrales, with the former including three families, the Rhizosoleniaceae, Probosciaceae and Pyxillaceae (Nikolaev & Harwood 2001). From the diatom phylogenetic tree produced by Medlin *et al.* (2000) it is clear that *Rhizosolenia* and *Corethron* may be closely related, however, *Chaetoceros* Ehrenberg appears elsewhere on the tree. Perhaps their most interesting finding is the closeness of *Proboscia* and *Leptocylindrus*, which do not seem to be related to *Rhizosolenia*. Jordan & Ito (2002) showed that *Proboscia* first appeared in the Late Cretaceous, and thus the distance between

Proboscia and *Rhizosolenia* on the phylogenetic tree seems justified. Apparently, the two genera also differ in "certain details of the cytoplasm during the cell cycle" (Pickett-Heaps pers comm in Medlin *et al*. 2000). *Leptocylindrus danicus* Cleve, the type species of *Leptocylindrus*, has many tile-like copulae, marginal flap-like projections and poroid valves, but forms resting spores after auxosporulation. A taxonomic position close to *Proboscia* must be considered doubtful at present. On the other hand, if the data of Medlin *et al.* (2000) is to be taken seriously, the inclusion of *Corethron* in the Leptocylindraceae by Hasle & Syvertsen (1996) does not seem to be justified given the distance between them on the tree. Whilst the creation of the Probosciaceae (Nikolaev & Harwood 2000) is wholly justified on morphological, genetic and stratigraphic grounds, the authors did not validate their new family in accordance with the ICBN (Article 36.2 and Recommendation 36A.1 of Greuter *et al.* 2000). As the family Probosciaceae is typified not descriptive, a Latin description and generitype citation are necessary, because the type species of *Proboscia* is the living species, *P. alata*. *Proboscia* must therefore be viewed as an extant genus with fossil members, and so the family is described below as new and provided with a Latin diagnosis.

Probosciaceae Jordan & Ligowski fam. nov.

Probosciaceae Nikolaev & Harwood 2000, p. 53 (invalid).

Cellulae cylindricae, copulae multae apertae. Valva calyptoformis in parte extrema in proboscidem tubularem prolongata. Proboscis longa, spinulae in margine apicis, ab apice in latere dorsali rima longitudinalis. Auxospora terminalis. Species marinae planctonicae.

Cells cylindrical, with many copulae (girdle bands). Valve calyptroform, extending distally into a tubular proboscis. Proboscis long with marginal spines at the apex and a longitudinal slit on the dorsal side. Planktonic, marine. Auxospores terminal. Early Cretaceous to Recent.

Type genus: *Proboscia* Sundström

Citation: Sundström 1986, p. 99.

Members of the family Probosciaceae: *Proboscia* Sundström, *Kreagra* Gersonde & Harwood.

Comments: Gersonde & Harwood (1990) were not prepared to classify the fossil *Kreagra* when they originally described it from Early Cretaceous sediments, as only the valve apices and "linking spines" were preserved. However, they did speculate on its possible relationship with a subgroup represented by *Microorbis* Gersonde & Harwood. Later, Nikolaev & Harwood (1999) noted that *Kreagra* bore some resemblance to *Trochus* Gersonde & Harwood, and speculated that the former genus could have been ancestral to the Trochuaceae. Strangely, *Kreagra* was omitted from their subsequent centric classification scheme (Nikolaev & Harwood 2000), but in a later paper it was placed in the Rhizosoleniaceae (Nikolaev & Harwood 2001). This sudden change in thinking was perhaps due in part to the fact that Jordan & Ito (2002) had previously proposed in an oral presentation in 1998 that *Kreagra* may have been the ancestor to *Proboscia*. Although specimens of Early Cretaceous *Kreagra* species possibly represent resting stage valves rather than vegetative valves, they are similar to specimens of Late Cretaceous *Proboscia* species because they possess two large spines supported by buttresses, a longitudinal groove perhaps analogous to the longitudinal slit, a small spine on either side of a notch just above the groove, and poroid calyptroform valves (Jordan & Ito 2002). Thus, from morphological and stratigraphic viewpoints it seems logical to place *Kreagra* in the Probosciaceae, as *bona fide Rhizosolenia* species have not been illustrated from Cretaceous sediments and are first recorded in the Late Palaeocene (Fenner 1991b), although highly branched isoprenoid alkenes associated with *Rhizosolenia* species are thought to have evolved about 90 Ma in the mid-Cretaceous (Sinninghe Damsté *et al*. 2004).

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