Taxonomy and distribution of *Gomphonema subtile* Ehrenberg (Bacillariophyceae) and six related taxa

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Abstract: This paper reports on *Gomphonema subtile* and related taxa which have been classified as varieties so far and for which the shape of the headpole has been considered to be extremely variable. In literature they are described as cosmopolitan. However, the shape of *G. subtile* proved to be quite constant and specimens with less inflated headpoles represent separate species with limited distribution. *G. subtile* and *G. sagitta*, together with related diatoms like *G. cathedrale*, *G. maclaughlinii* and *G. subsagitta* form a group which is distributed in holarctic regions. In tropical regions similar species like *G. pantropicum* or *G. pseudosubtile* occur. All the mentioned taxa are described in detail and for most of them SEM–images are presented for the first time. *G. pseudosubtile* and *G. subsagitta* are described as new species. *G. pantropicum* is a new name for *G. subtile* var. *malayense* which is raised to species rank. In addition a few similar diatoms from tropical regions are discussed briefly.

Key words: Bacillariophyceae, diatom morphology, *Gomphonema*, new species, distribution, taxonomy, ultrastructure

Introduction

Gomphonema subtile was described by Ehrenberg as early as 1841 (1843) from two locations in North America: A slender *Gomphonema* with pronounced capitate headpole. Later it was reported from many other regions worldwide. These findings led to the assumption that *G. subtile* is a wide spread or even cosmopolitan diatom (e.g. Hustedt 1930: 377 "Im Süßwasser überall verbreitet"; Krammer & Lange–Bertalot 1986: 369 "kosmopolitisch"), although some authors (e.g. Cholnoky 1954: 126, 1962a: 77) reported on deviating dimensions or other differences. In addition Gomphonemata with less capitate or even not at all inflated headpoles have been described and/or combined with *G. subtile* (e.g. *G. sagitta* Schum., *G. subtile* var. *malayense* Hust.) based on the opinion that the size of the capitate headpole varies to a high degree. Questionable representations and combinations in the literature as well as findings of similar forms made it clear that a revision of the complex is necessary.

Material and Methods

This study is based on investigations of many samples in my own collection. Micrographs from those samples are presented together with the material–number (in brackets) and short information on the locality.

Detailed LM and/or SEM studies were carried out with following samples:

S1131 coll. Reichardt. Manzanita Lake, 1814 m a.s.l., Lassen National Park, California, USA.
On fine root systems. Leg.: E. Reichardt, 10.8.1990.
Type material of *G. subsagitta*.

S1384 coll. Reichardt. Julma Ölkky near Kuusamo, Finnland.
Leg. A. & R. Dorn, 13.6.1992.
Material ex coll. Lange–Bertalot. See Lange–B. & Metzeltin (1996) for further data.
Type material of *G. cathedrale*. Contains also *G. sagitta*.

S1838 coll. Reichardt. Spring at Zion National Park, Utah, Washington Co.; USA. Leg. J.L. Stone, 23.5.1964.
Material ex coll. R.B. McLaughlin (Ref. slide coll. McLaughlin S843).
Type material of *G. maclaughlinii*.

S1911 coll. Reichardt. Okavango River about 40 km west of Maun, Botswana. On plants in running water. Leg.: H. & R. Schuwerk, 22.10.1997.
Type material of *G. pseudosubtile.* Contains also *G. pantropicum.*

S2716 coll. Reichardt. Cultured material from rice–field, Ifugao Province, Luzon, Philippines. Leg. et cult. J. Margraf. Contains *G. pantropicum.*

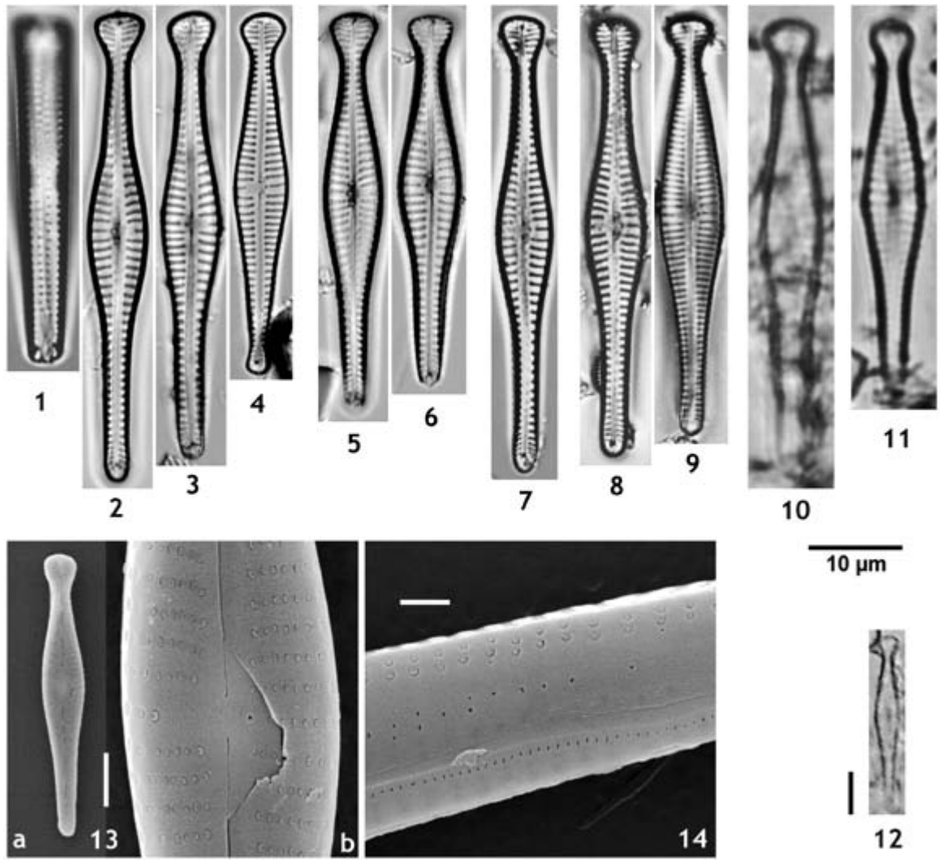
Measurements are also based on these materials and are confirmed by findings in additional materials (see figures). At least three slides with cover–glasses 18 mm square were scanned completely to find maximum and minimum sized

specimens. However, the full size–range of most of the species described is still unknown, since initial valves have not been found. The samples were prepared according to standard techniques by boiling in sulfuric acid and oxidation with nitric acid. Naphrax or Hyrax were used as mountants of the LM–slides. Light micrographs were taken with a digital camera Imagingsource DMK41AF02. For SEM studies the material was sputter coated with about 20 nm of gold and investigated in a modified Leitz AMR 1200B scanning electron microscop at an accelerating voltage of 15 kV. Holotypes are circled by a diamond marker.

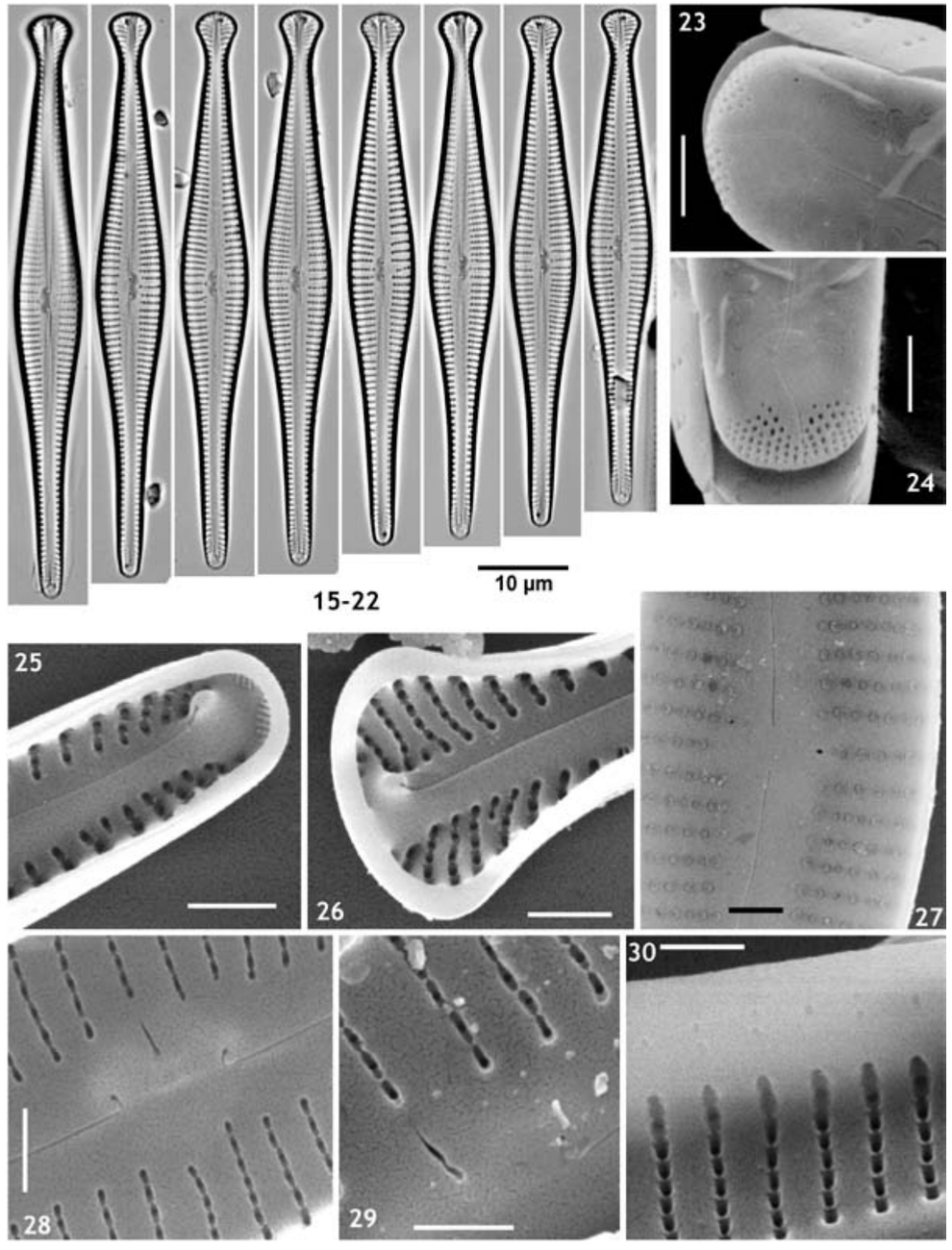
The following mica of C.G. Ehrenberg with marked specimens of *G. subtile* have been invesigated at the Ehrenberg Collection in Museum für Naturkunde in Berlin (BHUPM):
West–Point, New York. Case (Kasten) 26, book (Buch) 3, strip (Streifen) 1, mica 1, dark (violet?) paper ring. Epitype EC 260301 1v (Fig. 11).
Kymměne Gård. Case 34, book 10, strip 7, mica 4, green paper ring: EC 341007 4g (Fig. 10).
Loka. Case 34, book 9, strip 6, blue paper ring: EC 340906 bl (Fig. 12)

Results

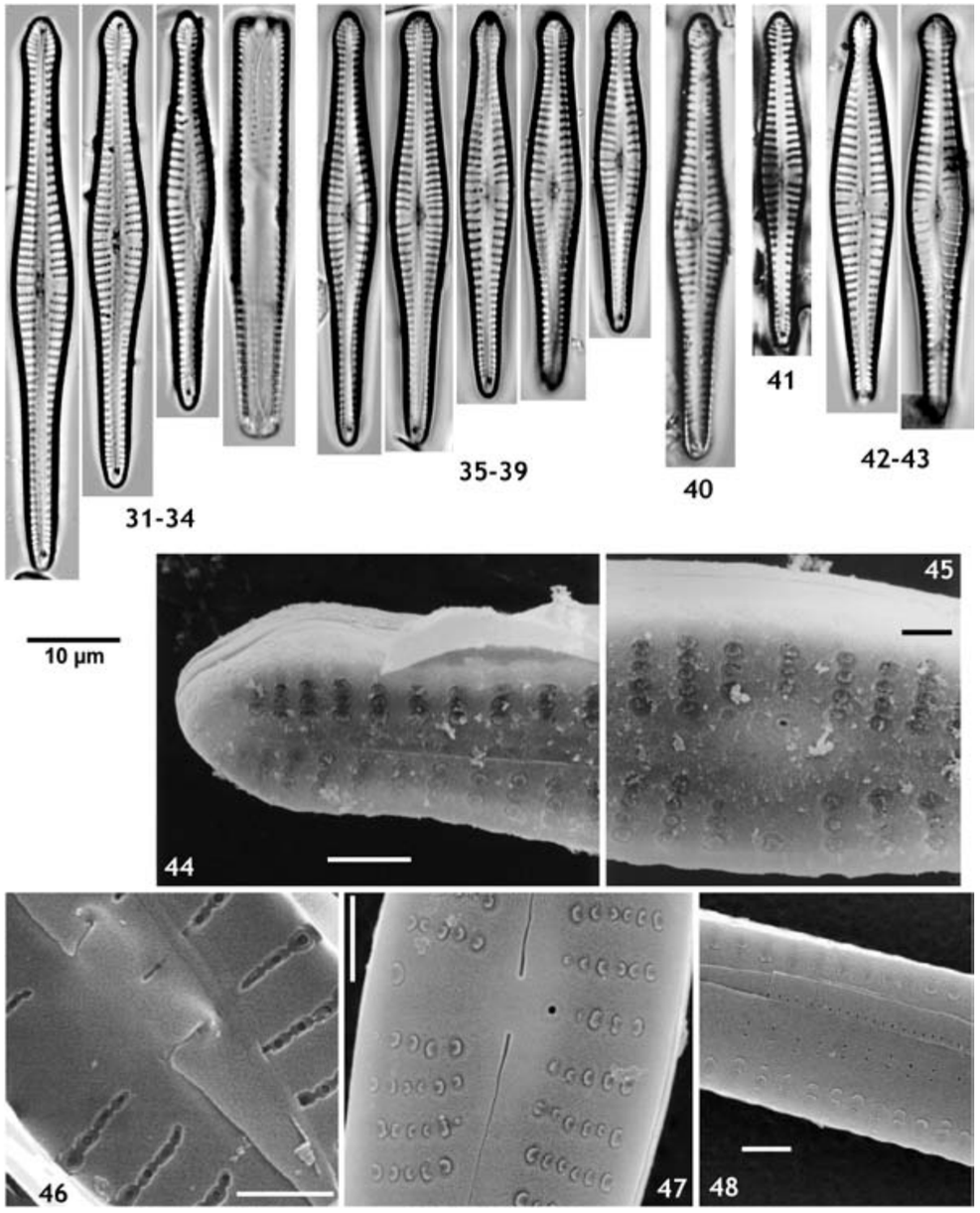
***Gomphonema subtile* Ehrenberg (Figs 1–14)**
G. subtile was first described from New York and Bridgwater, Mass. (Ehrenberg 1843: 416) and typified by Tuji (2009: 16). He designated the figure on Ehrenberg's drawing sheet 2253 as lectotype and the marked specimen on Ehrenberg's mica from New York (260301–1v) as epitype. However, figures of *G. subtile* can also be found on Ehrenberg's drawing sheet 685 from "New York", "Bridgwater" and "Kymměne"; they are cut outs from copies of the original drawing sheets. The first published figures appeared in the "Mikrogeologie" (Ehrenberg 1854) from New York (pl, 2/2.45), Loka (pl. 16/3.38), Kymměne (pl.



Figs 1–14. *Gomphonema subtile*, LM: (1–4) Lake Belanger, Canada, P.Q. (S1830), (1) Girdle view, (5–6) Jaquist River, Canada, P.Q. (McL25), (7) Lake Bosten Hu near Korla, China (S1796), (8–9) Lake Mittersee, Austria (phot. Lange–Bertalot), (10–12) Specimens marked by Ehrenberg on original mica, (10) Kymměne Gård; (11) West Point, New York, Epitype, (12) Loka, Sweden (bar 10 µm); SEM: Lake Castor, Canada, P.Q. (McL26): (13) Valve exterior with centre enlarged, (14) Girdle view with poroides in mantle. Scale bars (SEM) 2 µm, 10 µm (13a).

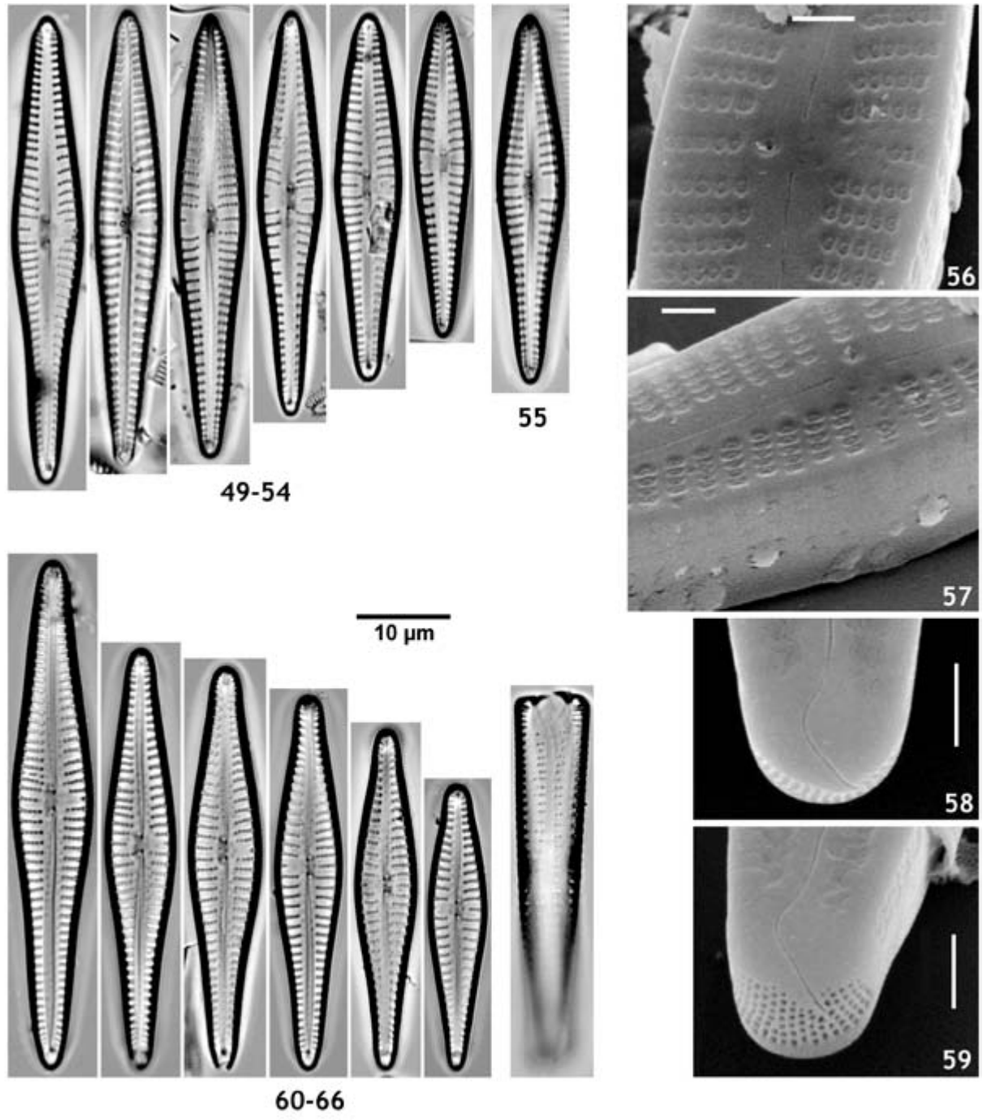


Figs 15–30. *Gomphonema pseudosubtile*, LM, type material: (17) Holotype; SEM, type material except 23, 24, 29 Okavango River near type locality (S1910): (23) Exterior of foot pole without tilting, pore field hardly extending onto valve face, (24) foot pole tilted 45°, (25) Interior of foot pole, (26) Interior of head pole, (27) Centre of valve exterior, (28) Centre of valve interior, (29) Valve interior showing alveoli with stubs, central raphe fissure and stigma opening, (30) Valve interior tilted 45° showing alveoli with stubs and poroids in the valve mantle. Scale bars (SEM) 2 µm.



Figs 31–48. *Gomphonema sagitta*, LM: (31–34) Lake Belanger, Canada, P.Q. (S1830), (34) Girdle view, (35–39) Trout Lake, Canada, P.Q. (McL18), (40) Van Heurck Types du Synopsis 484 "Angleterre", (41) Lake Mittersee, Austria (phot. Lange–Bertalot), (42–43) Julma Ölkky, Finland (S1384); SEM: (44–45) Exterior of head pole and valve centre, interruption of foramina at edge valve face/mantle (Island, phot. Lange–Bertalot), (46–48) McL18, (46) Centre of valve interior, (47) Centre of valve exterior, (48) Girdle view with poroides in mantle. Scale bars (SEM) 2 µm.

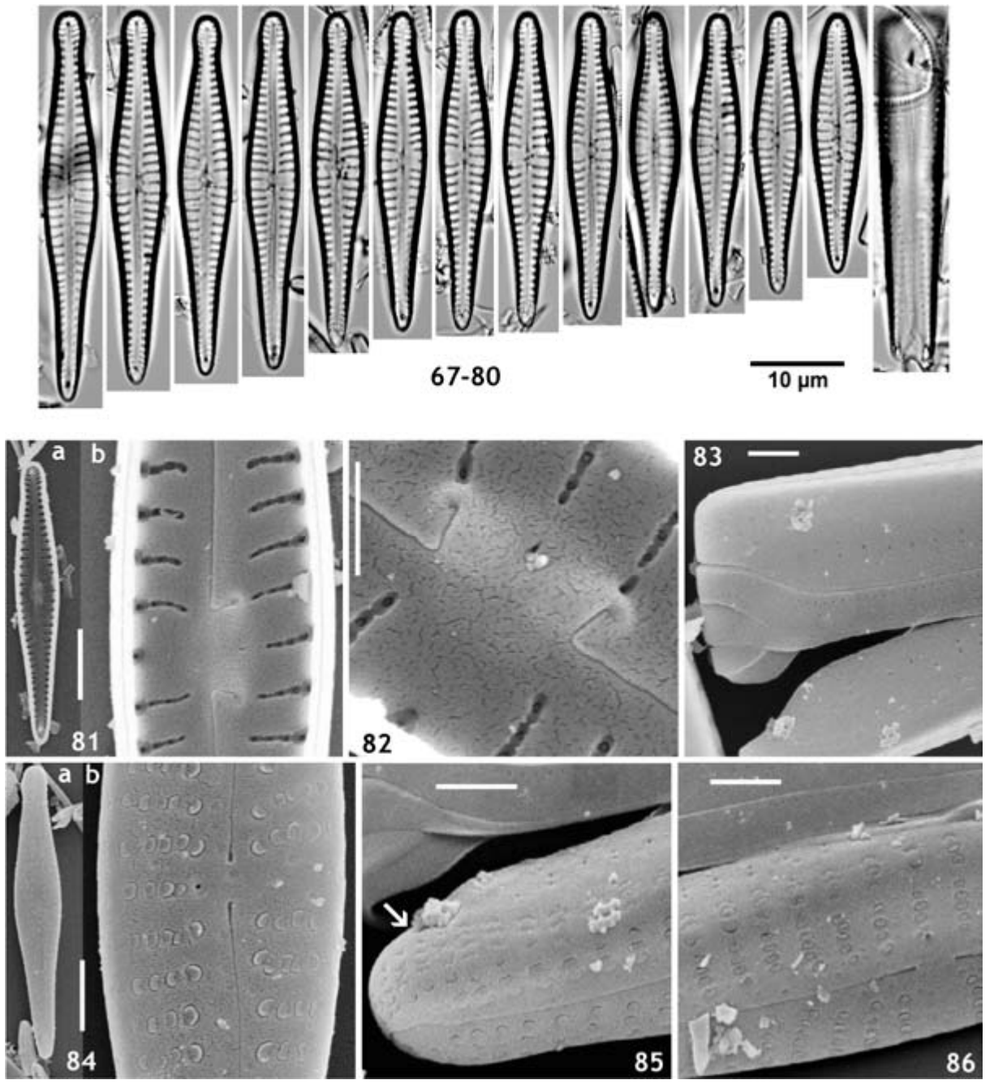
17/2.43) and Mourne, Ireland (pl, 15,A.90). In his catalogue, EHRENBERG gives the mica from New York and Kymměne with marked specimens as reference. With the exception of the drawing from Mourne, Irland all other figures are very similar and represent only one taxon. This is also confirmed by investigations of original preparations where marked specimens were found on mica from New York, Kymměne and Loka (Figs 10–12).



Figs 49–59. *Gomphonema cathedrale*, LM: (49–54) Type material (S1384); (55) Lake Castor, Canada, P.Q. (McL26); SEM, type material: (56) Centre of valve exterior tilted 40°, (57) Centre of valve exterior tilted 50° showing edge of valve face/mantle, (58) Exterior of foot pole without tilting, pore field restricted to polar mantle, (59) foot pole tilted 40°.
Figs 60–66. *Gomphonema maclaughlinii*, LM, type material (S1838).

The habitus of *G. subtile* is mainly characterized by a broadly capitate and flatly rounded headpole sitting on a narrow "neck". Sometimes the headpole shows a tendency to a somewhat oblique orientation. Length 39–51 µm, breadth 5.8–7.0 µm. Raphe lateral, external and internal central raphe endings distinguishable, the latter being wider apart and deflected to the same side. Axial area narrow, central area formed by only one short stria. On the opposite side, one not or only slightly shortened stria ends with a stigma which is clearly discernible. Striae slightly radiate or nearly parallel, 10–15 (mostly 11–13.5) in 10µm. Striae pores indistinct, though not too dense, about 28 in 10µm.

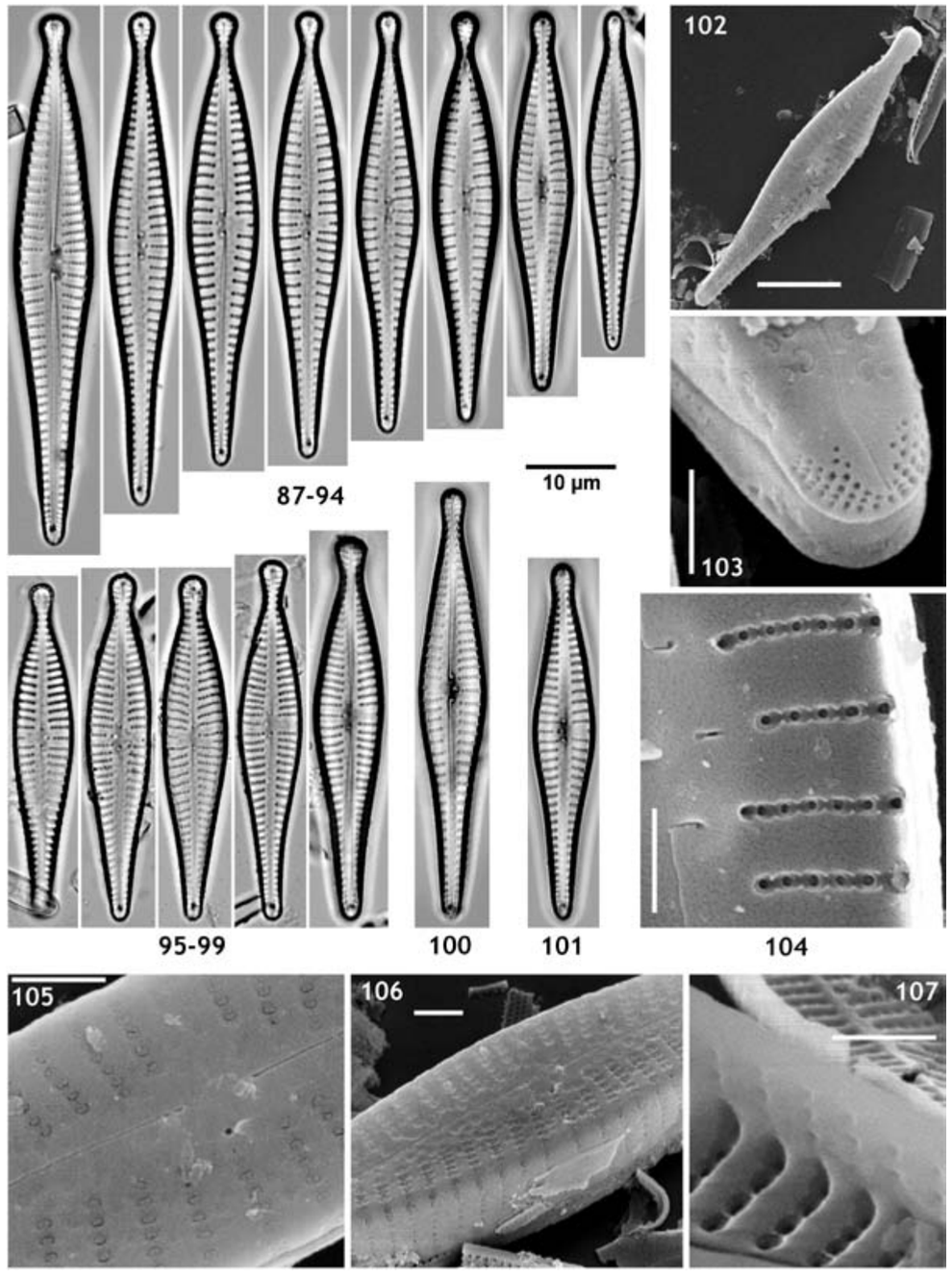
Ultrastructual details are similar as in *G. sagitta* described below, but there are slight differences: The foramina in *G. subtile* are somewhat smaller and more C– than kidney–shaped. Depressions around foramina



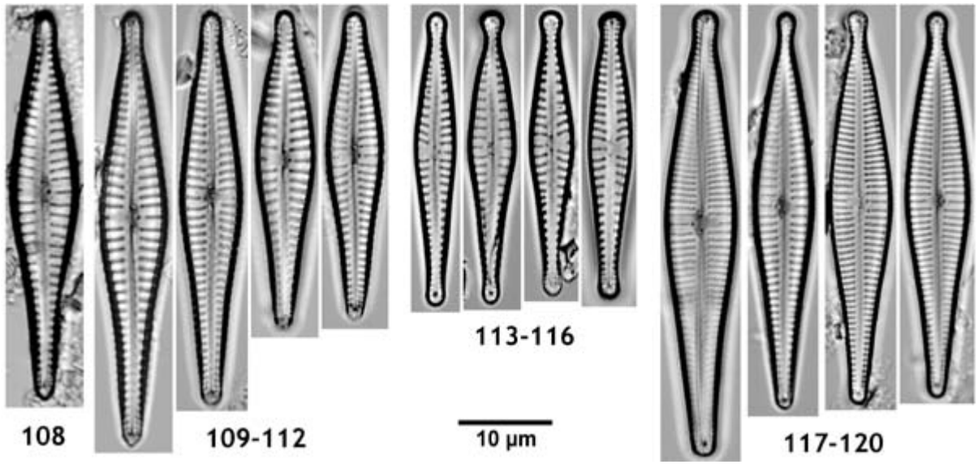
Figs 69–86. *Gomphonema subsagitta*, type material, LM: (70) Holotype, (80) Girdle view; SEM: (81) Valve interior with centre enlarged, (82) Inside view of valve centre showing alveoli with small stubs, central raphe fissures and stigma opening, (83) Girdle view of head pole showing poroids in the mantle, (84) Valve exterior with centre enlarged, (85) exterior of head pole showing valve face and mantle, foramina of striae running over the entire mantle near the apex (arrow), (86) Centre of valve, point of view as in Fig. 85. Scale bars (SEM) 2 µm, 10 µm (81a, 84a).

and external stigma opening are lacking and there is no or only indistinct interruption of foramina at the edge between valve face and mantle. External central raphe fissures simple, not or only slightly widened (Fig. 13).

G. subtile is distributed in holarctic regions, but in general, it is a rare taxon which occurs only scattered in the samples. The characteristic outline was found to be rather constant. Intermediate valves of specimens with less or slightly capitate headpoles as reported in literature (e.g. HUSTEDT 1937–39: 440) could not be found. Such forms or those from tropical regions represent different taxa.



Figs 87–107. *Gomphonema pantropicum*, LM: (87–94) Okavango River (S1911), (95–99) Ifugao, Philippines, cultured material from rice field (S2716), (100) Ifugao, Philippines, natural population from pond at rice field, (101) Victoria Falls, Zimbabwe (S1240); SEM, S2716 except 104 (S1911): (102) Exterior view of whole valve, (103) Foot pole with pore field, (104) Centre of valve interior, (105) Centre of valve exterior, (106) Exterior view of valve face and mantle, foramina running without significant interruption over the edge, (107) Valve interior tilted 45° showing poroids in valve mantle. Scale bars (SEM) 2 µm.



Figs. 108–120. *Gomphonema* spp., LM: (108–112) *Gomphonema* spec. aff. *pantropicum* with rostrate, not capitate headpole (108) Lake Bratan, Bali (S1713), (109–112) Lake Chembe, Zambia (S1262); (113–116) *Gomphonema* spec. Similar to *G. pantropicum* but much smaller. Okavango River (S1911); (117–120) *Gomphonema* spec. corresponding to SCHMIDT et al. (1902) pl. 234/19, (117) Waterfall Da–tanla, Vietnam (S1325), (118) My–son, Vietnam (S1326), (119–120) Lake Da–lat, Vietnam (S1323).

***Gomphonema peudosubtile* E. REICHARDT sp. nov. (Figs 15–30)**

Description: Valves lanceolate, constricted below the headpole. Apex truncated–capitate, flatly rounded. Length 61–83 µm, breadth 9–10 µm. Raphe lateral with slightly arched to nearly straight fissures. External and internal central raphe endings distinguishable, but less conspicuous than in *G. subtile*. Axial area somewhat lanceolate, moderately broad. No central area. One stigma near the end of one stria at mid–valve. Striae parallel or only very slightly radiate, (9) 10–12 in 10 µm with about 20 puncta in 10 µm.

Etymology: The epithet refers to the similarity with G. subtile and the fact that it has been misidentified as such.

Type Locality: Okavango River ca. 40 km west of Maun, Botswana (leg. Schuwerk, October 1997).

Holotype (desigatned here): Slide S1911–T02 Coll. Reichardt, Botanical Museum Berlin (B), represented by Fig. 17.

Isotype: ZU5/26, Hustedt Collection, Bremerhaven (BRM).

In SEM, the external views show C–shaped to semicircular foramina which are lacking at the edge between valve face and mantle. Central raphe fissures inconspicuous, simple endings of the raphe slit. Stigma opening somewhat oblong roundish (Fig. 27). A separated pore field is present at the foot pole and almost entirely restricted to the polar valve mantle (Figs 23, 24). Internal views show alveoli with stubs that form elongate chambers (Figs 28, 29). Central raphe fissures simply bent and recurved ending with a very small pore (Fig. 28). Stigma opening elongate to slit–like (also discernible in LM). Both poles show pseudoseptum–like thickenings of the cell wall (Figs 25, 26). Mantle with rows of one or mostly two rows of poroids (Fig. 30) with small c–shaped foramina externally.

CHOLNOKY (1962a: 77) first reported on much bigger specimens of "*G. subtile*" than known so far; over 80 µm long and about 10 µm broad. He did not name them, because he thought that intermediate forms exist. Later (CHOLNOKY 1966: 26) he gave some more detailed information on "*G. subtile*" from South Africa. Again he mentions the big ones, which represent *G. pseudosubtile* and he states that all other forms belong to *G. subtile* var. *malayense* HUST., hence he ascertained that *G. subtile* (sensu stricto) does not exist in South Africa.

G. pseudosubtile seems to be widespread in the Okavango region in southern Africa. Further findings are known from Transvaal (CHOLNOKY 1962a, see above) and Madagascar (Metzeltin & Lange–Bert. 2002, pl. 70/7)

***Gomphonema sagitta* SCHUMANN (Figs 31–48)**

Soon after its description (SCHUMANN 1862) GRUNOW (in VAN HEURCK 1880) combined this species with *G. subtile*. Since then this taxon has been reported as *G. subtile* var. *sagitta* (SCHUM.) GRUNOW, although MAYER (1928: 101) stated that it is a species of its own. Also LANGE–BERTALOT & METZELTIN (1996: 246) consider the combination as hardly convincing.

Unfortunately type material of *G. sagitta* was not available for this study, but there are findings which

agree with the protologue.

The most striking difference between both species is the shape of the headpole. Contrary to *G. subtile* it forms a small, somewhat rhombus–shaped head with cuneate apex in *G. sagitta*. Other structures visible in LM like raphe fissures, central raphe endings, areae, position of stigma, striae and puncta on valve mantles are very similar. Length 35–62 µm (suspected initial valves about 70 µm), breadth 5.5–7.0 µm, striae 10–12.5 in 10 µm with about 28 puncta in 10 µm (not always clearly distinguishable).

From the protologue, a breadth of only 4.5–5 µm can be calculated. But SCHUMANN'S figure (1862, pl. 9/29C) is about 5.8 µm broad and already MAYER (1928: 102) stated: "Unsere Exemplare sind verhältnismäßig etwas breiter als Sch. angibt" (our specimens are relatively somewhat broader than Sch. writes).

In SEM, the outside views show C– to kidney–shaped foramina positioned in weak depressions just as the round external stigma opening (Figs 45, 47). Central raphe fissures clearly widened (Fig. 47). The mantle bears rows of mostly two poroids clearly separated from the foramina of the transapical striae (Fig. 48). Foramina interrupted at the edge between valve face and mantle forming a narrow zone without structures at the margin of the valve (Figs 44, 45, 47). Inner central raphe fissure unilaterally bent approximately at a right angle ending in little recurved hooks. Alveoli with stubs, internal stigma opening clearly elongated to slit–like (Fig. 46).

G. sagitta is distributed in the same regions as *G. subtile* and often both taxa are associated. Their very similar habitus (the sum of all discernible characters), except for the very different shape of the headpole, makes their earlier combination in one species understandable. *G. sagitta* is sometimes reported as *G. sagittum*, but "sagitta" is a noun which means arrow.

***Gomphonema cathedrale* LANGE–BERTALOT et E. REICHARDT (Figs 49–59)**

This *Gomphonema* is closely related to *G. sagitta* and distinguished mainly by the lacking inflation of the headpole. The cuneate apex as well as other discernible characters resemble *G. sagitta* to a large extent. Ultrastructural details have been unknown up to now. External views in SEM show similar features, e.g. foramina and stigma opening are positioned in depressions. But the central raphe fissures are not significantly widened and the foramina are more clearly interrupted at the edge between valve face and mantle (Figs 56, 57). The apical pore field is restricted to the polar valve mantle (Fig. 58). There are rows of 2–3 (rarely 4) poroids in the valve mantle, whereas *G. sagitta* bears mostly 2 such poroids. Internal structures are still unknown, but a similar construction as in *G. sagitta* and related species has to be expected.

To our knowledge *G. cathedrale* is so far only known from its type locality (Julma Öllky, Finland). But it occurs in Canada, too (Fig. 55), and most probably also in Lassen National Park, California.

***Gomphonema maclaughlinii* E. REICHARDT (Figs 60–66)**

It was already pointed out in the protologue (REICHARDT 1999: 23) that *G. maclaughlinii* is related to *G. sagitta,* although at first glance it may appear that it belongs to the complex of *G. gracile* sensu auct. It differs from *G. cathedrale* and *G. sagitta* mainly by the narrowly rounded, not cuneate apex which is never inflated or capitate. The stigma is clearly separated from the adjacent stria. Structural details in general agree with *G. sagitta* resp. the group around *G. sagitta* (cf. REICHARDT 1999, pl. 22). Again we find foramina and stigma opening in slight depressions and there are rows of mostly two poroids in the valve mantle. Minor differences can be seen at the endings of the raphe and the internal opening of the stigma, which is only slightly elongated.

G. maclaughlinii was described from Zion National Park, Utah, where it is present in different samples.

***Gomphonema subsagitta* E. REICHARDT sp. nov. (Figs 67–86)**

Description: Cells moderately cuneate in girdle view with rows of 1–3 (mostly 2) clearly visible pores in the valve mantles.

Valves lanceolate, only slightly gomphonemoid–cuneate with small elongate–roundish capitate head poles (in larger specimens) to only weakly protracted head poles (in small specimens). Basal pole narrower and more acutely rounded. Length 28–43 µm, breadth 5–6 µm. Raphe lateral with curved fissures, external and internal central raphe endings distinguishable the latter are wider apart and deflected to the same side. Axial area moderately narrow, central area unilateral formed by a very short stria. Stria on opposite side not or only slightly shortened with a stigma near its end. Striae weakly radiate, here and there also nearly parallel, 10–12 in 10 µm with about 28 areolae in 10 µm.

Etymology: The epithet refers to the resemblance to *G. sagitta* but showing lower valve dimensions and less inflated headpoles.

Type Locality: Manzanita Lake, 1814 m a.s.l., Lassen National Park, California, USA (leg. Reichardt, August, 1990).

Holotype (designated here): Slide S1131–T02 Coll. Reichardt, Botanical Museum Berlin (B), represented by Fig. 70.

Isotype: ZU5/10, Hustedt Collection, Bremerhaven (BRM).

Characters in SEM mainly as in *G. sagitta*, but foramina not situated in depressions (Figs 84–86). Near the head pole the foramina (striae) run over the mantle a little bit like in *G. lateripunctatum* E. REICHARDT et LANGE–BERT. (Fig. 85). Interruption of foramina at the edge between valve face and mantle indistinct (Fig. 86). External central raphe fissures with very small drop–shaped central pores (Figs 84, 86). Internally the stigma opening is only slightly elongated (Figs 81, 82, rather corresponding to *G. maclaughlinii*).

G. subsagitta differs from *G. sagitta* mainly by smaller valves and the shape of the head pole which in larger specimens is elongate–capitate and rounded at the end contrary to the rhomboid and cuneate head in *G. sagitta*. Small valves with only protracted and not inflated head poles are very similar to *G. maclaughlinii* and single valves may not be distinguishable. However, *G. maclaughlinii* never develops capitate head poles. *G. subsagitta* was found in some lakes in Lassen National Park, California and in an old sample from Lake Arrowhead, San Bernandino Co., California (leg. Fleming 1933).

***Gomphonema pantropicum* E. REICHARDT stat. nov., nom. nov. (Figs 87–107)**

Synonym: *Gomphonema subtile* var. *malayense* HUSTEDT, Internationale Revue der gesamten Hydrobiologie und Hydrographie 42, p. 119, figs 258–260, 1942.

HUSTEDT (1937–39: 439) reported *G. subtile* from more than a dozen locations on Sunda Islands, although he noticed that the specimens here were partly larger and show only weakly capitate headpoles, even lacking in small valves. Later (HUSTEDT 1942) he described the specimens occuring on Sunda Islands and the Indomalayan Archipel as *G. subtile* var. *malayense*. CHOLNOKY following HUSTEDT reported corresponding individuals first as *G. subtile* (1954: 126, Fig. 20; 1958: 117, Figs 83–84) later as var. *malayense* (1962b: 323, Fig. 26), but in 1966 (p. 26, pl. 3/63) he stated that all of the many valves observed in the Okavango River may represent *G. subtile* var. *malayense* and that he did not see transitional forms to *G. subtile*. He also stated that the striae of these forms are more coarsely punctate. These observations were confirmed by CHOLNOKY (1970: 29) and in the present studies. Already CHOLNOKY (1970) was of the opinion, that species rank would be more appropriate. Because of *G. malayense* HUST. (1942: 115) a new name is necessary.

The main character of *G. pantropicum* is the shape of the capitate head pole which is very different from *G. subtile*. Compared with *G. subsagitta*, *G. pantropicum* is strongly constricted below the head. (Small) valves with lacking inflations as reported by HUSTEDT (1942) are rather rare in the populations and show narrow and sharply protracted apices (Fig. 94, cf. SIMONSEN 1987, pl. 424/10). In addition, the axial area is somewhat broader, the striae are more coarsely punctate and the valves are consistently broader. Length 34–65 µm, breadth 6–9 (mostly 7–8) µm, striae 8–12 in 10 µm, stria pores 20–26 (mostly around 24) in 10µm. Valves with dense striation (12 in 10µm) were found in cultured material from Luzon, Philippines (Figs 95–99), whereas valves from natural populations in the same region bear in general only 9–10 striae in 10 µm (Fig. 100).

In SEM, ultrastructural details are similar to *G. sagitta* and related taxa, but there are many minor differences: Externally the valve face appears somewhat uneven (visible with strong tilting only), but the foramina and especially the stigma opening are not situated in conspicuous depressions. Central raphe fissures inconspicuous, not significantly widened (Fig. 105). Foramina run continuously over the edge between valve face and mantle or show only slight interruptions (Fig. 106). Internally the deflected central raphe fissures are similar to *G. sagitta*, but somewhat shorter. Likewise the stigma opening is shorter, too (Fig. 104). There are 3–4 (rarely two) rows of small poroides in the mantle (Fig. 107).

G. pantropicum is widely distributed in tropical Africa, India and Southeast Asia, but there are also findings from tropical South America (RUMRICH, LANGE–BERTALOT & RUMRICH 2000, pl. 131/14–19). Hence pantropical distribution has to be supposed. In general it is reported as *G. subtile* or *G. subtile* var. *malayense* (e.g. CHOLNOKY l.c.; HUSTEDT l.c.; METZELTIN & LANGE–BERTALOT 2002, pl. 70/8–9; SARODE & KAMAT 1984, pl. 23/541). However, there exist similar taxa (see discussion below).

DISCUSSION

Diatom biogeography has become an increasingly studied subject and there are important results and discussions in more recent literature (e.g. WILLIAMS & REID 2006; LIU et al. 2013; ABARCA et al. 2014). The taxa described in this paper are a further example for the limited distribution of special diatoms or groups of diatoms respectively. In literature *G. subtile* is described to be a cosmopolitan diatom characterized by a capitate headpole that varies to a high degree. Both of these statements proved to be not true and evolved due to the fact, that separate species have not been differentiated. *G. subtile, G. sagitta, G. cathedrale, G. maclaughlinii* and *G. subsagitta* are closely related and seem to be restricted to holarctic regions. *G. subtile* should be unmistakable due to its characteristic outline which shows little variability. The other species differ chiefly by the shape of the headpole, partly by quantitative characters and minor ultrastructural details (Table 1).

Similar diatoms from tropical regions represent

separate taxa with *G. pantropicum* as principal species. As pointed out above, the structures of the latter and the holarctic species agree largely, indicating, that they may have common roots. But *G. pantropicum* developed many ultrastructural differences. In addition, there exist further more or less similar taxa in tropical waters. Some of these may be a reason for the assumption of HUSTEDT (1937–39: 440) that the shape of the capitate head is very variable. A few examples:

Figs 108–112 resemble *G. pantropicum*, but their headpole is only protracted without exception. It cannot be ruled out, that these forms belong to *G. pantropicum,* but specimens with corresponding length of e.g. Figs 108–110 in populations of *G. pantropicum* always show clearly capitate heads. Fig. 108 is from Lake Bratan, Bali. HUSTEDT (1937–39: 440; 1942: 119) reported "*G. subtile*" from this locality.

Figs 113–116 show a distinct species occurring in the region of the Okavango River, which is differentiated from *G. pantropicum* by consistently smaller valves (width only 4.7–5.0 µm). It was also observed by CHOLNOKY (1966, pl. 3/65), but not distinguished. CHOLNOKY'S (1954: 126) comment on small forms of only 28 µm length and 4.5 µm breadth possibly concern this species, too. Due to its rare occurrence SEM investigations were not possible. Therefore it is not described here.

Figs. 117–120 agree with M. SCHMIDT'S drawing in SCHMIDT et. al (1902) pl. 234/19, classified as "*G. parvulum* KÜTZ." Although they do not belong to *G. parvulum* (not even in a "latissimo" sense), this classification indicates, that they are not related to taxa around *G. subtile/sagitta/pantropicum.* Their kind of striation and other structural details give reason to believe that they belong to the huge cluster of taxa around *G. gracile* sensu auct. *G. subtiliforme* HUST. (1942) is a much more slender diatom and in spite of its name unmistakable compared to forms described in this paper.

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Table 1. Quantitative characters and minor ultrsstructure details of studied members from the genus *Gomphonema*.

	Head pole	Length (µm)	Width (µm)	Striae/10 µm	Areolae/10 µm
G. sagitta	rhombus–shaped, cuneate	35–62 (70)	5.5–7.0	10–12.5	ca. 28
G. cathedrale	not inflated, cuneate	45–70	7.0–10.0	8.10	ca. 20
G. maclaughlinii	not inflated, narrowly rounded	24–62	5.4–8.8	ca. 12	25–30
G. subsagitta	slightly capitate, elongate roundish	28–43	5.6	10.12	ca. 28

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