

Analysis of the type material of *Pinnularia divergentissima* (GRUNOW in VAN HEURCK) CLEVE (Bacillariophyceae)

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Abstract: The analysis of the type material of *Pinnularia divergentissima* (GRUNOW in VAN HEURCK) CLEVE revealed the presence of two distinct *Pinnularia* taxa in the same slide. Comparison with the original drawing of *P. divergentissima* by GRUNOW showed that recent taxonomic treatments of *P. divergentissima* are not in accordance with the original diagnosis. Both species in the type material are morphologically characterized and the correct identity of *P. divergentissima* is established whereas the second taxon is described as *P. pseudodivergentissima* sp. nov. Additionally, the type material of *P. fottii* J.BÍLÝ et MARVAN and *P. martinii* KRASSKE is likewise analysed and both taxa are separated from *P. divergentissima*. Finally, the morphological analysis of a fifth taxon from the sub–Antarctic Region resulted in the description of a new taxon, *P. lindanedbalovae* VAN DE VIJVER et MORAVCOVÁ sp. nov.

Key words: Antarctic Region, landmark analysis, morphology, new species, *Pinnularia divergentissima*, *P. fottii*, *P. martinii*, type material

Introduction

During a survey of the diatom flora influenced by a nesting site of the wandering albatross (*Diomedea exulans* L.) on the subantarctic island Ile de la Possession (Crozet Archipelago, southern Indian Ocean) (MORAVCOVÁ et al. 2010), several large populations of an unusual *Pinnularia* species were observed, showing affinities but likewise also marked differences with *Pinnularia divergentissima* (GRUNOW in VAN HEURCK) CLEVE as shown in KRAMMER (2000). The species was finally identified as *P. divergentissima* and later on also observed on other islands in the southern Indian Ocean such as the Prince Edward Islands, Iles Kerguelen and Heard Island (VAN DE VIJVER et al. 2001, 2002, 2004, 2008).

Pinnularia divergentissima was originally described as *Navicula divergentissima* GRUNOW in CLEVE et MÖLLER (1878, and not 1879 as

erroneously reported several times by various authors) reporting a list of species present in slide 186. However, this record should be considered as a *nomen nudum* since the name was published without a valid description nor diagnosis (ICBN art. 32; McNEILL et al. 2006). Two years later, in VAN HEURCK (1880), GRUNOW published a drawing of *N. divergentissima*, unfortunately without citing the specimen. CLEVE (1895, p. 77) subsequently transferred the species to the genus *Pinnularia*. KRAMMER (1992, 2000) reinvestigated the original material of *P. divergentissima*. KRAMMER (1992) also designated a lectotype for *P. divergentissima*. However, according to art. 9.1 of the International Code of Botanical Nomenclature (McNEILL et al. 2006), the drawing of Grunow presented on plate 6, fig. 32 in VAN HEURCK (1880) could be considered as the holotype (“If the author only uses one element, that one must be accepted as the holotype.”). But since Grunow had used the

new name prior to his valid publication linked to a slide deposited at Vienna (W), we use this as a strong argument for this slide being part of the original material. Therefore, Krammer's lectotypification of 1992 can be accepted, but not his taxonomic treatment of *P. divergentissima* because it does not "remain attached to that part which corresponds most nearly with the original description or diagnosis" (see McNeill et al. 2006, art. 9.12). Additionally, several other *Pinnularia* species (*P. fottii* J. BÍLÝ et MARVAN and *P. martinii* KRASSKE) were included within the concept of *P. divergentissima* by KRAMMER (1992) as synonyms.

In general, *P. divergentissima* is characterized in having relatively small valve dimensions (length less than 40 µm), the absence of external longitudinal lines on the striae and the presence of a distinct shift in stria orientation about halfway the central area and the valve apex. A similar shift can be observed in only a few other species such as *P. acoricola* HUST. (HUSTEDT 1935; LUÍS et al. 2012), *P. similiformis* KRAMMER (KRAMMER 1992), and *P. carteri* KRAMMER (KRAMMER 2000) but is absent in the majority of *Pinnularia* species.

When comparing *P. divergentissima* specimens in the type slide (slide 186 from the Collection of Cleve & Möller in the Grunow Collection in the Naturhistorisches Museum, Vienna, Austria, W), with the original drawing made by Grunow (kept at the National Botanic Garden of Belgium), it was clear that there were actually two species present in the slide showing comparable morphological features. Moreover, comparing the original drawing and the specimens related to this drawing from the Cleve & Möller slide, with the illustrations shown by KRAMMER (1992, 2000) taken from slide 186 from the Collection of Cleve & Möller (present at W), it was clear that *P. divergentissima* as Grunow described it and the specimens identified by KRAMMER (2000) as *P. divergentissima* do not belong to the same species. KRAMMER (1992) overlooked the admixture of two taxa and illustrated a single valve not corresponding to Grunow's original drawing. Therefore, the illustrations shown by KRAMMER (1992, 2000) belong to an undescribed species whereas only the specimens resembling Grunow's original drawing in KRAMMER (2000, plate 11, fig. 1) should be considered as the real *P. divergentissima*.

The present paper discusses the results of a comparison between several species resembling

P. divergentissima based on detail morphological observations and classical measurements of the type material. A reanalysis of the Cleve & Möller 186 slide resulted in the separation of the real *P. divergentissima* specimens from the second species present in the slide, describing the latter as a new species: *Pinnularia pseudodivergentissima* sp. nov. In addition to the analysis of the material of *P. divergentissima*, the type material of *P. fottii* and *P. martinii*, considered by KRAMMER (1992, 2000) as synonyms of *P. divergentissima* and some of its varieties, are likewise investigated. For a precise illustration of the quantitative morphological differences between individual taxa, we used the landmark-based geometric morphometrics of valve shapes (POTAPOVA & HAMILTON 2007; VESELÁ et al. 2009). With the geometric-morphometric registration of valve shapes, we were also able to identify the position of the original Grunow's type drawing of *P. divergentissima* in the morphospace so that the most similar specimens from the Cleve & Möller 186 slide could be determined. Finally, the sub-Antarctic species is described as a new species *Pinnularia lindanedbalovae* VAN DE VIJVER et MORAVCOVÁ sp. nov.

Material and Methods

Sample preparation. For this study, the type material of several small *Pinnularia* species belonging to the complex of *P. divergentissima* was investigated:

- *Navicula divergentissima* GRUNOW in CLEVE et MÖLLER 1879, slide 186, Fogstuen, Dovre, Norway (collected by Mr. O. Nordstedt) in the Grunow Collection (Lectotype slide present in the Naturhistorisches Museum, Vienna, Austria, W) and the Van Heurck Collection in the National Botanic Garden of Belgium (Belgium), BR (slide coll. n° II-7-B2)
- *Pinnularia fottii* J. BÍLÝ et MARVAN 1959, slide 575B IOK, Věčný déšť, Vysoké Tatry, Slovakia in the herbarium of the Botanical Institute of the Masaryk University, Brno (Czech Republic)
- *Pinnularia martinii* KRASSKE 1939, slide 4165 S. Vincente, Brandungshöhlen von Ramuncho, Krasske Collection, Kassel (Germany)

Additional material used in this study was collected on the sub-Antarctic island Ile de la Possession (Crozet Archipelago, southern Indian Ocean). Samples were taken from soils at the Champs des Albatros at Pointe Basse during the austral summer of 2004–2005. Details about the samples and the sampling location can be found in VAN DE VIJVER et al. (2002) and MORAVCOVÁ et

al. (2010). All soil samples were stored in 25 ml PVC bottles and fixed immediately with 3% formaldehyde. Diatom slides were prepared following the method described in VAN DER WERFF (1955). A small subsample was treated with H_2O_2 and $KMnO_4$ in order to remove all organic material. To speed up the reaction, samples were heated on a boiling plate for a short period. Following centrifugation, the resulting clean material was diluted with distilled water to avoid excessive concentrations of diatom valves that might obstruct the counting. Cleaned diatom valves were mounted in Naphrax®. Light microscopical observations were performed using an Olympus BX51 microscope equipped with Differential Interference Contrast optics (Nomarski®). Samples and slides are stored at the Department of Bryophyta and Thallophyta at the National Botanic Garden of Belgium in Meise. For scanning electron microscopy (SEM), part of the suspension was filtered through polycarbonate membrane filters with a pore diameter of 3 μm , pieces of which were fixed on aluminium stubs after air-drying. The stubs were sputter-coated with 50 nm of gold and studied in a JEOL-5800LV at 20 kV. Morphological terminology follows HENDEY (1964), ROUND et al. (1990) and KRAMMER (2000).

Geometric morphometrics. In total, 42 landmarks were delimited on valvar views of 335 *Pinnularia* frustules (Fig. 1) using TpsDig, ver. 2.16. (ROHLF 2010a). Landmarks were mostly placed along the valve outline, but they were also located in the central area, and at the raphe and stria endings. Of these 42 landmarks, there were 28 landmarks located in fixed

positions and 14 landmarks were allowed to slide along the abscissa connecting adjacent points (BOOKSTEIN 1991) (Fig. 1). As the apical ends of the valves could not be unambiguously identified, all the valves were symmetrised along the apical axis. Consequently, the asymmetric component of variation along the apical axis was eliminated from data and subsequent analyses were based entirely on symmetric configurations (KLINGENBERG et al. 2002). The general Procrustes superimposition (GPA) and the thin-plate spline analysis based on tangent space projections were conducted (BOOKSTEIN 1991; ZELDITCH et al. 2004).

The principal component analyses (PCA) of partial warps and the uniform component were conducted using the entire set of analysed objects in TpsRelw, ver 1.49. (ROHLF 2010b). The scores of the objects on all the non-zero PC axes were used for further analyses. The canonical variates analysis (CVA) of these data was conducted to evaluate discrimination among individual groups in PAST, ver. 2.12. (HAMMER et al. 2001). As there were only 9 objects in the smallest group, we only used the scores on the first 8 PC axes (spanning 97.3% of the total variation) for this analysis. The group assignments of all the valves were cross-validated by a leave-one-out procedure. Significance of two-group comparisons was evaluated by a set of permutational MANOVA's (ANDERSON 2001) in PAST, ver. 2.12. The Euclidean distance measure was used and the significance values were based on 9999 permutations of the original sets.

Results

Morphological observations

Pinnularia divergentissima (GRUNOW in VAN HEURCK) CLEVE 1895, p. 77, Figs 2–12

Basionym: *Navicula divergentissima* GRUNOW in VAN HEURCK 1880, plate 6, fig. 32.

Synonym: *Navicula divergentissima* GRUNOW in CLEVE & MÖLLER 1878, slide 186 (*nomen nudum*), non *Pinnularia divergentissima* (GRUNOW) CLEVE sensu KRAMMER 1992.

[first-step] Lectotype (designated by KRAMMER 1992: p. 62): coll. Cleve et Möller 1879, slide 186, Grunow Collection in the Naturhistorisches Museum, Vienna, Austria (W).

[second-step] Lectotype (designated here): valve on slide 186, coll. CLEVE & MÖLLER 1879, Grunow Collection in the Naturhistorisches Museum, Vienna, Austria (W), supporting Grunow's published drawing (GRUNOW in VAN HEURCK 1880: pl. 6, fig. 32) illustrated here as Fig. 4.

Locality of the lectotype: Fogstuen, Dovre, Norway (coll. Mr. O. Nordstedt).



Fig. 1. *Pinnularia divergentissima*. Positions of the landmark with fixed landmarks represented by empty circles and semilandmarks by filled circles.

Morphological observations (based on the taxon represented by the [second-step] lectotype): Valves strictly lanceolate with weakly convex margins, tapering towards the apices. Ends obtusely rounded, rostrate-capitate. Valve length 27–33 μm , width (middle) 4.5–5.5 μm , length–width ratio 5.4–6.6 ($n=9$). Axial area very narrow, linear, almost not widening towards the central area. Central area forming a wedge-shaped fascia, lacking shortened striae, never protruding rhombically into the axial area. Raphe branches straight, filiform. Proximal raphe endings very weakly deflected, extending well into the central area with expanded central raphe pores. Terminal raphe fissures shaped like question marks. Transapical striae very strongly radiate near the valve centre, extremely divergent with a sudden change in direction over a halfway distance from the valve centre to the ends, where the striae become strongly convergent with a blunt angle formed between the striae groups where they meet, 12–13/10 μm .

Taxonomical remarks: Since Grunow's original description includes only one single drawing, most likely based on the slide 186 from the Cleve & Möller Collection at W, the [first-step] lectotypification is accepted (according to art. 9.17 of the McNeill et al. 2006). Because of the admixture of two species we have decided to lectotypify the Grunow's species with a second-step lectotype in accordance with McNeill et al. (2006): art. 9.15. CLEVE & MÖLLER (1878) indicated that Grunow examined slide 186 and in the species list accompanying the slide, Grunow described *N. divergentissima*, unfortunately as

a *nomen nudum*. The specimens observed in slide 186 correspond entirely with the drawing Grunow published in VAN HEURCK (1880) but differ from the specimens showed by KRAMMER (1992, 2000) to illustrate *P. divergentissima*. The latter differ clearly in having more rostrate protracted apices, a different central area and less radiate striae (Table 1). For more morphological details on these specimens, see below under *P. pseudodivergentissima*.

***Pinnularia pseudodivergentissima* sp. nov.,**

Figs 13–21

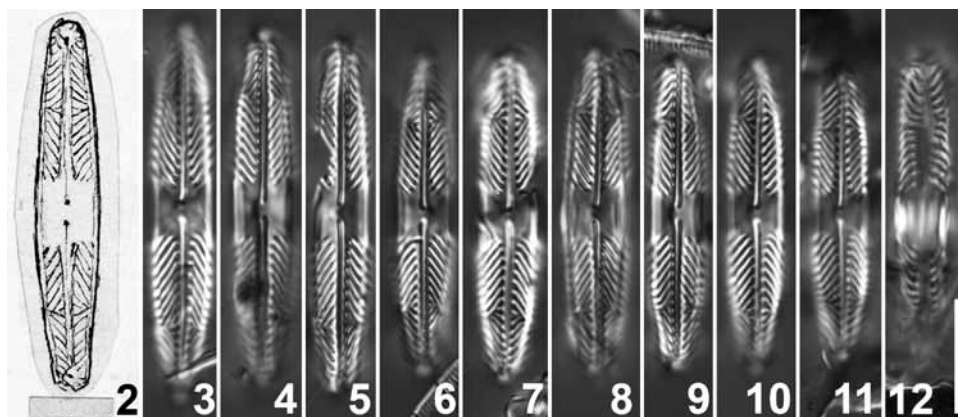
Synonym: *Pinnularia divergentissima* (GRUNOW) CLEVE sensu KRAMMER 1992, pl. 12, fig. 1.

Diagnosis: *Valvae lineares–lanceolatae marginibus parallelis ad leviter convexis, apicibus abrupte protractis, rostratis, late rotundatis. Longitudo 22–30 μm , latitudo 4.5–6.0 μm . Area axialis linearis, recta, graduatim dilatans in aream centralem. Area centralis formans fasciam latam, aliquando asymmetricam. Raphe recta, filiformis terminationibus proximalibus leviter deflexis, extensis in aream centralem. Striae transapicales fortiter radiatae in media parte valvae, magnopere divergentes, valde convergentes in apices, 13–17 in 10 μm . Lineae speciosae longitudinales nullae.*

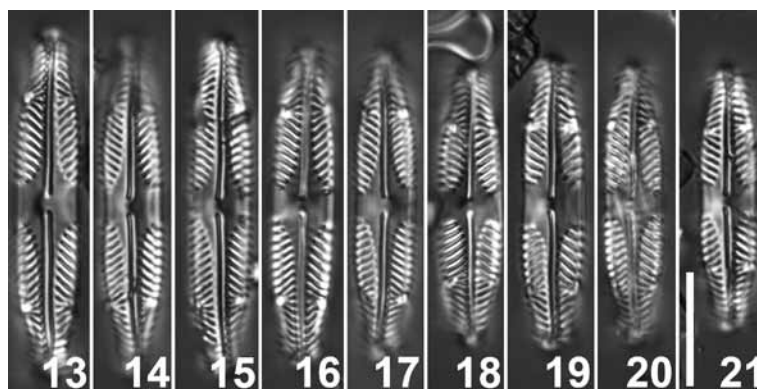
Holotype: coll. Cleve & Möller, slide 186 present in the Van Heurck Collection (National Botanic Garden, slide II–7–B2), the valve representing the holotype is illustrated as Fig. 13.

Type locality: Fogstuen, Dovre, Norway

Etymology: the specific epithet refers to the close resemblance with *Pinnularia divergentissima* s.s. as described by GRUNOW in VAN HEURCK 1880.



Figs 2–12. *Pinnularia divergentissima*: (2) original drawing by GRUNOW in VAN HEURCK (1880, plate 6, fig. 32), LM; (3–11) valve views; (12) girdle view. CLEVE & MÖLLER 1879, slide 186 (coll. n° II–7–B2), Fogstuen, Dovre, Norway in the Van Heurck Collection in the National Botanic Garden of Belgium (Belgium) (collected by Mr. O. Nordstedt). Scale bar 10 μm .



Figs 13–21. *Pinnularia pseudodivergentissima*. LM. Valve views. CLEVE & MÖLLER 1879, slide 186 (coll. n° II–7–B2), Fogstuen, Dovre, Norway in the Van Heurck Collection in the National Botanic Garden of Belgium (Belgium) (collected by Mr. O. Nordstedt). Scale bar 10 μ m.

Morphological observations: Valves linear–lanceolate with straight, parallel sometimes weakly convex margins and abruptly protracted, rostrate, broadly rounded apices. Valve length 22–30 μ m, width (middle) 4.5–6.0 μ m, length–width ratio 4.8–6.0 (n=14). Axial area linear, straight, gradually widening towards the central area. Central area forming a broad, occasionally asymmetrical fascia, lacking any shortened striae. Due to the shortening of the transapical striae towards the central area, the latter is protruding rhombically into the axial area. Raphe branches straight or weakly undulating, filiform. Central raphe endings very weakly deflected, extending well into the central area with small, slightly expanded pores. Terminal raphe fissures shaped like question marks. Transapical striae strongly radiate towards the valve centre, extremely divergent with a sudden change in direction over halfway distance from the valve centre to the ends where striae become strongly convergent with an acute angle formed between the striae groups where they meet, 13–17/10 μ m. Longitudinal lines absent.

Taxonomical remarks: There are several important morphological differences between *P. divergentissima* and *P. pseudodivergentissima* (Table 1). *Pinnularia divergentissima* has more convex valve margins resulting in a lanceolate valve outline with rostrate–capitate apices (Figs 3–12) whereas *P. pseudodivergentissima* has narrowly lanceolate valves with mostly parallel to slightly convex margins and clearly protracted rostrate apices (Figs 13–21). The main difference however is formed by the striation pattern. *P. divergentissima* has very strongly radiate striae

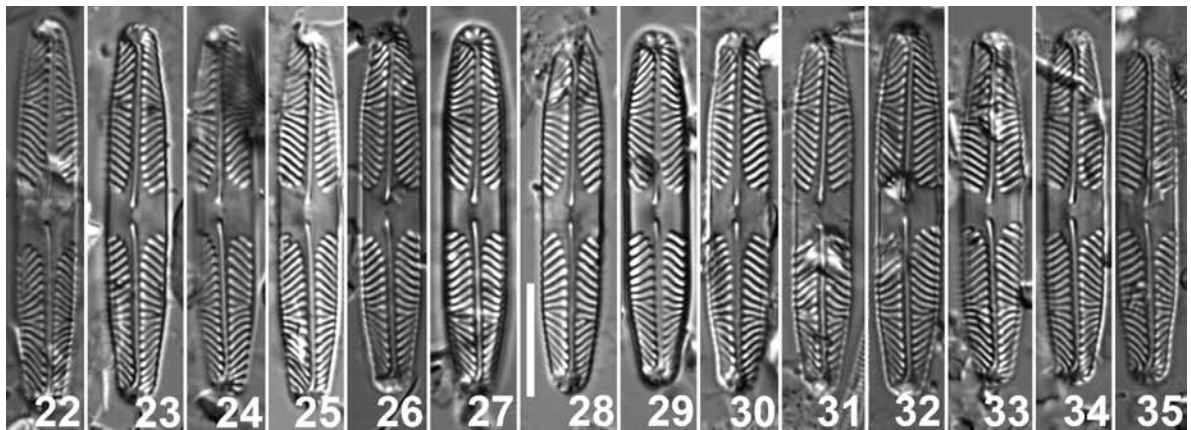
near the central area, rarely shortened reaching therefore almost always to the axial area. On the contrary, *P. pseudodivergentissima* shows radiate striae near the central area, gradually shortening towards the fascia showing a rhombical central area protruding into the axial area. *Pinnularia divergentissima* shows a very obtuse angle between the radiate striae and the convergent striae whereas in *P. pseudodivergentissima*, this angle is more acute. Finally, *P. divergentissima* has a lower stria density with only 12–13 striae in 10 μ m whereas *P. pseudodivergentissima* has 13–17 striae in 10 μ m. Based on these morphological differences, a separation of both species is justified.

***Pinnularia fottii* J.BÍLÝ et MARVAN 1959,**

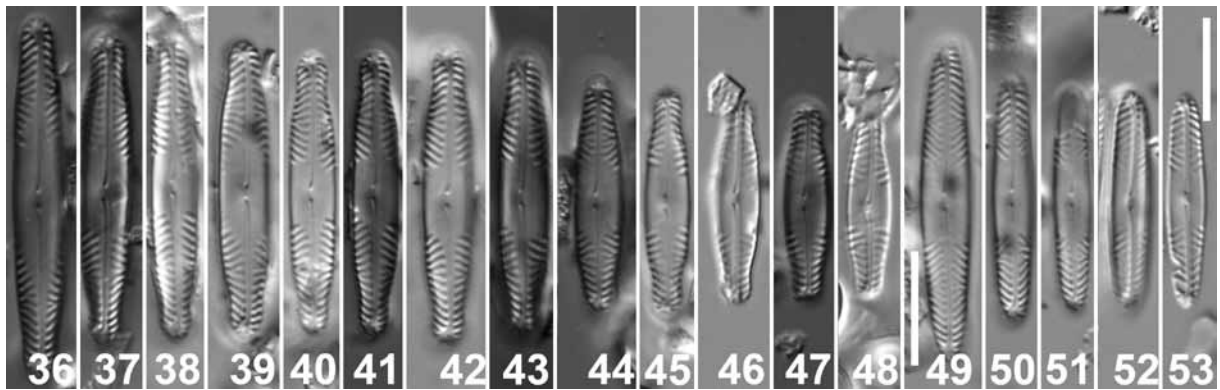
Figs 22–35

Type locality: slide 575B IOK, Věčný déšť, Vysoké Tatry, Slovakia

Morphological observations: Valves linear to narrowly lanceolate with parallel margins and broadly rounded, rostrate apices. Valve length 28–35.5 μ m, width 4.5–6.0 μ m, length–width ratio 4.6–7.2 (n=60). Axial area narrow, linear, only slightly widening towards the central area. Central area forming a large, wedge-shaped fascia. Striae bordering the axial area near the fascia clearly shortened. Raphe branches straight to weakly curved, filiform with deflected elongated pore-like proximal endings and “question marks”-shaped terminal fissures. Transapical striae strongly radiate near the central area, extremely divergent with a sudden change in direction over halfway from the valve centre to the ends where striae become strongly convergent with a rather acute angle formed between the striae groups where



Figs 22–35. *Pinnularia fottii*. LM. Valve views. Slide 575B IOK, Věčný déšť, Vysoké Tatry, Slovakia in the herbarium of the Botanical Institute of the Masaryk University, Brno (Czech Republic). Scale bar 10 μ m.



Figs 36–48. *Pinnularia martinii*. LM. Valve views. Figs 49–53. *Pinnularia martinii* f. *elliptica*. LM. Valve views. Slide 4165 S. Vincente, Brandungshöhlen von Ramuncho, Krasske Collection, Kassel (Germany). Scale bar 10 μ m.

they meet, 11–15 in 10 μ m.

Taxonomical remarks: *Pinnularia fottii* was considered by KRAMMER (1992, 2000) to be a younger synonym of *P. divergentissima*. Although belonging to the complex of *P. divergentissima* and showing similar valve dimensions (Table 1), the morphological comparison showed that the species differs morphologically from both *P. divergentissima* and *P. pseudodivergentissima*, as observed in the Cleve & Möller 186–slide. The former has more strongly radiate striae shifting with an obtuse angle to the quite convergent striae near the apices. The axial area in *P. pseudodivergentissima* is widening more distinctly towards the central area forming a much larger rhombically widened central area than in *P. fottii* where the axial area widens only close to the central area. Moreover, the valve outline of *P. fottii* shows more parallel margins with broadly rostrate, not suddenly offset rounded

apices whereas *P. pseudodivergentissima* has more clearly offset rostrate–capitate apices and *P. divergentissima* shows a more lanceolate outline with more capitate–rostrate apices.

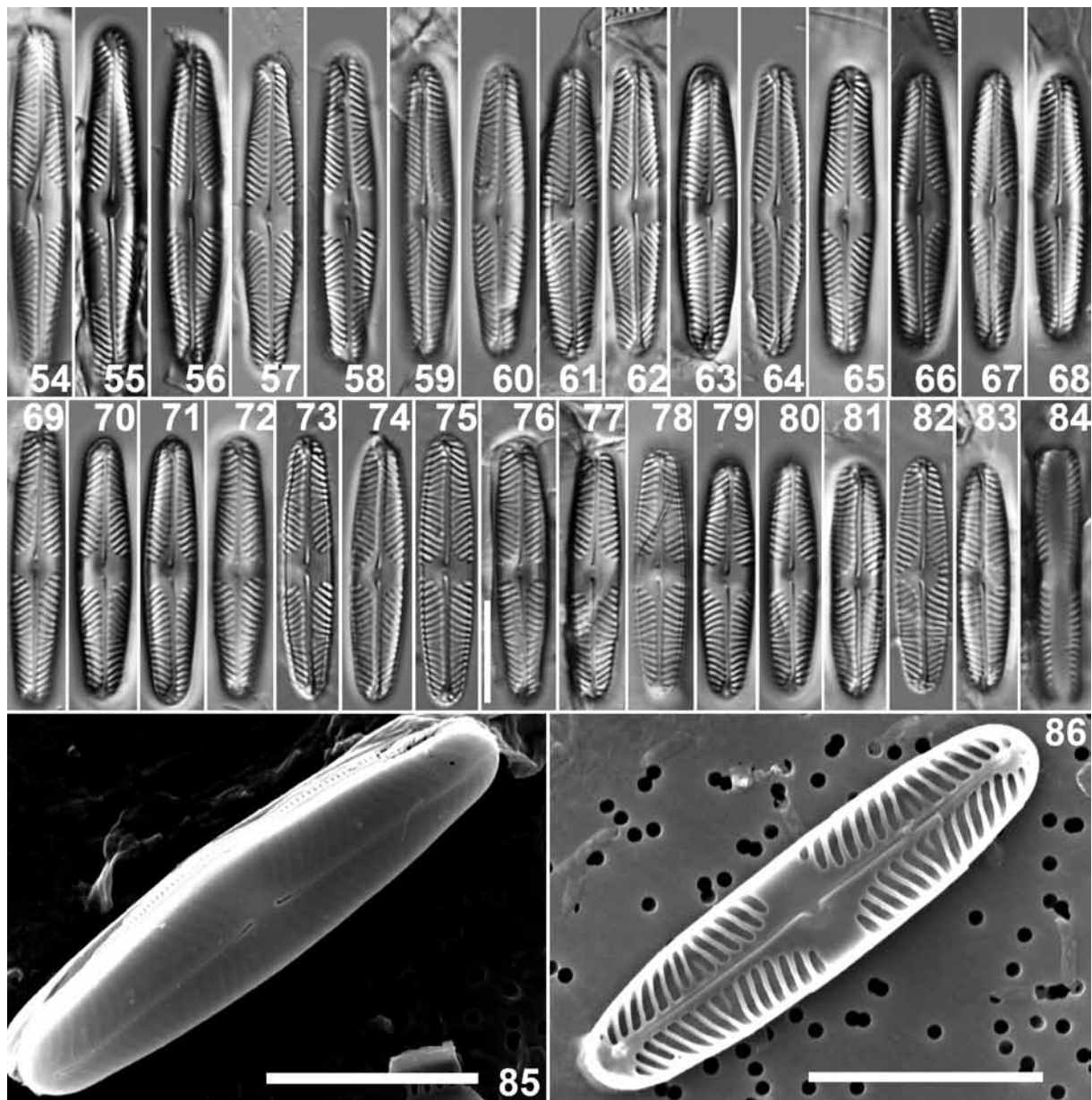
Two other *Pinnularia* species, *P. grudeensis* FOGED and *P. krammeri* METZELTIN in LANGE–BERTALOT et METZELTIN, described from Norway (FOGED 1970) and Finland (LANGE–BERTALOT & METZELTIN 1996) show a similar valve outline to *P. fottii* but can be distinguished based on their valve dimensions, having wider valves (6.7–7.8 μ m in *P. krammeri* and 9–10 μ m for *P. grudeensis*).

***Pinnularia martinii* KRASSKE 1939, Figs 36–48 (49–53?)**

Lectotype (designated by Thomas Lauser in Krammer 1992, p. 63): preparation D III 3, Krasske Collection, Kassel (Germany).

Type locality: slide 4165 S. Vincente, Brandungshöhlen von Ramuncho (Chile)

Synonyms: *Pinnularia divergentissima* var. *martinii* KRASSKE sensu KRAMMER (1992), *P. divergentissima*



Figs 54–86. *Pinnularia lindanedbalovae*: (54–83) LM Valve views; (84) LM. girdle view; (85) SEM external view; (86) SEM internal view. Scale bar 10 μ m.

var. *subrostrata* CLEVE sensu KRAMMER (2000).

Morphological observations: Valves narrowly elliptical to narrowly lanceolate with convex margins and protracted, rostrate–capitate to even capitate apices. Valve length 16.5–32.0 μ m, width 3.5–6.0 μ m, length–width ratio 4.6–7.2. Axial area narrow, gradually widening towards the central area. Central area forming a large rectangular to wedge-shaped fascia due to irregular shortening of striae delimiting the central area. Raphe branches weakly curved, filiform with slightly deflected, expanded, pore-like proximal endings and “question marks”-shaped terminal fissures.

Transapical striae strongly radiate near the valve centre, extremely divergent with a sudden shift in direction halfway between the valve centre and the apices where striae become strongly convergent with an acute angle formed between the striae groups where they meet, 11–16 in 10 μ m.

Taxonomical remarks: KRAMMER (1992) stated that *P. martinii* should be combined with *P. divergentissima* (sensu KRAMMER) as a variety and proposed the new combination *P. divergentissima* var. *martinii*, although a formal justification for this new combination was never presented and LANGE–BERTALOT et al. (1996) discussed

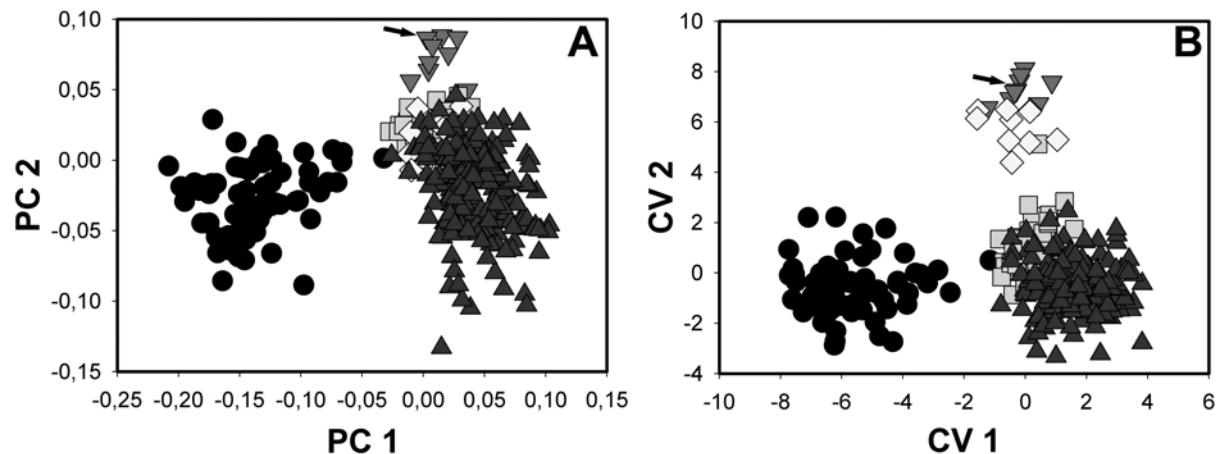


Fig. 87. Ordination plots representing first two axes of PCA (A), and first two axes of CVA (B). The arrows indicate position of the GRUNOW's original drawing (GRUNOW in VAN HEURCK 1880, plate 6, fig. 32) in the ordination spaces. Black circles: *P. martinii*; gray triangles: *P. lindanedbalovae*; light gray squares: *P. fottii*; white diamonds: *P. pseudodivergentissima*; dark gray inverse triangles: *P. divergentissima*.

Krammer's taxonomic view as unresolved with respect to biogeographical data. In 2000, KRAMMER considered *P. divergentissima* var. *martinii* as a younger synonym of *P. divergentissima* var. *subrostrata* CLEVE 1895 [and not CLEVE–EULER 1898 as written in KRAMMER (2000)]. KULIKOVSKIY et al. (2010) validated the (invalid) raise to species level of *P. subrostrata* (CLEVE) CLEVE–EULER proposed by CLEVE–EULER in 1955.

However, based on the analysis of the type material, KRAMMER's statement on the synonymy of both taxa should be contradicted. The central area in *P. martinii* forms a larger fascia with the proximal raphe endings extending much farther beyond the striae delimiting the fascia, contrary to *P. divergentissima* var. *subrostrata* that has only a small fascia, with the proximal raphe endings extending not far beyond the delimiting central striae.

In the same slide, KRASSKE (1939) separated the specimens lacking any protracted apices as *P. martinii* f. *elliptica* (Figs 49–53). Most of these *elliptica*-forms are smaller than 20 µm, although some larger valves (up to 28 µm) were found, overlapping with the smaller range of the rostrate-capitate *P. martinii*. Therefore, valve outline seems to be the only difference with *P. martinii*. Whether these forms should thus be considered as a separate species, a form of *P. martinii* or a synonym of *P. divergentissima* var. *ardnamurchan* KRAMMER is still unclear. The latter was described by KRAMMER in 2000 for all *divergentissima*-like specimens lacking rostrate or capitate apices. KRAMMER (2000) indicated that *P. martinii* f.

elliptica is similar to this new variety.

***Pinnularia lindanedbalovae* VAN DE VIJVER et MORAVCOVÁ sp. nov., Figs 54–86**

Diagnosis: *Valvae anguste lanceolatae marginibus leviter convexis, apicibusque protractis, subcapitatis ad subrostratis, obtuse rotundatis. Longitudo 18–42 µm, latitudo 4–6 µm. Area axialis linearis, angusta, leviter dilatans in aream centralem. Area centralis formans fasciam latam, aliquando asymmetricam. In speciminibus minoribus, fascia carens. Raphe leviter curvata ad leviter undulata, filiformis terminationibus proximalibus expansis, extensis in aream centralem. Striae transapicales distincte radiatae in media parte valvae, divergentes, valde convergentes in apices, 13–18 in 10 µm. Lineae speciosae longitudinales nullae.*

Holotype: BR–4240 (National Botanic Garden, Meise, Belgium), the valve representing the holotype is illustrated as Fig. 56.

Isotypes: PLP–188 (University of Antwerp, Belgium), BRM–ZUH8/50 (Hustedt Collection, Bremerhaven, Germany)

Type locality: Champs des Albatros, sample N3–10, Ile de la Possession, Crozet Archipelago, southern Indian Ocean (coll. B. Van de Vijver, coll. date: 12/01/2005)

Etymology: The species is named after our colleague Dr. Linda Nedbalová (Charles University in Prague, Czech Republic).

Morphological observations: Valves narrowly lanceolate with weakly convex margins. Smaller specimens with more elliptic-lanceolate outline and clearly convex margins (Figs 81–83). Valve

apices protracted, subcapitate to subrostrate, obtusely rounded. Smaller specimens sometimes with broadly rounded, non protracted apices (Figs 81–83). Valve length 18–42 μm , valve width 4–6 μm , length–width ratio 3.4–7.0. Axial area narrow, linear, only near the central area clearly widened. Central area forming a broad, sometimes asymmetrical fascia. Smaller specimens sometimes lacking a fascia due to the presence of gradually shortened striae. Raphe branches weakly curved to even slightly undulated, filiform with enlarged, elongated drop-like proximal raphe endings, extending into the central area. Distal raphe fissures “question mark”-shaped. Transapical striae distinctly radiate near the valve centre, divergent with a sudden change in direction over halfway between the valve centre and valve apices where striae become strongly convergent with an almost straight angle formed between the striae groups where they meet, 13–18/10 μm . Striae composed of alveoli with 3–4 series of small rounded pores (Fig 85). Internally, proximal raphe endings unilaterally hooked (Fig 86).

Taxonomical remarks: *Pinnularia lindanedbalovae* clearly belongs to the complex of species around *P. divergentissima* based on the presence of the clear shift in stria direction. In several papers dealing with the non-marine diatom flora of the islands, the species was identified as *P. divergentissima* (VAN DE VIJVER & BEYENS 1999; VAN DE VIJVER et al. 2001, 2002, 2004, 2008). However, both species differ in several ways (Table 1). Smaller valves of *P. lindanedbalovae* often lack a stauros with gradually shortened striae bordering the central area whereas this was never observed in *P. divergentissima*. Moreover, the striae orientation in *P. divergentissima* is much more radiate than in *P. lindanedbalovae*. The valve outline of *P. lindanedbalovae* usually shows a clear constriction before the valve apices, which was never observed in *P. divergentissima*. The axial area in *P. pseudodivergentissima* widens more clearly towards the central area whereas in *P. lindanedbalovae*, this widening is only present close to the central area. The absence of a fascia was never observed in *P. pseudodivergentissima*. *Pinnularia fottii* has usually parallel margins lacking a clear constriction before the apices. Usually, the valve margins are only near the apices clearly tapering towards the bluntly rounded apices whereas in *P. lindanedbalovae*,

the apices normally widen again slightly. A broad fascia was always observed in *P. fottii* contrary to *P. lindanedbalovae*, that lacks a fascia in a large part of its range.

Ecology and distribution: *Pinnularia lindanedbalovae* was observed (but always reported as *P. divergentissima*) on several islands in the southern Indian Ocean: Prince Edward Islands (VAN DE VIJVER et al. 2008), Crozet Archipelago (VAN DE VIJVER et al. 2002), Iles Kerguelen (VAN DE VIJVER et al. 2001) and Heard Island (VAN DE VIJVER et al. 2004). On Ile Amsterdam, the species was observed in small numbers (VAN DE VIJVER et al. 2012). Whether the species is also present in the southern Atlantic Ocean remains unclear due to confusion with other *Pinnularia* taxa.

The type population was observed in the disturbed very wet soil near an occupied albatross nest characterized by an acid pH (5.7), a high specific conductance value ($\pm 1100 \mu\text{S.cm}^{-1}$) and high nutrient values (VINCKE et al. 2007; MORAVCOVÁ et al. 2010). On Ile de la Possession (Crozet Archipelago), the species was in general mostly found in wet to very wet (60–85% of relative moisture) and acid (pH < 6) soils with higher specific conductance values ($>600 \mu\text{S.cm}^{-1}$) while in mosses and aquatic samples, the species was only rarely observed (VAN DE VIJVER et al. 2002). On the other islands, smaller populations were found usually in terrestrial mosses impacted by sea-spray or biotic influences.

Geometric morphometrics

The ordination plot representing the first and second PC axes spanned 79.3% of the total variation in the morphometric data (Fig. 87A). The first axis (57.4% of the variation) clearly separated *P. martinii* from the other taxa. Conversely, the second axis (21.9%) illustrated the differences between *P. divergentissima* (including Grunow's type drawing) and all the other taxa. The first two axes of the highly significant CVA (Wilk's $\lambda = 0.018$, $p < 0.0001$) clearly separated *P. martinii* and the pair *P. divergentissima*/*P. pseudodivergentissima* from the other taxa (Fig. 87B). However, the mean shape differences were highly significant among all the species pairs. The Bonferroni-corrected p -values were 0.001 in all the two-group permutational MANOVA comparisons. The cross-validation analyses of the canonical discriminant function revealed that 95.2% of the valves were correctly classified

Table 1. Table of comparison of the species belonging to the *Pinnularia divergentissima* complex.

	<i>divergentissima</i>	<i>pseudo-divergentissima</i>	<i>martinii</i>	<i>fottii</i>	<i>linda-nedbalovae</i>
	VAN HEURCK (1880)	this study	KRASSKE (1939)	BÍLÝ & MARVAN (1959)	this study
Length (µm)	27–33	22–30	8–30	28–35.5	18–35(43)
Width (µm)	4.5–5.5	4.5–6.0	2.5–5.0	4.5–6.0	4.0–6.7
L/W ratio	5.4–6.6	4.8–6.0	4.7	4.6–7.2	3.4–7.1
number of striae (in 10 µm)	12–13	13–17	12–13	11–15	13–18
outline	lanceolate	linear–lanceolate	elliptical, linear to lanceolate	linear to narrowly lanceolate	lanceolate
apices	not offset, rounded	rostrate	broadly rounded to capitate	broadly rounded, rostrate	broadly rounded, rostrate to subcapitate in large valves
shift in striae	clearly present	clearly present	clearly present	clearly present	present, absent in smaller valves
transition central–axial area	narrow, very abruptly, no deltoid–shape	broad deltoid–shaped	narrow deltoid–shaped	narrow deltoid–shaped	narrow deltoid–shaped
ecology	acid, oligotrophic, electrolyte–poor*	acid, oligotrophic, electrolyte–poor*	soils in coastal areas close to sea spray zone	–	soils, aerophilic, coastal areas
	*derived from dominating diatom composition				

into their species groups. The highest error rates concerned the pair of *P. lindanedbalovae* and *P. fottii*. In total, 5.6% of valves that were *a priori* assigned as *P. lindanedbalovae* were classified to the *P. fottii* group, and, conversely, 5.1% of valves *a priori* assigned as *P. fottii* were classified to *P. lindanedbalovae* (Table 2).

Discussion

Geometric morphometrics illustrated that differences in valve shape among all the taxa were significant. Grunow's type drawing was firmly nested within other frustules from the Cleve & Möller 186 slide that were assigned to the true *P. divergentissima* s.s. on the basis of microscopic

analysis. Conversely, frustules assigned as *P. pseudodivergentissima* were unambiguously separated from *P. divergentissima* by the cross-validation analyses. Geometric morphometric comparison of original type drawings or specimens from type slides with modern populations has already been used in diatom taxonomy (FRÁNKOVÁ et al. 2009). This study further illustrated that it can be highly useful in supporting (or disproving) the qualitative microscopic analyses and subsequent taxonomic conclusions. We should note that our analyses only concerned data from valves symmetrised along the apical axis. Neither the obvious left–right asymmetry of valves (indicated e.g. by central raphe poles), nor possible vertical asymmetry of valves were taken into account. The material analysed by geometric morphometrics in

Table 1. Cont.

	<i>acoricola</i>	<i>krammeri</i>	<i>obscura</i>	<i>diversa</i>	<i>osoresanensis</i>	<i>grudeensis</i>
	HUSTEDT (1935)	LANGE–BERTALOT & METZELTIN (1996)	KRASSKE (1932)	ØSTRUP (1901)	FUKUSHIMA et al. (2002)	FOGED (1970)
Length (µm)	8–35	26–45	12–34	23–39	7–29	35–40
Width (µm)	3–6	6.7–7.8	3.0–5.4	5–6	4.0–6.0	9–10
L/W ratio	2.4–6.5	3.7–5.8	3.7–6.0	5.8–7.0	3.0–5.1	3.7
number of striae (in 10 µm)	13–16	11–13	10–13	10–12	15–19	12
outline	elliptic–lanceolate to lanceolate, semirhomboidal	linear to linear–elliptical	linear–elliptical	rhombic–lanceolate	linear to lanceolate	almost linear
apices	small cuneiform, rounded to cuneate	broadly wedge-shaped, rounded	weakly rostrate or cuneiform, not offset and broadly rounded	not offset, obtusely cuneate or weakly capitate	cuneiform to rounded	broadly rounded
shift in striae	clearly present	clearly present	weakly present	clearly present	present to almost absent in smaller valves	clearly present
transition central–axial area	broad deltoid-shaped	narrow deltoid-shaped	narrow deltoid-shaped	narrow deltoid-shaped	broad deltoid-shaped	broad deltoid-shaped
ecology	oligosaprobic, electrolyte–poor waters	oligotrophic, electrolyte–poor waters	aerophillic, moist mosses, wet rocks	oligotrophic, oxygen rich, electrolyte poor moorland waters	inorganic, strongly acid waters	postglacial kieselguhr

this study was indeed too scarce (especially in *P. divergentissima* and *P. pseudodivergentissima*) to allow meaningful application of methods decomposing symmetric and asymmetric parts of variation (SAVRIAMA et al. 2010; SAVRIAMA & KLINGENBERG 2011). However, future morphometric studies of the genus *Pinnularia* should definitely also encompass the symmetry/asymmetry analyses that may help in defining quantitative morphological differences among species.

KRAMMER (1992, 2000) lumped several *Pinnularia* taxa showing comparable morphological features under *P. divergentissima*, considerably broadening that way not only the morphological variability of the latter but also its worldwide geographical distribution. However, taxonomic research on other diatom complexes/species

has indicated that both species drift, i.e. the continuous broadening of the original species description, and force fitting (TYLER 1996) as a result of the use of European or North American identification guides in other continents, are the two main reasons for underestimating the diatom diversity in remote areas (SABBE et al. 2003; VAN DE VIJVER et al. 2005; VAN DE VIJVER & MATALONI 2008; ZIDAROVA et al. 2010). This not only led to misinterpretations of the biodiversity of these areas but more important, has major implications on the biogeography of diatom species, creating a large set of cosmopolitan species showing a broad morphological variability.

Although the different taxa from the *P. divergentissima* complex including the newly described species can only be considered to be ‘*morphospecies*’ as data on their genetic structure is currently lacking, several recent

Table 2. The cross-validation matrix of the canonical variates analysis. Rows indicate the given groups and columns indicate the groups predicted by the discriminant function, respectively. Numbers correspond to valves classified to individual taxa.

	<i>P. martinii</i>	<i>P. divergentissima</i>	<i>P. fottii</i>	<i>P. pseudodivergentissima</i>	<i>P. lindanedbalovae</i>
<i>P. martinii</i>	63	0	1	0	0
<i>P. divergentissima</i>	0	9	0	0	0
<i>P. fottii</i>	0	1	36	0	2
<i>P. pseudodivergentissima</i>	0	0	0	10	0
<i>P. lindanedbalovae</i>	0	0	12	0	201

studies on other diatom taxa such as *Cyclotella meneghiniana* KÜTZ., *Sellaphora pupula* (KÜTZ.) MERESCHK. or *Pseudonitzschia*, indicated that there is a widespread occurrence of (semi)cryptic diversity in diatoms (BEHNKE et al. 2004; MANN et al. 2004, 2008; BESZTERI et al. 2005; POULÍČKOVÁ et al. 2010; VAN ELSLANDER et al. 2009). In most cases, the results of the morphological analyses were confirmed by molecular data. The distinction of the different taxa of the *P. divergentissima* complex, even based on subtle morphological differences, can therefore be considered highly probable.

Acknowledgements

Sampling on Crozet has been made possible thanks to the logistic and financial support of the French Polar Institute–Paul–Emile Victor in the framework of the terrestrial program 136 (Ir. Marc Lebouvier & Dr. Yves Frenot). Pierre Compère is thanked for his valuable taxonomical and nomenclatural comments. This research was financially supported by the Grant Agency of the Charles University in Prague (GAUK 139910) and partly by the project MSM N° 0021620828. Adéla Moravcová benefitted from an ERASMUS travel grant during her research stay in the National Botanic Garden of Belgium. Dr. Anton Igersheim, curator of the Cryptogam Collection at the Naturhistorisches Museum in Vienna is acknowledged for borrowing us the type slide of *P. divergentissima*.

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Received March 20, 2012

Accepted June 25, 2012