

Current taxonomic studies on the diatom flora (Bacillariophyceae) of the Bolivian Altiplano, South America, with possible consequences for palaeoecological assessments

EDUARDO A. MORALES¹*, CARLOS E. WETZEL², SINZIANA F. RIVERA¹, BART VAN DE VIJVER³ & LUC ECTOR²

¹Herbario Criptogámico, Universidad Católica Boliviana San Pablo, Calle M. Márquez esq. Plaza Jorge Trigo s/n, PO Box 5381, Cochabamba, Bolivia

²Public Research Centre – Gabriel Lippmann, Department of Environment and Agro-biotechnologies (EVA), 41 rue du Brill, L-4422 Belvaux, Luxembourg

³Botanic Garden Meise, Department of Bryophyta & Thallophyta, Domein van Bouchout, B-1860, Meise, Belgium

*Corresponding author (e-mail: edu_mora123@outlook.com)

ABSTRACT – The present investigation is based on detailed taxonomical analyses combining light microscopy (LM), scanning electron microscopy (SEM) and critical reviews of publications and type material. This method revealed a higher number of diatom taxa than that reported for the Altiplano, reports that are based on LM and SEM, but force-fitting the taxa into their European relatives. It also became evident that some taxa often reported from the Altiplano do not occur or are less common in this region and that misidentifications are the consequence not only of force-fitting, but also of misinterpretation of the original protologues and illustrations (taxonomic concept drift). These findings have important repercussions on past palaeoecological assessments for the Altiplano, which have been based on ecological information for taxa developing in ecosystems of highly contrasting conditions. Here we present the case of three araphid diatoms, which were reported as known taxa from Europe and elsewhere, but in fact correspond to taxa described as new for the Altiplano or unpublished taxa. It is recommended that: (1) a flora for this region is developed utilizing sound microscopical data and reviewing pertinent type material, (2) key common taxa used for past palaeoecological studies in the Altiplano are reviewed using a taxonomically thorough and critical method, and (3) future palaeoecological studies for the Andes are supported by prior detailed taxonomical analysis.

KEYWORDS: *Bacillariophyceae*, *diatoms*, *palaeoecology*, *palaeolimnology*, *type material*

INTRODUCTION

Montagne (1839) made the first identifications of diatoms from Bolivia from material collected from the Pacific coast by Alcide d'Orbigny. From the subsequent publications of Ehrenberg (1854a, b) to the most recent article by Morales *et al.* (2012), only 19 taxonomic publications have appeared in the literature for Bolivian diatoms. These references are concentrated on the Altiplano area and the great majority deals with palaeoecological assessments on a few ecosystems that are unrepresentative even for this part of the country (see list of publications and discussion in Morales *et al.*, 2008).

Palaeoecological works for the Altiplano frequently make reference or list taxa which include a great deal of names of species that were originally described from Europe or other continents, with only a few elements having a restricted South American origin (e.g. Bao *et al.*, 1999; Sylvestre *et al.*, 2001; Servant & Servant-Vildary, 2003; Vélez *et al.*, 2005; Ekdahl *et al.*, 2008, among many others). The recent major taxonomical study of Andean diatoms produced by Rumrich *et al.* (2000) also reported a low number of new species and a surprising high number of common elements (42% of 888 recorded taxa) with the European diatom flora (see discussion in Morales *et al.*, 2012). These data are paradoxical for a country counted among those with the highest biological diversity in the world (Ibisch & Mérida, 2003). Manguin (1964) expressed a similar view of predominant cosmopolitanism based on samples from the Andes near Lima, Peru (ranked higher than Bolivia as a biodiverse country), reporting the presence of 52.5% of cosmopolitan taxa out of a total of 392 from 10 samples; although at least two of these samples were from below 2000m above sea level (asl), indicating that they were not truly Altiplanic localities.

Morales *et al.* (2012) challenged this current view on Andean diatoms since their study of a single epipsammon sample from the Bolivian Desaguadero River yielded 228 taxa, more than a quarter of those reported by Rumrich *et al.* (2000) based on 350 samples and covering a geographical range from Argentina to Venezuela. Based on a taxonomic comparison with local regional and world-wide literature, Morales *et al.* (2012) determined that more than 80% of the taxa from Desaguadero River were not cosmopolitan, a fact most probably explained by the little human-related disturbance on the river collection site relative to the higher anthropic effects on the sites sampled by Rumrich *et al.* (2000). Although not clear from the site descriptions, it is also possible that the Peruvian localities studied by Manguin (1964) were influenced by anthropogenic effects. This is indicated by the reported proximity of such localities to Lima, smaller towns and rural communities.

Force-fitting into European and North American-based taxa concepts is an additional cause of the skewed view of the Bolivian Andean flora. As stated by Tyler (1996) and Kociolek & Spaulding (2000), force-fitting has been a major factor in the delay of our understanding of not only algal species distribution, but also of their true identity. Theriot *et al.* (1985) and Van de Vijver & Cocquyt (2009) touched on this aspect based on Peruvian samples and publications, while Morales *et al.* (2008; 2009) did the same for Bolivia. Force-fitting has not been exclusive to continental South America, but has also been a pervasive problem clouding diatom taxonomy and biogeography in the nearby Antarctic and sub-Antarctic regions (see discussions in Van de Vijver *et al.* 2010b; 2012).

Although, a high diversity of diatoms might not be common to all Altiplanic water bodies (see, for example, Álvarez-Blanco

et al. (2011) and Patrick (1961)); the probability for the existence of more sites comparable to the Desaguadero River leaves ample room to hypothesize that a great part of the Andean diatom flora is yet unknown and that the number of endemisms and new taxa could be much higher than those currently reported in the literature (Rumrich *et al.*, 2000; Rivera & Cruces, 2009). In fact, the number of new taxa published from the Andean region has increased in recent years (e.g. Tapia *et al.*, 2004; Maidana *et al.*, 2009; Van de Vijver & Cocquyt, 2009; Álvarez-Blanco *et al.*, 2011; Furey *et al.*, 2012).

The present article uses selected examples of araphid diatoms to demonstrate that misapplication of names has occurred in the diatom literature for the Bolivian Altiplano and that the implications for palaeoecological assessments could be detrimental, also producing skewed views of past environmental change. Published images of these selected taxa, identified with European names, are compared with our results of studies on type material. Although, it is not possible at present to make a reanalysis of the published palaeoecological data, mainly because the ecology of the analysed taxa is yet to be determined, some recommendations for the amendment of published data and for future taxonomic and applied studies are made.

MATERIAL AND METHODS

The following references were scanned to extract taxonomic information pertinent to the taxa used as examples in the present work: Servant-Vildary & Blanco (1984), Servant-Vildary (1986) and Servant-Vildary & Roux (1990). These references were chosen because they are among the few publications for the Bolivian Altiplano that contain taxonomic lists and light microscopy (LM) and scanning electron microscopy (SEM) images illustrating key taxa. Three araphid diatoms were selected to illustrate our arguments: *Fragilaria* (= *Pseudostaurosira*) *brevistriata* Grunow in Van Heurck, *Fragilaria* (= *Pseudostaurosira*) *elliptica* Schumann and *Fragilaria* (= *Staurosirella*) *pinnata* Ehrenberg. These taxa were selected because they are commonly reported from ecosystems around the world and seem to have been present in the Altiplano region for thousands of years as reported in, for example, Servant-Vildary & Mello e Souza (1993) and Sylvestre *et al.* (2001).

Type material and original type illustrations for the three taxa mentioned above were examined (Pl. 1 herein). The type of *Fragilaria brevistriata*, Van Heurck slide No. 318 (Pl. 1, figs 2–4 herein) and matching raw sample (Pl. 1, fig. 1 shows a SEM image of an individual from this sample) are housed at the Botanic Garden Meise (Belgium), Department of Bryophytes and Thallophytes. The material was originally collected by Delogne from a freshwater body in Brussels, Belgium (Van Heurck, 1885). The best available description of this taxon is found in Williams & Round (1987) and it is used here as basis for morphological discussions. In the case of *Fragilaria elliptica*, isotype material found at the Academy of Natural Sciences of Drexel University, in the form of a permanent slide labelled ANSP G.C. 11994 (Pl. 1, figs 6–8 herein) and raw material were analysed (SEM results are shown in Pl. 1, figs 5 and 9 herein); the original sample was collected by Schumann from Königsberg, Prussia (Schumann, 1867). For this taxon, the best description available is that of Edlund *et al.* (2006), upon which we base our discussions on morphology. Type material for *Fragilaria pinnata* is housed at the

Ehrenberg Collection, Institut für Paläontologie, Museum für Naturkunde in Berlin. This material belongs to a collection from ‘Moctezuma Flöss’, Mexico (‘*Mexiko, aus convergen des Moctezuma*’, unknown collector), which was prepared on micas by Ehrenberg (Pl. 1, figs 11–16 herein). The original type drawings by Ehrenberg (1843, figs 8a, b, c, d, e) are shown here in Plate 1, figure 10, clearly matching the LM images here provided in Plate 1, figures 11–16. In this case, the descriptions presented by Haworth (1975) and Williams & Round (1987) are used as bases for morphological discussions.

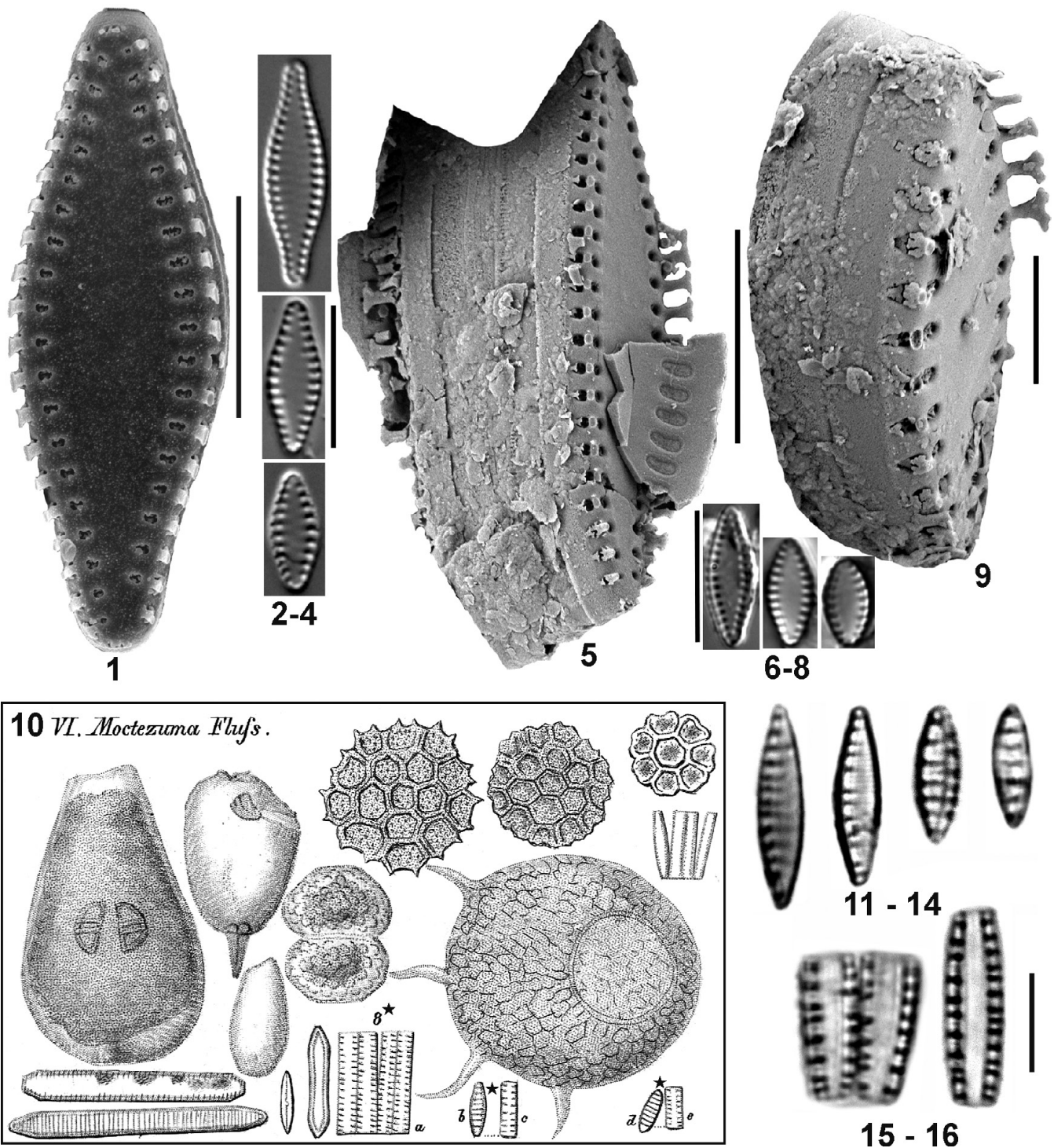
For LM analysis, Van Heurck’s slide No. 318 was viewed using a Leica DMRB microscope equipped with a DC500 high-resolution digital camera. Slide ANSP G.C. 11994 was analysed using a Nikon Microphot-FXA microscope equipped with a Spot Insight QE Model 4.2 Colour Digital Camera. From the Ehrenberg micas, photographs were taken at 400× using an Olympus BX51 light microscope and a Canon PowerShot A640 colour digital camera.

For SEM analysis, small portions of Van Heurck’s type materials were digested with 100 ml of hydrogen peroxide (35%) at a temperature of 210°C for 36 h. After settling and aspiration of the peroxide, 1 ml of hydrochloric acid (37%) was added to the samples and allowed to rest for 2–4 h. Samples were rinsed at least three times with distilled water. The material was filtered and rinsed with deionized water through glass fibre filters with a 3 µm pore diameter. Coating with platinum was accomplished using a BAL-TEC MED 020 Modular High Vacuum Coating System for 30 s at 100 mA. A Hitachi SU-70 electron microscope operated at 5 kV and 10 mm distance was used for the analysis. Also, a small portion of the Schumann isotype material was digested with nitric acid using the microwave method and washed by decanting using distilled water (Charles *et al.*, 2002). Aliquots of clean material were air dried on to 15 × 15 cm pieces of aluminum foil. Smaller pieces were trimmed and mounted on aluminum stubs with double-sided tape. The stubs were then coated with gold-palladium using a Polaron Sputter Coater for *c.* 1.5 min at 1.8 kV. A Leo-Zeiss 982-DSM electron microscope was used with an accelerating voltage of 2–4 kV.

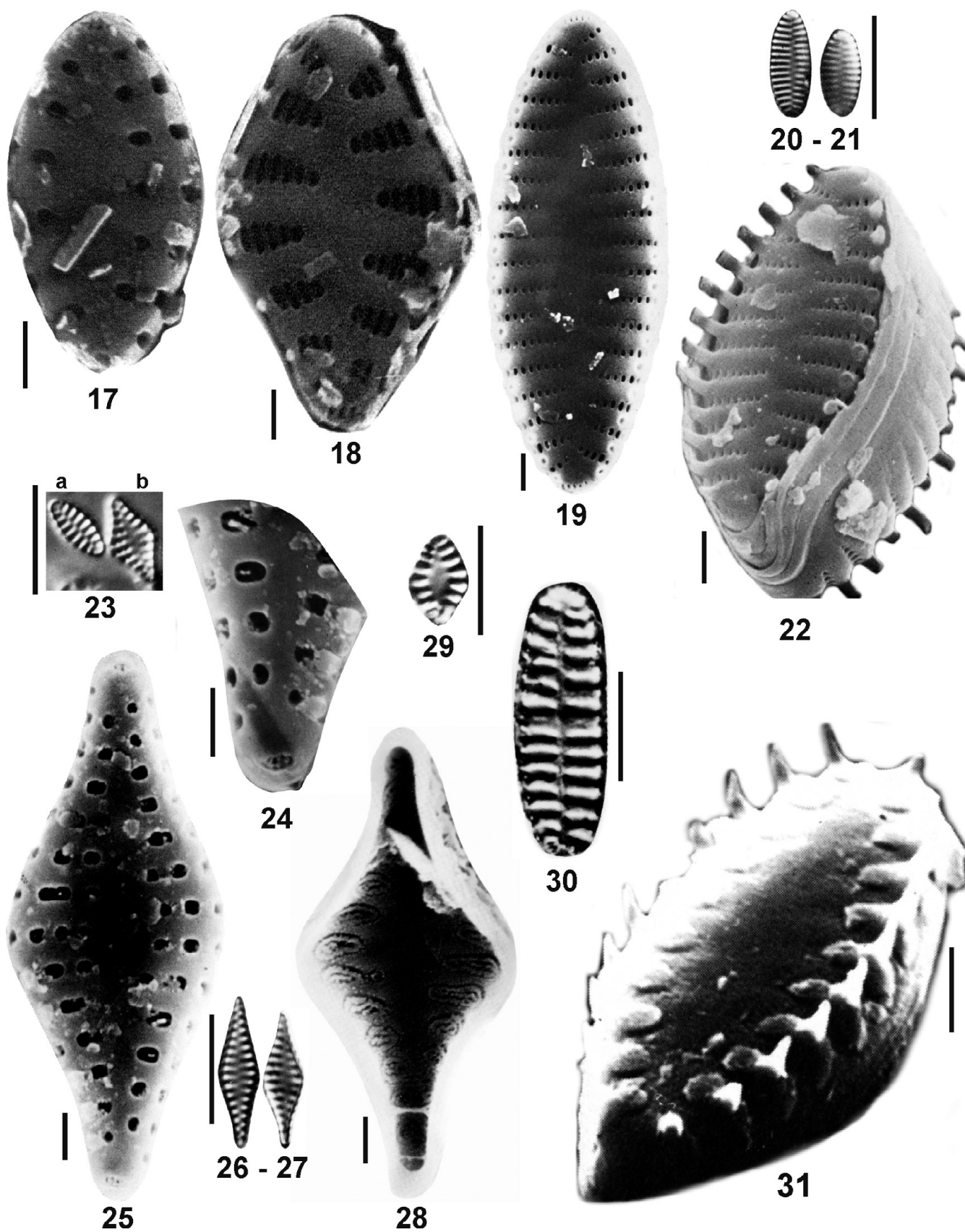
All micrographs and scanned material were digitally manipulated and plates mounted using Photoshop CS3.

RESULTS

Plate 2 shows araphid taxa identified from Bolivian material in Servant-Vildary & Blanco (1984), Servant-Vildary (1986) and Servant-Vildary & Roux (1990). Plate 2, figures 17, 23b, 25–28 and 31 show organisms identified as *Fragilaria brevistriata* Grunow, currently considered to be the generic type of *Pseudostaurosira* D.M. Williams & Round (Williams & Round, 1987) and currently bearing the name *Pseudostaurosira brevistriata* (Grunow) D.M. Williams & Round. From the figures cited above, it can be readily seen that the authors were using a very broad concept for this taxon, including in it a wide range of morphological variants. The examination of type material of *Fragilaria brevistriata* (Pl. 1, figs 1–4) shows that none of the variants reported from the Bolivian Altiplano belong to this taxon *sensu stricto*. The type of *F. brevistriata* includes individuals with lanceolate shape, wider than the valves represented by Servant-Vildary & Blanco (1984; Pl. 2, fig. 17 herein). Besides shape and width, the striation of valves from type material is less coarse



Explanation of Plate 1. figs 1–16. LM, SEM and scanned images of type material for *Fragilaria brevistriata*, *F. elliptica* and *F. pinnata*. **fig. 1.** SEM image of *F. brevistriata* from type material, Van Heurck No. 318, Botanic Garden Meise (Belgium); external view. **figs 2–4.** LM images from type material Van Heurck slide No. 318, Botanic Garden Meise (Belgium); valve views. **figs 5, 9.** SEM images of *F. elliptica* from isotype material housed at the Academy of Natural Sciences of Philadelphia of Drexel University; titled external views. **figs 6–8.** LM photographs from type material ANSP G.C. 11994 from the Academy of Natural Sciences of Philadelphia of Drexel University; valve views. **fig. 10.** Scanning of a plate presented in Ehrenberg (1843), illustrating material from the Moctezuma River, Mexico. Black stars mark the iconotype drawings of *F. pinnata*. **figs 11–16.** LM images of several individuals from the type material of *F. pinnata*, sample 1229, Institut für Paläontologie, Museum für Naturkunde, Berlin, seen in valve (figs 11–14) and girdle view (figs 15, 16). LM scales 10 µm; SEM scales 1 µm.



(c. 14 in 10 µm) than that in the Bolivian specimen (higher than 14 in 10 µm). The most striking difference between the type population and the Bolivian specimen is the absence of spines in the latter. Spines in species of the genus *Pseudostaurosira* are located between the areolae at the valve face–mantle junction. In a few species, such as *Pseudostaurosira robusta* (Fusey) D.M. Williams & Round (Williams & Round, 1987), the spines are located on the costae (between rows of areolae), but the Bolivian specimen photographed by Servant-Vildary & Blanco (1984) does not possess spines at this location either. There are other representatives of *Pseudostaurosira* that have incipient spines (e.g. *P. tenuis* E. Morales & Edlund (Morales & Edlund, 2003)) or lack spines altogether (*P. parasitica* (W. Smith) E. Morales (Morales, 2003)), but none compares morphologically with the valve pictured from the Bolivian material. Thus, although the Bolivian specimen is certainly not *P. brevistriata*, it does indeed belong in the genus *Pseudostaurosira*, but currently, it cannot be associated with any known taxon within this genus.

Plate 2, figures 23b, 25 and 28 also depict representatives of *Pseudostaurosira*, an identification that we base on the type or areolae and apical pore fields. However, a quick comparison with Plate 1, figures 1–4 clearly shows that this second variant from Bolivian material does not belong in *P. brevistriata* either. Two conspicuous features that distinguish these two entities are the rhomboid shape and inconstant production of incipient spines interrupting the rows of areolae at the valve face–mantle junction in the Bolivian specimens. Rumrich *et al.* (2000) presented *Staurosira laucensis* Lange-Bertalot & Rumrich (= *Pseudostaurosira laucensis* (Lange-Bertalot & Rumrich) E. Morales & M.L. Vis) from the Chilean Altiplano, the same geographical area as the site from where Servant-Vildary (1986) reported the specimens depicted in Plate 2, figures 23b, 25 and 28 (bottom of bog from the Ichu Khota region and downstream from outlet of Khara Khota Lake in the Bolivian Altiplano). The type of areolae, the infrequent production of incipient spines and the small apical pore fields at the valve apices readily associate *S. laucensis* with the Bolivian representatives. It should be mentioned that Servant-Vildary (1986) did not feel confident about the placement of these specimens in *F. brevistriata* and called them ‘*Fragilaria* aff. *brevistriata* Grunow’ in the text, further stating that the axial area was slender than that of *F. brevistriata* and that the specimens from Bolivia resembled those of *Fragilaria pseudoconstruens* Marciniak (now *Pseudostaurosira pseudoconstruens* (Marciniak) D.M. Williams & Round). This resemblance is only in overall valve shape, however, since *Fragilaria pseudoconstruens* has valves with rostrate ends and inflated central area. Also, spines are well developed and located between the striae in *F. pseudoconstruens* (Marciniak, 1982, 1986).

A third morphological variant presented by Servant-Vildary (1986) under the name *F. brevistriata* is represented in Plate 2, figures 26 and 27. The narrowly rhomboidal shape of these indi-

viduals is characteristic and cannot be associated with any known araphid taxon from the literature. Since the author did not present SEM images that could be related to these LM photographs, we cannot ascribe these two individuals to a genus with confidence. Certainly, *Pseudostaurosira* is a candidate, but *Staurosira* Ehrenberg would be as well, given the LM data that do not show the structure of the striae clearly.

The fourth variant identified by Servant-Vildary & Roux (1990) as *F. brevistriata* (Pl. 2, fig. 31 herein) has areolae occluded externally by a rota (solid siliceous disc). This is a feature not of *Pseudostaurosira*, but of *Pseudostaurosiropsis* E. Morales (Morales, 2001). In *Pseudostaurosira*, the occlusions are volae, branched siliceous rods originating from the areolar inner periphery as can be seen in the type material of *P. brevistriata* (Pl. 1, fig. 1). The genus *Pseudostaurosiropsis* has been reported from North America and Europe (Morales, 2001, 2002) and has been observed in South American collections from Brazil and Venezuela (D. Talgatti and C.E. Wetzel pers. comm.). Thus, Servant-Vildary and Roux’s report of this taxon from Bolivia (though under ‘*Fragilaria brevistriata*’) is not improbable. Morales *et al.* (2012) related this fourth variant to *Pseudostaurosira sajamaensis*, but due to the regularly round characteristic of the external rota (highly irregular in *P. sajamaensis*), this specimen imaged by Servant-Vildary & Roux (1990) is better placed in *Pseudostaurosiropsis*.

A similar comparative analysis can be presented for *Fragilaria elliptica*. The type material for this taxon was studied in detail by Edlund *et al.* (2006), who concluded that this taxon, instead of belonging to *Staurosira* (as had been reported in numerous previous publications from around the world), should be placed in *Pseudostaurosira* as *P. elliptica* (Schumann) Edlund, E. Morales & S.A. Spaulding. One of the reasons why this taxon had suffered such taxonomic concept drift (Van de Vijver *et al.*, 2009, 2010a) was that only one sketch drawing had been presented by Schumann (1867, Pl. 1, fig. 5), a representation that was subsequently misinterpreted and the same name misapplied to several taxa producing similar phenotypes at approximately the size of the diatoms depicted by such drawings. The proper identification of taxa with convergent morphology often requires population-level studies under SEM and detailed cross-checking with LM data (Morales *et al.*, 2001). Servant-Vildary (1986) identified specimens illustrated herein in Plate 2, figures 19–22 as ‘*F. elliptica* Schuman’, but a comparison with type material of *F. elliptica* (Pl. 1, figs 5–9 herein) makes this identification untenable. The specimens from the Bolivian material belong in fact to *Staurosira* and have close affinities with *S. venter* (Ehrenberg) Cleve & Möller, a taxon frequently reported from freshwaters around the world, but that also requires a thorough revision based on type material originally studied by Ehrenberg (1854b). Valve outline, areolae shape and structure, apical pore field and girdle features relate the Bolivian specimens to *Staurosira*.

Explanation of Plate 2. figs 17–31. LM and SEM images from publications based on material collected from the Bolivian Altiplano. **fig. 17.**

Fragilaria brevistriata Grunow *sensu* Servant-Vildary & Blanco (1984, pl. 3, fig. 1), external view. **fig. 18.** *Fragilaria pinnata*? Ehrenberg *sensu* Servant-Vildary & Blanco (1984, pl. 3, fig. 2), external view. **figs 19–22.** *Fragilaria elliptica* Schuman *sensu* Servant-Vildary (1986, pl. 2, figs 23, 22, 21 and 25, respectively). **fig. 23a.** *Fragilaria pinnata* Ehrenberg *sensu* Servant-Vildary (1986, pl. 3, fig. 31a). **figs 23b–28.** *Fragilaria brevistriata* Grunow *sensu* Servant-Vildary (1986, pl. 3, figs 31b–36). **fig. 29.** *Fragilaria pinnata* Ehrenberg *sensu* Servant-Vildary (1986, pl. 2, fig. 30). **fig. 30.** *Fragilaria pinnata* Ehrenberg *sensu* Servant-Vildary (1986, pl. 8, fig. 147). **fig. 31.** *Fragilaria brevistriata* Grunow *sensu* Servant-Vildary & Roux (1990, fig. 27). LM scales 10 µm; SEM scales 1 µm.

The case of the application of the name *Fragilaria pinnata* is more complicated given the tangled taxonomic history of this name (Morales *et al.*, 2013). The taxon was originally erected by Ehrenberg and its nomenclatural changes through time can be summarized as follows.

Basionym:

- *Fragilaria pinnata* Ehrenberg, 1843, p. 415, pl. 3 (6), figs 8a–e. Here as Plate 1, figure 10.

The name *F. pinnata* had already been used in 1841 by Ehrenberg, but it was not until 1843 that he provided a description and an illustration.

Later combinations found in the literature are:

- *Odontidium pinnatum* (Ehrenberg) Kützing (Kützing, 1844)
- *Nematoplata pinnata* (Ehrenberg) Kuntze (Kuntze, 1898).

The current name being used for this taxon is:

- *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round (Williams & Round, 1987).

A Google® search under the four names listed above yielded 45 613 hits (search done on 8 September 2012). Compared to hits on the same date for some of the most commonly reported taxa in the diatom literature, such as *Ulnaria ulna* (Nitzsch) Compère (= *Fragilaria ulna* (Nitzsch) Lange-Bertalot or *Synedra ulna* (Nitzsch) Ehrenberg: 252 900 compiled hits for the three names), *Eolimna minima* (Grunow) Lange-Bertalot (= *Navicula minima* Grunow: 66 300 hits for both names), *Nitzschia palea* (Kützing) W. Smith (42 500 hits), and *Gomphonema parvulum* Kützing (and *Sphenella parvula* Kützing: 39 560 hits for the two names), it is evident that ‘*pinnata*’ is, indeed, a widely used name. Conservatively, about 12 different morphological variants have been identified as *Fragilaria pinnata* or *Staurosirella pinnata* in the literature (consult references listed in Gaul *et al.* (1993) and Henderson & Reimer (2003)). Only the site <http://craticula.ncl.ac.uk/EADiatomKey/html/taxon13780050.html> (accessed on 8 September 2012) has six of these variants. One of the reasons for the wide concept applied to ‘*pinnata*’ is that one of the most common and influential floras world-wide, Krammer & Lange-Bertalot (1991), has been used as a basis for its identification. This publication presents ‘*pinnata*’ in plate 133, figs 1–18, 32, 32A, depicting what can be arguably separated into at least nine different morphological variants. In plate 134, fig. 8, these same authors include (with a question mark) yet another variant under the epithet ‘*pinnata*’. Although the concept used by Dr Lange-Bertalot’s research group has been drastically narrowed in recent years (e.g. Hofmann *et al.*, 2011), their shift has not been based on analysis of Ehrenberg’s type material. It is not clear why the name *Staurosira mutabilis* (W. Smith) Grunow has suddenly started to be used for some variants formerly placed under *Fragilaria pinnata* (e.g. Werum & Lange-Bertalot, 2004; Hofmann *et al.*, 2011; Kulikovskiy *et al.*, 2011), but it is not based on analysis of type material of *Odontidium mutabile* W. Smith either. Furthermore, it is not clear why the name *Staurosira pinnata* Ehrenberg, a different taxon altogether as can be evidenced from the type drawings in Ehrenberg (1854b), was used to

replace the name *Fragilaria pinnata* in some publications (e.g. Rumrich *et al.*, 2000; Schmidt *et al.*, 2004). Needless to say, thorough LM and SEM studies of type material of *Staurosira pinnata* have not been done to date.

As presented by Morales *et al.* (2013), examination of the original type figures of *Fragilaria pinnata* in Ehrenberg (1843; depicted in Pl. 1, fig. 10 herein, see black stars) reveals that this author had a completely different concept of this taxon from the one, albeit wide, that is used today. Ehrenberg’s drawings show valves in girdle and valve views that can be readily tied to the genus *Denticula* Kützing. LM analysis of the micas of *F. pinnata* confirms this association since the valve morphology, including the typically septate girdle bands, can be clearly observed (Pl. 1 figs 11–14). It is unclear when and where the notorious shift in the concept of ‘*pinnata*’ occurred, but the analysis of type material puts in evidence that the application of this name to an araphid diatom is mistaken.

Servant-Vildary & Blanco (1984) and Servant-Vildary (1986) used the epithet ‘*pinnata*’ to identify three morphological variants. Plate 2, figures 18 and 29 herein, depict the first variant. Plate 2, figure 18 was published in Servant-Vildary & Blanco (1984) and was ascribed to ‘*Fragilaria pinnata*? Ehr.’, but no discussion on this determination is included in the text. Plate 2, figure 29 was presented two years later (Servant-Vildary, 1986) and the author discussed that this ‘oval’ shape (rhomboid in our view) is mixed with the rounded (elliptical in our view) more frequent form (here depicted in Pl. 2, fig. 23a). The characteristics of the striae and spines described by Servant-Vildary (1986) certainly place these two variants in *Staurosirella* D.M. Williams & Round (Williams & Round, 1987), but, as we saw earlier, ascribing any araphid diatom to ‘*Fragilaria pinnata*’ is erroneous.

The third morphological variant used by Servant-Vildary (1986) is depicted here in Plate 2, figure 30. The linear-elliptical valve outline with a narrow sternum is characteristic of the depicted specimen and sets it apart from any other taxon currently known in *Fragilaria* or *Staurosirella* and probably represents a new species. As per our analysis of the type, the inclusion of this form in ‘*Fragilaria pinnata*’ is also flawed.

DISCUSSION

Given that before our study of Van Heurck’s type material the only reference to the type of *F. brevistriata* was an outline drawing in Van Heurck (1881, pl. 45, fig. 32), inclusion of several morphological variants under this name was not infrequent in the literature, Servant-Vildary’s (1986) publication not being the exception (see the references reported to contain SEM images of this taxon in Gaul *et al.* (1993) and Henderson & Reimer (2003) to demonstrate the wide concept currently used for ‘*brevistriata*’).

Likewise, at the time Servant-Vildary (1986) made her identifications of Altiplano material, the prevailing concept of *F. elliptica* (in the absence of type material studies) indeed included phenotypes like the ones she studied. Thus, her approach to the identification of the Bolivian specimens was the most likely given the base references she used for identification: Haworth (1975), Rosen & Lowe (1981) and Archibald (1983).

Again, Servant-Vildary and collaborators were using the bibliography available at that time, which in turn was not based on thorough analysis of type material and simply inherited and transmitted

a series of concepts greatly influenced by taxonomic drift. Therefore, the use of the epithet '*pinnata*' by Servant-Vildary and collaborators, as used by the bulk of other authors in the literature produced from that time until recently, is a natural consequence.

As presented thus far, taxonomic drift was not the only problem during identification of Andean material, but force-fitting of populations from this geographical area to concepts and names developed for Europe and elsewhere also produced a skewed view of diatom communities in the Andes. As a consequence, today we only have a partial idea of the composition and structure of those communities and we know very little about the ecology of even the most common, non-cosmopolitan taxa. Given that South America started its separation from Europe and Africa in the Permian–Jurassic (250–145 Ma) and that the Andes have a Mesozoic–Tertiary origin (250–2.6 Ma) (Oncken *et al.*, 2006), organisms in this mountainous region have had sufficient time to evolve and produce populations isolated from other continents and from other neighbouring ecosystems in South America (e.g. the lowlands of the Amazon or the coastal Pacific strip). In the Bolivian Altiplano, the average altitude of 4000 m asl of the western Andean mountain range and the equally high Eastern Cordillera constitutes a formidable barrier greatly reducing gene flow, as shown by the numerous animal and higher plant endemics (Aguirre *et al.*, 2009; Navarro, 2011). Although no comparable studies of endemism and gene flow exist for the algae, it is highly likely that similar processes occurred in populations and communities of these organisms. Therefore, use of European floras or taxonomic works for other regions of the world or even other South American ecoregions must be exercised with extreme caution (Morales *et al.*, 2008, 2009; Van de Vijver & Cocquyt, 2009). As we have seen in the case of araphids selected from publications for the Andes, in none of the three cases was the application of European concepts correct.

The lack of comprehensive floristic works for the Andes, works based on detailed LM and SEM analyses and cross-checking with type material, seriously affects applied fields such as ecology. The importance of having a sound taxonomic analysis prior to applied ecological interpretations can be witnessed in the literature for the Andes. In the case of *S. pinnata*, for example, there is no agreement regarding the range of ecological conditions in which this taxon can be found. While most authors agree that it is a benthic, epiphytic taxon (e.g. Cross *et al.*, 2000; McCulloch & Davies, 2001), regarding salinity some authors state that it is a taxon found in low pH and conductivity, and that it thrives in oligotrophic systems (e.g. Vélez *et al.*, 2006), while others state that it can be found in fresh to brackish conditions with variable pH, conductivity and trophic state (Borromei *et al.*, 2010; Fritz *et al.*, 2012). In Europe, this has been reported as an oligo to eutraphentic taxon, capable of growing in a wide range of salinities, but tolerating alkaline waters (Van Dam *et al.*, 1994).

Certainly, detailed studies of current populations and communities in the diverse aquatic ecosystems existing in the Andean area will lead to a better taxonomical and ecological characterization of extant organisms with beneficial implications for palaeolimnological assessments. Based on our analysis of the three araphid examples used herein, ecological misinterpretations of past conditions (e.g. Servant-Vildary & Mello e Souza, 1993; Sylvestre *et al.*, 2001) can be suspect and must be reassessed in the future.

We concur with Álvarez-Blanco *et al.* (2011), who state that there is a large number of unidentified taxa that have yet to be described for the Andes. We add that these taxa form part of communities particular to the Andes, communities that have not yet been characterized, thus impeding at present the reassessments we recommend.

CONCLUSION

The analysis of the literature presented herein shows that misapplication of European names to taxa from the Andean Altiplano has occurred. This misapplication happened because the taxonomy of European taxa was founded on inadequate original descriptions and sketchy original figures, which in turn led to taxonomic drift. Without a clearly defined protologue, the ecology was also ill-determined, leading to a series of – often contradictory – ecological requirements for a given taxon. Palaeoecological interpretations based on such undefined taxonomy and ecology could have led to erroneous interpretations of past ecological conditions in Andean settings and, thus, a reassessment based on studies of a combination of LM, SEM and critical reviews of publications and type material is needed.

The development of a taxonomically well-founded current and fossil flora for the Andes is urgently needed. Recent studies in this geographical area, using a combination of LM and SEM tools, show that at least some locations in the Altiplano could hold an unreported taxonomic richness and endemism that could change the current view of the diatom flora in this part of the world. Future palaeoecological studies encompassing a thorough taxonomical analysis and the use of a well-founded flora could yield more accurate interpretations of past ecological conditions.

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