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New epiphytic araphid diatoms in the genus *Ulnaria* (Bacillariophyta) from Lake Titicaca, Bolivia

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Two new epiphytic species of *Ulnaria* (Kützing) Compère, *U. titicacaensis* E. Morales, Ector & P.B. Hamilton and *U. macilenta* E. Morales, C.E. Wetzel & S.F. Rivera, are described from the Tiquina Strait, Lake Titicaca, Bolivia. The taxa have distinctive morphological features and their separation from morphologically related taxa and from each other is predominantly based on features of the valve central area and type of colonies. Whereas most morphologically similar taxa have a clear unilateral central area and form ribbon-like colonies, *U. titicacaensis* has a central area which is large and depressed internally, square to rectangular fascia, forms pin-cushion-like colonies mainly on *Cladophora* species, and has large polyphosphate bodies located toward the frustule apices. In contrast, *U. macilenta* has a similar central area to that in *U. titicacaensis*, but has narrower valves, forms short palisade groupings arranged in pin-cushion-like colonies, mainly on *Oedogonium* species and has polyphosphate bodies distributed throughout the frustule lumen. Morphological and ecological aspects of both new taxa are discussed in the light of available literature.

Keywords: *Altiplano, ancient lake, Andes, Fragilaria, new species, Synedra, taxonomy, Ulnaria*

Introduction

Despite the scientific importance of Lake Titicaca as an ancient lake (its basin began its geologic evolution at the transition between the Pliocene and the Early Pleistocene) and because it is the deepest high-altitude lake in the world (maximum depth of 285 m and elevation of 3814 m above sea level), very few taxonomic studies on diatoms have been published (Frenguelli 1939, Theriot et al. 1985, Servant-Vildary 1991, Tapia et al. 2004). However, there is a plethora of ecological studies including palaeoecological assessments (e.g., Cross et al. 2000, Sylvestre 2002, Abbott et al. 2003, Servant & Servant-Vildary 2003, Tapia 2003, Tapia et al. 2003, 2004, Ekdahl et al. 2008, Fritz et al. 2012) and determinations of algal productivity and community dynamics (e.g., Iltis 1991a, b, Richerson et al. 1991, Servant-Vildary 1991, Wurtsbaugh et al. 1991, Fontúrbel et al. 2006). Frenguelli (1939) and Servant-Vildary (1991) remain the only ones to have reported several diatom species from the benthos and plankton, respectively, for the Bolivian side of Lake Titicaca. Theriot et al. (1985) and Tapia et al. (2004) dealt with the purportedly endemic *Cyclostephanos andinus* (E.C. Theriot, Carney & Richerson) P.M. Tapia, E.C. Theriot, S.C. Fritz, Cruces & P. Rivera, which has subsequently been reported from other regions in the Altiplano (Hernández et al. 2008, 2011).

Besides these reports, there are no studies using combined light (LM) and scanning electron (SEM) microscopy or molecular tools.

These previous studies depicted a rather poor diatom flora, which is inconsistent with the high variability of potential habitats in the lake. The abundant submersed and emergent vegetation present on many of its shores, the rocky and sandy littoral zones, and the deep pelagic region should favor the growth of benthic and pelagic communities in Lake Titicaca (Iltis & Mourguiart 1991, Raynal-Roques 1991). There are also numerous bays and islands that are subjected to different types of anthropic influence, adding to the variety of conditions that might favor the development of diverse diatom communities (Lavenue 1991, Roche et al. 1991, Wirmann 1991).

A single sample from the Tiquina Strait revealed a rather diverse benthic diatom community. The Strait divides Lake Titicaca into the larger Lake Chucuito and the smaller Lake Huiñaimarca, and is known to be human-impacted and subject to heavy boat traffic. From this single sample, over 110 morphospecies were recorded using LM and SEM, with as many as 50% of them being left unidentified using local (Frenguelli 1939, Servant-Vildary 1991), regional (Manguin 1964, Rumrich et al. 2000) and worldwide floras (Krammer & Lange-Bertalot 1986, 1988, 1991a, b). This

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finding indicates that the diatoms from Lake Titicaca, at least in the benthos, remain largely unknown and that the potential for this lake to hold a rather diverse diatom flora is highly probable.

From the group of unknown diatoms found in the Tiquina Strait, two new species within the genus *Ulnaria* (Kützing) Compère are described. Given the common occurrence of these two diatoms, it is highly probable that they were misidentified in previous studies. These two species represent only a small part of the araphid diatom flora of Lake Titicaca, which is to be fully described at a later date. The taxonomy and ecology of both of the new taxa are compared and contrasted with that of morphologically similar taxa.

Materials and methods

The main samples used in this study were collected from the Tiquina Strait at San Pablo de Tiquina, Los Andes Province, Bolivia in February 2010 (Fig. 1). The Tiquina Strait has a width of c. 800 m and a minimum depth of 21 m. In the absence of a bridge, boat traffic in the Strait is heavy. Because boats are not controlled by the local authorities, gasoline and oil leakage, as well as organic and solid waste fall directly into in the water. Rapid development of the

towns of San Pablo and San Pedro de Tiquina on the eastern and western sides of the Strait have contributed to increased water contamination; many newly constructed households lack basic services, such as a proper sewage disposal.

In February 2010, the submersed portion of the cement and wooden pier at San Pablo de Tiquina was scraped using a stiff metallic brush and rinsed with lake water. Macroscopic filaments were also collected by hand and placed into the same flask as the scraped material. A second sample was collected from the same place 22 months after the first sampling in December 2012, in order to study freshly collected material and determine the growth type of the new *Ulnaria* species. At the time the last sample was collected, physico-chemical variables (temperature, pH, specific conductance and total dissolved solids) were measured *in situ* using a portable meter (HI 99300, Hanna Instruments S.L., Eibar, Spain) at a water depth of c. 15 cm and close to the collection area. Both samples had a final volume of c. 200 mL and were fixed with 10 drops of 40% formalin solution.

In the laboratory, drops of fixed material were analyzed by means of wet mounts using Lugol's solution to enhance contrast of cytoplasmic structures. Analysis was performed using a Zeiss Universal compound microscope equipped with differential interference contrast (DIC) optics at $\times 500$

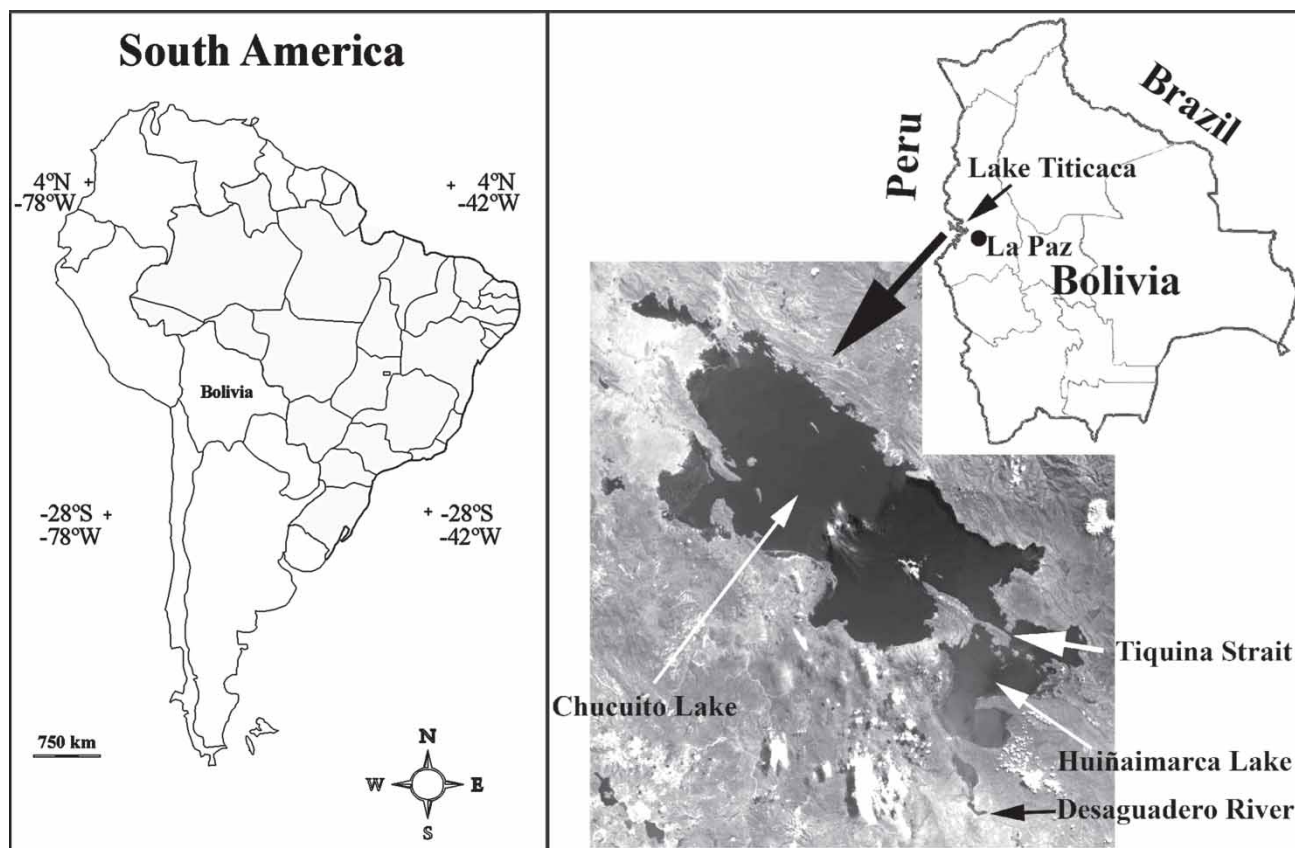


Fig. 1. Gauss–Krüger transverse projection map of Lake Titicaca shared by Bolivia and Peru, showing the Tiquina Strait where samples were collected. Lake Titicaca is divided into a larger basin called Chucuito Lake, and a smaller basin called Huiñaimarca Lake. The only outlet of the lake, the Desaguadero River, is also shown. Modified from Google Earth (2012).

magnification. Polyphosphate bodies were recognized as round, whitish structures usually lying outside the plastids. Oxidation of the organic matter was made using hot nitric acid and rinsed several times with distilled water until neutrality was reached. Aliquots of clean material were allowed to dry at room temperature on cover slips, which were then mounted permanently on glass slides using Naphrax[®]. At least 100 valves of each new species were measured in LM at $\times 500$ and $\times 1250$ magnifications using the microscope described above. Images were taken using a Jenoptik CF color digital camera and ProGres CapturePro v. 2.8 software. To determine the relative abundance of the taxa composing the community present in the first sample, 250 valves were counted on permanent slides along a random vertical transect, with a width determined by the microscope field of view at $1250 \times (140 \mu\text{m})$.

For SEM analysis, 10–20 mL aliquots of raw sample were digested with concentrated H_2O_2 and heated for 24 h in a sand bath. Then, the sample was allowed to cool and settle (c. 1 cm h^{-1}) and 80–90% of the supernatant was eliminated by vacuum aspiration. A 1 mL volume of 37% HCl was added and the preparation was allowed to settle for 2 h. The sample was then rinsed and decanted three times using deionized water. Aliquots (c. $100 \mu\text{L}$) of clean material were filtered and rinsed with deionized water through glass fiber filters of $3 \mu\text{m}$ pore size. 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 with a 10 mm working distance was used to examine diatom valves. Micrographs were digitally manipulated and plates containing LM and SEM images were mounted using Photoshop CS3[®] and CorelDRAW X5[®].

For comparative purposes, the type material of *Ulnaria colcae* Van de Vijver & Cocquyt was analyzed under SEM (Van de Vijver & Cocquyt 2009).

Morphological terminology follows Barber & Haworth (1981) for valve shape and stria pattern, Cox & Ross (1981) and Cox (2012) for lateral extensions and cross bars, Williams & Round (1987) and Round et al. (1990) for areolar substructures, apical pore fields and girdle bands, and Cox (1996) and Schmid (2001) for plastid shape and structure.

Results

The collection site had clear water with a pH of 8.9 and specific conductance of $1240 \mu\text{Scm}^{-1}$, indicating high electrolyte content and elevated pH. Despite contamination, the wooden and cement parts of the pier are heavily colonized by chlorophytes and macrophytes such as *Cladophora* sp., *Rhizoclonium* sp., *Oedogonium* sp. and *Elodea* sp. Outside the area influenced by boat traffic, there are profuse growths of *Schoenoplectus californicus* ssp. *tatora* (Kunth) T. Koyama and *Myriophyllum* sp., development of which is affected mainly by household effluents and solid waste.

Ulnaria titicacaensis E. Morales, Ector & P.B. Hamilton sp. nov. (Figs 2–13, 25–28, 31–45)

Description. Frustules rectangular in girdle view, attached to macroalgae by mucilaginous pads, producing pin-cushion-like colonies and only rarely forming ribbon-like groupings of more than two cells. Valves lanceolate, with substrate apices and a bilaterally gibbous central area. Valve face externally flat and internally slightly undulate due to raised virgae. Transition to mantle steep. Length: 15.5–98.5 μm , width: 4.0–6.5 μm , striae: 16–18 in $10 \mu\text{m}$ (number of specimens examined, $n = 50$). Central area with large, depressed, oval to square fascia, asymmetrical; sometimes conspicuously shifted to one side due to the presence of shortened striae, or completely clear in other specimens. Central sternum narrow, mostly linear and barely open at the central area. Striae parallel in the center, becoming slightly radiate toward the apices. Striae run continuously onto valve mantle reaching deep into it. Virgae wider than striae and conspicuously internally thickened and raised. Areolae round to oval; occlusions not observed. Spines absent. Ocellulimbus-type apical pore fields well-developed, broadly elliptical, bearing neatly arranged rows of round poroids. A single rimoportula present on one apex, aligned with second to fourth stria on valve face, angled with respect to the valve's transapical axis in internal view. Scab-like structures (blisters) faintly developed along the abvalvar mantle edge. Girdle bands bearing round perforations. Valvocopula bearing short fimbriae. Open/close nature of girdle bands not observed. Chloroplasts lobed in valve and girdle views, shaped in the form of an irregular H, positioned in the center of the frustule. Presence of polyphosphate bodies of different size; the largest ones mainly distributed toward the frustule apices.

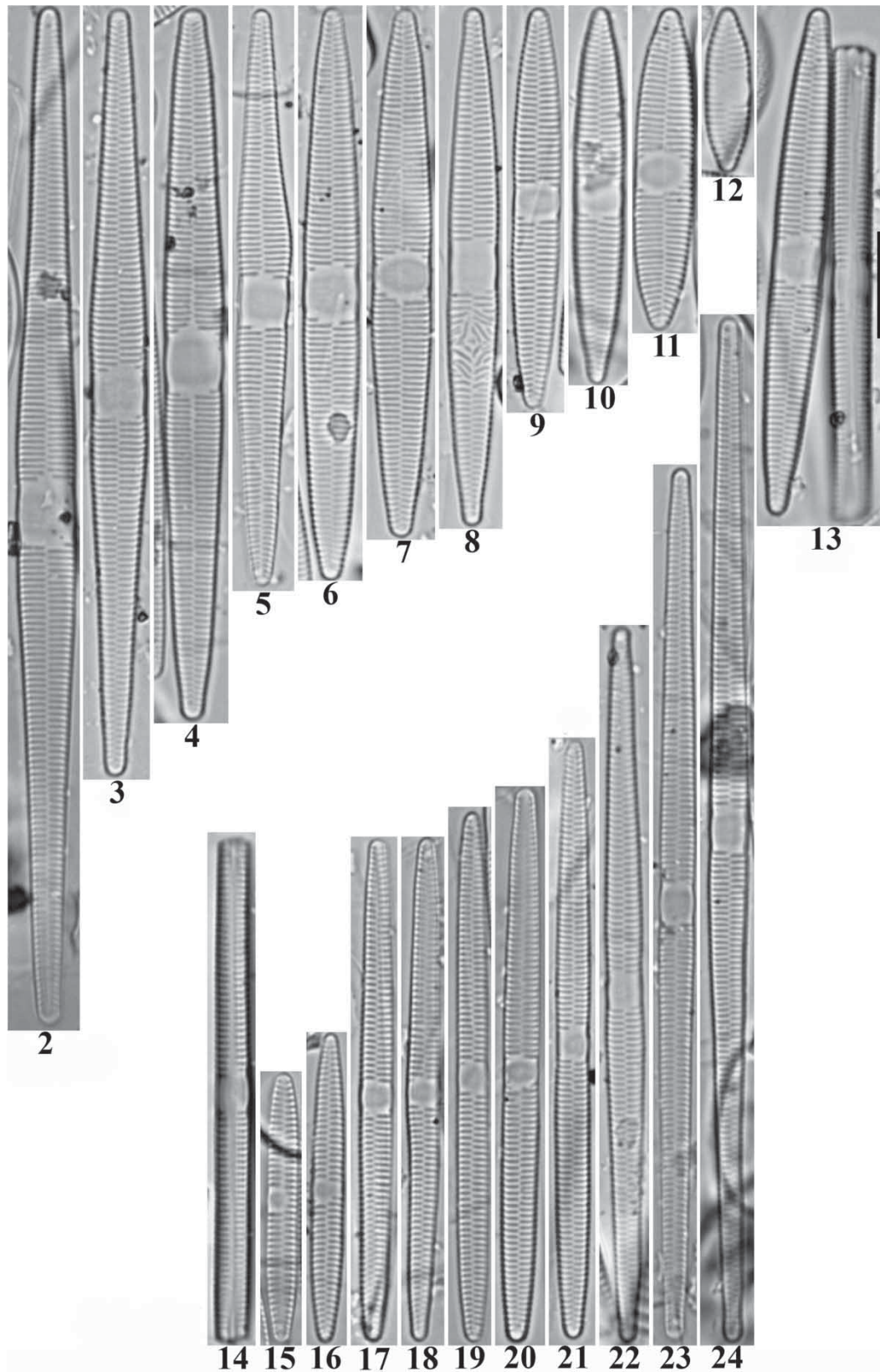
Holotype. Circled specimen on slide BR-4302, National Botanical Garden, Meise, Belgium. Figure 3 is of the holotype.

Isotype. Slide HCUCB D-275, Herbario Criptogámico, Universidad Católica Boliviana, San Pablo, Cochabamba, Bolivia.

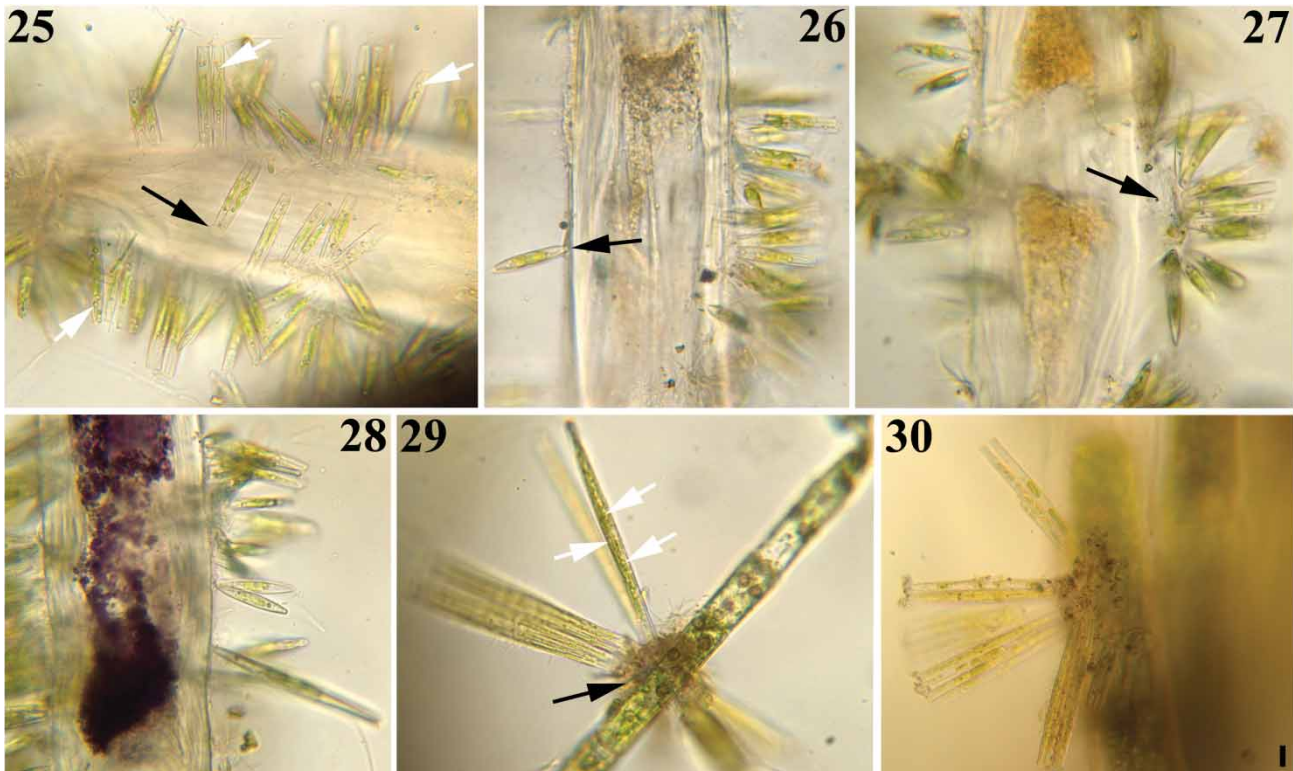
Type locality. Main pier in the eastern side of Tiquina Strait at San Pablo de Tiquina ($16^{\circ}13'S$, $68^{\circ}51'W$), Lake Titicaca, Los Andes Province, Department of La Paz, Bolivia, at 3830 m a.s.l. Collected by E.A. Morales and E. Fernández, 15 February 2010.

Etymology. The specific epithet refers to Lake Titicaca from where the new species was collected.

Ecology. Epiphytic, mainly on *Cladophora* sp., but also on *Rhizoclonium* sp. growing on cement and wooden substrata. Alkalibiontic, eutrathentic, living in shallow clear waters contaminated by motor oil, gasoline and solid waste.



Figs 2–24. Specimens of *Ulnaria titicacaensis* (Figs 2–13) and *U. macilenta* (Figs 14–24) from type material, LM. **Figs 2–13.** Valves showing size variation. **Fig. 3.** Holotype specimen. **Fig. 8.** Teratological valve. **Fig. 13.** Specimens in valve and girdle views. **Figs 14–24.** Valves showing size variation. **Fig. 14.** Frustule in girdle view. **Fig. 21.** Holotype specimen. Scale bar = 10 μm.



Figs 25–30. Epiphytic live material of *Ulnaria titicacaensis* and *U. macilenta* on macroalgae from Tiquina Strait, Lake Titicaca collected in December 2012, LM. **Figs 25–28.** *Ulnaria titicacaensis* growing on *Cladophora* sp. **Fig. 25.** Solitary and paired cells attached to a macroalga by mucilaginous pad (black arrow). White arrows denote the presence of large polyphosphate bodies toward the cell apices. **Fig. 26.** Lateral view of mucilaginous pad (arrow). **Fig. 27.** Pin-cushion-like colony attached to the macroalga by a large mucilaginous pad (arrow). **Fig. 28.** Variability in cell size attached to the macroalga. **Figs 29–30.** *Ulnaria macilenta* growing on *Rhizoclonium* sp. **Fig. 29.** Palisade subgrouping attached by mucilaginous pad (black arrow) to *Oedogonium* sp., with cells showing polyphosphate bodies (white arrows). **Fig. 30.** Several palisade subgroupings within a colony. Scale bar = 10 µm.

Taxonomic remarks. In LM, this species has the typical fragilarioid–synedroid shape in both valve and girdle views (Figs 2–13). Although the apices are in general subrostrate, this feature becomes less evident in larger and smaller valves, in which this region becomes rounded and cuneate, respectively (compare Figs 2–5 with Figs 9–12). The valve central area is very typical in this species, appearing as an oval or square clear region, which may occupy the whole central area (e.g., Figs 2–6) or be shifted to one side by the growth of short bordering striae (Figs 11–12). This fascia gives the impression of being raised because of a central depression that appears as a shadowed central area zone (Figs 2–11, 13).

Growth of this taxon as an epiphyte on *Cladophora* sp. and *Rhizoclonium* sp. (Figs 25–28) presumably starts with the deposition of a small mucilage pad (Fig. 25) that grows as the number of cells in the pin-cushion-like colonies increases (Fig. 27). Although the number of cells in a fully developed colony can be large, the mucilage pads remain relatively flat.

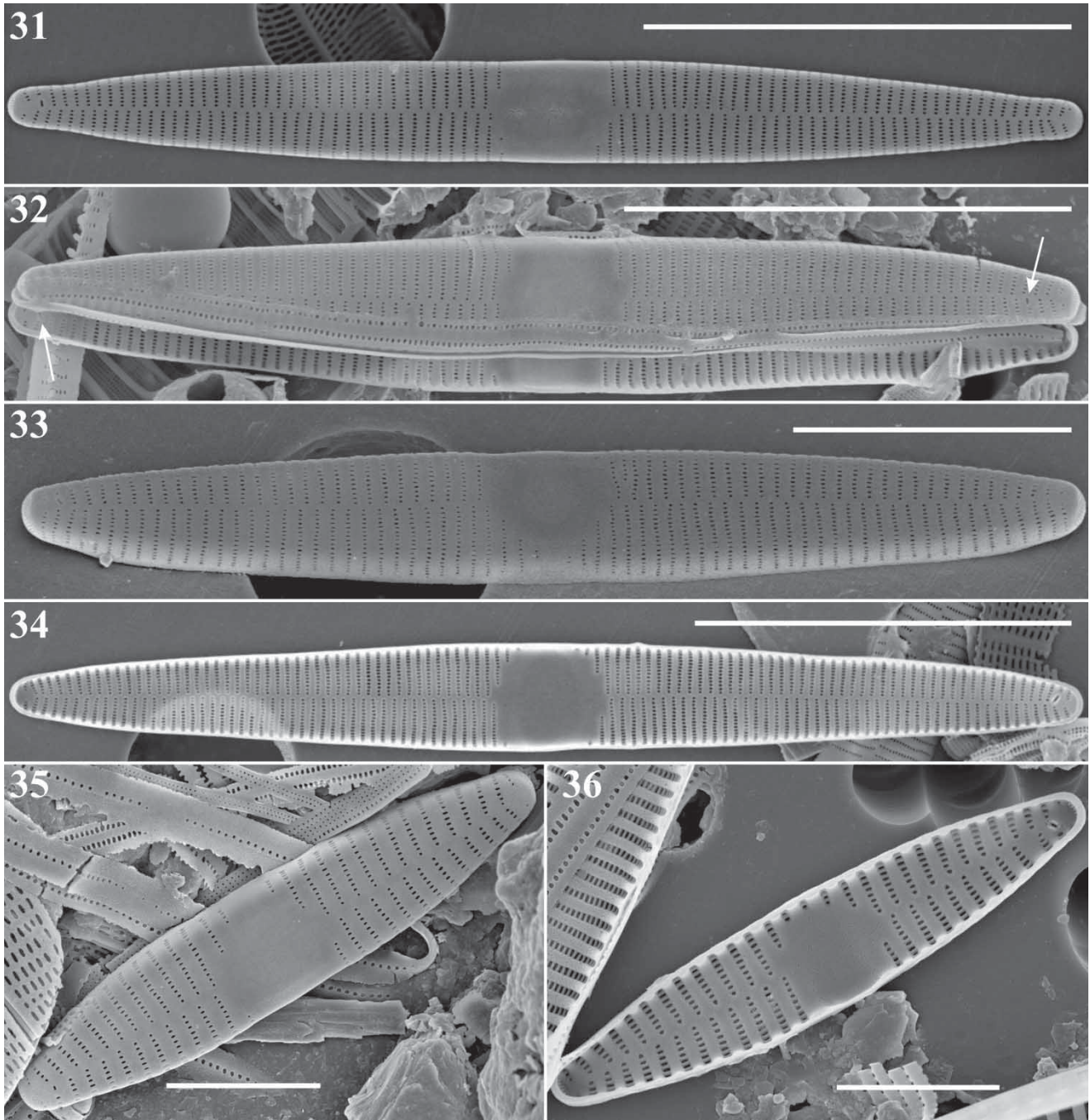
Polyphosphate bodies in live cells are clearly evident as whitish granules, which tend to be located toward the valve ends (Figs 25–28). Although in many cells the distribution

of these bodies does not seem to show a specific pattern, larger bodies are more frequent toward the valve apices (Figs 25–28).

In SEM, this fragilarioid–synedroid appearance is also noticeable (Figs 31–45). The valve outline, striae, rimoportula, apical pore fields and girdle bands resemble those in members of this fragilarioid–synedroid group. The transition between valve face and mantle is steep and no raised costae or depressed striae can be seen in external view (Figs 31–33, 35). The striae can be seen alternating along the axial area, which is consistent in all examined specimens (Figs 31–45). All observed valves show a conspicuous basal thickening along the entire perimeter of the abvalvar region of the valve mantle. However, the thickening is more conspicuous at the valve apices (Figs 34, 36–38, 40, 43, 45).

Ulnaria macilenta E. Morales, C.E. Wetzel & S.F. Rivera sp. nov. (Figs 14–24, 29–30, 46–55)

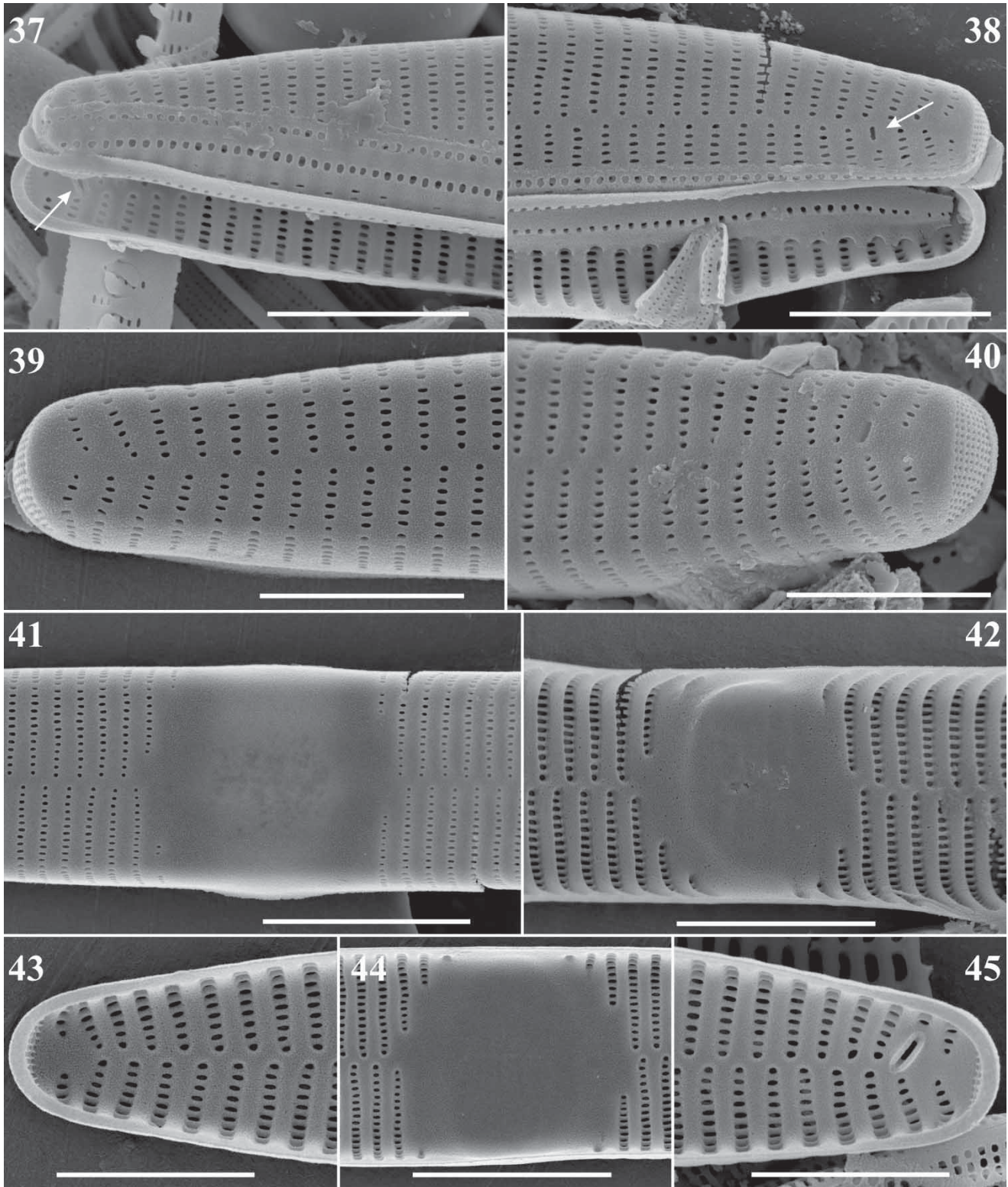
Description. Frustules rectangular in girdle view, attached to macroalgae by a mucilaginous pad, producing pin-cushion-like colonies composed of various palisade subgroupings. Valves linear–lanceolate, with subrostrate to



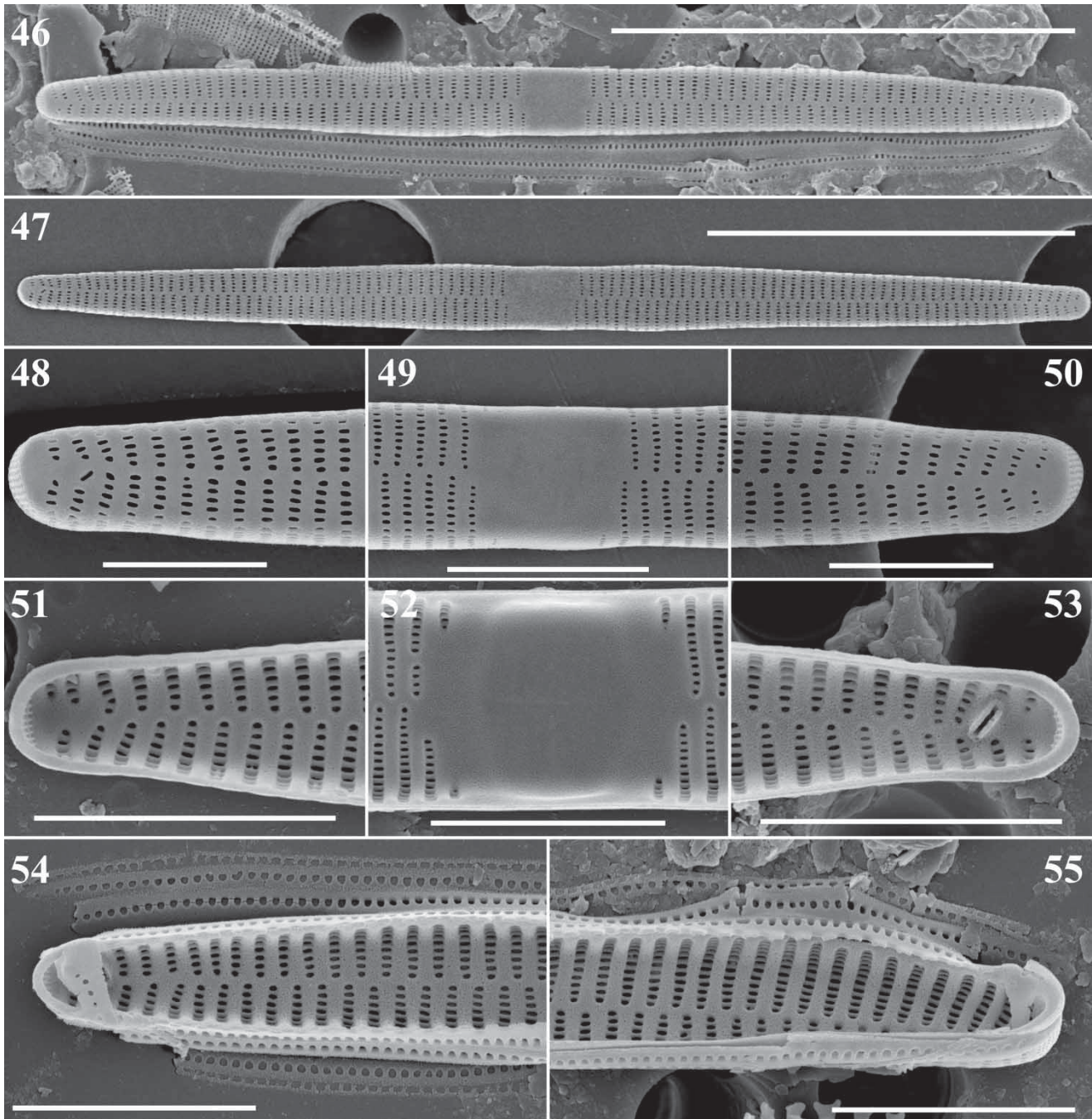
Figs 31–36. Valves of *Ulnaria titicacaensis* from type material, SEM. **Figs 31, 33.** External view of whole valves showing the characteristic axial and central areas, and the position of the rimoportula only present near one apex. **Fig. 32.** Frustule in valve view partially opened up showing dislodged girdle bands with one row of pores, and inner and outer openings of the rimoportula (arrows). **Fig. 34.** Internal view of whole valve showing depression in central fascia, narrow axial area, one rimoportula and striation pattern. **Fig. 35.** External view of a small valve. **Fig. 36.** Internal view of a small valve. Scale bars = 20 μm (Figs 31–32, 34); 10 μm (Fig. 33); 5 μm (Figs 35–36).

broadly rounded apices and a bilaterally gibbous central area. Valve face externally flat and internally slightly undulate due to raised virgae. Transition to mantle steep. Length: 18.5–95.0 μm ; width: 2.5–3.5 μm ; striae: 18–19 in 10 μm ($n = 50$). Central area with large, depressed, square to rectangular fascia, asymmetrical; sometimes conspicuously shifted to one side due to the presence of

shortened striae, or completely clear in other specimens. Central sternum narrow and linear. Striae parallel in the center to slightly radiate toward the apices. Striae run continuously onto the valve mantle, reaching deep into it. Virgae slightly wider than striae and conspicuously internally thickened and raised. Areolae round to oval, with no occlusions observed. Spines absent. Ocellulimbus-type



Figs 37–45. Specimens of *Ulnaria titicacaensis* from type material, SEM. **Figs 37–38.** Frustule apices showing external and internal views of the rimoportula (white arrows), respectively, and perforated girdle bands. Note short fimbriae in Fig. 38. **Figs 39–40.** Apical pore fields on same valve in external view. **Fig. 41.** Quadrangular central fascia in external view. **Fig. 42.** Central fascia in internal view with raised virgae. **Figs 43, 45.** Apices on same valve in internal view. **Fig. 44.** Central fascia in internal view. Scale bars= $5\mu\text{m}$ (Figs 41, 44); $4\mu\text{m}$ (Figs 37–38, 42); $3\mu\text{m}$ (Figs 39–40, 43, 45).



Figs 46–55. Specimens of *Ulnaria macilenta* from type material, SEM external (Figs 46–50) and internal (Figs 51–55) views. **Fig. 46.** Whole valve showing striation, central fascia and axial area, a single rimoportula at one apex and girdle bands with one row of pores. **Fig. 47.** Whole valve with axial area and central fascia, striation and one rimoportula at one apex. **Figs 48, 50.** Apical pore fields on same valve showing striation and only one rimoportula. **Fig. 49.** Central fascia more or less quadrangular in shape. **Figs 51, 53.** Apical region on same valve showing apical pore fields, striation with raised virgae and one rimoportula. **Fig. 52.** Central fascia. **Figs 54–55.** Part of same valve with girdle bands perforated by a single row of pores. Scale bars = 20 μm (Figs 46–47); 5 μm (Figs 49, 51–55); 3 μm (Figs 48, 50).

apical pore fields well-developed, broadly elliptical, bearing neatly arranged rows of round poroids. A single rimoportula present at one apex, aligned with second or third stria on valve face, angled with respect to the valve transapical axis in internal view. Scab-like structures (blisters) not present along abvalvar mantle edge. Girdle bands

bearing round perforations. Valvocopula bears short fimbriae. Open/closed nature of girdle bands not observed. Chloroplasts are plate-like in valve view, with very long tubular lobes in girdle view. They tend to be positioned along the entire cell lumen. Several small polyphosphate bodies present, distributed throughout the cell lumen.

Holotype. Circled specimen on slide BR-4303, National Botanical Garden, Meise, Belgium. Figure 21 is of the holotype.

Isotype. Slide HCUCB D-275, Herbario Criptogámico, Universidad Católica Boliviana, San Pablo, Cochabamba, Bolivia.

Type locality. Main pier in the eastern side of Tiquina Strait at San Pablo de Tiquina (16°13'S, 68°51'W), Lake Titicaca, Los Andes Province, Department of La Paz, Bolivia, at 3830 m a.s.l. Collected by E.A. Morales and E. Fernández, 15 February 2010.

Etymology. The specific epithet refers to the slender valves produced by this species.

Ecology. Epiphytic, mainly on *Oedogonium* sp., but also on *Cladophora* sp. and *Rhizoclonium* sp., growing on wooden and cement substrata. Alkalibiontic, eutrapihentic, living in shallow clear waters contaminated by motor oil, gasoline and solid waste.

Taxonomic remarks. In LM, as a similar valve construction to *U. titicacaensis*, however, the width of the valve is conspicuously much more reduced (Figs 14–24). The subrostrate valve apices are more noticeable in medium to large specimens (Figs 18–24) than in smaller ones. The latter tend to have cuneate (Figs 16–17) or blunt (Fig. 15) apices. The valve central area has a square to rectangular shape and may occupy the entire central area (Figs 17–24) or be shifted to one side of the valve due to the presence of short striae (Figs 15–16). The fascia has also a shadowed area due to the presence of a depression (Figs 15–24).

The epiphytic habit of this taxon on *Oedogonium* sp., *Cladophora* sp. and *Rhizoclonium* sp. is possibly due to the secretion of rather thick mucilage pads in which the cells are inserted by one of their apices (Figs 29–30). One other conspicuous feature of the colonies of this taxon is the production of palisades (Figs 29–30), which are different from the pin-cushion-like colonies produced by synedroid taxa and from the ribbon-like colonies produced by fragilarioid species. In the latter case, contiguous valves are attached by linking spines and in some cases only one of the terminal cell of the colony is attached to the substratum by a mucilage pad or stalk. As it happened in the case of *U. titicacaensis*, spines were not observed in this taxon and all the members of the palisade attach to the mucilage.

Ulnaria macilenta presents polyphosphate bodies which are much smaller, more difficult to see and are randomly distributed throughout the cytoplasm (more evident in Fig. 29).

In SEM, the valve outline, striae, rimoportula, apical pore fields and girdle bands resemble those in needle-like fragilarioid–synedroid diatoms. The transition between the valve face and mantle is also steep in this case, as it was in

U. titicacaensis, and the thickening at the abvalvar end of the mantle is also present (more conspicuous at the valve apices; see Figs 51–53). Also in this case, the striae can be seen alternating along the axial area, a constant feature among individuals (Figs 46–55).

The examination of the type material of *U. colcae* was inconclusive under SEM due to the poor preservation state of the valves. The species presence in the material is confirmed, as well as the fact that it is frequent in it, but valves are eroded to the point that clear images of critical features for comparative purposes could not be taken.

Discussion

The two new species from Lake Titicaca were placed in the genus *Ulnaria* following the criteria used by Van de Vijver & Cocquyt (2009), basically, the absence of spines and lack of ribbon-like colonies holding cells together by spines. Van de Vijver & Cocquyt (2009) also used the closed nature of the cingulum in *U. colcae* as a justification for placing it in *Ulnaria*. Unfortunately, the poor preservation state of the girdle bands in the Lake Titicaca samples has made it difficult to clearly observe the open/closed nature of the girdle bands. Most of these structures were broken or eroded, and only on a few occasions could some girdle bands, still attached to the valves, be observed and appeared to be closed.

Similar to the conclusion reached by Van de Vijver & Cocquyt (2009) for *U. colcae*, *U. titicacaensis* and *U. macilenta* were placed in the genus *Ulnaria*, but the decision is transitory and holds until the distinction between *Fragilaria* Lyngbye and *Ulnaria* can be established using stable synapomorphies (i.e., characters shared among taxa and also present in the most recent ancestor) and not only relying on purely nomenclatural argumentation, as is currently the case (Compère 2001). Recently, Williams (2011) implied that the closed nature of the girdle bands would be the single synapomorphic character to distinguish species in *Ulnaria* from other closely related genera. He disregarded characters such as the number of rimoportula (usually two in *Ulnaria*), the absence/presence and position of spines [usually absent in *Ulnaria*, but present on the virgae in *U. ungeriana* (Grunow) Compère (Morales 2003)], and the ability to form ribbon-like colonies (absent, except in *U. ungeriana*) as pleisiomorphic characters, which are widely distributed among several fragilarioid groups. However, since the type species of the genus *Ulnaria*, *Synedra ulna* (Nitzsch) Ehrenberg, has not been studied in detail in LM or SEM, it is difficult at present to accept closed girdle bands as 'appropriate evidence' in Williams' (2011) terms to define *Ulnaria* as a separate group from *Fragilaria*. As Williams (2011) discussed, it is true, that a large group of fragilarioid diatoms do have closed girdle bands. Williams also implied, and it is agreed, that it is highly probable that these taxa belong in a cohesive group. Furthermore, this group of diatoms should

be separated from *Synedra* Ehrenberg, now a genus comprising marine species which is in agreement with Compère (2001) and Williams (2011). However, it should be noted that *Ulnaria* is based on *U. ulna* (Nitzsch) Compère, a morphologically unknown and uncharacterized diatom at the moment, which is practically impossible to separate from *Fragilaria*. Thus, the use of the name *Ulnaria* remains a purely nomenclatural decision (Van de Vijver & Cocquyt 2009), lacking biological justification until examination of the type material of *Bacillaria ulna* Nitzsch is performed.

Ulnaria titicacaensis was abundant in the sample from Tiquina Strait contributing 28% relative abundance of the total diatom community, along with *Cocconeis* cf. *titicacaensis* Frenguelli and *Diatoma vulgare* Bory (Table 1). By contrast, *U. macilenta* contributed a low 4% relative abundance of the total diatom community. Most recorded taxa from Lake Titicaca that could be identified are commonly reported from eutrophic waters (Table 1; Krammer & Lange-Bertalot 1986, 1988, 1991a, b) and some specimens (<1%) showed valve abnormalities (e.g., Fig. 8) probably due to the presence of oil, gasoline and solid waste contaminants in the water. Both, plankton and epiphytic diatoms living on *Schoenoplectus californicus* ssp. *tatora* were observed under LM, but no valves of the new taxa were found. Whether the new taxa are growing only

on *Cladophora* sp., *Rhizoclonium* sp. and *Oedogonium* sp. requires further study.

These two new species have possibly been reported previously, but under a different name. *Synedra rumpens* var. *fragilarioides* Grunow illustrated by Frenguelli (1939, fig. 11) probably corresponds to *U. titicacaensis*. However, the undulation of the valve outline is somewhat exaggerated in his illustration, as are the subrostrate/subcapitate apices. *Synedra rumpens* var. *fragilarioides* was not observed in the several benthic (epiphyton, epilithon) and planktonic samples taken by us from Lake Titicaca. Servant-Vildary (1991) did not report any diatom similar to these new species of *Ulnaria*.

The valve dimensions and stria density are of limited use in distinguishing the new species from similar taxa; however, features around the central area and the lack of colonies seem more effective as separating characters (Table 2). The two new species of *Ulnaria* from Lake Titicaca show a clear bilateral central area as in *Fragilaria capucina* Desmazières, *F. parva* (Grunow) Tuji & D.M. Williams, *F. rhabdosoma* Ehrenberg, *F. fragilarioides* (Grunow) Cholnoky, *F. rumpens* var. *meneghiniana* (Grunow) H.P. Gandhi and *F. socia* (J.H. Wallace) Lange-Bertalot. However, all of the latter fragilarioid species form ribbon-shaped colonies with cells held together by spines, whereas both *U. titicacaensis* and *U. macilenta* form pin-cushion-like colonies, with palisade subgroupings in the case of *U. macilenta*. A unilateral central area is sometimes present in small specimens of *F. rhabdosoma* and *F. socia*, but this is unusual, just as it happens in smaller specimens of the new species from Lake Titicaca (see Figs 11–12, 15). It is, therefore, recommended that the type of colony be used for the identification of these species.

Fragilaria nyansae (G.S. West) Lange-Bertalot and *F. perminuta* (Grunow) Lange-Bertalot have a unilateral clear central area (absent in *F. nyansae*) and both form ribbon-like colonies, whereas the two new Lake Titicaca *Ulnaria* species have a bilateral clear central area and no ribbon-like colonies. *Fragilaria capitellata* (Grunow) J.B. Petersen is also different from the two Lake Titicaca species in that it does not produce ribbon-like colonies because it lacks spines (see Tuji & Williams (2008a)) and it has a unilateral central area. In addition, the valve outline is lanceolate with strongly apiculate apices in *F. capitellata*, different from the new Lake Titicaca *Ulnaria* taxa.

Ulnaria colcae is the closest species to *U. titicacaensis* and *U. macilenta* from Lake Titicaca (Van de Vijver & Cocquyt 2009). These three species cannot be easily distinguished in LM, therefore, SEM is required to observe features specific to each species. In LM, the valves of *U. colcae* are very similar to those of *U. titicacaensis*, but generally the shorter valves had a more broadly lanceolate outline and broadly rounded to subrostrate apices for *U. colcae*. However, these features are not reliable since they showed some variability in the population depicted by Van de Vijver & Cocquyt (2009). In SEM, the distinction

Table 1. Species composition and relative abundance of the diatom community in type material of *U. macilenta* sp. nov. and *U. titicacaensis* sp. nov. from Lake Titicaca.

Taxon	Abundance (%)
<i>Amphora</i> sp. 1 TITICACA	0.8
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	0.4
<i>Cocconeis</i> cf. <i>titicacaensis</i> Frenguelli	20.8
<i>Diatoma tenuis</i> C. Agardh	3.2
<i>D. vulgare</i> Bory	18.8
<i>D. vulgare</i> cf. var. <i>linearis</i> Grunow	0.8
<i>Encyonema auerswaldii</i> Rabenhorst	0.4
<i>Fragilaria</i> cf. <i>crotonensis</i> Kitton	0.8
<i>Gomphonema</i> cf. <i>minutum</i> (C. Agardh) C. Agardh	2.8
<i>G.</i> sp. 1 TITICACA	0.8
<i>G.</i> sp. 2 TITICACA	0.8
<i>Navicula gregaria</i> Donkin	2.0
<i>N. lanceolata</i> Ehrenberg	0.8
<i>N. perminuta</i> Grunow	0.8
<i>N. tripunctata</i> (O.F. Müller) Bory	1.6
<i>N. veneta</i> Kützing	0.8
<i>N.</i> sp. 2 TITICACA	2.4
<i>Nitzschia</i> cf. <i>capitellata</i> Hustedt	0.8
<i>N.</i> cf. <i>inconspicua</i> Grunow	0.4
<i>N.</i> cf. <i>radicula</i> Hustedt	1.2
<i>N. dissipata</i> (Kützing) Grunow	0.8
<i>N. paleacea</i> Grunow	2.0
<i>N. paleaeformis</i> Hustedt	3.6
<i>N. recta</i> Hantzsch ex Rabenhorst	0.4
<i>Ulnaria macilenta</i> sp. nov.	4.0
<i>U. titicacaensis</i> sp. nov.	28.0

Table 2. Comparison of biometric data and morphological features between *U. macilenta* sp. nov. and *U. titicacaensis* sp. nov. with closely related *Fragilaria* taxa from the literature.

Variables	<i>U. macilenta</i>	<i>U. titicacaensis</i>	<i>F. capitellata</i>	<i>F. capucina</i>	<i>F. nyansae</i>	<i>F. parva</i>	<i>F. perminuta</i>	<i>F. rhabdosoma</i>	<i>F. fragilarioides</i>	<i>F. rumpens</i> var. <i>meneghiniana</i>	<i>F. socia</i>
Valve length (µm)	18.5–95.0	15.5–98.5	20–39 ²	25.6–67.5 ³	91–150 ⁴	31.0–40.5 ⁴	9–24 ²	20.8 ⁵ 15.6–28.3 ⁶	40–60 ⁷ 35.5–55.2 ⁸ (24.4) 31.5–66.4 ⁹	43.0–48.2 ¹⁰	16–72 ¹
Valve width (µm)	2.5–3.5	4.0–6.5	3–4 ¹	3.1–3.8 ²	10–13 ³	2.5–3.0 ⁴	3.0–3.5 ¹	3.3–3.9 ⁶	4.2–4.5 ⁸ 3.4–4.9 ⁹	3.3–3.5 ¹⁰	3.5–4.0 ¹
Striae in 10 µm	18–19	16–18	17–19 ¹	ca. 15–16 ²	14–15 ³	ca. 20 ⁴	18–19 ¹	ca. 18–20 ⁶	10.0–10.5 ⁷ 11–12 ⁸ 9–14 ⁹	12.5–13.3 ¹⁰ 12–14 ¹¹	17 ¹
Valve outline	Linear–lanceolate	Lanceolate	Lanceolate	Linear	Linear	Lanceolate	Lanceolate	Linear–lanceolate	Lanceolate	Lanceolate	Lanceolate
Apex	Substrate to broadly rounded	Substrate	Strongly apiculate	Weakly rostrate	Protracted, subcapitate–rostrate, > 4 µm wide	Capitate	Slightly rostrate	Weakly rostrate	Weakly rostrate	Weakly rostrate	Weakly rostrate
Central area	Asymmetrical, with a large, depressed, square to rectangular fascia; sometimes shifted to one side or completely clear	Bilaterally gibbous; asymmetrical, with a large, depressed, square to rectangular fascia; sometimes shifted to one side or completely clear	Unilateral, often expanded just until the sternum	Rectangular to rhombic	Absent	Bilateral, characteristic swellings	Strongly unilateral	Characteristic swellings, slightly unilateral in small specimens, bilateral in larger specimens	Characteristic swellings, bilateral	Characteristic swellings, bilateral	Slightly unilateral, bilateral in larger specimens
Striation	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	n.d.	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices	Alternate, parallel to slightly radiate toward the apices
Ribbon-like colony	Present, but attached in pin cushion-like colonies	No	No	Present	n.d.	Present	Present	Present	Present	Present	n.d.
Number of rimoportula	1	1	1	2	n.d.	n.d.	n.d.	1	2	n.d.	n.d.
Apical pore field	Ocellulimbus-type, well-developed, broadly elliptical, bearing neatly arranged rows of round poroids	Ocellulimbus-type, well-developed, broadly elliptical, bearing neatly arranged rows of round poroids	Rectangular	Rectangular, bearing neatly arranged rows of poroids	n.d.	n.d.	n.d.	Rectangular, bearing neatly arranged rows of poroids	n.d.	n.d.	n.d.
Girdle band	Bearing round occlusions; open/close nature not observed	Bearing round occlusions; open/close nature not observed	n.d.	Open bands, each with a single row of small pores	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Spine	Absent	Absent	Absent	Present	n.d.	n.d.	n.d.	Present	n.d.	n.d.	n.d.
Reference	This study	This study	Tuji & Williams (2008a) ¹	Tuji & Williams (2006) ²	West (1907) ³	Tuji & Williams (2008b) ⁴	Tuji & Williams (2008a) ¹	Ehrenberg (1835) ⁵ , Tuji (2004) ⁶	Cleve-Euler (1953) ⁷ , Cholnoky (1963) ⁸ , Ludwig & Flôres (1997) ⁹	Gandhi (1964) ¹⁰ , Van Heurck (1881) ¹¹	Tuji & Williams (2008a) ¹

Notes: n.d.: no data.

Superindices in rows 1–3 indicate references from which measurements were taken. These references are listed in the last row of the table.

becomes more evident. The valve surface in *U. colcae* is undulate due to the raised virgae. In *U. titicacaensis*, this feature can also be seen, especially on the virgae in the valve–mantle area, but to a lesser extent than in *U. colcae* (compare Figs 39–40 with fig. 42 in Van de Vijver & Cocquyt (2009)). In addition, the striae extend deep onto the valve mantle in *U. colcae*, almost reaching the abvalvar margin where they stop before a thin ridge that runs along the entire abvalvar margin perimeter. This ridge is not present in *U. titicacaensis* and the striae stop shortly before the abvalvar mantle margin, leaving a clear unornamented area around the entire valve perimeter. A final difference is that there are small scab-like depositions on the abvalvar side of the mantle in *U. titicacaensis*, features that are absent in *U. colcae*. These siliceous depositions lie in the space between the stria ends and the edge of the mantle, space that is absent in *U. colcae*. The differences between *U. colcae* and *U. macilenta* are the same as those stated above (except that there is also an absence of scab-like structures in *U. macilenta*), but there are also notable differences in width and striation, *U. macilenta* being consistently narrower and having a higher stria density. These differences may appear subtle and will have to be confirmed with further studies of the type material of *U. colcae*. Even though an attempt was made to study this material, its state of preservation did not allow a clear observation of the diagnostic features. All comparisons presented here are based on Van de Vijver & Cocquyt (2009) at the time *U. colcae* was described.

The two new species from Lake Titicaca can be distinguished from each other using the growth form, the valve outline and the width of valves (Table 2). *Ulnaria titicacaensis* was found mainly on *Cladophora* sp. on which it produces extensive growths alongside *Diatoma vulgaris*. It was less abundant on *Rhizoclonium* sp. where it shares space with *U. macilenta*. *Ulnaria titicacaensis* cells grow in groups as pin-cushion-like colonies (Figs 25, 27), but can also be found solitary (Fig. 26) or in pairs (Fig. 25, arrow). By contrast, *U. macilenta* grows mainly on *Oedogonium* sp., sometimes solitary, but most commonly as palisade groupings (Figs 29–30), attached to the substrate by a large mucilaginous deposition (Fig. 29, arrow). This type of colony is reported in the genus *Ulnaria* for the first time and may serve as a reliable diagnostic feature for *U. macilenta*. This diatom was also observed growing on *Cladophora* sp. and *Rhizoclonium* sp. filaments, on which it forms the same type of colony.

Another difference between the two new *Ulnaria* species is the shape of the plastids, which are H-shaped in *U. titicacaensis* and plate-like in *U. macilenta*. Plastids have not been used to distinguish species within *Ulnaria*, but the differences observed in the Lake Titicaca material suggest that such features could be useful for this purpose.

Finally, the difference in the size and distribution of polyphosphate bodies in *U. titicacaensis* (large and mainly located near the apices) and *U. macilenta* (small and present

throughout the whole cell lumen) point towards another distinguishing feature between the two species and it suggests that there could be a wider diagnostic use of these structures for species within the genus. Round *et al.* (1990) stated that these bodies can be used reliably for some raphid diatoms, but their use for araphid diatoms merits further studies.

One other feature that seems different between the two species is the presence of blisters on the abvalvar mantle margin in *U. titicacaensis*, whereas these structures are absent in *U. macilenta*. Whether blisters are reliable diagnostic features cannot be determined from the literature and more studies are needed regarding this issue.

The reason for the lack of areolar substructures in both of the new species remains unclear. It is probable that occluding structures have been lost during preparation of the material, as frequently happens with most species of *Fragilaria* and *Ulnaria*. The observation of a high state of dissolution in diatoms from some epilithic and pelagic samples from Lake Titicaca might partly explain the lack of closing plates; however, as depicted from our SEM data, the rest of the valve features seem to be well preserved.

Ulnaria titicacaensis and *U. macilenta* are only two of several species that need to be described as new from Lake Titicaca. The frequent portrayal of the Lake Titicaca diatom flora as poorly diverse is rather unjustified as it was based on the analysis of a low number of samples (Freguelli 1939, Servant-Vildary 1991). Therefore, this flora needs to be updated through systematic studies which undoubtedly will yield a taxa list that is much larger than is currently known (Freguelli 1939, Theriot *et al.* 1985, Servant-Vildary 1991, Tapia *et al.* 2004).

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