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Morphology, ecology and biogeography of *Stauroneis pachycephala* P.T. Cleve (Bacillariophyta) and its transfer to the genus *Envekadea*

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Stauroneis pachycephala was described in 1881 from the Baakens River, Port Elizabeth, South Africa. Recently, it was found during surveys of the MacKenzie River (Victoria, Australia), the Florida Everglades (USA) and coastal marshes of Louisiana (USA). The morphology, ecology and geographic distribution of this species are described in this article. This naviculoid species is characterised by lanceolate valves with a gibbous centre, a sigmoid raphe, an axial area narrowing toward the valve ends, and capitate valve apices. The central area is a distinct stauron that is slightly widened near the valve margin. The raphe is straight and filiform, and the terminal raphe fissures are strongly deflected in opposite directions. Striae are fine and radiate in the middle of the valve, becoming parallel and eventually convergent toward the valve ends. The external surface of the valves and copulae is smooth and lacks ornamentation. We also examined the type material of *S. pachycephala*. Our observations show this species has morphological characteristics that fit within the genus *Envekadea*. Therefore, the transfer of *S. pachycephala* to *Envekadea* is proposed and a lectotype is designated.

Keywords: diatoms, morphology, *Stauroneis pachycephala*, ecology, *Envekadea*, biogeography, taxonomy, lectotype

Introduction

Recent revisionary efforts on the classification and phylogeny of diatoms have targeted the naviculoid diatoms and recognised the importance of valve ultrastructure, protoplast organisation, molecular sequences, ecological and geological ranges, sexual compatibility and biogeography in defining relationships and diversity within this heterogeneous group (Round & Sims 1981, Round et al. 1990, Mann 1999, Spaulding et al. 1999). Revisions have resulted in the resurrection of old or the description of numerous new genera, split off from the catch-all genus *Navicula* s.l. Bory de St. Vincent (Round et al. 1990). The genus *Envekadea* Van de Vijver et al. was described to include naviculoid diatoms with a sigmoid raphe, non-porous copulae, and large, rectangular to polygonal areolae closed by external hymenes (Gligora et al. 2009). Members of this genus are distributed across a broad ecological spectrum

from marine to oligotrophic freshwaters (Gligora et al. 2009). To date, five species of *Envekadea* have been recognised (Gligora et al. 2009, Graeff et al. 2013, Lee et al. 2013), including *Envekadea pseudocrassirostris* (Hustedt) Van de Vijver, Gligora, Hinz, Kralj & Cocquyt, *E. hedinii* (Hustedt) Van de Vijver, Gligora, Hinz, Kralj & Cocquyt, *E. metzeltinii* Lee, Tobias & Van de Vijver, *E. palestinae* (Gerloff, Natour & Rivera) Lee, Tobias & Van de Vijver and *E. vanlandinghamii* Graeff, Kociolek & S.R. Rushforth.

Stauroneis pachycephala P.T. Cleve has morphological features that conform to *Envekadea*. *Stauroneis pachycephala* was described in 1881 from the Baakens River, Port Elizabeth, South Africa, and was subsequently reported from Australia (Foged 1978, John 1983, 1993, Gell & Gasse 1994, Hodgson 1995, Vyverman et al. 1995, Hodgson et al. 1997, Haynes et al. 2007, Taukulis & John 2009), New Zealand (Foged 1979), Sweden (Cleve-Euler 1953), Sri

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Lanka, Cuba and Papua New Guinea (Foged 1976, 1984, Vyverman 1991).

In this article, we provide morphological, ecological and biogeographical analyses of *S. pachycephala* based on new collections from Victoria (Australia), Florida (USA), Louisiana (USA), and compare these with type material from South Africa. The transfer of *S. pachycephala* to *Envekadea* is proposed and a lectotype is designated.

Material and methods

Study sites

The MacKenzie River is located on the northern slopes of the Grampians National Park in Victoria, southeast Australia. The river receives a substantially modified and engineered flow regime since the construction of the Wartook Reservoir in 1887 (SKM 2002, Atazadeh *et al.* 2012). The river is one of the main tributaries of the Wimmera River and flows ~ 50 km from the Wartook Reservoir before joining the Wimmera River. The catchment lies to the south of the city of Horsham and covers an area of ~ 597 km² (WCMA 2004). The upstream section of the river receives water for most of the year, providing a water supply for the city of Horsham. However, the lower part of the river is ephemeral and flows vary depending on withdrawals for consumption (WCMA 2004). Despite the irregular flow regime, riparian vegetation is present along the length of the river and the river supports a range of aquatic fauna, such as brown trout (*Salmo trutta* Linnaeus), eastern gambusia (*Gambusia holbrooki* Girard) and platypus (*Ornithorhynchus anatinus* Shaw) (WCMA 2004).

The second site studied was the Florida Everglades, USA. This large wetland extends from Lake Okeechobee in the north to Florida Bay in the south, and includes both freshwater marsh in the interior and saline marsh along the coast. The Everglades has a distinct wet and dry season controlled by the subtropical climate and hydrologic management. Anthropogenic modification for water storage and flood control to support agricultural activity and urban populations beginning in the early 1900s have altered the broad, slow-moving sheet flow of water across the Everglades landscape into a complex network of channelised and controlled flow into distinct compartments, including Water Conservation Areas (WCAs) and the Everglades National Park (Light & Dineen 1994). Much of the Everglades has a shallow peat layer that allows biogeochemical interactions between the limestone bedrock, groundwater and biota, producing hard-water conditions and thick, calcareous periphyton assemblages (Gaiser *et al.* 2011, Hagerthey *et al.* 2011). In WCA-1 (the Arthur R. Marshall Loxahatchee National Wildlife Refuge), however, a much deeper peat layer produces soft-water conditions and loose, flocculent assemblages with a distinct species composition (Harvey & McCormick 2009, Gaiser *et al.* 2011). Common Everglades wetland vegetation includes sawgrass (*Cladium jamaicense*), spikerush (*Eleocharis* spp.) and

water lily (*Nymphaea odorata*), and common aquatic fauna include mosquitofish (*Gambusia holbrooki*), largemouth bass (*Micropterus salmoides*) and American alligator (*Alligator mississippiensis*) (Davis & Ogden 1994).

The third region studied was the coastal marsh in the Chenier Plain of southwest Louisiana, USA. The Louisiana coastal marsh can be divided into two geomorphic zones: the Mississippi Delta plain on the southeast coast and the Chenier Plain of the southwest with the dividing line located near Vermillion Bay (29°43'11"N, 91°58'34"W). The Chenier Plain extends from Vermillion Bay to the Texas state border and includes over 6000 km² of coastal marshes. It was formed by deposits of fine-grained sediments of the Mississippi River during the Middle to Late Holocene. A series of regressive–transgressive phases created relict beach ridges (called ‘cheniers’) within a 30-km wide coastal plain of low-energy fresh, brackish and saline marshes (McBride *et al.* 2007). The cheniers act as barriers, reducing tidal flow to some areas of the marsh. The sediments are largely fine-grained silts and clays, with large amounts of organics and peat. Vegetation follows a general north–south salinity gradient of fresh to brackish to saline marsh. Diatom samples were collected from a network of permanent wetland-monitoring stations located throughout coastal Louisiana, the Coastwide Reference Monitoring System (CRMS; Steyer 2010, Folse *et al.* 2012). The CRMS was designed to monitor coastal habitats in Louisiana and evaluate the effectiveness of wetland restoration strategies (<http://lacoast.gov/crms2/>; Steyer 2010, Smith 2012).

Benthic diatom samples from Australia were collected using standard methods (e.g. Stevenson & Bahls 2006). Physical and chemical characteristics of the water, including temperature, pH, specific conductivity and dissolved oxygen were measured *in situ* using a Horiba multimeter (Water checker U-10). Total nitrogen (TN), dissolved phosphorus (PO₄-P) and total suspended solids (TSS) were measured in the laboratory using a Hach DR 2800 spectrophotometer. Diatom samples were digested in 10% H₂O₂ at 90°C on a hotplate for two hours, after which two drops of 10% HCl were added. Samples were topped up with distilled water and left to settle overnight, the supernatant was discarded, and this process was repeated at least four times (Battarbee 1986). Permanent slides were prepared using the mountant Naphrax®. Diatoms were identified using a Nikon Eclipse 80i microscope equipped with differential interference contrast (DIC). For scanning electron microscopy (SEM), the rinsed samples were resuspended in a solution of deionised water and household bleach (50 : 1) for 30 min and rinsed three times in distilled water. Diatom suspensions were dried directly on 22 mm aluminium stubs and gold coated with a Dynavac Xenosput sputter coater. Frustules were imaged in a Philips XL30 field-emission scanning electron microscope, with a working voltage of 2.0 kV and spot size 2. Material and samples from Florida and Louisiana were collected and prepared as noted in Lee *et al.* (2013) and Smith (2012), respectively, and studied

using an Olympus BX51 light microscope equipped with full immersion DIC optics capable of $\times 1000$ magnification. Permanent slides (or duplicates) of all collections that were microscopically analysed have been deposited at the Academy of Natural Sciences of Drexel University in Philadelphia (ANSP), the National Botanic Garden of Belgium (BR; Meise) and the Canadian Museum of Nature (CANM).

Additional material examined for this study included exsiccatum Nr. 197 for *Stauroneis pachycephala* (Cleve & Møller 1879; South Africa [Cape of Good Hope] Baakens River, Port Elizabeth) from the Diatom Herbarium, ANSP and the isotype slide (ANSP GC64419) of *S. pachycephala* var. *alaskana* Foged (1981) from Kuzitrin Lake, Alaska.

Results

Envekadea pachycephala (P.T. Cleve) I. Atazadeh & M.B. Edlund comb. nov. (Figs 1–39)

Basionym. *Stauroneis pachycephala* P.T. Cleve 1881, p. 15; pl. 3, fig. 43.

Lectotype. Here designated as the specimen (Fig. 13) located 9.4 mm E \times 5.8 mm S from the origin marked on slide ANSP Cleve & Møller 197.

Remarks. *Stauroneis pachycephala* was included in Cleve & Møller's (1878, and not 1879 as erroneously reported several times by various authors) list of species present in exsiccatum 197. However, this record must be considered as a *nomen nudum*, because the name was published without a valid description or diagnosis (ICBN Art. 38, McNeill et al. 2012). Therefore the valid description in Cleve (1881) is taken as the basionym.

Australian material. Cells solitary, frustules rectangular in girdle view with rounded capitate apices (Figs 1–11). Valves linear–lanceolate with convex margins, gradually narrowing towards capitate, broadly rounded valve apices. Valve dimensions ($n = 30$): length 43.1–58.0 μm , breadth 7.0–9.0 μm , length : breadth 5.2 : 6.5, breadth of apex 5.4–6.7 μm , breadth of constriction 4.6–6.0 μm . Axial area very narrow, linear. Central area forming a large and distinct stauros, slightly widening towards the valve margin. Raphe straight and filiform. Proximal raphe ends slightly expanded. Distal raphe fissures hooked towards opposite sides and widening at their ends. Striae radiate in the middle becoming convergent near the apices, 27.0–30.3 in 10 μm .

South African material (lectotype; ANSP Cleve & Møller Nr. 197). The lectotype slide of *S. pachycephala* was examined during this study. Cleve described *S. pachycephala* in 1881 from the Baakens River, Port Elizabeth, South Africa:

(valves) Linear, gibbous in the middle and at the ends, which are broadly rounded and capitate. Striae oblique, very fine,

about 29 in 0.01 mm. (29 in 10 μm), reaching the median line. Stauros reaching the margin. Median line straight. Terminal nodules turned opposite direction. Length 0.055 mm (55 μm). Breadth 0.009 mm (9 μm).

Valves lanceolate with the valve outline narrowing abruptly from the valve centre to the subparallel sides, then expanding to the capitate valve apices (Figs 12–15). Valve dimensions ($n = 23$): length 44.8–60.0 μm , breadth 8.0–10.0 μm , length : breadth 5.2–6.5, breadth of apex 5.4–6.7 μm , breadth of valve constriction 4.5–6.0 μm . Central area forming a distinct stauros, abruptly widening near the valve margin. Raphe straight and filiform. Distal raphe fissures deflected in opposite directions. Striae fine, radiate in the valve centre, becoming parallel mid-valve and convergent at the valve ends, 24.4–29.4 in 10 μm .

African specimens show slight differences in valve outline compared with other populations, with margins that narrow more abruptly away from the valve centre, with larger specimens having nearly parallel sides tapering to capitate ends. The sample from South Africa contains an alkaline or brackish diatom assemblage dominated by *Mastogloia* G.H.K. Thwaites in W. Smith, *Plagiotropis* E. Pfitzer and several brackish *Navicula* J.B.M. Bory de Saint-Vincent species.

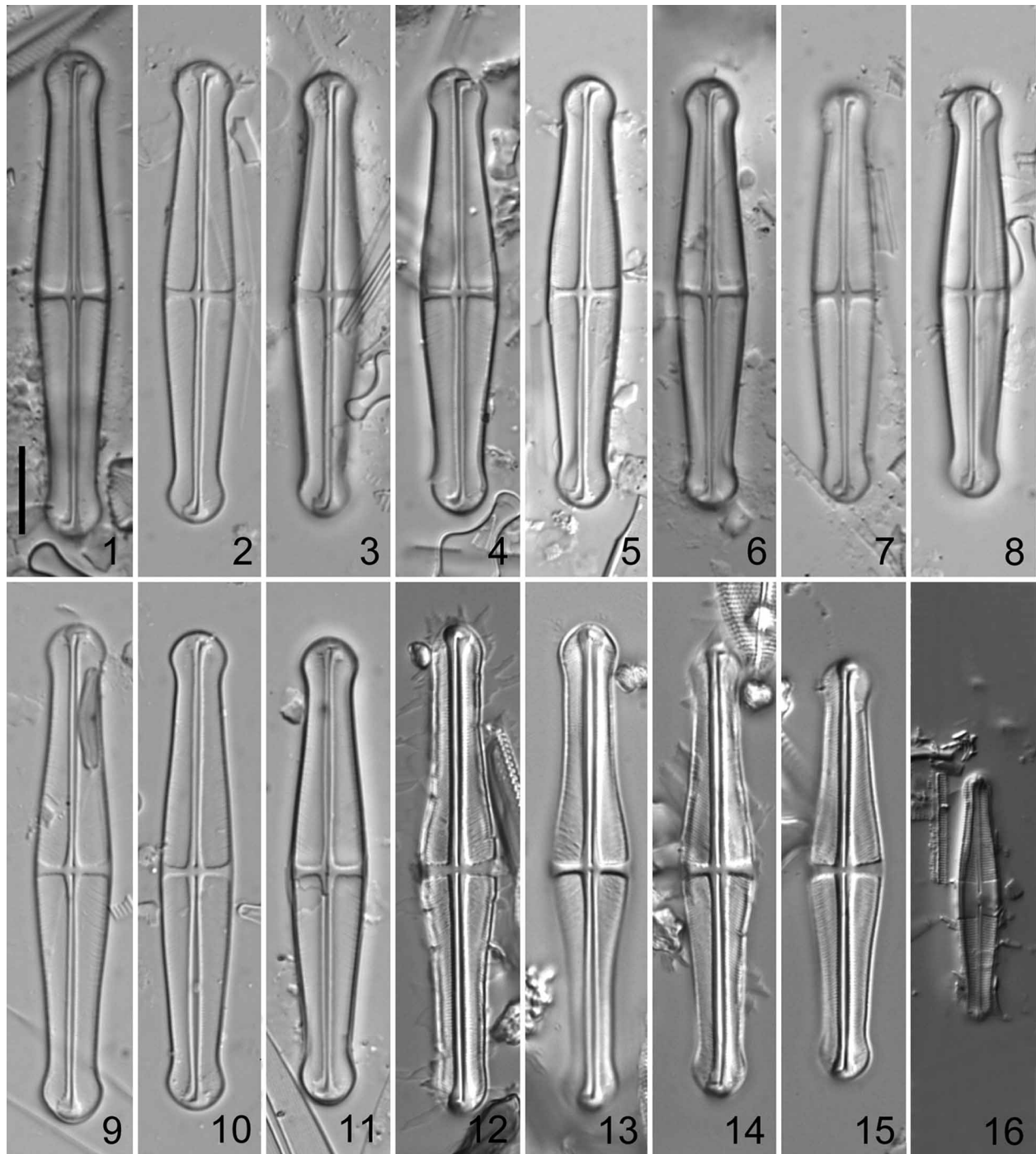
North American material. In 1981, Foged described *S. pachycephala* var. *alaskana* Foged from Alaska, USA. A specimen found on the isotype slide (Fig. 16) conforming to the original illustration and description of *S. pachycephala* var. *alaskana* belongs to *Caloneis* P.T. Cleve and is not treated further here. Recently, *E. pachycephala* was found during a survey in the Florida Everglades. The taxon is rare in Florida, but the highest abundances were observed in WCA-1, a distinctive, soft-water environment within the Everglades (E. Gaiser, unpublished data).

Valves lanceolate, raphe sigmoid, axial area narrowing toward the valve ends, and capitate valve apices. The central area a distinct stauros that is slightly widened near the valve margin (Figs 17–24). Valve dimensions ($n = 16$): length 34–46.4 μm , breadth 6.7–8.6 μm , length : breadth 5.2–6.2, constriction breadth 3.5–4.6 μm , apex breadth 4.9–5.7 μm , 27.8–29.4 striae per 10 μm .

Samples from Florida were dominated by acidophilic species such as *Brachysira brebissonii* R. Ross in Hartley and *Frustulia crassinervia* (Brébisson) Lange-Bertalot & Krammer in Lange-Bertalot & Metzeltin.

Additional North American populations of *E. pachycephala* were found in coastal marshes in Louisiana (USA; Smith 2012).

Valves lanceolate with an expanded valve centre that narrowed toward a constriction that subtended capitate valve apices (Figs 25–32). Valve dimensions ($n = 15$): length 34.8–50.3 μm , breadth 7.0–8.3 μm , length : breadth 5.0–6.4, breadth at constriction 3.6–4.6 μm , breadth at apex 4.8–6.2 μm . Striae radiate at the valve centre, becoming



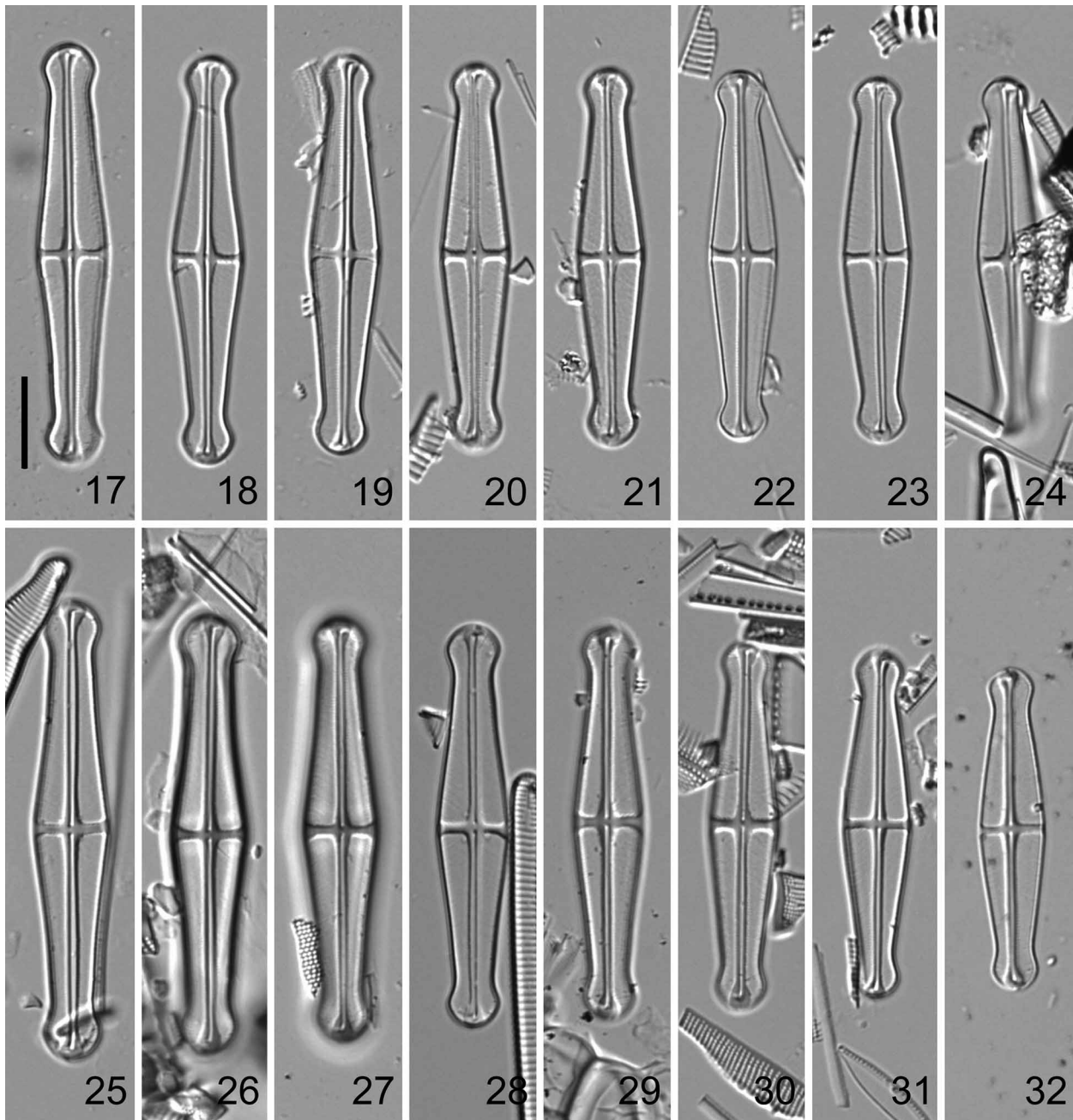
Figs 1–16. *Envekadea* species, light micrographs, DIC, scale bar = 10 μm . **Figs 1–8.** *Envekadea pachycephala* MacKenzie River, Wartook Outlet, Victoria, Australia (ANSP GC40128, CANA 87195, BR-4323). **Figs 9–11.** *Envekadea pachycephala* Wartook Reservoir, Victoria, Australia (ANSP GC40129, BR-4324). **Figs 12–15.** *Envekadea pachycephala*, Cl. & Møller exsiccatum Nr. 197 (ANSP Cleve & Møller 197), South Africa, Cape of Good Hope, Baakens River, Port Elizabeth. Fig. 13. Lectotype specimen. **Fig. 16.** Isotype slide of *Stauroneis pachycephala* var. *alaskana* Foged (1981) from ANSP GC64419 (Kuzitrin Lake, Alaska); this taxon belongs in the genus *Caloneis*.

parallel and eventually convergent at the valve ends, 26.3–30.3 striae per 10 μm .

In Louisiana, *E. pachycephala* was found in association with diverse *Eunotia* Ehrenberg and *Pinnularia* Ehrenberg species as well as *Nitzschia obtusa* W. Smith and

Nitzschia scalaris (Ehrenberg) W. Smith in brackish sites (Smith 2012).

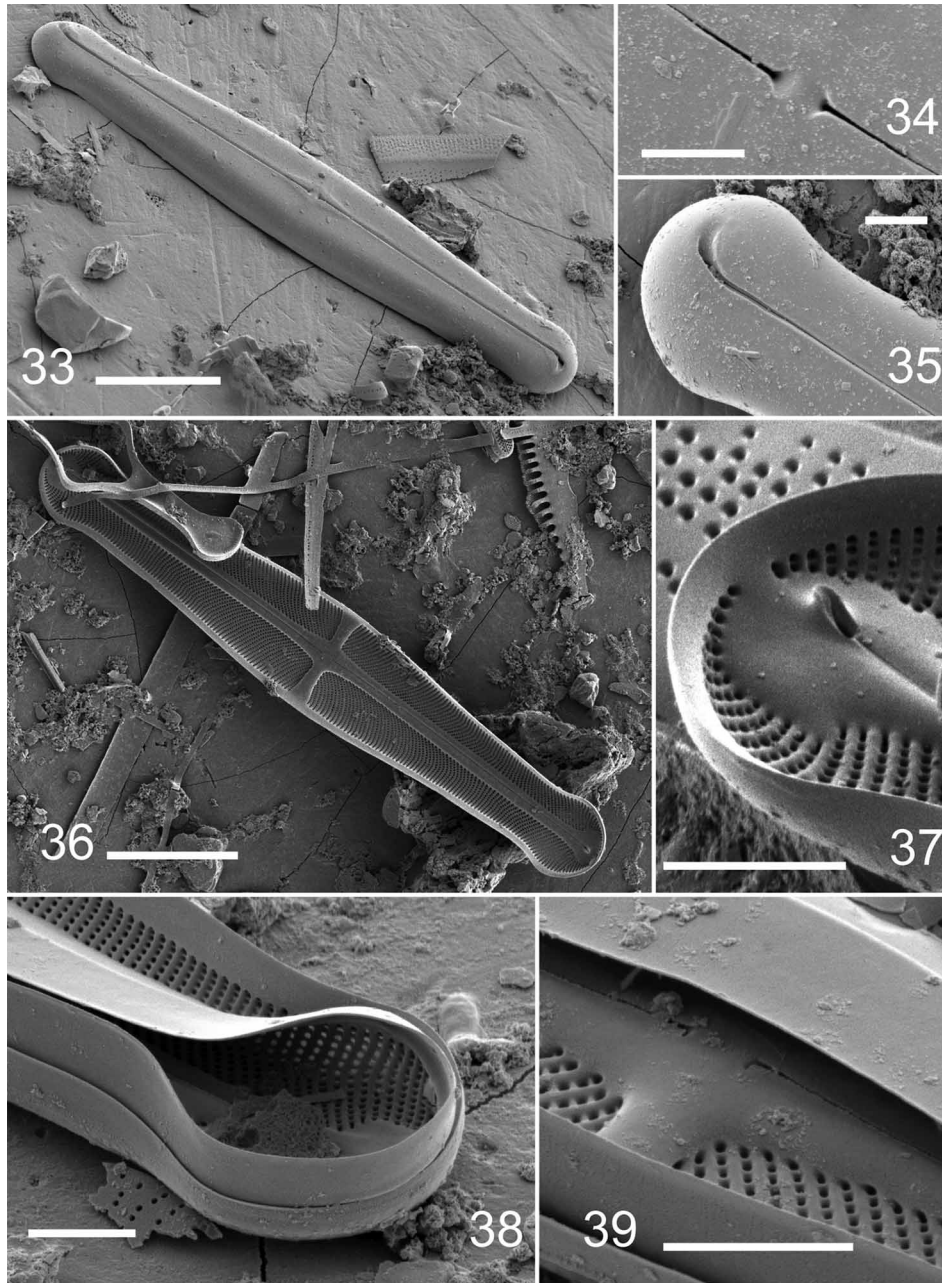
SEM observations of Australian material. Areolae are entirely covered by external hymenes, giving the valve a smooth outer surface and obscuring the external areolar



Figs 17–32. Size diminution series of *Envekadea pachycephala* from Florida Everglades and Louisiana, USA, light micrographs, DIC. All figures as same scale; scale bar (Fig. 17) = 10 μm . **Figs 17–24.** *Envekadea pachycephala*, Florida Everglades, USA (ANSP GC59136). **Figs 25–32.** *Envekadea pachycephala*, Louisiana, USA (ANSP GC65210).

features. The raphe branches are straight, located in a shallow, narrow groove, clearly widening towards the central area (Figs 33–34). The external proximal raphe ends are short but clearly unilaterally hooked (Figs 36, 39). Striae are slightly enlarged and terminate in expanded pore-free regions. The external distal raphe ends are widened and hooked in opposite directions (Figs 33, 35) giving the raphe a sigmoid path. Internal raphe branches are straight and located on a raised, thickened sternum (Figs 36–37). Internal distal raphe ends terminate on short but prominent helictoglossae, situated in an asymmetrically expanded

part of the raphe sternum, most likely corresponding with the external groove (Figs 36–37). Proximal raphe ends are short but clearly unilaterally hooked (Figs 36, 39). Striae are clearly visible in LM images and internal SEM views (Figs 36, 38). Striae are clearly bent and radiate near the central area, becoming more geniculate about one third of the way toward the valve apex. Striae become parallel and even convergent at the apices. Striae are uniseriate and internally open by small, rounded areolae. The striae are situated between slightly raised virgae and the areolae separated by



Figs 33–39. *Envekadea pachycephala*, MacKenzie River, Australia. **Fig. 33.** External valve view. **Fig. 34.** Central part of the valve with expanded proximal raphe ends, external view. **Fig. 35.** External distal raphe end. **Fig. 36.** Internal valve view. **Fig. 37.** Valve apex showing distal raphe end and helictoglossa. **Fig. 38.** Internal view of valve end showing unornamented valvocopula. **Fig. 39.** Central part of the valve with unilaterally deflected proximal raphe ends, internal view. Scale bars = 10 μm (Figs 33, 36) and 2 μm (Figs 34, 35, 37–39).

very narrow struts. Striae continue uninterrupted with a few areolae on the valve mantle. The valve mantle is bordered by a large, unornamented zone that becomes smaller near the apices (Figs 33, 35, 38). The central area is formed by a thickened stauros, extending from the central nodule to the valve margins, where it merges into the valve mantle. The girdle is composed of apparently open, smooth copulae lacking perforations (Figs 38, 39).

Taxonomic remarks. The morphological characteristics observed in *E. pachycephala*, such as the sigmoid raphe with the unilaterally deflected internal proximal ends, external distal raphe ends deflected in opposite directions and uniseriate, radiate striae occluded by external hymenes covering the entire valve, the internal structure of the areolae, and the unperforated copulae justify its transfer to *Envekadea*. The stauros, which is easily visible in the

interior the valve of *E. pachycephala*, is absent in other known *Envekadea* species (Gligora et al. 2009, Graeff et al. 2013, Lee et al. 2013).

Ecology

The pH in the MacKenzie River where *E. pachycephala* was reported was circumneutral to acidic and the specific conductivity, suspended solids and nutrient concentrations were low (Table 1). During this survey in the MacKenzie River, *E. pachycephala* was found only in the upper reaches of the MacKenzie River, especially near

Table 1. Minimum and maximum values of water quality parameters measured at the Lake Wartook head gauge at the MacKenzie River from November 2011 to October 2012 (GWMWC 2012).

Parameter	Minimum	Maximum	Units
Specific conductivity	69	85	$\mu\text{S cm}^{-1}$
Ammonia, NH_3	0.024	0.150	mg L^{-1}
Soluble reactive phosphorus, SRP	< 0.003		mg L^{-1}
Total Kjeldahl nitrogen, TKN	0.007	0.015	mg L^{-1}
Total phosphorus, TP	0.007	0.015	mg L^{-1}
Nitrate–nitrite, NO_x	< 0.003	0.014	mg L^{-1}
Chlorophyll- <i>a</i>	3.2	12	$\mu\text{g L}^{-1}$

the Wartook Reservoir. The most common diatom genera in the MacKenzie River were *Tabellaria* Ehrenberg ex F.T. Kützing, *Navicula*, *Gomphonema* Ehrenberg, *Frustulia* Rabenhorst, *Brachysira* Kützing, *Brevisira* K. Krammer, *Eunotia* and *Neidium* E. Pfitzer. The relative abundance of *E. pachycephala* was low (3–4%). It was found in standing or slowly flowing water.

By contrast, this species was present (maximum abundance 5.8%) in the Florida Everglades under higher specific conductances (96.9–5420 $\mu\text{S cm}^{-1}$) with slightly higher nutrient content (total phosphorus 163–595 $\mu\text{g g}^{-1}$) and pH from 5.23 to 7.67.

In Louisiana, the salinity optimum for *E. pachycephala* was estimated at 2.43 ppt, but the taxon was found at sites with salinities from 0.02 to 10.67 ppt (Smith 2012). The type material from South Africa showed that this species co-occurs with brackish species such as *Navicula*, *Mastogloia* and *Plagiotropis*. These results show that *E. pachycephala* has a wide ecological tolerance, from freshwater to brackish and low to high concentrations of nutrients.

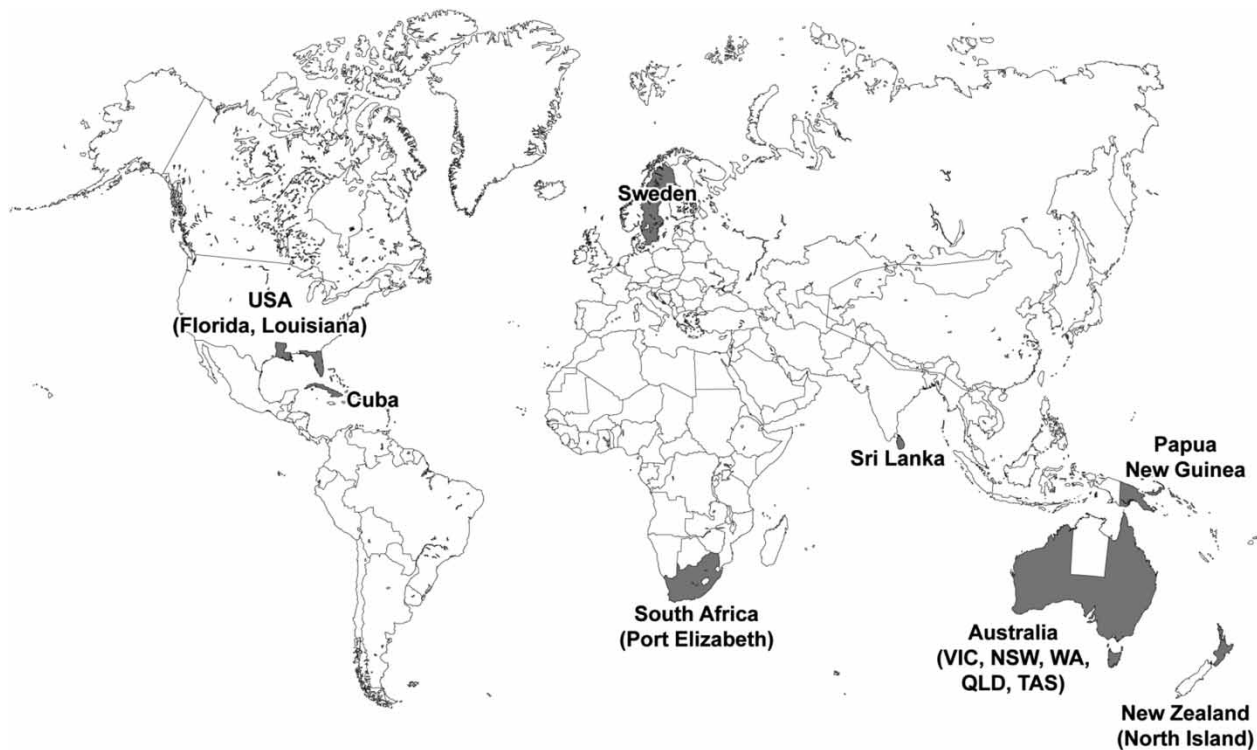
Discussion

In the original description by Cleve (1881), *E. pachycephala* (as *Stauroneis*) was reported from brackish water in South Africa. In 1953, it was reported by Cleve-Euler from both Sweden and the southern hemisphere, in fresh and brackish waters (Table 2). Cleve (1894) and Hustedt (1959) reported it in brackish water from Tasmania and South

Table 2. Morphological and ecological characteristics of *Envekadea pachycephala* populations.

Author (year)	Length (μm)	Width (μm)	Stria density (#/10 μm)	Habitat	Locality
Cleve & Moller (1881)	44.8–60.0	8.0–10.0	24.4–29.43	Brackish	South Africa
Cleve (1894)	40–55	7–9	29	Brackish	Tasmania, South Africa
Cleve-Euler (1953)	40–55	7–9	29	Fresh–brackish	Southern hemisphere, Sweden
Hustedt (1959)	40–60	7–9	30	Brackish	Tasmania, South Africa
Foged (1976)	35–41	7–8	30–35	Halophilous, alkaliphilous	Sri Lanka
Foged (1978)	35	6.5	30	Mesohalobous, alkaliphilous	NSW, QLD
Foged (1979)	46	7	–	Oligohalobous, alkaliphilous	New Zealand
John (1983)	36–40	6–7	30	Freshwater	Western Australia
Foged (1984)	40	8	dense	Oligo- to mesohalobe, alkaliphile	Cuba
Vyverman (1991)	44–45	7.9–8.1	28	Mesohalobous, alkaliphilous	PNG
Gell & Gasse (1994)	40–60	7–9	30	Freshwater	Victoria
Hodgson (1995)	52.5	7.7	–	Fresh–brackish	Tasmania
Hodgson et al. (1997)	33	5	30	Brackish	Tasmania
This study	43.1–58.0	7.0–9.0	27.0–30.3	Freshwater	Victoria, Australia
This study	38.8–45.6	6.9–7.8	27.8–29.4	Freshwater, alkaline	Florida
This study	34.8–50.3	7.0–8.3	26.3–30.3	Fresh–brackish	Louisiana

Notes: NSW: New South Wales; QLD: Queensland; PNG: Papua New Guinea.



Figs 40. Worldwide distribution of the records for *Envekadea pachycephala* (shaded area). South Africa (Cleve & Moller 1881, Cleve 1894, Hustedt 1959), Australia (Cleve 1894, Hustedt 1959, Foged 1978, John 1983, 1993, Gell & Gasse 1994, Hodgson 1995, Vyverman *et al.* 1995, Hodgson *et al.* 1997, Haynes *et al.* 2007, Taukulis & John 2009), New Zealand (Foged 1979), Sri Lanka (Foged 1976), Cuba (Foged 1984), Papua New Guinea (Vyverman 1991) and Sweden (Cleve-Euler 1953). In the present study, it is reported from Victoria (Australia) and Florida and Louisiana (USA).

Africa. According to Foged (1978), *E. pachycephala* is mesohalobous and alkaliphilous (Table 2). This taxon was also reported from the Swan River Estuary in Western Australia by John (1983). In our study, *E. pachycephala* was found in freshwater in Australia, whereas populations from Florida and Louisiana were growing in fresh to brackish conditions and across a wide nutrient spectrum. Based on its wide geographic range (including a report from Cuba [Foged 1984]), it is a subtropical species that is more common in the southern hemisphere (Fig. 40).

When originally described, *Envekadea* included species inhabiting a broad ecological spectrum, from brackish to freshwater (Gligora *et al.* 2009). There are relatively few diatom genera that inhabit both fresh and saline waters (e.g., *Surirella* P.J.F. Turpin, *Mastogloia*, *Navicula*, *Nitzschia* A.H. Hassall; Round & Sims 1981); most genera are restricted to fresh or saline habitats. Our study confirmed that *Envekadea* species tolerate a wide range of salinities, but in our case, we note that a single *Envekadea* species, *E. pachycephala*, is found across a wide range of salinity and nutrient conditions. For example, *E. pachycephala* has been reported from both brackish and freshwater in Australia and adjacent areas (Foged 1978, John 1983, Gell & Gasse 1994, Vyverman *et al.* 1995, Hodgson *et al.* 1997, this study). Several studies suggest that *E. pachycephala* is rare

in mesohalobous (Foged 1978) or brackish habitats (John 1983), which might suggest that these habitats are simply depositional areas where freshwater populations accumulate in fluvial sediments. However, Hodgson (1995) and Hodgson *et al.* (1997) studied both modern and fossil collections from Tasmania and noted that *E. pachycephala* has an ecological optimum in brackish waters, and that it was most abundant in Tasmania's Lake Fidler during a brackish water phase. Clearly, additional work on the ecophysiology of this taxon is warranted to define its salinity tolerance, because salinity is one of the strongest ecological gradients controlling diatom distribution (Gell & Gasse 1994, Smith 2012). Further evidence for the wide tolerance of this taxon is found in its species associations. In freshwater, it was most often associated with *Frustulia*, *Brachysira*, *Brevisira*, *Eunotia*, *Tabellaria*, *Navicula*, *Gomphonema* and *Neidium* species, whereas in brackish water it was associated with brackish species of *Navicula*, *Nitzschia*, *Mastogloia* and *Plagiotropis*.

There are slight morphological differences among the worldwide populations of *E. pachycephala*. We note that the MacKenzie River and type specimens from South Africa are slightly larger than those reported elsewhere, including the new populations from Florida and Louisiana, but the full range of valves encountered (length 34.8–60.0 μm)

encompasses the typical range of sizes expected for a single species (Edlund & Bixby 2001). The African specimens also show slight differences in valve outline, with margins that narrow more abruptly away from the gibbous valve centre, with larger specimens having nearly parallel sides tapering to capitate ends. However, efforts to identify non-reducible morphological groups within the populations we studied did not provide clear separation of any subset of specimens or populations to suggest that we are working with more than one taxon. The broad geographic range and environmental tolerance clearly invites future efforts to consider reproductive and molecular evidence that might support the recognition of separate species within this widespread taxon.

Conclusion

We examined the morphology, ecology and biogeography of *E. pachycephala* and demonstrated that this species has a wide geographic distribution with a broad ecological tolerance, from fresh to brackish water. However, its salinity tolerance requires further investigation. Based on its morphology, *S. pachycephala* is transferred to the genus *Envekadea* as *E. pachycephala* (P.T. Cleve) I. Atazadeh & M.B. Edlund. Until now, only five species had been included within *Envekadea* (Gligora et al. 2009, Graeff et al. 2013, Lee et al. 2013); this taxon adds another species to the genus.

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