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4 **Morphology, ecology and biogeography of *Stauroneis pachycephala* P.T. Cleve**
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6 **(Bacillariophyta) and its transfer to the genus *Envekadea***
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11 Islam Atazadeh*¹, Mark B. Edlund², Bart Van de Vijver^{3,4}, Keely Mills^{1,5}, Sarah A. Spaulding⁶,
12 Peter A. Gell¹, Simon Crawford⁷, Andrew F. Barton¹, Sylvia S. Lee⁸, Kathryn E.L. Smith⁹, Peter
13 Newall¹ and Marina Potapova¹⁰
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21 ¹*Centre for Environmental Management, School of Science, IT and Engineering, Federation*
22 *University Australia, Ballarat, Vic 3353, Australia (islam.atazadeh@gmail.com, *corresponding*
23 *author)*
24
25
26

27
28 ²*St. Croix Watershed Research Station, Science Museum of Minnesota, Marine on St. Croix, MN*
29 *55047, USA*
30
31

32 ³*Botanic Garden Meise, Department of Bryophyta & Thallophyta, B-1860 Meise, Belgium*
33
34

35 ⁴*University of Antwerp, Department of Biology-ECOB, Universiteitsplein 1, B-2610 Wilrijk,*
36 *Belgium*
37
38

39 ⁵*Department of Geography, Loughborough University, Leics LE11 3TU, UK*
40
41

42 ⁶*INSTAAR, University of Colorado, 1560 30th St, Boulder, CO 80309, USA*
43
44

45 ⁷*School of Botany, The University of Melbourne, Parkville, Vic 3010, Australia*
46
47

48 ⁸*Department of Biological Sciences, Florida International University, Miami, FL 33199, USA*
49
50

51 ⁹*United States Geological Survey, 600 4th Street South, St. Petersburg, FL 33701, USA*
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54 ¹⁰*Academy of Natural Sciences Philadelphia, Drexel University, PA 19103-1195, USA*
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Abstract

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 examined in the present paper. 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 stauros 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 frustule and copulae is smooth and lacks ornamentation. We also examined the type material of *Stauroneis pachycephala*. Our observations show this species has morphological characteristics that fit within the genus *Envekadea*. Therefore, the transfer of *Stauroneis pachycephala* to the genus *Envekadea* is proposed and a lectotype is designated.

Keywords: morphology, *Stauroneis pachycephala*, ecology, *Envekadea*, biogeography, 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 resulted in the resurrection and description of a large number of 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 separate naviculoid diatom taxa 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 freshwater species (Gligora et al. 2009). To date, five species have been recognised in the genus (Gligora et al. 2009, Graeff et al. 2013, Lee et al. 2013b) 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 presents morphological features that conform to the genus *Envekadea*. *Stauroneis pachycephala* was described in 1881 from Baakens River, Port Elizabeth, South Africa and has subsequently been reported in 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 Lanka, Cuba, and Papua New Guinea (Foged 1976, 1984, Vyverman 1991).

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In the present paper, we provide morphological, ecological, and biogeographical analyses of *Stauroneis pachycephala* based on new collections from Victoria (Australia), Florida (USA), Louisiana (USA) and compare these with type material from South Africa. Furthermore, 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, south-east Australia. The river receives a substantially modified and engineered flow regime since the construction of Wartook Reservoir in 1887 (SKM 2002, Atazadeh et al. 2012). The river is one of the main tributaries of the Wimmera River and flows approximately 50 km from Wartook Reservoir before joining the Wimmera River. The catchment lies to the south of the city of Horsham and covers an area of approximately 597 km² (WCMA 2004). The upstream section of the river receives water for most of the year providing water supply for the city of Horsham. The lower part of the river, however, is ephemeral and flows vary depending on withdrawals for consumptive use (WCMA 2004). Despite the irregular flow regime, riparian vegetation is present along the length of the river and the river has 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 the freshwater marsh in the interior and marine marsh along the coast. The Everglades has a distinct wet and dry season controlled by the subtropical climate and hydrologic management. Anthropogenic

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2
3 modification for water storage and flood control to support agricultural activity and urban
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5 populations beginning in the early 1900s have altered the broad, slow-moving sheet flow of
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7 water across the Everglades landscape into a complex network of channelised and controlled
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9 flow into distinct compartments, including Water Conservation Areas (WCAs) and Everglades
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11 National Park (Light & Dineen 1994). Much of the Everglades has a shallow peat layer that
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13 allows biogeochemical interactions between the limestone bedrock, groundwater, and biota,
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15 producing hard-water conditions and thick, calcareous periphyton assemblages (Gaiser et al.
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17 2011, Hagerthey et al. 2011). In WCA 1 (the Arthur R. Marshall Loxahatchee National Wildlife
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19 Refuge), however, a much deeper peat layer produces soft-water conditions and loose, flocculent
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21 assemblages with a distinct species composition (Harvey & McCormick 2009, Gaiser et al.
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23 2011). Common Everglades wetland vegetation includes sawgrass (*Cladium jamaicense*),
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25 spikerush (*Eleocharis* spp.), and water lily (*Nymphaea odorata*), and common aquatic fauna
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27 includes mosquitofish (*Gambusia holbrooki*), largemouth bass (*Micropterus salmoides*), and
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29 American alligator (*Alligator mississippiensis*) (Davis & Ogden 1994).
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36 The third region studied was the coastal marsh in the Chenier Plain of southwest Louisiana,
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38 USA. The Louisiana coastal marsh can be divided into two basic geomorphic zones: the
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40 Mississippi delta plain on the southeast coast and the Chenier plain of the southwest with the
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42 dividing line located near Vermillion Bay (29°43'11" N, 91°58'34" W). The Chenier plain
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44 extends from Vermillion Bay to the Texas state border and includes over 6,000 km² of coastal
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46 marshes. It was formed by the deposits of fine-grained sediments of the Mississippi River during
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48 the Middle to Late Holocene. A series of regressive-transgressive phases created relict beach
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50 ridges (called 'cheniers') within a 30-km wide coastal plain of low-energy fresh, brackish, and
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52 saline marshes (McBride et al. 2007). The cheniers act as barriers, reducing tidal flow to some
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3 areas of the marsh. The sediments are largely fine-grained silts and clays, with large amounts of
4 organics and peat. Vegetation follows a general north-south salinity gradient of fresh to brackish
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6 to saline marsh. Diatoms samples were collected from a network of permanent wetland
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8 monitoring stations located throughout coastal Louisiana called the Coastwide Reference
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10 Monitoring System (CRMS; Steyer 2010, Folse et al. 2012). CRMS was designed to monitor
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12 coastal habitats in Louisiana and evaluate the effectiveness of wetland restoration strategies
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14 (<http://lacoast.gov/crms2/>; Steyer 2010, Smith 2012).
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20 Benthic diatom samples from Australia were collected using standard methods (e.g.
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22 Stevenson & Bahls 2006). Physical and chemical characteristics of the water, including
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24 temperature, pH, specific conductivity and dissolved oxygen were measured *in situ* using an
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26 Horiba multimeter (Water checker U-10). Total nitrogen (TN), dissolved phosphorus (PO₄-P)
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28 and total suspended solids (TSS) were measured in the laboratory using a Hach DR 2800
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30 spectrophotometer. Diatom samples were digested in 10% H₂O₂ at 90°C on a hotplate for 2
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32 hours, after which 2 drops of 10% HCl were added. Samples were filled with distilled water and
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34 left to settle overnight, the supernatant was discarded, and this process repeated at least four
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36 times (Battarbee 1986). Permanent slides were prepared using the mountant Naphrax. Diatoms
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38 were identified using a Nikon Eclipse 80i microscope equipped with differential interference
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40 contrast (DIC). For scanning electron microscopy (SEM), the rinsed samples were resuspended
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42 in a solution of deionised water and household bleach (50:1) for 30 minutes and rinsed three
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44 times in distilled water. Diatom suspensions were dried directly on 22 mm aluminium stubs and
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46 gold coated with a Dynavac Xenosput sputter coater. Frustules were imaged in a Philips XL30
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48 field-emission scanning electron microscope, with a working voltage of 2.0 kV and spot size 2.
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50 Material and samples from Florida and Louisiana were collected and prepared as noted in Lee et
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3 al. (2013a) and Smith (2012), respectively, and studied using an Olympus BX51 light
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5 microscope equipped with full immersion DIC optics capable of 1000x magnification.
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8 Permanent slides (or duplicates) of all collections that were microscopically analysed have been
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10 deposited at the Academy of Natural Sciences of Drexel University in Philadelphia (ANSP),
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12 Botanic Garden Meise (BR) and the Canada Museum of Nature (CANA).
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15 Additional material examined for this study included exsiccatum Nr. 197 for *Stauroneis*
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17 *pachycephala* Cleve (Cleve & Møller 1879; South Africa (Cape of Good Hope) Baakens River,
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19 Port Elizabeth) from the Diatom Herbarium, Academy of Natural Sciences of Drexel University
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21 in Philadelphia (ANSP) and the isotype slide (ANSP GC64419) of *Stauroneis pachycephala* var.
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23 *alaskana* Foged (1981) from Kuzitrin Lake, Alaska.
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29 Results

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

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

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37 **Lectotype:** Here designated as the specimen (Fig. 13) located 9.4 mm E x 5.8 mm S from the
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39 origin marked on slide ANSP Cleve & Møller 197.

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41 **Remarks:** *Stauroneis pachycephala* was used in Cleve & Møller (1878, and not 1879 as
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43 erroneously reported several times by various authors) reporting a list of species present in
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45 exsiccatum 197. However, this record should be considered as a *nomen nudum* since the name
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47 was published without a valid description or diagnosis (ICBN Art. 32, McNeill et al. 2006).
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51 Therefore the valid description in Cleve (1881) is taken as the basionym.

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53 **Australian material:** Cells solitary, frustules rectangular in girdle view with rounded capitate
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55 apices (Figs 1-11). Valves linear-lanceolate with convex margins, gradually narrowing towards
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3 capitata, broadly rounded valve apices. Valve dimensions (n=30): length 43.1-58.0 μm , breadth
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5 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
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7 μm . Axial area very narrow, linear. Central area forming a large and distinct stauros, slightly
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9 widening towards the valve margin. Raphe straight and filiform. Proximal raphe ends slightly
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11 expanded. Distal raphe fissures hooked towards opposite sides and widening at their ends. Striae
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13 radiate in the middle becoming convergent near the apices, 27.0-30.3 in 10 μm .

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15 **South African material (lectotype; ANSP Cleve & Møller Nr. 197):** The lectotype slide of
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17 *Stauroneis pachycephala* was examined during this study. Cleve described *Stauroneis*
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19 *pachycephala* in 1881 from the Baakens River, Port Elizabeth, South Africa: "(valves) Linear,
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21 *gibbous in the middle and at the ends, which are broadly rounded and capitate. Striae oblique,*
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23 *very fine, about 29 in 0.01 mm. (29 in 10 μm), reaching the median line. Stauros reaching the*
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25 *margin. Median line straight. Terminal nodules turned opposite direction. Length 0.055 mm (55*
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27 *μm). Breadth 0.009 mm (9 μm)." Our analysis showed valves to be lanceolate with the valve
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29 outline narrowing abruptly from the valve center to the subparallel sides, then expanding to the
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31 capitata valve apices (Figs 12-15). Valve dimensions (n=23): length 44.8-60.0 μm , breadth 8.0-
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33 10.0 μm , length:breadth 5.2-6.5, breadth of apex 5.4-6.7 μm , breadth of valve constriction 4.5-
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35 6.0 μm . Central area forming a distinct stauros, abruptly widening near the valve margin. Raphe
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37 straight and filiform. Distal raphe fissures deflected in opposite directions. Striae fine, radiate in
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39 the valve center, becoming parallel mid-valve and convergent on the valve ends; 24.4-29.4 in 10
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41 μm . African specimens have slight differences in valve outline compared to other populations,
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43 with margins that more abruptly narrow moving away from the valve center, with larger
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45 specimens having nearly parallel sides tapering to capitata ends. The sample from South Africa
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3 has an alkaline or brackish diatom assemblage dominated by *Mastogloia*, *Plagiotropis* and
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5 several brackish *Navicula* species.
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8 **North American material:** In 1981, Foged described *Stauroneis pachycephala* var. *alaskana*
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10 Foged from Alaska, USA. A specimen found on the isotype slide (Fig. 16), and conforming to
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12 the original illustration and description of *S. pachycephala* var. *alaskana* belongs to the genus
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14 *Caloneis* and is not treated further in this paper. Recently, *Stauroneis pachycephala* [*Envekadea*
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16 *pachycephala*] was found during a survey in the Florida Everglades. The taxon is rare in Florida,
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18 but the highest abundances were observed in WCA-1, a distinctive, soft-water environment
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20 within the Everglades (E. Gaiser, unpublished data). Valves lanceolate, raphe sigmoid, axial area
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22 narrowing toward the valve ends, and capitate valve apices. The central area a distinct stauros
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24 that is slightly widened near the valve margin (Figs 17-24). Valve dimensions (n=16): length 34-
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26 46.4 μm , breadth 6.7-8.6 μm . length:breadth 5.2-6.2, constriction breadth 3.5-4.6 μm , apex
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28 breadth 4.9-5.7 μm , 27.8-29.4 striae per 10 μm . Samples from Florida were dominated by
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30 acidophilic species such as *Brachysira brebissonii* and *Frustulia crassinervia*.
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37 Additional North American populations of *E. pachycephala* were found in coastal
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39 marshes in Louisiana (USA; Smith 2012). Valves were lanceolate with an expanded valve center
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41 that narrowed toward a constriction that subtended capitate valve apices (Figs 25-32). Valve
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43 dimensions (n=15): length 34.8-50.3 μm , breadth 7.0-8.3 μm , length:breadth 5.0-6.4, breadth at
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45 constriction 3.6-4.6 μm , breadth at apex 4.8-6.2 μm . Striae radiate at the valve center, becoming
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47 parallel and eventually convergent at the valve ends, 26.3-30.3 striae per 10 μm . In Louisiana, *E.*
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49 *pachycephala* was found in association with diverse *Eunotia* and *Pinnularia* species as well as
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51 *Nitzschia obtusa* and *N. scalaris* in brackish sites (Smith 2012).
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3 **SEM observations on Australian material:** Areolae are entirely covered by external hymenes,
4 giving the valve a smooth outer surface and obscuring the external areolar features. The raphe
5 branches are straight, located in a shallow, narrow groove, clearly widening towards the central
6 area (Figs 33, 34). The external proximal raphe ends are slightly enlarged and terminate in
7 expanded hyaline regions. The external distal raphe ends are widened and hooked in opposite
8 directions (Figs 33, 35) giving the raphe a sigmoid shape. Internal raphe branches are straight
9 and located on a raised, thickened sternum (Figs 36, 37). Internal distal raphe ends terminate on
10 short but prominent helictoglossae, situated in an asymmetrically expanded part of the raphe
11 sternum, most likely corresponding with the external groove (Figs 36, 37). Proximal raphe ends
12 are short but clearly unilaterally hooked (Figs 36, 39). Striae are clearly visible in LM images
13 and internal SEM views (Figs 36, 38). Striae are clearly bent and radiate near the central area,
14 becoming more geniculate about 1/3 of the way toward the valve apex. Striae become parallel
15 and even convergent at the apices. Striae are uniseriate and internally composed of small,
16 rounded areolae. The striae are situated between slightly raised virgae and the areolae separated
17 by very narrow struts. Striae continue uninterrupted with a few areolae on the valve mantle. The
18 valve mantle is bordered by a large, unperforated, hyaline zone that becomes smaller near the
19 apices (Figs 33, 35, 38). The central area is formed by a thickened stauros, extending from the
20 central nodule onto the valve margins and fused with the valve mantle. The girdle is composed
21 of apparently open, smooth copulae lacking perforations (Figs 38, 39).

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48 **Taxonomic remarks:** The morphological characteristics observed in *Stauroneis pachycephala*,
49 such as the sigmoid raphe with the unilaterally deflected internal proximal ends, external distal
50 raphe ends deflected in opposite directions and uniseriate, radiate striae occluded by external
51 hymenes covering the entire valve, the internal structure of the areolae, and the unperforated
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3 copulae justify its transfer to the genus *Envekadea*. The stauros, which is easily visible in the
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5 interior part of the valve of *E. pachycephala*, is absent in other known *Envekadea* species
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8 (Gligora et al. 2009, Graeff et al. 2013, Lee et al. 2013b).
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10 **Ecology:** The pH in the MacKenzie River where *Envekadea pachycephala* was reported was
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12 circumneutral to acidic and the specific conductivity, suspended solids, and nutrient
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14 concentrations were low (Table 1). During this survey in the MacKenzie River, *E. pachycephala*
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16 was found only in the upper reaches of the MacKenzie River, especially near Wartook Reservoir.
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18 The most common diatom genera in the MacKenzie River were *Tabellaria*, *Navicula*,
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20 *Gomphonema*, *Frustulia*, *Brachysira*, *Brevisira*, *Eunotia*, and *Neidium*. The relative abundance
21
22 of *E. pachycephala* was low (3-4%). It was found in standing or slowly flowing water. In
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24 contrast, this species was present (maximum abundance 5.8%) in a higher range of specific
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26 conductance (96.9-5420 $\mu\text{S cm}^{-1}$) with slightly high concentrations of periphyton nutrient
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28 content (total phosphorus 163-595 $\mu\text{g/g}$), and pH from 5.23-7.67, in the Florida Everglades. In
29
30 Louisiana, the salinity optimum for *E. pachycephala* was estimated at 2.43 ppt, but the taxon was
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32 found in sites with salinities from 0.02 to 10.67 ppt (Smith 2012). The type material from South
33
34 Africa showed that this species co-occurs with brackish species such as *Navicula*, *Mastogloia*,
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36 and *Plagiotropis*. These results show that *E. pachycephala* has a wide ecological tolerance from
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38 freshwater to brackish and low to high concentrations of nutrients.
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48 **Discussion**

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50 In the original description by Cleve (1881), *Envekadea pachycephala* was reported from
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52 brackish water in South Africa. In 1953, this species was reported by Cleve-Euler from both
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54 Sweden and the southern hemisphere in fresh and brackish waters (Table 2). Cleve (1894) and
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3 Hustedt (1959) reported it from Tasmania and South Africa in brackish water. According to
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5 Foged (1978), *E. pachycephala* is mesohalobous and alkaliphilous (Table 2). This taxon was also
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7 reported by John (1983) from the Swan River Estuary in Western Australia. In our study, *E.*
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9 *pachycephala* was found in freshwater in Australia, whereas populations from Florida and
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11 Louisiana were growing in fresh to brackish conditions and across wide nutrient spectrum. Foged
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13 (1984) earlier reported this taxon from Cuba. Based on this wide geographic range, species
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15 distribution could be described as subtropical and more common in the southern hemisphere
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17 (Fig. 40).
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22 When originally described, the genus *Envekadea* included species inhabiting a broad
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24 ecological spectrum, from brackish to fresh waters (Gligora et al. 2009). There are limited
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26 diatom genera that inhabit both fresh and saline waters (e.g. *Surirella*, *Mastogloia*, *Navicula*,
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28 *Nitzschia*; Round & Sims 1981); most genera are limited in distribution to fresh or saline
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30 habitats. Our study confirmed that *Envekadea* species tolerate a wide range of salinities, but in
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32 our case, we note that a single *Envekadea* taxon, *E. pachycephala*, is also found across a wide
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34 range of salinity and nutrient conditions. For example, *E. pachycephala* has been reported from
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36 both brackish and freshwater collections in Australia and adjacent areas (Foged 1978, John 1983,
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38 Gell & Gasse 1994, Vyverman et al. 1995, Hodgson et al. 1997, this study). Several of the
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40 studies suggest that *E. pachycephala* is rare in mesohalobous (Foged 1978) or brackish habitats
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42 (John 1983), which might suggest that these habitats are simply depositional areas where
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44 freshwater populations accumulate in fluvial sediments. In contrast, Hodgson (1995) and
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46 Hodgson et al. (1997) studied both modern and fossil collections from Tasmania with *E.*
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48 *pachycephala* and noted that its ecological optimum was in brackish waters, and that it was most
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50 abundant in Tasmania's Lake Fidler during a brackish water phase. Clearly additional work on
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3 eco-physiology of this taxon is warranted to resolve the salinity tolerance of this species because
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5 salinity is one of the strongest ecological gradients controlling diatom distribution (Gell & Gasse
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8 1994, Smith 2012). Further evidence for the wide tolerance of this taxon is found in its species
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10 associations. In freshwater, it was most often associated with *Frustulia*, *Brachysira*, *Brevisira*,
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12 *Eunotia*, *Tabellaria*, *Navicula*, *Gomphonema* and *Neidium* species, while in brackish water it
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14 was associated with brackish species of *Navicula*, *Nitzschia*, *Mastogloia*, and *Plagiotropis*.
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18 There are slight morphological differences among the worldwide populations of
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20 *Envekadea pachycephala*. We note that the MacKenzie River and type specimens from South
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22 Africa are slightly larger than those reported elsewhere including the new populations from
23
24 Florida and Louisiana, but the full range of valves encountered (length 34.8-60.0 μm)
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26 encompasses a typical range of sizes expected for a single species (Edlund & Bixby 2001). The
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28 African specimens also have slight differences in valve outline, with margins that more abruptly
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30 narrow moving away from the gibbous valve center, with larger specimens having nearly parallel
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32 sides tapering to capitate ends. However, efforts to identify nonreducible morphological groups
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34 within the populations we studied did not provide clear separation of any subset of specimens or
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36 populations to suggest we are working with more than one taxon. The broad geographic range
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38 and environmental tolerance clearly invites future efforts to consider reproductive and molecular
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40 evidence that might support recognition of separate species within this widespread taxon.
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48 **Conclusion**

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50 We examined the morphology, ecology and biogeography of *E. pachycephala* and demonstrated
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52 that this species has wide geographic distribution with broad ecological tolerance from fresh to
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54 brackish water. The tolerance of this species for salinity, however, deserves further investigation.
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3 Based on the morphology of *Stauroneis pachycephala*, the species is appropriately transferred to
4 the genus *Envekadea* as *E. pachycephala* (P.T. Cleve) I. Atazadeh & M.B. Edlund. Until now,
5
6 only five species were included within the genus *Envekadea* (Gligora et al. 2009, Graeff et al.
7
8 2013, Lee et al. 2013). With the present paper, one more species is added to the genus.
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12 13 14 15 **Acknowledgements**

16
17 This research was supported by the Iowa Lakeside Laboratory scholarship and Federation
18
19 University Australia scholarship to IA. This project was funded by Grampians Wimmera Mallee
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21 Water (GWMWater, Australia). IA wishes to thank Peter J. van der Linden (Executive Director
22
23 of Iowa Lakeside Laboratory & Regent's Resource Center, USA) and all staff and students at the
24
25 Iowa Lakeside Laboratory for their help and cooperation. The authors would like to thank Rosie
26
27 Grundell, Jessica Reeves and Phuong Doan (Federation University Australia), and Rebecca
28
29 Bixby (University of New Mexico) for their help and cooperation. The authors also would like to
30
31 give special thanks to Evelyn Gaiser (Florida International University) for providing data on *E.*
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33 *pachycephala* in the Florida Everglades. We thank two anonymous reviewers and Lisa Osterman
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35 (U.S. Geological Survey) for their comments that improved the manuscript.
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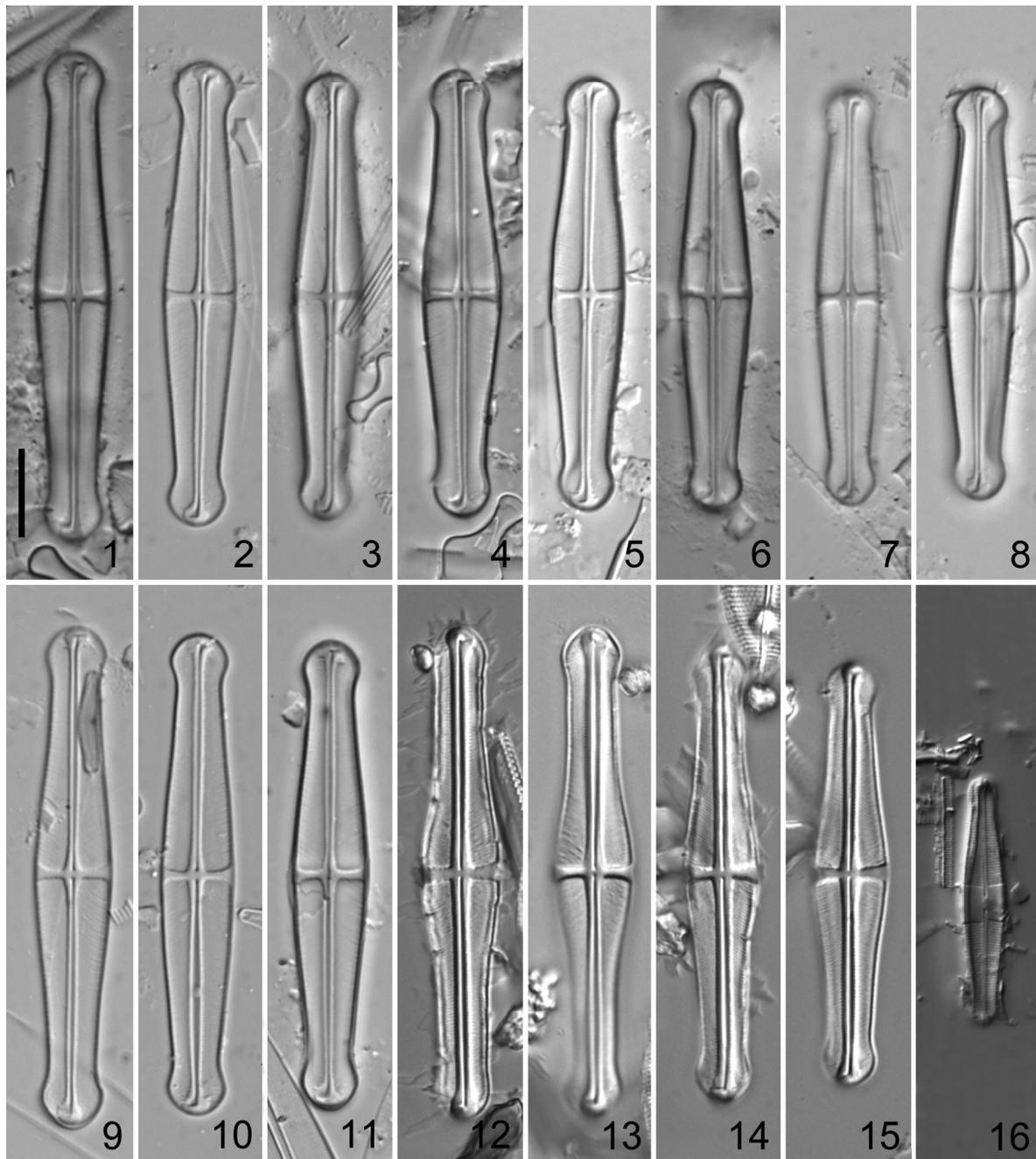
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Table 1. Minimum and maximum values of water quality parameters measured from November 2011 through October 2012 at the Lake Wartook head gauge at MacKenzie River (GWMWC 2012).

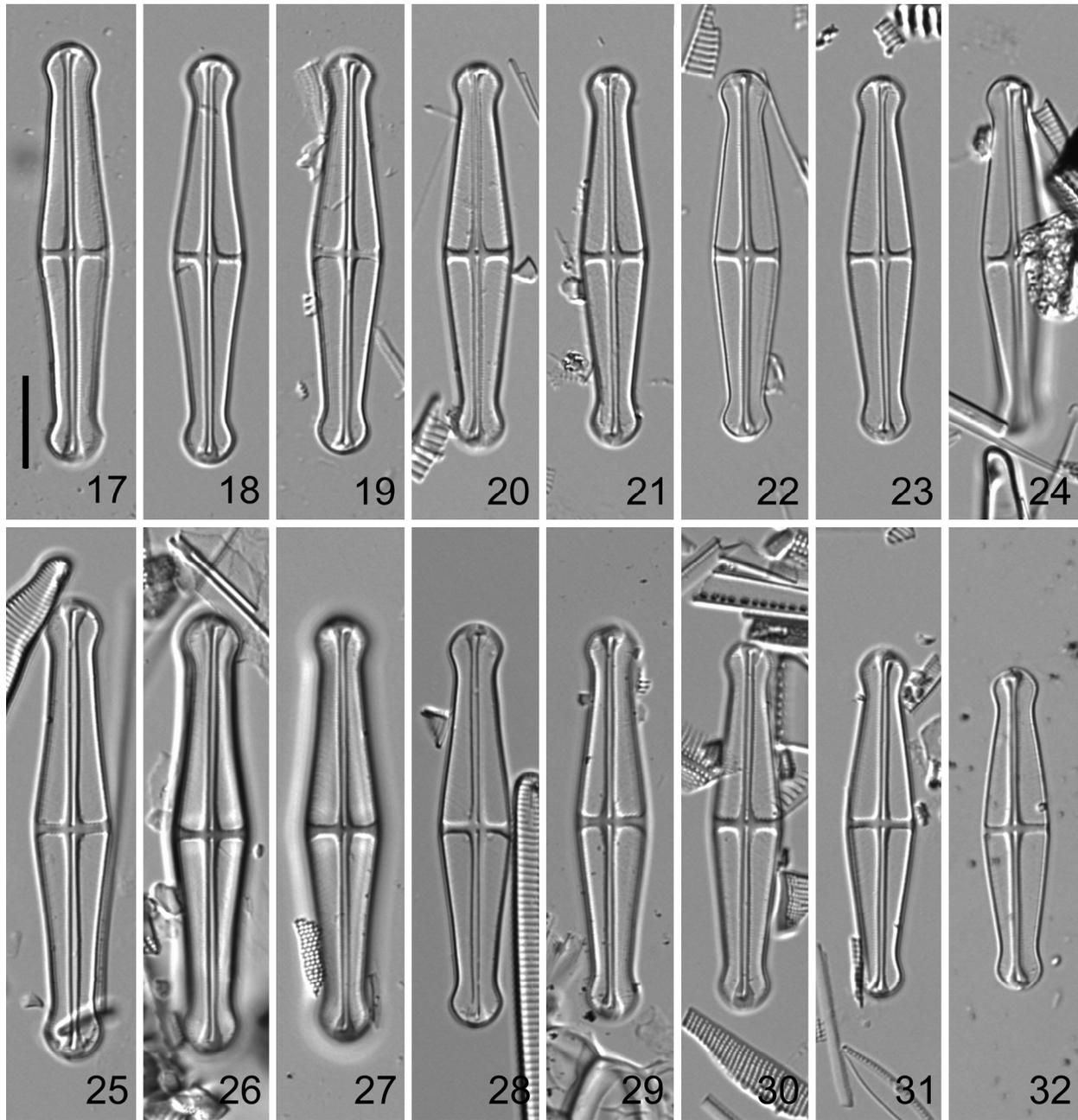
Parameter	minimum	maximum	units
pH	6.3	6.8	–
Specific conductivity	69	85	$\mu\text{S cm}^{-1}$
Ammonium, NH_3	0.024	0.150	mg L^{-1}
Soluble Reactive Phosphorus, SRP	<0.003		mg L^{-1}
Total Kjeldahl Nitrogen, TKN	0.007	0.015	mg L^{-1}
Total Phosphorus, TP	0.007	0.015	mg L^{-1}
Nitrate-Nitrite, NO_x	<0.003	0.014	mg L^{-1}
Chlorophyll <i>a</i>	3.2	12	$\mu\text{g L}^{-1}$

Table 2. Morphological and ecological characteristics of populations reported as *Envekadea pachycephala*. NSW = New South Wales, QLD = Queensland, PNG = Papua New Guinea

<i>Envekadea pachycephala</i>					
Author (year)	Length (μm)	Width (μm)	Striae Density (#/10 μm)	Habitat	Locality
Cleve <i>et</i> Moller 1881	44.8-60.0	8.0-10.0	24.4-29.43	Brackish	S. Africa
Cleve 1894	40-55	7-9	29	Brackish	Tasmania, S. Africa
Cleve-Euler 1953	40-55	7-9	29	Fresh-brackish	Southern Hemisphere, Sweden
Hustedt 1959	40-60	7-9	30	Brackish	Tasmania, S. 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 <i>et al.</i> 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

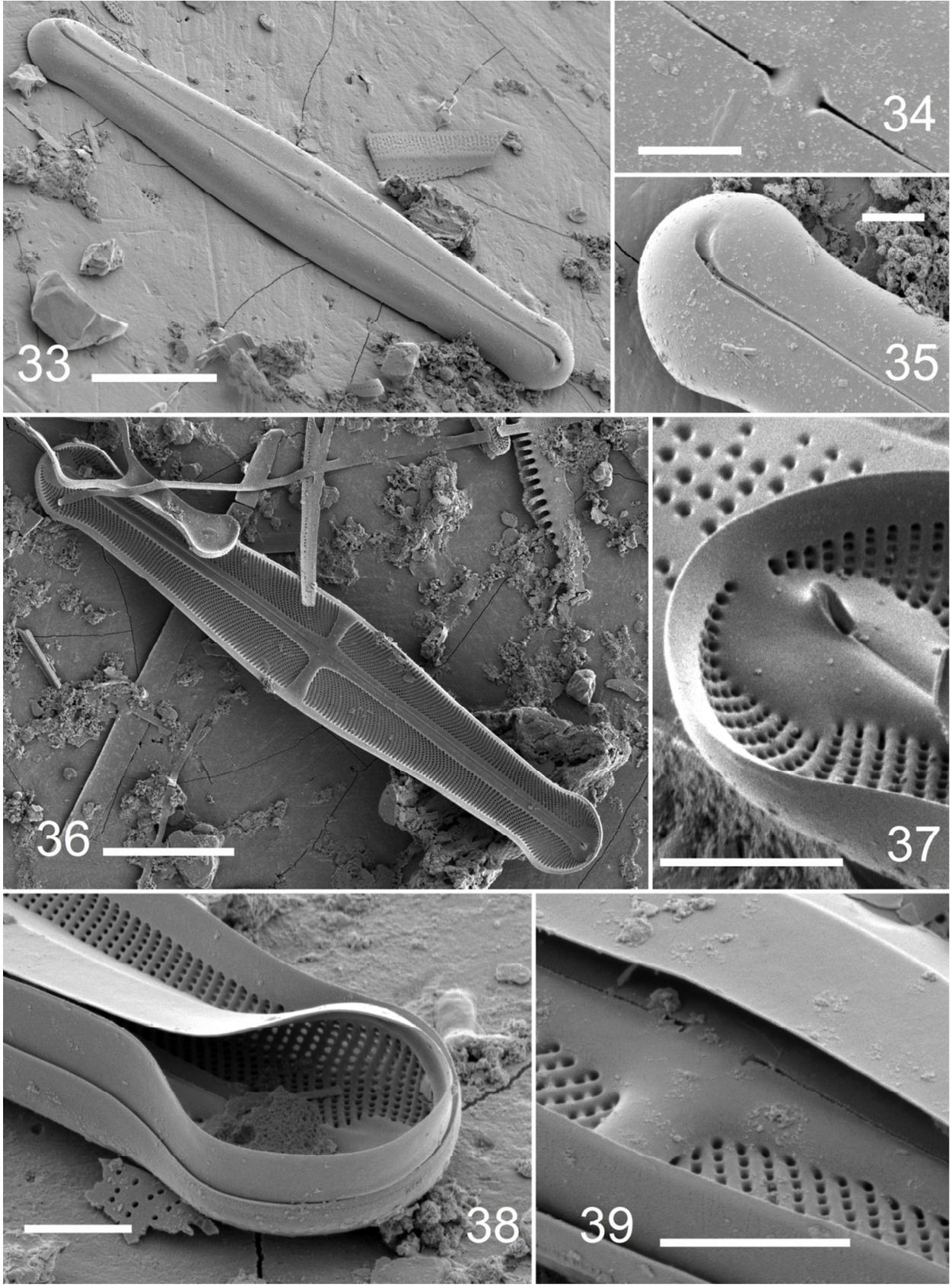


Figs 1-16. *Envekadea* species, light micrographs, DIC, scale bar = 10 μm . **Figs 1-8.** *Envekadea pachycephala* MacKenzie River, Wartook Outlet, Victoria, Australia (ANSP GC40128, CANA 87195, BR-4323). **Figs 9-11.** *Envekadea pachycephala* Wartook Reservoir, Victoria, Australia (ANSP GC40129, BR-4324). **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) shows this taxon clearly belongs in the genus *Caloneis*.



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 μ m.
Figs 17-24. *Envekadea pachycephala*, Florida Everglades, USA (ANSP GCxxxx). **Figs 25-32.** *Envekadea pachycephala*, Louisiana, USA (ANSP GCxxxx).

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Figs 33-39. *Envekadea pachycephala*, MacKenzie River, Australia. SEM. **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).

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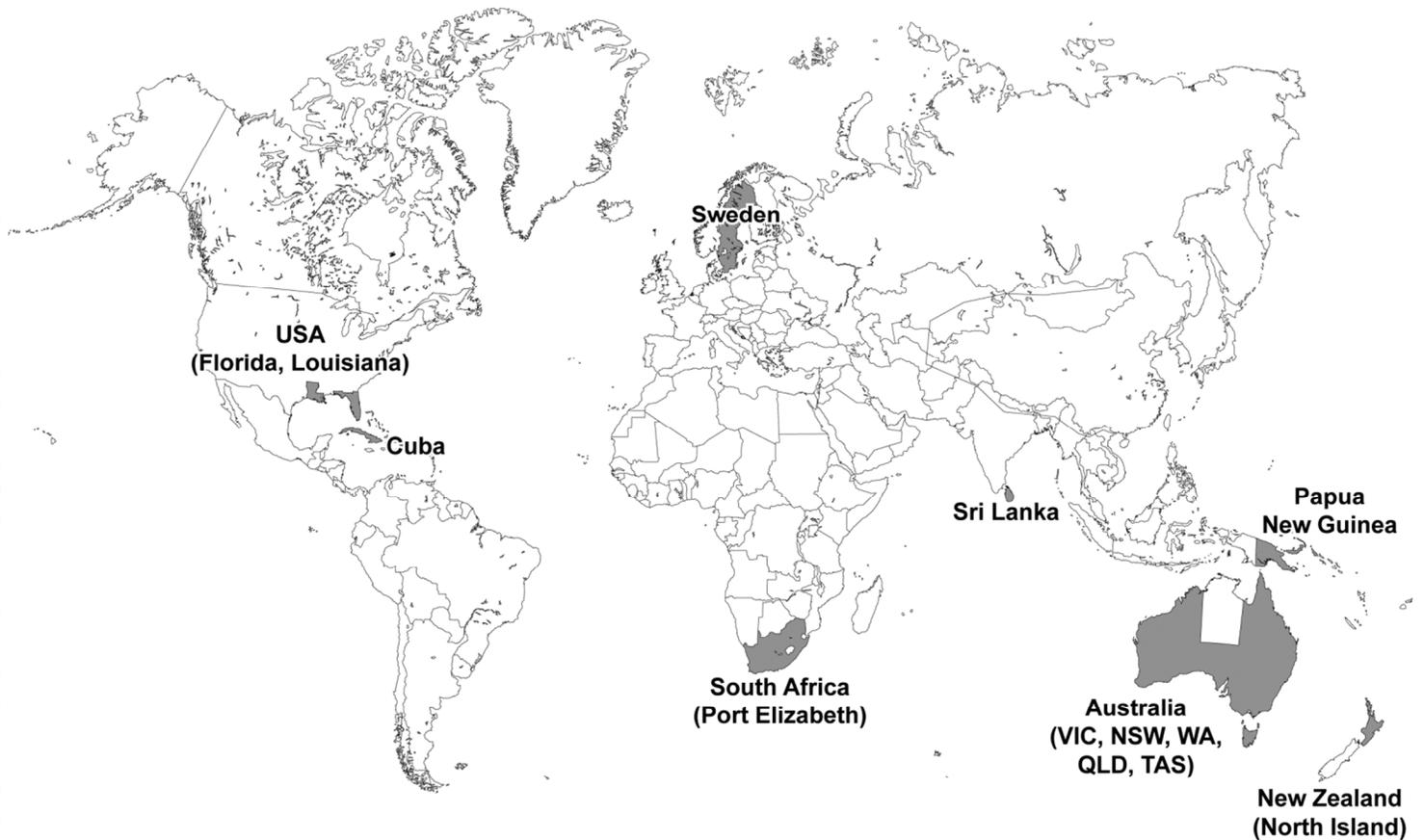


Fig. 40. World-wide distribution of the records for *Envekadea pachycephala* (shaded area). South Africa (Cleve et Moller 1881, Cleve 1894, Hustedt 1959), Australia (Cleve 1894, Hustedt 1959, Foged 1978, John 1983,1993, Gell & Gasse 1994, Hodgson 1995, Vyverman et al. 1995, Hodgson et al. 1997, Haynes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