Climaconeis desportesiae and C. leandrei (Bacillariophyta, Berkeleyaceae), two new curved species from Guam, Western Pacific

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Abstract – Two new curved species and a new record of a straight species are reported; neither new species has the craticular bars seen in the generitype. *C. desportesiae* resembles *C. guamensis* and *C. riddleae* in size and number of plastids (2 pairs) but has much finer striae (46-50 in 10 µm). *C. leandrei* has multiple plastids and is very long, like *C. koenigii* but more slender and with rectangular rather than circular areolae. Valvocopulae of this species are described for the first time in *Climaconeis* spp., which otherwise show no distinction among copulae. A straight species, provisionally identified as *C. scalaris*, is reported for the first time from tropical waters. An updated key to the 18 known species is provided.

Coral reefs / Berkeleyaceae / biodiversity / diatoms / Naviculales / taxonomy

INTRODUCTION

Climaconeis Grunow is a small genus of marine diatoms, some straight, some curved in valve view. Two straight ones, including the generitype C. lorenzii Grunow, bear ingrowths of the valvocopula (craticular bars) that gave the genus its name (from κλιμακας, ladder). Some species have a stauros. The genus was revised by Cox (1982); new species were added by Prasad et al. (2000), Ried & Williams (2002), Prasad (2003), and Lobban et al. (2010), so there are now 16 known species, almost all in warm waters. Cox (1982) emended the description, and Lobban et al. (2010) proposed a further emendment to account for the variety of substrata and to more accurately reflect the plastid characters. All species have paired plastids joined by a pyrenoid, with most species having several to many pairs. Very long taxa such as C. koenigii A.K.S.K. Prasad (curved) and C. petersonii Lobban, Ashworth & Theriot (straight) have 40–50 pairs of plastids. At the other extreme, four species, 3 of them curved, have only 2 pairs of plastids, one on each side of the central nucleus. The curved species are C. inflexa (Brébisson) Cox, C. riddleae A.K.S.K. Prasad, and C. guamensis Lobban, Ashworth & Theriot; Lobban et al. (2010) reported all of these from Guam. In C. riddleae the raphe is essentially central, following the arc of the valve, but in the other two the raphe branches are biarcuate (each having a curve distinct from that of the valve and coming closer to the dorsal side in the middle of each branch) and the central raphe endings are deflected toward the concave

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side of the valve. The raphe in *C. koenigii* follows the curve of the valve (and is therefore not *bi*arcuate as stated by Prasad *et al.* 2000) and central raphe endings are straight. In examining new samples from Guam, I encountered (1) a population of cells that appeared to be *C. guamensis*, but on examination with the SEM proved to have a much higher stria density than any known species, and (2) a long, slender species with numerous plastids that was similar to *C. koenigii*. Unlike other *Climaconeis*, this new species had a distinctive valvocopula and the length of the cells of the latter and its dominance in the sample allowed me to study copulae in this genus for the first time.

MATERIALS & METHODS

Samples were collected from farmer-fish territories in Guam by SCUBA diving at GabGab reef in Apra Harbor (details in Lobban *et al.*, 2012), Vecky's Reef, a continuation of the reef at GabGab toward the harbor mouth, and in Agat Bay. They were observed while fresh and material of interest from these slides was transferred to membrane filters and prepared for SEM as whole mounts. Additional aliquots of the raw samples were preserved, cleaned with nitric acid and observed in LM and SEM following usual procedures for the lab (details in Lobban & Ashworth, 2014; Lobban, 2015).

RESULTS

Order NAVICULALES Bessey Family BERKELEYACEAE D.G. Mann Climaconeis Grunow Climaconeis desportesiae sp. nov. Lobban

Figs 1, 5-11

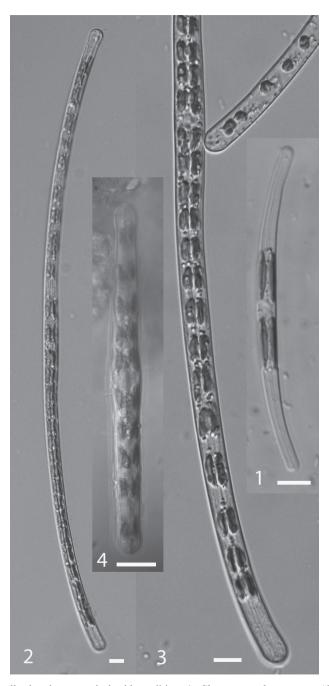
Diagnosis: Distinguished from other short, curved species lacking a stauros and having 2 pairs of plastids (e.g., *C. riddleae*, *C. guamensis*) by very fine stria density 46-50 in 10 μm.

Type material: Holotype: GU44BT-2, slide 2232 (Figs 5, 6), located at 11.5 mm E and 10.3 mm S relative to the reference mark (Sterrenburg *et al.* 2012); slide deposited at ANSP, accession number 20073. GabGab reef, Apra Harbor, Guam, 13.443 N, 144.643 E, on coarse red algal mat in a farmer fish (*Plectroglyphidodon lacrimatus*) territory at 10 m depth; collected by M. Schefter 26 Feb. 2017.

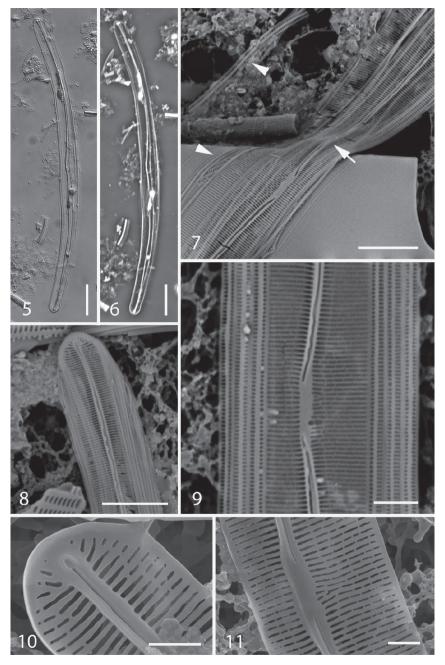
Additional records: GU76A-3, Vecky's Reef, Apra Harbor, Guam.

Etymology: This species comes from a sample collected by my wife, Maria Schefter, and I name it after her maternal 8th great-grandmother Hélène Desportes (1620-1675), the first white child born in Nouvelle France (to Pierre Desportes and Françoise Langlois in Champlain's Habitation, Québec) (Bennett, 2003; McNelly, 2013). We dedicate this also to the *Filles du Roi*, at least four of whom are among Maria's great-grandparents, and who, like Hélène, contributed greatly to populating the nascent colony.

Description: Cells of this species resemble *C. guamensis* in size, biarcuate raphe branches, number of plastids, and invisibility of the striae in LM. Frustules (Fig. 1)



Figs 1-4. Live cells showing natural plastid condition. 1. Climaconeis desportesiae (GU44BT-2). 2, 3. C. leandrei (GU76A-1). 4. C. scalaris (GU76A-1). Scale bars = $10 \mu m$.



Figs 5-11. Climaconeis desportesiae (GU44BT-2), SEM except Figs 5 and 6 LM. **5**, **6**. Holotype frustule in DIC and phase contrast illumination. **7**. External surface of acid-cleaned valve draped over debris, showing raised sternum thickenings (arrow) and copulae with two rows of pores and medial rib (arrowheads). **8**. Apex external details, acid cleaned. **9**. Central area, whole mount: valve with three copulae. **10**. Internal detail of apex showing helictoglossa and transapically elongate areolae. **11**. Internal detail of central area. Scale bars: Figs 5, $6 = 10 \mu m$, Figs 7, $8 = 5 \mu m$, Fig. $9 = 2 \mu m$, Figs 10, $11 = 1 \mu m$.

were very delicate. A pair of plastids was observed on each side of the nucleus (Fig. 1). Valves (Figs 5, 6) were 92-148 μ m long, curved in valve view, but the margin of the valve on the concave side was straighter through the middle half of the cell, making the cell gradually wider towards the central area (6-8 μ m vs 4-5 μ m). The length distribution in the sample was bimodal, with cells being about 97 μ m or about 140 μ m long. Stria density was 46-50 in 10 μ m, striae parallel except around the apices (Figs 7-11). Areolae transapically elongated (Figs 9-11), sometimes greatly so, and sometimes tapered (Fig. 10). The raphe branches were biarcuate (Figs 5, 6), the central raphe endings deflected toward the ventral side and separated from one another the distance of 10 striae; there was no stauros (Figs 5, 9). Terminal raphe endings were straight (Fig. 8). The sternum was irregularly thickened into flaps along the raphe (Figs 7, 8). Internally the valves were unremarkable; the helictoglossa was small (Figs 10, 11).

Cingulum with up to 6 copulae with two unequal rows of pores (Fig. 9). **Remarks:** The plastids of *C. desportesiae* are similar to those of *C. guamensis* and *C. riddleae* (Table 1), but long compared to those in multi-plastid species such as *C. silvae* A.K.S.K. Prasad (Prasad, 2003; Lobban *et al.*, 2010). At both sites, *C. desportesiae* co-occurred with *C. riddleae* (Figs 12, 13), from which it was readily distinguished in SEM by the stria density and the shape of the areolae.

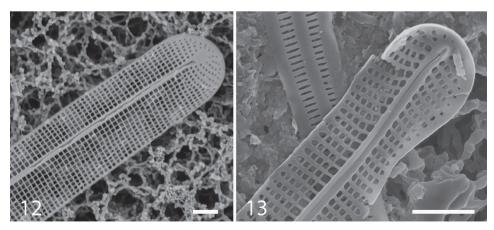
Climaconeis leandrei, sp. nov. Lobban

Figs 2, 3, 14-33

Diagnosis: Distinguished from other long curved species with numerous plastids and no stauros (e.g., *C. koenigii*) by the dimensions, the biarcuate raphe branches, and the transapically rectangular to square areolae.

Type material: Holotype: GU76A-1, slide 2366 (Figs 14, 15), located at 13.0 mm E and 3.1 mm S relative to the reference mark; slide deposited at ANSP; accession number 20074. Vecky's Reef, Apra Harbor, Guam, 13.449341 N, 144.62486 E, on *Halimeda* in or near a farmer fish (*Plectroglyphidodon lacrimatus*) territory at 12 m depth; collected by C. Lobban and M. Schefter 27 July 2017.

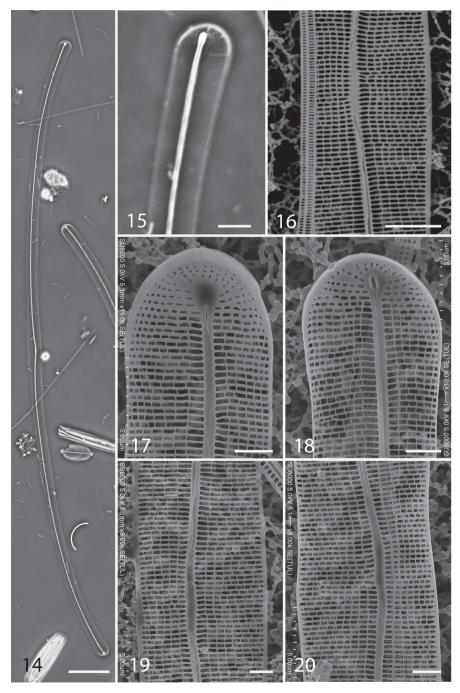
Etymology: Named for my wife's paternal 2nd great grandfather, Léandre Schoeffter (Schefter) (1812-1899), who emigrated from Soufflenheim, Alsace, to New Germany



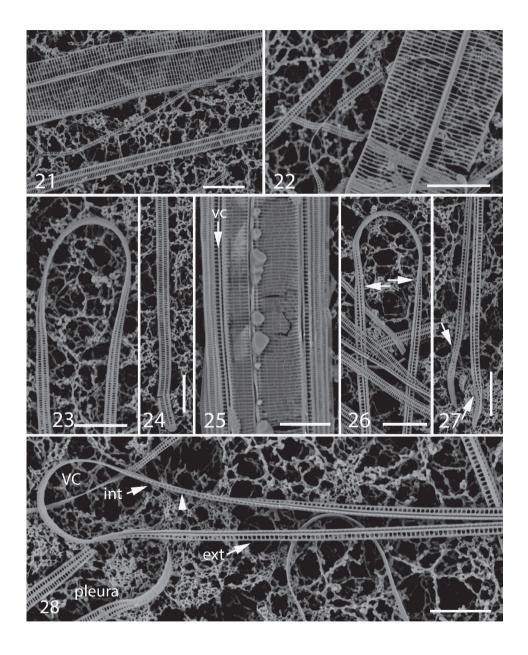
Figs 12, 13. *Climaconeis riddleae* from same collections as *C. desportesiae*, SEM, acid cleaned. **12.** External apex of valve (GU76A-3). Fig. 12. Internal apex (GU44BT-2). Scale bars = 2 μm.

Table 1. Comparison of characters of the new species and similar congeners. All these species are curved, lack a stauros, and lack craticular bars

	C. desportesiae	C. leandrei	C. guamensis	C. riddleae	C. inflexa	C. ghurbensis	C. koenigii	C. silvae
Length, µm	92-148	375-464	90-120	82-182	80-220	120-160	200-468	132-298
Max. width, µm	8-9	11-13	3-4	3-5	5-11	4-5	3.6-4.5	5-10
No. of plastid pairs	2	26-34	2	2	2	multiple	26	8-20
Stria density in 10 µm	46-50	29	33-34	24-27	19-23	31-34	24-27	28-35
Areola shape	Transapically elongated	Transapically rectangular	Transapically irregularly elongated	Quadrangular	Rounded quadrangular	Quadrangular	Circular	Transapically irregularly elongated
Raphe branch curvature	Biarcuate	Biarcuate	Biarcuate	Monoarcuate	Biarcuate	Biarcuate	Monoarcuate	Biarcuate
Irregular thickening of raphe sternum	Present	Present	Present	Present	Present	Present	Absent	Present
Provenance	Guam	Guam	Guam	Florida, Guam	Europe, Guam	Abu Dhabi (Persian Gulf)	Florida	Florida, Guam
References	This paper	This paper	Lobban et al. (2010)	Prasad 2003, Lobban <i>et al.</i> 2010	Cox 1982, Lobban <i>et al.</i> 2010	Reid & Williams Prasad et al. 2002 2000	Prasad <i>et al.</i> 2000	Prasad 2003, Lobban <i>et al.</i> 2010

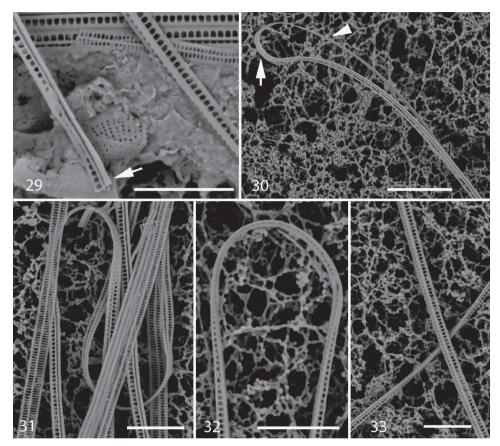


Figs 14-20. *Climaconeis leandrei* (GU76A-1) SEM except Figs 14 and 15 LM. **14, 15.** Holotype, phase contrast illumination; Fig 15 higher magnification of apex to show striae. **16.** External central area and a pleura, showing deflection in raphe. **17.** External apex. **18.** Internal apex. **19.** External central area. **20.** Internal central area. Scale bars: Figs $14 = 25 \mu m$, Figs $15, 16 = 5 \mu m$, Figs $17-20 = 2 \mu m$.



(Maryhill), Ontario, Canada in 1843 with his wife and children and became the ancestor of many of the Schefters in North America.

Description: Cells were curved, long and slender, 375-464 μ m long, 8-10 μ m wide, weakly inflated at the center to 11-13 μ m (Figs 2, 3, 14); live cells displayed 26-34 pairs of plastids. Striae 29 in 10 μ m, visible in LM (Figs 14, 15), parallel except



Figs 21-33. Climaconeis leandrei (GU76A-1) SEM of copulae. 21. Portion of valve (external view) with portions of a normal pleura (below) and two narrow pleurae (next to the valve). 22. Portions of narrow bands and a valve (internal view). 23. Closed end of a normal pleura, external surface. 24. Open end of normal pleura. 25. Whole mount of portion of valve showing relationship between valve, valvocopula (VC) and pleurae. 26, 27. Valvocopula: closed and open ends of the same specimen, external surface; arrows indicate where the band becomes flat. Several pleurae can also be seen in Fig. 26. 28. Labeled valvocopula (VC), closed end, advalvar edge toward the viewer, internal surface (int) of the upper half, external (ext) surface of bottom half, showing changing appearance at different angles. (Arrowhead explained in text.) 29. Detail of valvocopula showing broken end (arrow), internal surface, and part of another valvocopula in external view showing a wide ridge. 30. Oblique view of closed end of valvocopula (arrowhead indicates inner surface). 31, 32. Additional views of valvocopulae closed ends, Fig. 31 also showing several pleurae. 33. Portions of two valvocopulae at different angles. Scale bars: Fig. 30 = 10 μm; 21-29, Figs 31–33 = 5 μm.

for those radiating around the apex (Figs 17-20). The raphe branches were biarcuate and the external terminal and central endings slightly deflected from the curvature of the raphe branches (Figs 14-16, 19, 20). The external raphe slit was partially hidden by an irregular flap (Figs 17, 19). Internal terminal raphe endings were also straight both externally and internally, and internally ended in a characteristic

helictoglossa (Fig. 16). The central area was no wider than the sternum (Figs 17, 18) and there was no stauros. Areolae were generally transapically rectangular, especially towards the sternum, but irregularly shorter to quadrangular (Figs 16-18).

Copulae were open and bore two rows of pores, as in other species, but in this species the valvocopula was recognizably different from the other copulae (i.e., pleurae), notwithstanding the lack of craticular bars (Figs 21-33). Copulae varied in width, mostly 1.2-1.5 µm wide (Figs 21, 23, 24, 31), including the valvocopula, but there were some very narrow ones with two rows of quadrangular pores (540 nm) (Fig 21, 22). The pleurae were flat, with one row of slits ca. 42 in 10 μm on each side of a "midrib", the slits sometimes longer on the abvalvar side (Figs 21, 23, 24). The open ends were blunt (Fig. 24); none were seen to have a ligula. The valvocopulae, in contrast were pleated, pointed at the open end, and had much wider pores, ca. 27 in 10 um (Figs 25-33). The pleat was seen as a ridge from the outside, sometimes sharp, sometimes wider (Figs 26, 27 vs. 29), and as a groove from the inside (Figs 28, 29). There were two rows of pores, which were most clearly seen near the poles (Figs 26, 27, arrows), where the band was still flat. The advalvar row of pores continued around the apex (Figs 26, 30, 32). There was a row of large pores on the abvalvar edge, which sometimes extended onto the lower edge of the pleat. The row of smaller pores appeared to be on the opposite side of the pleat with another flat, non-perforated surface on the margin (Fig. 29, arrow), but several views suggested that the small pores were along the advalvar margin (Figs 28 and 30 arrowheads). Figs 26-32 show the valvocopula at a variety of angles. It is clear from Fig. 25 that the ridge was exterior.

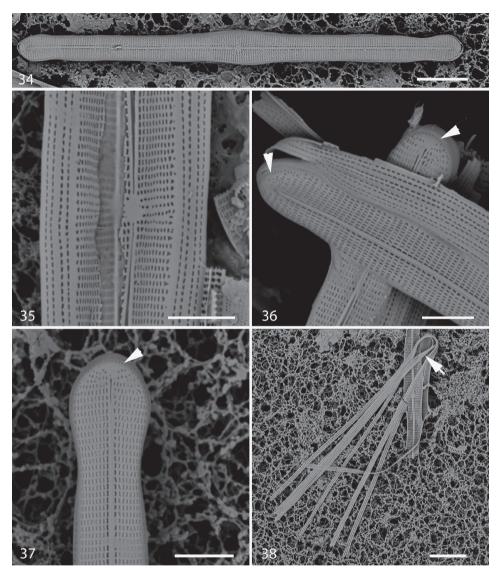
Remarks: The width, biarcuate raphe branches, and rectangular vs. circular areolae separate it from its nearest congener, the more slender *C. koenigii*, so far known only from Florida (Table 1). The most similar species in the Guam flora is *C. silvae*, which is shorter and has different areolae.

Climaconeis scalaris (Brébisson) Cox

Figs 4, 34-38

In addition to the two new curved species, I also recently collected a population of straight *Climaconeis* from Agat, Guam (GU75B-1). Cells were 88-91 µm long, 4.3-4.6 µm wide, center inflated to 5.5-6.3 µm and apices weakly capitate, 5.2 µm wide (Figs 4, 34); 10-12 pairs of plastids (Fig. 4); valves lacked a stauros, and the valvocopula lacked craticular bars. Striae 21 in 10 µm, parallel except weakly radiating adjacent to oval central area and weakly convergent approaching the apices, striae sparse and radiating beyond the terminal raphe ending (Figs 36, 37). Areolae rectangular, apically elongated, except porate in the central striae; central raphe endings straight (Fig. 35). Copulae had two rows of apically-elongated rectangular pores (Figs 35, 36, 38).

The cells differed from *C. scalaris* (*Navicula scopulorum* Brébisson "B") as described by Cox (1979, Figs 7, 11, 15-18, 28-34) in having inflated center and apices; in this regard they were similar to *C. undulata* (Meister) Lobban, Ashworth & Theriot and *C. fasciculata* (Grunow ex. Cleve) Hustedt, but differed from those two in valve dimensions and stria density. Particularly the SEM images in Cox (1979, Figs 28-34) show no significant differences from my material, so notwithstanding the minor shape variation and the absence of molecular data, I have provisionally identified it as *C. scalaris*, the correct name for the taxon according to Cox (1982). This is a new record for the region and brings the number of species in our flora to 11. The fact that it has previously been reported only from temperate European waters (Reid & Williams, 2002), one of three temperate *Climaconeis* species [the others are *C. inflexa* and *C. delicatula* (Cleve) E.J.Cox], suggests that



Figs 34-38. Climaconeis scalaris (GU75B-1), SEM of whole mount. **34.** Valve, showing shape and striae. **35.** Central area, whole mount, showing valve and copulae. **36.** Apices, one in oblique view, showing row of pores on mantle around apex (arrowheads) and copulae with apically-oriented rectangular pores. **37.** Apex, whole mount. **38.** Copulae from whole mount; only one pole present but open ends of copulae can be seen at arrow; note that there is no distinction between the various copulae. Scale bars: Figs 34, $37 = 10 \mu m$, Figs 35, 36, $38 = 4 \mu m$.

evidence from gene sequencing should be gathered when possible to confirm the identity. However, all three species have been rarely reported and *C. inflexa* also appears to occur in Guam (Lobban *et al.*, 2010).

DISCUSSION

Repeated sampling in Florida by Prasad and in Guam by myself suggest that there is still more diversity of *Climaconeis* to be discovered. In my experience they occur very sporadically; I have examined many collections since the earlier paper (Lobban et al., 2010) and seen occasional populations of C. silvae, C. guamensis, C. riddleae and individuals of C. lorenzii. Yet by chance the three new records are all from samples collected in 2017. There are also several species that closely resemble others and are easy to misidentify. Nevertheless, the genus has a surprising range of character states, including curved vs. straight, presence/absence of craticular bars and of a stauros, size of valves, number of plastids, density of striae, and the shape of the areolae. All species have distinct helictoglossae at the internal terminal raphe endings, as in other Berkeleyaceae, and the areolae are likely closed on the inside (Round et al. 1990). We did not publish gene sequences in Lobban et al. (2010) but Ashworth has sequenced several species more recently (C. riddleae, C. undulata (Meister) Lobban, Ashworth & Theriot, and an unidentified straight species from the Red Sea); they form a generic clade in phylogenetic trees (e.g., Ashworth et al., 2016).

The genus now includes 18 species, and I have extended the keys of Cox (1982) and Prasad (2003) to incorporate them all.

Of the recent publications that deal with *Climaconeis*, only one has a figure specifically of a girdle band (Prasad et al., 2000, Fig. 17, for C. koenigii), except for images of craticular valvocopulae in Round et al. (1990). My own images include a few with copulae but do not suggest a clear distinction between pleurae and valvocopula [i.e., Lobban et al., 2010, Fig. 36 (C. silvae) Figs 40, 43 (C. riddleae), Fig. 49 (C. guamensis), and the present study for C. desportseae (Figs 8, 9) and C. scalaris (Figs 35, 36, 38)]. So the usual situation (i.e., excluding the two species with craticular bars) is that all the bands are copulae, in contrast to situations where the valvocopula is distinct and the other (later formed) copulae referred to as pleurae, according to the terminology of von Stosch (1975). However, analysis of the cingulum in C. leandrei showed that the valvocopula is recognizably different, and that there is, among the pleurae one that is significantly narrower than the others. In Hanicella moenia Lobban & Ashworth, which has numerous copulae, Lobban & Ashworth (2014) found a narrow band that could be recognized as the 4th (last formed) pleura; in Climaconeis it has so far not been possible to determine the position of this narrow band in the sequence of pleurae, but it could well be the last-formed. While copulae within most species are indistinguishable, there are differences between species: pores in the bands of C. desportesiae and C. leandrei are transapical, whereas those in C. scalaris are apically oriented slits.

Although this is a small genus, it has already become necessary to use areola shape to help distinguish some like species, as used in the key, and this character should always be checked because we can expect both the list of species and the number of similar species to grow. Some additional valve features may become useful in future to distinguish similar species. (1) Some species of *Climaconeis* have a row of pores on the mantle around the apex [*C. koenigii, C. undulata, C. scalaris* [Figs 36, 37], *C. petersonii* Lobban, Ashworth & Theriot, *C. scopulorioides* (Hustedt) E.J.Cox] but others do not (*C. desportesiae* [Fig. 10], *C. leandrei* [Figs 17, 18], *C. silvae, C. riddleae*). (2) The striae at the apex commonly radiate around the end of the sternum (*C. leandrei* [Figs 17, 18], *C. riddleae* [Figs 12, 13], *C. silvae, C. undulata*) but may continue to be parallel (*C. petersonii*) or may

be nearly absent (*C. desportesiae* [Fig. 10]). (3) Raphe flaps do not occur in all species but are known from some other curved species – *C. silvae*, *C. riddleae* and *C. guamensis*, but not *C. koenigii* – as well as both new species here.

Finally, one may ask whether a case can be made for resurrecting the genus Okedenia T. Eulenstein ex G.B. De Toni emend. Mereschkowsky (Mereschkowsky 1901) for the curved species of *Climaconeis*. This genus was not originally conceived by De Toni (1891) or by Mereschkowsky (1901) as being defined by curved species. as it included several straight ones, but by the time of Cox's (1982) analysis, the curved species O. inflexa was the only one left. Cox (1982), after an exhaustive study of all the related taxa, and recognizing that information on many of them was partial, concluded that there should be only one genus and that by priority it would be Climaconeis, based on C. lorenzii, which has craticular bars. While species added since then (now the majority of the known taxa) have been thoroughly described, there is no evident synapomorphy that separates the curved and straight species, as curvature per se is not appropriate (several genera have both straight and curved species, e.g., Licmophora, Climacosphenia). Molecular data are presently scarce but, as noted above, Ashworth et al. (2016) have sequenced two straight and one curved species. There was 100% bootstrap support in the branch between the two straight species, but the curved species was sister to those with only 50% support. While this is tantalizing, sequencing of additional straight and curved species will be needed to get enough evidence to challenge the morphological conclusion. One may also ask how important is the craticular valvocopula in the straight species, for which Climaconeis was named? It occurs in only two species, neither of which has been sequenced.

KEY TO THE KNOWN SPECIES OF CLIMACONEIS

Notes. Plastids occur in pairs of plates often joined by a pyrenoid; plastid numbers are given in pairs. * Species reported from Guam

1.	Valves straight
1.	Valves curved
	2. Valve with central stauros.32. Stauros absent5
3.	Stauros without pores, valves 50-130 µm long, 3-7 µm wide, striae 35-38 in 10 µm
3.	Isolated pores in the stauros
	 4. Valves linear, striae 23 in 10 μm 4. Valves linear-lanceolate, striae 28-38 in 10 μm 6. scopulorioides 7. C. colemaniae
	Valvocopula with craticular bars 6 Craticular bars absent 7
	6. Central raphe endings deflected to one side, striae 16-20 in 10 μm
	6. Central raphe endings straight, striae 16 in 10 μm <i>C. coxiae</i> *
7.	Plastids 2 pairs, valves lanceolate, 26-65 μm long, striae ca. 40 in 10 μm
7.	Plastids > 2 pairs, valves linear, $> 65 \mu m long$, striae $< 30 in 10 \mu m$

8. Plastids > 40 pairs, valves 350-380 µm long	ı* 9
9. Valves robust, 10-12 μm wide; 90-120 μm wide, striae 17-19 in 10 μm	
C. fasciculata 9. Valves slender, ≤ 8 μm wide	0
10. Valves 68-92 μm long, 5.5-8 μm wide, striae \geq 20 in 10 μm <i>C. scalaris</i> 10. Valves 70-150 μm long, 8 μm wide, striae 18-20 in 10 μm <i>C. undulate</i>	s* 1*
11. Plastids 2 pairs	
11. Plastids numerous 1 11. Plastids not observed, proceed with ultrastructure characters 1	15 18
12. Striae 18-23 in 10 μm, valve arcuate-lunate	13
13. Striae very fine, 46-50 in 10 μm	?* [4
14. Striae 33-34 in 10 μm, raphe biarcuate (centrally deflected toward ventr side)	s *
14. Striae 24-27 in 10 μ m, raphe following valve curvature	
15. Plastids 8-20 pairs [assumed for <i>C. ghurbensis</i>], valves 120-210 (-298) μm lon external central raphe endings deflected	16
15. Plastids > 20 pairs, valves 200-470 μm long	
 16. Valves 5-10 μm wide, areolae irregularly elongate transapically <i>C. silvae</i> 16. Valves 4-5 μm wide, areolae quadrangular	is
17. Valves $< 5 \mu m$ wide, striae 24-27 in 10 μm , areolae circular to oval	
17. Valves 9-13 μm wide, striae 29 in 10 μm, areolae transapically rectangular	
18. Areolae circular throughout, cells very long (200-468 μm) and slende (2 μm wide except at poles and center)	er gii
19. Areolae square to apically rectangular	20
19. Areolae transapically elongate.	
20. Stria density 24-28 in 10 μm, areolae rectangular, apically elongate	
20. Stria density 18-23 in 10 μm, areolae circular except for larger apical elongate rows along sternum	ly
21. Stria density > 40 in 10 μm	2* 22
 22. Areolae square to rectangular	23 2*
23. Striae 29 in 10 μm, cells > 200 μm long	i*
24. Areolae square except along the sternum, cells 120-160 μm long	
24. Areolae transapically elongate throughout,	is
cells 90-120 µm long	s*

Acknowledgements. Some details of *C. desportesiae* and *C. leandrei* were imaged in Szczecin thanks to Rafał Wróbel, Zachodniopomorski Uniwersytet Technologiczny, Department of Technology and Chemical Engineering, and Andrzej Witkowski, University of Szczecin. The microscopes used at U. Guam were funded by NIGMS RISE award GM063682. I thank María Schefter for continuous support and encouragement with the diatom research, and Captain H.E. Sholley, Commanding Officer of Naval Base Guam for continued access to the collecting sites on the base. Thanks to one of the anonymous reviewers for the question about *Okedenia*.

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