

Typification and taxonomic status re-evaluation of 15 taxon names within the species complex *Cymbella affinis/tumidula/turgidula* (Cymbellaceae, Bacillariophyta)

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Abstract

Specimens belonging to the *C. affinis* / *C. tumidula* / *C. turgidula* species complex have many taxonomic problems, due to their high morphological variability and lack of type designations. Fifteen taxon names of this complex, distributed in five species, were re-evaluated concerning their taxonomic status, and lectotypified based on original material. In addition to light microscopy, some material was analyzed by electron microscopy. Four new combinations are proposed in order to reposition infraspecific taxa.

Keywords

Diatoms, typification, Cymbellales, *Cymbella tropica*, *Cymbella subturgidula*, *Cymbella rheophyla*, *Cymbella uenoi*

Introduction

The history of the genus *Cymbella* C.Agardh is replete with taxonomic complexities. Within these complexes many species are similar in valve morphology. Much of the confusion in these complexes was caused by poor species descriptions including specimen images and the lack of designation of types, which has been required by the International Code of Nomenclature for algae, fungi, and plants (ICN) only since 1958 (McNeill et al. 2012).

In the most recent revision of the genus *Cymbella*, Krammer (2002) characterized and emended species descriptions within the complex *C. affinis* Kütz. / *C. tumidula* Grunow / *C. turgidula* Grunow. This has generated confusion in the taxonomy of the group, specifically concerning the typification of *C. affinis*. The concept of *C. affinis* as proposed by Krammer (2002) involved the synonymization of *C. affinis* and *C. tumidula* Grunow, and the restoration of *C. excisa* Kütz. *Cymbella excisa* has previously been treated by some authors as a synonym of *C. affinis*, at the same or at an infraspecific rank (e.g. Cleve 1894, Grunow 1882, Patrick and Reimer 1975). According to Krammer (2002), the specimens treated as *C. affinis* have cymbelloid outlines, with the axial area straight to slightly curved and a prominent central area. In these specimens the valvar ends are more protracted and more densely striated and areolated than in *C. excisa*, which has the axial area curved and an indistinct central area. Moreover, *C. excisa* commonly has an excision in the ventral middle part of the valve.

Krammer in Krammer and Lange-Bertalot (1986) also designated a neotype for *C. turgidula*, a species with an outline very similar to *C. affinis* but with wider, fewer and uniformly distributed striae, and less-dense punctae in the striae. In the same contribution, Krammer also described the new species *C. subturgidula* Krammer, which he distinguished from *C. turgidula* by its narrower breadth, higher length/breadth ratio, and the size and shape of the central area.

Tuji (2007) designated a lectotype for *C. affinis* from an original illustration provided by Kützing (1844, Pl. 6, Fig. 15). Moreover, he assigned an epitype to a single specimen in preparation BM 18530 (Tuji 2007, Fig. 9) which was made from the original sample, which is Kützing's packet 333.

Tuji (2007) observed that the designation of a neotype for *C. turgidula* by Krammer in Krammer and Lange-Bertalot (1986) was inappropriate. This designation was made because Krammer was unable to locate the original samples or preparations (Krammer and Lange-Bertalot 1986). Tuji (2007) found the original slide (syntype) used by Grunow in Schmidt (1875) to describe *C. turgidula*, and designated an original illustration as a lectotype and one specimen on Grunow's slide as an epitype.

The material of *C. uenoi* Skvortsov was also revisited by Tuji (2007), which according to him would make *C. subturgidula* a synonym. He also proposed the new combination *C. uenoi* f. *nipponica* (Skvortsov) Tuji for *C. turgidula* var. *nipponica* Skvortsov [\equiv *Cymbella rheophila* Ohtsuka].

Despite the changes, the revision of Tuji (2007) did not resolve the status of taxa such as *C. tumidula* or *C. excisa*. Moreover, he overlooked some requirements by the ICN with respect to the validity of the name *C. uenoi*.

The aim of the present study was to elucidate the current taxonomic status of *C. tumidula*, *C. excisa* and *C. subturgidula*, as well as of *C. uenoi* and *C. uenoi* f. *nipponica* [\equiv *C. turgidula* var. *nipponica*; \equiv *Cymbella rheophila*]; to revisit the infraspecific taxa encompassed in this complex of species; and to lectotypify the ambiguous taxa.

Materials and methods

We analyzed the protologues and morphological features from materials of *C. affinis* var. *affinis*, *C. affinis* var. *procera*, *C. excisa* var. *excisa*, *C. excisa* var. *procera*, *C. excisa* var. *angusta*, *C. excisa* var. *subcapitata*, *C. tumidula* var. *tumidula*, *C. salinarum*, *C. turgida*, *C. tropica*, *C. subturgidula*, *C. turgidula* var. *nipponica*, *C. reophila*, *C. uenoi* f. *uenoi*, and *C. uenoi* f. *nipponica* (Table 1). The characterization of *C. salinarum* and *C. uenoi* f. *uenoi* was based on the illustration of the holotype provided by Krammer (2002, Fig. 25: 13) and of the epitypes illustrated by Tuji (2007, Figs 14–19).

Materials of *C. affinis* (BM18530), *C. excisa* (BM 18543), *C. tumidula* (BM 18543), *C. turgidula* var. *nipponica* (R 214.928, R 214.929, R 214.930, R 214.931 and R 214.932) were analyzed in the Laboratório de Ficologia, Museu Nacional, Rio de Janeiro, Brazil, using an Olympus BX 51 microscope (Olympus, Tokyo, Japan) fitted with an Olympus Q-Color digital camera. Images were processed with Q capture Pro QImaging© software.

Materials of *C. affinis* sensu Krammer (1198F IOK BRM) and *C. affinis* var. *procera* (714 IOK BRM) were examined in the laboratory of the Botanischer Garten und Botanisches Museum (BGBM), Berlin, Germany, using a Zeiss Axio Imager 4.2 microscope (Carl Zeiss MicroImaging GmbH, Berlin), and the images were captured through an MRC/MRM system (Carl Zeiss MicroImaging) and the software AxioVision Rel. 4.8 (Carl Zeiss MicroImaging).

We also analyzed materials *C. excisa* sensu Krammer (1131G IOK BRM), *C. excisa* var. *procera* (212A IOK BRM), *C. excisa* var. *angusta* (752 IOK BRM), *C. excisa* var. *subcapitata* (717A IOK BRM), *C. tropica* (1015D IOK BRM) and *C. subturgidula* (1046E IOK BRM) with a Zeiss Axioplan microscope (Carl Zeiss, Jena, Göttingen, Germany) with an Olympus XC50 capture system (Olympus, Tokyo, Japan) and the software analySIS Image Processing (Soft Imaging System, Münster, Germany), at the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Scanning Electron Microscopy (SEM) analyses were carried out only for *C. turgidula* var. *nipponica*. Samples were deposited on cover slips and attached to aluminum stubs using LeitSilver® (Sigma-Aldrich, Berlin, Germany). The material was coated with 150–200 Å of gold in an Emitech K 550 sputter coater (Quorum Technologies Ltd., Kent, UK). The material was analyzed in a Jeol JSM-6390 scanning electron microscope (Jeol, USA), operated at 6–8 kV, spot size 10–30, in the electron microscopy laboratory in the Museu Nacional, Rio de Janeiro, Brazil.

The term “degree of dorsiventrality” is used here to define how dissimilar the sides of the valvae are on the apical axis. The symbols “ \equiv ”, “=” and “–” preceding

Table 1. Metric features of the material of the complex *C. affinis/tumidula/turgidula* analyzed in this study ($n=29-34$ individuals).

Taxon (published name)	Current name	Material	Length (μm)	Breadth (μm)	L/B ratio	Striae in middle part (in 10 μm)	Striae close to the ends (in 10 μm)	Puncta (in 10 μm)	Stigmata
<i>C. affinis</i> Kürz. sensu Kramer (2002)	<i>C. tumidula</i> Grunow var. <i>tumidula</i>	Preparation 1198F IOK in BRM, from France, Normandy, Falaise, coll. Brébisson, in BRM (Figs 50–56)	25.4–29.8	7.8–8.7	3.4–3.9	10–15	12–19	26–33	2–3
<i>C. affinis</i> Kürzing (1844)	<i>C. affinis</i> Kürzing var. <i>affinis</i>	Lectotype designated by Tuji (2007), preparation BM 18530, from France, Falaise, coll. Brébisson, in BM (Figs 1–7)	22.5–26.7	7.0–8.5	2.9–3.4	9–12	11–18	19–27	1
<i>C. affinis</i> var. <i>procera</i> Kramer (2002)	<i>C. tumidula</i> var. <i>procera</i> (Krammer) W.Silva, comb. nov.	Holotype, preparation 714 IOK, from Serbia, Rogatica, 1976, in BRM (Figs 57–63)	27.0–40.3	9.0–10.2	2.9–4.2	9–13	13–18	25–31	2–5
<i>C. excisa</i> var. <i>procera</i> Kramer (2002)	<i>C. affinis</i> var. <i>neoprocera</i> W.Silva, comb. nov. et nom. nov.	Holotype, preparation 212A IOK, from West Germany, Eifel, Torenmaar, 2.2.1974, in BRM (Figs 22–28)	21.5–41.0	8.0–11.0	2.7–4.0	9–13	11–14	22–27	1
<i>C. excisa</i> Kürzing (1844)	<i>C. affinis</i> var. <i>excisa</i> (Kürz.) Grunow	Isolectotype, preparation 1131G IOK, Hauck No. 72 from Italy, 26.3.1837, in BRM (Figs 15–21)	23.1–28.5	7.0–9.5	2.7–3.9	9–12	11–17	24–26	1
<i>C. excisa</i> var. <i>angusta</i> Kramer (2002)	<i>C. affinis</i> var. <i>angusta</i> (Krammer) W.Silva, comb. nov.	Holotype, preparation 752 IOK, from Croatia, Lake Gavanovac, 18.5.1976, in BRM (Figs 29–35)	20.5–35.0	6.0–8.5	3.2–4.6	9–15	11–18	19–29	1
<i>C. excisa</i> Kürzing (1844)	<i>C. affinis</i> var. <i>excisa</i> (Kürz.) Grunow	Lectotype (designated here), preparation BM 18543, from Hauck No. 72 from Italy, 26.3.1837, in BRM (Figs 8–14)	21.5–26.5	7.0–8.7	2.6–3.5	9–13	11–16	21–25	1
<i>C. excisa</i> var. <i>subcapitata</i> Kramer (2002)	<i>C. affinis</i> var. <i>subcapitata</i> (Krammer) W.Silva, comb. nov.	Holotype, preparation 717A IOK, from Hungary, Balaton, 6.77, in BRM (Figs 36–42)	21.0–31.7	7.4–9.0	2.7–4.0	8–12	9–15	26–31	1

Taxon (published name)	Current name	Material	Length (µm)	Breadth (µm)	L/B ratio	Striae in middle part (in 10 µm)	Striae close to the ends (in 10 µm)	Puncta (in 10 µm)	Stigmata
<i>C. subburgidula</i> Kramer (2002)	<i>C. subburgidula</i> Kramer	Lectotype, preparation 1046E IOK, from Korea, Ulsin County, Kyungsang Pukdo, Kwangchun River, in BRM (Figs 71–77)	30.3–37.4	9.0–12.8	2.6–3.5	9–11	12–15	21–24	2
<i>C. tropica</i> Kramer (2002)	<i>C. tropica</i> Kramer	Holotype, preparation 1015D IOK, from Venezuela, Rio Manizanes, coll. Rumrich 4.4.1990, in BRM (Figs 64–70)	34.5–42.7	10.0–12.0	3.1–4.0	9–12	11–12	21–24	1
<i>C. tumidula</i> Grunow in Schmidt (1875)	<i>C. tumidula</i> Grunow var. <i>tumidula</i>	Lectotype (designated here); Epitype (designated here), preparation BM 18543, from Hauck No. 72, from Italy, 26.3.1837, in BM (Figs 43–49)	26.8–34.7	7.8–8.7	3.4–4.0	10–15	12–19	26–33	2–4
<i>C. salinarum</i> Grunow in Schmidt (1875)	<i>C. tumidula</i> var. <i>salinarum</i> (Grunow) Cleve	Holotype illustration provided Kramer (2002, Fig. 25: 13)	34.0	10.7	3.2	14	15	–	1
<i>C. turgidula</i> Grunow in Schmidt (1875)	<i>C. turgidula</i> Grunow	Epitype designated by Tuji (2007), preparation 1504, from Puerto Rico, in the Grunow Collection, in W	36.5–45.0	10.8–13.3	3.2–3.4	9–12	11–17	21–24	1–3
<i>C. turgidula</i> var. <i>nipponica</i> Skvortsov (1936) [= <i>C. rheophila</i> Ohtsuka in Ohtsuka and Tuji (2002); = <i>C. uenoi</i> f. <i>nipponica</i> (Skvortsov) Tuji (2007)]	<i>C. subburgidula</i> Kramer	Isolectotype, preparation R 214.928, from sample 0983 from Japan, Lake Biwa, coll. Tamiji Kawamura, 03.11.1915, in R (Figs 78–80)	28.1–39.0	10.0–13.2	2.8–3.0	9–12	12–15	21–26	1–2
		Preparations R 214.929 and R 214.930, from sample 1062, from Japan, Yamanoshita Bay in Lake Biwa, Otsu City, Shiga Prefecture, coll. Yasuko Iwao in 23.01.1993, in R (Fig. 81)	27.7–39.2	10.3–13.1	2.5–3.6	9–12	12–15	22–26	1–2

Taxon (published name)	Current name	Material	Length (µm)	Breadth (µm)	L/B ratio	Striae in middle part (in 10 µm)	Striae close to the ends (in 10 µm)	Puncta (in 10 µm)	Stigmata
		Preparations R 214.931 and R214.932, from from sample 1093, from Japan, cobble in Lake Biwa, at Uchidehama, Otsu City, Shiga Prefecture, coll. Yasuko Iwao, 03.03.1993, in R (Figs 82–84)	26.5–40.1	11.1–13.5	2.3–3.4	9–13	12–14	21–24	2–3
<i>C. uenoi</i> Skvortsov ex Tuji (2007)		Epitype and isotype illustrations provided Tuji (2007, Figs 21–24, 26)	26.3–41.0	9.0–12.7	2.9–3.2	9–11	12–15	21–24	2

specific and infraspecific names are used to represent homotypic or nomenclatural, heterotypic or taxonomic, and concept synonyms, respectively, as used in the ICN (McNeill et al. 2012).

Results

Cymbella affinis Kütz

Figs 1–7

Cymbella affinis Kütz., Bacill., 80, Pl. 6 Fig. 15, 1844.

Lectotype. 3rd figure from the left in Kützing (1844, pl. 6, Fig. 15) designated by Tuji (2007).

Type locality. “Falaise (France): De Brébisson! Herb. Binder., Schleswig: Herb. Binder.!”

Epitype. An individual on preparation BM18530, from Kützing packet 333, in the Natural History Museum (BM), designated by Tuji (2007, Fig. 9).

Epitype locality. Falaise, France, coll. De Brébisson.

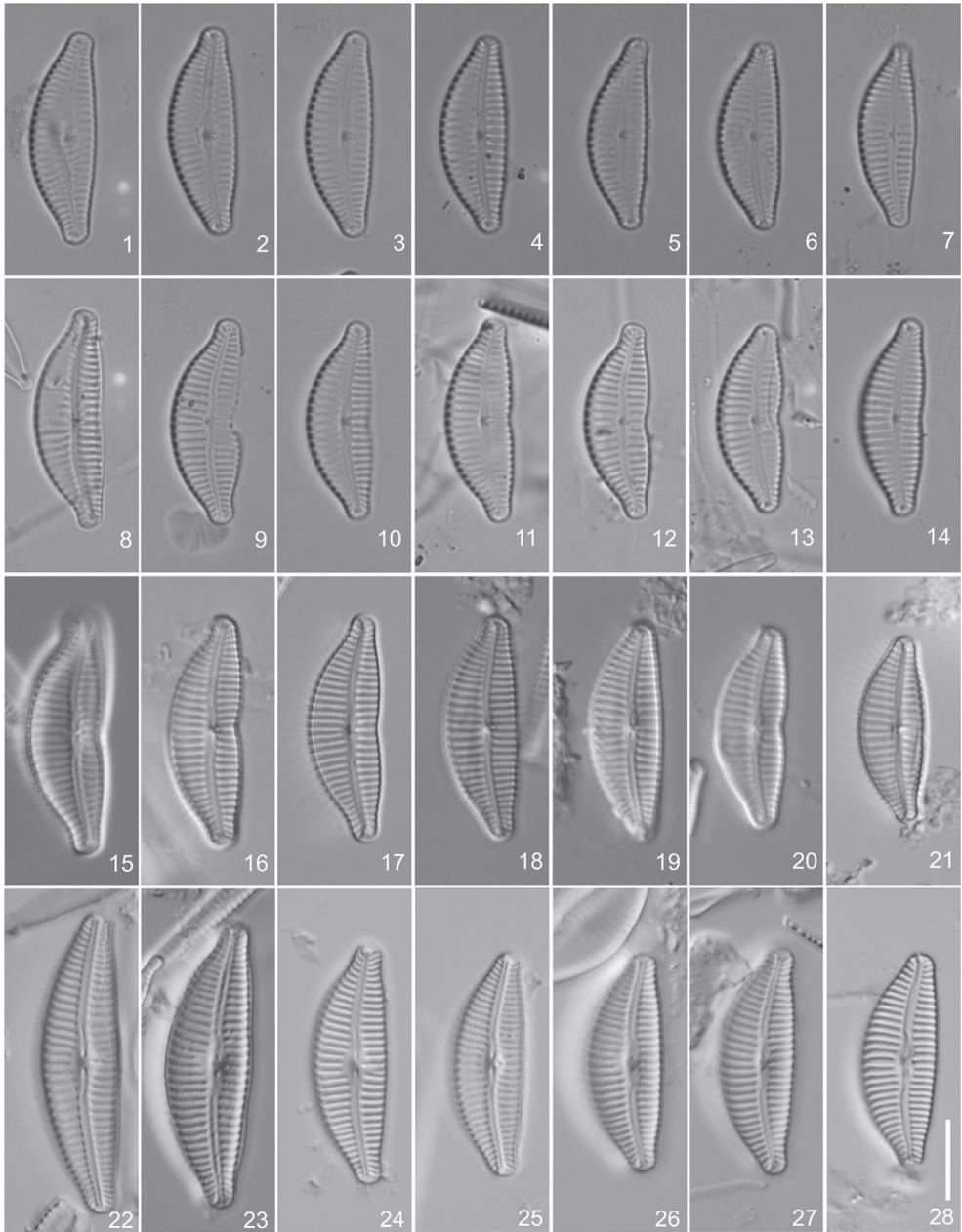
Valvae lanceolate, dorsiventral, dorsal and ventral margins convex; ends barely protracted, rounded, to slightly subrostrate or subcapitate; length 22.5–26.5 µm, breadth 7.0–8.5 µm, L/B ratio 2.9–3.4; axial area narrow, linear-arched, indistinct central area; striae 9–12 in 10 µm, becoming 11–18 towards ends, one isolated pore at end of central striae on ventral side; 19–27 punctae in 10 µm.

Remarks. Although Krammer (2002, p. 41) used material sampled by the same collector and from the same locality and related his new preparation to the type locality, his effort did not constitute a typification of *C. affinis* as ruled by the ICN (Art. 7.10, McNeill et al. 2012). On the other hand, Tuji (2007) was the first to consider the original material of this taxon and performed a lectotypification and epitypification, and as such, must be followed according to Articles 9.19 and 9.20 (McNeill et al. 2012).

The lectotype valve of *C. affinis* is similar to the lectotype valve of *C. excisa*, except for the excision in the middle part of the valve present in the majority of specimens (Figs 8–21). Populations of this complex from different parts of the world may or may not have excisions, but this character is present in the majority of specimens from the populations examined (Krammer 2002). Therefore, we consider *C. excisa* and *C. affinis* as belonging to the same species with differences at the varietal rank based on phenotypic expression and ecological modifications. Genetic studies are still to be completed.

The two taxa were both proposed by Kützing (1844, p. 80) and therefore have the same priority. In similar cases, Article 11.5 of the ICN rules that “the first such choice to be effectively published establishes the priority of the chosen name”.

Grunow (1882) proposed the new combination and the new status of *C. excisa* for *C. affinis* var. *excisa* (Kütz.) Grunow. This was the first publication that defined



Figures 1–28. *Cymbella affinis* species complex **1–7** *C. affinis* Kütz. var. *affinis* **8–14** *C. affinis* var. *excisa* (Kütz.) Grunow, specimens from Trieste in preparation BM 18543 **11** Lectotype, designated here **15–21** *C. affinis* var. *excisa* [– *C. excisa* sensu Krammer], specimens from Trieste in preparation 1131 IOK **16** Isolectotype, designated here **22–28** *C. affinis* var. *neoprocera* W.Silva, specimens from Germany in preparation 212A IOK, holotype **22** Lectotype, designated here. Scale bar: 10 μ m.

the priority of the epithet *affinis* over *excisa* at the specific level. Therefore, the name *C. affinis* must be considered to be the name of the species when *C. excisa* and *C. affinis* are considered to be the same species, in conformity with Article 11.5 of the ICN (McNeill et al. 2012).

Cymbella affinis valves sensu Patrick and Reimer (1975, p. 57) have similar outlines as *C. affinis* in the type population, but higher range of length and breadth values (length: 20–50 vs. 22.5–26.5 μm ; breadth: 7–12 vs. 7.0–8.3 μm , respectively). However, these authors (Patrick and Reimer 1975), included representatives of different localities that could encompass different varieties subscribed to this taxon. The density of striae in the material from USA was similar in the middle part of the valve compared to the type material (9–11 vs. 9–12 striae in 10 μm , respectively) and lower when comparing them close to the ends of the valvae (12–14 vs. 11–18 striae in 10 μm , respectively) (Patrick and Reimer 1975).

C. excisa var. *procera* Krammer (Figs 22–28), *C. excisa* var. *angusta* Krammer (Figs 39–35) and *C. excisa* var. *subcapitata* Krammer (Figs 36–42) also appear to be conspecific with *C. affinis*, but the types show slight differences in their outlines and metric characteristics (Table 1). Thus, all these taxa are here transferred to *C. affinis* using their respective infraspecific epithet.

***Cymbella affinis* var. *excisa* (Kütz.) Grunow**

Figs 8–21

Cymbella affinis var. *excisa* (Kütz.) Grunow, Beitr. Paläont. Österreich.-Ungarns Orients, 2: 142, Pl. 19(1), Fig. 26, 1882.

Basionym. *Cymbella excisa* Kütz., Bacill., 80, Pl. 6, Fig. 17, 1844.

Lectotype (designated here). An individual marked with blue ring on preparation BM 18543, from Hauck No. 72, 26.4.1837, in the Natural History Museum (BM), London, United Kingdom, represented by Fig. 11.

Isolectotype (designated here). An individual on preparation 1131G IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 16.

Type locality. “Unter Oscillatorien in Bächen bei Triest”, Italy, 26.4.1837.

Valvae dorsiventral, dorsal margin broadly convex, ventral margin straight, usually with an excision in middle portion; ends subrostrate to rostrate; length 21.5–28.5 μm , breadth 7.0–9.5 μm , L/B ratio 2.6–3.9; axial area narrow, linear-arched, central area indistinct; striae 9–13 in 10 μm , becoming 11–17 toward ends, one isolated pore at end of central striae on ventral side; 21–26 punctae in 10 μm .

Remarks. Similarly to *C. affinis*, the lectotypification of *Cymbella excisa* designated by Krammer (2002, p. 26) cannot be considered according to Article 7.10 of the ICN

(McNeill et al. 2012), because the phrase “designated here” or equivalent is required from 1 January 2001 and it was not included by Krammer (2002). Therefore, the lectotype designated by us cannot be considered a replacement of Krammer’s (2002) “lectotype”; rather, it is the first lectotypification of this taxon.

The main difference between *C. affinis* var. *excisa* and the nominate variety is the presence of an excision in the middle portion of the ventral side of the valve, a characteristic common to populations of this taxon around the world (Krammer 2002). Therefore, we consider that the presence of excisions in all populations, not present in the type material of *C. affinis*, constitutes sufficient grounds to consider *C. affinis* var. *excisa* different from the nominate variety, which conforms to the statement by Grunow (Schmidt 1875); and not a different species.

Krammer (2002) recorded populations in the isotype material of *C. affinis* var. *excisa* with length 17–41 μm , and breadth 6.0–10.7 μm , which were higher than populations in the lectotype material. Krammer (2002) was able to observe initial and post initial cells which were similar to the minimum and maximum length and breadth of this taxon. However, Krammer (2002) included specimens of the variety *excisa* and the nominate variety in his description.

***Cymbella affinis* var. *neoprocera* W.Silva, comb. nov. et nom. nov.**

Figs 22–28

Basionym. *Cymbella excisa* var. *procera* Krammer, *Diatoms Europe* 3: 159, Figs 9:1–7, 2002 (Figs 22–28).

Holotype. Preparation 212A IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Lectotype (designated here). An individual on preparation 212A IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany; represented by Fig. 22.

Type locality. Germany, Eifel, Totenmaar, 22.2.1974.

Valvae dorsiventral, dorsal margin broadly convex, ventral margin straight; ends not protracted, rounded, or subrostrate to rostrate; length 21.5–41.0 μm , breadth 8.0–11.0 μm , L/B ratio 2.7–4.0; axial area narrow, linear-arched, indistinct central area; striae 9–13 in 10 μm , becoming 11–14 toward ends, one isolated pore at end of central striae on ventral side; 22–27 punctae in 10 μm .

Remarks. The combination of *C. excisa* var. *procera* with *Cymbella affinis* would be illegitimate unless it was given a new name, because it would be a later homonym of *C. affinis* var. *procera* Krammer. Specimens designated by Krammer (2002), i.e., the preparation 212A IOK (BRM), were found to belong to more than one taxon therefore to clarify the taxonomy we designated a lectotype as established in Art. 9.11 of the ICN (McNeill et al. 2012).

A broader range of metric characteristics were highlighted in this study compared to the characterization of the type population (Krammer 2002, p. 28). We find smaller

(21.5–41.0 vs. 24–41 μm) and narrower (8.0–11.0 vs. 8.4–11.0 μm) representatives of this taxon compared to the Krammer's (2002) records. Still considering Krammer's (2002) findings, we observe more densely striated (9–13 vs. 9–11 striae in 10 μm) and less punctate (22–27 vs. 24–27 punctae in 10 μm) valves.

***Cymbella affinis* var. *angusta* (Krammer) W.Silva, comb. nov.**

Figs 29–35

Basionym. *Cymbella excisa* var. *angusta* Krammer, Diatoms Europe 3: 159, Figs 9: 8–13, 2002.

Holotype. Preparation 752 IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Lectotype (designated here). An individual on preparation 752 IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 29.

Type locality. Croatia, watercourse near Lake Gavanovac, Plitvice.

Valves dorsiventral, dorsal margin broadly convex, ventral margin straight, usually with excision in middle portion; ends not protracted to slightly protracted, rounded, subrostrate or subcapitate; length 20.5–35.0 μm , breadth 6.0–8.5 μm , L/B ratio 3.2–4.6; axial area linear-arched, indistinct central area; striae 9–15 in 10 μm , becoming 11–18 towards ends, one isolated pore at end of central striae of ventral side; 19–29 punctae in 10 μm .

Remarks. The material recorded here presented slight differences in the valve metrics compared to Krammer's (2002, p. 28) characterization from the same preparation; differences included valve length (20.5–35.0 vs. 17.0–34.0 μm), breadth (6.0–8.4 vs. 6.7–8.2 μm), striae (9–15 vs. 11–14 in 10 μm) and number of punctae (19–29 vs. 25–28 in 10 μm).

Similar to *C. affinis* var. *neoprocera*, specimens designated by Krammer (2002), i.e., the preparation 752 IOK (BRM), were found to belong to more than one taxon. Therefore we designated a lectotype for this taxon as established in Art. 9.11 of the ICN (McNeill et al. 2012).

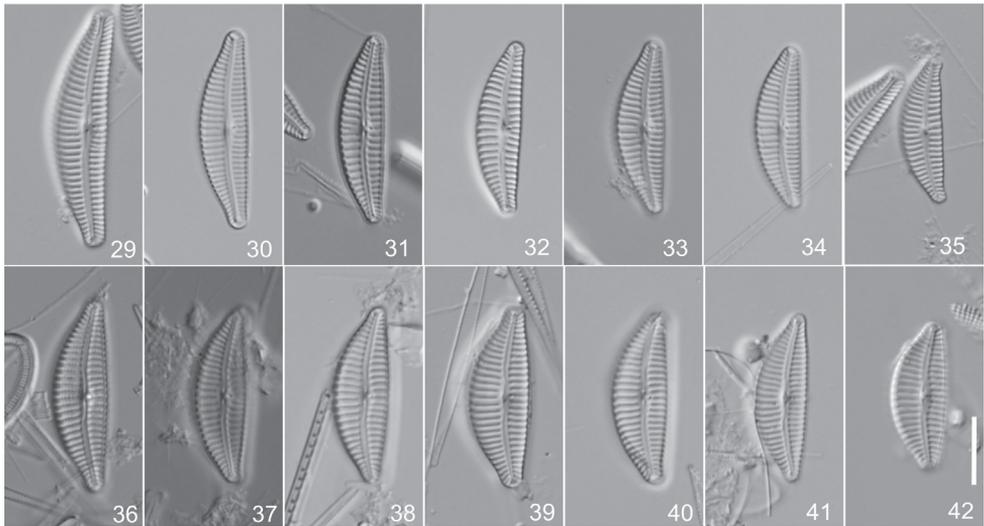
***Cymbella affinis* var. *subcapitata* (Krammer) W.Silva, comb. nov.**

Figs 36–42

Basionym. *Cymbella excisa* var. *subcapitata* Krammer, 2002, Diatoms of Europe 3: 159, Figs 10: 14–18.

Holotype. Preparation 717A IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Lectotype (designated here). An individual on preparation 717A IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 39.



Figures 29–42. *Cymbella affinis* species complex **29–35** *C. affinis* var. *angusta* (Krammer) W.Silva, specimens from Croatia in preparation 752 IOK, holotype **29** Lectotype, designated here **36–42** *C. affinis* var. *subcapitata* (Krammer) W.Silva, specimens from Hungary in preparation 717 IOK, holotype **39** Lectotype, designated here. Scale bar: 10 μ m.

Type locality. Hungary, Balaton.

Valves dorsiventral, dorsal margin broadly convex, ventral margin straight, usually with excision in middle portion; ends barely protracted, rounded, to broadly protracted, subcapitate; length 21.0–31.7 μ m, breadth 7.4–9.0 μ m, L/B ratio 2.7–4.0; axial area linear-arched, indistinct central area; striae 8–12 in 10 μ m, becoming 9–15 towards ends, one isolated pore at end of central striae of ventral side; 26–31 punctae in 10 μ m.

Remarks. Krammer (2002) distinguished this variety from the variety *excisa* based on the shape of the ends of the valvae. However, he (Krammer 2002, p. 28) did not provide metric characterizations of this the variety *subcapitata*, which we observed to agree with the characterizations of *C. excisa* sensu Krammer (2002), except for the density of striae that was slightly lower in the variety *subcapitata*.

Specimens designated by Krammer (2002), i.e., the preparation 717A IOK (BRM), were found to belong to more than one taxon. Therefore we designated a lectotype as established in Art. 9.11 of the ICN (McNeill et al. 2012).

Cymbella tumidula* Grunow var. *tumidula

Figs 43–56

Cymbella tumidula Grunow var. *tumidula*, in Schmidt, A. Schmidt's Atlas Diatom.-Kunde, Pl. 9, Fig. 33, 1875.

Synonym. *Cymbella affinis* Kütz. *sensu* Krammer, *Diatoms Europe* 3: 41, Figs 21:2–21, 22:1–20, 23:1–18, 2002. (Figs 50–56).

Lectotype (designated here). Plate 9, Fig. 33 from Schmidt (1875a) (Fig. 43).

Type locality. Italy, Trieste, 26.4.1837.

Epitype (designated here). An individual marked with a red ring on preparation BM 18543 from Hauck No. 72, 26.4.1837, in the Natural History Museum (BM), London, United Kingdom, represented by Fig. 49.

Isoepitype (designated here). An individual on preparation 1131G IOK, from Hauck No. 72, 26.4.1837, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 54.

Epitype locality. Italy, Trieste, 26.4.1837.

Valves lanceolate, dorsiventral, dorsal and ventral margins convex; subcapitate ends; length 25.4–34.7 μm , breadth 7.8–8.7 μm , L/B ratio 3.4–4.0; axial area linear-lanceolate, straight to arched, central area irregular to rounded; striae 10–15 in 10 μm , becoming 12–19 toward ends, 2–4 isolated pores at end of central striae on ventral side; 26–33 punctae in 10 μm .

Remarks. The lectotypification of *C. affinis* allowed us to consider *C. affinis* and *C. tumidula* [– *C. affinis sensu* Krammer], lectotypified and epitypified here, as independent species. *C. tumidula* has a more lanceolate outline, subcapitate ends, and a lower degree of dorsiventrality than *C. affinis*. The striae in the middle part of the valve are shorter and unevenly distributed in *C. tumidula*, forming a distinct central area (Figs 43–63), in contrast to *C. affinis* where the central area is indistinct and the striae are uniformly distributed. In addition, all specimens of the type material of *C. affinis* have only one stigma, whereas in *C. tumidula* 1–5 stigmata can be observed.

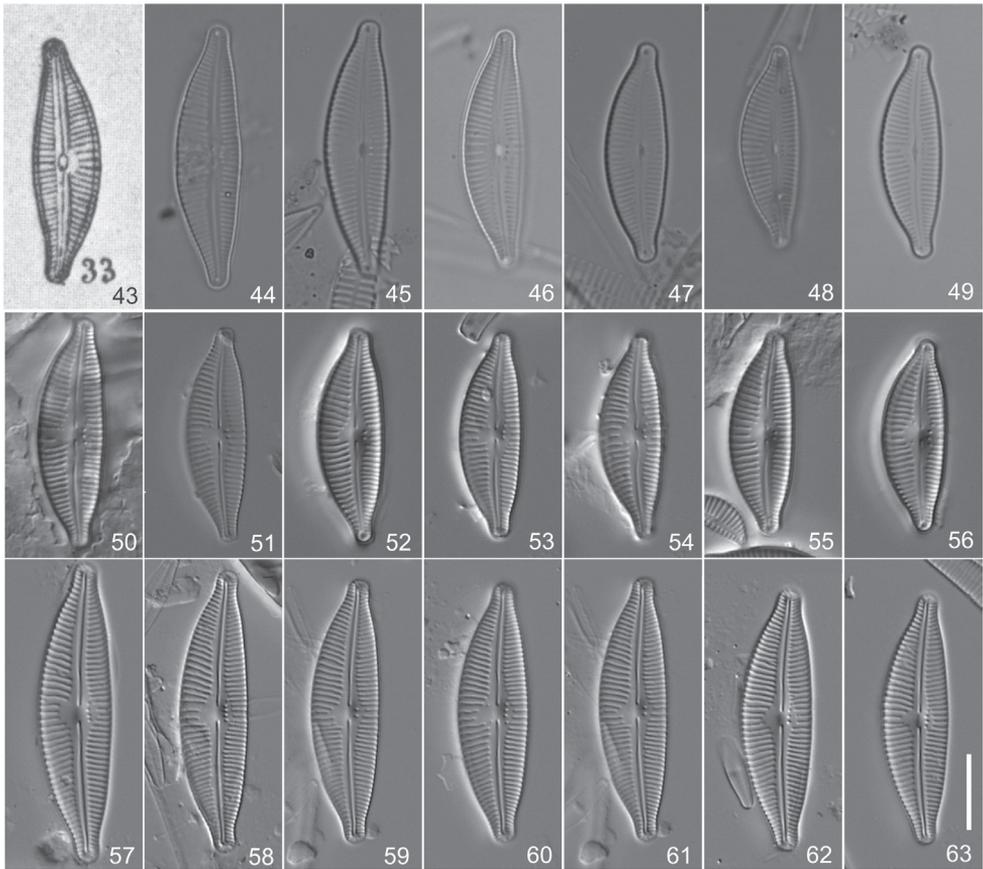
Specimens from the population of the holotype material of *C. affinis* var. *procera* were very similar in outline but larger and wider than *C. tumidula* var. *tumidula*, resulting in higher maximum length/breadth ratios. However, all metric characteristics of *C. affinis* var. *procera* intergraded with *C. tumidula* var. *tumidula*, and therefore this taxon was transferred to *C. tumidula* var. *procera*.

The characteristics of *C. affinis sensu* Krammer (2002, p. 41) were similar to the type population of *C. tumidula*, but with a wider range of values. This includes length (17–34 vs. 25.4–34.7 μm , respectively) and breadth (7.5–9.5 vs. 7.8–8.7 μm). *C. affinis sensu* Krammer (2002, p. 41) also presented narrower range of values of striae in 10 μm (10–13, becoming 13–15 toward ends vs. 10–15 in 10 μm , becoming 12–19 toward ends, respectively) and density of punctae (27–32 vs. 26–33 punctae in 10 μm) than *C. tumidula*.

***Cymbella tumidula* var. *procera* (Krammer) W.Silva, comb. nov.**

Figs 57–63

Basionym. *Cymbella affinis* var. *procera* Krammer, *Diatoms Europe* 3: 161, Figs 22: 8–13, 2002.



Figures 43–63. *Cymbella tumidula* species complex **43** Original illustration provided by Grunow in Schmidt (1875, Pl. 9, Fig. 33), lectotype, here designated **44–49** *C. tumidula* var. *tumidula*, specimens from Trieste in preparation BM 18543 **49** Epitype, here designated **50–56** *C. tumidula* var. *tumidula* [*C. affinis* sensu Krammer (2002)], specimens from Trieste in preparation 1131G IOK **54** Isolectotype, designated here **57–63** *C. tumidula* var. *procera* (Krammer) W.Silva, specimens from Serbia in preparation 714 IOK, holotype **57** Lectotype, designated here. Scale bar: 10 μm .

Holotype. Preparation 714 IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Lectotype (designated here). An individual on preparation 714 IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 57.

Type locality. Serbia, Rogatica (abundant in chalk-rich spring), 1976.

Valves lanceolate, dorsiventral, dorsal and ventral margins convex; ends subrostrate or subcapitate; length 27.0–40.3 μm , breadth 9.0–10.2 μm , L/B ratio 2.9–4.2; axial area linear-lanceolate, slightly arched, central area rounded; striae 9–13 in 10 μm , becoming 13–18 toward ends, 2–5 isolated pores; 25–31 punctae in 10 μm .

Remarks. According to Krammer (2002), this variety differs concerning wider valves (higher than 9.5 μm) from the nominate variety of *C. affinis* sensu Krammer. We recorded specimens of *C. tumidula* var. *procera* with 9 μm breadth, which were higher than the nominate variety (9.0–10.2 vs. 7.8–8.7 μm).

Specimen designated by Krammer (2002), i.e., the preparation 714 IOK (BRM), were found to belong to more than one taxon. Therefore we designated a lectotype as established in Art. 9.11 of the ICN (McNeill et al. 2012).

Cymbella tumidula var. *salinarum* Grunow

Cymbella tumidula var. *salinarum* (Grunow) Cleve, Kongl. Svenska Vetensk.-Akad. Handl., ser. 4, 26(2): 171, 1894.

Basionym. *Cymbella salinarum* Grunow in Schmidt, A. Schmidt's Atlas Diatom.-Kunde, Pl. 9, fig. 28, 1875.

Holotype. Preparation 1603 in the Grunow Collection in the Naturhistorisches Museum Wien (W).

Lectotype (designated here). An individual on preparation 1603, in the Grunow Collection in the Naturhistorisches Museum Wien (W), represented by the illustration in Krammer (2002, Fig. 25: 13).

Type locality. Salinen von Zaule (Trieste, Italy).

Valves lanceolate, dorsiventral, dorsal and ventral margins convex; ends subcapitate; length 34.0 μm , breadth 10.7 μm , L/B ratio 3.2; axial area linear-lanceolate, slightly arched, central area rounded; striae 14 in 10 μm , becoming 15 toward ends, 1 isolated pore.

Remarks. This taxon presents morphometric characteristics similar to *C. tumidula* var. *tumidula*, except it has wider valves. Cleve (1894) recorded specimens of *C. tumidula* var. *salinarum* with 27–40 μm length, 8–10 μm breadth, and 11 or 12 striae in 10 μm , and considered that the only difference between this taxon and *C. tumidula* var. *tumidula* was the shape of the ends. Although in poor condition, in preparation 1603 we did not find differences between the shape of the valvar ends of the variety *salinarum* and the nominate variety. However, *C. tumidula* var. *salinarum* has higher breadth values compared to the type population of *C. tumidula* var. *tumidula*, even in populations of this taxon as recorded by Krammer (2002) from Falaise where initial and post initial cells were found. Moreover, the occurrence of *C. tumidula* var. *salinarum* has been restricted to brackish waters.

Krammer (2002, Fig. 25: 13) provided the illustration of an individual of the type of *C. salinarum*. The individual represented by him (Krammer 2000) was similar to *C. tumidula* var. *tumidula*. However, it was larger and had only one isolated pore, differing from *C. tumidula*, which has more than two isolated pores (Figs 50–56). Thus, in contrast to Krammer (2002), who treated *C. salinarum* at the specific level, we consider this taxon at the infraspecific rank as did Cleve (1894).

***Cymbella turgidula* Grunow**

Cymbella turgidula Grunow, in Schmidt, A. Schmidt's Atlas Diatom.-Kunde, Pl. 9, Figs 23–26, 1875.

Lectotype. Plate 9, Fig. 23 in Schmidt (1875), designated by Tuji (2007).

Type locality. Puerto Rico and Kahyenmathay.

Epitype. An individual on slide 1504 in the Grunow Collection in the Naturhistorisches Museum Wien (W), designated by Tuji (2007, Fig. 15).

Epitype locality. Puerto Rico.

Valves lanceolate, dorsiventral, dorsal margins broadly convex and ventral margin convex; ends barely protracted, narrowly rounded, or subcapitate; length 36.5–45.0 μm , breadth 10.8–13.3 μm , L/B ratio 3.2–3.4; axial area linear, arched, central area indistinct to rounded; striae 9–12 in 10 μm , becoming 11–17 toward ends, 1–3 isolated pores; 21–24 punctae in 10 μm .

***Cymbella tropica* Krammer**

Figs 64–70

Cymbella tropica Krammer, *Diatoms Europe* 3: 61, Figs 44:1–10, 49: 12, 13, 2002.

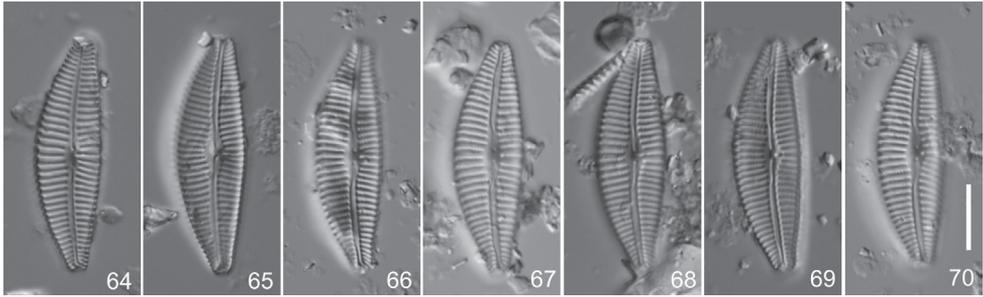
Holotype. Preparation 1015D IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Lectotype (designated here). An individual on preparation 1015D IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 64.

Type locality. Venezuela, Rio Manizanes, coll. Rumrich, 4.4.1990.

Valves lanceolate, dorsiventral, dorsal and ventral margins convex; ends barely protracted, rounded, or subcapitate, slightly deflected to ventral margin; length 34.5–42.7 μm , breadth 10.0–12.0 μm , L/B ratio 3.1–4.0; axial area linear, arched, central area indistinct to slightly rounded; striae 9–12 in 10 μm , becoming 11–12 toward ends, 1 isolated pore; 21–24 punctae in 10 μm .

Remarks. Krammer (2002) described *C. tropica* and recorded differences in the size, length/breadth ratio, and the presence of only one stigma as consistent diagnostic differences between this species and *C. turgidula*. Tuji (2007) recorded the occurrence of specimens of *C. turgidula* with 1–3 isolated pores, which was also observed by Krammer (2002) in his material. We observed a continuum between the metric characteristics of *C. tropica* and *C. turgidula*, even in those characters that were considered by Krammer (2002) as differentiating. However, the outline was more lanceolate, the ends more protracted and slightly deflected to the ventral side, and the degree of dorsiventrality was lower in *C. tropica* compared to *C. turgidula*.



Figures 64–70. *Cymbella tropica* Krammer from Venezuela in preparation 1015D IOK, holotype **64** Lectotype, designated here. Scale bar: 10 μm .

Cymbella subturgidula Krammer

Figs 71–97

Cymbella subturgidula Krammer, *Diatoms Europe* 3: 166, Figs. 44: 19–21, 2002.

Synonyms. = *Cymbella turgidula* var. *nipponica* Skvortzov, *Philipp. J. Sci.* 61: 283, Figs. 2:8, 4:4, 1936. (Figs 78–97)

– *Cymbella uenoi* Skvortzov in Skvortzov & Noda, *Sci. Rep. Niigata Univ., ser. D (Biol.)* 8: 19, Pl. 3, Fig. 3, 1971. (nom. inval.)

= *Cymbella rheophila* Ohtsuka in Ohtsuka & Tuji, *Phycol. Res.* 50: 245, Figs 7, 8, 2002.

= *Cymbella uenoi* Skvortzov ex Tuji, *Diatom* 23: 50, Figs 20–25, 2007.

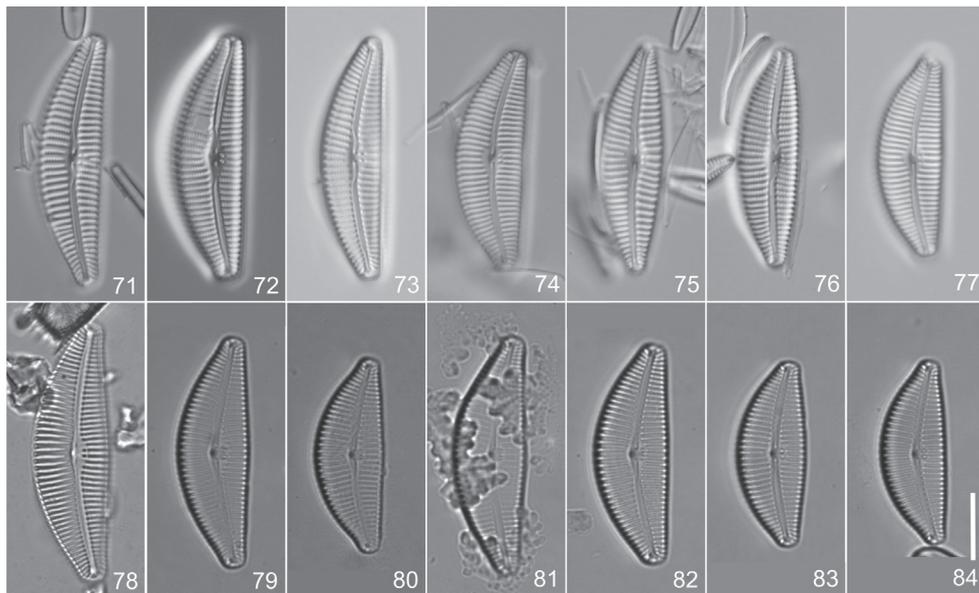
= *Cymbella uenoi* f. *nipponica* (Skvortzov) Tuji, *Diatom* 23: 54, Fig. 26, 2007.

Holotype. Preparation 1046E IOK [not “1046c IOK”], in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany.

Lectotype (designated here). An individual on preparation 1046e IOK, in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), Bremerhaven, Germany, represented by Fig. 73.

Type locality. Korea, Ulchin County, Kyungsang Pukdo, Kwangchun River.

Valvae slightly lanceolate to lanceolate, dorsiventral, dorsal margin broadly convex and ventral margin straight to convex; ends barely protracted, subrostrate to broadly subcapitate; length 26.3–41.0 μm , breadth 9.0–13.5 μm , L/B ratio 2.3–3.6; axial area linear to linear-lanceolate, arched, central area indistinct to slightly rounded; striae 9–13 in 10 μm , becoming 12–15 toward ends, 1–3 isolated pores; 21–26 punctae in 10 μm . In SEM, the striae showed lineolate punctae externally and internally, the striae are composed by an alveolus internally, surrounded by thick costae; the isolated pores are rounded externally; internally, the alveoli of the isolated pores are irregularly obovate and connected to intercostae, the margins with tooth-like structures (brocca); one apical pore field (APF) not divided by the external terminal fissure of the raphe can be observed on each pole of the valvae; the terminal nodule extends to the dorsal side,

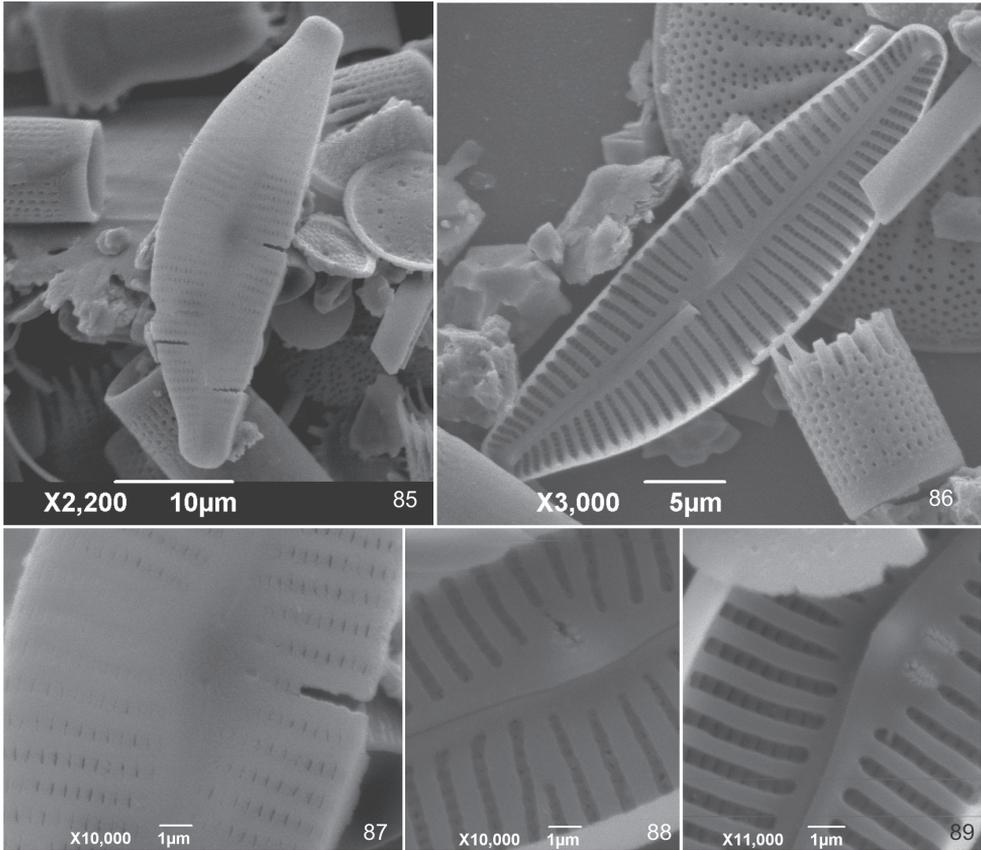


Figures 71–84. *Cymbella suburgidula* Krammer **71–77** Specimens from Korea in preparation 1046E IOK, holotype **73** Lectotype, designated here **78–80** Specimens from Japan in preparation R 214.928 **78** Isolectotype, designated here, of *C. turgidula* var. *nipponica* Skvortsov [\equiv *C. rheophila* Ohtsuka], heterotypic synonym of *Cymbella suburgidula* **81** Specimen from Japan in preparation R 214.930 **82–84** Specimens from Japan in preparation R 214.932. Scale bar: 10 μ m.

under the APF and has a short branch that penetrates the APF apically; the helictoglossae lie under the terminal nodule and are deflected to the dorsal side.

Remarks. Krammer (2002) described *C. suburgidula* based on preparation 1046c, which he designated as the holotype. This preparation was sought in the Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM), where the entire Krammer Collection was transferred. However, preparation 1046c IOK is from Argentina in South America, and not from the holotype designated from Korea. In the protologue of *C. suburgidula*, Krammer (2002, p. 278 and 279) illustrated three specimens from preparation 1046E IOK, from Korea. Thus, the existence of slide 1046c IOK from Argentina, which is incongruent with the type locality, and the existence of slide 1046E which was used by Krammer to illustrate *C. suburgidula*, led us to consider the indication of preparation 1046c IOK as a typographical error.

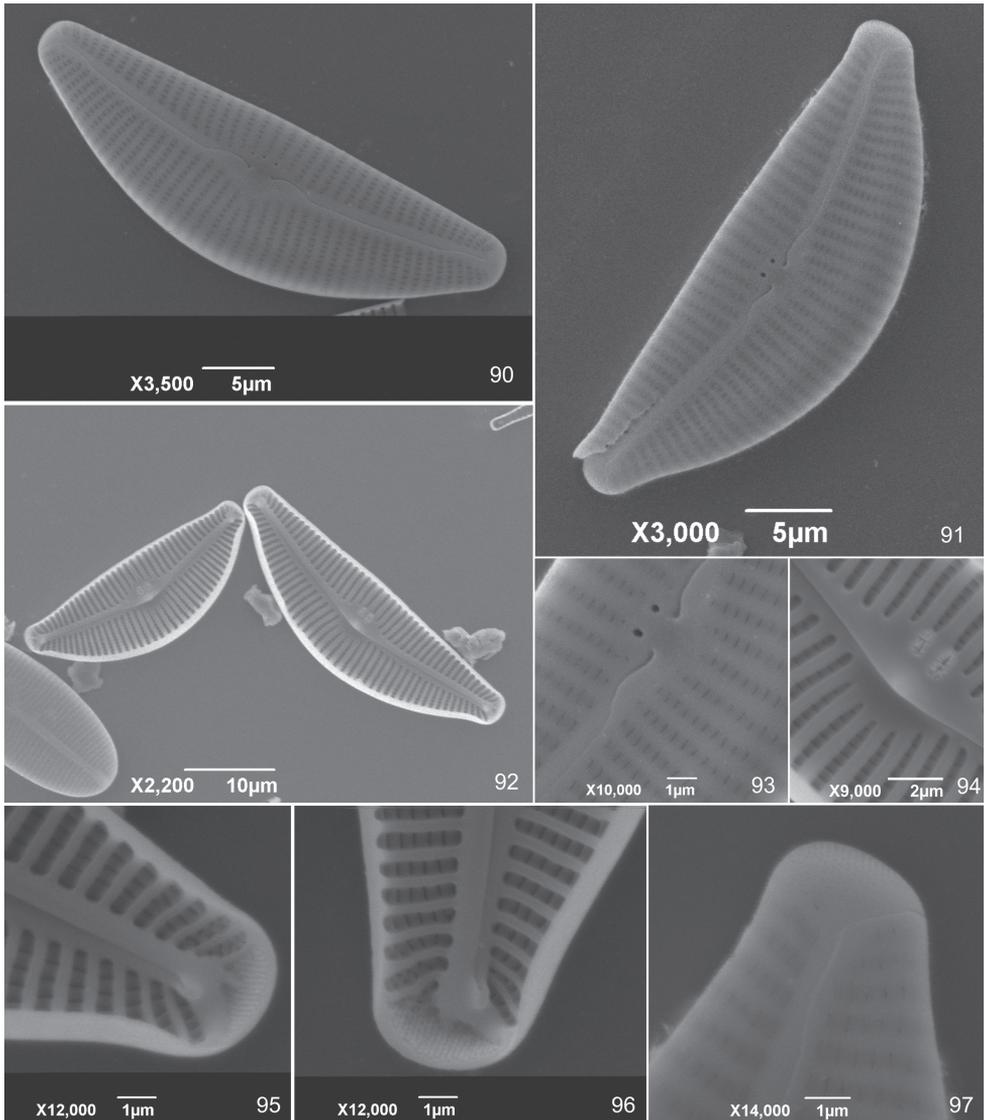
Cymbella suburgidula and *C. turgidula* are closely related species. However, *C. turgidula* is more lanceolate and has a higher degree of dorsiventrality than *C. suburgidula*. Moreover, *C. turgidula* is slightly broader than *C. suburgidula*, with a more prominent ventral side of the valve. The ends in the two species are different, being substrate-rounded in *C. turgidula* and slightly substrate-truncate in *C. suburgidula*. The central area is more distinct in *C. turgidula* than *C. suburgidula*. Although the number of punctae in 10 μ m is the same in both species, the striae in *C. suburgidula* seem to be more coarsely punctuated than in *C. turgidula*.



Figures 85–89. *Cymbella submarginata* Krammer from Japan, in the original material of *C. tumidula* var. *nipponica* Skvortsov [\equiv *C. rheophila* Ohtsuka], in sample 0983 **85, 87** External valvar view **86, 88, 89** Internal valvar view.

Cymbella tumidula var. *nipponica* was described by Skvortzow (1936). He considered that this taxon differed from the nominate variety due to the elongated valve, slightly undulate ventral margin, and broad rostrate ends. Ohtsuka and Tuji (2002) proposed that maintaining this taxon as a variety of *C. tumidula* was not appropriate. They based their arguments on the co-occurrence of the nominate variety and the variety *nipponica*. Therefore, they proposed the name *C. rheophila* T. Ohtsuka for this taxon at the specific rank.

Skvortsov and Noda (1971) described *C. uenoi* Skvortsov, but did not indicate any type. According to Article 40.1 of the ICN, names of new genera or taxa of lower ranks published after 1958 are valid only when the type is indicated (McNeill et al. 2012), and therefore *C. uenoi* is invalid. Tuji (2007), however, indicated a type for *C. uenoi*, fulfilling the conditions required by the ICN. Therefore, the author of the name becomes *C. uenoi* Skvortsov ex Tuji. Tuji (2007) also transferred *C. tumidula* var. *nipponica* [\equiv *C. rheophila*] to that species, resulting in the name *C. uenoi* f. *nipponica*, considering erroneously that the name *C. uenoi* had priority under the name *C. rheophila*.



Figures 90–97. *Cymbella subturgidula* Krammer from Japan in sample 1093 **90, 91, 93, 97** External valvar view **92, 94, 95, 96** Internal valvar view.

Tuji (2007, p. 54) suggested the conspecificity of *C. subturgidula* and *C. uenoi*. The observations of the type material of *C. uenoi* provided by Tuji (2007) and *C. uenoi* f. *nipponica* [\equiv *C. rheophila*], compared with the type material of *C. subturgidula* (i.e. morphometric characteristics), led us to agree with Tuji (2007). Since *C. uenoi* was validated only in 2007, the valid names of this species are either *C. rheophila* or *C. subturgidula*, both published in 2002, and not *C. uenoi* as stated by Tuji (2007). *C. subturgidula* was described in *The Diatoms of Europe*, volume 3, published by Kram-

mer on 28 January 2002 (Koeltz Scientific Books, pers. comm.), while *C. rheophila* was not published before 29 July 2002, the date of acceptance of the paper. Therefore, the epithet *subturgidula* has priority over the epithet *rheophila*.

The re-analysis of the type material of *C. subturgidula* allows us to broaden the metric data of this species compared to its original description. We observed a wider range of values for length (30.3–37.4 vs. 36–37 μm), breadth (9.0–12.8 vs. 10.0–11.0 μm), striae (9–11 vs. 10–11 in 10 μm) and punctae (21–24 vs. 24 in 10 μm) compared to Krammer's (2002) description. Metric characteristics of the original material of *C. turgidula* var. *nipponica* [\equiv *C. rheophila*; \equiv *C. uenoi* f. *nipponica*, isolectotype designated here (Fig. 78)] and *C. uenoi* (Table 1) also agree with the characteristics of the type population of *C. subturgidula* (Skvortzov and Noda 1971, Ohtsuka and Tuji 2002, Tuji 2007).

Krammer (2002) described two isolated pores in *C. subturgidula*. Similarly, Ohtsuka and Tuji (2002) and Tuji (2007) observed two isolated pores in the material of *C. turgidula* var. *nipponica* [\equiv *C. rheophila*; \equiv *C. uenoi* f. *nipponica*] and *C. uenoi*. However, in the original sample of the lectotype of *C. turgidula* var. *nipponica* we found some specimens with only one isolated pore (Fig. 88), and in recent material collected in Lake Biwa we found up to three isolated pores (Fig. 90).

Discussion

Few studies have discussed the criteria to delimit infraspecific ranks in diatoms. Cox (1997) reviewed this issue and found contradictions among the criteria adopted by different researchers over time. In order to resolve this question, she proposed a pragmatic solution to delimit infraspecific taxonomic ranks. According to Cox (1997), the term variety should be used “for populations (within the same species) which are ecologically and morphologically distinct, in which there is no evidence of morphological intergrading under intermediate conditions”.

However, taxonomic analyses of some species complexes in diatoms using molecular data have demonstrated that Cox's (1997) suggestions about the delimitation of varieties do not apply to every situation. *Sellaphora pupula* (Kütz.) Mereschk. sensu lato and *Nitzschia palea* (Kütz.) W.Sm. sensu lato, for example, have been shown to be an assemblage of pseudocryptic species that correspond, in the majority of instances, to populations with intergrading morphological characteristics (Mann et al. 2008; Trobajo et al. 2009). We have found a similar situation in populations that were clearly identified as *Cymbella tumida* (Bréb.) Van Heurck (unpublished data).

The criteria adopted by Krammer (2002, 2003) to delimit several specific and infraspecific taxa of *Cymbella* take into account variations between the type and similar individuals from other populations. It is important to note that, for Krammer (2002, 2003), types can be individuals marked or represented in some illustration, as well as a group of individuals mounted in a preparation, as defined in the ICN (McNeill et al. 2012).

Because of the lack of taxonomic studies on the *Cymbella affinis/tumidula/turgidula* species complex using molecular data, we opted to use Krammer's concept in order to attempt to organize this confusing group. This criterion is usual as a reference to circumscribe groups with similar morphologies, even if individuals with these morphologies sometimes overlap. Some authors prefer to define similar groups as “morphodemes”, which have no nomenclatural status. However, in some cases, this definition sounds more similar to the old taxonomy when any taxonomic unit could be denominated by different names, but scientifically by a long sentence that is more similar to the current “diagnosis”. Although the concept of varieties used here implies the publication of nomenclatural novelties, none of them are new proposals, but rather are simply adjustments of already existing names that are in confusing combinations, because of a misinterpretation by Krammer (2002) as well as the history of the taxa and the evolution of nomenclatural rules.

The criteria of delimitation of taxa and the weight of characters in diatoms are variable from group to group (Mann 1999). While in some groups the density of striae is a good morphological indicator of different species, in other groups this can be irrelevant (Abarca et al. 2014). Different sizes and valve outlines are not always good characters to delimitate taxa such as in the complex *Encyonema silesiacum/minimum/ventricosum* (unpublished data). Thus, it is common to find taxa with polythetic definitions, that is, in which a set of characteristics, sometimes interweaving with other taxa, are taken into account (Needham 1975). The delimitation of *Cymbella* taxa is a clear example of polythetism (Krammer 2002).

In this context, several characters must be considered in their characterization and identification of taxa. The degree of dorsiventrality of the valve, for example, is slightly higher in *C. affinis* than in *C. tumidula*, and even higher in *C. schilleri* Krammer (2002, Fig. 26: 7, 8) than in *C. orientalis* Lee (Krammer 2002, Fig. 26: 1–6). Another example is the thickness of the striae. The striae of *C. tumidula* are narrower than in individuals of *C. affinis* in LM, even in specimens of the same size. This is often the result of thick intercostae and the size of areolae, which can only be observed in SEM (Krammer 2002, Figs 5: 1, 23: 18). Thus, these characters, alone, seem to be unimportant but in combination with further features can provide a better concept of the taxa.

Ultrastructural characterizations by SEM are also important in diatoms, but not always possible using the original material. Records from the literature have demonstrated that representatives of the *C. affinis/tumidula/turgidula* species complex present similar internal ultrastructure of the isolated pores (i.e., aperture covered by small teeth) and the intercostae. This is the case of *C. affinis* (= *C. excisa* sensu Krammer 2002, Figs 5: 1), *C. affinis* var. *subcapitata* (Krammer 2002, Figs. 10: 16–18) *C. tumidula* var. *tumidula* (= *C. affinis* sensu Krammer 2002, Fig. 23: 18), and *C. subturgidula* (Figs 89, 94), which are similar to *C. cymbiformis* C.Agardh, type of the genus (Krammer 2002, Figs 5: 2, 3). However, the internal structure of isolated pores and the intercostae of these taxa are different to other species such as *C. aspera* (Ehrenb.) Perag. (Krammer 2002, Fig. 5: 4), *C. neolanceolata* W.Silva (= *C. lanceolata* sensu Krammer 2002, Fig. 5: 5), *C. neocistula* Krammer (2002, Figs 5: 6, 7). This demonstrates that the complex

C. affinis/*tumidula*/*turgidula* is morphologically closer related to the type of the genus, than to the other species of the same genus.

The economic and ecological uses of diatoms require a refined taxonomy, which is more detailed than simply species complexes. This is especially true for bioassessments using diatoms (European Committee for Standardization 2003). *Gomphonema lagenu- la* Kütz. has for a long time been treated as synonym of *G. parvulum* Kütz., since the variability in the shape of the ends were considered insufficient to distinguish the taxa (VanLandingham 1971). However, differences in the ecological preferences of these two taxa were recorded and the independence of the two species has been confirmed by molecular data (Kermarrec et al. 2013, Abarca et al. 2014). Differences between the ecological preferences of *Nitzschia palea* (Kütz.) W.Sm. var. *palea* and *N. palea* var. *debilis* (Kütz.) Grunow have also been recorded, and simply morphological characters are insufficient to separate the series of phenotypic expressions subscribed to *N. palea* (Trobajo et al. 2009). Thus, the efficiency in the use of diatoms in activities such as bioassessments needs accuracy and taxonomic harmonization (Manoylov 2014). But this will only be possible if important characteristics such as ecological preferences can be permanently attached to a taxon or an accessible designation, which is facilitated by the establishment of correct types and by the knowledge of these types.

Naturally, beside the knowledge of types, supplementary studies are necessary to record phenotypic plasticity resulting from different ecological conditions or by life cycles. Such studies should be carried out in natural or cultivated samples in order to observe a more realistic concept of the species (Mann 1999). These studies will allow us to observe slight changes in the morphology of the valves (i.e., outline, measures, etc.) such as some of those observed in the type population of the taxa discussed here. Moreover, these studies can possibly verify the relationship among morphological characters, which are associated in a polythetic way during the establishment of specific concepts and in their use in the identification of taxa of similar groups.

Conclusion

The process of lectotypification can markedly influence the identity of some taxa and can sometimes substantially change the relation to other taxa. The designation of a type for *C. affinis* resulted in a profound restructuring of *C. affinis*, *C. excisa* and *C. tumidula*. *C. excisa* has been shown to be the same taxon at the species level as *C. affinis*, but because of its specific morphology is treated herein at a different rank. The epithet *affinis* has priority over the epithet *excisa*, as defined by the criterion of the first effective publication. Thus, four infraspecific taxa of *C. excisa* were transferred to *C. affinis*.

The lectotypification of *C. tumidula* Grunow and comparisons with the lectotype of *C. affinis* allowed us to conclude that the two species are independent. *C. affinis* var. *procera* was treated as a new species, which is closer to *C. tumidula* than *C. affinis* because of morphological similarities. Infraspecific taxa described by Krammer (2002) within *C. affinis* had small differences in relation to the type of *C. tumidula*, and they are recombined herein.

The analysis of the type and the history of taxa such as *C. subturgidula* Krammer, *C. rheophila* Ohtsuka, and *C. uenoi* Skvortsov *ex* Tuji allowed us to conclude that these taxa are conspecific, and to determine that the epithet *subturgidula* has priority.

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A new species of *Centaurea* sect. *Pseudoseridia* (Asteraceae) from north-eastern Turkey

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Abstract

Centaurea ziganensis Yüzb., M. Bona & İ. Genç, a new species is described and illustrated from Gümüşhane province, NE Turkey. The new species grows in rocky places on the south face of Zigana Mountains, and is closely related to *C. drabifolioides*, from which it differs mainly in stem, achene and phyllary appendage characters. Micromorphological structures of achenes and karyological features of *C. ziganensis* and *C. drabifolioides* were examined in this study.

Keywords

Centaurea, new species, taxonomy, Turkey

Introduction

Centaurea L. *s.l.* is one of the largest and taxonomically most difficult genera of the Asteraceae (Dostál 1976). Recent approaches have split this taxon into four genera: *Centaurea*, *Rhaponticoides* Vaill., *Psephellus* Cass. and *Cyanus* Mill. (Wagenitz and Hellwig 2000, Greuter 2003, Hellwig 2004). The genus *Centaurea* was previously revised by Wagenitz (1975) for the *Flora of Turkey and the East Aegean Islands* without considering the splitting mentioned above. Even excluding the species now placed in these genera, Turkey is among the richest countries in *Centaurea* diversity (Wagenitz 1975, Davis et al. 1988, Güner 2000).

Recently *Centaurea s.l.* was revised for *Türkiye Bitkileri Listesi* by Dural (2012), Ertuğrul (2012) and Uysal (2012a, 2012b). According to revised system, the number of known *Centaurea* species in Turkey is 162 [(excluding 56 species which are now treated within *Psephellus* (33), *Cyanus* (16) and *Rhaponticoides* (7)].

In the *Flora of Turkey and the East Aegean Islands* (Wagenitz 1975), 34 sections of *Centaurea* were presented. Some sections of the Turkish *Centaurea* have been revised, but others, such as sect. *Pseudoseridia* Wagenitz, have not been revised recently. According to Wagenitz (1975) there were seven *Centaurea* species in section *Pseudoseridia*. Since then, six new taxa have been described for the section (Uzunhisarcıklı et al. 2005, 2007, Uysal et al. 2007, Aksoy et al. 2008, 2010, Bona 2015).

The present study is focused on the morphological, micromorphological and karyological criteria for distinguishing a new species in *Centaurea* sect. *Pseudoseridia*. Investigations on living and herbarium specimens suggest that this new species is morphologically most similar to *C. drabifolioides*.

Material and methods

Flowering and fruiting specimens of the *C. ziganensis* and of related species, *C. drabifolioides* were collected by the first author several times in 2013 and 2014 from type localities. The *Centaurea* material was examined and compared with material of similar taxa (sect. *Pseudoseridia*) in ISTE, ISTO, GAZI, ANK, HUB, E, K and G. The specimens were also cross-checked with various accounts of *Centaurea* in relevant floras, i.e. *Flora Orientalis* (Boissier 1875), *Flora Europaea* (Dostál 1976), *Nouvelle Flore du Liban et de la Syrie* (Mouterde 1983) and a taxonomic study on *Centaurea* in Iran (Negaresh et al. 2014). The measurements, colors and other details given in the description are based on both herbarium and living materials. Herbarium specimens were deposited in the herbaria of ISTE. Photographs of living material were taken with a Canon D60 digital camera (Canon EF 100 mm macro-lens) and the illustrations of the new species were made by using Adobe Photoshop CS4. The morphology of the new species was examined with the aid of a Leica S8AP0 stereo–binocular microscope.

During Scanning Electron Microscopy, 2 mature achenes from *C. ziganensis* (ISTE 104470) and *C. drabifolioides* (ISTE 104472) were selected and mounted onto stubs with double-sided adhesive tape, and were then coated with gold. The achene surfaces were examined from the lateral sides. For each sample, photographs of the testa were taken using the JEOL JSM-5600 at a magnification 500×, 1000×, and 3000×. The terminology of achene characteristics in this work was based on the descriptions used by Stearn (1992), Barthlott (1981), and Koul et al. (2000).

Chromosome number and karyological features of the *C. ziganensis* and *C. drabifolioides*, were determined from plant material collected from type localities. All karyological observations were carried out on root tips. Root-tip meristems were provided from achenes by germinating them on wet filter paper in petri dishes at room temperature. Firstly, root tips pretreated for 24 h in a-monobromonaphthalene at 4 °C, fixed

in 3:1 absolute alcohol-glacial acetic acid, then the root tips were hydrolyzed with 1 N HCL for 12 min at 60 °C and stained in Feulgen solution and squashed in aceto-orcein (Altınordu et al. 2014).

For karyotype analysis, the photographs were taken using OLYMPUS BX53 microscope with camera Kameram12 CCD attachment. Chromosome counts in mitosis metaphase and karyotype analyses were obtained based on three root tips, five metaphase cells for each individual. Measurements of somatic chromosomes were made with the program CAMERAM, they were calculated with formula of the relative variation in chromosome length (CV_{CL}) (Paszko 2006) and mean centromeric asymmetry (M_{CA}) according to Peruzzi and Eroğlu (2013). Chromosomes were classified according to the nomenclature of Levan et al. (1964) and Stebbins asymmetry types are given (Stebbins 1971).

Taxonomic treatment

Centaurea ziganensis Yüzb., M. Bona & İ. Genç, sp. nov.

urn:lsid:ipni.org:names:77148383-1

Fig. 1

Diagnosis. *Centaurea ziganensis* is related to *C. drabifolioides*, from which it differs mainly in its 2–4 (–8) branched and non-winged stem (not simple and winged), median phyllary appendages with 4–6 pairs of cilia (not 5–10); achenes 4.5–5 mm long, oblong, straw-colored, striate (not 5.5–6 mm long, lanceolate, blackish-chestnut, shiny); pappus straw-colored (not blackish-chestnut).

Type. TURKEY. **Gümüşhane:** Zigana pass–Gümüşhane road, c. 5. km, rocky places, 1450 m a.s.l., 20 Aug 2014, S. Yüzbaşıoğlu 4117 (holotype: ISTE 104470, isotype: ANK).

Description. Perennial herb with sterile leaf-rosettes and woody rootstock. Stems erect or erect-ascending, pubescent with short simple hairs, 30–70 cm long, not winged, usually 2–4 (–8) well developed one-headed branched from near middle. Basal leaves scabrid with multiseriate septate hairs, and densely covered transparent sessile glands on both surfaces, narrowly lanceolate, petiole 3.5–6.5 cm long, margins entire or sparsely toothed, c. 10 teeth on each side (c. 1 mm long), acute, attenuate, 10–20 × 0.5–1.5 cm (inc. petiole). Median and upper cauline leaves scabrid, linear-lanceolate, mucronate (c. 1 mm) at apex, margins entire; the median ones 5–10.5 × 0.8–1 cm, distinctly decurrent; the upper ones 1.2–3.5 × 0.2–0.4 cm, sessile, not decurrent, leaves decreasing to capitula, uppermost bract-like. Capitula 2–4 (–8), solitary at end of well-developed branches. Involucre ovoid, 15–20 × 12–15 (–18) mm. Phyllaries green, tomentose at apex; the outer ones ovate, 5–6 × 4–5.2 mm; the median ones lanceolate, 9.5–10 × 4.6–5 mm; innermost linear-lanceolate, 16–17 × 3.2–4 mm. Appendages small, not concealing basal part of phyllaries, 1.5–2 mm broad, dark brown, triangular, not decurrent, spreading or reflexed, with 4–6 pairs of cilia (1–3 mm), ending with a

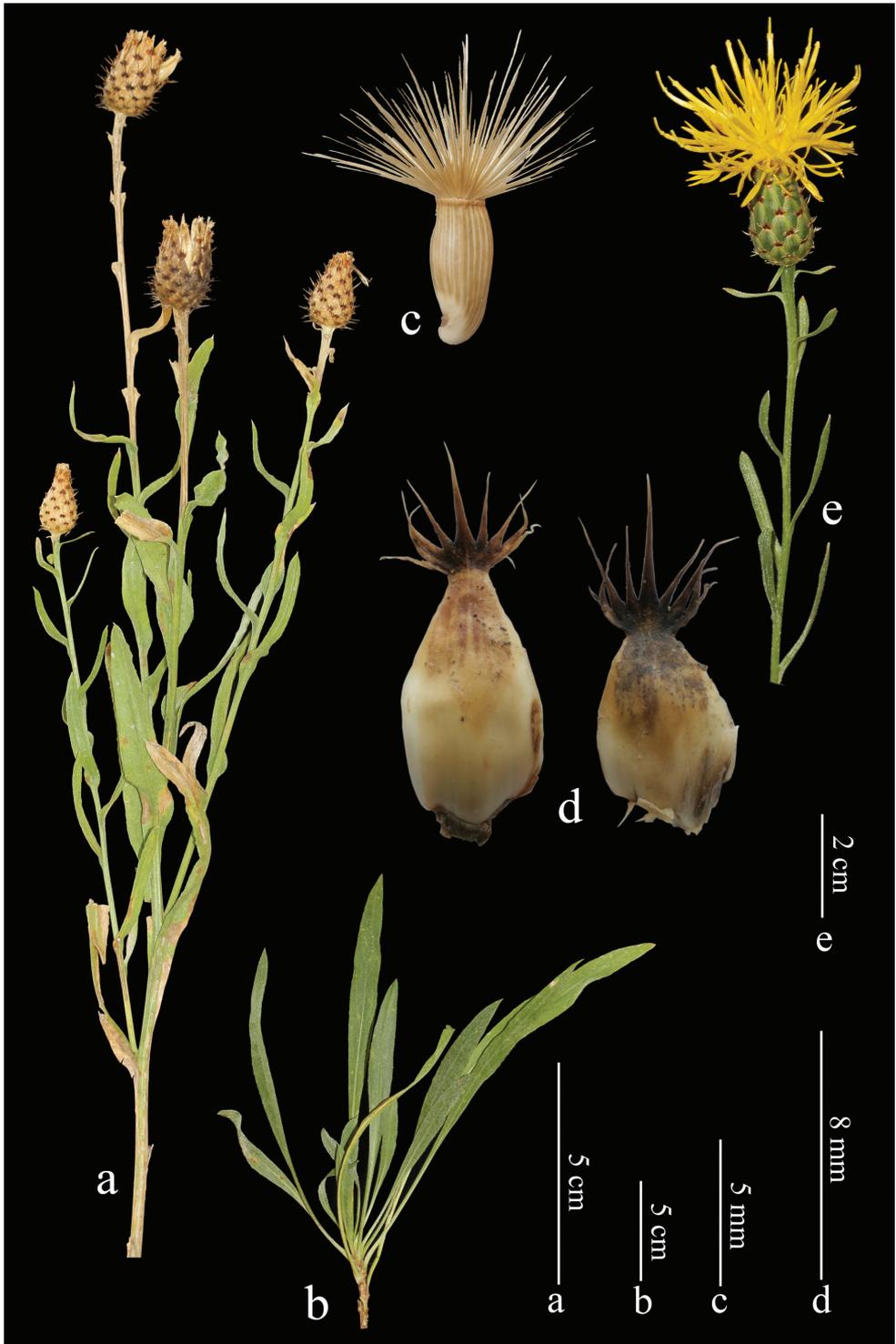


Figure 1. *Centaurea ziganensis* sp. nov. **a** habit **b** roset leaves **c** achene **d** median phyllaries **e** capitulum.

2–4 mm spinule. Florets yellow, marginal not radiant; corolla tube glabrous, 20 mm long, lobes 6–7 × 0.5 mm, linear, with 5 brown stripes along corolla tubes; anthers 10 mm, filaments 4 mm long. Achenes oblong, straw-coloured, glabrous, distinctly striate, 4.5–5 × 2–2.2 mm; pappus straw-coloured, biseriate, scabrous, outer series 5.3–6.2 mm long, inner series 1.5–1.8 mm long.

Phenology. *Centaurea ziganensis* flowers from the end of June to–July, and mature fruits are produced in August–early September.

Etymology. Named after the Zigana Mountains where it was discovered.

Ecology. The new species was only found on the southern slopes of Zigana Mountains and occurs on rocky slopes at c. 1500 m elevation. Within this area, the new taxon is associated with plants such as: *Allium rupestre* Steven, *Alyssoides utriculata* (L.) Medik., *Arenaria serpyllifolia* L., *Asplenium septentrionale* (L.) Hoffm., *Asyneuma lobelioides* (Willd) Hand.-Mazz., *Berberis vulgaris* L., *Campanula betulifolia* C. Koch, *Coronilla orientalis* Mill. var. *orientalis*, *Euphorbia condylocarpa* M. Bieb., *Fibigia clypeata* (L.) Medik., *Haplophyllum armenum* Spach, *Helianthemum nummularium* (L.) Mill., *Hypericum pruinatum* Boiss. & Bal., *Hyssopus officinalis* L. subsp. *officinalis*, *Juniperus oxycedrus* L. subsp. *oxycedrus*, *Lamium galactophyllum* Boiss. & Reuter, *Laser trilobum* (L.) Borkh., *Ornithogalum narbonense* L., *Psephellus pyrrhoblepharus* (Boiss.) Wagenitz, *Reichardia glauca* Matthews, *Rosa canina* L., *Salvia tomentosa* Mill., *Salvia verticillata* L., *Saxifraga paniculata* Mill., *Sempervivum transcaucasicum* Muirhead, *Silene dichotoma* Ehrh. subsp. *sibthorpiana* (Reichb.) Rech., *Sobolewsia clavata* Fenzl, *Teucrium polium* L. and species of *Acer* and *Quercus*.

Distribution and proposed conservation status. As presently known, *Centaurea ziganensis* is a narrow endemic and known only from the type locality, north eastern Anatolia (Gümüştane): where the extent of occurrence is less than 100 km² (criterion B1), with an estimated area of occupancy of less than 10 km² (criterion B2). According to our field observations, habitat destruction through human encroachment such as road construction is the principal threat in the area. Therefore, on the basis of our knowledge, we argue that the species is potentially Critically Endangered (CR), but more data are needed to estimate its real IUCN category of threat (IUCN 2014).

Karyology. The chromosome number of the new taxon is 2n = 18 (Fig 2a). The shortest chromosome length is 2.22 µm, the longest is 3.55 µm, and the haploid chromosome length is 24.17 µm. The karyotype formula of this taxon consists of 10 median pairs and 8 submedian pairs. Satellites were usually seen on the short arms of the longest sub-metacentric chromosomes. As for karyotype asymmetry, the karyotype of this species is classified according to the symmetry classes of Stebbins as 3A. Intra-chromosomal asymmetry (M_{CA}) is 20.90 and the interchromosomal asymmetry index (CV_{CL}) is 16.32. The karyogram is given in Figure 2b, and ideogram was drawn based on the centromeric index (Fig 2c).

Our study showed that the chromosome number of *C. drabifolioides* Hub.-Mor. is 2n = 18 (Fig 2d). The shortest chromosome length is 1.51 µm, the longest is 2.77 µm, and the haploid chromosome length is 18.64 µm. The karyotype formula of this taxon consists of 10 median pairs and 8 submedian pairs. Satellites were usually seen on the

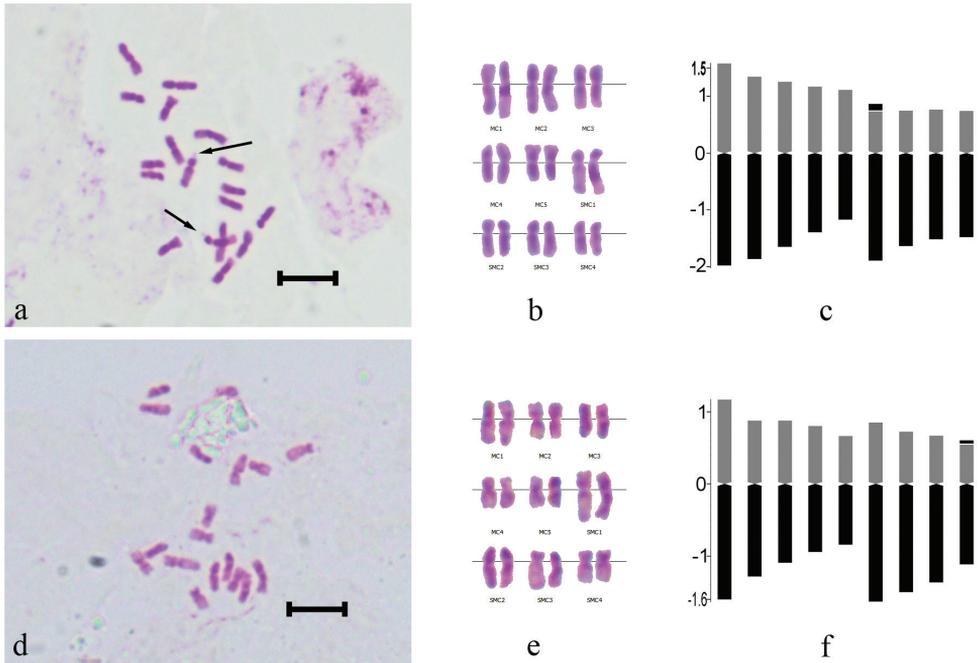


Figure 2. Somatic chromosomes, karyotype and idiogram of *C. ziganensis* (a–c); *C. drabifolioides* (d–f). Arrow indicates satellite. Scale bars = 5 μ m.

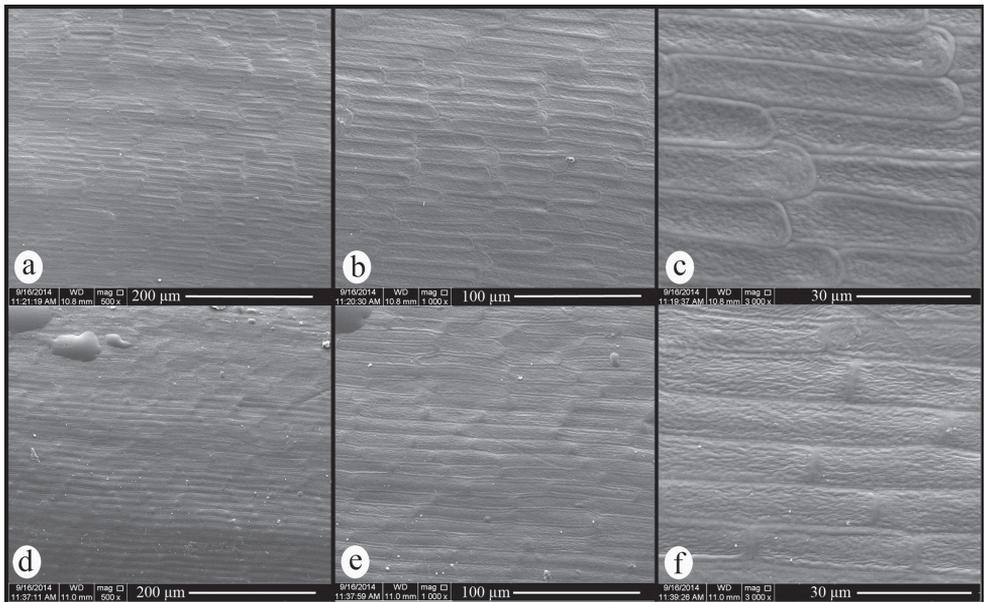


Figure 3. Scanning electron micrographs of achene surface. (a–c) *C. ziganensis*. (d–f) *C. drabifolioides*.

short arms of shortest sub-metacentric chromosomes. As for karyotype asymmetry, the karyotype of this species is classified according to the symmetry classes of Stebbins as 3A. Intrachromosomal asymmetry (M_{CA}) is 22.71 and the interchromosomal asymmetry index (CV_{CL}) is 17.95. The karyogram is given in Figure 2e, and ideogram was drawn based on the centromeric index (Fig 2f).

SEM observations. Seed surface pattern of *Centaurea ziganensis* is ruminant. Testa cells are regularly arranged, elongated parallel with the seed surface and the cells are apparently imbricate. The cell boundaries are thin and have smooth structure, and the boundaries raised above cell centre (Fig. 3a–c). Even seed surface pattern and testa cell arrangement of *C. drabifolioides* are similar to *Centaurea ziganensis*, the cell centres raised above the boundaries and testa cells are not apparently imbricate (Fig. 3d–f).

Discussion

In section *Pseudoseridia*, *C. hermannii* F.Hermann is unique taxon which has both orange flowers and lyrate leaves. *C. cheirolopha* (Fenzl) Wagenitz, *C. amanosensis* M. Bona, *C. lycopifolia* Boiss. & Kotschy ex Boiss., and *C. stevenii* M. Bieb. have short pappus and lyrate or pinnatifid leaves differing from the remaining taxa in the section. *C. glabroauriculata* Uysal & Demir, *C. kizildaghensis* Uzunh., E. Doğan & H. Duman, and *C. pseudokotschy* Wagenitz are also easily separated from the other *Pseudoseridia* taxa by their non decurrent leaves. Among the section *Pseudoseridia* taxa, only *C. drabifolioides*, *C. yaltirikii* N. Aksoy, H. Duman & A. Efe, *C. cheirolepidoides* Wagenitz, *C. marashica* Uzunh., Tekşen & E. Doğan have long pappus, and decurrent, simple leaves. The nearly cylindrical involucre and grey tomentose leaves of *C. cheirolepidoides* and *C. marashica* are different from the ovoid to ovoid-oblong involucre and scabrous leaves of *C. drabifolioides* and *C. yaltirikii*. Finally, *C. yaltirikii* is different with scabrous-barbellate pappus and a widely broad-winged stem (2–4 mm); while *C. drabifolioides* has scabrous and narrowly winged (0.5–1 mm) stems. In addition, *C. drabifolioides* has linear-lanceolate leaves compared with the broader and lanceolate, oblong, ovate or oblanceolate cauline leaves of *C. yaltirikii*.

Achene, pappus and phyllary characters provide the most reliable characteristics to separate *Centaurea* taxa from each other at sectional and specific level (Wagenitz 1975, Wagenitz and Helwig 2000, Bancheva and Gorgorov 2010). It is known that achene micromorphology also provides strong support in the delimitation of *Centaurea* taxa (Bagheri Shabestari 2013, Bona 2014). *C. ziganensis* closely related to *C. drabifolioides*. Even though they both have long pappus, simple, scabrous, decurrent, linear-lanceolate leaves, and are distributed close to each other in a similar habitat, *C. ziganensis* differs from *C. drabifolioides* in its stem, achene and pappus colour, appendage of phyllary, achene micromorphology and karyology. These two species are compared in Table 1 and Figures 2, 3, 4.

Huber-Morath named *C. drabifolioides* in 1967, and based his description of this species on plants collected from near Şebinkarahisar (Giresun), NE Turkey. It

Table 1. Morphological, micromorphological and karyological comparison of *Centaurea ziganensis* and *C. drabifolioides* (Abbreviations; SCL: shortest chromosome length; LCL: longest chromosome length; HCL: haploid chromosome length; M_{CA} : intrachromosomal asymmetry; CV_{CL} : interchromosomal asymmetry index).

Character	<i>C. ziganensis</i>	<i>C. drabifolioides</i>
Stem	non-winged, 2–4 (–8) well developed branched	winged, simple
Appendage	with 4–6 pairs of digitat cilia, very narrowly triangular	with 5–10 pairs of pinnat, cilia, triangular
Achene	4.5–5 mm long, oblong, straw colored, striate	5.5–6 mm long, lanceolate, blackish-chestnut, smooth, shiny
Pappus	straw colored	blackish-chestnut
Seed surface pattern	cell boundaries raised above cell center, testa cells rounded at apex and apparently imbricate	cell center raised above cell boundaries, cells not rounded at apex and not apparently imbricate
Karyology		
SCL	2.22 μm	1.51 μm
LCL	3.55 μm	2.77 μm
HCL	24.17 μm	18.64 μm
M_{CA}	20.90	22.71
CV_{CL}	16.32	17.95
Satellite	usually seen on the short arms of longest sub-metacentric	usually seen on the short arms of shortest sub-metacentric

is not a common plant throughout this range occurs in a relatively small area and has not been recorded from different part of Turkey, it is only known from the type locality. According to type description (Huber-Morath 1967) and Flora of Turkey (Wagenitz 1975) pappus color for *C. drabifolioides* was indicated as whitish (Huber-Morath 1967) and cream (Aksoy et al. 2008, Uysal et al. 2007). But, the observations we made in the type locality of *C. drabifolioides* indicate that the pappus color of mature achenes is the same as that of the achene, blackish-chestnut. We think that, the pappus color that is referred to in previous studies was from immature achenes.

In this paper, we describe a further new species for *Centaurea* section *Pseudoseridia*. The total number of sect. *Pseudoseridia* taxa known from Turkey with this new species, has increased to fourteen, twelve of these are endemic to Turkey. A new identification key for sect. *Pseudoseridia* in Turkey has been prepared according to Wagenitz (1975), Uzunhisarcıklı et al. (2007) and Bona (2015), and the new species may be inserted as follows:

- 1 Pappus short (0.5–3 mm) 2
- 2 Leaves grey-tomentose below 3
- 3 Perennial, stem erect or ascending, basal leaves lyrate or lanceolate
..... *C. cheirolopha*



Figure 4. The character comparison of the median phyllary appendages and achenes of *Centaurea ziganensis* (a) and *Centaurea drabifolioides* (b).

- 3' Biennial, stem decumbent, basal leaves pinnatifid *C. amanosensis*
- 2' Leaves not grey-tomentose below 4
- 4 Leaves or their terminal segments toothed; appendages of inner phyllaries brown *C. lycopifolia*
- 4 Leaves simple or divided, margins entire; appendages of inner phyllaries straw-coloured *C. stevenii*
- 1' Pappus longer (5–15 mm) 5
- 5 Cauline leaves non-decurrent 6
- 6 Stem leaves auriculate; terminal spinule of appendage distinctly longer than the other cilia *C. glabroauriculata*
- 6' Stem leaves non-auriculate; terminal spinule not distinct or slightly so 7

- 7 Stem ascending; leaves semi-amplexicaul; phyllary appendages with five to six pairs of cilia (cilia 3–5 mm) and ending in a 4–6 mm spinule..... *C. pseudokotschyi*
- 7' Stem erect; leaves sessile; phyllary appendages with two to four pairs of cilia (cilia c. 1 mm) and ending in a 1–1.5 mm spinule..... *C. kizildaghensis*
- 5' Cauline leaves decurrent 8
- 8 Basal or lower stem leaves lyrate..... *C. hermannii*
- 8' All leaves undivided, basal sometimes with a pair of teeth or lobes..... 9
- 9 Leaves scabrous; involucre ovate-oblong 10
- 10 Stem wings 2–4 mm broad; median stem leaves lanceolate-oblong, rarely ovate or oblanceolate, 0.7–2 cm broad, shortly decurrent *C. yaltirikii*
- 10' Stem wings absent or 0.5–1 mm broad; median stem leaves linear-lanceolate to linear, 0.4–0.6 cm broad, distinctly decurrent 11
- 11 Stem 2–4 (–8) well developed branched; phyllary appendages with 4–6 pairs of digitate cilia; achene straw coloured..... *C. ziganensis*
- 11' Stem usually simple; phyllary appendages with 5–10 pairs of pinnate cilia; achene blackish-chestnut..... *C. drabifolioides*
- 9' Leaves grey tomentose; involucre nearly cylindrical..... 12
- 12 Median and upper leaves with 0.5–2 mm long spinule at apex; phyllary cilia 1–1.5 mm, terminal spinule 1–2 mm *C. cheirolepidoides*
- 12' Median and upper leaves with 2.5–6 mm long spinule at apex; phyllary cilia 2–4 mm, terminal spinule 2–5 mm *C. marashica*

Additional specimens examined. *Centaurea ziganensis*: Turkey. Gümüşhane: Zigana pass–Gümüşhane road, c. 5. km, rocky places, 1450 m a.s.l., 04 Sep 2013, *S. Yüzbaşıoğlu 3903* (ISTE 104468); *ibid.*, 09 Jun 2014, *S. Yüzbaşıoğlu 4002* (ISTE 104469). ***Centaurea drabifolioides*: Turkey.** A7 Giresun: Şebinkarahisar–Dereli road, c. 9. km, within valley, rocky places, 1340 m a.s.l., 10 Jun 2014, *S. Yüzbaşıoğlu 4045* (ISTE 104471); *ibid.*, 23 Aug 2014, *S. Yüzbaşıoğlu 4118* (ISTE 104472); distr. Şebinkarahisar, Schlucht des Arslanyurdu Deresi 9–11 km nördlich von Şebinkarahisar, 1300–1330 m a.s.l., 01 Jul 1955, *A. Huber-Morath 13243!* (holotype, G); *ibid.*, 8 km N Şebinkarahisar, 1300 m a.s.l., 03 Aug 1989, *M. Nydegger 44650!* (G, HUB); *ibid.*, 9 km N Şebinkarahisar, 1300 m a.s.l., 19 Jul 1992, *M. Nydegger 46809!* (G).

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Revision of the fern genus *Orthiopteris* (Saccolomataceae) in Malesia and adjacent regions

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Abstract

A taxonomic revision of the Old-World representatives of the fern genus *Orthiopteris* is presented. We recognize eight species, one of which is newly described (*Orthiopteris samoensis*), and five varieties, of which two are newly described (*O. campylura* var. *insularis* and *O. campylura* var. *laxa*). *Orthiopteris acuminata*, *O. caudata*, *O. minor* and *O. kingii* are all reduced to varieties of *O. campylura*.

Keywords

Orthiopteris, taxonomy, new species, new varieties, Malesia, Madagascar, Polynesia, Melanesia, Saccolomataceae

Introduction

The genus *Orthiopteris* was first recognized by Copeland (1929a) to accommodate *Davallia ferulacea* Moore (= *Orthiopteris ferulacea* (Moore) Copel.) from Fiji. Later that year, Copeland (1929b) described the genus *Ithycaulon* Copel. to accommodate the species *I. moluccanum* (Blume) Copel. (= *Davallia moluccana* Blume.), *I. caudatum* (Copel.) Copel., and *I. inaequale* (Kunze) Copel., noting an affinity between *Ithycaulon* and *Saccoloma* Kaulf. However, in 1947, he (Copeland 1947) merged *Ithycaulon* with *Orthiopteris* (with *Orthiopteris* having priority), while maintaining the idea that *Orthiopteris* and *Saccoloma* are “near relatives”.

Copeland (1929b) considered *Ithycaulon* to be close to *Dennstaedtia* based on similarities in frond dissection and sori. In his *Genera Filicum* (1947) he arranged *Orthiopteris* next to *Dennstaedtia*. He was followed by most pteridologists (Holtum 1947; Jaman and Latiff. 1998; Kato 1996). Kramer (1990) sunk *Orthiopteris* into *Saccoloma*, a genus in the subfamily *Saccolomatoideae* of the *Dennstaedtiaceae*. Molecular phylogenetic studies ambiguously support this classification. Wolf (1995) placed *Saccoloma* in a group with mainly Pteridoid affinities, whereas others resolved *Saccoloma* at the base of the Polypod lineage (Pryer et al. 2004) or in a position more closely related to Lindsaeoid than to *Dennstaedtioid* ferns (Schuettpelz and Pryer 2007). Recent classifications treat *Orthiopteris* as one of the two genera within the family *Saccolomataceae* (Smith et al. 2006; Christenhusz et al. 2011). The description of the family *Saccolomataceae* Doweld was validly published only recently (Doweld and Reveal 2008).

The question whether *Orthiopteris* is distinct from *Saccoloma* within the *Saccolomataceae* is also controversial, and requires further study (Smith et al. 2006; Christenhusz et al. 2011). Many authors have treated *Orthiopteris* as a synonym of *Saccoloma* (Tryon and Tryon 1982b; Kramer et al. 1990; Parris et al. 1992; Smith et al. 2006). Both genera share a similar rhizome anatomical structure, sorus shape and spore morphology. In transverse section the rhizome of *Orthiopteris* spp. and *Saccoloma elegans* Kaulf. shows two concentric, somewhat discontinuous, rings of vascular bundles. Both genera have pouch-shaped sori and tetrahedral-globose, with a plain exospore and perispore with low branching ridges. However, *Orthiopteris* fronds are bipinnate or more decompound, unlike the simple-pinnate fronds of the type species of *Saccoloma*, *S. elegans* (Kramer 1990). Using a single *rbcL* gene phylogeny, Wolf (1995) found *Orthiopteris* as here circumscribed in two widely different clades. He reported *Saccoloma moluccanum* (based on a specimen from the Philippines, and therefore most likely corresponding with *O. campylura* var. *campylura*) in a clade with (American) *Saccoloma elegans*, and *Orthiopteris kingii* (based on a specimen from Indonesia) in a far more basal position. Since then there has not been any other phylogenetic study including representatives of both *Orthiopteris* and *Saccoloma*. Subsequent studies including only *Saccoloma* (Pryer et al. 2004; Schuettpelz and Pryer 2007; Rai and Graham 2010; Lehtonen et al. 2012) all place *Saccoloma* in a basal position, although with some uncertainty regarding the exact position (Lehtonen et al. 2012). We performed a reanalysis (not reported) of the *rbcL* marker of all accessions used in these studies, which placed all these in a clade with the *Orthiopteris* accession that Wolf (1995) placed in a basal position. A more densely sampled analysis is clearly needed to resolve the exact relationships between the two genera and their phylogenetic position.

Scope of this study

In the Malay-Pacific region, 11 *Orthiopteris* species have been reported: *Orthiopteris acuminata* (Rosenst.) Copel., *O. campylura*, *O. caudata* (Copel.) Copel., *O. cicurioides* (Baker) Copel., *O. ferulacea*, *O. firma* (Kuhn) Brownlie, *O. henriettae*, *O.*

kingii (Bedd.) Holttum, *O. minor* (Hook.) Copel., *O. tenuis* (Brack.) Brownlie, and *O. trichophylla* Copel. (Copeland 1950; Holttum 1954; Copeland 1958; Brownlie 1969; Parris 1992; Beaman et al. 1992; Whistler 1994; Kato 1996; Brownsey and Perrie 2011). There is, however, uncertainty about the taxonomic status and nomenclature of some of these names. Here, we attempt to elucidate the specific boundaries and geographic distributions of all taxa occurring in this region by revising the available material. We also include the Malagasy endemic species *O. henriettae* Baker (Tardieu-Blot 1958), to assess the status of this geographically isolated taxon. We hope this study will provide an impetus for a worldwide revision of *Orthiopteris* and *Saccoloma*, including also the American species *Orthiopteris domingensis* (Spreng.) Copel., *O. inaequalis* (Kunze) Copel., and *Saccoloma elegans*.

Material and methods

This study was based entirely on herbarium specimens. In total, 240 specimens have been examined from K, L, MICH, MO, NY, SING and additional images or on-line images provided by BM, K, MICH, P, and the JSTOR Global Plants database (plants.jstor.org). Herbarium abbreviations follow Index Herbariorum (Thiers continuously updated). Sheets seen as digital image only are marked with “*”. Data of all the studied specimens were entered into the BRAHMS database at L for storage and further analysis of geographic distribution. All studied specimens are listed in Appendix. We have selected lectotypes whenever necessary to resolve ambiguities in the application of a name. Most of the morphological characters were examined and measured with a stereo microscope or a compound microscope. In addition to light microscopy, scanning electron microscopy (using a Jeol JSM 7600F FEG-SEM) was used to study structure and ornamentation of the spores.

Morphology

Orthiopteris is often a large-sized fern; with a stout, erect rhizome and fronds often more than a meter long. Herbarium collections are often incomplete, and this makes an evaluation of the differentiating characters difficult. For the distinctions between the species, we have studied the following characters.

Rhizome

Due to lack of complete specimens, a thorough assessment of the variability of the rhizome morphology was impossible. From the available material, rhizomes can be assessed to be uniformly erect, and radially organized, and may form aerial trunks exceptionally to 1 m high. Characteristically, the vascular system shows two concentric

cylinders of meristeles (well-illustrated in Bower 1918; 1923). The morphology of the rhizome scales appears to show very little variation, and we have not found it useful for species distinction. In most of the species, rhizome scales are multistratose and pseudopeltate, tapering to a long narrow acumen from a rounded-cordate base, the margin usually being eroded and unistratose (Figure 4).

Fronid divisions

Division and venation of fronds are among the most confusing characters in *Orthiopteris* as the fronds are dissected to many levels, in many specimens reaching to quadripinnate. The gradual decrease in dissection from base to apex produces an almost perfectly fractal pattern, where the most basal pinnules are almost perfectly isomorphic with more apical pinnae (Figure 1). This makes it difficult to judge this character in fragmentary specimens unless it is known exactly from which part of a frond the fragment is taken. In our species descriptions, we concentrate on the major (pinnae) and on the ultimate divisions (segments) (Figure 1).

We define “ultimate segment” as the smallest distal unit with a branched venation around which lamina is incised completely, leaving no or very little lamina around the vein at its base. Margins are described as shallowly incised, crenate, dentate, or deeply lobed, with the degree of dissection quantified, when necessary, by the distance from the base of the shallowest sinuses to nearest costule/vein (Figure 2).

Sori

The most variable and important characters for distinguishing *Orthiopteris* species are found in the sori, the inner indusium and the outer indusium. The inner indusium is a thin membrane on the abaxial surface of the lamina. The outer indusium is continuous with the lamina on the adaxial surface. Each sorus thus forms a pouch-shaped structure that contains up to 30 sporangia, but mostly less, that are immersed within the indusium when young, but variously exerted when mature. We distinguish and classify several soral shape types as shown in Table 1 (see also Figure 3).

Table 1. Different types of soral shapes.

Length of sorus Widest at	equal to width	longer than width
	Mouth	Funnelform
Above middle	Wide obovate	Narrow obovate
At middle	Round/Ovate	Elliptic



Figure 1. Basal pinna of *Orthiopteris firma*, showing quadripinnatifid dissection and terminology. bipinnate segment 2nd order. isomorphic segments 2nd and 3rd order, arrows: ultimate segments. Franc 335 (K).

In addition, we use the following descriptive terms:

Outer indusium: (1) symmetric when it is not confluent with the margin but is abruptly set-off from the lamina margin on two sides (Figure 3a, b, c, d...); (2) asymmetric when it is confluent with the lamina margin on one side (Figure 3g, i, j...).

Inner indusium at apex: (1) obtuse-truncate without incision (Figure 3b, c, d,...), (2) extended into a lobe when it has a lobe $1/2$ – $2/3$ as wide as the entire sorus but shorter than $1/3$ the length of the sorus (Figure 3g, h, i, j...), (3) extended into a narrow tongue, when it has a lobe less than $1/2$ as wide as the entire sorus and longer than $1/3$ the sorus length (Figure 3l, m, n, o...). To assess this character, it is necessary to examine more than one sorus because they can show some variations even on the same frond. In most species, the sori are in the same plane as the frond, but sori may also be curved towards the abaxial surface.

Sporangia and spores

Characters of the sporangia are deemed not important for species distinction. Sporangia are stalked with a spherical to hemispherical capsule and a vertical, interrupted annulus with 16–24 indurated cells, which are more or less equal to distinctly unequal in size (Figure 5). Stalk and capsule are glabrous. All examined species have a more or less similar spore morphology resembling the American *Saccoloma elegans* (Tryon and Lugardon 1991: 269, fig. 90). Spores are trilete, tetrahedral-globose with a smooth or finely wrinkled exospore closely overlain with a perispore ornamented with ridges (Figure 6). The ridges strongly vary in width and density and in the degree to which they are sinuous and anastomosing.

Taxonomy

Orthiopteris Copel.

Orthiopteris Copel., Bernice P. Bishop Mus. Bull. 59: 14. 1929a.

Type: *Davallia ferulacea* T. Moore = *Orthiopteris ferulacea* (T. Moore) Copel.
Ithycaulon auct. non Copel., Univ. Cal. Publ. Bot. 16: 79. 1929b.

Type: *Davallia moluccana* Blume = *Ithycaulon moluccanum* (Blume) Copel.
See also Excluded names.

Description. Rhizome erect, stout, forming a trunk (2–)20–50(–100) cm high, in cross section showing two complete rings of vascular bundles, partly covered with scales, roots inserted on all sides of the rhizome especially in the older parts. Rhizome scales appressed at base, mostly basifix, pseudopeltate to peltate, mostly narrow lanceolate with long attenuate tips, thick, stiff, brittle, dark brown. Fronds tufted, erect, monomorphic.

Stipes (10–)30–70(–90) cm long, 0.4–0.8 cm thick (at base), scaly or slightly roughened due to scale traces towards base, greenish-brown. Lamina tri- to quadripinnate, anadromous, deltoid or lanceolate, gradually attenuate towards apex, (30–)100–150(–200) × (30–)40–60(–100) cm, herbaceous to papyraceous, bright-green to brownish-green when dry, abaxial surface sometimes with scattered small scales. Segments alternating, the acroscopic sides of all divisions larger than basiscopic sides, except for the first basiscopic pinnules of the lowest two pinnae; ultimate segments sessile or very short stalked, trapeziform, asymmetric at base, shallowly to deeply lobed. Rachis and costae grooved on adaxial surface, veins dichotomously forked, free. Sori terminal on veins, apical or lateral on the lobe, marginal to sub-marginal, reflexed or not when dry, funnellform, obovate or elliptic, formed by an outer indusium continuous with the lamina and an inner indusium, affixed at sides and usually with same colour as the vein. Sporangia (3–)5–15(–30) per sorus, immersed within indusium when young, exerted when mature. Annulus cells 16–24, more or less equal to distinctly unequal in size. Spores tetrahedral-globose, 25–38 µm in polar view, 20–25 µm in lateral view; perispore surface ornamented with branching sinuous ridges, exospore smooth or weakly scabrate.

Geographical distribution. *Orthiopteris* has seven species occurring in the Malay-Pacific region, one of which is widespread in the area and consists of a number of geographically more or less weakly delimited varieties (Figure 7), the remaining six are more or less narrow endemics in the eastern part of the region (Figure 8). On Madagascar, there is a single species.

Key to the species

- 1 Ultimate segments of fronds finely dissected, distance from base of sinuses to the nearest costule 0.1 mm or less; lobes usually with a single unbranched vein, or with 1–2 additional veins **2**
- Ultimate segments of fronds not finely dissected, distance from base of sinuses to the nearest costule more than 0.1 mm (usually more than 0.5 mm); lobes with veins pinnately branched into more than 3 veins **5**
- 2 Ultimate segments completely dissected to the veins, thus forming a single lobe for each vein, lobe not narrowed toward base; sori equal to or wider than the sterile lamina part below its base **3**
- Ultimate segments not completely dissected to the veins, with 2–3 veins per lobe, lobe narrowed towards base; sori narrower than the sterile lamina part below its base **4**
- 3 Sori elliptic-obovate, not reflexed when dried; inner indusium extending into a narrow tongue. Plant including rhizome not more than 1 m tall; stipes slender, 1–2 mm thick **3. *O. ferulacea***
- Sori funnellform, reflexed when dried, inner indusium extending into a narrow tongue. Plant including rhizome more than 1 m tall; stipes thicker than 2 mm **8. *O. trichophylla***

- 4 Outer indusium asymmetric; inner indusium lobed with lobe less than 2/3 width of sorus. Angle between ultimate segment and costa usually larger than 40° **2. *O. cicutarioides***
- Outer indusium symmetric; inner indusium obtuse, if lobed then lobe shallow and more than 2/3 width of sorus. Angle between ultimate segment and costa smaller than 40° **7. *O. tenuis***
- 5 Lamina margin with distinct yellow cartilaginous border; inner indusium extending into a narrow tongue about half the length of the entire sorus; sori elliptic to obovate **4. *O. firma***
- Lamina margin without distinct yellow cartilaginous border; inner indusium not extending into a narrow tongue, but truncate or with a shallow, obtuse lobe (about 1/4–1/3 length of sorus); sori funnellform **6**
- 6 Inner indusium distinctly shorter than outer, if almost equal then lamina thick and finely dissected **7**
- Inner indusium equal as or little shorter than outer, at least 2/3 as long; lamina thin and not finely dissected **8**
- 7 Lamina 140–150 cm wide, as wide as long or wider, papyraceous, thin; ultimate segments stalked, wide trapeziform; veins darker than lamina; sori nearly as wide as long, fertile vein swollen at the joint with base of sori; inner indusium emarginate and irregularly eroded, not lobed **5. *O. henriettae***
- Lamina 40–50 cm wide, longer than wide, herbaceous, not thin; ultimate segments sessile or very short stalked, narrow trapeziform; veins lighter than lamina; sori 2/3 as wide as long; fertile vein not swollen at the joint with base of sori; inner indusium entire, forming a shallow lobe **7. *O. tenuis***
- 8 Abaxial surface of lamina with scattered irregular triangular scales; apex of inner indusium lobed and eroded. Sori situated on both acroscopic and basiscopic sides of lobes **6. *O. samoensis***
- Abaxial surface of lamina without scales or with few hair-like scales; apex of inner indusium often entire and obtuse to truncate, if single-lobed then sori situated mostly on acroscopic side of lobes **9**
- 9 Sori asymmetric; inner indusium with single lobe; lobe width less than 2/3 width of sorus **10**
- Sori symmetric, inner indusium obtuse to truncate, if forming a lobe then lobe width at least 2/3 width of sorus **11**
- 10 Sori 0.6 mm or more wide **12**
- Sori not wider than 0.6 mm **1d. *O. campylura* var. *insularis***
- 11 Sori strongly reflexed when dry **1c. *O. campylura* var. *kingii***
- Sori in the plane of the lamina when dry **1a. *O. campylura* var. *campylura***
- 12 Lobes of ultimate segments blunt, obtuse; sori longer than wide; outer indusium not confluent with lamina margin on one side but incised **1e. *O. campylura* var. *laxa***
- Lobules of ultimate segments acute; sori almost as wide as long; outer indusium confluent with lamina margin on one side **1b. *O. campylura* var. *caudata***

1. *Orthiopteris campylura* (Kunze) Copel., Fern Fl. Philip. 1: 87. 1958.

Davallia inaequalis var. *minor* Hook., Sp. Fil. 1: 180, pl. 58A. 1846.

Lectotype (selected here): PHILIPPINES. Luzon, *Cuming 119* (K, on 2 sheets: K000794851*, K000794853*, isolectotypes: K: K000794864*, MICH: MICH1259585*).

Davallia campylura Kunze, Bot. Zeitung (Berlin) 8: 132. 1850.

Lectotype (selected here): PHILIPPINES. Luzon, *Cuming 119* (herb. Kunze, not traced, isolectotypes: K: K000794851*, K000794853*, K000794864*, MICH: MICH1259585*, see below).

Saccoloma campylurum (Kunze) Mett. Ann. Sci. Nat. Bot. sér. 4, 15: 80. 1861.

Type. Based on *Davallia campylura* Kunze

Saccoloma moluccanum (Blume) Mett. in Kuhn var. *stenolobum* Christ, Bull. Herb. Boissier, ser. 2 6: 1005. 1906.

Type. PHILIPPINES. Mabacal/Rizal, III, 1906, Loher s.n. (holo: P, on 4 sheets: P01566098*, P01566099*, P01566100*, P01566101*).

Saccoloma minus (Hook.) C.Chr., Gard. Bull. Straits Settlem. 4: 399. 1929.

Type. Based on var. *minor* Hook.

Ithycaulon minus (Hook.) C.Chr., Index. Fil. Suppl. 3: 116. 1934.

Type. Based on var. *minor* Hook.

Orthiopteris minor (Hook.) Copel., Gen. Fil.: 50. 1947.

Type. Based on var. *minor* Hook.

Type. PHILIPPINES. Luzon, *Cuming 119*

(K000794851 [<http://specimens.kew.org/herbarium/K000794851>],

K000794853 [<http://specimens.kew.org/herbarium/K000794853>],

K000794864 [<http://specimens.kew.org/herbarium/K000794864>];

MICH, 1259585 [<http://quod.lib.umich.edu/h/herb2ic/x-mich1259585/mich1259585.tif>]).

non *Saccoloma alatum* (Heward) (J. Sm.) Mett., Ann. Sci. Nat., Bot. sér. 4, 15: 80. 1861, nec *Microlepia alata* J. Sm., J. Bot. (Hooker) 3: 416. 1841, which is based on *Davallia alata* Heward, Mag. Nat. Hist. & J. Zool. II. ser. 2, 2: 465. 1838, nom. illeg, non Blume (1828).

Type. Jamaica, *Heward*. John Smith (1841) applied this name to the Asiatic specimen (*Cuming 119*, Luzon, Philippines) but as Smith's the name is validated by Heward's description it is typified by the Heward specimen from Jamaica.

Description. Rhizome erect, rising at least 20 cm above ground, diameter 1.5 cm. Rhizome scales pseudopeltate to peltate, 4–7 × 1.0–1.7 mm, narrowly lanceolate, attenuate toward apex. Fronds 100–130 × 40–50 cm; stipes slender, 37–40 cm long, 0.5–1 cm across (at base), dark brown; lamina deltoid, tripinnate, 70–100 × 40–50 cm, rather thick herbaceous, rigid, brown-green when dry, scaly; pinnae at 40–45° to rachis, largest at base, slightly overlapping, stalked 1 cm, including stalk up to 23–25 × 9–10 cm, lanceolate, first basiscopic pinnules of lowest pinnae enlarged; ultimate

segments 0.9–2.0 × 0.3–0.6 cm, sessile or very short-stalked, oblong trapeziform, apex obtuse to acute, margin with weak cartilaginous border; distance from vein to base of sinuses ca. 1.0 mm; crenate-dentate, shallowly to deeply incised, lobes obtuse to acute, veins in lobes 3–15 forks, light to dark brown, not strongly contrasting with lamina, percurrent. Scales on rachis mostly present at base of pinnae or pinnules, irregularly triangular, basifix, 0.7–0.9 × 0.3–0.4 mm.

Distribution. Sumatra, Peninsular Malaysia (Pahang, Perak, Selangor), Java, Borneo (Sabah, Kalimantan Timur), Philippines (Leyte, Luzon, Mindanao, Negros), Moluccas (Seram), New Guinea, Vanuatu (Aneityum), Fiji (Vanua Levu, Taveuni) (Figure 8).

Ecology. Terrestrial, mostly in shaded moist habitats, river banks, moist slopes, ravines etc., in primary or disturbed forest, at 0–2000 m altitude.

Discussion. *Orthiopteris campylura* is the most variable species within the genus. It is widely distributed from Western Malesia to Papua New Guinea and the Pacific, existing as different entities in each sub-geographical region, which in many cases have been recognized as individual species. However, we have regularly observed samples that were intermediate between the forms, and accordingly treat them here as varieties rather than as subspecies. Characters of the sori provide the best criteria to distinguish these varieties.

There are no data that suggest that any of the varieties is distinguished by a different ecology.

a. *Orthiopteris campylura* var. *campylura*

Figs 3a, b, 6d

Description. Sori protruding from the margin on distinct lobes, in one plane with lamina wings, 0.9–1 × 0.5–0.8 mm, symmetric, narrowly funnellform-obovate, widest at mouth; inner indusium brown, firm, equal to outer indusium, sometimes longer, apex similar to outer indusium; outer indusium truncate or obtuse, shallowly undulate; sporangia 7–12 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 15–20, clearly unequal; spores in polar view 35–45 μm, in lateral view 30–33 μm.

Distribution. Philippines (Leyte, Luzon, Mindanao, Negros), Moluccas (Seram), Papua New Guinea (Manus).

Discussion. Although in the shape of inner and outer indusium shape this species resembles *Orthiopteris campylura* var. *kingii*, the sori are not reflexed but usually flat even when dried. The distribution center of this variety appears to be in the Philippines.

b. *Orthiopteris campylura* var. *caudata* (Copel.) P.H.Hovenkamp & T.T.Luong, comb. nov.

urn:lsid:ipni.org:names:77148378-1

Figs 2e, 3g

Saccoloma caudatum Copel. Philipp. J. Sci. 30: 327. 1926.

Ithycaulon caudatum (Copel.) Copel., Univ. Calif. Publ. Bot. 16: 80. 1929b.

Type. Based on *Saccoloma caudatum* Copel.

Orthiopteris caudata (Copel.) Copel. Philipp. J. Sci. 78: 9. 1950.

Type. Based on *Saccoloma caudatum* Copel.

Type. PAPUA NEW GUINEA. Hydrographers Range, alt. 900 m, *King 462* (holo: MICH, 1190968* [<http://quod.lib.umich.edu/h/herb2ic/x-mich1190968/mich1190968.tif>]).

Description. Sori not protruding from the margin on distinct lobes, not reflexed when dry, in one plane with lamina wings, 0.7–0.9 × 0.6–0.7 mm, asymmetric, funnelform, widest at mouth of sori; inner indusium bright-brown, firm, usually shorter but not shorter than 2/3 length of outer indusium, apex with c. 0.2 mm long lobe (< 1/3 length of sorus); outer indusium emarginate to undulate-truncate; sporangia 17–21 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 17–20, clearly unequal; spores in polar view 28–32 µm, in lateral view 25–28 µm.

Distribution. North Moluccas, Papua New Guinea.

c. *Orthiopteris campylura* var. *kingii* (Bedd.) P.H.Hovenkamp & T.T.Luong, comb. nov.

urn:lsid:ipni.org:names:77148379-1

Figs 2g, 3c, 4d, e, f

Dicksonia kingii Bedd., Handb. Suppl.: 6. 1892.

Dennstaedtia acuminata Rosenst., Hedwigia 56: 350. 1915.

Type. PAPUA NEW GUINEA. Sattelberg, alt. 800 m, April 1914. *G. Bamler 139* (holo: B, B200044968* [<http://herbarium.bgbm.org/object/B200044968>];

iso: P, P00633321* [<http://coldb.mnhn.fr/catalognumber/mnhn/p/p00633321>],

P00633320* [<http://coldb.mnhn.fr/catalognumber/mnhn/p/p00633320>];

UC, 391869* [<http://plants.jstor.org/stable/10.5555/al.ap.specimen.uc391869>];

S, S-P-6347* [<http://andor.nrm.se/kryptos/fbo/kryptobase/large/S-P-006001/S-P-6347.jpg>], S09-41598* [<http://andor.nrm.se/kryptos/fbo/kryptobase/large/S09-041001/S09-41598.jpg>]).

Ithycaulon acuminatus (Rosenst.) Copel., Univ. Calif. Publ. Bot. 12: 395. 1931.

Type. Based on *Dennstaedtia acuminata* Rosenst.

Orthiopteris acuminata (Rosenst.) Copel. Philipp. J. Sci. 78: 9. 1950.

Type. Based on *Dennstaedtia acuminata* Rosenst.

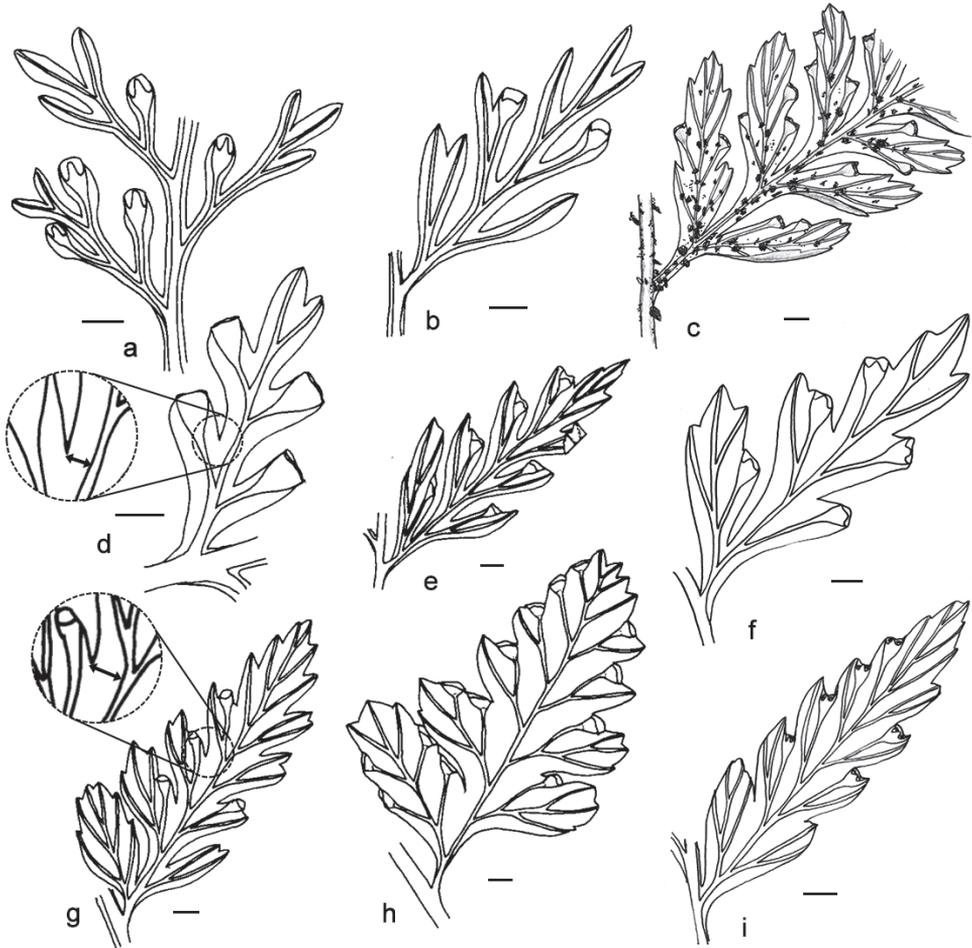


Figure 2. Ultimate segments. Arrows show distance from base of the shallowest sinuses to nearest costule/vein. **a** *Orthiopteris ferulacea*, Smith 8932 (K) **b** *O. cicutarioides*, Carr 13257 (K) **c** *O. samoensis*, Reinecke 97a (L) **d** *O. trichophylla*, Brass 12239 (L) **e** *O. campylura* var. *cautada*, Carr 12518 (L) **f** *O. campylura* var. *laxa* Mueller s.n. (L) **g** *O. campylura* var. *kingii*, Brass 12941 (MICH) **h** *O. henriettae*, Lam & Meeuse 5892 (L) **i** *O. campylura* var. *insularis* Braithwaite 4110 (L). All scale bars 1 mm.

Orthiopteris kingii (Bedd.) Holttum, Rev. Fl. Mal. 2: 306. f. 175. 1954.

Type. Based on *Dicksonia kingii* Bedd.

Saccoloma kingii (Bedd.) Parris in Parris, R.S. Beaman & Beaman, Pl. Mt. Kinabalu I. Ferns & Fern Allies: 151. 1992; G.B.Nair, J. Econ. Taxon. Bot. 16 (3): 645. "1992" [1994].

Type. Based on *Dicksonia kingii* Bedd.

Type. PENINSULAR MALAYSIA. Gunong Batu Puteh, August 1885, *King's collectors* 8058 (holo: K, 2 sheets: K000794854 [<http://specimens.kew.org/herbarium/>])

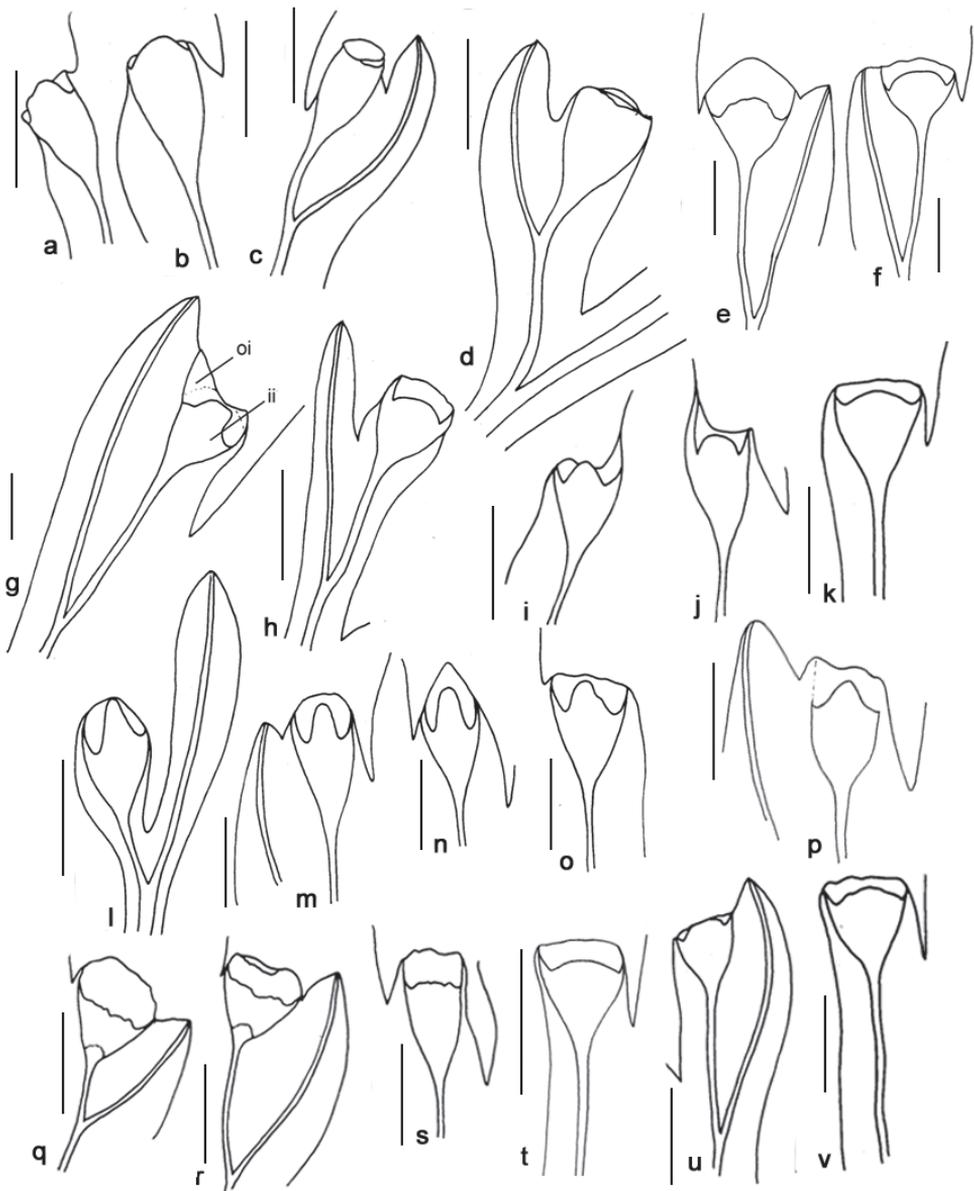


Figure 3. Sori of *Orthiopteris* seen from abaxial side. **a, b** *Orthiopteris campylura* var. *campylura* (Cuming 119, MICH) **c** *O. campylura* var. *kingii* (Brass 12941, MICH) **d** *O. trichophylla* (Brass 12239, L) **e** *Orthiopteris tenuis* (Smith 9154, L) **f** *Orthiopteris tenuis* (Smith 7274, L) **g** *O. campylura* var. *caudata* (Carr 12518, L) **h** *O. cicutarioides* (Carr 13257, K) **i, j** *O. campylura* var. *insularis* (Braithwaite 4110, L) **k** *O. tenuis* (small segment) (Degener 14648, L) **l** *O. ferulacea* (Smith 8932, K) **m, n** *O. firma* (Schlechter 14890, L) **o, p** *O. campylura* var. *laxa* (Mueller s.n., L) **q, r** *O. henriettae* (Lam & Meeuse 5892, L) **s** *O. henriettae*. **t** *O. samoensis* (Reinecke 97a, L) **u, v** *O. samoensis* (Vaupel 312, L). All scale bars 1 mm, oi = outer indusium, ii = inner indusium.

K000794854]; K000794855 [<http://specimens.kew.org/herbarium/K000794855>]; iso: SING, 0170905).

Description. Sori protruding from the margin, strongly reflexed when dry, in one plane with lamina wings, 0.9–1.0 × 0.5–0.8 mm, symmetric, narrowly funnelform-obovate, widest just below mouth; inner indusium dark-brown, firm, shorter or equal to outer indusium, apex similar to outer indusium; outer indusium truncate or obtuse, shallowly undulate tip; sporangia 6–12 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 17–20, clearly unequal; spores in polar view 28–30 µm, in lateral view 20–22 µm.

Distribution. Sumatra, Peninsular Malaysia (Pahang, Perak, Selangor), Java, Borneo (Sabah, Kalimantan Timur), Moluccas (Seram), Papua New Guinea.

Discussion. This variety is widespread in western Malaysia. It is easily recognized when dry by its distinctly protruding and reflexed sori. The ultimate segments of this variety may be the widest among the varieties of *Orthiopteris campylura*, although many collections from the Moluccas have narrow segments. The abaxial surface is scaly, but the scales are very small and not easily observed.

d. *Orthiopteris campylura* var. *insularis* P.H.Hovenkamp & T.T.Luong, var. nov.

urn:lsid:ipni.org:names:77148376-1

Figs 2i, 3i, j

Diagnosis. Sori asymmetric, not protruding from the margin, < 0.6 mm wide. outer indusium at one side strongly excurrent on lamina.

Type. SOLOMON ISLANDS. San Cristoval, Hinuahaoro, alt. 900 m, 22 September 1932, *Brass 2914* (holo: L, 0319881, iso: K, MICH).

Description. Sori not protruding from the margin, not reflexed, in one plane with lamina wings, 0.8–1.0 × 0.5–0.6 mm, asymmetric, narrow obovate, widest just below mouth sori; inner indusium bright-brown, firm, usually shorter, sometimes equal to outer indusium, apex with 0.1–0.2 mm long lobe; outer indusium deeply emarginate, at one side strongly excurrent on lamina; sporangia 10–15 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 17–22, clearly unequal; spores not seen.

Distribution. Papua New Guinea (Bougainville), Solomon islands, Vanuatu (Erromango).

Etymology. The varietal epithet refers to the archipelagic distribution of this taxon.

Discussion. This variety is quite widespread in the island archipelago stretching from Bougainville to the New Hebrides, but appears to be absent on the mainland of New Guinea.

e. *Orthiopteris campylura* var. *laxa* P.H.Hovenkamp & T.T.Luong, var. nov.

urn:lsid:ipni.org:names:77148377-1

Figs 2f, 3o, p

Diagnosis. Lobes of ultimate segments blunt. Sori symmetric, outer indusium truncate, not confluent with lamina margin on one side but incised.

Type. FIJI. Vanua Levu, Taveuni, 29 December 1933, *A.C. Smith 865* (holo: NY).

Description. Lamina not complete for measurement of size and shape, firm-herbaceous, yellowish-green, scales not found; ultimate segments 1.4–1.5 × 0.6–0.7 cm, sessile or very short-stalked, trapeziform, base asymmetric, cuneate, apex obtuse to acute, margin shallowly incised, distance from base of sinuses to costules 0.7–1.5 mm, lobes blunt; veins in lobes 3–15 forks, light to dark brown, not strongly contrasting with lamina, percurrent.

Ultimate segments 1.4–1.5 × 0.6–0.7 cm, sessile or very short stalked, trapeziform, Sori protruding from margin, not reflexed, 0.9–1.0 × 0.8 mm, symmetric, narrowly funnelform, widest at mouth; inner indusium brownish, firm, slightly shorter than outer indusium, apex with 0.2–0.3 mm long lobe, 1/4–1/3 length of sorus; outer indusium truncate, emarginate or undulate; sporangia 10–15 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 17–22, unequal in size; spores not seen.

Distribution. Vanuatu (Aneityum), Fiji (Vanua Levu, Taveuni).

Etymology. The varietal epithet refers to the general aspect of the fronds.

Discussion. The specimens grouped here have been confused with *Orthiopteris firma* mainly because of the similarity in the lobed inner indusium, but differ from that species in sorus shape and a less distinct cartilaginous border. The two available specimens examined here also show a considerable variation among themselves. More specimens or molecular evidence are needed to provide better support for the existence of this new variety.

2. *Orthiopteris cicutarioides* (Baker) Copel., Univ. Calif. Publ. Bot. 18: 217. 1942.

Figs 2b, 3h, 4a

Davallia cicutarioides Baker, J. Bot. 28: 106 (1890)

Leucostegia ?*cutarioides* (Baker) C.Chr., Index Filic., Suppl. III: 120 (1934)

Type. Based on *Davallia cicutarioides* Baker

Itthycaulon tenuisectum C.Chr., Brittonia 2: 285. 1937.

Type. PAPUA NEW GUINEA. Central Division, Dieni, alt. 700 m, 01 May 1933, *Brass 3139* (holo: BM n.v., iso: NY, 00127937*; MICH, 1190678*)

Itthycaulon cicutarioides (Baker) Alston, J. Bot. 77: 289. 1939.

Type. Based on *Davallia cicutarioides* Baker

Type. PAPUA NEW GUINEA. Mount Musgrave, alt. 700 m, 25 June 1889, W. Macgregor s.n. (Holo: K, 00794858*).

Description. Rhizome erect, rising at least 2 cm above ground, diameter unknown. Rhizome scales pseudopeltate, ca. 3.0×1.0 mm, lanceolate with long falcate acumen. Fronds 90–110 \times 30–50 cm; stipes stout, 35–45 cm long, 0.4–0.5 cm across (at base), light brown; lamina deltoid, tripinnate to quadripinnate, ca. 70 \times 30–50 cm, papyraceous, yellow-green when dry, glabrous or with few scattered scales; pinnae at 40–45° to rachis, largest at base, overlapping, stalk 2.0–2.5 cm, including stalk 25–35 \times 10–15 cm, lanceolate, first basiscopic pinnules of lowest pinnae enlarged; ultimate segments 1.0–2.0 \times 0.5–0.7 cm, sessile or very short stalked, trapeziform, apex acute, margin with weak cartilaginous border; deeply incised to less than 0.2 mm from veins; lobes oblanceolate, veins in lobes unbranched or with 1 fork, light brown and not strongly contrasting with lamina, percurrent. Scales on rachis mostly present at base of segment, hair-like. Sori apical on small lobes, lateral on larger lobes, symmetric, not reflexed, slightly concave with lamina wings slightly recurved, 0.7–0.8 \times 0.4–0.5 mm, wide obovate, widest just below mouth, not wider than the lamina below sorus; inner indusium brownish, firm, shorter than outer indusium, apex with c. 0.1 mm long lobe; outer indusium truncate-obtuse.

Distribution. Papua New Guinea (Boridi).

Ecology. Terrestrial, at 700–1500 m altitude.

Discussion. *Orthiopteris cicutarioides* has the least dissected fronds in the group of finely dissected-frond species, with usually more than one vein per lobe. The single specimen of this species that could be examined had sterile sori without sporangia, which might be an indication of a hybrid origin. The shape of the sorus and indusium of *O. cicutarioides* resembles those of *O. campylura* var. *caudata*, and it could represent a locally derived taxon.

3. *Orthiopteris ferulacea* (Moore) Copel., Bernice P. Bishop Mus. Bull. 59: 14. 1929a. Figs 2a, 3l, 4b

Davallia trichomanoides Hook., Sec. cent. Ferns T 64. 1861, non Blume 1828.

Davallia ferulacea T. Moore, Index Fil. (T. Moore): 294. 1861.

Type. Based on *Davallia ferulacea* T. Moore

Saccoloma ferulaceum (T. Moore) R.M. Tryon & A.F. Tryon, Rhodora 84: 127. 1982. 1982a.

Type. Based on *Davallia ferulacea* T. Moore

Saccoloma ferulaceum (T. Moore) G.B. Nair, J. Econ. Taxon. Bot. 16(3): 642. “1992” [1994].

Type. Based on *Davallia ferulacea* T. Moore

Type. FIJI. Naviti Levu, Dec. 1855, *Milne 315* (holo: K, 2 sheets: K00794861*, K00794862*).

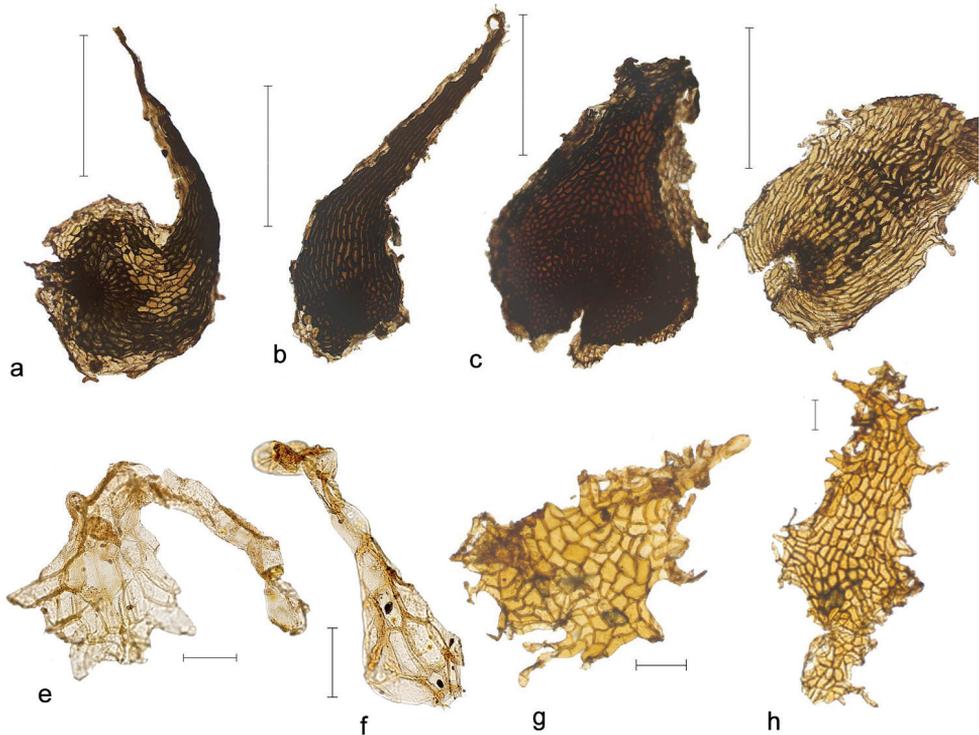


Figure 4. **a–d** Rhizome scales and **e–h** rachis scales of *Orthiopteris*. **a** *O. cicutarioides* (Carr 13257, L) **b** *O. ferulacea* (Smith 8932) **c** *O. firma* (Green 1793, K) **d** *O. campylura* var. *kingi* (Hoogland & Craven 10162, L) **e, f** *O. campylura* var. *kingi* (Larhing 6910, L) **g, h** *O. samoensis* (Reinecke 97a, L). Scale bars: 1 mm (**a–d**), 0.1 mm (**e–h**).

Description. Rhizome erect, rising at least 2–3 cm above ground, diameter 5–7 mm. Rhizome scales peltate or pseudopeltate, 2.5–3.0 × 0.7–0.9 mm, lanceolate with long falcate acumen. Fronds 30–80 × 10–30 cm; stipes slender, 10–30 cm long, 0.1–0.2 cm across (at base), light brown; lamina deltoid, tripinnate to quadripinnate, 20–50 cm × 10–30 cm, papyraceous, bright green when dry, glabrous; pinnae at 30–35° to rachis, largest at base, overlapping, stalk 0.5 cm, including stalk 15–25 × 6–9 cm, lanceolate, first basiscopic pinnules of the lowest pinnae enlarged; ultimate segments 1–2 × 0.5 cm, sessile or very short stalked, trapeziform, apex acute, margin without or with very weak cartilaginous border; deeply incised to less than 0.1 mm from veins; lobes narrowly oblanceolate, veins in lobes unbranched, light brown and not strongly contrasting with lamina, ending well below apex. Scales on rachis mostly at base of pinnae or pinnule, irregular triangular, basifixed. Sori apical on lobes, symmetric, not reflexed when dried, in one plane with lamina wings, 0.7–1.0 × 0.4–0.5 mm, elliptic, widest at middle or slightly above, wider than the sterile lamina below sorus; inner indusium brownish green, thin and slightly transparent, usually shorter, sometimes

equal to outer indusium, apex with narrow 0.2–0.3 mm long tongue, c. 1/2 length of sorus; outer indusium obtuse; sporangia 4–7 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 16–18, \pm equal; spores in polar view 26–30 μ m, in lateral view 20–25 μ m.

Distribution. endemic to Fiji (Viti Levu).

Ecology. Terrestrial in dense forest, bank of creek, at 50–1200 m altitude.

Discussion. *Orthopteris ferulacea* is the smallest species in the genus and the most easily recognizable among the species group with finely dissected fronds because of its relative small size and delicate and finely dissected frond. *Orthopteris trichophylla*, similarly dissected, has larger fronds and funnel-shaped sori without narrow tongue, whereas sori of *O. ferulacea* are elliptic with a narrow tongue.

4. *Orthopteris firma* (Kuhn) Brownlie, Fl. Nouv.-Calédonie & Dépend. 3: 112, t. 13, f. 9, 10. 1969.

Figs 3m, n, 4c, 5b, 6a, b

Saccoloma moluccanum var. *firmum* Kuhn, Verh. Zool.-Bot. Ges. Wien 19: 582. 1869.

Saccoloma firmum (Kuhn) C.Chr., Vierteljahrsschr. Naturf. Ges. Zürich 70. 221. 1925.

Type. Based on var. *firmum* Kuhn

Ithycaulon firmum (Kuhn) C.Chr., Index Filic., Suppl. III: 116. 1934.

Type. Based on var. *firmum* Kuhn

Lectotype (here designated). VANUATU. Erromango, *MacGillivray s.n.* (B, 200157508 [<http://herbarium.bgbm.org/object/B200157508>]).

Description. Rhizome erect, rising at least 20 cm above ground, diameter unknown (complete rhizome not seen). Rhizome scales basifixed, round to lanceolate, round scales 0.5–0.85 \times 0.6–1.0 mm, cordate scales 1.2–1.5 \times 1.1–1.5 mm, lanceolate scales 0.7–0.8 \times 0.–2.5 mm. Fronds ca 100–150 cm long; stipes stout, of unknown length, ca. 0.7–0.8 cm across (at base), dark brown; lamina deltoid, quadripinnate, complete fronds not seen, herbaceous, thick, dark green when dry, glabrous; pinnae at 50–60° to rachis, largest at base, separated or slightly overlapping, stalk 3 cm, including stalk up to 40 \times 25 cm, lanceolate, first basisopic pinnules of lowest pinnae enlarged; ultimate segments 2.0–3.0 \times 0.7–1.5 cm, sessile or very short stalked, narrow trapeziform, apex obtuse to acute, margin with distinct, thick, yellow cartilaginous border; shallowly incised to 1.0–2.0 mm from veins; lobes acute, veins in lobes 7–15 forks, bright green, clearly visible and contrasting with lamina, percurrent, joining with border. Scales on rachis only on rachis or veins, very sparse (few scales on an entire frond), irregular triangular, basifixed, 0.35–0.50 \times 0.25–0.4 mm. Sori apical on small lobes, lateral on larger lobes, symmetric, not or slightly reflexed, slightly concave with lamina wings usually recurved, 1.4–1.2 \times 0.8 mm, elliptic to narrowly obovate, widest at middle to 3/4 from base; inner indusium bright brown and contrasting in colour with lamina, firm, slightly shorter than outer indusium, sometimes equal, apex with

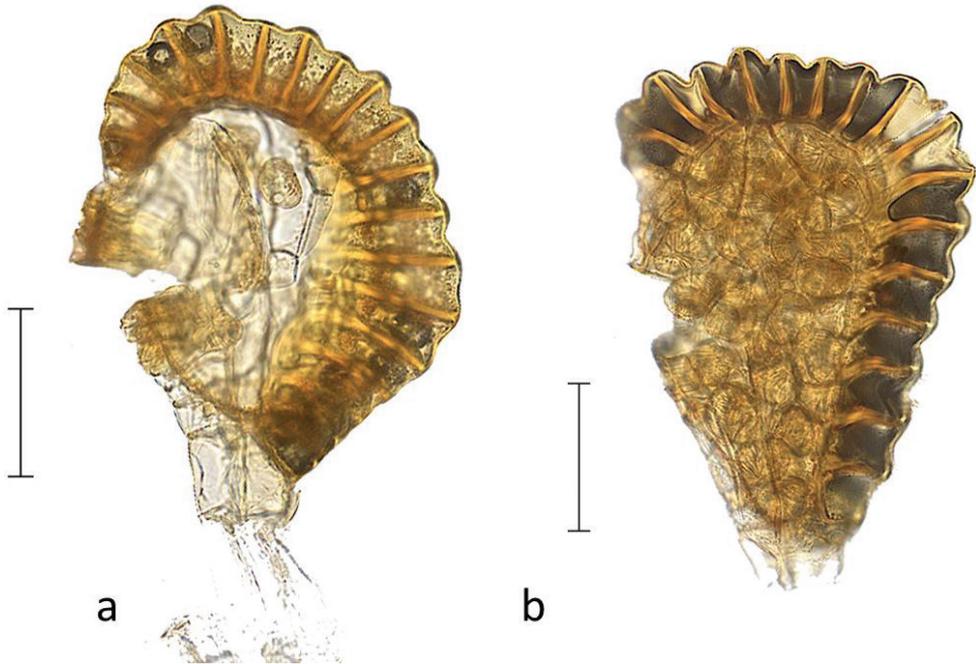


Figure 5. Sporangia of *Orthiopteris*, note the unequal-sized annulus cells. **a** *O. henriettae* (Malcomber et al. 2246, MO) **b** *O. firma* (Green 1793, K). All scale bar 0.1 mm.

narrow 0.35–0.45 mm long tongue, 1/3–1/2 length of sorus; outer indusium acute, obtuse, rarely truncate or emarginate; sporangia 9–15 per sorus, capsule rectangular-triangular with truncate apex, narrowed toward base, indurated annulus cells 17–20, unequal; spores in polar view 30–32 μm , in lateral view 25–27 μm .

Distribution. New Caledonia; New Hebrides (?), Fiji (?)

Ecology. Terrestrial on slopes or margin of humid montane forest, at 300–900 m altitude.

Discussion. This species is quite large and therefore often incompletely represented in collections. Rhizomes are usually missing and entire fronds are not preserved. The brightly colored, firm and large sori are very conspicuous on the dark green lamina. The majority of the specimens of *Orthiopteris firma* are from New Caledonia, except for the two specimens cited in the protologue and a single specimen from Fiji (*Betche s.n.*). All these represent records more than 100 years old for each respective location (collecting date is neither mentioned in literature nor indicated on specimen labels but collectors lived before 1913). For at least one of these specimens, a mistake in labeling is likely, as a similar specimen (*MacGillivray s.n.* B 200157509) is indeed labelled as originating from New Caledonia. All recent collections of *O. firma* are from New Caledonia, and therefore *O. firma* is best considered as an endemic for New Caledonia.

Kuhn (1869) described *Saccoloma moluccanum* var. *firma* based on two specimens: *Herus* 85 (Aneityum, New Hebrides) and *MacGillivray s.n.* (Erromango, New Hebrides).

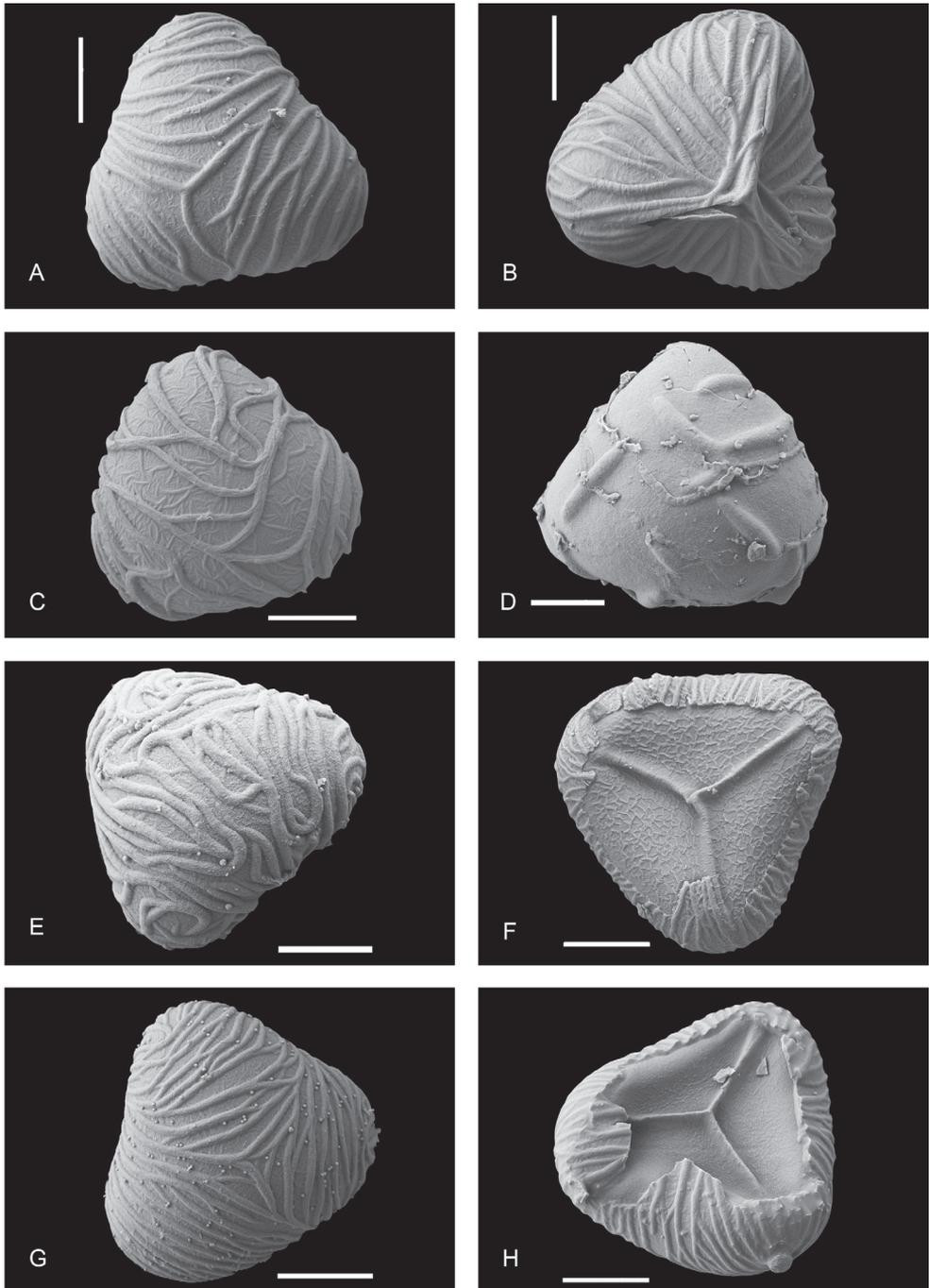


Figure 6. *Orthiopteris* spores. **a, b** *O. firma* (Guillaumin & Baumann-Bodenheim 10318, L) **c** *O. tenuis* (Smith 9154, L) **d** *O. campylura* var. *campylura* (Elmer 11717, L) **e** *O. campylura* var. *caudata* (Ridsdale 30654, L) **f** *O. henriettae* (Lam & Meeuse 5892, L) **g, h** *O. samoensis* (Sledge 1563, L). All scale bars 10 μm .

des, B200157508). Our study concludes that they belong to different taxa. *Herus* 85 is *O. campylura* var. *laxa*, *MacGillivray s.n.* is this taxon, although probably with an erroneous location, and is here selected as the lectotype for *Saccoloma moluccanum* var. *firmum* to maintain nomenclatural stability.

5. *Orthiopteris henriettae* (Baker) Copel., Gen. Fil.: 50. 1947.

Figs 2h, 3q, r, s, 5a, 6f

Dicksonia henriettae Baker in Hook. & Baker, Syn. Fil. (ed. 2): 462. 1874.

Microlepia henriettae (Baker) Kuhn, Reisen Ost-Afrika (Decken): 62. 1879.

Type. Based on *Dicksonia henriettae* Baker

Dennstaedtia henriettae (Baker) Diels, Nat. Pflanzenfam. 1: 4: 218. 1899.

Type. Based on *Dicksonia henriettae* Baker

Saccoloma henriettae (Baker) C.Chr., Dansk Botanisk Arkiv 7: 75, t. 25, f. 12–13. 1932.

Type. Based on *Dicksonia henriettae* Baker

Ithycaulon henriettae (Baker) C.Chr. Index Filic., Suppl. III: 116. 1934.

Type. Based on *Dicksonia henriettae* Baker

Type. MADAGASCAR. Antananarivo, *Baker s.n.* (holo: K, 000351013* [<http://specimens.kew.org/herbarium/K000351013>]).

Description. Rhizome erect, rising at least 5 cm above ground, diameter 1.5–2 cm. Rhizome scales pseudopeltate–peltate, 1.5–3.0 × 0.5–1.3 mm, narrow lanceolate with long sinuose acumen, thick. Fronds 110–150 × 100–150 cm (length fairly equal with width); stipes slender, 30–50 cm long, 0.4–0.6 cm across (at base), dark brown; lamina rhomboid–deltoid, widest at 3–5 cm above the base, tripinnate to quadripinnate (lowest lobe of ultimate segments free or nearly so), 60–110 × 140–150 cm, papery, thin, dull brown–yellowish green when dry, glabrous; pinnae at 45–50° to rachis, largest at the second from base, overlapping, stalk 3 cm, including stalk 30–50 × 10–15 cm, lanceolate, first acrosopic, sometimes first basisopic pinnule of the lowest pinnae enlarged; ultimate segments 3–5 × 1.5–2.5 cm, 1–2 mm stalked, ovate-trapeziform, with strongly asymmetric base, lowest lobe almost completely separated, apex obtuse, margin with weak cartilaginous border; shallowly incised to 1.5–2.5 mm from veins; lobes rounded, veins in lobes 8–9 forks, dark brown, not contrasting with lamina, percurrent. Scales on rachis a few hair-like scales only on veins (few scales on an entire frond), hair-like. Sori lateral on lobes, symmetric, not reflexed, sometimes concave with lamina wings recurved, 0.8–1.1 × 0.5–1.0 mm, wide funnellform-obovate, sometimes narrow funnellform, widest at mouth or just below mouth; inner indusium dull brown, papery, thin but tough, with swollen joint at base with distinct dark line at the joint, 1/2 – 2/3 as long as outer indusium, apex emarginate and irregularly eroded, not extending into a lobe; outer indusium truncate to obtuse;

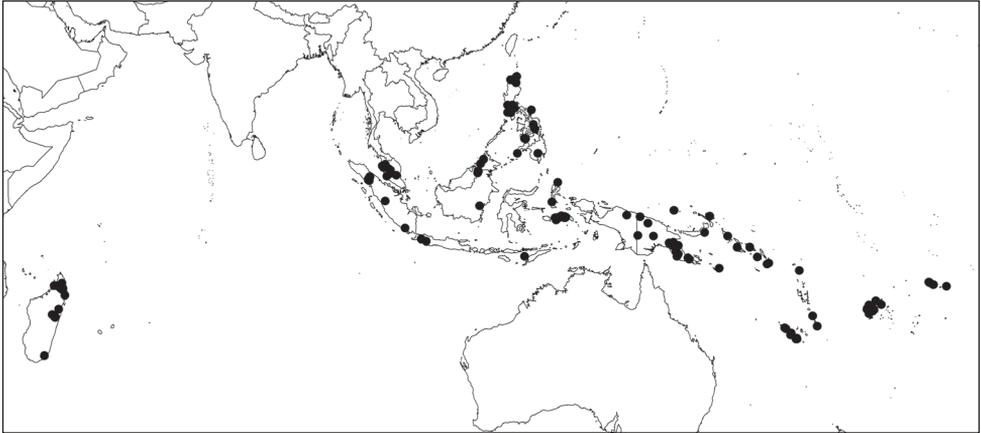


Figure 7. Distribution of *Orthiopteris* excl. *Saccoloma*.

sporangia 10–17 per sorus, capsule globose and rounded at apex, gradually narrow ed toward base, indurated annulus cells 18–24, unequal in size; spores in polar view 30–38 μm , in lateral view 22–25 μm .

Distribution. endemic to Madagascar (Toamasina, Antsiranana, Toliara, Tamatave, Antananarivo).

Ecology. Terrestrial in moist, shady, evergreen forest, on laterite soil derived from gneiss or in lowland dense disturbed forest with bamboo and Acanthaceae, border of the creek etc., at 350–1700 m altitude.

Discussion. *Orthiopteris henriettae* is the only representative of the genus in Madagascar, where it is not rare. It is clearly distinct from the Malay-Pacific species by its fronds having a papyraceous and thin texture, the ovate-trapeziform ultimate segments with shallowly crenate-dentate margin and usually swollen joints in the veins just below sori. The ultimate segments seem to be narrower in collections from higher altitudes.

6. *Orthiopteris samoensis* P.H.Hovenkamp & T.T.Luong, spec. nov.

urn:lsid:ipni.org:names:77148375-1

Figs 2c, 3t, 3u, v, 4g, h, 6g, h

Diagnosis. Differs from all other *Orthiopteris* species in relatively dense scales on lower surface of the lamina.

Type. SAMOA. Savai'i, 31 December 1905, *Vaupel* 312 (holo: L, 3 sheets: L0319870, L0319927, L0319847, iso: MO, U).

Description. Rhizome erect, rising at least 50 cm above ground, diameter unknown. Rhizome scales unknown. Fronds 150–200 cm (complete fronds not seen); stipes stout, ca. 70 cm long, 0.5–0.8 cm across (at base), light brown; lamina probably deltoid, quadripinnate, 100–150 cm long, at least 60 cm wide, firm- herbaceous, brownish green when dry, scaly with scattered scales on abaxial surface, denser at base of segments, and on veins

and base of rachis; pinnae at 45–50° to rachis, separated or slightly overlapping, stalk 1.6 cm, including stalk up to 30–45 × 15–20 cm, lanceolate; ultimate segments 1.0–2.0 × 0.4–0.8 cm, sessile or very short stalked, narrowly trapezoid, apex obtuse to acute, margin with weak cartilaginous border; shallowly incised to 0.3–1.0 mm from veins; lobes obtuse to acute, veins in lobes form 3–6 forks, yellow green, weakly contrasting with lamina, percurrent. Scales on rachis irregularly triangular, basifixed, 0.4–1.4 × 0.4–0.9 mm. Sori lateral on lobes, symmetric, not reflexed, in one plane with lamina wings, 0.5–0.8 × 0.6–0.75 mm, suborbicular to funnellform, widest at mouth; inner indusium brown to dark brown, firm, slightly shorter or equal to outer indusium, rarely longer, apex with a rounded to truncate, 0.1–0.2 mm long lobe, eroded, ca. ¼ length of sorus; outer indusium truncate, shallowly lobed or eroded; sporangia 5–10 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 17–19, clearly unequal; spores in polar view 30–33 µm, in lateral view 23–27 µm.

Distribution. endemic to Samoa (Upolu, Savaii).

Ecology. Terrestrial, medium wet forest, at 600–900m altitude

Etymology. The specific epithet refers to the type locality.

Discussion. The key character to separate this newly recognised species from the others are the many scales covering the abaxial surface of lamina. *Orthiopteris campylura* may have some scales on the lower lamina surface, but these are sparser, smaller and narrower. Apart from the laminal scales, *O. samoensis* most closely resembles *O. campylura* var. *caudata* in terms of frond and sori shape, but the inner indusia of *O. samoensis* are not lobed.

7. *Orthiopteris tenuis* (Brack.) Brownlie, Nova Hedwigia 55 (Pterid. Fl. Fiji): 115. 1977.
Figs 3e, f, k

Microlepia tenuis Brack., U.S. Expl. Exped., Filic. 16: 236. 1854.

Microlepia papillosa Brack. U.S. Expl. Exped., Filic. 16: 237, t. 34, fig. 1. 1854.

Type. FIJI. *U.S. South Pacific Exploring Expedition s.n.* (number 4 in Brackenridge 1854) (Holo: US, 00134882* [<http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00134882>]; iso: K, 000794859*).

Saccoloma tenue (Brack.) Mett., Ann. Sci. Nat., Bot. sér. 4, 15: 80. 1861.

Type. Based on *Microlepia tenuis* Brack.

Saccoloma papillosa (Brack.) Mett., Ann. Sci. Nat., Bot. sér. 4, 15: 80. 1861.

Type. Based on *Microlepia papillosa* Brack.

Type. FIJI. *U.S. South Pacific Exploring Expedition s.n.* (number 3 in Brackenridge 1854) (Holo: US, 00134883* [<http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00134883>]; iso: K & NY, K000794860*, NY 00127936*).

Description. Rhizome erect, rising at 5–60 cm above ground, diameter 1.5–10 cm. Rhizome scales pseudopeltate, 4–8 × 0.7–1 mm, narrow, linear lanceolate, usually falcate and suddenly contracted into a long thin acumen. Fronds 100–170 × 40–50

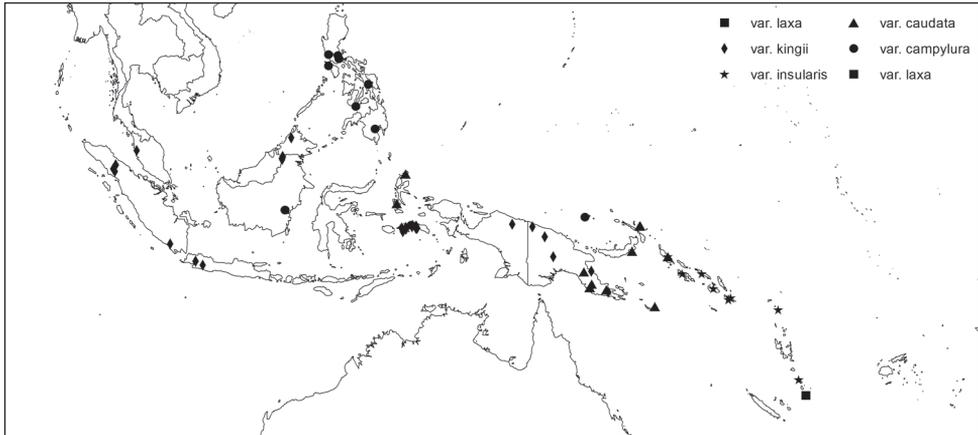


Figure 8. Distribution of *Orthiopteris campylura* and its varieties.

cm; stipes slender, 30–70 cm long, 0.3–0.8 cm across (at base), dark brown; lamina deltoid, widest at base, tripinnate, sometimes quadripinnate in large plants, ca. 70 × 40 cm, herbaceous, lively green when dry, glabrous; pinnae at 35–45° to rachis, largest at base, separated or slightly overlapping, stalk 1–2 cm, including stalk up to 26 × 12 cm, lanceolate, first basispicopic pinnules of lowest pinnae enlarged; ultimate segments 1.5–2.0 × 0.7–1.0 cm, sessile or very short stalked, trapezoid to narrowly so near frond apex, apex obtuse to acute or attenuate, margin with weak cartilaginous border; shallowly to deeply incised to 0.2–2.0 mm (see discussion) from veins; lobes acute, veins in lobes with 1–3 forks, bright green, strongly contrasting to the lamina, percurrent, sometimes ending just below apex. Scales on rachis absent, absent. Sori apical on small lobes, lateral on larger lobes, asymmetric, sometimes symmetric, not reflexed, in one plane with lamina wings, ca. 1.5 × 1 mm, funnellform, sometimes ovate, widest at middle to 2/3 from base; inner indusium yellow bright green, contrasting in colour with lamina, firm, 1/2–2/3 as long as outer indusium, apex with obtuse to acute lobe, slightly eroded, ca. 0.25–0.5 the length of inner indusium; outer indusium obtuse, sometimes acute, truncate or emarginate with 1–2 shallow sinuses; sporangia 7–10 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 17–22, ±equal; spores in polar view 30–35 μm, in lateral view 25–27 μm.

Distribution. Endemic to Fiji (Viti Levu, Vanua Levu, Ovalau).

Ecology. Terrestrial, dense forest, bank along stream, at 0–1000 m altitude.

Discussion. This species is highly variable in terms of frond dissection, and sorus shape. Plants from higher altitudes (above ca. 500 m) have larger fronds and furthermore differ from the lowland plants in ultimate segments being deeply incised (distance of lamina from base of sinuses to costules less than 0.5 mm), and sori with almost equally long inner- and outer indusium. In contrast, the lowland plants have ultimate segments more shallowly incised (distance of lamina from base of sinuses to costules more than 0.5 mm), and sori with a large difference in length between inner and outer indusia. We could not separate the two forms because of the presence of intermediate specimens.

8. *Orthiopteris trichophylla* Copel.

Figs 2d, 3d

Orthiopteris trichophylla Copel., Univ. Calif. Publ. Bot. 18: 217. 1942.*Saccoloma trichophyllum* (Copel.) G.B.Nair, J. Econ. Taxon. Bot. 16(3): 643. "1992" [1994].Type. Based on *Orthiopteris trichophylla* Copel.

Type. PAPUA NEW GUINEA. Idenburg River, 15 km southwest of Bernhard camp, alt.1800 m, 1939, *Brass 12027*, (erroneously cited as *Brass 12057* in Copeland 1942, holo: MICH, 1190791* [<http://quod.lib.umich.edu/h/herb2ic/x-mich1190791/mich1190791.tif>]; iso: BM, 001044444, BO 1510941)

Description. Rhizome erect. Rhizome scales not seen. Fronds 120–160 × 40–50 cm; stipes stout, 40–50 cm long, 0.4–0.6 cm across (at base), dark brown; lamina deltoid, widest at base, tripinnate to quadripinnate, 100–120 × 40–50 cm, herbaceous, dark brownish green when dry, glabrous or with few scattered scales; pinnae at 30–35° to rachis, largest at base, overlapping, stalk 0.5 cm, including stalk 15–25 × 6–9 cm, lanceolate, first basiscopic pinnules of lowest pinnae enlarged; ultimate segments 1.0–1.5 × 0.5 cm, sessile or very short stalked, trapezoid, apex acute, margin with weak cartilaginous border; almost completely dissected to less than 0.2 mm from veins; lobes narrowly oblong, veins in lobes unbranched or with 1 fork, dark brown and not contrasting with lamina, percurrent. Scales on rachis mostly at base of pinnae or pinnule, very few on veins, hair-like. Sori lateral or apical on lobes, symmetric, slightly reflexed, slightly concave with lamina wings slightly recurved, 1.0–1.2 × 0.6–0.7 mm, funnel-form, widest at mouth, not wider than the sterile lamina below sorus; inner indusium dull brown, firm, 4/5–2/3 as long as outer indusium, apex truncate; outer indusium truncate; sporangia 7–12 per sorus, capsule globose and rounded at apex, gradually narrowed toward base, indurated annulus cells 16–20, ±equal; spores in polar view not studied, in lateral view .

Distribution. Papua New Guinea (Idenburg River).

Ecology. Terrestrial in bottom of ravines, rain forest, at 1800 m altitude.

Discussion. This species can be mistaken for *Orthiopteris cicutarioides* because the frond morphology is similar, with fronds very finely dissected in both species. However, *O. trichophylla* is more finely dissected with a single vein per lobe (similar to *O. ferulacea*), while *O. cicutarioides* has 2 or 3 one veins per lobe. The sori and indusia of *O. trichophylla* resemble those of *O. campylura* var. *kingii*, being funnellform and slightly reflexed, and the possibility cannot be excluded that *O. trichophylla* is locally derived from *O. campylura* var. *kingii*. The single specimen we examined (*Brass 12239*) differs slightly from the type (studied from scanned image of *Brass 12027*) by its shorter lobes. However, the sori and indusia are identical, and they were collected on the same day and at the same locality. Unlike in *O. trichophylla*, which may represent a similar case of a locally derived taxon, both specimens of *O. cicutarioides* look very productive with many ripe sporangia spreading over the mouth of the sorus. Brass noted that the

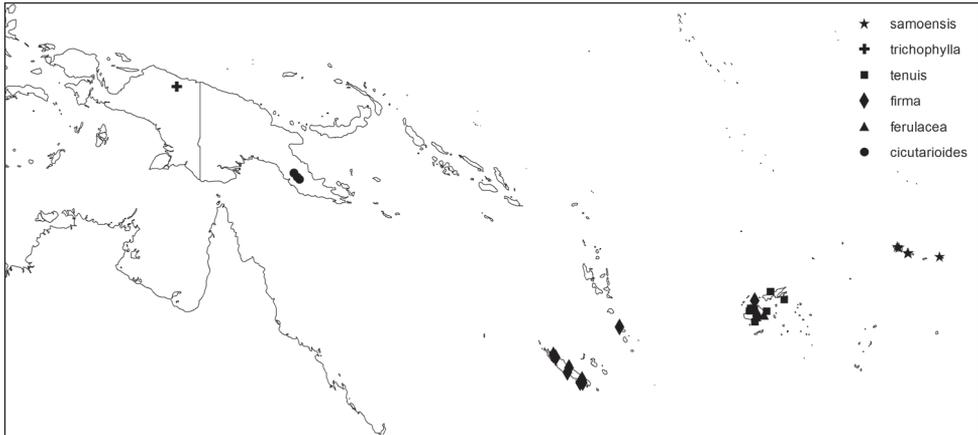


Figure 9. Distribution of *Orthiopteris* species in East Malesia and the Pacific.

species was very common and abundant at the collecting site (Idenburg river), but we have not seen any later collections than Brass's in 1939. Perhaps it is just abundant locally, and it may well be currently threatened.

Excluded names

Ithycaulon Copel., *Univ. Calif. Publ. Bot.* 16: 79. 1929b.

Type. *Ithycaulon moluccanum* (Blume) Copel.

Ithycaulon moluccanum (Blume) Copel, *Univ. Calif. Publ. Bot.* 16: 79. 1929b.

= *Saccoloma moluccanum* (Blume) Mett in Kuhn, *Verh. zool. bot. Ges.* 19. 581. 1869.

Both names *Ithycaulon moluccanum* and *Saccoloma moluccanum* are based on *Davallia moluccana* Blume, *Enum. Pl. Javae* 2: 237 (1828), for which the accepted name is now *Tapeinidium moluccanum* (Blume) C.Chr, *Gard. Bull. Straits Settlements* 4: 399. (1929). For more details of this misapplication see De Joncheere (1984).

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Appendix

Identification list Orthiopteris

- 1a. *O. campylura* var. *campylura*
- 1b. *O. campylura* var. *caudata*
- 1c. *O. campylura* var. *kingi*
- 1d. *O. campylura* var. *insularis*
- 1e. *O. campylura* var. *laxa*
2. *O. cicutarioides*
3. *O. ferulacea*
4. *O. firma*
5. *O. henriettae*
6. *O. samoensis*
7. *O. tenuis*
8. *O. trichophylla*

Alston, AHG 16940: 1b;
 anon. 1123: 6; 119: 6; 249: 6; s.n.: 6;
 Aridy, J; Rahajasoja, G; Moise 69: 5;
 Baker s.n.: 5;
 Bamler, MG ROS 116: 1b;
 Baudouin 1805?: 4;
 Baumann-Bodenheim, MG 10168: 4; 10236: 4; 15190: 4;
 Baumann-Bodenheim, MG; Guillaumin, A 10281: 4;
 Beer's collectors BSIP 7671: 1d;
 Betche, E s.n.: 4; s.n.: 6;
 Boerlage, JG 687: 1c; 687: 1c;
 Braithwaite, AF RSNH 2268: 1d; RSS 4110: 1d; RSS 4245: 1d;
 Brass, LJ 2914: 1d; 3050: 1d; 3919: 2; 12027: 8; 12239: 8; 12269: 1c; 12941: 1c;
 Brownlie, G 771: 3;
 Carr, CE 12518: 1b; 13067: 1b; 13257: 2;
 Chew, WL; Corner, EJH; Stainton, A 1578: 1c;
 Christophersen, E; Hume, EP 2032: 6; 2065: 6;
 Clemens, J; Clemens, MS 40386: 1c;
 Clemens, MS 3470: 1c; 5120: 1c;
 Copeland, EB 21777: 1a; PPE 67: 1a;
 Croft, JR 799: 1b; 1206: 1a; 1720: 1c; 1959: 1b; 2053: 1b;
 Cuming, H 119: 1a; 360: 1a;
 Curtis, C 2085: 1c;
 Degener, O 14648: 7; 14907: 3; 15162: 7;
 Dorr, LJ 3144: 5;

Edaño, GE BS 78693: 1a; BS 79627: 1a; PNH 807: 1a; PNH 11183: 1a; PNH 11187:
 1a; PNH 11223: 1a; PNH 17313: 1a;
 Elmer, ADE 9067: 1a; 9714: 1a; 10183: 1a; 11717: 1a;
 Franc (BONATI) 36: 4; (BONATI) 335: 4; (ROSENSTOCK) 4: 4;
 Gay, H 404: 1c;
 Germain, R s.n.: 4;
 Gillespie, JW 3326: 3; 4013: 7; 5124: 3;
 Green, PS 1793: 4;
 Grether, DF; Wagner, WH 4161: 1a;
 Guillaumin, A; Baumann-Bodenheim, MG 10318: 4;
 Herus 85: 1e;
 Hildebrandt, JM 3765: 5;
 Holttum, RE 11477: 1c; 15412: 1c; 31220: 1c;
 Hoogland, RD; Craven, LA 10162: 1c; 10386: 1c;
 Hovenkamp, PH; Arifiandy, NM; Iqbal, M 05/ 159: 1a;
 Humbert, H 14131: 5; 22461: 5; 23155: 5;
 Humbert, H; Capuron, R; Cours, G 24686: 5;
 Humbert, H; Cours, G 17864: 5;
 Iqbal, M; Usman 049: 1a;
 Iwatsuki, K; Kato, M; Ueda, K; Mahjar, UW C 302: 1c; C 1025: 1c;
 Janssen, T 2418: 5;
 John, H 18311: 3;
 Kajewski, SF 2672: 1d;
 Kato, M C 13703: 1c;
 Kato, M; Imaichi, R; Aso, K; Darnaedi, D; Ujang Hapid B 860: 1a;
 Kato, M; Okamoto, M; Walujo, EB B 9266: 1c; B 9584: 1c; B 10082: 1c; B 11308:
 1c; B 11498: 1c;
 Kato, M; Okamoto, M; Walujo, EB; Ueda, K; Darnaedi, D B 8363: 1c;
 Kato, M; Sunarno, B; Akiyama, H C 3224: 1c;
 Kato, M; Ueda, K; Fanani, Z C 11298: 1c; C 11350: 1c; C 11642: 1c; C 11683: 1c;
 C 12934: 1c; C 13231: 1c; C 13330: 1c; C 14106: 1c;
 Kato, M; Ueda, K; Mahjar, UW C 1248: 1c; C 1294: 1c; C 1771: 1c; C 2121: 1c; C
 2149: 1c; C 2160: 1c;
 Kato, M; Ueda, K; Mahjar, UW; Okamoto, M; Akiyama, H; Sunarno, B C 5372: 1c;
 C 5613: 1c; C 6548: 1c; C 6876: 1c; C 7159: 1c; C 7478: 1c;
 King's collector 2118: 1c; 8058: 1c;
 Koroiveibau, D; Saula 16119: 3;
 Kuhl, H; Hasselt, JC van s.n.: 1c;
 Lam, HJ 7222: 4;
 Lam, HJ; Meeuse, ADJ 5841: 5; 5892: 5;
 Loher, A s.n.: 1a; Copel. 6716: 1a;
 Lörzing, JA 5787: 1c; 6910: 1c; 14722: 1c;
 MacGillivray, J s.n.: 4;

Main s.n.: 1b;
Malcomber, S; Rakotomalaza, PJ; Raharilala, J 2246: 5;
Matthews, CG 649: 1c; s.n.: 1c;
McGregor, RC 24: 2;
McPherson, G 6528: 4;
Merrill, ED 5951: 1a;
Miller, JS 3545: 5;
Milner s.n. (313): 3; s.n. (315): 3;
Mohd Haniff 9081: 1c; 9083: 1c;
Morrison, A s.n.: 1e;
Mueller, F von s.n.: 1e;
Murton, HJ 26: 1c;
Nakaike, T 108: 1c;
Palmer, W; Bryant, O 547: 1c;
Pancher, M s.n.: 4;
Parks, HE 20050: 7; 20192: 7; 20861: 7; 212332: 3;
Parris, BS; Croxall, JP 7910: 1c;
Powell, T s.n.: 6;
Price, MG 2478: 1a; 3166: 1a;
Pullen, R 3453: 1b; 7889: 1c; 7924: 1c; 8263: 1b; 8265: 1b;
Raciborski, M 126: 1c;
Rakotondrainibe, F 3163: 5;
Rakotovaio, C; Felix, E; Razafindasy, R; Antilahimena, P; Razanatsoa, H 1233: 5;
Ramos, M BS 14795: 1a; BS 30424: 1a; BS 39545: 1a;
Randriambololomamonjy, O; Razakamalala, R; Jaowind 347: 5;
Ravololonanahary, H; Ralimanana, H; Birkinshaw, C; Randrianaivo, R; Ranaivoj 44: 5;
Razafitsalama, LJ 486: 5;
Reinecke 149 b: 6; 97 a: 6;
Reinecke, F 71: 6;
Ridley, HN 8634: 1c; 14000: 1c;
Ridsdale, CE; Lavarack, P NGF 30654: 1b; NGF 30656: 1d;
Robinson, HC s.n.: 1c;
Sands, MJS; Pattison, GA; Wood, JJ 2924: 1a;
Schlechter, R 14890: 4;
Schodde, R 1562: 1c;
Scortechini, B 306: 1c;
Seemann, B 753: 7;
Shim, PS San 81811: 1c;
Sledge, WA 1563: 6;
Smith, AC 4381: 7; 6463: 7; 6764: 7; 7274: 7; 8533: 7; 865: 7; 8875: 7; 8885: 3;
8932: 3; 9154: 7;
Stevens, PF; Lelean, Y LAE 58676: 1b;
Sulit, MD PNH 20294: 1a;

Surbeck, H 756: 1c; 1085: 1c; 1175: 1c;
Tabualewa, A 15613 a: 3; 15566: 7;
Turnau, EA 936: 1c;
U.S South Pacific Exploring Expedition s.n. 3: 7; s.n. 4: 7;
Vaupel, F 312: 6; 482: 6;
Venning, FEW MA 18: 1c;
Vieillard, E 1623: 4;
Wenzel, CA 646: 1a;
Werff, HH van der; McPherson, G 15906: 4;
Werff, HH van der; McPherson, G; Rapanarivo, S 13622: 5;
Whitmore, TC BSIP 1572: 1d;
Whitmore, TC; Grubb, PJ BSIP 2067: 1d;
Wiriadinata, H 1457: 1c;
Yapp, RH 427: 1c;
Zollinger, H 244: 1c;

Adiantum shastense, a new species of maidenhair fern from California

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Abstract

A new species of *Adiantum* is described from California. This species is endemic to northern California and is currently known only from Shasta County. We describe its discovery after first being collected over a century ago and distinguish it from *A. jordanii* and *A. capillus-veneris*. It is evergreen and is sometimes, but not always, associated with limestone. The range of *Adiantum shastense* Huiet & A.R.Sm., **sp. nov.**, is similar to several other Shasta County endemics that occur in the mesic forests of the Eastern Klamath Range, close to Shasta Lake, on limestone and metasedimentary substrates.

Keywords

Shasta Lake, maidenhair, Shasta snow wreath, new species

Introduction

The genus *Adiantum* L. (Pteridaceae) is found worldwide mostly in the tropics and subtropics, but about ten percent of species (of a total of ca. 225 spp.) are found in temperate regions. The majority of these occur in Asia but several are found in North America. There are nine species of *Adiantum* in the continental United States and Canada and eight of the nine are native (Paris 1993). Three are of tropical origin, occurring in restricted ranges that are at their northern most limits. The remaining five

species occur solely in temperate regions, with four having a broad geographic range: *Adiantum pedatum* L., *A. capillus-veneris* L., *A. aleuticum* (Rupr.) C.A.Paris and *A. jordanii* Müll.Hal. *Adiantum pedatum* and *A. capillus-veneris* are distributed beyond North America (Paris 1993); *A. capillus-veneris* is the most wide-ranging and occurs on six continents, whereas *A. pedatum* occurs widely in both North America and Asia. Cytological data for different geographic localities of these two species reveal differing chromosome numbers (diploids, tetraploids, dysploids), suggesting that they may both be species complexes (Löve and Löve 1997, Nakato and Kato 2005, Wagner 1963).

Of the four wide-ranging species, three *Adiantum capillus-veneris*, *A. aleuticum* and *A. jordanii* occur in California and none of these is endemic. They all are found in at least 30% of the counties, and their distributions span the entire state. *Adiantum aleuticum* is easily recognized by its distinct pseudopedate laminar morphology, while *A. jordanii* has a laminar architecture that is more similar to *A. capillus-veneris*; however, the two are not closely related (Huiet et al. unpublished). Juvenile and sterile forms of these taxa can sometimes be difficult to distinguish.

While investigating *Adiantum capillus-veneris* populations in California as part of a worldwide molecular phylogenetic study of the genus, a new endemic species was discovered. Here we describe this new taxon and discuss its remarkable discovery after it was first collected over 100 years ago.

Methods

Chromosome material of young sporangia was field-fixed in ethyl alcohol:acetic acid (3:1). Spore mother cells were stained with acetocarmine, and, using standard squash techniques, examined under a compound microscope. Meiotic cells were examined at diakinesis, metaphase I, and normal pairing of homologous chromatids was seen. The voucher is listed under paratypes.

Taxonomy

Adiantum shastense Huiet & A.R.Sm., sp. nov.

urn:lsid:ipni.org:names:77148382-1

Figs 1–2

Diagnosis. *Adiantum shastense* is similar to *A. jordanii* in having dark brown to purplish brown rhizome scales and 2–3-pinnate laminae. It differs by being persistent and green throughout the summer, and does not die back as does *A. jordanii*. *Adiantum shastense* can be distinguished from *A. capillus-veneris* by the darker rhizome scales, the rhomboid shape of the pinnulets, and the often, glaucous bluish green color of the laminae.

Type. UNITED STATES, California: Shasta County, north side of Lake Shasta. McCloud River arm, along Gilman Road, just W of intersection with Old Mill Road

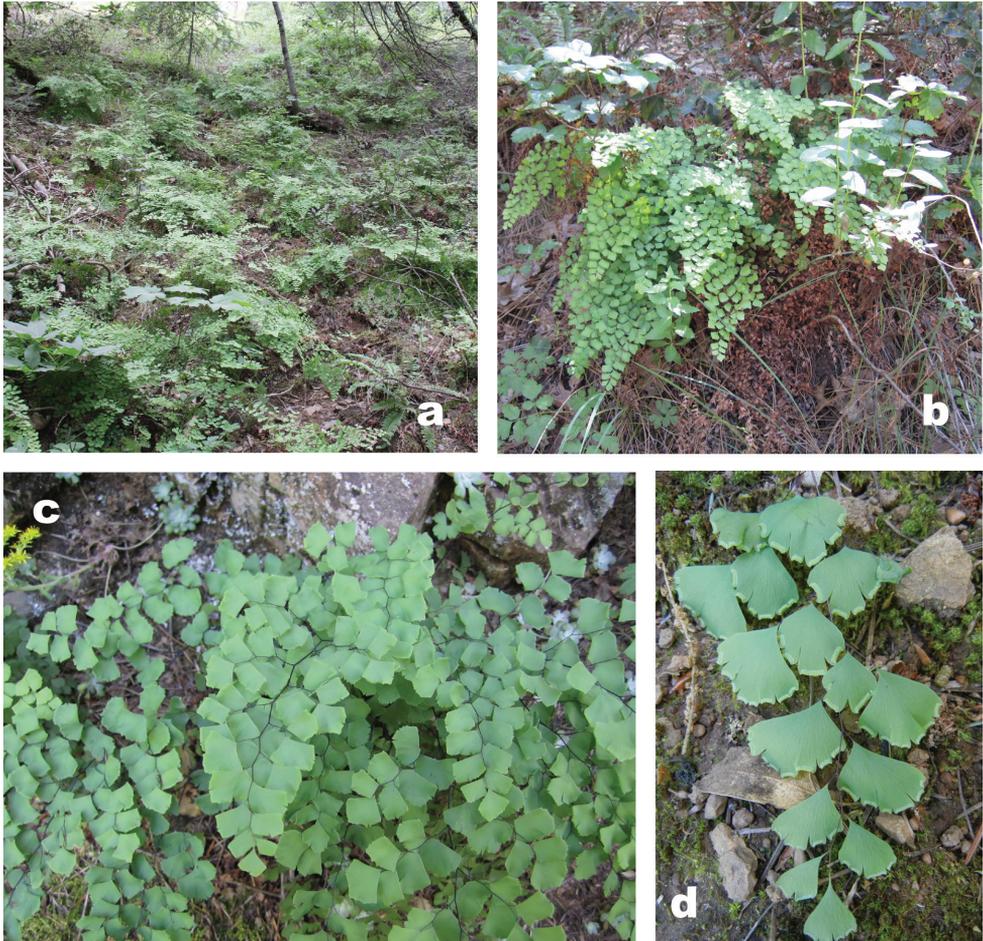


Figure 1. Photographs of *Adiantum shastense*. **A** Plants as dominant understory **B** Mature plant **C** Fronds **D** Young fertile pinnulets.

where Fall Creek intersects Gilman Road. 40°51.517200'N, 122°18.835800'W, 1222 ft, 14 May 2014, *Layne Huiet, Alan Smith, Joan Smith, Ellen Dean & Martin Lenz 162* (holotype: UC2030515!; isotypes: CAS!, DAV!, DUKE!, MO!, NY!, US!)

Description. Rhizomes short-creeping or ascending, usually buried in loose soil, 2–4 mm in diameter, sometime branching; stipes clustered, up to 10 fronds per 1 cm of rhizome length; rhizome scales (and those at stipe base) castaneous to dark brown, lustrous, concolorous, ovate to lanceolate, attenuate at tips, 1.5–5 × 0.3–0.6 mm, margins entire; fronds clustered, mostly (18–)30–60 cm long, arching, persisting (remaining green) through summer, fall, and into winter; older dead fronds remaining attached to rhizome behind new growth; stipes castaneous to atropurpureous, becoming blackish with age, sublustrous, sometimes slightly glaucous (especially proximally), terete, each with a single vascular bundle at bases, (10–)20–30 cm long, (0.6–)0.8–2.0 mm in diameter, ca. 1/2 the

frond length, glabrous except at very bases; laminae ovate to deltate, 2–3 times pinnate (depending on size), mostly (12–)20–35 × (6–)15–20 cm, broadest at or just above the bases, tapering gradually to apices, costae (pinna axes) ascending mostly 30–50 degrees from rachis, pinnae acroscopically branched, basal acroscopic pinnule longer, more dissected, and at a greater angle with respect to costa than basal basisopic branch (pinnae thus somewhat unequal-sided), laminae bluish green, often slightly glaucous; rachises castaneous to atropurpureous, glabrous, lustrous or slightly glaucous, terete to somewhat angled or obscurely sulcate adaxially (more so distally); pinnae of well developed laminae ca. 6–8 pinnate to bipinnate pairs below the 1-pinnate apical region (which is 3–5 cm long), decidedly alternate, stalked to ca. 2 cm (proximal pinnae); pinnules (ultimate segments) obovate, flabellate, or rhombic, sometimes semicircular, non-articulate except on very old laminae (stalks not breaking cleanly, not cupule-like at their apex), mostly 1–2 × 1–2 cm (to 2 × 3 cm in sterile segments of juvenile fronds), cuneate at bases ca. 90–135 degrees (more narrowly cuneate bases on distal segments), occasionally pinnulet bases truncate and the pinnules thus semicircular (especially proximal acroscopic pinnulet on well-developed pinnae), margins often cleft 1–4 mm, sterile pinnules generally more incised than the fertile, 1–3 clefts per pinnulet, sterile margins thickened, whitish, shallowly crenulate distally, color of stalks gradually diminishing at base of pinnules and passing slightly into pinnulet lamina; veins free, forking, in sterile laminae ending in small rounded crenulations (not in sharp teeth) of pinnulet margins, usually visible but only slightly raised, if at all, on both sides of laminae; indument lacking on both sides of laminae; idioblasts not apparent either abaxially or adaxially; sori 2–7 per pinnulet, confined to distal margins, sporangia borne on ± parallel veins on the strongly reflexed underside of the indusia (facing laminar tissue), mixed with sessile yellow-orange, cylindrical or clavate glands < 0.1 mm long; indusia mostly (1–)2–4 mm long, ca. 1 mm wide, entire or nearly so, oblong to slightly arcuate (not noticeably reniform), lacking hairs. $2n = 30$ II.

Distribution and ecology. *Adiantum shastense* is currently known only from an area of the Eastern Klamath range (Miles and Goudy 1997) surrounding Shasta Lake entirely within Shasta County, California. It is found in mesic hardwood-conifer forests, on the forest floor as well as on limestone and metasedimentary rock outcrops, including rocky road cuts, most often in shade and with northern or eastern exposures. It co-occurs with the local endemic Shasta snow wreath, *Neviusia cliffonii* Shevock, Ertter & D.W.Taylor. In some localities it can be the dominant understory plant (Fig. 1a). Associated species include *Pinus ponderosa* P.Lawson & C.Lawson, *Quercus chrysolepis* Liebm., *Acer macrophyllum* Pursh, and *Toxicodendron diversilobum* (Torr. & A.Gray) Greene. Collected from 1100–2740 ft (335–835 m) elevation.

Phenology. Sporulates mid to late spring and most likely throughout summer.

Etymology. It seems most appropriate to name this species *Adiantum shastense*, recognizing its restricted, currently known geographic localization to Shasta Co., California.

Suggested common name. Shasta maidenhair fern.

Conservation status. We recommend a California Rare Plant Rank of 4.3, a watch list for plants of limited distribution.



Figure 2. Holotype of *Adiantum shastense* Huiet & A.R.Sm. (Huiet et al. 162, UC)

Paratypes. U.S.A. California: Shasta Co.: 2.6 miles E of Nosoni Mountain on the west side of North Fork Squaw Creek, 2700 ft, 07 Apr 2009, *P.J. Alexander 994* (DUKE!, NMC, SP); Waters Gulch Trail ca. 05 mi N of Packers Bay Marina, 1200 ft, 27 Apr 1994, *Oswald & Ahart 6148* (CHSC, JEPS!); Bailey Cove Trail, W side of McCloud River arm of Shasta Lake, 1100 ft, 27 Apr 1994, *Oswald & Ahart 6121* (CHSC, JEPS!); Oak Run, 21 May 1894, *Baker & Nutting s.n.* (UC!); on limestone cliffs 0.5 mi E of Squaw Creek fire control station, 1750 ft, 19 Apr 1992, *Taylor 12599* (JEPS!); south side of Lake Shasta, Pit River Drainage along Fenders Ferry Rd, 1730 ft, 15 May 2014, *Huiet et al. 167* (DAV!, DUKE!, UC!); on arm of McCloud Reservoir across from boat ramp, ca. 8.5 air miles SSE of McCloud, 2740 ft, 27 May 2014, *Lenz & Nelson 5350* (DUKE!, UC!); along road to Deep Creek campground, ca. 5.2 air miles SE of Big Bend, 2395 ft, 27 May 2014, *Lenz & Nelson 5351* (DUKE!, UC!); along logging road on east side of Sacramento River across from Gibson, 2045 ft, 27 May 2014, *Lenz 5352* (DUKE!, UC!); McCandless Gulch ca. 5 miles E of Ingot, 1700 ft, 16 Sept 2014, *Taylor, Falscheer & Lindstrand 21512* (DAV!, UC!); Cedar Creek drainage, ca. 6 miles west of Round Mountain on Highway 299, 1450 ft, 6 Sept 2013, *Taylor 21418* (UC!); along Fender's Ferry Rd. ca. 6.5 road miles SE of McCloud Bridge, 1800 ft, 3 Jul 2014, *Alverson 2014-10* (OSC, UBC, WTC!); north side of Lake Shasta, McCloud River Arm, Bailey Cove Trail, 1135 ft, *Huiet et al. 156A* (DUKE! chromosome voucher).

Discussion

It was a surprise to discover that amongst the few herbarium collections of *Adiantum* from Shasta County, there was a previously unrecognized species. Before 2014, there were only 13 documented collections of *Adiantum* in the county (data from participants of the Consortium of California Herbaria, <http://ucjeps.berkeley.edu/consortium>). Amongst them were all the recognized taxa in California: *A. aleuticum*, *A. capillus-veneris*, and *A. jordanii*. It was while confirming the identity of a recent collection that we serendipitously stumbled upon the new species. DNA sequencing analysis revealed that this plant was neither *A. capillus-veneris* nor *A. jordanii*, but rather sister to *A. jordanii*. We confirmed that additional specimens collected near Shasta Lake gave the identical result (Huiet et al. unpublished). Subsequently, in spring 2014, we made collections from additional populations across a wider geographic range to confirm the earlier results and to examine material in the field.

Morphologically *Adiantum shastense* has rhizome scales that are essentially the same as in typical *A. jordanii*. However the pinnulets of *A. jordanii* are more fan-shaped and usually the sorus length is much longer so there are fewer sori per pinnulet than in *A. shastense*. No doubt because of the shorter sorus length and the more cuneate shape to the pinnulets, *A. shastense* has been identified by some as *A. capillus-veneris*, the only other species found in California with similar blade architecture. However, the sori of *A. shastense* have yellow farina among the sporangia, as does *A. jordanii*. Also, the rhi-

zome scales of *A. capillus-veneris* are golden or lighter brown than those of *A. shastense*. The most striking difference between *A. shastense* and *A. jordanii* is that *A. shastense* is not ephemeral. Green laminae are persistent throughout the summer, and the fronds appear to overwinter without dying back, perhaps until more than a year's persistence. After the fronds die back, they ring the base of the plant, surrounding the new growth.

The first collection of *Adiantum shastense* in Shasta County was over a century ago by Milo Baker and Frank Nutting, in 1894, and was identified by Baker as *A. jordanii*. No other collection was made of *A. shastense* until 1992 (Taylor 12599, UC) and that was identified as *A. capillus-veneris*. Subsequent collections were mostly identified as *A. capillus-veneris*. Thus far, the distribution of *A. shastense* appears to be limited to a region surrounding Shasta Lake and the rivers and watersheds that feed into it and their drainages. A survey of other specimens identified as *A. jordanii* and *A. capillus-veneris* from nearby areas (counties) did not reveal any additional collections of *A. shastense*. This includes a single collection of *A. capillus-veneris* from Siskiyou county (UC), collected in a cave at Lava Beds National Monument (Smith et al. 1993). We also have examined specimens of *A. jordanii* from Oregon and they too are correctly identified.

It appears that the Shasta maidenhair fern is another narrow endemic found in the area surrounding Shasta Lake. This region is host to a number of endemic plants and animals, most likely because of its unique geology, age and climate. These include the Shasta salamander, *Hydromantes shastae* Gorman & Camp, 1953 (Hammerson et al. 2004); the Shasta monkey flower, *Erythranthe taylori* Nesom (Nesom 2013); Shasta snow wreath, *Neviusia cliftonii* (Lindstrand and Nelson 2006); and the Shasta eupatory, *Ageratina shastensis* (D.W.Taylor & Stebbins) R.M.King & H.Rob. (Taylor and Stebbins 1993). Of these species, the Shasta maidenhair fern has one of the widest geographic ranges, perhaps due to its wind-borne spores. Currently we do not know if its range extends beyond the geologically unique Shasta Lake region into neighboring counties. Further field study may reveal more about this surprisingly new and unique California maidenhair fern. It currently is the only endemic species of *Adiantum* in the United States.

Key to species of *Adiantum* in California

- 1 Rhizomes stout, compact, short-creeping to suberect, usually 5–8 mm diam. (scales excluded); stipes mostly 1.5–3 mm diam. at bases; laminae palmate-pinnate (fan-shaped), proximal pinna pair 2–3-times basiscopically forked; pinnulets strongly inequilateral, 2–4 times longer than wide.... ***A. aleuticum***
- Rhizomes relatively narrow, short- to long-creeping (occasionally more compact in *A. shastense*), usually 1.5–3 mm diam (scales excluded); stipes mostly 0.5–1.5 mm diam. at bases; laminae 2–3-pinnate (not fan-shaped), proximal pinna pair 0–1 times basiscopically forked; pinnulets more or less equilateral (bilaterally symmetric), about as long as wide or sometimes to twice as long as wide in *A. capillus-veneris*.

- 2 Rhizome and stipe base scales golden brown or light brown; laminae usually 2-pinnate; pinnulets (especially sterile ultimate segments) cut or lobed often >1/4 or much more than (to 2/3) the way to base; dark color of stalks extending into base of ultimate segments; distal teeth of sterile segments usually >3 mm long, acute at tips; pinnulet margins at base diverging at 45–90°; sori (and false indusia) (2–)3–11 per pinnulet, generally < 5 mm long ***A. capillus-veneris***
- Rhizome and stipe base scales dark brown or dark purplish brown; laminae 2–3-pinnate, larger fronds with proximal pinnae usually having at least 1 or 2 pairs of pinnules divided (i.e., laminae 3-pinnate proximally); pinnulets (especially sterile ultimate segments) cut or lobed usually <1/4 of the way to base; dark color of stalks extending into base of ultimate segments or ending ± abruptly at base of ultimate segments; distal teeth of sterile segments 1–2(–3) mm long, rounded or acute at tips; pinnulet margins at base diverging at 90–180(–240)°; sori (and false indusia) 1–5 per pinnulet, some generally > 5 mm long.
- 3 Rhizomes short-to long-creeping, just below soil surface, stipe bases often > 5 mm apart; lamina tissue green; dark color of stalks ending ± abruptly at base of ultimate segments; ultimate segments often somewhat semi-lunate; mature fronds dying in late spring or early summer, completely dried and largely unseen in late summer, fall, and early winter; throughout California, but apparently rare in Shasta Co ***A. jordanii***
- Rhizomes short-creeping to suberect, often deeply buried, stipe bases < 5 mm apart; laminar tissue bluish green; dark color of stalks extending into base of ultimate segments; ultimate segments often somewhat rhomboidal; mature fronds persistent and evergreen through summer and into winter and following spring; Shasta Co., locally abundant ***A. shastense***

Note: a combination of characters must occasionally be used to separate *Adiantum capillus-veneris*, *A. jordanii*, and *A. shastense*, i.e., not all characters are reliable for all specimens seen. However, the species characters for separating these three species are reliable for 95% or more of specimens seen. For example, *Gross 2802* (UC), from Ventura Co., is undeniably *A. capillus-veneris* in rhizome characters, but blade characters resemble much more closely *A. jordanii*. Pinnulet characters (shape, distal margin) often vary, depending on size of fronds and extent of fertility. Rare, sterile hybrids showing intermediate morphology are known between *A. aleuticum* and *A. jordanii* (*A. ×tracyi* C.C.Hall ex W.H.Wagner), but no known hybrids are known between other species. In California, and probably elsewhere, the four species have rarely been found growing together. In Shasta Co., *A. aleuticum* and *A. shastense* have so far only once been found growing proximate to one another, but *A. jordanii*, does not co-occur with any of the other species, as far as we have observed.

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Two new species of *Hoya* R.Br. (Apocynaceae, Asclepiadoideae) from Borneo

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Abstract

Two new *Hoya* R.Br. species from Borneo are described and illustrated. The first, *Hoya ruthiae* Rodda was collected in Sabah on Bukit Baturong, a limestone outcrop. It is one of the few species in the genus to have clear exudate. It is compared with the morphologically related *Hoya uncinata* Teijsm. and Binn. The other, *Hoya bakoensis* Rodda, was collected in the kerangas forests of Bako National Park. It belongs to *Hoya* section *Acanthostemma* (Bl.) Kloppenb., a section with numerous members in the Philippines but under-represented in Borneo.

Keywords

Bako National Park, kerangas, limestone flora, Malaysia, Sabah, Sarawak, taxonomy

Introduction

Hoya R.Br. is a large and complex genus with more than 500 published species names (IPNI 2015). Kleijn and van Donkelaar (2001) estimated that these names might represent 200–300 species. However their estimate was very conservative. Since 2001 more than 200 new *Hoya* names have been published (IPNI 2015) and the species number estimate for the genus may therefore now lie in between 350 and 450, taking into account a large number of synonyms expected in a horticulturally significant genus. The genus is particularly diverse in the island of Borneo where Nutt (2001) listed

21 species while more recent research bring up the number to an estimated 60–70 species for Sabah alone (Lamb et al. 2014). In Brunei a preliminary checklist comprises 27 species including three undescribed taxa (Rodda 2014).

Numerous papers have been recently published documenting new *Hoya* species from Borneo (Green and Kloppenburg 2014; Rodda and Nyhuus 2009; Rodda and Simonsson 2010; 2011a; b; Rodda and Simonsson Juhonewe 2013a; b; Rodda et al. 2011; 2014a; b; Trần et al. 2011). More notably, Lamb et al. (2014) published eight new taxon names in the genus *Hoya* all described based on materials from Sabah originally collected sterile and brought into cultivation at Kipandi Park (Kampung Kipandi, Moyog, Sabah) where they bloomed and were identified as new taxa. An extensive introduction on the morphology and ecology of Bornean *Hoya* is also found in Lamb et al. (2014).

Two further new *Hoya* species from Borneo are here described. The first, collected by Ruth Kiew in Sabah, is also widely available in cultivation, and is here named *Hoya ruthiae* Rodda. The second was collected by the author in March 2015 during an expedition to Bako National Park (Sarawak, Malaysia) to which it is named after.

Species treatments

Hoya ruthiae Rodda, sp. nov.

urn:lsid:ipni.org:names:77148380-1

Figs 1, 2

Diagnostic characters. Similar to *Hoya uncinata* Teijsm. and Binn as both species have clear exudate, deeply lobed rotate corolla and corpusculum of the pollinarium almost as large as the pollinium. The flattened corolla is smaller (1.5–1.7 cm in diameter) with ovate lobes in *H. uncinata*, while the corolla of *H. ruthiae* is 1.8–2.2 cm in diameter with narrowly lanceolate lobes.

Type. Malaysia, Sabah, Lahad Datu, Bukit Baturong, on limestone, 7 July 2000, Kiew R RK5029 (SING, holotype; barcode SING0077484).

Description. Delicate lithophytic climber with clear exudate in all vegetative parts; all vegetative parts glabrous. Leafy stems cylindrical, slender, up to 4 mm in diameter, dark brown or grey, with membranaceous peeling bark; internodes 5–15 cm long. *Petioles* terete, fleshy, 5–15 × 1.5–3 mm in diameter, *lamina* lanceolate, fleshy, (5–)7–15 × 1.5–3 cm, apex acute-acuminate, base cuneate, light green above turning red in bright light with numerous grey spots, lighter green underneath; penninerved, secondary veins obscure. *Inflorescences* pseudo-umbelliform or globular, 3–4 cm in diameter, 4–20 flowered; *peduncles* persistent, extra-axillary, terete, 1–3 cm × 1.5–2.5 mm in diameter, glabrous; *pedicels* 10–15 mm × 0.5–0.8 mm in diameter, glabrous. *Buds* conical with a 5-ridged base, ca. 10 × 6 mm. *Calyx* lobes triangular, white-pink 1.3–1.5 × 0.7–1 mm, apex rounded, glabrous; basal *colleters* 1 in each sepal sinus, ovoid. *Corolla* rotate, deeply lobed, 1–1.5 cm in diameter, 1.8–2.2 cm when flattened, white tinged pink, thinly and minutely pubescent inside, outside glabrous, tube 1.5–2 mm long; *corolla lobes* narrowly



Figure 1. *Hoya ruthiae* photographed from Rodda M. MR606 (SING) prior to pressing **A** Flower, lateral view with two corolla lobes removed **B** Corolla, underneath **C** Corolla and corona, top view **D** Corona, underneath **E** Pedicel, calyx and ovaries **F** Pollinarium with twin pollinia. (Photographs by M. Rodda)

lanceolate with a triangular acuminate apex, 9–10 × 3–4 mm, laterally revolute, lobe tips recurved. *Gynostegium* stalked, corona column conical 1–1.2 × ca. 2 mm diam, glabrous; *corona* staminal, 2.5–3 mm high, 6–7 mm in diameter, fleshy, yellow with a purple



Figure 2. *Hoya ruthiae* photographed from Rodda M. MR606 (SING) prior to pressing **A** Inflorescence **D, E, F, G** Two leaves (**D, F** adaxial surface **E, G** abaxial surface). *Hoya uncinata* photographed from Rodda M MR607 (SING) prior to pressing **B** Flower, lateral view **C** Flower, top view. (Photographs by M. Rodda)

centre; *corona lobes* laterally compressed, ovate above, with revolute margins beneath, 2.8–3.2 mm × 1–1.2 mm, inner process erecto-patent, linear with an acute tip, as high as the anthers, outer process round. *Anthers* ovate, 650–750 × 300–400 µm, with apical round membranaceous appendage as high as the style-head apex. *Pollinia* oblong, with obliquely truncate apex and round base and evident pellucid margin, 550–630 × 150–200 µm; *caudicles* attached at the base of the retinaculum, elongate, ca. 150 µm long, *corpusculum* 600–650 × 250–300 µm; style-head 5-angled in cross section, with 5 spreading lobes alternating with the stamens; *style-head* apex columnar, 1–1.2 mm long, ca. 0.5 mm broad at the base, apex conical; *ovary* linear, ca. 2 mm long, each carpel ca. 0.5 mm wide at the base. *Fruits* and *seeds* unknown.

Etymology. This species is named after Ruth Kiew (1946–), tropical botanist based at the Forest Research Institute Malaysia and author of numerous publications on *Begonia* L. and Gesneriaceae, among others.

Distribution and ecology. *Hoya ruthiae* is only known from Bukit Baturong, Sabah, Malaysia, where it was found growing on limestone.

Conservation status. The distribution area, population size and possible threats to the habitat of *H. ruthiae* are not known, as it is only known from the type specimen and unlocalised cultivated material. It is therefore considered Data Deficient (DD) (IUCN 2014).

Notes. The most striking feature of *H. ruthiae* is its lack of coloured latex. Other species lacking coloured latex are the type species of the genus *Hoya carnosa* R.Br. and several morphologically similar taxa (Rodda and Simonsson Juhonewe 2012). All these have rotate corollas with thickly pubescent lobes within and rhomboid corona lobes with narrow inner and outer corona lobe processes. In Borneo only *Hoya monetteae* T. Green belongs to this group. *Hoya ruthiae*, as mentioned above, is morphologically very similar to *Hoya uncinata*, another non-laticiferous species known to occur in Java and Sumatra. Both species have deeply lobed rotate corollas, laterally compressed corona lobes and corpusculum of the pollinarium almost as large as the pollinium. *Hoya ruthiae* has larger flowers (1.8–2.2 cm in diameter when flattened vs. 1.5–1.7 cm) and the corolla lobes are narrowly lanceolate (vs. ovate in *H. uncinata*). The corona lobes of both species are ovate but in *H. ruthiae* the outer process is round while in *H. uncinata* it terminates in an incurved membranaceous apiculate appendage. Flowers of *H. uncinata* are illustrated in Fig. 2.

Additional specimens examined. Unlocalised (nursery origin), Cultivated in Thailand, Ratchaburi Prov., Ratchaburi, 23 March 2014, *Rodda M MR606* (SING).

***Hoya bakoensis* Rodda, sp. nov.**

urn:lsid:ipni.org:names:77148381-1

Figs 3–5

Diagnostic characters. Similar to *Hoya aeschynanthoides* Schltr. as both species have bilobed outer corona lobes, but differing in the size and colour of the flowers (3.5–4

mm in diameter, pink corolla, yellow and red corona lobes for *H. bakoensis*; ca. 5 mm in diameter and white for *H. aeschynanthoides*) and in the habit, that in *H. aeschynanthoides* is decumbent while *H. bakoensis* is a weak twining climber.

Type. Malaysia, Borneo, Sarawak, Bako National Park, along Tajor Trail, 20 March 2015, Rodda M MR1042b (SING, holotype; SAR, KEP, isotypes)

Description. Epiphytic climber with white exudate in all vegetative parts. *Stems* slender, weakly twining upward, internodes (1 mm–)2–7(–10) cm × 0.7–1.5(–2) mm, dull green, sparsely pubescent when young, scabrous; *adventitious root* sparsely produced along the stems and just under the nodes where they are paired. *Leaves* petiolate; petiole straight or recurved, 4–10 × 1–1.5 mm, dark green to maroon, sparsely pubescent; *lamina* ovate (lanceolate) (1.5–)2–4(–5) × 1–2.8 cm, base attenuate (acute), apex apiculate (cuspidate), dark green above, slightly pubescent on young leaves only, lighter green underneath with occasionally a slightly darker midrib and edge, glabrous, margin occasionally ciliate; penninerved, secondary veins obscure; *colleters* one at each lamina base, triangular to ovate 0.1–0.3 × 0.3–0.5 mm. *Inflorescence* pseudo-umbelliform, slightly convex, 10–15 flowered; *peduncle* 4–6 cm × 1–1.5 mm in diameter, dull green to brown, pubescent; rachis indeterminate (–7) × ca. 2 mm in diameter. *Pedicel* 3–7 × 0.7–0.9 mm in diameter, pale green with pink spots, papillose. *Calyx* lobes triangular, 0.7–1 × 0.5–0.8 mm, apex acute or round, light green with pink edge, sparsely ciliate; *basal colleter* one in each calyx lobe sinus, ovate, 150–200 × 80–100 µm. *Corolla* revolute, 3.5–4 mm in diameter, ca. 6 mm when flattened; *corolla lobes* basally fused, tube 1.2–1.5 mm long, lobes triangular, 2–3 × 2.4–2.7 mm, pink, pubescent inside, outside glabrous. *Corona* staminal, 2.8–3 mm in diameter, 0.9–1.1 mm high; *corona lobes* oblong, 1.2–1.4 × 0.7–0.8 mm, convex above, underneath sulcate with inrolled margins, outer process apex bifid, light yellow, inner process elongate, red, with a yellow round tip. *Anthers* broadly triangular, 400–450 × 550–650 µm, with apical triangular membranaceous appendage. *Pollinia* clavate, 200–250 × 90–110 µm, narrowing towards the base, apex obliquely truncate, with evident pellucid margin; *corpusculum* oblong, constricted in the middle, 80–100 × 50–60 µm; *caudicle* broad, spatulate, hyaline, 110–130 × 30–45 µm at the widest. *Style-head* 5 angled in cross section, with 5 lobes alternating with the stamens, style-head apex round, 200–300 µm long, ca. 0.5 mm broad at the base; *ovary* ovate with a narrow tip, 0.8–1 mm, each carpel ca. 0.3 mm wide at the base, light green. *Fruit* (unripe) a single linear follicle, 10 cm × 2 mm (widest), *seed* (unripe) narrowly lanceolate, 3–4 mm long, winged, long comose.

Etymology. The species is named after the collection locality of the holotype, Bako National Park (Sarawak, Malaysia).

Distribution and ecology. *Hoya bakoensis* is only known from Bako National Park, where it is common along Tajor Trail in moist, shady kerangas heath forest near a stream. The species is strictly epiphytic and it was found mostly germinating from the opening of small ant nests located inside hollow tree trunks (Fig. 4). The plants observed were forming small clumps of weakly climbing stems near the germinating point or more rarely were climbing towards the tree canopy potentially in response to low light.

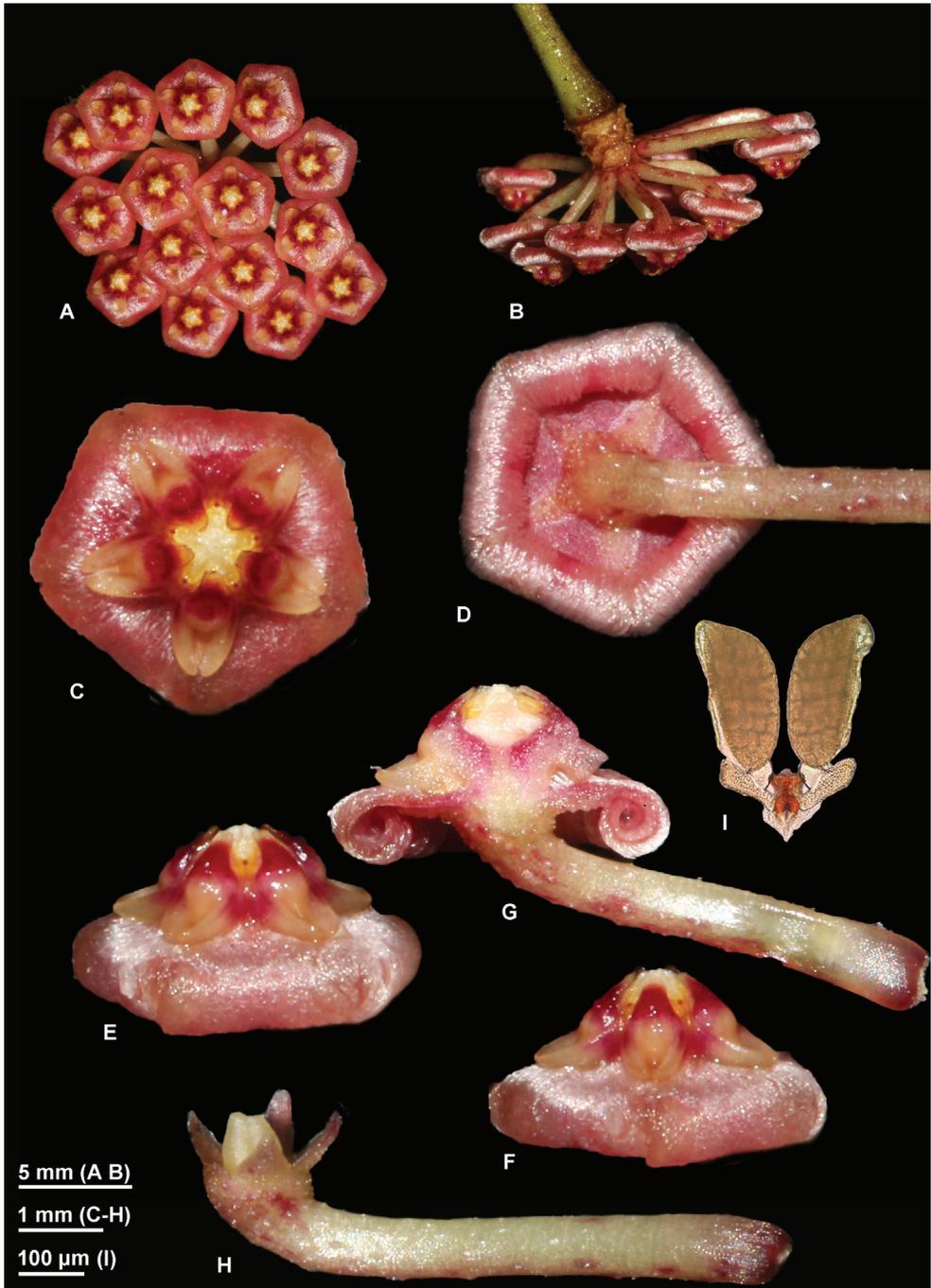


Figure 3. *Hoya bakoensis* photographed in the field from the type plant *Rodda M MR1042b* (SING) prior to pressing. **A** inflorescence, frontal view **B** Inflorescence, side view **C** A single flower, front view **D** Revolute margins of the corolla lobes, calyx and pedicel **E, F** Corolla, side view **G** Flower, longitudinal section **H** Pedicel, calyx and ovary **I** Pollinarium with twin pollinia. (Photographs by M. Rodda)



Figure 4. *Hoya bakoensis* in situ in Bako National Park (Sarawak, Malaysia) **A** Habitat, kerangas heath forest **B** Mature plant rooted inside the trunk of the host plant where an ant nest is located **C** Seedlings germinating from the opening of an ant nest in a hollow trunk.



Figure 5. *Hoya bakoensis* leaves photographed in the field from *Rodda M MR1042b* (**A, B, E, F**) and *Rodda M MR1042a* (**C, D**) (SING) prior to pressing. **A, C, E** Adaxial side **B, D, F** Abaxial side.

Conservation status. *Hoya bakoensis* is locally common and well protected inside Bako National Park. Its conservation status is therefore Least Concern (LC) (IUCN 2014).

Notes. *Hoya bakoensis* is one of the 11 Bornean *Hoya* species in *Hoya* section *Acanthostemma* (Bl.) Kloppenb. *Acanthostemma* species are characterised by revolute corolla lobes, bilobed outer corona lobes and pollinaria with broad, spatulate caudicles. The other Bornean species in *Acanthostemma* are *H. aeschynanthoides*, *Hoya acicularis*, T. Green, *Hoya beccarii* Rodda & Simonsson, *Hoya kloppenburgii* T. Green, *Hoya minutiflora* Rodda and Simonsson, *Hoya pubera* Bl., *Hoya revoluta* Wight ex Hook.f., *Hoya rundumensis* (T. Green) Rodda and Simonsson, *Hoya sigillatis* T. Green and *Hoya waymaniae* Kloppenb.

Most of these species can be easily separated from *H. bakoensis* because their flowers are larger (>5 mm in diameter) or their inflorescence is markedly concave (in *H. beccarii* and *H. revoluta*). As mentioned in the diagnosis *H. aeschynanthoides* has white, only slightly larger flowers than *H. bakoensis* (ca. 5 vs. 3.5–4 mm in diameter). Additionally the bilobed outer lobes of *H. aeschynanthoides* appear to be less pronounced than those of *H. bakoensis*, but this observation is based solely on the examination of the drawing attached to the type of *H. aeschynanthoides* as only small buds are present on the specimen while no other specimens have been found at present. The flowers of *H. pubera* are also comparable in size with those of *H. bakoensis*, but they are yellow-orange, the corolla lobes are only apically revolute and the corona is more markedly

raised in the centre. Lastly, *H. minutiflora* has the smallest flowers among all Bornean *Acanthostemma* (2.6–2.8 mm in diameter).

Additional specimens examined. Malaysia, Borneo, Sarawak, Bako National Park, along Tajor Trail, 20 March 2015, *Rodda M MR1042a* (KEP, SAR, SING)

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