RESEARCH ARTICLE

Synopsis of *Plazia* Ruiz & Pav. (Onoserideae, Asteraceae), including a new species from northern Peru

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Abstract

A synopsis of *Plazia* Ruiz & Pav. (Onoserideae, Asteraceae) is presented, including the description of a new species, *Plazia robinsonii* M.O.Dillon & Sagást., from a locality c. 20 km west of Huamachuco, Department of La Libertad in northern Peru. It most closely resembles *P. conferta* Ruiz & Pav., a narrow endemic from central Peru some 450 km to the south; however, the latter species has larger leaves and smaller capitula. *Plazia* is a small genus of four species confined to the Andean Cordillera of Peru, Bolivia, Chile, and Argentina. A distribution map of the four species, an illustration of the new species, a photograph of the holotype, and a key to species are provided.

Resumen

Se presenta una sinopsis del género *Plazia* Ruiz & Pav. (Onoserideae, Asteraceae), incluyendo la descripción de una nueva specie, *Plazia robinsonii* M.O.Dillon & Sagást., proveniente de una localidad c. 20 km al oeste de Huamachuco, Departamento de La Libertad, norte de Perú. Esta especie es similar a *P. conferta* Ruiz & Pav., un endemismo del centro de Perú, unos 450 km hacia el sur; sin emabrgo, esta última especie tiene hojas más grandes y capítulos más pequeños. *Plazia* es un género compuesto por cuatro especies restringidas a la Cordillera de los Andes de Perú, Bolivia, Chile y Argentina. Se inlcuye un mapa de distribución de las cuatro especies, una ilustración de la nueva especie, una fotografía del holotipo y una clave para las especies.

Keywords

Introduction

Plazia Ruiz & Pav. (Mutisioideae, Asteraceae) is a distinctive genus confined to the Andean Cordillera of Peru, Bolivia, Chile, and Argentina. It is easily recognized by its suffrutescent and decidedly woody habit with stems to a meter or more. The sessile leaves are tightly clustered and confined to the terminal 10–20 cm portions of the branch apices, the radiate capitula have ray florets with whitish to pink corollas and dark purple anthers long-exerted from the disc whitish florets.

Phylogenetic studies have shown that the genus *Plazia* belongs to the tribe Onoserideae, along with the genera *Aphyllocladus* Wedd., *Gypothamnium* Phil., *Lycoseris* Cass., *Onoseris* Willd., and *Urmenetea* Phil. (Panero and Funk 2008, Katinas et al. 2008, Luebert et al. 2009, Panero 2009). These studies also show that the genus *Plazia* forms a clade within the Onoserideae together with *Aphyllocladus* and *Gypothamnium*. Recently, Panero and Freire (2013) suggested the inclusion of the genus *Paquirea* Panero and S.E. Freire in the tribe Onoserideae, associating it with *Plazia*, but provided no phylogenetic evidence to support that.

The distribution of these genera involves the Atacama Desert, the high Andes of central and northern Chile, southern Peru, northwestern Argentina and western Bolivia, the Chaco and Monte Regions, as well as the inter-Andean valleys of central and northern Peru (Cabrera 1951, 1977, Ferreyra 1980, 1995, Moreira-Muñoz and Muñoz-Schick 2007, Luebert et al. 2009). *Plazia* is restricted to the high Andes between northern Peru and central Chile and Argentina (Fig. 1).

Taxonomy

***Plazia* Ruiz & Pav., Fl. Peruv. Prodr.: 92. 1794.**
http://species-id.net/wiki/Plazia

Aglaodendron J.Rémy, Ann. Sci. Nat., ser. 3, 12: 175. 1849. Type: *Aglaodendron cheiranthifolium* J.Rémy = *Plazia cheiranthifolia* (J.Rémy) Wedd.
Harthamnus H.Rob., Phytologia 45(6): 451. 1980. Type: *Harthamnus boliviensis* H. Rob. = *Plazia daphnoides* Wedd.

Type. *Plazia conferta* Ruiz & Pav.

Description. Shrubs 1–2 m tall, the branches erect to ascending; stems lacking spines. Leaves simple, sessile, in whorls at branch tips; blades lanceolate to oblanceolate, glabrous to glandular, usually appressed, the margins entire. Capitulescences of solitary, terminal heads, sessile. Capitula heterogamous, radiate or more rarely homogamous, discoid; involucres cylindrical to campanulate; receptacles plane, glabrous; phyllaries 5–7-seriate, lanceolate; ray florets 5–25, the corollas ligulate-bilabiate, the outer lip 4-nerved, tridentate, the inner lip bifid; styles cylindric, glabrous, bifid, the branches short, inconspicuous; disc florets 7–40, the corollas tubular, actinomorphic, glabrous, the limb deeply

Figure 1. Distribution map of the currently recognized species of *Plazia*. The shaded area indicates high-elevation areas of the Andes above 3000 m. Locality data were obtained from Cabrera (1951), Ferreyra (1995), Missouri Botanical Garden (http://www.tropicos.org/), Instituto de Botánica Darwinion (through http://www.gbif.org/) and the herbaria ASU, B, F, HUT, P, SGO, US.

5-lobed, the lobes greater than 1/3 the length of the corolla, coiled; anthers linear, the terminal appendages lanceolate, fused into a column, truncate, the bases caudate; styles claviform, the branches short, rounded. Achenes glabrous or glandular-pubescent; pappus of scabrid bristles, isomorphic, yellowish. Chromosome number: unknown.

Distribution. All species are confined to the Andean Cordillera and associated inter-Andean valleys (Fig. 1). Two species are confinded to Peru; both are rare and only known from a few collection localities. Another species is restricted to the Andes of central Chile. *Plazia daphanoides* Wedd. is the only wideranging species, being recorded from southern Peru and adjacent Argentina, Bolivia and Chile, usually in high-elevation, dry sites (Cabrera 1978, Ferreyra 1980, 1995).

Discussion. The genus *Plazia* was described by Ruiz López and Pavón (1794) and they subsequently published its first species, *P. conferta* Ruiz & Pav. (1798). All efforts at locating material corresponding to their type collection from Peru have not been successful (Cabrera 1960).

Weddell (1855) provided an emended generic description for *Plazia* and he recognized three species: *Plazia conferta* Ruiz & Pav., *P. cheiranthifolia* (J. Remy) Wedd., and *P. daphnoides* Wedd. Reiche (1905) picked up the implied transfers by Hoffmann (1890–1894) and treated *Plazia* in Chile as having three species: *P. cheiranthifolia*, *P. pinifolia* (Phil.) O.Hoffm. [= *Gypothamnium pinifolium* Phil.], and *P. virgata* (Phil.) O.Hoffmann [=*Aphyllocladus denticulatus* (J.Rémy ex Gay) Cabrera]. Recent floristic treatments have accepted *Plazia* as distinct from *Aphyllocladus* and *Gypothamnium* (e.g., Cabrera 1978, Ferreyra 1995, Hind 2009, Marticorena and Quezada 1985, Zuloaga and Morrone 1999). The addition of the northern Peruvian species described here brings the total number of recognized species to four.

Key to species of *Plazia*

1	Leaves oblong or oblong-spathulate, 8–18 mm long, 2–3.5 mm wide; capitula with 5–8(–10) ray florets, (7–)10–11(–12) disc florets; involucres cylindrical (Argentina, Bolivia, Chile, Peru) ....***Plazia daphnoides* Wedd.**
–	Leaves elliptic to oblanceolate or oblong, 22–42 mm long, 3–6 mm wide; capitula lacking obvious ray florets or more commonly with 15–25 ray florets, (9–)20–25(–40) disc florets; involucres campanulate **2**
2	Leaves oblong, 28–30 mm long, 7.5–8 mm; corollas more or less isomorphic, obvious ligules lacking (Central Chile) .... ***Plazia cheiranthifolia* (J.Rémy) Wedd.**
–	Leaves oblanceolate, 10–25 mm long, 1–3 mm wide; corollas dimorphic, outer florets with ligules obvious (Peru) **3**
3	Involucre 25–30 mm in diameter; ray florets 15–20, disc florets c. 40 ....***Plazia robinsonii* M.O.Dillon & Sagást.**
–	Involucre 12–16 mm in diameter; ray florets 18–20, disc florets 10–20......... ....***Plazia conferta* Ruiz & Pav.**

1. *Plazia cheiranthifolia* (J.Rémy) Wedd., **Chlor. Andina 1: 12. 1855.**
http://species-id.net/wiki/Plazia_cheiranthifolia

Aglaeodendron cheiranthifolium J.Rémy, Ann. Sci. Nat., ser. 3, 12: 175. 1849.

Type. CHILE, Región IV, Coquimbo, *C. Gay s.n.* (holotype: P00703596!; isotype: P00703598!).

Description. Shrubs to 1.5 m tall; stems very resinous. Leaves oblong, 28–30 mm long, 7.5–8 mm wide, sessile, apically acute, 3–5-nerved, entire, thickened, glabrous. Capitulescences of solitary terminal heads. Capitula solitary, sessile; involucres campanulate, 25–30 mm long, c. 25 mm wide; phyllaries 3–4-seriate; inner lanceolate, 25–28 mm long, c. 3 mm wide; florets numerous, isomorphic, the outer with corollas subligulate. c. 10, lobes strongly coilled, inner florets 20–25; all corollas lobes c. 7 mm long, c. 4 mm wide, the tube c. 13 mm long; pappus to 16 mm long. Achenes 6–7-ribbed, glabrous, linear oblong, c. 7.5 mm long, c. 1.2 mm wide.

Distribution. While it was once considered extinct, this species was recently rediscovered in the Precordillera of Ovalle (Faúndez and Saldivia 2008) and the description provided here is largely derived from the specimens and data in that publication. Since this species appears to be restricted to an area of no more than 2 km^2, it would be designated as "critically endangered" (IUCN 2001).

Discussion. *Plazia cheiranthifolia* is a rare shruby species apparently confined to the central Chilean region near Coquimbo. It has the longest leaves of any species of *Plazia* and large capitula with broadly campanulate involucres. Rémy described as his *Aglaodendron chieranthifolium* as homogamous, all with bilabiate corollas with lobes of varying lengths. From the photo in Faúndez and Saldivia (2008), it appears there are perhaps nine subligulate corollas.

Aglaeodendron cheiranthifolium J.Rémy was based upon a collection by Claudo Gay deposited in Paris (P00703596). The isotype, also in Paris (P00703598), contains a small piece of paper c. 1 cm square, with the number "176" afixed to the lower left hand corner. This number corresponds to the page number of the collection citation in Rémy (1849). It should not be considered as an accession number for Claudo Gay as has been published in internet sources.

Specimens examined. CHILE. Region IV. Prov. Limarí. Bocatoma Central Los Molles, Río Molles, 2590 m, 18 Jan 2007, *P. Saldivia et al. s.n.* (SGO154422!).

2. *Plazia conferta* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 187. 1798.
http://species-id.net/wiki/Plazia_conferta

Type. PERU. Junín: Acobamba [near Tarma], *H. Ruiz López & J.A. Pavón s.n.* (holotype: MA, n.v.).

Description. Shrubs, branched, branches glabrous. Leaves oblanceolate, 22–42 mm long, 5–6 mm wide, glabrous, sessile, acute-mucronate, margin entire. Capitula with involucres 18–22 mm high, 12–16 mm wide; phyllaries 6–7-seriate, glabrous, lanceolate, the inner 22–25 mm long, 3–3.5 mm wide, acute, the outer gradually smaller; ray florets 18–20, the corollas 26–28 mm long, the tube 10–11 mm long, glabrous, the outer lip 14–15 mm long, 5–6 mm wide, 4-nerved, tridentate, the inner lip bipartite; disc florets 40–42, the corollas 15–18 mm long, the tube glabrous, the lobes 9–10 mm long, 1–1.2 mm wide, coiled; anthers 6–7 mm long. Achenes [ray] 4–5 mm long, 1.5–1.6 mm wide, glabrous; pappus c. 12 mm long; [disc] 4.5–5 mm long, 1–1.2 mm wide; pappus c. 14 mm long.

Distribution. Endemic to an inter-Andean valley in central Peru from near Tarma; c. 3000 m. Given that this species appears confined to a single locality and of a few individuals, it would be considered "critically endangered" (IUCN 2001).

Discussion. *Plazia conferta* is a rare species, and type material has not been located. No new material had been collected since Ruiz López and Pavón's original gathering until a second collection was made by Felix Woytkowski at the type locality nearly 180 years after its original description. Cabrera (1960) was unsuccessful in locating Ruiz López and Pavón's type material in the major European herbaria, including Madrid. We made inquiries to the Real Jardín Botánico in Madrid, but no collection of *Plazia* has surfaced as yet. Ferreyra (1980) cited duplicates of *Woytkowski 52* as occurring at MO and F, but after exhaustive searching, no duplicate collections were located, and subsequently the duplicates were not cited in Ferreyra's Flora of Peru treatment (1995). Further, during this study, we were unsuccessful in our efforts to examine the Woytkowski collection at USM, and the description provided by Ferreyra (1995) was used to quantify the differences between that species and the new one described here.

There is an error in the citation of the generic description in Florae Peruvianae Chilensis Prodromus (1794), where page "104" is cited in Systema Vegetabilium Florae Peruvianae et Chilensis (1798) incorrectly, and the generic description is actually on page 92.

3. *Plazia daphnoides* Wedd., Chlor. Andina 1: 13. 1855.
http://species-id.net/wiki/Plazia_daphnoides

Plazia daphnoides α *villosa* Wedd., Chlor. Andina 1: 13. 1855.
Type. CHILE. XV Region, Prov. Parinacota: Cordillera de Tacora, entre Tacna et La Paz, *H. Weddell s.n.* (lectotype desiganted by Ferreyra 1995, pg. 83: P, P00703594!; isolectotype: ex P, F971331!).
Plazia daphnoides ß *glabrescens* Wedd., Chlor. Andina 1: 13. 1855.
Type. BOLIVIA. Tomas Frias: Potosi, *A. d'Oribigny 1386* (lectotype, chosen here: P00793599!; isolectotypes: BR0000552180!, GH, P00703595!).
Harthamnus boliviensis H. Rob., Phytologia 45(6): 451. 1980.

Type. BOLIVIA. Cochabamba: S E of Cochabamba, vicinity of Rodeo, 3500 m, 5 Mar 1979, *J. A. Hart 1739* (holotype: US2854177!; isotype: A, n.v.; photograph ex US, FM neg. 1944785!).

Description. Shrubs to 2 m, resinous. Leaves sessile; blades oblanceolate to lanceolate, 10–18(–20) mm long, (2–)3–4 mm wide, apically acute, basally cuneate, glandular-pubescent, the margins ciliate. Capitula with cylindrical involucres (15–)18–20 mm high, 7–8(–14) mm wide; phyllaries 3–6-seriate, lanceolate, the inner 20–21 mm long, 2.4–3 mm wide, the outer smaller; ray florets (5–)7–8(–10), the corollas 20–21 mm long, the tube 11–11.5 mm long, the outer lip 9–9.5 mm long, 2–3 mm wide, tridentate, the inner lip bipartite, 6–7 mm long; disc florets (7–)10–11(–12), the corollas white, 13–14 mm long, the tube 10–11 mm long, the lobes 7–8 mm long; anthers 5–6 mm long. Achenes [ray] 4.5–5 mm long, 1.2–1.4 mm wide, glandular; pappus c. 13 mm long; [disc] 5–5.5 mm long, 1 mm wide, glandular; pappus c. 12.5 mm long.

Distribution. In *Plazia, P. daphnoides* displays the widest distribution with collections from the Andean Cordillera of southern Peru, Bolivia, Chile, and Argentina (3000–4000 m). While locally it may come while locally may come under stress from habitat reduction, it would be considered as of "least concern" (IUCN 2001).

Discussion. This species is distinctive with the narrowest capitula with the fewest ray and disc florets within the genus. Ferreyra (1995) lists the type specimen as collected by H. Weddell near the locality of Tacora, which is now in northern Chile.

Weddell (1855) failed to describe a nominative variety (p. 13); however, the manner in which he presented the material examined in his studies suggests that his first variety represented his nominative variety [α *villosa,* foliis utrinque villosis]. Examination of a large suite of collections has failed to find consistant morphological variation combined with any geographic pattern to support recognition of varieties in this taxon.

Robinson's (1980) new genus and species, *Harthamnus boliviensis*, was discovered by him to be a synonym of *Plazia daphnoides* shortly after its publication.

Specimens examined. ARGENTINA. Jujuy: Dept. Humahusca, Mina Aguilar, Espinosa del Diablo, 3800 m, 12 Jan 1968, *A.L. Cabrera et al. 18985* (LP, n.v.; SI014474!). Dept. Tumbaya, El Angosto de San José del Chañi, 3550 m, 26 Feb 1972, *A.L. Cabrera, J. Frangi, A.M. de Frangi, R. Kiesling & E.M. Zardini 22463* (LP, n.v.; P04318222!). Salta: Dept. Poma, Colres, 31 Jan 1944, *A. L. Cabrera 8331* (LP, n.v.; F1549306!, P02405527!).

BOLIVIA. Cochabamba: Sivingani, 11,000 ft, 24 Mar 1950, *W.M.A. Brooke 6219* (F1547725!). Tarija: Cercado, Tarija, 3900 m, 20 Feb 1904, *K. Fiebrig 3101* (F520491!).

CHILE. Region XV. Prov. Parinacota. Putre, 3500 m, 29 Dec 1995, *L. Landrum & S. Landrum 8883* (ASU0061610!); Quebrada Murmuntani, 3800 m, 13 May 2008, *M.A. Trivelli s.n.* (SGO156326!); Cordillera de Chapiquiña, 3600 m, 7 Mar 1927, *C. Troll 3235* (B!).

PERU. Ayacucho, 83 km W of Puquio, 76 km E of Nazca, 3430 m, 22 Jun 1978, A. *Gentry, M. Dillon, P. Berry, & J. Aronson 23273* (F1918361!).

4. *Plazia robinsonii* M.O. Dillon & Sagást., sp. nov.

urn:lsid:ipni.org:names:77135762-1
http://species-id.net/wiki/Plazia_robinsonii
Figs 2, 3

Type. PERU. La Libertad: Prov. Huamachuco, Pallar – Huaguil, carretera a Tayabamba, 3000 m, 23 Jun 1974, *A. López M. & A. Sagástegui A. 8123* (holotype: HUT12930!, isotypes: F1863606!, US3266111!).

Diagnosis. Plaziae confertae affinis, a qua foliis minoribus, capitulis majoribus et radiis 15–20 differt.

Description. Shrubs to 1 m, the branches erect; stems lacking spines. Leaves simple, sessile, in whorls at branch tips; blades oblanceolate, 10–25 mm long, 1–3 mm wide, uninerved, adaxial and abaxial surfaces glabrous; margins entire. Capitulescences of solitary, terminal heads, sessile. Capitula heterogamous, radiate; involucres broadly campanulate, c. 25 mm wide, 30 mm in diameter; receptacles plane, glabrous; phyllaries 4–5-seriate, the outer ovate, 8–12 mm long, 4–6 mm wide, apically acuminate, the inner oblong 20–25 mm long, 4–5 mm wide, apically acute, ciliolate; ray florets 15–20, the corollas ligulate-bilabiate, whitish, the tube 4–5 mm long, the outer lip 4-nerved, 8–12 mm long, tridentate, the inner lip bifid; styles cylindric, glabrous, bifid, the branches short, inconspicuous; disc florets whitish, c. 40, the corollas tubular, actinomorphic, glabrous, the limb deeply 5-lobed, the lobes 5–8 mm long, c. 1/2 the length of the corolla, coiled; anthers linear, the terminal appendages lanceolate, fused into a column, truncate, the bases caudate; styles claviform, the branches short, rounded. Achenes [ray and disc] glabrous, 5-ribbed, 4–5 mm long; pappus of scabrid bristles, c. 15 mm long, isomorphic, pale yellow.

Distribution and conservation. Known only from the type locality in an inter-Andean valley at around 3000 m (7°47.22'S, 77°52.27'W). The entire area surrounding Huamachuco and the road east to Tayabamba has been intensely cultivated for many years and is now highly disturbed by human pressure with expanding cultivation. Only fragmented small pockets of original habitats remain, usually in steeper quebradas. This species has not been recollected for 40 years and should be considered "critically endangered" (IUCN 2001).

Discussion. The duplicates of the type collection of this new species were originally distributed under the generic name *Diplostephium* Kunth (1818), a member of the tribe Astereae. The overall morphology of the material does superficially resemble some members of *Diplostephium*, however, the bilabiate corollas, truncate style branches, and anther tails are typical for the Mutisieae not the Astereae. The new species was uncovered after the Flora of Peru treatment (Ferreyra 1995) was published and set aside for investigation. Only recently was the material encountered during routine filing, having been misplaced for nearly two decades.

The type locality is approximately 450 km north of its nearest congener, *Plazia conferta,* from near Tarma. Although the region where the original collections were made has been visited by numerous botanists, to our knowledge this species has not been recollected since 1974 when it was encountered by Abundio Sagástegui Alva and
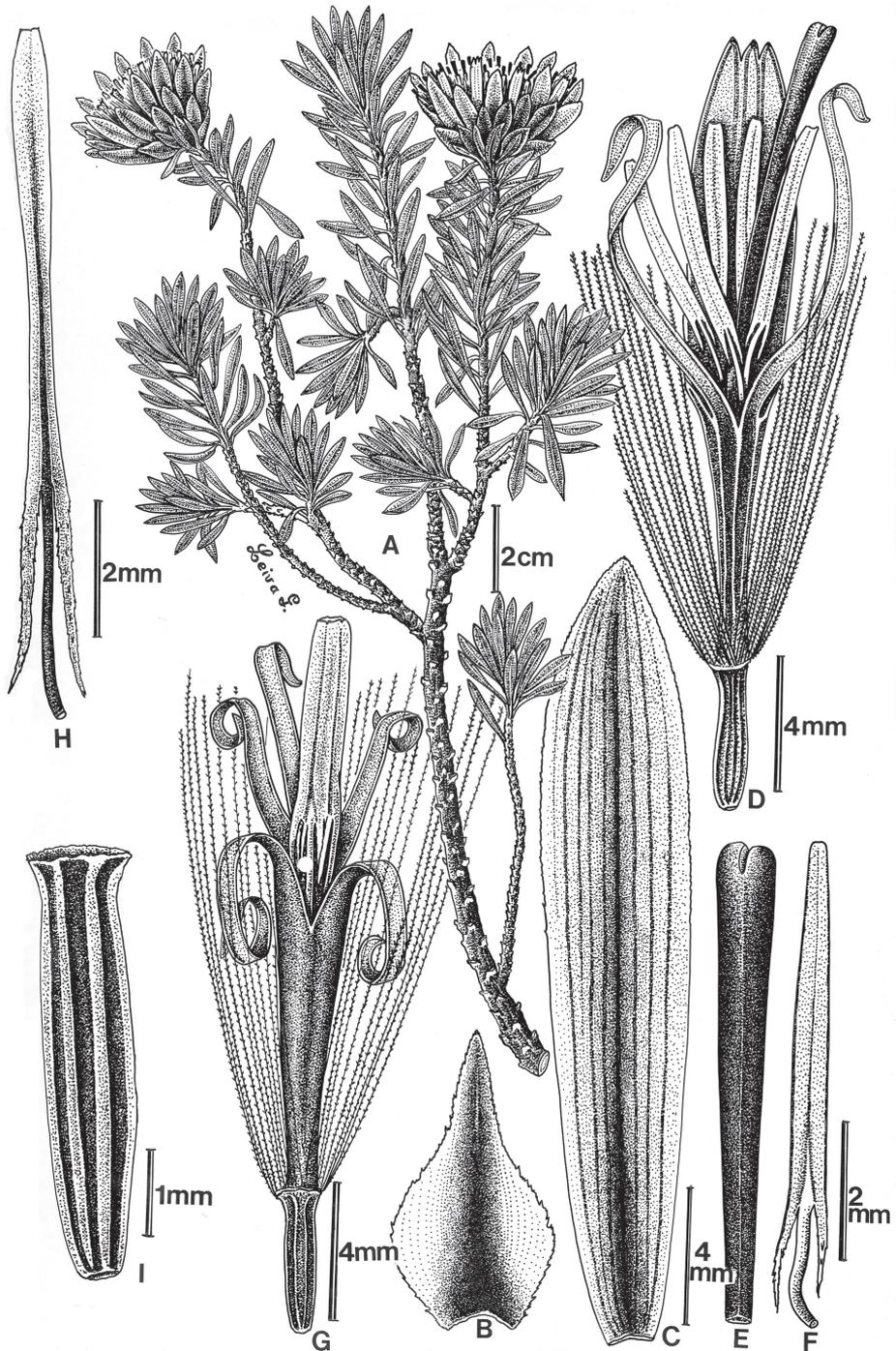
Figure 2. *Plazia robinsonii* M.O. Dillon & Sagást. (drawn from *A. López M. & A. Sagástegui A. 8123*). **A** Flowering branch **B** External phyllary **C** Internal phyllary **D** Ligulate floret **E** Terminal portion of the style of ligulate florets **F** Stamen from ligulate floret **G** Disc floret **H** Stamen from disc floret **I** Achene.

Figure 3. *Plazia robinsonii* M.O.Dillon & Sagást. Photograph of the holotype collection of *A. López M. & A. Sagástegui A. 8123* (HUT).

Arnaldo López Miranda. Casual efforts to find the plant again have not met with success. Given that the plant is quite showy and distinctive, it should not go undetected for long if it is indeed extant.

Etymology. This species honors Dr Harold Robinson, Senior Research Curator at the National Herbarium, Smithsonian Institution. He suggested with his annotation of the US sheet, designated as an isotype, that this taxon was perhaps a new species of *Plazia*, and not an unusual *Diplostephium*, as had been suggested on the original label.

Excluded names in *Plazia*

Plazia acaciifolia J.Koster = *Hyalis lancifolia* Baker
Plazia argentea (D.Don) Kuntze = *Hyalis argentea* D. Don ex Hook. & Arn.
Plazia decussata Hieron. (unpubl. herbarium name) = *Aphyllocladus decussata* Hieron.
Plazia ephedroides Hieron. (unpubl. herbarium name) = *Aphyllocladus ephedroides* Cabrera
Plazia lorentzii Hieron. = *Hyalis lancifolia* Baker
Plazia pinnifolia (Phil.) O.Hoffm. = *Gypothamnia pinnifolium* Phil.
Plazia spartioides (Wedd.) Kunth = *Aphyllocladus spartioides* Wedd.
Plazia virgata (Phil.) O.Hoffm. = *Aphyllocladus denticulatus* (J.Rémy ex Gay) Cabrera

Acknowledgements

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SHORT COMMUNICATION

The correct name for a subspecies of *Oenothera fruticosa* L. (Onagraceae)

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Abstract

In 1978 when Straley adopted the name *Oenothera fruticosa* L. subsp. *glauca* (Michx.) Straley for one of the two recognized subspecies of *O. fruticosa* it was the correct name for this taxon; however, since that time the botanical code has changed so that now an autonym is treated as having priority over the name or names of the same date and rank that established it. This change means that since 1981 *O. fruticosa* subsp. *glauca* was no longer the correct name. The appropriate combination for it is made here as *O. fruticosa* L. subsp. *tetragona* (Roth) W.L. Wagner. Original material for the basionym, *O. tetragona*, is no longer extant so a neotype is designated.

Keywords

Oenothera fruticosa, *O. tetragona*, *O. glauca*, nomenclature

Introduction

The superfluous nature of the combination *Oenothera fruticosa* subsp. *glauca* (Michx.) Straley (1978) was brought to my attention by John Wiersema so that the nomenclature could be corrected in advance of the forthcoming treatment of *Oenothera* in the *Flora of North America*.

In a revision of *Oenothera* sect. *Kneiffia* (Straley 1978) a common eastern North American species widely cultivated in gardens, *O. fruticosa*, was broadly delimited to include in synonymy a number of names previously recognized as distinct species.

Oenothera fruticosa was subdivided into two widespread subspecies with subsp. *fruticosa* occurring at lower elevations and having a more southerly geographic distribution and subsp. *glauca* occurring in more northerly areas and at higher elevations. In 1978 Straley made the new combination *O. fruticosa* subsp. *glauca* for the more northerly subspecies, based on *O. glauca* Michx. and including among its synonyms *O. tetragona* subsp. *glauca* (Roth) Munz and *O. tetragona* Roth. In 1978 Straley's new combination was the correct name for the taxon; however, since that time the botanical code of nomenclature has changed so that an autonym is treated as having priority over the name or names of the same date and rank that established it. This change means that since 1981, when this rule was added (Greuter 1981: 910, note 7), *O. fruticosa* subsp. *glauca* was no longer the correct name for this taxon.

This rule is now Art. 11.6 of the current code of nomenclature (McNeill et al. 2012), and it dictates that the autonym, *O. tetragona* subsp. *tetragona*, has priority over the name that created it, *O. tetragona* subsp. *glauca*. Since the type of *O. tetragona*, which is necessarily also the type of *O. tetragona* subsp. *tetragona* (Art. 7.6), was definitely included by Straley in the synonymy of *O. fruticosa* subsp. *glauca*, the correct name for this taxon must be the combination *O. fruticosa* subsp. *tetragona*, which has not been previously made. The name *O. fruticosa* subsp. *glauca*, although nomenclaturally superfluous (Art. 52.1), is not illegitimate (because it has a basionym; Art. 52.3) and is here placed into synonymy.

Nomenclature

Oenothera fruticosa tetragona (Roth) W.L. Wagner, comb. nov.
urn:lsid:ipni.org:names:77135763-1
http://species-id.net/wiki/Oenothera_fruticosa_tetragona

Basionym. *Oenothera tetragona* Roth, Catal. Bot. 2: 39. 1800.

Type. Grown in the garden of Wilhelm Koch, at Gnadau, near Barby, Germany, of American origin; no extant material located. Pennsylvania. Lancaster Co.: between Churchtown Rd. and Beartown, 6 September 1892, A.A. Heller 549 (neotype, here designated: US-58278; isoneotypes: G-Bois, G, MO, NY). Munz (1937) apparently saw the original type material in B, stating "Ex horto meo Vegesackii, 1799, *Oe, tetragona*, Herb. A. W. Roth." I contacted Robert Vogt at Berlin and there is currently no extant original material; however, he located a specimen grown from seeds provided by A. W. Roth "e semin. Rothianis in h. bot. Wratislav. colui 1823," but there is no way to clearly connect this material with the original material used when Roth described the species. I have here selected a neotype that fits Roth's description and was considered to represent this entity in its narrowest interpretation. It was annotated by Munz for his 1937 revision and also by Straley for his 1978 revision.

Synonym. *Oenothera glauca* Michx., Fl. Bor.-Amer. (Michaux) 1: 224. 1803. *Kneiffia glauca* (Michx.) Spach, Hist. Nat. Veg. Phan. 4: 374. 1835. *Oenothera fruticosa* L.

var. *glauca* (Michx.) H. Lév.*, Monogr. Onothera 107. 1902. *Oenothera tetragona* Roth subsp. *glauca* (Michx.) Munz, N. Amer. Fl., ser. 2, 5: 91. 1965. *Oenothera fruticosa* L. subsp. *glauca* (Michx.) Straley, Ann. Missouri Bot. Gard. 64: 403. 1978 ["1977"; published 26 May 1978].

Type. Hab. in sylvis remotis et occidentalibus flumini *Mississippi* confinibus, versus regionem Illinoensium, 1787 or 1789, A. Michaux s.n. (holotype: P, photograph GH; isotype: P). According to Straley (1978) the type is labeled "Ouest de Ohio, Route aux Illinois," but the plant is presumably from the southern Appalachians, in the Carolinas or Virginia where Michaux collected in June and July of 1787 and 1789.

Acknowledgments

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RESEARCH ARTICLE

Piper kelleyi, a hotspot of ecological interactions and a new species from Ecuador and Peru

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Abstract

We describe *Piper kelleyi* **sp. nov.**, a new species from the eastern Andes of Ecuador and Peru, named in honor of Dr. Walter Almond Kelley. *Piper kelleyi* is a member of the *Macrostachys* clade of the genus *Piper* and supports a rich community of generalist and specialist herbivores, their predators and parasitoids, as well as commensalistic earwigs, and mutualistic ants. This new species was recognized as part of an ecological study of phytochemically mediated relationships between plants, herbivores, predators, and parasitoids. Compared to over 100 other *Piper* species surveyed, *Piper kelleyi* supports the largest community of specialist herbivores and parasitoids observed to date.

Resumen

Describimos la nueva especie *Piper kelleyi* **sp. nov**., proveniente de la vertiente Este de los Andes en el Ecuador y Perú, y nombrada en honor al Dr. Walter Almond Kelley. *Piper kelleyi* forma parte del clado *Macrostachys* del género *Piper* y conforma la base alimenticia de una diversa comunidad de herbívoros, tanto generalistas como especialistas, depredadores y parasitoides de estos herbívoros, así como tijeretas comensales y hormigas mutualistas. Esta nueva especie fue reconocida como parte de una investigación ecológica de las interacciones, mediadas por fitoquímica, entre plantas, herbívoros, depredadores y parasitoides. En comparación con más de otras 100 especies de *Piper* estudiadas, *Piper kelleyi* hospeda la comunidad de insectos con mayor diversidad de herbívoros especialistas y parasitoides observada hasta ahora.

Keywords

Introduction

Documenting plant and phytochemical diversity is recognized as an important component of understanding interactions among plants, herbivores and predators, and for understanding the evolution of biodiversity (Ehrlich and Raven 1964). Ongoing ecological, evolutionary, and phytochemical studies that focus on the plant genus *Piper*, and its insect herbivores and mutualists, have revealed a network of complex interactions in which plant phytochemistry has an evolutionary impact across multiple trophic levels (Dyer and Palmer 2004, Miller and Dyer 2009, Wilson et al. 2012, Dyer et al. 2013). Through the course of these studies, dozens of new species of the *Piper* specialist lepidopteran herbivore *Eois* Hübner (Geometridae: Larentiinae) and their parasitoids have been discovered (Grinter et al. 2009, Inclán-Luna 2010, Strutzenberger et al. 2010, Inclán-Luna and Stireman 2013). Among the *Piper* species studied thus far, the one that supports the highest diversity of *Eois* and associated parasitoids is also a previously unrecognized species. In this paper we describe this new species of *Piper* from Ecuador and Peru, and discuss the diversity of organisms that it sustains.

Materials and methods

Morphology and species distribution modeling

Morphological data and locality information were taken from the personal collections of EJT, GRC, and AEG, the ecological studies mentioned above, and from specimens sent to EJT for identification. Although the new species occurs in Ecuador and Peru, the distribution model was restricted to Ecuador since the majority of collection data is from the northeast and southeast Andean slopes of Ecuador. Collection density was very high in Napo Province, Ecuador (where much of the project activity was focused) relative to other parts of the species range, and to avoid biased results due to this imbalance, locations were filtered so that the model was based on an even sample from across the species' range. The distribution model was calculated using the maximum entropy method (Maxent software package; Phillips et al. 2006) from 26 presence locations marked with GPS and 19 climatic parameters at the $25km^2$ scale, which were downloaded from WorldClim (www.worldclim.org; Hijmans et al. 2005). The model was calibrated using elevations at which the species is modeled to be present, against elevations at which the species was observed in the field. The methods are described fully in Rodríguez-Castañeda et al. (2012).

Natural history studies

Study sites were located in the northeastern Andes of Ecuador in the provinces of Napo and Sucumbíos along an elevational transect from Amazonian lowland rain forest (200 m)

to Andean páramo (3200 m). Mean temperature along this gradient drops linearly with elevation at a rate of approximately -0.5°C per 200 m elevation gain, and precipitation ranges from 3900–4500 mm yr^{-1} (Rodríguez-Castañeda et al. 2010). This area includes three mountain ranges: the Sumaco, Huacamayos and Reventador, as well as continuous lowland to montane rain forests (sensu Holdridge 1967) that are part of the Cayambe–Coca, Antisana, and Gran Sumaco nature reserves.

To document trophic interactions associated with the new *Piper* species, standard 10 m diameter plots were established inside the forest at the sampling sites (Dyer et al. 2010a). A mean of 9 ± 0.81 plots were sampled at 200 m intervals along an elevational range from 280–3200 m; the new species was encountered from 1200–2300 m along this transect. Inside each plot, the leaves and stems of all individuals of *Piper* present were harvested (leaving the roots intact) kept in a separate bag identified by plot number and plant number, and transported to laboratories at Jatun Sacha (400 m), Yanayacu Biological Station (2200 m), or Oyacachi (3200 m) for further study. At the laboratory, all leaves were carefully surveyed for caterpillars or other insects. When the plants had ants or other arthropods inside the petioles, these were collected and placed in 75% ethanol in labeled vials. Each caterpillar found chewing on *Piper* leaves was assigned a unique number, identified to morphospecies, and reared to an adult moth for identification, or in the case of parasitized caterpillars, to obtain parasitism rates and identify the parasitoids.

Taxonomic treatment

Piper kelleyi Tepe, sp. nov.
urn:lsid:ipni.org:names:77135933-1
http://species-id.net/wiki/Piper_kelleyi
Figs 1–2

Diagnosis. Piperi imperiali *(Miq.) C.DC. similis sed sinu foliorum laxe aperto (numquam angusto neque petiolum tegente) et tuberculis leviter elevatis differt.*

Type. Ecuador: Prov. Napo, Cantón Quijos, island in the Cosanga River near Las Palmas, 0°32'42"S, 77°52'36"W, 1875 m, 19 Jan 2009 (fl), E.J. Tepe & W. Simbaña 2615 (holotype: QCNE; isotypes: MO, MU).

Description. Shrub to small tree, 1.5–15 m tall, moderately branched; trunk of flowering individuals 5–8 cm d.b.h.; some individuals with prop roots. Stems glabrous, the nodes moderately to densely tuberculate, density of tubercules increasing distally along each internode, the internodes 6.5–9.6 cm long and 0.5–1.1 cm in diam.; shoot apex emerging from the sheathing leaf base. Prophyll minute and hidden by the sheathing leaf base. Leaves more or less distichous on flowering branches, with petioles 6–14 × 0.7–1 cm at flowering nodes, vaginate, and with persistent margins, the margins extending to the leaf base or projecting 1–10 mm beyond the insertion of lower leaf lobe, glabrous, sparsely to moderately tuberculate; laminae 25–50 × 15–42 cm, broadly
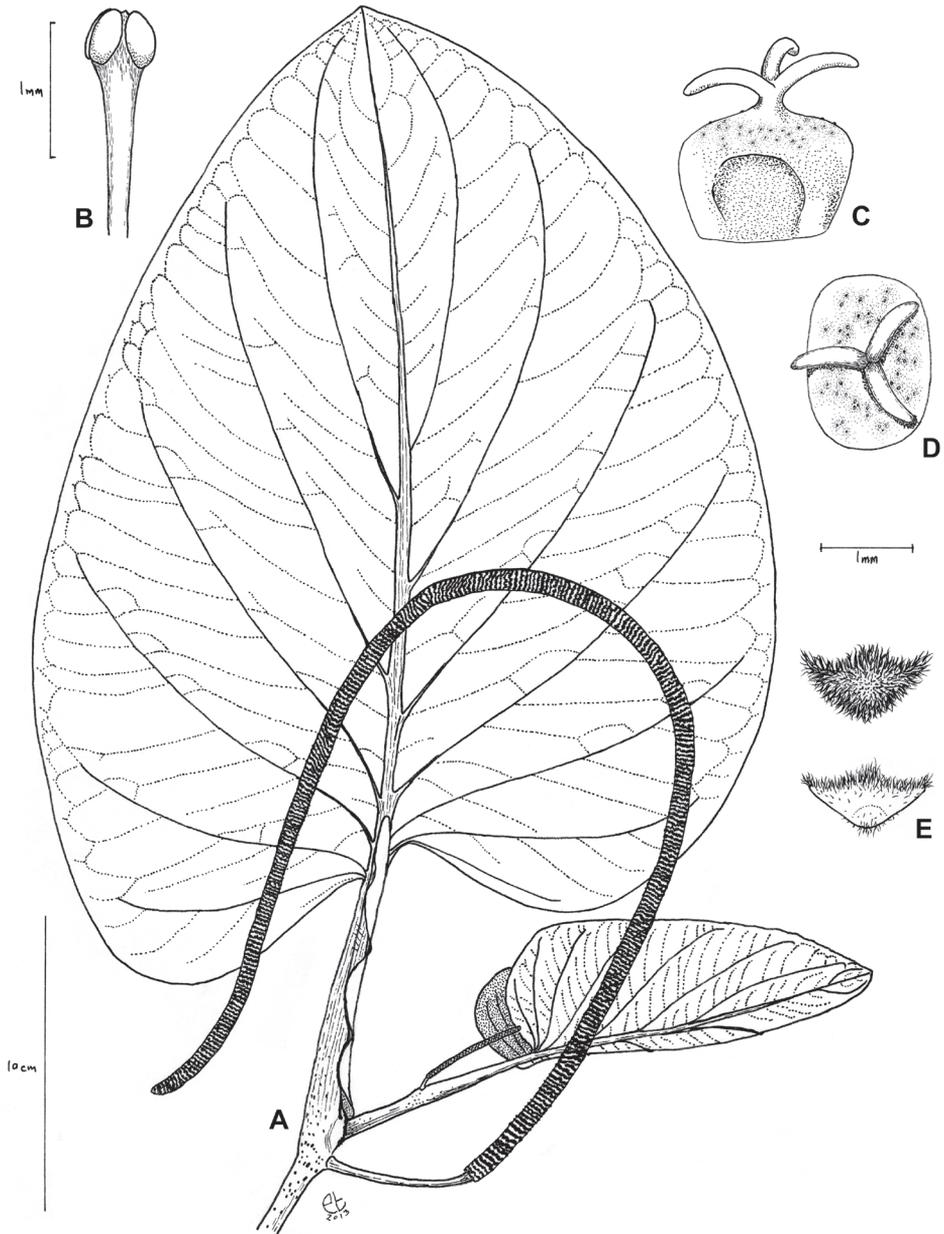
Figure 1. *Piper kelleyi* Tepe. **A** leaf and inflorescence **B** Stamen **C** fruit in lateral view **D** Fruit in apical view **E** Bracts in apical view. [**A** and **E** (lower) drawn from Tepe et al. 1597; **B–E** (upper) drawn from Tepe et al. 2615]

ovate, the apex obtuse, rounded, the base oblique, cordate, the lobes equal or more commonly somewhat unequal, extending 2–8 cm below the petiole attachment, divergent and never overlapping the petiole, the sinus open and the apices of the lobes

nearer the leaf margin than the petiole, the sides of the lamina arising 7–8 mm apart on the petiole, the lamina drying thickly chartaceous, densely glandular-dotted (usually blackish on dried specimens, 3–5 per mm^2, increasing in density along the leaf margin), glabrous above, glabrous to sparsely pubescent on the lamina below and moderately to densely pubescent on the veins below with much shorter trichomes (< 0.2 mm long; these more conspicuous on the secondary and tertiary veins, often lacking on the mid-vein), the 4–6 pairs of major secondary veins arising from the lower 2/3 of the mid-vein, arcuate-ascending, primary–tertiary veins somewhat impressed above, prominent below. Inflorescences free from the leaf base of the same node, pendulous, 40–72 × 0.4–0.8 cm in flower and 0.8–1.1 cm in diameter in fruit, the flowers densely crowded and +/- banded; peduncles 2.5–6 × 0.25–0.5 cm, white to green in fruit, glabrous; floral bracts 0.7–1.0 mm broad, triangular to triangular-rounded, nearly glabrous with upper margin white ciliate to densely pubescent throughout; stamens 4 per flower, the stamens maturing asynchronously such that only one or two are apparently visible per flower at one time, white, the anthers 1–1.5 mm long, the filaments clavate, the connective somewhat broadened between thecae and these divergent at ca. 45°, dehiscing laterally; fruits rounded or rectangular from above by compression, 1.5–2 × 1.2–2 mm, the apex truncate, glabrous, gland-dotted, stigma lobes 3(–4), 0.5–0.8 mm long, sessile or on a very short style, caducous; seeds rounded-square, flattened, 1.5–2 mm.

Distribution. *Piper kelleyi* is found in shaded understory habitats of primary and secondary lower montane rainforests (Neill 1999) on the eastern slopes of the Andes in Ecuador and northern Peru; elevation 1200–2400 m (Fig. 3A).

Phenology. Flowering specimens have been collected in Jan–Mar and Dec; fruiting specimens have been collected in Mar, Jul, and Sep.

Etymology. *Piper kelleyi* is named for Dr. Walter Almond Kelley (1942–2010). Dr. Kelley spent a good portion of his career focusing on taxonomy within the genus *Cryptantha* (Boraginaceae; e.g., Kelley and Wilken 1993), but became fascinated with *Piper* when he visited Costa Rica in 1997 to work with *Piper* species at La Selva Biological Station. He was interested generally in angiosperm evolution, evolution of unique morphologies, stem anatomy, and tropical biology and spent years working with *Piper* from Costa Rica and Ecuador (e.g., Tepe et al. 2009). He examined the unique morphology of *Piper*, and documented *Piper* stem anatomy. He had made considerable progress on understanding phyllotaxy and the notoriously complicated stem anatomy in *Piper*, and produced two substantive manuscripts on *Piper* biology. His extensive observations on *Piper* morphology, included the following comments:

There are three basic patterns of sympodial stem tip and leaf primordial (STLP) enclosure and protection in *Piper*. The first common pattern has the sympodial STLP enclosed in a prophyll only. A second common pattern has the sympodial STLP enclosed in a prophyll and a stipular wrap-over of the terminal subtending leaf. A third, rarer pattern occurs when the prophyll has become greatly reduced so that the sympodial STLP appears to be enclosed only by a stipular wrap-over of the terminal subtending leaf (W.A. Kelley, field journal).

Figure 2. *Piper kelleyi*. **A** Habit **B** Close-up of leaves showing characteristic red color of younger leaves [Tepe et al. 2381] **C** Close-up of inflorescence [Tepe et al. 2615] **D** Close-up of infructescence [Tepe et al. 1597].

Piper kelleyi exhibits the third of these patterns. He established the herbarium (MESA) at Colorado Mesa University, Grand Junction, Colorado (CMU), and cultivated a high diversity of *Piper* species at the CMU greenhouse, including *P. kelleyi*. These plants are still used for research today.

Preliminary conservation status. According to the IUCN Red List Categories (IUCN 2013), we deem it necessary to classify *P. kelleyi* as Data Deficient (DD). *Piper kelleyi* appears to occupy a relatively narrow elevational band along the eastern slopes of the Andes in Ecuador and northern Peru, but is fairly common in Ecuador between 1400–2200 m in Napo and between 1900–2000 m in Zamora-Chinchipe Provinces. These two areas have established field stations with projects focusing on *Piper* and, accordingly, collection of *Piper* has been comparatively intense in these areas. Scattered collections of *P. kelleyi* in other parts of its range, however, indicate the species' presence, but are not necessarily informative of its abundance. Collecting intensity across
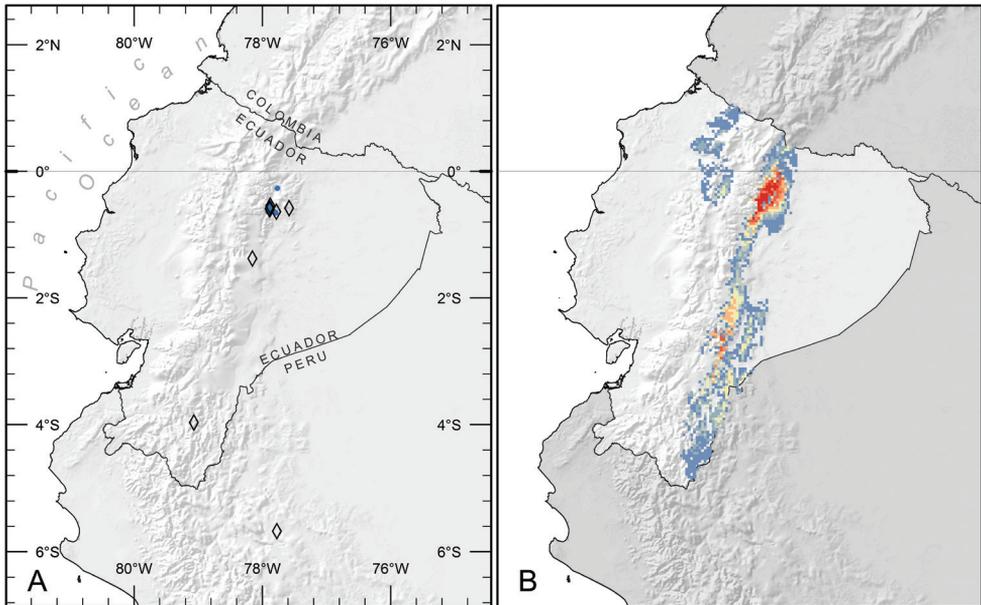
Figure 3. Distribution of *Piper kelleyi*. **A** Distribution of known localities based on collections (open diamonds) and study plots used to gather natural history data (blue circles) **B** Predicted distribution based on analysis of habitat parameters using the maximum entropy method. Areas in red are the most likely to have suitable habitat for *P. kelleyi* (probability = 0.75–0.87), and areas in blue (0.02–0.08) or unlabeled (< 0.02) are the least likely.

the Neotropics is decidedly uneven (Schulman et al. 2007) and virtually nothing is known about the density of individuals of this species outside of the two focus areas mentioned above. Consequently, we are presently unable to make an informed statement regarding the conservation status of *P. kelleyi*.

Specimens examined. ECUADOR. Napo: Yanayacu Biological Station, 3 km SW of Cosanga, 0°36'S, 77°53'W, 2080 m, 24 Sep 2005 (fr), J. Homeier, C. Chicaiza & B. Moreno 1646 (GOET, QCA, QCNE); Parque Nacional Sumaco-Galeras, southern slope of Sumaco Volcano, 0°35'S, 77°35'W, 1930 m, 19 Mar 2008 (fr), J. Homeier, M.A. Chinchero, E. Jaramillo & D. Simba 3362 (GOET, QCA, QCNE); Parque Nacional Sumaco-Galeras, Río Hollín watershed, 0°38.3'S, 77°46.9'W, 1490 m, 28 Mar 2008 (st), J. Homeier, M.A. Chinchero, D. Simba, L. Guachamin & M. Unger 3524 (GOET, QCA, QCNE); Cosanga, on road to the Yanayacu Biological Station, 0°35'09"S, 77°53'04"W, 2100–2200 m, 2 Mar 2006, (fl, fr), E.J. Tepe et al. 1597 (MO, MU, QCNE); Canton Quijos, ca. 4 km W of Cosanga on the Cosanga - Las Caucheras road, 0°35'52.1"S, 77°53'10.0"W, 2120 m, 16 Feb 2011 (fl), E.J. Tepe & M.P. Moreno 2999 (MO, QCA, QCNE); Parque Nacional Sumaco-Galeras, southern slope of Sumaco Volcano, 0°35'S, 77°35'W, 2015 m, 21 Nov 2006 (st), S. Trogisch, S. Moritz & J. Homeier 312 (GOET, QCA, QCNE). **Tungurahua:** Zuñag Scientific Station, 1°22'41"S, 78°09'20"W, 1581 m, 19 Jul 2012 (fr),

A. Glassmire, M. Habdas & A. Crespin B13 (CINC). **Zamora-Chinchipe**: Reserva San Francisco, 3°58'S, 79°04'W, 1950 m, 6 Sep 2008 (st), N. Cumbicus & J. Peña *643* (GOET, LOJA); Reserva San Francisco, road Loja-Zamora, ca. 35 km from Loja, 3°58'S, 79°04'W, 2000 m, 20 Mar 2009 (st), M. Ebinghaus 6 (MU). **PERU. Amazonas:** Road from Rioja to Pedro Ruiz, km 383 (old white markers), 5°40'39"S, 77°46'24"W, 2000 m, 16 Dec 2007 (infl), E.J. Tepe, S. Leiva, S. Stern & M. Zapata Cruz 2381 (MU, USM). The specimen database is available at http://hdl.handle. net/2374.UC/731268.

Results and discussion

Piper kelleyi is a striking species that stands out from its surroundings because of its long, white, pendulous inflorescences, large leaves, and the pinkish coloration characteristic of the young stems and leaves. These colorful young leaves have given this species the whimsical, informal name "pink belly," which was used in two previous works (O'Connor 2011, Wilson et al. 2012).

   Piper kelleyi is a member of the *Macrostachys* clade of *Piper*, species of which are most abundant in the shady understory of lowland and cloud forest habitats in the Andes and Central America (Jaramillo et al. 2008). Species of this clade have a prophyll that is highly reduced and completely obscured by the sheathing petiole, but can be most easily recognized by the typically large leaves with leaf bases that are strongly asymmetric and often prominently lobed, and the long, pendulous inflorescences that characterize most species. *Piper kelleyi* can be distinguished from other members of the clade by the unusually broad sinus between the basal lobes of the leaf (Fig. 1). In *P. kelleyi* the lobes are always divergent and never overlap the petiole, whereas in most species of this clade, including *P. imperiale* (Miq.) C.DC., which is the species perhaps most likely to be confused with *P. kelleyi*, the sinus is often narrow and one of the basal leaf lobes sometimes covers the petiole. Aside from leaf characters, this new species can be distinguished by the slightly raised tubercles on the stems and petioles (or their complete absence), as compared to the often conspicuously raised tubercles of *P. imperiale* (as much as 5 mm or more in some extreme specimens). The other species of *Piper* sect. *Macrostachys* that is likely to co-occur with *P. kelleyi* is *P. marsupiiferum* Trel.; however, this species is a slender shrub, short in stature (tall plants can reach 1.5 m with the majority being less than 1 m tall), with narrow, strongly asymmetric, deeply rugose leaves with a basal lobe that completely covers the petiole. In addition, the inflorescences of *P. marsupiiferum*, while pendulous, are a maximum of 15 cm long (vs. 40–72 cm in *P. kelleyi*). Other large-leaved pipers that co-occur with *P. kelleyi*, at least in the northern part of its range, include *P. baezanum* C.DC., which has coarsely rugose, symmetrical leaves, and the lianescent *P. schuppii* A.H. Gentry. Furthermore, both of these species are distinct from *P. kelleyi* in that they have inflorescences that are held upright during all stages of development.

Distribution

Ecological niche model performance was high (avg. train AUC: 0.99; avg. test AUC: 0.99; max. probability range: 0–0.86). Results predict that suitable habitat for *P. kelleyi* is more extensive than the distribution reported here, which is based on available collections and observations (Fig. 3B). The species favors montane elevations (ca. 1000–2500 m) and according to the model, important determinants of its habitat were intolerance to freezing temperatures and affinity for temperate climate (coldest month temperatures of ∼12.5°C). Further habitat suitability increases with high levels of precipitation during the coolest months (>1000 mm). The species seems to favor river or stream banks and sandy soils (pers. observation by GRC). The model predicts suitable habitat on both sides of the Andes, but *P. kelleyi* has never been recorded from localities west of the continental divide despite intensive *Piper* collection by EJT and surveys of *Piper* for caterpillars by AEG at several localities on the western slopes of the Andes. These collections included seven species of *Piper* sect. *Macrostachys*, but did not include *P. kelleyi*. It is possible that additional collecting will reveal the presence of the new species in these areas, but based on current collections it appears that *P. kelleyi* is restricted to limited localities on the eastern slopes of the Andes.

Ecology

Piper kelleyi is a focal component of a study aimed at understanding the influence of plant secondary chemistry on herbivores and their associated parasitoids (Wilson et al. 2012). The genus *Piper* produces a high diversity of multiple classes of secondary compounds, including biologically active amides and imides (Dyer et al. 2004), which are known to negatively affect generalist herbivores (Dyer et al. 2003). Preliminary evidence suggests that *P. kelleyi* is not palatable to generalist herbivores based on assays conducted by GRC and AEG during studies spanning 2005–2008 and 2011–2013 respectively (unpubl. data).

Plot data resulted in herbivory and parasitism rates, and measures of herbivore and parasitoid richness. Mean herbivory rates for the plant are close to 20%, and the only herbivores that are regularly found on *P. kelleyi* are species of the specialist herbivore *Eois*. Even in the absence of caterpillars, the presence of *Eois* can be identified by the characteristic feeding markings that they leave behind (see the herbivory key in Dyer et al. 2010b). These caterpillars scrape small portions of the under sides of leaves, leaving unpigmented windows (Fig. 4A) that are eventually lost, resulting in characteristic holes in the leaves. Apart from *Eois*, other lepidopteran herbivores reared from this host plant include members of t the families Erebidae, Hesperiidae, Noctuidae, Pyralidae, and Tortricidae. Over 3,000 caterpillars have been reared from *P. kelleyi*, yet only single individuals have been recorded from these other lepidopteran families (Dyer et al. 2013) suggesting that, unlike *Eois*, they are not likely to be *Piper* specialists.
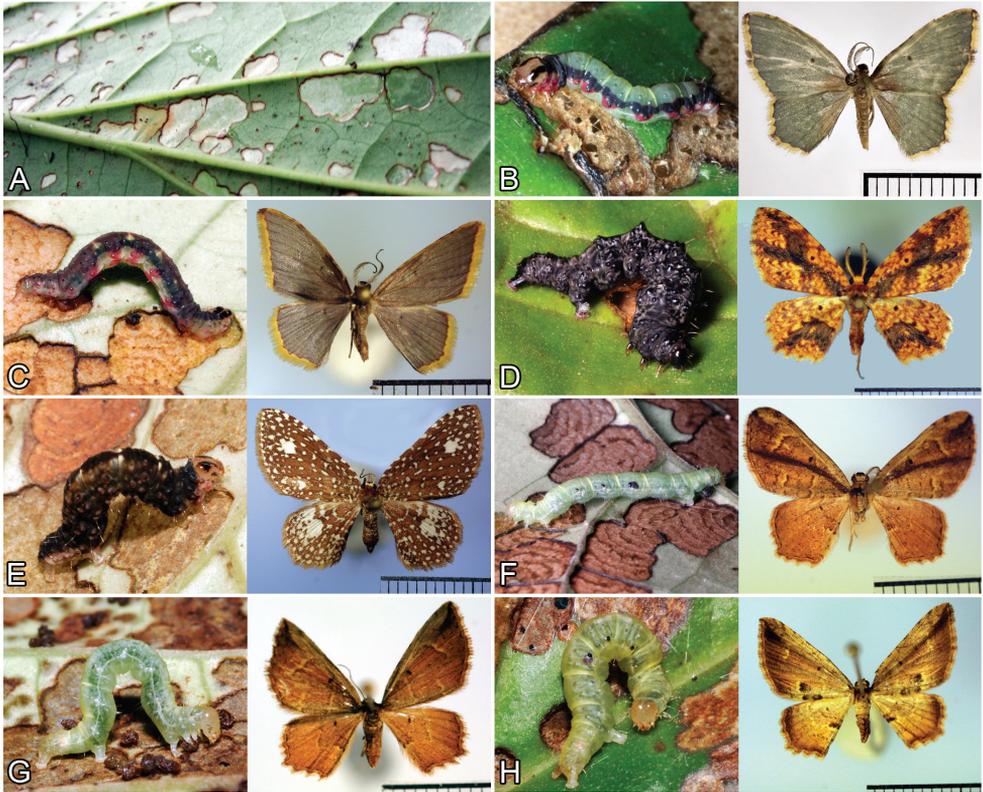
Figure 4. A Leaf of *Piper kelleyi* with characteristic herbivory marks or "windows" made by the specialist herbivore *Eois*; species of *Eois* that specialize on *Piper kelleyi* include **B** *Eois viridiflava* (Dognin) **C** *E*. aff. *viridiflava* (Dognin) **D** *E. ignefumata* (Dognin) **E** *E. planetaria* (Dognin) **F** *E*. aff. *pallidicosta* (Warren) **G** *E. encina* (Dognin) **H** *E*. aff. *encina* (Dognin).

Project collaborators have reared nearly 30,000 caterpillars and parasitoids from over 100 *Piper* species, and *P. kelleyi* is the host species with highest density and species richness of *Eois* found thus far. Since many of the *Eois* species and nearly all of the parasitoids reared from *Piper* were previously undescribed, the taxonomy of these insect groups currently lags behind that of their host plants. Nevertheless, *P. kelleyi* hosts at least 11 morphospecies of the specialist herbivore *Eois* and these include *Eois cancellata* (Warren), *E. encina* (Dognin), *E*. aff. *encina* (Dognin), *Eois goodmani* (Schaus), *Eois ignefumata* (Dognin), *Eois* aff. *necula* (Druce), *Eois olivacea* (Felder & Rogenhofer), *Eois* aff. *pallidicosta* (Warren), *Eois planetaria* (Dognin), *Eois viridiflava* (Dognin), and *E*. aff. *viridiflava* (Dognin) (Fig. 4B–H; Rodríguez-Castañeda 2009, Dyer et al. 2013: www.caterpillars.org). Seven of these species were recognizable from adult characters as distinct species, whereas additional cryptic species were recognized from a combination of molecular data and larval characteristics (Wilson et al. 2012). These results are not surprising since molecular identification has increased Geometrid estimates of diversity by 50% in the SE Andes of Ecuador (Strutzenberger et al. 2010).

Figure 5. A colony of *Pheidole* ants nesting inside a petiole of *P. kelleyi*.

The parasitism rate for all of the *Eois* collected from *P. kelleyi* was 8.63%. Parasitic wasps were the most frequent and included Eulophidae (Hymenoptera: Chalcidoidea) at 3.5%, followed by Braconidae (Microgastrine) at 2.7%, and Ichneumonidae at 1.5%. Tachinid flies (Diptera: Tachinidae) had the lowest parasitism rate at 0.9%. Within the subfamily Microgastrine (Braconidae), species of the genera *Cotesia* (Cameron)*, Glyptapanteles* (Ashmead), *Mesochorus* (Gravenhorst), *Parapanteles* (Ashmead), and *Protopanteles* (Ashmead) have been reared out of the *Eois* species feeding on *P. kelleyi*. The determined Tachinid species include *Erythromelana abdominalis* (Townsend), *E. cryptica* (Inclán & Stireman), and *E. jaena* (Townsend) (Inclán–Luna 2010, Dyer et al. 2013, Inclán–Luna and Stireman 2013).

Thus, to date, *P. kelleyi* is host to at least 17 species of specialist and generalist herbivores, and nine described and an estimated 20–30 undescribed species of parasitoids (unpubl. data). Moreover, *P. kelleyi* acts as a microcosm for other insect species. The sheathing leaf petioles occasionally host nests of *Pheidole* (Westwood) (Hymenoptera: Formicidae; Fig. 5), other ants, or small families of earwigs. Several species of the *Macrostachys* clade of *Piper* have specialized associations with ants that nest primarily within the petioles (Risch et al. 1977, Letourneau 1998, Tepe et al. 2004); however, when the large sheathing petioles of other species form a sufficiently closed chamber, a diversity of opportunistic, arboricolous ants take advantage of these chambers for nesting sites (Tepe et al. 2007). Also, predatory coccinellid beetle larvae and salticid spiders are frequently found on the leaves of *P. kelleyi* (GRC, personal observation).

Conclusions

Empirical evidence has been accumulating that supports the hypothesis that plant biochemistry helps drive the evolution of biodiversity, not only among herbivores that feed directly on plants, but among higher trophic levels as well (Ehrlich and Raven 1964, Forister and Feldman 2011, Wilson et al. 2012). *Piper kelleyi* represents a hotspot of these interactions. In fact, our group has surveyed lepidoptera feeding on *Piper* species for over

20 years, and *P. kelleyi* supports the highest diversity of *Eois* recorded to date. We have documented a large number of parasitoids as well, but, because parasitism rates are low and discoveries are still occurring, we expect the number of parasites to be similarly high.

Our description of *Piper kelleyi* is part of a larger effort to combine traditional taxonomy and natural history with newer integrative approaches. The purpose of this project is to successfully contribute to taxonomy and systematics while characterizing evolutionary patterns via molecular phylogenetics, studying community ecology, and increasing our understanding of functional diversity by quantifying specialized consumer-resource relationships and interaction diversity. The importance of traditional taxonomy and natural history data for these studies is essential (as argued in Dyer et al. 2010a) and descriptions of new species, such as *P. kelleyi*, are a necessary component of thorough research programs in ecology and evolutionary biology.

Acknowledgements

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RESEARCH ARTICLE

Lithocarpus orbicarpus (Fagaceae), a new species of Stone Oak from Phang Nga province, Thailand

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Abstract

A new species is described, *Lithocarpus orbicarpus* Strijk, collected from Ton Pariwat Wildlife Sanctuary, Mueang district, Phang Nga Province in the Peninsular Floristic Region of Thailand. We provide the first technical illustrations and colour photographs of the new species, as well as a description of its conservation status and the collecting locality. The species can be easily distinguished by its unique orbicular acorns, each covered with a dense pattern of irregularly placed scales, which completely conceal the nut, except for a tiny apical pore, and which are arranged in a dense cluster on an erect woody spike. We also provide an amendment to the existing diagnostic key to *Lithocarpus*, and discuss important differences with morphologically similar species found in Thailand and the surrounding region.

Keywords

Lithocarpus orbicarpus, new species, Stone Oaks, Fagaceae, Thailand, Ton Pariwat Wildlife Sanctuary

Introduction

Lithocarpus Blume is the second largest genus within Fagaceae, with over 300 species described (Camus 1948, 1954; Phengklai 2008; Soepadmo 1972; Wu et al. 1999). Members of the genus, commonly called Stone Oaks, can be found in (sub-)

tropical broad-leaved evergreen forests near sea level to mixed forests at altitudes of over 3200 m. The geographic distribution of *Lithocarpus* roughly covers southern and south-eastern Asia from eastern India to southern Japan, to the Philippines and southward to New Guinea. *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, the only North American member of the genus was recently moved to a new monotypic genus (Manos et al. 2008). All species within *Lithocarpus* are trees, ranging from small understory elements, to very large emergent trees. Many species have a geographically wide distribution and in some locations may constitute the main canopy forming elements together with other Fagaceae (*Lithocarpus*, *Quercus*, *Castanopsis*), Lauraceae and Theaceae. Leaves are simple, entire, rarely serrate, generally glabrous and mostly spirally arranged. Male and female flowers are white to pale whitish-yellow. Genders can be either on separate inflorescences, on the same inflorescence mixed throughout, or with female flowers below and male flowers terminal, arranged with dense indumentum on erect spikes. Male flowers are solitary or in clusters of three or more, with the perianth campanulate or cup-shaped, usually 6-lobed, partially united; stamens generally 12. Female flowers solitary or in clusters of three, perianth like male flowers but smaller; 12 staminodes; 3(-4) styles (Camus 1948, 1954; Phengklai 2008).

Previous studies and the most recent treatment for Thailand have recovered 57 species of *Lithocarpus* (Barnett 1940; Phengklai 2004, 2008). During fieldwork in remote Ton Pariwat Wildlife Sanctuary, carried out as part of ongoing research on the genomics, systematics, biogeography and evolution of Asian Fagaceae, we made collections of an individual tree with unique features that could not be matched with any previously described taxa in Fagaceae. After careful examination of herbaria and literature, comparison of other specimens collected during the fieldwork and consultation of specialists on the regional flora, we report this collection here as a new species, placed within the genus *Lithocarpus*.

Taxonomy

Lithocarpus orbicarpus Strijk, sp. nov.
urn:lsid:ipni.org:names:77135982-1
http://species-id.net/wiki/Lithocarpus_orbicarpus
Fig. 1, 2

Type. THAILAND, Ton Pariwat Wildlife Sanctuary, Mueang district, Phang Nga Province, 8°37'25"N; 98°33'14"E; alt. 455 m, 16 July 2013, Chamchumroon et al. 5823 (Holotype: BKF; Isotypes: E, K, L, SING).

Diagnosis. *Lithocarpus orbicarpus* is a small-medium sized tree. It differs from similar species by its unique orbicular acorns, each covered with a dense pattern of irregularly placed scales, which completely conceal the nut, except for a tiny apical pore, and which are arranged in a dense cluster on an erect woody spike. Unique for Thai species of *Lithocarpus*, almost the entire surface of the round nut is covered with scar area (re-

ceptacle tissue), leaving only the topmost part of the nut covered with a thin vestigial exocarp layer. Pending discovery of additional individuals, the species appears to be locally restricted to low-mid-elevation forests in the peninsular region of Thailand.

Description. Small-medium sized tree, up to 15 m tall. *Bark* smooth to slightly rough grey-green, with superficial horizontal lines. Sapwood white to yellow, with inner bark ridges forming light brown longitudinal slits in sapwood surface. *Branches* dark brown to grey brown, mostly glabrous, densely lenticellate; young twigs, leaf buds and old fruits with short, soft (occasionally long) gray indumentum. Leaf buds tiny and terminal buds solitary. *Leaves* simple; lamina elliptic to oblanceolate with (strongly) acuminate tip, 11.0–22.3 × 4.4–7.1 cm. Margin entire. Leaves often with slightly asymmetric lamina. Leaf apex acuminate to strongly acuminate, leaf base cuneate to slightly attenuate. Both surfaces generally glabrous except emerging leaf buds, terminal shoots and young leaves, which have soft grey indumentum. Young leaves light green, but turning dark green above and glaucous below when older. *Venation.* Pinnately veined; secondary venation discretely anastomosing near the leaf margin. Pairs of secondary veins 9–13, slightly raised and clearly visible on underside of leaf. *Peduncles* carrying fruits 5–11 cm long, up to 1 cm thick at the base, glabrescent, grey-brown and densely lenticellate. *Male and female inflorescences* not seen. *Infructescence* a woody spike, terminal, up to 15–21 cm long. Fruits sessile on thick woody peduncle, closely pressed against each other, but walls of individual units not fused. Number of fruits per infructescence very variable, ranging from 9–20 units. *Acorn.* Orbicular, globose, 2.7–3.4 by 2.9–3.5 cm (including cupule) and covered with glabrous, semi-concentric interlocking ridges when young, which transform over time into ridges with irregularly placed scales. Cupule nearly completely enclosing the nut, indehiscent, but showing small cracks when mature; fruit wall up to 4–6 mm thick, apical pore very small, 1–4 mm wide, exposing the persistent punctiform styles (3) and a tiny fraction of vestigial exocarp. Young cupule walls light green, ridges light to dark brown. Old cupule walls turning light brown to yellow-brown and pubescent with short (occasionally long), greyish-yellow indumentum. *Nut* 1 in each cupule, ball shaped, globose, 2.4–2.9 by 2.6–3.0 cm. Up to 95% of surface area of the nut made up of scar area (receptacle tissue), upper 5% of surface area of the nut slightly raised and made up of vestigial exocarp layer. Nut scar pale yellow-whitish, tiny exocarp layer light brown. Scar area covered with deep groves and red-brown to purplish vein-like lines, stretching down to the base of the nut. Up to 5/6 of the scar area of the young nut (from the base upward) covered with dotted pattern of small depressions. Cotyledons black when dried.

Flowering and fruiting. Flowering unknown, but thought to be around November-January. Infructescences on the ground in July, fruiting commencing possibly as early as April-May.

Distribution. This species is only known from Thailand, and has not been recorded outside Ton Pariwat Wildlife Sanctuary, Mueang district, Phang Nga Province. During our field survey, we found only one individual tree, located on a gentle sloping section of closed dense forest. Additional survey work will have to be undertaken to determine the actual population size of this species within the wildlife sanctuary.
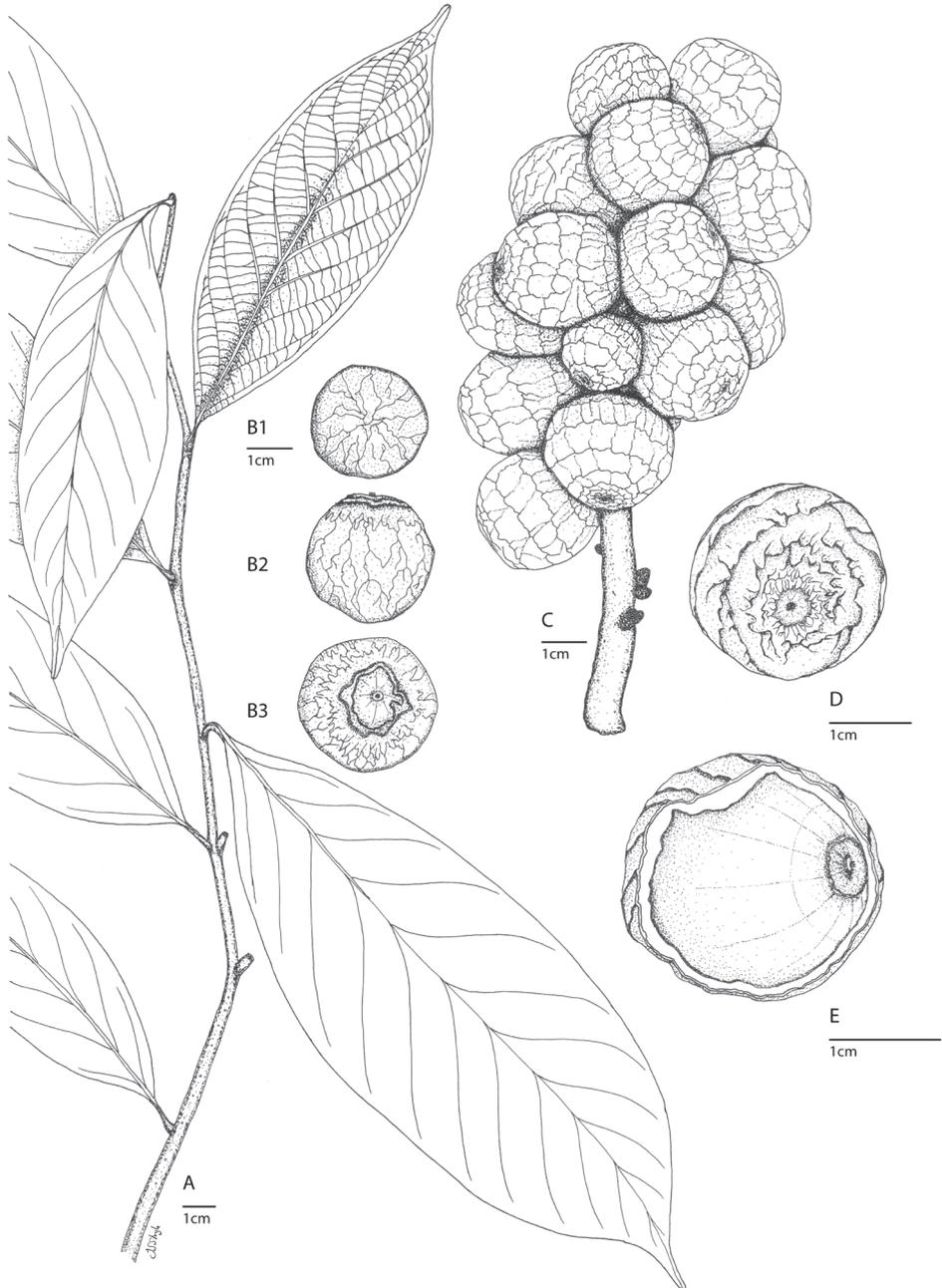
Figure 1. *Lithocarpus orbicarpus* Strijk, sp. nov. Chamchumroon et al. 5823 (BKF). Technical illustration. **A** Habit **B** Detail of glabrous young fruit with ridges and apical pore **C** Detail of interior of young fruit, showing nearly complete fruit scar, covered umbo and 'pitted pattern' on the nut surface **D** Infructescence with ripe fruits showing highly irregular scaly patterns on the fruit exterior **E** Details of seed, from left to right: bottom view, side view, top view. Note venation and crevice pattern on surface of fruit, and cover of the umbo section. All drawings by J.S. Strijk.

Ecology. This species grows in dense hillside forest at an elevation of around 450 m.

Vernacular name. Unknown.

Etymology. *Lithocarpus orbicarpus* is named after its unique orbicular acorns, arranged densely clustered on an erect spike, of which the cup almost completely encloses the nut (except for a tiny apical pore). The exterior of the cup is covered with a dense pattern of ridges, transforming with age into horizontal and vertical lines with irregularly placed scales. Apart for a tiny portion of the umbo which is covered with vestigial exocarp, the exterior surface of the nut is completely covered by scar. Although the cupule nearly completely covers the nut, the latter is free and not fused to the wall of the cupule – a condition which occurs throughout the genus (Cannon 2001; Cannon and Manos 2001). Upon drying, the shrinking of the cotyledons inside the nut causes the whole infructescence to make a rattling sound when shaken.

Discussion. Thailand has a total of 121 species, 2 subspecies and 2 varieties of Fagaceae in four genera indigenous to the country. Of these, nine species (*Castanopsis*: 4; *Quercus*: 1; *Lithocarpus*: 4) and 1 subspecies (*Quercus*: 1) are national endemics (Bunpha et al. 2011; Phengklai 2008). Three of the endemic *Lithocarpus* species (including *L. orbicarpus*) are restricted to small ranges in the peninsular region. Of the 58 *Lithocarpus* known to occur in Thailand (including this newly described species), 43 species (74%) can be found in the Peninsular floristic province making it the most diverse floristic region (in terms of *Lithocarpus* species) followed by the North (25 species – 43%). While the Northern (and North-eastern) floristic province is characterized by species that reach high elevation habitat (>75% can be found between 1200–2500 m), the Peninsular complement includes species that are restricted to lower elevations (21 species restricted <500 m asl). With two exceptions (*L. falconeri* (Kurz) Rehder and *L. erythrocarpus* (Ridl.) A.Camus), none of these species are shared with the North (or North-east). In contrast, four of the Peninsular lowland species (*L. lucidus* (Roxb.) Rehder; *L. maingayi* (Benth.) Rehder; *L. reinwardtii* (Korth.) A.Camus; *L. tubulosus* (Hickel & A.Camus) A.Camus) are shared with the South-eastern floristic province, in addition to *L. elephantum* (Hance) A.Camus and *L. pierrei* (Hickel & A.Camus) A.Camus, which can only be found in the South-eastern region.

Lithocarpus in Thailand can be further characterized based on their acorn (cupule+nut) properties. The open- or semi-open type, in which the cupule shape ranges from saucer shaped-flat to covering up to 4/5th of the nut is present in 37 species (64%), while the remaining 18 species have cupules that entirely cover the nut, in most cases leaving a tiny portion of the umbo uncovered. With one exception (*L. truncates* (King ex Hook.f.) Rehder), all closed-type species occur in the Peninsula, and eight are restricted to it (two shared with the Southeast). *L. orbicarpus* resembles species in this group, with its indehiscent and near-closed cupules, restricted geographical distribution and presence in lower elevation habitat, but is clearly distinct from them based on the structure and shape of the fruit, the infructescence and the properties of the nut.

During our field survey, we encountered and collected additional Fagaceae species, e.g. *Lithocarpus reinwardtii* (Korth.) A.Camus (Burma, Cambodia, Malaysia, Indonesia), *L. sundaicus* (Blume) Rehder (Malaysia, Indonesia, Brunei), *L. cantleyanus* (King ex Hook.f.)
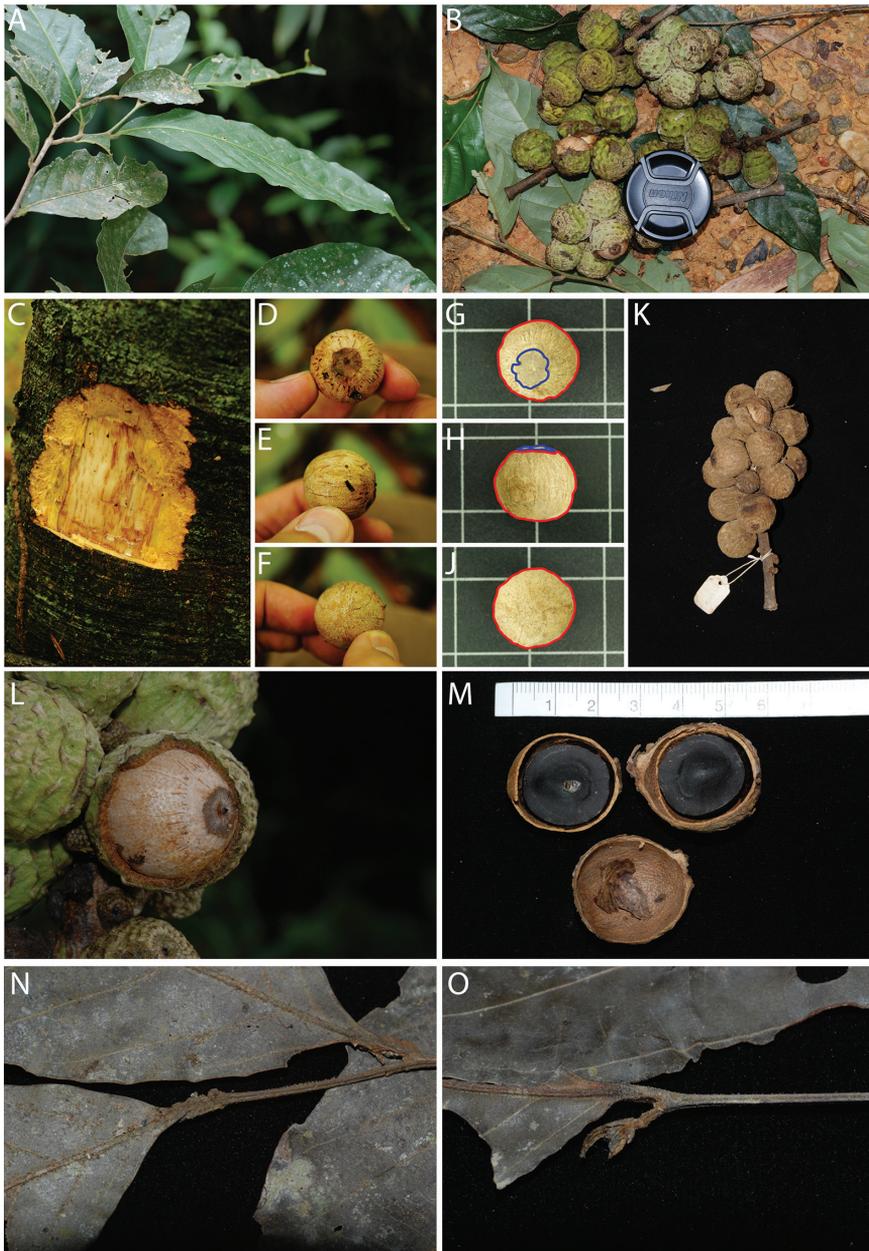
Figure 2. *Lithocarpus orbicarpus* Strijk, sp. nov. Chamchumroon et al. 5823 (BKF). Pictures from field collection. **A** Branch with leaves **B** Young infructescences **C** Bark and sapwood **D** Fresh fruit – top view **E** Fresh fruit – side view **F** Fresh fruit – bottom view **G** Dried fruit – top view **H** Dried fruit – side view **J** Dried fruit – bottom view (**G–J**: blue lines demarcate vestigial exocarp; red lines demarcate scar area (receptacle tissue)) **K** Dried infructescence **L** Young acorn, opened up to show dotted pattern of small depressions and surface structure of the umbo **M** Cross-section of fried nut, showing seed coat and black cotyledons **N** Terminal leaf, twig and very small terminal bud, showing grey indumentum **O** Young emerging leaf with soft grey indumentum. All pictures by S. Sirimongkol and J. S. Strijk.

Rehder (Burma, Malaysia, Singapore) and several, as of yet, unidentified collections. Additional species encountered in previous surveys in the wildlife sanctuary are: *Castanopsis javanica* (Blume) A.DC. (Vietnam, Malaysia, Singapore, Indonesia); *Castanopsis nephelioides* King ex Hook. f. (Malaysia, Singapore); *Castanopsis purpurea* Barnett (Thailand (endemic)); *Castanopsis wallichii* King ex Hook. f. (Malaysia, Singapore, Indonesia); *Castanopsis inermis* (Lindl.) Benth. & Hook. f. (Burma, Malaysia, Singapore, Indonesia, Philippines); *Lithocarpus bennettii* (Miq.) Rehder (Malaysia, Singapore, Indonesia); *Lithocarpus clementianus* (King) A.Camus (Malaysia, Indonesia); *Lithocarpus eucalyptifolia* (Hickel et A.Camus) A.Camus (Burma, Vietnam, Cambodia); *Lithocarpus falconeri* (Kurz) Rehder (Burma, Malaysia); *Lithocarpus garrettianus* (Craib) A.Camus (China, Burma, Laos, Vietnam); *Lithocarpus lucidus* (Roxb.) Rehder (India, Malaysia, Singapore, Indonesia, Brunei); *Lithocarpus macphailii* (Henders.) Barnett (Malaysia, Indonesia); *Lithocarpus wrayi* (King) A.Camus (Vietnam, Malaysia, Indonesia) and *Quercus oidocarpa* Korth. (Burma, Vietnam, Malaysia, Indonesia). Out of these 17 species, at least 14 have a geographic distribution that is primarily or completely located in the Sundaland biogeographic region. Conversely, only three species have a distribution that is mostly or entirely contained within the Indochinese biogeographic region. Despite the paucity of detailed biological records on this remote area, the distributional data shows us that the Fagaceae flora in Ton Pariwat Wildlife Sanctuary is distinctly Sundaic in composition, and differs substantially from forests in the more northern Indochinese region. This is in fact not surprising, as the Ton Pariwat Wildlife Sanctuary is located near the southern edge of one of the world's major phytogeographic and zoogeographic transition zones: the ~500km stretch between the biogeographically distinct and well-known Isthmus of Kra – the narrowest part of the connection between mainland Southeast Asia and the Malay Peninsula (10°30'N) – and the line between Kangar (Malaysia) - 6.°51'N, and Pattani (Thailand) 6°87'N. Within this relatively short distance, an abrupt and major shift takes place from northern Indochinese flora and fauna, to those distinct for the southern Sundaland region (Hughes et al. 2003; Meijaard 2009; Parnell 2013; Van Steenis 1950; Woodruff 2003; Woodruff and Turner 2009).

When looking at the Fagaceae flora in the wider region, some properties of *L. orbicarpus* resemble species in Peninsular Malaysia, such as *Castanopsis nephelioides* King ex Hook.f., but can easily be distinguished from species within *Castanopsis* (D.Don) Spach, based on the presence of bark ridges that penetrate the sapwood, the nut which is not fused to the cup and the orbicular shape of the fruit. Congeneric species from the Indo-Chinese zone that share some characters with *L. orbicarpus* are *L. rouletii* (Hickel & A.Camus) A.Camus (but fruit with basal scar, flattened, dehiscent; South Vietnam); *L. pachycarpus* (Hickel & A.Camus) A.Camus (but leaves with yellow indumentum, cupules pear-shaped, acorns not orbicular; Vietnam-Laos); *L. kontumensis* A.Camus (but cupules truncate, higher than acorn, cupules sometimes fused; Vietnam-Laos); *L. lepidocarpus* (Hayata) Hayata (but cupules truncate, sometimes fused, fruit not orbicular; central and south Taiwan); and *L. laoticus* (Hickel & A.Camus) A.Camus (but cupule ovoid, high elevation habitat (Tibet, south and central China, Vietnam) (Wu et al. 1999). Within Thailand, *L. orbicarpus* is unique in its combination of properties, and we outline some of the defining differences with Thai species in Table 1 below.

Table 1. Morphological differences between *L. orbicarpus* and other Thai species of Fagaceae.

Characters	*L. orbicarpus* Strijk	*L. encleisocarpus* A.Camus	*L. wrayi* (King) A.Camus	*C. nephelioides* King ex Hook.f.
1. Nut wall	Free from the cup	Free from the cup	Free from the cup	Fused to the cup
2. Cupule enclosure	Almost complete, but small apical pore showing flat umbo remains (≤5%). Indehiscent.	Almost complete, but raised umbo free (±5-10%). Easily dehiscent in irregular parts.	Almost complete, but raised umbo free (±5-15%). Indehiscent.	Enclosure complete. Indehiscent.
3. Nut shape	Orbicular.	Ovoid to globose.	Broadly conical.	Ovoid, usually depressed to one longitudinal side.
4. Cup surface	Spines absent. Small, flattened scales present. Irregularly intersecting lines present. Old acorns pubescent with short (occasionally long), greyish-yellow indumentum.	Spines and scales absent. Wall smooth, densely greenish-brown hairy.	Alternate pseudo-spines and free scales present; pseudo-spines incurved or erect.	Sparsely covered with short, woody spines, 2-3 branched reclining and decurved.
5. Acorn shape	Orbicular, symmetric; young fruits occasionally slightly skewered in young and dense infructescences	Ovoid or turbinate.	Broadly ovoid.	Obovoid, always asymmetric, usually flattened adaxially.
6. Leaf margin	Entire throughout.	Entire throughout.	Entire throughout.	Entire or serrate in the upper half.
7. Scar position, shape and size	Orbicular, covering ≥95% of the fruit, from the base upward.	Basal, slightly concave, ca. 1 cm in diameter.	Basal, concave, ca. 1.5 cm in diameter.	- (nut fused to wall).
8. Nut indumentum	Glabrous.	Greyish pubescent.	Sparsely sericeous then dull brown.	- (nut fused to wall).

This species is endemic to Thailand and is currently only known from one location in Ton Pariwat Wildlife Sanctuary. The sanctuary covers a region of low-lying forested mountains with a total area of approximately 100,000 ha at the southern end of the Phuket mountain range. As such it is an integrated part of the Southern Forest Complex of Thailand. The sanctuary is popular for its rich bird- and wildlife (e.g. Blue-banded Kingfisher (*Alcedo euryzona* Temminck, Alcedinidae) and Whitehanded Gibbons (*Hylobates lar* L., Hylobatidae) as well as rare flora, such as *Rafflesia kerrii* Meijer (Rafflesiaceae). Its unique species composition, high diversity and relatively intact forest structure underscore the importance of strengthening ongoing and future conservation measures at Ton Pariwat Wildlife Sanctuary, as a key element of wider conservation efforts in southern Thailand.

Updated key for the species of *Lithocarpus* occurring in Thailand

Following the treatment of Fagaceae for the Flora of Thailand (Phengklai 2008), no further updates have been published. In the updated key we include here, we incorporate the identification of *L. orbicarpus* and add several additional corrections.

Key to the thai species of *Lithocarpus*

(based on vegetative characters and acorns)

1	Outer surface of cupules with annular or lamellate markings or markings lacking	
2	Cupules without lamellae, chartaceous or subcoriaceous, enclosing nearly all of the nut, more or less dehiscent when mature	
3	Cupules weakly dehiscent from the apex, cupule surface distinctly undulate with vertical and horizontal lines	
4	Cupule urn-shaped	
5	Cupule base broadly conical, much broader than apex, skin distinct with many vertical filiform lines or without. Nut conical............**5. *L. blumeanus***	
5	Cupule base obconic, much narrow than apex, surface distinct with 3-4 horizontal filiform lines. Nut obconical....................................**33. *L. maingayi***	
4	Cupule top or globe shaped	
6	Cupule top-shaped, enclosing 4/5 of nut, surface with 2–6 distinct horizontal, filiform lines...**30. *L. macphailii***	
6	Cupule globe-shaped, enclosing nut completely, except for a tiny section at the apex, surface with distinct irregularly placed scales along 5–9 horizontal and vertical lines ....**36. *L. orbicarpus***	
3	Cupules readily dehiscent into irregular parts from the top, surface with 2–5 filiform, undulate, horizontal lines	
7	Cupules with 2 or 3 such lines .... **18. *L. encleisocarpus***	
7	Cupules with 4 or 5 such lines.......................................**37. *L. pattaniensis***	
2	Cupules with distinct lamellae, coriaceous, enclosing a variable amount of the nut, indehiscent	
8	Cupule enclosing not less than 1/2 of the nut	
9	Cupule enclosing about 1/2 of the nut	
10	Nuts ovoid to conical at apex, scar shallowly concave or flattened................. ....**24. *L. gracilis***	
10	Nuts subhemispheric or depressed at apex, scar deeply concave .... **8. *L. clementianus***	
9	Cupule enclosing not less than 3/4 of the nut	
11	Cupules obconic, enclosing nut almost completely except around the umbonate apex	
12	Nut longer than broad, ca. 1 by 0.7 cm ....**26. *L. hendersonianus***	
12	Nut shorter than broad, 1–2.7 by 2–3 cm ....**32. *L. magnificus***	
11	Cupules saucer-shaped, enclosing ca. 3/4 of the nut..............**1. *L. aggregatus***	
8	Cupule enclosing not more than 1/4 of the nut	
13	Nuts hemispheric or depressed on both sides	
14	Cupule enclosing 1/5 to 1/4 of the nut............................**39. *L. platycarpus***	
14	Cupule enclosed only the base of the nut	

15	Acorns sessile. Scar deeply concave..**15. *L. eichleri***
15	Acorns with stalk up to 0.5 cm long. Scar slightly concave.......**6. *L. cantleyanus***
13	Nuts conical to broadly ovoid, or with a dome-shaped apex
16	Cupule enclosing only the base of the nut
17	Acorns sessile. Leaves oblanceolate...**29. *L. lucidus***
17	Acorns with fruit-stalk up to 0.5 cm long. Leaves oblong..... **43. *L. reinwardtii***
16	Cupule enclosing ca. 1/4 of the nut
18	Nut with one horizontal ring around equator. Leaves ensiform to linearlanceolate ....**28. *L. loratefolius***
18	Nut without horizontal ring. Leaves ovate, ovate-oblong or narrowly elliptical
19	Nut ovoid or conical. Cupules cup or saucer-shaped. Leaves ovate or ovate-oblong, apex caudate...**3. *L. bancanus***
19	Nut broadly ovoid. Cupules slightly obconical to saucer-shaped. Leaves narrowly elliptical .... **41. *L. rassa***
1	Outer surface of cupules with alternate lamellae (resembling fish scales) or pseudospines
20	Mature cupules of one infructescence more or less fused together
21	Acorns broader than long, depressed both on top and at base. Cupules saucer- or cupshaped or obconic, some hardly distinct from each other through fusion
22	Infructescences with densely arranged cupules
23	Cupules barely distinct, resembling a large gall .... **13. *L. echinophorus***
23	Cupules distinct, saucer-shaped
24	Nut flattened or apiculate at apex, to 2.2 cm diam. Leaves cuneate at base ... .**16. *L. elegans***
24	Nut retuse at apex, not less than 3 cm diam. Leaves auriculate at base ....**2. *L. auriculatus***
22	Infructescences with spaces between cupules
25	Rachis of infructescence always with sub-branches. Acorns stalked .... **34. *L. mekongensis***
25	Rachis of infructescence without sub-branches
26	Acorns sessile ....**24. *L. finetii***
26	Acorns stalked...**50. *L. tenuinervis***
21	Acorns longer than broad, conical, ovoid or turbinate. Cupules cup-shaped or cylindric
27	Rachis of infructescence always with sub-branches. Acorns stalked, nuts shining
28	Acorn up to 1 cm high. Rachis up to 4 mm in diam...............**7. *L. ceriferus***
28	Acorn not less than 1 cm high (to 2.5 cm). Rachis not less than 4 mm in diam .... **40. *L. polystachyus***
27	Rachis of infructescence without sub-branches. Acorns sessile, nuts more or less shining
29	Twigs glabrous or sparsely pubescent then glabrous
30	Cupules cup-shaped, enclosing up to 1/2 of the nut ....**12. *L. dealbatus***

30   Cupules turbinate, enclosing the whole nut, open only around umbo ....
....**53.** *L. truncatus*

29   Twigs ferruginous or tomentose

31   Leaves glabrous except along midrib. Cupules enclosing up to 1/3 of the nut...**25.** *L. harmandianus*

31   Leaves densely tomentose especially on lower surface. Cupules enclosing 1/2 of the nut...**27.** *L. lindleyanus*

20   Mature cupules of one infructescence, free, not fused

32   Acorn longer than broad, conical, ovoid or obconical. Cupules cup- or saucer-shaped or obconic

33   Cupules enclosing nut completely or 2/3 of the nut

34   Cupules enclosing ca. 2/3 of the nut

35   Cupules slightly obconical-shaped, nuts hairy at style apex (if persistent)......
....**45.** *L. rufescens*

35   Cupules cup or saucer-shaped..**16.** *L. elegans*

34   Cupules enclosing nut completely, or up to the apex of the nut

36   Cupules dehiscent, obconic or ovoid

37   Cupules obovoid, sessile, surface with dense, long and narrow recurved pseudospines...**42.** *L. recurvatus*

37   Cupules ovoid, fruit stalk 2–3 mm long, surface finely ornamented with thin, triangular lamellae throughout...................................**35.** *L. neo-robinsonii*

36   Cupules indehiscent, ovoid, surface clothed with dense, triangular lamellae

38   Infructescences up to 18 cm long. Leaves up to 16 cm long.....**9.** *L. craibianus*

38   Infructescences not less than 20 cm long. Leaves not less than 20 cm long ...
....**19.** *L. erythrocarpus*

33   Cupules enclosing up to 1/2 of the nut

39   Acorns stalked

40   Cupules slightly obconic. Leaves ovate, ovate-oblong or obovate ....
....**48.** *L. sootepensis*

40   Cupules cup-shaped or saucer-shaped

41   Cupules cup-shaped. Leaves lanceolate to lanceolate oblong........**47.** *L. siamensis*

41   Cupules saucer-shaped to flattened. Leaves oblong to oblong-lanceolate.......
....**10.** *L. curtissii*

39   Acorns sessile

42   Acorns (mature) not less than 3.5 by 2.2 cm

43   Cupule lamellae bearing pseudo-spined reflexed towards the base. Leaves acute to obtuse at apex...**46.** *L. scortechinii*

43   Lamellae curved towards the cupule apex. Leaves acuminate at apex............
....**20.** *L. eucalyptifolius*

42   Acorns (mature) up to 3 by 2.2 cm

44   Infructescence with acorns in clusters, but not fused

45   Nuts ovoid. Leaves usually curved to one side...............**54.** *L. wallichianus*

45   Nuts strongly apically depressed, occasionally conic. Leaves not curved ....
        .... **51. *L. thomsonii***
44   Infructescence with acorns solitary, with spaces between them
46   Cupules saucer or cup-shaped, limb recurved. Leaves not less than 12 cm
        long .... **21. *L. falconeri***
46   Cupules obconical, limb not recurved. Leaves up to 11 cm long ....
        ....**4. *L. bennettii***
32   Acorns broader than long, hemisphaeric-depressed
47   Cupules enclosing the nut completely or up to the apex of the nut
48   Cupules more or less up to the apex of the nut, lamellae with erect or reflexed
        pseudospines which are not fused
49   Pseudo-spines erect or spreading. Leaves oblanceolate. Scar nearly 1/2 of the
        nut..**14. *L. echinops***
49   Pseudo-spines reflexed. Leaves oblong or oblanceolate
50   Infructescence with acorns packed close together, but not fused. Leaves
        slightly cuneate at base..**23. *L. garrettianus***
50   Infructescence with acorns solitary, with spaces between them. Leaves obtuse
        at base.. **54. *L. tubulosus***
48   Cupules enclosing the nut completely, except the umbo
51   Lamellae pointed, with narrowly pseudospines. Infructescence with acorns
        packed close together, but not fused .... **57. *L. wrayi***
51   Lamellae flattened and imbricate. Infructescence with acorns solitary, with
        spaces between them
52   Lamellae fused on lower half, the upper half free and adaxially curved..........
        ....**22. *L. fenestratus***
52   Lamentas fused almost to apex, only a short free lobe adaxially curved..........
        ....**52. *L. trachycarpus***
47   Cupules enclosing up to 1/2 of the nut
53   Acorns stalked, cupules enclosing only base of the nut
54   Stalk up to 1 cm long. Leaves glaucous on lower surface, petiole up to 1 cm
        long .... **49. *L. sundaicus***
54   Stalk not less than 1 cm long. Leaves pale on lower surface, not glaucous,
        petiole not less than 1 cm long.. **31. *L. magneinii***
53   Acorns sessile, cupules enclosing up to 1/2 of the nut
55   Acorns not less than 2 by 2.5 cm
56   Cupules slightly obconical. Leaves oblong, acute to caudate at apex, margin
        not revolute, petiole not less than 1 cm............................**11. *L. cyclophorus***
56   Cupules saucer-shaped. Leaves obovate, obtuse at apex, margin revolute, pet-
        iole up to 0.6 cm long..**44. *L. revolutus***
55   Acorns up to 1.5 by 2 cm
57   Nuts convex at the apex
58   Cupules saucer-shaped to flattened and discoid. Leaves not whorled
59   Lamellae usually fused throughout. Leaves up to 15 cm long...**38. *L. pierrei***

59   Lamellae fused at base only, apices free. Leaves not less than 18 cm ....
        long .... **17. *L. elephantum***
58   Cupules cup-shaped. Leaves usually whorled at the twig tips... **58. *L. xylocarpus***
57   Nuts flattened at the apex. Cupule cup-shaped, enclosing 1/5 to 1/2 of the
        nut. Leaves with unequal sides, usually curved to one side
60   Leaves oblong, elliptic oblong, not less than 10 by 3.5 cm, with 14–20 pairs
        of lateral nerves.. **55. *L. vestitus***

Acknowledgements

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RESEARCH ARTICLE

An interactive key to the *Chrysochromulina* species (Haptophyta) described in the literature

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Abstract

We present a general overview of features and technical specifications of an original interactive key web application for the identification of *Chrysochromulina* species. The list of species, originally described as belonging in the genus *Chrysochromulina*, is given and recent taxonomic changes in species and genera of the order Prymnesiales are provided. We briefly discuss the interest of such a key for the identification of phytoplanktonic species.

Keywords

Introduction

The genus *Chrysochromulina,* erected by Lackey (1939) is an important component of the marine and brackish phytoplankton although the type species occured in fresh water. Electron microscopy (EM) has been a key tool for a specific identification and Mary Parke & Irene Manton were pioneers in reviewing the type species (Parke et al. 1962) and describing more than ten species between 1955 and 1966. They remained for many years the specialists of the genus until Barry Leadbeater added some more new species so that almost half the number of species known today were described by 1974. With the extent of TEM (Transmission Electron Microscopy) or SEM (Scanning Electron Microscopy)

studies, the genus appeared worldwide distributed and some species were found to produce massive blooms, some of which were eventually toxic (Moestrup 1994). The 1988 bloom of *Chrysochromulina polylepis* Manton & Parke (Dahl et al.1989) was the first event of toxic bloom causing important economic impact, raising a considerable interest of the scientific community especially in Scandinavia. Two PhD thesis were submitted (Jensen 1998, Eikrem 1999) with an illustrated key for identification of species of this genus, based on morphological characters (Eikrem et al. 1998). With the 21th century molecular biology introduced changes in the delineation of classes and orders and the genus *Chrysochromulina* was considered as polyphyletic (Edvardsen et al. 2000).

The class name Haptophyceae was first used by Christensen in 1962 but Hibberd introduced the typified class name Prymnesiophyceae (Hibberd 1976), both names being considered as valid. More recently Silva et al. (2007) advise the use of the name Coccolithophyceae for this class, considering that the class name Coccolithophyceae Rothmaler 1951 had priority over Haptophyceae and Prymnesiophyceae. However this class name remains a matter of debate and therefore is not mentionned in the title.

Within the class, the genus *Chrysochromulina* was for a long time placed in the order Prymnesiales and the family Prymnesiaceae. However, from DNA phylogenies and morphological comparisons, Edvardsen et al. (2011) reviewed the taxonomy of the Prymnesiales. They emended the Family Prymnesiaceae W. Conrad ex O.C. Schmidt emend. Edvardsen, Eikrem & Medlin, (Edvardsen et al. 2011), placing five species of *Chrysochromulina* (*C. palpebralis*, *C. polylepis*, *C. kappa*, *C. chiton* and *C. minor*) in the genus *Prymnesium*, and five other species (*C. brevifila*, *C. ericina*, *C. fragaria*, *C. herdlensis* & *C. hirta*) in the new genus *Haptolina* Edvardsen & Eikrem (Edvardsen et al. 2011). An unnamed species, cited as *Chrysochromulina* sp4 (Eikrem & Edvardsen, 1999), is considered as the type species of the new genus *Pseudohaptolina* Edvardsen & Eikrem. They give a formal description of this species as *P. arctica* Edvardsen & Eikrem (Edvardsen et al. 2011). Because of these changes, the family Chrysochromulinaceae Edvardsen, Eikrem & Medlin is now restricted to the unique genus *Chrysochromulina* with the remaining species, all being saddle-shaped cells (Edvardsen et al. 2011).

As we are dealing here with an identification key, we have taken into consideration all species originally described as *Chrysochromulina* in the literature (or moved to this genus as for *Chrysocampanula spinifera* (Fournier) by Pienaar and Norris in 1979) but modifications of their taxonomic status are mentioned in the species descriptions. References are restricted to papers giving the original description of a species or an emended description.

Project description

Taxonomic coverage

The key covers 58 species originally described as *Chrysochromulina*. References for publications dealing with their description and occurrence are given. A detailed description

is provided and illustrations of a whole cell as well as for the different scale types, in some cases from unpublished material seen in SEM, are included. It is noticeable that two of them have different morphologies described as "forma": *C. polylepis* , now *Prymnesium polylepis*, "authentic" or "alternate" (Edvardsen and Paasche 1992, Edvardsen et al. 1996, Edvardsen and Medlin 1998); *C. palpebralis* f. *palpebralis* or *C. palpebralis* f. *bisquamata* (Seoane et al. 2009). As mentioned before, an additional species, referred to as *Chrysochromulina* sp. 4 (Eikrem and Edvardsen 1999) is now considered as the type species of the new genus *Pseudohaptolina* (Edvardsen et al. 2011). The terminal taxa of the key are 63 because all morphological forms are treated separately. A few of them (freshwater species) are poorly described (*C. inornamenta* Wujek & Gardiner, *C. chiton* var. *minuta* and *C. papillata* Gao, Tseng & Guo, *C. laurentiana* Kling) but still may be identified through this key.

List of the terminal taxa included in the current version of the database (last update, July 2013)

Chrysochromulina acantha Leadbeater & Manton (1971); *Chrysochromulina adriatica* Leadbeater (1974); *Chrysochromulina arenghotii* Jensen & Moestrup (1999); *Chrysochromulina alifera* Parke & Manton (1956) in Parke et al. (1956); *Chrysochromulina apheles* Moestrup & Thomsen (1986); *Chrysochromulina bergenensis* Leadbeater (1972); *Chrysochromulina birgeri* Hällfors & Niemi (1974); *Chrysochromulina brachycylindra* Hällfors & Thomsen (1985); *Chrysochromulina brevifilum* Parke & Manton (1955) in Parke et al. (1955), now *Haptolina brevifila* (Parke & Manton) Edvardsen & Eikrem 2011; *Chrysochromulina breviturrita* Nicholls (1978); *Chrysochromulina camella* Leadbeater & Manton (1969); *Chrysochromulina campanulifera* Manton & Leadbeater (1974); *Chrysochromulina chiton* Parke & Manton (1958) in Parke et al. (1958), now *Prymnesium chiton* (Parke & Manton) Edvardsen, Eikrem & Probert (2011); *Chrysochromulina chiton* var. *minuta* Gao, Tseng & Guo (1993); *Chrysochromulina cyathophora* Thomsen (1979); *Chrysochromulina cymbium* Leadbeater & Manton (1969); *Chrysochromulina discophora* Manton (1983); *Chrysochromulina elegans* Estep et al. (1984); *Chrysochromulina ephippium* Parke & Manton (1956) in Parke et al. (1956); *Chrysochromulina ericina* Parke & Manton (1956) in Parke et al. (1956), now *Haptolina ericina* (Parke & Manton) Edvardsen & Eikrem 2011; *Chrysochromulina fragaria* Eikrem & Edvardsen (1999), now *Haptolina fragaria* (Eikrem & Edvardsen) Edvardsen & Eikrem 2011; *Chrysochromulina fragilis* Leadbeater (1972); *Chrysochromulina herdlensis* Leadbeater (1972), now *Haptolina herdlensis* (B. Leadbeater) Edvardsen & Eikrem 2011; *Chrysochromulina hirta* Manton (1978b), now *Haptolina hirta* (Manton) Edvardsen & Eikrem 2011; *Chrysochromulina inornamenta* Wujek & Gardiner (1985); *Chrysochromulina kappa* Parke & Manton (1955) in Parke et al. (1955), now *Prymnesium kappa* (Parke & Manton) Edvardsen, Eikrem & Probert, 2011; *Chrysochromulina lanceolata* Chrétiennot-Dinet, Nezan & Puigserver (2003) in Puigserver et al. (2003); *Chrysochromulina latilepis* Manton (1982); *Chrys-*

ochromulina laurentiana Kling H.J. (1981); *Chrysochromulina leadbeateri* Eikrem & Throndsen (1998); *Chrysochromulina limonia* Jensen & Moestrup (1998); *Chrysochromulina mactra* Manton (1972); *Chrysochromulina mantoniae* Leadbeater (1972) ; *Chrysochromulina megacylindra* Leadbeater (1972); *Chrysochromulina microcylindra* Leadbeater (1972); *Chrysochromulina minor* Parke & Manton (1955) in Parke et al. (1955), now *Prymnesium minus* (Parke & Manton) Edvardsen, Eikrem & Probert, 2011; *Chrysochromulina novae-zelandiae* Moestrup (1979); *Chrysochromulina orbiculata* Rouchijajnen (1972); *Chrysochromulina pachycylindra* Manton & Oates (1981) in Manton et al. (1981); *Chrysochromulina palpebralis* Seoane, Eikrem, Edvardsen & Pienaar (2009), now *Prymnesium palpebrale* (Seoane, Eikrem, Edvardsen & Pienaar) Edvardsen, Eikrem & Probert, 2011; *Chrysochromulina papillata* Gao, Tseng & Guo (1993); *Chrysochromulina parkae* Green & Leadbeater, (1972); *Chrysochromulina parva* Lackey (1939); *Chrysochromulina pelagica* Estep, Davis, Hargraves & Sieburth (1984); *Chrysochromulina planisquama* Hu & Tseng (2005) in Hu et al. (2005); *Chrysochromulina polylepis* Manton & Parke (1962), now *Prymnesium polylepis* (Manton & Parke) Edvardsen, Eikrem & Probert, 2011; *Chrysochromulina pontica* Rouchijajnen (1966); *Chrysochromulina pringsheimii* Parke & Manton (1962); *Chrysochromulina pseudolanceolata* Chrétiennot-Dinet & Puigserver (2003) in Puigserver et al. (2003); *Chrysochromulina pyramidosa* Thomsen (1977); *Chrysochromulina quadrikonta* Kawachi & Inouye (1993); *Chrysochromulina rotalis* Eikrem & Throndsen (1999); *Chrysochromulina scutellum* Eikrem & Moestrup (1998); *Chrysochromulina simplex* Estep, Davis, Hargraves & Sieburth (1984) emend. Birkhead and Pienaar (1995); *Chrysochromulina spinifera* (Fournier 1971) Pienaar & Norris (1979) back to *Chrysocampanula spinifera Fournier 1971* (see Edvarsen et al. 2011); *Chrysochromulina strobilus* Parke and Manton (1959) in Parke et al. (1959); *Chrysochromulina tenuispina* Manton (1978a); *Chrysochromulina tenuisquama* Estep, Davis, Hargraves & Sieburt (1984); *Chrysochromulina throndsenii* Eikrem (1996); *Chrysochromulina vexillifera* Manton & Oates (1983).

Characters used in the key

The key matrix is based on one ecological character (habitat) and 19 morphological descriptors seen in light or electron microscopy, under live conditions or after fixation for EM observations. They range from cell shape to scale ornamentation. Details of scales can be obtained by specific techniques with TEM, such as direct preparations (Moestrup and Thomsen 1980, Jensen 1998) and cultures are generally needed. Although rarely used, SEM can also provide interesting results with natural samples (Puigserver et al. 2003). For fragile cells, 3 mL of sample are fixed with 50 µL of a 1:1 Lugol/Glutaraldehyde (25%) solution, centrifuged on a Thermanox cell culture coverslip coated with poly-L-lysine (0.1%) for a better adherence of cells, critical point dried and then examined with a field emission scanning electron microscope.

List of descriptors used in the key:

HABITAT: marine, brackish, freshwater
SHAPE: spherical-subspherical, elongate to round, lanceolate, saddle-shaped
CELL LENGTH, CELL WIDTH: min. and max. sizes are given for each form or
    species.
FLAGELLA: Two flagella are present and may be equal or sub-equal, in that case the
    length of the longer and shorter flagellum are given.
HAPTONEMA BEHAVIOR: coiling, rarely coiling, non coiling.
HAPTONEMA LENGTH: min. and max. size (in some cases, the haptonema may
    be very long)
NUMBER OF SCALE TYPES: in some cases, scales may be displayed in several layers and
    show up to four different types but there is always a layer of plate scales as cell covering.
SCALE APPENDICES: besides plate scales, a number of different appendices can be
    observed : spine, cylinder or another typical ornamentation.
PLATE SCALE LENGTH AND WIDTH: min. and max. sizes are given for all plate
    scales.

Software used

The interactive key is developed using Xper2 version 2.2 software. It is free software available with multilingual interface and compatible with different OS (Windows, MacOS and Linux) under a creative commons license (BY-CC-ND). You can download it on http://www.infosyslab.fr and find on this website a complete documentation with technical details, user manual and knowledge bases.

Xper2 offers an editor to structure and analyse descriptive data and an interface for interactive free access key (Ung et al. 2010). Keys of various taxonomic groups are already available with Xper2 (Kerner et al. 2011) (Mathieu et al. 2012) (Thomas and De Franceschi 2013).

We installed the interactive key on a web server with Apache2, choosing the English interface. This content is under a creative commons license (BY-CC-ND), except when a special information is attached to images.

The knowledge base

Xper2 manages structured descriptive data: all the terminal taxa of the key are described using the same terms (descriptor and character states labels), and so the taxa can be compared automatically.

Figure 1 presents the comparison of the two forms attributed to *Prymnesium palpebrale* (previously *Chrysochromulina palpebralis*). The different colors allow to point

Comparison

	Chrysochromulina palpebralis f. bisquamata = Prymnesium palpebrale	Chrysochromulina palpebralis f. palpebralis = Prymnesium palpebrale	UNION	INTERSECTION
Habitat	Marine	Marine	Marine	Marine
Shape	elongate to round	elongate to round	elongate to round	elongate to round
Cell length	Min:8.0 Max:13.0	Min:8.0 Max:13.0	[8.0;13.0] & [8.0;13.0]	[8.0;13.0]
Cell width	Min:6.0 Max:9.0	Min:6.0 Max:9.0	[6.0;9.0] & [6.0;9.0]	[6.0;9.0]
Flagella	Equal	Equal	Equal	Equal
Flagella length	Min:20.0 Max:27.0	Min:20.0 Max:27.0	[20.0;27.0] & [20.0;27.0]	[20.0;27.0]
Haptonema behavior	non coiling	non coiling	non coiling	non coiling
Haptonema length	Min:7.0 Max:15.0	Min:7.0 Max:15.0	[7.0;15.0] & [7.0;15.0]	[7.0;15.0]
Number of scale types	2	3	2, 3	
Scale appendices	Absent	Present	Absent, Present	
Scale appendices type	not applicable	Spine; Other	Spine, Other	
Spine length	not applicable	Min:0.5 Max:1.0	[0.5;1.0]	[0.5;1.0]
Other appendice characteristics	not applicable	eye-lash projections	eye-lash projections	
Plate scale sizes	Min:0.39 Max:1.25	Min:0.54 Max:0.93	[0.39;1.25]	[0.54;0.93]
Specific scale ornamentation	yes	yes	yes	yes

Legend: Discrimination / Partial discrimination / No discrimination

Save   Print   Close

Figure 1. Comparison of the two forms of *Prymnesium palpebrale*. The two forms are very similar and differ only on scales and appendices.

easily where the descriptions are distinct, overlap, or are the same. Here the two forms differ on scale type number and appendices.

In the same way the comparison of the five species (*Haptolina brevifila*, *H. ericina*, *H. fragaria*, *H. herdlensis* and *H. hirta*) previously known as *Chrysochromulina* but attributed in 2011 in the new genus *Haptolina* (Edvardsen et al. 2011) shows that these species share few attributes used in the key (Figure 2).

The online interactive key

Our key of the *Chrysochromulina* species is a free access key accessible at http://www.obs-banyuls.fr/chrysochromulina. It offers an interactive and flexible way to identify these phytoplanktonic species.

Figure 2. Comparison of the five species of the new genus *Haptolina*. The column «intersection» on the right side gives the values shared by the five species.

A classical polytomous key consists of a series of questions (characters), each one offering alternative statements (Hagedorn et al. 2010). A free access key is a more flexible identification key: the sequence of choices is defined by the user preventing these of characters difficult or impossible to observe.

Figure 3 shows the screen during an identification process. Each item (terminal taxon of the key) is documented by a text including nomenclatural data, type locality, literature references and morphological data, and is illustrated by several images. Descriptors and character states are also documented and illustrated.

At each step, the user may ask the software to find the best characters to distinguish the possible taxa. Three different measures are proposed Xper, Jaccard, and Sokal & Michener (as "Best descriptors" in the select box). For each pair of remaining taxa, each coefficient measurement compares the possible states and the final result is the sum for all the pairs. Xper coefficient checks only if there is no overlap (it means the two taxa may be completely distinct on this character) and so the measure for one pair of taxa is 0 (if overlapping) and 1 (if no overlapping). Jaccard coefficient was initially developed to compare sets of binary characters; here the states are considered as the binary characters and the
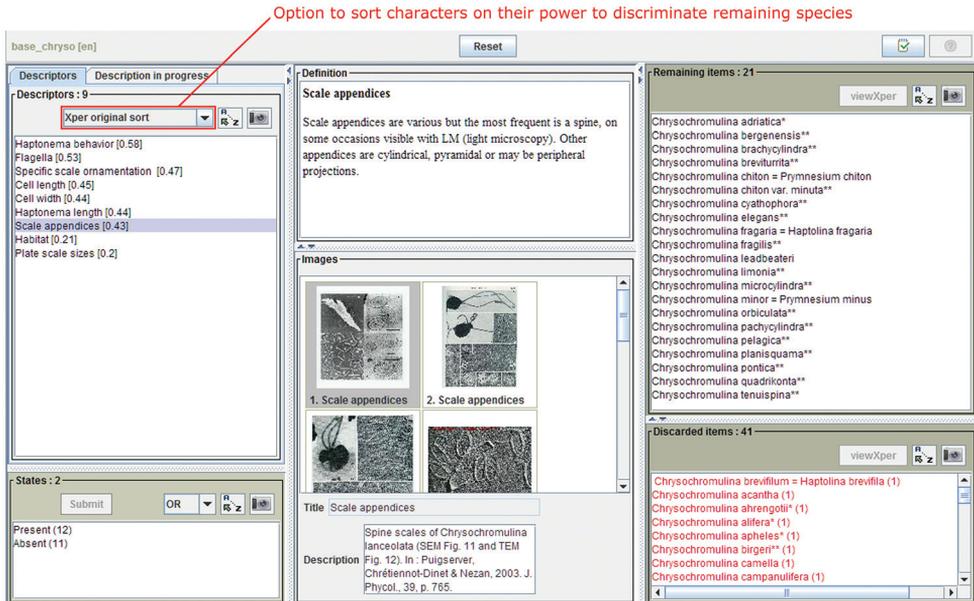
Figure 3. Example of screen of the free access key. On the left the user chooses descriptor and states with the help of the additional ressources, text and images in the center of the screen. On the right the lists of remaining and eliminated species.

comparison takes into account the ratio between the number of states possible for only one taxon of the pair and the number of states possible for at least one taxon of the pair. In the Sokal & Michener coefficient, the states which are not possible for the two taxa are also taken into account. The three measures are described in Burguière et al. (2013).

Conclusions

Identification of *Chrysochromulina* species has long been reserved to specialists as it is a major difficulty for most phytoplanktonologists. The cells are very small, often overlooked or placed as "unidentified" species in field studies. Cultures and specific preparations are generally needed to get relevant information on morphological features. A key for identification of Scandinavian species (Eikrem et al. 1998), based on TEM observations of cultures has only been published in PhD Theses (Jensen1998 and Eikrem 1999). A list of species as part of toxic haptophytes was published by Moestrup & Thomsen in a manual on harmful marine microalgae (Moestrup and Thomsen 2004). However original descriptions are not always available for researchers. In this interactive key, all species found in the literature are treated and information necessary for their identification is provided. This key is a very powerful tool for a taxonomic work on the genus and is therefore strongly recommended, especially for phytoplanktonologists working on nanoflagellates. The content of the key was carefully checked

Figure 4. Example of descriptors (in red) that allow differentiation between *C. lanceolata* and a specimen under identification.

and tested with information on species characteristics found in the Scandinavian key (Jensen 1998, Eikrem 1999) and unpublished data obtained by one author (M-J C-D). Among all descriptors used in this key, those concerning the scale description are most important and the mean number of required characters to identify a species is 4.3. SEM preparations from field samples seem promising for identification of these species (Puigserver et al. 2003 and unpublished illustrations shown in the key). The choice of characters introduced without order is also an important advantage as compared to a classical key: characteristics of a typical scale may be enough for a specific identification.

Acknowledgements

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