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Review of the flower-inhabiting water scavenger beetle genus *Cycreon* (Coleoptera, Hydrophilidae), with descriptions of new species and comments on its biology

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Abstract

The hydrophilid genus *Cycreon* Orchymont, 1919, previously known from two historical specimens only, is reviewed based on the numerous material collected recently from the inflorescences of various Araceae species in the Malay Peninsula and Borneo. Four species are recognized in the genus: *C. sculpturatus* Orchymont, 1919 from Sumatra, *C. armandi* Shatrovskiy, 2017 from Singapore, *C. adolescens* **sp. n.** from peninsular Malaysia, and *C. floricola* **sp. n.** with two subspecies, the nominotypical one from Peninsular Malaysia, and *C. floricola borneanus* **subsp. n.** from Borneo. All species are very similar, differing only by the pronotal punctation, shape of the clypeus and the mentum, and the form of the median lobe of the aedeagus. Specimens of *C. floricola* **sp. n.** and *C. adolescens* **sp. n.** were collected from inflorescences of various genera of the family Araceae. The field observations and analysis of mid gut contents indicates that they feed on organic material on internal organs of the inflorescences, including the pollen of the host plant. They were also observed to carry a large amount of pollen and are likely pollinators of their host species of Araceae.

Introduction

Among the water scavenger beetles (Polyphaga: Hydrophiloidea: Hydrophilidae), the members of the tribe Megasternini stand out in terms of species and morphological diversity, faster speciation rate and the wide array of microenvironments inhabited (Bloom et al. 2014; Fikáček et al. 2009, 2012). Most of the megasternine species are associated with various kinds of decaying organic matter, like mammal dung (e.g., Smetana 1978, Ryndevich 2008, Ryndevich et al. 2017, Arriaga-Varela et al. 2017, 2018), humid forest leaf-litter (e.g., Deler-Hernández et

al. 2015; Fikáček et al. 2009; Fikáček and Short 2006) or rotten seaweed (e.g., Smetana 1978; Ryndevich 2001). In contrast to this general pattern, few genera are known to inhabit the interior of various inflorescences: the Neotropical *Pelosoma* Mulsant has been collected inside *Heliconia* flowers (Archangelsky 1997), and the Neotropical *Nitidulodes* Sharp and Oriental *Cycreon* Orchymont, 1919 were recently reported to be associated to Araceae flowers (Bloom et al. 2014; Low et al. 2016; Hoe and Wong 2016; Hoe et al. 2018). However, very little is known about the biology and the systematics of these genera.

Only two specimens of *Cycreon* are known so far in the literature, representing two different species. The genus was described by d'Orchymont (1919) with *Cycreon sculpturatus* d'Orchymont, 1919 as the only species, based on a single female specimen collected in Palembang, Sumatra without any detailed collecting data. An additional male specimen from Singapore was later examined by d'Orchymont and labeled as '*Cycreon emarginatus* sp. n., however, whether is it not the male of *C. sculpturatus*', but never published. Both specimens were moreover on loan from d'Orchymont collection when M. Hansen was preparing a generic review of the hydrophiloid beetles (Hansen 1991). Shatrovskiy (2017) examined both these specimens and described the second specimen, male from Singapore, as *Cycreon armandi*.

Extensive sampling of insects associated with inflorescences of Malayan aroid plants was performed recently by Low et al. (2014, 2016), Hoe and Wong (2016) and Hoe et al. (2018) in order to study their pollination biology, and Takizawa (2010) in order to study the association of species of *Chaloenus* Westwood, 1861 (Chrysomelidae) with these inflorescences. As a result, a high number of *Cycreon* specimens from both Peninsular Malaysia and Borneo was accumulated. In this study, we use this material to redescribe and illustrate the genus *Cycreon* in detail, to revise the systematics of the genus, and to sum up the available data on the biology of the genus.

Material and methods

Examined specimens and depositories. A total of 1444 specimens of *Cycreon* were examined. Label data are reproduced verbatim; notes on the label data or additional information are written between square brackets []. List of examined specimens is available in DarwinCore-formatted spreadsheet file at Zenodo repository (https://doi.org/10.5281/zenodo.1258208). This file was also used to prepare the distribution map using QGIS software and freely available GLOBE altitude data and DIVA-GIS country borders data. The authors did not examine holotypes of *C. sculpturatus* and *C. armandi* as these are not accessible for the examination, and adopted the information about them from Shatrovskiy (2017). In addition, A. Shatrovskiy kindly provided a new photograph of ventral view of the head of *C. sculpturatus* used to illustrate the shape of the mentum of this species (Fig. 5P).

The examined specimens are deposited in the following collections:

BMNH Natural History Museum, London, United Kingdom (M.V.L. Barclay);
EIHU Hokkaido University Museum, Sapporo, Japan (M. Ôhara);
IBTP BORNEENSIS Collection, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah (P. Jimbau);
IRSNB Institute Royal des Sciences Naturelles de Belgique, Brussels, Belgium (P. Limbourg);
KMNH Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan (Y. Minoshima);
NHMW Naturhistorisches Museum, Wien, Austria (M. A. Jäch);
NMPC National Museum, Prague, Czech Republic (M. Fikáček);
SRBC Sergey Ryndevich collection, Baranovichy, Belarus;
ZIN Zoological Institute of the Russian Academy of Science, St. Petersburg, Russia (A.G. Kirejtshuk);
ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (J. Frisch, B. Jäger);
ZMUC Zoological Museum, Natural History Museum of Denmark (A.Yu. Solodovnikov).

Morphological studies. Specimens were dissected, with genitalia embedded in a drop of alcohol-soluble Euparal resin on a piece of glass glued to a small piece of cardboard attached below the respective specimen. Habitus photographs were taken using a Canon D-550 digital camera with attached Canon MP-E65mm f/2.8 1–5 macro lens. Pictures of genitalia were taken using a Canon D1100 digital camera attached to an Olympus BX41 compound microscope; combined pictures were were made with Helicon Focus software. Scanning electron micrographs were taken using Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum in Prague. Pictures used for plates were adapted in Adobe Photoshop CS6. All original pictures including additional views not presented in this paper are included in the dataset submitted to the Zenodo archive under doi 10.5281/zenodo.1258208.

All known species of *Cycreon* are very similar and share most structural characters. We therefore provide a generic description which includes shared morphological features, while the species descriptions are restricted mostly to species-specific characters.

Taxonomy

Cycreon Orchymont, 1919

Cycreon Orchymont, 1919: 119.

Types species. *Cycreon sculpturatus* Orchymont, 1919 (by original designation).

Diagnosis. (1) antennal grooves on prosternum small and marked by a weak ridge close to the lateral margins of prosternum (Fig. 2C–D); (2) mentum deeply excised anteromesally (Figs 1J, 2B, 5B, E, H, L, P) ; (3) mesoventral medial elevation reduced to a narrow carina (Fig. 2E–F); (4) grooves for reception of procoxae absent (Fig. 2E–F); (5) metaventrite without abdominal lines or demarcated anterolateral angles (Fig. 2E), (6) abdominal ventrite 1 not carinate medially (Fig. 2G); (7) aedeagus with the median lobe not fused to the bases of parameres, reaching into the phallobase; (8) median portion of male sternite 9 tongue-like (Fig. 3D, H, M).

Note. Orchymont (1919) mentioned the absence of antennal grooves, which were supposed by Hansen (1991) who did not have the chance to study specimens of this genus. Shatrovskiy (2017) revealed that antennal grooves are present although very small, and weakly marked by a faint ridge.

Differential diagnosis. *Cycreon* is distinct among Megasternini in lacking the median carina of abdominal ventrite 1 (Fig. 2G); in this character it only corresponds to the Megasternini genera *Pyretus* Balfour-Browne and *Acaryon* Hebauer. From *Pyretus*, *Cycreon* is easily diagnosed by the narrowly laminate elevation (in contrast to widely pentagonal and widely contacting metaventrite in *Pyretus*), simply carinate median portion of prosternum (forming an elevated prosternal plate in *Pyretus*), and small antennal grooves (antennal grooves are large and reaching lateral pronotal margin in *Pyretus*). The genus *Acaryon* from Madagascar is similar to *Cycreon* in many characters, including the relatively large eyes, simply carinate prosternum, antennal grooves not reaching pronotal margin, narrowly carinate elevation on mesoventrite, metaventrite without additional ridges, and dorsal punctation (with semicircular to circular punctures in *Cycreon*, and circular setiferous punctures intermixed with usual punctation in *Acaryon*). However, *Cycreon* can be distinguished from *Acaryon* by the shape of the mentum (deeply emarginate anteromedially in *Cycreon*, weakly sinuate on anterior margin in *Acycreon*), presence of the grooves for reception of procoxae at sides of the mesoventral elevation (absent in *Cycreon*, present in *Acaryon*) and the dorsal colouration (unicoloured or bicoloured in *Cycreon*, unicoloured yellow with dark central pronotal spot in *Acaryon*).

Description. Body (Fig. 1A–D) 2.2–3.4 mm long, elongate-oval, weakly convex. Colouration more or less reddish-brown, pronotum and underside usually somewhat paler (yellowish-brown), elytra usually darker.

Head. Clypeus with anterior margin with very fine bead, anteromedian margin slightly to strongly emarginate medially (Figs 1E, 5A, D, G, K, O), anterolateral angles rounded, antennal bases exposed; frontoclypeal suture distinct laterally, reduced in medial third; transverse ridges absent. Median portion of frons and clypeus not elevated above remaining surface. Dorsal surface glabrous, with dense punctation composed of shallow circular impressions (incomplete in some species), with a small puncture at anterior margin; interstices between punctures without visible microsculpture (Fig. 4A, D, G). Eyes moderately large, with dorsally visible portion slightly smaller than ventral one, separated by 4.9–5.5× the width of one eye in dorsal view. Labrum (Fig. 1I) ca. 0.4× as wide as head, membranous, largely retracted under clypeus, very weakly bisinuate at anterior margin, moderately densely pubescent dorsally, setae becoming longer on lateral portions. Mandible (Fig. 1F–H) with apex deeply bifid (teeth may be partially abraded in some specimens; compare Fig. 1F, G), curved; its external margin very weekly crenulate at basal half; prostheca with anterior third covered by long thin setae, distal group of these setae facing ventrally and proximal group of them facing mesally (Fig. 1H); mola with fine lamellae having poriferous structure. Maxilla of male with sucking disc on galea (Fig. 2B); maxillary palps with basal palpomere minute, palpomere 2 large, widened at apical half, 1.2× as long as palpomere 3, palpomere 3 slightly shorter than palpomere 4, slightly widening apicad, palpomere 4 fusiform, without digitiform sensilla. Mentum (Figs 1J, 2B, 5B, E, H, L, P) transverse, about twice as wide as long, lateral margins with few sparse setae, anterior margin very deeply emarginate; labial palps trimerous, palpomere 1 transverse, palpomere 2 subequal in width but slightly longer than palpomere 1 and with few long setae, palpomere 3 narrow, slightly longer than palpomere 2. Submentum with moderately dense setiferous punctures, gular sutures vaguely developed, rather widely separated from each other, tentorial pits small, almost rounded. Antenna with 9 antennomeres; scape (antennomere 1) long, cylindrical, constricted medially; pedicel (antennomere 2) rather short, bulbous basally; antennomeres 3–5 short, subequal in length, antennomere 5 much wider than preceding ones; cupule slightly asymmetrical, as long as antennomere 5; antennomeres 7–9 forming an elongate pubescent club (2.2× longer than wide), antennomeres 7–8 subequal in length, antennomere 9 slightly longer, roundly subacuminate at apex; sensorial antennal fields absent. Genal ridge absent.

Prothorax. Pronotum transverse, moderately convex, about as wide as bases of elytra combined; lateral margins minutely bordered; anterior and posterior angles rounded (Fig. 1E); punctation dense, composed of shallow circular impressions with one small puncture at posterior margin, circular impression sometimes incomplete (Fig. 4B, E, H). Prosternum (Fig. 2C) weakly raised medially, with faint longitudinal carina; prosternal process short, almost reaching midlenght of procoxal cavities, not bifurcate; precoxal part short. Procoxal cavities large, open posteriorly. Notosternal suture distinct. Antennal grooves present, very short, vaguely defined by thin ridge parallel to lateral notosternal suture, vanishing posteriad (Fig. 2C–D).

Mesothorax. Mesoventrite completely fused with anepisternum; anterior collar of mesothorax narrow. Median portion of mesoventrite simply tectiform, elevation forming a ridge shortly overlapping anterior margin of metaventrite. Grooves for reception of procoxae absent

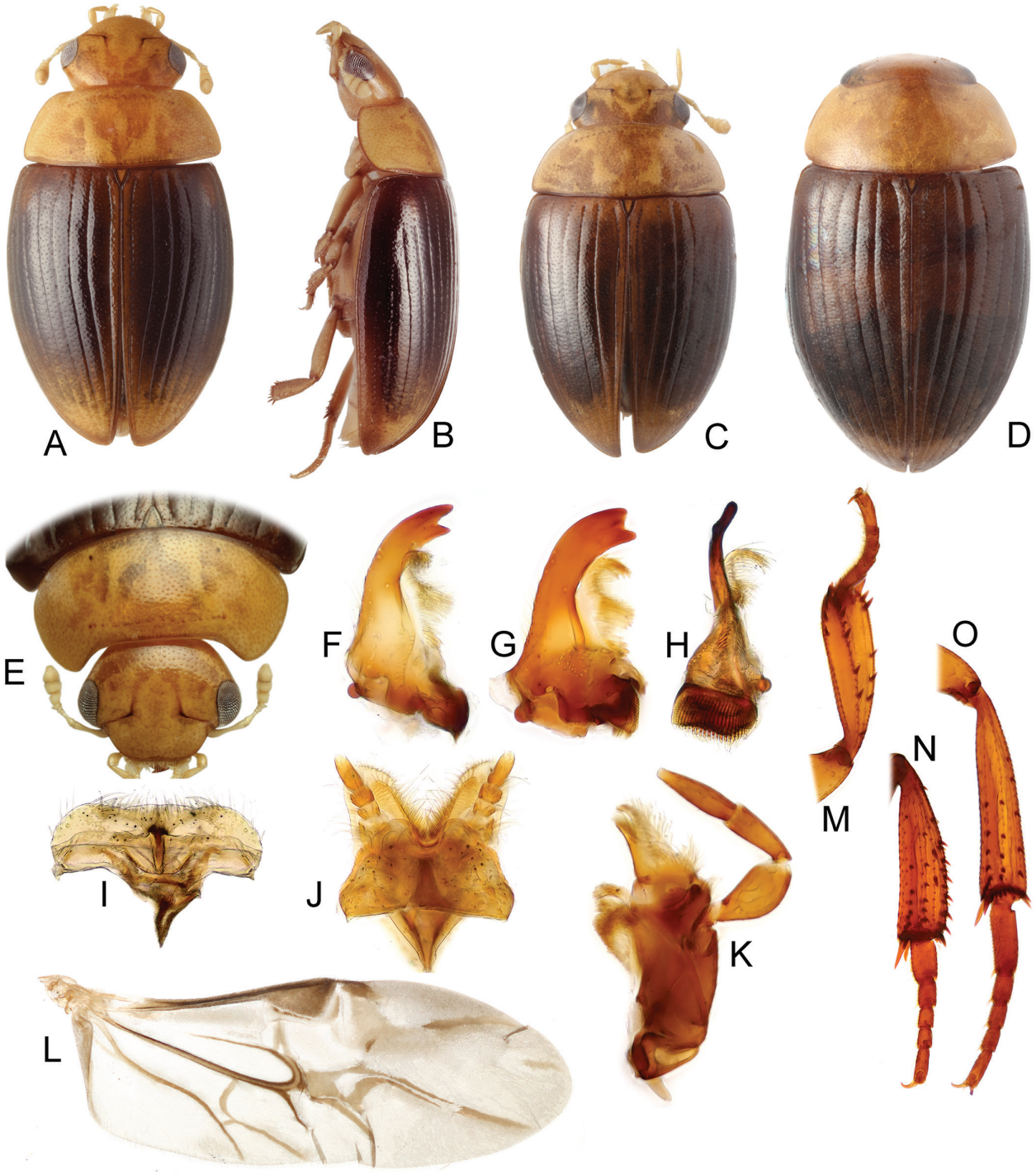

Figure 1. Habitus and morphology of *Cycreon* species. **A–D** – general habitus: **A–B** – *C. floricola floricola* ssp. n. (**A** – dorsal; **B** – lateral); **C** – *C. floricola borneanus* ssp. n., dorsal; **D** – *C. adolescens* sp. n., dorsal. **E–O** – morphology of *C. floricola floricola* ssp. n.: **E** – head and pronotum dorsally. **F–K** – mouthparts (**F** – mandible with unabraded apex; **G** – mandible with abraded apex; **H** – mandible, mesal view; **I** – labium; **J** – labrum; **K** – maxilla. **L** – metathoracic wing. **M–O** – tibiae and tarsi (**M** – prothoracic leg; **N** – mesothoracic leg; **O** – metathoracic leg).

(Fig. 2E–F). Mesepimeron moderately narrow, very weakly widening laterad. Mesocoxal cavities narrowly separated. Scutellar shield small, triangular, 1.1× as long as wide. Elytra weakly convex, weakly bordered laterally, each elytron bearing 10 series, series 1–9 consisting of foveate impressions (punctures) with a setiferous puncture on anterior margin (Fig. 4C, F, I); serial punctures situated in longitudinal sulci; series 1–4 and 9 reaching apex, series 5 and 8 enclosing series 6–7 subapically, series 9 and 10 fainter, series 10 reduced both anteriorly and posteriorly; epipleuron almost horizontal, gradually narrowing posteriad, vanishing behind level of posterior margin of metaventrite, bearing moderately dense short setae (Fig. 2E).

Metathorax. Metaventrite (Fig. 2E) with postcoxal line closely following posterior edge of mesocoxa and slightly deviating only in anterolateral angles; mesal elevate area flat and pentagonal, rather narrow, about as long as wide; lateral portions densely covered with short setae. Femoral lines and anterolateral ridges absent. Metanepisternum ca. 4.5× as long as wide, with anterior oblique ridge, metepimeron with minute ventral portion. Metafurca well developed. Hind wings (Fig. 1L) well developed, with transverse vein r4 arising from basal portion of radial cell, RP rather long, reaching ca. halfway to wing base, basal cubito-anal cell small, closed; wedge cell absent; transverse vein mp-cua joining to MP_{3+4}+CuA_{1+2}; anal lobe not defined.

Legs. Procoxae large, subglobular, transverse, with long setae, junction with trochanter; meso- and metacoxae wide, transverse. Tronchatero-femoral junction straight. Femora flattened, comparatively long, with very short setae; profemur without impressed parts; metafemur 1.1× as long as mesofemur (Fig. 1M–O). Tibiae rather long, triangular, flattened, straight or curved, especially on external margin, with short lateral and mesal spines. Tarsi pentamerous (Fig. 1N–O), tarsomeres densely covered by short stiff setae; metatarsomere 1 longer than metatarsomere 2 and 3 combined, metatarsomeres 2–4 continuously getting shorter, metatarsomere 5 about 0.4× than metatarsomere 1. Claws simple, arcuate; empodium bisetose.

Abdomen with five ventrites. Ventrite 1 without median carina (Fig. 1G), about as long as ventrites 2–4 together. Male sternite IX with tongue-like median projection with round to roundly acuminate anterior margin and rounded posterior margin, lateral struts almost reaching base of median projection (Fig. 3D, H, M). Aedeagus (Fig. 3A, E, J–K) simple; median lobe subparallel-sided to moderately sinuate, in *C. floricola* sp. n. enlarged basally and connected to phallobase by strong muscles; phallobase short, symmetrical to slightly asymmetrical, manubrium present, short; parameres simple. Female genitalia as in *Kanala* (see Fikáček 2010).

Key to the species of *Cycreon*

1 Clypeus strongly emarginated mesally (Figs 5K, O) 2
– Clypeus very weakly emarginated mesally (Figs 5A, D, G) 3
2 Pronotum with dense, completely ring-like impressions (punctures) (Fig. 5C); meso- and metatibiae straight (Fig. 5R) ..... *C sculpturatus* d'Orchymont, 1919
– Pronotum with moderately dense, half-moon shaped impressions (punctures) (Fig. 5M); meso- and metatibiae curved (Fig. 5S) ..... *C. armandi* Shatrovskiy, 2017
3 Pronotum with completely circular impressions (punctures). Mentum less transverse, 1.7× as long as wide (5B), with anteromedial emargination reaching 1/5 of length, and with many ring-like impressions (punctures) in posterior half. Aedeagus with parameres about as long as phallobase; median lobe wide, bluntly pointed at apex (Fig. 3I–J) ..... *C. adolescens* sp. n.
– Pronotum with completely ciruclar or semicircular impressions (punctures). Mentum more transverse, 2.0× as long as wide (Figs 5E, H), with anteromedial emargination reaching 1/3 of length, and with few ring-like impressions (punctures) in posterior half. Aedeagus with parameres longer than phallobase; median lobe abruptly narrowed into a long acute tip at apex (Figs 3A–H). *C. floricola* sp. n. 4
4 Pronotum with incomplete ring-like impressions (punctures) only (Figs 4H, 5I) ..... *C. floricola floricola* spp. n.
– Pronotum with all or vast majority of impressions (punctures) in shape of complete rings (Figs 4E, 5F) ..... *C. floricola borneanus* ssp. n.

Species accounts

Cycreon sculpturatus Orchymont, 1919

Fig. 5O–R

Cycreon sculpturatus Orchymont, 1919: 121.
Cycreon sculpturatus: Shatrovskiy (2017: 589, redescription).

Type locality. Indonesia: South Sumatra: Palembang [ca. 2.9861°S, 104.7555°E].

Material examined. None (information adopted from Shatrovskiy 2017).

Diagnosis. *Cycreon sculpturatus* can be distinguished from other species of the genus by the deeply incised clypeus, pronotum densely covered with complete ring-like impressions (punctures) and straight meso- and metatibiae.

Addition to description. Body 2.6 mm long; colouration light reddish-brown, with slightly darker head and elytra; clypeus about 2.5× as wide as long, with anterior margin conspicuously emarginate medially (Fig. 5O); frons and clypeus with punctation composed of complete circular impressions (punctures); mentum (Fig. 5P) subtrapezoid, widest at posterior fifth, about 2.0× wider than long, anteromedian emargination reaching about 0.2× the mentum length; pronotum with dense and moderately deep punctation consisting of complete circular impressions with a small setiferous puncture in posterior part (Fig. 5Q), punctation of approximately same diameter and density all over pronotum; meso- and metatibiae straight (Fig. 5R); male genitalia unknown (because male remains unknown for this species).

Distribution. Only know by a single female specimen from the type locality (Indonesia, Sumatra, Palembang) (Fig. 7).

Remark. According to Shatrovskiy (2017) the proportions of the clypeus were given as 4× as long as wide, however, the picture in the paper (Shatrovskiy 2017: 591) shows that the ratio is about 2.5×.

Cycreon armandi Shatrovskiy, 2017

Figs 3K–M, 5K–M

Cycreon armandi Shatrovskiy, 2017: 589.

Type locality. Singapore.

Material examined. None (information adopted from Shatrovskiy 2017).

Diagnosis. *Cycreon armandi* can be distinguished from other known species by the deeply incised clypeus, the semicircular impressions (punctures) on the pronotum, and the curved meso- and metatibae.

Addition to description. Body 3.3 mm long; colouration completely light reddish-brown; clypeus about 2× as wide as long, anterior margin of clypeus strongly emarginate medially (Fig. 5K); frons and clypeus with small and not so closely disposed punctures; mentum (Fig. 5L) subtrapezoid, widest at posterior fifth, about 1.8× wider than long, with a deep anteromedian emargination reaching beyond the anterior fourth of length; pronotum with dense and shallow, punctation consisting of small setiferous half-moon shaped punctures (Fig. 5M); meso- and metatibiae curved (Fig. 5S); median projection of sternite 9 rounded apically (Fig. 3M); aedeagus (Fig. 3L) with phallobase 0.6× as long as parameres, almost symmetrical, manubrium narrow and very; parameres continuously narrowing towards apex; median lobe moderately wide (Fig. 3K), slightly constricted in apical fourth; apex acuminate, triagular.

Distribution. Only known from the type locality in Singapore (Fig. 7).

Remarks. According to Shatrovskiy (2017) the proportions of the clypeus are given as 3× as long as wide, however, the picture in the paper (Shatrovskiy 2017: 591) shows that the ratio is closer to 2.0×.

Cycreon adolescens sp. n.

http://zoobank.org/C6503E49-3440-4820-B671-D35E579D6247

Figs 1D, 3I–J, 4J, 5A–C

Type locality. Malaysia, Pahang, Genting Highland [ca. 3.4233°N, 101.7930°E].

Type material. Holotype (male, teneral specimen): "Malaysia, PAHANG / Genting Highland / 24.X.2012 / H. Takizawa" (IBTP). **Paratypes: MALAYSIA: Pahang:** [same data as holotype] (2 females: NMPC, KMNH).

Additional material examined. MALAYSIA: Pahang: Cameron Highlands, Tanah Rata, Robinson Waterfall [ca. 4.461778°N 101.38803°E], in flowers of Araceae, 15.iii.2015, H. Takizawa lgt. (5 females: EIHE, KMNH, NMPC).

Diagnosis. This species is most similar to *Cycreon floricola borneanus* ssp. n. in the very weakly emarginate anterior margin of the clypeus and pronotal punctation consisting of circular punctures, and straight meso- and metatibiae. It differs from the latter in the structure of the male genitalia (relatively longer phallobase and widely pointed apex of the median lobe) and by the less transverse mentum (1.7× wider than long), with many ring-like impressions in posterior half.

Description. *Measurements.* 2.4–3.0 mm long (length of holotype: 2.8 mm), 1.7× as long as wide, widest at basal fifth of elytra; weakly convex, 3.3–3.5× as long as high (height of holotype: 0.82 mm). *Colouration*. Light brown with slightly darker elytra (Fig. 1D).

Head. Clypeus about 2.4× as long as wide, with anterior margin of clypeus margin very weakly emarginate medially. Frons and clypeus with punctation composed of complete circular impressions (punctures) with a small setiferous puncture on anterior margin (Fig. 4A). Interocular distance about 5.5× the width of one eye in dorsal view. Mentum (Figs 4J, 5B) subtrapezoid, widest at posterior fifth, about 1.7× wider than long, with a moderately pronounced emargination reaching about the anterior fifth of mentum length; lateral angles weakly marked; surface with few sparse, moderately long setae in anterolateral angles, posterior half glabrous, punctures moderately large and deep, vanishing mesally, 11–13 punctures close to posterolateral angles with ring-like impressions (punctures).

Prothorax. Pronotum transverse, widest at base 2.2× wider than long; 1.6× wider at base than between anterior angles, 1.7× wider than head including eyes. Punctation dense and shallow, consisting of circular impressions with one small setiferous puncture on posterior margin (Fig. 4B), punctation of approximately same diameter and density all over pronotum.

Pterothorax. Elytra widest at anterior fifth, 1.1–1.2× as long as wide, 2.9–3.0× as long as pronotum, 1.2–1.3× as wide as pronotum. Punctation on intervals composed of semicircular impressions with a setiferous puncture on posterior margin (Fig. 4C). *Legs.* Metatibiae wide and flattened, weakly curved on external margin, 0.35× as long as elytra, 5.0× as long as wide.

Male genitalia (Fig. 3I–J). Phallobase about 1.1× as long as parameres, slightly asymmetrical, manubrium slightly hooked, widely rounded. Parameres continuously narrowing apically, external margins straight, apex rounded. Median lobe wide throughout, apex triangularly acuminate, gonopore rather small, situated subapically. Median projection of sternite 9 not examined.

Etymology. The species name reflects the teneral condition of the holotype (from Latin *adolescens* = growing up, maturing).

Distribution. The species is only known two localities in Pahang province, Malaysia.

Biology. No details about collecting circumstrances are available for type specimens; additional specimens from Tanah Rata were collected from inflorescences of Araceae (H. Takizawa, pers. comm. 2018).

Cycreon floricola sp. n.

http://zoobank.org/16453A2C-31B9-425C-998E-88D0836C8DE7

Figs 1A–C, E-O, 2, 3A–D, E–H, 4G–I, 5D–F, G–I, 6A–B

Description. *Measurements.* 2.2–3.4 mm long (length of holotype: 2.9 mm), 1.8–2.0× as long as wide, widest

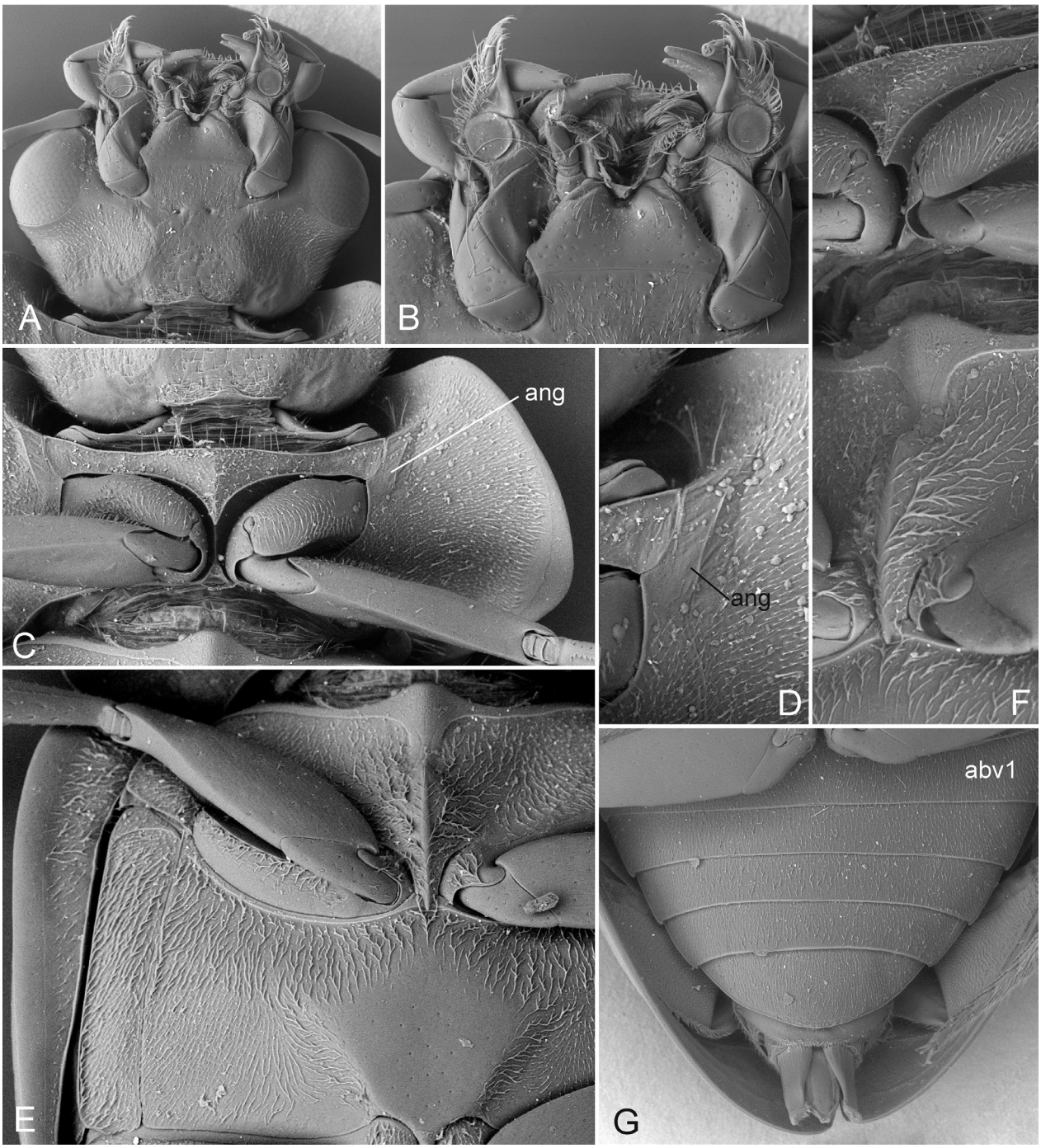

Figure 2. External morphology of *Cycreon floricola floricola* ssp. n. **A**– head, ventral view; **B** – detail of male mouthparts in ventral view; **C** – prothorax in ventral view; **D** – detail of the antennal groove; **E** – meso- and metaventrite; **F** – prosternum and mesoventral elevation in ventrolateral view; **G** – abdominal ventrites. Abbreviations: abv1 – abdominal ventrite 1; ang – antennal grooves.

at basal fifth of elytra; weakly convex, 3.1–3.4× as long as high (height of holotype: 0.9 mm). *Colouration*. Light brown with darker elytra (Figs 1A–C).

Head. Clypeus about 2.5× as wide as long, with anterior margin of clypeus margin very weakly emarginate medially. Frons and clypeus with punctation composed of complete circular impressions (punctures) with one small setiferous puncture on anterior margin (Figs 4G, D). Interocular distance about 4.9–5.2× width of one eye in dorsal view. Mentum (Figs 1J, 2B, 4K, 5E,H) subtrapezoid, widest at posterior fifth, about 2.1× as wide as long, with deep emargination reaching beyond anterior third of mentum length; surface with sparse, moderately long setae in anterior half, posterior half glabrous, punctures moderately large and deep, becoming smaller mesally, with 2–3 punctures with ring-like impressions close to posterolateral angles.

Prothorax. Pronotum transverse, widest at base, 2.2× as wide as long; 1.5–1.6× wider at base than at anterior

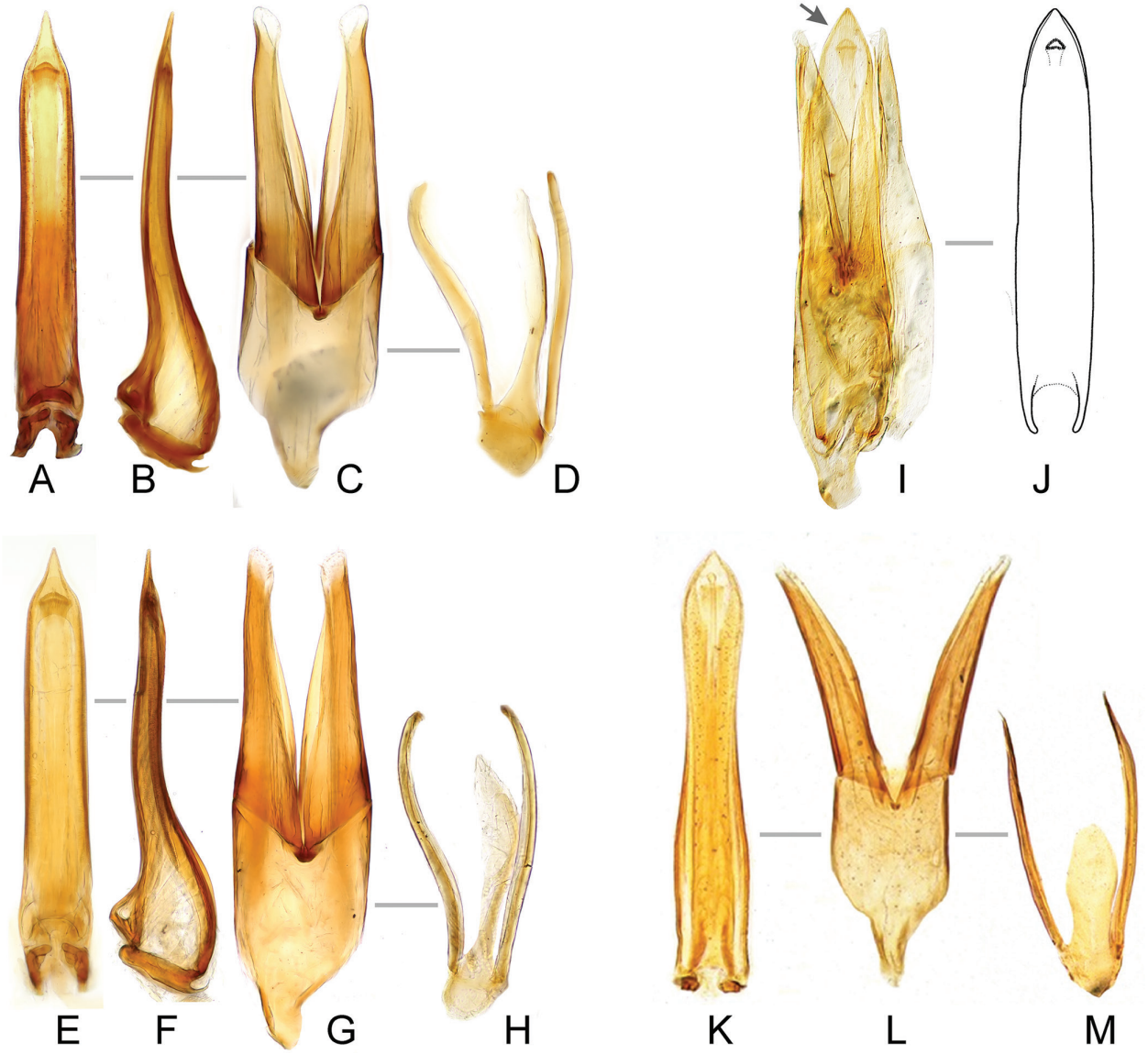

Figure 3. Male genitalia of *Cycreon* species (except *C. sculpturatus* for which male remains unknown). **A–D** – *C. floricola floricola* ssp. n., holotype; **E–H** – *C. floricola borneanus* ssp. n., holotype; **I–J** – *C. adolescens* sp. n., holotype; **K–M** – *C. armandi* Shatrovskiy, 2017, holotype. **A, E, K** – median lobe; **B, F** – median lobe in lateral view; **C, G, L** – tegmen; **D, H, M** – sternite 9; **I** – whole aedeagus; **J** – reconstructed shaped of the median lobe. **K–M** adapted from Shatrovskiy (2017).

angles, 1.6× as wide as head including eyes. Punctation dense and shallow, consisting of semicircular to complete ring-like impressions with a small setiferous puncture on posterior margin (Figs 4E, H, 5F, I), punctation approximately same in size and density all over pronotum.

Pterothorax. Elytra widest at anterior fifth, 1.1–1.2× as long as wide, 2.9–3.0× as long as pronotum, 1.1× as wide as pronotum. Punctation on intervals composed of semicircular impressions with setiferous puncture on posterior margin (Fig. 4F, I).

Legs. Metatibiae wide and flattened, very weakly curved, 0.35× as long as elytra, 4.8× as long as wide.

Male genitalia. Median projection of sternite 9 (Fig. 3D, H) rounded apically, with few short subapical setae, shorter than lateral struts. Phallobase (Fig. 3C, G) about 0.8× as long as parameres, asymmetrically narrowing towards base, manubrium acuminate and slightly hooked, with apex rounded. Parameres continuously narrowing from base to apex, but slightly widened at apex; external margins bisinuate; apex obliquely acuminate. Median lobe moderately wide (Fig. 3A–B, E–F), almost parallel-sided throughout, apex acuminate, with very acute tip, expanded basally and bent dorsally on lateral view, gonopore large, situated subapically.

Etymology. The species name reflects the association of this species with flowers, it consists of *flori-* (from Latin *flos, floris* = flower) and *-cola* (from Latin *incola* = inhabitant).

Comment. This species is composed of two phenotypically distinguishable forms which are geographically exclusive and are here descibed as subspecies. Morphological differences are mainly restricted to punctation on the pro-

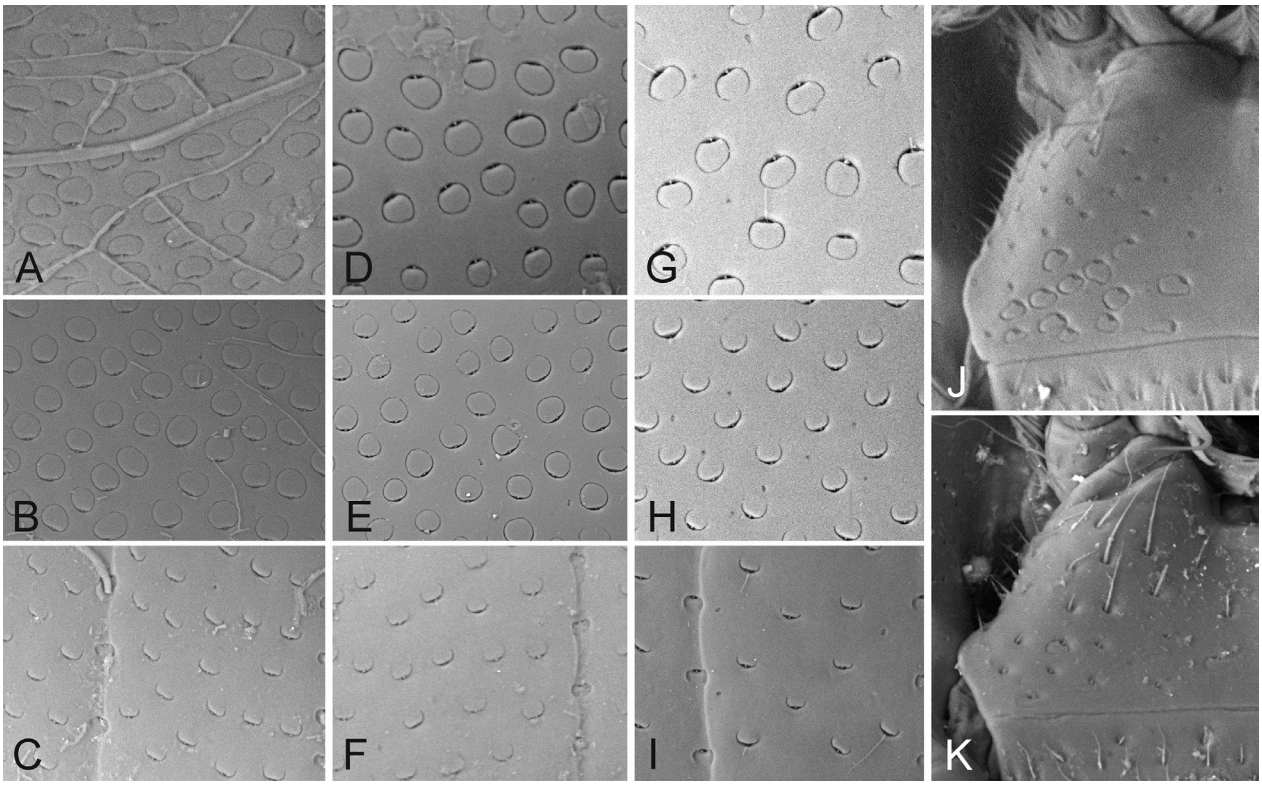

Figure 4. Surface sculptures of *Cycreon* species. **A–C, J** – *C. adolescens* sp. n., holotype; **D–F** – *C. floricola borneanus* ssp. n., paratype; **G–I, K** – *C. floricola floricola* ssp. n., paratype from the type locality. **A, D, G** – head punctation; **B, E, H** – pronotum punctation; **C, F, I** – elytral punctation; **J–K** – punctation of mentum.

notum, which consists exclusively of incomplete ring-like impressions in the mainland form (*C. f. floricola* ssp. n.), and exclusively or mainly of the completely ring-like forms in the specimens from Borneo (*C. f. borneanus* ssp. n.).

Cycreon floricola floricola ssp. n.

http://zoobank.org/953D42A0-7C3B-47BD-A2E5-26CB0ACAB588
Figs 1A–B,E–O, 2, 3A–D, 4G–I, K, 5G–I

Type locality. Malaysia, Kelantan, Guala Musang prov., Kuala Koh district, Taman Negara, 700 m from the entrance, 96 m a.s.l., 4°52.333′N 102°26.872′E.

Type material. Holotype (male: ZIN): "MALAYSIA: Kelantan AR-4332 / Guala Musang prov., Kuala Koh / distr., Taman Negara, 700 m / from entrance, 4°52.333′N / 102°26.872′E, 96m, 11.i.2014 / *Schismatoglottis* sp. HY Chen". **Paratypes: MALAYSIA: Johor:** Endau-Rompin N.P., NERC to Visitor Complex, Stream 1, 80 m, 2°25′12.8 ′ ″N 103°15′41.33″ E, flowering *Kiewia ridleyi*, 22.x.2008, Ooi Im Hin lgt. (AR-2602) (1: ZIN); Kota Tinggi, Hutan Simpan Panti, starting point of the trail to mount Panti, 14 m, 1°48.595′N 103°51.099′E, flowering *Schismatoglottis*, 4.xii.2013, Hoe Yin Chen lgt. (AR-4322) (21: ZIN, NMPC, IBTP); [same locality, except] 16 m, flowering *Schismatoglottis*, 4.xii.2013, Hoe Yin Chen lgt. (AR-4326) (11: ZIN); Kota Tinggi, Hutan Simpan Panti, starting point of the trail to mount Panti, 16 m, 01°48.565'N 103°51.104'E, flowering *Schismatoglottis*, 04.xii.2013, Hoe Yin Chen lgt. (AR-4328) (4: ZIN, NMPC); Kota Tinggi, Hutan Simpan Panti, Starting point of the trail to mount Panti, 16 m, 01°48.565'N 103°51.104'E, flowering *Schismatoglottis*, 13.xii.2013, Hoe Yin Chen lgt. (AR-4328) (6: ZIN, NMPC); **Kelantan:** Gua Musang, Kuala Koh, Taman Negara, 700 m away from the entrance gate (outside the park), 96 m, 4°52.333′N 102°26.872′E, flowering *Schismatoglottis*, 11.x.2014, Hoe Yin Chen lgt. (AR-4332) (237: ZIN, NMPC, IBTP, KMNH, EIHE, NHMW, BMNH, SRBC).

Diagnosis. This subspecies is very similar to *Cycreon floricola borneanus* ssp. n. with which it shares most of the external characters including genital morphology. *Cycreon floricola floricola* can be distinguished by the pronotal punctation consisting exclusively of the incomplete ring-like punctures. The dorsal coloration of the is slightly more contrasting in most specimens of *C. floricola floricola* than in representatives of *C. f. borneanus* ssp. n., with the pronotum darker compared to the elytra.

Description. *Measurements.* 2.4–3.2 mm long (length of holotype: 2.7 mm), 1.9–2.0× as long as wide, widest at basal fifth of elytra; weakly convex, 3.2–3.4× as long as high (height of holotype: 2.7 mm). *Colouration.* Pale yellowish-brown with dark-brown elytra (Fig. 1A–B).

Pronotum 2.2× wider than long; 1.6× wider at base than between anterior angles, with punctation dense and shallow, consisting of semicircular impressions (punctures) with a small setiferous puncture on posterior margin.

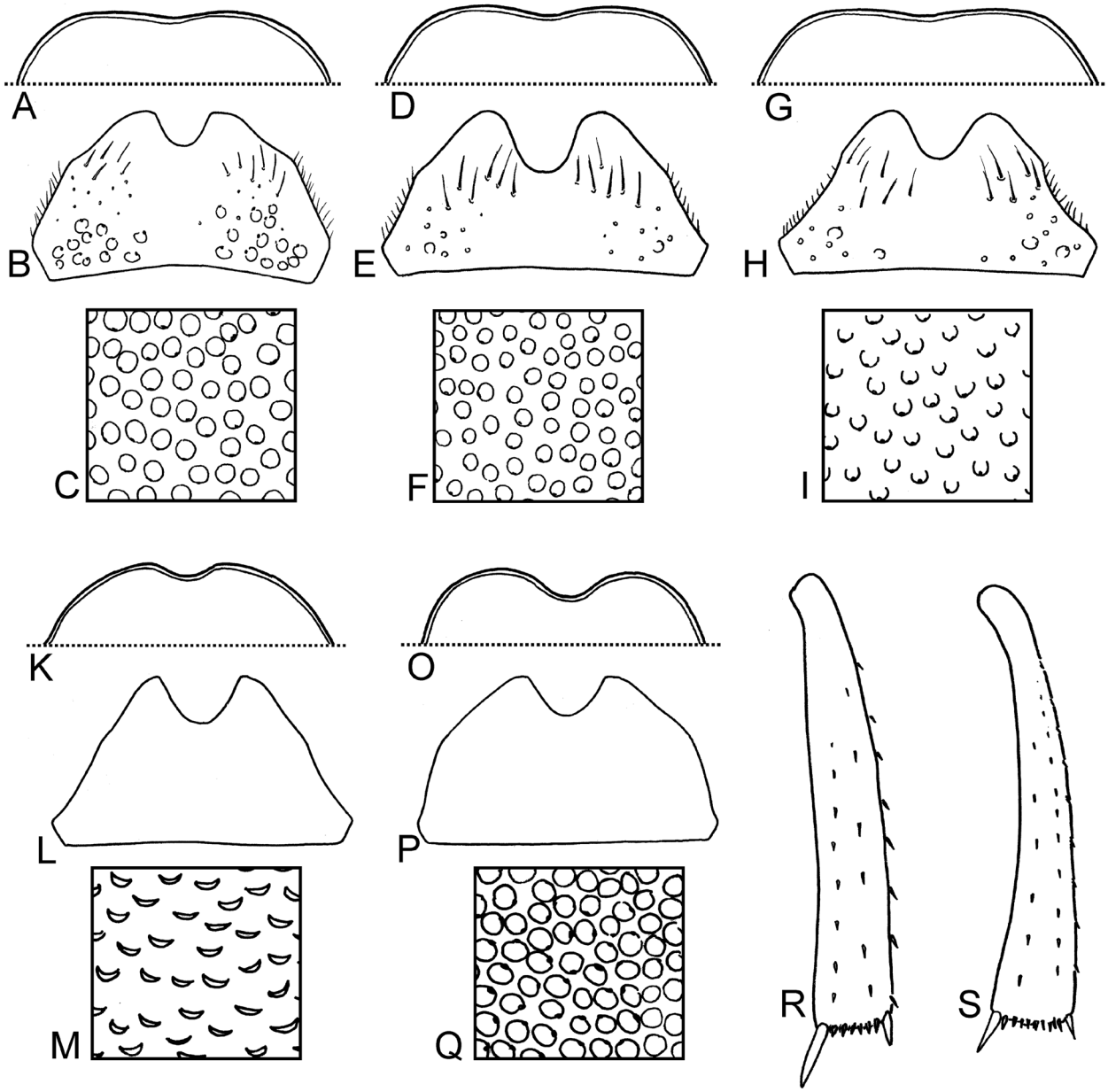

Figure 5. Diagnostic characters of known *Cycreon* species. **A–C** – *C. adolescens* sp. n.; **D–F** – *C. floricola borneanus* ssp. n.; **G–I** – *C. floricola floricola* ssp. n.; **K–L, S** – *C. armandi*; **O–R** – *C. sculpturatus*. **A, D, G, K, O** – anterior margin of clypeus; **B, E, H, L, P** – mentum (superficial sculpture omitted in **L** and **P**); **C, F, I, M, Q** – pronotal punctation; **R–S** – metatibia. **K, M–S** redrawn from Shatrovskiy (2017), **L** based on a photo provided by A. Shatrovskiy (pers. comm., 2017).

Punctation approximately same in size and density all over pronotum.

Elytra widest at anterior fifth, 1.1–1.2× as long as wide, 2.9–3.0× as long as pronotum, 1.1× as wide as pronotum. Punctation on intervals composed of semicircular impressions with one setiferous puncture on posterior margin.

Distribution. The subspecies is known from two regions in Peninsular Malaysia, in provinces of Johor and Kelantan.

Biology. Many specimens of *C. floricola floricola* were collected inside of inflorescences of *Schismatoglottis* species and *Kiewia ridleyi* (Low et al. 2018) (both Araceae).

Cycreon floricola borneanus ssp. n.

http://zoobank.org/ADFC83BC-973B-4A18-AE6F-B906027D49A1
Figs 1C, 3E–H, 5D–F, 6A–B

Type locality. Malaysia, Sabah, Tawau, Lahad Datu, Tawau Hills National Park, Kebun Botani, 305 m a.s.l., 4°23′59.4″N 117°53′17.2″E.

Type material. Holotype (male: ZIN): "MALAYSIA: Sabah AR-2659 / Tawau, Lahad Datu, Tawau Hills / NP, Kebun Botani, 305m / 04°23′59.4N 117°53′17.2E / *Schistamoglottis calyptrata* group, / 8.vii.2016, Wong Sin Yeng, / P. C. Boyce & Zaiety binti Thomas". **Paratypes: INDONESIA**: **Kalimantan Barat:** Bengkayang

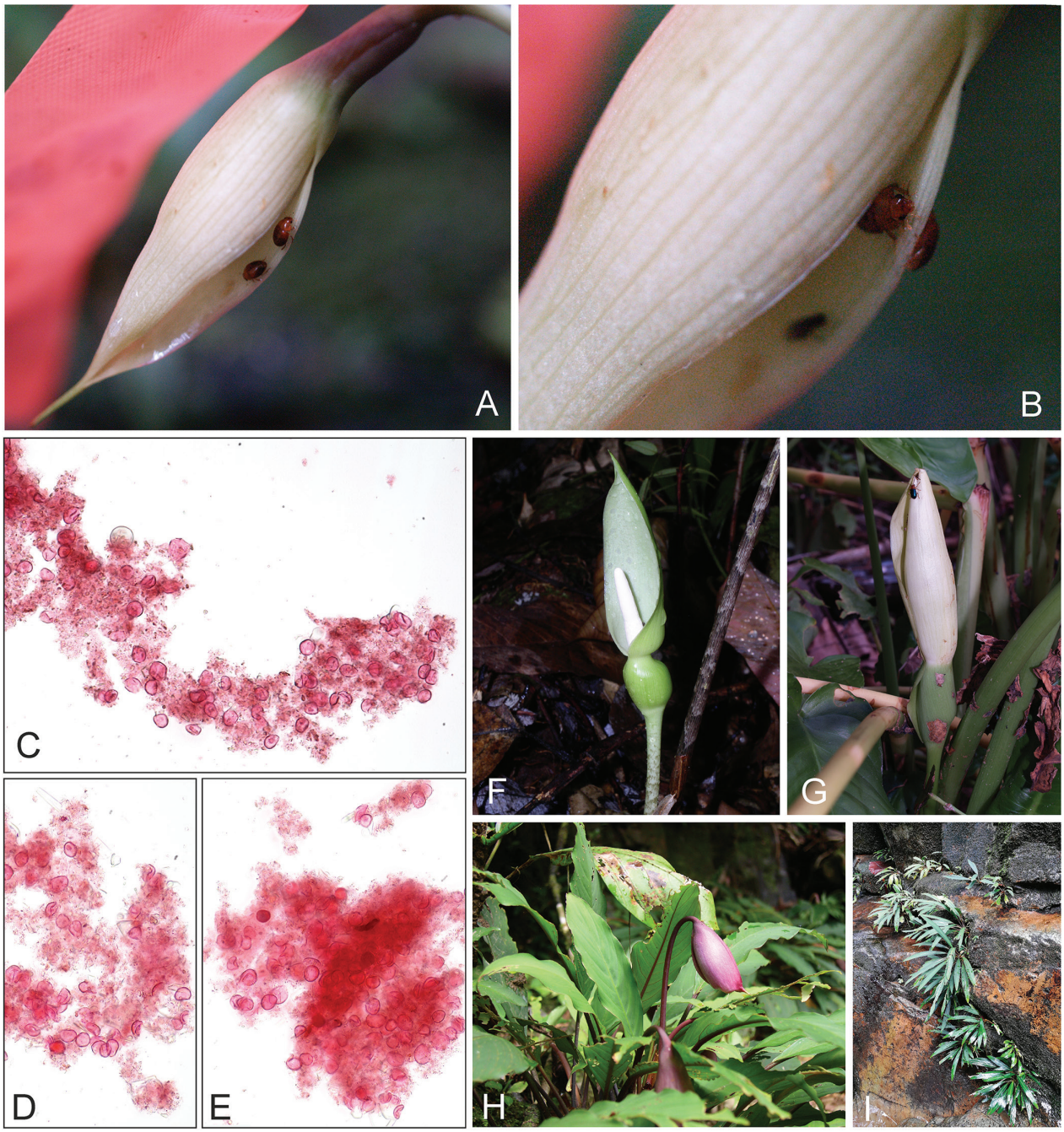

Figure 6. Biology of *Cycreon floricola* sp. n. **A–B** – alive specimens of *C. floricola borneanus* in the inflorescence of *Schottarum sarikeense* at Sebankoi Recreational Park, Betong, Roban, Sarawak in January 2010 (photo by S.-Y. Wong). **C–E** – safranine-dyed gut content of *C. floricola borneanus* collected from *Schismatoglottis calyptrata* complex in Tawau Hills, Kebun Botani on 8th July 2016 (collecting event AR-2659). **F–I** – examples of aroid plants on which the species were collected (**F** – *Alocasia longiloba*; **G** – *Schismatoglottis giamensis*; **H–I** – *Ooia glans*).

Pajintan, Ayer Terjun Sibohe, 80 m, 0°51’55.8”N 109°2’25.1”E, flowering *Schismatoglottis modesta*, 2.ix.2017, Wong & Boyce lgt. (AR-2812) (39: NMPC, ZIN). **Kalimantan Selantan:** ‘S.O. Borneo / Grabowsky S. V.’ (1: ZMNH); Kendangan, 15.5.1882, Grabowsky S. V. [ca.: S 2.592552°, E 115.028244°] (5: ZMNH). **MALAYSIA: Sabah:** Tawau, Lahad Datu, Tawau Hills NP, HQ Area, 304 m, 4°23′51.2”N 117°53′25.1”E, flowering *Alocasia longiloba* complex, 6.vii.2016, Wong Sin Yeng & P.C.Boyce lgt. (AL-315) (1: ZIN); [same locality] flowering *Schismatoglottis calyptrata* complex, 7. vii.2016, Wong Sin Yeng & P.C.Boyce lgt. (AR-2641) (101: ZIN, NMPC, IBTP, KMNH, NHMW); Tawau, Lahad Datu, Tawau Hills NP, Air Terjun Bukit Gelas, 315 m, 4°24′48.4”N 117°53′29.3”E, flowering *Gamogyne loi*, 6.vii.2016, Wong Sin Yeng & P.C.Boyce lgt. (AR-2638) (12: ZIN, NMPC); Tawau, Lahad Datu, Tawau Hills NP, Trail to Bukit Gelas, 319 m, 4°24′37.0”N

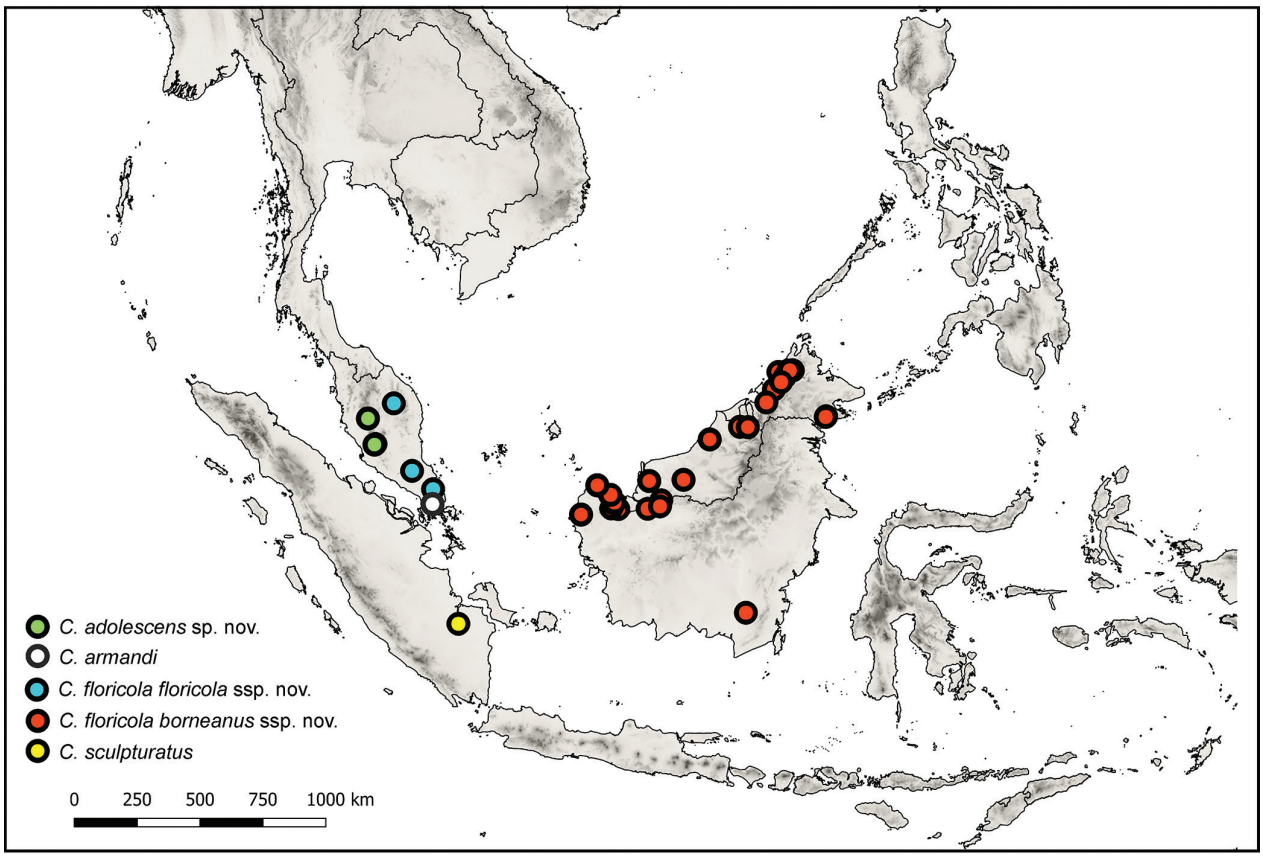

Figure 7. Known distribution of *Cycreon* species.

117°53′38.8”E, flowering *Homalomena hanneae* complex, 6.vii.2016, Wong Sin Yeng & P.C.Boyce lgt. (AR-2636) (18: ZIN, NMPC); [same locality] flowering *Schismatoglottis calyptrata* complex, 7.vii.2016, Wong Sin Yeng & P.C.Boyce lgt. (AR-2652) (36: ZIN, NMPC); Tawau, Lahad Datu, Tawau Hills NP, Kebun Botani, 305 m, 04°23′59.4″N 117°53′17.2″E, flowering *Schismatoglottis calyptrata* complex, 8.vii.2016, Wong Sin Yeng, P.C.Boyce & Zaiety binti Thomas lgt. (AR-2659) (116: ZIN, NMPC, IBTP, KMNH, NHMW, BMNH); Kg. Moyog, Jln. Tambunan, Penampang, 12.xii.2009, H. Takizawa lgt [ca. N 5.888455°, E 116.235335°] (11: EIHE, KMNH, NMPC, IBTP); [same locality and collector] 30.x.2008 (7: EIHE, KMNH); [same locality and collector,] 13.ix.2008 (7: EIHE, KMNH, IBTP); Poring park, Ranau, 19–20.ix.2008, H. Takizawa lgt [ca. N 6.047067°, E 116.703231°] (7: EIHE, KMNH, IBTP); [same locality and collector] 25–26.ix.2008 (5: EIHE, KMNH. IBTP); [same locality and collector] 8–9.i.2010 (7: EIHE, KMNH, IBTP); [same locality and collector] 11.xii.2008 (3: EIHE, KMNH); [same locality and collector] 27.v.2010 (1: EIHE); [same locality and collector] 25.ii.2009 (2: KMNH); [same locality and collector] 10.vii.2008 (1: EIHE); [same locality and collector] 12.iii.2009 (1: KMNH); [same locality and collector] 29.viii.2013 (1: KMNH); [same locality and collector] 12.iii.2009 (1: KMNH); [same locality and collector] 4–5.iv.2008 (3: KMNH, IBTP); [same locality and collector] 7.x.2012 (2: KMNH); Kg. Kiapad, Inanam, Kota Kinabalu, 7.ix.2008, H. Takizawa lgt [ca. N 5.988388°, E 116,190333°] (16: KMNH, EIHE, IBTP, NMPC); [same locality and collector] 2.i.2010 (3: KMNH, EIHE); [same locality and collector] 10.xi.2012 (16: KMNH, EIHE, IBTP, NMPC); [same locality and collector] 6.xii.2008 (18: KMNH, EIHE, IBTP, NMPC); [same locality and collector] 6.iv.2013 (7: KMNH, EIHE, IBTP); [same locality and collector] 5.vii.2008 (22: KMNH, EIHE, IBTP, NMPC); [same locality and collector] 4.x.2008 (3: KMNH); [same locality and collector] 7.xi.2009 (1: KMNH); Ulu Senagang subts., Keningau, 31.i.-2.ii.2011, H. Takizawa lgt. [ca. N 5.362946°, E 116.028679°] (14: KMNH, EIHE, IBTP); [same locality and collector] 24–26.vii.2010 (2: KMNH); Kinabalu PHQ, Ranau, 17–19.iii.2008, H. Takizawa lgt. [ca. N 6.021639°, E 116.542751°] (1: EIHE); Kinabalu Park, HQ, Ranau, 5.iii.2010, H. Takizawa lgt. [ca. N 6.021639°, E 116.542751°] (3: EIHE, KMNH); [same locality and collector] 14.iii.2012 (1: KMNH); [same locality and collector] 8.vii.2010 (2: KMNH); [same locality and collector] 23–25.iii.2010 (1: EIHE); [same locality and collector] 27–28.v.2008 (2: KMNH); [same locality and collector] 13–14.v.2010 (1: EIHE); [same locality and collector] 23–25.viii.2008 (2: KMNH); [same locality and collector] 23–25.vii.2008 (1: KMNH); [same locality and collector] 1.ii.2010 (1: KMNH); [same locality and collector] 23–24.ix.2008 (1: KMNH); [same locality

and collector] 17–19.x.2008 (1: KMNH); Muaya waterfall, Sipitang, 6–9.iii.2009, H. Takizawa lgt. [ca. N 4.903889°, E 115.760278°] (8: EIHE, KMNH, IBTP); Mahua waterfall, Crocker R. P., Tambunan, 26.vii.2011, H. Takizawa lgt [ca. N 5.797627°, E 116.408377°] (1: NMPC); Gn. Bombalai, Tawau Hills park, Tawau, 17. vi.2010, H. Takizawa lgt [ca. N 4.386858°, E 117.879748°] (4: EIHE, KMNH); Pk. Bundu Tuhan Kundasang, Ranau, 6.iii.2010, H. Takizawa lgt. [ca. N 5.996602°, E 116.528987°] (1: NMPC); Mesilau headgate, Kundasang, Ranau, 25.ii.2009, H. Takizawa lgt. [ca. N 6.044605°, E 116.596306°] (1: KMNH); Malangan, Kg. Tikolod, Tambunan, 12–14.iii.2010, H. Takizawa lgt. [ca. N 5.626763°, E 116.286933°] (1: EIHE); Pantai Barat, Kota Kinabalu, Inanam, Kionsom, Kionsom Waterfall, 230 m, 05 57 24.0N 116 12 25.3E, flowering *Schismatoglottis corneri*, 18.iv.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-4683) (7: ZIN, NMPC). **Sarawak:** Serian, Pichin, between Sugun Karang and Tahang Sipukam, Sungai Kakas, 48 m, 1°06′09.7″N 110°28′11.8″E, flowering *Schismatoglottis bulbifera*, 28.vi.2014, Ooi Im Hin & Jeland ak Kisai lgt. (AR-4832) (1: ZIN); Kuching, Padawan, Puncak Borneo, Jungle Trail, 890 m, 1°07′33.5″N 110°12′57.4″E, flowering *Ooia glans*, 15.ix.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-93) (92: ZIN, NMPC, IBTP, KMNH, NHMW); Kuching, Padawan, Puncak Borneo, Sungai Semangas, 472 m, 1°08′26.6″N 110°13′36.1″E, flowering *Ooia glans*, 16.ix.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-4979) (29: ZIN, NMPC, KMNH); Kuching, Matang, Kubah N.P., Sungai Bungen, 230 m, 1°36′30.9″N 110°11′35.0″E, flowering *Ooia glans*, 28.vii.2007, P.C.Boyce, Wong Sin Yeng & S.Maclean lgt. (AR-2118) (27: ZIN, NMPC, IBTP); [same locality] flowering *Schismatoglottis mayoana*, 28.vii.2007, Wong & Maclean lgt. (AR-2122) (1: ZIN); Kuching, Matang, Kubah N.P., Waterfall Trail, 190 m, 1°35′40.2″N 110°10′45.9″E, flowering *Ooia glans*, 28.vii.2007, P.C.Boyce, Wong Sin Yeng & S.Maclean lgt. (AR-2117) (10: ZIN, NMPC); Sri Aman, Lubok Antu, Sungai Engkari, Nanga Segerak, Sungai Serjanggut, 332 m, 1°24′46.5″N 112°00′18.5″E, flowering *Ooia* sp., 17.iii.2015, Wong Sin Yeng, P.C. Boyce & Bada ak Chendai lgt. (AR-5169) (11: ZIN, NMPC); Sri Aman, Lubok Antu, Engkilili, Tempat Rekreasi Sungai Raya, Sungai Raya, 13 m, 1°06′49.2″N 111°30′56.8″E, flowering *Schismatoglottis calyptrata* complex, 9. xii.2005, P.C.Boyce, Jeland ak Kisai, Jipom ak Tisai & Mael ak Late lgt. (AR-1632) (38: ZIN, NMPC, IBTP, KMNH); Sri Aman, Lubok Antu, Sungai Sepipit, 108 m, 1°11′54.9″N 111°57′29.4″E, flowering *Schismatoglottis petradoxa*, 27.vii.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-4894) (1: ZIN); Kuching, Siburan, Kampung, Giam, Sugun Jawan, 70 m, 1°19′20.7″N 110°16′21.4″E, flowering *Schismatoglottis giamensis*, 20.vi.2009, P.C.Boyce & Wong Sin Yeng lgt. (AR-2549) (56: ZIN, NMPC, IBTP, KMNH); Kuching, Siburan, Kampung Sikog, Air Terjun Baan Gong, 70 m, 1°20′16.1″N 110°20′09.6″E, flowering *Schismatoglottis baangongensis*, 26.vii.2009, P.C.Boyce & Wong Sin Yeng lgt. (AR-2588) (63: ZIN, NMPC, IBTP, KMNH); Miri, Marudi, Long Lama, Mulu N.P., Trail to Deer Cave, 60 m, 4°02′23.8″N 114°48′54.6″E, flowering *Phymatarum borneense*, 5.viii.2006, P.C.Boyce, Wong Sin Yeng, Jeland ak Kisai & Mael ak Litis lgt. (AR-1931) (23: ZIN, NMPC); Miri, Marudi, Long Lama, Mulu N.P., Trail to Deer Cave, 60 m, 4°02′02.0″N 114°49′00.0″E, flowering *Schismatoglottis muluensis*, 6.viii.2006, P.C.Boyce, Wong Sin Yeng, Jeland ak Kisai & Mael ak Litis lgt. (AR-1941) (110: ZIN, NMPC, IBTP, KMNH, NHMW); Kuching, Siburan, Kampung Giam, Air Terjun Giam, 37 m, 01°19’11.2”N 110°16’11.4”E, flowering *Homalomena giamensis*, 07.ii.2016, P.C.Boyce, Jeland ak Kisai & Wong Sin Yen lgt. (AR-1691) (13: ZIN, NMPC); Kampung, Sungai Temaga, trail to Gunung Pueh, 82 m, 01°46’58.6”N 109°43’06.6”E, flowering *Schismatoglottis*, 23.iii.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-4651) (1: ZIN); Kuching, Siburan, Air Terjun Baan Gong, 70 m, 01°20′16.1″N 110°20′09.6″E, flowering *Homalomena borneensis*, 26.vii.2009, P.C.Boyce & Wong Sin Yeng lgt. (AR-2575) (11: ZIN, NMPC); Kuching, Siburan, Sugun Jawan, 50 m, 01°19’16.1”N 110°16’16.7”E, flowering *Homalomena gastrofructa*, 09.vi.2009, P.C.Boyce & Wong Sin Yeng lgt. (AR-2559) (5: ZIN, NMPC); Miri, Niah N.P., Beside road margin, outside of the main entrance, 13 m, 03°49.598’N 113°45.683’E/03°49.577’N 113°45.710’E, flowering *Schismatoglottis*, 30.iii.2014, Hoe Yin Chen lgt. (AR-4665) (2: ZIN); Kuching, Sematan, Sungai Temaga, trail to Gunung Pueh, 82 m, 01°46’58.6”N 109°43’06.6”E, flowering *Homalomena caput-gorgonis*, 23.iii.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-4659) (2: ZIN); Kuching, Kampung Sebat Dayak, Air Terjun Sebat, 70 m, 01°48’05.6”N 109°43’09.6”E, flowering *Piptospatha elongata*, 21.iii.2014, Wong Sin Yeng & P.C.Boyce lgt. (AR-4367) (1: ZIN); Betong, Roban, Sebankoi, Taman Rekreasi Sebankoi, 154 m, 01°57′27.4″N 111°26′04.6″E, flowering *Homalomena ibanorum*, 05.xii.2005, P.C.Boyce, Jeland ak Kisai, Jepom ak Tisai, Mael ak Late & Wong Sin Yeng lgt. (AR-1538) (7: ZIN, NMPC); Kuching, Matang, Maha Mariamman Temple, trail to Indian Temple, 350 m, 01°35’25.7”N 110°13’12.8”E, flowering *Homalomena matangae*, 04.iii.2014, P.C.Boyce & Jeland ak Kisai lgt. (AR-230) (7: ZIN, NMPC); Kuching, Bau, Krokong, Gua Peri-peri, 30 m, 01°22’51.9”N 110°07’09.3”E, flowering *Schismatoglottis*, 09.v.2009, P.C.Boyce & Wong Sin Yeng lgt. (AR-2445) (2: ZIN); Kuching, Bau, Gua Angin, 45 m, 01°24’54.8”N 110°08’08.2”E, flowering *Schismatoglottis*, 21.vi.2005, P.C.Boyce & Jeland ak Kisai lgt. (AR-1240) (8: ZIN, NMPC); Roban, Sebankoi, Taman Rekreasi Sebankoi, Site 1, 154 m, 01°57’27.4”N 111°26’04.6”E, flowering *Schismatoglottis sarikeense*, 07.ii.2010, Low Shook Ling lgt. (AR-3001) (4: ZIN); Kuching, Siburan, Kampung Sikog, Air Tejun Baan Gong, 70 m, 01°20′16.1″N 110°20′09.6″E, flowering *Homalomena baangongensis*, 26.vi.2009, P.C.Boyce &

Wong Sin Yeng lgt. (AR-2574) (44: ZIN, NMPC, IBTP, KMNH); Kuching, Matang, Kubah N.P. Sungai Bungen, 230 m, 01°36′30.9″N 110°11′35.0″E, flowering *Ooia glans*, Ooi Im Hin lgt. (AR-2339) (2: ZIN); Kuching, Bau, Gua Angin, 45 m, 01°24'54.8"N 110°08'08.2"E, flowering *Schismatoglottis*, 21.vi.2005, P.C.Boyce & Jeland ak Kisai lgt. (AR-1240) (24: ZIN, NMPC). Miri, Miri, Marudi Long Lama, Mulu National Park, DC limestone, before Kenyalang trail junction, 65 m, 4°02'29.4"N 114°48'44.3"E, flowering *Schismatoglottis muluensis*, 25.xii.2017, SY Wang team lgt. (SK01) (38: NMPC); [same locality] DC limestone, before 2nd shelter, flowering *Schismatoglottis colocasioideae*, 27.xii.2017 (SK03) (11: NMPC); [same locality and host plant] 30.xii.2017 (SK07) (11: NMPC); [same locality] DC limestone, before Kenyalang trail junction, flowering *Schismatoglottis muluensis*, 1.i.2018 (SK10) (11: NMPC); [same locality] DC limestone, near Deer water cave, flowering *Schismatoglottis muluensis*, 1.i.2018 (SK11) (33: NMPC, IBTP); [same locality] DC limestone, canopy trail, flowering *Schismatoglottis colocasioideae*, 7.i.2018 (SK12) (13: NMPC); [same locality] BT right, flowering *Schismatoglottis serratodentata*, 8.i.2018 (SK13) (2: NMPC); [same locality and host plant] 23.i.2018 (SK17) (1: NMPC); [same locality] DC limestone, near Deer water cave, flowering *Schismatoglottis pellucida*, 30.i.2018 (SK18) (3: NMPC); [same locality] flowering *Schismatoglottis multinervia*, 31.i.2018 (SK19) (4: NMPC); [same locality and host plant] 3.ii.2018 (SK21) (3: NMPC); Kapit, Taman Rekreasi Sebabai, 84 m, 1°56'37.5"N 112°54'24.8"E, flowering *Ooia havilandii*, 22.ix.2017, Wong & Boyce lgt. (AR-3635) (23: NMPC, ZIN): Sarikei Bayong, Ulu Sarikei, Lubok Lemba, Rymah Nyuka, 55 m, 1°53'41.3"N 111°30'11.5"E, flowering *Ooia secta*, 3.vi.2017, Wong & Boyce lgt. (AR-2756) (1: NMPC); Kuching Lundu, Gunung Gading NP, waterfall 1, 200 m, 1°41'28.3"N 109°50'43.6"E, flowering *Homalomena*, 27.v.2017, Wong & Boyce lgt. (AR-2757) (3: NMPC); Sarikei Bayong, Ulu Sarikei, Lubok Lemba, Rymah Nyuka, 55 m, 1°53'41.3"N 111°30'11.5"E, flowering *Schismatoglottis erumpens* complex, 3.vi.2017, Wong & Boyce lgt. (AR-2753) (4: NMPC).

Diagnosis. This species is very similar to *Cycreon floricola floricola* with which it shares most external characters and genital morphology. *Cycreon floricola borneanus* ssp. n. can be distinguished from *C. floricola floricola* by the shape of the pronotal punctation consisting only or largely of complete ring-like punctures. The dorsal coloration of *C. floricola borneanus* sp. n. is usually more uniform, with elytral colouration not much darker than pronotal one.

Description. *Measurements.* 2.2–3.4 mm long (length of holotype: 2.9 mm), 1.8–1.9× as long as wide, widest at basal fifth of elytra; weakly convex, 3.1–3.3× as long as high (height of holotype: 2.8 mm). *Colouration.* Pale brown with weakly darker elytra (Fig. 1C).

Pronotum 2.2× wider than long; 1.5× wider at base than between anterior angles, 1.6× wider than head including eyes. Punctation dense and shallow, consisting of complete ring-like impressions with one small setiferous puncture on posterior margin (Figs 4E, 5F), punctation of approximately same in size and density all over pronotum.

Elytra widest at anterior fifth, 1.1–1.2× as long as wide, 2.9–3.0× as long as pronotum, 1.1× as wide as pronotum. Punctation on intervals composed of semicircular impressions with one setiferous puncture on posterior margin (Fig. 4F).

Variation. In most specimens examined from Borneo, the pronotal punctation consists exclusively of completely ring-like punctures. However, in few localities on the north-western coast of Borneo the punctation of 5-20% of specimens shows a mixture of complete and incomplete rings. In the absence of genetic data, we are unable to analyze this variation in detail, and hence temporarily treat even these specimens as *C. floricola borneanus*.

Etymology. The name of this species is derived from Borneo, the historical name of island where all the known specimens of this subspecies were collected.

Distribution. The species seems to be widespread in Borneo, it is recorded from Indonesia: Kalimantan Barat and Kalimantan Selantan and Malaysia: Sabah, Sarawak (Fig. 7)

Biology. This subspecies has been collected in inflorescences of a number of plant species belonging to the Araceae family. It was collected in high numbers in flowers of the genus *Schismatoglottis*: *S. calyptrata*, *S. colocasioideae*, *S. erumpens* complex, S. *giamensis* (Fig. 6G), *S. mayoana*, *S. modesta*, *S. muluensis*, *S. multinervia, S. pellucida*, *S. petradoxa* and *S. serratodentata.* It has been also collected in numbers close to one hundred specimens in an inflorescence of *Ooia glans* (Figs 6H–I) and *O. havilandii.* Other known records of host plants include *Alocasia longiloba* complex (Fig. 6F), *Gamogyne loi*, several species of *Homalomena* (this paper) *Phymatarum borneense* and *Schottarum sarikeense* (Fig. 6A–B) (Low et al. 2016). According to H. Takizawa (pers. comm. 2017), *C. borneanus* can be found in aggregations in a wide range of aroid inflorescences from lowlands to montane areas (ca. between 100–1500 m a.s.l), mainly in flowers on small open places like trail sides in or near well-preserved primary or secondary forests, or along small streams.

Biology of *Cycreon*

All specimens of both subspecies of *C. floricola* have been collected in inflorescences of various Araceae genera, often in high numbers, indicating their tight association with this microhabitat. The fact that there were only two specimens of the genus known up to now likely correspond with the biology of *Cycreon* beetles, since no study of flower-inhabiting beetles associated with Araceae in the Malaysian Peninsula and Sunda islands was performed previously.

Low et al. (2016) studied the biology of insects associated with inflorescences of Araceae in Borneo and demonstrated that *Cycreon floricola borneanus* specimens

are only present in the upper part of the inflorescences of *Phymatarum borneense* and *Schottarum sarikeense*, never in the pistillate zone (= bottom), and that they are not attracted by the smell of the inflorescences, unlike the co-occurring *Chaloenus* beetles (Chrysomelidae) and *Colocasiomyia* flies (Drosophilidae). Observations of few specimens covered by pollen grains were reported, but only *Colocasiomia* flies were considered as pollinators. Subsequent investigations of the pollination biology of the *Schismatoglottis calyptrata* complex (Hoe et al. 2018) revealed that *Cycreon floricola borneanus* visited all the investigated species except *Schismatoglottis calyptrata* and *S. laxipistillata*, but their abundance differed based on host plant species: they were very abundant in *S. giamensis, S. caesia and S. muluensis*, but present in single or few specimens only in *S. pseudoniahensis*, *S. pantiensis*, *S. adducta*, and *S. roh*. *Cycreon* beetles were observed to feed on the exudations from the interpistillar staminodes, mated on the pistillate zone and remained inside the lower spathe chamber. They were also revealed as the most effective pollen carriers, carrying 6–15 times more pollen than *Colocasiomyia* flies and hence considered as secondary pollinators (*Colocasiomyia* flies were 4–6 times more abundant and are hence considered as main pollinators). No hydrophilid larvae were found in the inflorescences, indicating that they may live in different microhabitat.

Mouthparts of *Cycreon* (Fig. 1F–K) are unusual when compared to other members of the tribe Megasternini examined so far, differing from them in three aspects: (1) structure of the mandible with two large teeth on the apex (Fig. 1F–G), (2) excision of the clypeus (varying from weak to very deep, depending of the species; Fig. 5), and (3) shape of the mentum, with deep anterior excision (Figs 1J, 2B, 5). The mandibles of other Megasternini examined so far bear simple apex (e.g., Fikáček 2010, Arriaga-Varela et al. 2018), while those of *Cycreon* have the apex deeply bifid and with two large teeth. When the mandible is examined in mesal view (Fig. 1H), both apical teeth are situated on sides of straight edge, and they become strongly abraded in some specimens (Fig. 1G). This may indicate that mandibular apex is used for processing of some hard/solid material, possibly for scraping organic material from internal parts of the aracean inflorescences, in agreement with the above observations by Hoe et al. (2018). The inspection of the gut contents of *Cycreon floricola borneanus* (Fig. 6C–E) revealed that the midgut contains two components, both stained by safranine dye: (1) pollen grains of the respective plant species and (2) the heterogeneous organic matter which cannot be further identified; it does not seem to be just remains of crushed pollen grains, as no partially crushed pollen grains or remains of their exine were found (safranine stains various organic compounds including cellulose, lignine, glucosamines and cell nuclei, and does not allow detailed identification of this component - it may represent organic detritus scraped by the beetles from interior of the inflorescence). The presence of this unspecified organic matter in the intestines indicates that *Cycreon* beetles are not specialized pollen feeders, but the presence of pollen grains in the midgut content confirms that pollen is part of the diet and may be possibly digested. When compared to specialized pollen-feeding New Zealand genus *Rygmodus* (Hydrophilidae: Cyclominae) analyzed by Minoshima et al. (2018), important differences in mandible morphology can be found, confirming that *Cycreon* is not specialized pollen feeder: (1) mandibular apex is simple and spoon-like in *Rygmodus*, whereas strongly bifid in *Cycreon*, (2) mola is simply tuberculate in *Rygmodus* (a supposed adaptation to disrupt the pollen exina by grinding), but bears poriferous lamellae in *Cycreon* and all other hydrophilids examined. Unlike in *Cycreon*, the midgut of *Rygmodus* contains nearly exclusively pollen grains, with very little fine organic matter (see Minoshima et al. 2018: fig 4).

The excised clypeus and anterior margin of mentum is unusual in the Megasternini. Excised mentum is only known in the Central American genus *Nitidulodes*, which is also associated with aroid inflorescences (Hansen 1991, Bloom et al. 2015). Excised clypeus is only present in *Cycreon*. Moreover, the strong variation of mentum and clypeus shape between different species of *Cycreon* is also unusual within Megasternini. Usually these characters are very similar in congeneric species and differ at most between genera. We suppose that this interspecific variation in *Cycreon* may indicate species-specific food and host-plant preferences. The data by Hoe et al. (2018) indicate some kind of specificity in host plants, which would be in agreement with this assumption. For example, various genera and species of Schismatoglottideae were sampled in Mulu National Park (Malaysia, Sarawak) from December 2017 to February 2018, but *Cycreon* beetles were only found in sampled species of *Schismatoglottis* (beetles were present in all sampled plants), whereas not a single specimen was found in inflorescences of *Anadendrum, Aglaonema, Alocasia, Bucephalandra* and *Lasia.* Additionally, the material collected from various inflorescences of the single aroid tribe Schismatoglottideae by Low et al. (2014, 2016), Hoe & Wong (2016) and Hoe et al. (2018) includes two very closely related subspecies only (*Cycreon floricola floricola* and *C. floricola borneanus*), despite consisting of more than 1000 specimens; not a single specimen of another *Cycreon* species was collected even in peninsular Malaysia, despite the sampled localities were close to those of two other species (*C. armandi* and *C. adolescens*). We suppose this may be caused by the focus on a single narrow group of host plants, and is congruent with the expected species-specific host preferences in *Cycreon* beetles.

Discussion

Interactions of *Cycreon* with aroid inflorescences can be interpreted as an initial stage of development of cantharophyly, i.e. interrelations between beetles and plant reproductive organs, in which only adult are associated with flowers (e.g., Kirejtshuk 1994, 1997). This type of inter-

relations is particularly possible in cases when blossoming period ends by decaying of part of flowers with fungal and microbial infection (Teichert et al. 2012). On the other hand, species of *Chaloenus* beetles (Chrysomelidae: Alticini) co-occurring with *Cycreon* may represents another type of interrelations with plants, connected with a secondary transition of adults from leaf-feeding to flower-feeding. Besides, one sample collected from *Leucocasia giganteum* in peninsular Malaysia included representatives of *Aethina* Erichson (Coleoptera: Nitidulidae: Nitidulinae); some species of the genus are known to be associated with fungi, others to feed on inflorescences (Kirejtshuk 1986). Few examined samples also included few staphylinids, possibly as occasional visitors of decaying aroid inflorescences.

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References

Archangelsky M (1997) Studies on the biology, ekology and systematice of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). Bulletin of the Ohio Biological Survey, New Series 12(1): 1–207.

Arriaga-Varela E, Seidel M, Deler-Hernández A, Senderov V, Fikáček M (2017) A review of the *Cercyon* Leach (Coleoptera, Hydrophilidae, Sphaeridiinae) of the Greater Antilles. ZooKeys 681: 39–93. https://doi.org/10.3897/zookeys.681.12522

Arriaga-Varela E, Seidel M, Fikáček M (2018) A new genus of coprophagous water scavenger beetle from Africa (Coleoptera, Hydrophilidae, Sphaeridiinae, Megasternini) with a discussion on the *Cercyon* subgenus *Acycreon*. African Invertebrates 59(1): 1–23. https://doi.org/10.3897/AfrInvertebr.59.14621

Bloom D, Fikáček M, Short AEZ (2014) Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. PLoS ONE 9(6): e98430. https://doi.org/10.1371/journal.pone.0098430

Fikáček M (2010) Hydrophilidae: The genus Kanala Balfour-Browne (Coleoptera). In: Jäch MA, Balke M (Eds) Water Beetles of New Caledonia, volume 1. Monographs of Coleoptera 3: 365–394.

Fikáček M, Short, AEZ (2006) A revision of the Neotropical genus *Motonerus* Hansen (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 1268: 1–38.

Fikáček M, Hebauer F, Hansen M (2009) Taxonomic revision of New World species of the genus *Oosternum* Sharp (Coleoptera: Hydrophilidae: Sphaeridiinae). I. Definition of species groups and revision of the *Oosternum aequinoctiale* group. Zootaxa 2054: 1–37.

Fikáček M, Jia FL, Prokin A (2012) A review of the Asian species of the genus *Pachysternum* (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 3219: 1–53.

Hansen M (1991) The Hydrophiloid beetles: phylogeny, classification and a revision of the genera (Coleoptera, Hydrophiloidea). Kongelige Danske videnskabernes selskab, Copenhagen, 367 pp.

Hoe YC, Wong SY (2016) Floral biology of *Schismatoglottis baangongensis* (Araceae: Schismatoglottideae) in West Sarawak, Borneo. Plant Systematics and Evolution 302: 1239–1252. https://doi.org/10.1007/s00606-016-1329-z

Hoe YC, Wong SY, Gibernau M (2018) Diversity of pollination ecology in the *Schismatoglottis Calyptrata* Complex Clade (Araceae). Plant Biology. doi:10.1111/plb.12687

Kirejtshuk AG (1986) Revision of the genus Aethina Er. (Coleoptera, Nitidulidae) of the fauna of the Oriental and Palaearctic Regions. Proceedings of the Zioological Institute of Academy of Sciences of USSR 140: 44–82. [In Russian]

Kirejtshuk AG (1994) System, evolution of the way of life, and phylogeny of the order Coleoptera. I. Entomological Review 73(2): 266–288 (in Russian). [English translation: 1995, 74: 12–31]

Kirejtshuk AG (1997) On the evolution of anthophilous Nitidulidae (Coleoptera) in tropical and subtropical regions. Bonner Zoologische Beitrage 47(1–2): 111–134.

Low SL, Wong SY, Boyce PC (2014) *Schottarum* (Schismatoglottideae: Araceae) substantiated based on combined nuclear and plastid DNA sequences. Plant Systematics and Evolution 300: 607–617. https://doi.org/10.1007/s00606-013-0906-7

Low SL, Wong SY, Ooi IH, Hesse M, Städler Y, Schönenberger J, Boyce PC (2016) Floral diversity and pollination strategies of three rheophytic Schismatoglottideae (Araceae). Plant Biology 18(1): 84–97. https://doi.org/10.1111/plb.12320

Low SL, Wong SY, Boyce PC (2018). Naming the chaos: generic redelimitation in Schismatoglottideae (Araceae). Webbia 72: 1–100. https://doi.org/10.1080/00837792.2017.1409940

Minoshima YN, Seidel M, Wood JR, Leschen RAB, Gunter NL, Fikáček M (2018) Morphology and biology of the flower-visiting water scavenger beetle genus Rygmodus (Coleoptera: Hydrophilidae). Entomological Science. https://doi.org/10.1111/ens.12316

Orchymont A (1919) Contribution a l'étude des sous-familles des Sphaeridiinae et des Hydrophilinae (Col. Hydrophilidae). Annales de Société Entomologique de France 88 : 105–168.

Ryndevich SK (2001) On identification of species of the Cercyon dux group (Coleoptera: Hydrophilidae). Zoosystematica Rossica 10(1): 79–83.

Ryndevich SK (2008) Review of species of the genus *Cercyon* Leach, 1817 of Russia and adjacent regions. IV. The subgenera *Paracycreon* Orchymont, 1924 and *Dicyrtocercyon* Ganglbauer, 1904 (Coleoptera: Hydrophilidae). Zoosystematica Rossica 17(2): 89–97.

Ryndevich SK, Jia FL, Fikáček M (2017) A review of the Asian species of the Cercyon unipunctatus group (Coleoptera: Hydrophilidae: Sphaeridiinae). Acta Entomologica Musei Nationalis Pragae 57(2): 535–576. https://doi.org/10.1515/aemnp-2017-0089

Shatrovskiy A (2017) A new species of *Cycreon* d'Orchymont, 1919 from Singapore (Coleoptera: Hydrophilidae: Megasternini). Zootaxa 4217 (3): 588–592. https://doi.org/10.11646/zootaxa.4317.3.11

Short AEZ, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51: 83–122.

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. https://doi.org/10.1111/syen.12024

Smetana A (1978) Revision of the subfamily Sphaeridiinae of America north of Mexico (Coleoptera: Hydrophilidae). Memoirs of Entomological Society of Canada 105: 1–292. https://doi.org/10.4039/entm110105fv

Takizawa H (2010) Revisional notes on the genus *Chaloenus* Westfood (Coleoptera: Chrysomelidae). In: Mohammed HJ, Ipor I, Meekiong K, Sapuan KA, Ampeng A (Eds) Lanjak Entimau Wildlife Sanctuary 'Hidden Jewel of Sarawak'. Proceedings of the Seminar: Lanjak Entimau Scientific Expeditions. Academy of Sciences Malaysia, 347–355.

Teichert H, Dötterl S, Framec D, Kirejtshuk A, Gottsberger G (2012) A novel pollination mode, saprocantharophily, in Duguetia cadaverica (Annonaceae): A stinkhorn (Phallales) flower mimic. Flora (Morphology, Distribution, Functional Ecology of Plants) 207(7): 522–529. https://doi.org/10.1016/j.flora.2012.06.013

Supplementary material 1

List of known specimens of Cycreon in DarwinCore format

Authors: Emmanuel Arriaga-Varela, Sin Yeng Wong, Alexander Kirejtshuk, Martin Fikáček

Data type: occurence

Link: https://doi.org/10.3897/dez.65.26261.suppl1