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Comparative morphology of immature stages and adults of *Hydroscapha* from Taiwan, with description of a new species from Hong Kong (Coleoptera: Myxophaga: Hydroscaphidae)

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Abstract. Hydroscaphidae is a small family of the beetle suborder Myxophaga comprising miniaturised aquatic beetles resembling some staphylinids. Surprisingly little is known about the taxonomy and biology of these beetles. In this study we present novel data based on freshly collected material of *Hydroscapha* LeConte, 1874, from Taiwan and Hong Kong. Morphology and DNA barcoding revealed two species: Taiwanese endemic *H. takahashii* Miwa, 1935, and *H. shuihau*, a new species, so far known only from Lantau Island of Hong Kong. Both species are (re)described, illustrated, and compared to the types of *H. hunanensis* Pu, 1948. Both species were found in algal mats in ephemeral hygropetric habitats; in two cases adults massed together with immature stages were observed. Larvae and pupae of *H. takahashii* were studied and illustrated using SEM and light microscopy. Comparisons of immature stages of Hydroscaphidae based on our new data and a detailed review of the literature reveals that principal differences between genera and species can be found in the modifications of the tracheal system both in larvae and pupae. Four larval instars were found in *H. takahashii*, corresponding to the number of instars known in the myxophagan family Torridincolidae. Based on our observations, we suggest that the minute body size of *Hydroscapha* may be one of the adaptations for colonising and exploiting ephemeral habitats.

Key words. skiff beetles, Oriental Region, new species, larva, pupa, DNA barcode

INTRODUCTION

Hydroscaphidae (skiff beetles) is one of four families of the beetle suborder Myxophaga (e.g., Reichardt, 1973; Yavorskaya et al., 2018). As with other members of the suborder, hydroscaphids are very small beetles, with a body length around 1 mm, which are associated with aquatic habitats with abundant algae (e.g., Falamarzi et al., 2010). The family contains four genera and 33 described species (Short et al., 2015; Raundez Reyes et al., 2019; Trujillo & Cañote, 2019; Perkins & Bergsten, 2019). Recent discoveries of new species (Raundez Reyes et al., 2019; Trujillo & Cañote, 2019; Perkins & Bergsten, 2019) suggest that the diversity of Hydroscaphidae could be distinctly higher. However, beetles are likely often overlooked due to their small body size and specific environmental requirements. The species-level systematics are further hindered by a highly uniform external morphology (e.g., Maier et al., 2010), problems associated with matching male and female of the same species (e.g., Fikáček & Šípková, 2009), and the fact that the limited number of species-specific morphological characters are only observable after careful dissection.

Of the four genera that the family comprises, three are confined to the Neotropics: *Confossa* Short et al., 2015; *Scaphydra* Reichardt, 1973, and *Yara* Reichardt & Hinton, 1976 (Short et al., 2015). Only the genus *Hydroscapha* LeConte, 1874 is widely distributed, recorded from the Palaearctic (five species), Oriental region (13 species), the Nearctics (two species), northern Neotropics (one species), and Madagascar (two species) (Short et al., 2015; Perkins & Bergsten, 2019). Asian species of *Hydroscapha* were revised by Löbl (1994) and Fikáček & Šípková (2009). The authors of both studies were unable to interpret the identity of *H. takahashii* Miwa, 1935 from Taiwan. The type material was considered as lost (Jäch, 1995), and no additional specimens were available. This made the identification of

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Hydroscapha in the region impossible — it was unclear whether the central Chinese species, *H. hunanensis* Pu, 1948, or the recently collected specimens from Hong Kong were conspecific with the Taiwanese species.

Our fieldwork from 2018 to 2020 resulted in the rediscovery of *Hydroscapha* in five localities in Taiwan, in two cases together with larvae of all instars and pupae. Examination of museum collections in Taiwan revealed that the types of *H. takahashii* had not been lost; they were found well-preserved and available to study. Knowing the identity of the Taiwanese species enabled us to ascertain that specimens collected in Hong Kong belong to a different species, which is described here as new. DNA barcode data are provided for both species, in order to facilitate future studies of Asian *Hydroscapha*.

MATERIAL AND METHODS

Specimen depositories.
AFCD – Agriculture, Fisheries and Conservation Department, Cheung Sha Wan Insect Collection, Hong Kong;
BMNH – Natural History Museum, London, UK (M. Barclay);
FSHC – Fang Shuo Hu collection, Taichung, Taiwan;
KMNH – Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan (Y. Minoshima);
NCHU – Department of Entomology, National Chung Hsing University, Taichung, Taiwan. (M.-M. Yang);
NHMW – Naturhistorisches Museum, Wien, Austria (M. A. Jäch);
NMNS – National Museum of Natural Science, Taichung, Taiwan (J.-F. Tsai);
NMPC – National Museum, Prague, Czech Republic (J. Hájek, M. Fikáček);
PCPA – Paul Aston collection, Hong Kong, China;
SYSU – Museum of Biology, School of Life Sciences, Sun Yat-sen University, Guangzhou, China (H. Pang, F.- L. Jia);
TARI – Taiwan Agriculture Research Institute, Taichung, Taiwan (C.-F. Lee).

Systematics and morphological studies. We have examined freshly collected specimens from Lantau Island and Taiwan, and the type specimens of *H. takahashii* (see under that species). For comparative purposes, we also examined the following paratypes of *H. hunanensis* (Figs. 3K–O, 4G–I): 1 male, 1 female (SYSU): "Hunan Hengshan [in Chinese] / 1941. IX. 4 [4 September 1941] // Hungshan / Hunan, China / Sept. 4 1941 [4 September 1941] / C. L. Pu // Hydroscapha / hunanensis / Pu // PARATYPE".

Dried uncoated adults were first examined using a Hitachi S-3700N electron microscope at the Department of Paleontology, National Museum in Prague, using low vacuum mode. Selected specimens were subsequently dissected using fine micro-pins (minuten pins) in glycerin; genitalia and terminal abdominal sclerites were photographed using a Canon D1100 digital camera attached to an Olympus BX41 compound microscope. Third instar larvae and pupae were first cleaned manually by brush and by sonicating in glass cleaner, then transferred from ethanol to hexamethyldisilazane (HMDS) in the following steps: (1) 50% ethanol for 15 mins, (2) 70% ethanol for 30 mins, (3) 80% ethanol for 30 mins, (4) 90% ethanol for 30 mins, (5) 96% ethanol for 30 mins, (6) two baths in 100% ethanol for 30 mins each, (7) 2 parts 100% ethanol + 1 part HMDS for 30 mins, (8) 1 part 100% ethanol + 2 parts HMDS for 30 mins, (9) two baths in pure HMDS 30 mins each, (10) drying the specimens overnight. Specimens were examined uncoated in low vacuum mode using the Hitachi S-3700N electron microscope (see above) or gold-coated in full vacuum mode using a JEOL JSM-6380LV electron microscope in the Laboratory of Electron Microscopy, Faculty of Science, Charles University, Prague.

Measurements of adults are based on dry-mounted specimens (n=25 for *H. takahashii*, n=10 for *H. shuihau*, new species); since the length of the abdomen varies due to the telescopic character of the segments, we provide the length of the forebody (= the distance between anterior margin of the head and posterior margin of elytra) in addition to the total body length. Measurements of larvae of *H. takahashii* are based on alcohol-fixed specimens (n=20 for body length, n=190 for the width of head capsule used to determine the number of larval instars).

Adults of all known *Hydroscapha* species are very similar in body shape, and only a few external characters, including size and body proportions, were found useful for identification (Löbl, 1994; Fikáček & Šípková, 2009; Maier et al., 2010): length of the forebody, proportions of antennomeres III and IX, and proportions of the mesoventral elevation. Most species-level diagnostic characters are present in the male and female genitalia and surrounding abdominal sclerites. All these characters are mentioned and illustrated. In larva and pupa, we illustrate and describe the characters we consider as diagnostic for the genus and the species, based on the comparison with published descriptions of immatures of the Hydroscaphidae (see Table 4 in the Discussion for reference). Additional characters of all stages may be seen in the supplementary photographs and SEM micrographs provided, see Online depositories of data below.

DNA extraction and sequence analysis. Complete genomic DNA was extracted from two specimens of *H. shuihau*, new species (male holotype and a female), and two specimens of *H. takahashii* (one from Heshe, another from Wulai), using the Tissue Genomic DNA Mini Kit (Geneaid Biotech Ltd., Taiwan) following the manufacturer's instructions, but with adapted incubation times (3.5 hours with proteinase K + GT buffer, 1 hour with proteinase K + GT buffer + LGT buffer). We amplified the 5′ fragment of the cytochrome oxidase I (*cox1*) mitochondrial gene (so-called barcoding fragment) using the standard LCO1490/HCO2198 primers (Folmer et al., 1994) with the following PCR protocol: 94°C for 3 mins, 35× (94°C for 30 s, 48°C for 45 s, 72°C for 1 min), 72°C for 8 mins. Our sequences were aligned with other available data for the genus *Hydroscapha* (European species: *H. granulum* (Motschulsky, 1844) from Pons et al., 2010; North American species: *H. natans* LeConte, 1874 and *H. redfordi*

Table 1. List of newly sequenced specimens and their GenBank accession numbers.

Species	Sex	Voucher #	Locality data	GenBank #
Hydroscapha shuihau, new species (paratype)	female	MF2430.1	Hong Kong, Lantau, Shui Hau, 14 April 2019, P. Aston lgt.	MT132897
Hydroscapha shuihau, new species (holotype)	male	MF2430.2	same data as MF2430.1	MT132899
Hydroscapha takahashii	male	MF2365	Taiwan: Nantou County, Heshe, Xinyi Township Tongfu Village; at bridge over Heshexi, 23.58767°N, 120.89027°E, 16 May 2018, Fikáček, Hu, Liang, Liu & Minoshima, lgt. (2018-TW35a)	MT132896
Hydroscapha takahashii	female	MF2456	Taiwan: New Taipei, Wulai City at Wulai Bridge, 24.86404°N, 121.5518°E, 18 May 2018; Fikáček & Minoshima lgt. (2018-TW09)	MT132898

Löbl, 1994 from Maier et al., 2010; *H. perijaensis* Hall & Short, 2010 from Short et al., 2015) using the MUSCLE algorithm in Geneious 6.1. Aligned data were analysed using maximum likelihood in the MEGA7.0 software (Kumar et al., 2018) using the GTR model; bootstrap values were calculated using 1000 replicates. We list genetic distances between species and specimens as uncorrected p-distances. Sequenced specimens are listed in Table 1.

Online depositories of data. Original unedited photos and SEM micrographs, including those only used for comparative purposes and not included in the printed version of this paper, were submitted as a .zip file to Zenodo archive under the doi.org/10.5281/zenodo.3537900 under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 license; this paper should be cited in each case when these data are used. Newly generated *cox1* sequences were submitted to GenBank under accession numbers MT132897, MT132899 (*H. shuihau*) and MT132896, MT132898 (*H. takahashii*).

RESULTS

Molecular Analysis. The *cox1* sequences are very similar for the male and female from Hong Kong (genetic distance 1.4%) and Taiwanese specimens from both localities (2.1%). These distances correspond to the intraspecific distances known in *H. natans* (1.4%) and are much smaller than the distance between Taiwan and Hong Kong specimens (14.8%). These results indicate that the material contains two species, one from Taiwan and one from Hong Kong. Maximum likelihood analysis reveals both species as moderately supported sister species (bootstrap bb=0.84) which are together more closely related to the European *H. granulum* than to the American species (Fig. 1). Results of the molecular analysis are corroborated by the morphological differences found between the Taiwanese and Hong Kong specimens (see below).

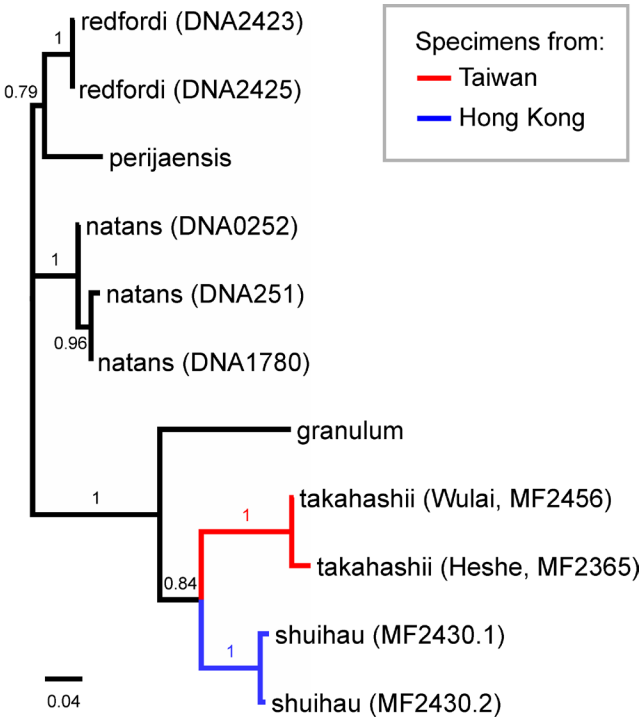

Fig. 1. Results of the maximum likelihood analysis of the *cox1* sequences of *Hydroscapha*. Sequences of the species treated in this study are highlighted in blue (Hong Kong specimens) and red (Taiwanese specimens).

SYSTEMATICS

Family Hydroscaphidae LeConte, 1874

Hydroscapha LeConte, 1874

Hydroscapha takahashii Miwa, 1935

Hydroscapha takahashii Miwa, 1935: 352.
Hydroscapha takahashii – Löbl, 1994: 32; Jäch, 1995: 33; Fikáček & Šípková, 2009: 43–45.

Table 2. Characters of male genitalia and abdominal sclerites (adapted from Fikáček & Šípková, 2009).

Species	Aedeagus				Sternite V		Sternite VI	Sternite VII		Tergite VII
	subapical region in lateral view	bent ventrad apically	angulate at dorsal face	shape in lateral view	chaetotaxy	posterior margin	posterior margin granulate	tufts of hairs	median part projecting	arrangement of posterolateral setae	posterior margin mesally
H. shuihau, new species	narrow	no	no	arcuate	two indistinctly divided tufts	weakly sinuate	no	no	weakly	serial	convex
H. takahashii	narrow	no	no	straight	two distinctly divided tufts	weakly sinuate	no	no	no	irregular	straight
H. hunanensis	narrow	yes	no	straight	two indistinctly divided tufts	weakly sinuate	no	no	weakly	irregular	convex

Type material examined. Syntypes: 1 male (TARI): "Shinten / Formosa / 14-VII.1935 [14 July 1935] / R. Takahashi // Hydroscapha / takahashii / Miwa / DET. Y. MIWA // 3056 // TYPE"; 2 females (TARI): "Shinten / Formosa / 14-VII.1935 [14 July 1935] / R. Takahashi // Hydroscapha / Takahashii / Miwa / DET. Y. MIWA"; 2 females (TARI): "Shinten / Formosa / 14-VII.1935 [14 July 1935] / R. Takahashi // Hydroscapha / Takahashii / Miwa / DET. Y. MIWA".

Additional material examined. 365 adults, 251 larvae, 15 pupae (NMPC, BMNH, KMNH, NCHU, NHMW, NMNS, SYSU, TARI): Taiwan: Nantou County, Heshe, Xinyi Township Tongfu Village; at bridge over Zhenyoulanxi, 23.58767°N, 120.89027°E, 16 May 2018, coll. Fikáček et al. (2018-TW35a), on exposed concrete wall with thin layer of flowing water and a layer of green algae. 9 adults (NMPC): Taiwan: New Taipei, Wulai City at Wulai Bridge, 24.86404°N, 121.5518°E, 05 and 18 May 2018; coll. Chang et al. (2018-TW09), seepage on concrete wall next to the Laka Rd., partly overgrown by the layer of algae. 1 male (NCHU): Taiwan: Kaohsiung City, Jingualiao bridge, Neiman Township, 16 April 2019, 23.0122700°N, 120.5207176°E, in stream, by net, coll. K-Y Zheng. 2 males (NCHU): Taiwan: Taichung City, Xiannv Waterfall, Taiping District, 24.1216°N, 120.8181°E, 04 January 2020, coll. H.-C. Liu. 210 adults, 9 larvae (FSHC): Taiwan: Taichung City, Tonglin, Wufeng District, 24.0712°N, 120.7524°E, 23 April 2020, coll. F.-S. Hu.

Type locality. Formosa, Shinten in Taihoku Province [= Taiwan, Xindian].

Diagnosis of adults. Males are most similar to *H. reichardti* Löbl, 1994 from Sulawesi in the following characters: two clearly divided tufts of setae on sternite V, sternite VI lacking lateral tufts of hairs, posterior margin of sternite VII only weakly convex, aedeagus evenly curved and narrowing towards apex, and proportions of antennomeres III and IX; they differ from *H. reichardti* in a slightly smaller body (forebody 0.69–0.76 mm in *H. takahashii*, 0.85–0.94 mm in *H. reichardti*) and a more elongate apex of the aedeagus (compare Fig. 3A with Löbl, 1994: fig. 55). Females are most similar to *H. jumaloni* Satô, 1972 from the Philippines in the following characters: simple posterior margin of sternite VI, slightly projecting posterior margin of tergite VI, and smaller body size. They differ from *H. jumaloni* in a sinuate posterior margin of female sternite V (straight in *H. jumaloni*). Males of *H. takahashii* may be distinguished from those of *H. shuihau*, new species, and *H. hunanensis* by distinctly divided tufts of setae on sternite V, sternite VI lacking median projection, and tergite VII being straight posteromedially. Females of *H. takahashii* may be distinguished from these species by a distinctly triangular (and hence pointed) posterior margin of tergite and sternite VI. The main diagnostic characters are listed in Tables 2 and 3 to be compared with those of other Asian species as listed by Fikáček & Šípková (2009).

Redescription of adults (Figs. 2D, 3A–E, 4A–C). Total body length: 1.0–1.2 mm. Length of the forebody (from

Table 3. Characters of female abdominal sclerites, body size, and proportions of antennomeres (adapted from Fikáček & Šípková, 2009). Antennomere III refers to second visible antennomere, antennomere IX to the ultimate one (see Fikáček et al., 2020 for details).

Species	Female sternite VI	Female tergite VI	Body	Antenna		Mesothorax
	shape apically	shape apically	length of fore body (mm)	antennomere III length/ width	antennomere IX length/ width	mesoventral elevation width/length
H. shuihau, new species	simple, widely rounded	widely rounded	0.70–0.75	1.3	2.4	2.1
H. takahashii	simple, widely triangular	with triangular median projection	0.69–0.76	1.6	2.6	2.0
H. hunanensis	simple, narrowly rounded	with narrowly rounded median projection	0.66–0.73	1.1	2.8	1.7

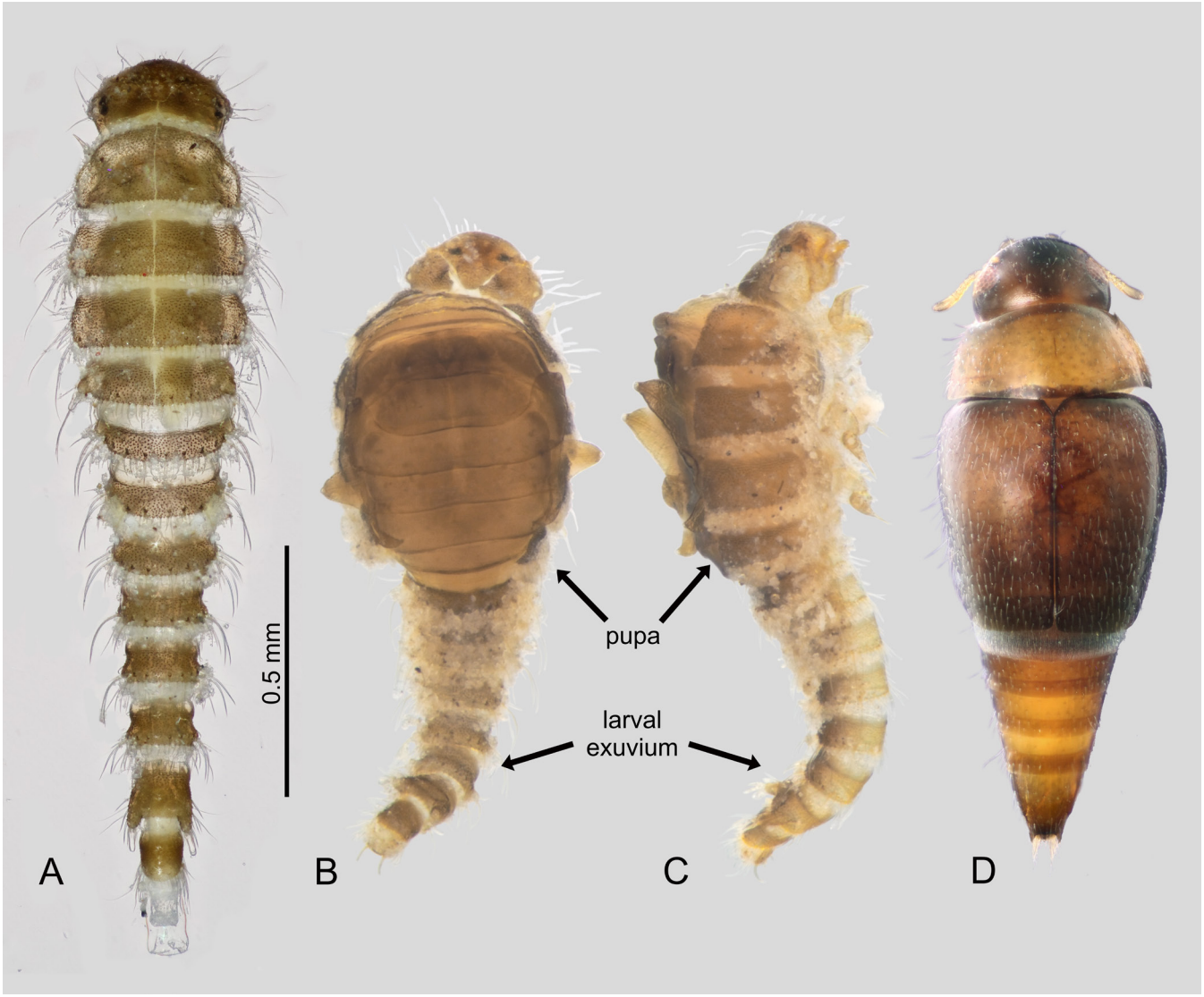

Fig. 2. Habitus of larva, pupa, and adult of *Hydroscapha takahashii*. A, last-instar larva in dorsal view; B, C, pupa in larval exuviae (B, in dorsal view; C, lateral view); D, adult in dorsal view.

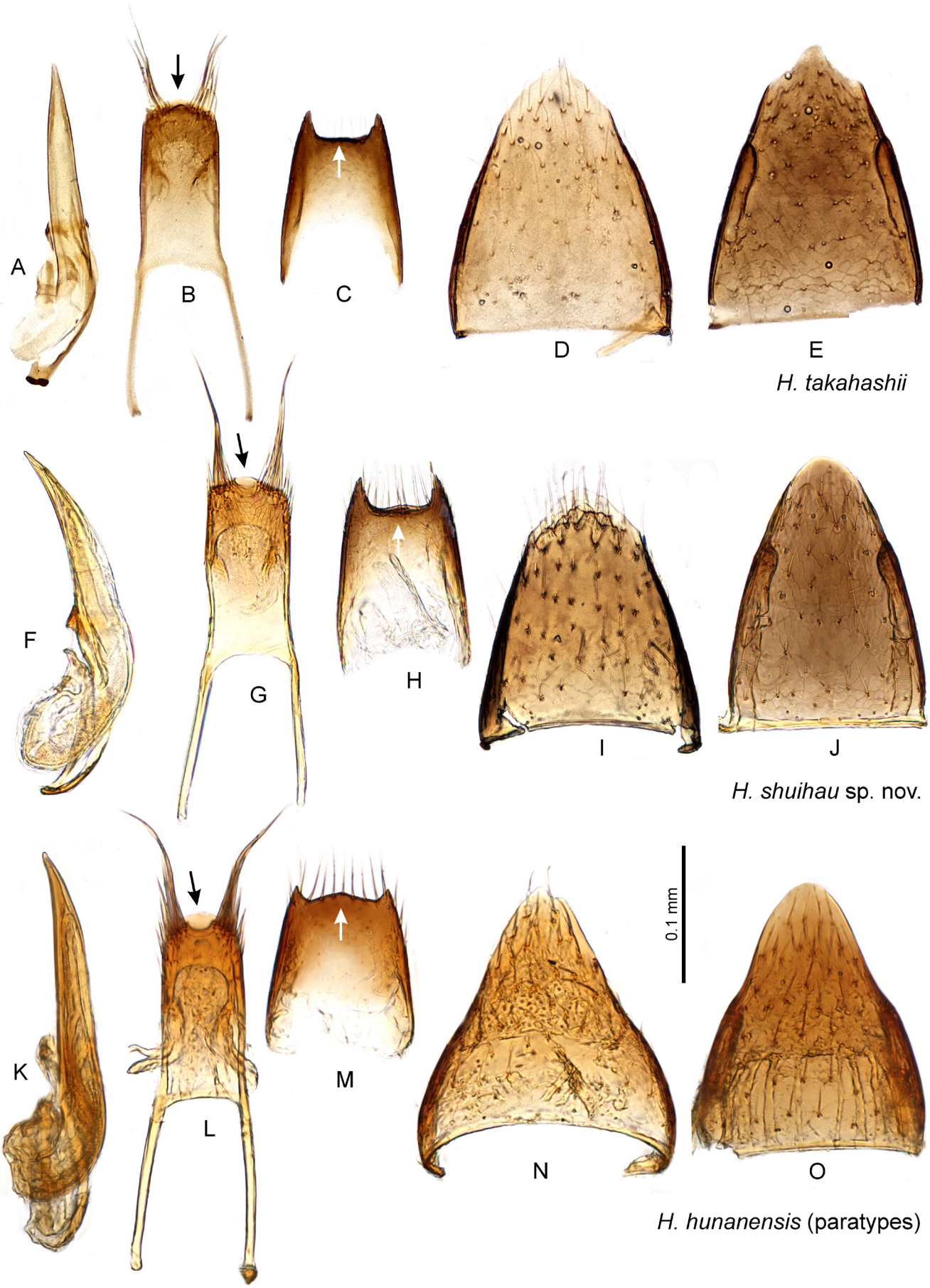

Fig. 3. Genitalia and terminal abdominal sclerites of *Hydroscapha takahashii* (A–E), *H. shuihau*, new species (F–J), and examined paratypes of *H. hunanensis* (K–O). A, F, K, aedeagus in lateral view; B, G, L, male sternite VII; C, H, M, male tergite VII; D, I, N, female sternite VI; E, J, O, female tergite VI. Only sclerites showing differences among species are illustrated. For illustrations of all taxonomically important sclerites see https://zenodo.org/deposit/3537900.

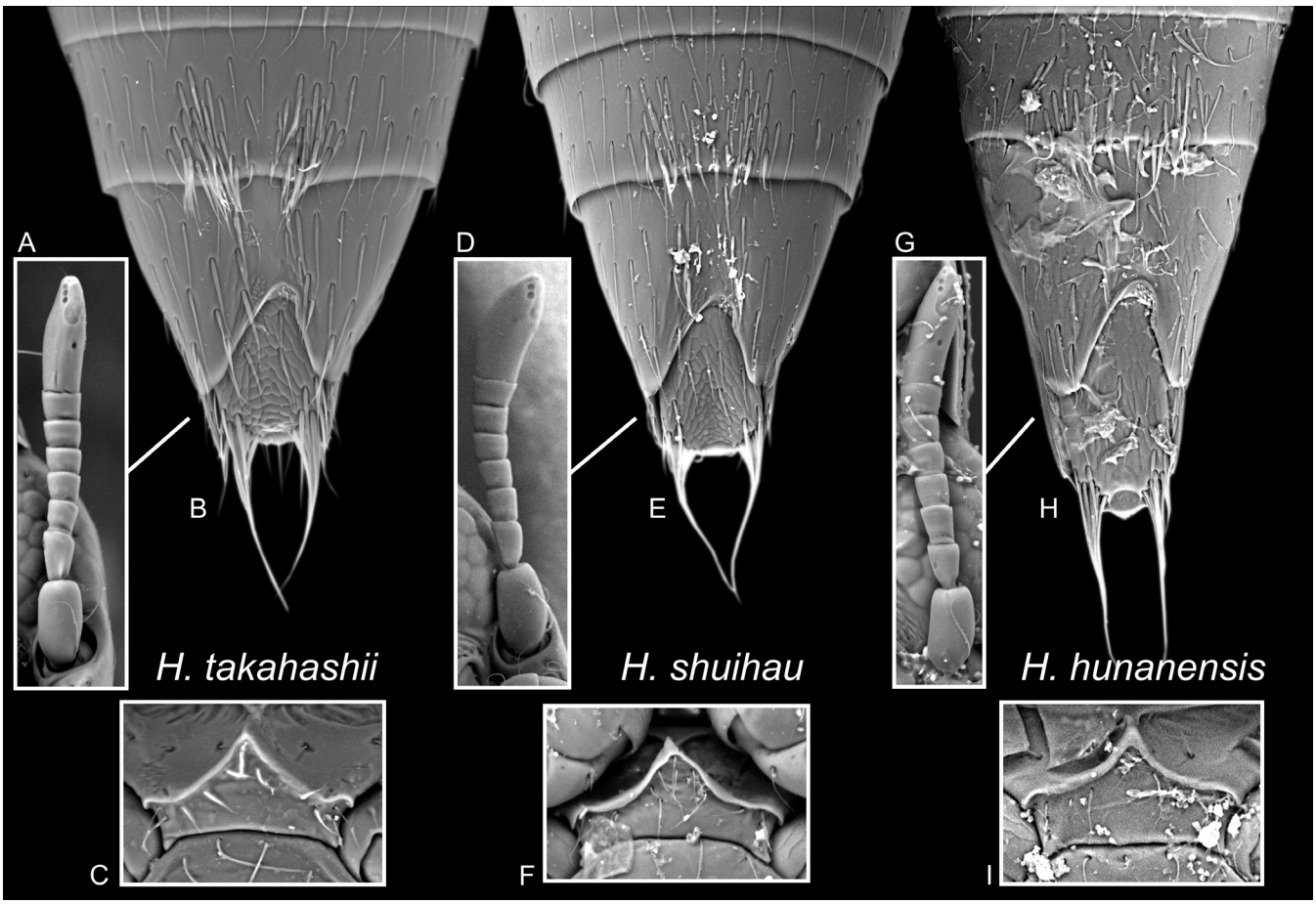

Fig. 4. External diagnostic characters of *Hydroscapha takahashii* (A–C), *H. shuihau*, new species (D–F), and *H. hunanensis* (G–I). A, D, G, antenna; B, E, H, male abdominal apex in ventral view with groups of setae on sternite V; C, F, I, mesoventral elevation.

anterior margin of head to posterior margin of elytra): 0.69–0.76 mm. Dorsal colouration reddish-brown to dark brown. Labrum angularly excised anteriorly, with two groups of setae dorsally. Antenna (Fig. 4A) with moderately long antennomere III (= second visible) and narrowly elongate slightly asymmetrical antennomere IX (= ultimate one); the latter with few apical sensilla. Mesoventral elevation subpentagonal, 2.0× wider than long (Fig. 4C).

Male. Protarsus with one sucking disc on basal tarsomere. Posteroventral margin of abdominal segment V weakly sinuate, ventral surface with two groups of setae distinctly separated from each other (Fig. 4B). Tergite VI truncated on posterior margin. Sternite VI without tufts of hairs. Sternite VII (Fig. 3B) without medioposterior projection. Tergite VII (Fig. 3C) entire posteromesally. Aedeagus (Fig. 3A) narrow basally, nearly straight in posterior two thirds, gradually narrowing towards apex.

Female. Protarsus lacking sucking disc. Abdominal sternite VI (Fig. 3D) and tergite VI (Fig. 3E) both triangularly pointed posteriorly.

Morphology of last instar larva (Figs. 2A, 5, 6). Body. Total length: 1.65–1.75 mm. Larva narrowly elongate. Legs largely hidden under body in dorsal view. **Head.** Width of head capsule: 0.29–0.30 mm. Head transverse, bearing fine dorsal microsculpture (Fig. 5C). Five pigmented spots (stemmata) are situated at side of head: four of them have lens-like cuticular structure (Fig. 5A: st), the fifth is not associated with lens-like structure. Genae projecting in wide genal folds (Fig. 5A, B: ge) bearing stout setae directed upwards; these folds adjoin lateral sides of labrum, together completely concealing mouthparts in dorsal and lateral views. Labrum fused with clypeus (Fig. 5A: lb), deeply concave on anterior margin (Fig. 5B: lb). Mandible not projecting, robust basally, with thin multidentate apex (Fig. 5E: md). Maxilla robust basally, apically projecting into narrow multidentate mala (Fig. 5E: mx). Labium largely covering mouthparts in ventral view; ligula large and robust (Fig. 5E: lig), bearing numerous specialised sensilla ('papilae', Fig. 5E: pa); labial palp with two palpomeres, lateral sensorial appendage with longitudinally ridged microsculpture (Fig. 5D: SA). **Thorax.** Each thoracic segment dorsally with large sclerite not subdivided mesally; surface with microsculpture similar to that on dorsal surface of head; anterior and posterior margins of protergum and posterior margins of meso- and metatergum bearing transverse row of setae (Fig. 6B), setae on lateral margins much longer than posterior ones; additional short setae also on disc, especially in mesal area. Pleural areas weakly sclerotised, with fine microsculpture (Fig. 6I, L). Sternal portion very narrow between closely adjacent articulations of legs (Fig. 6L). Legs (Fig. 6I) tetramerous, with large elongate coxa, long femur (likely fused basally with trochanter), relatively short tibiotarsus, and one long simple claw. **Abdomen** with

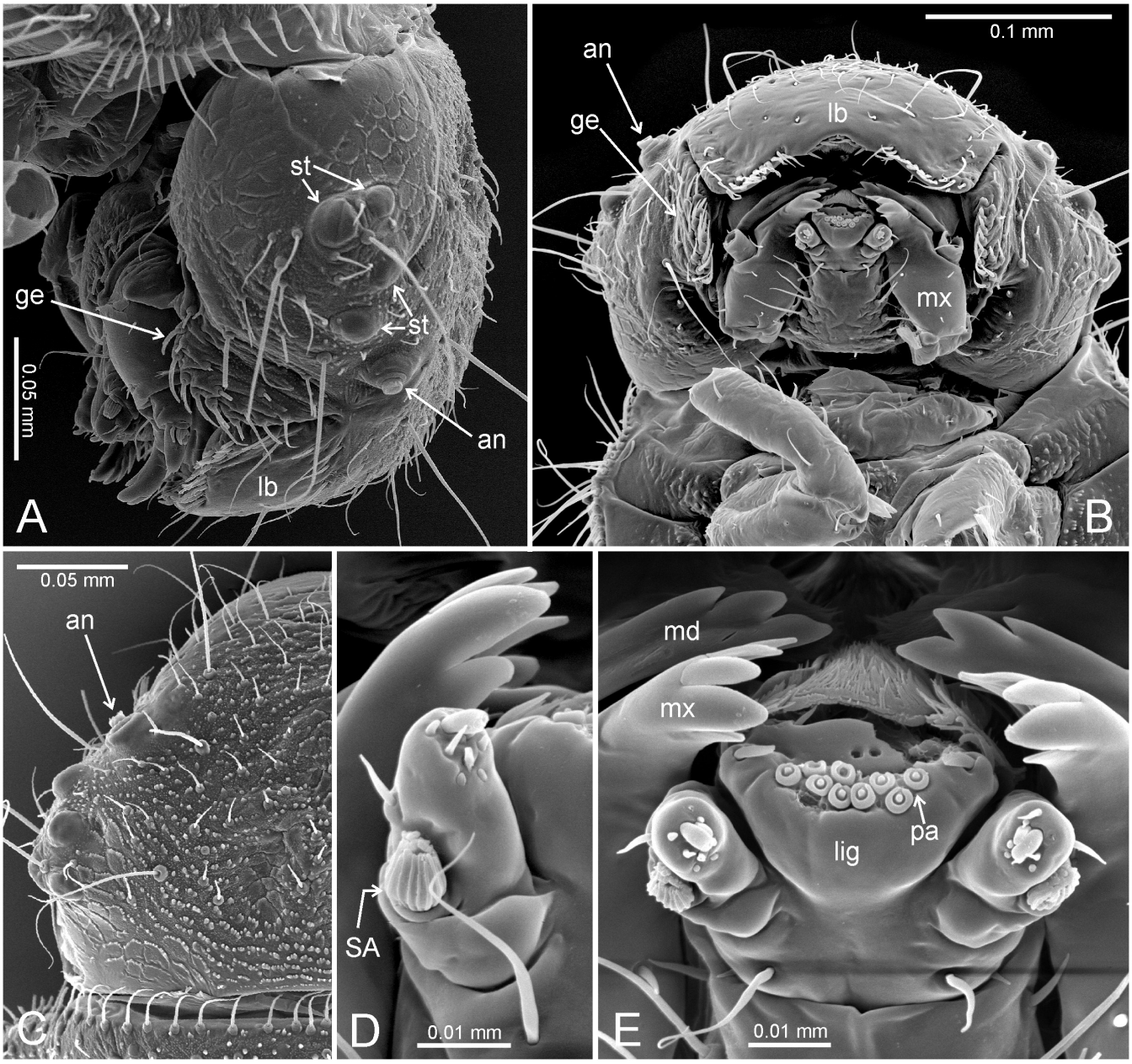

Fig. 5. Head morphology of the third instar larva of *Hydroscapha takahashii*, SEM micrographs. A, head in lateral view; B, head in ventral view; C, dorsal sculpture of the head; D, detail of labial palpus; E, detail of mouthparts in ventral view. Abbreviations: an, antennal articulation (antenna broke up); ge, genal lobe; lb, labrum; md, mandible; mx, maxilla; lig, ligula; pa, 'papilae', specialised sensilla of the ligula; SA, sensorial appendage of the labial palpus; st, stemma. For high resolution micrographs see https://zenodo.org/deposit/3537900.

10 segments (Fig. 6A). Segments III–IX with tergite and sternite fused into complete ring (Fig. 6A, J, K). Sclerites of segments I–VIII with fine microsculpture, series of long setae at posterior margin, and transverse series of stouter but more sparsely arranged setae slightly anterior to posterior margin (Fig. 6J, K). Segment X exposed as ventrally facing sclerotised plate with pair of hooks (Fig. 6G, H). Spiracles balloon-like (Fig. 6C–F), with fine walls enforced internally by longitudinal ridges, situated on posterolateral margin of protergum, laterodorsal part of abdominal segment I, and laterally on abdominal segment VIII. Thoracic spiracle ca. 2.5× as long as wide, on very short projection; spiracle on abdominal segment I ca. 2.5× as long as wide, on low wide tubercle; spiracle on abdominal segment VIII ca. 3.5× as long as wide, in a long finger-like projection.

Morphology of pupa (Figs. 2B, C, 7). Pupa short and wide, obtect, in natural condition resting within last larval exuvia (Fig. 2B, C). Head with exposed antennae, antenna with exposed scapus. Legs nearly completely covered by wingsheaths. Abdominal segments I–III dorsally flat, with lateral portions projecting anteriorly (segment I), laterally (segment II), and dorsally (segment III), apex of each lobe with open spiracle (Fig. 7D, E). Abdominal segments III–VII ring-like, segment IV with laterally situated open spiracle on small ventrally directed tubercle (Fig. 7G). Segments VIII–X minute (Fig. 7C, H).

Remarks on adult morphology. *Hydroscapha takahashii* was originally distinguished from other *Hydroscapha* by the presence of the median furrow on the pronotum as stated

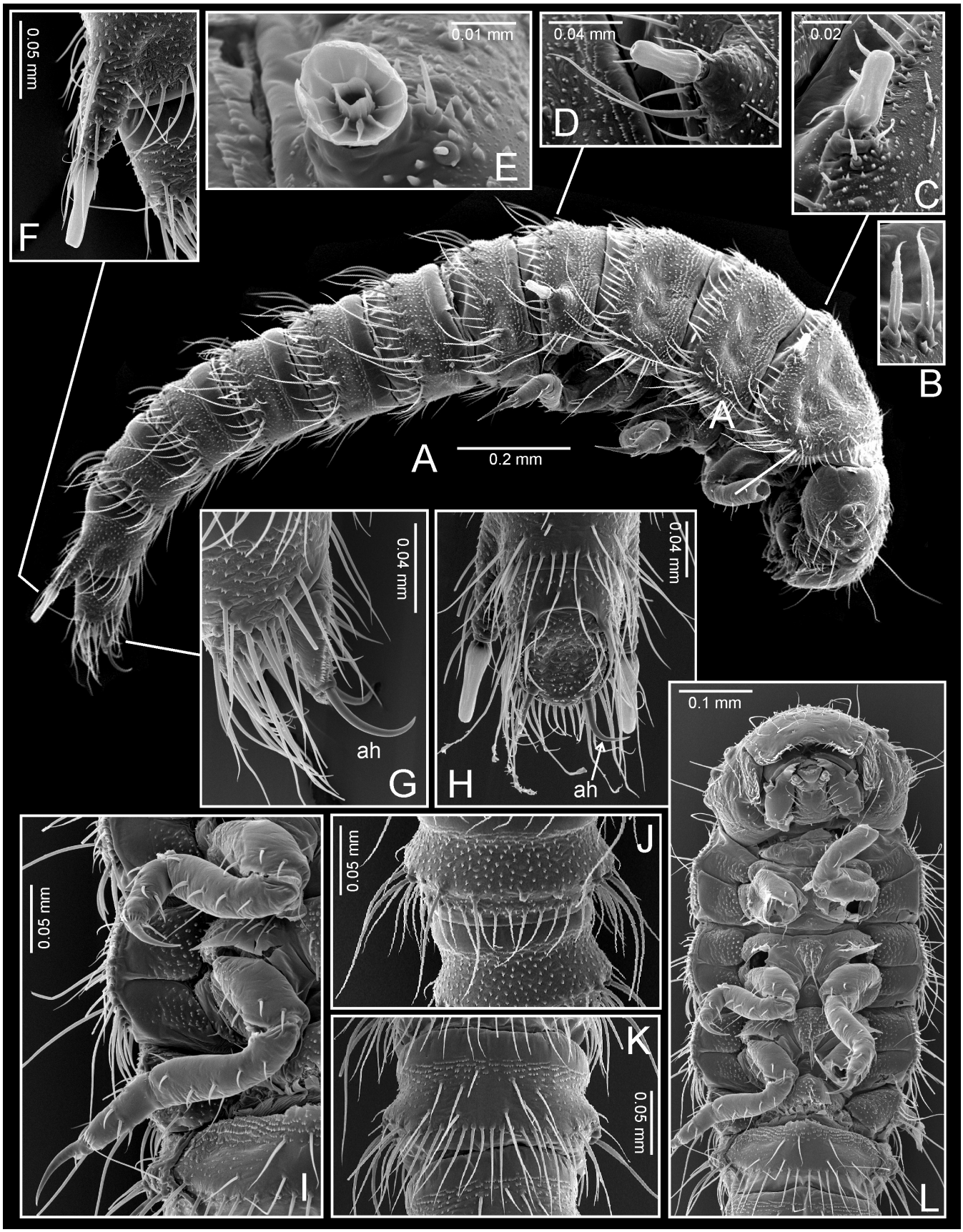

Fig. 6. Morphology of the third instar larva of *Hydroscapha takahashii*, SEM micrographs. A, whole larva in lateral view; B, detail of lanceolate setae on posterior margin of protergum; C, thoracic spiracular gill; D, spiracular gill of abdominal segment I; E, broken spiracular gill of abdominal segment VIII showing its internal structure; F, spiracular gill of abdominal segment VIII; G, abdominal apex with abdominal hooks, lateral view; H, abdominal apex, ventral view; I, meso- and metathoracic leg; J, detail of abdominal segments, dorsal view; K, detail of abdominal segments, ventral view; L, head, thorax, and abdomen in ventral view. Abbreviations: ah, abdominal hooks. For high resolution micrographs see https://zenodo.org/deposit/3537900.

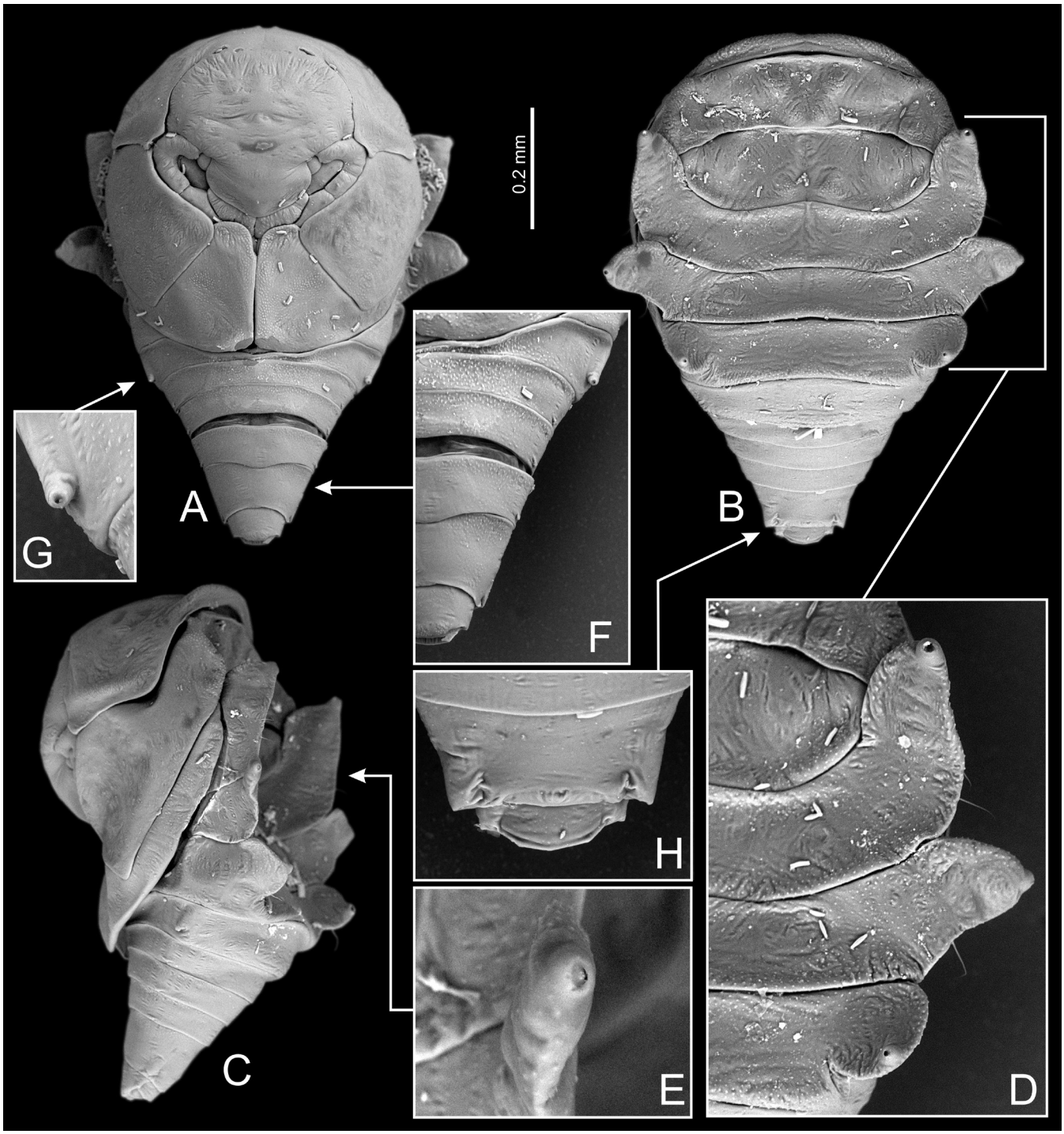

Fig. 7. SEM micrographs of the pupa of *Hydroscapha takahashii*. A–C, habitus (A, ventral view; B, dorsal view; C, lateral view). D, E, details of lateral lobes of abdominal segments I–III with spiracles; F, detail of lateral portions of abdomen, ventral view; G, detail of spiracle on abdominal segment IV; H, abdominal apex, dorsal view. For high resolution micrographs see https://zenodo.org/deposit/3537900.

in the original description (Miwa, 1935). As no specimens were available for study, this character was adopted by Löbl (1994) and Fikáček & Šípková (2009). However, the pronotum of *H. takahashii* is in fact smooth, and does not bear any furrow or impression (Fig. 2D), a feature shared by all other known *Hydroscapha* species. The first couplet in the keys by Löbl (1994) and Fikáček & Šípková (2009) is hence incorrect and has to be discarded.

Distribution. Endemic in Taiwan, but apparently widespread on the island. Presently, this species is known from five lowland localities in northern (New Taipei City), central (Nantou County, Taichung City), and southern Taiwan (Kaohsiung City). The newly collected specimens studied in detail and sequenced are from Wulai which is situated ca. 12 km south of the type locality. In this regard, this species is similar to other aquatic beetles in Taiwan associated with streams and rivers, which, even if they are widespread lowland species, are often endemic (e.g., Jäch, 1998; Jäch & Díaz, 1998; Fikáček & Liu, 2019).

Bionomics (Fig. 8A–C). In Wulai and Heshe, beetles were found on a wet concrete vertical wall with a small amount of very slow-flowing water, partly or entirely covered by algae. In Wulai (ca. 150 m a.s.l.), a small amount of algae was present and a low density of *Hydroscapha* adults; we did not find immature stages. *Oocyclus* and *Agraphydrus* hydrophilid beetles were collected from the same habitat. In Heshe (ca. 800 m a.s.l.), the habitat was completely covered with algal mats mixed with sandy mud. Numerous adults, all larval instars and pupae of *H. takahashii* were collected, together with adults and larvae of *Laccobius* cf. *hammondi* Gentili (Hydrophilidae, Coleoptera), adults and larvae of *Saldoida* sp. (Saldidae, Hemiptera), and larvae of Chironomidae, Dixiidae, and Psychodidae (Diptera). After the discovery of the locality on 16 May 2018, the authors (Hu & Liu) visited it again on 14 October 2018, but the habitat was found dry and no more beetles were found. The specimen from Neiman Township was collected with a net in a small stream; it is likely a specimen washed out from the side of the stream. In Wufeng, mass occurrence of adults and few larvae were found in algal mats at the muddy banks of a small stony river (Fig. 8F).

Hydroscapha shuihau, new species

Material examined. Holotype: male (NMPC): Hong Kong, Lantau, Shui Hau, coordinates, 22.220250°N, 113.916434°E, 14 April 2019, coll. P. Aston, washed out of small layer of slime in mud. Paratypes: 16 exs. (NMPC, SYSU, NMNS): same label data as the holotype; 14 exs. (NMPC, SYSU, PCPA, AFCD): same locality, 16 November 2013, coll. P. Aston; 18 exs. (PCPA): same locality, 5 November 2017, coll. P. Aston; 1 ex. (PCPA): same locality, 10 December 2013, coll. P. Aston.

Diagnosis of adult. *Hydroscapha shuihau*, new species, is very similar to *H. hunanensis* known from Central China (Hunan). However, it is easily distinguished by the shape of the female tergite VI and sternite VI, which are both only weakly narrowing posteriad (they are both strongly narrowed in the posterior third and projecting as a narrowly rounded posterior portion in *H. hunanensis*). Slight differences may be also found in the shape of the aedeagus (wider basally and evenly arcuate in apical half in *H. shuihau*, narrower basally and nearly straight in apical half except the apex in *H. hunanensis*) and in proportions of the terminal antennomere (relatively wider in *H. shuihau* than in *H. hunanensis*) and the mesoventral elevation (relatively shorter in *H. shuihau* than in *H. hunanensis*). For the differences between *H. shuihau* and *H. takahashii*, see under the latter species.

Using the keys by Fikáček & Šípková (2009), males of *H. shuihau* key to *H. hunanensis*, and females to *H. coomani*, *H. hunanensis*, and *H. reichardti* (which were keyed out together due to absence of distinguishing characters). It differs from *H. coomani* Löbl, 1994, in the shape of the male sternite V, which is weakly sinuate on the posterior margin (with a pair of pointed lobes in *H. coomani*, compare Fig. 4E to Löbl, 1994: fig. 17). It differs from *H. reichardti* in male sternite V lacking two distinctly separate tufts of setae (vs. two tufts in *H. reichardti*, compare Fig. 4E with Löbl, 1994: fig. 54). Both *H. coomani* and *H. reichardti* are also slightly larger than *H. shuihau* (with the length of forebody ranging 0.85–0.94 mm, compared to 0.70–0.75 mm in *H. shuihau*). Major diagnostic characters are listed in Tables 2 and 3 to be compared with those of other Asian species listed by Fikáček & Šípková (2009).

Description of adult (Figs. 3F–J, 4D–F). Total body length: 1.0–1.1 mm. Length of forebody (from anterior margin of head to posterior margin of elytra): 0.70–0.75 mm. Dorsal colouration reddish brown to dark brown. Labrum angularly excised anteriorly, with two groups of setae dorsally. Antenna (Fig. 4D) with short antennomere III (= second visible) and widely elongate asymmetrical antennomere IX (= ultimate one); the latter with few apical sensilla. Mesoventral elevation subpentagonal, 2.1× wider than long (Fig. 4F).

Male. Protarsus with sucking disc on basal tarsomere. Posteroventral margin of abdominal segment V weakly sinuate, ventral surface with longer setae indistinctly subdivided into two groups (Fig. 4E). Tergite VI widely rounded on posterior margin. Sternite VI without tufts of hairs. Sternite VII (Fig. 3G) with small medioposterior projection. Tergite VII (Fig. 3H) weakly convex posteromesally. Aedeagus (Fig. 3F) wide basally, arcuate in posterior two thirds, gradually narrowing towards apex.

Female. Protarsus without suckers. Abdominal sternite VI (Fig. 3I) widely subtriangular, tergite VI (Fig. 3J) widely rounded posteriorly.

Etymology. The new species is named after the village of Shui Hau on Lantau Island where the species was found. Noun in apposition.

Distribution. The species is only known from Lantau Island in Hong Kong.

Bionomics (Fig. 8D, E). At the type locality, the beetles have been found in filamentous algae in a hygropetric environment on the concrete footpath leading from Shui Hau village to the sea. The footpath is edged by a freshwater marsh on both sides, which is mainly grassy and grazed by water buffalo. The beetles only occur in the hygropetric areas where the footpath has sunken and is covered by a very thin, almost stagnant film of water over a thin layer of mud and the filamentous algae. The beetles are usually present from November to April (mostly in the dry season) when the slope of the marsh allows the hygropetric environment to flourish. The algae die off before the hot summer months and again start to form mats in September; despite this, the beetles were not present until 9 November 2019, even though the filamentous mats of algae were fairly large (80 cm^2). We did not find any beetles in similar-looking habitats in areas situated close to the agricultural land or closer to the sea. The specimens were collected from the green algae together with *Sphaerius* sp. (Sphaeriusidae), *Hydraena* sp. (Hydraenidae), and various Hydrophilidae including *Enochrus* (*Methydrus*) *esuriens* Walker, 1858, and *Paracymus* sp. Unfortunately,

Fig. 8. Habitats of *Hydroscapha* in Taiwan and Hong Kong. A–C, mass occurrence of *H. takahashii* in Taiwan, Heshe: A, detail of living beetles in algal mat at wet concrete wall; B, wet concrete wall with algae at sides of Zhenyoulanxi river; C, view of algal mat showing numerous adults and larvae. D, E, type locality of *H. shuihau*, new species, in Hong Kong: D, general view of marsh below Shui Hui village, with small seeps at concrete trail; E, microhabitat at sides of concrete trail from where beetles were collected; F, algal mats at side of a small river in Taiwan: Wufeng, with mass occurrence of *H. takahashii*.

Table 4. Review of published data on immature stages of Hydroscaphidae. Stages: L = larva, P = pupa.

Species	Stages	References
Hydroscapha natans LeConte, 1874	L (morphology), P (general habitus drawing)	Böving (1914)
	L (morphology)	Böving & Craighead (1931)
	L (spiracular morphology)	Hinton (1967)
	L, P (SEMs)	Reichardt & Hinton (1976)
	L (head morphology, SEMs)	Beutel & Haas (1998)
	L (morphology, SEMs)	Beutel et al. (1999)
Hydroscapha granulum (Motschulsky, 1855)	L (morphology, habitat data)	Richoux & Doledec (1987)
	L (habitat data, photos of living larvae)	Falamarzi et al. (2010)
Hydroscapha takahashii Miwa, 1935	L, P (morphology, SEMs, habitat)	This paper
Scaphydra angra (Reichardt, 1971)	L, P (morphology)	Reichartd (1974), Reichardt & Hinton (1976)
Yara marmontsedu Raundez Reyes et al., 2019	L, pharate adult (morphology, habitat)	Raundez Reyes et al. (2019)
Yara sp.	L (habitus photo, as '*Hydroscapha*')	Gutiérrez-Fonseca (2010)

during the autumn of 2019, material was taken out of the marsh, causing the marsh level to drop by 30 cm, resulting in the drying of the hygropetric areas, and by the end of January 2020 all the areas where the beetles were previously found, were totally dry. No specimens of *Hydroscapha* were found in the winter of 2019–2020.

DISCUSSION

Immature stages of Hydroscaphidae. Of the four genera presently recognised (Short et al., 2015), larvae and pupae are known for: *Hydroscapha*, *Scaphydra*, and *Yara* (Table 4). Based on the available information, the immatures of these three genera differ in the modification of the spiracular system both in larvae and pupae. The larva of *Hydroscapha* is characterised by three pairs of balloon-shaped spiracular gills: mesothoracic ones (moved to the posterior part of the prothorax), and those of abdominal segments I and VIII (Fig. 6C–F). The same configuration is found in larvae of *Sphaerius* (Sphaeriusidae), but the position of the gills is different (Britton, 1966; Hinton, 1967; Beutel et al., 1999). In contrast, the larva of *Scaphydra* bears bundles of filamentous gills in the position of the balloon-shaped gills of *Hydroscapha* (Reichardt, 1974). *Yara* has similar bundles of filament-like tracheal gills as *Scaphydra*, but only present on abdominal segment VIII; tracheal gills seem to be absent from the thorax and abdominal segment I (Raundez Reyes et al., 2019). *Yara* apparently also differs from *Hydroscapha* in the shape of the thoracic tergites, which project more distinctly laterally, the presence of lateral projections on abdominal segments III–VII, and in the more basal position of the sensorial appendage of the labial palp. No data on these structures are available, as compared to *Scaphydra* for which only very basic illustrations based on early instar larva are available (Reichardt, 1974; Reichardt & Hinton, 1976). The structural differences between pupae of the three genera also concern the tracheal system. The pupa of

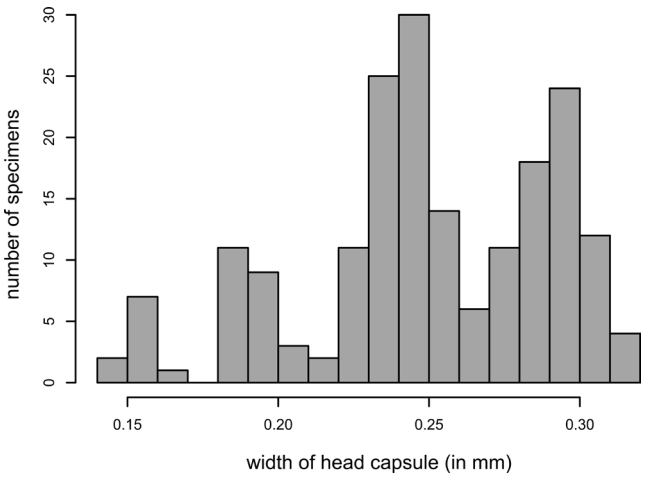

Fig. 9. Histogram of the head width measurements of 190 larvae of *H. takahashii* from Heshe, indicating the presence of four larval instars in the examined material.

Hydroscapha has four pairs of open spiracles, three of them (on abdominal segments I–III) situated on large projecting lobes (Fig. 7). In contrast, the pupa of *Scaphydra* bears three pairs of long spiracular gills on abdominal segments I–III (Reichardt, 1974). The 'pupa' illustrated by Raundez Reyes et al. (2019) is actually a pharate adult in the pupal exuvia. Although the pupal characters are not easy to observe, it appears that the pupa also has three pairs of spiracular gills.

Interesting discrepancies among the existing illustrations and descriptions of hydroscaphid larvae are found in (1) separation of labrum, (2) number of larval stemmata, and (3) number of leg segments. Based on our examination, the labrum is fused with the head capsule in later larval instars of *Hydroscapha* (Fig. 5A), as already shown for *H. natans* by Beutel & Haas (1998). The labrum is, however, illustrated as separated in *H. natans* by Böving & Craighead (1931) and in *S. angra* by Reichardt (1974). The illustrations of larval *Yara* by Raundez Reyes et al. (2019), although not properly

focusing on the head capsule, do not indicate a separate labrum. Our SEM micrographs (Fig. 5A), as well as those of Beutel & Haas (1998), show four stemmata present in *H. takahashii* and *H. natans*, respectively. Five dark spots are however present at the side of the head in *H. takahashii* examined by us, corresponding to illustrations of *H. natans* by Böving (1914) and Böving & Craighead (1931), the description of *H. granulum* by Richoux & Dodelec (1987), and illustrations of *S. angra* by Reichardt (1974). Raundez Reyes et al. (2019) illustrates five or six stemmata for *Y. marmontsedu*. It seems that one of the pigmented spots lacks a convex cuticular lens present in the other four stemmata, and is therefore not visible on SEM images. The reason for the presence of two different kinds of stemmata is not known. Legs are supposed to consist of five segments in all groups of Myxophaga (e.g., Beutel et al., 1999; Yavorskaya et al., 2018) which is true for larval Torridincolidae (e.g., Hájek & Fikáček, 2008). In *H. takahashii* examined here, only four articles were recognised (see Fig. 6I), which also corresponds to the finding of Raundez Reyes et al. (2019) in *Yara*. Based on these observations, it is possible that the trochanter is fused to the femur in *Yara* and *Hydroscapha*. This, however, does not agree with statements of Beutel et al. (1999), Lawrence et al. (2011), and Yavorskaya et al. (2018) on *Hydroscapha*, the drawings of *H. natans* by Böving (1914), and the description of larval *Scaphydra* by Reichardt (1974). Additional research is necessary in all these matters.

Immature stages of *Hydroscapha*. Immature stages are known for three *Hydroscapha* species (Table 4): the North American *H. natans* LeConte, 1874 (both larva and pupa), the European *H. granulum* (Motschulsky, 1844) (only larva), and the Taiwanese *H. takahashii* reported in this paper. Unfortunately, none of the previously published studies provides a detailed and complete account of the larval and pupal morphology, which impedes the comparison to *H. takahashii*. The general body shape of the larva of *H. takahashii* is narrower than that illustrated for *H. natans* by Böving & Craighead (1931) and Beutel et al. (1999), and for *H. granulum* by Richoux & Dodelec (1987). However, the living larvae of *H. granulum* photographed by Falamarzi et al. (2010) do not show such a wide thorax, indicating that the wide thorax may be partly an artefact of slide-mounted larvae (not the case of illustrations in Beutel et al. [1999] which were not examined on slides; Beutel, personal communication). The only differences found between *H. takahashii* and the larval head of *H. natans* illustrated by Beutel & Haas (1998) are the shape of the anterior margin of the labrum (more excised in *H. takahashii* than in *H. natans*) and possibly the superficial microsculpture of the sensorial appendage of palpomere 2 (ridged in *H. takahashii*, smooth in *H. natans*). Setae on the posterior margins of dorsal thoracic sclerites seem sparser and less lanceolate in *H. takahashii* than in *H. natans* (illustrated by Beutel et al., 1999). The most apparent difference, noticed already by Richoux & Dodelec (1987), is the shape of the balloon-like spiracles. These are rather short in the larva of *H. granulum* and longer in *H. natans* and *H. takahashii* (the first abdominal spiracle is ca. 1.5× longer than wide in *H. granulum*, 2.5× longer than wide in *H. takahashii*, and 4.1× longer than wide in *H. natans*; the eighth spiracle is ca. 1.8× longer than wide in *H. granulum*, but 3.5–4.0× longer than wide in *H. natans* and *H. takahashii*). The pupa of *H. takahashii* can be compared to that of *H. natans* illustrated by Reichardt & Hinton (1976) — the shape and proportions of the lateral spiracle-bearing lobes of abdominal segments I–III significantly differ between both species, indicating that they may be species-specific. Interestingly, the most apparent differences among the known immatures of *Hydroscapha* seem to be in the body parts related to breathing and oxygen intake.

Larval instars. No data are available on the number of larval instars of the Hydroscaphidae, except the note by Böving (1914) mentioning three instars in his material of *H. natans*. We measured the head capsule width of 190 larvae of *H. takahashii* collected from Heshe. The histogram of these values (Fig. 9) shows four peaks, indicating that four larval instars are present in our material. This corresponds to the data for the Torridincolidae, for which four larval instars are also recorded (*Ytu zeus*: Reichardt, 1973; *Delevea namibiensis*: Endrödy-Younga, 1997).

***Hydroscapha* in temporary habitats.** The localities of the *Hydroscapha* species reported here from Taiwan and Hong Kong have a temporal character (Fig. 7). We found the concrete wall in Heshe (central Taiwan) dried up few months after collecting *Hydroscapha* there. We also observed a high seasonality at the type locality of *H. shuihau*, new species, in Hong Kong where suitable microhabitats repeatedly dry up, and the algal mats repeatedly vanish during the year. Both observations indicate that *Hydroscapha* is capable of colonising ephemeral hygropetric habitats, either from permanent ones or from other ephemeral habitats in a different stage of succession (e.g., Wissinger, 1997). Typical adaptations for colonising and efficient exploitation of such ephemeral places include quick colonisation of the habitat, accelerated larval development and generally a short life cycle, continuous reproduction, high reproductive capacity, and small body size (e.g., Batzer & Wissinger, 1996; Lytle, 2008; da Silva Gonçalves et al., 2011). It is likely that this at least partly applies to *Hydroscapha*, although very limited data are available at the moment. Nothing is known about the dispersal abilities of *Hydroscapha*. However, all examined adult specimens are fully winged, and we did not observe any wing polymorphism as reported, for example, for *Satonius* species examined by Hájek et al. (2011). The duration of the larval development remains unknown. Many females collected have had an egg present in their abdomen, which may indicate a continuous reproduction once a suitable habitat is colonised. Interestingly, the egg is relatively large compared to the female body, which may enable faster larval development (since the larva is quite large when it hatches and/or may use the nutrients in the egg at the beginning of its ontogeny) or it may be the secondary consequence of a miniaturised body size (as in Ptiliidae: Polilov, 2008, 2016). Relatively large eggs are typical for all Hydroscaphidae and were reported for *Hydroscapha* (Böving, 1914; Fikáček & Šípková, 2009; Falamarzi et al., 2010), *Confossa* (Short et al., 2015), and *Yara* (Raundez Reyes et al., 2019). Usually one egg is present, but Raundez Reyes et al. (2019) observed

three eggs inside the female abdomen of *Yara*. Additional studies of *Hydroscapha* and related genera are needed to understand their ecology and natural history, and to evaluate to what extent the miniaturised body size of Hydroscaphidae is an adaptation (consequence) or exaptation (prerequisite) to utilise and exploit the ephemeral habitats.

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LITERATURE CITED

Batzer DP & Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Annual Review of Entomology, 41: 75–100.

Beutel RG & Haas A (1998) Larval head morphology of *Hydroscapha natans* (Coleoptera, Myxophaga) with reference to miniaturization and the systematic position of Hydroscaphidae. Zoomorphology, 118: 103–116.

Beutel RG, Maddison DR & Haas A (1999) Phylogenetic analysis of Myxophaga (Coleoptera) using larval characters. Systematic Entomology, 24: 171–192.

Böving A (1914) Notes on the larva of *Hydroscapha* and some other aquatic larvae from Arizona. Proceedings of the Entomological Society of Washington, 16: 169–174 + pls. XVII–XVIII.

Böving AG & Craighead FC (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. Brooklyn Entomological Society, New York, 351 pp. + 125 pls.

Britton EB (1966) On the larva of *Sphaerius* and the systematic position of the Sphaeriidae (Coleoptera). Australian Journal of Zoology, 14: 1193–1198.

da Silva Gonçalves C, Pereira Souza U & Vieira Volcan M (2011) The opportunistic feeding and reproduction strategies on the annual fish *Cynopoecilus melanotaenia* (Cyprinodontiformes: Rivulidae) inhabiting ephemeral habitats on southern Brazil. Neotropical Ichthyology, 9(1): 191–200.

Endrödy-Younga S (1997) Active extraction of water-dissolved oxygen and descriptions of new taxa of Torridincolidae (Coleoptera: Myxophaga). Annals of the Transvaal Museum, 36(24): 313–332.

Falamarzi S, Pütz A, Heidari M & Nasserzadeh H (2010) Confirmed occurrence of *Hydroscapha granulum* in Iran, with notes on its biology (Coleoptera: Myxophaga: Hydroscaphidae). Acta Entomologica Musei Nationalis Pragae, 50(1): 97–106.

Fikáček M & Liu HC (2019) A review of *Thysanarthria* with description of seven bew species and comments on its relationship to *Chaetarthria* (Hydrophilidae: Chaetarthriini). Acta Entomologica Musei Nationalis Pragae, 59(1): 229–252.

Fikáček M & Šípková H (2009) New Asian *Hydroscapha*, with comments on male-female association of co-occurring species (Coleoptera, Myxophaga, Hydroscaphidae). Zootaxa, 2286: 31–48.

Fikáček M, Beutel RG, Cai C, Lawrence JF, Newon A, Solodovnikov A, Ślipiński A, Thayer MK & Yamamoto S (2020) Reliable placement of beetle fossils via phylogenetic analyses–Triassic *Leehermania* as a case study (Staphylinidae or Myxophaga?). Systematic Entomology, 45(1): 175–187.

Folmer O, Black M, Hoeh W, Lutz R & Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3(5): 294–299.

Gutiérrez-Fonseca PE (2010) Guía ilustrada para el studio ecológico y taxonómico de los insectos acuáticos del Orden Coleoptera en El Salvador. In: Springer M & Sermeño Chicas JM (eds.) Formulación de una guía metodológica estandarizada para determinar la calidad ambiental de las aguas de los ríos de El Salvador, utilizando insectos acuáticos. Editorial Universitaria de la Universidad de El Salvador, San Salvador. Pp. i–v + 1–59.

Hájek J & Fikáček M (2008) A review of the genus *Satonius* (Coleoptera: Myxophaga: Torridincolidae): taxonomic revision, larval morphology, notes on wing polymorphism, and phylogenetic implications. Acta Entomologica Musei Nationalis Pragae, 48(2): 655–676.

Hájek J, Yoshitomi H, Fikáček M, Hayashi M & Jia FL (2011) Two new species of *Satonius* Endrödy-Younga from China and notes on the wing polymorphism of *S. kurosawai* Satô (Coleoptera: Myxophaga: Torridincolidae). Zootaxa, 3016: 51–62.

Hinton HE (1967) On the spiracles of the larvae of the suborder Myxophaga (Coleoptera). Australian Journal of Zoology, 67: 955–999.

Jäch MA (1995) Hydroscaphidae (Coleoptera). In: Jäch MA & Ji L (eds.) Water Beetles of China. Zoologisch-Botanische Gesellschaft & Wiener Coleopterologenverein, Vienna. Pp. 33–34.

Jäch MA (1998) Hydraenidae. II. The Taiwanese and Japanese species of *Ochthebius* Leach (Coleoptera). In: Jäch MA & Ji L (eds.) Water Beetles of China Volume II. Zoologisch-Botanische Gesellschaft & Wiener Coleopterologenverein, Vienna. Pp. 173–193.

Jäch MA & Díaz JA (1998) Hydraenidae. I. The Taiwanese species of the genus *Hydraena* Kugelann (Coleoptera). In: Jäch MA & Ji L (eds.) Water Beetles of China Volume II. Zoologisch-Botanische Gesellschaft & Wiener Coleopterologenverein, Vienna. Pp. 147–171.

Kumar S, Stecher G, Li M, Knyaz C & Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution, 35: 1547–1549.

Lawrence JF, Ślipiński A, Seago AE, Thayer MK, Newton AF & Marvaldi AE (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici, 61(1): 1–217.

LeConte JL (1874) Descriptions of new Coleoptera chiefly from the Pacific slope of North America. Transactions of the American Entomological Society, 5: 43–72.

Löbl I (1994) Les espèces asiatiques du genre *Hydroscapha* LeConte (Coleoptera, Hydroscaphidae). Archives des Sciences (Genève), 47: 15–34.

Lytle DA (2008) Life-history and behavioural adaptations to flow regime in aquatic insects. In: Lancaster J & Briers RA (eds.) Aquatic insects: challenges to populations. Proceedings of the Royal Entomological Society's 24th Symposium. Cab International, Wallingford. Pp. 122–138.

Maier CA, Ivie MA, Johnson JB & Maddison DR (2010) A new northern-most record for the family Hydroscaphidae (Coleoptera: Myxophaga), with description of a new Nearctic species. The Coleopterists Bulletin, 64(4): 289–302.

Miwa Y (1935) Description of a new species of Hydroscaphidae from Formosa. Transactions, Natural History Society of Formosa, 25: 352–353.

Motschulsky V (1855) Nouveautés. Etudes Entomologiques, 4: 82–84.

Perkins PD & Bergsten J (2019) New Myxophagan water beetles from Madagascar (Coleoptera: Torridincolidae, Hydroscaphidae). Zootaxa, 4657(1): 57–96.

Polilov AA (2008) Anatomy of the smallest Coleoptera, featherwing beetles of the tribe Nanosellini (Coleoptera, Ptiliidae), and limits of insect miniaturization. Entomological Review, 88(1): 26–33.

Polilov AA (2016) At the size limit- effects of miniaturization in insects. Springer, Berlin, 325 pp.

Pons J, Ribera I, Bertranpetit J & Balke M (2010) Nucleotide substitution rates for the full set of mitochondrial protein-coding genes in Coleoptera. Molecular Phylogenetics and Evolution, 56: 796–807.

Pu CL (1948) A new species of Hydroscaphidae from China (Coleoptera). Lingnan Science Journal, 22: 75–77.

Raundez Reyes SM, Cano Espinoza RA & Girón JC (2019) A new species and immature stages of the skiff beetle genus *Yara* Reichardt and Hinton (Coleoptera: Myxophaga: Hydroscaphidae) from Nicaragus. Zootaxa, 4544(1): 125–134.

Reichardt H (1973) A critical study of the suborder Myxophaga, with a taxonomic revision of the Brazilian Torridincolidae and Hydroscaphidae (Coleoptera). Arquivos de Zoologia, 24: 37–162.

Reichardt H (1974) Relationships between Hydroscaphidae and Torridincolidae, based on larvae and pupae, with the description of the immature stages of *Scaphydra angra* (Coleoptera, Myxophaga). Revista Brasileira de Entomologia, 18(4): 117–122.

Reichardt H & Hinton HE (1976) On the New World beetles of the family Hydroscaphidae. Papéis Avulsos de Zoologia, 30(1): 1–24.

Richoux P & Doledec S (1987) *Hydroscapha granulum* (Motschulsky, 1855) description of the larva and ecological notes. Aquatic Insects, 9(3): 137–144.

Satô M (1972) Description of a new species of Hydroscaphidae from Cebu Islands, the Philippines. Bulletin of the Japan Entomological Academy, 6: 25–27.

Short AEZ, Joly LJ, García M, Wild AL, Bloom DD & Maddison DR (2015) Molecular phylogeny of the Hydroscaphidae (Coleoptera: Myxophaga) with description of a remarkable new lineage from the Guiana Shield. Systematic Entomology, 40(1): 214–229.

Trujillo GA & Cañote J (2019) First confirmed species record of Hydroscaphidae from Peru: description of a new species of *Yara* Reichardt and Hinton, and key to species (Coleoptera: Hydroscaphidae). Zootaxa, 4638(3): 344–350.

Walker F (1858) Characters of some apparently undescribed Ceylon Insects. Annals and Magazine of Natural History, Series 3, 2: 202–209.

Wisinger SA (1997) Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biological Control, 10: 4–15.

Yavorskaya MI, Anton E, Jałoszyński P, Polilov A & Beutel RG (2018) Cephalic anatomy of Sphaeriusidae and a morphology-based phylogeny of the suborder Myxophaga (Coleoptera). Systematic Entomology, 43(4): 777–797.