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

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**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 Palaeartic (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...
Hydroscapha in the region impossible — it was unclear whether the central Chinese species, H. humanensis 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);
NMPC – National Museum, Prague, Czech Republic (J. Hájek, M. Fikáček);
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. humanensis (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...
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).

SYSTEMATICS

Family Hydroscaphidae Le Conte, 1874

Hydroscapha Le Conte, 1874

Hydroscapha takahashii Miwa, 1935


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 V, slightly projecting posterior margin of tergite VI, and smaller body size. They differ from *H. jumaloni* in a slender 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 posteriorly. 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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Female sternite VI</th>
<th>Female tergite VI</th>
<th>Body</th>
<th>Antenna</th>
<th>Mesothorax</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>shape apically</td>
<td>shape apically</td>
<td>length of fore body (mm)</td>
<td>antennomere III length/width</td>
<td>antennomere IX length/width</td>
</tr>
<tr>
<td><em>H. shuihau</em>, new species</td>
<td>simple, widely rounded</td>
<td>widely rounded</td>
<td>0.70–0.75</td>
<td>1.3</td>
<td>2.4</td>
</tr>
<tr>
<td><em>H. takahashii</em></td>
<td>simple, widely triangular</td>
<td>with triangular median projection</td>
<td>0.69–0.76</td>
<td>1.6</td>
<td>2.6</td>
</tr>
<tr>
<td><em>H. hunanensis</em></td>
<td>simple, narrowly rounded</td>
<td>with narrowly rounded median projection</td>
<td>0.66–0.73</td>
<td>1.1</td>
<td>2.8</td>
</tr>
</tbody>
</table>

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.
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. 6L). 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 tibiotsar, 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 & Diaz, 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 Agrapryphus 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. takahashi 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


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 posteriorly (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. takahashi, 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 cm²). 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. (Sphaerisiidae), Hydroena sp. (Hydraenidae), and various Hydrophilidae including Enochrus (Methydrus) esuriens Walker, 1858, and Paracyamus 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*.
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 I–III (Fig. 6A–F). The latter configuration is found in larvae of *Sphaerius*, which move the mesothoracic gills to the posterior part of the prothorax, and those of abdominal segments I and VIII (Britton, 1966; Hinton, 1967; Beutel et al., 1999).

The structural differences between pupae of the three genera also concern the tracheal system. The pupa of *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

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Stages</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hydroscapha natans</em> LeConte, 1874</td>
<td>L (morphology), P (general habitus drawing)</td>
<td>Böving (1914)</td>
</tr>
<tr>
<td></td>
<td>L (morphology)</td>
<td>Böving &amp; Craighead (1931)</td>
</tr>
<tr>
<td></td>
<td>L (spiracular morphology)</td>
<td>Hinton (1967)</td>
</tr>
<tr>
<td></td>
<td>L, P (SEMs)</td>
<td>Reichardt &amp; Hinton (1976)</td>
</tr>
<tr>
<td></td>
<td>L (head morphology, SEMs)</td>
<td>Beutel &amp; Haas (1998)</td>
</tr>
<tr>
<td></td>
<td>L (morphology, SEMs)</td>
<td>Beutel et al. (1999)</td>
</tr>
<tr>
<td><em>Hydroscapha granulum</em> Motschulsky, 1855</td>
<td>L (morphology, habitat data)</td>
<td>Richoux &amp; Doledec (1987)</td>
</tr>
<tr>
<td></td>
<td>L (habitat data, photos of living larvae)</td>
<td>Falamarzi et al. (2010)</td>
</tr>
<tr>
<td><em>Hydroscapha takahashii</em> Miwa, 1935</td>
<td>L, P (morphology, SEMs, habitat)</td>
<td>This paper</td>
</tr>
<tr>
<td><em>Yara marmontsedu</em> Raundez Reyes et al., 2019</td>
<td>L, pharate adult (morphology, habitat)</td>
<td>Raundez Reyes et al. (2019)</td>
</tr>
<tr>
<td><em>Yara sp.</em></td>
<td>L (habitus photo, as ‘Hydroscapha’)</td>
<td>Gutiérrez-Fonseca (2010)</td>
</tr>
</tbody>
</table>

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**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.**
focusing on the head capsule, do not indicate a separate larbum. 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. marmontseu. 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. 61), 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 we 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; Delevya 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. shuihua, 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 hygroptic 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 & Šipkóva, 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.

**ACKNOWLEDGEMENTS**

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**LITERATURE CITED**


