International Journal of Odonatology
2024, Vol. 27, pp. 11–18
doi:10.48156/1388.2024.1917250

The final-instar larva of *Bayadera strigata* Davies & Yang, 1996 from Yunnan, China (Odonata: Zygoptera: Euphaeidae)

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Abstract. The final instar of *Bayadera strigata* Davies & Yang, 1996, from Yunnan Province, China, is described and illustrated for the first time. This study confirms several characters as being typical of, or unique to, the genus *Bayadera* and discusses them in comparison to other genera. The larva of *B. strigata* is distinguished from its congeners by the presence of numerous distinct short spines on the genae, but no long spines. The gonapophyses are unusually long in both sexes. Notes on this species' habitat and behaviour are provided. The material examined will be stored at the Bioscience Museum of Dali University, Dali, Yunnan, China.

Key words. Dragonfly, morphology, naiad, Oriental region

Research Article

Published: 23 January 2024
Received: 11 August 2023
Accepted: 13 December 2023

Citation:
Yang & Orr (2024): The final-instar larva of *Bayadera strigata* Davies & Yang, 1996 from Yunnan, China (Odonata: Zygoptera: Euphaeidae). *International Journal of Odonatology, 27,* 11–18
doi:10.48156/1388.2024.1917250

Data Availability Statement:
All relevant data are within the paper and its Supporting Information file.

Introduction

Bayadera Selys, 1853 is the second largest genus of the family Euphaeidae, with 17 species (Paulson et al., 2023), occurring in from southern subtropical China to Indochina, Thailand, Myanmar and the eastern Himalayas (Kalkman et al., 2020; Zhang, 2019). Twelve species of this genus have so far been recorded from China (Zhang, 2019).

Because larvae and adults are frequently not present simultaneously in/at the same streams (Corbet, 1999), and since larvae typically conceal themselves beneath stones in flowing streams (Keetapithchayakul et al., 2020), it can be challenging to find the latter. Fewer than half of the larvae of the genus *Bayadera* are known and only five have been described to date, often in insufficient detail and sometimes with obviously inaccurate illustrations. These include: *B. brevicauda* Fraser, 1928 by Matsuki & Lien (1978), *B. indica* (Selys, 1853) by Needham (1911) and Kumar (1973), *B. bidentata* Needham, 1930 by Wan et al. (2011), *B. ishigakiana* Asahina, 1964 by Ishida (1996), and *B.serrata* Davies & Yang, 1996 by Keetapithchayakul et al. (2020). The last mentioned treatise contains the only comprehensive presentation of characters with detailed and accurate illustrations. Despite these publications, at present there is still paucity of reliable information on how to distinguish the larvae of *Bayadera* from those of other euphaeid genera, although some species are distinctive. Here, we describe the final instar of *B. strigata* from Yunnan Province, China. It is compared with known congeneric larvae and with larvae of other euphaeid genera, significantly reinforcing our knowledge of the genus.

Materials and methods

The larvae were collected from the Maer Mountains, HeQing County and Cangshan Mountains, Bai Autonomous Prefecture of Dali, Yunnan Province, China, in 2020 and 2023, and taken back to the laboratory. There they were placed in a plastic container, outfitted with an inlet pipe at the top and an outlet at the bottom to create a well-oxygenated running-water environment, and they were raised to adulthood on a diet of chironomid larvae. Emergence of two male damselflies occurred after 6–37 days in setup. Species identification was confirmed based on the examination of the caudal appendages of one of these males (Fig. 1). Pictures of *B. strigata* in life were taken in the field and in the laboratory with a digital camera (Nikon D7200) coupled with an 18–200 mm F/3.5-5.6ED zoom lens. Dissected specimens were photographed and measured in the laboratory using the Kuyence VHX-5000 (Japan) digital microphotography system; images of structural details are based on alcohol-preserved final-instar larval specimens. Mandibular terminology and formulae follow Watson (1956), S = abdominal segment(s), SS = simple setae, CVS = claviform setae, and SPS = spiniform setae. The term CVS is used in lieu of 'RLS' as introduced by Keetapithchayakul et al. (2020), and follows Needham & Gyger (1939), who first identified and accurately characterized these structures in the Euphaeidae. Some of these specialized setae have undergone a transition to a more rod-like structure and this is noted in the text where relevant.

The material examined will be stored at the Bioscience Museum of Dali University, Dali, Yunnan, China.

Descriptions of the larva

Bayadera strigata *Davies & Yang, 1996*
(Figs 1, 2, 3, 4, 5, 6, 7)

Material examined

1 ♀ larva, 6.iv.2020, ZiYang stream (25.74° N, 99.99° E, 2320 m a.s.l.), YangBi County, Bai Autonomous Prefecture of Dali, Yunnan Province, China, Guo-Hui Yang leg. The ZiYang is one of steams on Mt Cangshan in Dali, Yunnan. 2 ♀♀, 2 ♂♂ larvae, 27.iv.2023, same locality, Guo-Hui Yang leg. 1 ♂ F-0 adult emergence 2.vi.2023; 2 ♂♂ larvae, 27.ix.2023, Mt Maer (26.25° N, 100.13° E, 2750 m a.s.l.), HeQing County, Bai Autonomous Prefecture of Dali, Yunnan Province, China, Dong-Dong Zi leg. 1 ♂ F-0 successful emergence 4.xi.2023.

Description

Habitus. A medium-sized larva, somewhat flattened, robust build, with long heavy legs; colour brownish black, lacking a distinct pattern, with dark saccoid gills with blunt and pale tips (Fig. 2).

Head. Broad and pentagonal in shape, flat dorsally, covered with numerous fine setae on the dorsum except on the vertex (Figs 2, 3a). Labrum with long SS and scattered CVS on basal, and dense CVS and short SS at ⅘ of the base of the labrum (Figs 3a–b). Compound eyes broad and rounded, protruding anterolaterally. Occiput margin concave, with scattered SPS; postocular lobes strongly developed and rounded, but dense SPS at the posterior corners create a seemingly squared profile; anterior margin with CVS along the margins of the compound eyes, posterior margin intermingled with small spines, long SS and CVS. Genae large, with rows of SPS and CVS along the ventral margins of the compound eyes; anterior margin of right gena with rows of blunt and distinct spines (7–8) and a row of CVS infused with SPS and SS (Figs 3b–c); anterior margin of the left gena with a row of 9–10 dominant spines and row of CVS infused with SPS and SS (Figs 3d–e). Antennae unusually long (1.3 × length of head measured from occipital margin to labrum), filiform, 7-segmented; third antennomere longest, length of antennomeres (mm): 0.67:0.86:1.23:0.83:0.46:0.23:0.09, giving a total length of 4.37 (Fig. 4a). Prementum 1.4 × longer than wide, subpenta-

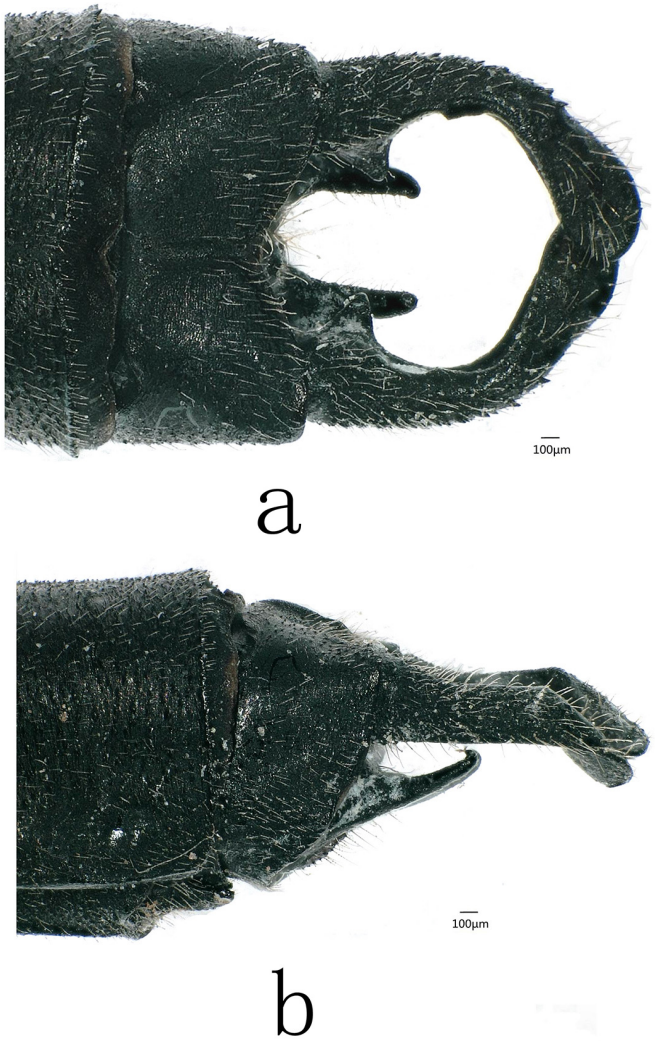

Figure 1. Caudal appendage of *Bayadera strigata*, (a) dorsal view; (b) lateral view.

Figure 2. Larval habitus of *Bayadera strigata*, dorsal view.

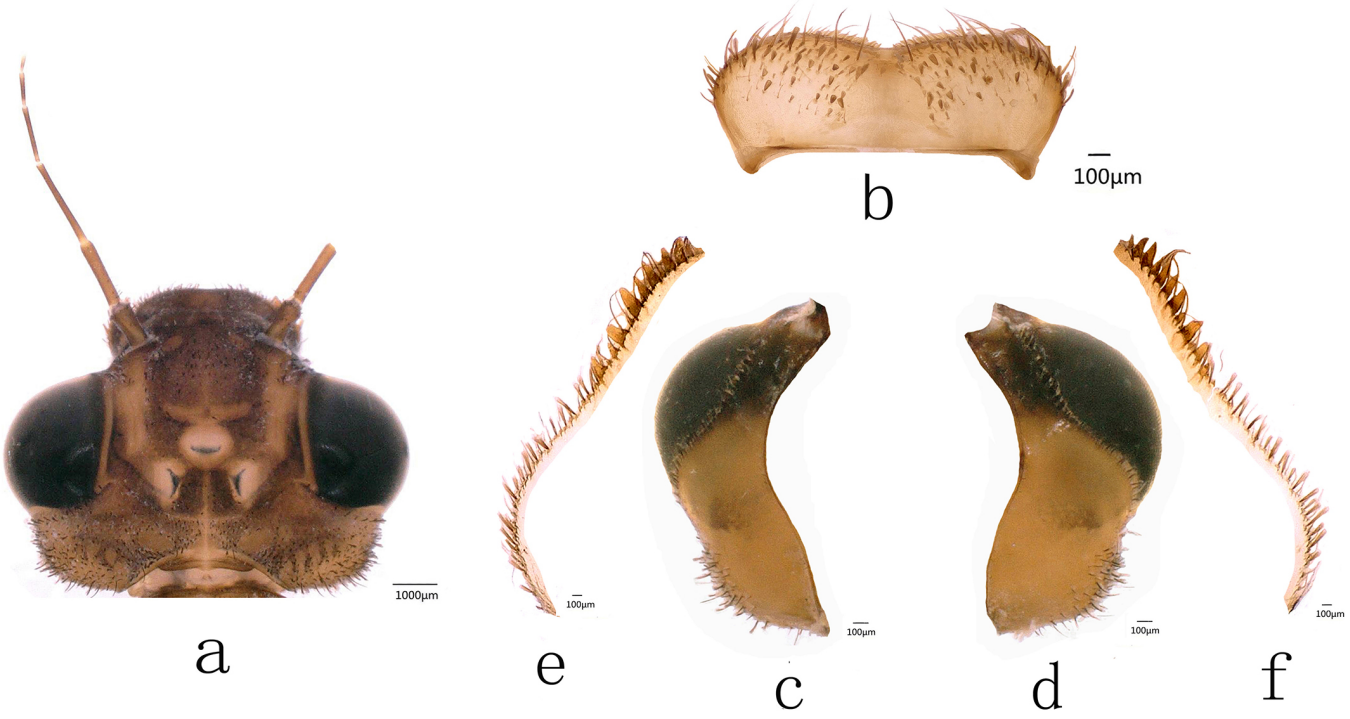

Figure 3. Head of a larva of *Bayadera strigata* and morphological details of the labrum and genae: (a) head, dorsal view; (b) labrum, dorsal view; (c) right genae; (d) left genae; (e) detail of arrangement of the spines and setae along the margin of the right genae; (f) detail of arrangement of the spines and setae along the margin of the left genae.

gonal in shape, with a row of 14–16 (left side) and 13–17 (right side) strong broad spines and numerous small spines (each spine bearing SS) along the lateral margin of each side (Figs 4b–c); ligula convex, its anterior margin finely serrated, with a tiny median cleft (Fig. 4d); labial palp long, 0.54 × as long as the prementum, outer margin with scattered SS and CVS, while SS, CVS and SPS are dense in the basal half, weakly serrated on the inner margin, distal end with three processes, the outer process moderately incurved with a wavy outer margin, the middle process largest, weakly unciate, the inner process short and securiform, movable hook about 0.44 × as long as the labial palp, acuminate, bent slightly inwards (Fig. 4e). Mandibles brown, formula:

L 1+1'2340 a($m^{1.2.3.4.5}$)b / R 1+1'234 y a(m^{0})b, asymmetrical, four incisors, well developed, 4>3>2>1+1'; molar crest with seven teeth (a>1=2=3=4=5>b) on left mandible; a>b, b very small on the right mandible (Figs 4f–i); Maxilla with seven hooks, four long and three short, sharply pointed, basally with short setae; maxillary palp bearing dense, long setae (Figs 4j–k).

Thorax. Prothorax trapezoidal, narrower than the head, with scattered CVS intermixed with SS. Procoxa arc-shaped, with a central protrusion, and supracoxal armament on prothorax circularly arc-shaped, with a depression in the middle, lateral margin of pronotal disc rounded (Figs 2, 3a). Synthorax nearly equal to head in width, covered with SS on its dorsal side. Wing sheaths divergent, forewing sheaths reaching the rear border of S5, hindwing sheaths extending to middle of S6. Legs long and robust; metafemur straight, reaching distal end of S7; all femorae and tibiae bearing SS and CVS; a row of claviform to rod-like setae on the distal end of the tibial comb; tarsal formula 3-3-3; claws small and simple (Figs 2, 5a).

Abdomen. Long, gradually narrowing from S1 to distal end, with scattered CVS and SS; seven pairs of pale lateroventral abdominal gills from S2 to S8. Male gonapophyses well developed, base stout, tips blunt, moderately divergent distally in ventral view, reaching more than halfway along S10, with a plate-like spine on the

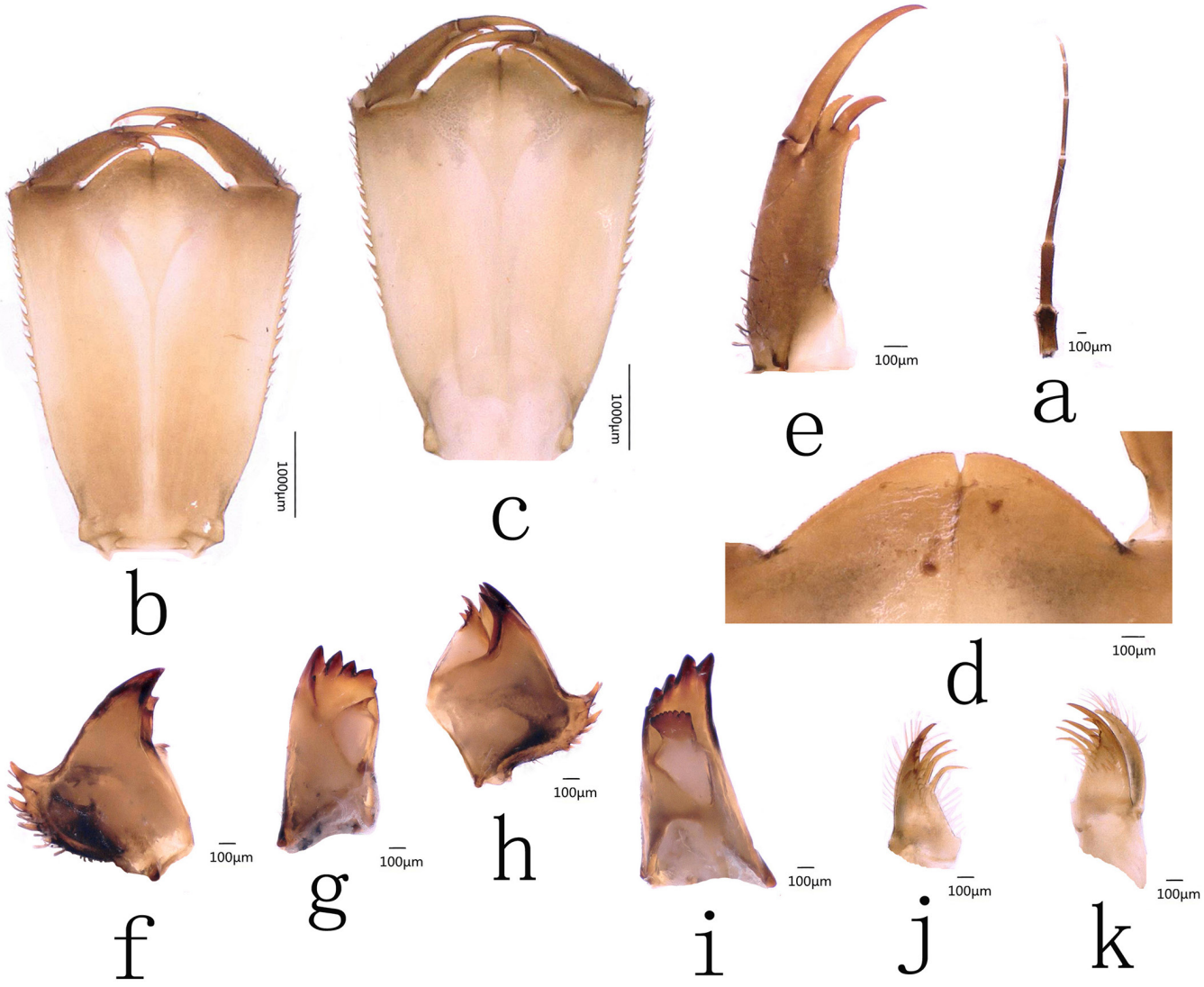

Figure 4. Details of the head and mouthparts of the final instar of *Bayadera strigata*: (a) right antenna; (b) labium, ventral view; (c) labium, dorsal view; (d) ligula, dorsal view; (e) labial palp, ventral view; (f) right mandible, ventral view; (g) right mandible, inner face; (h) left mandible, ventral view; (i) left mandible, inner face; (j) left maxilla; (k) right maxilla.

ventral side (Figs 5b–c); female gonapophyses rising from the distal end of S8 and basal S9 and extending almost to the distal margin of S10 (Figs 5d–e); lateral valvulae each with a nipple-shaped process at the tip and a plate-like spine on the ventral side; cerci in both sexes long, narrow, slightly curved with pointed tips, bearing claviform to rod-like setae; male paraprocts triangular. Caudal gills brownish black, swollen, saccoid-shaped, with a yellowish white terminal filament, covered with SS; median gill about as long as the lateral gills (Figs 5f–h).

Measurements (mm). Larvae (in alcohol, N = 7), body length (excluding antennae and caudal gills) 14.8–16.2; length of abdomen (including caudal gills) 14–15.4; maximum width of head 5; length of hind femur 5–6.5; lateral caudal gills 7–8.

Discussion

This study of *B. strigata* has increased the number of the known larvae of *Bayadera* to six species, and the

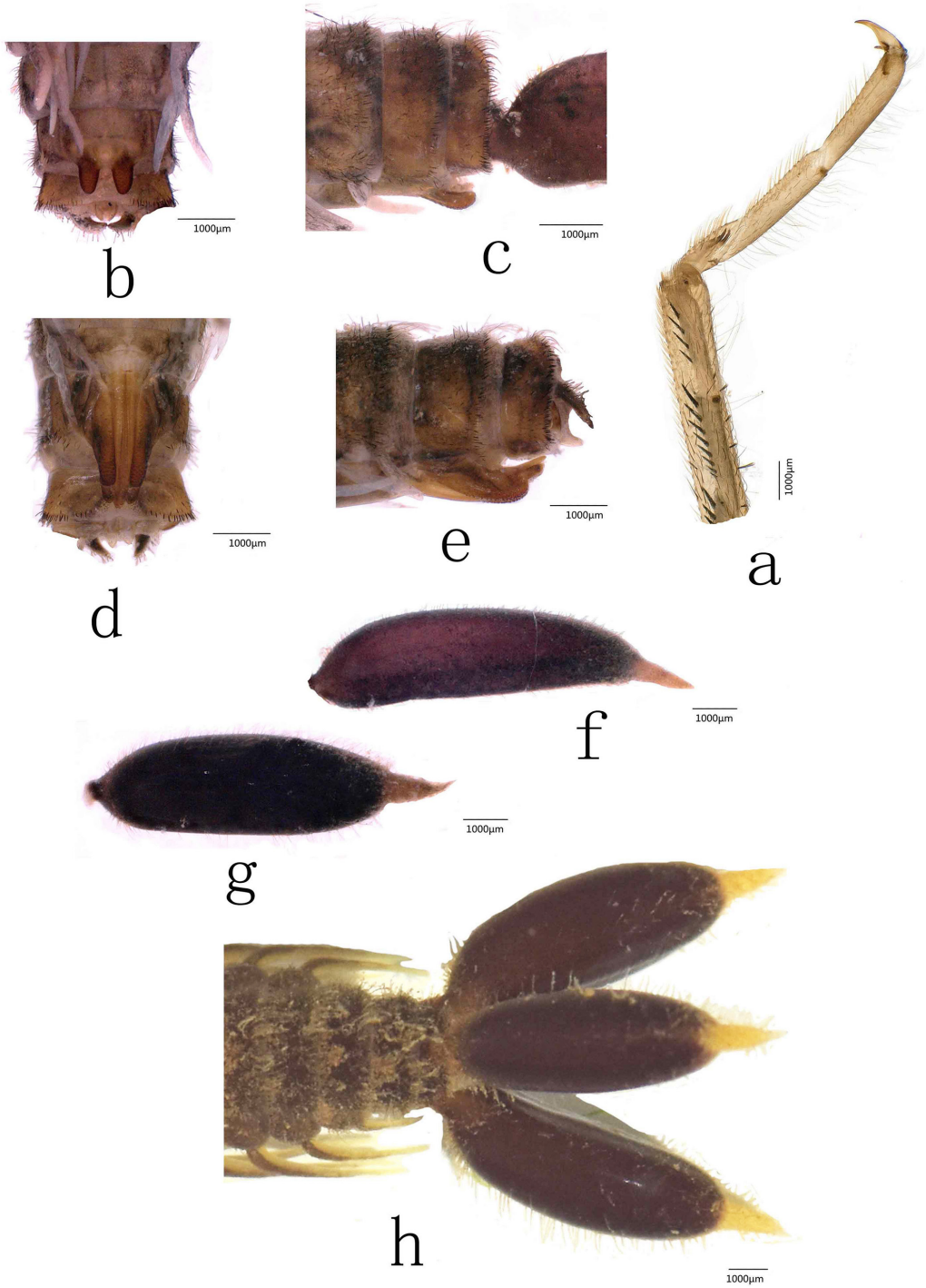

Figure 5. Morphological details of the tibia and S8–10 of *B. strigata*: (a) tibial comb and tarsi, dorsal view; (b) male gonapophyses, ventral view; (c) male gonapophyses, lateral view; (d) female gonapophyses, ventral view; (e) female gonapophyses, lateral view; (f) lateral caudal gill, lateral view; (j) median caudal gill, lateral view; (h) caudal gills, dorsal view.

other five species were discussed in detail by Keetapithchayakul et al. (2020). It confirms (along with Keetapithchayakul et al., 2020) several features that distinguish *Bayadera* from *Anisopleura* and *Euphaea*, the genera with which it is most likely to be confused (but note that the larvae of the sympatric *Cryptophaea* and *Schmidtiphaea* are as yet unknown). Firstly, in all photographed *Bayadera* (*strigata*, *serrata* and *indica* from Bhutan supplied to the second author by Vincent Kalkman), the caudal gills end in a short blunt cone, separated from the main body of the gills by a distinct constriction. This condition is also implied by all reliable drawings of other species, although some are highly stylised. In neither *Anisopleura* nor *Euphaea* does this condition normally occur, although in *E. superba* Kimmins 1936, the terminal filament approaches this form (Wu et al., 2019), but this species exhibits other marked differences from *Bayadera*, including the very well developed long spines on the gena. The terminal filament is attenuated and, especially in *Anisopleura*, tapers gradually from the body of the gill. It is furthermore distinguished from *Anisopleura* (but not *Euphaea)* by the length of the antennae (relatively shorter in *Anisopleura*), and the freely separated securiform inner process on the labial palp (reduced and adpressed to the central process in *Anisopleura*). It lacks small tubercles on the anterior face of the head and labrum (possibly universal in *Anisopleura*). Finally, all known euphaeid genera except *Bayadera* possess 2–7 long anterior subocular spines on the theie genae (Keetapithchayakul et al., 2020; Orr & Hämäläinen, in press). In *Bayadera*, such spines occur only in *B. serrata* (Keetapithchayakul et al., 2020). *Bayadera indica* possesses two short spines, which are a little longer than those found in *B. strigata*, and several smaller cone-like processes; *B. strigata* possesses numerous spines (Figs 3e, f), but they are much shorter than in the other genera. Another feature present only in *Bayadera* (only confirmed for *strigata* and *serrata*, and probably also in *indica*) is the wavy (undulating, sensu Keetapithchayakul et al., 2020) outer edge of the outer process of the labial palp. Finally, the male genital apophysis in *Bayadera* is long and sausage-shaped, versus spinose or cone-like in other genera.

The chief characters of the known species of *Bayadera* were tabulated and largely redrawn, with minor errors and omissions by Keetapithchayakul et al. (2020). It should be noted that, while reasonably faithful to the originals, these drawings have in some cases made the originals look more plausible than they are. For example, the highly stylized representation of the caudal gills provided by Matsuki & Lien (1978) could actually depict a normal set of gills, similar to the now well-known shapes in *B. serrata*, *B. strigata* and *B. indica*. The caudal gills of *B. indica* drawn by Kumar & Arun (1973) are clearly inaccurate, and the illustration provided by Needham (1911) should be supposed to be truer to the facts. The most unusual structure is the labial palp of *B. bidentata* as shown by Wan et al. (2011). This paper contains very small, coarsely produced drawings, but in general its proportions appear correct. The drawing of the prementum is surely reliable. It is possible that mistakes were made when drawing the smaller details of the labial palp, but given the overall accuracy of the other images we feel we must accept this as a genuine representation of the relevant structures; hence it is an aberrant form within the genus, unless it is proven otherwise by re-examination of the original or fresh material. The distal processes of the palp are distorted, with only the outer and central processes being well developed, the inner process is reduced to an inward-pointing, small, triangular spine at the base of the central process, and there is another, short, blunt process rising midway from along the inner margin of the palp that is unique to this species. There is no indication of a wavy margin on the outer process of the palp, but this is not surprising at this level of resolution, and a comparable character state is also lacking in other publications before 2020. Similarly, Ishida's (1996) drawings are often stylized and not photographically accurate. The long attenuations on the gills of *B. ishigakiana* may be artistic flourishes, especially as this species is morphologically close to *B. brevicauda*, with which it was once considered conspecific, and which has other similar structures, too.

Comparing *B. strigata* with *B. serrata*, several differences are obvious. The legs and antennae are longer in proportion to the rest of the body. The spines on the genae are much longer in *B. serrata*, but number only 1–3, whereas in *B. strigata*, they are short, but number 7–10. Other small differences are apparent, but these are mostly quite subtle and not suitable for diagnosis. Rather than repeat previous detailed analyses of other species we here present a tentative key to the known larvae of *Bayadera* species.

A key to the larvae of six species of the genus Bayadera

1. 1–3 long spines on genae; prementum long, ratio of length:width > 1.2 ..... *B. serrata*
1'. Spines on the genae either lacking or small and numerous 2
2. Genae with short spines 3
2'. Genae lacking obvious spines 4
3. Prementum short, ratio of length:width < 1.2, only two well-developed short spines on genae ..... *B. indica*
3'. Prementum long, ratio of length:width > 1.2,6–10, well-developed short spines on genae .... *B. strigata*
4. Labial palp with only two clear lobes; inner lobe vestigial and pointing inward ..... *B. bidentata*
4'. Labial palp with normal terminal processes, with three lobes 5
5. Ratio between max. head width and prothorax > 1.4 ..... *B. ishigakiana*
5'. Ratio between max. head width and prothorax < 1.4 ..... *B. brevicauda*

Biological notes

The larvae of *B. strigata* conceal themselves underneath large stones and boulders in clear streams in sections with riffles and rapids (Figs 6a–c, 7). Breeding adults frequently perch on twigs at the stream margins (Fig. 6d). The flight season ranges from May through October. During the breeding season (from June to September in the Dali region), many males of *B. strigata* lead tandemed females to lay their eggs on dead wood in fast-flowing streams (Fig. 6e).

On hatching in turbulent water, the larvae are washed into regions far from their hatching sites to develop. During the raising of captured larvae, a rather peculiar behaviour was noticed: when a larva sits on a flat stone or at the bottom of a container, it will cling with its legs well spread and from this strong base sway its abdomen and caudal gills back and forth horizontally, like the pendulum of a clock (Supplementary Video S1). This exercise was performed 12–15 times a day, and probably assists in absorbing oxygen by the abdominal gills (Norling, 1982) to all parts of the body, in order to compensate for the lower dissolved oxygen levels in the laboratory breeding environment than in their natural habitat with its high flow rates of oxygen-saturated water.

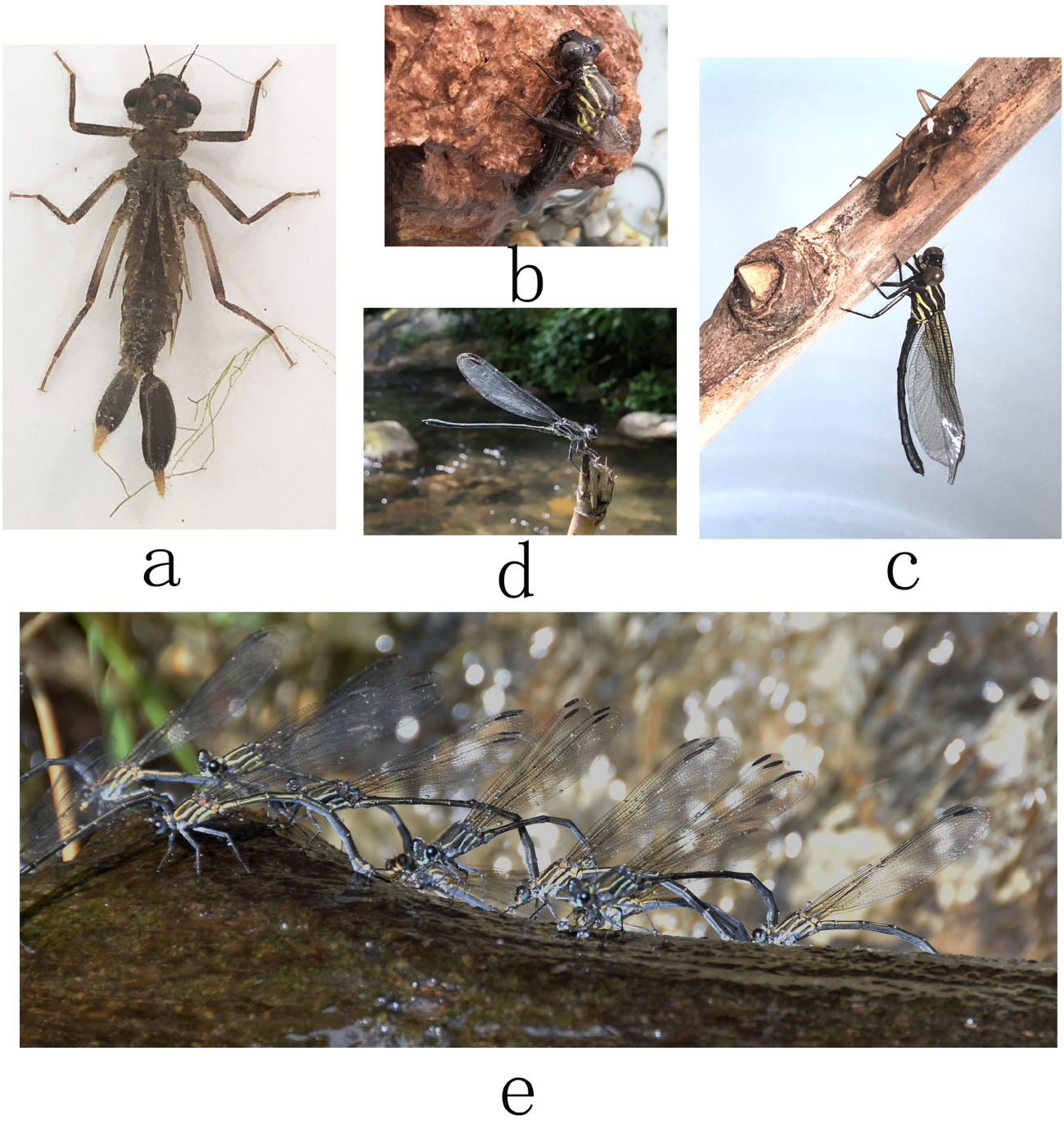

Figure 6. (a) Final instar of *Bayadera strigata* in the laboratory; (b) male imago emerging on 02.vi.2023; (c) emergence of a male on 04.xi.2023; (d) male of *B. strigata* perched on branches next to a stream; (e) numerous males of *B. strigata* taking females in tandem to lay eggs on wood in turbulent rivers.

Figure 7. Larval habitat of *Bayadera strigata*.

Acknowledgements

We are grateful to Dr Tosaphol Saetung Keetapithchayakul for his kind help in providing literature necessary for the present study, and we thank three anonymous referees for their helpful comments and suggestions. Vincent Kalkman kindly supplied AGO with detailed photographs of *Bayadera indica* larvae from Bhutan. This project was supported by a Dali University Research Project (KY2319103840).

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Supplementary Material

Supplementary Video S1. A video of a larva of *B. strigata* swaying left and right in the laboratory.