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Revision of the status of *Anaciaeschna donaldi* and *A. martini*, with allied species, and distributional notes (Odonata: Aeshnidae)

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Abstract. The taxonomic status of four Asian *Anaciaeschna* species, *viz. A. donaldi*, *A. kashmirense*, *A. martini*, and *A. montivagans*, has not yet been fully settled. Each of them is often treated as a good species in the major catalogues of World Odonata. However, the taxonomic relationship especially of *A. donaldi* and *A. martini* remains problematic, *i.e.*, the attribution of Indian and Nepalese populations is still confusing. This even includes museum collections which have used different references for identification. In this paper we review the complex background of the taxonomical history of *A. donaldi*, including *A. martini*, with distributional notes, and present the first record from Bhutan. A morphological comparison was made based on specimens from Nepal and Japan, including photographical analysis of *A. donaldi* type specimens from India. To support our morphological analysis, we also analysed nuclear and mitochondrial DNA from Japanese and Nepalese material. Our results showed there are no significant in morphological or molecular genetic differences between *A. donaldi* and *martini*; therefore we conclude that *A. donaldi* is a junior synonym of *A. martini*. Additionally, we confirmed the status of *A. montivagans*, once wrongly synonymised with *A. martini*, as a valid species.

Further key words. Dragonfly, Anisoptera, Nepal, Bhutan, India, Sri Lanka, Japan, junior synonym, *montivagans*

Introduction

The genus *Anaciaeschna* Selys, 1878, has nine valid species globally (Schorr & Paulson 2019). Of those, *A. trinagulifera* McLachlan, 1896, is distributed

in Africa, and three species are confined to the South Pacific, New Guinea (*A. megalopsis* Martin, 1908), the Solomon Islands (*A. melanostoma* Lieftinck, 1949), and the Maluku Islands (*A. moluccana* Lieftinck, 1930), respectively. *Anaciaeschna jaspidea* (Burmeister, 1839) occurs widely from Australasia to tropical Asia. The other four species are distributed from the Indomalayan region and East Asia. These are *A. donaldi* Fraser, 1922, *A. kashmirense* Singh & Baijal, 1954, *A. martini* (Selys, 1897), and *A. montivagans* Lieftinck, 1932. However, their classification is still confused; the taxonomic relationship of *A. donaldi* and *A. martini* remains problematic, and *A. montivagans* has been treated as a synonym of *A. martini* (Fraser 1943). So far no studies have investigated their morphology in detail. Therefore, a taxonomic revision of these species was badly needed.

Anaciaeschna kashmirense Singh & Baijal, 1954, is an enigmatic species. It was originally described from Srinagar, Dal Lake, Kashmir, India, based on a pair of specimens (holotype and allotype) by Singh & Baijal (1954). Since then, no further specimens have been collected. Hämäläinen (1989) supposed this species is »probably« a synonym of *A. jaspidea*. Sheela et al. (2016) published photos of the type specimens, which are unfortunately in poor condition. Therefore, we will not discuss this species further here.

In this paper, we review the complicated historical background of *A. donaldi*, *A. martini*, and *A. montivagans*. By examining available material, we compared the morphology of the three species. To test our hypothesis based on morphological analysis, we analysed nuclear and mitochondrial DNA extracted from material from Nepal and Japan.

Historical background and taxonomic treatment of *Anaciaeschna donaldi*

The identification record of *A. donaldi* begins with a brief description by Fraser (1922a) based on several females collected in Palni Hills (Kodaikanal in May 1908 and Sept. 1921, Oct. 1921) and neighbouring regions (Yercaud in Sept. 1921; Ootacamund in Sept. 1921) in South India. At the same time, he mentioned that he and his colleagues, after searching nearby jungle areas, could not find any adult males, although they found many exuviae along the lakes' sides. Fraser (1992b) again related their struggle to find males, »but all in vain«.

Fraser (1924) wrote that he finally obtained teneral males at Ooty Lake in Nilgiri (now Tamil Nadu state, India) in March 1922 and kept them in his room. The adults did not reach mature coloration since the wings of both males and females did not develop saffron coloration, and the »lateral thoracic stripes are most certainly apple green«. In addition, he synonymized *A. donaldi* with *A. martini*, following a personal communication by Friedrich Ris, suggesting that the characteristics of Fraser's female *A. donaldi* fit with those of males of *A. martini* (Fraser 1924). Although *A. martini* was originally described by Selys-Longchamps (1897) from »Yokohama« in Japan, based on an immature male, the locality was considered »erroneous«.

Fraser (1936) refined the taxonomic treatment of his 1924 paper, and for the first time described mature males of this species as well as mature females. He succeeded in catching two mature adult males, but, because of the colour dimorphism of mature males and females, wrote that »their relationship [between male and female] would be open to doubt had it not been proved by breeding experiments«. At the same time, Fraser introduced Ris' opinion that »[Selys' *A. martini*] had come from Java, and this opinion is strengthened by the recent discovery of a female by Lieftinck in Java which seems to me [Fraser] to be closely related to the present species«.

On the other hand, Lieftinck (1932) described a new species, *A. montivagans*, from mountainous areas of western and middle Java, based on five males and eight females. However, all males were immature and a mature specimen had not then been obtained, as in the case of *A. donaldi*. Lieftinck (1934) again emphasized the differences between *A. montivagans* and *A. martini* in terms of the colour of the stripe on the synthorax.

However, Fraser (1943) incorrectly synonymized *A. montivagans* with *A. martini*, and restored *A. donaldi* as a good species, on the grounds that »these two species [*donaldi* and *montivagans*] might equally claim to be the Selysian *A. martini* with this important difference, *viz*. that *montivagans* had been found in the *terra typica* of *martini*, whereas *donaldi* came from the continent of Asia«. But probably he did not directly compare any *A. montivagans* and the type of *A. martini* with his *A. donaldi*, and did not present any evidence that the type of *martini* came from Java, except the comment that »Fruhstorfer [from whose collection the type of *martini* had been supplied] had made his collections [in Java]«. Therefore, Lieftinck (1954) pointed

out Fraser's »erroneous synonymy«, and treated *A. montivagans* again as a good species.

Later, Kimmins (1966) designated the female specimen from »Kodaikanal, Palni Hills, S. India« on »May 1908« as the lectotype of *A. donaldi* (Figs 1d, e) and the male from »Varatapari, Annaimallai Hills, S. India« on »25.iv. 1933« as the allotype (Figs 1a–c) in the British Museum (Natural History).

Figure 1. Type specimens of *Anaciaeschna donaldi* from India in BMNH; a – habitus of allotype male in dorsal view; b – the same in lateral view; c – anal appendages of allotype male; d – habitus of lectotype female in dorsal view; e – the same in lateral view. Photos courtesy of Michael van der Poorten.

In summary, and in chronological order, Selys-Longchamps (1897) described *A. martini* from Yokohama, Japan. Fraser (1922a) described *A. donaldi* from Palni Hills, southern India. Fraser (1924) synonymized *A. donaldi* with *A. martini*. Lieftinck (1932) described *A. montivagans* from Java. Fraser (1943) synonymized *A. montivagans* with *A. martini* based on his misunderstanding that the type of the latter had come from Java, not Japan, and resurrected *A. donaldi* as a good species. However, Lieftinck (1934, 1954) confirmed *A. montivagans* was a good species, different from *A. martini*.

Thereafter, most of the World catalogues of Odonata (Bridges 1994; Steinmann 1997; Tsuda 2000; Schorr & Paulson 2019) list all three (*A. martini*, *A. donaldi*, *A. montivagans*) as good species. However this arrangement has never been satisfactorily proven.

Investigating the status of *A. donaldi*, we found the specimens from the Indo-Himalayan region deposited in museums were confusingly labelled. Some were identified as *A. donaldi* while others were labelled as *A. martini* – for example, the Indian Pusa Collection lists *A. martini* (Sharma et al. 2009). Later, in »The Fauna of India Checklist« (Subramanian & Babu 2017) *A. martini* is replaced by *donaldi*. In Nepal Natural History Museum there is a male specimen labelled *A. martini* from Ilam, Nepal, as documented by Shrestha & Mahoto (1984) but Vick (1989) listed it as *A. donaldi*.

Records of *Anaciaeschna donaldi* and *A. martini* from the Indo-Himalayan region

Anaciaeschna donaldi and/or *A. martini* have been recorded from the Indo-Himalayan region, in India, Sri Lanka, Nepal, and Bhutan.

In India, there have been no further records of these species since Fraser's aforementioned records, of which the last was made in 1933. Fraser (1936) described the distribution as »all montane lakes in the Nilgiris, Annaimallai Hills, and Palni Hills« (now in the states of Tamil Nadu, Kerala, Maharashtra, and Karnataka) in middle western to southern India.

In Sri Lanka, a single female (Fig. 3a) specimen from Hakgala gardens in 1924 was deposited in the National Museum of Natural History, Colombo, with the label *A. martini*, determined by Laidlaw (de Fonseka 2000).

Bedjanič et al. (2014) report records of *A. donaldi* at three separate locations near Nuwara Eliya in Sri Lanka in 2003. No other reports of *A. donaldi* have been published since then.

In Nepal, the first *Anaciaeschna* specimen was collected from Ilam, in eastern Nepal near the border with Sikkim. It is a teneral male, missing the terminal three segments, and is deposited in the Natural History Museum of Nepal (NHMN) in Kathmandu. It is labelled »*A. martini*« (Shrestha & Mahato 1984) and has probably been identified following Fraser (1936). However, Vick (1989) listed this specimen and an additional female from Godavari, south of Kathmandu, in the Annapurna History Museum under *A. donaldi*. Sasamoto & Ushijima (2000) reported five females from Godavari as *A. donaldi*. Two of us found a female (KC unpubl.) and a male of the same species (MSL unpubl.) at a small pond in the Godavari Knowledge Park in June 2012 and July 2017, respectively (Figs 2a–c).

In Bhutan, a female of the same species was recently photographed, ovipositing at a pond of Sherubtse College in Kanglung, Tashigang in eastern Bhutan at 1 775 m a.s.l. (27.288154'N, 91.524427'E) at around 10 h BTT (UTC + 06:00) on 01-vi-2019 (M. Gurung pers. comm.; Fig. 3b). This is the first and hitherto only record for the country.

As an aside, in East Asia, *A. martini* was originally described by Selys-Longchamps (1897) from Yokohama, Japan. This species is known to be widely distributed in the Japanese Archipelago, except for the northern regions and south-western islands (Ozono et al. 2012). In addition, it is locally found in the highlands of Taiwan (Lieftinck 1984; Wang 2000) and the southern Korean Peninsula (Lee 2001; Jung 2016). In the 21st century, it has been revealed that this species is distributed more broadly than expected in south central China (Zhang 2017, 2019) and Indochina (Thailand: Hämäläinen 2002; Vietnam: Karube 2004; Laos: Yokoi & Souphanthong 2014).

Material and methods

For morphological analysis, we compared Japanese specimens of *Anaciaeschna martini* with Nepalese and Indian specimens, previously identified as *A. martini* or *A. donaldi*, and studied the presence of potential differences. In addition, the same was done with *A. montivagans*.

The specimens were either examined directly or from digital photographs supplied by the museums listed below. Males of the specimens labelled as *A. donaldi* or *A. martini* in several collections were often teneral or imma-

Figure 2. *Anaciaeschna martini* (previously sometimes identified as *A. donaldi*) from Nepal (Godavari, Kathmandu); a – habitus of mature male in lateral view; b – detail of head and synthorax of living mature male; c – habitus of mature female in lateral view; d – the basal segments of abdomen of mature male in ventral view; e – *vesica spermalis* (immature stage); f – male anal appendages in lateral view (immature stage); g – same in dorsal view (immature stage).

ture, lacking full development and coloration. Many labels of the collections from India and Nepal have an original identification that has not been changed.

To test and validate our morphological analysis, we performed molecular phylogenetic analysis on nuclear DNA (ITS1, 5.8S rRNA, and ITS2) and mitochondrial DNA (mt16SrRNA and mtCOI) sequences, by the same method of Futahashi & Sasamoto (2012). The sequence data were deposited in the DDBJ/EMBL/GenBank databases (accession numbers LC466154-LC466165). Molecular phylogenetic analyses were conducted by neighbour-joining and maximum likelihood methods with MEGA7 (Kumar et al. 2016). The Maximum Composite Likelihood and Tamura Nei models were used for neighbour-joining and maximum likelihood analysis, respectively (Tamura & Nei 1993). Bootstrap values were obtained by 1 000 bootstrap replications. The DNA samples were extracted from Japanese and Nepalese specimens, but ones from India and Sri Lanka were not available in this study.

Material studied
Abbreviations: Hw – hind wing; Fw – Fore wing

Acronyms of museum collections:
NHM – Natural History Museum, London, UK
RMNH – Naturalis Biodiversity Centre, Leiden, The Netherlands
NMNH – National Museum of Natural History, Colombo, Sri Lanka
KPMNH – Kanagawa Prefectural Museum of Natural History, Odawara, Japan
NHMN – Natural History Museum of Nepal, Kathmandu, Nepal
ANHM – Annapurna Natural History Museum, Pokhara, Nepal

Indian material, examined by photographs
NHM: 1♂, allotype of *A. donaldi* (Figs 1a–c), 25-iv-1933, »on road side, Varatapari, Annaimalai Hills, S. India«, ex. coll. F.C. Fraser (Kimmins 1966); 1♀, lectotype of *A. donaldi* (Figs 1d, e), v-1908, »Kodaikanal, Palnai Hills, S. India«, ex. coll. F.C. Fraser (Fraser 1922a; Kimmins 1966).

RMNH (all »ex. coll. F.C. Fraser«):1♂ (1089755; teneral, »ex-larva«, labelled *A. martini*), iii-1921, »S. Pen. India, Nilgiris, Ooty«; 1♀ (1089756; labelled *A. martini*), 10-vi-1922, »S. Penins. India, Nilgiris, 7 250 ft. Ootacamund«; 1♂ (1089776;

the distal abdomen from 3rd segment missing, teneral, »ex-la[rva]«, without species label), date lacking, »S. Penins. India, Nilgiris, W. Ghats, Ooty Lake, 7 250 ft.«, leg. F.C. Fraser; 1♂ (1089777, teneral, »ex-larva«, labelled *A. martini*), iii-1921, »S. Pen. India, Nilgiris, Ooty«, leg. F.C. Fraser; 1♀ (1089779, teneral, labelled *A. martini*), date lacking, »Pen. India, loc. ?«, leg. F.C. Fraser.

Sri Lanka material, examined by photograph

NMNH: 1♀ (labelled *Anaciaeschna martini*) (Fig. 3a), vi-1924, Hakgala Botanical Gardens, Sri Lanka, det. Laidlaw (de Fonseka 2000).

Nepalese material, directly examined

ANHM: 1♀, Godavari (alt. 1 500 m), 17-vii-1986, leg. C. Smith; NHMN: 1♂ (teneral, damaged, labelled *A. martini*), 15-v-1979, Ilam District (alt. 1 000 m), leg. M. Mahato (Shrestha & Mahato 1984).

Authors' private collections: 1♂ (Figs 2a, b, d), 14-vii-2017, Godavari, Bagmati District (27°35'40"N, 85°23'22'E, 1 581 m a.s.l.), leg. K. Conniff; 1♀ (Fig. 2c), 14--xi-2012, same locality, leg. K. Conniff & N. van der Poorten; 4♀, 21-vii-1998, Godavari, leg. K. Ushijima (Sasamoto & Ushijima 2000); 4♂ 3♀ (immature, 21-iv–26-vii-1999 emergence, bred from egg, taken from a mature female caught in Godavari, 21-vii-1998) (Figs 2e–g), br. A. Sasamoto.

Japanese material of *A. martini*, examined by photograph

RMNH: 1♀ (1089778), 20-vii-1970, »Godaisau [sic!] Park, Kochi City, Kochi Pref.«; 1♂ (1089757) (Fig. 4c), 12-ix-1993, »Tsurugaike, Iwata City, Shizuoka Pref.«, leg. Ugai; 1♂ (1089780, teneral), 21-vi-1951, »Totisuka [sic!], Tokyo«, ex. coll. S. Asahina.

Japanese material of *A. martini*, directly examined

Authors' private collections: 3♂ 1♀, 18–28-vii-1999, Ichikawa City, Chiba, leg. K. Naruse; 1♂ 1♀, 21-vii–01-viii-2000, same locality and collector; 2♀, 29-vii–06--viii-2001, same locality and collector; 2♂ (Figs 4d–f), 28–29-viii-2001, Tenri City, Nara, leg. A. Sasamoto; 2♀, 22–27-vii-2002, Ichikawa City, Chiba, leg. K. Naruse; 9♂ 5♀, 07-vii–30-viii-2006, same locality and collector; 1♂ (Fig. 4a), 07-viii-2018, Tenri City, Nara, leg. A. Sasamoto; 1♀ (Fig. 4b), 05-viii-2019, same locality and collector.

Material of *A. montivagans*, examined by photograph

RMNH: 1♀ (1089782) (Figs 5d, e), 17-vii-1949, »W. Java, 1 700 m, Mt. Gedeh, Tjibeureum Rawa Gajonggong«, ex. coll. M.A. Lieftinck; 1♂ (1089783, teneral) (Figs 5a, b), »Larva ult: 15-xii-1929/ Imago: 1-ii-1930«, »Java occ. 1 400 m. Telaga Saät, Bij Poentjak-pas. (Gedeh)«, ex. coll. M.A. Lieftinck (Lieftinck 1932).

Figure 3. *Anaciaeschna martini* from Sri Lanka and Bhutan; a – female specimen from Sri Lanka, deposited in NMNH, ex. coll. F.F. Laidlaw in 1924. Photo courtesy of Michael van der Poorten; b – ovipositing female at a pond of Sherubtse College in Kanglung, Tashigang, eastern Bhutan, at around 10 a.m. (01-vi-2019). Photo: M. Gurung

Material of *A. montivagans*, directly examined

KPMNH: 1♀, 03-v-1990, Gn Sibayak, near Brastagi, Sumatra, Indonesia, leg. K. Mat.

Authors' private collections: 1♀, 30-iv-2001, Kg. Raja, Pahang, Malaysia, leg. A. Sasamoto (Sasamoto 2007).

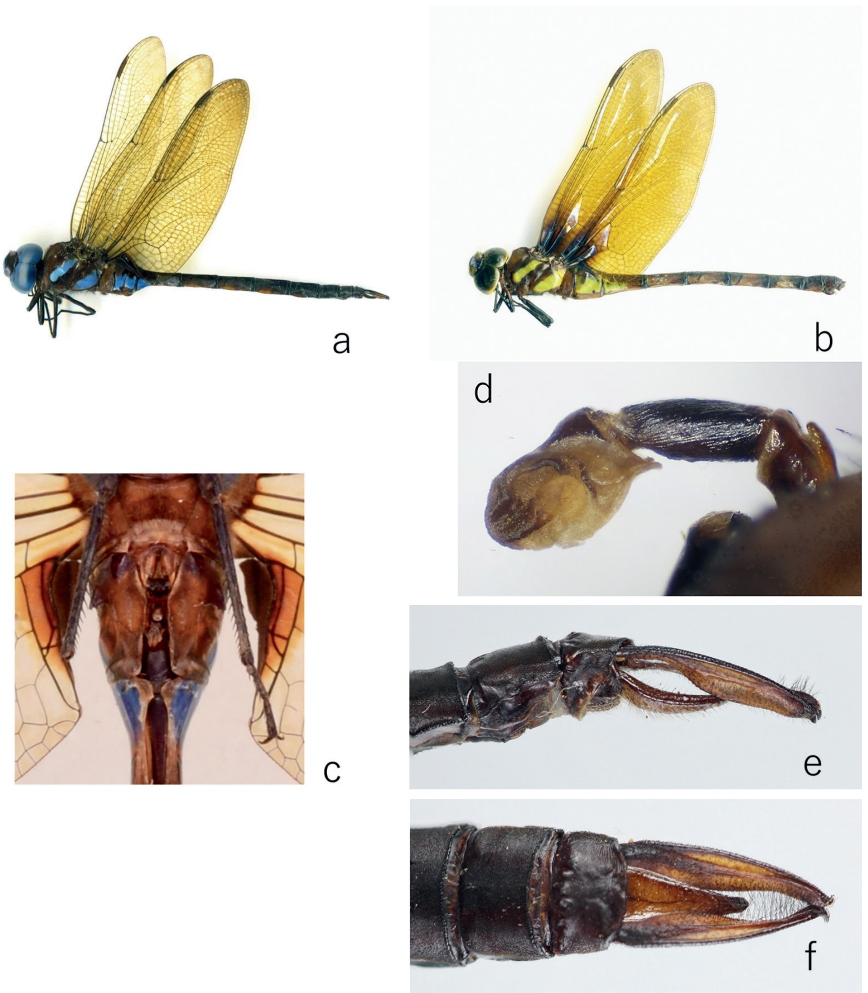

Figure 4. *Anaciaeschna martini* from Japan; a – habitus of mature male in lateral view; b – habitus of mature female in lateral view; c – the basal segments of abdomen of mature male in ventral view (RMNH 1089757); d – *vesica spermalis*; e – male anal appendages in lateral view; f – same in dorsal view.

Results

Morphological analysis

Anaciaeschna martini from Japan, the *terra typica*, has been well described and illustrated repeatedly in previous works (Selys-Longchamps 1897; Martin 1908; Hamada & Inoue 1985; Sugimura et al. 1999; Ozono et al.

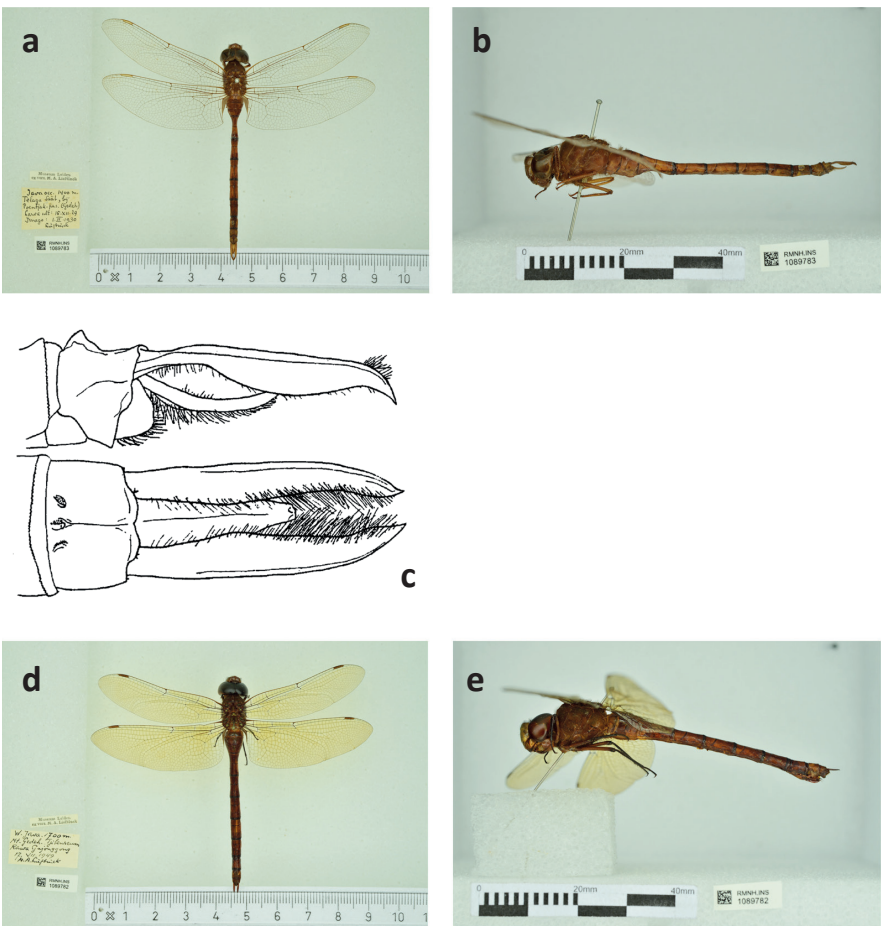

Figure 5. *Anaciaeschna montivagans* from Java Island in RMNH; a – habitus of immature male in dorsal view; b – same in lateral view; c – the figure of anal appendages of male after Lieftinck (1932); d – habitus of mature female in dorsal view; e – same in lateral view.

2012). Therefore, we do not describe this species here in detail, except for accessory genitalia, *vesica spermalis*, and male anal appendages, which are important for identification. Regarding coloration, it should be noted that the mature male of *A. martini* (Fig. 4a) has conspicuously azure blue eyes and maculation on the synthorax and basal abdomen on a reddish-brown ground colour. On the other hand, the mature female (Fig. 4b) has deep amber-coloured wings with a basal dark patch and apple green maculation on synthorax and basal abdomen, whereas immature individuals of both sexes have yellow maculation on the thorax instead of the vivid colour of the mature stage. Such colour features are peculiar and make *A. martini* easy to separate from the other species.

Accessory genitalia (Fig. 4c) as follows; lamina anterior with a large incurving spine; *hamulus anterior* has a complicated shape like a horse saddle; *hamulus posterior* is club- shaped but rudimentary. Auricle in ventral view is a triangle with usually two spines (rarely one or three) on distal side.

Vesica spermalis (Fig. 4d) with an apical segment that is prolate spheroid, with a wrinkled protuberance baso-laterally and with a chitinized curling expansion apically.

Anal appendages of male (Figs 4e, f), cercus (superior appendage) in dorsal view slender and gently curved inwards; the width gradually broader from base to a little proximal of the middle, then thinner distad, ending in a divergent tip at apex; cercus in lateral view slender at base, but suddenly broad ventrad at about proximal third, then gradually narrower distad. Epiproct (inferior appendage) in dorsal view slender triangular shaped, about ⅔ of cercus in length; the same in lateral view with gently arched shape, turning dorsad distally.

Nepalese specimens, which were labelled *ad hoc* as *A. martini* or *A. donaldi* in the past, have no substantial differences in morphology compared with Japanese *A. martini* (Figs 2a, b, c), including accessory genitalia (Fig. 2d), auricle and *vesica spermalis* (Fig. 2e; note that it is a little wrinkled due to post-mortem change of immature specimen) and anal appendages (Figs 2f, g). The body size of Nepalese specimens tends to be a little smaller than in Japanese specimens, but sizes are largely overlapping. Japanese specimens have the following size ranges: male abdomen (excluding anal appendages) 43–57 mm, male Hw length 41–47 mm, female abdomen 53–63 mm, Hw

length 44–50 mm (Ozono et al. 2012 and our material); Nepalese specimens have size ranges as follows: male abdomen (excluding anal appendages) 46–49 mm, male Hw length 40–42 mm, female abdomen 47–54 mm, Hw length 43–50 (our materials).

Examination of Indian and Sri Lanka specimens could only be carried out via photographs. The lectotype and the allotype of *A. donaldi* in NHM (Fig. 1), collected in southern India, are in good condition. As far as we see, there are no differences from Japanese and Nepalese specimens, including male anal appendages (Fig. 1c), although we were unable to examine the morphology of accessory genitalia and *vesica spermalis*. The female specimen from Sri Lanka (Fig. 3a) shows many characteristics of *A. martini*, such as dark brown wings and in the pattern of maculation. Fraser (1936) described the body measurements of Indian specimens as: male abdomen (excl. anal app.) 50, Hw 44, female abdomen 53, Hw 48 mm, all of which fall into the range of those of Japanese *martini*.

In contrast, *Anaciaeschna montivagans* (Fig. 5), which was synonymized with *A. martini* by Fraser (1943), but was resurrected as a good species by Lieftinck (1954), differs from *A. martini* and *A. donaldi* (Lieftinck 1934; Sasamoto 2007; Katatani 2008). The clear differences from *A. martini* are the lack of a mark on the upper frons, eyes greenish brown even when mature, no vivid colour maculation on the synthorax (Figs 5a, b, d, e), and anal appendages (Fig. 5c) longer and narrower than those of *A. martini*.

These morphological results strongly suggest that Japanese *A. martini* specimens and Nepalese, Indian, and Sri Lanka materials, either identified as *A. donaldi* or *A. martini* in the past, are conspecific. On the other hand, *A. montivagans* is apparently a different species from *A. martini*, although it was synonymised in the past.

Molecular phylogenetic analysis

To validate our morphological analysis, which suggest strongly that Japanese and Nepalese *martini*/*donaldi* belong to the same species, we performed molecular phylogenetic analysis on nuclear DNA (ITS1, 5.8S rRNA, and ITS2) and mitochondrial DNA (mt16SrRNA and mtCOI) sequences. The molecular phylogenetic tree of nuclear DNA indicated that they are genetically inseparable (Fig. 6a), and that of mitochondrial DNA showed

that there are only slight differences probably due to geographic variation (Fig. 6b), suggesting that they are the same species.

Discussion

Taxonomic treatment

Considering that there are no substantial morphological differences between Japanese *Anaciaeschna martini* and Nepalese/Indian *A. donaldi*, and there is no significant molecular genetic separation between Japanese and Nepalese

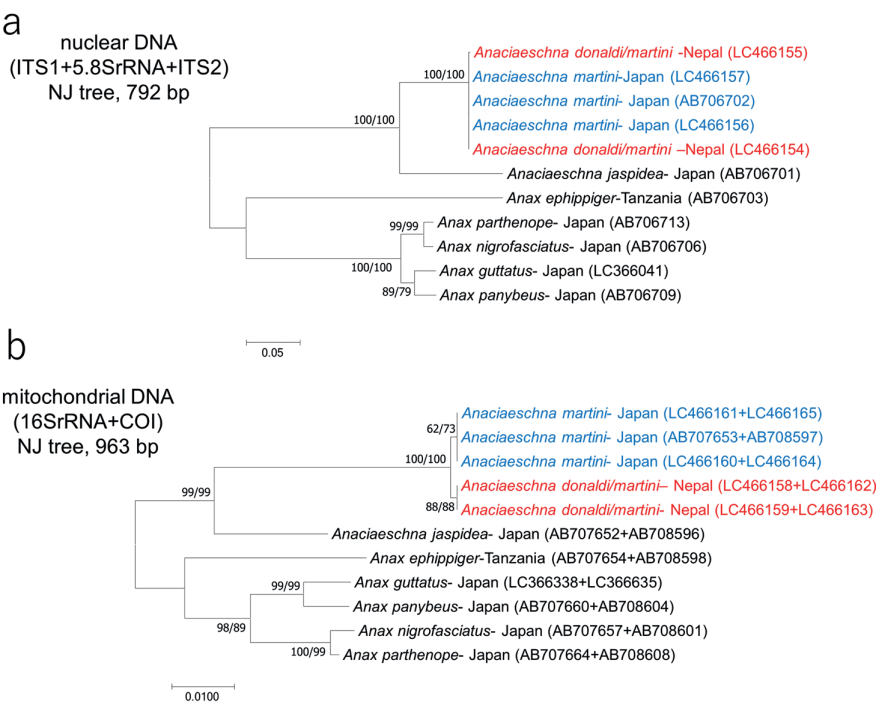

Figure 6. Molecular phylogenetic analysis of Japanese *Anaciaeschna martini* and Nepalese *A. martini/donaldi*, with allied species. A neighbour-joining phylogeny is shown; maximum likelihood phylogeny exhibited the same topologies. The blue specimens are from the Japanese population and the red ones are from the Nepalese population. On each node, statistical support values are indicated in the order of [bootstrap value of neighbour joining]/[bootstrap value of maximum likelihood]. Accession numbers are shown in parentheses; a – nuclear genes (ITS1-5.8S-ITS2, 792 bp); b – mitochondrial genes (16SrRNA and COI, 963bp)

populations, we consider them conspecific and conclude that *Anaciaeschna donaldi* Fraser, 1922, is junior synonym of *A. martini* (Selys, 1897).

Anaciaeschna martini (Selys, 1897)
= *Anaciaeschna donaldi* Fraser, 1922 (synonym)

Brief key of *Anaciaeschna* species in Indomalaya and East Asia (excluding *A. kashmirense*)

1a – synthorax uniform brown, without any vivid markings in both sexes ..... ***A. montivagans*** (Fig. 5) (South-East Asia: Java, Sumatra, Malay Peninsula)

1b – synthorax warm reddish-brown with strongly coloured (yellow, green or blue) markings on mesepimeron and metepimeron **2**

2a – Frons dorsally with rotated H black marking; synthorax with blue markings on mature male, apple green marking on mature female, and yellow on immature stage of both sexes; wings heavily enfumed in mature stages ..... ***A. martini*** (Figs 1–4) (temperate regions to tropics in East to South Asia)

2b – Frons dorsally with transverse black stripe; synthorax with yellow or pale green markings on both sexes even in mature stage; wings only lightly enfumed ..... ***A. jaspidea*** (subtropics and tropics in Australasia and Indomalayan realms)

Notes on distribution

A distribution map is given in Figure 7. In South Asia, *Anaciaeshna martini* (sometimes recognized as *donaldi*) has been recorded only locally in the Western Ghats in southern India, in Sri Lanka, and Nepal (Mitra 2010), and in Bhutan (this paper). On the other hand, in East Asia, the species is abundant and widespread in Japan and occurs locally in South Korea and Taiwan. In addition, it has recently been discovered in continental China (Zhang 2017, 2019) and at several localities in Indochina (Hämäläinen 2002; Karube 2004; Yokoi & Souphanthong 2014).

This update of the distribution of *A. martini* indicates that South Asian and East Asian populations are continuous and may have genetic interac-

tions. In the past, the distributional gap between populations of *A. donaldi* in South Asia and *A. martini* in East Asia was regarded as evidence of their specific segregation (Fraser 1943). However, recent research has narrowed the distribution gap and this study shows clearly that the populations of East Asia and South Asia are of the same species, *A. martini.* For this species, high mountains and oceans may not be strong barriers isolating populations. In fact, the allied *A. jaspidea* exhibits strong migratory behaviour and is sometimes found in remote habitats, where it can establish temporarily (Dow 2010; Ozono et al. 2012; Chaudhry et al. 2013). Similarly, *A. martini* is a

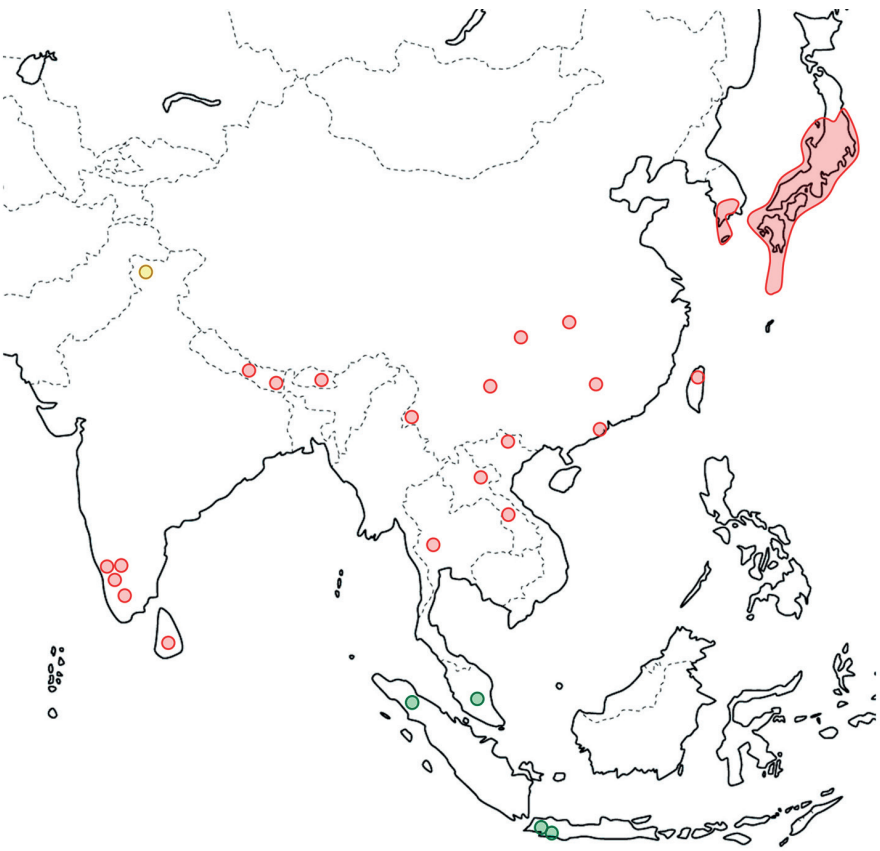

Figure 7. Distributional map of *Anaciaeschna* species in Asia (excluding *A. jaspidea*). Red – *A. martini*; yellow – *A. kashmirense*; green – *A. montivagans.*

strong flier (Yoshino 2016) and therefore is likely to migrate long distances in search of suitable habitat in which to settle. As *A. martini* is crepuscular and the male flies at high speed, they are difficult to collect and record reliably. Therefore, its distribution is probably more widespread than present records indicate. New discoveries of *A. martini*, for example, from central India and Myanmar can thus be expected.

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