



Six, not two, species of *Acisoma* pintail dragonfly (Odonata: Libellulidae)

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Abstract

The dragonfly genus *Acisoma* is revised based on adult male morphology and COI sequence data. Six species are recognised, including the new species *A. attenboroughi* sp. nov. Diagnoses and a key to males of all species and illustrations of all relevant characters are provided. *A. inflatum*, *A. variegatum* and *A. trifidum* are confined to continental Africa, while *A. panorpoides* is restricted to Asia. *A. ascalaphoides* is known only from threatened littoral forest fragments on the east coast of Madagascar, while *A. attenboroughi* is widespread across the island. The new species honours Sir David Attenborough on his 90th birthday.

Key words: Dragonfly, Odonata, *Acisoma*, taxonomy, new species, COI

Introduction

The African-Asian genus *Acisoma* Rambur, 1842 has been considered to include only two species, one with two subspecies, for more than a century. Rambur (1842) described the genus and two species: *A. panorpoides* based on both sexes from Asia and *A. ascalaphoides* based on two females from Madagascar. A specimen from Algeria was described as *Libellula panorpoides* by Selys (1849), but mentioned by him under the name *A. inflatum* in 1882. However, the latter name was introduced validly only when Selys (1889) provided a description. At the same time, Kirby (1889) named *A. trifidum* from Congo, subsequently describing *A. variegatum* from Malawi (Kirby 1898). Finally, Martin (1905) named *A. lacroixi*, which was rapidly synonymised with *A. trifidum* by Ris (1911).

In his revision of the Libellulidae, Ris (1911) considered *A. trifidum* from tropical Africa as a distinct species, but placed all other African, Malagasy and Asian specimens of the genus under *A. panorpoides* with two subspecies: *A. p. panorpoides* in Asia and *A. p. ascalaphoides* in Africa and Madagascar. Nonetheless, Ris (1911) noted morphologically distinct forms within his limited material from northern and eastern Africa, as well as Madagascar, which he associated with the species-group names *inflatum*, *variegatum* and *ascalaphoides* respectively.

Ris (1911) probably did not examine the female type material of *A. ascalaphoides* in detail or assumed extreme sexual dimorphism, as K. Schütte found two distinct male forms on Madagascar, one agreeing with the *A. ascalaphoides* female as figured by Rambur (1842) and another nearer typical *A. panorpoides*. As Ris (1911) had linked the name *ascalaphoides* to all *panorpoides*-like specimens from Africa and Madagascar, Schütte's discoveries demanded a reappraisal of *A. panorpoides* sensu Ris (1911), known colloquially as the Grizzled Pintail, across its entire range. This revision presents that reassessment based on morphological and molecular analyses and concludes that the genus *Acisoma* contains six species, of which the *panorpoides*-like one from Madagascar is described as new.

Material and methods

Morphological characters of 139 adult males and COI sequence data of 61 adults were compared. Additional collections and photographic records were checked and entered in ODA, the Odonata Database of Africa (Clausnitzer *et al.* 2012). The material lists provide details for examined males; further records (also unverified) are provided in Suppl. Tab. 1 available from <https://science.naturalis.nl/dijkstra>. Esri® ArcMap™ 10.0 was used to map distributions.

Acronyms of collections:

BMNH	Natural History Museum (London, United Kingdom)
ISNB	Institut Royale des Sciences Naturelles de Belgique (Brussels, Belgium)
MNHN	Muséum National d'Histoire Naturelle (Paris, France)
RMNH	Naturalis Biodiversity Center (Leiden, The Netherlands)
ZMUH	Zoologisches Museum Hamburg (Hamburg, Germany)

Morphology. The characters identified by Ris (1911) were tested and new characters found. Species were diagnosed by adult male characters only, following the style used by Dijkstra *et al.* (2015) in which shared features are listed with a letter (a; b; c etc.) and distinguishing features with a number (1; 2; 3 etc.). As in that publication, we provide a morphological diagnosis rather than a full holotype description for the new species identified, augmented with a photograph of the holotype (Fig. 11). Morphological nomenclature follows Dijkstra & Clausnitzer (2014), with these abbreviations: Ax (antenodal crossveins); Fw (fore wing); Hw (hind wing); Pt (pterostigma); S1–10 (first to tenth abdominal segments). See Fig. 1 for the carinae on S4–6 measured; data and proportions are summarised and compared in Tab. 2 and Fig. 3.

DNA extraction and amplification. Genomic DNA was extracted from legs using a NucleoMag 96 Tissue kit (Macherey-Nagel GmbH & Co.) on a KingFisher Flex magnetic particle processor (Thermo Scientific). A volume of 150 µl was used for elution. A 658 bp fragment of the mitochondrial COI gene was amplified using primer combinations provided in Tab. 1.

TABLE 1. Primer combinations used for amplification of COI.

Primer name	Direction	Sequence (5' to 3')	Reference
ODO_LCO1490d	F	TTTCTACWAACCAYAAAGATATTGG	Dijkstra <i>et al.</i> , 2014
ODO_HCO2198d	R	TAAACTTCWGGRTGTCCAAARAATCA	Dijkstra <i>et al.</i> , 2014
LepF1	F	ATTCAACCAATCATAAAGATATTGG	Hebert <i>et al.</i> , 2004
LepR1	R	TAAACTTCTGGATGTCCAAAAAATCA	Hebert <i>et al.</i> , 2004
LCO1490	F	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> , 1994
HCO2198	R	TAAACTTCAGGGTGACCAAAAAAATCA	Folmer <i>et al.</i> , 1994

Twenty-five microlitres of PCR reaction mixes contained 5 µL of 5x Phire II Reaction Buffer (Thermo Scientific), 1 µL of each primer (10 pM), 0.5 µL of Phire Hot Start II DNA Polymerase (Thermo Scientific), 0.5 µL of dNTPs and 1 µL of DNA template. The amplification protocol consisted of 30 sec at 98° C followed by 40 cycles of 5 s at 98° C, 5 s at 50° C and 15 s at 72° C, and a final 5 min at 72° C. Bi-directional Sanger sequencing was performed at BaseClear, Leiden, The Netherlands.

Sequences were edited with Sequencher 4.10.1 (Gene Codes Corporation) and checked for stop-codons in AliView (Larsson 2014). All sequence data and additional geographic and ecological data as well as photographs of the specimens (if available) were uploaded to the Barcode of Life Data System (BOLD; Ratnasingham & Hebert 2007). Sequences were also deposited in GenBank. GenBank accession numbers are provided in Suppl. Tab. 2 available from <https://science.naturalis.nl/dijkstra>.

Phylogenetic analyses. Multiple sequence alignments were performed using MAFFT version 7 (Katoh *et al.* 2009) under default parameters. Maximum likelihood and Bayesian inference were performed on the Naturalis OpenStack computing cloud.

Maximum likelihood analyses were run with RAxML 8 (Stamatakis 2014) using the GTRCAT model. The best maximum likelihood tree was calculated using the $-D$ parameter. A multiparametric bootstrap search was performed, which automatically stopped based on the extended majority rule criterion.

The Bayesian inference was performed with ExaBayes v1.4.1 (Aberer *et al.* 2014) using the GTR substitution model. Four independent runs with four Monte Carlo Markov Chains each, were run for 1,000,000 generations during which converge, with a standard deviation of split frequencies $< 1\%$, had been reached. The resulting trees were visualised in FigTree 1.4.2 (Rambaut 2014).

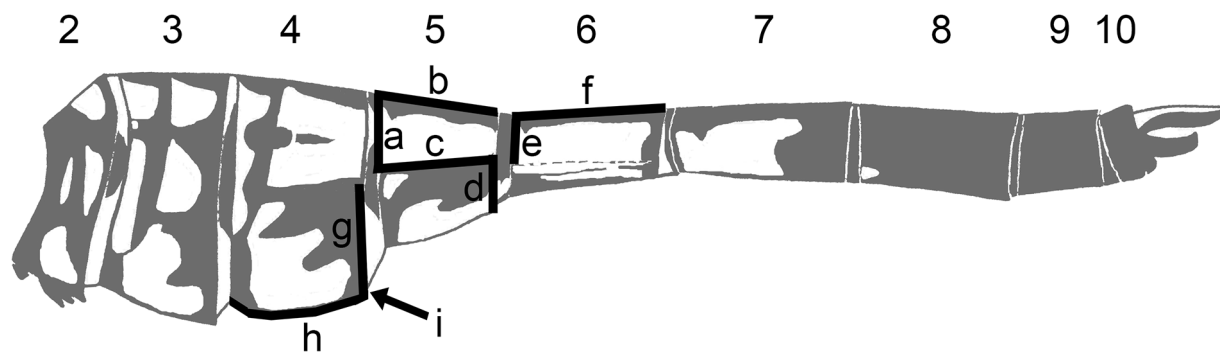


FIGURE 1. Abdomen of *A. inflatum* showing segment numbers and carinae measured; a: dorso-basal S5, b: dorsal S5, c: lateral S5, d: ventro-apical S5, e: dorso-basal S6, f: dorsal S6, g: ventro-apical S4, h: ventral S4, i: corner between ventro-apical and ventral carina S4.

Results and taxonomic discussion

Our results confirm the tentative assessment by Ris (1911) that his classification of *Acisoma* in two species (one with two subspecies) was an oversimplification and that the Afrotropics harbour at least three taxa aside from *A. trifidum*. Both morphologically and molecularly *A. trifidum* from continental Africa and the taxon that agrees with the female types of *A. ascalaphoides* from Madagascar in ISNB (K. Schütte personal observation) are highly distinct (Tab. 2; Fig. 2). COI data of the remaining specimens reveal three geographically separate and morphologically supported clusters from continental Africa, Asia and Madagascar, of which the latter is well separated from *A. ascalaphoides*.

Males from the African cluster can morphologically be assigned to two distinct groups, which differ most notably in abdominal proportions but also in markings and average size (Fig. 3). Not only are they discrete from each other, but the more slender one is also notably distinct from all other *Acisoma*, suggesting two species are involved. The two overlap widely in range and can occur at the same site and can thus not be considered subspecies (Fig. 9), while intermediates are expected if they were morphologically different forms of one species, as polymorphism in abdomen shape is unknown in odonates.

We conclude that the two are good species that diverged too recently to be separated in COI. From 4260 sequenced specimens of 585 sub-Saharan odonate species (80% of those known to occur there), Dijkstra *et al.* (2015) inferred that 9% of morphologically recognised species do not possess unique haplotypes for COI. The two *Acisoma* species thus belong to the estimated 65 sub-Saharan odonate species that cannot be identified by DNA-barcoding.

The more slender African species is limited to the south and east and agrees with the holotype of *A. variegatum* from Malawi in BMNH (K.-D.B. Dijkstra personal observation). The species found throughout the continent, including the type locality Algeria, corresponds with *A. inflatum*. Recognising these species implies that the well-defined Asian and Madagascan forms are treated as species too. The former agrees with typical *A. panorpoides* and the latter is named *A. attenboroughi* **sp. nov.** below.

Summarising, the “grizzled pintail” *A. panorpoides* in the widest traditional sense is split into five species. The former subspecies *ascalaphoides* is divided into the Stout Pintail *A. inflatum* with a large range in continental Africa, the Slender Pintail *A. variegatum* in eastern and southern Africa, the Littoral Pintail *A. ascalaphoides* in coastal East Madagascar and Attenborough’s Pintail *A. attenboroughi* **sp. nov.** elsewhere in Madagascar. The subspecies *panorpoides* from Asia is also raised to species level and dubbed the Asian Pintail *A. panorpoides*.

Although our revision is based on males only, the non-sexual morphological characters used appear to apply equally to the even more similar females.

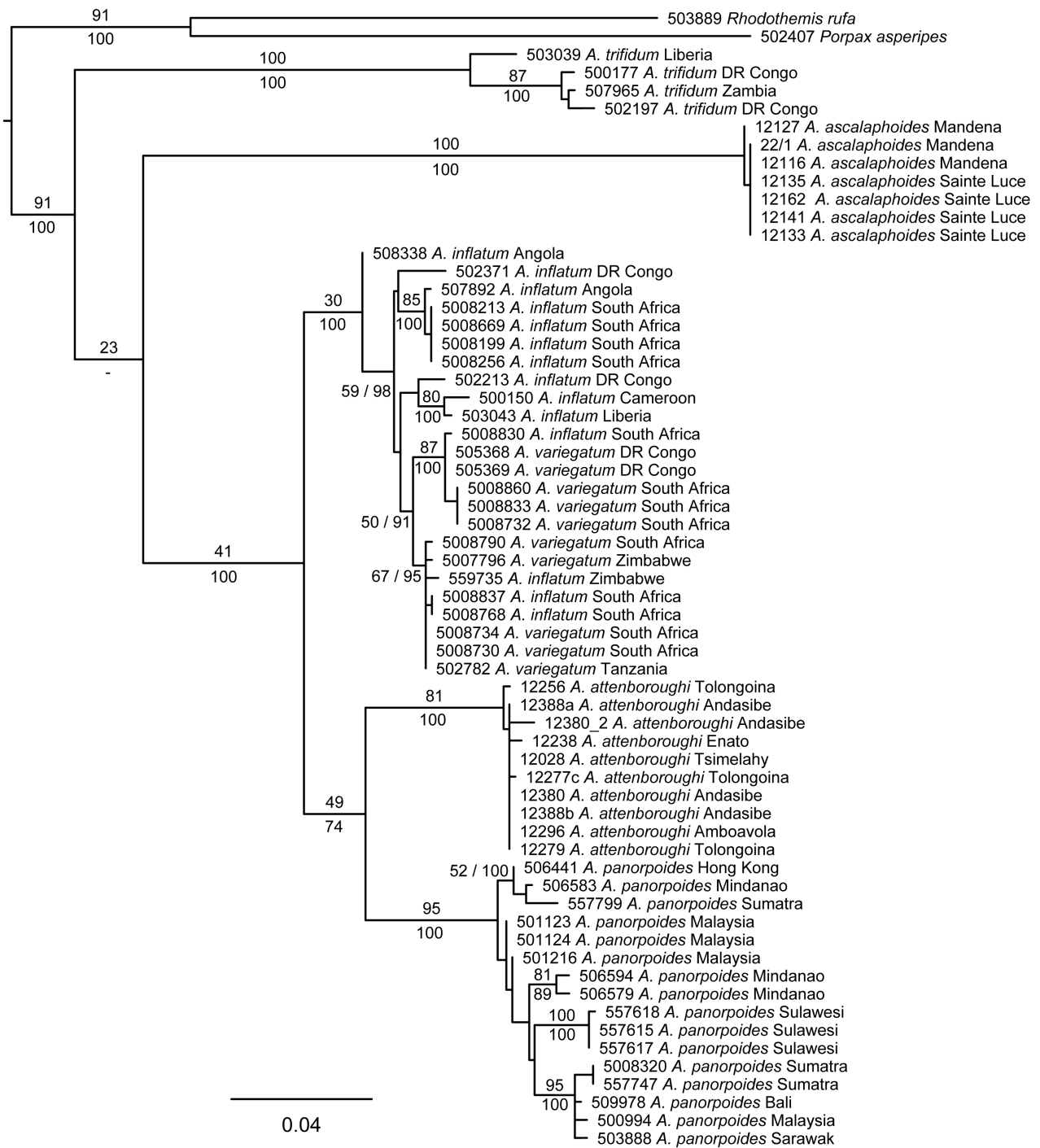


FIGURE 2. Best tree from Maximum Likelihood analysis of COI sequences for *Acisoma* and two outgroup taxa. For relevant branches bootstrap support is shown first, as are posterior probabilities from Bayesian inference (both as percentages). Six- and seven-digit numbers refer to RMNH.INS and RMNH collection codes respectively, other numbers to KS069 codes (these prefixes are omitted). Specimen details are provided in Suppl. Tab. 2 available from <https://science.naturalis.nl/dijkstra>.

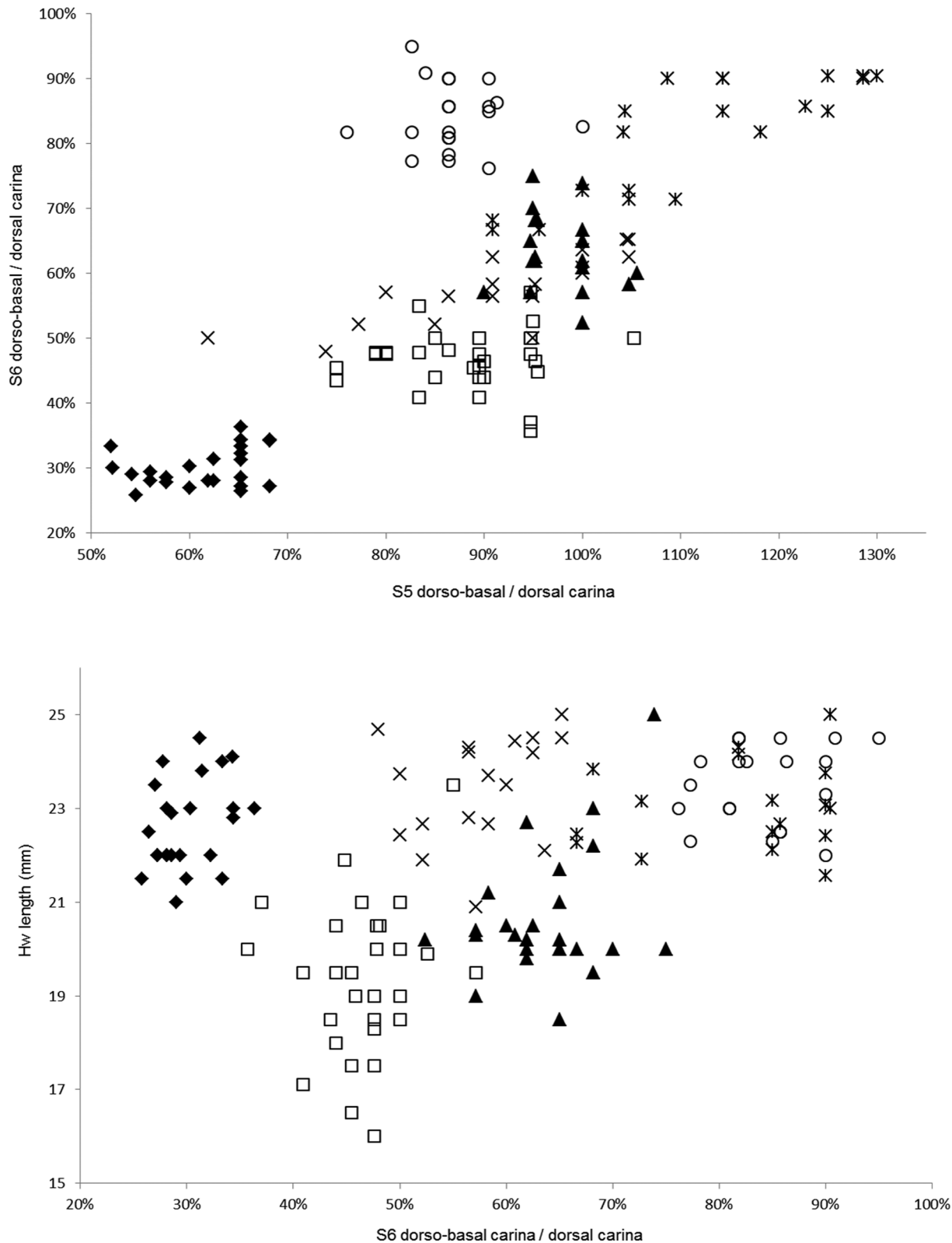


FIGURE 3. Scatter plots of (proportions of) the lengths of S5 and S6 carinae and Hw in *Acisoma* species; filled diamonds: *A. variegatum*, open squares: *A. inflatum*, filled triangles: *A. panorpoides*, crosses: *A. attenboroughi*, stars: *A. ascalaphoides*, open circles: *A. trifidum*. The relationship of the proportion between the ventro-apical and lateral carinae of S5 with the dorso-basal and dorsal carinae of S5 is similar to that of the latter with the dorso-basal and dorsal carinae of S6.

Taxonomy

Genus *Acisoma* Rambur, 1842

With over a thousand species, Libellulidae is the largest family of Anisoptera (Dijkstra *et al.* 2013). *Acisoma* belongs to the morphologically rather distinctive *Erythemis*-group (Pinto 2013), which also has strong molecular support (K.-D.B. Dijkstra unpublished). The group is largely tropical and has most species in the New World genera *Erythemis* Hagen, 1861, *Rhodopygia* Kirby, 1889, and *Carajathemis* Machado, 2012. *Acisoma* overlaps with the superficially very different genera *Cyanothemis* Ris, 1915, and *Porpax* Karsch, 1896, in Africa, *Viridithemis* Fraser, 1960, in Madagascar, and *Rhodothemis* Ris, 1909, in Asia. All genera have similar secondary genitalia and share the enlarged occipital triangle with rather straight borders, as a result of which the eyes touch at most over a distance less than half the triangle's length. Their coloration is also unusual, frequently including bright white, green or blue pigments that are otherwise rare in the family. These colours are often notably concentrated dorsally, e.g. the African genera have the frons and vertex ventrally black with contrasting dorsal markings.

Acisoma is easily recognised by the combination of its (1) small size, Hw 16–25 mm; (2) brown to black body with contrasting and fragmented (bluish) white markings; (3) open venation with only 6–9½ Ax in Fw and normally 1 cell in Fw triangle and 1 cell-row in all radial planates; (4) Hw with at most a small dark patch at their extreme base; (5) strongly swollen abdomen at base, narrowing abruptly between S5 and S7, with slender tip; and (6) S4 with transverse ridge of similar strength as that on S3 and the lateral carina of S4.

Key to males

1. Abdomen in lateral view narrows gradually throughout or on S5–6, at most S7–10 slender (Fig. 7E–F). Labrum, labium, thorax and underside of S3 and S6 largely brown to black; white markings on S2–5 solid and clean-cut, S7 (almost) entirely black (Fig. 4F–G, 5H–I, 6G–H, 7E–F). 8½ or 9½ (rarely 8) Fw Ax. 2 or 3 cells in Fw triangle, rarely 1. Fw Pt about 10–13% as long as Hw. Lobe of hamule with pointed or narrow tip (Fig. 8E–F). 2
 - Abdomen narrows abruptly on S5; S6–10 slender (Fig. 7A–D). Labrum, labium, thorax and underside of S3 and S6 extensively white; markings on S2–5 fragmented and frayed, S7 with large white lateral spots (Fig. 4A–E, 5A–G, 6A–F, 7A–D). 6–7½ Fw Ax, but about 20% up to 8½. 1 cell in Fw triangle, but about 10% has 2. Fw Pt about 11–16% as long as Hw. Lobe of hamule broad and triangular (Fig. 8A–D). 3
2. Abdomen narrows most on S7 and S8–10 slender (visible best in dorsal view); S7–8 of similar and intermediate length as S6 and S9; S4–5 with bold ventral white spots; dorsum of cerci largely white (Fig. 7F). Antefrons, clypeus, labrum and labium with bold black and white pattern (Fig. 4G, 5I). 3 cells in Fw triangle, but about 40% with 2. Lobe of hamule pointed (Fig. 8F). Tropical Africa *trifidum*
 - Abdomen narrows most on S5–6 and S7–10 slender (visible best in lateral view); S7–8 both distinctly longer than S6 and S9; S4–5 ventrally dark; dorsum of cerci black (Fig. 7E). Antefrons, clypeus, labrum and labium uniformly brown (Fig. 4F, 5H). 1 or 2 cells in Fw triangle. Lobe of hamule notched (Fig. 8E). East coast of Madagascar *ascalaphoides*
3. Abdomen more slender, with S6 about 2x to 4x as long as high, and ventral borders of S5 and S6 (almost) confluent; sublateral black marking on S4 concentrated on basal side of segment (Fig. 7A–B). Hook of hamule rather wide at base (Fig. 8A–B). Continental Africa. 4
 - Abdomen stout, S6 about 1x to 2x as long as high, and distinct 'step' between ventral borders of S5 and S6; sublateral black marking on S4 concentrated on apical side of segment (Fig. 7C–D). Hook of hamule more slender (Fig. 8C–D). Asia and Madagascar. 5
4. Carinae forming ventro-apical corner of S4 largely white; lateral carina of S5 usually partly white; S6 more than 2.5x as long as high (Fig. 7A). Hw 21–25 mm. Eastern and southern Africa. *variegatum*
 - Carinae forming ventro-apical corner of S4 entirely black; lateral carina of S5 all black; S6 at most 2.5x as long as high (Fig. 7B). Hw 16–22 mm, only rarely larger. Throughout Africa. *inflatum*
5. Mesepisternum with isolated black spot on its dorsal half that is connected to black humeral stripe in at most 5% of darkest specimens (Fig. 6C–D). Black band across antefrons narrow, 10–40% as wide as labrum is high; labrum without black spot or this very small and typically separate from base (Fig. 4C–D). Ventro-apical carina of S4 totally black, but partly white in about 15% of cases (Fig. 7C). Distal Ax in Fw complete in over 60% of cases. Asia. *panorpoides*
 - Dorso-central black spot on mesepisternum shifted toward and fused with black humeral stripe (Fig. 6E, F). Black band across antefrons wide, 40–80% as wide as labrum is high; black spot on labrum large, attached to base (Fig. 4E). Ventro-apical carina of S4 partly white, but all black in about 10% of cases (Fig. 7D). Distal Ax in Fw incomplete. Madagascar. *attenboroughi* sp. nov.

Species texts

Acisoma variegatum Kirby, 1898—Slender Pintail

(Figs. 4A, 5A–D, 6A, 7A, 8A, 10A)

Material. Tanzania: 8 males, Mpanda, 11-x-1970, J. Kieland (RMNH); 5 males, Sibweza, 20–23-v-1966/ 26-ix-1966/ 24-vi-1968/ 21-xi-1968, J. Kieland (RMNH); 1 male, Korogwe, 07-ii-1964, G.M.L. Bergers (RMNH).—D.R. Congo: 1 male, Katanga, Mutwale, 06-iv-1961, J.J. Symoens (RMNH); 1 male, Katanga, Mulandi, 11-ii-1963, J.J. Symoens (RMNH); 1 male, Katanga, Kiubo, 05-ix-2011, K.-D. B. Dijkstra (RMNH).—Kenya: 2 males, Amboseli, viii-1980, collector unknown (RMNH).—Uganda: 1 male, Entebbe, botanical garden, 30-iii-1999, V. Clausnitzer (RMNH).—South Africa: 2 males, KwaZulu-Natal, Ndumo Game Reserve, Mgagabhuleni, 31-ii-2014, K.-D.B. Dijkstra (RMNH); 1 male, KwaZulu-Natal, 7 km ESE of Manguzi, Kosi Bay area, inflow of Nhlanga and Amanzimnyama lakes, 02-iv-2014, K.-D.B. Dijkstra (RMNH); 1 male, KwaZulu-Natal, 15 km NE of Manguzi, Kosi Bay estuary, 03-iv-2014, K.-D.B. Dijkstra (RMNH).

Male diagnosis. Typical of the group lumped formerly under *A. panorpoides* by the (a) extensively white labrum, labium, thorax and underside of S3–7; (b) low number of Fw Ax, most often 7½ but sometimes 8½; (c) 1 cell in Fw triangle, but 2 cells in 24% of examined wings; (d) long Fw Pt, about 13–16% as long as Hw; (e) abdomen that narrows abruptly on S5 in lateral view, with S6–10 slender (Fig. 7A); (f) fragmented and frayed white markings on S2–5 and large white lateral spots on S7 (Fig. 7A); and (g) broad and triangular lobe of hamule (Fig. 8A). Unique within the genus by the (1) most slender abdomen, with the tergite of S5 below the lateral carina almost invisible in lateral view and S6 always more than 2.5x as long as high, and the ventral borders of S5 and S6 confluent (Fig. 7A); (2) almost always partly white ventral carina of S4, extending to an always white corner with the apical carina; and (3) always largely white and thus never wholly black lateral carina of S5. Overlaps with *A. inflatum* in eastern and southern Africa with which it shares the (4) sublateral black marking concentrated on the basal side of S4 (Fig. 7A); and (5) rather wide base of the hook of the hamule (Fig. 8A); but differs by the unique characters mentioned as well as its generally (6) larger size, with Hw 21–25 mm.

Range and ecology. More localised than *A. inflatum*, ranging from Ethiopia to Katanga and northern South Africa (Fig. 9B). Although the distribution seems to follow the more elevated Afrotropical part of the continent, the species appears to favour more open and eutrophic and often low-lying and expansive marsh habitat where it overlaps with *A. inflatum*, such as flood plains.

Acisoma inflatum Selys, 1889—Stout Pintail

(Figs. 4B, 5B–F, 6B–C, 7B, 8B, 10B)

Material. D.R. Congo: 2 males, Orientale, Kisangani, Scolasticat, 07/10-vi-2010, K.-D.B. Dijkstra (RMNH); 1 male, Equateur, Lower Itimbiri, Loeka river mouth, 11/16-v-2010, K.-D.B. Dijkstra (RMNH); 1 male, Bangala, Mobeka, xii-1934, collector unknown (RMNH).—Congo: 1 male, region de Kouilou, Pointe Noire, 03/04-iii-2010, P.H. Lambret (RMNH).—Gambia: 1 male, West District, Abuko, 15-xii-1980, M. Hämäläinen (RMNH).—Benin: 1 male, Department de l'Atlantique, So-Ava, 25-xii-2000, S.L. Tchibozo (RMNH).—Ghana: 1 male, Central Region, 12 km NW of Cape Coast, river below Brimsu dam, 20-iv-2000, K.-D.B. Dijkstra (RMNH).—Cameroon: 1 male, Centre Province, 55 km NW of Yaoundé, Sanaga River at Monatélé, 04-vi-2008, K.-D.B. Dijkstra (RMNH).—Liberia: 1 male, Nimba County, Mt Tokadeh, 02-x-2010, K.-D.B. Dijkstra (RMNH).—Gabon: 1 male, Haut-Ogooué, Mikouanga, Moanda, 01-vi-2009, N. Mézière (RMNH).—Angola: 1 male, Uíge, 5 km of Negage, lake at Canuango source, 24-xi-2012, K.-D.B. Dijkstra (RMNH).—Uganda: 1 male, Lake Nabugabo, 1999, V. Clausnitzer (RMNH); 1 male, Ddewe, vi-1949, E. Pinhey (RMNH).—Kenya: 1 male, coast south of Mombasa, 28-x-1990, V. Clausnitzer (RMNH).—Chad: 2 males, Chari-Baguirmi, N'Djaména, 02-viii-1992, H. Feijen (RMNH).—Algeria: 1 male, Algiers, 1892, coll. Albarda (RMNH).—Egypt: 4 males, Siwa oasis, 3 km of Siwa town, Fatnas spring, edge of Birket Siwa, 15-vi-2009, K.-D.B. Dijkstra (RMNH); 1 male, Dakhla oasis, Rashda, 27-x-1977, S. Thomas (RMNH).—South Africa: 1 male, KwaZulu-Natal, Himeville, Moorcroft Manor, 27-ii-2014, K.-D.B. Dijkstra (RMNH); 1 male, KwaZulu-Natal, 39 km W of Bergville, Royal Natal National Park, Mahai Dam, 02-iii-2014, K.-D.B. Dijkstra (RMNH); 2 male, Mpumalanga, 20 km ESE of Badplaas (= Emanzana), Teespruit River N of Lochiel on R545, 27-iii-2014, K.-D.B. Dijkstra (RMNH); 2 male, KwaZulu-Natal, 6 km NE of Manguzi, dam NW of Kosi Bay Lodge, 01-iv-2014, K.-D.B. Dijkstra (RMNH); 1 male, KwaZulu-Natal, 15 km NE of Manguzi, Kosi Bay estuary, 03-iv-2014, K.-D.B. Dijkstra (RMNH).

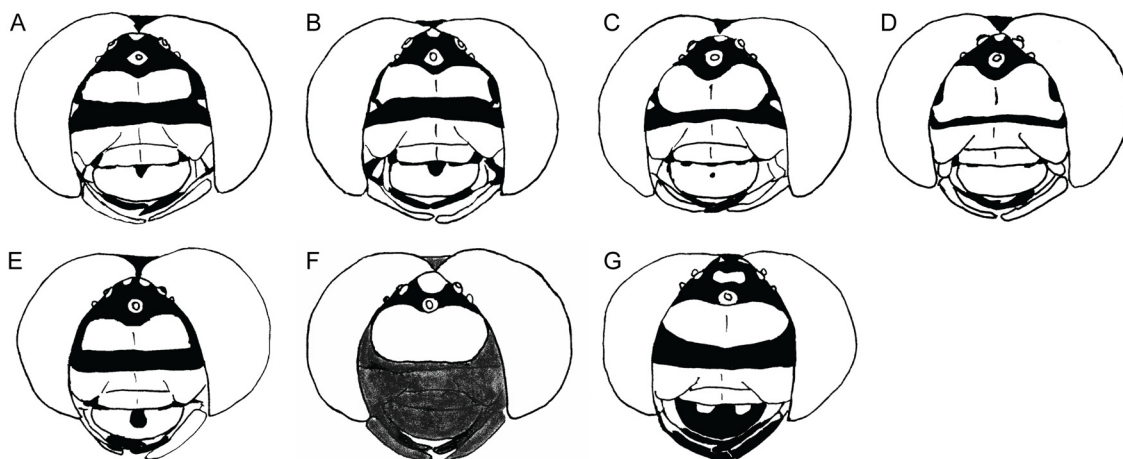


FIGURE 4. Head of *Acisoma* species in rostral view. A: *A. variegatum*, B: *A. inflatum*, C: *A. panorpoides* (typical), D: *A. panorpoides* (pale), E: *A. attenboroughi*, F: *A. ascalaphoides*, G: *A. trifidum*.

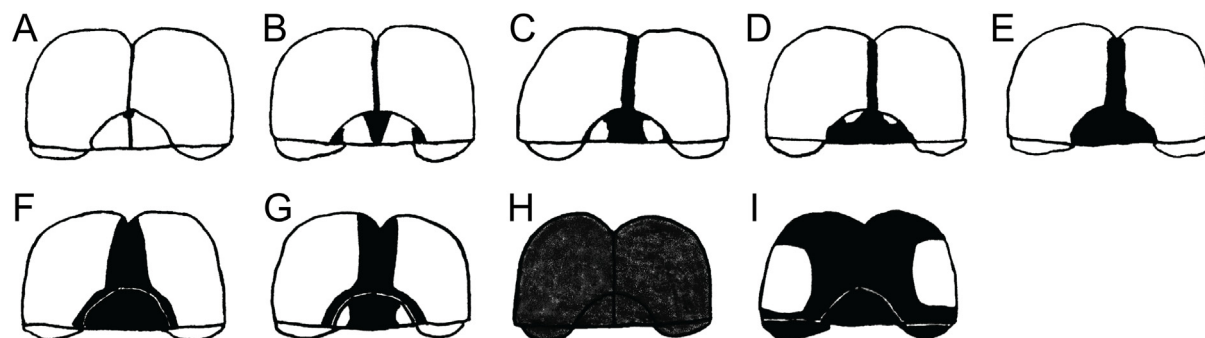


FIGURE 5. Labium of *Acisoma* species in ventral view. A–G: variations of *A. variegatum* (A–D seen), *A. inflatum* (B–F), *A. panorpoides* (A–C) and *A. attenboroughi* (A–C, F–G), H: *A. ascalaphoides*, I: *A. trifidum*.

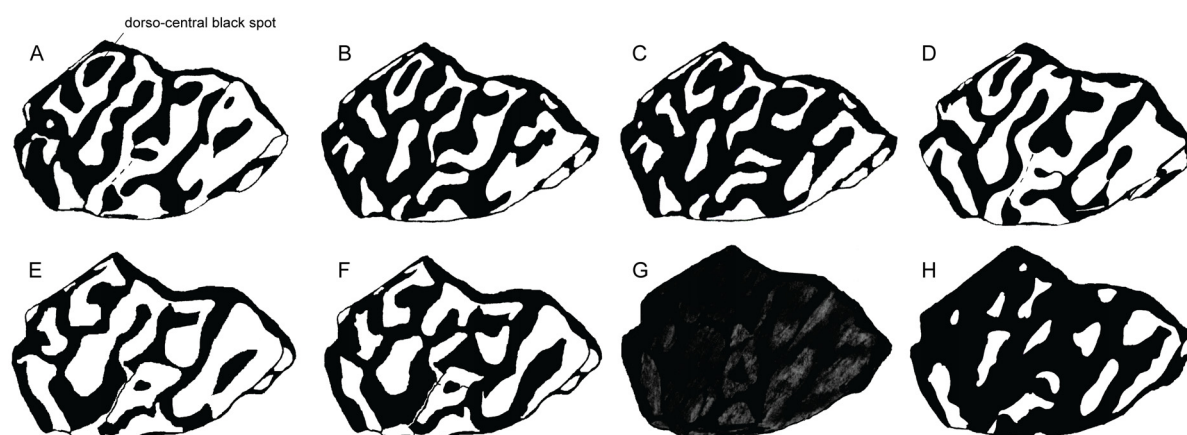


FIGURE 6. Thorax of *Acisoma* species in lateral view. A: *A. variegatum*, B: *A. inflatum* (typical), C: *A. inflatum* (dark), D: *A. panorpoides*, E: *A. attenboroughi* (typical), F: *A. attenboroughi* (dark), G: *A. ascalaphoides*, H: *A. trifidum*.

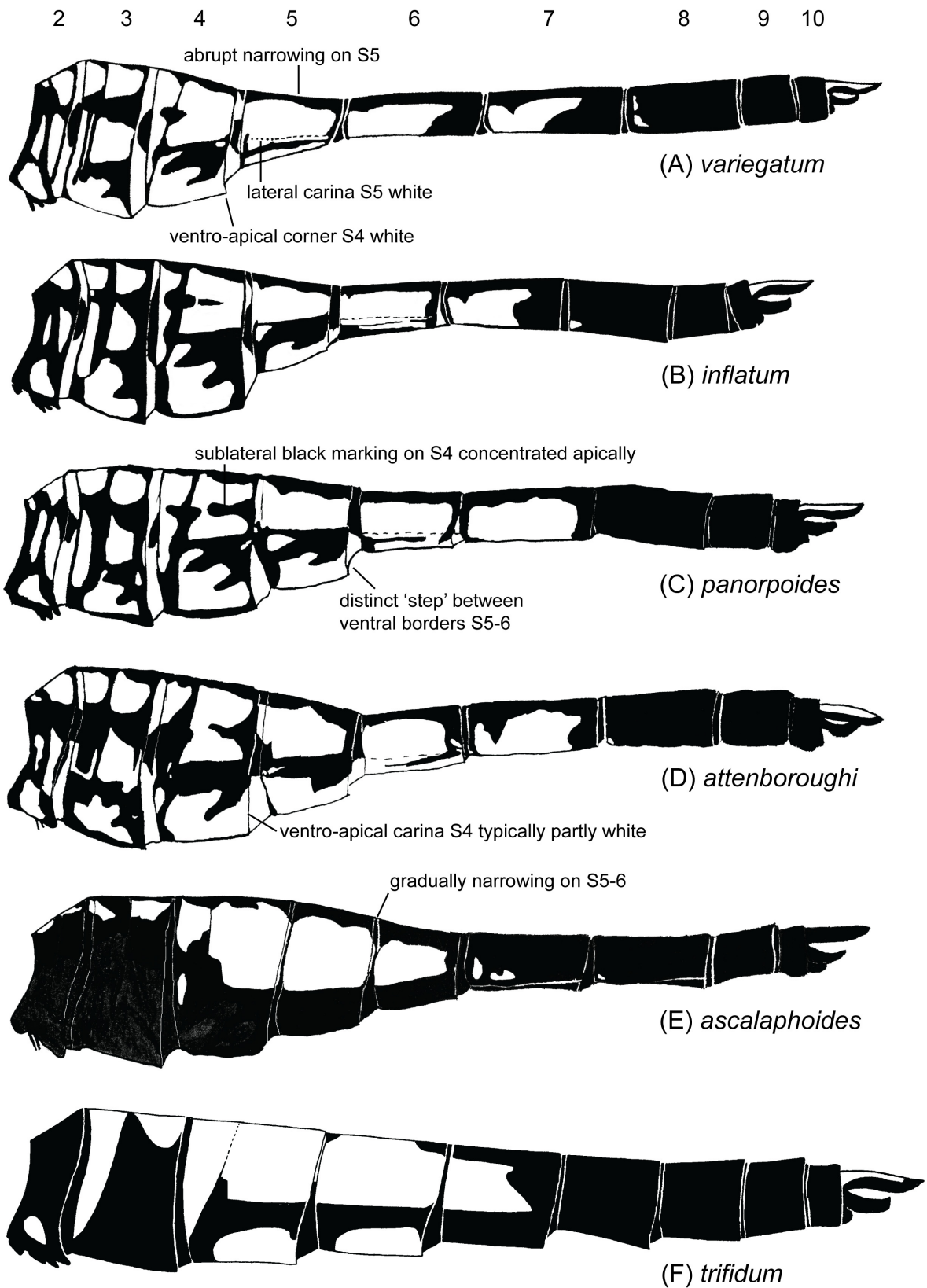


FIGURE 7. S2–10 of *Acisoma* species in lateral view, scaled to their average size. Segment numbers and relevant characters are indicated.

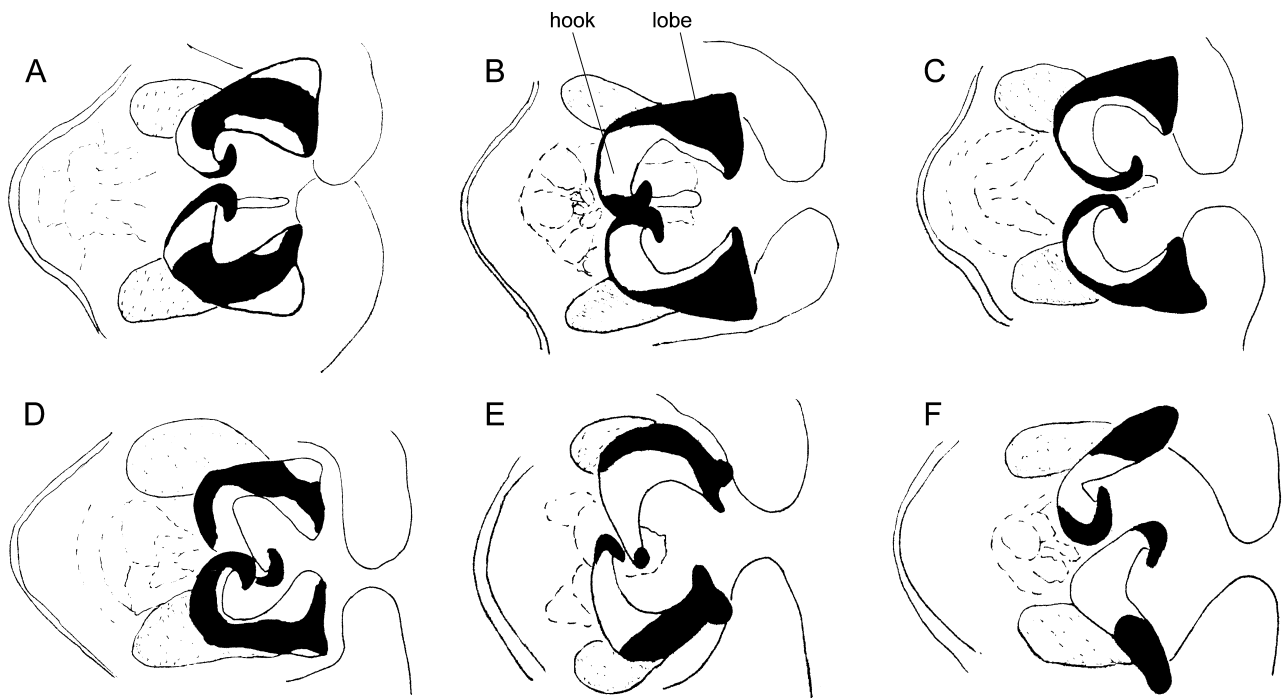


FIGURE 8. Secondary genitalia of *Acisoma* species in ventral view. A: *A. variegatum*, B: *A. inflatum*, C: *A. panorpoides*, D: *A. attenboroughi*, E: *A. ascalaphoides*, F: *A. trifoldum*. Structure of hamule indicated.

Male diagnosis. Typical of the group lumped formerly under *A. panorpoides* by the (a) extensively white labrum, labium, thorax and underside of S3–7; (b) low number of Fw Ax, usually 6½ or 7½, but sometimes 8½; (c) 1 cell in Fw triangle, but 2 cells in 11% of examined wings; (d) long Fw Pt, about 11–16% as long as Hw; (e) abdomen that narrows abruptly on S5 in lateral view, with S6–10 slender (Fig. 7B); (f) fragmented and frayed white markings on S2–5 and large white lateral spots S7 (Fig. 7B); and (g) broad and triangular lobe of hamule (Fig. 8B). The only species with no known unique structural or coloration characters, although it is the smallest species on average, with Hw shorter than in any of the other species in about a third of the specimens (Fig. 3). Being widespread in Africa, it must be separated with care from the more localised *A. variegatum* with which it shares the (1) relatively slender abdomen, with S6 usually over 2x as long as high, and ventral borders of S5 and S6 (almost) confluent; (2) sublateral black marking concentrated on the basal side of S4 (Fig. 7B); and (3) rather wide base of the hook of the hamule (Fig. 8B). Differs from that species by the (4) smaller size, with Hw 16–22 mm, although occasionally larger; (5) entirely black carinae forming the ventro-apical corner of S4; (6) all black lateral carina of S5; and (7) S6 at most 2.5x as long as high (Fig. 7B).

Range and ecology. Occurs throughout the geographic and habitat range (any calm grassy water body) formerly associated with *A. panorpoides* in continental Africa, including the relictual localities in northern Africa (Fig. 9A). Overlaps with *A. variegatum* in eastern and southern Africa (found at the same pond in coastal KwaZulu-Natal), but appears to be the only one of the pair in the more forested lowlands of western and central Africa.

***Acisoma panorpoides* Rambur, 1842—Asian Pintail**
(Figs. 4C–D, 5A–C, 6D, 7C, 8C, 10C)

Material. Philippines: 1 male, Mindoro, Mt Halcon, Calapan, vi-1991, R. Müller (RMNH); 1 male, Homonhon, Eastern Samar, Bitaoagan, 12-v-1988, R. Müller (RMNH); 1 male, Cebu, Lahug, 19-iii-2001, T. Borromeo (RMNH); 1 male, Dinagat, Surigao del Norte, Loreto, Danao lake, vii-1989, A. Buenafe (RMNH); 2 males, Mindanao, Mt Kalatungan, 06-iii-1996, R.A. Müller (RMNH); 1 male, Palawan, Busuanga Island, Coron, Mabentangen River, 04/07-v-1991, T. Borromeo (RMNH); 1 male, Visayas, Samar Island, Oras Municipality, 25/

31-vii-1992, T. Borromeo (RMNH).—Indonesia: 2 males, Kalimantan, Samarinda, 10-xii-1956, A.M.R. Wegner (RMNH); 1 male, West Java, Bantam, Kasemen, 17-v-1957, A.M.R. Wegner (RMNH); 1 male, Sulawesi, Sidaonta Palu, vi-1937, J.M.A. van Groenendaal (RMNH); 1 male, Pulau Panaitan, 03-vii-1955, collector unknown (RMNH); 1 male, Sumatra, Kuta Cane, Tanah Merah, 23-vi-1972 (RMNH); 1 male, Flores, Mborong, 01-iv-1958, A.M.R. Wegner (RMNH); 1 male, Billiton, Manggar, 18-ii-1936, F.J. Kuiper (RMNH).—Peninsular Malaysia: 1 male, Pahang, Krau Wildlife Sanctuary, Bukit Rengit, 5/8-vi-1997, M. Hämäläinen (RMNH).—Thailand: 1 male, Pu Pan NP, Kaengmoddaeng, 18-iv-1996, H. Malicky & P. Chantaramongkol (RMNH); 1 male, Bangkok, Kasetsart, 06/08-vi-1984, M. Hämäläinen (RMNH); 1 male, Chaiyaphum, Phu Khieo Wildlife Sanctuary, 09/10-vi-1984, M. Hämäläinen (RMNH).—India: 1 male, Uttar Pradesh, Doon Valley, Kulhal barrage on river Ahsan, 13-x-1986, M. Hämäläinen (RMNH).—China: 1 male, Guangxi, 7 km SE Guilin, 10-ix-1985, collector unknown (RMNH); 1 male, Fukien, Bohea Hills, 25-vi-1939, T.C. Maa (RMNH); 2 males, Shanghai, 23-vi-1934 and 04-vi-1936, E. Suenson (RMNH); 1 male, Guangdong, Guangzhou, 18-vii-1990, J. Silber (RMNH).

Male diagnosis. Only representative of the genus in Asia, typical of the group lumped formerly under *A. panorpoides* by the (a) extensively white labrum, labium, thorax and underside of S3–7; (b) low number of Fw Ax, typically 7 but varies between 6 and 8; (c) 1 cell in Fw triangle, but 2 cells in 6% of examined wings; (d) fairly long Fw Pt, about 11–14% as long as Hw; (e) abdomen that narrows abruptly on S5 in lateral view, with S6–10 slender (Fig. 7C); (f) fragmented and frayed white markings on S2–5 and large white lateral spots on S7 (Fig. 7C); and (g) broad and triangular lobe of hamule (Fig. 8C). Within this group has the (1) stoutest abdomen, with S6 between 1x and 2x as long as high and a distinct ‘step’ between the ventral borders of S5 and S6 (Fig. 7C). Latter recalls *A. attenboroughi* sp. nov. that also only shares the (2) rather slender hook of the hamule (Fig. 8C); and (3) sublateral black marking concentrated on apical side of S4 (Fig. 7C); but differs by the (4) totally black ventro-apical carina of S4, although this is partly white in about 15% of cases (Fig. 7C). Aside from distribution, unique within the genus by the (5) narrow black band across the antefrons, which is only 10–40% as wide as labrum is high (Fig. 4C–D); (6) labrum with no black or only a very small spot that is typically separated from the base (Fig. 4C–D); and (7) complete distal Ax in 62% of examined Fw.

Range and ecology. Common at marshy habitats from the Indian subcontinent to Japan, the Philippines and Indonesia.

Acisoma attenboroughi sp. nov.—Attenborough’s Pintail

(Figs. 4E, 5A–C, 5F–G, 6E–F, 7D, 8D, 10D, 11)

Type material. Holotype (Fig. 11): male, Andasibe, lake Toamasina, 12-xii-2006, K. Schütte (ZMUH).

Other material. Madagascar: 1 male, Ankarafantsika National Park, Ampijoroa, 06-iii-2001, G. Garcia (RMNH); 1 male, Tananarive, 21-iii-1985, F. Keiser (RMNH); 1 male, locality unknown, 1993, J.M. Elouard (MNHN); 1 male, Madagascar, Coll. Martin (MNHN); 7 males, Andasibe, lake Toamasina, 12-xii-2006, K. Schütte (ZMUH); 5 males, Andasibe, river Toamasina, 12-xii-2006, K. Schütte (ZMUH); 7 males, Fort-Dauphin, Amboavola, 28-xi-2006, K. Schütte (ZMUH); 1 male, Fort-Dauphin, Tsimelaha, 1.5km de accueil, 01-x-2006, K. Schütte (ZMUH); 1 male, Fort-Dauphin, Enato, 26-x-2006, K. Schütte (ZMUH); 1 male, Fianarantsoa, Ranomafana, ValBio field station next to river, 01-xi-2006, K. Schütte (ZMUH); 3 males, Tolongoina, coffee plantation, 10-xi-2006, K. Schütte (ZMUH); 1 male, Tolongoina, tavy in forest, 04-xi-2006, K. Schütte (ZMUH).

Etymology. The new species honours Sir David Attenborough on his 90th birthday. His documentaries inspired entire generations to love and conserve nature (Dijkstra 2016).

Male diagnosis. Confined to Madagascar, where easily identified by the characters typical of the group lumped formerly under *A. panorpoides*: (a) extensively white labrum, labium, thorax and underside of S3–7; (b) 1 cell in Fw triangle; (c) fairly long Fw Pt, about 11–14% as long as Hw; (d) abdomen that narrows abruptly on S5 in lateral view, with S6–10 slender (Fig. 7D); (e) fragmented and frayed white markings on S2–5 and large white lateral spots on S7 (Fig. 7D); and (f) broad and triangular lobe of hamule (Fig. 8D). Unique in the genus by the (1) dorso-central black spot on the mesepisternum that is shifted toward and fused with the black humeral stripe (Fig. 6 E–F); and (2) S4 typically with all black ventral carina but partly white ventro-apical carina, although the latter is all black in about 10% of cases (Fig. 7D). The shape and general appearance is intermediate between *A. panorpoides* from Asia and *A. inflatum* from Africa, with a (3) stout abdomen, with S6 about 1.5x to 2x as long as

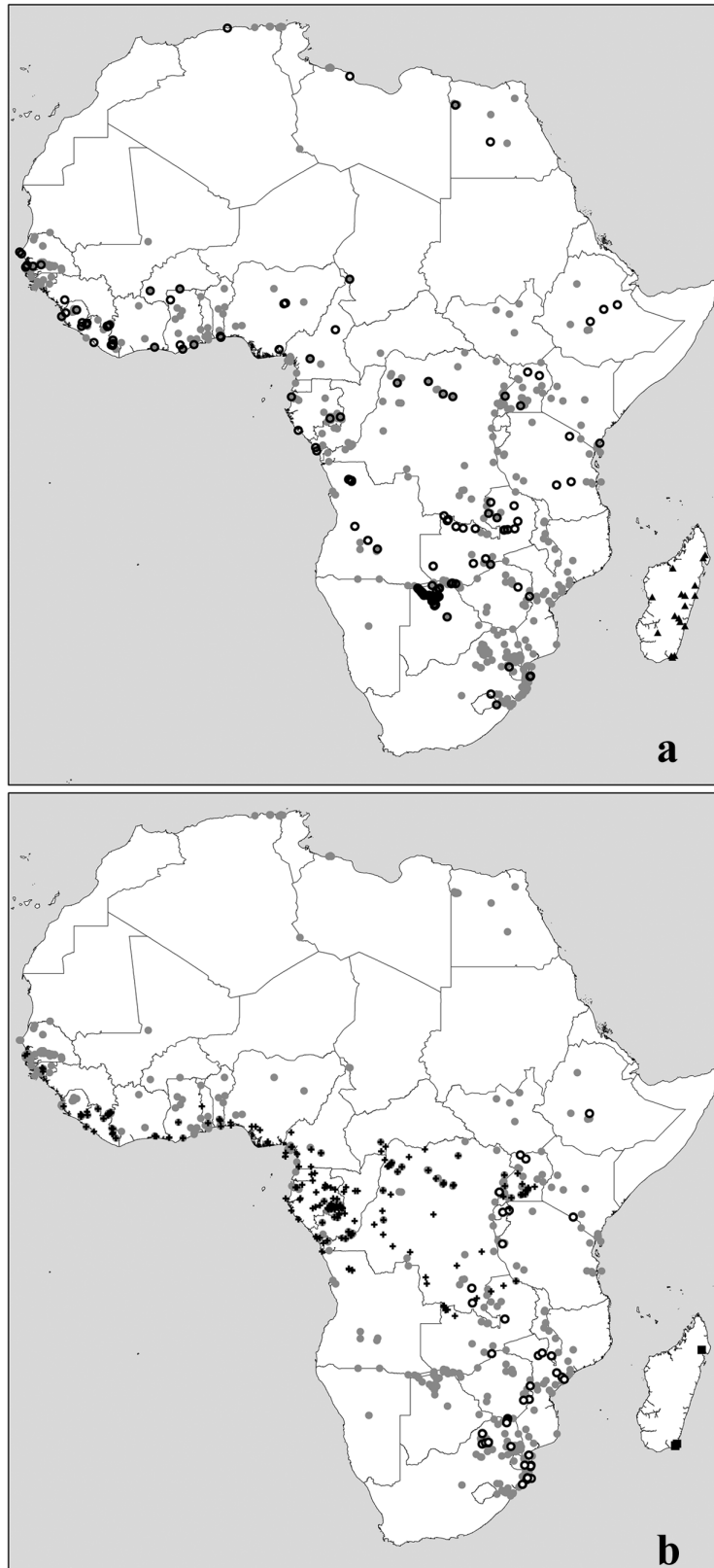


FIGURE 9. Distribution of Afrotropical *Acisoma* species based on examined specimens and verified records in Odonata Database of Africa (see supplementary materials): A: *A. inflatum* (circles), *A. attenboroughi* (triangles), unverified records of *A. inflatum* or *A. variegatum* (grey dots); B: *A. variegatum* (circles), *A. ascalaphoides* (squares), *A. trifoldum* (crosses), unverified records of *A. inflatum* or *A. variegatum* (grey dots). All records are provided in Suppl. Tab. 1 available from <https://science.naturalis.nl/dijkstra>.



FIGURE 10. Male habitus of *Acisoma* species. A: *A. variegatum* South Africa, 21-ii-2007 (mature), B: *A. inflatum*, The Gambia, 30-xi-2010 (mature), C: *A. panorpoides*, Hong Kong, China, 26-x-2011 (shortly after emergence, colours not fully developed), D: *A. attenboroughi*, Vohiparara, Madagascar, 13-i-2016, E: *A. ascalaphoides*, Sainte Luce, Madagascar, 19-x-2006 (mature), F: *A. trifidum*, Moanda, Gabon, 22-v-2013 (mature). Note characters such as the slender abdomen of *A. variegatum*, pale face and ventral ‘step’ between S5–6 in *A. panorpoides*, and shifted dorso-central black spot on mesepisternum in *A. attenboroughi*. Photographs by Wil Leurs (A–B), Erland Nielsen (C), Kai Schütte (E), Netta Smith (D) and Nicolas Mézière (F).



FIGURE 11. Holotype of *Acisoma attenboroughi* sp. nov., ZMUH.

high, and a fairly distinct ‘step’ between the ventral borders of S5 and S6 (Fig. 7D). Differs from *A. panorpoides* by the (4) wide black band across the antefrons, which is 40–80% as wide as the labrum is high (Fig. 4E); (5) large black spot on the labrum attached to its base (Fig. 4E); and (6) always incomplete distal Ax in Fw; and from *A. inflatum* by the (7) sublateral black marking concentrated on apical side of S4 (Fig. 7D); and (8) more slender hook of the hamule (Fig. 8D).

Range and ecology. Widespread across Madagascar, including the interior, at weedy ponds such as abandoned rice fields. Found down to the coast in the east (Toamasina, Tolagnaro) and west (Mahajanga) but not in the littoral forests where *A. ascalaphoides* occurs (Fig. 9A).

***Acisoma ascalaphoides* Rambur, 1842—Littoral Pintail**

(Figs. 4F, 5H, 6G, 7E, 8E, 10E)

Material. Madagascar: 3 male, Maroantsetra, Voloina, 30-xii-1971, P. & J. Minet (MNHN); 2 males, Tolagnaro, Mandena, 12-ii-2004/19-iii-2004, K. Schütte (RMNH); 4 males, Tolagnaro, Sainte Luce, Akaifira, 02-xii-2006, K. Schütte (ZMUH); 1 male, Tolagnaro, Sainte Luce, S8, forest, marecage, 18-x-2006, K. Schütte (ZMUH); 1 male, Tolagnaro, Sainte Luce, S9, marecage west, 01-iv-2004, P. Razafindraibe (ZMUH); 2 males, Tolagnaro, Mandena, bridge from M15 to M16, 13-x-2006, K. Schütte (ZMUH); 1 male, Tolagnaro, Mandena (Citronelle), 13-x-2006, K. Schütte (ZMUH); 5 males, Tolagnaro, Mandena, 17-iii-2004/18-iii-2004/ 19-iii-2004/ 22-iii-2004/ 27-iii-2004, P. Razafindraibe (ZMUH); 1 male, Tolagnaro, Mandena, marecage, 12-ii-2004, K. Schütte (ZMUH).

Male diagnosis. Distinctive species confined to the east coast of Madagascar that appears somewhat intermediate between *A. trifidum* and the species formerly treated under *A. panorpoidea*. Its unique characters are the (1) uniformly brown antefrons, clypeus, labrum and labium (Fig. 4F, 5H); (2) largely brown thorax with faint and limited paler markings (Fig. 6G); (3) mostly 2 cells in Fw triangle, although 37% of examined wings with 1 cell; (4) abdomen that narrows most on S5–6 while S7–10 are slender (Fig. 7E); (5) ventrally entirely dark abdomen with extensive dorsal white markings only on S3–6, which are solid and clean-cut but not confluent across dorsal carina (Fig. 7E); (6) narrow lobe of hamule with notched tip (Fig. 8E); and (7) black dorsum of cerci, not largely white (Fig. 7E). Similar only to *A. trifidum* are the (8) more numerous Fw Ax, usually 8½ but occasionally 8 or 9½.

Range and ecology. Known only from littoral forest fragments at the southern (Tolagnaro, formerly Fort Dauphin) and northern (Voloina) ends of Madagascar's east coast (Fig. 9B). Only about 10% of the original cover of these forests remains, all in small patches of which only 13% are protected (Consiglio *et al.* 2006). The species may occur elsewhere along the coast, but as it seems restricted to this habitat, could well be under threat (Schütte & Razafindraibe 2007). The larvae are possibly adapted to more acidic water than *A. attenboroughi* **sp. nov.**

***Acisoma trifidum* Kirby, 1889—Pied Pintail**

(Figs. 4G, 5I, 6H, 7F, 8F, 10F)

Material. D.R. Congo: 3 males, Orientale, Yaekela, 01/02-v-2010, K.-D.B. Dijkstra (RMNH); 1 male, Orientale, 9 km E of Kisangani, Old Buta road, 09-vi-2010, K.-D.B. Dijkstra (RMNH); 1 male, Orientale, East of Isangi, Yandja Rive to Yandja Lac, 06-v-2010, K.-D.B. Dijkstra (RMNH).—Congo: 2 males, Region de Kouilou, Conkouati National Park, 21/22-ii-2010, P. Lambret (RMNH).—Liberia, 2 males, Mt Tokadeh, 29-ix/02-x-2010 and 01-i-2011, K.-D.B. Dijkstra (RMNH); 1 male, northern bank Yah (Dayea) River near Gbapa, 05-i-2011, K.-D.B. Dijkstra (RMNH).—Angola: 1 male, 9 km WNW of Uíge, Cassanga stream and adjacent swamp, 17-xi-2012, V. Clausnitzer & K.-D.B. Dijkstra (RMNH); 1 male, 8 km SE of Negage, Gilangole stream, 25-xi-2012, K.-D.B. Dijkstra (RMNH).—Gabon: 1 male, Haut-Ogoué, Moanda, 24-iv-2009, N. Mézière & C. Vanappelghem (RMNH); 1 male, Haut-Ogoué, Plateau d'Okouma, Mounana, 01-vii-2009, N. Mézière (RMNH); 1 male, Moanda, 28-xi-2008, N. Mézière (RMNH).—Sierra Leone: 1 male, Eastern Province, Gola forest, 500 m north-east of Vaama, 08-iii-2011, K.-D.B. Dijkstra (RMNH).—Ghana: 1 male, Central Region, 12 km NW of Cape Coast, Brimsu Dam, 20-iv-2000, K.-D.B. Dijkstra (RMNH).—Benin: 1 male, 18 ESE of Zogbodomé, Sous-préfecture de Zogbodomé, Forêt de Lokoli, 09-vii-2002, S.L. Tchiboza (RMNH).—Gambia: 1 male, Brufut-Tanji, 16-xii-1980, M. Hämäläinen (RMNH).

Male diagnosis. The most distinctive species, confined to the more forested parts of equatorial Africa, with the following unique characters: (1) labrum black, only with two small white spots at base (Fig. 4G); (2) labium black, only with two large white spots on sides (Fig. 5I); (3) thorax largely black with limited and fragmented pale markings (Fig. 6H); (4) mostly 3 cells in Fw triangle, but 43% of examined wings with 2 cells; (5) generally shorter Fw Pt, about 10–12% as long as Hw; (6) abdomen dorsoventrally rather than laterally compressed, narrowing most visibly in dorsal view and most marked on S7, thus only S8–10 slender, with S7–8 of similar and intermediate length as S6 and S9, rather than both distinctly longer (Fig. 7F); (7) abdomen with solid and clean-cut white markings on S3–6, largely confluent across dorsal carina on S3–5, and bold ventral white spots on S4–5 (Fig. 7F); (8) lobe of hamule narrow and pointed (Fig. 8F). Similar only to *A. ascalaphoides* are the (9) more numerous Fw Ax, invariably 8½ or 9½.

Range and ecology. Occurs throughout western and central Africa, from Senegal to Uganda, Rwanda and northern Zambia, favouring more forested ponds than the frequently coexisting *A. inflatum* (Fig. 9B).

TABLE 2. Comparison of the *Acisoma* species. All measurements are given as average and (in brackets) range. Ratios between the lengths of abdominal carinae are given as percentages (Fig. 1).

Species (n=)	<i>A. variegatum</i> (24)	<i>A. inflatum</i> (31)	<i>A. panorpoides</i> (26)	<i>A. attenboroughi</i> (18)	<i>A. ascalaphoides</i> (20)
Antefrons (Fig. 4)	black band 40-70% as wide as labrum is high	black band typically 40-60% as wide as labrum is high; but 10% in 1 specimen	black band 10-40% as wide as labrum is high	black band 40-80% as wide as labrum is high	brown, with colour extending onto clypeus
Labrum (Fig. 4)	white, with one small black spot at base	white, with one small black spot at base	white, typically with tiny black spot loose of base, but no spot in 38% and basal black spot in 12%	white, with one small black spot at base	all brown
Central lobe of labium (Fig. 5)	partly white	typically totally black; but partly white in 10%	partly white	typically partly white; but totally black in 17%	brown
Lateral lobes of labium (Fig. 5)	white, centrally narrowly black	white, centrally broadly to narrowly black	white, centrally narrowly black	white, centrally broadly to narrowly black	entirely brown
Thorax (Fig. 6)	typically predominantly pale, but darker in 29%	typically predominantly dark, but paler in 13%	typically predominantly pale, but darker in 8%	predominantly pale in 56% and dark in 44%	uniform brown with faint paler pattern
Dorso-central black spot on mesepisternum (Fig. 6)	typically free; but attached to humeral stripe in 4%	typically free; but attached to humeral stripe in 10%	typically free; but attached to humeral stripe in 4%	shifted towards and always attached to humeral stripe	not distinct, as thorax is diffuse brown
Length Hw (mm)	22.7 (21.0-24.5)	19.4 (16.0-23.5)	20.6 (19.0-25.0)	23.5 (20.9-25.0)	23.0 (21.6-25.0)
Cells in subtriangle	1 although 2 in 24%	1 although 2 in 11%	1 although 2 in 6%	Always 1	2 although 1 in 37%
Number of subcostal (i.e. complete) Fw Ax	7.26 (7-8)	7.03 (6-8)	6.87 (6-8)	7.53 (7-8)	8.11 (8-9)

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Table 2. continued

Species (n=)	<i>A. variegatum</i> (24)	<i>A. inflatum</i> (31)	<i>A. panorpoides</i> (26)	<i>A. attenboroughi</i> (18)	<i>A. ascalaphoides</i> (20)	<i>A. trifidum</i> (20)
Last Fw Ax incomplete (lacks subcostal section)	in 100%	in 97%	in 38%	in 100%	in 89%	in 100%
FwPv/Hw	14.11% (13.18-15.79%)	14.27% (11.56-16.11%)	12.37% (10.81-14.14%)	12.79% (11.59-14.00%)	11.56% (10.48-13.04%)	11.19% (10.31-12.24%)
Lobe of hamule (Fig. 8)	broad and triangular, externally often white	broad and triangular, externally always black	broad and triangular, externally often black	broad and triangular, externally black or white	narrow and notched, externally always black	narrow and pointed, externally always black
Hook of hamule (Fig. 8)	wide at base, abruptly curved	wide at base, gradually curved	slender, gradually curved	slender, abruptly curved	wide at base, gradually curved	wide at base, gradually curved
Ventral white markings present on S3-5 (Fig. 7)	at least S3-5	at least S3-5	at least S3-5	at least S3-5	absent	only S4-5
Emphasis of sublateral black marking S4 (Fig. 7)	at base	at base	at apex	at apex	absent	absent
Ventral carina S4 (Fig. 7)	partly white, but all black in 4%	black	black	black	black	black
Ventro-apical carina S4 (Fig. 7)	partly white	typically black, but partly white in 19%	typically black, but partly white in 15%	typically partly white, but totally black in 11%	always black	always black
Ventro-apical carina S4 where it meets ventral carina S4 (Fig. 7)	always white	always black	typically black, but white in 8%	typically white, but black in 39%	always black	always black

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Table 2. continued

Species (n=)	<i>A. variegatum</i> (24)	<i>A. inflatum</i> (31)	<i>A. panorpoides</i> (26)	<i>A. attenboroughi</i> (18)	<i>A. ascalaphoides</i> (20)	<i>A. trifidum</i> (20)
Lateral carina S5 (Fig. 7)	largely white	largely or entirely black, but largely white in 3%	largely or entirely black	largely or entirely black	entirely black	entirely black
Narrowing of abdomen in lateral view (Fig. 7)	abrupt on S5	abrupt on S5	abrupt on S5	abrupt on S5	abrupt on S5-6	gradual throughout
S5: dorso-basal / dorsal carina* (Fig. 7)	61% (52-68%)	88% (79-105%)	98% (90-106%)	91% (62-105%)	112% (91-130%)	87% (76-100%)
S5: ventro-apical / lateral carina* (Fig. 7)	22% (19-26%)	40% (26-47%)	52% (43-63%)	44% (38-52%)	52% (53-58%)	48% (41-54%)
S6: dorso-basal / dorsal carina* (Fig. 7)	30% (26-36%)	47% (36-57%)	64% (52-75%)	58% (48-65%)	81% (67-90%)	84% (76-95%)
Apical border of white marking on S6 (Fig. 7)	distinctly skewed dorsally	typically moderately skewed dorsally or ventrally, but rounded in 13%	rounded	rounded	rounded	distinctly skewed ventrally
S7 (Fig. 7)	with one large lateral white spot	with one large lateral white spot	with one large lateral white spot	with one large lateral white spot	with two small white spots laterally	typically no white spots, but small dorsal spot in 10%
Base of S8 (Fig. 7)	typically with two white spots, but in 21% one or no spots	always one white spot	typically no spots, but in 31% one or two white spots	typically one white spot, but in 33% no spots	typically one white spot, but in 10% no spots	typically no spots, but in 10% one spot

Acknowledgements

Wil Leurs, Nicolas Mézière, Erland Nielsen and Netta Smith supplied field photographs and Jens Kipping records from the Odonata Database of Africa. Jean-Pierre Boudot provided comments on the description date of *A. inflatum*. Thure Dalsgaard imaged specimens. Bettina Scheel helped with lab work and Ralph Peters with preliminary genetic analysis. Molecular work at the Naturalis Biodiversity Center was enabled by a grant of the Economic Structure Enhancement Fund, and analyses were supported by Camiel Doorendeerd. Pierre Razafindraibe and Refaly Ernest assisted with field collections in Madagascar, where the Ministère de l'Environnement, des Eaux et Forêt provided collection and export permits.

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