Gone with the wind: westward dispersal across the Indian Ocean and island speciation in *Hemicordulia* dragonflies (Odonata: Corduliidae)

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Abstract

The taxonomy and biogeography of the western representatives of the largely Papuan-Australian genus *Hemicordulia* are discussed and compared with other alate fauna including butterflies, birds, bats and other dragonflies. Specimens from Malawi, Mozambique, Réunion, South Africa, Tanzania and Uganda were compared with Indian specimens of *H. asiatica*, with which they were previously regarded conspecific. They are found to be distinct and are described as the continental *H. africana* **n. sp.** and those from Réunion as *H. atrovirens* **n. sp.** The three species were compared with *H. similis* of Madagascar and *H. virens* of Mauritius. Insufficient material of the Seychelles taxon *H. similis delicata* was available; it may represent another insular endemic species. The distribution of *Hemicordulia* is discussed in the light of the dispersal capacity of Odonata and the biogeography of taxa with similar distributions in the region, with an emphasis on the survival of 'oceanic' species on the continent. Recent (i.e. in the last few million years) trans-oceanic airborne dispersal aided by westward storms, is the most likely explanation for the distribution of the genus in Africa and the Indian Ocean islands, as well as for other winged animals of Asian affinities in the region. The world range of *Hemicordulia* is largely insular, broadly excluding continents, and *H. africana* **n. sp.** demonstrates 'inverted insularity': all continental sites are in proximity to large water bodies, such as the great African lakes. This pattern may be related to the climatological instability of these sites, which offer suitable cool habitat where competition is (temporarily) reduced. *Hemicordulia* prefer cool conditions, but may be vulnerable to overheating and competition with more warm-adapted species.

Key words: Anisoptera, *Hemicordulia*, Africa, India, Indian Ocean islands, taxonomy, biogeography, key

Introduction

"The […] possibility can immediately be ruled out on good reasons: both the behavioural characteristics and habitat preference of this non-migrating, forest-dwelling […] species are fully incompatible with long-range flight over open seas. Hypothetically, only natural disasters like volcanic eruptions or tidal waves could force survivors […] to suddenly leave their habitats, and this too, only soon to reach the nearest safe forest habitat […]. Neither are the prevailing systems of trade winds […] in the Indian Ocean […] in any way favourable to transport viable propagules […] from the nearest landmass in the indo-malayan region to Madagascar."

Farkas's (1985) emphatic dismissal of westwards trans-oceanic dispersal of an alate forest animal, the passerine genus *Copsychus* in his case (Fig. 21), neatly summarises the opposition against the notion that eastern elements of the terrestrial fauna in the western Indian Ocean may have arrived airborne. Nonetheless, avian examples alone suggest that such dispersal from Asia towards Africa may be frequent (Keith 1980). Louette (1987) hypothesised that several overseas colonisations of the passerine genus *Hypsipetes* from India to Madagascar and surrounding islands gave rise to five similar species (Fig. 22). Phylogenetic reconstructions place Indian Ocean *Hypsipetes* and *Copsychus* within Asian radiations of their families (Farkas 1985; Jønsson & Fjeldså 2006; Moyle & Marks 2006). Thomassen *et al.* (2005) found the nearest relatives of Sey-

chelles and Mascarene endemic *Collocalia* swiftlets in the genus's centre of diversity in Sundaland, but did not sample species occurring in the Himalayas and southern India (Fig. 20). Groombridge *et al.* (2004) found molecular support for the trans-oceanic colonisation of Mauritius by a *Psittacula* parakeet from India, although samples of extinct species from the Seychelles and Rodrigues were unavailable. Of other alate fauna, about fifty *Pteropus* fruit bat species inhabit Australasia and the Pacific, while nine endemic taxa occupy all major Indian Ocean islands up to those on the Tanzanian coast (Bergmans 1990; Fig. 23). Preliminary phylogenetic results are compatible with long-range trans-oceanic dispersal from the east (Colgan & da Costa 2002; Giannini & Simmons 2003; Juste B. *et al.* 1999; O'Brien & Hayden 2004). Two endemic *Euploea* butterflies in the Seychelles and Mascarenes are western isolates of a large tropical Australasian genus, but their phylogeny is poorly resolved (Ackery & Vane-Wright 1984).

The distribution of the dragonfly genus *Hemicordulia* Selys (including the closely related *Procordulia* Martin) is similar to that of *Pteropus* (Fig. 18). The highest number of over fifty species and their greatest morphological and ecological variation is found in New Guinea and Australia (van Tol 1997; Tsuda 2000). Some species are strong migrants that are among the most abundant Papuan-Australian dragonflies, others are adapted to extreme habitats like isolated desert pools and high-altitude lakes or are endemic to remote oceanic islands (e.g. Asahina 1940; Lieftinck 1962). Outside Australia the group is local on continents, together accounting for less than one-tenth of known species. For instance, there are no records from mainland China, although *Hemicordulia* extends to Taiwan and the Ryukyus. The group ranges across the Pacific to New Zealand, French Polynesia and the Bonin Islands, and across the Indian Ocean to the Seychelles, Mascarenes and Madagascar. Pinhey (1961) first reported the Indian species *H. asiatica* (Selys) from eastern Africa, stating that "as Fraser has remarked to me, there seems to be no difference between Uganda and Indian examples". Couteyen & Papazian (2000) recorded the species from Réunion. However, similar populations found in-between, were treated as distinct species, with *H. virens* (Rambur) on Mauritius and *H. similis* (Rambur) on Madagascar and the Seychelles. The western distribution of *Hemicordulia* and the other groups, raises the question of their origin. Lieftinck (1942) described *Hemicordulia* as "one of the few 'modern' or ectogenic, Australian dragonflies that, having passed northward into the Papuan region, has spread far and wide beyond its Australian zoocentre. As is clearly shown by its distribution, the genus has most decided powers of dispersal but not generally a wide specific range." Fraser (1949) also wrote of "strong migratory tendencies", adding that "the genus is essentially a Papuan one, […] *H. asiatica* […] has extended into continental Asia […]. Two others, concerning which there is good evidence to show that they are lineal descendants of *H. asiatica*, are found in the Mascarene Islands and Madagascar [*H. virens*, *H. similis*]". On finding '*H. asiatica*' in South Africa, Pinhey (1985) indicated it was "possibly a migrant" but refrained from suggesting its origin. Van Tol (1997) found Fraser's remarks "in support of an Indo-Australian origin of the genus, with westward migration in a later phase" and Donnelly & Parr (2003) also stressed that *Hemicordulia* "seems to have wide powers of dispersal, and its occurrence in Madagascar (and in Africa, as well) suggests an origin from the east."

In Odonata, the distribution of *Hemicordulia* is mirrored by several groups (Fig. 26), especially the coenagrionid genus *Teinobasis* Kirby (Donnelly & Parr 2003; Fig. 19). Its less extensive range has a western Pacific centre of diversity, with a scattering of insular endemics (e.g. Paulson & Buden 2003). The genus is peripheral on continents, but *T. alluaudi* (Martin) occurs in the Seychelles, Madagascar and East Africa (Clausnitzer 2003). The south-eastern African aeshnid *Gynacantha immaculifrons* Fraser is related to endemics of the Seychelles, Madagascar and the Mascarenes, but their possible Oriental affinities are unresolved (Dijkstra 2005). Dijkstra *et al.* (2007) argued that the Comoros and Pemba (just off the Tanzanian coast) were colonised on two separate events by *Platycnemis* Burmeister damselflies from Madagascar, possibly crossing 1000 km of sea with the strong monsoon that follows the East African coast. Similar distributions in other freshwater insects, possibly established "with the aid of cyclones", are seen in *Aulonocnemis* beetles and *Setodes* and *Potamyia* caddisflies (Gibon 2003; Paulian & Viette 2003).

An emphasis on vicariance has led to the neglect of oceanic dispersal as a major factor in biogeography, in part because such dispersal is considered almost impossible to falsify: as dispersal can potentially explain any pattern, it could conclusively explain no pattern in particular (McGlone 2005). This has led to the arbitrary situation in which dispersal is generally accepted for oceanic islands, for lack of alternatives, but denied for continents and continental islands (de Queiroz 2005). Sanmartín & Ronquist (2004) found a general temporal and spatial mismatch between phylogenies of trans-oceanic groups and Gondwanan vicariance, although this was less pronounced for animals than plants, which were considered less vagile. However, winged fauna such as Odonata, may be equally mobile as these often wind-dispersed plants. Moreover, the direction of oceanic dispersal is not necessarily random. Muñoz *et al.* (2004) demonstrated that distribution patterns of cryptogams on sub-Antarctic islands were better explained by the direction of prevailing winds, than by their geographic proximities. Considering the dispersive heterogeneity of the studied taxa, they implied that wind transport in lower atmospheric layers should work for many other groups, including arthropods. Gillespie & Roderick (2002) considered that "butterflies and other large insects, such as dragonflies and sphinx moths, may have a wider range of dispersal than most insect groups" and found a good correlation between proportions of insect groups trapped in aerial nets over the ocean and those that make up oceanic island faunas. Zakharov *et al.* (2004) concluded that prevailing winds favour dispersal from Asia to the western Indian Ocean and from Madagascar to Africa, especially for vagile taxa such as large butterflies. This paper examines the anomalous distribution and taxonomy of western Indian Ocean *Hemicordulia* and discusses its origin in the light of the revived emphasis on long-distance dispersal in biogeography.

Method and material

The investigation of African '*H. asiatica*' was prompted by a note in the BMNH: "Pinhey calls these [three Ugandan specimens] *asiatica* Selys, I think they are a new species. Anal app[endages] and pt[erostigma] different. (C. Longfield 1955.)". Lieftinck (1962) wrote that *Hemicordulia* species "are much alike and extremely difficult to distinguish. Males can best be separated by slight differences in the genital organs, anal appendages, length of posterior femur and tibial keels; females, by the pubescence of the occiput, length and shape of the anal appendages, and wing color; both sexes in combination, by color, body size and (occasionally) venation." The Indian Ocean species can best be distinguished by the shape of the vulvar scale (Fraser 1949). I examined material of both sexes (see lists under species) of African and Asian '*H. asiatica*' for these and potential additional characters and, with this comparison as calibration, also the insular taxa *H. similis* and *H. virens*. Most western species are elusive and local; specimens are almost exclusively collected while hunting in open spaces in forest (e.g. Fraser 1936; Pinhey 1966; 1976). Therefore an effort was made to examine as many specimens as possible.

Abbreviations

Ax: antenodal cross-veins; Ax1: first antenodal (counted from base) etc.; Cux: cubital cross-vein; Fw: forewing(s); Hw: hindwing(s); Pt: pterostigma; Px: postnodal cross-veins; S1: first abdominal segment; S2–3: second and third abdominal segments etc.

Acronyms for collections

BMNH: Natural History Museum, London; ISNB: Institut Royal des Sciences Naturelles de Belgique, Brussels; MNHN: Muséum National d'Histoire Naturelle, Paris; NHRS: Naturhistoriska Riksmuseet, Stockholm; NMBZ: Natural History Museum of Zimbabwe, Bulawayo; NMKE: National Museums of Kenya, Nairobi; RMNH: Nationaal Natuurhistorisch Museum Naturalis, Leiden; SUEC: Stellenbosch University Entomology Collection, Stellenbosch; UMO: University Museum, Hope Entomological Collections, Oxford;

ZMMU: Zoological Museum of Makerere University, Kampala; ZMUH: Zoologisches Institut und Zoologisches Museum, Universität von Hamburg, Hamburg.

Results

Consistent differences were found between African and Asian '*H. asiatica*', especially in the shape of the male cerci and female vulvar scale, which were sufficient to regard them as distinct species (Table 1). No differences were found in the hamule, femora, tibiae and female cerci. The African '*H. asiatica*' was similar to Madagascan *H. similis* and Réunion '*H. asiatica*' to *H. virens* of nearby Mauritius, but the species in each pair were distinct by coloration (Table 2, Key). With all diagnosable entities confined to defined geographic areas, each is best treated as a species. Thus five species occur west of the Gulf of Bengal, which are discussed below ordered from east to west.

TABLE 1. Comparison of *Hemicordulia africana* **n. sp.** ('*H. asiatica*' from continental Africa) with typical *H. asiatica* from Asia (see Table 2 for measurements).

Character	Comparison
Size	Smaller, only 12.5% of *africana* and 17.6% of *asiatica* males had overlapping Hw lengths. Corresponding lower Px counts with mode of 5 (average 5.17) versus 6 (5.67).
Frons (♂)	Metallic green restricted to upper half of rough area on frons, leaving lower half yellow (best seen in dorsal view, where yellow is visible anteriorly). In *asiatica* green extends ventrally to cover entire rough area, leaving only smooth portion bordering postclypeus free.
Occiput (♀)	Paired rounded swellings bear a cluster of short thick brown bristles on each side, besides long pale hairs. These clusters are absent in *asiatica*.
Synthorax	Less intensely metallic green and pale markings more extensive. Markings of both species are extremely variable and their interpretation is complicated by age-related melanisation and often weak contrast between metallic (melanised) and pale (less melanised) parts. Teneral specimens are largely pale. Mature *asiatica* males tend to be more strongly melanised on synthorax. This results in more extensive areas of a deeper green, with a more brightly metallic lustre, which contrasts more sharply with less melanised parts.
Abdomen	Pale markings on abdomen less extensive, in contrast to state of synthorax. There is much variation and mature males may loose pale markings almost completely. *Asiatica* has prominent pale lateral markings on S2–7 or S2–8. In *africana* markings on S2–3 are much reduced, those on S4–5 are barely discernible (infused with melanin) or absent, and those on S6–8 tend to be clear. As darkening progresses, *asiatica* males loose marking on S8 before those on S5–6, the reverse in *africana*. A typical *asiatica* male thus has a string of pale marks from abdomen base to S7, whereas *africana* has an isolated string on S5–8 or S6–8. Females (in which pale markings are more extensive) differ in a similar way, the markings on S2–5 being relatively reduced in *africana*.
Pterostigma	Pt marginally shorter, an impression emphasised by small size. Fw Pt length was 13.2% (12.5–13.8) of the postnodal wing half in *africana* (n=10) and 14.2% (12.5–15.3) in *asiatica* (n=10).
Wing colour (♀)	Yellow in wing bases more extensive, up to arculus or even Ax2 in Fw and Hw in *africana*, whereas virtually indiscernible in Fw and at most a little past Hw Cux in *asiatica*.
Cerci (♂)	More slender and sinuous in dorsal view (Fig. 6). Rather thick halfway in *asiatica*, the outer border being less strongly curved inwards (Fig. 2). In lateral view ventral border is evenly concave in *asiatica* (Fig. 7), but has a distinctly convex bulge at midpoint in *africana* (Fig. 11).
Vulvar scale (♀)	Incision narrower, its sides nearly parallel: angle between them being 10–30° in *africana* (Fig. 17) versus 35–55° in *asiatica* (Fig. 12). Scale protrudes slightly further over sternite of S9, reaching 35–45% down sternite in *africana* versus 30–35% in *asiatica*.

Systematic part

Hemicordulia **Selys**

Cordulia nec Leach, 1815 – Rambur (1842: 146).
Cordulia (*Hemicordulia*) Selys, 1870: v [type species: *Cordulia australiae* Rambur, 1842; by original designation].
Hemicordulia Selys, 1870 – Kirby (1890: 46).

Diagnosis. The genus combines characters typical of Corduliidae with reductions shared with Libellulidae. 'Corduliid' features are: (1) posterior margin of eyes infracted; (2) male hind tibiae keeled; (3) S2–3 without transverse subbasal ridges; (4) body largely metallic green. 'Libellulid' features are: (1) anal triangle and angle of Hw reduced in males; (2) auricles on S2 reduced in males. Aside from aforementioned 'libellulid' features, a combination of venation characters in unique among Afrotropical 'corduliids': (1) only 6–9 Ax in Fw; (2) arculus lies between Ax1–2; (3) Hw arculus more or less aligned with proximal border of triangle; (4) only one bridge cross-vein in all wings; (5) supratriangles without cross-veins; (6) Hw with only one Cux; (7) subtriangle of 3 cells; (8) anal loop boot-shaped. The separation of the closely related Australasian genus *Procordulia*, which has an anal triangle, is not well resolved (van Tol 1997).

Key to Afrotropical *Hemicordulia* species

1 Fw usually with 8 Ax and 7 Px. Vulvar scale covering less than one third of sternite S9, not reaching paired processes on sternite (Figs 13–14). ♀ occiput only with long pale hairs. Distal third of ♂ cerci almost parallel-sided, tips abrubtly rounded (Figs 3–4, 8–9). Hw 32–38 mm in ♂, 35–39 in ♀. Mascarene Islands 2
- Fw usually with 7 Ax and 5 Px. Vulvar scale covering over one third of sternite S9, extending over bases of paired processes (Figs 16–17). ♀ occiput with cluster of short thick brown bristles on each side, in addition to long pale hairs. Distal third of ♂ cerci tapering to a blunt point (Figs 5–6, 10–11). Hw 27–32 mm in ♂, 28–33 in ♀. Africa, Madagascar and Seychelles 3
2 Yellow anterior to metallic area on frons not visible in dorsal view (perhaps marginally in ♀). Fore femora predominantly black. Synthorax predominantly metallic green. S6–8 entirely dark. Réunion.....................
   .... *atrovirens* **n. sp.**
- Yellow anterior to metallic area on frons visible in dorsal view. Fore femora predominantly yellow. Synthorax predominantly yellow. S6–8 dark with yellow lateral spots. Mauritius.....................................*virens*
3 Yellow anterior to metallic area on frons not visible in dorsal view (perhaps marginally in ♀). Labrum with two dark blotches at base. ♀ Hw at most yellow to Cux and Ax1, yellow almost absent in Fw. Madagascar and Seychelles ....similis
- Yellow anterior to metallic area on frons visible in dorsal view. Labrum all yellow. ♀ Fw and Hw at least yellow to arculus. Continental Africa...*africana* **n. sp.**
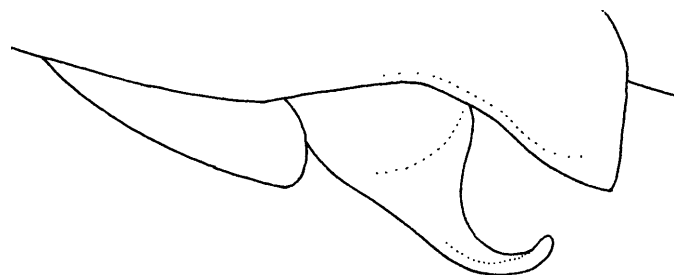

FIGURE 1. Secondary genitalia of *Hemicordulia africana* **n. sp.** in lateral view.

Hemicordulia asiatica (Selys)

Figs 2, 7, 12.

Cordulia (Hemicordulia) asiatica Selys, 1878: 186 (bulletin), 8 (reprint). Holotype ♂ with labels: handwritten "Khasiya Hills [India]", yellow, printed "Atkinson", handwritten by Selys "Hemicordulia asiatica S ♂", printed and handwritten by Martin "Collection Selys, Hemicordulia asiatica Sel. Type, Révision Martin 1906 Hemicordulia asiatica Sel.", printed red and handwritten by Martin "Type Hemicordulia asiatica Sel." (ISNB) [examined].

Hemicordulia asiatica (Selys, 1878) – Kirby (1890: 47).
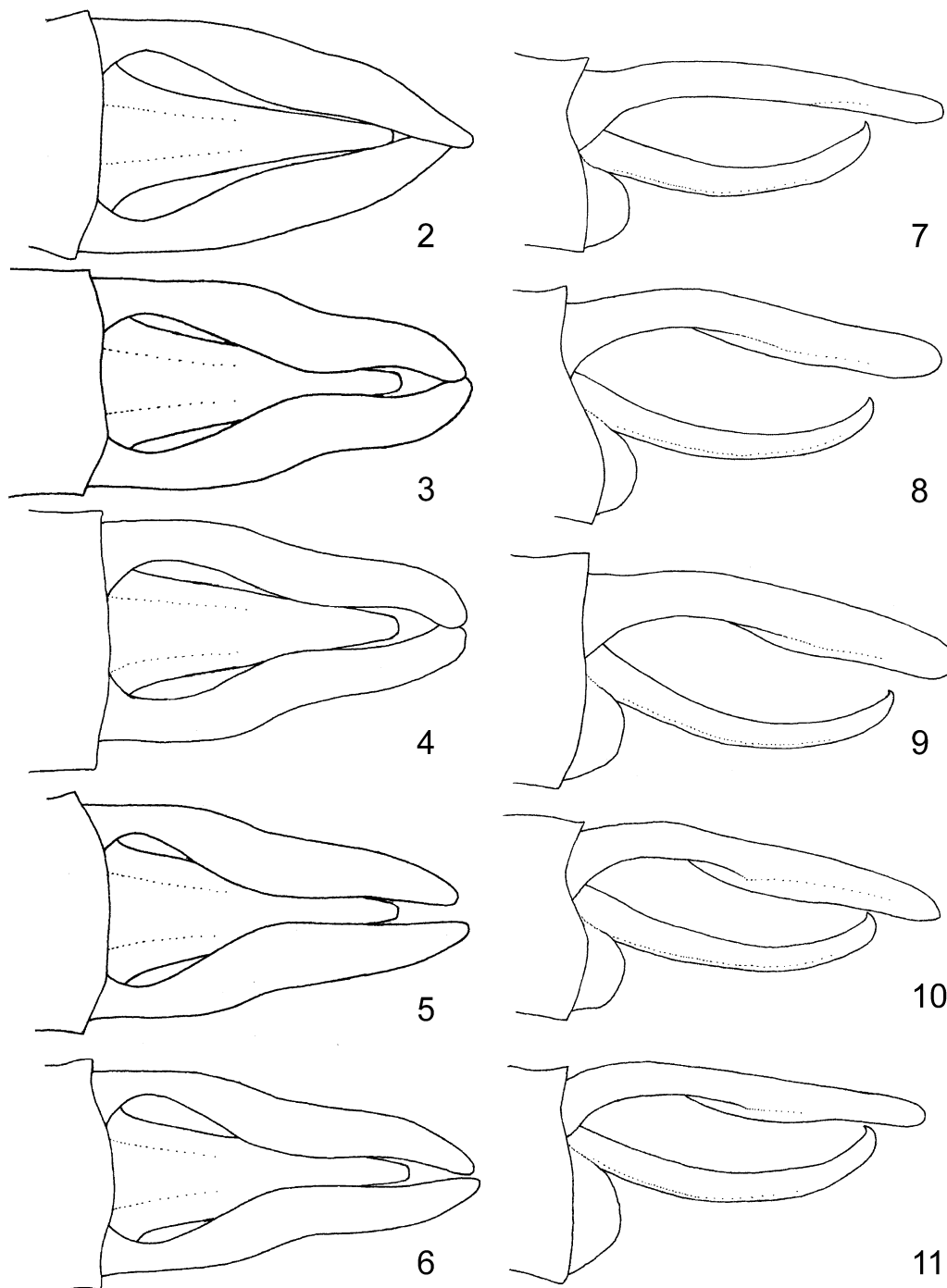
FIGURES 2–11. 2–6, Male appendages of *Hemicordulia* species in dorsal view. (2) *H. asiatica*; (3) *H. virens*; (4) *H. atrovirens* **n. sp.**; (5) *H. similis*; (6) *H. africana* **n. sp.; 7–11,** Male appendages of *Hemicordulia* species in lateral view. (7) *H. asiatica*; (8) *H. virens*; (9) *H. atrovirens* **n. sp.**; (10) *H. similis*; (11) *H. africana* **n. sp.**

Further material: INDIA (Karnataka): 1 ♂, Coorg, Fraserpet [= Kushalnagar]-Mercara Road, 3000 ft. (= 915 m), 25.v.1923, F.C. Fraser (BMNH). – INDIA (Kerala): 1 ♀, Mudis Hills, 14.v.1934, F.C. Fraser. – INDIA (Meghalaya): 1 ♂, Shillong, 1.ix.1919, Fletcher (BMNH); 1 ♂, Shillong, Assam, 10.viii.1928, J. Muller (ISNB). – INDIA (Tamil Nadu): 1 ♂, 1 ♀, Nilgiri Hills, Coonoor, Syms Park, 7–14.v.1921, F.C. Fraser; 5 ♂, 2 ♀, Nilgiri Hills, Ootacamund, 7250 ft (= 2210 m a.s.l.), 18.x.1921–18.xi.1922, F.C. Fraser & T.B. Fletcher; 1 ♂, Nilgiri Hills, Lovedale Lake, 7250 ft (= 2210 m a.s.l.), 8.x.1922, F.C. Fraser; 1 ♂, Nilgiri Hills, date & leg. unknown; 1 ♂, 1 ♀, Palni Hills [= Palani H.], Kodaikanal, Bear Stream, 2.vi.1923, Maj. Frere; 1 ♂, Bear Stream, date unknown, F.C. Fraser; 1 ♂, Annaimallai Hills [= Anaimalai H.], Varataparai, 7.v.1933, F.C. Fraser; 1 ♂, Annaimallai Hills, Varataparai, on hill-side road, iv–v.1934, F.C. Fraser; 1 ♂, Annaimallai Hills, date & leg. unknown (BMNH).

Diagnosis. Differs from all other species discussed in the shape of the male cerci (Figs 2, 7) and incision of the vulvar scale (Fig. 12). The greatly restricted yellow on the female wings is also distinctive.

Range and ecology. Known from two disjunct highland areas in the south-west and north-east of the Indian Subcontinent (Prasad & Varshney 1995), ranging into Myanmar (Asahina 1970). The status of *Hemicordulia* from northern Thailand and Vietnam is unclear relative to the Sundaic *H. tenera* Lieftinck, 1930 (Asahina 1987; Donnelly 1994; H. Karube pers. comm.). According to Fraser (1936) "the larva breeds in mountain lakes and, less often, in pools in montane streams". The adult "rarely strays far from its watery habitat and is to be found patrolling the borders of lakes or flying rapidly along open roads and glades on the hill-sides above the lakes. The females are rarely seen, and appear to keep to jungle, except for brief intervals when they come to oviposit and then depart again, pairing taking place during these short visits to water." Fraser (1949) indicated an altitudinal range of 915 to 2300 m in southern India.

Hemicordulia virens (**Rambur**)
Figs 3, 8, 13.

Cordulia virens Rambur, 1842: 147. Holotype ♀: Mauritius (UMO) [not examined].
Cordulia (*Hemicordulia?*) *virens* (Rambur, 1842) – Selys (1871: 253 (bulletin), 19 (reprint)).
*Hemicordulia* (?) *virens* (Rambur, 1842) – Kirby (1890: 47).

Further material: MAURITIUS: 4 ♂, 4 ♀, Moka, 30.vi.1945–30.xii.1948; J. M. Vinson (BMNH); 1 ♂, Macak'Rd, 11.v.1959, leg. unknown (MNHN); 1 ♀, F[ôre]t de Machabée, 19.iii.1981, L. Matilé (MNHN); 1 ♂, Cachette, Ruisseau Saint-Denis, 350 m a.s.l., 2.ii.1999, D. Grand (Coll. D. Grand); 1 ♂, Cachette, ruisselet forestier, 300 m a.s.l., 2.ii.1999, D. Grand (MNHN); 1 ♂, Rivière Tamarin, 1 m a.s.l., 2.ii.1999, D. Grand (MNHN); 1 ♀ (head missing), Black River, 120 m a.s.l., 7.iv.1999, A. Martens (Coll. A. Martens); 1 ♂, Rivière du Poste, W Grand Bassin, 645 m a.s.l., 12.iv.1999, A. Martens (Coll. A. Martens); 2 ♂, Black River, spring area, 680 m a.s.l., 16.iv.1999, A. Martens (Coll. A. Martens).

Diagnosis. Palest and one of the largest species. *H. atrovirens* from neighbouring Réunion, by contrast, is the darkest known. The two species agree in their large size, high Ax and Px counts, thick blunt-tipped cerci (Figs 3, 8) and the basal position of the vulvar scale (Fig. 13).

Remarks. The holotype was not seen, but is described as a large, pale specimen from Mauritius, conforming with the diagnosis. As morphological and geographic proximity suggest, *Hemicordulia* populations on Mauritius and Réunion are closely related. The extreme difference in coloration makes separation straightforward and warrants recognition at the species level. Similar differences separate Micronesian species (e.g. Buden & Paulson 2003). All specimens listed by Fraser (1949; 1950) were re-examined, and inconsistencies between my Fig. 13 and Fraser's (1949) illustration of the vulvar scale and S9 (where the segment is very short) result from a degree of variability in this structure and Fraser's inaccurate depiction thereof.

Range and ecology. Endemic to Mauritius, where restricted to the mountains in the south-west, which

harbour the island's main forest remnants. It is notable that records are from an altitudinal range of 120 to 680 m (Mauritius is only up to 823 m high), lower than most sites of its sibling species *H. atrovirens*. Breeds in pools in rocky streams and rivers, which are mostly forested. Males have been observed patrolling such streams in search of females. Adults have been observed from December to June (D. Grand & A. Martens in litt.).
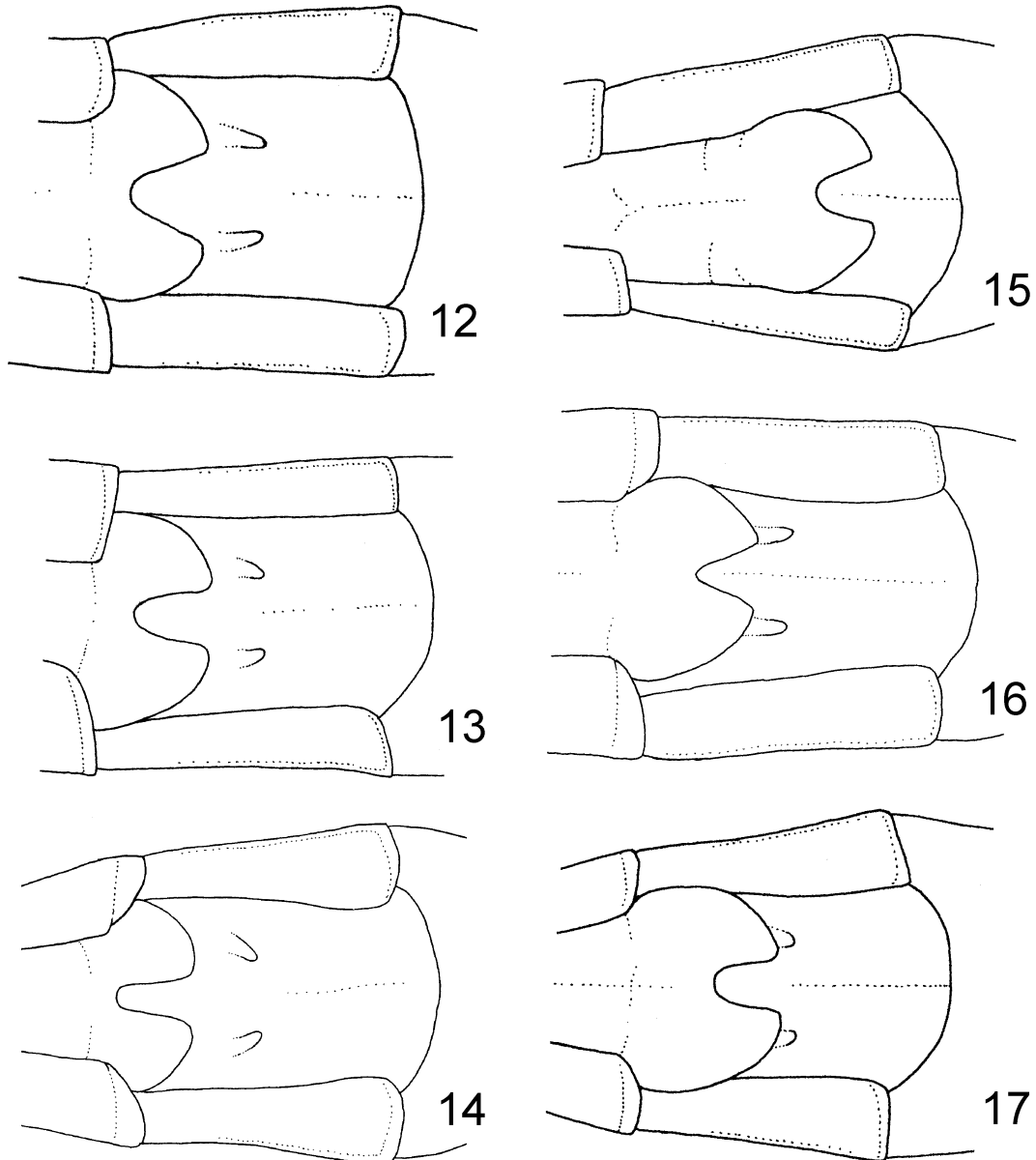
FIGURES 12–17. Vulvar scale and S9 of *Hemicordulia* species in ventral view. (12) *H. asiatica*; (13) *H. virens*; (14) *H. atrovirens* **n. sp.**; (15) aberrant *H. similis* (cf. Fraser 1949); (16) typical *H. similis*; (17) *H. africana* **n. sp.**

Hemicordulia atrovirens **n. sp.**
Figs 4, 9, 14.

Hemicordulia asiatica nec (Selys, 1878) – Couteyen & Papazian (2000: 107).
Hemicordulia atrovirens **n. sp.** Holotype ♂ and paratype ♀: Réunion, Rivière de Sainte-Suzanne, 730 m a.s.l., 8–9.iv.1996, A. Martens (RMNH) [examined].

Further material: RÉUNION: 1 ♀ (Coll. Martin), "Réunion" (MNHN); 2 ♂, Bras Cabot, 1325 m a.s.l., 4.iv.1996, A. Martens (Coll. A. Martens); 2 ♂, Rivière des Marsouins, 1330 m a.s.l., 4.iv.1996, A. Martens (Coll. A. Martens); 3 ♂, ravine near Rivière Langevin, 350 m a.s.l.,14.iv.1996, A. Martens (Coll. A. Martens); 1 ♂, Chemin-de-Ceinture, forêt de ravenales, 12.ii.1999, J. & Cl. Pierre (MNHN); 1 ♀, commune de Saint-Philippe, Ravine Basse Vallée, altitude 280 m a.s.l., 22.v.1999, S. Couteyen (Coll. M. Papazian); 1 ♂, Saint-Paul, old watermill, 2 m a.s.l., 1.v.2000, A. Martens (Coll. A. Martens); 2 ♂, Saint-Benoit, Bras Cabot, 1100 m a.s.l., xii.2001, S. Couteyen (Coll. M. Papazian); 1 ♂, La Plaine des Palmistes, Forêt de Bébour, Rivière des Marsouins, 1330 m a.s.l., 14.ii.2003, D. Grand (Coll. D. Grand).

Diagnosis. Largest and darkest species, with the most extensive and deepest metallic green markings of all species under consideration (see *H. virens*).

Description. Holotype male. Measurements (mm): entire length: 51, abdomen length (without appendages): 34, Fw length: 35, Hw length: 34.5, Fw Pt: 2.0. Labium beige, darker anteriorly (discoloured?). Mandibles, genae, labrum, clypeus and narrow area on lower frons brownish yellow; darker on edges. Vertex and dorsum of frons deep metallic green-blue, merging via a deep brown band into yellow area on antefrons (latter is not visible in dorsal view). Antennae, occipital triangle, occiput and postgenae black; paired rounded swellings on occiput lower than in *H. africana*. Labrum, clypeus, frons, vertex and occipital triangle with long bristly black hairs. Labium, genae and occiput with finer whitish hairs. Prothorax dark brown. Synthorax deep metallic green with weakly contrasting brownish yellow areas on anterior half of mesepisternum and centres of mesepimeron, metepisternum and metepimeron: metallic areas are much wider than the pale areas between them making entire synthorax almost uniformly green. Mesokatepisternum, metakatepisternum and synthoracic venter brownish yellow with metallic green lustre; poststernum posteriorly dark. Synthorax covered with dense pale long hairs, especially long on mesepisternum; shorter, darker and denser hairs on antealar sinus. Legs black save for yellow coxae and a hint at base of fore femora. Keels present on anterior face of apical half of fore tibiae and almost whole length of hind tibiae (just falling short of their bases), but absent on middle tibiae. Venation blackish. Wing membrane evenly but very lightly tinted brown, tinged yellower at extreme bases. Membranule dark brown, slightly paler at extreme base. Pt dark brown. Venation as for genus. 8 Ax in both Fw, 6 in Hw. 7–8 Px in Fw, 9 in Hw. Fw and Hw triangles with single cross-veins. Discoidal field of 2 rows of cells at base. Anal loops of 18 cells. Abdomen black with green- and blue-purple gloss, tergites unmarked except for an indistinct brownish yellow lateral spot on S2, S2–3 intersegmental ring and narrow streaks on lateral carinae S3. Sternites black. Cerci and epiproct slender, black (Figs 4, 9). Cerci with thick, blunt tips. Secondary genitalia similar to *H. africana* (cf. Fig. 1), hamule blackish brown.

Paratype female. Measurements (mm): entire length: 55, abdomen length (without appendages): 39, Fw length: 39, Hw length: 38, Fw Pt: 2.5. Larger and slightly paler than holotype. Paired rounded swellings on occiput more strongly swollen than in male, only with long pale hairs. Pale areas on synthorax larger and brighter, appearing as distinct spots. Fore femora ventrally largely pale. Basal yellow in wings more extensive than in male, to Cux and almost to Ax1 in Fw, and just beyond Cux and to Ax1 in Hw. 8–9 Ax in Fw, 6 in Hw. 7 Px in Fw, 9 in Hw. Anal loops of 19–21 cells. Vulvar scale appressed, dark brown, extending over less than a third of sternite S9, semi-circular with deep cleft (Fig. 14). Cerci black, long and slender, 2.5x longer than S10.

Variation. Limited. Pale markings are slightly more extensive in females; teneral specimens were not examined.

Etymology. The Latin *atrovirens* (being dark green) emphasises both the close relationship and the main difference with its Mauritian neighbour.

Range and ecology. Endemic to Réunion. The larval habitat has been said to range from torrents to stagnant water under closed cover, but is probably principally pools and calm sections of shady fast-flowing streams (Couteyen & Papazian 2000; Grand 2004; A. Martens in litt.). *H. atrovirens* seldom cohabits with any of the ten other anisopterans found on Réunion (Couteyen 2006): overlap (number of sites where two species

co-occur as percentage of sites where either or both occur) with each of the nine species shared with mainland Africa was at most 9%, while that with *Gynacantha bispina*, the only other Mascarene endemic on the island, was 12%. Moreover, within its usual altitudinal range of 300 to 1500 m (one record provided here is near sea level), below 750 m only forested habitats were occupied. Because all nine widespread species avoid forest and six are confined to lower altitudes, Couteyen (2006) suggested that both endemics are out-competed by the mainland species. However, the distribution may also be explained by different habitat preferences (A. Martens in litt.). Males fly along streams, both under forest cover and in full sun. In cloudy weather and towards dusk, adults appear in clearings and on the forest edge, making prolonged flights close to the vegetation (Couteyen & Papazian 2000; D. Grand in litt.). Adults have been observed from December to May.

Remarks. See *H. virens*. Paulson & Buden (2003) observed increasing size of *H. haluco* Asahina with increasing altitude on Pohnpei. The slight size difference seen between *H. atrovirens* and *H. virens*, and the darker colour of the latter, may be linked to the greater elevation of the Réunion habitats.

Hemicordulia similis (Rambur)
Figs 5, 10, 15–16.

Cordulia similis Rambur, 1842: 147. Holotype ♀ with labels: handwritten "Madagascar", handwritten "Ramb.", handwritten "Cordulia similata Rb.", handwritten by Selys "Hemicordulia similis, R. ♀", printed and handwritten by Martin "Collection Selys, Hemicordulia similis Rb. Type, Révision Martin 1906 Hemicordulia similis Rb.", printed red and handwritten by Martin "Type Cordulia similis Rb." (ISNB) [examined].
Cordulia similata Rambur – probably Selys (in litt., see above), *nomen nudum*.
Cordulia (Hemicordulia?) similis (Rambur, 1842) – Selys (1871: 252 (bulletin), 18 (reprint)).
Hemicordulia (?) similis (Rambur, 1842) – Kirby (1890: 47).
Hemicordulia delicata Martin, 1896: 105. Holotype ♂ with labels: handwritten by Martin "Hemicordulia Séchelles.", "Coll. R. Martin 1920 MUSEUM PARIS" (MNHN) [Martin (1896, 1907) did not specify the number of specimens from the Seychelles and presumably saw no females. Only this male was located in MNHN and it is assumed to be the holotype, although it bears no type labels.].
*Hemicordulia similis delicata* Martin, 1896 – Pinhey (1962: 208).

Further material: MADAGASCAR: 1 ♂, "Madag. Schauf[uss]." (BMNH); 2 ♂, blue handwritten by Selys "Madag. Schauf[uss].", handwritten by Selys "Hemicordulia similis, R. ♂", printed and handwritten by Martin "Collection Selys, Hemicordulia similis Rb., Révision Martin 1906 Hemicordulia similis Rb." (ISNB); 4 ♂, 2 ♀, "Madagascar" (MNHN); 1 ♂, 1 ♀, Madagascar (NMBZ); 1 ♂, "E. Madagascar" (MNHN); 2 ♂, 1 ♀, Miarinarivo (MNHN); 1 ♂, "Tamatave", "Madagask. Kaudern", "Hemicordulia similis Yngve Sjöstedt det." (NHRS); 3 ♂, 1 ♀, "Madagascar" (RMNH); 1 ♂, 1 ♀, Tananarive, 1919, G. Waterlot (MNHN); 1 ♀, Ambohimangana, 4.xii.1946, leg. unknown (BMNH); 1 ♂, Tananarive, Tsimbazaza, 24.xii.1947, leg. "A.R." (BMNH); 3 ♂, 10 km N of Tôlanaro (24°56'S 46°59'E), 17–20.iii.2004, K. Schütte (ZMUH); 2 ♂, 1 ♀, 33 km NE of Tôlanaro (24°46'S 47°10'E), 1–3.iv.2004, K. Schütte. – SEYCHELLES: 1 ♂, Mahé, slopes of Morne, xii.1952, Vesey Fitzgerald (NMBZ).

Diagnosis. Similar to *H. africana*, but marginally larger on average and with darker face, perhaps slightly straighter ends of cerci (Fig. 5), more triangular cleft of the vulvar scale (Fig. 16) and reduced yellow at the female wing bases: almost none in Fw and at most to Cux and Ax1 in Hw.

Remarks. Martin (1907) discussed the taxon *delicata* under *H. similis* without indicating whether it is a synonym or subspecies of the latter, but because he later omitted *delicata* he probably considered it a synonym (Martin 1914). That is also how Fraser (1949) treated it, but Pinhey (1962) considered it a subspecies. Each distinct geographic area studied had its single endemic species and therefore *H. s. delicata* may be a separate species too. The current status is however retained because only two males were seen and no female with its potentially diagnostic vulvar scale. The unusually stalked vulvar scale, as illustrated by Fraser (1949) was only seen on the BMNH female and must be aberrant (Fig. 15). All other examined females, including the

type, have an unstalked scale (Fig. 16).

Range and ecology. Widespread on Madagascar. Otherwise known only from Mahé, the largest of the granitic Seychelles (Blackman & Pinhey 1967; Martin 1896), where it was recently reported from a marsh at Police Bay (Gerlach 2003; A. Martens in litt.). Ecology unknown, but is probably similar to other species, as is the adult flight season.
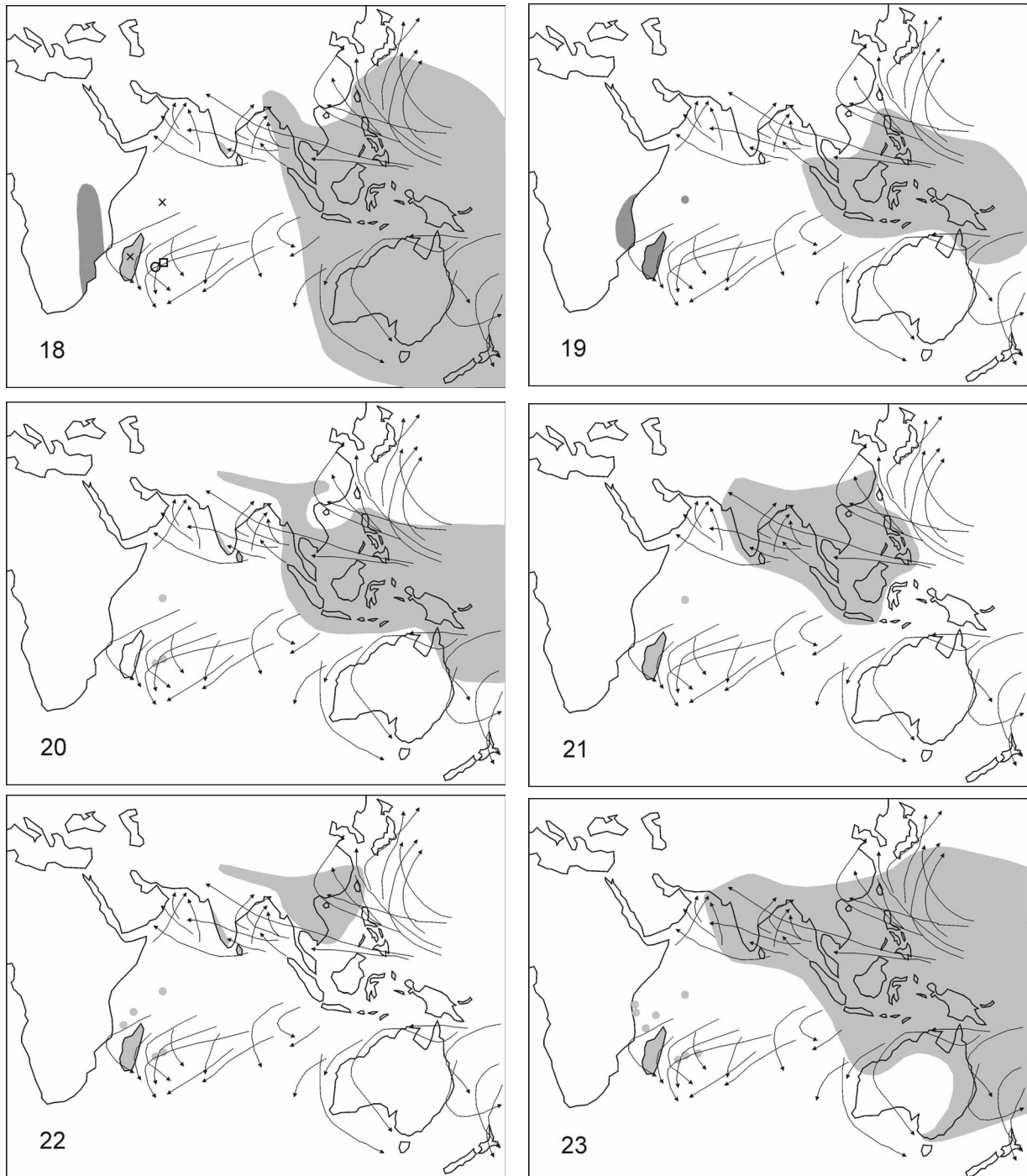
FIGURES 18–23. Distribution of discussed genera. The courses of storms from May to November in the northern hemisphere and November to May in the southern hemisphere are indicated by arrows (after Times Books 1997). (18) *Hemicordulia* and *Procordulia* dragonflies, pale shading: main range in Australasia and Pacific; dark shading: *H. africana* **n. sp.**; crosses and pale shading: *H. similis*; square: *H. virens*; circle: *H. atrovirens* **n. sp.**; (19) *Teinobasis* damselflies, pale shading: main range in Australasia and Pacific; dark shading: *T. alluaudi*; (20) *Collocalia* swiftlets; (21) *Copsychus* magpie robins; (22) *Hypsipetes* bulbuls; (23) *Pteropus* flying foxes.

Hemicordulia africana **n. sp.**
Figs 1, 6, 11, 17.

Hemicordulia similis nec (Rambur, 1842) – Martin (1906 in litt.).
Hemicordulia asiatica nec (Selys, 1878) – Pinhey (1961: 105).
Hemicordulia africana **n. sp.** Holotype ♂ and paratype ♀ with labels: printed "Van Someren, Katera Forest. Masaka
    Uganda, Oct.-Nov.1953" and printed "V.G.L. van Someren Collection. Brit. Mus. 1959-468." (BMNH) [examined].

Further material: MALAWI: 1 ♂, Nkhata Bay, Mkuwazi Forest, 6.v.1966, E. Pinhey (NMBZ). – MOZAM-
BIQUE: 1 ♀, blue, handwritten "Delagoa B. [= Maputo]", printed and handwritten by Martin "Collection
Selys, Hemicordulia similis Rb., Révision Martin 1906 Hemicordulia similis Rb. [but not listed by Martin
(1907).]" (ISNB). – SOUTH AFRICA (KwaZulu-Natal): 1 ♂, Lake St Lucia, pools near small river, *Bar-
ringtonia* trees, 24.xi.1995, G. Carchini; 1 ♀, Sodwana, small forest stream, 20.x.1996, G. Whiteley & J. Ban-
natyne; 1 ♀, Sodwana, stream in *Barringtonia* forest, 21.xi.1996, G. Whiteley; 1 ♀ (perching high up on twig
among trees, 100 m from water), Sodwana, near Lake Ngoboseleni, 9.ii.1997, M.J. Samways; 1 ♂ (hawking
up and down roadside in forest), Cape Vidal, 10.ii.1997, M.J. Samways; 4 ♂ (hawking among trees and open
bush next to forest), 1 ♀ (perching in shade, forest edge), Kosi Bay (26°57'S 32°49'E), among trees and bush,
45 m a.s.l., 16.xii.2000, M.J. Samways (SUEC). – TANZANIA: 1 ♂, Sibweza, 35 mi., Mpanda-Karema Rd.,
1050 m a.s.l., 5.xi.1966, J. Kielland (RMNH). – UGANDA: 1 ♂ (label states: "Hemicordulia asiatica Selys
F.C. Fraser det. 1953), Entebbe, 17.v.1952, E.C.G. Pinhey (BMNH); 1 ♂, Entebbe, v.1952, E.C.G. Pinhey
(NMKE); 2 ♂ (label states: "Hemicordulia ?asiatica or sp.n. det. Miss C. Longfield"), Entebbe, x.1952, E.C.G.
Pinhey (BMNH); 4 ♂, Entebbe, x.1952, E.C.G. Pinhey (NMKE); 6 ♂, 2 ♀, Katera Forest, Masaka, x–xi.1953,
V.G.L. van Someren (BMNH); 7 ♂, 1 ♀, Katera, xi.1953, T.H.E. Jackson (NMKE); 1 ♂, Zika, 28.iii.1962, P.S.
Corbet (BMNH); 1 ♀, Lake Nabugabo, 4.v.1999, V. Clausnitzer (Coll. V. Clausnitzer); 1 ♂, 1 ♀, Kibale
National Park, Kanyawara, Makerere University Biological Field Station (0°35'N 30°20'E), open area, 1500
m a.s.l., 8–30.v.2001, R.H.A. van Grunsven (RMNH); 1 ♂, Semliki Game Reserve, 16.i.2002, C. Williams
(ZMMU).

Diagnosis. Smallest species, with very extensively yellow wing bases in females (see *H. similis*).

Description. Holotype male. Measurements (mm): entire length: 44.5, abdomen length (without append-
ages): 29.5, Fw length: 29, Hw length: 28, Fw Pt: 1.7. Labium pale beige. Mandibles, genae, labrum, clypeus
and broad area on lower frons pale brownish yellow. Dorsum of frons metallic green-blue, contrasting weakly
with visible yellow on antefrons in dorsal view; vertex with weaker metallic lustre. Occipital triangle and
occiput brown; occiput with paired rounded swellings. Postgenae and antennae black. Labrum, clypeus, frons,
vertex and occipital triangle with long bristly black hairs. Labium, genae and occiput with finer whitish hairs.
Prothorax dark brown. Synthorax metallic green with weakly contrasting large pale brownish yellow areas on
anterior half of mesepisternum and centres of mesepimeron, metepisternum and metepimeron resulting in pat-
tern of metallic bands posterior to humeral and metapleural sutures, both of which are narrower than pale
areas between them. Mesokatepisternum, metakatepisternum and synthoracic venter pale brownish yellow,
with dark transverse band on posterior poststernum. Synthorax covered with dense pale long hairs, especially
long on mesepisternum; shorter, darker and denser hairs on antealar sinus. Legs black save for yellow coxae,
trochanters, most of fore femora and a hint at base of mid femora. Keels present on anterior face of apical half
of fore tibiae and almost whole length of hind tibiae (just falling short of their bases), but absent on middle tib-
iae. Venation blackish. Wing membrane clear, very narrowly and faintly yellow at extreme bases. Membran-
ule dark brown, slightly paler at extreme base. Pt dark brown. Venation as for genus. 7 Ax in both Fw, 5 in
Hw. 5 Px in Fw, 6–7 in Hw. Fw triangles with single cross-veins, Hw triangle uncrossed. Discoidal field of 2
rows of cells at base. Anal loops of 15 cells. Abdomen black with green-purple gloss, marked with weakly
contrasting brownish yellow: tergites S1–3 largely pale but darker dorsally (S1–3) and laterally (S3), S4–8
pale laterally and ventrally, from base to apex on S4–6 sides and almost to apex on S7–8; S9–10 all black.

Sternites blackish brown. Cerci and epiproct slender, black (Fig. 6, 11). Cerci with fairly pointed but blunt tips. Secondary genitalia as in Fig. 1, hamule blackish brown.

Paratype female. Measurements (mm): entire length: 46, abdomen length (without appendages): 32.5, Fw length: 31, Hw length: 30, Fw Pt: 2.0. Larger and paler than holotype. Occiput bears a cluster of short thick brown bristles on each side, besides long pale hairs. Metallic green areas reduced, e.g. broken into two blocks on frons by pale median line, almost no gloss on vertex, and only intense on synthorax behind humeral and metapleural sutures. Fore and mid femora largely pale. All tergites except S9–10 laterally and ventrally yellow. Sternites blackish brown, except on S9–10 paler brown. Basal yellow in wings extensive, to arculus and halfway Ax1–2 in Fw, and arculus and Ax2 in Hw. 7 Ax in both Fw, 5 in Hw. 5 Px in Fw, 7 in Hw. Anal loops of 15–17 cells. Vulvar scale appressed, pale brown, extending over almost half of sternite S9, semi-circular with deep cleft (Fig. 17). Cerci black, long and slender, 2.5x longer than S10.
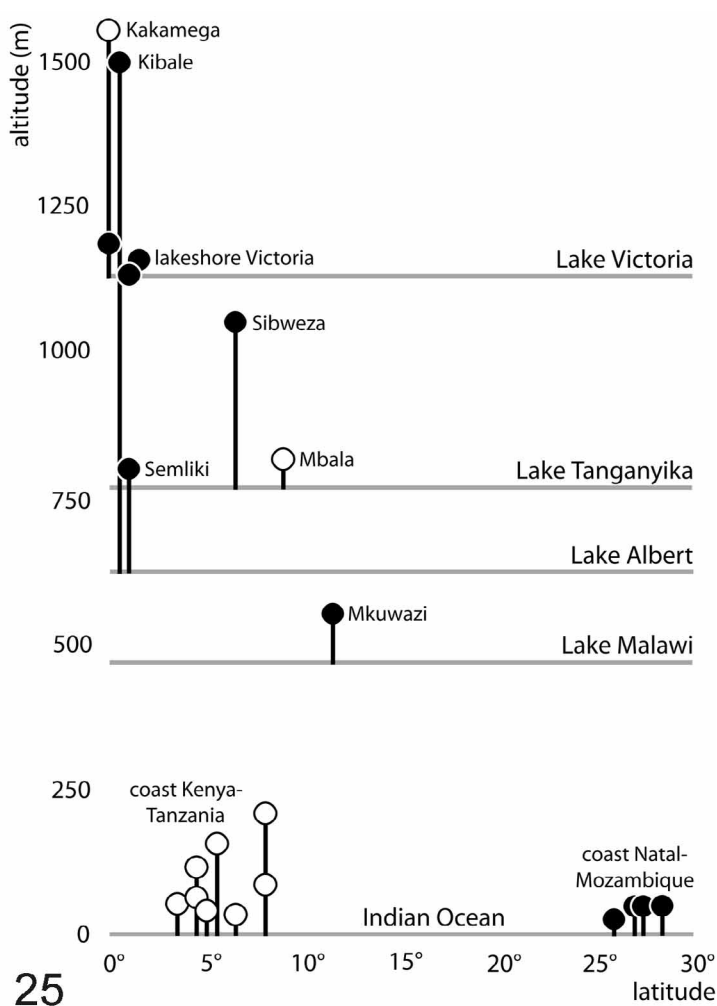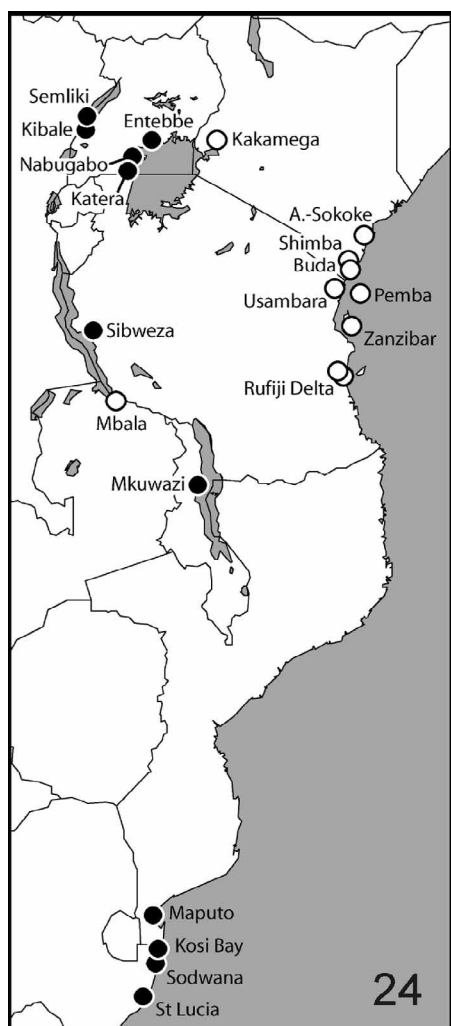
FIGURES 24–25. Geographic (24) and altitudinal (25) distribution of *H. africana* **n. sp.** relative to large water bodies. Filled circles are known records (present paper), open circles forested localities near large waterbodies that have recently been intensively surveyed by V. Clausnitzer (pers. comm.), except Mbala by Pinhey (1984). Many sites in the region away from large water bodies have also been researched. A line connects each site to the altitude of the nearest large water body.

Variation. Substantial. Pale markings are more extensive in females and younger specimens. Thorax and abdomen largely pale when teneral, but may loose pale markings almost completely when mature; typical mature males have restricted narrow lateral streaks on S5–8 or S6–8. The relative length of the vulvar scale and the shape of its cleft is variable, as in all species (Table 2).

TABLE 2. Comparison of the discussed *Hemicordulia* species. Figures represent averages for continuous measures and sums, and modi for counts (frequencies given), with ranges given in brackets. The extent of the vulvar scale along S9 is measured as the distance from the base of the scale to its tip, divided by the distance from its base to the tip of sternite S9. Relative characters are defined in comparison to *H. africana* **n. sp.** and *H. asiatica* (see Table 1 for details), e.g. the extent of yellow in female wing bases in *H. similis* is intermediate between the extensive state in *H. africana* **n. sp.** and the restricted state in *H. asiatica*.

	H. asiatica	*H. virens*	*H. atrovirens*	*H. similis*	*H. africana*
n (♂ : ♀)	17 : 5	11 : 6	13 : 3	24 : 9	33 : 10
Range	India to Myanmar	Mauritius	Réunion	Madagascar; Mahé	eastern Africa
Hw length (♂)	31.0 (30.0–32.5)	34.0 (32.0–36.0)	35.3 (32.5–37.5)	29.2 (27.5–31.5)	28.7 (27.0–30.0)
Hw length (♀)	33.2 (31.0–34.5)	36.4 (35.5–37.5)	38.5 (38.0–39.0)	31.3 (30.0–32.5)	29.8 (28.0–32.5)
Fw Ax	7 in 65% (7–8)	8 in 72% (7–9)	8 in 69% (7–9)	7 in 82% (6–8)	7 in 88% (7–9)
Fw Px	6 in 67% (5–6)	7 in 63% (6–8)	7 in 66% (6–9)	5 in 71% (5–6)	5 in 81% (5–6)
Paired dark blotches at base of labrum	absent or vague	absent	vague	distinct	absent
Green on frons	extensive	reduced	extensive	extensive	reduced
Extent of yellow in wing bases (♀)	restricted	intermediate	intermediate	restricted to intermediate	extensive
Angle of vulvar scale incision (♀)	35–55°	20–30°	0–15°	30–50°	10–30°
Extent of vulvar scale along S9 (♀)	30–35%	25–35%	25–35%	35–40%	35–45%

Etymology. The species is named for its native continent, after having been mistaken for a species named after Asia for about half a century.

Remarks. It is surprising that Fraser (in Pinhey 1961) did not recognise an African species, as the vulvar scale differs clearly from that of true *H. asiatica*. Pinhey (1985) indicated that his Natal material comprised of "all undersized males". The species is indeed small, although Pinhey did not explain the background of his remark. The continental taxon is very close to the Madagascan *H. similis*, but the slight differences appear stable and warrant specific distinction.

Range and ecology. Probably confined to eastern Africa (Fig. 24). The first records are from Entebbe, where also found recently (Pinhey 1961; Graves 1999). Later found in Malawi and KwaZulu-Natal (Pinhey 1966; 1985). Interestingly, the single Malawian site is also the only inland African locality for *Teinobasis alluaudi* and the only Malawian site for *Gynacantha immaculifrons*, two other suspected trans-oceanic arrivals (Fig. 26). The present records are the first for Mozambique and Tanzania, although Tsuda (2000) did list '*H. asiatica*' for Mozambique, probably because Pinhey (1981) predicted its presence. Lindley (1974) listed *H. asiatica* for the "high forest" of Côte d'Ivoire without providing details. This anomalous record may pertain to *Idomacromia* Karsch. *H. africana* "hawks up and down on the edges of forests or in forest glades, often high in the air" (Pinhey 1961), but its ecology is otherwise unknown. Adults have been observed from October up to February in South Africa and up to May elsewhere.

Discussion

Biogeographic hypothesis

The eastern Afrotropical distribution of *Hemicordulia* and its presence on all the major Indian Ocean islands match a biogeographic scenario with large, trans-oceanic distances covered in flight. Presently, the

shortest distance between Indian and insular *Hemicordulia* populations is the 2750 km to the Seychelles. Thence to continental Africa, Madagascar and Mauritius is 1300, 1050 and 1700 km respectively. The distance directly from India to Mauritius is 3800 km; Sumatra is 5000 km away. Summer storms move from east to west, providing a medium for trans-oceanic transport (Fig. 18). Whereas *Hemicordulia* includes well-dispersing species, there is also a tendency to quick speciation of isolated populations, producing closely similar island species. Differences between the studied species are too small for a robust phylogenetic analysis of morphology. However, the morphological diversity of the Papuan-Australian species, and the geographic and morphological proximity of those around the western Indian Ocean suggest an eastern origin of the genus and expansion westwards. Because the four westernmost species form two distinct sister-species pairs they may represent two, rather than one, colonisation events.

Odonate dispersal

Flight is an effective means of dispersal in adult Odonata, and long-range dispersal is frequent and widespread. Numerous observations are consistent with the transportation of dragonflies by wind across water over distances of up to 4000 km (Corbet 1999). Within the genus *Hemicordulia*, Armstrong (1978) inferred that *H. australiae* (Rambur) only colonised New Zealand in the 1930s. The American damselfly *Ischnura hastata* (Say) colonised the volcanic Galapagos Islands (925 km from Ecuador) and the Azores (3100 km from Maine and Bermuda), and has been collected at 300 m altitude with nets fixed to aeroplanes (Cordero Rivera *et al.* 2005). *Ischnura ramburii* (Selys) is not closely related to other American species of the genus, but probably shares a recent ancestor with the abundant Paleotropic *I. senegalensis* (Rambur) (Chippindale *et al.* 1999; Donnelly & Parr 2003; H.J. Dumont pers. comm.). *Anax ephippiger* (Burmeister) has reached French Guiana, Iceland and Japan from Africa and India, and *Anax junius* (Drury) Great Britain, France and eastern Siberia from North America (Haritonov & Malikova 1998; Machet & Duquef 2004; Meurgey 2004; Pellow 1999; Tuxen 1976; Ugai 1996). Belle (1988) treated a Surinam specimen of the African migrant *Tramea basilaris* (Palisot de Beauvois) as an accidental introduction, but prevailing winds make north-eastern South America the most likely place for Afrotropical arrivals in the Neotropics (see *A. ephippiger* above). The scale and effect of long-range odonate dispersal has best been studied in the most cosmopolitan species, *Pantala flavescens* (Fabricius). The well-documented arrival in New Zealand, where it probably cannot breed, indicated that over 2000 km of ocean were crossed with speeds of 18–50 km/hr (Corbet 1979). Observations of migratory swarms across the Chinese Bohai Sea indicated similar speeds and a flight height of up to 1000 m, but usually 200–500 m (Feng *et al.* 2006). *P. flavescens* is the only odonate to reach Easter Island, 1900 km from the Pitcairn Islands and 3600 km from Chile. Individuals in this population are darker, robuster, more asymmetrical, shorter-winged and have a weaker flight than continental populations, probably under extreme ecological and genetic stress (Dumont & Verschuren 1991; Moore 1993; Samways & Osborn 1998). The (partial) loss of flight in oceanic insects, whose ancestors are typically highly dispersive representatives of their group, is a paradoxical but recurrent feature of their evolution (Gillespie & Roderick 2002).

Timing and means of dispersal

The age of western Indian Ocean colonisations by alate terrestrial fauna may be inferred from the history of the occupied islands and prevailing weather patterns, and by phylogenies of groups with similar distributions calibrated by such events. *Platycnemis* species could only reach the Comoros airborne after these were created by volcanism at most 8 million years (Ma) ago (Dijkstra *et al.* 2007). Mauritius is about 8 Ma old, Réunion 2 Ma and Rodrigues 1.5 Ma (Austin *et al.* 2004; Shapiro *et al.* 2002). Estimates that *Psittacula* arrived on Mauritius 0.7–2.0 Ma ago and *Pteropus* colonised the western Indian Ocean in the last 1.5 Ma conform with these ages (Groombridge *et al.* 2004; O'Brien & Hayden 2004). Thomassen (2005) estimated that Indian Ocean *Collocalia* separated from a Sundaic ancestor 1.43–1.50 Ma ago, with the split between the Seychelles and Mascarene species at 0.50–0.65 Ma. Indian Ocean sunbirds represent two separate colonisation

events from Africa to Madagascar and the Comoros in the past 3.9 Ma, while the Seychelles were only reached 1–2 Ma and Aldabra 125 thousand years (ka) ago (Warren *et al.* 2003). In contrast, Shapiro *et al.* (2002) estimated that the flightless dodo of Mauritius and solitaire of Rodrigues separated 18–36 Ma ago, having diverged from an Australasian ancestor 32–56 Ma ago, supporting the suspected presence of dry land here in the late Oligocene. Present-day prevailing winds across the Indian Ocean blow westwards towards Madagascar. However, the island probably only moved into the belt of easterly trade winds in the Paleocene, becoming warmer and wetter, and lying fully in it by the early Oligocene, around 30 Ma ago. The current monsoon system, which seems especially suitable to transport airborne propagules across from Asia, only emerged in the last 8 Ma (Wells 2003). Flight speed estimates for *Pantala flavescens* imply that a windborne odonate can cover the distance between India and the Seychelles within two to six days, and with a suitable weather-system in place, dispersal may be ongoing. Considering this and the apparently limited morphological divergence between the species discussed, a long-term explanation for their distribution seems unnecessary (see de Queiroz 2005). The significant number of well-dispersing Oriental and Afrotropical species on the Seychelles, suggests frequent and contemporary long-range dispersal of Odonata across the Indian Ocean in two directions (Blackman & Pinhey 1967).

Alternative hypotheses

Hemicordulia could have been present in Africa, Madagascar, Seychelles and India before Gondwanaland fractured and later colonised the Mascarenes, or colonised Africa through south-western Asia, expanding later to Madagascar, the Seychelles and Mascarenes. The latter scenario incorporates Dumont's (1980) hypothesis of an overland route through the Middle East and along the Nile Valley before the present extent of aridity in the intervening regions. The additional evolutionary time (tens of millions of years) and space that these scenarios provide, predict a greater divergence of taxa, i.e. more different and more species. Within Odonata, for instance, morphologically distinct groups of *Zygonyx* occur in Africa, Madagascar, Seychelles and Asia, suggesting the first scenario, and Chlorocyphidae has great generic diversity in Asia and great species diversity in Africa but is absent on Madagascar and the Indian Ocean islands, conforming with the second. Neither scenario conforms with the emphasis of *Hemicordulia* occurrence on the Indian Ocean seaboard and both, especially the second, still require substantial trans-oceanic dispersal. Considering the morphological diversity of Indian Ocean *Pteropus*, Bergmans (1997) concluded that a trans-oceanic scenario implied multiple colonisations from various, sometimes very distant, sources. He preferred an overland scenario, relating the current absence on the mainland to extinction. This is difficult to accept for a predominantly insular genus (86% of species occurs on islands) with a possibly very recent western history (O'Brien & Hayden 2004). Bergmans accepted that trans-oceanic dispersal takes place, referring to records of vagrancy, but found the scale and frequency unacceptable. That argument is arbitrary and in reality dispersal is probably an extensive phenomenon.

Trans-oceanic species on the continent

The assumption that islands contribute little to continental biotas, including contributions to mainland Africa from Madagascar and the Indian Ocean islands, remains relatively untested (Gillespie & Roderick 2002; Zakharov *et al.* 2004). Island species may be at a competitive disadvantage on the continent, just as they are when islands are colonised by continental species. Competitive exclusion by already present *Zosterops* white-eyes may, for instance, explain the mysterious absence of *Nectarinia* sunbirds in the Mascarenes (Warren *et al.* 2003). However, the widespread Paleotropical lime swallowtails (*Papilio*) probably originated in Madagascar, possibly after the arrival of an ancestor from Asia (Zakharov *et al.* 2004). Some satyrine and acraeine butterflies may also have colonised Africa from Madagascar, as have chameleons and certain rodents (Jansa *et al.* 1999; Raxworthy *et al.* 2002; Torres *et al.* 2001).

Although many records of suspected trans-oceanic Odonata on the mainland are coastal, most species are also known well inland (Fig. 26). Their continental distribution cannot be attributed to research intensity, as large parts of Kenya, Malawi and Zambia (for instance) are well-studied, although some coastal regions remain unsampled. Especially surveys of Mozambique and southern Tanzania may improve the resolution of observed patterns. Because occupied island habitats are also seldom coastal in nature, the distribution of *Hemicordulia* and also *Teinobasis* (see Introduction) raises the question how they colonised islands but remained so localised on the mainland. *H. asiatica* and *H. atrovirens*, for instance, favour higher elevations and the apparent correlation between altitude and latitude in *H. africana* suggests that its absence on the equatorial coast is linked to higher ambient temperatures there (Fig. 25). All *H. africana* records are within 50 km of large water bodies, thus the inland localities are 'insular' in having 'sea' and 'habitat' in close proximity (Fig. 25). However, their elevation above some lakes excludes the possible importance of large water bodies as breeding habitats, which are more likely forest streams (Fig. 25).
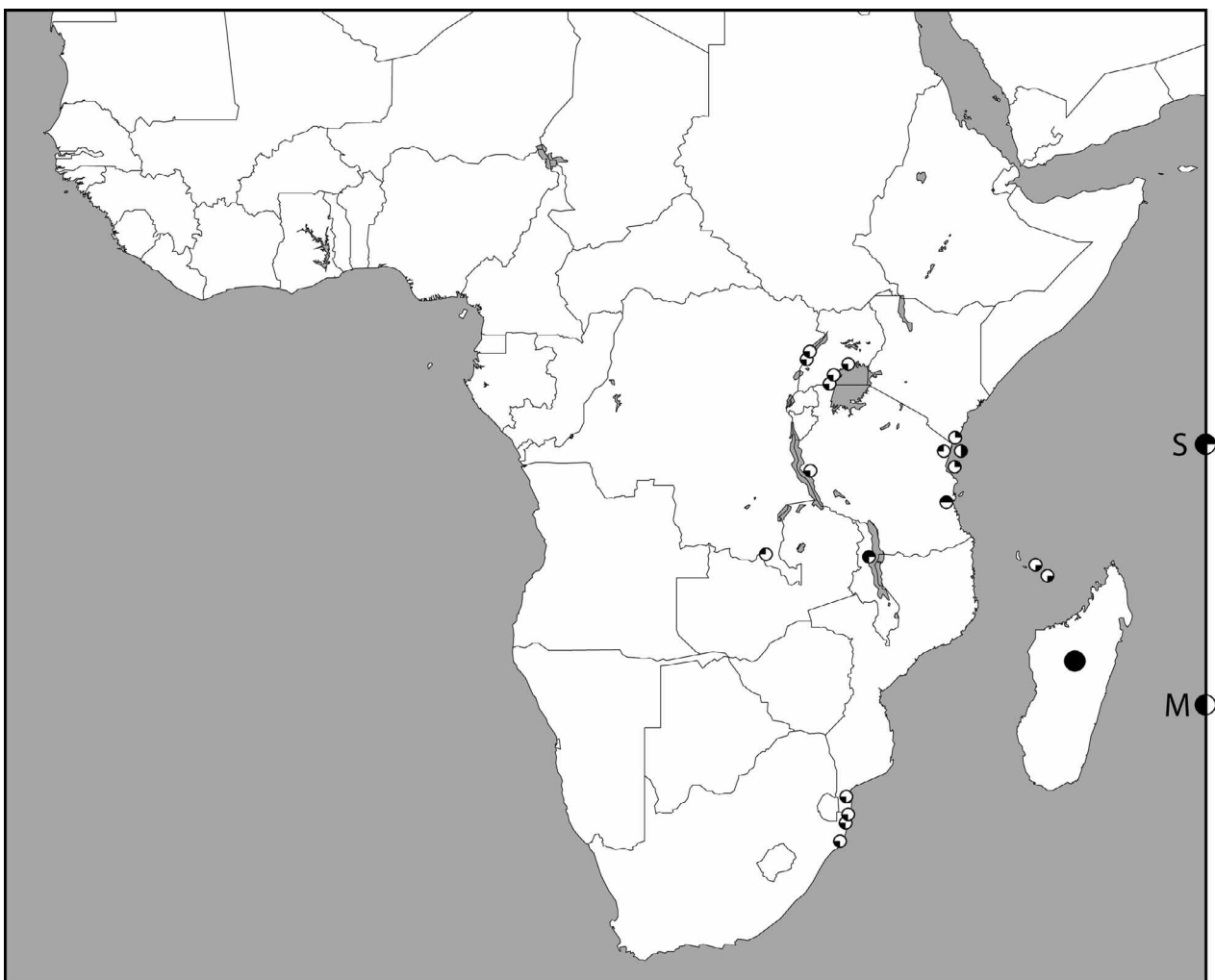

FIGURE 26. Distribution of suspected trans-oceanic Afrotropical Odonata (see Introduction). Black bottom-left quarter of circle: *Hemicordulia africana* **n. sp.**; bottom-right: *Platycnemis* species of Madagascan radiation; top-left: *Gynacantha immaculifrons*; top-right: *Teinobasis alluaudi*; enlarged circles: presence of these species or close relatives on Madagascar and the islands just east of the map's border, the Mascarenes (M) and Seychelles (S).

Recent climatic fluctuations especially affected local convectional rainfall near the great lakes (Fjeldså & Lovett 1997; Lovett 1993). The levels of Lakes Malawi and Tanganyika were lowered by 250–500 and 600 m before 25 ka ago and were also lowered about 12 ka ago (Scholz & Rosendahl 1988). Lake Victoria is only between 30 and 400 ka old and was largely dry about 14–17 ka ago (Griffiths 1993; Lovett 1993). Lake-generated rainfall may have remained erratic throughout the Holocene (Stager 2001), with high lake levels in Africa 7–10 ka ago (Diamond & Hamilton 1980). There was little or no lowland forest in Uganda before 12 ka ago, and its spread since was not as an advancing front, but by the wide dissemination of efficient dispersers and gradual coalescence of forest patches (Hamilton *et al.* 2001). The persistence of a diversity gradient here (marked eastwards impoverishment) shows that there is a long lag-period in the adjustment of forest ecosystems to a new equilibrium after a major climatic event (Hamilton 1981). Diamond & Hamilton (1980) argued that "competitive exclusion often prevents establishment by long-distance wanderers" and that it "is likely to be least important in new, [...] vacant areas of a particular habitat type, such as might be created by the spread of a vegetation type as a result of climatic change" and also "species that are at present restricted to montane forest may formerly have occurred also at lower altitudes and been forced to higher elevations as the lowlands were gradually colonized by species better adapted to lowland conditions".

The confinement of *Hemicordulia* to relatively unstable habitats would explain its distribution, including its absence on the equatorial coast. This is one of the climatologically most stable areas on the continent, in contrast to the coast further south that lies in Madagascar's rainshadow (Lovett 1993). White (1981; 1993) noted that montane plants with isolated lowland populations are often readily-dispersing pioneers (e.g. by birds or wind) that occupy rather specialised habitats (spray zones, poor soils) where competition with lowland species is reduced. *Hemicordulia* may indeed be a good disperser, but a poor competitor, as suggested by Couteyen (2006) for *H. atrovirens*. This could explain both the genus's insular distribution, where competition is reduced in impoverished faunas, as its continental distribution in areas where suitable habitat is comparatively recent and therefore impoverished (lakeshores, highlands). The competitive position of *Hemicordulia* may be related to thermoregulation. Holarctic Corduliidae are generally relatively cold-tolerant, but sensitive to overheating (Wildermuth 2006; A. Martens in litt.). Although the physiological limitations of tropical corduliids are largely unknown, the studied *Hemicordulia* species do prefer shaded habitats, often at greater elevations, and are active at cooler times of the day. The presence of trans-oceanic species on the continent may generally be a 'peripheral' phenomenon. Dijkstra *et al.* (2007) argued that reduced habitat availability during recent dry spells could have largely exterminated *Platycnemis* and *Teinobasis* damselflies in eastern Africa, where both genera are respresented by a single species. However, the *Platycnemis* species is confined to an island (Pemba) and the *Teinobasis* species to two islands (Pemba, Zanzibar) and other sites near sea or lake level, which are susceptible to frequent disturbances like submersion. Perhaps their survival depends on the persistence of suitable habitat in areas with reduced competition.

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