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Taxonomy and identification of the continental African *Gynacantha* and *Heliaeschna* species (Odonata: Aeshnidae)

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Abstract

The taxonomy of the *Gynacantha* and *Heliaeschna* species from continental Africa is problematic, and available keys are unsatisfactory. 'Traditional' characters such as venation and 'innovative' ones like abdominal denticulation are evaluated and their variability is measured and discussed. *G. quadrina* is a synonym of *G. africana* and not of *G. vesiculata*, *G. ochraceipes* is regarded a synonym of *G. vesiculata*, *G. victoriae* of *G. bullata*, *G. flavipes* and *G. sevastopuloi* of *G. nigeriensis*, *G. zuluensis* of *G. usambarica*, and *H. ukerewensis* of *H. trinervulata*. Analysis of the complex of large *Heliaeschna* species provides no basis for separating species and *H. lanceolata*, *H. libyana* and *H. raymondi* are treated as synonyms of the single variable species *H. fuliginosa*. The first records of *G. immaculifrons* and of specimens near *H. longfieldae* since their descriptions are provided. The probable male of *H. longfieldae* is diagnosed. Remarkable heterogeneity of characters in *G. manderica*, *G. villosa* and *H. longfieldae* is described. This may have taxonomic relevance, but study of more specimens is required. Afrotropical *Gynacantha* species can be assigned to three groups: the *africana*-, *bispina*- and *bullata*-groups. It is suggested that *Gynacantha* and *Heliaeschna* may not be monophyletic and that the *africana*-group may be more closely related to African *Heliaeschna* than to the other *Gynacantha* groups. Keys to the species of *Gynacantha* and *Heliaeschna* are provided for both sexes. Identification is still tentative for females of some species.

Introduction

Despite the study of African *Gynacantha* Rambur, 1842 by Fraser (1962), the genus needs to be revised, as was already stressed by Pinhey (1974). *Gynacantha* specimens are common in collections and are often misidentified, creating a need for reliable keys. *Heliaeschna* Selys, 1881 is encountered much less than *Gynacantha* and the species are even more similar to each other, making their taxonomic status especially problematic (Dijkstra 2003). The basis for a different approach to the identification of the African species of these genera, using innovative characters, was already laid down by Gambles (1956) and Balinsky (1961), but was ignored

by Fraser (1962). Instead of clarifying the taxonomy, Fraser's (1962) revision bares the weakness of the traditional characters such as venation and coloration. For the purpose of designing new identification keys I studied characters first investigated by Gambles (1956) and Balinsky (1961) as well as traditional and new characters on extensive series of Afrotropical species, including types of most taxa. When the observed variability of certain characters was taken into account, a number of synonyms arose. For convenience, the genera *Gynacantha* and *Heliaeschna* combined will further be referred to as Gynacanthini and gynacanthines in this paper, although the precise classification of Aeshnidae is still unsettled (von Ellenrieder 2002).

Taxonomy of the genera

African gynacanthines are placed in two genera, *Heliaeschna* and *Gynacantha*. African *Heliaeschna* forms a fairly homogeneous group of species. The *Gynacantha* species, including those of the Indian Ocean islands, are easily sorted into three groups. The grouping of the species is shown in Table 1, their diagnostic features in Table 2. Fraser's (1962) "Group I" is the same as the *africana*-group, while his "Group II" includes the *bispina*- and *bullata*-groups. The species within each of the four African groups share many potential apomorphies, but only a worldwide phylogenetic treatment of the Gynacanthini can positively demonstrate their monophyly. Moreover the genera *Gynacantha* and *Heliaeschna* may not be monophyletic: taking aside venation, African *Heliaeschna* bear little resemblance to the Oriental species of that genus, whose males have different hamular processes, cerci and epiproct and females typically bear a second pair of spines on S10. The presence of median cross-veins and the absence of brace veins are found in different groups of aeshnids and were probably achieved by convergence (von Ellenrieder 2002). Because the *africana*-group is distinctive in so many ways, including venation, it is surprising it was not given more weight by earlier workers. The group shares some characters with *Heliaeschna* but not with other African *Gynacantha* species (Table 2). This and the similarities between *G. sextans* and *Heliaeschna*, suggest that the *africana*-group may be more closely related to African *Heliaeschna* than *Gynacantha*, possibly warranting generic recognition.

Controversy exists concerning the usage of the genus names *Gynacantha*, *Triacanthagyna* Selys, 1883 and *Acanthagyna* Kirby, 1890 (Hedge & Crouch 2000; von Ellenrieder & Garrison 2003). Application 3294 to the ICZN by N. von Ellenrieder and R.W. Garrison is followed in the usage of *Gynacantha*.

Material and methods

The present paper is the result of a gradual build-up of data, obtained during numerous visits to collections, and not of a preconceived revision. Therefore no full lists of specimens studied can be given. Most specimens in MNHN (*Heliaeschna* only), BMNH, ISNB, MNMS, MRAC, NHRS, NMKE and RMNH were studied. Sample sizes and examined primary types are indicated in Tables 1, 3 and 4 and where relevant in the species texts.

Table 1. Grouping, synonyms and ranges of African Gynacanthini, including species of Indian Ocean Islands. Range information is approximate, and rather wide geographical definitions are used, e.g. Central Africa includes such peripheral areas as Cameroon, W Kenya and N Malawi, while East Africa stretches as far south as Natal. — *: primary types examined by author.

Genus / group **Species**	**Synonyms**	**Range**
Gynacantha / africana		
africana (Palisot de Beauvois, 1807)	*quadrina* McLachlan, 1896* *lieftincki* Compte Sart, 1964*	W and C Africa
cylindrata Karsch, 1891*		W and C Africa
radama Fraser, 1949		Madagascar
sextans McLachlan, 1896*	*schultzei* Le Roi, 1915* *maesi* Schouteden, 1917*	W and C Africa
vesiculata Karsch, 1891*	*ochraceipes* (Pinhey, 1960)	W and C Africa, Ethiopia
villosa Grünberg, 1902*		E Africa
Gynacantha / bispina		
bispina Rambur, 1842		Mauritius and Reunion
immaculifrons Fraser, 1956*		Katanga, Malawi, Tanzania
malgassica Fraser, 1962		Madagascar
stylata Martin, 1896		Seychelles
Gynacantha / bullata		
bullata Karsch, 1891*	*elongata* Fraser, 1957* *victoriae* (Pinhey, 1961)*	W and C Africa
hova Fraser, 1956		Madagascar
manderica Grünberg, 1902*		Tropical Africa
nigeriensis (Gambles, 1956)*	*flavipes* Fraser, 1956* *sevastopuloi* (Pinhey, 1961)*	W and C Africa, Ethiopia
usambarica Sjöstedt, 1909*	*zuluensis* (Balinsky, 1961)	E Africa
Heliaeschna		
cynthiae Fraser, 1939*		C Africa
fuliginosa Selys, 1883*	*lanceolata* Le Roi, 1915* *libyana* (Fraser, 1928)* *raymondi* Compte Sart, 1967*	W and C Africa
longfieldae Gambles, 1967*	? *sembe* Pinhey, 1962	C Africa
trinervulata Fraser, 1955*	*ukerewensis* Pinhey, 1961*	C Africa
ugandica McLachlan, 1896*	? *sembe* Pinhey, 1962	C Africa

The following acronyms for collections are used:

BMNH - Natural History Museum, London
ISNB - Institut Royal des Sciences Naturelles de Belgique, Brussels
MNHN - Muséum National d'Histoire Naturelle, Paris
MNMS - Museo Naçional de Ciencias Naturales, Madrid
MRAC - Musee Royal de l'Afrique Centrale, Tervuren
NHRS - Naturhistoriska Riksmuseet, Stockholm
NMBZ - Natural History Museum of Zimbabwe, Bulawayo
NMKE - National Museum of Kenya, Nairobi
RMNH - Nationaal Natuurhistorisch Museum Naturalis, Leiden
TMSA - Transvaal Museum, Pretoria
UCME - Departemento de Biologia, Universidad Complutense, Madrid
ZFMK - Zoologische Forschungsinstitut und Museum Alexander Koenig, Bonn
ZMHB - Museum für Naturkunde der Humboldt-Universität, Berlin
ZMUH - Zoologisches Institut und Zoologisches Museum, Universität von Hamburg

Characters

Coloration: The body of most species is largely brown to green, while legs and face often have a reddish or yellowish tinge. The antealar sclerites and markings on the abdomen may be blue. Coloration patterns of live specimens have diagnostic value, but must here be largely ignored because discoloration of preserved specimens is generally severe, dulling all colour and obscuring markings. In the past, species distinctions based on the more 'ferruginous' or 'ochraceous' nature of certain body parts were made, but only black markings, for instance on the frons, legs and metastigma (= metathoracic spiracle), are reliable characters (e.g. Figs 1, 2, 8). Gambles (1956) introduced the rim colour of the metastigma to distinguish between females of *G. nigeriensis* and *G. vesiculata* (erroneously identified as *G. villosa* by him); that of the latter has a black rim, contrasting with the colour of the synthorax. This character actually separates African *Gynacantha* into two distinct groups in both sexes (Table 2). Living specimens of *G. africana*, *G. cylindrata*, *G. immaculifrons*, *G. manderica*, *G. sextans*, *G. vesiculata*, *G. villosa*, *H. cynthiae* and *H. ugandica* have a pale blue crescent on the anterior side of the compound eyes (Table 1). The value of this lunule is difficult to assess, as it is easily lost in preserved specimens. Most species may develop smoky wings with age, this is particularly strong in *G. africana*. Especially in *Heliaeschna*, as well as some *Gynacantha* species, subcostal rays may be present (Figs 6a, 6d; Plate I). These are dark brown markings extending from the wing bases, concentrated in the subcostal spaces.
Venation: The variation of some venation characters is summarised in Tables 3 and 4. Although venation has been given much weight in gynacanthine taxonomy in the past, two important characters for African species have been overlooked. Typical *Gynacantha* possess a brace vein that – aligned with the proximal border of Pt – is much more oblique than other cross-veins below Pt (von Ellenrieder 2002). In *Heliaeschna* and the *africana*-group of *Gynacantha* there is no brace vein, all cross-veins below Pt being parallel (Figs 6a, 6d, 6e, 7a-c). Somewhat oblique veins at the position of the brace vein are occasionally encountered, but very rarely in all wings.

Table 2. Diagnosis of groups of African Gynacanthini by male characters. Rare aberrances – e.g. single median cross-veins sometimes seen in *Gynacantha* – excluded. For a full discussion of these characters see text.

	Gynacantha		***Heliaeschna***
***africana*-group**	***bispina*-group**	***bullata*-group**	
Rim of metastigma			
Black	Pale	Pale	Pale
Cross-veins in median spaces			
0	0	0	3-8
Cells in anal triangles			
3-6	3	3	3-6
Brace veins			
Absent	Present	Present	Absent
R2-R3 field proximal to Pt			
Many cells doubled	No cells doubled	No cells doubled	Few cells doubled at most
Shape of S3			
Cylindrical (3 spp.) or constricted (3)	Cylindrical (3 spp.) or constricted (1)	Constricted	Constricted
Basal fold of hamular process			
Very shallow, process flat	Deep, process tilted	Very deep, process tilted	Shallow, process tilted
Denticles along genital fossa			
Absent or irregular, mostly in posterior portion	Absent, at most a few in anterior portion	Neat rows in anterior portion	Irregular, mostly in posterior portion
Shape of cerci			
Bisinuous inner border, wide near apex	Sinuous inner border, wide near apex	Sinuous inner border, slender near apex	Sinuous inner border, leaf-like

The *africana*-group differs from other African Gynacanthini in having many cells in the field between R2 and R3 proximal to Pt doubled or tripled, resulting in 2 or 3 (instead of 1) rows of cells there. This may give the appearance of IR2 continuing almost to the subnodus (Fig. 6a). Large *Heliaeschna* specimens may also show some cell-doublings in this field (Fig. 6d). *Heliaeschna* differs from *Gynacantha* in the possession of 3-8 cross-veins in the median space of all wings (Figs 6d, 6e), although 1-2 are occasionally seen in the latter.

Secondary genitalia: The length and orientation of the paired spines on the anterior lamina differ among species, but are of little practical use because it is difficult to define the rather subtle differences. The anterior hamules terminate in flat hand-like extensions, the "anterior processes" of von Ellenrieder (2002), which may be tilted relative to their base, from which they are separated by a fold. The pronunciation of this basal fold differs among the groups (compare with von Ellenrieder & Garrison 2003). It is very shallow in the *africana*-group, where the processes are horizontal and lie in a single plain. In the other African Gynacanthini the fold is deeper, the processes are oblique to almost vertical, like the roof of a tent or hands

in prayer. In *Heliaeschna* the basal fold is round and shallow, in the *bispina*-group it is sharper and deeper, and in the *bullata*-group the process is even deeply incised at the fold. The shape of the auricles presents two extreme forms: a rounded auricle with the outer border strongly convex, curving gradually inwards (e.g. Fig. 3j), and a triangular auricle with a straighter outer border, abruptly curving inwards, resulting in a rather pointed outer angle (e.g. Fig. 3i). The pattern of denticles placed on ridges along the border of the genital fossa is diagnostic for many species; see paragraph on denticulation of the abdominal venter.

Constriction of S3: Most species have a distinct waist on S3 in both sexes: the lateral carinae converge strongly, the segment being narrowest about a third from the base (e.g. Fig. 3a). The lateral carinae are often absent or only weakly defined in the basal half of the segment, or they lie very closely against the ventral carinae. In some species S3 is not constricted but cylindrical in both sexes: the lateral carinae are (nearly) parallel and well-defined throughout, just falling short of reaching the base of the segment (e.g. Fig. 3b). In ventral aspect S3 therefore looks like S4. These species are *G. cylindrata*, *G. radama* and *G. vesiculata* of the *africana*-group and *G. bispina*, *G. immaculifrons* and *G. malgassica* of the *bispina*-group. In two apparently not closely related taxa S3 is constricted in the male and cylindrical in the female, these being *G. nigeriensis* in the *bullata*-group and *H. longfieldae*.

Denticulation of abdominal venter: The ventral portions of the tergites are demarcated by the lateral carinae exteriorly and the ventral carinae interiorly. The 'average' African gynacanthine bears denticles in a single row on the lateral carinae of S3-8, while the ventral carinae are bare. Species differ in their exceptions to this rule (mostly on distal segments), such as the expansion of single rows into irregular double (or even triple) rows. Variation is summarised in Table 5. Denticles are also placed on ridges along the anterior and posterior portions (separated at the point where the two sides of the fossa are closest) of the genital fossa border (S2).

Table 3. Variation of some wing characters in males of African *Gynacantha* species. Extreme variations are given in brackets. Note that for each specimen both wings have been quantified. Proposed taxonomic changes are included, e.g. *G. nigeriensis* includes (type) specimens of *G. flavipes* and *G. sevastopuloi*. *G. manderica* does not include the large Congo male (see species text). — Al: anal loop cells; At: anal triangle cells; Ax: antenodal cross-veins; Fw: forewing; Hw: hindwing; L: length [mm]; *: measurements of type specimens included (taken by author).

Species	***n***	**Hw L**	**Fw Ax**	**Hw At**	**Hw Al**
G. africana	12	49.5 - 56.0	28 - 34 (37)	3 - 5	15 - 26
*G. cylindrata**	22	47.0 - 50.0	22 - 29	3 - 5	10 - 17
*G. sextans**	12	46.0 - 51.0	26 - 31	3 - 6	15 - 27
*G. vesiculata**	12	44.5 - 47.5	21 - 25	3 - 4	11 - 17
*G. villosa**	26	47.0 - 53.0	22 - 28	3 - 5	10 - 20
*G. immaculifrons**	8	44.0 - 46.5	22 - 24	3	8 - 10
*G. bullata**	24	39.5 - 44.0	19 - 28	3 (4)	7 - 14
G. manderica	17	35.5 - 39.0	13 - 19	3	7 - 11
*G. nigeriensis**	19	43.0 - 46.5	22 - 27	3	8 - 13 (19)
*G. usambarica**	14	43.0 - 48.0	21 - 27	3	9 - 14

Denticulation is most pronounced in the *bullata*-group, where all species have a neatly aligned row of 8-20 denticles in the anterior portion (Figs 3g-j). This row is placed relatively far from the genital fossa, resulting in broad denticle-free edges along the fossa. Denticulation is (nearly) absent in the *bispina*-group (Fig. 3f). It is irregular in presence and pattern in the *africana*-group, the denticles being concentrated in the posterior portion (Figs 3a-e). Similarly, in *Heliaeschna* the denticles are concentrated in a row or irregular cluster in the posterior portion, extending somewhat onto the anterior portion.

Shape of cerci: The outer border of the cerci is nearly straight in all species (Fig. 4). The inner border is sinuous in most species: it gradually curves away from the outer border at the base, then curves back to the outer border at the apex, the apex often produced into a sharp spine. In the *africana*-group the inner border is bisinuous: it makes an additional curve about two-thirds from the base (Figs 4a-e). In *Heliaeschna* the curvature of the sinuous inner border is relatively abrupt, resulting in a leaf-like stalk and blade, an allusion that is strengthened by a midrib-like central ridge (Figs 4k-p). The stalked shape is also obvious in the long female cerci. Species differ in the position and extent of the widest point of the cerci: in *G. bullata* they are clearly widest just before the apex (Fig. 4g), though this widening is not as marked as in *G. immaculifrons* (Fig. 4f), while in *G. nigeriensis* they are more gradually widened, the widest point lying much further from the apex than in *G. bullata* (Fig. 4i). Larger species have a ventral (and slightly internal) thickening near the base of the cerci, which may appear as a low lump or blunt tooth, best seen on the inner border in dorso-lateral view (Figs 5b-d).

Behaviour and ecology: As far as is known, all Afrotropical *Gynacantha* species reproduce in seasonal pools and perhaps swamps in dense forest or bush. Oviposition in dry mud of depressions, weeks before they fill with water, has been observed in *G. africana*, *G. usambarica*, *G. vesiculata* and *G. villosa*, as well as non-African species (Gambles 1960; Miller 1995; Corbet 1999; V. Clausnitzer pers. comm.). Larvae and exuviae of *G. cylindrata* (Plate I), *G. manderica* and *G. vesiculata* (R.M. Gambles unpubl. manuscript "The Nigerian dragonflies"; K.-D.B. Dijkstra pers. obs.) have been found at such sites, once filled with water. I have observed a female of *G. immaculifrons* oviposit in the bank of a dry streambed. Gambles (1960) believed larval development in three Nigerian species lasted 2-3 months, while the remainder of the year (up to nine months between rains) was spent in the adult stage. Reproduction in tree-holes, known in tropical America for two *Gynacantha* species and two species of the related genus *Triacanthagyna*, is unknown from Africa (Corbet 1999). Adults rest in dense vegetation during the day (Plate I), and perhaps also in buildings: I have seen a large gynacanthine perched near the ceiling of a high room in Elmina Castle, Ghana, but it may have been attracted to light the previous night. Note that the holotype of *H. longfieldae* was caught in a cave. Resting adults often occur in small concentrations, probably at favourable sites (see also Neville 1960). Such an effect may explain "dormitories" seen by Fraser (1962) in India. Higher densities can be found in thick undergrowth along dry streambeds and bordering forested swamps. Males may be seen winding through the tangles at daytime, probably in search of females. All African species are crepuscular, flying at dusk and during rain, and may come to light at night. Large species like *G. cylindrata* fly fast and erratically in forest clearings, while small ones like *G. bullata* may hover cautiously along edges.

The habits of *Heliaeschna* are (probably) largely similar, but the species are much more localized and perhaps associated with more permanent water, like swamp forest or streams. The environs of Entebbe in Uganda are traditionally a hotspot for this genus (e.g. type locality of three or four taxa), possibly because specimens from the swampy forested surroundings have always been drawn to lighted houses at night. Lempert (1988) reports a larva of *H. fuliginosa* from a Liberian rainforest stream, and adults of both sexes flying along it. Neville (1960) saw *H. lanceolata* (= *fuliginosa*) "hawking over ponds all through the day until after dusk" and still heard them "when darkness fell", but did not mention whether the days were overcast. Flight behaviour included "long spells of hovering in one spot" 0.3-2 m above the ground and often for up to three minutes. Oviposition took place in "moist soil around the ponds".

Taxonomy of the species

Many of the species descriptions, among the recent ones especially those of Pinhey (1960, 1961, 1962b), are poor. The considerable variation observed may not only mask synonyms, but also specific distinctiveness. Moreover, the presence of distinct (female) morphotypes within so-called *G. manderica*, *G. villosa* and *H. longfieldae* suggests that the presented male-biased classification may be over-simplified. Nonetheless, I present here seven new cases where synonymy appears to be certain. The complex situation of the species near *H. fuliginosa* is difficult to resolve, but analysis of the available data suggests that considering all as one variable species is the most practical solution.

africana-group: *Gynacantha africana* (Palisot de Beauvois, 1807)

(Figs 3a, 4a, 8a)

Aeshna africana Palisot de Beauvois, 1807: 67 [no type specimen known: West Africa].
Gynacantha quadrina McLachlan, 1896: 414 [type: Mahambé, West Africa; BMNH]; junior synonym (R.M. Gambles unpubl. manuscript "The Nigerian dragonflies").
Gynacantha lieftincki Compte Sart, 1964: 15 [type: Bata, Equatorial Guinea; MNMS]; junior synonym (Legrand 1989).

Diagnosis

The largest African gynacanthine, Hw rarely shorter than 50 mm. It may be confused with its eastern counterpart *G. villosa*, with which it probably only overlaps in Uganda and E Democratic Republic of Congo (DRC). *G. villosa* has many denticles confined to the top of the ridge in the posterior portion of the genital fossa border (Fig. 3e), to no denticles at all. In *G. africana* denticulation is similar, but some denticles are scattered laterally onto the slope of the ridge (Fig. 3a). Denticulation is extensive on the ventral abdominal carinae in *G. villosa*, but not in *G. africana*.

The female of *G. africana* is unmistakable by the very large, leaf-like cerci. Both sexes tend to develop deeply amber-stained wings, whereas in *G. villosa* the wings more often (but not always) remain rather clear. Venation is very dense, as is apparent from the high Ax counts, but also from the cubital field that often has 2 (not 1) rows of cells at the base. The field between R2 and R3 usually has partly 3 (not 2) rows proximal to Pt. Similarly dense venation is only encountered in *G. sextans* (see that species).

Discussion

I confirm Gambles' opinion that *G. quadrina* is a synonym of *G. africana*, not of *G. vesiculata*. *G. quadrina* was described because the true identity of *G. africana* was obscure.

Gynacantha cylindrata Karsch, 1891

(Figs 3b, 4b; Plate 1)

Gynacantha cylindrata Karsch, 1891: 282, 308 [type: Chinchoxo, West Africa; ZMHB].

Diagnosis

The male is instantly recognised by the 'horse hoof' cerci (Fig. 4b). Both *G. vesiculata* and *G. cylindrata* have a cylindrical S3 and at most a few denticles restricted to the most posterior portion of the ridge along the genital fossa (Figs 3b, 3d). Reliable separation of females is difficult.

Gynacantha sextans McLachlan, 1896

(Figs 3c, 4c, 6a)

Gynacantha sextans McLachlan, 1896: 413 [type: Mongo-ma-Lobah, Cameroon; BMNH].
Gynacantha schultzei Le Roi, 1915: 347 [type: Benito, Equatorial Guinea; ZMUH]; junior synonym (Fraser 1962).
Gynacantha maesi Schouteden, 1917: 104 [type: Inongo, DRC; MRAC]; junior synonym (Fraser 1962).

Diagnosis

Venation characters combined with the dark subcostal rays generally suffice to identify both sexes (Fig. 6a). The species has rather dense venation, the number of Fw Ax and cells in the anal loop (AL) and anal triangle being high relative to its Hw length (Table 3). In males the ratio Hw/Fw Ax normally lies below 1.8 in *G. sextans* and above it in *G. cylindrata*, *G. vesiculata* and *G. villosa*. The ratio Hw/AL normally lies below and above 3 respectively. Only *G. africana* has similarly low ratios, which like *G. sextans* often has partly 3 (not 2) rows of cells proxi-

mal to Pt between R2 and R3. The ratios seem to apply to females too, the threshold values lying around 1.9 and 3.2. In contrast, *G. sextans* tends to have mainly 2 or 3 rows of cells in the fork of IR3, whereas the other *africana*-group species have 4 or 5. Compared with the other *africana*-group species, *G. sextans* has rather neatly aligned rows of denticles along the genital fossa extending anteriorly, but without the broad edge of the *bullata*-group (Fig. 3c, see paragraph on denticulation). Furthermore the hamular processes are more oblique, although not incised basally as in the *bullata*-group.

Discussion

The conditions of the genital fossa border and hamular processes are reminiscent of *Heliaeschna*, as are the subcostal rays, the few rows of cells in the fork of IR3 and the shape of S10 in the female. Added to the similarities shared by all *Heliaeschna* and *africana*-group species (Table 2), this suggests a close relationship between the two.

Gynacantha vesiculata Karsch, 1891

(Figs 3d, 4d, 5a)

Gynacantha vesiculata Karsch, 1891: 282, 307 [type: Chinchoxo, West Africa; ZMHB].

Acanthagyna ochraceipes Pinhey, 1960: 511 [type: Kasoge Base Camp, Tanzania; NMBZ]; new synonymy.

Diagnosis

The smallest species of the *africana*-group. The male is recognised by the shape of the cerci and S3 (Figs 3d, 4d, 5a). See also under *G. cylindrata*.

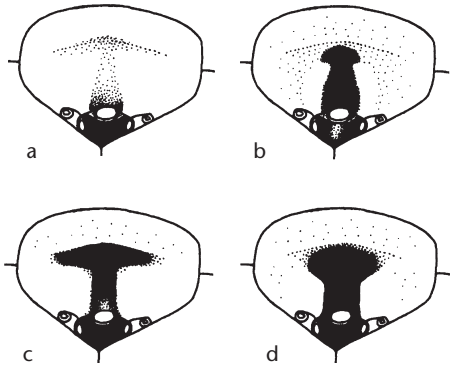

Figure 1: Frons, dorsal view — (a) *Gynacantha immaculifrons*; (b) *G. manderica*; (c) *G. nigeriensis*; (d) *G. usambarica*.

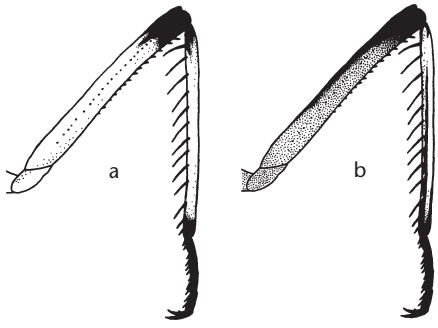

Figure 2: Hind leg, lateral view — (a) *Gynacantha bullata*; (b) *G. manderica*.

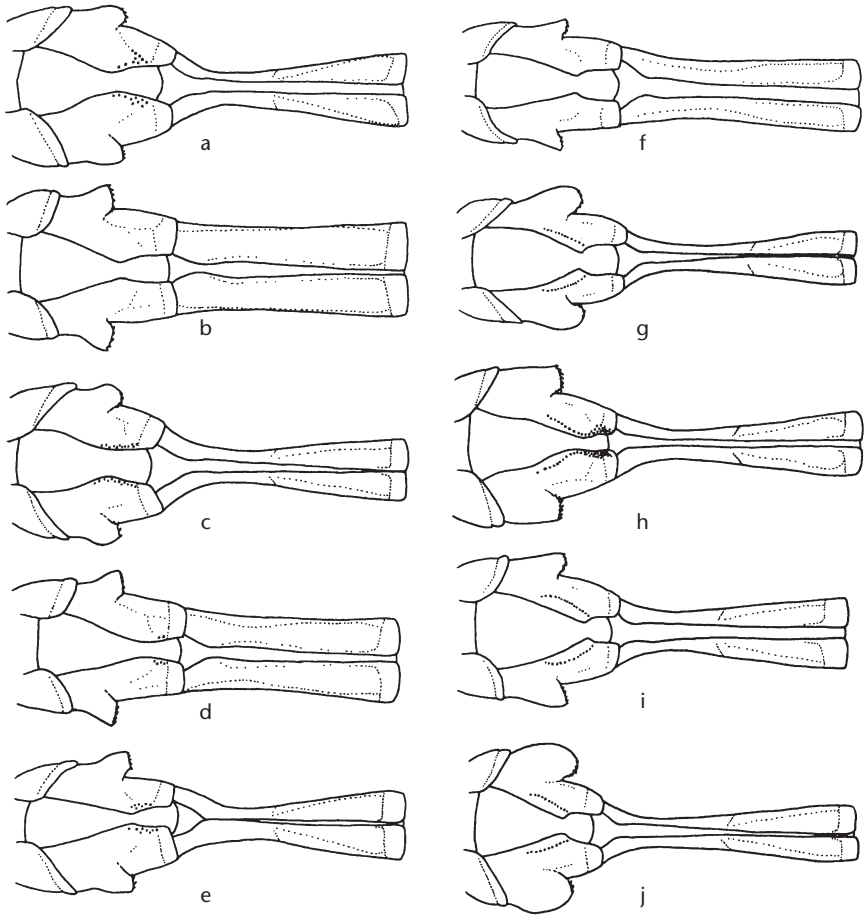

Figure 3: Male S2-3, ventral view — (a) *Gynacantha africana*; (b) *G. cylindrata*; (c) *G. sextans*; (d) *G. vesiculata*; (e) *G. villosa*; (f) *G. immaculifrons*; (g) *G. bullata*; (h) *G. manderica*; (i) *G. nigeriensis*; (j) *G. usambarica*.

Discussion

Pinhey (1960) described *G. ochraceipes* from the Mahale Mountains on the eastern shore of Lake Tanganyika. He later reported it from N Malawi and the Central African Republic (Pinhey 1984). Donnelly (2002) reported females from W Uganda, even though a good diagnosis for that sex has not been published. Pinhey (1960) provided only a very brief description for *G. ochraceipes*, and illustrated typical *G. vesiculata* cerci with only a slight basal swelling and a rather pointed apex. Pinhey (1960, 1984) stated that *G. ochraceipes* is much smaller than *G. villosa* and *G. vesiculata*. The Hw measurements he provided for *G. vesiculata* (50-51 mm) are

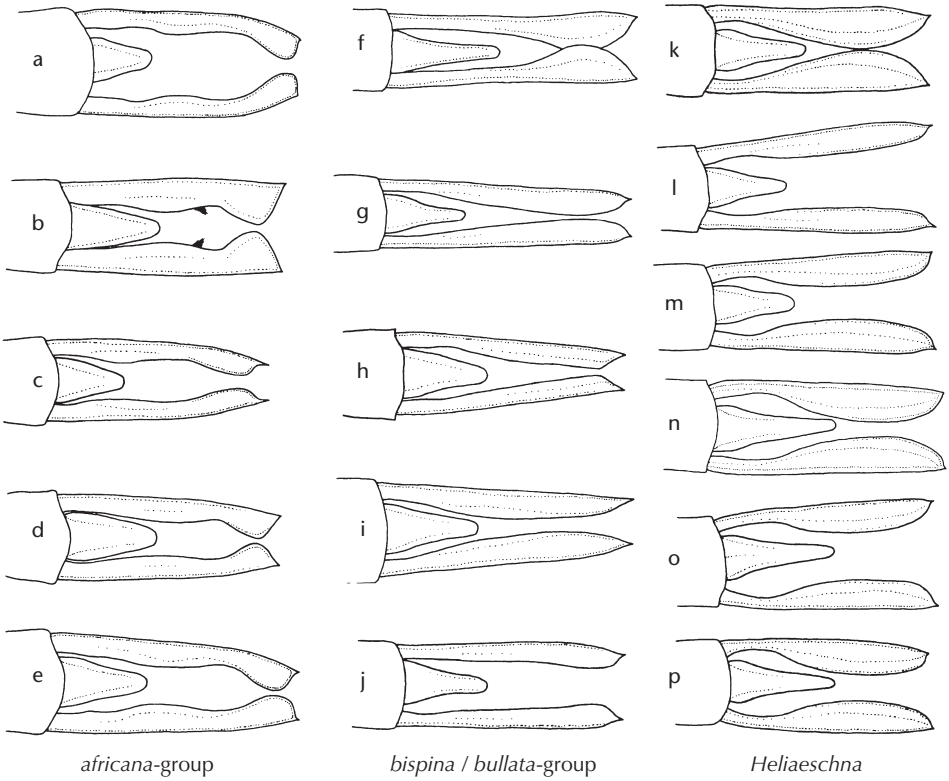

Figure 4: Male appendages, dorsal view — (a) *Gynacantha africana*; (b) *G. cylindrata*; (c) *G. sextans*; (d) *G. vesiculata*; (e) *G. villosa*; (f) *G. immaculifrons*; (g) *G. bullata*; (h) *G. manderica*; (i) *G. nigeriensis*; (j) *G. usambarica*; (k) *H. cynthiae*; (l) *Heliaeschna fuliginosa* Nigeria (= *'fuliginosa'*); (m) *H. fuliginosa* Uganda (= *'libyana'*); (n) *H. longfieldae*; (o) *H. trinervulata*; (p) *H. ugandica*.

too great for that species but match those of *G. villosa* (47-53 mm), while the measurement for the *G. ochraceipes* holotype (46 mm) agrees with those of *G. vesiculata* (44.5-47.5 mm). It is apparent from his East African records that Pinhey confused *G. vesiculata* and *G. villosa*, specimens of checked records of the first are referable to the latter (Clausnitzer 2003, and pers. comm.). On the other hand, I have re-identified males reported as *G. villosa* from PN Garamba by Pinhey (1966c) as *G. cylindrata* and *G. vesiculata*. With the name *G. vesiculata* being occupied by *G. villosa* specimens in his usage, Pinhey would thus have had to create a new name for true *G. vesiculata* specimens. There are three males and three females in the RMNH from Sibweza in the Mpanda District. This site lies in the same highlands as the *G. ochraceipes* type locality and the specimens agree entirely with typical *G. vesiculata* and with the description of *G. ochraceipes*. The latter name is thus considered a junior synonym of *G. vesiculata*.

Gynacantha villosa Grünberg, 1902
(Figs 3e, 4e, 5b)

Gynacantha villosa Grünberg, 1902: 233 [type: Langenburg, Tanzania; ZMHB].

Diagnosis

The only *africana*-group species in much of its range, which extends from coastal Kenya to E DRC, N Botswana and Natal. See under *G. africana*.

Discussion

As stated under *G. vesiculata*, that species has frequently been confused with *G. villosa*. Pinhey generally referred specimens of *G. villosa* to *G. vesiculata* (e.g. Pinhey 1960, 1961, 1984), while Gambles (1956) did the reverse. Examined females from Katanga, Rwanda and Uganda, differ from those from coastal Tanzania. The former have S3 strongly constricted, cerci broad and leaf-like (7.5x1 mm), S9 only slightly longer than S8, and ventral carinae S3-5 (almost) bare. The latter have S3 almost cylindrical (lateral carina slightly incurved towards base), cerci narrow and stiletto-like (6.5x0.6 mm), S9 almost twice as long as S8, and ventral carinae S3-5 denticulate. The coastal females are thus similar to *G. cylindrata* females, which have S3 cylindrical (lateral carina straight), cerci small and stiletto-like (5x0.3 mm), S9 just over to almost twice as long as S8, and ventral carinae S3-5 denticulate. Compared with males from Kenya, E Tanzania and Malawi (including the holotype), those from Rwanda, W Tanzania and Uganda are heavier in build with a more strongly constricted S3 and wider cerci, their apex being less acute and thus more square-cut. Denticulation on the genital fossa border is denser (often completely bare in coastal males) and the spines on the anterior lamina are larger and straighter, reaching beyond the hamular processes. Figs 3e, 4e and 5b show a male from Kampala, Uganda. Study of more specimens is needed to see if differences are stable and non-clinal, warranting separation of a western species.

bispina-group: *Gynacantha immaculifrons* Fraser, 1956
(Figs 1a, 3f, 4f)

Gynacantha immaculifrons Fraser, 1956: 385 [type: Lubumbashi, DRC; MRAC].

Diagnosis

The only member of the *bispina*-group on the mainland, the male is easily identified by its plain metastigma, genital fossa border with scarce denticles (0-4), at most slightly waisted S3 (Fig. 3f), and the shape of the cerci (Fig. 4f). The faintly marked frons is unique in African *Gynacantha* (Fig. 1a). The frons and S3 also identify the female.

Discussion

The species appears to be closely related to *G. bispina* and *G. malgassica*. Aside from the characters provided in Table 2, this is also apparent from the male's abdominal denticulation, which is the same in these insular species as in *G. immaculifrons* (see Table 5): The 'inversion' on S8 (lateral carinae bare, but ventral carinae denticulate) is unique in Afrotropical gynacanthines. Perhaps *G. immaculifrons* is a relatively recent oceanic arrival to the continent. It is one of the rarest African *Gynacantha* species. In addition to the types (a pair in MRAC and one female in BMNH) from Lubumbashi, I have seen specimens from near Nkhata Bay in N Malawi (one female, leg. K.-D.B. Dijkstra, RMNH) and from the Rufiji Delta (two males, one female, leg. & coll. V. Clausnitzer) and the Muheza District (one male, leg. anonymous, BMNH) of Tanzania. Four additional males and one female from Lubumbashi were found in MRAC.

bullata-group: *Gynacantha bullata* Karsch, 1891
(Figs 2a, 3g, 4g, 6b)

Gynacantha bullata Karsch, 1891: 282, 306 [type: Chinchoxo, West Africa; ZMHB].
Gynacantha bullata elongata Fraser, 1957: 339 [type: Eala, DRC; MRAC]; junior synonym (Pinhey 1966b).
Acanthagyna victoriae Pinhey, 1961: 101 [type: Entebbe, Uganda; BMNH]; new synonymy.

Diagnosis

The smallest African *Gynacantha* after *G. manderica*, both sexes instantly recognisable by the dark ringed 'knees' (Fig. 2a).

Discussion

Pinhey (1962b) stated "It seems probable that Fraser's subspecies *elongata* (1957) from the Congo, with its very long appendages, is a distinct species". Later however, after examining the holotypes of both *G. bullata* and *G. b. elongata*, Pinhey (1966b) noted that Fraser's (1957) measurements were exaggerated and concluded that "it is evident that *elongata* is not a distinct subspecies but at most a variety". He added that "it may be significant that Fraser (1962) omits *elongata* from his [...] revision." It must be noted that the allotype female of *G. b. elongata* belongs to *G. vesiculata*, adding further 'false distinctiveness' to this taxon. The brief description of *G. victoriae* by Pinhey (1961) offered no clue as to why he recognised the taxon as distinct from *G. bullata*, besides of the specimens being smaller and paler. *G. bullata* is one of the most widespread and abundant species of the genus and the type specimens and the long series of *G. victoriae* in the BMNH and NMKE fall within the variation range of *G. bullata* specimens examined from allover the continent. Pinhey (1966b) himself admitted that "this species [*G. bullata*],

found in many equatorial African forests, varies in size". The paleness of *G. victoriae* can be explained by the teneral state of the specimens involved. With no differences in other characters (e.g. auricles, constriction of S3, denticulation, appendages) I consider *G. victoriae* a junior synonym of *G. bullata*.

Gynacantha manderica Grünberg, 1902

(Figs 1b, 2b, 3h, 4h, 6c)

Gynacantha manderica Grünberg, 1902: 234 [type: Mandera (Ukami), Tanzania; ZMHB].

Diagnosis

The smallest African *Gynacantha* (the only species with Hw normally shorter than 40 mm), easily recognised by its short, rounded wings with low Ax count (Fig. 6c), markings on legs (Fig. 2b) and synthorax, the genital fossa denticulation (Fig. 3h) and the shape of the cerci (Fig. 4h). The species has a dark, triangular spot on the centre of the synthoracic venter, which the other species normally lack. A Congolese variety (see below) is darker and larger, with higher vein counts.

Discussion

G. hova from Madagascar is possibly conspecific (Fraser 1962). There are two females from DRC in ISNB (both from Kinshasa), three in MRAC (Elisabetha, Elisabethville, Binga) and one in RMNH (Mobeka), as well as single male in ISNB from Leopoldville (= Kinshasa). These are close to *G. manderica* by markings of the legs (although less contrasting, possibly due to staining), frons (although T-mark thicker, reminiscent of *Aeshna ellioti* Kirby, 1896) and synthorax, as well as abdomen shape and denticulation. The male cerci are relatively wider in their middle portion. The females are large (Hw 44-48.5 mm) and have rather dense venation (22-27 Fw Ax, 15-19 anal loop cells), the male is similar (Hw 44 mm, 22-24 Fw Ax, 16-17 anal loop cells). These values are well above those of normal *G. manderica* (see Table 3). Distinctive are dark basal rays in the females' wings, reaching about

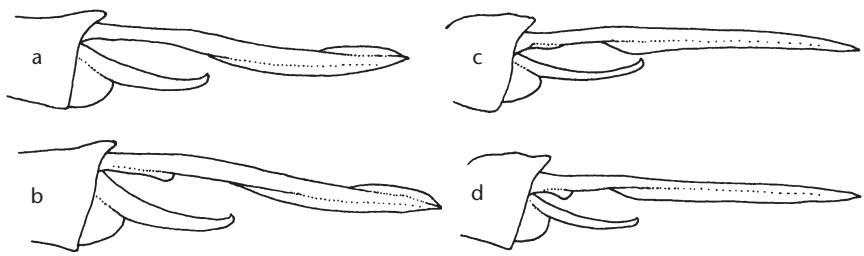

Figure 5: Male appendages, lateral view — (a) *Gynacantha vesiculata;* (b) *G. villosa;* (c) *Heliaeschna fuliginosa* Nigeria (= '*fuliginosa*'); (d) *H. fuliginosa* DRC (= '*lanceolata*').

to Ax2 or Ax3 in the subcostal spaces, for which they had been identified as *G. sextans*. Shorter and fainter rays are present in the cubital spaces. Females of *G. manderica* have faint rays too, but much more restricted. In the male the subcostal rays are shorter, reaching Ax1. Although the features of these Congolese specimens seem discrete, with only a handful of stained specimens and without diagnostic morphology, I hesitate to name them as a distinct taxon. I have seen normal *G. manderica* from DRC in these collections from PN Garamba, PN Upemba, Katanga and Kibombo. The records suggest some overlap of the forms at least in S DRC.

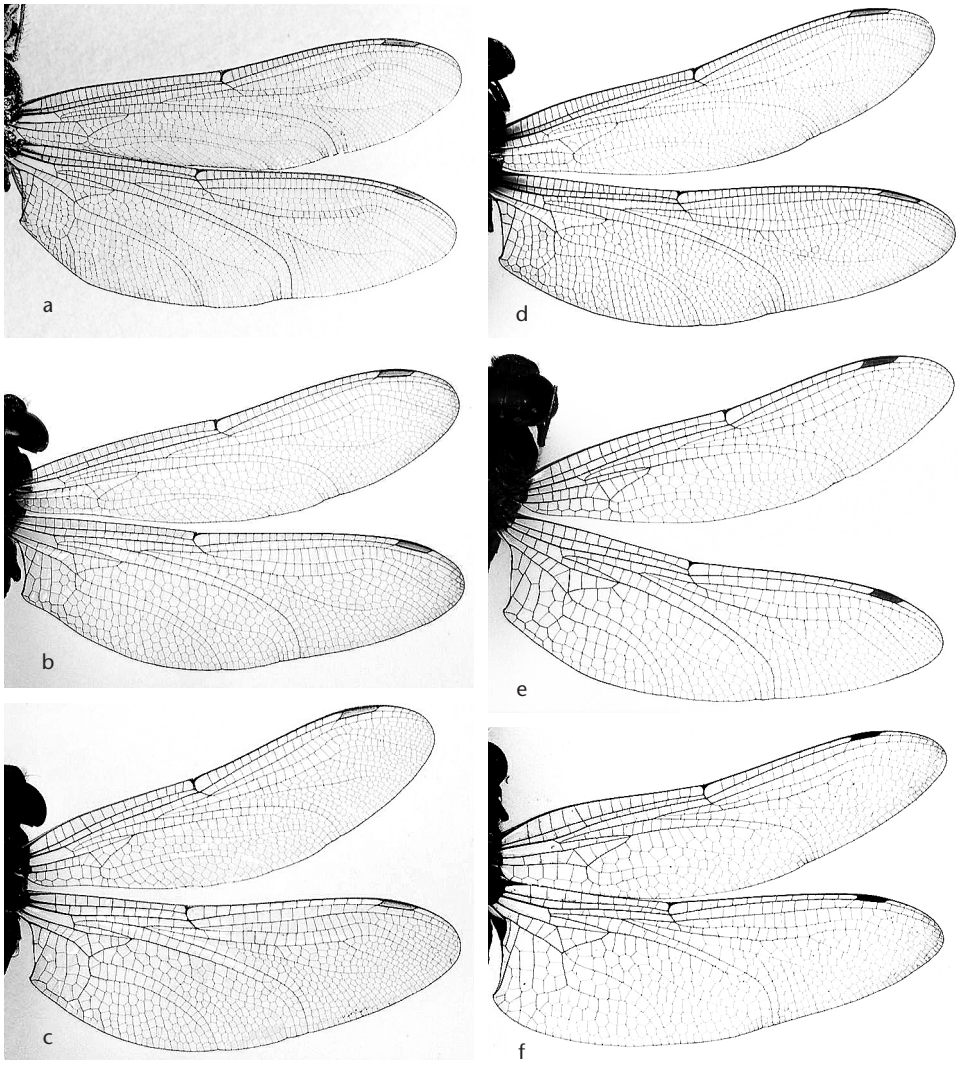

Figure 6: Male wings — (a) *Gynacantha sextans*; (b) *G. bullata*; (c) *G. manderica*; (d) *Heliaeschna fuliginosa* Uganda (= *'libyana'*); (e) *H. trinervulata*; (f) *Aeshna ellioti*.

Gynacantha nigeriensis (Gambles, 1956)
(Figs 1c, 3i, 4i)

Acanthagyna nigeriensis Gambles, 1956: 194 [type: Vom, Nigeria; BMNH].
Gynacantha flavipes Fraser, 1956: 386 [type: Lubumbashi, DRC; MRAC]; new synonymy.
Acanthagyna sevastopuloi Pinhey, 1961: 100 [type: Kampala, Uganda; BMNH]; new synonymy.

Diagnosis

Males have a diagnostic combination of characters: T-mark on frons with narrow stem (Fig. 1c), auricles small and triangular and S3 not so strongly constricted (Fig. 3i), ventral carinae of S8 with denticles tending to form a double row, and cerci evenly widened (Fig. 4i). Females are unusual for the *bullata*-group by the cylindrical S3 and long S9. The yellow face and legs of this species are distinctive in the field.

Discussion

Gambles (1956) described *G. nigeriensis* from Nigeria, Fraser (1956) *G. flavipes* from Katanga, and Pinhey (1961) *G. sevastopuloi* from Uganda. Neither of these species, described within such a short time-span from such widely separated areas, was compared to the others by their authors. Subsequently Gambles (unpubl. manuscript) reported his species from Sierra Leone and Congo, while Pinhey (1984) listed his for Zambia, Tanzania, Congo and "possibly westwards to Guinea", filling the distribution gap. Comparison of the three holotypes and seventeen additional males from Benin, Cameroon, Ethiopia, Ghana, Katanga, Nigeria and Uganda revealed no significant differences and showed that males share a set of characters that differs from all other African *Gynacantha*, as summarised in the diagnosis above. *G. nigeriensis* and *G. flavipes* further agree in the cylindrical S3 of the female, and the relatively bright yellowish face and legs. The female of *G. sevastopuloi* was not described, and the face and legs of its males are said to be more rufous (not apparent when holotypes compared). The three overlap in size and venation details. They appear to constitute one wide-ranging, scarce species, the name *G. nigeriensis* published in May 1956 taking priority over *G. flavipes* published in December of the same year.

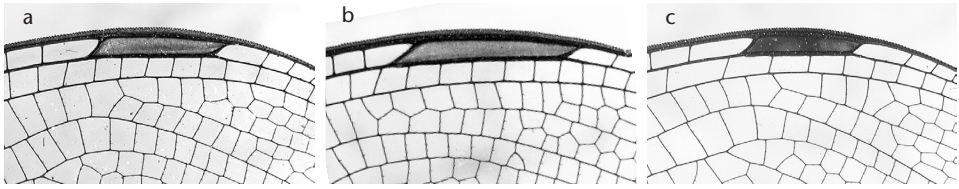

Figure 7: Pterostigma in male forewing — (a) *Heliaeschna cynthiae*; (b) *H. fuliginosa* Uganda (= *'libyana'*); (c) *H. ugandica*.

Gynacantha usambarica Sjöstedt, 1909
(Figs 1d, 3j, 4j)

Gynacantha usambarica Sjöstedt, 1909: 36 [type: Mombo, Usambara, Tanzania; NHRS].
Acanthagyna zuluensis Balinsky, 1961: 79 [type: Richard's Bay, Natal; TMSA]; new synonymy.

Diagnosis

The male is the only African *Gynacantha* with unmarked legs and metastigma as well as large rounded auricles (Fig. 3j). Whereas most African gynacanthines are largely marked green or brown, males of this species have all pale spots on the abdomen blue. Distinctive in both sexes are the tiny denticles on the centre of the first sternite, although this feature can be hard to see and may be present in some *africana*-group species (*G. cylindrata*, *G. sextans* and *G. vesiculata*).

Discussion

Balinsky (1961) described *G. zuluensis* from the Natal coast. Unlike most descriptions, his actually includes a comparison with the most similar species, *G. usambarica*. These two taxa are confined to – and were described from opposite ends of – the East Coast forest biome that stretches from S Somalia to NE South Africa (e.g. White 1983; Burgess & Clarke 2000). Records of *G. zuluensis* from near Beira in Mozambique and Nkhata Bay in Malawi by Pinhey (1966a; 1981) narrow the distribution gap between the two. Balinsky (1961) listed five structural differences, apparently based on comparison of Sjöstedt's (1909) description and illustration, but not of (type) specimens. These are the size of the denticles on the auricles (larger in *G. zuluensis*); position of tornus of Hw (reaching further relative to auricles); length of epiproct (longer); shape of frons (more pointed) and colour of legs (more reddish). In my experience, most of these characters are of dubious taxonomic value. Leg colour is influenced by age, the relative distance of tornus and auricles by the position of the wings. The auricle denticulation cannot be judged well from Sjöstedt's figure and the frons may be pushed in, as often happens with preserved specimens. In series of '*usambarica*' males from coastal Kenya and Tanzania and '*zuluensis*' from Malawi and Natal all these differences are not apparent or break down with variation. Moreover, the specimens agree in the shape of the appendages and the denticulation of the abdomen, including the diagnostic denticles on the first sternite. They also share the extensively blue-marked abdomen. From the specimens examined it is apparent that the species from Malawi and Natal is the same as that occurring in Tanzania and Kenya. The descriptions and illustrations of both *G. usambarica* and *G. zuluensis* are detailed and agree with this single East Coast species. The two names are therefore regarded as synonyms.

Heliaeschna cynthiae Fraser, 1939
(Figs 4k, 7a)

Heliaeschna cynthiae Fraser, 1939: 89 [type: Entebbe, Uganda; BMNH].

Diagnosis

Males are best recognised by the shape of the cerci (Fig. 4k). The female is similar to *H. ugandica*, Pt size being the most reliable distinction (Fig. 7a). In *H. cynthiae* it is about as long as 5-6 underlying cells in all wings, rather than 3-4 cells.

Heliaeschna fuliginosa Selys, 1883
(Figs 4l, 4m, 5c, 5d, 6d, 7b, 8b; Plate I)

Heliaeschna fuliginosa Selys, 1883: 38 [type: West Africa; ISNB].
Heliaeschna lanceolata Le Roi, 1915: 346 [type: Duma, Ubangi, DRC; ZMUH], new synonymy.
Gynacantha libyana Fraser, 1928: 136 [type: Entebbe, Uganda; BMNH], new synonymy.
Heliaeschna raymondi Compte Sart, 1967: 10 [type: Bata, Equatorial Guinea; UCME], new synonymy.

Diagnosis

Males are easily recognised by their large size and high vein counts (see Table 4), dark thoracic bands (Fig. 8b) and short epiproct (Figs 4l, 4m). Females combine the first three characters with a constricted S3.

Discussion

The large *Heliaeschna* specimens in the BMNH, ISNB, MNHN and MRAC have variably been placed under *H. fuliginosa*, *H. lanceolata* and *H. libyana*. Although largely similar to each other, the males differ subtly in size, vein counts, shape of cerci and extent of the subcostal rays. Variation in size and venation appears to follow a geographic pattern: Table 4 summarises this for 82 males assigned to five regions. Average size and vein counts decrease westwards: western African males (WA: Senegal to Cameroon) have 85% of anal triangles 3-celled, against only 6% in central Africans (CA: Gabon to Uganda). WA have 72% of Fw with ≤ 30 Ax, against 10% for CA. WA have 57% of anal loops with ≤ 13 cells, against 24% for CA. WA tend to have equal numbers of median cross-veins in Fw and Hw, whereas CA on average have an extra one in each Fw: 12% of WA males have both Fw with 1-3 cross-veins more than Hw, against 60% in CA. To give an indication of the discriminative power of these values: using just the most reliable character, the anal triangle, only 6% of the 82 specimens would have been assigned to the wrong region, while 7% would have been inconclusive (e.g. have one anal triangle 3- and the other 4-celled). If Fw Ax are added as a supporting character, just 4% would be assigned wrongly, but 28% would be inconclusive or conflicting (i.e. the characters not agreeing). With the median cross-veins as a third character, figures

would be 0% and 52%. The extent of the subcostal rays seems to vary locally, for instance being (almost) absent in the centre of the Congo Basin and prominent to beyond Ax2 in Uganda (Table I). Morphological differences are small and especially variable. Moreover, they cannot easily be quantified. The width of the cerci and the shape and thickness of the lump at their base can differ clearly among specimens. Series from single localities can be quite uniform – for instance having a thick almost tooth-like lump (Fig. 5d) – but contain single specimens having a slight one (Fig. 5c) or even none at all. Generally WA males tend to have narrower (Fig. 4l) cerci than CA ones (Fig. 4m), but specimens from Tai Forest in Côte d'Ivoire (MNHN) show both conditions.

The taxonomic situation of the large *Heliaeschna* is difficult. With our current knowledge it is possible to fairly reliably separate western and eastern specimens by venation, but with the observed paucity of morphological distinctiveness and stability there is no firm basis for separating clear-cut taxa. A complicating matter is the unclear identity of some types. The first valid description of *H. fuliginosa* is usually assigned to Karsch (1893). This author considered the name to be introduced by Selys (1883), but that was later regarded a nomen nudum (e.g. Pinhey 1962a; Bridges 1994), because Selys only mentioned the species name in a diagnosis of the genus. This diagnosis counts as the first valid description of *H. fuliginosa* because it is the only species incorporated (pers. comm. J. van Tol, L. Holthuis). Typical WA males in ISBN labelled as types of "*H. fuliginosa* Selys" by Martin thus constitute the primary types. This is fortunate, as Karsch's '*fuliginosa*' male belongs to *H. cynthiae*, although the female is *H. fuliginosa*-like. Pinhey (1962a) did not know the locality of the *H. lanceolata* holotype, but it is in ZMUH (Weidner 1962, 1977). The male – soft and faded by nearly a century in alcohol – still shows all characters of the large *Heliaeschna*. Specimens from the Congo Basin and Uganda (including the male holotypes of *lanceolata* and *libyana* respectively) cannot be separated, e.g. both have rather wide cerci. Compte Sart (1967) described *H. raymondi* from two females. They are typical large *Heliaeschna*, the holotype being unusual only by its long cerci (13 mm). This is probably an extreme state – *Heliaeschna* females have very long cerci and this is a large specimen (Hw 54 mm) – of a character whose variation cannot easily be assessed. In most females the cerci are largely lost, moreover specimens are scarce, especially of females associated with (similarly confusing) males. Indeed, even the paratype has broken cerci and cannot – with the only possibly diagnostic character gone – be positively associated with the holotype, other than by locality. In the light of the above, it seems best to treat all large *Heliaeschna* as one widespread and variable species.

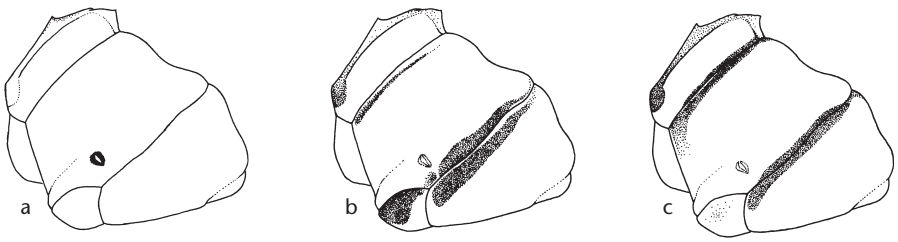

Figure 8: Male synthorax, lateral view — (a) *Gynacantha africana*; (b) *Heliaeschna fuliginosa* Uganda (= '*libyana*'); (c) *H. longfieldae*.

Heliaeschna longfieldae Gambles, 1967
(Figs 4n, 8c)

Heliaeschna longfieldae Gambles, 1967: 200 [type: Mount Cameroon; BMNH].
? *Heliaeschna sembe* Pinhey, 1962b: 39 [type: Sembe, Souanke, Congo; NMBZ]; possible synonymy.

Diagnosis

Males believed to be this species possess a unique combination of characters of the large (*H. fuliginosa*) and small species (*H. cynthiae*, *H. trinervulata* and *H. ugandica*) of *Heliaeschna*: The thorax is for instance marked similarly to the former (Fig. 8c), but appendages are shaped as in the latter (Fig. 4n). Their size is intermediate, while Pt size and venation is nearer to those of the large species, venation thus being rather dense (Table 4). Short subcostal rays are often present, but may also be absent. The cerci are about twice as long as the epiproct, with a wide blade and without a basal lump (Fig. 4n). The humeral and metapleural dark bands are almost equally broad in males, black being narrowly present on both sides of the sutures (Fig. 8c). In males of *H. fuliginosa* the black is very broad on both sides of the metapleural suture, but narrow on the humeral suture where it is confined to the posterior side (Fig. 8b). In *H. longfieldae*-like females the bands are more *fuliginosa*-like, with almost indiscernible humeral bands and broad metapleural bands. The females are the only African *Heliaeschna* with a cylindrical S3. They are large (Hw 51-53 mm) with numerous Fw Ax (30-38).

Discussion

Longfield (1936) described a distinctive female taken in a cave on Mount Cameroon, but in the absence of a male abstained from naming it. Gambles (1967) named the species in Longfield's honour, but the female – now the holotype – remained the only known specimen. Years later Pryce (1999) examined "a very broad, shallow, well shaded stream" near Muambong in SW Cameroon. He wrote: "I saw something moving rapidly in the shade and took a swipe at that. As it entered the net all I could make out was that it was a mating pair – of what I did not know. It turned out to be one of the highlights of the trip: a pair of the very poorly known genus *Heliaeschna*." Photographs of the pair are depicted in Silsby (2001) identified as *H. lanceolata*, but the cylindrical abdomen of the female suggests it is closer to *H. longfieldae*. Gambles (1967) remarked that "the unconstricted abdomen of the female carries no implication that the male will be similar in this respect", referring to the sexual dimorphism of the feature in *G. nigeriensis*. The Muambong male has a constricted abdomen, unlike the female. Gambles continued that "a character more likely to be useful [...], is the number of antenodal veins in the forewing", referring to the very high counts in the holotype of *H. longfieldae* (36-38). The Muambong female agrees in the high number of such veins (32-34), the counts of the male also being quite high (27-29). Following the recognition of the Muambong pair as being close to *H. longfieldae*, a similar male was located in BMNH, as well as seven males and two females in MRAC. All are from DRC: the BMNH male from Eala, the other males from Bambesa, Bobey, Kafakumba (2), Katompe, Lokasda and Thepaza; the females from Eala and Kapanga. MNHN has males from Gabon (2), Yéalé (at the foot of Mt Nimba in Côte d'Ivoire) and

Cameroon. NHRS has a male from Cameroon, presumably that reported from Bonge as *H. fuliginosa* by Sjöstedt (1900), and ZFMK five without locality data collected in December 1957.

With the Muambong pair as the key to solve the puzzle, augmented with the examination of the *H. longfieldae* holotype and the twenty additional specimens, it seems possible to diagnose both sexes of *H. longfieldae* (see above). Males possess a distinctive combination of *H. ugandica*-like appendages and *H. fuliginosa*-like thoracic markings, while the cylindrical S3 of the females is equally unique. The *H. longfieldae* puzzle seems to be solved, were it not for some features of the Muambong female: S9 is markedly longer (including the ovipositor that is also straighter) and the spines of S10 are directed backward more than in the holotype and DRC females. The 19 examined males appear to be uniform in their characters. A situation similar to that described for *G. manderica* and *G. villosa* reveals itself: characters (particularly of females) suggest the presence of more taxa, but specimens are limited, as are clear differences in males. Without sufficient specimens and clear differences in males and with one published name, I choose to consider each case as representing a single heterogeneous species. A parallel can be seen in the genus *Oligoaeschna* on Borneo where male forms are outnumbered by female forms by seven to eleven or more (Orr 2003). Adding to the problem, *H. sembe* was described from the NW corner of Congo-Brazzaville as a species similar to *H. ugandica*. The scanty information provided by Pinhey (1962b) neither gives strong clues for synonymy with that species, nor does it provide any truly diagnostic characters. The minimal differences described in size, leg coloration and appendages may fall within the variation of either *H. longfieldae* or *H. ugandica*. The description does not mention thoracic bands. Pt length would also be diagnostic: Pinhey (1962b) stated this is 2.5 mm in the *H. sembe* Hw, but in comparison writes that it is "only 3 mm" in *H. ugandica*, suggesting the former measurement is erroneous, the Pt actually being larger. If found to be conspecific, the name *H. sembe* will have priority over *H. longfieldae*.

Heliaeschna trinervulata Fraser, 1955

(Figs 4o, 6e)

Heliaeschna trinervulata Fraser, 1955: 16 [type: Entebbe, Uganda; BMNH].
Heliaeschna ukerewensis Pinhey, 1961: 103 [type: Ukerewe Island, Tanzania; NMKE]; new synonymy.

Diagnosis

The smallest African gynacanthine, rivalled only by *G. manderica*, and like that species always with under 20 Fw Ax (Fig. 6e). Morphologically it is similar to *H. ugandica*, tenerals of which may also have plain frons and legs.

Discussion

Pinhey (1961) described *H. ukerewensis* from Ukerewe Island in the S of Lake Victoria. He admitted that because Fraser (1955) did not provide illustrations, an adequate comparison could not be made with *H. trinervulata*, the type locality of which lies on the opposite side of the lake. The long epiproct, rather narrow cerci,

Table 4. Variation of some wing characters in males of African *Heliaeschna* species, ordered from largest to smallest, from east to west within *H. fuliginosa*. Variation is expressed as complete range observed (100%), range in median two-thirds of specimens (67%) and average (av.). Geographic indications for *H. fuliginosa* — East: Uganda, NE and SE DRC (incl. *H. libyana* holotype); Congo: Congo Basin (incl. *H. lanceolata* holotype); CamNig: Cameroon and Nigeria (incl. *H. fuliginosa* types); West: Ghana to Senegal; Al: anal loop cells; At: anal triangle cells; Ax: antenodal cross-veins; Fw: forewing; Hw: hindwing; L: length; Mx: median cross-veins; *: measurements of type specimens included (taken by author).

Species	***n***	**Hw L**			**Hw At**		
		av.	**67%**	**100%**	**av.**	**67%**	**100%**
H. fuliginosa East	16	49.3	47.0 - 51.5	47.0 - 52.0	4.3	4 - 5	3 - 6
H. fuliginosa Congo	26	50.1	48.5 - 51.5	47.5 - 53.5	4.0	4	3 - 5
H. fuliginosa Gabon	7	47.7	45.5 - 50.0	45.0 - 51.5	4.5	4 - 5	3 - 6
H. fuliginosa CamNig	23	48.9	48.0 - 50.0	46.5 - 50.5	3.1	3	3 - 4
H. fuliginosa West*	11	47.6	46.0 - 49.0	45.5 - 49.5	3.2	3	3 - 4
H. longfieldae	19	42.6	40.5 - 45.0	39.5 - 46.0	3.3	3 - 4	3 - 5
*H. cynthiae**	17	42.4	40.0 - 44.0	38.0 - 45.0	3.1	3	3 - 4
*H. ugandica**	16	39.8	39.0 - 41.0	37.0 - 42.0	3.2	3 - 4	3 - 4
*H. trinervulata**	5	36.2	35.0 - 38.0	35.0 - 38.0	3.0	3	3

Species	***n***	**Fw Ax**			**Hw Al**		
		av.	**67%**	**100%**	**av.**	**67%**	**100%**
H. fuliginosa East	16	31.6	30 - 33	27 - 35	14.6	13 - 16	9 - 18
H. fuliginosa Congo	26	32.3	31 - 34	29 - 35	15.4	13 - 17	11 - 20
H. fuliginosa Gabon	7	31.8	31 - 33	30 - 33	14.4	13 - 16	11 - 19
H. fuliginosa CamNig	23	29.8	28 - 31	26 - 36	13.5	12 - 15	10 - 18
H. fuliginosa West*	11	28.6	27 - 31	25 - 32	12.1	10 - 14	8 - 15
H. longfieldae	19	27.8	26 - 30	23 - 32	10.6	9 - 12	8 - 14
*H. cynthiae**	17	26.8	24 - 29	23 - 30	12.1	11 - 13	8 - 15
*H. ugandica**	16	22.4	20 - 25	20 - 27	9.2	8 - 11	7 - 13
*H. trinervulata**	5	17.1	15 - 19	15 - 19	6.1	5 - 7	5 - 7

Species	***n***	**Fw Mx**			**Hw Mx**		
		av.	**67%**	**100%**	**av.**	**67%**	**100%**
H. fuliginosa East	16	5.8	5 - 6	4 - 7	4.8	4 - 6	4 - 6
H. fuliginosa Congo	26	5.7	5 - 6	4 - 7	4.9	4 - 5	4 - 6
H. fuliginosa Gabon	7	6.5	6 - 8	5 - 8	5.5	5 - 6	5 - 7
H. fuliginosa CamNig	23	4.8	4 - 5	4 - 7	4.6	4 - 5	3 - 7
H. fuliginosa West*	11	4.6	4 - 5	4 - 7	4.5	4 - 5	3 - 6
H. longfieldae	19	5.5	5 - 6	4 - 7	4.8	4 - 5	4 - 6
*H. cynthiae**	17	4.8	4 - 5	4 - 6	4.6	4 - 5	4 - 6
*H. ugandica**	16	4.3	4 - 5	3 - 6	3.8	3 - 4	3 - 5
*H. trinervulata**	5	3.3	3 - 4	3 - 4	3.0	3	3

Table 5. Denticulation of abdominal carinae of African *Gynacantha* and *Heliaeschna* species. S1-2 and S9-10 tend to lack denticulate carinae. *Heliaeschna* species are uniform in their denticulation, and the condition is only given for the genus as a whole. — ○ : denticles absent; ▶: denticles present; !: row of denticles has tendency to double or triple. Combination and duplication of symbols and brackets indicate both variation and intermediate conditions, e.g. presence of only a few almost indiscernible denticles.

Males	**Carina**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**
G. africana	lateral	○ ▶	▶	▶	▶!	▶!!	▶!
	ventral	○	○	○	○ (▶)	○ ▶	○ ▶
G. cylindrata	lateral	▶	▶	▶	▶	▶	▶
	ventral	▶	▶	▶	▶	▶	▶!!
G. sextans	lateral	○ ▶	▶	▶!	▶!!	▶!!	▶
	ventral	○	○	○ (▶)	○ (▶)	○ ▶	○ ▶
G. vesiculata	lateral	▶	▶	▶	▶	▶	▶
	ventral	▶	▶	▶	▶	▶	▶(!)
G. villosa	lateral	▶(○)	▶	▶	▶	▶	▶
	ventral	○ ▶	▶(○)	▶	▶	▶	▶
G. immaculifrons	lateral	▶	▶	▶	▶	▶	○
	ventral	○ (▶)	○ (▶)	○ ▶	▶	▶	▶(!)
G. bullata	lateral	▶	▶	▶	▶	▶	▶(○)
	ventral	○	○	○	○	○	○
G. manderica	lateral	▶(○)	▶	▶	▶	▶	○ ▶
	ventral	○	○	○	○	○	○ (▶)
G. nigeriensis	lateral	▶	▶	▶	▶(!)	▶(!)	▶
	ventral	○	○	○ (▶)	▶(○)	▶(!)	▶!(!)
G. usambarica	lateral	▶	▶	▶	▶	▶(!)	▶(○)
	ventral	○	○	○ (▶)	▶(○)	▶	▶
Heliaeschna	lateral	▶	▶	▶(!)	▶!	▶!	▶!
	ventral	○	○ (▶)	○ ▶	▶(○)	▶(!)	▶(!)

Females	**Carina**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**
G. africana	lateral	○	○ ▶	▶	▶	○	○
	ventral	○	○	○	○	○	○
G. cylindrata	lateral	▶	▶	▶	▶	▶	○
	ventral	▶	▶	▶	▶	▶	○
G. sextans	lateral	○ ▶	▶	▶	▶	▶	○ (▶)
	ventral	○	○	○	○	○ (▶)	○
G. vesiculata	lateral	▶	▶	▶	▶	▶	○
	ventral	○ (▶)	○ ▶	▶(○)	▶	▶	○
G. villosa	lateral	▶(○)	▶	▶	▶	▶	○
	ventral	▶(○)	▶(○)	▶(○)	▶(○)	▶(○)	○
G. immaculifrons	lateral	▶	▶	▶	▶	▶	○
	ventral	○	○	▶	▶	○ ▶	○
G. bullata	lateral	▶	▶	▶	▶	▶	○
	ventral	○	○	○	○	○	○
G. manderica	lateral	○ ▶	▶	▶	▶	▶	○
	ventral	○	○	○	○	○	○
G. nigeriensis	lateral	▶	▶	▶	▶	▶	▶(○)
	ventral	○	○	○	○	▶	○ ▶
G. usambarica	lateral	▶	▶	▶	▶	▶	▶
	ventral	○	○	○	○ (▶)	▶	▶(○)
Heliaeschna	lateral	○ (▶)	○ ▶	○ ▶	○ ▶	○ ▶	○
	ventral	○	○	○	○	○	○

unmarked frons and small size (Hw 37 mm) described and illustrated for *H. ukerewensis* are characteristic of *H. trinervulata* and seem sufficient to synonymise the two. Moreover, the type locality of *H. ukerewensis* falls within the range of *H. trinervulata*, known from the N shore of Lake Victoria to N Malawi and Katanga (Pinhey, 1984). Examination of the *H. ukerewensis* holotype revealed an insect identical to *H. trinervulata*, but retaining only the base of the abdomen (S1-2 and half of S3). Comparison of the appendages has thus become impossible. The difficulties encountered to assign some specimens either to *H. trinervulata* or *H. ugandica*, suggest the two may be varieties of a single species, the latter being the large, dark, dense-veined extreme. A pale male from Boro (Central African Republic) in MNHN with Hw 38.5 mm and 20-21 Ax is an example of such an unassignable specimen. The specimens of *H. trinervulata* available for this paper were too limited to come to a convincing conclusion on this matter.

Heliaeschna ugandica McLachlan, 1896

(Figs 4p, 7c; Plate I)

Heliaeschna ugandica McLachlan, 1896: 419 [type: Uganda; BMNH].
? *Heliaeschna sembe* Pinhey, 1962b: 39 [type: Sembe, Souanke, Congo; NMBZ]; possible synonymy.

Diagnosis

Identified by the absence of the diagnostic characters of the other *Heliaeschna* species, such as the appendages of *H. cynthiae*, size and frons of *H. trinervulata*, and the thoracic markings of the larger species. Teneral specimens (with unmarked frons) and low Ax counts may be indistinguishable from *H. trinervulata*.

Discussion

See the remark on *H. sembe* under *H. longfieldae*. The somewhat nondescript (see above) nature of the species and its wide range, from Uganda to Cameroon, may mask a complexity similar to that of *H. fuliginosa*. In this regard, the possibility of *H. trinervulata* being a pale, small, open-veined variety of *H. ugandica* cannot yet be ruled out (see under that species).

Mystery *Heliaeschna*

A female in MNHN has a label by R. Martin reading "Assinié ? (indiqué Bancó)". Although the precise locality is unclear, this indicates Côte d'Ivoire as origin. The first impression is of a *Heliaeschna* with a cylindrical abdomen but without thoracic bands, an unknown combination in the genus. Other features are: Hw 50 mm; metastigma somewhat blackened; all wings with single cross-vein proximal to proximal primary Ax in subcostal space; 25-28 Fw Ax; 7 cross-veins in both Fw median spaces and 5 in Hw; 9 cells in both anal loops; brace veins absent; 2 rows of cells in fork of IR3; only 1-3 cells doubled between R2 and R3 proximal to Pt;

wings evenly smoky with not even a hint of subcostal rays; denticles present on lateral carinae of S2-7 and ventral carinae of S2-5; S9 as long as S8; ventral spines of S10 at angle of about 45° with axis of abdomen. The venation is typical of *Heliaeschna*, except for the single proximal subcostal cross-vein. In *Gynacantha* there are normally no cross-veins proximal to the proximal primary Ax, in *Heliaeschna* there are 1 or 2 costal and 1-3 subcostal ones. The specimen thus shows an intermediate state, which is only sporadically seen in *Gynacantha* or *Heliaeschna*. The numbers of Ax and anal loop cells are a bit on the low side for a *Heliaeschna* of this size. Large *Heliaeschna* usually have subcostal rays, most *Gynacantha* do not. The dark metastigma is diagnostic of the *africana*-group. Females of *Heliaeschna* have bare abdominal carinae, at most the lateral carinae of S2-7 are weakly denticulate, while *G. cylindrata* and *G. vesiculata* have both carinae of S2-7 clearly denticulate. The shape of S8-10 is nearer *Heliaeschna* than *Gynacantha*. If the specimen is really Ivorian, the characters suggest a *Gynacantha* x *Heliaeschna* hybrid; however it also displays a strong similarity with *H. bartelsi* Lieftinck, 1940 from SE Asia. The discussed female is therefore probably a mislabelled specimen with a remarkably misleading 'mixed' set of African gynacanthine characters.

Keys to continental African *Gynacantha* and *Heliaeschna*

Further differences among the groups, e.g. in the anterior processes of the hamules, and denticulation of genital fossa border, are given in Table 2, in the paragraphs about characters, among species in Tables 3-5, and in the species accounts. Variability of characters is also treated in these sections. The species of *Gynacantha* from the Indian Ocean islands are not included below, but *G. radama* will key out as *G. vesiculata*, *G. hova* as *G. manderica*, and *G. bispina*, *G. malgassica* and *G. stylata* as *G. immaculifrons*. Note that in these three species the T-mark is prominent, and *G. stylata* has a constricted S3.

Key to genera and groups

1. Frons 45-55% as wide as head (dorsal view); IR2 extends at most halfway under Pt; Hw cubital field of 2 rows of cells at base; anal triangle almost reaches tornus or is absent; membranule large, broadly bordering anal triangle (Fig. 6f) ..... other Afrotropical Aeshnidae

1'. Frons 35-40% as wide as head (dorsal view); IR2 usually extends more than halfway under Pt; Hw cubital field often of 1 row at base; anal triangle falls short of tornus by at least 1/3 of its length; membranule small, only touching extreme base of anal triangle (Figs 6a-e) ..... (Gynacanthini) **2**

2. 3-8 cross-veins in median space of all wings; 1-2 secondary Ax present proximal to proximal primary Ax; mainly 2 rows of cells in fork of IR3; brace veins absent (Figs 6d, 6e) ..... *Heliaeschna*

2'. No cross-veins in median spaces; no secondary Ax present proximal to proximal primary Ax; mainly 2-5 rows in fork of IR3; brace veins present or absent (Figs 6a-c) ..... (*Gynacantha*) **3**

3. Rim of metastigma black, in contrast with thoracic colour (Fig. 8a); inner border of cerci bisinuous, concave roughly 2/3 from base (Figs 4a-e); anal triangle of 3-6 cells; largely 2 or 3 rows of cells between R2 and R3 proximal to Pt; brace veins absent (Fig. 6a) ..... *africana*-group
3'. Rim of metastigma same colour as thorax; inner border of cerci sinuous or almost straight (Figs 4f-j); anal triangle of 3 cells; only 1 row between R2 and R3 proximal to Pt, at most some cells doubled; brace veins present (Figs 6b, 6c) **4**

4. Genital fossa border with distinct rows of 8-20 denticles; S3 of male distinctly constricted near base (Figs 3g-j) ..... *bullata*-group
4'. Genital fossa border with 0-4 scattered denticles; S3 of male usually cylindrical, of almost uniform width throughout (Fig. 3f) ..... *bispina*-group

Key to males of *africana*-group of *Gynacantha*

1. Cerci tapering to slender point (Fig. 4c); wing bases with dark subcostal rays; mainly 2 or 3 rows of cells in fork of IR3 in all wings (Fig. 6a) ..... *sextans*
1'. Cerci widened and sharply cut-off at end (Figs 4a, 4b, 4e, 4d); wings may be tinted, but without distinct subcostal rays; mainly 4 or 5 rows in fork of IR3 ... **2**

2. S3 constricted near base (Figs 3a, 3e); cerci with distinct ventral lump near base (Fig. 5b) **3**
2'. S3 cylindrical, of almost uniform width throughout (Figs 3b, 3d); cerci at most thickened somewhat near base (Fig. 5a) **4**

3. Ventral carinae S5-6 and usually S4 with denticles; 22-28 Fw Ax; 2 rows of cells between R2 and R3 proximal to Pt (save occasional cell) ..... *villosa*
3'. Ventral carinae S4-5 and usually S6 bare; 28-37 Fw Ax; at least partly 3 rows between R2 and R3 proximal to Pt ..... *africana*
4. Cerci with deep subapical excavation with a tuft of hairs at its basal side, like a hoofed leg in profile with a spur on heel (Fig. 4b); Hw 47-51 mm ..... *cylindrata*
4'. Cerci not so sharply excavated, hairs evenly spaced along its entire length (Fig. 4d); Hw 44-48 mm ..... *vesiculata*

Key to females of *africana*-group of *Gynacantha*

Identification is sometimes difficult, especially when the cerci are lost, which often happens. *G. cylindrata* and *G. vesiculata* cannot always be distinguished. See the species account of *G. villosa*, in which eastern females with a weak constriction of S3 can be confused with *G. cylindrata*.

1. S3 cylindrical, of almost uniform width throughout; cerci stiletto-like, usually smaller than 6x0.5 mm; ventral carinae S5-7 with denticles **2**
1'. S3 constricted near base; cerci leaf-like, usually larger than 6x0.5 mm; ventral carinae S5-7 may be bare **3**

2. S9 about 1.5x as long as S8; lateral carinae S2 weakly bent at midlength; Hw 50-54 mm ..... *cylindrata*
2'. S9 slightly longer than S8; lateral carinae S2 almost straight; Hw 46-50 mm ..... *vesiculata*

3. Wing bases with dark subcostal rays; mainly 2 or 3 rows of cells in fork of IR3; ventral spines S10 directed downwards, angle between them and axis of abdomen > 45°; ventral carinae S3-7 normally bare ..... *sextans*
3'. Wings may be tinted, but without distinct subcostal rays; mainly 4 or 5 rows of cells in fork of IR3; ventral spines S10 pointing backwards, angle between them and axis of abdomen < 45°; ventral carinae S3-7 may have denticles **4**

4. Cerci very large and leaf-like, more than 10x2 mm; ventral carinae S3-7 bare; lateral carinae S7 bare; S9 over 1.5x as long as S8; at least partly 3 rows of cells between R2 and R3 proximal to Pt; 28-37 Fw Ax ..... *africana*
4'. Cerci short and narrow, at most 8x1 mm; ventral carinae S3-7 often with denticles; lateral carinae S7 with denticles; S9 at most 1.5x as long as S8; 2 rows between R2 and R3 proximal to Pt (save occasional cell); 22-29 Fw Ax ..... *villosa*

Key to males of *bispina*- and *bullata*-groups of *Gynacantha*

1. Legs with dark markings, at least blackish on tarsi and around joints between femora, tibiae and tarsi (Figs 2a, 2b); ventral carinae S6-8 bare; Hw 35-44 mm **2**
1'. Legs uniformly pale, including tarsi and joints; ventral carinae S7-8 and usually S6 with denticles; Hw 43-48 mm **3**
2. Mid and hind legs dark, with pale streak on tibia (Fig. 2b); humeral and metapleural fossae darkened, forming distinct dots on sutures; posterior portion of genital fossa border densely set with denticles (Fig. 3h); 13-19 Fw Ax (22-27 in Congolese variety) ..... *manderica*
2'. Mid and hind legs pale, with dark rings around joints (Fig. 2a); no dots on humeral and metapleural sutures; posterior portion of genital fossa border bare (Fig. 3g); 19-28 Fw Ax ..... *bullata*

3. T-mark on frons with at least stem faint or absent (Fig. 1a); cerci distinctly widened just before apex (Fig. 4f); genital fossa border with 0-4 scattered denticles (Fig. 3f); lateral carinae S8 bare, in contrast with denticulate ventral carinae; S3 cylindrical, of almost uniform width throughout, at most slightly narrowed (Fig. 3f) ..... *immaculifrons*
3'. T-mark on frons distinct and black (Figs 1c-d); cerci of rather even width throughout (Figs 4i, 4j); genital fossa border with distinct rows of 8-20 denticles (Figs 3i, 3j); lateral carinae S8 normally with denticles, like ventral carinae; S3 distinctly constricted near base (Figs 3i, 3j) **4**

4. Outer border of auricles strongly convex, making them rounded in shape (Fig. 3j); stem of T-mark on frons thick, as long as wide (Fig. 1d); sternite S1 usually with denticles; ventral carinae S8 with denticles in 1 row ..... *usambarica*
4'. Outer border of auricles straight, making them triangular in shape (Fig. 3i); stem of T-mark narrow, 2x as long as wide (Fig. 1c); sternite S1 usually bare; ventral carinae S8 often with denticles in 2 or 3 irregular rows ..... *nigeriensis*

Key to females of *bispina*- and *bullata*-groups of *Gynacantha*

1. Legs with dark markings, at least blackish on tarsi and around joints between femora, tibiae and tarsi (Figs 2a, 2b); ventral carinae S6-7 bare **2**
1'. Legs, including tarsi and joints, uniformly pale; ventral carinae of either S6, S7 or both with denticles **3**

2. Mid and hind legs dark, with pale streak on tibia (Fig. 2b); humeral and metapleural fossae darkened, forming distinct dots on sutures; 13-19 Fw Ax (22-27 in Congolese variety) ..... *manderica*
2'. Mid and hind legs pale, with dark rings around joints (Fig. 2a); no dots on humeral and metapleural sutures; 19-28 Fw Ax ..... *bullata*

3. S3 constricted near base; stem of T-mark on frons thick, as long as wide (Fig. 1d); sternite S1 usually with denticles ..... *usambarica*
3'. S3 cylindrical, of almost uniform width throughout; stem of T-mark absent, faint or narrow, 2x as long as wide (Figs 1a, 1c); sternite S1 bare **4**

4. T-mark on frons distinct and black (Fig. 1c); S9 longer than S8; ventral carinae S5-6 bare, S7 with denticles ..... *nigeriensis*
4'. T-mark on frons with at least stem faint or absent (Fig. 1a); S9 about as long as S8; ventral carinae S5-6 with denticles, S7 may be bare ..... *immaculifrons*

Key to males of *Heliaeschna*

1. Metapleural and often humeral suture with dark band (Figs 8b, 8c); ≥ 26 Fw Ax (rarely 23); Hw 39-54 mm, usually over 45 mm **2**
1'. Without metapleural or humeral dark bands; ≤ 29 Fw Ax (rarely 30); Hw 35-45 mm **3**

2. Epiproct 1/4 to 1/3 length of cerci; cerci narrow, widest point of blade about 1.5-2.5x as wide as narrowest point of stalk (Figs 4l, 4m); cerci usually with ventral thickening near base (Figs 5c, 5d); metapleural band much broader than often indiscernible humeral band (Fig. 8c); Hw 45-54 mm ..... *fuliginosa*
2'. Epiproct about 1/2 length of cerci; cerci wide, widest point of blade about 2.5-3x as wide as narrowest point of stalk (Fig. 4n); cerci without ventral thickening near base; metapleural band about as broad as humeral band (Fig. 8b); Hw 39-46 mm ..... *longfieldae*

3. Widest point of blade of cerci closer to apex than to base of blade (Fig. 4k); Pt as long as 5-6 underlying cells in all wings (Fig. 7a); wing bases usually with dark subcostal rays; ≥ 24 Fw Ax (rarely 23) ..... *cynthiae*
3'. Widest point of blade of cerci at about midlength of blade (Figs 4o, 4p); Pt as long as 3-4 underlying cells in all wings (Fig. 7c); wing bases clear; ≤ 25 Fw Ax (rarely up to 27) **4**

4. Frons pale, at most with cross-bar of T-mark; cerci narrow, blade about 2.5x as wide as stalk (Fig. 4o); 15-19 Fw Ax; anal loop of 5-7 cells ..... *trinervulata*
4'. Frons completely dark or with stemmed T-mark; cerci wide, blade about 3x as wide as stalk (Fig. 4p); 20-27 Fw Ax; anal loop of 7-13 cells ..... *ugandica*

Tentative key to females of *Heliaeschna*

1. Metapleural suture with broad dark band (Fig. 8c); 28-38 Fw Ax; Hw 48-56 mm **2**
1'. Without metapleural band; 17-32 Fw Ax; Hw 36-48 mm **3**

2. S3 constricted near base ..... *fuliginosa*
2'. S3 cylindrical, of almost uniform width throughout ..... *longfieldae*

3. Pt as long as 5-6 underlying cells in all wings (Fig. 7a); wing bases normally with dark subcostal rays; 26-32 Fw Ax; Hw 43-48 mm ..... *cynthiae*
3'. Pt as long as 3-4 underlying cells in all wings (Fig. 7c); wings may be tinted, but without distinct subcostal rays; 17-26 Fw Ax; Hw 36-42 mm **4**

4. Frons pale, at most with cross-bar of T-mark; 15-19 Fw Ax; anal loop of 5-8 cells ..... *trinervulata*
4'. Frons with stemmed T-mark or completely dark dorsally; 19-26 Fw Ax; anal loop of 7-13 cells ..... *ugandica*

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