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THE *ATOCONEURA* PROBLEM REVISITED: TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF A DRAGONFLY GENUS IN THE HIGHLANDS OF AFRICA (ODONATA, LIBELLULIDAE)

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The genus *Atoconeura* previously comprised two species; one with five subspecies. Principal Component Analysis of 33 characters of 148 specimens and cladistic analysis of 28 characters revealed six discrete taxa, partly with narrowly overlapping ranges. Subspecies *aethiopica*, *kenya* and *pseudeudoxia* of *biordinata* are raised to specific rank; the synonymy of *chirinda* with *biordinata* is confirmed; *A. luxata* sp. n. is described from West Africa. A key to the species is provided and the poorly known behaviour, ecology and biogeography are discussed. The author has not witnessed oviposition; one report suggests that it may be perched, solitary and epiphytic, which is unusual within the family. The species are largely restricted to streams above 1000 m, except *A. luxata* sp. n. that is only known below that altitude, but always at the foot of highlands. Four species demonstrate a distribution pattern recalling a 'ring species' in highlands, circling Lake Victoria and the dry north of Tanzania. The phylogeny suggests an expansion of the genus from the western lowlands to the eastern highlands, or vice versa, followed by an expansion through the Albertine Rift and Eastern Arc Mts to the Kenyan and ultimately Ethiopian highlands. Especially in the case of a western origin there appears to have been a tendency of the species to occur at increasing altitudes in the course of their evolution.

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Key words. – Odonata; Anisoptera; *Atoconeura*; Afro-montane; systematics; keys.

In her paper 'The *Atoconeura* Problem' Longfield (1953) sketched the taxonomic disorder in the genus, caused by considerable variation in the sparse material available. Her solution was the recognition of two species based on epiproct morphology, *A. eudoxia* and *A. biordinata*, the latter with four subspecies differing mainly in markings: *A. b. biordinata* from highlands in Tanzania, Malawi and Katanga; *A. b. chirinda* in Zimbabwe; *A. b. kenya* in Kenya; and *A. b. pseudeudoxia* in W Uganda. Kimmins (1958) added *A. b. aethiopica* from Ethiopia, stating apologetically that 'one might question the wisdom of adding yet another subspecies'. Pinhey (1961a) remarked that 'Longfield has divided this [genus] into two species, but I think *kenya* may eventually prove to be a third species.' Later Pinhey (1982) suggested that 'it is possibly more correct to regard them [the subspecies] all as *biordinata*, with variable forms rather than subspecies'. Bridges (1991) listed *A. kenya* as a good species with the subspecies *A. k. aethiopica*, but made *chirinda* and *pseudeudoxia* synonyms of *A. biordinata*. The problem demands a more objective analysis of variation, as well as the study of new material and characters. This paper presents the outcome of that study, with a revised classification of the taxa and a reassessment of their biogeography.

Methods and material

To validate the views of Longfield (1953) and her contemporaries, the analysis was designed to test how well their characters applied to their classification. Most of Longfield's specimens (BMNH) were restudied, besides new material including West

African *Atoconeura*, which Longfield did not have. Previously used characters were translated to 33 ordered variables, of which 28 were applicable to males and 26 to females (see appendix 1). These were scored for 148 complete specimens (107 males; 41 females), and a portion of them for 15 incomplete specimens (12; 3), including most primary types and specimens from throughout the genus's range. Principal Component Analysis (PCA) of the complete specimens was performed using a correlation matrix (i.e. standardizing all data to a common mean and variance) in PC-ORD4 software (McCune & Mefford 1999). PCA performs excellently in the reduction of morphological data (e.g. Gardner & Mendelson 2004, Malhorta & Thorpe 2004, Tadauchi 1983). The resulting components were correlated with the character variables to establish which variation they describe. Data of incomplete specimens were only used to measure variability of characters within taxa (table 1).

After this analysis, further specimens (details are provided in separate material lists) were studied and additional characters investigated, including details of the penis with scanning electron microscopy (figs. 21-28). Characters used in the PCA were evaluated for use in cladistic analysis of the clusters identified by the PCA. Where necessary character states were simplified or fine-tuned, undiscriminating or uninformative characters (e.g. binary, with one state unique to a single species) were removed, and additional characters were incorporated. 22 'old' characters and six 'new' ones (all ordered and of equal weight) were adopted (see appendix 2 and table 2). Some characters were not scored for the outgroups, because of the absence of obvious putative homologies, especially in the penis. Analysis based on maximum parsimony was carried out using both an exhaustive search and parsimony bootstrap (1000 randomized runs). Both analyses were also performed with unordered characters. All analyses were run with PAUP* 4.0 Beta 10 (Swofford 2002) and three different outgroups: *Olpogastra lugubris* Karsch, 1895, *Malgassophlebia bispina* Fraser, 1958 and *Zygonyx flavicosta* (Sjöstedt, 1900).

Each recognised species was diagnosed and variation assessed. Full descriptions of known taxa were not prepared, those given by Longfield (1953) and Kimmins (1958) being sufficient. Order of species in the text and figures follows the cluster numbers from the PCA and also reflects the phylogenetic results, placing the more basal groups first (see Results).

Acronyms of collections

BMNH Natural History Museum, formerly British Museum (Natural History) (London, UK)
CGVL Collection Graham Vick (Little London, UK)
CVCH Collection Viola Clausnitzer (Halle, Germany)
ISNB Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)
MNHN Muséum National d'Histoire Naturelle (Paris, France)
MRAC Musee Royal de l'Afrique Centrale (Tervuren, Belgium)
MZUF Museo Zoologico 'La Specola' (Firenze, Italy)
NHRS Naturhistoriska Riksmuseet (Stockholm, Sweden)
NMBZ Natural History Museum of Zimbabwe (Bulawayo, Zimbabwe)
RMNH Nationaal Natuurhistorisch Museum Naturalis, formerly Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands)
UMMZ University of Michigan Museum of Zoology (Ann Arbor, USA)
ZMHB Museum für Naturkunde der Humboldt-Universität (Berlin, Germany)

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

Results

PCA of complete males resulted in 10 axes accounting for 93.0% of variation. 70.0% of variation was explained by the first three axes: Axis 1 (36.9% of variation) was correlated with variables related to abdomen shape, Ax count, head and thorax markings, and pruinosity. Axis 2 (18.9%) correlated with Px counts, markings of S3-9 and cercus shape, and Axis 3 (14.2%) with markings of S2 and epiproct shape. Plotted against Axis 1 and 2, four clusters were apparent (fig. 1): (1) all West African males, except one from Cameroon; (2) all *eudoxia* and *pseudeudoxia* males including holotypes, plus some Katangan '*biordinata*'; (3) all males from Zimbabwe including the *chirinda* holotype, plus most '*biordinata*' and one male from Cameroon; (4) holotypes of *aethiopica* and *kenya* and all other Ethiopian and Kenyan males, plus singles from Uganda (Ruwenzori) and Tanzania (Mt Meru). Introduction of Axis 3 (fig. 2) divided two clusters further: (2a) all *eudoxia*; (2b) remainder of cluster 2; (4a) non-Ethiopian material in cluster 4; (4b) all Ethiopian material.

PCA of complete females resulted in 10 axes accounting for 91.6% of variation. 60.9% of variation was explained by the first three axes: Axis 1 (32.3% of variation) was correlated with variables related to

abdomen shape, Ax and Px counts, head and thorax markings, and shape of vulvar scale. Axis 2 (15.3%) correlated with vertex colour, markings of S3-9, cercus shape and vulvar scale length, and Axis 3 (13.3%) with number of cells in Fw triangle and the colour of the antefrons. Plotting Axis 1 against 2 (fig. 3) and 3 (fig. 4) gave similar clusters as in males: (1) West African females; (2a) all females assigned to *eudoxia*; (2b) females from Uganda ('*pseudeudoxia*') and Katanga; (3) all females from Zimbabwe including the *chirinda* allotype, plus most '*biordinata*' and one from Kenya (Taita Hills); (4a) one Kenyan (*kenya* allotype) and four Tanzanian females (Mts Kilimanjaro and Meru); (4b) two Ethiopian females including the *aethiopica* allotype.

Males in cluster 2 (*eudoxia* and *pseudeudoxia*) shared distinctive setation of the hind femora and poststernum (figs. 14-15), while only 2a (*eudoxia*) had diagnostic abdominal setation. Compared with the third segment, all species have a notably short fourth segment of the penis when deflated (figs. 21-28): a short collar-like hood encloses a complex of smooth and scaly (i.e. covered with numerous, small and overlapping flattened spines) pleats, which are at least partly formed by the apical lobe (terminology follows Miller 1991). A pair of tusk-like cornua emerges from among the pleats in all examined penes, except of cluster 1, where clear sockets mark their position. Representatives of clusters 1, 2, 3 and 4 had differently shaped pleats and cornua, those of 4a (*kenya*) and 4b (*aethiopica*) were essentially similar, as were those of 2a (*eudoxia*) and 2b (*pseudeudoxia*), which are rather close to 3 ('*biordinata*'). These characters are discussed further in the species texts.

All cladistic analyses using ordered characters and *O. lugubris* and *Z. flavicosta* as outgroups produced the same topology (fig. 5), with bootstrap support of all nodes at 87% or higher. With *M. bispina* as outgroup the tree only differed in cluster 1 being the sister group to cluster 2, but bootstrap support of this node was only 49%. Analyses with unordered characters produced similar results, although some search combinations grouped either cluster 1 or 3 with cluster 2, but bootstrap support of these changes was 51% or lower. Fig. 5 reflects the PCA results, with cluster 1 being most basal, followed by clusters 2, 3 and 4; the apomorphies of the nodes are provided in appendix 3.

Discussion

The analysis testing Longfield's characters, specimens and taxa resulted in six discrete clusters of specimens, but some specimens were 'out of place' according to her views (figs. 1-4). Indeed Longfield (1953) observed that 'in the series I have examined, there have always been one or two specimens that did not exactly conform to either group and I prefer to give them only subspecific rank.' That discordance was not caused by imperfect separation of Longfield's subspecies by their characters, but by their geography: the distributions of her taxa *biordinata*, *kenya* and *pseudeudoxia* overlap. Pinhey (1961a) predicted the sympatry of *biordinata* and *kenya* on 'the northerly or westerly foothills of Mount Kilimanjaro or, perhaps, Mount Meru': both indeed occur on Kilimanjaro. *Biordinata* and *pseudeudoxia* overlap in Katanga (fig. 6).

The clusters corresponding with Longfield's taxa not only overlap geographically without intergrading in characters of size and markings, but are also discrete by characters of setation, appendages, penis and poststernum. Therefore I conclude that each cluster represents a good species. Pinhey (1960, 1984) found that the subspecies *chirinda* intergrades with nominotypic *biordinata*, which is confirmed by both PCAs. With all other former subspecies of *A. biordinata* raised to specific rank, I treat *A. aethiopica* equally, although it is close to *A. kenya* and perfectly allopatric. No name is available for cluster 1, which represents a sixth species of *Atoconeura* from western Africa.

Has 'the *Atoconeura* problem' now been solved? The genus comprises of six readily identifiable, broadly (but not entirely) allopatric species. More extensive overlap is suggested by single males of *A. biordinata* from Cameroon, *A. kenya* from W Uganda and the new species from Katanga, but see the discussion in each species account. Considerable geographic sampling gaps may harbour further overlap, but also possible areas of transition or undescribed species.

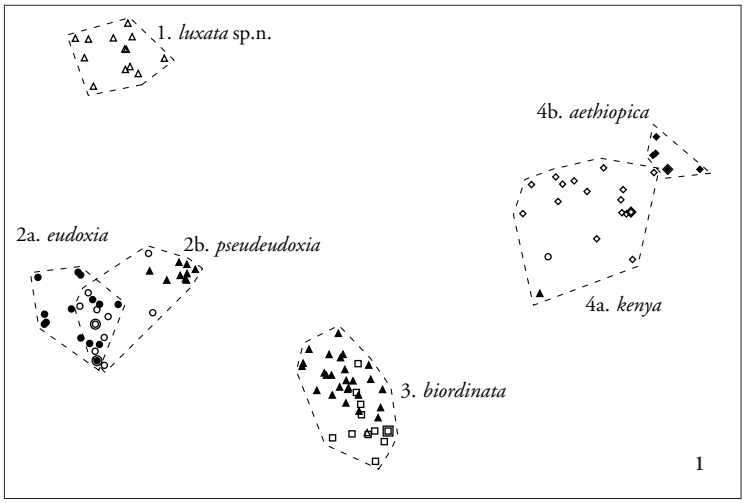
Taxonomic part

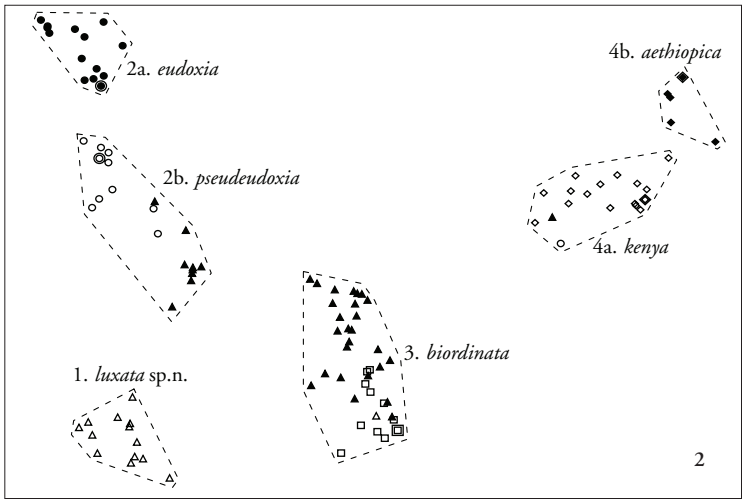
Atoconeura Karsch

Atoconeura Karsch, 1899: 371. Type species: *Atoconeura biordinata* Karsch, 1899 (by monotypy).
Accaphila Kirby, 1909: 59. Type species: *Accaphila eudoxia* Kirby, 1909 (by monotypy); junior synonym (Ris 1919: 1195).

Diagnosis

Fairly large libellulids (Hw 28-39 mm), predominantly glossy black marked with yellow. When not pruinose, the dorsal yellow spot on S7 is conspicuous (figs. 43-48), a feature seldom seen in African libellulids of similar size and behaviour. The following combination of venation characters is diagnostic in most cases: (1) distal Ax complete; (2) arculus distal of Ax2; (3) Fw discoidal field partly of two rows of cells; (4) Hw with 2 Cux; (5) Rspl subtending single row of cells. The species are best separated





Figs. 1-4. Scatter plots of males (1-2) and females (3-4) along the PCA Axes 1 (horizontal axis; figs. 1-4), 2 (vertical axis; 1, 3) and 3 (vertical axis; 2, 4). The symbols represent the original identification of specimens sensu Longfield, based mainly on range, the indicated clusters represent the revised classification (see Results). Legend. – ◆: specimens assigned to *aethiopica* by range (Ethiopia); ▲: to *biordinata* by range (Tanzania to Malawi and Katanga); □: to *chirinda* by range (Zimbabwe); ●: to *eudoxia* by epiproct or vulvar scale; ◇: to *kenya* by range (Kenya); ○: to *pseudeudoxia* by range (Uganda); △: unassigned specimens from West Africa; framed symbols: holotype.

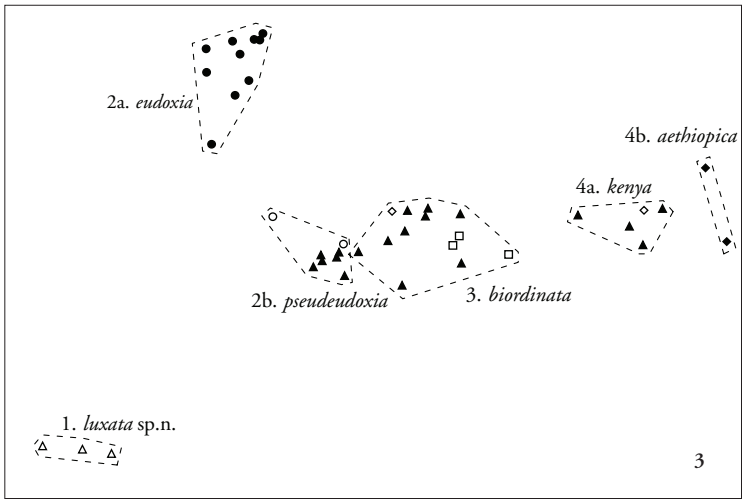
by markings (figs. 8-13, 17-19), male appendages and vulvar scales (figs. 29-42). The external secondary genitalia are remarkably uniform within the genus (fig. 20), but the species differ in the penis (figs. 21-28).

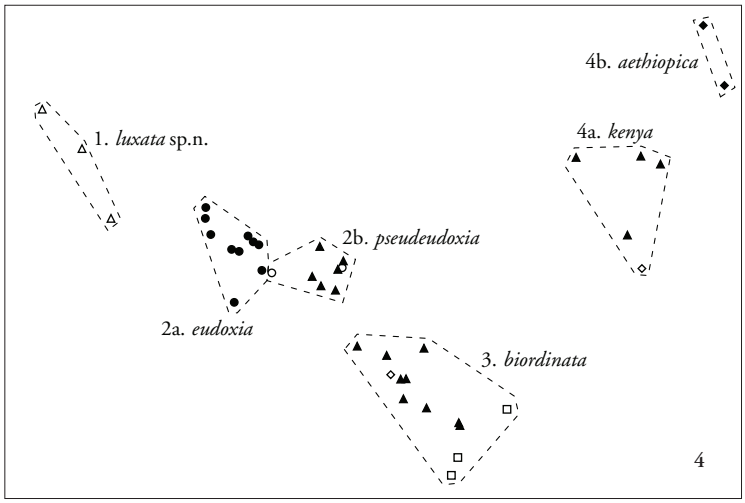
Affinities

Although *Atoconeura* is rather singular among African Libellulidae, Pinhey (1962) placed it close to *Trithemis* Brauer, 1868. The larva of *A. biordinata* shows a general similarity (own observations), but the adult differs by venation, pronotal hindlobe and penis. Preliminary molecular analysis placed the genus close to *Malgassophlebia* Fraser, 1956 and *Olpogastra* Karsch, 1895 (G. Fleck, M. Brenk & B. Misof pers. comm.). These genera are very distinct, but their combination of black-with-yellow coloration and claw-like hamule is shared only with *Atoconeura* in continental Africa. Ris (1912) considered his *Thalassothemis* of Mauritius close to *Atoconeura* and placed the two in the *Trithemis-Zygonyx* group of Libellulidae. The superficial resemblance between *A. luxata* sp. n. and *Z. flavicosta* is especially striking.

Ecology and biogeography

Longfield's (1953) summary still applies well: 'The genus *Atoconeura* inhabits forested regions and swift rivers from between about 4,000 and 9,000 feet





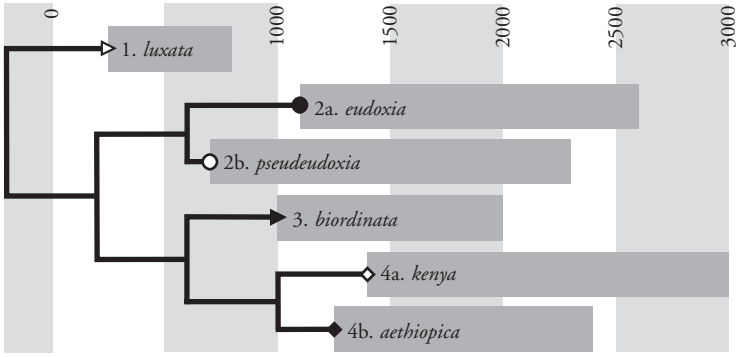


Fig. 5.
Phylogeny of *Atoconeura* species superimposed on their observed altitudinal range (m). PCA cluster numbers and plot/map symbols are provided for correspondence with figs 1-4 and 6. See appendix 3 for apomorphies of nodes.

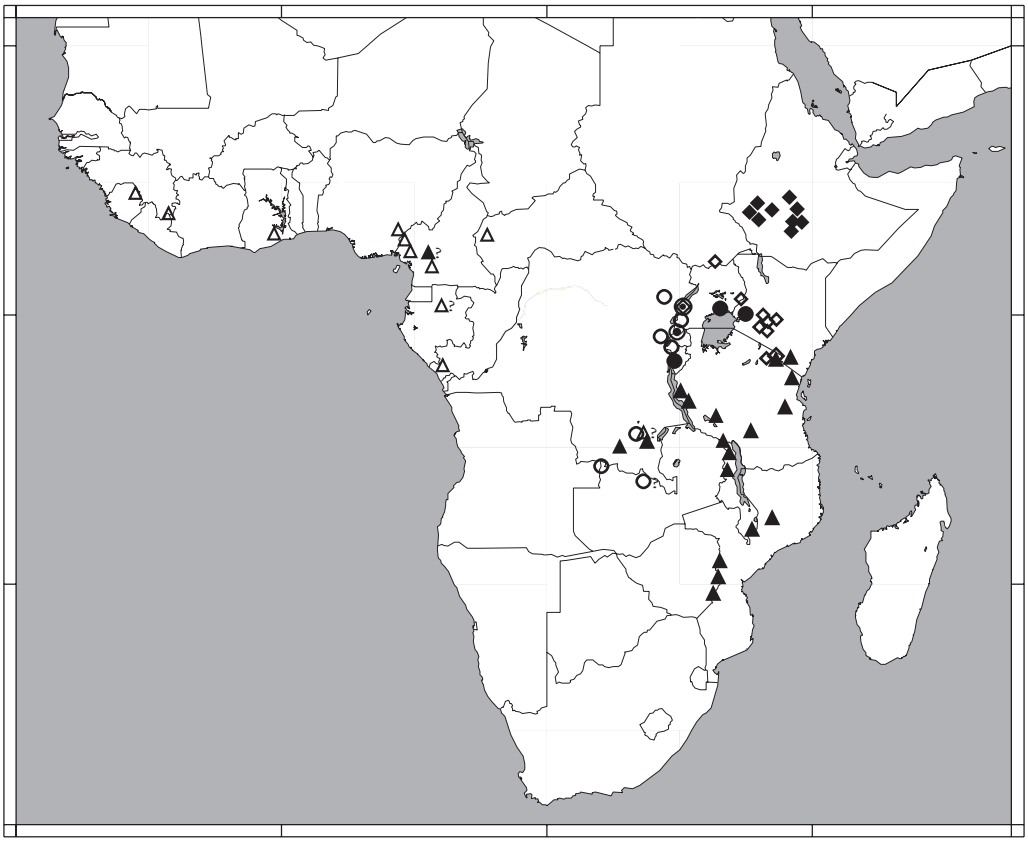


Fig. 6. Distribution of *Atoconeura* species, based on records and sources provided in the species accounts. Legend. – ◆: *A. aethiopica*; ▲: *A. biordinata*; ●: *A. eudoxia*; ◇: *A. kenya*; △: *A. luxata* sp. n.; ○: *A. pseudeudoxia*. Composite symbols indicate overlap of species, records with question marks are discussed in the text of the relevant species.

[1220-2745 m] altitude, and it is obvious that the dragonfly has been isolated for many generations in certain mountain and highland areas.' Pinhey (1961a) added: 'Whereas *biordinata* generally prefers fast running streams, often stony or rocky ones, and is partial to patches of riverine bush as well as forest (except *pseudeudoxia*, a forest insect), *eudoxia* is a forest dweller, inhabiting muddy, rather sluggish streams. It settles on overhanging twigs or on floating debris. However I have found that the *chirinda* race of *biordinata* also favours this sort of life, at Mount Selinda (November 1955).'

Atoconeura species (own observations) mainly inhabit streams between 1000 and 2500 m, and can be dominant above 1500 m: *A. biordinata* is the most common anisopteran on streams on the Mulanje and Namuli plateaus (about 2000 m) of S Malawi and N Mozambique. *A. kenya* probably ventures highest; between 1400 and 3000 m. All records of *A. luxata* sp. n. lie below 1000 m, but are concentrated around highlands (some not higher than 800 m) such as Loma, Nimba and Atewa in the Upper Guinea and Adamawa and Mayumbe in the Lower Guinea. This 'piedmont effect' is also seen in *A. pseudeudoxia*, which occurs at 700 m in the Semliki Valley at the foot of the Ruwenzori Mts. The species may be segregated in elevation in areas of overlap, but data are scarce. In sympatry, *A. eudoxia* and *A. pseudeudoxia* are found at calm and fast-flowing sections of streams respectively. All species occur in forest, but *A. aethiopica*, *A. biordinata* and *A. eudoxia* often enter adjacent open areas.

The genus's association with highlands is reflected by its distribution (fig. 6). Five of the six species occur only in eastern Africa, where the continent's main highlands lie. Four species form an interlocking chain of ranges around the dry plains of NW Tanzania (fig. 6), a pattern mirrored by morphology (figs. 1-4):

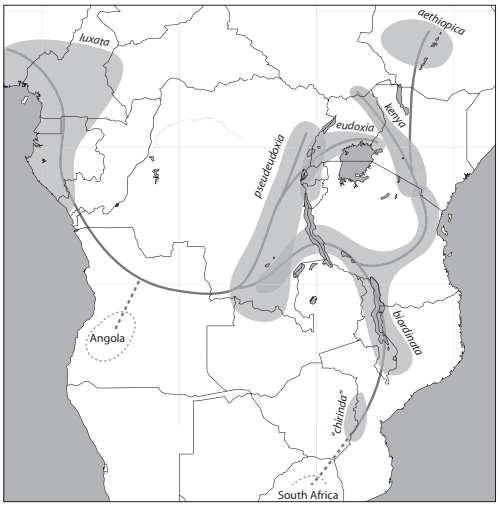


Fig. 7. A biogeographic hypothesis for *Atoconeura*. The phylogeny of the species is superimposed on their ranges, marking speculative expansion routes, but no direction along these routes is suggested. Species ranges are inferred by known records (questionable ones omitted) and the position of highlands, the clades follow these as much as possible. Note that the position of evolutionary splits within species ranges is an artefact of the presentation form and has no bearing on the hypothesis. Notable distributional gaps are indicated, marked by dashed area outlines and clades, as is the southern isolate of *A. biordinata* ('*chirinda*').

A. pseudeudoxia combines characters of *A. eudoxia* and *A. biordinata* and also lies in between geographically; *A. biordinata* shares further characters with its neighbour *A. kenya*. The morphologically most disparate taxa, *A. eudoxia* and *A. kenya* overlap north of Lake Victoria, closing the chain. This pattern recalls a 'ring species', suggesting expansion across montane stepping stones. The obtained phylogenetic hypothesis suggests an expansion of the genus from the western lowlands to the eastern highlands, or vice versa, followed by an expansion through the Albertine Rift and Eastern Arc Mts to the Kenyan and ultimately Ethiopian highlands (fig. 7). Especially in the case of a western origin there appears to have been a tendency of the species to occur at increasing altitudes in the course of their evolution (fig. 5). However, molecular analysis and more clarity of the genus's affinities are required to determine the relative age and direction of colonisations.

The absence of *Atoconeura* in two highland regions with high endemism and suitable habitat in southern Africa is notable: the South African highveld has been sufficiently surveyed, but would not have been colonised if cooler periods (when more stepping stones were available) coincided with harsher conditions, making it uninhabitable then and unreachable now. Angola has been poorly researched and *Atoconeura*, possibly a seventh species, could be found there.

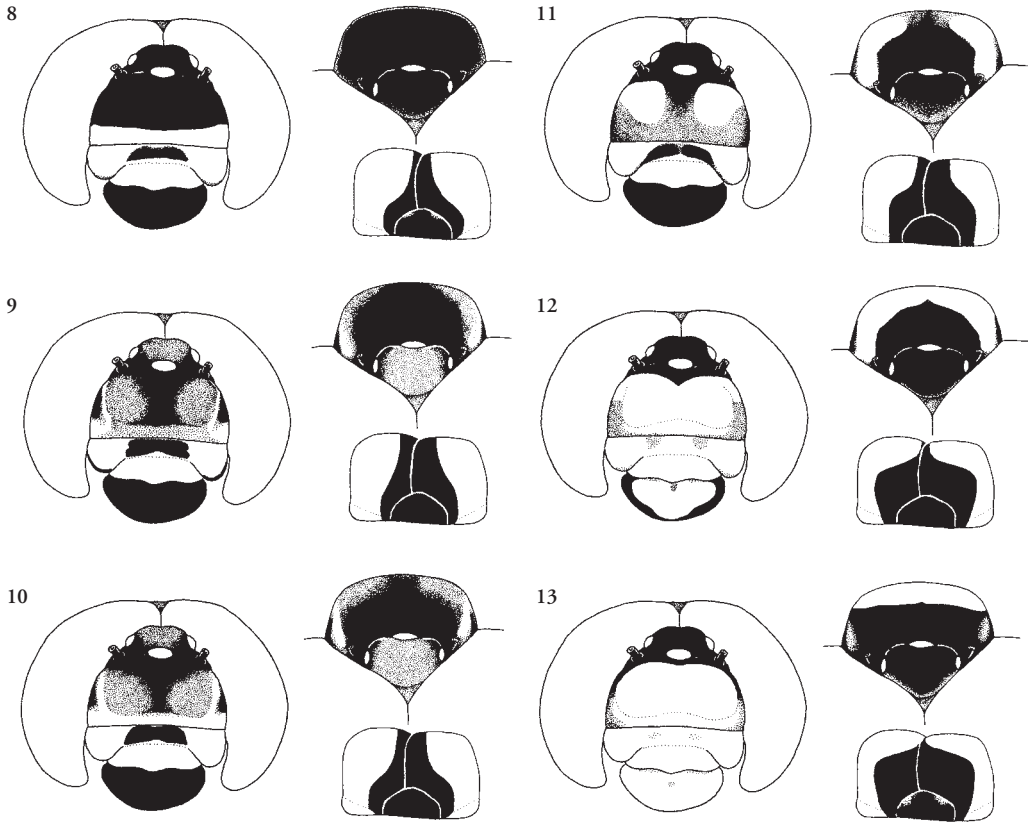
Behaviour

Males often perch prominently on rocks or twigs above streams, the abdomen held somewhat curved (figs. 43, 45-46). Males of *A. luxata* sp. n. in Ghana hovered persistently over rapid sections and near waterfalls in a manner recalling *Zygonyx* Hagen, 1867 and often perched only briefly (own observations). It is my impression that male behaviour at the waterside reflects the genus's phylogeny, with the proportion of time spent on the wing decreasing from the basal node upwards. This can only be confirmed by careful observations. Moreover, this effect may also be environmental, with lower ambient temperatures at greater elevations inhibiting sustained flight.

The reproductive behaviour is largely unknown. Despite being the commonest anisopteran on the Mulanje Plateau, I observed only three copulas of *A. biordinata* during 11 days of fieldwork there. They appeared to form at the streams and then go high up into the trees. S. Kyobe (pers. comm.) observed possible perched solitary epiphytic oviposition of *A. eudoxia* at Ruhija, Uganda: a female was reportedly laying on a twig floating on the stream surface and clad with bearded moss, while perched on twigs 1-3 cm above the substrate, repositioning herself once (by flight) before capture. Seated oviposition is uncommon and mainly facultative in Libellulidae: African *Tetrathemis* Brauer, 1868 females typically oviposit alone on substrates overhanging pools, while *Zygonyx natalensis* (Martin, 1900) tandems may use it to brave the torrential flow of waterfalls (Corbet 1999).

Key to males of *Atoconeura*

1. Labrum at least half pale (figs. 12-13). Mesepisternum with yellow hyphen bordering antealar sinus; abdomen often pruinose when mature (figs. 47-48). Cornua longer than half width of fourth segment of penis (fig. 28) 2
– Labrum all black or at most narrowly pale at base (figs. 8-11). Mesepisternum without hyphen; abdomen never pruinose (figs. 43-46). Cornua shorter than half width of fourth segment, or absent (figs. 25-27) 3
2. Dark area on frons rounded, sometimes with point down central groove (fig. 12; dorsal view) ..... *kenya*
– Dark area on frons with straight anterior edge (fig. 13) ..... *aethiopica*
3. Epiproct deeply bifid, its halves widely splayed,



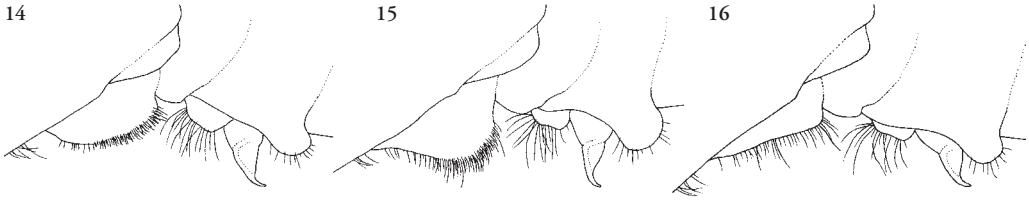
Figs. 8-13. Details of male head of *Atoconeura* species: face in rostral view (left), frons and vertex in dorsal view (top right) and labium in ventral view (bottom right). – 8, *A. luxata* sp. n.; 9, *A. eudoxia*; 10, *A. pseudeudoxia*; 11, *A. biordinata*; 12, *A. kenya*; 13, *A. aethiopica*.

like fishtail (fig. 39). Underside S7-9 with many long dark hairs ..... *eudoxia*
– Epiproct narrow and slender, with only slightly notched apex (fig. 38). Underside S7-9 at most with some fine hairs 4
4. S4-9 all black except for large dorsal spot on S7; basal spot S3 oval to triangular (fig. 17). Hw amber at base of subcostal and cubital spaces. Cerci rather straight and epiproct relatively long (figs. 29, 32). Cornua on fourth segment of penis absent (fig. 25) ..... *luxata* sp. n.
– S4-9 with basal yellow spots, which are lateral on S4-6 and ventral on S7-9; basal spot S3 crescent-shaped (fig. 19). Hw base clear. Cerci more sinuous and epiproct shorter (figs. 31, 34-35). Cornua on fourth segment present (figs. 26-27) 5
5. Hind femora anteriorly with dense long dark hairs. Poststernum strongly raised and with dense patch of short bristly hairs (fig. 15). Frons largely dark, lower border often paler; vertex brown (fig. 10). Hw 32-36.5 mm ..... *pseudeudoxia*
– Hind femora with only some fine hairs. Poststernum barely raised and with only scattered fine long hairs (fig. 16). Frons with pale areas on shields, contrasting with dark lower border; vertex usually glossy black (fig. 11). Hw 28-33.5 mm ..... *biordinata*

Key to females of *Atoconeura*

(couplets 4 and 5 are tentative)

1. Points of vulvar scale lie close to each other, normally well visible, space between them narrow, <60° (figs. 40-41). Postclypeus usually heavily marked with central black bar and darkened antero-lateral borders (figs. 8-9) 2



Figs. 14-16. Poststernum of *Atoconeura* species in lateral view (secondary genitalia included for reference). – 14, *A. eudoxia*; 15, *A. pseudeudoxia*; 16, *A. biordinata*.

– Points of vulvar scale wider apart, normally (partially) hidden under tergite, space between them wide, >60° (fig. 42). Postclypeus often not so heavily marked (figs. 10-13) 3
2. S4-9 with small yellow basal spots. Points of vulvar scale reach just beyond end of S8 (fig. 41). Cerci slightly longer than epiproct, blunt .... *eudoxia*
– S4-9 without basal spots. Points of vulvar scale reach as far as end of S8 (fig. 40). Cerci over twice as long as epiproct, with sharp point .... *luxata* sp. n.
3. Labrum at least half pale (figs. 12-13). Mesepisternum dark with pale markings including hyphen bordering antealar sinus, or uniformly brown 4
– Labrum all black or at most narrowly pale at base (figs. 10-11). Mesepisternum dark with pale markings, but without hyphen 5
4. Synthorax brownish black with yellow markings. Cerci about as long as epiproct ..... *kenya*
– Synthorax uniformly brown. Cerci almost twice as long as epiproct ..... *aethiopica*
5. Frons rather gradually darkening dorsally, palest along lower border (fig. 9). Hw 34-36.5 mm, 12-14 Fw Ax, seldom 11 ..... *pseudeudoxia*
– Frons with pale areas on shields, contrasting with darkened areas along lower border (fig. 11). Hw 30-33.5 mm, seldom up to 35.5. 10-11 Fw Ax, seldom 12 ..... *biordinata*

Atoconeura luxata sp. n.
(figs. 8, 17, 20-21, 25, 29, 32, 38, 40, 43-44)

Type material. – Holotype ♂: CAMEROON (SW): Meme, Atop, 1.5km from Ngusi, 250 m, 4.ix.1997, O. Mesumbe (CGVL). – Paratypes: CAMEROON (SW): 1♂, Tombel area, Lala, Lala and Ndibe streams, 18-22.iv.1995; 1♀, Meme, Atop, 1.5km from Ngusi, 250 m, 6.ix.1997, O. Mesumbe (CGVL); 1♂, Takamanda Camp, 568 m, 25.iv.2001, J. Groves (CGVL). [*A. b. pseudeudoxia* Karsch, 1899 [sic] in Vick (1999); *A. biordinata* in Vick (2002, 2003)].

Other material (included in PCA). – CONGO-BRAZZAVILLE: 1♀, Mts du Mayombe, Dimonika, 15.iv.1979, J. Legrand (MNHN). – GUINEA-CONAKRY: 8♂, 1♀, Mt Nimba, Bord du Zougué, galerie forestière, 12.xii.1983-15.i.1984, M. Lamotte & C. Girard (MNHN) [*A. biordinata* in Legrand (1985)]; 3♂, Mt Nimba, Zougué River, Plateau de Zougouepo station, env. Popote, ca. 750 m, 28.v-30.vi.1991, J. Legrand (MNHN) [*A. biordinata* in Legrand (2003)].

Other material (not included in PCA). – CAMEROON: 1♂, Mamfe, Gorilla Mt, 1700 ft (≈520 m), ii.1958; 1♂, Mamfe, ii.1958, E. Pinhey (NMBZ) [*A. b. pseudeudoxia* in Pinhey (1961c)]; 1♂, about 20 km W of Yaoundé, ca. 700 m, partly shady stream with sandy bottom in rainforest, 28.iv.1983, R. Niedringhaus (Coll. Niedringhaus, Oldenburg) [examined by T. Lieckweg]. – CENTRAL AFRICAN REPUBLIC: 1♂, Bouar, Artillery Range, 10.iv.1975, R.P. Lindley (NMBZ). – CONGO-KINSHASA: 1♂, 40 miles N of Quibo Falls, iii.1958, leg. unknown (NMBZ) [*A. b. biordinata* in Pinhey (1961c)]. – GHANA: 5♂, Eastern Region, Atewa Range Forest Reserve, Obeng-ne-obeng stream, 640 m, 17-21.vi.2006, K.-D.B. Dijkstra (RMNH). – NIGERIA (SE): 1♂, Ajassor-Ikom, ii.1958, E. Pinhey (NMBZ) [*A. b. pseudeudoxia* in Pinhey (1961c)]. – SIERRA LEONE: 1♀, Loma Mts, waterfall of Denkale river, ca. 800 m, 30.xi.1984, W. Rossi (MZUF) [*A. biordinata* in Carfì & d'Andrea (1994)].

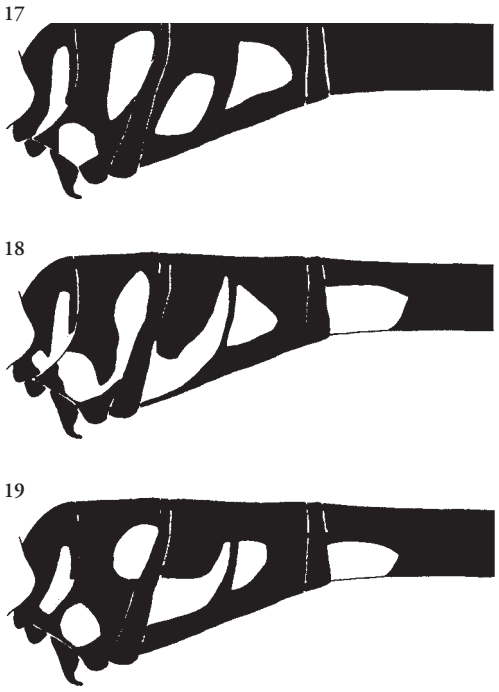
Diagnosis

Fairly large, dark and slender *Atoconeura* species, identified by the absence of basal spots on S4-9 in both sexes (fig. 17), the absence of penile cornua (figs. 21, 25), the slender male appendages (figs. 29, 32) and the vulvar scale (fig. 40). Males of other species usually have clear wing bases, but these are distinctly marked with amber in this species. Densely veined, the sum of Ax and Px in both Fw is on average 44.1 in males (range 39-48; n=18) against a range of 32-45 in other species (table 1).

Description

Holotype male. – Measurements (mm): entire length: 45, abdomen (without appendages): 33, Fw: 37, Hw: 35.5, Fw Pt: 3.5.

Prementum black, anteriorly with two small paired yellow blotches, and labial palps yellow with inner quarter black, this central black area of



Figs. 17-19.
Abdomen base of *Atoconeura* species in lateral view. – 17, *A. luxata* sp. n.; 18, *A. eudoxia*; 19, *A. biordinata*.

labium triangular, narrowing anteriorly and extending thinly along anterior border. Mandibles yellow, tipped black. Genae yellowish. Labrum glossy black. Ante- and postclypeus yellow, centre of postclypeus with blackish brown bar (above anteclypeus), anterolateral border brownish. Frons entirely black with blue sheen, except anterior part, which is yellow, sharply demarcated from black along lower border of frontal shields. Vertex black with blue sheen, glossy brown above anterior ocellus. Occipital triangle dark brown, blacker laterally. Postgenae and back of occiput black, browner internally, with small circular yellow spot about halfway along eye margin and similar streak bordering ventral end of margin. Antennae and their bases black. Labrum, clypeus, frons, vertex and occipital triangle with black hairs. Postgenae with pale hairs, these longer than black facial hairs.

Prothorax brown, darker on posterior lobe, which has dense long pale hairs. Synthorax brownish black with bluish gloss, marked with yellow as follows: middorsal carina yellow; antehumeral stripe complete but narrow, about as wide as one-sixth of mesepisternum; thin stripe on mesepimeron anterior to interpleural suture reaches dorsad about halfway metastigma and subalar ridge, and is aligned with isolated blotch on antero-dorsal corner of metepisternum; complete stripe (about as wide as antehumeral) on metepisternum anterior of metapleural suture, which is fused with mesepimeral stripe below metastigma, continuing onto largely yellow metakatepisternum; metepimeron with antero-dorsal spot and stripe along posterior carina, the latter about as wide as antehumeral. Mesokatepisternum yellow, anterior half darker. Synthoracic venter yellow, posterior stripe of metepimeron continuing onto venter, leaving it black anteriorly and posteriorly. Posterior border of poststernum black. Antealar sinus and sclerites brownish black. Synthorax entirely covered with long pale hairs, longest and densest on dorsal mesepisternum, darker latero-ventrally. Poststernum slightly raised posteriorly, with long, fairly dense pale hairs.

Legs black save largely yellow coxae, and yellow on interior sides of trochanters and basal three-quarters of interior side of fore femora. Trochanters and especially coxae with numerous pale and dark long hairs. Legs otherwise quite bare, save the usual black bristles and denticles, and patches of fine pale hairs on anterior face of hind femora, near base. These hairs quite dense and up to two-thirds as long as femur is wide.

Venation black. Wing membrane clear, amber at base of Hw and Fw, concentrated in subcostal and cubital spaces, most extensive in Hw cubital space where it reaches about halfway to Cux1. Membranule and Pt blackish brown. 14 Ax in both Fw, 10-11 in Hw. 10 Px in Fw, 10-11 in Hw. Arculus about halfway Ax2 and Ax3 in all wings. 1 Cux in both Fw, 2 in Hw. Fw triangles about 3x as long as wide, each with one cross-vein; Hw triangles uncrossed. Supratriangles without cross-veins, subtriangles of 3 cells. Discoidal field of 3 cells bordering triangle, then 2 rows for 6-8 cells, becoming 3 rows just proximal of nodus, Mspl scarcely defined. IR3 and Rspl enclosing single row of 9-10 cells in all wings. Anal field of 3 rows near rounded tornus. Anal loop of 21-23 cells, distinctly boot-shaped with pointed 'toe' and rectangular 'heel'. Bridge spaces with 1 cross-vein.

Abdomen slender, S7-9 slightly expanded, but not club-shaped. Abdomen black marked with yellow: S2-8 very thinly yellow along dorsal carina, most clearly on S2-4; S1 with long lateral mark; S2 with round spot above genital fossa and large wedge-shaped lateral spot posterior of transverse ridge; S3 with oval lateral spot anterior of transverse carina and large roundly triangular spot posterior of it, the former shifted somewhat ventrad relative to the latter; S4-6 and S8-10 unmarked; S7 with elongate dorsal spot, occupying about basal two-thirds of segment. Cerci and epiproct black. Cerci weakly sinuous in lateral view, straight in dorsal view; narrowed near base, swollen subapically, with slender pointed,

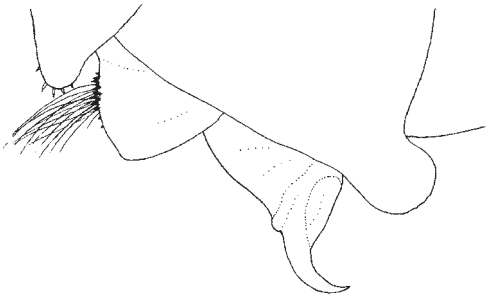


Fig. 20. Secondary genitalia of *Atoconeura luxata* sp. n. in lateral view.

somewhat up-curved tips; ventral ridge rather short with about 7 irregular, coarse teeth (figs. 29, 32). Epiproct long and rather narrow, almost reaching halfway ventral ridge and apex of cerci (figs. 32, 38). Cerci with bristly black hairs, abdomen otherwise rather bare, mainly with fine, short hairs along carinae. Venter of abdomen (sternites and ventral portions tergites) black, narrowly yellow along ventral carinae. Anterior lamina low and brown, with numerous long pale hairs and short black denticles. Hook of hamule blackish brown, strongly curved (fig. 20). Genital lobe black and short with many long pale hairs. Penis not extracted (see paratype).

Paratype males. – Similar to holotype but slightly smaller: Hw 34 (Tombel) and 34.5 mm (Takamanda). Tombel male has labium only narrowly black along inner border of palps, paired yellow blotches occupying most of prementum. Postclypeus slightly blacker laterally, vertex all black. Venation similar but 12 Ax in Fw, 9-10 in Hw. 8-9 Px in Fw, 9 in Hw. Discoidal field of 2 rows of cells from base to level of nodus. Anal loop of 21-24 cells. Takamanda male has labium as holotype but prementum all black. Postclypeus slightly darker laterally, vertex all black. Venation similar but 11-12 Hw Ax and 10 Hw Px. Anal loop of 20-23 cells. Penis of Takamanda male extracted: fourth segment relatively long with greatly developed pleats; ventral hump and cornua absent (figs. 21, 25).

Paratype female. – Measurements (mm): entire length: 49, abdomen (without appendages): 34, Fw: 38.5, Hw: 37, Fw Pt: 3.7. Similar to holotype but slightly more robust. Black on labial palps reduced to narrow band along inner borders. Antero-lateral borders of postclypeus blacker, frontal shields and vertex dorsum largely brown. Thorax alike, but spot and stripe on metepisternum are fused. Interior side of all femora yellow on basal half. Amber at wing bases deeper and more extensive, reaching Ax1 and Cux1. Venation similar but 12 Fw Ax, 10 Hw Ax and 11-12 Hw Px. Anal loop of 22-24 cells. The two lateral yellow markings of S2 fused. S4 with a yellow lateral streak on about middle third of segment. A similar, but almost indiscernible, streak on S5. Vulvar scale with two small points just reaching to end of S8, separated by U-shaped excavation that is about as wide as one point (fig. 40). Yellow along ventral carinae of tergites wider than in holotype. Cerci about 3x as long as epiproct and paraprocts, elongated with fine spiny point, with scattered black bristly hairs.

Variation

The males from Mt Nimba are slightly smaller (average Hw 33.6 mm, n=11) and paler than the type material (34.7, n=3). They often have paired pale spots at the labrum base and the postclypeus is normally all pale. The dark area on the frons dorsum is browner and less extensive, sometimes leaving the anterior half of the shields pale. The vertex is brown, rather than black. The basal spot on S3 may be larger and more crescentic (i.e. more like *A. biordinata*) and the dorsal spot of S7 is longer, about as long as 75% of the segment. Ghanaian males are intermediate in coloration, but even smaller (32.1, n=5).

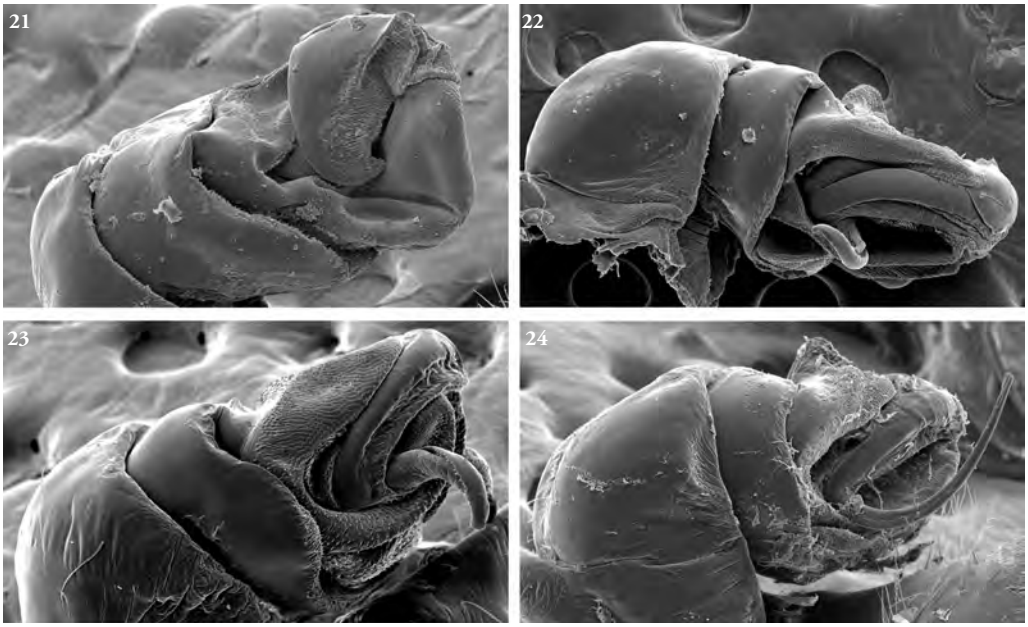
Etymology

The adjective *luxata* (dislocated) refers to the species's isolation by characters and geographic and altitudinal range.

Range

Known from Sierra Leone, Guinea-Conakry, Ghana, SE Nigeria, Cameroon, W Central African Republic and W Congo-Brazzaville (fig. 6) at 250-800 m, much lower and further west than other *Atoconeura*. The genus was collected in Gabon (J. Legrand pers. comm.), but no material was available for study. Pinhey (1961b, c) passed the Chutes de Kiubo in Katanga (9°31'S 27°02'E) on his way north in January 1958. However, the male from near 'Quibo Falls' is dated two months later and would originate from well outside the species's known geographic and altitudinal range (the site should lie south of Mitwaba above 1000 m). Pinhey collected *A. luxata* sp. n. in Cameroon a month later, but returned south by aeroplane. Perhaps the Quibo Falls specimen was mislabelled, although Pinhey's assistant returned overland and could have collected it then.

Males in Ghana preferred sunny spots on a shaded rainforest stream with rocks and gravel, hovering over the swiftest parts, for instance near a small waterfall (larvae were not found). This is corroborated by Legrand (1985) who found the species 'sur les petits cours d'eau forestiers, la larve, très rhéophile, se tient fixée sur les dalles rocheuses en plein courant' and the waterfall habitat in Sierra Leone.



Figs. 21-24. Electron microscope scans of penes of *Atoconeura* species in lateral view. – 21, *A. luxata* sp. n. (Takamanda, Cameroon); 22, *A. pseudeudoxia* (Kibale NP, Uganda); 23, *A. biordinata* (Mulanje, Malawi); 24, *A. kenya* (Mt Kenya, Kenya).

Atoconeura eudoxia (Kirby)
(figs. 9, 14, 18, 26, 30, 33, 39, 41, 45)

Accaphila eudoxia Kirby, 1909: 60. Holotype ♂: UGANDA: round label, white with red border 'Holotype', rectangular, blue '20 Jan 06 alt 6000 ft. [≈1830 m], Ruwenzori East', rectangular, white 'Accaphila eudoxia Kb. type.', leg. probably G. Legge & A.F.R. Wollaston (BMNH) [examined].

Atoconeura extraordinata Fraser, 1950: 56. Lectotype ♂ (designated by Kimmins 1966: 191): UGANDA: round label, white with purple border 'Lectotype', 'UGANDA Ruwenzori, Bwamba V., 6500-7500 ft. [≈2000-2300 m], 13-15.i.1926. G.D. Hale Carpenter.', rectangular, white 'Atoconeura extraordinata Fraser. ♂. TYPE. (Atoconeura eudoxia (Kirby) F.C. Fraser det., 1951', rectangular, white 'F.C. Fraser Bequest. Brit. Mus. 1963-234.' (BMNH) [examined]; junior synonym (Longfield 1953: 44).

Atoconeura eudoxia (Kirby, 1909) – (Longfield 1953: 44).

Diagnosis

Male is immediately identified by bifid epiproct (fig. 39) and the numerous long dark hairs on the underside of S7-9, female by vulvar scale (fig. 41). The male cerci are much more swollen medially than in other species: the dorsal profile is rather flat, the ventral ridge is shallow and drawn-out (fig. 33), and the apices diverge (fig. 30). Despite these unusal male characters, the female head morphology is similar to that of other species, although the vertex and occiput appear slightly flatter.

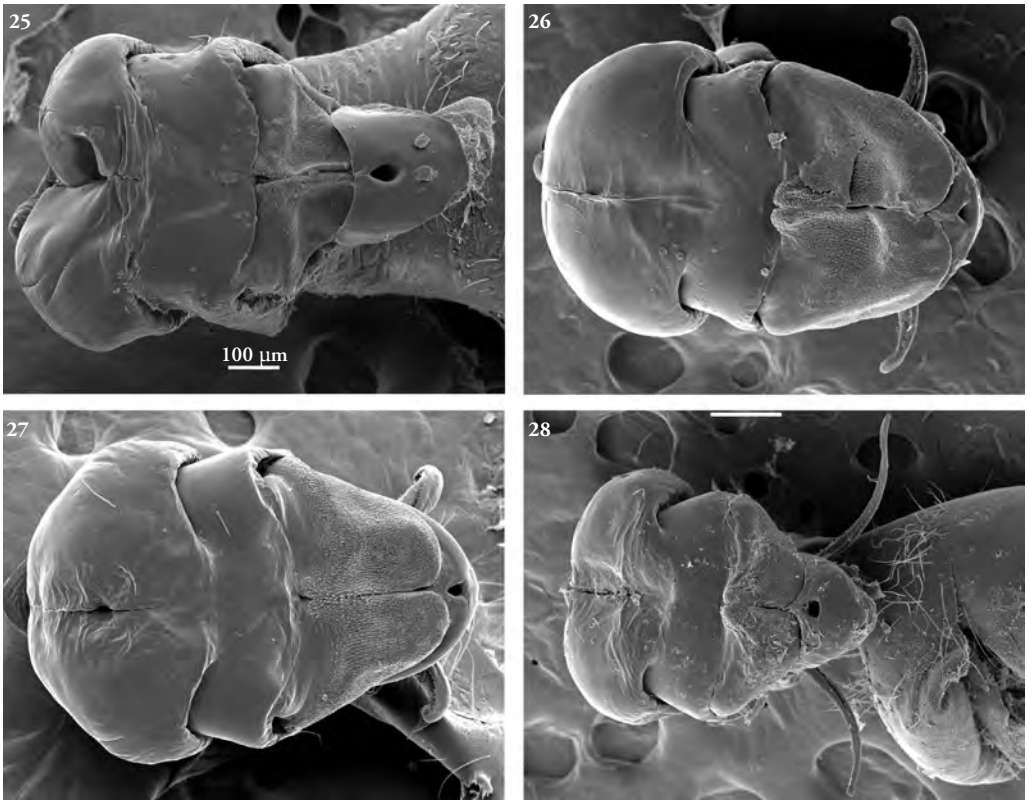
Although *A. eudoxia* differs from all other species by sexual characters, it is almost identical to the sympatric *A. pseudeudoxia* in five respects (see *A. pseudeudoxia* for a comparison): (1) Large size (table 1). (2) Cone-shaped labial marking, largely dark frons and brown vertex (figs. 9-10). Other species in eastern Africa have the labial marking on average wider at base but narrower at apex, the frons paler with more contrast and the vertex blacker (figs. 10-13). (3) Strongly swollen poststernum with medially a dense patch of short, bristly pale and dark hairs (figs. 14-15). This patch strengthens the 'pot-belly' and recalls a coconut fibre mat in lateral view. Female poststerna are similar, but with only sparse hairs. (4) Anteriorly densely, long and dark haired hind femora. The femoral surface appears rather rough where these hairs are present. (5) The fourth segment of the penis is relatively long and flat, with a clear ventral hump and distinct but short cornua (figs. 22, 26).

Variation

Not notable within small range.

Range

Most records are from S and W Uganda (fig. 6) at 1400-2600 m, e.g. Ruwenzori Mts and Bwindi Impenetrable NP. The Burundi record also lies within the Albertine Rift and suggests the species's presence



Figs. 25-28. Electron microscope scans of penes of *Atoconeura* species in ventral view. – 25, *A. luxata* sp. n. (Takamanda, Cameroon); 26, *A. eudoxia* (Bwindi Impenetrable NP, Uganda); 27, *A. biordinata* (Mulanje, Malawi); 28, *A. kenya* (Mt Kenya, Kenya).

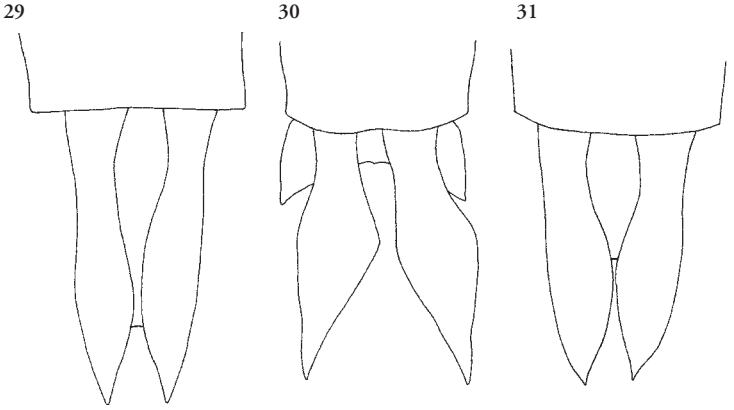
in Rwanda and E Congo-Kinshasa. Rather isolated populations occur in Mabira Forest near Kampala at 1100-1300 m (J.J. Kisakye pers. comm.) and Kakamega Forest, W Kenya.

Remarks

A. eudoxia is so similar to *A. pseudeudoxia* that Fraser (1950) found it to possess 'so strange an inferior anal appendage that I came to the conclusion [at first] that it must be a deformity'. Longfield (1953) did not 'consider it strange that, on comparing these [*A. pseudeudoxia*] specimens with the type of *A. eudoxia* from the same locality, and finding that the only apparent difference was the deeply bifid inferior appendage of the *eudoxia* type, I thought this was a structural anomaly.'

Further type material (included in PCA). – Paratype ♀ ('allotype') *eudoxia*: UGANDA: round label, white with red border 'Allotype', rectangular, white 'Nyamgasani Valley, 8-9,000ft. [≈2500-2700 m], D.R. Buxton', rectangular, white 'UGANDA: Ruwenzori Range, xii.1934-i.1935. B.M.E. Afr. Exp. B.M. 1935-203.', rectangular, white 'Atoconeura eudoxia Kirby allotype ♀ det. Miss C. Longfield.' (BMNH).

Other material (included in PCA). – BURUNDI: 1♂, Usumbura (=Bujumbura), 17.i.1934, Lefevre (MRAC). – KENYA: 4♂, Kaimosi Forest, Kakamega, i.1951-i.1953, E.C.G. Pinhey (BMNH); 1♀, Kakamega Forest, ca. 1600 m, i.1995, V. Clausnitzer (CGVL). – UGANDA: 1♀, Ruwenzori, Bwamba Pass, 6500-7000 ft. (≈2000-2100 m), 13-15.i.1925, G.D. Hale Carpenter (BMNH); 1♂, Ruwenzori Range, Nyamgasani Valley, 8-9,000 ft. (≈2500-2700 m), xii.1934-i.1935, D.R. Buxton (BMNH); 1♂, Ruwenzori Range, Namwamba Valley, 6,500 ft. (≈1980 m), xii.1934-i.1936; 1♀, Kigezi, Mafuga Rain Forest, vi.1951, T.H.E. Jackson (BMNH); 1♂, Kigezi, Mitano Rain Forest, vi.1951; 1♂, 2♀, Kigezi, Rutenga Forest, vi.1951-vi.1952; 1♂, 1♀, Kayonza Forest, Kigezi, iv.1951-xi.1953, V.G.L. van Someren (BMNH); 2♂, 1♀, Bwindi Impenetrable NP, Buhoma, Munyaga Valley, 1600 m, 17-18.v.2003; 1♂, 1♀, Bwindi Impenetrable NP, Rushamba, 1450 m, 21-23.v.2003; 1♀, Bwindi Impenetrable NP, Ruhija, 2100 m, 24.v.2003, K.-D.B. Dijkstra (RMNH).



Figs. 29-31.
Male appendages of *Atoconeura* species in dorsal view. – 29, *A. luxata* sp. n.; 30, *A. eudoxia*; 31, *A. aethiopica*.

Atoconeura pseudeudoxia Longfield stat. rev.
(figs. 10, 15, 22, 34)

Atoconeura biordinata pseudeudoxia Longfield, 1953: 46. Holotype ♂: UGANDA: round label, white with red border 'Holotype.', rectangular, white 'Uganda: Ruwenzori Range, Mobuku [=Mubuku] Valley, Bikoni Peak, 7000 ft. [≈2130 m] 30.XII.1937. C.E. Longfield', rectangular, white 'Atoconeura biordinata pseudeudoxia det. Miss C. Longfield. Type ♂ subsp.n.', rectangular, white 'Brit. Mus. 1952-581' (BMNH) [examined].

Diagnosis

Has a 'hybrid' appearance, being almost identical to *A. eudoxia* in many respects (see that species), but the vulvar scale and male appendages are close to *A. biordinata* (figs. 34, 42). However, the male cerci are more strongly sinuous than in other species: the tips are curved upwards more, while the extreme apices curve slightly down again, and the ventral ridge is so strongly sinuous that it appears as two separate short ridges in lateral view (fig. 34).

Although 'carbon-copy' *A. eudoxia* and *A. pseudeudoxia* probably exist, they tend to differ in details of markings (figs. 9-10). Both sexes of *A. eudoxia* always have black antero-lateral edges of the postclypeus, which are absent in most *A. pseudeudoxia*. The lower frons is more often pale in *A. pseudeudoxia*, in contrast with the shields. In *A. eudoxia* males the yellow lateral spots on S2 are often fused (fig. 18), but always separated by black in *A. pseudeudoxia* (cf. fig. 19). In *A. pseudeudoxia* the poststernum is most strongly raised posteriorly and slopes anteriad, giving a triangular profile in lateral view (fig. 15), but it is relatively high anteriorly and therefore plateau-like in *A. eudoxia* (fig. 14).

Variation

Specimens from Katanga are paler and smaller (average Hw 33.6 mm, n=10) than other specimens (34.6, n=12). Most notably the postclypeus is normally unmarked.

Range

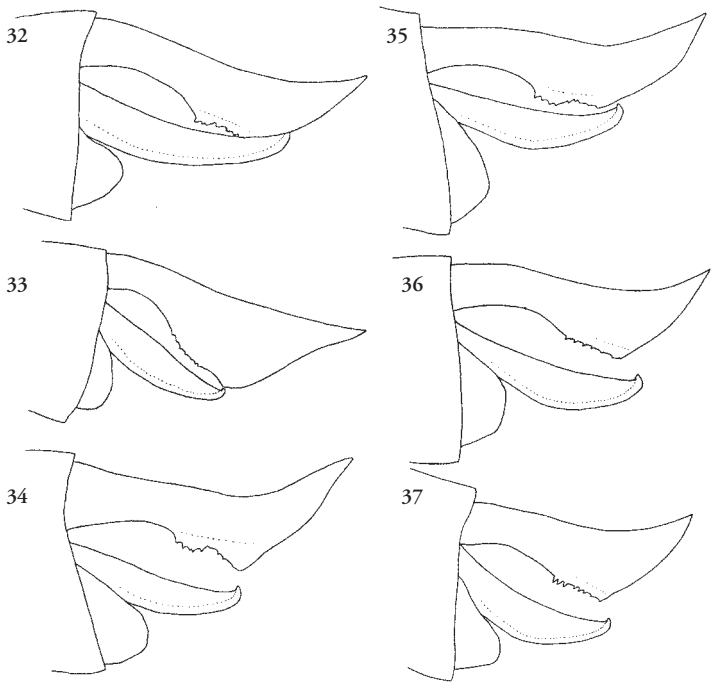
Described from S and W Uganda, from where it extends into E Congo-Kinshasa and through Katanga to N Zambia (fig. 6), occurring at 700-2300 m.

Remarks

Longfield (1953) remarked that 'when found, it [the female of *A. pseudeudoxia*] will be extremely difficult to determine'. None of the details of a female discussed by Pinhey (1961a) are diagnostic. Two kinds of females recalling *A. eudoxia* were studied. That treated as *A. eudoxia* by Longfield has a uniquely formed vulvar scale (fig. 41) and is known from W Kenya, where *A. pseudeudoxia* does not occur. The other is known from Uganda and Katanga, and has the scale similar to *A. biordinata*, and includes the presumed *A. pseudeudoxia* female found by Dijkstra & Dingemanse (2000).

Further type material (included in PCA). – Paratypes: UGANDA: 1♂, Bikoni, Mobuku valley, 7,500 ft. (≈2290 m), 31.xii.1934, leg. unknown (BMNH) [head belongs to another genus]; 1♂, Ruwenzori Range, Mpanga Forest, 25.i.1935, F.W. Edwards; 1♂, Ruwenzori, 6-8000 ft. (≈2130 m), xii.1895, Scott-Elliot (BMNH).

Other material (included in PCA). – CONGO-KINSHASA: 1♂, Région Lac Kivu, Kadjudju, 1930, G. Babault (MNHN); 9♂, 5♀, PN Upemba, River Mubale, 1480 m, 1-20.v.1947, G.F. de Witte (ISNB); 1♀, PN Upemba, River Mubale, 1480 m, 20.v.1947, G.F. de Witte (BMNH). – UGANDA: 1♂, Bwamba Valley, 2500 ft. (≈760 m), 8-12.i.1928, G.D. Hale Carpenter (BMNH); 1♂, Fort Portal, Bwamba Forest, 2400 ft. (≈730 m), iv.1951, E.C.G. Pinhey (BMNH); 1♂, Kigezi, Rutenga Forest, viii.1951, V.G.L. van Someren (BMNH); 1♂, Kalinzu Forest Reserve 4,700 ft. (≈1430 m), 25.vi.1994,



Figs. 32-37.
Male appendages of *Atoconeura* species in lateral view. – 32, *A. luxata* sp. n.; 33, *A. eudoxia*; 34, *A. pseudeudoxia*; 35, *A. biordinata*; 36, *A. kenya*; 37, *A. aethiopica*.

T. Graves (Coll. T. Graves); 1♂, Kibale NP, Kanyawara, 29.x.1995; 1♀, Kibale NP, Ngogo, 3.ii.1996; 3♂, Bwindi Impenetrable NP, Buhoma, Munyaga Valley, 1600 m, 17-18.v.2003; 1♂, Bwindi Impenetrable NP, Rushamba, 1400 m, 22.v.2003; 1♀, Semliki NP, Ntandi, Nkisi River, 700 m, 1.vi.2003, K.-D.B. Dijkstra (RMNH).

Other material (not included in PCA). – CONGO-KINSHASA: 1♂, Ituri Forest, ii.1958, E. Pinhey (NMBZ). – ZAMBIA: 1♂, Ikelenge, Sakeshi, v.1961; 1♂, Mwinilunga, v.1964, E. Pinhey (NMBZ); 1♂, Mwinilunga, Ikelenge, Lisombo River, 28.iv.1972, F.C. de Moor & E. Pinhey (NMBZ).

Atoconeura biordinata Karsch
(figs. 11, 16, 19, 23, 27, 35, 42, 46)

Atoconeura biordinata Karsch, 1899: 371. Holotype ♀: TANZANIA: Kitope [not found ZMHB, i.2004].

Atoconeura leopardina Förster, 1906: 38. Holotype ♂: TANZANIA: Nguelo (UMMZ) [not examined]; junior synonym (Ris 1912: 750).

Atoconeura biordinata chirinda Longfield, 1953: 46. Holotype ♂: ZIMBABWE: round label, white with red border 'Holotype', rectangular, white 'Chirinda For. Melsetter Dist. Dept. Agric. S. Rhodesia 27/12.1948', rectangular, white 'J.A. Whellan Collector', rectangular, white 'Atoconeura biordinata chirinda det. Miss C. Longfield. Type ♂ subsp.nov.' (BMNH) [examined]; junior synonym (Bridges 1991: VIII.9).

Oreoxenia leopardina Förster, label name – (Pinhey 1962: 266).

Atoconeura biordinata f. *chirinda* Longfield, 1953 – (Pinhey 1984: 47).

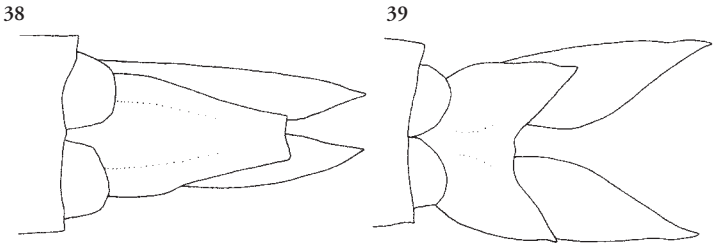
Oreocema leopardina Förster, label name – (Garrison et al. 2003: 58); possible misspelling.

Diagnosis

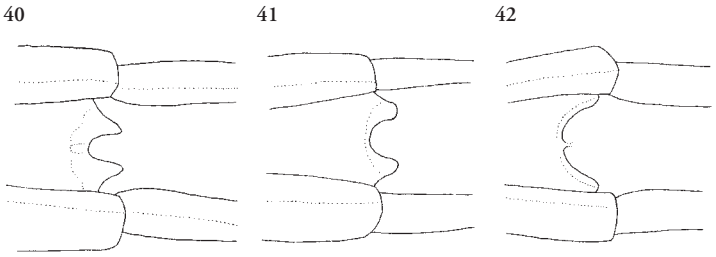
Smallest *Atoconeura* species, best separated from others with black labrum by frons: although this is variable, the pale shields always contrast with the dark area below them (fig. 11). It is otherwise rather intermediate between *A. pseudeudoxia* and *A. kenya* in markings (including labium), abdomen shape and cerci (fig. 35). The small size is reflected by venation: in males 79% of Fw have 10-11 Ax (range 9-13, n=86) while in *A. pseudeudoxia* 79% have 12-13 (10-14, n=43). 44% of *A. biordinata* males (n=43) have one or both Fw triangles uncrossed, whereas 100% of *A. pseudeudoxia* (n=22) have both crossed. The fourth segment of the penis is nearest that of *A. eudoxia*, with similar cornua, although the general shape is intermediate to *A. kenya*; the ventral hump is reduced (figs. 23, 27).

Variation

Specimens from Zimbabwe ('*chirinda*') are smaller with more open venation: most examined males (average Hw 28.9 mm, n=11) had Fw with 7 Px, 10 Ax and uncrossed triangles, while non-Zimbabwe



Figs. 38-39.
Male appendages of *Atoconeura* species in ventral view. – 38, *A. luxata* sp. n.; 39, *A. eudoxia*.



Figs. 40-42.
Vulvar scales of *Atoconeura* species in ventral view. – 40, *A. luxata* sp. n.; 41, *A. eudoxia*; 42, *A. biordinata*.

A. biordinata (31.2, n=32) more often had 8-9 Px, 11 Ax and crossed triangles in Fw.

Range

The first Kenyan record is from the Taita Hills, which (bio-) geographically are considered the northernmost outlier of the Eastern Arc Mts (Burgess et al. 1998). Ranges further from Mt Kilimanjaro and the Usambara Mts to Katanga, Malawi, Mozambique and Zimbabwe (fig. 6), occurring at 1000-2000 m and probably higher. Pinhey's (1984) Zambian records probably all pertain to *A. pseudeudoxia*. An old and poorly labelled male, already examined by Ris (1912), may indicate an isolated presence of *A. biordinata* in the Cameroon highlands. However, it is the only specimen seen from the region, and clusters with males from Zimbabwe (figs. 1-2).

Remarks

Longfield (1953) did not see the holotype of this species, a teneral female from central Tanzania, and I could not relocate it. By origin the present interpretation of its identity is probably correct. The description by Karsch (1899) contains little specific information, but the open Fw triangle in one wing and low measurements match the known female. Longfield's (1953) diagnosis of *A. biordinata* incorporated unpruinose specimens of *A. kenya* from N Tanzania: 'The Arusha [=Mt Meru] series [plural] vary considerably and in some, the colour-pattern resembles the subspecies from the Kenya Highlands [*A. kenya*], to a slight extent.' As a consequence, most of the characters in her key for *A. biordinata* refer to *A. kenya*.

Further type material (included in PCA). – Paratypes *chirinda*: ZIMBABWE: 1♀ ('allotype'), round label, white with red border 'Allotype'; rectangular, white 'Chibudzana R., Melsetter Dist. Dept. Agric. S. Rhodesia 26/2.1948', rectangular, white 'J.A. Whellan Collector', rectangular, white 'Atoconeura biordinata chirinda allotype ♀ subsp.n. det. Miss C. Longfield.' (BMNH); 1♂, Umtali District, 4.xii.1947; 3♂, Chirinda Forest, Melsetter District, 14.xi-27.xii.1948, J.A. Whellan (BMNH).

Other material (included in PCA). – 1♂, 'Cameroun', date and leg. unknown (MNHN) [origin doubted]. – CONGO-KINSHASA: 1♂, Katentania, v.1924, Ch. Seydel (MRAC); 1♂, PN Upemba, Kavizi (affl. Lusinga), 14.vii.1945, G.F. de Witte (MRAC). – KENYA: 1♀, Teita [=Taita] Hills, Wesu, vii.1947, V.G.L. van Someren (BMNH). – MALAWI (MISUKU HILLS): 1♀, Matipa Forest, 5.xii.1987; 1♂, Mughese Forest, 10.xii.1987, J.T. Wilson (CGVL). – MALAWI (MULANJE): 2♂, Lichenya Path, 1780 m, 8.xi.2001; 1♂, Lichenya Plateau, 2000 m, 8.xi.2001; 1♂, Muloza Stream, 1980 m, 10.xi.2001; 1♀, Nessa Path, 1860 m, 9.xi.2001; 4♂, Dzole Stream, 2000 m, 16.xi.2001; 2♀, Ruo Gorge, 1750 m, 17.xi.2001; 2♂, Ruo Gorge, 1090 m, 17-18.xi.2001; 1♀, Lichenya Path, 1200 m, 13.i.2002, K.-D.B. Dijkstra (RMNH). – MOZAMBIQUE (NAMULI): 3♂, Khurukani Stream, 1490 m, 4.xii.2001; 1♂, 1♀, Muretha Plateau, 1870 m, 6.xii.2001, K.-D.B. Dijkstra (RMNH). – TANZANIA: 2♂, W Kilimanjaro, Ngare-Nairobi, 4-5,000 ft. (≈1200-1500 m), i-ii.1937, B. Cooper (BMNH); 1♂, Kigoma, Mahale Mt. nr Ujamba, 2000 m, 28.viii.1966; 1♀, Sibweza, 35 mi, Mpanda-Karema Rd. (1050m), 26.xi.1968; 2♂, Sibweza,

Figs. 43-48. Males of *Atoconeura* species. Note characters of frons and mesepisternal 'hyphens'. – 43-44, *A. luxata* sp. n. in the Atewa Range, Ghana; 45, *A. eudoxia* near Ruhija, Uganda; 46, *A. biordinata* on Mulanje, Malawi; 47, *A. kenya* on Mt Elgon, Uganda; 48, *A. aethiopica* at Wushwush, Ethiopia. Photographs taken by author (43-46, 48) and V. Clausnitzer (47).

35 mi. Kampisa-Mpanda (1500m), 26.xi.1968; 2♂, 1♀, Kigoma, Ujamba at Mahale Ridge, 2000-2500 m, x.1969-4.ii.1972, J. Kielland (RMNH); 1♂, 1♀, Mts Uluguru, Chenzema, 1700 m, 21-22.vii.1971, L. Berger, N. Leleup & J. Debecker (MRAC); 2♂, Kigoma, Lukandamira, 1600-1700 m, viii.1971-ii.1972; 1♂, Mpanda District, Kampisa, 1500 m, ix.1971, J. Kielland (RMNH); 2♂, Mbizi Mts, Mkutwa, 1987-1988, leg. unknown (CGVL); 1♂, Kiwira River, Isongole, 1930 m, 23.ix.2001; 1♀, Kilimanjaro, Machame Gate, 1700 m, 19.iii.2002, V. Clausnitzer (CVCH). – ZIMBABWE: 1♂, Imbiza Valley, Umtali, 21.i.1948; 2♂, 1♀, Vumba Mt, Umtali S.R., x.1953; 1♀, Inyanga, i.1960, E.C.G. Pinhey (BMNH); 1♂, Inyanga, 2.i.1960, E.C.G. Pinhey (RMNH); 2♂, Inyanga NP, 1800 m, 17.x-6.xi.1964, G.F. Mees (RMNH).

Other material (not included in PCA). – TANZANIA: 1♂, Kilimanjaro, Kibonoto, 1300-1900 m, 15.v.1906, Y. Sjöstedt (NHRS).

Atoconeura kenya Longfield
(figs. 12, 24, 28, 36, 47)

Atoconeura biordinata kenya Longfield, 1953: 46. Holotype ♂: KENYA: round label, white with red border 'Holotype', rectangular, white 'B.E. Africa, Kenya, Meru. 29.I.1934. On swift stream. C.E. Longfield. 6,000 ft. [≈1830 m]', rectangular, white 'Atoconeura biordinata kenya det. Miss C. Longfield. Type ♂ subsp.n.', rectangular, white 'Brit. Mus. 1952-581' (BMNH) [examined].

Atoconeura kenya kenya Longfield, 1953 – (Bridges 1991: VIII.9).

Diagnosis

Medium-sized with relatively short, club-shaped abdomen (fig. 47). *A. kenya* and *A. aethiopica* (see latter for a comparison) differ from all other species by their pale labrum (figs. 12-13), mesepisternal 'hyphens', pruinose abdomen in mature males (figs. 47-48) and the distribution of black pigment. While the face is paler, the vertex is often black, and the labial black marking is large with its greatest extent shifted anteriad (fig. 12). The pale markings on the thorax and abdomen base are strongly broken up. Besides the characteristic 'hyphens', there is always a spot on the mesepimeron near the wing base just behind the humeral suture, unlike most individuals of other species. Altogether this gives the thorax a more spotted than striped appearance. The dorsal spot on S7 is relatively large (fig. 47) and the abdomen underside can be predominantly yellow. The cerci have an almost straight ventral ridge (fig. 36). In both species the fourth segment of the penis is very short, with a strong ventral hump and very long cornua (figs. 24, 28).

Variation

Pruinosity either develops slowly or is easily lost in preservation: of 20 examined males only 6 had an entirely pruinose abdomen, 10 were only pruinose at the base (fig. 47) and 4 lacked it completely. The width of the black labral border varies from fairly broad (fig. 12) to absent (cf. fig. 13; 2 of examined males).

Range

Most records are from Kenya's central highlands (e.g. Mt Kenya and Aberdare Mts), but also occurs on Mt Elgon (including Ugandan side), N Tanzania (Mts Meru and probably Kilimanjaro) and the Imatong Mts of S Sudan (fig. 6), at 1400-3000 m. Cooper collected *A. kenya* on Mt Meru in the same period that he obtained the only specimens known from Kilimanjaro, but his *A. biordinata* males from Kilimanjaro were collected earlier. Hale Carpenter collected three *Atoconeura* species in the Bwamba Valley in the W Ruwenzori, including the only *A. kenya* specimen known from the Albertine Rift. Both records require confirmation as mislabelling cannot be ruled out, although Hale Carpenter did concentrate his collecting in W Uganda.

Remarks

The larva is briefly described by Pinhey (1959), the karyotype by Wasscher (1985).

Further type material (included in PCA). – Paratypes: KENYA: 1♀ ('allotype'), round label, white with red border 'Allotype', rectangular, white 'Africa, Kenya, Thompson's Falls April 1950.R.W. Barney. B.M. 1952-582', rectangular, white 'Atoconeura biordinata kenya det. Miss C. Longfield. allotype ♀ subsp.n.' (BMNH); 1♂, Nairobi, xi.1926, leg. unknown (BMNH); 3♂, Nyeri, vi.1949, E. C. G. Pinhey (BMNH).

Other material (included in PCA). – KENYA: 1♂, Thiririka River, near Ruiro, date unknown, G.R.C. van Someren (BMNH); 1♂, Meru, viii.1937; 1♂, Katamayu, iii.1942, V. G.L. van Someren (BMNH); 1♂, Meru, Kasita River, 10,000 ft. (≈3050 m), iv.1947; 1♂, Meru, Kasita River, 6000 ft. (≈1830 m), iv.1947, G.R.C. van Someren (BMNH); 3♂, Nyeri, vi.1949, E.C.G. Pinhey (BMNH); 1♂, Naivasha, R. Gilgil (irrigation canal), North Lake Rd, 27.xii.1982, P.C. Barnard (BMNH); 1♂, Mt Kenya, Kentrout, iv.1983, V. Clausnitzer (CVCH); 1♂, Njoro, Ndaragu River, 12.x.1987, leg. 'AW' (BMNH). – TANZANIA: 2♂, 3♀, Mt Meru, 7500 ft. (≈2290 m), xii.1937-ii.1938; 3♀, W Kilimanjaro, 4500-5000 ft. (≈1400-1500 m), xii.1937-ii.1938, B. Cooper (BMNH). – UGANDA: 1♂ Bwamba Pass, Ruwenzori, ca 4500-5000 ft. (≈1400-1500 m), 13-15.i.1926, G.D. Hale Carpenter (BMNH); 1♂, Mt Elgon NP, 2.iv.1997, V. Clausnitzer (CVCH).

Other material (not included in PCA). – SUDAN: 1♂, Imatong Mts, south of Gilo, 2000 m, 12.ii.1981, M. Wasscher [*A. biordinata* in Wasscher (1985); specimen lost, photograph examined]. – TANZANIA: 2♀, Meru Niederung, 27.xii.1905, Y. Sjöstedt (NHRS).

Atoconeura aethiopica Kimmins
(figs. 13, 31, 37, 48)

Atoconeura biordinata aethiopica Kimmins, 1958: 357. Holotype ♂: ETHIOPIA: round label, white with red border 'Holotype', rectangular, white 'Ethiopia, Segheria, 25.iii.1948. K.M. Guichard. B.M. 1948-248.', rectangular, white 'Atoconeura biordinata ♂ aethiopica Kim D.E. Kimmins det. 1958 Type' (BMNH) [examined].

Atoconeura kenya aethiopica Kimmins, 1958 – (Bridges 1991: VIII.9).

Atoconeura aethiopica Kimmins, 1958 – (Clausnitzer & Dijkstra 2005: 126).

Diagnosis

Similar to *A. kenya* (see that species), but the epiproct was marginally shorter (fig. 37), the abdomen somewhat narrower and abdominal pruinosity complete in all examined males (fig. 48). The dark area on the frons has a straight anterior edge in *A. aethiopica* males, but is rounded in *A. kenya* (figs. 12-13). Facial

markings tend to be even paler and the marking on the labium is more variable: it can be exactly as in *A. kenya*, but is sometimes strongly reduced. The dark colour of the thorax is more brown than black, making pale markings ill-defined. Unlike other species, females are so light that their thorax appears uniformly brown.

Variation

The pattern on the labium is very variable (Kimmins 1958, Pinhey 1982). The labrum may be all pale (fig. 13) or have a narrow black border.

Range

Endemic to Ethiopia and not uncommon along clear streams and rivers (often with forest) at 1250-2400 m south of Addis Abeba (Clausnitzer & Dijkstra 2005).

Remarks

Only two females could be examined. Their all-brown appearance may be a preservation artefact, although I believe my interpretation of their lack of markings is correct.

Further type material (included in PCA). – Paratypes: ETHIOPIA: 1♀ ('allotype'), round label, white with red border 'Allotype', rectangular, white 'Ethiopia, Segheria, 25.iii.1948. K.M. Guichard. B.M. 1948-248.', rectangular, white 'Segheria, 25.3.48', rectangular, white 'Atoconeura biordinata ♀ aethiopica Kim D.E. Kimmins det. 1958 Allotype' (BMNH); 1♂, Segheria, 25.iii.1948; 1♂, Dilla, iv.1948; 1♂, Wondo, iv.1948, K.M. Guichard (BMNH).

Other material (included in PCA). – ETHIOPIA: 1♂, Lac Zouay, 19.iii.1914, leg. unknown (MNHN); 1♀, Segheria, 25.iii.1948, K.M. Guichard (BMNH).

Other material (not included in PCA). – ETHIOPIA: 1♂, Gubali, 4.iii.1934, leg. unknown (NHRS); 2♂, Baro River between Gordomo and Masha (1630m), 30 km south of Gore, 17.iii.2004; 1♀, stream near Gecha, 40 km north of Tepi, 17.iii.2004; 1♂, Wushwush Tea Plantation (1900m), 13 km west of Bonga, 19.iii.2004; 1♂, Borkana River near Yayu (1290m), 35 km east of Matu (Metu), 21.iii.2004, V. Clausnitzer & K.-D.B. Dijkstra (RMNH).

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Table 1. Measurements of the species. Figures represent averages for continuous measures and sums, and modi for counts, with ranges given in brackets.

	A. luxata sp. n.	*A. eudoxia*	*A. pseudeudoxia*	*A. biordinata*	*A. kenya*	*A. aethiopica*
♂ : ♀	19 : 3	15 : 9	22 : 8	43 : 14	20 : 7	5 : 2
Hw ♂ (mm)	33.4 (30.5 - 36)	34.5 (33.5 - 36)	34.1 (32 - 36.5)	30.6 (28 - 33.5)	32.5 (31 - 35)	32.4 (31 - 34)
Hw ♀ (mm)	36.8 (36.5 - 37)	36.8 (35 - 38.5)	35.3 (34 - 36.5)	32.1 (30 - 35.5)	32.8 (32 - 34)	34.5 (34 - 35)
Fw Ax ♂ ♀	12 - 13 (11 - 14)	11 - 12 (10 - 14)	12 - 13 (10 - 14)	10 - 11 (9 - 13)	10 - 11 (9 - 12)	9 - 10 (- 11)
Fw Px ♂ ♀	9 - 10 (8 - 11)	8 - 9 (7 - 11)	8 - 9 (7 - 11)	7 - 9 (6 - 10)	8 - 9 (- 10)	8 (- 9)
Σ Fw Ax Px ♂ ♀	44.4 (39 - 50)	40.6 (36 - 45)	42.7 (39 - 47)	37.0 (32 - 44)	38.8 (36 - 43)	35.4 (34 - 37)
Abd ♂ (mm)	30.3 (28 - 33)	31.5 (30 - 34)	31.6 (29 - 35)	27.2 (25 - 31)	27.0 (26 - 28)	27.2 (27 - 28)
% Abd / Hw ♂	89.6	91.2	92.5	89.1	82.8	84.0

Table 2. Character matrix for cladistic analysis. Numbers correspond to those in appendix 2.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
A. luxata	2	2	3	2	1	2	1	0	1	1	1	0,1	1	1	0	2	1	1	0	2	2	0	0	0	2	0	0	0
A. eudoxia	2	2	1	2	0	2	1	0,1	1	1	1	0	1	1	0	0,1	0	0	1	0	1	1	1	1	2	2	1	1
A. pseudeudoxia	2	2	2	2	0	2	1	0	1	1	1	0	1	1	0	1,2	0	2	2	0	0	0	1	1	2	2	1	1
A. biordinata	0	1	0	1	0	1	1	1	0	1	0	0,1	1	1	0	2	0	1	1	1	0	0	0	0	1	1	0	1
A. kenya	1	0	1	0,1	0	0	0	0,1	0	0	0	1	0	0	1	2	0	1	0	1	0	0	0	0	0	0	1	2
A. aethiopica	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	2	0	1	0	1	0	0	0	0	0	0	1	2
M. bispina	0	1	1	0	0,1	2	1	0	1	1	?	1	1	1	0	0	0	0	0	2	2	1	0	0	2	?	?	?
O. lugubris	2	2	3	2	1	2	1	0	1	1	1	1	0	1	0	2	0	1	0	1	2	0	0	0	2	?	?	?
Z. flavicosta	2	1	2,3	2	0,1	2	1	0	1	1	1	1	1	1	0	2	1	1	0	2	2	0	0	0	2	?	?	?

Appendix 1: Characters used in Principal Component Analysis.

States (all ordered) are arranged from small to large and from pale to dark as much as possible.

Size
1. Hw length: in mm.
2. Relative abdomen length (♂ only): abdomen length / Hw length.

Wings
3. Px: sum of both Fw.
4. Ax: sum of both Fw.
5. Fw triangles crossed: (0) neither; (1) one; (2) both.
6. Membranule: (0) beige; (1) brown with beige basal lining; (2) brown.
7. Amber wing base: (0) absent; (1) present.

Head
8. Lengthwise extent of labial black: (0) not reaching apex along inner edges; (1) narrow along entire inner edge; (2) broad along entire inner edge.
9. Breadthwise extent of labial black: (0) restricted to prementum; (1) reaching up to a third of length and breadth of labium; (2) up to two-thirds; (3) more than two-thirds.
10. Labrum: (0) all pale; (1) pale with thin black edge; (2) pale with broad black edge; (3) all black.
11. Centre of postclypeus: (0) all pale; (1) with paired black spots; (2) with black bar.
12. Antero-lateral edges of postclypeus: (0) pale; (1) marked with black.
13. Anterior edge of frons (antefrons): (0) pale; (1) brown; (2) shiny black.
14. Medial part of frons (shields): (0) pale; (1) brown; (2) shiny black.
15. Lengthwise extent of dark mark on frons: (0) restricted to base; (1) extends slightly down central groove; (2) extends well down the groove.
16. Breadthwise extent of dark mark on frons: (0) restricted to central groove; (1) laterally bordered pale; (2) extending over lateral sides.
17. Vertex: (0) pale; (1) brown; (2) shiny black.

Thorax
18. Yellow 'hyphens' anterior to antealar sinus: (0) obliterated by paleness of dorsum; (1) present; (2) absent.
19. Sides: (0) evenly brown; (1) black and yellow with extra spot near Fw base; (2) black with yellow spots.

Abdomen
20. Pruinosity (♂ only): (0) absent; (1) present only basally; (2) present throughout.
21. Yellow markings on S2 (♂ only): (0) joined; (1) narrowly severed; (2) broadly severed.
22. Basal yellow marking on S3: (0) crescentic; (1) ovoid or triangular.
23. Basal yellow spots on S4-9: (0) present; (1) absent.
24. Relative width of S7: (0) broad; (1) intermediate; (2) narrow.

Sexual characters ♂
25. Dorsal profile of cerci: (0) rather flat; (1) weakly curved up; (2) strongly curved up.
26. Ventral ridge of cerci: (0) straight; (1) weakly sinuous; (2) strongly sinuous.
27. Length of epiproct: (0) falls short of ventral angle of cerci; (1) reaches to angle; (2) reaches beyond angle.
28. Shape of epiproct: (0) entire; (1) bifid.

Sexual characters ♀
29. Length of cerci: (0) as long as epiproct; (1) slightly longer; (2) much longer.
30. Tip of cerci: (0) blunt; (1) pointed.
31. Epiproct: (0) bare; (1) sparsely hairy; (2) densely hairy.
32. Cleft of vulvar scale: (0) wide; (1) intermediate; (2) narrow.
33. Reach of vulvar scale: (0) to end of S8; (1) beyond end of S8.

Appendix 2: Characters used in cladistic analysis.

Numbers of corresponding characters in PCA are given in brackets. All character states are ordered and were taken from males only, except for female sexual characters.

Size

1. (1). Size, based on Hw length: (0) small; (1) medium-sized; (2) large.
2. (2/24). Abdomen shape: (0) S7 broad, abdomen length is about 80-85% of Hw length; (1) S7 intermediate, abdomen is about 85-90% of Hw; (2) S7 narrow, abdomen is about 90-95% of Hw.

Wings

3. (3/4). Density of venation, based on sum of Ax and Px in both Fw: (0) very open; (1) fairly open; (2) fairly dense; (3) very dense.
4. (6). Membranule: (0) beige; (1) brown with beige basal lining; (2) brown.
5. (7). Amber wing base: (0) absent; (1) present.

Head

6. (8/9). Shape of labial black: (0) relatively narrow at apex and with greatest extent subapically; (1) intermediate; (2) relatively broad at apex and with greatest extent at base.
7. (10). Labrum: (0) largely pale; (1) largely black.
8. (13). Anterior edge of frons (antefrons): (0) pale; (1) dark.
9. (14). Medial part of frons (shields): (0) pale; (1) dark.
10. (15). Lengthwise extent of dark mark on frons: (0) at most extends slightly down central groove; (1) extends well down the groove.
11. (16). Breadthwise extent of dark mark on frons: (0) laterally bordered pale; (1) extending over lateral sides.
12. (17). Vertex: (0) tends to be brown; (1) tends to be shiny black.

Thorax

13. (18). Yellow 'hyphens' anterior to antealar sinus: (0) present; (1) absent.
14. (19): Sides: (0) black and yellow with extra spot near Fw base; (1) black with yellow spots.

Abdomen

15. (20). Pruinosity: (0) always absent; (1) present when mature.
16. (21): Yellow markings on S2: (0) joined; (1) narrowly severed; (2) broadly severed.
17. (23). Basal yellow spots on S4-9: (0) present; (1) absent.

Sexual characters ♂

18. (25). Dorsal profile of cerci: (0) rather flat; (1) weakly curved up; (2) strongly curved up.
19. (26). Ventral ridge of cerci: (0) straight; (1) weakly sinuous; (2) strongly sinuous.
20. (27). Length of epiproct: (0) falls short of ventral angle of cerci or just reaches it; (1) reaches slightly beyond angle; (2) reaches well beyond angle.

Sexual characters ♀

21. (32). Cleft of vulvar scale: (0) wide; (1) intermediate; (2) narrow.
22. (33). Reach of vulvar scale: (0) to end of S8; (1) beyond end of S8.

Characters not corresponding with any used for PCA

23. Poststernum: (0) flat and sparsely hairy; (1) raised and densely hairy.
24. Hind femora: (0) sparsely hairy; (1) densely hairy.
25. Length of fourth segment of penis: (0) short; (1) intermediate; (2) long.
26. Apex of fourth segment of penis: (0) narrow; (1) intermediate; (2) broad.
27. Ventral hump on fourth segment of penis: (0) absent; (1) present.
28. Cornua of penis: (0) absent; (1) short; (2) long.

Appendix 3: Apomorphies of nodes in fig. 5.

Numbers of characters are given before, of states after the point. All characters refer to males only, except for female sexual characters. Ambivalent (i.e. variable within species) and homoplasious (prone to reversal or parallelism) characters were omitted (except 27).

Clusters 2, 3 and 4 (all species except *A. luxata* sp. n.):
5.0: Amber at wing base absent.
17.0: Basal yellow spots on S4-9 present.
20.0,1: Epiproct does not reach well beyond ventral angle of cerci.
21.0,1: Cleft of vulvar scale (rather) wide.
27.1: Ventral hump on fourth segment of penis present [reversal to absence (0) in cluster 3].
28.1,2: Cornua of penis present.

Cluster 2 (*A. eudoxia* and *A. pseudeudoxia*):
20.0: Epiproct falls short of ventral angle of cerci or just reaches it.
23.1: Poststernum raised and densely hairy.
24.1: Hind femora densely hairy.
26.2: Apex of fourth segment of penis broad.

Clusters 3 and 4 (*A. aethiopica*, *A. biordinata* and *A. kenya*):
1.0,1: Small or medium-sized.
2.0,1: S7 (rather) broad, abdomen length is about 80-90% of Hw length.
4.0,1: Membranule at least with beige basal lining, not all brown.
6.0,1: Labial black not relatively broad at apex but narrow at base.
9.0: Medial part of frons (shields) pale.
20.1: Epiproct reaches slightly beyond ventral angle of cerci.
25.0,1 Fourth segment of penis (rather) short.

Cluster 3 (*A. biordinata*):
1.0: Small size.
2.1: S7 intermediate, abdomen is about 85-90% of Hw.
6.1: Shape of labial black intermediate.
25.1: Length of fourth segment of penis intermediate.
26.1: Breadth of apex of fourth segment of penis intermediate.

Cluster 4 (*A. aethiopica* and *A. kenya*):
1.1: Medium-sized.
2.0: S7 broad, abdomen length is about 80-85% of Hw length.
4.0: Membranule all beige, only occasionally brown with beige basal lining (4.1).
6.0: Labial black relatively narrow at apex and with greatest extent subapically.
7.0: Labrum largely pale.
10.0: Dark mark on frons at most extends slightly down central groove.
13.0: Yellow 'hyphens' anterior to antealar sinus present.
14.0: Sides of thorax black and yellow with extra spot near Fw base.
15.1: Pruinosity present when mature.
25.0: Fourth segment of penis short.
28.2: Cornua of penis long.