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THE GENERA OF THE AFROTROPICAL "AESHNINI": AFROAESCHNA GEN. NOV., PINHEYSCHNA GEN. NOV. AND ZOSTERAESCHNA GEN. NOV., WITH THE DESCRIPTION OF PINHEYSCHNA WATERSTONI SPEC. NOV. (ANISOPTERA: AESHNIDAE)

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The generic names Afroaeschna, Pinheyschna and Zosteraeschna are introduced for 3 groups of Afrotropical dragonfly species, traditionally assigned to the paraphyletic taxon Aeshna. The phylogenetic relationships of these monophyla which are not immediately related to each other are discussed. The Ethiopian populations of Pinheyschna gen. n. are described and characterized as a new sp. (Pinheyschna waterstoni). Zosteraeschna ellioti (Kirby, 1896) and Z. usambarica (Förster, 1906) are regarded as distinct species. Only synonymy, information on status (if feasible) and distribution are given for the remaining species of the group, and a preliminary key to the adults of all but one species is presented.

INTRODUCTION

After the last transfer of American species into the huge and hierarchically differentiated monophyletic taxon *Rhionaeschna* Förster (VON ELLENRIEDER, 2003) about 40 species remained in the traditional genus *Aeshna* Fabricius, 1775. There are no traits synapomorphically characterizing the members of this assemblage (PETERS, 1987; VON ELLENRIEDER, 2003) which encompasses such disparate species as *Aeshna isosceles* (Müller), *A. petalura* (Martin), *A. scotias* Pinhey and *A. williamsoniana* Calvert. Thus, even with the removal of the *Rhionaeschna* species, *Aeshna* is a paraphyletic construct. Nonetheless there are several monophyletic units included with the genus, for instance around the Pal-

aearctic generotype A. grandis (L.).

The same paraphyletic status applies to the few *Aeshna* species, distributed in the Afrotropical region (PINHEY, 1961, 1962, 1964, 1981a, 1984; CLAUSNITZER & PETERS, 2003). Although they are geographically well-separated from the bulk of the "Aeshnini" (sensu BRIDGES, 1994) in the Holarctic, Neotropical and Oriental regions, thus appearing as a zoogeographically bounded complex, the Afrotropical "Aeshnini" do not appear to be monophyletic as a whole.

The first author was repeatedly asked by V. Clausnitzer and K.-D.B. Dijkstra to finally describe an *Aeshna* taxon from Ethiopia for which he already fixed the type material in the ZMHU and BMNH years ago. Honouring this request, we feel obliged to offer the results of extended studies on the Afrotropical "Aeshnini", in order to avoid assigning the new species to an obsolete taxon. These studies resulted in the recognition of the mentioned taxon as a new species and in the founding of new genera for three not closely inter-related groups of Afrotropical *Aeshna* species.

MATERIAL AND METHODS

The terminology used for the description of body pattern and wing venation largely follows PETERS & THEISCHINGER (2007).

Measurements are given in millimetres (mm).

The following abbreviations are used for material depositories:

BMNH British Museum (Natural History), London, England

MRAC Musee Royal de l'Afrique Centrale, Tervuren, Belgium

MSNG Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy

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", Leiden, The Netherlands

UMMZ University of Michigan Museum of Zoology, Ann Arbor, USA

ZFMK Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany

ZMHU Zoologisches Museum der Humboldt Universität, Berlin, Germany.

Abbreviations for common morphological terms: Ax: antenodal cross-veins, Ax1: first Ax from base, Fw: forewing(s), Hw: hindwing(s), Pt: pterostigma, Px: postnodal cross-veins, S1-S10: first – tenth abdominal segment.

The term cerci is used for male superior anal appendages, the term epiproct for male inferior anal appendage. The gender symbols (δ for male, φ for female) are used when appropriate.

THE MONOPHYLETIC TAXA OF THE AFROTROPICAL SPECIES FORMERLY PLACED IN AESHNA

The African "Aeshna" species south of the Tropic of Cancer constitute three units, which each have a special set of characters. Among odonatologists one has been known as the "Aeshna rileyi group" and a second as the "Aeshna ellioti group". Aeshna scotias belongs to neither group. It has a number of ancestral

traits and some autapomorphies which in their combination have not been found in other aeshnine taxa, *Aeshna* s. str. included. To recognise these disparities, it is desirable to create a new genus for each group.

AESHNA SCOTIAS

As already pointed out above, the particularity of the species reflecting its isolated phylogenetic position should be marked by the allocation of the generic name *Afroaeschna* gen. nov.

AFROAESCHNA GEN. NOV.

Etymology. - The prefix "Afro" is chosen in order to accentuate the Afrotropical distribution of this puzzling taxon.

Type species: Aeshna scotias PINHEY, 1952.

Species: Afroaeschna scotias (Pinhey).

DIAGNOSIS. – A fairly large dragonfly: total length 77-98 mm (male), 78-86 mm (female); Fw 49-53 mm (male), 53-56 mm (female). The most remarkable diagnostic characters are:

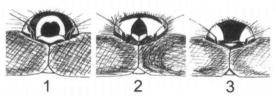
- eyes green
- incisura lateralis (posterior border of eye) well marked
- occiput small with posterior border concave
- all thoracic and abdominal stripes and spots green
- wing venation black
- high number of Ax and Px (19-24 and 14-16 in Fw)
- IR2 fork nearly symmetrical, in some specimens with 1-2 irregular inserted cells at level of branching (Fig. 9)
- MA-RP3/4 anastomosis badly marked (Fig. 9)
- one paranal cell (Fig. 9)
- anal loop with 3 rows of cells (Fig. 9)
- anal triangle 2-celled with the crossvein in posterior half (Fig. 4)
- membranule short (Fig. 4)
- auricles with 3-6 denticles
- cerci without ventrobasal tubercle, the elevated posterior portion of its dorsal crest with 3-6 denticles, apical portion of blades with deep insertion (Fig. 27)
- larvae with claw-like curved and sharply pointed labial palps and distinct paraglossae (Fig. 5 in CHELMICK, 2001) and with spiniform (single-pointed) epiproct.

DISCUSSION, DISTRIBUTION, HABITAT AND ECOLOGY. – As *Afroaeschna* is monotypic these accounts are presented below, under *Afroaeschna scotias*.

AFROAESCHNA SCOTIAS (PINHEY) COMB. NOV. Figures 4, 9, 23, 27

Aeshna scotias PINHEY, 1952: 14 [Type: Kamengo Forest, Uganda, BMNH]. Aeshna wittei FRASER, 1955: 15 [Type: Kaziba, DRC, MRAC], new synonymy.

DISTRIBUTION. — In contrast with the south-north extended distribution of *Pinheyschna, Zosteraeschna* and *Anaciaeschna triangulifera* throughout eastern Africa, *Afroaeschna scotias* is concentrated in the equatorial region and not only in its eastern part but also in the west. Its occurrence in west Africa was quite unpredictable: Southwest province of Cameroon (VICK, 1999; CHELMICK, 2001); Fernando Po (= Bioko) (5 specimens collected by W. Hartwig in 1962/63, not mentioned by PINHEY (1971)), in ZFMK. Until now no other "Aeshnini" has been reported from West Africa. In the eastern African tropics *A. scotias* is known from several places: Uganda: Kamengo and Matuma Forest (Terra typica) 20-30 miles W of Kampala (PINHEY, 1952, 1961) and Butolo Forest (1 \(\rapprox\) in NMBZ); Tanzania: Mpanda distr., Sitebi (1 \(\delta\) coll. Kieland in NMBZ); Congo: Katanga, Upemba Nat. Park, Kaziba and Kalumengongo (T. t. of *A. wittei*); Zambia: Ikelenge distr., N. Mwinilunga, Isombo River (*A. wittei*, see PINHEY, 1981b). In



Figs 1-3. Top of frons (modified from PINHEY, 1951): (1) Pinheyschna subpupillata; — (2) Zosteraeschna minuscula; — (3) Z. usambarica (as ellioti).

general, the distribution of A. scotias is known quite inadequately, even in East Africa where the species, confined to shaded mountain streams, should exist in many more places. Its occurrence in the southern edgings of the Congo basin and in Gabon, due to the poor odonatological

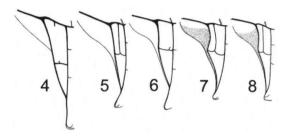
knowledge about these vast territories, cannot be ruled out. On the other hand its absence there could indicate a Cameroon highlands/Albertina rift disjunction as is known from other dragonfly species. Anyhow, at the present A. scotias is known from two disjunct regions on both sides of the Congo basin. On the Albertina Rift stretching from Uganda to NW Zambia, it overlaps with Pinheyschna and Zosteraeschna, and on the Cameroon highlands it is the only Aeshnini species.

HABITATS AND ECOLOGY. - Deeply shaded calm streams with moderate current. Lotic; ovipositing in dead wood or vegetation lying in the water. Larvae have been found among roots of branches hanging in the water.

DISCUSSION. – Aeshna wittei Fraser, 1955, with only 4 specimens known (see PINHEY, 1981b) is identical with Afroaeschna scotias. This conclusion, made from the study of specimens clearly identified as A. scotias and the detailed redescription of A. wittei by PINHEY (1981b), and agreed to by K.-D. DIJK-

STRA who saw the holotypes of both, seems to be the most acceptable hypothesis.

Afroaeschna scotias is the most enigmatic taxon of all Afrotropical hawkers. It is fairly "rich" in ancestral character states, and none of the few advanced expressions of traits unites the species with Pinheyschna, Zosteraeschna or Anaciaeschna Selys. The apomorphic state of a nar-



Figs 4-8. Anal triangle and mebranule of left Hw, male, ventral view: (4) Afroaeschna scotias (from Fernando Po); – (5) Pinheyschna rileyi; – (6) P. waterstoni; – (7) Zosteraeschna usambarica; – (8) Z. minuscula.

row 2-celled anal triangle and of 3 rows of cells in the discoidal field as well as a single paranal cell (instead of 2) has been brought about in a number of aeshnid taxa. Denticles on the dorsal crest of the cerci are met with in some species of Aeshna s. str. (crenata, eremita, osiliensis, serrata etc.). But with these taxa A. scotias does not share any other apomorphy. Supposedly only two characters seem to represent unambiguous autapomorphies: the claw-like bending and tapering of the larval labial palps (unknown to us from other Aeshnini) and the far-going reduction of pale/bright abdominal spots in the adults. Anterodorsal, medio- and posterodorsal spots are totally missing and the anterolateral ones are diminished to small antero-carinal lines. Reduction of abdominal spots, where not caused by rufinism (the potential of species to produce individuals more or less uniformly brown with little blue instead of green, yellow and blue marked with black) as for instance to different degrees in Andaeschna De Marmels, Amphiaeschna Selys, or "Aeshna" isoceles, has taken place also in Aeshna grandis, Anax speratus Hagen and Remartinia Navas. But reductions seldom can be discussed seriously as indications of synapomorphy, at last concerning the abdominal pattern or spots. Totally inadequate for systematic analysis, of course, are the numerous and conspicuous ancestral character states like green eyes, large incisura lateralis, short membranule, large number of auricle teeth, unforked larval epiproct and others. Afroaeschna scotias is not included in the comprehensive cladistic analysis of VON ELLENRIEDER (2003). Thus the determination of the phylogenetic position of the species remains a challenge for future research.

THE "AESHNA RILEYI GROUP"

Aeshna rileyi, the first Afrotropical species described of the genus, serves as the generotype of a complex of related species which is introduced as *Pinheyschna* gen. nov.

PINHEYSCHNA GEN. NOV.

Etymology. — The name is coined in honour of the late Elliot Charles Gordon Pinhey for his extensive and fruitful investigations of the Afrotropical dragonfly fauna. It is a composite of Pinhey and Aeschna. The gender of the name is feminine.

Type species: Aeschna Rileyi CALVERT, 1892.

Species: Pinheyschna meruensis (Sjöstedt), P. moori (Pinhey), P. rileyi (Calvert), P. subpupillata (McLachlan), P. waterstoni sp. n., P. yemenensis (Waterston).

DIAGNOSIS. - All *Pinheyschna* species share the following apomorphies:

- ocellus- (eye) like rounded stem of the "T-spot" (on top of frons) surrounded by a pale ring and potentially thinly connected with the cross-bar of that spot (Figs 1, 32)
- extended (down-running) membranule and shortened anal triangle (Figs 5,
 6)
- postero-ventrad protruding male genital lobe (Figs 13, 14)
- abdomen with dorsal and lateral pairs of bright intersegmental spots (repeated in Basiaeschna Selys, Aeshna umbrosa Walker and some species of Anax Leach.

Characters of some diagnostic value: females somewhat larger than males; eyes green (not blue); abdominal sternum 1 without tubercle; S2 dorsally without uninterrupted crossing ridge; auricles with 2-4 teeth; crossveins in basal portion of wings yellow (not black); IR2-fork symmetrical; anal triangle 2-3-celled, with apical cell longer than the basal one(s), and CuP ("anal crossing") usually situated in front of it (Figs 5, 6); membranule not distinctly two-coloured; cerci strongly hooked; larval epiproct bifid with apical cleft longer than wide. Additionally peculiarities of the male secondary genitalia (Figs 19-22) may be of systematic value.

DISTRIBUTION. – Yemen, Ethiopia, Kenya, Tanzania, Uganda, Zimbabwe, Cape.

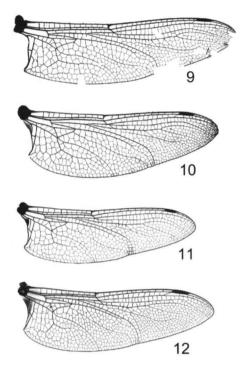
The six species of this monophylum form, according to venation density, shape of the extended male genital lobe and to the proportions of the larval anal pyramid, two species groups, a northern and a predominantly southern one with one species somehow suspended in between. The more northerly distributed group, termed *P. meruensis* group for the remainder of this paper, includes *P. meruensis* (CLAUSNITZER & PETERS, 2003), *P. yemenensis* (WATERSTON, 1985), the Ethiopian species described below and possibly *P. moori*. Its diagnostic characters include more open venation, in male a rather short, triangular genital lobe with apex pointed, and cerci without sub-basal inferior hump, and in the larvae a not particularly short and wide anal pyramid. The group of the southern species, termed *P. rileyi* group for the remainder of this paper, includes *P. rileyi* and *P. subpupillata* and possibly *P. moori*. It is characterized by denser venation, in male by a more or less funnel-like process of the genital lobe and a sub-basal inferior hump on the cerci, and in the larvae by a very short and broad anal

pyramid (SAMWAYS, CARCHINI & DI DOMENICO, 1993).

HABITAT AND ECOLOGY. – Pinheyschna, as compared to Afroaeschna and Zosteraeschna, favours more open country including highlands without forest. The habitats are fast-flowing, rocky open streams with limited shading. Lotic; oviposits in steep gravel banks, dead wood or bankside vegetation. Larvae among silt, gravel and pebbles under rocks in rapid stream sections.

DISCUSSION. – The first and third of the above listed autapomorphies are unique among the "Aeshnini".

The relatives and finally the sister group of of *Pinheyschna* have to be searched for among "Aeshnini" bearing an advanced type of hamular apparatus (to be characterized elsewhere) combined with an extended membranule. A "down-running" membranule which is the apomorphic counterpart of the short one, characterizes not only



Figs 9-12. Right Hw of males: (9) Afroaeschna scotias; – (10) Pinheyschna rileyi; – (11) Zosteraeschna usambarica; – (12) Anaciaeschna jaspidea.

the taxa more or less closely related to Zosteraeschna (see next paragraph) but also Adversaeschna Watson, Oreaeschna Lieftinck, Anax, "Aeshna" isoceles, mixta Latreille and affinis Vander Linden. In nearly all these groupings with Pinheyschna included, the extended membranule is associated with some other apomorphic trends [diminishing incisura lateralis and number of auricle teeth, expression of MA-RP3/4 anastomosis and presence of Rspl2 (Fig. 12)]. The only exception from this picture is "Aeshna" isoceles. But all the just listed advanced states may have been produced independently more than once in the evolutionary history of the taxa. Therefore the determination of the phylogenetic position of Pinheyschna in the first place depends on the phylogenetic evaluation of the combined character states. At the present we can only draw one preliminary conclusion: none of the mentioned taxa is the sister group of Pinheyschna. In a comprehensive cladistic analysis by VON ELLENRIEDER (2003), however, "Aeshna" rileyi + subpupillata, both assigned to Pinheyschna gen. n. in this paper, emerged as the sister group of Rhionaeschna.

PINHEYSCHNA MERUENSIS (SJÖSTEDT) COMB. NOV. Figure 19

Aeshna meruensis SJOSTEDT, 1909: 32 [Type: Mt Meru, Tanzania NHRS].

STATUS. – The species specific distinctness of *P. meruensis* and *P. yemenensis* is unquestionable, as well as the sympatry of *P. meruensis* and *P. rileyi* (CLAUSNITZER & PETERS, 2003; DIJKSTRA & CLAUSNITZER, 2005).

DISTRIBUTION. - Kenya, Tanzania and Uganda; ?Sudan, Angola (PINHEY, 1975).

PINHEYSCHNA MOORI (PINHEY) COMB. NOV.

Aeshna moori PINHEY, 1981: 64 [Type: Ikelenge, Zambia, NMBZ].

STATUS. – According to K.-D.B. Dijkstra, the holotype is in fairly good condition, only the abdominal markings are indiscernible. It is apparently a dark species, the synthorax is dark save three complete but narrow stripes on each side. The frontal mark is clearly preserved and although the extreme tip of the left lobe is lost, the tapering and strongly curved genital lobes do not represent a distortion or aberration. Combined with the dimensions stated, this indicates that *P. moori* is a good species. Hw 48.5 mm, Abd 54.8 (50.1 without appendages), Fw Pt 4.0, Hw Pt 3.9 mm. The allotype is more stained, but clearly shows a frontal mark like the holotype and is also large. Hw 52.8 mm, Abd 52.7 without appendages, Fw Pt 4.6, Hw Pt 4.1 mm.

DISTRIBUTION. – Zambia; known only from Kamankundju River and Isomo River in North Mwinilunga.

DISCUSSION. — *P. moori* is known only from a single poorly preserved male and a female from NW Zambia. According to PINHEY (1981b) it is near *P. rileyi* but the male has the genital lobes tapering to a fine, well-curved point, and the T-mark on the frons is not ocellate but a typical T with thick stem, although his note that the "stem [is] slightly more swollen near base and edged with yellow" suggests some similarity to a *rileyi*-type T-mark. The genital lobe, large size (Hw given as 49 mm), relatively short Pt (given as 3 mm) and appearance of the appendages (see also PINHEY, 1984) would have suggested that this specimen is close to *P. meruensis*, although the well-curved genital lobe is a feature of *P. yemenensis* and *P. waterstoni* spec. nov. PINHEY (1981b) may not have thought of *P. meruensis*, because he considered it synonymous with *P. rileyi* (see PINHEY, 1963). Anyway the position of *P. moori* will have to be re-assessed when more material is at hand.

PINHEYSCHNA RILEYI (CALVERT) COMB. NOV. Figures 5, 10, 22

Aeschna Rileyi CALVERT, 1892: 164 [Type: Kilimanjaro, N.E. Tanzania].

Aeshna rileyi raphaeli PINHEY, 1964: 112 [Type: Ikelenge, Zambia, NMBZ].

Aeshna rileyi form (or subspecies) raphaeli PINHEY, 1964 – PINHEY (1984: 28).

PINHEY (1984) downgraded his *P. raphaeli* to a form and supposed sympatry of both, *rileyi* and *raphaeli*, in eastern Zimbabwe. It appears that only a thorough revision of the widely scattered collection material may be able to answer the question about the status of *raphaeli* (see also the distribution map of *P. subpupillata* in TARBOTON & TARBOTON (2002) and the quotation of the latter species for Mozambique by CLAUSNITZER (2001).

DISTRIBUTION. - Kenya to Zimbabwe; ?Sudan; Angola (PINHEY, 1975).

PINHEYSCHNA SUBPUPILLATA (MCLACHLAN) COMB. NOV. Figure 1

Aeschna subpupillata McLACHLAN, 1896: 422 [Type: South Africa, BMNH].

STATUS. - PINHEY (1981b) confirmed the species status of *P. subpupillata* and *P. rileyi*.

DISTRIBUTION. - Zimbabwe to Cape.

PINHEYSCHNA WATERSTONI SP. NOV.

Figures 6, 13, 20, 28, 31, 32

Aeschna Rileyi nec CALVERT, 1892 - CALVERT (1896: 632).

Aeschna Ragazii Selys [Type: Shoa, Ethiopia, MCSN] – CALVERT (1896: 632), nomen nudum.

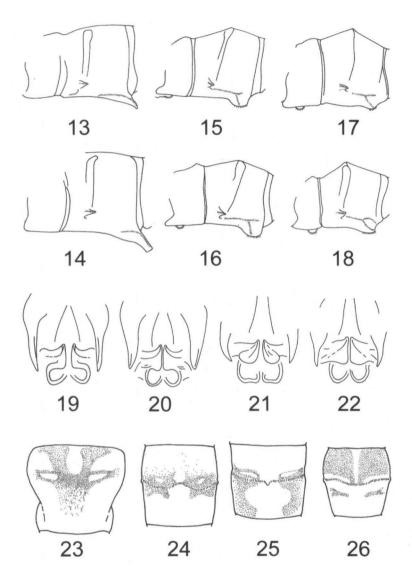
Aeshna ragazzi Selys - PINHEY (1962: 191), nomen nudum.

Aeshna meruensis waterstoni TELFER, 1992: 127 – CLAUSNITZER & DIJKSTRA (2005: 121), nomen nudum.

Aeshna sp. - CLAUSNITZER & PETERS (2003: 11).

Aeshna cf. yemenensis WATERSTON, 1985 - CLAUSNITZER & DIJKSTRA (2005: 121).

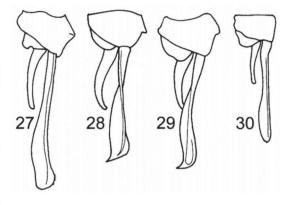
M a t e r i a l. – Holotype δ: Ethiopia, Antoto, north of Addis Abeba, V-1907, Kostlan, S. (with an original blue handwritten label "Abessynia Antoto V. 07 Kostlan, S.") (ZMHU). – Paratypes: 1 ♀, Sciotalit, 116. Luglis 1887, Non rari (MSNG); 1♀, Abyssinia near Djem-Djem Forest alt. 8000 ft, 20-IX-1926, I. Omer. Cooper (this specimen with an additional label added by A. R. WATERSTON in 1977: "Not A. rileyi CALV. but n. sp. near meruensis and yemenensis MS female"); 1 δ, C. Abyssinia, Managascha, 26-V-1914, O. Kovacs leg.; 1 δ, C. Abyssinia, Maraquo, 20-VIII-1914, O. Kovacs leg.; 1 δ, R. (or ?L.) Tana, 13-V-1915, O. Kovacs leg. (all BMNH). 1 δ, Akaki River, 2500 m (Addis), 23-IV-1971, Carfi; Nr. 2075 [Aeshna rileyi Calvert)] det. Carfi (MZUF). 1 δ, Ethiopia, Debre Libanos, 12-III-2004, V. Clausnitzer & K.-D.B. Dijkstra leg.; 1♀, Ethiopia, 15 km S of Sashemene, Wondo Genet,



Figs 13-26. (Figs 13-18) S1 and S2 of males, lateral view, with the outline of the ventral tubercle on sternum 1 (where present), the auricle and the genital lobe: (13) Pinheyschna waterstoni; — (14) P. subpupillata; — (15) Zosteraeschna minuscula; — (16) Z. usambarica; — (17) Anaciaeschna triangulifera; — (18) Rhionaeschna marchali. — (Figs 19-22) Anterior hamuli and spines of the anterior lamina, male, ventro-posterior aspect: (19) Pinheyschna meruensis; — (20) P. waterstoni (holotype); — (21) P. yemenensis; — (22) P. rileyi. — (Figs 23-26) Ridge (girdle, carina) across abdominal tergum 2, dorsal: — (23) Afroaeschna scotias (ridge absent); — (24) Zosteraeschna ellioti; — (25) Anaciaeschna jaspidea; — (26) Rhionaeschna elsia.

1650 m a.s.l., 7°05' N/38°36.77' E, 30-III-2004, V. Clausnitzer & K.D.B. Dijkstra leg.; 2 final instar exuviae (♀), Ethiopia, Nekemte, 15-III-2004, V. Clausnitzer & K.-D.B. Dijkstra leg.; 5 final instar exuviae (1 ♂, 4 ♀), Ethiopia, Wondo Genet, 30-III-2004, V. Clausnitzer & K.-D.B. Dijkstra leg. (all in RMNH).

Etymology. — The species is named in honour of the late Andrew Roger Waterston for his merits in the investigation of the south-Arabian odonate fauna, including his description of *P. yemenensis*.



Figs 27-30. S10, cerci and epiproct, male, lateral view: (27) Afroaeschna scotias; — (28) Pinheyschna waterstoni; — (29) P. yemenensis; — (30) Zosteraeschna ellioti.

MALE (Holotype). - Col-

ours faded; tips of right Fw and Hw missing.

H e a d. – Outer (posterior) eye margin with badly indicated incisura lateralis. Antennae 6-segmented. Top of frons with subpupillate black mark, connected thinly with the dark anterior border of frons (as in Fig. 9).

Thorax. – Bright synthoracic stripes with nearly parallel borders, antehumeral stripes not as bright as lateral stripes. Legs more brownish than black.

Wings. Nodal formula 12.17/18.13 (Fw), 13.12/12.13 (Hw); IR2 fork at level 3 postnodal cells proximal to Pt, symmetrical, with 3 rows of cells; forking of MA in front of the well developed "aeshnine groove" with branches of nearly equal thickness; discoidal triangles with 5 cells in Fw and 4 cells in Hw (basal cells divided); anal triangle 2-celled, occupying the inner border of the wing for about 2/3 of its length (Fig. 6); anal loop with 9/11 cells in 3 rows.

A b d o m e n. – A cross-extended spot, covered with hairs and low blackish denticles, in the anterior portion of sternum 1; dorsum 2 flat (not crossed by a ridge); laminar spines and anterior hamuli as in Figure 20; a complete set of bright spots on terga 3-8: the broad anterodorsals posteriorly extended to the intersegmental carina, laterally broadly connected with the anterolaterals, the paired mediodorsalia triangular in shape and not bluish but yellow, the pair of posterodorsals not connected with the posterolaterals and the latter not contacting the mediolaterals; intersegmental rings with pairs of bright dorsal and lateral spots; \$10 with a small mid-dorsal hump; cerci (Fig. 28) and ventral portions of abdomen more brownish than black.

Measurements. — Total length 66.0; Hw 43.5; abdomen 43.5; Pt of Fw 3.3; cerci 6.1; width of head 11.6.

Overall colouration and colour pattern (brown to black with largely pale greyish to greenish blue elements and some small yellow markings) of the live insect can be seen in Figure 32; little variational deviation from the basic description as given

for the holotype and from the photo has been found.

FEMALE (**Paratype** (allotype) from Djem-Djem Forest). — Wings with nodal formula 12.18/17.11 (Fw) and ?.11/12.12 (Hw).

Measurements. - Hw 45.1; Pt 3.3.

From the available (only old) material can be detected that the female much agrees in all details with A. meruensis.

LARVA. — Prementum nearly twice as long as its greatest width, just surpasses posterior side of mesocoxa; labial palps without bristles, lobe evenly wide with apex round to truncate; antennae generally 7-segmented; femora with two pale rings; lateral spines on S5-9, that on 5 tiny; ovipositor reaching just beyond end of S9; anal pyramid not particularly short and stout, fairly smooth, with paraprocts about 4 times as long as wide. Total length 37.0-41.0 mm

DISTRIBUTION. — *Pinheyschna waterstoni* is known to occur in the Ethiopian Highlands and mountain chains at elevations between 1650 and 2500 m. Some information is now available from Tesfaye Kebede (Addis Abeba) on the localities where the stored last century specimens have been taken: Antoto (=Entoto) is located halfway between Addis Abeba and Debre Markos; Djem-Djem Forest (=Gemgem) means forested river valley some 50 km north of Gima; Maraquo (=Maraki or Marequo) is a site in the Gojam Province near Debre Markos; the Akaki River flows through Addis Abeba; Wondo Genet lies south of Lake Awasha (250 km S Addis Abeba) and Nekemte in the province Welega (230 km W Addis Abeba). "Managascha" and Sciotalit" remain undeciphered (Scioa is the Italian version of the central province Shoa = Shewa).

As a mountain species, *P. waterstoni* is separated from its congeners in Ugandal Kenya (*P. meruensis*) and Yemen (*P. yemenensis*) by large stretches of low-level savannas and even desert, not to mention the Red Sea. An isolated population of *Pinheyschna* identified by LONGFIELD (1936) as *Aeshna rileyi*, occurs at Jebel Marra in the South Darfur Province of Sudan, some 1,400 km west of the Ethiopian Highlands. The presence of this taxon at Jebel Marra was confirmed by HAPPOLD (1966) and DUMONT (1988). Whether or not the population (documented by 3 specimens in BMNH) belongs to *P. waterstoni* remains to be seen.

HABITAT AND ECOLOGY. – The larvae live in running water (brooks, streams).

DISCUSSION. — This species has a long bibliographic history. CALVERT (1896) described a female from Ethiopia in MSNG, which he assumed to be *P. rileyi*, labelled "Aeschna Ragazzii, Selys typus! \(\Perp \)". However, by origin and description this female must pertain to *P. waterstoni*. Because CALVERT (1896) considered ragazzii as synonym of rileyi, the name ragazzii CALVERT, 1896 is unavailable (ICZN 1999: article 11.6). PINHEY (1962) lists it under *P. rileyi* as "Aeshna ragazzi SELYS (ined.; nom. nud.)". TELFER (1992), CLAUSNITZER & PETERS (2003) and CLAUSNITZER & DIJKSTRA (2005) discussed the species as A.

meruensis waterstoni, an unnamed Aeshna species and A. cf. yemenensis respectively. Lacking a description, the name waterstoni TELFER, 1992 is unavailable (ICZN 1999: article 13.1.1).

In both sexes of *P. waterstoni* the length of the Pt does not exceed 7.5% of Hw length (as opposed to 8.0-9.6% in individuals of the *P. rileyi* group) and the abdomen is relatively shorter [95.0-103.0% of Hw length (as opposed to 103.0-107.0%)]. In the males of *P. waterstoni* the anal triangle is 2-celled (with single 3-celled exceptions) as opposed to 3-celled, rarely 2-celled, in the *P. rileyi* group, and the genital lobes are not only downwardly extended, but also sharply pointed (Fig. 13).

The males of *P. waterstoni* differ from *P. meruensis* by the shape of the genital lobe (see Fig. 1 in CLAUSNITZER & PETERS, 2003). Differences between the females are still unknown.

Both sexes of *P. waterstoni* differ from *P. yemenensis* by the yellowish brown postgenae (black in *yemenensis*), the males by the predominantly 2-celled anal triangle and the abruptly (instead of gradually) rising dorsal crest of the cerci and their somewhat broader blade (Fig. 28). Cell- and crossvein-counts in different fields of the wings showed a somewhat denser venation in *P. waterstoni* and *P. meruensis* than in *P. yemenensis*. Also the hamular folds appear more roundish in *P. waterstoni* and *P. meruensis* than in *P. yemenensis* (Figs 19-21).

In summary, the small but nevertheless consistent differences between the adults of *P. waterstoni* and *P. yemenensis* are hardly or not at all detectable between *P. waterstoni* and *P. meruensis*. In the shape of the male genital lobe, however *P. waterstoni* strongly differs from *P. meruensis*, but is indistinguishable from *P.*

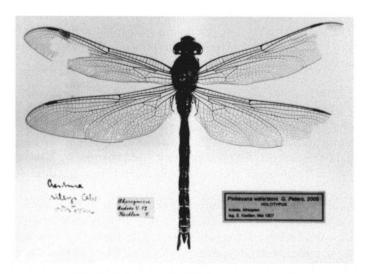


Fig. 31. Holotype male of Pinheyschna waterstoni.



Fig. 32. Live male of *Pinheyschna waterstoni* (Photo K.-D.B. Dijkstra).

yemenensis. Following the "biological species" hypothesis as defined by MAYR (1942) and acknowledging the close morphological affinities, P. waterstoni could be described as a subspecies of P. meruensis, which by chance achieved the same shape of male genital lobe as found in P. vemenensis. But there are some serious arguments not to proceed along this concept. Leaving aside the poorly known P. moori, the distribution ranges of the Pinhevschna taxa follow each other from South to North: subpupillata - rilevi - meruensis - waterstoni - yemenensis. But this chain is not in accord with subsequent changes of character states in the same, or in opposite, direction. The ancestral (plesiomorphic) 3-celled state of anal triangle is retained by the southern species

and in remote north-eastern *P. yemenensis* but not by the taxa situated between them (*P. meruensis* and *P. waterstoni*). Examples of return from the advanced 2-celled state to the 3-celled state (excluding atavism) are not known to us. But the tendency to produce 2-celled triangles in species usually bearing 3-celled ones can be found in different aeshnine taxa, for instance even in some *P. rileyi* specimens.

To the 3-celled condition of the anal triangle another "groundplan" character of the hypothetical *Pinheyschna* stem species can be added: the down-curved tip of the genital lobe (secondarily tube-like widened in the males of the *rileyi* group). If so, the down-turned extension of the genital lobe in *P. yemenensis* and *P. waterstoni* should be regarded as the plesiomorphic state, changed by *P. meruensis*, the sister species of *P. waterstoni*, apomorphically into a posteriorly directed pointed tip.

The opposite point of view, considering the contour of the genital lobe in *P. meruensis* as the ancestral state and thus as a groundplan character, fails, because this scenario would imply an even twofold return ("reversal") of an advanced anal triangle to the more ancestral type (in *rileyilsubpupillata* and in *yemenensis*) and because it would ignore a sister-species relationship between *P. meruensis* and

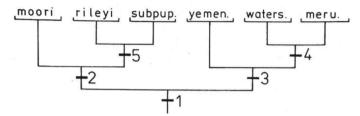


Fig. 33. Phylogram of *Pinheyschna* (autapomorphies of species omitted): 1: stem of T-spot ocellate, postero-ventrad protruding genital lobe (males); — 2: Pt longer than 7.9% of Hw length; — 3: male genital lobe funnel-like, abdomen as long as, or shorter than, Hw; — 4: male anal triangle predominantly 2-celled; — 5: antehumeral stripes shortened, epiproct (male) shortened.

P. waterstoni. And last not least, it would be impossible to explain the contradiction between the *meruensis*-like characters of *P. waterstoni* and the *yemenensis*-like shape of its genital lobe.

Thus, it appears an acceptable hypothesis on the phylogenetic relationships of the *Pinheyschna* species (if *P. moori* is included in the *P. rileyi* group) that the *Pinheyschna* stem species by splitting produced the stem species of *rileyilsubpupillata* (+ *moori*) and of *P. yemenensis*. Then the *yemenensis* stem species gave rise to *P. yemenensis* at one side and to the stem species of *waterstonilmeruensis* to the other (Fig. 33).

PINHEYSCHNA YEMENENSIS (WATERSTON) COMB. NOV. Figures 21, 29

Aeshna yemenensis WATERSTON, 1985: 461 [Type: Al 'Asr, Yemen, BMNH].

DISTRIBUTION. - Yemen.

THE "AESHNA ELLIOTI GROUP"

Three species of this third group of Afrotropical "Aeshna" species are very closely related, constituting a monophylum which is introduced as Zosteraeschna gen. nov.

ZOSTERAESCHNA GEN. NOV.

Etymology. - The prefix "Zostera", proposed by K.-D.B. Dijkstra (in litt.), points to the ringlike ornamental ridge, crossing in both sexes abdominal tergum 2 in its middle.

Type species: Aeshna ellioti KIRBY, 1896.

Species: Zosteraeschna ellioti (Kirby), Z. minuscula (McLachlan), Z. usambarica (Förster).

DIAGNOSIS. – Compared with Afroaeschna and Pinheyschna, the members of Zosteraeschna seem to be united by the following synapomorphies:

- Rspl2 usually well expressed (Fig. 11)
- apical cell of anal triangle "opened" posteriad to the anal angle of Hw (Figs 7, 8)
- membranule distinctly bicoloured (half white, half black) (Figs 7, 8)
- ridge across the middle of abdominal tergum 2 with central ornament (Fig. 24)
- angulated posterior part of male genital lobe markedly projecting ventrally (Figs 15, 16)
- number of auricle denticles reduced to 2
- S10 of male without distinct mid-dorsal tooth (Fig. 30)
- cerci along their central axis slanted inwardly (in lateral view the outer border of the blades appears as their upper border (Fig. 30))

Discriminating traits of uncertain phylogenetic orientation are:

- cerci without basoventral projection (only badly expressed rugosity present) (Fig. 30)
- larval labial palps and their movable hook with fine bristles (CHELMICK, 2001).

DISTRIBUTION. – Ethiopia, Tanzania, Kenya, Namibia, South Africa (except for Namibia within the range of *Pinheyschna*).

HABITAT AND ECOLOGY. – Variably shaded ponds, swamps, lakes and calm sections of streams with little or no current. Lentic; oviposition takes place in aquatic and riparian vegetation. Larvae probably live among detritus.

DISCUSSION. — By the majority of the listed advanced character states Zosteraeschna appears synapomorphically connected with aeshnine and anactine genera distributed outside of Africa. Among the taxa bearing a long membranule reaching the tornus, the ridge across the middle of abdominal tergum 2 is exposed not only in Zosteraeschna, but also found in all species of Anaciaeschna, Andaeschna and Rhionaeschna (in the sense of VON ELLENRIEDER, 2003). This ornamental carina is unique in Aeshnidae sensu PETERS & THEISCHINGER (2007) and therefore in all probability represents a synapomorphy of the four genera. The mid-dorsal tooth (cone, tubercle) on S10 of males is present in all species of Rhionaeschna and Anaciaeschna but, as in Zosteraeschna, it is missing also in Andaeschna (DE MARMELS, 1994).

The apomorphic trend "widening of anal triangle down to tornus" is broadly dispersed among taxa with long membranule. In parallel with Zosteraeschna it is realised in the Neureclipa Navas subgroup of Rhionaeschna, in Andaeschna and Anaciaeschna (most strikingly in A. martini Selys) and even in "Aeshna" isoceles.

The reduction of the number of auricle denticles to 2 has been achieved not only by Zosteraeschna, Rhionaeschna (except Marmaraeschna Calvert), Andae-

schna and Anaciaeschna, but is found also in Pinheyschna, Adversaeschna and Oreaeschna.

Additionally a usually well expressed Rspl2 (Figs 15-18) connects the first four of the just mentioned taxa.

Zosteraeschna is linked geographically with Anaciaeschna through the Afrotropical species A. triangulifera McLachlan. The collections of NHRS and of MSNG each contain a female of A. triangulifera, misidentified by Sjöstedt, respectively Nielsen, as Aeshna ellioti. Some similarities in eye diameter (eyes are not globular in A. triangulifera), colouration (large bright spots on S8-10; black and white tinted membranule) and in wing venation may produce identification difficulties. But all the otherwise highly individually characterized Anaciaeschna species differ from Zosteraeschna at least in four apomorphic traits partly shown in Figure 12: strongly slanting Ax1 in Fw, asymmetrical IR2-forking (as in Andaeschna), RP2-bulging and predominant existence of a prolonged cell (instead of two smaller ones) distal the MA-RP3/4 anastomosis.

With Rhionaeschna the Zosteraeschna species share the down-projected posterior borders of the genital lobes (Figs 15, 16, 18). But the more extensively and differently built genital lobes of Pinheyschna males seem to represent the advanced state in the evolution of these structures. If so, the similarities in the shape of genital lobes between Zosteraeschna and Rhionaeschna can be interpreted as symplesiomorphies.

From *Rhionaeschna* the *Zosteraeschna* species differ by the absence of a tubercle on the first abdominal sternum (VON ELLENRIEDER, 2003). Only *Z. minuscula* instead of a tubercle bears a slightly elevated central spot densely covered with small spinules.

The differences between Andaeschna and Zosteraeschna are striking. Reduction of the T-spot on the frons, uni-coloured body, rounded anal angle of Hw with widely opened anal triangle in male and asymmetrical IR2-fork with IR2b branching off posteriad represent advanced character states of Andaeschna, against which Zosteraeschna holds an ancestral position. The males of both genera agree in the reduction of the mid-dorsal tooth on S10 and in the very long cerci which (except in A. rufipes Ris) are simply constructed.

Among the above listed apomorphies, the absence of a tooth (tubercle) on S10, notwithstanding its parallel reduction in Andaeschna, seems to be the only obvious autapomorphy of Zosteraeschna. Its presence has to be interpreted as a "groundplan character" of the Aeshnini+Anactini+Polycanthagini sensu DAV-IES & TOBIN (1985), but including Oplonaeschna Selys and Basiaeschna Selys. Besides Zosteraeschna and Andaeschna there is only a small number of taxa with the status "tooth missing": Anax, the 7 species of the cyanea-group of Aeshna (constricta, cyanea, palmata, persephone, petalura, umbrosa, walkeri) and the closely related genera Castoraeschna Calvert, Remartinia Navas and Coryphaeschna Williamson. Badly detectable remnants of the tubercle are retained in some Anax

species, in Castoraeschna coronata (Ris) and even in one of the Zosteraeschna species (ellioti). In order to accentuate the value of this character the following remark should be added: Where present in the Gynacanthidae and Panbrachytronoda sensu PETERS & THEISCHINGER (2007), the tooth is not situated in the anterior half of the segment but in its rear portion, frequently just in front of its posterior border (Epiaeschna Hagen, Tetracanthagyna Selys, some Gynacantha Rambur and Heliaeschna Selys, Telephlebia Selys, Antipodophlebia Fraser, Austrophlebia Tillyard and the majority of species of Austroaeschna Selys). The deviating position of the cone and its rareness and scattered distribution call for non-homology and multiple origin of the trait among "ancestral" aeshnids.

Finishing with the comments on Zosteraeschna we repeat the main points: Zosteraeschna is a monophyletic taxon. Together with Anaciaeschna, Andaeschna and Rhionaeschna it appears to us to constitute a higher ranked monophylum based on the synapomorphy of an ornamental cross-bar on abdominal tergum 2 and a number of more or less shared apomorphic trends. In the elaborate cladogram of VON ELLENRIEDER (2003), however, "Aeshna" ellioti, assigned to Zosteraeschna in this paper, is nested together with Anaciaeschna, Andaeschna and some other "Aeshna" species in a monophylum representing the sister group of Rhionaeschna+("Aeshna" rileyi+ subpupillata). As the sister-taxon of "Aeshna ellioti" emerges "Aeshna" mixta (to which most probably "Aeshna" affinis can be added).

ZOSTERAESCHNA ELLIOTI (KIRBY) COMB. NOV.

Figures 24, 30

Aeschna Ellioti KIRBY, 1896: 124 [Type: Ruwenzori, BMNH].

STATUS. — Since PINHEY (1956) Aeschna usambarica generally was included in Aeschna ellioti as a distinct subspecies. Return to species rank is proposed for A. usambarica below, under Zosteraeschna usambarica.

DISTRIBUTION. - North Tanzania (Kilimandjaro) to eastern Congo and Ethiopia.

DISCUSSION. - See under Zosteraeschna usambarica.

ZOSTERAESCHNA MINUSCULA McLACHLAN COMB. NOV.

Figures 2, 8

Aeschna minuscula McLACHLAN, 1896: 421 [Type: Cape of Good Hope, South Africa, BMNH].

Aeschna dolabrata KARSCH, 1899: 48 [Type: Cape of Good Hope, South Africa, ZMHB].

DISTRIBUTION. – South Africa (except north-eastern and north-western) and Namibia.

ZOSTERAESCHNA USAMBARICA (FÖRSTER) COMB. NOV., STAT. Figures 3, 11, 16

Aeschna usambarica FÖRSTER, 1906: 48 [Type: Nguelo, Tanzania, UMMZ].

STATUS. – Since PINHEY (1956) Aeschna usambarica generally was considered as a subspecies of Aeschna ellioti. For the reasons discussed in the following we consider Zosteraeschna ellioti and Z. usambarica as two distinct species.

DISTRIBUTION. - South Kenya (Taita Hills) to north-eastern South Africa.

DISCUSSION. — None of the authors dealing with Zosteraeschna ellioti and its assumed subspecies usambarica seems to have had difficulties with the allocation of a certain specimen to one or the other of the two. Z. usambarica is distributed from the northern provinces of South Africa through Zimbabwe, Zambia and Malawi to the northeast of Tanzania (Usambara Mts) and the southeast of Kenya. Z. ellioti is known to occur in northern Tanzania, the most eastern parts of Congo, in Kenya, Uganda and Ethiopia. Nothing is known about the existence of Zosteraeschna in the mountain chains between the northern shores of Lake Nyasa (Nyika Plateau: Z. usambarica) and Lake Kiwu (Z. ellioti), including the mountain ranges on both sides of Lake Tanganyika. Whether or not (and to what extent) one or both species bridge this enormous distance along the western branch of the Rift Valley, remains to be explored.

As pointed out under Zosteraeschna, the Z. ellioti males retained a remnant of the mid-dorsal tooth on S10, but Z. usambarica and Z. minuscula did not. Additionaly Z. usambarica differs from Z. ellioti in colour markings and wing venation. The antehumeral stripes in *ellioti* are parallel sided, but wedge-shaped. with wider upper ends, in usambarica. Meso- and metepimeral stripes are also wider in usambarica: 14.6 and 17.4% of head diameter against 12.3 and 14.7% in ellioti. The white coloured portion of the membranule usually takes 1/3 of its area in ellioti and ½ in usambarica. Z. usambarica is characterised by a markedly denser venation: 15.0 Fw Ax against 14.0 in ellioti (14.4 in minuscula); cells along RP3/4 in Hw 23.3 against 20.9 (22.4 in minuscula); double cells between MP and CuA 6.7 against 4.4 in males and 9.4 against 6.8 in females (5.4 in both sexes of minuscula). All differences between the mean values are statistically significant. The proportions of the discoidal triangle differ between both species: in usambarica the Hw triangle reaches only 84% (females) and 88% (males) of the Fw triangle length against 90-92% in ellioti. The Hw triangle (exposed to Hw length) is distinctly narrower in usambarica (5.7% in males, 6.2% in females) than in ellioti (6.5% and 7.0%). These data have been sampled and calculated from 30 specimens of Z. usambarica and 11 of Z. ellioti as follows: Z. usambarica: Transvaal (3): Vumba Mts, Zimbabwe (2); Nyika Plateau, Malawi (8); Uluguru Mts, Tanzania (2); Usambara Mts, Tanzania (11); Taita Hills to the west of Voi, Kenya (4). Z. ellioti: north of Lake Kiwu (Sabinio), Congo (1); Kilimanjaro (Kibonoto),

Tanzania (2); Mt Elgon Nat. Park, Kenya (5); Saiwa Swamp (east of Mt Elgon), Kenya (1); Prov. Shewa (= Shoa), Ethiopia (2).

Considering the points made in the above discussion, it appears reasonable to accept Z. ellioti and Z. usambarica as distinct species. Notwithstanding allopatry and morphological similarity, both taxa are distinguished by integrated complexes of traits in colour markings, venation and proportions. This integrity of characters reveals the nature of a closed propagating community, meaning the nature of an independent evolutionary species (CLAUSNITZER & PETERS, 2003; PETERS, 1998). Hybrids of the two may occur, but no gradually deviating "intermediates" which usually exist in the transgression zones of subspecies. SJÖSTEDT (1909) collected typical Z. ellioti individuals on the slopes of Kilimanjaro, whereas Viola Clausnitzer took "normal" Z. usambarica at the adjoining Taita Hills in southeastern Kenya. On the other hand large distances seem not to have caused differences between the ellioti populations of Uganda/Kenya and Ethiopia. It should be added that the allopatry between Z. ellioti and Z. usambarica in east Africa (CLAUSNITZER, 1999) is repeated in the south of the continent by Z. usambarica and Z. minuscula which are morphologically quite different from each other (PINHEY, 1951; TARBOTON & TARBOTON, 2002).

It has to be pointed out here that what is presented under *Aeshna ellioti* in two popular books on the dragonflies of South Africa (TARBOTON & TARBOTON, 2002; SAMWAYS, 2008) has to be referred to *Z. usambarica*.

KEY TO THE ADULTS OF THE SPECIES OF AFROAESCHNA, PINHEYSCHNA AND ZOSTERAESCHNA (P. moori not included)

- Smaller species (Hw <45 mm); membranule blackish with strongly contrasting white base (Figs 7, 8); S2 prominently raised dorsally along transverse suture, forming a girdle (Fig. 24). Male: anal triangle 3-celled (Figs 7, 8); anal loop of 2 rows of cells (Fig. 11); auricles with 2 denticles; S10 without mid-dorsal tooth; cerci with apex flat, pointed, without denticles (Fig. 30)
- Membranule grey, almost without white at base. Pt 2.5-3.3 mm, 7.5-7.8% of Hw length; abdomen 95-103% of Hw length. Male: anal triangle mostly 2-celled, rarely 3-celled (Fig. 6); genital lobe

short and triangular, apex pointed (Fig. 13)
Male genital lobe rather straight rileyi - Space between lateral thoracic stripes black with pale marking near Fw base; costa pale yellow and
many cross-veins near base yellow, including those in triangles. Male genital lobe distinctly curved (Fig. 14)
6 From Kenya, Tanzania, Uganda, possibly Sudan and Angola. Male genital lobe straight
 From Ethiopia or Yemen. Male genital lobe curved, with apex twisted downwards
- From Yemen. Postgenae back. Male: anal triangle mostly 3-celled, rarely 2-celled; dorsal ridge of cerci rising gradually (Fig. 29)
8 Top of frons with distinct black T-mark made up of cross-bar and triangular stem (Fig. 2); antehumeral stripes narrow and parallel to each other; costa yellow; pale latero-basal spots of S4-7 larger than apical spots
 Top of from with solid black pentagon (Fig. 3); antehumeral stripes wider, converging dorsally; costa dark brown; latero-basal pale spots of S4-7 smaller than apical spots, or absent
9 From Tanzania to eastern Congo and Ethiopia. Antehumeral stripes parallel sided; pale lateral thoracic stripes narrow, space between them mor than twice as wide as one stripe ellioti
 From south Kenya to north-eastern South Africa. Antehumeral stripes wedge-shaped, with dorsal end much wider than ventral end; lateral thoracic stripes broad, space between them less than twice as wide as one stripe usambarica

CONCLUDING REMARKS

No matter what the results of further, most particularly molecular, research will be, already now it is obvious that Africa produced endemic supra-specific groups of "Aeshnini". This conclusion has some zoogeographical implications which previously were not traceable due to the camouflaging use of the traditional name Aeshna for the "Aeshnini" of the Afrotropical region. But for as long as the phylogenetic relationships of Pinheyschna, Zosteraeschna and Afroaeschna are not more firmly elucidated, nothing definite can be said about their zoogeographic connections. The absence of immediate relationships between the three sympatric taxa may refer to a relatively long period of independent evolutionary history. Anyway, besides all suggestions and speculations, the three new aeshnid genera add another enigma terminating in the question: What happened to the African odonate fauna during the Tertiary, keeping in mind the scarcity of endemic monophyla and the absence of Gomphaeschnidae and Panbrachytronoda sensu PETERS & THEISCHINGER (2007)?

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