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REVIEW OF THE GENUS *ZYGONOIDES*, WITH DESCRIPTION OF THE LARVAE AND NOTES ON 'ZYGONYCHINE' LIBELLULIDAE (ODONATA)

Dijkstra, K.-D.B., F. Suhling & O. Müller 2006. Review of the genus Zygonoides, with description of the larvae and notes on 'zygonychine' Libellulidae (Odonata). – Tijdschrift voor Entomologie 149: 275-292, figs. 1-42, tables 1-4. [ISSN 0040-7496]. Published 1 December 2006. Zygonoides Fraser, 1957 – formerly considered a subgenus of Olpogastra Karsch, 1895 – is reinstated as a genus. It comprises Z. fuelleborni (Grünberg, 1902), Z. fraseri (Pinhey, 1956), Z. lachesis (Ris, 1912) and Z. occidentis (Ris, 1912). The latter was formerly considered a subspecies or form of Z. fuelleborni, but is found to be a good species near Z. fraseri. The larvae of Z. fuelleborni, Z. fraseri and Z. occidentis are described. Adult and larval characters are compared with those of the other 'zygonychine' genera Celebothemis, Olpogastra, Onychothemis, Zygonychidium and Zygonyx. Identification, distribution and ecology of the species are outlined.

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Key words. – Odonata; Libellulidae; *Olpogastra*; *Zygonoides*; *Zygonyx*; Africa, systematics; biogeography; keys; larvae.

The species of Olpogastra Karsch, 1895 are large and aggressive animals, which are among the most charismatic African dragonflies (e.g. Clausnitzer 2001, Silsby 2001). The genus traditionally includes one Madagascar species (O. lachesis Ris, 1912) and three species confined to continental tropical Africa: O. fraseri Pinhey, 1956, O. fuelleborni Grünberg, 1902 (with subspecies occidentis Ris, 1912) and O. lugubris Karsch, 1895. Zygonoides Fraser, 1957 was originally introduced as a genus for all species of Olpogastra except O. lugubris, but it was subsequently made a subgenus of Olpogastra by Pinhey (1961). The revision of *Zygonoides* was made necessary by the discovery of O. fraseri - previously known only from the Ugandan type series - in western Africa, which made the status of O. fuelleborni occidentis unclear, and by discovery of larvae of all four mainland taxa. In this paper we (1) reassess the status of Zygonoides, (2) revise and diagnose its species, (3) describe larval

characters of all continental *Zygonoides* taxa, and (4) compare it with related genera.

METHODS AND MATERIAL

Adult (including relevant primary types) and larval specimens (including exuviae) of *Zygonoides* and the related genera *Celebothemis* Ris, 1912, *Olpogastra, Onychothemis* Brauer, 1868, *Zygonychidium* Lindley, 1970 and *Zygonyx* Hagen, 1867 were compared (see tables 1-4 and diagnoses). Association of larvae with adults was possible by their origin and relative size, and in some cases by observations of emergence (see material lists for details). Examined specimens of *Zygonoides* are listed under each species; other material studied for comparison includes:

Adults. – Olpogastra lugubris: Benin: 1 $\,$ $\,$ $\,$ Alibori River, 9.vii.2001; 1 $\,$ $\,$ $\,$ $\,$ Parc National du W, Mékrou

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River, 9.vii.2001; 1 \circlearrowleft , Ahouanzoumè, Ouémé River, 31.vii.2001; 1 \Lsh , Forêt de Lokoli, 15.x.2001; 1 \Lsh , Pessagou, 9.x.2003, S.L. Tchibozo (rmmh); congo-kinshasa: 1 \circlearrowleft , Lokutu, 27.x.2004, K.-D.B. Dijkstra (rmhh); ghana: 1 \circlearrowleft , Menuso, Menu River, 14.iii.1993, H.A. Olsvik (rmhh); Liberia: 1 \circlearrowleft , Gola National Forest, 29.xi.2005, K.-D.B. Dijkstra (rmhh); malawi: 1 \circlearrowleft , 1 \Lsh , Mkuwazi Forest Reserve, 13.xii.2001; 1 \circlearrowleft , Chisasira Forest Reserve, 25.xii.2001, K.-D.B. Dijkstra (rmhh); uganda: 1 \circlearrowleft , Semliki National Park, Semliki River, 4.vi.2003, K.-D.B. Dijkstra (rmhh). Additionally, specimens of various species of Celebothemis, Onychothemis and Zygonyx (rmhh) were examined, as was the description of Zygonychidium by Lindley (1970).

Larvae [final instar, unless stated otherwise]. - Olpogastra lugubris: TANZANIA: 1 larva, Luiche in Ujiji, River S of town, Kagera (4°55.966'S 29°42.339'E), 14.ix.2004, E. Michel (BMNH); NAMIBIA: several exuviae (two with emerged adults) and larvae of different stadia, several localities along Kunene, Okavango, Kwando and Zambezi Rivers, 2003-2005, F. Suhling (NMNW). - Onychothemis testacea Laidlaw, 1902: THAILAND: 1 exuvia, Pongpuron Kanchamburi, iv.2003, A.G. Orr (Coll. A. G Orr). - Zygonyx cf. flavicosta (Sjöstedt, 1900): côte d'ivoire: 1 exuvia, Kongo River, i.1992, K. Grabow (Coll. K. Grabow). - Zygonyx natalensis (Martin, 1900): NAMIBIA: >20 exuviae, Okavango River, xii.2004, F. Suhling (NMNW). - Zygonyx torridus (Kirby, 1889): NAMIBIA: several exuviae, Damaraland, Okavango River and Ongongo Falls, 2002-2005, F. Suhling & A. Martens (NMNW). Additionally, larval descriptions by Fraser (1956, 1962) of Zygonyx cf. speciosus, Z. hova and Z. ranavalonae were examined, although the species identifications are doubtful.

Acronyms for collections

BMNH Natural History Museum, formerly British Museum (Natural History) (London, UK)

Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)

MNHN Muséum National d'Histoire Naturelle (Paris, France)

MNMS Museo Naçional de Ciencias Naturales (Madrid, Spain)

Mrac Musee Royal de l'Afrique Centrale (Tervuren, Belgium)

NHRS Naturhistoriska Riksmuseet (Stockholm, Sweden)

NMKE National Museums of Kenya (Nairobi, Kenya)

NMNW National Museum of Namibia (Windhoek, Namibia)

RMNH Nationaal Natuurhistorisch Museum Naturalis, formerly Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands)

ZMHB Museum für Naturkunde der Humboldt-Universität (Berlin, Germany)

ZMUH Zoologisches Institut und Zoologisches Museum, Universität von Hamburg (Hamburg, Germany)

Abbreviations

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

TAXONOMIC TREATMENT

Zygonoides Fraser

Olpogastra; nec Karsch, 1895 – Grünberg (1902: 235). Zygonoides Fraser, 1957: 119. Type species: Olpogastra fuelleborni Grünberg, 1902 (by original designation). Olpogastra Karsch, 1895 (Zygonoides Fraser, 1957) – Pinhey (1961: 275)

Affinities

Fraser (1957) placed Olpogastra, Zygonoides and Zygonyx in the subfamily Zygonictinae (corrected spelling: Zygonychinae). Bechly (1996) ranked this subfamily as the subtribe Zygonychina of the tribe Onychothemistini and transferred O. lugubris to the subtribe Onychothemistina, which otherwise only includes the Oriental genus Onychothemis. This regrouping was on account of the reduced posterior hook of the tarsal claws, and implies polyphyly of Olpogastra if Zygonoides is included in it. The isolated monotypic genera Celebothemis and Zygonychidium were also placed close to these genera by their authors (Lindley 1970, Ris 1912). C. delecollei Ris, 1912 is endemic to the Indonesian island of Sulawesi and Z. gracile Lindley, 1970 is known only from a few specimens collected in northern Côte d'Ivoire. It remains to be seen if this 'zygonychine' complex is a natural group, but the term is used here to indicate these similar genera for convenience.

Diagnosis

Adult. – Large (Hw 34-47mm), robust libellulids. Venation characterised by following combination: (1) Fw with 11½-17½ Ax and 8-12 Px; (2) Pt long, 4.5-5.5mm, 10-14% of Hw length; (3) arculus stands between Ax1-2; (4) subtriangles of 3 cells, sometimes 4; (5) Fw discoidal field parallel-sided; (6) up to 8 cell-doublings between IR3 and Rspl in all wings; (7) proximal border of anal loop abruptly curved, almost rectangular.

For a comparison with *Olpogastra* (s.s.) see table 1. *Zygonyx* is superficially similar to *Zygonoides*, but the African species differ from it and also from *Olpogastra* (s.s.) in the following features: (1) Pt shorter, 7-10% of Hw length; (2) seldom any cell-doublings before Rspl; (3) hindlobe of pronotum smaller, without fringe of long pale hairs; (4) posterior hook of tarsal claws about as large as anterior hook, not distinctly

smaller (fig. 8); (5) tibial spines smaller and thinner; (6) hook of hamule more pointed; (7) males guard territories in flight, never perching intermittently, and the rest-posture is vertical, not horizontal. The ubiquitous *Z. torridus* differs from typical *Zygonyx* by its short tarsal hooks (fig. 9) and up to 5 cell-doublings preceding Rspl. Even its coloration recalls *Zygonoides*, but in other adult (and larval) characters it agrees with *Zygonyx*.

The fourth African 'zygonychine' genus (see Affinities), *Zygonychidium*, has tarsal claws like those of *Zygonoides* and venation and tibial armature nearest *Zygonyx*, but otherwise has numerous unique features (Lindley 1970): (1) banded eyes; (2) distinctive thoracic and abdominal markings; (3) small, slenderhooked hamule; (4) balloon-like distal segment of penis; (5) incredibly elongated cerci, about 5-6x as long as epiproct and 30% of abdomen length in male; (6) bilobed vulvar scale and enlarged sternite of S9 in female.

Larva. - For a comparison with *Olpogastra* (s.s.), Zygonyx and Onychothemis see table 3. The three available Zygonoides taxa are homogeneous in a number of characters separating the genus from Olpogastra (s.s.): (1) dorsal spines are present on S9-10 (figs. 18-20, 23-25); (2) prementum is slightly longer than wide and reaches only to the posterior borders of fore coxae (figs. 18-20); (3) legs are short and flattened. Olpogastra, in contrast, has dorsal spines only up to S8, a longer prementum reaching to the posterior border of the mid coxae, and longer cylindrical legs (figs. 21, 26). Zygonoides shares the three characters with the Zygonyx species examined (fig. 22), but the latter genus differs from both Zygonoides and Olpogastra by its: (1) blunt dorsal spines; (2) S8-9 not fused and suture between them straight; (3) laterally implanted legs; (4) projecting eyes; (5) prominent occipital processes; (6) relatively long anal pyramid. Altogether Zygonoides appears intermediate between Zygonyx and Olpogastra (s.s.) in larval characters, but two characters are neither intermediate nor shared with either: (1) lateral spines present on S5 (except Z. fuelleborni) and S6 (figs. 18-20, 23-25); (2) very short epiproct (figs. 33-35). The larva of Zygonychidium is unknown.

An interesting character is the dorsal fusion of S8-9. When softened with moisture, the dorsal suture functions as an inter-segmental hinge in *Zygonyx*, while the segments cannot move separately in the other genera examined. Ventrally the suture is almost straight in *Zygonyx*, but markedly kinked posterolaterally in the other genera, which share the dorsal fusion of S8-9 with *Gomphidia* Selys, 1854 (Müller et al. 2005) and *Ictinogomphus* Cowley, 1934 (own observations) in Gomphidae. These genera all have broad abdomens with a high dorsal ridge and

terminal segments partly enveloping each other, inhibiting their flexibility. The dorsal fusion of S8-9 may be an adaptation to the larval habitat; at least *Zygonoides* and *Gomphidia* seem to have a similar larval ecology (F. Suhling, own observations).

Status of genus

The sole foundation of *Zygonoides* is a brief note by Fraser (1957):

'Olpogastra Karsch (Ethiopian, as represented by lugubris Karsch, but excluding all others of the genus, which are here placed in a new genus Zygonoides; lugubris differs from all other species by its clawhooks almost obsolete, its abdomen longer than the wings and very slender, and lastly by its male genitalia, which is broadly different from all other species formerly placed in the genus. The type of Zygonoides is Olpogastra fuelleborni Grunberg.).'

Originally, however, Fraser (1949) was of the opinion that 'little separates the genus Olpogastra from Zygonyx'. Pinhey (1951) elaborated on the similarity of Olpogastra and Zygonyx, stating that 'the more robust one, fuelleborni, is somewhat like Zygonyx torrida [= torridus] in build, markings and genitalia [...], unlike the genotype *lugubris*. It seems possible to me that fuelleborni [...] might have to be placed in a separate genus or in a subgenus under Zygonyx.' Pinhey (1962) separated *Olpogastra* and *Zygonoides* in a key to genera, and argued: '... fuelleborni is nearer that genus [Zygonyx] in genitalia than to the present one [Olpogastra] and it is possible that this and fraseri are not true Olpogastra'. In conflict with these and earlier remarks, Pinhey (1961, 1962) ranked Zygonoides as a subgenus of Olpogastra, and not as a separate genus or as a subgenus of Zygonyx. Gambles (see Medler 1980) rejected Pinhey's opinion, emphasising in his unpublished manuscript 'The Nigerian Dragonflies' that 'there is only one species in [Olpogastra], O. lugubris.' Although Pinhey's (1962) catalogue is generally followed in considering Zygonoides a subgenus, we feel that consistent arguments to support his classification have not been put forward.

The considerable differences between *Zygonoides* and *Olpogastra* (s.s.), especially in the larvae, may warrant the restoration of *Zygonoides* as a genus. However, if all characters that distinguish *Olpogastra* from *Zygonoides* are apomorphies (tables 1, 3), splitting the two might create a paraphyletic taxon. Most characters that separate *Zygonoides* from *Olpogastra* are shared with *Zygonyx*, while those that separate it from *Zygonyx* are shared with *Olpogastra*. Nonetheless, the diagnostic shape of the secondary genitalia of the adult male (figs. 10-13), and the lateral spines on S5-6 and the short epiproct of larvae are possible

autapomorphies and serve to define Zygonoides.

Moreover, Olpogastra (s.s.) and Zygonoides may not be sister groups, as implied by Bechly (1996). The adult habitus of the Sulawesi endemic Celebothemis is surprisingly similar to that of O. lugubris. Indeed two syntype males and a female at ISNB each bear the handwritten label 'Olpog.? no. 2' and are accompanied by a poorly legible note: 'Olpogastra? no.2 Différences de lugubris: soies des tibias nombreux et fins, 1 seul rang entre An. [?] et spl. arc. dans le prol. [?] du △ inf.' ¹. The resemblance is created by: (1) an abnormally bulbous S1-3 combined with a thin and cylindrical S4-10, (2) the glossy black body with sharply contrasting yellow spots, and (3) the similar anterior lamina, bare and low. In some characters Celebothemis differs from both Olpogastra and Zygonoides. (1) Rspl subtends a single row of cells; (2) hind tibiae have an outer row of 14-15 fine spines; and (3) S4-10 are all black. In other features Celebothemis is nearer Zygonoides: (1) 3-4 cells in subtriangle; and (2) shape of appendages. The markings of the thorax, the shape of hamule and genital lobe and the size of the posterior hooks of the tarsal claws stand somewhat between Olpogastra and Zygonoides.

Ris (1912) was also struck by the similarity of Celebothemis with Olpogastra, but linked its leg armature to that of Zygonyx and its tarsal claws and secondary genitalia to those of Onychothemis. Onychothemis differs from this complex of genera by its curled hamular hook and robust abdomen. In larval characters O. testacea comes very close to Zygonoides (table 3). The mixture of characters combined with geographic reasons lead Ris (1912) to describe Celebothemis separately from Olpogastra. Whether Celebothemis stands among Olpogastra, Onychothemis and Zygonoides and is the sister group of any of these, remains to be seen. It would therefore be interesting to discover its larva. However, we believe that each morphological unit within the 'zygonychine' complex is best treated as a separate genus, and thus consider it incorrect to unite such disparate units as Zygonoides and Olpogastra.

Ecology and biogeography

Zygonoides is endemic to the Afrotropics, where the four species appear to have allopatric distributions (fig. 42). The somewhat disparate Z. lachesis is isolated on Madagascar. Z. fraseri and Z. fuel-leborni occupy the dry northern and south-eastern belts of continental Africa, while Z. occidentis is only

known with certainty from several localities in the Congo Basin and an unspecified site in Nigeria. The absence of records of the genus in Katanga and most of Zambia is notable, as these areas have been comparatively well surveyed (e.g. Pinhey 1984). All species inhabit principally open rivers and large streams (figs. 39-40, details provided under each species). Males perch above the water and make long and aggressive patrols, preferring sections of more movement, such as rapids, riffles and splash zones. Oviposition behaviour is unknown.

Identification

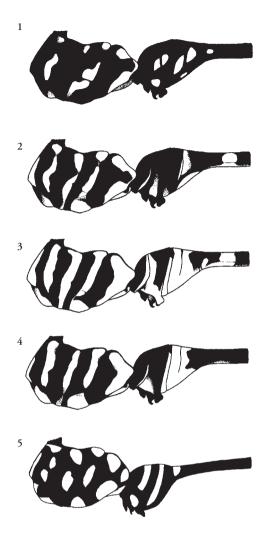
Zygonoides adults differ mainly in size and coloration (see key and table 2). The exuviae of the continental Zygonoides species are similar, but can be easily separated by their size and the shape, size and number of lateral and dorsal abdominal spines (see key and table 4).

Key to adult Zygonoides

- Postdorsal stripes present (figs. 2-4). Costa yellow to dark brown, paler than blackish Pt. Hook of hamule curved straight backwards (figs. 11-13), anteriorly with numerous short bristles. S2-3 without conspicuous spot-pairs (figs. 2-4). Pale band on S7 at segment midlength. At most abdomen venter and S3-4 dorsum becoming white pruinose in mature male. Hw 37-47 mm. Continental Africa

- 3. Hw base yellow, contrasting with dark brown membranule. Labrum and genital lobe largely pale (fig. 3). S4-7 with broad pale bands. Hw 40-45 mm. Northern Uganda to Côte d'Ivoire fraseri
- Hw base blackish brown, like membranule.

¹ Inversely, an *O. lugubris* female of unknown origin at zmuh is labelled 'Celebothemis n.sp. ♀ det. Dr. Erich Schmidt 1934'!



Figs. 1-5. Synthorax and S1-4 of *Zygonoides* and *Olpogastra* males in lateral view. Pruinosity omitted, i.e. teneral condition shown. – 1, *Z. lachesis*; 2, *Z. fuelleborni*; 3, *Z. fraseri*, 4, *Z. occidentis*; 5, *O. lugubris*.

Key to final stadium larvae of *Zygonoides* (*Z. lachesis* unknown)

 Lateral spines present on S6-9 only. Lateral spines on S8 reaching at most to apical border of S9.

- Lateral spines on S9 shorter than S9 (fig. 18, ventral view) fuelleborni
- Lateral spines present on S5-9. Lateral spines on S8 reaching at least beyond apical border of S9. Lateral spines on S9 as long as or longer than S9 (figs. 19-20)
- Lateral spines on S8 reaching to near apical border of S10. Lateral spines on S9 at most slightly longer than S9 (fig. 19) fraseri

Zygonoides lachesis (Ris) comb. n. (figs. 1, 10, 15)

Pseudomacromia n.sp. Ris, 1906: in litt. [see below].

Olpogastra lachesis Ris, 1912: 828. Syntype &: MADAGASCAR: blue, handwritten 'Rumena V. Mayanga (Madag)', white, handwritten 'Ps[eudomacromia]. no. 5', red triangle, white, handwritten '84'; syntype &: MADAGASCAR: blue, handwritten 'Rumena V. Mayanga (Madag)', white, handwritten 'Ps. no. 5'; syntype P: MADAGASCAR: blue, handwritten 'Nossibe', white, handwritten 'Ps. no. 5' [these three accompanied by three unattached labels, white, printed and handwritten 'Collection selys Pseudomacromia n.sp. Revision RIS 1906 TYPE Olpogastra lachesis Ris'] (ISNB) [all examined].

Pseudomacromia bella Lacroix, 1920: 175. Holotype &: MADAGASCAR: Miarinarivo (MNHN) [not examined]; junior synonym – Pinhey (1962: 279).

Diagnosis

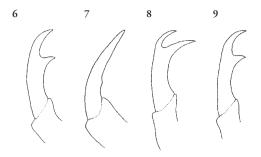
The smallest species of *Zygonoides*, and also the darkest, with generally more black on labium, frons, thorax, wing veins and S5-6 (see table 2). Distinct from continental taxa by colour pattern (fig. 1) and extent of pruinosity, Pt colour, hamule shape (fig. 10) and male appendages: the cerci appear compressed and therefore more sinuous and strongly heeled than in other *Zygonoides* species (fig. 15). Larva unknown.

Remarks

Initially considered to be related to *Zygonyx* (of which *Pseudomacromia* Kirby, 1889 is a synonym) by Ris (in litt.) and Lacroix (1920). Fraser's (1957) exclusion of all species except *O. lugubris* from *Olpogastra* suggested that he included *Z. lachesis* in *Zygonoides*, but Pinhey (1962) retained this species in *Olpogastra*. Although it is the most distinct *Zygonoides* species, it agrees with the generic diagnosis (table 1).

Range and ecology

Endemic to Madagascar. Males perch on sticks low over the current of sunny streams (S.W. Dunkle in litt.).



Figs. 6-9. Tarsal claw of Zygonoides, Olpogastra and Zygonyx in lateral view. – 6, Z. fuelleborni; 7, O. lugubris; 8, Z. natalensis; 9, Z. torridus.

Other material. – MADAGASCAR: $1\ \ \mathring{\sigma}$, $1\ \ \mathring{\varphi}$, Fianarantsoa Province, Ranomafana National Park, 10.xi.1993, S.W. Dunkle (Coll. S.W. Dunkle); $1\ \mathring{\sigma}$, $1\ \ \mathring{\varphi}$, 69km from Sambava on Andapa Rd., Hawantomby R. ($14^\circ 30.2^\circ S 49^\circ 48.0^\circ E$), 19.iv.1999; $1\ \mathring{\sigma}$, 83km Vill Antanumbao, Lokoho Br., 21.iv.1999; $1\ \mathring{\sigma}$, 60 km Tana-Toamasina Rd., Mandraka R. ($18^\circ 50^\circ S 48^\circ 05^\circ E$), 25.iv.1999, M.J. Parr (Coll. M.J. Parr).

Zygonoides fuelleborni (Grünberg) comb. n. (figs. 2, 6, 11, 18, 23, 28, 33, 38)

Olpogastra fülleborni Grünberg, 1902: 235. Holotype \mathfrak{P} : танханіа: blue, printed 'Nyassa-See, Langenburg, 9-19.VIII.98, Fülleborn S.', handwritten 'Olpogastra fülleborni Grünb.', handwritten 'Olpogastra ?' (ZМНВ) [examined].

Pseudomacromia torrida nec Kirby, 1889 – Brauer (in litt.) in Grünberg (1902: 235).

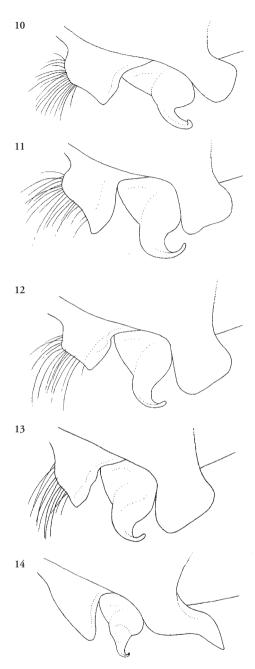
Diagnosis

The smallest mainland *Zygonoides*, separated from *Z. fraseri* and *Z. occidentis* by the narrowed or broken pale thoracic stripes, the absence of a broad pale ring at S3 base (fig. 2), and the development of extensive white pruinosity on the apical portion of S3. The latter is conspicuous as a white ring in the field (fig. 38). Secondary genitalia are similar to those of *Z. fraseri* and *Z. occidentis* but the lip of the anterior lamina appears more swollen, hamular hook more bristly and strongly curved, and anterior corner of genital lobe less developed (fig. 11).

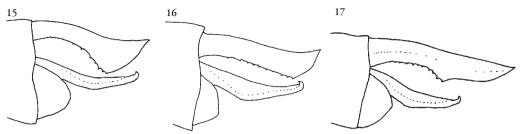
The exuviae are smaller than those of *Z. fraseri* and *Z. occidentis* and have also the relatively smallest abdominal spines (figs. 18, 23).

Remarks

Grünberg (1902) published this species as 'Olpogastra fülleborni K. nov.spec.'. 'K.' stands for Karsch, as is apparent in Grünberg (1903) where species like Mesocnemis singularis Karsch, 1891 and



Figs. 10-14. Secondary genitalia of *Zygonoides* and *Olpogastra* in lateral view. The hamular bristles of *Z. fuelleborni, Z. fraseri* and *Z. occidentis* have been omitted. – 10, *Z. lachesis*; 11, *Z. fuelleborni*; 12, *Z. fraseri*; 13, *Z. occidentis*; 14, *O. lugubris*.



Figs. 15-17. Male appendages of Zygonoides and Olpogastra in lateral view. - 15, Z. lachesis; 16, Z. fraseri; 17, O. lugubris.

Atoconeura biordinata Karsch, 1899 carry the same abbreviation. Following article 11.9.3.2 of ICZN (1999), Grünberg (1902) is the author of these names, because Karsch is not named explicitly in the work itself.

Range and ecology

Ranges from Kenya through Tanzania and Malawi to southern Africa (fig. 42). The only Sudan record is imprecise: the ancient Nubian specimen in NHRS is possibly the same mentioned by Grünberg (1902) as being in Vienna. References for Nigeria can be traced back to a record of *Z. occidentis*.

Pinhey (1981) mentioned that Z. fuelleborni 'settles on reeds or overhanging branches over well-flowing rivers and large streams'. Most records are from larger, open rivers where it appears to prefer rocky zones with rapid flow, such as Victoria Falls and the rapids at Katima Mulilo and Katambora on the Zambezi, Popa Falls on the Okavango, Epupa Falls on the Kunene and Malawi's Mpatamanga Gorge. It also inhabits the rocky shores of Lake Malawi, where wave motion emulates riverine conditions (fig. 39). Here males perch (abdomen held horizontally, slightly raised or in obelisk position) on tips of reeds or branches (or rocks, but favouring pole-like perches, fig. 38) making long, fast flights over areas of rock and moving water, rather like Zygonyx. Despite attempts to sample larvae at several places in Namibia, only exuviae were collected.

Other material. - KENYA: 1 &, Mzima Springs, Tsavo West National Park, 9.xii.2000; 1 &, Marich Pass, Morun River, 930m a.s.l., 14.i.2001, V. Clausnitzer (Coll. V. Clausnitzer). – MALAWI: 3 ♂, 2 ♀, Northern Region, Nkhata Bay District, Mwaya Beach (11°58.9'S 34°04.8'E), sandy shore of Lake Malawi with some rocks, 470 m a.s.l., 15.xii.2001, K.-D.B. Dijkstra (RMNH). – NAMIBIA: 1 д, Kunene River near Swaartboisdrift (17.291°S 13.762°E), 729 m a.s.l., 04.iii.2004, J. Ott (nmnw); 1 ♀, Okavango River at Popa Falls (18.121°S 21.532°E), 1030 m a.s.l., 16.xii.2004, E. Marais (nmnw). – sudan: 1 &, 'Marno Nubien 1871' [must refer to explorer Ernst Marno], 'Fuelleborni, det. H. Zerny' (NHRS). – TANZANIA: 1 ♀, Uluguru Mts, Ruvu River (7°01'S 37°48'E), 19.ix.2001, V. Clausnitzer (Coll. V. Clausnitzer). - ZAMBIA: 1 3, Katambora, Zambezi River, 2.ii.1965, E. Pinhey (Coll. D.R. Paulson). – ZIMBABWE: 1 ♂, 1 ♀, North Province, Zambezi River near Victoria Falls, 900 m, 1.xi.1997, D.R. Paulson (Coll. D.R. Paulson).

Larval material [exuviae]. - NAMIBIA (KUNENE RIVER): Epupa Falls (17.002°S 13.244°E), 639 m a.s.l., iii.2004; near Swaartboisdrift (17.291°S 13.762°E), 729 m a.s.l., iii.2004; Kunene River Lodge (17.555°S 13.882°E), 753 m a.s.l., iii.+xii.2004; E Kunene River Lodge (17.434°S 13.955°E), 767 m a.s.l., iii.2004; F. Suhling (NMNW). - NAMIBIA (OKAVANGO RIVER): W Nkurenkuru (17.586°S 18.577°E), 1095 m a.s.l., xii.2004; Hakusembe Lodge (17.852°S 19.676°E), 1071 m a.s.l., xii.2004; N'Kawzi Lodge (17.866°S 19.907°E), 1062 m a.s.l., xii.2004; Andara (18.058°S 21.448°E), 1035 m a.s.l., xii.2004; Suclabo Lodge (18.114°S 21.5879°E), 1028m a.s.l., ii.2004; Popa Falls (18.121°S 21.532°E), 1030m a.s.l., ii.+xii.2004; F. Suhling (NMNW). - NAMIBIA (ZAMBEZI RIVER): rapids at Katima Mulilo (17.476°S 24.248°E), 963 m a.s.l., ii.+xii.2004; F. Suhling (NMNW) [Several exuviae were collected at each site, therefore numbers are not indicated. No emerging adults were found, but because Z. fuelleborni is the only Zygonoides species at these sites and the exuviae are small and similar to those of Z. fraseri they could be assigned to this species.]

Zygonoides fraseri (Pinhey) comb. n. (figs. 3, 12, 16, 19, 24, 29, 34)

Olpogastra fraseri Pinhey, 1956: 39. Holotype &: UGANDA: round, with red ring, printed 'Holotype', handwritten and printed 'Aswa R., Madi Opei, Acholi, Uganda, March 1952, Т.Н.Е. Jackson', pink 'HOLOTYPE Olpogastra fraseri Pinh. 1954' (ВМNН) [examined].

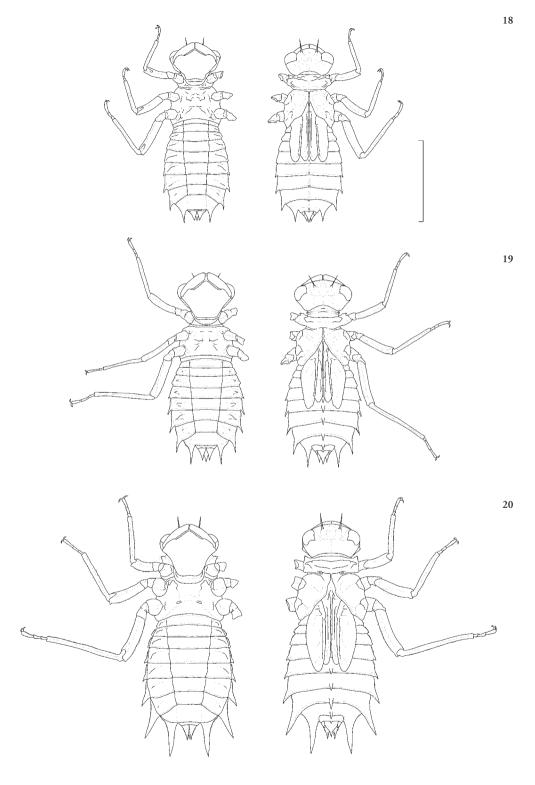
Zygonoides fuelleborni occidentis nec (Ris, 1912) – Gambles (1975: in litt.).

Olpogastra fuelleborni nec Grünberg, 1902 – O'Neill & Paulson (2001: 75).

Diagnosis

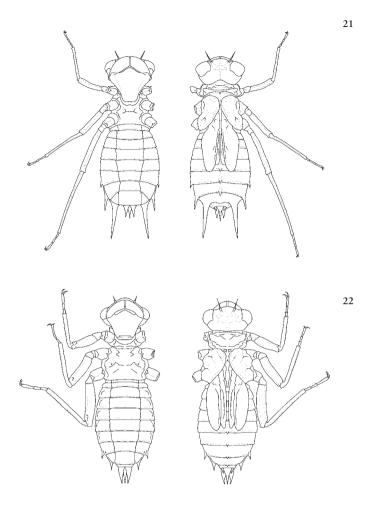
The palest species of *Zygonoides*, identified by the broadly striped thorax and boldly banded abdomen. The only continental *Zygonoides* with a yellow (not dark brown) patch at the Hw base. Intermediate in size (adult and larva) and larval characters between *Z. fuelleborni* and *Z. occidentis* (figs. 19, 24).

In flight, males recall the sympatric Zygonyx



Figs. 18-22.
Final stadium larva (drawn from exuviae) of *Zygonoides*, *Olpogastra* and *Zygonyx* in ventral (left) and dorsal (right) view. Drawn to scale (scale bar represents 10 mm).

– 18, *Z. fuelleborni*; 19, *Z. fraseri*; 20, *Z. occidentis*; 21, *O. lugubris*; 22, *Z. natalensis*.



torridus, but are of heavier build with wider pale markings (especially the band on S7 is apparent) and green (rather than dark brown) eyes. Patrols may be prolonged, but males occasionally perch at the waterside, unlike *Z. torridus* (K.-D.B. Dijkstra, own observations).

Remarks

The description of *Z. fraseri* appeared in 1956 and not in 1955, as already indicated by Pinhey (1962), but ignored by later authors (e.g. Bridges 1994). Gambles' label on the Ivorian male shows two points: (1) he regarded *Zygonoides* as a good genus (see Status of genus); (2) he indirectly suggested that *Z. fraseri* is the same as *Z. occidentis* (see under *Z. occidentis*). O'Neill & Paulson (2001) published their Ghana record as 'Olpogastra fuelleborni Ris,

1912 [not Grünberg, 1902]' and probably also meant O. f. occidentis Ris, 1912.

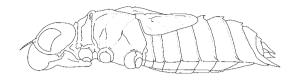
Range and ecology

Previously known only from northern Uganda, O'Neill & Paulson (2001) published the first western African record from Ghana, and we provide further records from there and Côte d'Ivoire. *Z. fraseri* probably occurs throughout the savannah belt between the Sahara and the equatorial forests, which stretches to Senegal (fig. 42).

All records are from open rivers (fig. 40), but the larval microhabitat is unknown.

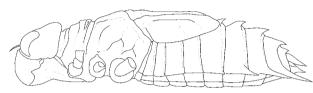
Other material. – côte d'ivoire: $1\ \$ Ç, 'Ivory Coast vii-viii '74 Alasdair J. Edwards', with note 'Zygonoides fuelleborni occidentis (Ris) det. R.M. Gambles 1975 $\$ (*) (BMNH); $2\ \$ $\$ (1 freshly emerged), Comoé River (8.45°N, 3.49°W),



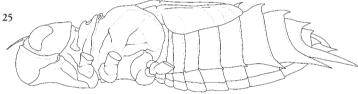


Figs. 23-27.
Final stadium larva (drawn from exuviae) of *Zygonoides*, *Olpogastra* and *Zygonyx* in lateral view, showing the length of the prementum relative to the legs and the number and shape of dorsal spines. Drawn to scale. – 23, *Z. fuelleborni*; 24, *Z. fraseri*; 25, *Z. occidentis*; 26, *O. lugubris*; 27, *Z. natalensis*.

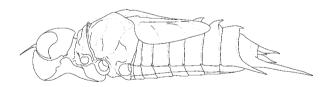




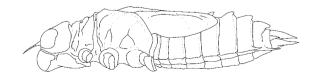


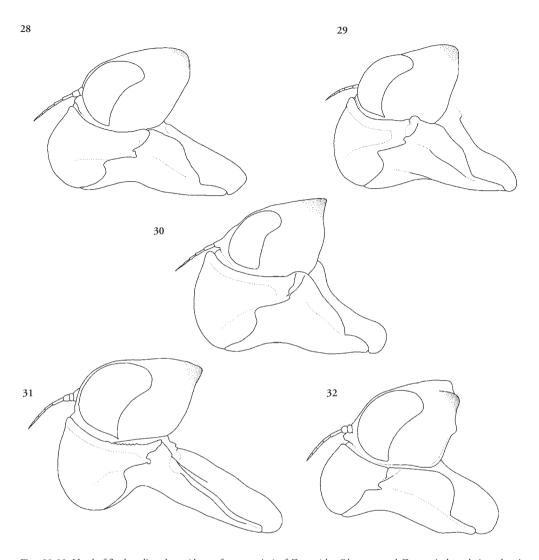


26



27



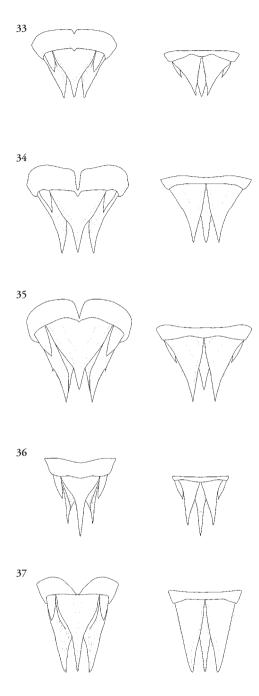


Figs. 28-32. Head of final stadium larva (drawn from exuviae) of *Zygonoides, Olpogastra* and *Zygonyx* in lateral view, showing the general shape of the labium and the occipital processes in *Zygonyx*. – 28, *Z. fuelleborni*; 29, *Z. fraseri*; 30, *Z. occidentis*; 31, *O. lugubris*; 32, *Z. natalensis*.

11.v.1991, K. Grabow (Coll. K. Grabow). — GHANA: 2 δ , Volta Region, Menu River, Menuso, 14.iii.1993, H.A. Olsvik (Coll. H.A. Olsvik); 1 δ , 1 ς , Brong Ahafo Region, Bui National Park, Black Volta River (8°20'N 2°19'W), 11.vii.1997, G. O'Neill (Coll. D.R. Paulson); 1 δ , Volta Region, south of Hohoe, Dayi river at Gbi-Wegbe (7°06'N 0°27'E), 12.vii.2006, K.-D.B. Dijkstra (RMNH). — UGANDA: 1 δ , Aswa R., Acholi, iii.1952, T.H.E. Jackson (BMNH); 2 δ (paratypes), Aswa R., Acholi, iii.1952, T.H.E. Jackson (NMKE); 1 δ (paratype), Aswa Riv. Bridge, Acholi, iv.1952, 1 ς (paratype), Ara, NW Madi, W Nile, v-vi.1954, V.G.L. van Someren (BMNH); 1 ς ('allotype'), with labels

round, with red ring 'Allotype', handwritten and printed 'Ara, West Madi, West Nile, Uganda, June 1954, T.H.E. Jackson', pink 'ALLOTYPE Olpogastra fraseri Pinh. 1954' (BMNH); 1 & (paratype), Ara, West Madi, West Nile, vi.1954.

Larval material [exuviae]. — côte d'ivoire: 7 exuviae, Comoé National Park, Comoé River (8.45°N, 3.49°W), 11.v.1991, K. Grabow (Coll. K. Grabow) [specific identity confirmed by one emerged adult]. — GHANA: 1 exuvia, Volta Region, south of Hohoe, Dayi river at Gbi-Wegbe (7°06'N 0°27'E), 12.vii.2006, K.-D.B. Dijkstra (rmnh).



Figs. 33-37. Anal pyramid of final stadium larva (drawn from exuviae) of *Zygonoides, Olpogastra* and *Zygonyx* in dorsal (left) and ventral (right), showing the proportions of the epiproct and paraprocts. Drawn to scale. – 33, *Z. fuelleborni*; 34, *Z. fraseri*; 35, *Z. occidentis*; 36, *O. lugubris*; 37, *Z. natalensis*.

Zygonoides occidentis (Ris) stat. n. (figs. 4, 13, 20, 25, 30, 35)

Olpogastra Fuelleborni occidentis Ris, 1912: 826. Syntype &: CONGO-KINSHASA: printed 'Kinchassa [= Kinshasa] Waelbroeck 1899', handwritten and printed 'Olpogastra' no. 3 Det. Dr. F. Ris', red triangle (plain, indicates illustration in Ris 1912), handwritten '158', accompanied by unattached label, printed and handwritten 'Collection selys Schizonyx corduloides Selys Revision RIS 1906 TYPE Olpogastra Fuelleborni occidentis Ris' (ISNB) [examined]. – Syntype &: CONGO-KINSHASA: pink 'Type', 'Musée du Congo Belge. Kasai, Lukenge. Fontainas.', handwritten 'Cotype Olpogastra fuelleborni occidentis Ris. Det. Dr. F. Ris', printed 'R. Det. B. 248' (MRAC) [examined]. Olpogastra fuelleborni occidentalis Longfield, 1947: 31.

Olpogastra fuelleborni occidentalis Longfield, 194/: 31.
– Misspelling.

Zygonoides fuelleborni occidentis (Ris, 1912) – Medler (1980:

28).
Zygonoides fuelleborni f. occidentis (Ris, 1912) – Pinhey (1981: 613).

Diagnosis

The largest and one of the darkest species of Zygonoides. According to Ris (1912), Z. occidentis differs from Z. fuelleborni as follows: (1) larger size; (2) lack of pruinosity; (3) abdomen with pale bands on S3 and S7, rather than spots on S3-6; (4) pale thoracic markings brighter and sharper, with antehumeral and metepisternal stripes complete, not broken (fig. 4). These characters agree with Z. fraseri, but Z. occidentis is much darker overall, having a shining black labrum, all-black legs and a blackish spot at Hw base. These features are more similar to Z. fuelleborni, although that species does have a pale labrum. Z. occidentis has a largely dark abdomen, except for the following pale markings: faint spots on S2 near genital fossa; broad basal ring on S3, just like in Z. fraseri; tiny ventral spots on S4-7 (at most extended slightly dorsally on S4), instead of broad bands up to S9; prominent medial crescent or band on S7 dorsum. The Kinshasa syntype has a sliver of white pruinosity on the postero-ventral border of S3 and underside of S4.

The exuviae of *Z. occidentis* are much larger than those of the two other continental species, with relatively large lateral spines (figs. 20, 25).

Remarks

Pinhey (1956) remarked that the taxon occidentis 'is evidently close to fraseri, with its body larger and yellower [but see diagnosis] than fuelleborni and also lacking pruinosity', but later considered it 'no more than a form, not race [of fuelleborni]' (Pinhey 1981, 1984). From the diagnosis and figures it is apparent that adult occidentis is closer to fraseri than fuelleborni; it is even larger than the relatively big fraseri and its markings are similarly configured. However, overall occidentis is darker than fuelleborni, while fraseri is the palest taxon. In larval characters, occidentis is also



Figs. 38-41. Habitus and habitat of *Zygonoides* species. Photographs by K.-D. B Dijkstra. – 38, male *Z. fuelleborni* at Mwaya Beach on Lake Malawi, Malawi; 39, lakeshore habitat at Mwaya Beach; 40, Dayi river near Hohoe, Ghana, males of *Z. fraseri* perched on stakes in midstream (background) and patrolled towards the riffles in the foreground, an exuvia was found among bank-side grass on the right; 41: Congo river near Lokutu, Congo-Kinshasa, where exuviae of *Z. occidentis* were found.

nearer *fraseri*, but surpasses both it and *fuelleborni* in the size of body and spines.

In this light, *occidentis* cannot be considered a subspecies of *fuelleborni*, unless *fraseri* is considered as such too. Morphological differences between the three taxa are negligible in adults (see *Z. fuelleborni*) and gradual in larvae. However, specimens of the three taxa are easily grouped by their size, range, extent and configuration of adult markings and the size of the larval spines. Therefore the taxa should be treated equally, as species.

Pinhey (1962, 1984) believed that a holotype from Kinshasa was at MRAC and a possible secondary type might be at ISNB. However, the Kinshasa male syntype figured by Ris (1912) is at ISNB, while another syntype is at MRAC. The name *Schizonyx corduloides* on the note placed near the *Z. occidentis* Kinshasa

syntype must refer to a metallic green *Zygonyx* from Sulawesi pinned nearby.

Range and ecology

The scarceness and location of records suggest this species inhabits very large rivers such as the Congo and Ubangi, where adults will be exceedingly difficult to catch. The exuviae were found along a more than 1 km broad channel of the Congo on a rocky face of a forested bank, and on an emergent stake under overhanging bushes (fig. 41). The only reliable record outside the Congo Basin is alledgedly from Nigeria, where suitable habitat may be present in the southeast, e.g. on the lower Niger (fig. 42). Longfield (1947) reported a female collected by Monard from Kakindo in southern Angola, but *Z. fuelleborni* occurs in nearby NE Namibia.

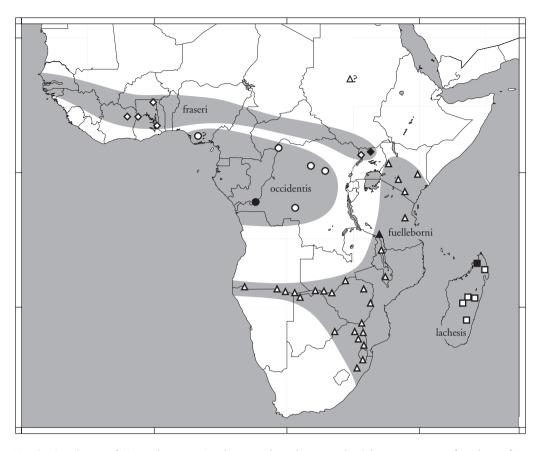


Fig. 42. Distribution of *Zygonoides* species. Based on records in this paper, the Odonata assessment of southern Africa (J. Kipping in litt.), Fraser (1956), Pinhey (1961, 1979) and a sight record of *Z. fraseri* by K.-D.B. Dijkstra at Nakpanduri in northern Ghana (29.vii.2006). Longfield's (1947) Angola record of *Z. occidentis* is omitted, as neither the identity nor the exact origin of the specimen could be determined. Legend. – squares: *Z. lachesis*; triangles: *Z. fuelleborni*; diamonds: *Z. fraseri*; circles: *Z. occidentis*; filled symbols: type localities; question mark: precise locality within nation unknown, but identity of specimen confirmed; grey shading: inferred ranges (Sudan record left out; see under *Z. fuelleborni*).

Other material. — CONGO-KINSHASA: 1 & (teneral; soft and faded after nearly a century in alcohol), 'Inner-Afrika-Expedition d. Herzog Adolf-Friedrich zu Mecklenburg 1910-1911, Belg. Kongo, Duma, Ubangi-Distr., Dr. H. Schubotz leg. 27.IX.1910' (ZMUH) [reported as this taxon by Le Roi (1915) and correctly identified judging from its measurements and (mere traces of) markings on S3]; 1 &, 'Musée du Congo, Stanleyville [= Kisangani], 9-IV-1912. Dr. Christy.', handwritten 'Olpogastra fuelleborni occidentis', 'R. Det. C. 248' (MRAC) [this and both other MRAC specimens were listed by Schouteden (1934)]; 1 \$\frac{9}{2}}, 'Musée du Congo, Leopoldville [= Kinshasa] 12-iv-1912. Dr. Bequaert', handwritten 'Olpogastra fuelleborni occidentis', 'R. Det. C. 248' (MRAC). — NIGERIA: 1 \$\frac{9}{2}} (very teneral and crushed), 'Nigeria', 'Olpogastra? no.3 Det. Dr. F. Ris', no other details (MNHN) [the identification, which Ris (1912) questioned].

Larval material [exuviae]. – CONGO-KINSHASA (ORIENTALE): 2 exuviae, Territoire de Basoko, Congo River at Lokutu (1°10'N 23°37'E), 370 m a.s.l., 8.xi.2004, K.-D.B. Dijkstra (RMNH) [identified as this species by locality, size and similarity to *Z. fraseri*].

Acknowledgements

Hans Duffels and Natalia von Ellenrieder gave comments that much improved the manuscript. Graham Vick kindly provided the unpublished writings of Gambles and Jens Kipping map details. Viola Clausnitzer, Sid Dunkle, Karsten Grabow, Ellinor Michel, Bert Orr, Mike Parr and Dennis Paulson provided material. Eliane de Coninck, Jos De Becker, Dave Goodger, Kjell Arne Johanson,

Wanja Kinuthia, Jean Legrand, Marc de Meyer, Laban Njoroge, Michael Ohl and Kai Schütte were helpful during visits to BMNH, MNHN, MRAC, NHRS, NMKE, ZMHB and ZMUH. The first author's work in BMNH, ISNB, MNHN and NHRS was supported by the SYS-RESOURCE, ABC, COLPARSYST and HIGH LAT infrastructures of the European Union IHP Programme. The International Dragonfly Fund made additional visits to BMNH, NMKE and ZMHB possible. The authors were supported by grants from the German Federal Ministry of Education and Research (BMBF, BIOLOG Programme, 01LC0025, 01LC0404 (KDBD), and 01LC0024 (FS and OM)), while RMNH provided working facilities (KDBD).

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Received: 28 July 2006 Accepted: 5 September 2006

Table 1. Comparison of adults of the genera Olpogastra and Zygonoides.

Character	Olpogastra	Zygonoides	
Pale markings of synthorax	broken up into spots, very contrasting (fig. 5)	merged into lines (more or less), generally less contrasting (figs. 1-4)	
Outer row of spines in hind tibiae usually of	9 spines (range 8-10)	10-12 spines (range 9-14)	
Posterior hook of tarsal claws	almost obsolete, a tiny dent (fig. 7)	prominent, up to half the size of anterior claw (fig. 6)	
Abdomen shape	S1-3 swollen and bulbous (S3 much higher than long with convex ventral carina). S4-10 very slender and cylindrical (S4 about 8x longer than wide), of even width (fig. 5)	S1-3 not bulbous (S3 about as high as long with straight ventral carina). S4-10 robust and flattened (S4 about 3x longer than wide), widest at S6-7 (figs. 1-4)	
Abdomen length (+ appendages)	105-115% of Hw length	80-95% of Hw length	
Subtriangle usually with	5 cells	3 cells (sometimes 4)	
Distal anal-discoidal area of Hw	with yellow wash	clear	
Anterior lamina	bare with low hump (fig. 14)	with long hairs and strong hump (figs. 10-13)	
Hook of hamule	small and abruptly curved (fig. 14)	large and gradually curved (figs. 10-13)	
Genital lobe	sickle-shaped (fig. 14)	roundly trapezoidal (figs. 10-13)	
Pale markings on S5-7 (when present)	basal spots	sub-basal or medial spots or bands	
Cerci	apical portion long, slender and straight, extending well beyond tip of epiproct (fig. 17)	apical portion short, thick and up-turned, extending just beyond tip of epiproct (figs. 15-16)	

Table 2. Comparison of adults of the species of *Zygonoides*. Characters apply to both sexes, unless stated otherwise. Average measurements are provided, with ranges between brackets.

Character	Z. lachesis (n=10)	Z. fuelleborni (n=11)	Z. fraseri (n=14)	Z. occidentis (n=6)
Hw	36.8 (34.5-39.0) mm	39.7 (37.5-42.0) mm	42.8 (40.0-45.0) mm	45.3 (44.5-46.5) mm
Fw Ax	13.1 (12½-14½)	12.6 (11½-14½)	14.4 (12½-15½)	16.0 (14½-17½)
Fw Px	9.1 (8-10)	8.4 (8-9)	9.8 (8-12)	10.8 (10-12)
Dorsal pruinosity (る)	grey, may cover entire thorax and abdomen	white, restricted to S3-4	none	none
Labium	all pale to largely black with narrow pale lateral edges	all pale	all pale	all pale
Labrum	all pale to black with two large triangular pale patches	all pale, sometimes with dark blotches	all pale	blackish, extreme base paler
Dorsum of frons	glossy black	pale, with broad brown basal band	pale, with glossy brown band over median groove	largely glossy brown
Eyes in life	green	grey blue	green	unknown
Pale markings of synthorax	strongly reduced and fragmented, e.g. post- dorsal pale stripe absent (fig. 1)	narrowed, reduced and fragmented, but post-dorsal stripe present (fig. 2)	broad and continuous stripes (fig. 3)	generally continuous stripes narrower, may be reduced and fragmented (fig. 4)
Femora	all dark	all dark	pale basally and ventrally	all dark
Costa and subcostal veins	black	pale	pale	dark brown
Pt	brown, paler than costa	black, darker than costa	black, darker than costa	black, darker than costa
Hw base	yellow to dark brown up to Ax1 and Cux	brown spot at least in extreme base of cubital space and often along the similarly coloured membranule	faint but fairly extensive yellow patch, contras- ting with dark brown membranule	blackish brown mainly along membranule and base of subcosta, may extend into cubital space
Hamule (♂)	curved back- and outwards (fig. 10), bare	curved backwards (fig. 11), anterior margin with many short bristles	curved backwards (fig. 12), anterior margin with many short bristles	curved backwards (fig. 13), anterior margin with many short bristles
Genital lobe (♂)	black, evenly rounded (figs. 1, 10)	black, roundly truncated (figs. 2, 11)	pale, sometimes with dark tip, roundly truncated (figs. 3, 12)	black, roundly truncated (figs. 4, 13)
Pale markings on S3	each side with three isolated lateral spots (fig. 1)	bands along transverse ridge and lower border (fig. 2)	basal three-quarters pale (fig. 3)	basal three-quarters pale (fig. 4)
Pale markings on S4-6	at most small basal spot on S4	large medio-lateral spots, often partly fused dorsally	all with broad medial band and S4 with basal spot	at most traces of medio-lateral spots
Pale markings on S7	sub-basal band, sometimes fragmented into a dorsal and two lateral spots	narrower medial band, sharply constricted dorsally	very broad medial band, of even width or widened slightly dorsally	at most narrow medial band, widest dorsally
Cerci (♂)	stouter and with thicker heel (fig. 15), all black	relatively slender (fig. cf. 16), all black	relatively slender (fig. 16), often with pale dorsal spot at base	relatively slender (fig. cf. 16), all black

Table 3. Comparison of larval characters of *Olpogastra, Zygonoides, Zygonyx* and the southern Asian *Onychothemis*. See larval diagnosis for explanation of S8-9 suture characters.

Character	Zygonoides	Olpogastra	Zygonyx	Onychothemis
Shape of eyes	not projecting (figs. 18-20)	not projecting (fig. 21)	projecting (fig. 22)	slightly projecting
Occipital processes	weak (figs. 28-30)	almost undeveloped (fig. 31)	very distinct (fig. 32)	weak
Prementum reaches to posterior border of	fore coxae (figs. 18-20)	middle coxae (fig. 21)	fore coxae (fig. 22)	fore coxae
Position of legs	ventro-lateral	ventro-lateral	lateral	ventro-lateral
Shape of femora	short, flattened	long, not flattened	short, flattened	short, flattened
Dorsal spines present up to segment	S10 (figs. 23-25)	S8 (fig. 26)	S10 (fig. 27)	S8
Shape of dorsal spines	pointed (figs. 23-25)	pointed (fig. 26)	blunt (fig. 27)	pointed
Lateral spines present on	S5-9 or S6-9 (figs. 18-20)	S7-9 (fig. 21)	S8-9 (fig. 22)	S6-9
Lateral spines on S9 reach to	tip of anal pyramid (figs. 18-19) or beyond (in <i>Z. occidentis</i> , fig. 20)	clearly beyond tip of anal pyramid (fig. 21)	tip of anal pyramid or beyond (in <i>Z. flavicosta</i> and <i>Z. speciosus</i> , fig. 22)	tip of anal pyramid
S8-9	dorsally fused	dorsally fused	dorsally flexible	dorsally fused (also S7-8)
Ventral S8-9 suture	kinked (figs. 18-20)	kinked (fig. 21)	straight (fig. 22)	kinked
Epiproct: S10 length	2-2.5x (figs. 33-35)	just over 3x (fig. 36)	5-6x (fig. 37)	about 2x
Paraprocts: epiproct	longer or as long (figs. 33-35)	slightly shorter (fig. 36)	longer or as long (fig. 37)	longer or as long

Table 4. Comparison of the larvae of continental African *Zygonoides* species. Spine length is measured on its inner margin, abdominal segment length medially on ventral side, head width dorsally at level of eyes. The wide variation measured in *Z. fuelleborni* is due to clear size differences between specimens from the Zambezi (larger) and Okavango (smaller).

Character	Z. fuelleborni (n = 10)	<i>Z. fraseri</i> (n = 6)	Z. occidentis (n=2)
Head width	6.1-7.2 mm	7.0-7.4 mm	7.4-7.5 mm
Hind tibia length	6.7-7.6 mm	8.5-8.9 mm	9.8-10.0 mm
Abdomen length	11.9-14.4 mm	12.1-13.9 mm	15.8-16.5 mm
Dorsal spines	small, not reaching over next segment (fig. 23)	large, reaching over next segment (fig. 24)	large, reaching over next segment (fig. 25)
Lateral spines present on	S6-9	S5-9	S5-9
Lateral spines on S8 reach to near	apical border of S9 (fig. 18)	apical border of \$10 (fig. 19)	tip of anal pyramid (fig. 20)
Length of lateral spine on S9	1.4-2.0 mm	2.0-2.3 mm	4.3-4.4 mm
Length ratio lateral spine S9 : S9	0.67-0.9	1.0-1.1	1.9-2.3
Length ratio lateral spine S9 : anal pyramid	1.3-1.5	1.2-1.4	2.3-2.7