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

Abbreviations

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

Taxonomic treatment

Zygonoidea Fraser


Affinities

Fraser (1957) placed Olpogastra, Zygonoidea and Zygonyx in the subfamily Zygonicinae (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 re-grouping was on account of the reduced posterior hook of the tarsal claws, and implies polyphyly of Olpogastra if Zygonoidea 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 Zygonoidea, 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

Acronyms for collections

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

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

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

MNMS Museo Nacional de Ciencias Naturales (Madrid, Spain)

MRCV 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, 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)
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 Zygonyx, 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 Zygonyx 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, slender-hooked 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 Onychochenus see table 3. The three available Zygonyx 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). Zygonyx shares the three characters with the Zygonyx species examined (fig. 22), but the latter genus differs from both Zygonyx 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 Zygonyx 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. fueleborni) 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 Zygonyx and Gomphidia seem to have a similar larval ecology (F. Suhling, own observations).

Status of genus

The sole foundation of Zygonyx 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 Zygonyx; lugubris differs from all other species by its claw-hooks 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 Zygonyx is Olpogastra fueleborni 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, fueleborni, is somewhat like Zygonyx torridus [= torridus] in build, markings and genitalia […]’, unlike the genotype lugubris. It seems possible to me that fueleborni […] might have to be placed in a separate genus or in a subgenus under Zygonyx.’ Pinhey (1962) separated Olpogastra and Zygonyx in a key to genera, and argued: ‘… fueleborni 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 Zygonyx as a subgenus of Olpogastra, and not as a separate genus or as a subgenus of Zygonyx. Gamble (see Medler 1980) rejected Pinhey’s opinion, emphasizing 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 Zygonyx a subgenus, we feel that consistent arguments to support his classification have not been put forward.

The considerable differences between Zygonyx and Olpogastra (s.s.), especially in the larvae, may warrant the restoration of Zygonyx as a genus. However, if all characters that distinguish Olpogastra from Zygonyx are apomorphies (tables 1, 3), splitting the two might create a paraphyletic taxon. Most characters that separate Zygonyx 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 Dif ferences de lugubris: soies des tibiaux nombreux et fins, 1 seul rang entre An. (?) et spl. arc. dans le prol. (?)’ 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 Afrotopics, where the four species appear to have allopatric distributions (fig. 42). The somewhat disparate Z. lachesis is isolated on Madagascar. Z. fraseri and Z. fuelleborni 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

1. Postdorsal stripes absent (fig. 1). Costa black, darker than dark brown Pt. Hook of hamule curved back- and outwards (fig. 10), bare. Both sides of S2-3 with paired pale spots at midheight (fig. 1). Pale band on S7 close to segment base. Abdomen and synthorax becoming entirely grey pruinose in mature male. Hw 34-39 mm. Madagascar ................................................................. lachesis

– 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 .................................................. fuelleborni

2. S3 largely dark at base (fig. 2), pruinosity (when present) extending onto dorsum S3 and often S4. Hw 37-42 mm, base with dark brown marking. Eyes blue in life. Eastern and southern Africa .......

– Base of S3 with broad pale ring occupying most of segment (figs. 3-4), pruinosity (when present) limited at most to underside of abdomen. Hw 40-47 mm, base marked with yellow; if brown Hw is 44-47 mm. Eyes green in life (unknown in occidentis). Western and central Africa ............ 3

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 .......

1 Inversely, an O. lugubris female of unknown origin at zmuh is labelled ‘Celebothemis n.sp. ♀ det. Dr. Erich Schmidt 1934’.
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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 ♀: MADAGASCAR: blue, handwritten ‘Nosibe’, 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].

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.).

Key to final stadium larvae of Zygonoides

(Z. lachesis unknown)

1. 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) ............................................ 2

2. Lateral spines on S8 reaching to near apical border of S10. Lateral spines on S9 at most slightly longer than S9 (fig. 19) ..................................... fraseri

- Lateral spines on S8 reaching to near tip of anal pyramid. Lateral spines on S9 much longer than S9 (fig. 20) ................................................ occidentis

Labrum and genital lobe largely black (fig. 4). S4-7 dark, only S7 frequently with pale band. Hw 44-47 mm. Congo basin to Nigeria .......... occidentis

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

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 fuelleborni K. nov.spec.’. ‘K.’ stands for Karsch, as is apparent in Grünberg (1903) where species like Mesocnemis singularis Karsch, 1891 and

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.


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.
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 to southern Africa (fig. 42). The only continental reference is the ancient Nubian specimen in NHRS (1999), nec Grünberg, 1902 – O’Neill & Paulson (2001: 75).


Diagnosis

The palest species of Zygonyx, identified by the broadly striped thorax and boldly banded abdomen. The only continental Zygonyx 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).
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 ♀, ‘Ivory Coast vii–viii ’74 Alasdair J. Edwards’, with note ‘Zygonoïdes fuelleborni occidentis (Ris) det. R.M. Gambles 1975 ♀’ (BMNH); 2 ♂ (1 freshly emerged), Comoé River (8.45°N, 3.49°W),

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).

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*. 
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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.
**Zygonoides occidentis** (Ris) stat. n.

(figs. 4, 13, 20, 25, 30, 35)

*Olpogastra Fuelleborni occidentis* Ris, 1912: 826. Syntype δ: CONGO-KINSHASA: printed ‘Kinchasa [= Kinshasa] Waelbroeck 1899’, handwritten and printed ‘Olpogast*ra? no. 3 Det. Dr. F. Ris’, red triangle (plain, indicates illustration in Ris 1912), accompanied by unattached label, printed and handwritten ‘Collection Selys Revision ris 1906 type Olpogast*ra Fuelleborni occidentis Ris’ (ttsn) [examined].


**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
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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 allegedly 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.
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 ♀, 'Musée du Congo, Leopoldville [= Kinshasa] 12-IV-1912. Dr. Bequaert', handwritten 'Olpogastra fuelleborni occidentis', 'R. Det. C. 248' (Mrac). – NIGERIA: 1 ♂ (very teneral and crushed), 'Nigeria', 'Olpogastra' no. 3 Det. Dr. F. Ris', no other details (MNNH) [the identification, which Ris (1912) questioned, is confirmed].

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, ZMBH and ZMUH. The first author’s work in BMNH, ISNB, MNHN and NHRS was supported by the SYRESOURCE, ABC, COLPARSYS and HIGH LAT infrastructures of the European Union HF Programme. The International Dragonfly Fund made additional visits to BMNH, NMKE and ZMBH 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).

References


Received: 28 July 2006

Accepted: 5 September 2006

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

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Olpogastra</em></th>
<th><em>Zygonoides</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Pale markings of synthorax</td>
<td>Broken up into spots, very contrasting (fig. 5)</td>
<td>Merged into lines (more or less), generally less contrasting (figs. 1-4)</td>
</tr>
<tr>
<td>Outer row of spines in hind tibiae usually of</td>
<td>9 spines (range 8-10)</td>
<td>10-12 spines (range 9-14)</td>
</tr>
<tr>
<td>Posterior hook of tarsal claws</td>
<td>Almost obsolete, a tiny dent (fig. 7)</td>
<td>Prominent, up to half the size of anterior claw (fig. 6)</td>
</tr>
<tr>
<td>Abdomen shape</td>
<td>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)</td>
<td>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)</td>
</tr>
<tr>
<td>Abdomen length (+ appendages)</td>
<td>105-115% of Hw length</td>
<td>80-95% of Hw length</td>
</tr>
<tr>
<td>Subtriangle usually with</td>
<td>5 cells</td>
<td>3 cells (sometimes 4)</td>
</tr>
<tr>
<td>Distal anal-discoidal area of Hw</td>
<td>With yellow wash</td>
<td>Clear</td>
</tr>
<tr>
<td>Anterior lamina</td>
<td>Bare with low hump (fig. 14)</td>
<td>With long hairs and strong hump (figs. 10-13)</td>
</tr>
<tr>
<td>Hook of hamule</td>
<td>Small and abruptly curved (fig. 14)</td>
<td>Large and gradually curved (figs. 10-13)</td>
</tr>
<tr>
<td>Genital lobe</td>
<td>Sickle-shaped (fig. 14)</td>
<td>Roundly trapezoidal (figs. 10-13)</td>
</tr>
<tr>
<td>Pale markings on S5-7 (when present)</td>
<td>Basal spots</td>
<td>Sub-basal or medial spots or bands</td>
</tr>
<tr>
<td>Cerci</td>
<td>Apical portion long, slender and straight, extending well beyond tip of epiproct (fig. 17)</td>
<td>Apical portion short, thick and up-turned, extending just beyond tip of epiproct (figs. 15-16)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Z. lachesis</em> (<em>n=10</em>)</th>
<th><em>Z. fuelleborni</em> (<em>n=11</em>)</th>
<th><em>Z. fraseri</em> (<em>n=14</em>)</th>
<th><em>Z. occidentis</em> (<em>n=6</em>)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hw</td>
<td>36.8 (34.5-39.0) mm</td>
<td>39.7 (37.5-42.0) mm</td>
<td>42.8 (40.0-45.0) mm</td>
<td>45.3 (44.5-46.5) mm</td>
</tr>
<tr>
<td>Fw Ax</td>
<td>13.1 (12½-14½)</td>
<td>12.6 (11½-14½)</td>
<td>14.4 (12½-15½)</td>
<td>16.0 (14½-17½)</td>
</tr>
<tr>
<td>Fw Px</td>
<td>9.1 (8-10)</td>
<td>8.4 (8-9)</td>
<td>9.8 (8-12)</td>
<td>10.8 (10-12)</td>
</tr>
<tr>
<td>Dorsal pruinosity (<em>♂</em>)</td>
<td>grey, may cover entire thorax and abdomen</td>
<td>white, restricted to S3-4</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Labium</td>
<td>all pale to largely black with narrow pale lateral edges</td>
<td>all pale to largely black with narrow pale lateral edges</td>
<td>all pale</td>
<td>all pale</td>
</tr>
<tr>
<td>Labrum</td>
<td>all pale to black with two large triangular pale patches</td>
<td>all pale, sometimes with dark blotches</td>
<td>all pale</td>
<td>blackish, extreme base paler</td>
</tr>
<tr>
<td>Dorsum of frons</td>
<td>glossy black</td>
<td>pale, with broad brown basal band</td>
<td>pale, with glossy brown band over median groove</td>
<td>largely glossy brown</td>
</tr>
<tr>
<td>Eyes in life</td>
<td>green</td>
<td>grey blue</td>
<td>green</td>
<td>unknown</td>
</tr>
<tr>
<td>Pale markings of synthorax</td>
<td>strongly reduced and fragmented, e.g. post-dorsal pale stripe absent (fig. 1)</td>
<td>narrowed, reduced and fragmented, but post-dorsal stripe present (fig. 2)</td>
<td>broad and continuous stripes (fig. 3)</td>
<td>generally continuous stripes narrower, may be reduced and fragmented (fig. 4)</td>
</tr>
<tr>
<td>Femora</td>
<td>all dark</td>
<td>all dark</td>
<td>pale basally and ventrally</td>
<td>all dark</td>
</tr>
<tr>
<td>Costa and subcostal veins</td>
<td>black</td>
<td>pale</td>
<td>pale</td>
<td>dark brown</td>
</tr>
<tr>
<td>Pr</td>
<td>brown, paler than costa brown spot at least in extreme base of cubital space and often along the similarly coloured membranule</td>
<td>black, darker than costa faint but fairly extensive yellow patch, contrasting with dark brown membranule</td>
<td>black, darker than costa blackish brown mainly along membranule and base of subcosta, may extend into cubital space</td>
<td></td>
</tr>
<tr>
<td>Hw base</td>
<td>yellow to dark brown up to Ax1 and Cux</td>
<td>black, darker than costa brown spot at least in extreme base of cubital space and often along the similarly coloured membranule</td>
<td>black, darker than costa blackish brown mainly along membranule and base of subcosta, may extend into cubital space</td>
<td></td>
</tr>
<tr>
<td>Hamule (<em>♂</em>)</td>
<td>curved back- and outwards (fig. 10), bare</td>
<td>curved backwards (fig. 11), anterior margin with many short bristles</td>
<td>curved backwards (fig. 12), anterior margin with many short bristles</td>
<td>curved backwards (fig. 13), anterior margin with many short bristles</td>
</tr>
<tr>
<td>Genital lobe (<em>♂</em>)</td>
<td>black, evenly rounded (figs. 1, 10)</td>
<td>black, roundly truncated (figs. 2, 11)</td>
<td>pale, sometimes with dark tip, roundly truncated (figs. 3, 12)</td>
<td>black, roundly truncated (figs. 4, 13)</td>
</tr>
<tr>
<td>Pale markings on S3</td>
<td>each side with three isolated lateral spots (fig. 1)</td>
<td>bands along transverse ridge and lower border (fig. 2)</td>
<td>basal three-quarters pale (fig. 3)</td>
<td>basal three-quarters pale (fig. 4)</td>
</tr>
<tr>
<td>Pale markings on S4-6</td>
<td>at most small basal spot on S4</td>
<td>large medio-lateral spots, often partly fused dorsally</td>
<td>all with broad medial band and S4 with basal spot</td>
<td>at most traces of medio-lateral spots</td>
</tr>
<tr>
<td>Pale markings on S7</td>
<td>sub-basal band, sometimes fragmented into a dorsal and two lateral spots</td>
<td>narrower medial band, sharply constricted dorsally</td>
<td>very broad medial band, of even width or widened slightly dorsally</td>
<td>at most narrow medial band, widest dorsally</td>
</tr>
<tr>
<td>Cerci (<em>♂</em>)</td>
<td>stouter and with thicker heel (fig. 15), all black</td>
<td>relatively slender (fig. cf. 16), all black</td>
<td>relatively slender (fig. cf. 16), often with pale dorsal spot at base</td>
<td>relatively slender (fig. cf. 16), all black</td>
</tr>
</tbody>
</table>
Table 3. Comparison of larval characters of *Olpogaster*, *Zygonoidea*, and the southern Asian *Onychothemis*. See larval diagnosis for explanation of S8-9 suture characters.

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

Table 4. Comparison of the larvae of continental African *Zygonoidea* 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).

<table>
<thead>
<tr>
<th>Character</th>
<th>Z. fuelleborni (n = 10)</th>
<th>Z. fraseri (n = 6)</th>
<th>Z. occidentis (n=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head width</td>
<td>6.1-7.2 mm</td>
<td>7.0-7.4 mm</td>
<td>7.4-7.5 mm</td>
</tr>
<tr>
<td>Hind tibia length</td>
<td>6.7-7.6 mm</td>
<td>8.5-8.9 mm</td>
<td>9.8-10.0 mm</td>
</tr>
<tr>
<td>Abdomen length</td>
<td>11.9-14.4 mm</td>
<td>12.1-13.9 mm</td>
<td>15.8-16.5 mm</td>
</tr>
<tr>
<td>Dorsal spines</td>
<td>small, not reaching over next segment (fig. 23)</td>
<td>large, reaching over next segment (fig. 24)</td>
<td>large, reaching over next segment (fig. 25)</td>
</tr>
<tr>
<td>Lateral spines present on S6-9</td>
<td>S6-9</td>
<td>S5-9</td>
<td>S5-9</td>
</tr>
<tr>
<td>Lateral spines on S8 reach to</td>
<td>apical border of S9 (fig. 18)</td>
<td>apical border of S10 (fig. 19)</td>
<td>tip of anal pyramid (fig. 20)</td>
</tr>
<tr>
<td>near</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of lateral spine on S9</td>
<td>1.4-2.0 mm</td>
<td>2.0-2.3 mm</td>
<td>4.3-4.4 mm</td>
</tr>
<tr>
<td>Length ratio lateral spine S9 : S9</td>
<td>0.67-0.9</td>
<td>1.0-1.1</td>
<td>1.9-2.3</td>
</tr>
<tr>
<td>Length ratio lateral spine S9 : anal pyramid</td>
<td>1.3-1.5</td>
<td>1.2-1.4</td>
<td>2.3-2.7</td>
</tr>
</tbody>
</table>