A remarkable new genus and species of dragonfly (Odonata: Anisoptera: Libellulidae) from Brazil and notes on its bionomics and phylogenetic affinities

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Abstract. *Orionothemis felixorioni* **n. gen., n. sp**. from Bahia state, Brazil, is described and illustrated from larvae, reared adults and an immature adult male taken in association with its possible larval shuck. This taxon exhibits remarkable features among the Odonata, such as enormous dorsal and lateral spines perpendicular to the body axis, totally fused last abdominal segments in the larva, strongly differentiated and sexually dimorphic posterior legs, and the incompletely chitinized eighth abdominal tergite of the adult. *Orionothemis* is closely related to *Elasmothemis* (Neotropical) and *Onychothemis* (South-East Asia). The larvae were collected in the abundant immersed vegetation in a clear and cool stream in the Brazilian 'planalto' (central plateau) in an area that is endangered by deforestation and irrigation. Better knowledge of the libellulid or more generally odonata larvae could help taxonomy and phylogeny of the group.

Résumé. Un nouveau genre et une nouvelle espèce remarquable de libellule (Odonata : Anisoptera : Libellulidae) du Brésil avec des notes sur sa bionomie et ses affinités phylogénétiques. *Orionothemis felixorioni* **n. gen., n. sp.** de l'état de Bahia, Brésil, est décrit et illustré sur la base de la larve, d'adultes élevés et d'un adulte immature capturé en association avec sa possible exuvie larvaire. Ce taxon possède des caractères remarquables, comme des derniers segments abdominaux complètement fusionnés et d'énormes épines dorsale et latérales perpendiculaires à l'axe du corps chez la larve, des pattes postérieures fortement différenciées et avec un fort dimorphisme sexuel ainsi qu'un huitième tergite abdominal incomplètement chitinisé chez l'adulte. *Orionothemis* est très proche du genre néotropical *Elasmothemis* et du genre indo-malais *Onychothemis*. Ces larves ont été collectées dans l'abondante végétation immergée d'une petite rivière aux eaux fraiches et claires du 'planalto' brésilien (plateau central) dans une zone mise en danger par la déforestation et l'irrigation. Une meilleure connaissance des larves de Libellulidae et plus généralement des Odonata pourrait aider à résoudre la taxonomie et la phylogénie de ce groupe.

Keywords: *Orionothemis*, *felixorioni*, Bahia State, biogeography, deforestation.

A few specimens of a strange dragonfly larva that differed strongly from those of any described genera were collected in July 2004 in a clear stream in the 'planalto' (central Brazilian plateau) in western Bahia State by one of us (NH). In October 2007, the first author collected a freshly emerged adult close to its possible exuviae and successfully reared a set of larvae, allowing for the description of a new genus and species based on larvae, males and females.

Wing terminology follows Fleck *et al.* (2003), primarily based in those of Riek & Kukalová-Peck (1984) and Nel *et al.* (1993). Abbreviations: S1–S10: abdominal segments 1–10.

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Orionothemis n. gen.

Type-species. *Orionothemis felixorioni* **n. sp.** by present designation.

Diagnosis. Ultimate stadium larva: (1) antennae very short and thin, with length approximately equal to distance between bases; (2) eyes pointed laterally and ending in two small blunt projections in dorsal view (Fig. 1); (3) occiput very large with each postero-lateral margin forming broad, ill-defined and rounded tubercle (Fig. 1); (4) distal part of labial palp with very shallow crenulations; (5) prothorax with well-developed ventral process on each side of labial mask near submentum-mentum articulation at level of mesocoxae (Fig. 2); (6) all legs very long and thin with elongated coxae and long, thin and poorly arched claws and with nearly cylindrical tibiae and femora (without distinct groove or carina) (Fig. 1); (7) lateral spines on S6 to S9, diminishing in size from S6 to S9 (Figs 1, 3); (8) lateral spines on S6 extraordinary strong, oriented perpendicular to body axis, their respective apex strongly sclerotized and sharply pointed; (9) dorsal hook on S8 extraordinarily strong and long, with apex strongly sclerotized and sharply pointed; this hook

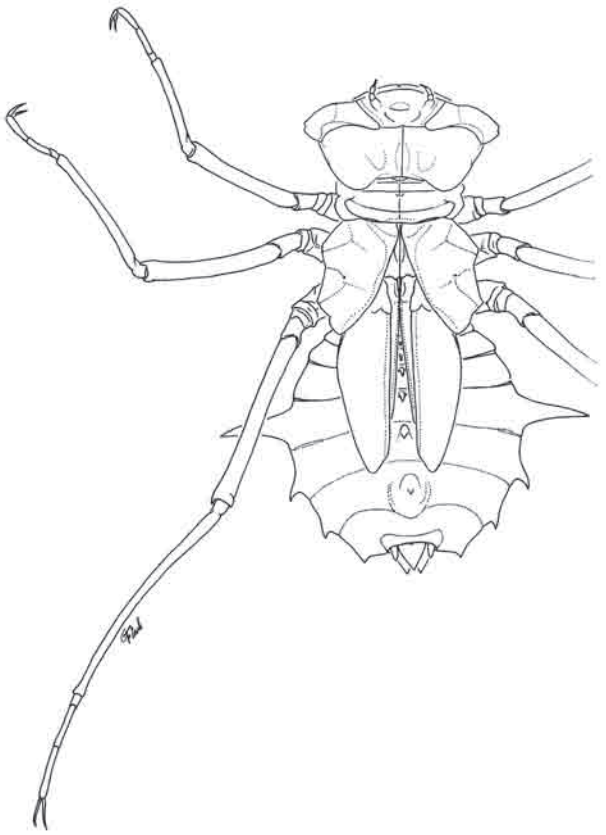
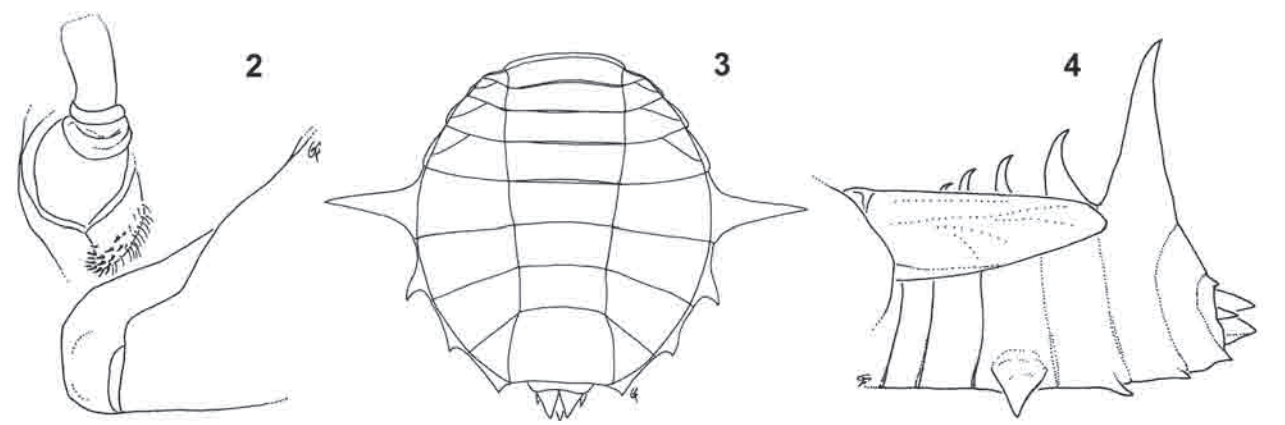


Figure 1
Orionothemis felixorioni **n. gen., n. sp**. Ultimate stadium larva in dorsal view (setae omitted).

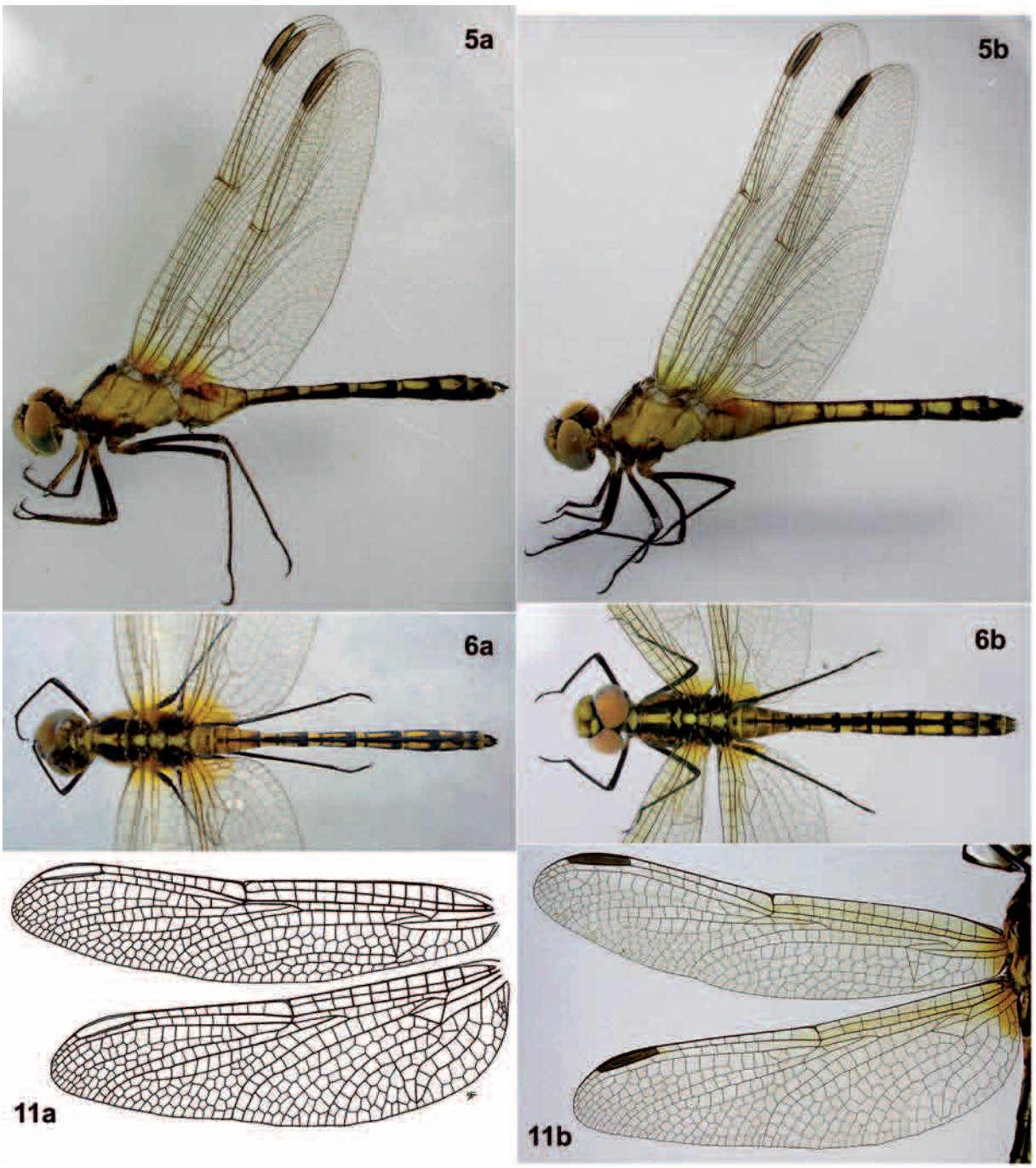
occupying entire dorsal length of segment in lateral view, and with full height of S8 greater than length of six last abdominal segments and anal pyramid taken together (Figs 4, 16); (10) five last abdominal segments completely fused together, i.e. segments strongly joined, with intersegmental membrane absent or strongly sclerotized, such that this assemblage forms a rigid box; (11) abdomen very short and large, much broader than long, including lateral spines, ratio width/length >1.3; (12) abdomen, not considering lateral spines, nearly circular in ventral view, with well developed pleurites on S6 to S8, and with elongated triangular pleurites bordering very large sternite on S9 (Fig. 3); (13) S9 partly embedded in S8 and with, in lateral view, its dorsal border strongly angled and nearly continuous with S8 dorsal hook (Fig. 4); (14) S10 small, annular and strongly embedded in S9; (15) all appendages of anal pyramid particularly short and moderately pointed (Figs. 1, 4).

Adult: (16) eyes in contact over rather short distance (Figs. 5, 6b); (17) posterior margin of eyes with small indentation, resembling corduliid condition; (18) pronotal posterior lobe poorly developed, not narrowed at base and fringed with pale long hair-like setae; (19) legs very long and thin, length of male metathoracic legs being about 80% as long as whole abdominal length (including anal appendages) (Figs. 5, 6); (20) distal part of trochanter with elliptical, bulging and strongly sclerotized structure, with finely reticulated surface, bordered by some strong setae (Figs. 7, 8); (21) femora sub-cylindrical with weak carina opposite comb; (22) male tibial comb of metathoracic leg with strong asymmetries (Figs. 7, 9) a) outer row with rather long and moderately strong spines, inner row with unusually small ones, b) outer row with about 15 setae, inner row with more than 35, consequently ratio (number of outer spines)/(number of inner spines) >2, c) proximo-distal organization differing between rows, outer row with spines diminushing in height and robustness distalward and with more than half of distal setae unusually short and weak, inner row with spines diminishing in length (but not in robustness) in basal fourth of row, then increasing in lenght and robustness until 2/5 of length of the row and increasing in robustness (but not in length) in distal 2/5 of row, d) longest spines of outer row strongly bent distalward, so acute angle between tibial axis and



Figures 2–4
Orionothemis felixorioni **n. gen., n. sp**. Ultimate stadium larva. **2,** latero-ventral view of thorax showing right ventral process close to mesocoxa, basal portion of mask indicated; **3,** abdomen in ventral view (setae omitted); **4,** abdomen (and pterotheca) in left lateral view (setae omitted).

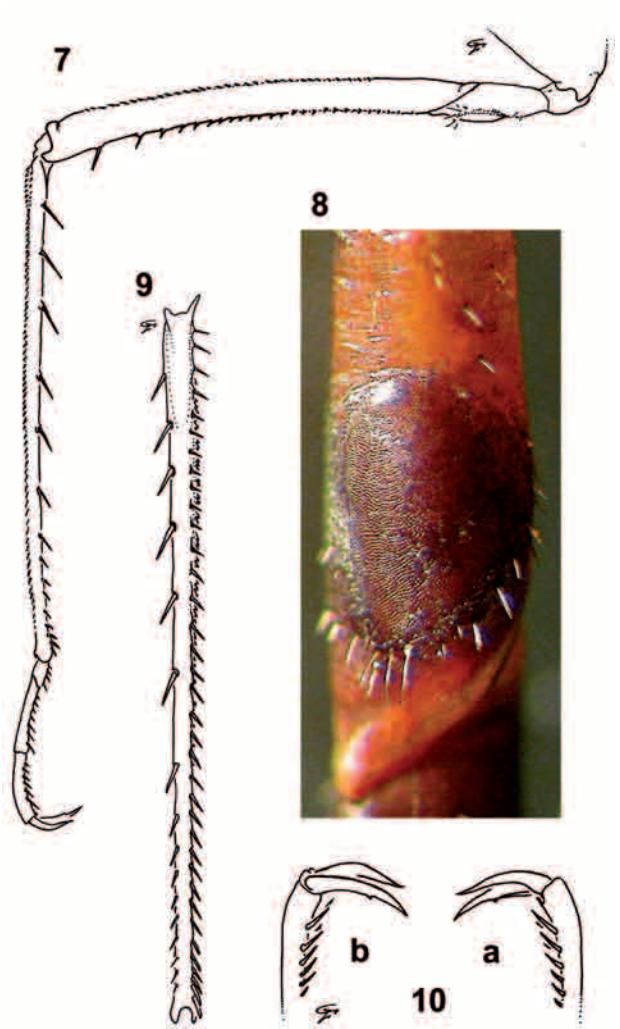
axis of spines about 30°, this angle about 45° in inner row; (23) all tarsal claws of prothoracic and mesothoracic legs and inner claws of metathoracic legs long, thin, poorly arched and bearing extremely reduced tooth; (24) outer claw of metathoracic legs without any trace of tooth, slightly shorter than inner claw in the female, and, in male, distinctly shorter than inner claw and with distinct apical inverted curvature (Fig. 10); (25) fore- and hindwing RP2 and IR2 not undulated or only with RP2 very slightly undulated (for wing venation characters see Fig. 11); (26) arculus opposite Ax2; (27) forewing last antenodal usually



Figures 5,6 and 11
Orionothemis felixorioni **n. gen., n. sp**. Adult male. **5a,** general habitus of holotype in lateral view; **6a,** head, thorax and abdomen of paratype in dorsal view; **11a,** holotype left pair of wings. Adult female. **5b,** general habitus of allotype in lateral view; **6b,** head, thorax and abdomen of paratype in dorsal view; **11b,** paratype right pair of wings in ventral view.

incomplete; (28) libellulid oblique vein very distinct and sigmoid; (29) one or two very broad cell(s) present at the level of the basal side of pterostigma between RP2 and beginning of the apical supplement; (30) hindwing cubito-anal field not strongly developed and with only two rows of cells between posterior wing margin and anal loop; (31) medio-dorsal part of S8 with structure resembling a crater with strong rounded border, covered in its centre by thin and soft membrane, and with clump of small and fine setae close to proximal part of border (Figs. 12, 13).

Characters (2), (8), (9), (11), (20), (22), (24) and (31) seem to be unique among the Odonata, and the characters (7), (10), (12) and (23) are shared with only a handful of species within the Libelluloidea or even within the Odonata.



Figures 7–10
Orionothemis felixorioni **n. gen., n. sp**. Adult male posterior leg. **7,** holotype right leg in lateral view; **8,** detail of the anterior face of the coxa showing the strongly sclerotized bulging formation covered by a fine reticulation and distally bordered by some rather strong setae; **9,** paratype anterior face of right tibia; 10, paratype tarsal claws of the right leg; a, external view; b, opposite view.

Remarks. Conditions (9) and (31) are very different and at first sight not related since one is a very strongly erected and heavily sclerotized hook in the larva and the other is a crater-like formation with a non-sclerotized depressed part in the adults despite of their obviously morphological correlation. At emergence, a large part of the larval dorsal hook is still visible and well developed in the very young imago (Fig. 14). The complete and rapid suppression of this protuberance in the fully developed adult a few minutes later leads to the unique weakly sclerotized structure described above.

The three enormous abdominal spines (the two laterals forming an angle of about 100° with the dorsal) and the merged segments reinforcing the rigidity of the abdomen could represent a passive system of defense against predators. Abdominal spines have been shown to differ slightly in *Leucorrhinia* with fish predator presence (Johansson & Wahlström 2002).

Etymology. The name is derived from Félix Orion Fleck, son of the first author, and the suffix "*themis*" commonly used in Libelluloid taxonomy. Gender masculine.

Orionothemis felixorioni n. sp. (Figs. 1–18)

Material. **Holotype** ♂: Brazil, Bahia, Luis Eduardo Magalhães municipality, Rio das Fêmeas (12° 29' S, 45° 53' W, at ca. 750 m above msl), Highway BR 020 between Luis Eduardo Magalhães and Roda Velha (Bahia, Brazil), 01.X.2007; exuviae dry stored and corresponding reared male adult stored in 92% ethanol (emerged 19.X.2007); **allotype** ♀: same data, but reared adult emerged 17.XI.07 and preserved in ethanol one day after emergence; *paratypes*: one ♂ and its possible exuviae, one ♀ (emerged 29.X.2007, stored in ethanol three days after emergence); ten ultimate instar larvae (F-0), all 01.X.2007, same data as the holotype (all G. Fleck leg.); two larvae (one F-1 and one F-0), 2 and 3.VII.2004, same data as the holotype (N. Hamada, M. Moraes Lima and R.S. Leite leg.).

All material except following is deposited in Instituto Nacional de Pesquisas da Amazônia, Manaus: two F-0 larvae deposited at the Museu Integrado de Roraima, Boa Vista; and two F-0 larvae at Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro.

Etymology. Named after Félix Orion Fleck, son of the first author.

Descriptions.

Male holotype. Exuviae of ultimate stadium larva. Body nearly uniformly light brown, irregularly covered with long and rather strong setae which are more abundant at frontal margin, between occipital muscle insertions, at lateral part of the prothoracic episternum, on legs, and at sides of the abdomen (Figs. 15, 16); body covered by small and rather strong spine-like setae, except legs, three last abdominal segments and anal pyramid, the pleurites and sternite of S7 and sternites of the remaining abdominal segments; mask large compared to body dimension, reaching the end of mesocoxae.

Antennae with seven segments; mask with 11 mental setae on each side, the eight most proximal ones nearly perfectly aligned and perpendicular to body axis, the three most lateral and distal setae well aligned and at right angle to more proximal ones; right labial palp with seven, left labial palp with eight palpal setae; external margin of palps with three (left) and two (right) proximal spine-like setae continued distally by row of long setae ending at two-third of distance between palp articulation and base of movable hook; distal margin of palps with eleven very shallow crenulations, most bearing three to five *setae raptores* each.

Thoracic pronotal shield rather well developed, with posterior margin rounded; propleuron with epimeron and episternum distinctly separated and with episternum well developed; wing pads with parallel costal margins and reaching anterior margin of S8.

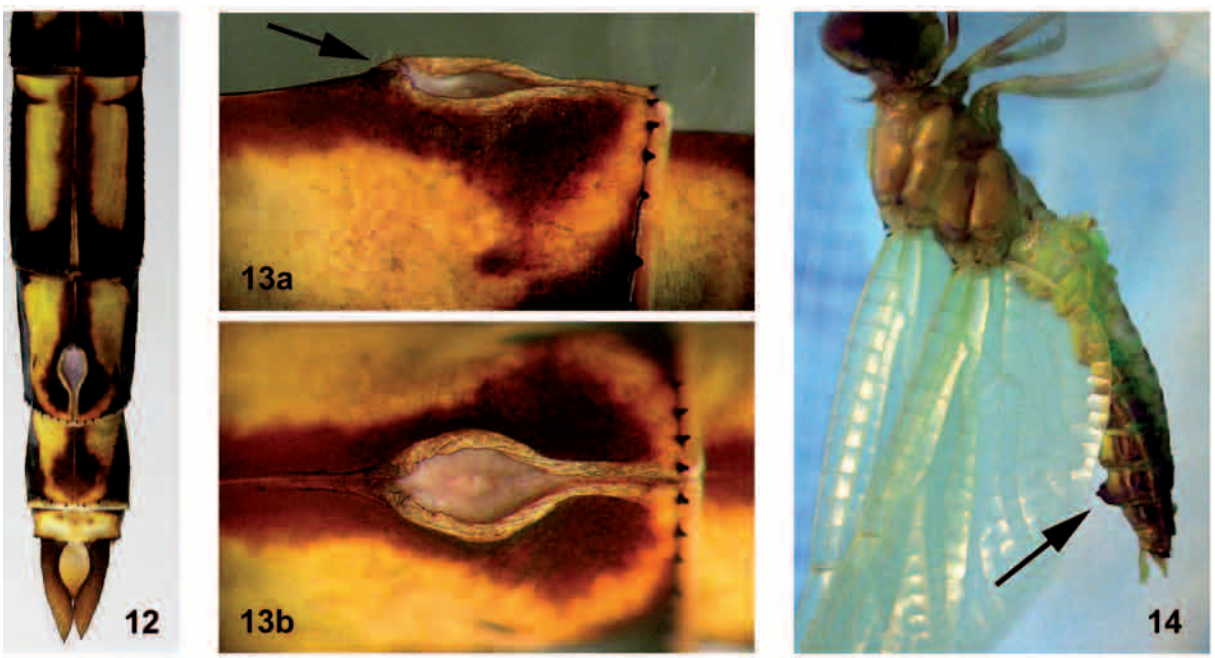
Abdominal dorsal hooks present on S3 to S8; all dorsal hooks very well developed dorso-ventrally with basal two-third straight and apex progressively directed backward (Fig. 4); S6–S9 lateral spines slightly directed downward; S10 with minute posterior indentation in medio-dorsal part; last five abdominal segments without antepleurite (Fig. 3); dorsal part of epiproct rounded in cross-section.

Corresponding reared adult. Medium-sized dragonfly; general body coloration yellow and brown to blackish, patterned as indicated in Figs. 5a, 6a and 12 and with mesothoracic episternal brownish stripes with distinct green metallic reflections.

Median lobe of labium light brown; palpi with lateral part yellowish becoming progressively light brown toward inner margin; labrum yellowish with brown frame along inferior margin and with median brown spot in contact with clypeus; clypeus yellowish; frons yellowish with brownish areas near eyes margins and small brownish spot in front of median ocellus; vertex simple, rounded.

Wings elongated with rather open venation and with basal orange spot (for wing characters, see Figs. 5a, 6a, 11a); sectors of arculus united over rather long distance, hypertriangles and hindwing discoidal triangles not crossed; no supplementary cross-vein in submedian spaces or above bridges; fore- and hindwing Mspl not strongly developed; first cross-vein beneath pterostigma in fore- and hindwing distinctly more oblique than others; base of pseudo-IR1 in fore- and hindwing at mid-longitudinal length of pterostigma; forewing post-discoidal area with three rows of cells from MAb to level of seventh antenodal cross-vein (Ax7), followed distally by two rows of cells and again with three rows of cells from level of base of RP3/4 nearly to wing margin; forewings with 11 and a half antenodal cross-veins (Ax), discoidal triangle two-celled, subtriangle three-celled and MA and MP almost parallel; pterostigmata long; hindwing with nine antenodal cross-veins.

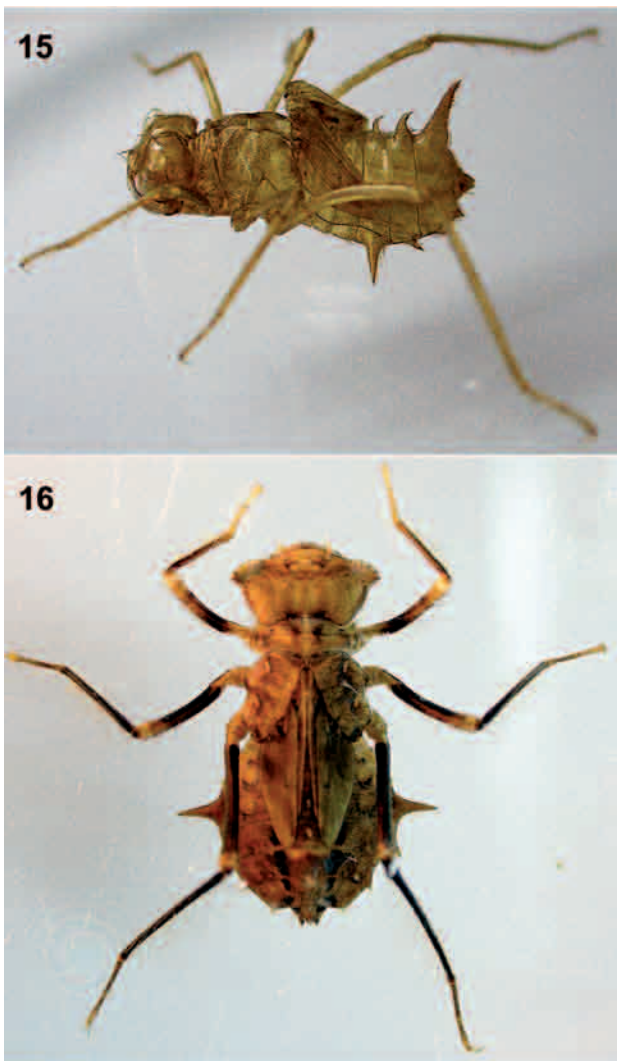
Abdomen dorso-ventrally swollen at base and slightly widened laterally, at S4 strongly constricted and again progressively expanded dorso-ventrally and laterally from S5 to S8 (Figs. 5a, 6a); S3 and S4 without supplementary transverse carina; median 2/3 of S9 with moderately developed longitudinal lateral carina on each side; genital lamina anterior broad, slightly higher than genital lobe but not plate-like, and with



Figures 12–14
Orionothemis felixorioni **n. gen., n. sp**. Adult abdomen. **12,** male last segments in dorsal view (paratype). Note the presence of a circular non-sclerotized formation on segment 8; **13,** structure resembling a crater on the dorsal part of segment 8; a, lateral view; b, dorsal view. Note the strong rounded border, and in the centre of this crater-like structure a thin and soft unpigmented membrane. The arrow indicates a clump of small and fine setae close to the proximal part of the border; **14,** freshly emerged adult male with the abdomen still not fully expanded (holotype). The arrow indicates a remnant of the larval abdominal segment 8 dorsal hook (beginning of the resorption).

posterior margin furnished with long and strong setae (Fig. 17); genital hamulus strongly developed, distinctly higher than lamina anterior, with broad basal part and longer and thinner hook-like distal part bearing at apex a short and strong spine directed toward lamina anterior (Fig. 17); genital lobes weak; penis without flagellae and with weakly developed posterior lobe *sensu* Santos (1945) (= lateral lobes *sensu* Westfall 1988); anal appendages short, slightly shorter than S9+S10 taken together; superior appendages (cerci) with rather broad distal half, shaped as illustrated (Figs. 18a, 18b), and with concave inferior margin bearing nine minute spines; inferior appendage (epiproct) short and wide, slightly bilobed at apex, with convex lateral margins (ventral view) (Fig. 18a), and bearing two small apical up-turned spines at apex (one of each terminal lobe) (Fig. 18c).

Dimensions (mm). Exuviae total length 15.7, width of head (between eyes) 6.1, width of abdomen (including lateral spines) 11.2, height of S8 (including dorsal hook) 6.8; adult: total length (including anal appendages) 42.3, hindwing length 32.0.



Figures 15–16
Orionothemis felixorioni **n. gen., n. sp**. Ultimate larval stadium. **15,** exuviae in dorso-lateral view (holotype); **16,** larva in dorsal view (paratype).

Female allotype similar to holotype but differing as follows.

Exuviae of ultimate stadium larva. Except a slightly larger body, general habitus and color nearly identical to those of holotype; mask with 12 mental setae on each side; right labial palps with eight palpal setae; most crenulations of palpal distal margin bearing each three or four *setae raptores*; cerci very small, distinctly smaller than those of the male holotype; epiproct triangular in cross-section.

Corresponding reared adult. Slightly more robust than male holotype, yellow markings slightly more extensive (Figs. 5b, 6b).

Hind leg very slightly shorter; distal femoral spines of the outer row stronger and longer; three ultimate distal femoral spines of inner row distinctly better developed, spine-like (in holotype male most spines of internal row appear as small sclerotized blunt tubercles); all femoral asymmetries present but slightly less marked; forewings with 12 and a half antenodal cross-veins.

Abdomen stouter and not strongly constricted dorso-ventrally at S4; cerci short; vulvar lamina weakly developed, appears as rim bordering the genital pore and bearing blunt medial triangular lug directed toward the front; S9 gonapophyses minute, very close to sagittal line and placed on a small, whitish, poorly sclerotized area; S9 sternal plate without carina, distally slightly down curved, with distal border rounded and slightly overlapping S10.

Dimensions (mm). Exuviae total length 16.0, width of head (between eyes) 6.3, width of abdomen (including lateral spines) 12.1, height of S8 (including dorsal hook) 6.6; adult: total length (including anal appendages) 42.5, hindwing length 34.0.

Variations in other specimens. Larvae. General coloration variable, from greenish to dark brown, with more sombre areas most frequently patterned as in Fig. 16; number of mental setae usually 11 or 12, exceptionally 10 (left row of one specimen) or 13 (right row of one specimen), the most central seta of one or both rows sometimes very small; number of palpal setae usually 8 or 9, exceptionally 10 (left palp of one specimen). **Adults.** ♂ paratype: right hindwing with eight antenodal cross-veins; ♀ paratype (S5 not fully developed): yellow areas of mesothorax and first abdominal segments slightly obscured (Fig. 6b); left forewing with 12 antenodal cross-veins, right forewing with 13 antenodal cross-veins, but the two parts of the last distal antenodal cross-veins not well aligned (Fig. 11b); area between costal margin and RP between base and nodus tinged with yellow. Difference in color observed in the two female specimens could be due to their different age. Allotype was placed in ethanol one day after emergence, whereas the other female was placed in alcohol three days after emergence.

Dimensions (in mm). Larvae (5 ♂ and 5 ♀): total length 15.2–16.2 (♂), 15.9–16.7 (♀), width of head (between eyes) 6.1–6.2 (♂), 6.3-6.4 (♀), width of abdomen (including lateral spines) 10.7–11.2 (♂), 11.1–11.9 (♀); possible exuviae of paratype adult ♂: total length 15.5, width of head 6.2, width of abdomen (including lateral spines) 10.7; paratype ♀ exuviae: total length 16.8, width of head 6.5, width of abdomen (including lateral spines) 11.4 ; paratype adult ♂: total length (including anal appendages) 43.0, hindwing length 31.5; paratype adult ♀: total length (including anal appendages) 39.5, hindwing length 34.0.

Discussion

Study area and bionomics

The type locality, Rio das Fêmeas stream, belongs to the sub-hydrographic basin of Rio Grande, a tributary on the left bank of the middle stretch of Rio São Francisco in the western portion of Bahia State. This area is covered mainly by 'cerrado' (central Brazilian savanna) vegetation and the regional topography is dominated by the Chapadão Central, a plateau located at 700–900 m. Annual precipitation in this area averages 1100 mm, with a rainy season occurring between October and April (Andrade *et al*. 2002)

Ongoing agroindustrial enterprises since the 1970's have resulted in sediment transport and silting of streams and rivers, affecting the recharge of aquifers and watercourses, and leaving the soil vulnerable to wind and water erosion (Andrade *et al*. 2002).

Despite the fact that the Rio das Fêmeas is located in a region that is under severe anthropogenic pressure, it still shows rather high dragonfly diversity. Only few dragonfly adults were seen and collected, but surveys of a few meters along the stream yielded many interesting larvae. Among the collected material, two new species of *Aeschnosoma* were recognized. The other collected material are: *Phyllogomphoides* (two spp.), *Castoraeschna* (two spp.), *Aeschnosoma marizae* Santos 1981, *Navicordulia* (one sp.), *Diastatops* (two spp.), *Elasmothemis* (two spp.), *Idiataphe batesi* (Ris 1913), *Brechmorhoga, Elga, Erythrodiplax*, *Gynothemis*, *Lepthemis* and ?*Macrothemis* (one sp. each). This stream also had two unique Simuliidae (Diptera, Nematocera), one undescribed species in the subgenus *Simulium* (*Ectemnaspis*) and the other, *S. cerradense* Coscarón, Cerqueira, Sato & La Salvia, described in 1992, was not collected in any other stream in the region, despite the sampling effort made by N.H.

The high diversity and unique fauna observed until now in this stream indicates that preservation actions should be urgently undertaken in this region, which is unprotected by any conservation units. Additional surveys should be conducted to obtain a complete inventory of the aquatic fauna of this area, which appears to contain endemic species of aquatic insect groups.

Taxonomic notes and phylogenetic affinities

In Borror's work (1945), the new genus keys with *Dythemis* Hagen, 1861 (which at that time also included the genus *Elasmothemis* Westfall, 1988). It falls 'between' *Dythemis* and *Elasmothemis* in the more recent key of Garrison *et al.* (2006).

Orionothemis **n. gen.** strongly differs from the genus *Dythemis* (illustrations and information on larvae and adults of *Dythemis* are available in Westfall 1988; Needham *et al.* 2000; Garrison *et al*. 2006).

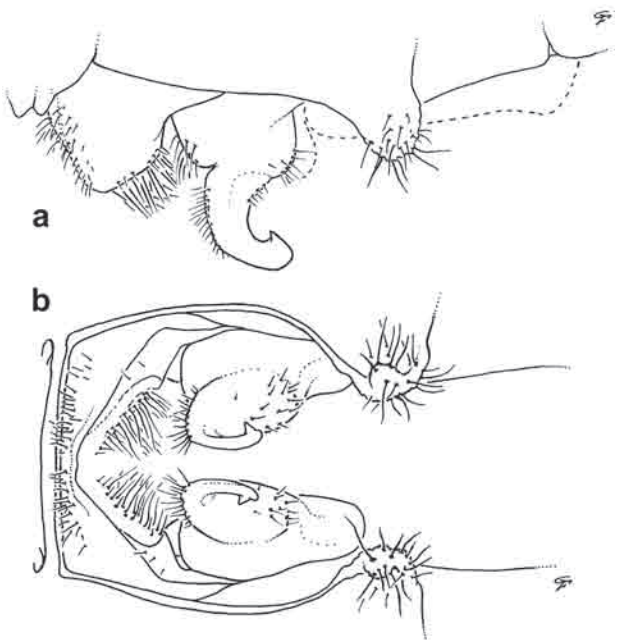


Figure 17
Orionothemis felixorioni **n. gen., n. sp**. Male secondary copulatory apparatus (paratype). a, left lateral view, the dashed line indicates the placement of *vesica spermalis*; b, same in ventral view (*vesica spermalis* not figured for greater clarity of the drawing).

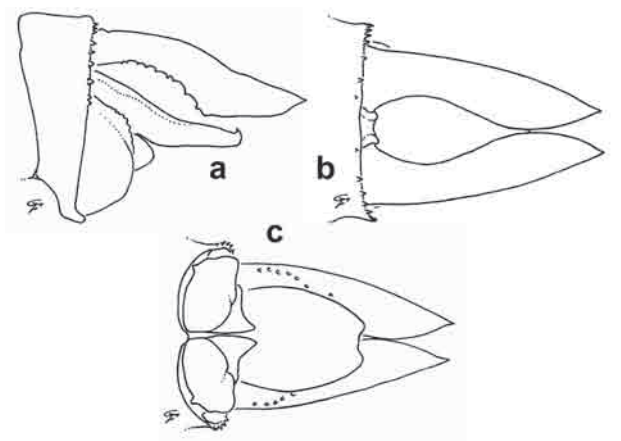


Figure 18
Male anal appendages (paratype). a, lateral view; b, dorsal view; c, ventral view.

Larvae are very different and none of the characters listed in the generic diagnosis above is shared by these two genera, except perhaps character (14) (character (4): the crenulations are not well marked in *Dythemis*, nevertheless they are much more distinct than those of *Orionothemis*). Adults also differ and genera do not share the characters (17), (19), (20), (21), (22), (23), (24), (25), (29), (30) and (31). Furthermore, eyes of *Dythemis*, though in contact over a moderately short distance, are in contact over a distinctly longer distance than for *Orionothemis*; pronotal posterior lobe, like *Orionothemis*, is low, but in contrast with this genus, it seems to be devoid of the fringe of numerous long hair-like setae; libellulid reversed oblique vein is distinctly less marked. *Dythemis* also has two rows of cells between IR2 and Rspl (one row in *Orionothemis*), a distinctly better-developed anal loop with a distinctly angled midrib, a male anterior lamina distinctly lower than genital lobes, genital lobes as high as hamuli, a male distal part of the abdomen not widened laterally, and male anal appendages distinctly thinner and less robustly built than those of *Orionothemis*.

Orionothemis differs from the genus *Elasmothemis* by numerous features (illustrations and information on larvae and adults of *Elasmothemis* available in Westfall 1988, Pujol-Luz 1990 and Garrison *et al*. 2006). The characters (2), (6), (7), (8), (9), (11), (15), (17), (17), (20), (21), (22), (23), (24), (25), (29), (30) and (31) of the generic diagnosis of *Orionothemis* are absent in *Elasmothemis*. Eyes of *Elasmothemis*, like those of *Dythemis*, are in contact over a distinctly longer distance; the abdomen of the larva (without considering lateral spines) is thick and short, but distinctly more elongated; S9 and S10 are also respectively embedded in S8 and S10, but not as strongly as those of *Orionothemis*. Larva of *Elasmothemis* is more strongly built, the body is somewhat more flattened, the labial palps less developed dorso-ventrally and the legs shorter and stouter. Adult of *Elasmothemis*, contrary to *Orionothemis*, has generally two rows of cells between IR2 and Rspl, a distinctly better-developed anal loop with a distinctly angled midrib, a better-developed plate-like lamina anterior, male genital hamulus with thinner terminal part distinctly shorter than wider basal part, last segment of penis with enormous posterior lobe (*sensu* Santos 1945) covering long flagellae (flagellae apparently reduced to short expensions in *E. williamsoni*, Fleck pers. obs.), and terminal segments of abdomen not widened dorso-ventrally.

The characters (2), (6), (7), (8), (9), (11), (15), (17), (17), (20), (21), (22), (23), (24), (25), (29), (30) and (31) of the generic diagnosis of *Orionothemis* are also absent in *Onychothemis* a closely related genus (Fleck *et al*. unpublished), see below.

The genera *Orionothemis* and *Elasmothemis* share the characters (1), (5), (10) and (14), considered as derived, in the above-mentioned generic diagnosis. The larvae of these two genera also have abdominal lateral spines on S6 to S9. This character and character (10) are clearly derived, and these two extraordinary characters are shared only by a handful of species belonging to a small monophyletic group within the Libellulidae (Fleck *et al*., unpublished). The larvae of the two genera also have a strongly developed occiput with two postero-lateral protuberances and a wide and short abdomen, and ventral tooth of claw of adult legs is at most weakly developed. These characters are then considered as synapomorphies since they are clearly not in the libellulid ground plan, and not in the ground plan of the libellulid related groups (even sometimes totally absent [character 10]): Urothemistidae, 'Corduliidae', Macromiidae, Synthemistidae. They are even absent of the ground plan of the Cavilabiata sensu Bechly (1996) (= Libelluloidea *sensu* Carle 1995); for example larval lateral abdominal spines on S6-S9 are only found in the 'Corduliidae' genera *Lauromacomia* and *Rialla* within the Cavilabiata non-Libellulidae and represent a clear convergence with the present studied group of Libellulidae.

All these characters are also shared (synapomorphies) by the Asian libellulid genus *Onychothemis* Brauer, 1868 and the general appearance of the larva of *Onychothemis* is so close to that of *Elasmothemis* that, at first glance, they could be attributed to the same genus (Fleck pers. obs.). Thus, we suppose that the genera *Orionothemis*, *Elasmothemis* and *Onychothemis* constitute a monophyletic group, nevertheless the phylogenetic affinities within this group are not clear and we prefer to consider their relationships unresolved for the present. The larva of the genus *Zygonyx* Hagen 1867 possesses small antennae and a fusion of the two last abdominal segments (Fleck *et al*. unpublished). As these characters are considered to be derived and shared with *Orionothemis*, *Elasmothemis* and *Onychothemis*. We consider the genus *Zygonyx* as a close sister group of the clade (*Orionothemis* & *Elasmothemis* & *Onychothemis*). Larva of *Dythemis* does not present these conditions, and *Dythemis* might constitute a more distant sister group of (*Zygonyx* (*Orionothemis* & *Elasmothemis* & *Onychothemis*)) or even might not be related to this group.

Remarks

Character (22b) as expressed in the generic diagnosis is not present in *Elasmothemis*, nevertheless a slight asymmetry seems to be present at least in some

Elasmothemis species. In a set of *E. cannacrioides* from Roraima state (Brazil), outer row of spines has 14-16 setae whereas the inner one has 23-25. The asymmetry between the numbers of spines of the outer and inner tibial combs could constitute a potential synapomorphy of the two genera. This character should be checked in the other species of *Elasmothemis*, and a phylogeny of the genus should be attempted to validate or not this potential synapomorphy between the genera *Elasmothemis* and *Orionothemis*.

An 'anterior lamina of male much thickened, plate-like and higher than genital lobe' is found in some other genera that may be related (in 'Trithemistinae' like *Celebothemis*, some *Brechmorhoga*, *Macrothemis* and *Gynothemis*, any *Trithemis* and *Zygonyx*, etc.) or not (*Misagria*, some *Dasythemis*, some *Oligoclada*, *Raphismia*, etc.) to *Elasmothemis*. Consequently, an anterior lamina distinctly higher than the genital lobes as encountered in *Elasmothemis* and slightly higher than genital lobes as encountered in *Orionothemis* should not be considered as a putative synapomorphy between these two genera.

Importance of larvae in taxonomy and phylogeny of Odonata

Westfall (1988) established the genus *Elasmothemis* on the basis of strong differences in the abdominal spines with some larvae of *Dythemis*. He listed a set of characters for the adult generic diagnosis. Nevertheless, none of these characters is a unique character of the genus (contrary to the clear cut larval characters), and each character is encountered in numerous other genera. Many of these adult characters are even variable within the genus *Elasmothemis*, as indicated by Westfall himself (see p. 422). Thus, the list of diagnostic characters should be regarded as a combination of characters allowing the differential separation between the genera *Dythemis* and *Elasmothemis*. Many females of other genera fall into the adult diagnosis proposed by Westfall, and also other genera for which the structure of male penis is unknown fall also in this diagnosis (for example the possible related genus *Celebothemis*). Westfall (1988: 420, 421, 425) following Buchholz (unpublished) planned first to place the aberrant species *Dythemis williamsoni* Ris 1919 in a monotypic genus because the adult of this species differs in several respects from other members placed by the author in *Elasmothemis*. Nevertheless, since the larva of *williamsoni*, is so similar to that of *cannacrioides* Westfall finally decided to place also *Dythemis williamsoni* Ris 1919 in the genus *Elasmothemis*.

The work of Westfall (1988), the present study for which the phylogenetic affinities are established on larval characters, and some other recent studies (Fleck 2001, 2004; Fleck & Nel 2003; Fleck & Legrand 2006; Fleck & Orr 2006; Fleck *et al*. 2008) suggest that the imaginal characters, and in particular wing venation, are much more often prone to homoplasious evolution than formerly supposed. Taxonomic or systematic works predominantly based on wing venation (and adult characters) might be in need of substantial revision, at least within the Libellulidae. The larvae, however, seem to maintain their general appearance despite ecological and imaginal diversification (Fleck 2004; Fleck & Nel 2003; Fleck & Orr 2006; Fleck *et al*. 2008; Legrand & Fleck 2005). It is obvious that the imaginal phase experiences most of the evolutionary change and it can be speculated that it is mostly this ontogenetic phase that drives speciation phenomena (see Fleck 2004; Fleck & Orr 2006; Fleck *et al*. 2008). From this it also follows that larval characters preserve more of the phylogenetic signal relevant to systematics within the Libellulidae and potentially in other families as well (Fleck 2001, 2004; Fleck & Nel 2003; Fleck *et al*. 2008).

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