PHYLOGENETIC RELATIONSHIPS OF PRISCAGRION ZHOU & WILSON, 2001, WITH A DESCRIPTION OF TEINOPODAGRION CROIZATI SPEC. NOV. FROM ECUADOR (ZYGOPTERA: MEGAPODAGRIONIDAE)

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The generic characters of *Priscagrion Zhou & Wilson*, 2001 are reviewed. It is shown that this genus is closely related with the Australo-Papuan 'Argiolestinae' and with the South American 'Megapodagrion-complex'. Hence, a Pacific origin for the whole group seems probable. *Teinopodagrin croizati* sp. n. (holotype &: Ecuador, Pichincha prov., 7.3 km W of Alluriquin, at Hotel Tinalandia, 20-VII-1977; deposited at MIZA, Maracay) is described and illustrated, and its position within the genus is outlined.

INTRODUCTION

The known subfamily arrangements of the megapodagrionid genera are based on wing venation (RACENIS, 1959; DAVIES & TOBIN, 1984; BRIDGES, 1994). However, already LIEFTINCK (1965: 231) stated, that "features of the venation do not [...] adequately reflect relationships" within the Megapodagrionidae. NEL et al. (1996: p. 205) rightly warned of the "presence of numerous homoplasies in the wing characters" of the Megapodagrionidae, and suggested that "a phylogenetic study of that family [...] should integrate the genital and the body characters". KENNEDY (1920) was perhaps the first to consider the penile characters. He also stated (p. 20), that "probably the major groups [within the Zygoptera] can be defined in larval characters when these are better known". Careful consideration of as many features as possible, of adults and larvae (as done by THEISCHINGER, 1998) is, therefore, indispensable if a natural suprageneric classification of the Megapodagrionidae has hopefully to

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emerge, someday in the future. On penile characters, DE MARMELS (2001) showed, that the closest relative of the South American 'Megapodagrion-complex' is a group of Australo-Papuan genera ('Argiolestinae' s. str.), a view which seemingly leads the two largest 'subfamilies' to collapse into one, the Megapodagrioninae, the limits of which are still unknown. In the present study, the recently described genus *Priscagrion* Zhou & Wilson, from South China, is evaluated on the basis of the information forwarded by its authors, who do not, in my opinion, adequately exploit the richness of their own data.

Since the conclusion of the work of DE MARMELS (2001), a new species of *Teinopodagrion* De Marmels from Ecuador has been discovered. This is described hereafter, following the terminology and methods outlined in the said publication.

NOTES ON PRISCAGRION ZHOU & WILSON, 2001

The authors characterize their new genus on the basis of four wing venation features and the "simple" penile organ. Since they presume the new genus is referable to the 'Megapodagrioninae' — apparently solely so on the evidence of the anal bridge configuration, this in itself an unreliable feature in megapodagrionid classification — they refrain from comparing *Priscagrion* with other genera from around the world that are supposedly not members of the 'Megapodagrioninae', and do not define the actual phylogenetic position of this genus. The "complete anal bridge" is, in this context, doubtless a plesiomorphy. The presence of accessory antenodal cross-veins in the costal space is considered "archaic" by the authors, but NEL et al. (1996) list that character as apomorphous in the Megapodagrionidae. The "elongate discal cell" is apomorphous, as are the numerous accessory longitudinal veins between IR1 and RP2. Contrary to the claim by the authors (under *Priscagrion pinheyi*, p. 121) that the pterostigma is "unbraced", their illustrations clearly show a braced pterostigma, in both species, which

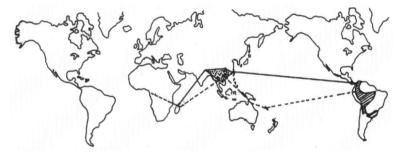


Fig. 1. Character geography: distribution of two penile character states in the Megapodagrionidae (localities connected by tracks). Broken line: internal fold enlarged; solid line: apical segment deeply split into two cornua; hatched area: range of Megapodagrion-complex, including Archaeopodagrion Kennedy and Philogenia Selys; stippled area: range of Asian genera Lestomima May, Mesopodagrion MacLachlan, Philosina Ris and Priscagrion Zhou & Wilson. Both tracks have trans-Pacific and trans-Indian Ocean baselines (CRAW et al., 1999). — [Modified from DE MARMELS, 2001].

is a plesiomorphous feature. The curious "stout projection" on the outer margin near the tip of the male cercus is not further discussed, and one wonders whether this "projection" may be homologous with the spine present in Tatocnemis robinsoni Schmidt, from Madagascar, or with that found in the genus Austroargiolestes Kennedy. The elongate ovipositor in female Priscagrion, an apomorphy, might have merited inclusion in the generic diagnosis. Unfortunately, the striking specializations of the penile organ were barely recognized by the authors. To dub the penis "simple", and hence "archaic", is perhaps a bit simplistic. The illustrations (figs 6 and 13) forwarded by the authors show that, from below the "simple" tip (= apical segment), a highly specialized internal fold protrudes, particularly so in P. kiautai. Surprisingly, this seemingly chitinized and grossly overdeveloped structure, which ends in a flagellumlike process, is not mentioned either in the generic diagnosis or in the species descriptions. Yet it is this highly apomorphous structure, which is the key to a correct phylogenetic placement of the genus *Priscagrion*. Fingering through LIEFTINCK's (1975) paper on the dragonflies of New Caledonia, one is struck by his excellent figure 3, which shows the penis of *Podopteryx selysii* (Förster). In *Podopteryx*, the apical segment has become as totally reduced as the internal fold has become hypertrophied and modified. With Podopteryx as the reference point, it is easy to interpret the "simple" tip of the penis in Priscagrion as an incipient state of reduction, rather than a primarily simple ("archaic") condition. Due to the widely different style of the illustrations provided by ZHOU & WILSON (2001) for each of the two Priscagrion species, it is not clear how the internal fold of P. pinheyi exactly looks like. At any rate, a large, membranous (?) structure with perhaps a short flagellum may seem an adequate interpretation of figure 13. In consequence, the closest relatives of Priscagrion appear to be the Australo-Papuan 'Argiolestinae', including Argiolestes Selys s. str., Caledargiolestes Kennedy, Caledopteryx Kennedy, Podopteryx and Trineuragrion Ris, together with the South American 'Megapodagrion-complex', with Megapodagrion Selys, Allopodagrion Förster, and Teinopodagrion De Marmels (DE MARMELS, 2001). The latter author includes in that study a map (his fig. 234), showing the geographic distribution of two penile characters in the Megapodagrionidae. This map is reproduced here and modified to incorporate Priscagrion (Fig. 1). The hypertrophied internal penis fold present in Priscagrion corroborates the transpacific track for this highly apomorphous character and, hence, a probable Pacific origin of this group of Megapodagrionidae.

TEINOPODAGRION CROIZATI SP. NOV.

Figures 2-6

Material. — Holotype &: ECUADOR: Pichincha prov., 7.3 km W of Alluriquin, at Hotel Tinalandia, 20-VII-1977, D. Paulson leg.; deposited at MIZA (No 16711), Maracay, Venezuela.

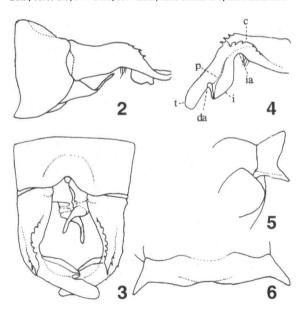
Etymology. — The species is dedicated to the great biologist and father of modern biogeography, Leon Croizat.

Methods and terminology used in description are those of DE MARMELS (2001).

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MALE (holotype). - Face black with inferior pale crossband recuced to a dot on each gena; ferruginous ocellar mark about half as wide as lateral ocellus is long; rest of head black; first antennal segment as long as second; occipital tubercles strongly prominent, pointed. Lateral processes of pronotal hind lobe long, triangular, pointed (Fig. 6); blue area of mature colouration on mesepisternum not yet defined, because of young age; black mesepimeral stripe wedge-shaped, reaching to about half-length of humeral suture. Wings hyaline, pterostigma pale; forewing (FW) with 15 (14 in right wing) postnodal cross-veins (px), 14 (13) in hindwing (HW); IR1 branching at ninth px in FW, at eighth px in HW; RP2 originating near seventh px in FW, near sixth in HW. Supplementary sectors reaching basalwards at most to last px before pterostigma. FW with four, HW with three cells in discal field. Terminal fold of penis convex. Crest of cercus low, almost indistinguishable in lateral view (Fig. 2); external spines small, weak; terminal branch not broadening apically; subapical internal keel absent; internal angle between proximal and distal portion of cercus deeply excavated and opening at less than 90°; internal plate weakly developed, not projecting caudad; internal branch hollowed-out basally at distal angle. Distal process of paraprocts slender, spindle-shaped (Figs 2-3).

Me a surements (in mm). — Total length (including caudal appendages) 37.4; abdomen (incl. app.) 28.3; cerci 1.0; FW 24.6; HW 22.9; hind femur 6.1; hind tibia 6.9.



Figs 2-6. Diagnostic structures of *Teinopodagrion croizati* (holotype 3): (2) abdominal segment 10 with caudal appendages, left lateral view; — (3) same, dorsal view; — (4) left cercus, right dorso-internal view (c = crest, da = distal angle, I = internal branch, ia = internal angle, p = internal plate, t = terminal branch); — (5) pronotal hind lobe, left lateral view; — (6) same, dorsal view.

FEMALE and LARVA unknown.

HABITAT. — "Forest stream" (collector's note).

DISTRIBUTION. — Known only from the type locality, in northern central Ecuador (Fig. 7).

REMARKS. — T. croizati keys out to T. macropus (Selys) in DE MARMELS (2001). It differs from T. macropus by the more slender cerci and paraprocts. The internal angle of the cerci is yet more acute in the new species. The cercal crest in T. macropus is strongly developed and elevated in a semicircle, but low, almost indistinguishable in lateral view, in T. croizati.

On the basis of its morphological features, T.

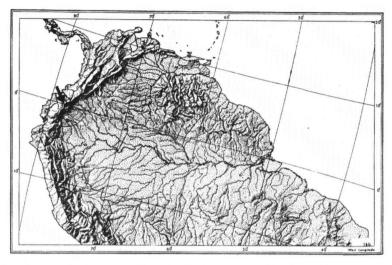


Fig. 7. Northwestern South America with type locality in northwestern Ecuador of *Teinopodagrion croizati* sp. n. – [Map courtesy of Dr O.S. Flint, Smithsonian Institution, Washington, D.C.]

croizati falls within the northern species group, hence corroborating the biogeographic and evolutionary scenario outlined by DE MARMELS (2001).

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