

**THE LARVA OF *ALLOPETALIA PUSTULOSA* SELYS, 1873
(ANISOPTERA: AESHNIDAE), WITH NOTES ON AESHNOID
EVOLUTION AND BIOGEOGRAPHY**

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Received May 7, 1999 / Reviewed and Accepted October 12, 1999

The larva is described and illustrated from four ultimate instar exuviae (2 ? reared) and from a younger larva, all from Venezuela. Main characters are a pointed epiproct and spinous mesial carinae of paraprocts. There is some general similarity with larvae of *Boyeria* McL., but the latter have angled occipital lobes, longer labium and, in some species, a bifid epiproct. Penis is strikingly similar in *Allopetalia* and *Boyeria*, the "cornua" coming closer to those found in *Gomphaeschna* Sel. than to the "flagella" as found in the brachytrine *Spinaeschna* Theisch. and in the austropetaliine *Rheopetalia* Carle. – The "pryeri-group" of *Oligoaeschna* Sel. is adscribed to Gomphaeschnata LOHMANN (1996, *Ent. Z., Essen* 106: 209-252), while the "poeciloptera-group" is considered a representative of the archaic Gynacanthini (Aeshnata). Biogeographical problems of Anisoptera, especially those of Gomphaeschnini and Gynacanthini, and of Euphaeida (Zygoptera) are discussed, considering the Pangaea-model and panbiogeographic criteria. Maps and a glossary of some panbiogeographic terms are added.

INTRODUCTION

Heretofore the genus *Allopetalia* Selys has justly been considered a somewhat enigmatic taxon, consisting of two little-known species, both confined to the Andes of South America. Indeed, these two happen to be the only representants of the Gomphaeschnini ("Boyeria-series" of WALKER, 1912) in South America.

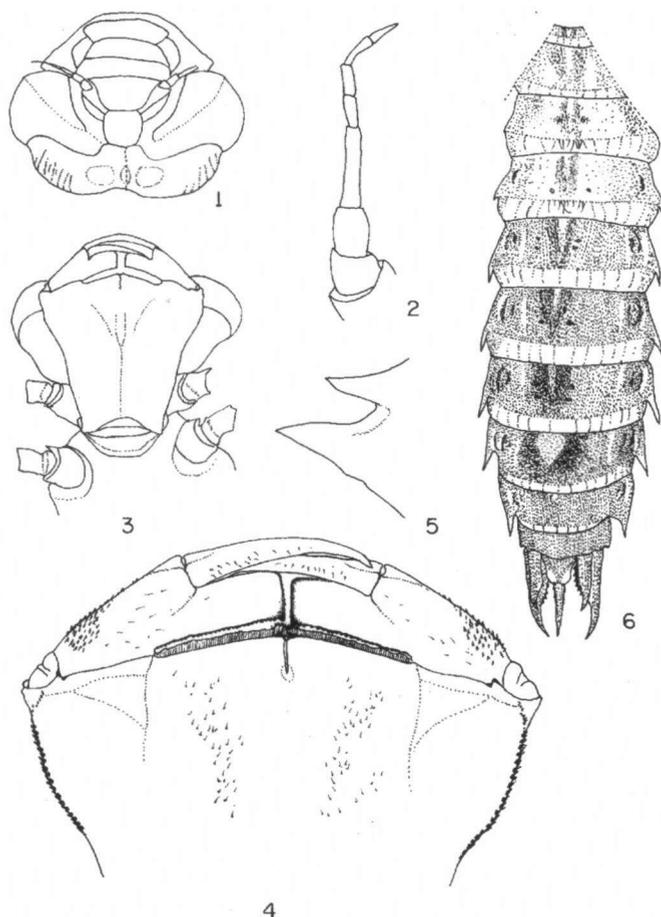
The discovery of the larva of *A. pustulosa* Selys and a careful study of the male accessory genitalia should now help to a better understanding of the taxonomic and biogeographic ties between *Allopetalia* and other Gomphaeschnini. Unfortunately, much of the recent "phylogenetic" systematic work (see below) almost

exclusively relies on morphology and does not pay much attention to the factors "space" and "time", which play, of course, a crucial role in evolution and taxonomy. Consequently, in this paper some emphasis is given to these two points.

DESCRIPTION OF THE LARVA

Figures 1-10

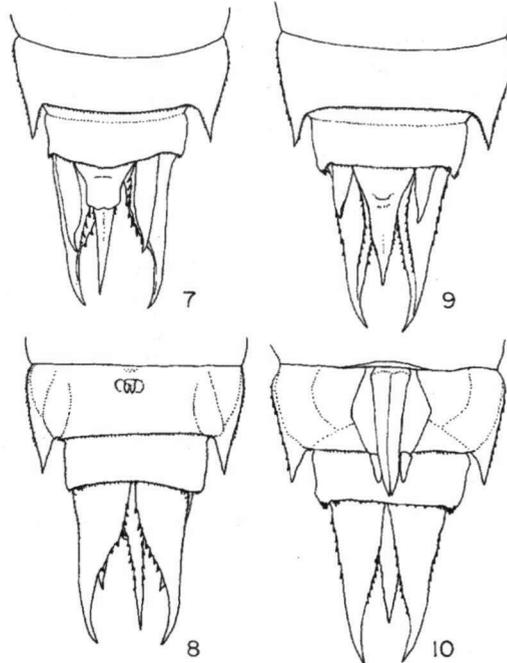
Material (3 ♂, 2 ♀). – VENEZUELA (Táchira State): San Vicente de La Revancha, Las Pesas, Fundo Piedra Blanca, alt. 2200 m, Tamá National Park, 1 ♂, ultimate instar exuviae (reared), 1 ♀, ultimate instar exuviae, 1 ♂, possible antepenultimate instar larva. Same locality, but alt. 2350 m, 1



Figs 1-6. *Allopetalia pustulosa*, ultimate instar exuviae: (1) female head, dorsal view; – (2) right antenna of male; – (3) female labium, ventral view; – (4) anterior portion of male labium, dorsal view; – (5) left prothoracic apophyses of male, dorsal view; – (6) male abdomen, dorsal view.

♀, ultimate instar exuviae; all specimens 30-XI/1-XII-1997, 1 ♂, reared, 13- I-1999, all J. De Marmels (MIZA).

DESCRIPTION. – Head dark, with rounded occipital lobes (Fig. 1); antenna as in Figure 2; hinge of labium between second pair of coxae (Fig. 3); median lobe of prementum with a low, broad, somewhat irregularly shaped “tooth”, on each side of median cleft; end hook of labial palp little larger than remaining, approximately thirty, teeth of inner margin of palp (Fig. 4). Prothoracic supracoxal processes in male long, slender, pointed (Fig. 5), in female little more robust. Femora with broad, dark cross-band in proximal half and with narrower one in distal half, tip also dark; tibiae with narrow, dark cross-band in proximal third, followed by a broader one over distal two thirds, tip also dark; tarsi pale, but basal and distal end of all segments dark. Wing cases reaching to beyond abdominal segment 3. Abdomen dark, with ill-defined, narrow, pale dorsomedian line, which suddenly broadens on segment 8, forming a pale spot (not well marked in female exuviae); two additional, interrupted, pale longitudinal lines between dorsomedian line and lateral margins of abdomen (best visible in female exuviae). Male has lateral spines on segments 4(5)-9, those on segment 4(5) very small (Fig. 6); in female there are lateral spines on segment 5-9, those on segment 5 very small; epiproct spiniform, sharply pointed, with spines along lateroventral carinae, in male little shorter than paraprocts, in female considerably shorter; male projection at base of epiproct with shallow apical emargination; male cerci about two thirds the length of paraprocts, in female one third this length; tip of paraprocts sharply curved mesiad, dorsal and ventral mesial carinae of paraprocts beset with sharp spines; in female these spines are weaker than in male, but the female has spines also along outer ventral margin of paraprocts, while in male these spines are reduced to blunt knobs (Figs 7, 9). Ovipositor not quite reaching to the end of segment 10 (Fig. 10).



Figs 7-10. *Allopetalia pustulosa*, caudal pyramid: (7) male, dorsal view; – (8) same, ventral view; – (9) female, dorsal view; – (10) same, ventral view.

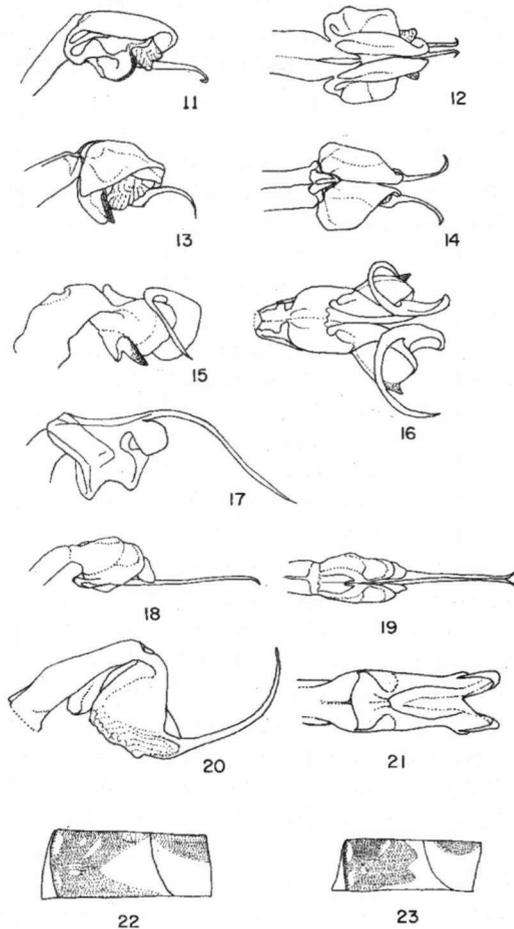
Measurements (in mm). – Total length (ultimate instar exuviae) 45.0-46.0; maximum width of head 10.0; female paraproct 4.8; male paraproct 4.5; hind femur (excl. trochanter) 7.5-7.9; hind tibia 8.4-8.5.

HABITAT. – At Las Pesas, a single adult male was observed flying along one of the several tiny streams, each less than 0.5 m wide and with very little flowing water, which drain a swampy plateau on an otherwise steep slope. Originally, the whole mountain side was covered with cloud forest, but the latter has largely been cleared for pasture land. The vegetation of the terrasse is composed mainly of grasses, sedges and *Juncus effusus* L. with many interspersed trees. The mentioned adult male *Allopetalia* repeatedly landed on the trunk of one of the trees for sunbasking, at about 10 a. m. The insect was almost indistinguishable from the lichen-covered bark. Unfortunately, it could not be secured on either of the three consecutive days. The female exuviae were collected from a tree trunk, about 1.5 m above ground and at a distance of 2 m from one of the streamlets. Additional larvae were not found here, in spite of intense searching. Other Odonata observed were a few *Aeshna marchali* Ramb. and *Erythrodiplax abjecta* (Ramb.), numerous *Cyanallagma tamaense* De Marmels and *Sympetrum gilvum* (Sel.). The two live larvae and the second female exuviae were collected from a stony stream on the same slope, but at about 2200 m elevation. This “quebrada” (rocky mountain stream) is about three metres wide and its margins are heavily forested. Only here and there the right bank had been cleared for pasture land (“potreros”). At one of these spots I found the larvae, clinging to the underside of stones in the middle of the stream, while the exuviae were hanging from a bush over the left bank, about 1.5 m above ground. Here, the accompanying adult odonate fauna was composed only of Zygoptera such as *Euthore f. fastigiata* (Sel.), *Hetaerina cruentata* (Ramb.) and “*Allopodagrion*” *oscillans* (Sel.), but a live larva of a libellulid (probably *Macrothemis*) was also collected.

REMARKS. – Among Venezuelan Aeshnidae, larvae of *Aeshna draco* Rácenis (Aeshnini), and *Racenaeschna angustistrigis* Calvert (Gynacanthini) have also spiniform, pointed epiproct (DE MARMELS, 1990). However, these species lack spines along mesial carinae of paraprocts and along lateroventral carinae of epiproct. In this feature, *Allopetalia* resembles several “brachytrine” genera, such as *Notoaeschna* Till., *Spinaeschna* Theisch. (see figs 159, 185 in THEISCHINGER, 1982), and to the “gomphaeschnine” *Boyeria* McL. (see fig. 10 in PETERS, 1991). The latter genus has, however, angled occipital lobes and longer labium. Similarly, larvae of *Spinaeschna* differ from *Allopetalia* in having six antennal segments, longer labium, with two triangular teeth on each side of median cleft, and differently shaped prothoracic processes, while larvae of *Notoaeschna* have unserrated, tapering labial palp, without an end hook, and bear middorsal spines on abdominal segments 2-9. Judging from the illustrations of the penes of *Notoaeschna* and *Spinaeschna*, given by THEISCHINGER (1982, figs 163, 171), the flagellae in these genera seem to originate ventrally and mesially and are probably of rather membranous structure, the whole penile organ resembling that of *Austroaeschna* Sel. The cornua

in *Allopetalia* and *Boyeria* are, on the contrary, anchored dorsally and mesially and are of a more sclerotized structure. The penes of the latter two genera are so overwhelmingly similar as to discard whatever doubt about the close relationship of *Allopetalia* with *Boyeria* (Figs 11-14). This is further corroborated by the similarity of their wing venation, which led NEL et al. (1996) to adscribe a fossil wing fragment first to *Allopetalia*, only to move it later to *Boyeria* (NEL, et al., 1997). It is perhaps noteworthy that even the rather peculiar abdominal pattern of *B. irene* (Fonsc.) is almost repeated in *Allopetalia pustulosa* (Figs 22-23). The penis of *Gomphaeschna* Sel. (Figs 15-16) looks rather different from *Allopetalia/Boyeria*, but the cornua are essentially of the same type and the organ as a whole is identical to the penis of "*Oligoaeschna*" Sel. of the "pryeri-group", as is apparent from an unpublished SEM photograph, taken and kindly put at my disposal by Mr Wen-chi Yeh, Taipei (Taiwan), from an undescribed Taiwanese species of the mentioned species-group. Curiously, LOHMANN (1996) included

only the two North American *Gomphaeschna* species in his new taxon "Gomphaeschnata" (an adelphotaxon of "Aeshnata" within "Palanisoptera"), but failed to place here also the "pryeri-group" of *Oligoaeschna*, which shares with *Gomphaeschna* most, if not all, of the purported "autapomorphies" of the latter,



Figs 11-21. Penes (left: right lateral view, right: ventral view) of: (11-12) *Allopetalia pustulosa*; - (13-14) *Boyeria irene* (Fonsc.); - (15-16) *Gomphaeschna furcillata* (Say); - (17) *Spinaeschna tripunctata* (taken from THEISCHINGER, 1982, fig. 171); - (18-19) *Limnetron debile*; - (20-21) *Rheopetalia apicalis* (Sel.). - Figs 22-23: Pattern of fourth abdominal segment (right lateral view) in males of (22) *Allopetalia pustulosa*; (23) *Boyeria irene*.

especially the ramhorn-like cornua. On the other hand, a rudimentary bilobulation of the first (basal) segment of the vesica spermalis is present even in *Allopetalia pustulosa* (as well as a slightly bifid epiproct). The “Gomphaeschniden-Lücke” (LOHMANN, 1996) is also found in “*Oligoaeschna*” *pryeri* Martin, and partly even in the species of the “poeciloptera-group” (the “true” *Oligoaeschna*) (see fig. 126 in MARTIN, 1909; LIEFTINCK, 1968, pls 12, 13). I suspect that this character is therefore plesiomorphous and part of the groundplan of Palanisoptera (Aeshnidae), outlined by LOHMANN (1996), together with the absence of cross-veins in the supratriangle. The species of the “pryeri-group” of “*Oligoaeschna*” lack cross-veins in the supratriangle, but the species of the “poeciloptera-group” (true *Oligoaeschna*) have cross-veins there.

It is clear that *Oligoaeschna* Sel. is polyphyletic, with the “pryeri-group” forming a separate genus (to be described by Mr Wen-chi Yeh) within LOHMANN’s (1996) “Gomphaeschnata”, while the species of the “poeciloptera-group” remain in *Oligoaeschna*, but fall in “Aeshnata” (Gynacanthini, see below).

EVOLUTION AND BIOGEOGRAPHY

CARLE (1995), adhering to the Pangaea concept, introduced the “trans-pangaean mountain system” into the discussion of the ancient Anisoptera evolution. Curiously, he interprets this paleogeographic feature as a “dispersal route”, along which the ancestral forms are supposed to have actively migrated forth and back over thousands of miles across Pangaea, first “in a southerly direction [in the American portion of that mountain chain], but later a northwards migration also occurred” (CARLE, 1995: 400). This is a surprising explanation, since in the same paper (p. 394) the author stated that the ancient Anisoptera were “inhabitants of [...] seepages and small streams”, and that their poor fossil record is due, “to relatively low vagility [and] small population sizes”. Nevertheless, “the North-South vicariance pattern between Austropetaliidae and Aeshnidae (i. e. *Gomphaeschna*)” must be, according to Carle, the result of migration of, I deduce, an archipelaline ancestor, from Chile to somewhere between Louisiana (USA) and southern Siberia, to “release” *Gomphaeschna* there, and become extinct, while “the relationships between Cordulegastridae and early non-cordulegastrid Libelluloidea show a reversed phylogenetic polarity” (l. c., p. 400). Obviously, in this case, a *Zoraena*-like ancestor must have migrated from New York to Chile where it gave origin to *Neopetalia*, and then disappeared, etc. It should also be noted that, in spite of such intense moves up and down along the western edge of South America, no Cordulegastridae, and only a single genus of “Gomphaeschnini”, namely *Allopetalia*, with only two species, happened to be left in existence in that subcontinent. In the meantime, LOHMANN (1996) has expressed the opinion that the “Austropetaliata” are not related to Aeshnidae, but must be rather placed within his “Neanisoptera”. This, however, does not alter the basic question as to the obvious discrepancy between

the currently accepted Anisoptera phylogeny and biogeography. I agree with CARLE (1995: 394) that “extant anisopterous superfamilies were well established before the break up of Pangaea”. Later (in litt., 13 July 1996), he emphasized that he “meant that they existed, not that they were widely distributed”. However, as “the most ancient representatives [of the northern Tachopterygidae, viz. *Tachopteryx* Sel. and the southern Petalurinae, viz. *Phenes* Ramb.] [...] inhabit the northern and southern remnants of the dispersal route” (p. 397), they must have got there prior to the break up of Pangaea, which occurred long before the end of the Jurassic (SCHUBERT & HUBER, 1989). By then, at least the Petaluroidea, the Hemeriscopidae [nothing less than the “potential stem-group representative of extant Chlorogomphoidea” (BECHLY et al., 1998: 149)], the Gomphoidea, and of course the Aeshnoidea, were already widely distributed. While even the true Aeshnidae [*Morbaeschna muensteri* (Germar)] were in existence in Germany as early as the Upper Jurassic (age of fossilization, not of origin!), the primitive Austropetaliidae were seemingly always confined to the trans-antarctic belt. Therefore an ancestor, common to both, must have been already widely distributed very much earlier. It is rather unparsimonious to postulate a “phylogenetic polarity” which requires

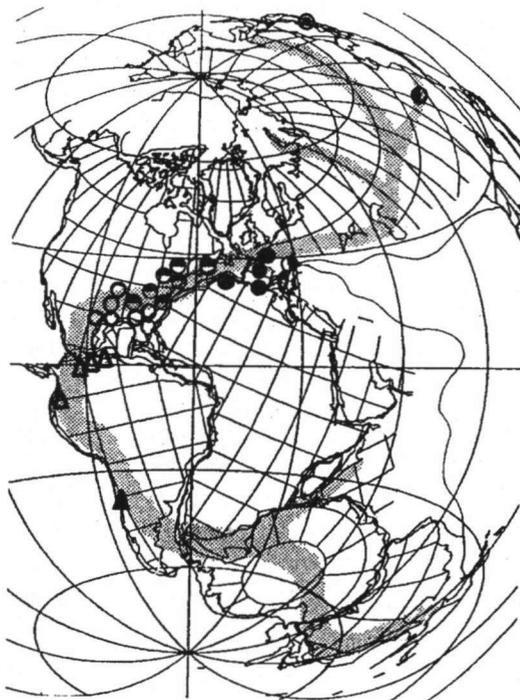


Fig. 24. Distribution of known species of extant *Allopetalia* and *Boyeria* projected on a paleocontinental map for Early Jurassic (ca 180 million years ago), taken from CARLE, 1995 (as modified from SMITH & BRIDEN, 1977). Shaded areas indicate the likely location of trans-pangaeian mountain system. Solid triangles = *Allopetalia reticulosa* Sel.; – empty triangles = *A. pustulosa*; – empty circles = *Boyeria vinosa* (Say); – circles with upper half black = *B. vinosa* + *B. grafiانا* (Williamson); – solid circles = *B. irene*; – circle with right half black = *B. cretensis* Peters; – circle with left half black = *B. sinensis* Asahina; – circle with enclosed solid circle = *B. maclachlani* (Selys). – [Distributional data for the American species of *Boyeria* were extracted from NEEDHAM & WESTFALL, 1955, and from WALKER, 1958; data for the other species were obtained either from the original descriptions or from DAVIES & TOBIN, 1985 and from TSUDA, 1991, or from the MIZA collection].

cross-wise transcontinental migrations, such as the “Tachopter[ylg]line (northern hemisphere) > Austropetaline (southern hemisphere) > Cordulegastridae (northern hemisphere) > Neopetaline (southern hemisphere) sequence” (Dr F.L. Carle, in litt., 13 July 1996; see also incongruence of cladogram with geography in WIGHTON & WILSON, 1986: 517). Who migrated when? It is difficult to imagine how all those journeys, with each consecutive taxon somehow branching from the preceding one (see arrows above), should have been accomplished before the definitive break up of Pangaea and the consequent subsidence of the supposed “dispersal route”.

Considering the “Gomphaeschnini” (corresponding approx. to WALKER’s [1912] “Boyeria-series”) alone, it is interesting to note that the ranges of many extant and fossil genera fall along the trans-pangaeian mountain system. This type of dispersal can be represented by a “track”, which follows the northern edge of Tethys geosyncline (see CROIZAT, 1964: 63, fig. 16; and pp. 66 ff), connected to the more northerly tracks (this paper, Figs 24-25). The dispersal of the ancient Anisoptera in general, and of the Gomphaeschnini in particular, skips Africa and those parts of South America, which formed, together with the West African shield, a joint Gondwanian shield in the Triassic and during some of the Jurassic, namely the Guyana shield plus the Brazilian shield. I agree with Dr F.L. Carle (in litt., 13 July 1996), that “... originally Protogondwana and later tropical Pangaea were probably devoid of the early ancestors of modern Anisoptera”. This explains why no ancient Anisoptera, and of course no Gomphaeschnini, might be expected to occur either in Pantepui (Guyana Highlands), the Amazon, or in southeastern South America (Figs 24-25). †“*Gomphaeschna*” *obliqua* Wighton, from the Lower Cretaceous of northeastern Brazil, has been removed (as “*Gomphaeschnoides*”) to the Gomphidae

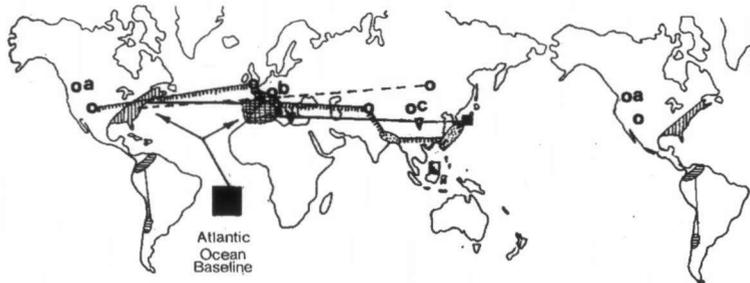


Fig. 25. Dispersal of extant Gomphaeschnini and of some fossil genera, which are or may be related to Gomphaeschnini: horizontally hatched areas = *Allopetalia*; vertically hatched = American *Boyeria*; – cross-wise hatched = *B. irene*; – solid triangle = *B. cretensis*; – empty triangle = *B. sinensis*; – solid square = *B. maclachlani*; – black and white square = *Linaeschna polli*; – stippled areas = range of “*Oligoaeschna*” (“pryeri-group”); – empty circles = fossil records. – Solid lines (tracks) connecting ranges of *Allopetalia* and *Boyeria*, respectively; – broken line connecting †*Gomphaeschna inferna* Pritykina with the range of the extant *Gomphaeschna*; – stippled line connecting the range of the extant “*Oligoaeschna*” (“pryeri-group”) with the fossil *Oligoaeschna*; – a = *Alloaeschna*, – b = *Morbaeschna* Needham, – c = *Gobiaeschna* Pritykina.

(CARLE & WIGHTON, 1990), but, as LOHMANN (1996) pointed out, it is referable to the Aeshnidae. However, while Lohmann (p. 226) claimed the species falls “zweifelsfrei” (“doubtless”) in his “Pan-Gomphaeschnata”, I am inclined to consider it a possible stem-group representative of the Gynacanthini, perhaps an early ancestor of *Limnetron/Racenaeschna* (broad wing base, comparatively ample anal loop, ample cubito-anal space, obsolescent “Gomphaeschniden-Lücke”, dense reticulation and southern distribution, but perhaps “still” with no cross-vein in the supratriangle). LOHMANN (1996: 226) stated, that †*Alloaeschna* Wighton & Wilson, from the Late Paleocene of Alberta, Canada, is an “eindeutige” (“inequivocal”) stem-group representative of his “Gomphaeschnata”. To me, this genus seems, if not a polyphyletic entity, a stem-group representative of the Aeshnini (in the traditional sense), because of the following characters, viz. ample base of hindwing, ample anal loop, comparatively dense reticulation, tendency to reduce the “Gomphaeschniden-Lücke”, occasionally crossed supratriangle and first trigonal cell, and northern distribution.

The South American genera *Limnetron* Förster and *Racenaeschna* Calvert exhibit some striking “gomphaeschnine” (= primitive) features, but these taxa more likely represent plesiomorphic Gynacanthini, annectent to forms such as the “poeciloptera-group” of *Oligoaeschna*, which is not related to the “pryeri-group” (see above), but rather close to some gynacanthine ancestor. Numerous characters of the “poeciloptera-group” point in this direction, viz. sombre colour, crepuscular habits, long interorbital suture, long and slender female cerci, easily breakable, auricles angled with fewer, sharply acute and incurved spinules, denser venation, crossed supratriangle, tropical distribution (see LIEFTINCK, 1968), and cornua of penis shortened (SCHMIDT, 1915: 161, fig c). The male of *Racenaeschna* is as yet unknown, but this genus and *Limnetron* stand “nearest” (CALVERT, 1958: 233) together. Also, the morphology of the larval labium indicates close relationship between *Limnetron* (see SANTOS, 1970) and *Racenaeschna* (see DE MARMELS, 1990). The former was adscribed to the “Gruppe Brachytron” by KARSCH (1891; as *Epiaeschna*), FORSTER (1907) and by SANTOS (1970: 15, “Brachytrinae, Brachytrini”). DAVIES & TOBIN (1985) listed *Limnetron* under “Gynacanthini”, but *Racenaeschna* under “Brachytronini”. As already mentioned, I consider these two genera as primitive Gynacanthini, which still conserve many plesiomorphous characters known from certain Gomphaeschnini, viz. cornua on the penis, anterior lamina with blunt spines, anterior hamuli with large, cephalad tapering process, enlarged base and greatly reduced hamular fold (WALKER, 1912: 19), auricles beset with numerous small denticles, female abdominal segment 10 with relatively short ventral projection bearing four or more small spines, small membranule, angled nose, rheophilous habits, oviposition into plant substrate in the water. Wing venation clearly identifies *Racenaeschna* (see DE MARMELS, 1993, fig. 18) as a member of the Gynacanthini, closely resembling *Plattycantha cornuta* (Förster) (see MARTIN, 1909, fig. 156).

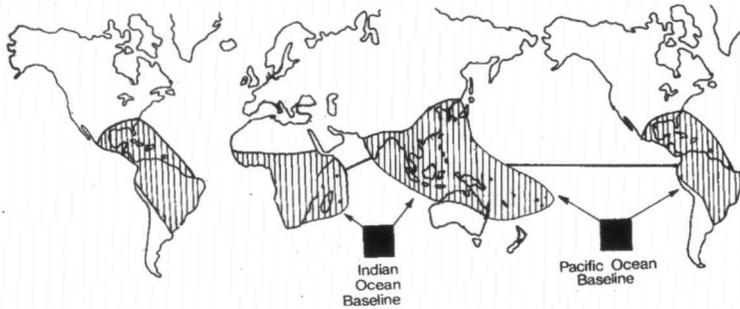


Fig. 26. Dispersal of the extant Gynacanthini, after DAVIES & TOBIN (1985) and TSUDA (1991). Discussion in text.

It follows that an ancestor of the modern Gynacanthini was present along a trans-Pacific track (see below) before the opening of the Pacific Ocean. This trans-Pacific track meets the Tethyan track and the Gondwanian track in Southeast Asia, an important “node” and “center of form-making” (CROIZAT, 1964: 83, 84). Therefore, many Australasian aeshnid genera (e.g. *Telephlebia* Sel.) should be carefully reexamined in order to ascertain whether they are referable to the “gomphaeschnine/brachytrine” or to the “gynacanthine”. Obviously, the classification of these groups cannot be based any longer on the “straight” or “curved” Rspl. In the same way, wing venation alone may not suffice for classifying the extinct taxa at higher taxonomic levels. The more ancient the remains, the more similar is their venation to be expected. In such cases, biogeography often furnishes additional criteria.

As already suggested, there is an alternative way to CARLE’s (1995) dispersalist scenario for looking at the evolution of the early ancestors of the modern Anisoptera, namely the panbiogeographic approach of CROIZAT (1958, 1964). In this model, a widespread, inherently polymorphic ancestor (see the discussion in HEADS, 1985; GREENAN & AINSWORTH, 1985) dissolves into a number of vicariant descendant taxa in situ. Similar or even identical taxa may develop independently in disjunction, separated by entities that are different (“wing dispersal”, CROIZAT, 1958, 1964; see HEADS, 1985), by polytopic recombination of ancestral characters. HENDERSON (1989: 500) pointed out that “it is simply fortuitous if one pair of taxa happen to share more characters than other pairs. If ancestors evolved over broad fronts, producing vicariant subtaxa all equally related to each other, the fuzzy phylogenies we see are exactly what would be expected. For biogeographic analysis of such problems, phylogenetic “information” must be ignored since it has no basis [...]”. If cladistic relationships do not really exist (as in the case of the Anisoptera discussed here), then dispersalist scenarios are not needed for the “explanation” of such relationships, either. Therefore, neither the *Cordulegastrata* (sensu LOHMANN, 1996) nor its immediate ancestor did migrate from North America to Chile to release

the Neopetaliata (sensu LOHMANN, 1996) there (or viceversa), in order to “save” the cladogram or “back up” some “phylogenetic polarity”. On the contrary, it can be assumed that the earliest ancestor of the Anisoptera had a Pangaeian distribution and that it was probably the proper orogeny of the transpangaeian mountain system itself, which initiated the evolution of the basal groups of Anisoptera. The continuing orogeny and the subsequent subsidence resulted in the events, which triggered the development of more or less similar taxa in a total disjunction (viz. Tachopteryginae in the North, Petalurinae in the South, Cordulegastridae in the North, Neopetaliidae in the South, and other taxon-pairs (see CARLE, 1995). These, in any cladogram, would fall close to each other, as so-called “sister-groups”. When one adds to this view of polycentric and, therefore, “polyphyletic” evolution (“by level”, see CROIZAT, 1978: 143; GREHAN & AINSWORTH, 1985: 177) the interference of epigenetic inheritance systems (JABLONKA & LAMB, 1995), then, too, one can expect that out of a common ancestral gene pool more or less similar descendant forms may arise in complete vicariance, if the interplay of the environment and the developmental processes is similar in each case. Consequently, these authors go on to state (p. 279), that “we may also have to amend some practices in theoretical population genetics and in phylogenetic analyses”. No doubt. An analogous view is expressed by STURM (1994: 260), discussing the reactivation of silent genes (“tendencies”) under developmental constraints (“Entwicklungszwänge”) in non-monophyletic taxa. Parallelisms (and I may add: many so-called “convergences”) are then phenomena, in which identical or similar genetic potentials become realised (STURM, 1994: 259; see also HEADS, 1985: 214). This is nothing but CROIZAT’s (1964) recombination of ancestral characters within a certain common type of organization.

The basic tenet of CROIZAT’s (1958, 1964, and all his major works) Panbiogeography and biological synthesis is: “Evolution = form-making + space + time”. It is surprising, that even in recent systematic papers, such as LOHMANN’s (1996) or BECHLY’s (1998), only the phyletic/cladistic aspects are considered. In over sixty pages on phylogeny of the Anisoptera, Lohmann brings the factors “space” and “time” into play at a single opportunity (p. 363). Similarly, BECHLY (1998), discussing the phylogeny of the Epallagidae, dedicated less than fourteen lines to “paleobiogeography” (p. 49). Without losing time in analyzing the distributional pattern and the factor “time” in the evolution of his “Euphaeida” (incl. the Epallagoidea and Polythoridae), he proceeds to claim (p. 49), that “the Epallagidae probably *originated in the Lower Tertiary of the Northern hemisphere*, possibly in the Nearctic region”, and “obviously became extinct in North America before this group could *invade* the Neotropical region. The absence from Africa and Australia *can thus far only be explained by mere contingency*” [italics added]. A glimpse at the distributional map of Euphaeida (Fig. 27) shows otherwise: There are two “main massings”, one in tropical South America (Polythoridae), the other in Southeast Asia (Epallagidae). The glaring absence of Euphaeida from Africa can certainly

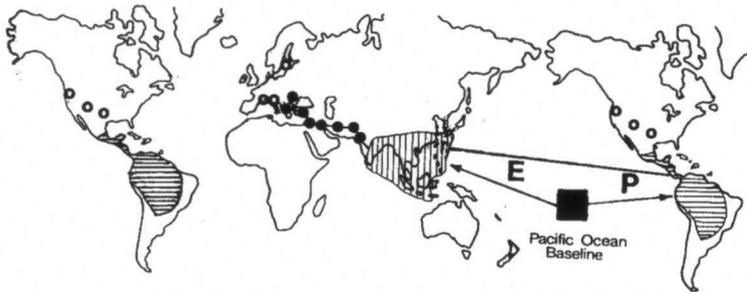


Fig. 27. Dispersal of Euphaeida: horizontally hatched areas = Polythoridae; – vertically hatched = Epallagidae; – solid circles = *Epallage fatime*; – empty circles = fossil Epallagidae (after BECHLY, 1998). – [General distributional data after DAVIES & TOBIN, 1984 and TSUDA, 1991].

not be “explained” invoking sheer chance. This taxon is missing from Africa simply because its ancestors did never live there! It follows that the Euphaeida dispersal is not Gondwanian, but Pacific, with a track right across the Pacific Ocean; the latter forming the “base line” of the dispersal of Euphaeida (CROIZAT, 1958; CRAW, 1988). Similarly, the absence of Euphaeida from Australia indicates that no ancestor of it was ever present on any land mass of the Antarctic belt. Taking into account plate tectonics [or rapid Earth expansion (SHIELDS, 1991)], the Epallagidae obviously cannot have “originated in the Lower Tertiary of the Northern Hemisphere” and certainly less so “in the Nearctic region” (BECHLY, 1998: 49). At this time (Eocene) all the mayor continental land masses were already well separated by the present oceans, except northern Europe and North America. So, by which “means” should Epallagidae have managed to “colonize” the Indomalayan archipelago? And, if the family “obviously became extinct in North America before this group could invade the Neotropical region” (p. 49), the Polythoridae may have come out of nothing? The map (Fig. 27) clearly shows that FRASER’s (1957:78) hypothesis on the “Oceanian [Pacific] origin” (in the sense of ancestral range) is correct, if applied to the whole of Euphaeida (incl. Polythoridae), whether or not the Australian *Diphlebia* Sel. is considered the closest relative of Epallagidae. The only recent outlier of Epallagidae to the West is *Epallage fatime* Charp. The dispersal of this relict species falls exactly along the northern edge of Tethys. Considering the scanty and poorly known “genuine” (BECHLY, 1998: 49) fossil Euphaeida, the following may be said: †*Parazacallites aquisextanea* NEL, 1988, *Epallage* spec. described by CAVALLO & GALLETTI (1987), and †*Indophaea* spec. by THEOBALD (1937), neatly fit in the dispersal North of Tethys and mark the ancient distribution of forms allied to the modern *Epallage fatime*. †*Litheuphaea ludwigi* BECHLY, 1998, from Baltic Amber (Upper Eocene), was assigned by his describer to this genus in spite of considerable venational differences. The type species of †*Litheuphaea* Fraser is †*L. carpenteri* Fraser, from Middle Oligocene of Goshen, Oregon (USA). This disjunction may indicate a transatlantic track for †*Litheuphaea*.

However, the locality of †*L. carpenteri* is situated West of the limit of the North American Craton, i. e. on a suspect terrane of Pacific origin (see CRAW & PAGE, 1988 and papers cited therein), therefore suggesting a northern Pacific track for disjunct Epallagidae. Future discovery of fossil Epallagidae and/or †Zacallitidae in East Asia would strongly support this latter hypothesis.

When comparing the map of Euphaeida (Fig. 27) with those of Gomphaeschnini (Fig. 25) and Gynacanthini (Fig. 26), the following becomes evident: the dispersal of Euphaeida, as elucidated above, is transpacific with a relic distribution along the northern edge of Tethys, the fossil forms indicating a once wider ancestral distribution across the Northern Hemisphere.

The Gynacanthini, at a first glance, seem to exhibit a very clear Gondwanian dispersal. However, the main massings of Gynacanthini are found in tropical South America and Australasia (ca 7 genera each), while the core of Gondwana, namely Africa plus India, are rather poorly stocked with Gynacanthini, *Heliaeschna* Sel. and *Gynacantha* Ramb. being the only genera present in Africa. The first is shared with Southeast Asia, while the pantropical *Gynacantha* is the sole genus occurring in India, Africa, and also in South America. Therefore any claim for a Gondwanian type of dispersal for the Gynacanthini seems unjustified and, hence, the Pangaea model inadequate to explain the dispersal of this tribe. Also in this case a trans Pacific track seems more convincing, together with a very feeble track between South Asia and tropical Africa, across the Indian Ocean.

Figure 25 shows that the dispersal of Gomphaeschnini runs essentially North of Tethys, touching Andean South America in the West (*Allopetalia*) and Indonesia (North Borneo) in the East (*Linaeschna polli* Martin). If the Brachytrini are included, the track follows straight South along eastern Australia, with some outlier in the southwestern corner of that continent. As mentioned above, a careful character analysis should be carried out with respect to many Australasian genera. The accessory genitalia of *Linaeschna polli* have never been examined. This genus could be as closely related to *Allopetalia* as is *Boyeria*. Based on the currently known distributional and taxonomic data that much can be said: the tracks of Gynacanthini and Gomphaeschnini are not congruent, since the track of the latter includes an Atlantic Ocean baseline, while that of Gynacanthini has Pacific and Indian Ocean baselines. The Pangaea model seems able to explain the dispersal of Gomphaeschnini, but not that of the Gynacanthini (and Euphaeida). Both tracks overlap in Southeast Asia, which is a known centre of form-making (CROIZAT, 1958, 1964). Morphological and biogeographical evidence further suggests, that *Allopetalia* and *Boyeria* are closely related.

GLOSSARY

Geographic distribution: "the records of occurrence at different points of the map of the modern world of consanguineous entities forming a taxon" (CROIZAT, 1964: 13).

- Dispersal*: "a coherent explanation of geographic distribution formulated in joint reference to form-making and translation in space. Translation in space does not necessarily require migration" (CROIZAT, 1964: 13, 14; see also HEADS, 1989).
- Wing dispersal*: "cases in which very similar when not identically the same subspecies, species and/or genera do recur at the wings of the affinity separated inbetween by entities that are different" (CROIZAT, 1964: 192).
- Track*: "A track is an estimate of the ancestral distribution of a taxon." (PAGE, 1987: 12). "A track is a line graph drawn on a map of the geographic distribution of a particular taxon (be it a species, species-group, genus or family) that connects the disjunct collection localities of the subordinate taxa belonging to the taxon" (CRAW, 1988: 411, 413; see also CROIZAT, 1960: 1615).
- Baseline*: "diagnostic character with respect to the organisms distributed in or around an ocean basin" (GREHAN, 1988: 579). "Tracks are oriented in terms of the sea or ocean basin that the track crosses or circumscribes. This allows a hypothesis of the baseline for that track to be proposed. The baseline is a primary biogeographic homology (i. e. diagnostic characteristic) for the group under analysis" (CRAW, 1988).
- Nodes*: "regions with a large number of tracks stemming from different baselines" (PAGE, 1987: 13); "areas where two or more natural biogeographic regions come into contact within the boundaries of present-day composite areas of endemism" (CRAW, 1983: 435).
- Main massing*: "can be understood as a numerical, genetical or morphological centre of diversity for a particular taxon or group of taxa" (CRAW, 1985: 7).

ACKNOWLEDGMENTS

I feel indebted to Drs JANIRA MARTINS COSTA and ALCIMAR DO LAGO CARVALHO (both Universidade Federal de Rio de Janeiro), to Prof. Dr ANGELO B. M. MACHADO (Universidade Federal de Minas Gerais), to Dr. JAN VAN TOL (Natural History Museum, Leiden), and to Dr GÜNTHER PETERS (Humboldt Universität, Berlin) for the loan of aeshnid material. A very fruitful conversation via e-mail with Mr WEN-CHI YEH (Taiwan Forestry Research Institute, Taipei), who also provided a SEM photograph and other illustrations of anisopterous penes, further contributed to the present paper. Field trips and costs of publication were covered by the "Consejo de Desarrollo Científico y Humanístico" (CDCH) of the Universidad Central de Venezuela (project number 01-38.2663.97, as well as additional funds).

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