Odonatologica 31(2): 139-150 *June 1, 2002*

A STUDY OF *CHROMAGRION* NEEDHAM, 1903, *HESPERAGRION* CALVERT, 1902, AND *ZONIAGRION* KENNEDY, 1917: THREE MONOTYPIC NORTH AMERICAN DAMSELFLY GENERA WITH UNCERTAIN GENERIC RELATIONSHIPS (ZYGOPTERA: COENAGRIONIDAE)

J. DE MARMELS
Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez" (MIZA),
Facultad de Agronomía, Universidad Central de Venezuela,
Apartado 4579, Maracay 2101-A, Venezuela

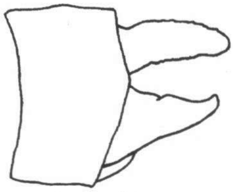
Received March 6, 2001 / Reviewed and Accepted July 10, 2001

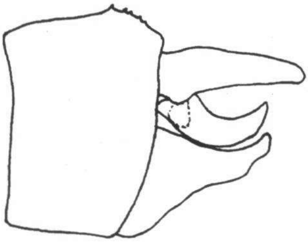
Comparative morphology identifies *Chromagrion* as the sister genus of *Pyrrhosoma* Charp. The genera *Hesperagrion*, *Anisagrion* Selys, *Apanisagrion* Kennedy and *Calvertagrion* St. Quentin probably form a monophyletic group as they share a bifid apical penis segment armed with a pair of sclerotized spine-like processes. A new interpretation of certain penis structures, and biogeographic considerations, suggest that *Zoniagrion* is probably a primitive genus, which occupies a basal position on the stem of the Acanthagrion-series, within the ischnurine Coenagrionidae.

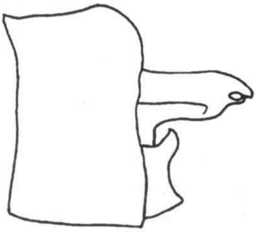
INTRODUCTION

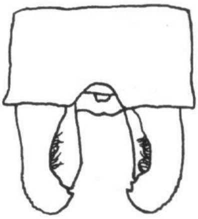
In their recent book on the "Damselflies of North America", WESTFALL & MAY (1996: 293) suggest that the North American genus *Chromagrion* Needham "may be closest related to the Palearctic *Erythromma*" Charpentier, 1840. Indeed, this was the opinion of all authors ever since NEEDHAM (1903) established the genus *Chromagrion*. However, already HAGEN (in SELYS, 1876: 1305) had placed *conditum* in *Erythromma* with a question mark, adding at the end of his description ("NB.", p. 197, reprint), that this species is fairly difficult to classify, falling close to *Erythromma* in view of its dominant blue colouration, but also to *Pyrrhosoma* Charpentier, 1840, when considering the long paraprocts. Curiously, this latter suggestion has never been taken up by subsequent authors. In the present study it will be shown, that *Chromagrion* is the vicariant sister genus of *Pyrrhosoma*, having nothing in common with *Erythromma*.

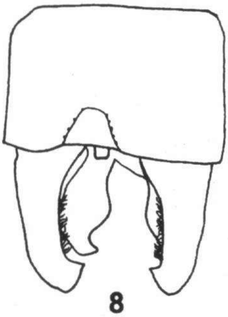
Hesperagrion Calvert is another monobasic genus with unclear relationships.

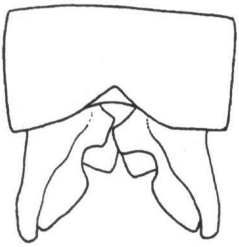

1

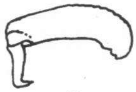

7

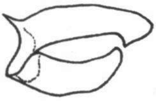

13

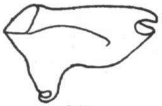

2


8

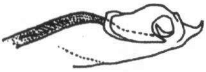

14

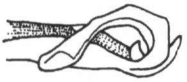

3

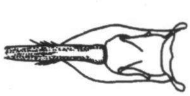

9

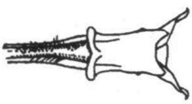

15

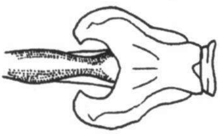

4

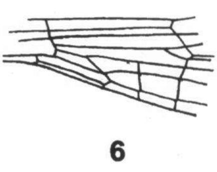

10

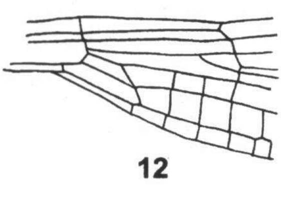

16

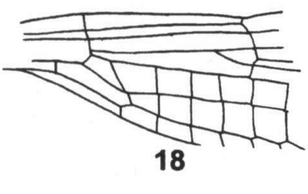

5


11


17


6


12


18

WESTFALL & MAY (1996) suggest, with some hesitation, a possible affinity with *Apanisagrion* Kennedy, 1920. The present work strongly supports the view of these authors.

A third monotypic genus of "rather uncertain affinities" (WESTFALL & MAY, 1996: 541) is *Zoniagrion* Kennedy. Westfall & May recognize "ischnurine affinities", but do not further elaborate on phylogenetic questions. Comparative character analysis and biogeographic considerations point towards a possibly primitive position of this genus within the Ischnurinae.

Male genitalia are crucial for establishing phylogenetic relationships between odonate genera, while wing venation and other structural characters, including larval features, are often of little informative value, or even misleading, when considered in isolation. However, the correct interpretation of penile structures is by no means easy, as evidenced in this paper. To decide whether some membranous transverse fold does or does not correspond to a "true" internal fold sensu KENNEDY (1916), may be, nevertheless, decisive for a correct phylogenetic arrangement of many coenagrionid genera, including those discussed in the present work.

METHODS

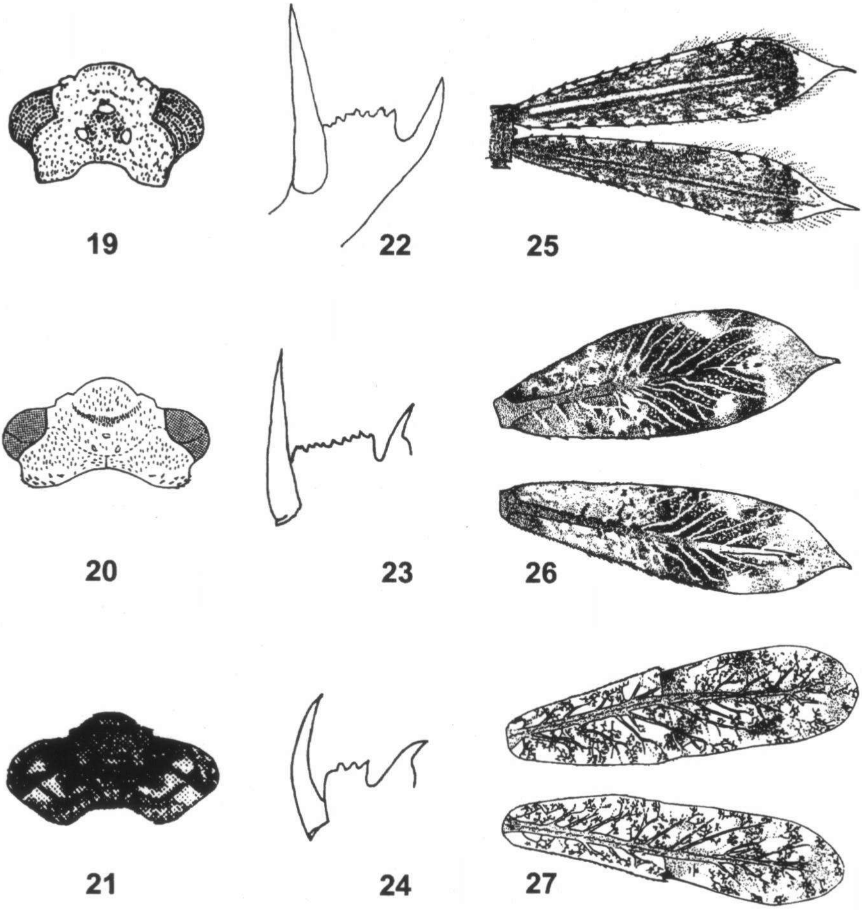
Wing venation, male genitalia and caudal appendages, as well as larval features, including morphology of the labium and caudal lamellae, are compared. Ecological data and behavior are also considered when relevant. Wing vein nomenclature follows RIEK & KUKALOVA-PECK (1984). Terminology of penis structures is that proposed by KENNEDY (1916). All specimens studied are deposited at the Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez" (MIZA), Facultad de Agronomía, Universidad Central de Venezuela, Maracay.

RESULTS

The penis of *Chromagrion* possesses an internal fold sensu KENNEDY (1916, textfig. p. 327), while the similarly looking membranous transverse fold present in *Hesperagrion* and *Zoniagrion* does not appear to be homologous with the former. Kennedy's internal fold sits at the end of the second segment. If the penis is softened with ammonia and the apical (third) segment is folded caudad with the help of a pin, a "true" internal fold

Figs 1-18. Male structural features of three coenagrionid genera: (1-6) *Chromagrion conditum*, from USA. (1) Caudal appendages, left lateral view (Topinabee, MI); — (2) same, dorsal view (Centre, PA); — (3) left cercus, left ventrolateral view (Topinabee, MI); — (4) penis, right lateral view (Topinabee); — (5) same, ventral view; — (6) base of left hind wing (same). (7-12) *Pyrrhosoma nymphula*, from Europe. (7) Caudal appendages, left lateral view (Sweden, Smoland, Aneboda); — (8) same, dorsal view; — (9) left cercus, left ventrolateral view (same); — (10) penis, right lateral view (Italy, Lombardia, Mantova); — (11) same, ventral view; — (12) base of left hindwing (Sweden, Aneboda). (13-18) *Erythromma najas*, from Germany. (13) Caudal appendages, left lateral view (Bavaria, Thalkirchen); — (14) same, dorsal view; — (15) left cercus, left lateral view (same); — (16) penis, right lateral view (Bavaria, Penzberg); — (17) same, ventral view; — (18) base of left hind wing (Bavaria, Thalkirchen). — [Figures to scale].

would not alter its orientation. In the case of *Hesperagrion* and *Zoniagrion*, however, the "accessory membranous transverse fold", as I call it here, present in these genera, is actually sitting at the base of the third segment. Hence, by pushing this segment caudad, the orientation of the accessory membranous transverse fold is also altered. A



Figs 19-27. Larval features of three coenagrionid genera (mostly from published references): (19, 22, 25) *Chromagrion conditum*: (19) head, dorsal view; – (22) tip of right labial palp, frontal view (modified from a sketch by K. Tennessen); – (25) epiproct (above) and paraproct (left lateral view). (20, 23, 26) *Pyrrhosoma nymphula*: (20) head, dorsal view; – (23) (probably left) labial palp, dorsal view; – (26) epiproct (above) and paraproct (left lateral view). (21, 24, 27) *Erythromma najas*: (21) Head, dorsal view; – (24) (probably left) labial palp, dorsal view; – (27) epiproct (above) and paraproct, left lateral view. – [Figures not to scale]. – [Figs 19 and 25 were taken or modified from WALKER (1953); Figs 20, 23, 24, 26 and 27 were taken from HEIDEMANN & SEIDENBUSCH (1993), with permission of the Erna Bauer Verlag, Keltern, Germany; Fig. 21 was adopted from ROBERT (1959)].

"true" internal fold can be observed in many genera, besides of *Chromagrion, Pyrrhosoma* and *Erythromma*, also in *Enacantha* Donnelly & Alayo, 1968, *Enallagma* Charpentier, 1840, and, especially well, in *Antiagrion* Ris, 1904. In *Ischnura* Charpentier, 1840, a true internal fold is present, but generally it is much reduced. In the species examined it can be seen best in *I. kellicotti* Wllmsn. The "true" internal fold may be functionally analogous to the "accesssory membranous transverse fold", but morphologically they are different structures. LEONARD (1977) (cf. also DE MARMELS, 1997) separated KENNEDY's (1920) "Acanthagrion series" from the "Enallagma series" on the basis of the presence or absence of a ("true") internal fold. Only the genera of the "Enallagma series" have such a fold.

CHROMAGRION Needham, 1903

Figures 1-6, 19, 22, 25, 35

Material. – ***Chromagrion conditum*** (Hagen *in* Selys, 1876) (4 ♂). – USA: Pennsylvania, Centre, Black Moshannon State Park, 1 ♀, 23-VI-1954, Beatty & Frost; Michigan, Cheboygan, Topinabee, 3 ♂, 13-VII-1965, Rácenis (all in MIZA).

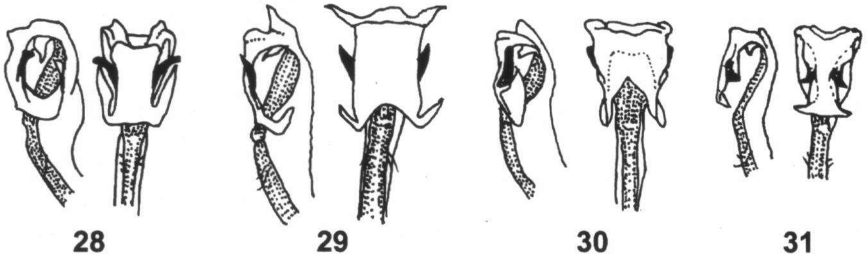
Even if the blue *Chromagrion conditum* looks strikingly different from the red *Pyrrhosoma nymphula* (Sulzer), both share important structural features which probably are synapomorphous and identify the two genera as sister taxa. The male cercus has an articulated(!) ventral branch. This is short and slender and directed ventrad, terminating in a pointed hook in *Chromagrion* (Fig. 3), while being much longer and more stocky, first arched ventrad and then distad in an even curve, in *Pyrrhosoma nymphula* (Fig. 9). It is interesting to note that in *P. elisabethae* Schmidt this ventral branch is seemingly intermediate between *C. conditum* and *P. nymphula* (cf. SCHMIDT, 1948: 71, figs 1a, c; ASKEW, 1988: 74, fig. 68). Otherwise the morphology of the caudal appendages is overwhelmingly alike in both genera (Figs 1-2, 7-8), while cerci and paraprocts of *Erythromma* are of a fundamentally different architecture (Figs 13-15).

Penis morphologies of *Chromagrion* and *Pyrrhosoma* are so close as to be inseparable at the generic level. This becomes evident when glancing over Figures 4-5 and 10-11, which illustrate the particular shape of the apical segment and of the terminal fold in these two genera. Both have also a "true" membranous internal fold and short setae on the penis shaft. In *Erythromma* the apical segment is deeply bilobate, the terminal fold entire, and setae are seemingly absent from the penis shaft (Figs 16-17).

The length of the hind wing quadrangle in *Chromagrion* has been emphasized by NEEDHAM (1903), WALKER (1953) and by WESTFALL & MAY (1996). Not surprisingly, also in *Pyrrhosoma* the hind wing quadrangle is lengthened, while in *Erythromma* it is short (Figs 6, 12, 18).

Additional congruent characters between *Chromagrion* and *Pyrrhosoma* can be found in the larval stage (Figs 19-20, 22-23, 25-26). WALKER's (1953: 159) description of the larva of *Chromagrion* includes the following characters: "noticeably angular postocular lobes [...] occipital margin strongly excavated in middle [...] mental setae 3, lateral [= palpal] setae 5; distal margin of lateral lobe with about 7 denticles, successively smaller laterad [...] Caudal lamellae slender oblanceolate [...] tapering to slender acuminate tips [...]". The larva of *Pyrrhosoma nymphula* is described by HEIDEMANN & SEIDENBUSCH (1993: 111, 112 and figures) [translated from german] as follows: "[...] head appearing very angulate caudad [...] the three procts [caudal lamellae] ending in accuminate tips [...] denticulated ridge of labial palp with well-marked teeth". Their figure 15d (p. 295), here reproduced as Figure 23, shows a broad ridge with about nine denticles, very similar to that found in the labial palp of *Chromagrion* (Fig. 22). The labial palp in *Erythromma* (Fig. 24) has a narrow dental crest with only four teeth (see also CONCI & NIELSEN, 1956: 224, fig. 121). The caudal lamellae have a nodal line, are parallel-sided and bluntly rounded distally, occasionally with a small, set-off point (Fig. 27).

The habitat of *Chromagrion conditum* has been described as "areas of clear streams, most often spring-fed, and some unpolluted lentic waters" (WESTFALL & MAY, 1996: 293), its flight season begins in March. WALKER (1953) characterizes the species as of "early summer" (p. 157), occurring at "partly shaded spring pools [...] or spring runs and the mouth of small tributary spring-fed streams", but also "about cut-off ponds close to rapids and in ditches dug through cold swamps" (p. 160). The adults are "commonly seen resting on foliage with their wings slightly spread [...]", the latter character was qualified as "nearly unique" among the North American Coenagrionidae" by WESTFALL & MAY (1996: 295). *Pyrrhosoma nymphula* "emerges early in the year, appearing in mid-April" (ASKEW, 1988: 72). Its German common name, "Frühe Adonislibelle", refers to the early flight season (ROBERT, 1959). The species inhabits "peat pools, lochans, ponds, ditches, seepages and sluggish streams" [...] and "more swiftly flowing water" in southern Europe (ASKEW, 1988: 72). During the day perching specimens always hold their wings half-spread (ROBERT, 1959: 149; 137, fig. 12J). Both, *Erythromma najas* (Hans., 1823) and *E. viridulum* (Charp.) inhabit lakes and large ponds and backwaters with slowly flowing water. They have pelagic habits and



Figs 28-31. Penes of *Hesperagrion* and related American genera (left: right lateral view; right: ventral view): (28) *Hesperagrion heterodoxum* (Mexico, Veracruz, Orizaba); — (29) *Apanisagrion lais* (Mexico, Oaxaca, Valle Nacional); — (30) *Anisagrion inornatum* (Venezuela, Trujillo, La Puerta); — (31) *Calvertagrion dicellulare* (Brazil, Amazonas, Porto Velho). — [Figures to scale].

rest on floating vegetation with their wings closed. Flight period begins in early summer, generally in May/June (ASKEW, 1988)

HESPERAGRION CALVERT, 1902

Figures 28, 36

Material. — ***Hesperagrion heterodoxum*** (Selys, 1868) (6 ♂, 5 ♀). — MEXICO: Morelos, La Fuente, Municipio Jiutepec, 10 km W of Cuernavaca, 1800 m, 1 ♂, 1 ♀, 17-IX-1983, R.W. Garrison leg.; — Veracruz, Orizaba, 3 ♂, 4 ♀, 31-VII-1959, Beatty leg.; — USA: Arizona, Portal, Cochise, 2 ♂, 30-VI--1958, Westfall leg. (all MIZA).

WESTFALL & MAY (1996: 432) found the penis of *Hesperagrion* (Fig. 28) "quite similar" to that of *Apanisagrion* (Fig. 29). Among the other Western Hemisphere coenagrionines only *Anisagrion* Selys, 1876 of Central America and northern South America, and the Amazonian *Calvertagrion* St. Quentin, 1960 have a similarly structured penis (Figs 30-31). This includes an accessory membranous transverse fold (not a "true" internal fold!) on the second penile segment, and a bifid apical segment, which bears a pair of chitinized spines of variable expression on its ental surface. While female *Hesperagrion* are armed with a vulvar spine on segment 8, such a spine is absent in *Anisagrion*, *Apanisagrion* and *Calvertagrion*. The male cercus of *Hesperagrion* is similarly structured as in *Anisagrion*. Paired dorsal horns distally on abdominal segment 10 are absent in *Hesperagrion*, *Apanisagrion* and *Calvertagrion*, but do occur in *Anisagrion*.The striking colour change during adult maturation observed in *Hesperagrion*, *Anisagrion* and *Apanisagrion* (not described so far in *Calvertagrion*) is perhaps worthwhile to be mentioned.

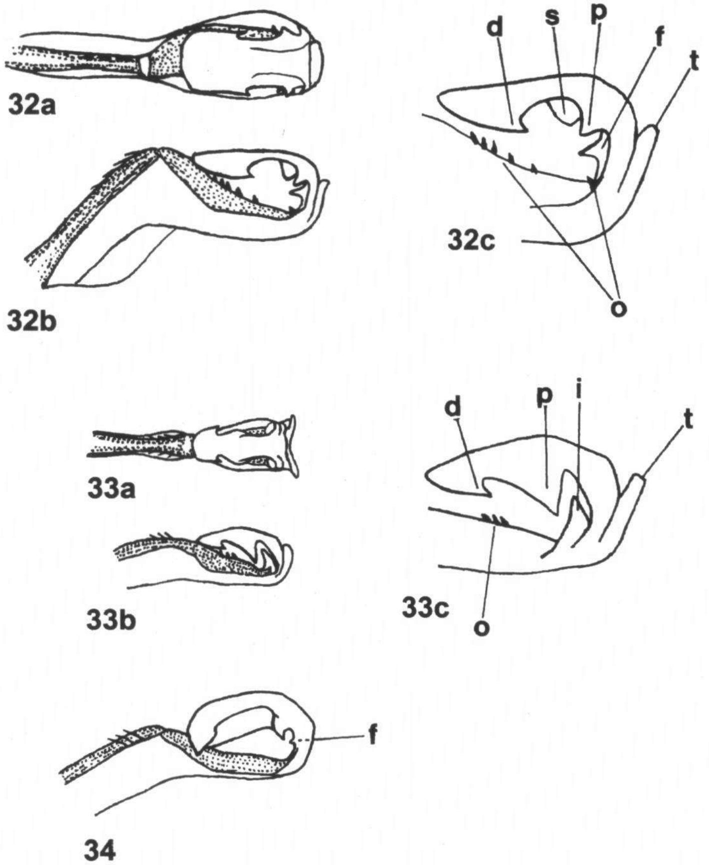
ZONIAGRION Kennedy, 1917

Figures 32, 37

Material. — ***Zoniagrion exclamationis*** (Selys, 1876) (4 ♂, 1 ♀). — USA: California, Marin Co., Lagunitas Creek at entrance to Samuel P. Taylor State Park, just W of Lagunitas, 2 ♂, 27-VI-1976; 1 ♂ (reared, with its exuviae), 12-II-1977 (emerg. 4-III-1977; 1 ♂, 1 ♀, 13-V-1978, all R.W. & J.A. Garrison leg. (MIZA).

When I saw for the first time a picture and figures of this species in WESTFALL & MAY (1996), I was struck by its similarity in colour pattern and wing venation with South American *Cyanallagma* Kennedy, 1920. Dr R.W. Garrison, (Azusa, California, USA) kindly sent to me the specimens listed above. A close inspection of the penis showed there was no "true" internal fold, but, instead, an "accessory membranous transverse fold". A few chitinized distal spinules mark the point where the internal fold should be expected to sit, if present (Fig. 32; cf. also KENNEDY, 1917, fig. 24; WESTFALL & MAY, 1996, fig. 56). The fold present in *Zoniagrion* (and in *Hesperagrion*, see above) is also found, although less developed, in certain species of

Acanthagrion (Fig. 34), or, as more elaborate paired protuberances, in some species of *Oxyagrion* Selys, 1876, such as *O. basale* Sel., or *O. rubidum* (Ramb.). In her revision of *Oxyagrion*, COSTA (1978: 43) interpreted these folds and paired teeth as actually representing Kennedy's "internal fold", but, as these structures are lacking in some *Oxyagrion* species, this seems unlikely. *Zoniagrion* might, therefore, be placed within the "Acanthagrion series" (which lacks any "true" internal fold). On the other hand, the curious spinules on the shaft of the second segment of the penis in *Zoniagrion* are not exclusive to this genus. Similar, probably homologous, though smaller spinules are present in *Enallagma divagans* Sel. (Fig. 33), *E. civile* (Hag.), *E. cyathigerum* (Charp.),



Figs 32-34. Penes of *Zoniagrion* and related American genera [a = ventral view, b = right lateral view, c = same, enlarged]: (32) *Zoniagrion exclamationis* (USA, CA, Marin, Lagunitas); — (33) *Enallagma divagans* (USA, NJ, Malaga, Scotland Run); — (34) *Acanthagrion imeriense* De Marmels, 1989 (Venezuela, Bolivar, Serrania de Maigualida), right lateral view. [d = distal lateral lobe, f = accessory membranous transverse fold, i = internal fold, o = teeth, p = proximal lateral lobe, s = internal swelling, t = terminal fold]. — [Figures (except c) to scale].

and possibly in other species, although not near the distal end of the second segment, as is the case in *Zoniagrion*, but restricted to the basal half. The rounded tip of the apical segment, too, is reminescent of *Enallagma* rather than of *Cyanallagma* (see figures in DE MARMELS, 1997). The membranous mound-like swelling on the internal surface of the apical segment of *Zoniagrion* (Fig. 32c) lacks a median process as usually present in *Cyanallagma*. In *Enallagma* even such a swelling seems to be altogether absent.

The presence of horns on the distal dorsal margin of abdominal segment 10, as well as the specific architecture of the cerci and the paraprocts as found in male *Zoniagrion* are known to occur, partly or jointly, in other ischnurine genera, such as *Cyanallagma, Enallagma, Acanthagrion* and *Ischnura*.

Wing venation of *Zoniagrion* has few noteworthy characteristics: CuP is always separated from the hind border of wing at least by its own length. The same condition is found in most species of *Enallagma*, while in *Cyanallagma* the distance of CuP from the hind border of wing is variable; in *Acanthagrion* CuP coincides with the end of the petiolus, i.e., it is not separated from the hind border of wing. The pterostigma is, in *Zoniagrion*, at least as high as long, and hence closely similar to the pterostigma found in many species of *Cyanallagma*.

WESTFALL & MAY (1996: 541) mention a "mound-like prominence" on the pterothoracic venter in *Zoniagrion*. A similarly developed metasternal tubercle occurs in *Protallagma titicacae* (Calvert) of the "Enallagma series".

According to KENNEDY (1917) the larva of *Zoniagrion* has 7-segmented antennae, as have *Acanthagrion* and *Cyanallagma*. However, in the exuviae of a single male in my possession I detected only six antennal segments, like in *Enallagma* larvae. WESTFALL & MAY (1996: 322) consider the number of antennal segments of "little practical use", due to the occurrence of *Enallagma* individuals with an apparent seventh segment and the often indistinguishable seventh segment in *Coenagrion* and *Ischnura*. The dentation of the distal margin of the labial palp consists in *Zoniagrion* of three well-defined teeth near the mesial end hook and a group of two or three very small teeth near the movable hook. This is the same pattern as found, for example, in *Enallagma civile* (Hag.), but also in *Acanthagrion fluviatile* (De Marmels) (DE MARMELS, 1990), in some *Ischnura*, and in the southern *Cyanallagma* species, viz. *C. bonariense* (Ris) and *C. interruptum* (Sel.) (BULLA, 1973). Curiously, the Andean species of the latter genus show a homogenous, very weak serrulation without individually defined teeth (DE MARMELS, 1997).

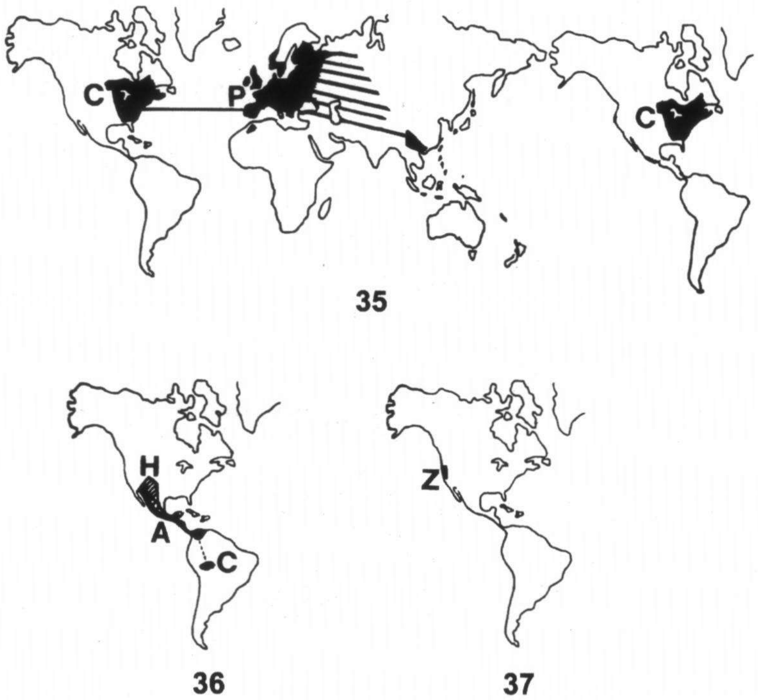
The *Zoniagrion* caudal gills lack a nodal line and end in a filamentous tip; they are similar to those in Andean *Cyanallagma*. In both genera the marginal serration is homogenous throughout the gills.

BIOGEOGRAPHY

In the case of *Chromagrion*, there is a standard transatlantic disjunction between this genus and *Pyrrhosoma* (Fig. 35). It would be futile to try to decide whether it was

Chromagrion which crossed the Atlantic and invaded Eurasia some time after the Oligocene to transform itself into *Pyrrhosoma* there, or it was *Pyrrhosoma* which migrated the other way around. More reasonably, this distributional pattern suggests that a common ancestor of both genera thrived approximately in the range, or part of it, now occupied by either genus, and that it was the opening of the North Atlantic Ocean which split the ancestral genus into a western (American) and an eastern (Eurasian) portion. Following this vicariance event, the western population evolved into *Chromagrion conditum*, while the eastern one yielded *Pyrrhosoma*, which across the vast extension of its range, produced three species, viz. *P. nymphula* (Sulz.) in the western Palearctic, *P. elisabethae* Schmidt in southeastern Europe (to India?, cf. TSUDA, 1991), and *P. tinctipenne* (McL.) in southwestern China (NEEDHAM, 1930: 245).

Hesperagrion occupies the northern part of the (combined) range of those genera that are characterized by a pair of chitinized spines on the bifid apical segment of the penis. The Amazonian distribution of the very small-sized *Calvertagrion* is disjunct (Fig. 36). The range of this group of genera across southwestern North America, Central America and northwestern South America could indicate phylogenetic relationships



Figs 35-37. Distribution maps: (35) transatlantic disjunction between *Chromagrion* (C) and *Pyrrhosoma* (P); – (36) total range of American coenagrionid genera with bifid apical penis segment beset with a pair of chitinized spine-like processes (A = *Anisagrion*+*Apanisagrion*, C = *Calvertagrion*, H = *Hesperagrion*); – (37) range of *Zoniagrion exclamationis* (Z) in northwestern California.

with the genera on the other side of the Pacific Ocean, but these were not evidenced so far.

Zoniagrion has a restricted range in northwestern California (Fig. 37). This could suggest quite unexpected relationships. HEADS (1999: 400) states that "the California--Chile disjunction is a taxonomically widespread distribution pattern found in many plants and animals with varied ecology and means of dispersal". A number of such taxa is listed in CHIN et al. (1991). There is only one coenagrionine genus endemic to Chile, viz. *Antiagrion*. The penis of *Antiagrion* has, however, a well-developed "true" internal fold, and the genus shows only limited similarity with *Zoniagrion* in other features. Possible transpacific relationships of *Zoniagrion* (and of *Antiagrion*) may also be considered. Many tracks linking disjunct related taxa on both sides of the Pacific Ocean have already been identified (CROIZAT, 1958, CRAW et al., 1999 and references cited therein). Comparative mitochondrial DNA analyses may perhaps solve such questions in the future, especially where comparative morphology alone yields ambiguous results. At present, the comparative morphological study suggests that *Zoniagrion* is a member of KENNEDY's (1920) "Enallagma-Acanthagrion series". Herein, *Zoniagrion* stands morphologically between *Acanthagrion* and *Enallagma*, combining also many adult and larval characters known in other ischnurine genera. It may be concluded, therefore, that *Zoniagrion* mirrors an evolutive condition probably present prior to the separate existence of the *Acanthagrion* and *Enallagma* lineages or, at least, an extremely basal position on the *Acanthagrion* stem. If so, *Zoniagrion* may be considered a primitive relic taxon, surviving along a limited stretch of the North American Pacific coast, including the Sacramento Valley.

ACKNOWLEDGEMENTS

I am thankfull to Dr ROSSER W. GARRISON (Azusa, CA, USA.) for helping with specimens and literature. Dr KENNETH TENNESSEN (Florence, AL, USA) provided a sketch of the labial palp of larval *Chromagrion conditum*. Mr ERICH BAUER, Verlag Erna Bauer of Keltern (Germany) kindly gave permission to reproduce some figures from Heidemann & Seidenbusch (1993). Ing. QUINTÍN ARIAS (MIZA) edited the plates. The "Consejo de Desarrollo Científico y Humanístico" (CDCH) of the Universidad Central de Venezuela covered the costs of publication.

REFERENCES

ASKEW, R.R., 1988. *The dragonflies of Europe*. Harley Books. Colchester.

BULLA, L.A., 1973. Revisión de dos especies argentinas del género Cyanallagma Kennedy (Odonata: Coenagrionidae). *Revta Soc. ent. argent* 34(1/2): 95-105.

CHIN, N., M. BROWN & M. HEADS, 1991. The biogeography of Macrocystis C. Agardh (Phaeophyta, Laminariales). *Hydrobiologia* 215: 1-11.

CONCI, C. & C. NIELSEN, 1956. *Odonata. Fauna d'Italia*. Vol. 1. Calderini, Bologna.

COSTA MARTINS, J., 1978. Revisão do gênero Oxyagrion Selys, 1876 (Odonata: Coenagrionidae). *Publçoes avuls. Mus. nac. Rio de J.* 61: 1-216.

CRAW, R.C., J.R. GREHAN & M.J. HEADS, 1999. *Panbiogeography: tracking the history of life*. Oxford

[*Biogeography* ser. 11].

CROIZAT, L., 1958. *Panbiogeography*, Vols. 1, 2a, 2b. The Author, Caracas.

DE MARMELS, J., 1990. Nota sobre dos "formas" en Acanthagrion fluviatile (De Marmels, 1984) y una descripción de la náyade (Odonata: Coenagrionidae). *Boln ent. venez.* (N.S.) 5(15): 116-122.

DE MARMELS, J., 1997. New and little-known species of Cyanallagma Kennedy, 1920 from the Andes and from Pantepui (Zygoptera: Coenagrionidae). *Odonatologica* 26(2): 135-157.

HEADS, M., 1999. Vicariance biogeography and terrane tectonics in the South Pacific: analysis of the genus Abrotanella (Compositae). *Biol. J. Linn. Soc.* 67: 391-432.

HEIDEMANN, H. & R. SEIDENBUSCH, 1993. *Die Libellenlarven Deutschlands und Frankreichs: Handbuch für Exuviensammler.* Erna Bauer, Keltern.

KENNEDY, C.H., 1916. Notes on the penes of Zygoptera (Odonata), 1. Species limits in the genus Acanthagrion. *Ent. News* 27: 325-330.

KENNEDY, C.H., 1917. Notes on the life history and ecology of the dragonflies (Odonata) of central California and Nevada. *Proc. U. S. natn. Mus.* 52: 483-635.

KENNEDY, C.H., 1920. The phylogeny of the zygopterous dragonflies as based on the evidence of the penes. *Ohio J. Sci.* 21: 19-29.

LEONARD, J.W., 1977. A revisionary study of the genus Acanthagrion (Odonata: Zygoptera). *Misc. Publs Mus. Zool. Univ. Mich.* 153: 1-173.

NEEDHAM, J.G., 1903. Aquatic insects of New York State. 3. Life histories of Odonata, suborder Zygoptera. *Bull. N. Y. St. Mus.* 68: 218-279.

NEEDHAM, J.G., 1930. A manual of the dragonflies of China: a monographic study of the Chinese Odonata. *Zool. sin.* (A) 11: 1-344, 20 pls excl.

RIEK, E.F. & J. KUKALOVA-PECK, 1984. A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Can. J. Zool.* 62(6): 1150-1166.

ROBERT, P.-A., 1959. *Libellen (Odonaten).* Kümmerly & Frey, Bern.

SCHMIDT, E., 1948. Pyrrhosoma elisabethae n. sp., eine neue Odonatenart aus Griechenland. *Opusc. ent.* 13: 69-74.

SELYS-LONGCHAMPS, E. de, 1876. Synopsis des agrionines, 5me légion: Agrion (suite). *Bull. Acad. Belg.* 41(2/3): 3-282 [reprint].

TSUDA, S., 1991. *A distributional list of World Odonata, 1991.* Tsuda, Osaka.

WALKER, E.M., 1953. *The Odonata of Canada and Alaska*, Vol. 1. Univ. Toronto Press.

WESTFALL M.J. & M.L. MAY, 1996. *Damselflies of North America.* Scient. Publishers, Gainesville, FL.