

Phylogeny and taxonomy of the damselfly genus *Enallagma* and related taxa (Odonata: Zygoptera: Coenagrionidae)

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Abstract. The zygopteran genus *Enallagma* has been the subject of numerous behavioural and ecological studies, but phylogenetic relationships among species have been examined only within eastern North America, and even the composition and diagnosis of the genus are unclear on a world-wide basis. Most authorities currently recognize about seventy species within *Enallagma*, comprising two major radiations, in North America and Africa. This study, using morphological data, demonstrates that the North American and a few related Palaearctic species form a monophyletic group that is quite distinct from the African species. The latter are themselves divided into at least three, and probably four, separate clades, one of which may be related to *E. parvum* of India. Consequently, three of Kennedy's long disused genera, *Africallagma*, *Amphiallagma* and *Proischmura* (Kennedy, 1920) are resurrected and two new genera, *Azuragrion* gen.n. and *Pinheyagrion* gen.n. are established for the remaining African taxa. Finally, *Enallagma* is divided into two subgenera, *Enallagma s.s.*, the typical 'bluets', including many North American, Holarctic and Palaearctic species, and *Chromatallagma* subgen.n., comprising a group of species of more variable colour that is confined to North America, the Caribbean and northernmost South America.

Introduction

Genus *Enallagma*, as it is usually understood today, is among the largest in Zygoptera, with about seventy species. It is also a biogeographical anomaly, with two strong, disjunct centres of diversity: in North America (c. forty species), especially eastern North America, and in sub-Saharan Africa (c. twenty species), with a scattering of species in the Palaearctic and Oriental Regions. The marked concentration of species in two areas that have been geologically separated since around the end of the Cretaceous (Windley, 1984), and that have no species in common, in itself suggests the independent evolution of at least two clades in these regions. The principal aim of this study was to investigate, using morphological characters and cladistic methods, the phylogeny of this genus, with an aim to resolving the apparent paradox of its distribution and determining, in broad outline, the pattern of evolutionary relationships within it.

These damselflies are of considerable interest, not only because they dominate coenagrionid assemblages in large sections of temperate North America and also include very common species in Europe and Africa, but also because they have been the subjects of extensive behavioural, ecological and evolutionary study, e.g. adult mating behaviour and reproductive success (Bick & Bick, 1963; Bick & Hornuff, 1966; Fincke, 1982, 1985, 1986; Martens & Grabow, 1994; Samways, 1994), adult dispersal (McPeck, 1989; Anholt, 1990), larval behaviour (Baker, 1986; Chowdhury & Corbet, 1989; McPeck, 1990b), population biology (Parr, 1976; Macan, 1977; Anholt, 1992), guild and community structure (Johnson *et al.*, 1984; McPeck, 1990a; McPeck & Brown, 2000), morphology of the reproductive system (Srivastava & Srivastava, 1986), morphological development of larvae (Pilon, 1982, 1994) and speciation (McPeck & Brown, 2000). To place these studies in a sound comparative context, information on the phylogeny of this group is essential. Brown *et al.* (2000) proposed a phylogeny including most of the North American species, based on morphology and on sequence data from the mitochondrial genes, COI and COII. The current study extends their results, using morphology alone, to allow a preliminary understanding of relationships among most of the species world-wide.

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Part of the difficulty in determining the composition of, and relationships among, many coenagrionoid genera lies in the facts that their venation is much reduced (Munz, 1919; Williamson & Williamson, 1924) and many attributes that have been treated as discrete are continuously distributed (O'Grady, 1998). This seriously restricts the utility of characters that are traditionally used to distinguish damselfly taxa. *Enallagma* is generally characterized as having the wing petiolation ending before Ac, postocular spots present, females with a vulvar spine on the sternum of abdominal segment 8, and M_2 separating from M_1 near the fifth and fourth postnodal crossveins in fore- and hindwings, respectively (de Selys-Longchamps, 1876; Westfall & May, 1996). These are all shared with numerous other taxa, however, and the last is not constant among *Enallagma*. In practice, *Enallagma* is to a large extent recognized by the absence of characters that distinguish related genera, e.g. the dorsoapical prominence of abdominal segment 10 in male *Ischnura*. Appropriate synapomorphies have not been recognized that could serve to delineate this genus unambiguously. This is the first cladistic analysis to focus on phylogenetic relationships among *Enallagma* and phenetically similar genera, as well as among species of *Enallagma*.

The results suggest that the North American assemblage, plus the Palearctic species closely related to *E. cyathigerum*, constitute a monophyletic group that can be subdivided into at least two, and possibly three, clades corresponding more or less to the three species groups proposed by Walker (1958). The Oriental and African species are probably polyphyletic and, at least in some instances, not closely related to true *Enallagma*. Kennedy (1920) proposed that the Oriental species, *E. parvum*, should be placed in a separate genus, *Amphiallagma*, and that the African species be assigned to three different genera, *Proischnura*, *Africallagma* and *Ischnallagma*. These genera have not been widely accepted, but evidence is provided for the probable validity of all but the last, and in addition two new genera and a new subgenus within *Enallagma* are proposed.

Methods

Character and species selection

Forty-seven morphological and one ecological/behavioural character (Appendix 1) were scored for sixty-six species of Coenagrionidae (Fig. 1; Appendix 3). Structural characters were examined and photographed using an Hitachi™ S510 scanning electron microscope after coating with gold-palladium.

For a number of species, especially from outside North America, some characters, mostly of larvae, could not be scored due to lack of material, although in a few cases information was supplemented from the literature. Character states are judged to be qualitatively discrete, although this was confirmed by morphometric analysis only for male stature (Appendix 1). Male or female secondary sexual characters are emphasized throughout much of this analysis and in Figs 3–8 because these are among the relatively few structural

features that vary consistently among these taxa (May, 1993), and certain suites of such characters seem to be very well correlated with cladistic groupings. Note that characters were selected based on personal and others' examination of *Enallagma*, in the broadest sense (i.e. Bridges, 1994), but not, for the most part, on Coenagrionidae generally. Thus, inferred relationships among species not placed in *Enallagma* by Bridges are suspect because characters thought to indicate those relationships, but judged not useful for *Enallagma*, are not included. These species were included because the sister taxon to *Enallagma* is unclear, so it seemed prudent to include several possibly related taxa.

The species include thirty-eight North American (among which are five principally Central American or Antillean species: *E. coecum*, *E. novaehispaniae*, *E. rua*, *E. semicirculare* and *E. truncatum*; and one Holarctic species, the type species, *E. cyathigerum*), one Oriental (*E. parvum*) and sixteen African species (including *E. granti* from Socotra Island) recognized and attributed to *Enallagma* by Bridges (1994), and nine species not included in *Enallagma*. Taxonomic changes subsequent to Bridges' list mostly follow May (1997): *E. camerunense* is transferred to *Pseudagrion*, *E. kauderni* is considered distinct from *E. nigradorsum*, *E. melanotum* is transferred to *Cercion*, *E. pseudelongatum* is considered distinct from *elongatum* and *E. strouhali* is regarded as a junior synonym of *E. risi*. I have subsequently examined the paratype male of *E. caputavis* Terzani & Carletti and found that it actually belongs in *Pseudagrion*, a conclusion with which the describers concur (Terzani, personal communication). Also, *Enallagma brevispina* Selys was earlier shown to be a synonym of *Ischnura senegalensis* (Rambur) (Asahina, 1956), and *E. kagiensis* (Matsumura) a synonym of *Agriocnemis pygmaea* (Rambur) (Liefstinck *et al.*, 1984).

Enallagma vaginale and *E. longifieldae* are doubtfully distinct (Pinhey, 1963) and are here considered a single taxon, although insufficient material was available to make a careful judgement of their relationship. Likewise the various forms of *E. coecum* (Westfall & May, 1996) are not distinguished here, although they may encompass more than one valid taxon. The following species are not included in this study due to lack of material: *E. ambiguum* Navás, *E. belyshevi* Haritonov, *E. buchholtzi* Pinhey, *E. deserti* (Selys), *E. insula* Fraser, *E. maldivensis* Laidlaw, *E. nigrolineata* Belyshev & Haritonov and *E. optimolocus* Miller & Ivie. *Thermagrion webbianum* Förster was placed by Bridges (1994) and others in *Enallagma*, apparently based on a speculation by Pinhey (1962). The type has not been re-examined to my knowledge, and its whereabouts is unknown (M. F. O'Brien, personal communication). The identity of the species is difficult or impossible to determine from the description of the single female specimen. Consequently, I see no basis for moving it to *Enallagma*, and it is not treated here.

Analysis

Cladistic analysis based on maximum parsimony was carried out using heuristic searches (100–1000 randomized

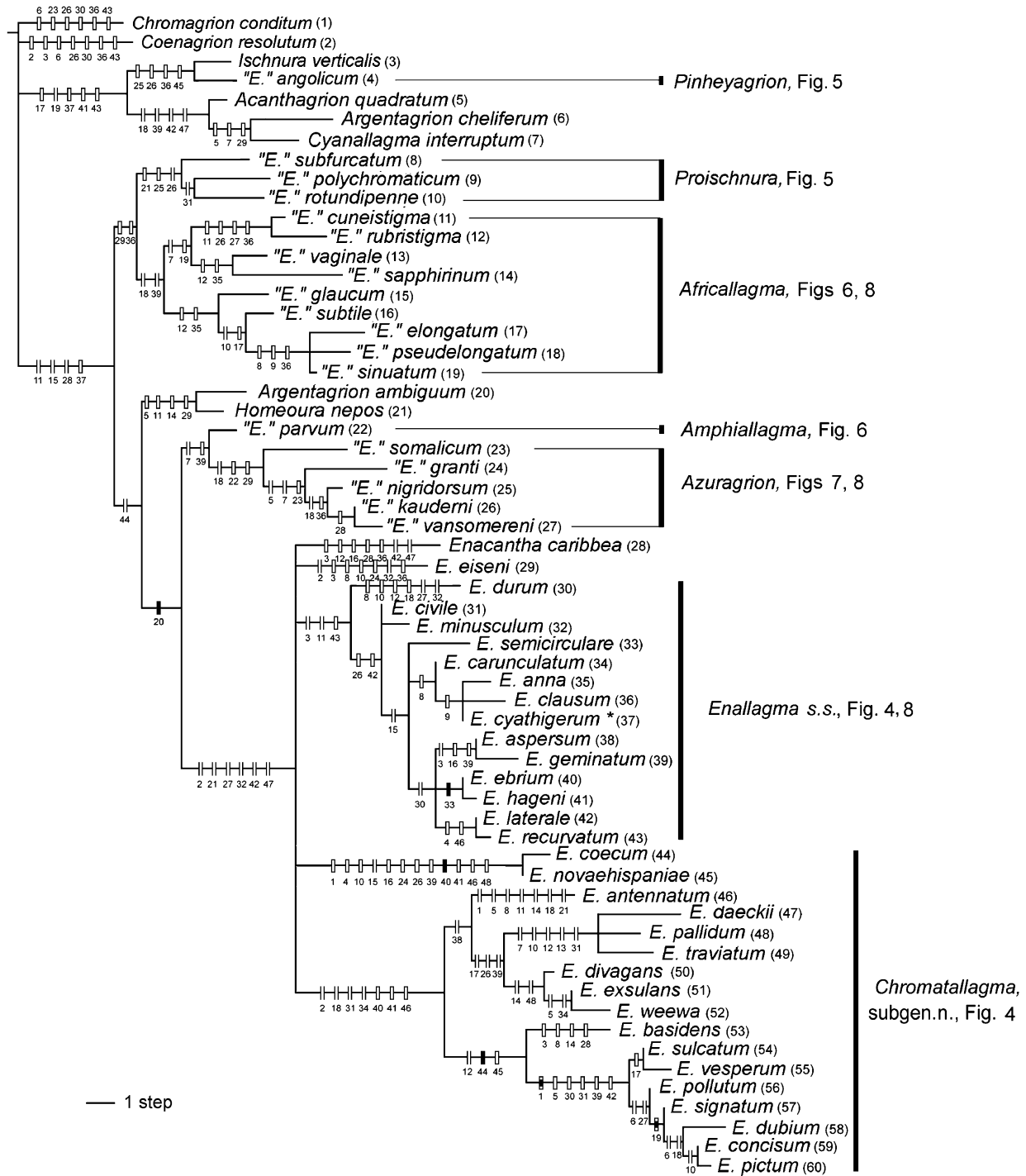


Fig. 1. Phylogram of strict consensus tree summarizing ninety-six shortest (190.50 steps) trees using 'scaled', equally weighted characters (see text) to estimate relationships among *Enallagma* and related genera. Character changes are shown as short vertical bars: filled, no homoplasy; half filled, unique appearance of one state of multistate character; unfilled closed, parallel homoplasy elsewhere on tree; open, multiple changes within clade where bar appears (note that, once a character of this category appears on a branch, subsequent changes are also shown using the open bar symbol, e.g. ch. 2 is also shown as open when changing 0 → 1 at the base of clade 28–60 and again when reversed in *E. eiseni* and clade 46–60). Changes are not shown on all terminal branches owing to space limitations. Generic identity of terminal taxa is shown as *E.* for species retained in *Enallagma*, '*E.*' for those transferred in this paper to other genera. Species are numbered consecutively from the basalmost clades, and these identifying numbers are used to designate species in Fig. 2 and Appendix 3. Species compositions of new or redefined genus-group taxa are indicated by vertical bars at right. Asterisk indicates *E. cyathigerum*, the type species of *Enallagma*.

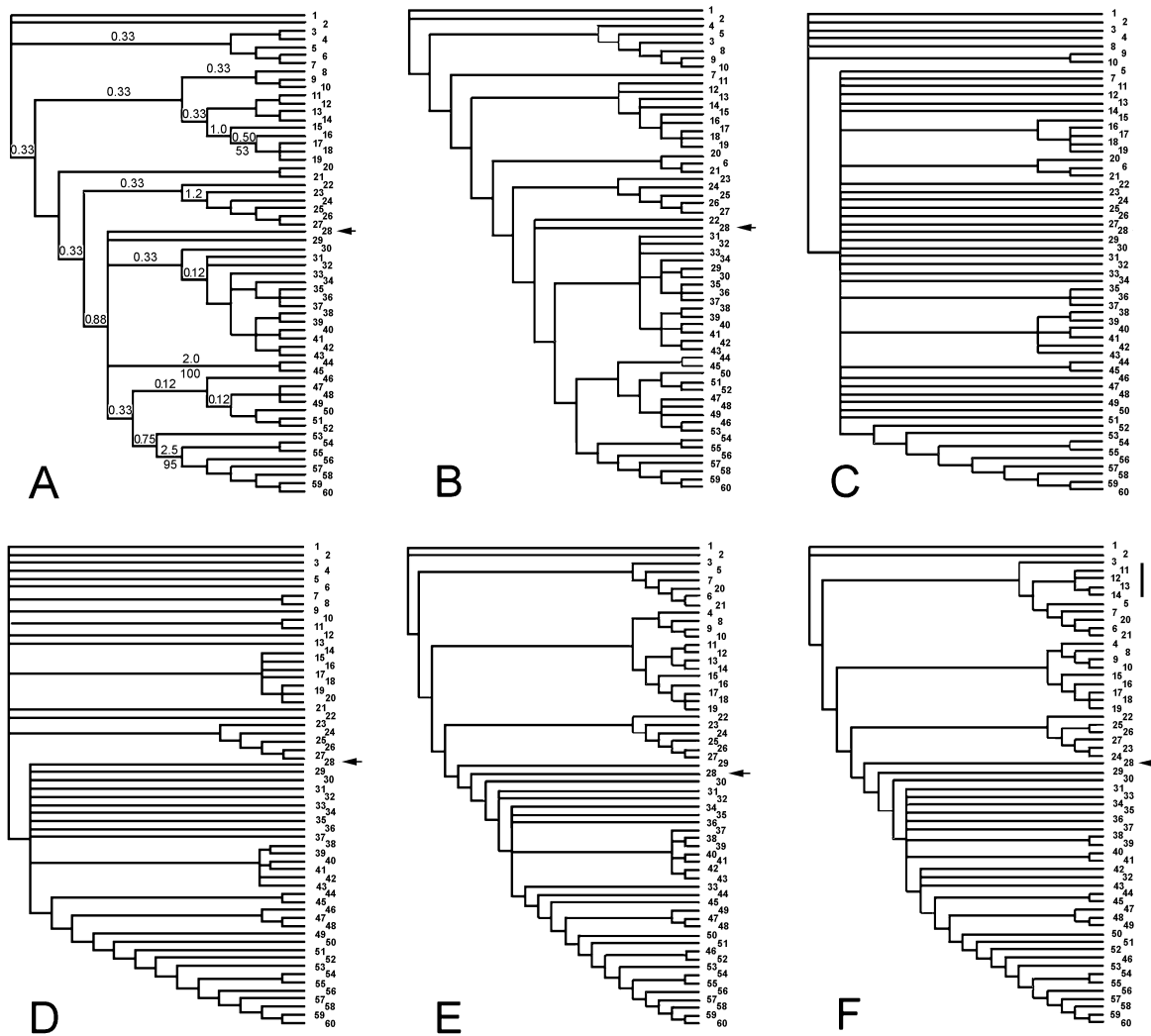


Fig. 2. Six strict consensus trees showing results of alternative character weightings (note that, because of different weightings, tree lengths are not directly comparable). A, Weighting and tree topology as in Fig. 1, numbers above and below branches are decay indices and bootstrap values $>50\%$, respectively; B, consensus of six trees, length 110.96, weighting as in A except that characters referring to colour or habitat preference were downweighted fivefold relative to structural characters; C, consensus of 501 trees, length 297, using 'unscaled' equal weighting, i.e. giving each character state transition equal weight regardless of the number of states per character; D, consensus of 444 trees, length 164.80, weighting as in C except that characters referring to colour or habitat preference were downweighted fivefold relative to structural characters; E, consensus of sixty-three trees, length 54.07, starting with the ninety-six trees summarized by Fig. 1 and iteratively reweighting each character by its RCI until constant length was attained; F, consensus of fifty trees, length 126.04, starting with 100 bootstrap trees reweighted according to RCI using 'best' option with multiple trees (Kjer *et al.*, 2001). Small arrowheads indicate position of *Enacantha caribbea*, vertical line in F indicates the unusual position of *Africallagma cuneistigma*, *A. rubristigma*, *A. sapphirinum* and *A. vaginale*.

replicates) on PAUP 4.0b4a (Swofford, 1999). Although several weightings were tested, except when otherwise noted, each character was weighted equally regardless of character type and the number of character states ('scaled' equal weighting). Because some characters have multiple states, state transitions were, in effect, downweighted in proportion to the number of states for these characters relative to binary characters. This results in fractional tree and branch lengths. Other weightings examined included equal weighting for each state change ('unscaled' equal weighting); downweight-

ing characters based on coloration and habitat (because these are often variable within species) by a factor of five, iterative reweighting (Farris, 1969) based on rescaled consistency index, and reweighting using the method of Kjer *et al.* (2001).

All characters are unordered, i.e. change is equally likely between any pair of states. In each analysis, trees were rooted using only *Chromagrion conditum* as the outgroup. Species with character scoring identical to another species were omitted to speed analysis without changing tree lengths; these species included *E. boreale*, *E. circulatum*,

and *E. risi* (identical to *E. cyathigerum*), *E. davisi* (= *E. recurvatum*), *E. doubledayi* (= *E. civile*), *E. praevarum* and *E. rua* (= *E. anna*) and *E. truncatum* (= *E. signatum*).

Decay indices (Bremer, 1988) were calculated for selected branches by searching for the shortest trees that excluded that branch, i.e. prevented monophyly of the clade originating from the ancestor represented by that branch. Support for separation of certain groups of taxa was evaluated by finding the shortest trees in which pairs of those groups were constrained to be monophyletic and comparing tree lengths with that of the shortest unconstrained trees. In addition, bootstrap analyses (100 bootstrap replicates, five random replicates per bootstrap replicate) were performed for the scaled equal weighting trees.

Results

A strict consensus tree of the ninety-six shortest trees (length 190.50) is presented in the form of a phylogram

(branch lengths approximately proportional to the number of character state changes) in Fig. 1. Bars to the right indicate hypothesized clades that I suggest should receive taxonomic recognition (see Discussion). Clearly, none of the major clades is strongly supported by either decay index or bootstrap values (Fig. 2A), but note that this is true also of basal branches where *Ischnurinae* (Davies & Tobin, 1984; spelling, see Fet & Bechly, 2000) separate from presumably much more distantly related taxa. Confidence in the reality of several important clades is substantiated by their refractoriness to various alternative weightings (Fig. 2).

North American *Enallagma* species appear to form a monophyletic group, except for the inclusion in the clade of *Enacantha caribbea*. Uncertainty exists about the placement of *Enacantha* (Fig. 2B,F), but otherwise this conclusion is supported by all weightings except unscaled equal weighting, which leaves almost the entire tree unresolved (Fig. 2C). The possibility clearly must be considered that *Enacantha* should be subsumed within *Enallagma*. The male

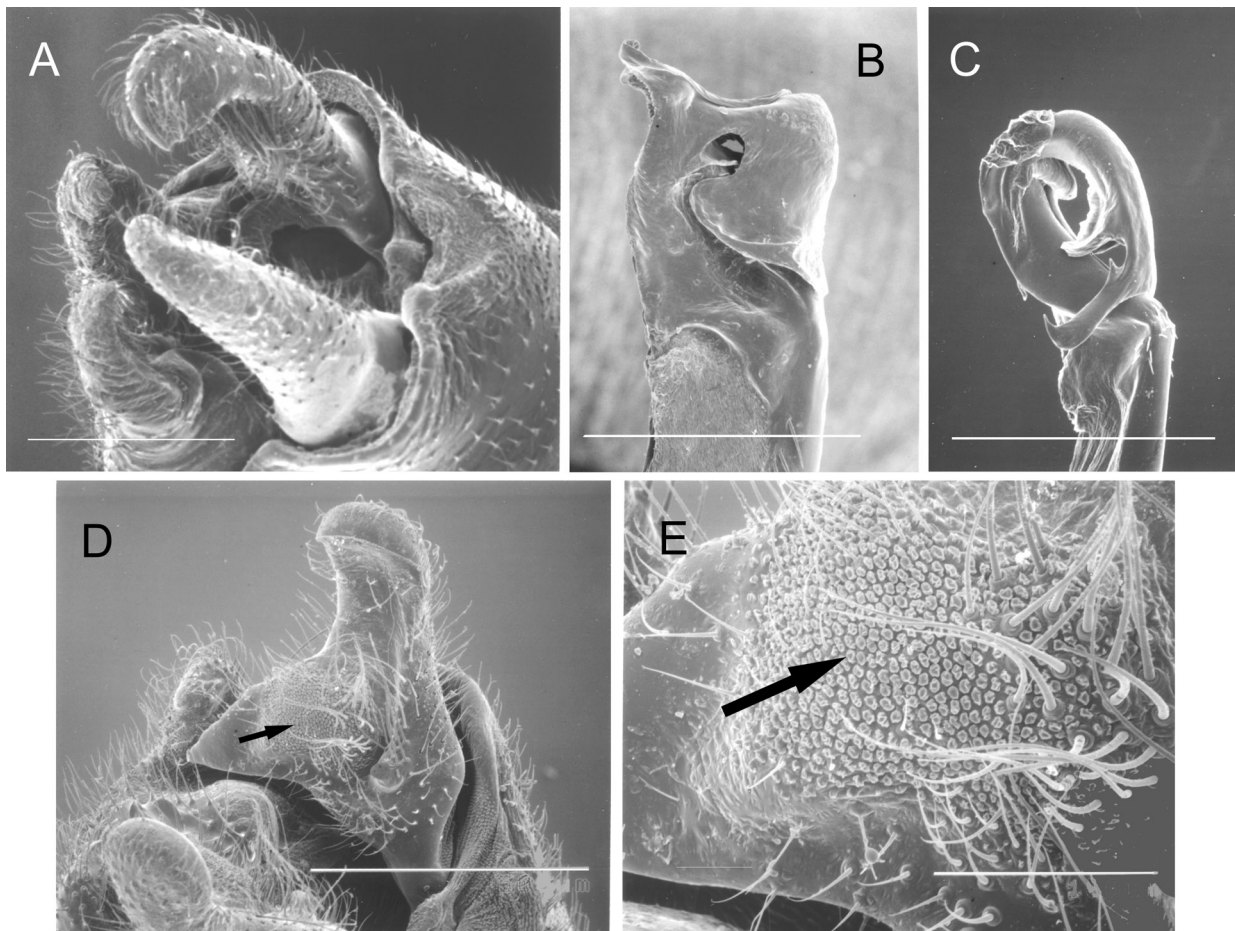


Fig. 3. Scanning electron micrographs of penes and male caudal appendages of putative outgroup genera. A, Oblique dorsolateral view of cerci and paraprocts of *Chromagrion conditum*; B, lateral view of distal portion of penis of *C. conditum*; C, ventrolateral view of distal portion of penis of *Enacantha caribbea*; D, oblique internal view of left cercus of *E. caribbea*; arrow indicates scalariform cuticle; E, detail of C. showing apparent scalariform cuticle (arrow). Scales = 0.05 mm (E); 0.25 mm (B,C); 0.50 mm (A).

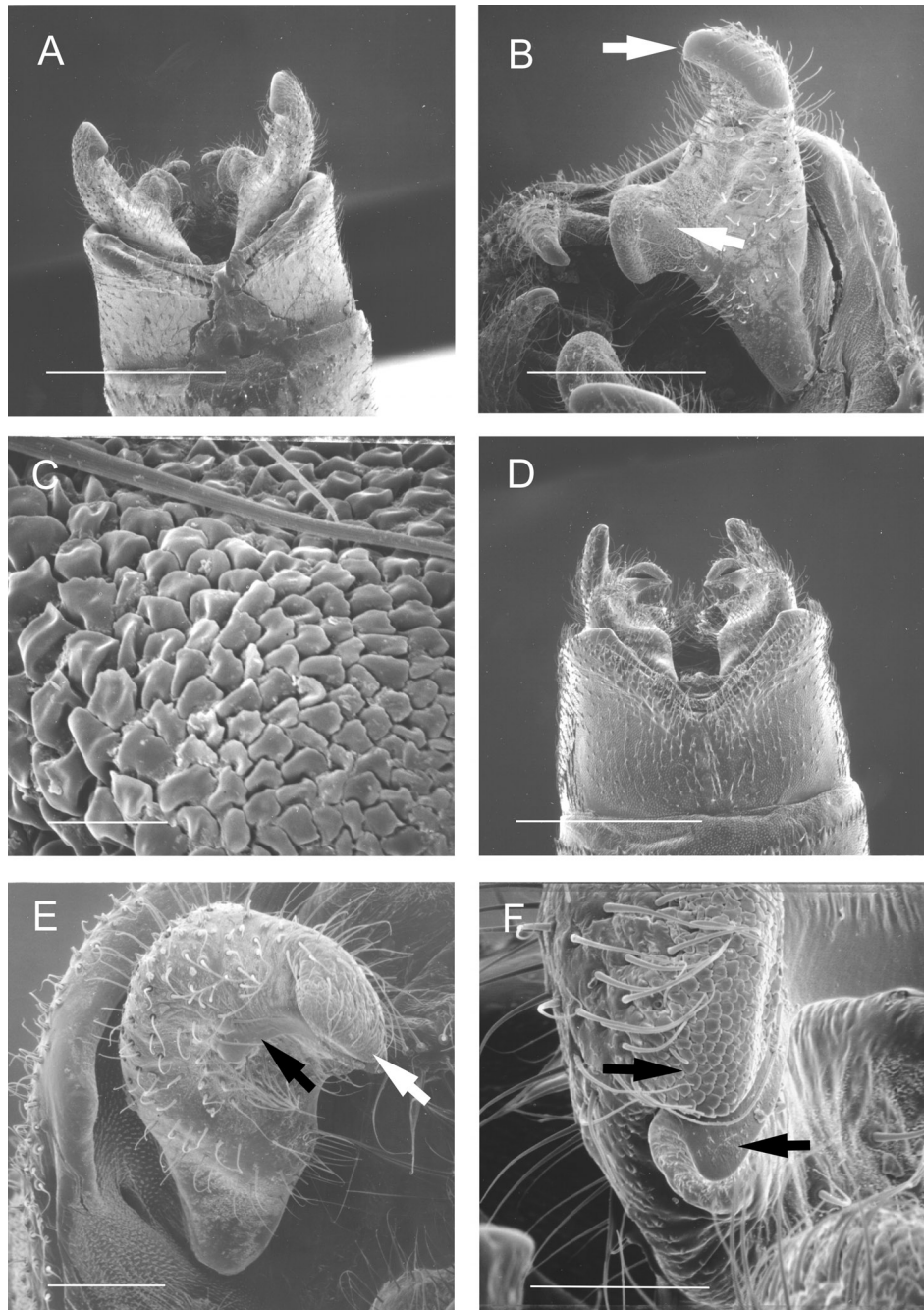


Fig. 4. Scanning electron micrographs of penes and male caudal appendages of representative *Enallagma*, including *Chromatallagma*, subgen.n. A, Dorsal view of caudal appendages of *E. (Enallagma) aspersum*; B, oblique internal view of left cercus of *E. aspersum* showing scalariform cuticle (arrow); C, detail of scalariform cuticle from B; D, as in A, *E. (Enallagma) cyathigerum*; E, as in B, *E. cyathigerum*, with transversely elongated terminal hook of reduced dorsal arm and scalariform cuticle overlapping terminal hook (arrows); F, extreme tip of right cercus of *E. cyathigerum* showing portion of terminal hook and overlapping scalariform cuticle (arrows); G, lateral view of male caudal appendages of *Enallagma eiseni*, with short, dorsally directed paraproct (arrow); H, as in B, *E. eiseni* (cf. Fig. 3D); I, oblique internal view of right cercus of *E. (Chromatallagma) signatum*, inferior branch fused to superior branch (arrows), scalariform cuticle covering medial surface of both; J, as in B, right side, *E. (Chromatallagma) antennatum*; K, detail of J., scalariform cuticle absent on inferior branch of cercus; L, ventral view of distal portion of penis of *E. cyathigerum*, showing distolateral and lateral lobes (arrows); M, as in L, *E. antennatum*; N, lateral view of distal portion of penis of *E. signatum*; arrow indicates large bladeliike internal spine. Scales = 0.01 mm (C); 0.10 mm (E,K); 0.25 mm (B,L,M); 0.50 mm (A,D,F,G–J,N).

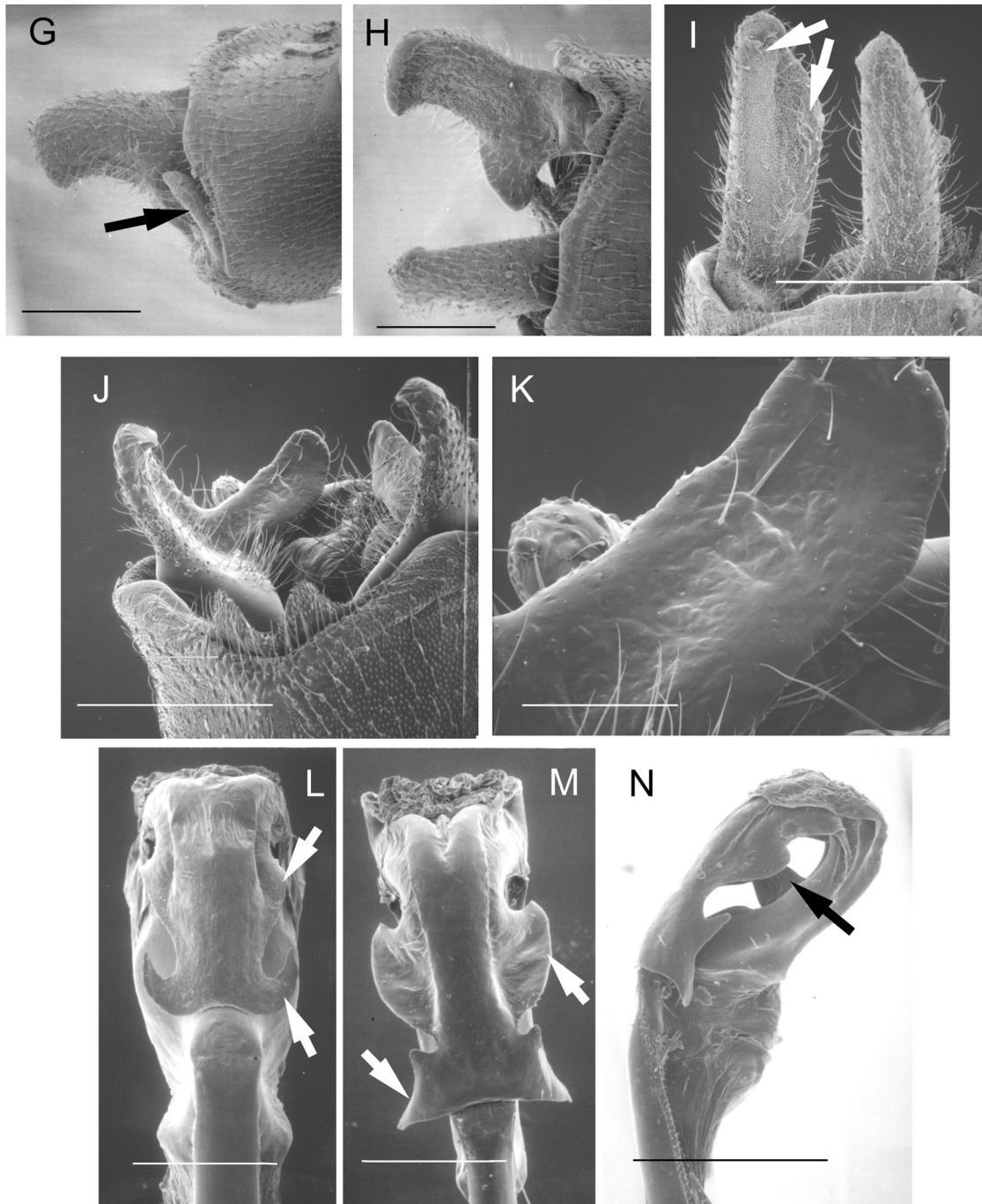


Fig. 4. Continued.

cerci are very similar, especially to *Enallagma eiseni* (Figs 3D, 4H) although, as noted by Donnelly & Alayo (1966), the penis of *Enacantha* is highly autapomorphic (Fig. 3C) and the male pterostigmata are bicoloured. Forcing monophyly between North American clade (excluding *Enacantha*) and the various African and Oriental taxon groupings increases tree length by one to four steps (Table 1). North American species are thus probably

monophyletic with respect to the other so-called *Enallagma*, although they may be close to *E. parvum* and the *E. nigridorsum* species group. They are unique in possessing scalariform cuticle (Fig. 4B,C,E,F; secondarily lost in *E. antematum*, Fig. 4K), a characteristic hook terminating the superior arm of the male cercus, and in penis structure (Fig. 4). The morphology of the cercus is shown very clearly by *E. aspersum* (Fig. 4A–C) and in considerably modified

Table 1. Added steps required to force the taxon sets indicated in columns 1 and 2 into monophyly, assuming 'scaled', equal character weighting, as in Fig. 1.

Merged taxon sets		Added steps
All African ' <i>Enallagma</i> '	N. A. <i>Enallagma</i>	4.00
' <i>E.</i> ' <i>angolicum</i>	N. A. <i>Enallagma</i>	4.12
' <i>E.</i> ' <i>subfurcatum</i> group	N. A. <i>Enallagma</i>	2.46
' <i>E.</i> ' <i>glaucum</i> group*	N. A. <i>Enallagma</i>	2.62
Extended ' <i>E.</i> ' <i>glaucum</i> group**	N. A. <i>Enallagma</i>	2.50
' <i>E.</i> ' <i>nigridorsum</i> group	N. A. <i>Enallagma</i>	1.12
' <i>E.</i> ' <i>parvum</i>	N. A. <i>Enallagma</i> + <i>Enacantha</i>	0.33
<i>E. signatum</i> group	Bluet group	5.71
<i>E. signatum</i> group	Bluet group + <i>E. durum</i>	3.83
<i>E. signatum</i> group + <i>E. basidens</i>	Bluet group	5.00
<i>E. signatum</i> group + <i>E. basidens</i>	Bluet group + <i>E. durum</i>	3.46
<i>E. divagans</i> + <i>E. traviatum</i> groups + <i>E. antennatum</i>	Bluet group	4.88
<i>E. divagans</i> + <i>E. traviatum</i> groups + <i>E. antennatum</i>	Bluet group + <i>E. durum</i>	4.33
<i>E. coecum</i> group	Bluet group + <i>E. durum</i>	2.00
<i>E. coecum</i> group	<i>E. signatum</i> + <i>E. divagans</i> + <i>E. traviatum</i> groups	0.00

*Excludes *E. cuneistigma*, *E. rubristigma*, *E. sapphirinum* and *E. vaginale*.

** Includes the four species above.

form by *E. cyathigerum*, in which the superior arm is greatly reduced (Fig. 4D–F) and *E. signatum*, in which the superior and inferior arms are fused (Fig. 4I).

Among North American species, two primary clades are evident, one including the typical bluets, *E. cyathigerum*, *E. civile*, etc. (Appendix 2), the second a visually diverse species assemblage including a number of relatively slender blue species, plus the very distinctive orange *E. signatum* species group. Only the *E. signatum* group has a relatively high decay index and bootstrap support. Of uncertain placement are *E. eiseni*, *E. coecum* + *E. novaehispaniae* and *E. durum* (Figs 1, 2). The bluet group itself has relatively weak support and is not recovered by all weightings, but other evidence (see Discussion) allows for some confidence in its monophyly. It is characterized in most species by extensive dorsal blue colour of the male abdominal segments and by the characteristic penis shape (Fig. 4G; also see Donnelly, 1963).

The second ('non-bluet') clade is recovered by all weighting schemes except unscaled equal weighting. In some cases (Fig. 2), *E. coecum* and *E. novaehispaniae* (the 'coecum-group') are included at the base of this clade. Salient characters include a dark male abdomen and, again, distinctive penis morphology (Fig. 4L,N; shared with *E. durum* and *E. eiseni*; Donnelly, 1963). Forcing the major subgroups of the non-bluet clade into monophyly with the bluets increases tree length by about 3.5–5.5 steps; some minimum-length trees place the *E. coecum* group in monophyly with the non-bluets whereas at least 2.0 additional steps are required to generate a clade grouping the former with the bluets (Table 1).

All species that were placed outside *Enallagma* by Bridges (1994), except *Enacantha caribbea*, group well away from North American *Enallagma*. Of the African *Enallagma*, *E. subfurcatum* and *E. rotundipenne*, placed by Kennedy in

Proischnura, are also well separated from their supposed congeners and closely grouped with the heretofore enigmatic *E. polychromaticum* (Fig. 1; in fact the penes and male cerci are rather similar, Fig. 5), with the former having triangular projections just before the distal flexure of the penis. This general placement is also supported by most weighting assumptions (Fig. 2), and is not inconsistent with the others. *Enallagma angolicum* also often is grouped with these three species (Fig. 2), with which it shares subterminal processes on the penis (Fig. 5), but it differs markedly in size, coloration, cercal structure and the form of the lateral penile projections. It seems safe to say that *E. angolicum* is not related to North American *Enallagma* nor, in all probability, to other African species outside the *E. subfurcatum* group. All these species have very well developed lappets on the male mesostigmal plates, as in the *E. glaucum* group (see below) but unlike any North American *Enallagma*.

Two additional clades are recovered consistently. The *E. glaucum* group (*E. glaucum*, *E. subtile*, *E. elongatum*, *E. pseudelongatum*, *E. sinuatum*) appears under all weightings, except that *E. vaginale* is included within it in one instance (Fig. 2D). A somewhat more heterogeneous group, consisting of *E. cuneistigma*, *E. vaginale*, *E. rubristigma* and *E. sapphirinum*, usually appears as a sister clade to the *E. glaucum* group (but see Fig. 2F). All of these species except *E. cuneistigma* share among themselves, and with *E. angolicum* and the *E. subfurcatum* group but not with any North American species, the possession by males of paraprocts that are clearly bifurcated in lateral view (Fig. 6) and all have distinct, raised ridges or lappets on the posteromedial corner of the mesostigmal laminae, that may serve to prevent intrasexual tandem pairing (Fig. 8; considered to be present only if this area was distinctly more elevated in males than females). Most of the *E. glaucum*

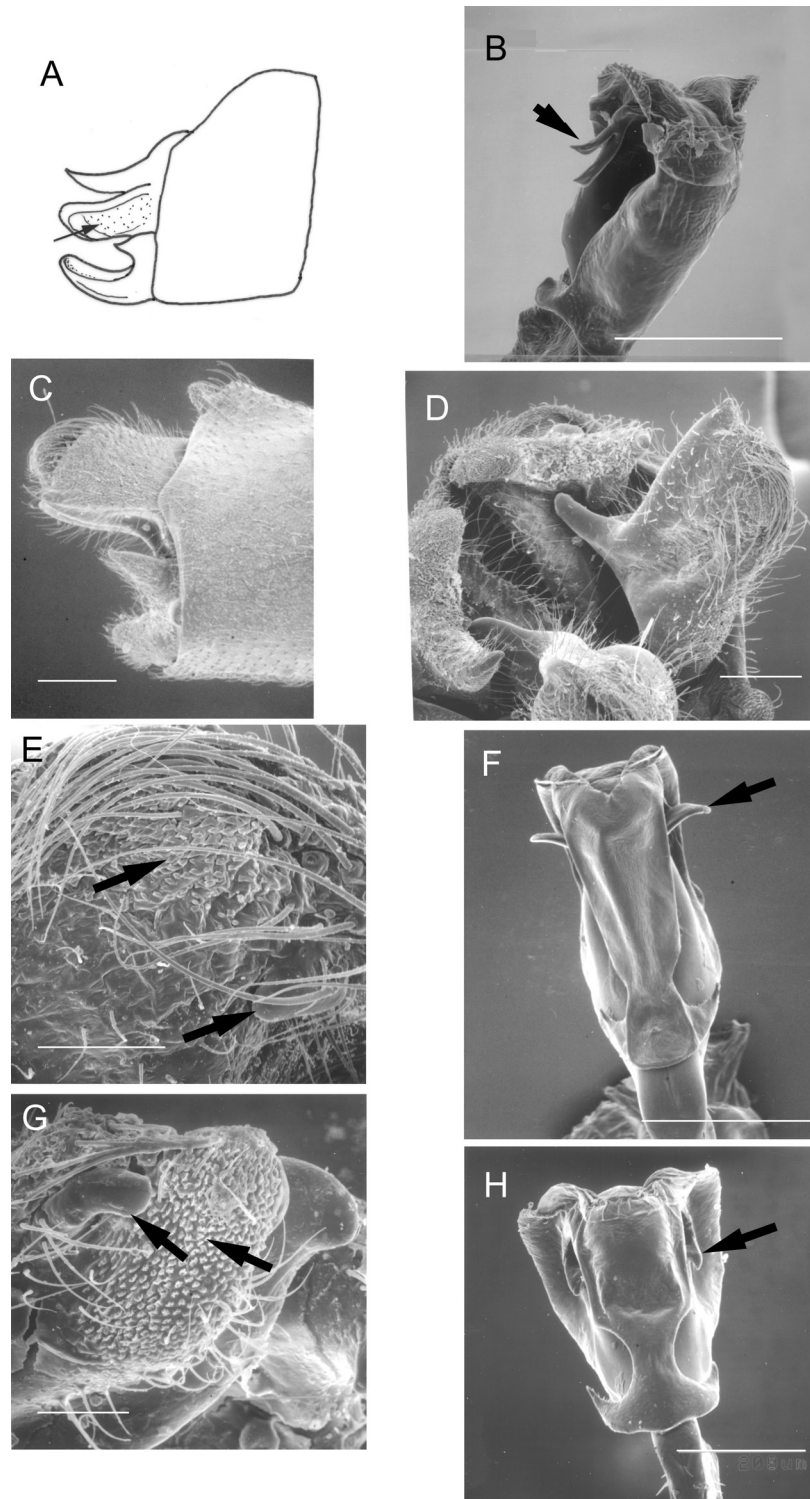


Fig. 5. Sketch and scanning electron micrographs of penes and male caudal appendages of species formerly placed in *Enallagma* but here transferred to *Pinheyagrion* and *Proischnura*. A, Lateral view of male caudal appendages of *Pinheyagrion angolicum*, arrow indicates pad of flexible cuticle; B, oblique ventrolateral view of distal portion of penis of *P. angolicum*, with bifurcated spine (arrow); C, lateral view of caudal appendages of *Proischnura subfurcatum*; D, oblique internal view of left cercus of *P. subfurcatum*; E, detail of D showing scalariform cuticle and glabrous thumblike projection (arrows); F, ventral view of distal portion of penis of *P. subfurcatum*, with tongue-like projection (arrow); G, as in E, *P. polychromaticum*; H, as in F, *P. polychromaticum*. Scales = 0.1 mm (E,G); 0.2 mm (B,F,H); 0.5 mm (D); 1.0 mm (C).

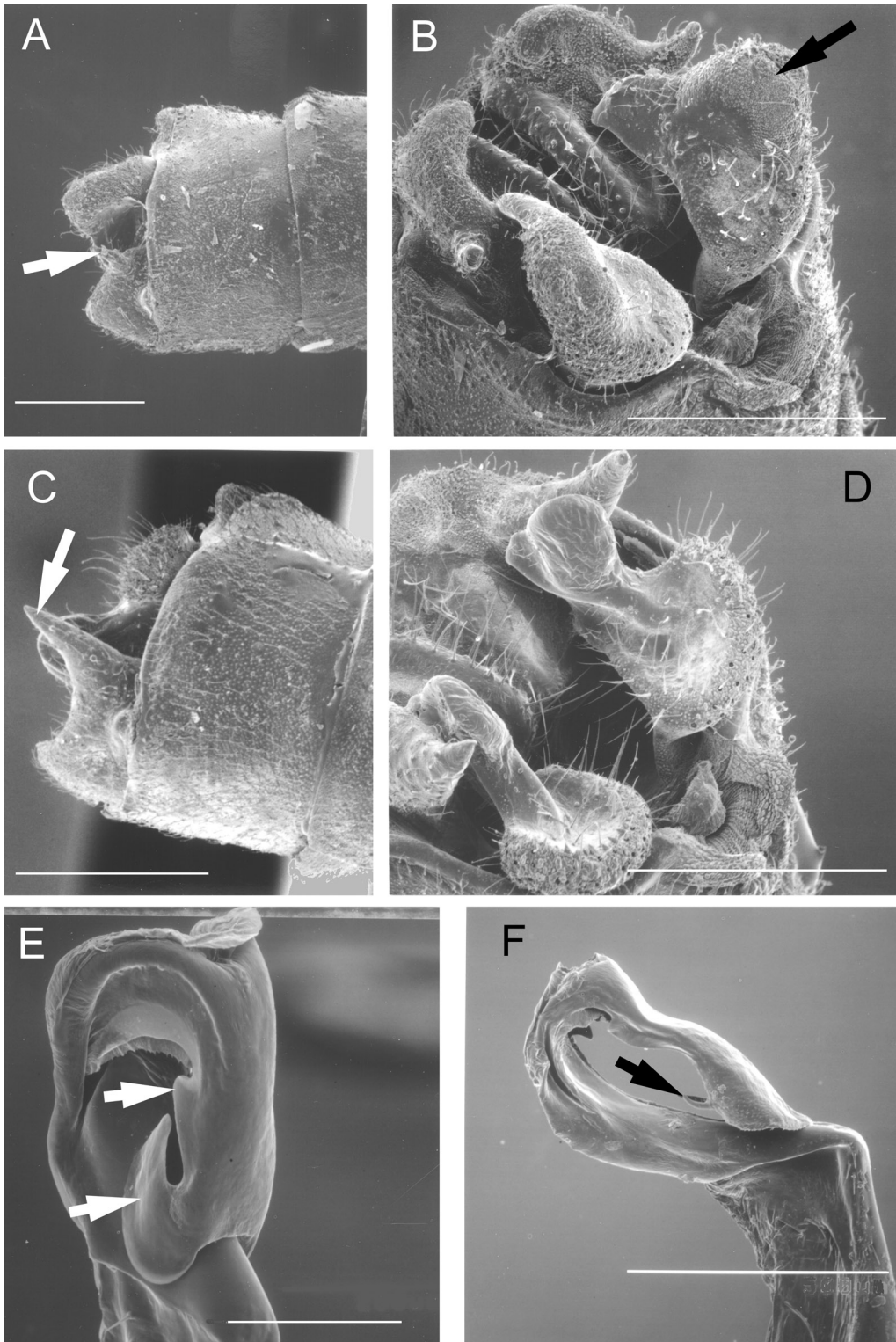


Fig. 6. Scanning electron micrographs of penes and male caudal appendages of species formerly placed in *Enallagma* but here transferred to *Africallagma*: A, Lateral view of male caudal appendages of *Africallagma glaucum*, arrow indicates superior branch of paraproct; B, oblique internal view of left cercus and paraproct of *A. glaucum* showing scalariformlike cuticle (arrow); C, as in A, *A. elongatum*; D, as in B, *A. elongatum*; E, ventrolateral view of distal portion of penis of *A. glaucum* showing distolateral and lateral lobes (arrows); F, lateral view of distal portion of penis of *A. (?) rubristigma* showing distolateral lobe (arrow). Additional figures of cerci in Fraser (1947: Fig. 1). Scales = 0.5 mm.

group are also characterized by a low anteromedial trough and flange on the female mesostigmal plate (Fig. 8).

The other African species, comprising the *E. nigradorsum* group (May, 1997), plus *E. parvum*, apparently form a clade with the North American species but as a group are sister to the North American species. Although decay index support is low, the African species are united by the very similar and distinctive structure of the male cerci (Fig. 7), with three longitudinal lobes, the upper one hooked medially and the middle one of rugose, slightly flexible cuticle (usually pale in life). *Enallagma parvum* is usually placed as sister taxon to the *E. nigradorsum* group but sometimes (Fig. 2B) to North American *Enallagma* plus *Enacantha*. The cercal structure of *E. parvum* is rather different from the African *E. nigradorsum* group (Fig. 7). All of these species agree with North American *Enallagma* in that male paraprocts are not bifurcated (a probable plesiomorphy). Lappets on the mesostigmal laminae are vestigially present (Fig. 8) except in *E. parvum*, where they are absent.

Discussion

A glance at RCI values in Appendix 1 clearly indicates one reason for the low branch support provided by conventional measures – most characters are subject to extensive homoplasy or loss, or both. Perhaps the most characteristic identifying feature of North American *Enallagma* is the presence on the inferior branch of the cerci (Fig. 4) of ‘scalariform cuticle’ (Jurzitza, 1975; this is probably an adaptation for gripping the female prothorax during tandem pairing), yet this appears to have been lost in *E. antennatum*, perhaps shifted to the superior branch in *E. eiseni*, and to be present in much reduced form in *E. basidens*. It should be noted at this point that many coenagrionids have areas of modified cuticle on the cerci that may function in tandem linkage (the ‘middle lobe’ on the cerci of the *E. nigradorsum* group of species is a likely example; Fig. 7). Scalariform cuticle, however, is specifically characterized as consisting of an array of small protrusions, usually closely spaced (Fig. 4C), by being relatively pale and flexible, at least in freshly mature specimens, and in its position on the inferior cercal branch or a structure identifiably derived from this branch.

In addition to the problem of homoplasy, scoring of some characters is uncertain. The broad triangular projections of the middle penis segment of *E. subfurcatum* are scored as the same character state as the bifurcated ones of *E. angolicum* (Fig. 5), or the spines in this position in *Ischnura verticalis* (see, e.g. Robinson & Novak, 1997), but there surely is room for doubt about the homology of these structures.

Character weighting is also problematic. Several characters have numerous possible states, notably thoracic colour and shape of the terminal penis segment. These could, of course, be resolved into sets of binary characters, but the result would be, in effect, to weight these characters very highly. For this reason, and because the result gives a very

well resolved tree (Fig. 1), I suggest the equally weighted tree using scaled characters as most likely to reflect the true phylogeny, but attention to other weighting possibilities is important. For example, downweighting colour and ecological characters by up to fivefold relative to structural ones does not change the main relationships, although it reduces resolution within some groups (Fig. 2), nor does specifically upweighting penis shape fourfold.

The North American portion of the tree receives very substantial support from the work of Brown *et al.* (2000). Although they examined fewer species, their data included a slightly different morphological dataset as well as sequence data from COI and COII mtDNA, and maximum likelihood as well as parsimony analysis. Their results very largely support those reported here, and in particular support the monophyly of the bluet clade, including *E. durum*, very strongly. Their results also suggest recent, very rapid morphological evolution within this clade, which may have made it more difficult to recover it consistently using morphological characters alone (Fig. 2).

More recent unpublished molecular data from these mitochondrial genes (McPeck, personal communication) places Palaearctic specimens of *E. cyathigerum*, as well as Palaearctic species not included here (*E. deserti* Selys, *E. risi*, *E. circulatum*), well within a monophyletic group including the North American bluets. Furthermore, the African *E. glaucum*, *E. nigradorsum* and *E. pseudelongatum* are all basal to *Ischnura ramburii* and *I. verticalis* in a tree rooted by *Coenagrion resolutum*, and thus they may be even more widely separated from North American *Enallagma* than suggested here.

The phylogenetic conclusions presented here suggest several taxonomic changes. For example, *E. subfurcatum*, *E. rotundipenne* and *E. polychromaticum* form a valid genus *Proischnura* that is distinct from *Enallagma s.s.*; they are clearly united by the extremely similar penile morphology and structure of the cerci (Barnard, 1937; Robertson & Patterson, 1982). Although *E. angolicum* could be included here, it is phenotypically so distinct that a very close relationship appears unlikely; it clearly is not an *Enallagma* but resembles in some respects *Ischnura aurora* and related species. I propose here a new, monotypic genus, *Pinheyagrion* gen.n., for this species (see Appendix 2 for diagnosis).

Substantial justification exists for separating the other non-North American species at the generic level. In particular, the *E. glaucum* group is well separated phenotypically and cladistically from true *Enallagma*. Thus, I propose that this group be recognized as genus *Africallagma* Kennedy (of which *Ischnallagma* becomes a junior synonym). The relationships of the four outliers to this group, i.e. *E. cumeistigma*, *E. vaginae*, *E. rubristigma* and *E. sapphirinum*, to one another and to the *E. glaucum* group are uncertain. In these species the male cerci or the penes, or both, differ somewhat from the core *E. glaucum* group, although these characters are somewhat variable within the latter as well (e.g. cerci of *E. glaucum* vs. *E. elongatum*, Fig. 6; in most species the cerci are more similar to those of *E. glaucum*).

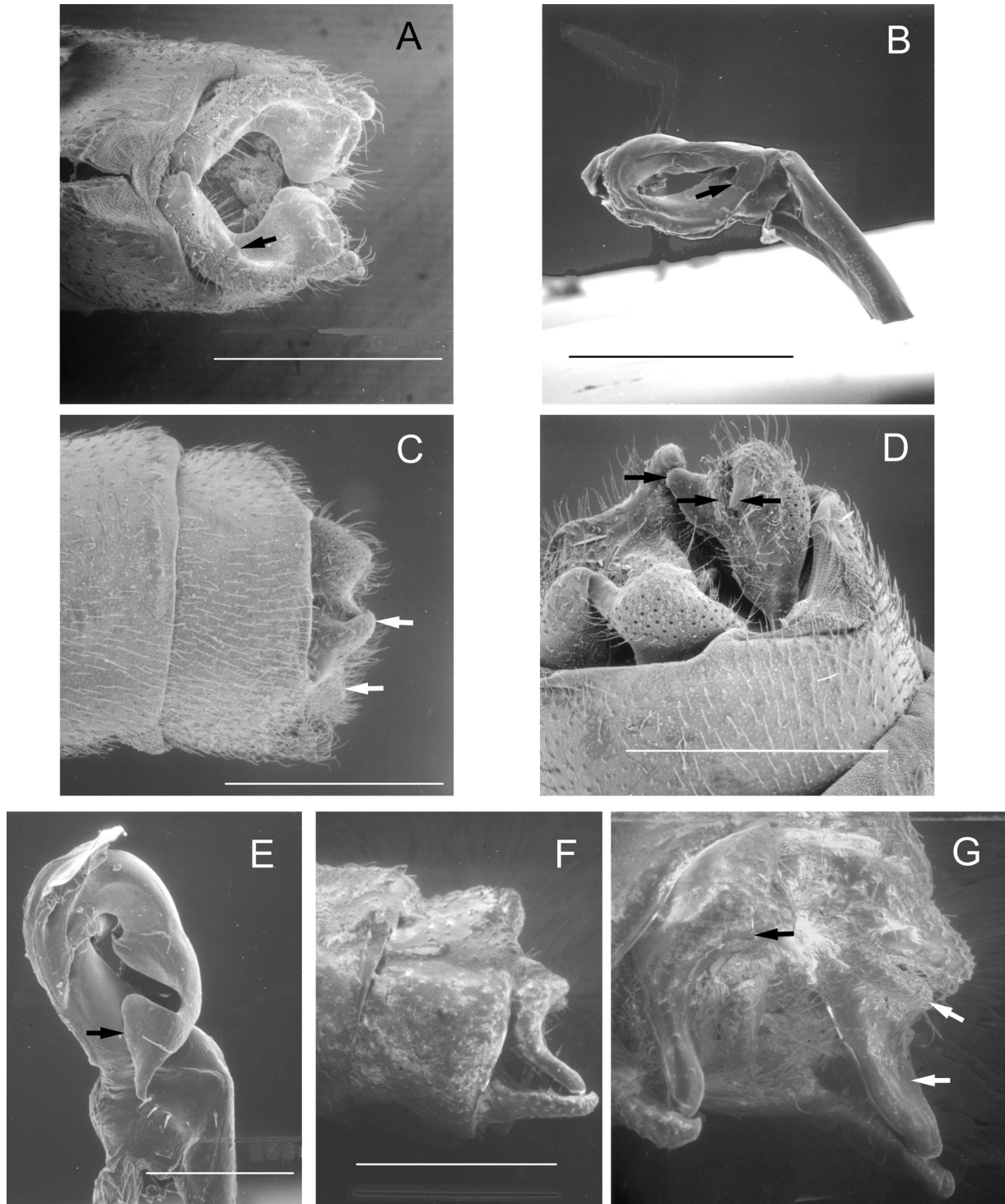


Fig. 7. Scanning electron micrographs of penes and male caudal appendages of species formerly placed in *Enallagma* but here transferred to *Amphiallagma* and *Azuragrion*. A, Dorsal view of male caudal appendages of *Amphiallagma parvum*, showing dorsal tubercle (arrow); B, lateral view of distal portion of penis of *A. parvum* showing distolateral lobe (arrow); C, lateral view of male caudal appendages of *Azuragrion nigridorsum* showing superior branch and inferior protrusion of paraproct (arrows); D, oblique internal view of left cercus and paraproct of *A. nigridorsum* showing subterminal dorsal hook, middle lobe, and inferior arm of cercus (arrows); E, lateral view of distal portion of penis of *A. nigridorsum* showing distolateral lobe (arrow); F, as in C, *A. somalicum* (specimen is uncoated); G, as in D, *A. somalicum* (uncoated). Additional figures in May (1997). Scales = 0.2 mm (B,E); 0.5 mm (A,C,D,F,G).

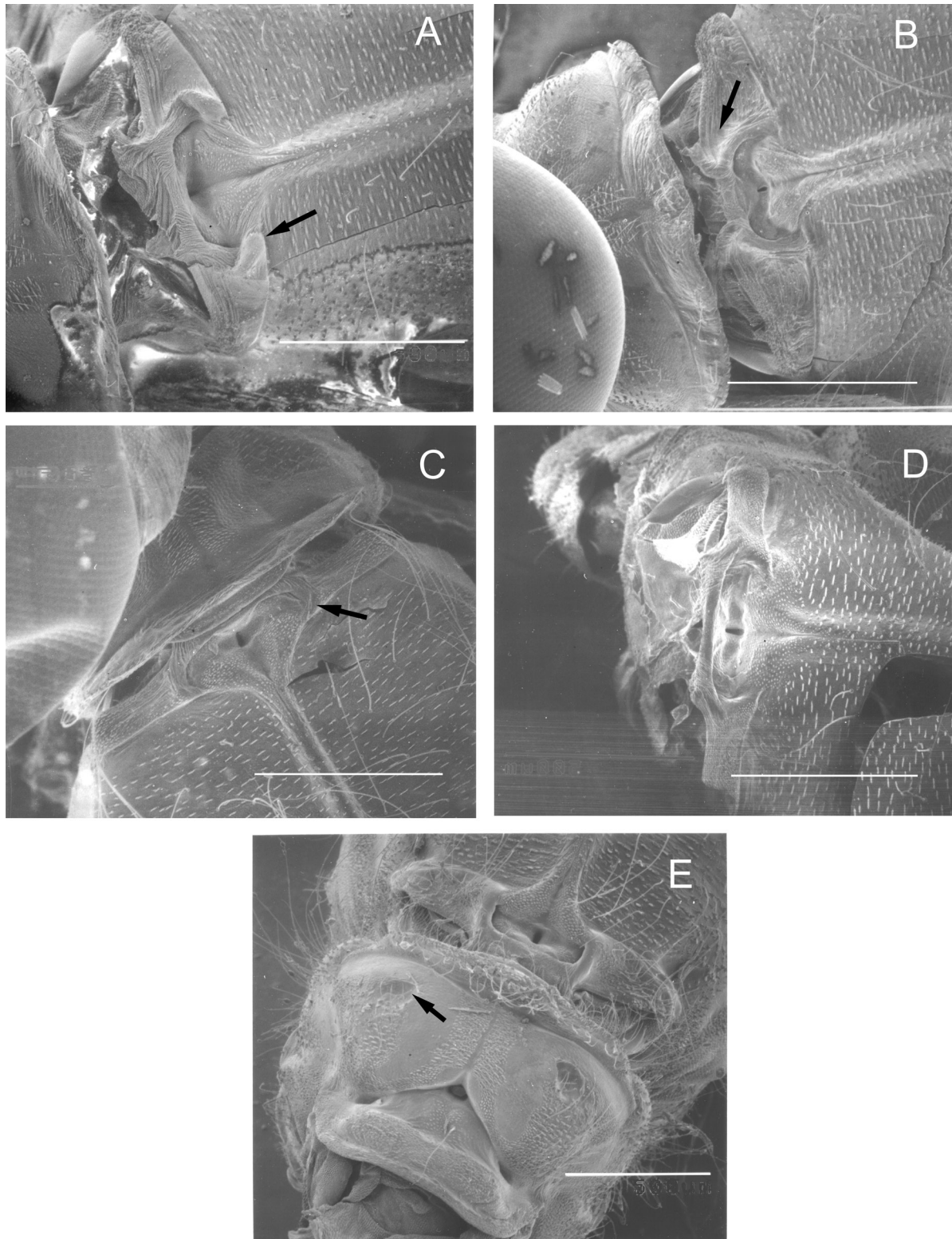


Fig. 8. Scanning electron micrographs of dorsal views of mesostigmal plates and posterior margin of pronotum. A, *Africallagma glaucum* male showing posteromedial lappet (arrow); B, *A. glaucum*, female showing anteromedial trough and flange (arrow); C, *Azuragrion nigradorsum*, male showing vestigial posteromedial lappet (arrow); D, *A. nigradorsum*, female; E, *Enallagma (Enallagma) aspersum*, female showing pronotal pits (arrow). Scales = 0.5 mm.

I suggest that all these species be placed provisionally in *Africallagma*, comb.n., pending a more detailed study.

Support for separation of the *E. nigradorsum* group is less strong, but in addition to the evidence based on the phylogeny itself, the biogeography supports independent evolution. This is especially true because the *Enallagma* that are geographically nearest to *E. nigradorsum* and its relatives, and that are clearly closely related to North American species (e.g. *E. deserti* in North Africa and south into Ghana; D'Andrea & Carfi, 1994), are probably among the most recently evolved species (Brown *et al.*, 2000) and are very different from all species of the *E. nigradorsum* group in coloration and genital structure. A similar argument for removal from *Enallagma* applies to *E. parvum*, for which the genus name *Amphiallagma* Kennedy is available. Whether or not the African *E. nigradorsum* group should also be placed in *Amphiallagma* is problematic. The very close similarity of the male cerci within this group, and the relative distinctiveness of those of *E. parvum*, support the monophyly of the African species convincingly. Given that fact, the geographical gap between the latter and *E. parvum*, and the relatively weak support for the monophyly of *E. parvum* plus the *E. nigradorsum* group, I suggest that the latter be placed in a new genus *Azuragrion* (see Appendix 2 for diagnosis), with *E. nigradorsum* designated herewith as the type of the genus. Clearly, information about the poorly known species, *E. insula* Fraser (mainland India) and *E. maldivensis* Laidlaw (Maldive Archipelago), might shed light on relationships of the African and Indian taxa, but these are known only from the type series, which are badly damaged (*E. maldivensis*; Laidlaw, 1919; Olsvik & Hämäläinen, 1992; personal observation) or of uncertain whereabouts (*E. insula*).

The taxonomy of North American species also deserves examination. The bluet and non-bluet species groups seem clear and consistent enough to deserve recognition at the subgeneric level. I therefore propose the name *Chromatallagma* subgen.n. for the latter, in reference to the bright and variable colour of these insects (see Appendix 2 for diagnosis and species composition); *Enallagma signatum* is herewith designated the type species. *Enallagma coecum* and *E. novaehispaniae* probably also belong here. It may eventually prove justifiable and useful to divide the new subgenus further, particularly in view of the strong differentiation of the *E. signatum* group and the molecular support (Brown *et al.*, 2000) for the sister-group relationship of the latter to *E. antennatum* and the *E. divagans* and *E. trivatum* groups.

The placement of *E. eiseni* remains uncertain, largely because of the unusual colour pattern, and because the larva is unknown. This may account for its position basal to *Enacantha* with some weightings. Clarification of its status requires further information on larval and molecular characters. In view of the strong phenotypic differentiation of *Enacantha caribbea* and the instability of its position, particularly with respect to *E. eiseni*, under different character weightings (Fig. 2), I propose that this monotypic genus continue to be recognized as such.

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Appendix 1. Character list.

Characters illustrated by Westfall & May (1996) are indicated as 'W & M: Fig. - ' ; other illustrations are in the present paper except for character 47. Note that character state designations have no significance with respect to polarity. Consistency (CI) and retention (RI) indices are modal values for the ninety-six shortest trees.

Colour (males)

- Pale thoracic colour*: (0) blue; (1) yellow/orange; (2) green; (3) violet; (4) otherwise. CI = 0.444, RI = 0.583.
- Black on dorsum of abdominal segment 2*: (0) extending more than half segment length; (1) less than half segment length. CI = 0.125, RI = 0.632.
- Abdominal segments 3–6 dorsally*: (0) extensively pale; (1) intermediate; (2) almost entirely dark; W & M: Fig. 12. CI = 0.250, RI = 0.625.
State 2 includes species with extensive lateral encroachment of pale colour but with a distinct middorsal dark stripe the length of all or most segments.
- Lateral or ventrolateral black markings on abdominal segment 8*: (0) present; (1) absent; W & M: Fig. 13. CI = 0.571, RI = 0.250.
- Abdominal segment 8 dorsally*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.273, RI = 0.529.
- Abdominal segment 9 dorsally*: (0) mostly blue; (1) mostly orange; (2) mostly dark. CI = 0.800, RI = 0.750.
- Abdominal segment 10 dorsally*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.333, RI = 0.333.
- Middorsal carina of male*: (0) almost entirely pale; mainly dark (1). CI = 0.357, RI = 0.357.
- Humeral stripe constricted before mesopleural fossa*: (0) commonly; (1) never. CI = 0.167, RI = 0.444.
- Postclypeus*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.429, RI = 0.273.
- Postfrons*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.300, RI = 0.731.
- Pale spots anterior to lateral ocelli*: (0) present; (1) absent. CI = 0.0.250, RI = 0.647.
- Area between ocelli*: (0) pale; (1) dark; W & M: Fig. 128. CI = 1.000, RI = 1.000.

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Colour (females)

- Humeral stripes*: (0) entire; (1) longitudinally divided for less than half their length; (2) longitudinally divided for most of length; W & M: Fig. 127. CI = 0.400, RI = 0.500.
- Black on dorsum of abdominal segment 1*: (0) covering more than basal two-thirds; (1) less than basal two-thirds. CI = 0.500, RI = 0.833.
- Abdominal segment 8 dorsally*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.400, RI = 0.182.
- Abdominal segment 9 dorsally*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.400, RI = 0.647.
- Abdominal segment 10 dorsally*: (0) mostly pale; (1) about equally pale and dark; (2) mostly dark. CI = 0.167, RI = 0.600.

Secondary sexual characters (males)

- Cerci with separate ventrobasal lobe*: (0) present; (1) secondarily fused; (2) absent; Figs 4–7. CI = 0.400, RI = 0.667.
- Cerci with dorsal lobe*: (0) hooked; (1) not hooked; Figs 4–7. CI = 1.000, RI = 1.000.
- Cerci with scalariform or scalariformlike cuticle*: (0) present on ventrobasal lobe; (1) present elsewhere; (2) absent; Figs 4–7. CI = 0.333, RI = 0.486. See text for explanation.
- Middle lobe of cerci*: (0) present; (1) absent; Figs 4–7. CI = 0.500, RI = 0.800.
- Paraprocts*: (0) distinctly bifid; (1) slightly bifid; (2) not at all bifid; Figs 4–7. CI = 0.286, RI = 0.750.
- Paraprocts*: (0) very short and directed upward; (1) not so; W & M: Figs 143 and 148. CI = 0.333, RI = 0.333.
- Lateral spines just proximal to distal flexure of penis*: (0) present; (1) absent; Figs 4–7. CI = 0.500, RI = 0.750.
- Penis with terminal segment*: (0) quadrilobate distally; (1) crescentic distally; (2) with earlike distolateral lobes; (3) with short, digitate distolateral lobes; (4) broad with subquadrate distolateral lobes; (5) with distolateral lobes recessed, long and spatulate; (6) with distolateral lobes filamentous; (7) very narrow, abruptly expanded distally to reflexed, undulate distolateral lobes; (8) very

short and broad with broadly rounded distolateral lobes; Figs 4–7. CI = 0.667, RI = 0.867.

The large number of character states partly reflects the diversity of penis shapes among outgroups; shapes were not combined into one state when very distinct to avoid providing artificial support for clades with disparate shapes.

27. *Shaft of penis*: (0) with 1 or 2 large, bladelike internal spines; (1) with several small spines; (2) without spines or with small denticles only; Figs 4–7. CI = 0.250, RI = 0.400.
 28. *Penis with distinct lateral lobes*: (0) present; (1) absent; Figs 4–7. CI = 0.143, RI = 0.538.
 29. *Mesepisternal lappets*: (0) present; (1) vestigial; (2) absent; Fig. 8. CI = 0.400, RI = 0.850.

Secondary sexual characters (females)

30. *Distinct pits on middle lobe of prothorax*: (0) present; (1) absent; Fig. 7; W & M: Fig. 130. CI = 0.250, RI = 0.786.
 31. *Posterior margin of pronotum with median tubercle*: (0) well developed; (1) vestigial; (2) absent; W & M: Fig. 132. CI = 0.250, RI = 0.625.
 32. *Posterior margin of pronotum*: (0) entire; (1) notched or undulating; Fig. 8. CI = 0.286, RI = 0.808.
 33. *Posteromedial tubercle of mesostigmal plates*: (0) present; (1) absent; W & M: Fig. 132. CI = 0.333, RI = 0.692.
 34. *Mesostigmal plates*: (0) very broad and posteriorly convex; (1) not so; W & M: Figs 151 and 152. CI = 1.000, RI = 1.000.
 35. *Anteromedial trough and flange on mesostigmal plates*: (0) present; (1) absent; Fig. 8. CI = 0.333, RI = 0.600.
 36. *Ovipositor valves*: (0) short, not extending caudad as far as end of paraprocts; (1) of medium length, extending beyond paraprocts but not to end of cerci; (2) long, extending beyond ends of cerci. CI = 0.750, RI = 0.933.
 37. *Vulvar spine*: (0) present; (1) absent; W & M: Figs 7 and 50. CI = 1.000, RI = 0.000.

Miscellaneous adult structures

38. *Vein Ac*: (0) distinctly basal to midway between antenodal crossveins; (1) at or distal to midway between antenodal crossveins. CI = 0.600, RI = 0.826.
 39. *Stature of males*: (0) slender, ratio of width to length of abdominal segment 3 < 0.12; (1) intermediate, this ratio between 0.12 and 0.14; (2) robust, this ratio > 0.14; CI = 0.182, RI = 0.609.

Larval structures

40. *Second and third antennal segments*: (0) relatively long; (1) short; W & M: Fig. 134. CI = 0.750, RI = 0.933.
 41. *Distinct dark pattern on eyes*: (0) present; (1) absent; W & M: Fig. 134. CI = 0.333, RI = 0.889.

42. *Posterolateral margin of head*: (0) prominent; (10) not prominent; W & M: Fig. 134. CI = 0.0.167, RI = 0.583.
 43. *Numerous stout setae on lateral carinae of abdomen*: (0) present; (1) absent; W & M; Fig. 135. CI = 0.222, RI = 0.875.
 44. *Lateral carinae of abdomen*: (0) projecting abruptly toward posterior end; (1) not so; W & M: Fig. 135. CI = 1.000, RI = 1.000.
 45. *Extensive and well defined areas of extra-tracheal pigmentation on gills*: (0) present; (1) absent; W & M: Fig. 136. CI = 0.333, RI = 0.778.
 46. *Well developed series of antenodal setae on median gill*: (0) present; (1) absent; W & M: Fig. 136. CI = 0.250, RI = 0.824.
 47. *Spine on labial palp*: (0) present; (1) absent; May & Corbet, 2001: Figs 1–5. CI = 0.333, RI = 0.600.

Habitat

48. *Primarily inhabiting*: (0) ponds; (1) streams. CI = 0.250, RI = 0.500.

Appendix 2. Diagnoses of adults of genus-group taxa introduced or treated in detail here.

The following characters apply to all the taxa described below and distinguish them from many other genera of Coenagrionidae: frons rounded in profile; postocular spots present, at least in males; thoracic colour pattern with distinct dark humeral stripe overlying the mesopleural suture, occasionally longitudinally divided or reduced to hairline within mesopleural suture, especially in females; venter of metathorax without distinct, moundlike prominence; tibial spurs at most only slightly longer than intervening spaces; inferior tooth of each tarsal claw normally developed; anal vein diverging from posterior wing margin proximal to Ac; pterostigmata of front and hind wings usually similar in colour and shape in both sexes; quadrangle with posterodistal corner moderately acute; dorsum of abdominal segment 10 of males without a marked, bifurcated prominence (sometimes with low protuberance or small, rounded distal scale on each side of midline, or both) and without tori (Westfall & May, 1996); dorsum of abdominal segment 10 of females not divided medially; male epiproct small, not visible in dorsal view; female with vulvar spine; penis without elongate distal flagellae.

Characters that discriminate these genus-group taxa, and the proposed composition of each taxon, are detailed below. Parenthetical question marks after species names indicate that I question whether these species actually are within a monophyletic group with the type species or I am uncertain of the identity of the species.

Africallagma Kennedy (1920)

Medium sized to very slender and elongate, male abdominal segments 3–6 largely dark dorsally, at least along and for

a short distance on either side of the midline. Pale thoracic colour usually blue but sometimes very pale tan, almost whitish, black humeral stripe never divided longitudinally, sometimes reduced to hairline in males and females. Pterostigmata pale grey to nearly black, vein Ac at or distal to midway between antenodal crossveins. Abdominal segment 10 of male without posterodorsal protuberance. Male paraprocts distinctly bifid in lateral view except in *A. cuneistigma*, with inferior arm much broader and usually shorter than superior; cerci variable but lacking a distinct inferior arm or middle lobe, generally curved ventromedially in distal third, or with recurved process at one-third to two-thirds length directed ventromedially, sometimes with scalariformlike cuticle (presumably not homologous with that of *Enallagma* because of its very different position on the cercus and because it appears to be normally sclerotized) on mediobasal surface. Penis with large rounded or recurved earlike distolateral lobes (narrow and digitate in *A. rubristigma*), distinct lateral lobes present, spines or projections not present just proximal to distal flexure. Male mesostigmal plates with prominent posteromedial lappets; female plates usually with wide anteromedial trough and flange (absent in *A. sapphirinum*, condition in *A. rubristigma* not known), posterior margin of pronotum sinuate, with distinct median prominence, or with median notch, middle lobe of pronotum never with well defined pits. Ovipositor valves of medium length or long, sometimes strikingly so. Figs 6, 8.

Type species: *Agrion glaucum* Burmeister, 1839. Other species: *Enallagma cuneistigma* Pinhey, 1969 (?); *Ischnura elongata* Martin, 1907; *Enallagma pseudelongatum* Longfield (1936); *Enallagma rubristigma* Schmidt, 1951 (?); *Enallagma sapphirinum* Pinhey, 1950 (?); *Enallagma simuatum* Ris, 1921; *Enallagma subtile* Ris, 1921; *Enallagma vaginale* Sjöstedt, 1917 (includes *E. longfieldae* Fraser, 1947) (?).

Amphiallagma Kennedy (1920)

Very small, male abdominal segments 3–6 largely dark dorsally. Pale thoracic colour mostly blue, black humeral stripe never divided longitudinally, sometimes reduced to hairline in (immature?) female. Pterostigmata tan to black, vein Ac at or distal to midway between antenodal crossveins. Abdominal segment 10 of male without posterodorsal protuberance. Male paraprocts not bifid in lateral view; cerci smoothly rounded distally, somewhat excavated dorsomedially, with very small conical tubercle along dorsal ridge at about one-third length, cuticle probably somewhat flexible dorsally on distal surface but scalariform cuticle absent, middle lobe absent, each cercus with dorsomedial projection at extreme base. Penis with small, quadrate earlike distolateral lobes, distinct lateral lobes absent, spines or projections not present just proximal to distal flexure. Male mesostigmal plates without posteromedial lappets; female plates without wide anteromedial trough and flange, posterior margin of pronotum undulate, middle lobe of pronotum never with well defined pits. Ovipositor valves short. Fig. 7.

Type species: *Enallagma parvum* Selys, 1876.

Azuragrion, gen.n.

Very small to large (*A. granti*), male abdominal segments 3–6 largely dark dorsally except largely blue in *somalicum*. Pale thoracic colour mostly blue in males, pale bluish green to brown in females, black humeral stripe never divided longitudinally, sometimes reduced to hairline in female. Pterostigmata grey to brown, vein Ac usually basal to midway between antenodal crossveins, sometimes at or distal to this point in *A. somalicum* and *A. granti*, especially in forewing. Abdominal segment 10 of male without posterodorsal protuberance. Male paraprocts not distinctly bifid but with a low ventral protrusion as well as an elongate dorsal process visible in lateral view; cerci with superior sclerotized arm with acute terminal or subterminal medial hook, middle lobe of about same length consisting of pale, flexible cuticle, inferior sclerotized arm from as long as to about twice as long as superior arm, scalariform cuticle absent. Penis with small to large quadrate or triangular earlike distolateral lobes, distinct lateral lobes usually absent (present in *A. nigradorsum*), spines or projections not present just proximal to distal flexure. Male mesostigmal plates with very low, vestigial posteromedial lappets; female plates without wide anteromedial trough and flange (sometimes with deep transverse trough and elevated anterior margin), posterior margin of pronotum with distinct median prominence, middle lobe of pronotum never with well defined pits. Ovipositor valves of short or medium length. Figs 7, 8.

Type species: *Enallagma nigradorsum* Selys, 1876. Other species: *Enallagma buccholzi* Pinhey (1971) (see Pinhey, 1971), *Ischnura granti* McLachlan, 1903; *Ischnura kauderni* Sjöstedt, 1917; *Enallagma somalicum* Longfield (1931); *Enallagma vasomerani* Pinhey, 1955.

Etymology: Named for the azure blue colour of males of most species.

Chromatallagma, subgen.n. of *Enallagma*

Medium sized to fairly large (*E. daeckii*), males usually slender, male abdominal segments 3–6 largely dark dorsally. Pale thoracic colour blue, violet, yellow, orange or red in males, pale blue, greenish, tan or dull yellow to orange in females, black humeral stripe sometimes divided longitudinally, occasionally reduced to hairline in males and females. Pterostigmata pale tan to nearly black, vein Ac usually basal to midway between antenodal crossveins. Abdominal segment 10 of male without posterodorsal protuberance but usually with rounded distal scale on each side of midline. Male paraprocts not bifid in lateral view; cerci with a superior arm ending in a glabrous hook whose sharp edge is somewhat elongated, distinct inferior arm bearing scalariform cuticle (absent in *E. antennatum*, reduced in *E. basidens*), this arm sometimes fused with superior arm. Penis with quadrate distolateral lobes produced at corners, distinct lateral lobes present, spines or projections not present just proximal to distal flexure. Male mesostigmal plates without posteromedial lappets; female plates without antero-

medial trough and flange, posterior margin of pronotum usually smoothly rounded but sometimes with distinct median tubercle, middle lobe of pronotum often with well defined pits. Ovipositor valves usually short. Fig. 4.

Type species: *Agrion signatum* Hagen, 1861. Other species: *Agrion antennatum* Say, 1839; *Enallagma basidens* Calvert, 1902; *Agrion coecum* Hagen, 1861 (?); *Enallagma concisum* Williamson, 1922; *Telagrion daeckii* Calvert, 1903; *Enallagma divagans* Selys, 1876; *Enallagma dubium* Root, 1924; *Agrion exsulans* Hagen, 1861; *Enallagma novaehispaniae* Calvert, 1907 (?); *Enallagma pallidum* Root, 1923; *Enallagma pictum* Morse, 1895; *Agrion pollutum* Hagen, 1861; *Enallagma sulcatum* Williamson, 1922; *Enallagma traviatum* Selys, 1876; *Enallagma truncatum* Gundlach, 1888; *Enallagma vesperum* Calvert, 1919; *Enallagma weewa* Byers, 1927.

Eymology: Named for the bright and varied colours of males within this group.

Enallagma Selys, *sensu stricto*

Medium sized, males usually robust, male abdominal segments 3–6 usually largely blue dorsally. Pale thoracic colour blue in males, pale blue, greenish or tan in females, black humeral stripe never divided longitudinally, not reduced to hairline. Pterostigmata pale tan to nearly black, vein Ac almost always basal to midway between antenodal crossveins. Abdominal segment 10 of male without posterodorsal protuberance but often with rounded distal scale on each side of midline. Male paraprocts not bifid in lateral view; cerci with a superior arm ending in (or sometimes reduced to) a glabrous hook whose sharp edge is somewhat elongated, distinct inferior arm bearing scalariform cuticle, this arm sometimes partly fused with superior arm when latter is reduced, so scalariform cuticle overlaps the latter. Penis usually with crescentic distolateral lobes (quadrate in *E. durum* and *E. eiseni*), distinct lateral lobes present, spines or projections not present just proximal to distal flexure. Male mesostigmal plates without posteromedial lappets; female plates variable but usually without anteromedial trough and flange, posterior margin of pronotum usually smoothly rounded (sinuate in *E. eiseni*) and without median tubercle, middle lobe of pronotum sometimes with well defined pits. Ovipositor valves short. Figs 4, 8.

Type species: *Agrion cyathigerum* Charpentier, 1840. Other species: *Enallagma ambiguum* Navás, 1936 (?); *Enallagma anna* Williamson, 1900, *Agrion aspersum* Hagen, 1861; *Enallagma belyshevi* Haritonov, 1975; *Aenallagma boreale* Selys, 1875; *Enallagma carunculatum* Morse, 1895; *Enallagma circulatatum* Selys, 1883; *Agrion civile* Hagen, 1861; *Enallagma clausum* Morse, 1895; *Enallagma davisi* Westfall, 1943; *Agrion deserti* Selys, 1871; *Agrion doubledayi* Selys, 1850, *Agrion durum* Hagen, 1861; *Agrion ebrium* Hagen, 1861; *Enallagma eiseni* Calvert, 1895 (?); *Enallagma geminatum* Kellicott, 1895; *Agrion hageni* Walsh, 1863; *Enallagma insula* Fraser, 1920 (?); *Enallagma laterale* Morse, 1895; *Enallagma maldivense* Laidlaw (1902) (?); *Enallagma minusculum* Morse, 1895; *Enallagma nigrolineata* Belyshev & Haritonov, 1975;

Enallagma opitimolocus Miller & Ivie, 1996 (?); *Agrion praevarum* Hagen, 1861; *Enallagma recurvatum* Davis, 1913; *Enallagma risi* Schmidt, 1961; *Enallagma rua* Donnelly, 1968; *Enallagma semicirculare* Selys, 1876; *Enallagma vernale* Gloyd, 1943. Except for *E. eiseni*, the species in this group whose names are followed by a question mark are of uncertain identity or validity. They are retained provisionally in *Enallagma* strictly for nomenclatorial convenience, not on the basis of evidence about their relationships.

Pinheyagrion, gen.n.

Very small, male abdominal segments 3–6 largely dark dorsally. Pale thoracic colour mostly blue or greenish in males, sometimes orange brown in females, black humeral stripe never divided longitudinally, sometimes reduced to hairline in (immature?) female. Pterostigmata of male bright pink, those of female brown, vein Ac at or distal to midway between antenodal crossveins. Abdominal segment 10 of male without posterodorsal protuberance. Male paraprocts distinctly bifid in lateral view, the inferior branch much longer than superior; cerci with 2 branches fused for about half their length, no middle lobe, the superior branch ending in an acute, spinelike, but not hooked, tip directed posterodorsally, the inferior asymmetrically rounded distally, somewhat dorsoventrally flattened and inclined slightly upward laterally, the ventral surface covered with padlike cuticle (probably somewhat flexible), scalariform cuticle absent. Penis with small, quadrate earlike distolateral lobes, distinct lateral lobes absent, with prominent bifurcated spine on each side just proximal to distal flexure. Male mesostigmal plates with very prominent posteromedial lappets; female plates without wide anteromedial trough and flange, posterior margin of pronotum undulate, middle lobe of pronotum never with well defined pits. Ovipositor valves long. Fig. 5.

Type species: *Enallagma angolicum* Pinhey, 1966.

Eymology: Named for the late Dr Elliot Pinhey in recognition of his many contributions to the taxonomy of African Odonata.

Proischnura Kennedy (1920)

Small to medium sized, male abdominal segments 3–6 largely dark dorsally. Pale thoracic colour blue or blue-green to violet in males, bluish green to tan in females, black humeral stripe never divided longitudinally. Pterostigmata of both sexes grey, brown or black, usually paler in female, vein Ac at or distal to midway between antenodal crossveins. Abdominal segment 10 of male with low, bifid posterodorsal protuberance. Male paraprocts distinctly or slightly (*P. polychromaticum*) bifid in lateral view, the superior branch longer; cerci with wide superior branch, broadly rounded distally with low nipplelike protrusion at tip, small glabrous thumblike process on dorsomedial edge, otherwise with dorsomedial area usually bearing numerous stiff setae except for small distal area of scalariformlike cuticle

(presumably not homologous with that of *Enallagma* because of its very different position on the cercus), narrow digitate inferior branch projecting ventromedially from base of superior branch. Penis with elongate crescentic distolateral lobes just beyond a distinct constriction, distinct lateral lobes present or absent, with prominent triangular or tongue-like projection on each side just proximal to distal flexure. Male mesostigmal plates with prominent posteromedial lappets; female plates without wide anteromedial trough and flange,

posterior margin of pronotum undulate, medially tuberculate or with prominent median notch, middle lobe of pronotum never with well defined pits. Ovipositor valves of medium length. Fig. 5.

Type species: *Enallagma subfurcatum* Selys, 1876. Other species: *Enallagma polychromaticum* Barnard (1937); *Enallagma rotundipenne* Ris, 1921.

Appendix 3. Character matrix. Numbers for characters and character states correspond to those in Appendix 1; species numbers correspond to those of Figs 1 and 2.

Species	Characters																																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48		
<i>Chromagrion conditum</i>	0	0	2	1	0	0	2	1	?	2	2	1	1	0	1	2	2	0	1	2	0	1	2	1	1	1	1	1	1	1	0	2	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1		
<i>Coenagrion resolutum</i>	0	1	0	1	0	2	1	1	0	1	2	2	1	0	1	2	2	0	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	
<i>Ischnura verticalis</i>	2	0	2	1	0	2	1	0	1	0,2	0,2	2	2	1	0	1	0	6	2	1	2	0	2	0	1	1	1	1	1	1	1	0	1	0	1	2	0	0	1	0	1	0	0	1	0	0	1	0	1	0
<i>Pinheyagrion angolicum</i>	0	0	2	1	2	0	2	1	0	1	2	0	2	1	0	1	4	2	1	0	0	2	1	1	1	1	1	1	1	1	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Acanthagrion quadratum</i>	0	0	2	1	0	2	1	1	0	1	2	0	2	1	1	0	7	2	1	2	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	
<i>Argentagrion cheliferrum</i>	0	0	2	1	2	0	1	2	1	1	2	0	1	1	0	1	1	2	0	1	1	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
<i>Cyanallagma interruptum</i>	2	1	2	1	2	0	1	1	2	1	2	1	1	0	1	2	1	2	1	2	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Proischnura subfurecatum</i>	0	0	2	1	0	2	1	1	0	0	2	2	0	1	1	0	4	0	1	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>P. polychromaticum</i>	3	0	2	0	0	2	1	0	0	2	2	0	1	1	0	4	2	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>P. rotundipenne</i>	0	0	2	1	0	2	0	1	0	1	2	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Africallagma (?) cuneisigma</i>	0	0	2	1	0	2	1	0	2	0	2	0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>A. (?) rubristigma</i>	0	0	2	1	1	0	2	1	0	2	1	1	0	1	1	1	3	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>A. (?) vaginale</i>	0	0	2	1	2	0	1	0	2	1	0	2	1	1	0	1	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>A. (?) sapphirinum</i>	0	0	0	1	0	2	1	0	2	1	2	1	1	1	0	1	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Africallagma glaucum</i>	0	0	2	1	0	1	0	2	2	0	2	1	1	0	1	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. subtile</i>	0	0	2	1	0	1	0	2	1	0	1	0	1	1	0	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. elongatum</i>	0	0	2	1	0	1	0	1	0	1	0	1	0	1	1	0	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. pseudelongatum</i>	0	1	2	1	0	1	0	1	0	1	0	1	0	1	1	0	1	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. sinuatum</i>	0	1	2	1	0	1	0	2	0	0	1	2	1	0	1	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Argentagrion ambiguum</i>	0	0	2	1	2	1	0	2	0	0	1	2	1	1	0	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Homeoura nepos</i>	0	0	2	1	2	1	2	0	2	2	0	1	1	0	1	1	1	2	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Amphiallagma parvum</i>	0	0	2	1	0	1	0	2	2	0	2	1	1	0	1	2	1	2	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Azuragrion somalicum</i>	0	0	0	1	0	1	0	2	1	0	0	2	0	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. granti</i>	0	0	2	1	0	2	1	0	2	2	0	0	2	0	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. nigradorsum</i>	0	0	2	1	1	0	2	1	0	2	2	0	1	1	0	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. kauderni</i>	0	0	2	1	1	0	2	1	0	2	2	0	2	0	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. vansomereni</i>	0	0	2	1	1	0	2	1	0	2	2	0	2	0	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Enacantha caribbea</i>	0	1	0	1	0	1	0	1	2	0	0	1	2	1	1	0	2	1	1	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Enallagma eiseni</i>	0	0	1	0	1	0	2	2	0	0	1	2	0	1	1	2	0	1	0	2	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>E. durum</i>	0	1	0	1	2	0	1	0	2	2	0	0	1	2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Appendix 3. Continued.

Species	Characters																																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48					
<i>E. civile</i>	0	1	0	1	0	0	2	1	1	2	2	1	1	0	0	2	2	2	0	0	0	1	2	1	1	1	1	2	0	2	0	2	0	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	1	0	0	1	0
<i>E. minusculum</i>	0	1	0	1	0	0	2	1	1	2	2	1	1	0	0	2	2	2	0	0	0	1	2	1	1	1	1	2	0	2	0	2	0	1	1	0	0	1	1	0	0	0	2	0	1	0	1	1	1	?	0		
<i>E. semicirculare</i>	3	1	0	1	0	0	1	1	2	0	1	0	1	0	2	2	0	0	1	2	0	1	2	0	1	1	2	0	2	0	1	1	0	0	0	1	1	0	0	0	1	2	0	1	0	1	1	0	0	0			
<i>E. carunculatam</i>	0	1	0	1	0	0	1	2	2	0	0	1	2	1	1	2	2	0	0	1	2	1	1	2	0	2	0	1	1	0	0	2	0	1	1	0	0	2	0	1	0	0	2	0	1	0	1	0	?	0			
<i>E. anna</i>	0	1	0	1	0	0	2	2	1	0	1	2	2	1	0	1	2	2	0	0	1	2	1	1	2	0	2	0	1	1	0	0	2	0	1	1	0	0	2	0	1	0	0	2	0	1	0	1	0	0	1		
<i>E. clausum</i>	0	1	0	1	0	0	2	2	1	0	1	0	1	0	1	2	2	0	0	1	2	1	1	1	2	0	2	1	2	0	1	2	0	1	1	0	0	2	0	1	0	0	2	0	1	0	1	0	1	?	0		
<i>E. cyathigerum</i>	0	1	0	1	0	0	2	2	1	0	1	0	1	0	0,2	2	2	0	0	1	2	1	1	1	2	0	2	0	2	0	1	2	0	1	1	0	0	2	0	1	0	0	2	0	1	0	1	0	0	0			
<i>E. aspersum</i>	0	1	2	1	0	0	1	1	2	2	0	1	0	1	1	2	2	0	0	1	2	1	1	2	0	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0				
<i>E. geminatum</i>	0	0	2	0	0	0	2	1	1	2	2	1	1	0	1	2	2	0	0	1	2	1	1	2	0	1	1	0	0	1	2	0	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0				
<i>E. ebrum</i>	0	1	0	1	0	0	1	2	2	1	0	1	2	1	0	2	2	0	0	1	2	1	1	2	0	1	1	0	0	2	0	1	2	0	0	1	1	0	0	2	0	1	0	0	2	0	1	0	1	0	0		
<i>E. hageni</i>	0	1	0	1	0	0	1	2	2	1	0	1	2	1	0	2	2	0	0	1	2	1	1	2	0	1	1	0	0	2	0	1	2	0	0	1	1	0	0	2	0	1	0	0	2	0	1	0	1	0	0		
<i>E. laterale</i>	0	1	0	0	0	2	1	1	2	2	1	0	1	0	1	2	2	0	0	1	2	1	1	2	0	1	1	0	0	2	0	1	2	0	1	1	0	0	1	0	0	2	0	1	0	0	1	0	0	0			
<i>E. recurvatum</i>	0	1	0	0	0	2	1	1	2	2	1	0	1	0	1	2	2	0	0	1	2	1	1	2	0	1	1	0	0	2	0	1	2	0	1	1	0	0	1	0	0	2	0	1	0	0	1	0	1	0	0		
<i>E. coecum</i>	3	1	2	0	0	2	1	1	0	1	0	1	0	1	0	2	2	0	0	1	2	0	1	1	2	0	2	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1		
<i>E. novaehispaniae</i>	3	1	2	0	0	2	1	1	0	1	0	1	0	1	0	2	2	0	0	1	2	0	1	1	2	0	2	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	1	0	1		
<i>E. antennatum</i>	2	0	2	1	2	0	0	1	2	2	1	1	0	2	2	2	0	2	0	2	1	2	1	0	2	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	2	1	0	0	1	1	0	0		
<i>E. daeckii</i>	0	0	2	1	0	0	0	1	2	0	0	0	1	2	0	0	1	2	0	0	1	2	1	1	2	0	2	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	
<i>E. pallidum</i>	0	1	2	1	0	0	1	0	0	0	0	0	0	0	0	2	2	0	0	0	1	2	1	1	2	0	2	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	
<i>E. traviatum</i>	0	0	2	1	0	0	2	1	0	0	0	0	1	0	0	1	0	0	0	1	2	1	1	2	0	2	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0		
<i>E. divagans</i>	0	0	2	1	0	0	2	1	0	0	0	0	1	2	0	0,2	2	0	0	1	2	1	1	2	0	2	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	
<i>E. exsulans</i>	0	0	2	1	2	0	1	2	0	0	0	1	2	0	0	1	2	0	0	1	2	1	1	2	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	1		
<i>E. weewa</i>	3	0	2	1	2	0	1	2	2	1	0	2	0,2	0,2	0	0	0	0	0	1	2	1	1	0	0	2	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	1		
<i>E. basidens</i>	0	0	0	1	0	0	2	1	2	0	0	1	2	0	2	2	0	0	0	1	2	1	1	0	2	1	2	0	0	1	0	0	1	0	0	1	0	0	0	0,1	2	1	0	0	1	0	0	1	0	0			
<i>E. sulcatum</i>	1	0	2	1	2	0	1	0	0	1	0	0	1	0	0	2	1	0	0	1	2	1	1	0	2	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0		
<i>E. vesperum</i>	1	0	2	1	2	0	1	0	0	1	0	0	2	1	0	2	1	0	0	1	2	1	1	0	2	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0		
<i>E. pollatum</i>	1	0	2	1	2	0	1	0	0	2	2	0	2	0	0	2	2	0	0	1	2	1	1	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0		
<i>E. signatum</i>	1	0	2	1	2	0	1	0	0	2	2	0	1	0	2	2	0	0	0	1	2	1	1	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0		
<i>E. dabium</i>	1	0	2	1	2	0	1	0	0	2	2	1	0	0	2	2	0	0	0	1	2	1	1	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0		
<i>E. concisum</i>	1	0	2	1	2	0	1	0	0	2	2	1	0	0	2	2	0	0	0	1	2	1	1	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0		
<i>E. pictum</i>	1	0	2	1	2	0	1	0	0	2	2	1	0	0	2	2	0	0	0	1	2	1	1	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0		