Hydrobiologia (2011) 665:195–203
DOI 10.1007/s10750-011-0622-7

PRIMARY RESEARCH PAPER

A preliminary phylogenetic study of Megapodagrionidae with focus on the Chinese genera *Sinocnemis* Wilson & Zhou and *Priscagrion* Zhou & Wilson (Odonata: Zygptera)

Xin Yu · Wenjun Bu

Received: 10 September 2010 / Revised: 20 December 2010 / Accepted: 6 February 2011 / Published online: 2 March 2011

Abstract A cladistic analysis of the megapodagrionid damseflies was performed on a data matrix of 44 morphological characters and 39 terminal taxa with emphasis on defining the phylogenetic position of the Chinese genera *Sinocnemis* Wilson & Zhou and *Priscagrion* Zhou & Wilson which have rarely been used in a cladistic study before. *Sinocnemis* is recovered as the sister group to all other reduced-venation groups, including *Chorismagrion* + *Perissolestes*, *Hemiphlebia*, and all coenagrionoids; *Priscagrion* is close to *Austroargiolestes*. *Sinocnemis henanensis* is confirmed as a good species.

Keywords Megapodagrionidae · *Sinocnemis* and *Priscagrion* · Phylogeny

Electronic supplementary material The online version of this article (doi:10.1007/s10750-011-0622-7) contains supplementary material, which is available to authorized users.

Handling editor: H. J. Dumont

X. Yu (✉) · W. Bu
Institute of Entomology, College of Life Sciences,
Nankai University, Tianjin 300071, China
e-mail: nk_yuxin@yahoo.cn

Introduction

Several recent cladistic studies of Odonata (Rehn, 2003; Dumont et al., 2005; Bybee et al., 2008; van Tol, 2009; Dumont et al., 2010) have established that the large group of the megapodagrionids are not monophyletic as previously believed (e.g. Fraser, 1957; Davies & Tobin, 1984 and Bridges, 1994 and Bechly, 1996), but its phylogenetic relationships remain controversial. Rehn (2003) obtained megapodagrionids as the pectinate basal group of a clade comprising all other zygopterans except *Philoganga*, *Diphlebia*, and the Caloptera. Bybee et al. (2008), using morphology, fossils and genes, recovered megapodagrionids as polyphyletic or paraphyletic. Both van Tol (2009) and Dumont et al. (2010), largely based on DNA sequences, recovered Megapodagrionidae as strongly polyphyletic.

Priscagrion Zhou & Wilson, a megapodagrionid genus endemic to China, only including two species presently, which has an unusual vein pattern by the presence of 1–2 additional cross veins in C-Sc space (Fig. 18) and is considered archaic by most authors, has never been used in a cladistic study yet. De Marmels (2002) has given a brief review on *Priscagrion* based on the original description and believes that Zhou & Wilson (2001) "do not adequately exploit the richness of their own data". According to De Marmels (2002), the original figures are questionable, and some significant morphological characters of *Priscagrion*, such as the striking specializations of the penile organ and projection on the outer margin near the tip of the male cercus, have so far been ignored. De Marmels (2002) believed the closest relatives of *Priscagrion* are species of the Australo-Papuan Argiolestinae.

Sinocnemis Wilson & Zhou, another China endemic, including three species presently, which has a relatively simple vein pattern by lacking of intercalated sectors between main longitudinal veins, was originally placed into Platycnemididae. Kalkman (2008) indicated that the diagnostic morphological characters for *Sinocnemis* in Wilson & Zhou (2000) are not common, if present, in platycnemidids at all. Furthermore, *Sinocnemis* lacks most of the important characters of platycnemidids while it displays some which are typical of megapodagrionids, such as having a lateral row of long setae along sides of genital ligula shaft and the fact of keeping its wings open at rest. Kalkman (2008) believed that *Sinocnemis* is not a platycnemidid but a megapodagrionid, close to *Mesopodagrion*. van Tol (2009) comfirmed that *Sinocnemis* is not a platycnemidid but failed to recover the phylogenetic position of this charming Chinese taxon. Dumont et al. (2010) supposed that *Sinocnemis* belong to neither Platycnemididae nor Megapodagrionidae.

This study, based on morphological data, is aimed at clarifying the phylogenetic position of *Priscagrion* and *Sinocnemis* as well as to test the phylogeny of megapodagrionids with cladistic methods.

Materials and methods

Taxa sampling and terminology

Based on the taxonomy of Bridges (1994), with reference also to Tsuda (2000), van Tol (2006), and Schorr et al. (2009), all currently recognized families and subfamilies within Lestoidea and Hemiphlebioidea were sampled with emphasis on megapodagrionids. Representatives of Coenagrionoidea and Caloptera were also included. In total, 39 genera belonging to 17 families and 27 subfamilies were included in our study, with genera as terminal taxa. Bybee et al. (2008), Carle et al. (2008), van Tol (2009) and Dumont et al. (2010) all supported Lestid-like damselflies (Lestidae + Synlestidae) as sister to other Zygoptera, therefore Lestid-like damselflies were chose as outgroups in this study. Specimens examined (Appendix 1 in Supplementary material) were deposited in the Institute of Entomology, Nankai University, Tianjin, China (NKU), the Institute of Zoology, Academia Sinica, Beijing, China (IZAS), and Life Sciences College, Hebei University, Baoding, Hebei, China (CHU). Specimens from Australian and New World were obtained through kind exchanges by Dr. Rosser W. Garrison from the California Department of Food & Agriculture, Sacramento, CA, USA. Character scores for which we had no specimens (16 species) of was obtained from the literature (Appendix 2 in Supplementary material). Terminology for the morphological characters in this study was followed Rehn (2003) with a few modifications and additions.

Cladistic analysis

The cladistic analysis was performed in PAUP* version 4.0 b10 (Swofford, 2002) using heuristic parsimony analysis, with 1000 random stepwise additions of taxa [tree-bisection-reconnection (TBR) branch swapping] under ACCTRAN optimization, characters unordered, qualitative and equal weight, MulTrees option in effect. Jackknife values for clades were calculated in 1,000 replicates using a general heuristic search; 10% of the data set was deleted for each jackknife replicate. The unambiguous characters were mapped by MacClade version 4.0 (Maddison & Maddision, 2000). Bayesian analysis was also performed using MRBAYES (version 3.1.2) (Ronquist & Huelsenbeck, 2003) for 1,000,000 generations using four chains with a sample frequency once per 100 generations and the burn-in value was set to 10,000 trees.

Characters

Forty-four adult morphological and biological characters were selected for coding. Characters 1–39 were taken from Rehn (2003), characters 40 and 42–44 from Pessacq (2008), with modifications and in many cases qualitative differences. Larval characters were excluded from this research owing to the unavailability of larva for Chinese genera emphasized in this study. The data matrix used in the analysis is shown in Appendix 3 in Supplementary material.

Head

1. *Shape of clypeus*: (0) rectangular, with anteclypeus and postclypeus forming distinct anterior and dorsal faces, respectively; (1) flattened, with anteclypeus tilted back and not distinct from dorsal facing postclypeus; (2) greatly swollen and rounded into prominent snout.
2. *Shape of labial palp*: (0) widest at base, tapering to tip; (1) external edge greatly expanded; (2) parallel-sided.
3. *Premental cleft*: (0) well developed, at least one-quarter the length of entire prementum; (1) poorly developed, no more than one-quarter the length of entire prementum.
4. *Shape of frons*: (0) smoothly rounded in profile; (1) angulate; (2) flattened.
5. *Length of pedicel and scape*: (0) pedicel longer than scape; (1) scape and pedicel equal in length.
6. *Ecdysial cleavage line*: (0) well developed; (1) partially developed; (2) absent.
7. *Postfrontal suture*: (0) vestigial or absent; (1) partially developed; (2) well developed.
8. *Inner dorsal margins of eyes*: (0) bent at a sharp angle so that a single point marks the narrowest space between them; (1) straight, so that no narrowest point exists between them.

Wing venation characters

9. *Number of antenodal crossveins (Ax)*: (0) at least 5, present in C-Sc space and Sc-R space, unaligned; (1) at least 5, present in C-Sc and Sc-R space, aligned; (2) between 2 to 5, present in C-Sc space only (except Ax0); (3) only 2 in C-Sc space and Sc-R space (viz. Ax0).
10. *Position of* IR_1: (0) closer to RP_1 than to RP_2; (1) equidistant from RP_1 and RP_2; (2) closer to RP_2 than to RP_1.
11. *Oblique vein between* RP_2 *and* IR_2: (0) absent; (1) present.
12. *Postnodal crossveins*: (0) unaligned in the C-RA and RA-RP spaces; (1) aligned in the C-RA and RA-RP spaces only; (2) aligned in a transverse series to beyond IR_2.
13. *Pterostigma* (Pt): (0) present; (1) absent in both sexes and replaced by a densely reticulate network of veins.
14. *Stigma brace vein*: (0) absent; (1) present.
15. *Path of MP distal to hind angle of quadrangle*: (0) continuing straight; (1) greatly arched forward.
16. *Posterior arculus*: (0) developed proximal to the RP/MA divergence; (1) developed at or distal of the RP/MA divergence; (2) absent.
17. *RA-RP space proximal to the end of ScP*: (0) crossed; (1) not crossed.
18. *Position of RP midfork*: (0) located beyond 25% wing length; (1) located at less than 25% wing length.
19. *Position of RP-*IR_2 *junction*: (0) at less than 25% wing length; (1) at 25-50% wing length; (2) beyond 50% wing length.
20. IR_2: (0) apparently joined to RP' with a crossvein; (1) fused directly to RP' at an acute angle, or with a gentle forward curve.
21. *Subdiscoidal crossvein*: (0) present between MP and CuA and aligned with discoidal vein; (1) absent resulting from the fusion of the posterior-apical corner of the quadrangle with the hind margin of the wing.
22. *CuA*: (0) not forked throughout its entire length; (1) with a basal bifurcation only; (2) pectinate basally; (3) reduced and ending on the subdiscoidal vein, or absent; (4) reduced and ending on the posterior side of the quadrangle.
23. *Distal angle of quadrangle*: (0) distinctly acute in both pairs of wings; (1) square in its distal angle in both pairs of wings.
24. *Position of nodus*: (0) located at one-third to one-half wing length; (1) located at one-quarter to one-third wing length; (2) located at less than one-quarter wing length.
25. RP_1*–*IR_1 *field*: (0) expanded and filled by intercalated veins; (1) narrow, with no RP_1 branches or intercalated veins.
26. IR_1*–*RP_2 *field, intercalated sectors*: (0) absent; (1) present.
27. RP_2*–*IR_2 *field, intercalated sectors*: (0) absent; (1) present.
28. IR_2*–*RP_3 *field*: (0) expanded and filled by intercalated veins; (1) narrow, with no RP_3 branches or intercalated veins.
29. RP_3*–MA field*: (0) expanded and filled by intercalated veins; (1) narrow, with no MA branches or intercalated veins.

30. *MA–MP field*: (0) expanded and filled by intercalated veins; (1) narrow, with no MA branches or intercalated veins.
31. *MP–CuA field*: (0) expanded and filled by intercalated veins; (1) narrow, with no CuA branches or intercalated veins.
32. *Basal proximity of IR_2 and RP_3*: (0) not positioned extremely close to one another near their origins for the length of several cells; (1) positioned extremely close to one another basally for the length of several cells.
33. *Apices of RA and RP_1*: (0) meeting the distal wing margin anterior to the apex of the wing itself; (1) meeting the distal wing margin posterior to the wing apex.

Miscellaneous characters

34. *Third segment of penis*: (0) with 2 lateral lobes only; (1) with 2 apical and 2 lateral lobes; (2) filamentous; (3) vestigial or absent; (4) present, but with no lobes.
35. *Anterior hamules*: (0) platelike and quadrate; (1) platelike and triangular.
36. *Shape of seminal vesicle* (SV): (0) rounded laterally, and anteriorly produced into 2 sclerotized tips connected by desclerotized membrane; (1) rounded laterally, anteriorly the 2 sclerotized tips fuse into a single tip with no membranous area.
37. *When resting*: (0) wings not held pressed together over the abdomen and body hanging downward to, or at least not parallel to the ground or substrate; (1) wings not held pressed together over the abdomen and body parallel to the ground or substrate; (2) wings held pressed together over the abdomen. Rehn (2003) gave a detailed discussion of this character, however, scores for many taxa were uncertain. Quite a number of taxa coded as holding wings vertically in Rehn (2003), such as *Bayadera* and *Megalestes*, definitely stretch their wings laterally. Here, we treated all taxa not holding their wings tightly over the abdomen as one state, no matter whether their wings were opened fully or partially. This character must be observed from mature adults (all Odonata may hold their wings tightly when just emerging) at a common resting state (not in copulation and so on). We believe the body orientation of resting Zygoptera relative to the roost (rocks or leaves etc.) is also phylogenetically informative.
38. *Cross vein basal of Cu crossing*: (0) present; (1) absent.
39. *Internal fold of ligula*: (0) not developed into a long filament; (1) developed into a long filament.
40. *Length of tibial spurs*: (0) longer than 1½ the intervals at least; (1) not longer than 1½ the intervals between them.
41. *Larva lives in*: (0) flowing water; (1) still water; (2) water-filled tree holes only. Taxa only found in running waters are state 0; mainly found in steady water are state 1, even though some of them can also live in running water. State 2 was only found in Central and South American Pseudostigmatids and East African *Coryphagrion grandis*.
42. *Pterostigma*: (0) covering at least 3 cells; (1) covering more than one cell but less than three cells; (2) covering only one cell; (3) absent. Here cells refer to those present in C-RA and proximal to pterostigma.
43. *Cerci*: (0) forcipate, without projections (such as spines or teeth) (Fig. 1A); (1) forcipate, with projections (Fig. 1B, C); (2) not forcipate (Fig. 1D).
44. *Paraprocts*: (0) vestigial or shorter than 1/2 length of cerci, obtuse, without projections (such as spines or teeth) (Fig. 1A, B); (1) shorter than 1/2 length of cerci, acute or with projections (Fig. 1C); (2) longer than 1/2 length cerci (Fig. 1D).

Results

The heuristic parsimony analysis resulted in 66 most parsimonious trees [length = 188, consistency index (CI) = 0.3564, retention index (RI) = 0.7237)]. Jackknife value was calculated on the 50% Majority-rule consensus of the 66 most parsimonious trees with status of all unambiguous characters indicated (Fig. 2). Bayesian analysis, using the Mk Model with 1,000,000 generations, resulted in a 50% majority-rule consensus tree (Fig. 3). Both heuristic parsimony analysis and Bayesian analysis recover a paraphyletic Megapodagrionidae, its members forming the basal

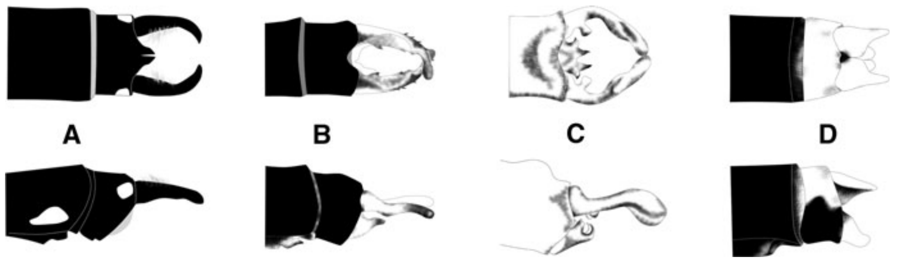


Fig. 1 Cerci and paraprocts of Zygoptera, dorsally and laterally **A** from Yu & Bu (2009) and **B–D** from Yu (2008). **A** *Mesopodagrion tibetanum*, **B** *Lestes japonicus*, **C** *Megalestes distans*, **D** *Prodasineura auricolor*

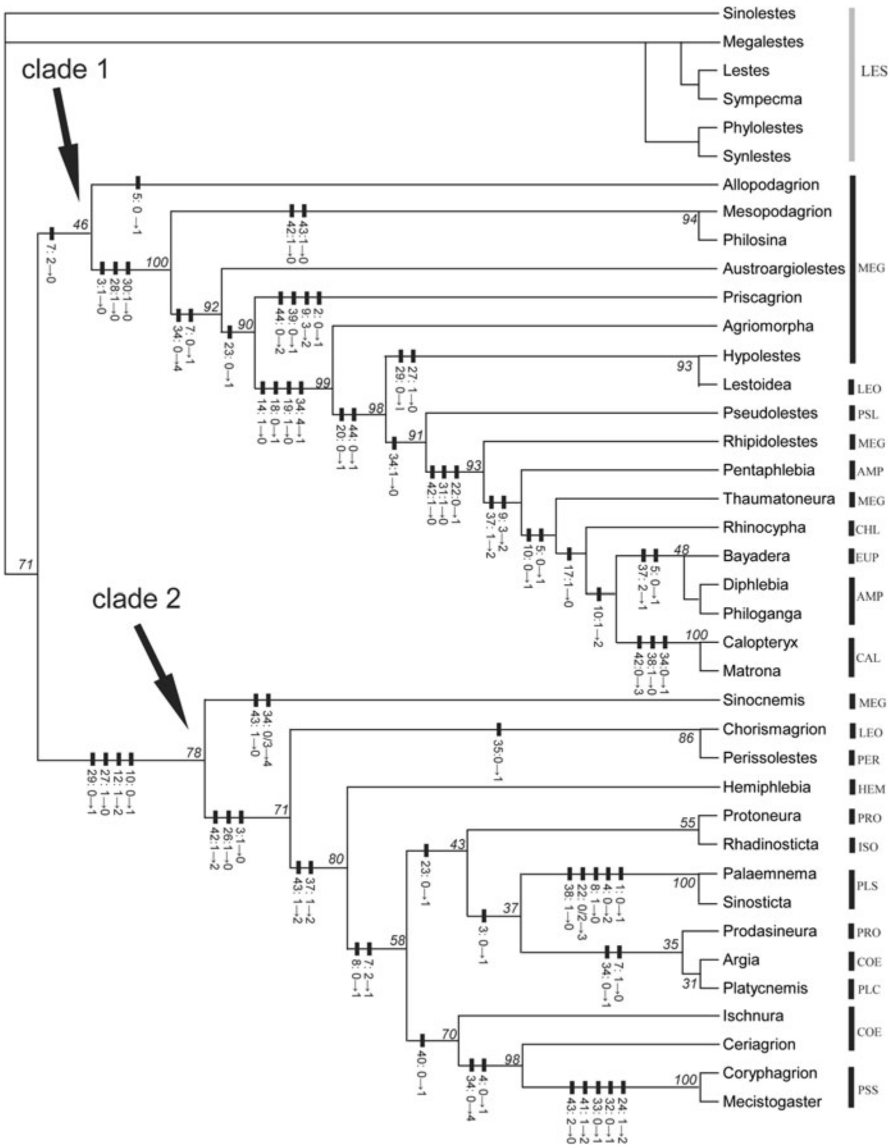
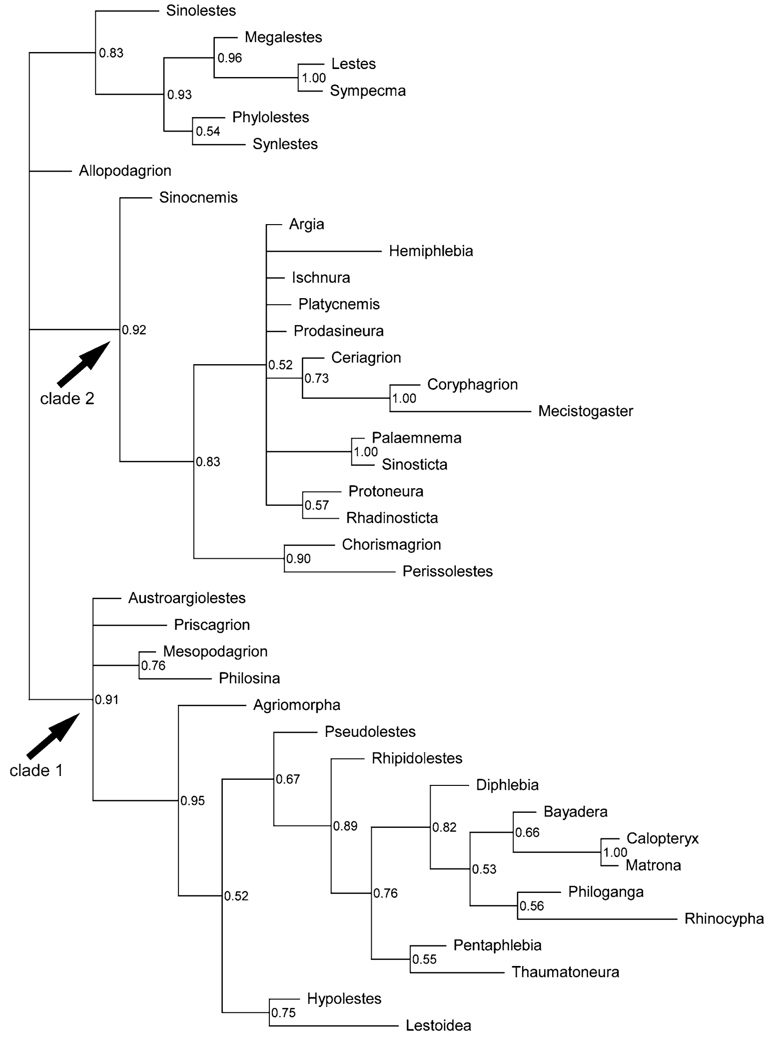


Fig. 2 The 50% Majority-rule consensus of the 66 most parsimonious trees (length = 188, consistency index (CI) = 0.3564, retention index (RI) = 0.7237) with jackknife value and unambiguous characters, Original families (according to Bridges, 1994) for ingroups and outgroups are indicated by *black* and *grey bars* respectively. *AMP* Amphipterygidae, *CAL* Calopterygidae; *CHL* Chlorocyphidae, *COE* Coenagrionidae, *EUP* Euphaeidae, *HEM* Hemiphlebiidae, *ISO* Isostictidae, *LEO* Lestoideidae, *LES* Leatid-like damselflies, *MEG* Megapodagrionidae, *PER* Perilestidae, *PLC* Platycnemididae, *PLS* Platystictidae, *PRO* Protoneuridae, *PSL* Pseudolestidae, *PSS* Pseudostigmatidae, *SYN* Synlestidae

Fig. 3 50% Majority-rule consensus tree generated via MrBayes with 1,000,000 generations using the Mk Model

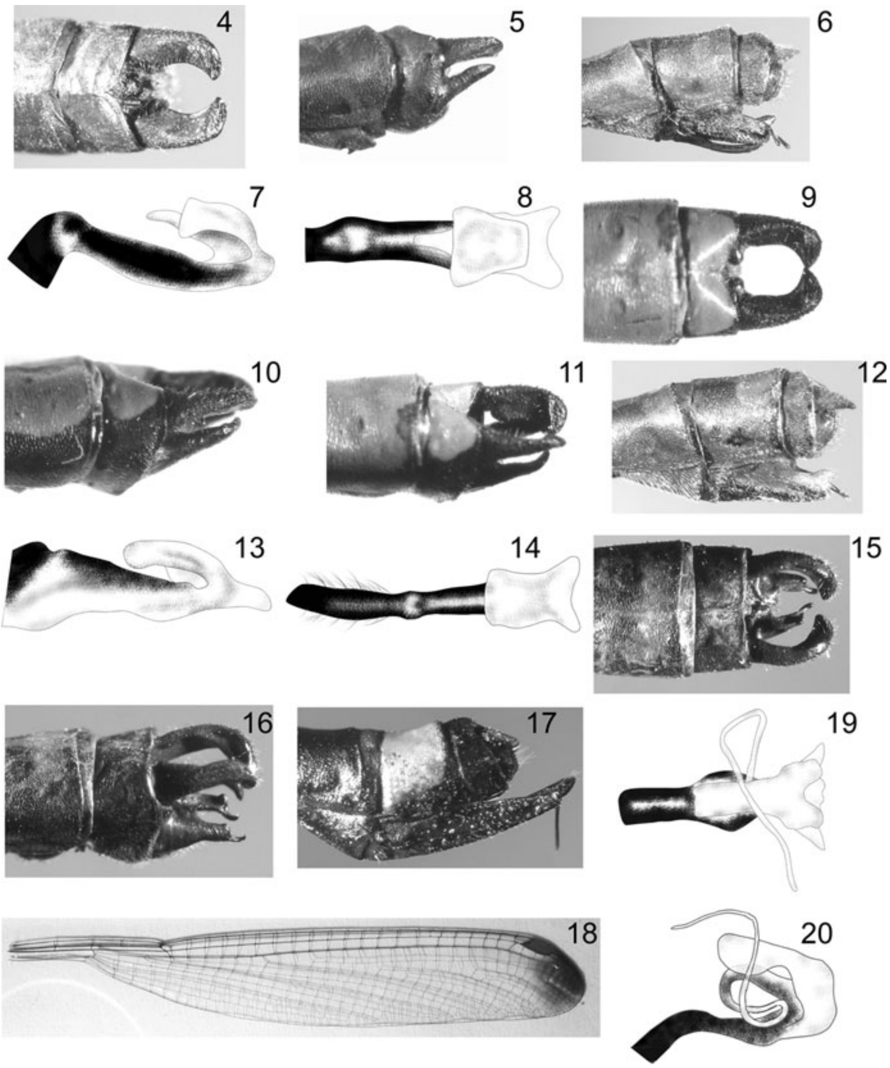


groups of a monophylum, clade 1 (Figs. 2, 3), together with Caloptera, Pseudolestidae and *Lestoidea*. *Sinocnemis* does not nest into Platycnemididae but is the most basal branch of another monophylum, clade 2 (Figs. 2, 3), composed of *Chorismagrion* + *Perissolestes*, *Hemiphlebia*, and all coenagrionoid groups. *Priscagrion* is close to *Austroargiolestes*. *Hypolestes* is the sister to *Lestoidea*. *Hemiphlebia* is sister to the monophyletic Coenagrionoidea in heuristic parsimony analysis with poor support.

Discussion and conclusion

Sinocnemis is confirmed not to be a platycnemidid species and also not, as Kalkman (2008) suggested, close to *Mesopodagrion*, or as van Tol (2009) indicated, the sister to all Zygoptera except lestids. Rather, it is recovered as the most basal branch of clade 2, strongly supported by both heuristic parsimony and Bayesian analysis (Figs. 2, 3). This result is consistent with the position of Dumont et al. (2010), i.e., *Sinocnemis* is neither a platycnemidid nor a megapodagrionid. Our study shows that reduced venation are synapomorphies for clade 2, i.e. characters 10 (0 → 1), 12 (1 → 2), 27 (1 → 0) and 29 (0 → 1). *Chorismagrion*, *Perissolestes* and *Hemiphlebia* all nest in clade 2 when *Sinocnemis* is included in the analysis rather than that it comes out close to Lestid-like damselflies (Rehn, 2003). Considering that homoplastic losses of veins may exist, a more comprehensive phylogenetic study is required to confirm this result. However, we do believe *Sinocnemis* is important for the phylogeny of the Zygoptera, since its characteristics may help to infer more accurately those of the common ancestor of the two clades. Possibly, *Sinocnemis* may deserve a family of its own, however we still need more works to establish it. Finally, Kalkman (2008) treated *Sinocnemis henanese*, a junior synonym of *S. yangbingi*, but after checking our specimens from Gansu, China we arrive at the conclusion that *S. henanese* is a valid species. Although characters of color pattern and caudal appendages are similar between *S. henanese* (Figs. 4–6 and *S. yangbingi* (Figs. 9–12) they are definitely different in the genital ligula: (1) *S. henanese* presents a short projection of the internal fold of the ligula (Figs. 7, 8) which was stated as 'terminal margin of distal segment of penis with a apophysis' in the original description and as a 'soft and probably inflatable area' in Kalkman (2008), whereas *S. yangbingi* lacks this structure (Figs. 13–14); (2) *S. henanese* has no long setae along sides of genital ligula shaft and *S. yangbingi* dose (Fig. 14). We agree with Kalkman (2008) that in terms of ICZN's rules the name '*S. henanese*' should be changed to '*S. henanensis*'.

Heuristic parsimony analysis recovers *Priscagrion* is close related to *Austroargiolestes* supported by characters 3 (1 → 0), 7 (0 → 1), 28 (1 → 0), 30 (1 → 0)



Figs. 4–20 *Sinocnemis henanese* (**4–8**): **4** caudal appendages dorsal, **5** caudal appendages lateral, **6** female caudal appendages lateral, **7** genital ligula lateral, **8** genital ligula ventral; *S. yangbingi* (**9–14**): **9** caudal appendages dorsal, **10** caudal appendages lateral, **11** caudal appendages dorsal–lateral, **12** female appendages lateral, **13** genital ligula lateral, **14** genital ligula ventral; *Priscagrion kiautai* (**15–20**): **15** caudal appendages dorsal, **16** caudal appendages lateral, **17** female caudal appendages lateral, **18** right forewing, **19** genital ligula ventral, **20** genital ligula lateral

and 34 (0 → 4) as well as a topology of (*Allopodagrion* (*Mesopodagrion* + *Philosina* (*Austroargiolestes* (*Priscagrion* +…)))) at base of clade 1 (Fig. 2), however the position of *Allopodagrion* is not strongly supported. In Bayesian analysis *Mesopodagrion* + *Philosina*, *Austroargiolestes*, and *Priscagrion* appear as a polytomy of four branches at base of clade 1. *Allopodagrion* is excluded from clade 1 and appears as one branch of the deepest three polytomous clades. Our result generally supports the suggestion of De Marmels (2002), i.e., the closest relatives of *Priscagrion* are Australo-Papuan 'Argiolestinae' together with South American 'Megapodagrion-complex'. We agree with De Marmels (2002) that the extended internal fold of genital ligula is a key morphological character and the original figures of *Priscagrion* in Zhou & Wilson (2001) are not clear enough. Thus we redrew this structure (Figs. 19, 20) and provided also photos (Figs. 15–18) of the caudal appendages and wing of *Priscagrion*.

Acknowledgments We would like to acknowledge Dr. Rosser Garrison for exchanging valuable specimens from New World and Australia with us, and for helping to check characters scores for some of the specimens. We are grateful to Dr. Michael L. May for his priceless suggestions on our study. We thank Dr. Qiang Xie for helping us with phylogenetic computer software analysis. We also thank Dr. Dennis Paulson and Dr. Klaas-Douwe B. Dijkstra for helping with character scoring. This project was supported by the Natural Science Foundation of China (No. J0930005 and No. 30725005).

References

Bechly, G., 1996. Morphologische Untersuchungen am Flugelgeader der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berucksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. Petalura, special volume 2: 1–402.

Bridges, C. A., 1994. Catalogue of the Family-Group, Genus-Group and Species-Group Names of the Odonata of the World, 3rd ed. The Author, Urbana.

Bybee, S. M., T. H. Ogden, M. A. Branham & M. F. Whiting, 2008. Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. Cladistics 23: 1–38.

Carle, F. L., K. M. Kjer & M. L. May, 2008. Evolution of Odonata, with Special Reference to Coenagrionoidea (Zygoptera). Arthropod Systematics & Phylogeny 66: 37–44.

Davies, D. A. L. & P. Tobin, 1984. The Dragonflies of the World, Vol.1. Societas Internationalis Odonatologica Rapid Communications (Supplements) No.3, Utrecht.

De Marmels, J. 2001. Revision of *Megapodagrion* Selys, 1886 (Insecta, Odonata: Megapodagrionidae). Dissertation, University of Zurich, Germany.

De Marmels, J., 2002. Phylogenetic relationships of *Priscagrion* Zhou & Wilson, 2001, with a description of *Teinopodagrion croizati* spec. nov. from Ecuador (Zygoptera: Megapodagrionidae). Odonatologica 31: 389–394.

Dumont, H. J., J. R. Vanfleteren, J. F. De Jonckheere & H. H. P. Weekers, 2005. Phylogenetic relationships, divergence time estimation, and global biogeographic patterns of calopterygoid damselflies (odonata, zygoptera) inferred from ribosomal DNA sequences. Systematic Biology 54: 347–362.

Dumont, H. J., A. Vierstraete & J. R. Vanfleteren, 2010. A molecular phylogeny of the Odonata (Insecta). Systematic Entomology 35: 6–18.

Fraser, F. C., 1957. A Reclassification of the Order Odonata. Royal Zoological Society of New South Wales, Sydney.

Kalkman, V. J., 2008. Taxonomy, behaviour, and habitat of *Mesopodagrion* and *Sinocnemis*. Notes on Old World Megapodagrionidae 3 (Odonata). International Journal of Odonatology 11: 185–193.

Kimmins, D. E., 1931. Description of the male *Coryphagrion grandis* Morton (Odonata). Annals & Magazine of Natural History 7: 215–217.

Maddison, D. R. & W. P. Maddision, 2000. MACCLADE, Version 4.0. Sinauer Associates, Massachusetts.

Morton, K. J., 1924. A new genus and species of dragonfly from East Africa belonging to the legion Podagrion (Odonata). The Entomologist 57: 217–220.

Novelo-Gutierrez, R., 1995. The larva of *Amphipteryx* and a reclassification of Amphipterygidae *sensu lato* based upon the larvae (Zygoptera). Odonatologica 24: 73–87.

Pessacq, P., 2008. Phylogeny of Neotropical Protoneuridae (Odonata: Zygoptera) and a preliminary study of their relationship with related families. Systematic Entomology 33: 511–528.

Rehn, A. C., 2003. Phylogenetic analysis of higher-level relationships of Odonata. Systematic Entomology 28: 181–239.

Ronquist, F. & J. P. Huelsenbeck, 2003. MrBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Schorr, M., M. Lindeboom & D. R. Paulson, 2009. World Odonata List [available on internet at http://www.ups.edu/x6140.xml]. Accessed May 2009.

Swofford, D. L., 2002. PAUP*—Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sinauer Associates, Massachusetts.

Theischinger, G. & J. Hawking, 2006. The complete field guide to dragonflies of Australia. CSIRO Publishing, Collingwood, Victoria.

Tsuda, S., 2000. A Distributional List of World Odonata. Privately published, Osaka.

van Tol, J., 2006. Global species database. Odonata. In Bisby, F. et al. (eds), Species 2000. Annual Checklist 2006 (Updated Version Published in 2008) [available on internet at http://www.odonata.info].

van Tol, J., 2009. Phylogeny and biogeography of the Platystictidae (Odonata). PhD Thesis, Leiden University.

Wilson, K. D. P. & W. B. Zhou, 2000. *Sinocnemis yangbingi* gen nov., sp. nov. and Sinocnemis dumonti sp. nov., new platycnemidids from south-west China (Odonata: Plactycnemididae). International Journal of Odonatology 3: 173–177.

Yu, X., 2008. A taxonomic study on the superfamilies Coenagrionoidea and Lestoidea (Odonata: Zygoptera) from China. Doctoral Dissertation, Nankai University, Tianjin, China.

Yu, X. & W. J. Bu, 2009. A Revision of *Mesopodagrion* McLachlan, 1896 (Odonata: Zygoptera: Megapodagrionidae). Zootaxa 2202: 59–68.

Zhou, W. B. & K. D. P. Wilson, 2001. *Priscagrion kiautai* gen nov., spec. nov. and P. pinheyi spec. nov., new damselflies from southwestern China (Zygoptera: Megapodagrionidae). Odonatologica 30: 117–121.