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THE *ENALLAGMA* OF THE WESTERN AND CENTRAL PALAEARCTIC (ZYGOPTERA: COENAGRIONIDAE)

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Six populations of the *Enallagma cyathigerum* complex from North Africa, Europe and West and Central Asia were examined, mainly using DNA analysis and scanning electron microscopy. The taxa *deserti* and *risi* are geographic ssp. to *E. cyathigerum*: although ♂♂ can unequivocally be identified from their superior anal appendages, their 18 S rDNA and intergenic spacers ITS 1 and 2 are identical. Moreover, morphological intermediates have become known between *deserti* and *cyathigerum*, and between *risi* and *cyathigerum*. The habitat choice (predatory fish tolerated but with difficulty) and salinity tolerance of all 3 are similar as well. It is concluded that they share a common origin, and only recently started to diverge.

INTRODUCTION

The status of the *Enallagma* species from the Mediterranean basin, Europe, and Western-Central Asia has been a problem for a long time (LIEFTINCK, 1966; JURZITZA, 1975; SEIDENBUSCH, 1997). In 1865, SÉLYS described *E. deserti* from Algeria. The male remained unknown until much later (RIS, 1928). SCHMIDT (1961) described *E. risi* from Afghanistan. This "species" soon proved to be widespread in Central Asia (HARITONOV, 1975; KOSTERIN, 2000), whence it was reported under various names (St QUENTIN, 1962; BENEDEK, 1968). MAY (1997) established order in the synonymy of this taxon. In contrast to the North African *deserti*, which has an occurrence in Ghana worthy of further study (D'ANDREA & CARFI, 1994), it covers a range that rivals that of *cyathigerum*, and was recently found (pers. observ. by H. Dumont) as far southeast as Beijing!

The genus *Enallagma* in Eurasia is an impoverished remnant of a preglacial fauna that may have been comparable in species richness to that of North America, where

around 40 species are currently recognized (WESTFALL & MAY, 1996). Recent progress in understanding the American clades was made when McPEEK & BROWN (2000) combined molecular, morphological and ecological information to derive a phylogenetic tree and reconstruct patterns of local and regional assemblages within the genus. A major factor eliciting radiation was the ability of species to co-exist with fish or not.

Here, we analyse a number of European (including the Maghreb and Turkey-in--Asia) and Mesasiatic populations representing the three "taxa" that are currently recognized in the region. As an outgroup, we analyzed two African and one Himalayan species.

MATERIAL AND METHODS

The origin of the specimens used for DNA-work in the present study is given in Table I. For morphological work, additional specimens from the Middle Atlas in Morocco in the collection of H. Dumont were re--examined (see DUMONT, 1972 for details about these populations, all classified under *E. deserti* in that paper), as well as numerous specimens collected from various localities in Afghanistan (DUMONT, 1975), the Altai mountains (Siberia), Inner Mongolia, and the Republic of Mongolia between 1999 and 2001. A particularly instructive population was that of the salt lake Ergol Nur in Mongolia, collected on 21 July 2001. Numerous specimens from Anatolia, including those from saline Burdur Lake and Aci Krater Gol mentioned in DUMONT (1977) were also rechecked.

Morphological information. – Structural parts of specimens were selected, glued to brass stubs, coated in a thin layer of gold and examined under different magnifications using a JSM-840 scanning electron microscope (SEM), at 15 KV. Some line drawings were made, using a drawing tube attachment, under a Wild M5 stereomicroscope.

Molecular information. – EXPERIMENTAL PROCEDURES. – Thoracic muscular tissue was dissected, and total DNA prepared according to the protocol of the Puregene ™ DNA isolation kit, type D-5000A (BIOzym, Landgraaf, The Netherlands). The entire nuclear ribosomal small subunit DNA (18S nrDNA), ITS1, 5.8S, ITS2, and the 5' part of the nuclear ribosomal large subunit DNA (28S nrDNA) were amplified by PCR, using Qiagen DNA polymerase (Westburg, Leusden, The Netherlands). External eukaryote-specific primers complementary to the 5'-terminus of the nuclear small subunit ribosomal (18S nrDNA) gene (FW primer: 5'-TYCCTGGTTGATYYTGCCAG-3') and the 5'-terminus of the nuclear large subunit ribosomal (28S nrDNA) gene (RV primer: 5'-GCTTAAATTCAGCGG-3') were used to amplify the complete coding and non-coding regions. PCR amplifications were done using a total volume of 100 µl, containing 1,5 mM $MgCl_2$, 0.5 µM each primer, 0.2 mM dNTP mixture, and 10x Taq polymerase reaction buffer, and 2.5 units of Taq DNA polymerase (Qiagen) was added to each reaction. The samples were covered with two drops of mineral oil, and PCR reactions were performed in a Progene thermal cycler (NBS-Techne). Cycling conditions were 95°C for 1 min, 52°C for 2.5 min, and 72°C for 3 min for 30 cycles. PCR products were used for direct sequencing using the BigDye™ technology, the protocol of the ABI Prism BigDye terminator cycle sequencing ready reaction kit, and consequently analysed on an ABI Prism 377 DNA sequencer (PE Applied Biosystems, Nieuwerkerk a/d IJssel, The Netherlands). External (see above) and internal primers in conserved regions of the 18S rDNA; 570C, 570, 1262C and 1262 (WEEKERS et al. 1994), 3'-RV (5'-TGATCCATCTGCAGGTTYCACCT-3'), ITS-FW (5'-TAGAGGAAGTAAAAGTCG-3'), and in conserved regions of the 5.8S rDNA; 5.8SFW (5'-GGATCGATGAAGAACG-3'), 5.8SRV (5'-GAATCGTGGGCTGCAAT-3') were used for sequencing. PCR products were used for direct sequencing using the BigDye™ technology, the protocol of the ABI Prism BigDye terminator cycle sequencing ready reaction kit, and thereafter analysed on an ABI Prism

Table I

Gene length, GC content and accession number of the ribosomal 18S and 5.8S genes and the ITS1 and ITS2 spacers, and geographical origin of the species used in this study. – [Collector's institutional affiliations are provided in the acknowledgments]

species/ sub-species	18S gene length	18S gene GC %	ITS-1 spacer length	ITS-1 spacer GC %	5.8S gene length	5.8S gene GC %	ITS-2 spacer length	ITS-2 spacer GC %	EMBL acc. number	geographical origin	collector's name
E. deserti	1857	52.23	188	44.15	172	54.65	202	58.91	AJ420945	Thala, Tunisia	R. Jödicke
E. deserti	1857	52.23	188	44.15	172	54.65	202	58.91	AJ420944	Tebessa, Algeria	B. Samroui
E. risi	1857	52.23	188	44.15	172	54.65	202	58.91	AJ420942	Hulun Nur, Inner Mongolia	H. Dumont
E. risi	1857	52.29	188	44.15	172	54.65	202	58.91	AJ420943	Teletskoe Lake, Altai, Russia	H. Dumont
E. risi	1857	52.23	188	44.15	172	54.65	202	58.91	AJ420941	Hohhot, Inner Mongolia, China	S. Rong
E. cyathigerum	1857	52.18	188	44.15	172	54.65	202	58.91	AJ420940	Kalmthout, Belgium	H. Dumont
E. parvum	1857	52.18	168	48.81	172	54.07	203	66.01	AJ420939	Asan Lake, N. India	H. Dumont
E. nigridorsum	1857	52.29	210	47.62	175	53.71	203	58.13	AJ420938	Socotra Island	K. Van Damme
E. granti	1857	52.29	156	57.05	173	56.65	202	68.81	AJ420937	Socotra Island	K. Van Damme

377 DNA sequencer (PE Applied Biosystems).

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS. – Sequences (18S, ITS1, 5.8S, ITS2 and partial 28S) were aligned automatically using CLUSTALW (THOMPSON et al., 1994) but visually optimized using the Eyeball Sequence Editor (ESEE) (CABOT & BECKENBACH, 1989). From this alignment a second dataset, containing only the ITS1, 5.8S and ITS2 sequences, was constructed and used in the phylogenetic analysis. Sequence divergence values were computed by the Kimura 2-parameter model (KIMURA, 1980) using the DNADIST program of PHYLIP (FELSENSTEIN, 1989). Phylogenetic reconstruction was performed using the neighbour-joining method and the JIN & NEI (1990) correction method of Treecon 1.3b (VAN DE PEER & DE WACHTER, 1994); bootstrap values were calculated with the same program (FELSENSTEIN, 1985).

RESULTS OF THE DNA STUDY

We obtained the complete, unambiguous sequence for the entire nuclear ribosomal small subunit DNA (18S), ITS1, 5.8S, ITS2, and the 5' part of the nuclear ribosomal large subunit DNA (28S) for all *Enallagma* listed in Table I. The length of the 18S gene is 1857 bp, and is the same for the ingroup and outgroup taxa; the GC content varies slightly (52.18-52.29%) (Tab. I). The length of the 5.8S gene is the same for all ingroup taxa (172 bp) but varies in the outgroup taxa (172-175 bp). Also the GC content of the 5.8S gene shows some variation (53.71-56.71%). The length of the ITS1 and ITS2 are the same for all ingroup taxa (resp. 188 and 202 bp). In general, the in- and outgroup taxa vary more in length of their ITS1 (156-210 bp) than in their ITS2 (202-203 bp). The same is true for the GC content. The GC content of the ITS1 and ITS2 of the ingroup taxa is resp. 44.15% and 58.91%.

Table II

Pairwise comparison of all ingroup (North Africa, Europe and Asia) and outgroup (India and Socotra Island) taxa in the analysis. Above the diagonal are absolute nucleotide differences. Below the diagonal are distances calculated for the combined 5.8S, ITS1 and ITS2 regions, using the Kimura 2-parameter model as correction method

Taxa	Edes(A)	Edes(T)	Eris(C)	Eris(R)	Erbo(IM)	Ecya	Epar	Egra	Enig
E. deserti (Algeria)	—	0	0	0	0	0	77	97	109
E. deserti (Tunisia)	0.0000	—	0	0	0	0	77	97	109
E. risi (E. Inner Mongolia)	0.0000	0.0000	—	0	0	0	77	97	109
E. risi (Altai, Russia)	0.0000	0.0000	0.0000	—	0	0	77	97	109
E. risi (C.Inner Mongolia)	0.0000	0.0000	0.0000	0.0000	—	0	77	97	109
E. cyathigerum (Belgium)	0.0000	0.0000	0.0000	0.0000	0.0000	—	77	97	109
E. parvum (N. India)	0.1609	0.1609	0.1609	0.1609	0.1609	0.1609	—	101	114
E. granti (Socotra Island)	0.2173	0.2173	0.2173	0.2173	0.2173	0.2173	0.2315	—	76
E. nigridorsum (Socotra Island)	0.2314	0.2314	0.2314	0.2314	0.2314	0.2314	0.2541	0.1639	—

The GC content for in- and outgroup taxa together shows a variation between 44.15-57.05% (ITS1) and 58.13-68.81% (ITS2) (Tab. I).

The highest interspecific sequence diversity between the taxa investigated is ca 25%. The interspecific sequence diversity of the ingroup is zero (0%), while for the outgroup it varies between 16% and 25% (Tab. II). Phylogenetic analysis, using the method described above, was used to construct a phylogenetic tree. Of 607 aligned positions from the ITS1, 5.8S and ITS2 regions of all taxa, 177 sites were variable, 59 of which were phylogenetically informative. The ITS1, 5.8S and ITS2 sequence data, used to construct a neighbour-joining tree using the Kimura 2--parameter correction method (Fig. 1), showed that the *cyathigerum-deserti-risi* complex (ingroup) is monophyletic (bootstrap values 100%) with no genetic distance between the taxa.

SCANNING ELECTRON MICROSCOPY

All three taxa have characteristic male superior appendages, with a diagnostic arrangement of the dorsal apical lip and a typically shaped subapical tooth.

In *deserti*, the male bears a chisel--shaped subapical tooth, separated from the lip by a cleft (Figs 2, 3, 7, 17). Numerous bifid spines are found on the inner surface of the second segment of the penis (Figs 10, 11).

In *cyathigerum* the male superior appendage has a finger-shaped, inwardly pointing subapical tooth, and an overhanging apical lip (Figs 4, 8, 16). The

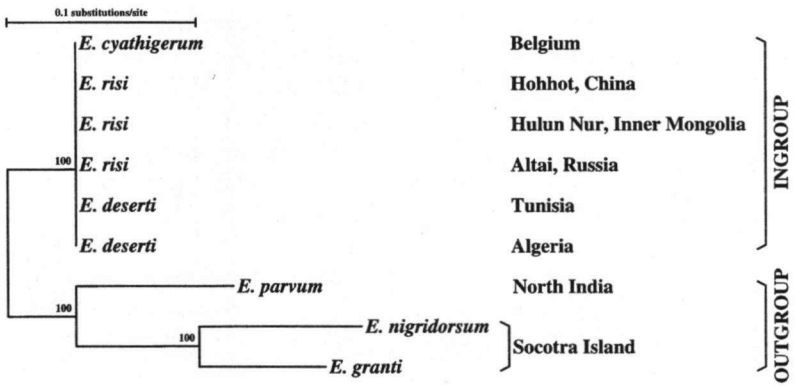


Fig. 1. Neighbour-joining distance tree inferred from ITS1, 5.8S and ITS2 sequence data showing biogeographical relationships between *Enallagma* taxa from different geographical origin. Evolutionary distances calculated by neighbour-joining using the Jin & Nei correction method in Treecon. The tree is rooted using *E. parvum* (Northern India), and *E. nigridorsum* and *E. granti* (Socotra Island) as outgroup. Bootstrap values are based on 1000 replicates and expressed as a percentage.

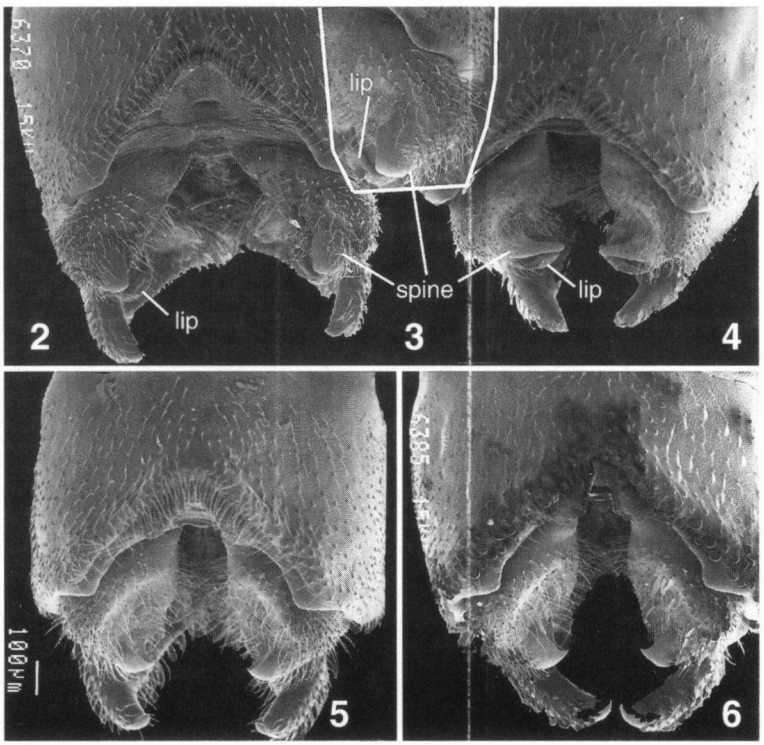
inner surface of the second segment of the penis bears only three simple spines (Figs 12, 13). Females have a somewhat sinuous depression (less pronounced than that of *E. risi*) of the hind ridge of the mesostigmal plates (Fig. 21).

In *risi* the male superior appendages have a claw-shaped, sharp subapical tooth, separated from the lip by a narrow cleft (Figs 5, 6, 9). The spines on the inner surface of the penis are partly bifid (Figs 14, 15) The anterior margin of the female lamina mesostigmalis is ridge-like and is raised above a depression (Fig. 20).

Within the range of *risi,* which we allow to begin east of the Caspian Sea but probably does not encompass the humid part of Siberia (KOSTERIN, 2000), we found transitory male specimens in the area of Teletskoe lake on the north slopes of the Altai mountains, exactly confirming a similar claim by KOSTERIN (loc. cit.). Furthermore, mixed with typical *risi,* we found the odd specimen of pure *cyathigerum* phenotype among series of specimens collected at Ergol Nur, a salt lake in Mongolia. Re-examining series of "*deserti*" collected in the Middle Atlas, Morocco, in July 1972, supplemented by specimens collected at the same sites in May 1996, we confirm that, beside *deserti* phenotypes, phenotypes close to pure *cyathigerum* occur (as claimed by LOHMAN, 1990), as well as intermediates (Figs 18, 19) in which the subapical tooth is more broad-based than in *cyathigerum*, and the apical lip either overhangs the tooth (Fig. 18) or not (Fig. 19).

DISCUSSION

Ever since the description of *E. deserti* (SÉLYS, 1865, 1871; RIS, 1928) and *E. risi* (SCHMIDT, 1961), the true relationship of these taxa and their distribution (allegedly



Figs 2-6. *Enallagma cyathigerum* group, SEMS of male terminalia: (2) *deserti* (Algeria); – (3) idem, more enlarged to show chisel-shape of subapical spine of appendix superior; – (4) *cyathigerum* (Kalmthout, Belgium); – (5-6) *risi* (Huhehot, Inner Mongolia and Teletskoe Lake, Altai, Siberia).

circumpolar for *E. cyathigerum*) has been a source of confusion.

Recent research by McPEEK & BROWN (2000) has revealed that it remains to be seen whether true *cyathigerum* really occurs in North America. It also stands to reason to blame the Pleistocene glaciations for the impoverished *Enallagma* flock of the Palaearctic, but where the origin of the *cyathigerum* group lies is still an unsolved question.

The lack of genetic divergence among the three *cyathigerum*-like taxa might reflect a slow rate of evolution of the genes involved (18S, 5.8S rRNA), but that does not apply to the intergenic spacers ITS1 and ITS2. We know of no other, even closely related odonate species or subspecies which display the same perfect homology, and think that they all stem from a recent parapatry, that has resulted in some morphologic but little or no genetic disgression.

Molecular and morphological data may conflict, as different loci can evolve at different rates. Morphological differences are sometimes greater than molecular differences

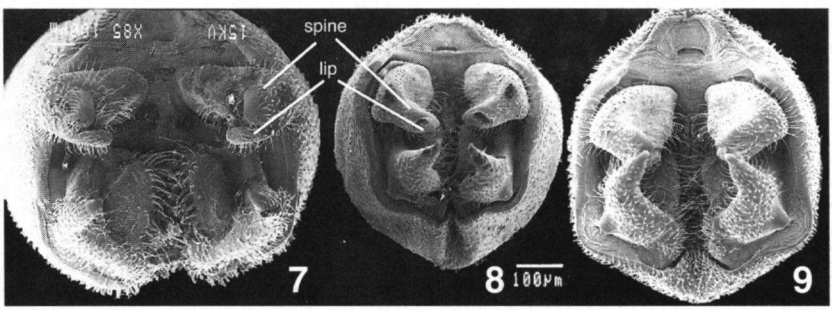
(MEYER et al., 1990). However, zero divergence is unusual, and cases of slight morphological differences with considerable molecular divergence appear to be much more common than the inverse (STURMBAUER & MEYER, 1992, 1997).

The shape of the anal appendages of *deserti* populations across North Africa (LIEFTINCK, 1966; SAMRAOUI & MENAI, 1999; JACQUEMIN & BOUDOT, 1999) and that of *risi* across Central Asia (SCHMIDT, 1961; DUMONT, 1975; MAY, 1997) and *cyathigerum* across Europe was thought to be invariable. However, both Kosterin's study, and the present observations now show that this is not the case.

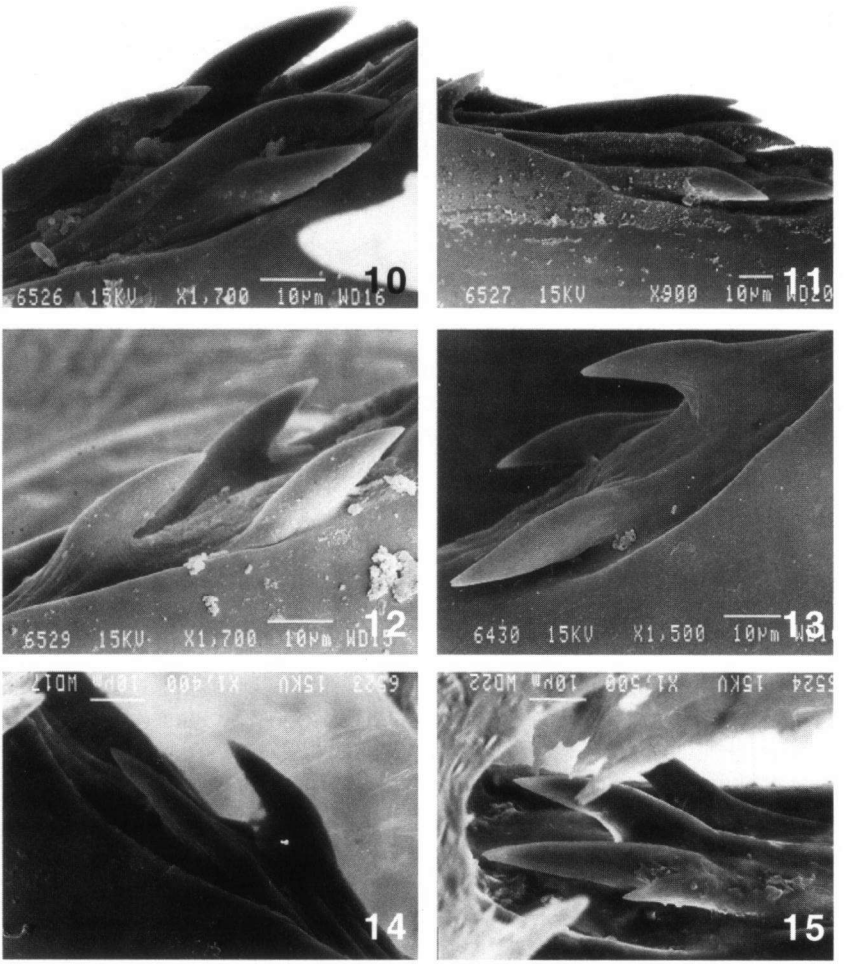
E. deserti and *E. cyathigerum* indeed coexist in the Moroccon Middle Atlas (LOHMANN, 1990; JACQUEMIN & BOUDOT, 1999), but structural intermediates form a cline here.

McPEEK & BROWN (2000) suggested that nonadaptive speciation processes may have been the driving force behind the relatively recent (ca 15,000 years old) *Enallagma* radiation in North America. These authors suggest that sexual selection fueled by random drift could explain the regional pattern of North American *Enallagma* assemblages characterized by an array of ecologically similar but reproductively isolated species. Neither *risi* nor *deserti* appear to be reproductively isolated from *cyathigerum*, however. A second factor to which McPEEK & BROWN (loc. cit.) give great weight is evolution (of the larvae) in the presence or absence of fish. In the *cyathigerum*-group, coexistence with fish is often the case, but larval losses to fish predation are high. However, *Enallagma* is common in acid waters, where fish predation is depressed, and, even more significantly, in fish-depleted saline waters. In the latter type of biotope, they may build huge population sizes. Examples of these have been cited from Anatolia (*cyathigerum*) (DUMONT, 1977), and from Mongolia (Dumont, pers. obs.) (*risi*). The senior author recently found *deserti* at lowland saline environments ("chotts") in Algeria too.

SEQUENCE VARIATION. – The complex (ingroup) under examination has short ITS1 and ITS2 regions (188 bp and 202 bp, respectively). The shortest ITS regions reported for animals are from nematodes, having respectively 215-224 bp (ITS1), and 107-120



Figs 7-9. SEMS of male terminalia in posterior view: (7) *deserti* (Algeria); – (8) *cyathigerum* (Belgium); – (9) *risi* (Inner Mongolia).

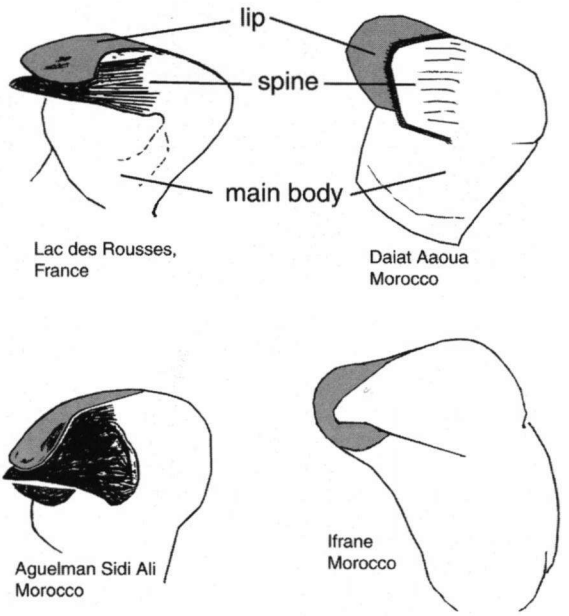


Figs 10-15. Spines on ligula of males of *Enallagma cyathigerum* group: (10-11) *deserti* (Algeria); – (12-13) *cyathigerum* (Belgium); – (14-15) *risi* (Altai, Russia).

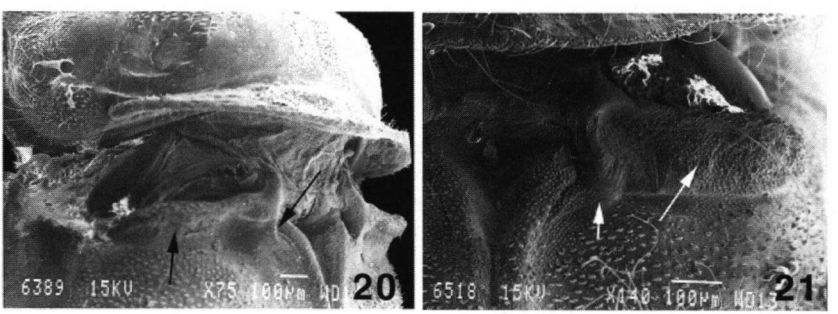
bp (ITS2) (HUGALL et al., 1999). Among plants the length of short ITS regions varies between 186-240 bp (ITS1) and 219-263 bp (ITS2) (Cucurbitaceae, JOBST et al., 1998; Papilionidae, KÄSS & WINK, 1997; Araliaceae, WEN & ZIMMER, 1996). The GC content of the ITS1 and ITS2 of all *Enallagma* taxa (in- and outgroup) are within the normal range for insects (data from Genbank/EMBL), and are also within the range of other animals and plants with relatively short ITS sequences; 50-67% (ITS1) and 52-83% (ITS2) (JOBST et al., 1998; KÄSS & WINK, 1997; HUGALL et al., 1999). However, the GC content in the ITS2 is in general higher than in the ITS1.

PHYLOGENETIC RELATIONSHIPS: INTER- AND INTRA SPECIFIC IMPLICATIONS. – Our

phylogenetic tree shows a separate clade for the *cyathigerum-deserti-risi* complex with bootstrap value 100%, and no genetic distance between the taxa. It therefore seems that the taxa *deserti* (Algeria, Tunesia), *risi* (China, Russia, Inner Mongolia) and *cyathigerum* (Belgium), even though from widely different geographical origins, are identical. Their spatial juxtaposition with marginal overlap and cline-formation in diagnostic morphological characters is consistent with the geographic subspecies concept. We therefore reduce *deserti* and *risi* to the status of subspecies to *cyathigerum*. The outgroup taxa, in contrast, stand far apart from *Enallagma cyathigerum*, and perhaps even from true *Enallagma*. We agree with WESTFALL & MAY (1996) that they had better be considered one (or perhaps two) separate genera. This, however, will form the subject of a separate study.



Figs 16-19. Diagrams of apical zone of male superior appendages: (16) typical *cyathigerum* (Lac des Rousses, France); – (17) typical *deserti* (Daiet Aaoua, Middle Atlas, Morocco); – (18-19) two intermediate specimens between *cyathigerum* and *deserti* from two locations in Morocco.



Figs 20-21. Hind margin of pronotum and lamina mesostigmalis in females of *Enallagma cyathigerum* group: (20) *E. risi*; – (21) *E. cyathigerum*. Small differences arrowed.

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