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Complex male genitalia (hemispermatophores) are not diagnostic for cryptic species in the genus *Euscorpius* (Scorpiones: Euscorpiidae)

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Abstract

Genital morphology is often used as a key character for distinguishing species in many arthropod groups. Regarding scorpions, male genitalia (hemispermatophores) have been increasingly used in species descriptions. In the present study we analyse hemispermatophores of four Central European species of *Euscorpius* Thorell, 1876, and those of *Euscorpius flavicaudis* (De Geer, 1778) from southern France. The main focus are the three morphologically cryptic species, *Euscorpius alpha* Caporiacco, 1950, *Euscorpius germanus* (C.L. Koch, 1837), and *Euscorpius gamma* Caporiacco, 1950. The clear, deep split between *E. alpha* and *E. germanus* previously shown from nuclear allozyme data and mitochondrial genetic markers is not found in hemispermatophore and other morphological characters. Even the hemispermatophore of *E. gamma*—a species branching off at the same genetic distance level as *E. alpha* and *E. germanus*, and clearly diagnosable on external morphological characters—is indistinguishable from those of *E. alpha* and *E. germanus*. Although hemispermatophores are complex, they are not more informative than other morphological characters. *Euscorpius* hemispermatophores may be useful for species discrimination, but in closely related species they are of limited taxonomic value.

Keywords: Scorpiones; *Euscorpius*; Hemispermatophores; Genital organ; Cryptic species

See also **Electronic Supplement** at http://www.senckenberg.de/odes/04-02.htm

Introduction

Rapid evolution and complexity in genitalia is a generally observed pattern in the morphological diversification of animals. Thus, animal genitalia have been recognised as especially useful in distinguishing closely related species in a wide variety of animal groups (Eberhard 1985). The term male genitalia sensu lato also includes packages of sperm (spermatophores), which are deposited by the males of some animal groups outside their bodies during mating (Eberhard 1985). This indirect form of mating is widespread in arachnids, e.g. in amblypygids, pseudoscorpions, mites, and scorpions (Angermann 1957; Weygoldt 1969, 2000; Schaller 1971; Polis 1990; Proctor 1998).

In scorpion taxonomy, the two hemispermatophores forming the spermatophore have been described as a useful character (Pawlowsky 1921; Vachon 1948; Lamoral 1979; Maury 1980; Stockwell 1989). Thus, this character is often used as a valuable trait in species

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descriptions (Lamoral 1979; Lourenço and Monod 2000; Volschenk et al. 2000, 2001). Hemispermatophore structure may even represent the only reliable character discriminating species, as shown for two cryptic species of the *Mesobuthus gibbosus* (Brullé, 1832) complex, where genetic data supported a deep split between two allopatric species (Gantenbein et al. 2000a).

The genus *Euscorpius* (Euscorpiidae) has been studied since the 1830s using "trichobothriotaxy" (= the use of trichobothrial patterns in taxonomy; Vachon 1974) as a valuable method to compare and separate different species (Birula 1917; Vachon 1962, 1972, 1974). Many subspecies were described, but their delimitation and distribution was very unclear (Caporiacco 1950; Kinzelbach 1975; Bonacina 1980). *Euscorpius* taxonomy changed considerably with the application of molecular methods (Gantenbein et al. 1998, 1999, 2000b, 2001; Scherabon et al. 2000; Fet et al. 2003). Currently, five species in Central Europe are regarded as valid: *Euscorpius alpha* Caporiacco, 1950, *Euscorpius tergestinus* (C.L. Koch, 1837) (elevated to species level out of the *E. carpathicus* complex by Fet and Soleglad 2002), *Euscorpius gamma* Caporiacco, 1950, *Euscorpius germanus* (C.L. Koch, 1837), and *E. italicus* (Herbst, 1800).

Recent phylogenetic studies on the two sibling species *E. alpha* and *E. germanus* revealed a clear separation, since populations were fixed for different alleles at eight out of the 18 scored allozyme loci (Gantenbein et al. 2000b). There was also no evidence for hybridisation at the nuclear loci. Moreover, additional mitochondrial (mt)DNA sequence data supported the phylogenetic tree found by allozyme analysis (Gantenbein et al. 2000b). However, the hemispermatophores of the two species were never studied in detail.

At present, *Euscorpius* taxonomy is therefore based mainly on molecular and somatic-morphological data. On the other hand, hemispermatophores have been shown to be the only species-discriminating morphological character in certain buthids (Gantenbein et al. 2000a). We therefore present here for the first time detailed descriptions and comparisons of the hemispermatophores of four Central European species of *Euscorpius*. In addition, we discuss the strongly deviating hemispermatophore of *Euscorpius flavicaudis* (De Geer, 1778) from southern France.

Material and methods

Fig. 1 shows the sampling sites for the different species and the respective numbers of specimens used. *E. italicus* specimens were collected by M.B. or A.J. The population samples of the other species are in the collection of B.G. (for details see the corresponding Organisms, Diversity and Evolution Electronic Supplement: http://www.senckenberg.de/odes/04-02.htm). The specimens were collected by hand, most were killed by deep-freezing (–80°C). A pedipalp was usually removed for biochemical analyses (Gantenbein et al. 2000b). After genetic analysis, specimens were transferred to 70–80% ethanol. For morphological analysis only adult males were used. All specimens are deposited in the Natural History Museum of Bern. A detailed list of specimens is given in Electr. Suppl. 04-02.

Preparation

To uncover the paraxial organs containing the hemispermatophores, the first six mesosomal segments were sectioned dorsally along the median line by using a small pair of scissors. With the help of tweezers the paraxial organ was taken out of the mesosoma, and the hemispermatophore was carefully removed from the surrounding tissue. This method has the advantage that the delicate hemispermatophores can be removed without damaging them. For other hemispermatophore preparation methods see Lamoral (1979) and Stockwell (1989). Usually, the left hemispermatophore was analysed.

Morphological characters

Vachon's (1948) nomenclature is used for the hemispermatophore analysis, with some emendations adapted from Stockwell (1989). Our illustrations (e.g. Fig. 2) show each hemispermatophore in an overview, as well as details of the capsule (cap) region. The latter contains three major lobes: the outer distal lobe (lde = lobe distal extern), the inner distal lobe (ldi = lobe distal intern), and the basal lobe (lb = lobe basal) which carries a number of short spikes (Fig. 2A). At the end of a long, transparent lateral lobe (ll), there is a "crown-like structure", the armature of the sperm duct opening (Stockwell 1989; cls in Fig. 2A).

We recorded the number of spikes on the cls at the end of the lateral lobe (llspikes), the number of spikes on the basal lobe (lbspikes), and the presence and structure of the ldi. For the comparison between *E. alpha* and *E. germanus*, two additional traits were included, namely the number of pectinal teeth of the right pecten (ptright) and the number of trichobothria on the ventral side of the right patella (tvright). This was done because, according to the data of Gantenbein et al. (2000b), the latter two characters allow the identification of some specimens of the two species.

Statistical tests

E. alpha and *E. germanus* were compared by multivariate statistics in a linear discriminant analysis. This method is based on multiple regressions and allows the

Fig. 1. Sampling sites (with number of specimens used). (○) *E. alpha*: 1 Fontainemore (6), 2 Monte (2), 3 San Carlo (2), 4 San Giovanni Bianco (31), 5 Isola di Fondra (5), 6 Carona (1), 7 Selvino (1), 8 Vigolo (1), 9 Bezecca (1), 10 Molina di Ledro (1). (●) *E. germanus*: 11 Sta Maria (3), 12 Müstair (1), 13 Schluderns (4), 14 Vetriolo (3), 15 Borca di Cadore (6), 16 Starkenbach (2), 17 Tarrenz (1), 18 Kranzach (2), 19 Schütt (2), 20 Federaun (1). (⊖) *E. gamma*: 21 Windisch Bleiberg (2), 22 Waidisch (2), 23 Trögerner Klamm (3), 24 Johannsenruhe (2), 25 Babucnikgraben (2). (Δ) *E. italicus*: 2 Monte (1), 26 Conthey (1), 27 Sala Capriasca (1), 28 Cugnasco (1), 29 Coglio (2), 30 Soazza (2), 31 Bodio (1).

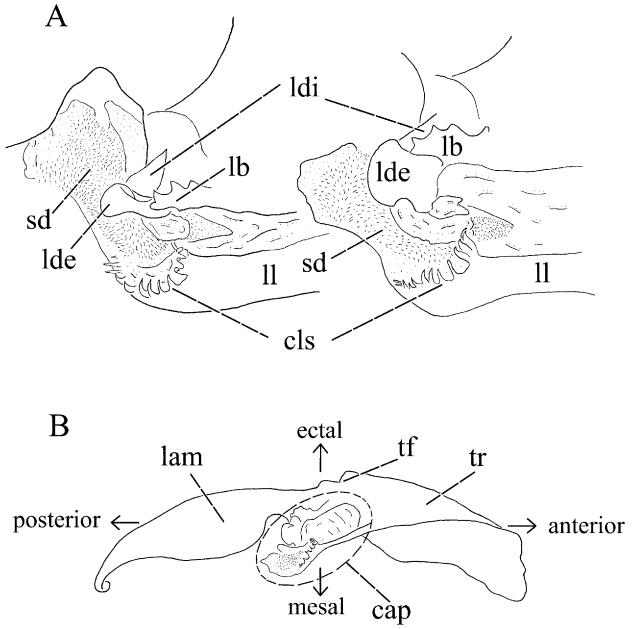

Fig. 2. Explanation of hemispermatophore structures, showing the hemispermatophore of *E. italicus* in an overview (B); and two different views of the capsular region (A). Abbreviations: cap = capsule, cls = crown-like structure, lam = distal lamina, lb = basal lobe, lde = outer distal lobe, ldi = inner distal lobe, ll = lateral lobe, sd = sperm duct, tf = truncal flexure, tr = trunk.

summing up of several morphological characters into one value per individual. For more detailed information about this procedure consult Flury and Riedwyl (1988). A χ^2 value with the Haber correction was used to compare the existence or reduction of the ldi. The number of spikes at the end of the ll and the number of spikes on the basal lobe were each tested for the four species using a Kruskal–Wallis test. If those tests showed significant differences, a Dunn test was performed to determine on which comparisons this significance was based. Linear discriminant analysis and Kruskal–Wallis tests were carried out using SPSS for Windows (release 11.0; SPSS Inc. 2001).

Results

Euscorpius hemispermatophores

In *Euscorpius*, the hemispermatophore is lamelliform, consisting of a trunk (tr), truncal flexure (tf), distal lamina (lam), and a capsule (cap) region with sclerotised lobes, situated mesally between trunk and lamina (Fig. 2). In four of the species studied (*E. alpha*, *E. germanus*, *E. gamma*, *E. italicus*), the outer surface of the sperm duct (sd) that connects the end of the ll with an extended region around the outer distal lobe is lined with numerous small spicules. The outer distal lobe is always distinctly pronounced and does not differ among the four species. In contrast, the occurrence of the inner distal lobe varies from distinctly pronounced to completely reduced even within one species. The number of spikes on the basal lobe varies from 1 to 8, the number of spikes on the cls from 4 to 15. The simplified hemispermatophore of *E. flavicaudis* does not fit this description (see below).

Euscorpius germanus and *E. alpha*

No differences between the two species were found regarding the shapes of the trunk, truncal flexure or distal lamella (Figs. 3 and 4). The complex region around the sperm duct provides more information. The ldi is completely reduced in 24% of *E. germanus* ($n = 25$) and 8.7% of *E. alpha* ($n = 23$), whereas in the remaining specimens it is weakly distinct. No significant difference was found by calculating a χ^2 value with the Haber correction ($\chi^2 = 1.352$, $df = 1$, $0.1 < p < 0.25$). Fig. 5 shows box plots of four characters that could potentially be used for the separation of the two species (see also Electr. Suppl. 04-02). By applying linear discriminant analysis, the coefficients shown in Table 1 are found. The best separation resulted when the three variables llspikes, tvright and ptright were included, but lbspikes omitted. Using the coefficients in Table 1 we can calculate the discriminant function scores shown in Fig. 6. Separation of the two species is clear, except for 8 out of 31 individuals. Therefore, the separation probability increases by using linear discriminant analysis, but a complete separation is not possible. The shape of the basal lobe (lb) is very variable in both species, and comparing the respective transition of the lb to its base does not give clear differences. In both species the intraspecific variation of hemispermatophore characters is very high, making it impossible to find unambiguous differences.

Euscorpius gamma

The hemispermatophore in *E. gamma* (Fig. 7) is practically identical to those in *E. germanus* and *E. alpha*. The ldi is also very weakly distinctive or reduced and does not differ in shape from those in the two other species. The degree of morphological variation in the capsular region is also very high.

Euscorpius italicus

Comparing the hemispermatophore of *E. italicus* (Fig. 8) to the three species described above, several differences are quite evident. Firstly, the *E. italicus* hemispermatophore is considerably larger than the

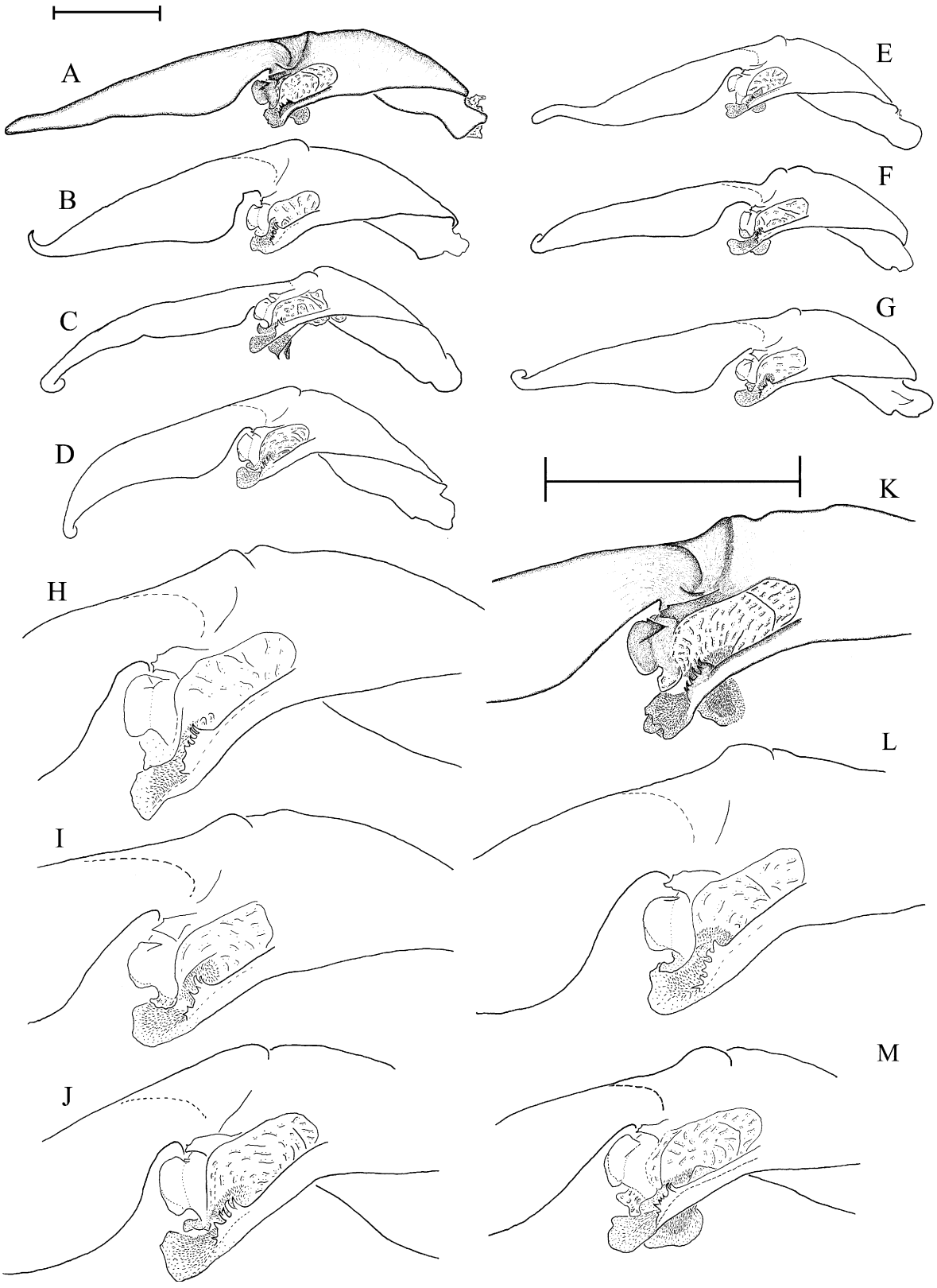

Fig. 3. *E. alpha* hemispermatophores; (A–G) overviews (scale bar at top left: 1 mm); (H–M) capsules (scale bar at center right: 1 mm). Sampling sites: (A,E,K,M) Isola di Fondra; (B,D,G–J,L) Fontainemore; (C) Vigolo; (F) Monte.

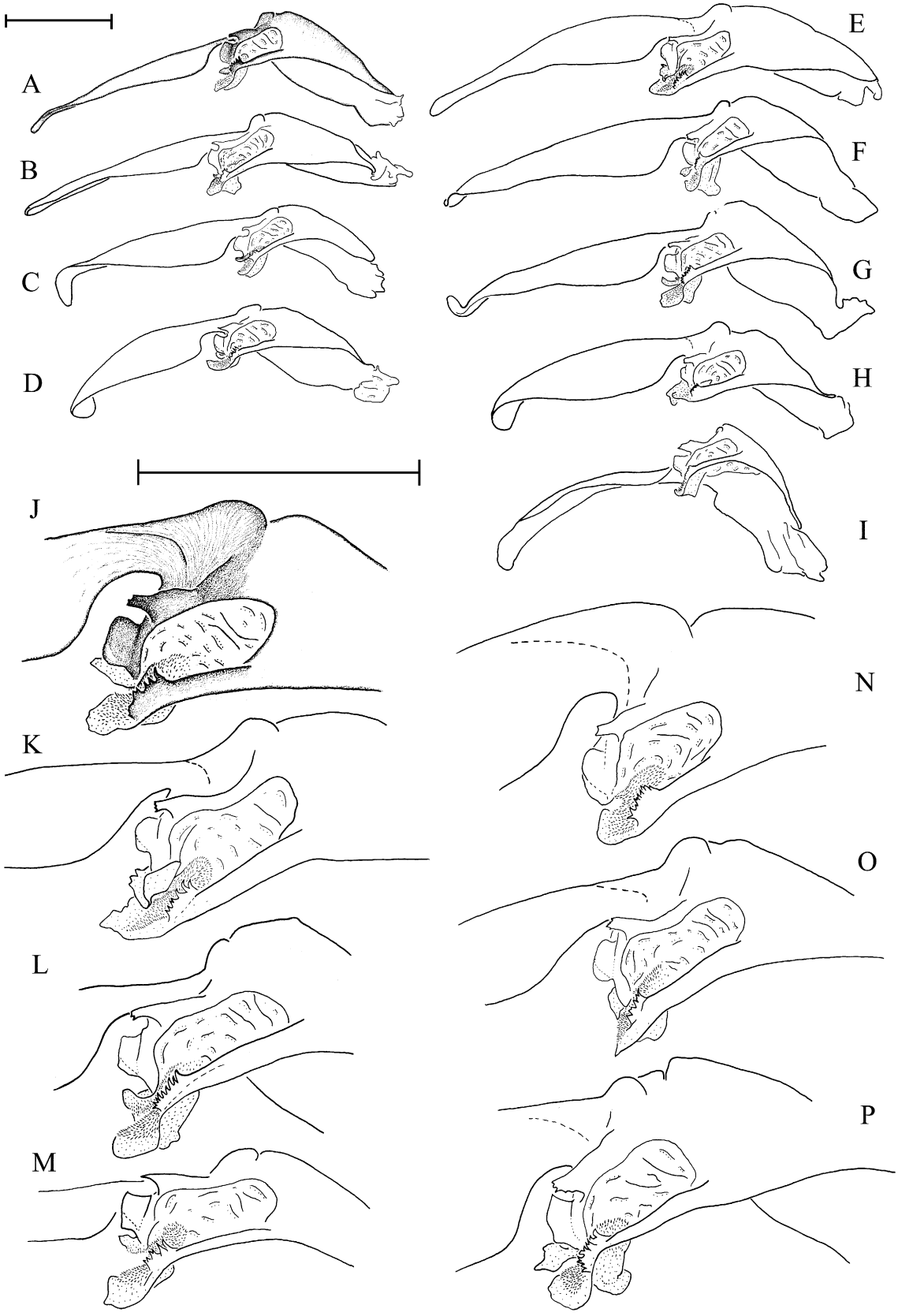

Fig. 4. *E. germanus* hemispermatophores; (A–I) overviews (scale bar at top left: 1 mm), (J–P) capsules (scale bar at center left: 1 mm). Sampling sites: (A,C,H,J,N) Vetriolo; (B) Schütt; (D) Tarrenz; (E, K) Starkenbach; (F,P) Kranzach, (G,L) Sta Maria; (I) Müstair; (M) Borca di Cadore; (O) Federaun.

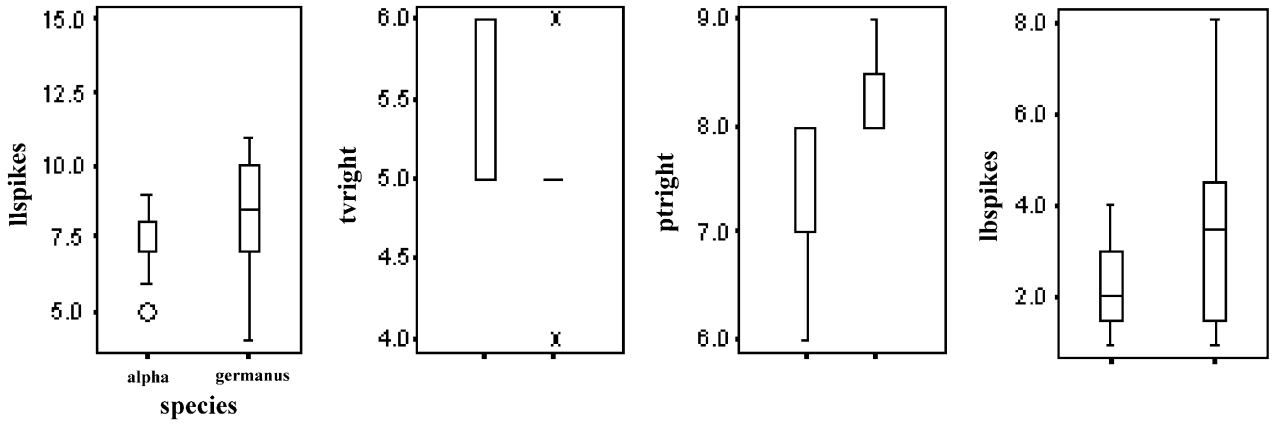

Fig. 5. Comparison of *E. alpha* (species 1) with *E. germanus* (species 2) regarding four morphological characters: llspikes = number of spikes on the cls ($n_1 = 21$, $n_2 = 24$); tvright = number of trichobothria on the ventral side of the right patella ($n_1 = 18$, $n_2 = 17$); ptright = number of pectinal teeth of the right pecten ($n_1 = 22$, $n_2 = 22$); lbspikes = number of spikes on the basal lobe ($n_1 = 23$, $n_2 = 24$). The median, first and third quartile, minimum and maximum values are shown; star symbol indicates isolated extreme value, circle symbol indicates an out lier.

Table 1. Coefficients of the linear discriminant analysis of the three characters, "llspikes" (number of spikes on the crown-like-structure), "ptright" (number of teeth on the right pecten), and "tvright" (number of trichobotria on the ventral side of the right patella); comparing *Euscorpius alpha* ($n = 16$) and *E. germanus* ($n = 15$)

E. alpha – E. germanus	
llspikes	0.036
ptright	0.453
tvright	–0.200

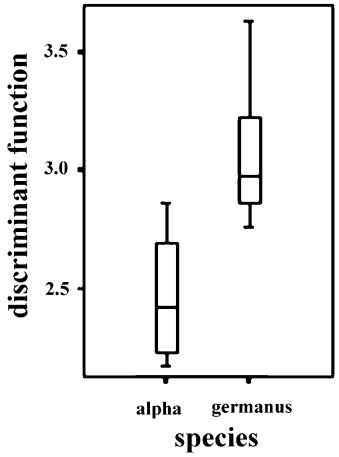

Fig. 6. Values of the discriminant function found in a discriminant analysis including the morphological markers llspikes (number of spikes on the cls), tvright (number of pectinal teeth of the right pecten), and ptright (number of trichobothria on the ventral side of the right patella). Species 1: *E. alpha* ($n = 16$); species 2: *E. germanus* ($n = 15$).

others. The ldi in *E. italicus* is clearly pronounced and never reduced as is the case in *E. germanus* and *E. alpha* (Figs. 3, 4 and 8). In addition, a well-recognisable edge clearly separates the lb from its base.

Statistical comparisons among the four species in Central Europe

No significant differences in reduction of the ldi were found when comparing all four species (values not shown).

On one hand, the Kruskal–Wallis test indicates no significant difference in the number of spikes on the basal lobe (lbspikes) ($\chi^2 = 6.499$, df = 3, $p = 0.09$) when comparing all four species (*E. alpha* $n = 23$, *E. germanus* $n = 24$, *E. gamma* $n = 9$, *E. italicus* $n = 11$; see also Electr. Suppl. 04-02). On the other hand, a significant difference was found in the number of spikes of the cls (llspikes) ($\chi^2 = 33.014$, df = 3, $p < 0.001$) (*E. alpha* $n = 21$, *E. germanus* $n = 24$, *E. gamma* $n = 9$, *E. italicus* $n = 10$). Thus, a Dunn test (corrected for ties) was carried out for llspikes, for all six comparisons among the four species. *Euscorpius italicus* differs significantly from the other three species, and *E. gamma* differs significantly from *E. alpha*, but not from *E. germanus* (Table 2). In Fig. 9, the means and standard deviations of the number of spikes on the cls and lb, respectively, as well as their significant differences are presented for the four species.

Euscorpius flavicaudis

The hemispermatophore of *E. flavicaudis* (Fig. 10) differs markedly in comparison to those of the other

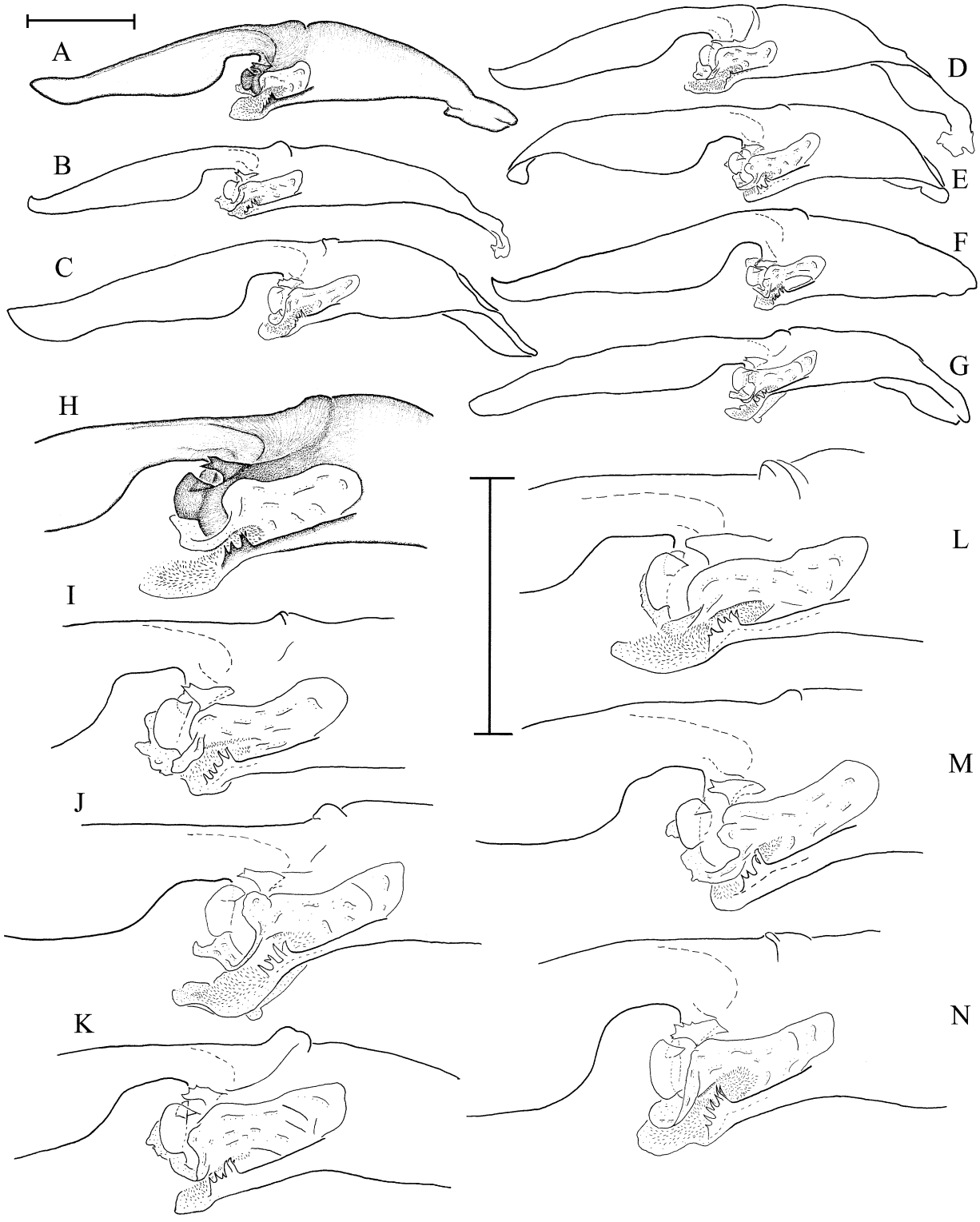

Fig. 7. *E. gamma* hemispermatophores; (A–G) overviews (scale bar at top left: 1 mm), (H–N) capsules (scale bar at center: 1 mm). Sampling sites: (A,H) Trögerner Klamm; (B,F,I,K) Waidisch; (C,G,J,N) Windisch Bleiberg; (D,L) Johannsenruhe; (E,M) Babucnikgraben.

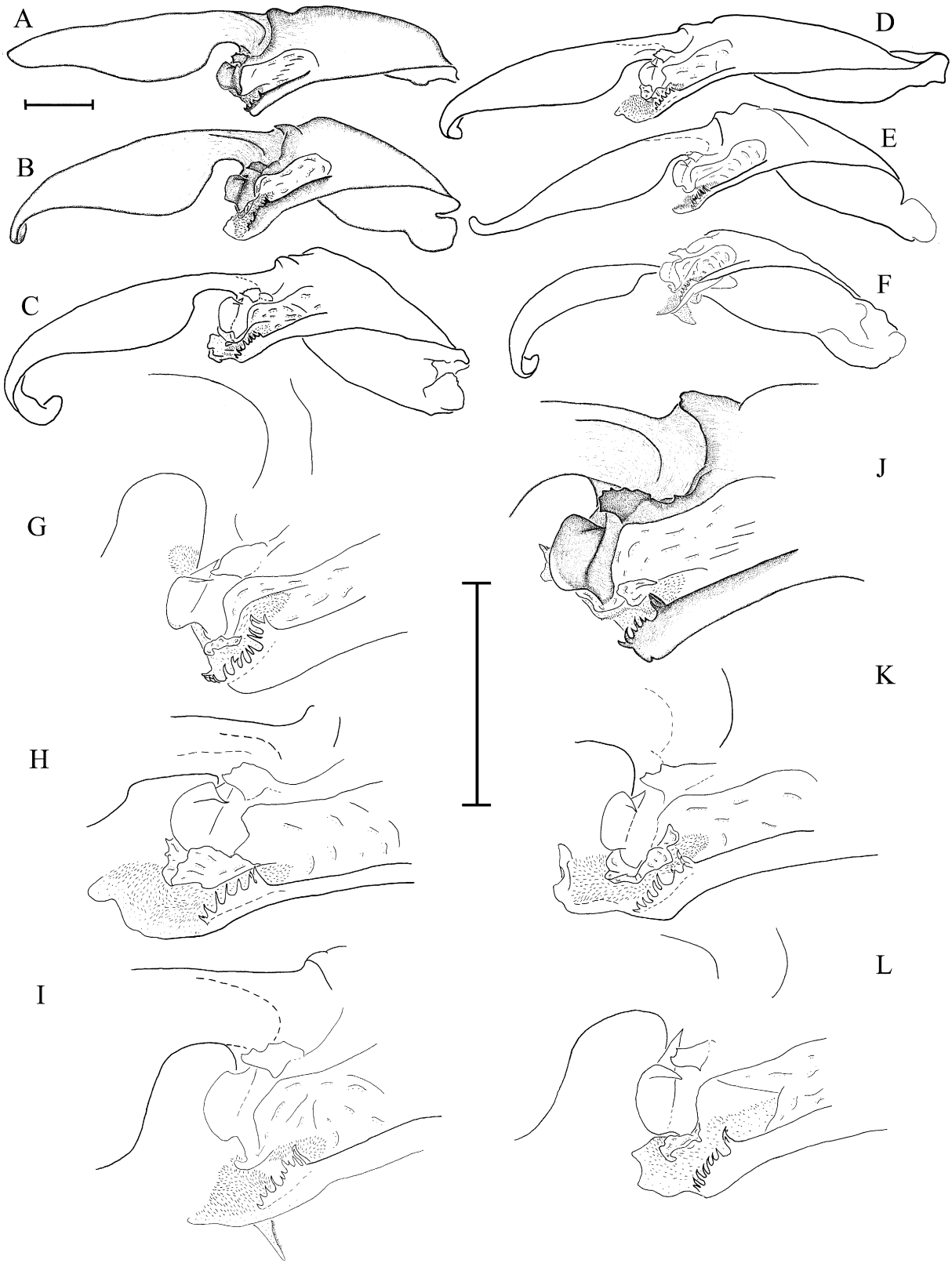

Fig. 8. *E. italicus* hemispermatophores; (A–F) overviews (scale bar at top left: 1 mm), (G–L) capsules (scale bar at center: 1 mm). Sampling sites: (A,J) Coglio; (B,G) Monte; (C,K) Soazza; (D,H) Cugnasco; (E) Conthey; (F,I) Sala Capriasca; (L) Bodio.

Table 2. Kruskal–Wallis test, corrected with Dunn, comparing the differences in number of spikes on the crown-like structure (llspikes) among four species of *Euscorpius*

Comparison (B vs. A)	Difference (RB−RA)	SE	Q	$Q_{0.5,4}$	p-values
3 vs. 4	44.928	8.381	5.361	2.639	$p<0.01$
3 vs. 1	34.016	5.863	3.402	2.639	$p<0.01$
3 vs. 2	24.257	7.267	4.681	2.639	$p<0.01$
2 vs. 4	20.671	7.008	1.557	2.639	$p>0.50$
2 vs. 1	9.759	5.450	1.791	2.639	$0.20<p<0.50$
1 vs. 4	10.912	6.865	3.011	2.639	$0.01<p<0.05$

The differences in mean ranks are indicated, standard error SE, Q, the critical value $Q_{0.5,4}$ with a confidence level of 5%. The four different species are: 1 = *Euscorpius alpha* ($n = 21$); 2 = *E. germanus* ($n = 24$); 3 = *E. italicus* ($n = 9$); and 4 = *E. gamma* ($n = 10$).

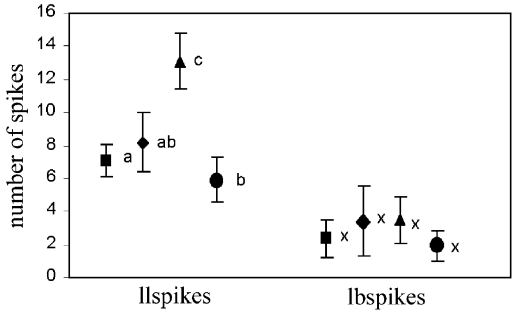

Fig. 9. Four-species comparisons of the number of spikes on the cls (llspikes) and on the basal lobe (lbspikes), respectively. Results are significantly different between those species labeled with different letters. (■) *E. alpha*: llspikes 7.095 ± 0.995, $n = 21$; lbspikes 2.348 ± 1.112, $n = 23$. (◆) *E. germanus*: llspikes 8.208 ± 1.793, $n = 24$; lbspikes 3.417 ± 2.083, $n = 24$. (▲) *E. italicus*: llspikes 13.111 ± 1.691, $n = 9$; lbspikes 3.444 ± 1.424, $n = 9$. (●) *E. gamma*: llspikes 5.900 ± 1.370, $n = 10$; lbspikes 1.909 ± 0.944, $n = 11$.

Euscorpius species. The lobe region shows the strongest distinctions. Instead of the three lobes lde, ldi and lb, only one single lobe exists, situated in the place of lde and ldi. This lobe consists of two spikes ($n = 6$). The cls of all individuals analysed consisted of only one tooth. Moreover, the lining of the sperm duct is smooth, and there are no small spicules as in the other species.

Discussion

Euscorpius flavicaudis

We can clearly separate *E. flavicaudis* and *E. italicus* from the other three *Euscorpius* species by using the shapes of the structures in the capsular region of the hemispermatophore (Figs. 3, 4, 7, 8 and 10). The separation of these two species from each other is also possible. Stockwell (1989) pointed out that the genus *Euscorpius* is closely related to the genus *Megacormus* Karsch, 1881 (Megacorminae, Euscorpiidae) from eastern Mexico. Arguments for this relationship include the following common hemispermatophore structures: truncal flexure, cls and lining of the sperm duct with numerous small spicules (Stockwell 1989). In contrast, *E. flavicaudis* has a smooth sperm duct without spicules, and only one spike at the cls. Thus, these two characters are reduced in *E. flavicaudis*, which may be regarded as an apomorphic condition if compared to other *Euscorpius* species and to *Megacormus*. The data of Fet and Soleglad (2002) support this conclusion. This separation of *E. flavicaudis* from the other *Euscorpius* species is also concordant with the molecular data of Gantenbein et al. (1999).

Statistical comparisons among four species in Central Europe

If we exclude *E. flavicaudis*, we find more differences in the hemispermatophores of the remaining four species by using statistical tests. No significant differences were found in the reduction of the ldi or the number of spikes on the basal lobe (lbspikes), but a significant difference was found in the number of spikes of the cls (llspikes).

There are significant differences between *E. italicus* and the three other included *Euscorpius* species, and between *E. gamma* and *E. alpha* (Table 2). This seems surprising, as according to current taxonomic knowledge (Scherabon et al. 2000) *E. gamma* belongs to the *Euscorpius mingrelicus* species complex, whereas the sister species *E. germanus* and *E. alpha* do not. This implies that *E. germanus* and *E. alpha* are more closely related to each other than to *E. gamma*. Our results, however, indicate a cline from west to east along which the number of spikes on the cls decreases, which could be interpreted such that all three species are very closely related to each other. Thus, if *E. germanus* and *E. alpha* are truly sister species, the similarity between *E. alpha* and *E. gamma* appears to be a homoplasy, or the

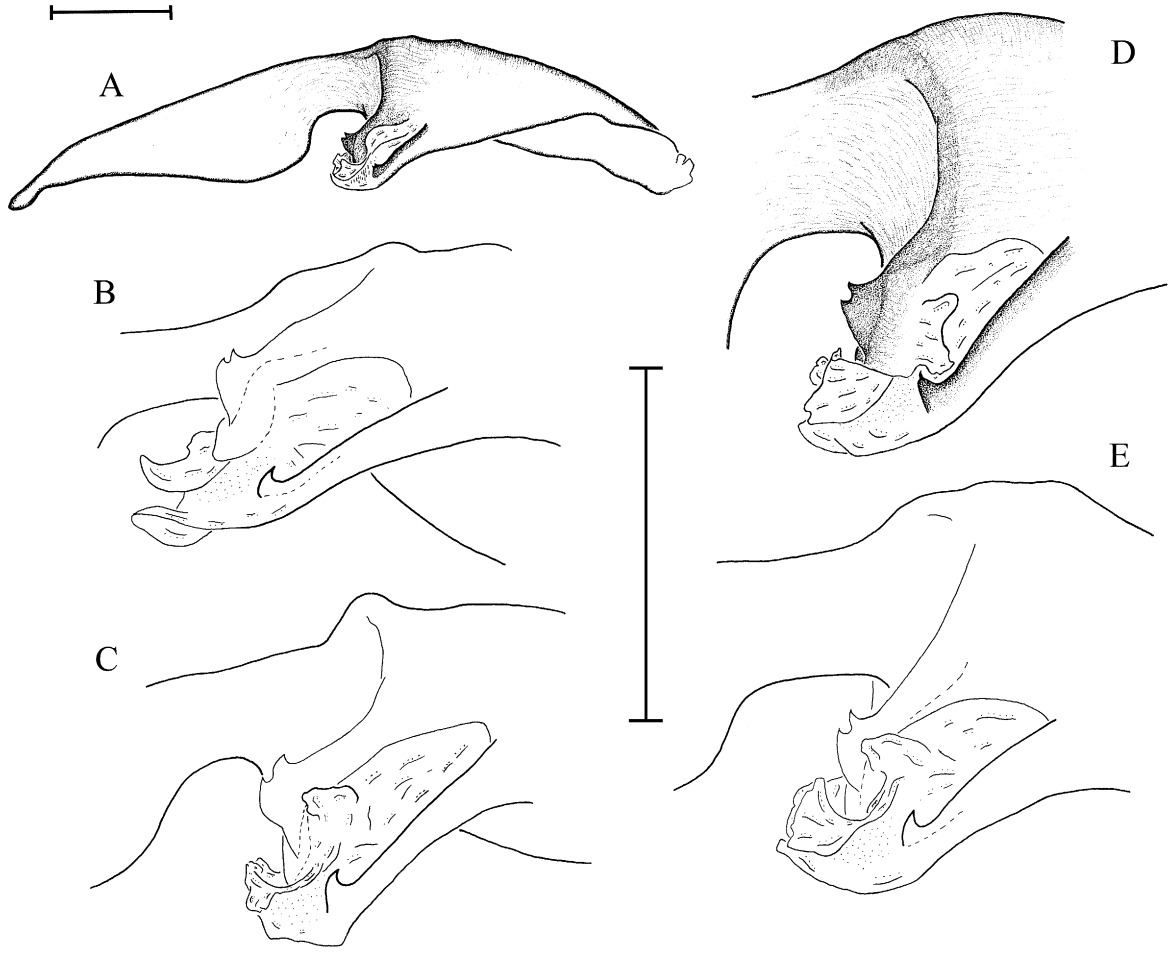

Fig. 10. *E. flavicaudis* hemispermatophores. (A) overview; scale bar at top left: 1 mm; sampling site: Balazuc. (B–E) Capsules; scale bar at center: 1 mm; sampling sites: (B,D) Balazuc, (C) Puget, (E) Marinianne.

relatively low number of llspikes in *E. alpha* and *E. gamma* may represent a plesiomorphic state.

The question of species specificity of *Euscorpius* hemispermatophores

Considering that complex animal genitalia are traditionally seen as species-specific, it is striking that this is not always the case in *Euscorpius*: the hemispermatophores of *E. germanus* and *E. gamma* provided not a single significant difference. Between *E. alpha* and *E. gamma*, significant differences were identified, but they do not allow unambiguous species differentiation. Nevertheless, the somatic morphology of *E. gamma* characterises this species unambiguously (Scherabon 1987; see below). This is evidence that hemispermatophores are not always diagnostic in "good" species in the genus *Euscorpius*.

The species status of *E. gamma* seems well justified from a morphological point of view. For example, the diameter of the male telson or the length of male leg IV in relation to the length of the male cauda are reliable characters that separate *E. gamma* from *E. germanus* unambiguously (Scherabon 1987). In addition, the number of trichobotria on tibiae of the pedipalps and the number of pectinal teeth in the female are of great importance to discrimination between *E. germanus* and *E. gamma* (Scherabon 1987). These morphological results are additionally supported by molecular data using the same set of allozymes and the same mitochondrial DNA sequence data as for the distinction between *E. alpha* and *E. germanus* (Scherabon et al. 2000). The phylogenetic analysis of the mt genetic data revealed a sequence divergence between *E. gamma* (=K-Form) and *E. germanus* (=T-Form) of 5.6–7.5%, which falls within the known range of divergence between congeneric species (Gantenbein et al. 1999, 2000b; Scherabon et al. 2000). Thus, solid evidence supports the independent specific status of *E. gamma*.

Euscorpius germanus and *E. alpha* cannot be clearly separated on hemispermatophore characters (Figs. 3

and 4). This result is supported by the data of Molteni et al. (1983), also analysing hemispermatophores of these species. Even by combining the most separating hemispermatophore character (llspikes) with other morphological characters (tvright and ptright) (Fig. 5), no absolute separation resulted (Fig. 6).

However, the population genetic analysis by Gantenbein et al. (2000b) of the same populations as used in the present study found two distinct gene pools, one belonging to populations of *E. germanus* and the other representing populations summarised under the taxon *E. alpha*. This allozyme study also found no evidence of hybrids between these population groups as proposed by Bonacina (1980). In fact, the genetic variation within populations was nearly zero, but the estimated genetic differentiation between *E. alpha* and *E. germanus* population groups pointed to well-separated gene pools due to the fixation of different alleles at 44% (8 out of 18) of all scored allozyme loci.

Furthermore, the identified mt haplotypes of *E. alpha* and *E. germanus* differ by approx. 7% sequence divergence (Gantenbein et al. 2000b), which is on the same order as the genetic divergence between the congeneric species *E. tergestinus* (formerly known as *E. carpathicus*) and *E. italicus* (approx. 6%; Gantenbein et al. 1998, 1999, 2000b; Fet and Soleglad 2002; Fet et al. 2003). Interpreting the 7% divergence with respect to time by using the recently calibrated molecular clock for mtDNA of the Aegean scorpion *M. gibbosus* (Brullé 1832) (Gantenbein and Largiadèr 2002), we end up with a divergence time of 7 M years between those lineages. This divergence estimate clearly predates the Pleistocene and excludes the possibility that these lineages emerged from the last ice ages. Geographically, these two population groups are separated by the river Adige in Italy, with *E. alpha* to the west and *E. germanus* to the east (Gantenbein et al. 2000b). As far as we know today, the distribution areas of the two sibling species normally do not overlap. Only in three cases has *E. germanus* been recorded on the opposite side of the river Adige: localities 29 (=locality 11 in the present paper) and 30 of Gantenbein et al. (2000b: 845; =locality 12 in the present paper). However, no hybrids have been found.

This level of genetic divergence (or similarity) has also been found between sibling or non-sibling species of the *Drosophila willistoni* Sturtevant, 1916 complex, and in sunfish of the genus *Lepomis* Rafinesque, 1819 (Avise 1994; Ayala et al. 1975). Accounting for the lack of hybrids and the clear-cut mitochondrial tree branching into two highly diverging scorpion lineages, one has to conclude that the species rank of the two sibling species is justified as was previously stated by Gantenbein et al. (2000b). Such morphologically cryptic species are known from Californian trap door spiders (Bond et al. 2001), and more recently from harlequin beetle-riding pseudoscorpions in Panamá (Zeh et al. 2003).

We classify the hemispermatophore as a taxonomic character on the same level of importance as the other characters (like trichobotria, cheliceral dentition, pedipalp chelal finger, etc.) usually used in scorpion taxonomy. *Euscorpius* hemispermatophores may be useful for species discrimination, but in closely related species they are of limited taxonomic value.

In general, our data confirm recent indications in other arthropod taxa that genitalia need not necessarily evolve rapidly or be species-specific (Tanabe et al. 2001; Huber 2003). In general, scorpion morphology seems to be highly conservative. Lourenço (2003), e.g., found a proto-element of Euscorpiidae from the Cretaceous of France with very similar morphology compared to extant euscorpiids.

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