

Phylogeny of the genus *Misolampus* (Coleoptera: Tenebrionidae)

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An account of the phylogeny of the genus *Misolampus* is proposed. This phylogeny is inferred by parsimony analysis of 23 morphoanatomical characters. The evolutionary trend of the female genitalia is examined. The biogeographical processes leading to the current distributional range of the species studied are discussed. Independent dispersal from two different source areas (eastern Iberian Peninsula and North Africa) is proposed to explain the presence of two congeneric species on the Balearic Islands (*M. goudoti* and *M. ramburi*).

Keywords: phylogeny, cladistics, female genitalia, biogeography, Western Mediterranean.

FILOGÈNIA DEL GÈNERE *MISOLAMPUS* (COLEOPTERA: TENEBRIONIDAE). Es proposa una hipòtesi de la filogènia del gènere *Misolampus*. Aquesta filogènia es basa en l'anàlisi de 23 caràcters morfoanatòmics pel mètode de la màxima parsimònia. S'examinen les tendències evolutives de l'aparell genital femení. Es discuteixen els processos biogeogràfics que han conduït a la distribució actual de les espècies considerades. La presència de les dues espècies que viuen a les Balears (*M. goudoti* i *M. ramburi*) és explicada per dispersió des de dues àrees diferents: l'est Ibèric i el nord d'Àfrica.

Paraules clau: filogènia, cladística, genitàlia femenina, biogeografia, Mediterrània Occidental.

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Introduction

The main goal of this contribution is to elucidate the phylogenetic relationships within the genus *Misolampus* (Coleoptera, Tenebrionidae). Immediate usefulness of the

inferred phylogeny is shown at two levels. First, evolutionary trend of the female genital tube is deciphered through phylogenetic reconstruction. The plesiomorphic state and the

evolutionary pathways followed are estimated *a posteriori* by optimizing the change of states over the phylogeny (Maddisson & Maddisson, 1992). Second, the species studied have restricted distributional ranges. They are flightless and seem to have limited dispersal abilities. Therefore, the paleogeographic events leading to their current distributions can be potentially elucidated (Palmer & Cambefort, in press).

Misolampini (*sensu* Gebien, 1934) are represented in the Western Mediterranean by the *Misolampus* genus only. It includes six species, one of them (*M. goudoti* Guérin) having three subspecies. Español (1949) proposed that the monotypic genus *Cybopiestes* Reitter is very close to *Misolampus*. However, recent contributions have introduced important systematic changes. Thus, the Misolampini (*sensu* Watt, 1974) are included within the Coelometopinae by Doyen and Tschinkel (1982). Furthermore, these authors modify the systematic position of many genera, leaving the limits of the Misolampini (*sensu* Doyen & Tschinkel, 1982) not very clear. In accordance, *Cybopiestes* is not assumed *a priori* to be the sister taxa of *Misolampus*, whereas one species of each the genera *Coelometopus* Solierand *Iphthimus* Truqui is included in the phylogenetic analysis.

Methods

A search for the most parsimonious phylogenetic tree was made by the exhaustive procedure of PAUP (Swofford, 1993). Descriptions of the 23 characters included in the analysis and their states are listed in Table 1. No *a priori* assumptions were made on the polarity of character states (all unordered option). All characters used concerned the external morphology, the male aedeagus, and the female genitalia. As many characters as possible were included in the analysis, as long as they respect the basic principle of descent heritability. Characters were excluded when i) they could not be plausibly postulated to be

heritable and ii) character states could not be plausibly postulated to be homologous in all the species concerned. Body size and punctation degree of the pronotum and elytra were excluded. They are currently used for species identification (e.g., Español, 1949) but the existence of primary homology (*sensu* de Pinna, 1991) is doubtful. Female genitalia dissections were made on dried museum specimens by treating them with NaOH, plus ulterior staining with Chlorazol Black. A minimum of two males and two females per species (or subspecies) were dissected, except for *Cy. csikii* because the small number of specimens available precluded it, hence only a single female was studied. The intrapopulation variability of some characters (i.e., number of spermathecal vesicles and shape of the bursa copulatrix) was tested and found to be negligible after dissection of 10 females of *M. goudoti erichsoni* from Mallorca (Balearic Islands). Structural interpretation of female genitalia follows Tschinkel & Doyen (1980).

Three other Coelometopinae species were added to the analyses as outgroups. Namely, *Iphthimus italicus* Truqui, *Coelometopus clypeatus* Germar and *Cybopiestes csikii* Reitter. *I. italicus* has been reported from the Italian Peninsula, Corsica, Sicily, Sardinia and several eastern Mediterranean sites. There are two described species of the genus *Coelometopus*. *Co. clypeatus* is a common species distributed along the north of the Iberian Peninsula (Español, 1956). *Co. cobosi* Español is only known from SE Iberia (Español, 1963) and no material was available for dissection. *Cybopiestes csikii* Reitter is known from a few sites of Atlantic Morocco (Grimm & Hellmann, 1985). Apparently only one genus of Coelometopinae (*sensu* Doyen and Tschinkel, 1982) with Mediterranean species has not been included as outgroup: *Metaclisia* Jacquelin Du Val (Cnodalonini). This genus has 2-3 Mediterranean species. However, they seem not to be closely related to *Misolampus*.

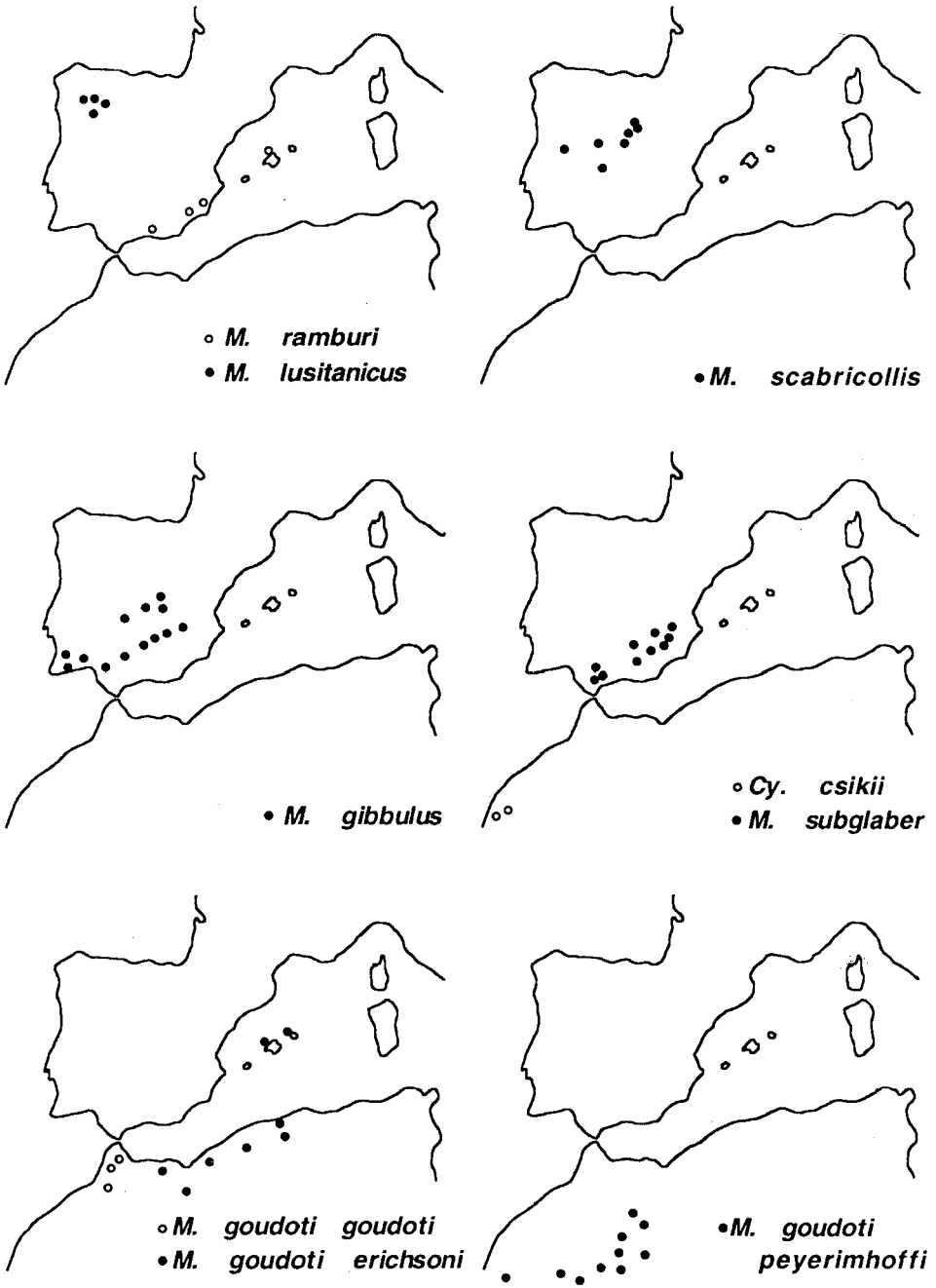


Fig. 1. Distribution of the species studied.

Fig. 1. Distribucions de les espècies estudiades.

Table 1. Description of characters and characters states
Taula 1. Descripcions dels caràcters i dels estats de cada caràcter.

1. Elytral striation tubercled (1) not (0).
2. Elytral striation simple (0) double (additional string of points in between) (1).
3. Pronote flattened (0) globular (1).
4. Dorsal part of the eye big and rounded (0) small and transverse (1).
5. Anterior angles of the pronote rounded (0), right (1), pointed (2).
6. Dorsal and ventral part of the eye separated by five or more strings of ommatidia (0) by one or two strings (1).
7. Metaepimerite wide at metacoxa level (0) narrow (1).
8. Tormae of epipharynx long (more than the posterior papillae) (0) short (1).
9. Mentum careened and pointed (1) not (0).
10. Prosternal appendix expanded and slow-stepped toward mesosternum (0) fast-stepped and rounded (1) fast-stepped and denticled or tubercled (2).
11. Metaesternum long (0) short (1).
12. Clypeal suture furrowed (0) manifest but not furrowed (1) imperceptible (2).
13. Posterior angles of the pronote pointed (0) rounded or obtuse (1).
14. Anterior area of the labium nearly vertical and delimiting a frontal furrow (0) dorsal and sternal parts of the labium progressively convergent (1).
15. Gular furrow well defined (0) imperceptible or very smoothed (1).
16. Arolium of the foreleg tarsus indented (0) truncated (1) pointed (2).
17. Internal face of the elytral striation with one single string of transverse cells (0) with two strings of rounded cells (1).
18. Head bent-down (1) not (0)
19. Elytral pseudopleura wide (wider than the mesoepimerite at its level) (0) similar sized (1).
20. Submentum with masive walls (0) not (1).
21. Brachipterous (0) apterous (1)
22. Primary bursa copulatrix (*sensu* Tschinkel and Doyen, 1980) hardly-developed but clear (0) vestigial, insertion point of the spermatheca conduct not apical (1) absent (2) secondary dorsal bursa copulatrix (3).
23. Spermatheca tapering (0), vesiculated (1), tubular-rolled (2)

Table 2. Data matrix used for cladistic analysis.
Taula 2. Matriu usada per a l'anàlisi cladística.

<i>I. italicus</i>	0000000?00010010?0?1030
<i>Coel. clypeatus</i>	00002000000000000000101
<i>Cibo. czikii</i>	0010000?00011010010110?
<i>M.g. goudoti</i>	10101000110111110111111
<i>M.g. erichsoni</i>	10101000110111110111111
<i>M.g. peyerimhoffi</i>	10101000110111110111111
<i>M. lusitanicus</i>	0011111?121111121111122
<i>M. subglaber</i>	00111110121211121111122
<i>M. scabricollis</i>	00111110121111121111122
<i>M. gibbulus</i>	01112111121111121111111
<i>M. ramburi</i>	01112111121211121111111

Outgroup permutation was done. Moreover, one of the outgroups (*I. italicus*) might be not very close to the other species considered (see below). In accordance, additional analyses were performed alternatively including and excluding this outgroup.

The evolution of the female genital tube deserves a more detailed analysis. Given the form of the phylogenetic tree, the states observed in the terminal taxa, and the assumptions regarding character evolution, McCLADE (Maddison & Maddison, 1992) assigned the state to the internal nodes of the tree that require the fewest evolutionary steps (i.e., the most parsimonious ancestral state).

Some methods allow to infer which paleographic events model species phylogeny

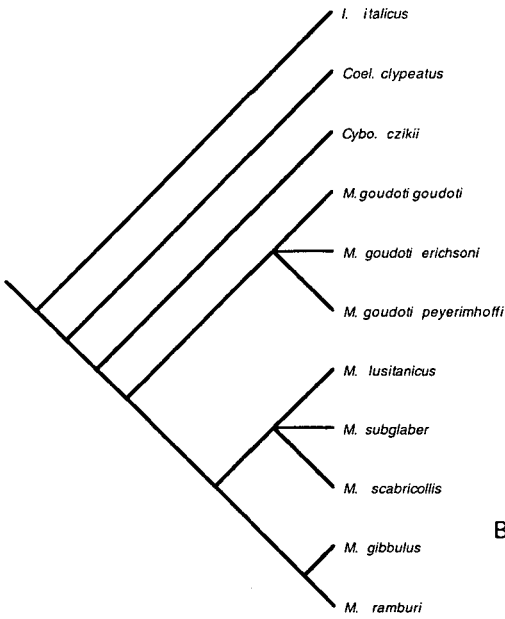


Fig. 2. Phylogenetic tree of the species studied. Tree length: 32 steps.

Fig. 2. Arbre filogènètic de les espècies estudiades. Longitud de l'arbre: 32 passos.



Fig. 4. Female genitalia of *Misolampus goudoti* Guérin. Scale bar: 1 mm.

Fig. 4. Genitàlia femenina de *Misolampus goudoti* Guérin. Escala gràfica: 1 mm.

by optimizing the most probable range of the successive ancestors (e.g., Morrone & Carpenter, 1994). Thus, a cladogram of area-relationships have been deduced for the *Misolampus* genus by Brooks parsimony analysis (Willey, 1988; Brooks, 1990). Reconciliation of this individual area-cladogram with a general paleogeographic area-cladogram allows to explain successive speciation events in terms of historical development. The paleogeographic area-cladogram

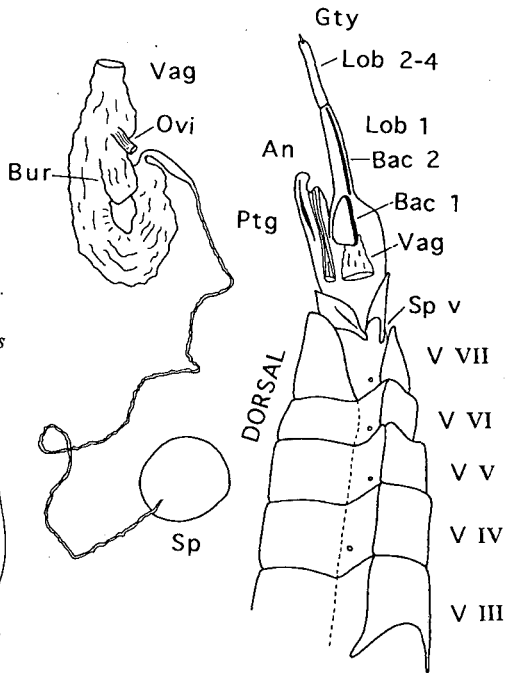


Fig. 3. Female genitalia of *Coelometopus clypeatus* Germar (Outgroup). Gty, gonostyle; Lob 2-4, lobes 2-4 of the coxite; Lob 1, lobe 1 of the coxite; Bac 1, baculus 1; Bac 2, baculus 2; Vag, vagina; Sp, spermatheca; Spv, spiculum ventrale; V VII to V III, ventrite 7 to 3; An, anus; Ptg, Proctiger; Ovi, Oviduct; Bur, bursa copulatrix.

Fig. 3. Genitàlia femenina de *Coelometopus clypeatus* Germar (Outgroup). Gty, gonostil; Lob 2-4, lobuls 2-4 del coxite; Lob 1, lobul 1 del coxite; Bac 1, baculus 1; Bac 2, baculus 2; Vag, vagina; Sp, espermateca; Spv, spiculum ventrale; V VII a V III, ventrites 7 a 3; An, anus; Ptg, Proctiger; Ovi, Oviduct; Bur, bursa copulatrix.

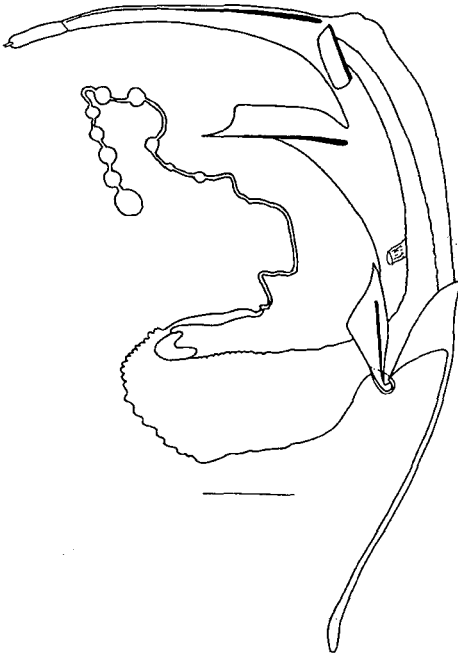


Fig. 5. Female genitalia of *Misolampus ramburi* Brême. Scale bar: 1 mm.

Fig. 5. Genitèlia femenina de Misolampus ramburi Brême. Escala gràfica: 1 mm.

adopted here is that proposed by Oosterbroek & Arntzen (1992), with some modifications (Palmer & Cambefort, in press).

Data on species distribution were checked at the Museum National d'Histoire Naturelle (Paris), the Museu de Zoologia de Barcelona and the collections MNM of the IMEDEA-CSIC (Palma de Mallorca). The very large number of specimens from old collections with non-detailed labels (e.g., Iberia, Andalucia or similar) were not considered. Checked data are presented in Fig. 1. They agree with the distributional data provided by Vauloger (1899), Escalera (1914), Antoine (1945-1947), Español (1949, 1953, 1955, 1956, 1960 and 1967), Kocher (1958), and Pons & Palmer (1996).

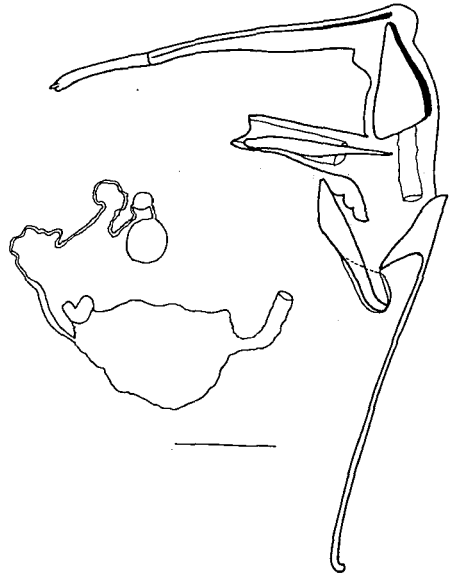


Fig. 6. Female genitalia of *Misolampus gibbulus* Hbst. Scale bar: 1 mm.

Fig. 6. Genitèlia femenina de Misolampus gibbulus Hbst. Escala gràfica: 1 mm.

There are few ecological data on these species. *M. goudoti* Guérin is found beneath bark or semi-decomposed wood of dead trees (e.g., *Quercus ilex* and *Pinus halepensis*), usually, but not only, in well preserved forested areas (Antoine, 1925; Pons & Palmer, 1996). *Misolampus* sp. has been recorded from fruit trees (Español, 1949).

Results and discussion

Taxonomic implications

Punctuation degree of the pronotum is the main difference among subspecies of *M. goudoti*. Well-differentiated specimens are found in the type localities (Grand Atlas, Tanger and North Argelia). However, some populations from the Middle Atlas (the contact area between *M. goudoti goudoti* and *M.*

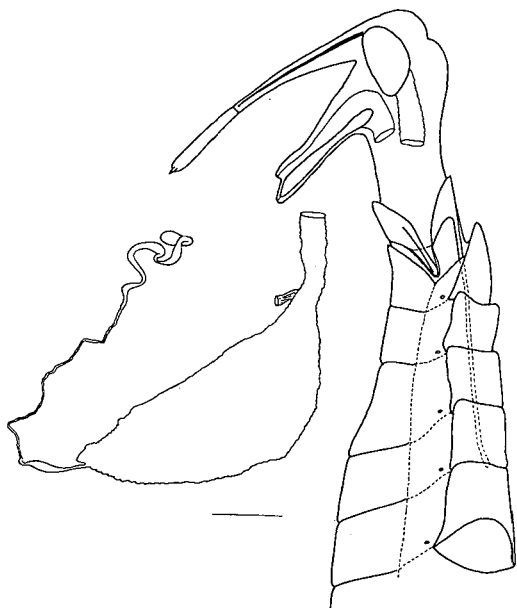


Fig. 7. Female genitalia of *Misolampus scabricollis* Graells. Scale bar: 1 mm.

Fig. 7. Genit lia femenina de Misolampus scabricollis Graells. Escala gr fica: 1 mm.

goudoti peyerimhoffi) display an intermediate punctuation degree, and also intermediate specimens between *M. goudoti goudoti* and *M. goudoti erichsoni*. There are also differences in the number of spermathecal vesicles. *M. goudoti peyerimhoffi* has 5 to 7 spermathecal vesicles, whereas *M. goudoti erichsoni* and *M. goudoti goudoti* have only 4 (Fig. 11). This character is not included in the cladistic analysis since homology cannot be plausibly established.

Antoine (1945-1947) casts doubts on the taxonomic status of these subspecies (considered as geographic variations of *M. goudoti*). Clinal variation of some morphoanatomical characters is usual among Tenebrionidae (e.g., Palmer, 1998). Genetic substructuring at the population level has been described in some species of Tenebrionidae (e.g., Finston & Peck, 1995). Therefore, I assume that variation in the punctuation degree of

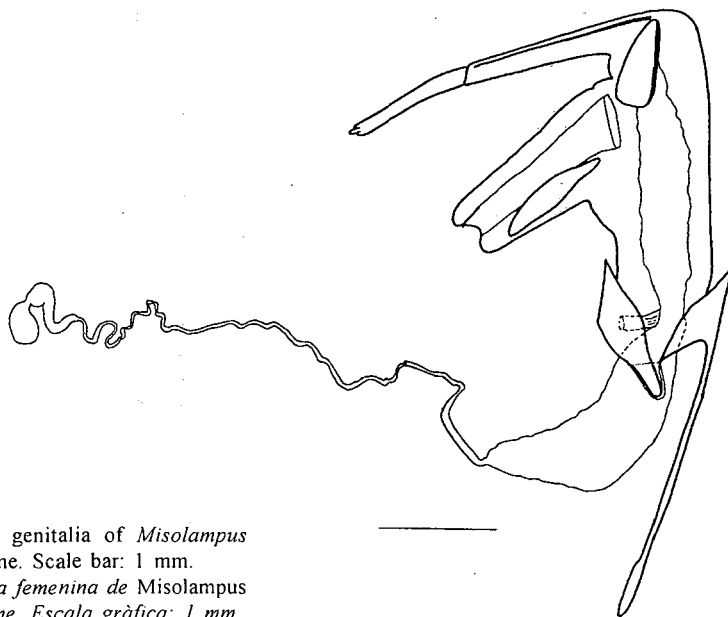


Fig. 8. Female genitalia of *Misolampus lusitanicus* Br me. Scale bar: 1 mm.

Fig. 8. Genit lia femenina de Misolampus lusitanicus Br me. Escala gr fica: 1 mm.

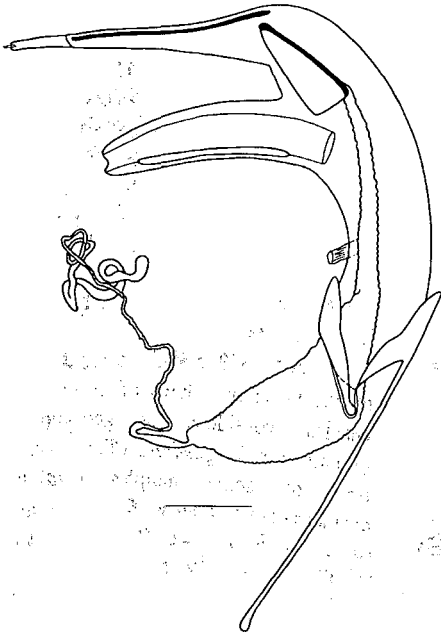


Fig. 9. Female genitalia of *Misolampus subglaber* Rosenhauer. Scale bar: 1 mm.

Fig. 9. Genitàlia femenina de Misolampus subglaber Rosenhauer. Escala gràfica: 1 mm.

Misolampus supports subspecies status since this type of morphoanatomical differentiation is potentially explainable by genetic differentiation and it could evidence partial isolation.

Similarly, differences between *M. subglaber* Rosenhauer, *M. lusitanicus* Brême and *M. scabricollis* Graëlls have plausibly a genetic basis. These species are close to each other but no objective data justifies the change their current species status. It should be noted that the characters differentiating these species (body size and punctuation degree of the pronotum and elytra) have been excluded from the cladistic analysis. Obviously, descent heritability of these characters is implicitly assumed. However, homology with other *Misolampus* species is doubtful.

Cladistic analyses

Character states of the studied species are presented in Table 2. The unique, most

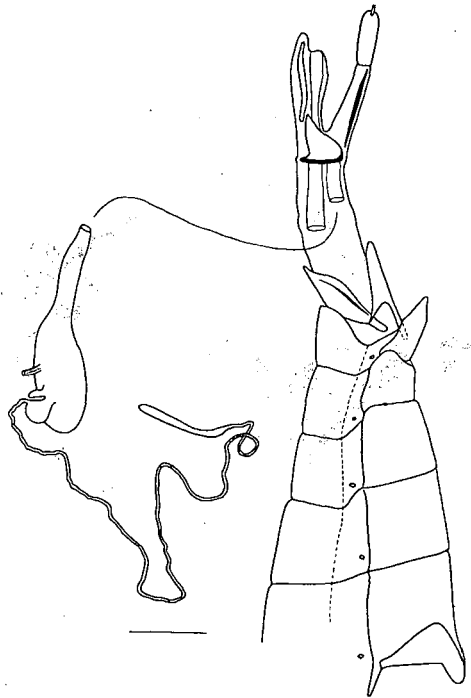


Fig. 10. Female genitalia of *Iphthimus italicus* Truqui. Scale bar: 1 mm.

Fig. 10. Genitàlia femenina d'Iphthimus italicus Truqui. Escala gràfica: 1 mm.

parsimonious tree is found at 32 steps. Its topology is presented in Fig. 2. Almost all internodes are defined by two or more character changes. Monophyly of *Misolampus* is supported on the shape of the mentum (9), the labium (14), and the size of elytral pseudopleures (19). However, the proposed phylogenetic tree is not fully resolved. There are two polytomies. Namely, the cluster of the three subspecies of *M. goudoti* and the cluster of *M. lusitanicus*.

Evolutionary trends of the female genital tube

The inferred phylogeny is used to decipher the evolutionary trend of the female genital tube. The evolutionary pathway requiring the fewest evolutionary steps is presented

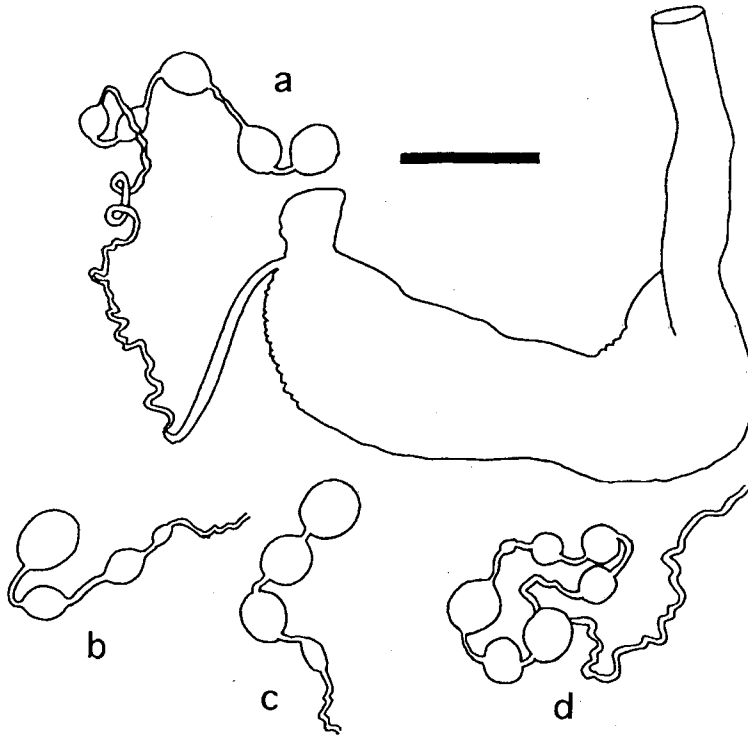


Fig. 11. Intraspecific variation in the internal tract of female genitalia. *a*, *Misolampus goudoti peyerimhoffi* Antoine, from Azrou, Middle Atlas, Morocco (this population shows some intermediate characters toward *M. g. goudoti* Guérin); *b*, *M. g. erichsoni* Vauloger from Pollença, Mallorca, Balearic Islands; *c*, *M. g. erichsoni* Vauloger from Tanger, Morocco (type locality); *d*, *M. g. peyerimhoffi* Antoine from Glaoumi, Grand Atlas (type locality). Scale bar: 1 mm.

Fig. 11. Variació intraespecífica del tracte intern de la genitèlia femenina. *a*, *Misolampus goudoti peyerimhoffi* Antoine, d'Azrou, Mitjan Atlas, Marroc (aquesta població mostra alguns caràcters a mig camí cap a *M. g. goudoti* Guérin); *b*, *M. g. erichsoni* Vauloger de Pollença, Mallorca; *c*, *M. g. erichsoni* Vauloger de Tànger, Marroc (localitat típica); *d*, *M. g. peyerimhoffi* Antoine de Glaoumi, Gran Atlas (localitat típica). Escala gràfica: 1 mm.

in Fig. 12 (from MacClade, Maddison & Maddison, 1992). Excluding *I. italicus*, the ancestral state seems to be the occurrence of a few developed but clear primary bursa copulatrix. *Co. clypeatus* shows this type of bursa (Fig. 3). The bottom of the vagina appears very developed and the spermathecal duct opens apically on it. Vestigial primary bursa (*M. goudoti*, *M. ramburi* and *M. gibbulus*; Figs. 4 to 6) is revealed by the subapical opening of the spermathecal duct. It

is absent in the three species of the *M. scabricollis* branch (Figs. 7 to 9). The most parsimonious evolutionary path seems to be a progressive reduction of the primary bursa copulatrix.

Concerning the spermatheca, the plesiomorphic state (*I. italicus* excluded) seems to be vesicled, but it tends to be tubular-rolled in the *M. scabricollis* branch. The number of vesicles is variable, and the trend

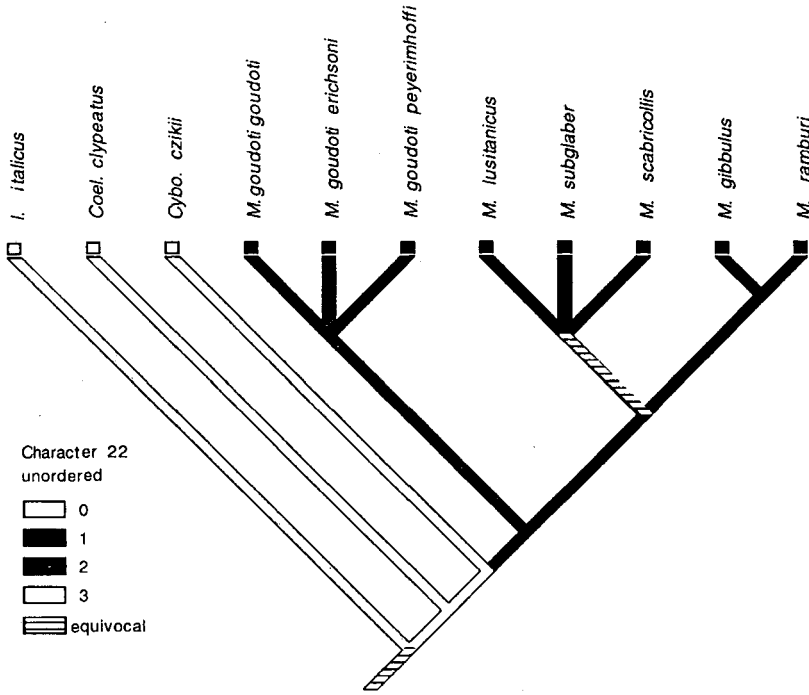


Fig. 12. Optimization of the evolutionary path of the female genitalia (character # 22, tables 1 and 2) over the phylogenetic tree.

Fig. 12. Optimització de l'evolució de la genitèlia femenina (caràcter # 22, taules 1 i 2) sobre l'arbre filogenètic.

is to pass from one vesicle (*Co. clypeatus*) to a poly-vesicled spermatheca. Finally, an elongated spiculum ventrale could be a synapomorphy of *Misolampus* and *Cybopiestes*.

The female genital tube of *I. italicus* suggests an independent phylogenetic pathway far removed from the other Coelometopinae studied here. It shows a dorsal secondary bursa copulatrix (*sensu* Tschinkel & Doyen, 1980) and a tapering spermatheca (Fig. 10).

Biogeographic implications

The increasing concern on phylogenetic inference in biogeographic studies is exemplified by the *Misolampus* genus. Some methods allow to infer which paleogeographic events

model species phylogeny by optimizing the most probable range of the successive ancestors. An individual cladogram of area-relationships for the *Misolampus* genus inferred by Brooks parsimony analysis is provided by Palmer & Cambefort (in press). Reconciliation of this area-cladogram with a general paleogeographic area-cladogram allows to explain successive speciation events in terms of historical development (Palmer & Cambefort, in press).

The *Misolampus* phylogeny has been modeled by paleogeographic events as follows (Palmer & Cambefort, in press). A vicariance event between the Maghribian and Iberian species probably took place after ±15 MY BP. Previous to this date, an ancestor of the Iberian

species dispersed by land to Iberia from the Maghrib. Diversification of *Misolampus goudoti* into three subspecies took place within North Africa and could be related to the occurrence of recent (Quaternary) volcanic activity across the sismo-tectonic range connecting Nékor and Agadir (Harmand & Moukadiri, 1986).

Diversification of the Iberian species (*M. lusitanicus* to *M. ramburi* in Fig. 2) implies the occurrence of two consecutive vicariance events within south Iberia. One between SE and SW Iberia is proposed to have occurred as a consequence of the rise of the Subbetic mountain ranges (± 15 MY BP). The vicariance event leading to the separation of the *M. lusitanicus* clade and the *M. gibbulus* clade remains unexplained. Speciation at the terminal nodes within the *M. lusitanicus* clade is well explained recurring to the establishment of climate refugia during the glaciations. The ancestor of this clade probably expanded its range from Andalusia toward the north during some glacial episode. The following interglacial period promoted the isolation of the three species in three separate altitudinal refugia, corresponding to their current distributions. The species of this "cold" clade occur above 1000 m a.s.l. (*M. subglaber*, in Sierra Morena and Sierra Nevada; *M. scabricollis*, in Sierra de Guadarrama and its Lusitanian extension; and *M. lusitanicus*, in several mountain ranges located in Pontevedra, Orense and León, North Iberian Peninsula). A similar explanation has been suggested by Coope (1979) for some Carabidae of Fennoscandia and the North Atlantic Islands.

The presence of two species of the genus *Misolampus* in the Balearic islands is remarkable. There are no differences between the Balearic populations and the mainland populations of *M. ramburi* and *M. goudoti erichsoni*. The last (potential) connection by land between the Balearic Islands and the mainland dates to ± 15 MY BP. It seems unlikely that after such a long time, there was no differentiation (even at subspecies level in

the case of *M. goudoti erichsoni*). Dispersal from Iberia to the Balearics during the Messinian has been claimed to explain the present distribution of some genera of beetles (e.g., *Thorectes*, Geotrupidae; Palmer & Cambefort, 1997). However, current *Misolampus* species are all linked to woodland. Therefore, it is plausible that the presumed paleoenvironment of the western Mediterranean basin during the Messinian (saline, arid or sub-arid conditions; Schüle, 1993) was an effective barrier for dispersal of *Misolampus* species. The alternative hypothesis of sea-surface dispersal (vegetal rafts; e.g., Bell, 1979 and Peck, 1994) or, more probably, human-mediated dispersal (wood commerce) is preferred.

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