

## **UC Merced**

### **Biogeographia - The Journal of Integrative Biogeography**

#### **Title**

Are Molopina of the Euro-Mediterranean region related to the Madagascan, South African and Australian Pterostichini? (Coleoptera, Carabidae)

#### **Permalink**

<https://escholarship.org/uc/item/7rc4v8bm>

#### **Journal**

Biogeographia - The Journal of Integrative Biogeography, 29(1)

#### **ISSN**

1594-7629

#### **Authors**

Casale, Achille  
Ribera, Ignacio

#### **Publication Date**

2008

#### **DOI**

10.21426/B6110141

Peer reviewed

# Are Molopina of the Euro-Mediterranean region related to the Madagascan, South African and Australian Pterostichini? (Coleoptera, Carabidae) <sup>1</sup>

ACHILLE CASALE, IGNACIO RIBERA\*

*Dipartimento di Zoologia e Genetica Evoluzionistica, Università di Sassari,  
Via Muroni 25, 07100 Sassari (Italy)  
e-mail: casale@uniss.it*

*\*Museo Nacional de Ciencias Naturales, Departamento de Biodiversidad y Biología  
Evolutiva, José Gutiérrez Abascal 2, 28006 Madrid (Spain)  
e-mail: i.ribera@mncn.csic.es*

Key words: Coleoptera, Carabidae, Molopina, Euro-Mediterranean region, Madagascar, biogeography

## SUMMARY

The disjunct distribution of supposedly related carabid taxa in different continents highly stimulated the curiosity of carabidologists interested in Biogeography, which resulted in the proposition of a long series of hypotheses and theories. The tribe Pterostichini, one of the most diverse groups in the family Carabidae and with a world wide distribution, has been the object of some recent phylogenetic analyses and classifications, based on both external and genital characters and on molecular data.

The main goal of the present contribution is the study, using a molecular approach, of the supposed close relationships between the Euro-Mediterranean taxa attributed to “Pterostichidae Molopini”, and some genera of South Africa, Madagascar, Australia and New Zealand.

1) Zoological researches supported by the Italian Ministero dell'Istruzione, dell'Università e della Ricerca Scientifica e Tecnologica (MIUR-PRIN 2004057217 “Zoogeography of Mediterranean - Southern African disjunct distributions by a multimethod approach”), and the UE program Interreg Sardinia-Corsica-Tuscany on Biodiversity. Molecular work supported by the project CGL2007-61665/BOS of the Spanish MEC.

We studied three representatives of the southern hemisphere “Molopina” sensu Jeannel, 1948, two of “abacomorphic” and “zabromorphic” facies (*Eucamptognathus (Heterabax) androyanus* and *Eucamptognathus (Mimozabrus) cf. oopterus*), and one of “carabomorphic” facies (*Eudromus striaticollis*). For their phylogenetic placement, we used published and newly obtained sequences of Euro-Mediterranean “true” Molopina (genera *Abax*, *Percus*, *Molops*, *Tanythrix* and *Styracoderus*), plus other genera of Palaearctic Pterostichini (*Pterostichus*, *Sterocorax*, *Corax*, *Poecilus*, *Astigis*). We sequenced eight gene fragments from tissue samples of the ethanol-preserved specimens, six mitochondrial (*cox1*, *nad1*, *nad5*, *rrnL*, *rrnS*, *tRNA-leu*) and two nuclear (SSU, LSU), with a total of 5303 aligned nucleotides.

Our preliminary data, exposed in the present contribution, show that the clade “Molopina”, including the genera *Molops*, *Tanythrix* (valid genus), *Percus* and *Abax*, but excluding *Styracoderus*, seems to be strongly supported. On the contrary, there is not any evidence to hypothesize that the Madagascan pterostichid beetles are related to the Euro-Mediterranean Molopina, which could be more likely derived from “Angarian” (Asiatic-European) lineages.

## INTRODUCTION

### Disjunct distributions in carabid beetles

The questions about phylogenetic relationships between faunas and floras of the northern and the southern hemispheres of the world, object of the last meeting of the Italian Society of Biogeography, has greatly fascinated biogeographers of every time. Many new data have been obtained, and in part already published on different zoological groups, thanks to the project “Zoogeography of Mediterranean-southern African disjunct distributions by a multimethod approach”, co-ordinated by the University Roma Tre (Prof. Marco Bologna), with the participation of students of the universities of Rome “Sapienza”, L’Aquila, Viterbo and Sassari.

A rich literature deals with this topic. Concerning carabid beetles, of which the importance as biogeographic indicators is widely acknowledged, this question has attracted much interest from several entomologists: the disjunct distribution of supposedly related carabid taxa in different continents highly stimulated the curiosity of carabidologists interested to Biogeography, which resulted in the proposition of a long series of hypotheses and theories. The original question, however, summarized by Thiele (1977) in one of the chapters of his outstanding book, is still the same: did carabids originate in the northern hemisphere, or in the southern part of the world?

Jeannel (1942a), for instance, in one of his classic and pioneer contributions to Biogeography, cited and illustrated some of these cases (among others, Carabidae Trechini of the so called Homaloderina group). Later, in one of his monographs, Jeannel (1957) stressed the markedly disjunct distribution of the small, endogean Carabidae Scaritinae of the subtribe Reicheina, currently known from a few extant representatives in South and Central Africa, and many genera and species distributed in the Euro-Mediterranean area, from the Iberian peninsula and Maghreb to the Caucasus. Other examples and cases have also been cited and discussed, among others, by Noonan (1979) and Erwin (1979).

A molecular approach to an example of disjunct distributions in carabids was recently presented by Prüser and Mossakowski (1998), concerning the so-called supertribe Carabitae, which occurs with two groups in the northern hemisphere (Carabini and Cychrini), another one with world wide distribution (Calosomini), and two isolated taxa (Ceroglossini and Pamborini) living in the southern hemisphere, in Chile and Australia respectively.

More recently, another remarkable example has been the object of both morphological and molecular studies: the Tribe Promecognathini. Known until a few years ago from North-Western America and South Africa, it was recently discovered in the Mediterranean area with an exceptional, troglobitic species (*Dalyath mirabilis* Mateu, 2002) in a “Sierra” of the Southern Iberian Peninsula (Mateu & Bellés, 2003; Ribera et al., 2005).

### The “Molopina case”

The tribe Pterostichini, one of the most diverse groups in the family Carabidae and with a world wide distribution, has been the object of some recent phylogenetic analyses and classifications, based on both external and genital characters and on molecular data, regarding mostly Palaearctic and Nearctic taxa (Bousquet, 1999; Maddison et al., 1999, Ober, 2002; Sasakawa and Kubota, 2007).

The main goal of the present contribution is the study of one of the examples proposed by Jeannel (1948), in his great monograph of the Madagascan carabid fauna, using a molecular approach. In this work, Jeannel proposed a close relationship between the Euro-Mediterranean taxa attributed to “Pterostichidae Molopini”, and some genera of South Africa, Madagascar, Australia and New Zealand. In general, and discussing with his usual competence some external and genital features, he proposed that Molopini Bonelli, 1810 “will have to include many Gondwanian genera”, previously included in different tribes (Sphodrosomini Tschitscherine, 1902, Abacomorphini Tschitscherine, 1902, Cyphosomatini Tschitscherine, 1902, Cratogastrini Tschitscherine, 1902).

Indeed, the resemblance of several Madagascan Pterostichini species of the genera *Eucamptognathus* (subgenera *Abacinus* Jeannel 1948, *Heterabax* Jeannel, 1948, *Mimozabrus* Jeannel, 1948), *Eudromus* Klug, 1835, *Eurypercus* Jeannel, 1948, *Molopinus* Jeannel, 1948 and *Peyrieraselus* Deuve, 1981 to species of Palaearctic Molopina (of the genera *Abax* Bonelli, 1810, *Percus* Bonelli, 1810, *Molops* Bonelli, 1810), and in some cases with some Carabina, Amarina and Sphodrina species, is impressive (Figs. 1-10).

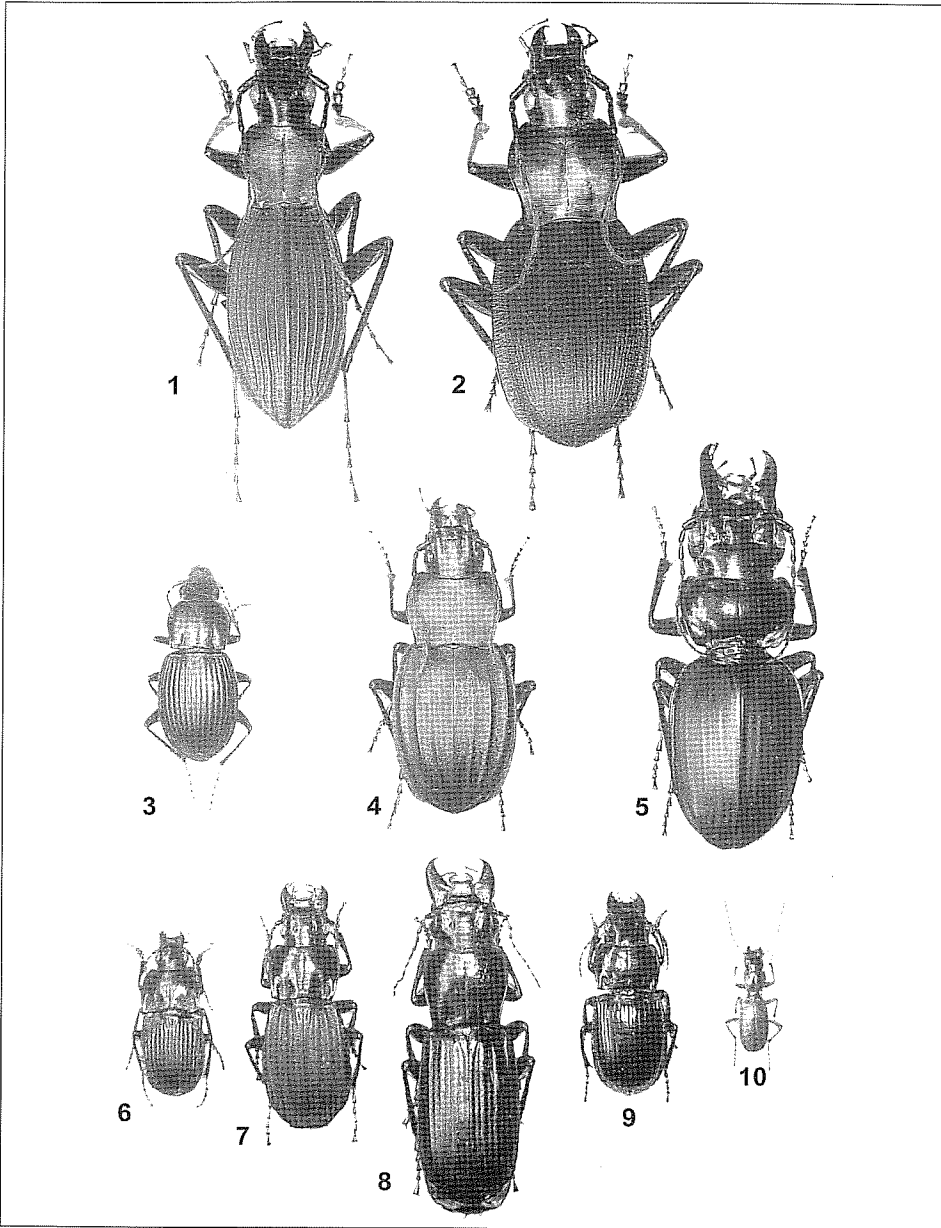
In the more recent literature, the question has not been treated in detail. In some catalogues (Lawrence et al., 1987; Löbl and Smetana, 2003; Lorenz, 2005), the genera that Jeannel included in his “Molopini” are currently treated as “Pterostichitae”, “Pterostichinae”, or “Pterostichini”, without further specification.

Some authors, however, recalled this question. Basilewsky (1967), for instance, treated some new Madagascan taxa as “Molopini”. More accurately, Deuve (1981, 1982, 1986), in describing some pterostichid taxa from Madagascar, specified that he was attributing them to “Molopini, sensu Jeannel”. In particular, in his first note (Deuve, 1981), he carefully discussed the question of the Jeannel’s taxonomic treatment, and recalled that the only character uniting the boreal with the austral Molopini was indeed a “negative” character, i.e. the loss of discal setiferous punctures on the elytra.

We are now able to furnish some further data on this question, thanks to the kindness of Michael Balke (Munich), who allowed us the study of some specimens of Madagascan Pterostichini preserved in absolute ethanol. Their study, together with molecular data from several taxa of “true” Euro-Asiatic Molopina and other Pterostichini, allowed us to assess the phylogenetic position of these carabids.

## MATERIAL AND METHODS

We studied three representatives of the southern hemisphere “Molopina sensu Jeannel, 1948”, two of “abacomorphic” and “zabromorphic” facies (*Eucamptognathus* (*Heterabax*) *androyanus* Tschitscherine, 1903 and *Eucamptognathus* (*Mimozabrus*) cf. *oopterus* Tschitscherine, 1898), and one of “carabomorphic” facies (*Eudromus striaticollis* Brullé, 1834) (Tab. I). For their phylogenetic placement we used published and newly obtained sequences of Molopina sensu Jeannel (1942b) and Mateu (1955) (genera *Abax*, *Percus*, *Molops*, *Tanythrix* and *Styracoderus*), plus other genera of Palaearctic Pterostichini (*Pterostichus*, *Sterocorax*, *Corax*, *Poecilus*, *Astigis*) (see Tab. I for details). As outgroups we used one example each of Brachininae, the sister group of Harpalinae (Ober, 2002; Ribera et al., 2005) and Carabinae, both clearly outside Pterostichini. The tree was rooted in *Carabus*.



Figs. 1-10 - Pterostichini "Molopina" in the widest sense of Jeannel (1948) from Madagascar (1 - 4) and Australia (5), and "true" Euro-Mediterranean Molopina (6-10), habitus, dorsal aspect. 1 - *Eudromus striaticollis* (Brullé, 1834); 2 - *Eucamptognathus (Eudromoides) gigas* (Basilewsky, 1967); 3 - *E. (Heterabax) violaceus* Jeannel, 1948; 4 - *E. (Eudromoides) opacus* (Fairmaire, 1892); 5 - *Mecynognathus damelii* W.J. MacLeay, 1873; 6 - *Abax (Abacopercus) carinatus sulcatus* A. Fiori, 1899; 7 - *A. (Abacopercus) schueppeli* Palliardi, 1825; 8 - *Percus (Percus) passerinii* (Dejean, 1828); 9 - *Molops striolatus* (Fabricius, 1801); 10 - *Speomolops sardous* Patrizi, 1955 (10).

Tab. 1. Taxa included in the analyses, with sources, locality data and collectors.

Species	voucher ref.	Country	Locality	date	Leg.	rrnS rrmL dRNA-leu cox1 nad1 nad5 SSU LSU
<b>Palearctic Molopina</b>						
<i>Abax angustatus</i>	GenBank					x
<i>Abax carinatus</i>	GenBank					x
<i>Abax exarvatus</i>	MNCN-A11295	Italy	Piemonte, Bocchetto Sessera	VII.2006	M. Negro	x x
<i>Abax oblongus oblongus</i>	GenBank					x
<i>Abax onalis</i>	GenBank					x
<i>Abax parallelepipedus contractus</i>	GenBank					x
<i>Abax parallelepipedus inferior</i>	GenBank					x
<i>Abax parallelepipedus lombardus</i>	GenBank					x
<i>Abax pyrenaicus</i>	MNCN-A1267	Spain			C. Hernando	x x
<i>Corax ghilianii</i>	MNCN-A11068	Spain	ES Ávila, Sa. , S. Puerto de Casillas	16.IX.2006	I. Ribera & A. Cieslak	x x
<i>Molops piceus</i>	MNCN-A1362	Slovakia	Nizke Tatry Mts., Janska dolina valley	26.VI.2005	F. Ciampor	x x
<i>Percus cf. strictus</i> (1)	GenBank P31					x
<i>Percus corsicus</i>	GenBank P39					x
<i>Percus cylindricus</i>	GenBank P14					x
<i>Percus guaraot</i>	GenBank					x
<i>Percus lineatus</i>	GenBank P12					x
<i>Percus parnelis</i>	GenBank					x
<i>Percus pilatus</i>	GenBank					x
<i>Percus politus</i>	MNCN-A1266	Spain			M. Baena	x x
<i>Percus reichei</i>	GenBank					x
<i>Percus strictus</i>	MNCN-A1265	Italy			A. Casale	x x
<i>Percus strictus laevirostris</i>	GenBank P03					x
<i>Percus strictus oberletmeri</i>	GenBank P40					x
<i>Percus strictus oberletmeri</i>	GenBank P41					x
<i>Percus stultus</i>	GenBank					x
<i>Percus villai</i>	GenBank					x
<i>Syracodenus atramentarius</i>	MNCN-A11181	Spain	Granada, Puerto de la Ragua	3.VI.2006	C. Andujar	x x
<i>Tanybrix edulis</i>	GenBank					x
<i>Tanybrix senilis</i>	MNCN-A1473	Italy	Piemonte, Val Sessera, Moncerchio	VI.2005	A. Casale	x x
<b>Southern Molopina</b>						
<i>Encampognathus (Heterabax) androyanus</i>	MNCN-A1477	Madagascar	Andasibe, PN Indri, forest stream, 980m	XI-XII.2004	M. Balke, R. Ranaivosolo, P. Razafindraite	x x
<i>Encampognathus (Mimazabrus) cf. oopernus</i>	MNCN-A1476	Madagascar	Andasibe, PN Indri, forest stream, 980m	XI-XII.2004	M. Balke, R. Ranaivosolo, P. Razafindraite	x x
<i>Eudromius sriaticollis</i>	MNCN-A1478	Madagascar	Andasibe, PN Indri, forest stream, 980m	XI-XII.2004	M. Balke, R. Ranaivosolo, P. Razafindraite	x x
<b>Pterostichini</b>						
<i>Astygis salzmanni</i>	MNCN-A11293	Italy	Piemonte, Bosco Marengo	2.VI.2006	G. Allegro	x x
<i>Poecilus crispus</i>	MNCN-A11294	Italy	Piemonte, Casale Monferrato	10.IV.2006	G. Allegro	x x
<i>Pterostichus niger</i>	GenBank					x
<i>Sterocorax globosus</i>	MNCN-A1474	Spain	Cáceres, Atroyo de la Vid	14.V.2005	I. Ribera	x x
<b>Brachiniac</b>						
<i>Brachinus sclopetu</i>	MNCN-A1511	Spain	Ciudad Real, Villarra	1.IV.2005	M. Garcia-Paris	x x
<b>Carabinae</b>						
<i>Carabus splendens</i>	GenBank					x

We sequenced eight gene fragments from tissue samples of the ethanol-preserved specimens, six mitochondrial (*cox1*, *nad1*, *nad5*, *rrnL*, *rrnS*, *tRNA-leu*) and two nuclear (*SSU*, *LSU*), with a total of 5303 aligned nucleotides (full details of sequencing methods, primers used and GenBank sequence accession numbers will be provided elsewhere, Ribera, Hernando & Casale, in preparation). Protein coding genes (*cox1*, *nad1*, *nad5*) were not length variable and the alignment was trivial. Ribosomal genes (*rrnS*, *rrnL*, *SSU*, *LSU*) and the *tRNA-Leu* sequences were aligned using multiple progressive pairwise alignment with secondary refinement as implemented in the software MAFFT online v. 6 using the Q-INS-i algorithm (Kato & Toh, 2008). The data matrix was completed with sequences obtained from published sources (Düring & Brückner, 2000; Brückner, 2002, 2004a, 2004b; Brückner & Mossakowski, 2006).

Bayesian analyses were conducted on a combined data matrix with MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001), using eight partitions, corresponding to the eight genes and a GTR+I+G evolutionary model with the parameters estimated independently for each partition. MrBayes ran for  $15 \times 10^6$  generations using default values, saving trees each 100. “Burn-in” values were established after visual examination of a plot of the standard deviation of the split frequencies between two simultaneous runs.

For comparative purposes we also conducted maximum likelihood searches in Garli v. 0.951 ([www.bio.utexas.edu/faculty/antisense/garli/Garli.html](http://www.bio.utexas.edu/faculty/antisense/garli/Garli.html)), which uses genetic algorithms (Zwickl 2006), with an estimated GTR+I+G model for the combined sequence and the default settings. Support was measured with 1000 bootstrap replicates (Felsenstein, 1985), reducing the number of generations without improving the topology necessary to finish the run to 5,000 instead of the default 10,000 to reduce the computation time.

## RESULTS

The two independent runs of MrBayes converged at a value of the standard deviation of the split frequencies of ca. 0.003 at  $13 \times 10^6$  generations, which was considered the burn-in value. The phylogram of the tree obtained with the last two millions generations of both runs is represented in Fig. 12. The topology was identical to that obtained with maximum likelihood (as implemented in Garli), and in both cases node support was generally very high (posterior probabilities higher than 0.95, bootstrap values above 70%).

There was strong support for the monophyly of “*Molopina sensu stricto*”, including the genera *Percus*, *Abax*, *Molops* and *Tanythrix*, but with the exclusion of *Styracoderus* and the Madagascan taxa.

*Styracoderus* was included among a group of genera related to *Pterostichus* with very high support (posterior probability 1, bootstrap value 100%):



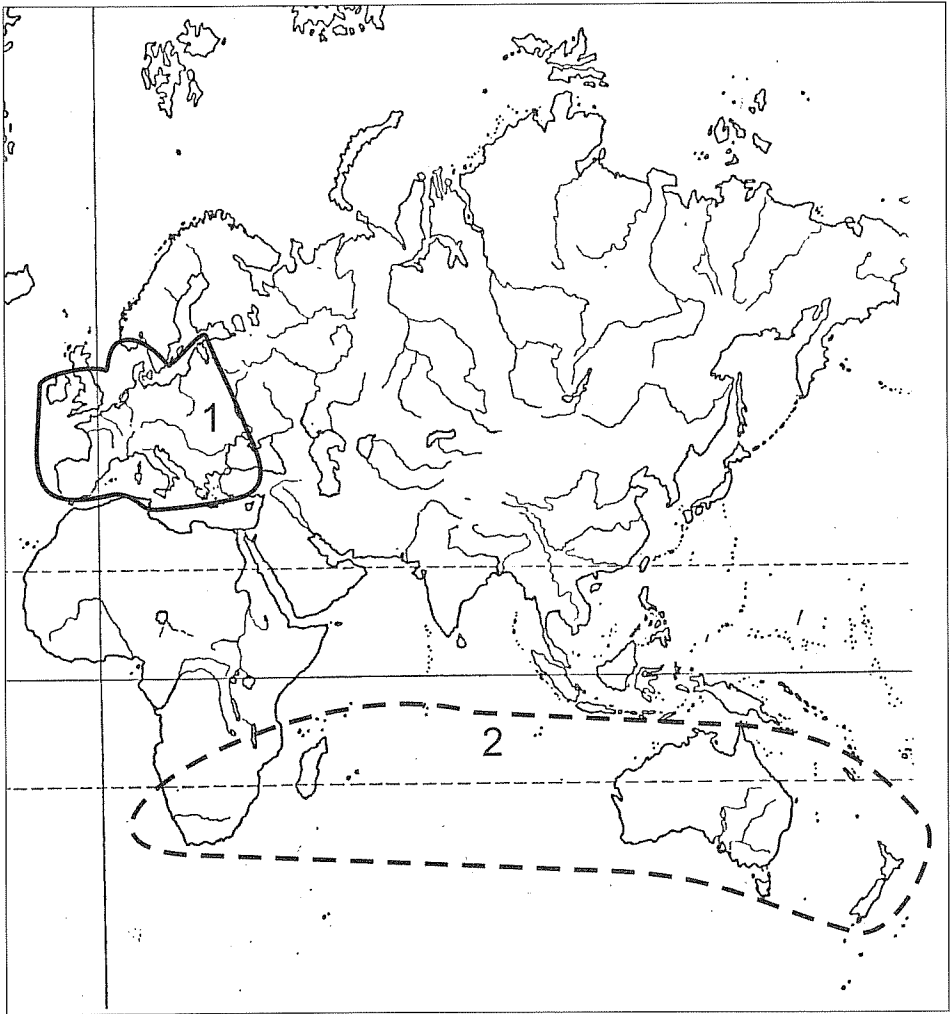


Fig. 11 - Geographical distribution of “true” Euro-Mediterranean Molopina (1), and additional taxa attributed to Molopina by Jeannel (1948) (2).

*Pterostichus*, *Sterocorax* and *Corax*. The northern-hemisphere Pterostichini were monophyletic and sister to the southern taxa, with high support in MrBayes (posterior probability of 1) but low for Garli (bootstrap value less than 50%).

Although the incomplete taxon sampling of Pterostichini (and other Harpalinae tribes) precludes the resolution of the phylogenetic position of the Madagascan taxa, from our tree we can conclude that they are not directly related to the Mediterranean Molopina, and the similarity in their general habitus should be due to convergence.

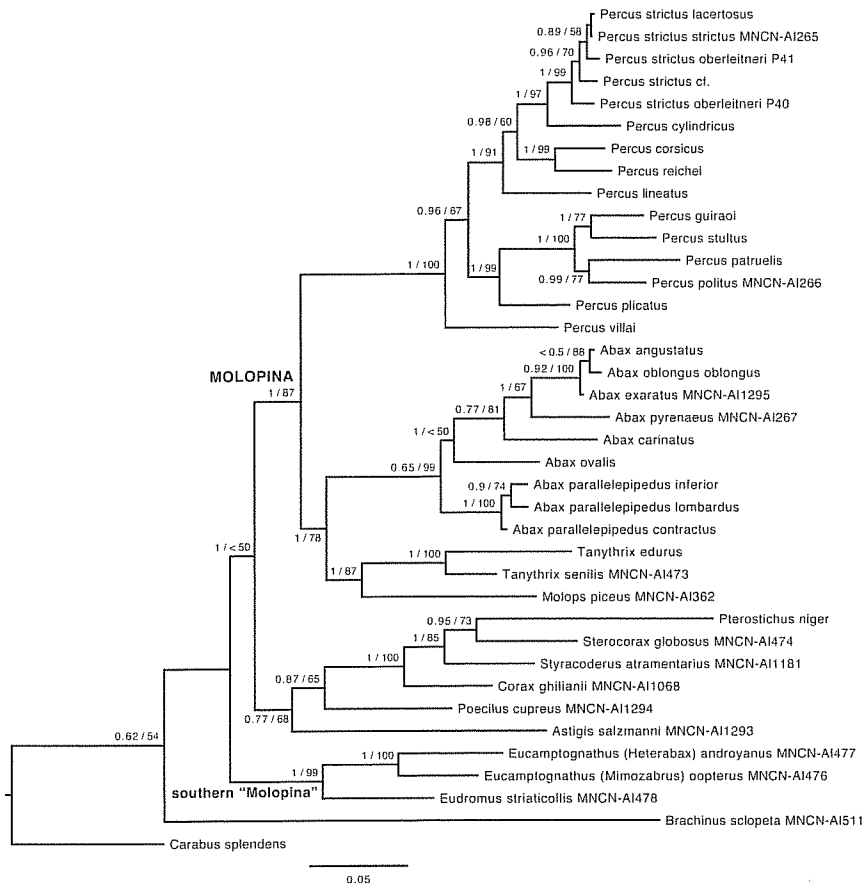


Fig. 12 - Phylogram reflecting the phylogenetic relationships among the studied taxa obtained with MrBayes. Numbers in nodes, posterior probabilities / Maximum likelihood bootstrap values, as obtained in Garli (see Methods for details). Codes after the name of species refer to voucher numbers of the sequenced specimens, data of species without codes were obtained from GenBank (see Tab. I for details).

## DISCUSSION AND CONCLUSIONS

From the morphological point of view, Euro-Mediterranean Molopina Bonelli, 1810, treated here as a subtribe of Pterostichini, appears as a moderately supported monophyletic unit. As recalled by Brandmayr and Zetto Brandmayr (1994) and by Düring and Brückner (2000), the group is characterized by some external features like the absence of discal setiferous punctures on elytra (we recall however that these are present, in the posterior half of the elytron disc, in *Tanythrix*), the presence of a keel on the seventh elytral stria (reduced or absent however in *Molops*: Brückner and Mossakowski, 2006), the lack of secondary sexual characteristics in the 7<sup>th</sup> abdominal segment in the

male (absent also in other groups of Pterostichini), and the presence of a membranous band at the base of the first antennomere in the larvae. The features of female genitalia do not give informative data on the homogeneity of Molopina (Giachino & Sciaky, 1991). Furthermore, some species of some genera are noticeable for having developed phenomena of parental care (Brandmayr and Zetto Brandmayr, 1979).

From the molecular point of view, among the genera currently attributed to this subtribe, the monophyly of the genera *Percus* Bonelli, 1810 and *Abax* Bonelli, 1810 (in the widest sense) appears however evident (Brückner and Mossakowski, 2006; Düring, 2004).

Our preliminary data, exposed in the present contribution, show that the clade “Molopina”, including the genera *Molops* Bonelli, 1810, *Tanythrix* Schaum, 1858 (treated as a distinct genus: see Vigna Taglianti, 1993), *Percus* Bonelli, 1810, and *Abax* Bonelli, 1910, but excluding *Styracoderus* Chaudoir, 1874 (a genus currently attributed to this subtribe: Mateu, 1955; Serrano, 2003), seems to be strongly supported (Fig. 12). *Styracoderus* seems to belong to the complex of genera related to *Pterostichus* Bonelli, 1810 (*sensu latissimo*), without close relationships to Molopina.

We can also anticipate that some of the subterranean taxa currently attributed to Molopina (genera *Molopidius* Jeannel, 1942, *Speomolops* Patrizi, 1955, *Henrotius* Jeannel, 1953, *Zariqueya* Jeannel, 1924, *Oscadytes* Lagar, 1975, *Typhlochoromus* Moczarski, 1913) are confirmed as members of this subtribe. Their phylogenetic position - with comments on their biogeographic history - will be discussed in another contribution (Ribera, Hernando and Casale, in preparation). Unfortunately, there is so far no molecular data available of the Balkan genera *Stenochoromus* L. Miller, 1866, and *Henrotiochoromus* Busulini, 1958.

Our phylogenetic analysis fully excluded that the Madagascan taxa, attributed by Jeannel (1948) to Molopina, belong to subtribe Molopina as re-defined here. Conversely, the few examined species, in spite of important differences in their morphological external features, form a monophyletic unit and a strongly supported clade. A molecular study with a better taxon sampling will be necessary to verify if all Madagascan Pterostichini, characterised by an impressive adaptive radiation, are derived from a single, or several colonization events of the island, to establish their relationships to South-African taxa, and to check a (possible) relationship to extant S.E. Asiatic and Australian Pterostichini. At that moment, the re-evaluation of some subtribes should be possible.

In any case, we do not have any evidence to hypothesize that the pterostichid beetles of the southern hemisphere are related to the “true” Euro-Mediterranean Molopina, which could be more likely derived from “Angarian” (Asiatic-European) lineages, with an early origin within the area. In particular, the distribution of the western Mediterranean Molopina (including some subterranean

taxa) presents the classical “Tyrrhenian” pattern, with morphologically highly derived species in the Iberian peninsula, Sardinia and Mallorca. This has traditionally been interpreted as the result of an ancient vicariant separation produced by the tectonic, Miocene drift of the West Mediterranean micro-plates, although there is still no genetic data to support this biogeographic hypothesis.

#### ACKNOWLEDGEMENTS

We are particularly indebted to Michael Balke for making the material of Madagascan Pterostichini available to us, and to G. Allegro, C. Andújar, M. Baena, F. Ciampor, C. Hernando, M. García Paris and M. Negro for specimens of European taxa. We also thank Ana Izquierdo (MNCN, Madrid) for laboratory work. For the help in sampling material in the field and the assistance in preparing some figures, we are particularly indebted to Paolo Marcia and Ivo Manca (University of Sassari, Dept. of Zoology).

#### REFERENCES

- BOUSQUET Y. 1999 - Supraspecific classification of the Nearctic Pterostichini (Coleoptera, Carabidae). *Faberies*, Supplement 9 : 1- 292.
- BASILEWSKY P. 1967 - Contribution à l'étude des Coléoptères Carabiques de la région malgache. III. Pterostichines nouveaux de la tribu des Molopini. *Bull. Soc. Entomol. France*, 72: 172-179.
- BRANDMAYR P., ZETTO BRANDMAYR T. 1979 - The evolution of parental care phenomena in Pterostichini, with particular reference to the genera *Abax* and *Molops*. In: den Boer P.J., Thiele H.U., Weber F. (eds.), *On the Evolution of Behaviour in Carabid Beetles*. *Miscellaneous Papers*, 18, Landbouwhogeschool Wageningen: 35-49.
- BRANDMAYR P., ZETTO BRANDMAYR T. 1994 - The evolutionary history of the genus *Abax* (Coleoptera, Carabidae). In: Desender K., Dufrière M., Loreau M., Luff M.L., Maelfait J-P. (eds.), *Carabid Beetles. Ecology and Evolution*. Kluwer Academic Publishers, series Entomologica, 51, Dordrecht, Boston, London: 19-24.
- BRÜCKNER M. 2002 - Phylogenie und biogeographie der Gattung *Percus* Bonelli 1810 (Coleoptera: Carabidae): eine molekularsystematische Analyse. PhD Dissertation, Verlag Mainz.
- BRÜCKNER, M. 2004a - Genetic differentiation in *Percus corsicus* (Coleoptera, Carabidae). *Mitt. Dtsch. Ges. allg. angew. Ent.*, 14: 83-86
- BRÜCKNER, M. 2004b - The phylogeny of the subgenus *Pseudopercus* (Coleoptera, Carabidae): conflicts between mitochondrial and nuclear DNA sequences. *Mitt. Dtsch. Ges. allg. angew. Ent.*, 14: 77-82
- BRÜCKNER M., MOSSAKOWSKI D. 2006 - Phylogeny of the genus *Percus* (Coleoptera: Carabidae) - nuclear genes and the basal splits. In: Serrano J., Koivula M., Lövei G. (eds.), *Proceedings of the XII European Carabidologists' Meeting*. *Entomol. Fenn.*, 17 (2006) : 195-199.
- DEUVE T. 1981 - Nouveaux Molopini, sensu Jeannel, de Madagascar [Col. Pterostichidae] (1<sup>er</sup> note). *Bull. Soc. entomol. France*, 86: 193-203.
- DEUVE T. 1982 - Nouveaux Molopini, sensu Jeannel, de Madagascar [Col. Pterostichidae] (2<sup>e</sup> note). *Bull. Soc. entomol. France*, 87: 204-211.
- DEUVE T. 1986 - Nouveaux Molopini, sensu Jeannel, de Madagascar [Col. Pterostichidae] (3<sup>e</sup> note). *Rev. Franç. Entomol.*, (n.s.) 8: 33-40.
- DÜRING A. 2004 - Molekularsystematische Untersuchungen am Carabidentaxon *Abax* Bonelli 1810 (Coleoptera, Carabidae). Dissertation zur Erlangung des Doktorgrades, Universität Bremen :1-363.
- DURING A., BRÜCKNER M. 2000 - The evolutionary history of the tribe Molopini: a first molecular approach. In: Brandmayr P., Lövei G., Zetto Brandmayr T., Casale A., Vigna Taglianti A. (eds.), *Natural History and applied ecology of Carabid Beetles*. Pensoft, Sofia-Moscow: 1-4.
- ERWIN T.L. 1979 - The American Connection, Past and Present, as a Model Blending Dispersal and Vicariance in the Study of Biogeography. In: Erwin T.L., Ball G.E., Whitehead D.R. (eds.), *Carabid beetles, their evolution, natural history, and classification*. Dr. W. Junk Publ., The Hague-Boston. London: 355-367.

- GIACHINO P.M., SCIAKY R. 1991 - Valore sistematico delle strutture genitali femminili in Pterostichinae (Coleoptera: Carabidae). Atti XVI Congr. Naz. Ital. Entomol., Bari-Martina Franca (TA), 23/18 settembre 1991: 885-892.
- FELSENSTEIN, J. 1985 - Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**: 783-791.
- HUELSENBECK J.P., RONQUIST F. 2001 - MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**: 754-755.
- JEANNEL R. 1942a - La Genèse des Faunes Terrestres. Éléments de Biogéographie. Presses Universitaires de France, Paris.
- JEANNEL R. 1942b - Coléoptères Carabiques. Deuxième Partie. Faune de France, **40**: 572-1173.
- JEANNEL R. 1948 - Coléoptères Carabiques de la Région Malgache (Deuxième Partie). Faune de l'Empire Français, X, Editions du Muséum: 373-765.
- JEANNEL R. 1957 - Révision des petits scaritides endogés voisins de *Reicheia* Saulcy. *Rev. franç. Entomol.*, **24**: 129-212.
- KATO H. & TOH H. 2008 - Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, in press (doi:10.1093/bib/bbn013).
- LAWRENCE J.F., MOORE B.P., PYKE E.J., WEIR T.A. 1987 - Zoological Catalogue of Australia. 4. Coleoptera: Archostemata, Myxophaga and Adephaga. Australian Government Publishing Service, Canberra.
- LÖBL I., SMETANA A. 2003 (eds.) - Catalogue of Palaearctic Coleoptera. 1. Archostemata, Myxophaga - Adephaga. Apollo Books, Stenstrup.
- LORENZ W. 2005 - Systematic list of extant ground beetles of the world (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae. incl. Paussinae, Cicindelinae, Rhysodinae). Tutzing.
- MADDISON D.R., BAKER M.D., OBER K.A. 1999 - Phylogeny of carabid beetles as inferred from 18S ribosomal DNA (Coleoptera: Carabidae). *System. Entomol.*, **24**: 103-138.
- MATEU J. 1955 - Los Molopini Bon. de la Península Ibérica. *Eos*, **31**: 297-301.
- MATEU J., BELLÉS X. 2003 - Position systématique et remarques biogéographiques sur *Dalyat mirabilis* Mateu, 2002 (Coleoptera: Adephaga: Promecognathidae), cavernicole du sud-est Ibérique. *Ann. Soc. Entomol. Fr.*, (n. s.) **39**: 291-303.
- NOONAN G. R. 1979 - The Science of Biogeography with Relation to Carabids. In: Erwin T.L., Ball G.E., Whitehead D.R. (eds.), *Carabid beetles, their evolution, natural history, and classification*. Junk Publ., The Hague, Boston, London: 295-317.
- OBER K.A. 2002 - Phylogenetic relationships of the carabid subfamily Harpalinae (Coleoptera) based on molecular sequence data. *Mol. Phylog. Evol.*, **24**: 228-248.
- PRÜSER F., MOSSAKOWSKI D. 1998 - Conflicts in phylogenetic relationships and dispersal history of the supertribe Carabiteae (Coleoptera: Carabidae). In: Ball G.E., Casale A., Vigna Taglianti A. (eds.), *Phylogeny and classification of Caraboidea*. *Mus. Reg. Sci. Nat.*, Torino: 297-328.
- RIBERA I., MATEU J., BELLÉS X. 2005 - Phylogenetic relationships of *Dalyat mirabilis* Mateu, 2002, with a revised molecular phylogeny of ground beetles (Coleoptera, Carabidae). *J. Zool. System. Evol. Res.*, **43**: 284-296.
- SERRANO J. 2003 - Catalogo de los Carabidae (Coleoptera) de la Peninsula Iberica. *Monogr. S.E.A.*, Zaragoza, **9**: 1-130.
- SASAKAWA K., KUBOTA K. 2007 - Phylogeny and genital evolution of Carabid beetles in the genus *Pterostichus* and its allied genera (Coleoptera: Carabidae) inferred from two nuclear gene sequences. *Ann. Entomol. Soc. Am.*, **100**: 100-109.
- THIELE H-U. 1977 - Carabid Beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour. Springer, Berlin, Heidelberg, New York.
- VIGNA TAGLIANTI A. 1993 - Coleoptera Archostemata, Adephaga (Carabidae). In: Minelli A., Ruffo S. & La Posta S. (eds.), *Checklist delle specie della fauna italiana*, **44**. Calderini, Bologna:1-51. (Errata-corrige cod. 3868, gennaio 1994)
- ZWICKL D. J. 2006 - Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin.