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Assessing relationships between Mediterranean and Afrotropical taxa of Cleonini (Coleoptera: Curculionidae: Lixinae): a survey based on Bayesian analysis and lineage geohistory reconstruction

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SUMMARY

Relationships between the Mediterranean and southern African genera of Cleonini (Curculionidae) were assessed using preliminary phylogenetic analysis and palaeohistorical reconstruction by maximum likelihood inference of ancestral distributions. Intergeneric relationships were found to be present only between sister taxa belonging to basal branches of the trees, suggesting that the faunas of the two regions were connected only during the early stages of radiation of the tribe. A critical revision of the species composition of some Afro-Mediterranean genera revealed that only *Pseudotemnorrhinus* has a disjunct Mediterranean-southern African distribution. This is regarded as having been determined by a recent expansion of the range of the genus from the Mediterranean region towards southern Africa via the eastern Africa grasslands.

INTRODUCTION

The Curculionidae subfamily Lixinae Schoenherr, 1823 is composed of about 100 genera, presently included in three tribes: Lixini Schoenherr, 1823; Rhinocyllini Lacordaire, 1863; and Cleonini Schoenherr, 1826. This last tribe accounts for most of the genera, more than 80. Its taxonomy is still based on Faust (1904), who also provided the only available key to all the genera. Lacking any comprehensive and comparative evaluation of characters, genera are not always clear and unequivocal; in some cases they seem to be paraphyletic taxa, with uncertain boundaries. A phylogenetic analysis of the tribe

is thus overdue and is now in progress (Meregalli and Silvestro, unpublished). This biogeographical contribution is based on the preliminary, but reliable cladograms so far obtained.

MATERIALS AND METHODS

Most of the specimens used in this study are preserved in coll. Meregalli. Other specimens were obtained on loan from several Museums. Whenever possible the type species of each genus was used; when this was not available we used the most morphologically similar taxon.

Phylogenetic analyses

The phylogenetic analyses were performed on a data set composed of 68 genera of Cleonini and one outgroup: the genus *Lixus* Fabricius, 1801. Thirty morphologic characters, 24 discrete and 6 continuous, were analyzed. Several characters were suggested by Anderson (1988) and Meregalli (2005).

Qualitative characters were divided into states after a comparative morphologic analysis and considered unordered, while dimensional ones were handled by a gap-weighting method (Thiele, 1993). They actually looked like continuous morphometric data and were discretized dividing their values into several equal categories each considered as a state. This calculation was performed using the program Morphocode 1.1. Morphometric characters were treated, during the phylogenetic analyses, as ordered. The number of resulting states was 26 for the parsimony optimality criterion and 6 for the Bayesian inference (the maximum number supported by the program MrBayes).

Parsimony analysis

The parsimony analysis was carried out using the program PAUP* version 4.0b10 (Swofford, 2002). Heuristic searches were performed with the following options: 100 random addition sequence (RAS) replicates, 1 tree held at each stepwise addition, and tree bisection-reconnection (TBR) branch swapping.

The characters were re-weighted according to their own rescaled consistency index (RC), following the iterative protocol of Farris (1969, 1989). Support for tree topology was not evaluated since these are draft analyses and the biogeographic reconstruction was based on the Bayesian analysis.

Bayesian analysis

The Bayesian searches were performed with the program MrBayes (Ronquist and Huelsenbeck, 2003); the following options were applied: two independent

analyses each with four simultaneous chains running for 1 million generations, sampling every 100 generations. The substitution model implemented for discrete morphological traits was the Mkv suggested by Lewis (2001). The "acquisition bias" (see Lewis, 2001) was corrected, in branch length calculation, by assuming that all characters in the matrix were variable and parsimony informative.

Across-site rate variation was allowed with the discrete gamma distribution model (Yang, 1994; 1996). Flat priors were used to reduce the subjectivity of parameters.

The final tree used for the subsequent analyses was a consensus of all compatible topologies sampled during the MCMC running. The trees found below the stationarity level (burnin generation) determined by plotting generations versus log likelihood were excluded.

Ultrametricizing the tree

The maximum likelihood method to infer ancestral areas on a phylogeny described by Ree et al. (2005) requires an ultrametric tree to be computed. For this reason the branch lengths were time-calibrated using the nonparametric rate smoothing (NPRS) suggested by Sanderson (1997). The ultrametric tree from the Bayesian phylogram was determined using the program r8s version 1.70 (Sanderson, 2004). Since no paleontological record indicating an absolute age for fixing at least one internal node was available, the root of the tree was fixed at an arbitrary age of 1.0 as suggested by Sanderson (2004). So all the internal node positions represent relative differences in time and are referred to the moment 1.0 in the past.

Biogeographical analyses

On the Bayesian phylogeny obtained as described above, the lineage geohistory was inferred through two different methods: dispersal-vicariance analysis (Ronquist, 1997) performed by the program DIVA 1.1 (Ronquist, 1996) and maximum likelihood inference of ancestral distributions (Ree et al., 2005) implemented using the program AReA 2.1 (Smith, 2007).

In the likelihood-based analysis the matrices of transition probabilities were obtained from 100,000 simulations, with the dispersal and extinction rates set at the values $D = 0.2$ $E = 0.5$, which seemed to maximize the likelihood of the reconstruction. The geographic model implemented in the analyses is shown in Fig. 3.

RESULTS

The Bayesian and parsimony trees are shown in Figs 1 and 2. They are similar, with minor differences in nodes and branches. A complete phylogenetic

analysis of the tribe is beyond the scope of this paper and will be the subject of further contributions, currently in preparation. Although based on only 30 characters, the analysis proved to be quite reliable (see Figure legends for reliability
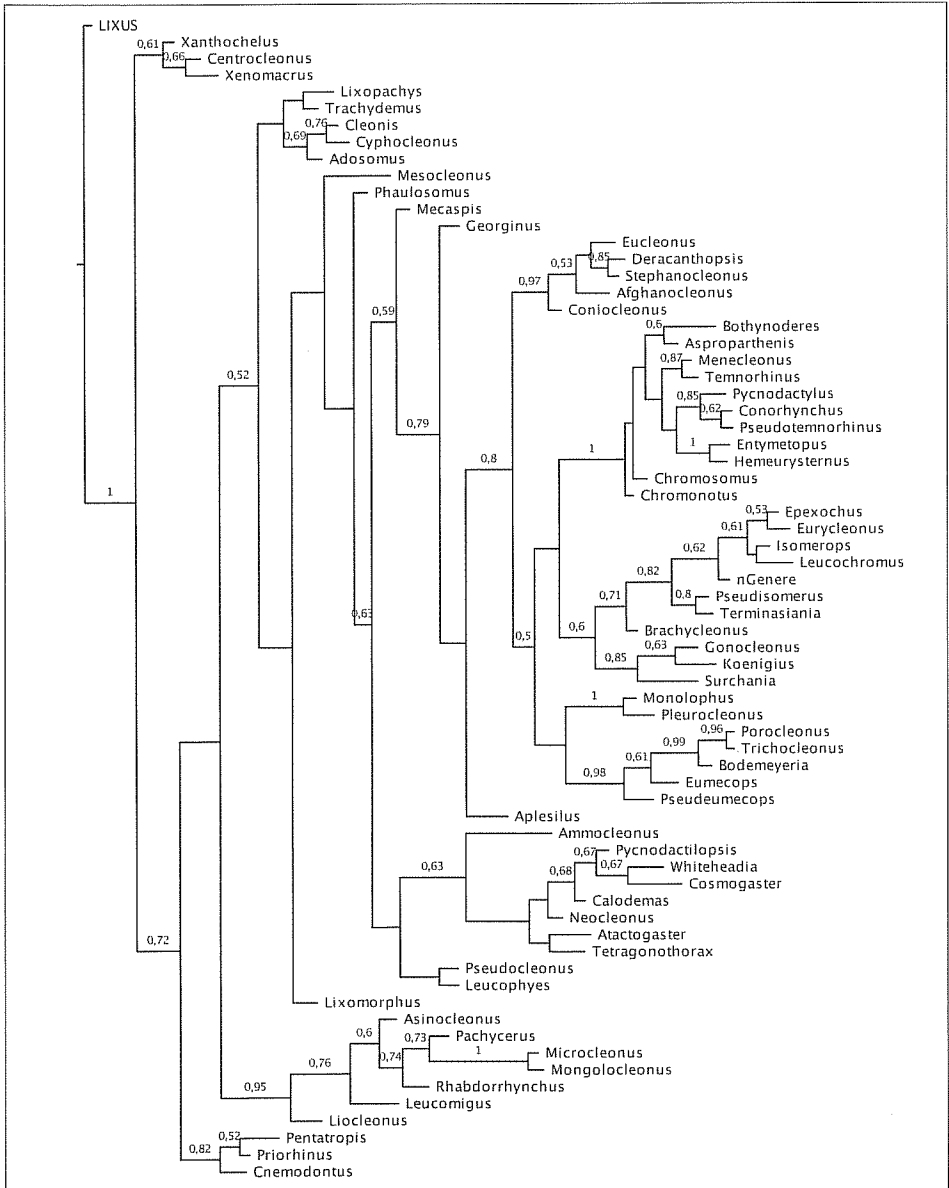

Fig. 1 - Bayesian Consensus tree showing all compatible groups with posterior probabilities above branches when greater than 0.50 and branch lengths. The tree is based on summarizing the 19,802 topologies sampled (excluding the burnin phase) during the 1million MCMC runs.

data). More complete matrixes, including more than 70 characters, are being elaborated. Their preliminary study confirms the general topology of the trees; a more precise resolution of some uncertain nodes will probably be obtained.
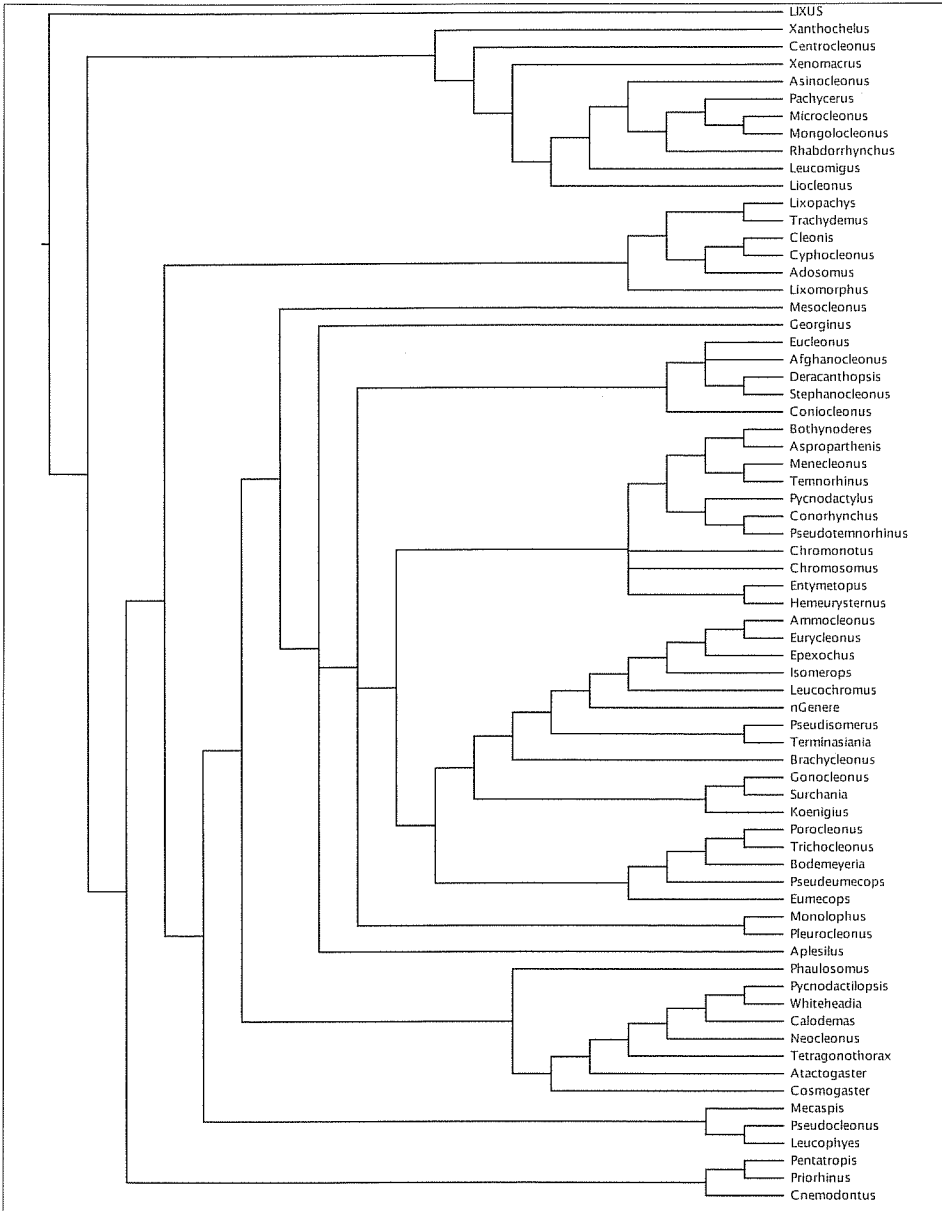

Fig. 2 - Parsimony Tree. Strict consensus of 700 most parsimonious trees obtained after 100 RAS replicates with TBR branch swapping. CI: 0.55; RI: 0.81; RC: 0.45; tree length: 211.

	S Africa	C Africa	E Africa	Mediterranean	Asia	Indo-Malayan
S Africa	-	1	1	1	0.5	1
C Africa	1	-	1	1	0.5	0.5
E Africa	1	1	-	1	1	1
Mediterranean	1	1	1	-	1	1
Asia	0.5	0.5	1	1	-	1
Indo-Malayan	1	0.5	1	1	1	-

Fig. 3 - Geographic model for the likelihood-based biogeographic analysis. This model shows connections between areas (see Ree et al., 2005) and is quite simple and generic, since the absence of an absolute dating of the nodes precludes any specific paleogeographic assumption.

The graphs of inferred lineage geohistory are shown in Figs. 4 and 5. The biogeographic analyses was performed on the whole phylogenetic tree; however, for graphic reasons, only the basal clades (including all the mainly southern African and Mediterranean taxa) are shown; the mainly Asian taxa, which
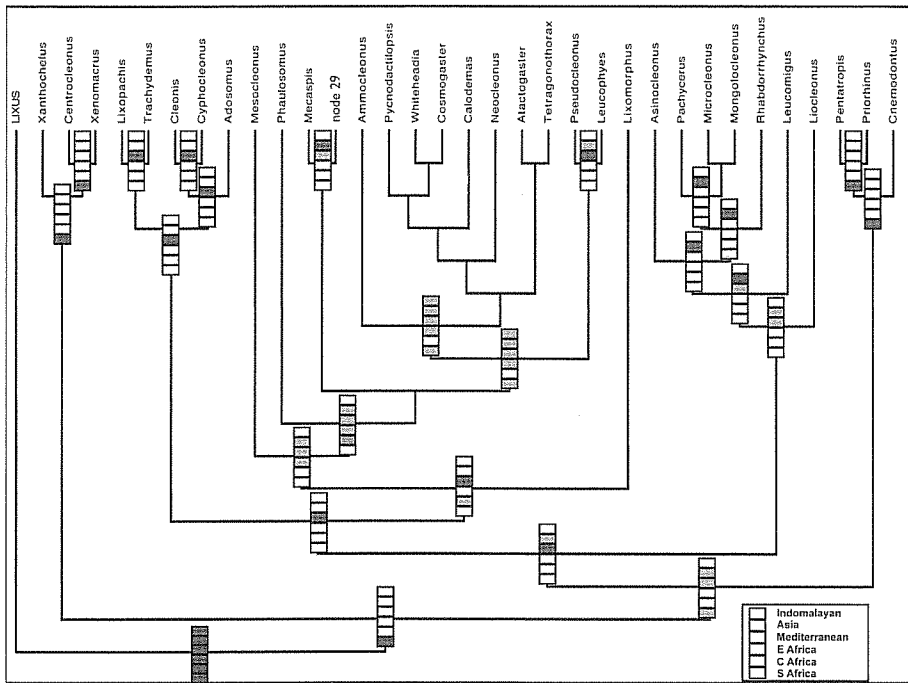

Fig. 4 - DIVA Reconstruction. This dispersal-vicariance reconstruction shows the ancestral distribution of the main basal ancestors. When the program found more than one most parsimonious reconstruction, distributions are depicted with grey rectangles.
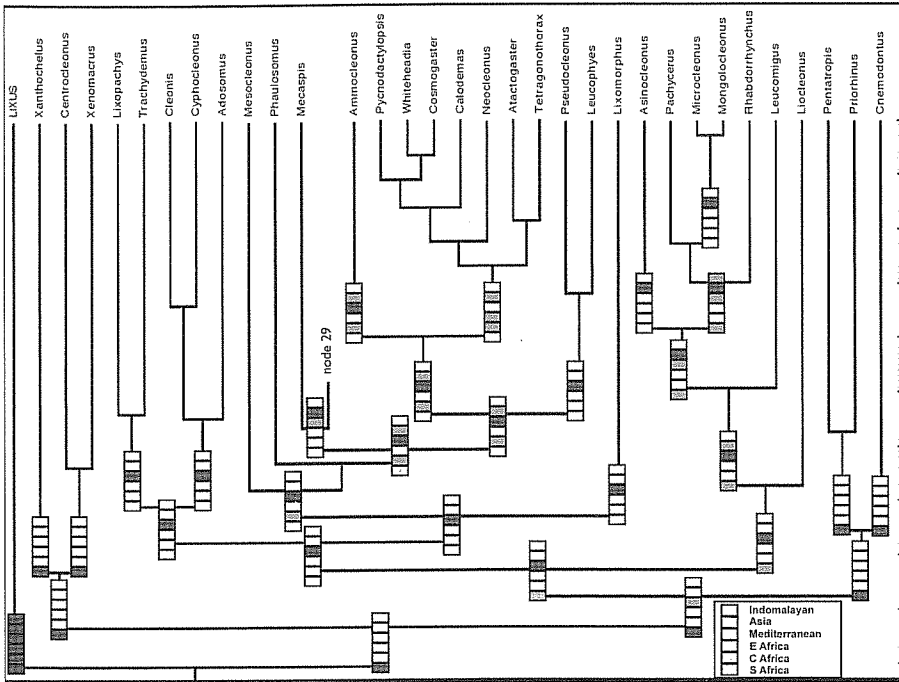
Fig 5 - AReA Reconstruction. This likelihood-based reconstruction shows the ancestral distribution of the main basal lineages immediately after the cladogenetic events. Black rectangles represent the strongly supported reconstructions, above the conventional cutoff value of two log-likelihood units (Edwards, 1992). Grey rectangles show alternative areas supported by less than two log-likelihood units. The log-likelihood of the reconstruction was -465.1.

differentiated from node number 29, are excluded from the Figures, not from the analysis.

The difference between the two representations consists in the absence of branch lengths in the cladogram of the DIVA reconstruction and in the position of the inferred ancestral areas. This is due to the difference in methods of extrapolating the ancestral distributions between the likelihood and dispersal-vicariance approaches. The maximum likelihood inference is calculated for descendents' distribution immediately after the cladogenetic event, whereas the analysis infers the ancestors' distribution. That is why, in the latter case, ancestral areas are situated in correspondence with the nodes. The two reconstructions are quite similar, but that based on likelihood gives a more significant support to the majority of the ancestral distributions, clearly showing the basal vicariance between southern African and Mediterranean branches. This is probably due to the information supplied by the branch lengths and the geographic model, which are lacking in the dispersal-vicariance analysis.
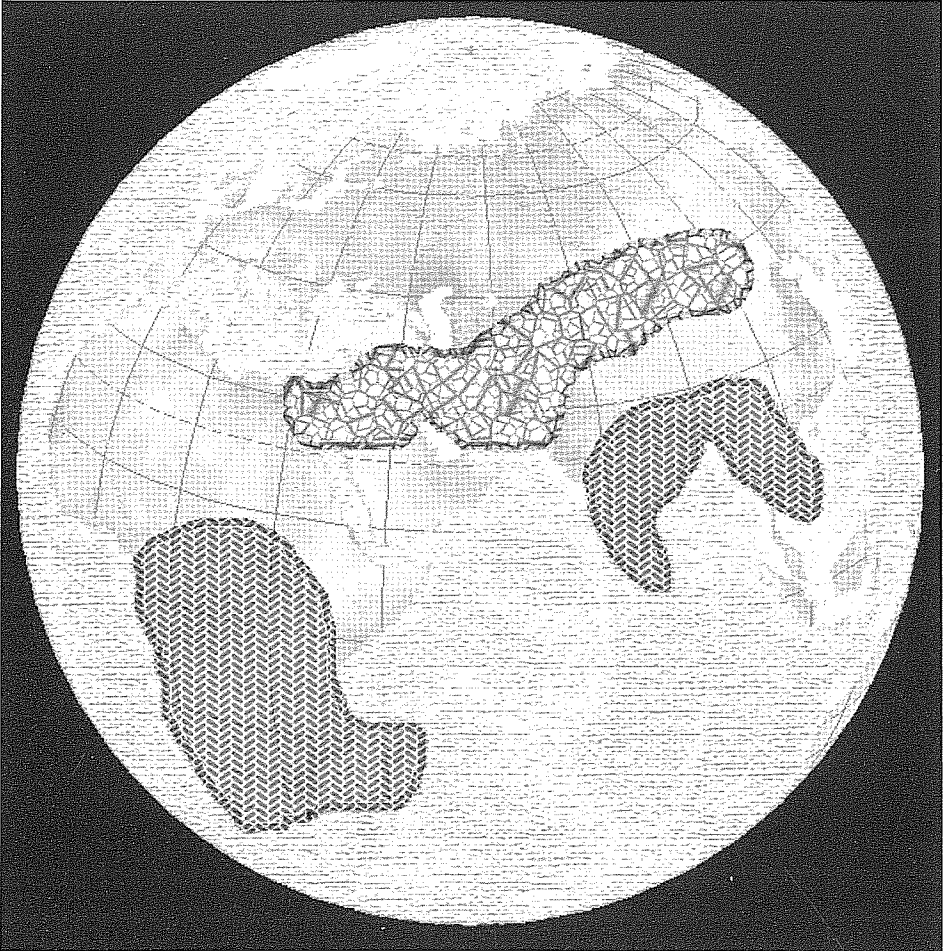
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Fig. 6 - Distribution of the genus *Xanthochelus* Chevrolat, 1873, showing the range of the Afro-Indian and the Palaearctic species-groups. This and the following maps were taken from Encarta World Atlas 2000 (Microsoft Corporation) and elaborated with Photoshop 7.0 (Adobe Systems Incorporated).

1. Intrageneric relationships

The recognition of intrageneric relationships between Mediterranean and southern African taxa would at least require boundaries among genera to be well defined, and the species composition of each genus well known. This, unfortunately, was not so far achieved, and the following remarks are based on a critical analysis of the composition of the genera as presently accepted.

Only four genera, considered in the "traditional" sense, seem to include Mediterranean and southern African species: *Xanthochelus* Chevrolat, 1873; *Pachycerus* Schoenherr, 1823; *Pseudotemnorrhinus* Voss, 1960 (= *Temnorhinus*

s. AA); and *Pycnodactylopsis* Voss, 1963 (= *Pycnodactylus* s. AA). Each case is here discussed.

Xanthochelus (Fig. 6). This genus clusters in a very basal clade and, together with two closely related genera, appears to be the sister taxon of the rest of the tribe. It includes about 20 species, distributed in southern and central Africa, the southeastern Mediterranean coasts (Egypt), Western and Central Asia, and tropical southeastern Asia. The type species, *Xanthochelus vulneratus* (Boheman, 1834) is found in South Africa. The tropical African species share several morphological similarities with the tropical southeastern Asian species, whereas the four Palaearctic taxa [the central Asian *X. eversmanni* (Fåhraeus, 1842) and *X. nomas* (Pallas, 1991); the Mediterranean-central Asian *X. cinctiventris* (Fåhraeus, 1842); and the eastern Mediterranean *X. longus* Chevrolat, 1873] are closer to some Palaearctic genera (namely, *Cleonis* Dejean, 1821) than their tropical counterparts. This genus seems to be polyphyletic and should be split into two genera, one encompassing the Asian and Mediterranean species, the other including the Afrotropical and Indomalayan species. Intrageneric relationships between Mediterranean and southern African taxa should be rejected, or at least considered to be very distant.

Pachycerus (Fig. 7). This is an interesting genus, with several species spread in the Mediterranean region, northern Africa, central Asia, India and Madagascar. It clusters in a quite basal clade, related to southern African genera. This genus is currently being revised by Meregalli (2002a; 2008; in press). Among the species previously ascribed to *Pachycerus* is *Lixus granulosus* Olivier, 1807, a southern African taxon. This is an enigmatic, apparently plesiomorphic species; its taxonomic position is still uncertain, but it was excluded from *Pachycerus* by Meregalli (2002a; 2008). Therefore, also in this case intrageneric relationships between Mediterranean and southern African taxa are rejected.

Pseudotemnorrhinus (Fig. 8). According to Arzanov (2005) the genus *Pseudotemnorrhinus* is here maintained separated from *Conorhynchus* Motschulsky, 1860, with which it was merged as a subgenus by Alonso Zarazaga and Lyal (1999) and Meregalli (2002b). It clusters in a derived clade, together with *Conorhynchus*, and includes species present in the Mediterranean region, central and western Asia, including the Arabian Peninsula, northern and eastern Africa, and southern Africa. The two endemic southern African species, *P. surdus* (Gyllenhal, 1834) and *P. longulus* (Fahraeus, 1842), are closely related to an apparently new species from Kenya, currently under study, and to some of the Mediterranean and Arabian species. This is the only genus including species occurring in the two faunistic regions, although there is not a sharp disjunction, since it is also present along the coasts of the Red Sea, in the Arabian peninsula and in Kenya.
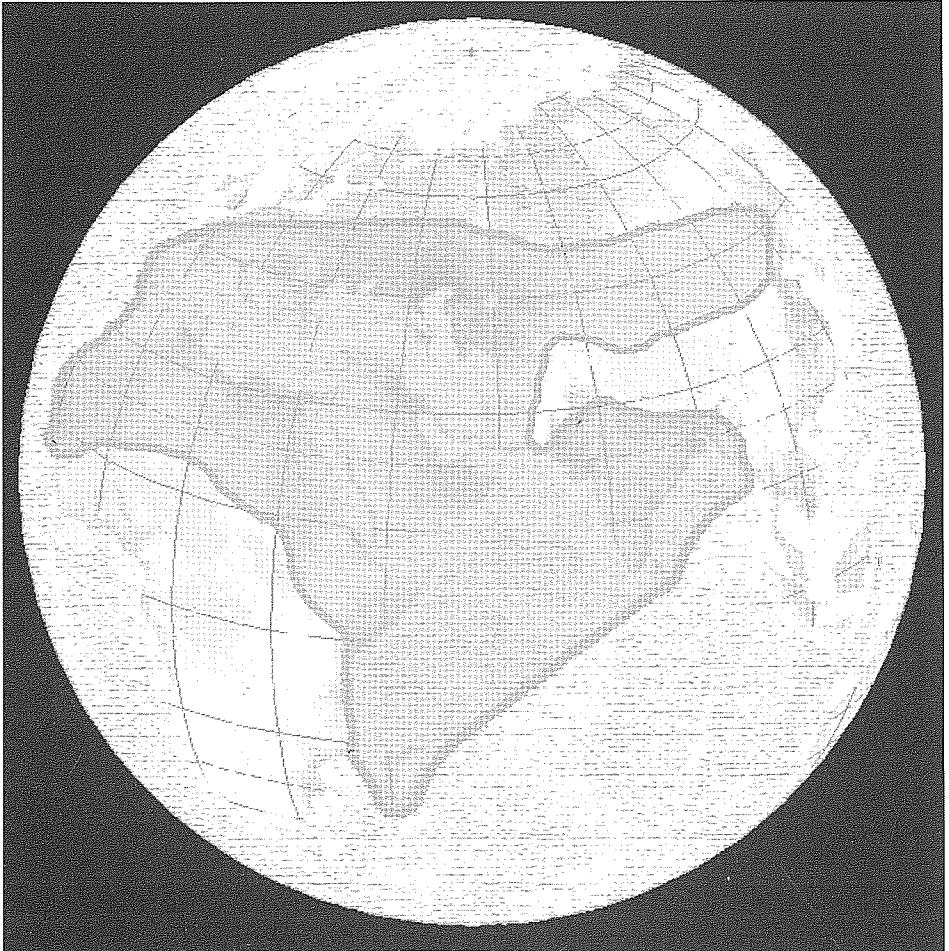
Fig. 7 - Distribution of the genus *Pachycerus* Schoenherr, 1823.

Osella et al. (1998) cited Mediterranean-southern African relationships also for the genera *Pycnodactylopsis* (as *Pycnodactylus*) [with *P. cretosus* (Fairmaire, 1868) and the sister taxon *P. tomentosus* (Fåhraeus, 1842) for the Mediterranean region and *P. fumosus* (Fåhraeus, 1842), *P. interstitialis* (Kolbe, 1883) and *P. mitis* (Gerstäcker, 1871) for southern Africa] and *Tetragonothorax* Chevrolat, 1873 [with *T. retusus* (F., 1801) and *T. senectus* (Gyllenhal, 1842) for the Mediterranean region and *T. angulicollis* (Fåhraeus, 1871) for southern Africa].

The three cited species of *Pycnodactylopsis* are widespread in central Africa and expand their range to marginal parts of southern Africa but are not native
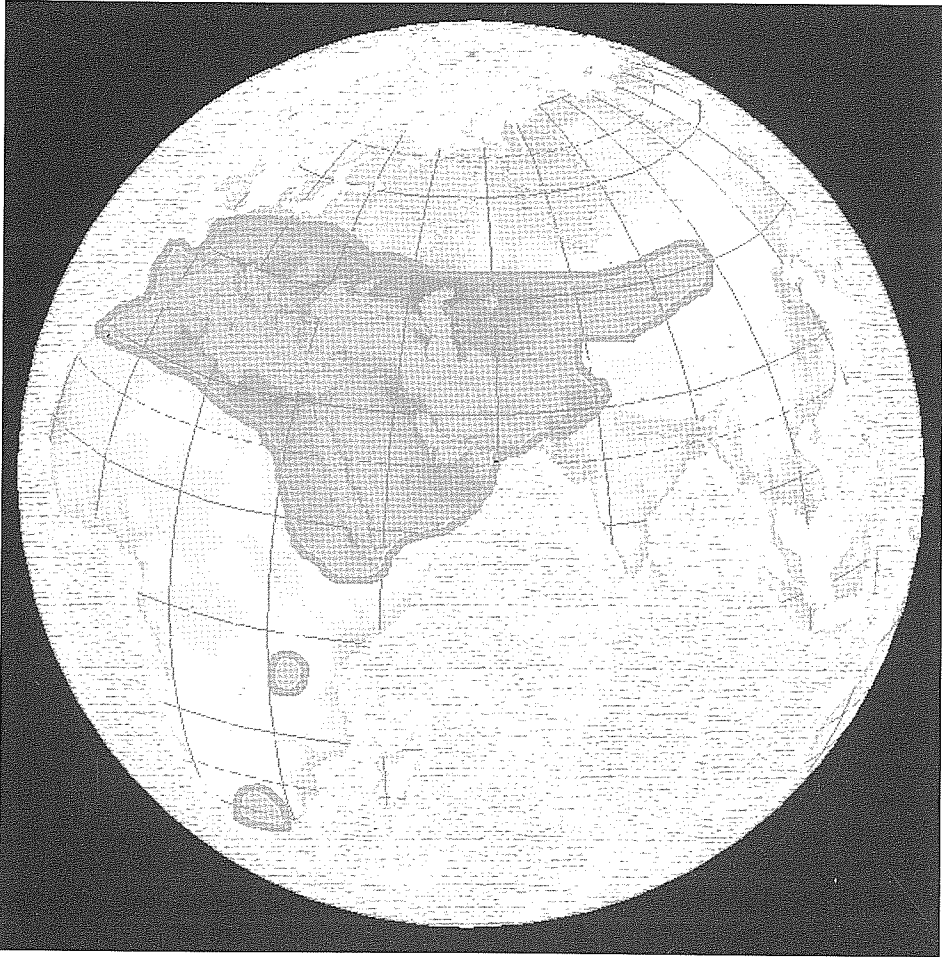
Fig. 8 - Distribution of the genus *Pseudotemnorrhinus* Voss, 1960.

to southern Africa. Moreover, the two Mediterranean species differ in many significant characters, including the structure of the female genitalia, so that their belonging to *Pycnodactylopsis* is anyway questionable. In any case, this genus does not present a disjunct Mediterranean-southern African distribution, being it widespread in central Africa.

In *Tetragonothorax* the two cited species occur in central and eastern Africa and reach their northernmost limit in the Sahel, but do not expand their range to the Mediterranean coasts and are thus not true Mediterranean elements. Also this case does not represent an example of disjunct Mediterranean-southern African range.

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2. Intergeneric relationships

The phylogenetic analysis of the 68 genera allows some considerations on intergeneric relationships, aiming at recognizing a possible disjunction between Mediterranean and southern African sister clades. We note that, differently from the southern African range, an endemic Mediterranean distribution pattern at genus rank is seldom recognizable. In fact, excepting a few cases, there is no clear division between Mediterranean and Asian taxa, since many of the genera present in the Mediterranean region expand their range to Palaearctic Asia, at least to its central part. In contrast, several taxa associated with the central Asian steppes are true endemics to this area.

All the southern African endemic genera cluster in basal clades. A first clade, apparently morphologically intermediate between the tribes Lixini and Cleonini (or even possibly referable to the Lixini), includes three taxa (*Xanthochelus*, *Centrocleonus* Chevrolat, 1873 and *Xenomacrus* Faust, 1904). The species of these genera are characterized by a round rostrum, with the scrobes not reaching its apex. The other southern African endemic genera (*Pentratropis* Faust, 1904, *Cnemodontus* Chevrolat, 1873 and *Priorhinus* Chevrolat, 1873) cluster basally to all the remaining genera of Cleonini.

A further relatively primitive branch includes three very closely related Asian-Mediterranean genera, *Cleonis*, *Cyphocleonus* Motschulsky, 1860 and *Adosomus* Faust, 1904. The southern Mediterranean *Lixopachys* Reitter, 1916 and the Mediterranean-Turanian *Trachydemus* Chevrolat, 1873 are also part of this group, possibly together with *Lixomorphus* Faust, 1904. These latter genera appear as basal to the *Cleonis* clade in the parsimony tree (Fig. 2); the first two also cluster in the same position in the Bayesian tree, whereas *Lixomorphus* falls in the following branch (Fig. 1).

All the central African genera cluster in a single clade, with so far unclarified relationships. It also includes a genus (*Atactogaster* Faust, 1904) expanding its range to the Indo-Malayan region. Several of the genera are also present in southern Africa, but only the two previously cited species of *Pycnodactylopsis* reach the Mediterranean region.

The "*Pachycerus*" clade clusters in a quite basal branch – in the parsimony tree sister to some of the southern African genera. The range of *Pachycerus* was already described; the other apparently related genera of this clade are known from the Mediterranean region, and Asia.

DISCUSSION

Our morphological and phylogenetic analysis of the tribe Cleonini indicates that in this tribe relationships between Mediterranean and southern African

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taxa are extremely limited in the present day fauna. Only *Pseudotemnorrhinus surdus* and *P. longulus* represent a case of a disjunct distribution. This genus belongs to a derived clade, sister to other Palaearctic taxa and is composed of a large number of species with central Asian and Mediterranean distribution. Since only a few species, reciprocally closely associated, are present in eastern and southern Africa, it appears that the African presence derives from an expansion of the range of the genus, likely from eastern Mediterranean habitats and in relatively recent times; this expansion apparently occurred along the coasts of the Red Sea, where three species, vicariant of Mediterranean taxa, are present, to colonize Kenya and finally southern Africa. The dry grassland corridor present at least since Middle Miocene in eastern Africa (Retellack, 1992) favoured faunistic communication between the two regions.

The case of *Pycnodactylopsis* is different. This genus belongs to the clade of the central African taxa and has a continuous Afrotropical distribution, reaching the southern Mediterranean coasts and the Turanian region with two species. There is no southern African endemic taxon, but three of the central African species expand their range to the northern part of southern Africa (one, *P. mitis*, also reaches the Arabian peninsula). Thus, the broad range of some of the central African species we consider as a case of diffusion of winged, apparently poorly specialized, taxa, whereas the two Palaearctic species probably derive from an ancient expansion of the ancestors of the genus.

Although in northern Africa the number of species of Cleonini decreases significantly with increasing distance from the coast, a few Asian-Mediterranean genera expand their range up to the Sahel. These are *Pachycerus, Ammocleonus* Bedel, 1907, and *Menecleonus* Faust, 1904. Whereas in the first case the Sahelian species are native to the region, and are not closely related to the true Palaearctic taxa, those of the other two genera are widespread along the southern Mediterranean coasts and reach Senegal and Mauritania, central Algeria and Sudan. Thus, it can be proposed that the Mediterranean region expands to the Sahel, at least for a limited number of species adapted to drier conditions and often associated with xerophytic vegetation, and is sharply limited to the south by the more humid, forested habitats of central Africa, where different, reciprocally related, genera are present. A few of the species belonging to these central African genera expand their range to the Sahelian area, again in Senegal and Sudan, but, with the notable exception of the two species of *Pycnodactylopsis*, they do not reach the Mediterranean coast. The Sahel thus represents, for the Cleonini, a transition zone between Afrotropical and Mediterranean faunas.

On a historical biogeography approach, the likelihood reconstruction of ancestral distributions (Fig. 5) fully supports the hypothetical considerations that can be drawn from the present day distribution. The tribe primarily dif-

ferentiated in southern Africa, where the most basal branches, including the endemic southern African genera, developed. A subsequent radiation, leading to some Asian-Mediterranean taxa, occurred probably along the southern coasts of the Tethys sea. This event originated the taxa belonging firstly to the *Lixopachys* and *Trachydemus*, and then to the *Cleonis,* clades. A final, very successful, radiation occurred in the central Asian dry habitats, where a large number of taxa differentiated. The Mediterranean distribution of some genera, particularly those belonging to the most apomorphic groups, may be secondary, deriving from the expansion toward the west of the range of taxa primarily differentiated in Asia.

The case of *Pachycerus* is intriguing. The genus, whose type species is the Palaearctic *P. segnis* (Germar 1824), includes well-differentiated groups of species, each restricted to a single biogeographic region, and there is even a probably very plesiomorphic, relict species in southern India (Meregalli, in press). Quite significantly, the maximum likelihood reconstruction gave the highest probability to a Mediterranean branching (the analysis was based on the characters of the Palaearctic *P. segnis*) but the possibility that the basal branch of the *Pachycerus* clade was in Africa was not ruled out (Fig. 5). Such an origin for the *Pachycerus* clade seems indeed quite likely. This lineage appeared independently from the other Mediterranean-Asian lineages, possibly from *Xanthochelus*-like ancestors in subtropical Africa or along the southern margin of the Tethys sea, and then spread to most of the Palaearctic region. Morphologically and geographically, *Pachycerus* may thus represent a link between African and Mediterranean taxa.

Determining the epoch of differentiation of the tribe is complex. Lacking molecular data, no chronological interpretation based on a molecular clock is available; however, fossils have been cited for Oligocene and Miocene European and northern American deposits (Heer, 1847; Alonso-Zarazaga and Lyal, 1999). In any case, the absence of species from South America and Australia suggests that the Cleonini appeared after the Gondwana fragmentation. The age of the further radiation of the tribe cannot be estimated precisely. Although true land connections between the African and the Eurasian plates were not re-established before late Oligocene, when several microplates were present into the Tethys Sea, and Arabia and Asia were connected via the Gomphotherium Landbridge (see Harzhauser at al., 2007, and references there cited), palinspastic restorations show that the western Tethys Sea has never been very broad, so that it cannot be considered as a true biogeographical barrier (Gelabert et al., 2002; Rosenbaum et al., 2002). Ancestral species having a good dispersal capacity may thus have invaded Eurasia in quite ancient times.

In conclusion, contemporary cases of disjunct southern African-Mediterranean distribution in the tribe Cleonini concern only two or three species of

Pseudotemnorrhinus out of nearly 1000 species known for the tribe. They seem to derive from the southern expansion of the range of an originally Mediterranean-Asian genus, likely occurring in relatively recent times, along the eastern African steppes. The central African taxa reach their northernmost expansion along the Sahel band, a region where a few Mediterranean species are also present. Relationships between the Cleonini of the Mediterranean region and of southern Africa exist only in sister basal branches, suggesting that a split between "Mediterranean" (better, Tethyan) and southern African taxa occurred during the early stages of the evolution of the tribe, and after that the two faunas did not have further connections. But it was from these Tethyan groups that a very successful radiation took place, leading to the colonization of all the steppe areas of the Mediterranean and central and western Asia.

ACKNOWLEDGEMENTS

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