Parsimony analysis of endemicity of enchodontoid fishes from the Cenomanian

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Abstract: Parsimony analysis of endemicity was applied to analyze the distribution of enchodontoid fishes occurring strictly in the Cenomanian. The analysis was carried out using the computer program PAUP* 4.0b10, based on a data matrix built with 17 taxa and 12 areas. The rooting was made on an hypothetical all-zero outgroup. Applying the exact algorithm branch and bound, 47 trees were obtained with 26 steps, a consistency index of 0.73, and a retention index of 0.50. The topology found with a majority rule consensus was: [(Mexico) + (United States) + (Morocco + Italy) + (Lebanon + Israel) + (Italy-Slovenia) + (Brazil)] + (D.R. Congo) + (Sweden) + (Germany) + (England). The procedure delimited two areas of endemism in the Tethys Ocean. They are Morocco and southern Italy and Lebanon and Israel. The area of endemism formed by Morocco + Italy represents the North African region of the Tethys Ocean, and that formed by Lebanon + Israel is in the mid-Tethyan Ocean. Our results are in partial agreement with the patterns of geographical distribution of certain invertebrate biota.

Key Words: Biogeography; parsimony analysis of endemicity; Late Cretaceous; Enchodontoidei

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Résumé : Analyse parcimonieuse d'endémicité des poissons Enchodontoidei du Cénomanien.- L'analyse parcimonieuse d'endémicité est réalisée pour expliquer la distribution cénomanienne des poissons Enchodontoidei. Le programme PAUP* 4.ob10 a été utilisé. L'analyse est basée sur une matrice construite à partir de 17 taxons provenant de 12 régions. L'enracinement se fait sur un groupe externe hypothétique. Par application de l'algorithme du "branch and bound", 47 arbres ont été obtenus à 26 pas, avec un index de consistance de 0,73 et un index de rétention de 0,50. Le consensus donne la topologie suivante : [(Mexique) + (Etats-Unis) + (Maroc + Italie) + (Liban + Israël) + (Italie-Slovénie) + (Brésil)] + (R.D. du Congo) + (Suède) + (Allemagne) + (Angleterre). Deux aires d'endémismes ont été identifiées en Téthys (Maroc et Italie du Sud; Liban et Israël). L'aire d'endémisme formée par le Maroc et l'Italie représente la région nord-africaine de la Téthys et celle formée par le Liban et Israël le centre. Nos résultats s'accordent partiellement avec la répartition géographique de certains biotopes invertébrés.

Mots-Clefs : Biogéographie ; analyse parcimonieuse d'endémicité ; Crétacé supérieur ; Enchodontoidei

Introduction

Parsimony Analysis of Endemicity (PAE) was originally developed by ROSEN (1988) in a paleontological setting. According to MORRONE & CRISCI (1995), PAE is a cladistic method that groups areas by their shared taxa based on the most parsimonious solution. This methodology allows an interpretation of the occupation of an area by taxa, to verify the relationships among areas, and to identify putative areas of endemism using a matrix built with taxa versus areas (or localities). Despite some criticisms (*i.e.*, HUMPHRIES & PARENTI, 1999; BROOKS & VELLER, 2003), PAE is a tool potentially useful in historical biogeography, because it allows an analysis of historical information from the geographic distribution of taxonomic groups, even if phylogenetic analyses are lacking. Additionally, in a recent paper of PAE review, NIHEI (2006) claimed that it remains as an insightful method for inferring historical patterns.

Recent papers have applied PAE to the study of faunal distributions, mainly those of extant taxa (*i.e.*, GLASBY & ALVAREZ, 1999; MORRONE *et alii*, 1999; BISCONTI *et alii*, 2001; GRAVE, 2001; RACHELI & RACHELI, 2004; SAMYN & TALLON, 2005; MORENO *et alii*, 2006; QUIJANO-ABRIL *et alii*, 2006). Biogeographical studies using only fossil taxa are very scarce (*i.e.*, FIELITZ, 1996;

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LIEBERMAN, 2003; CECCA *et alii*, 2005; GALLO *et alii*, in press) and PAE has been applied to the analysis of fossil assemblages in few studies (*i.e.*, SMITH, 1992; GERAADS, 1998; GALLO & SILVA, 2006). Generally, fossils in Biogeography are a very useful tool in the determination of the minimum age of a taxon, as well as for stratigraphic correlation, the more common objective. In some cases, the stratigraphic distribution seems to be more relevant than the geographic distribution. Certain papers with a biostratigraphic approach allude to the paleobiogeography of taxa over a short interval of time, using quantitative analyses based on similarity to infer the dynamics of their areas of distribution. However, these studies often do not emphasize historical relationships among taxa nor the areas of endemism. Their point of view is merely descriptive insofar as the recognition of spatial distribution patterns is concerned. The determination of the subjacent historical processes is intuitively proposed and depends on the geological data.

The Enchodontoidei are assigned to the Order Aulopiformes and are represented by extinct marine teleostean fishes, generally with an elongate body and a long and narrow strut maxilla included in the mouth gape (NELSON, 1994). The Order Aulopiformes consists of fifteen living (Alepisauridae, Aulopidae, Bathysauridae, Bathysauroididae, Bathysauropsidae, Chlorophthalmidae, Evermannellidae, Giganturidae, Ipnopidae, Notosudidae, Paralepididae, Paraulopidae, Pseudotrichonotidae, Scopelarchidae, and Synodontidae) and nine extinct (Apateopholidae, Cimolichthyidae, Dercetidae, Enchodontidae, Eurypholidae, Halecidae, Ichthyotringidae, Prionolepididae, and Serrilepidae) families of marine fish (NELSON, 1994, 2006). They form a morphologically very diversified group known as "lizardfishes", with both benthonic and pelagic habits. They are found in habitats ranging from estuaries to abyssal zones (BALDWIN & JOHNSON, 1996; NELSON, 2006).

The Enchodontoidei have a long temporal range: from the Early Cretaceous to the Early Eocene, and were most numerous in the Late Cretaceous. Geographically, they occur in the deposits of Tethyan Europe (Belgium, Czech Republic, England, France, Germany, Holland, Italy, Netherlands, Slovenia, and Sweden); Asia (Arabian Peninsula, India, Israel, Japan, Jordan, Lebanon, and Syria); Africa (Angola, Democratic Republic of Congo, Egypt, and Morocco); North America (Canada, Mexico, and United States), and South America (Bolivia and Brazil). In Brazil, enchodontoids are present in strata ranging in age from Cenomanian to Maastrichtian (*i.e.*, GOODY, 1969; CHALIFA, 1996; FIELITZ, 2004; FIGUEIREDO & GALLO, 2006).

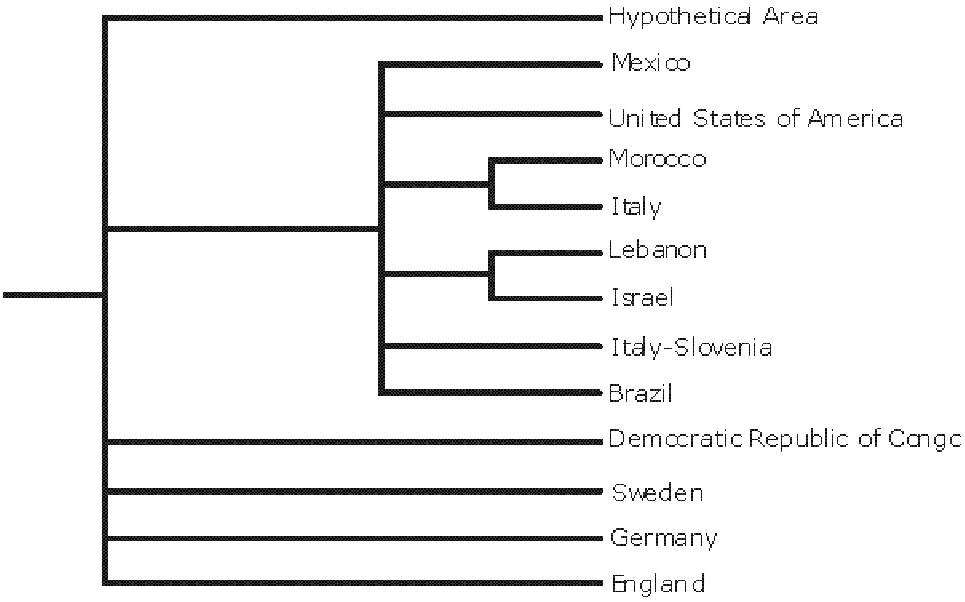

Figure 1: Majority rule consensus tree of the 47 most parsimonious cladograms obtained in the PAE from the enchodontoid distribution during Cenomanian.

FIELITZ (2004) proposed a hypothesis on the phylogenetic relationships of Enchodontoidea, that includes some living and extinct members of Aulopiformes. He concluded that Enchodontoidea is a monophyletic group and sister group of Cimolichthyidae, and this clade in turn is the sister group of the living Alepisauridae. In addition, he furnished an area cladogram of Enchodontoidea and suggested generalizations about the paleobiogeography of one of its genera, *Enchodus*. According to him, *Enchodus* originated in the mid-Tethyan Ocean (nowadays the Middle East), with some endemic and widespread species recorded in this area. Moreover, one clade comprising three other species is from North America, which is the sister group to a species from the northwestern region of the Tethys Ocean (nowadays western Germany), and this in turn is the sister group of species from the western edge of the Tethys

Ocean (nowadays Morocco) and North America.

In the absence of more methodologically sound biogeographical studies of Cretaceous enchodontoids, we applied PAE in order to analyze the distribution of these fishes occurring only in the Cenomanian (the first stage of the Late Cretaceous, with an estimated duration of about 4-5.4 My BP). The present paper is the first step in the paleobiogeographic reconstruction of the Late Cretaceous through the use of this methodology to analyze paleoichthyological assemblages.

Material and methods

The analysis is based on a data matrix (Appendix 1) built with taxa (columns) versus areas (rows). The areas are treated as taxa and the taxa as characters (ROSEN, 1988); character states are the presence/absence of taxa in the "terminal areas". The dataset consists of 16 genera distributed in eight families (*i.e.*, Ichthyotringidae, Apateopholidae, Dercetidae, Prionolepididae, Enchodontidae, Eurypholidae, Halecidae, and Serrilepidae), and one genus *incertae sedis* (*Yabrudichthys*), with most data obtained from the current literature. The genera are (Appendix 1): *Ichthyotringa* (1), *Apateopholis* (2), *Cyranichthys* (3), *Dercetoides* (4), *Hastichthys* (5), *Rhynchodercetis* (6), *Prionolepis* (7), *Rharbichthys* (8), *Palaeolycus* (9), *Eurypholis* (10), *Saurohamphus* (11), *Enchodus* (12), *Halec* (13), *Phylactocephalus* (14), *Hemisaurida* (15), *Serrilepis* (16), *Yabrudichthys* (17). The twelve areas are: Brazil, Mexico, United States, Democratic Republic of Congo, Morocco, Italy, Italy-Slovenia, England, Germany, Sweden, Lebanon, and Israel. The occurrences of the Messina and Lesina localities in southern Italy are referred to as "Italy". The occurrences in the Trieste-Komen Plateau are referred to Italy-Slovenia. Localities are listed in the Appendix 2.

The presence of the taxa in the several areas was coded as (1) and their absence as (0). A hypothetical area to root the tree with all the taxa absent was added to the data matrix. The data were analyzed using the computer program PAUP*4.0b10 (SWOFFORD, 2001), applying the branch and bound algorithm (BandB) to perform a search of the most parsimonious of all possible tree topologies.

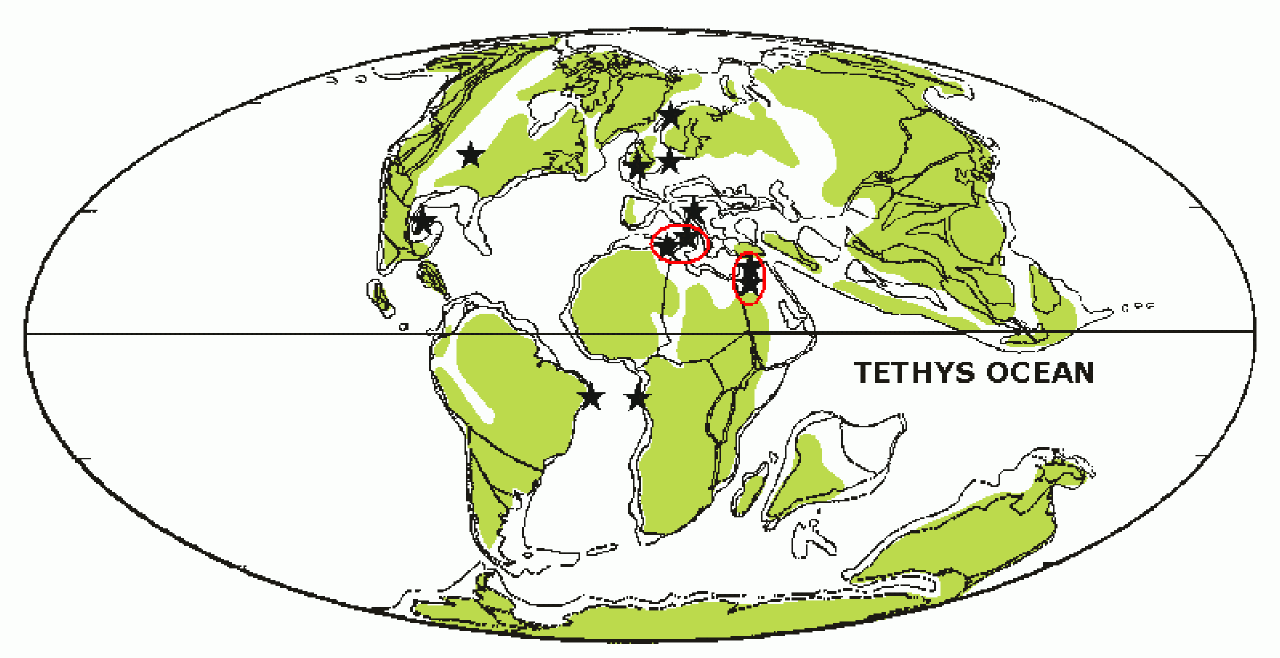

Figure 2: Paleocontinental map of the Cenomanian showing the localities used in the analysis (represented by stars) and the areas of endemism delimited in the PAE (encircled stars). Base map modified from SCOTESE (2002).

Results and conclusions

As a result, 47 trees were obtained with 26 steps, consistency index 0.73, and retention index 0.50. The majority rule consensus tree shows the topology (Fig. 1): [(Mexico) + (United States) + (Morocco + Italy) + (Lebanon + Israel) + (Italy-Slovenia) + (Brazil)] + (D.R. Congo) + (Sweden) + (Germany) + (England).

Two areas of endemism can be delimited in the Tethys Ocean: Morocco and southern Italy, Lebanon and Israel (Figs. 1 - 2). The first group appears in all trees, whereas the second one is present in 60 per cent of them. A unique clade found in 66 per cent of the trees contains these two areas of endemism, as well as four areas with unresolved relationships (*i.e.*, Mexico, United States, Italy-Slovenia, and Brazil). The relationships among the four other areas remain unknown (*i.e.*, D.R. Congo, Sweden, Germany, and England).

The area of endemism formed by Morocco and Italy represents the North African region of the Tethys Ocean, and that formed by Lebanon and Israel is in the mid-Tethyan Ocean (Fig. 2). These areas are congruent with those we obtained in the application of PAE to only one family of the Enchodontoidei, the Dercetidae, but over a wider temporal range, from the Late Cretaceous to the Paleocene (GALLO & SILVA, 2006).

SMITH (1992) accomplished a historical biogeography study of Cenomanian echinoids, applying PAE and cladistic vicariance analysis. Three regional groupings emerged: a North European grouping (England, Belgium, and Hungary), a Tethyan grouping (Algeria, Tunisia, Egypt, the Middle East, and Oman), and a Texas-Sergipe-Angola grouping. Morocco, Portugal, and the Charente remained with variable positions in the area cladograms, possibly explained by a vicariance event: the development of oceanic rifting along the line of the Bay of Biscay. Moreover, during the Cenomanian, an "Atlantic" biota was already differentiated from the North African biota; for the echinoid assemblages of the South Atlantic localities (Sergipe and Angola) are more closely related to those of Texas than to those of North Africa. These data are supported to some extent by our analysis, because Sergipe does not appear related to North Africa (*i.e.*, Morocco), which in our analysis is included in an area of endemism with southern Italy. Furthermore, according to ROMAN *et alii* (1989) and SMITH (1992), two subgroups can be separated within North Africa, the eastern and western echinoid faunas. This eastern subgroup may be related to the area of endemism Lebanon + Israel as delimited herein.

Our results are in agreement with the propositions of RAUP & JABLONSKI (1993) and CRAME (2000, 2001) regarding gradients of taxonomic diversity. According to these authors, during the Late Cretaceous, peak values of diversity occurred at the 30° – 40° N paleolatitudes. The high values of diversity were maintained at 40° – 50° N paleolatitudes, which may be explained by the existence of a reef belt there during Late Cretaceous times (STANLEY, 1995). The areas of endemism delimited herein are situated between the 20° - 30° N paleolatitudes, that is, near one of the paleolatitudes with higher values of diversity as pointed out by RAUP & JABLONSKI (1993) and CRAME (2001). In this context, Italy-Slovenia could form an area of endemism, because of its latitudinal position (30° N). If data regarding the southern hemisphere obtained during our current study are taken into account, high values of diversity could be placed in paleolatitudes 20° - 30° S. The high values that the above-cited authors found mainly in the northern hemisphere are probably nothing but only a taxonomic artifact produced by the greater emphasis on studies of North American and European taxa (*ibid.*).

HAUSDORF (2000) proposed a reconstruction of the historical biogeography of an extant taxon of Gastropoda, and so delimited the ancestral areas of the clades by using the method of Weighted Ancestral Area Analysis (WAAA). This author correlated the areas he found with the paleogeography postulated for Cretaceous and Tertiary times. Regarding Cenomanian paleogeography (HAUSDORF, 2000, fig. 2), two areas are split in the northern continents as a result of a vicariance event. The western area, delimited by the presence of the taxon Helicoidea, is partially congruent with the area of endemism Morocco + Italy described herein.

Comparing our data with those obtained by FIELITZ (2004) concerning the paleobiogeography of *Enchodus* above-cited, we confirm that in strata of Cenomanian age the highest number of occurrences of this genus is in the Middle East (Israel and Lebanon) (see Appendix 2). He concluded that *Enchodus* originated in the mid-Tethyan Ocean, which is represented now by the Middle East. Only one report of this genus is recorded in the North America and Morocco region, and there are none in Germany during this time. On the other hand, FIELITZ (*ibid.*) did not include in his analysis the records of the genus in Italy, Italy-Slovenia, and Brazil.

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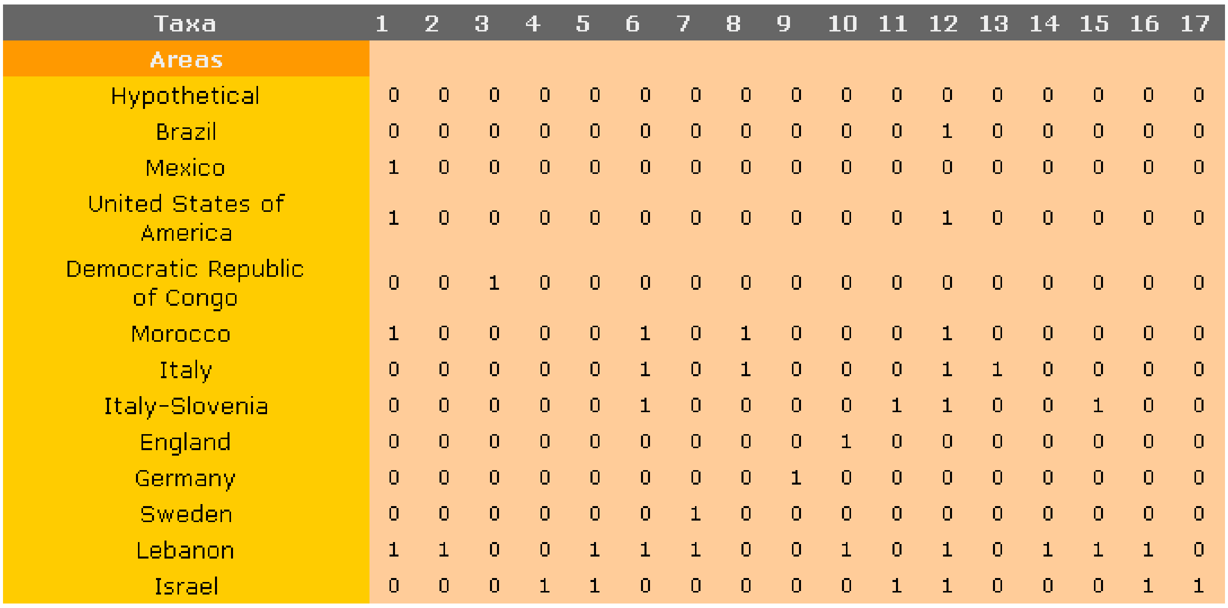
Taxa	Provenance	Country
Apateopholis	Haqel and En Nammoura	Lebanon
Cyranichthys	Kipala	Democratic Republic of Congo
Dercetoides	Ein-Yabrud	Israel
Enchodus	Ein-Yabrud and Givat-Shaul	Israel
	Haqel, Hgula, and En Nammoura	Lebanon
	Sage Creek	United States
	Messina	Italy
	Trieste-Komen	Italy-Slovenia
	Sergipe	Brazil
	Jbel Tselfat	Morocco
Eurypholis	Haqel, Hgula, and En Nammoura	Lebanon
	English Chalk	England
Halec	Lesina	Italy
	Trieste-Komen	Italy-Slovenia
Hastichthys	Ein-Yabrud	Israel
	En Nammoura	Lebanon
Hemisaurida	Trieste-Komen	Italy-Slovenia
	Haqel	Lebanon
Ichthyotringa	Haqel and Hgula	Lebanon
	Jbel Tselfat	Morocco
	Niobrara	United States
	Hidalgo	Mexico
Palaeolycus	Sedenhorst	Germany
Phylactocephalus	Haqel and Hgula	Lebanon
Prionolepis	Haqel and Hgula	Lebanon
	Tormarp	Sweden
Rharbichthys	Jbel Tselfat	Morocco
	Messina	Italy
Rhynchodercetis	Jbel Tselfat and Daoura	Morocco
	Messina	Italy
	Haqel, Hgula, and En Nammoura	Lebanon
	Trieste-Komen	Italy-Slovenia
Saurohamphus	Trieste-Komen	Italy-Slovenia
	Ein-Yabrud	Israel
Serrilepis	Ein-Yabrud	Israel
	En Nammoura	Lebanon
Yabrudichthys	Ein-Yabrud	Israel



Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Areas																	
Hypothetical	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brazil	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Mexico	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
United States of America	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Democratic Republic of Congo	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Morocco	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0
Italy	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
Italy-Slovenia	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0
England	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Germany	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sweden	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lebanon	1	1	0	0	1	1	1	0	0	1	0	1	0	1	1	1	0
Israel	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1

Appendix 1: Data matrix of taxa (columns) x areas (rows) of Enchodontoidei from the Cenomanian used in Parsimony Analysis of Endemicity (PAE).

◀ **Appendix 2:** Occurrences of enchodontoids in the Cenomanian included in the analysis. Most of data from: LUNDGREN (1889); ARAMBOURG (1954); LEONARDI (1966); GOODY (1969, 1976); CHALIFA (1985, 1989, 1996); RAAB & CHALIFA (1987); TAVERNE (1987); CAVIN & DUTHEIL (1999); MURRAY (2000); FOREY *et alii* (2003); FIELITZ & GONZÁLEZ RODRÍGUEZ (2005).

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