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Comparisons and relationships of the African and European Miocene carnivoran assemblages

George D. Koufos [a,*], Louis de Bonis [b]

[a] *Laboratory of Geology and Palaeontology, Department of Geology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece*
[b] *Université de Poitiers, UFR SFA, IPHEP, UMR 6046, 40, avenue du Recteur-Pineau, 86022 Poitiers cedex, France*

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Abstract

In the present article, the Middle and Late Miocene carnivoran faunas of Europe and Africa are compared for establishing their relationships. The Middle Miocene carnivoran assemblages from both continents are quite different at the specific and generic levels, less expressed in family composition. The comparison of the Late Miocene carnivoran assemblages indicates the following: the African carnivoran assemblage is different from the European ones both at the generic and specific level; the carnivoran faunas of Europe can be split into two geographic groups, "western" and "eastern"; the Turolian African assemblage is more diversified at the family level; the African carnivoran assemblage differs from the European ones in the presence of herpestids, the higher abundance of mustelids and the fewer hyaenids. It is more similar to the Late Miocene carnivoran assemblages of western and central Europe than eastern Europe. ***To cite this article: G.D. Koufos, L. de Bonis, C. R. Palevol 7 (2008).***

Résumé

Comparaisons et relations des faunes de Carnivora miocènes d'Europe et d'Afrique. Au Miocène moyen, les faunes sur les deux continents sont différentes aux niveaux spécifique et générique et, plus faiblement, au niveau familial. Les faunes du Miocène supérieur d'Afrique sont plus proches des faunes européennes que de celles du Miocène moyen d'Afrique. Au Miocène supérieur : la première moitié du Miocène supérieur, qui correspondrait au Vallésien, est particulièrement pauvre en carnivores et ne peut être comparée aux échantillons européens ; en Europe, nous trouvons deux ensembles bien distincts, l'un, occidental, l'autre, oriental ; la composition taxonomique des carnivores du Turolien africain est plus diversifiée au niveau familial ; les faunes africaines se caractérisent surtout par la présence des herpestidés, l'abondance des viverridès et la moindre diversité des hyènes, mais sont plus proche des faunes d'Europe orientale et centrale que de celles de l'occident. ***Pour citer cet article : G.D. Koufos, L. de Bonis, C. R. Palevol 7 (2008).***

Keywords: Europe; Africa; Carnivora; Mammalia; Comparisons; Relationships

Mots clés : Europe ; Afrique ; Carnivora ; Mammalia ; Comparaisons ; Relations

* Corresponding author.
E-mail addresses: koufos@geo.auth.gr (G.D. Koufos), louis.debonis@univ-poitiers.fr (L. de Bonis).

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Abbreviations

LAFR Late Miocene carnivoran assemblage of Africa
LEU Late Miocene carnivoran assemblage of Europe
LEEU Late Miocene carnivoran assemblage of eastern Europe
LCEU Late Miocene carnivoran assemblage of central Europe
LSEU Late Miocene carnivoran assemblage of southeastern Europe
LWEU Late Miocene carnivoran assemblage of western Europe
MAFR Middle Miocene carnivoran assemblage of Africa
MEU Middle Miocene carnivoran assemblage of Europe
N number of localities
n total number of species
TAFR Turolian carnivoran assemblage of Africa
TEEU Turolian carnivoran assemblage of eastern Europe
TCEU Turolian carnivoran assemblage of central Europe
TWEU Turolian carnivoran assemblage of western Europe
TSEU Turolian carnivoran assemblage of southeastern Europe

1. Introduction

The Miocene faunas of Europe, especially those of the Late Miocene, are rich and well known from a great number of fossiliferous sites dispersed throughout the continent, and include numerous taxa. For a long time, due to the less rich Miocene fossil record of Africa, the African Miocene faunas were less known. However, during the last two decades extensive fieldwork has remarkably increased the Miocene fossil record of Africa [3,5,9,10,13–19,26,27–29,32,34,37,40,42–44]. However, despite this significant increase, the African Miocene mammal record remains poorer when compared to the European one insofar as the number of European fossil bearing localities is still much higher.

The present article is an effort to compare the Miocene carnivoran assemblages of Europe and Africa in order to find their similarities or differences and to establish their possible relationships. Because carnivores are not as strongly tied to specific environments as herbivores are (whose dental and skeletal morphology reflect the palaeoenvironmental conditions), adaptation to the new conditions does not require as many special changes in the teeth and skeleton as occur in herbivores. Thus, it is expected that the geographic regions will have quite similar carnivoran assemblages. Although the faunal data from Africa are limited and do not include the complete fossil record, the comparison may yield some interesting results nonetheless.

This work was presented in the Revealing Hominid Origins Initiative (RHOI) workshop: Carnivores of Africa from the Middle Miocene to the Pleistocene: new data, systematics, evolution and biogeography, held in the University of Poitiers (France) on 20–23 May 2008.

2. Methods

The Middle Miocene fossil records from both Europe and Africa are not very rich. In Europe the record mainly originates from western and central Europe and is quite poor in eastern and southeastern Europe. In Africa it is also poor, and originates mainly from Eastern Africa. The Late Miocene carnivoran assemblages of Europe used in this study are based on several primary sources [2,6–8,12,21–24] and the NOW (2008) database. The data for Greece [21] have been updated with some new additions by one of us (G. D. K.). Those of African carnivores were taken both from the literature [1,4,11,17,18,20,25,29,30,31,33,35,37,38] supplemented with data of one of us (L. de B.).

All lists have been updated according to the most recent systematics in order to maintain the greatest possible homogeneity in the literature. The term “Middle Miocene assemblage” includes all the carnivoran taxa from the beginning of Langhian to the end of Astaracian; more precisely all the Carnivora from 16.5 Ma to 11.2 Ma [39]. Under the term “Late Miocene carnivoran assemblages” we include all the carnivoran faunas dated from the Vallesian to the end of the Turolian; more precisely, carnivoran taxa that lived from 11.2 to 5.3 Ma. The Middle Miocene data from Europe do not allow separation into subregions as the resulting lists are not comparable to each other. Thus, they are included as a single list under the name “Middle Miocene assemblage”. For a more detailed comparison, the Late Miocene European carnivores are divided into four subregions:

- western Europe (Portugal, Spain, France, Switzerland);
- central Europe (Austria, Italy, Czech Republic, Germany, Poland, Slovakia, Hungary);
- southeastern Europe (Romania, Bulgaria, Serbia, FYROM, Greece);
- eastern Europe (Moldova, Ukraine).

Although the Turolian (7.0–5.0 Ma) carnivoran faunas of Africa can be divided in two groups: one including the Toros-Menalla and Sahabi faunas (Chado-Libyan province) and the other the eastern and southern African faunas (Werdelin, this volume), to maximize taxonomic diversity, Africa is here considered one geographic region for both Middle and Late Miocene carnivoran faunas and is not divided into subregions. It is worth mentioning that the Late Miocene African faunal record comes mainly from eastern Africa, while few records are known from western and northern Africa.

The carnivoran assemblage for each subregion has been calculated using the faunal lists of all localities of each subregion. If a family is referred to in the faunal lists as "indet.," it is not included in the calculation of the families. If it is referred as "cf.," "aff." or with question mark, it is included in the calculation if the certain family is not included in the lists. Genera referred as "cf.," "aff." or with question mark are included in the calculation of the genera number if they are not certainly referred in the faunal lists. The same rule is also applied in the case of a species referred as "cf.," "aff." or with question mark.

The comparison of the Euro-African carnivoran assemblages was based on the faunal composition, faunal diversity and faunal similarity. The faunal composition was analyzed at the family level using the number of species per family and presented by pie-diagrams, giving their abundance per family. The same technique was done using number of genera per family, but this does not give very different results and thus is not included in this article. The carnivoran diversity was calculated using the number of species or genera per family with bar-diagram comparisons of the number of taxa. The faunal similarity was analyzed both at the generic and specific levels by Correspondence Factor and Cluster Analysis which can match the similar assemblages and also give their rate of similarity. The analysis and comparison of the carnivoran assemblages is made using MS Excel® for the pie- and bar-diagrams. The software PAST [16] is used for the comparisons by Correspondence Factor Analysis and Cluster Analysis. The comparison is given first for the whole Middle and Late Miocene carnivoran assemblages of each geographic region as well as between them. Then, the same comparison is given for the Turolian assemblages separately in order to check if there are changes during Late Miocene and to confirm the earlier comparisons. Unfortunately, the Vallesian carnivoran fossil record of Africa is very poor [40,41] and thus it is not compared with the European sample.

The study is principally based on large carnivores insofar as the small ones are quite rare in most of the localities except in some special sites, like Sansan (France) or Rudabanya (Hungary).

3. Middle Miocene Assemblages

The faunal composition of the Middle Miocene carnivoran assemblages based on the taxonomy (number of species per family) indicates that they are different (Fig. 1). The number of families is larger in MEU than in MAFR (ten families versus seven). The MEU assemblage differs from MAFR in the presence of the ursids, percrocutids, herpestids and barbourofelids, as well as the abundance of the amphicyonids. On the other hand, the MAFR assemblage differs from MEU in the presence of the stenoplesictids, the dominance of the mustelids and the higher abundance of the ailurids (Fig. 1).

The faunal diversity (number of species or genera per family) is given in the bar-diagrams of Fig. 2. It is quite clear from these diagrams that the carnivoran diversity is higher in the MEU assemblage both at generic and specific level. Although the hyaenids have similar

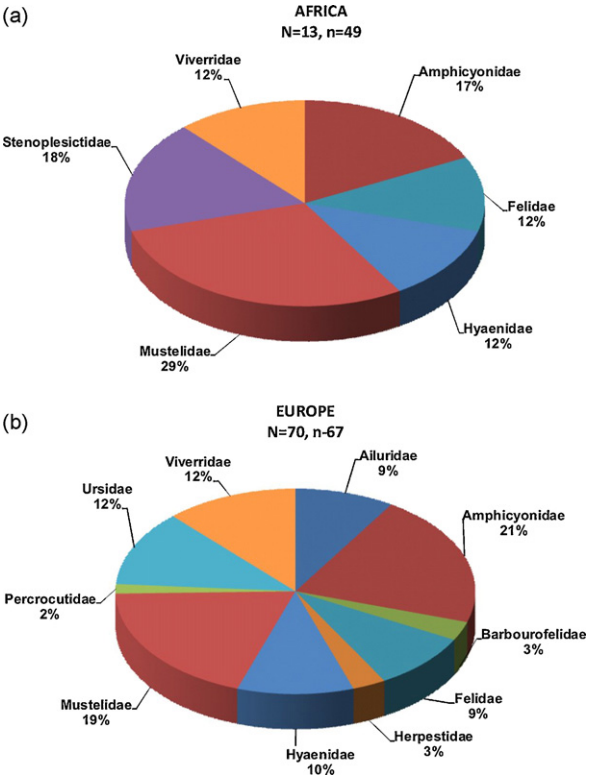

Fig. 1. Taxonomic composition (number of species per family) of the Middle Miocene carnivoran assemblages of (a) Europe and (b) Africa.
Fig. 1. Composition taxonomique (nombre d'espèces par famille) des faunes de carnivores du Miocène moyen (a) d'Europe et (b) d'Afrique.

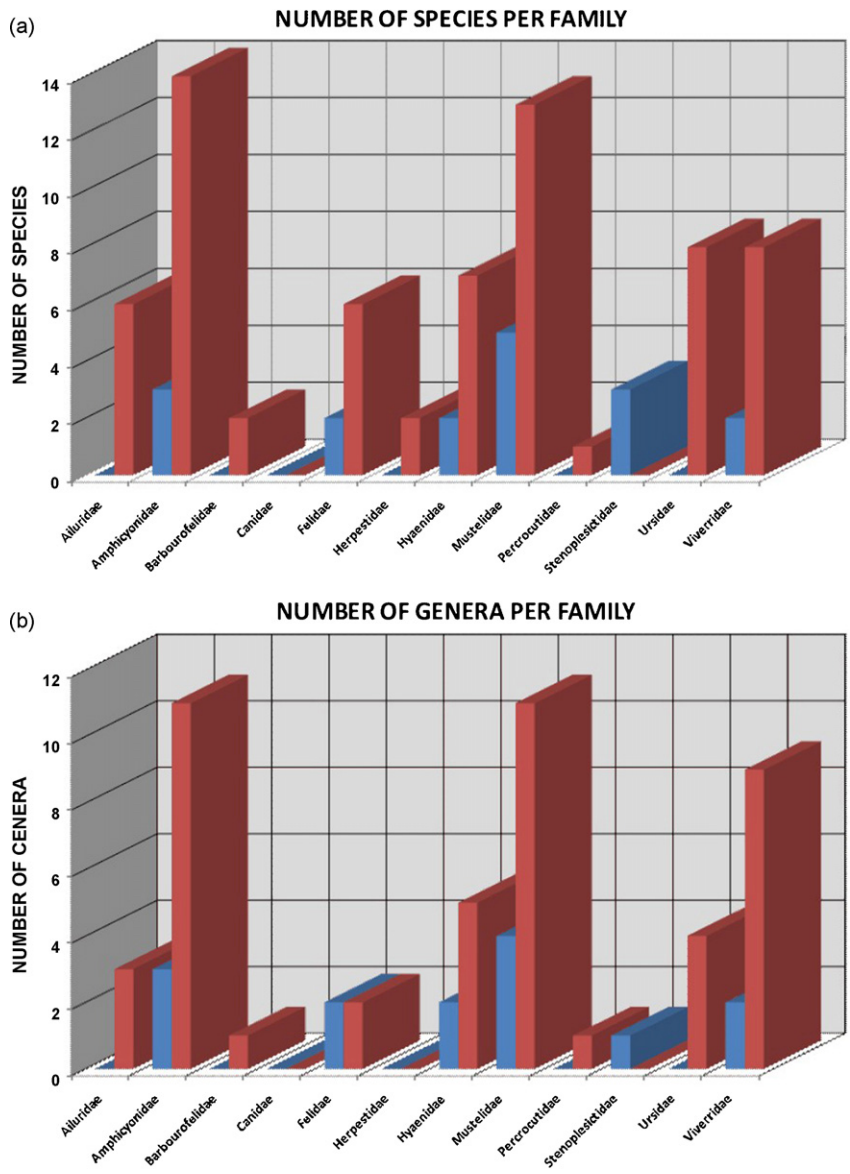

Fig. 2. Comparison of the African and European Middle Miocene carnivoran assemblages; (a) number of species per family and (b) number of genera per family.( )=MAFR, ( )=MEU.
Fig. 2. Comparaison des faunes de carnivores du Miocène moyen d'Afrique et d'Europe ; (a) nombre d'espèces par famille et (b) nombre de genres par famille. ( )=MAFR, ( )=MEU.

percentages in the faunal composition (Fig. 1) of both regions, they are more diversified in the MEU assemblage (Fig. 2); in MAFR there are two genera and two species versus seven and five in MEU, respectively. The mustelids dominate in the MAFR assemblage but the number of species (six) and genera (four) is smaller than those found in the MEU assemblage (13 species and 11 genera), indicating higher carnivoran diversity in the latter guild (Fig. 2).

The faunal composition and diversity of the Euro-African carnivoran assemblages indicates some similarities between geographic and temporal groups at the family level. However, it is necessary to check the relationships at lower taxonomic levels (generic or specific). Thus, the various assemblages are compared by multivariate and cluster analysis based on the presence/absence of the carnivoran lower taxa (genera or species).

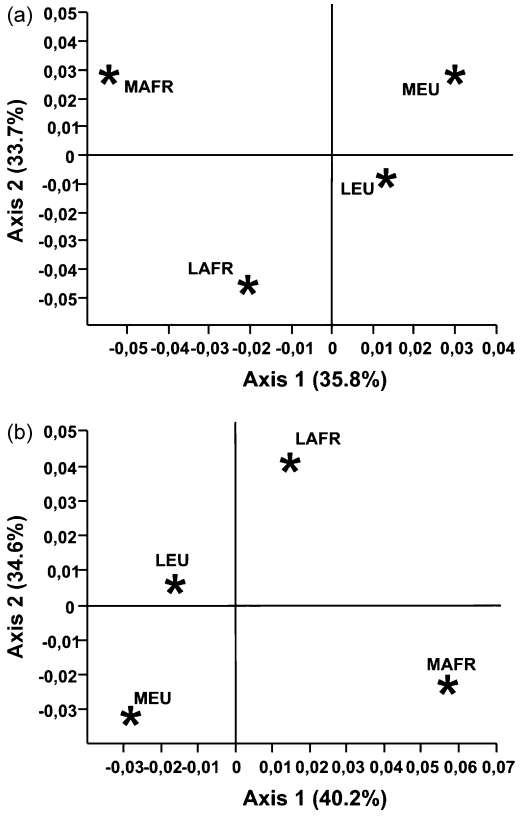

Fig. 3. Correspondence Factor Analysis (CFA) of the Middle and Late Miocene carnivoran assemblages of Africa and Europe at the specific (a) and, generic (b) levels.
Fig. 3. Analyses factorielles des correspondances (CFA) des faunes de carnivores du Miocène moyen et supérieur d'Afrique et d'Europe, aux niveaux spécifique (a) et générique (b).

The comparisons at specific and generic level (presence/absence matrix for 195 species and 107 genera respectively) of the various Middle and Late Miocene carnivoran assemblages have been analyzed by Correspondence Factor Analysis. The separation of the Middle and Late Miocene assemblages by axis-2 is quite clear at specific and generic level indicating that their taxonomic similarity is different (Fig. 3). The distinction of the African and European carnivoran assemblages is also quite clear by axis-1 both at specific and generic level (Fig. 3). Thus, the four different European assemblages are distinguishable from each other. The diagrams indicate that:

- although there were possible migrations between the two continents, the differences observed in the MAFR and MEU composition continue to exist in the Late Miocene (Fig. 3);
- the MEU and LEU assemblages are more similar each other than to those of MAFR and LAFR, indicating higher taxonomic similarity between MEU and LEU assemblages than those between MAFR and LAFR.

The same set of data is analyzed by Cluster Analysis at both the specific and generic levels using Jaccard's similarity index (Fig. 4). The clustering at the specific level separates two main clusters. The Cluster-A is distinguished in two subclusters, A1 and A2, including LAFR and LEU + MEU, respectively. The similarity between the Middle and Late Miocene carnivoran assemblages of Europe is ∼10% (Fig. 4a). The LAFR assemblage seems to be more similar to MEU than to MAFR, having a similarity of ∼5% with A2. The Cluster-B includes only MAFR and its similarity to LAFR is ∼2% (Fig. 4a). Similar clustering is taken at the generic level (Fig. 4b), but the similarity between the clusters and subclusters is higher. The MAFR has a similarity of ∼7% with LAFR, which has a similarity of ∼15% with MEU and LEU; both values are higher than those at specific level. The Cluster Analysis suggests that the Middle Miocene carnivores from both continents are quite different at specific level (the similarity ranges from 2–10%), while at generic level they are more similar (the similarity varies from 7–25%).

4. Late Miocene Assemblages

The faunal composition of the various Late Miocene carnivoran assemblages of Africa and Europe is given in Fig. 5. The LAFR assemblage is dominated by the mustelids (30%), hyaenas (24%), (the term hyaenas is used to express the sum of the hyaenids and percrocutids), and felids (14%), while the presence of herpestids distinguish it from the European ones (Fig. 5a). Herpestids are present in MEU (Fig. 1) but then disappeared in the Late Miocene European faunas, while they continue to exist in Africa. The LWEU and LCEU assemblages have similar carnivoran composition with abundant felids, hyaenids, mustelids and ursids. In this respect, the LAFR assemblage is closer to the LWEU and LCEU ones having more or less similar family composition (Fig. 5a–c). If we exclude the herpestids, the presence of the barbourofelids in LWEU and the decreased number of the felids, ursids and hyaenids are the small differences between these European carnivoran assemblages and LAFR. The LSEU and LEEU carnivoran assemblages are quite similar in their faunal composition which is characterized by the dominance of the hyaenas, felids and mustelids which represent 81–93% of the total carnivoran fauna. In this respect, the LSEU and LEEU assemblages differ clearly from LAFR, as well as from LWEU and LCEU (Fig. 5). Moreover, the

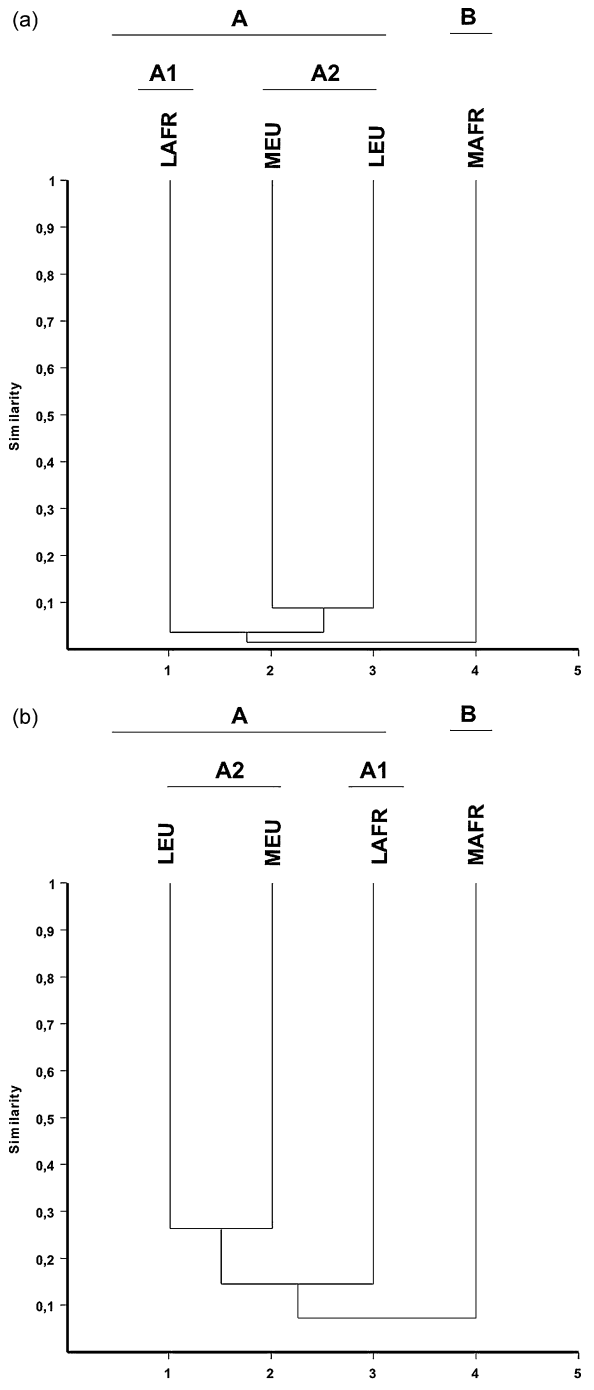

Fig. 4. Cluster Analysis of the Middle and Late Miocene carnivoran assemblages of Africa and Europe at the specific (a) and, generic (b) levels.

Fig. 4. Analyses de cluster des faunes de carnivores du Miocène moyen et supérieur d'Afrique et d'Europe, aux niveaux spécifique (a) et générique (b).

LSEU and LEEU assemblages are different from those of western and central Europe in their absence of the amphicyonids and canids (Fig. 5b–e). Thus, the LSEU and LEEU assemblages are distinguished from those of LWEU and LCEU, indicating the presence of two different carnivoran faunas in Europe, a "western" and an "eastern" one. The "eastern fauna" is characterized by the abundance of the hyaenas (40–50%), the absence of the canids and amphicyonids as well as a smaller number of ursids. The "western fauna" has fewer hyaenas (∼25%), more ursids, and rare, though present, amphicyonids and canids. Although the taxonomic abundance of the various families in LAFR is similar to that of the LWEU and LCEU (Fig. 5), it is clear that the carnivoran diversity is higher in the European assemblages. For example, the mustelids consist of 30% of the carnivoran fauna in LAFR and 18 and 23% in LWEU and LCEU assemblages respectively (Fig. 5), and the number of taxa in these assemblages is more or less similar at the specific level to the African one but less so at the generic level in TAFR (Fig. 6). Although other families (Hyaenidae, Felidae) have similar abundances (e.g. 16–25% hyaenids), they display remarkably higher diversity in the European assemblages (19–20 species in LWEU and LCEU versus eight in LAFR). On the contrary, the viverrids are more diversified in the LAFR assemblage than in the European ones, but even in this case the difference in the number of taxa is very small.

The Correspondence Factor Analysis (CFA) of the Late Miocene carnivoran assemblages based on a presence/absence matrix of 135 species and 60 genera from Europe and Africa indicates that the LAFR assemblage is clearly separated from the European ones by axis 1 (Fig. 7). This distinction suggests that the LAFR assemblage is composed of different genera and species than the European ones. Concerning the European assemblages, the axis-2 clearly distinguishes the LSEU and LEEU assemblages from LCEU and LWEU ones at specific level (Fig. 7a). The comparison at the generic level indicates that the LCEU, LEEU and LSEU assemblages group together and are separated from LWEU one (Fig. 7b). However, the distinction of the Late Miocene carnivoran assemblages of Europe at the specific level indicates a separation into two major groups with different composition. These groups correspond to a "western" (LWEU + LCEU) and an "eastern" (LSEU + LEEU) fauna confirming the above mentioned similar conclusion resulting from the comparison of the faunal composition (Fig. 5). At the generic level, only LWEU is separated from the three other European sets.

The same carnivoran set of data is analyzed by Cluster Analysis, using the Jaccard's similarity index. The

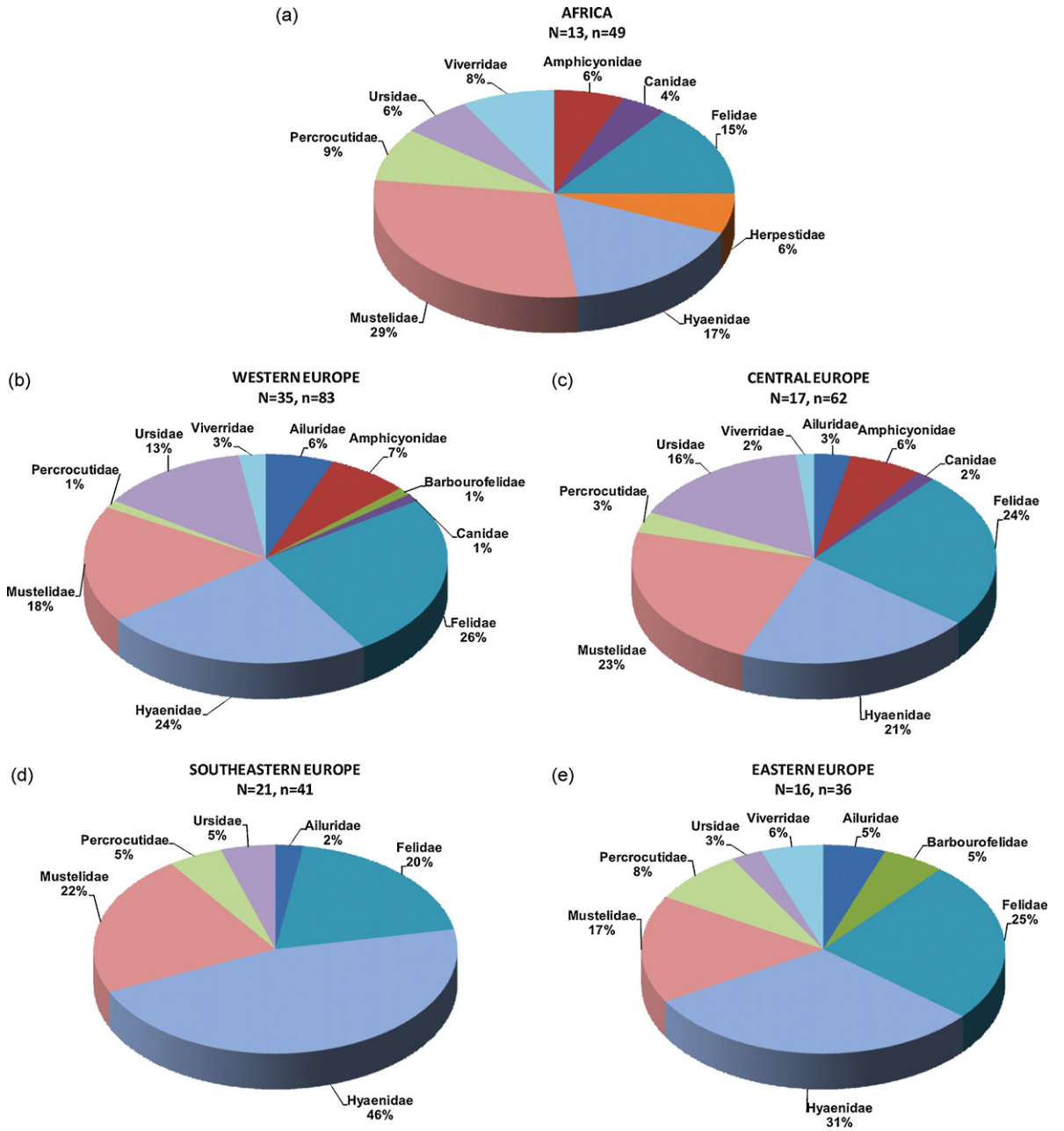

Fig. 5. Taxonomic composition (number of species per family) of the Late Miocene carnivoran assemblages of Europe and Africa.
Fig. 5. Composition taxonomique (nombre d'espèces par famille) des faunes de carnivores du Miocène supérieur d'Afrique et d'Europe.

dendrogram resulting from the clustering of similarities at the specific level (Fig. 8a) is divided in two clusters. The Cluster-A includes the LAFR assemblage which has a low similarity with the European ones (∼5%). The Cluster-B is divided in two subclusters, B1 and B2 including LSEU + LEEU and LWEU + LEEU assemblages, respectively (Fig. 8a). The similarity between the two subclusters is ∼25%. The clustering at the generic level suggests the presence of three clusters. Cluster-A includes only the LAFR assemblage which is clearly separated from the European ones. However, the similarity between them is ∼18%, larger than that at specific level (Fig. 8b), indicating that the LAFR assemblage has more genera than species in common with the European ones. Cluster-B is divided into three subclusters. B1 includes the LCEU and LEEU assemblages which have high similarity (∼60%). B2 includes the LSEU assemblage having a similarity of ∼45% with B1 and

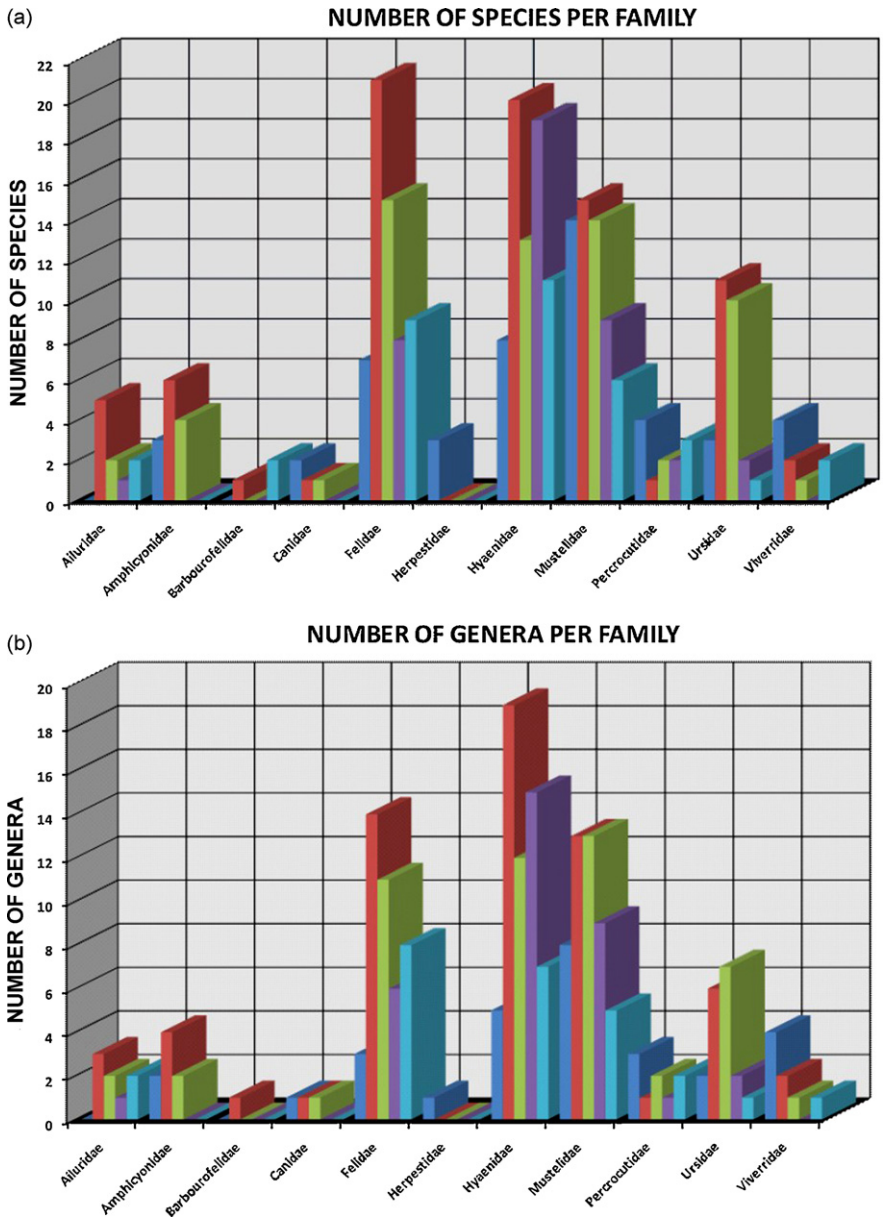

Fig. 6. Comparison of the African and European Late Miocene carnivoran assemblages; (a) number of species per family and, (b) number of genera per family. (■)=LAFR, (■)=LWEU, (■)=LCEU, (■)=LSEU, (■)=LEEU.

Fig. 6. Comparaison des faunes de carnivores du Miocène supérieur d'Afrique et d'Europe ; (a) nombre d'espèces par famille et (b) nombre de genres par famille. (■)=LAFR, (■)=LWEU, (■)=LCEU, (■)=LSEU, (■)=LEEU.

B3 LWEU assemblage having a similarity of ∼ 40% with B2.

Keeping in mind the above-mentioned comparisons, the LAFR assemblage is different than the European ones; its similarity to the European ones at the generic level is higher than that at specific level. However, its faunal composition is closer to LWEU and LCEU. Its faunal diversity is lower than that of the European carnivoran assemblages. The European carnivoran assemblages of the Late Miocene can be divided in two faunas an "eastern" one dominated by hyaenas and a "western" one with fewer hyaenas, more mustelids and ursids, as well as some amphicyonids.

5. Turolian carnivoran assemblages

The faunal composition of the Turolian carnivoran assemblages of Europe and Africa based on the number

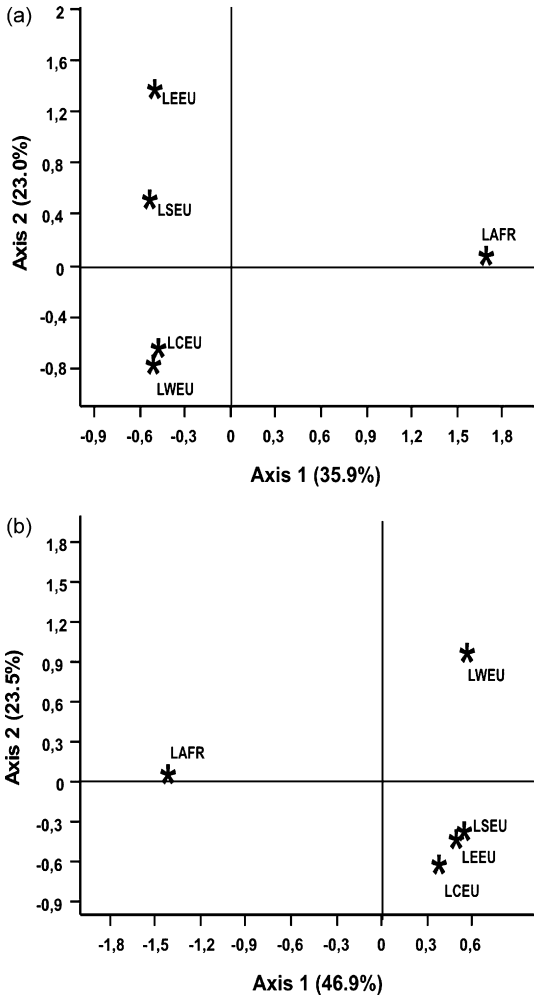

Fig. 7. Correspondence Factor Analysis (CFA) of the Late Miocene carnivoran assemblages of Africa and Europe at the specific (a) and, generic (b) levels.

Fig. 7. Analyses factorielles des correspondances (CFA) des faunes de carnivores du Miocène supérieur d'Afrique et d'Europe aux niveaux spécifique (a) et générique (b).

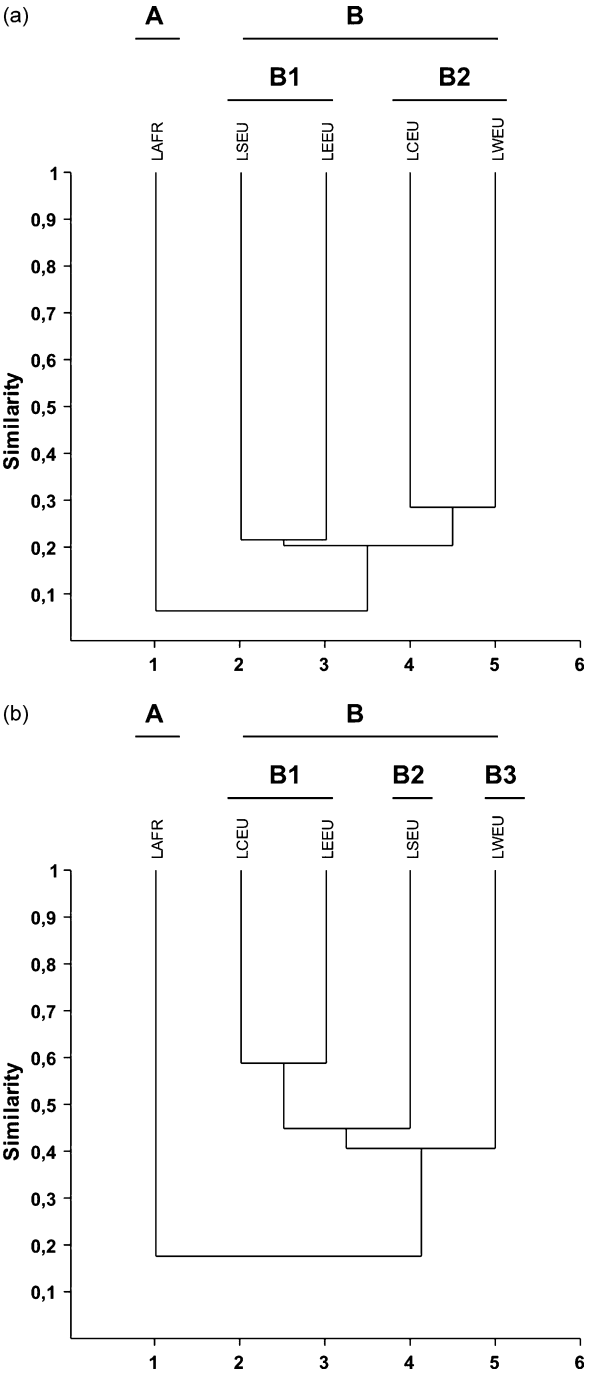

Fig. 8. Cluster Analysis of the Late Miocene carnivoran assemblages of Africa and Europe at the specific (a) and, generic (b) levels.

Fig. 8. Analyses de cluster des faunes de carnivores du Miocène supérieur d'Afrique et d'Europe aux niveaux spécifique (a) et générique (b).

of species per family is given in Fig. 9. The TAFR assemblage is richer in families than the European ones; it has nine families versus a maximum of seven in the European assemblages. It differs from the European assemblages in the presence of the herpestids, viverrids and amphicyonids, the dominance of the mustelids, and the relatively few hyaenas (Fig. 9a). The Turolian European carnivoran assemblages have fewer families than TAFR and include mainly hyaenas, felids and mustelids (Fig. 9b and c) providing a different taxonomic composition than TAFR. If we exclude the families of TAFR which are absent in Europe, then its taxonomic composition is closer to that of the TWEU and TCEU assemblages. Comparing the

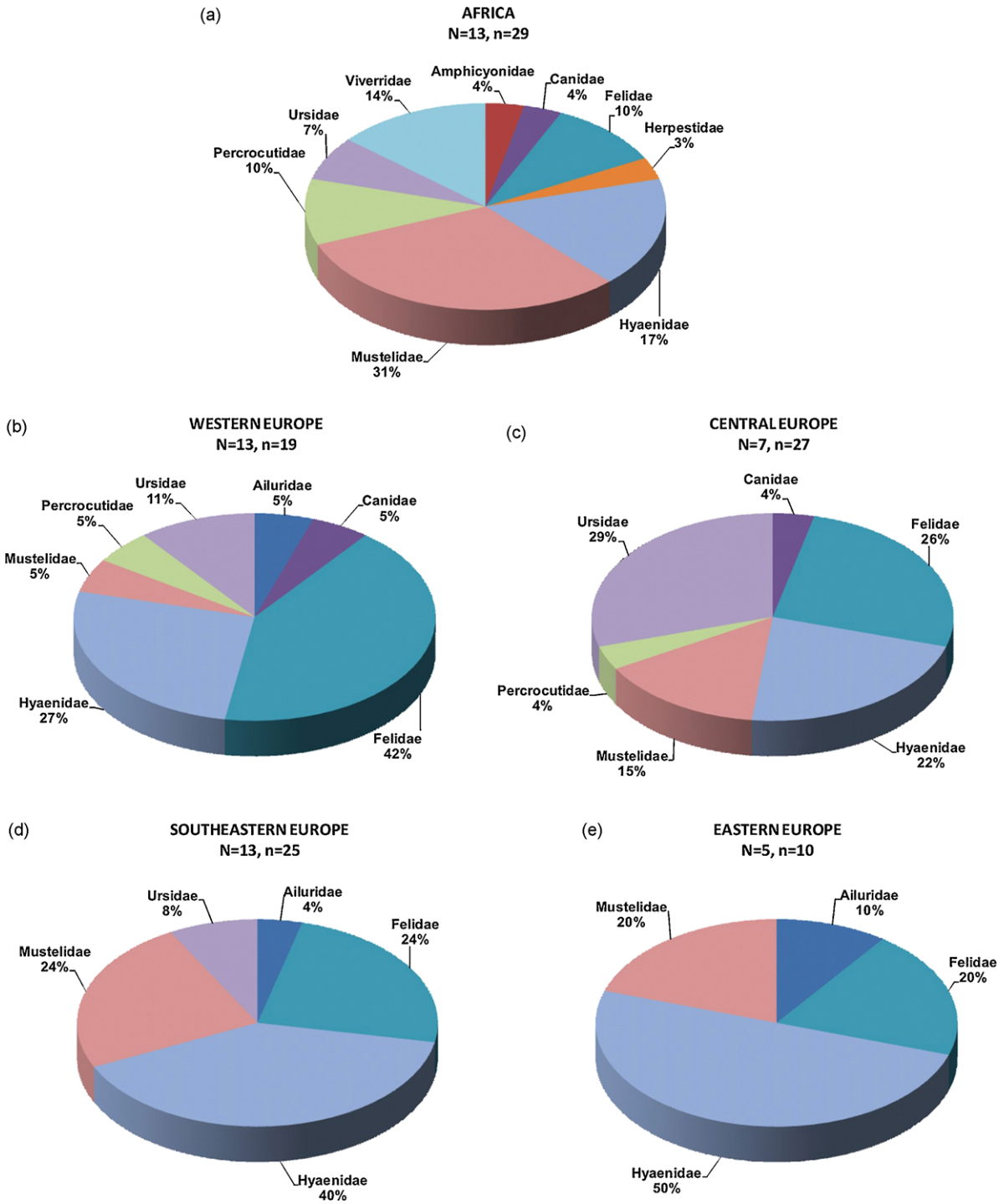

Fig. 9. Taxonomic composition (number of species per family) of the Turolian carnivoran assemblages of Africa and Europe.
Fig. 9. Composition taxonomique (nombre d'espèces par famille) des faunes de carnivores du Turolien d'Afrique et d'Europe.

TWEU and TCEU assemblages to those of the TSEU and TEEU, the former ones are separated by the presence of the percrocutids and canids as well as the more felids and ursids (Fig. 9). Based on these differences and mainly the high abundance of the hyaenas, the Turolian European carnivoran assemblages can be divided in two faunas the "eastern fauna" (40–50% hyaenas) and the "western fauna" (25–30% hyaenas).

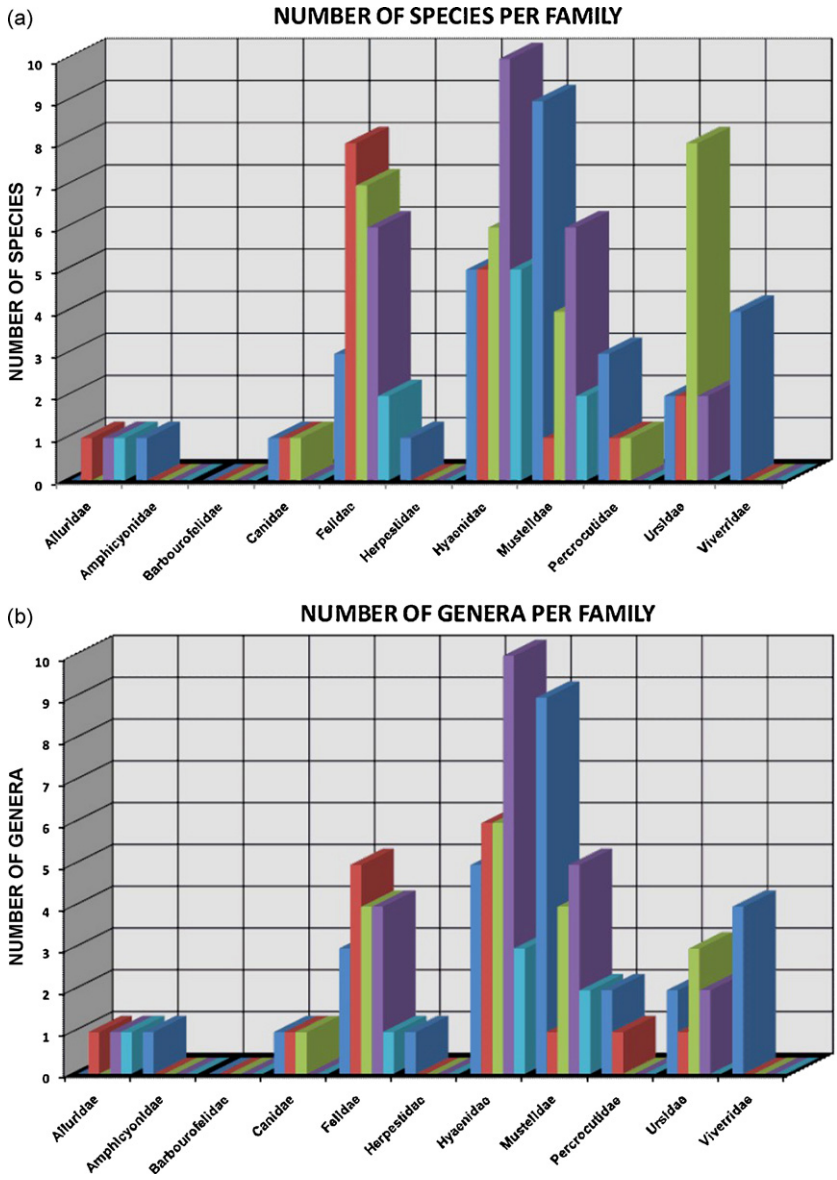

Fig. 10. Comparison of the Euro-African Turolian carnivoran assemblages; (a) number of species per family, and (b) number of genera per family. ( )=TAFR, ( )= TWEU, ( )=TCEU, ( )=TSEU, ( )=TEEU

Fig. 10. Comparaison des faunes de carnivores du Turolien d'Afrique et d'Europe ; (a) nombre d'espèces par famille et (b) nombre de genres par famille. ( )=TAFR, ( )= TWEU, ( )=TCEU, ( )=TSEU, ( )=TEEU.

The faunal diversity of the Euro-African Turolian assemblages (Fig. 10) indicates that it is fairly similar at both the specific and generic levels. The TAFR assemblage seems to be less diversified than the European ones. The mustelids in TAFR are more diversified than in the European Turolian assemblages (nine taxa versus one to six); but it is worth mentioning that the majority of those in the TAFR assemblage are lutrines. The faunal diversity of the Turolian carnivoran assemblages seems to be more homogeneous than that of the Middle and Late Miocene. If this is not due to issues of taxonomy, then we can consider a more diversified fauna at the end of Miocene.

The Correspondence Factor Analysis analyzed the presence/absence of a matrix of 86 species and 58 genera. The TAFR assemblage is clearly separated from the European ones at both the specific and generic levels by axis-1, indicating different generic and specific composition (Fig. 11). The European assemblages are separated into two groups at the specific level by axis-2. One group

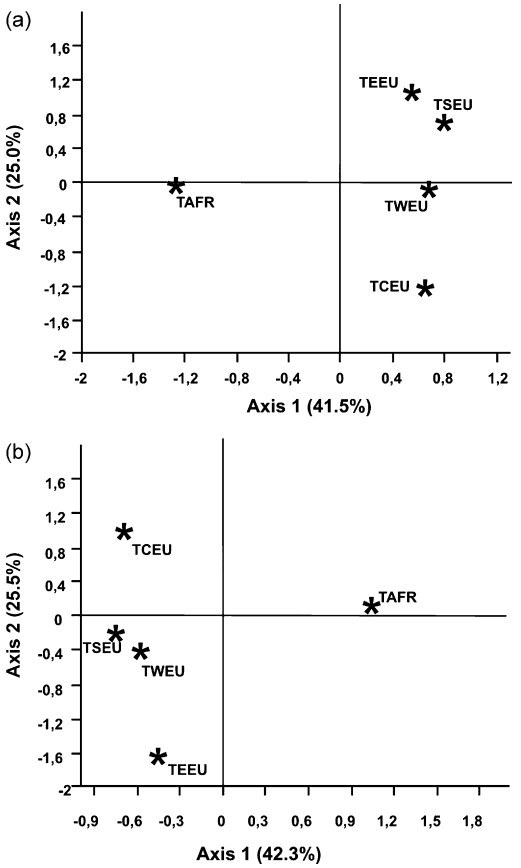

Fig. 11. Correspondence Factor Analysis (CFA) of the Turolian carnivoran assemblages of Africa and Europe at the specific (a) and, generic (b) levels.
Fig. 11. Analyses factorielles des correspondances (CFA) des faunes de carnivores du Turolien d'Afrique et d'Europe aux niveaux spécifique (a) et générique (b).

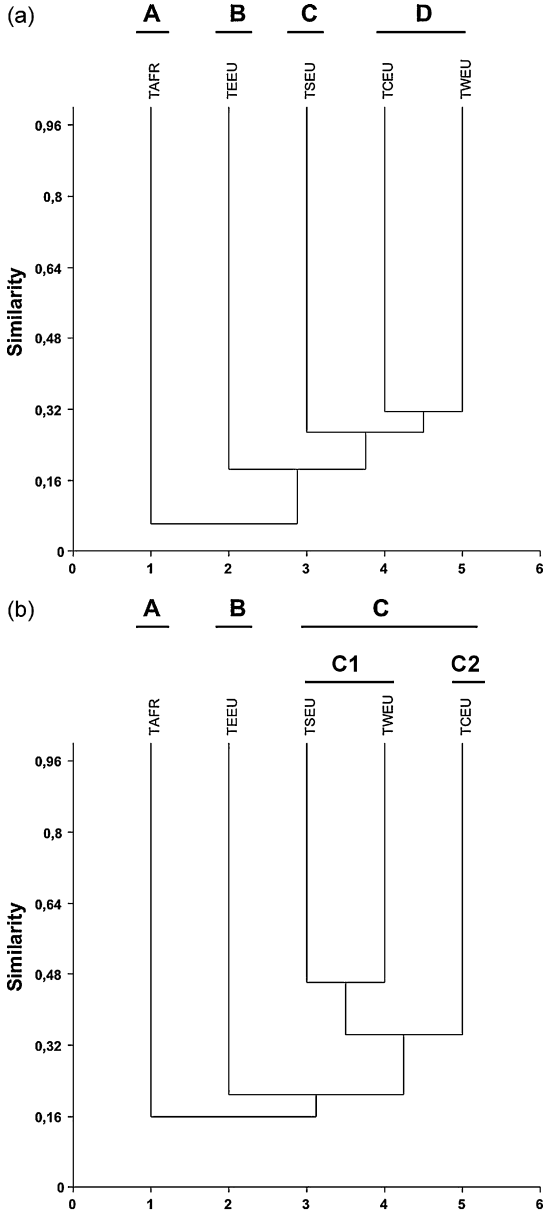

Fig. 12. Cluster Analysis of the Turolian carnivoran assemblages of Africa and Europe at the specific (a) and, generic (b) levels.
Fig. 12. Analyses de cluster des faunes de carnivores du Turolien d'Afrique et d'Europe aux niveaux spécifique (a) et générique (b).

includes the TEEU and TSEU assemblages and the other the TCEU and TWEU ones (Fig. 11a) confirming the separation of the European carnivoran assemblages in two faunas, an "eastern" and "western" one, as are mentioned above. At the generic level there are two groups too, the first one includes the TSEU, TEEU and TWEU assemblages, while the second one only includes the TCEU assemblage (Fig. 11b).

The Cluster Analysis of the same set of taxa using Jaccard's similarity index gives the dendrograms of Fig. 12. At the specific level there are four main clusters (Fig. 12a). Cluster-A includes the TAFR assemblage which is clearly distinguished from the European ones, having a similarity of ∼5% with them. Cluster-B includes the TEEU assemblage and Cluster-C is comprised of TSEU; these two clusters have a similarity of ∼20%. Cluster-D includes the TCEU and TWEU assemblages having a similarity of 25% with Cluster-C. The clustering at the generic level suggests the distinction of three main clusters (Fig. 12b). Cluster-A includes the TAFR assemblage and has a similarity of ∼15% with the European ones. Cluster-B includes the TEEU assemblage having a similarity of ∼22% with Cluster-C. Two subclusters can be distinguished in Cluster-C: C1 includes the TSEU and TWEU assemblages and C2 the TCEU one; their similarity is 35% (Fig. 12b).

The analysis of the Turolian carnivoran assemblages of Africa and Europe indicates that the TAFR assemblage is well separated from the European ones at both the generic and specific levels. Although the family composition is similar, the presence of the amphicyonids, herpestids and viverrids distinguishes the TAFR assemblage from the European ones. The similarity of TAFR with the European assemblages is higher at the generic and much smaller at the specific levels.

6. Discussion

The comparison of the Euro-African Miocene faunas gives interesting information about their relationships. The Middle Miocene carnivoran assemblages from both continents seem to be quite different; the similarity between them is less than 5% at both the generic and specific levels and this dissimilarity is due to the palaeoenvironment, palaeogeography or evolutionary history. The difference is less expressed in the family composition but it is very clear at the specific and generic levels. During the Middle Miocene in the wider Mediterranean Region, the palaeoenvironment was closed with evergreen tropical/subtropical forests [2] and cannot explain the difference between MEU and MAFR. The fact that the fossil records from both areas are quite poor, especially in Africa, is not a reliable explanation for this difference; if there were common taxa some of them would be found even in the few known localities from both regions. A possible explanation can be given by the palaeogeography. The communication of Africa and Eurasia was not possible until the upper part of the Early Miocene because the Mediterranean was connected with the Indo-Pacific Ocean through the Indo-Pacific Seaway (across the Middle East). During the end of the Early Miocene, Africa and Eurasia were connected by the "*Gomphotherium*-landbridge," allowing the migration of mammals [36]. The first immigrants from Africa were the proboscideans (gomphotheres and deinotheres) which arrived in Eurasia at ∼18.0–19.0 Ma. The presence of *Prodeinotherium bavaricum*, found in the Greek island of Lesvos with an age greater than 18.5 Ma is a strong evidence for this migration wave [24]. The establishment of the "*Gomphotherium*-landbridge" was not continuous and was broken and restored several times; thus, several migration waves and faunal exchanges between Eurasia and Africa and vice versa took place during Middle Miocene [36]. The taxonomic comparison of the carnivoran assemblages indicates that the carnivores did not follow these migrations rapidly but remained in their biotopes; very few taxa migrated, providing a small similarity between the MAFR and MEU assemblages, less than 5% (Fig. 4). There are only three common genera between the Middle Miocene carnivoran assemblages of Africa and Europe, including *Amphicyon*, *Agnotherium* and *Ictitherium*, and none is represented by common species. The comparison of the Euro-African Middle and Late Miocene assemblages indicates that the LAFR assemblage has more similarities to MEU and LEU than to MAFR (Figs. 3 and 4). Although the similarity is small at the generic level (∼15%), it means that the majority of the LAFR carnivoran genera possibly originated from the Middle Miocene European carnivoran assemblage (European immigrants). There are six common genera between LAFR and MEU, including the taxa *Agnotherium*, *Ictitherium*, *Indarctos*, *Herpestes*, *Percrocuta* and *Viverra*, and three between LAFR and MAFR (*Agnotherium*, *Ictitherium*, *Vishnuonyx*).

The analysis of the various Euro-African Late Miocene carnivoran assemblages by various methods indicates that:

- the African carnivoran assemblages are different from the European ones;
- their similarity is higher at the generic than at specific levels. This means that the immigrants from both continents rapidly evolved and adapted to the local conditions giving rise to new taxa. However, there are taxa, like *Adcrocuta eximia*, which are widespread in Eurasia during Late Miocene but present in Africa only in the Latest Turolian locality of Sahabi (Libya);
- the LAFR assemblage seems to be more similar to those of western and central Europe ("western fauna").

There are 16 common genera between LAFR and LEU assemblages including the following taxa: *Adcrocuta*, *Agnotherium*, *Agriotherium*, *Chasmaporthetes*, *Dinocrocuta*, *Eomellivora*, *Eucyon*, *Hyaenictis*, *Hyaenictitherium*, *Ictitherium*, *Indarctos*, *Machairodus*, *Mellivora*, *Metailurus*, *Plesiogulo* and *Simocyon*. However, there are only a few common species: *Adcrocuta eximia*, *Agnotherium antiquum*, *Hyaenictitherium parvum* (?), *Indarctos arctoides* (?), *Indarctos atticus*, *Machairodus aphanistus* (?), *Metailurus major* and *Plesiogulo monspessulanus*; the taxa with question mark are not certainly present in the LAFR assemblage. These data confirm the above-mentioned result but also indicate migration between Africa and Europe and vice versa. According to [37] the communication between the two continents was continuous during the Late Miocene, after the desiccation of the Indo-Pacific Seaway and thus the migration paths were open.

The European Late Miocene carnivoran assemblages constitute two faunas: a "western" (LWEU + LCEU) and an "eastern" (LSEU + LEEU) one. The distinction is mainly based on the high abundance of the hyaenas in the "eastern" fauna and it is possibly due to different palaeoenvironments. In western and central Europe the palaeoenvironment was more closed and humid during Vallesian, while in eastern Mediterranean it was open and relatively arid. Later, in the Turolian, the conditions became more homogeneous in all of Europe which became more open and dry [8,6,19,20]. The open environment of eastern Mediterranean favored the development of the hyaenas, as these animals were probably living in open areas, like the recent spotted hyaenas of Africa which live mainly in the open areas of Africa. This supports the high abundance of the hyaenas in the "eastern" fauna where the open-dry conditions existed since the beginning of Vallesian. During the Turolian, as the conditions became more similar throughout Europe, the hyaenas increased in western and central Europe (Fig. 9). Unfortunately, the Vallesian faunas of Africa are very poorly known and thus a comparison is impossible, but the TAFR assemblage seems to be quite similar to TWEU in the abundance of the hyaenas and could indicate similar conditions. Moreover, the otters are quite common in TAFR suggesting more wet conditions than in the Turolian of Europe. However, all these hypotheses need more faunal data from Africa and more analyses to be proved.

7. Conclusions

Comparison of the Middle Miocene faunas of Africa and Europe suggest the following:

- the Middle Miocene carnivoran assemblages from both continents seem to be quite different; the similarity between them is less than 5% at both the generic and specific levels;
- the difference is less expressed in family composition but it is very clear at the specific and generic levels;
- the faunal diversity is higher in the European carnivoran assemblage than in the African Middle Miocene one;
- the African Late Miocene carnivoran assemblage is more similar to the Middle and Late Miocene one of Europe than to the Middle Miocene of Africa. There are six common genera between LAFR and MEU, *Agnotherium*, *Ictitherium*, *Indarctos*, *Herpestes*, *Percrocuta* and *Viverra*, and only three between LAFR and MAFR (*Agnotherium*, *Ictitherium*, *Vishnuonyx*).

Although the Late Miocene fossil record of Africa is relatively poor compared to the European ones, the comparison of their carnivoran assemblages with various methods provides some interesting results:

- the faunal composition of the Late Miocene carnivoran assemblages of Africa differs from the European ones by a higher abundance of mustelids and few hyaenas. The presence of herpestids also distinguishes it from the European ones. It is more similar to the LWEU and LCEU assemblages. The family Ailuridae has never been recorded in Africa, the ancestry of the lesser panda seems to be holoactic;
- the faunal diversity of the Late Miocene European assemblages is higher than that of the African one;
- the LAFR is different from the European ones both at the generic and specific levels. Its similarity to the European ones is higher at the generic than at specific levels;
- the taxonomic composition of the TAFR is more diversified in its inclusion of more families. Although the amphicyonids disappeared in the Turolian of Europe, they still existed in Africa. The presence of the herpestids and the high abundance of the mustelids and viverrids distinguish the TAFR assemblage from the European ones;
- the taxonomic composition of the Late Miocene European assemblages indicates two carnivoran faunas: the "western" fauna, characterized by the high frequency of mustelids and ursids, as well as the presence of the amphicyonids. On the contrary, the "eastern" fauna is dominated by hyaenas (hyaenids + percrocutids) with a lot of felids and mustelids and few ursids.

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