

A spiny distribution: new data from Berg Aukas I (middle Miocene, Namibia) on the African dispersal of Erinaceidae (Eulipotyphla, Mammalia).

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Abstract : Material of Erinaceidae (Eulipotyphla, Mammalia) from Berg Aukas I (late middle Miocene, Namibia) is described. Originally identified as belonging to the gymnure *Galerix*, the specimens from Berg Aukas I are herein attributed to the hedgehog *Amphexinus* cf. *rusingensis*, and they represent the last known occurrence of *Amphexinus* in Africa. Its persistence in Northern Namibia may have been favoured by its generalist palaeoecology and the heterogeneous aridification of southern Africa during the middle Miocene. In addition, an update of the data acquired on African Erinaceidae is provided: a migration of the Galericinae to southern Africa is no longer supported; all attributions of African middle Miocene to Pliocene material to the genus *Galerix* are considered to be improbable; at least two migratory waves of *Schizogalerix* are recognized in northern Africa with *S.* cf. *anatolica* in the late middle Miocene (Pataniak 6, Morocco) and *S.* aff. *macedonica* in the late Miocene (Sidi Ounis, Tunisia).

Key Words : Erinaceidae, *Amphexinus*, Biogeography, Miocene, Africa.

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Introduction

While the family Erinaceidae (Eulipotyphla, Mammalia) is a frequent element of European and Asian Miocene faunas, little is known about the scarce African fossil record. Naturally, several factors have to be considered: the Palaeogene isolation of Africa, the highly heterogeneous distribution of known localities, the presence of already established insectivorous groups (e.g. Chrysochloridae, Tenrecidae) and the usual scarcity of Erinaceinae in small mammal deposits. Despite this, the suspected Miocene lineage *Gymnurechinus-Mellalechinus* suggests that Asian migrants evolved into better-adapted forms during their short stay in Africa.

The Otavi Mountains in Northern Namibia, yielded a rich quantity of fossiliferous cave breccias and fissure fillings with abundant remains of small mammals (Conroy *et al.* 1992; Senut *et al.* 1992; Rosina & Pickford, 2019; Peláez-Campomanes *et al.* 2020).

Unexpectedly, Eulipotyphla are poorly-represented. The only mentioned Erinaceidae is a specimen from Berg Aukas I (breccia block 63, extracted in 1991; middle Miocene) attributed to the well-known genus *Galerix*, whose subfamily had never previously been encountered in southern Africa. Another specimen, discovered in the breccia block 52 extracted in 1994, was considered to belong to the same species.

The occurrence of a Galericinae named *Galerix africanus* during the early Miocene of Eastern Africa (Butler, 1956, 1984) followed by the report of *Galerix* in Namibia (Conroy *et al.* 1992; Senut *et al.* 1992) led Butler (2010) to consider that *Galerix* may have dispersed throughout Africa. Since this genus already has a broad distribution in Europe and Asia (Van den Hoek Ostende, 2001), the first aim of the present note was to investigate the potential spread of *Galerix* in Africa.

Material and Methods

The material described here corresponds to two specimens extracted from breccias at the Namibian hominoid-bearing locality Berg

Aukas I (19°30'58"S, 18°15'10"E), during expeditions led in 1991 and 1994. The geological context was thoroughly described by

Pickford & Senut (2002, 2010), in which the oldest level of the palaeocave infilling at Berg Aukas I is estimated to date between 13 Ma and 12 Ma.

Engesser (1980) is followed for terminology and Prieto *et al.* (2010) for the measurement method of length (L), mesial width (W1) and distal width (W2). Measurements were obtained with a binocular LEICA

MZ16 A, a digital camera LEICA DFC420, two optical lights sources LEICA CLS 150X, and the programm Leica Application Suite (v. 4.5.0). Drawings were obtained with the software Autodesk SketchBook (v. 8.7.1). Specimens are figured in left orientation and housed at the National Earth Science Museum, Geological Survey of Namibia, Windhoek, Namibia.

Systematic Palaeontology

Order Eulipotyphla Waddell, Okada & Hasegawa, 1999

Family Erinaceidae Fischer, 1814

Subfamily Erinaceinae Fischer, 1814

Genus *Amphechinus* Aymard, 1850

Type species :- *Amphechinus arvernensis* (Blainville, 1839)

Species *Amphechinus* cf. *rusingensis* Butler, 1956

Partial synonymy :-

1992 *Galerix* sp. - Conroy *et al.*

1992 *Galerix* sp. - Senut *et al.*

Type locality :- Hiwegi Formation, locality R.1, Rusinga Island, Kenya; early Miocene.

Original diagnosis :- A species of *Amphechinus* that differs from *A. edwardsi* (Filhol) in the following characters: size smaller (C1/-M3/ inclusive: 13.2-13.5 mm); C1/ and P2/-p/2 less

Material and measurements :- BA 63'91, right P4/ (L=3.28, W1=2.68, W2=3.39); BA 52'94, right m/1 (L=3.12, W1=2.01, W2=2.01).

Description

The P4/ has a slightly S-shaped buccal margin because of a rounded parastyle and a curved and elongated metastyle. The paracone is a strong, upright cusp with a subtriangular base. From it starts a high and sharp metaloph reaching the pointed bucco-distal border. The metacone is distinguishable at the center of the crest only by a more worn aspect. A parastyle is attached to the mesio-buccal base of the paracone, without being connected to it by a crest. The distal border of the premolar is concave. The circular protocone is the tallest cusp of the lingual extension of the tooth. A thin

reduced; P2/ with two roots; buccal edge of M1/ slightly longer than that of P4/; M2/ slightly larger in proportion to M1/ (length M2/ - length M1/: 0.82) (Butler, 1956, p. 54).

Berg Aukas MM1, Otavi Mountains, Namibia; late middle Miocene (13-12 Ma) (Fig. 1).

bucco-lingual crest is present at the buccal base of this cusp. Another thin ridge is found between the protocone and the small rounded hypocone, which is situated more lingually. A barely distinguishable bulge is also present at the disto-lingual border of the premolar, from which starts a short mesial cingulum. This cingulum is stopped by a distinct notch situated lingually to the metaloph wall. Very narrow cingula are visible at the lingual and mesial base of the metaloph.

The trigonid of the first lower molar is slightly longer than the talonid. The paraconid

is the smallest cuspid of the trigonid. Mostly included in the paralophid, it is still distinguishable at the mesio-lingual corner of the tooth. The paralophid is a two-segmented crest connecting the paraconid to a triangular protoconid, the strongest cuspid of the molar. The metaconid has a circular base, smaller dimensions than the protoconid and is situated in a slightly more mesial position than the latter cuspid. Two thin ridges start from the median side of both cuspids, ending at the border of the trigonid distal wall without touching each other. The trigonid basin is open on its lingual side and is characterised by three valleys, the largest one having an almost bucco-lingual orientation. The

talonid is much lower than the trigonid. The subtriangular hypoconid is the smallest cuspid of the tooth. The smooth cristid obliqua is almost parallel to the lingual margin. The triangular entoconid is shorter than the paraconid. A weak hypolophid connects the two distal cuspids while a thin ridge joins the base of the entoconid to the base of the metaconid (there is no entocristid). This has led to a continuous closure of the deep and squared talonid basin. The postcingulid is large and connected to the entoconid without being in contact with the hypolophid. A narrow but continuous cingulid is present on the buccal margin.

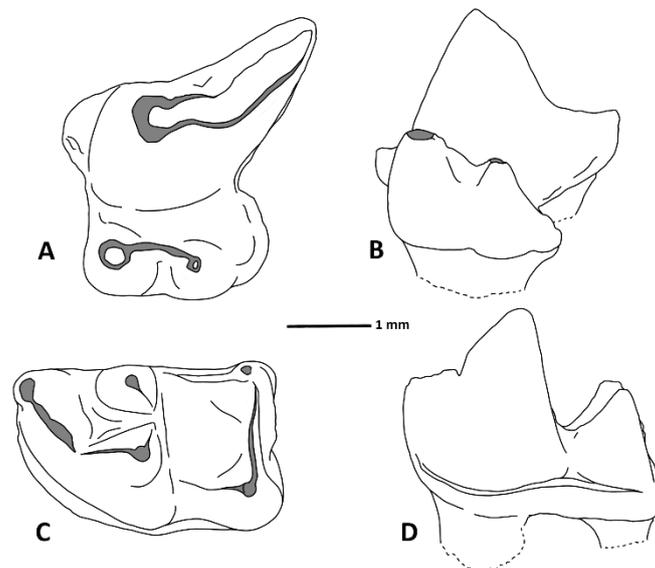


Figure 1. Interpretive line drawings of *Amphechinus* cf. *rusingensis* from Berg Aukas I. **A-B**) P4/ (BA 63'91, reversed). **C-D**) m/1 (BA 52'94, reversed). **A, C**) occlusal, **B**) lingual, **D**) buccal views (scale: 1mm).

Comparisons

While the species of Galericinae are known by their rounded and molarized P4/, the material from Berg Aukas I present a more angular shape with an elongated and sharp metaloph, which is the usual pattern found in Miocene Erinaceinae. A disto-lingual bulge is sometimes found in deciduous P4/ of Galericini (Ziegler, 1983), but the outline of this tooth is much more irregular than the described specimen. The distinctive notch present at the medio-distal margin (“anteroposteriorly compressed lingual region”, according to Butler, 1984:146) is usually found in *Amphechinus*, and is more pronounced than in the European *A. baudeloti*. This notch is not similar to the constriction of the lingual area observed in

Mellalechinus salis. There are no significant differences from the material of *A. rusingensis* from the Sperrgebiet (Mein & Pickford, 2008).

The two-segmented paralophid in m/1 is similar to that of Galericinae and *Amphechinus*, while *Gymnurechinus leakeyi* has a curved crest (Butler, 1984). The talonid of m/1 is lower and simpler than in Miocene Galericini. The postcingulid-entoconid connection is found in *Gymnurechinus*, *Mellalechinus* and *Amphechinus*, but also occurs in derived lineages of Galericini (Van den Hoek Ostende, 2001). The trigonid of the m/1 represents 58% of the total length of the tooth, while representing 60%-63% in *Amphechinus rusingensis* described by Butler

(1984). The first lower molar of *Mellalechinus salis* described by Lavocat (1961) is less compact, with a more stretched and open trigonid, as in *Gymnurechinus*. Moreover, the hypoconid of m/1 is situated in a more buccal position in *A. rusingensis* than in *M. salis*.

The dimensions of the two Berg Aukas specimens do not differ from the morphometric range of the early Miocene *Amphechinus rusingensis*. The size increase observed in the

material from Arrisdrift (Mein & Pickford, 2003) is not present in the sample from Berg Aukas. Because it is not possible to compare the Berg Aukas I material with the fossils of *Amphechinus* sp. from Fort Ternan, Kenya (13.7 Ma; Butler, 1984) and the lack of adequate diagnostic features, the two specimens from Namibia are attributed to a young form named *Amphechinus* cf. *rusingensis*.

Discussion

Palaeoecology of *Amphechinus*

The presence of *Amphechinus* at Berg Aukas I occurred at a time of global aridification. While environments were humid and forested during the early Miocene, the hyperarid Namib Desert emerged at the beginning of the middle Miocene (Pickford & Senut, 2002) which probably favoured the success of grazing mammals in southern Africa earlier than in the North-Eastern part of the continent (Pickford, 2008). The desertification of southern Africa was however heterogeneous and the Kalahari-Otavi area seems to have maintained more humid conditions (Senut *et al.* 2009; Rosina & Pickford, 2019), helping the preservation of less adapted forms during the middle Miocene.

A clear evolutionary history of *Amphechinus* is difficult to establish since the generic attribution of several species cannot be fully supported (Ziegler, 2005; Van Dam *et al.*

2020). At least, *Amphechinus* is for now recognized in Asia, Europe, Africa and North America. This suggests that the generalist ecomorphology of this genus allowed it to prosper in a lot of environments during the Oligocene and the Miocene. For instance, the North-American occurrences (Martin & Lim, 2004) coincide with the estimated immigration of several other Asian Eulipotyphla (Rich, 1981) usually considered as inadapted to cold environments, while European forms persisted even after the middle Miocene cooling event with *A. golpae* and *A. robinsoni*. Also, *Amphechinus* is identified in the well-known Spanish fossil record slightly before 16 Ma and survived there although the conditions became drier (Van Dam *et al.* 2020). This ubiquity could explain the longer persistence of *Amphechinus* in southern Africa compared to other Erinaceidae.

Overview of the African fossil record of Erinaceidae

Amphechinus is found in the Miocene of Africa with two other Erinaceinae: *Gymnurechinus* and *Mellalechinus* (previously *Protechinus* Lavocat 1961; see Zijlstra, 2012). Based on the comparisons of Lavocat (1961), *Mellalechinus* probably emerged from an undiscovered *Gymnurechinus*. However, the paucity of the fossil record means that this idea needs to be treated with caution. The first occurrences of *Amphechinus rusingensis*, *Gymnurechinus* and *Galerix africanus* in the Kenyan Koru and Legetet Formations (Fig. 2) are explainable by a single wave of dispersal, before 20 Ma. As for *Galerix africanus* and *Gymnurechinus*, the ancestral shape of *Amphechinus rusingensis* suggests a non-European ancestor. The only African representative of *Amphechinus* is mostly found

in the early Miocene but survived at least until the early middle Miocene (Mein & Pickford, 2003; Butler, 2010). While the material from Berg Aukas I confirms the survival of a form close to *A. rusingensis* in the late middle Miocene, the middle Miocene *Amphechinus* sp. from Fort Ternan indicates some morphological diversity and seems to highlight the acquisition of new characters in the African lineage.

From the middle Miocene to the early Pliocene, several occurrences of Erinaceidae are reported on the coastal side of northern Africa (Fig. 2). Almost all available data have been compiled by Stoetzel (2013) with the exception of the significant contribution of Engesser (1980). A large part of Erinaceidae occurrences are identified in the literature as *Galerix* and *Schizogalerix*, but since all the

described material show affinities with *Schizogalerix* (Engesser, 1980; Robinson *et al.* 1982; Aneur, 1984) the presence of the early to middle Miocene genus *Galerix* in the late Miocene and Pliocene of Africa is more than improbable. These materials attributed to *Galerix* should now be considered as “*Galerix*” indet. (or even as Galericinae indet.) since they probably correspond to *Schizogalerix*. Lavocat (1961) identified an incisor (or canine) from Beni Mellal (Morocco, middle Miocene) as belonging to ?*Galerix*, and considered another incisor to belong to *Palaeoerinaceus*?

(=*Amphechinus*). It is now well known that such isolated antemolar teeth do not allow precise identification, especially since Beni Mellal is the type-locality of *Mellalechinus*, whose dental variability is unknown. These doubtful identifications are thus not followed here. The last occurrence of the enigmatic *Mellalechinus* (*Mellalechinus* cf. *salis*) coincides with the first occurrence of Galericinae in the Moroccan late middle Miocene locality of Pataniak 6 (Stoetzel, 2013) based on an isolated M2/ attributed to the Galericini *Schizogalerix* cf. *anatolica* by Engesser (1980).

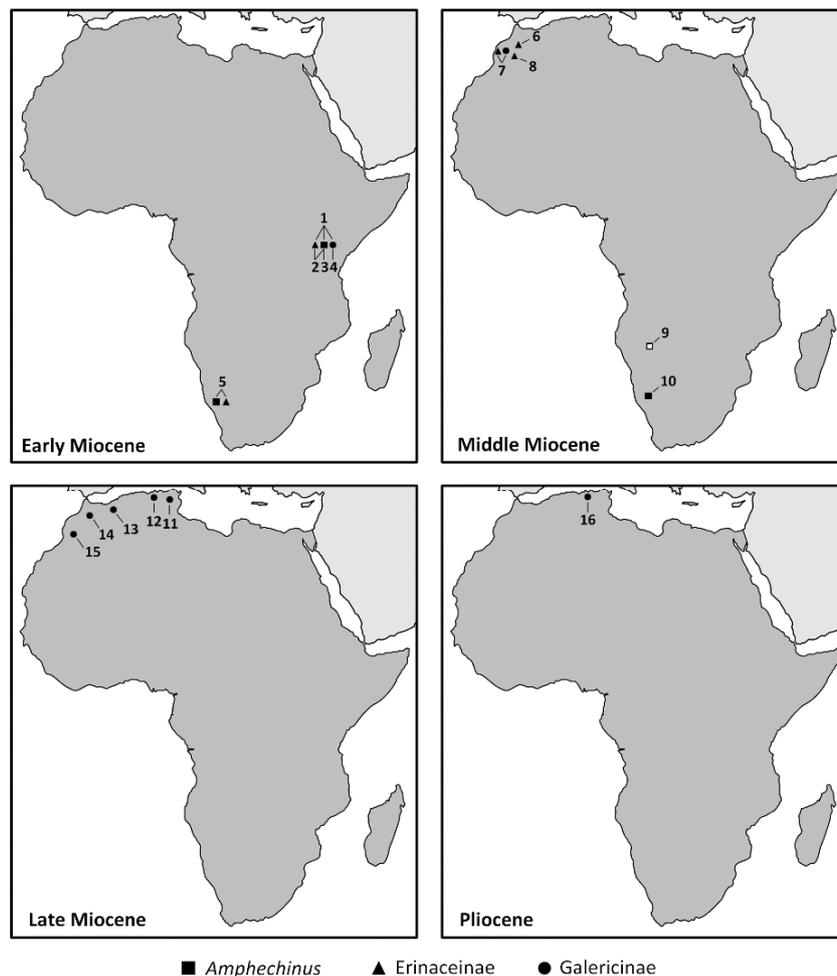


Figure 2. Updated distribution of Erinaceinae and Galericinae during the Miocene and Pliocene of Africa. *Amphechinus* is represented by squares, other Erinaceinae by triangles, and Galericinae by circles. 1) Legetet Formation, Hiwegi Formation and Kapurtay Agglomerates; Kenya. 2) Kulu Formation and Karungu; Kenya. 3) Maboko; Kenya. 4) Koru Formation; Kenya. 5) Sperrgebiet localities; Namibia. 6) Beni Mellal; Morocco. 7) Pataniak 6; Morocco. 8) Azdal 1, 3, 6 and 7; Morocco. 9) Berg Aukas I; Namibia. 10) Arrisdrift; Namibia. 11) Amama 1 and 2, Argoub Kamellal 1, Bab el Ahmar, El Hiout, Guergour Ferroudi and Smendou 6; Algeria. 12) Sidi Ounis; Tunisia. 13) Bou Hanifia 5, Koudiet el Tine and Sidi Salem; Algeria. 14) Oued Zra; Morocco. 15) Afoud 6, Asif Assermo and Oued Tabia; Morocco. 16) Amama 3; Algeria. Data are based on Engesser (1980), Aneur (1984), Butler (1984, 2010), Mein & Pickford (2003, 2008), Stoetzel (2013), Zouhri *et al.* (2017) and this work.

According to Robinson *et al.* (1982) the Turolian locality of Sidi Ounis (MDM locality, Tunisia) yielded a few teeth attributed by them to *Schizogalerix ?moedlingensis*. The Sidi Ounis specimens plot outside the metric range of variation of *S. moedlingensis*, and fit much better with *S. macedonica*, considered as belonging to the same lineage as *S. moedlingensis* by Doukas *et al.* (1995).

Robinson *et al.* (1982) mentioned the presence of a third cuspule on the lingual side of the M1/, between the protocone and the hypocone. This corresponds to a peculiar diagnostic feature of *S. macedonica*. Also, the trigonid of m/2 is not narrowed, compared to the trend observed in Turkish species (Furió *et al.* 2014). Despite this, it has to be noted that the extra cuspid found near the entoconid of m/1 and m/2 in *S. macedonica* and usually in *S. zapfei* is not described in Sidi Ounis lower molars. This lack also occurs in specimens from Pikermi (Greece) identified as *S. zapfei* by Rümke (1976). Moreover, Furió *et al.* (2014) had the opportunity to study the late Vallesian material of Kastellios Hill (Crete Island) and also found similarities with *S. macedonica* and *S. zapfei*, although the first discovered M2/ from this locality was attributed to *Schizogalerix sinapensis* by Van der Made (1996). The new clues from Kastellios Hill and Sidi Ounis imply a southward dispersal of the European lineage. The material from Sidi Ounis is here considered as belonging to a form named *Schizogalerix* aff. *macedonica*.

Engesser (1980) identified *Schizogalerix* in Oued Zra (Morocco), Amama 1 and Amama 2 (Algeria). The description of the small samples from Oued Zra and Amama 1 seems to imply the persistence into the Vallesian of the late middle Miocene migrant from Pataniak 6. The locality Bou Hanifia 5 (Morocco) may help to understand better the Vallesian record of *Schizogalerix* but only an unmeasured M3/ has been reported (Ameur, 1984). Apart from this, the even bigger *Schizogalerix* nov. sp. (*sensu* Engesser, 1980)

from the Turolian of Amama 2 is easily distinguished from all known species of the genus. It is clear that this material represents a new species that may have been derived from *Schizogalerix* aff. *macedonica*. Younger forms of *Schizogalerix* survived until the early Pliocene of Amama 3 (Algeria), where Galericinae are recorded for the last time in Africa (Stoetzel, 2013). Thus, at least two groups of *Schizogalerix* are identified in the late Miocene of Northern Africa and are related to two distinct dispersals. Finally, It is for now not possible to go further with the enigmatic fragment of M1/ found in the Lukeino Formation (Kenya, late Miocene) and attributed to an indeterminate Erinaceidae by Mein & Pickford (2006). A more southwards dispersal of the Galericini during the middle and late Miocene is considered to be unlikely.

While the ancestral Erinaceinae (*Amphechinus*, *Gymnurechinus*, *Mellalechinus*) disappeared during the Miocene, they were not immediately replaced by the recent dry-adapted genera *Atelerix* and *Paraechinus*. Even if the hypothesis of Mein & Ginsburg (2002) is correct by considering the existence of *Atelerix* in the French late Miocene of La-Grive-Saint-Alban (which is still a matter of debate), only a late diversification of *Atelerix* and also *Paraechinus* can be supported. Bannikova *et al.* (2014) estimated by molecular dating that the split between recent species of the two genera took place about 2.5 Ma. Concerning *Atelerix*, it seems to be related to a series of allopatric isolation events in northern Africa (Velo-Antón *et al.* 2019). The exclusively African distribution of recent *Atelerix* suggests an entrance of this genus before this split, during the Plio-Pleistocene transition, which is at least supported by the Plio-Pleistocene material from Ahl Al Oughlam (Zouhri *et al.* 2017). In southern Africa, the presence of *Atelerix* is only attested by a skull from an upper Pleistocene cave deposit of South Africa (Broom, 1937) attributed to *Atelerix major*.

Conclusion

The reassignment of Berg Aukas I fossil hedgehog material supports the persistence of ancestral erinaceids in southern Africa during the middle Miocene while greatly weakening the idea of a more southern expansion of Galericinae. The few occurrences of

Erinaceidae in Africa are mostly explained by a succession of dispersal events around the Mediterranean Basin during the early, middle and late Miocene while extant species seem to have emerged after the Plio-Pleistocene transition. Despite these clues, a large part of

Erinaceidae history in Africa still needs to be discovered.

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References

- Ameur, R. 1984. Découverte de nouveaux rongeurs dans la formation Miocène de Bou Hanifia (Algérie occidentale). *Geobios*, **17**, 167-175.
- Bannikova, A.A., Lebedev, V.S. & Abramov A.V. 2014. Contrasting evolutionary history of hedgehogs and gymnures (Mammalia: Erinaceomorpha) as inferred from a multigene study. *Biological Journal of the Linnean Society*, **112**, 499-519.
- Broom, R. 1937. Notices of a few more new fossil mammals from the caves of the Transvaal. *Annals and Magazine of Natural History*, Series 10, **20**, 509-514.
- Butler, P.M. 1956. Erinaceidae from the Miocene of East Africa - *Fossil Mammals of Africa*, **11**. British Museum (Natural History), London, 75pp.
- Butler, P.M. 1984. Macroscelidea, Insectivora and Chiroptera from the Miocene of East Africa. *Palaeovertebrata*, **14**, 117-200.
- Butler, P.M. 2010. Neogene Insectivora, In: Werdelin, L., & Sanders, W.S. (Eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, California, pp. 573-580.
- Conroy, G.C., Pickford, M., Senut, B., Van Couvering, J. & Mein, P. 1992. *Otavi-pithecus namibiensis*, first Miocene hominoid from southern Africa. *Nature*, **356**, 144-148.
- Doukas, C.S., Van den Hoek Ostende, L.W., Theocharopoulos, C.D. & Reumer, J.W.F. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). *Münchner Geowissenschaftliche Abhandlungen*, **A28**, 47-64.
- Engesser, B. 1980. Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. *Schweizerische Paläontologische Abhandlungen*, **102**, 47-149.
- Furió, M., Van Dam, J. & Kaya, F. 2014. New insectivores (Lipotyphla, Mammalia) from the Late Miocene of the Sivas Basin, Central Anatolia. *Bulletin of Geosciences*, **89**, 163-181.
- Lavocat, R. 1961. Le gisement de vertébrés miocènes de Beni Mellal (Maroc). *Notes et Mémoires du Services géologique du Maroc*, **155**, 29-94, 109-120.
- Martin, L.D. & Lim, J.D. 2004. New insectivores from the Early Miocene of Nebraska, USA and the Hemingfordian faunal exchange. *Mammalian Biology*, **69**, 202-209.
- Mein, P. & Ginsburg, L. 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). *Publications du Musée des Confluences*, **5**, 7-47.
- Mein, P. & Pickford, M. 2003. Insectivora from Arrisdrift, a basal Middle Miocene locality in southern Namibia. *Memoir of the Geological Survey of Namibia*, **19**, 143-146.
- Mein, P. & Pickford, M. 2006. Late Miocene micromammals from the Lukeino Formation (6.1 to 5.8 Ma), Kenya. *Bulletin mensuel de la Société linnéenne de Lyon*, **75**, 183-223.
- Mein, P. & Pickford, M. 2008. Early Miocene Insectivores from the Northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**, 169-183.
- Peláez-Campomanes, P., Mein, P. & Pickford, M. 2020. Fossil Sciuridae (Rodentia, Mammalia) from Berg Aukas (Otavi Mountains,

- Namibia). *Communications of the Geological Survey of Namibia*, **23**, 65-89.
- Pickford, M. 2008. Diversification of grazing mammals in southern and equatorial Africa during the Neogene and Quaternary. *Memoir of the Geological Survey of Namibia*, **20**, 529-537.
- Pickford, M. & Senut, B. 2002. The fossil record of Namibia. *Ministry of Mines and Energy, Geological Survey of Namibia*, Windhoek, Namprint, 39 pp.
- Pickford, M. & Senut, B. 2010. Karst Geology and Palaeobiology of Northern Namibia. *Memoir of the Geological Survey of Namibia*, **21**, 1-74.
- Prieto, J., Gross, M., Böhmer, C. & Böhme, M. 2010. Insectivores and bat (Mammalia) from the late middle Miocene of Gratkorn (Austria): biostratigraphic and ecologic implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **258**, 107-119.
- Rich, T.H.V. 1981. Origin and History of the Erinaceinae and Brachyericinae (Mammalia, Insectivora) in North America. *Bulletin of the American Museum of Natural History*, **171**, 1-116.
- Robinson, P., Black, C.C., Krishtalka, L. & Dawson, M. 1982. Fossil Mammals from the Kechabta Formation, Northwestern Tunisia. *Annals of the Carnegie Museum*, **51**, 231-249.
- Rosina, V.V. & Pickford, M. 2019. Preliminary overview of the fossil record of bats (Chiroptera, Mammalia) from the Miocene sites of Otavi Mountainland (Northern Namibia). *Communications of the Geological Survey of Namibia*, **21**, 48-58.
- Rümke, C.G. 1976. Insectivora from Pikermi and Biodrak (Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **B79**, 256-270.
- Senut, B., Pickford, M., Mein, P., Conroy, G. & Van Couvering, J.A. 1992. Discovery of 12 new late Cainozoic fossiliferous sites in palaeokarsts of the Otavi Mountains, Namibia. *Comptes Rendus de l'Académie des Sciences, Paris*, **314**, 727-733.
- Senut, B., Pickford, M. & Ségalen L. 2009. Neogene desertification of Africa. *Comptes Rendus Geoscience*, **341**, 591-602.
- Stoetzel, E. 2013. Late Cenozoic micromammal biochronology of northwestern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **392**, 359-381.
- Van Dam, J.A., Mein, P. & Alcalá, L. 2020. Late Miocene Erinaceinae from the Teruel Basin (Spain). *Geobios*, **61**, 61-81.
- Van den Hoek Ostende, L.W. 2001. A revised generic classification of the Galericiini (Insectivora, Mammalia) with some remarks on their palaeogeography and phylogeny. *Geobios*, **34**, 681-695.
- Van der Made, J. 1996. Pre-Pleistocene land mammals from Crete. In: Reese, D.S. (Ed.). *Pleistocene and Holocene fauna of Crete and its First Settlers*. Prehistory Press, Madison, Wisconsin, pp. 69-79.
- Velo-Antón, G., Boratyński, Z., Ferreira, C., Lima, V.O., Alves, P.C. & Brito, J.C. 2019. Intraspecific genetic diversity and distribution of North African hedgehogs (Mammalia: Erinaceidae). *Biological Journal of the Linnean Society*, **127**, 156-163.
- Ziegler, R. 1983. Odontologische und osteologische Untersuchungen an *Galerix exilis* (Blainville) (Mammalia, Erinaceidae) aus den miozänen Ablagerungen vom Steinberg und Goldberg im Nördlinger Ries (Süddeutschland). Unpublished PhD thesis, University of Munich, 224 pp.
- Ziegler, R. 2005. Erinaceidae and Dimylidae (Lipotyphla) from the Upper Middle Miocene of South Germany. *Senckenbergiana lethaea*, **85**, 131-152.
- Zijlstra, J.S. 2012. A *nomen novum* for *Protechinus* Lavocat, 1961 (Mammalia, Erinaceidae), a junior homonym of the valid name *Protechinus* Noetling, 1897 (Echinoidea, Arbacioidea). *Zootaxa*, **3233**, 67-68.
- Zouhri, S., Benammi, M., Geraads, D. & El Boughabi, S. 2017. Mammifères du Néogène continental du Maroc: faunes, biochronologie et paléobiogéographie. *Mémoires de la Société Géologique de France*, **180**, 527-588.