

## **FOSSILS AND MONOPHYLY OF AFROTHERIA: A REVIEW OF THE CURRENT DATA**

**A.O. Averianov<sup>1</sup>, A.V. Lopatin**

<sup>1</sup>*Zoological Institute, Russian Academy of Sciences; dzharakuduk@mail.ru*

Two groups of “afrotherians”, Macroscelidea and Paenungulata (Hyracoidea, Proboscidea, Sirenia) are related to archaic ungulates (“condylarthrs”) Apheliscidae and Phenacodontidae, respectively. In such a case, however, the clade including Apheliscidae, Macroscelidea, Phenacodontidae, and Paenungulata should also include Perissodactyla, which makes Afrotheria paraphyletic. Tenrecoidea are likely related to an insectivorous grade Adapisoriculidae, which may belong to a pre-zhelestid radiation of the stem placental mammals. This hypothesis, if correct, implies an enormous phylogenetic gap between Tenrecoidea and the clade including Macroscelidea and Paenungulata having originated from a more advanced group of archaic ungulates. The latter treatment invalidates the concept of Afrotheria as a group of closely related mammals originated in Africa. The origin of Tubulidentata is still obscure.

## **ПАЛЕОНТОЛОГИЧЕСКАЯ ЛЕТОПИСЬ И МОНОФИЛИЯ AFROTHERIA: ОБЗОР СОВРЕМЕННЫХ ДАННЫХ**

**А.О. Аверьянов<sup>1</sup>, А.В. Лопатин**

<sup>1</sup>*Зоологический институт РАН; dzharakuduk@mail.ru*

Две группы «афротериев», Macroscelidea и Paenungulata (Hyracoidea, Proboscidea, Sirenia), связаны происхождением с архаичными копытными («кондилартрами») Apheliscidae и Phenacodontidae, соответственно. В таком случае, однако, клада, включающая Apheliscidae, Macroscelidea, Phenacodontidae и Paenungulata, должна также включать Perissodactyla, что делает Afrotheria парафилетической группой. Tenrecoidea наиболее вероятно происходят от млекопитающих насекомоядного уровня организации, Adapisoriculidae, которые могут принадлежать к преджелестидной радиации стволовых плацентарных. Если эта гипотеза верна, то между Tenrecoidea и кладой, содержащей Macroscelidea и Paenungulata и происходящей от более продвинутых архаичных копытных, существует огромный филогенетический раз-

рыв. Эта трактовка делает концепцию Afrotheria, как группы возникших в Африке близкородственных млекопитающих, невалидной. Происхождение Tubulidentata пока не ясно.

## 1. Introduction

The mammal phylogenetic tree has been reshaped significantly during past decades by the molecular data (for review, see Averianov, Lopatin, 2014). The biggest surprise came from the clade of endemic African mammals that included Recent groups Tenrecoidea (tenrecs and golden moles), Macroscelidea (elephant shrews, or sengis), Tubulidentata (aardvarks), Hyracoidea (hyraxes), Sirenia (sea cows), and Proboscidea (proboscideans) (Springer et al., 1997, 1999, 2004; Stanhope et al., 1998a,b; Madsen et al., 2001; Murphy et al., 2001; van Dijk et al., 2001; Malia et al., 2002).

Several morphological characters has been proposed as the afrotherian synapomorphies, including high count of dorsal vertebrae (Sánchez-Villagra et al., 2007), characters of placenta (Mess, Carter, 2006), shape of ankle bones (Seiffert, 2007; Tabuce et al., 2007), and late eruption of permanent teeth (Asher, Lehmann, 2008). However, all these characters are either retention of plesiomorphic eutherian condition or parallelisms.

However, “afrotherians” appeared to be non-monophyletic on a morphology-based tree of Asher et al. (2003, fig. 3), in which Tubulidentata were shown to link to Xenarthra, Paenungulata to Ungulata, Afrosoricida to Lipotyphla, and Macroscelidea to Glires.

Few morphological phylogenetic analyses that include all afrotherian groups do not support monophyletic status of the Afrotheria. According to a combined analysis of morphological and molecular data by Asher et al. (2003), the crown group Afrotheria includes embrithopods, *Plesiorycteropus*, desmostylians, the “condylarths” *Hyopsodus*, *Meniscotherium*, and possibly *Phenacodus*.

Seiffert (2007) provided another combined analysis based on genomic data (nucleotide data, chromosomal associations, and retroposons) and 400 morphological characters scored across 16 extant and 35 extinct afrotherians. A NONA analysis of his morphological data matrix with 10,000 ratchet replications (Goloboff, 1999) produced 38 most parsimonious trees with their consistency index of 0.28 and retention index of 0.62. On the strict consensus tree, there were no monophyletic Afrotheria, with Tenrecoidea (= Afrosoricida) being nested within the Lipotyphla.

Tabuce et al. (2007) described new Tertiary mammals from North Africa they thought to “reinforce the molecular Afrotheria clade”. However, no any tenrecoide taxon was included in their data matrix and the clade being “reinforced” was actually just Macroscelidea + Paenungulata (Tabuce et al., 2007, fig. 4). There and in a previous analysis (Zack et al., 2005), macroscelideans and/or hyraxes are linked to the North American and European apfeliscid condylarths which disrupt the concept of Afrotheria as a monophyletic clade of the endemic African mammals.

In the most recent morphological analysis utilizing an enormous number of phenotypic characters (4541), a morphological consensus tree implies no monophyletic Afrotheria (O’Leary et al., 2013, supplementary fig. S2). Golden moles are linked to the true moles, tenrecs to the hedgehogs, and elephant shrews to the extinct North American leptictids adapted to ricocheted locomotion.

Evidently, both molecular sequence and parsimony morphological analyses have their own limitations. The lack of the intermediate taxa which would fill the gaps between the

Recent clades is critical for the both analyses. In such a situation, the only possible way to solve the afrotherian problem seems to be the tracing the possible ancestors of the modern clades in the fossil record. In this article, we review the known fossil record of the groups included in Afrotheria by the molecular data.

## 2. Review of the taxa

### 2.1. Tenrecoidea

The suprafamiliar nomenclature of this clade is confusing. We follow Asher (2005), Asher (2010), and Asher and Helgen (2010) in using Tenrecoidea (=Afrosoricida, = Tenrecomorpha) for the clade including Tenrecidae + Chrysochloridae. The adapisoriculids *Todralestes variabilis* and *Afrodon chleuhi* from the late Paleocene of Morocco (Gheerbrant, 1994, 1995) have been placed as stem tenrecoids in the phylogenetic analysis by Seiffert (2010).

#### 2.1.1. Tenrecidae

There are 30 modern species of this clade distributed in Africa (Potamogalinae) and Madagascar (Tenrecinae) (Asher, Hofreiter, 2006; Asher, 2010). Three extinct taxa from the early Miocene of Kenya and Uganda, *Protenrec tricuspis*, *Erythrozoetes chamerpes*, and *Parageogale aletris*, are members of the crown-group Tenrecidae (Butler, 1984; Poduschka, Poduschka, 1985; Asher, 2010). Another species, *Protenrec butleri*, is known from the early Miocene of Namibia (Mein, Pickford, 2003). *Jawharia tenrecoides* and *Qatranilestes oligocaenus* from the early Oligocene of Egypt and *Widanelfarasia bowni*, *W. rasmusseni*, and *Dilambdogale gheerbranti* from the late Eocene of Egypt are either stem tenrecids or stem tenrecoids (Seiffert, Simons, 2000; Seiffert et al., 2007; Seiffert, 2010). *Widanelfarasia* and *Dilambdogale* both have dilambdodont upper molars

and fully developed lower molar talonids, while *Qatranilestes*, known from the lower dentition only, has reduced molar talonids. *Widanelfarasia* is similar with *Protenrec* and some modern tenrecids in such derived characters as ectocrista and ectofossa on P4, distal root of P3 placed mesial to the P4 protocone, and “stepped” transition between P4 and anterior premolars (Seiffert et al., 2007). Thus phylogenetic position of *Widanelfarasia* as a stem tenrecid is a more preferable hypothesis (Seiffert et al., 2007; Seiffert, 2010). *Dilambdogale* was found to be a sister taxon to *Widanelfarasia* and it also shows incipient ectorista and ectofossa on P4 (Seiffert, 2010).

#### 2.1.2. Chrysochloridae

There are 21 modern species of golden-moles (Chrysochloridae) distributed in sub-Saharan Africa (Asher et al., 2010). The modern species, or distinct species very close to the modern ones, are known from the Pliocene-Pleistocene of South Africa (Broom, 1941, 1948; de Graaff, 1957; Asher, 2010; Asher, Avery, 2010). The generically distinct extinct golden mole *Prochrysochloris miocaenicus* is known from the early Miocene of Kenya and possibly Namibia (Butler, Hopwood, 1957; Butler, 1984; Mein, Pickford, 2003; Asher, 2010). It differs from the modern chrysochlorids by unreduced posterior molars (a normal M3 is present, M2 is widest upper molar), smaller and less molariform anterior upper premolars, and less reduced talonids on lower molars.

All these traits are plesiomorphic relative to the modern taxa, which have M3 lost or very reduced, M2 reduced, and lower molar talonids small single cusped or lacking altogether. Modern chrysochlorids and *Prochrysochloris* have zalambdodont dentition with reduced metaconid and talonid basin (McDowell, 1958; Asher, Sánchez-Villagra, 2005). The phylogenetic position of

*Prochrysochloris* is likely outside the crown group Chrysochloridae (Asher, 2010).

The oldest named stem taxon of Chrysochloridae is a poorly known *Eochrysochloris tribosphenus* from the early Oligocene of Egypt (Seiffert et al., 2007). *Eochrysochloris* has a single rooted p3, molariform p4, and lower molars with reduced but basined talonid. As it was discussed by Seiffert et al. (2007), the oldest stem chrysochlorid in Africa might be represented by an isolated upper molar (M2?) with greatly reduced metacone from the late Paleocene of Morocco, attributed to ?Proteutheria or ?Lipotyphla indet. (Gheerbrant, 1995, fig. 22a–c, pl. 1, figs. 1–3).

## 2.2. Macroscelidea

The order Macroscelidea includes a single family Macroscelididae with two extant and four extinct subfamilies (Corbet, Hanks, 1968; Holroyd, Mussell, 2005; Holroyd, 2010a). This classification is not phylogenetic, as two extinct subfamilies (Myohyracinae and Mylomygalinae) are within the crown-group and two other subfamilies (Metoldobotinae and Herodotiinae) are outside the crown-group (Holroyd, 2010a, fig. 8.3). The name Macroscelididae should be restricted to the crown group of elephant shrews, while other taxa should be considered as the stem macroscelideans. The 17 to 19 modern species of Macroscelididae are distributed in Africa either North (“*Elephantulus*” *rozeti*) or South to Sahara (other species) (Douady et al., 2003; Smit et al., 2011). The Miocene and younger extinct elephant shrews are known South to Sahara, while the Paleogene records came from North Africa and Namibia (Patterson, 1965; Novacek, 1984; Butler, 1995; Holroyd, 2010a).

The Eocene Macroscelidea are united in the subfamily Herodotiinae (Holroyd, 2010a), although monophyly of this group has not been demonstrated. These taxa are

*Herodotius pattersoni* from the late Eocene of Egypt, *Nementchatherium senarhense* from the middle-late Eocene of Algeria, *N. rathbuni* and *Eotmantsoius perseverans* from the middle-late Eocene of Libya, and *Chambius kasserinensis* from the early Eocene of Tunisia (Hartenberger, 1986; Simons et al., 1991; Tabuce et al., 2001, 2007, 2012). These taxa are known from dental and gnathic remains, except for the *Chambius* for which two petrosals have been described (Benoit et al., 2013b). Its petrosal lacks the anterior pneumatic fossa and well-developed *fossula cochleae* which correlated in modern macroscelideans with the middle ear pneumatization necessary for adaptation to low frequency hearing (Benoit et al., 2013b).

Apheliscid “condylarths” *Apheliscus* and *Haplomylys* from the late Paleocene to early Eocene of North America and louisinid “condylarth” *Paschatherium* from the late Paleocene to early Eocene of Europe share with macroscelideans a unique combination of tarsal characters associated with their cursorial and saltatorial adaptations and are also similar to them in dental characters. These taxa were placed as stem macroscelideans in the analysis by Zack et al. (2005); see also Penkrot et al. (2008). In the analysis by Tabuce et al. (2007), *Haplomylys* is a stem macroscelidean, while *Paschatherium* is a stem paenungulate, and *Apheliscus* is a sister taxon to the clade Macroscelidea + Paenungulata. In the analysis by Hooker and Russell (2012), *Chambius* was nested within Apheliscidae if postcranial characters were included, but within the Louisinidae if these characters were excluded.

## 2.3. Ptolemaiida

The Ptolemaiida is a small group of extinct African mammals known from the early Oligocene of Egypt (*Qarunavus meyeri*, *Ptolemaia lyonsi*, *P. grangeri*, *Cleopatrodon*

*ayeshae*, and *C. robusta*), late Oligocene of Kenya (*Ptolemaia* cf. *grangeri*), and early to middle Miocene of Kenya and Uganda (*Kelba quadeemae*) (Osborn, 1908; Bown, Simons, 1987; Simons, Bown, 1995; Cote et al., 2007; Gunnell et al., 2010; Miller et al., 2015). There are also remains of unidentified ptolemaiids from the late Eocene of Egypt (Gunnell et al., 2010). In the latest phylogenetic analyses, *Kelba* was placed as a sister taxon to Tubulidentata (Seiffert, 2007; Gheerbrant et al., 2014).

#### 2.4. Tubulidentata

There is a single Recent species of aardvarks, *Orycteropus afer*, distributed in Africa south to Sahara (Shoshani et al., 1988; Holroyd, 2010b). This species is known since the Pliocene in Africa (Lehmann, 2008; Holroyd, 2010b). There are at least two extinct species of *Orycteropus* from the Plio-Pleistocene of Africa, and five to seven extinct species of the closely related *Amphiorhycteropus* from the Mio-Pliocene of Africa, Europe, and Asia (Patterson, 1975; Lehmann et al., 2004, 2005, 2006; Lehmann, 2006, 2008, 2009; Holroyd, 2010b). There are two other extinct genera of Orycteropodidae, *Myorycteropus* with one to three species from the early–middle Miocene of Kenya and Uganda and *Leptorycteropus* with a single species, *L. guiljelmi*, from the upper Miocene of Kenya (Patterson, 1975; Pickford, 1975; Lehmann, 2009; Holroyd, 2010b). These extinct taxa are already very specialized and do not offer clues for the origin of Tubulidentata.

#### 2.5. Bibymalagasia

This order was erected for the genus *Plesiorycteropus* known from the Pleistocene of Madagascar (MacPhee, 1994; Werdelin, 2010). The rostral part of its skull and its dentition are unknown, its similarity in the postcranial skeleton to *Orycteropus*

was thought to be convergent (MacPhee, 1994). The collagen sequence data suggest *Plesiorycteropus* affinities to Tenrecoidea (Buckley, 2013). Results of the study of its bony labyrinth supported its ordinal distinctiveness (Benoit et al., 2015).

#### 2.6. Paenungulata

The Paenungulata includes Hyracoidea and Tethytheria (Simpson, 1945; Novacek, Wyss, 1986; Novacek et al., 1988; Gheerbrant et al., 2005a). In a recent phylogenetic analysis, the “condylarths” Phenacodontidae are considered as a sister taxon to the Paenungulata (Rose et al., 2014).

The authors just cited called the latter clade “Afrotheria”, but not a single tenrecoid was included in their analysis. The recently discovered stem paenungulate *Ocepeia* with two species from the middle Paleocene of Morocco was found to be a sister taxon to the clade Phenacodontidae + Paenungulata (Gheerbrant et al., 2014).

##### 2.6.1. Hyracoidea

The four Recent species of hyraxes classified within three genera (*Dendrohyrax*, *Heterohyrax*, and *Procavia*) of the family Procaviidae represent actually an insignificant remnants of the past vast diversity of the Hyracoidea which were among dominant herbivorous mammals in Afro-Arabic continent during the Paleogene and expanded their range to Eastern Asia in the Neogene (Rasmussen, 1989; Schwartz et al., 1995; Gheerbrant et al., 2005a; Rasmussen, Gutiérrez, 2010). The oldest known representatives of the crown Procaviidae from the late Miocene of Namibia and Kenya are *Heterohyrax auricampensis* and *Dendrohyrax* sp. (Rasmussen et al., 1996; Pickford, Hlusko, 2007). Other extinct taxa of Procaviidae include two species of *Procavia* and *Gigantohyrax maguirei* from the Pleistocene of

South Africa (Kitching, 1965; Rasmussen, Gutiérrez, 2010).

In the latest proposed classification of Hyracoidea, distinguished are four families of the extinct stem hyracoids (Geniohyidae, Saghatheriidae, Titanohyracidae, and Pliohyracidae), with Geniohyidae uniting these taxa by their most plesiomorphic traits of bunodont artiodactyl-like dentition (Rasmussen, Gutiérrez, 2010). However, according to the phylogenetic analysis by Barrow et al. (2010), the most basal clade of Hyracoidea is a group consisting of *Seggeurius amourensis* from the early Eocene of Algeria, *Microhyrax lavocati* from the early Eocene of Tunisia, and *Dimatherium patnaiki* from the late Eocene of Egypt (Court, Mahboubi, 1993; Tabuce et al., 2007).

### 2.6.2. Tethytheria

The above-order ranked taxon Tethytheria was initially proposed to include Sirenia, Proboscidea, and Desmostylia (McKenna, 1975; Domning et al., 1986; Novacek, 1986; Novacek, Wyss, 1986; Shoshani, 1986; Novacek et al., 1988; Tassy, Shoshani, 1988).

#### 2.6.2.1. Embrithopoda

This small extinct group was part of Simpson's concept of Paenungulata (Simpson, 1945), but was not included in the Tethytheria by McKenna (1975). The close relationships of Embrithopoda to Tethytheria were first proposed by Tassy and Shoshani (1988). The Arsinoitheriidae are endemic to Afro-Arabic continent and include *Namatherium blackcrowense* from the middle Eocene of Namibia, *Arsinoitherium zitteli* is known from the late Eocene to early Oligocene of Egypt, and *A. giganteum* is known from the late Oligocene of Ethiopia (Andrews, 1906; Court, 1990, 1992a,b, 1993; Sanders et al., 2004; Pickford et al., 2008; Sanders et al., 2010b). Remains referred to *Arsinoitheri-*

*um* sp. came from Angola, Libya, Tunisia, Kenya, and Oman (Al-Sayigh et al., 2008; Sanders et al., 2010b; Vialle et al., 2013). The Eocene Palaeomasiidae are known only outside of Africa and include *Crivadiatherium mackennai* and *C. iliescui* from Romania and *Palaeomasia kansui* and *Hypsamasia seni* from Anatolia (Radulesco et al., 1976; Sen, Heintz, 1979; Radulesco, Sudre, 1985; Kaya, 1995; Maas et al., 1998; Sanders et al., 2014). *Phenacolophus phalax* from the late Paleocene of Mongolia was considered a basal embrithopod by McKenna and Manning (1977), but this was questioned by some authors (Radulesco, Sudre, 1985; Gheerbrant et al., 2005a). In the recent phylogenetic analyses, *Phenacolophus* is placed as a sister taxon to Sirenia (Tabuce et al., 2007) or to Embrithopoda + Tethytheria (Gheerbrant, 2009). Among embrithopods, the complete skull and skeleton are known for *Arsinoitherium zitteli* only (Andrews, 1906; Court, 1992a, 1993); the other taxa are represented by gnathodental remains. *Arsinoitherium* was found to be a member of Tethytheria by analysis of cranial characters (Court, 1992a). Some petrosal characters link *Arsinoitherium* to Proboscidea (Court, 1990).

#### 2.6.2.2. Proboscidea

Proboscidea, one of the most diverse mammalian order in a not far past, nowadays is represented by but two species of *Loxodonta* and one species of *Elephas* of the family Elephantidae (Gheerbrant et al., 2005a; Rohland et al., 2010; Sanders et al., 2010a). A subrecent elephantid, the woolly mammoth *Mammuthus primigenius*, has become extinct in the historical times (Vartanyan et al., 1993; Guthrie, 2004). Proboscideans are divided into four superfamilies, two of which have radiated in the Eocene-Oligocene of Africa (Barytherioidea and Moeritherioidea), one in the Neogene of the Old World (Deinotheri-

oidea), while modern Elephantoida distributed in Africa, Eurasia and both Americas appeared as late as in the early Oligocene (Sanders et al., 2010a).

The oldest stem proboscideans came from the late Paleocene to early Eocene of Morocco: *Khamsaconus bulbosus*, *Eritherium azzouourm*, *Phosphatherium escuilieri*, and *Daoutherium rebouli* (Sudre et al., 1993; Gheerbrant et al., 1996, 1998, 2002, 2005b, 2012; Gheerbrant, 2009; Sanders et al., 2010a). This oldest proboscideans were already well differentiated in their size and morphology suggesting that origin of the entire group had occurred significantly earlier. The recent phylogenetic analyses placed Proboscidea as a sister taxon to Sirenia (Gheerbrant, 2009; Gheerbrant et al., 2014).

#### 2.6.2.3. Sirenia

Most of the diversity of Sirenia, just like in Hyracoidea and Proboscidea, was in the past. There are four families of Sirenia: Eocene Porastomidae and Protosirenidae, middle Eocene to Recent Dugongidae, and late Oligocene to Recent Trichechidae (Domning et al., 2010). There are but four currently extant sirenian species: Indo-Pacific *Dugong dugon* (Dugongidae) and three species of Atlantic *Trichechus* (Trichechidae) (Gheerbrant et al., 2005a; Domning et al., 2010). A North Pacific dugongid, the Steller's sea cow, *Hydrodamalis gigas*, has been exterminated in the 18th century (Anderson, 1995).

The oldest sirenian taxa are prorastomids, *Prorastomus sirenoides* and *Pezosiren portelli*, from the early–middle Eocene of Jamaica (Owen, 1855, 1875; Savage et al., 1994; Domning, 2001). Recently, a prorastomid vertebra has been reported from the middle Eocene of Senegal (Hautier et al., 2012). An isolated sirenian petrosal from the early–middle Eocene of Tunisia is more primitive than that in *Prorastomus*, which al-

lows to suggest an African origin of Sirenia (Benoit et al., 2013a).

#### 2.6.2.4. Desmostylia

This small order of the extinct marine mammals has no records in Africa, in contrast to other supposed afrotherians (Gheerbrant et al., 2005a). Two families of desmostylians, Palaeoparadoxiidae and Desmostylidae, are known only from the Oligocene–Miocene of North Pacific region. The oldest known taxa are *Behemotops proteus* (Palaeoparadoxiidae) from the middle–late Oligocene of Washington, USA, and *Ashoro alaticosta* from the late Oligocene of Japan (Desmostylidae) (Domning et al., 1986; Ray et al., 1994; Inuzuka, 2000; Beatty, 2009).

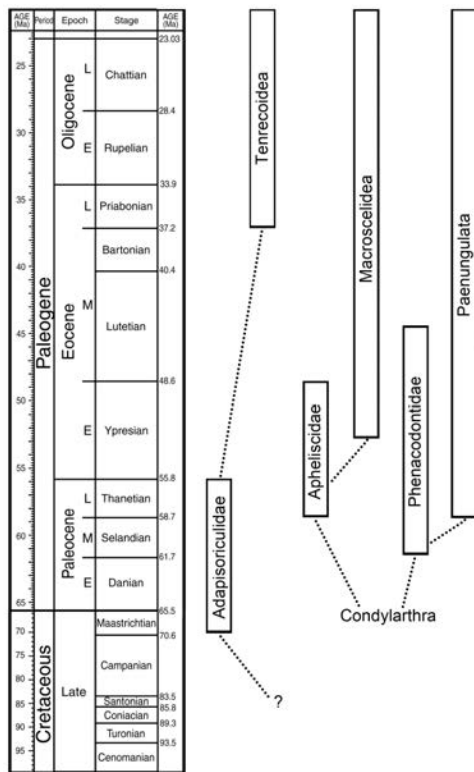
Traditionally, Desmostylia were considered as a part of the tethytherian radiation most closely linked to proboscideans and anthracobunids (Domning et al., 1986; Tassy, Shoshani, 1988; Gheerbrant et al., 2005a). However, in the recent phylogenetic analysis including Recent taxa constrained by a “molecular scaffold”, Anthracobunidae and Desmostylia were placed as stem perissodactyls (Cooper et al., 2014). In another analysis, Anthracobunidae are placed within the crown group Perissodactyla (Rose et al., 2014).

### 3. Discussion

Among the modern “afrotherian” clades, the origin of Tubulidentata is obscure.

Most likely, Tenrecoidea (Tenrecidae and Chrysochloridae) originated from the Adapisoriculidae, Macroscelidea originated from Apheliscidae, and Paenungulata (Hyracoidea + Proboscidea + Sirenia) originated from Phenacodontidae.

Apheliscidae and Phenacodontidae are members of Condylarthra, which is supposed to be a paraphyletic group of archaic ungulates (Archibald, 1998), while Adapiso-



**Fig. 1.** A likely origin of main “afrotherian” clades. The time scale is adapted from Gradstein et al. (2004).

**Рис. 1.** Вероятное происхождение основных клад «Afrotheria». Временная шкала согласно Gradstein et al. (2004).

riculidae is a group of insectivorous grade of the mammals.

The clade including Apheliscidae, Phenacodontidae, with their most recent common ancestor and all the latter’s descendants, should include also at least Perissodactyla (Rose et al., 2014), thus making Afrotheria paraphyletic in their current content.

There is a considerable morphological and phylogenetic gap between Adapisoriculidae and archaic ungulates (Fig. 1). Unfortunately, members of this group are known but from isolated teeth and jaw fragments

and few postcranial elements, with its oldest representative *Deccanolestes* having come from the Maastrichtian of India (Prasad et al., 1994, 2010; Boyer et al., 2010; Smith et al., 2010; Goswami et al., 2011). According to one of the recent phylogenetic hypotheses (Goswami et al., 2011), Adapisoriculidae belong to the very basal radiation of the stem placental mammals, prior to an offshoot of the zhelestid eutherians. This, if true, may explain many plesiomorphic features of the tenrecoids, including presence of cloaca and inefficient thermoregulation. What seems to be undoubted is that tenrecoids are not closely related to other “afrotherian” mammals which have originated from far more advanced archaic ungulates.

#### Acknowledgements

This work was supported by the Russian Scientific Fund (project 14-14-00015).

#### References

- Al-Sayigh A.R., Nasir S., Schulp A.S., Stevens N.J. 2008. The first described *Arsinoitherium* from the upper Eocene Aydim Formation of Oman: Biogeographic implications. — *Palaeoworld*, 17 (1): 41–46.
- Anderson P.K. 1995. Competition, predation, and the evolution and extinction of Steller’s sea cow, *Hydrodamalis gigas*. — *Marine Mammal Science*, 11 (3): 391–394.
- Andrews C.W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. London: British Museum of Natural History. 324 p.
- Archibald J.D. 1998. Archaic ungulates (“Condylarthra”). — Janis C.M., Scott K.M., Jacobs L.L. (eds). *Evolution of Tertiary mammals of North America*. Vol. 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. New York: Cambridge University Press. P. 292–331.
- Asher R.J. 2005. Insectivoran-grade placentals. — Rose K.D., Archibald J.D. (eds). *The rise of placental mammals: Origins and relationships of the major extant clades*. Baltimore,



- The Johns Hopkins University Press. P. 50–70.
- Asher R.J. 2010. Tenrecoidea. — Werdelin L., Sanders W.J. (eds). *Cenozoic mammals of Africa*. Berkeley: University of California Press. P. 99–106.
- Asher R.J., Avery D.M. 2010. New golden moles (Afrotheria, Chrysochloridae) from the early Pliocene of South Africa. — *Palaeontologia Electronica*, 13 (1): 3A.
- Asher R.J., Helgen K.M. 2010. Nomenclature and placental mammal phylogeny. — *BMC Evolutionary Biology*, 10: 102.
- Asher R.J., Hofreiter M. 2006. Tenrec phylogeny and the noninvasive extraction of nuclear DNA. — *Systematic Biology*, 55 (2): 181–194.
- Asher R.J., Lehmann T. 2008. Dental eruption in afrotherian mammals. — *BMC Biology*, 6: 14.
- Asher R.J., Maree S., Bronner G. et al. 2010. A phylogenetic estimate for golden moles (Mammalia, Afrotheria, Chrysochloridae). — *BMC Evolutionary Biology*, 10: 69.
- Asher R.J., Novacek M.J., Geisler J.H. 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. — *Journal of Mammalian Evolution*, 10 (1–2): 131–194.
- Asher R.J., Sánchez-Villagra M.R. 2005. Locking yourself out: diversity among dentally zalambdodont therian mammals. — *Journal of Mammalian Evolution*, 12 (1–2): 265–282.
- Averianov A.O., Lopatin A.V. 2014. High-level systematics of placental mammals: current status of the problem. — *Biology Bulletin*, 41 (9): 801–816.
- Barrow E., Seiffert E.R., Simons E.L. 2010. A primitive hyracoid (Mammalia, Paenungulata) from the early Priabonian (late Eocene) of Egypt. — *Journal of Systematic Palaeontology*, 8 (2): 213–244.
- Beatty B.L. 2009. New material of *Cornwallius sookensis* (Mammalia: Desmostylia) from the Yaquina Formation of Oregon. — *Journal of Vertebrate Paleontology*, 29 (3): 894–909.
- Benoit J., Adnet S., Mabrouk E.E. et al. 2013a. Cranial remain from Tunisia provides new clues for the origin and evolution of Sirenia (Mammalia, Afrotheria) in Africa. — *PLoS One*, 8 (1): e54307.
- Benoit J., Lehmann T., Vatter M. et al. 2015. Comparative anatomy and three-dimensional geometric-morphometric study of the bony labyrinth of Bibymalagasia (Mammalia, Afrotheria). — *Journal of Vertebrate Paleontology*, 35 (3): e930043.
- Benoit J., Orliac M., Tabuce R. 2013b. The petrosal of the earliest elephant-shrew *Chambius* (Macroscelidea: Afrotheria) from the Eocene of Djebel Chambi (Tunisia) and the evolution of middle and inner ear of elephant-shrews. — *Journal of Systematic Palaeontology*, 11 (8): 907–923.
- Bown T.M., Simons E.L. 1987. New Oligocene Ptolemaiidae (Mammalia: ?Pantolestia) from the Jebel Qatrani Formation, Fayum Depression, Egypt. *Journal of Vertebrate Paleontology*, 7 (3): 311–324.
- Boyer D.M., Prasad G.V.R., Krause D.W. et al. 2010. New postcrania of *Deccanolestes* from the Late Cretaceous of India and their bearing on the evolutionary and biogeographic history of euarchontan mammals. — *Naturwissenschaften*, 97 (4): 365–377.
- Broom R. 1941. On two Pleistocene golden moles. *Annals of the Transvaal Museum*, 20: 215–216.
- Broom R. 1948. Some South African Pliocene and Pleistocene mammals. — *Annals of the Transvaal Museum*, 21 (1–2): 1–38.
- Buckley M. 2013. A molecular phylogeny of *Plesiorcycteropus* reassigns the extinct mammalian order 'Bibymalagasia'. *PLoS One*, 8 (3): e59614.
- Butler P.M. 1984. Macroscelidea, Insectivora, and Chiroptera from the Miocene of East Africa. — *Palaeovertebrata*, 14 (3): 117–200.
- Butler P.M. 1995. Fossil Macroscelidea. — *Mammal Review*, 25 (1–2): 3–14.
- Butler P.M., Hopwood A.T. 1957. Insectivora and chiroptera from the Miocene rocks of Kenya colony. *Fossil Mammals of Africa*, 13. London: British Museum (Natural History). P. 1–35.
- Cooper L.N., Seiffert E.R., Clementz M.T. et al. 2014. Anthracobunids from the Middle Eo-

- cene of India and Pakistan are stem perissodactyls. — PLoS One, 9 (10): e109232.
- Corbet G.B., Hanks J. 1968. A revision of the elephant-shrews, family Macroscelididae. — Bulletin of the British Museum (Natural History), Zoology, 16 (2): 45–111.
- Cote S., Werdelin L., Seiffert E.R., Barry J.C. 2007. Additional material of the enigmatic Early Miocene mammal *Kelba* and its relationship to the order Ptolemaiida. — Proceedings of the National Academy of Sciences USA, 104 (13): 5510–5515.
- Court N. 1990. Periotic anatomy of *Arsinoitherium* (Mammalia, Embrithopoda) and its phylogenetic implications. — Journal of Vertebrate Paleontology, 10 (2): 179–182.
- Court N. 1992a. The skull of *Arsinoitherium* (Mammalia, Embrithopoda) and the higher interrelationships of ungulates. — Palaeovertebrata, 22 (1): 1–43.
- Court N. 1992b. A unique form of dental bilophodonty and a functional interpretation of peculiarities in the masticatory system of *Arsinoitherium* (Mammalia, Embrithopoda). — Historical Biology, 6 (2): 91–111.
- Court N. 1993. Morphology and functional anatomy of the postcranial skeleton in *Arsinoitherium* (Mammalia, Embrithopoda). — Palaeontographica, A: Palaeozoologie, Stratigraphie, 226 (4–6): 125–169.
- Court N., Mahboubi M. 1993. Reassessment of lower Eocene *Seggeurius amourensis*: Aspects of primitive dental morphology in the mammalian order Hyracoidea. — Journal of Paleontology, 67 (5): 889–893.
- de Graaff G. 1957. A new chrysochlorid from Makapansgat. — Palaeontologia Africana, 5: 21–27.
- Domning D.P. 2001. The earliest known fully quadrupedal sirenian. — Nature, 413 (6856): 625–627.
- Domning D.P., Ray C.E., McKenna M.C. 1986. Two new Oligocene desmostylians and a discussion of Tethytherian systematics. — Smithsonian Contributions to Paleobiology, 59: 1–56.
- Domning D.P., Zalmout I.S., Gingerich P.D. 2010. Sirenia. — Werdelin L., Sanders W.J. (eds). Cenozoic mammals of Africa. Berkeley: University of California Press. P. 147–160.
- Douady C.J., Catzeflis F.M., Raman J. et al. 2003. The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews). — Proceedings of the National Academy of Sciences USA, 100 (14): 8325–8330.
- Gheerbrant E. 1994. Les mammifères paléocènes du Bassin d'Ouarzazate (Maroc). II. Todralestidae (Proteutheria, Eutheria). — Palaeontographica, Abteilung A: Palaeozoologie, Stratigraphie, 231 (4–6): 133–188.
- Gheerbrant E. 1995. Les mammifères paléocènes du Bassin d'Ouarzazate (Maroc). III. Adapisoriculidae et autres mammifères (Carnivora, ?Creodonta, Condylarthra, ?Ungulata et incertae sedis). — Palaeontographica, Abt. A: Palaeozoologie, Stratigraphie, 237 (1–4): 39–132.
- Gheerbrant E. 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. — Proceedings of the National Academy of Sciences USA, 106 (26): 10717–10721.
- Gheerbrant E., Amaghaz M., Bouya B. et al. 2014. *Ocepeia* (Middle Paleocene of Morocco): The oldest skull of an afrotherian mammal. — PLoS One, 9 (2): e89739.
- Gheerbrant E., Bouya B., Amaghaz M. 2012. Dental and cranial anatomy of *Eritherium azzouzor* from the Paleocene of Morocco, earliest known proboscidean mammal. — Palaeontographica, Abt. A: Palaeozoologie, Stratigraphie, 297 (5–6): 151–183.
- Gheerbrant E., Domning D.P., Tassy P. 2005a. Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives). — Rose K.D., Archibald J.D. (eds). The rise of placental mammals. Origins and relationships of the major extant clades. Baltimore: Johns Hopkins University Press. P. 84–105.
- Gheerbrant E., Sudre J., Cappetta H. 1996. A Palaeocene proboscidean from Morocco. — Nature, 383 (6595): 68–70.
- Gheerbrant E., Sudre J., Cappetta H., Bignot G. 1998. *Phosphatherium esculliei* du Thané-

- tien du Bassin des Ouled Abdoun (Maroc), plus ancien proboscideen (Mammalia) d'Afrique. — *Geobios*, 31 (2): 247–269.
- Gheerbrant E., Sudre J., Cappetta H. et al. 2002. A new large mammal from the Ypresian of Morocco: Evidence of surprising diversity of early proboscideans. — *Acta Palaeontologica Polonica*, 47 (3): 493–506.
- Gheerbrant E., Sudre J., Tassy P. et al. 2005b. Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Éocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lo phodontes. — *Geodiversitas*, 27 (2): 239–333.
- Goloboff P.A. 1999. NONA (ver. 1.9). Software published by the author, S.M. de Tucuman, Argentina. [www.cladistics.org](http://www.cladistics.org).
- Goswami A., Prasad G.V.R., Upchurch P. et al. 2011. A radiation of arboreal basal eutherian mammals beginning in the Late Cretaceous of India. — *Proceedings of the National Academy of Sciences USA*, 27 (108): 16333–16338.
- Gradstein F.M., Ogg J.G., Smith A.I. 2004. A geologic time scale 2004. Cambridge (MA): Cambridge University Press. 589 p.
- Gunnell G.F., Gingerich P.D., Holroyd P.A. 2010. Ptolemaia. — Werdelin L., Sanders W.J. (eds). *Cenozoic mammals of Africa*. Berkeley: University of California Press. P. 83–87.
- Guthrie R.D. 2004. Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea island. — *Nature*, 429 (6993): 746–749.
- Hartenberger J.-L. 1986. Hypothèse paléontologique sur l'origine des Macroscelidea (Mammalia). — *Comptes rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre*, 302 (5): 247–249.
- Hautier L., Sarr R., Tabuce R. et al. 2012. First proramphid sirenian from Senegal (Western Africa) and the Old World origin of sea cows. — *Journal of Vertebrate Paleontology*, 32 (5): 1218–1222.
- Holroyd P.A. 2010a. Macroscelidea. — Werdelin L., Sanders W.J. (eds). *Cenozoic mammals of Africa*. Berkeley: University of California Press. P. 89–98.
- Holroyd P.A. 2010b. Tubulidentata. — Werdelin L., Sanders W.J. (eds). *Cenozoic mammals of Africa*. Berkeley: University of California Press. P. 107–111.
- Holroyd P.A., Mussell J.C. 2005. Macroscelidea and Tubulidentata. — Rose K.D., Archibald J.D. (eds). *The rise of placental mammals: Origins and relationships of the major extant clades*. Baltimore: The Johns Hopkins University Press. P. 71–83.
- Hooker J.J., Russell D.E. 2012. Early Palaeogene Louisinidae (Macroscelidea, Mammalia), their relationships and north European diversity. — *Zoological Journal of the Linnean Society*, 164 (4): 856–936.
- Inuzuka N. 2000. Primitive late Oligocene desmostylians from Japan and phylogeny of the Desmostylia. — *Bulletin of the Ashoro Museum of Paleontology*, 1: 91–123.
- Kaya T.T. 1995. *Palaeoamasia kansui* (Mammalia) in the Eocene of Bultu-Zile (Tokat-Northeastern Turkey) and systematic revision of *Palaeoamasia*. — *Turkish Journal of Earth Science*, 4: 105–111.
- Kitching J.W. 1965. A new giant hyracoid from the Limeworks Quarry, Makapansgat, Potgietersrus. — *Palaeontologica Africana*, 9: 91–96.
- Lehmann T. 2006. Biodiversity of the Tubulidentata over geological time. — *Afrotherian Conservation*, 4: 6–11.
- Lehmann T. 2008. Plio-Pleistocene aardvarks (Mammalia, Tubulidentata) from East Africa. — *Fossil Record*, 11 (2): 67–81.
- Lehmann T. 2009. Phylogeny and systematics of the Orycteropodidae (Mammalia, Tubulidentata). — *Zoological Journal of the Linnean Society*, 155 (3): 649–702.
- Lehmann T., Vignaud P., Likies A., Brunet M. 2005. A new species of Orycteropodidae (Mammalia, Tubulidentata) in the Mio-Pliocene of northern Chad. — *Zoological Journal of the Linnean Society*, 143 (1): 109–131.
- Lehmann T., Vignaud P., Likies A. et al. 2006. A sub-complete fossil aardvark (Mammalia, Tubulidentata) from the Upper Miocene of

- Chad. — *Comptes Rendus Paleovol*, 5 (5): 693–703.
- Lehmann T., Vignaud P., Mackaye H.T., Brunet M. 2004. A fossil aardvark (Mammalia, Tubulidentata) from the lower Pliocene of Chad. — *Journal of African Earth Sciences*, 40 (5): 201–217.
- Maas M.C., Thewissen J.G.M., Kappelman J. 1998. *Hypsamasia seni* (Mammalia: Embriothopoda) and other mammals from the Eocene Kartal Formation of Turkey. — *Bulletin of Carnegie Museum of Natural History*, 34: 286–297.
- MacPhee R.D.E. 1994. Morphology, adaptations, and relationships of *Plesiorycteropus*: and a diagnosis of a new order of eutherian mammals. — *Bulletin of the American Museum of Natural History*, 220: 1–214.
- Madsen O., Scally M., Douady C.J. et al. 2001. Parallel adaptive radiations in two major clades of placental mammals. — *Nature*, 409 (6820): 610–614.
- Malia M.J., Adkins R.M., Allard M.W. 2002. Molecular support for Afrotheria and the polyphyly of Lipotyphla based on analyses of the growth hormone receptor gene. — *Molecular Phylogenetics and Evolution*, 24 (1): 91–101.
- McDowell S.B. 1958. The Greater Antillean insectivores. — *Bulletin of the American Museum of Natural History*, 115: 113–214.
- McKenna M.C. 1975. Towards a phylogenetic classification of the Mammalia. — Lockett W.P., Szalay F.S. (eds). *Phylogeny of the Primates*. New York: Plenum Press. P. 21–46.
- McKenna M.C., Manning E.M. 1977. Affinities and palaeobiogeographic significance of the Mongolian Paleogene genus *Phenacolphus*. — *Geobios, Memoire Special*, 1: 61–85.
- 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.
- Mess A., Carter A.M. 2006. Evolutionary transformations of fetal membrane characters in Eutheria with special reference to Afrotheria. — *Journal of Experimental Zoology. Part B: Molecular and Developmental Evolution*, 306 (2): 140–163.
- Miller E.R., Rasmussen D.T., Kappelman J. et al. 2015. *Ptolemaia* from West Turkana, Kenya. — *Bulletin of the Peabody Museum of Natural History*, 56 (1): 81–88.
- Murphy W.J., Eizirik E., Johnson W.E. et al. 2001. Molecular phylogenetics and the origins of placental mammals. — *Nature*, 409 (6820): 614–618.
- Novacek M.J. 1984. Evolutionary stasis in the elephant-shrew, *Rhynchocyon*. — Eldredge N., Stanley S.M. (eds). *Living Fossils*. New York: Springer. P. 4–22.
- Novacek M.J. 1986. The skull of leptictid insectivores and the higher-level classification of eutherian mammals. — *Bulletin of the American Museum of Natural History*, 183: 1–112.
- Novacek M.J., Wyss A.R. 1986. Higher-level relationships of the Recent eutherian orders: morphological evidence. — *Cladistics*, 2 (3): 257–287.
- Novacek M.J., Wyss A.R., McKenna M.C. 1988. The major groups of eutherian mammals. — Benton M.J. (ed). *The phylogeny and classification of the Tetrapods, Vol. 2: Mammals*. The Systematics Association, Special Volume. 35B: 31–71.
- O’Leary M.A., Bloch J.I., Flynn J.J. et al. 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. — *Science*, 339 (6120): 662–667.
- Osborn H.F. 1908. New fossil mammals from the Fayum Oligocene, Egypt. — *Bulletin of the American Museum of Natural History*, 24: 265–272.
- Owen R. 1855. On the fossil skull of a mammal (*Prorastomus sirenoides*, Owen) from the island of Jamaica. — *Quarterly Journal of the Geological Society of London*, 11: 541–543.
- Owen R. 1875. On *Prorastomus sirenoides* (Ow.). — Part II. — *Quarterly Journal of the Geological Society of London*, 31: 559–567.
- Patterson B. 1965. The fossil elephant shrews (family Macroscelididae). — *Bulletin of the Museum of Comparative Zoology*, 133 (6): 297–336.
- Patterson B. 1975. The fossil aardvarks (Mammalia: Tubulidentata). — *Bulletin of the*

- Museum of Comparative Zoology, 147 (5): 185–237.
- Penkrot T.A., Zack S.P., Rose K.D., Bloch J.I. 2008. Postcranial morphology of *Apheliscus* and *Haplomyilus* (Condylarthra, Apheliscidae): Evidence for a Paleocene Holarctic origin of Macroscelidea. — Sargis E.J., Dagosto M. (eds). *Mammalian Evolutionary Morphology. A Tribute to Frederick S. Szalay*. Dordrecht: Springer. P. 73–106.
- Pickford M. 1975. New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. *Orycteropus minutus* sp. nov. and *Orycteropus chemeldoi* sp. nov. — *Netherlands Journal of Zoology*, 25 (1): 57–88.
- Pickford M., Hlusko L.J. 2007. Late Miocene procaviid hyracoids (Hyracoidea: *Dendrohyrax*) from Lemudong'o, Kenya. — *Kirtlandia*, 56: 106–111.
- Pickford M., Senut B., Morales J., Mein P., Sanchez I.M. 2008. Mammalia from the Lutetian of Namibia. — *Memoir of the Geological Survey of Namibia*, 20: 465–514.
- Poduschka W., Poduschka C. 1985. Zur Frage des Gattungsnamens von "*Geogale*" *altris* Butler und Hopwood, 1957 (Mammalia, Insectivora) aus dem Miozän Ostafrikas. — *Zeitschrift für Säugetierkunde*, 50: 129–140.
- Prasad G.V.R., Jaeger J.-J., Sahni A. et al. 1994. Eutherian mammals from the Upper Cretaceous (Maastrichtian) Intertrappean Beds of Naskal, Andhra Pradesh, India. — *Journal of Vertebrate Paleontology*, 14 (2): 260–277.
- Prasad G.V.R., Verma O., Gheerbrant E. et al. 2010. First mammal evidence from the Late Cretaceous of India for biotic dispersal between India and Africa at the KT transition. — *Comptes Rendus Palevol*, 9 (1–2): 63–71.
- Radulesco C., Iliesco G., Iliesco M. 1976. Découverte d'un Embrithopode nouveau (Mammalia) dans la Paléogène de la dépression de Hateg (Roumanie) et considération générales sur la géologie de la région. — *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* (11): 690–698.
- Radulesco C., Sudre J. 1985. *Crivadiatherium iliescui* n. sp., nouvel embrithopode (Mammalia) dans le Paleogene ancien de la Depression de Hateg (Roumanie). — *Palaeo-vertebrata*, 15 (3): 139–157.
- Rasmussen D.T. 1989. The evolution of the Hyracoidea. — Prothero D.R., Schoch R.R. (eds). *The Evolution of Perissodactyls*. New York: Oxford University Press. P. 57–78.
- Rasmussen D.T., Gutiérrez M. 2010. Hyracoidea. — Werdelin L., Sanders W.J. (eds). *Cenozoic mammals of Africa*. Berkeley: University of California Press. P. 123–145.
- Rasmussen D.T., Pickford M., Mein P. et al. 1996. Earliest known procaviid hyracoid from the Late Miocene of Namibia. — *Journal of Mammalogy*, 77 (3): 745–754.
- Ray C.E., Domning D.P., McKenna M.C. 1994. A new specimen of *Behemotops proteus* (Mammalia: Desmostylia) from the marine Oligocene of Washington. — Berta A., Deméré T.A. (eds). *Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr.* Proceedings of the San Diego Society of Natural History, 29: 205–222.
- Rohland N., Reich D., Mallick S., Meyer M., Green R.E., Georgiadis N.J., Roca A.L., Hofreiter M. 2010. Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. — *PLoS Biology*, 8 (12): e1000564.
- Rose K.D., Holbrook L.T., Rana R.S. et al. 2014. Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. — *Nature Communications*, 5: 5570.
- Sánchez-Villagra M.R., Narita Y., Kuratani S. 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. — *Systematics and Biodiversity*, 5 (1): 1–7.
- Sanders W.J., Gheerbrant E., Harris J.M. et al. 2010a. Proboscidea. — Werdelin L., Sanders W.J. (eds). *Cenozoic mammals of Africa*. Berkeley: University of California Press. P. 161–251.
- Sanders W.J., Kappelman J., Rasmussen D.T. 2004. New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. — *Acta Palaeontologica Polonica*, 49 (3): 365–392.
- Sanders W.J., Nemeč W., Aldinucci M. et al. 2014. Latest evidence of *Palaeoamasia* (Mammalia, Embrithopoda) in Turkish Anatolia.

- Journal of Vertebrate Paleontology, 34 (5): 1155–1164.
- Sanders W.J., Rasmussen D.T., Kappelman J. 2010b. Embrithopoda. — Werdelin L., Sanders W.J. (eds). Cenozoic mammals of Africa. Berkeley: University of California Press. P. 115–122.
- Savage R.J.G., Domning D.P., Thewissen J.G.M. 1994. Fossil Sirenia of the west Atlantic and Caribbean region. V. The most primitive known sirenian, *Prorastomus sirenoides* Owen, 1855. — Journal of Vertebrate Paleontology, 14 (3): 427–449.
- Schwartz G.T., Rasmussen D.T., Smith R.J. 1995. Body-size diversity and community structure of fossil hyracoids. — Journal of Mammalogy, 76 (4): 1088–1099.
- Seiffert E.R. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. — BMC Evolutionary Biology, 7: 224.
- Seiffert E.R. 2010. The oldest and youngest records of afrosoricid placentals from the Fayum Depression of northern Egypt. — Acta Palaeontologica Polonica, 55 (4): 599–616.
- Seiffert E.R., Simons E.L. 2000. *Widanelfarasia*, a diminutive placental from the late Eocene of Egypt. — Proceedings of the National Academy of Sciences USA, 97 (6): 2646–2651.
- Seiffert E.R., Simons E.L., Ryan T. et al. 2007. New remains of Eocene and Oligocene Afrosoricida (Afrotheria) from Egypt, with implications for the origin(s) of afrosoricid zalambdodonty. — Journal of Vertebrate Paleontology, 27 (4): 963–972.
- Sen S., Heintz E. 1979. *Palaeoamasia kansui* Ozansoy 1966, embrithopode (Mammalia) de l'Eocene de Anatolie. — Annales de Paléontologie (Vertébrés), 65 (1): 73–91.
- Shoshani J. 1986. Mammalian phylogeny: comparison of morphological and molecular results. — Molecular Biology and Evolution, 3 (3): 222–242.
- Shoshani J., Goldman C.A., Thewissen J.G.M. 1988. *Orycteropus afer*. — Mammalian Species, 300: 1–8.
- Simons E.L., Bown T.M. 1995. Ptolemaiida, a new order of Mammalia, with description of the cranium of *Ptolemaia grangeri*. Proceedings of the National Academy of Sciences USA, 92 (8): 3269–3273.
- Simons E.L., Holroyd P.A., Bown T.M. 1991. Early tertiary elephant-shrews from Egypt and the origin of the Macroscelidea. — Proceedings of the National Academy of Sciences USA, 88 (21): 9734–9737.
- Simpson G.G. 1945. The principles of classification and a classification of mammals. — Bulletin of the American Museum of Natural History, 85: I–XVI +1–350.
- Smit H.A., Jansen van Vuuren B., O'Brien P.C.M. et al. 2011. Phylogenetic relationships of elephant-shrews (Afrotheria, Macroscelididae). — Journal of Zoology, 284 (2): 133–143.
- Smith T., De Bast E., Sigé B. 2010. Euarchontan affinity of Paleocene Afro-European adapisoriculid mammals and their origin in the late Cretaceous Deccan Traps of India. — Naturwissenschaften, 97 (4): 417–422.
- Springer M.S., Amrine H.M., Burk A., Stanhope M.J. 1999. Additional support for Afrotheria and Paenungulata, the performance of mitochondrial versus nuclear genes, and the impact of data partitions with heterogeneous base composition. — Systematic Biology, 48 (1): 65–75.
- Springer M.S., Cleven G.C., Madsen O. et al. 1997. Endemic African mammals shake the phylogenetic tree. — Nature, 388 (6637): 61–64.
- Springer M.S., Stanhope M.J., Madsen O., Jong W.W., de 2004. Molecules consolidate the placental mammal tree. — Trends in Ecology and Evolution, 19 (8): 430–438.
- Stanhope M.J., Madsen O., Waddell V.G. et al. 1998a. Highly congruent molecular support for a diverse superordinal clade of endemic African mammals. — Molecular Phylogenetics and Evolution, 9 (3): 501–508.
- Stanhope M.J., Waddell V.G., Madsen O. et al. 1998b. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. — Proceedings of the National Academy of Sciences USA, 95 (17): 9967–9972.
- Sudre J., Jaeger J.-J., Sigé B., Vianey-Liaud M. 1993. Nouvelles données sur les Condylarthres du Thanétien et de l'Yprésien du Bas-

- sin d'Ouarzazate (Maroc). — *Geobios*, 26 (5): 609–615.
- Tabuce R., Coiffait B., Coiffait P.-E. et al. 2001. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: a possible origin for elephant-shrews. — *Journal of Vertebrate Paleontology*, 21 (3): 535–546.
- Tabuce R., Jaeger J.-J., Marivaux L. et al. 2012. New stem elephant-shrews (Mammalia, Macroscelidea) from the Eocene of Dur At-Talah, Libya. — *Palaeontology*, 55 (5): 945–955.
- Tabuce R., Marivaux L., Adaci M. et al. 2007. Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. — *Proceedings of the Royal Society B: Biological Sciences*, 274 (1614): 1159–1166.
- Tassy P., Shoshani J. 1988. The Tethytheria: elephants and their relatives. — Benton M.J. (ed.). *The phylogeny and classification of the Tetrapods, Volume 2: Mammals. The Systematics Association Special Volume. 35B*. Cambridge (UK): Cambridge University Press. P. 283–315.
- van Dijk M.A.M., Madsen O., Catzeflis F.M. et al. 2001. Protein sequence signatures support the African clade of mammals. — *Proceedings of the National Academy of Sciences USA*, 98 (1): 188–193.
- Vartanyan S.L., Garutt V.E., Sher A.V. 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. — *Nature*, 362 (6418): 336–339.
- Vialle N., Merzeraud G., Delmer C. et al. 2013. Discovery of an embrithopod mammal (*Ar-sinoitherium?*) in the late Eocene of Tunisia. — *Journal of African Earth Sciences*, 87: 86–92.
- Werdelin L. 2010. *Bibymalagasia* (Mammalia *Incertae Sedis*). — Werdelin L., Sanders W.J. (eds). *Cenozoic Mammals of Africa*. Berkeley: University of California Press. P. 113–114.
- Zack S.P., Penkrot T.A., Bloch J.I., Rose K.D. 2005. Affinities of “hyopsodontids” to elephant shrews and a Holarctic origin of Afrotheria. — *Nature*, 434 (7032): 497–501.