NEW SAUDI ARABIAN MIOCENE JUMPING MOUSE (ZAPODIDAE): SYSTEMATICS AND PHYLOGENY

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ABSTRACT — Early Miocene zapodids from Saudi Arabia are represented by two closely related species: *Arabosminthus quadratus* and *Arabosminthus isabellae* sp. nov. The new taxon differs from the other species of Asiatic zapodids in lacking the anteroconid on m1. A cladistic analysis involving species of *Arabosminthus*, *Heterosminthus*, *Parasminthus*, and *Shamosminthus* provides evidence that "*Heterosminthus*" *gansus*, and perhaps "*Gobiosminthus*" *qiui*, and "*Parasminthus*" *huangshuiensis* should be reallocated to *Arabosminthus*. This genus appears to represent an important clade of zapodid rodents basal to *Parasminthus* spp.+ *Heterosminthus* spp.

KEY WORDS: Rodentia, Zapodidae, Miocene, Saudi Arabia, phylogeny.

INTRODUCTION

The Saudi-French paleontological Research Project carried out between 1977 and the early 1980s resulted in the discovery of several Early and Middle Miocene mammal localities near the coast of the Arabian Gulf, Saudi Arabia (Fig.1). The Dam Formation in the As Sarrar area is less than 80 km from the coast and all its sections display interbedded continental and marine indicating the proximity of the sea shore (Thomas and Battail, 1980). Thus, during deposition of the Dam Formation, the area of As-Sarrar was a transitional zone, particularly sensitive to environmental changes (Thomas and Battail, 1980). Thomas et al. (1982) published preliminary results of this field work and recognised at least 66 species from the late Early Miocene faunas of the As-Sarrar area.

Four sites have yielded rodent remains in the As-Sarrar area. Among these, locality 21 has produced representatives of the Zapodidae (jumping mice). In this paper, we follow the classification adopted by Daxner-Höck (1999), according to which the two families Zapodidae and Dipodidae are independent. Extant zapodids, which are essentially restricted to the palearctic and nearctic biogeographic realms, are typically divided in Zapodinae and Sicistinae. Nevertheless, there is presently no consensus as to the classification of extinct zapodids at the sub-family level.

The aim of this paper is to provide (1) a systematic determination of zapodid teeth from Saudi Arabia including description and comparison of new specimens; (2) a cladistic analysis of the relationships among the species currently ascribed to *Parasminthus*, *Heterosminthus*, *Arabosminthus*, *Gobiosminthus*, and *Shamosminthus* and a discussion on their systematics.

The terminology used in the tooth descriptions follows the standard rodent dental terminology of Wang (1985), with some adjustments taken from Klingener (1963), see Fig. 2.

Acronyms — **AS**, As Sarrar; **GIN**, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; **IAUU**, Institute of Earth Sciences, Universiteit Utrecht, The Netherlands; **IPSP**, Institutul Pedagogic de Stat "T. Shevchenko", Laboratoriia paleontologii, Kishinev, Moldavia; **IVPP**, Institute of Vertebrate Paleontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHM**, Natural History Museum, London, United Kingdom; **NHMW**, Naturhistorisches Museum, Wien, Austria; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **PIU**, Paleontologisk Institut, Uppsala Universitet, Sweden; **T.b.**, Taben-buluk.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family ZAPODIDAE Coues, 1876

Genus *ARABOSMINTHUS* Whybrow, Collinson, Daams, Gentry, and McClure, 1982

Arabosminthus isabellae sp. nov.

Etymology — In honor of María Isabel Antoñanzas Asso.

Holotype — AS21-1200 (Fig. 3A), a left m1.

Paratypes — AS21-1201 (Fig. 3B), right m1; AS21-1202 (Fig. 3C), AS21-1203 (Fig. 3D), AS21-1204 (Fig. 3E), left m2s; AS21-1205 (Fig. 3F), right m2; AS21-1206

(Fig. 3G), left M1, AS21-1207 (Fig. 3H), left M1. All material is housed in the collections of MNHN. Size data for each tooth is provided in table 1.

Type locality — Loc. 21, As Sarrar area, Saudi Arabia (26°59'01"N; 48°23'14"E).

Horizon — Dam Formation (Lower Miocene).

Age — late Early Miocene (c. 15-17 Ma).

Diagnosis— Species of *Arabosminthus* with bunodont teeth; m1 with the four main cusps isolated, but with mesostylid and a well-developed ectostylid, and lacking anteroconid, mesolophid, and ectomesolophid; m2 with no protoconid-anteroconid connection, lacking mesolophid, anterior and posterior arms of the protoconid, and often mesoconid, and metalophulid II, but having a short metalophulid I; roughly quadrangular upper molars having very short mesoloph and metaloph II, and a very small valley behind the metacone.

Differential diagnosis— *Arabosminthus isabellae* differs from *Arabosminthus quadratus* in having a short mesoloph on M1, in the absence of mesoconid on m1 and frequently on m2. *Arabosminthus isabellae* differs from *Parasminthus cubitalus*, *Parasminthus tangingoli*, *Parasminthus parvulus*, *Parasminthus asiaecentralis*, *Parasminthus debruijini* in the absence of mesolophid on the lower molars, and a short mesoloph on the upper molars. *Arabosminthus isabellae* is distinct from *Parasminthus quartus* in having isolated main cuspids, in lacking anteroconid and mesolophid on m1 and metalophulid II, mesostylid, and mesolophid on m2. *Arabosminthus isabellae* differs from *Parasminthus xiningensis* and *Parasminthus lajeensis* in having a short mesoloph, a poorly developed metaloph II and an extremely small valley behind the metacone on the upper molars. *Arabosminthus isabellae* differs from *Parasminthus huangshuiensis* in having a short mesoloph on the upper molars.

Arabosminthus isabellae is distinct from *Heterosminthus orientalis*, *H. firmus*, and *H. honestus* in lacking ectomesolophid on m1 and metalophulid II on m2, and in having a short mesoloph on the upper molars. *Arabosminthus isabellae* is distinct from *H. jucundus*, *H. nanus*, and *H. erbajevae* in lacking ectomesolophid on the lower molars, and in having a short mesoloph on the upper molars. *Arabosminthus isabellae* differs from *H. mugodzharicus* in having no ectomesolophid on m1 nor anterostyle, protostyle, mesostyle, and metaloph II on the upper molars. *Arabosminthus isabellae* is distinct from "*H.*" *gansus* in lacking ectomesolophid on m1 and in having the occlusal surface of M1 square in outline. *Arabosminthus isabellae* differs from *H. lanzhouensis* in having no ectomesolophid on m1 nor protoconule on M1. *Arabosminthus isabellae* is different from *H. intermedius* in the lack of ectomesolophid and mesolophid on the lower molars and in having a short mesoloph on the upper molars.

Remark — An isolated left M1 (MS2-NMPC7) referred to as *Heterosminthus* sp. from the Marada Formation, Jebel Zelten, Libya (Wessels et al., 2003), possibly pertains to *Arabosminthus isabellae*.

DESCRIPTION

m1 — The two complete m1 found are roughly trapezoidal in outline, being narrower in their anterior part. They are distinctly bunodont and two rooted. There is no anteroconid and the four main cusps (protoconid, hypoconid, metaconid, and entoconid) are isolated. The main anterior cusps, as well as the posterior ones, are close to each other in opposite positions. AS21-1201 shows a weak V-shaped connection between protoconid and metaconid. The protoconid and metaconid are subequal in size, but the former is slightly more posteriorly located than the latter. The mesolophid and

ectomesolophid are absent. The entoconid is shifted forwards and transversely aligned with the well-developed ectostylid. The hypoconid is situated posterior to the entoconid. The posteroconid is pronounced and the posterolophid lacks a labial arm, whereas the lingual one is attached to the posterolingual edge of the entoconid.

m2 — The occlusal outline of m2 is rectangular. The four main cusps alternate, with the lingual ones being anterior to the labial ones. In AS21-1204, the anterolophid arises from the anteroexternal side of the protoconid. Except for this specimen, in which the metaconid and the anteroconid are merged in the anterolophid, these cusps appear differentiated. There is no protoconid-anteroconid connection. Thus, the postmetaconid fold meets the preprotoconid fold and forms a continuous S-shaped anterior sinusid. There is no anterior and no posterior arm of the protoconid. The mesolophid and metalophulid II are lacking, and a short metalophulid I connects the anteroconid with the metaconid. In all second molars, the ectostylid and ectomesolophid are absent, and only AS21-1203 shows a mesoconid, which is fused with the hypolophid. The protoconid-hypolophid-entoconid connection is continuous and very oblique. Except for AS21-1204, the hypoconid and the posterolophid are not connected. The connection between the prehypoconid and postentoconid folds is interrupted centrally. The posterolophid has no labial arm and its lingual arm continues onto the entoconid. The posteroconid is a pronounced oval cuspid lower than the remaining cusps.

M1 — They are roughly quadrangular in occlusal outline and their cusps are rounded. The lingual cusps are anteriorly situated with respect to the labial ones. The anterior arm of the protocone is continuous with the anteroloph, which does not extend to the antero-labial corner of the tooth. The connexion between the paracone and the protocone is simple; there is no double connection. The posterior arm of the protocone joins with the paracone, forming the protoloph II. The mesoloph and the metaloph II are

extremely short. The valley behind the metacone is very small. The posteroloph is developed and joins with the posterior arm of the hypocone. The sinus is broad and oblique antero-externally.

COMPARISONS

Comparison with *Arabosminthus quadratus* Whybrow, Collinson, Daams, Gentry, and McClure, 1982 — The holotype of this species (NHM M43024, Fig. 4B) is a right M2 (Whybrow et al., 1982:5) from the Lower Miocene locality of Jabal Midra ash-Shamali, Hadrukh Formation, Saudi Arabia (Fig. 1). The tooth morphology of this species is very close to that of *Arabosminthus isabellae*. The M1 of *A. quadratus* show a long mesolophid (Fig. 4A) whereas in *A. isabellae* it is very short. One of the differences between the m1 of *A. quadratus* (Fig. 4C) and that of *A. isabellae* is the presence of a mesoconid only in the former species. Only one very worn m2 of *A. quadratus* (Fig. 4D) has been found and its anterior part is missing. Its posterior morphology is very close to that of *A. isabellae*. However, whereas the m2 of *Arabosminthus quadratus* has a well developed mesoconid, only one of the three m2s of *Arabosminthus isabellae* shows a small mesoconid.

Asiazapus Lopatin and Zazhigin, 2000

This genus was established by Lopatin and Zazhigin (2000:452) on the basis of one tooth from the Lower Miocene Akzhar Formation of Batpaksunde (Eastern Kazakhstan). This specimen was believed to be a first lower molar of Zapodinae, more than twice as long as the m1 of all living and extinct species of the genus *Zapus* (and other Zapodinae). In fact, it is similar to d4 of *Sayimys* aff. *obliquidentis* from the middle

members of the Chul'adyr Formation (Lower Miocene) of the Aktau Mountains, Kazakhstan (Kordikova and de Bruijn, 2001). Both teeth have a metalophulid II, an isolated anteroconid, a nearly transverse hypolophid, and the metaflexid not anteriorly directed. The size of the d4 described and figured by Kordikova and de Bruijn (2001) is, at 2.05 x 1.28 mm, smaller than that given by Lopatin and Zazhigin (2000), but both can reasonably be considered as within the intra-specific range of size variation of the d4 of *S. obliquidens*.

Consequently, the holotype of *Asiazapus ingens* should be recognized as from *Sayimys obliquidens*, the holotype of which (Bohlin, 1946) comes from the Lower Miocene (?) locality of Taben-buluk (Gansu, China). *Asiazapus ingens* Lopatin and Zazhigin, 2000 is invalid; it is a junior synonym of *Sayimys obliquidens* Bohlin, 1946.

Bohlinosminthus Lopatin, 1999

Lopatin (1999:433) coined this genus for material from the Lower Miocene Altynshokysu locality of the Aral Formation, North Aral Region, Kazakhstan (Fig. 1). He reallocated *Parasminthus parvulus* Bohlin, 1946 and *Parasminthus quartus* Shevyreva, 1970 to this new genus. He argued that *Bohlinosminthus* differs from *Parasminthus* in being smaller, in lacking metaloph II on the M1 and protoloph II on the M2, and in having a greater development of the mesolophid in relation to the posterior arm of the protoconid on the m2. The presence of a metaloph II is a variable character; on the M1 of *P. asiaecentralis* from Ulanatal only 50% of the specimens show a metaloph linking with the posteroloph or posterior arm of hypocone ("metaloph II" sensu Wang, 1985:fig. 1) whereas in the remaining specimens the metaloph joins the central side of the hypocone ("metaloph" sensu Wang, 1985:fig. 1) (Huang, 1992:275). Consequently, both genera can hardly be differentiated in this respect.

According to Lopatin (1999:433), the M2 of *Bohlinosminthus* lacks the protoloph II. However, it appears that this genus has a developed a protoloph II on the M2 (see Lopatin, 1999:fig. 3n). In addition, this is also a very variable character; on the M2 of *Parasminthus asiaecentralis* from Ulanatal (Huang, 1992:276), some specimens have only a protoloph I, a few specimens show double protoloph, whereas the remaining ones present a weak protoloph II. Finally, the structural mesolophid variants described by Lopatin (1999:435) for the m2 of *Bohlinosminthus* are very similar to those described by Huang (1992:276) for *Parasminthus*.

For all these reasons, the characters put forth by Lopatin (1999) to distinguish *Bohlinosminthus* from *Parasminthus* appear of poor utility. In addition, the genus *Bohlinosminthus* as composed by Lopatin (1999) appears paraphyletic (see below).

In conclusion, it appears that *Bohlinosminthus* Lopatin, 1999 is a junior synonym of *Parasminthus* Bohlin, 1946. Thus, we reallocate to the genus *Parasminthus* the three species (*Parasminthus parvulus* Bohlin, 1946, *Parasminthus quartus* Shevyreva, 1970, and *Bohlinosminthus cubitalus* Lopatin, 1999) assigned by Lopatin (1999:433) to *Bohlinosminthus*.

Parasminthus Bohlin, 1946

The genus *Parasminthus* was erected by Bohlin (1946:15) based on zapodid material found in Taben-buluk, Gansu, China (Fig. 1). Later, more material of *Parasminthus* was recorded in the "middle" Oligocene of Ulanatal, Nei Mongol (Huang, 1992) (Fig. 1). Huang (1992) gave a diagnosis of this genus on the basis of this new material and Bohlin's (1946) descriptions.

Whether *Parasminthus* is distinct is controversial. In fact, some authors consider it a junior synonym of *Plesiosminthus* (Stehlin and Schaub, 1951:152; [Schaub](#),

1958:788; Kowalski, 1974:168; Li and Qiu, 1980; Li and Ting, 1983:48; McKenna and Bell, 1997:133) or a subgenus of *Plesiosminthus* (Wilson, 1960:86; Shevyreva, 1970; Lindsay, 1977). On the other hand, on the basis of ungrooved upper incisors and four roots on the upper molars of *Parasminthus*, other authors consider this genus to be different from *Plesiosminthus* (Engesser, 1979; Hugueney and Vianey-Liaud, 1980; Wang, 1985:362-363; Martin, 1994:102; Wang and Qiu, 2000; Dawson, 2003), the alternative we opt for. As mentioned above, Lopatin (1999:432) included *Parasminthus parvulus* and *Parasminthus quartus* in the new genus *Bohlinosminthus*, and he reallocated *Parasminthus xiningensis* to *Shamosminthus* and *Parasminthus lajeensis* to *Gobiosminthus*. However, we agree with Wang (1985) in recognizing all these species as *Parasminthus* representatives, following the results of the cladistic analysis conducted below.

Comparison with *Parasminthus asiaecentralis* Bohlin, 1946—The holotype of this species (T. b. 593 b) is a left maxillary fragment with P4-M3 (Bohlin, 1946), from a horizon at Taben-buluk, Gansu, China (Fig. 1), that is possibly Early Miocene in age (Wang et al., 2003a). This species has been also recorded in the "middle" Oligocene of Ulanatal, Nei Mongol (Huang, 1992), from the Late Oligocene Xianshuihe Formation, in Shangxigou, Lanzhou Basin of Gansu (Wang and Qiu, 2000), from Late Oligocene beds of the "Ulunguhe" Formation at Tiersihabahe, Junggar Basin of Xinjiang, China (Ye et al., 2003), and from the Late Oligocene-Early Miocene biozone D of the Loh Formation, Central Mongolia (Höck et al., 1999:118) (Fig. 1). *Parasminthus* cf. *asiaecentralis* is also mentioned from the Early and Late Oligocene (biozones B and C respectively) of the Hsanda Gol-Loh formations, Central Mongolia (Höck et al., 1999:115-116) (Fig. 1). The *Parasminthus* cf. *asiaecentralis* from the Early Miocene of

the Suosuoquan Formation of the Tieersihabahe-Chibaerwoyi cliffs, Junggar Basin, Xinjiang, China, would actually represent a still unpublished new species (Qiu and Li, 2003; Ye et al., 2003).

The m1 of *Parasminthus asiaecentralis* are distinct from those of *Arabosminthus isabellae* in having a metalophulid II, a small but distinctive mesoconid, and a mesolophid very developed. In addition, the m2 of *A. isabellae* lack the mesolophid or the pseudomesolophid, whereas one of them is always present in *P. asiaecentralis*. Finally, the morphology of the upper molars of *P. asiaecentralis* differs from that of the only specimen of *A. isabellae* in having a well-developed mesolophid, a mesostyle in most specimens, and a metalophid. The teeth of *P. asiaecentralis* are slightly longer, but similar in width to those of the Arabian species.

Comparison with *Parasminthus tangingoli* Bohlin, 1946—The holotype of this species (T.b. 593 a) is a fragmentary right maxilla with P4-M2 (Bohlin, 1946:23) from the Lower Miocene (?) of Taben-buluk, Gansu, China (Fig. 1). This species has been subsequently recorded in the "middle" Oligocene of Ulantatal, Nei Mongol (Huang, 1992), in the Late Oligocene Xianshuihe Formation, in Xiagou and Shangxigou, Lanzhou Basin of Gansu (Wang and Qiu, 2000), in the Late Oligocene beds of the "Ulunguhe" Formation at Tieersihabahe, Junggar Basin of Xinjiang, China (Ye et al., 2003), and in the Late Oligocene biozone C of the Hsanda Gol-Loh formations, Central Mongolia (Höck et al., 1999:115-116) (Fig. 1). *Parasminthus* aff. *tangingoli* was mentioned in the Early Miocene Aral Formation of Kazakshtan by Bendukidze (1993:43-44) and, more recently, Bayshashov et al. (1999) cited *P. tangingoli* at Ayakoz (Early Miocene, Eastern Kazakstan) (Fig. 1).

The m1 of *Parasminthus tangingoli* show a strong mesolophid and a mesoconid, which are absent in the specimens of *Arabosminthus isabellae*. The m2 of *P. tangingoli* differs from that of *A. isabellae* in the presence of the mesolophid. The M1 morphology of *P. tangingoli* mainly differs from that of *A. isabellae* in having a mesocone, a very developed mesoloph, and a metaloph that generally connects with the central side of the hypocone.

Comparison with *Parasminthus parvulus* Bohlin, 1946—The holotype (T.b. 592 a) of this species is a right maxillary fragment with root of P4, the posterior half of the crown of M1 and complete M2 and M3 (Bohlin, 1946:30) from the Lower Miocene (?) of Taben-buluk, Gansu, China (Fig. 1). This species has been also recorded in the Upper Oligocene of the Xianshuihe Formation, in Xiagou and Shangxigou, Lanzhou Basin of Gansu, (Wang and Qiu, 2000), in Late Oligocene beds of the "Ulunguhe" Formation at Tieersihabahe, Junggar Basin of Xinjiang, China (Ye et al., 2003), and from the Upper Oligocene biozones C and C₁ of the Hsanda Gol-Loh formations, Central Mongolia (Höck et al., 1999:115-116) (Fig. 1). *P. parvulus* may be also present in the Early Miocene of the Baiyinbaolidao Sumu area, Nei Mongol, China (Qiu and Wang, 1999).

This species has a long mesoloph on the upper molars that reaches the labial border of the tooth, the valley behind the metacone is large, and the metacone connects with the hypocone at the middle of this cusp. In contrast, the M1 of *Arabosminthus isabellae* have a very small valley behind the metacone, a very short mesoloph, and the metacone connecting to the posteroloph at its labial part.

The m1 in *Parasminthus parvulus* shows an isolated anteroconid, a long mesolophid, and the main cusps connected by crests. The m1 of *Arabosminthus isabellae* has isolated cusps and lacks anteroconid and mesolophid. On the m2 of *P. parvulus*, the protoconid and metaconid are separated from the anterolophid by a groove

and a mesolophid or pseudomesolophid is present, whereas in *A. isabellae* the anteroconid and metaconid are separated from the protoconid by a groove and there is no mesolophid or pseudomesolophid.

Comparison with *Parasminthus cubitalus* (Lopatin, 1999)—The holotype of *Parasminthus cubitalus* (IAUU ALT 115) is a fragmentary left mandible with m2 (Lopatin, 1999:fig. 3u, 2004:fig. 33h), from the Lower Miocene Aral Formation of Altynshokysu, western Kazakhstan (Fig. 1).

Parasminthus cubitalus is distinguished from *Arabosminthus isabellae* by the presence of distinct anteroconid, mesoconid, and mesolophid on m1. In addition, the first lower molars of the Arabian species show an isolated mesostylid, whereas the mesostylid is connected to the mesoconid by a mesolophid in *P. cubitalus*. The m2 of *P. cubitalus* shows a long mesolophid and a mesostylid, which is absent on the m2 of *A. isabellae*. With regard to the upper molars, those of *P. cubitalus* show a well developed metaloph joining the central side of the hypocone (metaloph sensu Wang, 1985). In contrast, on the M1 of *A. isabellae*, the metaloph is poorly developed and connects to the posteroloph (metaloph II sensu Wang, 1985). *P. cubitalus* has the mesoloph well developed, whereas it is weak in *A. isabellae*. Besides the differences in molar morphology, *P. cubitalus* is smaller than *A. isabellae*.

Comparison with *Parasminthus quartus* Shevyreva, 1970—

Synonym: *Parasminthus parvulus*: Bohlin, 1946 (partim)

The holotype of this species (2259-430) is a left m1 from the Early Oligocene of Kyzyl-Kak, Betpakdala Svita, Central Kazakhstan (Shevyreva, 1970:88) (Fig. 1). The m1 of *P. quartus* shows an isolated anteroconid, a developed mesolophid, and the main

cusps connected by crests. In contrast, the Arabian m1 lacks the anteroconid and the mesolophid, and has the main cusps isolated.

The m2 of *Parasminthus quartus* shows the metalophulid II, a well developed mesostylid, the anteroconid joining the protoconid, and the metastylid and the mesolophid connecting to the metaconid. In contrast, m2 in *Arabosminthus isabellae* lacks metalophulid II, mesostylid and mesolophid, and the anteroconid does not join the protoconid.

Comparison with *Parasminthus debruijni* Lopatin, 1999—The holotype of this species (IAUU ALT 49) is a right M2 (Lopatin, 1999: fig. 3c, 2004: fig. 32c) from the Lower Miocene Aral Formation at Altynshokysu, Kazakhstan (Fig. 1).

The M1 in *Parasminthus debruijni* shows a mesocone connected to a mesostylid by a long and narrow mesoloph and a very developed metaloph. Conversely, the M1 in *Arabosminthus isabellae* has no mesocone or metaloph, and shows a very short mesoloph. The Arabian m1 differs from those of *P. debruijni* in having the main cusps isolated and in the absence of mesoconid and mesolophid. The m2 morphology is also very different: whereas in *P. debruijni* shows the mesolophid, mesoconid, mesostylid, and, in most specimens, a pseudomesolophid, in *A. isabellae* these structures are lacking and only AS21-1004 shows the mesoconid.

Comparison with *Parasminthus xiningensis* (Li and Qiu, 1980) — The holotype of this species (IVPP V 5996) is a complete right maxilla with P4-M3 from the Early Miocene Xiejia village, Huangzhong County, Qinghai Province, China (Li and Qiu, 1980) (Fig. 1). No lower molar of this species has been found so far. Lopatin (1999:433), without justification, reallocated this species to the genus *Shamosminthus*.

Yet Huang (1992:283) established *Shamosminthus* on the basis of some characters such as the presence of metaloph II (metaloph joining the posterior arm of the hypocone) on M1. In contrast, *Parasminthus xiningensis* does not show metaloph II but metaloph I (metaloph connecting with the anterior arm of the hypocone) and should not be reallocated to *Shamosminthus* (contra Lopatin, 1999:433).

Parasminthus xiningensis is distinct from *Arabosminthus isabellae* in having a long mesoloph, a well developed mesocone, a mesostyle, a metaloph I and a large valley behind the metacone on the upper molars.

Comparison with "*Parasminthus*" *huangshuiensis* (Li and Qiu, 1980) — "*Parasminthus*" *huangshuiensis* is known so far only from the Lower Miocene of the Xiejia village, Huangzhong County, Qinghai Province, China (Li and Qiu, 1980) (Fig. 1). The holotype (IVPP V 5997) and unique specimen of this species is a left maxillary fragment with M1 and M2 (Li and Qiu, 1980:fig. 5, incorrectly mentioned as right in the caption). "*Parasminthus*" *huangshuiensis* differs from *Arabosminthus isabellae* in being much larger and in having a long mesoloph on the upper molars. As explained below, this species may prove to belong in *Arabosminthus*.

Comparison with *Parasminthus lajeensis* (Li and Qiu, 1980) — The holotype and unique specimen of this species (IVPP V 5998) is a left M1 (or M2) that comes from the Early Miocene of Xiejia Village, Huangzhong County, Qinghai Province, China (Li and Qiu, 1980) (Fig. 1). Lopatin (1999:433) without justification reallocated this species to *Gobiosminthus*. According to Huang (1992:281), *Gobiosminthus* is characterized by a metaloph II linked with the posteroloph, whereas in *P. lajeensis* it is linked to the center of the hypocone. Additionally, the valley behind the metacone is

open and small in *Gobiosminthus* (Huang, 1992:fig. 2) whereas it is large and closed in *P. lajeensis* (Li and Qiu, 1980:fig. 6). Therefore, we reject the proposal of Lopatin (1999) to reallocate *P. lajeensis* to *Gobiosminthus*, whose validity is questioned below.

The M1 of *Parasminthus lajeensis* shows a lophate molar morphology and has a long mesoloph. In contrast, the M1s of *Arabosminthus isabellae* show an extremely short mesoloph.

Heterosminthus Schaub 1930

Comparison with *Heterosminthus orientalis* Schaub, 1930 —

Synonyms: *Paracricetulus schaubi* (partim) Young, 1927

Protalactaga tunggurensis Wood, 1936

Young (1927:figs. 7-9, pl. II) originally described this species as *Paracricetulus schaubi* on the basis of three right and two left mandibular fragments and one left maxilla from the uppermost Middle Miocene (Xianshuihe Formation) of Xianshuihe, Gansu, China (Fig. 1). According to Schaub (1930:627), the maxilla described by Young (1927:fig. 7, pl. II) was indeed a Cricetinae, but the mandibular fragment (Young, 1927: figs. 8-9, pl. II), which was designated as the new species *Heterosminthus orientalis*, should be referred to Sicistinae. Based on rodent material from the Middle Miocene Tunggur Formation of Nei Mongol (Fig. 1), Wood (1936) coined the species *Protalactaga tunggurensis*. According to Qiu (1996:189), the holotype of *Protalactaga tunggurensis* is identical to the type of *Heterosminthus orientalis* and very similar to all specimens pertaining to this species. We agree with Qiu (1996, 2000) and with Wang et al. (2003b) in considering this species a junior synonym of *Heterosminthus orientalis*.

The holotype (PIU unnumbered) of this species is a fragmentary right mandible with m1-m3 (Young, 1927:figs. 8-9, pl. II; Schaub, 1930:fig. 10). *Heterosminthus orientalis* has been recorded in a number of localities in the Tunggur Formation of Nei Mongol (Qiu and Qiu, 1995; Qiu and Wang, 1999; Wang et al., 2003b:table 1), in which it is the most common rodent. Additional material has been reported (as the case may be as *Protalactaga tunggurensis*) from the lowermost Middle Miocene Chetougou Formation at Longzhigou (Minhe County) and Danshuilu (Huzhu County), Qinghai (Qiu et al., 1981; Qiu, 1996), from the Middle Miocene of the Dingjiaergou Village area (Tongxin County), Ningxia (Qiu and Qiu, 1995), from the Upper Miocene "Amuwusu beds" of Nei Mongolia (Qiu, 1988; Qiu and Wang, 1999), China, and from the Middle Miocene Oshin Formation in Kazakhstan at the localities Sharga 1 and 2, Naran-Bulak, and Khirgis-Nur 1, 2 (Zazhigin and Lopatin, 2000) (Fig. 1). In addition, the presence of *H. orientalis* in the Early Miocene of the Baiyinbaolidao Sumu area, Nei Mongol, China, is pointed out by Qiu and Wang (1999). Ünay et al. (2003b) mentioned the presence of *H. orientalis* in the Middle Miocene of Anatolia. This material is still awaiting description.

The M1 in *Heterosminthus orientalis* have a complete mesoloph, and both the lingual and labial arms of the posteroloph are well developed, whereas on the M1 of *Arabosminthus isabellae* the mesoloph is short and the posteroloph has only the labial arm. Contrary to the condition observed in *A. isabellae*, the m1 in *H. orientalis* have an anteroconid and a developed ectomesolophid. In addition, whereas the m2 in *H. orientalis* show a metalophulid II, those of *A. isabellae* lack it.

Comparison with *Heterosminthus firmus* Zazhigin and Lopatin, 2000 — The holotype of this species is a fragmentary right maxilla with M1 and M2 (PIN 4051/105)

that comes from the Lower Miocene locality of Ayaguz, eastern Kazakhstan (Zazhigin and Lopatin, 2000) (Fig. 1). This species has been also recorded from the Early-Middle Miocene biozone D₁ of the Loh Formation, Central Mongolia (Daxner-Höck, 2001:368). *Heterosminthus* cf. *firmus* has been mentioned in Late Oligocene-Early Miocene biozones (C₁ and D) of the Loh Formation, Central Mongolia (Daxner-Höck, 2001:370) (Fig. 1). In addition, *H.* cf. *firmus* could be present in Turkish Oligo-Miocene boundary sites such as Kargi 2 (Ünay et al., 2003a:fig. 2, 2003b), though apparently the material has been previously suggested to belong to *H. orientalis* (Theocharopoulos, 2000:table 6). Finally, we believe that the *Heterosminthus* sp. 2 ("small species") from the Early Miocene Suosuoquan Formation, West of the Chibaerwoyi area, Junggar Basin, Xinjiang, China (Ye et al., 2003:fig. 25.1h, i), fits well with *Heterosminthus firmus*.

The morphology of the lower molars of *Heterosminthus firmus* is very distinct from *Arabosminthus isabellae*. The m1 in *H. firmus* show a well developed anteroconid, a mesoconid, a strong metalophulid II, hypolophid, and ectomesolophid. In contrast, all these structures are absent on the m1 of *A. isabellae*. In the m2 of *H. firmus* (Daxner-Höck, 2001:figs. 8, 11, pl. 4), the long anterior arm of the protoconid and the short metalophulid I connect with the anteroconid, whereas in those of *Arabosminthus isabellae*, the anterior arm of the protoconid is very short or absent. The M1 of *H. firmus* is rectangular in shape, the labial part of the anteroloph joins or nearly joins the paracone, and it shows a complete mesoloph and a metaloph I. In contrast, the M1 in *A. isabellae* are quadrangular in shape, show a very short mesoloph, and lack the metaloph.

Comparison with *Heterosminthus mongoliensis* Zazhigin and Lopatin, 2000 — The holotype of this species (GIN 960/11) is a fragmentary left mandible with m1 and m2 from uppermost Lower Miocene sediments at Ulaan-Tolgoi (Loh Formation), Central Mongolia (Zazhigin and Lopatin, 2000) (Fig. 1). Other specimens of this species were also collected in Lower Miocene sediments of the Loh Formation at the type and Ulaan-Tolgoi localities, Central Mongolia (Daxner-Höck, 2001:371) (Fig. 1). Ünay et al. (2003b) mentioned *Heterosminthus* cf. *mongoliensis* in the Middle Miocene of Anatolia, but no detail was provided.

The M1 of this species differs from *Arabosminthus isabellae* in having a long arm of the protocone, a long mesoloph, and a metaloph. Contrary to the condition in the m1 of *A. isabellae*, the m1 of *H. mongoliensis* shows a short mesolophid and a long and pronounced ectomesolophid, which are absent in the Arabian specimens. The m2 in *H. mongoliensis* are distinct from those of *A. isabellae* in showing a pseudomesolophid or a metalophulid II and in bearing occasionally a short ectomesolophid.

Comparison with *Heterosminthus honestus* Zazhigin and Lopatin, 2000 — The holotype of this species (PIN 4059/2115) is an isolated right M2 from the Early Miocene Batpaksunde locality, Kenderlyk, Akzhar Formation, eastern Kazakhstan (Zazhigin and Lopatin, 2000) (Fig. 1). The main difference between the M1 of this species and those of *Arabosminthus isabellae* is the presence in the former of a complete mesoloph, a long metaloph and a posteroloph with both arms well developed. In addition, the m1 of *H. honestus* usually show a complete mesolophid and ectomesolophid, which are absent in *A. isabellae*. In the m2 of *H. honestus*, the posterior arm of the protoconid forms a metalophulid II or a pseudomesolophid, and

sometimes the ectomesolophid is developed. In contrast, the m2 of *A. isabellae* lack a metalophulid II and a pseudomesolophid, and no specimen shows an ectomesolophid.

Comparison with *Heterosminthus nanus* Zazhigin and Lopatin, 2000 — The holotype of this species (PIN 4059/2121) is an isolated right M1 from the Lower Miocene (Akzhar Formation) locality of Batpaksunde, eastern Kazakhstan (Fig. 1). Additional specimens come from the Lower Miocene Kensirik and Vertoletnaya localities of Eastern Kazakhstan (Zazhigin and Lopatin, 2000) (Fig. 1).

Heterosminthus nanus is distinct from *Arabosminthus isabellae* in having generally an endostyle, a complete mesoloph, and a large metaconule on the M1 as well as a mesolophid and ectomesolophid on the lower molars. *H. nanus* is also significantly smaller.

Comparison with *Heterosminthus jucundus* Zazhigin and Lopatin, 2000 — The holotype of this species (PIN 2977/4020) is an isolated right M2 from the Middle Miocene (Sarybulak Formation) locality of Point "I", eastern Kazakhstan (Zazhigin and Lopatin, 2000) (Fig. 1). Additional material comes from the Lower Miocene Point "I" and Middle Miocene Belyi Pup localities, Eastern Kazakhstan (Zazhigin and Lopatin, 2000) (Fig. 1).

This species is distinguished from *Arabosminthus isabellae* in bearing a complete mesoloph, a double anteroloph, and a large metaconule on the M1, and in having ectolophid on the m1 and ectomesolophid on the m2.

Comparison with *Heterosminthus mugodzharicus* Zazhigin and Lopatin, 2000 — The holotype (GIN 1106/2) of this species is a fragmentary mandible with m1 from the

lowermost Upper Miocene locality of Shet-Irgiz, western Kazakhstan (Zazhigin and Lopatin, 2000:fig. 5o) (Fig. 1). The M1 of *H. mugodzharicus* is distinct from that of *Arabosminthus isabellae* in having the anterostyle, protostyle, mesostyle, metaloph II, and very developed labial and lingual arms of the posteroloph. The m1 in *H. mugodzharicus* shows a very developed ectomesolophid which is lacking in *A. isabellae*.

Comparison with "*Heterosminthus*" *gansus* Zheng, 1982 —

Synonyms: *Heterosminthus simplicidens* Zheng, 1982

Bujoromys olarui Lungu, 1981

Sarmatosminthus gabunia Lungu, 1981 (partim)

This species was described and illustrated by Zheng (1982:141, figs. 3A-C) on the basis of one left mandibular fragment with m1 and m2 (the holotype, V6305) and a left isolated m2 from the Upper Miocene (Qiu, 1996:189) Tianzhu locality 80007, Gansu Province, China (Fig. 1). According to Qiu (1996:189-191), all species from the Tianzhu locality would be in fact *Lophocricetus gansus*. However, Zazhigin and Lopatin (2000) pointed out that the connection of cusps in the lower and upper molars of "*Heterosminthus*" *gansus* rather recalls the condition in *Heterosminthus* than in *Lophocricetus*. Recently, much more additional material of this species has been recorded from the Upper Miocene (Loh Formation) locality of Builstyn Khudag, Mongolia (Daxner-Höck, 2001:371) (Fig. 1). Based on this abundant material, Daxner-Höck (2001:373) agreed with Zazhigin and Lopatin (2000) in accepting the combination "*Heterosminthus*" *gansus*. According to her, "*H.*" *gansus* is a very advanced species of *Heterosminthus*. Actually, the cladistic analysis conducted below suggests that this species should be reallocated to *Arabosminthus*. The morphology of the teeth of "*H.*"

gansus is close to that of *Arabosminthus isabellae*, but the M1 are larger and more rectangular in "*H.*" *gansus* than in *Arabosminthus isabellae*. In addition, these teeth sometimes show a protoconule, absent in *A. isabellae*. The m2 of both species are similar and the m1 only show slight differences like the presence of ectomesolophid in "*H.*" *gansus*. "*H.*" cf. *gansus* is mentioned in the Late Miocene of the Baogedawula Formation at Abaga Qi, Nei Mongol (Qiu and Wang, 1999) and in the Late Miocene of the Bahe Formation in the Lantian area, Shaaxi, China (Qiu et al., 2003) (Fig. 1).

Sarmatosminthus gabuniai (Lungu, 1981:75, figs. 6, 7a-b, 8a-b, pl. XII) was named on the basis of isolated M2, m1 and m2 (IPSP 2 (243-245)) from a lowermost Upper Miocene horizon near Bujor (Moldavia) (Fig. 1). Lungu (1981) referred this new genus to the subfamily Sicistinae. Later, Topachevsky et al. (1984) reallocated *Sarmatosminthus* to the Lophocricetinae. According to Zazhigin and Lopatin (2000:322), due to the similar dental pattern of this species with that of later members of *Heterosminthus* (such as "*Heterosminthus*" *gansus*), *S. gabuniai* must be reallocated to the genus *Heterosminthus*. The m1 and m2 of this species (Lungu, 1981:figs. 7a-b and 8a-b, pl. XII) are similar in size and morphology to the m1 and m2 of "*H.*" *gansus*, and probably pertain to this species. However, the M2 of *Sarmatosminthus gabuniai* (Lungu, 1981:fig. 6, pl. XII) does not seem to conform with "*H.*" *gansus*.

Bujoromys olarui was originally described by Lungu (1981:86, figs. 1a-d, pl. XII) on the basis of 11 m1s from a lowermost Upper Miocene horizon near Bujor (Moldavia) (fig. 1). The holotype m1 of this species is IPSP 2 (387). The morphology and size of the teeth correspond exactly with those of "*Heterosminthus*" *gansus* (Zheng, 1982:figs. 2A-B; Daxner-Höck, 2001:pl. 7), and we consider this species a junior synonym of "*H.*" *gansus*.

Comparison with *Heterosminthus lanzhouensis* Wang and Qiu, 2000 — The holotype of this species (IVPP V11773.1) is a left m1 (Wang and Qiu, 2000:fig. 2B, pl. III, 1-8) recorded from the Upper Oligocene Lower Member of the Xianshuihe Formation at Xiagou and Shangxigou, Lanzhou basin, Gansu, China (Fig. 1).

The M1 is distinct from those of *Arabosminthus isabellae* in having a protoconule, a complete mesoloph, a mesocone, and a large valley behind the metacone. The m1 of *Heterosminthus lanzhouensis* differ from that of *A. isabellae* in showing a developed anteroconid, a complete mesolophid, a distinct mesoconid, an ectomesolophid, but no ectostylid. Some differences between the m2 of *H. lanzhouensis* and those of *Arabosminthus isabellae* rest in the connection of the anterior arm of the protoconid with the anteroconid and the posterior arm with the metastylid or the posterior wall of the metaconid. In addition, some m2 of *Heterosminthus lanzhouensis* show a metalophid whereas in those of *Arabosminthus isabellae* is lacking.

Comparison with *Heterosminthus intermedius* Wang, 2003 — The holotype of this species (IVPP V 13597) is a fragment of muzzle with right I2, left and right P4-M2, a right mandibular fragment with i2 and m1-m3, and a left mandibular fragment with i2 and m1-m2, probably belonging to the same individual (Wang, 2003:101). This material comes from the middle part of the Tiejiaogou Formation, of probably Early Miocene age, at Aksay Kazak, Gansu, China (Wang, 2003) (Fig. 1).

The m1 in *Heterosminthus intermedius* shows an isolated anteroconid, a V-shaped metalophid II, a well developed mesolophid, and a long and transverse ectomesolophid. In contrast, all these structures are lacking in the m1 of *Arabosminthus isabellae*.

The dental pattern of m2 in *Heterosminthus intermedius* and *Arabosminthus isabellae* are very different. *H. intermedius* shows a well developed mesoconid, mesolophid, and a weak ectomesolophid whereas in *A. isabellae* the mesoconid is often absent (except for AS21-1203) and there is no mesolophid nor ectomesolophid.

The M1 in *Heterosminthus intermedius* are distinct from those of *Arabosminthus isabellae* in being more rectangular, and in having a strong protoconule and mesoloph, and a developed posterior arm of the protocone.

Comparison with *Heterosminthus erbajevae* Lopatin, 2001 — The holotype of this species (PIN 4800/3) is a right mandibular ramus with m1 from the Middle Miocene Aya locality, Yelantsy, Baikal region, eastern Siberia (Lopatin, 2001:200) (Fig. 1).

Heterosminthus erbajevae is very different from *Arabosminthus isabellae*. The m1 of *H. erbajevae* shows a very small anteroconid connecting to the metaconid by a narrow crest. Besides, it has a well developed metalophulid II, a mesolophid and ectomesolophid, which are absent in the m1 of *A. isabellae*. The upper molars of *H. erbajevae* are also distinct from those of *A. isabellae* in being rectangular, and in having a strong mesocone connecting to a long mesoloph, anterostyle, and protostyle.

Comparison with "*Gobiosminthus*" *qiui* Huang, 1992 — The holotype of this species is a right maxillary fragment with M1-M3 (IVPP V10167, UTL7a) from the "middle" Oligocene of the Ulanatal area, Nei Mongol (Huang, 1992) (Fig. 1). No lower molar of this species has been found to date.

One of the differences between "*Gobiosminthus*" *qiui* and *Arabosminthus isabellae* is the characteristic upper molar morphology of "*G.*" *qiui* with deep and

narrow sinuses. Besides, the M1 in *A. isabellae* show a very short mesoloph, whereas it is long in "*G.*" *qiui*.

Comparison with *Shamosminthus tongi* Huang, 1992 — The holotype of this species (IVPP V10315, UTL8b) is a fragment of maxilla with P4-M3. It comes from the "middle" Oligocene of the Ulanatal area, Nei Mongol (Huang, 1992) (Fig. 1). No lower molar of this species has been found so far.

M1 in *Shamosminthus tongi* is more rectangular than in *Arabosminthus isabellae*. In addition, in *S. tongi* the valley behind the metacone is larger and the mesoloph longer than in the M1 of *A. isabellae*.

Comparison with "*Shamosminthus*" *sodovis* Daxner-Höck, 2001 — The holotype of this species is a fragmentary left maxilla with M1-M2 (NHMW 2001z0034/0001/1) from the Early Oligocene biozones A and B of the Hsanda Gol Formation, Valley of Lakes, Central Mongolia (Daxner-Höck, 2001:366) (Fig. 1). Other Early Oligocene localities of the Valley of Lakes, Central Mongolia, have yielded additional material of this species (Daxner-Höck, 2001) (Fig. 1). "*S.*" cf. *sodovi* [sic] is mentioned in the Early Oligocene of the Anatolian locality of Yeniköy (Ünay et al., 2003a:fig. 2).

The morphology of the teeth of "*Shamosminthus*" *sodovis* is very different from that of *Arabosminthus isabellae*. The m1 in "*Shamosminthus*" *sodovis* shows a V-shaped metalophulid II, a short mesolophid, and a well developed mesoconid, whereas the m1 in *A. isabellae* lacks all these structures. The m2 in "*Shamosminthus*" *sodovis* has a mesolophid, which is absent on the m2 of *A. isabellae*. The upper molars have a protoloph I and a medium mesoloph in "*Shamosminthus*" *sodovis*, while the M1 in *A. isabellae* lacks protoloph I and has a shorter mesoloph.

As explained below, the validity of the genus *Shamosminthus* is questionable and "*Shamosminthus*" *sodovis* may have to be reallocated to another genus in the future.

SYSTEMATICS AND PHYLOGENY

The relationships of zapodid rodents remain very poorly and partially known despite several investigations by Chinese authors. According to Qiu et al. (1981:table 1), the lineage *Parasminthus parvulus*-*P. lajeensis* is an early offshoot of a phylogenetic tree in which the lineages *Parasminthus asiaecentralis*-*Parasminthus huangshuiensis* and *Parasminthus tangingoli*-(*Protalactaga* spp. + *Parasminthus xiningensis*) are "sister-groups". Later, Wang (1985:fig. 26) presented a cladogram of early zapodids according to which *Parasminthus* + *Sinosminthus* is the sister group of *Heosminthus* + *Plesiosminthus*; however, this phylogenetic reconstruction was not based on a computer-assisted processing of a character/taxon matrix with parsimony analysis. In contrast, Wang and Qiu (2000) provided a cladogram of zapodid taxa using the Branch and Bound search of PAUP 3.1.1 (Fig. 5). They found that *Banyuesminthus*, *Allosminthus*, *Sinosminthus*, *Heosminthus*, *Plesiosminthus*, *Parasminthus parvulus*, *Parasminthus tangingoli* + *Parasminthus asiaecentralis*, *Gobiosminthus*, and *Shamosminthus* constitute a sequence of successive sister-taxa to (*Heterosminthus*, *Protalactaga*). Qiu (1996:figs. 47 and 49) previously suggested the paraphyly of *Parasminthus* by proposing the existence of two lineages: *Parasminthus parvulus*-*Heterosminthus*-*Lophocricetus* and *Parasminthus asiaecentralis*-*Protalactaga*-*Allactaga*.

Further, Russian researcher Lopatin (1999) thought that *Heosminthus* gave rise independently to *Plesiosminthus* and *Bohlinosminthus*, and considered *Sinosminthus* (or

a closely related form) to be the ancestor of *Parasminthus*, *Gobiosminthus*, and probably *Shamosminthus*. From *Shamosminthus* would have subsequently originated *Heterosminthus*, whereas *Gobiosminthus* could make a good candidate for the ancestor of *Protalactaga* (Lopatin, 1999; Zazhigin and Lopatin, 2000).

To clear up species level relationships within *Arabosminthus*, *Heterosminthus*, *Parasminthus*, and "*Shamosminthus*", a cladistic analysis using PAUP version 3.1.1 (Swofford, 1993) was conducted (fig. 6). The ingroup comprises *Arabosminthus isabellae* sp. nov., *A. quadratus*, *Heterosminthus erbajevae*, *H. firmus*, "*H.*" *gansus*, *H. honestus*, *H. intermedius*, *H. jucundus*, *H. lanzhouensis*, *H. mongoliensis*, *H. mugodzharcus*, *H. nanus*, *H. orientalis*, *Parasminthus asiaecentralis*, *P. cubitalus*, *P. debruijini*, *P. parvulus*, *P. tangingoli*, and "*Shamosminthus*" *sodovis*. The species "*Gobiosminthus*" *qiui*, "*P.*" *huangensis*, *P. lajeensis*, *P. quartus*, *P. xiningensis*, and "*S.*" *tongi* have been first excluded from the analysis as they are known at best by only lower or upper dentitions. Test runs of the analysis considering only upper or lower dentition characters resulted in largely unresolved trees. Polarity was determined by comparison with the outgroup taxon, *Allosminthus*, chosen essentially based on the phylogenetic analysis of Wang and Qiu (2000). *Allosminthus* probably represents an early side branch of the "general stock" of small dipodoids and forms a sister group to all the other known later zipodids according to Wang (1985:361).

Of 28 phylogenetically informative dental characters (Appendix 1), 23 are binary and 5 are multistate. Amongst the latter 5, three (3, 18, and 19) have two derived states while two (18 and 19) have five. Due to the lack of a priori information, the weight of all characters is identical (1). Because there is no rationale to order the multistate characters, all possible transformations of one state into another will cost one step. The relatively high number of terminal taxa and characters precluded the use of

exact algorithms, so a heuristic search by stepwise addition ('closest' option) was performed.

Three most parsimonious trees were generated, with the following characteristics: tree length = 77, CI = 0.481, RI = 0.680. The main features of the 50 % majority-rule consensus tree (Fig. 6) are as follows:

- 1) *Shamosminthus sodovis* is the most basal taxon of the ingroup.
- 2) "*Heterosminthus*" *gansus*, *Arabosminthus quadratus*, and *A. isabellae* form the sister-group to a clade including the remaining species of the ingroup. Whatever the optimization, this clade is supported by two exclusive synapomorphies located on m2: anteroconide-metaconide connection and continuous anterior sinusid.
- 3) Except for "*Heterosminthus*" *gansus*, included species of *Heterosminthus* form a monophyletic group, in which *H. lanzhouensis* is the most basal species. This clade is supported by two non exclusive synapomorphies whatever the optimization: M1 with protostyle and m1 with ectomesolophid.
- 4) All the species of *Parasminthus* form a monophyletic group. This clade is supported by one non exclusive synapomorphy whatever the optimization: m2 with mesostylide.

Contrary to Zazhigin and Lopatin (2000:331) and Daxner-Höck (2001:373), "*Heterosminthus*" *gansus* is not a highly advanced species of *Heterosminthus*. The topology of all three trees is consistent with a re-allocation of "*Heterosminthus*" *gansus* to *Arabosminthus*. *Arabosminthus* therefore appears as a key taxon to settle zapodid phylogeny. It bridges a previously unrecognized evolutionary "gap" between "*Shamosminthus*" *sodovis* and the species of *Parasminthus* plus *Heterosminthus*.

Contrary to recent suspicions (Qiu et al., 1981; Qiu, 1996; Wang and Qiu, 2000), *Parasminthus* is probably a monophyletic genus.

With respect to *Heterosminthus* phylogeny, Zazhigin and Lopatin (2000) and Lopatin (2001) proposed two lineages, one comprising *Heterosminthus firmus*, *H. honestus*, *H. jucundus*, *H. nanus*, and "*H.*" *gansus* on the one hand, and *Heterosminthus mongoliensis*, *H. erbajevae*, *H. orientalis*, and *H. mugodzhharicus* on the other hand. The topologies of our trees are not consistent with this hypothesis, but do support the suggestion of Daxner-Höck (2001:369), who placed *H. firmus* "intermediate" between *H. lanzhouensis* and *H. mongoliensis*. Our results also support Wang's (2003) opinion that *Heterosminthus intermedius* is more primitive than *H. orientalis*, but more advanced than *H. lanzhouensis*. In our analysis, the species of *Heterosminthus* are distributed in four main "lineages": 1) *H. lanzhouensis*, 2) *H. intermedius*, 3) *H. mongoliensis* + *H. orientalis*, and 4) the remaining species of *Heterosminthus*.

By adding in turn to the present analysis each of the incomplete species cited above, more can be suggested on **zapodid phylogeny**:

1) "*Gobiosminthus*" *qiui* branches as the sister-species of *Arabosminthus quadratus*, without further perturbing the topology of the cladogram as described above. Therefore, "*Gobiosminthus*" *qiui* **could eventually** be reallocated to *Arabosminthus*.

2) *Parasminthus lajeensis* falls within an unresolved node comprising also *P. cubitalus*, *P. debruijini*, and *P. parvulus*, with the remaining topology unchanged. The inclusion of "*Plesiosminthus*" *lajeensis* in *Parasminthus* is thus substantiated as is its closer relationship with *P. parvulus* than with the *Parasminthus asiaecentralis* + *Parasminthus tangingoli* clade (Wang, 1985). In contrast, the suggestion to transfer *P. lajeensis* to the genus *Gobiosminthus* (Lopatin, 1999:433) is unsupported.

3) *Parasminthus xiningensis* lies in an unresolved node with *P. parvulus* and *P. cubitalus*. The remaining part of the tree is unaffected. According to Wang (1985:363), "*Plesiominthus*" *xiningensis* should be reallocated to *Parasminthus* due to its affinity

with *P. asiaecentralis* and *P. tangingoli*. This reallocation is justified, though *P. xiningensis* is actually closer to *P. parvulus* and *P. cubitalus* than to *P. asiaecentralis* and *P. tangingoli*. The proposal of Lopatin (1999:433) to transfer *P. xiningensis* to *Shamosminthus* is in sharp contradiction with the present result.

4) "*Parasminthus*" *huangshuiensis* emerges as the sister-species of *Arabosminthus quadratus*, in a cladogram otherwise identical. Therefore, once better known this species might prove to represent *Arabosminthus* and not *Parasminthus*, in contrast to Wang's (1985:363) suggestion based on superficial resemblances with *P. asiaecentralis* and *P. tangingoli*.

5) *Parasminthus quartus* appears in an unresolved node with *P. asiaecentralis* + *P. tangingoli* and *P. debruijni* + (*Parasminthus cubitalus* + *Parasminthus parvulus*). The adjacent topology is not disturbed. The generic attribution of this species is therefore substantiated and the proposal to reassign it to the genus *Bohlinosminthus* (Lopatin, 1999:434), along with *Parasminthus cubitalus* and *Parasminthus parvulus*, is not sustained.

6) *Shamosminthus tongi* forms an unresolved clade with "*Heterosminthus*" *gansus* and *Arabosminthus isabellae* + *A. quadratus*; otherwise the tree is not changed. As *Shamosminthus tongi* is the type-species of the genus, *Shamosminthus* may prove to be a junior synonym of *Arabosminthus*, while *Shamosminthus sodovis* may merit a new genus name. With *Shamosminthus* a synonym of *Arabosminthus*, the suggestion of Zazhigin and Lopatin (2000:331) and Daxner-Höck (2001:370) to consider the former an ancestor of *Heterosminthus* makes more sense. On the contrary, the hypothesis in which *Heterosminthus* originates from *Parasminthus* (Qiu, 1996; Wang and Qiu, 2000) receives no support in the present analysis.

CONCLUSION

By Miocene times, zapodid rodents were a highly diversified group in Asia while curiously they are less often encountered in the rest of the Old World. The Lower Miocene of Saudi Arabia has yielded the two closely related species, *Arabosminthus quadratus* and *Arabosminthus isabellae* nov. sp. From an evolutionary viewpoint, *Arabosminthus* appears to be an important clade of zapodid rodents basal to *Parasminthus* spp. + *Heterosminthus* spp. It may have included as many as five species (*A. quadratus*, *A. isabellae* nov. sp., "*Heterosminthus*" *gansus*, "*Gobiosminthus*" *qiui*, "*Parasminthus*" *huangshuiensis*). The results of the systematic and phylogenetic survey that we have presented suggest that *Arabosminthus* representatives such as "*Heterosminthus*" *gansus* should be found in the Miocene of the northern regions of the Middle East. Given this, search for zapodids in the Miocene of the Middle East should be encouraged. As the possible Saudi-Libyan distribution of *Arabosminthus isabellae* suggests this region could have been a focal point in the dispersal of zapodids.

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FIGURE 1. Main distribution of the species of zapodid rodents analysed in this work. **1**, Bujor (Moldavia); **2**, Shet-Irgiz (Kazakhstan); **3**, Altynshokysu (Kazakhstan); **4**, Kyzyl-Kak (Kazakhstan); **5**, Ayakoz and Ayaguz (Kazakhstan); **6**, Batpaksunde, Kensirik and Vertoletnaya (Kazakhstan); **7**, Sarybulak (Kazakhstan); **8**, Aya (Siberia); **9**, Naran-Bulak and Khirgis-Nur (Mongolia); **10**, Sharga (Mongolia); **11**, Valley of Lakes (Central Mongolia); **12**, Tieersihabahe (Xinjiang, China); **13**, Aksay Kazak (Gansu, China); **14**, Shangxigou and Xiagou (Gansu, China); **15**, Tianzhu (Gansu, China); **16**, Xianshuihe (Gansu, China); **17**, Taben-buluk (Gansu, China); **18**, Danshuilu, Longzhigou and Xiejia (Qinghai, China); **19**, Dingjiaergou (Ningxia, China); **20**, Ulantatal (Nei Mongol, China); **21**, Amuwusu, AMNH Tairum Nor lower red bed, AMNH Tairum Nor upper red bed, AMNH Wolf Camp, IVPP Huerguolajin, IVPP Moergen level II, IVPP Moergen level V, 482, IVPP Roadmark 482, Abaga Qi (Nei Mongol, China); **22**, Jabal Midra ash-Shamali (Saudi Arabia); **23**, As-Sarrar (Saudi Arabia); **24**, Jebel Zelten (Libya).

FIGURE 2. Dental zapodid terminology used in this paper. Scale bar equals 1

mm.

FIGURE 3. *Arabosminthus isabellae* sp. nov. **A**, left m1 (AS21-1200, holotype, occlusal view). **B**, right m1 (AS21-1201, occlusal view). **C**, left m2 (AS21-1202, occlusal view). **D**, left m2 (AS21-1203, occlusal view) **E**, left m2 (AS21-1204, occlusal view). **F**, left m2 (AS21-1202, occlusal view). **G**, left M1 (AS21-1206, occlusal view). **H**, left M1 (AS21-1207, occlusal view). Scale bar equals 1 mm.

FIGURE 4. *Arabosminthus quadratus* **A**, right M1 (M43021, occlusal view). **B**, right M2 (M43024, holotype, occlusal view). **C**, right m1 (M43372, occlusal view). **D**, right m2 (M43028, occlusal view). Scale bar equals 1 mm.

FIGURE 5. Cladogram of Paleogene dipodids generated by Branch and Bound search of PAUP 3.1.1 taken from Wang and Qiu (2001).

FIGURE 6. Cladogram illustrating the relationships among *Arabosminthus*, *Heterosminthus*, *Parasminthus*, *Shamosminthus*, and *Gobiosminthus* species and the phylogenetic position of *Arabosminthus isabellae* sp. nov. Tree length 77, consistency index 0.481, and retention index 0.680. Bremer Index support values are circled at the appropriate nodes (which are designed by numbers 38 to 21)

TABLE 1. Occlusal measurements (mm) of the teeth of *Arabosminthus isabellae* sp. nov. from As-Sarrar (all obtained with Mitutoyo measuring equipment).

	Specimen	Length	Width
m1	AS21-1200	1.397	1.137
m1	AS21-1201	1.394	1.170
m2	AS21-1202	1.315	1.124
m2	AS8-1203	1.238	~0.940
m2	AS21-1204	1.286	1.045
m2	AS21-1205	1.357	1.212
M1	AS21-1206	1.373	1.224
M1	AS21-1018	—	—

APPENDIX I

Characters used in phylogenetic analysis. 23 characters are binary whereas 5 are multistate. The plesiomorphic state (0) was obtained by outgroup comparison with *Allosminthus ernos* Wang, 1985.

M1-2

1. Mesoloph on M1: (0) absent or short; (1) well developed.
2. Posterior concavity between the hypocone and posteroloph: (0) absent or weak; (1) well developed.
3. Number of roots: (0) three; (1) three or four; (2) four.
4. Protoloph I on M1: (0) present; (1) absent.
5. Protoloph II on M2: (0) absent or short; (1) present.
6. Protoloph I on M2: (0) present; (1) absent.
7. Metaloph on M1: metaloph or metaloph I (0); metaloph II (1).
8. Metaloph on M2: metaloph or metaloph I (0); metaloph II (1).
9. M1 valley behind metacone: (0) big; (1) small.
10. Arms of posteroloph: (0) labial arm developed; (1) labial and lingual arms developed.
11. Mesostyle on M1: (0) absent; (1) present.
12. Protostyle on M1 (0) absent; (1) present.
13. Anterostyle on M1 (0) absent; (1) present.

m1-2

14. Main cusps on molars: (0) not alternate; (1) alternate.

15. Anteroconid on m1: (0) isolated; (1) absent (2) joins protoconid; (3) joins metaconid; (4) joins metaconid and protoconid; (5) merged in anterolophid.
16. Anteroconid on m2: (0) isolated; (1) absent (2) joins protoconid; (3) joins metaconid; (4) joins metaconid-protoconid; (5) merged in anterolophid.
17. Anterior sinusid on m2: (0) interrupted; (1) continuous.
18. Mesolophid on m1: (0) absent or weak; (1) short; (2) long.
19. Mesolophid on m2: (0) absent or weak; (1) short; (2) long.
20. Pseudomesolophid on m2: (0) absent (1) present.
21. Ectolophid on m1: (0) present (1) absent.
22. Ectostylid on the m1: (0) absent; (1) present.
23. Mesostylid on m1: (0) absent; (1) present.
24. Ectostylid on m2: (0) absent; (1) present.
25. Mesostylid on m2: (0) absent; (1) present.
26. Metalophulid I on m1: (0) absent or weak; (1) present.
27. Ectomesolophid on m1 (0) absent; (1) present.
28. Ectomesolophid on m2 (0) absent; (1) present.

APPENDIX 2

Matrix of character codings used in the analysis of relationships of species of *Arabosminthus*, *Gobiosminthus*, *Heterosminthus*, *Parasminthus*, and *Shamosminthus*.

Characters are listed in Appendix I. *Allosminthus ernos* is used as outgroup. Character codings: 0, postulated plesiomorphic condition of character; 1 to 5, postulated derived conditions of character; -, uncodable character; ?, character state uncertain.

Taxa	Characters																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>Allosminthus ernos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parasminthus parvulus</i>	1	0	2	1	1	1	0	0	0	0	1	0	0	0	-	5	0	2	2	1	0	0	1	0	0	0	0	0
<i>P. tangingoli</i>	1	1	2	1	1	0	1	0	1	0	1	0	0	0	4	5	0	2	2	0	0	0	1	0	1	0	0	0
<i>P. asiae-centralis</i>	1	1	2	1	1	0	1	0	1	0	1	0	0	0	0	5	0	2	2	0	0	0	1	0	1	0	0	0
<i>P. quartus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	5	0	1	2	0	0	0	1	0	1	0	0	0
<i>P. cubitalus</i>	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	5	0	2	2	1	0	0	1	0	1	0	0	0
<i>P. debruijini</i>	1	0	1	1	1	0	1	0	0	0	1	0	0	0	1	5	0	2	2	1	0	1	1	0	1	1	0	0
<i>P. lajeensis</i>	1	0	?	?	?	1	1	?	0	?	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"P." <i>huangshuiensis</i>	1	0	2	1	1	1	1	1	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>P. xiningensis</i>	1	0	2	1	1	1	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Heterosminthus orientalis</i>	1	1	2	1	1	1	1	0	1	1	1	1	1	1	0	5	0	2	0	0	1	1	0	0	0	0	1	0
<i>H. mongoliensis</i>	1	1	2	1	1	1	1	?	1	1	1	1	1	1	0	4	0	2	0	1	1	1	1	0	0	0	1	0
<i>H. erbajevae</i>	1	1	2	1	1	1	1	0	1	1	1	1	1	1	3	?	0	0	?	?	1	1	0	?	?	1	1	?
<i>H. firmus</i>	1	1	2	1	1	0	1	0	1	1	1	0	1	1	3	5	0	2	1	0	0	1	1	0	0	1	1	0
<i>H. honestus</i>	1	1	2	1	1	0	1	0	0	1	1	0	1	1	3	5	0	2	1	0	0	1	1	1	0	1	1	1
<i>H. nanus</i>	1	1	2	1	1	0	1	0	1	1	1	0	1	1	3	5	0	2	1	0	0	1	1	1	0	1	1	1
<i>H. jucundus</i>	1	1	2	0	1	1	1	0	1	1	1	1	1	1	3	5	0	1	0	0	0	1	0	0	0	1	1	1
<i>H. mugodzhariensis</i>	0	1	2	1	?	?	?	1	?	1	1	1	1	1	2	?	?	1	?	?	1	1	0	?	?	1	1	?
<i>H. lanzhouensis</i>	1	1	2	1	1	1	1	0	1	0	1	1	0	1	4	4	0	2	2	0	0	1	1	0	0	0	1	0
<i>H. intermedius</i>	1	1	2	1	1	1	1	0	1	1	1	1	0	1	5	5	0	2	2	0	0	1	1	0	0	0	1	0
<i>Arabosminthus quadratus</i>	1	0	2	1	1	1	1	1	1	0	1	0	0	1	1	?	1	0	0	0	1	1	1	0	?	0	0	0
"H." <i>gansus</i>	0	1	2	1	1	1	1	0	1	0	0	1	1	1	0	3	1	0	0	0	0	1	0	0	0	0	1	0
<i>A. isabellae</i> sp. nov.	0	1	2	1	?	?	?	1	?	1	0	0	0	0	1	1	3	1	0	0	0	1	1	1	0	0	0	0
" <i>Gobiosminthus</i> " <i>qiui</i>	1	0	0	1	1	1	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
" <i>Shamosminthus</i> " <i>sodovis</i>	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	4	0	0	1	0	1	1	1	0	1	0	0	0
" <i>Shamosminthus</i> " <i>tongi</i>	0	1	2	1	1	1	1	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?