

**A brief review of the updated fossil vertebrate fauna of the upper
Eocene Ergilin Dzo Formation, southeastern Mongolia**

モンゴル南東部の上部始新統エルギリン・ゾー層における最新の化石脊椎動物相

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Abstract.

We briefly review the fossil vertebrate fauna of the upper Eocene Ergilin Dzo Formation of southeastern Mongolia. The Ergilin Dzo vertebrate fauna currently consists of 104 species of five classes: two species of the Osteichthyes, one species of the Amphibia, nine species of the Reptilia, 11 species of the Aves, and 81 species of the Mammalia. The Ergilin Dzo mammalian fauna currently consists of 11 orders, including six species of the Eulipotyphla, one species of the Anagalida, two species of the Mesonychia (= Acreodi), one species of the Cimolesta, two species of the Leptictida, four species of the Rodentia, four species of the Lagomorpha, five species of the Carnivora, eight species of the Hyaenodontida (= Hyaenodontidae), 13 species of the Artiodactyla, and 33 species of the Perissodactyla. In terms of the collected specimen numbers, the brontotheriid and rhinocerotid perissodactyls and ruminant artiodactyls are dominant among the vertebrate taxa of the formation.

Key words: Ergilin Dzo Asian Land Mammal Age (ALMA), Ergilin Dzo fauna, faunal list, Mammalia, Eocene, Vertebrata

Introduction

The upper Eocene Ergilin Dzo Formation (= Ergilin Dzo Svita in Russian literature) of southeastern Mongolia has been famous for yielding many terrestrial vertebrate fossils, including fish, amphibians, reptiles, birds, and mammals, since the early 20th Century (Berkey and Granger, 1923; Matthew and Granger, 1923a, 1923b, 1924, 1925a, 1925b; Osborn, 1923, 1924, 1925; Berkey and Morris, 1927; Wetmore, 1934; Burke, 1941; Kretzoi, 1942; Granger and Gregory, 1943; Rozhdestvenskiy, 1949; Belyayeva, 1952, 1954; Gromova, 1952a,

1952b, 1954, 1958, 1959; Trofimov, 1952, 1957, 1958; Yanovskaya, 1954, 1976, 1980; Kozlova, 1960; Dashzeveg, 1964, 1965, 1966, 1970, 1974, 1975, 1976a, 1976b, 1985; Radinsky, 1965, 1967; Van Valen, 1967; Kielan-Jaworowska and Dovchin, 1968; Młynarski, 1968; Wood, 1970; Shevyreva, 1972; Belyayeva *et al.*, 1974; Gabunia and Dashzeveg, 1974; Kurochkin, 1976, 1981; Yanovskaya *et al.*, 1977; Reshetov, 1979; Kurochkin and Dashzeveg, 1979; Devyatkin, 1981; Lucas, 1982; Wall, 1982; Dashzeveg and Devyatkin, 1986; Russell and Zhai, 1987). The fossil mammals from the formation define the type fauna of the Ergilin

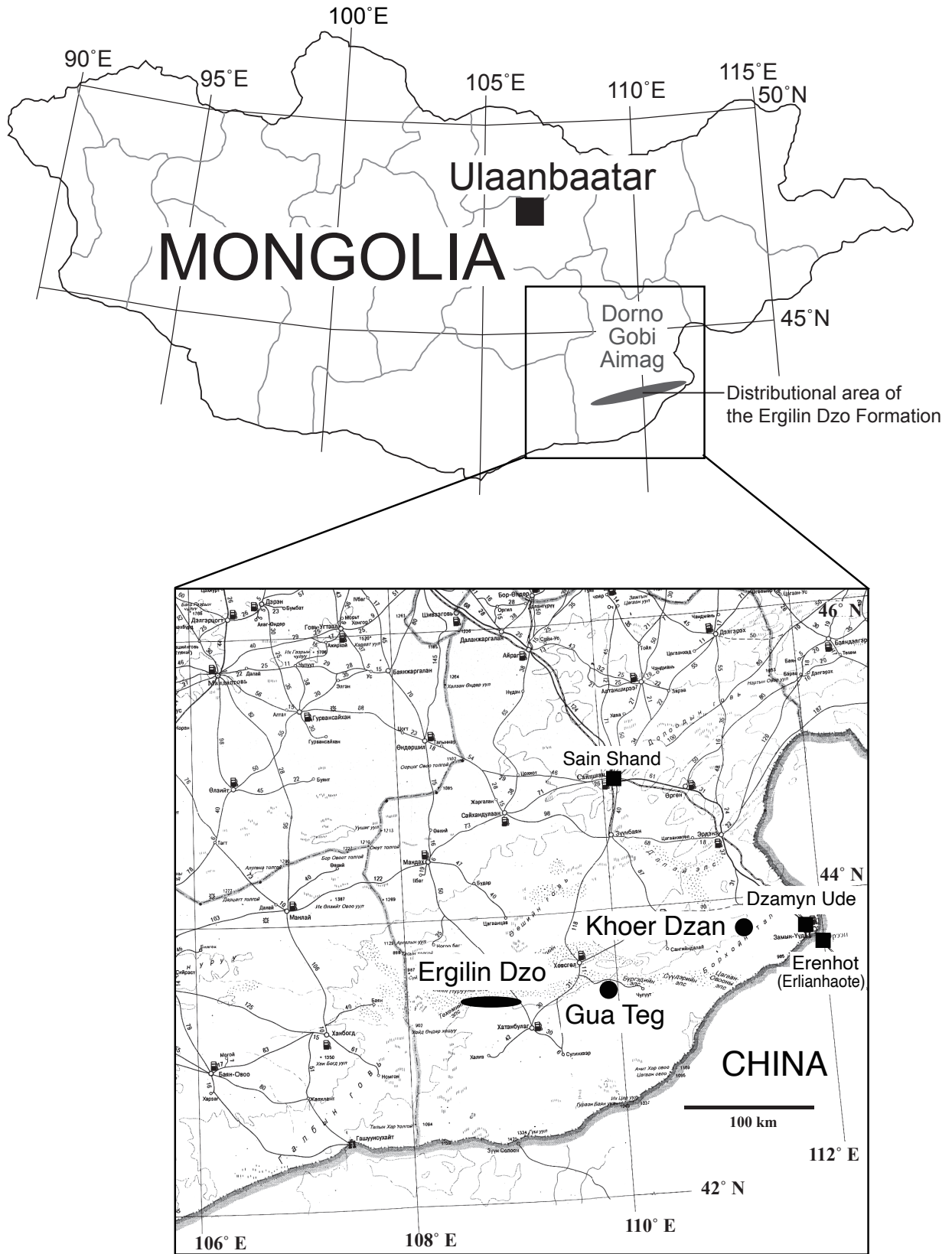


Figure 1. Map of Mongolia showing the distributional area of the upper Eocene Ergilin Dzo Formation, showing three of the fossil localities of the formation: Ergilin Dzo, Gua Teg, and Khoer Dzan localities (after Tsubamoto and Tsogtbaatar, 2008).

Asian Land Mammal Age (Russell and Zhai, 1987; Dashzeveg, 1993; Ducrocq, 1993; Ducrocq *et al.*, 1995; Meng and McKenna, 1998). Despite the recent progress of the discoveries and descriptions of its vertebrate fossils (Gabunia and Dashzeveg, 1988; Lange-Badré and Dashzeveg, 1989; Dashzeveg, 1991, 1996a, 1996b; Dashzeveg and Russell, 1992; Dashzeveg and Hooker, 1997; Lopatin, 1997, 2005, 2020; Vislobokova, 1998; Lavrov, 1999, 2019; Tsubamoto *et al.*, 2006, 2008, 2010, 2011a, 2011b, 2012a, 2012b, 2013a, 2013b; Tsubamoto and Tsogtbaatar, 2008; Muhlbachler, 2008; Egi *et al.*, 2009, 2016; Tsubamoto, 2010; Suzuki *et al.*, 2010; López-Torres and Fostowicz-Frelik, 2018; Iijima *et al.*, 2019) since Russell and Zhai (1987), who summarized the Paleogene mammals of Asia, the current composition of its fossil vertebrate fauna is not well documented due to the lack of comprehensive reviews based on the latest data. Here, we briefly review the fossil vertebrate fauna of the formation.

Geological and paleontological settings

The Ergilin Dzo Formation (Dashzeveg, 1993) (= Ardyn Obo Formation by Berkey and Granger, 1923) is distributed in the southern part of Dornogobi Aimag (eastern Gobi Desert), southeastern Mongolia (Figures 1–4; Dashzeveg, 1993, fig. 1; Clarke *et al.*, 2005, fig. 1; Tsubamoto and Tsogtbaatar, 2008, fig. 1). There are several fossil localities of the formation (Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Dashzeveg, 1993, 1996a; Saneyoshi *et al.*, 2010): Ergilin Dzo (sublocalities: Novozhilov Hills, Sevkul Khuduk, Ergil Obo [= Ardyn Obo], Ergil Ula, Ikh Uldziyn, Amar Uldziyn, Aman Us, Aman Usny Khyar, Shavag [= Zavag], Bayan Tsav Obo, Khetsu Tsav, and Sangin Obo), Gua Teg, Khoer Dzan (sublocalities: Ikh Dzan and Baga Dzan), and a locality near the Dzamyn Ude Railway Station. Nevertheless, it should be noted that more precise geological surveys are indeed necessary to test whether the deposits of all the localities cited above are really assigned to the single ‘formation,’ in a strict sense, in terms of the current guidelines of the lithostratigraphic units in geology. This is because there is no key bed (*e.g.*, characteristic tuff bed useful for the stratigraphic correlation) in the formation, and because the formation consists of fluvial deposits (Saneyoshi *et al.*, 2010; *contra* Dashzeveg, 1993; Dill *et al.*, 2005), which generally contain little evidence useful for the stratigraphic correlation.

Dashzeveg and Devyatkin (1986) and Dashzeveg (1993) subdivided the formation into six members: in stratigraphic ascending order, the Khubsugul, Zangut, Sevkul, Shavag, Ergilin, and Khetsu Tsav members (Figure 2). Most of the vertebrate fossils come from the

Sevkul and Ergilin members according to Dashzeveg and Devyatkin (1986) and Dashzeveg (1993). At the Ergilin Dzo locality, all members of the formation are exposed (Dashzeveg, 1993). Around the uppermost part of the formation (= around the Khetsu Tsav Member) at the Ergilin Dzo locality, many fossil specimens of the Amynodontidae (Mammalia, Perissodactyla) were collected during the 2004 and 2008 field seasons (Suzuki *et al.*, 2010; Tsubamoto *et al.*, 2010). It should be noted that the Khetsu Tsav Member is not distributed (or cannot be observed due to the erosion) at the Khoer Dzan locality, which is one of the most fossiliferous localities in the formation (Dashzeveg, 1993).

The Ergilin Dzo Formation is currently correlated to the upper Eocene on the basis of the comparison with the contemporaneous terrestrial mammalian fauna. The formation was traditionally correlated to the lower Oligocene (*e.g.*, Dashzeveg, 1966, 1970; Liskun and Badamgarav, 1977; Belyayeva *et al.*, 1974; Dashzeveg, 1974; Yanovskaya *et al.*, 1977; Russell and Zhai, 1987). Later, Dashzeveg and Devyatkin (1986) and Dashzeveg (1991, 1993, 1996a, 1996b) stated that there is the Eocene-Oligocene boundary between the Shavag and Ergilin members (Figure 2). More recently, Ducrocq (1993), Ducrocq *et al.* (1995), Meng and McKenna (1998), and Tsubamoto *et al.* (2004, 2008) concluded that all of the formation is correlated to the upper Eocene. The Khetsu Tsav Member (Figure 2) yields brontotheriid perissodactyl fossils (Yanovskaya *et al.*, 1977; Russell and Zhai, 1987), strongly implying the upper Eocene correlation for the member (Berggren and Prothero, 1992; Prothero, 1994). As another information on the geological age of the formation, Sakamoto *et al.* (2021) performed a preliminary paleomagnetostratigraphic study of the formation at the Ergilin Dzo locality and implied that there is at least one geomagnetic reversal within the formation.

The paleoenvironment of the Ergilin Dzo Formation is estimated to be relatively hot/warm and humid with a relatively-closed area on the basis of the presence of the Brontotheriidae (Mammalia, Perissodactyla) and the dominance of the low-crowned plant-eating mammals (Prothero, 1994; Tsubamoto *et al.*, 2005). This is also supported by the cenogram analysis of the Ergilin Dzo fossil mammalian fauna by Ducrocq *et al.* (1995). Nevertheless, the very few collected specimen number (currently only one specimen) of the crocodyliforms and the absence of the primates (Mammalia) imply that the paleoenvironment of the fauna appears to be more arid with some more open areas than the contemporaneous faunas of the southern and middle part of eastern Eurasia, such as the late middle Eocene Heti fauna (Rencun and Zhaili faunas) of central China, the late middle Eocene Pondaung fauna of Myanmar, and the late Eocene Krabi

Ergilin Dzo Formation	Khetsu Tsav Member	Poorly-sorted gravelly sandstones with cross lamination
	Ergilin Member	Yellowish gray sandstones with minor mudstones
	Shavag Member	Mudstones with very minor gravelly sandstones
	Sevkhol Member	Well-sorted white sandstones with red mudstones
	Zangut Member	White sandstones with minor mudstones
	Khubsuguk Member	Red mudstones

Figure 2. Generalized composite stratigraphy of the upper Eocene Ergilin Dzo Formation suggested by Dashzeveg (1993), with some comments from Saneyoshi *et al.* (2010) and Tsubamoto *et al.* (2011a).

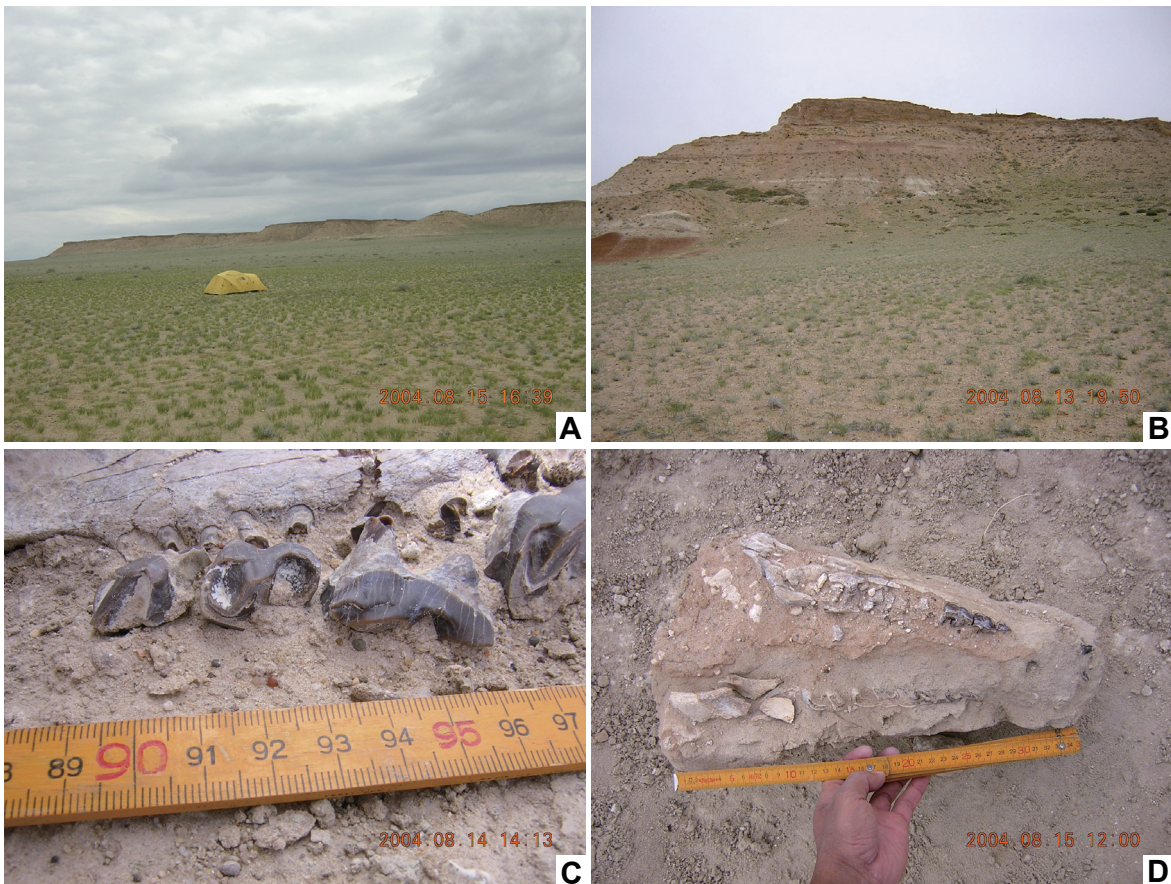


Figure 3. Some photos at the Ergilin Dzo locality (Figure 1) in 2004. **A**, landscape of the Ergilin Dzo locality around the Ergil Obo (= Ardyn Obo) sublocality; **B**, close-up of the Ergil Obo (= Ardyn Obo) sublocality; **C**, mode of occurrence of a right mandible with teeth of the Amynodontidae; **D**, right and left mandibles with teeth of the Amynodontidae *in situ* before plaster jacketing.

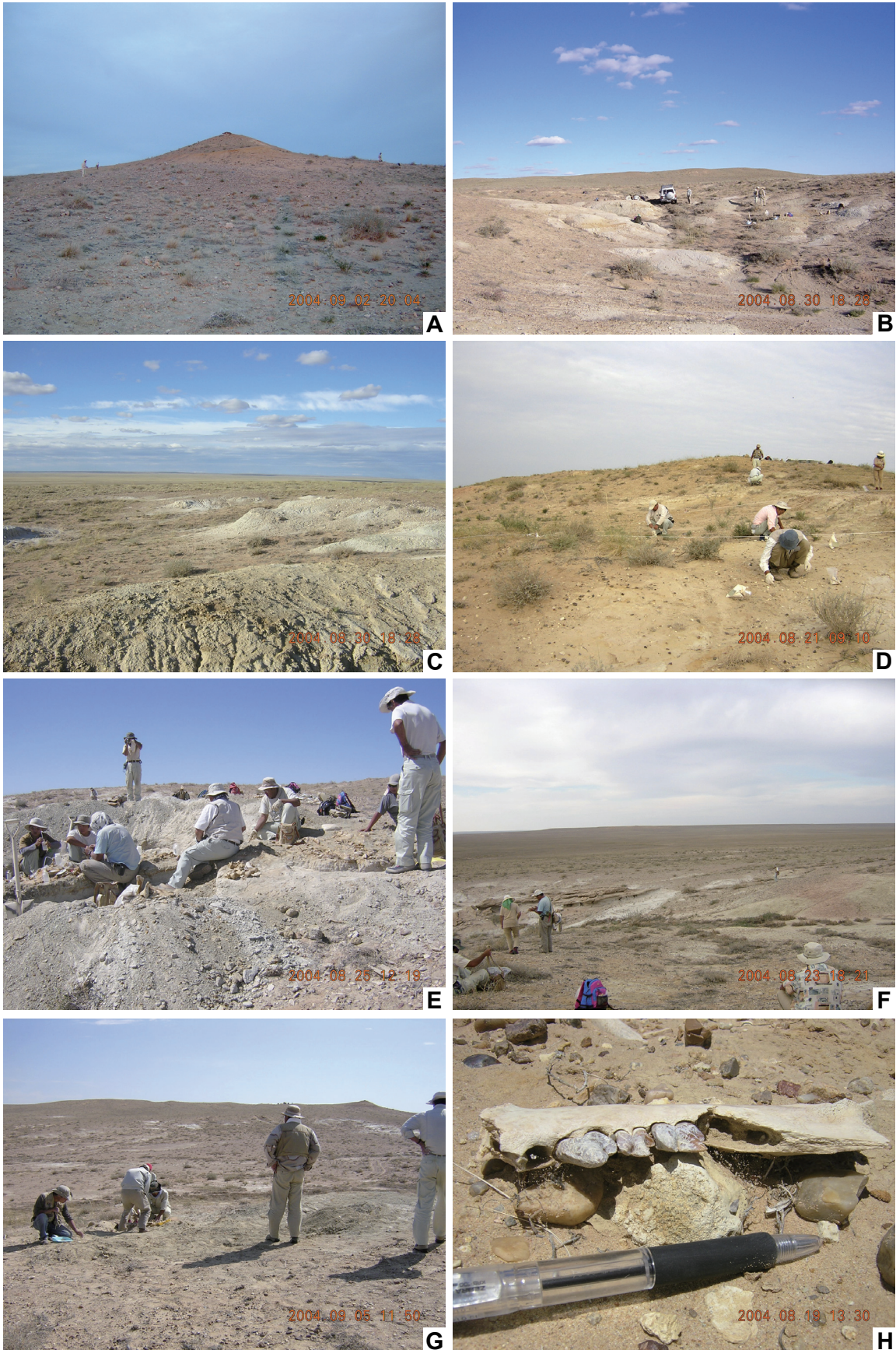


Figure 4. Some photos at the Ikh Dzan sublocality of the Khoer Dzan locality (Figure 1) in 2004. **A–G**, landscapes of the Ikh Dzan sublocality; **H**, mode of occurrence of a left mandible with p4–m2 of *Hyainodon incertus*.

fauna of Thailand (Russell and Zhai, 1987; Ducrocq *et al.*, 1995; Tong, 1997; Tsubamoto *et al.*, 2004, 2005).

The Ergilin Dzo fossil vertebrate fauna

The Ergilin Dzo vertebrate fauna currently consists of five classes, 22 orders, 49 families, 77 genera, and 104 species (Table 1). A list of some synonyms of the vertebrate taxa discovered from the formation are indicated in Table 2. Other synonyms and early versions of the faunal list are provided mainly by Belyayeva *et al.* (1974), Devyatkin (1981), Yanovskaya *et al.* (1977), Russell and Zhai (1987), Dashzeveg (1993), Meng and McKenna (1998), Tsubamoto *et al.* (2004), and Lopatin (2020).

Osteichthyes

The bony fish fauna consists of two orders, two families, two genera, and two species (Table 1). The two fish from the formation, *Amia* sp. and *Parasilurus* sp., were cited by Yanovskaya *et al.* (1977). The siluriform specimen from the formation figured by Tsubamoto *et al.* (2006) might perhaps be assigned to *Parasilurus* sp. of Yanovskaya *et al.* (1977).

Amphibia

Only one species (indeterminate urodelan) of the Amphibia has been reported (Table 1). It was cited by Yanovskaya *et al.* (1977), although it has not been described yet.

Reptilia

The reptilian (excluding birds) fauna consists of three orders, seven families, nine genera, and nine species (Table 1). The reptiles from the formation were studied or cited by Matthew and Granger (1923b), Młynarski (1968), Ckhikvadze (1972), Dashzeveg (1974, 1993), and Yanovskaya *et al.* (1977). According to Yanovskaya *et al.* (1977), six species (four families) of turtles and two species (two families) of lizards have been recognized in the formation (Table 1). The testudinid tortoise (or turtle), *Ergilemys insolitus*, was first described as a new species *Testudo insolitus* by Matthew and Granger (1923b). Later, this species was assigned to the genus *Geochelone* by Młynarski (1968); and this revised classification was followed by Dashzeveg (1974). *G. insolitus* was assigned to the new genus *Ergilemys* as the type species by Ckhikvadze (1972) (Table 2); and this revised classification was followed by Yanovskaya *et al.* (1977) and Dashzeveg (1993). *Palaeochelys? elongata* was renamed as *Melanochelys elongata* by Ckhikvadze (1971) (Table 2). Iijima *et al.* (2019) described a crocodyliform tooth. This discovery implied that southeastern Mongolia probably fulfilled thermal

requirements of crocodyliforms during the late Eocene (Iijima *et al.*, 2019).

Aves

The avian (bird) fauna consists of five orders, seven families, nine genera, and 11 species (Table 1). The birds from the formation were reported and cited by Wetmore (1934), Kozlova (1960), Kurochkin (1976, 1981), and Yanovskaya *et al.* (1977). *Ergilornis minor* was first described as a new genus and species *Proergilornis minor* by Kozlova (1960) (Table 2). The species was assigned to the genus *Ergilornis* by Kurochkin (1981). Clarke *et al.* (2005) considered that the Ergilornithidae is synonymous with the Eogruidae, although we provisionally and conservatively retain the Ergilornithidae in this article.

Mammalia

The fossil mammals from the formation were mainly summarized by Belyayeva *et al.* (1974), Yanovskaya *et al.* (1977), Devyatkin (1981), Russell and Zhai (1987), Dashzeveg (1993), and Lopatin (2020). The Ergilin Dzo mammalian fauna based on the progress of recent studies are briefly reviewed below.

The Ergilin Dzo fossil mammalian fauna

The mammalian fauna of the Ergilin Dzo Formation currently consists of 11 orders of 81 species (Table 1): six species of the Eulipotyphla, one species of the Anagalida, two species of the Mesonychia, one species of the Cimolesta, two species of the Leptictida, four species of the Rodentia, four species of the Lagomorpha, five species of the Carnivora, eight species of the Hyainodontida, 13 species of the Artiodactyla, and 33 species of the Perissodactyla. In terms of the species diversity, the perissodactyls are dominant in the fauna (33 perissodactyl species among the 81 mammalian species and the 104 vertebrate species). In terms of the collected specimen numbers, brontotheriid and rhinocerotid perissodactyls and ruminant artiodactyls are dominant among the vertebrate taxa from the formation (*e.g.*, Tsubamoto *et al.*, 2010).

Eulipotyphla

Three families, six genera, and six species of eulipotyphlans (= ‘insectivorans’) have been recognized (Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Lopatin, 2005). Lopatin (2005) described an indeterminate tupaiodontine changlelestid, *Oligochenus grandis* (Erinaceidae, Galericinae), and *Amphechinus* sp. (Erinaceidae, Erinaceinae, Amphechinini; McKenna and Bell, 1997) from the formation. However, he did not mention the other eulipotyphlans from the formation

Table 1. Composite fossil vertebrate faunal list of the Ergilin Dzo Formation. The list was compiled mainly after Kurochkin (1976, 1981), Yanovskaya *et al.* (1977), Russell and Zhai (1987), Dashzeveg (1993), and Meng and McKenna (1998), with other references. Selected references for the citation of each species in the Ergilin Dzo fauna are indicated in square brackets at each species.

OSTEICHTHYES

Amiiformes

Amiidae

Amia sp. [Yanovskaya *et al.*, 1977]

Siluriformes

Siluridae

Parasilurus sp. [Yanovskaya *et al.*, 1977]

AMPHIBIA

Urodela

Family indet.

Gen. et sp. indet. [Yanovskaya *et al.*, 1977]

REPTILIA

Chelonia

Testudinidae

Ergilemys insolitus (Matthew and Granger, 1923b) Ckhikvadze, 1972 [Yanovskaya *et al.*, 1977]

Platysternidae

Gen. et sp. indet. [Yanovskaya *et al.*, 1977]

Emydidae

?*Melanocheilus elongata* (Gilmore, 1931) Ckhikvadze, 1971 [Yanovskaya *et al.*, 1977]

Chrysemys sp. [Yanovskaya *et al.*, 1977]

Gen. et sp. indet. [Yanovskaya *et al.*, 1977]

Trionychidae

Gen. et sp. indet. [Yanovskaya *et al.*, 1977]

Lacertilia

Family indet.

Gen. et sp. indet. [Yanovskaya *et al.*, 1977]

Iguania

Agamidae

Gen. et sp. indet. [Yanovskaya *et al.*, 1977]

Crocodyliformes

Family indet.

Gen. et sp. indet. [Iijima *et al.*, 2019]

AVES

Gruiformes

Grues

Rallidae

Gen. et sp. indet. [Kurochkin, 1976]

Gruoidea

Ergilornithidae

Ergilornis minor (Kozlova, 1960) Kurochkin, 1981 [Yanovskaya *et al.*, 1977]

Ergilornis rapidus Kozlova, 1960 [Yanovskaya *et al.*, 1977; Kurochkin, 1981]

Ergilornis sp. [Kurochkin, 1981]

Eogruidae

Eogrurus sp. [Yanovskaya *et al.*, 1977]

Sonogrurus gregalis Kurochkin, 1981

Anseriformes

Anseres

Anatidae

Gen. et sp. indet. [Kurochkin, 1976]

Ciconiiformes

Ardeae

Ardeidae

Gen. et sp. indet. [Kurochkin, 1976]

Cygninae

Gen. et sp. indet. [Kurochkin, 1976]

Falconiformes

Accipitridae

Gen. et sp. indet. [Kurochkin, 1976]

Charadriiformes

Lari

Family indet.

Gen. et sp. indet. [Kurochkin, 1976]

Table 1.—continued.

MAMMALIA

Eulipotyphla

Changlestidae
Tupaiodontinae
Ictopidium? sp. [Yanovskaya *et al.*, 1977]
Gen. et sp. indet. [Lopatin, 2005]

Erinaceidae
Galericinae
Oligocheilus grandis Lopatin, 2005
Erinaceinae
Amphechinini
Amphechinus sp. [Lopatin, 2005]
Palaeoscaptor? sp. [Yanovskaya *et al.*, 1977]

Soricidae
Soricinae
Gen. et sp. indet. [Russell and Zhai, 1987]

Anagalida

Anagalidae
Zofiagale ergilinesis López-Torres and Fostowicz-Frelik, 2018

Mesonychia (= Acreodi)

Mesonychidae
Mongolestes hadrodens Szalay and Gould, 1966 [Dashzeveg, 1985, 1993; Russell and Zhai, 1987; Tsubamoto *et al.*, 2012a; This study]

Hapalodectidae
Metahapalodectes sp. [Dashzeveg, 1993; This study]

Cimolesta

Pantolestida
Pantolestidae
Dyspterninae
Gobiopithecus khan Dashzeveg and Russell, 1992 [Tsubamoto *et al.*, 2011b]

Leptictida

Didymoconidae
Ergilictis reshetovi Lopatin, 1997
Ardynictis furunculus Matthew and Granger, 1925a [Russell and Zhai, 1987]

Rodentia

Cylindrodontidae
Ardynomys silentiumis (Shevyreva, 1972) [Dashzeveg, 1993]
Ardynomys olseni Matthew and Granger, 1925a [Dashzeveg, 1993]
Ardynomys sp. [Dashzeveg, 1993]

Cricetidae
Eucricetodon sp. [Russell and Zhai, 1987]

Lagomorpha

Ochotonidae
Desmatolagus robustus Matthew and Granger, 1923a [Russell and Zhai, 1987; Dashzeveg, 1993]
Desmatolagus gobiensis Matthew and Granger, 1923a [Burke, 1941; Gureyev, 1960; Sych, 1975; Dashzeveg, 1993]
Desmatolagus ardynense Burke, 1941 [Dashzeveg, 1993]

Family indet.
Gen. et sp. indet. [Russell and Zhai, 1987]

Carnivora

Nimravidae
Nimravus mongoliensis (Gromova, 1959) [Dashzeveg, 1996b, Peigné, 2003; Egi *et al.*, 2016]
Eofelis sp. [Egi *et al.*, 2016]

Amphicyonidae
Gen. et sp. indet. [Egi *et al.*, 2009]

Family indet.
Asiavorator gracilis (Matthew and Granger, 1924) Egi *et al.*, 2016 [Dashzeveg, 1996b]
Alagtsavbaatar indigenus (Dashzeveg, 1996b) Egi *et al.*, 2016

Hyaenodontida

Hyaenodontidae
Hyaenodontinae
Hyaenodon pumilus Lavrov, 2019
Hyaenodon chunkhtensis Dashzeveg, 1985 [Tsubamoto *et al.*, 2008]
Hyaenodon eminus Matthew and Granger, 1925a [Tsubamoto *et al.*, 2008]
Hyaenodon pervagus Matthew and Granger, 1924 [Tsubamoto *et al.*, 2008]
Hyaenodon incertus Dashzeveg, 1985 [Tsubamoto *et al.*, 2008]
Hyaenodon mongoliensis (Dashzeveg, 1964) Van Valen, 1967 [Tsubamoto *et al.*, 2008]
Hyaenodon gigas Dashzeveg, 1985 [Wang *et al.*, 2005; Tsubamoto *et al.*, 2008; This study]

Proviverrinae
Gen. et sp. indet. [Tsubamoto *et al.*, 2008]

Table 1.—continued.

Artiodactyla (*sensu* Prothero *et al.*, 2022)

Anthracotheriidae
 cf. *Bothriodon* sp. [Tsubamoto and Tsogtbaatar, 2008]
 Gen. et sp. indet. [Tsubamoto and Tsogtbaatar, 2008]

Entelodontidae
Entelodon gobiensis (Trofimov, 1952) Brunet, 1979 [Russell and Zhai, 1987; Lucas and Emry 1996b; Tsubamoto *et al.*, 2011b]
Brachyhyops trofimovi (Dashzeveg, 1976b) [Russell and Zhai, 1987; Wang and Qiu, 2002; Tsubamoto *et al.*, 2011b]
Brachyhyops? sp. [Trofimov, 1952; Brunet, 1979; Russell and Zhai, 1987; Tsubamoto *et al.*, 2011b]

Ruminantia

Hypertragulidae
Praetragulus gobiae (Matthew and Granger, 1925b) Vislobokova, 1998 [Russell and Zhai, 1987]
Praetragulus electus Vislobokova, 1998

Lophiomerycidae
Lophiomeryx angarae Matthew and Granger, 1925b [Russell and Zhai, 1987]
Lophiomeryx sp. [Russell and Zhai, 1987]

Leptomerycidae
Miomeryx altaicus Matthew and Granger, 1925b [Russell and Zhai, 1987]
Miomeryx sp. [Russell and Zhai, 1987]
Gbiomeryx dubius Trofimov, 1957 [Russell and Zhai, 1987]

Pecora

Cervidae
Eumeryx sp. [Russell and Zhai, 1987]

Perissodactyla

Brontotheriidae
Embolotherium andrewsi Osborn, 1929 [Russell and Zhai, 1987; Dashzeveg, 1993; Mhlbachler, 2008]
Embolotherium grangeri Osborn, 1929 [Russell and Zhai, 1987; Dashzeveg, 1993; Mhlbachler, 2008]
Embolotherium sp. [Russell and Zhai, 1987; Dashzeveg, 1993]
Eubrontotherium clarnoensis Mhlbachler, 2007 [Mhlbachler *et al.*, 2004; Mhlbachler, 2008]
Protbolotherium efremovi Yanovskaya, 1980 [Russell and Zhai, 1987; Mhlbachler, 2008]
 cf. *Nasamplus progressus* (Granger and Gregory, 1943) [Mhlbachler, 2008]
 Gen. et sp. indet. [Russell and Zhai, 1987]

Chalicotherioidea

Chalicotheriidae
Schizotherium avitum Matthew and Granger, 1923b [Russell and Zhai, 1987]

Eomoropidae
Eomoropus sp. [Dashzeveg and Devyatkin, 1986; Dashzeveg, 1993]

Rhinocerotoida

Rhinocerotidae
Ronzotherium brevirostris (Belyayeva, 1954) Heissig, 1969 [Russell and Zhai, 1987; Meng and McKenna, 1998]
Ronzotherium orientale Dashzeveg, 1991
Ronzotherium sp. [Dashzeveg, 1991, 1993]

Eggsodontidae
 cf. *Allacerops* sp. [Dashzeveg, 1991; Qiu and Wang, 1999; This study]

Hyracodontidae (*sensu* Bai *et al.*, 2020b)
Ardynia praecox Matthew and Granger, 1923b [Radinsky, 1967; Russell and Zhai, 1987; Dashzeveg, 1991, 1993; Bai *et al.*, 2018]
Ardynia sp. [Dashzeveg, 1991]
Armania asiana Gabunia and Dashzeveg, 1988 [Dashzeveg, 1991]
Prohyracodon meridionalis [Dashzeveg, 1993]
Prohyracodon obrutschewi Dashzeveg, 1996a
 ?*Prohyracodon parvum* Dashzeveg, 1991

Paraceratheriidae (*sensu* Qiu and Wang, 2007; Bai *et al.*, 2020b)
Juxia borissiakii (Belyaeva, 1959) [Russell and Zhai, 1987; Lucas and Sobus, 1989; Dashzeveg, 1991; Qiu and Wang, 2007]
Paraceratherium parvum (Chow, 1958) [Russell and Zhai, 1987; Lucas and Sobus, 1989; Qiu and Wang, 2007; This study]
 Gen. et sp. indet. [Lucas and Sobus, 1989; Dashzeveg, 1991, 1993; This study]

Amynodontidae
Cadurcodon ardynensis (Osborn, 1923) Kretzoi, 1942 [Russell and Zhai, 1987]
Cadurcodon sp. [Russell and Zhai, 1987]
Cadurcotherium progressus (Gromova, 1954) Wall, 1982 [Russell and Zhai, 1987; Meng and McKenna, 1998]
 cf. *Zaisanamyndon* sp. [Wall, 1989; Lucas and Emry, 1996a; Lucas *et al.*, 1996]
Amynodon sp. [Dashzeveg, 1993]
Amynodontopsis lunanensis (Chow *et al.*, 1964) [Dashzeveg, 1993, 1996a]
Sharamyndon mongoliensis (Osborn, 1936) Kretzoi, 1942 [Russell and Zhai, 1987; Dashzeveg, 1993]

Tapiroidea or Rhinocerotoida

Deperetellidae
Teleolophus magnus Radinsky, 1965 [Russell and Zhai, 1987; Dashzeveg and Hooker, 1997; Tsubamoto *et al.*, 2012b]
 cf. *Deperetella* sp. [Dashzeveg and Devyatkin, 1986; Dashzeveg and Hooker, 1997; Tsubamoto *et al.*, 2005; This study]

Tapiroidea

Helaletidae
Paracolodon inceptus (Matthew and Granger, 1925b) Bai *et al.*, 2017 [Russell and Zhai, 1987]
Paracolodon sp. [Russell and Zhai, 1987; Bai *et al.*, 2017; This study]

Table 2. Synonym list concerning several fossil vertebrate taxa from the Ergilin Dzo Formation. Selected references concerning each synonymy are indicated in the square bracket at each synonymy. Other synonymies concerning the mammalian taxa from the Ergilin Dzo Formation are largely indicated in Russell and Zhai (1987), Dashzeveg (1993), and Lopatin (2020).

<i>Testudo insolitus</i> = <i>Geochelone insolitus</i> = <i>Ergilemys insolitus</i> [Matthew and Granger, 1923b; Młynarski, 1968; Ckhikvadze, 1972; Dashzeveg, 1974, 1993; Yanovskaya <i>et al.</i> , 1977]
<i>Palaeochelys? elongata</i> = ? <i>Melanochelys elongata</i> [Gilmore, 1931; Ckhikvadze, 1971]
<i>Proergilornis minor</i> = <i>Ergilornis minor</i> [Kozlova, 1960; Kurochkin, 1981]
Mesonychidae gen. et sp. indet. in Dashzeveg (1985), Russell and Zhai (1987), and Tsubamoto <i>et al.</i> (2012a) = <i>Mongolestes hadrodens</i> in Dashzeveg (1993) = ? <i>Mongolestes hadrodens</i> [This study]
<i>Metahapalodectes</i> in Dashzeveg (1993) = ? <i>Metahapalodectes</i> sp. [This study]
<i>Ardynomys vinogradovi?</i> = <i>Ardynomys vinogradovi</i> = <i>Ardynomys chihi</i> = <i>Ardynomys olseni</i> [Wood, 1970; Russell and Zhai, 1987; Dashzeveg, 1993; Wang and Meng, 2009]
<i>Morosomys silentiumis</i> = <i>Morosomys silenti</i> = <i>Ardynomys silentii</i> = <i>Ardynomys silentiumis</i> [Russell and Zhai, 1987; Dashzeveg, 1993]
<i>Desmatolagus vetustus</i> = <i>Procaprolagus vetustus</i> = <i>Desmatolagus gobiensis</i> [Matthew and Granger, 1923a; Burke, 1941; Gureyev, 1960; Sych, 1975; Dashzeveg, 1993]
<i>Cynodictis?</i> sp. = Amphicyonidae gen. et sp. indet. [Matthew and Granger, 1923b; Dashzeveg, 1974; Yanovskaya <i>et al.</i> , 1977; Russell and Zhai, 1987; Egi <i>et al.</i> , 2009, 2016]
<i>Megalopterodon mongoliensis</i> = <i>Hyaenodon mongoliensis</i> [Dashzeveg, 1964, 1993; Lange-Badré and Dashzeveg, 1989; Tsubamoto <i>et al.</i> , 2008]
<i>Macropterodon zelenovi</i> Lavrov, 1999 = <i>Hyaenodon gigas</i> [Wang <i>et al.</i> , 2005; Morlo and Nagel, 2006; Egi <i>et al.</i> , 2007; This study]
<i>Aelurogale mongoliensis</i> = <i>Nimravus intermedius</i> from the Ergilin Dzo Fm in Peigné (2003) = <i>Nimravus mongoliensis</i> [Dashzeveg, 1993; Egi <i>et al.</i> , 2016]
<i>Brachyodon gobiensis</i> = <i>Ergilgobia gobiensis</i> = <i>Entelodon gobiensis</i> [Trofimov, 1952, 1958; Brunet, 1979; Russell and Zhai, 1987; Dashzeveg, 1993]
<i>Entelodon orientalis</i> = <i>Entelodon gobiensis</i> [Lucas and Emry, 1996b]
<i>Archaeotherium?</i> sp. in Trofimov (1952) = <i>Entelodon?</i> sp. = <i>Brachyhyops?</i> sp. [Brunet, 1979; Russell and Zhai, 1987; Dashzeveg, 1993; Tsubamoto <i>et al.</i> , 2011a]
<i>Eoentelodon</i> = <i>Brachyhyops</i> [Wang and Qiu, 2002; Tsubamoto <i>et al.</i> , 2011a]
<i>Lophiomeryx gobiae</i> = <i>Praetragulus gobiae</i> [Matthew and Granger, 1925b; Russell and Zhai, 1987; Vislobokova, 1998]

cited by Yanovskaya *et al.* (1977), *Ictopidium?* sp. (Tupaiodontinae) and *Palaeoscaptor?* sp. (Erinaceinae, Amphelchinini).

Anagalida

Only one anagalidan species has been reported. López-Torres and Fostowicz-Frelik (2018) described a new genus and species of the Anagalidae, *Zofiagale ergilinsensis*, from the formation at the Ergilin Dzo locality on the basis of a mandibular fragment with p3–m3. This is one of the latest records of the anagalids (López-Torres and Fostowicz-Frelik, 2018).

Mesonychia (= Acreodi)

Two families, two genera, and two species of mesonychians is recognized here. In their faunal lists of the Ergilin Dzo Formation, Dashzeveg (1985) and Russell and Zhai (1987) cited an indeterminate mesonychid. This mesonychid was reidentified as *Mongolestes hadrodens* by Dashzeveg (1993) in his faunal list of the formation. Dashzeveg (1993) cited a small mesonychian *Metahapalodectes* (Hapalodectidae) from the formation. However, these three studies did not provide figures or any information on the specimens. Therefore, the existence of the mesonychians in the Ergilin Dzo fauna had not been confirmed at that

Table 2.—*continued.*

<i>Embolotherium insigne</i> = <i>Titanodectes ingens</i> ? = <i>Embolotherium loucksii</i> = <i>Embolotherium grangeri</i> [Yanovskaya, 1980; Russell and Zhai, 1987; Dashzeveg, 1993; Muhlbachler, 2008]
<i>Embolotherium ergilense</i> = <i>Embolotherium andrewsi</i> [Dashzeveg, 1975, 1993; Russell and Zhai, 1987; Muhlbachler, 2008]
<i>Metatitan relictus</i> = <i>Parabrontops gobiensis</i> = <i>Eubrontotherium clarnoensis</i> [Russell and Zhai, 1987; Muhlbachler <i>et al.</i> , 2004; Muhlbachler, 2007, 2008]
<i>Epimanteoceras robustum</i> = cf. <i>Nasamplus progressus</i> [Russell and Zhai, 1987; Muhlbachler, 2008]
<i>Symphysorrhachus brevisrostris</i> = <i>Ronzotherium brevisrostris</i> [Heissig, 1969; Russell and Zhai, 1987; Meng and McKenna, 1998]
<i>Allacerops</i> sp. (Rhinocerotidae) in Dashzeveg (1991) = cf. <i>Allacerops</i> sp. (Eggysodontidae) [Qiu and Wang, 1999; This study]
<i>Parahyracodon mongoliensis</i> = <i>Ardynia mongoliensis</i> = <i>Ardynia praecox</i> [Radinsky, 1967; Russell and Zhai, 1987; Dashzeveg, 1991, 1993; Bai <i>et al.</i> , 2018]
<i>Prohyracodon</i> sp. in Russell and Zhai (1987) = <i>Prohyracodon meridionalis</i> [Dashzeveg, 1993]
<i>Forstercooperia ergiliensis</i> = <i>Juxia borissiaki</i> [Russell and Zhai, 1987; Lucas and Sobus, 1989; Dashzeveg, 1991; Qiu and Wang, 2007]
<i>Forstercooperia</i> sp. in Dashzeveg (1991) = deleted [This study]
<i>Indricotherium parvum</i> = <i>Paraceratherium parvum</i> [Russell and Zhai, 1987; Lucas and Sobus, 1989; Qiu and Wang, 2007; This study]
<i>Urtinotherium</i> (or <i>Indricotherium</i>) sp. in Dashzeveg (1991, 1993, 1996a) = Paraceratheriidae gen. et sp. indet. [Lucas and Sobus, 1989; Qiu and Wang, 2007; This study]
Indricothere or amynodont indet. in Lucas (1982) and Russell and Zhai (1987) = deleted [This study]
<i>Caenolophus promissus</i> = <i>Amynodon</i> sp. [Dashzeveg, 1993]
<i>Hypsamynodon progressus</i> = <i>Cadurcotherium progressus</i> [Wall, 1982; Russell and Zhai, 1987; Meng and McKenna, 1998]
<i>Amynodon lunanensis</i> = <i>Amynodontopsis lunanensis</i> [Chow <i>et al.</i> , 1964; Dashzeveg, 1996a; Wang <i>et al.</i> , 2020]
<i>Gigantamynodon</i> = (<i>nomen dubium</i>) = cf. <i>Zaisanamynodon</i> sp. [Wall, 1989; Lucas and Emry, 1996a; Lucas <i>et al.</i> , 1996]
<i>Amynodon giganteus</i> = <i>Gigantamynodon cessator</i> = cf. <i>Zaisanamynodon</i> sp. [Wall, 1989; Dashzeveg, 1993; Lucas and Emry 1996a; Lucas <i>et al.</i> , 1996]
<i>Deperetella</i> sp. in Dashzeveg and Devyatkin (1986) = <i>Deperetella</i> cf. <i>birmanica</i> in Dashzeveg and Hooker (1997) = cf. <i>Deperetella</i> sp. [Tsubamoto <i>et al.</i> , 2005; This study]
<i>Colodon inceptus</i> = <i>Paracolodon inceptus</i> [Matthew and Granger, 1925b; Radinsky, 1965; Russell and Zhai, 1987; Bai <i>et al.</i> , 2017]
<i>Colodon</i> sp. = <i>Paracolodon</i> sp. [Yanovskaya <i>et al.</i> , 1977; Russell and Zhai, 1987; Bai <i>et al.</i> , 2017; This study]

time. Tsubamoto *et al.* (2012a) described some dental fossils of a *Mongolestes hadrodens*-like indeterminate mesonychid from the formation. Here, we provisionally recognize two mesonychians, ?*Mongolestes hadrodens* and ?*Metahapalodectes* sp., in the faunal list of the formation (Table 2).

Cimolesta

Only one cimolestan species has been reported. Dashzeveg and Russell (1992) described a dyspternine

pantolestid *Gobiopithecus khan* from the formation at the Khoer Dzan locality. Tsubamoto *et al.* (2011b) described an additional specimen of *G. khan* discovered from the same locality. This species is the only representative of the Dyspterninae recorded in East Asia.

Leptictida

One family (Didymoconidae), two genera, and two species of leptictidans have been reported (Matthew and Granger, 1925a; Russell and Zhai, 1987; Lopatin,

1997). The Didymoconidae are an endemic group in the Paleogene of Asia (McKenna and Bell, 1997).

Rodentia

Two families, two genera, and four species of rodents have been recognized (Matthew and Granger, 1925a; Wood, 1970; Shevyreva, 1972; Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Dashzeveg, 1993). Wood (1970) and Wang and Meng (2009) considered that *Ardynomys chihi* is a junior synonym of *Ardynomys olseni* (Table 2). Dashzeveg (1993) considered that *Morosomys silentiumis* (= *Morosomys silenti*) is assigned to the genus *Ardynomys* (Table 2).

Lagomorpha

Possible two families, two genera, and four species of lagomorphs have been recognized (Matthew and Granger, 1923a; Burke, 1941; Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Dashzeveg, 1993). Gureyev (1960) established a new genus *Procaprolagus* for *Desmatolagus vetustus*. Later, Synch (1975) synonymized *Procaprolagus vetustus* (= *D. vetustus*) with *Desmatolagus gobiensis* (Table 2).

Carnivora

Three families, five genera, and five species of carnivorans have been recognized (Matthew and Granger, 1923b; Gromova, 1959; Dashzeveg, 1974, 1996b; Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Peigné, 2003; Egi *et al.*, 2009, 2016). Egi *et al.* (2016) summarized the carnivoran fauna of the formation.

Hyaenodontida (= Hyaenodontidae)

Hyaenodontidans (or hyaenodontids) were reported by Matthew and Granger (1925a), Gromova (1952a), Dashzeveg (1964, 1974, 1985), Lange-Badré and Dashzeveg (1989), Lavrov (1999, 2019), and Tsubamoto *et al.* (2008, 2013a). Tsubamoto *et al.* (2008) reviewed the hyaenodontid fauna of the formation and recognized three genera and eight species of the Hyaenodontidae in the formation: six species of *Hyaenodon*, *Macropterodon zelenovi*, and an indeterminate proviverrine. More recently, Lavrov (2019) described additional one species (*Hyaenodon pumilus*) and one indeterminate species (*Hyaenodon cf. chunkhtensis*) from the formation.

Here, we recognize two genera and eight species (seven species of *Hyaenodon* and an indeterminate proviverrine) of the Hyaenodontidae in the formation (Table 1). *Macropterodon zelenovi* established by Lavrov (1999) on the basis of a specimen from the formation appears to be assigned to *Hyaenodon gigas* as implied by Wang *et al.* (2005), Morlo and Nagel (2006), and Egi *et al.* (2007). The mandibular specimens described by Lavrov (2019) from the formation as *Hyaenodon*

cf. chunkhtensis appear to be probably assigned to *Hyaenodon eminus* or *Hyaenodon chunkhtensis* on the basis of its size and morphology and do not appear to indicate an additional species in the Ergilin Dzo fauna. *Hyaenodon pumilus* established by Lavrov (2019) on the basis of the fossil from the formation is the smallest-sized species of the genus in the formation, although it should be noted that the sizes of p4 and m1 of *H. pumilus* are almost identical to those of *H. chunkhtensis*.

Artiodactyla (sensu Prothero *et al.*, 2022)

Six families, nine genera, and 13 species of artiodactyls have been recognized.

Anthracotheriidae: Tsubamoto and Tsogtbaatar (2008) recognized two genera and two species (*cf. Bothriodon* sp. and a bunodont and small indeterminate species) of anthracotheriids. The other studies on the anthracotheriids from the formation are as follows: Matthew and Granger (1923b), Dashzeveg (1974), Belyayeva *et al.* (1974), Yanovskaya *et al.* (1977), Devyatkin (1981), Dashzeveg and Devyatkin (1986), Russell and Zhai (1987), Dashzeveg (1993), and Tsubamoto (2010).

Entelodontidae: Tsubamoto *et al.* (2011a) recognized two genera and three species of entelodontids. The other studies on the entelodontids from the formation are as follows: Trofimov (1952, 1958), Dashzeveg (1965, 1976b), Yanovskaya *et al.* (1977), Brunet (1979), Russell and Zhai (1987), Lucas and Emry (1996b), Tsubamoto *et al.* (2013b), and Tsubamoto (2015).

Ruminantia: Four families, five genera, and eight species of ruminants have been recognized (Matthew and Granger, 1923b, 1925b; Trofimov, 1957; Yanovskaya *et al.*, 1977; Kurochkin and Dashzeveg, 1979; Yanovskaya, 1980; Russell and Zhai, 1987; Vislobokova, 1998). On the basis of our preliminary unpublished study on the ruminant specimens collected from the formation by the Hayashibara-Mongolian Paleontological Expeditions (Suzuki *et al.*, 2010; Tsubamoto *et al.*, 2006, 2010), at least three (large-, medium-, and small-sized) species of the Lophiomerycidae, which have a mesiolingually and widely open trigonid basin on the lower molars, appears to be recognized in the formation. Nevertheless, this information is not reflected in Table 1 because it is tentative.

Perissodactyla

10 families, 24 genera, and 33 species of perissodactyls have been recognized.

Brontotheriidae: Four genera and seven species of the brontotheriids have been recognized (Osborn, 1925, 1929; Granger and Gregory, 1943; Yanovskaya, 1954, 1976, 1980; Belyayeva *et al.*, 1974; Dashzeveg,

1975; Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Muhlbachler *et al.*, 2004; Muhlbachler, 2007, 2008).

Chalicotherioidea: Two family, two genera, and two species of chalicotherioids have been recognized (Matthew and Granger, 1923b; Dashzeveg and Devyatkin, 1986; Russell and Zhai, 1987; Dashzeveg, 1993). However, *Eomoropus* sp. (Eomoropidae) from the formation was only cited by Dashzeveg and Devyatkin (1986) and Dashzeveg (1993) and is neither described nor figured, and thus the presence of Eomoropus and Eomoropidae in the formation has not been confirmed yet. The genus *Eomoropus* is recorded mainly in the middle Eocene, except for this alleged record of the Ergilin Dzo Formation and the record of the late Eocene Krabi fauna of Thailand (Lucas and Schoch, 1989; Ducrocq *et al.*, 2021).

Rhinocerotidae: One genus and three species of rhinocerotids (= true rhinoceroses) have been recognized (Belyayeva, 1954; Heissig, 1969; Russell and Zhai, 1987; Dashzeveg, 1991, 1993).

Eggsodontidae: Dashzeveg (1991) described some specimens of *Allacerops* sp. from the formation and assigned it to the Allaceropinae within the Rhinocerotidae. Currently, *Allacerops* is assigned to the Eggsodontidae, which are closely related to true rhinoceroses (Wang *et al.*, 2016, Bai *et al.*, 2020b). Qiu and Wang (1999) doubted the generic identification of the specimens from the formation described as *Allacerops* sp. by Dashzeveg (1991) because the materials are very poorly preserved and their sizes are much smaller than those of *Allacerops*.

Hyracodontidae (sensu Bai *et al.*, 2020b): Three genera and six species of hyracodontids have been recognized (Matthew and Granger, 1923b; Gromova, 1952b; Kurochkin and Dashzeveg, 1979; Radinsky, 1967; Russell and Zhai, 1987; Gabunia and Dashzeveg, 1988; Dashzeveg, 1991, 1993, 1996a; Bai *et al.*, 2018).

Paraceratheriidae (sensu Qiu and Wang, 2007; Bai *et al.*, 2020b): three genera and three species of paraceratheriids (= huge rhinocerotoids) have been recognized (Gabunia and Dashzeveg, 1974; Dashzeveg, 1976a, 1991, 1993; Russell and Zhai, 1987; Lucas and Sobus, 1989; Qiu and Wang, 2007). *Forstercooperia* sp. was described from the formation by Dashzeveg (1991, p. 51–52). According to Dashzeveg (1991, table 13), it is based on a right mandibular fragment with p2–p4 (a specimen of Paleontologo-stratigraphic section of the Geological Institute of the Mongolian Academy of Sciences; specimen number: PSS no. 21-27), which is as half as that of *Juxia borissiaki* (= *Forstercooperia ergiliensis*) in size. On the contrary, judging from its drawing by Dashzeveg (1991, fig. 23), the teeth preserved in the specimen are not p2–p4 but dp2–dp4 because the central tooth preserved on PSS

no. 21-27 has a mesially elongated trigonid, which is a typical dp3 character of perissodactyls. Therefore, the specimen might be a juvenile specimen of *J. borissiaki*. Consequently, *Forstercooperia* sp. described by Dashzeveg (1991) is deleted from the faunal list of the formation in this paper (Tables 1–2).

It should be noted that a fragmentary dental specimen described as *Hypercoryphodon* sp. (Pantodonta, Coryphodontidae) from the formation by Kurochkin and Dashzeveg (1979) was assigned to an indeterminate indricothere or amynodont (Perissodactyla, Rhinocerotidae) by Lucas (1982). This specimen appears to be assigned to one of the species of the Paraceratheriidae or Amynodontidae listed in the Ergilin Dzo fauna and does not appear to indicate an additional species in the Ergilin Dzo fauna (Tables 1–2). Therefore, we delete ‘indricothere or amynodont indet.’, which was listed in the faunal list of the Ergilin Dzo Formation at the Khoer Dzan localit by Russell and Zhai (1987), from the faunal list of the formation in this paper.

Amynodontidae: Six genera and seven species of amynodontids have been recognized (Osborn, 1923, 1924, 1936; Gromova, 1954, 1958; Kurochkin and Dashzeveg, 1979; Wall, 1982, 1989; Russell and Zhai, 1987; Dashzeveg, 1993, 1996a; Lucas and Emry, 1996a; Lucas *et al.*, 1996). The genus ‘*Gigantamynodon* Gromova, 1954’ is now considered to be a *nomen dubium* (Table 2; Wall, 1989; Lucas and Emry, 1996a; Lucas *et al.*, 1996).

Deperetellidae: Two genera and two species of deperetellids have been recognized (Russell and Zhai, 1987; Dashzeveg and Devyatkin, 1986; Dashzeveg and Hooker, 1997; Tsubamoto *et al.*, 2012b). Dashzeveg and Devyatkin (1986) cited *Deperetella* sp. in the formation. Later, Dashzeveg and Hooker (1997) probably assigned this taxon to *Deperetella* cf. *birmanica*, describing a fossil specimen. On the other hand, Tsubamoto *et al.* (2005) elected a new genus *Bahinolophus* for *Deperetella birmanica* from the middle Eocene Pondaung Formation of Myanmar. Because *Bahinolophus* is currently endemic to the Pondaung Formation, here we provisionally cite the species under discussion discovered from the Ergilin Dzo Formation as cf. *Deperetella* sp. (Tables 1–2).

The superfamily to which the Deperetellidae are assigned is currently controversial (Koenigswald *et al.*, 2011; Bai *et al.*, 2019, 2020a, 2020b). This family has been traditionally assigned to the superfamily Tapiroidea because of its bilophodont molariforms (Radinsky, 1965; Bai *et al.*, 2019, 2020a). In contrast, Koenigswald *et al.* (2011) concluded that this family is assigned to the superfamily Rhinocerotidae because of the presence of dental cementum in some genera of the family. In the phylogenetic studies by Bai *et al.* (2020b), on the other hand, the parsimonious phylogenetic analysis implies

the tapiroid affinity of the family, but the Bayesian phylogenetic analysis implies the rhinocerotid affinity.

Helaletidae: One genus and two species of helaletids have been recognized (Matthew and Granger, 1925b; Radinsky, 1965; Yanovskaya *et al.*, 1977; Russell and Zhai, 1987; Dashzeveg and Hooker, 1997; Bai *et al.*, 2017). Russell and Zhai (1987) recognized two species of the helaletids, *Colodon inceptus* and *Colodon* sp., in the formation. Bai *et al.* (2017) assigned *Colodon inceptus* to the genus *Paracolodon*. Here, in addition, we provisionally assign *Colodon* sp. from the formation to the genus *Paracolodon* because the only named species of the helaletids from the formation, *Paracolodon inceptus* (= *C. inceptus*), was assigned to the genus *Paracolodon* by Bai *et al.* (2017) (Tables 1–2).

Concluding remarks

The fossil vertebrate fauna of the Ergilin Dzo Formation currently consists of five classes (the Osteichthyes, Amphibia, Reptilia, Ave, and Mammalia), 22 orders, 49 families, 77 genera, and 104 species, and its fossil mammalian fauna consists of 11 orders (the Eulipotyphla, Anagalida, Mesonychia, Cimolesta, Leptictida, Rodentia, Lagomorpha, Carnivora, Hyaenodontida, Artiodactyla, and Perissodactyla), 32 families, 56 genera, and 81 species (Table 1). The recent discovery of a crocodyliform tooth by Iijima *et al.* (2019) implies that southeastern Mongolia probably fulfilled thermal requirements of crocodyliforms during the late Eocene. In terms of the species diversity, perissodactyls are dominant in the fauna (Table 1; 33 perissodactyl species among the 81 mammalian species and the 104 vertebrate species), supporting that the Ergilian Asian Land Mammal Age is correlated to the late Eocene (Ducrocq, 1993; Ducrocq *et al.*, 1995; Meng and McKenna, 1998; Tsubamoto *et al.*, 2004, 2008). In terms of the collected specimens, the brontotheriid and rhinocerotid perissodactyls and ruminant artiodactyls are dominant among the vertebrate taxa of the formation (*e.g.*, Tsubamoto *et al.*, 2010). Compared with the early Oligocene mammalian faunas of northern Asia, taxonomic diversity and collected specimen numbers of the rodents, lagomorphs, and carnivorans appear to be low in the Ergilin Dzo mammalian fauna on the basis of the currently available evidence. In contrast, the perissodactyls in the Ergilin Dzo fauna are more common in terms of the relative abundance of the collected specimens as well as the taxonomic diversity than those of the early Oligocene faunas of northern Asia. The taxonomic diversity of the Hyaenodontida in the Ergilin Dzo fauna is as high as those of the early Oligocene faunas of northern Asia (Tsubamoto *et al.*, 2008). However, the relative numbers of the collected

hyaenodontid specimens in the Ergilin Dzo fauna are higher than those in the early Oligocene faunas of northern Asia, on the basis of the specimens collected by the Hayashibara-Mongolian Paleontological Expeditions in 2004, 2008, and 2010 (*e.g.*, Suzuki *et al.*, 2010; Tsubamoto *et al.*, 2006, 2010).

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References

- Bai, B., Meng, J., Janis, C. M., Zhang, Z.-Q. and Wang, Y.-Q., 2020a: Perissodactyl diversities and responses to climate changes as reflected by dental homogeneity during the Cenozoic in Asia. *Ecology and Evolution*, **2020(10)**: 6333–6355.
- Bai, B., Meng, J., Mao, F.-Y., Zhang, Z.-Q. and Wang, Y.-Q., 2019: A new early Eocene deperetellid tapiroid illuminates the origin of Deperetellidae and the pattern of premolar molarization in Perissodactyla. *PLoS ONE*, **14(11, e0225045)**: 1–26.
- Bai, B., Meng, J., Zhang, C., Gong, Y.-X. and Wang, Y.-Q., 2020b: The origin of Rhinoceroidea and phylogeny of Ceratomorpha (Mammalia, Perissodactyla). *Communications Biology*, **3(509)**: 1–16.
- Bai, B., Wang, Y.-Q., Mao, F.-Y. and Meng, J., 2017: New material of Eocene Helaletidae (Perissodactyla, Tapiroidea) from the Irдин Manha Formation of the Erlian Basin, Inner Mongolia, China and comments on related localities of the Huheboerhe Area. *American Museum Novitates*, **3878**: 1–44.
- Bai, B., Wang, Y.-Q. and Zhang, Z.-Q., 2018: The late Eocene hyracodontid perissodactyl *Ardynia* from Saint Jacques, Inner Mongolia, China and its implications for the potential Eocene–Oligocene boundary. *Palaeoworld*, **27(2)**: 247–257.
- Belyayeva (= Beliajeva), E. I., 1952: The primitive rhinocerotoids of Mongolia [Primitivnyye nosorogobraznyye Mongolii]. *Transactions of the Palaeontological Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **41**: 120–142. (*in Russian*)
- Belyayeva (= Beliajeva), E. I., 1954: Some data on the Oligocene rhinoceroses of Mongolia [Nekotopyye dannyye po oligotsenovym nosorogam Mongolii]. *Transactions of the Palaeontological Institute, Academy*

- of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **55**: 190–205. (in Russian)
- Belyayeva (= Beliajeva), E. I., 1959: Sur la découverte de Rhinocéros tertiaires anciens dans la Province Maritime de l'U.S.S.R. *Vertebrata Palasiatica*, **3(2)**: 81–92.
- Belyayeva (= Beliajeva), E. I., Trofimov, B. A. and Reshetov, V. Yu., 1974: Basic stages in the evolution of mammals in the late Mesozoic-Paleogene in Central Asia [Osnovnyye etapy evolyutsii mlekopitayushchikh v pozdnem mezozoye-paleogene Tsentral'noy Azii]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy]*, **1**: 19–45. (in Russian with English summary)
- Berggren, W. A. and D. R. Prothero, 1992: Eocene-Oligocene climatic and biotic evolution: An overview. In, Prothero, D. R. and Berggren, W. A., eds., *Eocene-Oligocene Climatic and Biotic Evolution*, p. 1–28. Princeton University Press, Oxford.
- Berkey, C. P. and Granger, W., 1923: Later sediments of the desert basins of Central Mongolia. *American Museum Novitates*, **77**: 1–16.
- Berkey, C. P. and Morris, F. K., 1927: *Geology of Mongolia-A Reconnaissance Report Based on the Investigations of the Years 1922–1923 (Natural History of Central Asia, Volume II)*, xxxi + 475 p. Central Asiatic Expeditions, American Museum of Natural History, New York.
- Brunet, M., 1979: *Les Grands Mammifères Chefs de File de l'Immigration Oligocène et le Problème de la Limite Éocène-Oligocène en Europe*, 281 p. Éditions de la Fondation Singer-Polignac, Paris.
- Burke, J. J., 1941: New fossil Leporidae from Mongolia. *American Museum Novitates*, **1117**: 1–23.
- Chow, M., 1958: Some Oligocene mammals from Lunan, Yunnan. *Vertebrata Palasiatica*, **2(4)**: 263–268, pls. I–II. (in Chinese with English summary)
- Chow, M., Xu, Y.-X. and Zhen, S.-N., 1964: *Amynodon* from the Eocene of Lunan, Yunnan. *Vertebrata Palasiatica*, **8(4)**: 355–361, pl. I. (in Chinese with English summary)
- Ckhikvadze, V. M., 1971: New turtles from the Oligocene of Kazakhstan and systematic position of some fossil species from Mongolia [Nouvelles tortues de l'Oligocène du Kazakhstan et position systématique de quelques espèces fossiles de Mongolie]. *Bulletin of the Academy of Sciences of the Georgian SSR [Soobshcheniia Akademii Nauk Gruzinskoi SSR]*, **62(2)**: 489–492. (in Russian)
- Ckhikvadze, V. M., 1972: About systematic position of the oldest land tortoises of Palearctic. *Bulletin of the Academy of Sciences of the Georgian SSR [Soobshcheniia Akademii Nauk Gruzinskoi SSR]*, **65(3)**: 745–748. (in Russian)
- Clarke, J. A., Norell, M. A. and Dashzeveg, D., 2005: New avian remains from the Eocene of Mongolia and the phylogenetic position of the Eogruidae (Aves, Gruoidea). *American Museum Novitates*, **3494**: 1–17.
- Dashzeveg, D., 1964: On two Oligocene Hyaenodontidae from Erghilyin-Dzo (Mongolian People's Republic). *Acta Palaeontologica Polonica*, **9**: 263–274, pl. 1.
- Dashzeveg, D., 1965: *Entelodon orientalis* n. sp. (Suiformes) from the Oligocene of the Gobi Desert, Mongolia. *Acta Palaeontologica Polonica*, **10(2)**: 281–285, pl. 1.
- Dashzeveg, D., 1966: New data on the stratigraphy of the Paleogene sediments of eastern Mongolia [Novyye dannyye o stratigrafii paleogenovykh otlozheniy Vostochnoy Mongolii]. *Reports of the USSR Academy of Sciences [Doklady Akademii Nauk SSSR]*, **168(3)**: 647–649. (in Russian)
- Dashzeveg, D., 1970: Stratigraphy and fauna of the upper Paleogene of the Mongolian People's Republic [Stratigrafiya i fauna verkhnego paleogena Mongol'skoy Narodnoy Respubliki]. *Transactions of the N. R. Scientific-Research of the Geological Institute, Mongolian Academy of Sciences, [Akademiya Nauk Mongolii, N. R. Nauchno-issledovatel'skaya Geologicheskogo Instituta, Trudy]*, **1**: 45–56. (in Russian)
- Dashzeveg, D., 1974: The chalicothere *Schizotherium avitum* Matthew et Granger from Oligocene deposits in East Gobi (locality Ergilin-Dzo) and a short review of vertebrate fauna of the same locality [Khalicoteryy *Schizotherium avitum* Matthew et Granger iz oligotsena Ergilin-Dzo vostochnoy Gobi i obzor pozvonochnykh iz etogo mestonakhozhdeniya]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy]*, **1**: 74–79. (in Russian with English summary)
- Dashzeveg, D., 1975: New representatives of the genus *Embootherium* from the Oligocene of Mongolia [Novyye predstavityel' roda *Embootherium* iz oligotsena Mongolii]. *Paleontological Journal [Paleontologicheskii Zhurnal]*, **3**: 150–152. (in Russian)
- Dashzeveg, D., 1976a: Discovery of an indricothere tooth in the early Oligocene of Mongolia [Nakhodka zuba indrikoteriya v nizhnem oligotsenye Mongolii]. *Paleontological Journal [Paleontologicheskii Zhurnal]*, **2**: 138–139. (in Russian)
- Dashzeveg, D., 1976b: New data on Entelodontidae (Artiodactyla, Suiformes) from the Oligocene of Mongolia [Novyye dannyye ob Entelodontidae (Artiodactyla, Suiformes) iz oligotsena Mongolii]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy]*, **3**: 47–50. (in Russian with English summary)
- Dashzeveg, D., 1985: Nouveaux Hyaenodontinae (Creodonta, Mammalia) du Paléogène de Mongolie. *Annales de Paléontologie (Vertebrata-Invertebrata)*, **71**: 223–256.
- Dashzeveg, D., 1991: Hyracodontids and rhinocerotids (Mammalia, Perissodactyla, Rhinoceroidea) from the Paleogene of Mongolia. *Palaeovertebrata*, **21(1–2)**: 1–84.
- Dashzeveg, D., 1993: Asynchronism of the main mammalian

- faunal events near the Eocene-Oligocene boundary. *Tertiary Research*, **14**(4): 141–149.
- Dashzeveg, D., 1996a: A new hyracodontid (Perissodactyla, Rhinoceroidea) from the Ergilin Dzo Formation (Oligocene, Quarry 1) in Dzamyn Ude, eastern Gobi Desert, Mongolia. *American Museum Novitates*, **3178**: 1–12.
- Dashzeveg, D., 1996b: Some carnivorous mammals from the Paleogene of the eastern Gobi Desert, Mongolia, and the application of Oligocene carnivores to stratigraphic correlation. *American Museum Novitates*, **3179**: 1–14.
- Dashzeveg, D. and Devyatkin, E. V., 1986: Eocene-Oligocene boundary in Mongolia. In, Pomel, C. and Premoli-Silva, I. eds., *Terminal Eocene Events. Developments in Paleontology and Stratigraphy*, **9**: 153–157.
- Dashzeveg, D. and Hooker, J. J., 1997: New ceratomorph perissodactyls (Mammalia) from the Middle Eocene of Mongolia: their implications for phylogeny and dating. *Zoological Journal of the Linnean Society of London*, **120**: 105–138.
- Dashzeveg, D. and Russell, D. E., 1992: Extension of dyspternine Pantolestidae (Mammalia, Cimolesta) in the early Oligocene of Mongolia. *Geobios*, **25**(5): 647–650.
- Devyatkin, E. V., 1981: The Cenozoic of Inner Asia (stratigraphy, geochronology and correlation). *Transactions of the Joint Soviet-Mongolian Scientific-Research Geological Expedition*, **27**: 1–196. Nauk, Moscow. (in Russian).
- Dill, H. G., Khishigsuren, S., Melcher, F., Bulgamaa, J., Bolorma, Kh., Botz, R. and Schwartz-Schampera, U., 2005: Facies-related diagenetic alteration in lacustrine-deltaic red beds of the Paleogene Ergilin Zoo Formation (Erdene Sum area, S. Gobi, Mongolia). *Sedimentary Geology*, **181**: 1–24.
- Ducrocq, S., 1993: Mammals and stratigraphy in Asia: is the Eocene-Oligocene boundary at the right place? *Comptes Rendus de l'Academie des Sciences, Paris, Série II*, **316**: 419–426.
- Ducrocq, S., Chaimanee, Y., Jaeger, J.-J., Yamee, C., Rugbunrung, M., Grohé, C. and Chavasseau, O., 2021: New fossil remains from Bang Mark locality, Krabi Basin, southern Thailand. *Journal of Vertebrate Paleontology*, **e1988624**. doi: 10.1080/02724634.2021.1988624.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V. and Jaeger, J.-J., 1995: Mammalian faunas and the ages of the continental Tertiary fossiliferous localities from Thailand. *Journal of Southeast Asian Earth Sciences*, **12**: 65–78.
- Egi, N., Tsubamoto, T., Saneyoshi, M., Tsogtbaatar, Kh., Watabe, M., Mainbayar, B., Chinzorig, Ts. and Khatanbaatar, P., 2016: Taxonomic revisions on nimravids and small feliforms (Mammalia, Carnivora) from the Upper Eocene of Mongolia. *Historical Biology*, **28**(1–2): 105–119.
- Egi, N., Tsubamoto, T. and Takai, M., 2007: Systematic status of Asian “*Pterodon*” and early evolution of hyaenaelurine hyaenodontid creodonts. *Journal of Paleontology*, **81**(4): 770–778.
- Egi, N., Tsubamoto, T. and Tsogtbaatar, Kh., 2009: New amphicyonid (Mammalia: Carnivora) from the Upper Eocene Ergilin Dzo Formation, Mongolia. *Paleontological Research*, **13**(3): 245–249.
- Gabunia, L. K. and Dashzeveg, D., 1974: On the Oligocene specimen of *Forstercooperia* (Hyracodontidae) from Mongolia [Ob oligotsenovom predstavivelye *Forstercooperia* (Hyracodontidae) iz Mongolii]. *Bulletin of the Academy of Sciences of the Georgian SSR [Soobshcheniya Akademii Nauk Gruzinskoy SSR]*: **75**(2): 497–500. (in Russian with English summary)
- Gabunia, L. K. and Dashzeveg, D., 1988: A peculiar rhinocerotid from the upper Eocene of Mongolia. *Biology Bulletin of the Academy of Sciences of USSR [Izvestiya Akademii Nauk SSSR, Seriya Biologicheskaya]*, **14**(14): 244–248. (in Russian)
- Gilmore, C. W., 1931: Fossil turtles of Mongolia. *Bulletin of the American Museum of Natural History*, **59**(4): 213–257, pls. I–XI.
- Granger, W. and Gregory, W. K., 1943: A revision of the Mongolian titanotheres. *Bulletin of the American Museum of Natural History*, **80**(10): 349–389.
- Gromova, V., 1952a: On primitive carnivores of the Paleogene of Mongolia and Kazakhstan [O primitivnykh khishchnikakh iz paleogena Mongolii i Kazakhstana]. *Transactions of the Palaeontological Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **41**(1): 51–77. (in Russian)
- Gromova, V., 1952b: Primitive tapiroids from the Paleogene of Mongolia [Primitivnyye tapiroobraznyye iz paleogena Mongolii]. *Transactions of the Palaeontological Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **41**(1): 99–119. (in Russian)
- Gromova, V., 1954: The swamp rhinoceroses (Aminodontidae) of Mongolia. *Transactions of the Palaeontological Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **55**: 85–189.
- Gromova, V., 1958: Nouvelles trouvailles des aminodontidés en Mongolie. *Vertebrata Palasiatica*, **2**(2–3): 107–116.
- Gromova, V., 1959: Première découverte d'un chat primitif au Paléogène d'Asie Centrale. *Vertebrata Palasiatica*, **3**(2): 59–72.
- Gureyev, A. A., 1960: Lagomorphs (Lagomorpha) from the Oligocene of Mongolia and Kazakhstan [Zaytseobraznyye (Lagomorpha) oligotsena Mongolii in Kazakhstana]. *Transactions of the Palaeontological Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **77**(4): 5–34. (in Russian)
- Heissig, K., 1969: Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim bei Ingolstadt in Bayern und ihre phylogenetische Stellung. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche*

- Klasse, Neue Folge*, **138**: 1–133. München.
- Iijima, M., Tsubamoto, T., Tsogtbaatar, Kh., Chinzorig, Ts. and Baasankhuu, S., 2019: Discovery of a crocodyliform tooth from the upper Eocene Ergilin Dzo Formation, Mongolia. *Acta Palaeontologica Polonica*, **64**(4): 775–778.
- Kielan-Jaworowska, Z. and Dovchin, N., 1968: Narrative of the Polish-Mongolian Paleontological Expeditions 1963–1965. *Palaeontologia Polonica*, **19**: 7–30, pls. I–IV.
- Koenigswald, W. von, Holbrook, L. T. and Rose, K. D., 2011: Diversity and evolution of Hunter-Schreger Band configuration in tooth enamel of perissodactyl mammals. *Acta Palaeontologica Polonica*, **56**: 11–32.
- Kozlova, E. V., 1960: New fossil birds from the southeastern Gobi [Novye iskopaemye ptitsy iz jugo-vostochnoj Gobi]. *Transactions of Problem and Thematic Meetings USSR Academy of Sciences, Zoological Institute [Trudy Problemykh i Tematicheskikh Soveshchaniy Akademija Nauk SSSR, Zoologicheskij Institut]*, **9**: 323–329. (in Russian)
- Kretzoi, M., 1942: Ausländische Säugetierfossilien der Ungarische Museen. *Földtani Közlemény*, **72**: 139–148.
- Kurochkin, E. N., 1976: A survey of the Paleogene birds of Asia. In, Olson, S. L. ed., *Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore*, p. 75–76.
- Kurochkin, E. N., 1981: New representatives and evolution of two archaic gruiform families in Eurasia. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Trudy Sovmestnaja Sovetsko-Mongolskaja Paleontologicheskaja Ekspeditsija]*, **15**: 59–85. (in Russian)
- Kurochkin, E. N. and Dashzeveg, D., 1979: New occurrence of coryphodon from the Oligocene of Mongolia [Novaya nakhoda korifodona v oligotsenye Mongolii]. *Transactions of The Joint Soviet-Mongolian Paleontological Expedition [Trudy Sovmestnaja Sovetsko-Mongolskaja Paleontologicheskaja Ekspeditsija]*, **8**: 7–9. (in Russian)
- Lange-Badré, B. and Dashzeveg, D., 1989: On some Oligocene carnivorous mammals from Central Asia. *Acta Palaeontologica Polonica*, **34**(2): 125–148, pls. 9–14.
- Lavrov, A. V., 1999: New material on the Hyaenodontidae (Mammalia, Creodonta) from the Ergilin Dzo Formation (Late Eocene of Mongolia) and some notes on the system of the Hyaenodontidae. *Paleontological Journal*, **33**(3): 321–329.
- Lavrov, A. V., 2019: New material on small hyaenodonts (Hyaenodontinae, Creodonta) from the Paleogene of Mongolia. *Paleontological Journal*, **53**(4): 418–431.
- Liskun, I. G. and Badamgarav, D., 1977: Lithology of the Cenozoic of Mongolia [Litologija kaynozoya Mongolii]. *Transactions of the Joint Soviet-Mongolian Scientific-Research Geological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Nauchno-issledovatel'skaya Geologicheskaya Ekspeditsiya, Trudy]*, **20**: 1–159. (in Russian)
- Lopatın, A. V., 1997: New Oligocene Didymoconidae (Mesonychia, Mammalia) from Mongolia and Kazakhstan. *Paleontological Journal*, **31**(1): 108–119.
- Lopatın, A. V., 2005: Late Paleogene Erinaceidae (Insectivora, Mammalia) from the Ergilin Dzo locality, Mongolia. *Paleontological Journal*, **39**(1): 85–92.
- Lopatın, A. V., 2020: A review of the Mesozoic and Cenozoic mammals of Mongolia. *Paleontological Journal*, **54**(7): 779–808.
- López-Torres, S. and Fostowicz-Frelik, Ł., 2018: A new Eocene anagalid (Mammalia: Euarchontoglires) from Mongolia and its implications for the group's phylogeny and dispersal. *Scientific Reports*, **8**(13955): 1–9.
- Lucas, S. G., 1982: The phylogeny and composition of the Order Pantodonta (Mammalia, Eutheria). In, Mamet, B. and Copeland, M. J., eds., *Third North American Paleontological Convention (Montreal, August 5–7, 1982) Proceedings*, **2**: 337–342.
- Lucas, S. G. and Emry, R. J., 1996a: Biochronological significance of Aynodontidae (Mammalia, Perissodactyla) from the Paleogene of Kazakhstan. *Journal of Paleontology*, **70**(4): 691–96.
- Lucas, S. G. and Emry, R. J., 1996b: Late Eocene entelodonts (Mammalia: Artiodactyla) from the Inner Mongolia, China. *Proceedings of the Biological Society of Washington*, **109**(2): 397–405.
- Lucas, S. G., Emry, R. J. and Bayshashov, B. U., 1996: *Zaisanamynodon*, a Late Eocene aynodontid (Mammalia, Perissodactyla) from Kazakhstan and China. *Tertiary Research*, **17**(1–2): 51–58.
- Lucas, S. G. and Schoch, R. M., 1989: Taxonomy and biochronology of *Eomoropus* and *Grangeria*, Eocene chalicotheres from the western United States and China. In, Prothero, D. R. and Schoch, R. M., eds., *The Evolution of Perissodactyls*, p. 422–437. Oxford University Press, Oxford.
- Lucas, S. G. and Sobus, J. C., 1989: The systematics of indricotheres. In, Prothero, D. R. and Schoch, R. M., eds., *The Evolution of Perissodactyls*, p. 358–378. Oxford University Press, Oxford.
- Matthew, W. D. and Granger, W., 1923a: Nine rodents from the Oligocene of Mongolia. *American Museum Novitates*, **102**: 1–10.
- Matthew, W. D. and Granger, W., 1923b: The fauna of the Ardyn Obo Formation. *American Museum Novitates*, **98**: 1–5.
- Matthew, W. D. and Granger, W., 1924: New Carnivora from the Tertiary of Mongolia. *American Museum Novitates*, **104**: 1–9.
- Matthew, W. D. and Granger, W., 1925a: New creodonts and rodents from the Ardyn Obo Formation of Mongolia. *American Museum Novitates*, **193**: 1–7.
- Matthew, W. D. and Granger, W., 1925b: New ungulates from the Ardyn Obo Formation of Mongolia, with faunal list and remarks on correlation. *American Museum Novitates*, **195**: 1–12.
- McKenna, M. C. and Bell, S. K., 1997: *Classification*

- of *Mammals above the Species Level*, xii + 631 p. Columbia University Press, New York.
- Meng, J. and McKenna, M. C., 1998: Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. *Nature*, **394**: 364–367.
- Mihlbachler, M. C., 2007: *Eubrontotherium clarnoensis*, a new genus and species of brontothere (Brontotheriidae, Perissodactyla) from the Hancock Quarry, Clarno Formation, Wheeler County, Oregon. *PaleoBios*, **27**(1): 19–39.
- Mihlbachler, M. C., 2008: Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia: Perissodactyla). *Bulletin of the American Museum of Natural History*, **311**: 1–475.
- Mihlbachler, M. C., Lucas, S. G. and Emry, R., 2004: A new brontothere (Brontotheriidae, Perissodactyla, Mammalia) from the Eocene of the Ily Basin of Kazakhstan and a phylogeny of Asian “horned” brontotheres. *American Museum Novitates*, **3439**: 1–43.
- Młynarski, M., 1968: Notes on tortoises (Testudinidae) from the Tertiary of Mongolia. *Palaeontologia Polonica*, **19**: 85–97, pls. VIII–IX.
- Morlo, M. and Nagel, D., 2006: New remains of Hyaeodontidae (Creodonta, Mammalia) from the Oligocene of Central Mongolia. *Annales de Paléontologie*, **92**: 305–321.
- Osborn, H. F., 1923: *Cadurcotherium* from Mongolia. *American Museum Novitates*, **92**: 1–2.
- Osborn, H. F., 1924: *Cadurcotherium ardynense*, Oligocene, Mongolia. *American Museum Novitates*, **147**: 1–4.
- Osborn, H. F., 1925: Upper Eocene and Lower Oligocene titanotheres of Mongolia. *American Museum Novitates*, **202**: 1–12.
- Osborn, H. F., 1929: *Embolotherium*, gen. nov., of the Ulan Gochu, Mongolia. *American Museum Novitates*, **353**: 1–20.
- Osborn, H. F., 1936: *Amynodon mongoliensis* from the Upper Eocene of Mongolia. *American Museum Novitates*, **859**: 1–9.
- Peigné, S., 2003: Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta*, **32**(3): 199–229.
- Prothero, D. R., 1994: *The Eocene-Oligocene Transition: Paradise Lost*, xviii + 291 pp. Columbia University Press, New York.
- Prothero, D. R., Domning, D., Fordyce, R. E., Foss, S., Janis, C., Lucas, S., Marriott, K. L., Metais, G., Naish, D., Padian, K., Rössner, G., Solounias, N., Spaulding, M., Stucky, R. M., Theodor, J. and Uhen, M., 2022: On the unnecessary and misleading taxon “Cetartiodactyla.” *Journal of Mammalian Evolution*, **29**(1): 93–97.
- Qiu, Z.-X. and Wang, B.-Y., 1999: *Allacerops* (Rhinocerotidae, Perissodactyla), its discovery in China and its systematic position. *Vertebrata Palasiatica*, **37**(1): 48–61, pl. 1. (in Chinese with English summary)
- Qiu, Z. and Wang, B., 2007: Paraceratheres fossils of China. *Palaeontologia Sinica*, **Whole no. 193** (New Ser. C, no. 29): i–xi, 1–396, pls. I–XLVI. (in Chinese with English summary)
- Radinsky, L. B., 1965: Early Tertiary Tapiroidea of Asia. *Bulletin of the American Museum of Natural History*, **129**(2): 181–264.
- Radinsky, L. B., 1967: A review of the rhinocerotoid family Hyracodontidae (Perissodactyla). *Bulletin of the American Museum of Natural History*, **136**(1): 1–46.
- Reshetov, V. Yu., 1979: Early Tertiary Tapiroidea of Mongolia and the USSR [Rannetretichnye tapiroobraznye Mongolii i SSSR]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition*, **11**: 1–144. (in Russian with English summary)
- Rozhdestvenskiy, A. K., 1949: Some early Tertiary mammal localities from Mongolia [Nekotoryye mestonakhozhdeniya drevnyetretichnykh mlekopitayushchikh v Mongolii]. *Reports of the USSR Academy of Sciences [Doklady Akademii Nauk SSSR]*, **66**(3): 463–466. (in Russian)
- Russell, D. E. and Zhai, R., 1987: The Paleogene of Asia: mammals and stratigraphy. *Mémoires du Muséum National d'histoire Naturelle, Série C, Sciences de la Terre*, **52**: 1–488.
- Sakamoto, S., Hatakeyama, T., Kitahara, Y., Saneyoshi, M., Tsogtbaatar, Kh., 2021: Geochronological study of the Ergilin Dzo Formation, Paleogene, Mongolia. *Abstracts with Programs, The 2021 Annual Meeting, The Palaeontological Society of Japan (July 2–4, 2021, Online, Okayama)*, p. 21. (in Japanese with English title)
- Saneyoshi, M., Tsubamoto, T., Watabe, M. and Tsogtbaatar, Kh., 2010: Lithostratigraphic and sedimentological analysis of the upper Eocene Ergilin Dzo Formation of Ergilin Dzo locality, Mongolia. *Hayashibara Museum of Natural Sciences Research Bulletin*, **3**: 149–153.
- Shevyreva, N. S., 1972: New rodents from the Paleogene of Mongolia and Kazakhstan [Novyye gryzuny iz paleogena Mongolii i Kazakhstana]. *Paleontological Journal [Paleontologicheskii Zhurnal]*, **3**: 134–145. (in Russian)
- Suzuki, S., Watabe, M. and Tsogtbaatar, Kh., 2010: Report of the HMNS-MPC Joint Paleontological Expedition in 2004. *Hayashibara Museum of Natural Sciences Research Bulletin*, **3**: 1–9.
- Sych, L., 1975: Lagomorpha from the Oligocene of Mongolia. *Palaeontologia Polonica*, **33**(6): 183–200, pls. LI–LIV.
- Szalay, F. S. and Gould, S. J., 1966: Asiatic Mesonychidae (Mammalia, Condylarthra). *Bulletin of the American Museum of Natural History*, **132**(2): 127–173, pls. 9–12.
- Tong, Y., 1997: Middle Eocene small mammals from Liguangqiao basin of Henan Province and Yuanqu basin of Shanxi Province, central China. *Palaeontologia Sinica*, **Whole no. 186** (New Ser. C, no. 26): i–xiv, 1–256, pls. I–XII. (in Chinese with English summary)
- Trofimov, B. A., 1952: New entelodontids from Mongolia and Kazakhstan [Novyye entelodontidy iz Mongolii i Kazakhstana]. *Transactions of the Palaeontological*

- Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **41**: 144–154. (in Russian)
- Trofimov, B. A., 1957: Nouvelles données sur les Ruminantia les plus anciens d'Asie. *Cursillos y Conferencias del Instituto "Lucas Mallada"*, **4**: 137–141.
- Trofimov, B. A., 1958: On a new name for the entelodont *Brachyodon* Trofimov, 1952, *Ergilobia* nom. nov. [O pereimenovanii entelodona *Brachyodon* Trofimov, 1952, v. *Ergilobia* nom. nov.]. *Materials for the Fundamentals of Paleontology [Materialy k Osnovam Paleologii]*, **2**: 119. (in Russian)
- Tsubamoto, T., 2010: Additional specimens of the Anthracotheriidae (Mammalia; Artiodactyla) from the upper Eocene Ergilin Dzo Formation of Mongolia. *Hayashibara Museum of Natural Sciences Research Bulletin*, **3**: 143–147.
- Tsubamoto, T., 2015: Rare anomalous dental morphologies found in raccoon dog (*Nyctereutes procyonoides*) and their implication to dental morphology of fossil mammals. *Journal of the Geological Society of Japan*, **121(6)**: 185–189.
- Tsubamoto, T., Egi, N., Takai, M., Sein, C. and Maung M., 2005: Middle Eocene ungulate mammals from Myanmar: A review with description of new specimens. *Acta Palaeontologica Polonica*, **50(1)**: 117–138.
- Tsubamoto, T., Saneyoshi, M., Tsogtbaatar, Kh., Chinzorig, Ts., Khatanbaatar, P., Mainbayar, B. and Suzuki, S., 2010: Report of the HMNS-MPC Joint Paleontological Expedition in the Gobi Desert of Mongolia, 2008. *Hayashibara Museum of Natural Sciences Research Bulletin*, **3**: 29–39.
- Tsubamoto, T., Saneyoshi, M., Watabe, M., Tsogtbaatar, Kh. and Mainbayar, B., 2011a: The entelodontid artiodactyl fauna from the Eocene Ergilin Dzo Formation of Mongolia with comments on *Brachyhyops* and the Khoer Dzan locality. *Paleontological Research*, **15(4)**: 258–268.
- Tsubamoto, T., Takai, M. and Egi, N., 2004: Quantitative analyses of biogeography and faunal evolution of middle to late Eocene mammals in East Asia. *Journal of Vertebrate Paleontology*, **24(3)**: 657–667.
- Tsubamoto, T. and Tsogtbaatar, Kh., 2008: New specimens of anthracotheriid artiodactyls from the upper Eocene Ergilin Dzo Formation of Mongolia. *Paleontological Research*, **12(4)**: 371–386.
- Tsubamoto, T., Tsogtbaatar, Kh., Chinzorig, Ts., Mainbayar, B., Egi, N., Saneyoshi, M. and Nishido, H., 2013a: Dental morphology of '*Pterodon* sp.' (Mammalia; Hyaeodontidae) described from the Eocene Ergilin Dzo Formation, Mongolia. *The Bulletin of Research Institute of Natural Sciences, Okayama University of Science*, **39**: 43–44.
- Tsubamoto, T., Tsogtbaatar, Kh., Saneyoshi, M., Mainbayar, B., Watabe, M., Chinzorig, Ts., Suzuki, S., Khatanbaatar, P., Ishigaki, S. and Barsbold, R., 2011b: A new specimen of *Gobiopithecus khan* (Mammalia; Pantolestia) from the Eocene Ergilin Dzo Formation, Mongolia. *Journal of Fossil Research*, **44(1)**: 20–23.
- Tsubamoto, T., Tsogtbaatar, Kh., Saneyoshi, M., Mainbayar, B., Watabe, M., Chinzorig, Ts., Khatanbaatar, P. and Nishido, H., 2013b: New specimens of *Entelodon gobiensis* (Mammalia; Artiodactyla; Entelodontidae) from the Eocene Ergilin Dzo Formation, Mongolia. *The Bulletin of Research Institute of Natural Sciences, Okayama University of Science*, **39**: 37–41.
- Tsubamoto, T., Tsogtbaatar, Kh., Saneyoshi, M., Mainbayar, B., Watabe, M., Chinzorig, Ts., Suzuki, S., Khatanbaatar, P., Ishigaki, S. and Barsbold, R., 2012a: Fossil evidence of a mesonychid mammal from the upper Eocene Ergilin Dzo Formation, Mongolia. *Paleontological Research*, **16(2)**: 171–174.
- Tsubamoto, T., Tsogtbaatar, Kh., Watabe, M., Saneyoshi, M. and Chinzorig, Ts., 2012b: The function of the crown cementum of *Teleolophus*, an Eocene deperetellid perissodactyl. *Journal of Fossil Research*, **44(2)**: 78–79.
- Tsubamoto, T., Watabe, M., Suzuki, S. and Tsogtbaatar, Kh., 2006: Fossil vertebrate assemblage from the upper Eocene Ergilin Dzo Formation of Mongolia. *Journal of the Geological Society of Japan*, **112(3)**: V–VI. (in Japanese)
- Tsubamoto, T., Watabe, M. and Tsogtbaatar, K., 2008: *Hyaenodon chunkhtensis* and the hyaeodontid fauna from the upper Eocene Ergilin Dzo Formation of Mongolia. *Journal of Vertebrate Paleontology*, **28(2)**: 559–564.
- Van Valen, L., 1967: New Paleogene insectivores and insectivore classification. *Bulletin of the American Museum of Natural History*, **135(5)**: 217–284.
- Vislobokova, I., 1998: A new representative of the Hypertraguloidea (Tragulina, Ruminantia) from the Khoer-Dzan Locality in Mongolia, with remarks on the relationships of the Hypertragulidae. *American Museum Novitates*, **3225**: 1–24.
- Wall, W. P., 1982: Evolution and biogeography of the Amyndontidae (Perissodactyla, Rhinoceroidea). In, Mamet, B. and Copeland, M. J., eds., *Third North American Paleontological Convention [Montreal, August 5–7, 1982] Proceedings*, **2**: 563–567.
- Wall, W. P., 1989: The phylogenetic history and adaptive radiation of the Amyndontidae. In, Prothero, D. R. and Schoch, R. M., eds., *The Evolution of Perissodactyls*, p. 341–354. Oxford University Press, Oxford.
- Wang, H., Bai, B., Meng, J. and Wang, Y., 2016: Earliest known unequivocal rhinocerotid sheds new light on the origin of Giant Rhinos and phylogeny of early rhinocerotoids. *Scientific Reports*, **6(39607)**: 1–9, doi: 10.1038/srep39607.
- Wang, B.-Y. and Meng, J., 2009: *Ardynomys* (Cylindrodontidae, Rodentia) from Nei Mongol, China. *Vertebrata Palasiatica*, **47(3)**: 240–244. (in Chinese with English summary)
- Wang, B. and Qiu, Z., 2002: A new species of Entelodontidae (Artiodactyla, Mammalia) From late Eocene of Nei Mongol, China. *Vertebrata Palasiatica*, **40(3)**: 194–202.
- Wang, X., Qiu, Z. and Wang, B., 2005: Hyaenodonts and

- carnivorans from the early Oligocene to early Miocene of Xianshuihe Formation, Lanzhou basin, Gansu Province, China. *Palaeontologia Electronica*, **8(1:6A)**: 1–14.
- Wang, X.-Y., Wang, Y.-Q., Zhang, R., Zhang, Z.-H., Liu, X.-L. and Ren, L.-P., 2020: A new species of *Amyndontopsis* (Perissodactyla: Amyndontidae) from the Middle Eocene of Jiyuan, Henan, China. *Vertebrata Palasiatica*, **58(3)**: 188–203.
- Wetmore, A., 1934: Fossil birds from Mongolia and China. *American Museum Novitates*, **711**: 1–16.
- Wood, A. E., 1970: The Early Oligocene rodent *Ardynomys* (family Cylindrodontidae) from Mongolia and Montana. *American Museum Novitates*, **2418**: 1–18.
- Yanovskaya (= Janovskaja), N. M., 1954: A new genus of Embolotheriinae from the Paleogene of Mongolia [Novyy rod Embolotheriinae iz paleogena Mongolii]. *Transactions of the Palaeontological Institute, Academy of Sciences of the USSR [Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR]*, **55(3)**: 5–43. (in Russian)
- Yanovskaya (= Janovskaja), N. M., 1976: *Epimanteoceras amplus* sp. nov. (Mammalia, Perissodactyla, Brontotheriidae) from Mongolia [*Epimanteoceras amplus* sp. nov. (Mammalia, Perissodactyla, Brontotheriidae) iz Mongolii]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy]*, **3**: 38–46. (in Russian with English summary)
- Yanovskaya (= Janovskaja), N. M., 1980: The brontotheres of Mongolia [Brontoterii Mongolii]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy]*, **12**: 1–220. (in Russian with English summary)
- Yanovskaya (= Janovskaja), N. M., Kurochkin, E. N. and Devjatkin, E. V., 1977: Ergeleen-Dzo locality—the stratotype of lower Oligocene in South-East Mongolia [Mestonakhozhdeniye Ergilin-Dzo—stratotip nizhnego oligotsena v yugo-vostochnoy Mongolii]. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition [Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy]*, **4**: 14–33. (in Russian with English summary)