

## 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.

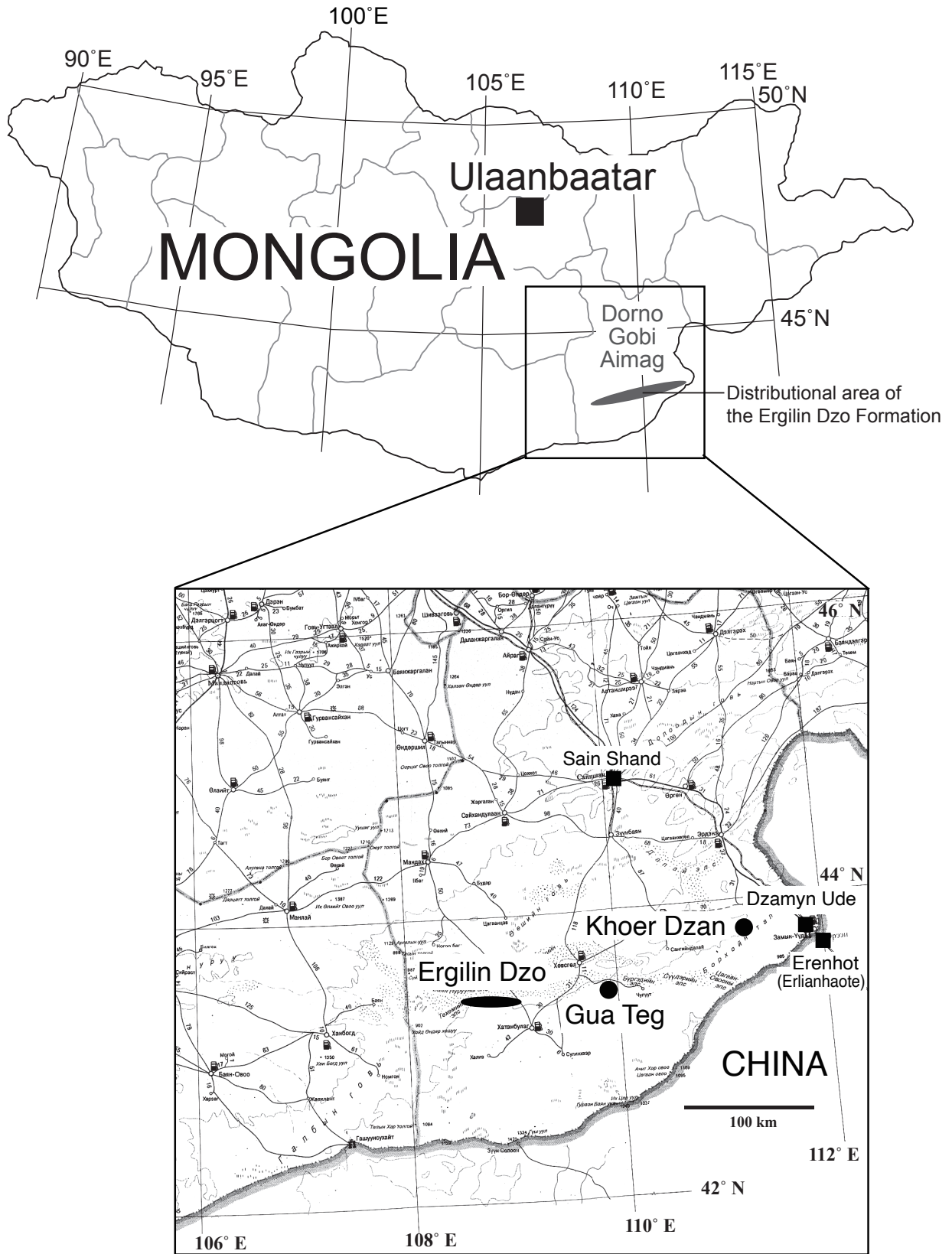
We briefly review the fossil vertebrate fauna of the upper Eocene Ergilin Dzo Formation of southeastern Mongolia. The Ergilin Dzo vertebrate fauna currently consists of 104 species of five classes: two species of the Osteichthyes, one species of the Amphibia, nine species of the Reptilia, 11 species 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; Mhlbachler, 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

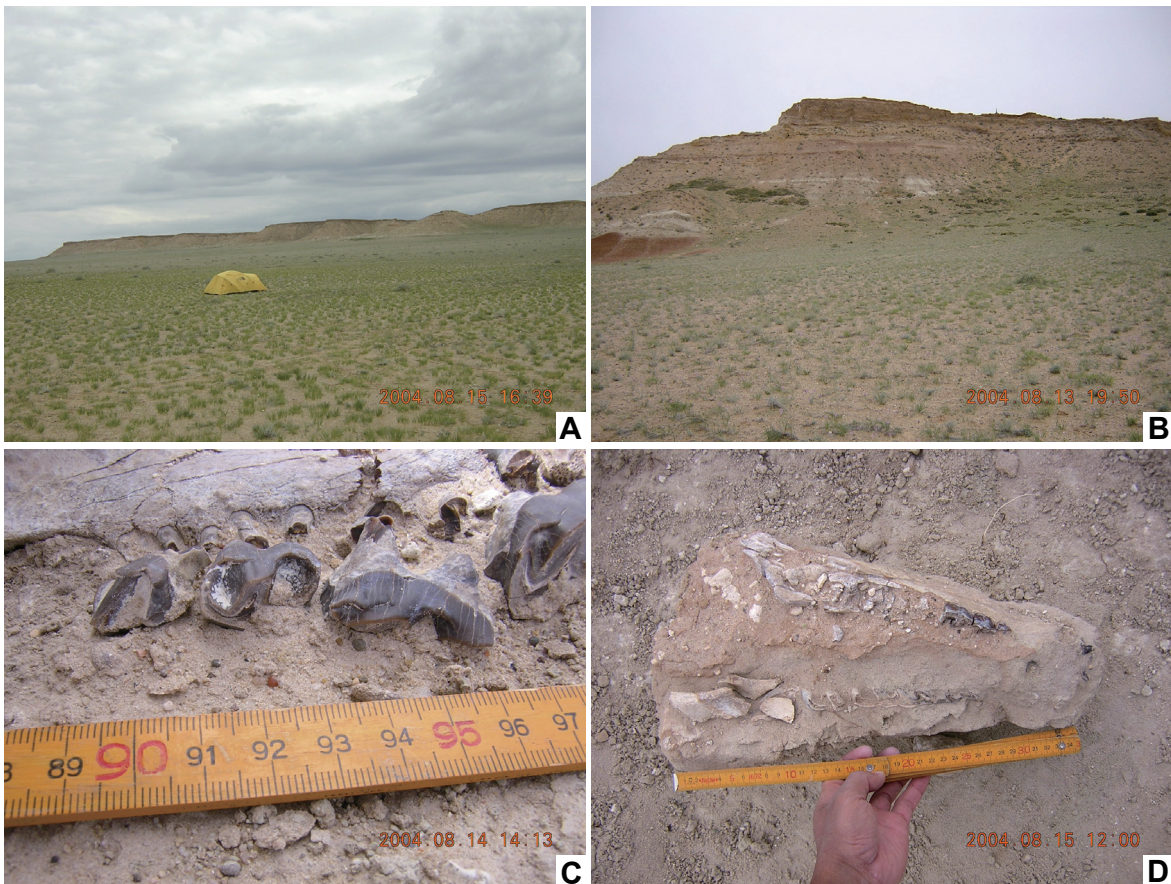
Sevkul and Ergilin members according to Dashzeveg and Devyatkin (1986) and Dashzeveg (1993). At the Ergilin Dzo locality, all members of the formation are exposed (Dashzeveg, 1993). Around the uppermost part of the formation (= around the Khetsu Tsav Member) at the Ergilin Dzo locality, many fossil specimens 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.

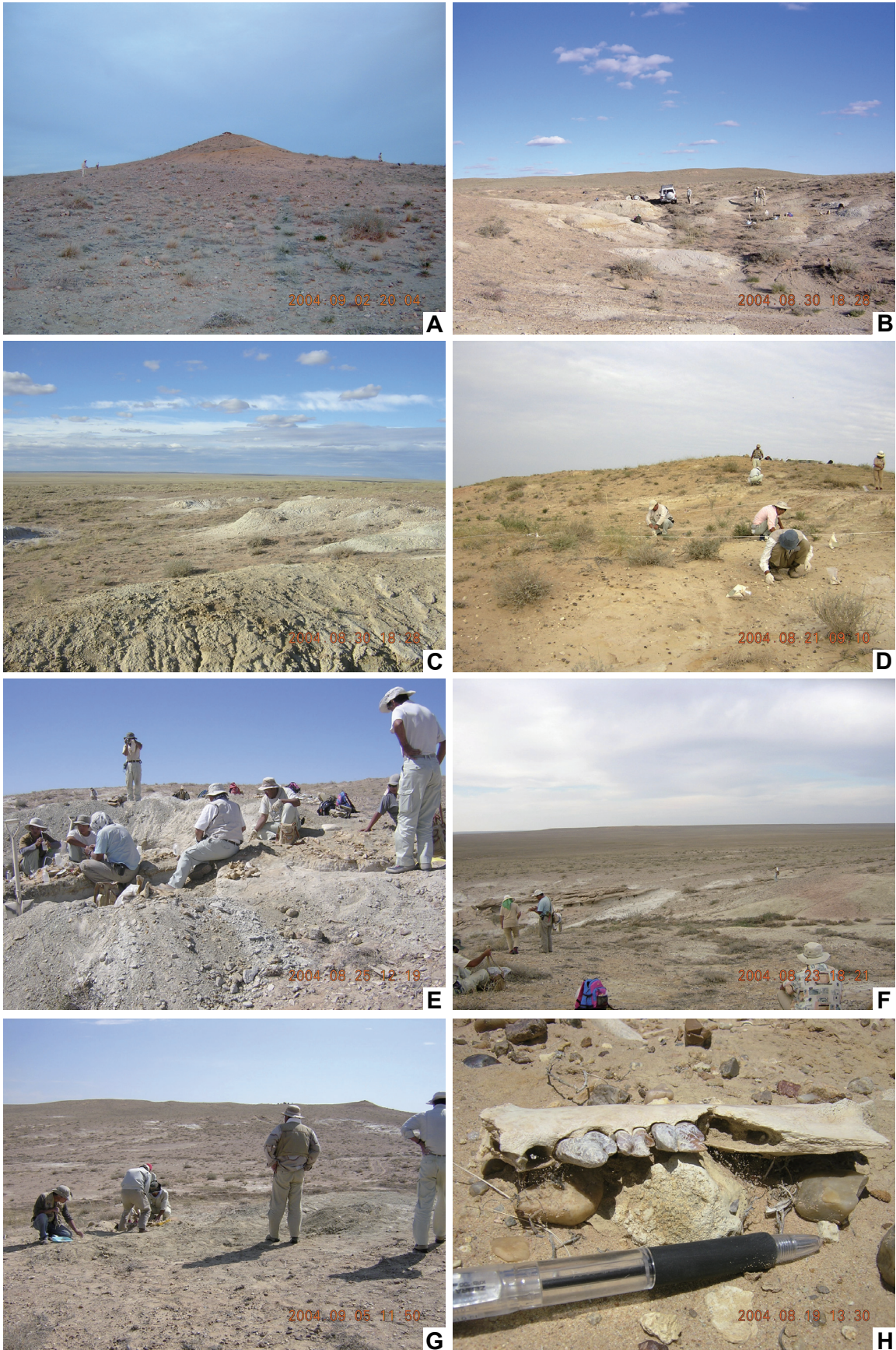
The paleoenvironment of the Ergilin Dzo Formation is estimated to be relatively hot/warm and humid with a relatively-closed area on the basis of the presence of the Brontotheriidae (Mammalia, Perissodactyla) and the dominance of the low-crowned plant-eating mammals (Prothero, 1994; Tsubamoto *et al.*, 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 *Hyaeodon 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.

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**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]

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Table 1.—continued.

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**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]

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Table 1.—*continued.*


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**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]

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**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).

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<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]

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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 ergilinesis*, 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.*

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<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]

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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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