A New Species of *Ardynictis* (Didymoconidae, Mammalia) from the Middle Eocene of Mongolia

A. V. Lopatin

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: alopat@paleo.ru

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Abstract—*Ardynictis captor* sp. nov., a new didymoconid species from the Middle Eocene Khaychin Formation of the Khaychin-Ula 2 locality in Mongolia, is described. It differs from the type species *A. furunculus* Matthew et Granger from the terminal Eocene–basal Oligocene of Mongolia by being twice as small, the shape and structure of P^4 and M^1, and the high paraconid and relatively low trigonid of M_1 and M_2. The subfamily Ardynictinae includes the genera *Ardynictis, Archaeoryctes*, and *Hunanictis* (and, possibly, *Mongoloryctes*). It differs from the Didymoconinae sensu stricto in the absence of metacone on P^3 and the absence of hypocone on P^4–M^2, broad stylar shelves on P^4–M^2, only weakly molarized P^4 and P_4, and bi- or unicuspid cutting talonids of M_1 and M_2.

Key words: Didymoconidae, Middle Eocene, Mongolia, Asia.

INTRODUCTION

The Didymoconidae is a family of Paleogene Asian insectivores of uncertain phylogenetic relationships. Currently, the Didymoconidae are usually considered to be related to the Lipotyphla (Meng *et al.*, 1994) or Leptictida (McKenna and Bell, 1997) or ranked as a separate order, the Didymoconida (Lopatin, 2001a), of the superorder Insectivora (sensu Novacek, 1986). The Didymoconidae are characterized by a reduced dental formula, $I^3/_2C^1/_1P^3/_3M^2/_2$; the presence of the bony pre-incisor rostrum; large canines; a specific structure of the cheek teeth; a specialized structure of the auditory region of the skull (Meng *et al.*, 1994); and a number of features of postcranial skeleton associated with the digging mode of life (Gromova, 1960; Wang *et al.*, 2001).

The Oligocene Didymoconidae have been thoroughly examined (Matthew and Granger, 1924; Gromova, 1960; Lopatin, 1997; Wang *et al.*, 2001; Morlo and Nagel, 2002), while the data on earlier representatives of the family are rather scarce (Gingerich, 1981; Russell and Zhai, 1987; Meng, 1990; Lopatin, 2001a). The following four genera and species of the Didymoconidae were recorded in the Eocene: Early Eocene *Hunanictis inexpectatus* Li *et al.*, 1979 (China, Hunan, Lingcha Formation) and Middle Eocene *Archaeoryctes borealis* Meng, 1990, *Mongoloryctes auctus* (Matthew et Granger, 1925), and *Kennatherium shirensis* Mellett et Szalay, 1968 (China, Inner Mongolia; Arshanto, Irdin Manha, and Ulan Shireh formations, respectively). These species were described on the basis of isolated and poorly preserved specimens: in *Hunanic-*

tis, an anterior skull region with strongly damaged teeth (Li *et al.*, 1979; Gingerich, 1981); in *Archaeoryctes*, a lower jaw fragment with P_4 and poorly preserved molars (Meng, 1990); in *Mongoloryctes*, isolated M^1 (Matthew and Granger, 1925b); and in *Kennatherium*, a posterior region of a lower jaw with a strongly worn M_1 (Mellett and Szalay, 1968). A fragmentary skull of *Hunanictis* sp. (Meng *et al.*, 1994) was discovered in the Yuhuangding Formation dated as the terminal Early or basal Middle Eocene (Hubei, China). In addition, Wang *et al.* (2001) discovered a new undescribed form in the Eocene Ulan Gochu locality in Inner Mongolia.

Hsiangolestes youngi Zheng et Huang, 1984 from the Early Eocene of China was originally referred to as the Didymoconidae (Zheng and Huang, 1984; Russell and Zhai, 1987); however, when more complete specimens were found, it was assigned to soricomorph insectivores of the family Micropternodontidae (Ting and Li, 1987; Ting, 1998). McKenna and Bell (1997) placed *Hsiangolestes* and *Mongoloryctes* in the subfamily Wyolestinae of the order Cimolesta.

The Didymoconidae from the Ergilian Asian Land Mammal Age (the terminal Eocene to the basal Oligocene) are represented by two forms from Mongolia, i.e., *Ardynictis furunculus* Matthew et Granger, 1925 and *Ergilictis reshetovi* Lopatin, 1997 (Matthew and Granger, 1925a; Lopatin, 1997). *Ardynictis* sp. was recorded in the Upper Aksyir Formation of the Zaisan Depression in eastern Kazakhstan (Gabounia and Chkhikvadze, 1997).

Below, a new *Ardynictis* species from the Eocene of Mongolia is described. The material includes 17 jaw fragments, five isolated teeth, and a fragmentary humerus from the Khaychin Formation of the Khaychin-Ula 2 locality (collection PIN, no. 3107, collected by the Southern Gobi Team of the Joint Soviet–Mongolian Paleontological Expedition headed by V.Yu. Reshetov in 1970–1973 and 1978). The locality is aged to the Middle Eocene (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987; Averianov and Godinot, 1998). In addition to the new *Ardynictis* species, the fauna from this locality contains three representatives of the Didymoconidae, including *Kennatherium shirensis* and two new forms.

The following abbreviations are used in the present study: (AMNH) American Museum of Natural History, New York; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow.

SYSTEMATIC PALEONTOLOGY

Order Didymoconida Lopatin, 2001

Family Didymoconidae Kretzoi, 1943

Subfamily Ardynictinae Lopatin, 1997

Ardynictinae: Lopatin, 1997, p. 119; Morlo and Nagel, 2002, p. 125.

T y p e   g e n u s. *Ardynictis* Matthew et Granger, 1925.

D i a g n o s i s. P^3 lacking metacone. P^4 weakly molariform, substantially longer and narrower than molars, metacone fused with paracone, and hypocone absent. Stylar shelves of P^4–M^2 wide. Hypocone of M^1 and M^2 undeveloped; occasionally, rudimentary cingular projection located in place of hypocone. P^2 single- or double-rooted and P_2 single-rooted. P_4 semimolariform and lacking metaconid and prominent cusps on talonid. Talonid of M_1 and M_2 uni- or bicuspid (since entoconid and (or) hypoconulid reduced), lingually open, and possessing high cutting cristid oblique. Coronoid process of lower jaw straight, high, and narrow; angular process strongly curved medially.

C o m p o s i t i o n. *Archaeoryctes* Zheng, 1979, Upper Paleocene to Middle Eocene of Central Asia; *Hunanictis* Li *et al.*, 1979, Lower Eocene of China; *Ardynictis* Matthew et Granger, 1925, Middle Eocene to basal Oligocene of Mongolia and terminal Eocene to basal Oligocene of eastern Kazakhstan; and *?Mongoloryctes* Van Valen, 1966, Middle Eocene of China.

C o m p a r i s o n. The subfamily considered differs from the Didymoconinae sensu stricto by the absence of a metacone on P^3, weakly molariform P^4 and P_4, a rudimentary or completely undeveloped hypocone on P^4–M^2, wide stylar shelves of P^4–M^2, single-rooted P_2, the structure of the talonid of P_4–M_2, and by the shape of the coronoid and angular processes of the lower jaw.

R e m a r k s. The genus *Mongoloryctes* is only tentatively referred to the Ardynictinae on the basis of a similar general structural pattern of M^1 in *M. auctus*

(Matthew and Granger, 1925b; Van Valen, 1966) and unquestionable ardynictines.

The Didymoconinae sensu stricto include didymoconids that show the following characters: P^3 has the metacone; P^4 is clearly molariform, approximately equal in length and width to M^1, and has a separate metacone and paracone; the stylar shelves of P^4–M^2 are narrow; the hypocone on P^4–M^2 is well developed; P^2 is double-rooted, P_2 is single- or double-rooted; P_4 is molariform and has the metaconid and a well-developed talonid; the talonid of P_4–M_2 is tricuspid or bicuspid, i.e., has the hypoconid, entoconid, and hypoconulid (positioned close to the hypoconid) or only the first two cusps, these cusps are located at the posterior edge of the occlusal surface; the coronoid process of the lower jaw is relatively low and broad; and the angular process only weakly curves medially.

The subfamily Didymoconinae includes *Ergilictis* Lopatin, 1997 from the terminal Eocene–basal Oligocene of Mongolia; *Didymoconus* Matthew et Granger, 1924 [= *Tshelkaria* Gromova, 1960, see Morlo and Nagel, 2002, p. 130] from the Oligocene of Mongolia, northern China, and Kazakhstan; *Archaeomangus* Lopatin, 1997 from the terminal Lower Oligocene of Mongolia; *Tshotgoria* Lopatin, 1997 from the Upper Oligocene of Mongolia; and an undescribed form from the Khaychin-Ula 2 locality (Didymoconinae indet.), which is the earliest member of the subfamily discovered in the Middle Eocene of Mongolia.

Apparently, *Zeuctherium* Tang et Yan, 1976 from the Lower Paleocene of China (Tang and Yan, 1976) and *Kennatherium* Mellett et Szalay, 1968 from the Middle Eocene of northern China and Mongolia belong to neither the Didymoconinae nor the Ardynictinae and are referred to as Didymoconidae incert. sed.

Genus *Ardynictis* Matthew et Granger, 1925

Ardynictis: Matthew and Granger, 1925a, p. 2.

T y p e   s p e c i e s. *Ardynictis furunculus* Matthew et Granger, 1925; terminal Eocene–basal Oligocene of Mongolia.

D i a g n o s i s. Small and medium-sized members of subfamily. P^2 double-rooted. P^3 lacking parastyle and possessing well-developed protocone. M^1 and M^2 lacking hypocone, metastylar wing of M^1 and parastylar wing of M^2 moderately developed, and metacone of M^2 strongly reduced. Main cusp of P_4 conical. Talonid of M_1 with hypoconid and entoconid. Talonid of M_2 strongly reduced, possessing hypoconid only.

S p e c i e s   c o m p o s i t i o n. *A. furunculus* Matthew et Granger, 1925, terminal Eocene–basal Oligocene of Mongolia and *A. captor* sp. nov., Middle Eocene of Mongolia.

C o m p a r i s o n. *Ardynictis* differs from *Archaeoryctes* by the absence of a rudimentary cingular hypocone on M^1 and M^2 and parastyle on P^3, reduction of the metacone on M^2, weaker stylar shelves of M^1 and M^2,
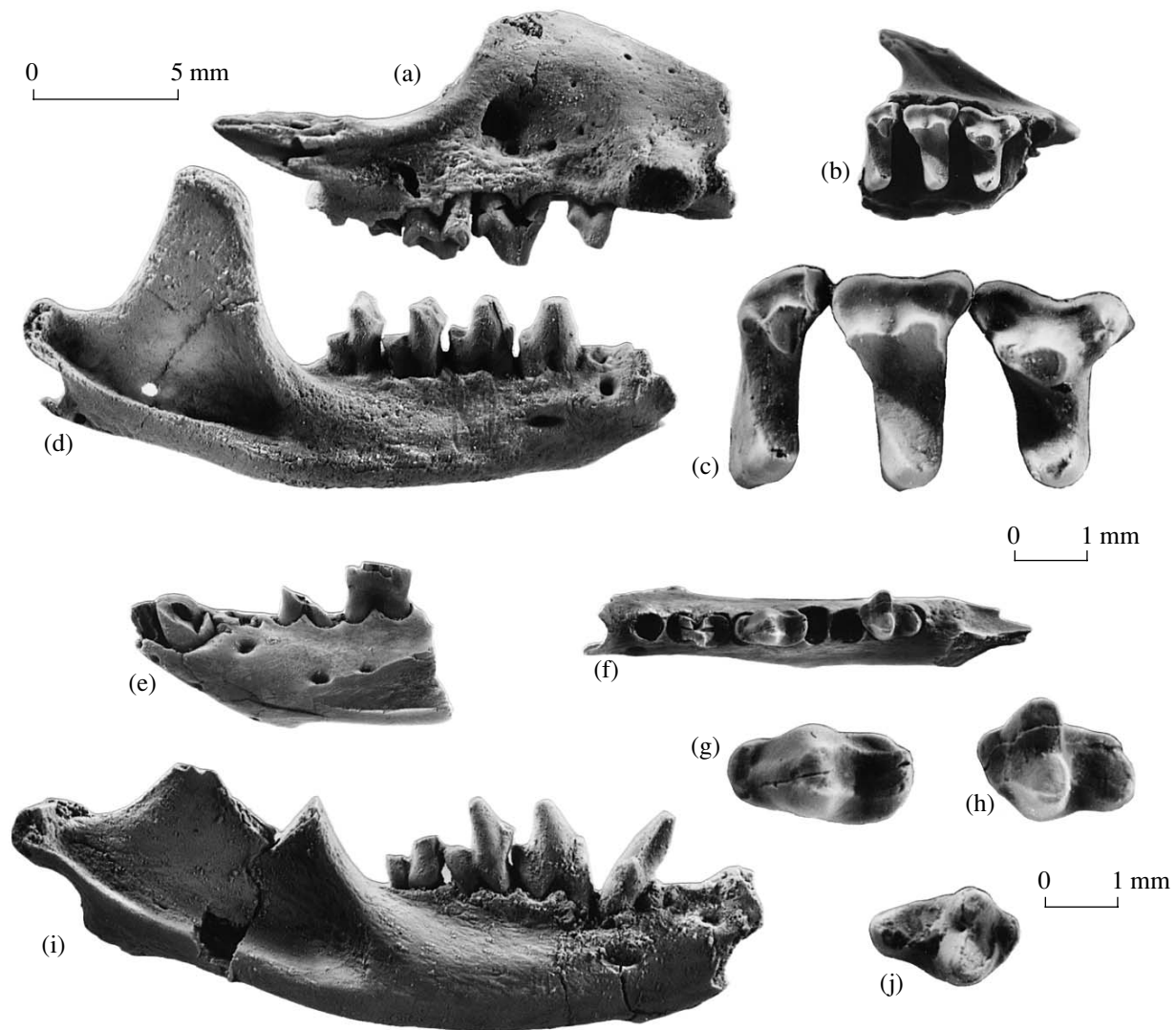
Fig. 1. *Ardynictis captor* sp. nov.: (a) specimen PIN, no. 3107/330, fragmentary right maxilla with P^2–P^4, labial view; (b, c) holotype PIN, no. 3107/333, fragmentary right maxilla with P^4–M^2, occlusal view: (b) general appearance and (c) P^4–M^2; (d) specimen PIN, no. 3107/362, fragmentary right dentary with P_3–M_2, labial view; (e) specimen PIN, no. 3107/340, fragmentary left dentary with damaged canine, P_3, and P_4, labial view; (f–h) specimen PIN, no. 3107/346, fragmentary left dentary with P_4 and M_2, occlusal view: (f) general appearance, (g) P_4, and (h) M_2; (i) specimen PIN, no. 3107/372, fragmentary right dentary with P_3–M_2, labial view; and (j) specimen PIN, no. 3107/345, isolated right M_2, occlusal view.

the conical shape of the main cusp on P_4, the absence of hypoconulid on P_4–M_2, the presence of the entoconid on M_1, reduction of the talonid of M_2, and by double-rooted P^2. It differs from *Hunanictis* by the better developed protocone on P^3, a larger stylar shelf of P^4, and double-rooted P^2; it differs from *Mongoloryctes* by better developed styles of M^1.

Ardynictis captor Lopatin, sp. nov.

E t y m o l o g y. From the Latin *captor* (capturer).

H o l o t y p e. PIN, no. 3107/333, fragment of the right maxilla with P^4–M^2; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

D e s c r i p t i o n (Figs. 1–3; 4a, 4b, 5). A small-sized didymoconid; the P_2–M_2 row is 10–11 mm long, P_4–M_2 is 6–7 mm long, the lower jaw is approximately 27 mm long, and the reconstructed skull is approximately 4 cm long. The rostral region of the skull is strongly narrowed (in specimen PIN, no. 3107/330, the palatine process of the maxilla is 3.2 mm wide at P^2 and 5.2 mm wide at the boundary between P^3 and P^4). The lateral region of the maxilla is convex, smooth, and pierced by several small nutritious foramina located near the nasomaxillary suture and the infraorbital foramen. Rough areas are observed dorsal to the alveoli of the canine and P^2, anterior to the infraorbital foramen, and at the base of the zygomatic arch.
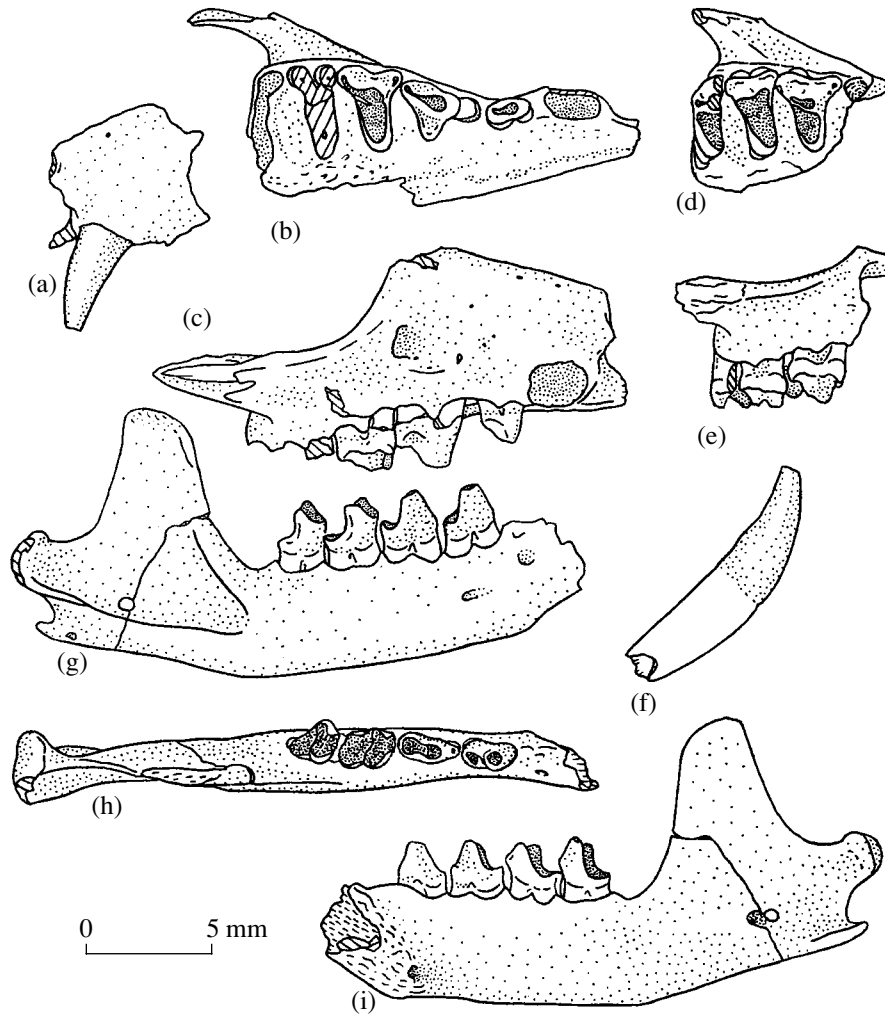
Fig. 2. *Ardynictis captor* sp. nov.: (a) specimen PIN, no. 3107/329, fragmentary left maxilla with a canine; (b, c) specimen PIN, no. 3107/330, fragmentary right maxilla with P^2–P^4, base of M^1 and alveoli of the canine and M^2: (b), occlusal and (c) labial views; (d, e) holotype PIN, no. 3107/333, fragmentary right maxilla with P^4–M^2: (d), occlusal and (e) labial views; (f) specimen PIN, no. 3107/335, isolated right lower canine; (g–i) specimen PIN, no. 3107/362, fragmentary right dentary with P_3–M_2: (g) labial, (h) occlusal, and (i) lingual views.

The infraorbital canal is short; anteriorly, it opens in line with the posterior labial root of P^4; the posterior opening is in line with the middle part of M^1. These foramina are rounded angular, the lateral and dorsal walls of the canal are straight. Ventromedial to the anterior foramen of the infraorbital canal, there is a small canal providing passage for a vessel and a nerve and extending to P^3. The orbital floor is pierced by stout lingual roots of P^4 and molars. The lachrymal is connected to the maxilla above the infraorbital canal.

The posterior edge of the base of the zygomatic arch is in a line with the parastylar wing of M^2. The zygomatic arch is thin. Judging from an available fragment (specimen PIN, no. 3107/330; Figs. 1a, 2c), the jugal laterally overlies the zygomatic process of the maxilla;

the anterior boundary between these bones is in line with M^2.

The upper incisors are not preserved. The canine is relatively short and stout, only slightly curved, and noticeably compressed transversely (Fig. 2a). P^2 is small, its anterior root is substantially narrower than the posterior root. The crown is extended, the wear facet of the main cusp extends along its posterior edge to the metastyle which is weakly developed. P^2 is separated from the canine and P^3 by small spaces.

P^3–M^1 are three-rooted. The lingual root is long and stout, while the labial roots are small. M^2 is double-rooted, its labial roots are completely fused.

P^3 is triangular. The paracone is large and high; as it is worn, a stout cutting crest connects it with the well-

developed metastyle. The internal projection is weak and the protocone is small. The parastyle and labial cingulum are absent.

P^4 is partially molarized. The stylar shelf is large, the parastyle and metastyle are well developed and large, and a prominent labial cingulum is a present. A small supplementary cuspule is located lingual to the parastyle; in a substantially worn teeth, it becomes fused with the parastyle. The paracone is large, the metacone is relatively small and weakly outlined. The cutting crest of the metacrista connects the metacone with the metastyle. The protocone strongly projects lingually, so that the crown is T-shaped in plan. M^1 is noticeably shorter than P^4 and differs from the latter by the presence of a well differentiated metacone and relatively weakly developed styles and cingulum. The parastyle is substantially larger than the metastyle. M^2 has a very small metacone and lacks a metastylar wing; M^2 is substantially inferior to M^1 in length. The posterior three cheek teeth slightly increase in width from P^4 to M^2.

The lower jaw has a thin and low horizontal ramus and a long coronoid region. The symphysis reaches the level of the middle of P_3. A deep postsymphyseal fossa is present. The anterior mental foramen is located under P_2, the posterior mental foramen is in line with the posterior root of P_3 or under the space between P_3 and P_4; an additional relatively large foramen is located on the anterior side of the dentary under the incisors. Occasionally, small supplementary foramina are observed under the anterior root of P_3 or P_4 and under the incisors and canine.

The lower edge of the dentary is slightly curved. The angle between the ascending and horizontal rami is approximately 110°–120°. The masseteric fossa is deep, clearly outlined, and reaches anteriorly the level of the base of the anterior edge of the coronoid process. The sharp crista condyloidea extends from the lateral side of the articular condyle and outlines the masseteric fossa ventrally. The coronoid process is high and paddle-shaped and has a gently sloping posterior edge and rounded thickened apex with a rough surface. The articular process is long. The neck of the condyle is extended and only slightly curved dorsally. The condyle is wide, high, and located in line with crowns of the cheek teeth. The transverse axis of the condyle is slightly posterolaterally inclined. The articular surface covers a sector about 180° and faces mainly posterodorsally. The mandibular foramen is oval and located under the incisure between the coronoid and articular processes somewhat anterodorsal to the angular process. In a senile (specimen PIN, no. 3107/362), a round through foramen is located immediately posterior to the mandibular foramen (Figs. 1d, 2g, 2i); since it is regular in shape and has smooth edges, it was most likely formed during the animal's lifetime as an aberration. The incisure between the articular and angular pro-
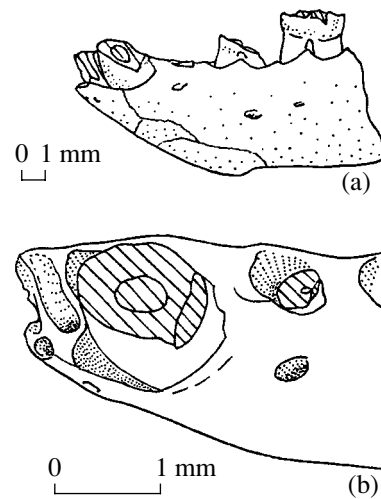

Fig. 3. The structure of the anterior region of the lower jaw of *Ardynictis captor* sp. nov. based on specimen PIN, no. 3107/340, fragmentary left dentary with broken canine, P_3, and P_4: (a) general appearance, labial view, and (b) anterior region of the jaw, dorsomedial view.

cesses is relatively deep. The angular process is small, pointed at the end, and strongly curved medially.

The lower incisors are not present. In specimen PIN, no. 3107/340 (Figs. 1e; 3), two alveoli for incisors are preserved anterior to the canine; they are located along the axis of the tooth row and inclined somewhat anteriorly. The anterolabial edge of the jaw is preserved and its shape gives evidence that the third alveolus was absent. A small round foramen located ventrolateral to the alveolus of the anterior incisor (Fig. 3) is undoubtedly a mental foramina (it is present in other didymoconids as well). Thus, only two incisors were present. Apparently, the idea that *Ardynictis* had three pairs of lower incisors (Matthew and Granger, 1925a; Gromova, 1960) is erroneous.

The canine is slightly transversely compressed and has a long and massive root and a relatively short and weakly curved crown with a flattened lingual surface and a weak posterior crest (Fig. 2a).

The P_2–M_2 row is separated from the canine by a small space. P_2 is not available. Its alveolus is small and round. In a senile (specimen PIN, no. 3107/362) showing strongly worn cheek teeth, the alveolus of P_2 is absent; only weak rugosity and superficial pits are observed in its place (Figs. 2g, 2h). Apparently, this tooth was lost during the animal's life and its alveolus was filled by bony tissue (similar cases were previously described in extinct mammals; see, e.g., Palmqvist *et al.*, 1999; Lopatin, 2001b). The absence of P_2 and its alveolus may be attributed not only to the loss of a damaged or sore tooth but also to the fact that the anterior premolar of didymoconids belongs to the deciduous generation; the large root of the deciduous canine and the rudimentary permanent canine completely occupy the space for the P_2 rudiment; therefore, DP_2 remained

and functioned almost over the entire animal's lifetime; as it came out at a late ontogenetic stage, the alveolus was filled by bony tissue (see also Morlo and Nagel, 2002, p. 139).

P_3 is narrow and has a high main cusp and a poorly pronounced supplementary posterior cuspule. The main cusp of P_4 is high, massive, conical, and slightly transversely expanded. Its wear facet is apical and descends along the posterior wall of the main cusp. The paraconid is well developed, relatively low, and narrow or expanded at the base. The talonid is higher than the paraconid and at least as wide as the main cusp. The cristid oblique is well developed. The wear facet of the talonid is connected to the wear facet on the posterior wall of the main cusp. Occasionally, a small but distinct projection is observed at the base of the posterior region of the lingual wall of the talonid (Fig. 1g).

M_1 has a wide trigonid and a narrow talonid. The paraconid is substantially higher than the talonid, expanded transversely, and slightly displaced lingually. The protoconid and metaconid are fused at the base, while their apices are clearly separated from each other by a notch. The protoconid is more massive and higher than the metaconid. The apices of the hypoconid and entoconid are displaced to the posterior edge of the occlusal surface. The entoconid is strongly compressed longitudinally and is noticeably smaller than the hypoconid.

M_2 has a small paraconid; a broad trigonid; and a strongly reduced, short, and narrow talonid. The paraconid is semicircular in plan. The protoconid is substantially higher and more massive than the metaconid. The talonid has only one cusp (hypoconid) strongly projecting posterolabially.

The humerus is typical of didymoconids (see Gromova, 1960), being distinguished by a relatively short and broad diaphysis, general shortening and flattening, and a weakly developed deltopectoral ridge.

M e a s u r e m e n t s, mm. Holotype: length of P^4–M^2, 5.35; length × width of P^4, 2.2 × 2.8; M^1, 1.95 × 3.0; and M^2, ca. 1.2 × 3.1. Specimen PIN, no. 3107/330: alveolus of C, 2.2 × 1.8; length of C–M^2 along the alveoli, 13.0; length of P^4–M^2, 8.5; length × width of P^2, 1.6 × 0.85; P^3, 2.65 × 1.9; and P^4, 2.35 × 3.2. Specimen PIN, no. 3107/334: length × width of P^4, 2.05 × 3.0; M^1, 1.7 × 3.2. Specimen PIN, no. 3107/332, P^3, 2.4 × 2.1.

Length of the upper canine crown (PIN, no. 3107/329) externally, along a straight line, 3.6; diameters at the base, 1.75 × 1.35. Diameters of the lower canine bases: (no. 3107/335) 1.7 × 1.2, (no. 3107/336) 2.0 × 1.3; and (no. 3107/340) 2.2 × 1.3. Length × width of the alveolus of P_2: (no. 3107/361) 0.9 × 0.9, (no. 3107/337) 1.0 × 0.9, (no. 3107/346) 1.05 × 0.95, (no. 3107/340) 1.1 × 1.0, (no. 3107/363) 1.15 × 0.8, (no. 3107/359, 385) 1.2 × 0.9, (no. 3107/372) 1.3 × 0.95, and (no. 3107/364) 1.4 × 0.9.

Length of P_2–M_2 along the alveoli: (PIN, no. 3107/385) 9.3, (no. 3107/359) 10.0, (no. 3107/346) 10.2, (nos. 3107/337, 361) 10.8, and (no. 3107/372) 11.0. Length of P_4–M_2: (no. 3107/359) 6.0, (no. 3107/362) 6.35, (no. 3107/346) 6.5, (no. 3107/361) 6.7, (no. 3107/372) 6.75, and (no. 3107/337) 7.0.

Length × width of lower premolars: P_3: (PIN, no. 3107/362) 1.95 × 1.0, (no. 3107/341) 1.95 × 1.2, and (no. 3107/361) 2.1 × 1.05; P_4: (no. 3107/362) 2.25 × 1.15, (no. 3107/372) 2.4 × 1.1, (no. 3107/340) 2.4 × 1.2, (no. 3107/343) 2.45 × 1.35, and (no. 3107/346) 2.5 × 1.3.

Measurements of lower molars, length × width of the trigonid–width of the talonid: M_1: (PIN, no. 3107/362) 2.15 × 1.5–1.25, (no. 3107/372) 2.35 × ?–1.3, and (no. 3107/344) 2.45 × 1.75–1.3; M_2: (no. 3107/362) 1.9 × 1.7–1.1, (no. 3107/345) 2.0 × 1.45–0.9, (no. 3107/372) 2.0 × ?–0.9, (no. 3107/346) 2.05 × 1.5–1.05, and (nos. 3107/359, 361) ? × ?–0.9.

Measurements of the horizontal ramus of the lower jaw:

Specimen PIN, no. 3107/	337	338	340	346	359	361	362	363	364	372	385
Depth at P_3	3.7	–	3.8	4.0	3.8	3.9	3.7	3.8	3.8	4.4	3.2
at P_4	4.25	–	4.2	4.45	4.3	4.9	4.0	–	4.0	4.5	2.9
at M_1	4.25	–	–	4.6	4.5	5.0	3.9	–	–	4.6	3.3
at M_2	4.1	4.3	–	4.4	4.25	4.9	3.8	–	–	4.5	3.6
Thickness at M_2	2.3	2.15	–	2.35	2.2	2.35	2.0	–	–	2.6	2.4

Measurements of the ascending ramus of the lower jaw: height of the coronoid region, 9.5 (PIN, no. 3107/362); segment from the posterior edge of the articular condyle to the posterior edge of M_2, 10.2 (no. 3107/362) and 12.5 (no. 3107/372); the same to the anterior base of the coronoid process, 9.0 (no. 3107/362) and 12.0 (no. 3107/372); the same to the anterior edge of the masseteric fossa, 9.0 (no. 3107/362) and 12.0 (no. 3107/372); thickness of the articular condyle, 1.9 (no. 3107/362) and 2.3 (no. 3107/372); width of the articular head, 2.8 (no. 3107/362) and 3.4 (no. 3107/372); dorsal length of the neck plus the head, 3.0 [2.0 + 1.0] (no. 3107/362) and 3.5 [2.2 + 1.3] (no. 3107/372); and the length and height of the angular process, 3.0 and 1.6, respectively (no. 3107/362).

The width and thickness of the humeral diaphysis at the narrowest point (above the crista epicondyli lateralis), 3.8 and 2.8, respectively (no. 3107/390).

V a r i a b i l i t y. Available lower jaw fragments allow one to estimate ontogenetic and, probably, sexual variability in measurements of *A. captor*. Specimen PIN, no. 3107/385 is a juvenile because its M_2 has not erupted. The alveolar edge of the jaw is incompletely formed and low on the labial side. The alveoli of DP_3 and DP_4 are smaller than the alveoli of P_3 and P_4 in adults and have thicker interalveolar septa. The septum between the alveoli of M_1 is undeveloped. Only the anterior alveolus of M_2 is open; deep in the alveolus, the protoconid and metaconid are seen. The alveolus for P_2 is similar in shape and structure to that of adults. The horizontal ramus of this specimen is approximately 75–80% as deep as that of adults. The senile stage (specimen no. 3107/362) is characterized by considerable tooth wear and, probably, the loss of P_2.

Among adults and seniles, irrespective of the extent to which the teeth are worn (consequently, irrespective of individual age), two size groups are distinguished. In the first group, the horizontal ramus at P_4–M_2 is less than 4.5 mm in depth and the P_2–M_2 row is approximately 10 mm long. Two larger specimens (PIN, nos. 3107/361, 372) differ in having a more massive jaw, a deeper horizontal ramus (4.6–5.0 mm), and a longer row of cheek teeth (ca. 11 mm). This differences are most likely associated with sexual dimorphism.

C o m p a r i s o n. The new species differs from the type species by having half as large measurements (Fig. 4); the shape and structure of P^4 (the protocone is strongly compressed longitudinally, the styles are well developed, and the metacone is small and only slightly outlined); a weakly developed metastyle of M^1; and by certain structural details of the lower molars, i.e., a high position of the paraconid and a relatively lower trigonid of M_1 and M_2 (in *A. captor*, the trigonid is approximately twice as high as the talonid; in *A. furunculus*, it is 3.5 times as high).

M a t e r i a l. In addition to the holotype, three maxillary fragments: (PIN, no. 3107/329) with a canine, (no. 3107/330) with P^2–M^1 and the anterior region of the zygomatic arch, and (no. 3107/334) with P^4 and M^1; (no. 3107/332) isolated P^3; 13 fragmentary dentaries: (no. 3107/340) with the alveoli of incisors, canine base, and damaged P_3 and P_4; (no. 3107/361) with P_3–P_4, and M_2; (nos. 3107/362, 372) with P_3–M_2 and ascending ramus; (no. 3107/363) with P_3 and P_4; (no. 3107/343) with P_4; (no. 3107/344) with P_4 and M_1; (nos. 3107/346, 359) with P_4 and M_2; (no. 3107/385) with unerupted M_2; and (nos. 3107/337, 338, 364) edentulous; four isolated lower teeth: (nos. 3107/335, 336) two canines, (no. 3107/341) P_3, and (no. 3107/345) M_2; and (no. 3107/390) fragmentary humerus. All specimens come from the type locality.
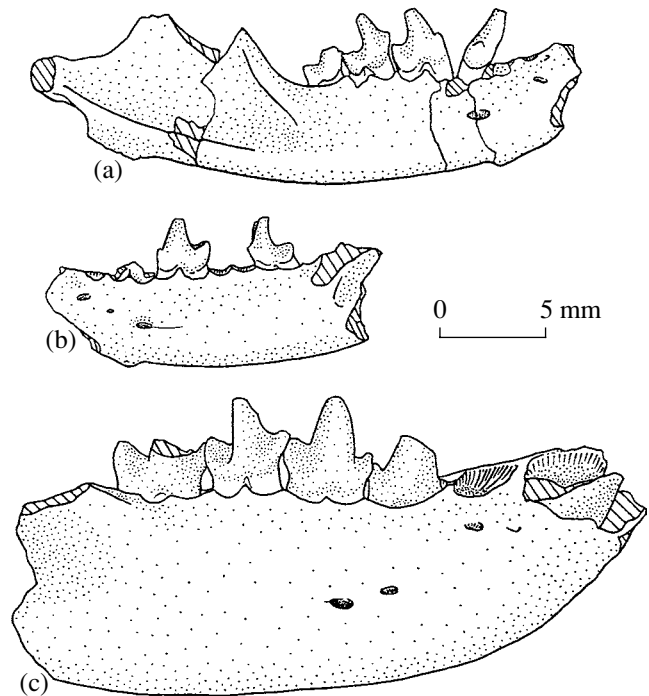

Fig. 4. Comparison of measurements of (a, b) *Ardynictis captor* sp. nov. and (c) *A. furunculus* Matthew et Granger from Mongolia: (a) specimen PIN, no. 3107/372, fragmentary right dentary with P_3–M_2, labial view, one of the largest individuals; (b) specimen PIN, no. 3107/346, fragmentary left dentary with P_4 and M_2, labial view, medium-sized individual; Middle Eocene, Khaychin Formation, Khaychin-Ula 2 locality; and (c) specimen PIN, no. 3109/246, fragmentary right dentary with P_3–M_2, labial view; terminal Eocene–basal Oligocene, Lower Member of the Ergilin-Dzo Formation, Ergilin-Dzo locality.

DISCUSSION

The Ardynictinae are clearly distinguished from the other Didymoconidae by the characters indicated in the diagnosis of the subfamily. Judging from the distinctions in the structure of cheek teeth, the Ardynictinae and Didymoconinae sensu stricto diverged at least as early as the Paleocene. The Late Paleocene ardynictines *Archaeoryctes notialis* Zheng, 1979 and *A. euryalis* Lopatin, 2001 had a weakly molariform P^4, M^1 and M^2 with very wide stylar shelves and cingular projections which occupy the position of the hypocones, nonmolariform P_4 with a bladelike main cusp, and lower molars with small paraconids and without entoconids but with large hypoconulids (Zheng, 1979; Lopatin, 2001a). These characters of the lower teeth are preserved in Eocene *A. borealis* Meng, 1990. *A. notialis* and, especially, *A. euryalis* are relatively large, the skull of the latter species is more than 10 cm long (Lopatin, 2001a).

In *Ardynictis captor* and *A. furunculus*, the hypocone on P^4–M^2 is absent, the entoconid on M_1 is preserved, and the hypoconulid on M_2 is lost. In a young *A. furunculus* (Matthew and Granger, 1925a, p. 4, text-figs. 6, 7, AMNH, no. 20 366), DP_4 is molarized to a
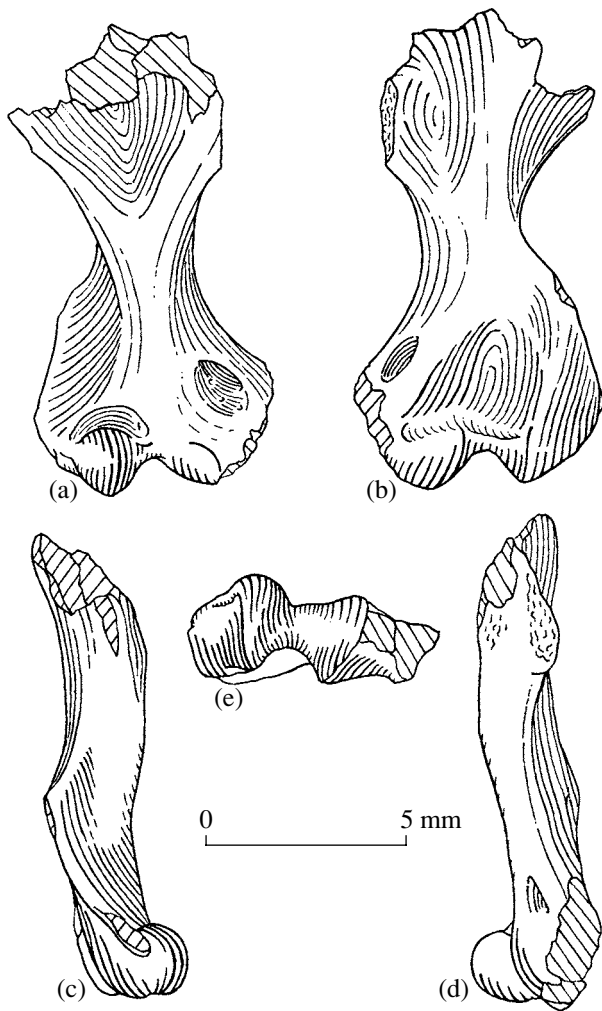
Fig. 5. Fragmentary right humerus of *Ardynictis captor* sp. nov., specimen PIN, no. 3107/390: (a) frontal, (b) rear, (c) lateral, and (d) medial views; and (e) trochlea, distal view.

substantially greater extent than the P_4 of adults (AMNH, no. 20 365; PIN, no. 3109/246); DP_4 has a clearly differentiated trigonid with the metaconid and bicuspid talonid and differs from the molar only by the larger paraconid. In contrast to the P^3 of adult *Ardynictis*, DP^3 of specimen AMNH, no. 20 366 has a metacone. Thus, the deciduous teeth of the Ardynictinae are similar to the permanent teeth of the Didymoconinae in the presence of the metacone on the middle upper premolar and in the extent of molarization of the posterior lower premolar. Deciduous premolars of the Didymoconinae are also quite molariform (Gromova, 1960; Morlo and Nagel, 2002). Apparently, a trend to progressive molarization of $(D)P^{3-4}/(D)P_4$, which is characteristic of all members of the Didymoconidae, was realized only in the deciduous generation of the Ardynictinae and in both the deciduous and permanent generations of the Didymoconinae; moreover, the gradual evolutionary

changes of P_4 clearly manifest themselves in the *Ergilictis–Didymoconus* lineage (Lopatin, 1997).

The Didymoconinae reached the acme of their development in the Early Oligocene, when the Ardynictinae had already become extinct; in the Ergilian Age, the latest ardynictine *Ardynictis furunculus* co-occurred with *Ergilictis reshetovi*, a form positioned at the base of the Early Oligocene adaptive radiation of didymoconines (Lopatin, 1997). Certain structural features of the postcranial skeleton of the Didymoconinae (short and stout forelimbs combined with relatively weak hind limbs, a massive clavicle, extended ulnar process, long and stout anterior claw phalanges) suggest adaptation to digging (Gromova, 1960) and even a specialized fossoriality for these animals (Wang *et al.*, 2001). The short and broad humerus of *Ardynictis captor* (Fig. 5) is even better adapted to digging than the humerus of the Didymoconinae. In the cranial structure, which has been examined in both the Oligocene Didymoconinae and the Paleocene–Eocene Ardynictinae (Gromova, 1960; Meng *et al.*, 1994; Lopatin, 2001a; Wang *et al.*, 2001), a number of characteristics are tentatively associated with the underground mode of life; this is primarily the general skull design where the facial region is stout and broad and the posterior region is extended and flattened. The specific structure of the middle ear region with an increased epitympanic sinus (Meng *et al.*, 1994) is likely associated with a high sensitivity to low-frequency sounds characteristic of subterranean animals (Wang *et al.*, 2001).

Cheek teeth of the Didymoconidae show a functional similarity to those of some zalambdodont insectivores feeding on worms and insects. The upper and lower tooth rows form a system of massive transverse crests and blunt cusps functioning as a crushing and cutting apparatus; thus, a food object is subject to chopping. The strong tooth wear characteristic of cheek teeth of the Didymoconidae is likely accounted for by soil particles seized together with food objects, which is inevitable in the case when an animal consumes food containing soil.

At the same time, the above structural features of the forelimb bones of didymoconids are developed to a lesser extent than in highly specialized diggers leading an underground mode of life (Gromova, 1960, p. 72). The large canines, well-developed zygomatic arches, stout symphysis, massive horizontal ramus, and relatively weakly developed articular and angular processes of the lower jaw substantially differ the Didymoconidae from specialized digging insectivores; however, these features are characteristic of predators (Carnivora, Creodonta, and Mesonychia) and carnivorous Insectivora (for example, *Tenrec ecaudatus*). Thus, the Didymoconidae were most likely carnivorous–insectivorous animals that obtained the main part of their food by digging through the upper layers of soil with the use of their snout and forelimbs (Gromova, 1960).

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