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The Skull Structure of *Archaeoryctes euryalis* sp. nov. (Didymoconidae, Mammalia) from the Paleocene of Mongolia and the Taxonomic Position of the Family

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Abstract—An almost complete skull with teeth of *Archaeoryctes euryalis* sp. nov., one of the earliest members of the family Didymoconidae, is described from the Tsagan-Khushu locality in Mongolia (Upper Paleocene, Naran Bulak Formation, Zhigden Member). Examination of the specimen corroborates data on the cranial features of the Didymoconidae, previously based only on relatively fragmentary material, and enlarged the characteristics of the family. Judging from the skull structure, didymoconids belong to Insectivora *sensu lato*; however, substantial differences from Lipotyphla and Leptictida suggest that they should be ranked a separate order, Didymoconida ordo nov.

INTRODUCTION

In 1983, V.Yu. Reshetov (Paleontological Institute of the Russian Academy of Sciences, PIN) found an almost complete skull of a mammal belonging to the family Didymoconidae in the Zhigden Member of the Naran Bulak Formation of the Tsagan-Khushu locality (Mongolia). Subsequently, this specimen was mentioned in a number of papers as Didymoconidae gen. et sp. indet. (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987). A unique feature of the specimen is a rather fine preservation of the teeth, rostral and occipital regions, and zygomatic arches. Examination has shown that the skull belongs to a new species of the genus *Archaeoryctes*, previously known from the Paleocene and Eocene of China (Zheng, 1979; Gingerich, 1981; Meng, 1990; Wang *et al.*, 1998).

The Zhigden Member is currently dated as terminal Late Paleocene, the fauna from the member belongs to the Gashatan Asian Land Mammal Age (Ting, 1998). The Paleocene Didymoconidae are also known from China (Tang and Yan, 1976; Zheng, 1979; Ting, 1998); these are *Zeuctherium niteles* Tang et Yan, 1976 (Early Paleocene, latter half of the Shanghuan Mammal Age) and *Archaeoryctes notialis* Zheng, 1979 (Late Paleocene, beginning of the Nongshanian Mammal Age). However, they are represented only by incomplete tooth rows; a skull of *A. cf. notialis*, the finding of which was indicated by Wang *et al.* (1998) and has not yet been described. The craniology of the Didymoconidae was examined on the basis of isolated incomplete specimens of relatively late forms, i.e., Oligocene *Tshelkaria rostrata* Gromova, 1960 (see Gromova, 1960) and Eocene *Hunanictis* sp. (Meng *et al.*, 1994). In the first case, the skull base was not preserved; in the second, the rostral region, zygomatic arches, and teeth were not preserved. Thus, the considerable geological

age and good preservation of the new specimen make it important for the clarification of the taxonomic position of Didymoconid, which is still poorly understood.

The following abbreviations are used in this paper: (PIN) the Paleontological Institute of the Russian Academy of Sciences, Moscow, and (IVPP) the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

SYSTEMATIC PALEONTOLOGY

Family Didymoconidae Kretzoi, 1943

Genus *Archaeoryctes* Zheng, 1979

Archaeoryctes euryalis Lopatin, sp. nov.

E t y m o l o g y. From Greek *Euros* (east).

H o l o t y p e. PIN, no. 3104/292, almost complete skull with canines and two series of cheek teeth; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran Bulak Formation, Zhigden Member.

D e s c r i p t i o n (Figs. 1–5). A large member of the family, the skull is approximately 100 mm long. In general, the skull is wedge-shaped. The base is broad; the zygomatic arches are spread strongly apart; the facial region and, in particular, the rostral region are narrowed.

The skull is strongly deformed, broken, and obliquely sloping to the right. Most bones are fragmentary, some are displaced. The right premaxilla, the major part of the right zygomatic arch, and certain fragments of bones of the skull base are lost. As a result of deformation, the lateral part of the left squamosal is strongly raised; therefore, as the cranial fragments were pasted together, the posterior ending of the zygomatic arch occupied a position under the latter.

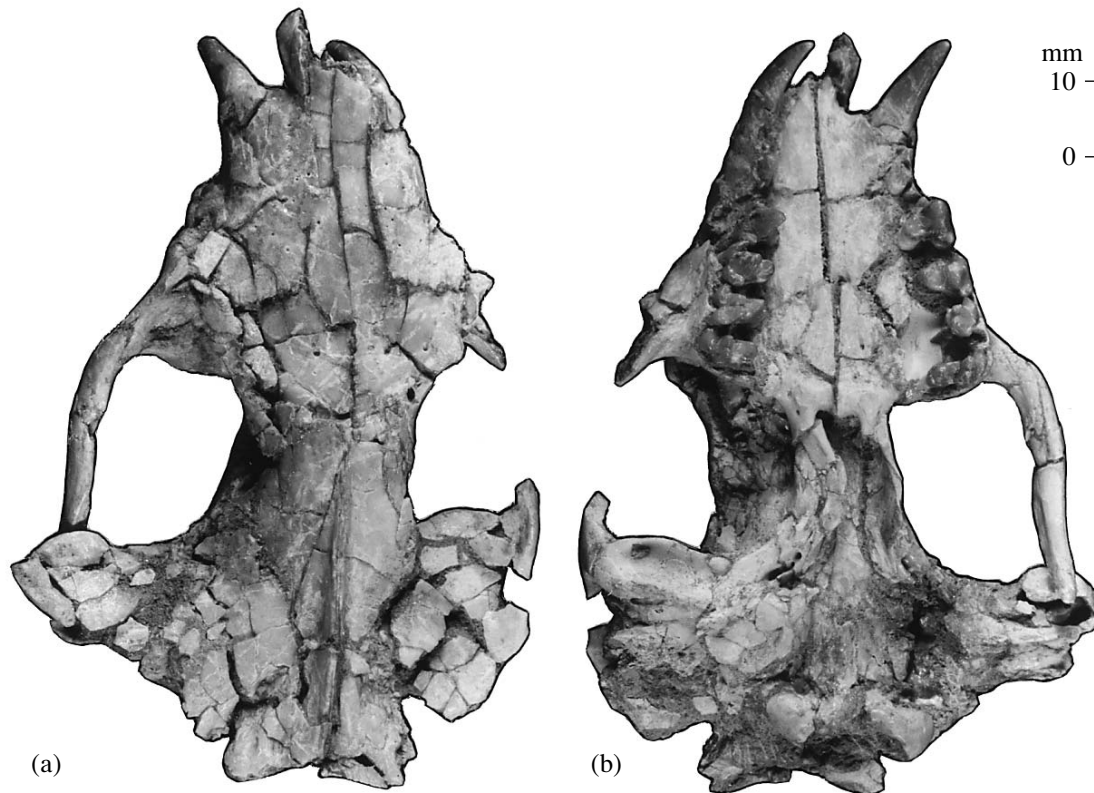


Fig. 1. *Archaeoryctes euryalis* sp. nov., holotype PIN, no. 3104/292, skull: (a) dorsal and (b) ventral views.

Judging from the position of preserved fragments, the premaxillae formed the lateral and lower walls of the anteriorly extended narrow rostrum that was covered dorsally by the nasals. The lateral portion of the suture between the premaxilla and the maxilla is located at the base of the rostrum, on level with the canine alveolus. At the boundary between the lateral and dorsal surfaces of the rostrum, the premaxillar-nasal suture is distinctly seen, and the premaxilla lacks a dorsal component. In the anterolateral part, just above the alveolus of I^1 , there is a small, round foramen. The lateral surface is convex in the region of the incisors, in particular, near I^2 . The ventral portion of the suture between the premaxilla and maxilla is short. The incisive foramen located between these bones is large and extended-oval. The premaxilla is broken off anteriorly; therefore, it is impossible to estimate the extent to which it projected beyond the incisors.

The nasals are narrow, long, and convex anteriorly; they extend posteriorly somewhat farther than the anterior ending of the zygomatic arches. The most anterior parts of both nasals are broken off; therefore, it is difficult to determine the point to which the nasals extended anteriorly. In the middle region of the nasals, relatively close to the lateral edge, there are two foramina open dorsally; the anterior foramen is small, and the posterior foramen is larger. The sutures between the nasals and the maxillae are well pronounced and expanded as

a result of bone displacement because of deformation. The suture between the nasals and the frontals is W-shaped in projection.

The maxillae form the major part of the facial region of the skull and the anterior part of the zygomatic arches; dorsally, they adjoin the premaxillae, nasals, frontals, and lachrymals. The dorsal and lateral surfaces of the rostral region are uneven, fine-porous, bearing numerous small pits and foramina. Near the contact with the nasals, there are relatively extensive round depressions; each contains a series of tiny pits. On the better preserved left bone, three depressions form a regular longitudinal row (Fig. 1a). In the first two, all pits are superficial; in the third, one pit is rather deep but blind-ended. Within the rostral part, there are also several supplying foramina: two very small foramina and a larger foramen ahead of the longitudinal series of depressions (open anterodorsally), a small dorsal foramen between the middle and posterior depressions, two medial to the posterior depression, and one posterolateral to the latter. Three small foramina are located on the dorsolateral surface of the facial region. The foramen which occupies the most medial position is open dorsally, the other two face posterolaterally. The pits and depressions possibly served for the attachment of tendons of the muscle that moved the extended snout of animal (*musculus nasolabialis profundus superficialis*).

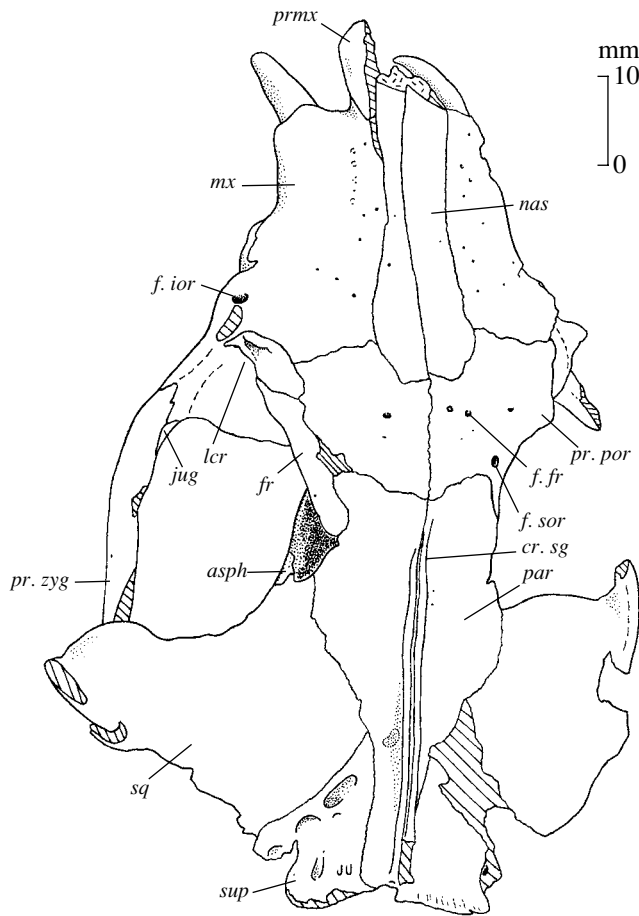


Fig. 2. *Archaeoryctes euryalis* sp. nov., holotype PIN, no. 3104/292, skull, dorsal view, structural scheme. Designations: (*asph*) alisphenoid; (*cr. sg*) sagittal crest; (*f. fr*) frontal foramen; (*f. ior*) infraorbital foramen; (*fr*) frontal bone; (*f. sor*) supraorbital foramen; (*jug*) jugal; (*lcr*) lachrymal bone; (*mx*) maxilla; (*nas*) nasal; (*par*) parietal; (*pr. por*) postorbital process; (*prmx*) premaxilla; (*pr. zyg*) zygomatic process of the squamosal; (*sq*) squamosal; and (*sup*) supraoccipital.

The lateral wall of the maxilla is perforated by a short, rounded infraorbital canal open anteriorly as a large infraorbital foramen located on level with P⁴. Lateral to the infraorbital canal, the base of the zygomatic process bears a weakly concave rough area, the presumable attachment site of a muscle (musculus maxillonasalis). The zygomatic process of the maxilla is broad and stout. Within the zygomatic arch, it is bounded by the zygomatic process of the squamosal (dorsally and laterally) and by the jugal. The maxilla forms the anteroventral region of the orbital margin and, primarily, the orbital floor. The anterior region of the orbital floor is perforated by small and round foramina and is pierced by the lingual root of M². Within the orbital wall, the maxilla is connected to the frontal; as a result, it isolates the lachrymal from the palatine. The boundary between the maxilla and the lachrymal

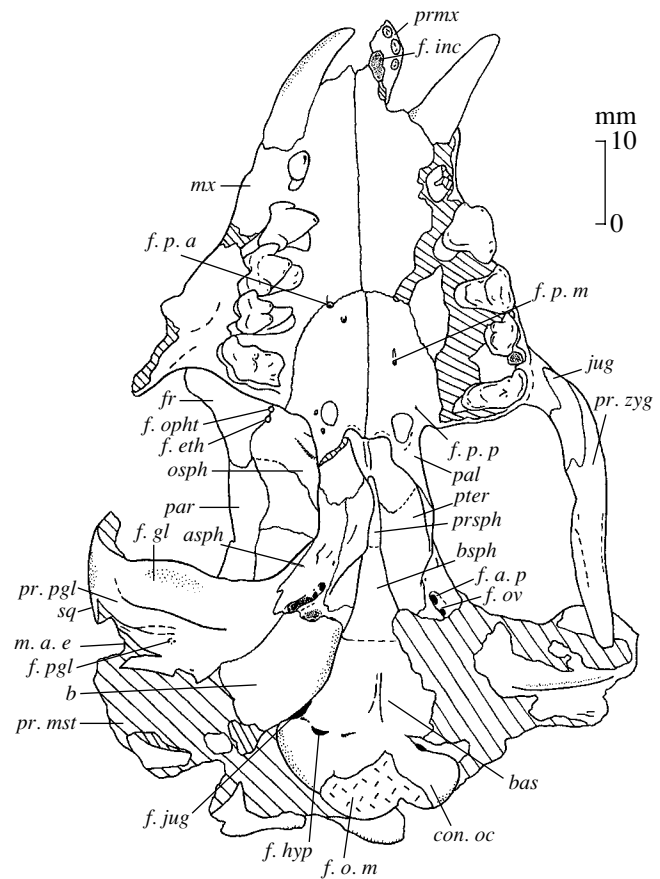


Fig. 3. *Archaeoryctes euryalis* sp. nov., holotype PIN, no. 3104/292, skull, ventral view, structural scheme. Designations: (*b*) tympanic bulla; (*bas*) basioccipital; (*bsph*) basisphenoid; (*con. oc*) occipital condyle; (*f. a. p*) posterior foramen of the alisphenoid canal; (*f. eth*) ethmoid foramen; (*f. gl*) glenoid; (*f. hyp*) hypoglossal foramen; (*f. inc*) incisive foramen; (*f. jug*) jugular foramen; (*f. o. m*) foramen magnum; (*f. opht*) ophthalmic foramen; (*f. ov*) foramen ovale; (*f. p. a*) anterior palatine foramen; (*f. pgl*) postglenoid fossa; (*f. p. m*) middle palatine foramen; (*f. p. p*) posterior palatine foramen; (*pal*) palatine; (*pr. pgl*) postglenoid process; (*pr. mst*) mastoid process of the petrosal; (*prsph*) presphenoid; and (*pter*) pterygoid. For other designations, see Fig. 2.

extends above the posterior foramen of the infraorbital canal and reaches the anterior contact between the lachrymal and the frontal. The positions of the palatine–maxillary suture and sphenopalatine foramen are uncertain because of the deformation of the specimen.

On the ventral side of the skull, the surface of the palatine processes of the maxillae is uneven and fine-porous. Medial to P⁴, the palatine–maxillary suture bears the anterior palatine foramen; anteriorly, it is connected to a broad and superficial groove. The palatine–maxillary suture extends almost in parallel to the longitudinal axis of the skull from the posteromedial edge of the posterior molar along the lingual side of the tooth row to the level of the middle of P⁴; at this point, it

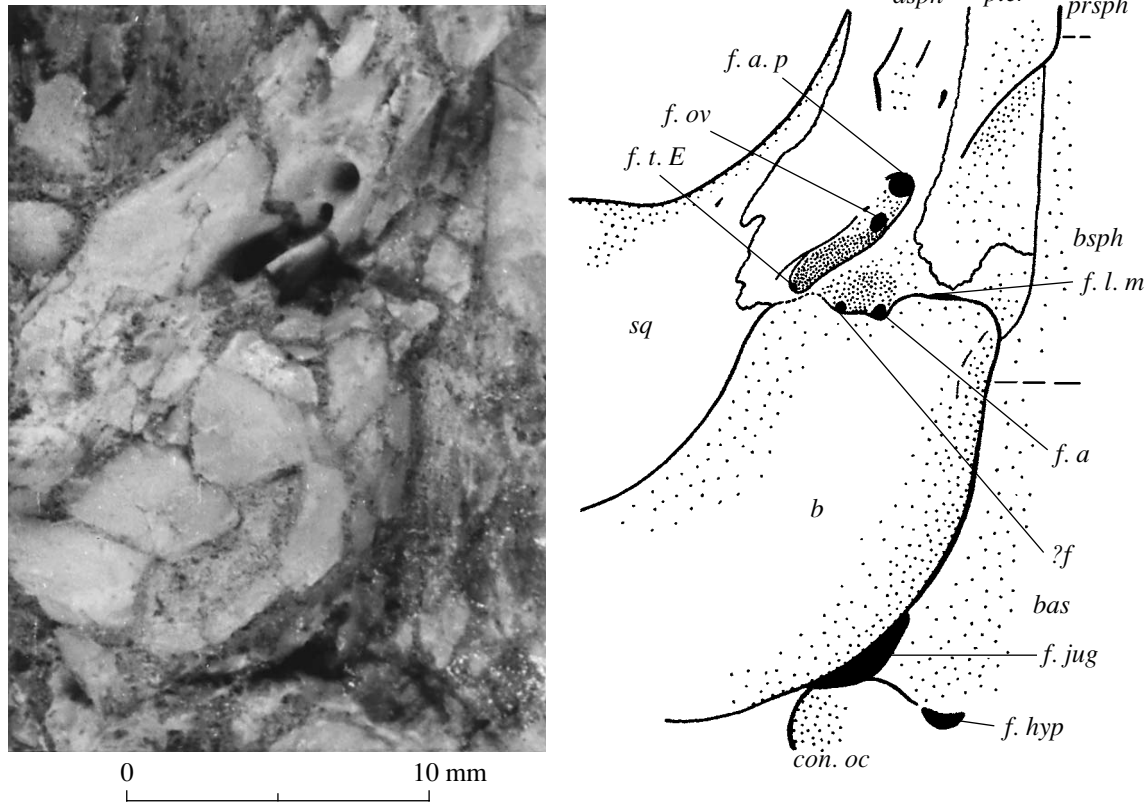


Fig. 4. *Archaeoryctes euryalis* sp. nov., holotype PIN, no. 3104/292, structure of the auditory region, right side. Designations: (?f) presumable foramen for the internal carotid nerve; (f. a) foramen for the internal carotid artery; (f. l. m) middle lacerate foramen; and (f. t. E) foramen of Eustachian tube. For other designations, see Figs. 2 and 3.

abruptly turns medially and adjoins the suture of the opposite bone pair.

The jugal forms a relatively small part of the zygomatic arch. It is clearly visible only on the ventral side of the skull and forms a small, longitudinally extended element in the anterior quarter of the ventromedial side of the zygomatic arch. Laterally, posteriorly, and dorsomedially, the bone is bounded by the zygomatic process of the squamosal; anteriorly and anteromedially, by the zygomatic process of the maxilla. Thus, ventrally and medially, it isolates the zygomatic processes of the maxilla and the squamosal from each other but does not break the contacts between them on the dorsal and lateral sides of the zygomatic arch. The ventral portion of the squamosal–jugal suture extends from the extreme lateral point of the zygomatic arch (located anterior to the caudal curvature) along the midline of the arch for one-fourth of its length and abruptly turns dorsomedially; on the dorsomedial surface, it adjoins the squamosal–maxillary suture and becomes the jugal–maxillary suture extending anteroventrally on the same side and terminating at the curvature of the zygomatic arch.

In ventral view, the palatines terminate on a level with P⁴. On the left bone, a small, oval middle palatine foramen is located on level with M¹; anteriorly, the

foramen is connected to a superficial and short groove. The latter contains two detached foramina; the lateral foramen is larger and opens anteromedially, and the medial foramen is smaller and opens anterolaterally. On the right bone, the foramen is slitlike, located opposite M¹ and opens anteriorly. Posteromedial to M², there is a small posterior palatine foramen. It is oval and opens ventrally. The posterior edges of the palatal processes form a stout postpalatine torus. Just ahead of the choanae, the torus bears a raised and round area on each bone (probably, for the attachment of epithelial fascicles). Laterally, the torus is pierced by relatively large and round foramina (open laterally). Apparently, each is connected by a canal to the corresponding posterior palatine foramen. On level with the choanal orifices, the postpalatine torus is divided into three processes. The lateral processes are narrow, long, and extend to the anterior base of the alisphenoid and pterygoid. The central postpalatal process isolating the choanal orifices from each other extends posteriorly up to the presphenoid.

Within the orbit, the palatine appears as a small element bounded by a projection of the frontal and by the alisphenoid. The contact of the palatine and other bones within the orbital wall are uncertain because of deformation.

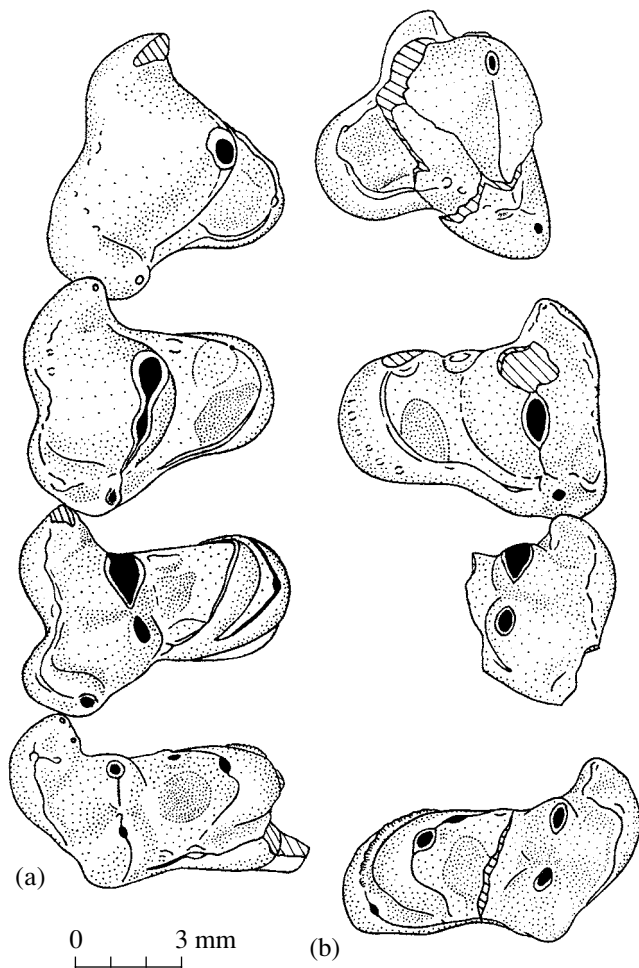


Fig. 5. *Archaeoryctes euryalis* sp. nov., holotype PIN, no. 3104/292, P³–M²: (a) right and (b) left.

The lachrymals are small with an extensive intraorbital region and a small facial process (visible in dorsal view because of deformation of the specimen, Fig. 2). The facial process is a very narrow band, the medial part of which forms a small lachrymal tubercle overhanging a large fossa that contains the lachrymal foramen and is bounded anteriorly and posteriorly by a ctenoid bone expansion. The foramen of the lachrymal canal is small and opens posterolaterally. Within the orbit, the lachrymal is bounded anteriorly and ventrally by the lachrymal–maxillary suture and posteriorly by the lachrymal–frontal suture. The major part of the orbital plate of the lachrymal is flat and located posteromedially to the fossa of the lachrymal foramen. A short lateral process overlaps the maxilla above the posterior part of the infraorbital canal. The ventral portion of the lachrymal–maxillary suture extends somewhat above the canal; thus, the lachrymal does not contribute to the formation of the dorsal wall of the posterior opening of the latter.

The frontals are short, approximately one-third as long as the parietals and half as long as the nasals. The

anterior edges of the bones are approximately on level with the infraorbital canals, and the posterior edges are somewhat posterior to the postorbital processes. The surface of these bones is flat. On the left bone, two foramina for the rami V₁ are distinguishable; a large frontal foramen is in the anterior region (open dorsally) and a much smaller foramen is posterior to the latter (slitlike and open anterodorsally). On the right bone, the number of these elements is doubled; in addition, a relatively large foramen is near the postorbital process (open anterodorsally). The surface of the postorbital process is covered by numerous small grooves and pits which are possibly the traces of the attachment of a ligament enclosing the orbit posteriorly. The frontal–parietal sutures are located in the narrowest part of the roof and extend transverse to the skull axis.

On the lateral side, the frontal descends into the orbit and forms a large part of the orbital wall. Within the orbit, it is bounded anteriorly by the lachrymal; ventrally, by the maxilla and palatine; and posteriorly, by the orbitosphenoid and alisphenoid. A stout supraorbital crest extends posteriorly from the lachrymal tubercle and ends as the postorbital process; a circular supraorbital foramen is located posterior to the latter. Within the frontal–orbitosphenoid suture, there are two other relatively large foramina, i.e., the ethmoid and ophthalmic foramina.

The parietals form the main part of the skull roof. They gradually expand posteriorly to the point where they are covered by the squamosals. The medial regions of a convex dorsal surface of the parietals rise abruptly upward and form a stout sagittal crest. The latter extends from the boundary of the frontals, gradually increasing in height, to the posterior edge of the dorsal surface of the skull where it abruptly becomes lower. Wedge-shaped posterior parts of the parietals are covered by the dorsal expansion of the supraoccipital and divide the latter into two triangular portions. The lateral spread of the parietals is small.

The squamosals are strongly splintered. These are the largest skull bones. They form a large part of the temporal region and basicranium. The squamosals are bounded anteriorly by the squamosal–parietal sutures and posteriorly by the squamosal–supraoccipital sutures. The dorsal surface is smooth and slightly concave.

At the base, the zygomatic process of the squamosal is directed anterodorsally. It forms a large part of the zygomatic arch, approximately three-fourths of the entire length. Judging by the preserved fragment of the left arch, the zygomatic process was relatively high, broad, and gently curved. Dorsally and laterally, it was bounded by the zygomatic process of the maxilla; ventrally and medially, it embraces the jugal. In the middle one-third, the process is pierced by a narrow canal providing passage for a nerve or a vessel; the anterior and posterior openings of the canal are on the medial and lateral sides of the bone, respectively. The lateral surface is convex and smooth and bears a well-pronounced

low crest in the lower part of the middle third of the arch; the crest isolates a rough ventrolateral area for the attachment of muscular fibers. A substantially larger and distinctly detached rough area for the attachment of muscles is located in the posterior region of the medial surface just posterior to the foramen.

The glenoid fossae and postglenoid processes are well-pronounced and large. The anterior edge of the glenoid fossa is clearly outlined and weakly curved anteriorly. The articular surface is smooth, deeply concave in the center, inclined anteroventrally, and crescent in lateral view. The postglenoid process is wide and rounded-triangular in rear view. Posteriorly, it adjoins the mastoid process of the petrosal; medially, it is bounded by the ectotympanic bone. A true postglenoid foramen is absent. However, in the center of the posterior surface of the postglenoid process, there is a relatively large fossa containing three small foramina (one in each lateral wall and one in the posterior wall); the latter were probably connected to the venous emissaries. The lateral foramen is the largest. In ventral view, the suture between the right squamosal and the alisphenoid is visible on the lateral side of the ectopterygoid process. Posteriorly, this suture terminates at the anterolateral angle of the tympanic bulla. The suture between the squamosal and the ectotympanic extends posteriorly. Notwithstanding the breakage of the bones, it is visible in lateral view that the squamosal forms the dorsal, anterior, and ventral walls of the external auditory canal (posteriorly, it is covered by the mastoid of the petrosal). The external auditory meatus was probably oval in outline.

The presphenoid is narrow and triangular; laterally, it is connected to the pterygoid and posteriorly, to the basisphenoid. The basisphenoid is trapezoid and adjoins laterally the alisphenoid and tympanic bulla; posteriorly, it is bounded by the basioccipital.

The pterygoids are clearly isolated from the alisphenoids, palatines, and presphenoid. They contribute to the formation of the internal walls of the posterior nasal passage and adjoin the presphenoid in the roof of the posterior nasal opening. The entopterygoid crests are transversely compressed and weakly inclined (the right crest is strongly deformed).

The alisphenoids form a large part of the lateral walls of the braincase. The dorsal processes of the alisphenoids almost reach the skull roof and adjoin the parietals. Anteriorly, the alisphenoid is bounded by the frontal and orbitosphenoid; within the sphenorbital fissure, it is bounded by the palatine. The suture between the palatine and the alisphenoid curves ahead of the sphenorbital fissure and extends posteriorly along the lateral side of the ectopterygoid process on the ventral side of the skull. Posteriorly, the alisphenoid clearly contacts with the squamosal. In the temporal region, the alisphenoid–squamosal suture extends vertically; lateral to the ectopterygoid process, it stretches along the crest marking the edge between the lateral wall and the

floor of the braincase. The ventral portion of the suture is turned posteriorly and extends along the lateral side of the ectopterygoid crest to the tympanic bulla. The anterior edge of the alisphenoid reaches the middle part of the lateral side of the posterior process of the palatine. At this point, the palatine–alisphenoid suture meets the pterygoid–alisphenoid suture. The latter extends posteriorly along the lateral base of the entopterygoid process; in this part, it is characterized by a peculiar serration. A narrow posterior portion of the suture ascends along the medial wall of choanae and adjoins the pterygoid–presphenoid suture.

Anterior to the tympanic bulla, the following elements are observed within the alisphenoid (Figs. 3 and 4). The ectopterygoid process of the alisphenoid is located lateral to the process of the pterygoid. It is compressed transversely and has a broad base and narrow apex turned ventrolaterally. Medial to the latter, near the pterygoid–alisphenoid suture, a small round foramen that looks like a short and deep groove extends posteriorly. A large, longitudinally extended depression containing three large foramina is located at the posterior base of the ectopterygoid process. The two foramina in the anterior wall open posteriorly. The larger foramen of this pair is the posterior opening of the alisphenoid canal. It is round in outline and located in the anteroventral region of the depression. The second is the foramen ovale; it is half as large, separated from the first by a narrow bone bridge, and located dorsoposteriorly. A little ventrally, the lateral wall of the depression contains a very small foramen (observed only on the right side of the skull). The posterior region of the depression is narrowed and forms a deep trough, the posterior wall of which is pierced by a small, narrow foramen. The latter opens anteriorly and lies somewhat above the foramen ovale. Since it is located in a long groove, it can be interpreted as the anterior opening of the bone part of the auditory (Eustachian) tube. Medially, the depression and the groove are bounded by a high ridge along the entire extent. Medial to the posterior region of the ridge, an additional deep depression is located just ahead of the tympanic bulla. The posterior wall of the depression (the anterior wall of the tympanic bulla) contains two foramina separated from each other by a vertical lamina; the medial foramen is relatively large, and the lateral foramen is smaller. The first is probably the opening of the internal carotid artery. The second probably provided passage for the internal carotid nerve. The middle lacerate foramen is detached and located in the extreme medial region of the base of the anterior wall of the tympanic bulla; it is large, broad, and oval.

The orbitosphenoid is bounded anteriorly, posteriorly, and ventrally by the frontal, alisphenoid, and palatine, respectively. In the central region, it bears a wide groove descending posteroventrally and bounded posteriorly by a high ridge. Apparently, the groove contained the optic foramen at the edge. A large sphenorbital fissure is located posteroventrally.

The occipitals are strongly broken and displaced. The foramen magnum is large and oval. The supraoccipital above the latter is pentagonal in outline; it is very thick with a weakly concave central region. The dorsal process is well developed and exposed on the skull roof; it is divided by the parietals into two triangular portions of approximately equal size. Two large, oval depressions are located near the occipital–squamosal suture. The surface of the posterior margin is grooved. The occipital–mastoid suture extends ventrally from the lambdoidal crest to the lateral side of the occipital condyle. In ventral view, the basioccipital is visible; it is bounded anteriorly by the basisphenoid and laterally by the tympanic bulla and the mastoid. It gradually expands posteriorly and bears a weak longitudinal keel. The occipital condyles are relatively small and convex; the anterior edge is weakly concave posteriorly. A large hypoglossal foramen is located just ahead of each condyle. A slitlike jugular foramen is positioned slightly anterolaterally at the boundary between the tympanic bulla, occipital, and petrosal.

At the skull base, the mastoid process of the petrosal (mastoid) forms a semicircular region bounded anteriorly and laterally by the squamosal and anteromedially by the tympanic bulla. On the right side, there is a small foramen facing ventrolaterally and positioned somewhat posteromedial to the postglenoid fossa. In occipital view, the mastoid is strongly flattened. A more detailed description is impossible because of strong fragmentation of both mastoids.

The tympanic bulla is completely ossified and bean-shaped, and the long axis is inclined anteromedially. In lateral view, it is weakly flattened, and the medial region is convex. The anterior edge is located approximately on level with the transverse axis of the glenoid fossa. The bulla entirely envelops the tympanic cavity; it is bounded medially by the basisphenoid and basioccipital and anteriorly, laterally, and posteriorly by the alisphenoid, squamosal, and mastoid, respectively. Consequently, the walls of the bulla are formed by only the tympanic bones. The ventral surface of the bulla lacks a suture.

Dentition (Figs. 1 and 5). The teeth are well preserved; there are alveoli of three incisors, a canine, and P²–M² in the left row, and a canine and P²–M² in the right row. Moreover, the canines and almost all the cheek teeth are completely preserved.

Judging from the alveoli, the incisors were very small and round in cross section; probably, I¹ < I² > I³. The canine is large, of a general carnivorous pattern, and weakly curved. P² is single-rooted, simple conical, and weakly compressed transversely. P³–M² are three-rooted, with a large lingual root and two smaller labial roots. The posterior labial root of M² is strongly reduced. P³ and P⁴ are substantially longer than the molars. The styler shelves of P³–M² are well developed.

P³ has a single large high cusp, the paracone. The parastyle and metastyle are well-pronounced, the labial

cingulum is absent. The internal projection is relatively extensive; however, the protocone projects slightly above the main dental surface and marginal crests.

P⁴ differs from P³ by a greater degree of molarization; this involves the presence of a weak labial cingulum, a rudimentary metacone (completely merged with the paracone but possessing a separate apical wear facet), and a well developed protocone. A small protoconule is developed. The posterolingual region of the occlusal surface bears a small depression, probably indicating the initial detachment of the cingulum. The middle part of the lingual side of the crown of the left P⁴ is covered by small, widely spaced tubercles.

M¹ is Y-shaped. The parastylar and metastylar wings strongly project anteroexternally and posteroexternally, respectively. A distinct labial cingulum connects the styles. The paracone and metacone are isolated from each other by approximately one-fourth of their height. The paracone is substantially more massive than the metacone and possesses a larger wear facet. The protocone is triangular and connected by long, low crests to the bases of the lateral parts of the lingual walls of the paracone and metacone. The protoconule and metaconule are weakly developed. The posterolingual cingulum, resembling a relatively wide band, is located substantially dorsally to the main surface of the internal projection. It bears a small rudimentary hypocone. A very narrow anterolingual cingulum is connected to the hypocone and covered by fine tubercles.

The crown of M² is reverse L-shaped, since a strongly developed parastylar wing projects far anteroexternally and the metasyle is strongly reduced. In addition to the parastyle, the parastylar wing bears two small cusps in the anterior region. The labial cingulum extends from the parastyle to the center of the metacone. Other structural elements of the occlusal surface are similar to those of M¹, although the metacone is developed to a substantially lesser extent and the hypocone is more strongly displaced posteriorly with reference to the protocone.

Measurements, mm. Condylbasal length of the skull is approximately 95; basal length, approximately 102 (because of transverse and vertical deformation, only longitudinal measurements can be estimated; moreover, it should be taken into account that most of the rostrum is broken off). The measurements of individual teeth are given in the table.

Length of tooth rows: (I¹–M²) 49; (C–M²) 39; (P²–M²) 28; (P³–M²) 24 on the right and 26 on the left; and (P⁴–M²) 17 on the right and 18 on the left.

Comparison. The new species is distinguished from the Late Paleocene *A. notialis* Zheng, 1979 from Southern China by its larger size, the better developed internal projection of P³, the relatively shorter P⁴, the structure of M² (strongly developed parastylar region and reduced metastylar region), and by the more strongly developed posterolingual cingulum on M¹ and M². The new species is distinguished from the Middle

Tooth measurements on (sin) left and (dex) right sides (incisors measured along the alveoli)

Tooth	I ¹ sin	I ² sin	I ³ sin	C		P ² dex	P ³		P ⁴		M ¹ dex	M ²	
				sin	dex		sin	dex	sin	dex		sin	dex
Length	1.9	2.3	2.0	5.5	5.5	3.3	7.5	7.3	6.0	6.2	5.5	4.8	4.8
Width	1.8	2.3	2.0	4.0	4.0	2.0	6.3	6.0	7.3	7.0	7.9	8.0	—

Eocene *A. borealis* Meng, 1990 from Northern China by the lower teeth and the substantially larger measurements of the new species.

Remarks. Regarding the shape and structure of P³–M², the new species strongly resembles the type species of the genus *Archaeoryctes*, *A. notialis* (Zheng, 1979, pl. 1, fig. 1b; Gingerich, 1981, p. 534, fig. 4A). The well developed lingual cingulum on M¹ and M² and the larger sizes of *A. euryalis* probably indicate that *A. euryalis* was a more highly evolved taxon than *A. notialis*. This is consistent with the geological age of these forms.

Material. Holotype.

THE TAXONOMIC POSITION OF THE DIDYMOCONIDAE

The primitive general pattern of the dental structure combined with twinned main cusps of the trigon and trigonid and the reduced formula of cheek teeth (P³/₃ M²/₂) have been interpreted as evidence of relationships between didymoconids and various mammal groups, such as the Oxyaenidae, Leptictidae (Matthew and Granger, 1925), Palaeoryctidae (Van Valen, 1966; Mellett and Szalay, 1968), Miacididae (Kretzoi, 1943), Anagalidae (McKenna, 1963), Zalambdalestidae (Szalay and McKenna, 1971), Arctocyoniidae (Gromova, 1960), Mesonychidae (Wang, 1976; Gingerich, 1981), and Deltatheridiidae (Romer, 1966; McKenna *et al.*, 1971). According to estimates of the taxonomic position of these families, the Didymoconidae were placed in the orders of carnivores (Carnivora or Ferae), creodonts (Creodonta or Deltatheridia), so-called carnivorous condylarthrans (Condylarthra, Eparctocyonia, Arctocyonia, Mesonychia, or Acreodi), so-called proteutherians, insectivores, anagalids, or were regarded as Mammalia inc. sed.

Comparison of didymoconids with the Leptictidae and Anagalidae was performed only on the supposition of the analogous structure of teeth and skeletons. The combination of a deep masseteric fossa, lingually turned angular process, and a clear medial postalveolar projection of the dentary observed in certain Didymoconidae (Mellett and Szalay, 1968) and early leptictids, such as *Gypsonictops*, was also interpreted as a functional similarity (Clemens, 1973). The idea of close relationships with the Zalambdalestidae was based on the presence of molariform P⁴ and P₄, longitudinally compressed talonids, and a trend to the lingual hypsod-

onty of the upper cheek teeth in the late Didymoconidae; however, didymoconids are strongly distinguished from all members of the Anagalida by the structure of the incisors, canines, and anterior premolars, the reduced dental formula; and by the structure of the skeleton.

The association of didymoconids with oxyaenids, miacids, and arctocyoniids was based on the presence of primitive and, at the same time, aberrantly specialized cheek teeth combined with a general carnivorous pattern of the dental system; this was regarded as the result of early deviation of the group from the common stock of Carnivora (in the broad sense, including true carnivores, creodonts, arctocyoniids, and mesonychids) and subsequent long independent development. The hypothesis for the origin of Didymoconidae from Deltatheridiidae (McKenna *et al.*, 1971), currently assigned to the Metatheria (Marshall and Kielan-Jaworowska, 1992), was based on an erroneous interpretation of the dental formula of *Deltatheridium* (I²⁴/₂ C¹/₁ P⁴/₄ M²/₃ instead of I²⁴/₃ C¹/₁ P³/₃ M⁴/₄).

The relationships between didymoconids and Mesonychidae were proposed by Wang (1976) and Gingerich (1981). According to Gingerich, common characters comprise the molariform P⁴ and P₄, reduced or absent M³ and M₃, almost symmetric upper molars lacking the metacrista, and the presence of a longitudinally slanting cristid of the lingually open talonid on the lower molars that occluded with the centrocrista of the upper molars. Gingerich believed that didymoconids originated from primitive Paleocene mesonychids, such as *Yantanglestes*. When criticizing this hypothesis, Meng *et al.* (1994) indicated that in the primitive Didymoconidae (*Archaeoryctes* and *Ardynictis*), P₄ was nonmolarized; the slanting cristid is only weakly expressed in didymoconids; the absence and, in particular, reduction of M³ and M₃ have been observed in various mammals; and simple and high trigonids and lingually open talonids (with reduced entoconids) were characteristic of many Cretaceous and Paleogene mammals. Thus, didymoconids and mesonychids lack shared derived characters in their dental structure (Meng *et al.*, 1994). The Didymoconidae and the Mesonychidae also lack synapomorphies in the skull structure. However, didymoconids show certain cranial characters in common with the Hapalodectidae, the other family of the Mesonychia (Ting and Li, 1987): a wide contact between the maxillae and the frontals in the facial region, a contact between the maxilla and the

frontal within the orbit, the absence of the facial process of the lachrymal, the absence of contacts between the lachrymal and the jugal, the shape and positions of the nasals and palatines, and the presence of the supraorbital foramen. At the same time, they differ strongly from each other in the structure of the rostral and occipital region of the skull, zygomatic arch, and auditory region (Ting and Li, 1987); thus, they should not be regarded as close relatives.

The study on the skull of *?Hunanictis* sp. from the Eocene of China (Meng *et al.*, 1994) has shown that among all mammals, members of the superorder Insectivora *sensu* Novacek (1986) are most similar in cranial morphology to the Didymoconidae. However, didymoconids were assigned neither to Leptictida nor to Lipotyphla. There is no consensus of opinion among the authors of the cited paper regarding the taxonomic position of this family; the opinion concerning the assignment of the Didymoconidae to Insectivora *sensu lato* was proposed by only Meng (see Meng *et al.*, 1994). In recent reviews, Didymoconidae are considered to belong either to Leptictida (McKenna and Bell, 1997) or Insectivora *inc. sed.* (Wang *et al.*, 1998), or Mammalia order *indet.* (Ting, 1998).

In the skull of *?Hunanictis* sp., IVPPV-5788 (Meng *et al.*, 1994), the teeth, rostral region, and the zygomatic arches are not preserved; this substantially complicated the estimation of the taxonomic significance of available cranial data. Therefore, in the previous paper, I upheld the viewpoint proposed by Gingerich (1981) and considered didymoconids within the composition of the Mesonychia (Lopatin, 1997). However, the skull of *Archaeoryctes euryalis* sp. nov. described above and undoubtedly belonging to Didymoconidae has much in common with that of *?Hunanictis* sp.

The main shared characters of didymoconids and Insectivora (Meng *et al.*, 1994) are as follows: (1) the jugal is reduced to an insignificant element of the zygomatic arch located between the processes of the maxilla and the squamosal and lacking contact with the lachrymal; (2) a wide contact exists between the maxilla and the frontal within the facial part, (3) a contact exist between the latter bones within the orbit, excluding contacts between the palatines and the lachrymals; (4) a relatively short infraorbital canal; (5) a large common depression for the sphenopalatine and dorsal palatine foramina; and (6) the lachrymals lacking a facial process.

A more specialized structure of the middle ear of didymoconids in comparison with those of insectivores (Meng *et al.*, 1994) is an autapomorphy. Of the other diagnostic features of Insectivora, Didymoconidae lack only one, i.e., the sharp sigmoid outlines of the anterior edge of the ventral surface of the occipital condyle.

Within Insectivora *sensu lato*, Lipotyphla or Insectivora *sensu stricto* are distinguished by the presence of a mobile snout or proboscis, a large orbital process of the maxilla adjoining the frontal inside the orbit, and by

reduced or absent jugals. Didymoconidae are similar to Lipotyphla in the entire set of these characters. An elongated snout of didymoconids is reconstructed on the basis of the peculiar structure of the bone rostrum formed by the premaxillae and nasals (Gromova, 1960; Meng *et al.*, 1994). In addition, a high mobility of the snout of *Archaeoryctes euryalis* is proposed, since the rostral part of the skull bears traces of the attachment of a well developed and differentiated muscle interpreted as the musculus nasolabialis profundus superficialis, according to the terminology proposed by Gambaryan (1989). However, in most living insectivores, the proboscis is attached to the nasal opening by a cartilaginous tube partitioned by a longitudinal cartilaginous plate; the elements resembling the bone rostrum of didymoconids have not been discovered in the Lipotyphla.

All of the above enables us to conclusively refute the theory of didymoconids belonging to the Mesonychia, and supports the hypothesis of their close relationships with insectivores. Thus, Didymoconidae should be referred to the superorder Insectivora.

The following characters are considered to be the main autapomorphies of Didymoconidae (see also Meng *et al.*, 1994): (1) the presence of a bone rostrum formed by the nasals and the premaxillae; (2) the walls of the external auditory canal formed by the squamosal and mastoid; (3) the tympanic bulla completely ossified and formed by merged tympanic bones; and (4) the formula of the cheek teeth reduced to $P^{3/3} M^{2/2}$, the molars bearing twinned cusps of the trigon and trigonid, and $P^{4/4}$ are molarized to a certain extent. The above characters taken together clearly distinguish didymoconids from Lipotyphla and Leptictida and do not allow their assignment to any of these orders. I therefore propose that Didymoconidae be ranked as a separate order, *Didymoconida ordo nov.*

Probably, *Didymoconida* deviated early from the common stock of insectivores, i.e., not later than the Late Cretaceous when Leptictida and Lipotyphla had already been formed. In the Paleogene, they were presented by a large number of forms varying in sizes and dental morphology; this gives evidence for a wide adaptive radiation of didymoconids and reflects their taxonomic diversity (Lopatin, 1997). As far as we know, the range of didymoconids was limited to Central Asia and Kazakhstan in the Recent.

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