

*We dedicate this paper to the memory
of Lev A. Nessov (1947–1995)*

Earliest eutherian mammal skull, from the Late Cretaceous (Coniacian) of Uzbekistan

MALCOLM C. MCKENNA, ZOFIA KIELAN-JAWOROWSKA, and JIN MENG



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We describe a partially crushed skull and dentaries of a sub-adult individual of *Daulestes nessovi* sp. n., from the Coniacian of Uzbekistan. This is the earliest known eutherian skull (about 87 Ma) and the sixth genus of Cretaceous eutherians in which a skull is available. Because the skull of *D. nessovi* is sub-adult, certain plesiomorphic features may be ontogenetic and should be interpreted with caution. Four upper premolars and five lower premolariform teeth were in use (possibly to become four lowers when fully adult). The upper cheek-teeth have winged conules; M2 has large parastylar and small metastylar projections. Pre- and postcingula are lacking on DP4 and the upper molars. The talonids of dp4-m2 are about 90% as wide as the trigonids, with widely separated entoconid and hypoconulid. The skull has a large sphenorbital fissure, no foramen rotundum, and apparently no pterygoid process of the sphenoid. A large orbital wing of the palatine prevents maxilla-frontal contact within the orbit. The zygomatic arch is slender. The cochlea has one full turn, with an expanded apex, which suggests that a lagena might have been present. A large malleus with a robust anterior process, and a large promontorium may be due to young age of the individual or a primitive retention, as in the platypus. Because of the similarity to Asioryctidae in both cranial structure and dentition, we assign *Daulestes* tentatively to Asioryctitheria Novacek *et al.* 1997, family *incertae sedis*.

Key words: Skull, Eutheria, *Daulestes*, *Asioryctes*, Coniacian, Cretaceous, Uzbekistan.

Malcolm C. McKenna [mckenna@amnh.org], Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY 10024-5192, USA.

Zofia Kielan-Jaworowska [zkielan@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Jin Meng [jmeng@amnh.org], Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY 10024-5192, USA.

Introduction

We describe a Late Cretaceous mammal skull from the Coniacian of the Kyzylkum Desert, Uzbekistan (Fig. 1). It is the earliest known eutherian mammal skull in a reasonably interpretable state of preservation. It is, however, somewhat distorted and telescoped by crushing, notably in the braincase region. The skull is designated *Daulestes nessovi* sp. n., which we tentatively assign to the order Asioryctitheria Novacek *et al.* 1997, family *incertae sedis*. *Daulestes* Trofimov & Nessov 1979, in Nessov¹ & Trofimov (1979), was known previously only from a fragment of a dentary.

When the review book on Mesozoic mammals by Lillegraven *et al.* (1979) was submitted for publication in 1978, only fourteen designated Cretaceous eutherian genera were known from the entire world (Kielan-Jaworowska *et al.* 1979; Clemens *et al.* 1979). Since that time, new Cretaceous eutherian taxa from various parts of the globe have been described or discussed by many authors. In their book on the classification of mammals, McKenna & Bell (1997) cited 32 eutherian genera from the Cretaceous. In the same year, the posthumous book by Lev A. Nessov was published (Nessov 1997), in which the author established three new Cretaceous eutherians. These are: *Eozhelestes* Nessov, 1997; *Ortalestes* Nessov, 1997 (possibly congeneric with *Aspanlestes*, see 'Note added in proof' in Nessov *et al.* 1998); and *Sazlestes* Nessov, 1997, with a single species *Sazlestes tis* Nessov, 1997. The latter species has, however, not been figured and is very poorly known. After the book by McKenna & Bell (1997) was published, the following Cretaceous eutherian genera have been erected: *Ukhaatherium* Novacek *et al.* 1997, *Eoungulatum* Nessov, Archibald, & Kielan-Jaworowska, 1998, and *Montanalestes* Cifelli, 1999.

Sloan & Van Valen (1965), Van Valen & Sloan (1965), and Van Valen (1978) listed six eutherian genera from the Hell Creek Formation of Montana, including taxa from channels at the top, regarded at that time as of latest Cretaceous age. These channels, the Bug Creek channels, are Paleocene in age (Lofgren 1995; see also McKenna & Bell 1997), and eutherian taxa from them are accordingly omitted. McKenna & Bell (1997) questioned *Cretasorex* Nessov & Gureev, 1981, described originally as a Cretaceous soricid, which might be a Late Cenozoic soricoid (with a pocketed coronoid process of the dentary), possibly wrongly attributed to Cretaceous rocks. Pocketed coronoid processes are also found in apternodontids.

Among about 40 designated Cretaceous eutherian genera, only five monotypic ones from the Late Cretaceous of the Gobi Desert (*Kennalestes*, *Asioryctes*, *Zalambdalestes*, *Barunlestes*, and *Ukhaatherium*) have been reported from fairly complete skulls. *Daulestes* is the sixth Cretaceous eutherian genus for which a skull has been found, and is also the earliest. Originally, *Daulestes* was regarded somewhat uncertainly as a zalambdalestid, but in subsequent papers Nessov (e.g., Nessov *et al.* 1994 and references therein) assigned it to the Palaeoryctidae.

¹ In the paper by Nessov & Trofimov (1979), the name of Nessov as the author of the paper was spelled with one 's', but with 'ss' as the author of a taxon. Nessov used to spell his name in English with 'ss', although according to rules of Cyrillic transliteration his name should be spelled with just one 's'. Because he changed the 1979 spelling with a single 's' himself in the Nessov *et al.* (1994) paper, we follow him and we cite his name in English always as Nessov.



Fig. 1. Generalized topographic map of south-western Asia, showing the position (triangle) of Dzharakuduk locality (modified from Nesson *et al.* 1994).

Beginning in 1978, the late Dr Lev A. Nesson collected Cretaceous mammals (among other vertebrates) at several localities in the Republic of Uzbekistan (Nesson 1982, 1984, 1985a, 1985b, 1987, 1988; Kielan-Jaworowska & Nesson 1990, 1992; Nesson & Kielan-Jaworowska 1991; Nesson *et al.* 1994; Nesson 1997; Averianov & Kielan-Jaworowska 1999). During field work in 1989 near Dzharakuduk (referred to also as Dzhyrakuduk and Dzharakuduk) in the central part of the Kyzylkum Desert, a phosphatic nodule containing an unknown amount of the fossilized skull of a small mammal (Fig. 2) was found by Vyacheslav Trikhin, a member of Nesson's team, in the Bissekty Formation (Nesson 1990; Nesson *et al.* 1998; Archibald *et al.* 1998). In 1990 the nodule was brought to Oslo and then to New York. It was subsequently prepared by William Amaral of Cambridge, Massachusetts, who skillfully removed the specimen from the containing matrix and separated its tiny jaws from interlocking occlusion, revealing the dentition and ventral parts of the sub-adult skull.

In the description that follows we compare the cranial features of *Daulestes nessonii* sp. n. primarily with those of *Kennalestes gobiensis* Kielan-Jaworowska, 1969, *Asio-ryctes nemegetensis* Kielan-Jaworowska, 1975a, *Zalambdalestes lechei* Gregory & Simpson, 1926, and *Barunlestes butleri* Kielan-Jaworowska, 1975a (see Gregory & Simpson 1926; Kielan-Jaworowska 1969, 1975a, 1981, 1984a, b, c; Kielan-Jaworow-

ska & Trofimov 1980). The skull of *Ukhaatherium nessovi* Novacek *et al.*, 1997 has received a preliminary description only (Novacek *et al.* 1997) and we refrain from extensive comparisons with it. Inasmuch as all these Cretaceous genera are monotypic, we refer to them merely by their generic names. Among these, *Kennalestes* is especially interesting because, among the various specimens from Mongolia, there is a sub-adult individual (ZPAL MgMI/1) represented by the skull and jaws, whose deciduous dentition is in the process of replacement; almost the same stage of development of the skull and jaws of *Daulestes nessovi* from Uzbekistan, described here.

Among Cretaceous eutherian taxa proposed by Nesson, *Daulestes* and *Taslestes* are here subjectively considered congeneric. In spite of the fragmentary nature of the holotypes of the type species involved, we believe that they differ from *Daulestes nessovi* sp. n. at the specific level (see Table 1). Another genus proposed by Nesson from the same area and formation, which is of comparable size, is the monotypic *Kumlestes* Nesson, 1985a. Only a fragment of a left dentary with two broken teeth (holotype of *Kumlestes olzha* Nesson, 1985a, CCMGE 1/12176) is available. It has been figured by Nesson (1985a: pl. 2: 15), Nesson & Kielan-Jaworowska (1991: fig. 1), Nesson *et al.* (1994: pl. 2: 2) and Nesson (1997: pl. 45: 7). Only talonids of the teeth (apparently m1 and m2) are preserved, the trigonids being virtually unknown. As the dental formula and the trigonids are unknown, the difference between it and other taxa of comparable size from the Bissekty Formation cannot be demonstrated. We follow the suggestion of A.O. Averianov (letter of June 14, 1999 to ZKJ) and regard *Kumlestes olzha* as a *nomen dubium*; we shall cite it further in quotation marks.

Terminology and abbreviations

Anatomical terms not otherwise specified follow Gregory (1910), Kielan-Jaworowska (1975a, b), Novacek (1986), Wible (1990), and Fleischer (1973). We denote upper teeth with capital letters and lower teeth with lower case letters: I/i, incisor; C/c, canine; P/p, premolar; M/m, molar. In the case of deciduous teeth we use D/d in addition.

Abbreviations: Ma, million years; f., foramen; fen. fenestra; proc., process.

Institutional: CCMGE, Czernyshev's Central Museum of Geological Exploration, St. Petersburg; ZIN, Zoological Institute of the Russian Academy of Sciences, St. Petersburg; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Description

Class Mammalia Linnaeus, 1758

Cohort Eutheria Huxley, 1880

Order ?Asioryctitheria Novacek, Rougier, Wible, McKenna, Dashzeveg & Horovitz, 1997

Family *incertae sedis*

Genus *Daulestes* Trofimov & Nesson, 1979, in Nesson & Trofimov (1979)

Synonym: *Taslestes* Nesson, 1982.

Type species: *Daulestes kulbeckensis* Trofimov & Nessov, 1979, in Nessov & Trofimov (1979: p. 952).

Other species assigned: *Taslestes inobservabilis* Nessov, 1982 and *Daulestes nessovi* sp. n.

Revised diagnosis. — Upper premolars 4, upper and lower molars 3, as in eutherians but not primitive metatherians. Shares with *Asioryctes*, *Ukhaatherium*, *Bobolestes*, *Cimolestes incisus*, *C. propalaeoryctes*, *C. cerberoides*, *Otlestes*, *Prokennalestes*, some specimens of *Procerberus*, and Zalambdalestidae the plesiomorphic lack of pre- and postcingula, thus differing from *Gypsonictops*, *Batodon*, *Kennalestes*, *Sailestes*, *Zhelestes*, some specimens of *Procerberus*, and several other species referred to *Cimolestes*. Shares with *Asioryctes* and *Ukhaatherium* a strongly asymmetrical styler shelf on the upper molars, especially on M2, with a large parastylar and small metastylar region, and differs in this respect from other Asian Cretaceous eutherians. Differs from *Prokennalestes* and *Otlestes* in lacking a single labial mandibular foramen, in lacking the preparastyle (Kielan-Jaworowska & Dashzeveg 1989), and in having the talonid almost as wide as the trigonid (rather than markedly narrower). The entoconid and hypoconulid are not twinned. Differs from *Pappotherium*, *Holoclemensia*, *Tribotherium*, *Prokennalestes* and deltatheroidans (but not from *Asioryctes*, *Batodon*, *Bobolestes*, *Bulaklestes*, *Gypsonictops*, *Kennalestes*, *Otlestes*, *Sailestes*, *Zhelestes*, *Zalambdalestes*, and many Cenozoic mammals) in having winged conules. Apparently differs from *Kennalestes*, *Asioryctes*, and *Barunlestes* in lacking the pterygoid process of the sphenoid. Shares with *Asioryctes* generally similar proportions of the alisphenoid and orbitosphenoid and arrangement of alisphenoid/orbitosphenoid foramina. The large sphenorbital fissure transmitted the nerves III, IV, V1, V2, and VI. A foramen dorsal to sphenorbital fissure and artifactually merged with it is interpreted as the ?sinus canal foramen. The optic nerve (II) and ophthalmic artery probably passed through an optic foramen situated low in the orbitosphenoid. A large foramen for carotid distribution (Vidian artery?) is still present within the sphenoid, as in *Asioryctes*, metatherians, pantolestids, early Eocene didymoconids (Meng *et al.* 1994: p. 539), and *Thrinaxodon* (Estes 1961). Differs from metatherians, *Zalambdalestes*, and *Barunlestes*, but not from *Asioryctes* and *Kennalestes*, in having the foramen rotundum confluent with the sphenorbital fissure (i.e., there is no foramen rotundum per se; V2 shares an exit through the sphenorbital fissure with V1 and other structures). Cochlea with but one full turn. Differs from all known Asian Cretaceous eutherians in being much smaller.

Distribution. — Late Cretaceous (late Turonian–Coniacian, Bissekty Formation) of Kyzylkum Desert, Uzbekistan.

Comments on age

The holotypes of *Daulestes kulbekensis* and *Taslestes inobservabilis* were recovered from the lower part of the Bissekty Formation, whereas the holotype of '*Kumlestes olzha*' is from the middle part of the Bissekty Formation. The holotype of *D. nessovi* was found in the upper part of the Bissekty Formation and is stratigraphically younger than two other species of *Daulestes* and '*Kumlestes olzha*'. The lower part of the Bissekty Formation, previously known as the Taykarshi Beds of Sochava (1968), site CDZH-17a, was referred to by Nessov & Mertiniene (1986) and Nessov (1993, 1997)

as late Turonian. Nesson *et al.* (1994) and Nesson *et al.* (1998) regarded the lower part of the Bissekty Formation as possibly late Turonian, and the middle and upper parts as Coniacian in age, an idea accepted by Averianov (1999). We follow this assessment. The total amount of time represented by the Bissekty Formation is perhaps several million years at most and the skull of *D. nessovi* is about 87 million years old (see Gradstein *et al.* 1994, 1995).

***Daulestes nessovi* sp. n.**

Figs 2–19, Tables 1–4.

Skull of a proteutherian; Nesson & Kielan-Jaworowska 1991: fig. 1.

Skull with two lower jaws of Eutheria of the new genus and species, 107/12455; Nesson 1993, fig. 1: 4.

Skull of a small eutherian under study; Nesson *et al.* 1994: p. 79.

Skull of a placental mammal, probably *Daulestes* sp. nov., ZIN C. 79066, site CBI-5; Nesson 1997: pl. 48: 1.

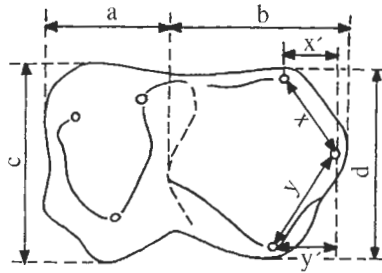
Holotype and only known specimen: ZIN C. 79066², a nearly complete but posteriorly crushed skull with articulated dentaries of a sub-adult individual, including a mix of deciduous and replacement teeth, but lacking premaxillae and upper incisors because of breakage, associated with an incomplete atlas and separate tympanic bone. The specimen was preserved in a phosphatic nodule. Originally the skull was associated with a slightly damaged spinous process of a mammalian vertebra (possibly an axis), adhering to the posterior part of the skull. It is seen in Figs 5 and 6, but has now been separated from the skull. The vertebra is relatively large in proportion to the skull, and we are not sure whether it belonged to the same animal as the skull.

Type horizon and locality: Channel in the upper part of the Coniacian part of the Bissekty Formation (Nesson 1990: p. 59; Nesson *et al.* 1994: p. 73), locality CBI-5a (Nesson's field locality, unpublished field notes; CBI = central Kyzylkum, Bissekty), about 10 m higher in the stratigraphic section than locality CBI-14 (Kielan-Jaworowska & Nesson 1992). East of Dzharakuduk, central part of the Kyzylkum Desert, Uzbekistan.

Diagnosis. — Smallest species of *Daulestes* (based on the size of m2, see Table 1); differs from the holotypes of *D. inobservabilis* and *D. kulbeckensis* in having m2 about 85% of their size. *D. nessovi* and *D. kulbeckensis* differ in structure of p2, which is double-rooted in the new species (unless it is dp2) and single-rooted in *D. kulbeckensis* (see also discussion on dental formula of *D. kulbeckensis* in Nesson *et al.* 1994: p. 56). Differs from *D. inobservabilis* in having three talonid cusps symmetrically arranged on m2, while in *D. inobservabilis* the hypoconid is set off, and the hypoconulid and entoconid are slightly approximated (see Nesson *et al.* 1994: pl. 1: 4a). The dentary of *D. nessovi* is much less robust (shallower below m2) than in *D. inobservabilis*, which, however, is in part due to the youth at death of ZIN C. 79066. The only other described taxon from Uzbekistan that falls within the same size category as species of *Daulestes* is *Otlestes meiman* Nesson, 1985a, from the early Cenomanian. *D. nessovi* differs from *O. meiman* in having four lower premolars and a temporarily retained dp2 instead of five permanent lower premolars, less molarized p3, and lack of labial mandibular foramen, which do not indicate a close relationship.

² According to A. Averianov (personal communication 2 February, 1999), 107/12455 (cited by Nesson 1993) was a number intended to be, but that was not actually listed in the catalogue for the collections of Chernyshev's Geological Museum, St. Petersburg. After Nesson's death all of Nesson's unpublished specimens were transferred to the Zoological Institute of the Russian Academy of Sciences. The proper number for the specimen described here is therefore ZIN C. 79066.

Table 1. Measurements (in mm) of holotype of *Taslestes inobservabilis* (= *Daulestes inobservabilis*); right (r) and left (l) m2s of *Daulestes nessovi*; m2 of holotype of '*Kumlestes olzha*' (*nomen dubium*); m1 of holotype of *Daulestes kulbeckensis*, and m2 of holotype of *Otlestes meiman*. Measurements and explanatory drawing are taken from Nesson *et al.* (1994: table 1 and fig. 1), augmented by optical micrometer measurements of the *Daulestes nessovi*, ZIN C. 79066, taken with Shopscopesm equipment. See drawing for explanation of the symbols: a, anteroposterior length of trigonid; b, remaining length of tooth to rear of hypoconulid; c, width of trigonid; d, width of talonid; x, direct distance between apexes of entoconid and hypoconulid; y, direct distance between apexes of hypoconid and hypoconulid; x', anteroposterior distance from entoconid apex to level of hypoconulid; y', anteroposterior distance from apex of hypoconid to level of hypoconulid; a+b, total anteroposterior length of tooth. Anteroposterior = parallel to tooth row.



Species	a	b	c	d	x	y	x'	y'	a+b
<i>Taslestes</i> , m2	0.65	0.67	0.90	0.84	0.26	0.37	0.22	0.16	1.32
<i>D. nessovi</i> , r m2	0.53	0.59	0.84	0.68	0.31	0.33	0.11	0.23	1.13
<i>D. nessovi</i> , l m2	0.51	0.61	0.84	0.76	0.33	0.32	0.15	0.21	1.12
' <i>Kumlestes</i> ', m2	0.55?	0.56	0.70	0.64	0.27	0.32	0.20	0.25	1.11?
<i>D. kulbeckensis</i> , m1									1.33
<i>Otlestes</i> , m2	0.61	0.69	1.02	0.76	0.34	0.35	0.21	0.32	1.30

Skull as a whole (Figs 2–7, Table 2)

The anterior aspect of the snout (the most anterior part of which is missing) is narrow and tubular. Its posterior end widens abruptly in front of the anterior opening of the infraorbital canal, at the level of P3. The anterior margin of the orbit is above the anterior margin of M1. The zygomatic arch, preserved on the left side, is very slender and only slightly expanded laterally, which may be ontogenetic and/or partly caused by distortion. There is a slight interorbital constriction, but no postorbital process. Although ZIN C. 79066 was sub-adult at death, we have had difficulty in delimiting sutures between various bones, especially in the orbit. We interpret this as the result of at least partial fusion. Also, the bones of the sphenoid complex (presphenoid, basisphenoid, orbitosphenoid, and alisphenoid) are fused, and our description of them as individual is conjectural. Fusion of skull sutures is also true of *Solenodon*, *Nesophontes*, many soricoids (McDowell 1958), and some bats.

The posterior end of the skull is broken, variously displaced, and distorted. In palatal view, the left side of the snout has been displaced at the midline about 0.9 mm poste-

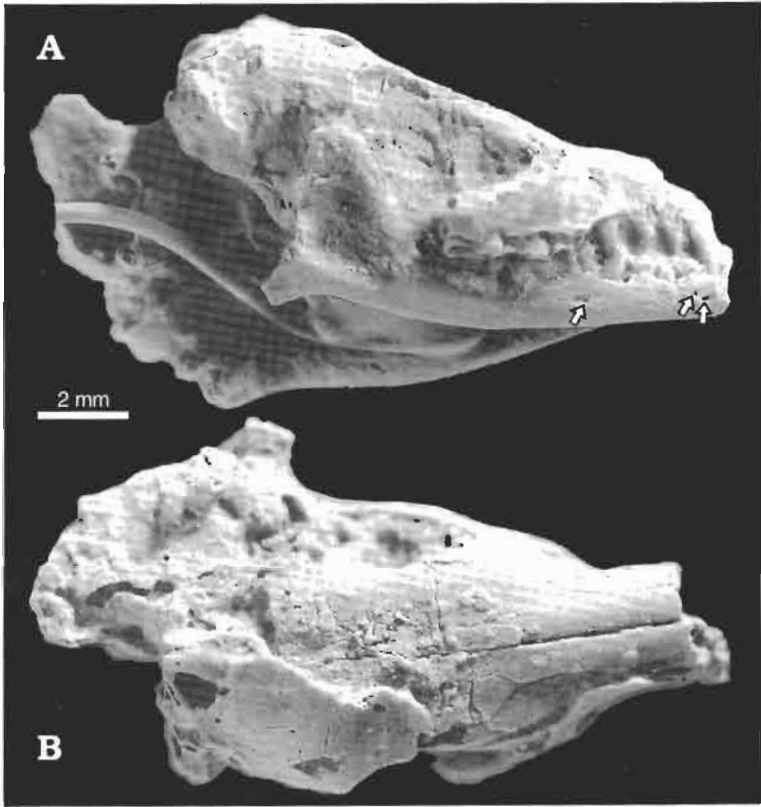
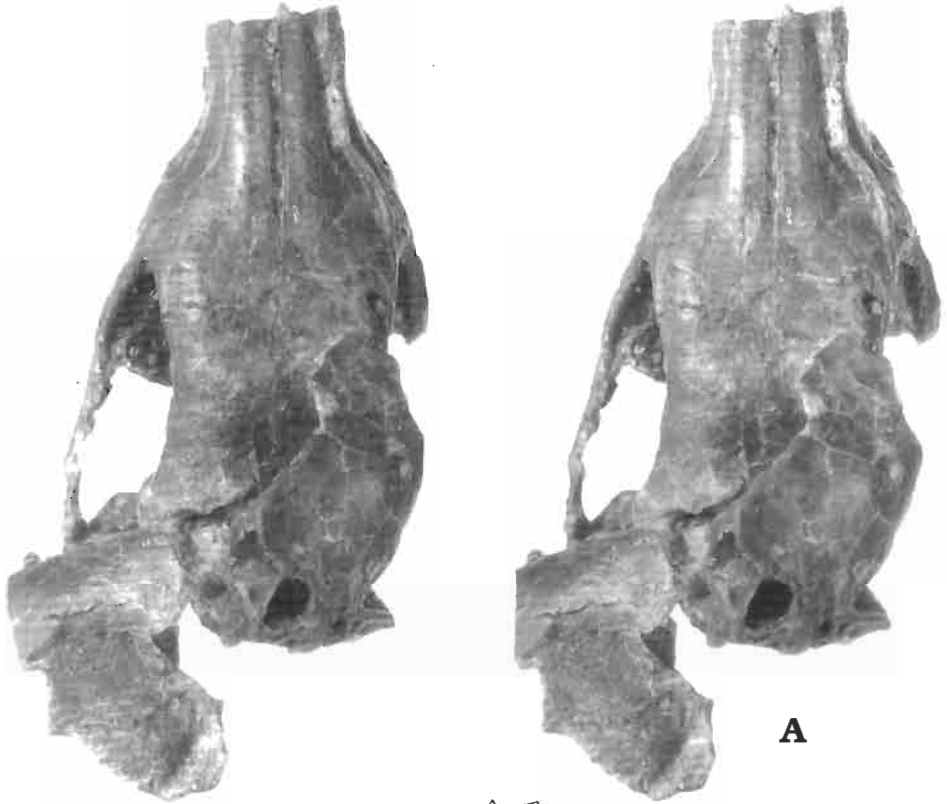


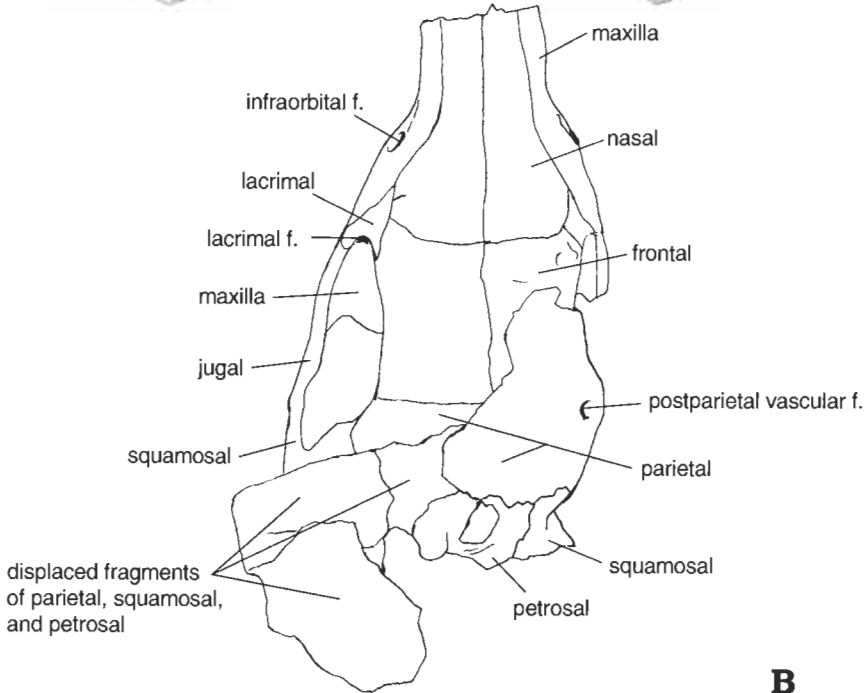
Fig. 2. Lateral (A) and dorsal (B) views of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066) in its originally preserved condition. Arrows in A point to the mental foramina.

riorly with respect to the right side, so that homologous teeth are no longer opposite one another (Fig. 4). On the dorsal aspect of the anterior part of the skull the left side is not displaced, although fracturing resembling displaced sutures has taken place. The basicranium has been bent upward toward the rear, such that the right petrosal now lies higher than the parietal on the skull roof. In addition to the upward displacement, the right squamosal and otic region have been telescoped forward and laterally with respect to the right alisphenoid. The left petrosal, although separate now from adjoining bone except the squamosal anteriorly, is more nearly in place with respect to the alisphenoid than is the right petrosal. The left basicranial region is largely broken, with only the basisphenoid and the promontorium preserved. The breakage goes through the left fenestra vestibuli and the fenestra cochleae; the left vestibule and semicircular canals posterior to this breakage are all missing. The promontorium is nonetheless preserved in good condition and is approximately in its original position with regard to the basisphenoid, although it is now strongly rotated outward (as seen from the rear).

Fig. 3. A. Stereophotograph showing dorsal view of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066), $\times 7$. B. Explanatory drawing for the same.



A



B

Table 2. Optical micrometer measurements (mm) of skull and dentary of *Daulestes nessovi* sp. n., ZIN C. 79066, taken with Shopscopesm equipment.

Length of preserved skull	11.55
Length of hypothetically undamaged sub-adult skull (Fig. 7)	15.6
Length of adult skull (estimated by analogy with <i>Kennalestes</i>)	19–20
Length from condyle to anteriormost preserved part of dentary	12.36
Depth of jaw buccally, beneath dp4	1.2
Depth of jaw buccally, beneath m2	1.1
Length from front of DC to the rear of M2, projected on sagittal plane	5.86
Length from front of DC to rear of M2, not projected on sagittal plane	6.17

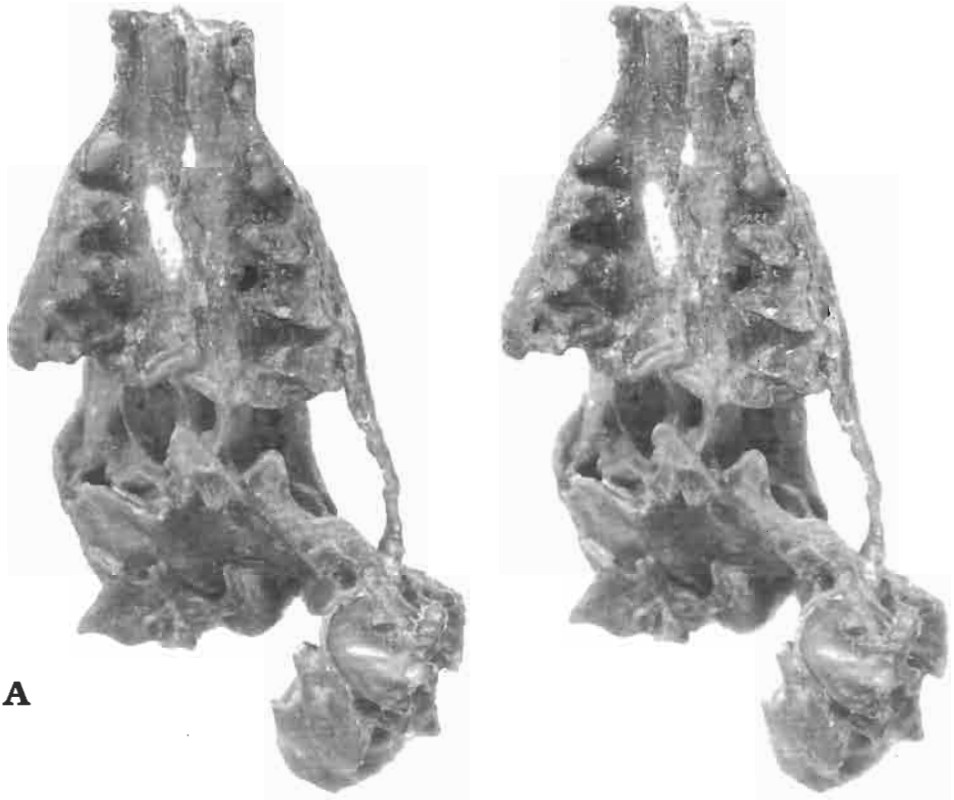
On the right side, the skull was fractured ventrally, approximately at the level of the pterygoid; the fracture runs dorsally along the posterodorsal edge of the orbit. The entire half of the cranium posterior to the fracture was rotated counterclockwise about 25° (as seen from the rear) and was pushed dorsally and slightly anteriorly; consequently, the preserved skull is now appreciably shorter than it was in life. Because of distortion and displacements at the rear of the skull, the position of the occipital plate with respect to the plane of the teeth is conjectural. Despite the bending and fracturing of the posterior part of the cranium, the ear region in regard to its surrounding elements remains roughly with many of its original topological relations and is the best preserved and most informative part of the skull.

In Fig. 7 we present a tentative reconstruction of the skull of *Daulestes*, according to which the length of a skull of an undamaged sub-adult individual would have been 15.6 mm. By analogy with *Kennalestes*, we estimate the length of an adult skull to have been between 19 and 20 mm (Table 2).

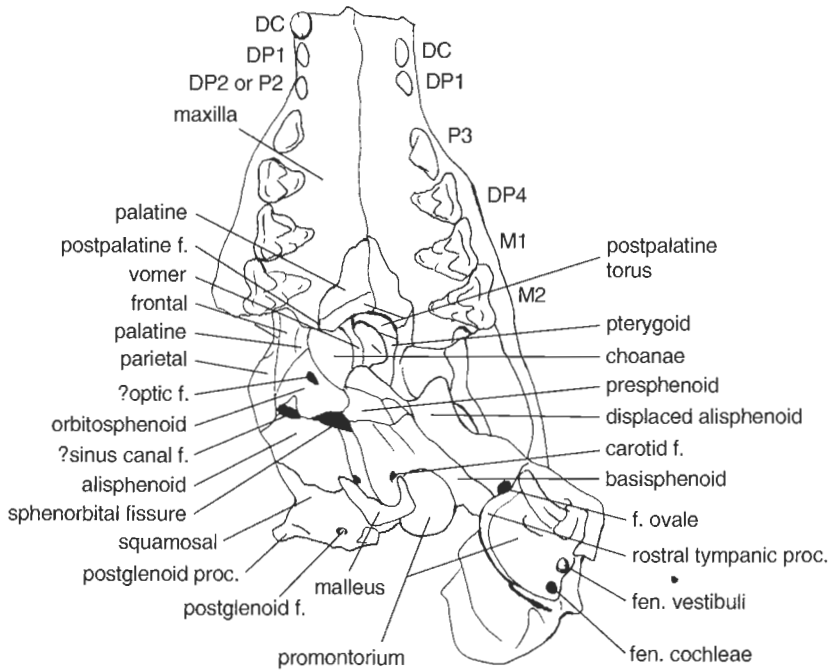
Bones of the skull (Figs 2–9)

The nasals (Figs 2, 3) are not complete anteriorly. Anteriorly narrow, they broaden sharply on the dorsal side of the snout, above the infraorbital canal. Each nasal contacts the maxilla laterally, and the lacrimal posterolaterally, as in more plesiomorphic synapsids (Gregory 1920). A broad contact with the frontal is present posteriorly. The suture with the frontal is faintly discernible, and is convex posteriorly as it crosses the roof of the skull from side to side above the anterior part of the orbit. The anterior ends of the nasals are arched in cross-section, and each nasal is overlapped by the maxilla throughout the entire length of the contact between them. Anteriorly the nasals are completely unfused; posteriorly the sagittal suture between them becomes less separate but is still distinct.

Fig. 4. A. Stereophotograph showing ventral view of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066), × 7. B. Explanatory drawing for the same. Vidian foramina are not seen in this view.



A



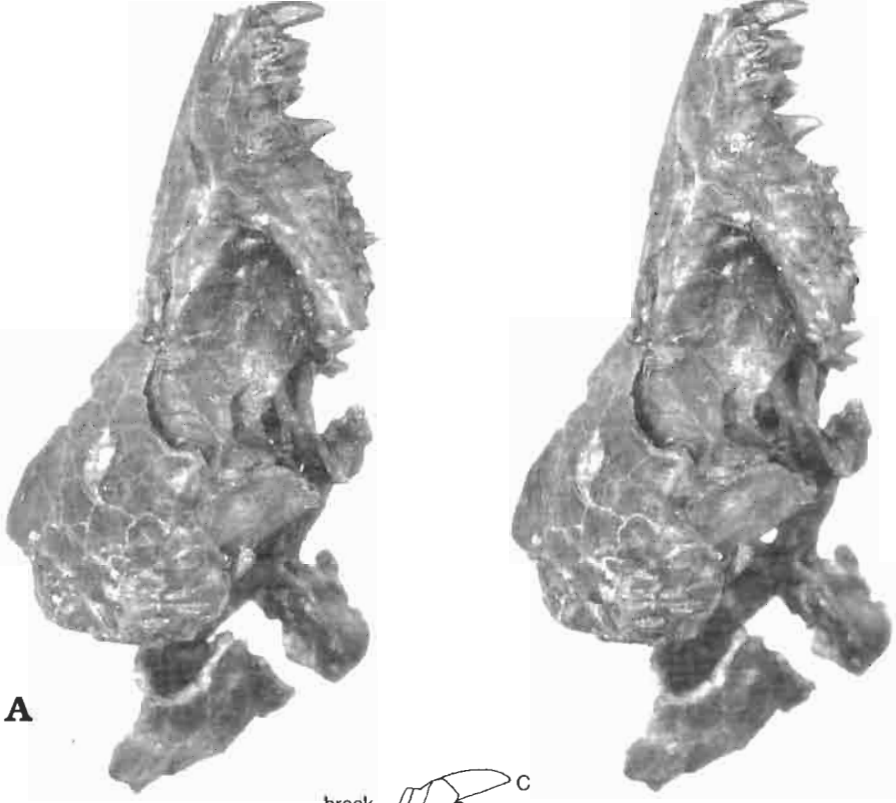
B

The premaxilla and its incisors are missing; thus the position of the suture between the premaxilla and maxilla is unknown other than that it must have been completely in front of, rather than at, the alveolus of the upper caniniform tooth (interpreted as DC).

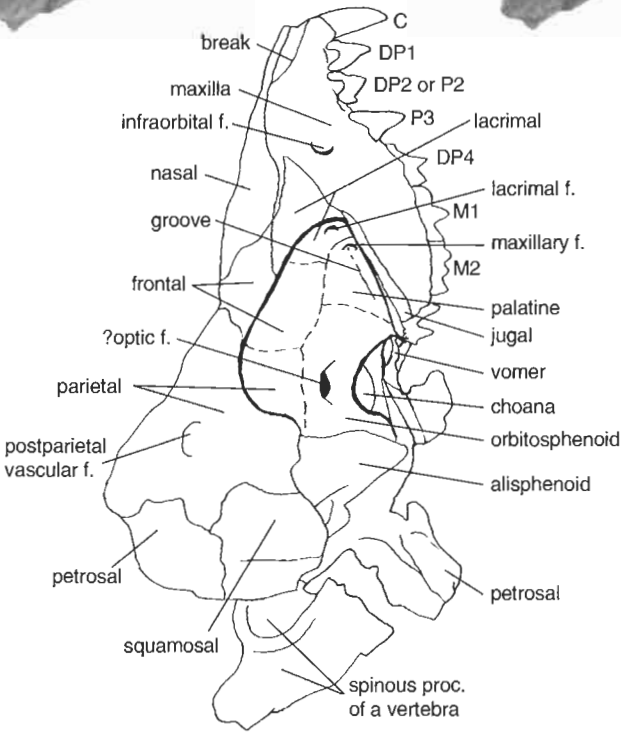
The maxilla (Figs 4–7) makes up the side-wall of the snout, but contributes little to the anterior end of the zygomatic arch. We do not know how far the maxilla extended in front of the alveolus for DC, but the latter lies wholly within the maxilla. The infraorbital foramen is 0.6 mm high. Leading anteriorly from the infraorbital foramen is a short, groove-like depression, in front of which the lateral wall of the maxilla is slightly concave and then flares slightly at the level of the tooth that we identify as either DP2 or P2. On the palate (ventral view) the maxilla is not fenestrated (Fig. 4). No traces of incisive foramina are visible at the anterior edge of the palate; therefore, incisive foramina must have been in the premaxilla, anterior to the level of the canine tooth. The anterior end of the preserved part of the skull has been slightly twisted, such that the left maxilla is displaced somewhat posteriorly with regard to the right one and also rotated slightly ventrally. At the rear of the palate the right and left maxillae have also been telescoped medially, so that the left maxilla and the horizontal part of the palatine have come to dorsally overlap the right maxilla and palatine. M3 was not yet erupted. Each maxilla of an adult would thus bear a canine and (presumably) seven postcanine teeth. The posterior margin of the palatal wing of the maxilla, the medial part of which has been preserved on the left side, is thickened (Fig. 4). Its lateral part (where the incompletely developed M3 was contained), and the whole margin on the right side, are broken. On the left side, to the rear of M2, we recognize the lingual part of an alveolus for M3, and tentatively the broken lingual root of the developing but now missing M3. A fragment of bone that (in ventral view) obscures the left side of the sphenoid (presphenoid) is possibly a broken part of the right maxilla. Between the trigons of the upper cheek-teeth there is some indication of shallow pitting of the maxilla for reception of cusp apices of the trigonids of lower cheek-teeth.

Within the orbit there is a large, horizontal, triangular maxillary plate that ventrally floors the anterior part of the orbit. We interpret the contact of the maxilla with the palatine's orbital wing to occur in the angle between the horizontal maxillary plate and the vertical orbital wall. The maxilla does not contribute to the orbital wall above the medial side of the horizontal maxillary plate. Rather, an extensive orbital wing of the palatine lying above and posterior to the maxilla bars contact of the maxilla with the frontal within the orbit, as in *Potamogale* but not other lipotyphlans (MacPhee & Novacek 1993: p. 18). The anterior end of the orbital floor continues anteriorly as the floor of the infraorbital canal. The dorsal ends of roots of M1 and M2 are exposed on the dorsal surface of the maxillary plate, on the orbital floor. The posterior end of the infraorbital canal (maxillary foramen) opens above the level of the M1 paracone. The boundary between the horizontal maxillary plate and the vertical orbital process of the palatine is marked by a groove for nerves and vessels ('groove' in Fig. 5), which leads to the ventromedial corner of the maxillary foramen and further to the infraorbital canal. Within the left orbit, the area bearing this groove is broken but could have housed a

Fig. 5. **A.** Stereophotograph showing right view of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066). **B.** Explanatory drawing for the same. ?Sinuous canal foramen and sphenorbital fissure are not seen in this view. Spinous process of a vertebra (possibly an axis), found with the skull, is preserved, $\times 7$.



A



B

sphenopalatine foramen; in the right orbit this foramen is only weakly suggested and would have been very small, if correctly identified.

The palatine is nearly complete on each side but, because of distortion, the left one is partly hidden from ventral view on the palate by the ventrally overlapping right one. On the palate the horizontal part of the palatine extends anteriorly up to the level of the anterior part of M1 (Fig. 4). An anterior palatine foramen has not been found. However, a partly hidden opening occurs at the anterior edge of the palatal process of the left palatine bone. This opening seems to be too large to be only the anterior palatine foramen; it may represent a foramen expanded by breakage and filled with matrix. Similar but even more extensive breakage filled with matrix occurs on the right side. Leading from these openings are very shallow grooves that extend anteriorly on the maxilla, bolstering the conclusion that foramina were present. The choanal margin, placed opposite the future site of an erupted M3, forms a gentle arch, possibly without a medial postpalatine spine. The curved postpalatine torus is more prominent and wider laterally than medially. It forms the posterior edge of the palate. The torus delimits the floor of the choanal opening. At its buccal left end, in the suture with the maxilla, a short furrow is tentatively recognized as a fissure-like posterior palatine foramen (Fig. 4). On the orbital wall (Figs 5, 6), the exposure of the palatine is extensive, but its boundaries are indistinct. The palatine contacts the maxilla anteroventrally, the frontal and lacrimal anterodorsally, and the orbitosphenoid posteriorly, but its boundary with the orbitosphenoid is conjectural.

The lacrimal is large, and has on the facial region a prominent triangular antorbital wing that wedges between the maxilla and the nasal. There is an extensive contact of the lacrimal with the broad rear part of the nasal, a plesiomorphic feature (Gregory 1920). Posterodorsally, the lacrimal contacts the frontal. The extent of the lacrimal within the orbit is also large; it contacts the frontal, maxillary and palatine bones there. There is no lacrimal tubercle. The single lacrimal foramen is prominent, lying just within the orbit and facing rearward. Beneath the lacrimal foramen, the lacrimal has a small zygomatic wing that extends a short distance back along the rim of the orbit, dorsally overlapping the anteriormost part of the jugal. Within the orbit and medial to this overlapping, the lacrimal forms the dorsal roof of the posterior opening of the infraorbital canal (maxillary foramen).

The orbitosphenoid (Figs 5–9) is preserved on both sides of the skull. The boundaries of this bone with others are mainly conjectural, especially so on the animal's left side. The orbitosphenoid is either mostly or totally fused to the palatine anteroventromedially, the frontal anterodorsally, and the parietal dorsally. The posterior margin is better preserved. It is marked by two large foramina (sphenorbital fissure and ?sinus canal foramen) at the boundary with the alisphenoid, which on the right side slightly overlaps the orbitosphenoid. At the postero-ventral part of the orbitosphenoid there is a large foramen, possibly enlarged on the left side by damage, but intact on the right side. This foramen faces anteroventrolaterally, and within the wall of the orbit it has ramifying passages. We identify it as the ?optic foramen as in *Asioryctes* (Kielan-Jaworowska 1981: fig. 3). A small opening (or breakage), connected with the ?optic foramen by a tiny groove, lies posteroventrally to it, at the presumed boundary with the presphe-

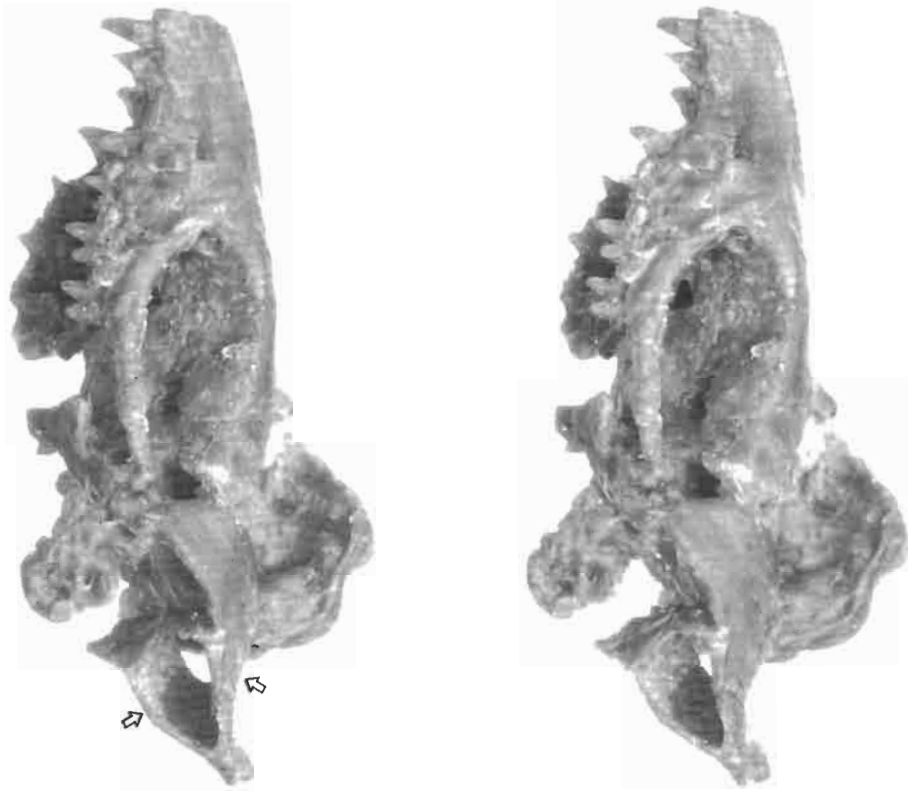


Fig. 6. Stereophotograph showing left view of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066). Arrows point to the spinous process of a vertebra (possibly an axis), found with the skull, $\times 7$.

noid. We cannot identify it. A small ethmoid foramen for the recurrent, ethmoid branch of the ophthalmic division (V1) of the trigeminal nerve is seen on the left side of the skull anterodorsal to the 'sinus canal foramen' at what appears to be the boundary of the orbitosphenoid and frontal.

The jugal forms the ventrolateral margin of the orbit, and at its anterior end lies above the maxilla (Figs 5–7), where its pointed anterior tip is dorsally overlapped for a short distance by the posterolaterally projecting zygomatic wing of the lacrimal. These relationships can be seen on the right side of the skull, although the more posterior parts of the zygomatic arch are missing on that side. Above the maxilla the height of the jugal gradually increases posteriorly to reach its deepest point opposite the ectoflexus of M2 and then tapers away beyond that point. The body of the slender left jugal extends posteriorly to reach approximately the glenoid area of the left squamosal, but that area is damaged and telescoped. The posterior end of the left zygomatic arch has been displaced; the expected suture between the jugal and a dorsally overlapping zygomatic process of the left squamosal has not been seen. Part of the squamosal contribution to the zygomatic arch, if any, may be missing or even covered by the rotated left petrosal. In its current distorted condition, the rear end of the preserved part of the jugal now unnaturally contacts

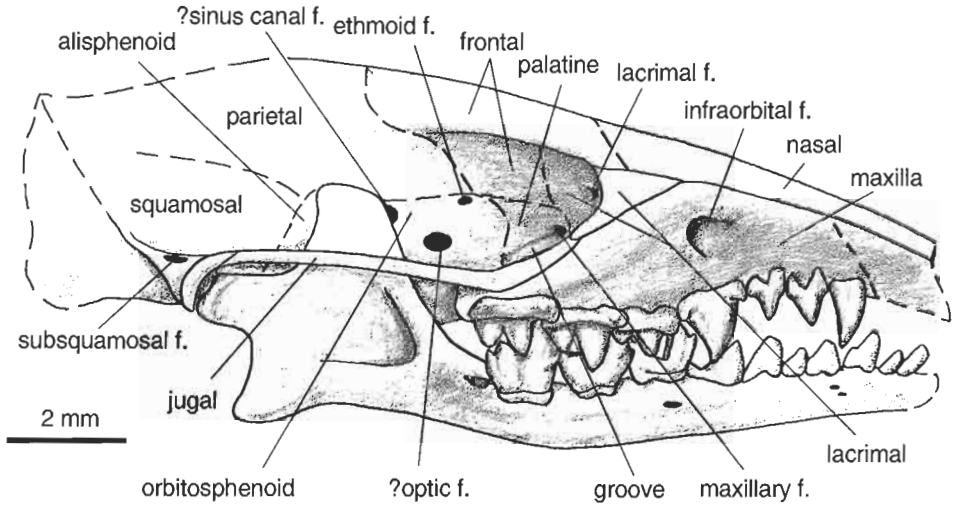


Fig. 7. Tentative reconstruction of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066) in lateral view.

the anterior margin of the petrosal as well as the alisphenoid near the foramen ovale, instead of reaching an anterior projection of the squamosal near the glenoid fossa.

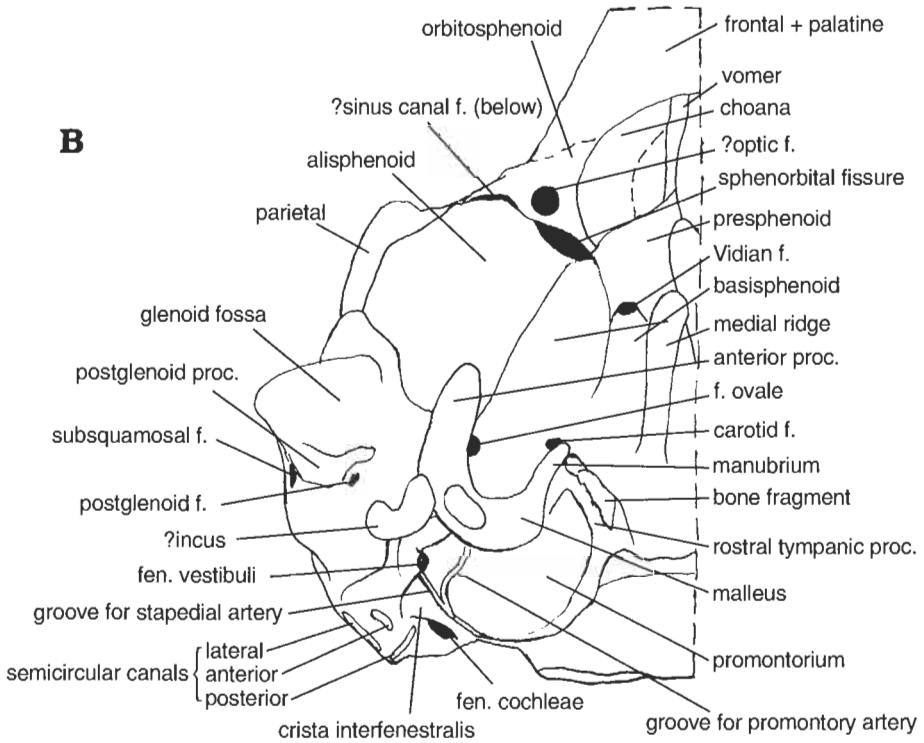
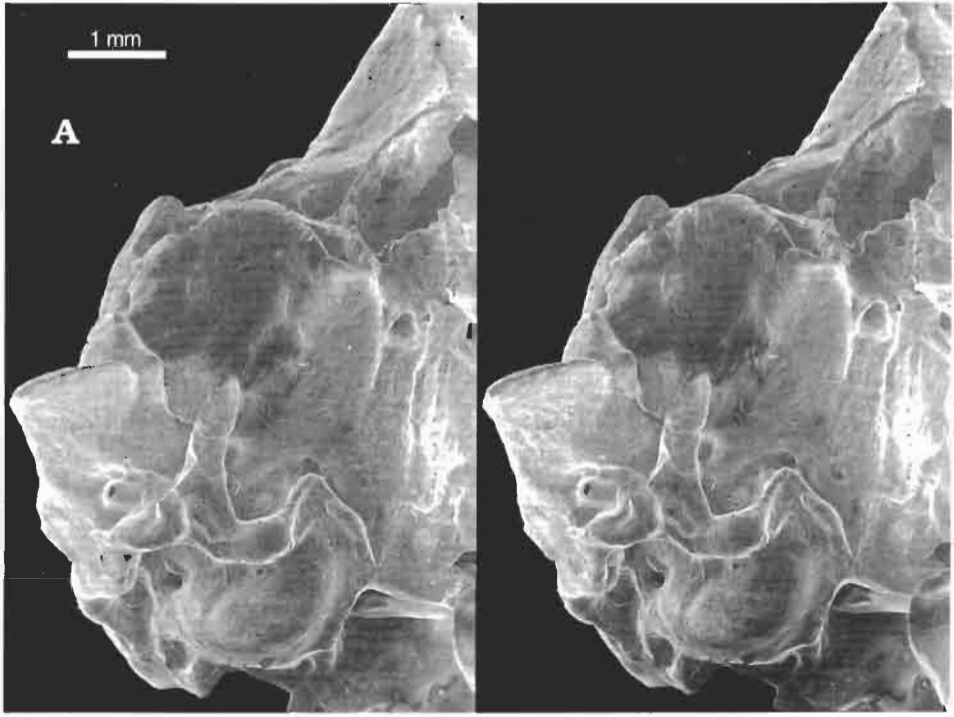
The pterygoid probably forms the posterior part of the lateral wall of the choanal channel, but the suture with the anterior part (built from the palatine) is conjectural (Fig. 4). The roofs and sides of both the right and left choanae are broken due to dislocation of the basicranium with regard to the anterior part of the skull. Also as the result of distortion and breakage, the lateral margins of the choanae probably converge posteriorly more strongly than in life.

The vomer (Figs 4, 8) is possibly represented by a longitudinal central ridge, as revealed by breakage of the roofs of the choanae. The ridge may lie too far back to be a part of the vomer. At present the possible vomer is separated from the presphenoid by postmortem damage.

The presphenoid (Figs 4, 8) has been shifted posthumously because of translation and rotation of the basicranium with respect to the more anterior part of the skull. The anterior end of the presphenoid now touches the ventral floor of the right choana (out of the midline) and has been separated from the vomer. Its anterior margin is possibly missing. There was a median ridge, only the base of which has been preserved. There is no suture (as opposed to breakage) between the presphenoid and basisphenoid.

The basisphenoid (Figs 4, 8) is estimated to be 2.6 mm long at the midline in ventral view, continuous laterally with the alisphenoid, as in *Asioryctes* and *Kennalestes*. This medial part of the basisphenoid is roughly trapezoidal, strongly widening posteriorly. A prominent ridge extends along its midline for the anterior third and gradually fades posteriorly. The ridge also persists onto the presphenoid as a club-like process. Several

Fig. 8. A. SEM stereomicrograph showing ventral view of the right basicranial region of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066) B. Explanatory drawing for the same.



pits of various sizes on the surface of the medial part possibly represent nutrient foramina that are filled with matrix. Anteriorly, an opening on each side of the skull occurs at the presumed transition between the presphenoid and basisphenoid. If they represent original foramina, these foramina are very large and occur at the entrance of the choanae. By position, they are unlikely to be anterior carotid foramina, because the latter are much more posteriorly positioned in *Asioryctes* (Kielan-Jaworowska 1981: fig. 3) and in many fossil and living marsupials (Marshall *et al.* 1995; entocarotid foramen of Gregory 1910: fig. 16). These foramina are tentatively identified as paired Vidian foramina that in life would have conveyed the Vidian artery (McDowell 1958), but the large size of these foramina, even allowing for damage, is puzzling. On the right side of the basisphenoid, a faint groove starts anterior to the ear region and extends to the Vidian foramen. Closer to the foramen, the groove becomes increasingly broader. It appears that the main groove leads to the foramen, while a smaller one branches off and courses by lateral to the foramen. This groove compares with the pharyngeal sulcus that contains the pharyngeal nerve and artery, as in leptictids (Novacek 1986).

Posteriorly, the medial part of the basisphenoid appears completely preserved but the basioccipital is entirely broken off beyond the suture between them.

The alisphenoid (Figs 4, 5, 7–9) is nearly complete on the right side of the skull and broken into two parts on the left. The alisphenoids form broadly rounded ridges, projecting ventrally, anterior to the tympanic region (in *Asioryctes* a similar structure extends along the medial border of the alisphenoid). The ridges define a valley that is wider posteriorly than anteriorly. The ectopterygoid process (flange) of the alisphenoid, which occurs at the boundary of the basisphenoid with the alisphenoid in *Kennalestes* and *Asioryctes* (Kielan-Jaworowska 1981), is apparently absent in *Daulestes*. On the right side the alisphenoid has been pushed somewhat anteriorly over the orbitosphenoid, while the squamosal has been pushed over the alisphenoid posteriorly. As preserved, an extensive gap is present at the anterior and lateral sides of the alisphenoid. Sutures delimiting the alisphenoid are not clear. We assume the broken edges of the bone to approximate the anterior and lateral sutures. Given these assumptions, the alisphenoid appears to be a very extensive, roughly fan-shaped extension of the sphenoid in the lateral wall of the braincase, with a rounded and thickened anterior margin that is convex anteriorly and that forms the posterior boundary of the sphenorbital fissure. The breakage gap anterior to the alisphenoid has left two large openings, which are partly separated by a bony bar. The ventral opening is identified as the sphenorbital fissure (foramen lacerum anterius) for nerves III, IV, V₁, V₂, and VI. This foramen is positioned lateral to the suture between the basisphenoid and presphenoid. The second opening, lying dorsolateral to the sphenorbital fissure, is probably enlarged as a result of breakage. We identify it as the ?sinus canal foramen. On the right side the ?sinus canal foramen lies at the mutual contact of the three bones (alisphenoid, orbitosphenoid and parietal) (Figs 8, 9). On the left side of the skull the sphenorbital fissure is also broken, and the anterior margin of the detached alisphenoid projection builds the posterolateral margin of the fissure. There is no alisphenoid canal. It seems that the posterodorsal margin (obscured by the squamosal) and the ventral margin of the alisphenoid converge posteriorly toward the foramen ovale. On the right side of the skull the foramen ovale is blocked from view ventrally by the anteriorly displaced

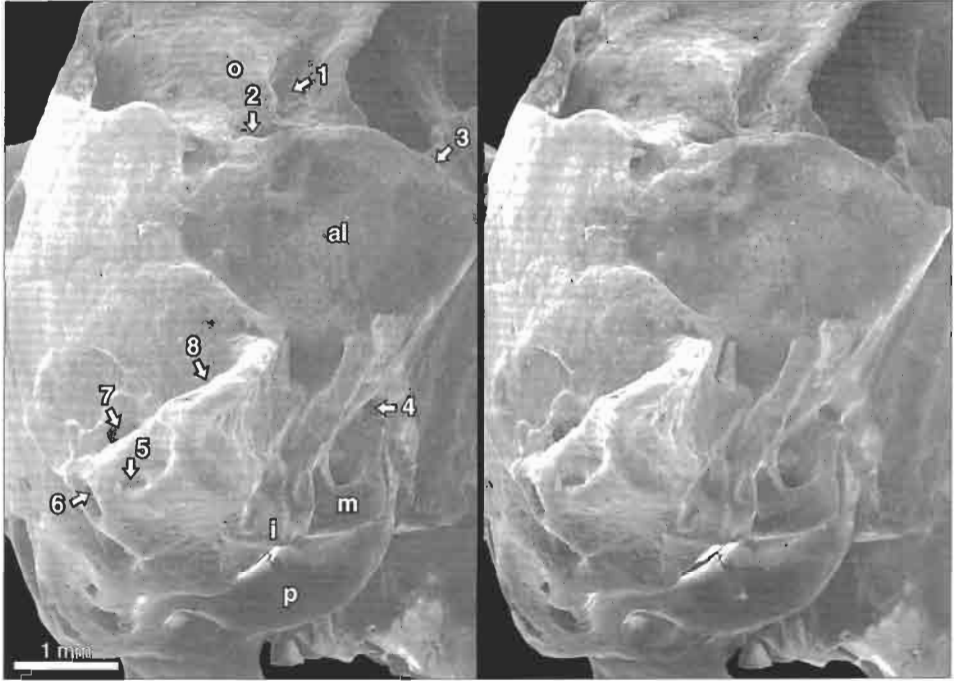


Fig. 9. SEM stereomicrograph showing ventro-lateral view of the right basicranial region of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066); al, alisphenoid; i, ?incus; m, malleus; o, orbitosphenoid; p, promontorium; the arrows point to: 1, ?optic foramen; 2, ?sinus canal foramen; 3, sphenorbital fissure (obscured by overthrust margin of the alisphenoid, only ventral part is partly seen); 4, carotid foramen; 5, postglenoid foramen; 6, subsquamosal foramen; 7, 8, additional vascular foramina. The postglenoid foramen looks double on this micrograph, which might be an artifact.

malleus. Between the posteromedial part of the alisphenoid and the anteromedial corner of the petrosal there is a large carotid foramen, well preserved on the right side (Fig. 8). On the left side of the skull only the anterior margin of this opening has been preserved, because the petrosal is broken across it. On the left side the medioventral part of the alisphenoid has been broken off and extends posterolaterally toward the promontorium as a process-like, laterally concave projection (Fig. 4). The anterior part of this projection is partly obscured by two displaced bone fragments. On the left side of the skull, the dorsal part of the alisphenoid has been pushed medially, resulting in a large gap in the middle of this part of the alisphenoid.

Frontal and parietal (Figs 2, 3, 5–7). The suture between the frontal and parietal is unclear; most likely it runs transversely, anterior to the breakage and posterior to the narrowest region of the skull, on the left side of the skull roof, as shown in Fig. 3. No frontal foramina have been seen. The frontal has a large extent in the orbit, but a postorbital process is not developed. The parietal is broad but does not form a lambdoidal crest (ontogenetic feature?). Given the shape of the preserved skull and the large parietal, the general outline of the skull is broad in the basicranial region. Dorsal to the fracture that separates the parietal and the alisphenoid, the transparent bone dis-

plays a light colored line that most likely represents a canal within, or a groove on the medial side of the parietal. By position, this canal or groove is similar to that of the ophthalmic sulcus for the ophthalmic artery and vein in the skull of leptictids (Novacek 1986). A large opening on the parietal (Figs 3, 5) represents a vascular postparietal foramen (Cope 1880). For taxa that have a broad temporal region, on which musculature must have attached, a vascular foramen, or several foramina, is frequently present as passageway for arteries and/or veins, as in *Eoryctes* (Thewissen & Gingerich 1989) and didymoconids (Meng *et al.* 1994: p. 536). These are temporal branches of the orbitotemporal system.

The squamosal (Figs 4, 5, 7–9) is well shown on the right side. Although displaced forward and rotated clockwise along with the right petrosal (in lateral view), the right squamosal is largely preserved. The left squamosal is now almost totally missing. Anteriorly, the right squamosal is separated from the alisphenoid by a break, where the squamosal is thrust forward and ventrally over the alisphenoid. Because the alisphenoid is thus overthrust, the anterior edge of the squamosal overlaps the alisphenoid for some distance ventrally. However, the relations of the squamosal to the parietal dorsally, and to the petrosal posteriorly, remain undistorted. The undistorted (and reconstructed) relationships are generally similar to those of *Asioryctes*, *Didelphis*, and leptictids, but in contrast to the latter, the squamosal in *Daulestes* apparently does not send an anterior process to intrude deeply between the alisphenoid and parietal. The squamosal is moderate in size, particularly so compared with the extensive petrosal; therefore, its contribution to the sidewall of the braincase is probably limited. Ventrally, the contribution of the squamosal to the zygomatic arch is not known. On the right side, however, the displaced and rotated squamosal bears an almost complete glenoid fossa. The fossa is moderately concave, delimited posteriorly by a transverse short postglenoid process, the medial part of which is narrower and bent anteriorly. There are two vascular foramina in this region. By comparison with *Kennalestes* and *Asioryctes*, we identify (Figs 7–9) the fissure-like, longitudinally directed opening, situated posterolateral to the postglenoid process, as a subsquamosal foramen (Cope 1880; Gregory 1910; Butler 1956; in *Leptictis* called a suprameatal foramen by Novacek 1986). In the squamosal, above and behind the glenoid process, small openings in the squamosal correspond to additional vascular foramina discussed by these authors, e.g., a postsquamosal foramen ('7' and '8' in Fig. 9). A prominent circular opening, slightly posteromedial to the postglenoid process, is identified as the postglenoid foramen (Figs 8 and 9). It opens ventromedially from a posterodorsally located sinus in the squamosal (to which other foramina in the squamosal also connect) for primarily venous drainage (sphenoparietal vein). A bony projection (entoglenoid process) limits the foramen immediately posteromedially. The projection would actually lie more on the posterior side of the foramen if the distorted basicranium were restored to its original shape. This would be a similarity to asioryctitherians. The medial contribution of the squamosal to the ear region is obscured by the somewhat displaced malleus.

Ear region (Figs 8–11)

The petrosals are relatively well preserved (Figs 4, 8–10). Both promontoria are present. The right one is in anatomical position with respect to the basisphenoid and

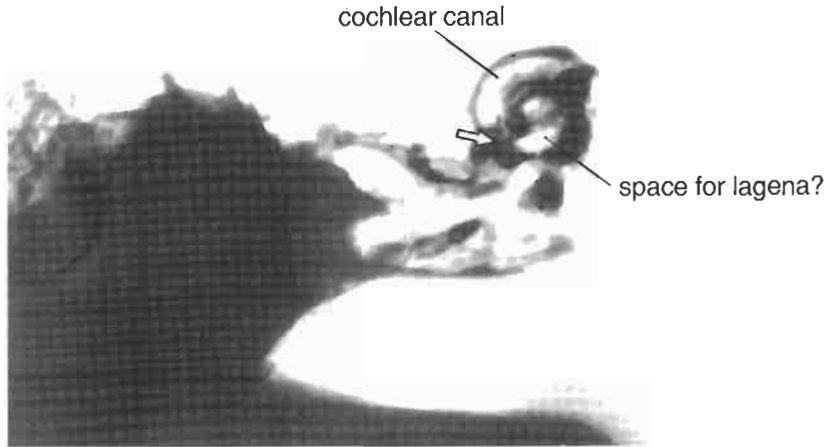


Fig. 10. Radiographic photograph revealing the shape of the cochlear canal in the left petrosal of *Daulestes nessovi* sp. n. (ZIN C. 79066), approx. $\times 7$. The arrow indicates a narrow area between the cochlear canal and the space probably for the lagena. See text for further discussion.

alisphenoid, and more or less with the squamosal (shifted anteriorly and rotated). In Fig. 8B we draw the position of the promontorium with its long axis directed obliquely anteromedially-posterolaterally as preserved, which is less longitudinally oriented than in certain other primitive eutherian mammals (e.g., *Asioryctes*, *Barunlestes*, *Palaeoryctes*, and others). The left promontorium has been displaced ventrally and tilted laterally in an unnatural way; however, it is still connected with the basicranial region by the displaced medial part of the alisphenoid. The promontory wall is very thin (possibly because of the youth of the individual). The shape of the cochlea is partly visible. Along the medial and anterior margins of the promontorium there is a flat bony shelf (rostral tympanic process of MacPhee 1981), which begins some distance in front of the fenestra cochleae and extends up to the carotid foramen. This shelf is well preserved on the left side of the skull, but partly obscured by unidentified minute bone fragments on the right side.

The promontorium is large relative to the skull size (Figs 4, 8, 9), possibly due in part to the animal's immaturity. The fenestra vestibuli is round-oval, about 0.5 mm in diameter, similar in dimension to the same structure in marsupials but significantly less elongate than that of known Late Cretaceous eutherians (MacIntyre 1972; Archibald 1979; Wible 1990; Meng & Fox 1995a, b). The fenestra is slightly inclined toward a horizontal position. Separated from the fenestra vestibuli by a broad bony bridge (crista interfenestralis), the fenestra cochleae is more posteromedially positioned. The fenestra cochleae, still blocked with matrix, is seen at the base of a pocket that is medially bounded by a bony ridge. The ridge, which marks the medial boundary of the posterior half of the petrosal, runs backward to end at the gyrus of the posterior semicircular canal. It is unclear whether an aqueductus cochleae (canaliculus cochleae) is present or whether the bony ridge is the processus recessus that divides the fenestra cochleae and the aqueductus in therians. On the medial side of the ridge, a small artifactual hole is present, penetrating the petrosal wall into the cochlear canal at the medial end of the promontorium.

At first sight, judged from the external shape of the promontorium only, the cochlear canal appears to have a broad basal section and then gradually taper apically. However, the X-ray photograph of the left ear region (Fig. 10), which is broken posterior to the vestibule, shows that the cochlear canal is actually not tapering; its apical part is as broad as its basal section. At the medial base of the canal, a narrow tunnel represents the connection between the fenestra cochleae and the cochlear canal. The X-ray photograph reveals a narrow region of the cochlear canal at about a turn of 180° from the base. This morphology differs from the osseous canal of the cochlea in either non-therian mammals, such as monotremes and multituberculates (Luo & Ketten 1991; Fox & Meng 1997), or in early therians (Meng & Fox 1995a, b). Two possibilities may be considered. First, the centerward area of the narrowed region is an artifact representing underexposure resulting from blockage of the X-rays by bone (for instance, the modiolus) and X-ray opaque matrix filling in the internal auditory meatus. Second, the narrow region is a true structure and is the boundary between the space of the cochlear canal and the space of the lagena. The latter implies that *Daulestes* possessed a large lagena, which would be unique among therian mammals. Among mammals, monotremes and, probably, multituberculates have a lagena, which is indicated osteologically by an expanded apex of the cochlear canal (Pritchard 1881; Gray 1908; Griffiths 1968, 1978; Fox & Meng 1997 and references therein).

The cochlear canal curves laterally, as in other mammals, and has just one full coil as has been reported for *Zalambdalestes* (Kielan-Jaworowska 1984b: p. 162 and fig. 2). The coiling is slightly less extensive than that of a therian taxon from the Late Cretaceous Milk River Formation of Canada (Meng & Fox 1995a). In the Milk River specimen, the apex of the cochlear canal overlaps the basal canal, but in *Daulestes* there is no overlap. At the center or vertical axis of the coiling, which is on the medial side of the broad basal cochlear canal, a dimple is formed on the external surface of the promontorium of the *Daulestes* petrosal. This morphology differs from that of all known Cretaceous mammals in which the cochlear canal is fully coiled (MacIntyre 1972; Archibald 1979; Kielan-Jaworowska 1984b; Wible 1990; Meng & Fox 1995a, b; Wible *et al.* 1995) or partially coiled, such as *Vincelestes* (Bonaparte & Rougier 1987; Rougier *et al.* 1992). In those forms, the surface of the promontorium is universally convex and 'almond-shaped'. In non-therians, such as multituberculates and triconodonts (Kermack 1963; Kermack *et al.* 1981; Kielan-Jaworowska *et al.* 1986; Graybeal *et al.* 1989; Luo 1989; Luo & Ketten 1991; Fox & Meng 1997) in which the cochlear canal is slightly curved, the promontorium is usually elongate, although its medial edge (which is usually the lateral boundary of the tensor tympani fossa) may suggest the curvature of the cochlear canal in some multituberculates (Fox & Meng 1997). The degree of curvature of the cochlear canal in *Daulestes* (Fig. 10) cannot be determined with precision, but it seems more curved than that of monotremes and *Vincelestes*, but less so than in any other known therian mammals. This may represent a primitive condition occurring in the common ancestor of marsupials and placentals.

The three semicircular canals are well-preserved in the left petrosal (Figs 8, 9). As in other mammals (Meng & Fox 1995b), the lateral canal surrounds the fossa for the stapedius muscle. The posterior part of the lateral canal is broken, exposing the empty canal within. Also as in other mammals, the gyrus of the anterior canal forms the rim of the subarcuate fossa on the intracranial side of the petrosal. The subarcuate fossa is

very deep; its roof is broken, forming a large, artifactual opening between the posterior and lateral semicircular canals on the posterior surface of the petrosal. The crus commune, formed by the posterior and anterior canals, bounds the posterior rim of the subarcuate fossa, near which the intracranial orifice of the aqueductus vestibuli is not observed. Among the three canals, the anterior one is the largest in diameter of the loop, but measurements of the canals are difficult to make, given the orientation and incomplete exposure of the structures.

Because of breakage at the occipital region, the intracranial side of the right petrosal is partly visible, but not well enough to be illustrated. Detailed morphology of the internal acoustic meatus is obscure because of matrix filling, but it is clear that on the ventral side of the subarcuate fossa a depression, the internal acoustic meatus, is present. The meatus is further divided by a bony ridge into a more anterior opening (presumably for the facial nerve, VII) and a posterior fossa in which no foramen for auditory nerve VIII can be seen because of matrix filling. The area anterior to the petrosal is covered by matrix, further removal of which would be likely destructive to the bone. Therefore, although it can be said that the petrosal contributes a great deal to the posterolateral wall of the braincase, it is impossible to determine how large the petrosal actually is and whether it has an anterior process.

The intracranial side of the displaced left petrosal is better exposed but poorly preserved. It shows a somewhat different morphology from the right one, probably owing to breakage, and does not merit description.

On the ventral surface of the right promontorium, two shallow grooves are visible, suggesting presence of the internal carotid artery (promontory artery) and stapedia artery (Figs 8, 9). The starting (medial) points of the two grooves are anteromedial to the fenestra cochleae. Judged from their tendencies, the branching point of these grooves, not imprinted on the bone, is close to the proximal ends of the two grooves. This situation differs from the condition of *Vincelestes*, in which the branching point of the promontory artery and stapedia artery is very close to the ventral rim of the fenestra vestibuli (Rougier *et al.* 1992). The groove presumably for the promontory artery extends anterolaterally to the concave region of the promontorium; further anteriorly, the course of the groove is blocked from ventral view by the displaced malleus. The groove presumably for the stapedia artery travels laterally toward the fenestra vestibuli; its destiny on the lateral side of the fenestra vestibuli is indeterminable, owing to poor preservation. On the right promontorium (Fig. 4), the groove for the promontory artery is present but is less distinctive than the one on the left, whereas because of breakage the stapedia groove is not preserved.

The ectotympanic is preserved as an isolated element found in the matrix at the rear of the skull (Fig. 11). The size of the ectotympanic matches the skull. It is roughly U-shaped, consisting of a transverse part that arcs ventrally and two limbs. Because it is not in its original anatomical position, the side of the skull to which the bone belongs is in doubt. However, we believe the bone is the left ectotympanic for two reasons: first, the longer limb – the anterior one according to our identification – bears a trough on the medial (if the bone was placed vertically) or the dorsal (placed horizontally) side of the limb. This trough is undoubtedly for articulation of the anterior process of the malleus; it compares well with those of horseshoe-shaped ectotympanics in extant mammals, such as *Didelphis*. In extant mammals, a similar trough occurs at the same position on the left ectotympanic, although it varies in size and shape among various taxa. In any

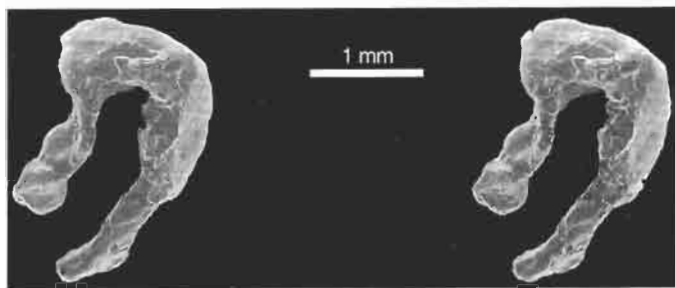


Fig. 11. SEM stereomicrograph of the left ectotympanic of *Daulestes nessovi* sp. n. (ZIN C. 79066).

case, the trough on the anterior limb helps to confirm its identity as the ectotympanic. Second, given our identification, the bone converges laterally (when vertically placed) so that the lateral opening is smaller in diameter and irregular in shape, suggesting formation of an external auditory meatus; in contrast, the medial side is more regularly oval-shaped with a larger diameter, in keeping with an oval-shaped ear drum.

The best preserved ectotympanic yet described in a Cretaceous eutherian is that of *Asioryctes* (see Kielan-Jaworowska 1981). The ectotympanic of ZIN C. 79066 is similar to that of *Asioryctes* in that its ventral (if vertically placed) or anteromedial (if horizontally positioned) transverse portion is slightly expanded, more so than the ring-shaped bone of *Didelphis*. However, the expansion in *Daulestes* is less than that in *Asioryctes*. The external surface of this expanded part is smooth and convex, whereas its medial side is concave, although in ZIN C. 79066 the medial side is still covered with some matrix and glue. A distinctive groove for attachment of the tympanum is absent, probably damaged during preservation. The anterior limb of the ectotympanic appears longer and slimmer than that of *Asioryctes*. The most notable morphology of the ectotympanic of *Daulestes*, assuming that it is complete, is its U-shaped outline. In several extant placentals, the ectotympanic at an early stage of development takes a U-shape and progresses to become more horseshoe-shaped in adult forms. Although the U-shaped ectotympanic in *Daulestes* may be attributed to its immaturity, or possibly to the loss of a part, two other possible interpretations come to mind. First, the posterior limb may have been displaced and pushed closer to the anterior limb than in its original condition. This is likely because a break occurs at its midpoint, where the posterior limb assumes the unusual shape. A second possibility is that the supposed posterior limb is not a part of the ectotympanic at all. Possibly, this little piece of bone might represent a part of another ear ossicle, secondarily attached to the ectotympanic at the break. Mentally removing this part makes the general shape of the remaining ectotympanic look more 'normal' but, on the other hand, enlarges the gap between the two ends of the bone. That gap, however, can be filled by the relatively large malleus.

The malleus is nearly complete on the right side of the skull (Figs 4, 8, 9) and is partly preserved on the left side. In fact, the right malleus is the best preserved malleus among known Cretaceous mammals. The right malleus has been moved from its original position anteriorly and is rotated slightly within the horizontal plane, with its anterior end more laterally shifted whereas the posterior end is more medially shifted. Consequently, the anterior process (goniale) now points anteriorly. In life, it would have

pointed more anteromedially. The anterior process is long, although its tip may be incomplete. The process appears to be robust, but its thickness is likely exaggerated by glue and by attached matrix on its dorsal side. However, removal of these alien materials might prove to be destructive to the bone. Owing to the indeterminate surface condition, we are unable to determine whether the foramen for the chorda tympani is present, as in monotremes (Doran 1878; Fleischer 1973) and multituberculates (Meng & Wyss 1995), but the homology of the anterior process (goniale) with the nonmammalian synapsid prearticular is assumed. The width of the anterior process matches the trough on the medial (or dorsal) side of the ectotympanic, as described above. The lamina (body) of the malleus is in all aspects typically therian (Doran 1878; Fleischer 1973). Its ventral surface is concave, and laterally the body is bounded by a distinct ridge. This ridge represents part of thickness formed at what appears to be the incus-malleus articulation. Although the actual articulation facet is not well seen, the ridged structure suggests that the incus is placed posterior to the malleus, as in living therians. In monotremes, in which the incus occurs on the dorsal side of the malleus, the ridge, if any, is very low and blunt (personal observations). In multituberculates the incus also is dorsal to the malleus (Meng & Wyss 1995; Hurum *et al.* 1996; Rougier *et al.* 1996b). The neck of the malleus is slightly narrower than the lamina and, on its medial end, thickens to form a somewhat rounded base for the manubrium. This morphology is almost identical to that of living therians. Surprisingly, the manubrium, or at least the most basal portion of the manubrium, is preserved nearly in the original position. It is a very thin process, extending from its rounded base anteriorly (in original position it would be directed anteromedially) about half the length of the anterior process. The anterior end of the manubrium, at least in the position in which it is preserved, presently abuts against the carotid foramen. The manubrium parallels the anterior process in ventral view; however, these two processes do not extend in the same plane. As in living mammals (monotremes and therians alike), the manubrium extends in a plane that is more dorsally tilted than that of the anterior process; the angle between the two planes varies among taxa. In ZIN C. 79066, the angle is about 30°. The tip of the manubrium is probably broken; if present, the tip should be wider than the body of the manubrium and it should bear a flat ventral surface for attachment of the tympanum.

The ?incus, interpreted here to be preserved on the right side of the skull (Fig. 9), adheres to and ventrally partly covers the posterolateral border of the malleus. If this bone is indeed an incus, it has apparently been overturned posterolaterally. On the left side of the skull an incus cannot be identified with any certainty. There is, however, a small bit of bone that adheres to the lateral margin of the transverse part of the left malleus, which might possibly be an incus.

The ?stapes cannot be identified with any certainty. On the left side of the skull a rounded piece of bone that may be a part of the stapes is closely associated with and may actually enter the fenestra vestibuli (Fig. 4). We cannot say anything meaningful about the shape of the stapes or about a stapedia foramen.

Atlas and occipital condyle (Fig. 12)

Separated from the skull are two fragmentary bones that are stuck together. One piece is a left half of the atlas vertebra, with the intercentrum missing (transferred to become the odontoid process of the missing axis vertebra?). The preserved atlas is similar to

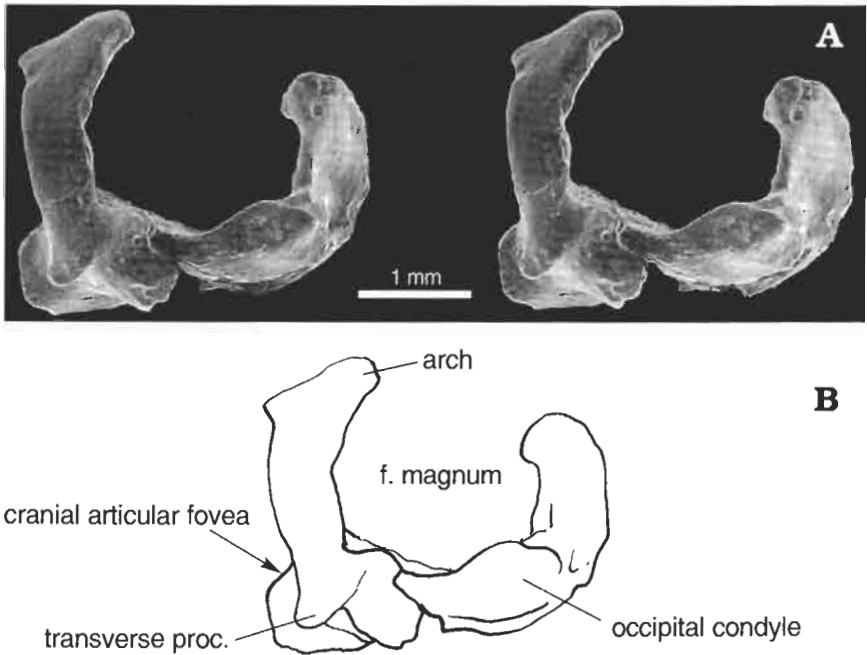


Fig. 12. A. SEM stereomicrograph of two fragmentary bones of *Daulestes nessovi* sp. n. (ZIN C. 79066); the left piece is a left part of the atlas; the right one is a partial right exoccipital with the occipital condyle. B. Explanatory drawing for the same.

those of *Asioryctes* and *Kennalestes* (Kielan-Jaworowska *et al.* 1979) in having a short transverse process and lacking a transverse foramen. The articular facet for the occipital condyle of the skull is oval and gently concave. The medial (distal) end of the arch is wider than the lateral (proximal) end. Unlike *Asioryctes* or *Kennalestes*, the sulcus arteriae vertebralis is shallower in *Daulestes*. In *Asioryctes* the right and left arches are fused, although no ridge or process is formed at the junction. In *Daulestes* the two arches appear separate, because the preserved arch has a straight, smooth medial (distal) edge; breakage is unlikely to have produced such a shape, had the arches fused. This morphology reflects either unfused structure in an immature individual, such as in juvenile dogs, or a more primitive condition than that of *Asioryctes*, or both.

The other piece of bone is a large part of the basioccipital and exoccipital of the skull, the latter bearing an occipital condyle. The condyle is flat and rough-surfaced. At its anterior margin, a laterally directed condyloid foramen occurs. On the dorsal side of the basioccipital (within the braincase in life), the intracranial opening of the condyloid foramen appears filled with matrix that is homogenized with surrounding bone by glue; applying acetone to this region reveals it.

Mandible (Figs 2A, 13–15)

Both dentaries are present. The right dentary bears a probably deciduous canine and eight postcanine teeth (including dp2 – wholly behind p2, and a developing m3, Fig.

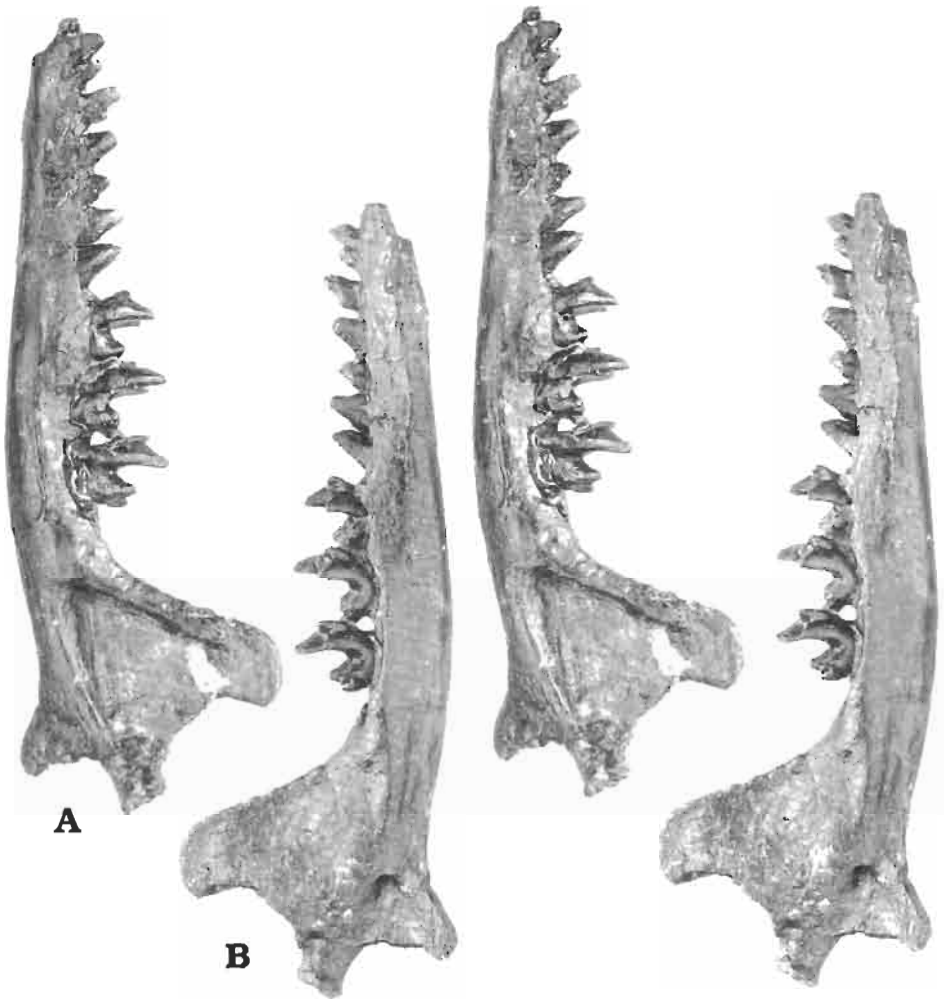


Fig. 13. Stereophotographs of the left dentary of *Daulestes nessovi* sp. n. (ZIN C. 79066). A. Lateral view. B. Medial view. $\times 8.5$.

15). The left dentary (Fig. 13) bears the alveolus of at least one now-missing anterior incisor. At least two additional incisors lie behind it, the anterior of which is large and possesses a slightly expanded crown and the posterior of which is minute and closely appressed to the posterior part of its anterior neighbor (Figs 13, 14). Following these single-rooted teeth is a double-rooted caniniform tooth that we interpret to be a deciduous canine. Following the caniniform tooth are four premolariform teeth that we identify as the following linear sequence: dp1, p2, dp2, and the erupting p3. Following p3 are four molariform teeth: dp4 not yet shed, two erupted molars, and a developing m3 in its alveolus. Both right and left dentaries are quite shallow, surely an ontogenetic feature. The dentary condyle, preserved on the left dentary, is best seen in posterior (slightly posterodorsal) view, in which it appears roughly circular. In posterior view it consists of two rounded ridges. The dorsomedial ridge is larger, the small ventrolateral



Fig. 14 **A.** SEM stereomicrograph of the left lower dentition, occlusal view, of *Daulestes nessovi* sp. n. (ZIN C. 79066). **B.** SEM micrograph of the medial view of the same. Scale bar is for **A** and **B**. See Fig. 16 for identification of the dentition. **C.** Stereophotograph of the left dentary of the same in occlusal view, $\times 8.5$.

one protrudes more strongly posteriorly. In lateral and medial views, the condyle is directed anterodorsally-posteromedially but the situation is the reverse of that seen in shrews, in which the lower capitular facet is placed more internally than the upper one. Two condyles occur in advanced Soricidae, but there is little reason to believe that the

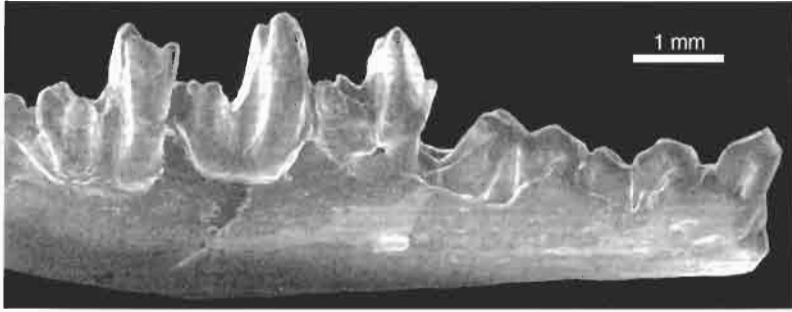


Fig. 15. SEM micrograph of the right lower dentition of *Daulestes nessovi* sp. n. (ZIN C. 79066), in lateral view. The mental foramen beneath the anterior root of dp4 is obscured by SEM artifact.

double condyle in *Daulestes* is homologous to that of the non-heterosoricine Soricidae or *Nesophontes* or *Solenodon* (Fearnhead *et al.* 1955; McDowell 1958: figs 3, 30; Mills 1966: fig. 12). It seems more probable that it is due to the youth of ZIN C. 79066, in which the condyle may be interpreted as not having been entirely ossified.

In buccal view, the coronoid process arises at about a 60° angle from the horizontal ramus (Fig. 13). It is not pocketed medially. There is a deeply pocketed masseteric fossa, which is floored by a shelf running forward from the condyle. Three and possibly more tiny vascular foramina lie at the anteroventral end of the masseteric fossa, in place of a single buccal foramen (labial mandibular foramen) at this site in some Cretaceous mammals, e.g., *Kielantherium*, *Otlestes*, and *Prokennalestes* (Marshall & Kielan-Jaworowska 1992: p. 365). These tiny foramina are visible on the right dentary; those on the left are still obscured by matrix and a preservative coating. Two mental foramina occur beneath the anterior part of right dp1, and a slit-like depression containing one or more mental foramina occurs under the anterior root of dp4 in both dentaries (Figs 2A, 7, 15). The position of such foramina in a fully adult individual may well have been somewhat different. In lingual view the symphysis extends from the front of the jaw to a point approximately beneath dp1 (Fig. 13B). At the anterodorsal base of the somewhat inflected angular process of the dentary a mandibular foramen is seen. Extending anteriorly from the mandibular foramen is a very shallow groove (present on both dentaries) that becomes narrower and more distinct anteriorly and disappears at a point below the posteriormost alveolus. This groove is less obvious than a groove referred to as a remnant of the Meckelian groove in *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989: figs 17, 20, 23). Above the groove the dentary is slightly swollen.

Dentition (Figs 13–19)

ZIN C. 79066 appears to be only slightly more mature than the juvenile skull of *Kennalestes gobiensis*, ZPAL MgM-I/1, described by Kielan-Jaworowska (1981). All the teeth of ZIN C. 79066 are similar in color (in juvenile *Kennalestes* the deciduous teeth are lighter in color), which cannot help to distinguish between deciduous and successional teeth. However, comparison with both the dental formula and the premolar morphology of *Kennalestes* helped us to hypothesize the dental formula of *Daulestes* at the ontogenetic stage represented by ZIN C. 79066 as follows. Upper incisor

count unknown, DC, (D)P1, either DP2 or a replacement P2, erupting P3 (DP3 already shed), DP4 still in place and presumably covering a replacement P4 if that tooth had formed yet, M1, M2, and fragments of the developing M3. In the lower jaw the following sequence of teeth is present: di1 or i1 (in the left dentary in front of di2 there is a root identified as di1 or i1), di2 or i2, di3 or i3, di4 or i4 (or some combination of at least three of these), dc, (d)p1, erupting p2, dp2 still present but lying wholly behind p2 rather than above it (resulting in a premolar count of 5 in use at one time), erupting p3, dp4 still in position over the site of a presumably developing p4, erupted m1 and m2, and m3 developing in its crypt but unerupted. We postulate that an adult specimen of *Daulestes* would have had an unknown upper incisor count but possibly more than three, C, (D)P1, P2, P3, P4, M1, M2, M3 / lower incisor count of at least three, c, (d)p1, p2, p3, p4, m1, m2, m3.

Lower dentition (Figs 13–16, Table 3). Incisors. — A partial root of an apparently large anterior incisor, designated di1 (or i1) and the last two incisors are preserved in the left dentary. Because of ambiguity concerning the number of lower incisors, we assign di1 (or i1) to the first tooth for which the root is preserved. The next incisor (di2 or i2), which is the first tooth with a completely preserved crown (penultimate incisor) projects anterobuccally from its alveolus at about 45°, bears a simple, blunt apex, and has a somewhat oval cross-section with anterior and posterior cresting. It is wider posteriorly than anteriorly. Lingual to its alveolus is a second, empty alveolus that either housed an additional incisor or possibly a deciduous predecessor of the penultimate incisor. The ultimate incisor (di3 or i3) is a very small, simple, peg-like tooth, projecting also at about 45° and lying somewhat posterolingual to the penultimate incisor, to which it is closely appressed. Although there are three or possibly more lower incisors, the retention of deciduous teeth among replacement incisors cannot be discounted.

The lower deciduous canine is double-rooted as seen from the buccal side, the anterior root being the smaller of the two. There is an anteriorly located, transversely appressed main cusp and a low heel at the rear, giving the tooth a premolariform aspect. In view of the depth of the jaw supporting it, it is difficult to imagine a larger tooth at this locus at the stage of ontogeny represented, so we regard this tooth as a deciduous rather than replacement lower canine. It occludes in front of the much larger, single-rooted upper caniniform tooth, which we also interpret to be deciduous on the basis of its similarity to DC of *Kennalestes*.

The first lower premolar (dp1 or p1), which usually is called dp1 in placentals except tapirs (see Simpson 1945), is a moderate-sized, completely erupted premolariform tooth; it is double-rooted and has a blade-like apex. A distinct, small heel cusp lies at the posterior end of the tooth. A sharp crest runs from the heel cusp all the way to the apex of the main cusp. Compared to its neighbors, the tooth leans somewhat lingually.

The second lower premolar (interpreted here as a p2 that did not displace the dp2 behind it during eruption; Luckett 1993) is a small, double-rooted tooth almost fully erupted on the animal's left side and incompletely erupted on the right side. Its morphology is generally similar to that of its neighbors, which tightly confine it. Full eruption of p2 and p3 would doubtless push dp2 out of the dentary. Posterior to p2 is a double-rooted, antepenultimate, lower premolar that we interpret as a non-shed dp2. This tooth formed and erupted behind, rather than above, p2. The posterior root of dp2 is

Table 3. Optical micrometer measurements (mm) of lower dentition of *Daulestes nessovi* sp. n., ZIN C. 79066, taken with Shopscopetm equipment. (AP, anterior-posterior).

Length (front dc – m2) projected on sagittal plane (estimated)	6.5
AP length right dc at alveolus, projected on sagittal plane	0.53
AP length left dc at alveolus, projected on sagittal plane	0.52
Width right dc at alveolus	0.33
Width left dc at alveolus	0.26
AP length right dp1 at alveolus, projected on sagittal plane	0.57
AP length left dp1 at alveolus, projected on sagittal plane	0.58
Width right dp1 at alveolus	0.28
Width left dp1 at alveolus	0.31
AP length right p2 at alveolus, projected on sagittal plane	0.47
AP length left p2 at alveolus, projected on sagittal plane	0.47
Width right p2 at alveolus	0.29
Width left p2 at alveolus	0.21
AP length right dp2 at alveolus, projected on sagittal plane	0.59
AP length left dp2 at alveolus, projected on sagittal plane	0.58
Width right dp2 at alveolus	0.31
Width left dp2 at alveolus	0.31
AP length incompletely erupted right p3, on angle, projected on sagittal plane	0.82
AP length left p3, on angle, projected on sagittal plane	0.72
Width, right p3	0.41
Width, left p3	0.45
AP max. length right dp4, paraconid to hypoconulid, projected on sagittal plane	1.06
AP max. length left dp4, paraconid to hypoconulid, projected on sagittal plane	1.09
Width trigonid right dp4	0.68
Width talonid right dp4	0.58
Width trigonid left dp4	0.65
Width talonid left dp4	0.58
AP max. length right m1, paraconid to hypoconulid, projected on sagittal plane	1.20
AP max. length left m1, paraconid to hypoconulid, projected on sagittal plane	1.21
Width trigonid right m1	0.79
Width talonid right m1	0.68
Width trigonid left m1	0.79
Width talonid left m1	0.68
AP max. length right m2, paraconid to hypoconulid, projected on sagittal plane	1.16
AP max. length left m2, paraconid to hypoconulid, projected on sagittal plane	1.14
Width trigonid right m2	0.80
Width talonid right m2	0.71
Width trigonid left m2	0.83
Width talonid left m2	0.68

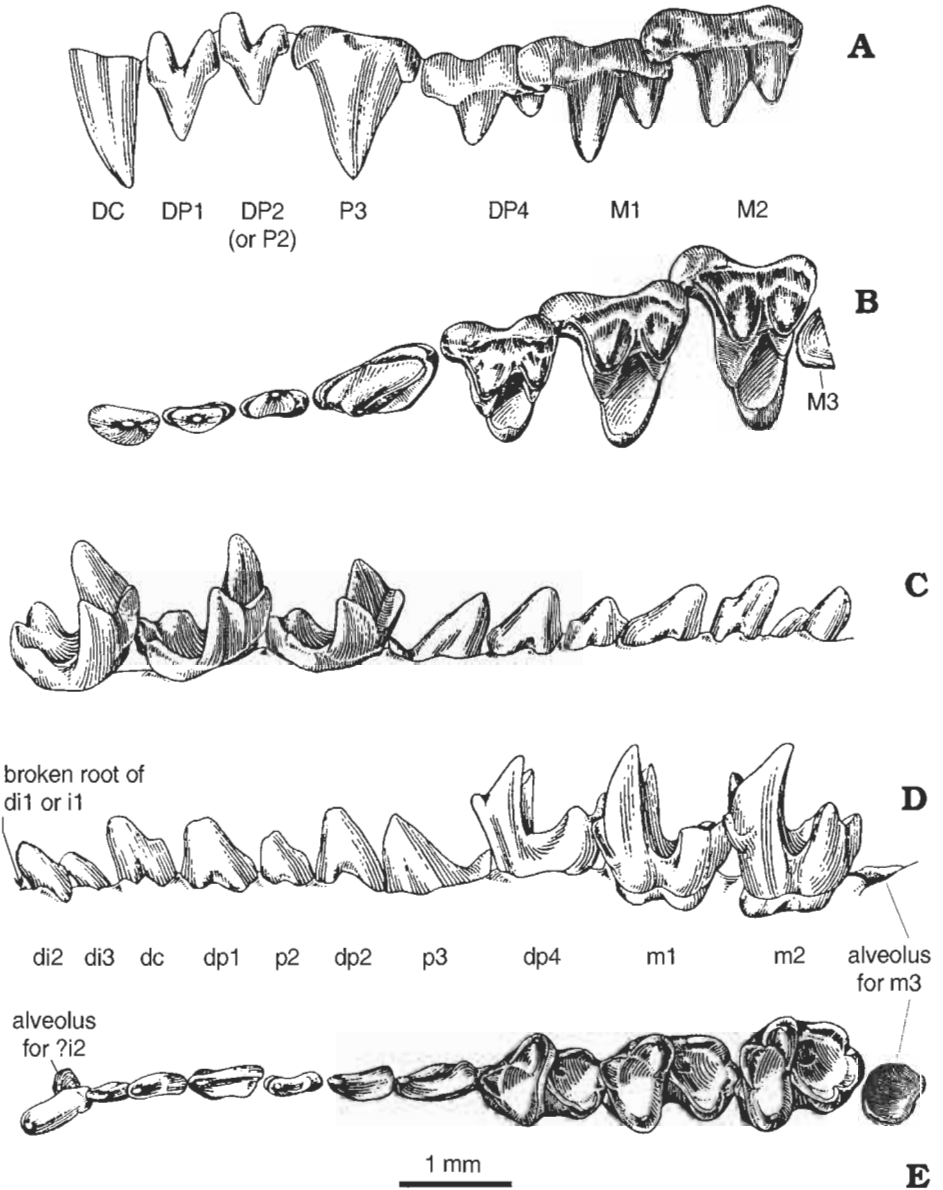


Fig. 16. Slightly diagrammatic drawing of the left upper and lower dentitions of *Daulestes nessovi* sp. n. (ZIN C. 79066). A, B. Upper dentition in lateral and occlusal views. C-E. Lower dentition in medial, lateral, and occlusal views.

noticeably larger than its anterior one. The crown of dp2 has a steeply rising anterior edge and a sloping posterior edge somewhat more blunt than is found in neighboring premolars. There is only a small posterobasal heel cusp (seen in buccal view).

On the right side, p1, p2 and dp2 appear heavily worn or broken; the latter interpretation is favored because the erupting p2 should not have extensive wear. The penulti-

mate lower premolar (p3) is incompletely erupted in both lower jaws. The talonid is below the alveolar margin in both rami. Had the animal lived longer, the tooth probably would have rotated somewhat more during the last stage of its emplacement. However, it is nearly in the position it would have had in an adult, but not yet so highly projecting. There is a single, high trigonid cusp, presumably the protoconid, without trace of either paraconid or metaconid. The crest leads from the protoconid apex posterolingually, ending at the trigonid base. A large, single, blade-like heel cusp projects strongly to the rear.

Four molariform lower teeth are indicated: dp4, m1, m2, and m3. Of these, the first three have erupted, whereas the last molar is represented only by a large dentary alveolus and fragmentary remains within the left alveolus. The size of the erupted teeth increases from dp4 through m2. If our assumption that M3 was reduced (see above) is true, one can presume that m3 might also have been relatively small. At least dp4, m1, and m2 are double-rooted, but the number of roots of the developing m3 is unknown.

The first molariform lower tooth is believed to be dp4. Although its wear does not show any significant difference from the molars, X-ray photography (not figured) reveals that the tooth has thinner enamel and more open roots than the molars. Moreover, a p4 germ is visible between the roots of dp4 within the dentary in a radiographic photograph. The dp4 has a more open trigonid than the succeeding teeth. Its paraconid juts forward as a short blade ending anterolingual to the protoconid, reaching approximately the mid-point of the anterior face of the trigonid. The protoconid is higher than the metaconid and those two cusps together form a high, nearly straight, posteriorly facing wall. On all molariform teeth, the three cusps of the talonid are symmetrically arranged (hypoconulid and entoconid are not twinned). On dp4 the entoconid is low and somewhat crested, the hypoconulid centrally located, the hypoconid the highest of the three cusps. A crest from the entoconid (entocristid) runs forward to the posterolingual margin of the rear wall of the trigonid. A crest from the hypoconid (cristid obliqua) reaches the central part of the base of the rear wall of the trigonid. Both of these crests, especially the cristid obliqua (better preserved in the left lower jaw) are rounded and wide rather than sharp, which is due to the youth of the individual and consequent lack of wear. Between the entocristid and cristid obliqua the talonid basin is a deep rounded depression; to the rear the talonid basin gradually raises. There are no cingulids, but a faint swelling may be seen along the buccal base of the paraconid.

The first lower molar has a more compressed trigonid than the preceding molariform tooth (dp4), with the metaconid less protruding posterodorsally. The talonid is wider, with a larger hypoconulid that points posterodorsally. A strong anterior cingulid rises steeply on the anterior slope of the protoconid, terminating at the boundary between the bases of the protoconid and the paraconid. Other details are essentially the same as in dp4.

The second lower molar has a somewhat compressed and recurved trigonid, with a blade-like paraconid more lingually placed than in the preceding molariform teeth, sharply delimiting a deep trigonid basin. The talonid is similar to that of m1, but the hypoconulid points dorsally rather than posterodorsally. An anterior cingulid like that of m1 is present. There is a faint trace of a posterobuccal cingulid below the hypoconid and hypoconulid.

Only a trace of the developing crown of m3 is preserved in the incompletely formed alveolus at the rear of the cheek-tooth row of the left dentary.

Upper dentition (Figs 4–6, 16A, B, 17, 19; Table 4). — Upper incisors are not preserved. However, they probably were numerous, judged from the lower dentition. The upper caniniform tooth (DC) is the most anterior tooth present, partly broken on the left side and originally completely preserved on the right side but now missing, only an alveolus being preserved. It is a projecting and canine-like tooth, oval in cross section and with a simple apex. We interpret it to be a fully erupted but not yet shed deciduous canine like that of a juvenile skull of *Kennalestes*, ZPAL MgMI/1 (Kielan-Jaworowska 1981), not an incompletely erupted replacement tooth. There apparently was a single root, as in ZPAL MgMI/1. The dorsal end of the root is bordered posteriorly by the maxilla, but it may have been bordered anteriorly either by the maxillary or by the missing premaxilla. If the caniniform tooth should prove to be a replacement tooth, its single root would be a profound difference from the double-rooted and shorter-crowned replacement upper canine of *Kennalestes*, *Asioryctes*, *Zalambdalestes* and other taxa with double-rooted permanent upper canine teeth. At the same time, a single-rooted upper permanent canine would be a similarity to *Hyotheridium*, *Ukhaatherium*, carnivores, creodonts, and cimolestids. However, the single-rooted condition observed in *Barunlestes* (Kielan-Jaworowska 1975a) is obviously convergent, associated with reduction of the anterior teeth other than the enlarged incisors.

Projecting less than the deciduous upper canine (or possibly its partly erupted replacement), the first tooth of the upper premolar series is double-rooted and somewhat elongate and laniate. It bears a high paracone, a faint indication of an anterobasal cusp, and a weak posterior basal swelling suggestive of a heel. The anterior surface of this premolar is slightly convex and oriented nearly vertically, whereas the posterior slope of the main cusp is more sloped. There is no indication of a replacement tooth within the maxilla dorsal to the roots. We identify the preserved tooth as the tooth usually called DP1 in placentals other than tapirs (Simpson 1945).

A double-rooted second premolar (DP2 or P2) is preserved on the right side of the skull but is missing on the left side, making a gap there that separates DP1 from P3. The right tooth is much lower and apparently more worn than the first premolar, and immediately follows it. The second premolar is essentially a small replica of the first, as in *Ukhaatherium* and *Asioryctes* but not *Kennalestes* (Novacek *et al.* 1997; Kielan-Jaworowska 1981).

P3 had almost completed its eruption in the right maxilla, but is somewhat less erupted on the left side of the skull. At this stage in ontogeny P3 lies anteroventral to the anterior opening of the infraorbital canal; its position when fully erupted may have shifted. Although primarily an anteroposteriorly trenchant tooth, P3 appears to have three roots: anterior, posterolingual, and posterobuccal. P3 is the highest upper cheek tooth. The crown is a very high, blade-like structure consisting of a paracone and its associated cutting edges. The anterior cutting edge is vertically oriented as a convex curve that joins a basal cusp anteriorly. A concave crest runs from the paracone apex posterodorsally to a point just lingual to a posterior basal heel cusp that appears to be supplied with short cingula extending a short distance forward along the lingual and buccal sides of the crown base. The posterior end of the lingual cingulum is slightly enlarged. There is no trace of a metacone on this tooth. P3 resembles the penultimate upper premolar of *Prokennalestes* in its stage of molarization, although in *Prokennalestes* the posterolingual cingulum is possibly slightly more prominent. It is less ad-

Table 4. Optical micrometer measurements (mm) of upper dentition of *Daulestes nessovi* sp. n., ZIN C. 79066, taken with Shopscope[™] equipment. (AP, anterior-posterior).

AP length DC at alveolus, projected on sagittal plane	0.45
Width right DC at alveolus	0.38
AP length right DP1, projected on sagittal plane	0.59
AP length left DP1, projected on sagittal plane	0.51
Width right DP1	0.27
Width left DP1	0.29
AP length right DP2 or P2, projected on sagittal plane	0.69
AP length left DP2 or P2, projected on sagittal plane	0.63
Width right DP2 or P2	0.24
Width left DP2 or P2	0.27
AP length right P3, parastyle to metastyle, on angle, projected on sagittal plane	1.05
AP length left P3, parastyle to metastyle, on angle, projected on sagittal plane	1.14
Width right P3, normal to sagittal plane	0.62
Width left P3, normal to sagittal plane	0.73
AP length right DP4, parastyle to metastyle, projected on sagittal plane	0.89
AP length left DP4, parastyle to metastyle, projected on sagittal plane	0.93
Width right DP4, normal to sagittal plane	1.14
Width left DP4, normal to sagittal plane	1.15
AP length right M1, parastyle to metastyle, projected on sagittal plane	1.17
AP length left M1, parastyle to metastyle, projected on sagittal plane	1.16
Width right M1, normal to sagittal plane	1.42
Width left M1, normal to sagittal plane	1.49
AP length right M2, parastyle to metastyle, projected on sagittal plane	1.15
AP length left M2, parastyle to metastyle, projected on sagittal plane	1.17
Width right M2, normal to sagittal plane	1.62
Width left M2, normal to sagittal plane	1.68

vanced in this respect than that of *Kennalestes*, in which P3 has a distinct heel. We have not seen any traces of root remnants of the shed DP3.

DP4 is the smallest of the erupted sequence of molariform teeth. A tooth germ representing P4 is present in the maxilla above it. DP4 is less transverse than the preserved molars but is by no means equilateral. As a molariform tooth, it bears a fully developed protocone, paracone and metacone, of which the high, somewhat forward-leaning paracone is the largest cusp. The metacone is present posterior to the paracone and is about half its height. The bases of the paracone and metacone are not conjoined, in contrast to M1. Extending along the anterior margin of the paracone is a narrow groove for reception of the protoconid of dp4. Anterior to the groove the tooth margin is



Fig. 17. SEM stereomicrograph of the right upper dentition, occlusal view, of *Daulestes nessovi* sp. n. (ZIN C. 79066).

incurved. A strong protocone lies lingually. The tooth has weakly developed winged conules, of which the paracone is larger and projects somewhat anterolingually. The paracone is connected by a short anterior cingulum to the parastylar area. The metacone is merely a swelling along the crest from the protocone apex to the posterolingual base of the metacone. The prominent parastylar projection incorporates a poorly developed parastyle and stylocone. The labial edge of the stylar shelf posterior to the stylocone is raised as a ridge and appears to bear two or more tiny cuspsules, the most posterior of which would be the metastyle. A ridge runs from the metastyle to the posterolabial side of the metacone, extending up to its apex. There are three roots.

M1 is triangular and is more transverse than DP4 but less so than M2. The high paracone dominates the much lower metacone and is basally conjoined with it. The paracone leans slightly forward and has a convex anterior surface and a concave crest-like posterior one continuous with the crest-like, transversely appressed metacone. The metacone is about half the height of the paracone. At the tooth's lingual apex the protocone is narrow and juts slightly forward, aligning with the paracone. A strong, winged paracone lies at the anterolingual base of the paracone and juts anteriorly. The metaconule is much smaller than the paracone, being a swelling along the crest

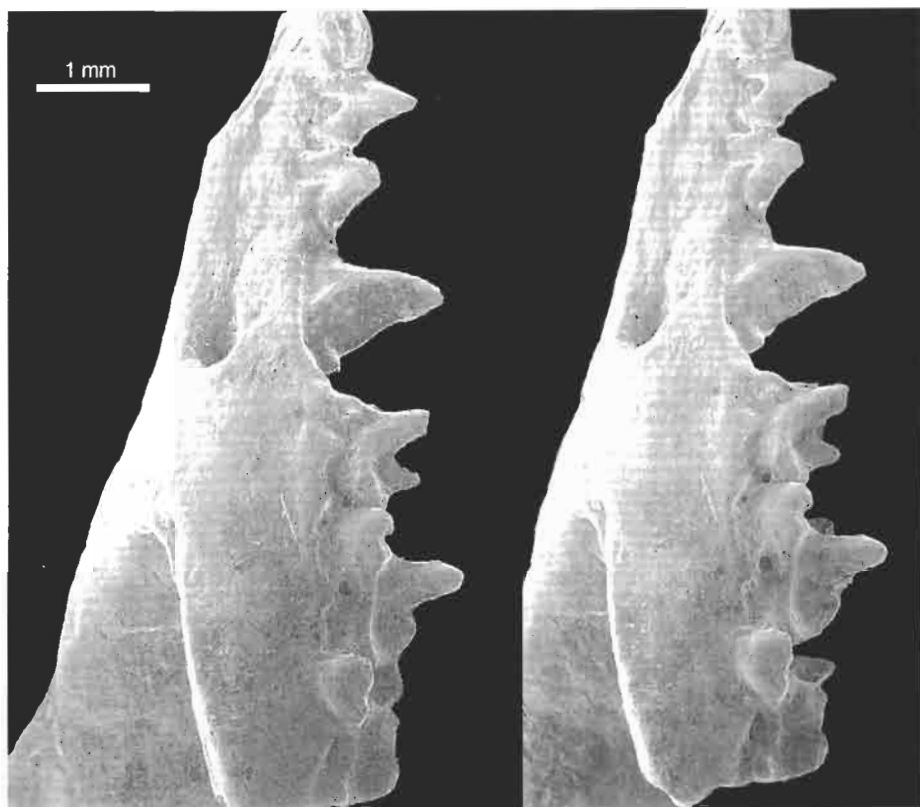


Fig. 18. SEM stereomicrograph of the right upper dentition, lateral view, of *Daulestes nessovi* sp. n. (ZIN C. 79066).

from the protocone to the posterior base of the metacone. The prominent antero-lingually placed paraconule and somewhat more posteriorly located metaconule are situated on the anterior and posterior edges of the trigon, respectively, with the deepest concavity of the trigon basin between them, in contrast to a more lingually placed trigon basin in many mammals. The parastylar wing juts sharply anteriorly from the anterolabial base of the paracone and bears a low parastyle and a low stylocone. In occlusal view the parastylar wing is partially hidden by the metastylar area of DP4, and therefore appears smaller than if viewed laterally. In lateral view, the parastyle protrudes slightly ventrally dorsal to the ventral margin of the parastylar wing, whereas the stylocone has an appearance of a rounded cusp. A crest (preparacrista) connects the paracone and stylocone. The groove for receiving the protoconid is wider than that of DP4. The ectoflexus is gently curved, being slightly shallower than on DP4 and much shallower than on M2. The metastylar wing is more prominent than on DP4 and bears several tiny cuspules at its raised buccal margin. A swelling extends between the parastylar and metastylar regions along the ectoflexus, at the end of which in the metastylar region small cuspules protrude slightly ventrally. Posterior and anterior cingula are not present. There are three roots.

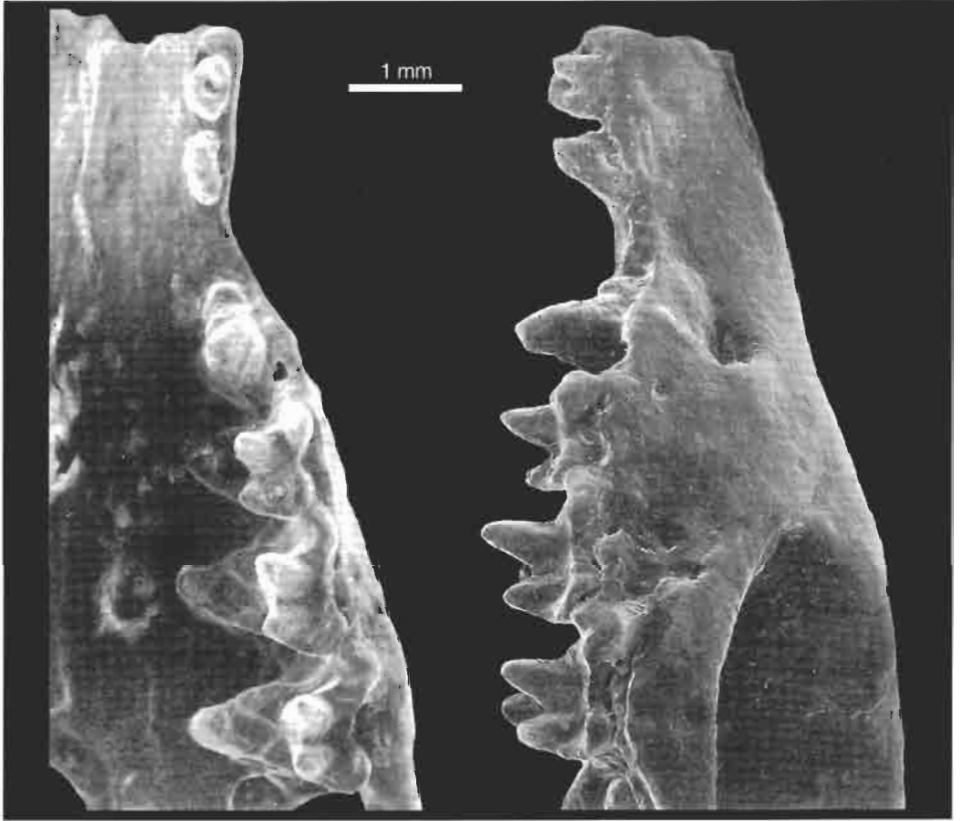


Fig. 19. SEM micrographs of the left upper dentition of *Daulestes nessovi* sp. n. (ZIN C. 79066). A. Occlusal view. B. Lateral view.

M2 is the widest of the erupted molariform series. It differs from M1 not only in proportions (see dimensions), but especially in having a strongly asymmetrical stylar shelf (see below). As on M1, the paracone and metacone are conjoined at their bases but each is slightly smaller than the corresponding cusp on M1. As on M1, the paracone leans anteriorly, whereas the smaller metacone points ventrally. The protocone is a high and piercing cusp, connected anteriorly by a low crest to a prominent paraconule, from which a preparaconule crista continues as the anterior edge of the tooth to the base of the parastyle. A postparaconule crista runs from the paraconule apex posterolabially toward the posterolingual base of the paracone. The winged paraconule is larger than the metaconule and, as on M1, the paraconule is more lingually placed, being closer to the protocone than to the paracone. Although occupying the anterior edge of the tooth, the paraconule projects less anteriorly than that of M1. The metaconule is a tiny cuspsule that lies along the postprotocrista from the protocone to the posterior base of the metacone; it is, however, V-shaped, with short conule crests. The parastylar region is very prominent and protrudes more labially than that of M1 so that the ectoflexus is deeper than on M1. In occlusal view the parastylar region is larger than that of M1, but appears slightly smaller in lateral view. It bears two cusps:

a more anterior and prominent parastyle and a barely developed stylocone, situated close to the ectoflexus. In occlusal view, the anterior margin of the parastyle is slightly obscured by the posterior margin of the metastylar area of M1, which erupted earlier. In lateral view, the stylocone is more rounded than on M1. The groove for the reception of the protoconid of m2 is similar to that of M1. Lingual to the parastyle, the anterior margin of the tooth is strongly incurved. Extending anterolabuccally from the anterobuccal side of the paracone to about the middle of the parastylar lobe, there is a weak crest. In contrast to the very prominent parastylar wing, the metastylar one is much less developed. The labial margin of the metastylar wing is gently rounded and only weakly protrudes labially. There is no metastylar cusp, but a ridge extends along the buccal margin of the metastylar shelf, bearing several poorly defined cusps, better seen on the left M2 than on the right one. The metacrista extends along the posterior margin of the tooth to the base of the metacone. In lateral view, the metacrista has the appearance of a tiny cuspsule.

The crown of M3, normally the last tooth erupted in the molariform sequence in placentals, is not preserved. Because of the immature stage represented by ZIN C. 79066, M3 simply was not yet fully formed and is poorly fossilized. There are, however, some clues about its size. Large parastylar and reduced metastylar wings of M2 occur in animals in which M3 is reduced or lost, so that M2 becomes M3-like (e.g. in *Deltatheroides*, see Kielan-Jaworowska 1975b: fig. 1). The difference in size of the parastylar and metastylar wings of M2 in *Daulestes* suggests reduction of M3. The preserved alveolus also suggests a reduced but still three-rooted M3. Traces of an apparently reduced, three-rooted tooth can be seen at the rear of the left maxillary plate (Figs 16B and 19).

Anatomical comparisons

Groove for internal carotid and stapedia arteries. — Early ideas of Gregory (1910), Matthew (1909), MacIntyre (1972), McKenna (1966), and others have been replaced by a concept that the promontory and ‘medial branch’ of the carotid artery (entocarotid artery) are one and the same (Presley 1979; MacPhee 1981; Wible 1987).

Conroy & Wible (1978: p. 84) cautioned that ‘measurements of the promontory canal in mammalian paleontological studies do not provide unequivocal evidence of the size or, indeed, the presence of the promontory artery in fossil forms’. In addition, presence of a stapedia foramen in the stapes does not necessarily imply presence of the stapedia artery, because the artery is absent in marsupials and some placentals in which a stapedia foramen persists (Bugge 1974; Wible 1987). Nonetheless, arteries are commonly reconstructed for fossils that have, or even lack sulci or grooves, as in *Probainognathus*, *Morganucodon*, multituberculates, *Vincelestes*, various eutherians, and the Khoobur (Khovboor) petrosal from the Early Cretaceous of Mongolia (Kielan-Jaworowska *et al.* 1986; Miao 1988; Luo 1989; Wible 1990; Rougier *et al.* 1992; Wible & Hopson 1995; Wible *et al.* 1995). Without a groove to dictate the course of a possible artery, reconstruction of the blood vessels becomes highly arbitrary, as shown, for instance, by three different patterns of the internal-stapedia arteries proposed for *Morganucodon* (Wible 1990: fig. 7A; Rougier *et al.* 1992: fig. 8B; Wible & Hopson 1995: fig. 6B). Given inferred soft structure to be unreliable as characters in

fossils, we adopt Cifelli's (1982) criterion that only grooves on the promontorium are counted as characters. Taxa bearing grooves on the promontorium, possibly for the internal carotid artery and/or stapedia artery, include multituberculates, *Vincelestes*, eutherians, and *Daulestes*. One petrosal of an unidentified tribosphenic therian possesses a groove similar to that of *Vincelestes* (Meng & Fox 1995a). The position of the groove for the promontory artery in *Daulestes* demonstrates, again, that the transpromontorial condition is primitive for placentals (Wible 1987).

Fenestra cochleae and aqueductus cochleae. — The fenestra cochleae ('fenestra rotunda', or 'round window') and aqueductus cochleae are structures related to the perilymphatic system of the inner ear, which functions as the route that channels fluid vibrations and releases pressure provided by sounds conducted to the petrosal by way of the stapes (Gray 1908; de Beer 1937; Wever 1978); therefore, they are important for hearing function. Meng & Fox (1995b) have summarized several features of this region typical for therian mammals: (1) merging of the perilymphatic recess with the basal part of the scala tympani within the petrosal (Gray 1908); (2) true fenestra cochleae and aqueductus cochleae resulting from development of the processus recessus (de Beer 1937; Zeller 1985a, b; Wible 1990); (3) distant separation of the fenestra cochleae and fenestra vestibuli by a bony bridge; and (4) the basal part of the secondary spiral lamina extends on the inner surface of the bony bridge between the two fenestrae, implying a basal elongation of the basilar membrane to this area.

In most nontherian mammaliaforms, such as Morganucodontids, multituberculates, and monotremes, the perilymphatic duct is not enclosed by a bony canal, but held by a narrow sulcus confluent with the lateral aperture of the perilymphatic recess (recessus scalae tympani; see Fox & Meng 1997, for review). The perilymphatic recess is a pouch medial (proximal) to the perilymphatic foramen, holding the perilymphatic sac, in nonmammalian amniotes and monotremes (Gray 1908; de Beer 1937; Wever 1978; Kuhn 1971; Zeller 1985a, 1985b, 1993). Such a pouch is present in multituberculates, illustrated by many (e.g., Kielan-Jaworowska *et al.* 1986; Luo 1989; Lillegraven & Hahn 1993; Wible & Hopson 1993, 1995), which is explicitly identified as the perilymphatic recess by Fox & Meng (1997). External to the recess in multituberculates is the opening, the lateral aperture of the perilymphatic recess, over which the secondary tympanic membrane is presumably stretched. Previously, the lateral aperture in nontherian mammaliaforms, except monotremes, was not recognized and the perilymphatic foramen was variably and incorrectly called 'fenestra cochleae', 'fenestra rotunda', or 'round window' (e.g., Kermack *et al.* 1981; Kielan-Jaworowska *et al.* 1986; Wible 1990, 1991; Lillegraven & Hahn 1993; Luo 1994; Luo *et al.* 1995; but see Wible & Hopson 1993). Neither the perilymphatic foramen nor the lateral aperture of the perilymphatic recess should be equated with the 'fenestra cochleae', 'fenestra rotunda', or 'round window', which are only correctly applied to the condition in which the aqueductus cochleae is formed. Coining the term 'processus recessus' to substitute Voit's (1909) 'processus intraperilymphaticus', de Beer (1929) rejected Gaupp's (1900) hypothesis that the fenestra cochleae (rotunda) and aqueductus cochleae are formed as subdivisions of the perilymphatic foramen; instead, de Beer (1937: p. 402) proposed that the secondary tympanic membrane stretches over the lateral aperture of the recessus scalae tympani, part of which becomes the fenestra co-

chleae. The lateral aperture, therefore, can be viewed as the progenitor for the fenestra cochleae.

In other than tribosphenic therians, a true fenestra cochleae (round window, fenestra rotunda) has been recorded in *Vincelestes* and the Khoobur petrosal from the Early Cretaceous of Mongolia (Rougier *et al.* 1992, 1996a; originally, a perilymphatic foramen was reported from the latter by Wible *et al.* 1995). Neither of these have a fully coiled cochlear canal (= a full turn of 360°). The fossil record shows that development of the fenestra cochleae and aqueductus cochleae occurred prior to the full coiling of the cochlear canal. Whether the secondary spiral lamina is developed in *Daulestes* is unknown, but it was coded for *Vincelestes* (Wible *et al.* 1995), of which the inner ear has yet to be described.

Curvature of cochlea. — In most reptiles, the cochlea (or its equivalent) is short and ventral to the vestibule (Miller 1966, 1968; Baird 1970a, b, 1974; Wever 1978; Lewis *et al.* 1985). The cochlear duct of a crocodile, among reptiles, is elongate (Manley 1970; Wever 1967, 1978) and bends anteroventrally (Baird 1970a, b: p. 260, fig. 27; Wever 1978). In birds, the cochlear duct is also elongate and bends medially, in a direction opposite to that of monotremes and therians (Pritchard 1881). In nonmammalian cynodonts, the cochlea is generally short and is anteroventral to the vestibule (Estes 1961; Quiroga 1979; Allin & Hopson 1992), with the exception of the reconstruction of a cynodont cochlea that is elongate and extends anteroventrally and then anteriorly (Simpson 1933). The cochlear canal of multituberculates is in a somewhat horizontal position and bent laterally in variable degrees (Simpson 1937; Luo & Ketten 1991; Fox & Meng 1997). Recent study (Fox & Meng 1997) demonstrates that the cochlear canals in monotremes curve around 180°, differing from the convention that the platypus has a cochlea with a 270° curvature; consequently, the monotreme condition is not significantly distinctive from that of multituberculates. In *Vincelestes* the cochlear canal curves about 270° (Rougier *et al.* 1992; Wible & Hopson 1993). The cochlear curvature in *Daulestes* is greater than that of monotremes, close to a full circle of coiling. Like the cochlear canal with a constant diameter throughout its entire length in monotremes (Gates *et al.* 1974), and like a petrosal of an unidentified tribosphenic therian (Meng & Fox 1995a), the cochlear canal of *Daulestes* does not taper, and has an expanded apex as in monotremes.

Ectotympanic. — Besides monotremes and therians, a fully suspended ectotympanic has been reported in multituberculates (Miao & Lillegraven 1986; Meng & Wyss 1995; Rougier *et al.* 1996b). The ectotympanic in multituberculates does not expand ventrally, differing from the condition in *Asioryctes* (Kielan-Jaworowska 1981) and *Daulestes*; however, it bears an internal groove for attachment of the tympanic membrane, as in extant mammals. The conditions in *Asioryctes* and *Daulestes* appear more derived than in multituberculates and didelphid marsupials in the ventral expansion of the ectotympanic, but a slender, ring-shaped ectotympanic is often found within eutherians, such as leptictids (Novacek 1986).

Malleus. — The malleus is nearly complete, the best preserved among known Cretaceous mammals. As in the case of the ectotympanic, the only non-monotreme, nontherian mammals in which the malleus is recorded are multituberculates (Miao &

Lillegraven 1986; Meng & Wyss 1995; Hurum *et al.* 1996; Rougier *et al.* 1996b). Again, the best morphology of the multituberculate malleus is from *Lambdopsalis*, in which the composite nature of the malleus – a combination of the articular, goniale, and prearticular (de Beer 1937; Allin & Hopson 1992) – is shown by presence of the foramen for the chorda tympani nerve in the massive anterior process (Meng & Wyss 1995). Although the condition of preservation impedes identification of this foramen in the malleus of *Daulestes*, we assume a composite malleus in *Daulestes*. One of the features that distinguish monotremes from therians is the dorsal placement of the incus: the articulation facet is on the dorsal side, at the anterior part of the body, of the malleus. A fossa at the same position in the malleus of *Lambdopsalis* suggested the dorsoventral incudo-malleus relationship in multituberculates (Meng & Wyss 1995, 1996), although this was questioned by Rougier *et al.* (1996b), based on a specimen (Miao & Lillegraven 1986) in which displacement was suspected. A detailed discussion concerning the shape and position of the malleus and incus in multituberculates was provided by Rougier *et al.* (1996b). In *Daulestes* the articulation of the incus and malleus is therian, demonstrated by a thickened articular area posterior to the body of the malleus.

Dentition. — Kielan-Jaworowska (1984c: p. 178) stated that: ‘...the Late Cretaceous Asian eutherian genera, although differing from each other in the coronal structure of the molars, are similar in the general appearance and organization of the dentition, when seen in lateral view. All have a strong double-rooted upper canine (secondarily single-rooted in *Barunlestes*), situated some distance to the rear of the premaxillary-maxillary suture, followed, after a short space, by small P1 and P2 that are double-rooted and do not come into occlusion with the lower premolars. In all genera P3 is the strongest tooth of the whole series, with a high, piercing paracone and P4 is semi-molariform.’

Daulestes shares with Mongolian Late Cretaceous eutherian genera *Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes* the above-described pattern of the premolar and molar sequence, but differs from adults of the first three genera in having a single-rooted upper canine as in *Hyotheridium* and *Ukhaatherium*. We believe, however, that the tooth at the canine locus of the juvenile skull of *Daulestes* is deciduous rather than permanent, and thus it is not excluded that the upper canine of adults could have been double-rooted. The situation would then be as has been demonstrated for juvenile vs. adult specimens of *Kennalestes* (Kielan-Jaworowska 1981). Because the permanent upper canine in *Daulestes* remains to be found, for the time being we tentatively accept that it was single-rooted. As in the other Mongolian Cretaceous genera mentioned, the upper deciduous canine of *Daulestes* could be some unknown distance behind the premaxillary-maxillary suture, but it could as well be bordered anteriorly by the now-missing premaxilla. Comparison with the Early Cretaceous Mongolian *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989; Sigogneau-Russell *et al.* 1992) cannot be made, because in *Prokennalestes* neither the upper canine nor its deciduous predecessor have yet been found.

The dentition of *Daulestes* shows a mixture of primitive and advanced characters. The lack of pre- and postcingula (shared with *Otlestes*, *Asioryctes*, *Ukhaatherium*, *Zalambdalestidae* and some *Palaeoryctidae*, *Cimolestidae*, and miscellaneous zalamb-

dodont mammals), the sequence of premolars and molars mentioned above (shared with *Prokennalestes* as well as the Mongolian Late Cretaceous genera), the possible (but uncertain) presence of four lower incisors, and perhaps the apparent presence of both dp2 and p2 in place at the same time (of indefinite duration), one in front of the other, are all primitive characters.

DP1 and the second upper premolar (DP2 or P2) in *Daulestes* are very similar to those of *Kennalestes* and *Asioryctes*, and do not come in contact with the lower premolars; the difference is that, in *Daulestes*, there is no diastema in front of DP1, or between DP1 and the second upper premolar, or between it and P3, although this may be the result of the relative youth of the new specimen, ZIN C. 79066. P3 of *Daulestes* resembles the penultimate upper premolar of *Prokennalestes* in its stage of molarization, although in *Prokennalestes* the posterolingual cingulum is possibly slightly more prominent. *Daulestes* is less advanced in this respect than *Kennalestes* or *Asioryctes*, wherein P3 is provided with a distinct heel. In Zalambdalestidae P3 is widely transverse and has developed a true protocone.

P4 in Mongolian Late Cretaceous genera and its equivalent, the last upper premolar in *Prokennalestes*, are semimolariform and transversely wide, but lack development of more than a trace of a metacone. In juvenile *Daulestes* DP4 is completely molariform. It is shorter than M1 or M2 and its metacone is well developed, although lower than the paracone. As we identify the last premolar of *Daulestes* as DP4, we are ignorant of whether its permanent successor is molariform.

Features of *Daulestes* that are advanced include the winged molar conules and a very special structure of the styler region, in which the metastylar projection is reduced as in *Asioryctes* (see Crompton & Kielan-Jaworowska 1978) and *Ukhaatherium* (Novacek *et al.* 1997), indicating an apparent reduction of M3.

Allocation to and within Eutheria

Allocation of *Daulestes* to Eutheria is supported by its dental formula and the general similarity to various Cretaceous basal eutherians. We do not compare *Daulestes* with metatherians or with the so-called 'tribotheres'. Butler (1978) proposed the infraclass Tribotheria for Albian tribosphenic mammals from Texas, but subsequently withdrew his infraclass (Butler 1990) and the group is now used informally. Some of the 'tribothere' genera, such as *Pappotherium*, *Holoclemensia*, *Kermackia* and *Slaughteria*, have been regarded by some authors as possible eutherians (see Marshall & Kielan-Jaworowska 1992, for summary), but we regard them as *Theria incertae sedis*.

Novacek (1986) made an attempt at the classification of higher categories of Recent and selected fossil eutherians, in which Cretaceous eutherians were not included. This was unfortunate, as his classification was subsequently used in current textbooks of vertebrate paleontology (e.g., Carroll 1988; Benton 1990). Moreover, the diagnosis of 'Eutheria' given by Novacek (1986, see also Novacek 1982) was based almost exclusively on soft anatomy and physiology appropriate for extant placentals. The only osteological characters given by him (1986: p. 81) were 'relatively narrow styler shelves on upper molars' (a vague diagnostic character) and 'epipubic bones absent'. Given that the majority of purported early placentals are known exclusively from teeth

or fragments of jaws with teeth, identification of them as belonging to eutherians using Novacek's (1986) definition is virtually impossible. The presence of epipubic bones is plesiomorphic for mammals (Lillegraven 1969). Epipubic bones are absent in all extant and post-Cretaceous eutherians, but do occur in zalambdalestids and *Ukhaatherium* (Novacek *et al.* 1997). Kielan-Jaworowska (1975c) first provided indirect evidence that they might have been present in the Late Cretaceous *Barunlestes*. They have been lost in later placentals, possibly in relation to the prolongation of the gestation period (Lillegraven 1969, 1975; Lillegraven *et al.* 1987).

An assignment of *Daulestes* to a known eutherian higher systematic category poses difficulties, as is the case with most Cretaceous eutherians. Nessov *et al.* (1994) assigned *Daulestes*, poorly known at that time, to Palaeoryctidae, while Nessov (1997: explanation to plate 48), identified CCMGE 1/12176 as 'Skull of a placental mammal, probably *Daulestes* sp. nov.' Kielan-Jaworowska (1981) assigned *Asioryctes* (placed in her new subfamily Asioryctinae) to Palaeoryctidae. This assignment, accepted by Thewissen & Gingerich (1989), was rejected by McKenna & Bell (1997). McKenna & Bell placed Palaeoryctidae in magnorder Epitheria, grandorder Ferae, order Cimolestia. The only Late Cretaceous cimolestean recognized by these authors is *Cimolestes*, assigned to the Didelphodontidae, classified earlier as a didelphodontine palaeoryctid (e.g., Lillegraven 1969; Clemens 1973; Fox 1984, 1989). McKenna & Bell (1997) did not use Asioryctinae and assigned *Asioryctes* to magnorder Epitheria, without further qualification. Novacek *et al.* (1997) erected Asioryctitheria (no systematic rank), into which they placed Asioryctidae Kielan-Jaworowska, 1981 (assigning family rank to it). Characters used to diagnose asioryctitherians include (1) a tall, curved crista interfenestralis that links the paroccipital process to the promontorium; (2) a strong entoglenoid process; and (3) a postglenoid foramen that opens inside the glenoid area. Novacek *et al.* (1997) attributed to Asioryctidae two genera, *Asioryctes* and *Ukhaatherium*, the latter genus only preliminarily described.

Daulestes is similar to the asioryctid genera *Asioryctes* and *Ukhaatherium* in both the dentition and skull structure (the latter described fully only in *Asioryctes*). *Daulestes* shares with asioryctid genera postcanine dental formula (the number of incisors is unknown) and reduced metastylar projection on the molars. It shares with *Ukhaatherium* a single-rooted upper canine (as here interpreted; double-rooted in *Asioryctes*), lack of pre- and postcingula, winged conules, and an enlarged parastylar region. It differs from both genera in having upper molars wider antero-posteriorly and less elongated transversely, with a well-developed metaconule, which disappeared in *Asioryctes* (Crompton & Kielan-Jaworowska 1978); *Asioryctes* is highly specialized in this respect. *Daulestes* differs further from both genera in having a less molarized P3, without even an incipient protocone, and an apparently less molarized p3.

The snout is similarly shaped in *Daulestes* and *Asioryctes*, and the arrangement of bones, as far as can be reconstructed, is similar. The lacrimal is poorly preserved in *Asioryctes*, but, as stated by Kielan-Jaworowska (1984: p. 30) 'The lacrimal is provided by a facial wing, probably pointed anteriorly...', which is also the case in *Daulestes*. There is a postpalatine torus in both, and a postpalatine foramen, developed in *Asioryctes* as a notch. The braincase (incomplete in *Daulestes*) is generally similar to that of *Asioryctes*, although the mesocranial region, very long in *Asioryctes*, is relatively shorter in *Daulestes*. The shortening concerns in particular the size of the

presphenoid and orbitosphenoid, which are relatively smaller in *Daulestes* (a juvenile character?). The alisphenoid has a thickened anterior margin in both genera and overhangs ventrally the smaller orbitosphenoid. There are four foramina in this region in both genera, the difference being that the sinus canal foramen in *Asioryctes* (Kielan-Jaworowska 1984) is placed more dorsally, and is clearly separated from the sphen-orbital fissure, while in *Daulestes* these foramina are hardly separated (possibly due to damage). The optic foramen is placed low in the orbitosphenoid in both genera. The ethmoid foramen is more obvious in *Asioryctes*, but is recognizable on the left side of the skull in *Daulestes*. The difference between *Asioryctes* and *Daulestes* concerns the apparent lack of the pterygoid process of the sphenoid in *Daulestes*, which, however, may be easily lost in fossilization, and its lack may be due to the state of preservation. The structure of the postglenoid process and arrangement of vascular foramina in the squamosal is similar, but not identical, in both genera. The promontorium is very large in both, but possibly more horizontally arranged in *Daulestes*. The ectotympanic is horseshoe-shaped in *Asioryctes* and U-shaped in *Daulestes*, which, however, may be a juvenile character in the latter.

The relationships between *Daulestes*, *Asioryctes*, and *Ukhaatherium* on the one hand, and Palaeoryctidae, on the other, cannot be demonstrated (*contra* Kielan-Jaworowska 1981). Asioryctidae and Palaeoryctidae resemble one another in having upper molars very narrow and strongly elongated transversely (the transverse elongation is less strongly pronounced in *Daulestes*); all have an enlarged parastylar region. They differ in having differently shaped lower molars and premolars and differ in dental formulae (four premolars in Asioryctidae, three in Palaeoryctidae). The similarity of *Daulestes* and Palaeoryctidae is that, in both, i_2 is larger than i_3 (in *Daulestes* possibly di_2 and di_3), which is not the case in Asioryctidae. The most dramatic difference concerns the skull structure (see Thewissen & Gingerich 1989 and references therein, for description of palaeoryctid taxa). In Palaeoryctidae, in contrast to Asioryctidae, the mesocranial region is very short, there is no Vidian foramen, no sphenorbital fissure, the optic foramen is placed far anteriorly, and there is an alar canal. In Palaeoryctidae the glenoid fossa is placed much more anteriorly with respect to the promontorium than in *Asioryctes* and *Daulestes*, and the whole basicranial region has a very different structure. In view of these differences it seems reasonable to presume that the similarities in upper molar structure of Asioryctidae and Palaeoryctidae are due to convergence, rather than relationship.

Another early eutherian that invites comparison with *Daulestes* is the Early Cretaceous *Prokennalestes* Kielan-Jaworowska & Dashzeveg, 1989 (see also Sigogneau-Russell *et al.* 1992). *Prokennalestes* has been assigned by Kielan-Jaworowska & Dashzeveg (1989) to the paraphyletic order Proteutheria, superfamily Kennalestoidea, family Otlestidae, but by Sigogneau *et al.* (1992) to Eutheria *incertae sedis*. The order Proteutheria was erected by Romer (1966) to include *incertae sedis* eutherians then known from the Early Cretaceous, as well as non-lipotyphlan Cretaceous and Tertiary insectivorous mammals grouped into the Leptictoidea and Apatemyoidea. Butler (1972) recommended use of Proteutheria, but pointed out its waste-basket nature; he stated (p. 264): 'Further research should reduce the size of the Proteutheria, by discovering the relationships of some of its groups to other orders, and possibly by making new orders out of other groups.' Many authors assigned Cretaceous or early Tertiary genera to Proteutheria (see e.g., Lillegraven *et al.* 1979 and references therein). McKenna & Bell (1997) arbitrarily as-

signed *Prokennalestes* and *Kennalestes* to Gypsonictopidae within the superorder Leptictida. However, *Kennalestes* differs from other Leptictida (McKenna 1975; Novacek 1986) in the lack of an entotympanic bulla and alisphenoid canal.

The skull and complete dental formula of *Prokennalestes* are unknown. *Daulestes* shares with *Prokennalestes* a plesiomorphic lack of pre- and postcingula, but differs in having four premolars (five in *Prokennalestes*), different structure of the upper molars with reduced metastylar region (not reduced in *Prokennalestes*), winged conules, di2 or i2 larger than di3 or i3 (subequal in *Prokennalestes*), paraconid and metaconid higher with respect to protoconid, and lack of single labial mandibular foramen.

Among Cretaceous eutherians, the skull is also known in *Kennalestes* and Zalambdalestidae. *Kennalestes* is known from an almost complete dentition, in which only the number of incisors is uncertain (Kielan-Jaworowska 1969, 1981). *Daulestes* differs from *Kennalestes* in having upper molars without pre- and postcingula, with reduced metastylar region, and possibly a single-rooted upper canine. The basicranial region in *Kennalestes* (less completely preserved than in *Asioryctes*) differs from *Daulestes* in the presence of an extensive pterygoid process of the sphenoid and in having the sphenoid wing (referred to by Kielan-Jaworowska as a basisphenoid wing) in the form of a fossa, which, however, may be an artifact of preservation. Kielan-Jaworowska (1981) reconstructed the lateral wall of the braincase in *Kennalestes* on the *Asioryctes* pattern, but the homology of some details is not certain.

Daulestes shares with Zalambdalestidae the plesiomorphic lack of pre- and postcingula on the upper molars, but differs in the otherwise very different structure of the dentition and skull. The differences are: larger stylar shelf on the upper molars in *Daulestes* than in Zalambdalestidae, strongly reduced metastylar region (especially on M2), paracone and metacone relatively higher and placed more lingually, and more prominent and more lingually placed conules. P3 of *Daulestes* is less molarized than in Zalambdalestidae, without a spur-like protocone. *Daulestes* differs from *Zalambdalestes* probably in having a single-rooted upper canine and, if so, is convergent in this character with *Barunlestes*. The lower molars are very differently shaped than in Zalambdalestidae, having a greater difference in height between the trigonid and talonid. Further, *Daulestes* differs from Zalambdalestidae in the lack of enlarged, procumbent anterior lower incisor, lack of labial mandibular foramen, and lack of a strongly elongated snout. In braincase structure the differences are dramatic and concern the lack of the pterygoid process of the sphenoid in *Daulestes*, presence of the Vidian foramen, lack of a separate foramen rotundum, relatively larger alisphenoid and orbitosphenoid, different distribution of alisphenoid/orbitosphenoid foramina and different pattern of other characters of the basicranial region (Kielan-Jaworowska 1969, 1984c; Kielan-Jaworowska & Trofimov 1980). McKenna & Bell (1997) assigned Zalambdalestidae to the grandorder Anagalida in the superorder Preptotheria McKenna, 1975.

Finally, a remarkably diversified eutherian clade that made its appearance in the Late Cretaceous comprises insectivorans, formally classified as Lipotyphla (see Butler 1956, 1988; McDowell 1958; Novacek 1986; MacPhee & Novacek 1993). McKenna & Bell (1997) assigned three Late Cretaceous genera (known only from teeth and dentaries) to Lipotyphla. These are:

(1) *Batodon*, which was usually assigned together with *Cimolestes* to Didelphodontinae in Palaeoryctidae (e.g., Lillegraven 1969; Clemens 1973; Archibald 1982;

Fox 1984; see also cladograms in Nessov *et al.* 1998: fig. 24). Poorly known upper molars of *Batodon* are of *Cimolestes* pattern and do not resemble those of *Daulestes*, being more elongated transversely, having pre- and postcingula, less prominent conules, and smaller styler region without a reduced metastylar part.

(2) *Otlestes* (see Nessov 1985a, 1997; Nessov *et al.* 1994); Kielan-Jaworowska & Dashzeveg (1989) assigned *Otlestes* and *Prokennalestes* to the Otlestidae Nessov, 1985a, but some of the characters that unite the two genera are plesiomorphies (see comparison of *Daulestes* with *Prokennalestes* above).

(3) *Paranyctoides* (Fox 1979, 1984; Lillegraven & McKenna 1986; Cifelli 1990) was for a long time regarded as the oldest North American eutherian mammal, but see Cifelli (1999); it shows unequivocal lipotyphlan affinities (family ?Nyctitheriidae). *Daulestes* differs from *Paranyctoides* in lacking pre- and postcingula and in having asymmetry of the styler region, a smaller ectoflexus, trigon basin more elongated transversely, and generally more gracile structure of the upper molars. On lower molars the main difference concerns the position of the paraconid, which in *Daulestes* is shifted from the lingual side anteriorly and placed symmetrically between the protoconid and metaconid.

Taking into account the characters of advanced lipotyphlans, *Daulestes* cannot be assigned to this group because it has a long jugal largely contributing to the lower edge of the orbit, a long infraorbital canal (but see McKenna & Simpson 1959), a palatine contributing to the orbital wall, contacting the lacrimal, and a true postglenoid process. We are aware of the caution of MacPhee & Novacek (1993) that, out of a suite of lipotyphlan characters given by Butler (1988), only two (hindgut simplification with correlated absence of cecum, and pronounced reduction of the pubic symphysis) are strong synapomorphies of Lipotyphla. However, neither of them can be applied for *Daulestes*.

We believe that the anatomy of the skull is more conservative and better reflects the affinities of mammalian taxa than the dentition, which easily changes with demands of the environment. In that we lack knowledge on skull structure of most Cretaceous mammals, conclusions on their relationships are often based on the dentition only. *Daulestes*, however, is represented by a large part of the skull, although it is immature. Comparison with other Cretaceous mammals in which skull has been preserved shows close similarity of the skull design of *Daulestes* to that of *Asioryctes*, more so than to *Kennalestes*, and very different from Zalambdalestidae. The skull similarities are also strongly supported by similarities in the dentition. The foregoing comparisons show that, of known Cretaceous Eutheria, *Daulestes* is most similar to *Asioryctes* and *Ukhaatherium*. We refrain from creating a separate family for *Daulestes*. Because of similarities and differences with Asioryctidae we assign *Daulestes* tentatively to Asioryctitheria Novacek *et al.*, 1997, family *incertae sedis*. *Daulestes* appears to belong to the asioryctitherian stem-group.

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Najstarsza czaszka ssaka łożyskowego z późnej kredy (koniaku) Uzbekistanu

MALCOLM C. MCKENNA, ZOFIA KIELAN-JAWOROWSKA i JIN MENG

Streszczenie

W pracy opisano częściowo uszkodzoną czaszkę młodego osobnika określonego jako *Daulestes nessovi* sp. n. z koniaku Uzbekistanu. Jest to najwcześniejsza czaszka ssaka łożyskowego, licząca ok. 87 milionów lat. *Daulestes* jest szóstym rodzajem kredowego ssaka łożyskowego, którego czaszka jest znana. Ponieważ czaszka *D. nessovi* należy do młodocianego osobnika, niektóre cechy plezjomorficzne mogą być związane z wczesnym stadium rozwojowym. W czaszce występują cztery górne przedtrzonowce i pięć dolnych, jest jednak możliwe, że w stadium dorosłym dolnych było też tylko cztery. Na górnych zębach policzkowych występują konule ze skrzydełkami. Na M2 wyrostek parastylarny jest duży, metastylarny – mały. Pre- i postcingula nie występują na mlecznym czwartym przedtrzonowcu ani na trzonowcach. Talonidy dp4–m2 mierzą ok. 90 % szerokości trygonidów, a entokonidy są oddalone od hipokonulidów. W czaszce występuje duża szczelina klinowo-oczodołowa i zapewne brak wyrostka skrzydłowego kości klinowej. Duże skrzydło oczodołowe kości podniebiennej powoduje, że brak jest kontaktu między szczęką a kością oczodołową w obrębie oczodołu. Wyrostek jarzmowy jest delikatny. Błędnik ma jeden pełny skręt z rozszerzonym wierzchołkiem, co może wskazywać na obecność lageny. Duży młoteczek z silnym wyrostkiem przednim oraz duże promontorium mogą być związane z młodym wiekiem osobnika lub zachowaniem cechy plezjomorficznej (jak u dziobaka). W związku z podobieństwem do Asioryctidae zarówno w budowie czaszki, jak i uzębienia, *Daulestes* został zaliczony do Asioryctitheria Novacek *et al.* 1997, rodzina *incertae sedis*.