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CATOPSALIS (MULTITUBERCULATA) FROM ASIA AND NORTH AMERICA AND THE PROBLEM OF TAENIOLABIDID DISPERSAL IN THE LATE CRETACEOUS

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Djadochtatherium Simpson, 1925 is a junior synonym of *Catopsalis* Cope, 1882. Known species of *Catopsalis* (*Djadochtatherium* included) form a morphological sequence, beginning with Asian ?Late Santonian and/or Early Campanian *C.matthewi*, and ?Middle Campanian *C.catopsaloides*, through the following North American species: Late Maastrichtian *C.joyneri*, Paleocene *C.foliatus*, *C.utahensis*, *C.fissidens* and *C.calgariensis*. Morphological changes involved an increase in size, a reduction of the number of upper premolars, relative reduction of the size of the lower fourth premolars, and an increase of the number of cusps on the molars. It is believed that *Catopsalis*, and possibly the family Taeniolabididae originated in Asia, developed there during the ?Late Santonian — ?Middle Campanian and spread to North America during the Late Campanian or Early Maastrichtian.

Key words: Cretaceous, migrations, Multituberculata, Paleocene, Taeniolabididae.

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INTRODUCTION

The genus *Catopsalis* was erected by Cope in 1882 for *C. foliatus* from the Lower Paleocene of New Mexico (Cope 1882, 1885, Granger and Simpson 1929, Matthew 1937). *C.foliatus* was based upon a fragmentary mandible with P₄, M₁ and M₂.

Until 1965 *Catopsalis* was known only from the Paleocene rocks of North America, where it is represented by four species: *C.foliatus* Cope from the Puercan (Lower Paleocene), *C.utahensis* Gazin from the Upper

Puercan and Lower Torejonnian (Middle Paleocene), *C.fissidens* Cope from the Torejonnian and *C.calgariensis* Russell from the Tiffanian (Upper Paleocene) — see Gazin (1939, 1941), Russell (1926), Simpson (1927), Granger and Simpson (1929), Van Valen and Sloan (1966). Sloan and Van Valen (1965) described *C.joyneri* from the Late Maastrichtian Hell Creek Formation of Montana.

Simpson (1925) erected genus *Djadochtatherium* for *D.matthewi* from the Djadokhta Formation of Mongolia, currently believed to be of ?Late Santonian and/or ?Early Campanian age (Gradziński *et al.* 1977). *D.matthewi* was based upon a partial skull with incomplete upper dentition associated with both mandibles and an incomplete postcranial skeleton (Simpson 1928, McKenna 1961). Simpson (1926) suggested that *Djadochtatherium* should be placed in a family of its own, but did not erect it. Sloan and Van Valen (1965) suggested assignment of *Djadochtatherium* to the Eucosmodontidae. Kielan-Jaworowska (1974a) described *D.catopsaloides* from the ?Middle Campanian Barun Goyot Formation of Mongolia and assigned *Djadochtatherium* to the Taeniolabididae. She stated (1974:42): "... it is very probable that *D.catopsaloides* is an ancestor of *C.joyneri*, or it is very close to the form that gave rise to *Catopsalis*".

Comparison of all known Asian and North American species of *Djadochtatherium* and *Catopsalis* led us to the conclusion that the two genera do not differ at the generic level.

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Abbreviations used:

AMNH The American Museum of Natural History, New York.

UCM Museum of Colorado University, Boulder.

ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

DESCRIPTION

Family Taeniolabididae Granger and Simpson, 1929

Genus *Catopsalis* Cope, 1882

(Synonym: *Djadochtatherium* Simpson, 1925)

(figs. 1—3)

Revised diagnosis. — Medium sized to large taeniolabidids, length of the skull varying from 5 cm to ca. 14 cm (estimated from the size of the molars). Snout roughly triangular, truncated; zygomatic arches confluent with lateral margins of

Table 1

Comparison of known species of *Catopsalis* Cope

Species	<i>C. matthewi</i> (Simpson, 1925)	<i>C. catopsaloides</i> (Kielan-Jaworowska 1974)	<i>C. joyneri</i> Sloan and Van Valen, 1965	<i>C. foliatus</i> Cope, 1882	<i>C. utahensis</i> Gazin, 1939	<i>C. fissidens</i> Cope, 1884	<i>C. calgariensis</i> Russell, 1926
Geographical distribution	Asia	Asia	N. America	N. America	N. America	N. America	N. America
Stratigraphical range	Djadokhta Fm. ?Late Santonian and/or Early Campanian	Barun Goyot Fm. ?Middle Campanian	Hell Greek Fm. Late Maastrichtian	Puercan Early Paleocene	Upper Puercan and Lower Torrejonian late Early Paleocene and Early Middle Paleocene	Torrejonian Middle Paleocene	Tiffanian Late Paleocene
Number of upper premolars	3	2	unknown	unknown	unknown	unknown	unknown
P ₃	present	present	unknown	absent	unknown	unknown	unknown
P ⁴ — length and cusp formula	unknown	3.8 mm 5:1	3.3 mm 1:5:1	unknown	unknown	unknown	unknown
M ¹ — length and cusp formula	unknown	6.1 mm 5—6:5—6:4	8.1 mm 7:8:8	unknown	unknown	unknown	unknown
M ² — length and cusp formula	unknown	3.6 mm 2:2—3:2—3	5.2 mm 1:3:3	unknown	unknown	unknown	unknown
P ₄ — shape, length and number of cusps	roughly parabolic 3.2 mm long 4 cusps	roughly parabolic 3.8 mm long 3 cusps	triangular, truncated 3.2 mm long 3 cusps	triangular 3.5—74.2 mm long, 2—3 cusps	unknown	unknown, alveolus present	unknown
M ₁ — length and cusp formula	4.7 mm 4:4	6.1 mm 4:4	7.0 mm 5:4	?8.2—10.7 mm 5:4	12—13 mm 6—7:5	14 mm 6:5	unknown
M ₂ — length and cusp formula	unknown	3.6 mm 2:2	5.5 mm 3:2	?6—6.6 mm 4:2—3	unknown	9.2 mm 3:2 accessory internal row of cusps present	9.2 mm 3:2 no internal accessory row of cusps

Remark: Question marks at some measurements of *C. foliatus* indicate doubts concerning the identification of UCM 34979 as *C. foliatus*.

the snout. Premaxilla with long nasal process, maxilla long, orbit in dorsal view comparatively small, situated far posteriorly. In ventral view the anterior margin of the zygomatic arch poorly defined, the posterior margin situated opposite the P^4-M^1 embrasure. Infraorbital foramen rounded, opposite the P^3-P^4 embrasure. Post-orbital process very long, peg-like. Frontals rounded posteriorly. Glenoid fossa more square than oval. Mandible strongly elongated, coronoid crest prominent, masseteric crest weak. Enamel on upper and lower incisors sharply limited. Upper dentition is known only in Cretaceous species. P_3 present until Campanian, absent in Maastrichtian and Paleocene. Fourth upper and lower premolars small. P_4 roughly rectangular in older forms, becoming triangular and relatively smaller in Maastrichtian and Early Paleocene, probably disappearing in the Late Paleocene. Molars large, increasing in size through time coeval with an increase in the number of cusps.

Species assigned — See Table I.

Stratigraphical and geographical range. — ?Late Santonian-?Middle Campanian of Asia, Late Maastrichtian and Paleocene of North America.

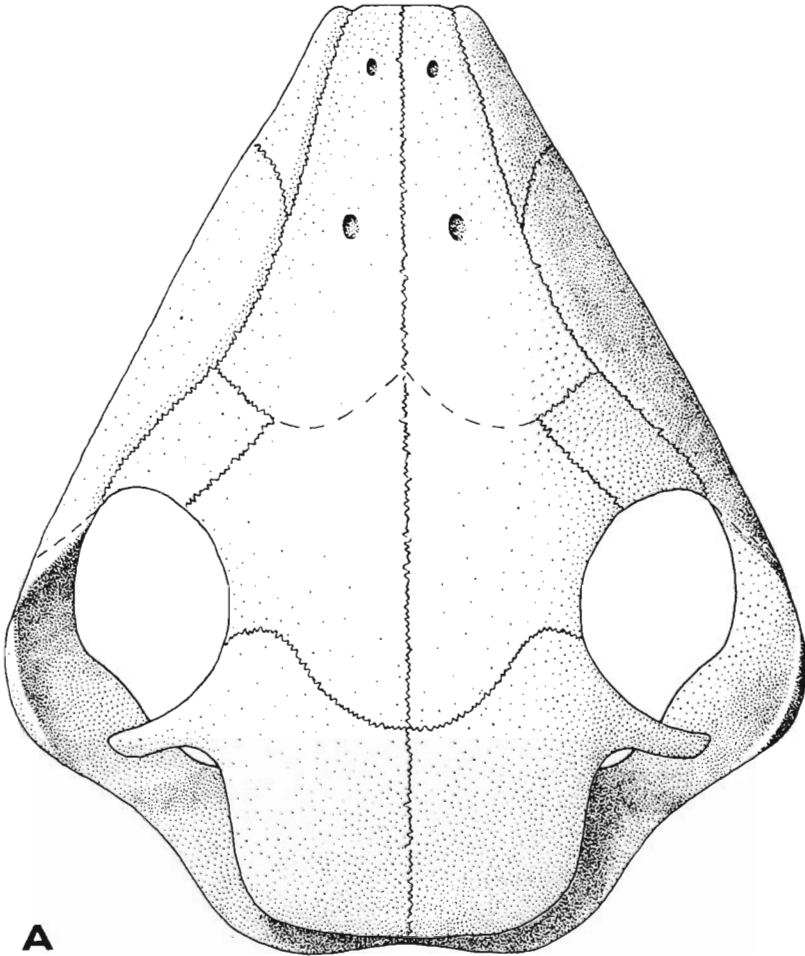
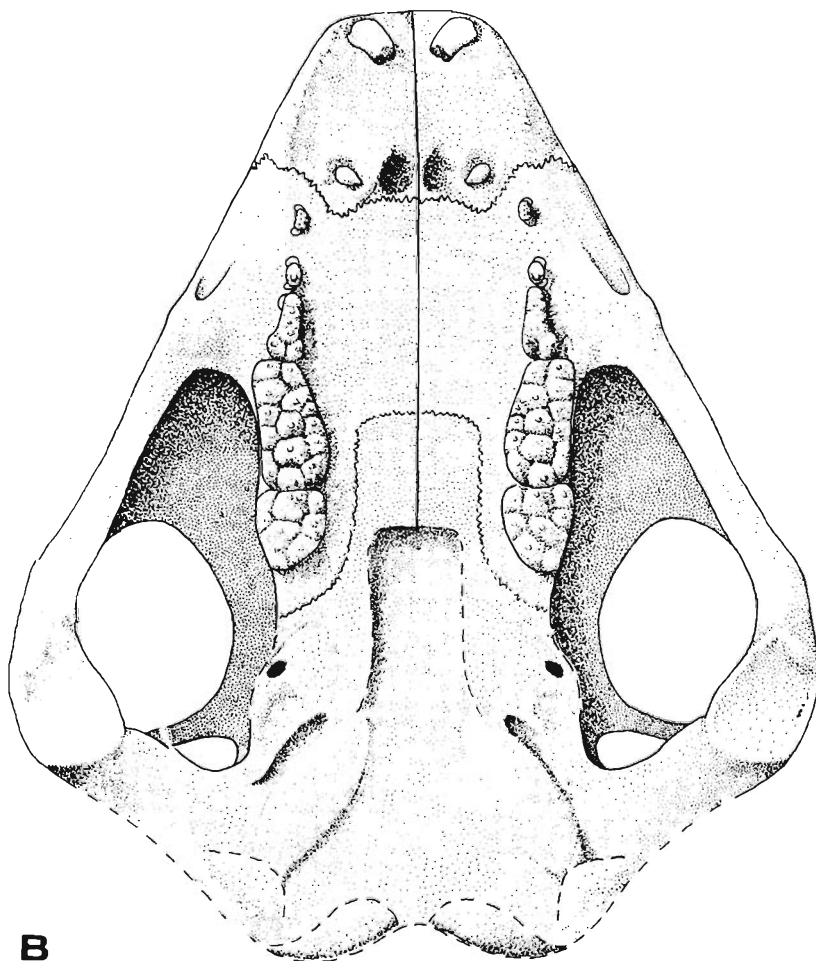
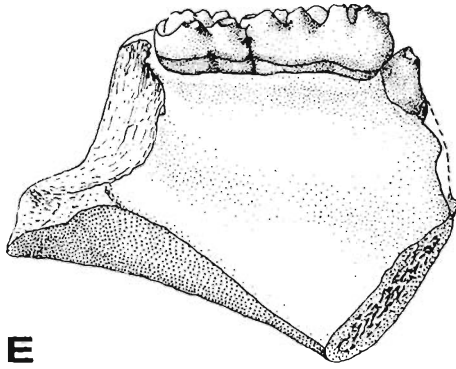


Fig. 1. *Catopsalis catopsaloides* Kielan-Jaworowska, reconstruction of the skull based upon ZPAL MgM-I/78, ZPAL MgM-I/79 and ZPAL MgM-I/80. A dorsal view, B ventral view, $\times 2$.

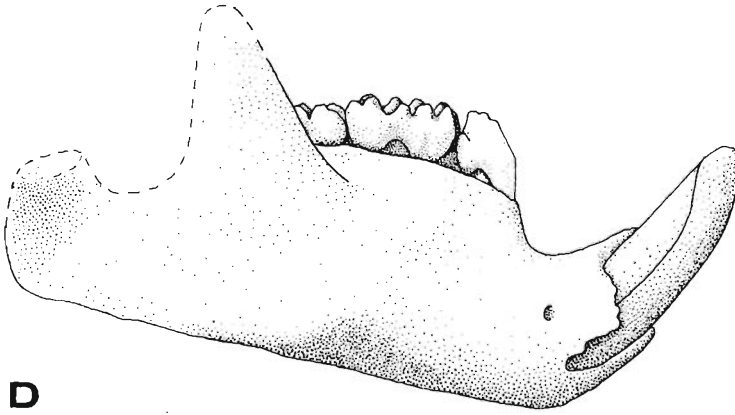
DISCUSSION

It follows from the data presented in Table I that known species of *Catopsalis* constitute a sequence of morphological changes, which vaguely corresponds to their stratigraphical range. *Catopsalis* makes its appearance in ?Late Santonian and/or Early Campanian of Mongolia (*C.matthewi*), continues in the ?Middle Campanian of Mongolia (*C.catopsaloides*) and then passes to North America, where it makes its appearance of the first time in the Late Maastrichtian Hell Creek Formation (*C.joyneri*). It is important to note that *Catopsalis* is unknown in the Campanian and Early Maastrichtian formations of North America where other multituberculate genera are fairly common (Clemens 1963, Lillegraven 1969, Sahni 1972),

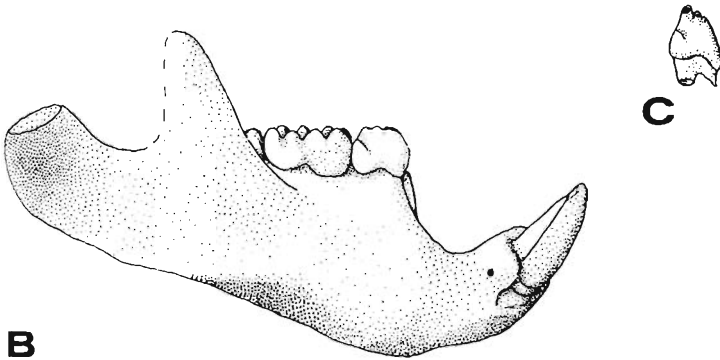
**B**



E

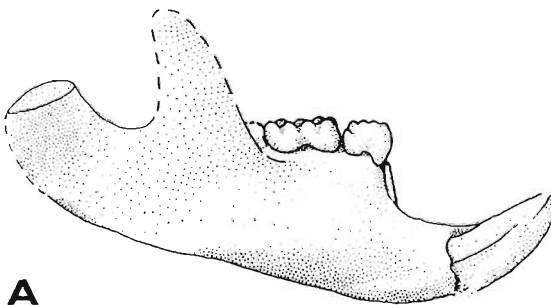


D



C

B



A

Fox 1971 and 1972). Beginning with Late Maastrichtian *Catopsalis* continues in North America in Lower, Middle and Upper Paleocene rocks, where it is, however, rare. The earliest known North American representative of *Catopsalis* (*C. joyneri*) is known from fragments of skulls and almost complete upper and lower dentition. Four North American Paleocene species are known only from lower dentition, sometimes from isolated lower molars. In spite of the scarcity of Paleocene material of *Catopsalis* there are no doubts that the above discussed Paleocene species are congeneric with Cretaceous Asian and North American representatives of *Catopsalis*.

It is interesting to note that *Catopsalis* has not been reported from the Paleocene of Asia. However, until now only two monotypic Asian Paleocene genera *Prionessus* and *Sphenopsalis* are known (Matthew and Granger 1925, Matthew *et al.*, 1928, Granger and Simpson, 1929). *Prionessus lucifer* Matthew and Granger is related to *C. catopsaloides*, but is smaller than Cretaceous Asian representatives of *Catopsalis*. For the time being, we regard *Prionessus* as a separate genus, although it cannot be excluded that when entire skulls of this genus are discovered, it may prove to be congeneric with *Catopsalis*.

It would be naïve to presume that seven discussed species of *Catopsalis* form an evolutionary line, in which each older species is an ancestor of the next one in a stratigraphic sequence. They presumably represent only a small percent of *Catopsalis* representatives which lived in Asia and North America during the discussed period of time. Nevertheless comparison of their morphology casts light on evolutionary changes in *Catopsalis*. These involved an increase in the size of the animal of about 3 times from the smallest known skull *C. matthewi* ca. 5 cm long, to the skulls of Middle and Late Paleocene species, the estimated length of which (based upon the length of lower molars) is ca. 14 cm.

This has been followed by an increase of the length of upper and lower molars. M^1 increased from 4.7 mm in *C. matthewi* to 14 mm in *C. fissidens*; M^2 from 3.6 mm in *C. catopsaloides* (unknown in *C. matthewi*) to 9.2 mm in *C. fissidens*. The number of cusps increased from 4:4 in M_1 in *C. matthewi* to 6-7:5 in *C. utahensis* and from 2:2 in M_2 in *C. catopsaloides* to 4:2-3 in *C. foliatus*, but 3:2 in *C. calgariensis*. An increase in the absolute size of the animal and the cusp number of the molars has been correlated with a relative decrease in size of the fourth premolars. In *C. matthewi*

Fig. 2. Comparison of mandibles and P_4 in the representatives of *Catopsalis* Cope: A *C. matthewi* (Simpson), reconstruction based upon AMNH 20440; B *C. catopsaloides* (Kielan-Jaworowska) — reconstruction based upon ZPAL MgM-I/78 and ZPAL MgM-I/80; C *C. joyneri* Sloan and Van Valen, P_4 (from Sloan and Van Valen 1965); D mandible identified in collection of UCM as *C. foliatus*, but distinctly smaller than the type specimen; the drawing is of the cast of UCM 34979; E *C. foliatus*, type specimen AMNH 3035 (from Matthew 1937, reversed). All $\times 2$.

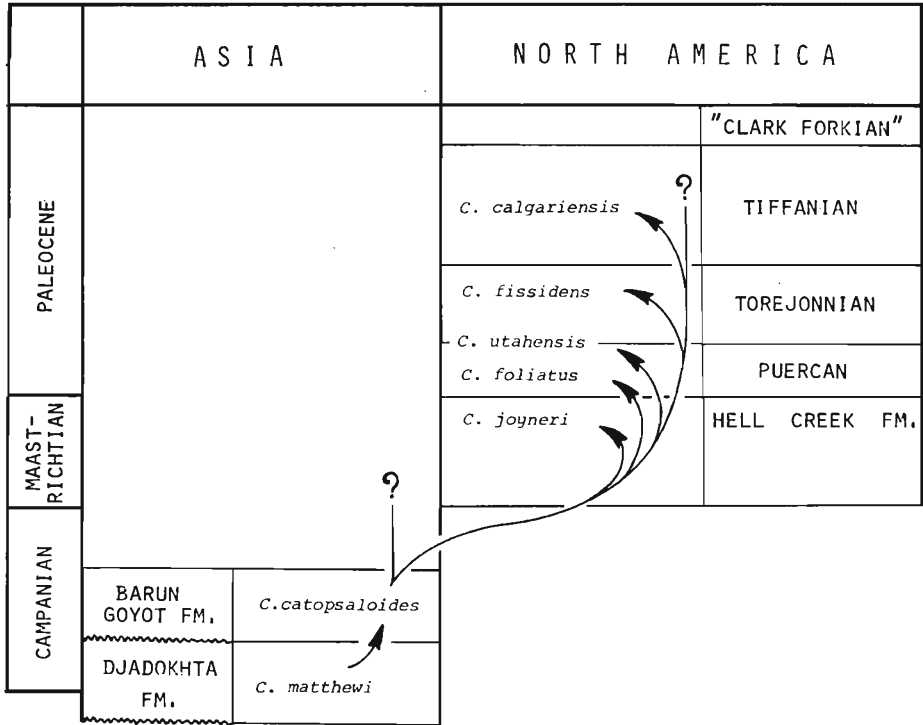


Fig. 3. Diagram showing the distribution of *Catopsalis* species in Asia and North America.

and *C. catopsaloides* P₄ is roughly parabolic 3.2 mm long with 4 cusps and 3.8 mm long with 3 cusps respectively, in *C. joyneri* it forms a truncated triangle and is 3.3 mm long, but one should remember that *C. joyneri* is about 10% larger than *C. catopsaloides*; in *C. foliatus* P₄ forms a small triangle (it appears relatively more reduced in the type specimen AMNH 3035 than in UCM 34979 figured in this paper). It seems that P₃ disappeared in the evolution of *Catopsalis*, it is present (vestigial) in *C. matthewi* and *C. catopsaloides*, unknown in *C. joyneri* and lost in *C. foliatus*.

It is probable that *C. matthewi* is a direct ancestor or remains close to the ancestor of *C. catopsaloides* (see Kielan-Jaworowska 1974a). It is not excluded that *C. catopsaloides* is in the ancestry of *C. joyneri*, but one can visualize at least one or two intermediate species between them. The evolution of North American Paleocene genera cannot be discussed in detail because of the incompleteness of the material.

It follows from the foregoing comparisons that, as suggested by Kielan-Jaworowska (1974b) *Catopsalis* and probably the Taeniolabididae originated in Asia and reached North America during the Late Campanian or Early Maastrichtian.

ADDENDUM

When the present paper was submitted to publication a paper by Minchen and Qi (1978) appeared, in which the authors describe Paleocene mammalian fauna from Nomogen Formation of China. This fauna contains among others the multituberculates, all of which belong in our opinion to family Taeniolabididae discussed in this paper. That is why we have thought it desirable to discuss some of the conclusions of Minchen and Qi.

Minchen and Qi described a new multituberculate genus and species *Lambdopsalis bulla*, characterized among others (1978: 78, free translation from Chinese): "...by the presence of a pair of very large, closed tympanic bullae. The tympanic bulla extends for more than 1/3 of the width of the posterior region of the skull, its diameter attaining 22 mm. The bulla occupies the whole posterolateral corner of the skull and protrudes posteriorly beyond the occipital region..."

Minchen and Qi (1978, pl. 1: 1) mislead in our opinion the inflated and probably somewhat ventrally displaced tabulars and paroccipital processes with the tympanic bullae. The basicranial region of *Lambdopsalis* does not differ from these in known multituberculates (see e.g. basicranial region in *Kamptobaatar* figured by Kielan-Jaworowska 1971, pl. 1: 2b), and the details of its structure, such as the position of the paroccipital process with regard to the promontorium are the same as in *Kamptobaatar* and in other multituberculate genera. The ear region in *Lambdopsalis* is open ventrally as in all known multituberculates and there is no tympanic bulla.

It seems that there are also mistakes either in the enlargements of the photographs published by Minchen and Qi, on pl. 1, or in the measurements given on p. 78 in the text and on the table, as some of these measurements differ distinctly from those obtained from the photographs.

We are of the opinion that *Lambdopsalis* does not merit an assignement to a separate family Lambdopsalidae. It is a typical representative of the Taeniolabididae, very close to *Prionessus*. The Lambdopsalidae Minchen and Qi, 1978 is a junior synonym of the Taeniolabididae Granger and Simpson, 1929. It cannot be also excluded that *Lambdopsalis* is a junior synonym of *Sphenopsalis* but the decision is left to the authors of *Lambdopsalis*.

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CATOPSALIS (MULTITUBERCULATA) Z AZJI I Z PÓŁNOCNEJ AMERYKI ORAZ
PROBLEM MIGRACJI TAENIOLABIDIDAE W PÓŹNEJ KREDZIE

Streszczenie

Wykazano, że azjatycki rodzaj *Djadochtatherium* Simpson, 1925 jest młodszym synonimem północno-amerykańskiego rodzaju *Catopsalis* Cope, 1882. Znane gatunki rodzaju *Catopsalis* (zaliczając tu i *Djadochtatherium*) można ułożyć w szereg morfologiczny, zaczynający się od azjatyckiego ?późno-santonńskiego lub wczesno-kampańskiego *D.matthewi*, po którym następuje ?środkowo-kampański *C.catopsaloides*, następnie północno-amerykański późno-mastrychski gatunek *C.joyneri*, do serii północno-amerykańskich paleoceńskich gatunków: *C.foliatus*, *C.utahensis*, *C.fissidens* i *C.calgariensis*. Zmiany morfologiczne w tym szeregu obejmowały wzrost wielkości, od *C.matthewi*, którego czaszka mierzy około 5 cm długości, do *C.fissidens* i *C.foliatus*, których długość czaszki obliczona na podstawie długości dolnych zębów wynosi około 14 cm. Zmianom tym towarzyszyła redukcja ilości górnych przedtrzonowych, względna redukcja wielkości i zmiana kształtu dolnego czwartego przedtrzonowego, od formy parabolicznej, poprzez ścięty trójkąt, do niewielkiego zaostrego trójkąta, oraz zwiększenie ilości guzków na zębach trzonowych. Autorzy uważają, że, jak wykazała Kielan-Jaworowska (1974a i 1974b), rodzaj *Catopsalis* powstał w Azji, gdzie rozwijał się od santonu do środkowego kampanu i przedostał się do Ameryki Północnej w późnym kampanie lub wczesnym mastrychcie. Jest prawdopodobne, że nie tylko rodzaj *Catopsalis*, ale cała rodzina Taeniolabididae jest azjatyckiego pochodzenia.
