A NEW CORYPHODONT FROM MONGOLIA, AND ON EVOLUTION AND DISTRIBUTION OF PANTODONTA

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Coryphodonts spread on three continents of the Northern Hemisphere. Up to the present, they have been known from the localities lying for apart from one another. Though represented abundantly in the Upper Paleocene and the Lower Eocene of the United States of America, some of the coryphodonts have also been found in the Lower Eocene of Europe (Hebert, 1856—1857; Gervais, 1859; Teilhard de Chardin, 1927; Cauleux, 1945). Besides, a rather large material on Pantodonta was collected by some expeditions of the American Museum of Natural History in Mongolia, such as, genus Eudinoceras (Osborn, 1934) in the Upper Eocene of Irdin Maziha, Hypercoryphodon in the Middle Oligocene of Iren Dabasu (Osborn and Granger, 1932), and the representative of the new family Pantolambodonton (Granger et Gregory, 1934) in the Upper Eocene of Shara Murun. The Mongolian Paleontological expedition of the Academy of Sciences of the U. S. S. R. found the remains of small-sized Pantodonta. Iuchaelambota referred to the new family Archaeolambididae in the Lower Eocene of Nemegtu depression in the South Gobi (Ferow, 1952).

Such geographic and stratigraphic distribution indicates that only a small part of these archaic Mammals is known and probably many new forms of Pantodonta would be discovered in future.

Fragments of lower jaws of Pantodonta found by the Mongolian Paleontological Expedition of the Academy of Sciences of the U. S. S. R. in 1949 in Hashiatto are of great interest. They serve as the confirmation of the above supposition of presence in future of still more new forms of this group. Remains belonging to a small animal like Coryphodonts—the structure of its teeth make us change a little the viewpoint on the history of Pantodonta.

Order Pantodonta
Family Coryphodontidae

Procoryphodon gen. nov.

Type: Procoryphodon primacus sp. nov. Upper Paleocene, Hashiatto, Mongolia.

Diagnosis: Smallest Coryphodont. Lower molars are low, elongated, with length larger than breadth. W-shaped: wings of V-shaped crescents (triangles) are complete:
anterior wing of posterior triangles touches posterior wings (protoconid-metaconid) of anterior triangle in a distance roughly of 1/3 that from metaconid. $M_2$ has paraconid, protoconid, and metaconid approximately of the same height as hypoconid and entoconid. $M_3$ has protoconid and metaconid a little higher than hypoconid and entoconid; protoconid has nearly the same height as metaconid (protoconid is equal to metaconid), and paraconid is rather lower than metaconid; it is well developed in the form of separate cusp. Anterior and posterior triangles on both teeth are nearly equal, the posterior triangle of $M_2$ being a little narrower than the anterior triangle. Cingulum is strong on the back parts of $M_2$ and $M_3$, but weak on the front and external parts.

Measurements (in mm):

<table>
<thead>
<tr>
<th></th>
<th>Length of $M_2$</th>
<th>14.7</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height of $M_2$ (crown)</td>
<td>7.5</td>
</tr>
<tr>
<td>entoconid</td>
<td>7.5</td>
<td></td>
</tr>
<tr>
<td>hypoconid</td>
<td>7.3</td>
<td></td>
</tr>
<tr>
<td>protoconid</td>
<td>8.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Length of $M_3$</td>
<td>15.8</td>
</tr>
<tr>
<td></td>
<td>Height of $M_3$ (crown)</td>
<td>6.2</td>
</tr>
<tr>
<td>entoconid</td>
<td>6.2</td>
<td></td>
</tr>
<tr>
<td>metaconid</td>
<td>8.4</td>
<td></td>
</tr>
<tr>
<td>protoconid</td>
<td>9.3</td>
<td></td>
</tr>
<tr>
<td>paraconid</td>
<td>5.7</td>
<td></td>
</tr>
</tbody>
</table>

**Procoryphodon primaeus sp. nov.**

Type: Fragment of left lower jaw with $M_2$ and $M_3$ N476-I, Paleontological Institute of the Acad. of Sci. of U.S.S.R.

Locality: Hashiato, Mongolia.

Horizon: Upper Paleocene.

Material: Besides the type, there is a piece of right lower jaw with broken $M_2$ and anterior part of $M_3$ N476-2, Paleont. Inst. of the Acad. of Sci. of U.S.S.R. Probably it belongs to the same specimen as type.

Diagnosis: The same as in genus.

Comparison: Judging from the description and illustrations of teeth, the new upper Paleocene genus by structure of lower molars is more closely related to the true Coryphodont than to Pantolambda. The last has isolated anterior and posterior triangles, while **Procoryphodon** has $M_2$ with an incomplete anterior wing of posterior triangle. The Lower molars of **Procoryphodon**, are similar to the molars of *Coryphodon testis*, but smaller in size. Coryphodonts have a reduction of anterior wings of V-shaped triangles. *Eudinoceras* of the Upper Eocene has lower molars more similar to the teeth of the lophiodont type.
Coryphodonts of Eurasia form two groups. The first one, which is similar to the American representatives, includes two genera: 

1) **Coryphodon** known in the Upper Paleocene and Lower Eocene of North America and the Lower Eocene of Europe, 
2) **Hypercoryphodon** in the Middle Oligocene of Mongolia. 

The upper premolars (P₂, P₃, P₄)
with a protocone from the top of which two crests go backward and forward in the form of half-moon horns are characteristic of this group.

One genus *Eudinoceras* referred to the second group is specifically Asiatic and differs pronouncedly from the American Coryphodonts. It is characterized by the simple conic protocone without crest on the upper praemolars (\(P^2\), \(P^3\), \(P^4\)).

Archaeolambda (Flerow, 1952) of which the upper praemolars have a simple conic protocone with one small crest directed forward is close to the last type. Back crest is completely absent, but in its stead there lies part of cingulum, which is strongly developed, has the function of back crest. Thus the teeth of Archaeolambda look like an intermediate between the two types mentioned above.

Fig. 2. Last upper praemolars. 1—*Pantodonta*; Coryphodont, Hypocoryphodont type; 2—*Eudinoceras* type; 3—*Archaeolambda* type. Not to scale.

The following stages can be pointed out in the changes of lower molars of Pantodonta during their evolution.

I. Lower molars are W-shaped, the protoconid and metaconid are much higher than the hypoconid and entoconid. The wing of triangle is completely developed. The anterior wing of the posterior triangle comes almost to the metaconid. The protoconid is slightly lower than the metaconid and forms a well distinct cusp. On \(M_2\) the anterior triangle is equal to the posterior triangle, while on \(M_3\) the posterior triangle is broader than the anterior one.

II. Lower molars are W-shaped. The protoconid, hypoconid, entoconid, and the crests joining them are low. The height of the hypoconid and entoconid of \(M_2\) is nearly equal to that of the protoconid and metaconid; the protoconid and metaconid of \(M_3\) are a little higher than the hypoconid and entoconid. The metaconid is approximately equal to the protoconid. The wings of the V-shaped triangle are complete; the anterior wing of the posterior triangle wedges to the posterior wing of the anterior triangle, falling back 1/3 from the metaconid. The protoconid is a little lower than the metaconid and forms a distinct cusp. The anterior and posterior triangles of \(M_3\) are equal. Of \(M_2\), the posterior triangle is a little narrower than the anterior triangle. The anterior
crest of the posterior triangle is plane concave and has the same bend as the posterior —*Procoryphodon*.

III. Lower molars are W-shaped. The protoconid, metaconid, hypoconid, entoconid and the crests joining them are high. The protoconid and metaconid of M₂ and M₃ are rather higher than the hypoconid and entoconid; the metaconid is the largest. The reduction of the anterior wings of triangles begins. The anterior wing of the posterior triangle is not up to the posterior wing of the anterior triangle and has an end nearly against the middle of it. The paraconid is much lower than the metaconid and does not form a distinct cusp. The anterior wings of triangles are much weaker and lower than the posterior ones (protoconid-metaconid and hypoconid-entoconid). The anterior crest of the posterior triangles is strongly concave in plane, more than posterior; that is why the posterior triangle is much narrower than anterior —*Coryphodon*.

IV. Lower molars with the transverse crests are close to the lophiodont type. On M₂ and M₃ the protoconid and metaconid are almost of the same height as the hypoconid and entoconid. The anterior wings of triangles are preserved only in the form of slightly distinct rudiments —*Eudinoceras*.

Thus the gradual change of lower molars is observed; the anterior wings of triangles are reduced to take the place of the W-shaped teeth. They become of the lophiodont type. As Simpson (1929) suggests, *Pantolambda* cannot be a direct ancestor of *Coryphodon*. Direct ancestry is impossible for, while it would form a suitable basis for the coryphodont dental specialization, *Pantolambda* does not show any actual beginning of this advance.

The discovery of new genus from Mongolia quite confirms Simpson’s point of view. We can consider that *Procoryphodon* is closer to the ancestor of true *Coryphodon* than to *Pantolambda*, in spite of the fact that the first two were contemporaneous. Probably in Asia this early type survived longer. While in North America true *Coryphodonts* already appeared, the archaic type was still present in Mongolia.

On the base of some data of evolution of teeth and feet of Pantodonta the following supposition of their changes of living is introduced.

I. Pantolambda and other archaic terrestrial omnivorous animals with digitigrade forefeet and semiplantigrade hindfeet.

II. *Procoryphodon* and early *Coryphodon (C. testis* type). Foot-digitigrade, gradual transition to semiaquatic living taking place; plantivorous animals feeding more and more on aquatic plants (in more late *Coryphodon*).

III. Eudinoceras and *Hypercoryphodon* —— semiaquatic mammals, feeding on aquatic plants (the same as in the case of tapirs).

**Distribution of Pantodonta:**

Up to the present Pantodonta have been known only from North America and only the representatives of genus *Coryphodon* have been found in Europe: England, North
France, Belgium (Owen, 1946; Hebert, 1856—1857; Gervais, 1859; Teilhard de Chardin, 1927; Cailleux, 1945). For the last 30 years some original groups from the order Pantodonta have been discovered in Mongolia by the Central Asiatic expeditions of the American Museum of Natural History and the Mongolian paleontological expeditions of the Academy of Sciences of the U.S.S.R. Asia as well as North America is abundant with representatives of this order. But it is necessary to notice that the paleontological research of the
American continent was conducted on a larger scale than that on Asia. That is why the fossil mammals of America are better known than the Asiatic ones. It may be supposed that a great number of species of Pantodonta would be discovered in Asia and it is quite probable that Pantodons are richer in Asia than in America. Pantodons so far found are distributed in the following way:

The distribution of pantodonta so far found may be tabulated as follows:

<table>
<thead>
<tr>
<th>Time</th>
<th>Europe</th>
<th>Asia</th>
<th>North America</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palaeocene</td>
<td>Coryphodontidae</td>
<td>Archaeolambia</td>
<td>Coryphodontidae</td>
</tr>
<tr>
<td></td>
<td>Coryphodon</td>
<td>Archaeolambda</td>
<td>Coryphodon</td>
</tr>
<tr>
<td>Eocene</td>
<td>Coryphodontidae</td>
<td>Archaeolambia</td>
<td>Coryphodontidae</td>
</tr>
<tr>
<td></td>
<td>Coryphodon</td>
<td>Archaeolambda</td>
<td>Coryphodon</td>
</tr>
<tr>
<td></td>
<td>Sparactolambda</td>
<td>Titanotheres</td>
<td>Barylambidae</td>
</tr>
<tr>
<td></td>
<td>Eo-coryphodon</td>
<td></td>
<td>Basilambda</td>
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<td></td>
<td></td>
<td></td>
<td>Hadolambda</td>
</tr>
</tbody>
</table>

As may be seen from the above table Asia and North America each has a local complex of pantodons. This complex consists of endemic genera and even families. In
other words, on both continents pantodonta developed in quite different phyla independent of one another for a very long time. The contrary is the case with Europe, where as shown in the table, representatives of Pantodonta closely related to American genus Coryphodon were found. They differ from the American Coryphodon only in that the latter is taken as a different species. It is characteristic that European Coryphodonts (Coryphodon coecenus R. Owen, C. croydonensis Newton, C. oweni Hebert) were found in England, North France, and Belgium.

The similarity of the American and European coryphodonts and their considerable difference from the Asiatic form prove that in Late Paleocene and early Eocene Europe was joined with North America through Greenland and Iceland besides Asia which at that time was separated from Europe. West Europe was isolated from its eastern parts. That is why coryphodonts could not invade far to the East. Undoubtedly more late junction between North America and Europe also took place and it was closer because Brontotheria found in Europe are more similar to the American forms than to the Asiatic; they join with them just the same as coryphodonts in general genus (genus Menodus). Undoubtedly this more late connection spread rather far to the East as the remains of Brontotheria were discovered on the Balkan Peninsula. Brontotheria did not spread far to the East and Oligocene faunas of Kazakhstan have already the forms similar to the Mongolian and Chinese ones. All this confirms the presence of large separation between Europe and Asia in Eocene and Oligocene.

To a considerable extent the distribution of Dinocerats shows the same. They are known in Paleocene and Eocene of Mongolia and North America, but completely absent in rather well-studied, correlated beds of Europe.

In this case, such distribution can be explained by the fact that Dinocerats, the origin of which is in Asia, separated in Paleocene and Eocene from Europe, migrated to North America through the Bering Sea. They formed there a specific independent phylum without invading into Europe and became extinct in the end of Eocene.

As to the place of origin of all pantodonta, this question is still under discussion. The presence in Asia of archaic forms of this order—Upper Paleocene primitive Procoryphodon and Lower Eocene Archaeolambda—makes us suppose that at any rate there must have happened very early separation and independent evolution of this group in Asia and America.

References

蒙古 Coryphodontidae 科的一新屬，並論
鈍腳目 (Pantodonta) 的進化與分佈

（摘要）

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本文記述了蘇聯古生物研究所蒙古學考察隊在蒙古哈西河古新統中發現的一個 Coryphodontidae 科的一新屬新種——Procoryphodon primaeus。

P. primaeus 是一種小型的 Coryphodont。根據它胃窩的存在，P. primaeus 與 Coryphodon testis 相近，但體重比較小。

根據鈍腳目這一類動物的牙齒和腳的進化關係，它們的生活方式的改變，概述如下：

1. Pantolambda 和其他原始的類型——前腳，陸行。後腳，步飛行。陸生，植食性動物。

2. Procoryphodon 和早期的 Coryphodon (以 C. testis 爲典型代表)——翼，陸行。由陸生漸漸轉變為半水棲的生活，植物性動物。

3. Endinoceras 和 Hypecoryphodon——半水棲的哺乳動物，以水生植物為食料。

鈍腳目在亞洲和美洲分佈很廣；在歐洲僅發現於英國、法國和比利時，而且只有 Coryphodon 這一屬。但是鈍腳目究竟是起源於美洲或普通亞洲？這仍然值得討論。假如不是所有的類都起源於亞洲，無論如何它們在美洲和亞洲是早早就分化和獨特進化的。（胡長康譯）