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PALEOBIOGEOGRAPHY OF SOME PALEOGENE RHINOCEROTOIDS (MAMMALIA) IN EUROPE

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Abstract. Four genera of the superfamily Rhinocerotoidea OWEN, 1845 from the Paleogene of Europe are presented: *Epiaceratherium* ABEL, 1910 and *Ronzotherium* AYMARD, 1856 (Rhinocerotidae), additionally *Prohyracodon* KOCH, 1897 and *Eggysodon* ROMAN, 1910 (Hyracodontidae). A new description of *Ronzotherium kochi* (KRETZOI, 1940) from the Transylvanian Basin (Romania) is given. The paleobiogeography of these four genera is recorded. The phylogenetic origin of these rhinocerotoids and the route of immigrants of the „Grande Coupure" are discussed.

Keywords: Vertebrate paleontology, Paleogene, Transylvania, Mammalia, Romania, paleobiogeography, Rhinocerotoidea, Grande Coupure.

INTRODUCTION

The superfamily Rhinocerotoidea includes four families: the Rhinocerotidae OWEN, 1845, the Hyracodontidae COPE, 1879, the Indricotheriidae BORISSIAK, 1923 and the Amynodontidae SCOTT & OSBORN, 1833 (Heissig 1989 b: 403-405, fig. 21.3.).

The cheek teeth of these four families are lophodont: The upper premolars and molars have one labial crest (ectoloph) and two transversal crests (protoloph and metaloph); the lower molars possess two crests, mostly bent at right angles, the labial side of the back crest (hypolophid) being connected with the front crest (metalophid) (Müller 1989: 529).

The four families are distinguished principally because of their body-construction and the specialization of their front dentition. In the often massivly constructed rhinocerotids (from Upper Eocene until today) the I1 and the i2 are enlarged, the only about sheep-sized, cursorial hyracodonts (from Middle Eocene to the Late Oligocene) possessed mostly a complete front dentition with incisors of nearly same sizes, in the gigantic indricotheres (from Upper Eocene until Lower Miocene) the first incisors were enlarged, and the hippo-like amynodonts (from Eocene until Lower Miocene) had enlarged canines (Radinsky 1966: 635-638, fig. 2, 3; Prothero, Guerin & Manning 1989: 321; Prothero & Schoch 1989: 509).

In this paper four genera of the Rhinocerotoidea from the Paleogene of Europe are considered in detail: two members of the family Rhinocerotidae: *Epiaceratherium* ABEL, 1910 and *Ronzotherium* AYMARD, 1856, and in addition two members of the family Hyracodontidae: *Prohyracodon* KOCH, 1897 and *Eggysodon* ROMAN, 1910.

PALEOBIOGEOGRAPHY OF *EPIACERATHERIUM* ABEL, 1910 AND *RONZOTHERIUM* AYMARD, 1856 (RHINOCEROTIDAE) FROM THE OLIGOCENE OF EUROPE

1. *Epiaceratherium* ABEL, 1910

This genus is represented by several more or less complete skulls (Dal Piaz 1930: 15-17, pl. I-IV). *Epiaceratherium* was hornless. The skull has not any rough spots, wich could point at a possession of horns. *Epiaceratherium* had a size similar to the living tapir (Uhlig 1999: 232, tab. 153). The front dentition was still almost complete, only the third lower incisor and the lower canine were absent. The upper premolars were pre- to submolariform, consequently they show a slight molarisation (Dal Piaz 1930: 11, 12, pl. II, IX, X and Uhlig 1999: 65, 69, 70, fig. 43, 49).

From the postcranial skeleton some bones are known. The construction of the feet is remarkable. The hind foot had three hoofs, the fore foot four (Dal Piaz 1930: 19-35, pl. XIV-XX and Uhlig 1999: 91-118, fig. 62-80). The little lateral hoof is a primitive feature within the rhinocerotids. In the course of the history of this group it was completely reduced (Heissig 1989 b: 401).

Epiaceratherium was spread in the Oligocene of Europe with four taxa: *E. bolcense* ABEL, 1910, *E. magnum* UHLIG, 1999, *E.* aff. *magnum* UHLIG, 1999 and cf. *Epiaceratherium* sp. (fig. 1).

E. bolcense is found only at Monteviale, a locality, wich in all probability is to range in the earlieast MP 21 (Hellmund 1992: 38, fig. 1 and Uhlig 1999: 209).

E. magnum occurrs in a few lokalities of Middle and West Europe from the MP 21-Zone until the MP 23-Zone: Soumaille, Möhren 16, Grafenmühle 11, Kleinblauen, Villebramar, Möhren 13, Markvartice, Grafenmühle 7, 12, Ronheim 1, Detan and Saint-Paul-des-Landes (Uhlig 1999: 209-216).

Recently, *E. magnum* has been also known from the Mainz-Basin (Böhme, oral communication, 1999): From Waldböckelheim („Unterer Meeressand", MP 22-Zone ?) a d4, sin. (Llab: 28 mm; Bant: 17 mm; Bpost: 20 mm; H: 12 mm) exists. This tooth is similar to the specimen 1972 XI 2077 of Möhren 13 (compare Uhlig 1999: 56, fig. 30).

E. aff. *magnum* is known from Offenheim in the Mainz-Basin (reworked in the Upper Miocene „Dinotheriensand", primary presumable MP 23-Zone) and from Monclar de Quercy (Aquitaine, probably MP 23-Zone) (Uhlig 1999: 88-91, 217, fig. 61, pl. II / 21).

Four isolated teeth of cf. *Epiaceratherium* sp. exist from Habach 5 (subalpine Molasse, Southern Bavaria, MP 25-Zone) (Uhlig 1999: 218, 122, 123, fig. 81).

2. *Ronzotherium* AYMARD, 1856

The construction of the skull of this rhinocerotid is almost completely known (Roman 1912: 46-47, pl. V and Brunet 1979: 131-137, fig. 13-15, pl. IX, X, XVII). The frontal does not show any rough spots. The nasals are not preserved completely, but so slender, that the possession of a horn in this area is rather improbable. *Ronzotherium* was clearly bigger than *Epiaceratherium* (except *R. kochi*) (compare Uhlig 1999: 80, 81, 119).

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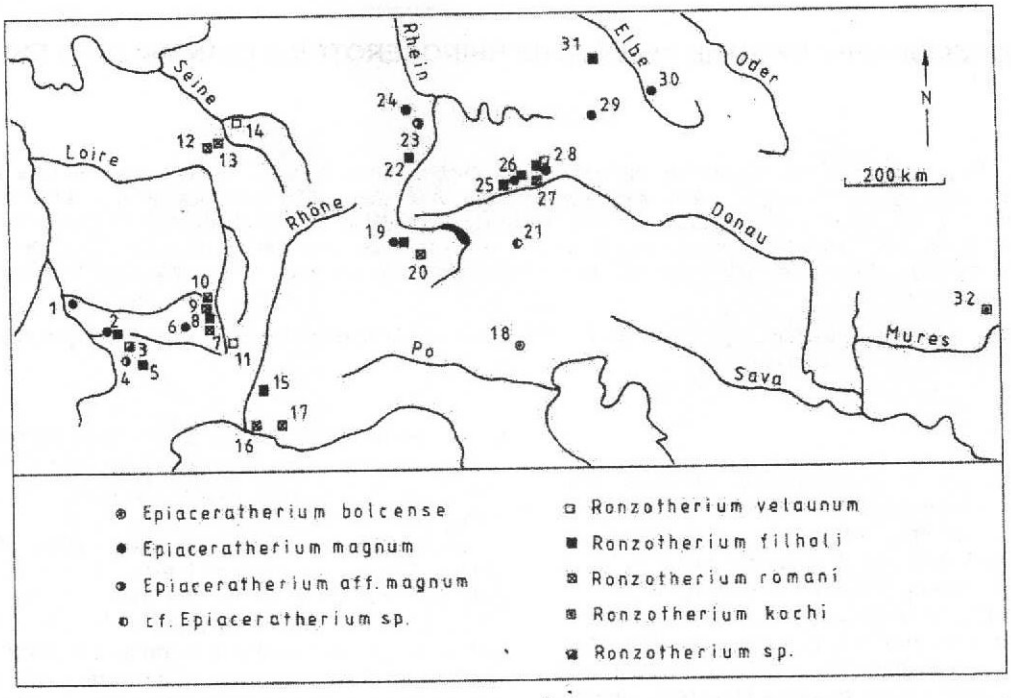

Figure 1 - Map of localities where *Epiaceratherium* and *Ronzotherium* (Rhinocerotidae) were found in Europe. 1: Soumaille; 2: Villebramar; 3: Garouillas and Itardies; 4: Monclar-de-Quercy; 5: Montans; 6: St.-Paul-des-Landes; 7: Brons and Vendèze; 8: Bournoncle St. Pierre; 9: Vodable; 10: Cournon; 11: Ronzon; 12: Etampes; 13: La Ferté-Alais; 14: Lagny-Thorigny; 15: Pernes; 16: St. Henri and St. André; 17: Les Milles; 18: Monteviale; 19: Kleinblauen; 20: Rickenbach; 21: Habach 5; 22: Pechelbronn; 23: Offenheim; 24: Waldböckelheim; 25: Burgmagerbein 8; 26: Ronheim 1; 27: Gaimersheim; 28: Möhren 4, 7, 13, 16, 19, 20, Grafenmühle 6, 7, 11, 12 and Haag 2; 29: Detan; 30: Markvartice; 31: Espenhain; 32: Cluj-Napoca.

The front dentition of *Ronzotherium* was already strongly reduced. The third incisors and the canines were absent. The I1 was enlarged, but still pointed; therefore it did not show any approaches to a chisel-like transforming (Heissig 1969: 19 and Brunet 1979: 102, fig. 3).

The upper premolars show the following characters: the second upper premolar is already semimolariform to molariform, however the fourth premolar is still pre- to submolariform. Premolars and molars may have a strong labial and lingual cingulum. As a rule the furrow in front of the protoloph is absent in the M2 and the M3 of the Lower Oligocene *Ronzotherium*-species (Heissig 1969: 21, 39, 43, fig. 6, 8, 12, 14, 15 and Brunet 1979: 115-128, fig. 9-11, pl. XII, XIII).

From the postcranial skeleton some bones are known (Brunet 1979: 136-149, pl. XX-XXV). However, the question, if the fore foot had three or four hoofs, cannot be answered with this material.

Ronzotherium was spread in the Oligocene of Europe with five taxa: *R. velaunum* (AYMARD, 1853), *R. filholi* (OSBORN, 1900), *R. romani* KRETZOI, 1940, *R. kochi* (KRETZOI, 1940) and *Ronzotherium* sp. (fig. 1).

R. velaunum is known from Möhren 20, Ronzon, Lagny Thorigny and Haag 2. These localities are ranged in the MP 21-Zone (Brunet 1979: 152; Heissig 1987: 107; Aguilar et al. (ed.) 1997: 780).

R. filholi appears from the MP 21-Zone until the MP 23-Zone in the following localities: Möhren 19, 7, 16, 20, 4, Bournoncle St. Pierre, Montans, Burgmagerbein 8, Pechelbronn, Grafenmühle 6, Villebramar, Kleinblauen, Pernes and Ronheim 1 (Brunet 1979: 105, 180, 183; Heissig 1987: 107; Aguilar et al. (ed.) 1997: 780). From the „Phosphoritknollenhorizont" (MP 22-Zone) of Espenhain near Leipzig (NW-Saxony) *R. filholi* is also recorded (Böhme, in press).

R. romani is known from the MP 24-Zone until the MP 29-Zone in the following localities: La Ferté - Alais, Etampes, Vendèze, Brons, Vodable, St. Henri, St. André, Les Milles, Cournon, Gaimersheim and Rickenbach (Brunet 1979: 154, 182-184; Aguilar et al. (ed.) 1997: 780).

R. kochi is known only from the Lower Oligocene of Cluj-Napoca (Transylvania, Romania). This rhinocerotid was described for the first time by Koch 1911 under the synonym *Praeaceratherium minus*. The material (a right fragment of a palate with P2-M3) is kept in the Museum of Paleontology at the Babes-Bolyai University Cluj-Napoca. In 1999, I studied this skull fragment.

In the upper premolars the paracone is fairly cranial situated, the paracone rib is strongly developed, the metacone rib is slightly weaker. The upper premolars do not show the furrow in front of the protoloph. The P2 is semimolariform to molariform, the bridge is deeply notched. The P3 is submolariform, the P4 premolariform. In the P2 and P3 the postfossette is rather shallow and only weakly notched; at the P4 the postfossette is notched ca. 2 mm below the posterior cingulum. In all three premolars, the labial cingulum is ca. 4 mm high. In the P2 it continues from anterior and posterior to the labial side, in the P3 it is interrupted below the paracone, and in the P4 this cingulum is continuous.

Also in the upper molars the paracone is fairly cranial situated. The paracone rib is strong, the metacone rib is only weakly developed. The furrow in front of the protoloph is deeply notched in the M1, at the basis of the M2 it is quite shallowly dented, and in the M3 this furrow is absent. The furrow at the backside of the protoloph is weak in the M1 and M3, however, in the M2 this furrow is strongly notched. In the M1 and M2 the furrow in front of the metaloph (furrow of hypocone) is absent, in the M3 this furrow is weakly developed. In all three molars, the

antecrochet is formed quite weakly. The medisinus has no labial pit. The narrow postfossette is incised below the posteriore cingulum ca. 2 mm.

The labial cingulum in the upper molars is ca. 3 mm high; in the M1 and M2 it continues from posterior to the labial side until below the metacone. In the M3, a very weak cingulum is developed below the paracone, it is absent labial. In the M3, the edge of ectoloph (below the metacone) is drawn too small by Koch. Rather, there exists a wide ectoloph edge. The upper molars do not have a continuous lingual cingulum, as it is illustrated by KOCH. In reality, the cingulum is interrupted in the M1 below the proto- and hypocone, and in the M2 and M3 below the protocone.

The following features suggest a membership of this tooth material to *Ronzotherium*:

- the molarisation of the premolars: The P2 is already semimolariform to molariform, however, the P4 is still premolariform. In *Epiaceratherium*, the P2 is only sub- to semimolariform, in *Eggysodon* it is submolariform.
- in the upper molars, the lingual cingulum is strongly developed and nearly continuous. This is never the case in *Epiaceratherium* and *Eggysodon*.
- there exists a labial cingulum. In *Epiaceratherium* a thin cingulum is rarely developed only in the P1 and M1, otherwise it is absent.
- the M3 has no furrow in front of the protoloph, in the M2 this furrow is only weakly developed. In *Epiaceratherium* this furrow is already developed in the earlieast Oligocene.

R. kochi is distinctly smaller than the *Ronzotherium*-species of Middle and West Europe. Its size is similar to *Epiaceratherium magnum*. However, this low size is judged as a primitive feature, wich does not indicate a relationship to *Epiaceratherium*.

Also the rather cranially situated, narrow paracone rib in the upper premolars is looked as a primitive feature, wich can be observed also in *Forstercooperia* from the Eocene of Asia and North America (compare Radinsky 1967: fig. 8). The development of a flat paracone rib more posteriorly situated is judged as a specialization of the *Ronzotherium*-species in Middle and West Europe.

Therefore, *R. kochi* from the Lower Oligocene of Cluj could be the smallest and most primitive member of the genus *Ronzotherium*. Thus, the *Ronzotherium*-species of Middle and West Europe and *R. kochi* of Transylvania may have a common origin in the Upper Eocene.

Some remains of *Ronzotherium* wich can only be determined as *Ronzotherium* sp. are known from Itardies und Garouillas (Bonis & Brunet 1995: 184; Aguilar et al. (ed.) 1997: 791).

PALEOBIOGEOGRAPHY OF *PROHYRACODON* KOCH, 1897 AND *EGGYSODON* ROMAN, 1910 (HYRACODONTIDAE) FROM THE PALEOGENE OF EUROPE

1. *Prohyracodon* KOCH, 1897

In this small hyracodont the number of the lower incisors is reduced to two. The upper premolars are pre- to submolariform. The upper molars have only a very weak antecrochet and not any secondary furrows. In the M3, the ectoloph and the metaloph do not form an angle against each other any more (Koch 1897: pl. XII; Abel 1910: pl. I; Teppner 1914: pl. I, II and Heissig 1989 b: 355).

Prohyracodon is represented in the Eocene of Europe with two taxa: *P. orientale* KOCH, 1897 and *P. telleri* (ABEL, 1910) (fig. 2).

P. orientale is known only from the locality Radaia (formerly Andrásháza), eight kilometers in the west of Cluj-Napoca. The deposit is ranged in the Upper Eocene (Codrea 1993: 72). The material, presented by Koch 1897, is kept mainly in the Museum of Paleontology at the Babes-Bolyai University Cluj-Napoca.

P. telleri from Motnik (Slowenia) was described by Abel in 1910 (p. 26-32, pl. I) as *Meninatherium telleri*. Heissig (1989 a: 355) included this material rightly in *Prohyracodon*. Heissig (1990: 58) and Codrea (1993: 72) suppose an Upper Eocene - age of the deposit. The type is lost. Other remains, a fragment of a palate and two jaws, described by Teppner in 1914, are kept in the Joanneum in Graz.

A small fragment of a palate from the Upper Eocene - locality Bobov Dol (Bulgaria), described by Nikolov & Heissig (1985: 68, pl. I/6) as *P.* aff. *meridionale* does not belong to this genus (Heissig, oral communication, 1999).

2. *Eggysodon* ROMAN, 1910

Two fragments of palates and a few jaws are known (Rámes 1886: 359, 360, pl. XVII/ 1-3; Roman 1912: 11, 19, 20, fig. 2, pl. I / 1, 2, VI / 1, 2; Stehlin 1930: 645-648, fig. 1-3; Uhlig 1999: pl. III). The canines were enlarged. A sexual dimorphism was proved at the lower canine (Uhlig 1999: 142-144, fig. 95, 96).

As in *Prohyracodon*, the number of the lower incisors is reduced to two. The upper premolars are pre- to submolariform. The upper molars always have a weak antecrochet and shallow secondary furrows. In the M3, the ectoloph and the metaloph form still an angle against each other (Uhlig 1999: 125).

From the postcranial skeleton, some elements are known (Uhlig 1999: 155-167, fig. 99-107). The metapodials are constructed slender and indicate a cursorial locomotion of *Eggysodon* (Uhlig 1999: 235).

Eggysodon is spread in the Oligocene of Middle- and West Europe with five taxa: *E. osborni* (SCHLOSSER, 1902), *E.* cf. *osborni*, *E. gaudryi* (RAMES, 1886), *E. pomeli* ROMAN, 1912 and *E. reichenaui* (DENINGER, 1903) (fig. 2).

E. osborni is known from the MP 21-Zone until the terminal MP 22-Zone respectively in the basal MP 23-Zone in the following localities: Möhren 19, Weissenburg 16, Grafenmühle 11, Lagny Thorigny, Veringenstadt, Haag 2, Kleinblauen, Villebramar, Möhren 13, Grafenmühle 7, Ronheim 1, and besides in the phosphorits of Quercy (Uhlig 1999: 153, 154, 209-215).

In addition, from the „Phosphoritknollenhorizont" of Espenhain near Leipzig a lower molar is known of a small rhinocerotoid (Böhme, in press). This molar is a m3?, dext. (Lmax: 27 mm; Bmax: 15 mm; H: 11 mm) of *E.* cf. *osborni*. The tooth has nearly the same size as *E. osborni* (compare Uhlig 1999: fig. 111); but no cingular ridge across the basis of the labial furrow is present, wich is an important feature within *E. osborni*.

E. gaudryi is in all probability a younger relative of *E. osborni*. However, it is established not earlier than in the MP 24-Zone (La Ferté-Alais). Other localities with *E. gaudryi* are: Brons, Las Peyres, Latou, Puylaurens and the phosphorits of Quercy. The stratigraphically youngest deposit of this species is most probably Puylaurens, a locality with an estimated age of MP 27-28-Zone (Uhlig 1999: 174-176, 204, 217-220).

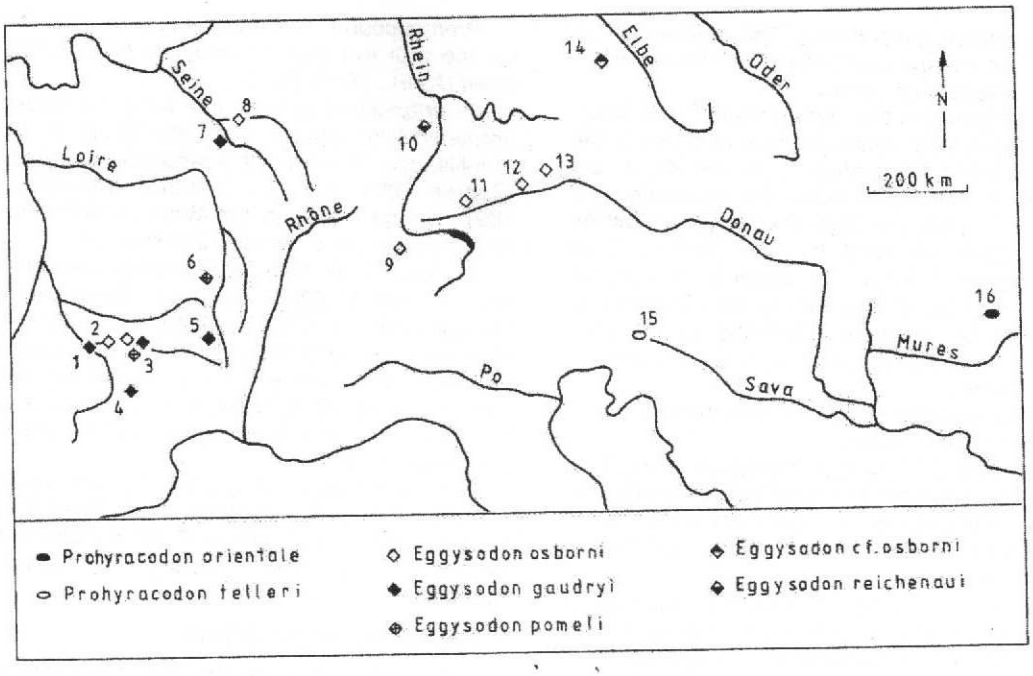

Figure 2 - Map of localities where *Prohyracodon* and *Eggysodon* (Hyracodontidae) were found in Europe. 1: Las Peyres and Latou; 2: Villebramar; 3: Quercy; 4: Puylaurens; 5: Brons; 6: Gannat; 7: La Ferté-Alais; 8: Lagny-Thorigny; 9: Kleinblauen; 10: Weinheim; 11: Veringenstadt; 12: Ronheim 1; 13: Möhren 13, 19, Grafenmühle 7, 11, Haag 2 and Weissenburg 16; 14: Espenhain; 15: Motnik; 16: Radaia

E. pomeli, the youngest member of the line *E. osborni* - *E. gaudryi* - *E. pomeli*, is known only from the terminal Oligocene of Gannat and from the phosphorits near Escamps (Uhlig 1999: 179, 219-220).

E. reichenaui is considered to be a separate line within the genus *Eggysodon*. This species is known only by its holotype from the „Unterer Meeressand" of Weinheim in the Mainz - Basin (MP 23-Zone ?) (Deninger 1903 93-97, pl. VI, VII and Uhlig 1999: 216).

THE PHYLOGENETIC ORIGIN OF *EPIACERATHERIUM, RONZOTHERIUM, PROHYRACODON* AND *EGGYSODON*

Epiaceratherium is known only from the Oligocene of Europe. However, *Trigonias* LUCAS, 1900 from the Oligocene of North America is very similar to this genus. Perhaps, both genera go back to *Teletaceras* HANSON, 1989 from the Upper Eocene of North America. This small rhinocerotid still has a complete front dentition, and the I1 already shows first approaches of a chisel-like shape.

Ronzotherium is known outside Europe with two species from the Lower Oligocene (Upper Eocene after Meng & McKenna 1998) of Mongolia: *R. orientale* DASHZEVEG, 1991 und *R. brevirostre* (BELIAJEVA, 1954). *Ronzotherium* with its primitive, pointed shape of the I1 is related probably to the Eocene genus *Forstercooperia* with equal sized incisors (Heissig 1989 b: 404, fig. 21.3 and Uhlig 1999: 197, 199).

There are remains of *Prohyracodon* outside of Europe in the „Lumeiyi Formation" of China: *P. meridionale* and *P. progressa* CHOW & XU, 1961. The age of the deposit cannot be dated more exactly than Middle- until Upper Eocene (Russel & Zhai 1987: 126). *Prohyracodon* is probably originated near *Hyrachyus* from the Eocene of Eurasia and North America (Uhlig 1999: 206).

There are no remains of *Eggysodon* outside of Europe. However, this genus is very similar to *Prohyracodon*, but nearly of double size. However, the development of the ectoloph and the metaloph in the M3 do not support a direct relationship. Both crests do not forme an angle against each other in *Prohyracodon*. Compared to *Eggysodon* this is considered to be a more progressive feature. Accordingly *Eggysodon* and *Prohyracodon* may have a common origin in the Middle until Upper Eocene of South East Europe or Asia.

CONCLUSIONS

Prohyracodon, coming from Asia, immigrated in the Upper Eocene to the Balkan-peninsula wich was still separated at that time from the European continental masse (Heissig 1979: 87). *Epiaceratherium* is probably originated in the Upper Eocene of North America, and *Ronzotherium* in the Middle until Upper Eocene of Asia. *Eggysodon* is probably originated in the Middle until Upper Eocene of South East Europe or Asia.

From their centers of evolution, these rhinocerotoids immigrated together with numerous other mammals at the Eocene - Oligocene boundary into Europe. This change of faunal assemblages is named after Stehlin (1909: 503-509) „Grande Coupure".

The route of these immigrants is an „old discussion". After Vianey-Liaud (1976: 77, 78) the immigrants came from the eastern Ural over the depression of Turgai. On the other hand, Heissig (1979: 83, 84, 87) and Hellmund & Heissig (1994: 279) suppose that the alpine orogenic belt between Asia and Europe was the land bridge in the uppermost Eocene, because there were earlier immigrants in South East Europe, the immigration took place simultaneously and the Polish lowland was a marine barrier at this time.

In my opinion, the finds of paleogene rhinocerotoids in South East Europe with close relationships to the

rhinocerotoids of Middle and West Europe support Heissig`s hypothesis.

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