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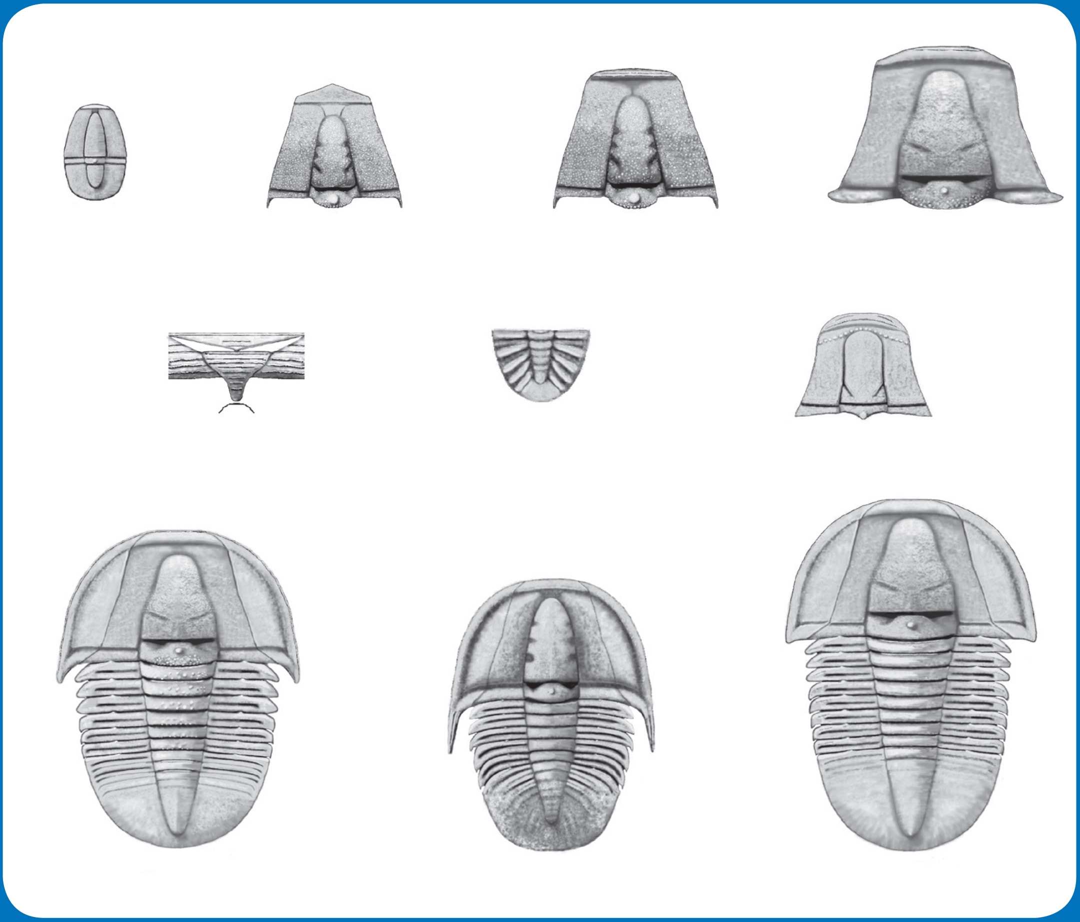

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Cover illustration: Tentative reconstructions of different taxa and ontogenetic stages in the trilobite genus *Drevermannia*, as well as of *Silesiops*? sp. For details, see Basse, M.: Revision und Ontogenie des Trilobiten *Drevermannia schmidti* Richter 1913 aus dem Oberdevon des Bergischen Landes, pp. 9–58 in this issue.
Back cover: Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbild: Rekonstruktionsversuche für verschiedene Taxa und ontogenetische Stadien der Trilobitengattung *Drevermannia* sowie für *Silesiops*? sp. Für weitere Informationen siehe Basse, M.: Revision und Ontogenie des Trilobiten *Drevermannia schmidti* Richter 1913 aus dem Oberdevon des Bergischen Landes, S. 9–58 in diesem Heft.
Rückseite: Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

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The American genus *Penetrigonias* Tanner & Martin, 1976 (Mammalia: Rhinocerotidae) as a stem group elasmothere and ancestor of *Menoceras* Troxell, 1921

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Abstract

A detailed character study of the early Oligocene skull of *Penetrigonias dakotensis* (Peterson, 1920) kept in the Bavarian State Collection of Paleontology and Geology at Munich, Germany, and comparisons of this specimen with geologically older species of the genus has resulted in the recognition of features characterizing this lineage of small-sized rhinoceroses of North America. Morphological trends recognizable in the upper cheek teeth of *P. dakotensis* are present also in the early Elasmotheriini, suggesting that the genus *Penetrigonias* may represent a stem group representative of this tribe. At the same time, the more advanced characters of the latest early Oligocene species *P. dakotensis* suggest that the genus *Menoceras* with its Eurasian and American species may represent the successor of this species. A cladistic analysis of the characters of early Rhinocerotidae from America results in a scheme explaining how and when this family may have split into its different tribes.

Key words: Elasmotheriini, North America, *Menoceras, Penetrigonias*, Paleogene, Phylogeny, Rhinocerotidae

Kurzfassung

Eine genaue Untersuchung des unteroligozänen Schädels von *Penetrigonias dakotensis* (Peterson, 1920) in der Bayerischen Staatssammlung für Paläontologie und Geologie und Vergleiche mit älteren Arten der Gattung erlauben es, den typischen Merkmalsbestand dieser phyletischen Linie kleinwüchsiger Nashörner Nordamerikas zu erfassen. Spezifische morphologische Trends der oberen Backenzähne stimmen mit denen früher Elasmotheriini überein, so dass die Gattung *Penetrigonias* als Stammgruppen-Vertreter dieses Tribus gelten kann. Zugleich lässt die jüngste, unteroligozäne Art, *P. dakotensis*, in ihren fortschrittlichen Merkmalen erkennen, dass die untermiozäne Gattung *Menoceras* mit ihren amerikanischen und eurasischen Vertretern wohl als Nachkomme dieser Art anzusehen ist. Eine cladistische Analyse der Merkmale früher Rhinocerotidae Amerikas ergibt ein Schema, das zeigt wie und wann sich die Familie in ihre verschiedenen Tribus aufgespalten haben könnte.

Schlüsselwörter: Elasmotheriini, Nordamerika, *Menoceras, Penetrigonias*, Paläogen, Phylogenie, Rhinocerotidae

1. Introduction

In 1998, the Bavarian State Collection in Munich (BSPG) acquired an unprepared, vertically compressed skull of a small rhinoceros from Dakota. Unfortunately, the precise age and provenance of the fossil have not been reported by the merchants. The only indication provided reads “90 km south of Roundup, Dakota”, which, however, does not make sense. The adhering matrix, a greenish, heavily calcified sandstone, apparently is the typical sediment of the *Protoceras* channels of the Whitneyan. After preparation, the dentition allowed the identification of the specimen as *Penetrigonias dakotensis* (Peterson, 1920). The specimen today is deposited in the Bavarian State Collection of Paleontology and Geology in Munich, Germany, under accession number BSPG 1998 I 34.

The combination *Penetrigonias dakotensis* (Peterson, 1920) was first used by Prothero (2005: 29), who also assigned to this species (as a junior synonym) the Eocene type species *P. hudsoni* Tanner & Martin, 1976. The characters of the Munich specimen, however, are so peculiar that a more detailed study on the phylogenetic significance is mandated. The fundaments of this analysis are, on the one hand, the survey of the known specimens of the genus by Prothero (2005: 29–35) and, on the other hand, the casts of several specimens obtained from the South Dakota School of Mines in Rapid City. For comparison with Old World Elasmotheriini the specimens housed in the Bavarian State Collection from Anatolia and Pakistan, as well as a sample of casts from the same collection were used, completed by published illustrations of material from the works of various authors.

2. Material and Methods

2.1 Specimens included in this study

- BSPG : Bavarian State Collection of Paleontology and Geology
- *Penetrigonias dakotensis*: 1998 I 34
- *Menoceras zitteli:* AS 340 holotype, casts of specimens from Paulhiac (1968 XVI 144), Velleron (1968 XVI 141) and Flörsheim (Orig. M 6748)
- *Menoceras arikarense:* 1964 X 107, 108
- *Caementodon oettingenae:* 1956 II 364, 1968 XVI 57
- *Bugtirhinus praecursor:* casts 1968 XVI 58
- *Hispanotherium grimmi:* holotype 1968 VI 1, 2 and others

Specimens in other collections used for direct comparison:
- AMNH: American Museum of Natural History, New York
- *Penetrigonias dakotensis*: 1110 holotype
- F:AM: Frick Collection in the AMNH
- *Penetrigonias.hudsoni*: 105019
- MNB: Museum für Naturkunde der Humboldt-Universität Berlin
- *Penetrigonias dakotensis:* Ma 42545
- MNHN: Muséum National d'Histoire Naturelle, Paris
- *Pleuroceros pleuroceros*: Type skull
- NHM : The Natural History Museum, London
- *Bugtirhinus praecursor:* M 15361
- NMB: Naturhistorisches Museum Basel
- *Menoceras zitteli:* Figured specimen of Viret (1958: fig. 77)
- SDSM: South Dakota School of Mines and Technology, Rapid City
- *Penetrigonias hudsoni:* 5331
- *Amphicaenopus platycephalus*
- SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/M
- *Menoceras zitteli*: M 3748, M 6773
- UCBL: Centre de Palóntologie stratigraphique et Paléoécologie,
- Université Claude Bernard Lyon, Villeurbanne
- *Menoceras zitteli:* cast of the cheek teeth of the Paulhiac skull 9600,

Additional specimens cited from the literature are housed in the following collections:
- DMNH: Colorado Museum of Nature and Science, Denver, CO.
- FMNH: Field Museum of Natural History, Chicago, IL.
- IVAU: Instituut voor Aardwetenschappen, Rijks Universiteit Utrecht,
- LACM: Natural History Museum of Los Angeles County, CA.
- LSUMG: Louisiana State University Museum of Geology, Baton Rouge, LA.
- MHNT: Muséum d'Histoire Naturelle, Toulouse
- PIUU : Paleontological Institute , University of Uppsala
- ROM: Royal Ontario Museum, Toronto
- SMNH: Saskatchewan Museum of Natural History, Regina, Sask.
- TMM: Texas Memorial Museum, University of Texas, Austin, TX.
- UCMP: University of California Museum of Paleontology, Berkeley, CA.
- UNSM: University of Nebraska State Museum, Lincoln, NE.

2.2 Methods

The terminology used for the morphological description of the dentition follows Osborn (1898: 107), modified by Heissig (1969: 11–12), and that for the skeletal elements primarily Heissig (1972: pl. 13). The different grades of molarisation of the upper premolars are named according to Heissig (1969: 15–16, fig. 4). Upper teeth are asigned capital letters, while lower teeth are indicated by lower case letters: I, i = incisors, C, c = canine, P, p = premolars, M, m = molars, D, d = deciduous molars, combined with numbers. E.g. dc = lower deciduous canine, D4 = fourth milk molar.

The cladistic analysis was performed without the use of mathematical processes, but rather by weighting the importance of characters. The characters are sorted into three categories, i.e. (a) "unique", (b) "important but homoplastic in different rhino clades" and (c) others of unknown importance. This method may be somewhat subjective, but selecting and separating characters is generally subjective, regardless of whether they subsequently are treated mathematically or not. Furthermore, no argument can be produced to justify the equal weighting of characters. Characters occurring in all members of a large clade (e.g. a tribe) must be treated as more important than characters that differ in closely related species. Both are of different importance as general trends in rhino evolution, as, for instance, the molarisation of premolars or the reduction of incisors, which do not allow reversals. Genera or species without known autapomorphies are accepted as valid to keep the taxonomy stable, if they cannot be synonymized. Although this approach does not concur with the cladistic orthodoxy, it is useful especially if only a few characters are known for the species considered.

2.3 Special characters

Many of the taxa included in this study show a considerable variability in characters that are rather stable in most rhinos. In the upper molars the position of the secondary folds is inconsistent, and thus the dominating fold sometimes arises from the metaloph as a “crochet”, while in other specimens it is borne from the ectoloph as a “crista”. In the upper premolars there occur irregular crests in much higher frequency than in other rhino groups. If a crest arising from the lingual side of the mesostyle reaches the lingual edge of the tooth, it should be named a mesoloph, notwithstanding that this structure does not represent an element of the normal rhinoceros tooth pattern.

Most ungulates with hypsodont or even mesodont molars develop a cement cover on the crown that is already complete in erupting tooth germs. This is also the case in most Elasmotheriini. In contrast to this condition, however, a secondary cover of the enamel is formed only above the gingiva margin in the mesodont molars of *Menoceras*. This substance is not identical to the cement formed within the alveoli of the teeth, but may enlarge the abrasion surface in a similar manner. If the secondary cover shows wear facets, I call it functional tartar. It is probably a unique feature within the ungulates.

2.4 Stratigraphical distribution of American stem group rhinoceroses

According to Prothero (2005), the earliest true Rhinocerotidae appear during the Duchesnean North American Land Mammal Age (NALMA) (late Middle Eocene, 40 – 37,2.MA). Most stem group rhinoceroses occur no later than Whitneyan (late Early Oligocene, 32 – 30.6.MA). The surviving genera *Menoceras* and *Diceratherium* have been reported to the middle Hemphillian (17 MA, Early Miocene).

3. The Munich skull of *Penetrigonias dakotensis* (BSPG1998 I 34; Plate 1)

3.1 Description

The skull is severely crushed and dorsoventrally compressed, but still displays several distinctive traits. The separate nasals are thin and laterally arched. They are narrow and show the typical lateral notch of the most primitive genera. The nasal incision ends high above the anterior half of P2; its lower border is formed by a long tiny posterior process of the premaxilla, which contacts the nasal. The infraorbital foramen opens on a much lower level above the posterior half of P2. The probable contact of the nasals with the lachrymals is masked by multiple fractures on both sides, but there seems to be no contact of the maxilla with the frontal. The frontal region is very broad above the orbits, rapidly tapering in front and to the rear. The temporal lines occur in the form of thick and broad ridges, which unite above the tips of the zygomatic arches to form a long, but not elevated sagittal line. A small postorbital process and a moderately developed supraorbital swelling are present. The occiput is not preserved.

The robust jugal contacts the lachrymal; the foramen lacrimale is not preserved. The posterior end of the jugal reaches the glenoid fossa. The zygomatic arch branches off the maxilla lateral to M3. Its rough lower face, however, continues in a facial crest to the front side of M2. Its upper side is formed by the squamosal behind the orbit. Its upper elevated edge shows a feeble rugosity, and ends with a high point above a deep notch behind. The postglenoid process is relatively short and does not contact with the still shorter posttympanic process.

The entire right and tip of the left premaxillae are broken. Only the posterior rim of the I1 alveolus is preserved. Approximately 1 cm behind this structure follows a small, knob-like I2 with no traces of wear but a small polished tip. The anterior tip of the maxilla is broken, so that it remains doubtful if there was any trace of an obliterated alveolus of an early lost canine. The medium-sized diastema is formed by a strong ridge. The palatine foramen opens at a level between the premolar and the molar region. The choanae are opening with a small central spine at the hind half of M1. A maxillary tubercle behind M3 is lacking, probably because the individual was an early adult with a nearly fresh third molar. The palatine ridge is not preserved intact. There is a posterior process of the pterygoid, which is constantly tapering and ends shortly after bridging the alisphenoid channel. A prominent point on the basisphenoid continues in the form of a sharp central crest that separates two muscular scars.

The cheek teeth are preserved intact. One of the most striking features of the dental row is the great difference of wear within the molar series. The last molar had just entered the occlusal surface when the first one had already lost more than half of his height. The premolars are rather short compared to the molars. The ectoloph of all cheek teeth is covered with a thick layer of tartar foreshadowing the development of functional tartar in *Menoceras*.

The triangular D1 has lost all internal structures by wear. The poor enamel is present only on the lingual and the labial walls. A deep indentation delimits the parastyle lingually. The adjacent premolars are comparatively short and fully molariform. The metaloph is generally narrower than the protoloph, but longer in P2 and P3. Both cross lophs run parallel and form a rather acute angle with the ectoloph. The protoloph has a strong, high connection with the ectoloph, which is slightly bent backwards in P2, giving space for a very small prefossette. In the following premolars the protoloph connects anterior to the paracone. The protocone is somewhat swollen but not constricted in the premolars. The metaloph is connected to the ectoloph clearly anterior to the metacone. Its front side is characterized by a few tiny, irregular secondary folds. In P2 there is an oblique lamella bridging the medisinus from the protocone to the crochet position. This fold is higher in the right P2 than in the left one. However, the hypocone of this tooth forms a hook-like extension from the metaloph to the rear, whereas in the following premolars it is fully integrated in the metaloph. As a result, the long and wide postfossette is two fold in P2, but simple in P4. The P3 is intermediate.

The labial enamel wall is more or less straight in the premolars, with three flat, narrow ribs marking the paracone, the mesostyle and the metacone, which is somewhat broader. The mesostyle is absent in P2. The parastyle is of medium length, and thick in P2 but slim in P3 and P4. It has the same direction as the ectoloph, but in a parallel, more lingual plane. The parastyle fold is narrow and somewhat inclined backwards. Lingually there is one short crista in the usual position. The medisinus is straight, with a wide curvature around the thick protocone in P3. The postfossette is quite deep with a long extension between the metaloph and metacone. In P2 there is a second extension between the metaloph and hypocone hook.

The lingual cingulum is complete, and confluent with the anterior and posterior one. It is thick and high without depressions at the medisinus or postfossette. It is lingually oblique, and therefore passes closer to the hypocone, but without any special elevations.

The M1 and M2 are long and narrow with a deeply inflected ectoloph, covered labially by tartar, which does not reach the same thickness as that of the premolars. A metacone rib is absent. The paracone rib is sharp and narrow, and separated apically from the slim, tapering parastyle by a broad and deep parastyle groove. The mesostyle forms a broad, flat swelling. The wing-like metastyle is strongly elongated. There is a faint labial cingulum at the enamel base from the middle of the ectoloph to the metastyle edge. The metaloph is short and runs parallel to the more massive protoloph. It shows a faint crochet, but the main obstruction of the medisinus comes from a long and massive crista positioned just in front of the metaloph connection to the ectoloph. This fold occupies the space normally occupied by the crochet in rhinoceroses. A more anterior, smaller cristella is located in the position that is normally occupied by the crista in rhinoceros molars. This pattern of secondary folds is seen clearly in M2. The M1, however, is too much worn to display these folds. There are faint traces of a protocone constriction by two grooves and a basal swelling of the antecrochet. So the medisinus is narrow and undulating. The postfossette is deep, narrow, and longitudinal. There is no lingual cingulum around the protocone. It begins deeply inflected into the medisinus where it forms a small cusp and rises steeply to the hypocone base where it is nearly disappearing. There is a deep incision behind the postfossette.

The last molar shows first traces of wear, but its base is not yet fully erupted from the bone. It has the usual triangular shape of rhinoceros molars, but the metastyle line is moved considerably to the lingual edge of the ectometaloph. So the posterior cingulum, which is linked to this remnant on the back side, is not transversely orientated, but rather forms a short, blunt, shelf-like rim perpendicular to the oblique direction of the ectoloph. This rim, however, is not characterized by a rounded single edge as usual, but rather is split into two parallel, sharp edges descending from the top. In the right M3 the base of the hypocone is continuing lingually in a swollen shelf, completing the posterior edge of the triangular outline of the tooth. This point exhibits a low pillar separated from the ectometaloph like in some *Menoceras* specimens that have a high pillar in this position. The anterior part of the ectoloph and the protoloph are analogous to the other molars, but a protocone constriction is missing. There is one strong crochet somewhat lingually of the centre of the ectoloph. The lingual cingulum is absent at the protocone. At its back side it reappears, but then disappears beneath a thick cover of tartar in the entrance of the medisinus .

3.2 Comparison to the Berlin skull (MA 42545)

The specimen kept in the Museum für Naturkunde Berlin, Germany, which was ascribed to this species and described in detail by Wood (1929: 67), consists of a fragmentary skull with a fragment of the mandible preserved as well. The mandible is very similar in size and characters to the type, so that the specific identity of the Berlin specimen is indisputable. It is this specimen that shows the greatest similarity to the Munich skull described above. The characters of the preserved part of the skull are identical in the Munich and Berlin specimens. However, minor differences occur with regard to the dentition. In the premolars of the Berlin specimen, the connection of the cross lophs to the ectoloph is weaker. Moreover, even the somewhat more worn teeth, especially the metalophs of all teeth but also the protoloph of P2, are not yet confluent with the ectoloph. On the other hand, the hook-like extension of the hypocone in P2 is fused to the rest of the metaloph by wear. The oblique secondary fold bridging the medisinus is lacking in P2, but present in P3. There are two faint secondary folds in the crochet region of P4. The lingual cingulum is less complete and vanishes at the hypocone edge, in P2 also on the protocone edge. With regard to the molars, the only differences between the Munich and Berlin skulls are with regard

Plate 1

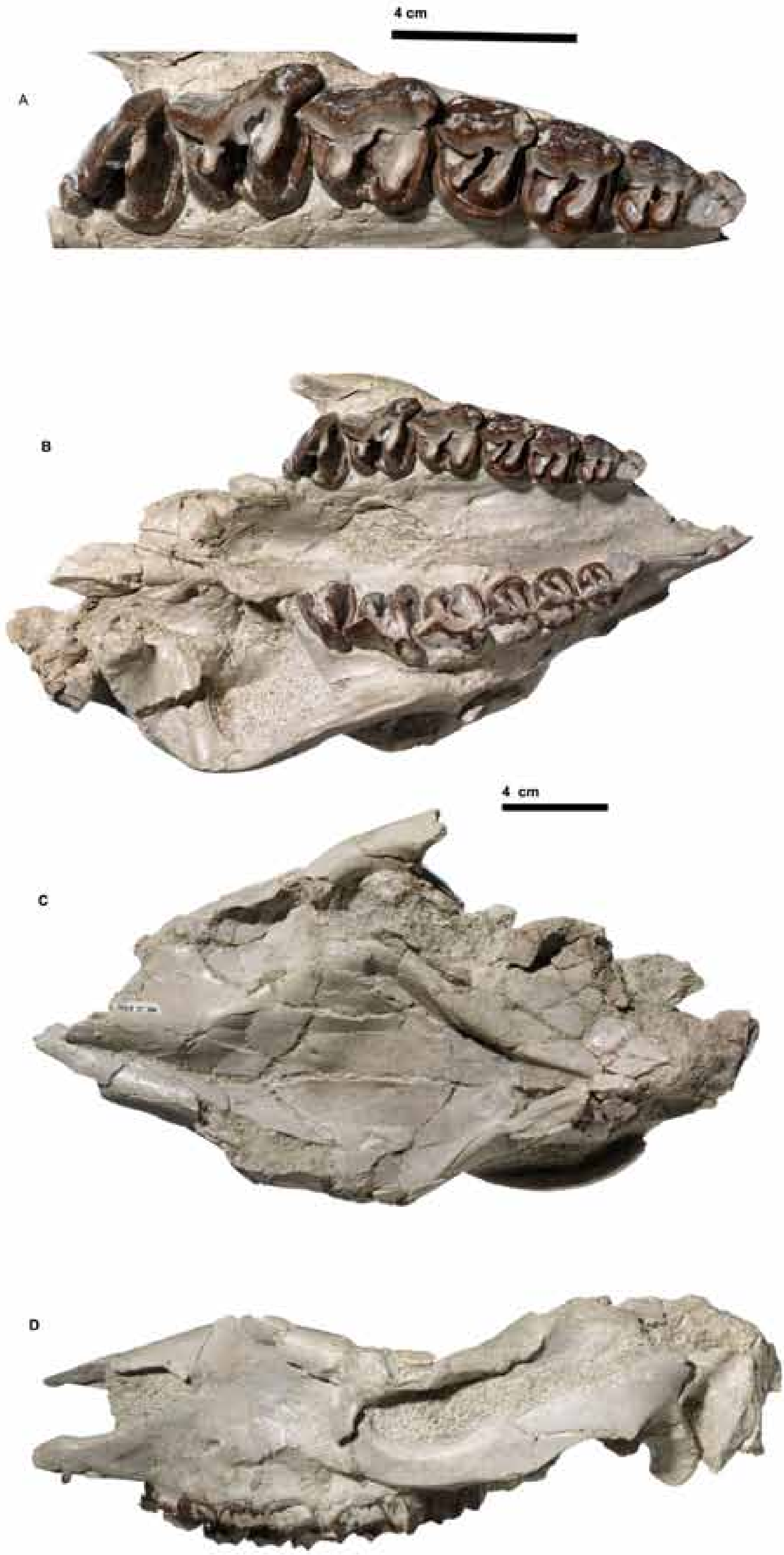

Plate 1: *Penetrigonias dakotensis* (Peterson, 1920), South Dakota, BSPG 1998 I 34. **(A)** Right upper dentition. **(B)** Skull, ventral view. **(C)** Dorsal view. **(D)** Left lateral view. Scale bar = 4 cm.

to the M3, which displays a normal, rounded lingual edge of the ectometaloph in the Berlin specimen, whereas the Munich specimen exhibits a swollen shelf and a low pillar, completing the posterior edge of the triangular outline of the tooth. The higher pillar, which occurs only in some *Menoceras* specimens, shows a common tendency to form individual extra elements in this place. In the Berlin specimen the crochet of the M3 is positioned more lingually than in the Munich skull. The strong crista in the M2, which replaces the faint crochet, is even more pronounced than in the Munich specimen.

These characters confirm that the oblique fold extending from the protocone to the crochet region in the premolars, the lengthening of the metastyle and the strong crista in the molars are not characters specific to the Munich specimen, but rather represent general characters – or at least tendencies – of the population.

3.3 Comparison of the holotype with the Berlin mandible

The Munich specimen lacks the mandible. Thus, to confirm Wood's (1929: 68) identification of the mandibular fragment of the Berlin specimen it needs to be compared to the holotype. Both specimens are of nearly the same size; they represent in fact the smallest specimens of the Oligocene true rhinoceroses of America. One striking character is the great difference in the wear stages of m1 to m2, indicating a delayed eruption of m2. The talonid is short compared to the trigonid in both specimens, and the connection of the hypolophid to the metalophid is low in both. The paralophid is comparatively long. All these characters are plesiomorphic, but no character can be used to challenge the specific identity of the specimens.

4. Taxonomy

4.1 Status of the genus *Penetrigonias* and its species

The genus *Penetrigonias* was introduced by Tanner & Martin (1976: 212) based on the new species *hudsoni* from the Chadronian (late Eocene) of Nebraska. Despite the clear difference with regard to the molarisation of the upper premolars and the difference in temporal provenience of both types, Prothero (2005: 29) considered the type species *P. hudsoni* Tanner & Martin, 1976 from the Chadronian as synonym of the Whitneyan (late Early Oligocene) *"Caenopus" dakotensis* Peterson, 1920, and, consequently, referred to the species *dakotensis* as the type species of the genus.

4.2 *Penetrigonias hudsoni* and *Penetrigonias dakotensis*

The type specimen of *"Caenopus" dakotensis* Peterson, 1920 is a mandible exhibiting both molar series and the nearly complete premolar series of one side, but lacking the front teeth, showing only their roots and alveoli. The rather uniform pattern of the lower cheek teeth make them nearly valueless for interspecific comparison. The most important character, however, is their small size. Consequently, all upper dentitions and skull remains of small size and similar age have been referred to this species.

As the type specimen of *P. hudsoni* Tanner & Martin, 1976 is an upper premolar series, comparisons to *P. dakotensis* are restricted to referred specimens of both species with complete upper cheek teeth. These show clearly that there are fully molarised premolars in the Whitneyan species *P. dakotensis*, whereas these teeth are still premolariform in the Duchesnean (late Middle Eocene) and Chadronian *P. hudsoni*, which have been lumped together in the same species by Prothero (2005: 32). This difference therefore requires reconsideration. Prothero's assumption that molarisation is a highly variable character rests upon the well known sample of *Trigonias osborni* Lucas, 1900 from the Chadronian *Trigonias* Quarry. The specimens from this sample represent in fact all possible molarisation stages. On the other hand, there exist quite a number of equally rich populations of other species that do not, or only faintly, show variability of this feature. We therefore have to accept that not only the molarisation stage, but also the range of variation may differ from one species to another. A general overview (e.g. Antoine 2002) shows that there are a few species of rhinoceroses that consistently posses non-molariform premolars and numerous others in which the variability includes only molariform and semimolariform stages (stages 5 and 6 in the sense of Prothero 2005: fig. 2.7). A greater variability is found in species just within the process of transformation (e.g. *Trigonias*) and may be restricted to these forms.

There is, indeed, a considerable variation in the premolar morphology of *P. hudsoni*, but specimens exhibiting all premolars in a fully molariform stage have not been described to date. This variability includes rather irregular patterns, especially the presence of a third cross loph in the second and third premolars of specimen no. 105019 of the Frick collection formed by a straight connection of the crista with the protocone by the lack of a hypocone in P4 and an oblique connection of a crochet with the protocone in P2.

As none of the currently known specimen of *P. dakotensis* with well preserved premolars differ in the degree of molarisation, there is no reason to assume a wide variation with regard to this character in this Whitneyan species. As a result, *P. hudsoni* cannot be considered a synonym of *"C." dakotensis*.

Other characters are apomorphic in *P. dakotensis* as well. The plesiomorphic, well developed metacone ribs of the premolars in *P. hudsoni* are not present in the Whitneyan species. Rather, the latter show, as a special trait, a large crista occupying the position of the crochet, which is also present but very small. *P. hudsoni* from the Chadronian of Julians loc., Bates hole (F:AM 105019), does neither possess a crista nor a crochet. There is already a narrow distance between the distinct metastyle ridge and the hypocone edge in M3 in *P. hudsoni*. In *P. dakotensis* the metastyle ridge is shifted even more lingually and combined with a rather lingual position of the crochet. This character represents a synapomorphy with *Menoceras.*

4.3 Uniformity of the genus *Penetrigonias*

As Prothero (2005: 34) noted the genus *Penetrigonias* occurs in the Duchesnean and Chadronian, is missing from the Orellan (earliest Oligocene), but reappears in the Whitneyan. This raises the question as to whether the older and younger groups of specimens in fact are belonging to the same genus. At first glance it is the smaller size that discriminates *Penetrigonias* from the more common genera *Trigonias* and *Subhyracodon*, as well as from the larger-sized genus *Amphicaenopus*, which shows the same interrupted occurrence as *Penetrigonias*. Another common character of Eocene and Oligocene *Penetrigonias* species is the flat skull profile.

There are several other very peculiar characters mainly in the molars that unite the Eocene with the Oligocene specimens. The first and second upper molars have an unusually long metastyle, which is deeply inflected. On the other hand, the metaloph is short and very oblique. The great difference in wear between M1 and M2, caused by a delayed eruption of the latter tooth, does equally occur in *Penetrigonias* and *Teletaceras* Hanson, 1989, and thus may be plesiomorphic. This feature has also been observed in the lower molars of the type specimen. The metastyle rudiment of the M3, i.e. a narrow ridge running down from the ectometaloph crest to the base, has shifted closely to the lingual edge of the ectometaloph in *P. dakotensis*, and thus the cingular flange at the back side is very short. *P. hudsoni* also displays this character, but not quite as extreme, better comparable to the grade of early Rhinocerotini. This shift occurs in different rhinoceros clades at a much later time. Here it begins already in the earliest specimens and is completed in the Whitneyan. These characters have not been observed in any other Eocene or early Oligocene rhinocerotid from America. As a result, the Eocene and Oligocene species should be accepted as congeneric.

4.4 *Penetrigonias hudsoni* and *Penetrigonias sagittatus*

Based on the preceding considerations, *Penetrigonias hudsoni* Tanner & Martin, 1976 is regarded as the type species of the genus *Penetrigonias*. The question as to whether *Subhyracodon sagittatus* Russell, 1982, transferred to *Penetrigonias* by Prothero et al. (1986), represents a separate species can be resolved only based on comparisons to additional specimens of *P. hudsoni*.

4.4.1 Intraspecific variability of *Penetrigonias hudsoni*

Penetrigonias hudsoni from the Chadronian of Nebraska was erected based on three non-molariform premolars of small size and whithout labial cingulum but with tartar deposits on the ectoloph. It turned out to be the smallest individual of the species. A specimen in the South Dakota School of Mines with much worn premolars but including the molars from the Yoder formation of Goshen Co. is somewhat larger than the type but still smaller than another specimen from Julians loc., Bates Hole in Natrona County in the Frick collection (F:AM 105019) with submolariform P2 and P3, but both with an additional ridge connecting the protocone to the crista like the mesoloph in the D2 of *Menoceras*. The P4, however, shows a non-molariform pattern in both specimens. The metaloph is short and has no lingual connection in the first, curved forward to the protoloph in the second. In both the hypocone is attached ony to the protocone but not the metaloph. The other characters are similar to the type specimen which, however, has a deeper lingual groove separating the protocone from the hypocone. This cusp is vestigial in the P4 of the type and the Julians loc. specimens.

In the molars there is less variability. The metacone rib may be present only on M1 or on M1 and M2. The lingual cingulum is present at the protocone and may be interrupted or continuous on its lingual edge, not depending on the tooth position. Secondary folds are absent. The protocone constriction is indistinct. Only the M2 of the Julians loc. Specimen possesses a distinct anterior groove.

4.4.2 Comparison of *P. sagittatus* with *P. hudsoni*

Penetrigonias sagittatus shows the common characters of the genus: The lengthening of the molars, their great difference in wear, and the lingually positioned metastyle stria in M3, as well as the absence of labial cingula in the premolars. On the other hand, it differs from both *Penetrigonias hudsoni* and *P. dakotensis* with regard to the degree of molarisation of the premolars. In the type specimen both P2 are submolariform with an oblique bridge crossing the medisinus in the P2 of both sides. The P3 are molariform, but the cross lophs are less oblique than in *P. dakotensis*. The last premolar, by contrast, is absolutely non-molariform and lacks a hypocone. The short metaloph assumes the plesiomorphic half moon shape frequently seen in primitive rhinocerotoids. This difference in the molarisation within one tooth row shows that it may be only a variation within the variability of morphologies of an incipient molarisation known for *P. hudsoni*. Two nearly unworn premolars from the same sample as the type, figured by Russell (1982: fig. 27), are of the same size. While the P3 is molariform as in the type, the P2 shows a separate hypocone behind the long metaloph that is reminiscent of the hook-like extension in *P. dakotensis*. Both specimens of *P. sagittatus* fit well into the described variability of *P. hudsoni*. As in this species, there are no secondary folds and the cross lophs of the premolars are nearly perpendicular to the ectoloph. All of them possess a second, labial point of the postfossette, pointing to the incomplete fusion of the metaloph with the hypocone. Based on the known dental material, it is not possible to decide if *P. sagittatus* actually represents a separate species. It should be noted that the oblique bridge in the second premolars corresponds with the same character in the Munich specimen (BSPG 1998 I 34) of *P. dakotensis*, whereas the Berlin specimen (MNB Ma 42545) exhibits this feature in P3.

Two cranial characters have been used by Prothero (2005: 34) to separate the species. The very short "postcanine" diastema separating the last upper incisor from the first milk molar in *P. sagittatus* is most probably due to a post mortem crushing near the maxillary premaxillary joint. Even the difference in nasal width may not necessarily serve as a separating character as long as sex differences in this respect are unknown in *Penetrigonias*. In other rhinocerotid species this character is affected by sex differences, as documented by Antoine (2002), among others.

4.5 Comparison of *Penetrigonias* to other genera

4.5.1 *Penetrigonias* and *Menoceras*

Wood (1931: fig. 1) was the first to draw a conjectural line from *"Caenopus" dakotensis* to *"Menoceras cooki"*, the smaller representatives of the pair-horned rhinoceroses of the Early Miocene. Unfortunately, the American species of this genus are the most specialized ones, and thus the common characters are masked by additional autapomorphic traits. It is therefore necessary to include the more primitive and dolichocephalic species of Europe in such comparisons as well.

4.5.2 The European species of *Menoceras*

Only one skull has been reported to date from Europe that exhibits the high, knob-like horn bases of the *Menoceras* type, and therefore the determination of other specimens must rely exclusively on dental characters. On the other hand, the famous skull from France, *Pleuroceros pleuroceros* (Duvernoy, 1853), has laterally directed horns and represents the *Diceratherium* type. Its teeth are absolutely worn down, so that the only visible character is the continuous cingulum around the back side of M3. This is the reason why the most recent study of this genus (Antoine et al. 2010) is based essentially on referred specimens, mainly the postcranials published by De Bonis (1973: textfigs 43–47), but also the skull from Paulhiac in the NMB figured by Viret (1958: fig. 77). This skull, however, cannot be referred to *Pleuroceros pleuroceros* because of its upright horn bases near the midline and the lack of a continuous cingulum around the posterior side of M3. The latter character, indeed, frequently occurs in American *Diceratherium* species.

Unfortunately, it has not yet been possible to determine other specimens of this taxon based on dental characters. The misinterpretation of specimens with *Menoceras*-like horn bases as *Pleuroceros* or even *Diceratherium* (e.g. De Bonis 1973: 149) has caused considerable confusion. The study of Antoine et al. (2010) rests upon dental and skeletal remains of European representatives of the *Menoceras* clade, erroneously referred to *Pleuroceros*.

The first named species from the early Miocene of Europe with dental traits resembling the American *Menoceras* is *Diceratherium zitteli* described by Schlosser (1902: 224). The type specimen from an Early Miocene fissure filling near Pappenheim in Bavaria, Germany, is a fragment of a juvenile maxilla containing milk molars and well preserved germs of the premolars. These are fully molariform and have strongly oblique cross lophs, including a very narrow medisinus. On the other hand, the postfossette is very wide, precisely as in *Penetrigonias dakotensis*. The strongly worn D2 shows a lingual contour reminiscent of the three-lophed D2 of the American *Menoceras arikarense* (Peterson 1920: pl. 65, fig 2). More complete dental series show also the molar characters and provide an idea of the variability. *Menoceras* first appears in the earliest Miocene of Paulhiac (Viret 1958: fig 77) in southern France; another, slightly younger specimen comes from Flörsheim near Frankfort (Heller 1933: 299), and a third one from Velleron (Roman 1912: 112) in Switzerland. All specimens exhibit a shortened back side of the M3 with a very short cingulum in this place. The first and second molars generally are of the rhinocerotid outline, with a less pronounced antecrochet than in *Menoceras arikarense*. Their crochet is short and forms an angle with the metaloph. The protocone grooves are variable. In the premolars the lingual cingulum is not continuous. The metaloph is very oblique, and sometimes its connection to the ectoloph is not located at the metacone, but rather occurs more anteriorly, like the pseudometaloph of Antoine (2002: 148) .

All these specimens form one size group. *Diaceratherium floersheimense* Heller, 1933 is a junior synonym of *Menoceras zitteli*. The skull fragment from Wischberg in Switzerland, described as *Pleuroceros pleuroceros* by Schaub & Hürzeler (1948: 364), is also a representative of *Menoceras* in Europe. Its description notes a certain elongation of the ectoloph, especially the metastyle, which is less pronounced than in *Penetrigonias*. It was determined by its similarity to the skull from Paulhiac (Viret 1958: fig. 77), which differs from *Pleuroceros* in the position of the horns close to the midline and more terminally on the nasals. If all the postcranials figured and described by De Bonis (1973: 150–157) from Paulhiac belong in fact to this genus, then the taxonomic affiliation is doubtful and in need of revision. Especially the entocuneiform (De Bonis 1973: fig. 46, no. 6) is morphologically more similar to *Aceratherium* than to *Menoceras*.

4.5.3 *Menoceras arikarense* (Barbour, 1906)

The type species of the genus *Menoceras* is more specialized than its European relatives. Its skull is considerably shorter and there are thick layers of tartar on the ectoloph, thinner ones on the lingual side. The protocone constriction is much more advanced and the crowns of the cheek teeth are higher. The lingual cusps are more massive than in the European species. Moreover, the medisinus is very narrow, especially in the premolars, but the postfossette is also narrow. The secondary folds in the crochet region are more complex. There may be more than one fold, forming a series of projections from the crochet to the crista. This tendency is most clearly expressed in M3, but in some specimens does also occur in other molars. The lingual cingulum may be continuous, but one or two interruptions are more common. In all cheek teeth the ridges on the outer wall are less prominent than in the European species. The postcranial bones are long and slender compared to the specimens described by De Bonis (1973: 150–157).

4.5.4 *Menoceras* and *Penetrigonias dakotensis*

In *P. dakotensis* we find several characters foreshadowing the later development of *Menoceras* that are not present in the Chadronian *Penetrigonias* species. Especially the straight and oblique cross lophs of the premolars and wide postfossette are similar to this condition in *M. zitteli*. The molars of *P. dakotensis* show only a short crochet, but a very strong crista in the space that is occupied by the crochet in other rhinoceroses. This crista is situated near the origin of the metaloph, not more mesially as in most rhinoceroses. In a similar way the crochet and crista may form a continuous series of folds in some specimens of *Menoceras arikarense*.

The back side of the M3 is shortened in both genera. In *Menoceras* the outline of the other molars, however, is more similar to non-elasmotherine rhinoceroses. It has a longer metaloph and shorter metastyle of the first two molars compared with *Penetrigonias*. In the premolars of *Menoceras* there are no irregular crests or bridges, which are found in several specimens of *Penetrigonias* (see Fig. 1a, b). In the second milk molar of *Menoceras*, however, a mesoloph is present that connects the crista to the lingual cingulum.

4.6 American genera possibly related to *Menoceras* and *Penetrigonias*

The small-sized *Gulfoceras westfalli* Albright, 1999 from the Texas gulf coast, contemporaneous with *Menoceras*, is similar in size and M3 back side

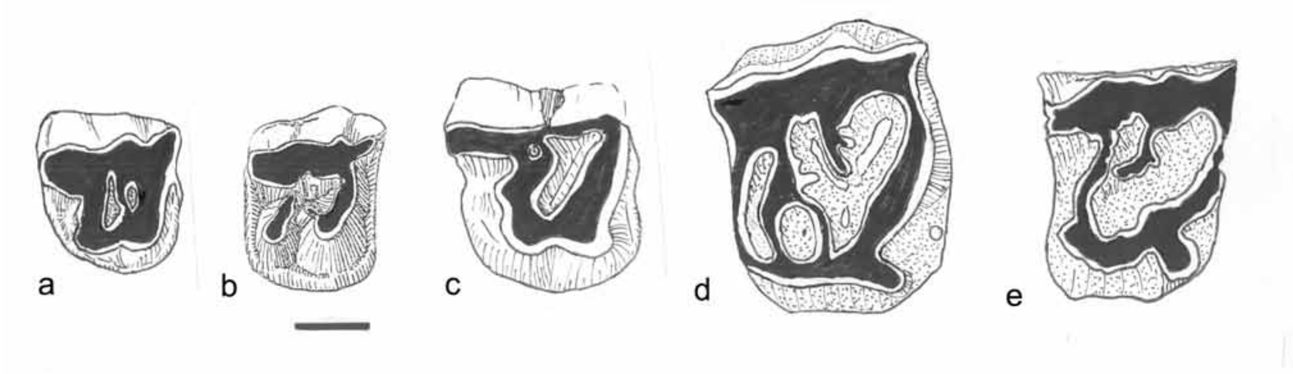

Figure 1: Upper premolars of *Penetrigonias* and some Elasmotheriini. **(a)** *P. hudsoni*, F:AM 105019, right P3. **(b)** *P. dakotensis*, MNB 42545, right P3 (after Wood 1929: fig. 5). **(c)** *Bugtirhinus praecursor*, MNHN Pak 725, right P4 (after Antoine & Welcomme 2000: pl. 1, fig. 7a). **(d)** *Hispanotherium grimmi*, BSPG 1968 VI 1, right P3; scale bar = 1 cm. **(e)** *Sinotherium lagrelii*, PIUU, left P4 (inverted) (after Ringström 1924: pl. 12, fig. 4); scale bar = 0,5 cm. Black = dentine, dotted = functional tartar or cement.

to *Penetrigonias dakotensis*, but shows an aberrant lingually situated crochet. This crochet position may sometimes also occur within the variability of *Menoceras*. Also the crown height is similar to this genus. Other teeth than M3 have not been described to date. There is no reason to separate *G. westfalli* from *Menoceras* generically until other parts of the dentition exhibiting characters different from this genus become available. The small size, however, may not be the result of dwarfing, but rather of not increasing over the size of *Penetrigonias.* Also an assignment to this genus might therefore be possible.

Skinneroceras manningi Prothero, 2005 from the early Arikareean is a small rhinoceros with a narrow, long skull and exaggerated temporal cristae. The diastema is long and there is no trace of an I2. The teeth are worn and show only a few characters, especially a large antecrochet similar to that seen in aceratheres. The outline of the M3 is not triangular but trapezoid. This latter character, together with the narrow skull form and the large antecrochet of the M3, exclude the specimen from the Menoceratini and render a relationship to the Aceratheriini more probable. The tooth dimensions are slightly larger than in *Penetrigonias.*

Prothero (2005: 33) ascribed an isolated tetradactyle manus from the late Whitneyan to *Penetrigonias dakotensis* because of its small size. This determination may be debated because the size of this fossil also fits *Skinneroceras*. *Skinneroceras* indeed is a rare genus, and its only specimens occur in a rather short stratigraphical distance after the cited manus. As a result, the fossil does not present evidence in favor of a tetradactyle manus in *Penetrigonias*.

5. *Penetrigonias* and the origin of the Elasmotheriini

In his cladistic analysis Antoine (2002: 35) established a close relationship between the American pair-horned rhinoceros *Menoceras* Troxell, 1921, and the one horned Old World Elasmotheriini. This astonishing result rests upon a sound complement of important characters.

According to Prothero et al. (1989: 328), *Menoceras* appeared as an immigrant in North America with no known closer relatives. If this is the case, then the probable common ancestor of this genus and the Elasmotheriini would be located somewhere in Eurasia. Establishment of a close relationship between *Penetrigonias* and *Menoceras*, as well as the discovery of an European *Menoceras* species, makes it more puzzling to follow the history of *Penetrigonias*. As to whether *Menoceras* actually immigrated into North America from Asia or evolved in a non-fossiliferous region of North America remains unclear.

5.1 Small early Elasmotheriini

Forster-Cooper (1934: 602, pl. 65, figs 26, 28–30) first described rare remains of a very small rhinocerotid from the Bugti Beds of Pakistan as *Ceratorhinus tagicus*, a name that is not valid, but was applied in that time to nearly all small rhinoceroses. The taxon was believed to be of early Miocene age. Heissig (1972: 57) established its parenty with the new genus *Caementodon*, a predominantly Middle Miocene elasmothere.

French expeditions between 1995 to 1999 yielded additional material of this small species. It was named *Bugtirhinus praecursor* by Antoine & Welcomme (2000: 798), and its age was determined as earliest Miocene (Antoine et al. 2010: 140). As a result, we now have decent knowledge of the upper cheek teeth, whereas the lower ones and the postcranial elements are known only partially. The most striking character of this species is the small size compared to that of all later members of the tribe. The upper molars have a very long metastyle, which is deeply inflected and therefore a short metaloph. There are thick layers of functional tartar (see p. xxx of this paper) – not cement as frequently written in the literature. Crochet and antecrochet, as well as strong protocone grooves, are normally developed. The antecrochet is thick and well rounded at its base, and forms a sharp and narrow pillar at the top. In the M2 there is a tiny secondary fold on the protoloph opposing the crochet. M1 has a small pillar in the medisinus entrance.

The last molar is triangular with a far lingually displaced metastyle rudiment and only faint cingular traces on the back side. Its crochet may be simple or plicated. There is a small cingular pillar in the medisinus entrance.

Most of the molar characters are also present in the larger and geologically younger *Caementodon oettingenae* Heissig, 1972, with the exception of special characters of the secondary folds. The ectoloph is more flattened labially. The back side of M3 is equally short, its crochet is forked. Generally there is much more tartar covering the teeth.

The premolars of *Bugtirhinus* (see Fig. 1c) are rather short and submolariform. Their ectolophs are strongly undulating and show a markedly narrow metacone rib. The postfossette is two-fold basally divided by a longitudinal swelling that joins the cingulum. The lingual part is shallower and, as a result, in later stages of wear only a short labial triangular stub of the postfossette remains. The swelling forms a posterior bulge on the metaloph. There is a rather labially situated crochet. The lingual cingulum is absent or occurs in the form of a short ledge behind the protocone. The metaloph is shorter than the protoloph in the last premolar in a way that the lingual side is oblique, with a shallow groove between the two cusps.

In *Caementodon* the submolariform premolars are more advanced but not yet semimolariform. The lingual groove of the postfossette is lacking, which excludes this genus from the ancestry of all later Elasmotheriini where the two-fold postfossette is preserved until *Elasmotherium*. The lingual separation of the protocone and metacone is more accentuated. The crochet is considerably longer. The greatest differences occur in the flattened ectoloph and the increased crown height.

Later genera of the Elasmotheriini often show irregular crest connections in the upper premolars (see Fig. 1d, e). It is questionable whether these variations have been present since *Penetrigonias hudsoni*, or document the loss of morphological stability due to increasing hypsodonty. Similar traits have also been observed in *Coelodonta* connected with a moderate hypsodonty.

5.2 Comparison of early Elasmotheriini with *Penetrigonias* and *Menoceras*.

The prolongation of the metastyle and the strictly triangular M3 are characters uniting *Bugtirhinus, Caementodon,* and *Penetrigonias*. *Menoceras arikarense*, however, has a shorter metastyle, even if the triangular last molar and the strong development of tartar are common characters. A look at the premolars reveals that the early elasmotheres have less molarized premolars than all *Menoceras* species and also than *Penetrigonias dakotensis* whose premolars are fully molariform.

The upper premolars of the early elasmotheres, including *Hispanotherium (Aegyrcitherium) beonense* Antoine, 1997, retain the strongly undulating ectoloph and two-fold postfossette of the Eocene and early Oligocene *Penetrigonias* species. It remains unclear whether these species had a rather short first upper incisor as seen in the early elasmotheres. On the other hand, already *Bugtirhinus* has reduced lingual cingula of the premolars that are retained in all American relatives of this genus. The number of upper incisors remains unknown. As the size of *Bugtirhinus* barely exceeds that of *Penetrigonias dakotensis* and the molarisation of the upper premolars is intermediate between the Eocene and late Oligocene species of this genus, the reduction of cingula, heavier development of tartar and later occurrence of the rather similar *Caementodon* in the same region are the only few arguments that could be used to exclude *Bugtirhinus* from *Penetrigonias* and regard it as an early representative of the true elasmotheres. The most conspicuous character, i.e. the development of a median horn, has not been documented to date for either *Bugtirhinus* or *Caementodon.* No species of *Penetrigonias*, however, shows any trace of a horn on frontal or nasals.

A quick look at the Middle Miocene elasmotheres shows that the larger sized genera have retained the two-fold postfossette and submolariform stage of the premolars. *Hispanotherium* Crusafont & Villalta, 1947 and *Beliajevina* Heissig, 1974 possess a strongly curved metaloph reminiscent of very early premolariform stages, as in *Teletaceras* or *Forster-*

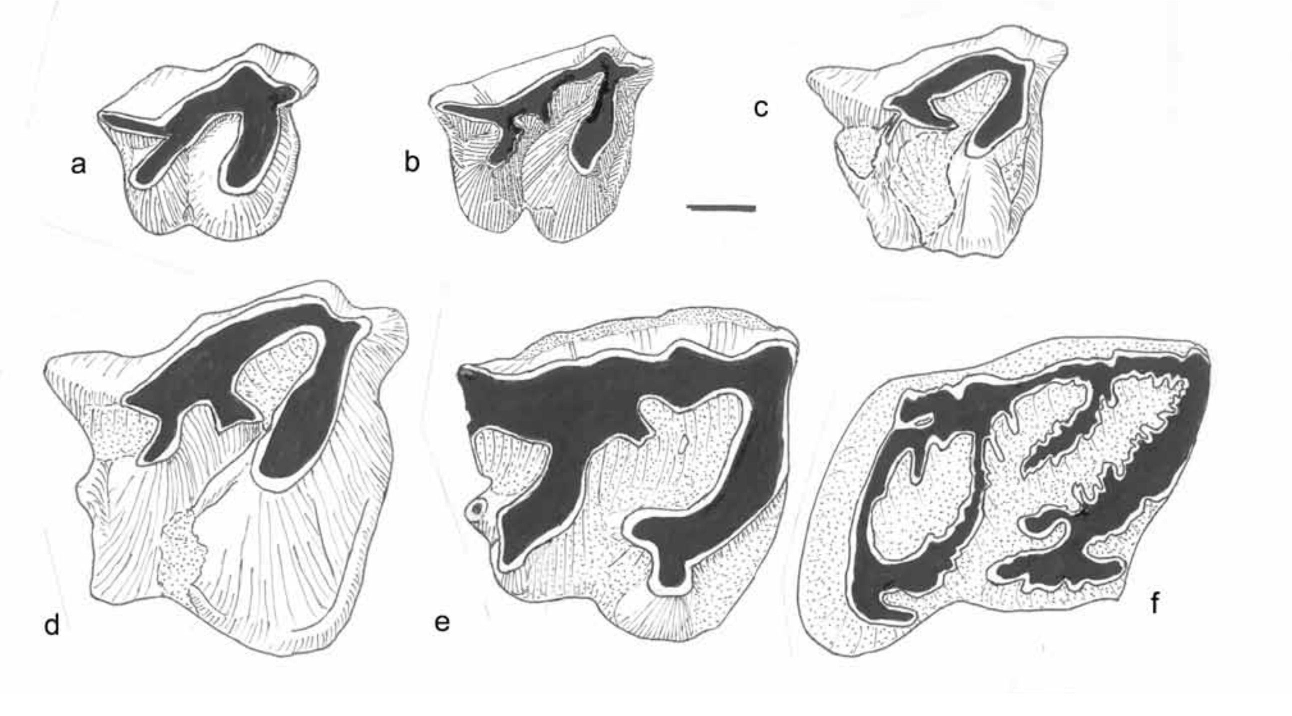

Figure 2: Upper molars of *Penetrigonias* and some Elasmotheriini. **(a)** *P. hudsoni*, F:AM 105019, right M2. **(b)** *P. dakotensis*, MNB 42545, right M2 (after Wood 1929: fig. 5). **(c)** *Caementodon oettingenae*, BSPG 1956 II 364, right M2. **(d)** *Hispanotherium (Aegyrcitherium) beonense*, MHNT Béon SN2615, left M2 (inverted) (after Antoine 2002: fig 124a). **(e)** *Hispanotherium grimmi*, holotype, BSPG 1968 VI 1; scale bar = 1 cm. **(f)** *Elasmotherium caucasicum*, PIN 31, right M2 (after Borissiak 1914: pl. 1, fig. 2); scale bar = 0,5 cm. Black = dentine, dotted = functional tartar or cement.

cooperia Wood, 1939. The postfossettes of these taxa are extremely short and tend to disappear. Furthermore, there is a tendency in these taxa to develop irregular folds, which are extremely rare in other rhinoceroses, but have been documented in the few known specimens of *Penetrigonias hudsoni*. From the beginning of the size increase in *Hispanotherium (Aegyrcitherium)* the crista is enlarged, sometimes at the expense of the crochet, as seen in *Penetrigonias dakotensis* (see Fig. 2b–f). Much later, in the late Miocene *Sinotherium* Ringström, 1924 and the Pleistocene *Elasmotherium* Fischer, 1808 the premolars became molariform.

6. Comparison with early Rhinocerotini

Rhinocerotini share with the Elasmotheriini several apomorphic characters. Their earliest appearance is a little later in the Middle Miocene of South Asia and Europe with the scarcely divergent genera *Lartetotherium* Ginsburg, 1974 and *Gaindatherium* Colbert, 1934. These taxa are characterized by a tridactyle manus, triangular last upper molars and double rooted first lower premolars. If we consider the articulation of the ulna with the lunar as a functional consequence of tridactyly, this may explain why this character occurs in both groups, but arises in elasmotheres not earlier than their first Asian member *Bugtirhinus* (Antoine 2000: 811). Both groups share well developed median horns. The general loss of lingual cingula in the upper premolars and the additional folds in the crista and crochet region are highly homoplastic characters and often reversed depending on the feeding habits.

On the other hand, the earliest Rhinocerotini are larger than the contemporaneous Elasmotheriini. Their premolars are molariform or semimolariform within the variation and have a one-fold postfossette as in all other rhinocerotid tribes. In the postcranials the ulna articulates with the lunar, and this bone has not only a rear articulation with the scaphoid, but also a prolongation of the distal articulation with the quadrate to the rear.

The loss of the posterior articulation of scaphoid and lunar already in *Bugtirhinus* is a typical elasmotherine apomorphy that excludes this genus from the ancestry of Rhinocerotini. The common characters shared by both tribes, nevertheless, point to a closer relationship than with other tribes that acquired tridactyly only in some members and much later. All early tridactyle rhinoceroses known to date come from North America. The first tridactyle Teleoceratini from Europe are of late early Miocene (MN 4) age; tridactyle Aceratheriini occur as late as the late Miocene.

7. Branching of the early Rhinocerotidae

Phylogenetic analysis of the early rhinoceroses

Characters: **Unique and important, Important but known as otherwise homoplastic,** Supporting the nodes but of unknown importance

1. **Lower i2 enlarged**
2. **Metastyle of M3 reduced or lost**
3. **Upper I1 enlarged, meeting the lower one**
4. **Reduction of lower canine and i3**
5. Size increase
6. **Entoconid present in p4**
7. **Tridactyle manus**
8. Delay of M2 eruption diminished
9. **Proximal MT IV facet extended caudally**
10. **Skull profile concave**
11. **Double rooted p1 within the variation**
12. Beginning of molarisation in upper premolars
13. **Moderate shortening of M3 back side**
14. **Tendency to irregular crests in upper premolars and crista enlargement in molars**
15. **M1-M2 metastyle lengthened**
16. **M2 metaloph shortened**
17. **Upper I3 lost**
18. **Upper canine lost**
19. Interruption of lingual cingulum in P
20. **Indistinct Crista or Crochet in Molars**
21. **Postfossette of P wide and long**
22. **Complete molarisation of P3 and P4**
23. **M3 crochet far lingual**
24. **Metaloph of P oblique, in front of Metacone**
25. **Postcingulum of M3 extremely shortened**
26. **Flattening of ectoloph pillars**
27. **I1 elongated and chisel like**
28. **Most upper premolars molarised to submolariform stage**
29. **Hypocone constriction in M**
30. **Crochet in upper premolars**
31. **M1-2 large crista instead of crochet**
32. **Submedian pair horn bosses**
33. M1-2 crochet definitely at metaloph bend.
34. **Articulation of the ulna with the lunate**
35. **Functional tartar on cheek teeth**
36. **Median single or tandem horns**
37. **No posterior scaphoid and lunate joint**
38. **Postfossette of upper premolars simplificated**
39. **Lateral horn formation**
40. **Additional lengthening of the distal articulation of lunate and pyramidal**
41. **p1 generally single rooted**
42. **i2 greatly enlarged and upturned**
43. **I2 lost**
44. **Small median split horn base, which is often reduced**

8. Early history of the Rhinocerotinae

8.1 Stem group Rhinocerotidae

The earliest known Rhinocerotidae are already more advanced with regard to the evolution of a prolonged, blade like upper incisor than the *Amphicaenopus* and *Ronzotherium* group, which appear somewhat later. Their common ancestor must have been similar to the indricotheriid genus *Forstercoo-*

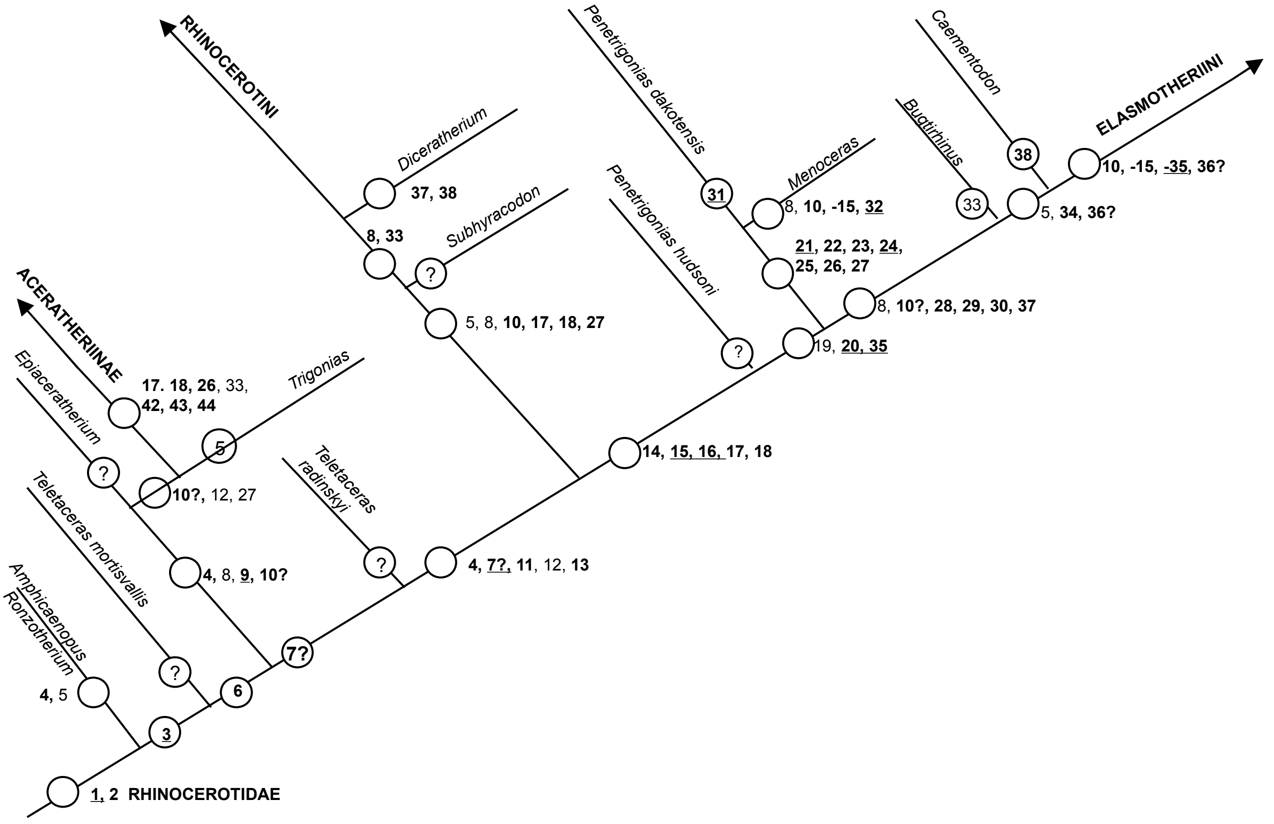

Figure 3: Phylogenetic relations of early Rhinocerotinae (? with number = possible introduction of apomorphy, ? without number = taxon without known autapomorphy)

peria, but different in the enlargement of the second lower incisor and a beginning reduction in size of the upper canines. These characers are not yet present in the Uintan (Middle Eocene) genus *Uintaceras* (Holbrook & Lucas, 1997), which therefore cannot be included in the Rhinocerotidae. The plesiomorphic tetradactyle manus of this genus also occurs in early rhinoceroses, as well as in early Indricotheriidae. A slightly reduced metastyle of the last upper molar is still present in *Teletaceras*, the earliest known true rhinoceros of middle Eocene age (late Uintan or Duchesnean). In early rhinoceroses the structure of the molars and premolars is so similar to that of indricotheres that it is generally not possible to assign isolated cheek teeth with confidence to either of the groups. This similarity and a tetradactyle manus are the prime arguments used to keep the indricotheres separate from the tridactyle hyracodonts and consider them a sister group of the Rhinocerotidae. *Forstercooperia* and *Uintaceras*, if it makes sense to keep it separate, may form a stem group, both without enlargement of i1 or i2.

The first split within Rhinocerotidae occurred at an evolutionary level where the ectoloph of the upper molars was undulating in the same manner as in indricotheres, meaning with broad para- and metacone bulges without any distance in between. The shearing complex of upper and lower enlarged incisors was not yet established. The prolonged but not blade-like upper incisors therefore met the lower ones punctually and without much wear. This first tetradactyle group comprising the Eurasian *Ronzotherium* and the American *Amphicaenopus* had more enlarged lower incisors than other contemporaneous rhinoceroses, but in a straight horizontal position and with a tear drop-shaped cross section. The triangular or even knob-like first upper incisors, however, remained in a rather primitive stage and were only slightly elongated. The upper small canine or third incisor was still present but smaller than the second one. The lower premolars were not molarised, with an incomplete hypolophid, sometimes even without an entoconid.

The earliest known true rhinoceros of North America, *Teletaceras,* already had a somewhat curved lower tusk with a triangular section, which is characteristic of all later rhinoceroses. This genus was thought to be tridactyle by its author (Hanson 1989: 390). However, the indirect evidence provided in the original publication is not persuasive. It still had a full set of upper incisors and a canine of similar size, precisely as the later and larger *Trigonias*, a clearly tetradactyle genus.

Near this evolutionary level the most important split separated the tridactyle American stock from the Eurasian tetradactyle lineages. Both had also representatives on the other continent, but in the late Oligocene no tetradactyle rhinoceroses survived in America, whereas the tridactyle *Menoceras* had a holarctic distribution. All tridactyle rhinoceroses of this time possessed a last upper molar characterized by a more or less narrow back side and triangular outline, whereas in the tetradactyle group this tooth has a trapezoid outline with a broad back side. The only indisputable tetradactyle rhinoceros in the late Eocene of America with a fully evolved shearing incisor complex, *Trigonias*, has also a trapezoid last upper molar. Also in other characters it remained plesiomorphic, especially with regard to the incomplete hypolophid of one or several of the lower premolars. This combination of plesiomorphic characters, combined with a pentagonal proximal articulation of the fourth metacarpal, represents the onset of the Aceratheriinae, including the small *Epiaceratherium* (Abel, 1910), which in Europe is most similar to *Trigonias*. The following history of the Aceratheriinae will not be dealt with here.

8.2 The Rhinocerotinae

The other subfamily, the Rhinocerotinae, however, shares the following synapomorphies: (1) a triangular last upper molar, (2) a tridactyle manus and (3) a triangular outline of the proximal facet of the fourth metacarpal bone. The most striking character of all middle Miocene and later members of this group is the evolution of rather large median horns that appeared later, probably independently in both of its tribes. No indication of any horm-like structure on the nasals or frontals is seen in the earliest members. However, also in the Aceratheriinae the presence of a small median horn base, mostly split by the internasal suture, first appears in the late Oligocene. As a result, it can be assumed that any dermal display structure was preforming the later horn but left no trace on the nasal bone. The size increase of the horn occurred probably independently in Rhinocerotini and Elasmotheriini.

8.2.1 The Rhinocerotini

The only extant tribe of Rhinocerotidae is characterized by a slightly elongated metastyle only in one early species and no tendency of irregular patterns in the premolars. A closer parenty with *Penetrigonias* is therefore less probable than with *Subhyracodon* (Brandt, 1878) or *Diceratherium* (Marsh, 1875). The latter tridactyle genera retain a second upper incisor, precisely as the early Rhinocerotini. However, *Subhyracodon*, the earliest Chadronian (late Eocene) genus of this group, was hornless. *Diceratherium* had paired laterally directed horn bosses. Both genera are very close to one another with regard to dental and cranial characters. If they represent stem Rhinocerotini, then the splitting of the Rhinocerotinae into two tribes occurred prior to the first appearance of *Subhyracodon* in the late Eocene.

The Rhinocerotini evolved a blade like first upper incisor relatively early in *Subhyracodon*, a consequence of its shearing function with the second lower incisor. The first horns in *Diceratherium* have been paired, but more laterally positioned (not subterminal as in *Menoceras*). The third upper incisor and canine became reduced relatively early, but the second upper incisor remained until incisors disappeared in some later lineages. The molarisation was completed already in *Diceratherium*, which was the latest member of the tribe in America. There is a considerable gap in the record of this tribe to the first appearance in South Asia, where its first record in the late early Miocene represents already two or three lineages. Even there the record is scarce with regard to most species, and thus the individual lineages cannot be followed, with the exception of the one leading to the recent unicorn. All known skull remains from the middle and late Miocene show the typical median subterminal horn base on the nasals.

8.2.2 The Elasmotheriini

The first elasmotheriine, *Penetrigonias* from the late Duchesnean (latest Middle Eocene), was characterised by the lengthening of its upper molars, a trend to develop irregular crests in the upper premolars, and a changing position of crista and crochet. *Penetrigonias* was rather small sized and developed molarised premolars in its latest species, *P. dakotensis*. This taxon probably gave rise to *Menoceras*, which evolved a blade like incisor and was the first within this tribe to produce paired paramedian horns. The molars were reduced in relative length. The manus of *Penetrigonias* remains unknown, that of *Menoceras* is tridactyle. As a result, we do not know if tridactyly represents a true synapomorphy of Elasmotheriini and Rhiocerotini or is homoplastic, as in some genera of other tribes.

The bulk of Elasmotheriini did not follow the general rhino trends. They remained plesiomorphic in the pointed shape of the upper incisor before it was entirely reduced in later genera. Also the premolars remained in a submolariform stage until the late Miocene and retained a two fold postfossette.

This leads to the conclusion that the typical elasmotheres must have split from the *Penetrigonias-Menoceras* lineage before the Whitneyan (late early Oligocene).

Its earliest Eurasian member, the early Miocene *Bugtirhinus praecursor* from South Asia, was still characterized by submolariform premolars and first

Table 1: Comparative measurements (in mm) of upper cheek teeth of early elasmotheres. (1) from Antoine & Welcomme (2000: tab. 3), (2) M3 in IVAU from Mochiwala, Lower Chinji, (3) from Antoine (1997: tab. 1)

Species	*Penetr. hudsoni*	*Penetr. hudsoni*	*Penetr. dakotensis*	*Menoceras zitteli*	*Menoc. arikarense*	*Bugtirh. praecursor*	*Caementod. oettingenae*	*Hisp. (Aeg. beonense*
Locality	Goshen co.	Julians loc.	South Dakota	Paulhiac	Agate Springs	Dera Bugti 1)	Kadirpur /Mochiwala 2)	Montréal du Gers 3)
Collection	SDSM	F:AM	BSPG	NMB	BSPG	NHM	BSPG / IVAU	MNHT
Nr.	5331	105019	1998 I 34		1964 X 107		1956 II 364	Béon 1989
P2-M3	119	129	138	168	157	--	--	--
P2-P4	51	55,5	58	75	66	--	--	--
M1-M3	71	75	84	100	98	--	--	--
M1 LxW	20 x 24	21 x 29	25 x 28	31 x 39	32,5 x 38	29 x 30,5	34 x 42	50 x 51
M2 LxW	24 x 30	30 x 29	31,5 x 33	36 x 39	34,5 x 39	35 x 32	43 x 45	57 x 56
M3 LxW	28,5 x 27	28 x 28	35 x 32	38 x 39	34,5 x 34	34 x 39	44 x --	56 x --

developed functional tartar in its cheek teeth. One of its successors, *Caementodon oettingenae*, lost the plesiomorphic lingual branch of the postfossette of the upper premolars, while the others, which began with the size increase and formation of median horns, retained it. This character, along with the flattening of the outer wall of the premolars, indicate that *Caementodon* was an early side branch of the elasmotherine clade that was more advanced in these traits than most later genera of the group. The first upper incisor remained triangular in this lineage and was reduced and finally lost during the Miocene.

The lineage of the early elasmotheres is further corroborated by the size development, which proceeds at a slower rate than in most other rhinoceros lineages, before the adaptation to abrasive food started in the Eurasian Elasmotheriini. In this lineage the size increased rapidly during the Miocene until they topped all other rhinoceroses in the late Miocene (Tab. 1).

There are two reversals in the cladogram (Fig. 3): The functional tartar was lost when enough cement was added to the tooth crown already in the germs of the cheek teeth. The lengthened metastyle of the upper molars is reduced to "normal" proportions both in *Menoceras* and the later Elasmotherini. This prolongation can be interpreted as an early adaptation to a rather harsh diet bacause it is also observed in the Amynodontidae. The teeth probably became broader as a consequence of higher tooth crowns in *Menoceras* and most later Elasmotheriini which produced additional cement to withstand abrasive food. The re-appearance of a metastyle of the last upper molar in at least two forms, i.e. the Pleistocene woolly rhinoceros *Coelodonta* and the latest Plio-Pleistocene elasmotheres, is an adaptation to the maximum enlargement of the molar surface. It suggests that the genetic information for this structure was not abandonned, but rather was suppressed when these molars became triangular.

8.3 Systematical consequences

The analysis allows a simplification of the systematic arrangement proposed by Heissig (1973: 30) in the following way:

Family: Rhinocerotidae
Stem group Rhinocerotidae: *Teletaceras, Amphicaenopus, Ronzotherium*
Subfamily Aceratheriinae
    Stem group Aceratheriinae: *Epiaceratherium, Trigonias*
    Tribe: Aceratheriini – not resolved in this analysis
    Tribe: Teleoceratini – not resolved in this analysis
Subfamily Rhinocerotinae
    Tribe: Rhinocerotini
        Stem group Rhinocerotini: *Subhyracodon, Diceratherium*

Subtribes: Rhinocerotina, Dicerotina, Dicerorhinina, (Coelodontina)

Tribe: Elasmotheriini

Stem group Elasmotheriini: *Penetrigonias, Menoceras*

Subtribe: Caementodontina: *Bugtirhinus, Caementodon*

Subtribe: Hispanotheriina: *Hispanotherium, Begertherium, Beliajevina, Tesselodon?, Gobitherium, Kenyatherium, Huaqingtherium*

Subtribe: Elasmotheriina: *Iranotherium, Ningxiatherium, Sinotherium, Parelasmotherium, Elasmotherium*

Despite the results of the analysis the morphological similarity of *Penetrigonias dakotensis* to the type species *Penetrigonias hudsoni* is so strong. As a consequence, I hesitate to propose a separate genus for it as an orthodox cladist might be inclined to. The similarity of several characters to *Menoceras*, however, prove that the species belongs to a separate side branch, and thus cannot be affiliated to this genus.

9. Conclusions

The Munich specimen of *Penetrigonias dakotensis* from the early Oligocene of Dakota represents a key fossil for bridging the gap between the Eurasian Elasmotheriini and their American stem group, the genus *Penetrigonias*. Among the rhinoceroses displaying numerous homplastic trends this tribe exhibits a few specific characters and resists the general tendencies of molarisation of the premolars for a long time, until the late Miocene. Only one side-branch, represented by the species *Penetrigonias dakotensis* and the genus *Menoceras*, develops molariform premolars and a blade-like upper incisor, whereas this tooth remains pointed in the main lineage until lost. It is impossible at present to determine whether the most striking characters uniting the tribes of Elasmotheriini and Rhinocerotini, i.e. the huge median horns and the tridactyle manus, represent true synapomorphies. The seemingly less important traits of a triangular last upper molar and the joint of ulna and semilunar in the carpus are most probably true synapomorphies of the subfamily Rhinocerotinae.

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