Kansu. -*Acta. Paleont. Sinica*, 4: 447-460.

Zhai, R. (1977): Supplementary remarks on the age of Changxindian Formation. -*Vert. PalAsiatica*, 15: 173-176.

Zhang, Y., You, Y., Ji, H., and Ting, S. (1978): Cenozoic stratigraphy of Yunnan.

-*Prof. Pap. Strat. Paleont.*, 7: 1-21.

Zheng, J., Tang, Y., Zhai, R., Ting, S., and Huang, X. (1978): Early Tertiary strata of Lunan Basin, Yunnan. -*Prof. Pap. Strat. Paleont.*, 7: 22-29.

20. *TELETACERAS RADINSKYI*, A NEW PRIMITIVE RHINOCEROTID FROM THE LATE EOCENE CLARNO FORMATION OF OREGON

C. BRUCE HANSON

Teletaceras, a new genus of rhinocerotid, includes the most primitive members of the family. A large quarry sample from the uppermost Clarno Formation (Duchesnean) of north-central Oregon provides the hypodigm for the type species, *T. radinskyi*, the least derived and probably earliest representative of the genus and family. It exhibits the derived incisor tusk complex characteristic of the Rhinocerotidae, while retaining an unreduced dental formula, strongly ribbed premolar ectolophs, and many skull characters primitive for the superfamily Rhinocerotoidea. Its tridactyl manus may also be primitive for rhinocerotids and hyracodontids, as are most other carpal and tarsal characters.

Two species originally referred to *Eotrigonias* are transferred to *Teletaceras*, extending its known geographic range to southern California, United States, and Maritime Province, Soviet Union, and its known temporal range to early Chadronian.

Introduction

The Rhinocerotidae, as now characterized, include previously described forms (*Penetrigonias* and *Trigonias*) as old as Chadronian and possibly latest Duchesnean. *Trigonias* Lucas (1900) has been long recognized as a very primitive rhinocerotid because of its nearly complete incisor formula and presumed primitive tetradactyl manus. Tanner and Martin (1976) described *Penetrigonias* on the basis of an unfortunately incomplete type, but numerous congeneric specimens in existing collections (e.g., the Calf Creek l.f. species "*Subhyracodon*" *sagittatus* Russell, 1982--see discussion following), now document its phyletic position as a rhinocerotid even more primitive than *Trigonias*.

Nonetheless, substantial differences remain between *Penetrigonias* and *Hyrachyus*, a genus historically implicated in rhinocerotid ancestry.

Other "primitive rhinoceroses" of similar or greater age (Wood, 1927, 1929, 1938, 1963) had been assigned to the Rhinocerotidae primarily on the basis of characters now known to have arisen independently in hyracodontids, and they are now placed in the latter family in the classifications of Radinsky (1966) and Prothero, Manning, and Hanson (1986). The Asian genus *Ilianodon* Chow and Xu (1961) bears a tusk thought to be an I_2, but its relatively erect orientation suggests that it is a canine and that *Ilianodon* is a hyracodontid as well.

Teletaceras radinskyi, the type species of the new genus described here, predates *Penetrigonias* and *Trigonias*. While exhibiting the key rhinocerotid synapomorphies, I^1/I_2 tusks and reduced premaxilla, it retains many more primitive character states than those genera, bridging much of the remaining "morphologic gap" between *Hyrachyus* and the rhinocerotids. The phyletic relationships of *Teletaceras*, inferred from the type species, have already been reported in Prothero *et al.* (1986) and in Prothero, Guérin, and Manning (this volume, Chapter 16), where it is identified as the "Clarno rhino," the sister taxon to all other rhinocerotids.

T. radinskyi is the most abundantly represented species in its type locality, Hancock Quarry, a prolific bone deposit in Wheeler County, Oregon. Hancock Quarry

(UCMP locality no. V-75203) is situated within the uppermost subunit of the Clarno Formation, about 10 m below a welded tuff at the base of the overlying John Day Formation. K-Ar dates on this tuff (37.1 and 37.5 Ma; Fiebelkorn *et al.* 1983) are consistent with biostratigraphic correlations of the Hancock Quarry l.f. to the dated interval bracketed by the Porvenir l.f. and Candelaria l.f. of Texas (Wilson, 1977). The combined data places the age of Hancock Quarry in the mid-Duchesnean, about 38 to 39 Ma.

Abbreviations

AMNH	American Museum of Natural History, New York
Fm.	Formation
l.f.	local fauna
LACM	Los Angeles County Museum
LACM (CIT)	California Institute of Technology Collection, now at LACM
Ma	million years before present
OMSI	Oregon Museum of Science and Industry, Portland
SDSM	South Dakota School of Mines and Technology, Rapid City
SMNH	Saskatchewan Museum of Natural History, Regina
TMM	Texas Memorial Museum, Austin
UCMP	University of California Museum of Paleontology, Berkeley
UM	University of Minnesota, Minneapolis
UOMNH	University of Oregon Museum of Natural History, Eugene
UW	University of Wyoming, Laramie
WSM	Burke Memorial Washington State Museum, Seattle.

Systematic paleontology

Family Rhinocerotidae Owen (1845)
Teletaceras new genus

Eotrigonias (?): Stock (1949) (not Wood, 1927)
Eotrigonias: Beliaeva (1959) (not Wood, 1927)
Pappaceras: Radinsky (1966) (in part) (not Wood, 1963)
Juxia: Lucas, Schoch, and Manning (1981) (in part) (not Chow and Chiu, 1964)

Etymology.- Greek, *teleta*, initiation, +*a*, without, +*keras*, horn; with reference to the initial phyletic position relative to the family and to the absence of the nasal horn possessed by living members of the family.

Type species. - Teletaceras radinskyi new species.

Included species. - Type species, *T. mortivallis* (Stock, 1949), new combination, and *T. borissiaki* (Beliaeva, 1959), new combination.

Known distribution. - Late Eocene (Duchesnean to early Chadronian) of central Oregon and southeastern California, United States, and Maritime Province, Soviet Union.

Generic diagnosis. - Dental formula = I3/3, C1/1, P4/4(-3), M3/3. Small rhinocerotids with I^1 and I_2 tusk complex characteristic of the family, but not as enlarged as in other incisor-bearing rhinocerotids. Differs from all other rhinocerotids in the possession of an unreduced anterior dental series, sharp crease between molar parastyles and paracones, more lingually inflected molar metacone axes, and low connection of molar metalophids to protolophids. Differs additionally from "*Subhyracodon*" *sagittatus* Russell (1982) by the presence of a marked postcanine diastema and single-rooted P_1.

Teletaceras radinskyi new species

Etymology. - Named in honor of the late Dr. Leonard Radinsky in recognition of his insightful contributions to the knowledge of Paleogene ceratomorphs.

Holotype. - UCMP 129000, nearly complete skull lacking premaxillae, portion of right zygoma, and occipital crest.

Type locality. - UCMP Loc. V75203,

Hancock Quarry, uppermost unit of the Clarno Formation, Wheeler County, Oregon.

Hypodigm. - Skulls – Type and UCMP 129001, 129002; UOMNH 27698; OMSI 616, OMSI (2 unnumb. specimens); maxillae and upper cheek teeth -- UCMP 129003 to 129006, 129012 to 129022; UOMNH 20447, 20452, 20478, 20485, 20539, 20540, 20927, 20928, 21125, 21378, 21381, 21384, 21388, 21390, 21391, 21394, 21401, 21403, 21419, 21426, 27376, 27644, 27647, 27649, 27719, 28311, 28317, 28319; OMSI 829, 830; incisors -- UCMP 129008 to 129010; UOMNH 20483, 28339; canines--UCMP 129011, 129024; UOMNH 20486; dentaries and lower cheek teeth – UCMP 129026 to 129031, 129033 to 129048, 129051 to 129054; UOMNH 20442, 20445, 20546, 20924, 20937, 20938, 21124, 21383, 21396, 21398, 21406, 21407, 21421, 21432, 21433, 21435, 27645, 27648, 27650 to 27655, 27657 to 27660, 28309, 28312, 28316, 28322, 28325, 28327, 28329, 28333, 28335, 28343, 28347; OMSI 612, WSM 56949, 56952; podials -- UCMP 129055 to 129069; UOMNH 20435, 20443, 20941, 28330, 28338.

Known distribution. - Type locality only; Duchesnean (late Eocene) of north-central Oregon.

Specific diagnosis. - Paracone and metacone ribs on P^{2-4} ectolophs prominent, subequal, and contiguous (not separated by intervening flat area). Dentition larger and more brachydont than *Teletaceras mortivallis*, smaller than *T. borissiaki*. Mean length M^{1-3}, 64 mm; M_{1-3}, 65 mm. Crown height index, 0.66 ± 0.02.

Description

In the following description, comparisons are made with *Hyrachyus* (the most primitive member of the Rhinocerotoidea; outgroup for Rhinocerotidae + Hyracodontidae), *Triplopus* and *Hyracodon* (primitive hyracodontids), and *Penetrigonias, Trigonias* and *Subhyracodon* (more derived Paleogene rhinocerotids). As analysis of all characters has already demonstrated the phyletic positions of these taxa relative to *Teletaceras* (Prothero *et al.*, 1986 and

Prothero, Guérin, and Manning, this volume), the comparisons will serve to imply the polarities of the described characters.

Skull. - The available Hancock Quarry sample of this species includes five nearly complete adult skulls, a sixth lacking the posterior cranium, and the posterior half of a seventh skull. Although none is complete or undistorted, this suite provides enough information for confident graphic reconstruction of all parts of the skull except the premaxilla (Fig. 20.1).

Dorsal aspect: The elongate appearance of the skull in dorsal view is enhanced by the unusually long, gently tapering nasals. Anterior to the orbits, the lateral margins of the dorsal surface converge gradually, describing uniform, laterally concave arcs.

Slightly convex zygomatic arches nearly parallel the midline as in *Hyracodon* and *Hyrachyus*, in contrast with straighter, anteriorly convergent arches in *Subhyracodon occidentalis* and more convex arches in *Penetrigonias sagittatus* and *Trigonias*.

The supratemporal crests converge in smooth arcs from the rear of the supraorbital processes, meeting at the midline to form a low, narrow sagittal crest marked by a medial groove as in *P. sagittatus* and *Subhyracodon copei* but differing from the separate parasagittal crests in *S. occidentalis*. A distinct, rounded notch interrupts the occipital crest at the midline, as in *P. sagittatus*. The crests of *S. occidentalis* and *Trigonias* bear broader indentations. The braincase is less expanded than in other rhinocerotids except *Trigonias*, but comparable to that of *Hyrachyus*.

Lateral aspect: The skull presents an elongate profile, varying little in depth from front to rear. A shallow saddle above the orbits separates the convex dorsal profiles of the muzzle and braincase regions. The convex braincase profile resembles that of most hyracodontids, *Hyrachyus*, and many other perissodactyls, but contrasts with the straight or concave profile of other rhinocerotids.
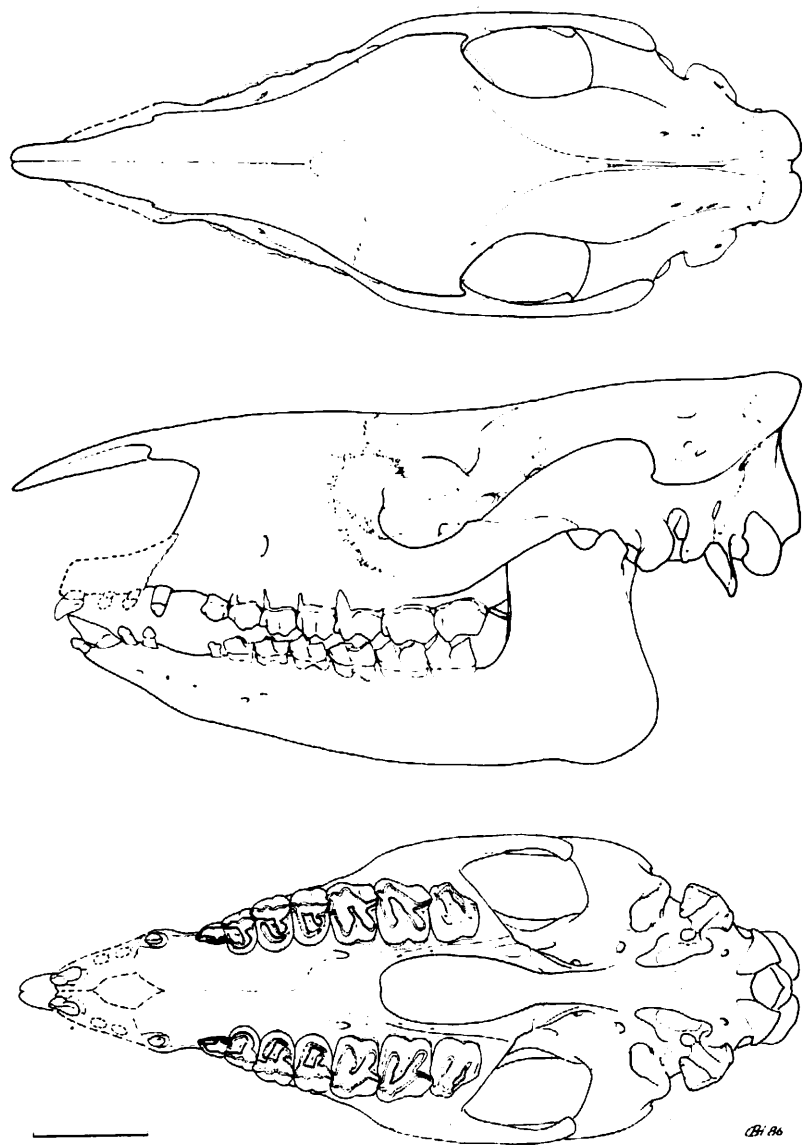
Strikingly elongate nasals extend

Fig. 20. 1. Composite reconstruction of skull of *Teletaceras radinskyi*. Dorsal (top), lateral (middle), and ventral (bottom) views. Reconstruction based primarily on type specimen (UCMP 129000), supplemented by UCMP 129001 (lateral dimensions), UCMP 129039 (dentary). Scale bar is 5 cm.

further forward than any reasonable reconstruction of the premaxillae. On the ntrolateral side, above the rear of the .sal incision, the nasal bone bears a small but prominent anteriorly directed process similar to that of *P. sagittatus* and *Hyracodon nebrascensis*. The nasal incision extends only to a point above the postcanine diastema, less deep in relation to the dental series than that of other rhinocerotids, but undercutting the nasals to an extent omparable to that of *Trigonias*. The premaxillary suture extends about halfway up the anterior margin of the maxilla, well separated from the nasals.

The center of the orbit lies midway along both the anteroposterior and dorsoventral dimensions. The skull does not exhibit the postorbital extension of *Subhyracodon* and *Trigonias*, but the position f the antorbital rim above anterior M^3 is common to all three.

The cheek tooth series is nearly straight in lateral view, and parallel to the dorsal profile of the skull, in contrast with the upward flexure of the anterior cheek-tooth row of later rhinocerotids. The relatively low-crowned teeth and shallow root-bearing portion of the maxilla are argely responsible for the shallow appearance of the mid-portion of the skull compared to that of other rhinocerotids except *P. sagittatus*.

A notch undercuts the posterodorsal end of the zygomatic arch as it does in *Trigonias* and *Subhyracodon* but not *Hyrachyus*.

The postglenoid, posttympanic, and paroccipital processes do not extend as far below the glenoid surface and the external auditory meatus as they do in *Subhyracodon* and *Trigonias*.

Ventral aspect: The narrow palate of *T. radinskyi* bears relatively straight, parallel cheek tooth rows, lacking the slight anterior convergence of the tooth rows of *S. occidentalis*, or the inward curvature of the anterior teeth exhibited by *P. sagittatus* and *Trigonias*. *T. radinskyi* compares more favorably with *Hyrachyus douglassi* (UW 1937; see discussion following) in this respect.

Behind M^3, the posterior margin of the maxilla is nearly straight, extending from the root of the zygomatic arch to the pterygoid crest, as in *Hyrachyus* and *P. sagittatus*, but differing from the convex margins in *Trigonias* and *Subhyracodon*. The posterior narial opening incises the palate to the level of the anterior border of M^2, farther than any of the compared taxa.

The basicranium of *T. radinskyi* resembles that of *Hyrachyus douglassi* more than that of either *Trigonias* or *Subhyracodon*. The postglenoid processes of the two former species are proportionately shorter with more strongly concave anterior faces, and have thicker (more rounded) posterolateral borders with distinct bulges partly enclosing the external auditory meatus ventrally. In *Teletaceras* and *Trigonias*, a shallow open groove (probably for n. chorda tympani) extends around the medial base of the postglenoid process, whereas in *S. occidentalis* this channel is partly enclosed by a bony bridge. The posttympanic process of *Teletaceras* is triangular in cross section, relatively stout, and has a longer free portion than the compared taxa. As in *Hyrachyus*, the paroccipital processes are quite slender in the lateral dimension. The foramen ovale lies medial to the anterior margin of the postglenoid process, distinctly separated from the middle lacerate foramen.

Dentary. -The dentary of *T. radinskyi* resembles that of *Subhyracodon* in relative proportions, though the former is considerably smaller. The cheek teeth occupy proportionately less of the total length of the jaw, and the ascending ramus is more slender. The symphysis extends back to a point below the anterior end of P_2, as in *Subhyracodon* and *Trigonias*, but the symphyseal portion of the jaw is proportionately longer in *T. radinskyi*, as it accomodates a long diastema and two more teeth (I_3 and C_1) than are usually present in the others. The angle of the jaw has a radius of curvature proportionately smaller
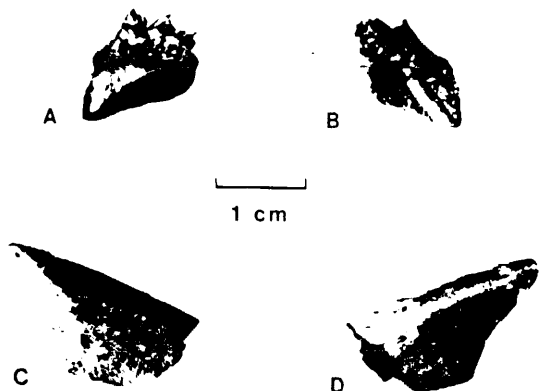
1 cm

Fig. 20. 2. Incisor tusks referred to *Teletaceras radinskyi*. A. Labial and B. lingual views of left I^1, UCMP 129009; C. lingual and D. labial views of right I_2, UOMNH 2085. Both specimens from type locality.
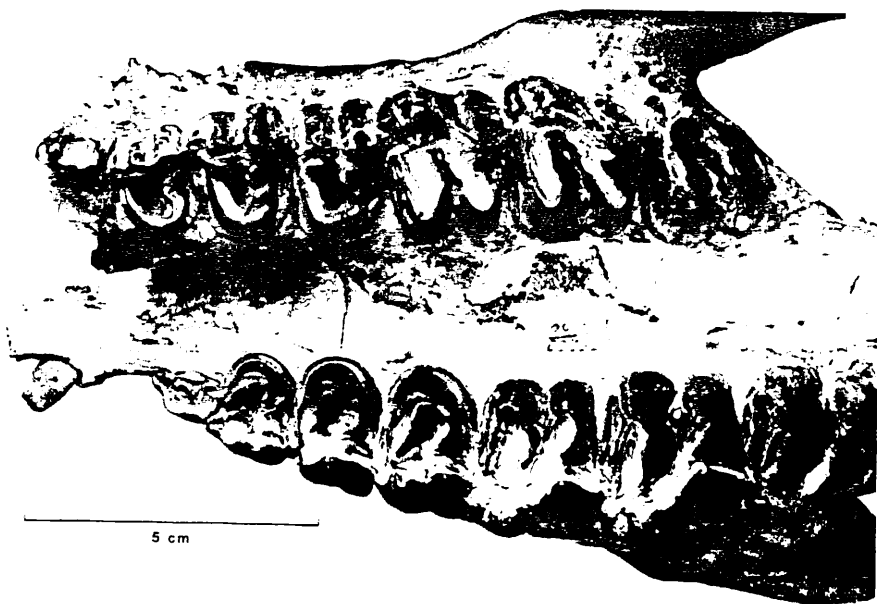

5 cm

Fig. 20. 3. Ventral view of palate of type specimen of *Teletaceras radinskyi*, UCMP 129000.

than those of *Subhyracodon* and *Trigonias*, and is delimited by more distinct indentations below the prominent postcotyloid process and on the ventral border of the jaw. A pair of mental foramina appears below P_2 and anterior P_3, and nutrient foramina (usually three on each side) penetrate the ventrolateral sides of the symphysis.

Dentition.- Upper teeth: Although the premaxilla is not represented in any of the Hancock Quarry specimens, isolated teeth and wear on incisors in dentaries reveal some aspects of the upper anterior dentition. Three isolated teeth are inferred to be first upper incisors. UCMP 129009 (Figs. 20.2A and B) is a nearly unworn crown, which is relatively small but otherwise similar to the I^1 of *Subhyracodon* and *Trigonias*. It has a wear facet compatible with the facets of I_2 of referred jaws. The crown is elongate anteroposteriorly and teardrop-shaped in occlusal view, with its greatest transverse dimension near the rear. The medial side is creased near its midline.

The presence of I^2 is indicated by a small wear facet on the I_2 of UCMP 129039, lateral to the posterior end of the thegosis facet produced by the I^1 tusk.

A portion of an I^3 root appears to remain in the type specimen (UCMP 129000) just anterior and internal to the left C^1. A wear facet on the anterolingual side of C_1 in a well-preserved jaw (UCMP 129039) is compatible only with an I^3.

C^1 is preserved in the type specimen and in UCMP 129003. The crown is small, but the root is proportionately long and massive. Prominent ridges mark the anteromedial and posterior edges of the crown.

The upper cheek teeth (Fig. 20.3) appear quite primitive compared to those of other rhinocerotids. The crowns are low (crown height index = 0.66 ± 0.02; see Radinsky, 1967) and irregular, and the morphological difference between the premolars and molars is conspicuous in lateral as well as occlusal view.

P^1 (five specimens) has a narrow, rounded triangular outline; its length is nearly twice its width. The large, centrally situated paracone dominates the labial face of the ectoloph, and shallow grooves delimit the small parastyle and metacone. The lingual cusps are quite small and anteroposteriorly elongate, especially the paracone. Cross-lophs are very weak or absent. The lingual cingulum extends only from the tip of the parastyle to the anterior end of the protocone. The size and shape of the hypocone, size of the protocone, and relative tooth width vary within the sample.

P^2 through P^4 (Fig. 20.4) retain many of the primitive characters of the superfamily. Most of the labial surface on each tooth is occupied by a pair of prominent, subequal, rounded ridges, the paracone and metacone ribs. The curved surfaces of these ribs meet medially, forming a cleft, except near the occlusal edges of unworn teeth. The parastyle is similar in size and shape to the metastyle. The resulting mirror symmetry about the median cleft approximates that seen in *Hyrachyus* and *Triplopus* but differs from the flatter, asymmetrical ectolophs of most rhinocerotids. In occlusal view, the crown outlines of P^{2-4} are also nearly symmetrical fore and aft. The lingual margins range from semicircular on P^2 to parabolic on P^4.

The protoloph incorporates the protoconule, protocone, and hypocone of P^{2-4} of all specimens except one: the P^2 of UOMNH 20447 has a distinct hypocone that appears to have had a metaloph connection. The protoloph of P^{2-4} is isolated from the ectoloph by a deep saddle (most pronounced in P^2) in lightly worn teeth. The short metaloph tapers labially from the metaconule to the ectoloph but connects more firmly than does the protoloph. A small flange on the metaconule of most of the specimens may be directed toward the protocone or the small hypocone. The strength of this flange generally decreases from P^2 to P^4 in a given individual, and the connection is usually
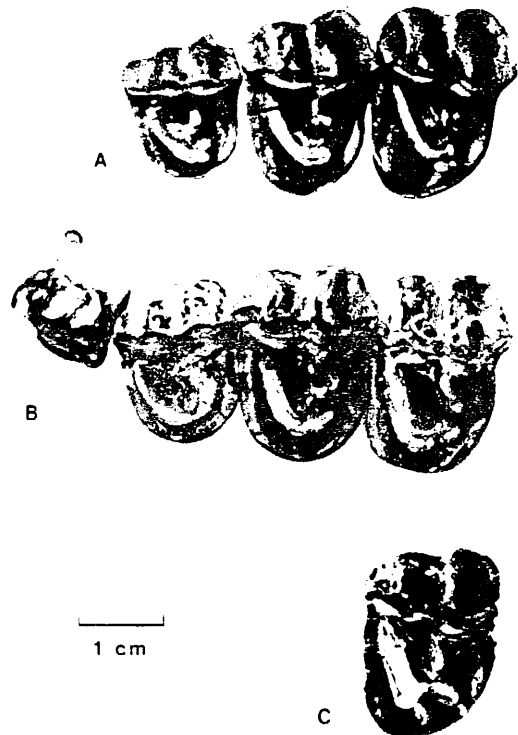
Fig. 20. 4. Occlusal views of upper premolars of *T. radinskyi* showing individual variation. A. P$^{2-4}$, UOMNH 21125; B. P$^{1-4}$, UCMP 129000 (type); C. P^4, UOMNH 21391.
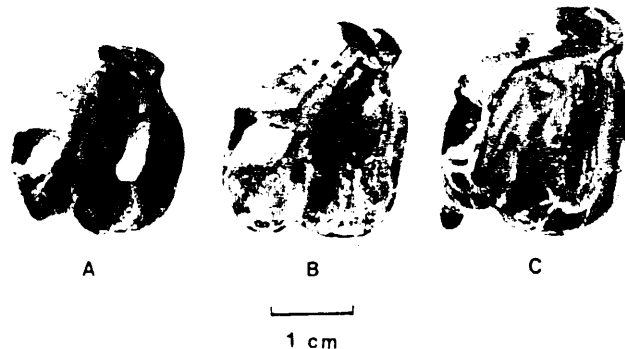

Fig. 20. 5. Occlusal views of third upper molars of *T. radinskyi* showing individual variation. A. UOMNH 21390; B. UCMP 129000 (type); C. UCMP 129019.

with the hypocone in P^2 and with the pro-tocone in P$^{3-4}$. The median valleys of P$^{3-4}$ open toward the rear until advanced wear. P^2 typically has a closed protoloph-met-aloph loop enclosing a central fossette, though one specimen (Fig. 20.4A) has a posterior opening and another a lingual opening. In general, premolar ectoloph features exhibit less intrapopulation vari-ability than do features of the protoloph-metaloph complex.

All specimens lack labial cingula on P$^{2-4}$, but possess anterior and posterior cingula. The lingual cingulum is variable, but any given individual exhibits a progressive decrease in the strength and extent of the lingual cingulum from P^2 through P^4. It is complete in three of nine P^{2}s, two of thirteen P^{3}s, and none of fourteen P^{4}s.

The roughly square outline of M^1 has gently curved anterior and posterior sides, which tend to converge lingually. In unworn teeth, the parastylar fold is smoothly con-cave near the occlusal edge and narrows to a sharp crease toward the base, but does not continue to the base of the enamel. The ec-toloph bears a very prominent dorsoven-trally curved paracone rib and a distinct metacone rib. The axis of the metacone cants inward about 45 degrees relative to the sagittal plane (more than in other rhinocerotids) and the ectoloph is rela-tively short. This forces the metaloph into near alignment with the paracone and midsection of the ectoloph. The protocone bears shallow, rounded grooves delimiting a very weak antecrochet. A metaconule fold is lacking (in most specimens) or very ob-scure, and cristae are absent. The postfos-sette is proportionately as large as in *Sub-hyracodon*. One or two small accessory cus-pules or low bulges (sometimes asymmetri-cal) occur near the lingual end of the me-dian valley in three M^1 specimens, includ-ing the type, but are absent in eight others. The anterior cingulum extends from the lin-gual side of the parastyle to the anterolin-gual side of the protocone. Its edge in oc-clusal view is a simple arc, convex anteri-orly, and in anterior view describes a ven-trally concave curve, but with a slight bump where it passes the protoconule in some specimens. This shape is comparable to that of *Hyrachyus*, intermediate between the nearly straight anterior cingulum of *Triplopus* and the more complex curvature in *Subhyracodon*. A short, high posterior cingulum extends straight (in occlusal view) from the ectoloph to the posterolabial side of the hypocone and bears a slight notch behind the postfossette. None of the upper molars has a labial or lingual cingulum.

M^2 differs from M^1 in its larger size, more labially situated protocone, and more open parastylar fold. The junction of the occlusal edge of the unworn protoloph with the ectoloph is more nearly centered on the parastyle. The cross-lophs diverge a bit more than in M^1, and the occlusal surface of the metaloph aligns directly with the paracone in moderate wear stages. The me-dian valleys of both M^{2}s of the type bear single accessory cuspules, not present in the other specimens.

Except for the reduction of the metastyle, M^3 differs little from M^2. The portion of the ectoloph between the para-cone and metacone is a bit more oblique and the parastylar fold is more open and lacks the sharp crease at its basal termination. The metaloph is slightly expanded at the hypocone as it is in the preceding molars, in contrast with the anteroposteriorly flat-tened M^3 hypocone of *Subhyracodon*. The large M^3 sample (22 individuals) exhibits a range of variation in the prominence of the metastyle (Fig. 20.5) extending from the condition seen in the type of *Triplopus rhinocerinus* to that in some specimens of *Subhyracodon*. This structure typically arises as a sharp ridge at the labial end of the postfossette and becomes more rounded and flattened toward its occlusal end. In most specimens (including the type; Fig. 20.5B), the ridge apparently extended nearly to the unworn occlusal edge of the

ectometaloph, but one specimen (not shown) bears a short ridge extending only 2 mm from the cingulum and has no rounded extension. At the slightly worn M^3 occlusal surface of the type, both the inner and outer sides of the ectometaloph have slight parallel flexures at the position of the metastyle. A somewhat variable postfossette extends anterolabially along the ectometaloph farther than in the other rhinocerotids, but less than in *Hyrachyus douglassi*. A small accessory cuspule near the opening of the median valley appears in 3 of 20 specimens. Another has a more extending from the antecrochet to the metacone.

All of the permanent upper cheek teeth have at least patches of cement on the surface of the ectoloph, in the median valley, and in the postfossette. Cement covers the outer surface of the ectoloph of M^1 of the type except at the tip of the metacone, parastyle, and along the paracone. Other teeth have lesser amounts, usually restricted to concave areas.

A nearly unworn dP^2 has an asymmetric cordate outline, conspicuously notched between the paracone and metacone and narrowing posterolingually to a rounded point at the hypocone. The ectoloph resembles that of the permanent premolars. The more molariform lingual portion bears a well-developed metaloph and a very oblique protoloph which barely contacts the ectoloph. A small, sharp cingular cuspule blocks the lingual end of the median valley, and a well-defined cingulum extends from here along the protoloph to the ectoloph. The posterior cingulum extends lingually to the posterolingual side of the hypocone. The specimen lacks a crista.

DP^3 and dP^4 resemble M^1 in most respects, except their smaller size, proportionately lower crowns, and the presence (at least in dP^3) of a crista. The dP^4 specimen has a small cusp near the lingual end of the median valley, and a comparable feature appears to have been broken from the dP^3.

Lower teeth: None of the referred jaws has the first lower incisor crown in place, but the three specimens with intact anterior symphyses have roots or alveoli for a small, procumbent I_1.

Three jaws include complete I_2s, and UOMNH 20483 (Fig. 20.2C and D) is an isolated I_2 crown. These teeth are the enlarged, procumbent tusks characteristic of the Rhinocerotidae, but are proportionately smaller than those of other members of the family. The crown cross-section near the base is teardrop-shaped, with the narrow end directed ventromedially. Most of the dorsomedial surface of the crown lacks enamel. A low ridge on the dorsolateral surface of the tooth extends from the base of the enamel toward the tip, decreasing in prominence distally.

All adequately preserved specimens have two alveoli between I_2 and the diastema, indicating the presence of both I_3 and C_1. No I_3 crowns are preserved in place, but the alveoli suggest the I_3 is smaller than I_1 and slightly procumbent. The root of C_1 is larger and more erect than that of I_3. Its crown resembles that of the upper canine described earlier. The diastema between C_1 and P_1 averages 23 mm and ranges from 21 to 26 mm (five specimens).

(D)P_1 is a small, simple single-rooted tooth which was retained throughout life in all but one of the individuals adequately preserved. The crown is only a bit longer than that of the C_1, but not as high. It is lozenge-shaped in occlusal view and has a single anteroposterior ridge along the occlusal surface, terminating at a very faint posterior cusp.

P_2 is laterally compressed with distinct paralophid and metalophid, but small, oblique cross-lophids. The labial surface lacks the pronounced fold seen in *Subhyracodon* at the posterior end of the paralophid. The talonid is proportionately smaller and the paraconid less distinct than in other rhinocerotids, though both features vary within the sample. P_2 bears faint anterior and posterior cingula, but

1 cm

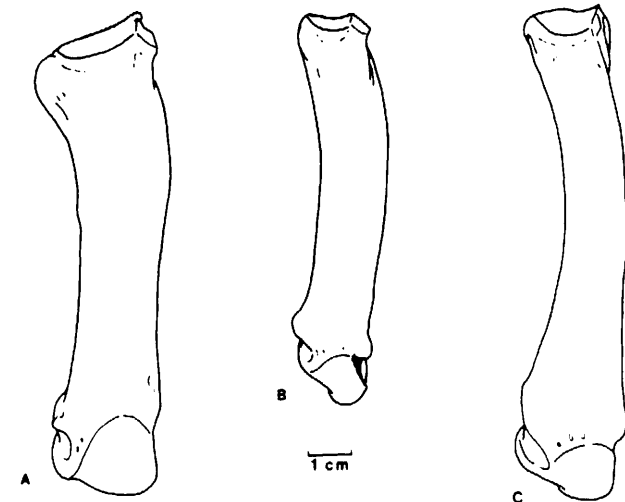Fig. 20. 6. Occlusal view of P_2-M_3 of *T. radinskyi*. UOMNH 21407.

1 cm

Fig. 20. 7. Right fourth metacarpals of rhinocerotids. A. *Trigonias* sp., a tetradactyl form (UCMP 32011, reversed); B. *T. radinskyi*, (UOMNH 28330); C. *Menoceras arikarense*. a tridactyl form (UCMP 39960). Facet for unciform (shaded) slants laterally in known tetradactyl ceratomorphs and medially in known tridactyl forms, indicating tridactyl manus for *T. radinskyi*.

lacks lingual and labial cingula.

P3 has a nearly molariform trigonid, but the talonid is low and flat with an incomplete hypolophid. A small entoconid appears on most specimens, separated from the abbreviated hypolophid by a shallow cleft. A weak cingulum arches across the anterior face of the crown. The posterior cingulum is restricted to the area of contact with P4 in most specimens, but extends around the talonid in a small percentage of the sample.

P4 is proportionately wider and more molariform than P3, but again the hypolophid is incomplete. The entoconid is even more distinct than in P3 and, in most cases, is situated anterior to the lingual end of the hypolophid. The cingula are similar to those of P3 in distribution and variability.

The lower molars also bear features intermediate between those of *Hyrachyus* and previously recognized rhinocerotids. Indentations on the anterior faces of the transverse lophids accentuate their component cusps so that the lingual and labial ends of the wear surfaces appear expanded, especially at the metaconid. The weak concave paralophid and convex metalophid descend steeply from their posterior connections with the cross-lophids in unworn teeth. The height of the junction between the metalophid and protolophid is little more than one-third the height of the unworn protoconid. The paralophid bends sharply inward near the anterolabial corner of the tooth, much as in *Hyrachyus*, but contrasting with the smoothly arcuate, longer paralophid of *Triplopus*. The anterior cingulum extends only around the transverse portion of the paralophid. The posterior cingulum occupies only the straight medial portion of the posterior molar face, and is weak or absent on M3. No traces of lingual or labial cingula exist. Overall size and the angle between the paralophid and protolophid increase from M1 to M3.

DP2 greatly resembles its permanent successor except in its lower crown, thinner enamel, and long, narrow proportions. The trigonid is especially elongate, and the weak metalophid slants backward more than in the permanent P2.

DP3 likewise differs from P3 in its very long, narrow trigonid, but the talonid is almost fully molariform, differing from M1 only in its narrower dimensions, slightly more oblique cross-lophids, lower crown, and thinner enamel.

Manus. -The prepared material from Hancock Quarry includes only one element referred to the manus of *T. radinskyi* -- a complete right fourth metacarpal (UOMNH 28330) -- but it is especially significant as it bears evidence that this species possessed a tridactyl manus. Its size, similarity to the fourth metacarpal of other rhinocerotids, and taphocoenotic association with abundant tooth-bearing specimens of *T. radinskyi* leave little doubt about the taxonomic assignment.

The specimen is 89 mm long and has a maximum transverse diameter of 20 mm across the distal end. In general proportions, it resembles metacarpal 4 of *"Caenopus" mitis*, not as slender as in *Menoceras arikarense* or *Subhyracodon occidentalis* (Fig. 20.7). The distal articular surface, however, differs from all of these and from *Trigonias osborni* (but resembles *Hyrachyus*) in its stronger convexity and in the marked step between the lateral and extended medial portions. The latter portion bears a very weak median keel. The triangular proximal end bears subdivided facets for both metacarpals 3 and 5.

Evidence of the lack of a fourth digit is offered by the orientation of the facet for the unciform (Fig. 20.7). This facet is saddle-shaped (transversely concave) in all ceratomorphs, and in *T. radinskyi* the lateral border of the facet is distinctly higher than the medial border. This condition is shared with *"Caenopus" mitis*, *Subhyracodon occidentalis*, *Menoceras*, *Hyracodon*, and *Colodon*, all ceratomorphs with a tridactyl manus, whereas in the tetradactyl forms (e.g., *Trigonias, Metamynodon, Za-*

isanamynodon, Heptodon, and *Tapirus*), the unciform facet slants laterally downward and the unciform is subequally shared by metacarpals 4 and 5.

While retaining some of the characters primitive with respect to other rhinocerotids, the metacarpal clearly differs from the long, slender elements which characterize even the least derived hyracodontids.

Pes. -The available assemblage from Hancock Quarry includes many more specimens pertaining to the pes of *T. radinskyi* (Fig. 20.8) than to its manus. These specimens were directly compared with elements referred to *Eotrigonias* (?) *mortivallis* Stock (1949) from the Titus Canyon Formation of California, Fig ured in his description.

Five astragali closely match a specimen [LACM (CIT) 3556] referred to *E.* (?) *mortivallis*. All of the major dimensions of the latter fall within the range of the Hancock Quarry sample. The most apparent difference is the more oblique orientation of the trochlear ridges of *T. radinskyi* with respect to the distal articulation for the navicular. It also has a more pronounced "neck" between the proximal and distal articulations, most noticeable on the lateral side, although in one specimen the medial trochlear ridge encroaches almost as closely on the navicular facet as it does in *E.* (?) *mortivallis*. *T. radinskyi* bears a slight lip on the lateral side of the trochlea, which, as Stock (1949) noted, is absent in *E.* (?) *mortivallis*.

The calcaneum of *T. radinskyi* is represented by four specimens. In addition to its more slender proportions, it differs from the calcanea of both *Subhyracodon occidentalis* (figured in Scott, 1941) and *Trigonias osborni* (UCMP 32011) in the high position and perpendicular orientation of the sustentaculum relative to the main body of the calcaneum. The oval astragalar facet on the sustentaculum compares with that of *Trigonias* but differs from the subquadrate facet in *Subhyracodon*. Just proximolateral to this facet is a
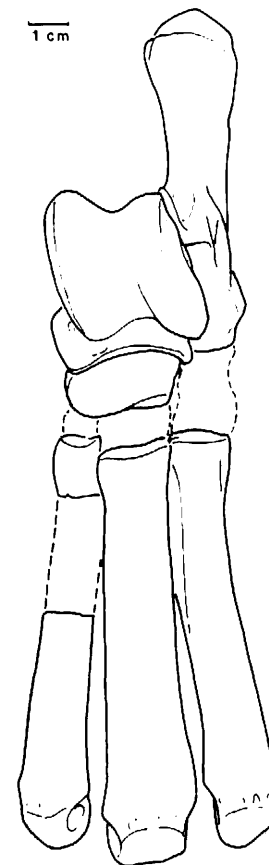

Fig. 20. 8. Composite reconstruction of left tarsus and metatarsus of *T. radinskyi*, dorsal view. Astragalus, UCMP 129061; calcaneum, UCMP 129057; navicular, UCMP 129066; proximal metatarsal 2, UCMP 129066; distal metatarsal 2, UCMP 129067; metatarsal 3, UCMP 129064; metatarsal 4, UOMNH 28338 (reversed).

shallow but distinct depression (absent in both *Trigonias* and *Subhyracodon*), probably homologous to a pit noted by Radinsky (1965) in the calcaneum of *Heptodon* to accomodate the tip of the fibula in extreme tibio-tarsal flexion. Two naviculars from the quarry differ slightly in thickness, and the thinner one resembles that of *S. occidentalis* in overall proportions.

Two incomplete metatarsal 2 specimens resemble the second metatarsal of *E* (?) *mortivallis* except in the more convex facets for metatarsal 3. Metatarsal 3 is proportionately narrower than that of either *Subhyracodon* of *Trigonias* and only slightly wider than the adjacent matatarsals. The proximal end is not expanded as in those genera. The fourth metatarsal of *T. radinskyi* (three specimens) is virtually identical in size and morphology to that of the cotype of *E.* (?) *mortivallis*. These show almost none of the reduction and lateral compression which characterize the medial and lateral metatarsals of the later rhinocerotids.

The distal articulations of all metatarsals are strongly biconvex and weakly keeled, and in metatarsals 2 and 4, the portion nearest the axis of the foot is extended. These are retained primitive characters modified in other rhinocerotids.

An isolated proximal phalanx may have belonged to either the second or fourth tarsal digit. It also closely resembles a comparable element of the *E.* (?) *mortivallis* cotype, but it tapers more toward the distal end. These elements are slightly longer than wide, intermediate in proportions between *Subhyracodon* and the stouter *Trigonias* phalanges.

Referred Species
Two species, originally referred to *Eotrigonias* but subsequently transferred to other genera, resemble *Teletaceras radinskyi* closely enough to warrant their inclusion in the same genus.

The genus name *Eotrigonias* is no longer available, as Radinsky (1967) transferred its type species, *E. rhinocerinus*, to *Triplo-*

pus, an assignment with which I agree. Although *E. rhinocerinus* bears a very reduced M^3 metastyle, it otherwise resembles other species of *Triplopus* more than it does *Teletaceras*. Compared with the latter, the teeth are more brachydont and the M^{1-2} postfossettes are smaller (primitive characters relative to *Teletaceras*), while the premolar ectolophs bear less prominent ribs and parastyles (derived features).

The lower cheek teeth of *Eotrigonias* (?) *mortivallis*, Stock (1949) from the Titus Canyon Formation, Inyo County, California, closely resemble those of *T. radinskyi*. The only known teeth of the former species are those of the type [LACM (CIT) 3564], with complete M_2 and broken M_1 and M_3) and a subsequently identified jaw fragment representing an older individual (LACM 61303, with incomplete P_4-M_2 from the same locality--CIT 254). The two species share the steeply descending molar paralophids and metalophids with low, weak connections of the metalophids to protolophids. These contrast with the higher, stronger crests of "*Trigonias* species C" of Russell (1982) (probably referable to *Penetrigonias*) and other more derived rhinocerotids. Short, sharply bent paralophids and high crowns compare more favorably with *T. radinskyi* than with *Triplopus*. *E.* (?) *mortivallis* differs from *T. radinskyi* in its less obtuse metalophid-hypolophid angle, slightly less elongate trigonid, the absence of a distinct P_4 entoconid, and smaller size. The mean length of M_1 of *T. radinskyi* exceeds that of *E.* (?) *mortivallis* by 5 mm (4.7 standard deviations), and M_2 is even longer in proportion. There is no overlap in the ranges of any tooth measurements. Wood (1963) commented on this species, stating: "As will be shown fully elsewhere (MS), *Eotrigonias* (?) *mortivallis*. . . . is a composite form composed of hyracodont teeth and caenopine [i.e. rhinocerotid] foot bones. The specific name *mortivallis* must go in the genus *Hyracodon*, whatever its validity as a species."

Table 20.1. Statistical summary of upper cheek tooth measurements (in mm) for *Teletaceras*. A-P, anterior-posterior dimension along midline; Tr, transverse dimension from paracone across protocone; N, sample size; SD, standard deviation; CV, coefficient of variation. Measurements for *T. borissiaki* from Beliaeva (1959)

			T. radinskyi hypodigm				*T. borissiaki*
		N	Mean	Range	SD	CV	
P^1	A-P	5	12.2	10.9 - 13.7	0.95	7.83	
	Tr	5	8.7	8.0 - 9.4	0.50	5.71	
P^2	A-P	10	12.6	11.1 - 13.5	0.66	5.24	
	Tr	10	16.3	15.0 - 18.5	1.05	6.45	
P^3	A-P	11	14.7	13.4 - 16.0	0.68	4.64	
	Tr	10	20.1	17.7 - 23.0	1.32	4.58	
P^4	A-P	14	15.6	13.8 - 17.2	1.80	5.15	--
	Tr	12	22.5	31.0 - 25.1	1.03	4.58	31
M^1	A-P	15	20.1	18.4 - 21.9	0.84	4.18	27 *
	Tr	11	24.4	23.5 - 26.5	0.90	3.70	33
M^2	A-P	18	22.6	20.9 - 25.4	0.96	4.23	
	Tr	14	26.7	25.0 - 28.8	0.98	3.68	
M^3	A-P	20	22.1	20.5 - 25.5	1.26	5.70	
	Tr	17	25.8	23.2 - 27.7	1.09	4.24	
P^{1-4}		4	55	53.0 - 58	1.85	3.35	
M^{1-3}		13	64	59.0 - 70	2.67	4.17	
P^{1-3}		3	121	119.0 - 124	2.05	1.70	

* Estimated from figure: Length given by Beliaeva (31.0) is along ectoloph.

Table 20.2. Statistical summary of lower cheek tooth measurements (mm) for *Teletaceras*. A-P, anterior-posterior dimension along midline; TrA, transverse dimension across trigonid; TrP, transverse dimension across talonid; N, sample size; SD, standard deviation; CV, coefficient of variation; @, approximate.

| | | *T. radinskyi* hypodigm | | | | | *T. mortivallis* | |
| | | LACM | | | | | LACM (CIT) | |
		N	Mean	Range	SD	CV	3564	61303
P_1	A-P	6	7.5	6.9 - 7.8	0.31	4.2		
	TrA	5	4.5	4.2 - 4.7	0.21	4.6		
P_2	A-P	16	12.9	12 - 15.4	0.76	5.9		
	TrA	18	7.7	7.1 - 8.8	0.41	5.3		
P_3	A-P	25	15.9	14.6 - 17.5	0.66	4.1		
	TrA	24	9.7	8.9 - 10.9	0.50	5.1		
	TrP	23	9.7	8.7 - 10.8	0.60	6.1		
P_4	A-P	35	16.6	14.7 - 18.6	0.85	5.1	13 @	
	TrA	31	11.4	10.2 - 12.4	0.49	4.3		
	TrP	32	11.2	10.4 - 12.1	0.52	4.7		
M_1	A-P	24	19.4	18 - 21.7	0.99	5.1	15.2	13.6
	TrA	23	12.7	11.3 - 14.0	0.71	5.6	10.2	
	TrP	27	13.2	11.6 - 14.5	0.66	5.0		
M_2	A-P	38	22.6	20.5 - 24.8	1.03	4.6	16.7	18 @
	TrA	33	14.2	13.3 - 15.5	0.61	4.3	11.1	
	TrP	32	14.7	12.8 - 17.2	0.87	6.0	11.9	
M_3	A-P	31	23.7	22 - 25.7	0.88	3.7	11 @	
	TrA	28	14.7	13.6 - 16 @	0.56	3.8		
	TrP	32	13.9	12.7 - 15.3	0.58	4.1		
P_{1-4}		13	50.2	44 @ - 57.2	3.54	7.1		
M_{1-3}		26	64.8	60 - 70.5	2.38	3.7	49	
P_1-M_3		10	113.1	105.5 - 124.3	5.01	4.4		
dP_2	A-P	1	14.5					
	TrA	1	7.2					
dP_3	A-P	1	20.5					
	TrA	1	8.6					
	TrP	1	10.4					
dP_4	A-P	2	17.9	17.0 - 18.8				
	TrA	2	10.0	9.7 - 10.3				
TrP		2	10.4	10 - 10.8				

The mentioned manuscript apparently was never published, but Stock's (1949) referral of the teeth and foot bones to a single species now appears justified by their similarity (discussed earlier) to comparable elements of *T. radinskyi*. The resemblances are great enough to dictate assignment of the two populations to the same genus, but differences in the size and morphology of the cheek teeth warrant species-level separation. I therefore transfer *E. (?) mortivallis* to *Teletaceras*.

The fauna associated with *T. mortivallis* indicates an early Chadronian age (Stock, 1949), somewhat younger than the Hancock Quarry l.f.

Eotrigonias borissiaki Beliaeva (1959) has suffered a complex nomenclatorial history, at least partly owing to the limitations of the type material. This consists of a maxillary fragment with M^1 and incomplete P^4 from the Artém coal field, Maritime Province, Soviet Union. Wood (1963) transferred the species to his new genus *Pappaceras*, despite several noted differences and only one positive comparison, "the distinction of the parastyle of M^1, much as in *Pappaceras confluens*." Even this similarity is questionable, given the available illustrations. Radinsky (1967) nonetheless agreed with this assignment but synonymized the entire genus *Pappaceras*, as well as *Juxia*, with *Forstercooperia*. Most recently, Lucas, Schoch, and Manning (1981) reassigned *E. borissiaki*, along with *Juxia sharamurenense* Chow and Chiu (1964) to a single monotypic species, *Juxia borissiaki*, citing similar size and "morphologically identical" P^4 and M^1 of the types of *E. borissiaki* and *J. sharamurenense*. The type of the latter species strongly resembles that of *F. ergiliinensis*, and these may well be conspecific. However, the type of *E. borissiaki* bears much greater resemblance to *Teletaceras radinskyi* and differs from *J. sharamurenense* in the following characters: 1) parabolic rather than semicircular lingual margin of P^4; 2) incomplete lingual P^4

cingulum bearing a bulge at the posterolingual side, as opposed to a complete, uniform lingual cingulum; 3) lingually convergent, rather than subparallel anterior and posterior sides of M^1; 4) small, anteriorly directed M^1 parastyle, not large and labially deflected; 5) strong paracone rib on M^1 ectoloph; 6) narrow connection of M^1 protoloph to inner side of parastyle rather than broad connection at paracone ; 7) M^1 metaloph short, aligned with paracone at moderate wear stage, and lingually divergent from protoloph--narrow median valley; 8) M^1 hypocone smaller with roughly teardrop-shaped (not circular) basal outline; 9) small bridge connecting midpoint of anterior cingulum to protoloph of M^1; 10) posterior M^1 cingulum short and broad, terminating at posterolabial (vs. posterolingual) side of hypocone; 11) large, anteroposteriorly elongate postfossette; and 12) larger M^1 antecrochet. The thickened posterior part of the M^1 ectoloph, cited by Beliaeva, may resemble that of *J. sharamurenense* more than *T. radinskyi*, though this is difficult to ascertain from the Fig ures. In size, *E. borissiaki* falls between known specimens of those species, and produces exceptionally large tooth size ranges when considered conspecific with *F. ergiliinensis* .

Eotrigonias borissiaki differs somewhat less from the North American genus *Penetrigonias* (discussed later) than from *Juxia*. However, except for its size, it differs from *Penetrigonias* and resembles *T. radinskyi* in its weaker M^1 antecrochet, more lingually inflected metacone, more prominent metacone rib, and more directly aligned metaloph, mid-ectoloph, and paracone. Its P^4 lingual cingulum is much less complete than in *Penetrigonias*. I therefore recognize *E. borissiaki* as a species of *Teletaceras*.

Notably, the only other published taxon from the Artém l.f., a large amynodontid, *Procadurcodon orientalis*, is congeneric with an undescribed species from

Hancock Quarry. The ages of these faunas therefore appear similar, but it is not clear which is older.

Discussion

Teletaceras and *Penetrigonias* exhibit few autapomorphic characters and fill much of the morphologic gap which formerly separated *Hyrachyus* and known rhinocerotids. Details of this transition can now be re-examined at higher resolution. A number of unpublished or incorrectly referred specimens demonstrate pertinent characters of the related taxa, and deserve mention here.

A well-preserved skull and mandible, UW 1937, from the Washakie B (early Uintan), Sweetwater County, Wyoming, bears a dentition (including unspecialized lower incisors) which closely resembles the type of *Hyrachyus douglassi* Wood (1934). The UW specimen is tentatively referred to that species for purposes of the present discussion. Most of the major skull characters of this advanced *Hyrachyus* are retained in *T. radinskyi*; dorsal skull profile nearly parallel to the tooth row; gently convex, narrow sagittal crest; skull elongate in dorsal view; and occipital crests short transversely and separated by a small medial notch. The basicranium of UW 1937 is almost identical with that of *T. radinskyi* except that the posttympanic and paroccipital processes are slightly shorter in the former. Derived skull characters of *T. radinskyi* relative to *H. douglassi* are narrower free portion of nasals, small process on nasals above nasal incision, straighter nasal-maxillary suture, reduced premaxilla not contacting nasals, slightly reduced sagittal crest, slightly upturned occipital crest, notch at posterior end of zygomatic arch, and the dental features described above. Although the skulls are virtually identical in size, the cheek tooth series of *T. radinskyi* is about 25% longer than that of *H. douglassi*, the postcanine diastema is correspondingly reduced, and the canines are slightly smaller. Overall, the skull of *T. radinskyi* resembles that of *Hyrachyus douglassi* more than it does

other rhinocerotids.

Several Chadronian localities in North America (other than Titus Canyon) have yielded specimens of small rhinocerotids which resemble *Teletaceras* in some features but exhibit a number of derived characters. For one of these specimens, Tanner and Martin (1976) named a new genus and species, *Penetrigonias hudsoni*, based on a specimen with P^{2-4} from Sioux County, Nebraska, for which familial assignment was uncertain. These premolars are almost indistiguishable from those included in a nearly complete and clearly rhinocerotid palate (with P^1-M^3; University of Minnesota, unnumbered specimen) from the Chadron Formation, Pennington County, South Dakota. The two specimens almost certainly represent the same species. Other specimens from the Yoder Formation in Goshen County, Wyoming (SDSM 6353), Porvenir l.f., Texas (TMM 40807-6; Wilson and Schiebout, 1984), the White River Group in Natrona County, Wyoming (AMNH 105019), and the Cypress Hills Formation in southwestern Saskatchewan (SMNH P1635.2, type of *Subhyracodon sagittatus* Russell, 1982, its hypodigm, and SMNH P1635.1, "*Trigonias* species C " in Russell, 1982), all resemble *Penetrigonias hudsoni* to varying degrees. They may represent two or three additional species of that genus, as dental differences are greater than usually seen in a single rhinocerotid species, though all are similar in size (M^{1-3} length 72 to 79.5 mm—about 3-15% larger than the largest *T. radinskyi*). These specimens were assumed congeneric in the analysis presented in Prothero, Manning, and Hanson (1986). Table 1, character set 28 of that paper summarizes the characters which distinguish *Penetrigonias* (and more derived rhinocerotids) from *Teletaceras*.

Of particular interest is the sequence of changes in three characters which have almost invariably entered discussions of the initial evolution of rhinocerotids: the incisor complex, the M^3 metacone, and the fourth carpal digit.

Teletaceras demonstrates that the lineage ultimately leading to modern rhinos had acquired the uniquely specialized I^1/I_2 tusks before the primitive M^3 metastyle was completely lost. Specimens here referred to *Penetrigonias* bear either a very faint M^3 metatsyle ridge or no trace of a metastyle. This further verifies Radinsky's (1966) contention that more than one rhinocerotoid group independently lost the metastyle (it is also completely lost in some hyracodontids), and underscores the limitations of this character in phyletic interpretation.

The evidence for a tridactyl manus in *Teletaceras* is more surprising in light of the generally primitive morphology of the genus and the entrenched assumption that a tetradactyl manus was primitively retained in some of the more advanced rhinocerotids, such as *Trigonias*. Though still open to the interpretation that the loss of metacarpal 5 is an autapomorphic character of *Teletaceras* (independent of its loss in other rhinocerotids), this evidence suggests an alternative hypothesis, that a tridactyl manus is primitive for rhinocerotids plus hyracodontids. A secondarily "revived" fourth digit has already been proposed for the Aceratheriinae (Prothero, et al., 1986). The same may be true for *Trigonias*. The manus is unknown for both *Hyrachyus douglassi* and *Penetrigonias*.

Acknowledgments

Bibliography

Beliaeva, E. I. (1959): Sur le découverte de rhinoceros tertiares anciens dans la Province Maritime de l'U.R.S.S. -*Vert. PalAsiatica*, 3: 81-91.

Chow, M., and Chiu, C. (1964): An Eocene giant rhinoceros. -*Vert. PalAsiatica*, 5: 264-267.

Chow, M., and Xu, Y. (1961): New primitive true rhinoceroses from the Eocene of Iliang, Yunnan. -*Vert. PalAsiatica*, 5: 291-304.

Fiebelkorn, R. B., Walker, G. W., MacLeod, N. S., McKee, E. H., and Smith, J. G. (1983): Index to K-Ar determinations for the state of Oregon. -*Isochron West*, 37: 3-60.

Gabunia, L., and Dashzeveg, D. (1974): Ob Oligotsenovom predstavitele *Forstercooperia* (Hyracodontidae) iz Mongolii [On the Oligocene representatives of *Forstercooperia* (Hyracodontidae) from Mongolia]. -*Soobshcheniya Akad. Nauk Gruz. SSR*, 75: 497-500.

Lucas, F. A. (1900): A new rhinoceros, *Trigonias osborni* , from the Miocene of South Dakota. -*U.S. Nat. Mus. Proc.*, 23: 221-224.

Lucas, S. G., Schoch, R. M., and Manning, E. M. (1981): The systematics of *Forster-*

cooperia , a middle to late Eocene hyra-codontid (Perissodactyla: Rhinocero-toidea) from Asia and western North America. -*J. Paleont.*, 55: 826-841.

Owen, R. (1845): *Odontography; or a treatise on the comparative anatomy of teeth.*- London (Hippolyte Bailliere).

Prothero, D. R., Guérin, C., and Manning, E. M. (1989): The history of the Rhinocerotoidea (this volume).

Prothero, D. R., Manning, E. M., and Hanson, C. B. (1986): The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). -*Zool. J. Linn. Soc.*, 87: 341-366.

Radinsky, L. B. (1965): Evolution of the tapiroid skeleton from *Heptodon* to *Tapirus*. -*Bull. Mus. Comp. Zool.*, 134: 69-106.

Radinsky, L. B. (1966): The families of the Rhinocerotoidea (Mammalia, Perissodactyla). -*J. Mamm.*, 47: 631-639.

Radinsky, L. B. (1967): A review of the rhinocerotoid family Hyracodontidae (Perissodactyla). -*Bull. Amer. Mus. Nat. Hist.*, 136: 1-46.

Russell, L. S. (1982): Tertiary mammals of Saskatchewan, Part VI: The Oligocene rhinoceroses. -*Royal Ont. Mus. Life Sci. Contrib.*, 133: 1-58.

Scott, W. B. (1941): Perissodactyla. -In: Scott, W. B. and Jepsen, G. L. (eds.): The mammalian fauna of the White River Oligocene. -*Trans. Amer. Phil. Soc.*, n.s., 28: 747-980.

Stock, C. (1949): Mammalian fauna from the Titus Canyon Formation, California.

-*Publ. Carnegie Inst. Wash.*, 584: 229-244.

Tanner, L. G., and Martin, L. D. (1976): New rhinocerotoids from the Oligocene of Nebraska. -In: Churcher, C. S. (ed.), *ATHLON: Essays in Paleontology in honor of Loris Shano Russell: Royal Ont. Mus. Life Sci. Misc. Publ.*, pp. 210-219.

Wilson, J. A. (1977): Stratigraphic occurrence and correlation of early Tertiary vertebrate faunas, Trans-Pecos, Texas, Part 1: Vieja area. -*Tex. Mem. Mus. Bull.*, 25: 1-42.

Wilson, J. A., and Schiebout, J. (1984): Early tertiary vertebrate faunas, Trans-Pecos Texas: Ceratomorpha less Amynodontidae. -*Texas Mem. Mus. Pearce-Sellards Ser.*, 39: 1-47.

Wood, H. E., II (1927): Some early Tertiary rhinoceroses and hyracodonts. -*Bull. Amer. Paleont.*, 13: 165-264.

Wood, H. E., II (1929): *Prohyracodon orientale* Koch, The oldest known true rhinoceros. -*Amer. Mus. Novit.*, 395: 1-7.

Wood, H. E., II (1934): Revision of the Hyrachyidae. -*Bull. Amer. Mus. Nat. Hist.*, 67: 181-295.

Wood, H. E., II (1938): *Cooperia totadentata*, a remarkable rhinoceros from the Eocene of Mongolia. -*Amer. Mus. Novit.*, 1012: 1-20.

Wood, H. E., II (1963): A primitive rhinoceros from the late Eocene of Mongolia. -*Amer. Mus. Novit.*, 2146: 1-11.

21. THE RHINOCEROTIDAE

KURT HEISSIG

The phylogeny and classification of the Rhinocerotidae are revised on the basis of the newly introduced characters presented by Prothero, Manning, and Hanson (1986) and Groves (1983) and my own observations since the revised classification of Heissig (1973a). The characters used here are discussed in detail, especially to avoid too many parallelisms. The presence of a functional fifth metacarpal in the two fore feet of *Juxia sharamurunense* Chow and Xiu in the American Museum serves the key to the controversy over whether the first true rhinoceroses had a tridactyl or tetradactyl manus. The evidence of a strong relationship of the American *Diceratherium* group with the basic stock of the rhinoceroses, especially the genus *Trigonias*, and on the other hand, the fundamental differences from *Menoceras*, as stated by Prothero, Manning and Hanson (1986), have modified our knowledge of the early history of the family. The hypothesis of a common ancestry of the Teleoceratini and the Rhinocerotinae, brought forward by the same authors, is rejected here. Some characters limiting the adaptational potential of subfamilies and tribes are analyzed in relation to the behavior of the animals.

the 1970s by Guérin, Ginsburg, and Heissig in Europe, Radinsky a little earlier in the United States, and, later, Fortelius in Finland, all authors have felt that a thorough revision of the classification was needed. The basis of the classification was fixed by Radinsky (1966) by restricting the family to members with the chisel-tusk shearing complex of I_2 and I^1, and their descendants. The later attempts by Heissig (1973a) as well as the phylogenetic and systematic hypotheses presented in this volume, must remain provisional until the materials already collected are described and used as a base of a new classification. We are still far from this goal, but we now need a classification to work with and to arrange our materials. A revised version of my classification (1973a) is presented here, changed by a better understanding of the American species and some strong arguments of my American colleagues.

Introduction

During the nearly thirty years in the middle of our century, when no specialists in the western world were concerned with detailed study or classification of the rhinoceroses, a huge mass of undescribed material was stored in the museums and collections all over the world. Modern means of transportation led to more extensive digging, and as a result, vast and only partially identified collections of fossil rhinoceroses were waiting for their adequate descriptions or monographs. Since the group was again taken into consideration in the beginning of

Characters and parallelisms in the Rhinocerotidae

Using characters for a phylogenetic analysis means avoiding parallelisms. Most gradually changing characters are an expression of a general tendency among the whole group whereas discrete characters, especially when new structures are formed, may be unique and therefore key characters for the analysis. The loss of an element or a structure may occur very easily and is always suspected to be subject to parallelisms. Nevertheless, we can even use parallel evolved structures, if they follow different ways in different subgroups. In the following list, a lot of single characters currently