

A New Helaletid Tapiroid (Perissodactyla, Mammalia)
from the Paleogene of Hokkaido, Japan, and the
Age of the Urahoru Group

By

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Abstract—*Colodon kushiroensis* sp. nov. is described from northern Japan based primarily on its non-molariform upper premolars and its large size. *C. kushiroensis* is morphologically most similar to *C. ? hancocki* known from the Chadronian of western North America. Although the close morphological similarity does not by itself indicate their definite age relationship, if it is accepted, the geologic age assignments of the Urahoru Group based on the mammalian fossil (Chadronian in North American "scale") and on the megafflora (Kummerian — "Goshen type" in North American "scale") are consistent with each other. The correlation of these North American "scales" to the European standard is presently unsettled, but an early Oligocene age for the Urahoru Group is tentatively assigned.

Introduction

Paleogene mammalian fossils have been very rarely found in Japan. About ten specimens from four localities are presently known. Most of those represent an amynodontid rhinocerotoid, "*Amyndodon watanabei*" (TOKUNAGA, 1926; TAKAI, 1950); others include fragmental teeth of a helaletid tapiroid (TAKAI, 1945) and an isolated tooth of an anthracothere (TAKAI, 1961). The above specimens have all been assigned to the late Eocene in age.

A new occurrence of another Paleogene mammal has recently attracted attention. It was found in 1968 by Messrs. Shun-ichi and Norio NAKAI at the sea cliff, east of Kushiro City, Hokkaido. But the fossil has been kept in the specimen storage room of the Kushiro City Museum without any attention until 1982 when all the specimens in the Museum were examined prior to moving to a new building.

The specimen is a palate of helaletid tapiroid with nine cheek teeth preserved. Although the teeth are fairly worn, it apparently represents a new species of the genus "*Colodon?*" as described below. The specimen is important biogeographically as it indicates close relationship with a North American Chadronian (early Oligocene) species and is also important as it forms a new member of the poorly known Paleogene terrestrial fauna of Japan. This discovery may also contribute to the age assignment of the Urahoru Group, which has been controversial.

Geology of the Locality Area

The locality of the specimen is the middle of the sea cliff, about 5.5 km east of Konbumori, Kushiro-cho, Kushiro-gun (Fig. 1); or more precisely, the cliff facing the Todo Iwa (sea-lion rock), an uneroded block of rocks in the sea.

The fossil bearing beds are the Ten-neru Conglomerate Member of the Chorobetsu Formation of KAWAI (1956) or the Ten-neru Formation of OKAZAKI (1966). I follow OKAZAKI (1966) for the stratigraphic nomenclature of the area (Fig. 2). The Urahoro Group that includes the Ten-neru Formation unconformably overlies the Nemuro Group that consists of mainly fine-grained, marine sediments deposited during the latest Cretaceous — early Paleocene. The maximum geologic age of the Nemuro Group is somewhat unsettled, but there is a consensus that at least the lower half of the group includes the latest Cretaceous (Maastrichtian) (OKAZAKI, 1966).

The Urahoro Group is well known as it contains rich coal. It consists of 400–1,000 m in total thickness of mainly fresh water sediments and is divided into seven formations (Fig. 2). From the Beppo Formation through Yubetsu Formation are fresh water sediments, and the Harutori Formation contains main coal seams of the Kushiro coal field. Although the Ten-neru Formation consists mainly of characteristic reddish brown pebble-sized conglomerates, it also contains the sandstones and mudstones. The helaletid tapiroid described in the present paper was found in a fine sandstone bed near the middle of the formation. The thickness of the formation is approximately 90 m at this area.

The Urahoro Group is overlain unconformably by the Onbetsu Group that consists mainly of marine mudstones at the western part of the Kushiro coal field, but the Onbetsu Group is all eroded at the eastern part where the tapiroid fossil was found,

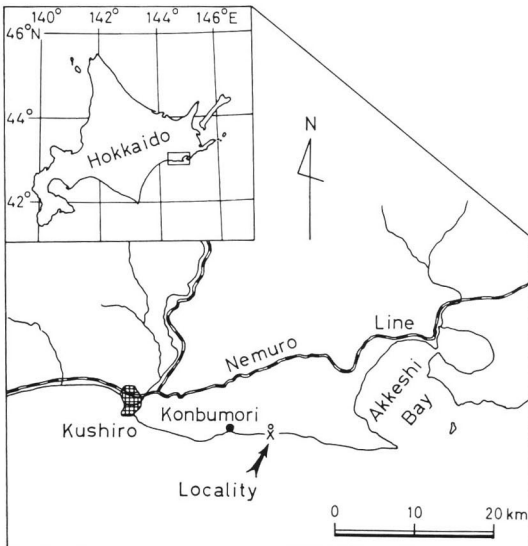


Fig. 1. Map showing the fossil locality.

AGE	FORMATIONS	T. (m)	FACIES	SED. ENV.	
Tertiary	Onbetsu G.	1000-1200	mudst., sd.st. tuff breccia	M	
			Charo F.		mudst.
			Omagari F.	sandst.	B
	Urahoro Group	Shakubetsu F.	400-1000	sd.st., mudst. coal seams	F-B
		Shitakara F.		sandst. mudst.	M-B
		So-un F.		mudst.	B
		Yubetsu F.		sd.st., mudst. coal seams	F
		Ten-neru F.		congl.-mudst. coal seams	
		Harutori F.		sd.st., mudst. coal seams	
		Beppo F.		congl.	
	Cret.	Nemuro Group	3000+	mudst. sandst. congl.	M

Fig. 2. General stratigraphy of the Kushiro area, compiled from OKAZAKI (1966). The geological age column is not the same as him. T: thickness; congl.: conglomerate, sd. st.: sandstone, mudst.: mudstone; M: marine, B: brackish, and F: fresh water environments.

and the Urahoro Group is overlain directly by the Quaternary sediments (OKAZAKI, 1966). For the geologic age of the Urahoro and Onbetsu groups, see the "Age of the Urahoro Group" section below.

Systematic Paleontology

Superfamily Tapiroidea GILL, 1872

Family Helaletidae OSBORN, 1892

Genus *Colodon* MARSH, 1890

Discussion: RADINSKY (1963, 1965) exhaustively reviewed the early Tertiary tapiroids then known from North America and Asia, respectively. The genus *Colodon* includes the most advanced species of the subfamily Helaletinae (*sensu* RADINSKY, 1967) and is characterized in part by the following diagnostic features (RADINSKY, 1963): 1) P¹ with lingual loph or cusp; 2) P²⁻⁴ essentially molariform, metaloph as prominent as protoloph and extending to hypocone; 3) M¹⁻² metacone flat to concave; 4) P₂₋₄ with relatively large entoconids; 5) nasals reduced. RADINSKY (1963) described *C. ? hancocki* that is characterized by barely submolariform upper premolars,

convex metacones of M^{1-2} , and other features. Although he indicated possibility of assignment of the species to a separate genus, he avoided to erect a new genus and questionably referred it, as well as *C.?* *cingulatus*, to the genus *Colodon* because of the poor knowledge of the advanced helaletids and lack of postcranial anatomy of the species at that time. In his review of Asiatic forms, RADINSKY (1965) also questionably referred "*Desmatotherium*" *grangeri* to the genus *Colodon*. He mentioned the close similarity of *C.?* *grangeri* with *C.?* *hancocki* and pointed out that these two species may be generically distinct from *Colodon*, but again did not erect a new genus because of the poor knowledge of those species.

Since RADINSKY (1965) did not mention the similarity of *C.?* *cingulatus* with these two species, it is not clear if he still refers it to this possible "new genus" or not. But, at any event, it is obvious that at least two species, *C.?* *hancocki* and *C.?* *grangeri*, represent a group of species of a same genus. The *Helaletes*-like characters that this group shares (although not all the characters can be observable on both species) are: 1) P^{2-4} non-molariform to barely submolariform; 2) M^{1-2} metacones convex, rather than concave; 3) P_{3-4} with small entoconids. The *Colodon*-like characters are: 1) P^{2-4} relatively short and wide; 2) P^{3-4} metalophs nearly or as prominent as protolophs; and 3) nasals much reduced.

A new species as described below also shares the same characters (where observable), and it is suggestive that this species also a member of the same group. During the course of examining the specimen of the new species I also had strong impression that these species may be generically distinct from *Colodon* based mainly on the retarded molarization of the upper premolars, which distinguish this group from the main *Helaletes* — *Colodon* line. Similar distinction is also observable between the genus *Dilophodon* and the main *Helaletes* — *Colodon* line (RADINSKY, 1963).

However, the only specimens that I have been able to examine directly are, in addition to the holotype of the new species, a plaster cast of the holotype of *C.?* *hancocki* and epoxy casts of two upper molars of *C. hodosimai* among the specimens of the closely related genera and species. Thus, I hesitate to discuss further on the generic status of the species *hancocki*, *grangeri*, and a new species described below until I am able to examine more specimens of the related genera and species. Thus, for the present I prefer to leave the generic status of these species as RADINSKY (1963, 1965) did which is to assign them questionably to the genus *Colodon*.

Colodon kushiroensis sp. nov.

(Plate 1)

Holotype: Laterally crushed rostrum with right P^{1-3} , partly broken $P^4 - M^2$, left P^{2-4} , and roots of M^1 preserved, Kushiro City Museum (KCM) - A89, which is the only known specimen.

Distribution: Presently known only from eastern Hokkaido, Japan; Ten-neru Formation, Urahoro Group (see "Geology of the locality area" section above).

Age: Probably early Oligocene (see next section).

Etymology: Named for Kushiro, general geographic name of the locality area.

Diagnosis: Size about equal to or may be slightly larger than *C.? cingulatus*, the largest previously known species of the genus, from which it differs in having less molariform upper premolars. P¹ with posterolingual widening but no lingual cusp nor cingulum. P² with an isolated anterolingual cuspule instead of protoloph. P³⁻⁴ with poorly developed posterolabial cingula.

Description: P¹ is a small, low, two-cusped, two-rooted tooth with a slight posterolingual widening; no cingulum present. The posterior cusp is much smaller and lower than the anterior one and thus may better be called a cuspule. The posterior root is wider than the anterior.

P² is roughly triangular in outline, with two distinct labial and a single lingual cusps, an anterolingual cuspule, and a small parastyle. No protoloph is present, and instead, the isolated anterolingual cuspule is present at the position of the protoloph. Weak metaloph extends from the protocone toward the anterolingual corner of the metacone but is not connected with it. The posterior cingulum is present.

P³⁻⁴ are relatively short and wide. P³ is roughly triangular in outline, with the apex of the triangle slightly skewed posteriorly. Because of the wear, the shape and number of lingual cusp(s) are not clearly observable. But, it is inferred from the general outline and from the absence of lingual groove that there is only a single cusp, protocone, on the lingual side of the tooth. The protoloph and metaloph are about equal in prominence, they extend toward the anterolingual corners of the paracone and metacone, respectively, but are not connected with them. The size of the parastyle is larger than in P² and smaller than in P⁴. The posterior cingulum is well developed. Both posterolabial and anterolingual cingula are incipient.

P⁴ is basically similar to but larger than P³. The position of the protocone is not skewed posteriorly and is wider than that of P³. The protoloph and metaloph are weakly connected to the anterolingual corners of the paracone and metacone, respectively.

In M¹ much of the morphology of the main cusps and lophs is not observable because of the wear and damage. The metacone is slightly convex labially, and is not displaced lingually as much as other species of the genus *Colodon* but it is shortened as in other species of the genus. The parastyle is well developed. The anterior cingulum is present, and the posterolabial cingulum is fairly well developed.

Not much can be observable on M². The metacone is nearly flat labially and shortened, and the posterolabial cingulum is developed as in M¹.

Table 1. Measurements (in mm) of the holotype of *Colodon kushiroensis*, KCM-A89.

Right	P ¹	P ²	P ³	P ⁴	M ¹	M ²
Length	9.3	13.2	14.0	ca. 14.8	ca. 19.3	ca. 23.1
Width	8.3	15.5	ca. 19.0	19.9	—	—

The infraorbital foramen is exposed above the anterior half of P^4 . For the measurements of the teeth see table 1.

Comparison: As described above, the *Colodon*-like characters of *C. kushiroensis* are: 1) P^{3-4} metaloph as prominent as protoloph, 2) P^{3-4} relatively short and wide, and 3) M^{1-2} metacones shortened; the *Helalestes*-like characters are: 1) P^1 simple, 2) P^{2-4} non-molariform, and 3) M^1 metacone slightly convex. These characters indicate the close similarity with *Colodon? hancocki* known from western North America (RADINSKY, 1963). In fact, except for the size difference and the degree of lingual displacement of molar metacone, KCM-A89 is nearly identical with the holotype of *C.? hancocki*, University of Oregon Vertebrate Paleontology (UO)-20377. KCM-A78 is approximately 30% larger than *C.? hancocki*, and I believe that this size difference exceeds possible intraspecific variation.

In P^2 of UO-20377 the anterolingual cuspule is connected with the protocone, and thus alternatively it can be interpreted as a widened protoloph. In both UO-20377 and KCM-A89 the anterolingual cuspule is much smaller than the main lingual cusp and is located much labial in comparison with the main lingual cusp. Therefore, I prefer to call the main lingual cusp a protocone when the molar terminology is applied to P^2 of these specimens.

C. kushiroensis is also similar to *C.? grangeri* known from northern Korea (TOKUNAGA, 1933; TAKAI, 1939). Except for a single lower molar, all the described specimens including the holotype are either destroyed during the World War II or cannot be located at present. Although RADINSKY (1965) mentioned that P^2 of *C.? grangeri* has a shallow lingual groove, I cannot see it on any of TOKUNAGA's and TAKAI's photographs (and TOKUNAGA does not mention it either), though they are not clear enough to confirm definitely. In P^4 of *C.? grangeri* a shallow lingual groove is present indicating incipient separation of the hypocone as TOKUNAGA (1933) mentioned. *C.? grangeri* is about 20% smaller than *C.? hancocki* and is nearly 40% smaller than *C. kushiroensis*. Three badly preserved lower teeth referred to *C.? grangeri* are known from western Japan (TAKAI, 1945). Because of the lower dentition the direct comparison is not available, but sizewise they are smaller than *C.? hancocki*.

C. kushiroensis is about equal to or only slightly larger than *C.? cingulatus* known from western North America (RADINSKY, 1963), but differs from it in having less molariform and slightly narrower upper premolars.

Judging from the description and illustrations of WORTMAN and EARLE (1893), KCM-A89 also closely resembles *Protapirus simplex* in general outline with having single lingual cusp on the upper premolars and in size. Although the upper molars of *P. simplex* is not known, those of other species of the genus (FIHOL, 1877; WORTMAN and EARLE, 1893; HATCHER, 1896; SCOTT, 1941) show the differences: in *Protapirus*, 1) labial convexity of molar metacone is stronger; 2) posterolabial cingulum of the molars is less developed; and 3) the length of upper premolar series relative to the length of molar series is longer than in *C. kushiroensis*. For the last point above, the ratio of the length of upper premolar series over that of molar series in *P. obli-*

quidens is 0.93 and *P. validus* 0.92 (calculated from SCOTT, 1941), while *C.?* *hancocki* 0.84 and *C. kushiroensis* about 0.78 (approximate estimate with an analogy that the length of M³ is about the same as that of M² in helaletids). In later forms of tapiroids the ratio is usually more than 1, while it is usually closer to 0.8–0.85 in helaletids except for a couple of species (RADINSKY, 1963). Thus, although *C. kushiroensis* closely resembles *P. simplex* in upper premolar morphology and in size, the morphology and relative size of upper molars indicate that it is rather a member of helaletids and is closer to *C.?* *hancocki* than the genus *Protapirus*.

Geologic Age of the Urahoro Group

The geologic age assignment of the Urahoro Group has been discussed by many workers, together with the correlations with Ishikari Group at the Ishikari coal field, central Hokkaido (Fig. 3). Previous age assignments of these groups have been based on three taxonomic groups of fossils: molluscs, foraminifers, and plants.

Among the many investigators, MIZUNO (1964) summarized Paleogene molluscan faunas of northern Japan and recognized four successive faunas: the Lower, Middle, and Upper Ishikarian, and Poronaiian faunas in ascending order. The marine molluscs from the Urahoro Group and those of the Onbetsu Group belong to his Upper Ishikarian and Poronaiian faunas, respectively. Based on the comparison with the Tertiary molluscan fossils, especially the Blakeley fauna, of the Pacific Coast of North America, he considered the Upper Ishikarian fauna, hence the Urahoro Group, belongs to the early to middle Oligocene and the Poronaiian fauna, hence the Onbetsu Group, belongs to the late Oligocene in age.

ASANO's (1962) interpretation of the stratigraphic relations between the Ishikari and Poronai groups, which is that the marine Poronai Group changes laterally into

ISHIKARI COAL FIELD		KUSHIRO COAL FIELD	
Poronai Group		Onbetsu Group	
Ishikari Group	Upper	Ashibetsu F. Hiragishi F. Ikushunbetsu F.	Urahoro Group Shakubetsu F. Shitakara F. So-un F. Yubetsu F. Ten-neru F. Harutori F. Beppo F.
	Middle	Akabira F. Bibai F. Wakkanabe F.	
	Lower	Yubari F. Horokabetsu F. Noborikawa F.	

Fig. 3. Correlation of the Paleogene beds in the Ishikari and Kushiro coal fields (slightly changed from TANAI, 1970). F: Formation

the fresh-water and brackish Ishikari Group, is quite inconsistent with the interpretation of most other workers (Fig. 3). Nevertheless, his conclusion on the geologic age assignments of both the Urahoro and Onbetsu groups are the Late Eocene (Priabonian), based on the benthic foraminiferal fauna and the findings of the planktonic foraminifers, *Globorotaloides suteri* (Late Eocene to "Middle" Oligocene) and *Globigerina cf. linaperta* (Eocene), in the Poronai Group by UJIIÉ and WATANABE (1960).

TANAI (1970) described in detail the fossil floras from the Urahoro Group and discussed its geologic age. He recognized four successive floras within the Urahoro Group: the Harutori, Ten-neru, Yubetsu, and Shakubetsu floras in ascending order. The Ishikari Group at the Ishikari coal field also includes several floras. From the correlations and analyses of the floras at these two areas he inferred the climatic trend during the time range that the Ishikari and Urahoro groups were deposited: subtropical climate as its warmest peak is represented by Bibai flora; then the climate gradually changed to warm-temperate during deposition of the Ikushunbetsu-Harutori floras, and further to temperate as indicated by the Yubetsu and Shakubetsu floras (Fig. 3).

Comparing with the Eocene and Oligocene floras of western North America, TANAI (1970) concluded that the Harutori flora is younger than the Clarno and Comstock floras and is somewhat older than the Bridge Creek and Ruby Basin floras. Based on the climatic trend mentioned above and on the then knowledge that the Clarno flora is Late Eocene and the Bridge Creek flora is early "Middle" Oligocene in age, TANI (1970) concluded that the Harutori flora is Early Oligocene and the Yubetsu and Shakubetsu floras are probably "Middle" Oligocene in age.

According to a recent study on megafloal chronology in western North America (WOLFE, 1981), the middle Clarno flora belongs to the late Ravenian, the Clarno nutbed flora to the Kummerian, and the Bridge Creek flora to the early Angoonian of Pacific North American megafloal stage. It is not clear whether TANAI's (1970) Clarno flora is the same as the middle Clarno flora of WOLFE (1981) or not (it is true that TANAI's Clarno flora does not include the Clarno nutbed flora), but if it is true, then, it is inferred that the Harutori flora is younger than the late Ravenian and is older than the early Angoonian stages of North American "scale" (Fig. 4).

As pointed out in the above section, *C. kushiroensis* is most similar in morphology to *C. ? hancocki* from the Clarno Formation of North America. The locality of *C. ? hancocki* is "Clarno mammal quarry" of the University of Oregon, and the associated fauna from the quarry indicates its age to be the early Chadronian or late Duchesnean (EVERNDEN *et al.*, 1964). Since the phylogenetic relationships among the species of the genus "*Colodon*?" have not been clear, the fact that *C. kushiroensis* is morphologically most similar to *C. ? hancocki* does not by itself indicate their definite age relationship. But, if it is accepted, and in addition, if the general trend of size increase seen among the early Tertiary tapiroids is applicable to the species of the genus "*Colodon*?", *C. kushiroensis* may be about the same age or more probably be slightly younger than *C. ? hancocki*. Thus, mammalian faunal evidence alone indicates the

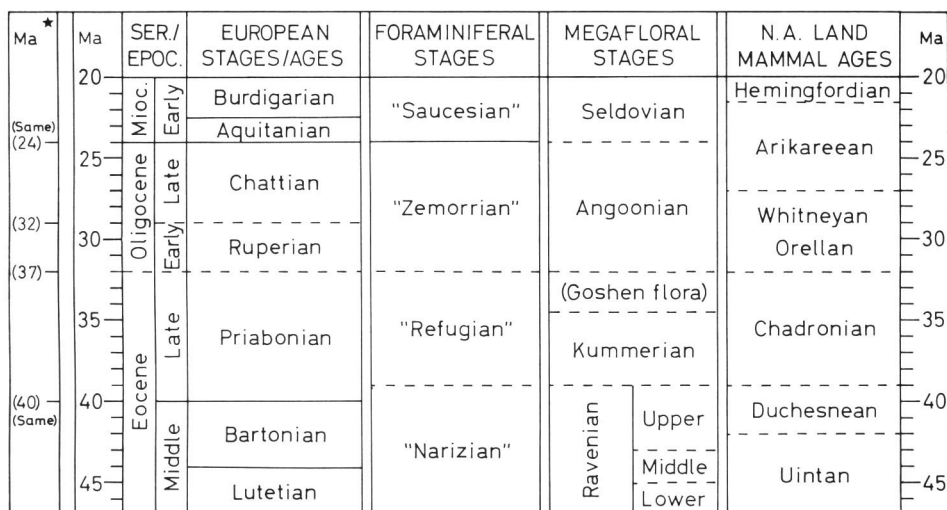


Fig. 4. Correlation of Cenozoic chronostratigraphic units for Oregon and Washington, redrawn from ARMENTROUT (1981, p. 145), but only slightly changed. ★ The dates at far left column are those by HARDENBOL and BERGGREN (1978), as in ARMENTROUT (1981).

age of the Ten-neru Formation, at least, to be sometime during the Chadronian of the North American land mammal "time scale".

The Clarno nutbed flora has been dated as 34.9 Ma (EVERNDEN and JAMES, 1964). The K-Ar dates published before 1979 are, in the present paper, recalculated following DALRYMPLE (1979). The Clarno mammal quarry is 60 m stratigraphically above the nutbed site, but the time gap between them is probably not much. The date 34.9 Ma is somewhat inconsistent with the age (late Duchesnean — early Chadronian) inferred from the mammalian faunal composition (EVERNDEN *et al.*, 1964), if the time range of the Chadronian is calibrated as approximately 39–32 Ma (Fig. 4). But, since the identification of the mammal fauna is tentative (EVERNDEN *et al.*, 1964, p. 182), that inconsistency should not be emphasized too much, and thus the Clarno mammal fauna can be assigned as Chadronian age.

WOLFE (1981) and ARMENTROUT (1981) correlated the Kummerian and "Goshen type" megafloreal stages to the "Refugian" foraminiferal stage, and then to the Priabonian stage of the European standard. They also correlated the Kummerian and "Goshen type" to the Chadronian land mammal age (Fig. 4). Although they place the Eocene — Oligocene boundary at the Priabonian — Ruperian boundary as other workers do (for example, HARDENBOL and BERGGREN, 1978; BERGGREN *et al.*, 1978), they differ from others in calibration of absolute age of that boundary. Thus, according to their correlation, the Chadronian is the late Eocene age.

Although the valuation of their correlations is still unsettled, if following WOLFE (1981) and ARMENTROUT (1981), 1) ASANO's (1962) age assignment of the Urahoro

Group to the Priabonian, 2) TANAI's (1970) age assignment of the Harutori flora to the post-Ravenian — pre-Angoonian, and 3) the Chadronian age of the Ten-neru Formation inferred from the *C. kushiroensis* are not inconsistent with each other.

The Bridge Creek flora of Oregon has been dated as 31.9 Ma and 32.3 Ma (EVERNDEN *et al.*, 1964), and TANAI (1970) pointed out that the Yubetsu and Shakubetsu floras are rather similar to the Bridge Creek flora. Recently a K-Ar date of 32.6 ± 1.7 Ma was obtained from the Nuibetsu Formation of Onbetsu Group (SHIBATA and TANAI, 1982). This date may be somewhat inconsistent with the age of the Yubetsu and Shakubetsu floras, which is inferred from the correlation with the Bridge Creek flora, but since that correlation is based only on the floral similarity, the precision of the order of 1–2 million years cannot be expected. Thus, I believe that the radiometric dates in the above discussion are all fairly consistent with each other.

In conclusion, the Harutori and Ten-neru formations, at least, and probably the Urahoru Group as a whole may be correlated to the Chadronian land mammal age or Kummerian and “Goshen type” megafloral stage of North American “scales”, that is the early Oligocene in traditional correlation and is late Eocene in the recent correlations by WOLFE (1981) and ARMENTROUT (1981) (Fig. 4). Since the material described in the present paper is a mammal and since the valuation of the correlations by WOLFE and ARMENTROUT is not settled, I prefer at present the early Oligocene age for the Chadronian as traditionally assigned. Secondly, the time gap represented by the unconformity between the Urahoru and Onbetsu groups is probably not much.

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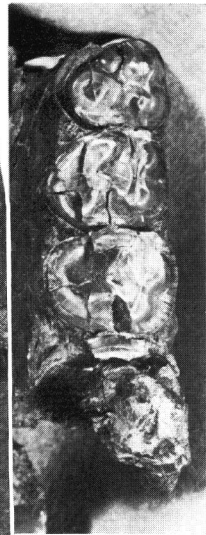
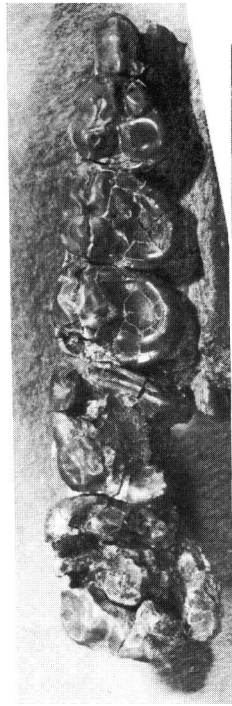
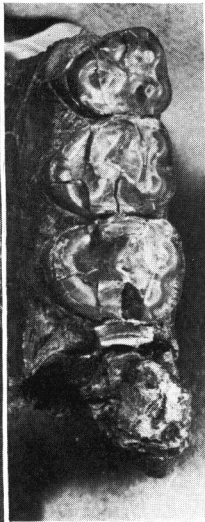
References Cited

- ARMENTROUT, J. M., 1981. Correlation and ages of Cenozoic chronostratigraphic units in Oregon and Washington. *Geol. Soc. Amer. Spec. Pap.*, (184): 137–148.
- ASANO, K., 1962. Japanese Paleogene from the view-point of foraminifera with descriptions of several new species. *Contr. Inst. Geol. Paleont. Tohoku Univ.*, (57): 1–32, pl. 1. (in Japanese with English abstract and descriptions)

- BERGGREN, W. A., M. C. MCKENNA, J. HARDENBOL, & J. D. OBRADOVICH, 1978. Revised Paleogene polarity time scale. *Jour. Geol.*, **86**: 67–81.
- DALRYMPLE, G. B., 1979. Critical tables for conversion of K-Ar ages from old to new constants. *Geology*, **7**: 558–560.
- EVERNDEN, J.F. & G.T. JAMES, 1964. Potassium-argon dates and the Tertiary floras of North America. *Amer. Jour. Sci.*, **262**: 945–974.
- , D. E. SAVAGE, G. H. CURTIS, & G. T. JAMES, 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. *Amer. Jour. Sci.*, **262**: 145–198.
- FILHOL, H., 1877. Recherches sur les phosphorites du Quercy. Etude des fossiles qu'on y rencontre et spécialement des mammifères. *Ann. Sci. geol. (Paris)*, **8** (1): 1–340, pls. 1–28.
- HARDENBOL, J. & W. A. BERGGREN, 1978. A new Paleogene numerical time scale. *Amer. Assoc. Petr. Geol., Studies Geol.*, **6**: 213–234.
- HATCHER, J. B., 1896. Recent and fossil tapirs. *Amer. Jour. Sci., 4th ser.*, **1**: 161–180.
- KAWAI, M., 1956. Explanatory text of the geological map of Japan: 1/50,000 Kombumori. *Geol. Survey Japan*, 59+8 pp. (in Japanese with English summary).
- MIZUNO, A., 1964. Summary of the Paleogene molluscan faunas in North Japan. *Rep. Geol. Survey Japan*, (207): 1–28.
- OKAZAKI, Y., 1966. Geology of Kushiro. Kushiro City Government, 326 pp. (in Japanese)
- RADINSKY, L., 1963. Origin and early evolution of North American Tapiroidea. *Bull. Peabody Mus. Nat. Hist. Yale Univ.*, (17): 1–106, pls. 1–4.
- , 1965. Early Tertiary Tapiroidea of Asia. *Bull. Amer. Mus. Nat. Hist.*, **129**: 181–264, pls. 1–4.
- , 1967. *Hyrachyus*, *Chasmotherium*, and the early evolution of helaletid tapiroids. *Amer. Mus. Novitates*, (2313): 1–23.
- SCOTT, W. B., 1941. Perissodactyla. In SCOTT, W. B. & G. L. JEPSEN, The mammalian fauna of the White River Oligocene. Part V. *Trans. Amer. Philos. Soc.*, **28**: 747–980, pls. 79–100.
- SHIBATA, K. & T. TANAI, 1982. K-Ar age of Tertiary volcanic rocks in Hokkaido. In TANAI, T. (ed.) Recent progress of Neogene biostratigraphy of Hokkaido, p. 75–79, Sapporo, Hokkaido Univ. (in Japanese)
- TAKAI, F., 1939. Eocene mammals found from the Hosan coal-field, Tyosen. *Jour. Fac. Sci. Imp. Univ. Tokyo, Sec. II*, **5** (6): 199–217, pls. 1–5.
- , 1945. Eocene mammals from the Ube and Hosan coal-fields in Nippon. *Proc. Imp. Acad. Tokyo*, **20** (10): 736–741. (for 1944)
- , 1950. *Amynodon watanabei* from the latest Eocene of Japan with a brief summary of the latest Eocene mammalian faunule in eastern Asia. *Rep. Geol. Survey Japan*, (131): 1–14, pl. 1.
- , 1961. A new anthracothere from the Shiramizu Group in the Joban coal-field, Japan, with notes on its geological age. *Proc. Japan Acad.*, **37** (5): 255–260.
- TANAI, T., 1970. The Oligocene floras from the Kushiro coal field, Hokkaido, Japan. *Jour. Fac. Sci. Hokkaido Univ., Ser. IV*, **14** (4): 383–514, pls. 3–20.
- TOKUNAGA, S., 1926. Fossils of Rhinocerotidae found in Japan. *Proc. Imp. Acad. Tokyo*, **2** (6): 289–291.
- , 1933. A list of the fossil land mammals of Japan and Korea with descriptions of new Eocene forms from Korea. *Amer. Mus. Novitates*, (627): 1–7.
- UJIIÉ, H. & H. WATANABE, 1960. The Poronai Foraminifera of the northern Ishikari coal-field, Hokkaido. *Sci. Rep. Tokyo Kyoiku Daigaku, Sec. C*, **7**: 117–136.
- WOLFE, J., 1981. A chronologic framework for Cenozoic megafossil floras of northwestern North America and its relation to marine geochronology. *Geol. Soc. Amer. Spec. Pap.*, (184): 39–47.
- WORTMAN, J. L. & C. EARLE, 1893. Ancestors of the tapir from the Lower Miocene of Dakota. *Bull. Amer. Mus. Nat. Hist.*, **5**: 159–180.

Explanation of Plate 1

Figs. 1-3. *Colodon kushiroensis* sp. nov., KCM-A89. Fig. 1. right P¹-M²; fig. 2. left P²⁻⁴, both stereophotographs of occlusal views. Fig. 3. left lateral view. All $\times 0.9$.



1

2



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