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PALEOCENE GENUS *PSEUDICTOPS* MATTHEW, GRANGER & SIMPSON 1929 (MAMMALIA) AND ITS REVISION

(PALEOCENSKI RODZAJ *PSEUDICTOPS* MATTHEW, GRANGER & SIMPSON, 1929
(MAMMALIA) I JEGO REWIZJA)

(Plates X—XIV)

Abstract. — The Paleocene genus *Pseudictops* is revised on the base of material collected during the Polish-Mongolian Palaeontological Expeditions (1963—1965) in Naran Bulak and Tsagan Khushu (Nemegt Basin) in the Mongolian People's Republic. The monotypic family Pseudictopidae (Eutheria incertae sedis) closely related to Anagalidae SIMPSON, 1931, is erected. *Pseudictops arilophiodon* TROFIMOV, 1952, from Naran Bulak is regarded a synonym of *P. lophiodon* MATTHEW, GRANGER & SIMPSON, 1929. Revised diagnosis of *P. lophiodon* is given, full upper and lower dentition, hind limb and other fragments of postcranial skeleton of this species being described. Considerations as to the systematic position and age of *P. lophiodon* are included.

INTRODUCTION

During the Polish-Mongolian Palaeontological Expedition in 1963, a few mandibular and maxillar fragments with teeth and fairly numerous isolated teeth of a primitive mammal of the genus *Pseudictops* were found in the Lower Tertiary beds of Naran Bulak in the Nemegt Basin (GRADZIŃSKI *et al.*, 1968, p. 53, Text-fig. 11). In the following year, more intensive exploration was carried out in the same area (KIELAN-JAWOROWSKA & KOWALSKI, 1965; KIELAN-JAWOROWSKA & DOVCHIN, 1968). As a result, new bone material, in particular fragments of a postcranial skeleton were collected.

Exploratory work was carried out in several places and horizons at Naran Bulak. Two places in particular yielded numerous and interesting remains: a small hill with fish (5), and a layer with micromammals (6) (see GRADZIŃSKI *et al.*, 1968, Text-figs. 11—12). The small hill, where the biggest bones were recovered, is at the south-eastern end of the northern walls of Naran Bulak. The bones were found in the upper part of the section which is composed of sandstone or greyish-white coloured sand overlying a not very thick layer of conglomerate with fish. Here the expedition found their first bone remains of *Pseudictops* in 1963.

In the layer with micromammals (6), in addition to numerous maxillar and mandibular fragments with teeth *in situ* (one maxilla fragment with complete dentition!) numerous remains of other mammals such as notoungulates (*Palaeostylops*), lagomorphs (*Eurymylus*) and multituberculates (*?Prionessus*) were also found. The latter layer is some 40—50 m east of the small hill with fish (5), lying in the section, under the upper bone-bearing layer with *Pseudictops*.

The rest of the *Pseudictops* remains from Naran Bulak were recovered from places lower than the afore-mentioned localities, i.e. from the lower fossiliferous horizon (3) (GRADZIŃSKI *et al.*, 1968, Text-figs. 11—12). In the one site, a strongly silicified mandible with very poorly preserved teeth was found, and in the second also a strongly silicified fragment of the maxilla with badly worn tooth crowns.

Some 8—9 km north-west of Naran Bulak, at Tsagan Khushu (GRADZIŃSKI *et al.*, 1968, Text-figs. 8, 10), in Lower Tertiary beds, the expedition came across a new locality with micromammalian bones. These remains were embedded in a lens of weakly consolidated light gray sand, situated at a distance of about 2—2.5 km south-east of Cretaceous beds with dinosaur bones, and about 1 km west of White Sayr. Here mandible fragments, some with badly damaged teeth, others without, were collected. These remains belong to *Pseudictops lophiodon*. Various fossil bones of other micromammals were also found in this place, among them mandibles and maxillae with teeth of the genus *Palaeostylops*.

The material collected by the three successive Polish-Mongolian Palaeontological Expeditions (1963—1965) in the above mentioned localities permitted observations to be made on the morphology and variability of dentition of the genus *Pseudictops*, as well as a revision of the previous diagnoses and systematic position of this genus.

As regards the fragments of the postcranial skeleton, the limb bones were not found together with the jaw fragments in anatomical arrangement, however, as they were all within a radius of 2 m, it is more probable than not that they belong to the same individual. This is also supported by fact that in the small hill with fish (5), no bone remains of any other big mammal were found, to whom the postcranial skeleton could be ascribed. Moreover, as additional evidence, the proportions and size of the bones are in keeping with those of the jaws.

The bone material of the genus *Pseudictops*, collected by the Polish-Mongolian Palaeontological Expeditions, is at present in the collection of the Palaeozoological Institute of the Polish Academy of Sciences in Warsaw.

The preparation and conservation of the bone material, the text illustrations, and the retouching of photographs was carried out by the author, with photographs by Miss M. CZARNOCKA.

The following abbreviations are used:

- Z. Pal. — Institute of Palaeozoology, Polish Academy of Sciences, Warsaw.
A. M. N. H. — American Museum of Natural History, New York.
PIN — Institute of Palaeontology, USSR Academy of Sciences, Moscow.

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THE HISTORY OF INVESTIGATIONS ON THE GENUS *PSEUDICTOPS*

MATTHEW, GRANGER & SIMPSON, 1929

The first remains of the genus *Pseudictops* were found by the Central Asiatic Expedition of the American Museum of Natural History, probably in 1924, in the red and orange sandstone of the Khashaat (= Gashato) formation, situated about 7 km W of the outcrops of Bayn Dzak (= Shabarakh Usu) and were described as *P. lophiodon* by MATTHEW, GRANGER and SIMPSON in 1929. The sediments of this formation were determined as Upper Paleocene or late Cretaceous (MATTHEW & GRANGER, 1925b), on the base of the mammalian assemblage, mainly multituberculates, discovered there (*l. c.*, pp. 1-2). In the opinion of the American authors, the genus *Palaeostylops* from Khashaat showed some relationship to the Paleocene American genus *Arctostylops* from the Torrejon (Wasatch) formation, however, the remaining mammalian fauna (with the exception of the multituberculates) could not be definitely correlated with other mammalian assemblages of that period (MATTHEW & GRANGER, 1925b; MATTHEW *et al.*, 1929; TROFIMOV, 1952). The bone remains at Khashaat were found lying not *in situ*, in or at the foot of several small eroded clay hills, or at their foot and were fragmented, badly preserved and strongly silicified.

The American *Pseudictops lophiodon* material consisted of a left mandible with P_3 - M_3 (A. M. N. H. No. 21727), two right maxillae — one with $M^{1-2(?)}$ (A. M. N. H. No. 21712) and a second with P^4 (DP^4) — M^1 (A. M. N. H. No. 21722), and a detached P_1 , described by MATTHEW and GRANGER (1925b, p. 4, Fig. 4) as *Palaeostylops* sp.

This material, judging from casts obtained from Dr. MCKENNA, appears to be not very well preserved, which could account for the discrepancies in the determination and morphology of some of the teeth. This species was assigned by MATTHEW *et al.* in 1929 to the order Insectivora and, in spite of its large dimensions, to the family Leptictidae. These authors stated, however, that the molarisation of the premolars is more advanced in *Pseudictops* than in the representatives of Leptictidae. The bilophodonts of trigons and trigonids also in their opinion do not correspond in both groups. Moreover, hypocone in leptictids, as they correctly stated, cannot be compared with the posterior cingulum in *Pseudictops*. Finally the molars in the latter increase posteriorly, which is not the case in leptictids.

The mentioned authors suggested a certain similarity between the genus *Pseudictops* and the Upper Cretaceous insectivore *Zalambdalestes*, but failed to find any close genetic connection between them. A certain resemblance to the representatives of Amblypoda was also suggested on the base of the complication of the premolars lophodonts, reduction of the paraconid on the lower cheek teeth, short talonids and the triangular outline of the upper molar crowns. In the end, however, the authors came to the conclusion that leptictids were perhaps the closest to the genus *Pseudictops*.

In 1948 or 1949 the Mongolian Palaeontological Expedition of the USSR Academy of Sciences (EFREMOV, 1954; ROZHDESTVENSKY, 1954, 1957a, b; NOVOZHILOV, 1954; TROFIMOV, 1952, and others), recovered in Khashaat a partial face belonging to the genus *Pseudictops*, as well as the remains of a micromammal (Insectivora?), and a fragment of another big mammal, probably also Insectivora? (NOVOZHILOV, 1954). The first of these specimens was described by TROFIMOV (1952) as *P. lophiodon*, while the other remains have so far not been systematically elaborated.

The partial face (PIN No. 476—7) is silicified with almost complete dentition on both sides. This specimen supplied new data as to the structure of the palate (shape, length and width,

the angle between the tooth rows), the presence of diastema and the position of the zygomatic arch. To the diagnoses and descriptions of *P. lophiodon*, already given by MATTHEW *et al.* in 1929, TROFIMOV added a tentative dental formula and a character, which he considered as primitive and characteristic of the genus *Pseudictops*, namely a tendency towards V-shaped transversal crests on the trigons and trigonids of the cheek teeth (*l. c.*, p. 8). This character, in TROFIMOV's opinion, suggests a closer relationship between this genus and the representatives of the Leptictidae, while at the same time, excluding the possibility of assigning *Pseudictops* to the order Carnivora. He also considered that, in the structure of teeth, *Pseudictops* is close to erinaceoids (Erinaceoidea), and especially to *Zalambdalestidae*. However, the presence of several archaic features and certain tendencies to specialization in *Zalambdalestes* seemed to exclude a closer connection between *Pseudictops* and *Zalambdalestes*. TROFIMOV considered the genus *Pseudictops* as a representative of the family Leptictidae in spite of its bigger measurements and difference in dentition. According to him, *Pseudictops* is a member of the Asiatic lineage of old erinaceoids, developing parallelly to the true line of development of the American leptictids. Finally, on the base of the analogy between its dentition and that of pantodonts, he put forwards the suggestion that *Pseudictops* was a herbivorous animal. ROZHDESTVENSKY (1957, pp. 52—53) and FLEROV (1952, 1957) came to the same conclusion.

In 1949, the Mongolian Palaeontological Expedition of the USSR Academy of Sciences (ROZHDESTVENSKY, 1957) worked in the region of Naran Bulak, discovering a fragment of a left mandible with M_{2-3} *in situ* and preserved alveoli for P_2 and M_1 . This specimen was assigned by TROFIMOV (1952, pp. 11—12, Text-figs. 2—4) to a new species *P. arilophiodon*. The sediments, in which the latter jaw was found, as well as those of other mammals (Dinocerata, Pantodonta), were determined by Soviet scientists as Lower Eocene. In the diagnosis of *P. arilophiodon*, TROFIMOV mentioned only three features, distinguishing it from *P. lophiodon*: trigonids, much higher than talonids, strongly developed crests on trigonids and better defined cusps on talonids. He stated that the front crest of the trigonid was lower and shorter than the back, and that on the base of the alveolar part of the jaw, M_1 had four roots¹.

SABAN (1958, p. 871), while accepting in principle the former diagnosis of genus *Pseudictops*, stressed that the incisors and canines had a similar structure and were of the same size. Also, in no case did the posterior cingulum of the upper molars form hypocone. In his opinion, trigonids increase as a result of reduction of the paraconids, the cusps of the talonids becoming in consequence more marked.

GROMOVA (1962) based his diagnosis of genus *Pseudictops* on the investigations of MATTHEW *et al.* (1929) and TROFIMOV (1952). Just as the latter author, GROMOVA assigned this genus to the family Leptictidae and to order Insectivora.

MCKENNA (1963) compared the dentition of genus *Anagale* and *Anagalopsis* with that of *Pseudictops* and stated a considerable resemblance between the cheek patterns of all the discussed genera. The resemblance extends also to the specific structure of the posterior limb bones, and in particular the metatarsal bones and ungual phalanges.

VAN VALEN (1964) carried out a detailed analysis of the dentition of the genus *Eurymylus* and put forwards some conclusions as to the possible relationship of this genus with genus *Pseudictops*. This work is discussed on page 126.

Recently (see ROMER, 1966, p. 380), the genus *Pseudictops* was placed in the order Insectivora and family Anagalidae. Assignment of this genus to Anagalidae is probably the result of MCKENNA's (1963) further investigations on the representatives of this family.

¹ On the illustration given by TROFIMOV (1952, p. 11, fig. 2) as on the specimen (observation of the present author), this tooth has two roots just as the remaining teeth, with the exception of P_1 .

MATERIAL INVESTIGATED

The bone material of the genus *Pseudictops* came from three localities in Southern Mongolia: Khashaat (= Gashato), Naran Bulak and Tsagan Khushu. The list given below also includes specimens already described in literature.

Khashaat (=Gashato)

1. A. M. N. H. No. 21727 — type specimen: fragment of a left mandible with P_3-M_3 (MATTHEW *et al.*, 1929, p. 5, fig. 1A-B).
2. A. M. N. H. No. 21712: fragment of a right maxilla with M^{1-2} (MATTHEW *et al.*, 1929, p. 6, fig. 2A-B).
3. A. M. N. H. No. 21722: fragment of a right maxilla with P^{3-4} (see VAN VALEN, 1964, p. 484; there DP^{4-M^1}).
4. A. M. N. H. No. 20426: topotype *Palaeostylops* sp.: isolated P_1 (MATTHEW & GRANGER, 1925b, p. 4, fig. 4).
5. PIN No. 476-7: partial face with almost complete dentition on both sides (TROFIMOV, 1952, p. 9, fig. 1).

Naran Bulak (Nemegt Basin)

The majority of bone material was found in the two main localities of Naran Bulak: 1) a small hill with fish (5), and 2) the upper bone layer with small mammals (6). Moreover two fragments, one of a mandible and the other of a maxilla, were recovered from the middle and lower bone levels(3).

6. PIN No. 533-121a: type specimen of *Pseudictops arilophiodon* (TROFIMOV, 1952): fragment of a left mandible with M_2-M_3 , and P_2 and M_1 alveoli (TROFIMOV, 1952, p. 11, figs. 2-3; p. 12, fig. 4).
7. Z. Pal. No. MgM-II/1: fragment of a right maxilla with I^1-M^3 (6).
8. Z. Pal. No. MgM-II/2: fragment of a right maxilla with P^1-M^3 (5).
9. Z. Pal. No. MgM-II/3: fragment of a right maxilla with $C-M^3$ (without P^2) (6).
10. Z. Pal. No. MgM-II/4: fragment of a left maxilla with P^2-M^3 (3).
11. Z. Pal. No. MgM-II/5: fragment of a left maxilla with P^2-M^1 (5).
12. Z. Pal. No. MgM-II/6: fragment of a left maxilla with I^{1-3} (5).
13. Z. Pal. No. MgM-II/7: fragment of a right maxilla with I^{2-3} (5).
14. Z. Pal. No. MgM-II/8: fragment of a left maxilla with P^3-M^1 (6).
15. Z. Pal. No. MgM-II/9: isolated right I^3 , C, P^1 (6).
16. Z. Pal. No. MgM-II/10: two upper canines (5).
17. Z. Pal. No. MgM-II/11: isolated left I_1 , I_2 , DC?, P_2 , P_3 , P_4 , M_1 and M_2 (6).
18. Z. Pal. No. MgM-II/12: isolated right I_2 , I_3 , DC?, P_1 , P_2 , P_3 , P_4 , and M_1 or M_2 (6).
19. Z. Pal. No. MgM-II/13: isolated left I_1 , I_2 , I_3 and C (5).
20. Z. Pal. No. MgM-II/14: isolated right I_1 , I_2 , C (5).
21. Z. Pal. No. MgM-II/15: fragment of a right mandible with P_1-M_3 (5).
22. Z. Pal. No. MgM-II/16: fragment of a left mandible with P_2-M_3 (5).
23. Z. Pal. No. MgM-II/17: fragment of a left mandible with P_4-M_3 (5).
24. Z. Pal. No. MgM-II/18: fragment of a right mandible with P_3-M_3 (M_2 lacking) (3).
25. Z. Pal. No. MgM-II/19: fragment of a right mandible with P_4-M_3 (6).
26. Z. Pal. No. MgM-II/20: left C with a damaged crown (3).
27. Z. Pal. No. MgM-II/21: anterior fragment of a right mandible with roots (6).
28. Z. Pal. No. MgM-II/22: a few fragments of lower teeth enamel (6).
29. Z. Pal. No. MgM-II/23: a few fragments of upper teeth enamel probably of I and P (6).

Postcranial skeleton

All specimens mentioned below were found in the small hill with fish (5):

30. Z. Pal. No. MgM-II/33: left femur: the head without neck, the proximal extremity with three trochanters and trochanteric fossa, as well as distal extremity (condyles only) all preserved.
31. Z. Pal. No. MgM-II/34: left tibia.
32. Z. Pal. No. MgM-II/35: left fibula without head and distal extremity.
33. Z. Pal. No. MgM-II/36: left calcaneum; the distal part of shaft damaged.
34. Z. Pal. No. MgM-II/37: left astragalus.
35. Z. Pal. No. MgM-II/38: left cuboideum.
36. Z. Pal. No. MgM-II/39: left naviculare.

37. Z. Pal. No. MgM-II/40: left metatarsal bone I (Mt. I); the base, middle part of shaft with head, and digital phalanges 1, 2.
38. Z. Pal. No. MgM-II/41: left metatarsal bone II (Mt. II), and digital phalanges 1, 2, 3.
39. Z. Pal. No. MgM-II/42: left metatarsal bone III (Mt. III); the base with proximal part of shaft, head, and digital phalanges 1, 2, 3.
40. Z. Pal. No. MgM-II/43: left metatarsal bone IV (Mt. IV), and digital phalanges 1, 2, 3.
41. Z. Pal. No. MgM-II/44: left metatarsal bone V (Mt. V); the base with proximal part of shaft, head, and digital phalanges 1, 2.
42. Z. Pal. No. MgM-II/45: four left sesamoid bones.
43. Z. Pal. No. MgM-II/46: left calcaneum, partially preserved.
44. Z. Pal. No. MgM-II/47: the middle part of left astragalus.
45. Z. Pal. No. MgM-II/48: right calcaneum.
46. Z. Pal. No. MgM-II/49: right astragalus.
47. Z. Pal. No. MgM-II/50: five digital phalanges of a hind or fore limb (I), a fragment of metatarsal bone II or III?, probably of the right hind limb.
48. Z. Pal. No. MgM-II/51: distal extremity (part) of the humerus?
49. Z. Pal. No. MgM-II/52: left tarsal bone 3.
50. Z. Pal. No. MgM-II/53: indeterminate bone fragments, probably of the hind limb.

Tsagan Khushu (Nemegt Basin)

All specimens mentioned below were discovered in the lens with micromammal bones, on the southern slope of White Sayr:

51. Z. Pal. No. MgM-II/24: fragment of a left mandible with P_3-M_3 .
52. Z. Pal. No. MgM-II/25: fragment of a left mandible with badly preserved P_4-M_3 , and with C, P_{1-3} alveoli.
53. Z. Pal. No. MgM-II/26: fragment of a left mandible with P_4-M_1 (the crowns of M_{2-3} missing).
54. Z. Pal. No. MgM-II/27: fragment of a left mandible with P_3-M_3 .
55. Z. Pal. No. MgM-II/28: fragment of a left mandible with partially preserved angular process.
56. Z. Pal. No. MgM-II/29: fragment of a left mandible with C, P_{1-3} alveoli.
57. Z. Pal. No. MgM-II/30: fragment of a left mandible with C, P_{1-2} alveoli.
58. Z. Pal. No. MgM-II/31: fragment of a right mandible with M_{2-3} alveoli.
59. Z. Pal. No. MgM-II/32: a few fragments of lower cheek teeth enamel.

TERMINOLOGY

The terminology used in the present paper for the description of dentition is mostly that of VAN VALEN (1966), with some exception. On the upper molars (M^{1-2}) of *Pseudictops* the conules are lacking, therefore crests connecting the protocone with the paracone, and the protocone with the metacone are named: the paraloph and the metaloph respectively. Terms as: preprotocrista, postmetaconule wing, premetaconule wing and postprotocrista, proposed by VAN VALEN, are used for teeth on which conules occur.

The only new term introduced by the present author is: posteroloph, to designate the crista in M^1 and M^2 , which extends from the protocone towards the posterior cingulum.

ABBREVIATIONS

Upper dentition (Text-fig. 1)

Anterior crista — ACR }
Posterior crista — PCR } (on I^{1-3} and C).

Lingual crista — LGCR (on I^1-P^3).

Lingual cusps — 1, 2, 3... (on LGCR; on I^1-I^1 , I^2-I^1 , 2, I^3-I^1 , 2, 3 and more. On C absent. The posterior lingual cusp 2 occurs on P^2).

Posterior lobes — I, II, III (on PCR; on P^3 lobe III is lacking; these lobes occur on P^{1-3}).

Parastyle — PAST (present on P^1-M^3 , uncertain on I^{2-3} and C, lacking on I^1).

Paracone — PAC (present on P^1-M^3 , uncertain on I^{1-3} and C).

- Metacone — MTC (on P^1-M^3).
 Metastyle — MTST (on P^2-M^2).
 Stylocone — STC (on P^{1-2}).
 Protocone — PRC (on P^3-M^3 ; protocone and lingual cusp 1 on P^2 uncertain).
 Protofossa — PRF (on P^1-M^3).
 Centrocrista — CECR (on P^{3-1} only, not typical).
 Styler shelf — ST SH (on P^3-M^3).
 Anterior cingulum — ACIN (on P^4-M^3 , sometimes on P^2).
 Posterior cingulum — PCIN (on P^3-M^3 ; postcingulum + metacingulum — VAN VALEN'S (1966, pp. 7-8),
 Metaloph — MTLPH } (on P^3-M^3).
 Paraloph — PALPH }
 Posteroloph — POLPH (on M^{1-2} only).
 Incipient hypocone — inc. HYC (on M^{1-2} , sometimes on M^3).

Lower dentition (Text-fig. 2)

- Protoconid — PRD (present, except in I_{1-3} , where uncertain).
 Paraconid — PAD (present, except for I_{1-2} ; on I_3 and C uncertain; on P_4 very small, vestigial).
 Posterior lobes — I, II (on PCRD; on I_{1-3} only).
 Anterior cingulum — ACIN (on P_{1-2} , on P_4 very weak).
 Posterior cingulum — PCIN (on C and P_{1-2}).
 Metaconid — MTD (on P_1-M_3).
 Antero-labial cingulum — ALBCIN (on P_3 and M_{1-3}).
 Parastylid — PASTD (on M_{1-3} , sometimes on P_3).
 Hypoconid — HYD
 Entoconid — END
 Crista obliqua — CROB
 Hypoflexid — HYFXD } (on P_3-M_3).
 Paralophid — PALPHD }
 Metalophid — MTLPHD }
 Postfossid — POFD }
 Profossid — PREFD (on P_2-M_3).
 Hypoconulid — HYLD (on M_{1-3}).
 Metacristid — MTCRD (on M_{1-3} very rare from the metaconid side).
 Entoconulid — ENLD (on M_3 only).
 Trigonid — TGD (on P_2-M_3).
 Talonid — TLD (on P_3-M_3 ; on P_2 as a pseudo-talonid).

DESCRIPTION

Class MAMMALIA

Infraclass EUTHERIA

Order incertae sedis

Family PSEUDICTOPIDAE n. fam.

Type genus: *Pseudictops* MATTHEW, GRANGER & SIMPSON, 1929.

Diagnosis. — Dental formula: $I_3^3 C_1^1 P_4^4 M_3^3$.

Dimensions similar to the small red fox or badger. The length of palate somewhat greater than the width between M^3-M^3 (labial sides). The angle between sagittal axis of the palate and a tooth-row ca. 20° . Zygomatic arch probably full and slender. Infraorbital foramen above P^3 .

Horizontal ramus of the mandible moderately long, thick and high. The symphysis extends to the anterior border of P_2 . P_3 - M_3 tuberculo-sectorial structure with square (lower teeth) and triangular (upper teeth) outlines. The crests of trigons and trigonids short and sharp. Upper cheek teeth twice as wide as long. Trigonids two or three times higher than talonids. P^3 - M^3 without hypocones or with incipient ones (on M^{1-2} only, sometimes on M^3). Progressive backwards molarisation of upper and lower premolars. Protoconid on P_{3-4} higher, and on M_{1-3} lower than the metaconid. The paraconid on P_3 - M_3 vestigial or fully reduced (especially on P_4). Paralophid short, steep and lower than the metalophid. The talonids of M_{1-3} with three or four cusps (on M_3). The pentadactyl hind limb, probably semiplantigrade or semidigitigrade. The claw phalanges on the hind limb fissured and with proximal enlargement. Astragalar foramen present, small. Astragalar trochlea almost symmetrical. The tibia and fibula separate. The calcaneum antero-posteriorly elongated with well-developed tuber calcis. The metatarsal bones II—IV long (the longest being metatarsal III), while metatarsal bones I and V are reduced in length. The cuboideum and naviculare similar to the astragalus — primitive insectivore — carnivorous type.

Remarks. — The new family is monotypic, erected to include *Pseudictops* MATTHEW, GRANGER & SIMPSON, 1929. See also discussion on page 124.

Genus *PSEUDICTOPS* MATTHEW, GRANGER & SIMPSON, 1929

Pseudictops lophiodon MATTHEW, GRANGER & SIMPSON, 1929

(Pls. X—XIV; Text-figs. 1—4)

1925. *Palaeostylops* sp.; W. D. MATTHEW & W. GRANGER, Fauna and correlation ..., p. 4, Fig. 4.
 1929. *Pseudictops lophiodon* MATTHEW, GRANGER & SIMPSON; W. D. MATTHEW, W. GRANGER & G. G. SIMPSON, Additions to the fauna..., pp. 1-6, Figs. 1 A-B, 2 A-B.
 1952. *Pseudictops lophiodon* MATTHEW, GRANGER & SIMPSON; B. A. TROFIMOV, O rode Pseudictops..., pp. 8-9, Fig. 1.
 1952. *Pseudictops arilophiodon* TROFIMOV; B. A. TROFIMOV, *Ibid.*, pp. 10-12, Figs. 2-4.
 1962. *Pseudictops lophiodon* MATTHEW, GRANGER & SIMPSON; I. V. GROMOVA, Osnovy paleontologii (pars Insectivora) ..., pp. 78-79, Figs. 35-36 A-B.
 1964. *Pseudictops lophiodon* MATTHEW, GRANGER & SIMPSON; L. VAN VALEN, A possible origin..., p. 486, Fig. 1A.

Type locality: Khashaat (= Gashato), Gobi Desert, The Mongolian People's Republic.

Type horizon: Upper Paleocene.

Occurrence: Khashaat (= Gashato), Naran Bulak and Tsagan Khushu, Gobi Desert.

Type specimen: The fragment of mandible with P_3 - M_3 (A. M. N. H. No. 21727) (MATTHEW, GRANGER & SIMPSON, 1929, p. 5, Figs. 1 A-B). Further materials from Khashaat, see page 105.

Material. — A full list of specimens of this species is given on pp. 105-106.

Revised diagnosis. — Palate rather short and narrow anteriorly (from I^1 to P^3), wide posteriorly (from P^4 to M^3). The anterior root of the zygomatic arch extends from between P^4 and M^1 , to half-length of M^3 . Two mental foramina present — an anterior below P_1 and a posterior, as a rule, between P_2 and P_3 . The cusp arrangement on trigons and trigonids in a triangle, on talonids crescentshape. I_1 - P_1^1 one-rooted, P_2 - M_3 two-rooted, and P^2 - M^3 three-rooted (sometimes P^2 is two-rooted). The protocone on P^3 - M^3 lower than the paracone and metacone. These latter cusps sharp and separate at tips. The paracone on M^{1-2} rather higher than metacone. P^4 - M^3 with anterior and posterior cingula, P^3 most often with the anterior cingulum very reduced. Progressive backward molarisation of premolars — P_2^2 30—40%, P_3^3 70—80%, P_4^4 80—90%. The

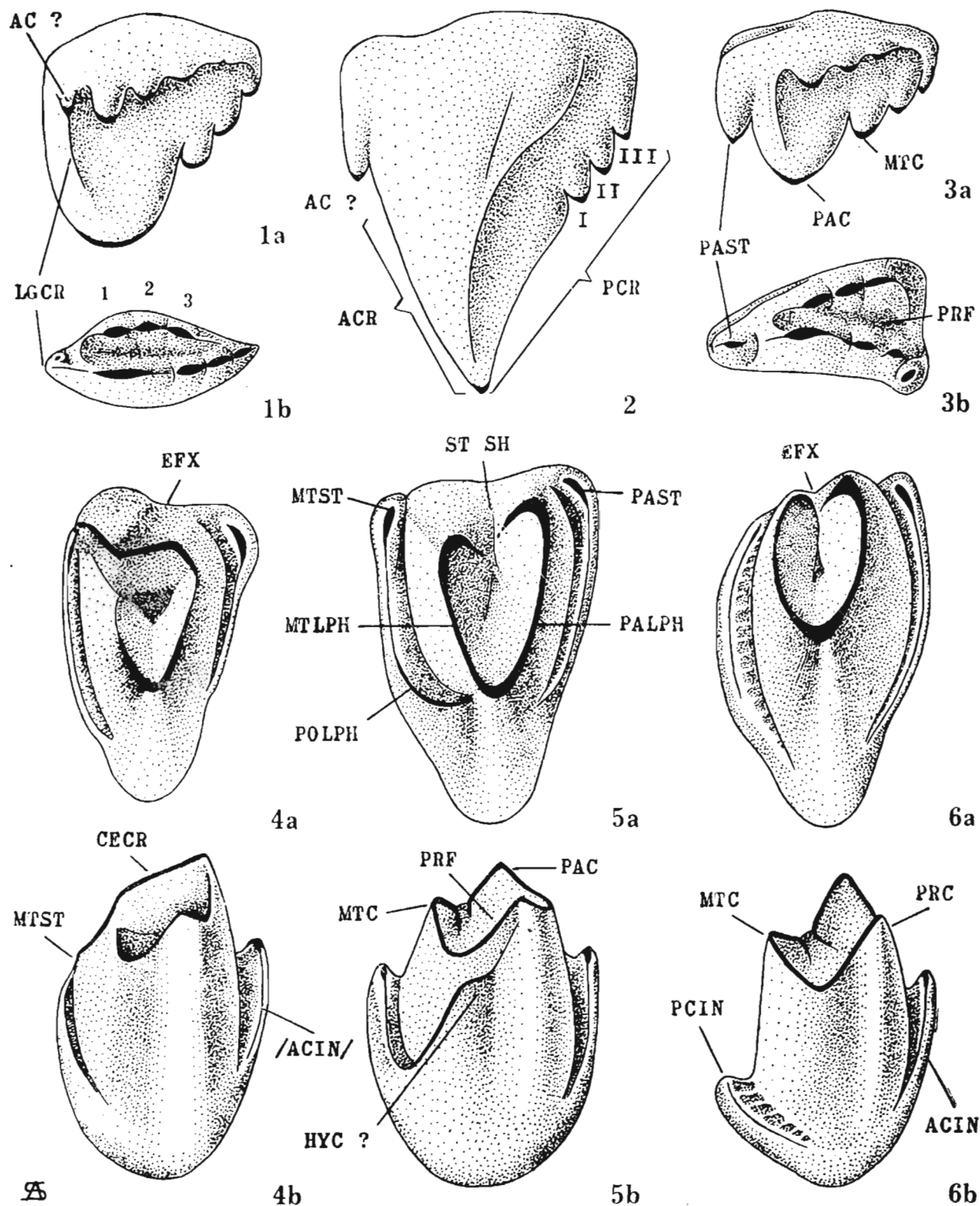


Fig. 1. *Pseudictops lophiodon* MATTHEW, GRANGER & SIMPSON. Structure of the upper teeth (drawings slightly schematic): 1 — I^{1-2} , 2 — C (lingual view), 3 — P^{1-2} , 4 — P^{3-4} , 5 — M^{1-2} , 6 — M^3 . Figs. 1, 3 a lingual view, b occlusal view, Figs. 4-6 a occlusal view, b lingual view. Explanations of abbreviations see in text. All ca. $\times 7.5$.

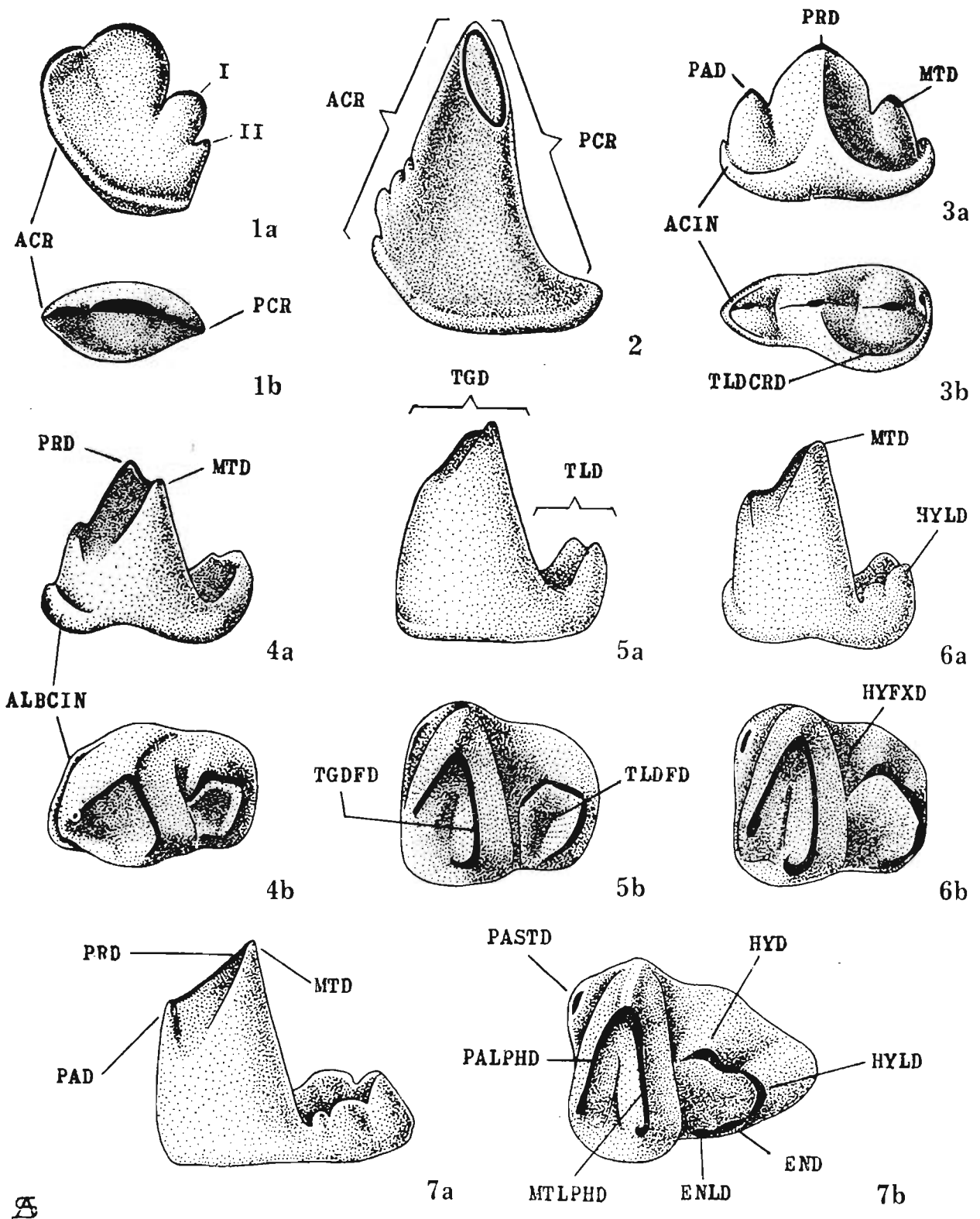


Fig. 2. *Pseudictops lophiodon* MATTHEW, GRANGER & SIMPSON

Structure of the lower teeth (drawings slightly schematic): 1—I₁₋₃, 2—C (lingual view), 3—P₁₋₂, 4—P₃, 5—P₄, 6—M₁₋₂, 7—M₃. Figs. 1, 3-7 a lingual view, b occlusal view. Explanations of abbreviations see in text. All ca. ×7.5.

parastyle an isolated cusp or labial swelling on the anterior cingulum. M^3 with a cut off postero-labial angle of the crown, without metastyle. The parastylid is a small cusp or antero-labial thickening on the cingulum. Lower molars without metastylids. The talonid on M_3 longer than trigonid, with three cusps, the hypoconulid being the greatest. P_3 - M_3 without a posterior cingulum. First and fifth dactyls of the hind limb reduced in length. The femur probably short, massive, and wide in extremities.

Description. — *Maxilla.* The infraorbital foramen above P^3 or somewhat displaced backwards (Pl. XII, figs. 9, 10). At this point there is a distinct narrowing of the maxilla. The anterior root of zygomatic arch extends from between P^4 and M^1 , to half-length of M^3 . Judging from the broken surface of the zygomatic arch, it was probably slender and full. The palate is somewhat longer than the width M^3 - M^3 (labial sides of maxilla). Angle between tooth-rows ca. 40° . Palatine process of the maxilla concave transversally. Anterior foramen (preserved only in one specimen — Z. Pal. No. MgM-II/3; Pl. XII, fig. 1) situated opposite the anterior edge of M^2 . Palatine groove very short, deep and narrow, disappearing probably at the level of M^1 - P^4 embrasure. This, however, is not certain, as part of the anterior portion of the maxillary palatine process between P^4 - P^1 is not preserved. The maxillo-palatine suture cannot be determined. To the rear of the anterior palatine foramen, there is another foramen, smaller than the anterior, situated opposite the M^2 - M^3 embrasure.

Upper dentition (Tbl. 1). I^1 one-rooted. Root twice as long as height of crown, and round in cross-section. The crown compressed antero-posteriorly, convex labially and concave lingually. The anterior cutting-edge of the crown, sharp, without cusps. The posterior cutting-edge possesses three or four lobes which, with the lobes of the following incisors, canine and two first premolars, form an irregular cutting-edge. This, in conjunction with the corresponding lower edge, acted somewhat as a saw (Text-fig. 3). Apart from main lobe I, there are two or three smaller lobules separated by notches. The last lobe, III or IV, placed at the posterior base of crown. On the lingual side of the crown, there is a small cusplule 1. Labial side of crown without cingulum. The enamel surface of incisor smooth.

I^2 one-rooted, somewhat larger than I^1 . The structure of crown and root as in I^1 . I^2 differs from I^1 in the presence of a distinct lingual heel with two cusplules 1, 2.

I^3 one-rooted. Tooth structure as in I^1 - I^2 , but somewhat larger than I^2 . I^3 differs from the first two incisors in having a well developed lingual heel with two or three cusplules 1, 2, 3, situated on the lingual crest (LGCR).

Canines are one-rooted. Root oval or round in cross section, and twice as long (or more) as the height of crown. Crowns laterally compressed with two sharp cutting-edges. The anterior with a weak cusp, the posterior with three cusps at the base of crown. Crown-tips sharp. Crown $1/3$ (or more) higher than those of incisors and first premolars crowns. Canine enamel smooth. On the lingual side of crown, small heel or cingulum absent. Crown inclined backwards and outwards. On the cutting-edges of the deciduous teeth, especially the back one denticles occur. In adult or senile individuals, in addition to the changes caused by the wearing of crowns, the posterior cutting-edge becomes more saddle-like with a distinct posterior-lingual polish.

Premolars, four in number. Increasing posteriorly, the structure of their occlusal surface gradually becoming more complicated. The degree of molarisation being P^2 30—40%, P^3 70—80% and P^4 80—90%.

P^1 one-rooted. Root twice as long as the height of crown and round in cross-section. The crown low, similar to that of incisors but more elongated antero-posteriorly, labial cingulum absent. On the sagittal edge of crown there are three cusps: anterocone small and separated

Table 1
Measurements of skull and upper dentition (in mm)

| Measurements | PIN No. 476—7 | A. M. N. H. No. 21712 (paratype) | A. M. N. H. No. 21722 | Z. Pal. No. MgM-II/1—8 |
|---|------------------|--|--------------------------|------------------------|
| Palate length | ca. 50.0 | — | — | ca. 48.0 |
| Palate width in M ³ and M ³ (labial side) | ca. 35.0 | — | — | ca. 37.0 |
| Length I ¹ —M ³ | 50.0 | — | — | 48.0 |
| Length C—M ³ | 38.0 | — | — | 38.0 |
| Length P ¹ —M ³ | 31.5 | — | — | 32.0—34.0 |
| Length P ¹ —P ⁴ | 20.0 | — | — | 19.0—20.3 |
| Length P ³ —P ⁴ | 10.0 | — | 9.0 | 8.9—10.3 |
| Length M ¹ —M ³ | 15.0 | — | — | 14.0—15.0 |
| Length M ¹ —M ² | 10.5 | 9.5 | — | 9.5—10.1 |
| Length I ¹ | — | — | — | 3.3— 4.0 |
| Width I ¹ | — | — | — | 2.2— 2.3 |
| Length I ² | — | — | — | 3.5— 4.0 |
| Width I ² | — | — | — | 2.3— 2.8 |
| Length I ³ | — | — | — | 3.8— 4.0 |
| Width I ³ | — | — | — | 2.4— 2.9 |
| Length C | 3.0 _a | — | — | 4.2— 4.9 |
| Width C | 3.2 _a | — | — | 2.8— 3.0 |
| Length P ¹ | — | — | — | 4.0— 4.6 |
| Width P ¹ | — | — | — | 2.3— 2.7 |
| Length P ² | 5.0 | — | — | 4.5— 5.2 |
| Width P ² | 3.0 | — | — | 3.5— 3.7 |
| Length P ³ | 5.0 | — | 5.0 | 4.8— 5.2 |
| Width P ³ | 5.0 | — | 8.0 | 6.9— 9.2 |
| Length P ⁴ | 5.0 | — | 4.0 | 4.7— 5.0 |
| Width P ⁴ | 7.0 | — | 7.5 | 7.6—10.0 |
| Length M ¹ | 5.0 | 4.5 | — | 4.5— 5.0 |
| Width M ¹ | 7.5 | 8.0 | — | 8.0—10.0 |
| Length M ² | 5.5 | 5.0 | — | 4.8— 5.1 |
| Width M ² | 7.5 | 8.0 | — | 8.1—11.0 |
| Length M ³ | 4.5 | — | — | 5.0— 5.3 |
| Width M ³ | 7.5 | — | — | 8.2—10.0 |

Remarks:

A. M. N. H. No. 21712 and 21722 — measured on MATTHEW's *et al.* illustration (1929, Fig. 2) and verified with the casts.

PIN No. 476—7 — measurement according to TROFIMOV's data and illustration (1952, pp. 10—11, Fig. 1) and verified with the original specimen.

a — measured along the alveoli.

from paracone, paracone high, blunt and somewhat laterally compressed, and a low metacone (?). Crown, almost flat labially, convex lingually, with a well defined protoconal crest (PRCR). Protoconal crest flanks a deep valley, opening posteriorly on the lingual side of crown. In one of the specimens the protoconal crest has a small thickening (probably incipient protocone). Anterocone, sometimes shifted lingually and joined to the protoconal crest. Anterior edge of the crown sharp and steep, while the posterior is gently sloping with two cusps. Between P^1 and P^2 there is a small diastema about 2.5 mm in length.

P^2 two-rooted, sometimes three-rooted (in adult and senile individuals). Crown outline subtriangular, with a broadened posterior base. Anterocone visible, small and sharp. Paracone high and broad at the base. Metacone lower than anterocone. The labial side of crown almost

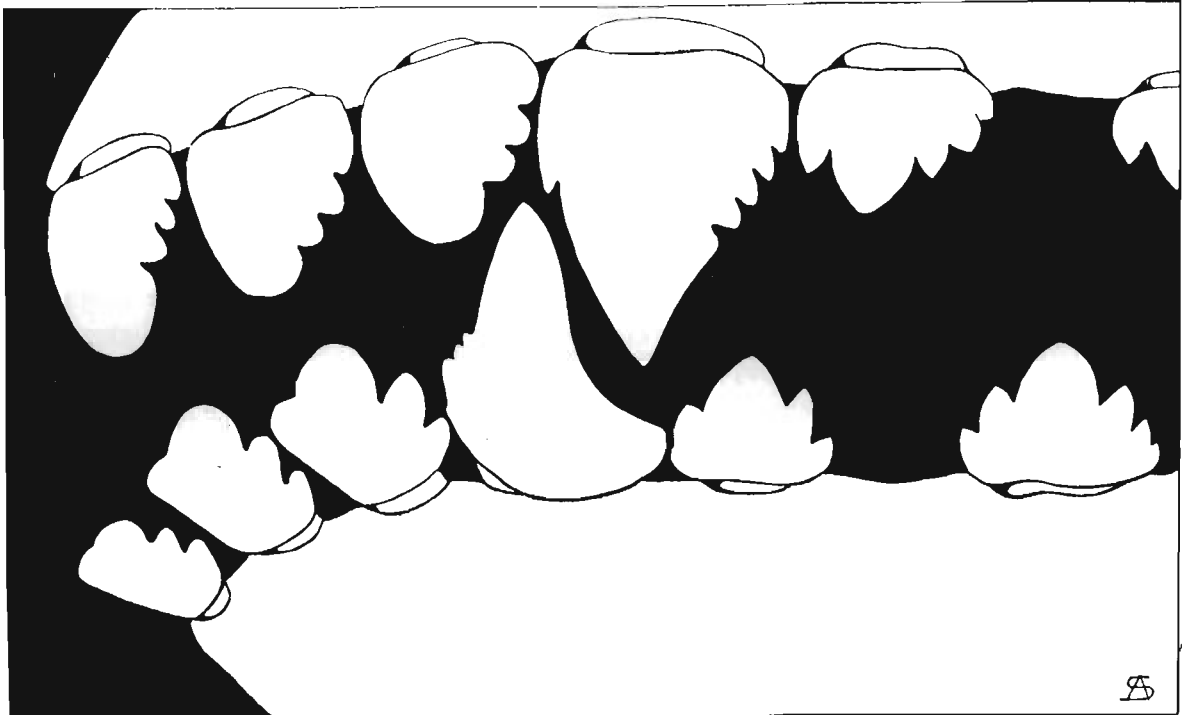


Fig. 3

Pseudictops lophiodon MATTHEW, GRANGER & SIMPSON
Upper and lower anterior teeth from labial side (scheme).

flat, the lingual — convex. Protoconal crest with a similar course as that in P^1 . In the posterior labial part of crown there is a weak posterior cingulum. Lingual cingulum absent. Two-rooted teeth have similar crowns, but are more elongated antero-posteriorly. On such teeth all cusps are in a rectilinear row. Posterior root almost twice as big and thick as anterior, with a tendency to divergence.

P^3 three-rooted, lingual root big and transversely oriented to the longitudinal axis of the maxilla, labial roots tiny and round in cross-section. Crown triangular, with base directed labially, apex — lingually. The same shape of crown also occurs in the remaining cheek teeth. P^3 crown, short and wide, almost twice as wide as long. Parastyle low and separated from paracone. Anterior cingulum, as a rule, absent or only as a faint trace. Paraloph (PALPH) joining paracone to protocone, metaloph (MTLPH) not reaching metacone, but finishing at its base.

Metacone, weakly defined, lying on the central crest (CECR) which joins the paracone with metacone. Posterior cingulum well developed, running from the posterior edge of metacone to the lingual border of protocone. On several teeth the parastyle is shifted anteriorly, not passing into the anterior cingulum which only occurs as a trace of at all. Antero-labial root directed more forwards than the postero-labial. On older teeth metaloph is joined to metacone. In addition, the protocone is high, but always lower than paracone. Metastyle appears as a thickening with metacone usually crestlike. On one specimen the paracone and metacone are distinctly separated and on the posterior cingulum, here rather wide, there is a fairly small swelling (incipient hypocone?) by the lingual border of the crown.

P⁴ three-rooted, bigger than P³. Parastyle small and joined to anterior cingulum. On several teeth it is more pronounced and separated from anterior cingulum. Anterior cingulum slender, low, reaching to 1/2 or 1/3 the width of the crown. Paracone and protocone joined by a high sharp paraloph. Metacone low, weaker than paracone, and joined to protocone by a low metaloph. In young individuals and sometimes in adult, the metacone and paracone are joined, in addition, by a central crest. Posterior cingulum wide, running towards lingual border of protocone. Posteroloph on P⁴ missing. Metastyle small or absent. The specimen Z. Pal. No. MgM-II/8 possesses a rather small thickening on the postero-lingual part of the posterior cingulum.

M¹ always three-rooted, smaller than M². Crown triangular, equal or slightly smaller than that of P⁴. Parastyle low, separated from paracone and joined to anterior cingulum. Anterior cingulum reaches to 1/2 or 2/3 crown width. The paracone is usually higher than the metacone, but sometimes they are of equal height. The protocone low and prismatic. Paraloph and metaloph high and sharp. Arrangement of crests in the form of a V. Posteroloph (POLPH) runs towards the posterior cingulum, joining it at about half its length. The posterior cingulum occupies 1/2 or 1/3 of the crown width. Labial cingulum in the form of a slight basal bulging. Metastyle joining the posterior cingulum. In young individuals the paracone is high, metacone low, both are sharp. Lingual root, large, antero-posteriorly compressed, while the labial is small and round in cross-section. At the junction of the posteroloph with the posterior cingulum there is a small thickening — incipient hypocone. This is specially visible on specimen Z. Pal. No. MgM-II/8. In addition, in young individuals the anterior cingulum is wide, strong, with a clearly visible parastyle and metastyle separated from main cusps.

M² three-rooted, triangular crown as in M¹. Arrangement of main cusps and crests also as in M¹. On several specimens, anterior cingulum is narrower and lower, and the paraloph more strongly developed. Posteroloph and a small incipient hypocone are present.

M³ three-rooted, subtriangular crown but with cut off postero-labial edge. Metastyle vestigial or absent. Parastyle small, low, joining anterior cingulum. The latter is almost as long as the width of the crown. Paracone high, metacone low. Paraloph and metaloph short, the latter lower than the former. Posterior cingulum well developed. In young individuals it is wide and almost as long as the width of the crown. Root structure as in M¹⁻². M³ is sometimes bigger than M² with higher and sharper paracone. Posteroloph on this tooth, absent.

All upper molars, short and wide, as a rule, twice as wide as long. Hypocone as a well defined cusp, does not appear, on the other hand, on some specimens of M¹⁻² (and only on these teeth) there is a small thickening at the junction of posterior cingulum and posteroloph. This thickening could be considered here as an incipient hypocone.

Mandible (Tbl. 2). The horizontal ramus is rather long, high and thick. Symphysis wide, reaching anterior border of P₃. On two specimens, part of the base of the coronoid process is preserved, showing it to have been probably wide and high. Angular process (Pl. XI, fig. 4)

Table 2
Measurements of mandible and lower dentition (in mm)

| Measurements | A. M. N. H. No. 21727 (type) | PIN No. 533—121 a | A. M. N. H. No. 20426 | Z. Pal. No. MgM-II/ 15—20, 25—27 |
|----------------------------|---------------------------------|----------------------|--------------------------|-------------------------------------|
| Height below P_1 — P_2 | — | — | — | 13.6—16.0 |
| Height below M_3 | — | 12.5 | — | 13.0—15.0 |
| Thickness below M_1 | 6.5 | 7.0 | — | 6.4— 8.0 |
| Thickness below M_3 | 6.0 | 7.5 | — | 7.0— 8.5 |
| Length P_1 — M_3 | — | — | — | 38.0—41.0 |
| Length P_3 — M_3 | 27.0 | — | — | 26.0—29.0 |
| Length P_4 — M_3 | 21.5 | — | — | 20.0—23.5 |
| Length M_1 — M_3 | 16.5 | — | — | 15.0—18.5 |
| Length M_2 — M_3 | 12.3 | 12.0 | — | 11.0—13.0 |
| Length I_1 | — | — | — | 3.7— 4.0 |
| Width I_1 | — | — | — | 2.1— 2.7 |
| Length I_2 | — | — | — | 3.6— 4.2 |
| Width I_2 | — | — | — | 2.3— 2.9 |
| Length I_3 | — | — | — | 3.8— 4.0 |
| Width I_3 | — | — | — | 2.5— 2.7 |
| Length C | — | — | — | 4.0— 5.2 |
| Width C | — | — | — | 3.0— 4.5 |
| Length P_1 | — | — | 4.4 | 4.0— 4.5 |
| Width P_1 | — | — | 2.1 | 2.0— 2.1 |
| Length P_2 | — | 5.0 a | — | 5.0— 5.5 |
| Width P_2 | — | 3.0 a | — | 2.7— 3.0 |
| Length P_3 | 5.3 | — | — | 5.0— 6.0 |
| Width P_3 | 4.3 | — | — | 3.5— 4.3 |
| Length P_4 | 4.3 | — | — | 4.8— 5.5 |
| Width P_4 | 5.2 | — | — | 3.9— 5.5 |
| Length M_1 | 4.7 | 5.0 a | — | 4.0— 5.0 |
| Width M_1 | 4.8 | — | — | 4.0— 4.8 |
| Length M_2 | 5.0 | 5.3 | — | 4.5— 5.5 |
| Width M_2 | 5.6 | 5.3 | — | 4.6— 5.0 |
| Length M_3 | 7.3 | 6.8 | — | 6.5— 7.5 |
| Width M_3 | 5.5 | 5.6 | — | 4.8— 5.6 |

Remarks:

A. M. N. H. No. 21727 and 20426 — measured on MATTHEW's *et al.* illustration (1929, Fig. 1) and verified with the casts and TROFIMOV's data (1952, p. 11).

PIN No. 533—121 a — measurements according to TROFIMOV's data and illustrations (1952, pp. 10—12, Figs. 2—4) and verified with the original specimen.

a — measured along the alveoli.

was probably long and well developed. The fossa and masseteric crest, judging from the preserved fragments of the lower part of mandibles, seem to have been well developed. The horizontal ramus, in the section P-C, becomes lower and narrower, widening again in the symphysis. Mental foramina, two in number, the front one usually under P_1 , sometimes between C and P_1 , the other between P_2 and P_3 or under posterior root of P_2 . Crowns of P_2 — M_3 tuberculo-sectorial in type, with well developed high, sharp cusps and crests.

I_1 one-rooted. Root twice as long as the height of the crown and directed posteriorly in relation to the crown base at an angle of ca. 45° . Cross-section of root round. Crown compressed laterally, with three lobes forming a sharp dentate irregular cutting-edge. Anterior lobe I big, separated from the middle one by a deep notch. Middle lobe II not large, separated from the posterior one, III, by a wide, deep notch. Round the labial base of the crown there is a weak pseudo-cingulum. On several teeth, in addition to the posterior lobe, an accessory basal cuspule is visible.

I_2 one-rooted. Root round in cross-section and twice or three times as long as the height of the crown, inclined posteriorly at an angle of 40° . Crown laterally compressed, with three or four lobes on the cutting-edge. Arrangement of lobes as in I_1 . Main lobe II high and spade-like.

I_3 one-rooted, root twice as long as the height of the crown, inclined posteriorly at an angle of ca. 35 — 40° . Crown bigger than I_2 crown. Main lobe often with a slight notch in the middle. Labial side of crown weakly convex, lingual strongly. Last lobe small, situated at the base of crown. Lingual side of crown possesses a rather small basal bulging.

Canines with one big root, oval in cross-section and twice or three times longer than the height of crown. Canine crowns are, as a rule, twice as high as incisors and first premolars. They are one-cusped, with two sharp cutting-edges. Anterior edge has a tiny cusp at the base, while the posterior is without. Tip of canine slightly bent posteriorly and outwards. Anterior cutting-edge of crown steep, posterior gently sloping, slightly saddle-like. Posterior edge arched from the tip of the crown, forming at its posterior base a slight thickening. In young individuals the crown is low, more compressed laterally, possessing a small cusp on the posterior cutting edge. The height of the crown of such teeth does not differ greatly from that of incisors and first premolars.

P_1 one-rooted, which is round in cross section and twice as long as the height of the crown, inclined posteriorly at an angle of 30° . Crown antero-posteriorly elongated, with three cusps on its sagittal cutting edge. Anterior paraconid low, middle protoconid big and high, posterior metaconid also low and the same height as paraconid. P_1 crown slightly convex on both sides. On the anterior and posterior base of the crown occur delicate anterior and posterior cingula.

P_2 two-rooted. Roots round in cross-section, the back one slightly bigger than the front. Crown antero-posteriorly elongated, with three or four cusps on sagittal cutting edge. Paraconid and metaconid low and sharp. The biggest of the cusps is protoconid, possessing an anterior and posterior cutting-edge. On the posterior part of the crown, somewhat on the lingual side there is a fairly small widening in the form of a heel, while on the labial there is a tiny cuspule. Anterior and posterior cingula well defined. Specially well developed is the talonid crestid (TLDCRD) on the posterolingual side of the crown.

P_3 two-rooted. Roots antero-posteriorly compressed and transversely oriented to the longitudinal axes of the jaws. Crown more molarised than the first two premolars. Trigonid, as a rule, wide and long, talonid very low and short, with weakly developed entoconid and hypoconid. Paraconid visible, small and shifted towards the front. Most often it is situated mesially in relation to the trigonid. At the labial anterior base of the crown, under the paraconid and protoconid, there is a parastylid or a widened, rather short anterior cingulum. Protoconid

on P_3 usually higher than metaconid. Paralophid and metalophid sharp. The former distinctly lower and shorter than the latter. Hypoconulid does not appear on talonid. In young individuals, the root are round in cross-section and the crown weakly molarised. The talonid in these teeth is a small posterior heel. Paraconid is considerably lower than metaconid, forming an isolated and sharp cuspule. Parastylid does not develop but appears as a basal thickening. In young individuals, as well as in adult there is a depression — hypoflexid (HYFXD) on P_3 , between trigonid and talonid on the labial side.

P_4 two-rooted. Structure and arrangement of roots as on P_3 . Crown more molarised than P_3 . Trigonid longer and wider than the talonid, the latter being considerably lower. Paraconid appears here as an insignificant mesial swelling on else is not developed at all. Protoconid the same height as metaconid. Both cusps are high, sharp, with a wide base. Paralophid and metalophid high and sharp, the former much lower and steeper than the latter. Talonid relatively big, with cuspules, but the hypoconulid is still only weakly marked. Labial and lingual cingula completely not developed. On several teeth the paraconid is tiny, vestigial or in the form of a mesial small crest. Anterior cingulum missing, parastylid tiny situated at the base of paraconid. Height of protoconid and metaconid variable, depending on the degree of wear of the crown. These cusps usually of the same height, but sometimes the first is higher. The proportion between length of trigonid and talonid varies, but most often it is in the ratio 2 : 1. Similar to P_3 , there is on P_4 a hypoflexid and a well defined oblique crest (CROB).

The molar crowns increase posteriorly. M_1 smaller than P_4 and M_3 is the biggest of all teeth.

M_1 two-rooted. Structure and arrangement of roots as in P_{3-4} . Trigonid and talonid almost the same length, the latter slightly narrower than the former. Paraconid small and low, situated at the level of half the height of metaconid. At the base of paraconid there is a well developed parastylid in a form of a cusp, passing into a sharp crest on the antero-lingual side of trigonid. Protoconid and metaconid high and broad at base, the second usually higher than the first. Paralophid and metalophid high, sharp, however, the posterior one is always higher than the anterior. Talonid possesses three well developed cusps: hypoconid, entoconid and hypoconulid. Between trigonid and talonid, on labial side, a hypoflexid is visible and a well developed oblique crest. In individuals with well worn crowns protoconid and metaconid are almost the same size. Arrangement of crests and cusps on trigonid V-shaped, and on talonid crescent-like. A certain variability is observed in the position and size of cusps on the talonid. As a rule, hypoconid is the best developed cusp, while entoconid is tiny. The height of cusps on trigonid and talonid depends not only on the degree of crown wear, but also on the manner and angle of gnawing. On the American specimen (A. M. N. H. No. 21727 — type) paraconid is high, somewhat higher than protoconid, and the trigonid is wider and longer than talonid. In addition, parastylid in this specimen is weakly developed and joined to anterior cingulum. The metalophid is only slightly higher than paralophid. This arrangement of cusps and crests should be considered as a feature of individual variability.

M_2 two-rooted. Structure of roots and crown, arrangement of crests and cusps are almost the same as on P_4 — M_1 . Variability concerns height of main cusps, paralophid and metalophid, size of talonid cusps and parastylid and anterior cingulum. On the Russian specimen (PIN No. 533-121 a), the paraconid is placed fairly high, just as in the examined specimens. Paralophid in this specimen is also high and sharp, but distinctly lower than metalophid. Trigonid and talonid cusps are only slightly worn, indicating that this specimen belongs to a young individual. Trigonid M_2 in this specimen is distinctly wider than talonid, and parastylid has the character of an anterior cingulum rather than a cusp. On the American specimen (see above), M_2 possesses a better developed parastylid. This also applies to metaconid and talonid cusps.

M₃ two-rooted. Front root antero-posteriorly compressed, the other — laterally. The latter is large, long and directed backwards. Trigonid short and wide, talonid clearly longer than the trigonid, narrower, with three well developed cusps. Of these the best developed is hypoconulid, which forms the apex of the subtriangular talonid. Paraconid small, low, joined to the protoconid by a steep, sharp paralophid. Parastylid small, situated on the antero-labial side of crown. The highest of the trigonid cusps is the metaconid. Metalophid high, sharp and higher than paralophid. Parastylid on M₃, as a rule, fairly small, having the character of an isolated, sharp, conical cuspule or thickening on the anterolabial side of trigonid. In young individuals, the length of trigonid and talonid is almost equal. In addition, protoconid and metaconid are of the same height, and metalophid is higher than paralophid. Parastylid in such teeth is tiny, basal and adheres to the base of paraconid. In both the investigated and comparative material, the talonid of the last molars possesses a small accessory cusp — entoconulid (ENLD), on the lingual side near the posterior wall of the trigonid. All the molars have trigonids twice or two and half times higher than talonids. Paralophids are lower than metalophids. In addition, on P₃—M₃ (except P₄) the anterior cingulum or parastylids are clearly visible. Finally, metaconids on molars are higher than protoconids and lower or equal to protoconids on premolars.

Postcranial skeleton. Z. Pal. No. MgM-II/33: *right femur* (Pl. XIII, fig. 1) consisting of part of the head without neck, shaft with damaged proximal extremity and part of the distal extremity with condyles.

Head oval with small fossa. Neck missing, but it seems to have been rather long and well developed. Shaft of the femur composed of proximal extremity with trochanter major, distinct intertrochanteric crest, deep trochanteric fossa, trochanter minor and a crestlike trochanter tertius. Trochanter major, strong, fairly wide, divided by a notch into two tubercles. Anterior tubercle bigger than the posterior. The intertrochanteric crest runs downwards from the trochanter major, smoothens out and passes into the trochanter minor. From the place where the intertrochanteric crest smoothens out, a rugged longitudinal swelling extends downwards along the surface of the shaft. Trochanter tertius well developed as a flat, short, rather high crest with an uneven lateral ridge. Distal extremity of the femur consists of only a medial and lateral condyle. The medial condyle better developed, with a well visible medial patellar crest, comparatively wide and extensive. The lateral side of the condyle bears an irregular depression. Intercondylar groove, separating the two condyles, rather deep and the patellar surface comparatively wide and extensive. Lateral condyle not so well preserved, but the lateral patellar crest is well defined although weaker.

Measurements of femur (in mm):

| | |
|---|------|
| Medio-lateral diameter of head | 12.0 |
| Antero-posterior diameter of head | 11.0 |
| Medio-lateral thickness of shaft | 14.0 |
| Medio-lateral thickness of shaft below tro- | |
| chanters | 11.0 |
| Intertrochanteric distance (majori-minori) . . | 29.0 |
| Intertrochanteric distance (majori-tertius) ca. | 34.0 |

Z. Pal. No. MgM-II/34: *left tibia* (Pl. XIII, fig. 2) well preserved, with slightly damaged condylar testa. Lateral and medial tubercles of spine and sagittal crest missing. Condylar testa (Text-fig. 4), trapezium shaped, medial surface of the medial condyle slightly concave posteriorly and almost the same size as the lateral surface of the lateral condyle. This latter convex and trapezium shaped. Between them, behind the tibial bones, a weak posterior intercondylar fossa is visible. An equally small anterior fossa occurs in front. A small, slightly concave

anterior surface over the tibial tuberosity. From the front, between this surface and the articular surface of the lateral condyle there is a deep notch. From the medial side, the tibial bone is flat, without any marked sculpture. Laterally, the proximal extremity has two depressions: anterior, extensive, running along the lateral surface of tibial crest, disappearing at mid-length of the tibial bone, and a posterior, also extensive, forming at the top a deep depression to accommodate the fibular head. The tibial crest high, fairly sharp, ending at mid-length of tibial bone. The middle part of the tibial shaft narrow, slender and roundish, slightly ridged in cross-section. The distal extremity of the tibia (Text-fig. 4) is not so broad as the pro-

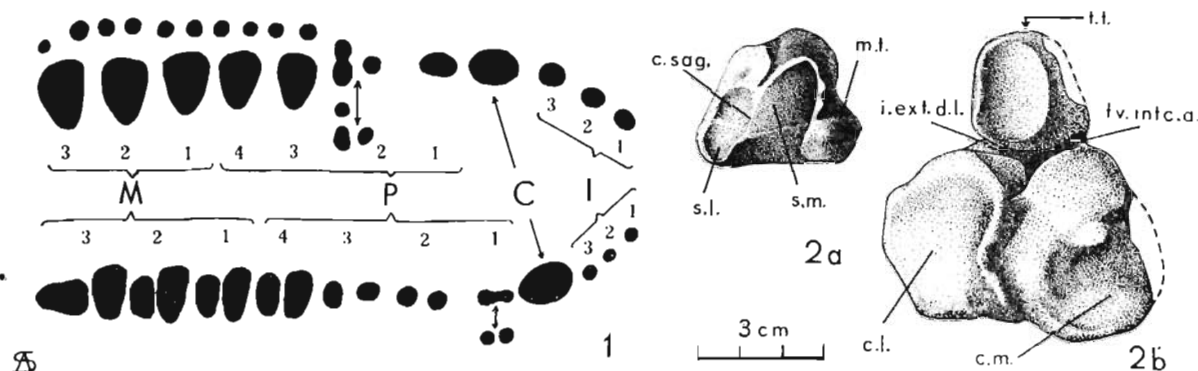


Fig. 4

Pseudictops lophiodon MATTHEW, GRANGER & SIMPSON

1 — alveolar rows of the upper and lower teeth (composition); 2 — tibia (Z. Pal. No. MgM-II/34): a distal articular surface (facies astragalea), b proximal articular surface (testa condyloidea) (schematic). Abbreviations: s. m. medial groove, s. l. lateral groove, c. sag. sagittal crest, m. t. tibial malleolus, c. l. lateral condyle, c. m. medial condyle, t. t. tibial tuberosity, i. ext. d. l. notch of extensor digiti longus, fv. intc. a. anterior intercondylar fovea.

ximal, its articulation having the characteristic appearance of an irregular trapezium. The medial side of articulation is a well developed tibial malleolus. The distal surface also bears two grooves: a medial, deep and narrow, and a lateral, shallower and slightly wider, with a sagittal crest running between them. Both grooves directed somewhat laterally (from the front) and medially (from the back). On the lateral side of the distal extremity of the tibia there is a rugged surface for coalescence with the fibula.

Tibia measurements (in mm):

| | |
|--|-------|
| Complete length of tibia | 110.0 |
| Width of proximal extremity (antero-lateral) | 23.0 |
| Width of proximal extremity (lateral) | 17.0 |
| Width of distal extremity (antero-lateral) | 11.0 |
| Width of distal extremity (lateral) | 11.5 |
| Width of shaft below tibial crest (antero-posterior) | 8.0 |
| Width of shaft below tibial crest (lateral) | 7.0 |

Z. Pal. No. MgM-II/35: *fibula* (Pl. III, fig. 2). The fibular bone is decidedly reduced in width. The proximal extremity broadened, with a rather small flat surface. Fibular head missing. The shaft slender and styliiform. Distal extremity absent, probably it existed and coalesced with the distal extremity of the tibia. Between the tibial bone and fibular there is a free, although narrow interosseous space, visible only along the proximal extremity. Apart from this, both bones are in close contact. It cannot be excluded that the fibula does not take part in the astragalar articulation or is not loosely joined to the calcaneum and astragalus.

Fibula measurements (in mm):

| | |
|--|------|
| Length of bone (without distal extremity) | 84.0 |
| Probable total length. | 98.0 |
| Width of proximal extremity (lateral) | 7.0 |
| Width of proximal extremity (antero-lateral) | 7.5 |
| Diameter of shaft | 3.0 |

Z. Pal. No. MgM-II/37: *left astragalus* (bone slightly damaged in the anterior part of lateral trochlear crest); Z. Pal. No. MgM-II/47: *left astragalus* (middle part of bone); Z. Pal. No. MgM-II/49: *right astragalus* (Pl. XIII, fig. 3; Pl. XIV, figs. 3, 5). The astragalus is rather wide, low and shortened in its proximo-distal axes. The dorsal side of the astragalar trochlea wide, with well defined crests and an extensive deep groove. The lateral trochlear crest slightly higher, better developed and longer than the medial, sharp in the anterior part, gentle in the posterior. The medial, on the other hand, is slightly shorter, lower and sharper in the posterior part, while gentle in the anterior. Medial and lateral malleolar surfaces of the trochlea, well defined and slightly concave. Specially well developed is the medial surface for articulation with the tibial malleolus. The presence, on some specimens, of lateral malleolar surface much less developed, seems to indicate the existence of some articulation with the fibular malleolus. Between the astragalar crests of the trochlea, in the posterior part of the groove, there is a tiny astragalar foramen. This is present on specimens Z. Pal. No. MgM-II/37 and 47. Curvature of trochlea pronounced (Pl. XIV, fig. 3c), semilunar, with a small radius. Posteriorly, the trochlea bends sharply, and anteriorly it runs gently towards the subtrochlear fovea. The fovea rather deep and extensive. The trochlear axis of the astragalus and its crests are oriented slightly obliquely in relation to the long axis of the astragalus. In addition, the posterior part of trochlea is directed somewhat medially, the anterior — laterally (the lateroventral type of trochlea). The astragalar neck, rather wide, shortened, but narrower than the width of the head, is directed medially. The angle between the trochlear axis and axis of the neck strongly obtuse about 150—155°. The astragalar head protrudes slightly beyond the medial trochlear ridge. It is wide, massive and dorsoventrally constricted, so that, looking from the front, the articular surface for the navicular bone is directed obliquely. Its proximal part oriented laterally, its distal towards the medial side of the head. On the medial side of the head there is a flat, slightly rugged surface, which does not directly form part of the tibio-astragalar articulation, but serves as an attachment for the medial astragalar ligament. On the other hand, on the lateral side of the head, there is a distinct, slightly rugged depression for the attachment of the lateral astragalar ligament.

Ventral side: this side bears four articular facets, namely: 1) lateral facet articulating with the lateral surface of the calcaneum, lying on the peroneal process; it is strongly concave, oval, and elongated; 2) the medial astragalar facet articulating with the main, anterior part of the sustentacular surface of the calcaneum, oval, elongated, convex and joined anteriorly by a narrow isthmus to facet 3; 3) this facet is a flat, rather small antero-lateral articular surface of the astragalar head. This latter articulates with a small, narrow, elongated antero-medial calcaneal surface. Between the lateral and medial astragalar facets, there is a pronounced deep groove, with a strong, posteriorly directed depression. On the antero-medial side of the head, runs a medially directed oval articular surface for the navicular, as an elongation from the antero-lateral side of the head, and finally 4) a transversal astragalar facet. This is a small surface, transversally oriented towards the astragalar axis, slightly concave and extending on the posterior part of the sustentacular surface of the calcaneum. Between this facet and the

medial astragalar facet there is a transversal astragalar groove. Articulation between the astragalus and the cuboideum absent.

Astragalus measurements (in mm):

| | |
|-------------------------------------|---------|
| Length of bone along trochlear axis | 13.0 |
| Width perpendicular to bone axis | 11.0 |
| Length of lateral trochlear crest | 9.0 |
| Length of medial trochlear crest | 8.0 |
| Width of trochlea | 10.0 |
| Head dimensions | 7.5×6.0 |

Z. Pal. No. MgM-II/36, 46 and 48: *calcaneum* (Pl. XIII, fig. 4; Pl. XIV, fig. 2) long, almost the same width along all its length. The proximal part of the bone somewhat widened posteriorly. Tuber calcis with two tubercles, a smaller — lateral and a bigger — medial. The tuber calcis itself somewhat concave posteriorly and uneven for the tendon attachment of gastrocnemius. The shaft of the calcaneum slightly flattened medio-laterally, so this thickness is somewhat smaller than the antero-posterior, in the ratio 1 : 1.5. The distal part of the calcaneum somewhat widened anteriorly, but without a medial tuberosity. The middle part of the bone bears three articular facets, corresponding to the astragalar facets. They are: 1) lateral facet, on the peroneal process, strongly convex, and somewhat diagonally oriented to the longitudinal bone axis, articulating with the lateral astragalar facet; 2) medial facet on the sustentaculum of the calcaneum, pronounced, concave and oval. The sustentaculum itself lies more or less perpendicular to the peroneal process. The sustentacular surface articulates with the medial astragalar surface; 3) the posterior sustentacular facet, narrow, slightly convex, articulating with the transversal astragalar surface. Between the sustentacular surface and the peroneal, there is a rather small calcaneal groove, overlying the astragalar groove, forming a small calcaneo-astragalar sinus. A long, wide, smooth groove for the tendon of the flexor muscle (*hallucis longus*) extends posteriorly at the base of the sustentaculum. On the medial side of the anterior part of the calcaneum there is a small, diagonal, antero-medial calcaneal facet for articulation, with the antero-lateral facet of the astragalar head. In addition to a peroneal facet, the peroneal calcaneal process has, on its proximal lateral surface, an accessory convex articular smoothness for loose articulation with the fibular malleolus. For articulation with the cuboideum the anterior articular surface of the calcaneum is transversally oval, wide, roughly triangular in outline and diagonally flattened in relation to the longitudinal bone axis.

Calcaneum measurements (in mm):

| | |
|--|---------|
| Complete length | 28.0 |
| Width of shaft (medio-lateral) | 4.5 |
| Width of shaft (antero-posterior) | 7.0 |
| Width of medio-lateral articular part of calcaneum | 11.0 |
| Dimensions of tuber calcis | 7.0×7.0 |

Z. Pal. No. MgM-II/39: *navicular bone* (Pl. XIV, fig. 6). With the exception of the astragalus, this bone is the most characteristic of the tarsal bones. It is small, vertically shortened and possessing a small reduced, free plantar tuberosity, directed somewhat laterally to the cuboideum and also anteriorly. A strong concave posterior navicular surface forms the boundary between the navicular and the articular surface of the astragalar head, while distally it is separated from the three facets of the tarsal bones (t. 1, 2, 3) by three secondary irregular articular facets of varying height. The lateral concave ridge of the navicular articulates with the cuboideum

through the cuboidal surface of the navicular. The above mentioned facets for articulation with the tarsal bones occur on the anterior side of the navicular. The medial facet for tarsal bone 1 is small, lying in the proximal part of the medial depression of the navicular. Facet for tarsal bone 2 is bigger than that for tarsal bone 1, and is roughly triangular in shape. Facet for tarsal bone 3 is dorso-ventrally elongated, a fairly marked crest-like swelling, forming the boundary between it and the facet of tarsal bone 2. Laterally it articulates with the big, oval medial cuboid facet.

Navicular measurement (in mm):

Length (antero-posterior) 5.0
 Thickness (dorso-ventral) 10.0
 Thickness at widest point
 (medio-lateral) . . . 7.5

Z. Pal. No. MgM-II/38: *cuboideum* (Pl. XIV, fig. 4), formed by the coalescence of tarsal bones 4 and 5, is proximo-distally shortened. As the medio-posterior part of bone is damaged, it is difficult to state whether it had an articular facet for the astragalar head. From the arrangement of these bones, it can be supposed that they were not in close contact. The proximal part of the cuboideum has an articular surface for articulation with the calcaneum. It is big, obliquely slanted in a slightly dorso-ventral direction in relation to the bone axis, unlike the calcaneal surface. The plantar side of the cuboideum forms a strong, wide, blunt cuboid tuberosity. Over the tubercle, from anterior side, there is a cuboid groove, to which the tendon of the long fibular muscle is attached. The medial ridge of the cuboideum is shallowly notched with facets for the navicular, one — situated proximally, and two, button-like, a distal and proximal for articulation with tarsal bone 3. Between the medial ridge of the cuboideum and the lateral ridge of tarsal bone 3, there is a small tarsal channel. The distal cuboid surface for articulation, with metatarsal bones IV and V, has the shape of a wide, oval, undivided triangle and is slightly concave.

Cuboideum measurement (in mm):

Length (antero-posterior) 11.0
 Width (medio-lateral) . . 7.0
 Width (dorso-ventral) . . 8.0

Z. Pal. No. MgM-II/52: *tarsal bone 3* (Pl. XIV, fig. 7), although somewhat damaged, the following characters are visible: bone dorso-ventrally elongated, laterally concave, medially convex with three articular surfaces: 1) posterior, the same shape as the antero-lateral navicular surface; 2) anterior, similar in outline to the articular surface of the metatarsal bone III. Both surfaces are almost flat and fit closely together. The third is a lateral facet, articulating with the medial articular surface of the cuboideum. In the examined material, tarsal bone 2 is missing. Tarsal bone 1 is probably coalesced with the proximal extremity of metatarsal I.

Tarsal bone 3 measurement (in mm):

Length (antero-posterior) 4.0
 Width (medio-lateral) . . 5.0

Metatarsal bones and digital bones of the hind foot. These bones represent almost all categories of anterior part of foot. What is missing here, can easily be reconstructed. Most probably, all the bones described below belong to a left hind limb.

Z. Pal. No. MgM-II/40: metatarsal bone I (the base, part of the shaft with head) and digital phalanges 1, 3; Z. Pal. No. MgM-II/41: metatarsal bone II and digital phalanges 1, 2, 3;

Z. Pal. No. MgM-II/42: metatarsal bone III (the head, part of the base with proximal fragment of shaft) and digital phalanges 1, 2, 3; Z. Pal. No. MgM-II/43: metatarsal bone IV and digital phalanges 1, 2, 3; Z. Pal. No. MgM-II/44: metatarsal bone V (part of base with proximal fragment of shaft and head) and digital phalanges 1, 2; Z. Pal. No. MgM-II 45: digital sesamoid bones.

Metatarsal bone I (Pl. XIV, fig. 1). The extremity enters the medial navicular depression from both the medial side and distally, articulating with it through a roundish lateral articular surface. The shaft slender, narrow, from the side of the base curved. The distal extremity with head somewhat widened, the trochlea almost symmetrical and transversal with a delicate posteriorly situated sagittal crest. On dorsal side, over the trochlea, there is a depression and, on both sides of the head, pits for the attachment of the tendons of flexor muscles.

Metatarsal bone II (see above). Bone complete and well preserved. Bone base widened, obliquely oriented to background. The articular surface of the base probably similar in shape to the articular surface of tarsal bone 2. From the medial side of metatarsal bone there is a well defined, free interosseous space. Laterally, the proximal extremity has an extensive coalescent field, with the proximal extremity of metatarsal bone III. This field extends distally to approximately half the length of the shaft. The shaft of metatarsal bone II thick, more massive than metatarsal bones I and V. From the plantar side the shaft is arched. The distal extremity widens, possessing on both sides supratrochlear epicondyles for the attachment of the extensor tendons of digits. The trochlea asymmetric, the medial condyle smaller than the lateral. Trochlear sagittal crest prominent, lying in the posterior half of trochlea. Over the trochlea a depression and on both sides pits.

Metatarsal bone III (see above). The proximal articular surface of this bone is similar in shape to the distal articular surface of tarsal bone 3. Laterally this surface articulates for a short distance with the medial part of the distal cuboid articular surface. From the medial side, the proximal extremity coalesced (during life) with the lateral coalescent field of the proximal extremity of the metatarsal bone II, while from the lateral side it was in close contact with the proximal extremity of metatarsal bone IV. This latter surface is also extensive and uneven. Besides, the mentioned fragment there is also a head with an almost symmetric trochlea, bearing more or less equal condyles, and a well developed sagittal crest. Metatarsal bone III is the longest of these bones.

Metatarsal bone IV (see above) complete and well preserved. Base wide, with large proximal articular surface, which joins the cuboid articular surface. From the medial side the proximal extremity articulates or coalesces with the lateral rugged coalescent field of the proximal extremity of the metatarsal bone III, while, on the lateral side, its equally extensive rugged coalescent field medially closely contacts the proximal extremity of metatarsal bone V. Distal extremity with head, widened, but trochlea asymmetrical with medial condyle bigger than the lateral, and sagittal crest situated in posterior half of trochlea. Here also pits occur on both sides of the trochlea and there is a depression over. The whole shaft arched from medial and plantar sides as in the previous metatarsal bones. All metatarsal bones, from the plantar side, form a plantar metatarsal groove.

Metatarsal bone V (see above). The bone base is untypical, similar to the base of metatarsal bone I, but more laterally flattened, the medial crescent field contacting the lateral coalescent field of metatarsal bone IV. Length of bone unknown, but probably longer than metatarsal bone I. The head of metatarsal bone V is typical in structure, similar to the head of metatarsal bone I.

All the metatarsal bones, except I, contact each other basally and during life were coa-

lesced. Spaces between these bones are narrow, visible only in anterior part of metatarsalia.

Digital bones 1 and 2 (see above). Widened at the base and in distal extremities, narrowed in the shaft, with pronounced depressions on both sides of the head. Measurements and proportions vary, the biggest — the digital phalanx 2 of the digit III, so the remaining bones of this digit are longer and stronger. The smallest are the phalanges of digits I and V, which are under-developed in length. The most characteristic of digital phalanges are the claw phalanges (3). They are better developed on digits II—IV. Basally they are widened, with a concave proximal articular surface for articulation with digital phalanges 2. On either side of the base of the claw phalanges, are small swellings and small deep foramens. Anteriorly, the bone shaft narrows, while on the tip it widens laterally. Anteriorly, at the place where it is widened and flattened, there is a fairly deep fissure, extending approximately to 1/3 (or less) the length of the phalanx. This fissure is especially visible on the claw phalanges of digits II-IV. The plantar side of the shaft possesses a wide longitudinal plantar tuberosity, which occupies half the length of the phalanx. The widening at the tip is separated from the shaft by two delicate longitudinal depressions.

Measurements (length/width) of metatarsal bones and digital phalanges (in mm):

| Metatarsale | 1 | 2 | 3 |
|--|----------|--------------|----------|
| I ca. 33.0/2.5 | 10.0/2.0 | — | 4.0/2.0 |
| II 40.0/4.0 | 15.0/4.0 | 9.0/3.5 | 8.0/3.0 |
| III ca. 44.0/5.0 | 16.0/4.0 | 12.0/3.5 | 10.0/3.0 |
| IV 40.0/4.0 | 15.0/4.0 | ca. 10.0/2.5 | 9.0/3.0 |
| V ca. 36.0/2.5 | 7.0/2.5 | 5.5/2.5 | — |
| Width of the metatarsale (II—IV) at the base | | | 15.0 |
| Length of the digit I | | | ca. 47.0 |
| " " " II | | | 70.0 |
| " " " III | | | ca. 81.0 |
| " " " IV | | | ca. 72.0 |
| " " " V | | | ca. 52.0 |

In addition, the examined material contains: some digital phalanges and metatarsale of the right hind limb, some digital phalanges, probably fore limb and other bones, which either do not differ morphologically from the above described bone elements or are fragments, whose morphology cannot be described in more detail.

Sesamoid bones (Text-fig. 4). Small, elongated, half-crescent bones, which occur in the posterior part of the distal extremity of metatarsal bones.

DISCUSSION

A review of investigations of the genus *Pseudictops* (see p. 103) reveals two controversial problems: a) the problem of the age of the fauna in which the discussed genus occurs, and b) the question of its systematic position. Proposing a solution for the first of these problems, is not the intention of the present author, however it should be mentioned that the fauna from Naran Bulak and Tsagan Khushu shows a strong degree of similarity in its generic composition to that from Khashaat (= Gashato). There are no doubts but that the Lower Tertiary beds of Naran Bulak, Tsagan Khushu and Khashaat are contemporaneous. Whether they are of Paleocene or Eocene age, remains an open question. In the present paper,

they are provisionally regarded as Paleocene (see KIELAN-JAWOROWSKA & DOVCHIN, 1968, p. 16).

The majority of authors investigating the genus *Pseudictops* were of the opinion that this genus, in spite of its different and characteristic dentition features, should be considered as a representative of the order Insectivora and most probably of the family Leptictidae (MATTHEW *et al.*, 1929; TROFIMOV, 1952; GROMOVA, 1962, and others). Establishing the proper systematic position of this genus was, however, difficult due to incomplete bone material and the presence of several mixed features of dentition. Its assignment to the family Leptictidae was based on the similarities in the structure of molar crowns, especially the triangular shape of trigones and trigonids, degree of molarisation of premolars and situation of zygomatic arch.

Leptictidae, besides being decidedly smaller than *Pseudictops*, reveal several basic differences. According to RUSSELL (1964, pp. 44-45; see also BUTLER, 1956; SCOTT & JEPSEN, 1936), in leptictids molarisation of premolars is less advanced, the paraconid is well developed (with a few exceptions, where this cusp occurs in the form of a crest); upper molars (including P⁴), in addition to labial cingula, have more or less developed hypocones, last lower molar reduced in length, with a short talonid; in mandible, e.g. in *Ictops*, there are four chisel-like incisors of very simple structure, and big, sharp, conical canines, much larger than the neighbouring teeth. Apart from many other features of dentition, which in leptictids are clearly different from the corresponding ones in *Pseudictops*, there are also differences, equally significant, in the build of tarsal bones. In *Prodiacodon* (see SZALAY, 1966), both the astragalus and calcaneum, as well as the remaining tarsal bones, show considerable differences in comparison with those of *Pseudictops*. This applies to the measurements, structure, shape and position of articular surfaces, articulation of individual bones and development of astragalar canal and foramens. These differences exclude the assignment of the genus *Pseudictops* to the family Leptictidae. ROMER (1966, p. 380), probably on the base of MCKENNA's (1963) and VAN VALEN's (1964) investigations, referred this genus to the family Anagalidae. The similarity, in general morphology of face and dentition, of this genus to anagalids is rather striking. This applies not only to dentition, but also to the postcranial skeleton. Even though *Pseudictops*, in general, is closest to anagalids, there are, however, significant differences. The latter is distinguished from former by having less transversally placed upper molars with developed hypocones, more hypsodont molar crowns, wide talonids (wider than trigonids) on lower molars, and a reduced but easy to distinguish paraconid. They are similar in having a general reduction of paraconid on P₄ and molars, and a weakly developed metacone on P³⁻⁴. In *Pseudictops* the typical hypocone is missing and the molar teeth are triangular in outline. The canines structure in *Pseudictops* (these teeth, just as incisors, previously unknown) are very characteristic, differing from both the canines of anagalids and leptictids. They are fairly large, protruding beyond the wear level of the neighbouring teeth, their crowns bearing on the posterior cutting edge, accessory cusps or denticles.

The lingual hypsodontism of the upper molars in *Pseudictops* (MCKENNA, 1963; VAN VALEN, 1964) is considerably less than that observed in anagalids. In addition, such a feature as the molar enamel passing into the alveoli is not observed in *Pseudictops*, this feature being confined to anagalids (*Anagalopsis*). To the similarities and differences in dentition between anagalids and *Pseudictops*, it is necessary to add the resemblances and differences in the bone structure of the hind limb. The tibia and fibula are free in both anagalids and *Pseudictops*, and the astragalus and navicular in general structure similar. Individual bones, however, in both groups are different. In anagalids, tibia and fibula are comparatively short, with a large space between them, almost for their whole length. In *Pseudictops*, on the other hand, the bones

are elongated, slender and distally contact each other, furthermore the interosseous space is narrow and limited to the proximal part of both bones. The astragalar bones in *Anagale* and *Pseudictops* are rather short, with short neck and roundish heads, a plantar foramen is visible (term of SZALAY, 1966). Considerable differences can be seen, however, in the structure of the last claw phalanges. Whereas in *Anagale* the phalanges are distally widened without a sagittal fissure, in *Pseudictops* the phalanges have a distinct, although shallow fissure. Therefore a close relationship between anagalids and *Pseudictops*, or vice versa, cannot be stated with complete certainty. The many common features can only point to the not very distant descent of these forms from a still unknown common Cretaceous ancestor.

On the base of the morphological comparisons of dentition and postcranial skeleton of the representatives of the above mentioned families with *Pseudictops*, the author came to the conclusion that the latter genus cannot be assigned to either leptictids or anagalids. This conclusion is also based on the following facts: neither in leptictids nor in anagalids can one find, the characteristic *Pseudictops* structure of incisors, canines and first premolars of both jaws, the hind limb with a tendency to reduction of first and fifth digit, while at the same time the III and IV (third being the longest) are enlarged, different articulation of the tarsal bones, especially astragalus in relation to calcaneum, tibia in relation to the astragalus, and a missing or only weakly developed incipient hypocone on the upper molars. On the base of the above, it seems to the author appropriate to erect a new family Pseudictopidae n. fam., represented, for the time being, by one specimen *Pseudictops lophiodon*.

VAN VALEN (1964, p. 484) not finding any definite data as to the ancestry of lagomorphs considered that the Mongolian genus *Pseudictops* "provides the most probable indication of this ancestry". Assuming that the morphological data of dentition and postcranial skeleton are indeed characteristic for *Pseudictops*, there is no probability that this genus is closely related to eurymylids. The differences between *Pseudictops* and *Eurymylus*, a representative of eurymylids, are so great and so numerous that even if some relationship exists, it is very distant.

The genus *Pseudictops* can clearly not be assigned as Carnivora because of the character of its dentition, non reduction of premolars, lack of carnassials, lack of reduction of the last molars, as well as the primitive lateroversal build of astragalar trochlea. Only a certain resemblance to primitive creodonts can be seen in the rather well differentiated canines, comparatively short, although massive, mandibles, situation of mental foramina, shortening of face, build of astragalus (arrangement of crests, presence of astragalar foramina) and fissure of claw phalanges. A comparison of the build of the astragalus in *Pseudictops* with the same bone in *Protictis* (Carnivora) (MAC INTYRE, 1966, pp. 149, 164, Pl. 10, figs. 2—3, 6—7) reveals similarities in the arrangement of articular facets, presence of astragalar plantar foramen, structure of head, angle of its inclination to the bone axis, shape of the articular facets for the navicular bone and the build of sustentacular and peroneal parts of calcaneum. Differences here refer to the bone dimensions (in *Pseudictops* astragalus is twice as big) and the length of the trochlear crests (in *Protictis* crests are of varying length).

Pseudictops, in spite of resemblances in the general structure of dentition (triangular build of upper molars and trigonids of the lower cheek teeth, similar molarisation of premolars and other features) (FLEROV, 1952; SIMONS, 1960; KIELAN-JAWOROWSKA, 1968) cannot be assigned to pantodonts. Most probably they were adapted to a similar type of life condition, which could account for the resemblance between them.

Could *Pseudictops* be a condylarthr? An answer to this question is not easy. The resemblance between the genus *Pseudictops* and these primitive preungulates is seen mostly in the build of the hind limb: in the well developed trochanter tertius on the tibia and the presence of

plantar and superior foramina on the astragalar trochlea. Just as in *Pseudictops*, in condylarthrs digit I and V are reduced, while the middle digits are overgrown (with slight elongated of third digit). In both *Pseudictops* and condylarthrs the claw phalanges are in their distal part dorso-ventrally flattened and at the top shallowly fissured. Such phalanges could serve either as an attachment for the weakly developed claws or a base for the development of primitive small unguals.

In spite of the definite similarity of this limb, and its components, *Pseudictops* differs significantly from condylarthrs in the morphology of its dentition. The upper molars, in these latter, are four-cusped with a well developed hypocone, and four-sided crowns, while the lower molars, as a rule, have reduced paraconids, four-sided crowns, and possess four instead of five cusps. In addition, the molarisation of premolars in condylarthrs is much more advanced than in *Pseudictops*.

On the base of these differences and the investigations carried out, up to now, on *Pseudictops*, the author comes to conclusion that this genus cannot be considered as a condylarthr. Perhaps, as yet unknown, bones of the fore limb of *Pseudictops* could throw further light on this problem.

MATTHEW *et al.* (1929), TROFIMOV (1952) and other authors suggested a similarity and certain relationship between *Pseudictops* and *Zalambdalestes* (GREGORY & SIMPSON, 1926), however, in the light of new data, these seem to be of only a general character. In these genera one can only state a similar degree of molarisation of premolars, triangular build of crown of upper cheek teeth, lack of conules, similar arrangement of crests and other features. However, considerable differences also exist. These are visible in the structure and number of incisors, build of canines, degree of diastemas development, reduction of last upper molar, build of individual cusps of lower cheek teeth and the construction of the face.

Because a place could not be found for the genus *Pseudictops* in any of the known orders, the present author has placed it tentatively in the subclass Eutheria, recognizing it as a representative of an unknown order. The present author is of the opinion that *Pseudictops*, as well as Anagalidae represent most probably a new order of mammals or, should new material support the supposition of condylarthrs ancestry for the *Pseudictops*, than this latter should be assigned to the order Condylarthra rather than to Insectivora.

The genus *Pseudictops arilophiodon* from Naran Bulak, described by TROFIMOV (1952, pp. 10—12, figs. 2—4), both from the point of view of the morphology of its dentition and identical measurements to *P. lophiodon*, is considered here as a synonym of the latter species.

Palaeozoological Institute
of the Polish Academy of Sciences
Warszawa, January 1967

REFERENCES

- BOHLIN, B. 1951. Some mammalian remains from Shih-eh-r-ma-ch'eng, Hui-hui-p'u area, Western Kansu. In: Hedin Sven, Rep. Sci. Exp. north-west. prov. China, 6. — *Vertebrate Paleontology*, 5, 1-47, Stockholm.
- BUTLER, P. M. 1956. The skull of *Ictops* and the classification of the Insectivora. — *Proc. Zool. Soc. London*, 126, 3, 453-481, London.
- EFREMOV, I. A. — see ЕФРЕМОВ, И. А.
- FLEROV, K. K. — see ФЛЁРОВ, К. К.

- GRAJDIŃSKI, R., KAŹMIERCZAK, J. & LEFELD, J. 1968. Geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. Results of the Polish-Mongolian Palaeontological Expeditions, I. — *Palaeont. Pol.*, **19**, 33-82, Warszawa.
- GREGORY, W. K. & SIMPSON, G. G. 1926. Cretaceous mammal skulls from Mongolia. — *Amer. Mus. Novit.*, **225**, 1-20, New York.
- GROMOVA, V. I. — see ГРОМОВА, В. И.
- MAC INTYRE, G. T. 1966. The Miacidae (Mammalia, Carnivora). Part I. The systematics of Ictidopappus and Protictis. — *Bull. Amer. Mus. Nat. Hist.*, **131**, 2, 115-209, New York.
- McKENNA, M. C. 1963. New evidence against tupaoid affinities of the mammalian family Anagalidae. — *Amer. Mus. Novit.*, **2158**, 1-16, New York.
- KIELAN-JAWOROWSKA, Z. 1968. Archaeolambdidae Flerov (Pantodonta) from the Paleocene of the Nemegt Basin, Gobi Desert. Results of the Polish-Mongolian Palaeontological Expeditions, I. — *Palaeont. Pol.*, **19**, 133-140, Warszawa.
- & DOVCHIN, N. 1968. Narrative of the Polish-Mongolian Palaeontological Expeditions 1963—1965. Results of the Polish-Mongolian Palaeontological Expeditions, I. — *Ibidem*, **19**, 7-30.
- & KOWALSKI, K. 1965. Polish-Mongolian Palaeontological Expeditions to the Gobi Desert in 1963 and 1964. — *Bull. Acad. Pol. Sci., Sér. sci. biol.*, **13**, 3, 170-175, Warszawa.
- LAVOCAT, R. 1956. Condylarthra. In: PIVETEAU, J. ed., *Traité de Paléontologie*, **6**, 2, 1-27, Paris.
- MATTHEW, W. D. & GRANGER, W. 1924. New Carnivora from the Tertiary of Mongolia. — *Amer. Mus. Novit.*, **104**, 1-9, New York.
- & — 1925a. New creodont and rodents from the Ardyn Obo Formation of Mongolia. — *Ibidem*, **193**, 1-7.
- & — 1925b. Fauna and correlation of the Gashato Formation of Mongolia. — *Ibidem*, **189**, 1-12.
- , — & SIMPSON, G. G. 1929. Additions to the fauna of the Gashato Formation of Mongolia. — *Ibidem*, **376**, 1-12.
- NOVOZHILOV, N. I. — see НОВОЖИЛОВ, Н. И.
- PIVETEAU, J. 1961. Carnivora. *Traité de Paléontologie*, **6**, 1, 641-820, Paris.
- ROMER, A. S. 1966. Vertebrate Paleontology. Univ. Chicago Press, 3 ed., 1-468, Chicago—London.
- ROZHDESTVENSKY, A. K. — see РОЖДЕСТВЕНСКИЙ, А. К.
- RUSSELL, D. E. 1964. Les Mammifères paléocènes d'Europe. — *Mém. Mus. Nat. Hist.*, n. s., **13**, 1-324, Paris.
- SABAN, R. 1958. Insectivora (Leptictidae). In: PIVETEAU, J. ed., *Traité de Paléontologie*, **6**, 2, 822-909, Paris.
- SCOTT, W. B. & JEPSEN, G. L. 1936. The mammalian fauna of the White River Oligocene. I: Insectivora and Carnivora. — *Trans. Amer. Phil. Soc. Philad.*, n. s., **28**, 1-153, Philadelphia.
- SIMONS, E. L. 1960. The Paleocene Pantodonta. — *Ibidem*, **50**, 6, 1-81.
- SIMPSON, G. G. 1931. A new insectivore from the Oligocene Ulan Gochu horizon of Mongolia. — *Amer. Mus. Novit.*, **505**, 1-22, New York.
- 1945. The principles of classification and a classification of Mammals. — *Bull. Amer. Mus. Nat. Hist.*, **85**, 1-350, New York.
- SZALAY, F. S. 1966. The tarsus of the Paleocene leptictid Prodiacodon (Insectivora, Mammalia). — *Amer. Mus. Novit.*, **2267**, 1-13, New York.
- TROFIMOV, B. A. — see ТРОФИМОВ, Б. А.
- VAN VALEN, L. 1964. A possible origin of rabbits and fossils. — *Evolution*, **18**, 484-491, New York.
- 1966. Deltatheridia, a new order of Mammalia. — *Bull. Amer. Mus. Nat. Hist.*, **132**, 1, 1-126, New York.
- ZITTEL, K. 1925. Textbook of paleontology, III. 1-316, London (1964).
- Громова, В. И. 1952. О примитивных хищных из палеогена Монголии и Казахстана. — *Тр. Палеонт. Инст. АН СССР*, **41**, 51—77, Москва.
- 1960. О новом семействе (Tschelkariidae) примитивных хищников (Creodonta) из олигоцена Азии. — *Ibidem*, **77**, 41—78.
- 1962. Млекопитающие (Insectivora). In: Ю. А. Орлов (ред.), Основы палеонтологии. Гос. Науч.-техн. изд., 72—85, Москва.
- Ефремов, И. А. 1948. Предварительные результаты работ первой Монгольской Палеонтологической Экспедиции Академии Наук СССР 1946 года. — *Тр. Монг. Ком. АН СССР*, **38**, 5—28, Москва.
- 1950. Тафономия и геологическая летопись. — *Тр. Палеонт. Инст. АН СССР*, **24**, 1, 1—177, Москва.
- 1954. Палеонтологические исследования в Монгольской Народной Республике (Предварительные результаты экспедиций 1946, 1948 и 1949 гг.). — *Тр. Монг. Ком. АН СССР*, **59**, 3—32, Москва.
- Новожилов, Н. И. 1954. Местонахождения млекопитающих нижнего эоцена и верхнего палеоцена Монголии. — *Ibidem*, **59**, 33—46.

- Рождественский, А. К. 1949. Некоторые местонахождения древнетретичных млекопитающих в Монголии. — *Докл. АН СССР*, **66**, 3, 463—466, Москва—Ленинград.
- 1954. Местонахождения верхнетретичных млекопитающих на западе Монгольской Народной Республики. — *Тр. Монг. Ком. АН СССР*, **58**, 48—53, Москва.
- 1957а. За динозаврами в Гоби. Гос. Изд. Геогр. Литер., 1—214, Москва.
- 1957б. Краткие итоги изучения ископаемых позвоночных Монголии по материалам Монгольской Палеонтологической Экспедиции Академии Наук СССР в 1946—1949 г. — *Vertebr. Palasiat.*, **1**, 3, 169—183, Peking.
- Трофимов, Б. А. 1952. О роде *Pseudictops*, своеобразном насекомоядном из нижнетретичных отложений Монголии. — *Тр. Палеонт. Инст. АН СССР*, **41**, 7—12, Москва.
- Флёров, К. К. 1952. Пантодонты (*Pantodonta*) собранные Монгольской Палеонтологической Экспедицией Академии Наук СССР. — *Ibidem*, **41**, 43—50.
- 1957. Диноцераты Монголии. — *Ibidem*, **67**, 1—82.
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P L A T E S

A. SULIMSKI: PALEOCENE GENUS *PSEUDICTOPS*

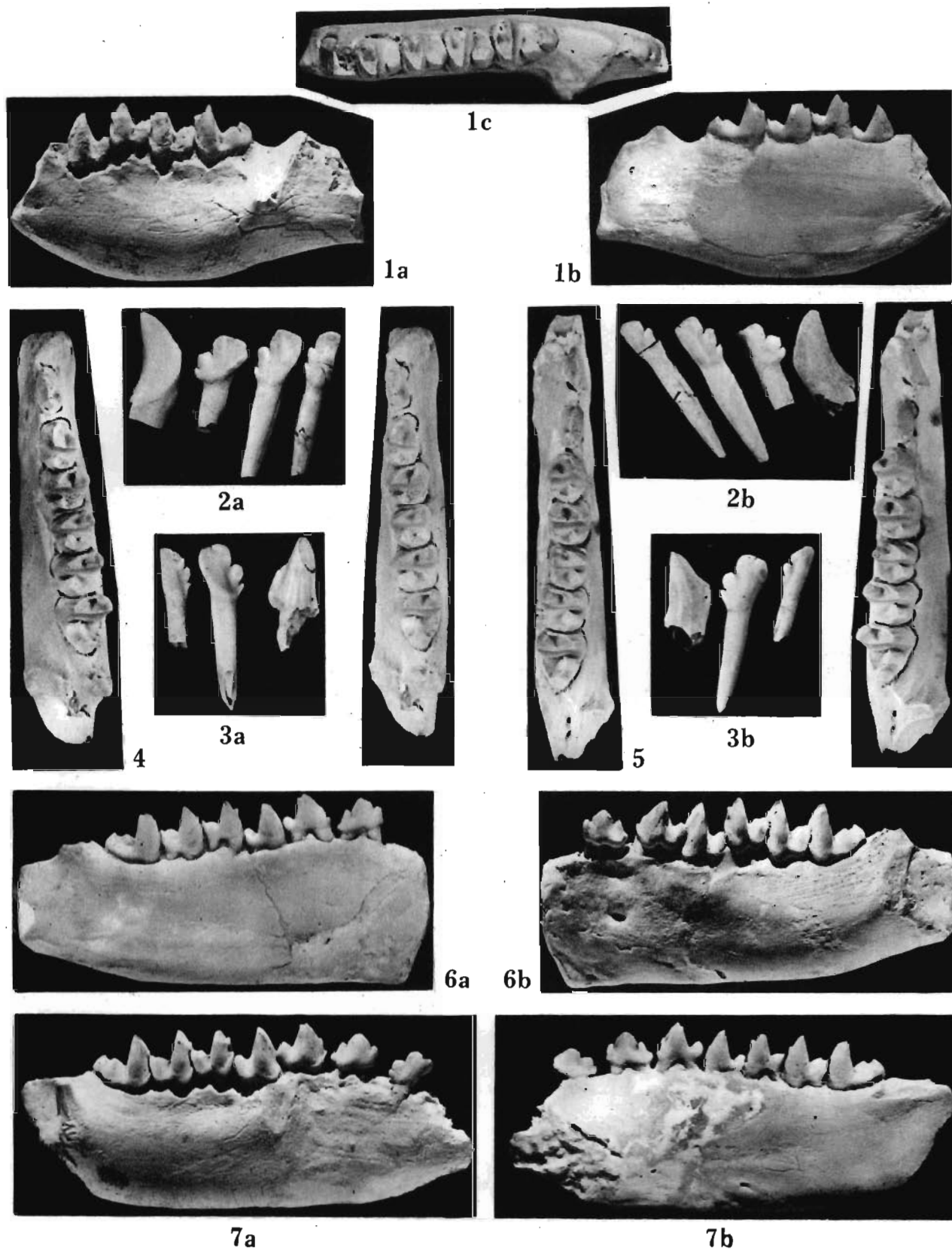
PLATE X

| | Page |
|---|------|
| <i>Pseudictops lophiodon</i> MATTHEW, GRANGER & SIMPSON | 108 |
| (Naran Bulak) | |

- Fig. 1. Left mandible with P₄-M₃: *a* labial view, *b* lingual view, *c* occlusal view (Z. Pal. No. MgM-II/17); ×1.5.
Fig. 2. Left isolated I₁₋₃, and C: *a* lingual view, *b* labial view (Z. Pal. No. MgM-II/13); ×2.
Fig. 3. Right isolated I₁₋₂, and C: *a* lingual view, *b* labial view (Z. Pal. No. MgM-II/14); ×2.
Fig. 4. Left mandible with P₂-M₃, occlusal view, stereo-photograph (Z. Pal. No. MgM-II/16); ×1.5.
Fig. 5. Right mandible with P₁-M₃, occlusal view, stereo-photograph (Z. Pal. No. MgM-II/15); ×1.5.
Fig. 6. Left mandible with P₂-M₃: *a* lingual view, *b* lateral view (Z. Pal. No. MgM-II/16); ×1.5.
Fig. 7. Right mandible with P₁-M₃: *a* labial view, *b* lingual view (Z. Pal. No. MgM-II/15); ×1.5.

(see also Plates XI—XIV)

Photo: M. Czarnocka



A. SULIMSKI: PALEOCENE GENUS *PSEUDICTOPS*

PLATE XI

Page

Pseudictops lophiodon MATTHEW, GRANGER & SIMPSON 108

(Tsagan Khushu)

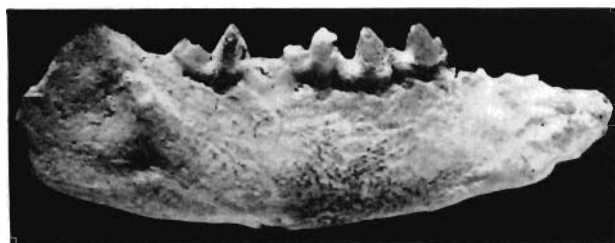
- Fig. 1. Right mandible with P_3 - M_3 , old individual: *a* labial view, *b* lingual view (Z. Pal. No. MgM-II/18).
Fig. 2. Left mandible with P_3 - M_3 : *a* lingual view, *b* labial view (Z. Pal. No. MgM-II/27).
Fig. 3. Left mandible with destroyed M_{1-2} , labial view (Z. Pal. No. MgM-II/26).
Fig. 4. Fragment of angular process of left mandible, labial view (Z. Pal. No. MgM-II/28).
Fig. 5. Anterior fragment of left mandible without teeth, young individual: *a* labial view, *b* lingual view (Z. Pal. No. MgM-II/29).
Fig. 6. Anterior fragment of left mandible without teeth, old individual: *a* labial view, *b* lingual view (Z. Pal. No. MgM-II/30).
Fig. 7. Left mandible with P_3 - M_3 : *a* lingual view, *b* labial view, *c* occlusal view (Z. Pal. No. MgM-II/24).
Fig. 8. Left mandible with P_4 - M_3 and alveoli of anterior teeth: *a* lingual view, *b* labial view, *c* occlusal view (Z. Pal. No. MgM-II/25).

All specimens $\times 1.5$

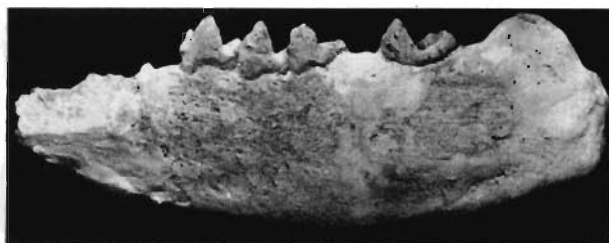
Specimen on Fig. 1 from Naran Bulak

(see also Plates X, XII—XIV)

Photo: M. Czarnocka



1a



1b



2a



2b



5a



3



7c



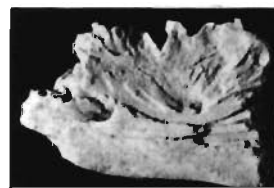
5b



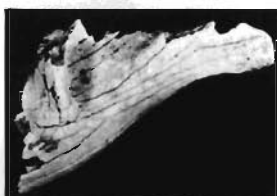
7a



7b



6a



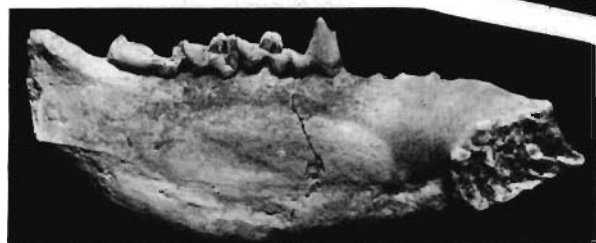
4



8c



6b



8a



8b

A. SULIMSKI: PALEOCENE GENUS *PSEUDICTOPS*

PLATE XII

Page

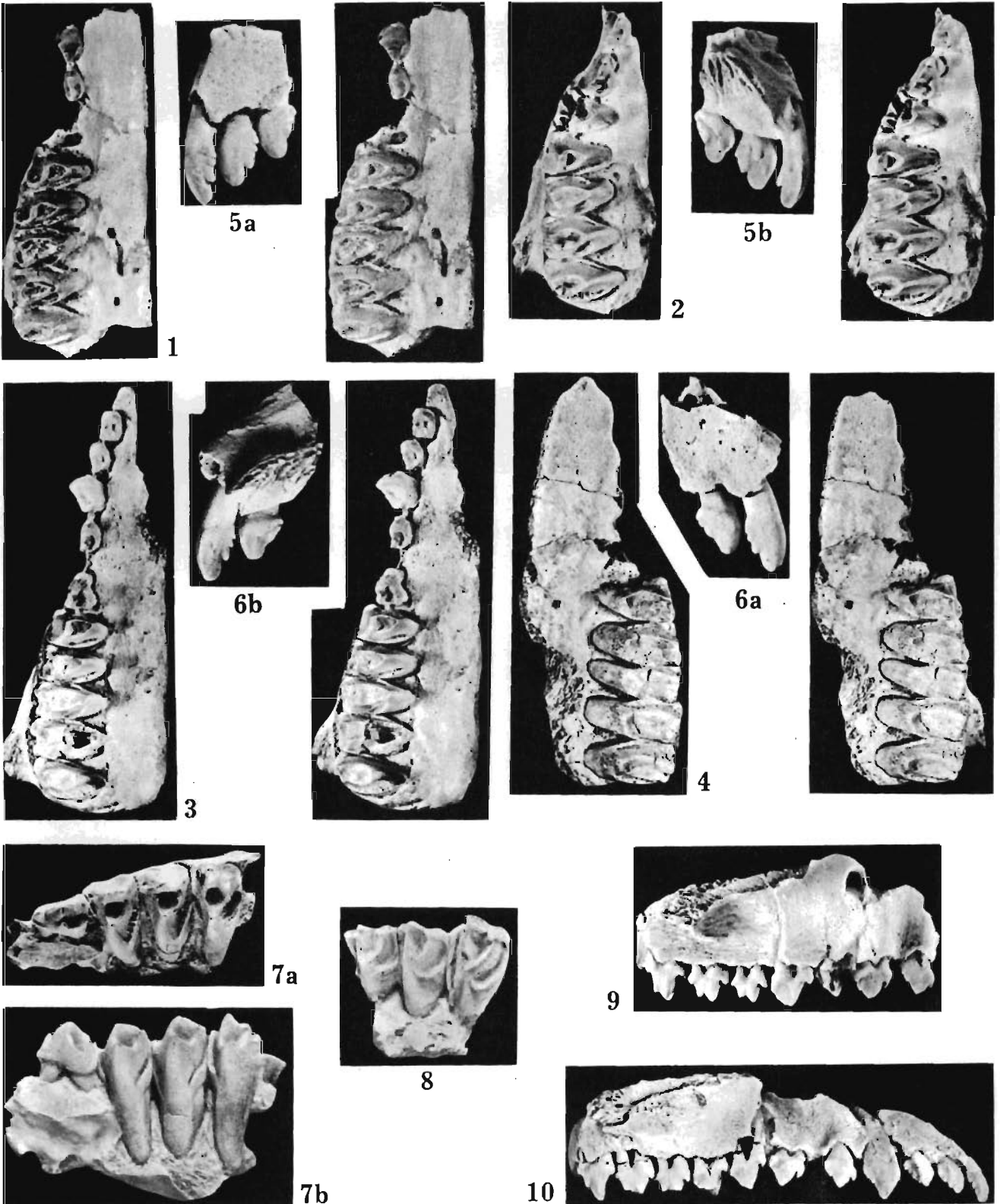
Pseudictops lophiodon MATTHEW, GRANGER & SIMPSON 108

(Naran Bulak)

- Fig. 1. Right maxilla with C-P¹, and P³-M³, occlusal view, stereo-photograph (Z. Pal. No. MgM-II/3); ×1.5.
Fig. 2. Right maxilla with P¹-M³, occlusal view, stereo-photograph (Z. Pal. No. MgM-II/2); ×1.5.
Fig. 3. Right maxilla with I¹-M³, occlusal view, stereo-photograph (Z. Pal. No. MgM-II/1); ×1.5.
Fig. 4. Left maxilla with P³-M³, occlusal view, old individual, stereo-photograph (Z. Pal. No. MgM-II/4); ×1.5.
Fig. 5. Left I¹⁻³ *in situ*: *a* labial view, *b* lingual view (Z. Pal. No. MgM-II/6); ×2.
Fig. 6. Right I²⁻³ *in situ*: *a* labial view, *b* lingual view (Z. Pal. No. MgM-II/7); ×2.
Fig. 7. Left maxilla with P²-M¹: *a* occlusal view, *b* occluso-lingual view (Z. Pal. No. MgM-II/5); ×2.
Fig. 8. Left maxilla with P³-M¹, occluso-lingual view (Z. Pal. No. MgM-II/8); ×2.
Fig. 9. Right maxilla with P¹-M³, labial view (Z. Pal. No. MgM-II/2); ×1.5.
Fig. 10. Right maxilla with I¹-M³, labial view (Z. Pal. No. MgM-II/1); ×1.5.

(see also Plates X, XI, XIII, XIV)

Photo: M. Czarnocka



A. SULIMSKI: PALEOCENE GENUS *PSEUDICTOPS*

PLATE XIII

| | Page |
|---|------|
| <i>Pseudictops lophiodon</i> MATTHEW, GRANGER & SIMPSON | 108 |
| (Naran Bulak) | |

Fig. 1. Right femur, lateral view: *a* proximal extremity with trochanters and head, *b* distal extremity with condyles, *c* anterior view of proximal extremity (Z. Pal. No. MgM-II/33); nat. size.

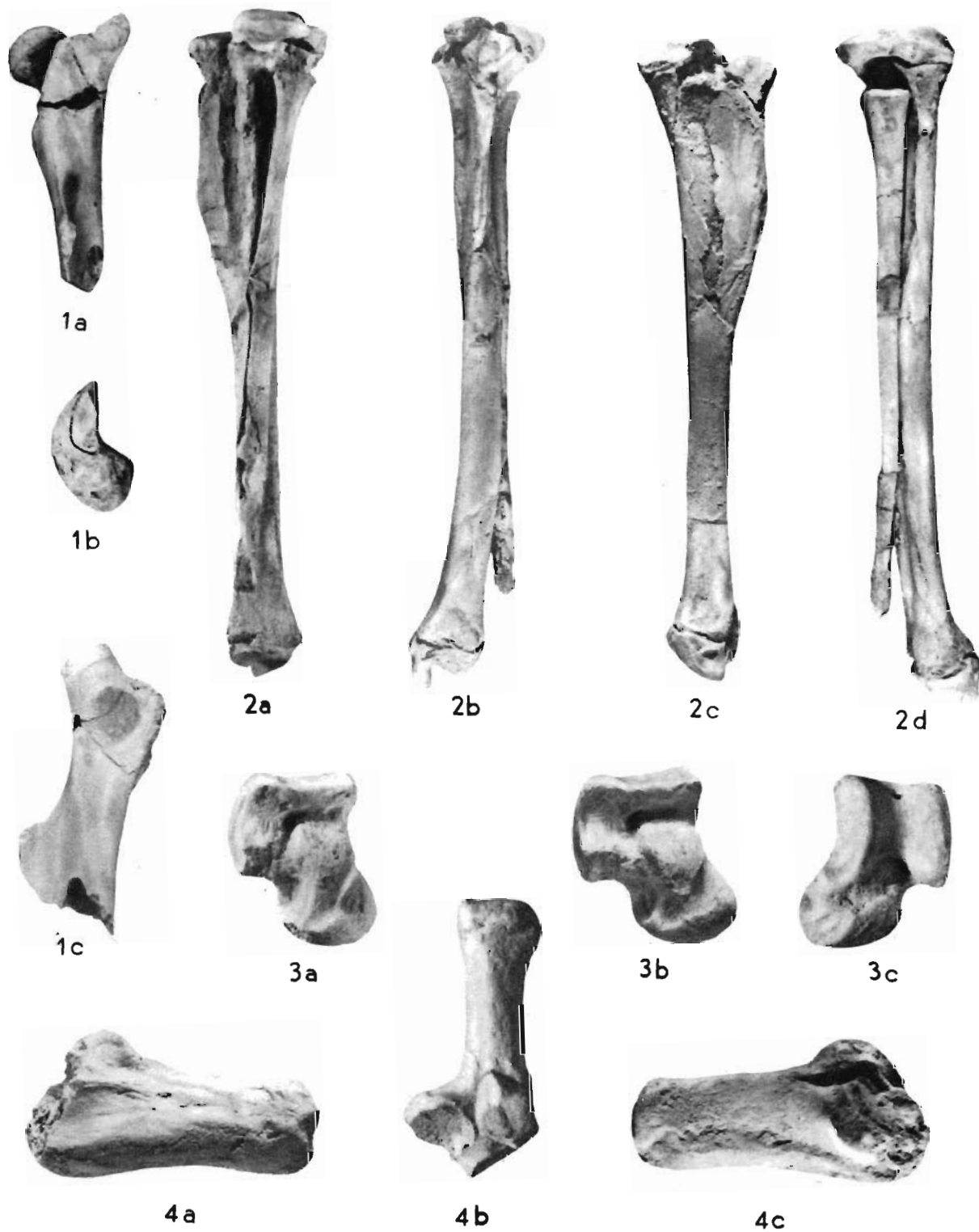
Fig. 2. Left tibia and fibula together: *a* lateral view, *b* anterior view, *c* medial view, *d* posterior view (Z. Pal. No. MgM-II/34 and 35); nat. size.

Fig. 3. Left astragalus: *a* plantar view, *b* the same, *c* dorsal view (Z. Pal. No. MgM-II/37); $\times 2$.

Fig. 4. Left calcaneum: *a* lateral view, *b* dorsal view, *c* medial view (Z. Pal. No. MgM-II/36); $\times 2$.

(see also Plates X—XII, XIV)

Photo: M. Czarnocka



A. SULIMSKI: PALEOCENE GENUS *PSEUDICTOPS*

PLATE XIV

Page

Pseudictops lophiodon MATTHEW, GRANGER & SIMPSON 108

(Naran Bulak)

- Fig. 1. Left hind foot, dorsal view, reconstructed; nat. size.
Fig. 2. Right calcaneum: *a* plantar view, *b* medial view, *c* dorsal view (Z. Pal. No. MgM-II/48).
Fig. 3. Right astragalus: *a* plantar view, *d* dorsal view, *c* lateral view (Z. Pal. No. MgM-II/49).
Fig. 4. Left cuboideum: *a* lateral view, *d* dorsal view, *c* medial view (Z. Pal. No. MgM-II/38).
Fig. 5. Trochlear fragment of left astragalus: *a* dorsal view, *b* plantar view (Z. Pal. No. MgM-II/47).
Fig. 6. Left naviculare: *a* dorsal view, *b* anterior view (Z. Pal. No. MgM-II/39).
Fig. 7. Left tarsal bone 3, dorsal view (Z. Pal. No. MgM-II/52).
Fig. 8. Left claw phalanx of digit IV: *a* dorsal view, *b* medial view (Z. Pal. No. MgM-II/43).
Fig. 9. Left claw phalanx of digit III: *a* dorsal view, *b* medial view (Z. Pal. No. MgM-II/42).

Figs. 2—9 $\times 2$

(see also Plates X—XIII)

Photo: M. Czarnocka

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