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MORPHOLOGY OF SKULL OF ASIATIC EOCENE TAPIROID (*LOPHIALETES EXPEDITUS* MATTHEW ET GRANGER, 1925)

(Mammalia, Perissodactyla, Tapiroidea)

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ABSTRACT

The paper describes the skull of the Asiatic Eocene tapiroid *Lophialetes expeditus* Matthew et Granger and discusses some peculiar features of skull structure and its functional significance.

Tapiroids, a primitive group of suborder Ceratomorpha/Perissodactyla/ was widely distributed in the Paleogene throughout Europe, North America and Asia. Presently about 20 localities of Eocene mammals containing remains of tapiroid forms are known in Asia (Belajeva, Reshetov, Trofimov, 1974; Reshetov, 1975). The representatives of the endemic family Lophialetidae Radinsky (1965a) prove to be the most numerous ones among the Asian Tapiroidea. They were widely spread in the second half of Eocene in the moderate zone of the mainland. Their finds are known from the Northern China, the Mongolian People's Republic and from the Asiatic areas of the USSR/Kazakh SSR, Kirghiz SSR/. The skull morphology of Asiatic early Tertiary Tapiroidea is hardly studied. Suffice it to note that very brief information related to the skull of *Lophialetes expeditus* and *Sholosseria magister* Matthew et Granger is found only in L. B. Radinsky's paper (1965, a).

This gap ought to be ascribed mainly to the scarcity of materials and the relatively rare findings of well-preserved skulls. The Joint Soviet-Mongolian Paleontological Expedition of 1969-1973 permitted to collect numerous materials on the Eocene Tapiroid forms of Mongolia. Special attention was paid to the well-preserved skulls of Lophialetides related to *Lophialetes expeditus* Matthew et Granger, 1925 and found at the locality of the Middle Late Eocene mammals of Khaichin-Ula III (Shuvalov, Reshetov, Barsbold, 1974).

A brief description of these materials is given below.

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SYSTEMATIC DESCRIPTION

Family Lophialetidae Radinsky, 1965

Subfamily Lophialetinae Matthew et Granger, 1925

Genus *Lophialetes* Matthew et Granger, 1925

Lophialetes expeditus Matthew et Granger, 1925.

Holotype: Maxilla with right P^4-M^3, coll. AMNH N 19163, Matthew et Granger, 1925, pp. 5-7, fig. 6. Northern China, Irdyn-Manha, lower part of the Upper Eocene.

Material: Two skulls with a well-preserved mandible belonging to adult specimens, coll. Paleontological Institute, USSR, Academy of Sciences, N 3403-Ia, b; 2a, b and one complete skull of the juvenile specimen, coll. Paleontological Institute, USSR Acad. Sciences, N 3403-5a, b.

Diagnosis[1]: Tapiroids of large size (for the family). The premolar series is shorter than the molar one. The metacones on the premolar teeth are of elongated and flat form. Transversal crests are relatively high, their tops are sharpened. The premolar teeth are nomolarized. M^{2-3} have comparatively long and narrow crowns. Some specimens lack P_1. The skull is elongated, the nasal bones shortened. The sagittal and occipitalc rests are strongly developed. The tarsus and metatarsus are of tridectylous pattern.

[1]The diagnosis is based on L. B. Radinsky's paper (1965a) with some amendments and changes.

Table 1

Skull sizes (mm) of *Lophialetes expeditus* Matthew et Granger, 1925; Mongolian People's Republic, locality Khaichin-Ula III, Middle-Lowest Upper Eocene.

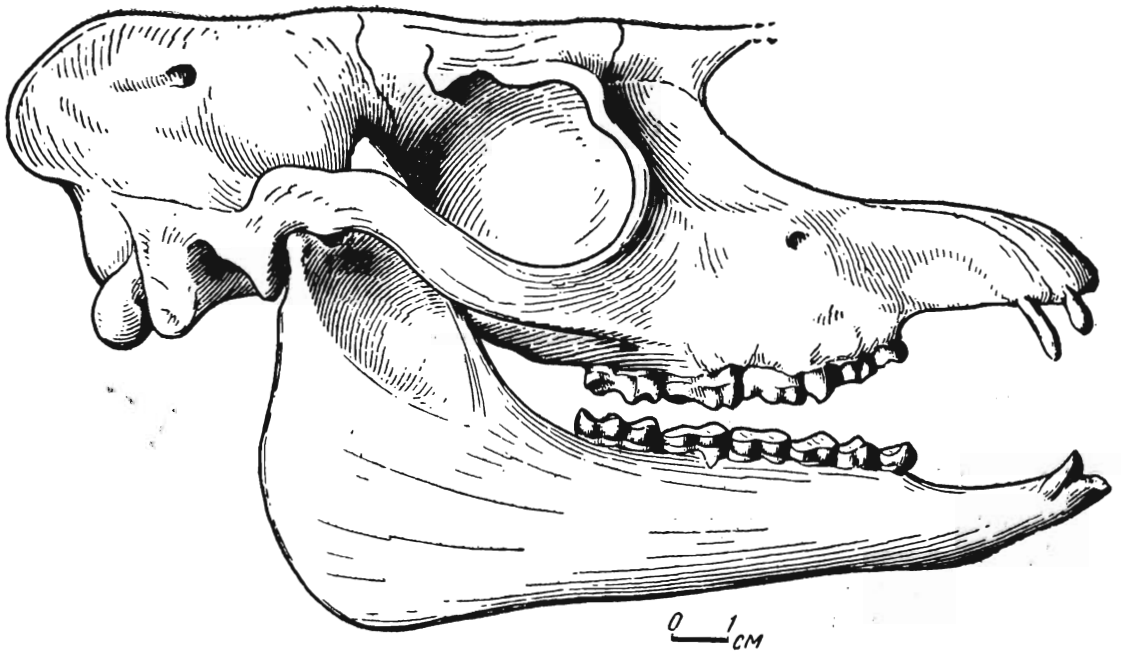
Item of measurement	coll. Paleontol. Institute USSR Ac. Sc. N 3403-Ia	coll. Paleontol. Institute USSR Ac. Sc. N 3403-2a	coll. Paleontol. Institute USSR Ac. Sc. N 3403-5a
1. Length from prosthion to posterior margin of condylus occipitale ..	184,0	190,0	?134,0
2. Length from prosthion to lower margin of foramen occipitale ..	173,5	177,5	?127,0
3. Length from prosthion to anterior margin of orbit (facial area) ..	86,0	90,0	60,0
4. Length from orbit's anterior margin to posterior margin of condylus occipitale (brain area) ..	98,0	100,0	?74,0
5. Length from anterior margin of nasalia to posterior margin of crista sagittalis (incomplete) ..	138,0		..
6. The least width (in temporal narrowing) ..	30,0	30,0	30,0
7. The utmost width (at zygomatic arch level) ..	79,0	79,0	60,0
8. Height above P^2 ..	19,0	18,0	..
9. Height above M^3 ..	58,0	?51,0	..
10. Occipum height from Basion to top of crista occipitale	51,0	51,5	..
11. Skull's width at processus jugularis level ..	38,5	40,0	..
12. Width between lateral margins of condyli occipitale	30,0	32,0	..
13. Length of diastema between I^3 and C ..	4,5	5,0	..
14. Length of diastema between C and P^1 ..	16,2	15,1	..
15. Length P^1—M^3 ..	?61,0	61,5	..
16. Length P^1—P^4 ..	....	25,5	..
17. Length M^1—M^3 ..	36,0	36,0	..

Description: The skull of *Lophialetes expeditus* (fig. Ia, b, c, Table I) is elongated, relatively low and narrow. The saggittal and occipital crests are well-developed. In adult specimens the orbit's front margin is above M^3. The nasal bones are strongly shortened. The brain case is elongated, the post-orbital (temporal) narrowing well pronounced. The brain area exceeds (in length) the facial one. Supraocular processuses are well-developed; there is a fronto-parietal depression. The orbits are of large and rounded shape.

Face. The boundary of the skull's facial and brain sections is provisionally drawn along the orbit's front margin. The skull's facial area changes most strikingly during postnatal development/V. N. Orlov, 1961/. In *L. expeditus* the face area is shorter than the brain one. Its average length is 90 mm. The nasal cavity is relatively broad and high. The nasal incisures broad and run far back having rounded above M^2 in adult specimens. The rostral area narrows in the diastema region, while the incisive area, on the contrary, is somewhat widened. The skull's width, along the orbit's front margins, is 65 mm., above the diastema 22 mm., above I^3—23,5 mm. The maxilla's height above M^3 is 58 mm. In juvenile forms the face is still more shortened compared to the brain-case (63 mm.), the maximall height of the face area (above P^4-M^1)-41,5 mm.; the length above the diastema-18,0 mm., above I^3—19,5 mm. The maxillas are somewhat bent in dorsal direction. Thus,the skull's shape resembles a bulldog's head.

Intermaxillaria are low, not knitted, stretched in the anterio-posterior direction. In their anterior part they bear 3 incisions on each side and extend back up to P^2 level; they gradually narrow. The maximal length (from the prosthion to the hind margin)-45 mm., maximal height (above I^3)—14 mm. At the front margin there is a tuberosity for the attachment of musculus levator nasolabialis. In juvenile specimens intermaxilla is more roundly outlined. Its maximum length 27,5 mm., height-11 mm. (above I^3) and it fringes the front extremity fissura palatina.

Maxilla. A relatively high bone. Its utmost height above the hind wall of M^2—47 mm., utmost length 99 mm. Foramen infraorbitalis positioned above the front margin of M^1 is a relatively large fenestra. Crista facialis is gently protruding in the middle, the highest part of maxillara. It gradually descend to naught at the M^1—M^2 level. The maxilla's upper part together with ossa lacrimale, frontale and nasale form a well pronounced fossa praeorbitalis and an outlined oblong depression—diverticulum where musculus levator labii maxillaris is attached. Maxilla's supraalveolar part is strongly tuberosed. Here the points of fixation of musculus masseter and of lip muscles are distinctly pronounced. The surface of palatine bone is smooth and flat. The palutina bone is almost not vaulted. Fissura palatina is long and narrow. Its utmost length is 15,5 mm. and in width it does not exceed 4 mm. Choans open at M^3 level.



Fig, 1a

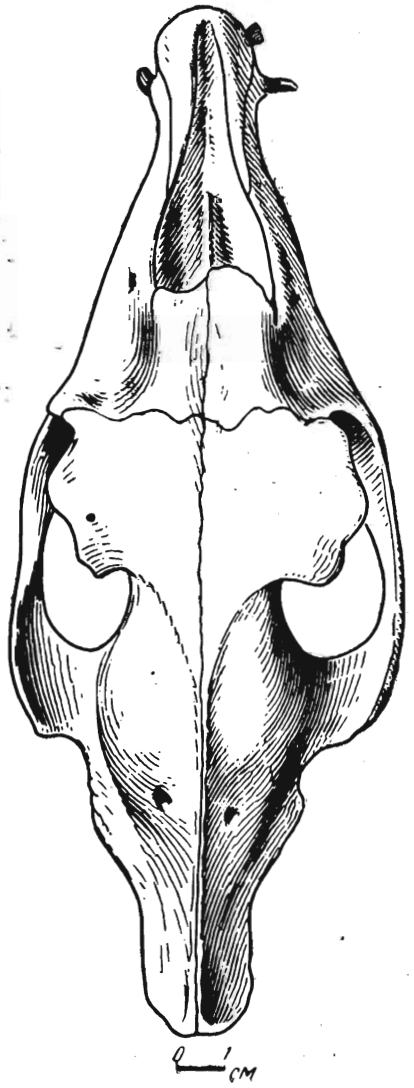


Fig. 1b

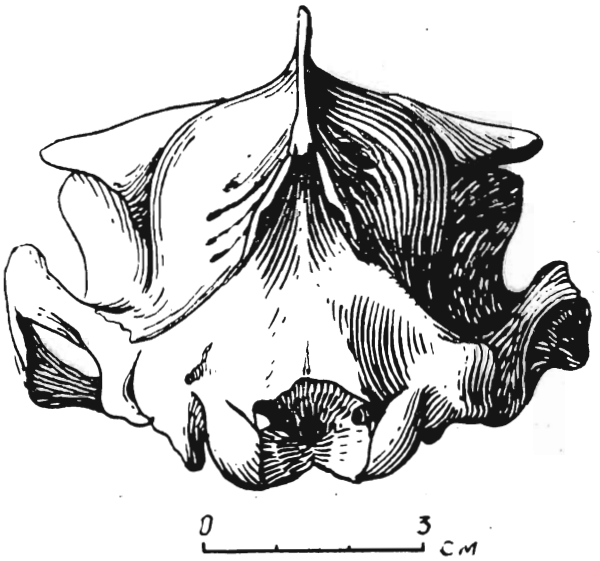


Fig. 1c

Fig. I, a, b, c. Skull of *Lophialetes expeditus* Matthew et Granger, 1925.

a—lateral view.
b—dorsal view.
c—occipital view.

In juvenile specimens os maxilla is relatively higher (max. height 37,5 mm.) and shorter (max. length 61,0 mm.). Foramen infraorbitale is above the hind margin of dP^2. Fissura palatina is relatively shorter and wide. Choans open at M^1 level.

Os nasale. In a well-preserved specimen their very ends are broken (coll. Paleontological Institute USSR Acad. Sciences, 3103, N Ia, fig. Ia, b). However, one observes that os nasale are strongly shortened. It appears that their front margins did not extend beyond the anterior margin of P^2. The nasal incisuras are very large, their hind margins are positioned above M^2. Os nasale are oriented in a somewhat dorsal direction. This is especially emphasized by the fronto-parietal depression. The nasal cavity is vast, however, its internal structure has not been preserved. Fossa praeorbitalis is deep, slightly extended in the dorsoventral direction and positioned above the orbit's anterior margin. Along the suture, separating both nasalia runs a deep small valley. Os nasale's horizontal and vertical planes are lie to each other at an angle close to a right one.

Os lacrimale. Positioned at the boundary of the skull's facial and brain sections. Covers a rather large area of the orbit's front part. Processus lacrimalis is a rather large trapeziform body. It screens the orbit from the anterio-dorsal side.

Brain-case. The brain case is rather low, of elongated form. The cranial cavity is moderately developed. It is about 1,5 times less in volume than in dogs of the same size. The orbits are large, processus supraorbitalis is strongly developed. The skull is very narrow in its postorbital narrowing (width—30.0 mm.) Zygomatic archs are not wide (the maximal width between extreme points—79 mm.). The occipital and sagittal crests are strongly developed. The facial and brain sections ratio in adult specimen is 88%, while in juvenile forms, about 80%.

Os zygomaticum. The lower margin of the zygomatic bone forms an acute tuberous crest-the attachment point, musculus masserter. The jugal processus is long and not wide.

Os frontale is large with a strongly developed processus supraorbitalis enclosing the orbit from the dorsal side. Os frontale covers a major part of the orbit and forms in it a trapeziform body restricted from the front side by a lacrimo-frontal suture and from behind by a fronto-parietal and ventro-spheno frontal suture. The dorsal side of os frontale is strongly concaved. In 1/3 of its rear part there is a distinctly pronounced crista frontalis externa—the line of attachment of the anterodorsal portion of musculus temporalis. Crista frontalis externa diminishes to naught at the base of the sagittal crest. The fronto-parietal suture is distinctly seen in specimen N 3403-2a. At the rear of the orbital portion of os frontale there is foramina ethmoidea through which nervous ethmoideus and arteria ethmoidalis pass.

Os parietale covers a rather large area restricted from its front by a distinct visible fronto-parietal suture, latero-horizontally directed tempoparietal suture, and in its rear part by occipito-parietal suture.

The junction of parietal bones forms a sigittal crest which is increasing backwards. A rounded paired foramen for vessels is opened on the posterio-dorsal surface of the parietal bone as well as distinctly pronounced furrows and tuberosities for attachment of musculus temporalis.

In the orbit area (fig. 2) there are consecutive openings of an internal foramen for canalis infraorbitalis, extremely large, through which a large arteria infraorbitalis, and a branching of the second branch of V pair the brain

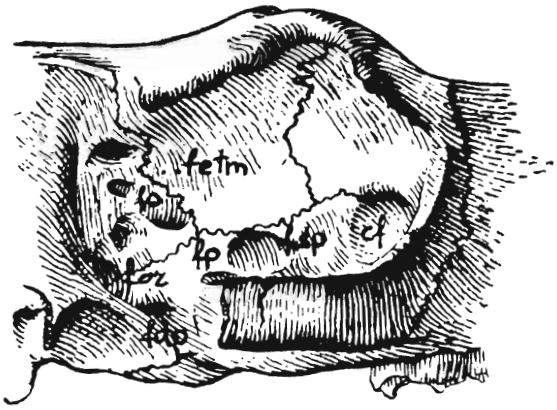


Fig. 2. Fenestra of the skull's orbital part *Lophialetes expeditus* Matthew et Granger, 1925:
fo—foramen opticum.
cf—canalis facialis.
fsp—foramen schaenopalatium.
fp—foramen palatinum.
for—fissura orbitalis.
fao—foramen alare orale.

cranial nerves-nervus infraorbitalis pass. Below, at the boundary of the area of the orbital part of os schenoides there is a very large ovally-shaped foramen sphaenopalalatinum and a much smaller foramen palatinum following it. Both of them serve for passing of the respective vessels and nerves. In one third of the orbit's rear part, in the area of distribution of os sphaenoides orbital part, there are consecutive openings of a rounded foramen opticum for nervus opticum and a ventrally positioned large foramen extended in dorso-ventral direction, on its position it corresponds to fissura orbitalis through which nerves of III pair (n. oculomotorius), IV pair (n. trochealis) and V pair (n. trigeminus) and of VI pair (n. abducens) pass. Foramen alare orale, an entry into

canalis alaris, is opened ventrally to fissura orbitalis. A large arteria maxillaris runs through canalis alaris. We failed to find foramen rotundum owing to the deformation of bone walls. However, the probability of its existence is not excluded.

The squama of ossae temporalis are vertically raised, however, they do not extend too high owing to the strongly developed parietal area. The molar processus of ossae temporalis is not wide and relatively short; it sharply ascends and forms with ossae temporalis a small, but deep cavity. Fossa mandibularis is relativelydeep and narrow in the anteroposterior direction, slightly raised in its dorso-lateral part. Processus retroarticularis is well-developed, wide and large, restricts the auditory section from the front. Crista temporalis is strongly developed and ventrally restricts the area of distribution of musculus temporalis. In the front it transforms into the molar processus of the squama bone and in its rear part it merges with crista occipitalis. Pars mastoidea is massive and tuberous; it restricts the auditory section of the rear.

Os occipitalis (fig. 1c) is characterized by a strongly developed crista occipitalis dorsally joined with crista sagittalis and laterally with crista temporalis. The sagittal, occipital and temporal crista neatly restrict the area of distribution of musculus temporalis. In their profile the occipital and sagittal crests are strongly ventrally bent. On the internal surface of crista occipitalis there is a distinct site for the attachment of musculus obliqua capitits medialis. The skull's occipital surface, in its plan view, reminds a triangle with a sharp dorsal angle. Condyli occipitale are narrow, elongated, directed backwards and ventrally. Foramen occipitale is large. Processus jugularis is relatively massive and short. A paired large foramen nervus hypoglossus for the XII pair of nerves-nervus hypoglossus opens from the ventral side. Basioccipitale is relatively long, tuberculi pharingei large and strongly protruding ventrally. This testifies to the development of a respective muscle. From the lateral side of basi-occipitale open foramen lacerum which serves for the passing of IX, X and XI pairs of nerves (nervus glossopharyngeus, nervus vagus, nervus, nervus accessorius). And the large arteria carotica interna feeds the brain at this very site. About 7 mm. ahead and somewhat more laterally there is foramen ovale through which the third branch (nervus mandibularis) of the V pair of nerves passes. The boundary of basioccipitale is below the anterior margin of fossa mandibularis.

Auditory area. The auditory bones are flat, semicircular from the lateral side; Porus acusticus externa is very large.

Bullae tympanici are absent. Processus muscularis has a wide base, its terminal part is destroyed.

The lower jaw is well preservedi n specimens 3403-Ib, 3403-5b (fig. Ia, table 2). It was initially described

Table 2

Size (mm) and indices (%) of lower jaw of *Lophialetes expeditus* Matthew et Granger, 1925, coll. Paleontological Institute, USSR Academy of Sciences, N 3403-Ib, Mongolian People's Republic, locality Khaichin-Ula III, middle-Lowest Upper Eocene.

1.	Length from symphysis anterior point to processus coronoideus	124,0
2.	Ditto to processus articularis	139,0
3.	Length of symphysis	32,5
4.	Utmost width of symphysis area	18,2
5.	The least width of symphysis area	14,9
6.	Length of diastema	29,0
7.	Height of horizontal branch under P_2	17,0
8.	Ditto beneath P_4—M_1	20,1
9.	Height of ascending branch up to the top of processus coronoideus (incomplete because of damage)	81,0
10.	Ditto to the top of processus articularis	66,0
11.	Width of ascending branch (max.)	49,0
12.	Width of incisura between processuses of ascending branch	4,5
13.	P_2—P_4 length	23,0
14.	P_2—M_3	61,9
15.	M_1—M_3 length	38,9
	Indices (%, %)	
1.	$\frac{\text{Length of symphysis (3)}}{\text{Jaw's length (1)}}$	26,2
2.	$\frac{\text{Length of symphysis (3)}}{\text{Jaw's length (2)}}$	23,4
3.	$\frac{\text{Least width of symphysis area (5)}}{\text{Utmost width of symphysis area (4)}}$	81,9
4.	$\frac{\text{Least width of symphysis area (5)}}{\text{Length of symphysis (3)}}$	45.8
5.	$\frac{\text{Utmost width of symphysis (4)}}{\text{Length of symphysis (3)}}$	56,0
6.	$\frac{\text{Height of ascending branch (9)}}{\text{Jaw's length (1) (9)}}$	65,3
7.	$\frac{\text{Height of ascending branch (9)}}{\text{Jaw's length (2)}}$	58,9
8.	$\frac{\text{Length of diastema (6)}}{\text{Length of symphysis (3)}}$	89,8
9.	$\frac{P_2\text{—}P_4 \text{ length (13)}}{P_2\text{—}M_3 \text{ length (14)}}$	38,1
10.	$\frac{P_2\text{—}P_4 \text{ length (13)}}{M_1\text{—}M_2 \text{ length (15)}}$	57,9
11.	$\frac{\text{Length of diastema (6)}}{P_2\text{—}M_3 \text{ length (14)}}$	46,0

by Radinsky (1965a, 238-239.) Its horizontal branch is relatively low and gradually decreases from M_3 to P_1. The diastema is relatively long and narrow. Its symphysial part is broadened and somewhat elongated. At the diastem level and beneath P_2 there are two small holes. The ascending branches are very wide at the base. The mandibula's posterior angle is of rounded shape. It smoothly protrudes backwards in relation to the upper part of ascending branch. Fossa masseterica is deep, distinctly pronounced and covers about 1/3 of the lateral surface of ascending branches.

This points to the strong development of the inner part of musculus masseter. Processus articularis is low processus condylaris is elongated and slanted to the mandibula's internal surface. Processus coronoideus is much higher than processus articularis. It is of uniform width throughout its entire length and its upper third portion is slanted back. The mandibulla's posterior margins are somewhat bent in the medial direction, restricting a vast area from the inner surface. The posterior portion of musculus pterigoideus is attached to this area. In juvenile specimens the mandibulla reveal relatively lower and inflated horizontal branches.

Teeth. I^1-3 with extended flattened crowns. I^3 is not enlarged compared to other incisers. C is separated from the incisers by a small diastem (4-5 mm.); it is of triangular shape, flat with a sharp top. P^1-P^4 are nonmolarized, P^1 of triangular shape, P^2 – subquadratic shape. The cingulum is well developed on the premolar teeth. Protoloph and metaloph form an U-shaped figure. M^1-M^3 is larger than the premolar teeth. M^1-M^2 are of quadratic shape. M^3 has a much shorter posterior wall compared to M^1-^2. The parastyle is not large. It is isolated sufficiently well. The metacone is well-developed and flattened. I_1-_3 with flattened extended crowns, I_3 is slightly larger than I_1-_2. There is no diastem between C and the incisers. C-triangular, rounded tooth. P_1 is absent in some specimens. Crowns P_2-_4 are of rectangular shape. M_{13} have relatively high and acute protolophides and hypolophides. Paralophides and metalophides are of elongated form. In M_3 one observed a developed hypoconulid.

Deciduous teeth dP^1 is similar to P^1, while dP_1-P_1, as assumed by Radinsky (1965a, p. 191) dp_1 possibly does not change in *L. expeditus*. DP^2 is submolarized, dP^3-^4 fully molarized. DP_2 is similar to P_2, but of less size, dP_3 submolarized, dP_4 fully molarized.

Comparison and remarks: In may ways the skull of *Lophialetes expeditus* is akin to the early Eocene American tapiroid of family Helaletidae-*Heptodon posticus* Cope, 1882 (Radinsky, 1965b). However, the skull of *L. expeditus* has some features of specialization distinguishing it from the initial primitive type characteristic of all early perissodactylys, for example, *Hyracotherium* and *Heptodon* (Kitts, 1956; Radinsky, 1965b). These differences refer firstly to the facial area—in *L. expeditus* it is shortened (in *Heptodon* the facial area excels to the brain area in length), the nasal bones are strongly reduced compared to those in *Heptodon* and *Hyracotherium* (in *Heptodon* os nasale extends ahead up to the symphysis area and contacts with inter-maxillaria). The nasal incisuras are respectively increased, while in *Heptodon* the posterior margins of nasal incisuras are positioned above P^1 and in *Lophialetes expeditus*, above M^2. Fossa praeorbitalis are also more strongly developed in *L. expeditus*. In the latter the front margin of crista facialis is positioned above M^2-M^3, whereas in *Heptodon* it is above M^1. There is also a difference in the structure of the occipial section. Crista sagittalis and crista occipitalis are developed in *L. expeditus* to a greater degree than in *Heptodon*. In the former both crests are more strongly swerved ventrally. The location of cranial foramens in *L. expeditus* is close to that in *Heptodon*.

However, it differs from their location observed in most ancient representatives of Perissodactyla-*Hyracotherium* (Kitts,—1956). In *Hyracotherium* in the orbit's posterior part one finds a single large opening for the passage of n. opticum, n. oculomotorious, n. trochlearis, n. adbucens and two branches of n. trigeminus (Kitts, 1956; Simpson, 1952). And at the same time we observe a merging of foramen ovale with foramen lacerum (Edinger, Kitts, 1954). And, in ancestors of Perissodactyla-Condylarthra (for example, in Phenacodus) one observes a common foramen for the passage of the orbit's vessels and nerves. Yet, it appears that in the latter nervus opticum ran through a separate opening. In Condylarthra foramen ovale and foramen lacerum are positioned separately. A similar location of these foramens was intitially peculiar to all placentic animals. However, in the course of evolution in different groups it has occured a merging of both fenestae. In Equidae it seems to have happened at the very early development stages, in Tapiroids it occured only in Oligocene (Edinger, Kitts, 1954). In all Tapiroids o' the Eocene era foramen ovale was apparently separated from foramen lacerum.

The peculiar features of skull structure in *L. expeditus* permit some suppositions about their functional role. The shortened and somewhat dorsally elevated nasalia, the increased nasal incisures as well as the deep fossa praeprebitalis lifted above the orbit's front margin point to the development of respective muscles in the facial area of *L. expeditus*. The well-developed fossa praeorbitalis testifies to strongly developed musculus levator labi

maxillaris proprius while the distinct tuberosity on the orbit's anterior margin reveals a corresponding development of musculus levator nasolabialis which in its muzzle part is subdivided into two portions: one of them is attached at diastema level, the other, at the anterior margin of intermaxillaria where tuberosity is observed in *L. expeditus*.

All these specific features point to a strong development of a mobile proboscidiformis upper lip in Lophialetidae which, however, was functionally weaker than in recent Tapirus. The development of a proboscidiformic upper lip in *L. expeditus* is an example of parallelism within the Tapiroidea superfamily. This organ developed independently in representatives of Helalitidae (Helaletes, Colodon) and somewhat later in Tapiridae.

The development of the teeth system in Lophialetidae ran along the lines of Lophodoncity-separate tubers in *Lophialetes expeditus* are merged into transversal crests; the metacone is enlarged and flattened, the ectoloph well developed and elongated. Such teeth structure permits-transversal movements of mandible along with intensive friction along the ectoloph. This pattern of teeth structure formed independently in Hyracontidae and Amynodontidae (Radinsky. 1969).

In *L. expeditus* the anterior margin of crista facialis (the point of m. masseter attachment is above M^2 in connection with the intensified masticatory function. The large crista sagittalis, and crista occipitalis, and crista temporalis point to an extremely strong development of M. temporalis and a group of occipital muscles. However, as a whole the brain case of *L. expeditus* is rather primitive in its structure and many of its features remind those observed in much earlier Condylarthra and even some predators.

The skull's structure in *L. expeditus* is an example of a combination of a fairly high specialization of the animal's face with rather primitive features of its braincase.

Geological age and geographic distribution: Middle-Lowest Upper Eocene. North China-locality of Irdyn-Manga, Ulan-Shire; the Mongolian people's Republic-locality Kholboldzhi-Nur; upper horizon of Khaichin-Ula II, Khaichin-Ula III.

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