



TRAGULUS NAPIS

THE MOUSE DEER OF THE RHIO-LINGA ARCHIPELAGO: A STUDY OF SPECIFIC DIFFERENTIATION UNDER UNIFORM ENVIRONMENT.

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The mouse deer are small Ungulates forming a special group, the *Tragulidae*, somewhat intermediate in anatomical characters between the deer, camels, and pigs. Two living genera are known, the Indian and Malayan *Tragulus* and the West African *Hyomoschus*. In appearance the larger members of the family show some resemblance to the musk deer; while the smaller species of *Tragulus*, which scarcely exceed a rabbit in size, suggest an Agouti with unusually long legs. Among the Malayan members of the family two groups of species are found, the larger nampus and the smaller kanchils, distinguished from each other by differences in size comparable to that between hares and rabbits, and by certain other slight peculiarities. On the Malay Peninsula and the larger islands members of these two groups appear everywhere to occur together, but on the smaller islands either may be absent. At no single locality have two forms of the same group yet been found.^a

In habits as well as in appearance the Malayan *Tragulidae* show a curious analogy to the South American agoutis. They are nocturnal and they live in jungle, where, owing to the denseness of the undergrowth, they are seldom seen, but where they may be readily caught with snares set in their runways. So perfectly protected from observation are these animals that I have been unable to find any detailed published account of their habits. Even the field notes of Dr. W. L. Abbott, to whose explorations of the Malay Archipelago most of our knowledge of the species is due, contain no definite observations, a fact that becomes especially significant when it is recalled that his col-

^a With the single exception of Pulo Mansalar, Tapamuli Bay, western Sumatra, where two species of nampus, *Tragulus amoenus* and *T. jugularis*, apparently occur together.

lections now contain about 550 specimens of *Tragulus*. Owing to this secluded mode of life the Malayan members of the family are subjected to an essentially uniform environment throughout their

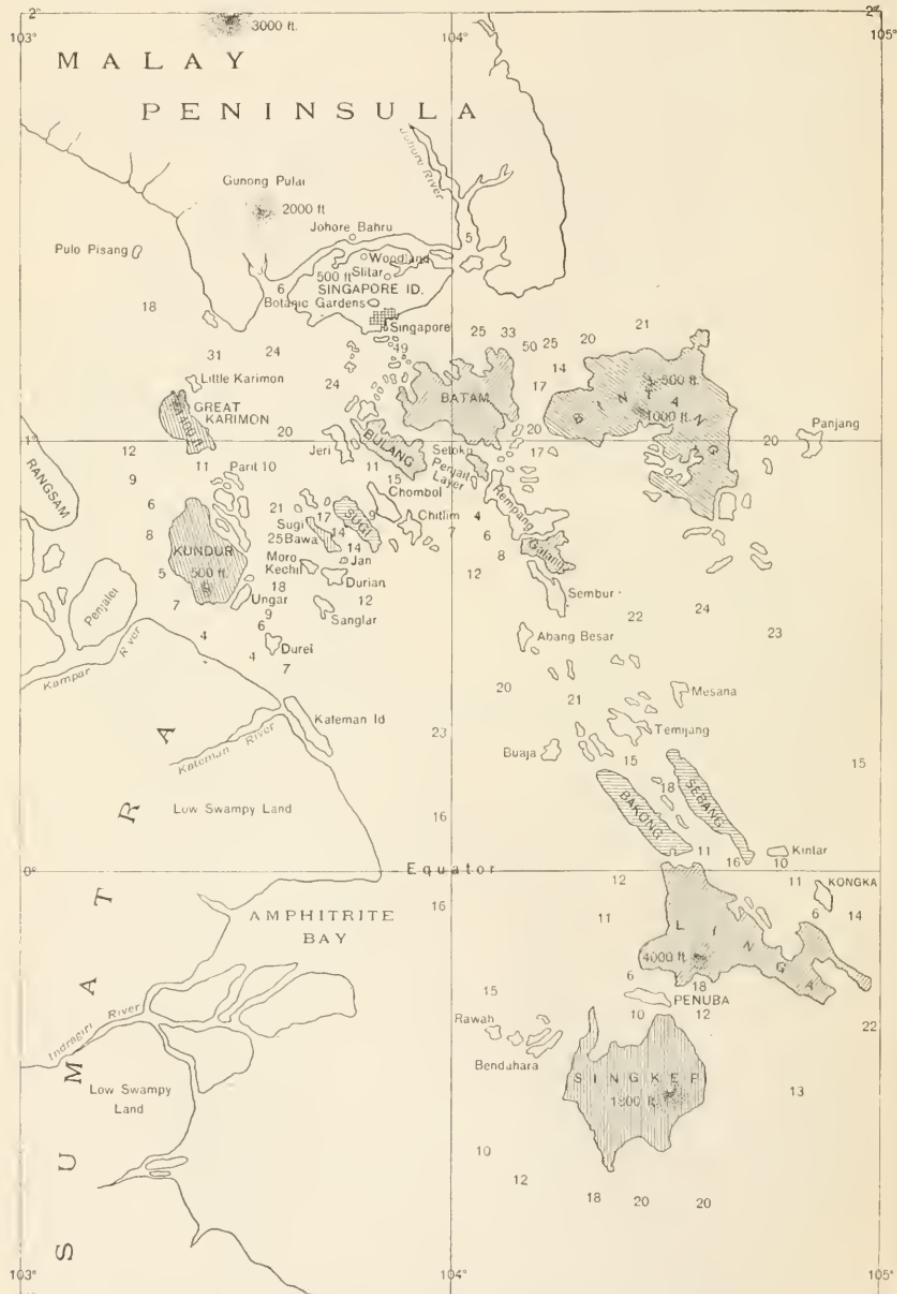


FIG. 1.—MAP OF RIAU-LINGA ARCHIPELAGO SHOWING DISTRIBUTION OF *TRAGULUS NAPU* GROUP, MEMBERS OF WHICH HAVE BEEN TAKEN ON ISLANDS SHADED.

range. Absence of any special tendency toward specific differentiation would be anticipated to result from such conditions. It is found as regards the animals inhabiting the large land masses of Sumatra

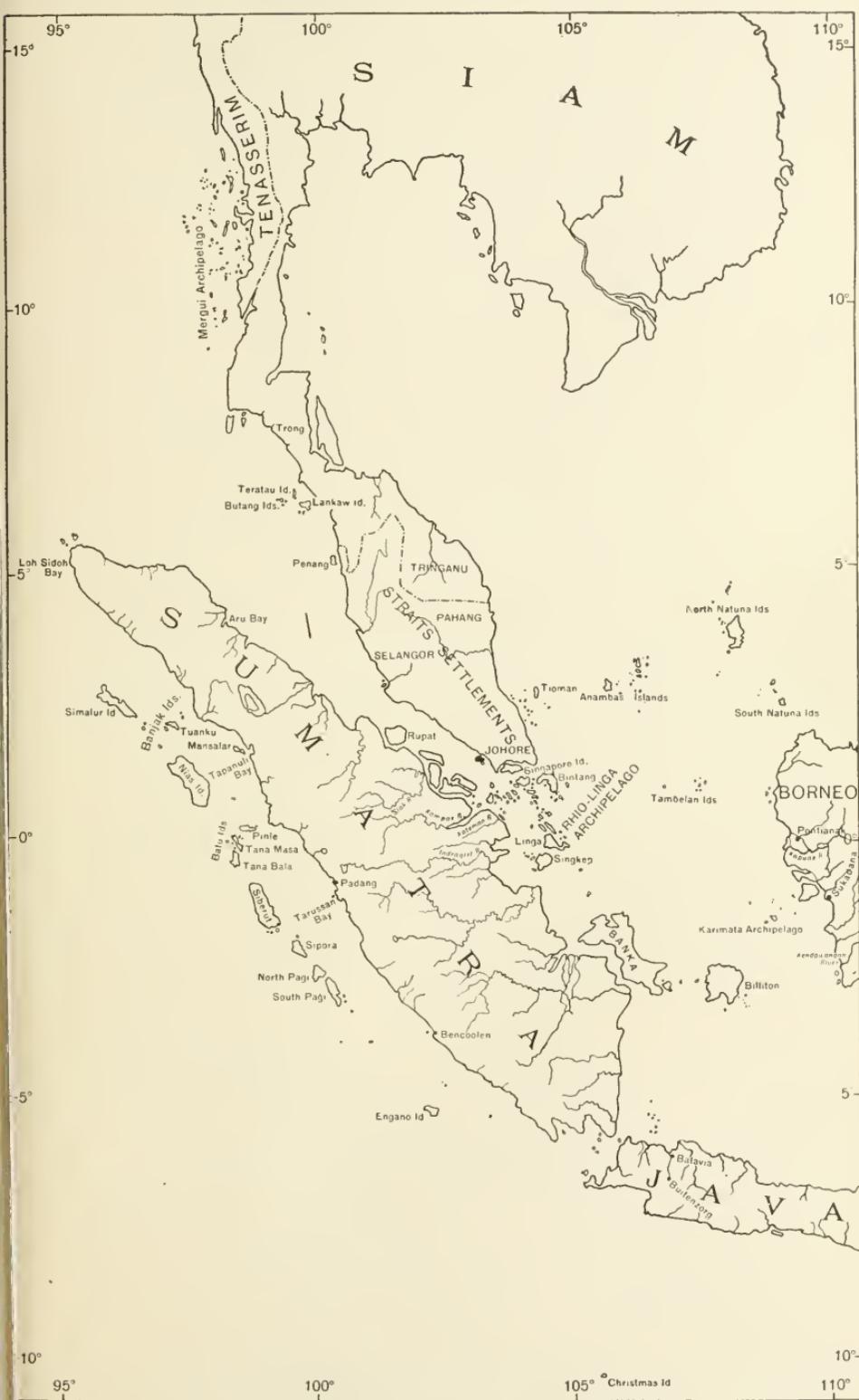


FIG. 2.—MAP OF A PART OF THE MALAY REGION SHOWING RELATIVE SIZE OF RHIO-LINGA ARCHIPELAGO.

and the Malay Peninsula,^a on which the number of known forms is only four or five. On the smaller islands of the archipelago, however, both kanchils and napus, but especially the latter, show an excessive tendency to differentiate into local forms, no less than 41 of which are now known.^b A particularly striking example of this tendency is furnished by the napus of the Rhio-Linga Archipelago.

The Rhio-Linga Archipelago is a series of small islands extending southeastward along the east coast of Sumatra from the southern extremity of the Malay Peninsula (see map, fig. 1). The northernmost of the islands, Karimon, Batam, and Bintang are separated from the mainland by the narrow Malacca Strait on the west and Singapore Strait on the east, the average width of which is only about 10 miles. Singapore Strait contains a mass of small islands on the north side, west of Singapore, which narrows the open water at that point to 5 miles. The easternmost, Karimon, Kundur, and Durei, are equally near the coast of Sumatra. From Karimon, the northwesternmost of the group, to the south shore of Sinkep, the southernmost, is a distance of about 150 miles, while that from Karimon east to Panjang is about 125 miles. Near the middle the archipelago is partly divided by the Rhio Strait into two main groups, the Rhio^c Archipelago proper at the north and the Linga Archipelago at the south. The principal islands of the Rhio Archipelago, the main axis of which extends east and west, are: Karimon, Kundur, Durei, Durian, Sugi, Chombol, Bulang, Batam, Rempang, Galong, Bintang, and Panjang. Of the Linga Archipelago, the main axis of which is nearly north and south, the more important islands are Sebang, Bakong, Linga, and Sinkep. In addition to these, the largest of which, Bintang, Linga, and Sinkep, are from 25 to 35 miles across, and roughly some 500 to 700 square miles in area, the archipelago contains an almost infinite number of smaller islands and islets. The entire group lies in shallow water, mostly within the 20-fathom line; though Malacca and Singapore straits reach a depth of about 30 fathoms, while an isolated sounding of 49 fathoms is recorded between Singapore Island and Batam. The average depth of the water between the archipelago and Sumatra is less than in the straits, that separating the Linga group from the larger island nowhere exceeding 20 fathoms, while that between the Rhio group and the coast scarcely reaches 10 fathoms. The size of the archipelago as compared with that of Sumatra and the Malay Peninsula is difficult to

^a Perhaps of Java and Borneo, also; but the material from these islands is at present unsatisfactory.

^b All but nine of the described forms of *Tragulus* have been discovered by Doctor Abbott.

^c The spelling Rhio is found on most German, English, and American maps; according to the Dutch authorities it should be Riouw.

estimate exactly (see map, fig. 2), but the total area which it covers, land and water together, is approximately one-thirtieth of the former and one-twentieth of the latter. Estimating the land area of the archipelago as one-third of the whole and the relative amount of jungle suited to the needs of *Traguli* as the same on the large land masses and the islets of the archipelago, the area inhabited on the archipelago would be about one-ninetieth that on Sumatra and one-sixtieth that on the peninsula, or only one one-hundred-and-fiftieth of the two combined. Physical conditions on the islands are remarkably uniform. Lying under the equator they are subjected to no seasonal variations of temperature; while the small extent of the group, the uniformity in depth of the surrounding water, and the absence of all influence of great ocean currents preclude the possibility of regional differences. The surface of the islands is mostly rather high, though not sufficiently so to produce altitudinal contrasts of temperature. In his notes Doctor Abbott makes frequent allusion to the uniformity of vegetation and general conditions from island to island. Slight local changes have been made here and there by cultivation, but never to an extent sufficient to alter the conditions under which the *Traguli* exist.

Notwithstanding its geographic insignificance and its lack of climatic or other contrasts, the archipelago is inhabited by no less than eight distinct species of napu; while from the whole of Sumatra, as well as of that part of the Malay Peninsula extending north to Tenasserim, the napus are, so far as known, essentially of a single type.^a The characters of these animals, some of the more conspicuous of which are figured in Plates 1 to 3, are briefly as follows:^b

^a The common peninsular *Tragulus canescens* differs very slightly, if at all, from the Sumatran *T. napu*. In naming it I was under the misapprehension that the napu of Linga Island (*T. pretiosus*) represented the Sumatran animal. The little-known *Tragulus stanleyanus*, from the interior of the Malay Peninsula, may for the present be disregarded as perhaps not strictly a member of the *napu* group.

^b Detailed descriptions of the recently discovered species of *Tragulus* will be found in the following papers:

Bonhote, Ann. and Mag. Nat. Hist., 7th ser., vol. 11, pp. 291–296 (*hosei*, *everetti*, *pierreii=rarus* Miller.)

Lyon, Proc. U. S. Nat. Mus., vol. 31, pp. 576–581, (*bancanus*, *billitonis*, *luteicollis*); idem, vol. 34, pp. 628–632 (*longipes*, *fulvicollis*).

Matschie, Sitz.-Ber. Gesellschaft Naturforsch. Freunde, Berlin, 1897, p. 157 (*annae*).

Miller, Proc. Washington Acad. Sci., vol. 2, pp. 227–228 (*rufulus*) ; Proc. Biol. Soc. Washington, vol. 13, pp. 185–186 (*canescens*) ; idem, pp. 191–192 (*umbrinus*) ; Proc. Washington Acad. Sci., vol. 3, pp. 113–117 (*bunguranensis*, *pallidus*) ; Proc. Acad. Nat. Sci. Philadelphia, 1902, pp. 144–147 (*pretiosus*, *nigricollis*) ; Proc. Biol. Soc. Washington, vol. 15, pp. 173–175 (*rarus*, *borncanus*) ; Proc. U. S. Nat. Mus., vol. 26, pp. 439–446 (*amoenus*, *jugularis*, *brevipes*, *russicus*) ; Proc. Biol.

TRAGULUS NAPU (F. Cuvier). The wide-ranging form of Sumatra and the Malay Peninsula (Plate 1).

Upper parts orange-buff, clouded with blackish, the dark clouding not in excess of under color in general effect; sides noticeably grayish, in marked contrast with back; nape with a fairly well defined median dark stripe; throat markings normal, the outer dark band essentially concolor with sides of neck. Average and extremes of nine adults from eastern Sumatra: Head and body, 572 (550-600) mm.; tail, 94 (83-110); hind foot, including hoofs, 149 (145-156).

TRAGULUS PRETIOSUS Miller. Linga (Plate 2, upper figure).

Colors much richer and more yellow than in *Tragulus napu*, but pattern in no way abnormal; ground color of back orange-ochraceous, darkening toward ochraceous-rufous on sides of neck and outer surface of legs, and lightening to orange-buff on sides of body. Back uniformly clouded, the black slightly in excess of the under color; sides inconspicuously "lined" with black. Nape stripe blackish, normal in extent, sharply defined. Dark throat stripes a mixture of black and dull ochraceous-rufous. White throat stripes normal. Average and extremes of five adults: Head and body, 566 (545-580) mm.; tail, 88 (80-95); hind foot, including hoofs, 141 (140-142).

TRAGULUS PRETIELLUS Miller. Bakong and Sebang.

Color as in *Tragulus pretiosus*, but size less and teeth relatively larger. Average and extremes of eight adults from Pulo Bakong: Head and body, 501 (473-515) mm.; tail, 77 (65-90); hind foot, including hoofs, 122.7 (119-126).

TRAGULUS FORMOSUS Miller. Bintang.

Size and general appearance as in *Tragulus pretiosus*, but color even more reddish, particularly on sides of neck, and dark nape stripe narrower and less well defined. Average and extremes of seven adults: Head and body, 549 (530-593) mm.; tail, 82 (75-100); hind foot, including hoofs, 141.7 (137-145).

TRAGULUS LUTESCENS Miller. Sugi Bava, Jan.

Color pattern normal, the nape stripe clear black, well defined; size scarcely larger than in *Tragulus pretiellus*; ground color paler than in the three preceding species, the back orange-buff, fading rather abruptly on sides through straw-yellow to cream-color; clouding due to black hair tips, essentially as in *T. pretiosus* or somewhat less. Average and extremes of seven adults (two from Sugi Bava, the others from Jan): Head and body, 508 (488-540) mm.; tail, 78 (72-90); hind foot, including hoofs, 130 (128-133).

Soc. Washington, vol. 16, pp. 31-44 (*lutescens*, *flavicollis*, *formosus*, *focalinus*, *virgicollis*=*hosei* Bonhote, *natura*=*everetti* Bonhote, *subrufus*, *ruberus*, *ravulus*, *lanceensis*, *lampensis*); Smithsonian Misc. Coll., vol. 44, pp. 2-4 (*batnanus*, *russulus*); Proc. U. S. Nat. Mus., vol. 31, pp. 55-57 (*carimata*); idem, pp. 250-255 (*nigrocinctus*, *perflavus*, *pretiellus*).

Thomas, Ann. and Mag. Nat. Hist., 6th ser., vol. 9, p. 254 (*nigriceps*).

TRAGULUS FLAVICOLLIS Miller. Sugi.

General color about as in *Tragulus lutescens*, but nape stripe absent, its position barely indicated by a few dark hairs; throat markings normal, the dark stripes scarcely mixed with black; size probably greater than in *T. lutescens*: Head and body (type, not fully adult), 55 mm.; tail, 80; hind foot, including hoofs, 132.

TRAGULUS PERFLAVUS Miller. Batam, Bulan, Galong, Setoko (Plate 2, lower figure).

In general like *Tragulus flavicollis*, but even more yellow, the nape without dark hairs; dark throat stripes clear, brownish, ochraceous-buff, noticeably encroaching on area of white markings; size rather large. Average and extremes of six specimens from Batam: Head and body, 605 (583–635) mm.; tail, 80 (77–85); hind foot, including hoofs, 131 (127–137).

TRAGULUS NIGRICOLLIS Miller. Singkep (Plate 3, upper figure).

Back as in *Tragulus pretiosus*, but more clouded with black; sides a light buff much like that of *T. lutescens*; entire neck black, clear above, sprinkled with yellowish-brown annulations at sides, especially along edge of lateral white stripes; throat markings normal, the dark stripes black, speckled with brown like sides of neck. Size large, average and extremes of five adults: Head and body, 566 (540–590) mm.; tail, 81.4 (77–85); hind foot, including hoofs, 143.8 (138–148).

TRAGULUS NIGROCINCTUS Miller. Kunder, Great Karimon (Plate 3, lower figure).

Back and sides rich and dark, essentially as in *Tragulus pretiosus*, but black shading heavier, almost completely obscuring the under color along mid-dorsal region; neck and throat clear black, the throat stripes absent; no white on under parts, the lower side of tail yellowish brown, a character unique among the species occurring in the archipelago. Size medium, average and extremes of ten adult males from Kunder: Head and body, 502 (490–520) mm.; tail, 86.5 (80–100); hind foot, including hoofs, 136 (132–142).

The only general feature in which the insular species differ from *Tragulus napu* is their tendency toward richer, less grayish coloration, especially of the sides of body. In other respects they show great diversity. In fact, among them are presented the extreme phases of a tendency manifest throughout the *napu* group for each local species to assume a type of marking referable to some phase in one of the two lines of variation most readily^a followed in diverging from the primitive type represented by the continental form. The

^a A mere inspection of the manner in which the colors are combined in the normal pattern is sufficient to show that the two courses followed are mechanically the most feasible; this is further shown by the fact that the not very extensive individual variations in a large series of Sumatran *Tragulus napu* can nearly all be referred to the earliest stages of divergence of the same two lines.

main characters of this primitive type are: (1) Neck mixed brown and black, the black concentrating along nape to form an evident nape stripe; (2) throat with a median white longitudinal stripe, on each side of which is a similar but somewhat oblique stripe, the three meeting in a broad white mass covering posterior portion of interramial region; space between median and lateral stripe brown like side of neck or somewhat darker; a brown transverse band or collar separates the stripes from white of chest. The two lines of variation are (1) toward predominance of yellowish brown and (2) toward predominance of black.

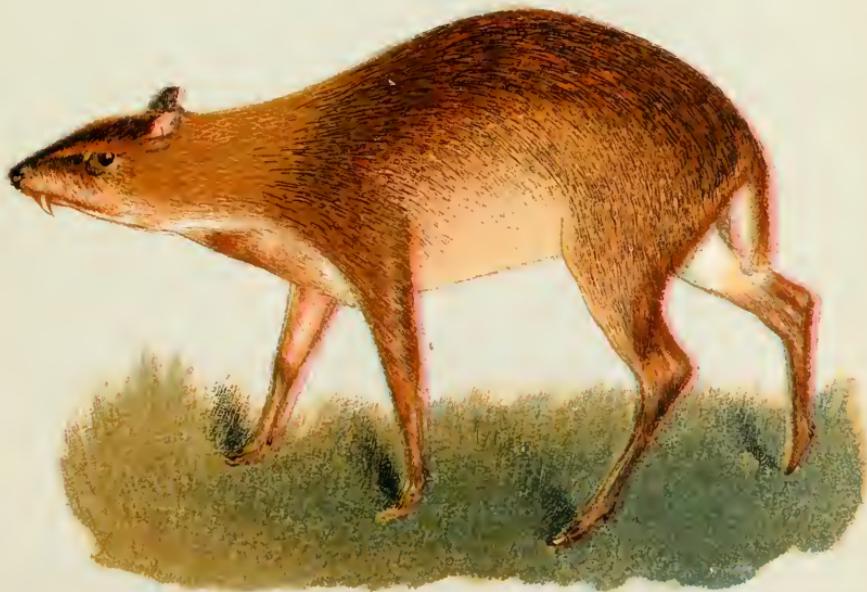
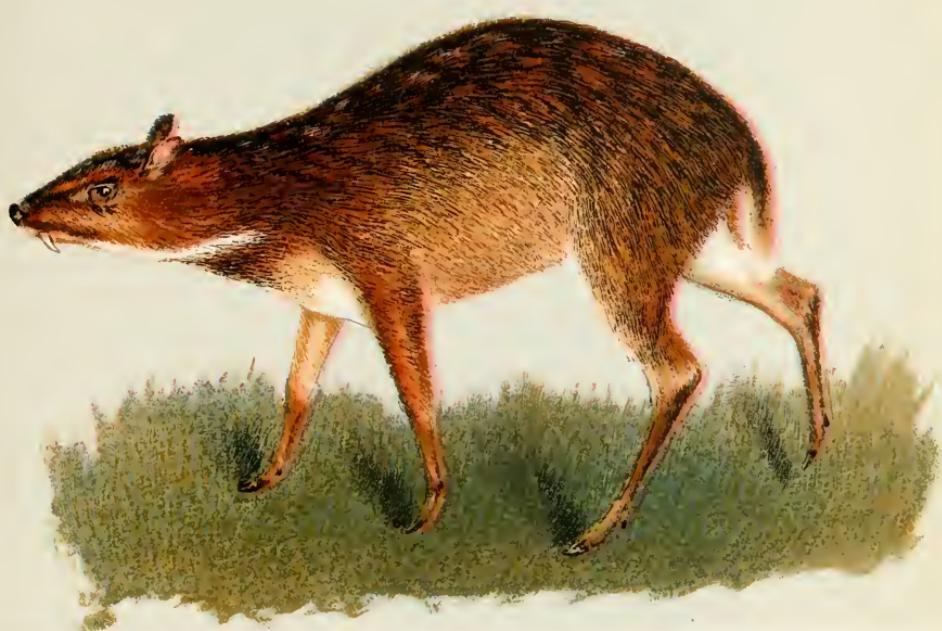
Variants of the primitive stage are shown by *Tragulus pretiosus* (color rich, pattern normal, size normal), *T. pretiellus* (like the last, but size reduced), and *T. lutescens* (size reduced, color yellowish, pattern normal). In *T. formosus* the first step is taken toward predominance of brown. The black nape stripe is narrower and less well defined than in the normal phase, though the throat markings retain their usual character. A further advance in the same direction is shown by *T. floricollis*, in which the nape stripe has disappeared, all but a few scattered dark hairs, but in which the throat markings remain normal. The extreme of this tendency, so far as now known, is presented by *T. perflavus*. Here the entire neck is yellowish brown without trace of dark hairs, and the white throat-stripes are noticeably narrowed by encroachment of the contiguous brown areas. The final stage, with white completely replaced by brown, has not yet been discovered, though there is little reason to doubt that it exists.

The first steps in the series leading toward dominance of black are not shown by any of the Rhio-Linga species. In *T. umbrinus* of Pulo Lankawi, off the west coast of the Malay Peninsula, the dark nape stripe has become diffuse, spreading over entire neck, though not to the exclusion of the brown. A further stage is represented by *T. amarus* of Pulo Mansalar, Tapamli Bay, west Sumatra. Here the neck is definitely black, though with much brown speckling at sides. Returning to the Rhio-Linga Archipelago, we find that in *T. nigricollis* the neck is black, slightly speckled with brown laterally; throat pattern normal. The next stage, in which the black begins to encroach on white of throat (corresponding to that represented by *T. perflavus* in the brown series), is represented by *T. bunguranensis* of Bunguran Island, North Natunas, and *T. nigricans* of Balabac. In *T. jugularis* of Pulo Mansalar the white is obliterated, but the position of the light markings is indicated by brown annulations on the hairs of the region normally occupied by the white stripes. The final stage is represented by a Rhio-Linga species, *T. nigrocinetus*, in which the entire neck and throat are clear black.

Allusion to the uniformity of environment under which the mouse deer exist has already been made. The geographic distribution of the various forms is a further indication that the characters of the species can not be explained as the result of local conditions. Linga and Singkep are only 7 miles apart, but the napu of the former has retained the primitive color pattern, while that of the latter is well advanced toward the dark extreme. The species representing intermediate stages are found 400 and 500 miles away, on the coasts of the Malay Peninsula and west Sumatra. Similarly the phase that lies between the Singkep form and the extreme represented by that of Kunder and Great Karimon occurs in the North Natuna Islands, at a distance of 300 miles, and on Balabac, more than twice as far away. On the other hand, the islands of Great Karimon and Bulang, within 25 miles of each other, are inhabited, respectively, by the most extreme black form and brown form now known.

The only conclusion that seems justified is that the *Tragulus napu* group consists of a series of local species whose color pattern, probably for some physiological reason, is varying along two main lines of divergence, both of which are independent of external conditions as ordinarily understood. Each series is equally incapable of explanation by the hypotheses of Lamarek, Darwin, or De Vries. On the larger land masses such changes as may be taking place are uniform over wide areas and relatively slow, while in the regions which, by submergence, have become divided into small land areas separated by water the changes are irregular and rapid, though progressing on different islands at a very unequal rate.^a

^aA somewhat parallel series of color changes in the African monkeys of the genus *Colobus* has recently been described (Lydekker, Proc. Zool. Soc. London, vol. 2, 1905, pp. 325-329).

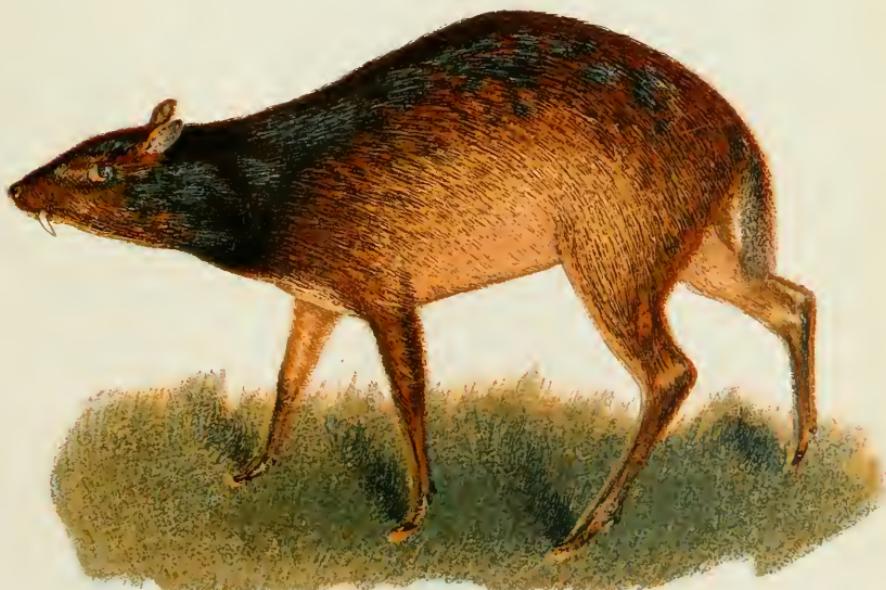


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