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AT HARVARD COLLEGE

Vol. 120, No. 1

THE HERPETOLOGY OF SOUTHERN RHODESIA
PART I. SNAKES

By Donald G. Broadley

Honorary Keeper of Herpetology,
National Museum of Southern Rhodesia

With Six Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March, 1959

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The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 1 — *The Herpetology of Southern Rhodesia. Part 1. Snakes.*

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CONTENTS

INTRODUCTION

This is the first comprehensive Check List of the Snakes of Southern Rhodesia to be published. The paper has been expanded to include much original ecological material and with the addition of a systematic key it should serve as a sound basis for the serpentology of the colony.

This work has been undertaken at the suggestion of Dr. E. E. Williams of the Museum of Comparative Zoology, after I had submitted a brief outline of the herpetology of Southern Rhodesia to Mr. Arthur Loveridge at that Museum.

The material examined consists of all the specimens in the National Museums of Southern Rhodesia at Bulawayo and Salisbury, plus a collection made by the Umtali Branch of the Herpetological Association of Rhodesia. I have also obtained the data for all Southern Rhodesian specimens in the Transvaal Museum and the British Museum (Natural History). Finally, I have examined a large number of snakes which were too badly decomposed or damaged to preserve. Altogether I have collated the data for 1385 specimens representing 61 species or races. Chubb's 1909 list contained 30 species from Matabeleland, and subsequent additions brought the total up to 52. The following forms are recorded from Southern Rhodesia for the first time:

Leptotyphlops longicauda (Peters)
Lycodonomorphus rufulus mlanjensis Loveridge
Meizodon semiornata semiornata (Peters)
Philothamnus ornatus Bocage
Prosymna sundevallii sundevallii (A. Smith)
Dromophis lineatus (Duméril and Bibron)
Psammophis angolensis (Bocage)
Aparallactus lunulatus lunulatus (Peters)
Naja melanoleuca Hallowell

There are very few taxonomic alterations. *Naja nigricollis mossambica* Peters is revived for certain light-coloured cobras with 21-25 midbody scale rows, which are found in Southern Rhodesia and Mozambique, extending north into Northern Rhodesia, Nyasaland and Tanganyika, and south into the Union of South Africa. Matabeleland specimens of *Aparallactus capensis* are regarded as intermediates between the typical form and the western race *bocagei*. Most specimens of *Atractaspis bibronii* from Southern Rhodesia prove to be intermediates between the typical form and the northern race *rostrata*.

Systematic Discussion. In this section is presented all the information at present available on the snakes of Southern Rhodesia. The subjects covered are best discussed under the headings employed.

Citations of literature. The original description of each form is given in full and these references are consequently omitted from the Bibliography on pp. 81-84. This is followed chronologically by every reference to Southern Rhodesian material in the herpetological literature that I have been able to trace.

Native Names. The present generation of Africans use very few names for snake species and the few that I have recorded were gleaned from the older men. There is much confusion among the younger generation. In Matabeleland, *Pimpi* is the name correctly applied to the Spitting Cobra (*Naja n. mossambica*), but it is now often applied to any grey or brown snake, even a female Boomslang (*Dispholidus typus*). A full list of English names is included in the systematic key on pp. 88-95.

Size. Where a specimen is referred to by a registered museum number, the following prefixes are used:

NM — National Museum of Southern Rhodesia, Bulawayo.
SM — Queen Victoria Museum, Salisbury.
UM — Umtali Museum, Umtali.
TM — Transvaal Museum, Pretoria.
MCZ — Museum of Comparative Zoology, Harvard.
BM — British Museum (Natural History).

Variation, Colouration, Size, Sexual dimorphism, Breeding, Diet, Parasites, Enemies, Defence, Venom, Habits and *Habitat.* These data are based on Southern Rhodesian material only.

Localities. Under this heading are listed: all Southern Rhodesian localities found in the literature; the localities of all specimens in the six museums listed above and the additional material examined by myself or members of the Herpetological Association of Rhodesia; a few localities are based on personal positive sight records.

Key to the Snakes of Southern Rhodesia. This is based purely on local material and the couplets do not necessarily hold good for other regions.

Plates and Text Figures. Live subjects were used for all the photographs. The text figures illustrating the key (Figs. 7-10) were personally drawn from local specimens.

ACKNOWLEDGEMENTS

The opportunity is taken of thanking Mr. Arthur Loveridge and Dr. E. E. Williams of the Museum of Comparative Zoology for their constant encouragement and advice leading to the production of this paper. I am indebted to Mr. Loveridge and Dr. Vivian FitzSimons of the Transvaal Museum for identifying specimens, answering numerous queries and supplying me with data for Southern Rhodesian material in their charge. I would also express my thanks to Mr. J. C. Battersby and Captain C. R. S. Pitman for supplying me with information on the relevant material in the British Museum (Natural History).

I am most grateful to Mr. R. H. Smithers and the staff of the National Museum of Southern Rhodesia for their help and cooperation. Much valuable material has been collected by the Herpetological Association of Rhodesia, particularly W. Arm-

itage, D. K. Blake and S. Warren of Umtali Branch and A. H. Siemers of Salisbury. Father K. Tasman, S.J., very generously supplied me with much useful information from his notes, compiled during many years of collecting in Rhodesia.

Thanks are also due to Dr. G. Theiler of the South African Veterinary Department for identifying the ticks, and Dr. F. Zumpt of the South African Institute for Medical Research for identifying the mites.

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TYPHLOPIDAE

TYPHLOPS DELALANDII Schlegel

Typhlops lalandii Schlegel, 1844, Abbild. Serp., p. 38, pl. xxxii, figs. 17-20.
Typhlops delalandii Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1910, p. 498; FitzSimons, F. W., 1912, pp. 52, 54.

Variation. (8 specimens.) Midbody scale rows 28. Diameter included in total length 41-50 times.

Colouration. Pink in life, each dorsal scale with a grey centre.

Size. Largest (NM/M.781) 295 (291+4) mm. from Bulawayo.

Habitat. One was found in a nest of small black ants under a stone at Richardson's Kop, Essexvale. An Irisvale specimen was taken in a pile of loose gravel on a quartz reef.

Distribution. South Matabeleland, extending as far north as Sawmills.

Localities. Sawmills; Bulawayo; Essexvale; Irisvale; Bembesi; Heany.

TYPHLOPS SCHLEGELII MUCRUSO (Peters)

Onychocephalus mucruso Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 621. FitzSimons, F. W., 1912, pp. 52, 54; Hewitt and Power, 1913, p. 160;
Typhlops mucruso Boulenger, 1902, p. 17; 1910, p. 498; Chubb, 1909a, p. 595; FitzSimons, F. W., 1912, pp. 52, 54; Hewitt and Power, 1913, p. 160; Tasman, 1953, p. 19; Rose, 1955, p. 75.
Typhlops schlegelii (not Bianconi), Boulenger, 1902, p. 17; 1910, p. 499 (part); FitzSimons, F. W., 1912, pp. 52, 54 (part).
Typhlops macruso (misprint), Chubb, 1909b, p. 35.
Typhlops dinga Boulenger, 1910, p. 499; FitzSimons, F. W., 1912, pp. 52, 54; Rose, 1955, p. 75.
Typhlops schlegelii mucruso FitzSimons, V. F., 1939, p. 20.
Typhlops schlegelii schlegelii Bogert, 1940, p. 15.

Native name of Zambezi Blind-Snake. *Inyorka umshlaba* (Sindebele); *N'dinga* (Cheshona).

Variation. (56 specimens.) Midbody scale rows 32-36. Diameter included in total length 21-53 times. These specimens cannot be separated from Northern Rhodesian material, so the typical form probably does not occur north of the Limpopo.

Colouration. Two colour varieties occur; 33 snakes represent the lineolate phase, which is blue-grey with dark-edged dorsal scales, becoming uniform brown with age; 23 snakes represent the blotched phase (var. *varius*), blue-grey to whitish, with irregular black blotches.

Size. Largest (UM/R.1) 817 (809+8) mm. from Umtali. Smallest (NM/M.780) 190 (187+3) mm. from Bulawayo. Seventeen specimens exceed 600 mm. in length.

Breeding. On 31.v.57 a 645 mm. ♀ from Bulawayo contained 37 eggs measuring 17 x 10 mm.

Diet. Termites and their larvae.

Enemies. A large specimen about two feet in length had been swallowed by a 40″ *Calamelaps u. miolepis* at Odzi.

Defence. When picked up, the blind-snake pushes its terminal spine into the hand of the captor, giving rise to the legend of a snake with a "sting" in its tail. Also it discharges the contents of the cloaca.

Habits. Often found wandering about on the surface during the rains. Small specimens are often found under stones, the adults apparently living at greater depths.

Distribution. Common throughout Southern Rhodesia.

Localities: Mazoe; Salisbury; Chishawasha; Marandellas; Monte Cassino; Inyazura; Odzi; Umtali; Odzani Falls; West Sebungwe; Gatooma; Selukwe; Turk Mine; Glenorchy, Insiza; Bulawayo; Matopos; Cyrene; Syringa; Empandene; Legion Mine; Bushtick Mine; Essexvale; Balla Balla; Irisvale; Sinkukwe; Stanmore; Chikore; Mount Silinda.

LEPTOTYPHLOPIDAE

LEPTOTYPHLOPS CONJUNCTA (Jan)

Stenostoma conjunctum Jan, 1861, Arch. Zool. Anat. Fisiol., vol. 1, p. 189.

Glauconia conjuncta Boulenger, 1910, p. 500; FitzSimons, F. W., 1912, pp. 56, 57.

Leptotyphlops conjuncta FitzSimons, V. F., 1939, p. 20; Rose, 1955, p. 75.

?*Leptotyphlops emini* (not Boulenger) Bogert, 1940, p. 14.

Variation. (6 specimens.) Midbody scale rows 14.

Colouration. Black, blue-grey when about to slough.

Size. Largest (UM/R. 30) 156 (140+16) mm. from Umtali.

Habitat. Taken under stones on a hillside at Umtali and under a stone within a few yards of the Tanganda River.

Distribution. Eastern districts of Southern Rhodesia.

Localities: Umtali; Changadzi River; Tanganda River; Mount Silinda; Charter Estates.

LEPTOTYPHLOPS SCUTIFRONS (Peters)

Stenostoma scutifrons Peters 1854, Monatsb. Akad. Wiss. Berlin, p. 621.
Glauconia nigricans (not Schlegel) Boulenger, 1902, p. 17.
Glauconia scutifrons Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1910, p. 500; FitzSimons, F. W., 1912, pp. 56, 57.

Variation. (29 specimens.) Midbody scale rows 14.

Colouration. Silver-grey to black.

Size. Largest (NM/M .921) 223 (209+14) mm. from Balla Balla.

Diet. Small termites and their larvae.

Habitat. Usually taken under stones or uncovered during gravel-pit clearing operations. Sometimes found wandering about on the surface during the rains.

Distribution. Common throughout Mashonaland and Matabeleland.

Localities: Mount Hampden; Salisbury; Chishawasha; Gatooma; Bulawayo; Essexvale; Balla Balla; Irisvale; Glass Block; Stanmore.

LEPTOTYPHLOPS LONGICAUDA (Peters)

Stenostoma longicaudum Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 621.

Variation. (11 specimens.) Midbody scale rows 14. Diameter into length 51-71 times. Tail length .13 to .18 of the total.

Colouration. Flesh pink to pale brown above (in life), flesh pink below.

Size. Largest (NM/M.1400) 205 (178+27) mm. from Irisvale.

Breeding. The largest specimen contained two eggs on 22.xi.57; these measured 21 x 4 mm.

Habitat. Ten specimens were taken, together with four *Leptotyphlops scutifrons*, on a quartz reef, well wooded but with little undergrowth. Another snake was taken on a granite outcrop three miles away.

Distribution. These are the first specimens to be taken south of the Zambezi since Peters described the species from Tete.

Localities: Irisvale.

BOIDAE

PYTHON SEBAE (Gmelin)

Coluber Sebae Gmelin, 1788, Syst. Nat. (ed. 13), p. 1118.

Python sebae Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1910, p. 442; FitzSimons, F. W., 1912, p. 58; Tasman, 1953, p. 18; Isemonger, 1955, p. 66.

Native Name of Python. *Shatu* (Cheshona and Sindebele).

Variation. (16 specimens.) Midbody scale rows 81-89; ventrals 270-284; subcaudals 63-81. Tail length .10 to .13 of the total.

Size. Largest 3810 (3430+380) mm. from Umtali.

Breeding. On 24.xii.56 a 13-foot ♀ was discovered coiled round her eggs in a hole in a bank beside a small dam near Umtali. Three newly hatched young were basking outside the hole. A coil of the mother was visible from outside. As I pulled out the big python the leathery shelled eggs split open and I had to remove handfuls of young snakes at intervals in order to avoid crushing them. Only three unruptured eggs remained and these hatched the same evening, bringing the total number of hatchlings to 39. This clutch appeared to be 100 per cent fertile. The hatchlings measured between 600 mm. and 633 mm. in total length.

Diet. A python killed at Salisbury contained a Springhare (*Pedestes cafer*). Captive specimens consumed various dead mammals and birds: rats (*Rattus, Tatera, Mus* spp.); hares (*Lepus saxatilis micklemi*); hyraxes (*Heterohyrax syriacus rhodesiae*); muishond (*Ictonyx s. striatus*); genet (*Genetta felina pulchra*); nightjars (*Caprimulgus* spp.); colies (*Urocolius indicus pallidus*). The hatchlings fed freely on rats and small birds and one took a shrew (*Crocidura* sp.).

Parasites. Ticks found in the nostrils of the Umtali ♀ were identified by Dr. Theiler as *Amblyomma nuttalli* and *Aponomma exornatum*.

Habits. Sluggish during the day, when much of the time is spent in basking. Becomes more active after dark, when most of the hunting is probably done. The python shows the usual serpentine lack of intelligence when feeding. The prey, when manipulated to suggest that it is alive, is seized and held by the numerous sharp recurved teeth, while several coils are rolled around it. The snake constricts until it feels that life is extinct, then begins to search for the head with flickering tongue. This search may last for up to half an hour if the head happens to be concealed by the coils. When the head is finally discovered, the python gapes and commences to swallow the prey head first. The animal is usually held by a coil to enable the snake to pull against it. An adult python has considerable difficulty in swallowing a small rat or bird, as the prey is not large enough to hold with a coil. The snake usually gets the animal across the jaws and has to juggle with it to arrange it lengthways.

Habitat. An 8½-foot ♀ was found basking at the top of a bank above a small stream at Chishawasha; only 100 yards away was a native kraal. The python slid down the bank and into the stream, where I discovered her coiled up close to the bank with only her nostrils showing above the water. Pythons are rarely found at any great distance from water.

Distribution. Widely distributed throughout Southern Rhodesia.

Localities: Mazoe; Salisbury; Domboshawa; Chishawasha; Nyamaropa; Odzi; Old Umtali; Umtali; Mtao Forest; Selukwe; Umshagashe River; Fort Victoria; Shabani; Bulawayo; Fort Usher; Syringa; Springvale; Essexvale; Beitbridge; Matopos.

COLUBRIDAE

COLUBRINAE

LYCODONOMORPHUS RUFULUS RUFULUS (Lichtenstein)

Coronella rufula Lichtenstein, 1823, Verz. Doubl. Mus. Berlin, p. 105.

Ablabophis rufulus Boulenger, 1896, p. 318; FitzSimons, V. F., 1939, p. 21; Tasman, 1953, p. 35; Isemonger, 1955, p. 67.

Lycodonomorphus rufulus Rose, 1955, p. 90.

Lycodonomorphus rufulus rufulus FitzSimons, V. F., 1958, p. 209.

Variation. (22 specimens.) Midbody scale rows 19; ventrals 166-175; anal entire (divided in one Glen Lorne snake); subcaudals 55-74; upper labials 8, the fourth and fifth entering the orbit[1]; lower labials 8, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2. Tail length .18 to .27 of the total.

Colouration. Dark brown to olive above. Below, pinkish or

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[1] Rarely 9, the first five in contact with the anterior sublinguals (one Vumba Snake).

yellowish, subcaudals with a dark median line, dark edged, or uniform greyish.

Size. Largest ♂ (T.M.22408) 575 (432+143) mm. from Pungwe Causeway. Largest ♀ (NM/M.625) 691 (567+124) mm. from Glen Lorne, Salisbury.

Diet. A juvenile taken at Leopard Rock, Vumba Mountain, disgorged a large sedge frog (*Hyperolius* sp.). Captive snakes from the same locality took frogs (*Rana* spp.), constricting only the larger ones.

Habitat. Six large adults were killed in the foundations of a bridge demolished at Glen Lorne, Salisbury. Two juveniles taken at Leopard Rock were under stones on the edge of two shallow dams, which were the breeding grounds of enormous numbers of *Kassina senegalensis.* One of these snakes shared its retreat with a Vumba Skink (*Scelotes arnoldi*).

Distribution. Mashonaland and the Eastern Districts of Southern Rhodesia. None of these Water-Snakes seems to have been recorded from Matabeleland since the single specimen, without a precise locality, listed by Boulenger in 1896.

Localities: Glen Lorne, Salisbury; Pungwe Causeway; Vumba Mountain; "Matabeleland."

LYCODONOMORPHUS RUFULUS MLANJENSIS Loveridge

Lycodonomorphus rufulus mlanjensis Loveridge, 1953, Bull. Mus. Comp. Zool., vol. 110, p. 253.

Variation. (3 specimens.) Midbody scale rows 21; ventrals 164-166; anal entire; subcaudals 56-73; upper labials 8, the fourth and fifth entering the orbit; lower labials 8, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2. Tail length of ♂ .25 of total, of ♀ .18 of total.

Colouration. Glossy olive-black above. Upper and lower labials white, lowest lateral scale row and edges of preceding one white. Immaculate white below, tail with a dark median line.

Size. ♂ (NM/M. 619) 460 (340+120) mm. from Nyamaropa. ♀ (UM/R. 37) 700 (575+125) mm. from Nyamaropa.

Breeding. A ♀ from the Macheke River, near Monte Cassino, contained 10 eggs (Tasman, *in litt.*).

Habitat. The ♂ was taken by W. W. Armitage in a boulder-strewn stream at Nyamaropa, north of Inyanga.

Distribution. Northeastern corner of Southern Rhodesia. *Localities:* Nyamaropa; Monte Cassino.

BOAEDON FULIGINOSUS FULIGINOSUS (Boie)

Lycodon fuliginosus Boie, 1827, Isis von Oken, vol. 20, col. 551.

Boodon lineatus Boulenger, 1902, p. 17; 1910, p. 446; Chubb, 1909a, p. 595; 1909b, p. 35; FitzSimons, F. W., 1912, p. 84; Hewitt and Power, 1913, p. 161.

Boaedon lineatus FitzSimons, V. F., 1939, p. 21; Tasman, 1953, p. 35: Rose, 1955, p. 89.

Boaedon lineatum Isemonger, 1955, p. 68.

Boaedon fuliginosus fuliginosus Loveridge, 1957, p. 251.

Variation. (70 specimens.) Midbody scale rows 26-33 (i.e., 26 in 1; 27 in 18; 28 in 1; 29 in 31; 31 in 3; 33 in 2); ventrals 198-228; anal entire; subcaudals 45-68; upper labials 8, the fourth and fifth entering the orbit; lower labials 8-10, the first three or four in contact with the anterior sublinguals; loreal 1; preoculars 1 or 2; postoculars 2; temporals 1+2 (usual), 1+3 (2+3 in one Bulawayo snake). Tail length .11 to .17 of the total.

Colouration. Dark red-brown to yellow-brown above, a light grey "V" extending from the snout through the upper eye to the back of the head. This marking is distinct in juveniles, less so in adults. Juveniles often have dark maroon spots and mottled stripes on the body, but these markings usually fade out in the adult. Below, "mother of pearl" white.

Size. Largest ♂ 725 (600+125) mm. from Umtali. Largest ♀ 1170 (1040+130) mm. from Umtali.

Sexual dimorphism. In 22 males the range of ventrals is 198-216; the range of subcaudals is 56-68; and the tail is .14 to .17 of the total length. In 34 females the range of ventrals is 210-226; the range of subcaudals is 45-57; and the tail is .11 to .13 of the total length.

Breeding. Captive snakes found in coitu on 16th and 17th of September. A captive 705 mm. ♀ laid 7 eggs on 10th November.

Diet. Juveniles subsist mainly on lizards; adults take rats. This powerful constrictor can kill a full-grown rat in a matter of seconds. Captive snakes have taken skinks (*Mabuya s. striata; Mabuya v. varia; Mabuya q. margaritifer*) and rats. Captive specimens at Umtali took frogs (*Rana* spp.) and one ate a shrew. One small snake, 487 mm. in length, swallowed four *Mabuya v. varia* in three days.

Enemies. A small House-Snake was found near Mount Hampden with its head and neck devoured, the trade mark of a mongoose.

Habits. Never found abroad during the day, the House Snake emerges at dusk to hunt. Although it may bite fiercely and draw blood when captured, this snake soon becomes docile with a little handling.

Habitat. Ubiquitous, but most plentiful around human settlements, where skinks and rats abound. Young snakes are often found under stones and rubbish heaps. I found one specimen under a stone in a waterlogged pasture on Vumba Mountain, a more suitable spot for *Lycodonomorphus* or *Natriciteres!*

Distribution. Common throughout Southern Rhodesia.

Localities: West Sebungwe; Trelawney; Mazoe; Mount Hampden; Salisbury; Marandellas; Odzi; Umtali; Vumba Mountain; Nyamashatu River; Mount Silinda; Que Que; Gwamayaya River; Shangani River; Sawmills; Bulawayo; Khami; Westacre; Empandene; Essexvale; Irisvale; Selukwe; Bembesi; Heany; Mount Darwin.

LYCOPHIDION CAPENSE CAPENSE (A. Smith)

Lycodon capensis A. Smith, 1831, S. African Quart. Journ., vol. 1, p. 18.

Lycophidium capense Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1910, p. 447; FitzSimons, F. W., 1912, p. 85; Hewitt and Power, 1913, p. 162.

Lycophidion capense capense FitzSimons, V. F., 1939, p. 21.

Lycophidion capense Tasman, 1953, p. 35; Rose, 1955, p. 92.

Lycophidion capensis Isemonger, 1955, p. 68.

Variation. (51 specimens.) Midbody scale rows 17; ventrals 165-192; anal entire; subcaudals 25-39; upper labials 8, the third, fourth and fifth entering the orbit; lower labials 8, the first five in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2. Tail length .08 to .14 of the total.

Colouration. Jet black to brownish black above, each scale tipped with white. Below, uniform white or uniform steel-grey to brownish, more often white with dark blotches. Head black, uniform or with an intricate pattern of fine white lines. A specimen from Westacre differed from all others examined in having a double row of large black dorsal blotches against the normal black and white speckled background.

Size. Largest 504+ (470+34+) mm. from Salisbury. Smallest (NM/M. 297) 155 (140+15) mm. from Bulawayo.

Breeding. The very large female recorded above laid 5 eggs in early November. On 16th December at Bulawayo a 405 mm. ♀ contained 7 eggs measuring 21 X 10 mm. On 29th December at Bulawayo a 340 mm. ♀ contained 6 eggs measuring 18 X 7 mm. Another 367 mm. Bulawayo ♀ contained 4 eggs measuring 22 X 10 mm.

Diet. The Cape Wolf-Snake seems to subsist almost entirely on skinks. *Mabuya s. striata* and *Mabuya v. varia* are taken readily by captive snakes; stomachs examined invariably contained the same species or *Ablepharus wahlbergii.*

Habits. A nocturnal species, often found under stones and rubbish during the day. Only once have I found one in the open during the hours of daylight; this snake was basking in the afternoon sun on a newly cut firebreak near Mount Hampden.

Distribution. Common in Mashonaland and Matabeleland, this species seems to be rather scarce in the Eastern Districts.

Localities: Trelawney; Mount Hampden; Salisbury; Hunyani; Chishawasha; Marandellas; Odzi; Umtali; Mount Silinda; Selukwe; Matetsi; Fatima; Lupane; Sawmills; Nyamandhlovu; Turk Mine; Bulawayo; Matopos; Westacre; Irisvale; Lumane; Bembesi.

MEHELYA CAPENSIS CAPENSIS (A. Smith)

Heterolepis capensis A. Smith, 1847, Ill. Zool. S. Africa, pl. lv.

Simocephalus capensis Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1910, p. 506; FitzSimons, F. W., 1912, p. 85.

Mehelya capensis capensis Loveridge, 1939, p. 142 (Generic revision).

Mehelya capensis Tasman, 1953, p. 35; Rose, 1955, pp. 91, 92; Isemonger, 1955, p. 69.

Native name of Cape File-Snake. *N'kwakwa* (Sindebele); *N'dara* (Cheshona).

Variation. (17 specimens.) Midbody scale rows 15; ventrals 195-220; anal entire; subcaudals 44-58; upper labials 7, the third and fourth entering the orbit (one Essexvale snake has 8 labials on one side and 7 on the other, where only the third enters the orbit); lower labials 8, the first four in contact with the anterior sublinguals; loreal 1; preocular 1; postoculars 2; temporals 1+2 (2+3 on one side of an Essexvale snake). Tail length .11 to .14 of the total.

Colouration. Purplish brown to black above, the vertebral rows of prominent bicarinate scales ivory white, outer scale rows white at the base, exposed skin between the widely spaced scales mauve. Below, ivory white with dark markings at the ends of the ventrals.

Size. Largest ♂ 1220+ (1085+135+) mm. from Irisvale. Largest ♀ (NM/M. 1769) 1625+ (1500+125+) mm. from 14 miles north of Bulawayo.

Breeding. On 15.x.57 a 4-foot Irisvale ♀ contained 5 eggs, measuring 55 X 20 mm. She was killed in a cattle pen, where she may have retired to lay.

Diet. A 53-inch ♀, killed after dark in a native hut at Essexvale, was engaged in swallowing an adult skink (*Mabuya s. striata*). Another Essexvale snake disgorged a toad (*Bufo carens*) after capture. A captive Essexvale ♂ took a 9-inch White-lipped Snake (*Crotaphopeltis h. hotamboeia*), seizing it in the middle of the body and swallowing it without any attempt at rearrangement. He also took toads (*Bufo regularis* and *Bufo carens*). He showed no interest in juvenile *Psammophis s. subtaeniatus* or *Causus defilippii*, but was terrified of a young *Naja n. mossambica*. A Bulawayo snake contained an adult *Agama cyanogaster*.

Parasites. The extensive areas of exposed skin between the widely spaced scales of this species make it particularly vulnerable to the attentions of ticks (*Aponomma latum*). My captive Essexvale ♂ succumbed to nematodes.

Defence. A four-foot Essexvale ♀ constricted my wrist when captured and emitted a cloacal discharge, unpleasant, but not in the same class as that of the common English *Natrix*. Neither of my captive specimens ever attempted to bite.

Habits. Strictly nocturnal and most in evidence during the rains. Most of the specimens examined were either killed in native huts or were road casualties. One was captured while hunting toads on a veranda and another had fallen into a reservoir with vertical sides.

Distribution. Throughout Southern Rhodesia.

Localities: Trelawney; Salisbury; Chishawasha; Odzi; Tanganda River; Selukwe; Bulawayo; Figtree; Essexvale; Balla Balla; Irisvale; Filabusi; Mavuradona Mts.; Mount Darwin; Glass Block.

MEHELYA NYASSAE (Günther)

Plate 2, upper figure

Simocephalus nyassae Günther, 1888, Ann. Mag. Nat. Hist., ser. 6, vol. 1, p. 328.

Mehelya nyassae Bogert, 1940, p. 25; Isemonger, 1955, p. 69.

Variation. (5 specimens.) Midbody scale rows 15; ventrals 173-184; anal entire; subcaudals 60-68; upper labials 7, the third and fourth entering the orbit; lower labials 8, the first five in contact with the anterior sublinguals; preocular 1; postocular 1; temporals 1+2 or 1+3. Tail length .18 to .20 of the total (but truncated in 2 snakes).

Colouration. Above, blackish brown, skin between scales pink. Below, paler brown, each ventral edged with white.

Size. Largest (NM/M. 1079) 575 (470+105) mm. from Fatima.

Distribution. Widely distributed throughout Southern Rhodesia.

Localities: Fatima; Umtali; Mount Silinda.

NATRICITERES OLIVACEA OLIVACEA (Peters)

Coronella olivacea Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 622.

Tropidonotus olivaceus Boulenger, 1910, p. 455; FitzSimons, F. W., 1912, p. 82; Tasman, 1953, p. 35.

Natriciteres olivacea olivacea Loveridge, 1953, p. 250 (Generic Key).

Neusterophis olivaceus Rose, 1955, p. 92; Isemonger, 1955, p. 67.

Native Name of Olive Marsh-Snake. *Vusamanzi* (Sindebele).

Variation. (17 specimens.) Midbody scale rows 19; ventrals 140-149; anal divided; subcaudals 63-70; upper labials 8, the fourth and fifth entering the orbit; lower labials 9-10, the first five in contact with the anterior sublinguals; preocular 1; postoculars 3, rarely 2 (both sides of a Selukwe snake); temporals 1+2. Tail length .22 to .28 of the total (but often truncated).

Colouration. Above, dark slate-grey to dark olive, with a dorsal stripe 5 scales wide, which is bordered with minute white dots. This stripe is usually, but not always, darker than the rest of the body; in some specimens it is a handsome maroon shade. Below, yellow or orange, with the outer third of the ventrals on either side slate-grey or olive. Upper labials white with black sutures.

Size. Largest (SM/R. 17) 527 (407+120) mm. from Victoria Falls. Smallest (NM/M. 963) 152 (115+37) mm. from Selukwe.

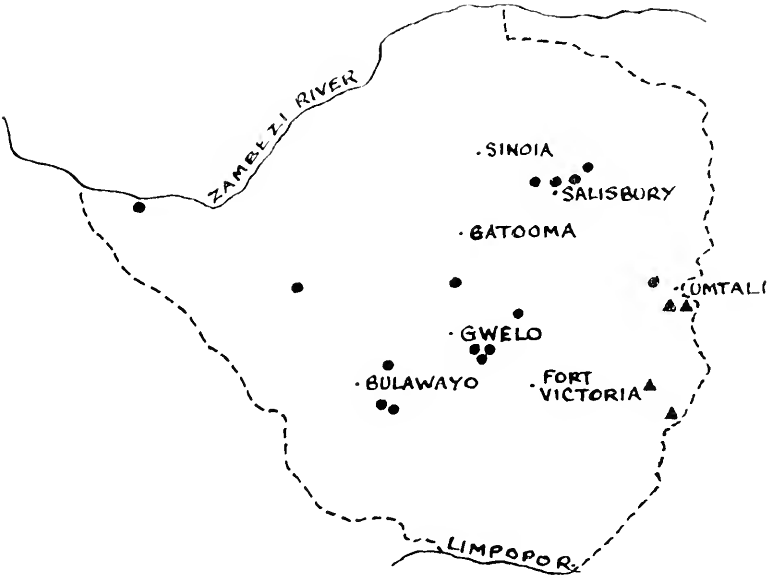

Fig. 1. Recorded localities for *Natriciteres.*
● *Natriciteres olivacea olivacea* (Peters)
▲ *Natriciteres olivacea uluguruensis* (Loveridge)

Diet. Captive specimens feed readily on small frogs (*Rana* spp.; *Kassina senegalensis; Phrynobatrachus natalensis*) and ranid tadpoles.

Enemies. A high percentage of specimens have truncated tails, due to the attentions of birds of prey, particularly the Hammerhead (*Scopus umbretta*), and crabs.

Habitat. This species prefers vleis and marshes to open streams. One specimen was taken under a stone in a vlei at Mount Hampden and another under a pile of stones in a stream bed at Domboshawa. Two were killed in the foundations of an old bridge demolished at Glen Lorne, Salisbury. At Essexvale, one snake was resting on rocks beside a dam spillway, another was found in a garden. A large specimen turned up on the Guardroom veranda at Lewellin Barracks, Heany.

Distribution. Mashonaland, extending east to Odzi, where it meets with the race *uluguruensis.* North Matabeleland, extending as far south as Essexvale.

Localities: Mount Hampden; Salisbury; Glen Lorne; Domboshawa; Odzi; Victoria Falls; Fatima; Que Que; Driefontein; Selukwe; Heany; Essexvale.

NATRICITERES OLIVACEA ULUGURUENSIS (Loveridge)

Natrix olivacea uluguruensis Loveridge, 1935, Bull. Mus. Comp. Zool., vol. 79, p. 7.

Natrix olivaceus (not Peters) FitzSimons, V. F., 1939, p. 20.

Natriciteres olivacea uluguruensis Loveridge, 1953, pp. 251, 252.

Variation. (12 specimens.) Midbody scale rows 17, rarely 15 (NM/M. 629 from Vumba Mtn. only)[1]; ventrals 132-141; anal divided; subcaudals 62-72; upper labials 8, the fourth and fifth entering the orbit; lower labials 8, the first four in contact with the anterior sublinguals; preocular 1; postoculars 3; temporals 1+2. Tail length .26 to .29 of the total.

Colouration. Blackish, slate-grey or olive above, with a darker dorsal stripe 5 scales wide, which is bordered by minute white dots. Below, bright orange or yellow, with the dorsal colouration extending onto the ends of the ventrals. Specimens from Chirinda Forest are described by Dr. V. FitzSimons as grey-brown or reddish above, with a blackish dorsal stripe; yellow to yellowish white below, the ends of the ventrals being grey or bright red, the latter colour extending onto the subcaudals.

Size. Largest (UM/R. 20) 396 (280+116) mm. from Vumba Mountain.

Habitat. One Vumba snake taken beside the spillway of a dam, others under stones beside small dams and another under a stone

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[1] Rarely 19 (NM/M. 1952 from Vumba Mtn. only).

on the edge of a strip of riverine forest. Dr. V. FitzSimons took three specimens as they basked on the edges of clearings in the Chirinda Forest.

Distribution. The Eastern Districts of Southern Rhodesia.

Localities: Vumba Mountain; Nyamashatu River; Sabi Experimental Station; Chirinda Forest.

MEIZODON SEMIORNATA SEMIORNATA (Peters)

Coronella semiornata Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 622.

Data of unique specimen. Midbody scale rows 21; ventrals 184; anal entire; subcaudals 74; upper labials 8, the fourth and fifth entering the orbit; lower labials 8, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2. Tail length .24 of the total.

Colouration. Above, grey, with black staggered cross-bars, broad on the neck becoming narrower and fading out soon after midbody. Head black, pre- and postoculars and the labials immediately below them white; a light cross band immediately behind the parietals. Chin white, ventrals and subcaudals black, edged with white.

Size. (NM/M. 870) 345 (262+83) mm. from Sebungwe.

Breeding. This specimen contained two eggs.

Distribution. Probably confined to the Zambezi valley.

Localities: Sebungwe.

PHILOTHAMNUS HOPLOGASTER (Günther)

Ahaetulla hoplogaster Günther, 1863, Ann. Mag. Nat. Hist., ser. 3, vol. 11, p. 286.

Chlorophis natalensis (not Smith), Boulenger, 1902, p. 17.

Chlorophis hoplogaster Boulenger, 1910, p. 507; FitzSimons, F. W., 1912, pp. 86, 87; Hewitt and Power, 1913, p. 162; FitzSimons, V. F., 1939, p. 22; Tasman, 1953, p. 35; Rose, 1955, p. 93; Isemonger, 1955, p. 70.

Chlorophis neglectus Boulenger, 1910, p. 507; FitzSimons, F. W.. 1912, pp. 86, 87; Rose, 1955, p. 93; Isemonger, 1955, p. 70.

Philothamnus hoplogaster Broadley, 1957a, p. 53.

Variation. (30 specimens.) Midbody scale rows 15; ventrals 148-160; anal divided; subcaudals 77-103; upper labials 8, the fourth and fifth entering the orbit (an Umtali snake has only 7 labials on one side, the third and fourth entering the orbit);

lower labials 9-11, the first four or five in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+1. Tail length .25 to .30 of the total.

Colouration. Light blue-green to grass-green above, olive-green when about to slough; white below. Some specimens have up to a dozen black blotches on the neck.

Size. Largest (B.M. 02.2.12.87), 945 (685+260) mm. from Mazoe. Smallest (SM/R. 19) 234 (164+70) mm. from Odzi.

Breeding. A 618 mm. ♀ from Cleveland Dam laid 4 eggs on 18.xi.55. A 484 mm. ♀ from the Umvumvumvu River laid 4 eggs measuring 28 x 9 mm. on 20.i.57.

Diet. A Cleveland Dam snake fed readily in captivity on frogs (*Rana* spp.; *Hyperolius* spp.) and took a small skink (*Mabuya v. varia*).

Enemies. A Spitting Cobra (*Naja n. mossambica*), captured beside the N'sese River at Irisvale, disgorged the tail of a Southeastern Green Snake. At Selukwe I was given an account of a crab killing and devouring a small green snake, probably referable to this species.

Defence. Unlike the next two species of *Philothamnus*, this snake does not inflate the throat or try to bite when captured.

Habitat. At Salisbury *hoplogaster* frequents the reedy vleis to the west of the city, extending east to Cleveland Dam. In the more open sandveld streams farther east it is replaced by *P. i. irregularis.* The two species occur together in the Eastern Districts and at Selukwe.

Distribution. Common in Mashonaland and the Eastern Districts. Very scarce in Matabeleland.

Localities: Eldorado; Trelawney; Mazoe; Mount Hampden; Salisbury; Cleveland Dam; Odzi; Nyamaropa; Inbeza; Vumba Mountain; Umvumvumvu River; Haroni-Lusitu Junction; Chirinda Forest; Selukwe; Driefontein; Umshagashe River; Irisvale; Lumane; Mount Darwin.

PHILOTHAMNUS ORNATUS Bocage

Philothamnus ornatus Bocage, 1872, Jour. Sci. Lisboa, vol. 4, p. 80.

Data of unique specimen. Midbody scale rows 15; ventrals 161; anal divided; subcaudals 96; upper labials 9-10, the fourth, fifth and sixth (normally the third, fourth and fifth) entering the orbit;

lower labials 10, the first five in contact with the anterior sublinguals: preocular 1; postoculars 2; temporals 1+1. Tail length .30 of the total.

Colouration. Emerald green above, with a red-brown dorsal stripe three scales in width, narrowly edged with yellow. The anterior dorsal scales edged with black. Labials and belly white with a bronze tint.

Size. ♂ (NM/M.621) 599 (420+179) mm. from Reitfontein, Salisbury.

Discussion. I found this specimen freshly killed on the road where a bridge spans a vlei on the outskirts of Salisbury. It agrees well with a series of nine *ornatus* collected by Monsieur H. J. Bredo in the Mweru-wa-Ntipa area of Northern Rhodesia and examined by me through the courtesy of the Musée Royal d'Histoire Naturelle de Belgique. The Salisbury snake differs only in having the fourth, fifth and sixth upper labials entering the orbit instead of the third, fourth and fifth as in all nine of Bredo's specimens. The head of this species is more rounded in profile than that of *irregularis* and resembles *hoplogaster* more in this respect. In any case *ornatus* must be restored to specific status; its range in the Rhodesias overlaps that of *P. i. irregularis*, so it can no longer be regarded as a race of the latter.

Distribution. Uncertain.

Localities. Reitfontein, Salisbury.

PHILOTHAMNUS IRREGULARIS IRREGULARIS (Leach)

Coluber irregularis Leach, 1819, in Bowdich, Mission to Ashantee, p. 494.

Chlorophis irregularis Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1910, p. 508; FitzSimons, F. W., 1912, p. 87; FitzSimons, V. F., 1939, p. 22; Bogert, 1940, p. 53; Rose, 1955, p. 94; Isemonger, 1955, p. 70.

Philothamnus irregularis irregularis Broadley, 1957a, p. 53.

Variation. (35 specimens.) Midbody scale rows 15; ventrals 154-169; anal divided; subcaudals 94-115; upper labials 9 (10 on one side only of two snakes), the fourth, fifth and sixth (fifth, sixth and seventh on one side of a Nyamashatu River snake) entering the orbit; lower labials 9-11, the first five (rarely six) in contact with the anterior sublinguals; preocular 1; postoculars 2 (3 on one side of an Imbeza snake); temporals 1+1 or 1+2. Tail length .27 to .33 of the total length.

Colouration. Brilliant emerald green above, some scales on anterior part of body black edged, but not forming regular cross-bars. Below, light green to yellow green. Eye with a handsome golden iris.

Size. Largest (NM/M. 736) 978+ (898+80+) mm. from Umzilizwe River. Largest perfect specimen (NM/M.1471) 1106 (810+296) mm. from Umzilizwe River.

Rate of growth. A Domboshawa ♂ grew from 698 to 763 mm. in 12 months of captivity, during which time he consumed 19 frogs (*Rana*); 9 toads (*Bufo*) and a pigmy mouse (*Leggada* sp.). A Chishawasha ♂ grew from 779 to 798 mm. in 14 months of captivity, during which time he consumed 14 frogs and 13 toads.

Diet. Captive specimens fed readily on frogs (*Rana* spp.: *Hyperolius* spp.; *Phrynobatrachus natalensis*) and toads (*Bufo regularis; Bufo carens*); one took a pigmy mouse (*Leggada* sp.).

Defence. When captured or molested, this snake inflates its throat vertically and strikes fiercely. A large Chishawasha ♀ drew blood on my top lip as I was admiring my capture, then she left six rows of bleeding tooth marks on my proffered hand.

Habitat. The Western Green-Snake prefers open, free running streams with plenty of shade. At Chishawasha it was abundant where a small stream flowed between high banks with plenty of overhanging trees. Four of these snakes were killed in the foundations of the demolished bridge at Glen Lorne. One Chishawasha snake was living in a crab hole beside a culvert, where many natives came to wash their clothes. The species is plentiful in reedbeds along the Umzilizwe River and elsewhere in the Eastern Districts. Like *P. hoplogaster* it often rests in small trees overhanging the water.

Distribution. Mashonaland and the Eastern Districts, extending southwest to Selukwe.

Localities: Victoria Falls; Glen Lorne, Salisbury; Domboshawa; Chishawasha; Odzi; Imbeza; Umtali; Umvumvumvu River; Umzilizwe River; Chirinda Forest; Selukwe; Moonies Creek; Pungwe River. 2200′; Nyamashatu River.

PHILOTHAMNUS SEMIVARIEGATUS SEMIVARIEGATUS (A. Smith)

Dendrophis (*Philothamnus*) *semivariegata* A. Smith, 1840, Ill. Zool. S. Africa, Rept., pls. lix, lx, lxiv, figs. 1a, 1b.

Philothamnus semivariegatus Boulenger, 1902, p. 17; 1910, p. 508; Hewitt and Power, 1913, p. 162; Tasman, 1953, p. 35; Rose, 1955, p. 94; Isemonger, 1955, p. 71.

Philothamnus semivariegatus semivariegatus FitzSimons, V. F., 1939, p. 22; Broadley, 1957a, p. 53.

Native name of Variegated Bush-Snake. *N'dlondlo* (Sindebele), but is mistaken for a young Boomslang (*Dispholidus typus*).

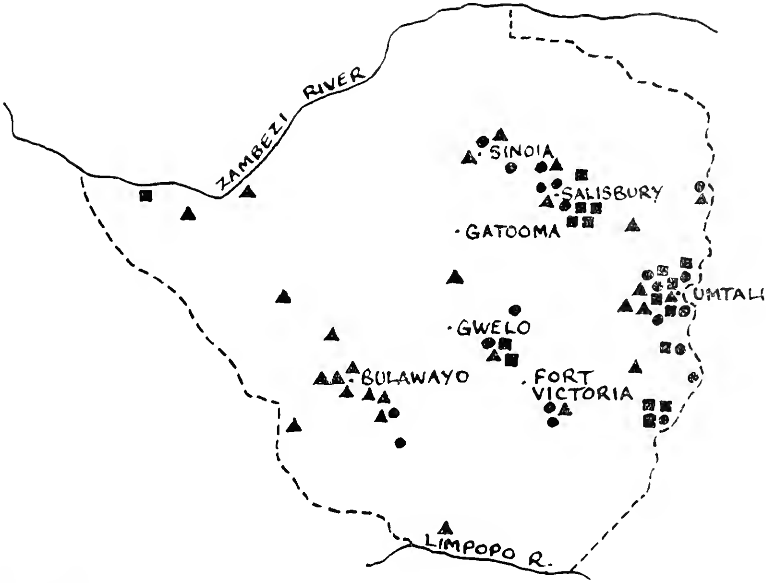

Fig. 2. Recorded localities for *Philothamnus.*
● *Philothamnus hoplogaster* (Günther)
■ *Philothamnus irregularis irregularis* (Leach)
▲ *Philothamnus semivariegatus semivariegatus* (A. Smith)

Variation. (31 specimens.) Midbody scale rows 15; ventrals 179-204; anal divided; subcaudals 121-142; upper labials 9, the fourth, fifth and sixth entering the orbit (10, the fifth, sixth and seventh entering the orbit, on one side only of a Bembesi snake); lower labials 10 (rarely 9), the first five (rarely 4) in contact with the anterior sublinguals; preocular 1; postoculars 2[1]; temporals 1+2 or 2+2. Tail length .28 to .34 of the total.

Colouration. Head blue-green, anterior third of the body blue-green with narrow black cross-bars, fading out to uniform bronze on the posterior of body and tail. Chin white, throat bright yellow, rest of underside cream. Eye with a golden iris.

Size. Largest 1108 (780+328) mm. from Umshagashe River.

Breeding. On 26.i.56 the huge Umshagashe ♀ laid 8 eggs, measuring 26 X 10 mm.

Diet. Captive specimens at Umtali feed freely on dwarf geckos (***Lygodactylus c. capensis***). The Umshagashe ♀ swallowed two frogs (***Rana*** sp.), but later disgorged them.

Defence. This snake is extremely truculent and is slow to settle down in captivity. The record specimen was found crawling slowly through the grass beside the Umshagashe River. She made no attempt to dash for cover, but inflated her throat vertically, at the same time lifting her head and neck to display the yellow patch and hissing fiercely. She struck viciously and repeatedly when picked up, drawing blood several times.

Habits. This species is more persistently arboreal than the two previous ones. Tasman (*in litt.*) states, "I have seen one (*P.s. semivariegatus*) go some way up the somewhat sloping trunk of a gum tree and later make quite a good jump to a lower stump or branch." The Bush-Snake has the same build and strongly keeled ventrals as the "Flying Snakes" (***Chrysopelea***) of Southeast Asia and it may be that it shares their ability to glide from tree to tree. Loveridge received reports of green snakes which behaved in his manner while he was collecting in Tanganyika, where *P.s. semivariegatus* is common.

Habitat. Most plentiful along shady streams with plenty of trees and bushes. This species is less dependent on water than the other species in the genus, feeding as it does mainly on geckos. I was called to remove a young Essexvale snake from the engine of a lorry, while another is recorded as having been found on the steps of the Bulawayo Public Library!

Distribution. Common throughout Southern Rhodesia, but most abundant in the eastern districts.

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[1] One on both sides of a Bembesi Snake (NM/M. 2060).

Localities: Sinoia; Eldorado; Mazoe; Salisbury; Monte Cassino; Kondo; Odzi; Umtali; Nyamaropa; Zambezi-Sebungwe Junction; Wankie; Fatima; Mohem Mine; Que Que; Selukwe; Bulawayo; Khami Dam; Essexvale; Irisvale; Empandene; Umshagashe River; Devuli River Bridge; Beitbridge; Umvuma; Bembesi.

PROSYMNA SUNDEVALLII SUNDEVALLII (A. Smith)

Plate 3, upper figure

Temnorhynchus sundevallii A. Smith, 1849, Ill. Zool. S. Africa, Rept., App., p. 17.

Variation. (2 specimens.) Midbody scale rows 15; ventrals ♂ 154, ♀ 181; anal entire; subcaudals ♂ 28, ♀ 23; prefrontal 1, but a small section split off above one eye in the ♀; internasals 2, separated by a median suture of the prefrontal and rostral; upper labials 6, the third and fourth entering the orbit; loreal 1; preocular 1; postoculars 2; temporals 2+2 or 2+3. Tail length .08 (♀) to .11 (♂) of the total.

Colouration. Purplish-brown above, with a dull red blotch on the frontal and parietals and a broad orange dorsal stripe, which is broken up by darker markings (see Plate). Lower one and a half lateral scale rows and ventrum white.

Size. ♂ (NM/M.1728) 284 (252+32) mm. from 8 miles south of Bulawayo. ♀ (NM/M. 635) 338 (311+27) mm. from Essexvale.

Discussion. Loveridge identified the ♀ as *Prosymna sundevallii bivittata*[1], but Dr. V. FitzSimons has examined the same specimen and regards it as a typical *sundevallii*. The ventral count of 181 is high for typical *sundevallii*, but I refer these snakes to the typical form until such time as further collecting can clarify the position.

Defence. When disturbed this snake coils and uncoils violently to try and intimidate the enemy.

Habitat. The ♀ was found under a stone on the verge of the main Bulawayo-Beitbridge road at Essexvale. The ♂ was taken at night by Mr. V. Hobbs, who found it lying in the middle of the same road, but only 8 miles from Bulawayo.

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[1] See Bull. Mus. Comp. Zool., vol. 119, p. 137.

Distribution. Matabeleland.
Localities: 8 miles south of Bulawayo; Essexvale.

PROSYMNA LINEATA (Peters)

Plate 3, lower figure

Temnorhynchus lineatus Peters, 1871, Monatsb. Akad. Wiss. Berlin, p. 568.

Variation. (7 specimens.) Midbody scale rows 15; ventrals ♂♂ 147-148, ♀♀ 157-170; anal entire; subcaudals ♂♂ 26, ♀♀ 17-23; prefrontal 1; internasals 2, forming a median suture; upper labials 6, the third and fourth entering the orbit; preocular 1; postoculars 2; temporals 1+2, 2+2 or 2+3. Tail length in the male .11, in the females .07 to .08 of the total.

Colouration. Head pale brown, a darker spot at junction of frontal and parietals, a dull orange blotch on the frontal, a dark line connecting the eyes along the rear edge of the prefrontal, a large dark blotch on the nape immediately behind the parietals. Body pale brown above, a paired vertebral series of dark brown longitudinal streaks, a similar series of lateral streaks; outer two scale rows and ventrum white. An Irisvale ♀ is a much darker brown than the rest.

Size. Largest ♂ (NM/M. 1889) 207 (180+27) mm. from Bulawayo. Largest ♀ (B.M. 02.2.12.00) 307 (282+25) mm. from Salisbury.

Discussion. These specimens were identified as *P. lineata* by Loveridge, but V. FitzSimons regards them as *P. sundevallii* and reports (*in litt.*) that 25 specimens in the Transvaal Museum collection show every stage from internasals in good contact to widely separated. I have not examined any extralimital material, but there certainly seem to be two distinct species in S. Rhodesia. clearly distinguished by scale counts, habitus and colouring. I follow Loveridge[1] and refer these specimens to *P. lineata* until such time as this difficult genus can be fully revised.

Defence. When disturbed, this snake coils and uncoils violently like a watch spring.

Habitat. A small male was discovered on the surface during gravel pit clearing operations on a quartz reef at Balla Balla, where the topsoil was grey sand. An adult ♀ was found lying

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[1] See Bull. Mus. Comp. Zool., vol. 119, p. 138.

in the hot sun, beside a road leading to a gravel pit at Government House, Bulawayo. She died a few hours later. Another big ♀ was taken while she was digging a hole in the bare sandy soil of a firebreak at Irisvale.

Distribution. Widely distributed, but scarce.

Localities: Salisbury; Selukwe; Bulawayo; Plumtree; Balla Balla; Irisvale.

PROSYMNA AMBIGUA STUHLMANNI (Pfeffer)

Ligonirostra stuhlmanni Pfeffer, 1893, Jahrb. Hamburg Wiss. Anst., vol. 10, p. 78, pl. 1, figs. 8-10.

Prosymna ambigua (not Bocage) Boulenger, 1902, p. 17; 1910, p. 509; Fitz-Simons, F. W., 1912, p. 88; Isemonger, 1955, p. 71.

Variation. (6 specimens.) Midbody scale rows 15; ventrals 132-153 (162); anal entire; subcaudals 23-31; prefrontal 1; internasal 1; upper labials 6, the third and fourth entering the orbit; preocular 1; postoculars 2; temporals 1+2. Tail length .09 to .16 of total.

Colouration. Black above, each scale with a blue-grey spot. Brownish-black below, chin and throat mottled with white.

Size. Largest ♀ (B.M. 1902.2.12.91) 280 (250+30) mm. from Mazoe.

Habitat. A 258 mm. snake was taken under a stone in leaf mould at the base of a granite kopje at Hillside Dams, Bulawayo.

Discussion. Two ♀ ♀ from Bulawayo have ventral counts of 160 (NM/M. 1944) and 162 respectively: the only race with ventral counts above 160 is *bocagii*, which does not range farther south than the northern Belgian Congo. Perhaps these specimens should be referred to *P. a. transvaalensis* Hewitt, for the types came from Tzaneen, just south of Beitbridge. A higher ventral count in ♀ ♀ is the only feature distinguishing *transvaalensis* (155-158) from *stuhlmanni* (144-155), so it appears likely that the range of ventrals in the latter race will have to be extended to 162 in order to include the Tzaneen and Bulawayo populations. The status of *transvaalensis* cannot be satisfactorily established until further material is available.

Distribution. Widely distributed, but scarce.

Localities: Mazoe; Imbeza; Odzi; Bulawayo; Umtali; Salisbury.

PSEUDASPIS CANA (Linné)

Plate 2, lower figure

Coluber canus Linné, 1758, Syst. Nat., ed. 10, vol. 1, p. 221.

Pseudaspis cana Chubb, 1909a, p. 595; 1909b, p. 35; Boulenger, 1902, p. 17; 1910, p. 507; FitzSimons, F. W., 1912, p. 86; Tasman, 1953, p. 33; Rose, 1955, pp. 86-88; Isemonger, 1955, p. 69.

Variation. (13 specimens.) Midbody scale rows 25-27; ventrals 181-208; anal divided; subcaudals 52-68; upper labials 7, the fourth entering the orbit; preoculars 1-2; postoculars 3; temporals 1+3, 1+4, 2+3, 2+4, 2+5, 3+3 and 3+4. Tail length .13 to .19 of the total.

Colouration. Juveniles: Above, light red-brown with a double row of dark brown dorsal spots, which are usually fused together to form either cross-bars or, more often, a zigzag wavy line. The dorsal markings are flanked by a series of white blotches and there is a further row of dark spots on the sides. The lower three lateral scale rows and the underside are white. Adults: Uniform light grey or pale brown, with black tipped scales (see Plate), lower three rows of lateral scales and underside cream to yellow, the ends of the ventrals often being dark edged.

Size. Largest ♂ 986 (804+182) mm. from Selborne Estates, Inyanga. Largest ♀ (NM/M. 656) 1230 (1065+165) mm. from Bulawayo.

Sexual dimorphism. In 6 males the range of ventrals is 181-193; range of subcaudals is 62-68; and the tail length is .18 to .19 of the total. In 5 females the range of ventrals is 198-208; range of subcaudals 52-56; and the tail length is .13 to .16 of the total.

Diet. A Nyamandhlovu juvenile contained a shrew (*Crocidura* sp.). A captive Irisvale snake readily constricts and swallows gerbilles (*Tatera* sp.) and other rats. A half-grown Inyanga snake took a skink (*Mabuya q. margaritifer*) in captivity at Umtali.

Enemies. The young Nyamandhlovu snake was being swallowed by a cobra when found by Mr. D. Young, the donor.

Defence. When disturbed, the Mole Snake coils and hisses loudly, striking viciously if approached.

Habits. An adult ♀ was found freshly killed on the road near Bulawayo at 3 p.m. The Irisvale snake was basking at 10 a.m.

Distribution. Widely distributed, but nowhere common.

Localities: Banket; Mazoe; Salisbury; Monte Cassino; Inyanga; Triashill; Chilimanzi; Driefontein; Sawmills; Nyamandhlovu; Bulawayo; Plumtree; Irisvale; Killarney Mine; Gazuma Pan.

DUBERRIA LUTRIX RHODESIANA Broadley

Duberria lutrix rhodesiana Broadley, 1958, Occ. Papers Rhod. Mus., vol. 22B, p. 215.

Homalosoma lutrix (not Linné) Boulenger (part), 1910, p. 509; FitzSimons, F. W. (part), 1912, p. 90.

Duberria lutrix (not Linné) Tasman, 1953, p. 36; Rose (part), 1955, p. 85; Isemonger (part), 1955, p. 71.

Duberria lutrix lutrix (not Linné) FitzSimons, V. F., 1939, p. 21; 1958, p. 209; Loveridge (part), 1944, p. 144 (Generic revision).

Variation. (18 specimens.) Midbody scale rows 15; ventrals 124-137; anal entire; subcaudals 21-38: upper labials 6, the third and fourth (second, third and fourth on both sides of an Umtali snake) entering the orbit; lower labials 6 (5 on one side of an Umtali snake, 7 on both sides of a Salisbury snake), the first three (two on one side of the Umtali snake) in contact with the anterior sublinguals; loreal 1 (absent on one side only of an Umtali snake); preoculars 1 (2 in an Umtali snake); postoculars 1 (2 in a Vumba Mtn. snake); temporals 1+2. Tail length .10 to .19 of the total.

Colouration. Plumbeus to olive-brown above, with a faint vertebral series of fine dark dashes; bases of lateral scales bluish-white, giving a mottled effect. Below, bluish-white, with a pair of large irregular black blotches situated at the base of each ventral, forming parallel longitudinal rows.

Size. Largest ♂ (NM/M.915.Paratype) 293+ (265+28+) mm. from Umtali. Largest ♀ (NM/M.914.Paratype) 307 (275+32) mm. from Umtali. Smallest (new-born) (NM/M.917.Paratype) 95 (79+16) mm. from Umtali.

Sexual dimorphism. In 8 males the range of ventrals is 124-127; of subcaudals 34-38; and the tail length is .17 to .19 of the total. In 10 females the range of ventrals is 130-137; of subcaudals 21-29; and the tail length is .10 to .12 of the total.

Discussion. Although a number of individual variations are recorded above, this longer series agrees very well with the type series. The race is distinguished from the typical form by the single postocular (2 in 87 per cent of *lutrix*), lower subcaudal count (21-38 as against 25-51 for *lutrix*), and the ventral markings. It differs from *Duberria l. shirana* in the presence of a loreal.

Breeding. The 307 mm. paratype gave birth to 7 young on 27.xii.56.

Diet. Captive Umtali snakes took slugs. Six of the young snakes mentioned above were swallowed by adult Slug-eaters.

Enemies. An Imbeza snake was disgorged by a cobra (*Naja n. mossambica*).

Habits. A Mount Hampden snake was dug out of leaf mould in a plantation; another was found crossing a footpath at 10 a.m. The Chishawasha holotype was found basking on the roadside at 9 a.m.

Distribution. Restricted to the wetter parts of the colony over 4,500 feet.

Localities: Mount Hampden; Salisbury; Chishawasha; Monte Cassino; Imbeza; Umtali: Vumba Mountain; Tsetsera; Nyamaziwa. Chubb's Bulawayo record of 1909 is rejected; this specimen is not in the National Museum now. The specimen that FitzSimons (1939) recorded from Mount Silinda actually came from Vumba Mtn.

TELESCOPUS SEMIANNULATUS SEMIANNULATUS A. Smith

Telescopus semiannulatus A. Smith, 1849, Ill. Zool. S. Africa, Rept., pl. lxxii.

Tarbophis semiannulatus Chubb, 1909a, p. 596; 1909b, p. 35; Boulenger, 1910, p. 510; FitzSimons, F. W., 1912, p. 119; Tasman, 1953, p. 31; Rose, 1955, p. 114; Isemonger, 1955, p. 74.

Variation. (20 specimens.) Midbody scale rows 19; ventrals 202-241; anal divided; subcaudals 58-70; upper labials 8 or 9, rarely 7 (both sides of a Bulawayo snake), the third, fourth and fifth or fourth, fifth and sixth (rarely third and fourth or fourth and fifth) entering the orbit; preocular 1; postoculars 2 (rarely 1 or 3); temporals 2+2 or 2+3. Tail length .13 to .18 of the total.

Colouration. Salmon pink to orange above, with from 26 to 40 black dorsal blotches on body and tail. Pale salmon pink below.

Size. Largest (NM/M. 837) 897+ (795+102+) mm. from Bulawayo. Smallest (NM/M.834b) 246 (205+41) mm. from Bulawayo.

Diet. Geckos (*Pachydactylus p. punctatus*) were recovered from the stomachs of Tjolotjo and West Sebungwe snakes. A Bulawayo snake contained a subadult *Chamæleo d. dilepis.*

Habitat. A Tiger snake was taken under a boulder on the top of a granite kopje at Hillside Dams, Bulawayo.

Distribution. Widely distributed throughout Southern Rhodesia.

Localities: West Sebungwe; Zambezi River; Odzi; Umtali; Selukwe; Tjolotjo; Sawmills; Umgusa Valley; Bulawayo; Valindre; Cyrene; Plumtree; Empandene; Balla Balla; Freda Mine.

CROTAPHOPELTIS HOTAMBOEIA HOTAMBOEIA (Laurenti)

Coronella hotamboeia Laurenti, 1768, Syn. Rept., p. 85.

Leptodira hotamboeia Chubb, 1909a, p. 596; 1909b, p. 35; Boulenger, 1910, p. 510; FitzSimons, F. W., 1912, p. 120; Hewitt and Power, 1913, p. 163.

Crotaphopeltis hotamboeia Tasman, 1953, p. 31; Rose, 1955, p. 112; Isemonger, 1955, p. 74.

Crotaphopeltis hotamboeia hotambocia FitzSimons, V. F., 1939, p. 22.

Native name for the White-lipped Snake. *Pimpi* (Sindebele), but as a result of mistaking this for a young cobra, to which this name is properly applied.

Variation. (65 specimens.) Midbody scale rows 19, rarely 18, 20 or 21 (one snake with each figure); ventrals 154-168; anal entire; subcaudals 30-46; upper labials 8, the third, fourth and fifth, or fourth and fifth, entering the orbit (rarely 7, the third and fourth entering the orbit); lower labials 9-10, the first four or five in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2, rarely 1+1. Tail length .11 to .15 of the total.

Colouration. Plumbeus to olive above, usually with numerous tiny white flecks, which are only prominent when the body is inflated in anger. Sides of head iridescent blue-black, upper labials and underside white.

Size. Largest ♂ 616 (535+81) mm. from Essexvale. Largest ♀ 702+ (610+92+) mm. from Nyamaropa. Smallest (NM/M. 587) 143 (123+20) mm. from Selukwe.

Diet. Stomachs examined contained amphibian remains. Captive snakes took toads and frogs (*Bufo regularis; Bufo carens; Kassina senegalensis; Phrynobatrachus natalensis; Rana d. delalandii; Xenopus l. lævis.*

Parasites. Mites (*Ophionyssus natricis*) on an Essexvale snake.

Defence. When molested, this snake coils up, flattening the head to show off the iridescent black temporal patches and inflating the body, to display numerous white flecks which are normally concealed. If approached, the snake strikes viciously and repeatedly. If allowed to bite a finger, it chews vigourously, leaving a row of bleeding fang punctures.

Venom. The bite of this species can be regarded as harmless to man. Numerous bites from specimens up to two feet in length have all produced the same effects. The actual bite is painful and followed by local smarting. The fang punctures bleed freely, which must soon flush all the venom from the system. The bleeding stops within a few minutes and there are no after effects. On one occasion I induced an 18″ snake to bite the tip of my little finger. The snake was more ambitious and started to swallow the digit, reaching the second joint before I disengaged him with some difficulty. The experience was rather painful, for as each side of the jaw "walked" forward in turn the corresponding fang was driven deep into the flesh. The same thing happens when the White-lipped Snake swallows its prey.

Habits. This species is strictly nocturnal. Several were picked up at night during the rains, but most specimens were found under stones. While collecting sedge frogs (*Hyperolius* spp.) along the Umzilizwe River at night, a *Crotaphopeltis* was found 18″ from the ground, in a shrub that harboured several frogs. A few yards away another snake was climbing the rough bark of a tree and was about two feet off the ground.

Distribution. Common throughout Southern Rhodesia.

Localities: Victoria Falls; Sinoia; Eldorado; Trelawney; Mount Hampden; Salisbury; Nyamaropa; Odzi; Umtali; Rowa Division; Gatooma; Que Que; Driefontein; Selukwe; Bulawayo; Syringa; Essexvale; Balla Balla; Irisvale; Lumane; Mazeppa Mine, Gwanda; Mount Silinda; Umzilizwe River; Turk Mine; Cyrene; Mount Darwin.

CHAMAETORTUS AULICUS AULICUS Günther

Chamaetortus aulicus Günther, 1864, Proc. Zool. Soc. London, p. 310: Zambezi; FitzSimons, F. W., 1912, p. 120.

Discussion. This rare species was originally described by Günther from a specimen collected on the Zambezi by Sir John Kirk. F. W. FitzSimons included Southern Rhodesia within its range in his "Snakes of South Africa." As *Chamaetortus* is known from Mozambique and N. E. Transvaal it may well occur in the eastern districts of Southern Rhodesia. East African specimens are usually associated with bamboos or palms.

DISPHOLIDUS TYPUS (A. Smith)

Bucephalus typus A. Smith, 1829, Zool. Journ., vol. 4, p. 441.

Dispholidus typus Boulenger, 1902, p. 18; 1910, p. 515; Gough, 1908, p. 33; Chubb, 1909a, p. 596; 1909b, p. 36; FitzSimons, F. W., 1912, p. 127; FitzSimons, V. F., 1939, p. 23; Tasman, 1953, p. 29; Rose, 1955, pp. 105-107; Isemonger, 1955, p. 73.

Native Name of Boomslang. *N'dlondlo* (Sindebele); *Coracundu* (Cheshona).

Variation. (87 specimens.) Midbody scale rows 19, rarely 17 (one Salisbury snake) or 21 (3 specimens); ventrals 171-196; anal divided; subcaudals 104-130; upper labials 7, rarely 8, the third and fourth (rarely fourth and fifth or fourth only) entering the orbit; lower labials 8-12, the first four (rarely three or five) in contact with the anterior sublinguals; preocular 1; postoculars 3, rarely 4; temporals 1+2, rarely 1+1 or 2+2. Tail length .25 to .30 of the total.

Colouration. Juveniles: Head uniform brown or blackish above, upper labials and chin white, uniform or more often speckled with black. Body blackish above, with numerous small blue spots, situated at the tips of dorsal scales and arranged in pairs vertically. These spots normally only appear as "warning colouration" when the body is inflated in anger. Sides of body greyish, passing to white below, very heavily peppered with dark maroon or grey to resemble a lichen covered branch. Iris of eye brilliant emerald green.

Adult males: Usually bright leaf green above, with black-edged scales and ventral scutes. A Fatima specimen had the head vermiculated with black. Some specimens from the eastern districts are uniform leaf green or blue-green. Several males from the Essexvale area are dark olive-green above and pale blue below. A single male from Essexvale was olive-brown. Iris of eye grey.

Adult females: Usually blackish-brown to olive, pale "biscuit" brown or light grey above. Below, dirty white to pale olive. Iris of eye grey or brown.

Size. Largest ♂ (UM/R.21) 1750 (1290+460) mm. from Umtali. Largest ♀ (NM/M.413) 1625 (1210+415) mm. from Essexvale.

Breeding. A pair of captive Boomslangs were found in coitu on 29.i.56.

Diet. The full stomachs examined all contained chamaeleons (***Chamaeleo d. dilepis***) except two, which contained three fledglings. A black ♀ Boomslang, just over five feet in length, lived for 21 months in captivity. In that time she consumed 25 chamaeleons, 3 agamas (*Agama h. distanti* and *Agama kirkii fitzsimonsi*), 1 dead snake (*Psammophylax t. tritaeniatus*), 6 fledglings. Only one snake, a ♂ captured swimming in a small stream at Odzi, would take frogs (*Rana* spp.). A dark olive ♂ from Balla Balla took dead rats readily, but rodents were ignored by eight other Boomslangs in the cage. Birds' eggs were taken readily when offered. Other lizards taken by captive snakes were: *Mabuya s. striata; Mabuya q. margaritifer* and *Agama cyanogaster* (juvenile).

Defence. The Boomslang is normally good natured, but when roused to anger first the throat, then the whole body, is inflated with air, making the snake appear twice its normal size. If further molested, the snake strikes with gaping jaws almost in one plane, so although the fangs are situated below the eye, it is not difficult for an adult snake to bring them into action. The fangs are approximately ¼″ in length, longer than in a cobra of the same size. Although this species is probably the commonest snake in Southern Rhodesia, bites are extremely rare. The Boomslang dashes to the top of the nearest tree at the least sign of danger and is seldom encountered at close quarters except by the herpetologist.

Venom. An adult snake normally takes about 20 minutes to kill a full-grown chamaeleon, longer than does a Vine Snake

(*Thelotornis*). The venom may be more effective against warm-blooded prey, as fledglings die quickly and the effects on a human are very severe if not fatal.

Habits. Mainly arboreal, often staying in the same tree, or group of trees, for several days. I have taken several along stream banks, where they were presumably searching for frogs. Large numbers are killed on the roads, which indicates the abundance of the species.

Distribution. Abundant throughout Southern Rhodesia.

Localities: Trelawney; Mazoe; Mount Hampden; Salisbury; Lake McIlwaine; Odzi; Old Umtali; Umtali; Que Que; Gatooma; Selukwe; Lukosi; Fatima; Turk Mine; Bulawayo; Empandene; Essexvale; Balla Balla; Irisvale; Stanmore; Beitbridge; Mtao Forest; Dadaya; Shabani; Lundi River; Nyaratedzi River; Birchenough Bridge; Mount Silinda; Chirinda Forest; Mount Darwin.

THELOTORNIS KIRTLANDII OATESII (Günther)

Dryophis Oatesii Günther, 1881, in Oates, Matabeleland and the Victoria Falls, App., p. 330, col. pl. D: Matabeleland, Southern Rhodesia.

Thelotornis kirtlandii (not Hallowell) Boulenger, 1896, p. 185; 1910, p. 515; Chubb (part), 1909a, p. 596; 1909b, p. 36; FitzSimons, F. W. (part), 1912, p. 126; Hewitt and Power, 1913, p. 164; Isemonger (part), 1955, p. 78.

Thelotornis kirtlandii capensis Loveridge (part), 1944, p. 154 (generic revision); Broadley (part), 1957c, p. 297.

Thelotornis kirtlandii oatesii Loveridge, 1953, pp. 277-279.

Native name of Oates' Vine-Snake. *Kotikoti* (Sindebele).

Variation. (11 specimens.) Midbody scale rows 19; ventrals 163-174; anal divided; subcaudals 140-159; upper labials 8, the fourth and fifth entering the orbit; lower labials 11-12, the first four in contact with the anterior sublinguals; preocular 1; postoculars 3, rarely 4; temporals 1+2, rarely 1+3. Tail length .36 to .38 of total.

Colouration. Top of head pale green speckled with pink and black, this speckling is normally restricted to a Y-shaped marking, whose stem lies along the interparietal suture and its arms extend across the posterior portion of the frontal to the supraoculars (in a Matopos specimen the speckling extends along the frontal to the internasals). A band of pink, black-edged, scales runs from the nostril through the orbit and lower temporals to the back of the head. Upper labials are white with a black streak extending from the eye to the full width of the sixth labial; there is usually a row of black spots on the lips. Chin white, the lower labials heavily speckled with black. Body light grey with diagonal cross bars of whitish blotches; the sides are adorned with scattered touches of pink or orange and black. Ventrum pinkish-white heavily mottled with dark grey. On the sides of the neck are one or two vivid black blotches.

Size. Largest (NM/M.972) 1417 (900+517) mm. from Gatooma.

Diet. A Matopos snake contained an immature Plated Rock-Lizard (*Gerrhosaurus v. validus*). The large Gatooma snake recorded above lived for 6 months in captivity before being killed by a large Boomslang (*Dispholidus typus*) in a dispute over a chamaeleon. In that time she consumed 11 *Chamaeleo d. dilepis*, an *Agama h. distanti* and two bird's eggs.

Defence. When molested the Vine-Snake inflates its throat enormously to display the vivid black and white markings. If further tormented it strikes viciously with gaping jaws.

Venom. See under *Thelotornis k. capensis.*

Distribution. Northwestern parts of Southern Rhodesia, extending south to a line Matopos-Bulawayo-Gatooma-Norton which more or less follows the principal watershed.

Localities: Trelawney; Donnington Farm, Norton; Gatooma; Bulawayo; Khami Dam; Matopos; Karoi.

THELOTORNIS KIRTLANDII CAPENSIS A. Smith

Thelotornis capensis A. Smith, 1849, Ill. Zool. S. Africa, 3, App., p. 19.

Thelotornis kirtlandii (not Hallowell) Chubb (part), 1909a, p. 596; 1909b, p. 36; FitzSimons, F. W. (part), 1912, p. 126; FitzSimons, V. F., 1939, p. 23; Tasman, 1953, p. 29; Isemonger (part), 1955, p. 78.

Thelotornis kirtlandii capensis Loveridge (part), 1944, p. 154 (generic revision); Broadley (part), 1957c, p. 297.

Theletornis (*sic*) *kirtlandii*, Rose, 1955, pp. 114-119.

Native name of Cape Vine-Snake. *Kotikoti* (Sindebele); *Kumtumuti* (Cheshona).

Variation. (38 specimens.) Midbody scale rows 19; ventrals 146-163; anal divided; subcaudals 127-166; upper labials 8, rarely 9, the fourth and fifth entering the orbit; lower labials 11-12, the first four in contact with the anterior sublinguals; preocular 1; postoculars 3, rarely 2; temporals 1+2, rarely 1+3. Tail length .33 to .40 of total.

Colouration. As in *Thelotornis k. oatesii,* except that in specimens from the south (Balla Balla-Lumane) the speckling extends over the whole of the top of the head. However, specimens from the Eastern Districts have either uniform green heads or the markings are reduced to a few spots arranged in the Y-shape typical of *oatesii.* The pink and black band on the side of the head is replaced by a uniform dark brown streak. Tanganyika specimens are similar. Because of this confusion in head markings the two forms can only be distinguished by their ventral counts[1].

Size. Largest 1440 (910+530) mm. from Umtali. Smallest (NM/M.613) 637 (410+227) mm. from Selukwe.

Diet. An Irisvale snake was swallowing a young Tree Agama (*Agama cyanogaster*) when captured. Captive specimens fed readily on lizards (*Mabuya s. striata; Mabuya q. margaritifer; Agama h. distanti; Agama h. armata; Agama cyanogaster; Platysaurus g. rhodesianus*), chamaeleons (*Chamaeleo d. dilepis*) and frogs (*Rana* spp.). Although birds and their eggs were occasionally taken, cold-blooded prey seems to be preferred.

Defence. See under *Thelotornis k. oatesii.*

Venom. On 1.x.57 I spotted a pair of Vine-Snakes mating in a tree at Lumane. As I tried to get both snakes into the bag at the same time, while perched at the top of the tree, the larger snake fastened on to the middle finger of my right hand. I descended to the ground and had some difficulty in disengaging the snake's fangs. The time was 3.30 p.m. I sucked the bite and then went after the second snake which I had been obliged to release. Although I failed to dislodge it from a thick bush I finally captured it two days later in the original tree. The finger was slightly swollen after half an hour and there was some slight haemorrhage from the fang punctures by 5 p.m. By 9 o'clock the finger was very swollen and discoloured at the joint. There was persistent haemorrhage from the fang punctures and teeth

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[1] In 8 specimens of *capensis* from Zululand, which may be considered topotypes, the head speckling is confined to the Y-shape characteristic of *oatesii*!

marks, also from numerous scratches on my legs (received while climbing the thorn tree after the snakes) and small shaving cuts. There was no pain whatsoever. The haemorrhage continued all night and all the next day. The blood was very slow to clot and I left pools of blood wherever I went. There were purple patches round all cuts, etc. By 9 p.m. on the 2nd the haemorrhage was easing off and confined to the scratches on my legs. The bleeding had stopped altogether by the next morning although the finger was still swollen and the hand puffy. There was slight bleeding from the fang punctures about 7 p.m. There was no haemorrhage on the 4th and the hand started to return to normal the following day.

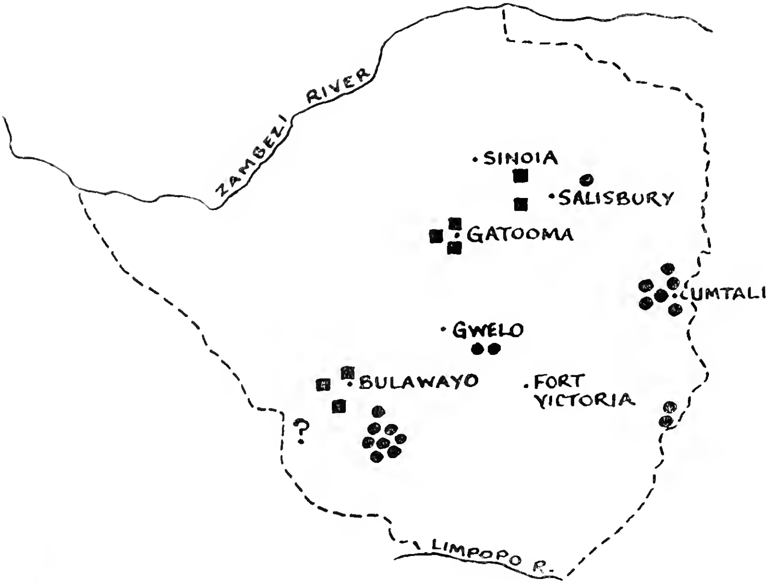

Fig. 3. Recorded localities for *Thelotornis.*
■ *Thelotornis kirtlandii oatesii* (Günther)
● *Thelotornis kirtlandii capensis* A. Smith

I think that the numerous cuts and scratches on my body acted as safety valves and prevented the dreadful internal haemorrhage which was a prominent feature when F. J. de R. Lock died from a *Thelotornis* bite in Tanganyika[1]. The snake concerned in the latter case was a juvenile 2′5″ in length; I was bitten by an adult of just over 4 feet.

Habits. This species is abundant in the dry Mopani bush at Lumane where there is very little undergrowth. It is also plentiful at Irisvale and in the Eastern Districts, where the vegetation is more varied and provides better cover. The snakes are usually found in bushes or on dead tree stumps not far from the ground where they can spot any lizards or frogs passing below. They remain motionless even when passed within a few inches.

Distribution. Southeastern districts of Southern Rhodesia, extending as far north as a line Balla Balla-Selukwe-Salisbury.

Localities: Salisbury District; Odzani; Odzi; Umtali; Selukwe; Balla Balla; Irisvale; Sinkukwe; Lumane; Mount Silinda; Pungwe River, 2400′. The specimens recorded from Empandene by Chubb (1909b) probably belong to this race, but are now missing from the National Museum collection.

HEMIRHAGERRHIS NOTOTAENIA NOTOTAENIA (Günther)

Coronella nototaenia Günther, 1864, Proc. Zool. Soc. London, p. 309, pl. xxvi, fig. 1.

Amplorhinus nototaenia Hewitt, 1913, p. 481.

Hemirhagerrhis nototaenia Isemonger, 1955, p. 75.

Variation. (6 specimens.) Midbody scale rows 17; ventrals 164-168; anal divided; subcaudals 72-83; upper labials 7 or 8, the third and fourth or fourth and fifth entering the orbit; lower labials 9, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2, rarely 1+3. Tail length .23 to .27 of the total.

Colouration. Dark ash grey or grey-brown above; top of head black, continuing as a vertebral stripe about three scales in width, which is black on the neck, but less well defined on the rest of the body. A row of black spots merges with the vertebral stripe on either side. These may be opposed to form cross-bars or alternated to form a zigzag. A dark streak on either side of the head passes through the eye and fades out on the neck. Below, mottled in ash grey or grey-brown and dirty white.

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[1] See Loveridge (1956), pp. 12-13.

Size. Largest (UM/R.332) 370 (280+90) mm. from Mount Darwin.

Habitat. A Bark-Snake was taken at 11 a.m. as it was crawling on the ground under Mopani trees with no undergrowth. This was in the Wedza Reserve, between the Macheke and Sabi rivers (W. Armitage).

Distribution. Found in the low-lying river valleys of Southern Rhodesia. The species seems to be closely associated with dry Mopani bush.

Localities: Zambezi River, 40 miles east of Chirundu; Matetsi; Macheke-Sabi Junction, Wedza Reserve; Devon Farm, Odzi River; Ramaquabane River; Beitbridge; Mount Darwin.

AMPLORHINUS MULTIMACULATUS A. Smith

Amplorhinus multimaculatus A. Smith, 1847, Ill. Zool. S. Africa, Rept. pl. lxii. FitzSimons, V. F., 1958, p. 209.

Variation. (2 specimens.) Midbody scale rows 17; ventrals 140-141; anal entire; subcaudals 58-75, the anterior five single, the remainder paired; upper labials 8, the fourth and fifth entering the orbit; five lower labials in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 2+2. Tail length .22 of total.

Colouration. Dark green to olive green above, with a paler dorsolateral and a longitudinal series of elongate black spots on either side; scattered scales narrowly edged with bluish white, especially over anterior half of body; upper labials each bearing a yellowish-white spot or irregular vertical streak. Chin yellow to yellowish-white, scales edged with bluish grey; underside of body and tail uniform bluish grey (V. F. FitzSimons).

Size. Largest (T.M.22407) 488 (383+105) mm. from Pungwe River Causeway.

Distribution. Mountains on the eastern border of Southern Rhodesia.

Localities: Nyamaziwa; Pungwe River Causeway.

PSAMMOPHYLAX TRITAENIATUS TRITAENIATUS (Günther)

Rhagerrhis tritaeniatus Günther, 1868, Ann. Mag. Nat. Hist., ser. 4, vol. 1, p. 423, pl. xix, fig. 8.

Coronella tritaenia, Günther, 1881, in Oates, Matabeleland, p. 329, pl. C.

Trimerorhinus tritaeniatus, Boulenger, 1896, p. 139; 1902, p. 18; 1910, p. 512; Chubb, 1909a, p. 596; 1909b, p. 35; FitzSimons, F. W., 1912, p. 121; Hewitt and Power, 1913, p. 163; Tasman, 1953, p. 33; Rose, 1955, p. 111; Isemonger, 1955, p. 76.

Psammophylax tritaeniatus, Broadley, 1956, p. 215.

Native name of Three-lined Grass-Snake. *N'shwazi* (Sindebele), but also applied to *Psammophis s. subtaeniatus.*

Variation. (56 specimens.) Midbody scale rows 17; ventrals 150-168; anal divided; subcaudals 54-67; upper labials 8, the fourth and fifth entering the orbit; lower labials 9-11, the first five, rarely four or six, in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 2+3, rarely 2+2[1]. Tail length .19 to .22 of the total.

Colouration. Top of head light brown; vertebral scale row dark brown, the superior halves of the scales flanking it are black, forming a sharp-edged vertebral stripe 2 scales wide; this is flanked by a pale brown, grey or yellowish stripe 3 scales wide followed by another dark brown, black-edged stripe 3 scales wide, which begins at the snout and runs through the eye; outer 1½ scale rows white, with a broken orange or pinkish line running through the outer row. Upper labials, chin and throat white; underside white, cream or lemon yellow, with some salmon or pink flecking at the ends of the ventrals.

Size. Largest (SM/R.70) 851 (680+171) mm. from Salisbury. Smallest 172 (140+32) mm. from Essexvale.

Breeding. A captive ♀ from West Nicholson, 728 mm. in length, laid 4 eggs between 27th and 30th November, when she died with 10 eggs still in her ovaries.

Diet. The huge Salisbury specimen, recorded above, contained a partially digested rat. Captive specimens took mice (*Rhabdomys* and *Leggada* sp.); lizards (*Chamaeleo d. dilepis* juv.; *Mabuya s. striata; Mabuya v. varia; Mabuya q. margaritifer; Agama h. distanti*), and frogs (*Kassina senegalensis; Breviceps mossambicus; Rana* spp.).

Enemies. A juvenile was found swimming alongside a drift on the Umgusa River, near Bulawayo. It had been cut clean in half just forward of the vent, almost certainly the work of one of the numerous crabs living in the drift.

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[1] 1+3 on both sides of a Bembesi snake

Defence. This species rarely attempts to bite when captured.

Habits. When basking, this snake's body becomes kinked in a most unnatural manner. The first time I observed this phenomenon was when I found a 20″ specimen basking on a sandbank of the Hunyani River at Sinoia. I thought that the snake was dead and it made no movement until I picked it up, appearing to be completely oblivious of its surroundings. I have since observed the same behaviour in many snakes both in captivity and in the wild state. This habit may account for many of the Striped Grass-Snakes killed on the roads and must make the species very vulnerable to the numerous birds of prey.

Distribution. Common throughout Southern Rhodesia.

Localities: Sinoia; Mazoe; Mount Hampden; Salisbury; Hunyani; Monte Cassino; Odzi; Umtali; Que Que; Driefontein; Selukwe; Bembesi; Bulawayo; Khami; Plumtree; Empandene; Essexvale; Balla Balla; Glass Block; Stanmore; West Nicholson; Mount Silinda; Mount Darwin; Umvuma.

RHAMPHIOPHIS OXYRHYNCHUS ROSTRATUS Peters

Rhamphiophis rostratus Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 624. Isemonger, 1955, p. 79, pl. opp. p. 36.

Rhamphiophis oxyrhyneus (misprint), Tasman, 1953, p. 33.

Variation. (4 specimens.) Midbody scale rows 17; ventrals 165-186; anal divided; subcaudals 100-105; upper labials 8, the fifth entering the orbit; lower labials 10-12; the first four or five in contact with the anterior sublinguals; preoculars 3; postoculars 2; temporals 2+3; 3+4. Tail length .29 to .31 of the total.

Colouration. Pale brown above, each scale edged with darker brown. White below.

Size. Largest (NM/M.1817) 1280 (880+400) mm. from Mavurandona Mts.

Distribution. Restricted to the dry sandveld at the lower altitudes.

Localities: Mtoko; Matetsi; West Sebungwe; Fatima; Lupane; Beitbridge; Mavuradona Mts.; Mount Darwin.

DROMOPHIS LINEATUS (Duméril and Bibron)

Dryophylax lineatus Duméril and Bibron, 1854, Erpet. Gen., 7, p. 1124.

Data of unique specimen. Midbody scale rows 17; ventrals 149; anal divided; subcaudals ?; upper labials 8, the fourth and fifth entering the orbit; first four lower labials in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2.

Colouration. Head dark brown above, two light hair-lines crossing back of head; pre- and postoculars yellow; upper labials and chin greenish white. Body grey-brown above; the vertebral scale row lighter, the next three rows edged with black, then a faint lighter stripe merging into grey-brown below; the outer row of scales edged with the black above and yellowish-white below. Ventrals yellowish-white, a black *transverse* marking at the end of each ventral for the anterior two-thirds of the body. Subcaudals bluish-white.

Size. (NM/M.529) 705+ (600+105+) mm. from Nampini.

Diet. This snake was swallowing a rat when it was shot by Mr. M. P. Stuart Irwin on the bank of the Zambezi.

Distribution. This is the most southerly specimen yet recorded. Mr. Irwin suggests that the distribution of this species may, like that of some bird species, be linked with the Papyrus swamps, which do not extend downstream below Nampini. Extralimitally this snake may occur in the swamps of the Chobe River, the border of Bechuanaland and the Caprivi Strip.

Localities: Nampini.

PSAMMOPHIS SIBILANS SIBILANS (Linné)

Coluber sibilans Linné (part), 1758, Syst. Nat., ed. 10, p. 222.

Psammophis thomasi Gough, 1908, p. 30, fig.

Psammophis sibilans Boulenger, 1902, p. 18; 1910, p. 514; Chubb, 1909a, p. 596; 1909b, p. 36; FitzSimons, F. W., 1912, pp. 123, 125; Hewitt, 1912, p. 273; Tasman, 1953, p. 33; Rose, 1955, p. 108; Isemonger, 1955, p. 77.

Psammophis furcatus (not Peters) Boulenger (part), 1910, p. 513; FitzSimons, F. W. (part), 1912, pp. 122, 123; Hewitt (part), 1912, p. 270.

Psammophis sibilans sibilans Loveridge, 1940, p. 30 (generic revision).

Native name of the Olive Grass-Snake. *N'dlondlo* (Sindebele), but confused with the brown phase of *Dispholidus typus.*

Variation. (35 specimens.) Midbody scale rows 17; ventrals 167-177; anal divided; subcaudals 92-107; upper labials 8 (9 on one side of an Essexvale snake), the fourth and fifth entering the orbit; lower labials 9-10, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 2+2, 2+3, rarely 2+1 (through fusion on both sides of two snakes). Tail length .26 to .31 of the total.

Colouration. Head brown above, uniform, or with an intricate pattern of chestnut markings; sides of head brown, preocular sometimes yellow, lower half of upper labials yellow, usually spotted with black; chin and throat yellow, speckled with black or with a series of black-edged ocelli on the lower labials. Body grey-brown to olive above, uniform, or with a series of narrow black dorsal stripes formed by black scale edgings, the vertebral scale row often lighter than the rest. Yellow to white below, uniform, or with a double row of obscure olive blotches.

Size. Largest (SM/R.34) 1740 (1253+487) mm. from Salisbury.

Sexual dimorphism. The sexes cannot be separated on scale counts. Sexing is made difficult by the small size of the hemi penes. The everted hemipenes of a 1466 mm. Essexvale ♂ were only 12 mm. in length and 2 mm. in diameter.

Breeding. On 2.x.57 a 1197 mm. Bulawayo ♀ laid 19 eggs, which hatched on 22.ii.58.

Diet. Stomachs examined contained skinks (*Mabuya s. striata*) and a frog (*Rana* sp.). Captive specimens took rats, lizards (*Mabuya s. striata; Mabuya v. varia; Ichnotrophis capensis*) and frogs (*Rana d. delalandii; Phrynobatrachus natalensis*)[1].

Venom. I have been bitten three times by adult snakes while catching them. Full bites from a 3-foot Essexvale snake and a 4-foot Bulawayo snake produced in each case only slight local pain and inflammation, which passed off within an hour. On 16.viii.57 I captured a 3′9″ ♂ at Bulawayo. I had dug the snake out of a pile of thornbush and debris and was lying on the ground under the thorn branches when I seized the snake, who promptly fastened onto my finger and chewed. It took me a minute or two to back out of my tunnel and disengage the snake's fangs from the base of my finger. After 10 minutes the finger started to swell up and I scarified and sucked the punctures. The whole hand was swollen and tender within an hour, but there was no pain. The swelling started to subside after 24 hours and was back to normal after 48 hours.

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[1] A four-foot specimen, captured by D. S. Rider at Umvuma, disgorged a juvenile mamba (*Dendroaspis p. polylepis*) a little over two feet in length.

Habits. This is a very active snake, and as it usually frequents reedbeds or long grass in vleis, it is not easy to capture. When pursued, it makes a short dash and then lies low until you are on top of it, then it makes another dash. This goes on until the snake eventually escapes into thick cover or a reedbed. Although it usually bites when captured, this species settles down very rapidly in captivity and likes being handled. Several of my specimens have learned to associate my appearance with food. They will come to the cage door and take lizards and frogs from my fingers. I captured one snake at Mount Hampden while it was engaged in swallowing a lizard (*Mabuya s. striata*). I put snake and lizard in the same bag and when I got home I discovered that the lizard was inside the snake!

Habitat. Although probably the best known species in the genus, *Psammophis s. sibilans* is definitely not a *sand* snake and I have never heard one hiss! "Hissing Sand-Snake," the direct translation of the scientific name, is most inappropriate and should be dropped. This species is restricted to shady localities along rivers and in vleis, orchards and similar situations. I found it abundant along the Umzilizwe River, below Mount Selinda, where specimens seem to attain a greater average length than usual. A specimen from the Umgusa River, Bulawayo, was dug out of a termitarium.

Distribution. Found throughout Southern Rhodesia, where conditions are suitable.

Localities: Sinoia; Mazoe; Mount Hampden; Salisbury; Hunyani; Kutama; Norton; Selukwe; Gwamayaya River; Fatima; Crosby Farm; Inyati; Bulawayo; Essexvale; Irisvale; Odzi; Umtali; Threespanberg Pass; Chipinga; Umzilizwe River; Mount Darwin; Umvuma.

PSAMMOPHIS SUBTAENIATUS SUBTAENIATUS Peters

Psammophis sibilans var. *subtaeniata* Peters, 1882, Reise nach Mossambique, 3, p. 121.

Psammophis subtaeniatus Chubb, 1909a, p. 596; 1909b, p. 35; Hewitt, 1912, p. 274; FitzSimons, V. F., 1939, p. 23; Tasman, 1953, p. 53.

Psammophis bocagii Boulenger, 1910, p. 514; FitzSimons, F. W., 1912, pp. 123, 124.

Psammophis notostictus (not Peters) Isemonger, 1955, p. 76.

Native name of Stripe-bellied Sand-Snake. *N'shwazi* (Sindebele), but also applied to *Psammophylax t. tritaeniatus.*

Variation. (35 specimens.) Midbody scale rows 17; ventrals 158-175; anal divided; subcaudals 105-123; upper labials 9, the fourth, fifth and sixth entering the orbit (except for 3 snakes from South Bulawayo and Filabusi, which agree with the northern race *sudanensis* in having 8 upper labials, the fourth and fifth entering the orbit); lower labials 9-10, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2 (3 on one side of a Beitbridge snake); temporals 2+2 or 2+3 (1+1 on one side of a Balla Balla snake; 1+2 on one side of a Hope Fountain snake). Tail length .32 to .36 of the total.

Colouration. Head above brown, uniform, or more often with a series of grey transverse markings, which continue onto the neck as a series of cross-bars; upper labials, chin and throat white, liberally speckled with black (immaculate lemon yellow in a Beitbridge snake). The seven dorsal scale rows are brown, sometimes with black scale edgings; a yellow or white dorsolateral stripe is black-edged above and followed by a chestnut to brown band 2½ scales wide; the lower half of the outer row of scales is white. Ventrals are yellow in the centre, with a pair of sharply defined black lateral lines; the ends of the ventrals are white. The black hair lines tend to fade out on the subcaudals.

Size. Largest (NM/M.465) 1155 (763+392) mm. from Beitbridge and (NM/M.861) 1155 (745+410) mm. from Bulawayo. Smallest (NM/M.286) 396 (268+128) mm. from Inyati.

Diet. Captive specimens took lizards (*Mabuya s. striata; Mabuya v. varia; Nucras intertexta holubi*) and frogs (*Rana* spp.).

Habits. A very fast moving snake. When disturbed on the granite outcrops, where it is abundant, it rapidly vanishes into the nearest jumble of loose rock. These snakes are extremely plentiful at Beitbridge, where they are fond of basking on the sand spruits which run down to the Limpopo. The large Beitbridge specimen was in such a situation when D. T. Crow and myself tried to cut her off from the nearest cover. However, she eluded us, shot up a bank and vanished. We eventually discovered her in a thorn tree and after much manoeuvering, succeeded in catching her. Another specimen, flushed in a sand spruit at Tod's Hotel, West Nicholson, took refuge in a hole among the roots of a tree.

Habitat. Truly a "sand" snake, common throughout Matabeleland in the dry savanna and on granite outcrops. Often occurs side by side with *P. s. sibilans* in the same districts, but not together.

Distribution. Very common throughout Matabeleland. Apparently absent from Salisbury District and much of Mashonaland, although it occurs sparingly in the Northeast.

Localities: Victoria Falls; Zambezi-Sebungwe Junction; Lupane; Sawmills; Inyati; Shiloh; Bulawayo; Hope Fountain; Matopos; Empandene; Essexvale; Balla Balla; Filabusi; Irisvale; Stanmore; Lumane; Tod's Hotel; Beitbridge; Makumbi; Shawanoe River; Mtoko; Nyamaropa; Umtali; Odzi; Birchenough Bridge; Lundi River; Que Que; Mount Darwin; Sebungwe River.

PSAMMOPHIS JALLAE Peracca

Psammophis jallae Peracca, 1896, Boll. Mus. Zool. Torino, vol. 11, No. 225, p. 2, figs.: Kazungula to Bulawayo; Boulenger, 1910, p. 514; Hewitt, 1912, p. 275; FitzSimons, F. W., 1912, pp. 123, 125; Loveridge, 1940, p. 62 (generic revision).

Variation. (5 specimens.) Midbody scale rows 15; ventrals 159-175; anal divided; subcaudals 89-100; upper labials 7, the third and fourth entering the orbit; lower labials 9, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 2+2 (2+1 on one side of the Springvale snake). Tail length .31 to .33 of total.

Colouration. Grey-brown above, with ill-defined light dorsolateral stripes. Whitish below.

Size. Largest (T.M.24392) 1135 (762+373) mm. from Wankie.

Distribution. Matabeleland, extending east to Driefontein and Salisbury.

Localities: Wankie; Kazungula to Bulawayo; Importuni District; Salisbury; Driefontein; Springvale.

PSAMMOPHIS CRUCIFER (Daudin)

Coluber crucifer Daudin, 1803, Hist. Nat. Rept., 7, p. 189.

Psammophis crucifer Boulenger, 1896, p. 169; Loveridge, 1940, p. 64 (generic revision); Rose, 1955, pp. 107, 108; FitzSimons, V. F., 1958, p. 210.

Variation. (5 specimens.) Midbody scale rows 15; ventrals 144-157 (118 in an aberrant Nyamaziwa snake); anal divided; subcaudals 61-73 (46 in the Nyamaziwa snake); upper labials 8, the fourth and fifth entering the orbit; lower labials 9, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 2+3. Tail length .20 to .23 of the total.

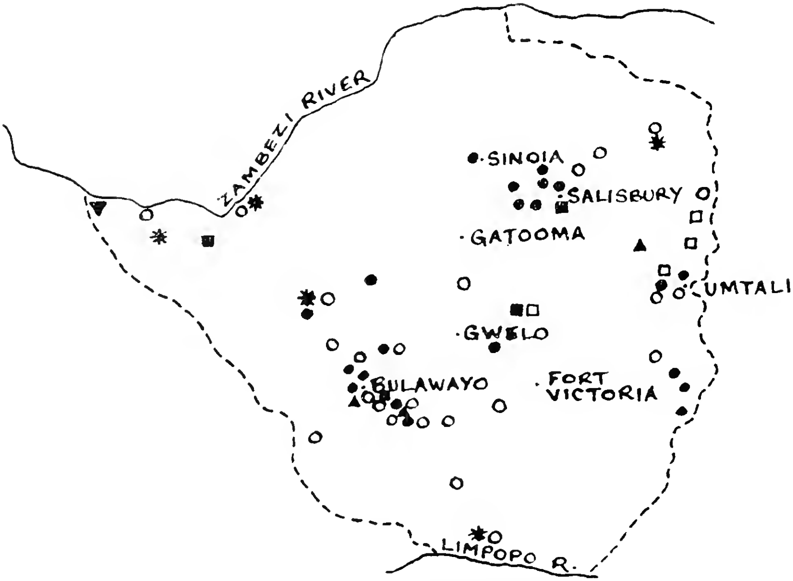

Fig. 4. Recorded localities for *Rhamphiophis, Dromophis* and *Psammophis.*
* *Rhamphiophis oxyrhynchus rostratus* Peters
▼ *Dromophis lineatus* (Duméril and Bibron)
● *Psammophis sibilans sibilans* (Linné)
○ *Psammophis subtaeniatus subtaeniatus* Peters
■ *Psammophis jallae* Peracca
□ *Psammophis crucifer* (Daudin)
▲ *Psammophis angolensis* (Bocage)

Colouration. Head grey, a dark red-brown, black-edged stripe extending from the snout, dividing on the frontal and again on the parietals, in each case enclosing a grey centre, continuing onto the body as a dorsal stripe; pre- and postoculars white;

upper labials, chin and throat white, blotched or speckled with black. A three-scale wide, black-edged dorsal stripe, red brown in colour, separated by a thin white line from a grey dorsolateral stripe two scales in width; a dark grey-brown lateral stripe, 2½ scales wide, inferior half of outer scale row white. Below, pale orange with a broken black lateral line.

Size. Largest (NM/M.620) 375 (287+88) mm. from Odzani.

Habitat. The largest specimen was found run over on the Umtali-Inyanga road near Odzani. The steep rocky hillside on either side of the road was searched for more, but the only reptile found was a zonure (*Cordylus c. rhodesianus*).

Distribution. Eastern Districts of Southern Rhodesia. The only specimens from other parts of the colony are two from "Matabeleland" recorded by Boulenger (1896) and a single specimen taken by the Rev. K. Tasman, S.J. at Driefontein 20 years ago.

Localities: Nyamaziwa; Odzani; Odzi; Driefontein; "Matabeleland."

PSAMMOPHIS ANGOLENSIS (Bocage)

Amphiophis angolensis Bocage, 1872, Jour. Sci. Lisboa, vol. 4, p. 82.

Variation. (3 specimens.) Midbody scale rows 11; ventrals 140-162; anal divided; subcaudals 72; upper labials 8, the fourth and fifth entering the orbit; lower labials 7, the first four in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2 (1+1 on one side of the Bulawayo snake). Tail length .29 to .30 of total.

Colouration. Head dark brown, three narrow yellow bands crossing the back of the head; upper labials white. Neck dark brown with a grey cross-band which broadens laterally; a broad, dark brown, dorsal band 4 scales wide; greyish to yellowish laterally; the Rusape snake has black hair lines through the outer two scale rows. Lower half of outer scale row and underside white or yellowish, uniform, or with an ill-defined lateral series of dark flecks.

Size. Largest (UM/R.16) 385 (270+115) mm. from Rusape.

Distribution. Apparently widely distributed, but scarce. The Balla Balla specimen in the British Museum (Natural History) seems to be the most southerly record.

Localities: Rusape; Bulawayo; Balla Balla.

CALAMELAPS UNICOLOR MIOLEPIS Günther

Plate 4, upper figure

Calamelaps miolepis Günther, 1888, Ann. Mag. Nat. Hist., ser. 6, vol. 1, p. 323.

Calamelaps concolor (not Smith) Chubb, 1909b, p. 36.

Calamelaps warreni Hewitt, 1912, p. 276; 1913, p. 480.

Calamelaps polylepis (not Bocage) Hewitt, 1913, p. 480.

Calamelaps unicolor (not Reinhardt) FitzSimons, V. F., 1939, p. 24.

Calamelaps unicolor polylepis Loveridge (part), 1944, p. 162 (generic revision).

Calamelaps unicolor warreni Loveridge (part), 1944, p. 163 (generic revision).

Calamelaps unicolor miolepis Witte and Laurent, 1947, p. 31 (generic revision).

Variation. (23 specimens.) Midbody scale rows 19 or 21; ventrals 168-214; anal divided; subcaudals 19-29; upper labials 6, the third and fourth entering the orbit, the third in contact with the prefrontal, the fifth largest and in contact with the parietal; lower labials 7 (8 in an Essexvale snake), the first four (five in the Essexvale snake) in contact with the anterior sublinguals; supraocular 1; postocular 1; temporal 0+1. Tail length .06 to .10 of the total.

Colouration. In life, iridescent purplish-black above and below, becoming opaque bluish-grey when about to slough. Difficult to distinguish from *Atractaspis* in the field.

Size. Largest ♂ (NM/M.411) 550 (495+55) mm. from Essexvale. Largest ♀ (B.M. ?) 1014 (952+62) mm. from Odzi.

Sexual dimorphism. Ten males all have 19 midbody scale rows; the range of ventrals is 168-185; range of subcaudals is 25-29, and the tail length is .10 of the total. Thirteen females all have 21 midbody scale rows; the range of ventrals is 195-214; range of subcaudals is 19-24 (but 6 tails are truncated) and the tail length is .06 to .07 of the total.

Discussion. Laurent has recently (1956) proposed the consolidation of the races *polylepis*, *miolepis* and *hildebrandti* under the older name *polylepis*. Although more material is needed before the question can be finally settled, I prefer to retain these races for the time being. From the material at present available it appears that *polylepis* of Angola always has 21 midbody scale rows; *miolepis* of the Rhodesias, Nyasaland, S.W. Tanganyika, Mozambique, Transvaal and Zululand has 19 (usually males) or 21 (usually females) scale rows, and *hildebrandti* of Kenya and Tanganyika has 17 or 19 scale rows.

Diet. The huge Odzi ♀ contained a Blind-Snake (*Typhlops s. mucruso*) approximately two feet in length. A captive Bulawayo ♂ readily takes Blind-Snakes (*Typhlops s. mucruso*) and Worm-Snakes (*Leptotyphlops scutifrons*), also lizards (*Mabuya v. varia; Nucras intertexta holubi*).

Enemies. A 3-foot ♀ was killed by a cat at Umtali.

Distribution. Widely distributed throughout Southern Rhodesia, but rarely encountered because of its fossorial habits.

Localities: Nyamaropa; Imbeza; Umtali; Odzi; Salisbury; Gatooma; Driefontein; Bulawayo; Matopos; Empandene; Essexvale; Gwanda; Birchenough Bridge; Zimbabwe.

CALAMELAPS VENTRIMACULATUS WEBSTERI FitzSimons and Brain

Calamelaps ventrimaculatus websteri FitzSimons, V. F. and Brain, 1958, Occ. Papers. Rhod. Mus., 22B, p. 202.

Variation. (3 specimens.) Midbody scale rows 15; ventrals 187-191; anal divided; subcaudals 23-25; upper labials 5, the second and third entering the orbit, the second in contact with the prefrontal, the fourth largest and in contact with the parietal, the third separated from the parietal by a postocular, by which the fourth is in short contact; lower labials 5, the third very large and just making contact with its fellow behind the sublinguals; supraocular 1; postocular 1; temporal 0+1. Tail length .08 of the total.

Colouration. Head black with white sutures. A dorsal band, 7 scales wide, is black with each scale white edged, giving a reticulated appearance. Upper labials, lateral scale rows and underside are white.

Largest. (NM/M.671. Holotype) 145 (132+13) mm. from Sawmills.

Habitat. This type series was found by Mr. R. E. Webster in the sand at the bases of tree stumps.

Distribution. Known only from the type locality, Sawmills, in the Kalahari sands 55 miles northwest of Bulawayo.

XENOCALAMUS BICOLOR BICOLOR Günther

Xenocalamus bicolor Günther, 1868, Ann. Mag. Nat. Hist., ser. 4, vol. 1, p. 415, pl. xix, fig. A: Zambezi; Boulenger, 1896, p. 248.
Xenocalamus bicolor bicolor FitzSimons, V. F., 1946, p. 39; Witte and Laurent, 1947, p. 45.

Data of type. Midbody scale rows 17; ventrals 218; anal divided; subcaudals 24; upper labials 6, the third and fourth entering the orbit, the fifth very large and in contact with the parietal; lower labials 6, the first three in contact with the anterior chin shields, the third very large; rostral and frontal very large, the latter in broad contact with the internasals; prefrontals very small and widely separated by the frontal, so that they resemble preoculars; supraocular 1; postocular 1; temporal 0+1. Tail length .07 of the total.

Colouration. Black above; upper labials, outer two scale rows and underside white.

Size. Type measures 430 (400+30) mm. from the Zambezi.

Distribution. This rare fossorial species was first described by Günther from a specimen collected on the Zambezi by Chapman. Dr. V. F. FitzSimons has recorded specimens from Northern Transvaal, so this remarkable snake should be found along the dry western border of Southern Rhodesia. Several subspecies have been described from Bechuanaland and South West Africa.

Localities: Zambezi.

CHILORHINOPHIS GERARDI GERARDI (Boulenger)

Apostolepis gerardi Boulenger, 1913, Rev. Zool. Afr., vol. 3, p. 103, fig.
Parkerophis gerardi Parker, 1927, p. 82, fig. 1.
Chilorhinophis gerardi Pitman, 1938, p. 183; Witte and Laurent, 1947, p. 55.
Chilorhinophis gerardi gerardi Loveridge, 1951, p. 194.

Variation. (4 specimens.) Midbody scale rows 15; ventrals 274-288; anal divided; subcaudals 20-31; upper labials 4, the third entering the orbit; lower labials 5, the first three in contact with the anterior sublinguals; preocular 1; postocular 1; temporal 0+1. Tail length .08 of total.

Colouration. Top of head and neck black, extending laterally on the neck to form a half collar as in *Aparallactus capensis;* a pair of yellow spots on the sutures of supraoculars and parietals, sometimes another pair of light spots behind the parietals; black stripes extending through the eye to the mouth and from the parietal to the angle of the jaw; rest of upper labials and chin yellow. Body yellow, with a black vertebral stripe 2 scales wide, followed by an interspace 2 scales wide, then a black lateral stripe 1 scale in width. Below, bright orange. Posterior third of the blunt tail is black, blotched with white, to simulate the head.

Size. Largest (NM/M.246) 423 (390+33) mm. from Karoi.

Distribution. Restricted to the northern parts of Southern Rhodesia, i.e. the Zambezi and its tributaries.

Localities: Karoi; Sinoia; Lukosi; Gatooma.

APARALLACTUS LUNULATUS LUNULATUS (Peters)

Uriechis lunulatus Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 323.

Variation. (9 specimens.) Midbody scale rows 15, ventrals 148-173; anal entire; subcaudals 55-62; upper labials 6, the third and fourth entering the orbit; lower labials 6, the first pair making good contact behind the mental, the first four in contact with the anterior sublinguals; preocular 1; postocular 1; temporals 1+1 (1+2 on one side of a Fatima snake). Tail length .19 to .23 of the total.

Colouration. Juveniles: (a) Odzi. Grey-brown above with light-edged scales; a black "collar" followed by 12 black cross bands; (b) Balla Balla. Uniform plumbeus above, dark grey below. Adults: Head pale brown. Body light grey with the base of each dorsal scale black, giving a reticulated effect; a black half "collar" on neck, followed by up to 12 black spots (these markings are often very faint). Below, uniform white.

Size. Largest (NM/M.925) 428 (345+83) mm. from Essexvale. Smallest (NM/M.452) 161 (125+35) mm. from Balla Balla.

Diet. The largest Essexvale snake took two centipedes while in captivity. I was fortunate enough to witness one of these being overcome. The snake seized the three-inch centipede in the middle of its body and chewed towards the head. Meanwhile the centipede tried to drive its fangs into the snake's neck, but was foiled by the smooth scales. Drops of venom were visible on the snake's neck. The venom of the Centipede-eater soon took effect and the myriapod ceased to struggle and was rapidly swallowed head first.

Habitat. Specimens taken under slabs of granite at Balla Balla and Irisvale.

Distribution. Possibly absent from the higher altitudes, but widely distributed throughout Southern Rhodesia.

Localities: Victoria Falls; West Sebungwe; Fatima; Odzi; 9 miles south of Bulawayo; Essexvale; Balla Balla; Irisvale; Nyamaropa.

APARALLACTUS GUENTHERI Boulenger

Aparallactus Guentheri Boulenger (part), 1895, Ann. Mag. Nat. Hist., ser. 6, vol. 16, p. 172; 1902, p. 18; 1910, p. 516; FitzSimons, F. W., 1912, p. 128; Loveridge, 1953, p. 284; Rose, 1955, p. 119.

Variation. (4 specimens.) Midbody scale rows 15; ventrals 153-163; anal entire; subcaudals 55-59; upper labials 6, the third and fourth entering the orbit; fifth largest and in contact with the parietal; lower labials 5, the first pair not in contact behind the mental, the first three in contact with the anterior sublinguals; preocular 1; postocular 1; temporals 0+1+1. Tail length .21 to .23 of the total.

Colouration. Head dark grey, a narrow sulphur-yellow band crossing rear of parietals, broadening laterally to cover the sixth labial; this is followed by a black interspace 7 scales wide, then another sulphur-yellow band 2 scales wide, expanding on the sides. Chin and throat white or greyish. Rest of body, above and below, iridescent steel-blue. In life, an extremely handsome little snake.

Size. Largest (NM/M.676) 357 (275+82) mm. from Umtali.

Distribution. Apparently replaces *Aparallactus l. lunulatus* at the higher altitudes in Mashonaland and the Eastern Districts.

Localities: Mazoe; Umtali.

APARALLACTUS CAPENSIS CAPENSIS A. Smith

Aparallactus capensis A. Smith, 1849, Ill. Zool. S. Africa, Rept., App., p. 16; Boulenger, 1902, p. 18; 1910, p. 516; Gough, 1908, p. 33; FitzSimons, F. W., 1912, p. 128; FitzSimons, V. F., 1935, p. 323; 1939, p. 24; Tasman, 1953, p. 33; Rose, 1955, p. 119.

Aparallactus capensis capensis Loveridge (part), 1944, p. 205 (generic revision); Witte and Laurent, 1947, p. 122 (generic revision); FitzSimons, V. F., 1958, p. 210.

Variation. (32 specimens.) Midbody scale rows 15; ventrals 137-170; anal entire; subcaudals 30-51; upper labials 6, the third and fourth entering the orbit, the fifth largest and in contact with the parietal; lower labials 5-6, the first three in contact with the anterior sublinguals, the first pair not in contact behind the mental; preocular 1, in contact with the nasal; postocular 1: temporals 0+1+1. Tail length .13 to .20 of total.

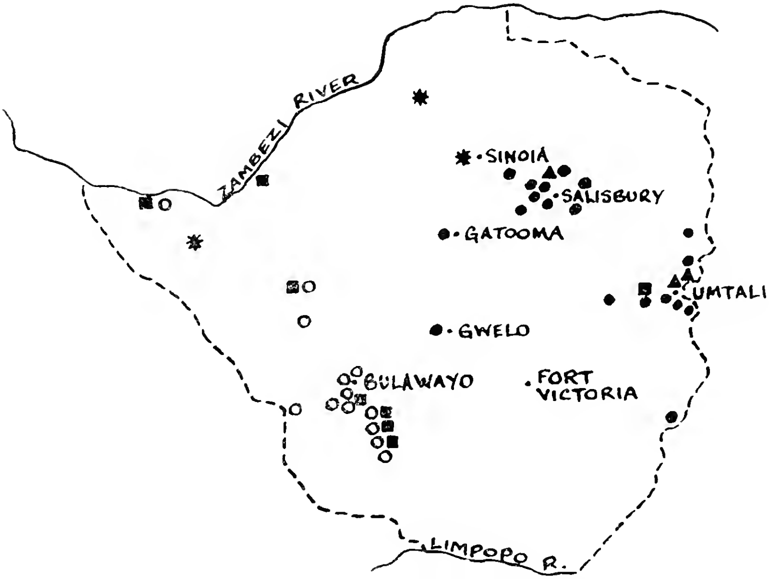

Fig. 5. Recorded localities for *Chilorhinophis* and *Aparallactus*.

* *Chilorhinophis gerardi gerardi* (Boulenger)

■ *Aparallactus lunulatus lunulatus* (Peters)

▲ *Aparallactus guentheri* Boulenger

● *Aparallactus capensis capensis* A. Smith

○ *Aparallactus capensis capensis* × *bocagei*

Colouration. Top of head and neck black, descending on the sides of the neck to form a half "collar"; sometimes a pair of light elongate spots extending back from the ends of the parietals; sides of head black from snout to anterior edge of the fifth labial. Body light grey-brown to bright red-brown, uniform, or with a narrow darker vertebral line, or with five evenly spaced narrow dark lines. Below, uniform white.

Size. Largest (NM/M.1190) 331 (268+63) mm. from Odzi.

Diet. A three-inch centipede recovered from the stomach of a Gatooma snake.

Enemies. The tail of a Cape Centipede-eater was disgorged by a Burrowing Adder (*Atractaspis bibronii* intermediate) taken at the Mchingwe River, Belingwe.

Habits. Taken under stones in many different types of country.

Distribution. Common throughout Mashonaland and the Eastern Districts. I regard Matabeleland specimens as intermediates between the typical form and the race *bocagei* described from Angola (*vide infra*).

Localities: Mazoe; Trelawney; Mount Hampden; Salisbury; Hunyani; Domboshawa; Chishawasha; Kondo; Odzi; Umtali; Imbeza; Nyamaziwa; Vumba Mtn.; Gatooma; Gwelo; Mount Silinda.

APARALLACTUS CAPENSIS CAPENSIS × BOCAGEI

Aparallactus capensis Chubb, 1909a, p. 596; 1909b, p. 36.

Aparallactus capensis capensis Loveridge (part), 1944, p. 205 (generic revision).

Variation. (17 specimens.) Midbody scale rows 15; ventrals 156-181; anal entire; subcaudals 44-63. Lepidosis otherwise as in the typical form. Tail length .17 to .22 of total.

Colouration. As in the typical form except that no specimens have the bright red-brown colouring found in some Mount Hampden snakes. Most specimens have the pair of light spots behind the parietals.

Size. Largest (NM/M.495) 348 (285+63) mm. from Tuli Hill.

Diet. Captive specimens took small centipedes.

Distribution. Matabeleland.

Localities: Victoria Falls; Fatima; Gwaai; Bulawayo; Matopos Dam; Bambata Cave, Matopos; Tuli Hill; Plumtree; Essexvale; Balla Balla; Irisvale; Lumane; Syringa.

Discussion. Analysis of the data for 49 specimens of *Aparallactus capensis* from Southern Rhodesia shows a definite increase in ventral and subcaudal counts from east to west. The lowest ventral counts are 137 and 138 for two Vumba Mountain snakes. At the other extreme are two snakes from the Matopos with 178 ventrals. The Matabeleland snakes, while not approaching the high ventral count of *bocagei* (175-191), do not fall within the accepted range of the typical form, and are best regarded as intermediates. The average counts for the material examined are: *A. c. capensis* . . . ventrals 157, subcaudals 43. *A. c. capensis* × *bocagei* . . . ventrals 167, subcaudals 50.

DASYPELTINAE

DASYPELTIS SCABRA (Linné)

Coluber scaber Linné, 1758, Syst. Nat., ed. 10, 1, p. 223.

Dasypeltis scabra Boulenger, 1894, p. 354; 1902, p. 17; 1910, p. 509; Chubb, 1909a, p. 595; 1909b, p. 35; FitzSimons, F. W., 1912, pp. 90-91; Tasman, 1953, p. 35; Rose, 1955, pp. 98-104; Isemonger, 1955, p. 72.

Variation. (27 specimens.) Midbody scale rows 21-27; ventrals 192-248; anal entire; subcaudals 45-70; upper labials 7, rarely 6, the third and fourth entering the orbit; no loreal; preocular 1 (2 on both sides of a Zambezi snake and one side of a Bulawayo snake); postoculars 2; temporals 2+3; 2+4 or 3+4. Tail length .11 to .17 of the total.

Colouration. Two phases occur. The commonest is the rhombic phase: Light brown or greyish above with a dorsal row of dark elongated blotches and a lateral series of dark vertical bars. A broad V-shaped mark on the neck is usually preceded by a narrower V on the head (sometimes two). A Fatima snake has a double row of coalescing dorsal blotches. Some specimens from Mashonaland and the Eastern Districts are uniform red-brown; this phase seems to predominate around Salisbury. Ventrum white, usually with some brown flecking at the ends of the ventrals.

Size. Largest (UM/R.6) 724 (630+94) mm. from Umtali.

Diet. Captive specimens would take only birds' eggs. Hatchlings consistently refused fresh gecko eggs, which seem quite suitable fare.

Distribution. Found throughout Southern Rhodesia, but scarce.

Localities: Zambezi River, 40 miles east of Chirundu; Mazoe; Salisbury; Chishawasha; Musami; Odzani Falls; Imbeza; Odzi; Umtali; Tandaai; Fatima; 25 miles north of Bulawayo; Bulawayo; Springvale; 9 miles south of Bulawayo; Mount Silinda; Mount Darwin; Bembesi.

ELAPIDAE

ASPIDELAPS SCUTATUS SCUTATUS (A. Smith)

Plate 4, lower figure

Cyrtophis scutatus A. Smith, 1849, Ill. Zool. S. Africa, Rept., App. p. 22.

Aspidelaps scutatus Chubb, 1909a, p. 597; Boulenger, 1910, p. 519; FitzSimons, F. W., 1912, pp. 165-166; Tasman, 1953, p. 24; Isemonger, 1955, p. 85.

Aspidelaps scutata Chubb, 1909b, p. 35.

Variation. (9 specimens.) Midbody scale rows 21; ventrals 113-123; anal entire; subcaudals 23-31; upper labials 6, the fourth entering the orbit; lower labials 7, the first three or four in contact with the anterior sublinguals; preocular 1; postoculars 2-3; temporals 2+4, 2+5 or 2+6, the lower anterior temporal very large, lying between the fifth and sixth labials (in a Kezi snake this shield reaches the lip, excluding the fourth labial). Tail length .14 to .17 of the total.

Colouration. Head black, chin and throat white, with black intrusions at the angle of the jaw; a broad black band, approximately 12 ventrals wide, encircling the neck. Body bright orange flecked with brown, a dorsal series of brown blotches. Ventrum white.

Size. Largest ♂ (NM/M.250) 545 (455+90) mm. from Kezi. Largest ♀ (NM/M.1478) 547 (490+57) mm. from Zezani.

Diet. The big Zezani ♀ took frogs (*Rana d. delalandii; Rana o. oxyrhynchus*) in captivity.

Habitat. The enormous rostral, in broad contact with the prefrontals, immediately distinguishes this fossorial species; it favours sandy localities.

Distribution. Matabeleland.

Localities: Lupane; Bulawayo; Kezi; Sun Yat Sen Mine; Empandene; Zezani; Beitbridge.

ELAPSOIDEA SUNDEVALLII DECOSTERI Boulenger

Elapsoidea Decosteri Boulenger, 1888, Ann. Mag. Nat. Hist., ser. 6, vol. 2, p. 141; Rose, 1955, p. 150; Isemonger, 1955, p. 86.

Elapechis guentheri (not Bocage) Chubb, 1909a, p. 596; 1909b, p. 35; Boulenger, 1910, p. 519; FitzSimons, F. W., 1912, pp. 166-167; Hewitt and Power, 1913, p. 165.

Elapsoidea (*Elapechis*) *guentheri* Tasman, 1953, p. 24.

Elapsoidea guentherii Rose, 1955, p. 150; Isemonger, 1955, p. 86.

Elapsoidea sundevallii decosteri Loveridge, 1944, p. 217 (generic revision).

Variation. (30 specimens.) Midbody scale rows 13; ventrals 137-162; anal entire; subcaudals 14-29; upper labials 7, the third and fourth entering the orbit; the first three or four lower labials in contact with the anterior sublinguals; preocular 1, in contact with the nasal; postoculars 2; temporals 1+2; Tail length .07 to .10 of the total.

Colouration. Juveniles: Head white or greyish, with a black goblet-shaped marking extending along the parietal suture onto the frontal. Body black, with 11 to 14 white cross-bars approximately one third the width of the black interspaces, a further 1 to 3 cross-bars on the tail. Below, chin white, rest of underside dark grey. While the snake is between 200 and 350 mm. in length, the white cross-bars fade out, through a gradual darkening of each scale from the centre. Adults are uniform black above, black or greyish below.

Size. Largest (SM/R.47) 593 (540+53) mm. from Salisbury District. Smallest (NM/M.1178) 178 (160+18) mm. from Bulawayo.

Distribution. Widely distributed throughout Southern Rhodesia, but scarce in Mashonaland and the Eastern Districts.

Localities: Miami; Eldorado; Salisbury District; Kutama; Gatooma; Umtali District; Deka; Wankie; Selukwe; Bulawayo; Matopos; Irisvale; Mavuradona Mts.

NAJA HAJE HAJE (Linné)

Plate 5

Coluber haje Linné, 1758, Syst. Nat., ed. 10, p. 255.

Naia haie Boulenger, 1902, p. 18; 1910, p. 517; Gough, 1908, p. 35; Chubb, 1909a, p. 596; 1909b, p. 36; FitzSimons, F. W., 1912, pp. 163-164; Hewitt and Power, 1913, p. 164; Tasman, 1953, p. 21; Isemonger, 1955, p. 83.

Naia haie var. *annulifera* Chubb, 1909a, p. 597; 1909b, p. 36; Hewitt and Power, 1913, p. 164.
Naja haie Rose, 1955, p. 132.

Native names of Egyptian Cobra. *Pimpi* (Sindebele), but properly applied to *Naja n. mossambica*, sometimes confused with *Dendroaspis p. polylepis* and called *Imamba; Makure* or *Mungu* (for the black phase) (Cheshona). The Banded Cobra (var. *annulifera* of Peters) is known as *Lume* in Sindebele and *Nyamafingu* in Cheshona.

Variation. (79 specimens.) Midbody scale rows 19 (17 in three cobras from Chishawasha, Bulawayo and Essexvale; 18 in one Essexvale snake); ventrals 186-203; anal entire; subcaudals 53-66; upper labials 7, the sixth largest (rarely 6, the fifth largest), normally excluded from the orbit by the suboculars (entering the orbit in three Bulawayo snakes: (a) third labial on each side; (b) second on one side and third on the other; (c) third on one side and third and fourth on the other); preocular 1; suboculars 2-3; postoculars 2, rarely 3; temporals 1+2 or 1+3. Tail length .14 to .18 of the total.

Colouration. Juveniles: Head brown, body dull yellow with a broad black band encircling the neck, ventrum bright yellow. Hatchlings belonging to the variety *annulifera* have barely discernible light and dark yellow bands. The first yellow band is clearly visible against the black on the back of the hood.

Adults: Head dark brown to black, body grey-brown (most Mashonaland snakes) to ashy black (most Matabeleland snakes). Below, yellow more or less mottled with brown, a broad (ca. 10 ventrals wide) purplish-brown band on the throat. In many Matabeleland cobras the belly gradually darkens from the tail towards the head, adults often becoming uniform black above and below with only the chin left yellow. Occasional specimens retain the lighter colouring of the juvenile and become an attractive orange-brown, with pink interstitial skin.

In the variety *annulifera* Peters the yellow livery of the juvenile is partially retained, while the rest of the body becomes even darker than usual. The normal colouring is: Head dark brown, body blue-black with from 7 to 11 bright yellow or creamy white cross bands, which are normally about half the width of the black interspaces. The belly is bright yellow, uniform, or more often blotched with black where the cross bands would continue.

In some specimens the body is completely ringed in black and yellow. The first band, in the centre of the "hood," is very narrow and is often broadened in the centre with a black median spot, reminiscent of the hood marking of the "monocellate" variety of *Naja naja*. One Umtali snake had a series of yellow dorsal blotches instead of bands. Another Umtali snake had a single yellow band just before the vent, the rest of the body being uniform black.

Size. Largest ♂ (NM/M.1373) 2285 (1905+380) mm. from Nyamandhlovu. Largest ♀ (NM/M.393) 2238 (1900+338) mm. from 7 miles north of Bulawayo. Smallest (T.M.) 302 (250+52) mm. from Amandas. This species appears to reach a length in excess of 10 feet.

Discussion. Naja haje var. *annulifera* Peters is represented by 26 of the 79 specimens for which data is available. The only difference in scale counts is a slightly higher average for subcaudals in *annulifera*. All the specimens of *annulifera* that I have sexed have been males, but some typical *haje* are also males, so there is no clear-cut sexual distinction. Unlike most species, the males seem to grow at least as large as the females. The record Nyamandhlovu specimen is an *annulifera*, as are two other big males of 2118 and 1943 mm. This handsome variety has not been recorded north of the Zambezi, but is known from Mozambique (Tete, type locality), Transvaal and Bechuanaland.

Diet. The largest ♀ contained a ♀ *Bitis a. arietans* 2′5″ in length, which in turn contained 19 fully formed young. A 6½-foot *annulifera* from Redbank had also swallowed an adult puffadder. A 5-foot cobra, captured on the Umzingwane River at Essexvale, disgorged five toads (*Bufo regularis*). Stomachs examined usually contained toads or amphibian remains. Cobras are persistent raiders of poultry runs. A 6-foot cobra killed at Irisvale contained two well-grown chickens. The Rev. K. Tasman, S.J. records (*in litt.*) a cobra of 7′1″ (killed in a poultry run) which contained 12 eggs. Another snake contained five ducklings. Tasman reports that 7 out of 17 stomachs with recognisable prey contained warm-blooded animals (rats and ducklings). Captive specimens took toads (*Bufo regularis; Bufo carens*); frogs (*Rana* spp.); chamaeleons (*Chamaeleo d. dilepis*) and snakes (*Boaedon f. fuliginosus; Psammophis s. sibilans; Naja n. mossambica; Causus defilippii*); one took a rat.

Parasites. Many specimens harbour ticks (*Aponomma latum*). The largest male was full of nematodes.

Enemies. While collecting along the N'sese River on the edge of the Matopos, I disturbed a fine Martial Eagle (*Polemaetus bellicosus*), which rose with a dead six-foot cobra in its talons.

Defence. Normally a cobra tries to escape when disturbed, but if taken by surprise or cornered, it rears and spreads a broad "hood," but does not strike unless molested. If left alone, it soon drops to the ground and tries to escape. Occasional specimens will attack if provoked; twice, cobras have turned and come straight at me when I attempted to catch them; both were *annulifera*. Some specimens sham death after capture. The first cobra I ever captured was a 4′9″ *Naja h. haje* which "played possum" very convincingly. I measured the "corpse," took all the scale counts, removed numerous ticks, examined the fangs and washed some sand out of the mouth. The cobra seemed quite lifeless, which puzzled me as I had not been rough while catching it. While I was getting out my skinning knives, the "corpse" came to life and started to glide across the floor!

Venom. The glands of an adult cobra contain a large quantity of the powerful neurotoxic venom. The only bite received personally was from a two-foot juvenile, which quietly started to chew my finger while I was handling it. I ligatured the finger at the base, cut and sucked the punctures and had no symptoms of poisoning whatsoever.

Habits. Cobras do most of their hunting at night, but may often be found basking near their holes during the day, particularly in the early morning. The usual lair is a disused termitarium, but rat holes and mole runs are sometimes used. I have no records of this species taking to the water or climbing trees.

Habitat. This species does not share the Spitting Cobra's preference for waterside localities, but I found it abundant near Mount Hampden in an extensive vlei which is inundated during the rains. The cobras lived in the numerous large termitaria, the only dry spots.

Distribution. Common throughout Southern Rhodesia.

Localities: Trelawney; Horseshoe Block; Mazoe; Amandas;

Mount Hampden; Salisbury; Chishawasha; Marandellas; Monte Cassino; Odzi; Umtali; Vumba Mountain; Zambezi-Sebungwe Junction; Gwelo; Nyamandhlovu; Redbank; Bulawayo; Matopos; Plumtree; Springvale; Essexvale; N'cema Dam; Balla Balla; Irisvale; Stanmore; Tod's Hotel, West Nicholson; Umshagashe River; Bubye River; Umvuma; Cyrene; Figtree.

NAJA HAJE ANCHIETAE Bocage

Naja anchietae Bocage, 1880, Jour. Sci. Lisboa, vol. vii, pp. 89, 98.

Discussion. This race is distinguished from the typical form by having only 17 midbody scale rows. Two cobras from Chishawasha and Bulawayo have 17 scale rows, as does an *annulifera* from Essexvale, but as they occur in the midst of a population of typical *haje* with 19 rows I regard them as aberrant specimens.

As *Naja haje anchietae* has been recorded from Livingstone in Northern Rhodesia and Kabulabula in N.E. Bechuanaland, both on the Southern Rhodesian border, this race probably occurs in the northwest corner of the colony.

NAJA NIGRICOLLIS MOSSAMBICA Peters

Plate 6, upper figure

Naja mossambica Peters, 1854, Monatsb. Akad. Wiss. Berlin, p. 625.

Naia nigricollis (not Reinhardt) Boulenger, 1902, p. 18; 1910, p. 518; Chubb, 1909a, p. 597; 1909b, p. 36; FitzSimons, F. W., 1912, pp. 164, 165; Hewitt and Power, 1913, p. 65; Tasman, 1953, p. 22.

Naja nigricollis (not Reinhardt) Rose, 1955, pp. 128-132; Isemonger, 1955, p. 84.

Native Name of the Mozambique Spitting Cobra. *Pimpi* (Sindebele), correctly applied to this species, but often applied to other brown, grey or blackish snakes.

Variation. (79 specimens.) Midbody scale rows 21-25 (68 snakes have 23); ventrals 182-203; anal entire; subcaudals 54-70; upper labials 6-7, the third, rarely the fourth, entering the orbit; preoculars 2; postoculars 3; temporals 2+4, 2+5, 3+4, 3+5, 3+6 or 3+7. Tail length .15 to .19 of the total.

Colouration. Above, head light brown, body light grey to grey-brown, scales black tipped. Below, salmon-pink to yellowish, with an irregular series of black cross-bands and blotches on the throat.

Size. Largest (NM/M.973) 1543 (1285+258) mm. from Essexvale. Smallest (NM/M.765) 292 (240+52) mm. from Chirinda Forest. This is a smaller species than *Naja h. haje*, averaging less than 4 feet in length.

Discussion. The species of the genus *Naja* are sorely in need of revision, none more so than *Naja nigricollis.* Two well-defined races occur in Rhodesia. *Naja nigricollis crawshayi* Günther ranges through Northern Rhodesia as far south as Lusaka and Fort Jameson. *Naja nigricollis mossambica* Peters occurs in the south of Northern Rhodesia, Nyasaland and S.W. Tanganyika, ranging south through Southern Rhodesia and Mozambique into the Union of South Africa. These races may be separated as follows:

Midbody scale rows 17-21 (usually 19); above, dark brown to black; below, yellowish to grey, with a *single* broad black band on the throat . . . *Naja nigricollis crawshayi* Günther.

Midbody scale rows 21-25 (usually 23); above, light grey or brown with black-tipped scales; below, pinkish or yellowish white, with a *series* of black bands and blotches on the throat . . . *Naja nigricollis mossambica* Peters.

Diet. A cobra captured beside the N'sese River at Irisvale disgorged the posterior half of South-eastern Green Snake (*Philothamnus hoplogaster*). An Imbeza snake disgorged a Slug-eater (*Duberria l. rhodesiana*). Numerous stomachs examined contained amphibians. This species also raids poultry runs, a 4-foot Irisvale cobra contained four small chickens. Captive specimens took toads (*Bufo regularis; Bufo carens*); frogs (*Rana* spp.); dead snakes. This species is truly cannibalistic, for a 4-foot cobra swallowed a 12″ juvenile when it was placed in the same cage.

Parasites. Most specimens carry a few ticks, but an aestivating cobra, killed when a culvert was demolished near Bulawayo, yielded 21 adults and 35 larvae of *Aponomma latum;* many more escaped.

Defence. Although it invariably tries to escape from man if possible, this cobra needs little provocation to make it start "spitting." The snake rears and spreads a long narrow "hood," very different from that of *Naja h. haje.* Occasionally a cobra will rear higher and higher until it is supported by little more than its tail. In these circumstances the snake will repeatedly overbalance, but a cobra with no more than a third of its length on the ground can balance itself beautifully, recoiling from a strike like a piece of sprung steel. When "spitting," the cobra draws the head back, opens the mouth, then, as the venom is forced down the fangs and through the bend at the tip, the head is thrown forward and a blast of air from the glottis assists the twin jets of venom to reach the target. The cobra aims for the eyes and is very accurate. A four-foot cobra has a range of from six to eight feet; although drops of venom travel farther than this, the range is too great for them to reach eye level. A cobra can continue to spit almost indefinitely; I have never managed to exhaust the supply of venom except by persuading the snake to discharge its venom repeatedly for several days. Even then the supply of venom is replenished in a day or two. This species seems to rely primarily on blinding an aggressor with venom and rarely tries to bite in the normal way.

Habits. This cobra is very plentiful along streams in Matabeleland. It often takes to the water when disturbed, swimming strongly on the surface with head down. Although often found living in termitaria, this is the only snake that I regularly find in rock crevices. Whenever a stream flows past fissured rocks, there will be found *Naja n. mossambica*, or at least the tell-tale sloughs. A well-populated fissure, in a granite outcrop at Irisvale, contained two four-foot Spitting Cobras, a dozen geckos (*Pachydactylus bibronii*), a few other lizards and a big scorpion (*Opistopthalmus*)! This species sometimes climbs trees. One evening, while in camp at Beitbridge, I found a Spitting Cobra climbing the tree that I was reclining against! I have also taken a juvenile on a branch ten feet from the ground at Irisvale.

Distribution. Abundant in south Matabeleland, where it is probably the commonest snake. The species is less common elsewhere in the colony and is extremely scarce around Salisbury.

Localities: Sinoia; Eldorado; Trelawney; Mazoe; Bindura; Salisbury District; Penhalonga; Imbeza; Odzi; Umtali; Hunter's Road; Wankie; Deka; Ntabezinduna; Nyamandhlovu; Bulawayo; Syringa; Empandene; Essexvale; Balla Balla; Filabusi; Irisvale; Sinkukwe; Glass Block; Mazeppa Mine, Gwanda; Beitbridge; Umzilizwe River; Chirinda Forest; Mount Darwin; Umvuma.

NAJA MELANOLEUCA Hallowell

Plate 6, lower figure

Naja haje var. *melanoleuca* Hallowell, 1857, Proc. Acad. Nat. Sci. Philadelphia, p. 61.

Data of unique specimen. Midbody scale rows 19; ventrals 215; subcaudals 67; upper labials 7, the third and fourth entering the orbit, the sixth largest and in contact with the postoculars; preocular 1; postoculars 3; temporals 1+2 or 1+3. Tail length .17 of the total.

Colouration. Light grey-brown above, freely speckled with black, tail dark brown. Belly bright yellow, heavily spotted with black, no bands on the throat. Upper labials yellowish, with only faint traces of the back sutures characteristic of the species.

Size. 1690 (1410+280) mm. from Mount Silinda.

Diet. The only food taken while in captivity consisted of two dead rats and two Blind-snakes (*Typhlops s. mucruso*).

Parasites. Numerous ticks found on this cobra were identified as *Aponomma latum* by Dr. G. Theiler.

Defence. This is a much faster species than the other local cobras. When cornered it rears and spreads a long narrow hood, similar to that of *Naja n. mossambica.* It is a formidable reptile to capture.

Temperament. In captivity, this specimen is much quieter and less nervous than the other cobras; it never spreads a hood or strikes at the glass when I pass the cage, as specimens of *Naja h. haje* invariably do.

Habitat. This specimen was taken as it emerged from a hole a yard from the edge of a strip of forest, where it borders mealie lands on the summit of Mount Silinda. On an earlier expedition I disturbed a huge cobra about eight feet in length, which was basking on a mat of floating grasses on the Umzilizwe River, below Mount Silinda. The cobra slid to the edge of the vegetation and dived to the bottom of a deep pool.

Distribution. Liable to be found in suitable localities anywhere along the Eastern Border of Southern Rhodesia.

Localities: Umzilizwe River; Mount Silinda.

DENDROASPIS ANGUSTICEPS (A. Smith)

Naia angusticeps A. Smith (part), 1849, Ill. Zool. S. Africa, Rept., pl. lxx.
Dendroaspis angusticeps Loveridge, 1950, p. 251.

Data for unique specimen. Midbody scale rows 17 (usually 19); ventrals 214; anal divided; subcaudals 120; upper labials 8-9, the fourth entering the orbit. Tail length .25 of the total.

Size. ♂ (M.C.Z. 29182) 1702 (1275+427) mm. from Mount Silinda.

Distribution. The Green Mamba may be found in any of the forested areas of the Eastern Districts.

Localities: Mount Silinda.

DENDROASPIS POLYLEPIS POLYLEPIS (Günther)

Dendraspis polylepis Günther, 1864, Proc. Zool. Soc. London, p. 310.
Dendraspis angusticeps Boulenger (part) 1910, p. 520; FitzSimons, F. W. (part), 1912, pp. 169, 170.
Dendroaspis angusticeps Tasman, 1953, p. 20.
Dendroaspis polylepis Rose, 1955, pp. 143-147; Isemonger, 1955, p. 81.

Native Name of the "Black" Mamba. *Imamba* (Sindebele); *N'zayo* (Cheshona).

Variation. (24 specimens.) Midbody scale rows 21-25; ventrals 256-275; anal divided; subcaudals 115-131; upper labials 8-9, the fourth[1] entering the orbit; preoculars 3; postoculars 3-4 (1, through fusion, on one side of a Selukwe snake); temporals 2+3 (usual), 2+4 or 3+3. Fusion of head shields common, particularly the sixth labial and lower anterior temporal. Tail length .20 to .22 of total.

Colouration. Above, very dark olive-green when freshly sloughed, rapidly becoming dark brown, grey-brown or olive, sometimes mottled with blackish-brown towards the tail. Below, dirty white or greenish white, often with dark mottlings posteriorly.

Size. Largest (NM/M.372) 2875 (2280+595) mm. from 20 miles north of Bulawayo. Detailed measurements are available for only 10 specimens, the rest consisting of skins and heads. The species reaches a length of 14 feet.

Parasites. Ticks from an Odzi specimen were identified as

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[1] Fifth on one side of a Bubye River snake.

Aponomma latum by Dr. G. Theiler. Most mambas have a few of these ticks on the neck.

Defence. Normally the mamba receives ample warning of the approach of man and quietly glides into cover. If taken by surprise or cornered, the mamba usually attempts to intimidate the enemy. This was well demonstrated by a huge mamba I found in a gravel pit near Balla Balla. The snake was at least 12 feet in length and was basking between a large termitarium and a track. I cut off the mamba from its anthill and pushed a noose in front of it as it made for home. As it reached the noose, the mamba reared up to the level of my face, spread a broad "hood" and opened its mouth, displaying the black interior and formidable fangs. With that terrible head only 18″ from my nose, I lost much of my enthusiasm and recoiled. Thereupon the mamba dropped to the ground and streaked down a hole in the termitarium[1].

Habitat. Mambas are often found on granite kopjes, where they live in rock crevices. In open thorn-bush they usually occupy disused termitaria.

Distribution. Throughout Southern Rhodesia, excluding the highlands over 5,000 feet. Most plentiful in the low-lying river valleys.

Localities: Inyazura; Odzi; Grand Reef; Umtali; Hot Springs; Umvumvumvu River; Hartley; Que Que; Wankie; West Sebungwe; Fatima to Bulawayo; Turk Mine; Heany; Selukwe; Inyati; Nyamandhlovu; Plumtree; Matopos; Balla Balla; Beitbridge; Shabani; Devuli River; Bubye River; Umvuma.

VIPERIDAE

Atractaspis bibronii bibronii A. Smith

Atractaspis bibronii A. Smith, 1849, Ill. Zool. S. Africa, Rept., pl. lxxi.

Variation. (7 specimens.) Midbody scale rows 21; ventrals 218-236; anal entire; subcaudals 19-26, single; upper labials 5, the third and fourth, rarely fourth only, entering the orbit; lower labials 5, the first pair in contact behind the mental, the first three in contact with the anterior sublinguals, the third much the larg-

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[1] Enemies — a 26½″ mamba was disgorged by a *Psammophis s. sibilans* captured at Umvuma by D. S. Rider.

est; preocular 1; postocular 1; temporals 1+2. Tail length .05 to .07 of the total.

Colouration. Uniform purplish black above and below.

Size. Largest (SM/R.52) 538 (510+28) mm. from Umtali.

Venom. At 5 p.m. on 20.viii.55 I was bitten by a 318 mm. ♂ Burrowing Adder. I turned over a stone on an Umtali hillside and exposed the snake, which promptly dived down its hole. I seized the tail and pulled steadily, but the snake reversed suddenly and bit me twice on the left index finger and once on the right before I got it into a bag. As the adder was only a juvenile I decided to let the venom run its course and observe the effects. After 15 minutes the left finger was slightly swollen and a feeling of depression was observed. By 9 p.m. the left hand was swollen but not very painful and the depression had gone.

During the night the hand and wrist became excessively swollen; the index finger was twice its normal size and painful. The right index finger, having received a smaller amount of venom, was only slightly swollen, but the glands under both armpits were swollen. I was persuaded to go to the hospital, and was admitted at 7.30 a.m. I was given 10 cc. of Polyvalent Serum and also penicillin injections every six hours. The left hand was poulticed and this helped to bring the hand down to normal size after four days. A large blood blister formed at the fang punctures; this was cut open and drained for several days. On the 28th August a rash appeared on my limbs and spread throughout my body before disappearing. I was discharged from the hospital the following day, but exercise brought on a severe recurrence of the serum reaction. This time, in addition to the rash, I suffered paralysis of the knees and fingers. I returned to the hospital, where calcium injections loosened the joints after 24 hours. I had violent recurrences of the rash for another three days. The dead flesh around the fang punctures sloughed away, leaving a pit ¼ inch deep. I finally left the hospital on September 3rd.

Habits. This fossorial species is usually found under stones; a burrow often extends downwards for a foot or so, providing the snake with a more secure retreat.

Distribution. The eastern districts of Southern Rhodesia. The rest of the colony is inhabited by a population of intermediates.

Localities: Odzi; Imbeza; Umtali.

ATRACTASPIS BIBRONI × ROSTRATA

Atractaspis bibronii (not A. Smith) Chubb, 1909b, p. 36; Tasman, 1953, p. 27; Isemonger, 1955, p. 90.

Variation. (23 specimens.) Midbody scale rows 21-23; ventrals 217-252; anal entire; subcaudals 20-27, mostly single; upper labials 5, the third and fourth entering the orbit (4, the second and third entering the orbit, on one side of an Essexvale snake); lower labials 5, the first pair in contact behind the mental, the first three in contact with the anterior sublinguals, the third much the largest; preocular 1; postocular 1; temporals 1+2 (1+3 on one side of a Chishawasha snake). Tail length .05 to .07 of the total.

Colouration. Uniform purplish-black above and below. Five snakes from Nyamandhlovu, Plumtree, Irisvale and Mchingwe River have the outer two rows of dorsal scales and the whole of the ventrum white. A Chishawasha snake has the sides and belly brownish with white blotches.

Size. Largest (NM/M.720) 553 (524+29) mm. from Chishawasha.

Diet. A Bulawayo snake contained a *Nucras intertexta holubi* with a head and body length of 75 mm. A Plumtree snake disgorged another lizard of the same species. A small specimen taken near the Mchingwe River disgorged the tail and partially digested body of a Cape Centipede-eater (*Aparallactus c. capensis*).

Venom. On 30.ix.55 I was bitten on the tip of the second finger of my left hand by the large Burrowing Adder from Chishawasha, recorded above. As I pinned the snake down, it twisted round and struck with one fang. This species does not open its mouth to bite; instead the lower jaw is contracted and the fangs brought down on each side of it. I ligatured the digit at the base and made some longitudinal cuts before squeezing out as much venom as possible. The finger became swollen during the night, with the characteristic throbbing pain. By the following day the pain had almost gone and I was fit enough to capture a ten-foot python.

Habits. As for the typical form. One specimen was taken at night as it was crossing a road.

Distribution. These snakes are intermediate between the typical form of South Africa and the race *rostrata* found north of the Zambezi. Whereas typical *bibronii* normally has 21 midbody scale rows and the race *rostrata* 23 rows, throughout most of Southern Rhodesia snakes with 21 and 23 scale rows occur side by side.

Localities: West Sebungwe; Trelawney; Chishawasha; Sawmills; Nyamandhlovu; Bulawayo; Plumtree; Essexvale; Balla Balla; Irisvale; Mchingwe River, Belingwe District; Bembesi.

CAUSUS RHOMBEATUS (Lichtenstein)

Sepedon rhombeatus Lichtenstein, 1823, Verz. Doubl. Mus. Berlin, p. 106.

Causus rhombeatus Boulenger 1902, p. 18; 1910, p. 521; Gough, 1908, p. 38; Chubb, 1909b, p. 36; FitzSimons, F. W., 1912, pp. 215, 216; Hewitt and Power, 1913, p. 165; FitzSimons, V. F., 1939, p. 24; Tasman, 1953, p. 27; Rose, 1955, pp. 166-167; Isemonger, 1955, p. 87; Broadley, 1957b, p. 115.

Native names of Rhombic Night-adder. *Changwa* (Sindebele); *Cheewa* (Cheshona).

Variation. (48 specimens.) Midbody scale rows 17-18, rarely 19; ventrals 138-151; anal entire; subcaudals 24-32; upper labials 6, excluded from the orbit; preoculars 1-3; suboculars 1-2; postoculars 1-2; temporals 2+3. Tail length .09 to .12 of the total.

Colouration. Above, pinkish, grey-brown or grey-green, with a darker forward-directed "V" on the head and a series of large, white or yellow-edged, dorsal rhombs. These markings may be very faint, often only visible when the body is inflated in anger. A Mount Hampden ♂ was uniform pinkish brown without a trace of markings. A series of dark lines radiate from the orbit. Ventrum, mother of pearl white to pinkish grey or black.

Size. Largest (UM/R.13) 813 (735+78) mm. from Odzani. Smallest (NM/M.806) 224 (203+21) mm. from Essexvale.

Breeding. A 578 mm. snake laid 14 eggs on 8.x.57.

Diet. Toads (*Bufo regularis* and *Bufo carens*) form the greater part of the night-adder's diet. Frogs (*Rana* spp.) are also taken.

Enemies. A Selukwe snake was killed by a chicken.

Defence. The normal reaction to a disturbance is to coil up and inflate the body with air, at the same time hissing loudly. Occasionally a specimen will flatten its neck after the manner of a cobra and make off slowly.

Venom. W. Armitage of Umtali was bitten on the tip of his left index finger by an adult nightadder, which penetrated with only one fang. A burning pain was felt at the fang puncture. A ligature was applied and the bite cut open; it proved impossible to induce bleeding. After half an hour sporadic pains were experienced as far as the wrist. Patient hot and flushed. The following day found the victim depressed and suffering from a headache and sore throat. Another 24 hours brought pains in the kidneys and the next day saw the patient confined to bed with a fever which broke the same evening, 72 hours after the bite.

Habits. This species mainly hunts its amphibian prey at night, although it may often be found basking during the day. A large uniform grey male, taken on Vumba Mountain, was engaged in swallowing a large *Bufo regularis* at 3 p.m. on a sunny day.

Longevity. A Mount Hampden snake lived for 27 months in captivity and grew from 560 mm. to 720 mm. in total length.

Distribution. Widely distributed throughout Southern Rhodesia. Common in Mashonaland and the Eastern Districts but rather scarce in Matabeleland.

Localities: Trelawney; Mazoe; Mount Hampden; Salisbury; Hunyani; Prince Edward Dam; Chishawasha; Marandellas; Odzi; Inyanga; Odzani; Vumba Mtn.; Chirinda Forest; Gatooma; Selukwe; Bulawayo; Tuli Reservoir; Hope Fountain; Matopos; Cyrene; Empandene; Essexvale.

CAUSUS DEFILIPPII (Jan)

Heterodon De Filippii Jan, 1862, Zool. Anat. Fisiol., 2, p. 225.

Causus defilippii Boulenger, 1902, p. 18; 1910, p. 521; Chubb, 1909a, p. 597; 1909b, p. 36; FitzSimons, F. W., 1912, pp. 215, 216; FitzSimons, V. F., 1939, p. 24; Tasman, 1953, p. 27; Broadley, 1957b, p. 115.

Causus dephillippii (*sic*) Rose, 1955, p. 167.

Causus defillippii (*sic*) Isemonger, 1955, p. 88.

Native name of Snouted Night-adder. *Changwa* (Sindebele), but generic.

Variation. (53 specimens.) Midbody scale rows 17, rarely 16 or 18; ventrals 112-127; anal entire; subcaudals 10-19; upper labials 6-7, excluded from the orbit (3rd labial enters orbit on one side of a Chirinda Forest snake); preoculars 2; suboculars 1-2 (rarely 0 or 3); postoculars 1-2; temporals 2+3. Tail length .05 to .09 of the total.

Colouration. Above, pink, mauve or pale brown, with a broad, slightly darker, dorsal stripe and a vertebral series of large, dark brown, blotches or backward-directed chevrons. A well-defined "V" on the back of the head has its apex on the frontal. A dark band passes through the orbit and the labial sutures are black. Below, glossy black in juveniles, becoming lighter in adults.

Size. Largest 410 (380+30) mm. from Umtali. Smallest (NM/M.715) 102 (95+7) mm. from Bulawayo.

Sexual dimorphism. In 24 males the range of ventrals is 112-117; range of subcaudals is 14-19, and the tail length is .07 to .09 of the total. In 22 females the range of ventrals is 120-127; range of subcaudals is 10-16, and the tail length is .05 to .07 of the total.

Breeding. A captive ♀ laid two eggs on 1.i.56 and was seen to mate the following day. Many hatchlings are killed while basking on the roads in February and March.

Diet. Captive specimens took small toads (*Bufo regularis; Bufo carens*) and frogs (*Rana delalandii; Phrynobatrachus natalensis*). A captive specimen at Umtali is reported to have seized and swallowed a small *Boaedon f. fuliginosus* in mistake for a frog while being fed. The bulky meal was later disgorged (D. K. Blake).

Defence. These small snakes behave like a puffadder when disturbed, inflating the body with air and hissing fiercely. They seem rather reluctant to bite.

Venom. W. Armitage and D. K. Blake were both bitten on the hand by Umtali specimens within two hours. No treatment was given. In each case the hand became swollen to the wrist and a dull throbbing pain was observed. The swelling subsided after three days, leaving a feeling of stiffness. There was no sloughing away of flesh.

Habits. The prominent upturned rostral suggests fossorial habits, but the habits of this smaller species do not seem to differ from those of *C. rhombeatus.*

Distribution. Widely but rather patchily distributed throughout Southern Rhodesia. This species is locally abundant at Umtali, where it seems to completely replace *C. rhombeatus.* At

Odzi, only 20 miles away, the latter species is common and *defilippii* very scarce.

Localities: Karoi; Trelawney; Mazoe; Salisbury; Musami; Umtali; Vumba Mountain; Chirinda Forest; 165 miles north of Bulawayo; Gwaai; Turk Mine; Bulawayo; Khami; Matopos; Figtree; Empandene; Essexvale; Balla Balla; Irisvale; Mount Darwin.

BITIS ARIETANS ARIETANS (Merrem)

Cobra lachesis Laurenti, 1768, Syn. Rept., p. 104.

Vipera (Echidna) arietans Merrem, 1820, Vers. Syst. Amphib., p. 152.

Bitis arietans Boulenger, 1902, p. 18; 1910, p. 522; Gough, 1908, p. 39; Chubb, 1909a, p. 597; 1909b, p. 36; FitzSimons, F. W., 1912, pp. 216, 217; Hewitt and Power, 1913, p. 165; FitzSimons, V. F., 1939, p. 24; Tasman, 1953; p. 25; Rose, 1955, pp. 156-161; Isemonger, 1955, p. 88.

Native names for the Puffadder. *Ibululu* (Sindebele); *Chiva* or *M'vumbi* (Cheshona).

Variation. (52 specimens.) Midbody scale rows 31-36; ventrals 126-141; anal entire; subcaudals 17-36; smooth; upper labials 12-15. Tail length .05 to .16 of the total.

Colouration. Dark grey to reddish brown above, with backward-directed yellow or white and black chevrons. Yellow below with black markings.

Size. Largest ♂ (NM/M.958) 915 (800+115) mm. from Khami. Largest ♀ 990 (920+70) mm. from Umtali. New-born young measure just over 200 mm. in total length.

Sexual dimorphism. In 23 males the range of ventrals is 126-136; range of subcaudals is 30-36, and the tail length is .12 to .16 of the total. In 27 females the range of ventrals is 131-141; range of subcaudals is 17-25, and the tail length is .06 to .09 of the total.

Breeding. Captive specimens observed mating on 26.viii.56. A 30″ ♀ produced a brood of 35 young on 2.xii.57 at Essexvale. Another Essexvale specimen, 2′8″ in length, contained 37 well-developed young at the beginning of November.

Diet. All stomachs containing food held rats. Captive specimens took rats readily. When hungry, some specimens would take toads (*Bufo carens; Bufo regularis*) rather reluctantly, other consistently refused to take anything but rats and starved to death rather than swallow a toad. On the other hand, juveniles fed readily on small toads and frogs (*Rana delalandii*). One took a shrew (*Crocidura* sp.).

Enemies. On two occasions large cobras (*Naja h. haje*) were found to contain adult puffadders. Both this species and *Naja n. mossambica* readily devoured new-born puffadders in captivity.

Defence. Although it may sometimes try to escape when approached, more often than not the puffadder remains motionless and its colouration makes it difficult to see in dry grass. As it often lies on footpaths through long grass, waiting for an unwary rat, this species is responsible for the majority of the cases of snakebite. Often the puffadder gives warning of its presence by inflating the body with air and hissing fiercely; at the same time the head is drawn back over the body in a striking coil.

Venom. As puffadder bites are invariably received on the limbs, prompt treatment can usually localise the venom and prevent death. The effects are unpleasant, local haemorrhage often causes an area around the bite to turn black and slough away and sloughing of the skin often recurs for several years afterwards.

Habits. The Puffadder does most of its hunting at night, but is often found basking during the day. It frequently becomes a road casualty.

Distribution. Common in Matabeleland but less plentiful in other parts of the colony. This species seems to be very scarce in Salisbury District.

Localities: Sinoia; Mazoe; Hunyani; Gatooma; Salisbury; Marandellas; Odzi; Umtali; Mount Silinda; Chikore; Victoria Falls; Zambezi-Sebungwe Junction; Shangani River; Gwaai; Bulawayo; Khami; Essexvale; Balla Balla; Irisvale; Glass Block; Gwanda; Tod's Hotel; Beitbridge; Mount Darwin; Bubye River; Umvuma.

Bitis gabonica gabonica (Duméril and Bibron)

Echidna gabonica Duméril and Bibron, 1854, VII, p. 1428, pl. lxxxb.
Bitis gabonica Isemonger, 1955, p. 88; FitzSimons, V. F., 1958, p. 211.

Variation. (4 specimens.) Midbody scale rows 39-46; ventrals 134-136; anal entire; subcaudals 19-22; upper labials 16-17. Tail length .06 to .09 of the total. All four specimens are females.

Colouration. Head buff, a dark brown triangular wedge, running from the orbit straight down to the lip and diagonally back to the angle of the jaw; this marking is divided by a narrow light line or spot. A vertebral series of sharply defined buff rectangles are connected by hour-glass shaped rich brown markings. The lateral markings consist of a complex geometrical pattern, composed of bold triangles in shades of buff, purple, brown and pink. The ventrum is buff with dark grey infuscations.

Size. Largest (UM/R.25) 1266 (1196+70) mm. from Dzoroka, Chipinga Dist.

Distribution. This massive viper ascends the river valleys from Mocambique and is liable to be found anywhere along the Eastern Border. It is reported to be not uncommon in the Inyanga Tea Estates. The Stapleford specimen was taken on the edge of a plantation at 6,000 feet.

Localities: Pungwe Valley; Hondi Valley; Stapleford; Dzoroka.

BITIS CAUDALIS (A. Smith)

Vipera caudalis A. Smith, 1839, Ill. Zool. S. Africa, Rept., pl. vii.
Bitis caudalis Chubb, 1909a, p. 597; 1909b, p. 36; Boulenger, 1910, p. 523; FitzSimons, F. W., 1912, pp. 217, 218; Isemonger, 1955, p. 89.
Bitis candalis (misprint) Tasman, 1953, p. 27.

Variation. (8 specimens.) Midbody scale rows 24-27; ventrals 120-134; anal entire; subcaudals 16-26; upper labials 11-13. Tail length .07 to .11 of the total.

Colouration. Males — Head light red-brown passing to grey on the temples, a yellow line connecting the supraocular "horns," dark lines radiating from orbit to mouth, a U-shaped dark red-brown marking on back of head extending as a pair of bars on the neck. Body blue-grey dorsally, with a series of dark red-brown, yellow-edged, blotches, large and more or less oval in shape. Laterally light red-brown with a series of oval markings, which are grey above and dark red-brown, edged with yellow, below. Ventrum white, tinged with orange laterally. Females — Light sandy brown with indistinct rows of dorsal and dorsolateral blotches, which are only slightly darker than the ground colour. Ventrum buff.

Size. Largest ♂ (NM/M.357) 301 (270+31) mm. from Beitbridge. Largest ♀ (NM/M.939) 322 (300+22) mm. from Bulawayo.

Defence. A very truculent and "explosive" little viper. Hisses very loudly for so small a snake and strikes fiercely at anything within range.

Habits. A Horned Viper from Bulawayo could not be induced to "sidewind." Local conditions seem unsuitable for a species which has become specialised for life in loose sand. It would seem that these Bulawayo specimens have spread out of their normal environment.

Distribution. Matabeleland.

Localities: Insiza; Bulawayo; Westacre; Beitbridge.

BITIS ATROPOS (Linné)

Coluber atropos Linné, 1754, Mus. Ad. Frid., p. 22, pl. xiii, fig. 1.
Bitis atropos Isemonger, 1955, p. 90; FitzSimons, V. F., 1958, p. 210.

Variation. (7 specimens.) Midbody scale rows 29-31; ventrals 121-134; anal entire; subcaudals 18-25; upper labials 11-12. Tail length .07 to .11 of the total.

Colouration. Above, grey-brown with a double series of dark dorsal blotches arranged in pairs on either side of the vertebral line: these abut against an ill-defined lighter dorsolateral line, below which there is a similar series of dark blotches. There are some dark markings on the top of the head. Below, chin white or cream with some sharply-defined black markings on the lower labials, ventrum white to dark grey.

Size. Largest ♂ (NM/M.1702) 347 (310+37) mm. from Chimanimani Mts. (5.500′). Largest ♀ (NM/M.1704) 288 (268+20) mm. from Chimanimani Mts. (8,000′).

Diet. A juvenile from Inyanga North, in captivity at Umtali, gorges himself on toads (*Bufo regularis*) until he cannot coil up (D. K. Blake).

Venom. W. W. Armitage of Umtali was bitten on the thumb at 9.30 a.m. on 12.xii.57 by a 5½ inch *Bitis atropos* from Inyanga North. One fang penetrated deeply, the other merely scoring the surface. Cuts were made through the fang punctures, but little bleeding was induced by squeezing. By 9.45 the thumb had begun to swell up and was very painful; the pain eased off after 15 minutes. By 10.45 the patient was light-headed and had difficulty in focusing his eyes. This gradually became worse and his sense of balance was also impaired. By 11 a.m. the patient was staggering and cross-eyed, the eyes being heavy-lidded and vision blurred. Armitage then received a total of 3 cc. polyvalent serum in the thumb and biceps. He was admitted to the hospital 10 minutes later, now only semiconscious and staggering. He had by now lost all sense of taste and smell. The patient was given 20 cc. of polyvalent serum in the buttocks and put to bed. By 11.30 the hand was swollen up to the wrist; the pupils were dilated and showed no reaction to light. By noon the patient was again fully conscious.

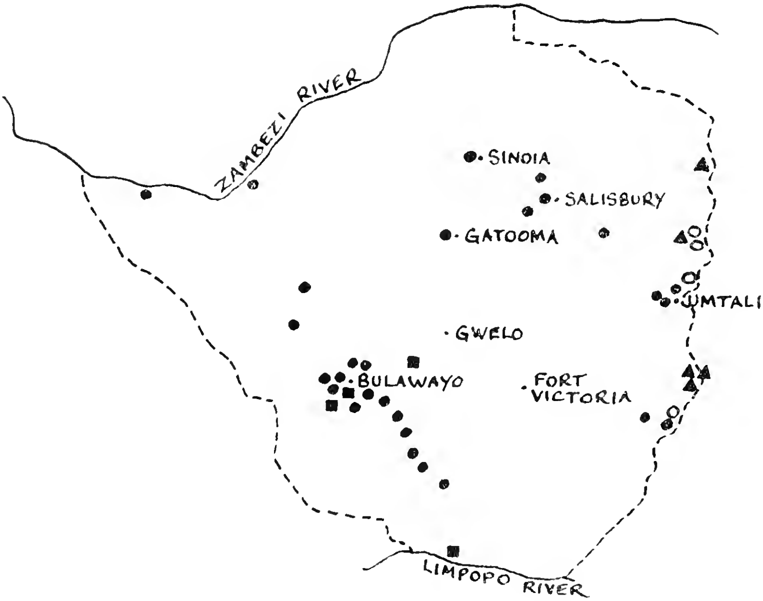

Fig. 6. Recorded localities for *Bitis*.

- ● *Bitis arietans arietans* (Merrem)
- ○ *Bitis gabonica gabonica* (Duméril and Bibron)
- ■ *Bitis caudalis* (A. Smith)
- ▲ *Bitis atropos* (Linné)

Armitage's condition showed no change on the following day, followed by a slight improvement on the 14th. By the 15th, the hand was back to normal, the thumb remaining swollen. The pupils were normal, but the left eyelid remained closed, the right being half open. There was still no sense of taste or smell. Both eyes were fully open the next day and Armitage was discharged from the hospital. His sense of smell returned on the 17th, but focusing of the eyes was still slow. The sense of taste returned the following day. The site of the bite was numb, but there was no sloughing of flesh around the fang punctures, which is a normal feature of viperine bites.

Habitat. The University of Cape Town sent an expedition to the Chimanimani Mountains on the Eastern Border of Southern Rhodesia in February 1958. A member of the Expedition, Mr. J. R. Grindley, collected 4 specimens of *Bitis atropos* and presented them to the National Museum. His field notes on these Mountain Vipers are given verbatim: (NM/M.1701) . . . "In long grass by stream on floor of Bundi Valley at 5,300 ft." (NM/M.1702) . . . "On path to Martin's Falls in open grassland at 5,500 ft." (NM/M.1703) . . . "In grassland above Martin's Falls at 5,000 ft." (NM/M.1704) . . . "In grass near summit of Point 71 at 8,000 ft."

Distribution. The Eastern Districts of Southern Rhodesia. Not entirely restricted to the mountains, for the Inyanga North specimen came from an altitude of approximately 2,500 feet.

Localities: Inyanga North (ca. 2,500′); Pungwe River Causeway (ca. 5000′); Chimanimani Mountains (5,000′ to 8,000′).

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Glossary of Scientific Terms.

Anal, the shield immediately preceding the vent.

Chin-shields, see sublinguals.

Frontal, see Fig. 10.

Internasal, see Fig. 10.

Loreal, see Fig. 10.

Labial, one of the shields bordering the mouth.

Lower labial, see Fig. 10.

Mental, see Fig. 10.

Midbody scales, those, other than ventral shields, encircling the body at a point midway between snout and vent.

Nasal, see Figs. 8, 9, 10.

Ocular, see Figs. 8, 9.

Parietal, see Fig. 10.

Postocular, see Fig. 10.

Prefrontal, see Figs. 8, 9, 10.

Preocular, see Figs. 8, 10.

Rostral, see Figs. 8, 9, 10.

Subcaudals, the series of scales beneath the tail, which may be single or (more often) paired.

Sublinguals, see Fig. 10.

Subocular, see Fig. 10.

Supraocular, see Figs. 8, 9, 10.

Symphysial, see Mental.

Temporal, see Fig. 10.

Upper labial, see Figs. 8, 9, 10.

Ventrals, the series of broad plates on the belly.

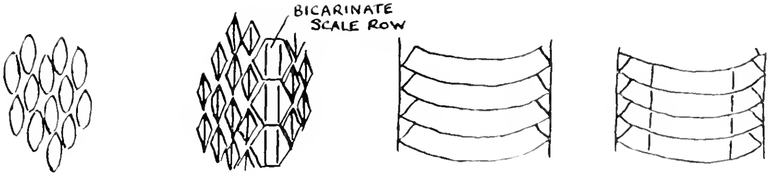

Fig. 7. From left to right, dorsal scales, smooth, dorsal scales, keeled, ventral scales, smooth, ventral scales, keeled.

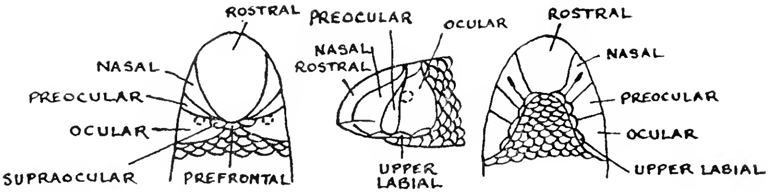

Fig. 8. Head shields of *Typhlops schlegelii mucruso* (Peters).

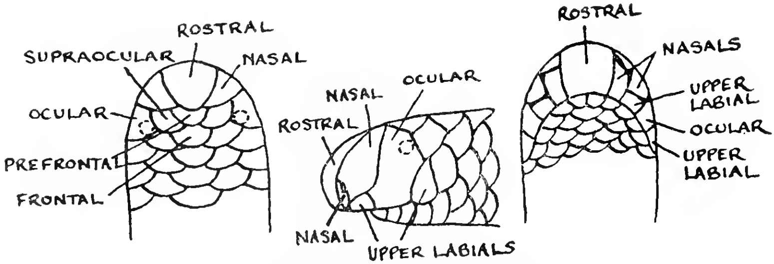

Fig. 9. Head shields of *Leptotyphlops longicauda* (Peters).

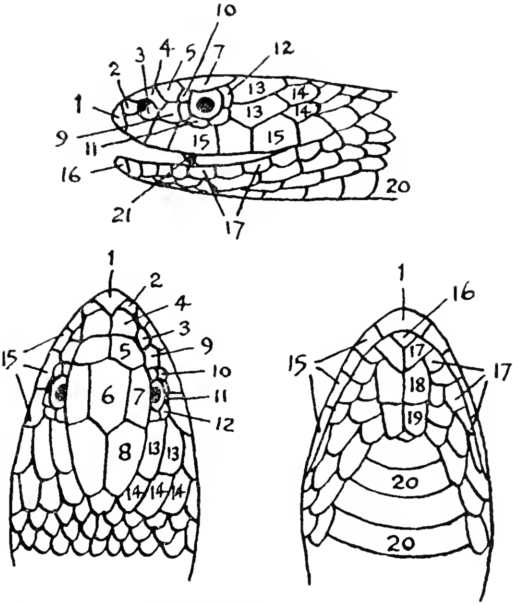

Fig. 10. Head shields of *Causus rhombeatus* (Lichtenstein).

1. rostral;
2. anterior nasal;
3. posterior nasal;
4. internasal;
5. prefrontal;
6. frontal;
7. supraocular;
8. parietal;
9. loreal;
10. preocular;
11. subocular;
12. postocular;
13. anterior temporal;
14. posterior temporal;
15. upper labial;
16. mental;
17. lower labial;
18. anterior sublingual;
19. posterior sublingual;
20. ventral;
21. poison fang.

A Key to the Snakes of Southern Rhodesia

A. *Key to Families*

1. Body encircled by small scales more or less uniform in size; 3 or 4 scales immediately preceding vent; eye minute, when distinguishable, beneath a shield 2

   Body not encircled by small scales owing to the presence on the belly of a longitudinal series of transversely enlarged plates, known as ventrals; 1 or 2 scales immediately preceding vent; eye clearly visible beneath a transparent "watchglass" scale 3

2. Ocular shield not bordering mouth; 18 or more scales round middle of body; tail as long as or only slightly longer than broad; size small to moderate . . . . *TYPHLOPIDAE* (B)
   (Blind-Snakes)

   Ocular shield bordering mouth; 14 scales round middle of body; tail much longer than broad; size very small, wormlike . . . . *LEPTOTYPHLOPIDAE* (C)
   (Worm-Snakes)

3. Ventral shields much narrower than body; midbody scale rows more than 75; vestigial limbs present, discernible as a pair of "claws" before the vent . . . . *BOIDAE* (D)
   (Boas and Pythons)

   Ventral shields as broad as, or nearly as broad as body; midbody scale rows less than 50; no vestigial limbs present 4

4. No enlarged poison fangs at *front* of jaw[1] . . . . *COLUBRIDAE* (E)
   (Typical Snakes)

   One or more pairs of enlarged poison fangs at front of jaw 5

5. Poison fangs immovable, not enclosed in a sheath of membrane . . . . *ELAPIDAE* (F)
   (Cobras, Mambas, etc.)

   Poison fangs movable and very large, so folded back when not in use, encased in a sheath of membrane . . . . *VIPERIDAE* (G)
   (Adders and Vipers)

B. *Key to the TYPHLOPIDAE* (Blind Snakes) *of Southern Rhodesia*

Midbody scale rows 28; diameter into length 41-50 times . . . . *Typhlops delalandii*
(Delaland's Blind-Snake)

Midbody scale rows 30 or more; diameter into length 21-53 times . . . . *Typhlops s. mucruso*
(Zambezi Blind-Snake)

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[1] Warning: Snakes of the genus *Psammophis* have a pair of greatly enlarged fang-like teeth below the anterior border of the eye, the grooved fangs being situated below the posterior border of the eye.

C. *Key to the LEPTOTYPHLOPIDAE* (Worm-Snakes) *of Southern Rhodesia*

1\. Rostral in contact with supraocular; black or grey in colour 2
Rostral separated from supraocular by the nasal; flesh pink in colour *Leptotyphlops longicauda* (Long-tailed Worm-Snake)

2\. Rostral very large, more than twice width of nasal *Leptotyphlops scutifrons* (Peters' Worm-Snake)
Rostral narrow, less than twice width of nasal *Leptotyphlops conjuncta* (Jan's Worm-Snake)

D. *Key to the BOIDAE* (Pythons) *of Southern Rhodesia*

Only one species occurring south of the Zambezi *Python sebae* (African Python)

E. *Key to the COLUBRIDAE* (Typical Snakes) *of Southern Rhodesia*

1\. Subcaudals mostly in pairs 2
Subcaudals single 39

2\. A loreal shield present between postnasal and preocular 3
No loreal shield present 35

3\. Pupil round (horizontal only in *Thelotornis*) AND anal divided 12
Pupil vertically sub-elliptic AND/OR anal entire 4

4\. Dorsal scales smooth 5
Dorsal scales strongly keeled in 15 rows at midbody 11

5\. Snout rounded; prefrontals and internasals paired 6
Snout with angular horizontal edge; prefrontal usually single 22

6\. Midbody scale rows 25-33 *Boaedon f. fuliginosus* (Common House Snake)
Midbody scale rows 15-21 7

7\. Midbody scale rows 15; a single postocular *Duberria l. rhodesiana* (Rhodesian Slug-eater)
Midbody scale rows 17 or more; two or three postoculars 8

8\. No pair of enlarged grooved fangs situated below the posterior border of the eye 9
A pair of enlarged grooved fangs situated below the posterior border of the eye, separated by an interspace from the preceding teeth 24

9\. Midbody scale rows 19-21; subcaudals more than 50; nostril directed upwards from between two nasals; semi-aquatic 10
Midbody scale rows 17; subcaudals less than 50; nostril directed outwards from a single nasal; terrestial *Lycophidion c. capense* (Cape Wolf Snake)

10. Midbody scale rows 19 . . . *Lycodonomorphus r. rufulus* (Brown Water Snake)

Midbody scale rows 21 . . . *Lycodonomorphus r. mlanjensis* (Mlanje Water Snake)

11. Ventrals 195-220; subcaudals 44-58; vertebral scale row and ventrals ivory white . . . *Mehelya c. capensis* (Cape File-Snake)

Ventrals 173-184; subcaudals 60-68; vertebral scale row blackish, ventrals brown . . . *Mehelya nyassae* (Nyasa File-Snake)

12. Midbody scale rows 25-27; snout pointed . . . *Pseudaspis cana* (Mole Snake)

Midbody scale rows 11-21 . . . 13

13. Pupil round . . . 14

Pupil horizontal; body extremely slender and vine-like . . . 27

14. Scales smooth . . . 15

Scales strongly keeled . . . *Dispholidus typus* (Boomslang)

15. A broad dark vertebral band with numerous short cross-bars or staggered to form an irregular zig-zag line; underside dark grey flecked with brown; not exceeding 450 mm. in length . . . *Hemirhagerrhis n. nototaenia* (Eastern Bark-Snake)

Markings and colouration not as above . . . 16

16. No pair of enlarged grooved fangs situated below the posterior border of the eye . . . 17

A pair of enlarged grooved fangs situated below the posterior border of the eye, separated by an interspace from the preceding teeth . . . 28

17. Midbody scale rows 21; ventrals 175-204 . . . *Meizodon s. semiornata* (Semiornate Snake)

Midbody scale rows 19 or fewer . . . 18

18. Midbody scale rows 19; ventrals 140-149 . . . *Natriciteres o. olivacea* (Olive Marsh-Snake)

Midbody scale rows 17 or fewer . . . 19

19. Midbody scale rows 17 (rarely 15); ventrals 132-141; 3 postoculars; colour in life not green . . . *Natriciteres o. uluguruensis* (Montane Marsh-Snake)

Midbody scale rows 15; ventrals 148 or more; 2 postoculars; colour in life green . . . 20

20. Ventrals 148-169; subcaudals 77-115, rounded or angular but without keels . . . 21

Ventrals 179-204; subcaudals 121-142, angular and strongly keeled like the ventrals . . . *Philothamnus s. semivariegatus* (Variegated Bush-Snake)

21\. Usually two labials entering orbit; subcaudals 77-103 .... *Philothamnus hoplogaster*
(Southeastern Green-Snake)
Usually three labials entering orbit; subcaudals 94-115 .... *Philothamnus i. irregularis*[1]
(Western Green-Snake)

22\. Internasal single; snout horizontal .... *Prosymna a. stuhlmanni*
(Eastern Shovel-snout)
Internasals paired; snout upturned 23

23\. Internasals forming a median suture; habit moderate .... *Prosymna lineata*
(Peters' Shovel-snout)
Internasals separated by rostral; habit slender .... *Prosymna s. sundevallii*
(Sundevall's Shovel-snout)

24\. Midbody scale rows 19 25
Midbody scale rows 17 26

25\. Ventrals 202-241; salmon pink above with black dorsal blotches .... *Telescopus s. semiannulatus*
(Tiger Snake)
Ventrals 154-168; black to olive above, flecked with white .... *Crotaphopeltis h. hotamboeia*
(White-lipped Snake)

26\. Ventrals 172-195; eye large with vertically elliptical pupil .... *Chamaetortus a. aulicus*
(Cross-barred Tree-Snake)
Ventrals 133-149; eye moderate with round pupil .... *Amplorhinus multimaculatus*
(Many-spotted Snake)

27\. Ventrals 163-176; range northwest of colony .... *Thelotornis k. oatesii*
(Oates' Vine-Snake)
Ventrals 146-164; range southeast of colony .... *Thelotornis k. capensis*
(Cape Vine-Snake)

28\. Rostral shield on snout prominent, beak-like; colour above pinkish-brown .... *Rhamphiophis o. rostratus*
(Eastern Brown Beaked-Snake)
Rostral shield on snout rounded normally 29

29\. Maxillary teeth form a continuous series up to the interspace which separates them from the posterior pair of enlarged grooved fangs 30
Maxillary teeth interrupted below the anterior border of the eye by two greatly enlarged fang-like teeth, separated before and behind by an interspace, followed by more small maxillary teeth, then a third inter-

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[1] If a brown dorsal stripe is present, refer to *Philothamnus ornatus* (Ornate Green-Snake).

space preceding the enlarged grooved fangs situated below the posterior border of the eye 31

30\. Usually a single anterior temporal; subcaudals 83-105; ventral markings consist of short black *transverse* dashes at ends of ventrals .... *Dromophis lineatus* (Buff-striped Grass-Snake)

Two anterior temporals; subcaudals 50-67; pink flecking at ends of ventrals .... *Psammophylax t. tritaeniatus* (Three-lined Grass-Snake)

31\. Midbody scale rows 17 32

Midbody scale rows less than 17 33

32\. Habit robust; uniform olive above or with black scale edgings forming narrow black longitudinal lines; yellow or white below, uniform or with an ill-defined series of longitudinal, discontinuous dashes; subcaudals 92-107; 8 upper labials, the fourth and fifth entering the orbit .... *Psammophis s. sibilans* (Olive Grass-Snake)

Habit slender; brown above, with a pair of yellow dorsolateral stripes; below, two narrow but well-defined black lines; subcaudals 105-123; normally 9 upper labials, the fourth, fifth and sixth entering the orbit .... *Psammophis s. subtaeniatus* (Southern Stripe-bellied Sand-Snake)

33\. Midbody scale rows 15 34

Midbody scale rows 11 .... *Psammophis angolensis* (Dwarf Sand-Snake)

34\. Ventrals 159-175; subcaudals 89-100 .... *Psammophis jallae* (Rhodesian Sand-Snake)

Ventrals 144-157; subcaudals 61-73 .... *Psammophis crucifer* (Cross-marked Grass-Snake)

35\. Midbody scales keeled in 21-27 rows; pupil vertical . *Dasypeltis scabra* (Common Egg-eater)

Midbody scales smooth in 15-21 rows; pupil round 36

36\. Habit extremely slender; head and tail black and similar in appearance, body with black and yellow longitudinal stripes; one labial entering orbit .... *Chilorhinophis g. gerardi* (Western Striped Burrowing-Snake)

Habit moderate; plumbeus or reticulated in black and white above; two labials entering orbit 37

37\. Prefrontals in broad contact; midbody scale rows 15, 19 or 21 38

Prefrontals widely separated by the frontal and much reduced in size so that they resemble preoculars; internasals in broad contact with the frontal; midbody scale rows 17 .... *Xenocalamus b. bicolor* (Bicolored Burrowing-Snake)

38. Midbody scale rows 19-21; 6 upper labials, the third and fourth entering the orbit . . . . *Calamelaps u. miolepis*
(Nyasa Purple-glossed Snake)
Midbody scale rows 15; 5 upper labials, the second and third entering the orbit . . . . *Calamelaps v. websteri*
(Webster's Burrowing Snake)
39. First lower labial in good contact with its fellow behind the mental . . . . *Aparallactus l. lunulatus*
(Reticulated Centipede-eater)
First pair of lower labials separated by the anterior sublinguals 40
40. Nostril normally in a divided nasal; subcaudals 55-59; above, steel-blue to black with two sulphur yellow nuchal collars; below, steel-blue . . . . *Aparallactus guentheri*
(Black Centipede-eater)
Nostril normally in an entire nasal; subcaudals 30-63; above, brown or reddish with a black head and neck; below, yellowish white . . 41
41. Ventrals 137-170; range Mashonaland and the Eastern Districts . . . . *Aparallactus c. capensis*
(Cape Centipede-eater)
Ventrals 156-181; range Matabeleland . . . . *Aparallactus capensis capensis* × *bocagei*
(Intermediates between the Cape and Angola Centipede-eaters)

F. *Key to the ELAPIDAE* (Cobras, Mambas, etc.) *of Southern Rhodesia*

1. Head short; snout broader than long; subcaudals less than 90 . 2
Head long and narrow; snout not broader than long; subcaudals more than 90 7
2. Scales in 13 rows at midbody; nostril between two nasals . . . . *Elapsoidea s. decosteri*
(Southeastern Garter-Snake)
Scales in 17 or more rows at midbody; internasal bordering the nostril 3
3. Rostral very large, detached at sides; ventrals less than 150; subcaudals less than 40 . . . . *Aspidelaps s. scutatus*
(Shield-Snake)
Rostral moderate, not detached at sides; ventrals more than 150; subcaudals more than 40 4
4. Eye separated from upper labials by suboculars 5
Eye in contact with third, or third and fourth upper labials . . 6
5. Midbody scale rows usually 17; range northwest of colony . . . . *Naja h. anchietae*
(Anchieta's Cobra)

Midbody scale rows usually 19; range all S. Rhodesia except the extreme northwest . . . . *Naja h. haje*
(Egyptian Cobra)

6. Midbody scale rows 21-25; sixth upper labial not largest, not in contact with postoculars . . . . *Naja n. mossambica*
(Mozambique Spitting-Cobra)

Midbody scale rows 17-19; sixth upper labial largest and deepest, in contact with the postoculars . . . . *Naja melanoleuca*
(Forest Cobra)

7. Midbody scale rows 17-21; ventrals 201-232; buccal membranes inside mouth bluish white . . . . *Dendroaspis angusticeps*
(Southern Green-Mamba)

Midbody scale rows 21-25; ventrals 242-282; buccal membranes inside mouth bluish grey to black . . . . *Dendroaspis p. polylepis*
(Southern Brown-Mamba)

G. *Key to the VIPERIDAE* (Adders and Vipers) *of Southern Rhodesia*

1. Top of head covered with large symmetrical shields; pupil round; reproduction oviparous 2

Top of head covered with numerous small scales; pupil vertical; reproduction ovo-viviparous 5

2. No loreal shield present; eye minute; ventrals more than 200; subcaudals mostly single; dorsal scales smooth; habit slender 3

A loreal shield present; eye moderate; ventrals less than 160; subcaudals paired; dorsal scales obtusely keeled; habit moderately robust . . . 4

3. Midbody scale rows 21; range Eastern Districts . . . . *Atractaspis b. bibronii*
(Southern Bibron's Burrowing-Adder)

Midbody scale rows 21-23; range S. Rhodesia excluding Eastern Districts . . . . *Atractaspis bibronii bibronii* × *rostrata*
(Intermediate Bibron's Burrowing-Adder)

4. Snout more or less rounded; ventrals 120-156; subcaudals 24-32 . . . . *Causus rhombeatus*
(Rhombic Night-Adder)

Snout prominent, the rostral more or less upturned; ventrals 110-128; subcaudals 10-19 . . . . *Causus defilippii*
(Snouted Night-Adder)

5. Midbody scale rows 39 or more; often a pair of horns on the snout . . . . *Bitis g. gabonica*
(Eastern Gaboon Viper)

Midbody scale rows less than 39; no horns on snout . 6

6. Midbody scale rows 24-27; a pair of supraocular horns; subcaudals strongly keeled distally . . . . *Bitis caudalis* (Horned Viper)

   Midbody scale rows 31-37; no supraocular horns; subcaudals smooth . . 7

7. Nostril directed upwards; a dorsal series of backward directed yellow and black chevrons; habitat savanna . . . . . *Bitis a. arietans* (Puff-Adder)

   Nostril directed upwards and outwards; four longitudinal dorsal series of large dark spots; habitat usually mountainous terrain . *Bitis atropos* (Mountain Viper)

ALPHABETICAL INDEX OF LOCALITIES IN SOUTHERN RHODESIA

A

Amandas, Mazoe Dist., 35 mls. N of Salisbury.

B

Balla Balla, Umzingwane Dist., 35 mls. SE of Bulawayo.
Bambata Cave, Matobo Dist., 30 mls. SSW of Bulawayo.
Banket, Lomagundi Dist., 50 mls. NW of Salisbury.
Beitbridge, Gwanda Dist., Limpopo River.
Belingwe, Belingwe Dist., 15 mls. SW of Shabani.
Bembesi, Bubi Dist., 25 mls. NE of Bulawayo.
Bindura, Mazoe Dist., 40 mls. NE of Salisbury.
Birchenough Bridge, Sabi River, 70 mls. S of Umtali.
Bubye River, affluent of Limpopo River, Matabeleland.
Bulawayo, Provincial Capital of Matabeleland.
Bushtick Mine, Umzingwane Dist., 30 mls. E of Bulawayo.

C

Changadzi River, affluent of Sabi River, just N of Birchenough Bridge.
Charter Estates, Charter Dist., near Enkeldoorn.
Chikore, Chipinga Dist., 12 mls. W of Mount Silinda.
Chilimanzi, Chilimanzi Dist., 35 mls. N of Fort Victoria.
Chimanimani Mts., Melsetter Dist., on the Mozambique border.
Chipinga, Chipinga Dist., 85 mls. S of Umtali.
Chirinda Forest, Chipinga Dist., on summit of Mount Silinda.
Chirundu, Urungwe Dist., Zambezi River, Salisbury-Lusaka road bridge.

Chishawasha, Goromonzi Dist., 12 mls. E of Salisbury.
Cleveland Dam, 6 mls. E of Salisbury.
Crosby Farm, 25 mls. N of Bulawayo.
Cyrene, Matobo Dist., between Westacre and Matopos.

D

Dadaya, Belingwe Dist., 8 mls. W of Shabani.
Deka, Wankie Dist., 10 mls. W of Wankie.
Devon Farm, Umtali Dist., 30 mls. S of Umtali on Odzi River.
Devuli River Bridge, 7 mls. W of Birchenough Bridge.
Domboshawa, Goromonzi Dist., 16 mls. N of Salisbury.
Donnington Farm, Hartley Dist., near Norton.
Dragon's Tooth, Chimanimani Mts., above the Haroni valley.
Driefontein, Chilimanzi Reserve, 15 mls. SE of Umvuma.
Dzoroka Farm, Chipinga Dist., 20 mls. SE of Chipinga.

E

Eldorado, Lomagundi Dist., 3 mls. E of Sinoia.
Empandene, Bulalima-Mangwe Dist., 15 mls. S of Plumtree.
Enkeldoorn, Charter Dist., 85 mls. S of Salisbury.
Essexvale, Umzingwane Dist., 25 mls. SE of Bulawayo.

F

Fatima, Nyamandhlovu Dist., 95 mls. NW of Bulawayo.
Figtree, Matobo Dist., 22 mls. SW of Bulawayo.
Filabusi, Insiza Dist., 50 mls. SE of Bulawayo.
Fort Usher, Matobo Dist., 15 mls. S of Bulawayo.
Fort Victoria, Victoria Dist., 145 mls. E of Bulawayo.
Freda Mine, Gwanda Dist., 15 mls. W of Gwanda.

G

Gatooma, Hartley Dist., 75 mls. N of Gwelo.
Gazuma Pan, Wankie Dist., on Bechuanaland border 65 mls. W of Wankie.
Glass Block, Gwanda Dist., 22 mls. N of Gwanda.
Glen Lorne, 10 mls. NE of Salisbury.
Glenorchy, near Insiza.
Grand Reef, Umtali Dist., 15 mls. W of Umtali.
Gwaai River, affluent of Zambezi River, Matabeleland.
Gwaai (Siding), Nyamandhlovu Dist., 85 mls. NE of Bulawayo.

Gwamayaya River, affluent of Shangani River, flowing into it from the north at a point 100 mls. N of Bulawayo.
Gwanda, Gwanda Dist., 60 mls. SE of Bulawayo.
Gwelo, Gwelo Dist., 95 mls. NW of Bulawayo.

H

Haroni-Lusitu Junction, Melsetter Dist., 20 mls. SE of Melsetter.
Hartley, Hartley Dist., 25 mls. NE of Gatooma.
Headlands, Makoni Dist., 70 mls. SE of Salisbury.
Heany, Umzingwane Dist., 15 mls. NE of Bulawayo.
Hondi Valley, Inyanga Dist., 30 mls. N of Umtali.
Hope Fountain, Umzingwane Dist., 8 mls. SE of Bulawayo.
Horseshoe Block, Umvukwes Range, 40 mls. NW of Salisbury.
Hot Springs, Melsetter Dist., 50 mls. S of Umtali.
Hunter's Road, Gwelo Dist., 20 mls. N of Gwelo.
Hunyani, now site of Lake McIlwaine Dam-wall, 20 mls. W of Salisbury.
Hunyani River, affluent of the Zambezi River, Mashonaland.

I

Imbeza, Umtali Dist., 5 mls. N of Umtali.
Insiza, Insiza Dist., 50 mls. NE of Bulawayo.
Inyanga North, Inyanga Dist., 100 mls. N of Umtali.
Inyati, Bubi Dist., 35 mls. NNE of Bulawayo.
Inyazura, Makoni Dist., 95 mls. SE of Salisbury.
Irisvale, Umzingwane Dist., 40 mls. SE of Bulawayo.

K

Karoi, Urungwe Dist., 110 mls. NW of Salisbury.
Kariba, Urungwe Dist., Zambezi River, 35 mls. S of Chirundu.
Kazungula, Wankie Dist., on Zambezi River, where N. Rhodesia, S. Rhodesia, Caprivi Strip and Bechuanaland meet.
Kezi, Matobo Dist., 55 mls. S of Bulawayo.
Khami Dam, Bulawayo Dist., 10 mls. W of Bulawayo.
Killarney Mine, Insiza Dist., 5 mls. E of Filabusi.
Kondo, 45 mls. WSW of Umtali.
Kutama, Lomagundi Dist., 45 mls. W of Salisbury.

L

Lake McIlwaine, 20 mls. W of Salisbury.
Legion Mine, Matobo Dist., 90 mls. S of Bulawayo.
Leopard Rock, Umtali Dist., on summit of Vumba Mountain.

Lukosi, Wankie Dist., 10 mls. S of Wankie.
Lumane, Gwanda Dist., 12 mls. N of Gwanda.
Lundi River, affluent of the Sabi River, Matabeleland.
Lupane Valley, Nkai Dist., 80 mls. N of Bulawayo.

M

Macheke, Marandellas Dist., 55 mls. SE of Salisbury.
Makumbi, Goromonzi Dist., 25 mls. NE of Salisbury.
Marandellas, Marandellas Dist., 40 mls. SE of Salisbury.
Matetsi, Wankie Dist., 25 mls. S of Victoria Falls.
Matopos Dam, Matobo Dist., 18 mls. S of Bulawayo (Schist).
Matopos Hills, Matobo Dist., 25 mls. S of Bulawayo (Granite).
Mavuradona Mountains, 20 mls. N of Mount Darwin.
Mazeppa Mine, Gwanda Dist., 10 mls. ESE of Gwanda.
Mazoe, Mazoe Dist., 25 mls. N of Salisbury.
Mchingwe River Bridge, Belingwe Dist., 20 mls. W of Shabani.
Melsetter, Melsetter Dist., 60 mls. S of Umtali.
Miami, Urungwe Dist., 120 mls. NW of Salisbury.
Mohem Mine, near Bembesi.
Monte Cassino, 5 mls. SE of Macheke.
Moonies Creek, 5 mls. S of Selukwe.
Mount Darwin, Darwin Dist., 80 mls. NNE of Salisbury.
Mount Hampden, Salisbury Dist., 10 mls. NW of Salisbury.
Mount Silinda, Chipinga Dist., 100 mls. S of Umtali.
Mrewa, Mrewa Dist., 50 mls. ENE of Salisbury.
Mtao Forest, Chilimanzi Dist., 10 mls. SE of Umvuma.
Mtoko, Mtoko Dist., 80 mls. ENE of Salisbury.
Musami, Mrewa Dist., 50 mls. ENE of Salisbury.

N

Nampini, Wankie Dist., Zambezi River, 50 mls. above Victoria Falls.
N'cema Dam, Umzingwane Dist., 5 mls. SE of Essexvale.
Norton, Hartley Dist., 25 mls. W of Salisbury.
N'sese River, affluent of the Umzingwane River, flowing into it at a point 10 mls. SE of Balla Balla.
Ntabezinduna, Bubi Dist., 20 mls. NE of Bulawayo.
Nyamashatu River, 12 mls. SSW of Umtali.
Nyamandhlovu, Nyamandhlovu Dist., 30 mls. NW of Bulawayo.
Nyamaropa, Inyanga Dist., 75 mls. N of Umtali.
Nyamaziwa, Inyanga Dist., 5 mls. E of Rhodes Estate, 5-6,000 ft.
Nyaratedzi River, Chibi Dist., 18 mls. NE of Shabani.

O

Odzi, Umtali Dist., 20 mls. W of Umtali.
Odzi River, affluent of the Sabi River.
Odzani Falls, Umtali Dist., 15 mls. N of Umtali.
Old Umtali, Umtali Dist., 5 mls. NW of Umtali.

P

Penhalonga, Umtali Dist., 6 mls. N of Umtali.
Plumtree, Bulalima-Mangwe Dist., 55 m's. WSW of Bulawayo.
Prince Edward Dam, Salisbury Dist., 10 mls. S of Salisbury.
Pungwe River Causeway, Inyanga Dist., 40 mls. N of Umtali.

Q

Que Que, Gwelo Dist., 35 mls. N of Gwelo.

R

Ramaquabane River, Bulalima-Mangwe Dist., on the Bechuanaland border, S of Plumtree.
Redbank, Nyamandhlovu Dist., 20 mls. NW of Bulawayo.
Rowa Division, Umtali Dist., 10 m's. S of Umtali.
Rusape, Makoni Dist., 90 mls. SE of Salisbury.

S

Salisbury, Federal and Territorial Capital.
Sawmills, Nyamandhlovu Dist., 55 mls. NW of Bulawayo.
Sebungwe River, affluent of the Zambezi River, flowing into it at a point 90 mls. E of Victoria Falls.
Selukwe, Selukwe Dist., 20 mls. SE of Gwelo.
Shabani, Belingwe Dist., 100 mls. E of Bulawayo.
Shamva, Mazoe Dist., 50 mls. NE of Salisbury.
Shangani River, affluent of the Gwaai River, Matabeleland.
Shangani (Siding), Insiza Dist., 55 mls. NE of Bulawayo.
Shawanoe River, Mrewa Dict., 40 mls. ENE of Salisbury.
Shiloh, 25 mls. of Bulawayo.
Sinkukwe, Umzingwane Dist., 10 mls. S of Balla Balla.
Sinoia, Lomagundi Dist., 65 mls. NW of Salisbury.
Sipolilo, Sipolilo Dist., 85 mls. NNW of Salisbury.
Springvale, Umzingwane Dist., 16 mls. SE of Bulawayo.
Stanmore, Gwanda Dist., 15 mls. S of Balla Balla.

Stapleford, Umtali Dist., 20 mls. NNE of Umtali.
Sun Yat Sen Mine, Matobo Dist., near Kezi.
Syringa, Bulalima-Mangwe Dist., 45 mls. SW of Bulawayo.

T

Tandaai, Melsetter Dist., 45 mls. S of Umtali.
Tanganda River, affluent of the Sabi River, 12 mls. SE of Birchenough Bridge.
Tanganda Tea Estate, Chipinga Dist., 20 mls. SE of Birchenough Bridge.
Threespanberg Pass, Chipinga Dist., 10 mls. NW of Chipinga.
Tjolotjo, Nyamandhlovu Dist., 60 mls. NW of Bulawayo.
Tod's Hotel, Gwanda Dist., 20 mls. SE of West Nicholson.
Trelawney, Lomagundi Dist., 45 mls. NW of Salisbury.
Triashill, Inyanga Dist., 40 mls. NNW of Umtali.
Tsetsera, Umtali Dist., 20 mls. SE of Umtali.
Tuli Hill and Tuli Reservoir, 10 mls. SE of Bulawayo.
Turk Mine, Bubi Dist., 35 mls. NNE of Bulawayo.

U

Umgusa River, affluent of the Gwaai River, Matabeleland.
Umshagashe River, Victoria Dist., affluent of the Mtilikwe River.
Umtali, Umtali Dist., 135 mls. SE of Salisbury.
Umvukwes Range, 40 mls. NW of Salisbury.
Umvuma, Chilimanzi Dist., 110 mls. SSW of Salisbury.
Umvumvumvu River, Melsetter Dist., 40 mls. S of Umtali.
Umzilizwe River, Chipinga Dist., 5 mls. N of Mount Silinda.

V

Valindre, Matobo Dist., 10 mls. SW of Bulawayo.
Victoria Falls, Zambezi River.
Vumba Mountain, Umtali Dist., 10 mls. SE of Umtali.

W

Wankie, Wankie Dist., 55 mls. SE of Victoria Falls.
Wedza Reserve, Marandellas Dist., 60 mls. W of Umtali.
Westacre, Matobo Dist., 18 mls. SW of Bulawayo.
West Nicholson, Gwanda Dist., 25 mls. ESE of Gwanda.
Woodvale, Bulawayo Dist., 10 mls. N of Bulawayo.

Z

Zambezi-Sebungwe Junction, Sebungwe Dist., 90 mls. E of Victoria Falls.
Zezani, Gwanda Dist., on the Umzingwane River near Beitbridge.
Zimbabwe, Victoria Dist., 15 mls. SSE of Fort Victoria.

PLATES

PLATE I

Map of Southern Rhodesia.

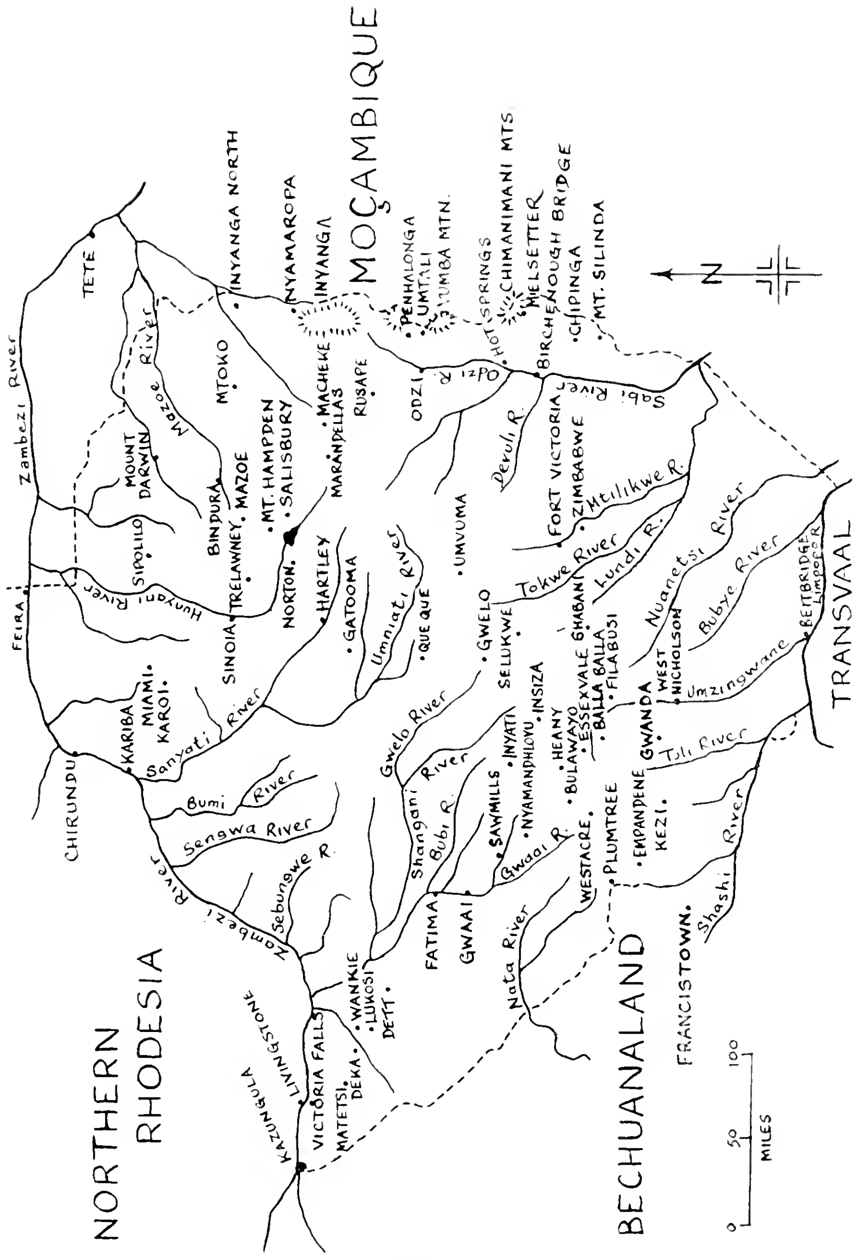
NORTHERN RHODESIA
MOÇAMBIQUE
BECHUANALAND
TRANSVAAL
N
0
50
100
MILES
Zambezi River
Zambezi River
Hunyani River
Mazoe River
Sanyati River
Bumi River
Sengwa River
Sebungwe R.
Umniati River
Gwelo River
Shangani River
Bubi R.
Gwaai R.
Nata River
Odzi R.
Sabi River
Devuli R.
Mtilikwe R.
Tokwe River
Lundi R.
Nuanetsi River
Bubye River
Umzingwane
Tuli River
Shashi River
Limpopo R.
TETE
FEIRA
CHIRUNDU
KARIBA
MIAMI
KAROI
SINOIA
SIPOLILO
MOUNT DARWIN
BINDURA
MAZOE
TRELAWNEY
MT. HAMPDEN
SALISBURY
NORTON
HARTLEY
GATOOMA
QUE QUE
MTOKO
INYANGA NORTH
NYAMAROPA
INYANGA
MACHEKE
MARANDELLAS
RUSAPE
PENHALONGA
UMTALI
VUMBA MTN.
ODZI
HOT SPRINGS
CHIMANIMANI MTS
MELSETTER
BIRCHENOUGH BRIDGE
CHIPINGA
MT. SILINDA
UMVUMA
FORT VICTORIA
ZIMBABWE
GWELO
SELUKWE
SHABANI
INSIZA
INYATI
NYAMANDHLOVU
HEANY
BULAWAYO
ESSEXVALE
BALLA BALLA
FILABUSI
GWANDA
WEST NICHOLSON
BEITBRIDGE
SAWMILLS
FATIMA
GWAAI
WESTACRE
PLUMTREE
EMPANDENE
KEZI
FRANCISTOWN
WANKIE
LUKOSI
DETT
DEKA
MATETSI
VICTORIA FALLS
LIVINGSTONE
KAZUNGULA

PLATE I

PLATE 2

Upper, Nyasa File Snake (*Mehelya nyassae*). This specimen came from Fatima Mission, between Bulawayo and the Victoria Falls. The photograph clearly shows the bicarinate vertebral scale row. The tail is much more slender than in *Mehelya c. capensis*, and can be seen coiled beneath the body, on the right.

Photo by D. G. Broadley

Lower, Mole Snake (*Pseudaspis cana*). This four-foot Bulawayo snake is the largest so far recorded from Southern Rhodesia. The stout body and the relatively small head readily identify this powerful constrictor.

Photo by D. G. Broadley

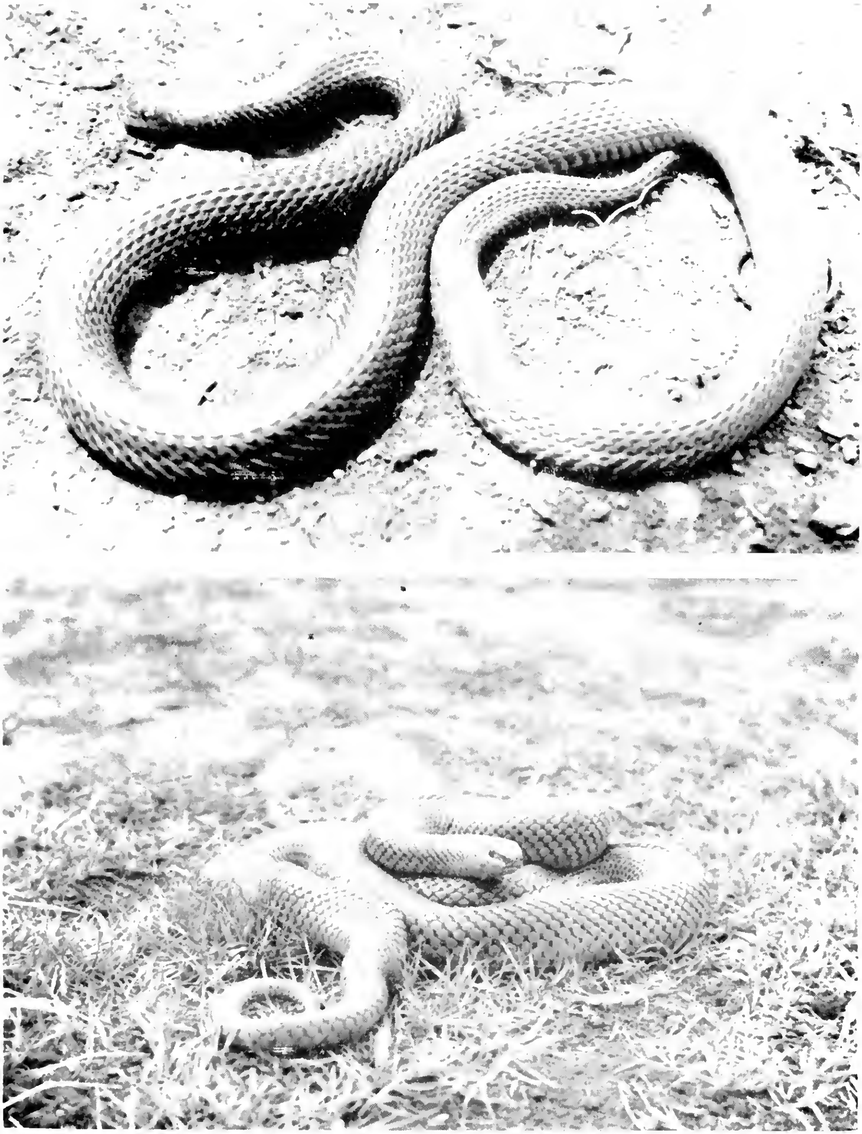

PLATE 2

PLATE 3

Upper, Sundevall's Shovel-snout (*Prosymna s. sundevallii*). This adult female was taken under a stone by the roadside at Essexvale. The dorsal stripe is bright orange against a purplish brown background. Apart from the colouring, this species is distinguished from the lower one by its more slender body.

Photo by D. G. Broadley

Lower, Peters' Shovel-snout (*Prosymna lineata*). This adult female was collected near Bulawayo. It is pale brown with darker markings and is more stoutly built than the one pictured above.

Photo by D. G. Broadley

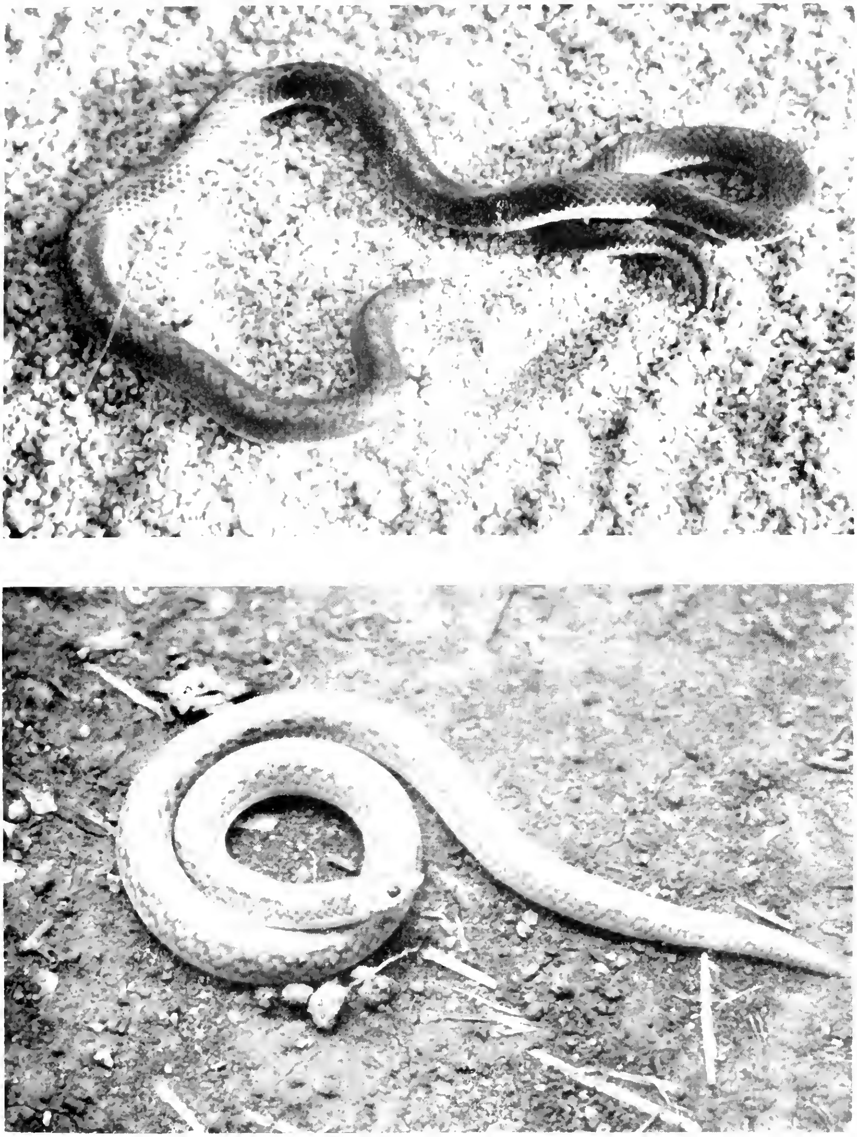

PLATE 3

PLATE 4

Upper, Nyasa Purple-glossed Snake (*Calamelaps unicolor miolepis*). This eighteen inch male came from a farm 15 miles north of Bulawayo. The iridescence of the glossy black scales can be clearly seen. This snake preys upon other burrowing species, particularly *Typhlops* and *Leptotyphlops*.

Photo by D. G. Broadley

Lower, Shield Snake (*Aspidelaps s. scutatus*). This fine female came from near Beitbridge. The enormous rostral shield, detached at the sides and in broad contact with the prefrontals, is a good distinguishing feature. The dorsal scales on the posterior part of the body and the tail are strongly keeled.

Photo by D. G. Broadley

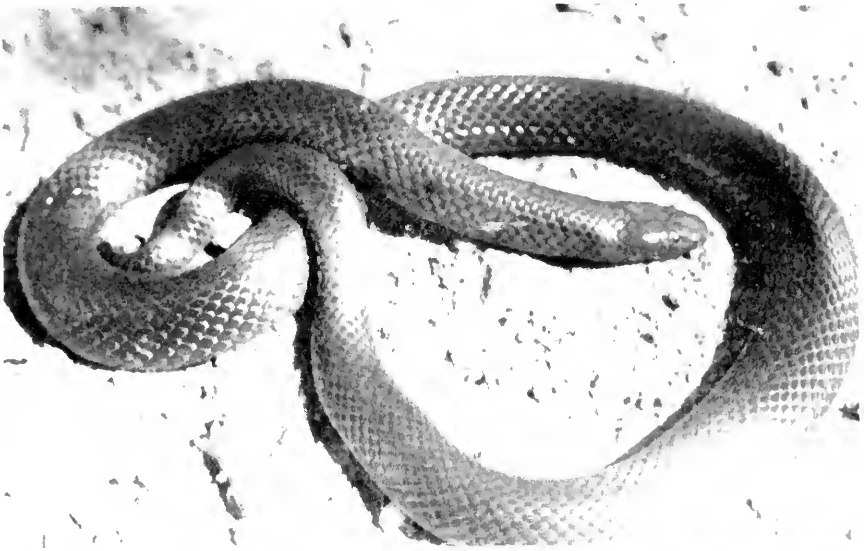

PLATE 4

PLATE 5

Upper, Egyptian Cobra (*Naja h. haje*). This massive cobra, seven feet in length, was captured at Irisvale. This is the all black phase commonly found in Matabeleland. Compare the broad "hood" of this species with the long narrow hoods spread by *Naja n. mossambica* (Pl. 6, upper) and *Naja melanoleuca* (Pl. 6, lower).

Photo by D. G. Broadley

Lower, Banded Cobra (*Naja h. haje*, var. *annulifera*). I pulled this fine cobra out of a termitarium adjoining my camp at Irisvale. This 6′8″ specimen is blue-black with 10 creamy-white cross-bands on body and tail. The photograph clearly shows the suboculars which exclude the labials from the orbit.

Photo by W. W. Armitage

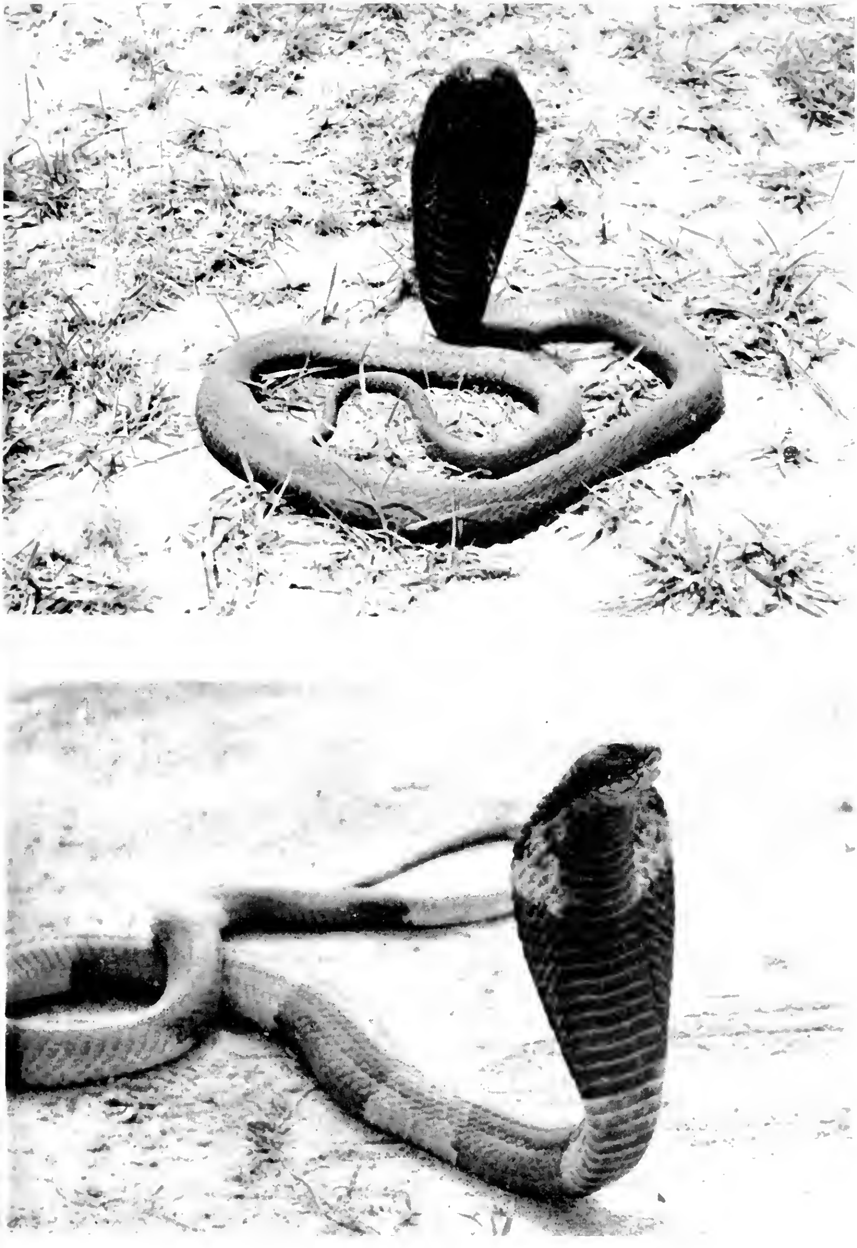

PLATE 5

PLATE 6

Upper, Mozambique Spitting Cobra (*Naja nigricollis mossambica*). The largest of 76 specimens examined, this Essexvale cobra is 5 feet 1 inch in length. The characteristic irregular series of bands and blotches on the throat, together with the light grey-brown, black-edged dorsal scales, help to distinguish this form from the race *crawshayi* found farther north.

Photo by D. G. Broadley

Lower, Forest Cobra (*Naja melanoleuca*). This specimen, five and a half feet in length, is the first to be taken in Southern Rhodesia. It was captured on the edge of a strip of forest on the summit of Mount Silinda. The long narrow hood is very different from that spread by the Egyptian Cobra.

Photo by D. G. Broadley

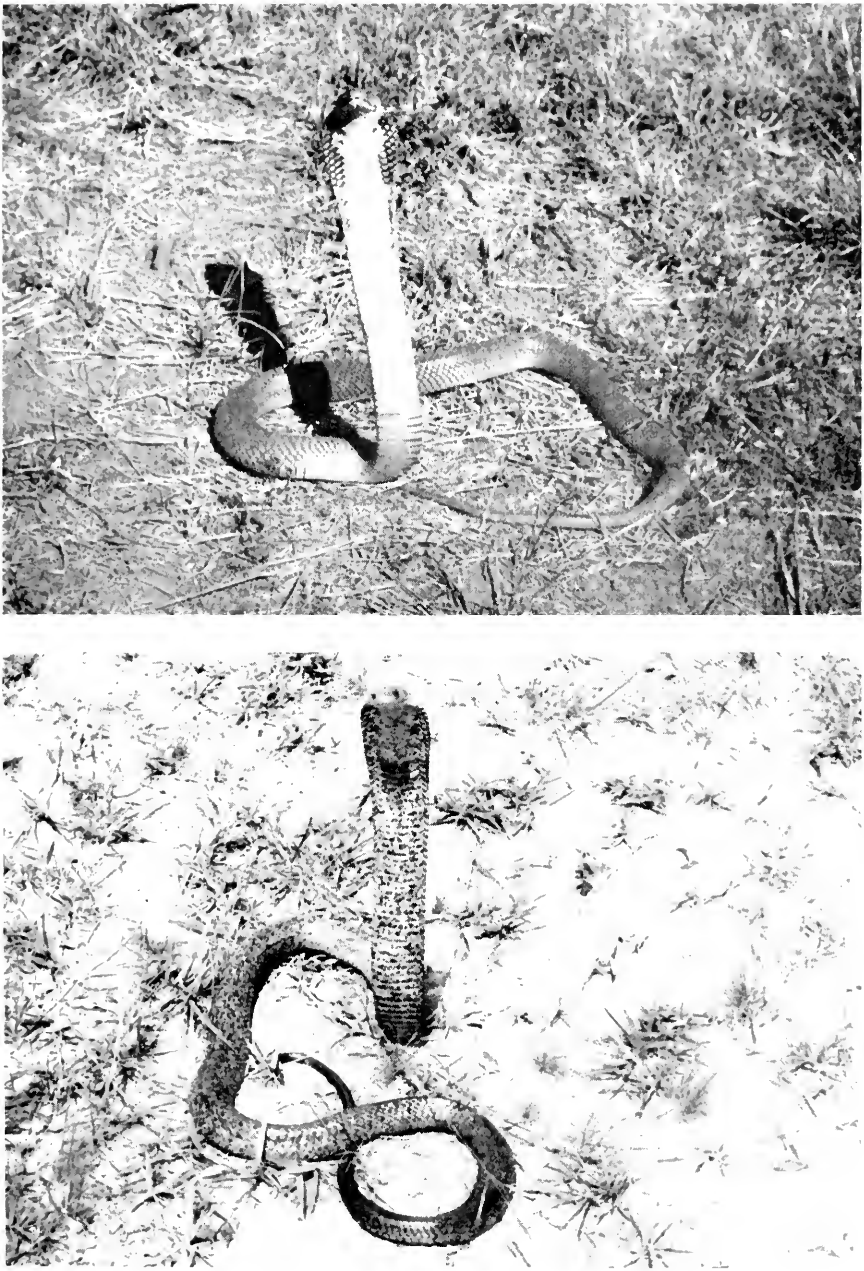

PLATE 6

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 120, No. 2

STUDIES ON THE COMPARATIVE EMBRYOLOGY OF THE REPTILIAN NOSE

By Thomas S. Parsons
Harvard Biological Laboratories

With Seven Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March, 1959

PUBLICATIONS ISSUED BY OR IN CONNECTION
WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

BULLETIN (octavo) 1863 — The current volume is Vol. 120.

BREVIORA (octavo) 1952 — No. 101 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 38 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 22 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 2 — Studies on the Comparative Embryology of the Reptilian Nose

By Thomas S. Parsons

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INTRODUCTION

Purpose and Scope. The following paper is a survey of the embryological development and adult anatomy of the nasal cavities and their epithelial walls in the living orders of the Reptilia; the embryology is considered in greater detail than the anatomy. Although the investigation was started as a study of Jacobson's organ, it soon became apparent that the remainder of the nasal organ would also have to be considered, if any valid conclusions were to be reached. Despite this widening in the scope of the study, special emphasis has still been placed on Jacobson's organ.

There is a very large body of literature on the nasal area of reptiles, a fact made apparent by the size of the bibliography at the end of this work. However most of the previous studies have been rather limited in their scope. Thus there remain many lacunae in our knowledge of the nasal embryology of most groups, and much disagreement persists over the interpretation of the observed structures, especially concerning the presence and nature of Jacobson's organ in turtles and crocodilians. In the following descriptions and discussions, an attempt has been made both to collect the various observations by earlier investigators, and to fill in some of the major gaps in our knowledge by studying a large number of reptilian embryos.

Naturally, a detailed study of the whole nasal area in the entire class was impossible. One major limitation is imposed by the availability of material. Thus only four embryos of *Sphenodon* were seen, so that no intensive investigation of the nasal embryology of this form was possible. The suborder Lacertilia has been studied far more carefully than any other comparable group, and therefore is not discussed in detail here. Similarly the skeleton of the nasal area, although important for a complete understanding of the olfactory organs, is not treated here, since it is better known than the soft parts of the region. However, some knowledge of the nasal glands and olfactory nerves is essential for a consideration of Jacobson's organ, and they are therefore discussed briefly.

Acknowledgements. This investigation was carried out as a thesis problem under the supervision and guidance of Professor Alfred S. Romer; to him I wish to express my deepest gratitude for his careful and constructively critical reading of the manuscript, and constant aid with the many problems which arose in its preparation. Also to Dr. Ernest E. Williams, I extend sincere thanks for his assistance on countless points during the course of this study. Many other people have patiently listened to my problems, and rendered valuable assistance; to all of them, I am most grateful.

I am indebted to numerous people for the loan of most of the material studied. The late Dr. G. B. Wislocki and Dr. R. O. Greep of the Harvard Medical School have kindly allowed me to borrow large numbers of slides from the Minot Collection of embryos. Further embryological slides were loaned to me by Dr. A. M. Reese of West Virginia University, Dr. F. J. Ryan of Columbia University, and Dr. E. E. Williams of Harvard University. My thanks are also due to Dr. A. Fleminger for an adult *Crotalus*, and to Dr. P. P. Vaughn for an immature *Alligator* and an adult *Pseudemys*.

Among the many people who assisted me in other ways, I should like especially to thank the librarians at the Museum of Comparative Zoology. Their constant help in locating many, often obscure, works for me is greatly appreciated.

A portion of this investigation was carried out during the tenure of a National Science Foundation Predoctoral Fellowship.

Finally, my deepest gratitude is due to my wife, Margaret C. Parsons. Besides making all the drawings for this work, she has assisted in countless other ways, including reading much of the manuscript, typing large sections of it, and making several of the dissections. Without her aid the work could not have been completed.

Materials and Methods. Embryos representing all four orders of recent reptiles were studied. These embryos were borrowed from the Minot Collection of the Harvard Medical School, from Columbia University, and from Drs. E. E. Williams and A. M. Reese. Most of the series were stained with alum cochineal, borax carmine, cochineal, hematoxylin, or iron hematoxylin, and counterstained with eosin, Lyon's blue, orange G, picric acid, or saffranin. The following forms were available: *Chrysemys* (80 embryos), *Emys* (9), *Chelydra* (9), *Trionyx* (3), *Sphenodon* (4), *Lacerta* (59), *Aristelliger* (32), *Iguana* (5), *Sphaerodactylus* (2), *Anniella* (1), *Lygosoma* (1), *Thamnophis* (70), *Oxybelis* (3), and *Alligator* (31).

Material representing all of the recent reptilian orders except the Rhynchocephalia was dissected for this study; normally the nasal cavities were opened sagittally, as shown in the figures of the dissections. The specimens dissected were: *Pseudemys* (1 specimen), *Chelonia* (1), *Drymarchon* (1), *Crotalus* (1), and *Alligator* (3). Besides this material, one series of sagittal sections through the head of an adult *Storeria* was studied.

All of the specimens which are mentioned above were studied in detail, but no reconstructions were made. Although models or other reconstructions would have been most useful in certain cases, the time involved in their preparation would have prevented the examination of as many specimens as were actually studied. In view of the comparative nature of this investigation, the use of as large a sample as possible appeared more desirable than the more concentrated study of a smaller number of embryos.

Most of the drawings were made by tracing photographs of the sections or dissections. The eye, brain, integument, and nasal epithelium are colored black while other tissues are stippled in the figures showing sections through the nasal areas of the embryos. In most cases the nerves are not indicated. Such a method gives an extremely accurate picture of the area, although in some cases the boundary between the nasal epithelium and the surrounding mesoderm is not, on the actual specimen, as sharp as the figures would indicate.

Terminology. The differences in nasal anatomy between the various orders of reptiles are of sufficient magnitude to necessitate the use of a different system of terminology for each order. Therefore discussions of the anatomical terms are most conveniently included in the sections on the various orders. In general, an attempt has been made to follow either the terminology in most general usage, or that proposed in the most recent paper dealing with any specific group; however in some cases, none of the available terms appeared to be suitable, and new ones are introduced.

In most cases the forms mentioned are identified only to genera, and specific names are not cited. The classification is, unless otherwise noted, that of Romer (1956). In all discussions of the literature, the generic names are those suggested by Romer; the following list includes the synonyms which are used in the papers cited or on the slides studied. The first name is that used elsewhere, and the second the one employed in the present work. Spelling variants, such as *Crocodilus* for *Crocodylus*, are not included, and specific names are considered only when necessary.

Alligator cynocephalus = *Caiman*
Alligator sclerops = *Caiman*
Aspidonectes = *Trionyx*
Boa constrictor = *Constrictor*
Caiman niger = *Melanosuchus*
Callopeltis = *Elaphe*
Chersydrus = *Acrochordus*
Chelonia cauana = *Caretta*
Chelone imbricata = *Eretmochelys*
Cistudo = *Terrapene*
Coluber aesculapii = *Elaphe*
Coluber natrix = *Natrix*
Crocodilus gangeticus = *Gavialis*
Dryophis = *Ahaetulla*
Enhydris hardtwickei = *Hydrophis*
Eutaenia = *Thamnophis*
Gavialis schlegelii = *Tomistoma*
Hatteria = *Sphenodon*
Pelias = *Vipera*
Platurus = *Laticauda*
Sphargis = *Dermochelys*
Tropidonotus = *Natrix*

OBSERVATIONS

Order Chelonia

General. Despite a fairly extensive literature on the anatomy of the nose in turtles, only a few genera have been adequately studied. The most important papers are those by Seydel (1896), Nick (1912), and Fuchs (1915). Hoffmann (1879-1890) describes a large series of forms, but never in detail. The other works cited below are of lesser importance, although they are mainly on forms not considered in the major papers. The most careful recent review is that of Matthes (1934).

Terminology poses a major problem in chelonian nasal anatomy. Most authors have followed Seydel (1896) in this regard, although Nick (1912) expresses doubt on the propriety of some of the terms, and Fuchs (1915) uses an essentially new system. In the following descriptions the terms adopted are mainly those of Seydel, while Nick is followed for some of the specialized structures of sea turtles. However, in some cases it is felt that none of the available terms are appropriate, and new ones have been made.

The most important new usage concerns the *partes olfactoria* and *respiratoria* of Seydel. In turtles these terms have come to be used in a purely topographic sense while in mammals they refer to the histological nature of the epithelium. The pars olfactoria is the dorsal or posterodorsal portion of the nose, typically separated from the remaining portions by a pair of horizontal ridges, one lateral and one medial, the *Grenzfalten* of Seydel. As far as is known, its walls are always almost entirely covered by olfactory epithelium; it thus corresponds closely to the pars olfactoria in the mammalian sense despite its definition on topographic rather than histological criteria. However, the pars respiratoria of Seydel, essentially the remainder of the *cavum nasi proprium*, bears not only non-sensory respiratory epithelium, but also has certain sensory zones. Since by definition a pars respiratoria is non-sensory, this term is obviously an undesirable one.

However, the only major paper since 1896 which has not followed Seydel in the use of these terms is that by Fuchs (1915). There, the pars olfactoria of Seydel is named the *recessus* *superior posterior.* The latter term, while descriptive of the condition found in sea turtles, is inappropriate for most forms. Fuchs gives no corresponding term for Seydel's pars respiratoria which is treated as a series of separate parts.

In the absence of any other available terms, Seydel's pars olfactoria is here designated *regio olfactoria* and his pars respiratoria as *regio intermedialis.* The former at least preserves the familiar term in part, and the latter is descriptive of the general position in the nose as a whole for this rather variable region.

Another set of new terms apply to the furrows in the surface of the regio intermedialis which bear sensory epithelium. Seydel and most later workers refer to them as *partes* of Jacobson's organ. Since in the present paper this sensory epithelium is not considered to constitute a Jacobson's organ, other names are necessary. The furrows are here called *sulci.* Thus Seydel's pars anterior is the *sulcus anterior*, his pars ventralis the *sulcus ventralis*, and his pars dorsalis the *sulci medialis* and *lateralis.*

Two other terms require comment. *Concha* is used by different authors in very different senses. Gegenbaur (1873) and Solger (1876) proposed a restricted definition, but this has not been generally accepted. A possible homolog of the concha of other reptiles is the laterale Grenzfalte of turtles; however a lateral outpocketing of the wall of the regio olfactoria, which is analogous to the saurian concha in that it increases the surface covered by olfactory epithelium, occurs in some turtles and is sometimes referred to as the concha (e.g. Plate, 1924). To avoid confusion, Seydel's term *Muschelwulst* is here used for such an outpocketing, and concha not at all in reference to turtles. Finally, *ductus nasopharyngeus* is used instead of *ductus choanalis.* Fuchs (1915) objects to the former term on the basis of embryological differences between the structure in mammals and in turtles, but as it is most often used in a general sense for any duct-like connection of the nasal cavity with the mouth, it is here retained.

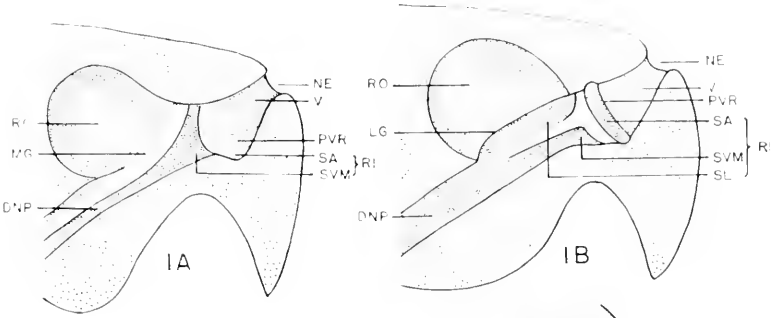
For descriptive purposes, the turtles may be split into four groups, only two of which are known in any detail. These are the ordinary land and pond turtles (Chelydridae and Testudinidae including Emydinae) and the sea turtles (Cheloniidae and Dermochelyidae). Two groups about which much less is known are the Trionychidae and the Pleurodira. Apparently nobody has studied the nose of the Dermatemydidae or Carettochelyidae.

Morphologically, turtles can be arranged in a series showing a greater or lesser degree of adaptation of the nose for an aquatic life. The greater this adaptation, the more important and complex is the regio intermedialis and the smaller is the regio olfactoria. Using those genera which have been most studied, such a sequence would be, in order of increasing aquatic adaptation: *Testudo; Chelydra; Emys, Chrysemys,* and *Pseudemys; Pelomedusa; Trionyx;* and *Chelonia, Caretta, Eretmochelys,* and *Dermochelys.* Naturally such a sequence is not phylogenetic, but represents the end points of various lines.

Adult Anatomy. The Chelydridae and Testudinidae display the simplest arrangement of the nasal cavities found in turtles, and are probably closer to the primitive chelonian condition than any other living groups. *Chelydra* may be taken as a possible starting point, with *Testudo* somewhat specialized for terrestrial and the emydines for aquatic life. *Chelydra* has been carefully studied by Nick (1912), and the following description and Figure 1 are taken from his paper with only slight modifications in terminology.

Figure 1. The nasal cavity of *Chelydra* (after Nick, 1912). A, lateral view of the right nasal cavity to show the medial wall. B, medial view of the left nasal cavity to show the lateral wall.

Figure 2. The nasal cavity of *Chelonia.* A, medial view of the left nasal cavity to show the lateral wall. B, lateral view of the right nasal cavity to show the medial wall.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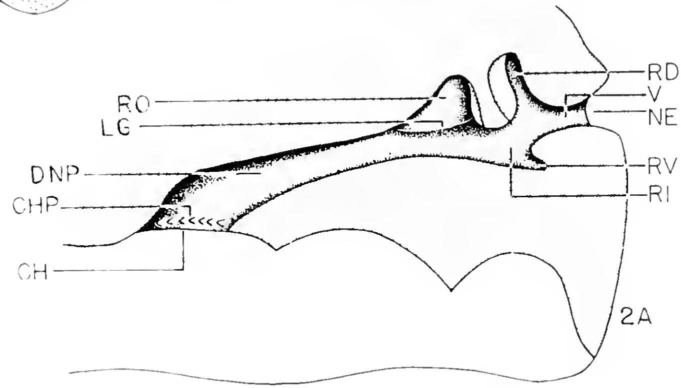
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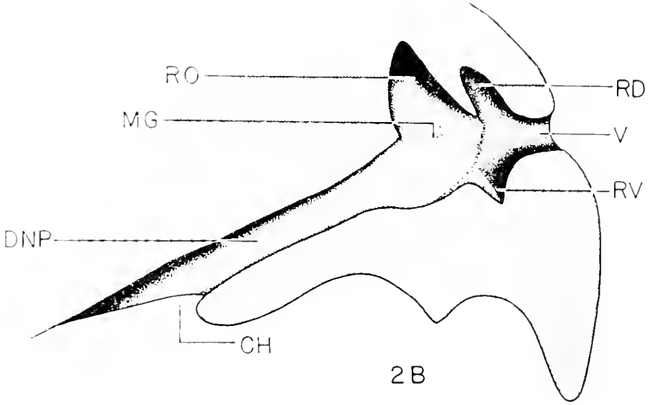
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The *vestibulum* is fairly short and straight. In *Chelydra* it runs ventrally as well as posteriorly from the *naris externus,* but this is probably a specialized condition; in most turtles it runs directly posteriorly. In transverse section it is circular anteriorly, becoming higher and oval posteriorly. The vestibulum is separated from the cavum nasi proprium by a slight ridge which is most prominent laterally (the *Grenzwall* of Nick, 1912, and Seydel, 1896, here referred to as the postvestibular ridge).

The cavum nasi proprium is divided into regiones olfactoria and intermedialis by prominent mediale and laterale Grenzfalten. These ridges both start on the dorsal wall of the cavum nasi proprium just posterior to its juncture with the vestibulum and run posteroventrally to the dorsal margin of the ductus nasopharyngeus. The mediale Grenzfalte is slightly ventral to the laterale and divides posteriorly, with the smaller dorsal arm meeting the dorsal border of the ductus as described above, and the larger ventral one continuing along the medial wall of the ductus nasopharyngeus.

The regio olfactoria is a large chamber lying posterodorsal to the regio intermedialis. It is roughly semicircular in sagittal, and oval in transverse section. Its ventral surface is open to the regio intermedialis except at its posteriormost extremity. The posterior half of its lateral wall projects slightly into the nasal cavity forming a distinct Muschelwulst whose ventral margin is part of the laterale Grenzfalte.

The regio intermedialis forms an oval tube with the dorsoventral axis greater than the mediolateral. It runs posteroventrally from the vestibulum to the nasal end of the ductus nasopharyngeus so that all three structures make one continuous and straight tube. The walls bear low ridges which form the boundaries of three shallow grooves. Seydel (1896) and most later workers term these grooves Jacobson's organ. The first ridge forms a circle in the wall of the regio intermedialis just posterior to the boundary with the vestibulum, thus forming a circular groove, the sulcus anterior, between it and the postvestibular ridge. A second ridge runs posteroventrally from the first along the lateral wall approximately halfway between the floor of the regio intermedialis and the laterale Grenzfalte. It becomes less pronounced posteriorly, disappearing near the start of the ductus nasopharyngeus. The groove between this ridge and the laterale Grenzfalte is the sulcus lateralis while the ventral and medial walls of the regio intermedialis are the sulcus ventralis et medialis. Nick was unable to distinguish differences in the epithelium of the ridges and sulci.

The ductus nasopharyngeus continues posteroventrally from the regio intermedialis, from which it is not sharply divided. The ductus bears low columnar epithelium which gradually merges with the thicker sensory epithelium of the cavum nasi proprium. As previously mentioned, the mediale Grenzfalte continues posteriorly as a low ridge along the medial wall of the ductus. Lateral and somewhat dorsal to the anterior part of the ductus is a small blind sac opening posteriorly into the ductus, the *recessus ducti nasopharyngei* (the *sinus maxillaris* of von Mihalkovics, 1898, and Nemours, 1930). Nick does not describe the *choanae*.

Kinosternon is the only other genus of the Chelydridae whose nose has been studied, and it is, judging from the diagrammatic figures and brief description in Hoffmann (1879-1890), entirely unlike that of any other turtle. Until this genus is restudied in greater detail, it is impossible, profitably, to compare the nasal cavity of *Kinosternon* with that of other turtles.

Among the Testudininae (Testudinidae) the only genus which has been studied is *Testudo*, and its anatomy is known from a brief account by Hoffmann (1879-1890) and the detailed work of Seydel (1896). In this genus the regio olfactoria is large with a very well developed Muschelwulst. The mediale Grenzfalte is more prominent than in *Chelydra*. On the other hand, *Testudo* possesses a simpler regio intermedialis. There is only one small ridge which runs posteroventrally from the ventral part of the postvestibular ridge along the medial wall of the nose. Between this ridge and the mediale Grenzfalte, there is a very shallow sulcus medialis. Seydel found vomeronasal epithelium only in this sulcus, with the remainder of the regio intermedialis bearing non-sensory respiratory epithelium.

Few genera of the Emydinae (Testudinidae) have been studied; all seem very similar and quite like *Chelydra* or *Testudo*. The best known form is *Emys*, which has been briefly noted by Solger (1876) and described in detail by Seydel (1896), who also studied *Chrysemys*. McCotter (1917) has written on "*Chrysemys punctata*." It is uncertain just what form this is; however, it is almost certainly either *Chrysemys* or *Clemmys*. Finally, Nemours (1930) briefly describes *Pseudemys*.

An adult *Pseudemys* was dissected for the present investigation and found to agree closely with most of the previous studies, especially that of Seydel. Emydines differ from *Chelydra* primarily in the reduction of the size of the regio olfactoria and increased complexity of the regio intermedialis. The Muschelwulst, if present at all, is very small. In the regio intermedialis there are ridges similar to those found in *Chelydra*, but there is also a third ridge along the medial wall, separating the sulci ventralis and medialis. According to Seydel, all four sulci bear vomeronasal epithelium, with non-sensory respiratory epithelium being found on the Grenzfalten and ridges. Figure 31, which shows a late embryo of *Chrysemys*, illustrates the relationships of the sulci.

The sea turtles show extreme adaptation to the aquatic environment in the great development of the regio intermedialis and the comparative reduction of the regio olfactoria. For this study an adult *Chelonia* was dissected as is shown in Figure 2.

The vestibulum is a short tubular structure without any marked increase in height posteriorly. Its juncture with the cavum nasi proprium is not marked by any postvestibular ridge, but is sharply defined by the sudden increase in cross-sectional area of the cavity.

The cavum nasi proprium is divided into regiones olfactoria and intermedialis by the laterale and mediale Grenzfalten as in the forms already described, but the olfactoria has become restricted to the posterodorsal third of the cavum. The complex regio intermedialis is divided into several sections which do not seem comparable to the sulci of other turtles. Unfortunately most of these sections have received several names, many of which are rather confusing.

The regio intermedialis may be thought of as a roughly tubular structure with several anterior outpocketings. The central tube is not generally given a separate name; however it corresponds to the anterior half of the *cella media* plus the *pars posterior* of the *recessus inferior* of Fuchs (1915). This tube runs from the vestibulum to the ductus nasopharyngeus so that the three form a straight passage from the naris externus to the choana. In the floor of this central portion of the regio intermedialis there is a shallow groove running anteromedio-posterolaterally.

The first outpocketing to be considered is the *recessus ventralis*. It is the *untere Ausbuchtung* of Gegenbaur (1873), the *recessus inferior* of Nick (1912), and the *pars anterior* of the *recessus inferior* of Fuchs (1915). This deep recessus is narrow anteroposteriorly, but lateromedially it is wider than the central part of the regio intermedialis due to its extending into the medial wall as a shallow groove. This groove pushes posteromedially into the septum, reaching dorsally to the level of the top of the vestibulum where a small ridge separates it from the recessus dorsalis (see Fig. 2B). It also reaches slightly lateral to the cella media of Fuchs (1915) where it expands as a wider but shallower pocket. The ventral portion of the recessus ventralis curves anteriorly so that its deepest point is the anteriormost part of the cavum nasi proprium.

The *recessus dorsalis* (the *obere Ausbuchtung* of Gegenbaur, the *recessi superior* and *medialis* of Nick, and the *recessus superior anterior* of Fuchs) is somewhat more complex. The main part of it is a deep groove similar to the recessus ventralis in its anteroposterior narrowness and lateromedial width. Medially, it is separated from the recessus ventralis by the narrow ridge already mentioned; laterally, the recessi are widely separated. The medial section of the recessus dorsalis extends posteriorly in the septal wall for a short distance, and this portion is often, as by Nick, described as a separate recessus medialis (see Fig. 2A). It is not open into the remainder of the regio intermedialis ventrally, but only into the central part of the recessus dorsalis, and is therefore here considered merely a part of that recess, as suggested by Fuchs.

The regio olfactoria (the *innere Riechgrube* of Gegenbaur and the *recessus superior posterior* of Fuchs) forms another large recess which is roughly two-thirds of a sphere in shape. It lacks a Muschelwulst. The laterale Grenzfalte is a small but distinct ridge running from the ventral end of the bar of tissue separating the recessus dorsalis from the regio olfactoria to the juncture of the cavum nasi proprium and the ductus nasopharyngeus. This ridge is the concha of Gegenbaur and Fuchs. The mediale Grenzfalte is less marked, but since the regio olfactoria extends farther medially than the adjoining section of the regio intermedialis, there is a distinct angle in the wall of the nose to represent it.

The ductus nasopharyngeus is a long simple duct, not sharply set off from the regio intermedialis. The mediale Grenzfalte continues along the dorsomedial wall as a low ridge which slowly disappears posteriorly. *Chelonia* lacks a recessus ducti nasopharyngei. Along the lateral margin of the choana there is a series of about twelve small stiff papillae; these are described in a separate paper (Parsons, 1958).

There is a moderately extensive literature on the nasal cavities of sea turtles; all appear to be very similar, although the similarity has been somewhat obscured by the variation in terminology. *Chelonia* has been studied by Solger (1876) and Nick (1912), *Caretta* by Gegenbaur (1873), *Eretmochelys* by Hoffman (1879-1890) and Fuchs (1915), and *Dermochelys* by Hoffmann (1879-1890) and Nick (1912). Deraniyagala (1939) and Parsons (1958) discuss the variation in the choanal papillae. All the forms which have been studied possess the same basic pattern of recessi dorsalis and ventralis in the regio intermedialis, although in *Dermochelys* the entire nasal cavity is shorter and the recessus ventralis smaller than in the members of the Cheloniidae. According to Nick, the sensory (vomeronasal) epithelium of the regio intermedialis is restricted to the recessi in *Dermochelys*, and to the recessi plus a narrow midventral band in *Chelonia*.

The nose of the highly specialized genus *Trionyx* has been but little studied. The most complete account is that of Hoffmann (1879-1890); Seydel (1896) compares it to *Emys*, but unfortunately without any detailed description or figures. The general pattern appears to resemble that found in *Emys*, but with reduction of the regio olfactoria and greater development of the regio intermedialis. Hoffmann figures some irregularities in the surface of the latter regio, but these do not appear to be comparable to the sulci found in *Emys*.

Little can be said concerning the nose of pleurodires. The only description available in the literature appears to be that of van der Merwe (1940) on *Pelomedusa*, in which he is mainly concerned with the skull and treats the nasal cavities only briefly. Both recessi and sulci are said to occur in the regio intermedialis, but their relationships are not made clear.

Early embryology. There have been few studies made on the early development of the nose in turtles. Seydel (1896) describes a small series of *Chrysemys* embryos, and Voeltzkow (1903) considers the general embryology of the face in *Eretmochelys*, giving excellent figures of the external appearance of the nose in his embryos. Dohrer (1912) discusses the nose briefly in his paper on *Chelydra*. More recently, Loew (1956) considers *Emys*, mainly in relation to the homologies of Jacobson's organ. The other papers which must be considered, Fuchs (1907 and 1915; *Emys*) and Thäter (1910; *Chrysemys*), are concerned primarily with the development of the palate and therefore give little detail on the earlier stages. Since the findings of all these investigations are similar, at least insofar as these stages are concerned, and in essential agreement with the present study, no extensive review is necessary.

The youngest *Chrysemys* embryos used in the present study which display any nasal differentiation have well developed nasal placodes without any conspicuous inpocketing (see Figs. 3 and 4). These placodes are located ventrolaterally on the heads, extending from the anterior end of the optic vesicles almost to the tip of the snout. They are nearly circular, with the ventral margin slightly flattened. In none of the series studied are the placodes in actual contact with the wall of the brain; there is always a small amount of undifferentiated mesenchyme interposed between the two. As in most of the early stages, there is as yet no visible nuclear differentiation, but the ectodermal tissues, both neural and integumentary, are distinguished from the intervening mesoderm by their darker-stained cytoplasm. The placodes are three to four times as thick as the simple cuboidal epithelium of the head with which they gradually merge without any sharp boundaries. The thickest part of the placode is posterodorsal to its center. In the youngest series, the nasal epithelium is simple columnar, but in a slightly more advanced embryo it is either stratified or pseudostratified, probably the latter since Voeltzkow (1903) simply describes it as "hohe Cylinderepithel" in a somewhat later stage in *Eretmochelys*. In the placode the nuclei tend to be basally situated, instead of being central as in the general body epithelium.

The nasal placode is, in the next stage, slightly indented, as shown in Figure 5. Its position is much as in the preceding stage, but it does not now reach as close to the anterior end of the snout as formerly, and it is separated from the brain by a greater thickness of mesenchyme. The nasal epithelium has become noticeably thicker, being up to five nuclei in depth. Whether it is stratified or pseudostratified could not be told from the available material; this stage appears, however, slightly less advanced than Voeltzkow's (1903) embryo mentioned above. The tendency for the nuclei to be basal is most clearly marked in the region of greatest indentation. However, there are more mitotic figures peripherally than basally. The greatest inpocketing is in the thickest region of the placode, posterior and dorsal to its center. Thus, although there is nowhere a clear separation between nasal and general body epithelium, the transition is most abrupt posterodorsally.

The indentation in the placode continues to deepen to form a simple pit. At this stage the indentation is still strongest dorsally, so that the dorsal wall is almost horizontal and the ventral wall vertical. However, now the deepest part is central when seen in frontal section instead of being posterior (see Fig. 6; Fig. 7 shows this stage in sagittal section). The nasal anlage is still ventrolateral and subterminal on the snout. Voeltzkow's (1903) figure 1 on plate 28 shows the external appearance of this

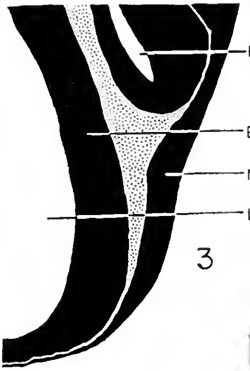
Figure 3. *Chrysemys* 1049 (4.8; MC). Frontal section through the nasal area (section 33). 160x.

Figure 4. *Chrysemys* 1050 (4.8; MC). Transverse section through the nasal area (section 13). 160x.

Figure 5. *Chrysemys* 1055 (6.2; MC). Transverse sections through the nasal area. A, section 74; B, 7 sections posterior to A; and C, 6 posterior to B. 90x.

Figure 6. *Chrysemys* 1060 (5.6; MC). Frontal sections through the nasal area. A, section 90; B, 4 sections ventral to A; and C, 6 ventral to B. 90x.

Figure 7. *Chrysemys* 1481 (5.0; MC). Sagittal section through the nasal area (section 16). 78x.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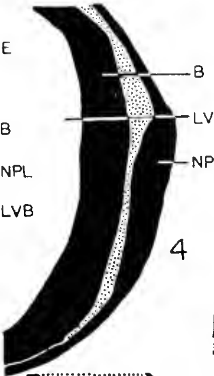
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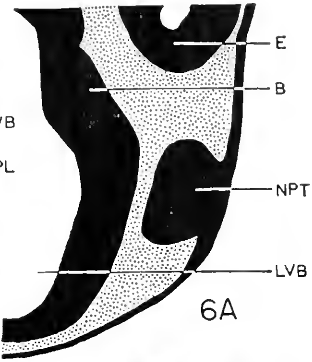
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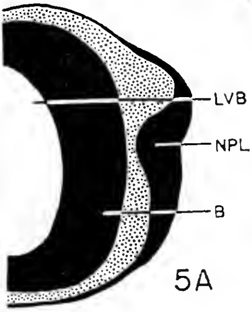
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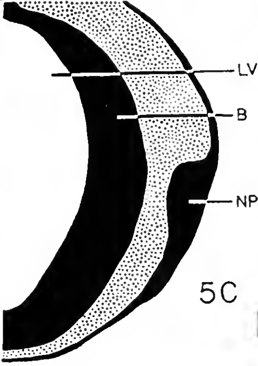
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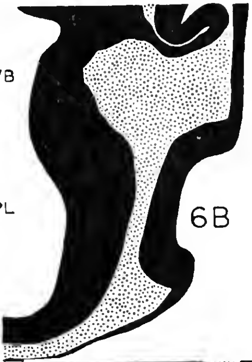
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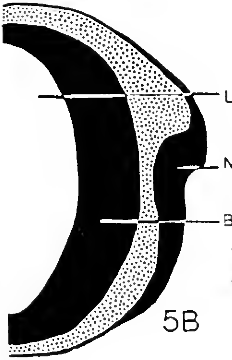
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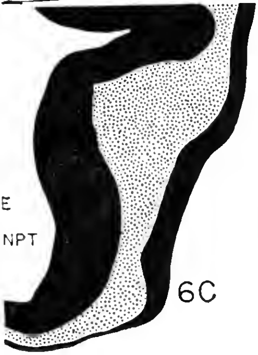
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stage; the pit is circular with its margins slightly raised, apparently more so in *Eretmochelys* than in *Chrysemys.* The thickened wall still merges gradually with the general body epithelium, which is one or occasionally two cells thick. The transition is most gradual ventrally. The placode appears but little thicker than in the preceding stage and is histologically much the same, although the basement membrane is now very distinct, showing low gentle undulations, and the peripheral concentration of mitoses is more marked.

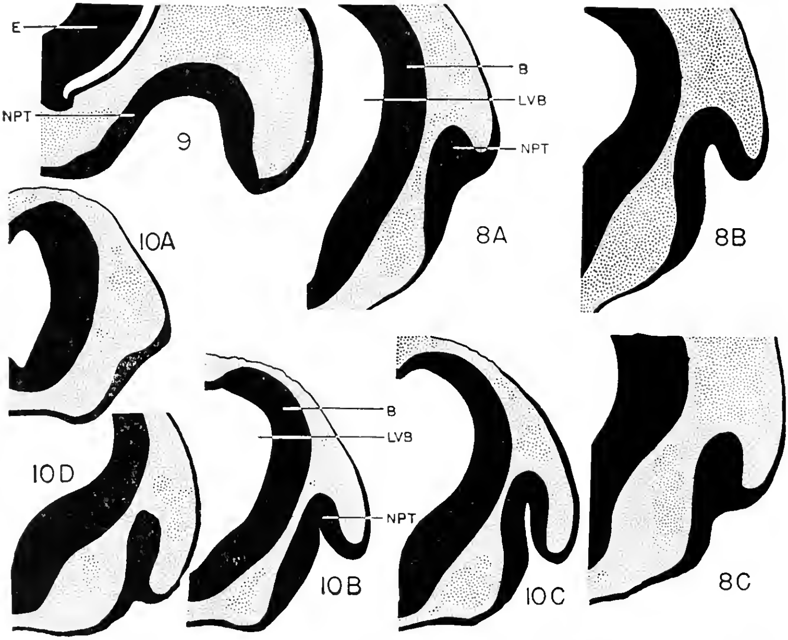


Figure 8. *Chrysemys* 1061 (7.6; MC). Transverse sections through the nasal area. A, section 87; B, 6 sections posterior to A; and C, 9 posterior to B. 60x.

Figure 9. *Chrysemys* 1062 (6.5; MC). Sagittal section through the nasal area (section 23). 60x.

Figure 10. *Chrysemys* 2132 (7.0; MC). Transverse sections through the nasal area. A, section 189; B, 11 sections posterior to A; C, 11 posterior to B; and D, 6 posterior to C. 42x.

The pit increases in depth, growing dorsally from the original placode (see Fig. 8). In some of the more advanced series of this stage its dorsal end is slightly lateral to the naris. The nasal pit is no longer round, but has become elongate so that the naris is oval, with the long axis anteroposterior. Anteriorly, the naris is wide; it narrows as it goes posteriorly and slightly ventrolaterally. The pit is deepest in the anterior half, especially in the more advanced embryos, where it is approximately as high as long (see Fig. 9). At the posterior end it becomes very low and is no more than a small band of thickened epithelium before it finally blends with the general body epithelium. The lumen is widest anteriorly. At this stage there appears the start of differential thickening of the nasal epithelium; it is thickest dorsally and medially, especially in the anterior two-thirds of the pit. Seydel (1896), however, in a *Chrysemys* embryo of similar stage noted no differences in thickness between various regions of the nasal epithelium. His description is otherwise in agreement with that given above.

Histologically there are few changes. There is still no visible nuclear differentiation. The previously noted concentration of nuclei basally and mitotic figures peripherally is still marked near the apex of the pit, but is not clearly seen elsewhere. The nasal epithelium appears to be up to six nuclei deep, but the cell shape and arrangement could not be distinguished. Seydel reports high columnar epithelium. The basement membrane tends to disappear dorsally, so that the boundaries of the nasal epithelium and the wall of the brain with the intervening mesodermal tissues are hard to distinguish. However, there appears to be no direct contact between the brain and nasal tissue. As before, the epithelia of the nose and of the rest of the head are continuous and not marked by any sharp separation.

The final stage before the fusion of the lateral and medial nasal processes (*Nasenfortsätze* of the German literature) is that of a deep, dorsally-extending pit. The shape is basically as in the preceding stage. Transverse sections of this stage are shown in Figure 10. A slightly more advanced embryo is shown in Figure 11, while Figure 12 shows frontal sections of a similar embryo. The naris is widely open anteriorly, but becomes a long narrow slit posteriorly. It is most lateral near its center, curving medially at both ends. Its anterior end is well dorsal to the posterior. Above the naris, the pit is dorsally and slightly laterally directed, with a wide lumen anteriorly and ventrally and a very narrow slit-like one dorsally, especially in the posterior half.

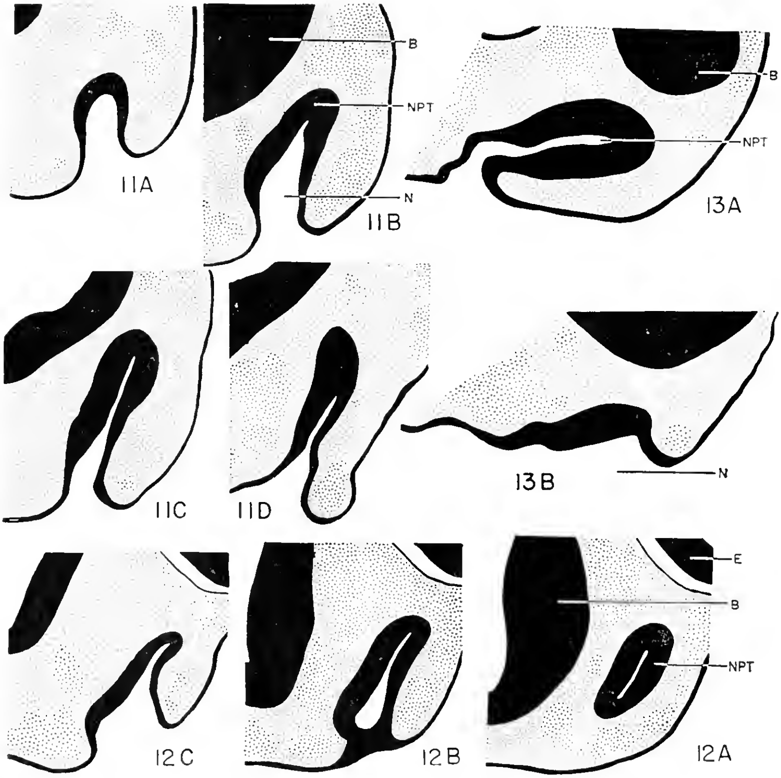


Figure 11. *Chrysemys* 1073 (9.5; MC). Transverse sections through the nasal area. A, section 171; B, 5 sections posterior to A; C, 5 posterior to B; and D, 8 posterior to C. 40x.

Figure 12. *Chrysemys* 1075 (8.4; MC). Frontal sections through the nasal area. A, section 73; B, 6 sections ventral to A; and C, 10 ventral to B. 40x.

Figure 13. *Chrysemys* 1074 (8.6; MC). Sagittal sections through the nasal area. A, section 121; and B, 11 sections medial to A. 40x.

The pit is deepest in the anterior half as is shown most clearly in sagittal section (see Fig. 13). The posterior wall is now nearly vertical, but in the more advanced embryos of this stage the naris continues anteriorly as a shallow, almost directly dorsally directed groove which runs a short distance anterior to the deep part of the pit. Anteriorly, the lumen turns laterally at the naris, thus forming a concavity in the ventromedian wall. This is shown best in Figures 12B and C. It lies at approximately the place where a Jacobson's organ might be expected to develop. There are, however, no signs of any differentiation of this area, and were a concavity not specifically looked for here on the basis of the nasal embryology of other forms, it would hardly be considered worthy of any note. The position of the naris on the snout is the same as in earlier stages, although due to an increase in the mesodermal tissue of the head, it now reaches anterior to the brain.

The differential thickening of the epithelium in different parts of the nose has become very marked, as is shown in the several figures of this stage. In general the walls are very thick anteriorly and dorsally, and thin in the entire posterior third and ventrally. They are thicker medially than laterally, and the much thickened part reaches farther ventrally on the median wall. It usually becomes thinner in the region of the concavity mentioned above so that the possible Jacobson's organ has walls of very variable thickness in different embryos — a condition markedly different from that in forms where such an organ is typically developed. However, in some of the series there does appear to be some definite thickening of the epithelium of this region.

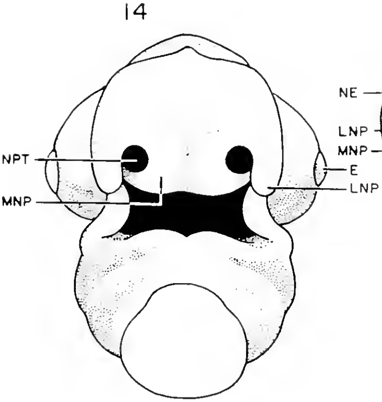
The histology shows few changes. The basement membrane of the nasal epithelium is not at all clear dorsally, but the nose appears not to touch the wall of the brain at any point, although they are in very close proximity. Near the apex of the pit the distribution of nuclei and mitotic figures previously described is still found, but farther ventrally there are few mitoses visible and the nuclei seem rather evenly distributed in the epithelium or even concentrated towards the lumen. There is still no sharp separation of nasal and general body epithelium.

Besides the *Chrysemys* material, a few other turtle embryos of this stage were examined. An embryo of *Chelydra* showed almost no differences from the descriptions already given. The only noteworthy point is that in this embryo the ventromedian concavity has quite thick walls. Two *Trionyx* embryos also possess the same pattern. Some details show slight differences from the *Chrysemys* studied, but these are not basic or even obvious.

Most of the papers dealing with the early embryology of the nasal region figure this stage. However, for the most part they show very little. Seydel (1896) shows a *Chrysemys*, slightly more advanced than any specimen available for the present study, in which the still single naris has become much constricted and is almost closed near its anterior end, thus separating the naris externus from the primitive choana. The only other difference from the embryos described above is that the ventromedian indentation is more pronounced than in any of the material used in the present study, or than figured by other workers except Loew (1956), although it is still far less conspicuous than the Jacobson's organ of a snake or lizard of a similar stage. Thäter's (1910) figures of a *Chrysemys* are too diagrammatic to show more than that it is of this stage, and Fuchs' (1907) *Emys* agrees with the *Chrysemys* examined except that the nasal pits seem to lean farther laterally in his material.

The external appearance in *Eretmochelys* is clearly shown by Voeltzkow (1903), whose figure 4a is reproduced in Figure 14. This needs no comment except to call attention to the prominent nasal processes which in section merely appear as the lateral and medial walls of the nasal pit. Other papers showing the external appearance at this stage are Dohrer (1912, *Chelydra*), Parker (1880, *Chelonia*), and Deraniyagala (1932 and 1939, *Dermochelys*). Thus the nasal pits of all turtles so far studied, and very probably of all cryptodires at least, are exceedingly similar at this stage.

Unfortunately, there were no series available for the present study which show the actual fusion of the medial and lateral nasal processes separating the nares externi from the primitive choanae. Voeltzkow (1903) summarizes the process in *Eretmochelys* as follows (p. 187): "Wie wir sahen, erfolgte der Verschluss der Nasenrinne durch Aneinanderlegen des lateralen und medialen Nasenfortsatzes, wobei jedoch eine primitive Choana vom Verschluss ausgeschlossen blieb. Durch Verwachsung beider Fortsätze und Verschmelzung der bindegewebigen Grundlagen mit Verdrängung der trennenden Epithelschicht ist nunmehr eine solide Scheidewand zwischen Nasendach und vorderstem Abschnitt der Mundhöhle, der sogenannte primitive Gaumen, gebildet." Such a stage is shown in Figure 15, which is taken from Voeltzkow's paper. Sections of this stage are figured by Fuchs (1907 and 1915). His embryo is only very slightly younger than some of those considered in the following section; the description agrees with that of Voeltzkow. Thäter (1910) also studied this stage using *Chelydra*, and his conclusions are dealt with at some length by Fuchs (1915). Their rather acrimonious dispute reflects differences more in the terminology used than in the processes observed, so it need not be treated here.



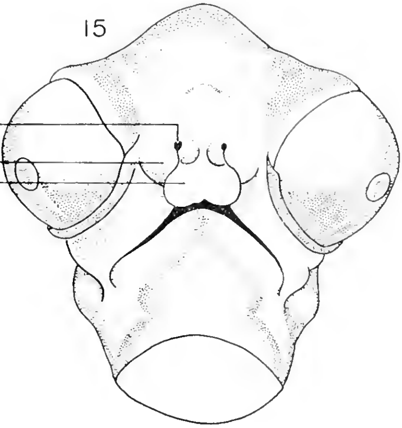


Figure 14. Anteroventral view of the head of an *Eretmochelys* embryo (after Voeltzkow, 1903). 11x.

Figure 15. Anteroventral view of the head of an *Eretmochelys* embryo slightly older than that shown in Fig. 14 (after Voeltzkow, 1903). 7x.

Later embryology. The major part of the study of the stages following the fusion of the nasal processes was made on *Chrysemys*, of which a very good series of embryos was available.

Supplementary observations were made on *Emys*, *Chelydra*, and *Trionyx*.

The stage immediately following the fusion of the nasal processes in *Chrysemys* is shown in Figure 16. In general shape the nasal cavity closely resembles the earlier stages, but the long narial opening has been divided into an anteroventral naris externus and a long slitlike choana on the palate. Anteriorly, the nasal cavity is oval in shape while posteriorly it becomes a long slit, due mainly to a marked dorsal extension. In the region of the choana there is a small lateral groove at the ventral margin of the nasal cavity. Although the nasal processes are

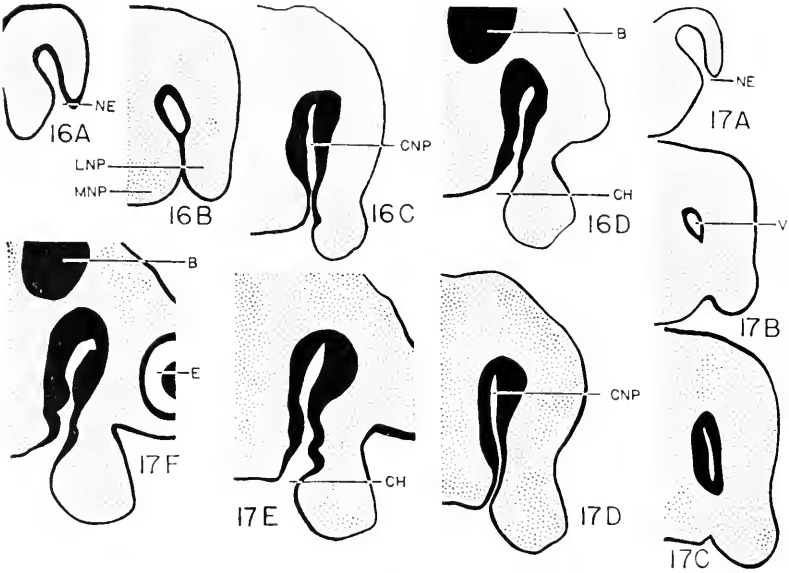


Figure 16. *Chrysemys* 1076 (10.4; MC). Transverse sections through the nasal area. A, section 264; B, 13 sections posterior to A; C, 11 posterior to B; and D, 11 posterior to C. 23x.

Figure 17. *Chrysemys* 972 (9.2; MC). Transverse sections through the nasal area. A, section 250; B, 8 sections posterior to A; C, 10 posterior to B; D, 6 posterior to C; E, 5 posterior to D; and F, 5 posterior to E. 23x.

fused, their epidermal epithelium is still visible as a band running from the ventral border of the nasal cavity to the face and palate, as shown in Figure 74.

Histologically, there is still little differentiation. The nasal epithelium is markedly thicker dorsally and medially than in the ventrolateral portions, but there are no sharp boundaries between the regions. However, the thicker portion appears to be well innervated, while no branches of the olfactory nerve could be traced to the thinner parts, and the former shows a greater

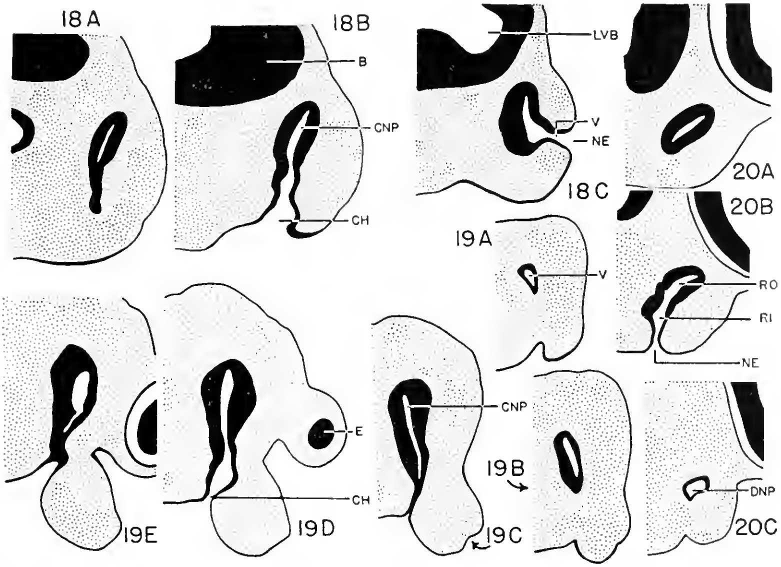


Figure 18. *Chrysemys* 973 (7.0; MC). Sagittal sections through the nasal area. A, section 80; B, 8 sections medial to A; and C, 10 medial to B. 18x.

Figure 19. *Chrysemys* 1079 (9.6; MC). Transverse sections through the nasal area. A, section 240; B, 7 sections posterior to A; C, 10 posterior to B; D, 6 posterior to C; and E, 5 posterior to D. 18x.

Figure 20. *Chrysemys* 1080 (9.6; MC). Frontal sections through the nasal area. A, section 80; B, 17 sections ventral to A; and C, 22 ventral to B. 18x.

concentration of mitotic figures near the lumen. There is a slight hint of a thinner line approximately two-thirds of the way dorsal on the medial wall which could indicate the future line of separation between the regiones olfactoria and intermedialis, but since this division is so vague and is absent in some older embryos, this seems unlikely. There is as yet no distinct vestibulum or ductus nasopharyngeus.

The next group of embryos shows a very similar condition but with the line of fusion of the nasal processes no longer marked by a band of epithelial cells, although in some embryos traces of one may still remain. Figures 17 and 18 illustrate this stage.

The naris externus is at the anterior tip of the snout and leads into a short and rather indistinct vestibulum. This chamber has a distinctly oval lumen in contrast to later stages in which it becomes more nearly circular. Histologically, the epithelium of the vestibulum shows something of a transition between the nasal epithelium and the epidermis, although it resembles the former more closely in being columnar rather than cuboidal.

The cavum nasi proprium remains essentially as in the preceding stage. The dorsal half, the presumptive regio olfactoria, possesses thicker walls and is somewhat lateral to the more ventral anlage of the regio intermedialis, but the separation between the regiones is not well marked. Such a division is most clearly seen in sagittal section (see Fig. 18B). The epithelium is generally slightly thicker than before, but otherwise unchanged.

A ductus nasopharyngeus is not yet present; the cavum nasi proprium opens directly into the mouth cavity by a slitlike choana along the posterior half of its ventral margin. The lumen is, at this time, wider here than in any other part of the nasal cavity. At this stage the small lateral groove along the choana reaches its greatest development.

The next stage is represented by fourteen embryos of *Chrysemys*. During the period covered by these series many changes occur, but the order in which they take place is not constant, so that further division into shorter stages is impractical. The description, therefore, is general rather than based on a few selected embryos. Figures 19, 20, and 21 illustrate this stage.

The vestibulum is more distinct than previously, but still tends to merge gradually with both the cavum nasi proprium and the external covering of the snout. It may be either circular or oval in transverse section. Throughout this stage it increases in length to the condition shown in Figure 21C. The presence of a moderately large lumen differentiates this from the following stages in which the vestibulum becomes virtually solid. As would be expected from the shape of the snout, the naris externus is the most medial part of the nose.

The cavum nasi proprium is becoming considerably more complex. In most of the series the regiones olfactoria and intermedialis can be distinguished, although this is not universally true. The lateral border is marked by the transition from the thicker epithelium dorsally to thinner ventrally; at the end of this stage the transition is quite abrupt. Medially, the entire wall of the cavum is thick, but a line of demarcation is starting to develop between the regiones. Most commonly this is simply a horizontal line of thinner epithelium appearing as a groove along the basal surface of the epithelium. Occasionally there are two such grooves with a third parallel groove between them in the superficial edge of the epithelium (see Fig. 20B). There is also a developing tendency for the lumen to be wider in the regio intermedialis than further dorsally. The regio olfactoria reaches farther ventrally on the lateral than the medial wall.

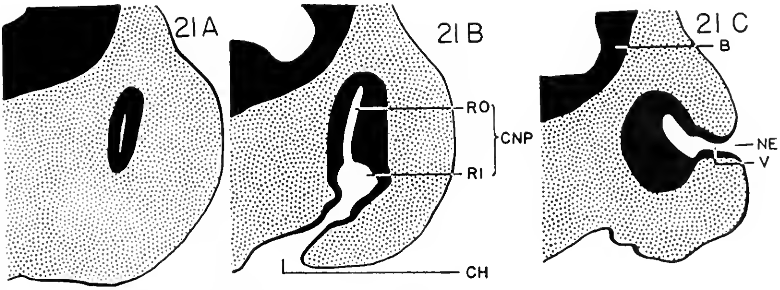


Figure 21. *Chrysemys* 1085 (9.0; MC). Sagittal sections through the nasal area. A, section 91; B, 10 sections medial to A; and C, 8 medial to B. 23x.

The cavum is in general closer to the midline anteriorly than posteriorly. This is most marked dorsally where the lumina of the regiones olfactoriae of opposite sides are at approximately right angles to each other; ventral to the nares externi the two sides are nearly parallel. Seen in transverse section the regio intermedialis is almost vertical. At the start of this stage the regio olfactoria appears to lean slightly laterally, but by its end this is true only posteriorly. Anteriorly, the dorsal part of the cavum becomes slightly median to the ventral. In frontal sections the posterior part of the regio olfactoria can be seen to turn laterally, thus producing a convexity in its lateral wall; this is the first appearance of the Muschelwulst.

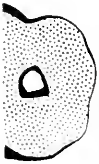
Histologically, there is very little regional differentiation visible in the available material, aside from the thickness of the epithelium. In some of the oldest embryos of this stage the thicker and presumably sensory portions show a clear cytoplasmic zone peripherally which has very few nuclei, while in the thinner portions, including the vestibulum and ductus nasopharyngeus, the nuclei are evenly distributed throughout the epithelial layer. However, this distinction is not marked. The pattern of thickening is well shown in the figures.

With the continued posterior growth of the primary palate, the choanae become more restricted, and a short ductus nasopharyngeus is formed (see Fig. 21B). This possesses a very wide lumen. The ductus runs slightly medially as well as ventrally from the cavum, but the choanae, which open into shallow grooves on the palate, are widely separated.

The next stage (see Fig. 22) displays few but important changes. The vestibulum is longer and generally quite circular.

Figure 22. *Chrysemys* 2136 (8.8; MC). Transverse sections through the nasal area. A, section 346; B, 10 sections posterior to A; C, 20 posterior to B; D, 16 posterior to C; E, 20 posterior to D; F, 11 posterior to E; and G, 12 posterior to F. 22x.

Figure 23. *Chrysemys* 1472 (10.8; MC). Transverse sections through the nasal area. A, section 313; B, 16 sections posterior to A; C, 12 posterior to B; D, 9 posterior to C; E, 6 posterior to D; and F, 8 posterior to E. 22x.



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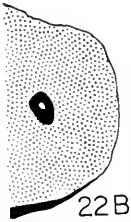

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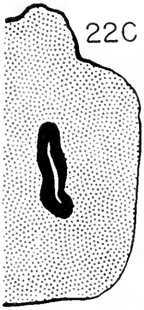

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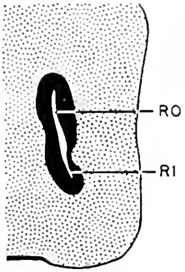

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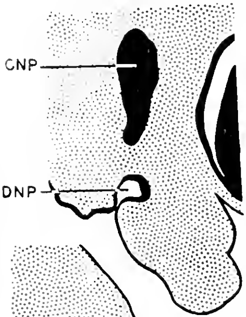

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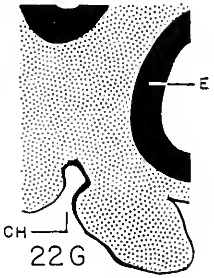
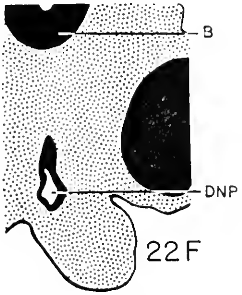


22G



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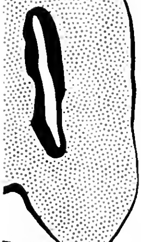

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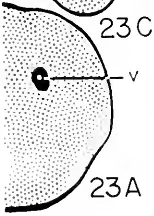

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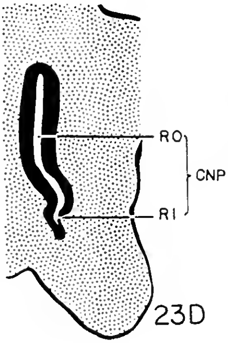

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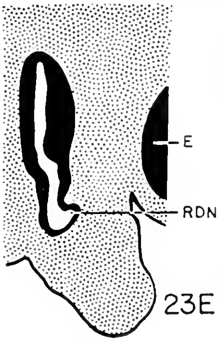
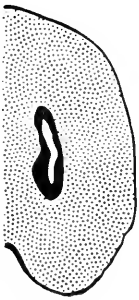


23E



23B

The most conspicuous development is that its walls have greatly thickened so that its lumen is much reduced in diameter. The cavum nasi proprium is exactly the same shape as described above, although the lumen is generally narrower and the regio olfactoria proportionately larger. However, the regio intermedialis now bears thickened epithelium not only medially, but also ventrally and ventrolaterally. This thickening appears to proceed progressively around the ventral margin from the medial wall. Posteriorly there is far less of the thick epithelium on the

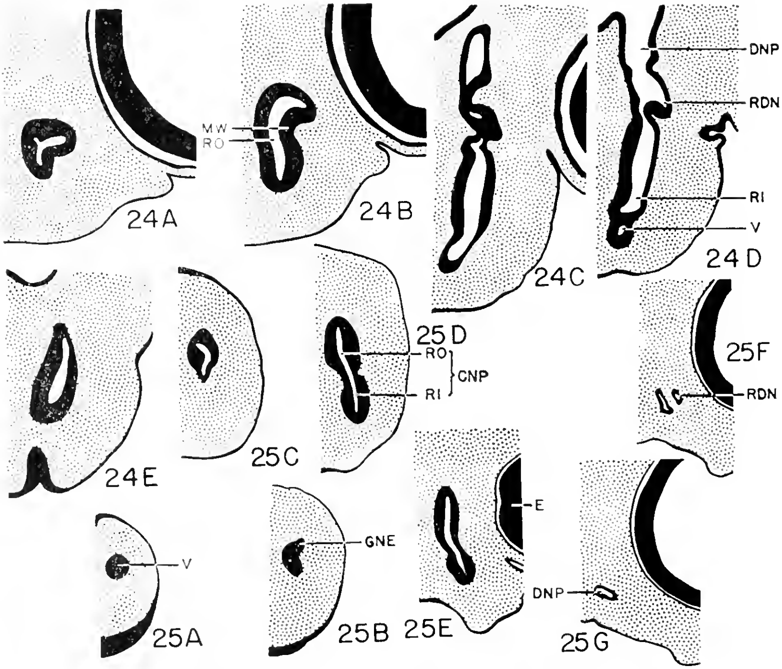


Figure 24. *Chrysemys* 1473 (9.8; MC). Frontal sections through the nasal area. A, section 183; B, 16 sections ventral to A; C, 18 ventral to B; D, 5 ventral to C; and E, 6 ventral to D. 21x.

Figure 25. *Chrysemys* 2141 (10.2; MC). Transverse sections through the nasal area. A, section 452; B, 17 sections posterior to A; C, 13 posterior to B; D, 20 posterior to C; E, 32 posterior to D; F, 24 posterior to E; and G, 24 posterior to F. 13x.

lateral wall than there is anteriorly. The circular ductus nasopharyngeus is considerably longer than previously so that the choanae are now completely posterior to the cavum nasi proprium.

The following stage (see Figs. 23 and 24) is unfortunately represented by only three embryos. The vestibulum is essentially as in the preceding stage, but the lumen is even smaller; in at least one series it appears to be completely solid for a short distance.

The cavum nasi proprium is also relatively unchanged. The regio olfactoria is generally slightly medial to the more ventral regio intermedialis, but the cavum is very close to vertical. The cava of opposite sides are now parallel. The Muschelwulst is highly developed as can be seen in Figure 24B. Surprisingly, the older embryos of this group seem to have less of the thickened epithelium ventrolaterally than in the preceding stage. There is, however, still some anteriorly. Histologically, the epithelium appears uniform except for the previously mentioned tendency for a peripheral zone lacking nuclei in the thickened areas; such zonation is not found in the areas of thinner epithelium. Figure 75 illustrates this feature. Posteroventrally the cavum becomes very narrow in the region of its junction with the ductus nasopharyngeus.

It is in the ductus that the greatest changes have occurred. The lumen is large and circular except at its anterior or nasal end where it connects with the cavum by a thin slit along its medial edge. The anterolateral end continues slightly anteriorly as a small blind pocket best shown in Figure 24D. This is the first stage in the development of the recessus ducti nasopharyngei.

The next stage, as shown in Figures 25 and 26, displays increased complexity in all regions, but most especially in the vestibulum. This is a quite long tubular structure with the anterior three-fourths circular in transverse section. Posteriorly, it becomes oval with the long axis vertical. The walls are very thick, and the lumen very restricted or completely obliterated. The histological character of the epithelium now reaches the condition which persists throughout the later development. There is an outer layer or two of columnar cells surrounding a thicker zone of cuboidal cells which gradually merges with the

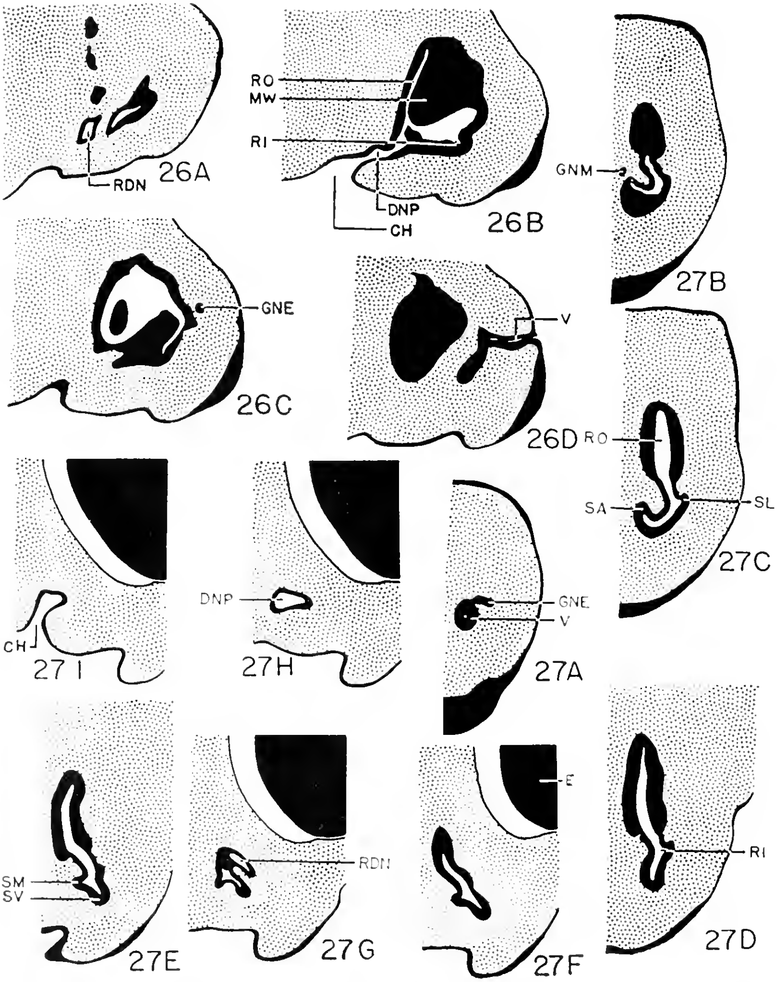


Figure 26. *Chrysemys* 1088 (11.0; MC). Sagittal sections through the nasal area. A, section 180; B, 6 sections medial to A; C, 6 medial to B; and D, 5 medial to C. 14x.

Figure 27. *Chrysemys* 1092 (16.7; MC). Transverse sections through the nasal area. A, section 30; B, 13 sections posterior to A; C, 7 posterior to B; D, 11 posterior to C; E, 11 posterior to D; F, 13 posterior to E; G, 16 posterior to F; H, 17 posterior to G; and I, 11 posterior to H. 22x.

stratified squamous epithelium actually lining and often filling the lumen. Such a pattern is clear in Figure 76 although the embryo figured is considerably more advanced. The nares externi are somewhat dorsal on the snout and very close to the midline.

More important are the appearances of two outgrowths of the vestibulum. The first to develop is the anlage of the *glandula nasalis externa*. This arises as a short solid prong growing dorsolaterally and slightly posteriorly from the dorsolateral surface of the vestibulum, very near its posterior end (see Fig. 25B). By the end of this stage there may be signs of a lumen within the prong, but this is variable. The subsequent development of the gland is described separately. From the same level or slightly further posteriorly another solid process may be seen medially on the dorsal edge of the vestibulum in the later embryos of this stage. This structure is found in all the older series, but has apparently not been previously described. Neither its ultimate fate nor its function are known; it is here termed the "dorsal recess of the vestibulum."

Within the cavum nasi proprium the changes are slightly less marked but important. The regiones olfactoria and intermedialis are divided as described above. Anteriorly, the former regio reaches farther ventrally on the lateral than on the medial wall, but posteriorly the reverse is true. The regio olfactoria is in general vertical, with the dorsal part somewhat medially directed near the anterior end. The more ventral regio intermedialis is also vertical in the anterior two-thirds of the nose, although with a strong medial twist at its ventral end in the anterior one-third. Posteriorly, this regio is more laterally directed, as shown in Figure 25. Thus the regio olfactoria is mostly medial to the intermedialis. The Muschelwulst is well developed. The cavum has a narrow lumen at this stage.

Histologically, there is little to add to the earlier descriptions. The regio intermedialis tends to have slightly thinner epithelium than the regio olfactoria, but this distinction is not always shown. The regio intermedialis possesses much thickened epithelium medially and, in the anterior two-thirds, ventrally and laterally as well. Although the anteromedial curve gives some indication of their future development, the sulci are not yet differentiated.

The ductus nasopharyngeus has a very small lumen anteriorly, but widens into a large circular tube posterior to the entrance of the recessus ducti nasopharyngei. The recessus is larger than in the preceding stage, but its walls are thicker so that the lumen is but little increased. It lies lateral and slightly dorsal to the anterior end of the ductus. Posteriorly, the ductus again narrows and becomes a small horizontal oval. The choanae are now closer to the midline, and those of opposite sides open into a single median groove in the palate by the end of this stage.

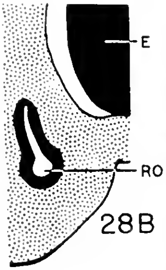
The embryos of the next stage start to assume the adult form with the development of the complex pattern of sulci in the regio intermedialis. Figures 27 and 28 illustrate this stage.

The vestibulum shows further differentiation with the development of the *glandula nasalis medialis*. It appears as a solid rod growing posteroventrally from the medial surface of the vestibulum, just anterior to the border of the regio intermedialis. It is further discussed in the section on nasal glands. The dorsal recess of the vestibulum is somewhat larger and, in the oldest embryos of this stage, is beginning to acquire a lumen. In frontal section it is oval as shown in Figure 28C. There are no visible histological changes, and the vestibulum remains essentially a thick-walled horizontal tube.

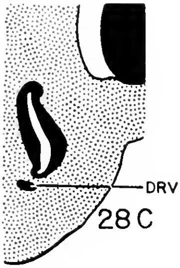
Figure 28. *Chrysemys* 1090 (16.8; MC). Frontal sections through the nasal area. A, section 204; B, 16 sections ventral to A; C, 20 ventral to B; D, 16 ventral to C; and E, 10 ventral to D. 22x.

Figure 29. *Chrysemys* 1096 (27.0; MC). Transverse sections through the nasal area. A, section 52; B, 27 sections posterior to A; C, 23 posterior to B; D, 28 posterior to C; E, 20 posterior to D; and F, 29 posterior to E. 17x.


28A



28B



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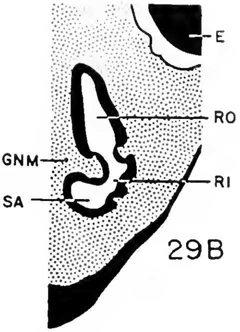

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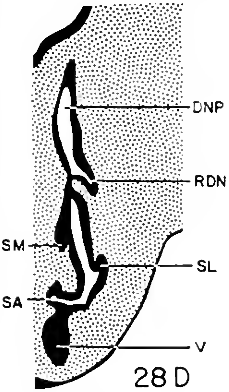

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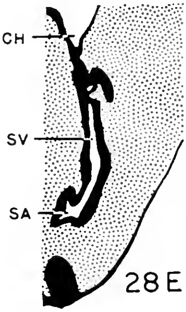

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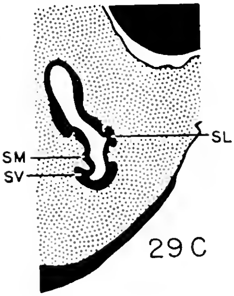

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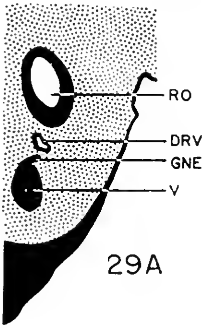
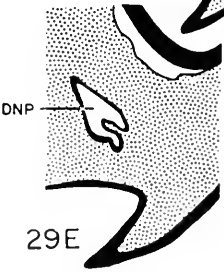


29A



29E

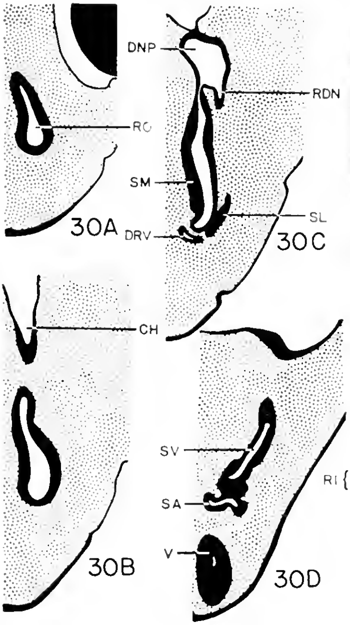
The regio olfactoria is quite simple. Its walls are everywhere very thick with a sharp boundary to the thinner epithelium of the regio intermedialis, except posteroventrally where they thin gradually. The lumen is wider than in the preceding stage, especially anteriorly. The regio olfactoria is virtually vertical, but posterolaterally there is a very small Muschelwulst so that this regio is slightly concave laterally in either transverse or frontal sections. The posterior ends are closer to the midline than the anterior. Grenzfalten are not yet formed, although there are faint signs of the medial one.

The regio intermedialis now possesses all four sulci. These are present as narrow grooves rather than as the adult condition of shallow troughs separated by ridges. Histologically, the epithelium shows no differentiation. It is all thinner than that of the regio olfactoria, most markedly so along the dorsal margins where the Grenzfalten will develop. There is frequently a clear peripheral zone lacking nuclei in the thinnest portions by this stage, so that such a zone can no longer be used as a criterion for presumptive sensory areas.

The shape of this regio as a whole can be seen in the figures. The regio is most medial anteriorly where the vestibulum enters its anterodorsal wall. In this region it is J-shaped with the hook directed medially. Posteriorly, it soon becomes vertical, and then the ventral end is turned away from the midline. The posterior ends of either side converge towards the midline so that in frontal section it appears concave medially. Throughout most of its length it is lateral to the regio olfactoria. The regio intermedialis slopes posteroventrally at an angle of approximately twenty-five degrees to the horizontal.

The pattern of the sulci is best shown in Figure 27. The sulcus anterior is ventromedian in the anterior quarter of the cavum, thus forming the hook of the J mentioned above. Starting at its posterior end and imperfectly separated from it, the sulcus ventralis runs along the ventral margin of the regio to its junction with the ductus nasopharyngeus. The smaller sulcus lateralis is prominent in the anterior three-quarters of the cavity, while the slightly more ventral sulcus medialis is present only in the posterior third of the regio intermedialis where it reaches to the start of the ductus.

The ductus nasopharyngeus shows fewer changes. It is very narrow anteriorly, but increases in diameter posterior to the recessus. The latter is now dorsolateral and larger, with an extensive lumen. Posteriorly, the ducti converge slightly to enter a medial groove in the palate. There is only a very slight posterior thinning at this stage and the caudal portion of the ductus is triangular (see Fig. 27H) rather than oval as in previous stages.



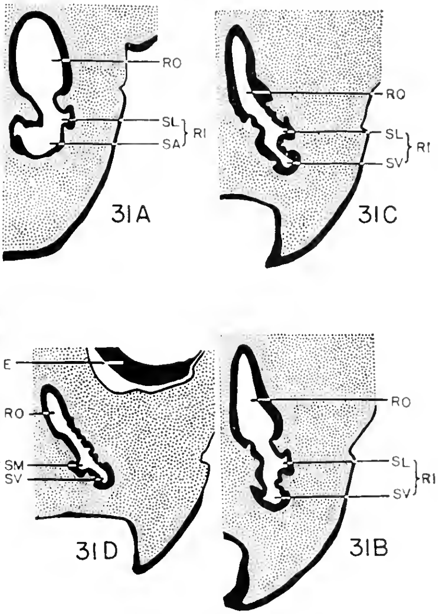


Figure 30. *Chrysemys* 1098 (28.1; MC). Frontal sections through the nasal area. A, section 133; B, 26 sections ventral to A; C, 11 ventral to B; and D, 29 ventral to C. 15x.

Figure 31. *Chrysemys* 1653 (32.0; MC). Transverse sections through the nasal area. A, section 55; B, 14 sections posterior to A; C, 9 posterior to B; and D, 19 posterior to C. 13x.

A final stage is represented by nine *Chrysemys* embryos. The pattern is very close to that of the adult, although in general the various ridges are less marked in the embryos. Figure 29 shows transverse sections of an embryo of this stage, and Figure 31 the cavum nasi proprium of a slightly older one. Frontal and sagittal sections are shown in Figures 30 and 32.

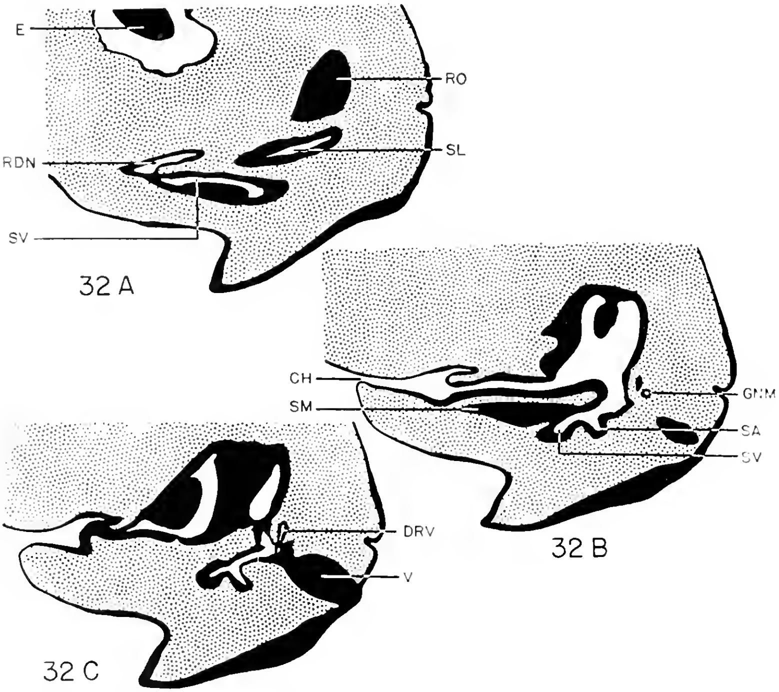


Figure 32. *Chrysemys* 1099 (26.4; MC). Sagittal sections through the nasal area. A, section 520; B, 11 sections medial to A; and C, 6 medial to B. 15x.

The vestibulum is very like that in the preceding stage. Anteriorly it is a long circular tube with very thick walls and a small lumen which is probably not continuous in most of the series. Histologically, its epithelium still shows a transition from columnar cells basally to squamous cells centrally as shown in Figure 76. Posteriorly, the vestibulum is, in transverse section, oval with the long axis vertical. Here the epithelium shows a transition to that of the cavum nasi proprium — the term vestibulum is thus used in a topographic sense without implying any specific histologic structure. The duct of the glandula nasalis externa enters the dorsolateral surface of the vestibulum well posteriorly, and that of the glandula nasalis medialis enters the medial surface at its extreme posterior end. Both ducts have large lumina at this stage. Between the two on the dorsomedial surface is the dorsal recess which is a dorsally-directed projection lying within the cartilaginous nasal capsule. It has a very small lumen and is lined by quite high columnar epithelium like that of the surrounding parts of the vestibulum. It is most clearly seen in Figure 32C, while its crescentic shape in frontal section is shown in Figure 30C.

The only gross differences from the preceding stage in the regio olfactoria are the further and nearly complete reduction of the Muschelwulst and a progressive widening of the lumen (compare Figs. 27, 29, and 31). The lumen is largest anteriorly and thins rapidly towards the rear so that both lateral and medial walls are concave inwards; the concavity is most marked medially. The general shape of this regio is of a laterally compressed hemisphere.

Histologically, several changes relating to glandular developments have occurred. The sensory portions, that is, all except the extreme posteroventral wall, possess high columnar epithelium with numerous Bowman's glands as shown in Figure 77. The last will be described subsequently when the glands are considered.

The small non-sensory area has lower columnar epithelium consisting mainly of goblet cells (see Fig. 78). The nuclei are thus all basal, with the peripheral area clear and very weakly staining. In some series this type of epithelium is present posterodorsally in the regio intermedialis, but this is not the usual condition, although isolated or even small clusters of goblet cells are common there and in the anterior end of the ductus nasopharyngeus and its recessus. Seydel (1896) describes small tubular "Schleimdrüsen" (which are made up of cells similar to those described above) throughout the non-sensory portions of the nasal cavities of adults of *Testudo* and *Emys*.

The regio intermedialis is separated from the regio olfactoria by well-developed Grenzfalten anteriorly (see Fig. 31A), but posteriorly these disappear and the regiones are less distinct, although there is usually a histological boundary. The general shape of the regio intermedialis remains essentially the same, but the sulci have developed further to approach closely their adult condition. They are now generally wider and more conspicuous. The sulcus anterior is restricted to the anteroventral corner of the regio but now extends well laterally as well as medially (see Fig. 30D). Thus the sulcus ventralis extends farther anteriorly than in the preceding stage. The sulcus medialis also reaches farther anteriorly; by the end of this stage it stretches for three-fourths the length of the regio. The sulcus lateralis is little changed. The various figures give the relations of these sulci. There are also small minor grooves in the wall, especially postero-laterally, as shown in Figure 31D. However, these are very variable and inconstant.

The epithelium of the regio intermedialis is moderately high columnar throughout. It is highest in the sulci, but otherwise there is no apparent differentiation in the material studied. Figure 79 shows its general appearance. Bowman's glands are not found in any part of the regio intermedialis.

The ductus nasopharyngeus shows only minor changes such as increased length. Its lumen is wider in all regions, but still smallest at the anterior end. The recessus ducti nasopharyngei is now more dorsal than lateral to the anterior fifth of the ductus. It too has an extensive lumen. The epithelium is low columnar to cuboidal; whether or not it is stratified could not be told from the available slides, but in some areas there appear to be two layers of cells. The choanae are similar to the preceding stage, although the palatal groove into which they open is now proportionately smaller than previously.

In general, the *Emys* embryos resemble very closely those of *Chrysemys,* and no detailed descriptions of individual stages are necessary. Minor differences which were observed between the genera include slight variations in the time of appearance of the different glands, an earlier and greater development of the Muschelwulst, and a lesser development of the dorsal vestibular recess in *Emys.* The oldest turtle embryo which was studied is of this genus; the sulci are wider and shallower than in any of the *Chrysemys* embryos, and thus approach more closely the adult form.

The *Chelydra* embryos studied are also quite similar to the *Chrysemys* material, although not as closely similar as are the *Emys*. The differences are those which would be expected from the descriptions of the adult anatomy, such as a larger Muschelwulst in *Chelydra*. The material is not advanced enough to show the development of the sulci.

The only available embryo of *Trionyx* which shows the nasal cavities after the fusion of the nasal processes is imperfectly sectioned and too young to show any of the specializations of this genus. In general it closely resembles the *Chrysemys* material, thus serving only to show that probably most turtles possess very similar nasal cavities at this stage.

There is relatively little literature which treats the nasal embryology of turtles and the major portion of that is on one problem — the nature of the palate and the ductus nasopharyngeus. Almost the entire body of papers concerned with this problem consists of a series of arguments of polemic nature between Fuchs and the students of Fleischmann, especially Thäter. Much of the controversy appears to be the result of using different terminology rather than basic differences in concept, although the latter do exist. The arguments will be reviewed only briefly here. A few earlier papers touch on this topic, but are adequately reviewed in the works cited below.

Fuchs (1907, 1908, 1911, and 1915) studied embryos of *Emys* and *Eretmochelys*. He emphasizes that, in the stage immediately following the fusion of the nasal processes, the choanae continue posteriorly for some distance as grooves along the roof of the mouth. These grooves are considered to be part of the original nasal involution, that is, of nasal, not buccal, origin. In later stages there is a progressive fusion from anterior to posterior along the ventral edge of this groove, thus forming a tube. The so-called secondary palate of turtles is thus essentially a continuation of the primary palate, and the secondary choanae are the posterior ends of the primary choanae. In order to differentiate these formations from the very different secondary palate and choanae of mammals, Fuchs in 1908 (but not in 1907) proposes the terms *tegmen oris primarium commutatum* and *choanae reliquae*.

He also, as previously noted, suggests the use of Choanengang rather than ductus nasopharyngeus in this group.

Thäter (1910 and 1912) worked primarily with *Chrysemys*, but also studied the models of *Chelydra* made and described by Dohrer (1912). In the only basic point of disagreement, Thäter points out that the total length of the nose is greater in older embryos, and thus postulates that the nasal cavities have grown. This Fuchs does not dispute. However, Thäter (1910) states that this growth occurs in such a manner that the choanae have become displaced posteriorly "ohne dass irgendwie eine Verwachsung notwendig wäre" (pp. 498-499). Both workers agree on the nasal origin of the ductus nasopharyngeus.

On the dispute over the processes involved, it would seem that both growth and fusion are necessary. Certainly the nasal cavities are far larger in the adult than in the early embryos, and therefore have presumably grown. However, the long slit-like choanae of early stages become nearly circular in the mature animal which would seem to require the ventral fusion of their anterior parts. Differential growth could possibly account for the changes, but the pattern observed in the embryos does not seem to support such a view, and the skeletal relationships in adult cheloniids would be very difficult to explain by such a hypothesis.

The terminology used to describe the adult palate appears to be a far less important problem. No worker would dispute that in many turtles the palate is far more extensive than the primary palate of amphibians or *Sphenodon* and also very different from the secondary palate of mammals or crocodilians; Fuchs' (1908) term tegmen oris primarium commutatum serves to call attention to these differences.

The first paper attempting to cover the general embryology of the nose in a turtle appears to be that of Seydel (1896), who had material of both *Emys* and *Chrysemys*. In general his observations agree well with those given above in the descriptive section, and only the differences need to be mentioned. In the younger stages of *Chrysemys*, Seydel describes the regio intermedialis as quite clearly separable from the regio olfactoria by means of the far more extensive lumen of the former. However, in later stages this distinction disappears, and he separates them by means of the pattern of epithelial thickening concerning which his observations do not differ from those given previously. Seydel's *Chrysemys* embryo IV (carapace 4 mm.) has a somewhat more prominent Muschelwulst than was seen in any of the material studied for the present work, but the difference is slight. His older *Emys* embryos agree closely with those already described, except that he shows the sulcus anterior (the Pars anterior des Jacobson'sches Organs of Seydel) as more restricted, with the sulcus ventralis reaching farther anteriorly.

Loew (1956) also describes a series of *Emys* embryos in a very recent paper; since his figures are very diagrammatic and his text is concerned primarily with the problem of Jacobson's organ, it adds comparatively little here. In general his account agrees with that already given and with Seydel's, but there is one very important difference. Loew calls attention to the early development of a ventromedian groove which he considers to be Jacobson's organ. This is present in all of his embryos in which the nasal processes are completely fused, and seems to correspond to the medial part of the sulcus anterior and the sulcus medialis of the present work. However, in the earliest stages in which he describes it, these are not distinct, and his groove appears to be merely the ventromedian corner of the regio intermedialis.

Four other papers figure, but do not discuss in any detail, the nasal cavities of emydine embryos. Fuchs (1907 and 1915) studied *Emys* in connection with his work on the palate, figuring two early stages. Kunkel (1912) in describing the embryology of the skull has drawings of two later *Emys* embryos. Finally, Thäter (1910) gives highly diagrammatic figures of *Chrysemys* embryos. None of these accounts adds any information to that already given.

The only other turtles whose nasal embryology has even been figured are the Cheloniidae; no descriptions are available. Parker (1880) shows several sections through the nasal area in his paper on the skull of *Chelonia*, and Fuchs (1907, 1911, and 1915) figures *Eretmochelys* in his discussions of the palate. The total information which can be gained from these sources is, however, far too meager to permit any description of the various stages or comparisons with the emydines.

Jacobson's Organ. There has been much disagreement in the literature concerning the nature of this organ in turtles. In the present discussion the various theories are presented, and then considered in the light of the observations made in the present study. Due to the marked differences in their nasal anatomy, the literature on the marine turtles is separately described.

The first paper mentioning Jacobson's organ in turtles is Seydel's 1896 monograph, which remains the most detailed and influential account of the nose in this order. His thesis is that all of the sensory epithelium of the regio intermedialis (the pars respiratoria of his paper) represents Jacobson's organ. A large part of his paper is devoted to an attempt to prove the homology of this sensory area with the supposed Jacobson's organ in the amphibians which he had previously studied. However, since the exact homologies in that group are also disputed, his arguments concerning them need not be given here. Other evidence which he presents in support of his theory includes the innervation of his Jacobson's organ by branches of the medial division of the olfactory nerve and the absence of Bowman's glands throughout the regio intermedialis. Seydel recognized that, according to this theory, Jacobson's organ would essentially equal the entire ventral part of the nose, rather than being restricted to a pocket in the medial wall as in the other amniotes. However, he puts forward two points which he believes should eliminate this as a problem. First, in *Testudo* the sensory epithelium of the regio intermedialis is restricted to the medial wall, and he assumes that this is the primitive condition in turtles. Second, in *Chrysemys* embryos the first areas of thickened and presumptive sensory epithelium, which he observed ventrally, were medial, and only in later stages did they spread to the ventrolateral wall. The latter fact considered with the innervation from the medial nerve trunk strongly suggests a primitive medial position for this sensory area.

Seydel's theory received strong support from McCotter (1917), who studied the nervous connections of the regio intermedialis in "*Chrysemys punctata*." McCotter describes a distinct accessory olfactory bulb receiving the fibers of the medial olfactory trunk. This bulb he considers to be the homolog of the accessory bulb in other amniotes in which it receives the nerve fibers from Jacobson's organ. The evidence presented in these two papers has been thought convincing by many later workers, and Seydel's theory that the entire sensory area of the regio intermedialis represents Jacobson's organ is accepted in many general works including the important review by Matthes (1934).

The next theory to be put forward is that Jacobson's organ is present as a small tubular structure in the septal wall of the nose, and has at its deep end a prominent gland. This is the structure considered by Seydel and other workers to be the duct of the glandula nasalis medialis. Such a theory was first proposed by von Mihalkovics (1898), who calls attention to the gross similarity between this duct in *Emys* and the Jacobson's organ of some mammals such as the mouse, which he also studied in some detail. He further states that a portion of the duct is lined by sensory olfactory epithelium and is strongly innervated by the medial trunk of the olfactory nerve. The only other worker to accept this theory is von Navratil (1926) who agrees with von Mihalkovics in all respects. Other investigators, such as Zuckerkandl (1910a) who also studied *Emys*, were unable to find any sensory epithelium in the duct, and thus could not consider it to be Jacobson's organ.

The most recent theory on the nature of this organ in turtles is that of Loew (1956), who studied a series of *Emys* embryos. In these he finds a rather small but distinct horizontal groove in the ventromedial wall of the nasal cavity — apparently the medial part of the sulcus anterior plus the sulcus medialis in the terminology used in the present paper. This groove first appears shortly after the fusion of the nasal processes has separated the naris externus from the choana. Although Loew notes that this is a relatively advanced stage for the appearance of Jacobson's organ, he considers it quite similar in general form to the anlage of that organ in *Natrix*, which he used for comparison. The groove remains relatively constant in the later development of *Emys* and is present in the adult. In denying that the lateral portion of the regio intermedialis is also part of Jacobson's organ, he states that only the medial wall of the nose is innervated by the medial division of the olfactory nerve. Thus he flatly contradicts the main evidence that Seydel put forward to support his theory.

The other workers who have studied the nose in turtles have generally refused to commit themselves on the problem of Jacobson's organ, although some tend towards the belief that it is completely absent in this order. The latter point of view enjoys a popularity equal to that of Seydel's theory, in general textbooks and reviews.

The first major work which casts doubt on both theories previously proposed is Peter's (1901) chapter in Hertwig's *Handbuch*. Although he did not actually study any turtles, his paper is so widely cited and important that it must be considered. Seydel's theory is discussed, but, in the absence of any transitional forms, Peter could not consider as probable the homology of the Jacobson's organ of lizards and snakes with a structure so radically different in pattern as the regio intermedialis of turtles. The relatively late embryonic development of Seydel's Jacobson's organ is also considered a major objection to such a homology. Von Mihalkovics' theory is mentioned, but, in the absence of any embryological evidence, Peter refuses to speculate on its validity.

Zuckerkandl (1910a) briefly describes the relationship of the olfactory nerve to the various parts of the nose in *Emys*. He definitely denies von Mihalkovics' conclusions, as stated above, but although he reviews Seydel's theory and states that he was able to confirm that author's anatomical findings, he nowhere states any opinion on the homology of Jacobson's organ. In another paper Zuckerkandl (1910b) again reviews the previous literature, and concludes that further study of a greater number of forms is necessary for any solution to this problem.

Nick (1912), in describing the nose of *Chelydra*, states that he considers Seydel's identification of Jacobson's organ probably correct if turtles have any such organ at all. However, he refuses to commit himself further on this point.

In his study of *Pelomedusa*, van der Merwe (1940) could not find any structure which he would consider to represent Jacobson's organ.

Finally the literature on sea turtles must be noted. The first paper to consider Jacobson's organ in this group is Seydel's (1896). His conclusions are based entirely on the study of published figures; he had no actual material. It is his belief that only the posterodorsal recess of the nasal cavity represents the regio olfactoria and that all the remainder of the cavum nasi proprium is the regio intermedialis. This division has found general acceptance and is used in the present paper. Thus, by

Seydel's theory, any sensory epithelium to be found in the recessi dorsalis or ventralis or the areas between them would constitute Jacobson's organ. He was, of course, unable to tell which areas were actually sensory.

Nick (1912) studied both *Chelonia* and *Dermochelys*. Although he mentions Jacobson's organ only in connection with the former, he considers them quite similar in nasal anatomy, so presumably his comments would apply to both genera. He found that the sensory epithelium of the regio intermedialis is restricted to the various recesses, but hesitates to give any opinion on the homologies of the area. He states only that if any Jacobson's organ is present, it is either the total sensory area of the regio intermedialis as postulated by Seydel, or else it is found in the medial part of the recessus dorsalis (the recessus medialis). The latter possibility is suggested by the gross form and topographical position of that recessus.

The last paper on sea turtles is that of Fuchs (1915) which is based on *Eretmochelys* and contains an extensive discussion of the problem. First, he gives four criteria which he considers essential for a Jacobson's organ: independence from the nasal epithelium, connection with the mouth rather than the nose in the adult, innervation by the medial division of the olfactory nerve, and a medial and ventral position. Clearly, turtles possess no organ fulfilling these requirements. However, on the medial wall of the recessus ventralis there is ventromedian sensory epithelium innervated by the medial trunk of the olfactory nerve. This Fuchs considers the probable homolog of Jacobson's organ, and for it he suggests the term pars vomeronasalis. The other sensory areas of the regio intermedialis, including the recessus medialis of Nick, are tentatively rejected as probable homologs of that organ on topographical grounds despite his own demonstration that all the sensory areas of this regio are medially innervated. In so doing Fuchs points out that it is probably incorrect to assume that the entire medial division of the olfactory nerve innervates only Jacobson's organ in other reptiles, so that there is no reason to assume that it does in this group. However, he also admits that, in the absence of any embryological data, these ideas remain speculative. Finally, he briefly comments on the phylogenetic importance of his ideas concerning Jacobson's organ in turtles, preferring to consider their condition primitive rather than derived from some form already possessing a distinct Jacobson's organ.

The observations previously described in this paper and those in the subsequent sections on the nasal glands and nerves shed considerable light on certain aspects of this problem. First, it now seems possible to deny the validity of von Mihalkovics' theory on several grounds. In none of the available material is there any evidence of a sensory area in the duct of the glandula nasalis medialis; rather, its epithelium appears uniform throughout, as reported by Zuckerkandl (1910a). Equally important is the very late embryonic appearance of the gland, which first forms as a solid rod of cells exactly similar to the anlage of the glandula nasalis externa, and totally unike that of Jacobson's organ in any other group. The evidence of the innervation is less clear. The gland itself is definitely supplied by fibers from the trigeminal nerve; however, it is impossible to show that no fibers from the olfactory nerve reach it. Even with the innervation questionable, the embryological argument appears sufficient to eliminate the duct as a possible Jacobson's organ.

Loew's theory seems almost as improbable as von Mihalkovics'. In the material used in the present study, the sulci anterior and medialis do not appear as early as was reported by him, and the thickened epithelium in which they form appears to be part of the single area which gives rise to all the sulci. Besides these embryological considerations, the innervation of the area does not bear out his assertions. The present work confirms the descriptions of Seydel (1896), Zuckerkandl (1910a), and McCotter (1917) rather than that of Loew in that all the sensory epithelium of the regio intermedialis receives fibers from the medial division of the olfactory nerve. Thus, this entire sensory area would appear to be a single unit rather than at least two distinct sensory regions as postulated by Loew.

That leaves only Seydel's theory. As mentioned in the preceding paragraph, his evidence from the pattern of innervation is confirmed by the present study. Even more important, the relationship to a distinct accessory olfactory bulb, first reported by McCotter (1917), is also confirmed. It is this neurological evidence that has convinced such workers as Matthes (1934) of the correctness of Seydel's identification. To deny its validity, it would appear necessary to deny the true homology of the accessory olfactory bulb of turtles with that of other forms, and to consider them independent developments, a step no one has advocated. Seydel's evidence from the absence of Bowman's glands remains unchallenged. In all tetrapods, except certain neotenous urodeles and possibly some aquatic snakes, such glands are present in the sensory olfactory epithelium; they are absent in Jacobson's organ, the regio intermedialis of turtles, and the various ventral sensory areas in modern Amphibia.

Next, what are the main arguments against Seydel's theory? The basic one is that the adult form and position of his Jacobson's organ in turtles are radically different from those in other forms possessing a typical Jacobson's organ — that is, snakes, lizards, and most mammals. However, neither form nor position can be considered necessarily accurate guides to homology. Furthermore, embryonically the epithelium of the regio intermedialis first becomes thickened on the medial wall, hence in the position where Jacobson's organ develops in other groups. Fuchs (1915) states that a connection with the mouth by a duct is characteristic of that organ. This is true of most forms, but in some mammals it retains its primitive connection with the nasal cavities, thus making an oral connection invalid as a criterion. Fuchs also cites independence of Jacobson's organ from its parent tissue: "diese Selbständigkeit ist morphologisch eigentlich ja im Begriffe 'Organ' gefordert. Denn was zu seinem Mutterboden in Unselbständigkeit beharrt, ist eben kein Organ für sich, sondern nur Teil eines Organes" (p. 169). This rather semantic argument seems stronger, but it attacks only the use of the name Jacobson's organ, not the acceptance of the homology as proposed by Seydel.

It seems, therefore, that the sensory epithelium of the regio intermedialis of turtles is indeed to be considered homologous with the Jacobson's organ of other amniotes, but in turtles it does not assume the definitive form. Hence the term is best not used in describing the nasal cavities of members of this order. Fuchs (1915) proposed the term pars vomeronasalis for the area of sensory epithelium which he believed to represent Jacobson's organ. This term could be useful if taken in a histological sense as opposed to pars olfactoria and pars respiratoria, the last two referring to normal olfactory epithelium and non-sensory epithelium, respectively, as is the case in mammalian anatomy. However, since in turtles the partes have generally been used in a topographical sense, as by Seydel, this usage would now be most confusing. The sensory areas of the regio intermedialis are in discontinuous patches of variable pattern so that any term would necessarily be rather vague with histological but no morphological significance. Such a term would, at best, have questionable value, and therefore none is proposed here.

The acceptance of the homology advocated in the preceding paragraph is of great phylogenetic importance. Two alternate hypotheses seem possible. First, it is possible that primitive tetrapods had considerable areas of sensory epithelium in the ventral half of their nasal cavities, and that the pattern of restricting this to a small area on the medial wall (which embryologically forms a distinct pocket, the definitive Jacobson's organ) did not arise until after the turtles were already established as a group. The other possibility is that turtles arose from forms having a typical Jacobson's organ, but during their evolution modified its development greatly to reach their present condition. Consideration of these alternatives is deferred to the general discussion on phylogeny.

ORDER RHYNCHOCEPHALIA

Adult Anatomy. No adult specimens of *Sphenodon* were available for the present study so the following review is based entirely on the literature. The earliest careful account of the nose of this genus is that of Osawa (1898). Later workers, including Broom (1906), Fuchs (1908), Hoppe (1934), and Malan (1946), studied very late embryonic material which shows essentially adult conditions. Finally, Pratt (1948) very briefly describes the nasal area in his paper on lizards. The most detailed paper is that by Hoppe, and the following description is based primarily on his work.

Figure 33 shows the lateral wall of the nasal cavity of an immature *Sphenodon* . The naris externus leads into a small vestibulum which is an essentially tubular chamber with its axis running lateromedially. Its medial end is somewhat expanded and separated from the cavum nasi proprium by a slight fold in the nasal wall. The ducts of the glandulae nasales externa and medialis both empty into the vestibulum on the posterior and ventral walls, respectively.

In describing the complex cavum nasi proprium, Hoppe uses in part new terms and in part the terminology of Beecker (1903) and Fuchs (1908). The area anteroventral to the conchae which lies between the vestibulum and the choana is termed the *Choanengang*. It is a relatively simple, non-sensory zone and extends dorsally ventrolateral to the concha anterior as the *dorsale Tasche des Choanengangs*. Most of the remainder of the cavum consists of the complex *Muschelzone* containing the conchae. Posterior to this is the small *Antorbitalraum*.

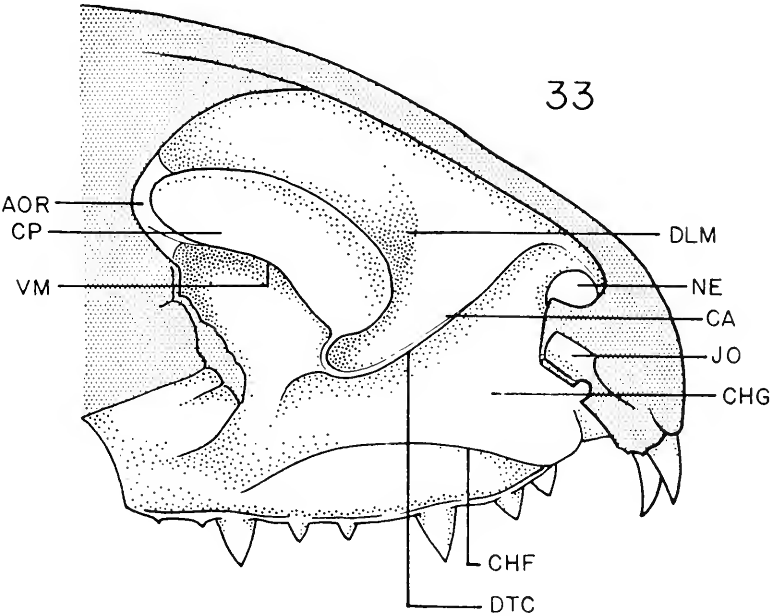


Figure 33. Medial view of the left nasal cavity of an immature *Sphenodon* to show the lateral wall (after Hoppe, 1934).

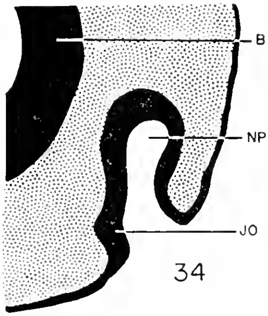
Hoppe distinguishes two conchae, the *concha anterior* and *concha posterior* (the *vordere* and *hintere Muscheln*). Both are simple lamellar projections of the lateral nasal wall containing cartilaginous processes from the nasal capsule. The anterior runs posteroventrally from the posterodorsal corner of the vestibulum, thus forming a diagonal ridge across the anterior half of the cavum nasi proprium. It projects medially and ventrally into the nasal cavity. The posterior end of the concha anterior turns dorsally and is continuous with the anterior end of the concha posterior. From there the latter structure extends posteriorly and somewhat dorsally nearly to the posterior end of the nasal cavity. Its free end is slightly inrolled so that in section the concha appears J-shaped.

The space dorsal and lateral to the concha posterior is termed the *dorso-lateraler Muschelraum* by Hoppe; it corresponds to the *Sakter* of Beecker (1903) and Fuchs (1908). Ventral to this concha there is another recess, the *ventraler Muschelraum* of Hoppe. This is considered a part of the Choangengang by Beecker and Fuchs.

There is no palatal fusion posterior to the premaxillae in *Sphenodon* and the choanae run almost the entire length of the cavum nasi proprium. They are widely open throughout their length. However, they appear to enter the mouth from the side rather than leading directly ventrally from the nasal cavity, due to the large *Vomerpolster* (Busch, 1898) which forms a horizontal plate at the ventral end of the nasal septum. The lateral margin of the choana is marked by a prominent ridge extending medially from the boundary between the nasal and oral cavities. This *Choanenfalte* is ventral to the Vomerpolster.

Jacobson's organ retains its primitive position, opening into the anterior end of the choana. In *Sphenodon* it is a tubular structure which lies along the ventromedial wall of the nose. According to Hoppe the anterior end of the organ turns laterally to enter the anteroventral end of the Choanengang on the lateral side in common with the lachrymal duct. The posterior end of Jacobson's organ is slightly dorsal to the anterior. Only the dorsal wall bears thickened epithelium, and it lacks the *mushroom body* (= *pilzenförmige Wulst* or *concha of Jacobson's organ*) found in the Squamata.

In general, most of the other descriptions of the nose in *Sphenodon* agree closely with that given above. However, there are two points which require further comment. The first of these concerns the conchae. Osawa (1898), Fuchs (1908), and Pratt (1948) all mention a single concha. This certainly corresponds to Hoppe's (1934) concha posterior; whether the concha anterior is considered part of this or is not considered to be a conchal formation is not clear from their papers. Malan (1946) calls attention to this difference, but does not express any opinions on the problem. DeBeer (1937) states that *Sphenodon* lacks a concha completely, but he apparently restricts the term to outpocketings of the capsule while *Sphenodon* has only lamellar projections from the surface of the capsule.



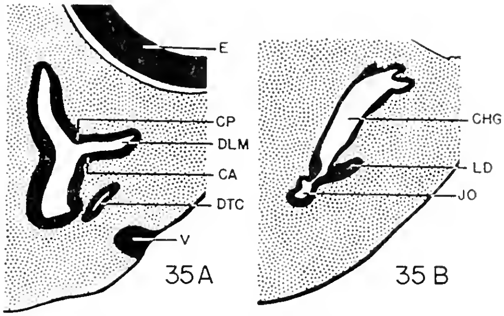


Figure 34. *Sphenodon* 1491 (7.9; MC). Transverse section through the nasal area (section 198). 46x.

Figure 35. *Sphenodon* 1507 (17.4; MC). Frontal sections through the nasal area. A, section 144; and B, 43 sections ventral to A. 16x.

The second debated point concerns the connection of Jacobson's organ with the nasal cavity. The description above is based on Hoppe (1934). Previous workers, Osawa (1898), Broom (1906), and Fuchs (1908), had stated that the very short duct of Jacobson's organ ran laterally from the center of the tubular organ to enter the medial wall of the anterior end of the choana. The opening of the lachrymal duct was reported to be just opposite or slightly posterior to it on the lateral wall. Hoppe claims that their opinions result from studying only transverse sections and that his models show the true situation. However, Malan (1946), Pratt (1948), and Bellairs and Boyd (1950) all corroborate the earlier workers.

Early Embryology. The early nasal embroyology of *Sphenodon* is poorly known, but appears to resemble that of other reptiles very closely. For the present study two series showing nasal pits were available. In both, the pits are moderately shallow, but already dorsally directed. The older of the two is shown in Figure 34. As in the other groups, the epithelium is thickest dorsally and medially, but no histological differentiation is visible, and the nasal and epidermal epithelia are not distinctly separate. At this stage the pit possesses a wide lumen throughout its extent and its dorsal end leans slightly laterally. The naris forms a long, widely-open slit which is on the lateral surface of the snout anteriorly, but becomes ventral posteriorly. There is a ventromedial band of thickened epithelium which is presumably the first stage in the development of Jacobson's organ; it is lacking in the younger series. At this stage there is still no real inpocketing for that organ.

Only three papers mention such early stages. Schauinsland (1903) shows the nose in his figures of the general external appearance of several *Sphenodon* embryos, but gives no descriptions. The nasal placode is shown as a roughly circular depression with the margins somewhat raised. This rim is first seen dorsally, but soon completely surrounds the nasal tissue. In slightly older embryos the placode has become a nasal pit, and the naris is elongated with the posteroventral end pointed and the anterodorsal round.

Hoppe (1934) considers one embryo which is slightly more advanced than the series described above. In his specimen the anlage of Jacobson's organ is more noticeably indented, but it is very small and the general appearance of the nasal pit is the same as in the younger embryo. The pit extends slightly anterior to the naris, thus forming a small *apikale Blindsack*. The pattern of epithelial thickening shows no changes, and the nasal epithelium is still not distinctly set off from the epidermis.

Finally, Fuchs (1908) studied early stages of *Sphenodon*, but states only that they closely resemble lizard embryos.

Later Embryology. The most detailed study of the later stages in the development of the nose of *Sphenodon* is that of Hoppe (1934) who constructed wax models of three embryos. Other papers, such as Broom (1906) and Malan (1946), figure only single very late stages and have already been considered. Fuchs (1908) deals with the embryology of the palate, but does not treat the general nasal development in any detail. The following description is based on Hoppe and a study of the two older *Sphenodon* embryos available for the present work.

Hoppe's stage 2 embryo already has both conchae well formed. In this and in a slightly older series studied in the present investigation (see Figs. 35 and 80), they are parallel ridges in the lateral wall of the cavum nasi proprium which run dorsally and somewhat posteriorly from the anteroventral corner of the cavum. As in the adult, the ventral ends of the two conchae are joined so that they form a narrow U with the slit-like dorso-lateraler Muschelraum between them. The ventraler Muschelraum and Antorbitalraum are only weakly developed, but the dorsale Tasche des Choanengangs is present. Hoppe shows the choana opening beneath only the anterior half of the nasal cavity; in the series which I studied it extends nearly the entire length of the cavum. A more important point of disagreement concerns the connection between Jacobson's organ and the nose. In all of his models Hoppe shows the anterior end of that organ passing laterally to enter the anterolateral corner of the Choanengang in company with the lachrymal duct. This is not the case in the series shown in Figure 35B. There the center of Jacobson's organ opens into the anteromedial corner of the nasal cavity and the lachrymal duct into the anterolateral with the latter slightly the more posterior.

In his two later embryos Hoppe shows a gradual development towards the adult condition. The concha anterior becomes vertical and then continues to rotate so that its ventral end is posteroventral to the dorsal. This rotation, coupled with a proportional lowering of the posterodorsal end of the concha posterior, results in a great enlargement of the dorso-lateraler Muschelraum which becomes a wide cavity rather than a narrow slit. The ventraler Muschelraum, Antorbitalraum, and dorsale Tasche des Choanengangs also show increases in size relative to the nasal cavity as a whole, and the choana is now figured as stretching more nearly the length of the cavum nasi proprium. The conchae increase in length, but do not thicken in proportion to the general growth of the area, so that they appear lamellar as in the adult, while in the younger embryos they are wide ridges in the nasal wall.

An older series, which is shown in Figure 36, resembles closely Hoppe's stage 4 embryo. The vestibulum runs medially and slightly posteroventrally from the naris externus to enter the cavum nasi proprium. As in other forms, the external end of the vestibulum is a solid cylinder of epithelial cells at this stage. The cavum nasi proprium is very similar to that of the adult *Sphenodon* although the ventraler Muschelraum is not yet fully developed. As is shown in the figures, the anterior end of the concha posterior is projected anteriorly from its line of attach-

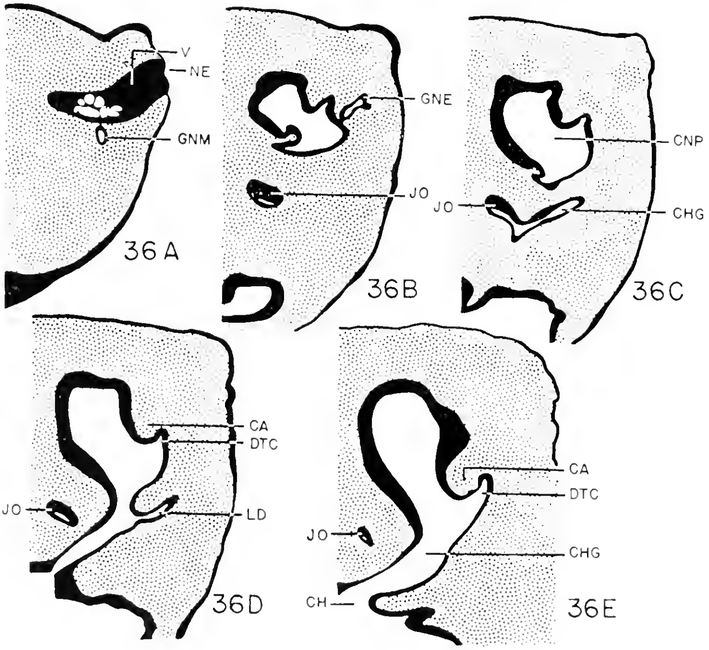


Figure 36. (First half). *Sphenodon* 1490 (25.2; MC). Transverse sections through the nasal area. A, section 43; B, 13 sections posterior to A; C, 7 posterior to B; D, 6 posterior to C; and E, 11 posterior to D. 16x.

ment, so that in transverse section it appears to lie free in the nasal cavity. The choana is ventral to the central part of the cavum nasi proprium and approximately two-thirds its length. Both Choanenfalten and Vomerpolster are well developed and resemble the adult structures.

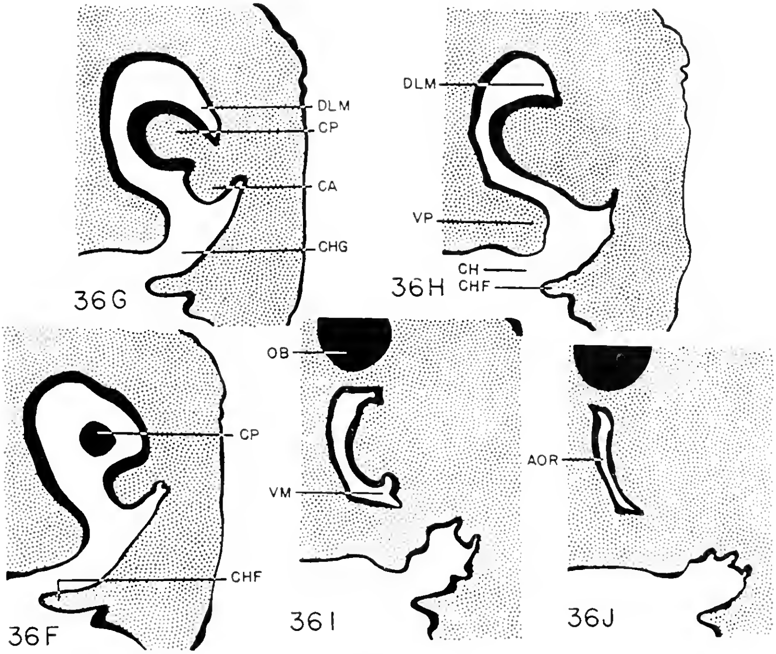


Figure 36. (Second half). *Sphenodon* 1490 (25.2; MC). Transverse sections through the nasal area. F, 7 sections posterior to E; G, 8 posterior to F; H, 7 posterior to G; I, 11 posterior to H; and J, 10 posterior to I. 16x.

Jacobson's organ also appears essentially adult in this series. It apparently enters the nasal cavity medially and quite separately from the lachrymal duct (see Figs. 36C and D). The structure of this region thus appears exactly as described and figured by Broom (1906), Fuchs (1908), and Bellairs and Boyd (1950). Despite careful study of both available series, I am unable to see any evidence for Hoppe's statements on the juncture of the lachrymal duct with a duct from the anterior end of Jacobson's organ. This cannot be caused by the use of only transverse sections; one of the series studied is cut in the frontal plane.

The questions on the nature and homologies of the two conchae are more difficult to answer. Certainly there seem to be two distinct lamellae, as described by Hoppe. Although they are, in all stages which have been studied, joined ventrally, their position in the embryos (see Fig. 80) makes it appear extremely unlikely that *Sphenodon* possesses a single concha comparable to that of the Squamata. In its general position and structure the concha posterior resembles the saurian concha very closely and their homology seems probable. However, the concha anterior of *Sphenodon* is less easily explained; this problem is discussed in a subsequent section.

ORDER SQUAMATA

General. The Squamata include a majority of the living reptiles and display a far greater range of morphological diversity than any of the other orders. It is also the order which has been most studied with respect to nasal anatomy and embryology. However, the preponderance of the earlier work treats the suborder Lacertilia; the Ophidia are less well known. Therefore, since snakes will serve as well as lizards as examples of the Squamata for comparison with members of the other orders, only the Ophidia are described in the following account.

The major works on the nasal anatomy of lizards may be briefly noted. Leydig's (1872a) great monograph of the German species forms the starting point for all the more recent studies of the anatomy and histology of the nasal region. The classic works on the nasal embryology of the Lacertilia are those of Born (1879) and Peter (1900). Two other early papers, Beecker (1903) and Fuchs (1908), made major contributions to our knowledge of both the adult form and the development of the nasal area, and established the terminology now generally used for all members of this order.

There are many recent works treating the nasal cavities and Jacobson's organs of lizards. Especially noteworthy are the many papers on cranial anatomy published by the South African school of anatomists, de Villiers, du Toit, and their students. The following list includes only major works which consider a variety of forms and which, in most cases, have extensive bibliographies: Matthes (1934), Malan (1946), Pratt (1948), Stebbins (1948), and Bellairs and Boyd (1950). For detailed descriptions and many further references, the reader is referred to these papers.

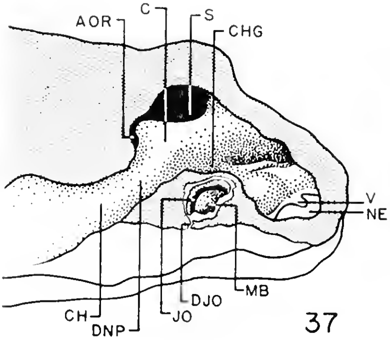
Adult Anatomy. The gross form of the nasal cavities is relatively simple in adult snakes. Anteriorly, there is typically a very small tubular vestibulum, running medially from the naris externus to the anterior end of the cavum nasi proprium. The posterior end of the cavum is connected to the oral cavity by the rather short and wide ductus nasopharyngeus. Certain authors, most notably Fuchs (1908), would prefer to restrict the term ductus nasopharyngeus to the crocodilian or mammalian condition, in which a well formed secondary palate is present; however, as in the case of turtles, the term is here retained and used in a topographic sense. Since this problem is discussed in the section on turtles, the arguments need not be reviewed again.

The cavum nasi propium is a large chamber, with its greatest height and width generally near the posterior end. It is thus somewhat ovate in either frontal or sagittal section. The concha is a prominent ridge along the posterior two-thirds of the ventrolateral wall of the cavum. Beecker (1903) proposed a series of terms for the various parts of the cavum. These were adopted by Fuchs (1908), and are now in fairly standard usage. Therefore, they are employed in the present work, except in one case where Beecker's term appears to be rather confusing. It must be emphasized at the start that these subdivisions of the cavum do not have any definite boundaries, but, despite their vagueness, they are most useful descriptively.

First, the cavum nasi proprium is divided into three main zones. The largest of these is the conchal zone; all of the cavum anterior to the concha is here termed the anterior caval zone, and the smaller part posterior to it is the Antorbitalraum. Secondly, the conchal zone is subdivided into three parts. The portion of the cavum lateral and dorsolateral to the concha is the *Sakter*. This is continuous with the dorsomedial *Stammteil,* while the ventromedial third of the cavum is termed the Choanengang.

The relationship of these three parts of the conchal zone is best seen in transverse sections such as are shown in Figure 58. Beecker and Fuchs term the anteriormost of the three main divisions of the cavum the *Nasenvorhof;* however, since other workers, such as Kathariner (1900), have used it to designate the vestibulum, the term is not employed in the present work. The only other difference in usage is that the ductus nasopharyngeus of the present paper is considered to be a part of the Choanengang by Beecker and Fuchs.

In the descriptions of Jacobson's organ, the anteroventral projection into its lumen is here termed the mushroom body. This structure is generally known by that term or a variant such as pilzenförmige Wulst or fungiform eminence, but is sometimes referred to as the concha of Jacobson's organ.



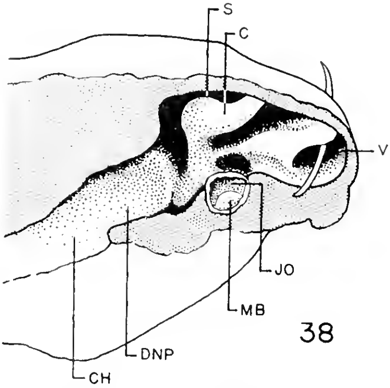


Figure 37. Medial view of the left nasal cavity of *Drymarchon* to show the lateral wall.

Figure 38. Medial view of the left nasal cavity of *Crotalus* to show the lateral wall. The bristle passes through the naris externus.

Three genera were studied in the present investigation. Dissections were made of the heads of *Drymarchon corais* and *Crotalus adamanteus*, and slides of an adult *Storeria dekayi* were also examined. Unfortunately, the last is an incomplete series and many of the sections are not in ideal condition, so that the bulk of the description is based on the first two forms.

Figure 37 shows the lateral wall of the nasal cavity of *Drymarchon.* The naris externus is a large, nearly circular opening very near the tip of the snout. From it, the very short vestibulum runs medially and slightly anteriorly to enter the anterior end of the cavum nasi proprium. On the anteromedial wall there is no macroscopically visible boundary between these two regions, but there is a marked, though rather moderate swelling along the lateral part of the anterior margin of the cavum. The duct of the glandula nasalis externa opens well dorsally on the posterior wall of the vestibulum, approximately halfway from the naris to the cavum.

The shape of the cavum nasi proprium is well shown in the figure. Its anterior half is a simple, nearly circular tube, with its dorsoventral diameter slightly greater than the lateromedial. Posteriorly, the cavum enlarges quite markedly. The concha is a prominent ridge attached along its anterior and ventrolateral edges. The dorsal margin turns slightly laterally, especially posteriorly. The Sakter is a quite large space, but does not extend anterior to the anterior line of attachment of the concha. Thus in transverse section the conchal zone is shaped rather like a question mark, and its three parts, the Sakter, Stammteil, and Choanengang, form a continuous cavity without any visible boundaries between them. The Antorbitalraum is very small.

Posteroventrally the Choanengang is continuous with the rather short but very wide ductus nasopharyngeus. The latter is a circular tube which enters the oral cavity at the anterior end of the large median palatal trough. Although they are not joined together further anteriorly, the ducti of opposite sides thus have a common opening into the mouth. Along the walls of the ductus there are many very small, but macroscopically visible grooves, probably of a glandular nature. These grooves continue posteriorly into the midpalatal trough, and also, though less obviously, anteriorly into the Choanengang. In all regions they run parallel to the long axis of the nasal cavity.

Jacobson's organ is, as in all snakes, well developed as a roughly spherical structure. In *Drymarchon* it lies ventromedial to the Choanengang. The mushroom body forms a large hemispherical projection from the anterior and anteroventral third of the wall of Jacobson's organ, thus restricting the lumen of that organ to a rather narrow, bowl-shaped space (see Fig. 37). From the anteroventral part of Jacobson's organ, the extremely narrow duct runs ventrally to enter the mouth well anterior to the choana.

The other snake which was dissected, *Crotalus*, is shown in Figure 38. Although the naris externus closely resembles that of *Drymarchon*, the vestibulum is considerably longer and better developed, and runs anteroventrally as much as medially. The latter is, however, still a very simple tube. No trace of the duct of the glandula nasalis externa could be found. As in the case of *Drymarchon*, the vestibulum and the cavum nasi proprium are not macroscopically distinguishable anteriorly. Posterolaterally, however, their boundary is sharply marked by a very large ridge in the anterolateral wall of the cavum.

This ridge, which is well shown in Figure 38, represents the greatest difference in nasal anatomy between *Drymarchon* and *Crotalus*. It runs more than half the length of the cavum nasi proprium, from the anterodorsal corner of the lateral wall to the ventral caval wall and the posteroventral part of the conchal attachment. There is a rather shallow groove in the lateral wall of the cavum ventral to this ridge and a somewhat deeper one dorsal to it; thus in transverse section the anterior portion of the cavum is more C-shaped than circular. In its gross form the ridge is somewhat reminiscent of the concha anterior of *Sphenodon:* however, its embryology is completely unknown, so that it is impossible to determine whether the two structures are actually the same. The ridge found in *Crotalus* appears to be a great elaboration of the small postvestibular swelling mentioned in *Drymarchon*. In the absence of any sectioned material of *Crotalus*, it is not possible to tell if any special structure is contained within the ridge, although it can be seen that the facial pit is well posteroventral to the area in question.

Posteriorly and dorsally the cavum nasi proprium of *Crotalus* is very similar to that of *Drymarchon*. The concha of *Crotalus* is slightly shorter and more dorsally situated, but is essentially the same shape. Its posterodorsal margin is laterally directed. The Antorbitalraum is considerably larger than in *Drymarchon*, but it remains simple and, as far as can be seen from gross dissection, unmodified in any way.

The ductus nasopharyngeus and choana of the two genera are also very similar, as is shown by a comparison of Figures 37 and 38. The only difference worth noting is the occurrence of a small ridge, separating the ductus from the cavum nasi proprium, which is found in *Crotalus* but not *Drymarchon*. No grooves could be seen in the walls of the ductus in the former genus, but the preservation of the specimen is not good enough to permit a denial of their presence there.

The only noticeable difference between the Jacobson's organs of *Drymarchon* and *Crotalus* is the smaller mushroom body and correspondingly larger lumen of the latter. However, the duct could not be dissected out in the rattlesnake studied, so its structure and exact location are not known.

Unfortunately, the slides of *Storeria* show little of the gross anatomy of the nasal cavity. The cavum nasi proprium appears to be approximately the same shape as in *Drymarchon*, with a well developed concha containing part of the glandula nasalis externa. Anteriorly, the sections are almost all broken, so that nothing can be determined concerning the form of the vestibulum. The ductus nasopharyngeus is proportionately longer than in *Drymarchon*, but not otherwise different. Jacobson's organ is large, and appears exactly like that of *Drymarchon*. The dorsal end of its duct leaves the posteroventral corner of that organ; the ventral end including its connection with the lachrymal duct is missing on the available slides.

There is a moderately sizable body of literature on the nasal anatomy of adult snakes, but the structure in many major groups is totally unknown; even in the commoner and larger families, very few forms have been studied. The only embryological paper which contributes anything to a comparative study of the nasal cavities of snakes is that by Pringle (1954); it is discussed in the subsequent section on the later nasal embryology. Major review papers considering this group include Hoffmann (1879-1890), and Matthes (1934). Zuckerkandl (1910b) reviews the earlier literature on Jacobson's organ.

The following genera have been described or figured: *Typhlops* (Zuckerkandl, 1910a), *Xenopeltis* (Bellairs, 1949), *Python* (Solger, 1876; and Dieulafé, 1904-1905), *Constrictor* (Gegenbaur, 1873), *Natrix* (Leydig, 1872b; Solger, 1876; von Mihalkovics, 1898; Kathariner, 1899 and 1900; Broman, 1920; and von Navratil, 1926), *Thamnophis* (Macallum, 1884), *Elaphe* (Nemours, 1930), *Acrochordus, Cerberus, Hydrophis, Pelamis, Laticauda* (the last five all by Kathariner, 1899 and 1900), *Vipera* (Solger, 1876; and Bellairs, 1942), and *Crotalus* (Solger, 1876). Finally Bellairs and Boyd (1950) investigated the relationship between the lachrymal duct and Jacobson's organ in a large series of forms including representatives of a majority of the families.

Almost all these descriptions appear essentially similar, and no detailed review is necessary. There is some variation in the attachment of the concha with the wall of the nasal cavity; in *Python* it is attached dorsally for the anterior two-thirds of its length, and hence the Sakter forms a large blind pocket, while in *Drymarchon* the concha is connected to the nasal wall only ventrolaterally. More conspicuous variations are found in the aquatic snakes studied by Kathariner (1900). In such forms the concha is reduced or absent, the sensory area restricted, and the vestibulum modified so as to prevent the entrance of water when the animal is submerged. Jacobson's organ is well developed in all snakes thus far studied. Otherwise, there are no basic differences reported within this suborder.

Early Embryology. The early stages in the nasal embryology of snakes have been little studied. Five papers mention the subject, all of them dealing with *Natrix natrix* and all written before 1890. The first is Rathke's (1839) classic monograph in which the nasal placodes and pits are described and the origin of Jacobson's organ (Nasendrüse of Rathke) is noted. In 1878 both Parker and Fleischer published papers which add little to Rathke's account. Born (1883) is concerned primarily with the development of the lachrymal duct and thus does not treat early stages in great detail. Finally Beard (1889) observed the embryology of the nose in connection with his studies on the olfactory nerve and Jacobson's organ. Specific points from these papers will be noted in the descriptions given below; therefore, no detailed review of the earlier literature is necessary.

The following account is based primarily on the study of a large series of *Thamnophis* embryos. At least two species, *T. radix* and *T. sirtalis,* are represented, but there does not appear to be any difference between them, and therefore they are here treated as one. Three embryos of *Oxybelis* were also available and serve to fill in one gap left in the *Thamnophis* series.

The first sign of nasal differentiation is the formation of the nasal placode which is, in its earliest stages, nothing more than a thickened area of epithelium without any indentation. It is roughly circular and located on the ventrolateral surface of the snout as shown in Figures 39 and 40. The greatest thickening, up to ten times that of the unmodified epidermis, occurs some-

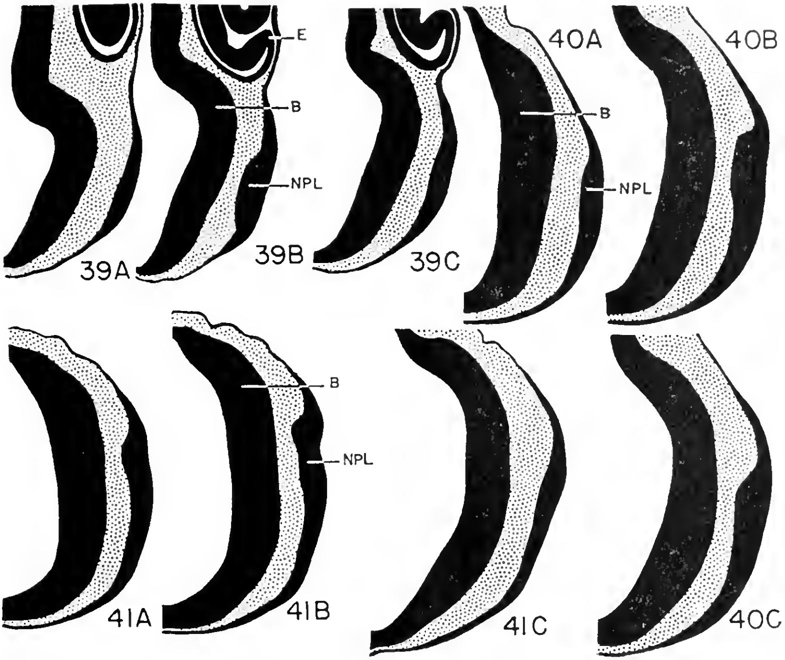


Figure 39. *Thamnophis* 1559 (3.7; MC). Frontal sections through the nasal area. A, section 52; B, 6 sections ventral to A; and C, 5 ventral to B. 42x.

Figure 40. *Thamnophis* 1592 (3.3; MC). Transverse sections through the nasal area. A, section 123; B, 7 sections posterior to A; and C, 5 posterior to B. 42x.

Figure 41. *Thamnophis* 1589 (3.5; MC). Transverse sections through the nasal area. A, section 94; B, 3 sections posterior to A; and C, 5 posterior to B. 42x.

what dorsal to the center of the placode so that the transition is most abrupt dorsally and most gradual ventrally, but there is nowhere a visibly distinct boundary between the nasal epithelium and the surrounding epidermis. The transition tends to be slightly more abrupt posteriorly than anteriorly. In some of the older embryos of this stage the placode exhibits a marked central thickening with an only slightly thickened ring surrounding it (see Fig. 39); in other embryos there is no such differentiation within the placode. Although there may be a small anlage of the olfactory nerve present, the placode is, at this stage, generally well separated from the brain by an intervening layer of mesenchyme.

The epithelium of the nasal placode is high columnar centrally, becoming low columnar near the periphery where it merges with the simple cuboidal epidermal epithelium. It is probably simple throughout; however, the available slides do not show cell boundaries so that it is impossible to be certain about this point. The nuclei are generally concentrated in the basal half of the epithelium, but mitotic figures appear to be most numerous near the lateral or external surface. In many of the embryos there is a very distinct basement membrane separating the nasal epithelium from the underlying mesenchyme. In some series, probably slightly more advanced, this disappears beneath the center of the placode, but is still present toward the edges. When it is present, the basement membrane is, for the most part, not smooth, but shows gentle undulations.

The first major change in the structure of the placode is the development of a small indentation in the area of greatest thickness (see Figs. 41 and 42). The placode still extends over a large part of the ventrolateral surface of the snout, but the inpocketing is almost directly lateral. Another change which occurs at approximately the same time concerns the establishment of a distinct cellular anlage of the olfactory nerve; the structure and further development of this are discussed in a subsequent section. As in the preceding stage, the nasal placode is continuous with, and indistinctly set off from, the epidermis. The transition in thickness remains most abrupt dorsally and most gradual ventrally.

Histologically, there are no essential differences between the unindented and indented nasal placodes. Throughout its early development the nasal epithelium slowly becomes thicker, but the general picture of high columnar epithelium with somewhat basally located nuclei does not change. The basal position of the nuclei is most marked in the area of indentation, but, as in the previous stage, mitotic figures are concentrated along the external surface of the placode.

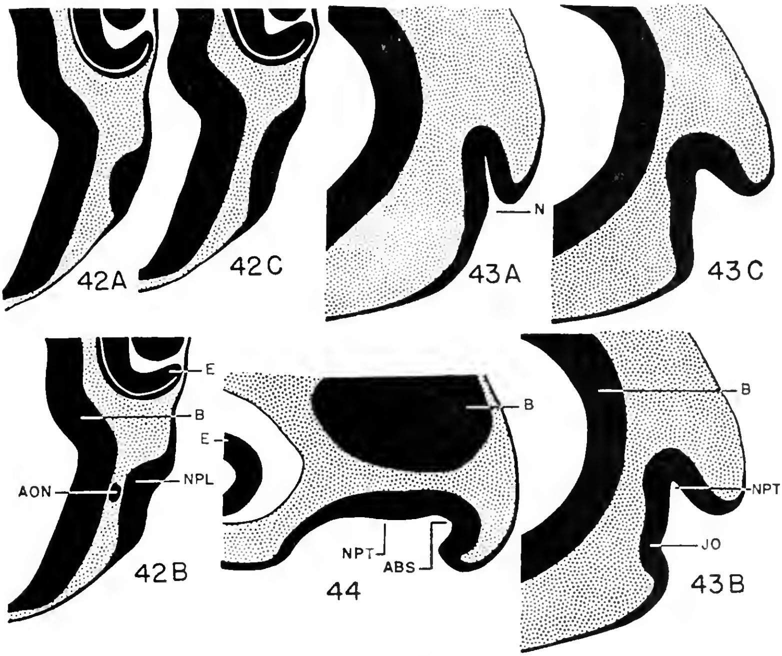


Figure 42. *Thamnophis* 1643 (3.4; MC). Frontal sections through the nasal area. A, section 71; B, 3 sections ventral to A; and C, 4 ventral to B. 42x.

Figure 43. *Oxybelis* 1528 (6.9; MC). Transverse sections through the nasal area. A, section 166; B, 8 sections posterior to A; and C, 5 posterior to B. 39x.

Figure 44. *Thamnophis* A2 (16.0; EEW). Sagittal section through the nasal area (section 26). 39x.

The invagination of the placode continues so that a nasal pit is formed. Early stages showing such a pit are poorly represented in the available *Thamnophis* material, but the three *Oxybelis* embryos make detailed description possible (there appear to be no important differences between these two genera in the younger stages; thus the *Oxybelis* material may be inserted into the series of *Thamnophis* embryos without breaking the continuity of the description). As is shown in Figure 43, the pit is, at this stage, relatively shallow and possesses a wide lumen ventrally. It extends dorsomedially from the dorsal part of the original placode. The inpocketing occurs along the horizontal length of the nasal epithelium so that the naris is formed as a slit whose anterior end is slightly dorsal to its posterior. At this stage the naris extends the full length of the nasal pit although the anterior wall of the nose is very nearly vertical. The epithelium of the pit is thickest dorsally and medially, but the regional differences are very slight and the histological appearance is exactly as in the preceding stage.

The most important development during the early nasal pit stage is the appearance of Jacobson's organ. Parker (1878), Born (1883), and Beard (1889) all report the presence of a small depression representing this organ while the nose is still in the placode stage, but none could be seen in any of the embryos used in the present study. Rathke (1839) also seems not to have found Jacobson's organ until after the start of nasal invagination, although his description is not perfectly clear on this point. In the youngest *Oxybelis* embryo, Jacobson's organ is a very slight ventromedian groove in the wall of the nasal pit (see Fig. 43B). It is somewhat posterior to the center of the naris. This groove gradually lengthens and becomes very large, reaching a size equal to that of the main nasal pit. With further growth of the nose, Jacobson's organ comes to lie medial to the center of the naris. Histologically, it does not differ in any way from the main portion of the nasal pit.

The next stage in the development of the nasal pit of *Thamnophis* is shown in Figures 44, 45, and 46. The pit has become moderately deep, with its long axis essentially vertical when seen in transverse section. As in the previous stage, the naris is a long slit with the posterior end ventral to the anterior.

The lumen is widest anteriorly and ventrally, but it is generally far less extensive than in younger embryos. Anteriorly a small portion of the pit extends anterior to the naris, thus forming a rather indistinct recess, the apikale Blindsack of Peter (1901). Posteriorly, the naris continues slightly posterior to the nasal pit as a shallow groove in the palate. The posterior part of the nose is slightly lateral to the anterior, but there is as yet no indication of a concha laterally. Jacobson's organ is, at this stage, relatively huge, having a size equal to that of the entire remainder of the nasal organ. It is a roughly spherical mass on the ventromedial wall of the nasal pit. The large lumen of this organ is widely open into the nasal pit medial to the center of the naris.

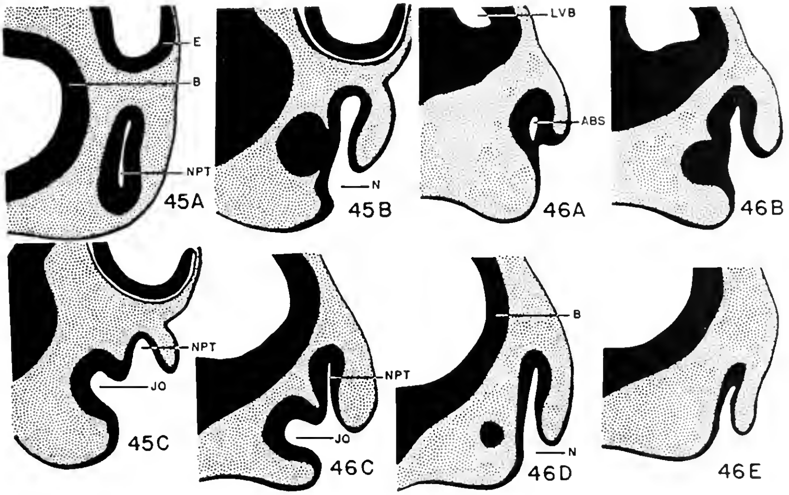


Figure 45. *Thamnophis* K (19.0; EEW). Frontal sections through the nasal area. A, section 52; B, 8 sections ventral to A; and C, 5 ventral to B. 38x.

Figure 46. *Thamnophis* 1348 (5.8; MC). Transverse sections through the nasal area. A, section 154; B, 4 sections posterior to A; C, 6 posterior to B; D, 9 posterior to C; and E, 6 posterior to D. 38x.

Histologically, the nasal epithelium shows rather few changes. It is still mainly high columnar and merges gradually with the epidermal covering of the snout. In the available material it is impossible to tell whether any of the epithelium is stratified or whether it is all simple. Considerable differential thickening has now occurred. The thickest epithelium is that of Jacobson's organ, while in the nasal pit the epithelium is thicker anteriorly, especially dorsomedially, than posteriorly. Throughout the markedly thickened areas the nuclei are still concentrated basally and mitotic figures are commonest toward the lumen; however in the thinner zones both are evenly distributed throughout the epithelium.

The final stage before the fusion of the lateral and medial nasal processes resembles closely that described above. Considerable growth has occurred and the extension of the lateral nasal process causes the naris to lie along the edge of the ventral surface of the snout rather than on its lateral face (see Figs. 47 and 48). The lumen is generally quite restricted, but expands ventrally near the naris and anteriorly where the apikale Blindsack is very strongly developed. The most striking change in the form of the nasal pit is the appearance of the concha as a projection of the lateral wall. This is most clearly seen in Figure 48D. Unfortunately, there is some distortion in the series figured; however, the drawings show the general form of the nose at this stage. With the formation of the concha, that portion of the nasal pit dorsal and lateral to it becomes recognizable as the Sakter. There appear to be no histological changes in the nasal epithelium at this stage.

Jacobson's organ continues to enlarge. It is still an essentially spherical organ opening into the ventromedian part of the nasal cavity, now slightly anterior to the center of the naris. The connection between its lumen and that of the main nasal pit has become slightly constricted, but is still very wide. All of the epithelium of Jacobson's organ is markedly thickened, but ventrolaterally it is somewhat thinner than elsewhere. In most of the series of this stage, the nasal pit has increased in size more rapidly than has Jacobson's organ so that it is considerably larger than the latter (see Fig. 47); however in one specimen (see Fig. 48), this is not the case, and Jacobson's organ is still fully as large as the nasal pit.

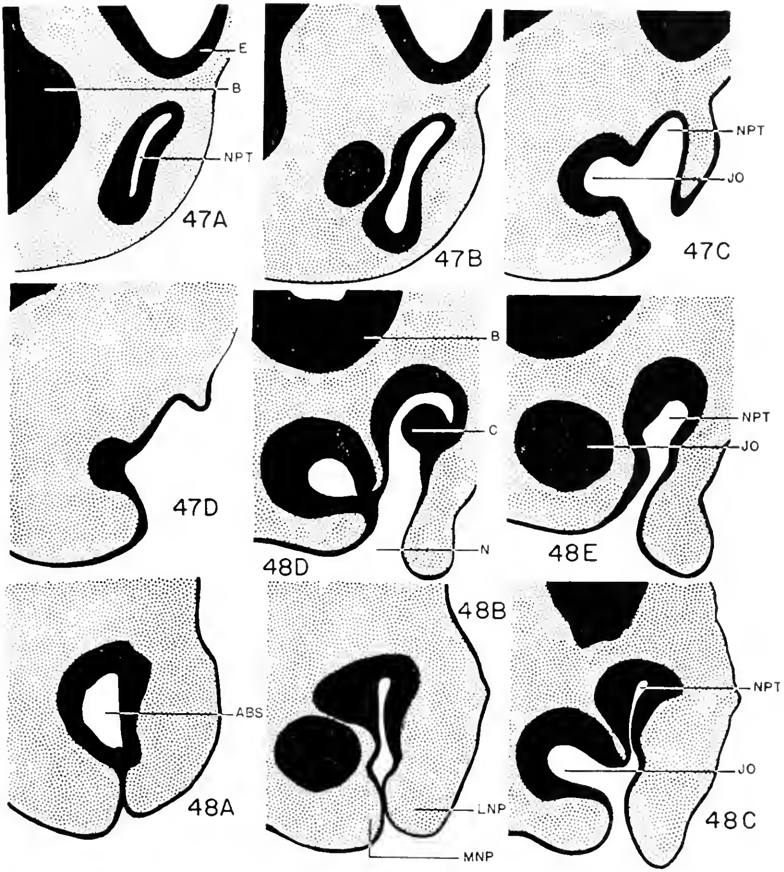


Figure 47. *Thamnophis* 1361 (6.0; MC). Frontal sections through the nasal area. A, section 99; B, 7 sections ventral to A; C, 7 ventral to B; and D, 5 ventral to C. 43x.

Figure 48. *Thamnophis* G (33.0; EEW). Transverse sections through the nasal area. A, section 162; B, 4 sections posterior to A; C, 4 posterior to B; D, 6 posterior to C; and E, 2 posterior to D. 43x.

None of the available embryos show the stages immediately preceding the actual fusion of the lateral and medial nasal processes. However, some of those to be described in the following section on the later embryology are very close to that stage, and therefore the process is best discussed when they are considered.

Later Embryology. The following account is based on the study of a large number of *Thamnophis* embryos. As in the case of the earlier stages, these are of two species, *T. radix* and *T. sirtalis.* However, since there appear to be no differences between the two, only one description is necessary. Unfortunately, material of other genera was not available.

As far as could be told from the available material, the fusion of the lateral and medial nasal processes follows a slightly different pattern in snakes from that described for turtles. Unfortunately, certain critical stages were not represented, but observations on lizards (mainly *Aristelliger*) and the accounts in the literature, to be discussed subsequently, appear to substantiate the impression gained from the *Thamnophis* embryos. In snakes the processes meet throughout almost all of the length of the anterior third of the nasal pit, leaving an open slit-like choana beneath the posterior two-thirds. There is, however, a very small naris externus, the lumen of which is almost immediately obliterated. The processes very quickly fuse and the apposed epithelial layers disappear throughout most of their extent, but anteriorly no such fusion occurs. There the cells clearly retain their epithelial character, and form a solid tubular vestibulum. In turtles the nasal processes fuse and, at a slightly later stage, the naris externus is closed as the vestibulum becomes a solid tube; in snakes the two events occur almost simultaneously.

With the fusion of the lateral and medial nasal processes, the nose takes on the form shown in Figure 49. The vestibulum is a short, nearly tubular structure, although its diameter is slightly greater dorsomedially than ventrolaterally and it is slightly flattened dorsoventrally. The naris externus is ventrolaterally placed very near the anterior end of the snout, and the vestibulum runs dorsomedially from it to the anterior end of the cavum nasi proprium.

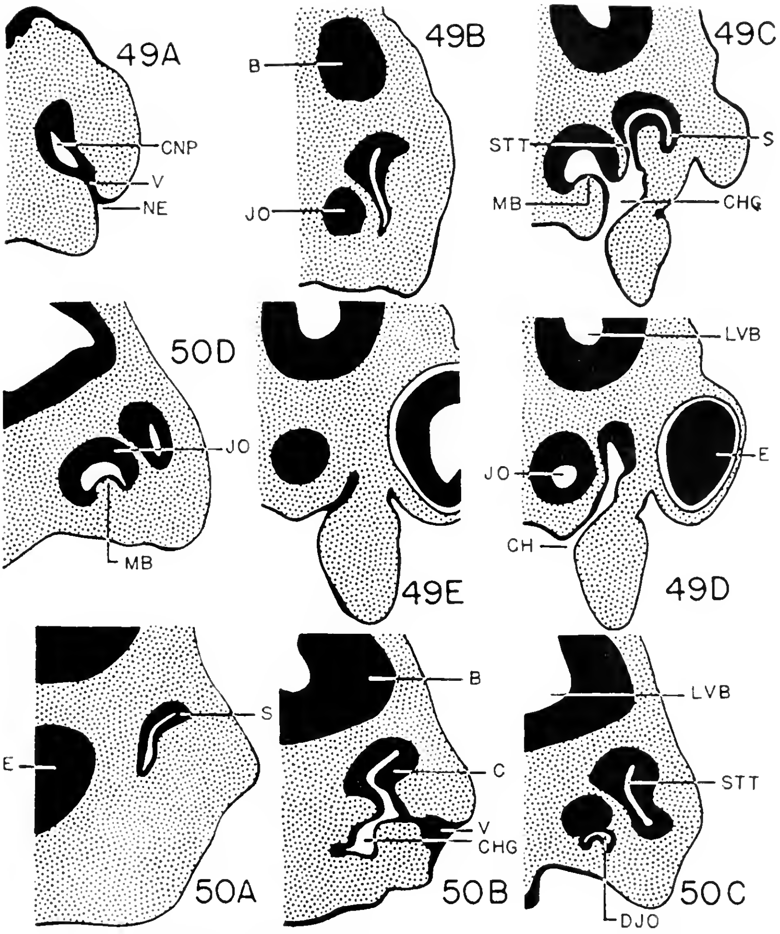


Figure 49. *Thamnophis* 1350 (7.4; MC). Transverse sections through the nasal area. A, section 174; B, 11 sections posterior to A; C, 10 posterior to B; D, 6 posterior to C; and E, 4 posterior to D. 28x.

Figure 50. *Thamnophis* 1372 (headlength, 4.4; MC). Sagittal sections through the nasal area. A, section 116; B, 11 sections medial to A; C, 4 medial to B; and D, 7 medial to C. 28x.

The latter chamber has already attained a considerable degree of complexity. Anteriorly, it is an oval tube which is nearly vertical except at the extreme anterior end where the dorsal portion leans somewhat medially. At the level of the anterior end of Jacobson's organ, the dorsal end begins to curl laterally and then ventrally around the concha. At the same level the ventral margin of the cavum extends ventrally and ventromedially to enter the oral cavity at the choana (see Fig. 49C). In this region the cavity can be roughly divided into the three zones, described by Beecker (1903) and Fuchs (1908); that section lateral and dorsolateral to the concha is the Sakter, the dorsomedial third is the Stammteil, and the ventromedial segment leading to the choana is the Choanengang. As in the later stages, there are no definite boundaries between these three regions. The concha is a large inpocketing of the wall of the cavum which is attached anteriorly and ventrolaterally. Posteriorly, it may project freely a short way into the lumen, but this is variable. Although the concha does not reach the posterior end of the cavum, the Antorbitalraum is very small and not in any way a distinctly separate region. The choana extends to the posterior end of the cavum, and even slightly posterior to it as a groove along the surface of the palate, but there is still no ductus nasopharyngeus. Posteriorly, the Choanengang becomes more ventromedially directed as the dorsal part of the cavum nasi proprium comes to lie farther from the midline. Thus, in frontal section, the nasal cavities of opposite sides show a marked posterior divergence dorsally and anteriorly, but are almost parallel posteroventrally.

The lumen of the cavum is generally very narrow. There are however three areas where it expands slightly. The first of these is the anteriormost part, anterior to Jacobson's organ and the concha. Even here the lumen is narrower than it would appear in transverse sections, as its long axis is transverse. Another expansion occurs in the anterodorsal part of the Choanengang lateral to the connection between Jacobson's organ and the nasal cavity. The third and last is at the posterior end of the concha, that is, in the Antorbitalraum. Despite the general restriction of the lumen, the choana is open throughout its length.

During this stage there are important changes in the form of Jacobson's organ. When the nasal processes first fuse, it is still a large spherical organ opening into the medial wall of the nasal cavity at the level of the anterior end of the choana. Very soon thereafter, however, the anteroventral wall of the sphere pushes into the large central lumen, thus forming the mushroom body (see Fig. 49C). With this development the lumen of Jacobson's organ is considerably reduced, although it is still quite sizable, and the connection with the main nasal cavity, although open, becomes greatly narrowed. Jacobson's organ still extends as far posterior as does the cavum nasi proprium.

Histologically, the picture appears to remain essentially similar to that in the earlier stages. The vestibulum possesses one or two layers of moderately low columnar cells basally and is filled with a mass of irregular, probably roughy isodiametric cells, the Füllgewebe of Weber (1950). The remainder of the nasal cavity is lined by two epithelial types which are not distinctly separable, but gradually merge along their boundaries. First, there is a conspicuously thickened and presumably potentially sensory epithelium. This occurs anteriorly and dorsally in the cavum nasi proprium and throughout in Jacobson's organ except on the surface of the mushroom body. It possesses a clear peripheral zone containing many mitotic figures and a thicker basal zone with many rows of circular nuclei. The thinner posteroventral area of the cavum and the mushroom body are covered by simple or bilaminar low columnar epithelium. The distribution of simple versus stratified epithelium is difficult to determine in the available material, but does not appear to follow any definite pattern. At the choana this non-sensory epithelium merges with the simple cuboidal epidermal epithelium without any visible break. The details of the pattern of thickening are clear in Figure 49 and require no description.

Slightly older embryos show very few changes; two such series are shown in Figures 50 and 51. The naris externus is still very well ventral, and the vestibulum therefore runs dorsomedially to its juncture with the cavum nasi proprium. However, its dorsoventral diameter is somewhat increased, especially superficially, so that the vestibulum is now slightly flattened in the transverse plane.

The basic shape of the cavum nasi proprium is unchanged, but some minor differences are noticeable. Anteriorly, it has extremely thick epithelium covering the small transverse segment

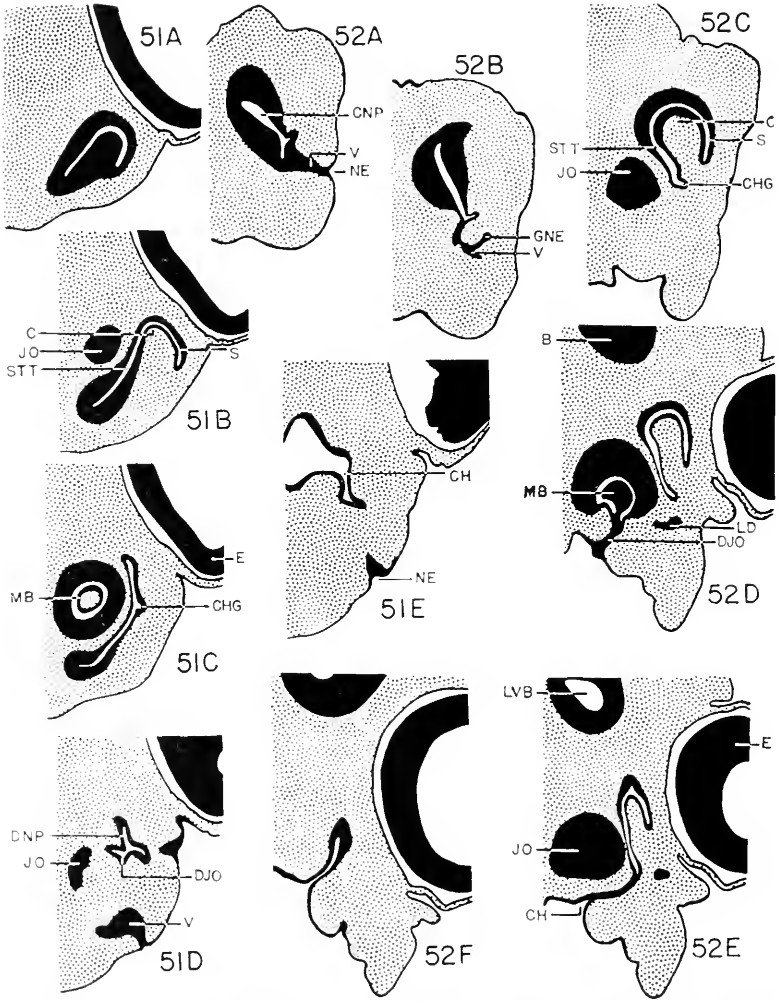


Figure 51. *Thamnophis* 1364 (10.0; MC). Frontal sections through the nasal area. A, section 135; B, 10 sections ventral to A; C, 13 ventral to B; D, 11 ventral to C; and E, 5 ventral to D. 22x.

Figure 52. *Thamnophis* 1415 (12.0; MC). Transverse sections through the nasal area. A, section 213; B, 5 sections posterior to A; C, 11 posterior to B; D, 15 posterior to C; E, 5 posterior to D; and F, 12 posterior to E. 22x.

just anterior to Jacobson's organ. However, the lumen is now as narrow there as in most of the conchal zone. The thickness of the epithelium anteriorly causes that wall of the cavum to project slightly anterior to the vestibulum. The concha is slightly larger than previously, but its shape remains the same, although the connection between the Sakter and Stammteil extends further ventrally posterior to the concha. Another change affects the somewhat expanded area of the Choanengang opposite Jacobson's organ. An anteroventral ridge has developed which results in the partial formation of a duct of Jacobson's organ. This runs slightly posterodorsally as well as laterally before entering the cavum (see Fig. 51D). However Jacobson's organ still opens into the anteromedial part of the Choanengang. Posteroventral to Jacobson's organ, the cavum becomes a rather small oval slit leading to the choana. Although this slit is not yet distinctly separated from the remainder of the Choanengang, it may now be considered the anlage of the ductus nasopharyngeus. The choana is still a moderately long slit which continues posteriorly along the palate as a shallow groove.

The mushroom body of Jacobson's organ increases in size so that the lumen of that organ becomes quite thin. However, there is no change in its shape. The thinning of the lumen reaches its extreme at the entrance to the short duct which is now virtually, if not actually, closed in several of the embryos. On its basal or external surface, the thickened epithelium of Jacobson's organ presents an irregular surface, with many small hemispherical projections into the surrounding mesodermal tissue. These represent the first stage in the development of the epithelial columns. Their later development and significance are considered in the section on Jacobson's organ, and no attempt has been made to indicate them in the various drawings of the embryos.

Histologically, these embryos appear exactly like those of the preceding stage. In most places the non-sensory epithelium probably is two cells thick, but the available material does not permit any definite statements on this.

The next stage is shown in Figure 52. Further differentiation is noticeable in almost all regions of the nose, but the changes are probably most marked in the vestibulum. During the period represented by the several embryos of this stage, the naris externus starts to move further dorsally on the snout, although this process of movement is far from complete, even at the conclusion of this stage, and the vestibulum still runs slightly dorsally, as well as medially, to reach the cavum nasi proprium. The posteroventral portion of the vestibulum is extended posteriorly as a small flange. From the dorsal surface of this projection, a solid rod-like process reaches a short distance dorsolaterally and posteriorly; this process is the anlage of the glandula nasalis externa, and is considered in the section on glands.

The anterior end of the cavum nasi proprium has also developed considerably. It remains an oval tube with the long diameter dorsomedial to ventrolateral. The walls are very thick except at the ventrolateral end where the cavum possesses small dorsolaterally and ventromedially directed extensions. Thus in transverse section this region resembles an inverted T. The medial edge of the posteroventral flange of the vestibulum is continuous with the end of the ventromedial caval extension (see Fig. 52B). This pattern persists posteriorly to the level of the anterior end of Jacobson's organ where the dorsal end of the cavum turns laterally dorsal to the concha and the ventral processes are lost. A slight trace of the more lateral of these extensions may, however, reach posteriorly into the conchal region.

The concha is very large, nearly filling the posterior two-thirds of the cavum. As shown in Figure 52, its shape is very similar to that of the preceding stages, although the ventrolateral line of attachment is proportionately narrower. The small area posterior to the concha, the embryonic Antorbitalraum, is unchanged. Near the posterior end of Jacobson's organ, the Choanengang becomes nearly vertical, and its ventral end turns sharply medially to reach the slitlike choana. The posterior extension of the choana as a palatal groove is now becoming shorter. In most of the series of this stage, the lumen is almost totally obliterated in the ventral portion of the Choanengang. When one is present, it is typically largest near the posterior end; this fact would support Fuchs' (1908 and 1911) theories on the formation of the choanae, which are discussed below.

Jacobson's organ shows no real changes, but its duct has developed considerably. It starts as a semicircle around the posteroventral end of the mushroom body and runs ventrally to the choana. At the beginning of this stage the duct enters the anterior wall of the Choanengang well dorsally, but by the end of the period it joins the ductus nasopharyngeus at the latter's ventral margin, that is, actually at the choana. The duct is solid. Although not yet connected directly to Jacobson's organ, the lachrymal duct now reaches to the anterolateral wall of the Choanengang. This area thus displays a pattern closely comparable to that found in the adult *Sphenodon.*

The non-sensory portions of the cavum nasi proprium typically have a basal layer of low columnar cells with central to basal nuclei, weakly staining cytoplasm, and a very distinct basement membrane. Usually there is a thinner layer of cuboidal or squamous cells facing the lumen, but in some areas, especially posteromedially, this inner layer appears to be lacking. Such epithelium is found at the ventral end of the anterior oval section of the cavum, throughout the Choanengang, on the posteroventral third of the Sakter, and on the posterior wall of the nasal cavity. The vestibular and sensory epithelia appear exactly as in the younger series, except for some increase in thickness. As shown in Figure 52, the sensory epithelium is thickest in Jacobson's organ; in the cavum nasi proprium, it is thicker dorsally and anteriorly than further ventrally or posteriorly.

In slightly older embryos, there is further growth but almost no change in form (see Fig. 53). The posteroventral flange on the vestibulum is slightly more marked, extending from the naris externus to the cavum nasi proprium as a thin shelf. Within the cavum there is great variation in the extent of the lumen: in some embryos it is clearly open throughout, and even wide in some areas such as the anterior quarter, but in others it is as restricted as in the previous stage. This same variation is found in the choana and duct of Jacobson's organ, although most commonly both of these are almost entirely without a lumen in the material studied. The concha is now recognizable further posteroventrally than before, extending ventral to the level at which the posteroventral part of the Choanengang (or anterior part of the ductus nasopharyngeus; the two are not really distinct) turns posteromedially towards the choana (see Fig. 53C).

Jacobson's organ has very nearly attained its adult structure. It is a large roughly spherical organ, with the ventral surface rather flattened. The mushroom body forms a large hemispherical process which extends inwards from the anteromedial corner of its ventral surface and nearly fills the lumen. Thus the cavity is the shape of an inverted bowl. The duct of Jacobson's organ runs ventrally from the posterior part of the organ, and is semilunar in frontal section, with the convex side posterolateral. In its ventral course the duct is slightly spiraled so that the convex side comes to lie posteriorly and finally, in this stage, posteromedially. The available embryos show some variation in the degree of separation between this duct and the choana; gen-

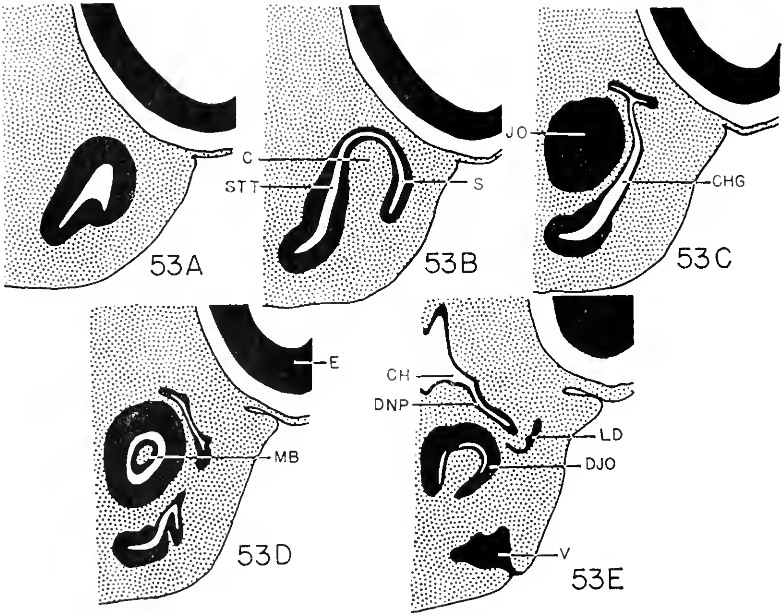


Figure 53. *Thamnophis* 1365 (10.2; MC). Frontal sections through the nasal area. A, section 105; B, 10 sections ventral to A; C, 16 ventral to B; D, 6 ventral to C; and E, 9 ventral to D. 23x.

erally the duct enters the roof of the mouth at the anterior end of the choanal groove. Although very close to the duct of Jacobson's organ, the lachrymal duct still appears to enter the choana. All of these openings occur along the dorsolateral corner of a large median trough in the palate; at this stage the trough is comparatively wide and shallow.

The histology appears to be very similar to that of earlier stages. In the presumably non-sensory areas of the cavum nasi proprium, the epithelium most commonly appears to be two or even three cells thick, but some areas still seem to have simple columnar epithelium. One embryo possesses small projections of the dorsolateral sensory epithelium which could be the first appearance of Bowman's glands; however the other embryos lack them, and their nature cannot definitely be determined in the series in question. Some embryos of this and earlier stages lack a distinct basement membrane under parts of the sensory epithelium, and the epithelial boundary becomes very vague in such areas.

The nasal cavity continues slowly to assume its adult form without any really marked changes. Figure 54 shows an embryo slightly more advanced than those described above. Here the vestibulum has become perfectly horizontal, and the naris externus is directly lateral on the snout, quite near, but not at, its anterior end. The posteroventral vestibular flange is very well developed, as shown in Figure 54A. Histologically, the vestibulum cannot always be differentiated from the non-sensory ventral portion of the cavum nasi proprium, but in some series minor differences can be found which indicate that the former region forms only the short and solid horizontal tube.

Anterior to Jacobson's organ, the cavum nasi proprium still resembles an inverted T when seen in transverse section. The dorsal end is well medial to the ventral, so that the long central arm of the T forms an angle of approximately 30 degrees with the midline (see Fig. 54B). Around the ventral projections, the epithelium is thin, but the central portion possesses the thickest epithelium of any part of the cavum, even as far ventral as the vestibulum. Posteriorly, in the conchal zone, the ventromedial projection disappears, but the ventrolateral one reaches almost to the posterior end of Jacobson's organ. The Sakter is now very large. It extends farthest anteriorly near its ventrolateral end; that is, the concha is attached dorsally as well as ventrally at its anterior end. For most of its length, the ventral end of the Sakter is turned slightly medially where it lies dorsal to the ventrolateral extension of the Choanengang. Thus the line of attachment of the concha is a quite thin lamellar band (see Fig. 54D). Ventrally the epithelium is non-sensory in type; dorsally it remains thick.

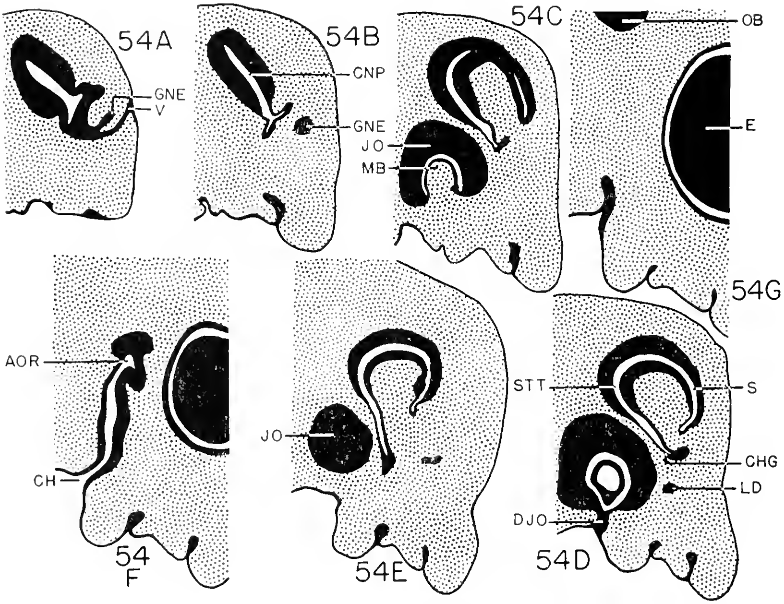


Figure 54. *Thamnophis* 1399 (12.1; MC). Transverse sections through the nasal area. A, section 273; B, 12 sections posterior to A; C, 14 posterior to B; D, 12 posterior to C; E, 13 posterior to D; F, 6 posterior to E; and G, 5 posterior to F. 23x.

Near the level of the posterior end of Jacobson's organ, the Choanengang becomes more nearly vertical, thus making the attachment of the concha ventral rather than ventrolateral. The Antorbitalraum is still not well developed; it forms a small vertical slit which is continuous ventrally with the ductus nasopharyngeus. The latter turns ventromedially to reach the choana, which is a quite short and narrow slit opening into the dorsolateral corner of the large median trough in the palate. A small groove still runs a short way posterior from the end of the choana. As can be seen in Figure 54, the epithelium is thicker dorsally than ventrally or posteriorly.

Jacobson's organ is unchanged, but its duct is now clearly separated from the choana. The duct is the same shape as in the preceding stage and remains solid. It leads ventrally from Jacobson's organ to the palate. Like the choana, it enters the dorsolateral corner of the median trough, but is well anterior to that structure. The lachrymal duct enters the roof of the mouth between the choana and the duct of Jacobson's organ; it is slightly closer to the latter.

The histology remains basically the same. A single basal layer of columnar cells is found in the vestibulum, with the center filled by rather irregular, but essentially isodiametric cells. The thickened sensory epithelium shows no changes at all. It is darkly staining and contains many nuclei except in the thin clear zone bordering the lumen; there, mitotic figures are common. In the thinner non-sensory zones, there is a basal layer of low columnar cells with central nuclei and weakly staining cytoplasm. Between these and the lumen are one or two layers of very thin irregular cells. Jacobson's organ has sensory epithelium resembling that of the cavum, except in its greater thickness and in the columns found at its basal surface. The mushroom body is covered by bilaminar cuboidal epithelium.

Slightly older embryos are shown in Figures 55 and 56. As in the previous stages, the changes are not great. The posteroventral flange of the vestibulum remains well developed, but is now most conspicuous laterally. Otherwise that region is unchanged.

Elongation of the snout has resulted in a corresponding elongation of the cavum nasi proprium, especially anteriorly. There, the segment anterior to Jacobson's organ no longer appears as a transverse slit in frontal section, but now runs anteromedially to posterolaterally. Both anteroventral extensions are present, with the lateral one tending to turn dorsally at its lateral end, and the medial one extending ventrally as much as medially. The latter does not reach posteriorly as far as the conchal zone, but the former extends nearly to the posterior end of Jacobson's organ as part of the Choanengang. There is little change in the conchal region, except for the further narrowing of the attachment of the concha. As in the other stages, that structure may possess a small posterior end projecting freely into the lumen; most commonly, however, it is connected with the ventrolateral wall of the nasal cavity throughout its length.

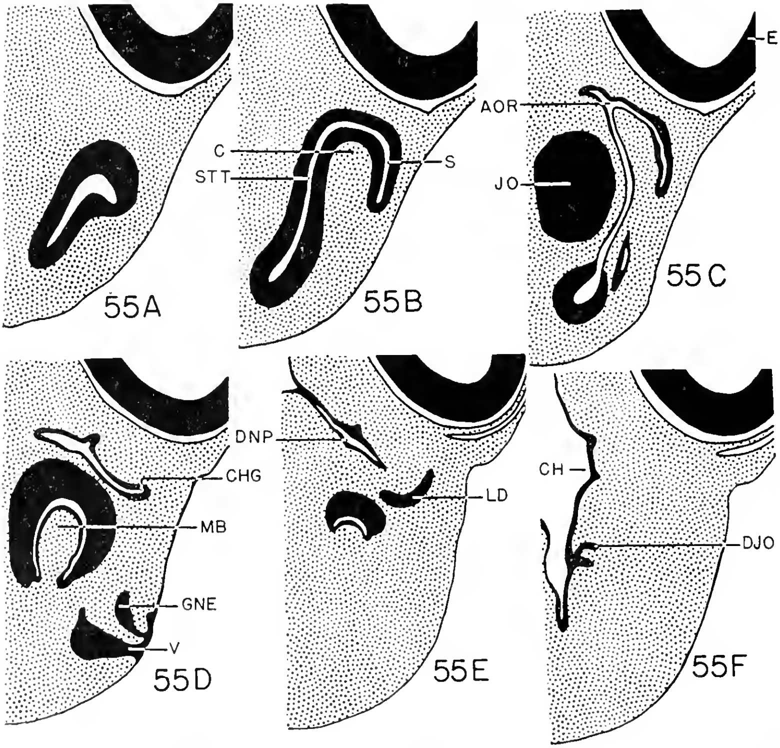


Figure 55. *Thamnophis* 1366 (12.0; MC). Frontal sections through the nasal area. A, section 105; B, 12 sections ventral to A; C, 20 ventral to B; D, 14 ventral to C; E, 14 ventral to D; and F, 8 ventral to E. 26x.

During this stage, the Antorbitalraum becomes a somewhat more distinct and complex region. The posteromedial part of the cavum which leads ventrally to the choana increases in height,

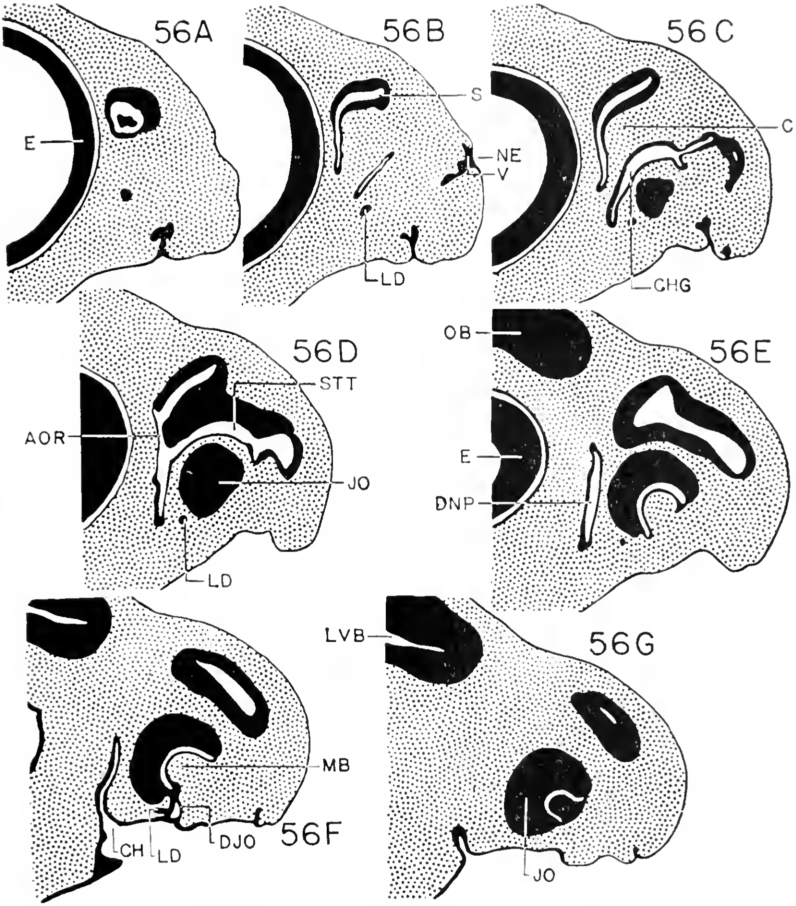


Figure 56. *Thamnophis* 1395 (10.4; MC). Sagittal sections through the nasal area. A, section 59; B, 8 sections medial to A; C, 11 medial to B; D, 6 medial to C; E, 7 medial to D; F, 8 medial to E; and G, 5 medial to F. 20x.

so that it now extends dorsally into the conchal zone (see Fig. 55C). By the end of the stage, the posteroventral portion of the Antorbitalraum starts to develop a small lateral pocket and a larger medial one. However, it still merges gradually with the more anterior concha zone and ventral ductus nasopharyngeus. The ductus is a moderately narrow tube which runs medially as well as posteroventrally to the choana. Although narrow, it typically possesses an uninterrupted lumen at this stage. The choana is much like that of the preceding stage, but it continues to shorten and become more posteriorly located. During this period it is a small oval opening, with only a short groove extending posteriorly from it.

The duct of Jacobson's organ, now well separated from the choana, is slightly more spiraled than before. At its ventral end the convex side is medial. The lachrymal duct becomes more closely associated with that from Jacobson's organ, and by the end of this stage, typically enters the palate at the posterior end of the latter duct. Both of these are still solid structures, at least at their palatal terminations. Dorsally the duct of Jacobson's organ may possess a narrow lumen.

Only two comments on the histology are necessary. Bowman's glands are becoming more common in the posterodorsal part of the Sakter, but they are still very rudimentary and absent from the remaining sensory areas. Secondly, in the non-sensory epithelium of the cavum nasi proprium, the basal columnar cells now have the nuclei towards the lumen. In the vestibulum, the nuclei remain central; thus the two regions may be separated on histological grounds, although the transition between them is often quite gradual.

With further growth, the nasal cavity attains the condition shown in Figure 57. The vestibulum remains a very short solid tube running directly medially from the lateral naris externus. A prominent flange still extends posteroventrally from the ventral margin of the vestibulum, especially near its lateral end.

The most conspicuous change in the cavum nasi proprium is a general increase in the size of the lumen. However the ductus nasopharyngeus, and frequently also the posterior conchal region, remains as narrow as in the preceding stages. The increase is most marked near the anterior end of the cavum, where it results in a relative decrease in the size of the anteroventral extensions. Slightly posterior, however, these extensions reach their maximum development (compare Figs. 57B and C). The anterior end of the concha is at approximately the level of the center of Jacobson's organ, and, as in previous stages, it is attached to the wall of the cavum dorsally as well as ventrally; thus the Sakter possesses a small anterior pocket. There is no change in the shape of the concha. From the posterior end of its line of attachment, a slight ridge continues posteriorly and curves around the

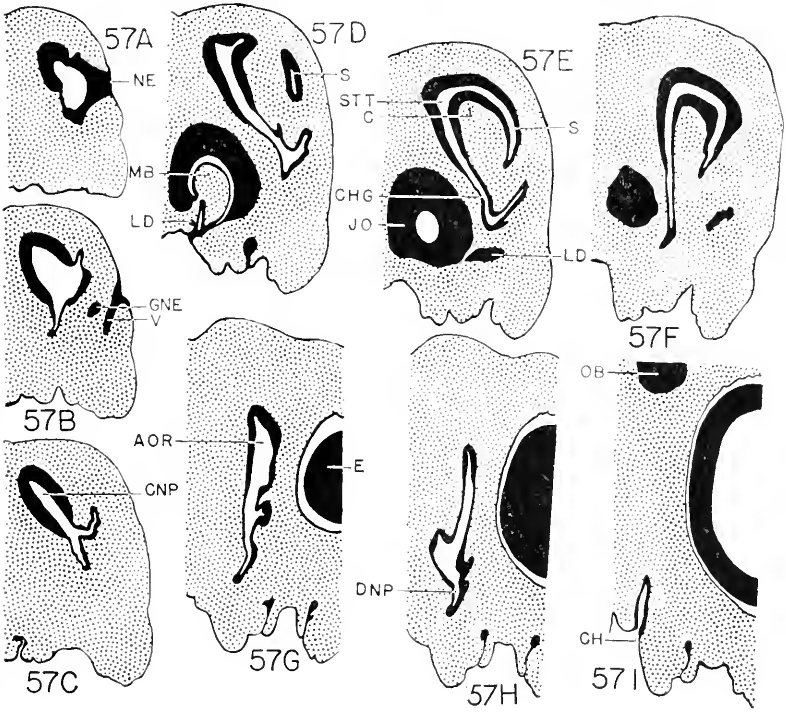


Figure 57. *Thamnophis* 1328 (12.0; MC). Transverse sections through the nasal area. A, section 182; B, 12 sections posterior to A; C, 17 posterior to B; D, 24 posterior to C; E, 8 posterior to D; F, 15 posterior to E; G, 11 posterior to F; H, 7 posterior to G; and I, 15 posterior to H. 18x.

back wall of the cavum. The medial end of this ridge is ventral to the lateral part. Thus there is now a moderately definite line of demarcation between the Antorbitalraum and the ductus nasopharyngeus. The former chamber is still a vertical slit of rather small extent; ventrally it possesses two small extensions, a vertical slitlike opening in the medial wall and a small lateral pocket.

The ductus nasopharyngeus continues to increase in length. It forms a narrow tube running from the posteroventral corner of the cavum to the small, nearly circular choana. The ducti of opposite sides converge posteriorly, so that the choanae are very close to the midline. Between them a narrow vertical slit is developing in the palate. With the increased length of the ductus, the choana is now well posterior as well as ventral to the cavum nasi proprium.

Jacobson's organ is relatively little changed. The mushroom body arises from the anteroventral wall, slightly farther anterior than previously, but retains the same form. Thus the entire organ appears to have been tilted slightly posteriorly from its former position. By this stage the lachrymal duct joins the ventral end of the duct of Jacobson's organ, and the two enter the oral cavity together. The former runs anteromedially from the eye to a point posteromedial to the duct of Jacobson's organ, and then turns anterolaterally to enter the anteromedial corner of the latter duct.

Histologically, the vestibulum is unchanged. The sensory areas of the cavum have slightly thicker epithelium than in earlier stages, but show no real differences, although Bowman's glands are becoming commoner and more widely distributed. Sensory epithelium is found in the dorsomedial two-thirds of the region anterior to the concha, the anterodorsal half of the conchal zone, and the dorsal wall of the Antorbitalraum. However, in the non-sensory caval regions a major change is starting to occur. Much of the thin epithelium, especially anteroventrally in this early stage, is becoming folded to produce shallow grooves. The cells of these small crypts, which are presumably glandular in the adult, appear to be identical with those of other non-sensory areas; they show no changes from the preceding stages.

Figure 58 shows a slightly older embryo in which the posterior part of the nasal cavity approaches closely the adult condition.

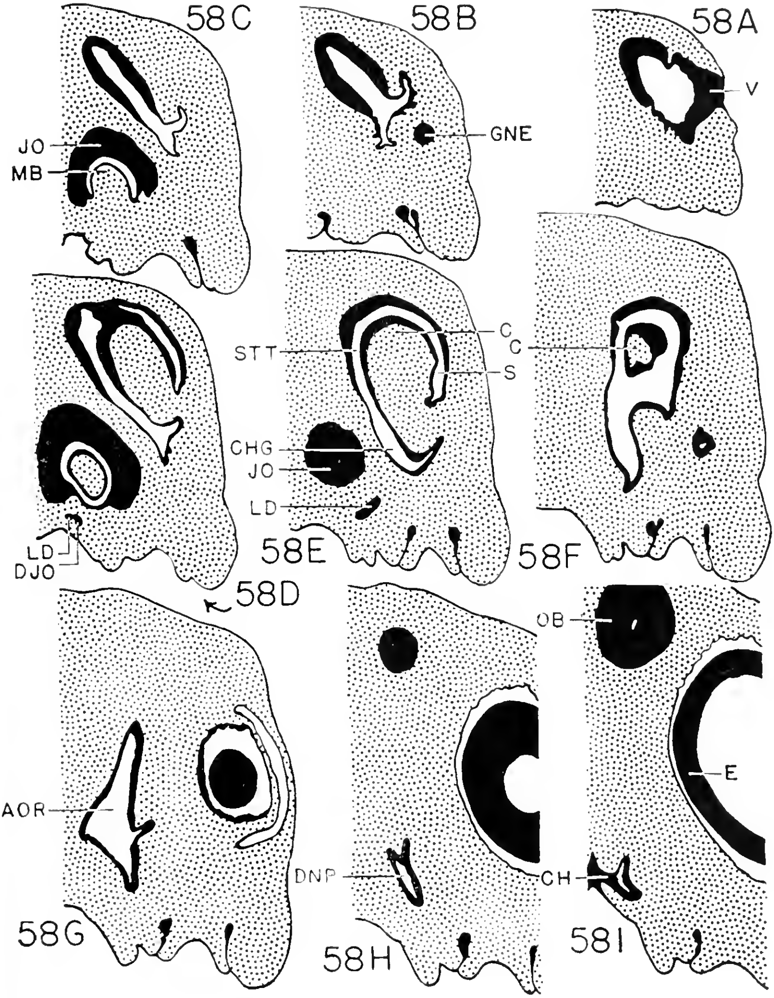


Figure 58. *Thamnophis* 1326 (headlength, 8.0; MC). Transverse sections through the nasal area. A, section 369; B, 24 sections posterior to A; C, 19 posterior to B; D, 20 posterior to C; E, 21 posterior to D; F, 15 posterior to E; G, 10 posterior to F; H, 14 posterior to G; and I, 16 posterior to H. 21x.

Anteriorly, the anatomy is essentially the same as in the preceding stage; comparison of Figures 57 and 58 renders description unnecessary. The Antorbitalraum is now a large open cavity posterior to the concha. Ventrolaterally, there is a prominent ridge continuing posteriorly from the line of attachment of the concha, and dorsally the end of that structure projects freely into the lumen. Farther posteriorly the cavity narrows and its dorsal wall slopes posteroventrally. The two posteroventral extensions are present, and the medial one is quite large, so that in transverse section the posterior portion of the Antorbitalraum appears triangular (see Fig. 58G).

The ductus nasopharyngeus is an oval tube with the long diameter dorsomedial to ventrolateral. As in earlier stages, it runs posteromedially to the choana. The latter has, however, changed considerably. A narrow cleft rises dorsally from the center of the large trough in the palate. The medial sides of the ducti of either side open into this cleft. At their posterior ends, the ventral walls of the ducti tend to disappear too, so that the choanae open in part directly into the mouth, but at this stage their lumen is very small. Thus the choanae have attained their adult pattern, in that there are no longer any conspicuous grooves continuing posteriorly from them.

The histology is little changed. Figure 81 shows the vestibulum at this stage; there is a single basal layer of columnar epithelium with basal nuclei. The remainder of the region is filled by an irregular mass of more or less isodiametric cells. In the sensory epithelium of the cavum nasi proprium (see Fig. 82), the Bowman's glands are still rather sparsely scattered and small. The epithelium itself appears to be in three indistinct layers. First, there is still a thin inner enucleate zone with occasional mitotic figures, although these are becoming quite rare by this stage. The central zone, which is intermediate in thickness, is filled with very darkly-staining, oval nuclei. Basally there is a very thick area filled with circular nuclei. Although these nuclei do, in some cases, appear to be aligned in radial rows, there are no indications of the columnar structure found in Jacobson's organ. Slight irregularities do occur in the basement membrane, but these show no real resemblance to even the earliest stages in the development of the columns. The only change in the non-sensory epithelium of the cavum is the greater development of the folds and small crypts described above. At this stage they are found in all the non-sensory areas of the cavum, but are still most common and highly developed anteroventrally (see Fig. 83). The nuclei of the basal columnar cells are typically near the surface facing the lumen. In a few sections some of this epithelium appears to be simple, but in most places it is stratified, as shown in the figure.

In the oldest available embryo, the vestibulum shows no changes in its gross form, but its histology indicates that the embryo must have been very close to hatching. It possesses thin epithelium, two or three cells thick, with some indications of cornification. Within it are loose masses of irregular cells, the remains of the solid epithelial plug of earlier stages. The naris externus is not present on the slides; thus it cannot be told if the vestibulum is actually open or not.

The lumen of the cavum nasi proprium is greatly enlarged in all regions. Anteriorly, this results in a considerable decrease in the size of the ventral extensions. With the increased growth, the anterior part of the cavum retains its oval shape, but the greatest diameter is nearly horizontal in transverse section, with the former ventral end now lateral. The concha is little changed: it is a shelf-like horizontal projection of the lateral nasal wall which expands into a large cylindrical mass dorsomedially. The free posterior end is very small. Posterior to it there is a large Antorbitalraum which is quite similar to that of the preceding stage except in its increased volume. From the posteroventral corner of the Antorbitalraum, the ductus nasopharyngeus extends posteroventromedially as before.

The histology of the sensory epithelium shows no changes, although it appears to be proportionately thinner, due to the great growth of the nasal area; its distribution is also like that described for the earlier stages. However the non-sensory areas are markedly different. There the epithelium is either simple or of a very low stratified type with the basal layer of cells low columnar. The development of the small crypts has progressed to the point where almost all of the non-sensory epithelium is thrown into folds. At the bases of these, and often elsewhere, the epithelium is simple and appears to consist entirely of goblet cells with basal nuclei and clear peripheral cytoplasm. Such crypts are very marked anterolaterally, as in the preceding stage, but now reach their maximum development in the posterior portion of the Antorbitalraum. Shallower, but basically similar grooves occur in the walls of the ductus nasopharyngeus.

The choanae are also somewhat further developed. As in the preceding stage, the ducti nasopharyngei converge towards the midline, and there is, between them, a very narrow median cleft in the palate. However the anterior end of this cleft is no longer open ventrally to the oral cavity. The two ducti and the cleft join ventrally to produce a median tube, the whole resembling the letter E in transverse section (with the open side dorsal). A short distance posterior to the juncture of the ducti nasopharyngei, this tube opens into the mouth by a narrow median slit. This choanal slit widens posteriorly, and the nasal and oral cavities possess a moderately wide connection by this stage.

The literature on the later stages in the nasal embryology of snakes is surprisingly meager. Rathke's (1839) great work on *Natrix* deals only briefly with the development of the nasal cavities. There are three other early papers based on studies of series of *Natrix* embryos. Fleischer (1878) and Beard (1889) are concerned primarily with the nature of Jacobson's organ, and neither author gives any detailed descriptions, so that their papers need no further comment here. However, Born (1883) does consider the general nasal embryology at some length, and his work has long been the classic in this field. It remains so, not only because of its early date and its quality, but also because there appear to be no more recent studies of a comparable nature.

In general, Born's account agrees well with the description given above. There are no differences concerning the development of the duct of Jacobson's organ and its relationship to the nasal cavity and to the lachrymal duct, points discussed in some detail in his paper. Born gives shorter descriptions of the cavum nasi proprium in most of his stages; a review of his findings would add nothing to the preceding section of this paper. However, Born's material included stages showing the fusion of the lateral and medial nasal processes more clearly than any available for the present study. He states (pp. 194 and 195) that: ". . . der lappen- oder vorhangförmige äussere Nasenfortsatz . . . legt sich mit seiner Spitze und mit den grössten Theile seines

Vorderrandes an die Aussenfläche des inneren Nasenfortsatzes vor den oberen Hälfte des zum Jacobson'schen Organ führenden Loches an und verschmilzt mit derselben. Nur oben bleibt eine ganz kleine punktförmige Öffnung, die Apertura externa, frei und dies auch nur auf kurze Zeit, denn sehr bald legen sich auch hier die Epithelflächen an einander und die Öffnung wird verlegt." The choanae are described as broad slits which run obliquely posterolaterally. Along the line of fusion of the nasal processes, Born found some traces of their original epithelial covering, but these quickly disappear. In the embryos used for the present study, there is virtually no trace of such remnants.

Several other papers mention or figure individual stages in the nasal embryology of snakes, although generally without detailed descriptions. The majority of these works are based on *Natrix*. Dieulafé (1904-1905) describes a single embryo of 40 mm. total length (uncoiled); it is of the stage immediately following the fusion of the nasal processes, and is, judging by his figure and discussion, probably identical in structure with the *Thamnophis* embryo shown in Figure 49. Three papers considering the palate and choanae, Fuchs (1908 and 1911) and Thäter (1910), figure sections through the nasal cavities of *Natrix* embryos; they appear to be in agreement with the observations recorded previously in this paper. Only one earlier paper deals with any embryonic material of *Thamnophis*. Macallum (1884) studied a specimen of 6 mm. headlength, but gives almost no information on its anatomy.

Apparently only two papers contain even a passing mention of other forms; both of them are concerned primarily with the development of the skull, but do figure sections through the nasal area. Peyer (1912) studied *Vipera*. Judging by his figures, moderately late embryos of this genus resemble very closely those of *Thamnophis*. Finally Pringle (1954) describes the chondrocrania of four South African snakes, *Lamprophis, Dasypeltis, Causus*, and *Hemachatus*. In each case he studied a series of embryos, but has few figures of the nasal region, generally all of one stage. All four genera appear relatively similar to *Thamnophis*, with the greatest differences occurring in *Hemachatus*. In that genus the concha is attached dorsally as well as ventrally for an unstated distance at its anterior end; thus the anterolateral portion of the Sakter extends anteriorly as a conspicuous pocket. Posteriorly the form of the concha shows another point of difference. There is a lateral projection of the concha which results in an increase in the medial twist at the ventral end of the Sakter. Although such a curving of that region is also seen in *Thamnophis* (see Fig. 54D), in *Hemachatus* the lateral conchal projection is supported by a simple lamellar extension from the conchal cartilage; no such support is present in *Thamnophis*.

As was the case with turtles, there is considerable literature on the embryology of the ducti nasopharyngei and palates of snakes. Early papers considering this problem include those of Rathke (1839) and Born (1883); their conclusions are summarized in the later papers and need no comment here. The views of Born are, in the main, substantiated by Fuchs (1908). Another viewpoint is put forward by Thäter (1910), and this last paper is answered by Fuchs (1911) who reiterates his former stand. Much of the last two papers is polemic in nature, and the arguments are here reviewed only briefly. For details the reader is referred to the papers cited, especially Fuchs (1911).

Fuchs' (1908) observations agree very well with those given above. When the choana is first formed, it stretches almost the entire length of the conchal zone of the cavum nasi proprium. During the later stages, Fuchs believes that fusion occurs in the ventral portion of the Choanengang, and between the palatal "processes" lying on either side of the primitive choana. The anteroventral corner of the choana remains open as the duct of Jacobson's organ, but posterior to this the fusion progresses nearly to the end of the choana. Thus he considers the situation in the adult snake to resemble closely that in turtles, and uses the same terms in both groups (choanae reliquae and tegmen oris primarium commutatum). Since the ductus nasopharyngeus of the present paper is formed from the posterior part of the nasal cavity rather than from a part of the oral cavity, Fuchs suggests that it is better termed part of the Choanengang.

Thäter's (1910) observations do not differ markedly from those of other workers; however his interpretations are quite radically opposed to those of Born and Fuchs. The only descriptive difference requiring note is Thäter's denial that the choanae are long slits, even at a stage in which Jacobson's organ is still connected to the medial wall of the nasal cavity. Rather he states that they are very small apertures. Thus Thäter believes that there is no marked shortening of the choanae in the embryo, and denies that fusion has occurred. He explains the changes in the position of the duct of Jacobson's organ by "eine aktive Umformung . . . so dass das Jacobsonsche Organ durch Wachstum oral vom Choanengang weggelagert wird" (p. 489).

Fuchs' (1911) answer adds little to the discussion. He points out that Thäter's youngest embryos are larger than those in which he had previously described the long choanal slits, thus denying the validity of much of Thäter's argument.

The observations made in the present study seem to support Fuchs' contentions. Although in later stages the choanae are very small, they appear to be long slits in younger embryos. As reported by Fuchs (1911), they become not only relatively, but absolutely shorter as they develop. Therefore some fusion seems to be required. However, there is almost certainly some differential growth involved in the early changes in the position of the duct of Jacobson's organ.

One final paper must be considered here. Weber (1950) describes in detail the histological changes involved in the closure of the vestibulum and naris externus. His observations were made on a large series of *Natrix* embryos. The epithelial lining of the vestibulum and the central plug of tissue, the *Füllgewebe* of Weber, are at first very similar. However, the former develops into columnar epithelium and becomes cornified, while the Füllgewebe remains a mass of more or less isodiametric cells which eventually degenerate. They are sloughed away after hatching.

Thus, a review of the literature shows that in only one genus of snakes, *Natrix*, has the later nasal embryology been studied in any detail. As might be expected from their close relationship, it resembles almost perfectly *Thamnophis*, as here described. The amount of information available does not permit any conclusions concerning the other groups of snakes, or generalizations for the suborder as a whole.

Jacobson's Organ. Since the adult anatomy and embryology of this organ have been discussed in previous sections of this paper, only two points need to be considered here. There has been little question of the homology of Jacobson's organ in the Squamata, and the history can be reviewed very briefly. The problem of the nature of the cellular columns forming the basal three-fourths of the sensory epithelium also merits some note.

The first description of Jacobson's organ in a member of this order appears to be Rathke's (1839) account of the embryology of the structure which he termed the Nasendrüse in *Natrix*. In 1854 Stannius noted the similarities between this "gland" in snakes and the Jacobson's organ of mammals, but not until 1872 was their homology definitely suggested. In that year Leydig described the organ both in lizards (1872a) and snakes (1872b), and stated that it was an accessory olfactory organ. Although in 1878 Parker referred to the structure as a nasal gland, Leydig's proposed homology has been accepted by all later workers, and has, to my knowledge, never been questioned.

The epithelial columns found in the dorsal wall of Jacobson's organ have long been known, and their nature was, for a considerable time, much discussed in the literature. More recently, however, they have received no attention, although many papers do figure them (e.g. von Navratil, 1926, and Pringle, 1954). Such columns are also known in certain lizards, and are considered in that group by Beard (1889) and von Mihalkovics (1898).

Figures 84, 85, 86, and 87 show stages in the development of these columns in *Thamnophis;* all are equally magnified. The sensory epithelium of Jacobson's organ becomes very greatly thickened as soon as the organ is formed as a distinct medial pocket. During the later development, the epithelium continues to thicken, but at a much reduced rate. Early in its development, the basal surface of the epithelium becomes irregular, and the columns are first formed as small bumps pushing into the surrounding mesodermal tissue. A network of capillaries appears between these anlagen of the columns, and is found at their base in all subsequent stages. With further growth, the columns increase greatly in length, and the undivided epithelium lining the lumen of Jacobson's organ becomes thinner, both relatively and absolutely. Another change which occurs is that the columns become thinner in cross-section, and hence more numerous. How this occurs is not known; none were seen dividing or growing out between already existing columns in the present study. In cross-section the columns appear polygonal. They do not possess a lumen.

The material used in the present work is not suitable for detailed histological study. At all stages there is a very narrow zone in the sensory epithelium facing the lumen in which there are few nuclei, but in which mitotic figures are common. The remaining portion of the epithelium contains many densely-packed circular nuclei in the early stages. Later a small central zone with more darkly stained oval nuclei develops between the thick basal and clear peripheral portions. The entire length of the columns lies completely within the basal zone as does part of the undivided epithelium. Precise tracing of nerve fibers was not possible in the available material. Certainly most of these leave the ends of the columns, but whether or not some run between them after leaving the epithelium at their bases could not be determined. Thus the histological picture is identical with that of the olfactory epithelium of the nose, except that the epithelium of Jacobson's organ is somewhat thicker, and its basal portion is divided into these cellular columns with capillaries and other mesodermal tissue between them.

The earlier literature contains two theories on the nature of these columns. The more generally accepted one was that they are formed of ganglionic cells. Leydig (1872a) first proposed such a theory, and Wright (1883), Macallum (1884), and Beard (1889) all supported it. The other theory is that the columns are simple tubular glands. Born (1883) proposed such an explanation on the basis of his embryological studies, but no other workers have concurred with his opinion.

The important paper by Retzius (1894) should have settled the controversy; however, it seems generally to have been overlooked. By a study of Golgi preparations of the epithelium of Jacobson's organ, Retzius determined that the columns are an integral part of the epithelium which is completely comparable with that of the sensory areas of the nose. It contains two cell types, sustentacular and sensory. The former are long thin cells extending the entire thickness of the epithelium. Their nuclei lie in a zone near the lumen, thus corresponding to the darker oval nuclei mentioned previously in the description of the material used in the present study. The sensory cells have round nuclei located at various levels in the epithelium. One process from each cell runs to the lumen, and another process emerges from the opposite surface of the epithelium and continues to the brain as a fiber of the olfactory nerve. There is no sign of any glandular structure, and Retzius mentions no ganglion cells.

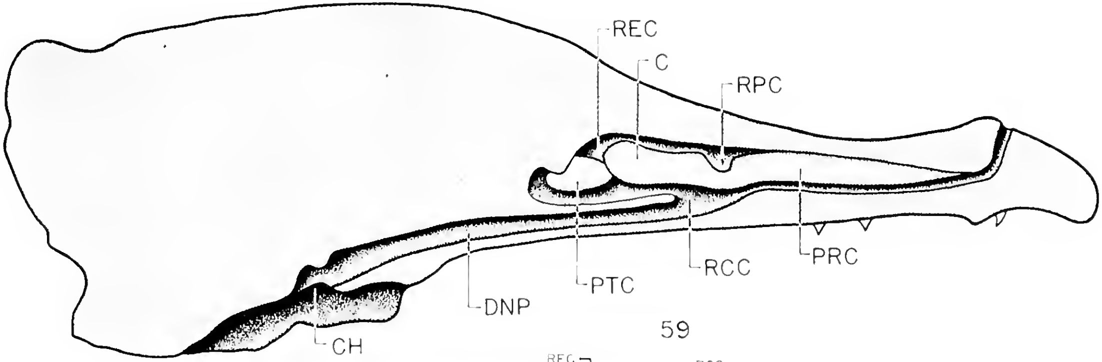
A few later papers, including Leydig (1897), von Mihalkovics (1898), and Zuckerkandl (1910b), further discuss the problem without reference to Retzius' discoveries, although his work may be cited in their bibliographies. Their works add no new information on the columns.

Thus there is no evidence for the presence of any secretory cells in the Jacobson's organ of snakes, and the occurrence of ganglionic cells in any numbers would be most surprising in view of present knowledge of the development and structure of the olfactory (including the vomeronasal) nerve. The observations made in the present study add only one point of interest. A capillary network is present at all stages in the development of the columns, not, as was stated by Beard (1889), only after they are well formed. Whether or not there is any causal relationship between this network and the form of the columns, as suggested by Wright (1883), remains unknown.

ORDER CROCODILIA

Adult Anatomy. The crocodilians possess by far the most complex nasal cavities of any reptiles. For the present study three immature specimens of *Alligator* were dissected; one of these is shown in Figure 59. Since the observations agree well with the accounts found in the literature, only one description is necessary. Major papers considering this group include those of Rathke (1866; *Alligator, Caiman, Crocodylus,* and *Tomistoma*), Gegenbaur (1873; *Alligator*), Solger (1876; *Crocodylus*), Hoffmann (1879-1890; *Crocodylus*), Nemours (1930; *Alligator*), and Bertau (1935; *Alligator, Melanosuchus,* and *Crocodylus*). Matthes (1934) and von Wettstein(1954) present rather detailed summaries of earlier work.

As with the other groups which have been described, there are many problems concerning terminology. In the following descriptions that of Bertau (1935) will be followed unless otherwise noted. The diagram shown in Figure 60, which is based in



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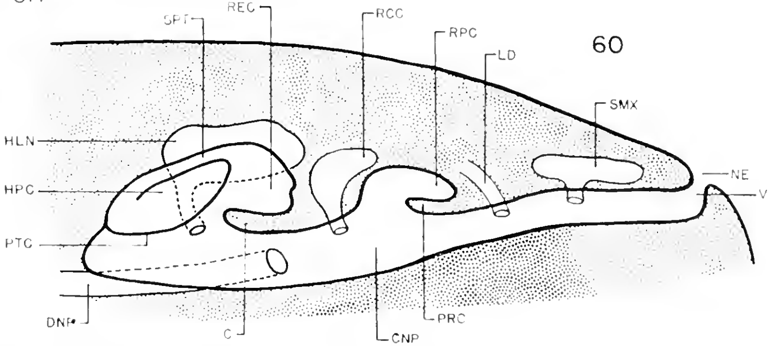

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Figure 59. Medial view of the left nasal cavity of an immature *Alligator* to show the lateral wall.

Figure 60. Diagram of the nasal cavity of a crocodilian in frontal view. The anterior end is toward the top of the page (mainly after Bertau, 1935).

large part on Bertau's Abbildung 18, includes most of the regions to be described.

The nose may be divided into three main parts comparable to those in other reptiles: an anterior vestibulum, a large cavum nasi proprium, and a ductus nasopharyngeus leading to the mouth. The short vestibulum (*Vorhöhle* of Bertau) is a vertical tube leading from the naris externus to the anterior end of the long horizontal cavum nasi proprium. The ducts of the glandula nasalis externa enter its posterior wall well ventrally.

The cavum nasi proprium is a large complex chamber, containing several concha-like projections of the lateral wall, and including a series of well-defined recesses or sinuses. It has often been treated as two somewhat separate parts, one lying anterior to the nasal end of the ductus nasopharyngeus and one lying posterior. The former has sometimes been considered as part of the vestibulum, as by Gegenbaur (1873). Bertau points out the incorrectness of this identification and treats the entire cavum as one region which he refers to as the *Haupthöhle;* this interpretation is followed here.

There are three projections of the lateral wall into the cavum which have been referred to as conchae. Gegenbaur (1873) and Solger (1876) proposed a restricted definition of this term, and considered only the middle projection as a true concha, calling the other two *pseudoconchae.* Almost all the more recent workers have used the terms *preconcha, concha,* and *postconcha.* The preconcha is a quite pronounced convexity of the lateral wall running from a short distance posterior to the vestibulum to the start of the ductus nasopharyngeus, thus making the anterior half of the cavum crescentic in transverse section.

The concha (= middle or true concha) is more complex, consisting of a thin projection from the lateral wall which extends medially and then posteriorly and ventrally. It stretches from the region of the ductus nasopharyngeus approximately two-thirds of the distance to the posterior wall of the cavum. In the *Alligator* material dissected for the present study the anterior two-thirds is essentially horizontal and the posterior third turns dorsally (see Fig. 59). In a late embryo of this genus, Bertau (1935) shows the posterior portion as larger and more distinctly separated from the anterior by a groove across the surface of the concha. He also shows a horizontal groove along the medial face of the anterior portion. In *Crocodylus*, the concha is simpler in having a fairly straight line of attachment which runs diagonally posterodorsally from the posterior end of the preconcha (Bertau). In both genera the anteroventral end of the concha is connected to and continuous with the posteroventral corner of the preconcha.

The postconcha is a very prominent convexity in the posterolateral wall of the nose. Its anterior end, which lies partly ventral to the posterior part of the concha, is pointed while its posterior end is rounded so that the projection is wedge-shaped in medial view.

Crocodilians possess a large number of recesses and sinuses connected to the nasal cavity. The first of these, the *recessus preconchalis*, enters the cavum nasi proprium between the preconcha and the concha just dorsal to their connection. It expands, especially anteriorly, under cover of the posterior end of the preconcha. The larger cavity lateral and ventral to the concha is the *recessus extraconchalis* which opens into the cavum by a diagonal slit between the concha and postconcha. From the ventrolateral corner of the posterior wall of this recessus a small duct-like passage, the *sinus postturbinalis*, runs posteriorly to the posterolateral corner of another large cavity. The last lies entirely within the postconcha and is termed only the *Höhle in der Postconcha* by Bertau. All of these chambers lie within the cartilaginous nasal capsule.

Three more sinuses lie outside the nasal capsule. The most anterior of these is the *sinus maxillaris* which enters the cavum ventral to the anterior end of the preconcha and expands into a longitudinal cavity in the maxilla ventral to the preconcha. The *recessus caviconchalis* is a rather digitiform sinus lying just anterior and parallel to the recessus extraconchalis. Its opening to the cavum is ventral to the anterior portion of the concha. In *Crocodylus*, Bertau found a small connection between this recessus and the Höhle in der Postconcha; such a connection is not present in the other genera which have been studied. Finally, ventral to the postconcha lies the *hintere laterale Nebenhöhle* of Bertau. It possesses a small connection with the cavum ventral to the postconcha and is of considerable extent ventrolateral to the nasal capsule. This sinus is well developed in *Alligator;* Bertau also found it in *Melanosuchus,* but reports its absence in *Crocodylus.*

The lachrymal duct also enters the cavum nasi proprium. Its opening is ventral to the center of the preconcha. In crocodilians this duct is much enlarged and bears an anterior extension, the *saccus lacrimalis*, which resembles another small paranasal sinus.

The ductus nasopharyngeus is a long simple tube leading from the floor of the cavum in the region of the anterior portion of the concha to the posterior end of the extensive secondary palate. Its position is well shown in Figure 59. The ducti of opposite sides are separated by a thin septum throughout their entire lengths.

The pattern just described appears to be relatively constant in all the living forms that have been studied. *Crocodylus* has a longer snout than *Alligator*, and thus the anterior parts of the nasal cavity are relatively longer, but the differences are very slight. *Melanosuchus* closely resembles *Alligator* in all regards. The nasal anatomy of *Gavialis* is known only from a figure in Brühl (1886); it appears to have the same pattern as the other genera. However, the crocodilian pattern is quite different from that of any other group, and the homologies of several of the structures are debated.

Thus the crocodilian sinus maxillaris is a sinus within the maxilla, but is almost certainly not phylogenetically related to the mammalian sinus maxillaris. Both the other extracapsular sinuses, the recessus caviconchalis and the hintere laterale Nebenhöhle (e.g. Bertau), are also within the maxilla and have been proposed as the true homolog of the mammalian sinus. However, since paranasal sinuses are not of frequent occurrence in reptiles and are absent in pelycosaurs (A. S. Romer, personal communication), it seems almost certain that these cavities arose independently in crocodilians and mammals. Therefore, there are probably no strict homologies between the sinuses of these two groups. The hintere laterale Nebenhöhle of crocodilians has also been compared to the orbital sinus of birds, but here again there is no general agreement (see Matthes, 1934). The homologies of the conchal formations will be considered in the general discussion at the end of this paper.

A final consideration is the extent of the sensory areas of the crocodilian nose. Since the only relatively mature material used in the present study was grossly dissected, no original observations were made on this point. In general, as in the other reptiles, the posterodorsal half of the cavum nasi proprium is said to be sensory and the anteroventral part is not (Bertau, 1935, and others).

Early Embryology. The only previous paper on the early embryology of the crocodilian nose is that of Voeltzkow (1899), who describes a series of embryos of *Crocodylus niloticus* (*C. madagascariensis* of Voeltzkow) in some detail. Unfortunately, the sizes of the embryos are not given. Rough approximations can be obtained from the figures of the entire heads, dividing the length of the figures by the stated magnifications; such are used in the following discussion.

Voeltzkow, in a series of excellent figures (his plate IX), shows the external appearance of the nasal placodes and pits. In the stages of headlengths 2.1, 2.4, and 4.0 mm. they appear as small circular depressions with a slightly raised rim, first on the lateral and then the ventrolateral surface of the snout, fairly near, but not at, its anterior end. In larger embryos (6.0 and 4.4 mm. headlength[1]), the nose has become a slit which is rounded anteriorly, and posteriorly passes into the developing mouth cavity. It is ventrolateral and nearly terminal in position. Embryos with headlengths of 5.8 and 6.5 mm. have the nares externi and choanae separated by the fusion of the lateral and medial nasal processes. The nares externi are nearly vertical slits which lean slightly towards the midline at their dorsal ends. At this stage the secondary palate has not yet formed.

In the text, Voeltzkow describes briefly the early nasal embryology, using very diagrammatic drawings of transverse sections of several stages. These stages agree quite closely with those seen in *Alligator* in the present study, and will be mentioned further in the following descriptions.

The early embryology of the nasal cavities of *Alligator*, which has to my knowledge never before been studied, is here described in some detail. In the youngest embryos displaying any nasal differentiation, there are distinctly thickened nasal placodes, covering most of the sides of the snout anterior to the eyes.

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[1] The former of these embryos seems very large for its stage of development; either there is considerable variation, or Voeltzkow's figure 70 on plate IX is mislabeled as to magnification.

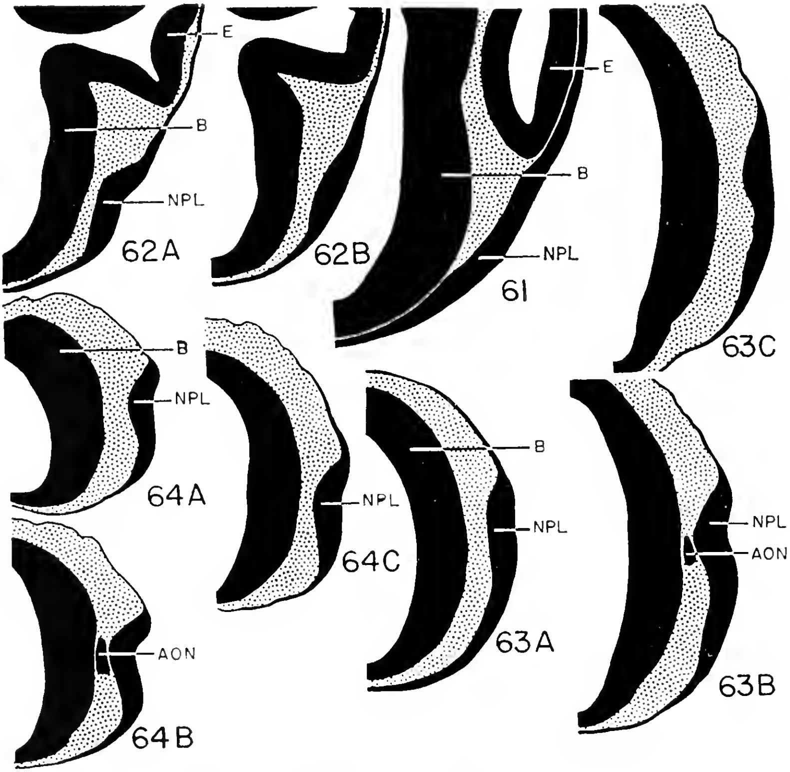

Figure 61. *Alligator* 059 (?; AMR). Frontal section through the nasal area (section 15). 115x.

Figure 62. *Alligator* I-7 (?; AMR). Frontal sections through the nasal area. A, section 394; and B, 10 sections ventral to A. 77x.

Figure 63. *Alligator* I-14 (?; AMR). Transverse sections through the nasal area. A, section 136; B, 6 sections posterior to A; and C, 5 posterior to B. 77x.

Figure 64. *Alligator* L-20 (?; AMR). Transverse sections through the nasal area. A, section 264; B, 9 sections posterior to A; and C, 8 posterior to B. 77x.

They are still convex, conforming to the general outline of the head without any indentation. The placode is up to three nuclei in depth in one embryo, and five in a second, while the general body epithelium has but a single layer. There is, however, no histological distinction between the placodal and general body epithelium other than the thickness, and the two merge without any sharp boundary. Anteriorly, the transition is sharper than elsewhere. The epithelium possesses a clear basement membrane throughout. The major difference between the placodes of the two available series of this stage is in their relation to the brain: in the younger the anterior half of the placode is in direct contact with it (see Fig. 61), while in the older, mesodermal tissue has pushed forward and separated these two structures. In the latter embryo a small bud of cells is formed which runs from the center of the placode towards the brain. It represents the anlage of the olfactory nerve, and its form and subsequent development are described in the section on that nerve.

The placode next starts to invaginate to form the nasal pit. Early stages in this process, however, are better described as indented placodes than pits (see Figs. 62 and 63). The indentation is a shallow symmetrical cone. The placodes are slightly more restricted in area than in the preceding stage, being ventrolateral and subterminal on the snout. Voeltzkow's (1899) earliest embryo (2.1 mm. headlength; his fig. 1, p. 43) is of this or possibly the following stage.

There is still no histological differentiation of nasal versus general body epithelium except in thickness. The indented section of the placode, somewhat dorsal to its center and hence lateral in position, shows five or six layers of nuclei, while most of the remainder of the placode is two or three layers; the general body epithelium remains a single layer. Thus the transition is sharpest dorsally and most gradual ventrally, with the anterior sharper than the posterior; however, in no case is there any definite boundary. The basement membrane is distinct under the placode, but elsewhere it disappears in the older series. This membrane is not smooth, but has low gentle undulations.

The next stage is that of a small conical nasal pit which is still quite symmetrical without any noticeable dorsal extension (see Figs. 64 and 65). Its depth is equal to its width in the youngest series and, again, in the oldest; it is less in the intermediates, due to a greater growth in area than in depth for a short period. Although the placode does not greatly increase in size, the much thickened and indented portion comes to assume a larger percentage of the total area, with only the ventral third remaining slightly thickened. Histologically, there is still little differentiation. All the nuclei appear the same, but the cytoplasm stains more densely in the epithelium, both nasal and

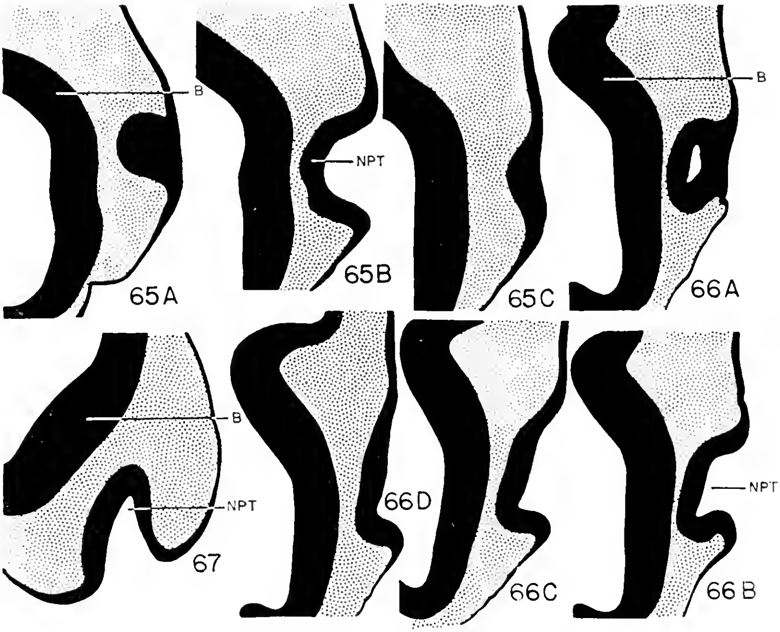

Figure 65. *Alligator* X-no. 4 (?; AMR). Frontal sections through the nasal area. A, section 132; B, 4 sections ventral to A; and C, 7 ventral to B. 42x.

Figure 66. *Alligator* F-7 (?; AMR). Frontal sections through the nasal area. A, section 107; B, 3 sections ventral to A; C, 7 ventral to B; and D, 8 ventral to C. 31x.

Figure 67. *Alligator* F-9 (?; AMR). Transverse section through the nasal area (section 118). 31x.

epidermal, and the brain than in the intervening mesodermal tissue. The walls of the nasal pit are everywhere the same, with a slight tendency for the concentration of nuclei toward the deep surface, but with more mitotic figures peripherally.

The nasal pit next starts to extend dorsally, probably in part by further invagination, and certainly in part by the anteroventral extension of the lateral nasal process (seitliche Nasenfortsatz of the German literature). Figure 66 shows this stage in frontal section and Figure 67 gives some idea of the height of the pit, although the section is not perfectly transverse. The pit now extends slightly anterior as well as dorsal to the naris so that in frontal section it appears as a parallelogram with the acute angles approximately 45 degrees. At the ventral end, the posterior wall tends to become more confluent with the epithelium of the head than anterodorsally, and the nasal pit thus appears more as a simple notch when seen in section. The naris is lateral anteriorly, but at its posterior end is on the ventral surface of the snout; the pit therefore appears deepest posteriorly.

Histologically, there are few changes. The walls of the pit are evenly thickened and are, in one case, up to ten nuclei deep. The boundaries of the nasal epithelium are fairly sharp, based on thickness, but are marked by no other changes. Posterior to the nasal pit, the epidermal epithelium is now two nuclei thick; elsewhere it has a single layer. The growth of the pit and also of the brain is reflected in the approximation of these two organs, with considerably less intervening mesodermal tissue than in the preceding stage.

With the further growth of the nasal pit and the lateral nasal process, the pit becomes a narrow but deep, dorsally directed groove on the side of the snout (see Fig. 68). Voeltzkow's (1899) *Crocodylus* embryo of headlength 2.4 mm. (his fig. 2, p. 43) is of this stage. In *Alligator* the pit still has its apex pointed; it is more rounded in Voeltzkow's *Crocodylus*. The naris is widely open at its anterior end where it is lateral and subterminal, but posteriorly it becomes a narrow slit along the lateral edge of the ventral surface of the snout. Anteriorly and posteriorly, the walls of the pit are very nearly vertical, as is the lateral wall, while the medial slants slightly laterally. The anterior portion of the pit is slightly curved when seen in transverse section, with the convexity medial. The lumen is widest ventrally and anteriorly, but is, in most cases at least, open throughout.

Histologically, there is some differentiation, but it is not great. The epidermal epithelium of the head is now thicker, having two or three layers of nuclei. In at least one series, it has a distinct basement membrane. There is thus no sharp boundary between it and the nasal epithelium, although the latter is everywhere considerably the thicker. A major change is the development of differences between the sensory and non-sensory portions of the nasal epithelium. The former, the dorsal third of the pit, especially anteriorly and medially, is thicker and lacks a basement membrane. The non-sensory portion has such a membrane and shows a tendency for the concentration of its nuclei toward the exposed, primitively lateral surface. This tendency is also

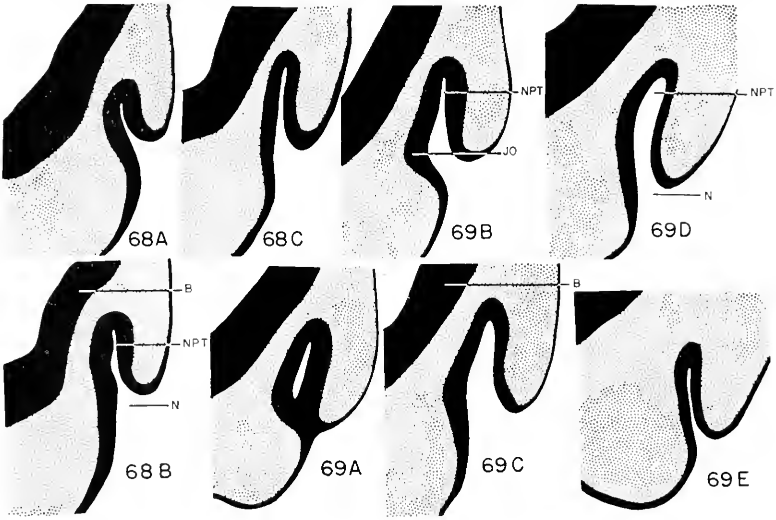

Figure 68. *Alligator* X-13 (?; AMR). Transverse sections through the nasal area. A, section 4 on slide M; B, 9 sections posterior to A; and C, 11 posterior to B. 36x.

Figure 69. *Alligator* H-22 (?; AMR). Transverse sections through the nasal area. A, section 335; B, 4 sections posterior to A; C, 21 posterior to B; D, 14 posterior to C; and E, 11 posterior to D. 36x.

present, but far less marked, in the sensory areas. In the older series of this stage there is a second area of much thickened epithelium: a band running along the anterior part of the medial wall approximately half way between its dorsal and ventral ends. This band is in the position where Jacobson's organ typically develops and apparently represents the earliest anlage of that organ. However, at this stage it shows no indentation; in fact, it may bulge out into the lumen of the pit.

Another embryo represents essentially the same stage, but the development of Jacobson's organ renders separate description necessary, and is shown in Figure 69. The pit is as in the preceding stage, although the lumen is slightly wider than before. The size of the lumen seems to vary from series to series and may represent either very small differences in distortion in the sectioning or a somewhat variable feature of the nasal embryology in this species. Histologically, there are no changes, thus still no nuclear differentiation. In the nasal epithelium, the layer of nuclei closest to the lumen shows many mitotic figures. Jacobson's organ is represented by a distinct, though very shallow, groove along the medial wall of the nasal pit in the same position as the thickened band of epithelium noted above (see Fig. 69B). It is apparent only in the anterior half of the nose. Since it is in the proper location, shows the expected form, and gives rise to many nerve fibers, there seems little reason to doubt that this groove is the Jacobson's organ of *Alligator*. The literature on

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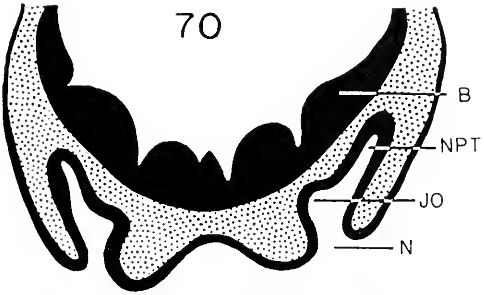

Figure 70. Transverse section through the nasal area of a *Crocodylus* embryo (after Voeltzkow, 1899). 26x.

this problem is reviewed separately, however, and further discussion is included there.

Voeltzkow (1899) describes two *Crocodylus* embryos, head-lengths 4.0 and 6.0 mm. (his figs. 3 and 4, p. 44; see second paragraph of this section), which are of a comparable stage. The first of these possesses a Jacobson's organ very like that just described, but much more conspicuous (see Fig. 70). Whether this difference in size is a generic one between *Crocodylus* and *Alligator* or merely due to Voeltzkow's having obtained an embryo showing more nearly the maximum development of the organ than any of those used in the present study, I am unable to say. In the very slightly more developed series shown in his figure 4, Jacobson's organ seems to have disappeared almost completely, although there is still a very slight indentation in the

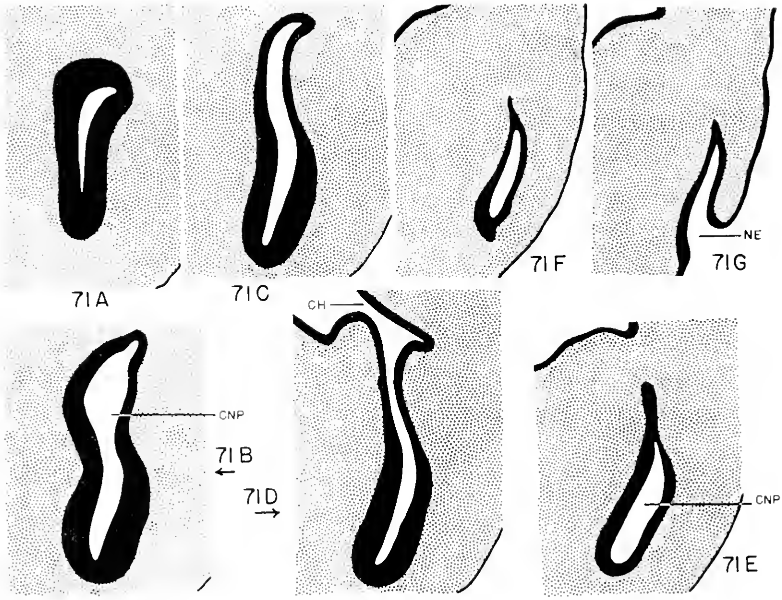

Figure 71. *Alligator* 24 (10.0; AMR). Frontal sections through the nasal area. A, section 367; B, 32 sections ventral to A; C, 15 ventral to B; D, 12 ventral to C; E, 12 ventral to D; F, 11 ventral to E; and G, 7 ventral to F. 42x.

same area. It appears, however, to have thinner epithelium than in the preceding series.

Two other differences between these series and the *Alligator* material are: the greater development of the lateral nasal process in *Crocodylus*, and the development of a dorsomedial outpocketing of the nasal epithelium in the posterior part of the nose in Voeltzkow's material. There is nothing corresponding to the latter in the *Alligator* embryos studied. This outpocketing produces an apparent medial pocket; however, it seems dorsal to Jacobson's organ. Whether or not the two are connected is not mentioned and cannot be told from the figures. On the basis of comparison with the *Alligator* material and Voeltzkow's figures of later stages, it appears unlikely that they are related.

The last series to be described here is shown in Figure 71. Unfortunately the plane of section is rather oblique, so that in all the figures the lateral edge of the section is slightly ventral to the medial. The nose is still a fairly simple pit, but the lateral and medial nasal processes have fused to separate the naris externus from the primitive choana. This is apparently a very recent occurrence; a double layer of epithelium with no intervening cavity extends about half way ventrally from the nasal cavity toward the roof of the mouth to mark the line of fusion. Both nares and choanae are widely open and well ventral. The concha (= middle concha) is starting to form laterally; it is directed somewhat posteriorly so that the nasal cavity, especially dorsally, has a lateral twist at its posterior end. The nasal pits are farther apart posteriorly than anteriorly (the choanae are widely separated at this stage), and each is slightly curved with the convexity lateral. There is no Jacobson's organ visible in this series; a transverse section might show a small remnant, but this seems unlikely, since there is no increase in the width of the lumen in the region where it would be expected. The lumen is widest about midway dorsal at its posterior end, but there is no sign of any dorsomedial projection into it at that point. Histologically, the only real differentiation within the nasal epithelium remains that of thickness. It is thickest dorsally and medially, and thinnest at the choanae.

Voeltzkow's (1899) 4.4 and 5.8 to 6.5 mm. headlength stages (his figs. 5 and 6, pp. 45 and 46) are comparable. The former is slightly less developed than the series described above; in his figure, the nasal processes do not appear to be fused as yet, although the lumen is obliterated ventrally between the nares externi and the choanae. The second embryo seems to be at almost exactly the stage shown in Figure 71. Both *Crocodylus* embryos appear to have a somewhat narrower lumen than that of the *Alligator* studied, but this is a very minor difference. A far greater one concerns the development of the dorsomedial outpocketing mentioned above. In Voeltzkow's figure 5b it has become very prominent so that the nasal cavity is Y-shaped. Such a structure is not figured in his succeeding stage. The medial arm of the Y appears to be the pocket considered to be Jacobson's organ by Shiino (1914) in his *Crocodylus* embryo of headlength 5 mm. (see his fig. 24, p. 319); this is an older embryo and is discussed in the section on Jacobson's organ. However, in Voeltzkow's figure 5 there is no sign of the more anterior and ventral groove here considered to represent that organ. Whatever this outpocketing may represent, it is apparently present only for a very limited time in *Crocodylus* and probably not at all in *Alligator*, although it could be formed in the latter genus for so short a period that none of the embryos used in the present study possessed it.

Later Embryology. The later stages of the nasal embryology have been very well described in several crocodilians, and no descriptions are necessary here. Early accounts include those of Rathke (1866), Meek (1893 and 1906), Reese (1901), and Shiino (1914). More important are the detailed studies by Meek (1911; *Crocodylus*) and Bertau (1935; *Alligator*, *Melanosuchus*, and *Crocodylus*); both of these papers include excellent figures of models of several stages. Finally, Fuchs (1908) described the formation of the ductus nasopharyngeus and secondary palate of *Crocodylus* in detail. For the present investigation, eleven *Alligator* embryos were studied; they did not differ appreciably from those figured and described by Bertau (1935). The later stages show a gradual development of the complex pattern of conchae and recesses and the long ductus nasopharyngeus found in adult crocodilians.

Jacobson's Organ. The literature concerning Jacobson's organ in the crocodilians is quite extensive. However, there is much disagreement, especially concerning the earlier stages, as to what structures, if any, represent the rudiment of this organ.

The earlier descriptions of crocodilian noses do not mention Jacobson's organ at all, and neither the texts nor the figures give any indication of one. Such works include those of Rathke (1866) who studied a variety of forms, Gegenbaur (1873) who studied a young *Alligator*, and Solger (1876) who employed *Crocodylus*. Beard (1889) was unable to find any trace of Jacobson's organ in an embryo crocodile, and Hoffman (1879-1890) cites its absence as a major difference between crocodilians and lizards.

However, in 1891 Howes started a great search for this organ by reporting a small vesicular structure (which he thought might represent a vestigial Jacobson's organ) at the anterior end of the vomer in a young *Alligator*. He was led to consider the possibility of finding such a vestige by a study of the skull of *Melanosuchus* in which the vomers extend farther anteriorly than in the other crocodilians and contain a small cavity. From a comparison with mammals, Howes believed that this cavity should contain Jacobson's organ. Unfortunately, he lacked preserved material of *Melanosuchus* in which to check this.

The first description of Jacobson's organ in embryonic crocodilians is that of Sluiter (1892). In his 20 mm. *Crocodylus*, the nasal cavity was, amazingly, exactly like that of a lizard with a very well developed Jacobson's organ opening into the roof of the mouth just anterior to the choana. In a younger stage (16 mm.) he was also able to find the anlage of that organ.

Meek (1893), in the first of a series of papers, presents a rather confusing picture, based on a series of *Crocodylus* embryos, in which he admits that, had it not been for Sluiter's paper of the preceding year, he would consider Jacobson's organ absent. In his youngest stage (5.0 and 5.75 mm. headlength), he considers a very small depression in the anteroventral wall of the ductus nasopharyngeus to represent a rudimentary Jacobson's organ, although he gives no reasons for this conclusion. In a slightly larger embryo (7.0 mm. headlength), he describes what appears to be an entirely different structure as Jacobson's organ. It is a slight fold enclosing a small space on the medial wall of the cavum nasi proprium. An embryo of headlength 7.75 mm. showed no trace of this, nor was he able to find any remnant of the organ in still larger series. He concludes that at least some trace of Jacobson's organ is probably present in all crocodilians, but that in *Crocodylus* it is present only for a very short period during development.

Röse (1893a) clarifies the situation somewhat. His rather extensive *Crocodylus* material included much of that used by Meek and Sluiter. By studying organs other than the nose, he was able to show that the critical embryo (20 mm.) of Sluiter's was, in fact, not a crocodile at all, but a lizard. In the *Crocodylus* embryos, he recognized the structure which Meek (1893) considered to be Jacobson's organ, but denied that it had any relation to that organ.

Röse, instead, describes a small pit on the posterodorsal wall of the ductus nasopharyngeus (which was noted in passing by Meek) as the true anlage of Jacobson's organ. It is shown in Figure 72 (his fig. 1). This pocket was found in embryos of from 5.0 to 12 mm. headlength and was also macroscopically visible in a young crocodile (headlength 42 mm.). No reason is stated for his designation of this pit as Jacobson's organ other than its general position near the primitive choana.

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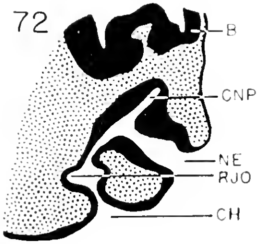

Figure 72. Sagittal section through the nasal area of a 5 mm. headlength *Crocodylus* embryo, showing the pocket which Röse (1893a) considers to represent Jacobson's organ (after Röse, 1893a).

Von Mihalkovics (1898), having no material of crocodilians available, used Röse's (1893a and b) descriptions, but reached very different conclusions. He calls attention to the dorsomedial point of entrance of the duct of the glandula nasalis externa into the nasal cavity, and postulates that the nasal end of this duct may be the true rudiment of Jacobson's organ in this group.

In his detailed study of the early embryology of the crocodilian nose, Voeltzkow (1899) never mentions Jacobson's organ at all.

However, an early stage of *Crocodylus*, shown in Figure 70 (his fig. 3a), has a distinct concavity in the ventral part of the median wall of the nasal pit which many later workers consider to be the anlage of Jacobson's organ. In later stages, after the nasal processes have fused, this small medial deepening apparently disappears; it is certainly not evident in Voeltzkow's figures of later stages.

Probably the most generally cited and accepted ideas on Jacobson's organ in the crocodilians are those of Peter (1901). His descriptions are based primarily on Voeltzkow's (1899), although most of the early works are cited. Peter was the first to call attention to Voeltzkow's figure 3a which he believed to show this organ "deutlich in typischer Lage und Form" (p. 43). Sluiter's (1892) and Röse's (1893a) theories are definitely denied and some doubt is expressed concerning Meek's (1893), although in the last case Peter could not be certain. His doubt is based in large part on the absence of sensory epithelium in the area, which he considers an important, if not diagnostic, characteristic of Jacobson's organ.

Reese (1901) describes very briefly one moderately well developed stage in *Alligator*, unfortunately without giving the size. He apparently accepts Röse's (1893a) identification of Jacobson's organ which is here described as a tubular mass of cells, without a lumen for most of its length. This so-called Jacobson's organ is made up of "typical mesoblast cells" (p. 462) similar to those of the ductus nasopharyngeus. It runs posteroventrally medial to the nasal cavity and enters the dorsal surface of the ductus. From the figures it would seem that the point of juncture is well posterior to the separation of the ductus nasopharyngeus from the cavum nasi proprium — thus in the portion which, according to Fuchs (1908), represents part of the primitive palatal rather than the nasal wall. The length of this organ seems far greater than that reported by Röse (1893a) or that of the embryos used in the present study.

Dieulafé (1904-1905) had available only an adult *Crocodylus;* he could find no trace of a Jacobson's organ. In his review of the literature he ventures no opinion on the various suggested embryonic anlagen.

In his paper on palatal embryology, Fuchs (1908) makes only passing reference to the absence of Jacobson's organ in crocodilians, although he does mention the possibility of an anlage of this organ in early stages, citing Voeltzkow's figure mentioned above. His material was mainly late stages of *Crocodylus* from Voeltzkow's collection.

Zuckerkandl (1910a), in connection with his studies on the olfactory bulbs, searched for Jacobson's organ in both *Alligator* and *Crocodylus;* he found no trace of it nor of the associated nerves and accessory olfactory bulb. However, he did not have early embryonic stages. In another paper, Zuckerkandl (1910b) discusses the various earlier accounts briefly, dismissing all reports except that of Peter (1901) based on Voeltzkow's figure. He considers further investigation to be necessary before crocodilians can be thought definitely to possess even a transitory anlage of Jacobson's organ.

The next major paper is that of Meek (1911); the main points of this paper are also present in abstract form in his note of 1906. In this paper he presents better figures of the same stages as were used in his earlier (1893) paper and rather cautiously reiterates his former conclusions. The figures of his 5.0 mm. headlength stage (his nos. 5 and 6, p. 363) show a small pocket in the floor of the cavum nasi proprium, just anterior to the ductus nasopharyngeus, which he calls Jacobson's organ. He then rather qualifies his conclusion (p. 364): "At all events, whether this be the representative or not of the primitive median moiety of the nose, there is nothing else at this stage which can be identified with a Jacobson's organ." It is in the non-sensory area. However, the same figures also show a small pocket in the anterior wall of the ductus nasopharyngeus which appears to me more like the one described and figured in his earlier paper. He could find no trace of the organ in embryos of headlength 12.0 mm. or larger. Meek supported Peter's (1901) conclusions, and admits that further study is needed to show whether or not the pit described by him has any relation to that figured by Voeltzkow.

Shiino (1914) is concerned primarily with the development of the skeletal structures in the head, but does include a little information on the nose. In a 5.0 mm. headlength *Crocodylus* he briefly describes and figures a medial pocket which he believes to be that figured by Voeltzkow (1899) and mentioned by Peter (1901). Shiino considers it the true Jacobson's organ. The orientation of his figure (no. 24, p. 319) is rather confusing, but the embryo is considerably more advanced than Voeltzkow's (the nasal processes have already fused), and the pocket appears to be the more posterior one shown by Voeltzkow and discussed in the section on the early embryology of the nose. Shiino was apparently unable to find any sign of Jacobson's organ in more advanced embryos.

Nemours (1930) studied a young (155 mm. in length) *Alligator* and found no trace of a Jacobson's organ. He mentions its absence in both young and adult material although he cites only the single specimen.

Matthes (1934) very briefly reviews all the earlier literature. Jacobson's organ is said to be definitely absent in the adult crocodilians. After disagreeing with the opinions of Sluiter (1892), Meek (1893), Röse (1893a), and Reese (1901), Matthes presents Peter's (1901) and Shiino's (1914) work, concluding (p. 921), "Danach lässt sich nicht mehr bezweifeln, dass sehr junge Krokodilembryonen ein Jacobsonsches Organ in typische Weise anlegen." However, he describes as still unknown the fate of this anlage in later embryos. Similar views are expressed in other recent reviews, e.g. von Wettstein (1954) and Gérard (1954).

Finally Bertau (1935) was unable to find Jacobson's organ in any of his material (late embryos of *Alligator, Melanosuchus*, and *Crocodylus*). He disagrees with the ideas of most earlier workers, and cites Peter's (1901) opinions without comment, concluding that it is doubtful that crocodilians possess any Jacobson's organ.

Of the *Alligator* embryos used in the present study, only one possesses an anlage of Jacobson's organ (see Fig. 69), although two slightly younger series show a slight thickening of the epithelium in the same area. This anlage, as described in the section on early nasal embryology, is definitely the same as that figured by Voeltzkow (1899), and first considered to be Jacobson's organ by Peter (1901). There is no trace of it in later stages. Since it is in the usual position, has the usual form, and gives rise to a large part of the olfactory nerve in early embryos, there seems to be no reason to doubt the homology. The organ is thus formed in early stages of *Alligator*, as in most other amniotes, as an inpocketing of the medial wall of the nasal pit, but it never develops to any great extent. In fact it very rapidly disappears. The situation would appear to be the same in *Crocodylus*, judging from Voeltzkow's (1899) figures. There, too, it is not shown after the lateral and medial nasal processes have fused.

None of the other structures described as Jacobson's organ in crocodilians appears to have any relation to that organ. The small vesicular structure found by Howes (1891) is reported only by him and from nearly adult material; what it may represent I do not know, but it seems unrelated to any of the various pits described in embryonic material.

Meek (1893, 1906, and 1911) presents what seem to be several structures. The fold in the medial wall of the nose (his 7.0 mm. headlength stage) has been reported by no other workers, and it is possibly if not probably formed by folding or breakage of the sections. A small depression does occur, in some series, in the ventral surface of the cavum nasi proprium or ductus nasopharyngeus, but none is present in the stages immediately following the disappearance of the typical anlage, so that aside from its being in the general area where Jacobson's organ might be expected, there is nothing to support such an identification. The same argument holds for the dorsal pocket in the ductus nasopharyngeus described by Röse (1893a) and Reese (1901). This last also appears to be posterior to the primitive nasal tissue of placodal origin, which makes the suggested homology most unlikely.

Von Mihalkovics' (1898) suggestion that the medial duct of the glandula nasalis externa may represent the organ in question is not supported by embryological study, for, aside from its lack of relation to the early anlage, the duct and, in fact, nasal glands in general are formed quite late in the development of the nose while Jacobson's organ is typically present in very young stages. Also the duct arises from the wall of the vestibulum, not the cavum nasi proprium as would be expected if it represented Jacobson's organ.

Finally, the posteromedial pocket which Shiino (1914) describes must be considered. As mentioned in describing Voeltzkow's (1899) *Crocodylus* embryos, this pit does not seem to be connected with the structure here considered to be Jacobson's organ. It does not occur in the *Alligator* material studied. While it is possible that this indentation may represent a part of that organ, it seems unlikely on the basis of Voeltzkow's figures: if it should, *Crocodylus* embryos retain the anlage of Jacobson's organ longer than *Alligator*, but still lose it completely early in their development.

NASAL GLANDS

General. All terrestrial vertebrates possess various glandular outgrowths of the nasal epithelium. Fish typically, if not universally, lack such glands (Broman, 1939, believes that lungfish may possess an embryonic rudiment of a nasal gland). Those tetrapods which are secondarily adapted for an aquatic, and especially for a marine, life tend to lose the glands, as is seen in many neotenous urodeles, marine turtles, some sea snakes, and whales. Birds, however, do not follow this pattern; in that class, typically, the nasal glands are most developed in marine forms, and salt water can be shown to stimulate the development of the major gland (Schildmacher, 1932; Marples, 1933; and Technau, 1936). A recent note by Schmidt-Nielsen et al. (1957) states that in *Phalacrocorax* this gland actually functions to excrete excess salt.

The glands are very variable, even within orders and smaller taxonomic units, and since they do not relate closely to the problem of Jacobson's organ, no detailed treatment of them will be given here. However, in view of some theories as to the homology of their ducts with Jacobson's organ, in certain forms (von Mihalkovics, 1898), some consideration of their nature and development is necessary.

Glandula Nasalis Externa. The glandula nasalis externa (= glandula nasalis lateralis, g. n. dorsalis, g. n. superior, or sometimes simply glandula nasalis) is, in all four Recent orders of reptiles, the largest of the nasal glands, and generally the first to appear in the ontogeny of the animal. It is here termed the external nasal gland as it lies outside of the cartilaginous nasal capsule, although generally within the dermal skull roof, in most forms; it may be either dorsal or lateral (or even, rarely, posterior) to the nasal cavity.

In all the forms which were studied for the present investigation, this gland arises as a solid rodlike outgrowth of the posterior or dorsolateral wall of the vestibulum. Although it is the first of the nasal glands to develop, there is never any indication of the anlage until well after the fusion of the nasal processes. The exact stage at which it first appears has already been noted in the sections on the nasal embryology of the various groups. The rodlike anlage of the gland increases in length, growing posteriorly and, in most cases, somewhat dorsally. Its further development is primarily a matter of repeated branching near its posterior end, thus forming a mass of tubules which make up the body of the gland. These findings are in agreement with the observations of Born (1883) and Röse (1893b) who studied the development of the glandula nasalis externa in *Natrix* and *Crocodylus* respectively; there appear to be no other embryological studies on this gland in reptiles.

Histologically, the earlier stages in the development of the gland resemble those of the vestibulum. In older embryos, the duct is rather variable, but generally possesses rather low columnar epithelium; although most commonly simple, it may be low stratified. The distal tubules have simple cuboidal epithelium with very large circular nuclei. In very late embryos, the epithelium of the secretory tubules becomes high columnar, and the nuclei tend to be basally located. There is little lumen in either the gland or its duct in most of the embryos, and never in the material studied was the duct open throughout its length. Presumably the lumen is formed and the gland becomes active only at the time of hatching.

In most adult turtles, the glandula nasalis externa forms a single middorsal plate lying between the nasal capsule and the skull roof; in sea turtles, both cheloniids and *Dermochelys*, it is completely absent (Nick, 1912, and Fuchs, 1915). Judging by the few forms which have been studied, this gland is larger in terrestrial forms, such as *Testudo*, than in aquatic genera, such as *Emys*. The gland possesses, on either side, a single duct which enters the dorsolateral wall of the vestibulum well posteriorly, hence in exactly the same position as in the embryonic material which has been studied. Studies of the adult structure of the gland include those of Seydel (1896; *Testudo* and *Emys*), Nick (1912; *Chelydra*), and van der Merwe (1940; *Pelomedusa*). Hoffmann (1879-1890) also mentions this gland in most of the forms which he studied, but his findings with respect to nasal glands do not always agree with those of more recent workers.

The only description of the external nasal gland of *Sphenodon* is that by Hoppe (1934). He states that the duct runs posterodorsally from the posterolateral surface of the vestibulum, very close to the boundary of that area with the cavum nasi proprium. Posteriorly, its few branches form a fairly compact mass embedded in the connective tissue lateral to the concha anterior. Pratt (1948) mentions only that it is much less highly developed in *Sphenodon* than in most lizards.

In snakes, the prominent glandula nasalis externa is an oval mass lying lateral to the nasal cavity, between the nasal capsule and the skull roof. It is almost universally present in this suborder; of the over fifty genera which have been examined, only one is said to lack the gland completely. This is *Pelamis* (Kathariner, 1900), a hydrophid, but its absence is not typical of the sea snakes since Kathariner (1900) and Smith and Bellairs (1947) have found it in three other genera of that family. Papers considering the structure of this gland in snakes include almost all of those cited in the discussion of the nasal anatomy of snakes and that of Smith and Bellairs (1947). Other works mention it, but do not add much information. There is considerable variation in the size of the external nasal gland, but the variation does not show any obvious relationship to either habits or phylogenetic groups. When the gland is large, it typically has a lobe lying within the cavity of the conchal cartilage; this lobe is lacking in forms with smaller glands.

The most detailed description of the histology of this gland in snakes is that by Reese (1925). Although he considers it to be acinar, other workers, such as Baumeister (1908), call it tubular. This difference is almost certainly one of terminology only: Leydig (1873) describes the gland as consisting of tubules whose ends are slightly swollen.

In most snakes, a single duct runs anteriorly from the body of the gland to enter the posterolateral wall of the short vestibulum, exactly as in *Sphenodon*. However, Baumeister (1908) states that in *Rhinophis* the duct enters the anteromedial glandular area which he terms the median nasal gland, and Smith and Bellairs (1947) mention, without listing genera, that there may be more than one duct from each external nasal gland.

Although the glandula nasalis externa of crocodilians was described in 1848 by Stannius, it has been little studied, and two authors (Hoffmann, 1879-1890, and Dieulafé, 1904-1905) have even denied its existence. The three papers which do treat it are those of Röse (1893b), Reese (1925), and Bertau (1935). As in other forms, the gland is an oval body lying dorsolateral to the nasal cavity between the nasal capsule and the skull roof. There may be either one or two ducts on each side which open into the vestibulum close to its junction with the cavum nasi proprium. One duct is generally posterolateral, and the other, which is apparently present in most cases, enters the posteromedial vestibular wall. The latter duct, to reach the medial side of the nasal cavity, passes dorsal to the anterior end of the cavum. The histology of the gland is much like that found in other reptiles (Reese, 1925).

An apparently similar glandula nasalis externa is found in most other tetrapods. It is present in all three orders of Recent amphibians, with the body of the gland forming a mass of tissue within the fenestra narina and with one or more ducts entering the lateral wall of the vestibular region (Matthes, 1934). The most detailed description of this gland in any amphibian is that given by Schuch (1934) who studied *Triturus*. In the birds, this gland is best developed in marine forms, as was noted above. It most often lies superficially in the orbital region (see Marples, 1933, and Technau, 1936, for detailed descriptions). There are two ducts on each side, one entering the lateral and the other the medial wall of the vestibulum, except in the Galliformes which possess only the medial duct. Although this pattern of two ducts is somewhat similar to that found in crocodilians, the two groups have probably developed the medial one independently; in birds the medial duct passes ventral to the cavum nasi proprium. The homology of the glandula nasalis externa in amphibians, reptiles, and birds is suggested not only by its position, but also by its innervation. Gaupp (1888) found that in all cases this is by the nervus externus narium of the ophthalmic ramus of the trigeminal nerve.

In mammals, Steno's gland is the major lateral nasal gland, and has generally been considered the homolog of the glandula nasalis externa as first postulated by Jacobson (1813). Peter

(1901) disagreed because he believed that Steno's gland developed from the cavum nasi proprium rather than from the vestibulum. Broman (1921) and Kangro (1928), however, state that the gland does arise from the vestibulum. Thus, although Steno's gland typically lies within the cartilaginous capsule, the homology as suggested by Jacobson seems probable.

Glandula Nasalis Medialis. A distinct median nasal gland is found in most turtles and *Sphenodon;* it is absent in all members of the Squamata and Crocodilia as far as is known.

In the embryos of *Emys* and *Chrysemys* which were used in the present study, the glandula nasalis medialis arises at approximately the same time as does the glandula nasalis externa or slightly later. Its anlage is first a solid rodlike process of cells projecting posteriorly or posteroventrally from the medial wall of the nasal cavity. In all the embryos it appears to arise from the vestibulum, but it is very close to or at the boundary of that region with the cavum nasi proprium. The pattern of further development and histology of this gland is identical to that already described for the glandula nasalis externa.

Studies of the adult anatomy of the median gland include those of Seydel (1896), Nick (1912), and van der Merwe (1940). It is absent in sea turtles (Nick, 1912, and Fuchs, 1915), but in the other forms which have been studied it forms a mass of tubules lying between the medial wall of the regio intermedialis and the nasal septum. In *Testudo,* where it is very highly developed, it may even reach ventral to the nasal capsule (Seydel, 1896); however, the gland is normally entirely contained within the capsule. Van der Merwe (1940) reports multiple ducts entering the nasal cavity in *Pelomedusa*, but other authors have found only one. In the adult the duct is said to enter the extreme anterior end of the regio intermedialis of the cavum nasi proprium rather than the vestibulum.

The glandula nasalis medialis of *Sphenodon* was first described by Hoppe (1934) and is also mentioned by Pratt (1948). In both Hoppe's material and the embryos used in the present study, the gland is an unbranched rod of cells running ventrally and slightly posterolaterally from the vestibulum. It joins the anteroventral surface of that structure well medially. Hoppe suggested that this rod was the homolog of the chelonian glandula nasalis medialis, and the embryology would appear to support such a view.

Gaupp (1888) homologized the glandula nasalis medialis of turtles with the median nasal gland of amphibians on the basis of their innervation by the nervus septi narium, a branch of the ophthalmic trunk of the trigeminal nerve. This homology has been generally accepted. In amphibians this gland normally lies ventromedial to the nasal cavity within the nasal capsule, with one or more ducts entering the unterer Blindsack (see Wiedersheim, 1879; Seydel, 1895; Schuch, 1934; and Matthes, 1934).

Birds lack a median nasal gland, although, as has already been noted, the glandula nasalis externa possesses a duct entering the medial wall of the vestibulum. Mammals, too, have no gland which would appear homologous to the glandula nasalis medialis of lower tetrapods, but many forms, especially rodents, do possess medially located glands, often in association with Jacobson's organ (Broman, 1921).

Bowman's Glands. Bowman's glands or glandulae olfactoriae are typically present in the sensory olfactory epithelium of all tetrapods except certain neotenous urodeles. The only reported exceptions to this rule occur in the hydrophid snakes in which Kathariner (1900) states that they are greatly reduced in number in *Pelamis* and totally absent in *Hydrophis.*

In all the forms studied for the present investigation, Bowman's glands appear only in very late stages in the development of the embryos. They are, in all cases, simple flask-shaped glands. The body of the gland is composed of simple cuboidal epithelium, while the very narrow duct is formed by squamous cells (see Figs. 77 and 82). Similar descriptions based on adult material have been given by Seydel (1896; *Emys* and *Testudo*), Osawa (1898; *Sphenodon*), and Macallum (1884; *Thamnophis*), although the latter two authors also report finding a few branched Bowman's glands. Hoffmann (1879-1890) also discusses these glands, mainly in turtles, but his descriptions do not agree well with those of other workers.

One very important point concerning the distribution of Bowman's glands was first made by Seydel (1896): they are common in the regio olfactoria of turtles but never found in the regio intermedialis. This observation has been confirmed by all later workers, and forms a major line of evidence for the homology of the chelonian regio intermedialis with the Jacobson's organ of other amniotes. Previously, Seydel (1895) had shown that the unterer Blindsack of amphibians, which he also considers the homolog of Jacobson's organ, lacks these glands. Bowman's glands have never been reported from the Jacobson's organ of the Squamata or mammals.

Bowman's glands similar to those of reptiles have been described in amphibians (Schuch, 1934) and birds (Ishihara, 1932). In the last class they are usually simple, but may be branched in certain forms. However, in mammals they are typically rather long and branched tubules which are quite contorted (Dogiel, 1886, Paulsen, 1886, and many others).

Other Nasal Glands. A variety of other small glands are associated with the nasal cavities in many forms. Such glands may occur in any part of the nasal cavity; for example, Ishihara (1932) reports goblet cells in the sensory epithelium of an owl, *Athene*, and Maeda (1954) describes numerous glands in the vestibulum of mammals. The great variety is best shown by Broman (1921) who studied mammals. Among the reptiles, glands other than those described above have been found in members of the orders Chelonia and Squamata.

Seydel (1896) found large numbers of pyriform and tubular mucous glands (*Schleimdrüsen*) in all non-sensory parts of the nasal cavities of *Testudo* and *Emys*. They may occur singly or in clusters. None of the embryos studied for the present work possessed these tubular glands which presumably develop only when the animal is hatched. However, as was noted in describing the nasal embryology, there are areas in which the epithelium does contain massed goblet cells. It is possible that these areas invaginate to form the tubules reported by Seydel; it is also possible that they are merely another type of glandular development not previously reported in turtles.

In snakes there is even greater development of glandular epithelium in the non-sensory portions of the nasal cavities. Late embryos of *Thamnophis* possess many folds or shallow crypts lined by goblet cells which have already been described. Macallum (1884), von Mihalkovics (1898), and Kathariner (1900) report similar structures in various colubrids and hydrophids.

At least certain adult snakes display slightly more complex glandular formations. In the *Storeria* which was used in the present study, many of the sections are unfortunately broken and difficult to interpret, but anteriorly there appear to be glandular tubules as well as crypts entering the cavum nasi proprium. Kathariner (1900) reports a similar condition in *Natrix*. Finally, Baumeister (1908) describes a saccular outgrowth at the anteromedial corner of the nasal cavity of *Rhinophis*. This he terms a median nasal gland or *Internasaldrüse*, with the latter term intended to differentiate it from the glandula nasalis medialis of turtles. In view of the variation in structure and the small sample which has been studied, no generalizations can be made concerning these glands, and further discussion is not profitable.

OLFACTORY NERVES

Early Development of the Olfactory Nerve. A large number of workers have studied the embryology of the olfactory nerves, but there is still much disagreement over many points. However, since none of the material used in the present investigation was specifically stained for neurological study, little can be added here. Thus, the following description is concerned primarily with those points which appear to be necessary for an understanding of the morphological significance of the various parts of the nasal cavity.

The embryology of the olfactory nerve can conveniently be divided into two main stages, which will be discussed separately. The first extends from the time of the initial appearance of the nerve until approximately the period at which the nasal processes fuse; during this stage the various elements forming the nerve become differentiated, or at least recognizable, and the basic histological pattern of olfactory innervation is established. Subsequently, during the remainder of the embryonic period, the nerve gradually assumes the gross anatomical pattern found in the adult.

In all vertebrates there appear to be two distinct elements in the anlage of the olfactory nerve; both originate from the epithelium of the nasal placode and migrate inwards toward the anterior end of the brain. First there are nerve fibers which grow out from cells remaining within the epithelium, and secondly there are cells which move medially along the course of the developing nerve. These two parts may be called the fibrous and cellular anlagen of the nerve, respectively. Since the appearance of Disse's paper of 1897, the fibrous anlage has almost universally been considered the source of the adult olfactory nerve. The fate of the cellular anlage is still disputed. Disse and many later workers (e.g. Pearson, 1941b) have believed that they become Schwann cells, but others, including Groth (1938), deny this.

A further source of confusion has been the nervus terminalis. This nerve also develops from the epithelium of the olfactory placode by inward migration. However, it is a ganglionated nerve, and cells migrate inward and then form fibrous processes.[1] Therefore, it is now generally assumed that any ganglion cells which are found to migrate inward from the nasal epithelium are to be considered part of the terminalis. As has been pointed out by Belogolowy (1909-1910) and Simonetta (1933), this means that birds possess at least a histologically recognizable remnant of the nervus terminalis even though it cannot be distinguished grossly — both these authors as well as Disse (1897), Tello (1923), Locatelli (1927), and Ishihara (1932) have reported ganglion cells along the course of the olfactory nerve in birds.

In the three reptiles studied in the present investigation, the olfactory nerve appears either just before the nasal placode first becomes indented (*Thamnophis* and *Alligator*), or immediately thereafter (*Chrysemys*). In all three forms there appears to be considerable variation in the timing of the development of this nerve relative to that of the nasal epithelium; although this is probably caused in part by the non-specific methods of staining, it is almost certainly partly natural. The cellular anlage of the nerve forms as a massive columnar ingrowth of cells from the nasal placode in *Alligator*. It extends to the brain, but is, in all the material studied, sharply separated from the brain by a distinct basement membrane (see Figs. 63B and 64B). Due

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[1] See Pearson (1941a) for a discussion of the embryology of the nervus terminalis.

to this darkly staining cellular mass, it is very difficult to see any nerve fibers in the earliest stages, although they are probably present as soon as the cellular anlage is formed. In *Chrysemys*, on the other hand, the fibrous anlage is the first formed. At all times there are nuclei among the fibers; presumably at least some of these have migrated inward from the nasal epithelium, but there is never a distinct cellular anlage separated from the surrounding mesodermal tissue by a basement membrane. *Thamnophis* shows an intermediate condition in which the cellular anlage is well formed (but not as large as in *Alligator*), and in which nerve fibers may be seen in most embryos.

After the placode has formed a nasal pit, the nerve appears predominantly fibrous throughout its length in all three forms. However, there are always abundant nuclei among the fibers; these are most abundant in *Alligator* and least in *Chrysemys*. The nerve arises from the medial surface of the nasal pit at or just anterior to its apex. It runs anterodorsally as well as medially to reach the wall of the telencephalon near the anterior end of that structure; the olfactory bulbs are not yet distinct. All the fibers of the nerve appear to enter the telencephalon at one point which is marked by the absence of any nuclei. This restricted enucleate zone gives the first indication of the myelospongium, the outermost layer of the adult olfactory bulb.

The subsequent changes in the structure of the nerve in the stages preceding the fusion of the nasal processes are concerned primarily with an increase in the area of the olfactory epithelium which gives rise to fibers. In *Chrysemys* the nerve arises from most of the median and dorsal walls of the pit, that is from the most conspicuously thickened areas of epithelium, and forms several small trunks which do not unite until they have run approximately half the distance to the brain. As soon as the anlage of Jacobson's organ is formed in *Thamnophis*, two portions of the olfactory nerve may be distinguished. The first arises from the dorsomedial wall of the nasal pit, especially anteriorly, and the second from the dorsal surface of Jacobson's organ. By the end of this period a few fibers may be seen entering the first trunk from the dorsolateral surface of the nasal pit. Finally, in *Alligator* the fibers arise from the dorsal half of the medial wall of the pit and, as in *Chrysemys*, may form several small trunks. Of especial interest is the fact that the small rudimentary anlage of Jacobson's organ, in the one embryo in which it is clearly present, gives rise to many nerve fibers, although in most cases few if any fibers may be found this far ventrally.

In none of the embryos studied could a nervus terminalis be recognized, nor is there any convincing evidence of specialization of the nuclei of the cellular anlage of the olfactory nerve. In some *Chrysemys* embryos these nuclei appear oval rather than circular, but such is not always the case. As was noted by Beard (1889) who studied *Natrix*, the nuclei may, in *Thamnophis*, be more abundant in that portion of the nerve which arises from Jacobson's organ; however this is not a constant feature, but shows considerable variation.

Later Development of the Olfactory Nerve. The major points of interest in the later developmental stages of the olfactory nerve concern the pattern of branching and the areas innervated; these must be described separately for the various orders. However, a few general statements may be made first. With the growth of the snout region, the olfactory nerve, which previously ran anteromedially, becomes medially and finally posteromedially directed in all forms. The nuclei found associated with the fibers of the nerve gradually change from a circular to a long oval or even fusiform shape, with their long axes paralleling the course of the nerve fibers. Their ultimate fate could not be determined from the available material. Finally, in the absence of specially prepared material, ganglion cells could not be recognized. On the basis of the studies on birds mentioned above, their presence may be suspected, but none could be demonstrated in the present investigation.

In *Chrysemys* embryos the pattern of distribution of the olfactory nerve remains very simple until the stage when the sensory epithelium of the regio intermedialis spreads onto the lateral wall. All the thickened portions of the epithelium, that is, the dorsal half of the lateral and entire medial wall of the nasal cavity, give rise to olfactory nerve fibers, while the thinner-walled ventrolateral portion does not. The fibers tend to be collected into two main divisions, the so-called lateral and medial trunks. Each of these "trunks" is generally made up of several small bundles, and frequently the separation between the two is not clear. The branches of the lateral trunk innervate the dorsolateral portion of the cavum nasi proprium, and those of the medial innervate the ventromedial portion. The dorsomedial area appears, in most cases, to be innervated by the larger lateral trunk. However, the lack of a distinct separation between the two trunks renders a definite generalization impossible; in many cases the medial trunk also appears to receive fibers from the dorsomedial area.

As the nerve approaches the olfactory bulb, or in earlier stages the surface of the telencephalon, the bundles become more closely associated, and may even form one massive trunk. In general, the fibers of the medial trunk first lie medial to those of the lateral, and then gradually assume a dorsomedial and finally a dorsal position as the bulb is reached. Thus the lateral trunk tends to enter the main olfactory bulb, while the medial leads to the accessory bulb. Despite references in the literature (e.g. McCotter, 1917) to the lack of any fiber interchange between the two trunks, the rather netlike appearance of the nerve as it nears the bulb makes such a definite statement impossible, at least in the material available for the present study.

A further problem with the nerves of this area concerns the nervus terminalis. The literature on this nerve is considered subsequently, but since the terminalis could not be definitely identified in the available materal, it is mentioned here. In most of the series there is a small band of fibers along the medial edge of the olfactory nerve which contains many nuclei. This band appears to run to the posteromedial end of the accessory olfactory bulb. Not until the latest embryonic stages were any fibers seen running posteriorly along the medial surface of the bulbs to the cerebral hemispheres. It appears probable that these fibers form the nervus terminalis, but I cannot be certain.

In more advanced embryos in which the lateral wall of the regio intermedialis bears thickened and presumably sensory epithelium, there is only one major change in the pattern of innervation. The lateral trunk of the olfactory nerve appears to be exactly the same as before; however, the medial now extends ventral to the nasal cavity, and then turns dorsally along its lateral margin, thus innervating the newly thickened ventrolateral areas. In only one case was there any indication that any branches of the lateral trunk might arise from the regio intermedialis; even in that embryo the fibers could not be traced with certainty, so that, in view of the situation in other embryos, such innervation seems very unlikely. This pattern was observed in both *Emys* and *Chelydra* as well as in *Chrysemys*.

There is some disagreement in the literature over the degree of distinctness between the lateral and medial trunks of the olfactory nerve. Seydel (1896) and Zuckerkandl (1910a) do not appear to consider the distinctness as marked, while Ogushi (1913) denies its existence. However, Johnston (1913), McCotter (1917), and Hanson (1919) describe them as completely separate at all levels. All these works are based on late embryos or adults of testudinid turtles except for those of Ogushi and Hanson which treat *Trionyx* and *Chelydra* respectively.

The most important differences in the previous statements on this nerve concern the course of the fibers arising from the lateral wall of the regio intermedialis. The pattern described above, in which the medial trunk receives branches which pass ventral to the nasal cavity from this area, was first reported by Seydel (1896). His findings were confirmed by Zuckerkandl (1910a), Johnston (1913), Ogushi (1913), and McCotter (1917). Such a pattern is denied by Hanson (1919) and Loew (1956). The former states, without further amplification, that the entire medial trunk arises from the medial wall of the nose. Loew studied *Emys*, and reports that the lateral portion of the regio intermedialis is innervated not by the medial trunk, but by other parts of the olfactory nerve, hence presumably the lateral trunk. The descriptions given by Loew are thus in marked disagreement with the observations made in the present study.

Finally, the olfactory nerve in a sea turtle has been described but once. Fuchs (1915) found that in *Eretmochelys* there are lateral and medial trunks comparable to those in other forms. The former innervates only the regio olfactoria (recessus superior posterior of Fuchs), while all the sensory epithelium of the recesses of the regio intermedialis sends olfactory fibers to the bulb through the medial trunk. The latter is composed of two main branches, one of which courses posterodorsally along the septum from the recessus ventralis; the other runs posteriorly from the recessus dorsalis.

The few available specimens of *Sphenodon* do not permit any detailed consideration of that form. In late embryos the olfactory nerve appears to arise by many bundles from the dorsal half to two-thirds of the cavum nasi proprium. These findings agree closely with those of Osawa (1898) and Hoppe (1934). Olfactory fibers also arise from the dorsal surface of Jacobson's organ; these fibers join bundles from the medial wall of the nasal cavity, so that a distinct vomeronasal nerve is not present. Wyeth (1924) was similarly unable to recognize a vomeronasal nerve in a late *Sphenodon* embryo (stage Q of the Dendy collection).

In *Thamnophis*, at the time of the development of Jacobson's organ, the olfactory nerve becomes divided into two trunks, or more exactly groups of bundles, of approximately equal size. One division of the nerve innervates Jacobson's organ, and is generally termed the vomeronasal nerve. However, the second part, which innervates the cavum nasi proprium, is referred to as the olfactory nerve. Since the vomeronasal nerve is now almost universally considered to be an integral part of the olfactory nerve, the latter term is used in two quite different senses. In order to avoid ambiguity, the nerve trunk innervating the cavum nasi proprium is here termed "the olfactory nerve proper."

In the younger embryos, the division into trunks is not very clear cut. The olfactory nerve enters the anteroventral surface of the brain as a rather irregular collection of bundles. The more lateral of these run dorsally from the anterodorsal portion of the cavum nasi proprium, while the medial bundles run somewhat anterodorsally to reach the olfactory bulb. Most of the medial division originates from Jacobson's organ, but many small branches from the posteromedial wall of the cavum nasi proprium run to, and enter the lateral side of the vomeronasal nerve. Since the bundles are, in the proximal third of their extent, frequently contiguous, it is impossible to determine whether there is any interchange of fibers between them.

In later stages, the two trunks become more distinct, with the olfactory nerve proper entering the anteroventral end of the olfactory bulb as a circular ring of from five to ten bundles. The vomeronasal nerve joins the accessory bulb posterodorsal to the main bulb; this nerve typically consists of only one to three bundles proximally. There is, during development, a gradual decrease in the number of small branches of the vomeronasal nerve which arise from the cavum, and they disappear almost completely with the formation of the capsule of Jacobson's organ.

Distally, fibers of the olfactory nerve proper arise from the entire sensory area of the cavum nasi proprium — that is, all of the regions previously described as having thickened epithelium. In early stages, the majority of the fibers are found anterodorsally, but they are soon present over the entire dorsal half of the cavum. The concha comes to be especially well innervated. These fibers are irregularly collected into larger and larger groups until the bundles are formed. The entire posterodorsal surface of Jacobson's organ gives rise to many nerve fibers, all of which run posterodorsally and pass out of the capsule of that organ at the posterior end of the septomaxilla. One very large and rather loose bundle is formed, which then runs dorsally and only slightly posteriorly. It therefore crosses the medial surface of the olfactory nerve proper. At the level of the anterior end of the olfactory bulb, the vomeronasal nerve turns posteriorly, and, as two or three bundles, runs along the medial wall of the olfactory bulb to reach the accessory bulb.

Despite a careful search for it, no trace of a nervus terminalis could be found. While it is possible that some of the fibers and nuclei within the olfactory nerve actually represent the terminalis, none of the fibers run posteriorly along the medial wall of the telencephalon posterior to the accessory olfactory bulbs. Therefore, although there could be cellular rudiments of it, there is no morphologically distinct nervus terminalis. This is in agreement with the findings of Bellairs (1942 and 1949), who reports the absence of that nerve in *Vipera* and *Varanus*. The literature appears to contain no other references to the terminalis in any member of the Squamata.

The literature on the olfactory nerve of adult snakes in general agrees well with the observations made on late embryonic material in the present study. Important papers include those of Leydig (1872b, *Natrix*; and 1897, *Natrix*, *Coronella*, and *Vipera*), Lee (1893, *Typhlops*), Macallum (1884, *Thamnophis*), Zuckerkandl (1910a, *Typhlops*), McCotter (1912, "snake"), and Bellairs (1942, *Vipera*). Most of the disagreement which does exist concerns the degree of separation between the two trunks, and whether or not the vomeronasal nerve supplies all the fibers innervating Jacobson's organ and no others. Since the proximity of the two trunks makes fiber interchange a possibility, this does not appear to be a very important point.

The available embryos of *Alligator* do not permit any detailed study of the later developmental stages of the olfactory nerve. In the series studied, nerve fibers appear to arise from the greater part of the surface of the cavum nasi proprium, even well ventrally and anteriorly. However, Bertau (1935) found sensory epithelium only in the posterodorsal third of the cavum in the oldest of his embryos of *Alligator*, *Melanosuchus*, and *Crocodylus*. Shiino (1914) and Nemours (1930) describe intermediate conditions. Thus it appears probable that the olfactory nerve fibers are originally formed by a large part of the caval epithelium, but during the course of later development become much restricted in their areas of origin. Further study is necessary before any detailed accounts of olfactory nerve distribution in crocodilians would be profitable.

Olfactory Bulbs. Although any detailed consideration of the olfactory bulbs is outside the province of this study, their structure and development are of importance with respect to questions on the homology of Jacobson's organ. Therefore, a brief treatment is included here. Special emphasis is placed on the occurrence and nature of the *accessory olfactory bulb* (=*area vomeronasalis* or *Nebenbulbus*) which typically receives the nerve fibers from Jacobson's organ.

As in the other parts of this paper, the snakes are taken as examples of the Squamata, and the lizards are not discussed. However, the extreme variation found in the degree of development of the accessory bulb in the latter group, and its correlation with the size of Jacobson's organ are of great interest; the lizards present convincing evidence for the relationship of Jacobson's organ and the accessory bulbs. Major papers which consider the lizards include those of Zuckerkandl (1910a), Krabbe (1939), and Crosby and Humphrey (1939).

Terminology, as usual, poses certain problems. The term olfactory bulb is frequently used in a topographic sense as a synonym of rhinencephalon; such is done in the present paper.

When it is necessary to distinguish those areas which are histologically the olfactory bulb — that is, the areas possessing olfactory glomeruli, the term bulbar formation is used. The region receiving fibers from the vomeronasal nerve or its homolog, when such is a separate zone, is the accessory olfactory bulb; the region receiving fibers from the olfactory nerve proper is here termed the main bulb.

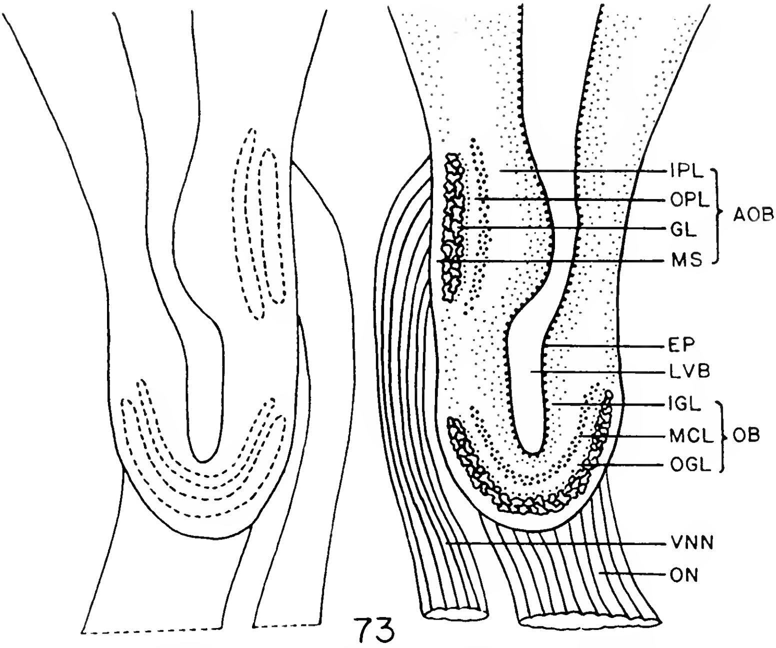

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Figure 73. Diagram of the olfactory and accessory olfactory bulbs of a reptile in frontal section to show the various cell layers mentioned in the text. Detailed structure is shown on the right side only.

Typically the olfactory bulb of the adult displays a rather definite layered structure; Figure 73 shows, in very diagrammatic fashion, those zones mentioned in the text. In no reptile are these zones as distinct as they are shown in the figure; in most cases the outer granular layer, especially, is not separate, but represented by periglomerular cells within the glomerular layer. The terminology used is based on the papers of Krabbe (1939), Crosby and Humphrey (1939), and Allison (1953). The last of these presents the most recent review of the nature and functions of the various layers, and of the structure of the central portions of the olfactory system in general; the reader is referred to that work for further discussions and an extensive bibliography.

There have been few studies on the embryology of the olfactory bulbs in reptiles. Krabbe (1939) considers the development of their gross form, but does not discuss the various cellular layers in any detail. His descriptions are similar to the observations which were made on *Chrysemys, Thamnophis,* and *Alligator* in the present study. In all cases differentiation of the bulbs starts before they are morphologically distinct from the telencephalic hemispheres. The region to become the olfactory bulb is first on the ventrolateral surface of the telencephalon, near but not at its anterior end. With the growth of the brain it gradually assumes its characteristic terminal position. Soon after the beginning of histological differentiation, the presumptive bulbar area forms a small protrusion of the wall of the telencephalon; it contains a narrow, digitiform extension of the lateral ventricle. Further development is essentially a matter of the elongation of the olfactory bulb with the formation of a thinner olfactory tract between it and the hemisphere. The extension of the lateral ventricle also elongates, and extends to the center of the bulb at all stages.

In all three forms studied, the development of the bulbar lamination is very similar. At the start of its differentiation there are two layers recognizable: an outer layer composed almost entirely of nerve fibers with almost no nuclei, and an inner zone with many small circular nuclei. The latter zone soon divides in two with the innermost half remaining the same and the outer half now containing fewer nuclei. At a later stage, the outermost enucleate zone can be seen to form an outer, still enucleate, zone, the *myelospongium* of the adult, and an inner zone with scattered nuclei. Simultaneously, the central layer with few nuclei becomes differentiated into a thin outer zone with many nuclei and a thicker inner one which is almost entirely fibrous; these are the *mitral cell* and *inner plexiform layers* respectively. Finally two more divisions of zones occur. The myelospongium is unchanged, but inside that the zone with scattered nuclei forms a *glomerular layer* containing the olfactory glomeruli and scattered periglomerular cells, and a fibrous *outer plexiform layer.* Continuing inwards, the mitral cell and inner plexiform layers remain as before, and the innermost, densely nucleate zone is divided into a thick *inner granular layer* and a thin layer of *ependymal epithelium* actually lining the ventricular cavity.

In adult turtles, it has long been recognized that the olfactory bulb may be divided into two major areas, a larger anteroventral one which includes the tip of the bulb and a smaller posterodorsal one. This division is described by Haller (1900), Zuckerkandl (1910a), Johnston (1915), McCotter (1917), and Crosby and Humphrey (1939). The last two of these papers consider the smaller posterodorsal area to be an accessory olfactory bulb receiving the nerve fibers from Jacobson's organ or its homolog. The older *Chrysemys* embryos studied in the present investigation correspond exactly with these earlier descriptions, with the absence of the outer layers of the bulbar formation, especially of the glomerular zone, marking the boundary between the main and accessory bulbs.

As far as I am aware, only one author has denied this pattern. Schepers (1948b), describing *Testudo geometrica* (= *Psammobates oculifer* of Loveridge and Williams, 1957), states that there is no definite separation into dorsal and ventral parts in either the olfactory nerves or bulbs. In an earlier paper Schepers (1948a) describes a deep invagination of the posterolateral wall of the olfactory bulbs in this form which greatly increases the circumferential area of the bulb, and results in the virtual obliteration of the bulbar part of the lateral ventricle. No other worker has reported such an invagination. In his second paper, Schepers suggests the possibility that this invagination may be somehow related to the vomeronasal nerve, but at the same time states that he was unable to identify any such nerve.

Although the olfactory bulbs of *Sphenodon* have been described by several workers, including Osawa (1898), Unger (1914), Cairney (1926), and Christensen (1927), only one previous paper, that of Wyeth (1924), mentions the accessory bulb. Unger may also have recognized it, but his description does not make this clear. In the oldest embryo used in the present study, as in the specimens described by Wyeth, the accessory bulb is a small circular or oval area on the dorsomedial wall of the posterior part of the olfactory bulb. As in the case of turtles, it is separated from the main bulb by a narrow region lacking the outer layers of the bulbar formation.

In the snakes, an accessory olfactory bulb has long been known and is universally recognized. Previous descriptions include those by Herrick (1893), Rabl-Rückhard (1894), Leydig (1897), Zuckerkandl (1910a), and Crosby and Humphrey (1939). The main bulb forms, in the adults studied by these authors, a small cap on the olfactory bulb. Posterior to it, the medial wall is enormously thickened and forms a very large accessory bulb. Due to its size, the ventricle of the bulb is displaced laterally, and often the surface of the accessory bulb contains an indentation, presumably to increase the surface area for entering nerve fibers. One exception has been described: in *Typhlops* the accessory bulb is posterodorsal rather than posteromedial to the main bulb (Zuckerkandl, 1910a).

Embryos of *Thamnophis* present an essentially similar picture. There is no indentation in the wall of the accessory bulb in any of the series studied, but this could easily form after the animal is hatched. One interesting point is that when the accessory bulb first appears in the embryo, it is dorsal, as in *Typhlops,* rather than medial. In later embryos it gradually becomes dorsomedial in position. Presumably it does not become truly medial until the time of hatching; it is still somewhat dorsal in the most mature embryos used in the present study.

There are no reports of an accessory bulb in any crocodilian. None was present in any of the *Alligator* embryos studied in the present investigation, thus confirming the studies of Herrick (1890), Zuckerkandl (1910a), Unger (1911), and Crosby (1917), and the statements in more general works by Kappers (1934), Kappers, Huber, and Crosby (1936), Crosby and Humphrey (1939), and Allison (1953). Herrick, and later Crosby, describe an "olfactory fossa" in which a thickening of the glomerular layer results in an unfolding of the inner zones of the bulbar formation. According to Crosby (1917), this lies in the ventromedial wall of the bulb near its anterior end. However, it does not appear to bear any relation to an accessory bulb, and could not be found by any of the other workers who studied crocodilians.

Nervus Terminalis. Although, as was previously noted, a nervus terminalis could not be definitely identified in any of the material used in the present study, it should be mentioned here since it has often been confused with the vomeronasal nerve (e.g. Kappers, 1934, p. 457). As far as is known, the terminalis is completely lacking in crocodilians (Haller, 1934; and Kappers, Huber, and Crosby, 1936) and in squamates (Bellairs, 1942 and 1949). The only report of its occurrence in *Sphenodon* is that by Wyeth (1924); he admits that he is unable to be certain about the identification, and describes only the proximal end of the structure in question.

However, in turtles, three workers have been able to locate the terminalis: Johnston (1913, *Emys*); Hanson (1919, *Chelydra*); and Larsell (1919, *Chrysemys*). According to Johnston and Larsell, the nerve is associated with the medial trunk of the olfactory nerve and forms a plexus in the median wall of the nasal cavities. Larsell believes that this nerve is probably primarily autonomic, but its function is not understood at all.

DISCUSSION

Major Subdivisions of the Nasal Cavity. Throughout this work the nasal cavity has been considered to consist of three main parts — an anterior vestibulum, a posterior ductus nasopharyngeus, and, between them, a cavum nasi proprium.

The vestibulum has, unfortunately, been defined in three different ways: on the basis of embryological development, of histological structure, and of gross anatomy. Theoretically, the first of these would be preferable in a consideration of the homologies of the nasal area. According to the embryological definition, the vestibulum is that part of the nasal cavity whose walls develop from essentially unmodified ectoderm rather than from the nasal placode, and are, at some stage in ontogeny, invaginated to form a tubular connection between the naris externus and the tissue of placodal origin. This definition, while frequently cited, is but rarely actually followed; it is rendered vague and impractical by the lack of any distinct boundary between the placode and the surrounding epidermal epithelium, at least in reptilian embryos.

In mammalian anatomy, the vestibulum is most commonly defined by its histology, as that portion of the nasal cavity whose walls bear stratified squamous epithelium comparable to the skin, rather than columnar epithelium as in the remainder of the nasal cavity. However, in reptiles, the transition between these epithelial types can occur at very different parts of the nasal cavities, even in members of the same family (see Eckart, 1922, on agamids), so that a histological definition also appears to be unsatisfactory.

The third definition of the vestibulum, that based on the gross form, is used in the present paper. In most reptiles, it forms a rather distinct anterior tubular region. In the orders Rhynchocephalia and Squamata it is typically separated from the cavum nasi proprium by a small ridge on the lateral wall of the nasal cavity. Turtles may, as in the Testudinidae, possess such a postvestibular ridge, but in others, such as the Cheloniidae, no ridge is present. However, the great and abrupt increase in cross-sectional area at the posterior end of the vestibulum provides a sharp boundary in all turtles. Crocodilians do not display so obvious a division between the vestibulum and cavum; the former region is the vertical segment of the nasal cavity, while the cavum is horizontal. Throughout the reptiles, the duct of the glandula nasalis externa enters the nasal cavity in the posterior part of the vestibulum (as here defined), thus providing evidence that the postvestibular boundary is closely comparable in all groups. Although such a morphological definition does not appear to be satisfactory for all other classes of tetrapods, it is the most useful in any discussion of the reptilian nose.

In almost all reptiles, the vestibulum forms only a small portion of the nasal cavity. However, in certain lizards, such as some iguanids and agamids, it may form a long and variously curved tube. Such elongation is most probably a specialization for desert life in many cases; the longer and more complex structure would tend to prevent particles of sand from becoming lodged within the sensory areas (Stebbins, 1948). Modifications enabling the animals to close the nares externi are found in certain aquatic groups, both among the snakes (Kathariner, 1900) and crocodilians (Bellairs and Shute, 1953). Otherwise, the vestibulum is a simple, essentially tubular structure, without conspicuous variation among the reptilian orders, although its length and diameter are markedly different in different forms.

As stated in the section on turtles, the term ductus nasopharyngeus is used in the present paper for any tubular structure leading from the nasal cavity to the choana, although Fuchs (1908) proposes the name ductus choanalis for those cases in which no secondary palate is formed. The distinction made by Fuchs — that a ductus choanalis is a part of the nasal cavity, while a ductus nasopharyngeus is a part of the buccal cavity which is separated from the remainder of that cavity by a secondary palate — is useful in considering the embryology, but appears to be rather arbitrary as far as the adult anatomy is concerned. A practical problem is that Fuchs' definitions depend on the recognition of an exact boundary of the nasal tissues: such an exact boundary is not generally recognizable. For a further discussion of this problem, the reader is referred to the works of Fuchs, especially his paper of 1908.

Among the recent reptiles, there is considerable variation in the length of the ductus nasopharyngeus. In *Sphenodon*, the cavum nasi proprium opens directly into the mouth cavity, so that there is no ductus. However, in the Squamata, the ductus is present, although generally short, especially in lizards. Turtles possess a well-developed ductus, which Fuchs considers to be a ductus choanalis similar to that of snakes, although it is typically somewhat longer in the Chelonia. The crocodilians have a highly developed secondary palate and an exceedingly long ductus nasopharyngeus. In all cases, the ductus is a very simple tube; many turtles, such as *Testudo*, *Emys*, and *Chrysemys*, possess a small dorsolateral diverticulum near the anterior end of the ductus, the recessus ducti nasopharyngei, but otherwise there are no gross structural modifications reported in reptiles.

The third major section of the nasal cavity is termed the cavum nasi proprium. It can be delimited only as the region lying between the vestibulum and the ductus nasopharyngeus, and thus its definition varies with those of the other portions of the nasal cavity. In most cases, the cavum is a large cavity, bearing sensory olfactory epithelium on a part of its walls; such sensory epithelium is not found in the vestibulum or ductus. Since the form of the cavum varies greatly among the reptilian orders, no generalizations can be made concerning its form, other than that there are usually one or more projections of its lateral wall extending into the cavity. Many names have been applied to the different parts of the cavum; all of these are defined in terms of the lateral projections, generally termed conchae, which must, therefore, be considered next.

The term concha has been used in several different senses. Most commonly it is applied to any process of the lateral wall of the nasal cavity, or the extension of the nasal capsule into such a process. This general usage is followed in the present paper. However, at least two more restricted definitions have been proposed, or at least used. Gegenbaur (1873) and Solger (1876) apply the term concha only to simple lamellar processes; all other projections of the wall are termed pseudoconchae. Hence a structure such as the concha of most squamates, which is U-shaped in section and frequently contains a portion of the glandula nasalis externa within its center (the cavum conchale), is not considered to be a true concha by these workers. On the other hand, deBeer (1937) applies the term concha only to those projections which do contain a cavum conchale.

The problems of conchal homologies among the various amniotes have received much attention in the literature, but there is, as yet, no general agreement. In the following discussion only the epithelial relationships are considered, and the nasal capsules are not treated. This limitation prevents a complete discussion of the problem, but several aspects can still be satisfactorily dealt with.

Turtles do not possess a concha, although the convexity of the dorsolateral wall (the Muschelwulst) has sometimes been referred to by that term. The latter structure, however, is well developed only in the Testudininae (*Testudo*), and is small or absent in most other groups including the Emydinae. Since the testudinines are believed to have been derived from emydine ancestors (Loveridge and Williams, 1957), it seems probable that a prominent Muschelwulst is a specialization within that subfamily. Gegenbaur (1873) and Fuchs (1915) consider the laterale Grenzfalte of sea turtles to be the homolog of the saurian concha. The Grenzfalte is in approximately the position where a concha might be expected, but its form is not at all like that of the concha of any other group.

It cannot, of course, be demonstrated whether the absence of a concha in turtles is primitive, or whether that structure has been secondarily lost within the order; certainly there is no evidence which would tend to cast doubt on the former theory. None of the modern Amphibia possess any conchae. Although these forms are very specialized in many respects, their nasal regions are, according to Jarvik (1942), very similar to those of the crossopterygians. Thus, in the absence of paleontological evidence, there is no reason to assume that any amphibians or primitive reptiles possessed a concha, or that its absence in turtles is not primitive, although both are entirely possible.

All other amniotes have at least one concha. Among the remaining reptilian orders, the Rhynchocephalia possess two, the Squamata one, and the Crocodilia three. However, in the last case, the preconcha and concha develop as a single projection of the lateral wall which subsequently divides into two parts, so that there are only two elements whose homologies must be considered. In the birds there are three conchae; the most anterior of these, the *concha vestibulae* (or "preconcha"), is on the wall of the vestibulum, and thus quite distinct from all other conchal formations. Mammals typically possess a maxilloturbinal, a nasoturbinal, and a series of ethmoturbinals; Peter (1901) also describes a small concha obtecta in the posterodorsal part of the nasal cavity.

The most commonly accepted system of homologies of these various conchae is that proposed by Peter (1901). He considers the concha of squamates, concha media of birds, and maxilloturbinal of mammals to be primary conchae laterales anteriores, while the postconcha or Riechhügel of birds, nasoturbinal of mammals, and possibly the postconcha of crocodilians are termed secondary conchae laterales anteriores. All the other conchae are believed to be independently developed and not related one to another. More recent authors, such as Fuchs (1908) and Bertau (1935), have added the concha (= the concha posterior?) of *Sphenodon* and the preconcha plus concha of crocodilians to the list of primary conchae laterales anteriores. Matthes (1934) and other workers have questioned the homology of the postconcha of crocodilians and birds with the mammalian nasoturbinal, but have, for the most part, accepted Peter's ideas.

However, at least one recent paper presents a quite different scheme. Hoppe (1934) recognized two conchae, anterior and posterior, in *Sphenodon*. The latter he considers to be the homolog of the concha of squamates; the former he compares to what he terms the "Lippe am Choanengang" of lizards. This lip is a small ridge along the lateral side of the choana described by Beecker (1903), who attached no importance to it. Hoppe also compares *Sphenodon* to crocodilians and birds, equating the concha posterior of the first with the postconcha, and the concha anterior with the middle concha of crocodilians and birds. Thus, he believes the concha of squamates to be homologous to the postconcha of crocodilians.

Hoppe's proposals do not appear to be very satisfactory. The concha posterior of *Sphenodon* does resemble closely the concha of the Squamata, and their homology seems probable. However, the similarities between the concha anterior and the lacertilian Lippe am Choanengang are slight, and are found only in the adults. The rhynchocephalian concha anterior is first formed as a ridge which extends dorsoventrally along the lateral wall of the cavum nasi proprium; during its embryonic development, it rotates to the more nearly horizontal position typical of the adult (see Fig. 33, and the figures in Hoppe, 1934). The Lippe of lizards, on the other hand, forms in place as a horizontal ridge along the Choanengang at the nasal end of the ductus nasopharyngeus. With regard to crocodilians, Hoppe's suggestions seem improbable. On the bases of both gross form and position within the cavum, the squamate concha appears to be far more readily comparable to the crocodilian middle concha than to the postconcha. Admittedly neither form nor position are infallible guides to homology; however, the position of the postconcha, posterior to the nasal end of the ductus nasopharyngeus, and thus in the region corresponding to the squamate Antorbitalraum, is radically different from the location of the concha of any squamate.

Therefore, it seems most probable that the concha posterior of *Sphenodon*, the concha of squamates, the preconcha plus concha of crocodilians, the concha media of birds, and the maxilloturbinal of mammals are all to be considered as homologous. It may be noted that this is typically the first of the conchae to appear in ontogeny in all groups, although in some mammals (e.g. *Lepus*, Peter, 1901) the nasoturbinal may also arise at an equally early stage.

The only other proposed conchal homology which must be considered is that of the postconchae of crocodilians and birds with the mammalian nasoturbinal. The latter structure is typically dorsal or anterodorsal to the maxilloturbinal, while the postconcha is posterior or posterodorsal to the concha, so that their positions are not readily comparable. In form, the postconcha is merely a marked outpocketing of the lateral wall, while the nasoturbinal is most commonly a more elongate and frequently lamellar formation. Actually, there appears to be no convincing evidence for their homology. It therefore seems more probable that, in the course of their evolution, both archosaurs and synapsids independently developed a second lateral concha. Unfortunately, there appears to be little paleontological evidence on the origin of conchae. Watson (1913) reports the presence of ethmoturbinals in at least two genera of therapsids; in 1951, he states that the nasoturbinal and maxilloturbinal were also present, but gives no details on their structure.

Thus a single concha was probably developed at a very early stage in the evolution of reptiles, before the separation of the line leading to mammals. The Squamata retain this primitive condition, but other groups have independently acquired other conchal structures. This theory is supported by the lack of evidence for further homologies; the idea of the gradual acquisition of various projections of the nasal wall in different groups seems to be a more reasonable working hypothesis than the supposition that a rather complex pattern appeared suddenly in primitive reptiles and has persisted, although often much modified, to the present. Conclusive evidence can come only from paleontology, and will probably never be available.

There is no need to make further comparisons of the nasal cavities of reptiles with those of other tetrapods, since all the problems relating to the cavum nasi proprium are basically concerned with the conchae, and the other regions are generally simple. Matthes (1934) gives excellent descriptions of the nasal cavities of all groups, considering the embryology as well as the adult anatomy; the reader is referred to his paper for further information and references on these topics.

Jacobson's Organ. Any discussion of the evolution of Jacobson's organ must necessarily start with the amphibians; unfortunately, there is no general agreement on the interpretation of the nasal cavities of that class, despite the existence of a very large body of literature on all aspects of the organ's form and development. In the following review only a few of the major papers are cited. Many more references can be found in the review by Matthes (1934). Special attention should also be called to Helling's (1938) study of the Anura.

Although there is considerable variation in nasal anatomy among the three living orders of amphibians, representatives of all three possess what may be called the *unterer Blindsack*, a conveniently vague term first employed by Born (1876). In most adult urodeles, ignoring the neotenous forms, this unterer Blindsack forms a small groove along the lateral margin of the main nasal chamber with which it is connected throughout its length. The remaining two orders possess a more complex structure. In the Gymnophiona, the Blindsack is a tubular inpocketing of the nasal wall which extends anteriorly from the anterolateral margin of the choana and lies ventral to the posterolateral portion of the main nasal cavity. The nasal anatomy is more variable among the Anura, but there is typically a series of quite distinct saccular extensions of the main nasal chamber. The unterer Blindsack lies ventral to the main chamber, and the two are joined by a narrow vertical slit which runs nearly the length of the nasal cavity. At the ventral end of this slit, the Blindsack extends laterally and, in its anterior half, also medially, so that in transverse section it resembles an inverted letter T. Seydel (1895) considered the untere Blindsäcke of all three orders to be homologous, but the radical differences in their forms and positions caused many workers to doubt this. However, subsequent embryological studies, such as that of Hinsberg (1901) have tended to support Seydel's opinions, and the proposed homology is now commonly accepted (see Matthes, 1934).

In all three orders, the wall of the unterer Blindsack bears an area of sensory epithelium; this area was termed the Jacobson's organ by many early workers, most notably Seydel (1895).

Other investigators questioned the homology of the Blindsack with the Jacobson's organ of amniotes, and there is still no general agreement on the subject. Matthes (1934) states that there is now little doubt that the structures are homologous, but Francis, in the same year, claims that "there is evidently a growing consensus of opinion . . . against Seydel's view" (p. 303). In the urodeles the sensory epithelium lines the posterior half of the Blindsack, while in anurans it is found in the anteromedial portion only. According to Wiedersheim (1879), the entire Blindsack of the Gymnophiona is lined by sensory epithelium, but Sarasin and Sarasin (1887-1890) report that only its ventral surface is sensory.

Seydel's arguments in favor of the proposed homology include the innervation of the sensory areas of the Blindsack by the ventral branch of the olfactory nerve, which corresponds to the medial trunk of that nerve in reptiles. He further cites the absence of Bowman's glands in this area, and states that, in all cases, both in amphibians and amniotes, Jacobson's organ is used to smell the contents of the mouth. A final major point is the presence of glandula nasalis medialis associated with the Blindsack in all three groups of amphibians.

The major objections raised against Seydel's identification of Jacobson's organ in amphibians are based on the adult topography of the nasal area. The lateral position of the Blindsack in *Salamandra* caused von Mihalkovics (1898) to consider it to be the homolog of the maxillary sinus rather than of Jacobson's organ, although he accepts Seydel's conclusions with respect to *Rana* in which the sensory portion is medially situated. That the sensory area of the urodele Blindsack has the same function as the Jacobson's organ of amniotes, is not denied by von Mihalkovics; however, as he points out, analogy is an unreliable guide to homology.

Supporters of Seydel's theory argue that the embryological development of the Blindsack demonstrates its primitive medial position, even in the urodeles. In *Triturus* (= *Triton* of authors), the Blindsack is said first to be present as a small inpocketing in the ventral half of the medial wall, and to assume its adult position through a rotation of the wall of the nasal cavity around its long axis. The first major paper describing this mode of development is that of Hinsberg (1901); more recently, Schuch (1934) has confirmed his results. However, the early embryology of the amphibian nose is still not at all well understood (see the discussion in the subsequent section of this paper), and thus Hinsberg's findings are subject to some doubt.

Another objection which is frequently raised is that the amphibian Blindsack does not typically develop until after the formation of the choanae, although at a stage before the lumen of the nasal cavity is continuous with that of the mouth. In amniotes, on the other hand, Jacobson's organ generally appears at a much earlier stage. However, in *Xenopus,* Föske (1934) finds a small ventromedial inpocketing, the anlage of the Blindsack, while the nose is still in the placodal stage. The significance of this case, which appears to be exceptional, is, of course, open to question.

Seydel's evidence from the glands remains virtually unchallenged. Almost all workers seem to accept the homology of the glandula nasalis medialis throughout the Amphibia, which is one of Seydel's main arguments, and Matthes (1934) states that Bowman's glands are never found in the sensory epithelium of the unterer Blindsack.

As in the case of the turtles, the neurological evidence is of prime importance; however, interpretations vary. The first major paper on the olfactory bulbs of the amphibians is that of Zuckerkandl (1910a). He recognized the main and accessory bulbs, but was generally unable to determine the relationship between the subdivisions of the bulb and specific areas of sensory nasal epithelium. In *Rana,* the ventral nerve trunk is thought to enter, in part, the accessory bulb. Zuckerkandl stresses that in all amphibians the olfactory fibers enter the anterior and lateral surfaces of the bulb; none are present medially. The accessory bulb lies at the posterolateral end of the main bulb, and may be either dorsolateral (*Hypogeophis*) or ventrolateral (*Rana*). In amniotes, on the other hand, many olfactory fibers enter the medial surface of the bulb and the accessory bulb typically lies posteromedially. The difference is so great that Zuckerkandl believes that two somewhat parallel lines are present, but that there is no homology between the accessory bulbs of amphibians and those of amniotes. Therefore, he does not accept Seydel's theory on the Jacobson's organ of the Amphibia.

Whether the medial position of the accessory bulb is actually of basic importance appears to be debatable. In turtles and most mammals it is more dorsal than medial, and in at least two mammals, *Blarina* and *Scalopus*, Crosby and Humphrey (1939) report a dorsolateral position. Therefore, Zuckerkandl's arguments cannot be considered conclusive.

McCotter (1917) studied *Rana*, and describes a vomeronasal nerve as arising from the medial portion of the unterer Blindsack. This nerve runs posteriorly along the medial wall of the nasal cavity, and then turns laterally, passing ventral to the remainder of the olfactory nerve. Finally, it runs posteriorly along the lateral surface of the olfactory bulb to reach the accessory bulb. McCotter, like most later workers, reports some intermingling of fibers from the two parts of the olfactory nerve, but states that it is slight. He accepts Seydel's theories.

The most important work on the urodeles is that of C. J. Herrick; of his many papers which consider this problem, those of 1921, 1924, and 1948 will suffice for the present discussion. In both *Ambystoma* and *Necturus,* he identifies an accessory olfactory bulb at the posterolateral end of the main bulb, but notes that the two are only indistinctly separated. The accessory bulb is said not only to receive the nerve fibers from the unterer Blindsack, but also many from the main nasal chamber. Herrick therefore concludes that a Jacobson's organ is becoming differentiated within the Urodela, and reaches its definitive condition in the Anura. Like Seydel, he appears to consider the modern Amphibia to be a phylogenetic series, an idea which invalidates his evolutionary conclusions.

Thus the amphibians appear to possess certain areas of sensory epithelium within the untere Blindsäcke which are, in many respects, comparable to the Jacobson's organ of amniotes. However, there are also important differences in embryology, anatomy, and neurological connections. That the unterer Blindsack is, at least in part, homologous to Jacobson's organ seems probable, but the use of the latter term does not appear to be advisable.

The Jacobson's organs of the four Recent reptilian orders have been discussed in previous sections, and only a short summary is necessary here. In the turtles, the ventral or anteroventral half of the cavum nasi proprium (the regio intermedialis) contains areas of sensory epithelium which are thought, on the basis of neurological and other evidence, to be homologous with Jacobson's organ. However, as in the case of the amphibians, these sensory areas are quite different from the definitive Jacobson's organ found in mammals and squamates, and the use of that name is therefore not recommended.

In all other reptiles, a depression is formed in the ventromedial wall of the nasal pit; this depression, which is the anlage of Jacobson's organ, appears well before the nasal processes fuse to separate the naris externus from the choana. The anlage rapidly disappears in the crocodilians, in which Jacobson's organ is lacking in adult animals, but in the Rhynchocephalia and Squamata it typically enlarges to form a tubular or spherical pocket off the median nasal wall. In some lizards, such as *Chamaeleo* (Haas, 1947), Jacobson's organ may be much reduced, but some trace of it appears to persist in all members of these two orders. Jacobson's organ remains as a pocket off the medial wall of the choana in the adult *Sphenodon*, while in squamates its duct opens into the mouth cavity, and is separated from the nasal cavity by the closure of the anterior half of the primitive choana.

Adult birds do not possess a Jacobson's organ. Correlated with this is the complete lack of an accessory olfactory bulb in the forms studied by Crosby and Humphrey (1939); even in *Apteryx*, in which the nasal cavity is far more complex than in other birds, Craigie (1930) reports the total absence of that structure. However a very small, though apparently typical anlage of Jacobson's organ has been found in embryos of at least three species. Cohn (1902) first reported such an anlage in chicks of 5.6 to 5.9 mm. headlength in which the nasal cavity is a very simple pit; in these, Jacobson's organ forms as a small groove in the ventromedial wall of the nasal pit, but quickly disappears. No trace of it was found in any later stages. Cohn's observations have more recently been confirmed by Zuckerkandl (1910b; *Vanellus*) and Schüller (1938; *Sterna*).

Two other workers reached very different conclusions on the basis of adult structure. Ganin (1891; also published in abstract in 1890) suggested that the medial duct of the glandula nasalis externa might represent, in part, the Jacobson's organ of birds. This duct enters the anteromedian wall of the nasal cavity. His suggestions received support from von Mihalkovics (1898), but more recent workers have not accepted the theory. The arguments against it are the same as those already given against von Mihalkovics' proposed homology between the duct of the chelonian glandula nasalis medialis and the Jacobson's organ of other amniotes, and need not be reviewed here.

A Jacobson's organ is typically present in mammals, although in some groups, such as the Chiroptera, Cetacea, and higher Primates, it is absent. The anatomy of this organ has been described in a large series of forms by many different workers, starting with Jacobson (1950; the original papers were published in 1811 and 1812). In the adult, its relationships are somewhat variable, but it is always ventromedially located within the nasal area. Most often the organ becomes associated with the nasopalatine duct (= incisive or Steno's duct), which represents the anterior end of the primary choana; thus it lies in a position closely comparable to that in *Sphenodon*. In almost all cases the organ is a tubular structure whose anterior end opens into the nasal cavity or nasopalatine duct, and whose posterior end terminates blindly along the surface of the nasal septum. Herzfeld (1888) describes the range of variation found within this class.

The early embryology of the mammalian Jacobson's organ is virtually identical with that of the Squamata. Its anlage forms as a small pit or groove in the medial nasal wall, at approximately the center of its ventral margin. This indentation appears at a very early stage, when the nose is represented by a simple nasal pit. Jacobson's organ grows larger and soon becomes a tubular structure. Subsequent changes in its structure are concerned primarily with the establishment of the various adult conditions, and do not need further comment.

Thus in all amniotes, except the turtles, Jacobson's organ arises in a similar fashion, and there is no reason to question its strict homology in all these forms. The modern Amphibia display a variety of conditions in the adults, and the embryology of the nose is poorly understood. In the Gymnophiona and especially in the Anura, the unterer Blindsack does appear to be very similar to the Jacobson's organ of amniotes; however, the variation among the Amphibia and the very different structure of the chelonian nasal cavities raises the possibility that some of the resemblances may be the result of parallel evolution.

Among the amniotes in which Jacobson's organ is unquestionably present, it generally becomes associated with the buccal rather than the nasal cavity of the adult. However, this is not universally true; rodents and lagomorphs possess well-developed Jacobson's organs whose lumina are joined to the nasal cavities only. It therefore appears to be impossible to assume, as some workers have, that the organ always functions in the testing of the mouth content. Since the Jacobson's organ of *Sphenodon* retains its embryonic position in the wall of the nasal cavity, it is generally assumed that the oral connection of that organ in mammals and squamates is a parallel development rather than a trait inherited from a common ancestor; this assumption appears to be supported by the differences in the embryology of that connection in the two groups. However it is very difficult to conceive of the rodents and lagomorphs being the only mammals to retain the primitive condition; in these cases, a suspicion that the nasal connection is a secondary retention of an embryonic character would appear to be justified.

Early Embryology of the Nasal Cavities. In all vertebrates, the earliest stage in the differentiation of the nasal cavities is the formation of a thickened area of ectoderm, the nasal placode, on the lateral surface of the snout. The placode soon becomes inpocketed to form the nasal pit in most forms; in amphibians there is still dispute concerning the mode of origin of the pit. Reports vary slightly on the sharpness of the boundary between the nasal epithelium of the placode and pit and the epidermal epithelium surrounding them. In all the reptilian embryos studied in the present investigation, there is a gradual transition, without any definite line of division. Such an absence of a boundary is probably characteristic of the youngest stages in amniotes generally; Cohn (1902) found none in the chick until the nasal pit was well developed. At that time, ridges appear at the margins of the nasal epithelium, and a teloderm or superficial epithelial layer is formed over the epidermal epithelium. No teloderm was seen in the reptilian material used in the present study. In early mammalian embryos, various workers, such as Seydel (1899) and Frets (1912), have described a transition between nasal and epidermal epithelia. However, a majority of the investigators who have studied amphibians report a quite sharp boundary between the two areas.

Another difference between the Amphibia and the amniotes concerns the histological structure of the placode. In the former class, the epithelium in which the placode forms is generally said to be two layered (Hinsberg, 1901 and 1902; Kurepina, 1931; Schuch, 1934; *et al.*); the thin outer layer is termed the *Deckschicht*, and the thicker inner layer the *Sinnesschicht*. The thickening which forms the placode occurs entirely within the latter inner zone. Hinsberg, Kurepina, and other workers believe that the Deckschicht disappears in the area which will become sensory, and that the first indentation of the nasal pit is formed by the loss of this layer. However, Schuch considers it to be more likely that the layers fuse in the presumptive sensory area; the inpocketing would then be the result of active growth of the placodal epithelium. At least one investigator, Marcus (1930), has denied the existence of two distinct layers within the epithelium on the basis of his studies of *Hypogeophis;* his observations are questioned by most other workers.

The nasal pit enlarges and, in all amniotes, becomes a deep groove which extends dorsally or dorsolaterally from a rather slit-like naris along the ventrolateral margin of the snout. During this period of growth, many mitotic figures are seen in the nasal epithelium, and it is believed that the increase in the depth of the pit is primarily the result of the growth of the epithelium (Peter, 1900, *Lacerta;* and Frets, 1912, mammals). The development of lateral and medial nasal processes on either side of the original pit also aids in this increased deepening. As in most questions on nasal development, the situation in the Amphibia is unclear: Schuch (1934) reports a similar formation of the pit through epithelial growth, but Hinsberg (1901) states that the cavity is formed by a "Dehiscenz der Zellen der Geruchsplatte" (p. 476).

The next major step in the nasal embryology of all tetrapods is the development of separate anterior and posterior openings, the nares externi and choanae respectively. Since the reptiles are the only group which was actually studied in the present investigation, and since they are believed to display the primitive method of choanal formation, they are here considered first.

In all the reptiles which have been studied, the single primitive naris is a long slit whose anterior end is near the tip of the snout and whose posterior end lies within the roof of the developing mouth cavity. The portion of the head lateral to the nasal pit grows ventrally and anteriorly to form the lateral nasal process; the median nasal process develops simultaneously at the ventromedial margin of the pit. The ventral ends of these two processes meet and become fused ventral to the central portion of the nasal pit. However they do not join at either the anterior or posterior ends of the primitive naris; thus the nasal cavity remains open at either end, and becomes tubular. The smaller anterior opening lies on the ventrolateral surface of the snout and is the naris externus, while the larger posterior one forms the primary choana which lies on the roof of the mouth. The bar of tissue between the naris externus and the choana, which is composed of the fused ends of the nasal processes together with the maxillary process, is the primary palate. In birds the formation of the choanae occurs in precisely the same manner as in reptiles (von Kölliker, 1860; Cohn, 1902; and many other authors).

Certain modifications of this method of choanal formation occur in the mammals, but the process is still generally considered to be quite comparable to that described for reptiles and birds. The earlier descriptions of mammalian nasal embryology, e.g. von Kölliker (1860), report the fusion of the nasal processes as taking place exactly as described above. However, Hochstetter (1891) states that in the rabbit and the cat the nasal and maxillary processes fuse ventral to the entire posterior portion of the nasal pit, leaving only a single anterior opening, the future naris externus. He also appears to deny that the posterior end of the nasal pit was continuous with the mouth cavity before the fusion of the processes, but his paper is not absolutely clear on this point. Ventral to the central portion of the pit, there is formed a primary palate similar to that in reptilian embryos, but further posteriorly there is only a thin ectodermal membrane, the *membrana bucco-nasalis*, separating the buccal and nasal cavities. This membrane soon ruptures and the primary choana is thus formed. In the following year, 1892, Hochstetter extended his observations to man, and Keibel (1893) found a similar development of the choanae in the pig and other mammals.

Since 1893 Hochstetter's views have been virtually universally accepted. However, Seydel (1899) was unable to find the membrana bucco-nasalis in *Echidna* embryos, and believes that the condition there resembles that in reptiles. Others workers, such as Peter (1901), have questioned Seydel's conclusions, doubting that his series of embryos was complete enough to enable him to reach any definite decision on the absence of the membrana.

Unfortunately, most of the subsequent discussions of the choanal formation in mammals are not entirely clear on one major point. If the pattern observed in mammals is a modification of the reptilian condition, then one should expect that the membrana bucco-nasalis is composed of the epithelium of the posterior parts of the nasal processes, and that the primary choanae formed by its rupture lie in the same position as did the posterior ends of the primitive nares before the fusion of the nasal processes. Such expectations are fulfilled according to the observations of His (1901; human embryos) and Frets (1912; mice). Thus the only modification is that the primary choana is secondarily closed by a membrane for a short period. However, other workers, including Hochstetter (1891 and 1892), Peter (1901), and Burns (1925), deny that the primitive naris extends posteriorly as far as the mouth cavity; Peter summarizes Hochstetter's conclusions as follows (p. 55): "Die primären Choanen der Säuger . . . entstehen also erst durch Eröffnung des hinteren Endes des Nasenblindsackes, nach Durchreissen der Membrana bucconasalis, und es existiert bei Säugern keine primäre Verbindung der Nasenhöhle mit der Mundhöhle, keine Mundnasenrinne." Should this statement be correct, then it would be very difficult to consider the pattern of choanal formation in mammals as a modification of the process observed in reptiles. Rather, the mammalian condition would appear to be basically different, and any comparison of the primary choanae throughout the amniotes would be open to doubt. Most general texts, including that of Matthes (1934), do not differentiate between the two possibilities outlined above, or give any clear indication of which interpretation they believe to be correct.

Concerning the Amphibia opinions differ, and it is impossible to reach any general conclusions about the formation of the primary choanae in this class. The Gymnophiona show a pattern somewhat comparable to that seen in amniotes, and are therefore considered first. In *Hypogeophis,* Hinsberg (1902) describes a small furrow running from the nasal pit posteroventrally to reach the roof of the mouth. Epithelial cells resembling the epidermal rather than the nasal type grow inwards to form a ridge along the basal surface of the epithelium of the snout underneath this furrow. As the embryo develops, mesodermal elements separate this ridge from the remainder of the epithelium so that it forms a narrow and solid cylinder of epithelial cells which runs from the nasal pit to the roof of the mouth. The primitive choana is developed by the creation of a lumen within the epithelial cylinder. Thus in the larvae of *Hypogeophis* there is a rather long tubular *Nasengaumengang* connecting the main nasal cavity with the mouth; in the adult, the tube is shorter, and the sensory region of the nasal cavity reaches to the choanal region. Marcus (1930) also studied *Hypogeophis*, and his observations agree well with those of Hinsberg, except that the former author recognizes a small lumen within the Nasengaumengang at the time of its formation. Thus in gymnophionans, the groove observed by Hinsberg appears to represent the posterior end of the nasal pit of amniotes, and the tissue on either side of it, the nasal processes.

However, in both urodeles and anurans, Hinsberg (1901) and most other early workers report a very different situation. In *Rana* and *Triturus*, Hinsberg could find no groove connecting the nasal pit with the roof of the mouth. Instead a solid process of epithelial cells from the wall of the pit grows posteroventrally through the intervening mesoderm to reach and fuse with the buccal epithelium. The choana is formed, as in the Gymnophiona, by the extension of the nasal cavity into the solid epithelial process, and finally by the breakdown of the epithelium of the roof of the mouth at the point where the epithelial process has fused with it. According to Hinsberg, this point of fusion is posterior to the pharyngeal membrane; therefore the primitive choana lies within the endodermal portion of the mouth, while in all amniotes and gymnophionans it is the ectodermal region. Such a development is so radically different from that found in other forms that Peter (1901) has questioned the homology of the amphibian choana with that in amniotes; thus he also expressed doubt that the unterer Blindsack can be homologized with Jacobson's organ because of the general incomparability of the nasal cavities of amphibians and amniotes.

Several more recent authors, most notably Kurepina (1931), have disagreed with most of Hinsberg's observations. In a series of six species of anurans and urodeles, Kurepina reports the presence of a small *oro-nasale Furchen* connecting the nasal pit and the mouth cavity. This groove is small, and is present only in very early larvae. The choanae are formed by a strand of epithelial cells which becomes separated from the oro-nasale Furchen in a manner precisely similar to that described by Hinsberg (1902) for *Hypogeophis;* they lie within the ectodermal portion of the mouth. Thus Kurepina believes that the amphibian nasal cavities develop by means of the same processes which have been described in reptiles.

There is still no general agreement concerning these problems. Föske (1934) reports the formation of the choana in *Xenopus* from an oro-nasale Furchen similar to that described by Kurepina, but in the same year Schuch repeats Hinsberg's major conclusions on the basis of his study of *Triturus.* Much of the solid epithelial strand between the nasal pit and the roof of the mouth is believed to be formed from endodermal cells of the latter area by Schuch, while Hinsberg considers it to be primarily an outgrowth of the nasal pit, but this difference is relatively slight.

Thus the Gymnophiona, Reptilia, and Aves all display a similar mode of choanal formation. If the observations of Kurepina (1931) on urodeles and anurans and those of Frets (1912) on mammals are to be credited, then this mode is common to all tetrapods. However, if Hinsberg (1901) and Peter (1901) present a more accurate picture of amphibian and mammalian development, then the choanae are formed in a very different manner in these two groups; in fact, three somewhat different patterns would be present if the amphibian choanae are actually in the endodermal portion of the palate. Further comparison of these patterns does not appear to be profitable until greater agreement has been reached concerning the choanal embryology of the Urodela, Anura, and Mammalia.

There is no need for any discussion of the later embryonic stages. In all groups, the nasal cavities slowly assume their adult configuration by the development of the various conchae and other structures already mentioned. The reptilian orders have already been described. Papers previously cited which consider later stages in amphibians include those of Hinsberg (1901 and 1902), Föske (1934), and Schuch (1934); Schüller (1938) presents the best account of the nasal embryology in a bird.

References to the literature on mammals may be found in the recent paper by Keilbach (1954) which, although concerned primarily with the nasal skeleton, contains an excellent bibliography on nasal anatomy and embryology in all mammals.

Phylogenetic Considerations. In conclusion, a discussion of the phylogenetic implications of this study is in order. However, since I am presenting these ideas in some detail in a separate paper (Parsons, in press), the discussion here will be very brief.

The most important point is the general similarity of the nasal anatomy and embryology in all groups of amniotes with the exception of turtles. *Sphenodon*, lizards, snakes, crocodilians, birds, and mammals typically possess at least one concha (the maxilloturbinal of mammals) which appears to be homologous in all these groups: it is absent in turtles and also in amphibians. Similarly all amniotes (except turtles) possess, in early embryonic stages, a distinct ventromedial inpocketing of the nasal epithelium. This inpocketing is the anlage of Jacobson's organ. However in turtles and amphibians the structures which are probably homologous to that organ do not exhibit the same mode of development. In the absence of any evidence to the contrary, it seems most probable that the ancestors of turtles had separated from the basic reptilian stock at a very early stage, before the divergence of the lines leading to the other modern amniote groups; before the latter division had occurred, a concha was formed and a typical Jacobson's organ developed.

Naturally, the theory stated in the preceding paragraph cannot be accepted as proven. It is possible that some of the resemblances between various amniote groups are due to parallel evolution or that the turtle ancestors possessed a concha and a typical Jacobson's organ. However the embryology of the nasal organ, as described in this paper, does not appear to support either of these possibilities. Since the early history of the reptiles has been much debated in the literature, it is most interesting to find another anatomical complex, the nasal cavities and Jacobson's organ, which may give some evidence concerning this problem.

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EXPLANATION OF FIGURES

Unless it is otherwise noted in the caption, all text figures are oriented as follows: transverse sections with the dorsal surface toward the top of the page and the midline to the left; frontal sections with the anterior end toward the bottom and the midline to the left; and sagittal sections or views with the dorsal surface toward the top and the anterior end to the right.

In all figures of the embryological series studied in the present investigation, the number of the series is given and then, in parentheses, its size in millimeters (if known) and its source. The abbreviations for the last are: AMR, Dr. A. M. Reese; EEW, Dr. E. E. Williams; and MC, the Minot Collection of the Harvard Medical School.

The abbreviations used on the figures are as follows:

ABS — apikale Blindsack
AOB — accessory olfactory bulb
AON — anlage of the olfactory nerve
AOR — Antorbitalraum
B — brain
C — concha
CA — concha anterior
CH — choana
CHF — Choanenfalte
CHG — Choanengang
CHP — choanal papillae

CNP — cavum nasi proprium
CP — concha posterior
DJO — duct of Jacobson's organ
DLM — dorso-lateraler Muschelraum
DNP — ductus nasopharyngeus
DRV — dorsal recess of the vestibulum
DTC — dorsale Tasche des Choanengangs
E — eye
EP — ependyma
GL — glomerular layer
GNE — glandula nasalis externa
GNM — glandula nasalis medialis
HLN — hintere laterale Nebenhöhle
HPC — Höhle in der Postconcha
IGL — inner granular layer
IPL — inner plexiform layer
JO — Jacobson's organ
LD — lachrymal duct
LG — laterale Grenzfalte
LNP — lateral nasal process
LVB — lateral ventricle of the brain
MB — mushroom body
MCL — mitral cell layer
MG — mediale Grenzfalte
MNP — medial nasal process
MS — myelospongium
MW — Muschelwulst
N — naris
NE — naris externus
NPL — nasal placode
NPT — nasal pit
OB — olfactory bulb
OGL — outer granular layer
ON — olfactory nerve
OPL — outer plexiform layer
PRC — preconcha
PTC — postconcha
PVR — postvestibular ridge
RCC — recessus caviconchalis

RD — recessus dorsalis of the regio intermedialis
RDN — recessus ducti nasopharyngei
REC — recessus extraconchalis
RI — regio intermedialis
RJO — Jacobson's organ of Röse (1893a)
RO — regio olfactoria
RPC — recessus preconchalis
RV — recessus ventralis of the regio intermedialis
S — Sakter
SA — sulcus anterior
SL — sulcus lateralis
SM — sulcus medialis
SMX — sinus maxillaris
SPT — sinus postturbinalis
STT — Stammteil
SV — sulcus ventralis
SVM — sulcus ventralis et medialis
V — vestibulum
VM — ventraler Muschelraum
VNN — vomeronasal nerve
VP — Vomerpolster

PLATE 1

Figure 74. *Upper figure*. *Chrysemys* 1076 (10.4; MC). Transverse section showing the fused ends of the lateral and medial nasal processes. The nasal cavity is to the right and the oral cavity to the left (section 256; see Fig. 16). 380x.

Figure 75. *Lower figure*. *Chrysemys* 2137 (8.9; MC). Transverse section howing (right) the lateral band of thin epithelium between the dorsal and ventral areas of thickened nasal epithelium. The dorsal surface is toward the bottom of the page (section 350). 380x.

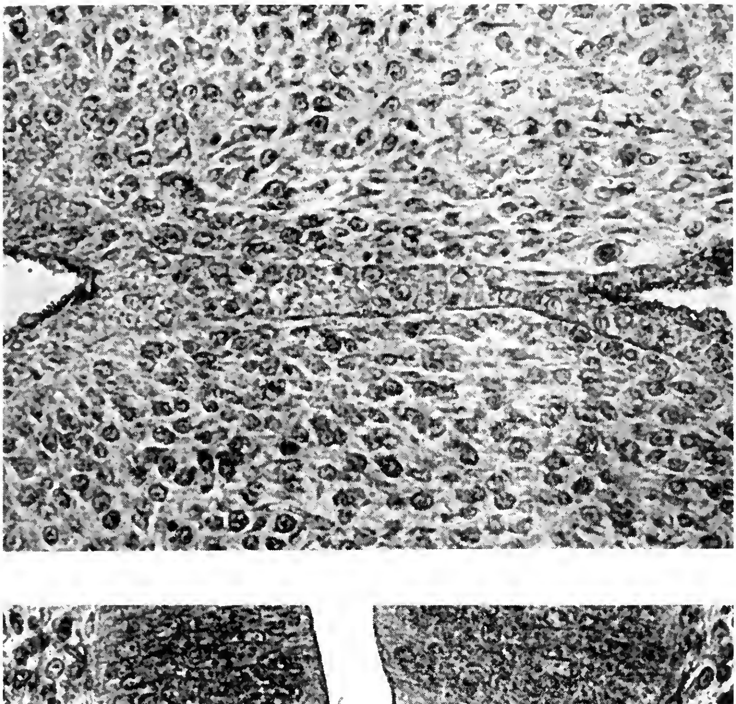
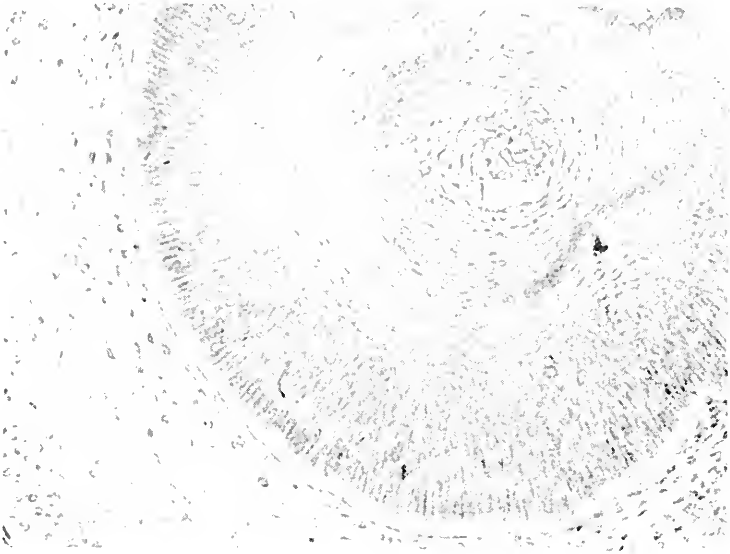


PLATE 1

PLATE 2

Figure 76. *Upper figure. Chrysemys* 1653 (32.0; MC). Transverse section through the vestibulum. The dorsal surface is to the right and the midline toward the top (section 25). 275x.

Figure 77. *Lower figure. Chrysemys* 1098 (28.1; MC). Frontal section through the sensory epithelium of the regio olfactoria showing a Bowman's gland. The anterior end is to the left and the midline toward the top (section 132). 275x.



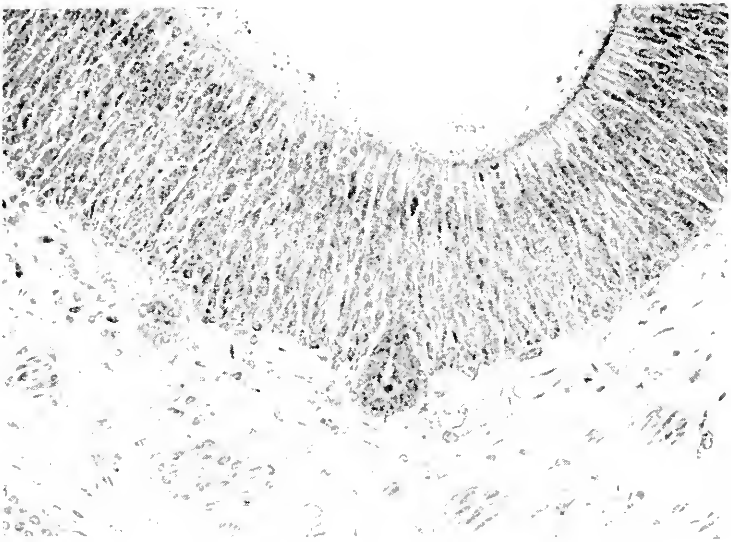


PLATE 2

PLATE 3

Figure 78. *Upper figure. Chrysemys* 1127 (32.0; MC). Transverse section through the non-sensory epithelium of the posteroventral portion of the regio olfactoria. The dorsal surface is to the right and the midline toward the top (section 97). 275x.

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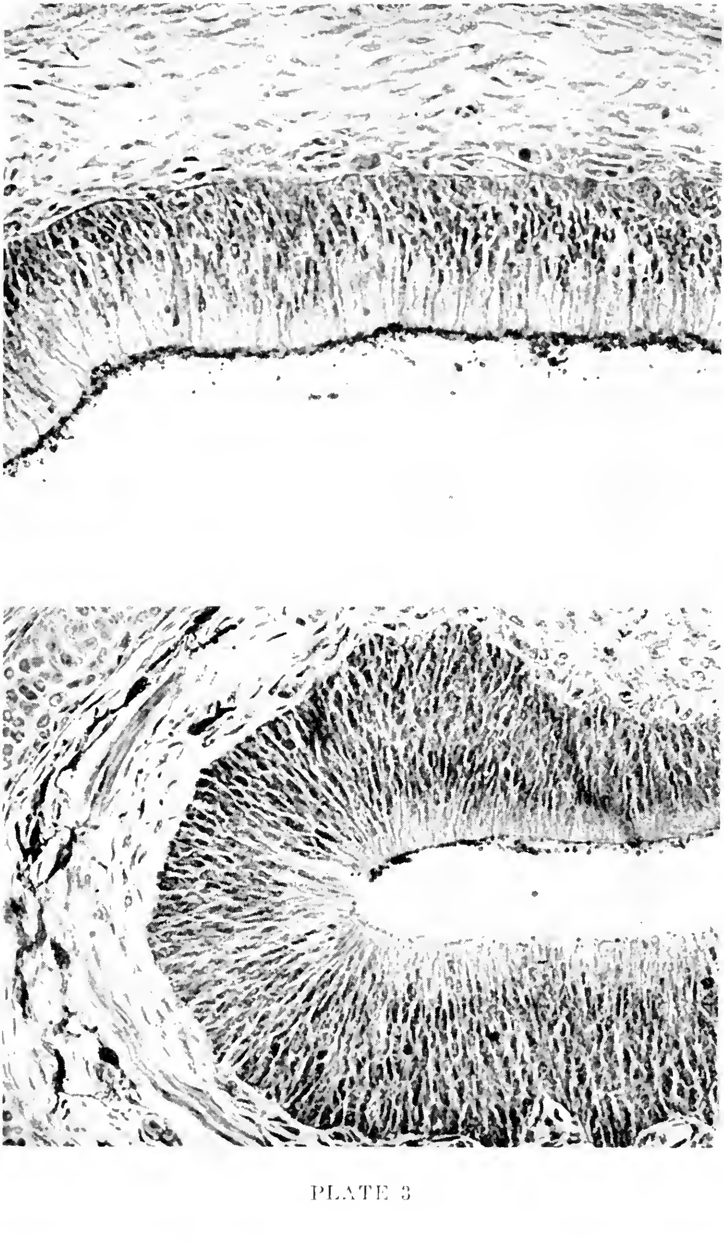

PLATE 3

PLATE 4

Figure 80. *Upper figure. Sphenodon* 1507 (17.4; MC). Frontal section through the nasal area to show the relationships of the conchae anterior and posterior. The anterior end is to the left and the midline toward the top (section 155). 35x.

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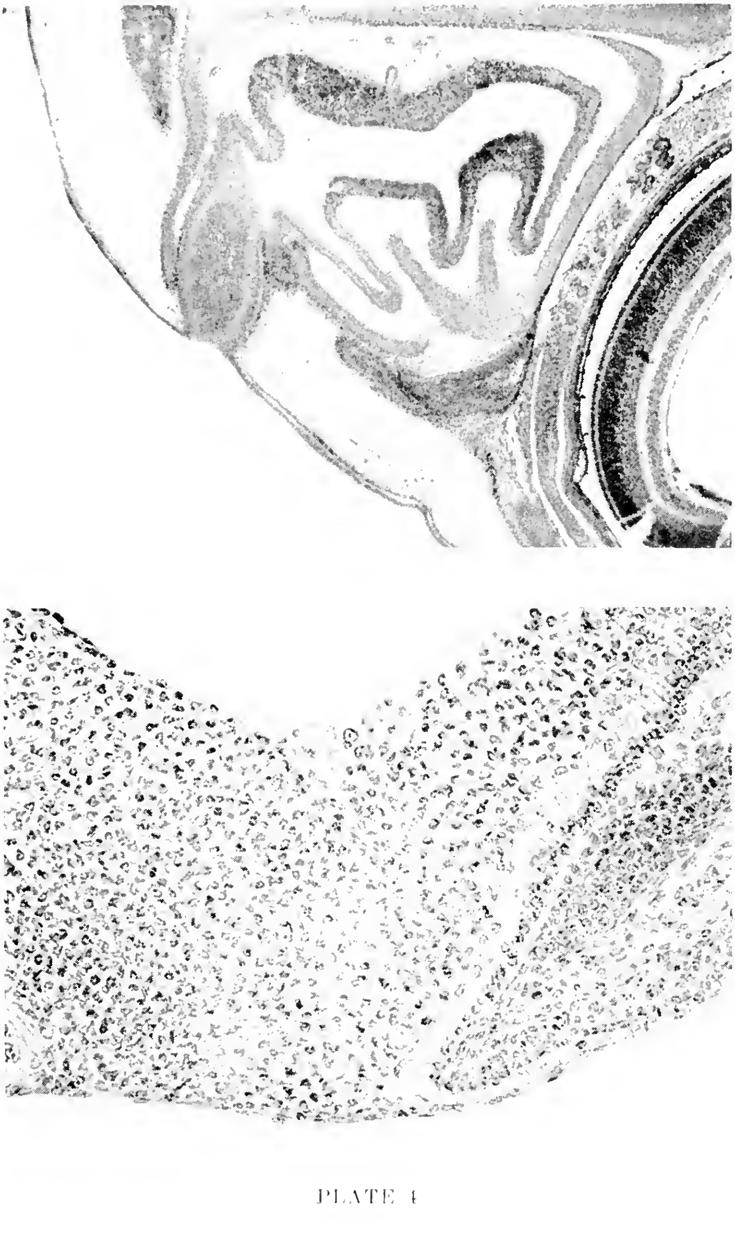

PLATE 4

PLATE 5

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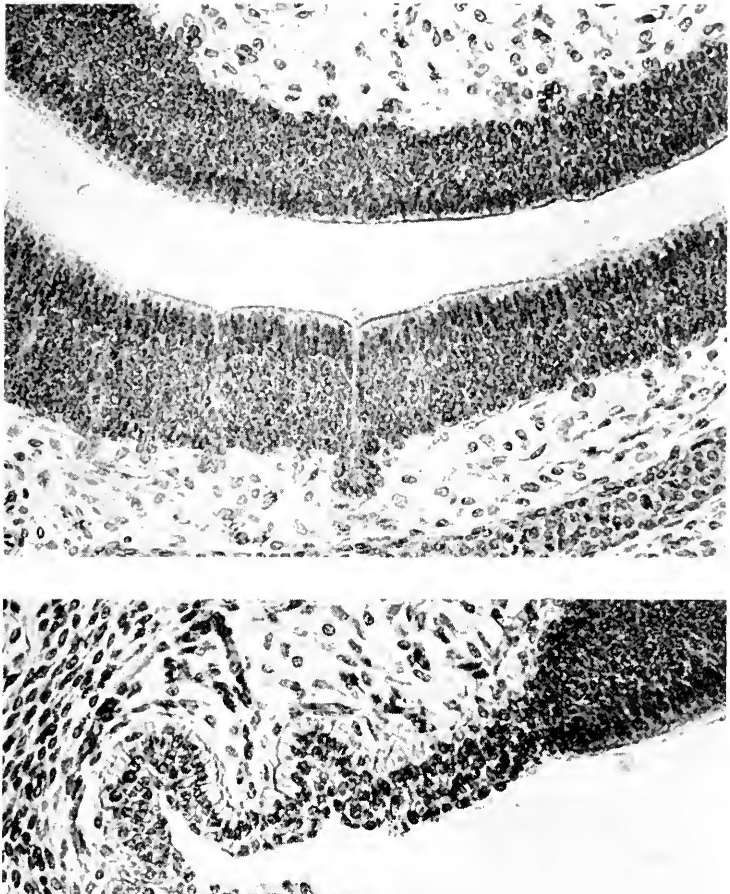

PLATE 5

PLATE 6

Figure 84. *Upper figure. Thamnophis* 1350 (7.4; MC). Transverse section through Jacobson's organ at a stage immediately preceding the formation of the columns. The dorsal surface is to the right and the midline toward the top (section 194). 275x.

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PLATE 6

PLATE 7

Figure 86. *Upper figure.* *Thamnophis* 1323 (11.0; MC). Transverse section through Jacobson's organ showing the continued growth of the columns. The dorsal surface is to the right and the midline toward the top (section 226). 275x.

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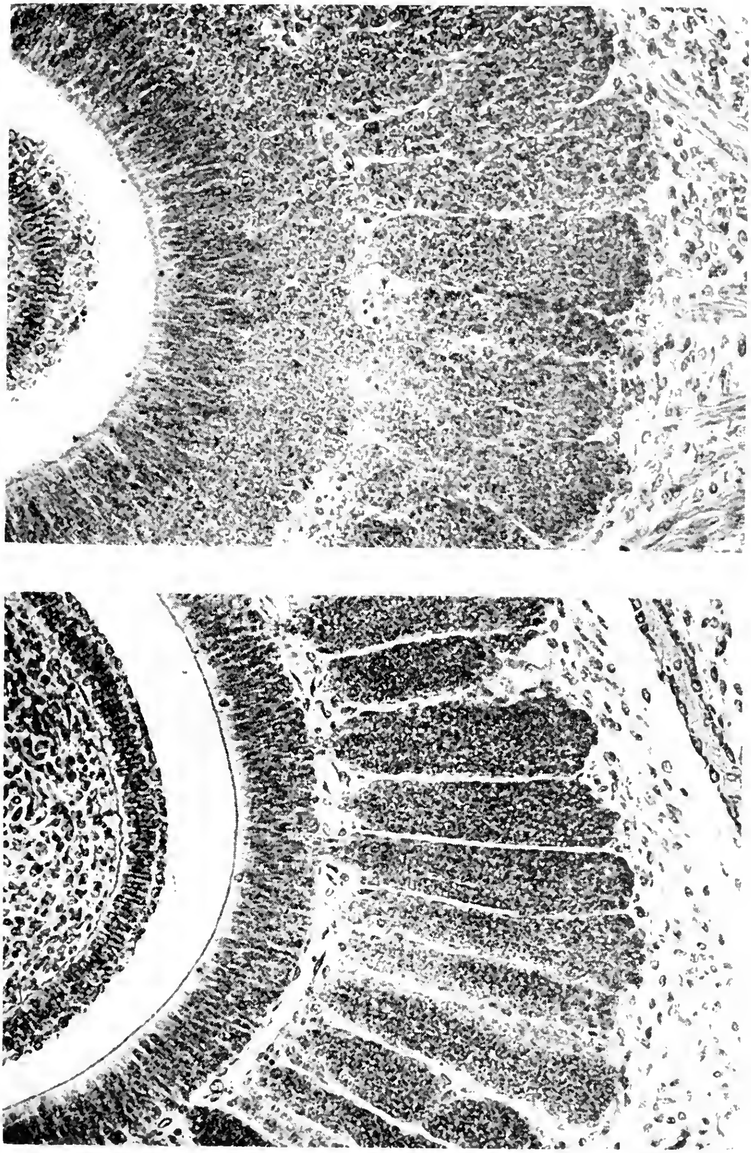

PLATE 7

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

VOL. 120, NO. 3

THE RODENTS OF THE DESEADAN OLIGOCENE OF PATAGONIA AND THE BEGINNINGS OF SOUTH AMERICAN RODENT EVOLUTION

By ALBERT E. WOOD AND BRYAN PATTERSON

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
MAY, 1959

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No. 3 — *The Rodents of the Deseadan Oligocene of Patagonia and the Beginnings of South American Rodent Evolution*

BY ALBERT E. WOOD AND BRYAN PATTERSON

CONTENTS

INTRODUCTION

Several years ago, one of us (Wood, 1949) undertook the study of two excellent rodent skeletons from the Deseadan of Patagonia in the collections of The American Museum of Natural History. This work emphasized the need for a review of the Deseadan rodent fauna as a whole, a project that we had had in mind for many years and for which each of us had been taking notes in somewhat desultory fashion. A first draft, based on material in the Amherst collection, was written by Wood. This was revised and extended by Patterson on the basis of specimens in Chicago Natural History Museum, The American Museum of Natural History, and the Muséum National d'Histoire Naturelle. A second draft, on which we collaborated, was then prepared. After this had been completed, the opportunity to convert the review into a monograph was afforded by the award of a John Simon Guggenheim Memorial Foundation Fellowship to Patterson for work in Argentina. Study of the types and other specimens in the Ameghino Collection revealed so much that was interesting and unexpected that the second draft had to be extensively revised. We then collaborated on the writing of a third draft. This was finally rewritten to include a discussion of the series of important papers on rodent phylogeny that have appeared during the last eight years. The work has indeed been a long time in preparation, but we believe that its present completeness fully justifies the delay.

The number of specimens available is surprisingly large. There are approximately 70 (mainly isolated teeth) in the Muséum

National d'Histoire Naturelle; 54 (including many complete jaws or upper dentitions) in the Amherst College Museum; 27 in the Ameghino Collection, now preserved in the Museo Argentino de Ciencias Naturales; 9 in Chicago Natural History Museum; 9 in the Yale Peabody Museum; 5 in the Museum of Comparative Zoology; and 11 in The American Museum of Natural History; a total of over 185. Loomis (1914, p. 20) mentions 102 rodent specimens, all but 6 being *Cephalomys,* collected by the Amherst Expedition (not by the Princeton Expeditions, as stated by Landry, 1957a, p. 53 — the Princeton Expeditions, to Hatcher's sorrow, never saw the Deseado). In his text, however, (pp. 189, 190 and 192) Loomis gives totals of specimens under individual species of *Cephalomys* that add up to 79, for a total rodent collection of 85. We have found 74 numbered specimens collected by Loomis (54 in Amherst, 9 in the Yale Peabody Museum, 5 in the Museum of Comparative Zoology and 6 in the American Museum of Natural History). Some of these consist of groups of isolated teeth. We do not know whether this is Loomis' entire collection, or whether there are, in other museums, additional specimens, or lots, that we have not been able to locate.

The locality known as Cabeza Blanca on the Río Chico del Chubut, Province of Chubut, has yielded the largest number of specimens. All of the specimens in Amherst, Yale and the Museum of Comparative Zoology, all but two of the Chicago specimens, and all but three of the American Museum specimens are from here. To judge from the color, preservation, adhering matrix and one of two labels preserved with them,[1] all but one

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[1] This label reads "Gran yacimiento del Pyroterio-Río Chico," which can only mean Cabeza Blanca. Other labels clearly referring to this locality read "Ier yacim. Pyroth. Río Chico," i.e. the first Deseadan (*Pyrotherium* beds) locality encountered on the way up the valley of the Río Chico del Chubut. It might be assumed from the wording that this was *the* first Deseadan locality found by Carlos Ameghino, but such is not the case. Isolated remains of Deseadan mammals from Neuquen (*Pyrotherium romeri, Trachytherus spegazzinianus, Parastrapotherium ephebicum*) reached Florentino Ameghino during 1885-1889, and Carlos had come across Deseadan localities in Santa Cruz and Chubut during 1888-1892, but was prevented by unfavorable circumstances from making collections. It was not until his seventh expedition to Patagonia, 1893-4, that Carlos was able to collect a Deseadan fauna and to prove that the beds lay beneath the Patagonian formation. The material collected during this expedition formed the basis of Florentino's first paper on this fauna, his "Première Contribution" (Ameghino, 1895, pp. 603-606). Judging from the forms represented, the color and preservation of the specimens, the adhering matrix and such labels as are present, there can be no doubt that the locality or area was that now known as La Flecha in Santa Cruz Province, situated a little distance to the south of the inlet of the Río Deseado. This, then, should be considered the type locality. By a happy coincidence, most of the Deseadan material, collected by Tournouër and studied by Gaudry, who proposed the name Deseado, came from this locality. The localities at Cabeza Blanca and Lake Colhué-Huapí were not discovered by Carlos Ameghino until 1894-1896, and material from them was first described by Florentino Ameghino in his "Deuxième Contribution" (1897c).

of Ameghino's specimens are also from this locality. The *Platypittamys* material in the American Museum is from the Scarritt Pocket, Rinconada de los Lopez, Chubut. All of the material in the Muséum National d'Histoire Naturelle is from La Flecha, Santa Cruz, as are the specimens not from Cabeza Blanca in Chicago Natural History Museum and in the Ameghino Collection. The specimens in the Ameghino Collection were, of course, collected by Carlos Ameghino; those in the Muséum National d'Histoire Naturelle by André Tournouër; those obtained by the Amherst College expedition were collected by Frederick B. Loomis, William Stein, Waldo H. Shumway and Phillip L. Turner; in Chicago Natural History Museum by Elmer S. Riggs, John B. Abbott and George F. Sternberg; and those from the Scarritt Expedition, in The American Museum of Natural History, by George Gaylord Simpson, Coleman S. Williams and Justino Hernandez. Tournouër was the only collector who found rodents in numbers at La Flecha. He very probably happened upon a small pocket containing them. The fact that Carlos Ameghino, who clearly had a magnificent eye for minute specimens, found only one isolated molar there is sufficient proof that they are really rare at the locality. The Chicago specimens from there consist of a ramus, and of an isolated molar that was found, during preparation, in the matrix surrounding a large mammal.

To date, seven genera have been described from the Deseadan: *Cephalomys*, *Asteromys* and *Orchiomys* Ameghino 1897, *Eosteiromys* Ameghino 1903, *Scotamys* and *Litodontomys* Loomis 1914, and *Platypittamys* Wood 1949. The Deseadan species *medianus*, referred by Ameghino to *Eosteiromys* (type species *E. homogenidens* Ameghino 1902 from the Colhué-Huapí) is here made the type of a distinct genus, *Protosteiromys*, and two other new genera, *Deseadomys* and *Chubutomys*, are proposed. *Orchiomys* is shown to be a synonym of *Cephalomys*. Eight genera and twelve species of Deseadan rodents are now known, but fragmentary remains too incomplete for formal description show that we are as yet far from a complete knowledge of the fauna. The phylogenetic relationships are very interesting and, for the most part, quite determinable. Six families, representing all four of the currently recognized superfamilies of South American rodents, are represented. Despite this apparent diversity, the Deseadan is not far from showing the basic stage from which the indigenous Neotropical rodent fauna has been derived.

Each of the adequately known forms has been compared with its possible ultimate ancestors, particularly the North American Paramyidae and Sciuravidae, the European Theridomyidae, and the African forms included by Wood (1955, p. 172) in the Phiomyidae, although these comparisons may not always be discussed in detail. In no case does the material here considered warrant the statement that any known form from the rest of the world is definitely ancestral to the Deseadan rodents. It is possible, however, to arrive at what we consider to be reasonable inferences as to the source of the South American rodents, and we have gone into this matter at length after the description of the fossils.

In addition to the Guggenheim Foundation Fellowship, this study has been assisted by grants to Wood from the Marsh Fund of the National Academy of Sciences, by tenure of a Cutting Traveling Fellowship from Columbia University by Wood, which afforded the opportunity for first hand study of numerous theridomyids, by tenure of a Carnegie Corporation Grant-in-aid for Travel awarded to Patterson by the American Association of Museums, which made possible a preliminary examination of the Deseadan material in the Muséum National d'Histoire Naturelle, and by a grant from the National Science Foundation to Wood, which permitted, incidental to other work, the statistical analysis of the material belonging to *Cephalomys*. We wish to express our sincere thanks to Professor Camille Arambourg, Muséum National d'Histoire Naturelle; Dr. George Gaylord Simpson, The American Museum of Natural History; Dr. J. T. Gregory, Yale Peabody Museum; and Drs. Agustín E. Riggi, Noemí Cattoi and Jorge L. Kraglievich, Museo Argentino de Ciencias Naturales, for their kindness in permitting the study and description of material in their charge. We are especially obliged to Professor Arambourg for sending the Tournouër Collection to us for detailed study. The statistical studies were made by Frances W. Wood, for whose assistance in this and in many other ways we are deeply appreciative. Regression lines were calculated by Mr. Craig C. Black. The aid of Mrs. William D. Turnbull and of Mrs. Elizabeth E. Wareham in preparing several

drafts of the manuscript is gratefully acknowledged. Figures 21, 24 and 26 were drawn by Señorita Estela Lescano, Figure 1 by Mrs. Dorothy Marsh; the remainder are by Wood.

The following abbreviations are employed: A.C.M., Amherst College Museum; A.M.N.H., The American Museum of Natural History; C.N.H.M., Chicago Natural History Museum; M.A.C.N., Museo Argentino de Ciencias Naturales; M.C.Z., Museum of Comparative Zoology: M.N.H.N., Muséum National d'Histoire Naturelle; and Y.P.M., Yale Peabody Museum.

MOLAR TERMINOLOGY AND MEASUREMENT

As discussed in detail on later pages, we believe that all indigenous South American rodents were derived from ancestors whose molars had four transverse crests on each tooth, both uppers and lowers. Adopting the terminology suggested by Wood and Wilson (1936), we employ the following terms for these crests: anteroloph, protoloph, metaloph and posteroloph in the upper teeth; anterolophid, metalophid, hypolophid and posterolophid in the lowers (Fig. 1). There is some uncertainty, due to a tendency to shift position, as to whether the terms protoloph and metaloph in the upper teeth, and metalophid and hypolophid in the lowers, are strictly applicable throughout, or whether such terms as protolophule II or hypolophulid I should be employed in some cases. The crests are strictly homologous throughout this group of rodents, however, and we have therefore thought it best to employ a uniform nomenclature rather than to introduce new terms whenever shifts occur in the relation of, say, the protoloph to the protocone or of the hypolophid to the hypoconid.

For the valleys between these crests, we have borrowed terms from Stirton's nomenclature for castorid teeth (1935), as modified by Black and Wood (1956). In the uppers, these are: paraflexus, mesoflexus and metaflexus (external) and hypoflexus (internal); in the lowers: hypoflexid (external) and anteroflexid, mesoflexid and metaflexid (internal). Whenever a valley is converted into a lake, either by wear or by the complete union before wear of the extremities of the flanking crests, the endings -flexus and -flexid become -fossette and -fossettid, e.g. parafossette, metafossettid (Fig. 1). In general, our terminology agrees with that of Fields (1957, Fig. 2). We do not, however, agree with his use of parafossettid and paraflexid in the lower teeth since we cannot accept the implied suggestion that these teeth incorporate a paraconid, and we therefore prefer the terms anterofossettid and anteroflexid. A second point of disagreement concerns the ter-

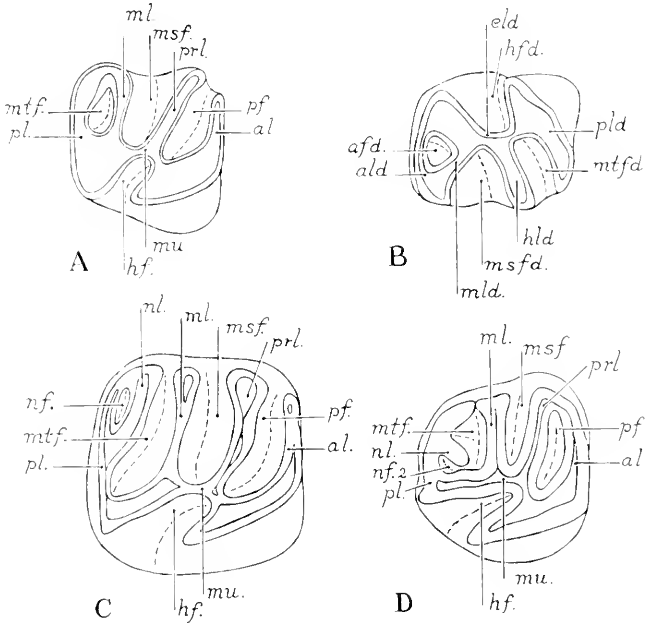

Fig. 1. Key to terminology applied to crests and valleys of molar teeth. *A* and *B*, RM^1 and RM_1 of *Deseadomys arambourgi* gen. et sp. nov.; *A*, A.C.M. no. 3163; *B*, type, M.N.H.N. no. 1903-3-1. *C*, LM^1, reversed, of *Protosteiromys medianus* (Ameghino), A.C.M. no. 3014. *D*, RM^3 of *Erethizon dorsatum epixanthum* Brandt, M.C.Z. no. 36718. *A-C*, x 6; *D*, x 3.

Abbreviations: *afd.*, anterofossettid; *al.*, anteroloph; *ald.*, anterolophid; *eld.*, ectolophid; *hf.*, hypoflexus; *hfd.*, hypoflexid; *hld.*, hypolophid; *ml.*, metaloph; *mld.*, metalophid; *msf.*, mesoflexus; *msfd.*, mesoflexid; *mtf.*, metaflexus or metafossette; *mtfd.*, metaflexid; *mu.*, mure; *nf.*, neofossette; *nf.2*, lingual neofossette; *nl.*, neoloph; *pf.*, paraflexus; *pl.*, posteroloph; *pld.*, posterolophid; *prl.*, protoloph.

minology in the lingual side of the upper teeth, where Fields calls the valley that separates the anteroloph from the protocone the hypoflexus, instead of using that term, as did Stirton and as do we, for the valley between the protocone and the hypocone.

There is a rather common tendency among South American rodents for the development of a fifth crest in the upper molars. Less commonly, a fifth crest may arise in the lower molars. These crests arise from the posteroloph above and from the anterolophid below. As pointed out farther on (pp. 334-336), they have nothing to do with the mesoloph and mesolophid of the Theridomyidae and other rodents; such crests do not occur in the permanent molars of caviomorphs. For descriptive convenience, we employ the terms neoloph and neolophid for these fifth crests, and neofossette and neofossettid for the lakes isolated by them. Fields' entoflexus and entofossette are the same as our neoflexus and neofossette.

We prefer definite names for these crests and valleys to such more general terms as first, second, etc. anticlinals and synclinals employed by Stehlin. The latter have the merit of simplicity but the defect of implying homology wherever used. A five-crested caviomorph molar and a five-crested theridomyid molar, for example, do not, we believe, have all their crests and valleys homologous.

The molar terminology is applied to structures on premolars that occupy the same position, relative to the tooth as a whole, as those on molars. It is recognized, however, that some of them, at least, may have had a different history. At the present time, the evolutionary sequence in rodent premolar development is often clouded. The development of the premolars in the Caviomorpha is a case in point.

The tooth measurements given are the maximum diameters, in millimeters, of the various areas measured. Depending on the nature of the specimen, they may be either diameter of the wear surface, maximum diameter of the extra-alveolar portions of the teeth, or the maximum diameter whether extra-alveolar or intra-alveolar. The second group of these measurements has been marked † and the last *. The diameters given are averages of two to four measurements. There is considerable variation in some of the high-crowned teeth as to the location of the maximum diameter. The measurements made from figures will not necessarily agree with those listed. The drawings have been made looking down perpendicularly on the wear surface. In many specimens, however, the wear surface is oblique to the long axis of the tooth, so that the drawing will show, for example, a considerable expanse of the lower part of the tooth on the lingual side of the crown, without indicating that there is an extensive overhang on the buccal side.

TAXONOMY AND MORPHOLOGY

Suborder CAVIOMORPHA Wood and Patterson 1955 (*in* Wood, 1955)

The Caviomorpha may be defined as follows: rodents with enlarged infraorbital foramen, through which progressively passes M. masseter medialis, pars anticus; infraorbital foramen frequently approaching orbit in size; angle of jaw of hystricognath type; malleus and incus fused or separate; dental enamel of multiserial type but derivable from an ancestral stock with enamel of pauciserial type; cheek teeth derived from an ancestral stock with four transverse crests on both upper and lower molars; permanent molars without mesoloph or mesolophid; metaloph and metalophid frequently unstable, disappearing in some groups; neoloph and neolophid arising in some groups from posteroloph and anterolophid respectively; restricted to the New World. Known distribution: Oligocene to Recent, South America; Pleistocene to Recent, North and Central America and Antilles.

In addition to these characteristics, several supplementary myological features may be cited. M. palmaris longus generally arises from the olecranon or is lost, though in the erethizontids and caviids it arises in the primitive manner from the medial epicondyle, as it does in the Old World hystricomorphs. M. trapezius is generally divided into two or three separate elements, although it is a continuous sheet in the erethizontids, as in *Aplodontia* and *Hystrix;* in the African *Petromus* there are three elements. M. omohyoideus is progressively lost, whereas it is present in the Old World Hystricomorpha. M. sternoscapularis is present in its entirety, but the fibers of the two halves are separated at the clavicle, as in *Petromus,* whereas they are continuous in *Hystrix* and *Thryonomys.* There is a tendency to lose the inner head of M. brachialis. The insertion of M. pronator teres has shifted from the distal to the proximal part of the radius.

Perhaps these muscle variants are of no great importance in themselves, but it appears to us that they are as significant in separating the Caviomorpha from the Old World Hystricomorpha as are myological characters sometimes cited as favoring the union of the two groups. Of all the characteristics that have been used to classify rodents, there are none so subjective as variations in muscles, no two authors ever seeming to give the same description for a given group of muscles. There are also few systems in the order where individual variation is less well understood.

Some caviomorphs possess five-crested molars, but the fifth crest (neoloph, neolophid), which was evidently acquired after the group had reached South America, is not homologous with the mesoloph or mesolophid of the Theridomyidae nor (probably) of the Hystricomorpha. In dm_4, of certain echimyids (*Protacaremys, Prospaniomys*) and erethizontids (*Erethizon* and *Coendou*) and in P_4 of some Santacruzian octodontids (*Sciamys*), a short crest may develop from the ectolophid posterior to the metalophid. Topographically, this occupies the position of the mesolophid in theridomyids and other rodents, but it is certainly an independent acquisition and does not extend posteriorly to the molar series. Within *Sciamys*, there is evidence that this and other minor crests posterior to the anterolophid developed essentially at random in P_4 (Patterson and Kraglievich, ms.).

On the basis of serology, Moody and Doninger (1956) conclude that there is no indication of special affinity between the Hystricomorpha and the Caviomorpha, based on studies of *Hystrix, Erethizon, Cavia* and *Dasyprocta.* Still another line of evidence that may be cited is that of ectoparasites, Vanzolini and Guimarães (1955 a and b) pointing out that there is no special relationship between the lice of caviomorphs and of hystricomorphs.

We believe that the indicated relationships warrant the separation of the South American rodents as a distinct suborder, the Caviomorpha. We believe that it can be considered as demonstrated that the South American forms were not descended from the European Theridomyidae, whether or not any of the Old World forms were. There does not seem to be any possibility that the Old and New World rodents generally placed in the "Hystricomorpha" (*sensu lato*) could have had a common ancestor later than the Early Eocene members of the Paramyidae. The similarities between the Old and New World forms must then all be examples of parallelism. Cabrera (1927) has reached broadly comparable conclusions, although without presenting supporting evidence. Lavocat (1951b) expressed a similar opinion, although he continued to place the Old and New World forms in a common group, based on jaw structure, and distinct from that in which the Paramyidae are placed. In another paper (1951a), he questioned there being any special relationship between the two groups, although later (1956), as discussed below, he returned to the possibility of special, though not close, relationships. Schaub (1953 a and b), Viret (1955), and Landry (1957a) have supported affinity between the Old and New World "hystricomorphs," which we do not accept for a variety of reasons given in detail below.

Since there are morphologic grounds on which the Old and New World "hystricomorphs" can be separated from each other, and since the paleontologic and particularly the paleogeographic evidence is against the two groups having a common ancestor later than the Early Eocene, we feel entirely justified in establishing a suborder for the South American forms, even though the morphologic criteria for doing so may appear to be neither exceptionally strong nor exclusive to the group. Similar situations will almost certainly be encountered as knowledge of rodent phylogeny improves. The classic subordinal divisions do not, it seems to us, stand on a secure foundation, and, in view of the abundantly demonstrated prevalence of parallelism in the order, can hardly be expected to stand unmodified indefinitely.

The microstructure of the dental enamel provides an interesting case in point, and one with a direct bearing on the present question. Over a hundred years ago, in his classic work on the microstructure of rodent enamel, Tomes (1850) showed that the crossing enamel layers in the incisors of "hystricomorphs" were each composed of several laminae of enamel prisms, a character that set them apart from other rodents. Here, seemingly, was a character as fundamental as the zygomasseteric structure for uniting Old World and New World "hystricomorphs" in the same suborder. Korvenkontio's magnificent work on the same subject (1934) suggests another interpretation, however. The "hystricomorphs" are indeed characterized, as Tomes showed, by crossing enamel layers composed of several laminae, Korvenkontio's multiserial type, in contrast to "sciuromorphs" and "myomorphs," which have the crossing layers composed of a single lamina, the uniserial type. Korvenkontio shows, however, that early, very primitive rodents have a type of enamel structure, which he calls the pauciserial type, that is intermediate between the two extremes, having neither as many laminae to a layer as in the multiserial nor as few as in the uniserial. The pauciserial type occurs both in paramyids and in some theridomyids.[2] It seems clear to us, therefore, that enamel of multiserial type could have been evolved independently by the ancestors of both the Hystricomorpha (*sensu stricto*) and the Caviomorpha; the evidence from the histology of the teeth does not now conflict with other evidence derived from gross morphology and from distribution. Sections of an isolated incisor from the Deseadan, probably of *Scotamys*, have been prepared. These show that, as might have been anticipated, multiserial enamel had already been acquired by this time.

The relations of the malleus and incus provide a similar case. Doran (1878, p. 418) stated that in the "Hystricomorpha" these ossicles were almost invariably fused in adults. Tullberg (1899, p. 69) gave such fusion as a character of his Hystricognathi, and Landry has recently (1957a, p. 16) given it great prominence as an item of evidence in favor of the unity of the Hystricomorpha (*sensu lato*). It must be noted, however, that Cockerell and Miller (*in* Cockerell, Miller and Printz, 1914, p. 372) found these ossicles to be separable in *Proechimys*.[3] We find that in *Echimys armatus*,

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[2] Because some theridomyids have the pauciserial type of enamel and some have the uniserial type, Landry (1957a, pp. 27-28) following Korvenkontio, considers that the Theridomyidae are a composite group, with members belonging to two suborders. This appears to us to be a misinterpretation of the data, which merely indicate that, in this feature, the Theridomyidae are in process of passing from a pauciserial to a multiserial type. The discovery of such transitional forms should, of course, come as no surprise.

[3] These authors also questioned one of Doran's exceptions, a young specimen referred by him to *Octodon*, stating that this looked very sciurine to them. They were quite right; a malleus and an incus of *O. degus* extracted by us from a skull are typically caviomorph in structure and bear no close resemblance to the bones so labeled by Doran.

Octodon degus, Spalacopus poeppigii and *Aconaemys* sp. the malleus and incus are not fused. Since the Octodontidae and Echimyidae are the most generalized of the caviomorph families, we strongly suspect that the lack of fusion in their auditory ossicles indicates that such fusion was acquired independently within the Caviomorpha.[4] The condition of the malleus and incus of *Pedetes* is of some interest in this connection, as showing that very close union is not confined to caviomorphs and hystricomorphs. Landry, following Tullberg, states that in this form the ossicles are separate, and that "this character, therefore, has proved useful in separating dubious groups from the Hystricomorpha" (*op. cit.*, p. 16). Doran had stated that these ossicles were fused in *Pedetes*. Upon investigation we have found them to be separable but with opposing surfaces complexly interlocking in both the vertical and horizontal planes. There is clearly even less possibility of movement between the two bones than in octodontids and echimyids. This anomalous rodent thus exhibits a "sciurognath" mandible, a "hystricomorph" zygomasseteric region, "hystricomorph" enamel, a "sciurognath" pterygoid fossa, and a malleus and incus at least as "hystricomorph" in degree of union as are some of those occurring in caviomorphs. *Pedetes* is, in fact, a standing warning against too dogmatic statements as to what does and what does not characterize major groups of rodents.

Our suborder Caviomorpha is not a new concept. The word "caviomorphs" was used by Simpson (1950, p. 376) for exactly the same group that we are including in the Caviomorpha, but without being formally proposed as a subordinal term, and without definition. Lavocat (1951b, p. 72) proposed a number of divisions of the rodents including one, the "Orthohystricognathes," for the forms we include in the Caviomorpha. Schaub (1953a) established an Infraorder Nototrogomorpha for the same group. Wood (1955, p. 180) proposed the suborder Caviomorpha, crediting it to the present authors. For reasons which we elaborate below, we feel that both Lavocat's and Schaub's

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[4] As Fields (1957, p. 347) implies, the auditory ossicles of rodents merit more study than they have received. As a minuscule contribution to this subject, we may record the following additional data as to fusion: *Abrocoma cinereus*, juv., separable; *Abrocoma bennetti murrayi*, adult, inseparable; *Ctenomys magellanicus*, adult, inseparable; *Thryonomys swinderianus angolae*, juv., inseparable, area of fusion involving part of crus longus of incus.

terms contain phylogenetic implications that we distrust, and we are therefore continuing to use Caviomorpha, which, we feel, carries the minimum of phylogenetic implications involving other groups. The rules of priority do not apply to subordinal units, but it is possible to make a legalistic (although not very impressive) argument, if one wanted, that Simpson's usage establishes the priority and that neither Lavocat nor Schaub provided diagnoses or definitions. In any event, we feel that the entire problem of the subordinal and superfamilial arrangement of the rodents is at present in a state of flux, and that the next decade will see a considerable alteration in our knowledge of rodent relationships as indicated by subordinal terminology, so that the precise terminology now employed makes little difference.

Superfamily OCTODONTOIDEA Simpson 1945

Family OCTODONTIDAE Waterhouse 1839

Acaremyinae Ameghino 1902
Acaremyidae Wood 1949

The most surprising result of a revision of the *Acaremys-Sciamys* group and a comparison of these forms with Pliocene and Recent octodontids (Patterson and Kraglievich, ms.) was the realization that the former could not be separated from the latter, either as a family or as a subfamily. Winge (1924, pp. 73, 78) would appear to have been right in his reference of "*Acaromys*" and "*Sciomys*" to his Octodontini, Octodontes. A gap exists in our knowledge of the Octodontidae between the Santacruzian and the Huayquerian, but *Sciamys* on one side of this gap and the Pliocene forms on the other are sufficiently close to each other in dental and cranial characters as to permit no doubt on this score. *Sciamys* has rooted molars but, in contrast to those of the contemporary *Acaremys*, these were well on the way toward attaining the hypsodont condition. This trend was carried to completion, and cement added, during the hiatus in the history of the family. The later forms are nearly all hypselodont, but the Huayquerian to Hermosan *Phtoramys* does develop roots in old age, and the changes in crown pattern that it displays are very similar to those seen in *Sciamys* and, more fleetingly, in *Acaremys*. The postcranial skeleton of the Deseadan

Platypittamys (Wood, 1949) is amazingly similar to that of *Octodon* itself (with which Wood did not have an opportunity to compare it), considering the vast time interval between the two. The chief differences lie in the proportions of the hind limb elements, and even these are not great. The tibia and fibula and the metatarsals are somewhat longer in the Recent form. The intersegmental indices of *Octodon* are: humerus/radius = 1.06; femur/tibia = 0.83: intersegmental index, $\frac{R + H \times 100}{T + F} = 67.3$; the corresponding figures for *Platypittamys* (Wood, 1949, pp. 42-43) are 1.04, 0.99 and 67.0. The tibia and fibula remain separate in *Octodon* as in *Platypittamys*, as indeed they do in many caviomorphs. In old individuals in several families, the expanded proximal portion of the fibula fuses with the tibia, but, in all skeletons we have examined, the distal ends are separate. We interpret fusion of either end of these bones, then, as a progressive character of the modern Caviomorpha (whatever it may have been in the Old World forms). We feel that the distribution of proximal fusion of these bones within the suborder very clearly demonstrates that the two bones were separate in the ancestral stock, a conclusion diametrically opposed to that reached by Landry (1957a, p. 19). It would appear that, apart from the hypselodont cheek teeth, *Octodon* and other nonfossorial octodontids are among the most generalized of living caviomorphs.

It must also be noted (see below, p. 300) that the Acaremyinae of Ameghino, Scott and others (Wood's Acaremyidae) included a number of forms that are in reality members of the very closely related Echimyidae. We may also note in passing that the supposed Colhuehuapian octodontid "*Eoctodon*" is also an echimyid (see p. 302), and not an "acaremyine" as stated by Landry (1957a, pp. 39 and 56).

On the basis of his study of *Platypittamys*, Wood concluded that the "Acaremyidae" were ancestral, at least structurally, to all rodents here included in the Caviomorpha, with the possible exception of the Erethizontidae. This conclusion stands unchanged, except that the word "Acaremyidae" must be replaced by "primitive Octodontidae."

PLATYPITTAMYS Wood

Platypittamys Wood, 1949, p. 5.

PLATYPITTAMYS BRACHYODON Wood

P. brachyodon Wood, 1949, pp. 6-43, Figs. 1-6, 8.

P. brachydon (*sic*), Landry, 1957a, pp. 92, 93.

Horizon and locality. Deseado formation; Scarritt Pocket, Rinconada de los Lopez, Chubut.

This genus has been described in detail by Wood, and there is no need to repeat his account. This opportunity is taken to point out that he erroneously labeled Figure 3C as left instead of right and Figure 3D as right instead of left.

The work reported on here and studies of later octodontids (Patterson and Kraglievich ms.) necessitate some discussion of the previous interpretation of P^4. The pattern of this tooth in *Platypittamys* is such that it could not have been derived from that of any described paramyid except by considerable reduction or degeneration. A recently discovered but still undescribed lower Gray Bull paramyid, however, has a premolar that could readily have given rise to that of *Platypittamys:* this suggests the possibility that there has been no secondary reduction in P^4 of the Caviomorpha.

By comparison with later members of the family, a terminology of the parts of the premolar has been adopted with the avowed intention of making the premolar terminology of the later octodontids agree with that of the molars, with the full understanding that the homologies suggested may be incorrect. This may or may not be phylogenetically justifiable, but is certainly convenient.

On this basis, we now interpret the premolar of *Platypittamys* as having a lingual protocone, and a buccal paracone and metacone, widely separated, the former incorporated in the protoloph and the latter in the posteroloph. No trace of a separate metaloph is present. There is a well-developed anterior cingulum, approaching the stage where it would be called an anteroloph. The Santacruzian *Sciamys* shows that the metaloph in octodontids was a later addition to the premolar crown that arose as a low, inconspicuous ridge on the anterior slope of the posteroloph.

Available evidence strongly suggests that in all caviomorphs the metaloph is the last of the premolar crests to come into existence, being formed in some groups by a progressive division of the posteroloph that begins with the development of a minute fossette in this crest.

Wood regarded the single posterior crest of P_4 of *Platypittamys* as the hypolophid. Conditions in *Sciamys* tend to confirm this interpretation. In that genus, some examples of P_4 occur in which the talonid is as simple as that of *Platypittamys;* others show various stages in the formation of a posterolophid by development of a cingulum posterior to the internal half of the hypolophid. In one individual (M.A.C.N. no. A 1879), however, the entoconid is connected to the ectolophid by a crest anterior to, and obviously formed later than, that joining the entoconid to the hypoconid. Development of a notch posterior to the entoconid in this specimen would have converted what is clearly the equivalent of the hypolophid in other individuals into a posterolophid. Such differences are trivial but they do show that the two talonid crests of the caviomorph P_4 could have arisen in different ways in various groups. Conditions in P_4 of the Deseadan cavioid *Asteromys* in fact suggest that the hypolophid arose in a manner comparable to that of the anterior crest in the aberrant *Sciamys* just discussed.

On the other hand, there still remains the possibility that there is no direct connection between the undescribed Gray Bull form and *Platypittamys,* in view of the very considerable time gap. A gap of this size is certainly too large to permit phylogenetic conclusions to be drawn with any confidence. The possibility should not be lost sight of that P^4 of *Platypittamys* is secondarily simplified. Such a simplification would not be entirely unexpected, and the possible sequence of events would be as outlined in the following paragraphs.

Among various groups of rodents, there has quite obviously been reduction of the premolars. In no known rodents are there more than two upper and one lower premolars. No one doubts that this is a reduction from the primitive placental formula. A premolar formula of $\frac{2}{1}$ is retained by only a few rodents, including most of the typically Eocene Ischyromyoidea, and the Sciuridae. Many other rodents show varying traces of reduction, to P^1_1 or P^1_0, before we reach the cricetid and murid condition of P^0_0. We explicitly accept this dental formula for these families, without any prejudice as to other families where dm^4_4 may have been retained and M^3_3 lost, which is surely not true of the Muroidea. The Caviomorpha retain one upper and one lower premolar. They must, therefore, have lost the third upper premolar, which is present in the paramyids.

Obviously, there must have been a reduction of the premolars, in the Paleocene rodents, giving us a paramyid condition by the late Paleocene. There was then a halt in the reduction, until middle Eocene or later, when a number of groups continued the reduction of premolars, first losing P^3, then P_4, and finally P^4. It seems evident to us that this tendency to lose premolars must have been accompanied by a simplification of the pattern before the loss took place.

According to this interpretation, the premolars of *Platypittamys* (especially P^4) would represent a simplification from the *Paramys* pattern, which was followed by a secondary redevelopment of complexity in this tooth in the later Caviomorpha. While this would be a case of reversibility of an evolutionary trend, it nevertheless is still an entirely logical explanation of what happened among the Caviomorpha.

Platypittamys is extraordinarily primitive, for a caviomorph, in the small size of the infraorbital foramen. The two available specimens are both badly crushed but, despite this, the structure of the zygomasseteric region can be determined with reasonable assurance. The foramen can hardly have been appreciably larger than shown in Wood's figure (1949, Fig. 2). Landry (1957a, p. 93), reports that he was unable to confirm Wood's account of the size of this structure, stating that "if this is true, Wood has here an exact intermediate in zygomasseteric structure between the ischyromyids and one of the three advanced groups, something no one else has ever been able to find." An independent check of the specimens by both of us, however, has convinced us that Wood was correct in his interpretation. Perhaps some of Landry's difficulty in visualizing what has happened in the crushing of this part of the fossil may be explained by the fact that he has confused M^3 and P^4. As a result, a shifting of the palate to restore the break and to put M^3 in its proper place would move the lateral wall of the infraorbital foramen much less than would have been the case if Landry had been correct and the tooth had been P^4. The fact that there is no definitely marked area on the mandible for the insertion of M. masseter medialis, pars antieus, is in accord with the small size of the foramen, since it indicates that this division of the muscle (which is the one that passes through the foramen) was at best poorly developed. A recheck of the specimen again confirms Wood's statement that the masseter was apparently limited to the ventral surface of the zygoma, since there is no suggestion that any part of the muscle passes through the foramen. As Landry states (1957a, p. 93), the specimens are so crushed that it cannot be told whether the muscle had invaded the orbit. The contemporary *Cephalomys*, the only other Deseado rodent for which we have any knowledge of the skull, has an enormous infraorbital foramen, relatively larger than in its much later relative *Neoreomys*. It is very possible therefore that *Platypittamys* was a persistently primitive, little-modified survivor, in this respect at least, of the basic immigrant stock. In the Colhuehuapian species of *Acaremys* there is a well-defined area of insertion on the mandible for M. masseter medialis, pars antieus, indicating that this part of the muscle, and hence presumably the foramen through which it passed, was nearly, if not quite, as developed as in the Santacruzian species. Landry (1957a, pp. 93-94) questions whether it is likely that the enlargement of the foramen took place independent of the movement of the muscle. We agree that this independence of development may seem improbable, but the evidence seems to indicate that it took place.

As stated by Wood (1949, p. 29), there is an entepicondylar foramen on the humerus, and the proximal ends of the tibia and fibula are not fused (*op. cit.*, p. 36), which makes it difficult to accept Landry's thesis that the primitive "hystricomorphs" were characterized by proximal fusion of the tibia and fibula and by loss of the entepicondylar foramen (Landry, 1957a, pp. 19, 20).

The suggestion has been made that the Scarritt Pocket, in which *Platypittamys* occurs, may be somewhat older than the other Deseadan local faunas of Patagonia, but this does not now appear to be the case. The evidence strongly suggests that these faunas were all very nearly of the same age, since there is no indication of evolutionary change from one to another.

Platypittamys is the only known Deseadan octodontid. The family is actually a rare one in the Oligocene and Miocene. Only the Santacruzian *Sciamys* is reasonably common, and there are but four known specimens from the earlier horizons. The relatively abundant Colhuehuapian *Protacaremys*, as noted below, is not an octodontid, but an echimyid. A tentative approximation of a phylogeny of the Miocene and earlier forms is shown in Figure 2.

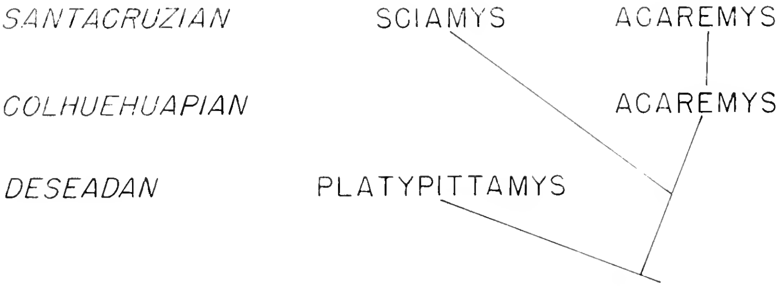

Fig. 2. Tentative phylogeny of the Oligocene and early Miocene Octodontidae.

Family ECHIMYIDAE Miller and Gidley 1918

The earliest Echimyidae are very similar to the earliest Octodontidae in molar structure, so much so that several of them have been placed in the latter family (in the guise of "Acaremyinae") by Ameghino, Scott and others. The similarities are so close that we have no hesitation in referring them to the same superfamily. Landry (1957a, p. 56) separates the two families widely, placing the Echimyidae in his Erethizontoidea. We feel that this disagreement is to some degree more apparent than real, since he, in common with most other authors, refers the earlier octodontids, as "Acaremyinae," to the Erethizontidae, and between these early octodontids and the early echimyids there is a very close affinity. Landry includes *Capromys* and its relatives as a subfamily of the Echimyidae and separates the nutrias (*Myocastor*) as a distinct family, which he places in the Octodontoidea. The echimyids and capromyids seem to be definitely related, and we believe that the nutrias also belong in the same major group, although we have no strong feelings as to the precise taxonomic rank that should be given them. Study of post-Deseadan members of the Echimyidae and Octodontidae (Patterson and Kraglievich, ms.) has revealed that the Colhuehuapian *Protacaremys* and "*Acaremys*" *preminutus*, and the Santacruzian "*Acaremys*" *minutus* and "*A.*" *minutissimus* and "*Sciamys*" *tenuissimus* are all echimyids. The molars of these forms may be distinguished from those of octodontids by the deeper anterior and posterior fossettes and fossettids, the somewhat more oblique lophs and lophids, the somewhat deeper paraflexus and metaflexid, a marked tendency toward reduction and loss of the metalophid (starting with M_3), and by the somewhat greater length as compared to width of unworn crowns. The most obvious difference in the dentition lies, however, in the retention of dm$^4_4$ and the suppression of P^4_4. This was first pointed out by Friant (1936a), who noted that in certain Recent and Pleistocene forms the anterior cheek tooth is invariably more worn than the molars and that there is no evidence that it was ever replaced. The abundant material examined by Patterson and Kraglievich shows that this is also true for all Tertiary forms from the Colhuehuapian on. From one Santacruzian specimen, they were even able to extract the crown of a premolar, of the *Acaremys* type, from deep within the ramus, below the first lower cheek tooth. It is virtually certain that this tooth would never have erupted.

Four Deseadan specimens, representing two distinct species of a new genus, *Deseadomys*, are certainly referable to this family on the basis of molar structure. The anterior cheek tooth is preserved in two of them and in both it is clearly an octodontid-like premolar and not a milk molar. This suggests that retention of dm$^4_4$ in the Echimyidae came about between Deseadan and Colhuehuapian time.

The phylogeny of the Echimyidae was evidently very complex, and the available material is insufficient to trace it in any great detail. A tentative phylogeny, however, is given in Figure 3, adapted from Patterson and Kraglievich (ms.). *Deseadomys* seems to be ancestral to the comparatively specialized *Adelphomys* group, composed of the Santacruzian *Adelphomys* and *Stichomys* and an undescribed Colhuehuapian genus, but not including *Protadelphomys*. The molars of *Deseadomys* are actually higher crowned than those of the Colhuehuapian *Protacaremys* and *Prospaniomys*. These last are sufficiently similar to suggest that their common ancestors may have lived in Deseadan time. The primary radiation of the Echimyidae was evidently in progress during the Deseadan and presumably had begun not long prior to it. Derivation from the primitive octodontid stem is clearly indicated. The Colhuehuapian *Eoctodon* Ameghino is neither valid nor an octodontid. The type species, *E. securiclatus*, is a synonym of *Protacaremys prior* and the larger *E. crassiusculus* is a synonym of *Prospaniomys priscus*. Both these forms are echimyids. The Santacruzian *Spaniomys* is highly variable, and *Gyrignophus complicatus* and *Graphimys provectus* appear to have been based on extreme variants of *S. modestus*.[5]

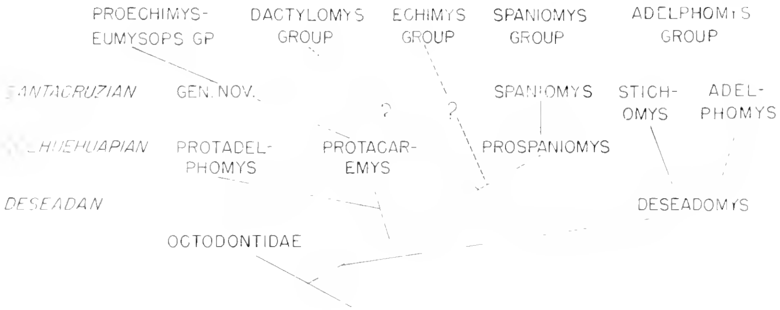

Fig. 3. Tentative phylogeny of the Oligocene and early Miocene Echimyidae.

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[5] J. L. Kraglievich (1957, p. 37) believes the "*Eumysops* group" (cf. Fig. 3) to be part of the subfamily Heteropsomyinae Anthony. The Pliocene genera *Proatherura* and *Proaguti* of Ameghino cannot be separated from *Eumysops*.

DESEADOMYS gen. nov.

Asteromys Loomis, 1914, pp. 194-195 (in part), *nec* Ameghino 1897c; Wood, 1949, pp. 4, 15, 16, 18-20; Schaub *in* Stehlin and Schaub, 1951, p. 60.

Type species. D. arambourgi sp. nov.

Distribution. Deseadan; Patagonia.

Diagnosis. Differing from all other known echimyids in replacement of dm$_4^4$ by P$_4^4$; cheek teeth mesodont, lower crowned than in *Adelphomys* and *Stichomys*, higher crowned than in *Protacaremys* and *Prospaniomys*, with unilateral hypsodonty in uppers but not in lowers; P^4 (known only in type species) not molariform, without metaloph, protoloph concave anteriorly; M^3 (known only in type species) more circular in outline and with hypocone less internal than in *Adelphomys* and *Stichomys;* P$_4$ (known only in type species) not molariform, without anterolophid, metaconid separated from protoconid by narrow cleft, metalophid rudimentary; lower molars more advanced in metalophid reduction than in *Protacaremys* and *Prospaniomys.*

A second species, *D. loomisi* sp. nov., somewhat more advanced than the type, is referred to the genus. The two species appear to have been trending toward the two Santacruzian genera, the type toward *Stichomys* and *D. loomisi* toward *Adelphomys.*

DESEADOMYS ARAMBOURGI[6] sp. nov.

Figs. 4-6

Asteromys prospicuus Loomis, 1914, p. 195 (in part), Fig. 128 (*nec* Ameghino 1897c); Schaub *in* Stehlin and Schaub, 1951, p. 60, Fig. 72.

Type. M.N.H.N. no. 1903-3-1, right mandible with I, P$_4$-M$_3$.

Hypodigm. Type and A.C.M. nos. 3163, right P^4-M^2 (described and figured by Loomis as *Asteromys prospicuus*)[7] and 3071, left M^3.

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[6] Named for Professor Camille Arambourg, as a slight return for his kindness in entrusting to us the Deseado rodents in his charge.

[7] These three teeth are isolated with no trace of connecting bone. They were, however, associated in the field (Loomis, personal communication to Wood, February, 1935) and presumably represent a single individual. Loomis' figure shows four teeth. The one figured by him as M^3 has a wear facet on both the front and the rear, proving it to be one of the central molars. On the basis of wear, it is interpreted as M^2 and Loomis' M^2 as M^1. The tooth figured by him as M^1 is not in the Amherst collections, and was apparently lost sometime between Loomis' description of the material in 1914 and Wood's visit to Amherst in 1935. As the specimen was mounted, there was a space between P^4 and Loomis' M^2 (our M^1), where a tooth obviously had been, and whence it had been lost.

Horizon and localities. Deseado formation; La Flecha, Santa Cruz (type), Cabeza Blanca, Chubut (Amherst specimens).

Diagnosis. Metalophid absent on M_3, interrupted on M_2, present on M_1; teeth somewhat lower crowned than in *D. loomisi.*

Loomis' reason for referring A.C.M. no. 3163 to *Asteromys*, whose upper dentition is not certainly known, presumably lay in his identification of an isolated cheek tooth (A.C.M. no. 3054), shown in his Figure 129, as M_2 of *A. prospicuus.* This species, as pointed out below, is actually a synonym of *Cephalomys plexus;* A.C.M. no. 3054 is not referable to it. The specimen appears to be an upper cheek tooth of an eocardiid, perhaps, although not surely, of *Asteromys punctus,* which is without question a member of this family (see below, p. 376). Since A.C.M. no. 3054 does show a certain resemblance to the lower molars of *A. punctus,* which were figured by Ameghino, Loomis' generic identification of it was as good as he could have made. As regards the specific identification, he should have noted that his tooth was much larger than Ameghino's syntype specimens of "*A. prospicuus.*" The small, ephemeral mesofossette of A.C.M. no. 3054 definitely excludes the specimen from the Echimyidae and Octodontidae. The reference of the upper cheek teeth, A.C.M. no. 3163, to the same species as no. 3054 was presumably made chiefly on the basis of size, general similarity, and occurrence in the same deposit. It was, however, definitely erroneous. Having made it, Loomis went on to observe the close general resemblance between the cheek teeth of A.C.M. no. 3163 and those of "*Acaremys*" *minutus* and *minutissimus*[8] figured by Scott, and to conclude that "*Asteromys* appears to be the direct ancestor of *Acaremys.*" Unfortunately, as already noted, "*A.*" *minutus* and *minutissimus* are not octodontids ("acaremyines"), as Ameghino and Scott supposed, but echimyids. As a result of this cumulative series of errors, *Asteromys* has been, since 1914, listed as a member of the "Acaremyidae" or Erethizontidae, "Acaremyinae."

A.C.M. no. 3163 is certainly an echimyid, possessing every one of the molar characters mentioned above that separate the early members of this family from the early Octodontidae. Our

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[8] Loomis did not specifically mention these species, but they are the only ones among those referred to *Acaremys* by Scott for which crown details are shown, and it is to Scott's publication that he would obviously have turned.

reasons for referring the specimen to *Deseadomys arambourgi* are as follows: the teeth are higher-crowned than those of the Colhuehuapian *Protacaremys* and *Prospaniomys*, and in this feature and in crown structure resemble the *Adelphomys* group; the lower molars of *Deseadomys* definitely resemble those of the *Adelphomys* group in both height and structure; within this group A.C.M. no. 3163 is closer to *Stichomys* than to *Adelphomys* in molar structure; the same is true of the lower molars of *D. arambourgi;* A.C.M. no. 3163 and the type of *D. arambourgi* agree perfectly in size. The two specimens are from different localities — Cabeza Blanca and La Flecha, respectively — but this is no obstacle to regarding them as conspecific, since many species, among them rodents, are common to both.

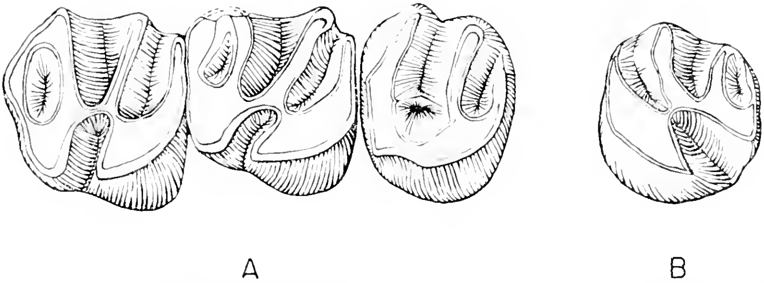

Fig. 4. *Deseadomys arambourgi* gen. et sp. nov. x 10. *A*, RP^4-M^2, A.C.M. no. 3163; *B*, LM^3, A.C.M. no. 3071.

P^4 is considerably smaller, simpler and more oval in outline than the molars (Fig. 4A). The anteroloph runs outward from the large protocone for about two-thirds of the way across the anterior face of the tooth, falling well short of the paracone. The protoloph is slender and somewhat concave anteriorly. As in *Platypittamys*, there is no trace of a metaloph. The posteroloph forms the posterior third of the tooth. This crest differs from that of *Platypittamys* in that there is a definite enlargement at the postero-internal corner, so that we may consider that there is a hypocone as well as a metacone in the posteroloph. The paraflexus is rather shallow, the mesoflexus deep. The protocone and hypocone are only very slightly separated, there being a faint groove on the lingual face indicating incipient separation. It is too faint to be called a hypoflexus. Near the middle of the tooth, there are crests extending into the mesoflexus from both the protoloph and the posteroloph, which partially dam the mesoflexus (and would split it in half at an advanced stage of wear). These crests seem to suggest the initial stages of a mure, as in the molars, but it seems clear that the molar pattern was not developed in this manner, but rather by a deepening of the hypoflexus until the connection between the protocone and hypocone came to lie near the center of the tooth. The tooth is definitely more advanced than P^4 of *Platypittamys*, but the advances were of no significance for the later history of the family, the premolars being destined to disappear from the functional dentition.

M^{1-2} (Fig. 4A) have the usual four transverse crests which are longer and more lophate than in *Platypittamys*. The anteroloph is better developed than in P^4, but does not extend as far externally as does the protoloph. The latter crest is thin and inclined anteriorly, markedly so on M^1. It is united with the anterior end of the mure rather than directly with the protocone, to which it is connected by a thin isthmus. The metaloph and posteroloph unite externally at an early stage of wear to enclose a metafossette that is worn away before the mesoflexus is isolated to form a fossette. The paraflexus is more widely open than in early octodontids, but would be isolated to form a lake while the deep lingual end of the metafossette was still present. The mesoflexus is widely open, but would ultimately be converted to a mesofossette. The hypoflexus is of nearly uniform depth throughout so that it might never be converted to a fossette. The protocone is elongate anteroposteriorly. These teeth closely resemble those of *Stichomys* and *Adelphomys*, and agree with those of *Stichomys* in all characters in which they differ from those of *Adelphomys*. These differences are: anteroloph not extending as far externally as the protoloph; paraflexus notably shallower than mesoflexus; metafossette relatively large and persistent; hypoflexus deep and persistent. The hypoflexus does not extend as far externally into the base of the protoloph in all molars of *Descadomys* as it does in the Santacruzian forms.

M^3 (Fig. 4B) is slightly smaller and has a rounder outline than its predecessors. The metaloph and posteroloph are just in process of uniting, so that decision as to whether there is a metaflexus or a metafossette is purely a matter of terminology. There was clearly a metaflexus at an earlier stage of wear. The hypocone is quite external in position, more so than in *Platypittamys*, and the posterior portion of the tooth is notably smaller than the anterior. *Adelphomys* has a smaller, less elongate M^3 than *Stichomys*, a point of resemblance to *Descadomys* and presumably a primitive feature. *Stichomys* resembles the Deseadan form in nearly all details of crown structure, including the presence of a metaflexus.

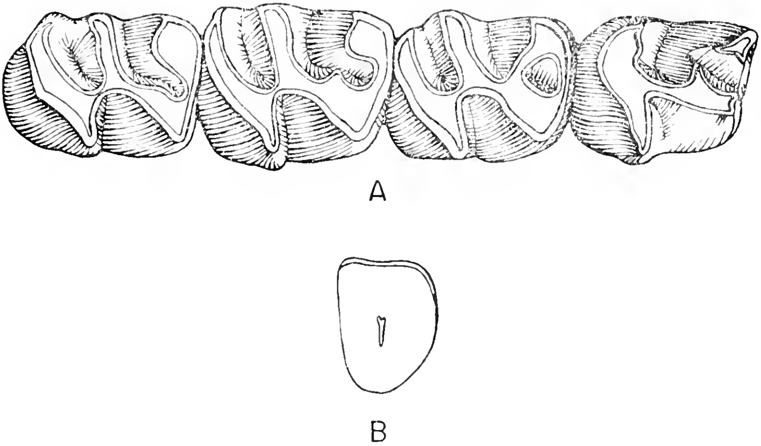

Fig. 5. *Deseadomys arambourgi* gen. et sp. nov. x 10. Type, M.N.H.N. no. 1903-3-1. *A*, RP$_4$-M$_3$; *B*, cross-section of RI$_1$, posterior view.

The lower premolar (Fig. 5A) is very similar to that of *Platypittamys* (Wood, 1949, Fig. 3 C, D), but is slightly less molariform. The protoconid is connected with the center of the hypolophid by a nearly straight, slightly obliquely directed, and nearly centrally located ectolophid, as in *Platypittamys*. The hypolophid forms the posterior margin of the crown, uniting the prominent anteroposteriorly compressed hypoconid with the very large and more rounded entoconid. As in *Platypittamys*, there is no suggestion that more than one crest is present at the rear of the tooth. Anteriorly, the protoconid sends a blunt spur linguad —the rudiment of the metalophid. The metaconid is a stout, four-sided cusp, separated from the protoconid by a narrow, fairly deep mesoflexid. With extreme wear, the central part of this would form a mesofossettid, as it does in a much earlier stage of wear in *Platypittamys*. The posterior corner of the metaconid is formed by a very short, blunt spur that projects in the direction of the tip of the metalophid rudiment. There is no anterolophid, nor any indication of a mesoconid or mesolophid. External and internal valleys are long and of nearly equal length.

The lower molars are longer relative to width than those of *Platypittamys* and are considerably more specialized in the reduction and loss of the metalophid, which is progressive from M_1 to M_3 (Fig. 5A). On M_1, this crest is short, inclined more anteriorly than in *Platypittamys* and joined to the internal rather than to the posterior face of the metaconid. On M_2, it is interrupted, being represented only by a short, blunt spur from the protoconid, which would unite with the metaconid only after extreme wear. On M_3, the metalophid is extremely reduced, and barely present at all. It would never reach the metaconid. A tendency toward reduction and loss of the metalophid occurs sporadically in caviomorphs. It is characteristic of echimyids, occurs in the later members of the Luantinae among eocardiids, in the *Capromys* group of capromyids, and may be seen in a few individuals of the octodontid *Sciamys*. This crest is the weakest of the four on the lower molars (as Wood noted [1949, p. 21], the anterolophid provides the main connection between protoconid and metaconid), and this no doubt accounts for the tendency toward loss. Curiously enough, there is a compensatory tendency in the *Proëchimys-Eumysops* group of echimyids for a neolophid to arise in place of the metalophid subsequent to its disappearance.

The deep hypoflexid is much less oblique than in *Platypittamys* — a point of resemblance to *Stichomys* and *Adelphomys*. The internal flexids are wider, due in part to the reduction of the metalophid and in part to the greater length of the teeth relative to width. The mesoflexid is vertically the deepest of the valleys, being slightly deeper than the hypoflexid, and is of essentially even depth throughout its course. The narrower metaflexid is shallower but deepens sharply buccad, so that a metafossettid would be isolated by further wear. The posterolophid is made up of the hypoconid and the posterior cingulum. There does not seem to be any swelling of this crest that could reasonably be considered to be the entoconid. The hypolophid therefore must contain the entoconid at the lingual margin of the tooth. In the upper Eocene paramyid *Rapamys* (Wood, 1950, Fig. 2B), there is a hypolophid extending from the entoconid to the anterior corner of the hypoconid at the point where the ectolophid arises. Apparently, with the gradual reduction of the metalophid, the entoconid and particularly the buccal end of the hypolophid have swung forward, giving the diagonal direction to this crest that characterized *Deseadomys*, where the hypolophid joins the ectolophid rather than the hypoconid. With the reduction of the metalophid, there is a corresponding increase in the width of the flexids. As in *Stichomys* and *Adelphomys*, there is no tendency toward unilateral hypsodonty. The depths of the hypoflexid and mesoflexid and the shallowness of the metaflexid relative to the mesoflexid are points of resemblance to *Stichomys*. In this genus, there is no trace of a metalophid on M_{2-3}, but in approximately a third of the specimens in the Ameghino Collection this crest is present, although very small, on M_1, connecting the protoconid with the junction of the anterolophid and metaconid.

The incisor (Figs. 5B, 6) is moderately stout and extends back to a point beneath M_3. The anterior face is nearly flat, but has a very faint longitudinal sulcus down the center, which is probably an individual peculiarity, since such faint sulci are very variable in many groups of rodents, including both the Paramyidae and the Santacruzian Echimyidae. The enamel extends for over a third of the way around on the outer side and is barely reflected over to the inner. In cross-section, the pulp cavity is elongate. The incisor of *Stichomys* has a much more curved anterior face.

The mandible (Fig. 6) is robust, deep through the masseteric fossa and symphysis, and the symphyseal region is elongate, extending back to a point beneath P_4. The genioglossal pit is poorly marked. The masseteric fossa begins beneath the posterior part of M_1 and the ventral margin is markedly everted, so that the fossa is deep; there is almost no dorsal boundary. The specimen is broken in the region of the angle and it is therefore impossible to say whether or not this was inturned, although it presumably was. The coronoid arises near the front of M_3. The mental foramen is about a third to a half of the way down the side of the mandible, about the middle of the diastema. The chin is slightly indicated. The symphysis shows very minor irregularities, and it seems probable that some movement between the two halves of the jaw was possible and that a small M. transversus mandibulae was present. In nearly every respect, the jaw closely resembles those of *Stichomys* and *Adelphomys.*

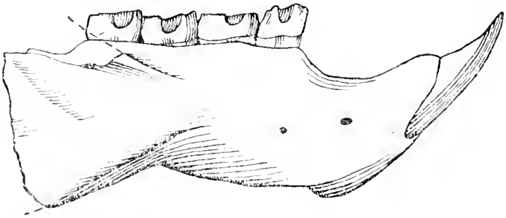

Fig. 6. *Deseadomys arambourgi* gen. et sp. nov. x 3. Type, M.N.H.N. no. 1903-3-1, right ramus, lateral view.

Apart from slight differences in the general shape of the incisor and in the contour of its anterior surface, *D. arambourgi* resembles *Stichomys* very closely. Since development and loss of shallow sulci and changes in the shape of the incisor may occur frequently in rodents, it is even possible that this species may be in the direct ancestry of the Santacruzian genus.

For measurements, see Table 1.

DESEADOMYS LOOMISI[9] sp. nov.

Fig. 7

Type. A.C.M. no. 3087, right mandible with I, M_{1-2}, alveoli of P_4, M_3.

Hypodigm. Type only.

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[9] Named for the late Professor Frederick B. Loomis, who organized and led the Amherst Patagonian Expedition of 1911-12.

Horizon and locality. Deseado formation; Cabeza Blanca, Chubut.

Diagnosis. Metalophid entirely absent; teeth slightly larger and molars somewhat higher-crowned than in *D. arambourgi;* mesoflexid deeper than in *D. arambourgi;* metaflexid fairly shallow, so that lingual ends of hypolophid and posterolophid approach more closely than in *D. arambourgi.*

The cheek teeth (Fig. 7A) are medium-crowned, but, as in *Adelphomys* and *Stichomys,* show no indications of unilateral hypsodonty. As in the type species, M_2 is the largest tooth. M_3 (as determined from the alveolus) was the smallest of the series. P_4 appears to have been about the size of M_1, which is an advanced character. There is no trace in either molar of any remnants of the metalophid, so that the teeth are entirely three-lobed on the lingual side. The mesoflexid and hypoflexid are about equally deep, and much deeper than the metaflexid. With wear, the metafossettid would persist until after the formation of the mesofossettid and hypofossettid, but would be worn away shortly thereafter. The hypofossettid is slightly deeper than the mesofossettid.

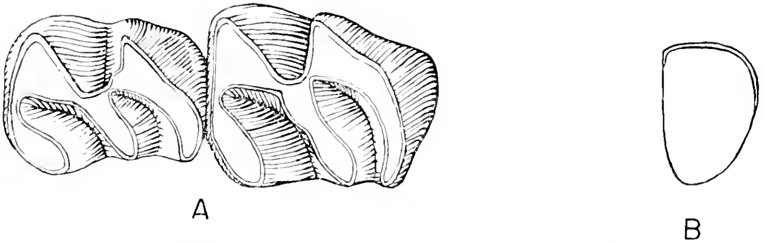

Fig. 7. *Deseadomys loomisi* sp. nov. x 10. Type, A.C.M. no. 3087. *A*, RM_{1-2}; *B*, cross-section of RI_1, posterior view.

The anterior face of the lower incisor is straight for the median two-thirds and gently curved on the buccal third (Fig. 7B). There is no suggestion of a sulcus. The enamel extends nearly halfway around the buccal side of the tooth, but only a short distance onto the lingual face. The two sides of the tooth are nearly parallel, as in *D. arambourgi.* The pulp cavity is long and narrow, but its details could not be determined. The incisor extends back to beneath M_2, thus not as far as in *D. arambourgi*. The lower incisor in *Adelphomys* is relatively larger, wider, and has a plane anterior surface.

The mandible differs from that of the type species in that the anterior end of the masseteric crest is beneath P_4 instead of M_1. This is a primitive character encountered in octodontids, *Protacaremys, Prospaniomys,* etc. The symphyseal surface is essentially plane.

As far as the available evidence goes, there is nothing to oppose the view that *D. loomisi* was in or near the ancestry of *Adelphomys*.

The tooth measurements are given in Table 1.

TABLE 1

Tooth measurements (in mm.) of *Descadomys*

Upper Teeth			Lower Teeth			
		D. arambourgi A.C.M. no. 3163, right			*D. arambourgi* M.N.H.N. no. 1903-3-1, right	*D. loomisi* A.C.M. no. 3087, right
P^4,	anteroposterior	2.09	Incisor			
	width protoloph	2.03*		anteroposterior	1.76	ca. 1.9
	width posteroloph	2.12*		transverse	1.31	1.29
M^1,	anteroposterior	2.25	P_4	anteroposterior	2.12	
	width protoloph	2.25*		anterior width	1.68*	
	width metaloph	2.04*		width hypolophid	1.90*	
M^2,	anteroposterior	2.42	M_1	anteroposterior	2.41	2.63
	width protoloph	2.61*		width metalophid	1.92*	2.10*
	width metaloph	2.41*		width hypolophid	1.96*	1.92*
		A.C.M. no. 3071, left	M_2	anteroposterior	2.52	2.64
				width metalophid	2.05*	2.47*
M^3,	anteroposterior	2.14		width hypolophid	2.18*	2.29*
	width protoloph	2.35*	M_3	anteroposterior	2.32	
	width metaloph	1.88*		width metalophid	1.90*	
				width hypolophid	1.89*	

* = Maximum diameter of tooth.

Superfamily CHINCHILLOIDEA L. Kraglievich 1940

As discussed below under Dasyproctidae (p. 327), we now suspect that a number of caviomorph families should be included in this superfamily.

Family CHINCHILLIDAE Bennett 1833
SCOTAMYS Loomis 1914

Scotamys Loomis, 1914, p. 192; Stehlin and Schaub, 1951, p. 260.

Type species. *Scotamys antiquus* Loomis 1914.

Distribution. Deseadan; Patagonia.

Emended diagnosis. Teeth very high-crowned, apparently rootless and ever-growing; crown pattern rapidly lost: hypoflexus and hypoflexid very deep; small third lobe on unworn upper molars; enamel missing from anterior part of lower molars and posterior part of uppers after little wear; cement present; incisors proportionately small.

SCOTAMYS ANTIQUUS Loomis 1914
Figs. 8-10

Scotamys antiquus Loomis, 1914, p. 192-193, Figs. 125-126; Stehlin and Schaub, 1951, Fig. 434, p. 260.

Type. A.C.M. no. 3063, a left lower jaw with I, P_4-M_2, from Cabeza Blanca, Chubut.

Hypodigm. Type and a series of isolated teeth in collection of Muséum National d'Histoire Naturelle (3 P^4, 15 $M^{1 \text{ or } 2}$, 3 M^3, 3 P_4, 9 $M_{1 \text{ or } 2}$, 1 M_3 and 11 incisors), all from La Flecha, Santa Cruz.

Diagnosis. As for the genus; tooth measurements as shown in Table 2.

It is often very difficult to determine with certainty the position in the tooth row of the isolated teeth. The patterns of P^4, M^3 and P_4 are sufficiently distinctive so that these teeth can be readily identified. M_3 can, we believe, be identified by the narrow talonid. $M^{1\text{-}2}$ cannot be separated from each other, as is also the case with $M_{1\text{-}2}$. The upper molars have a greater curvature of their vertical axes, both anteroposteriorly and transversely, than do the lowers, and the two have been separated on this basis. The interruption of the enamel in upper molars is generally the mirror image of that in the lowers.

No unworn cheek teeth are available. The general resemblance between *Scotamys* and the better known *Cephalomys* is sufficiently close, however, so that it seems justifiable to interpret such structure as can be seen in the former in terms of the latter.

P^4 (Fig. 8A) has a very large combined anteroloph and protocone that, together, forms all of the anterior and much of the external and internal faces of the tooth. This curving crest is separated from the paracone and its crest by a cleft, the hypoflexus, that extends nearly to the buccal margin of the tooth, though, in contrast with the situation in *Cephalomys*, it is open at the lingual end. This lingual opening does not extend far down the tooth, however, so that, with wear, the valley becomes a fossette, as in *Cephalomys*. The paracone is central in position and continues into a short crest, the protoloph, that describes a curve similar to that of the much larger anteroloph. The metacone is posteroexternal and united by wear to the paracone. A narrow crest, the posteroloph, runs internally from the metacone, forming the posterior margin of the tooth and joining the protoloph posterointernally. A small, shallow mesofossette is isolated between protoloph and posteroloph. Metacone, mesofossette and posteroloph are situated on a posteriorly overhanging portion of the crown, so that all trace of these structures disappears after

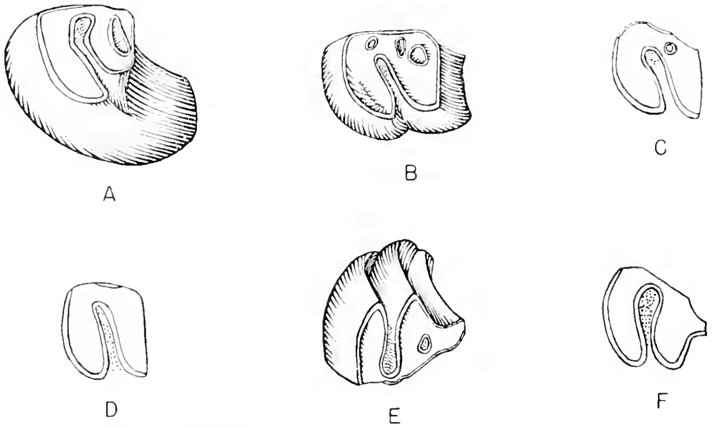

Fig. 8. *Scotamys antiquus* Loomis x 5. *A*, LP^4, M.N.H.N. no. 1903-3-8; *B*, LM$^{1 \text{ or } 2}$, M.N.H.N. no. 1903-3-9; *C*, *LM*$^{1 \text{ or } 2}$, M.N.H.N. no. 1903-3-10; *D*, LM$^{1 \text{ or } 2}$, M.N.H.N. no. 1903-3-11; *E*, RM^3, M.N.H.N. no. 1903-3-12; *F*, LM^3, M.N.H.N. no. 1903-3-13. *C*, *D* and *F* show crown outlines at wear surface.

a little wear, leaving a bilobed crown that then persists until after the closure of the hypoflexus. There is no indication that a metaloph was ever present. The enamel is interrupted early in life at the postero-buccal corner of the tooth, and then along the rest of the buccal side.

The least worn $M^{1 \text{ or } 2}$ in the series (M.N.H.N. no. 1903-3-9, Fig. 8B) shows a pattern consisting of two lobes separated by a narrow hypoflexus that extends about three-quarters of the way from the lingual to the buccal margin. Buccad of the hypoflexus is a small fossette and in the buccal portion of the posterior lobe are two more. All three are shallow. The anterior is the smallest, the middle the deepest, and the posterior the largest. From these remnants, the unworn crown pattern can readily be reconstructed. It was clearly very similar to that of the unworn *Cephalomys* molar without the fifth crest, consisting of a large anteroloph, a stout protoloph, a metaloph that was more transverse than in *Cephalomys*, a posteroloph and a hypoflexus that undermined the paraflexus (i.e., the paraflexus extended more linguad on the unworn crown than was the case farther down in the tooth, so that, as wear proceeded, the paraflexus diminished in length and the hypoflexus increased). Thus interpreted, the three fossettes in M.N.H.N. no. 1903-3-9 are the parafossette, mesofossette and metafossette. A basic similarity to the *Platypittamys-Deseadomys* pattern is evident. The posteroloph protrudes beyond the main body of the tooth and is soon eliminated by wear. In M.N.H.N. no. 1903-3-9, the enamel is complete all the way around the crown, although it would be interrupted at the anterior and posterior buccal corners after very little additional wear. In the next least-worn tooth (M.N.H.N. no. 1903-3-10, Fig. 8 C), which only shows a single fossette (the mesofossette) in the posterior lobe, the enamel is interrupted antero-buccally and posteriorly, as is the case with most of the other teeth. The pattern shown in Figure 8D (M.N.H.N. no. 1903-3-11) is quickly attained, and persists indefinitely as far as can be told from the available material.

Of the three specimens believed to be M^3, two are complete and one is broken. All three, however, show a characteristic three-lobed pattern, the posterior lobe being smaller than in *Perimys*. One tooth (M.N.H.N. no. 1903-3-12, Fig. 8E) is relatively little worn. In this specimen, the enamel is interrupted at the antero-buccal corner and the extreme posterior end of the tooth. The two anterior lobes are sharply angulate, and the third lobe is quite small. A small mesofossette is present. In a more worn specimen (M.N.H.N. no. 1903-3-13, Fig. 8F), the mesofossette is lost, the second lobe is larger, and the angulation of the tooth is reduced. The enamel is interrupted along the whole buccal surface of the third lobe. As far as the base of the prism, there is no further reduction of the enamel. To judge from the structure of the anterior molars, the posterior lobe is probably formed from the posterior cingulum. The differences between the teeth shown in Figures 8E and 8F are entirely due to wear.

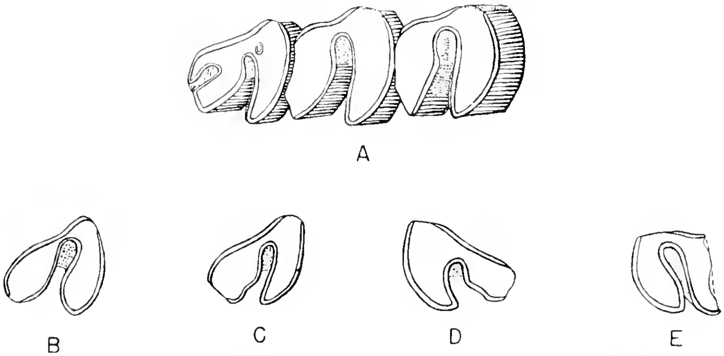

Fig. 9. *Scotamys antiquus* Loomis x 5. *A*, LP$_4$-M$_2$, type, A.C.M. no. 3063; *B*, LP$_4$, M.N.H.N. no. 1903-3-4; *C*, LP$_4$, M.N.H.N. no. 1903-3-5; *D*, RP$_4$, M.N.H.N. no. 1903-3-6; *E*, RM$_3$ (incomplete anteriorly), M.N.H.N. no. 1903-3-7. *B* to *E* show crown outlines at wear surface.

The central valley of all lower cheek teeth curves antero-linguad. At least in the stage of wear represented by most of the lower molars, each lobe is simple, all fossettids having been worn away. In unbroken lower molars, the prism may be over 7 mm. high, with no change in tooth pattern in this distance.

The least worn P$_4$ is that of the type. This tooth is bilobed, but there is a small antero-buccal valley in the anterior lobe and a minute fossettid, evidently a metafossettid, postero-linguad of the head of the central buccal valley (Fig. 9A). The metafossettid, however, has almost been eliminated by wear, and the anterior valley would be converted to a fossettid by a very slight additional amount of wear. This valley is directed nearly forward, partly because the protoconid has shifted forward at its buccal margin, and partly because the anterior cingulum is short at the lingual margin of the tooth. The anterior valley is filled with cement, as is the central part of the hypoflexid. This anterior valley is probably that between protoconid and anteroconid. None of the three Muséum National d'Histoire Naturelle specimens possesses an anterior valley, even as a fossettid. They apparently show a progressive transverse narrowing of the tooth with wear (Figs. 9B-D). On M.N.H.N. no. 1903-3-6, the hypoflexid ends about half way down the crown. On the lower half of the tooth, another valley appears buccally, as well as one on the lingual side, so that the pulp end of this tooth shows a figure-eight outline. This is the most worn lower premolar available. In the area with the figure-eight outline, the enamel was not laid down on the anterior face or on most of the lingual face, being present on the latter side only in the lingual valley.

In addition to those of the type, there are nine first or second lower molars in the M.N.H.N. collection. These all agree in pattern with those of the type (Fig. 9A), showing the enamel absent along the entire anterior face of the tooth and at the posterointernal corner. The central part of the hypoflexid is filled with cement, which extends part way along the sides of the flexid. Cement is also present on the posterolateral corners of the teeth. There is little or no change in pattern in the molars once the stage shown in Figure 9A has been reached. Although no unworn lower molars are preserved, there is no reason to suppose that the pattern of the lower molars was not a mirror image of that of the uppers.

M_3 (M.N.H.N. no. 1903-3-7, Fig. 9E) is similar to the anterior molars except that the talonid is appreciably narrower than the trigonid, at least at the wear surface. The difference is much less marked after further wear. The tooth is the smallest of the lower cheek teeth.

The crowns, particularly of the upper teeth, change in outline as wear proceeds. The internal cleft in P^4 disappears with wear, which gives the tooth an old *Cephalomys-Neoreomys* aspect, though arrived at in a different manner. The two sides of this cleft approach each other rather closely in old specimens of *Perimys* (e.g. A.M.N.H. no. 29673, Colhué-Huapí). Upper and lower molars of *Scotamys* are more ragged looking than in *Perimys*; they lack the neat, regimented appearance of the teeth of that form.

Three fragments of upper incisors are present in the Muséum National material. These are essentially identical in pattern with the lower incisors, but the anterior face is slightly more rounded and the pulp cavity is more nearly a straight slit than a dumb-bell shaped cavity (Fig. 10A). The lower incisor extends back to a point below M_2. It does not run beneath the cheek teeth, but rather medial of them, due to their excessive hypsodonty. The anterior face is slightly curved, and the enamel rather thick. The lateral face is markedly rounded. The enamel extends only a short distance onto the lateral side, and nearly as far on the median side (Fig. 10B). The pulp cavity is quite unusual, having a dumb-bell shape near the tip of the incisor, though it comes closer to the shape of the incisor itself several millimeters nearer the pulp end.

Both upper and lower incisors are stocky but very small in comparison to the size of the cheek teeth, a combination also true of *Cephalomys*. On this basis, *Scotamys* appears to have been a very poor gnawer. Coupled with the powerful masseter muscle and the hypselodont cheek teeth, this suggests an approach toward a grazing adaptation.

The mandible (Figs. 10C, D) is very massive and thick, with a broad, rather flat shelf on the ventral surface. The large mental foramen is in the ventral half of the jaw beneath the anterior end of P_4; two minute foramina are present above it. The chin is heavy and the symphyseal area large; the ventral margin forms a straight line terminating posteriorly in a strong mental process. The anterodorsal extemity of the symphysis extends upward above a line extended forward from the outer alveolar border of the cheek teeth. The pit for the genioglossal is pronounced. The masseteric crest is very strong, slopes gently downward and extends laterally for a considerable distance. On the dorsal side of the crest, within the masseteric fossa, there is a series of interrupted grooves. The cheek teeth are inclined laterally, as in all chinchillids and their open pulps are external to the incisor. The latter extended at least as far back as the end of the molar series, and the surrounding bone forms a shelf on the inner face of the ramus (Fig. 10D). Externally, the alveolar border of M_3 is broken away; the ascending ramus may have begun to arise from this region, as in other members of the family. For a member of the Chinchillidae, this is a primitive jaw. In the living forms the masseteric crest is reduced to the vanishing point; in *Perimys* this is much less salient than in *Scotamys*. The anterodorsal extremity of the symphysis extends as far upward in *Perimys* as in *Scotamys*, and nearly as much so in *Chinchilla* and *Lagidium*, but is low relative to the alveolar border of the cheek teeth in *Lagostomus*. The incisor extends back to M_3 in *Lagostomus*, to M_2 in *Chinchilla* and *Lagidium* and

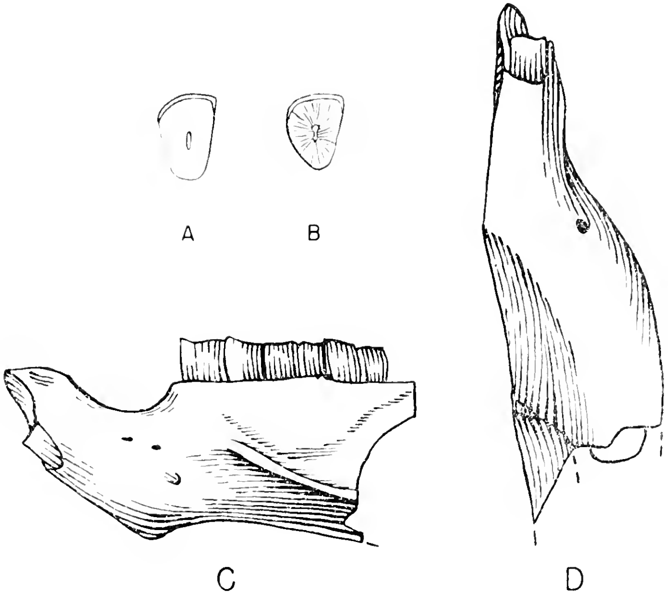

Fig. 10. *Scotamys antiquus* Loomis. Cross-sections of incisors x 5. *A*, right upper, anterior view, M.N.H.N. no. 1903-3-14; *B*, left lower of type, anterior view, A.C.M. no. 3063. Left mandible of type, A.C.M. no. 3063 x 2; *C*, lateral view; *D*, ventral view.

to varying distances in *Perimys*. The mental foramen is in the same position in *Perimys* as in *Scotamys*; much higher on the mandible in the living forms.

As regards hypselodonty, *Scotamys* is the most specialized Deseadan rodent known. Loomis (1914) placed this genus in the Chinchillidae and considered it to be ancestral to *Scotaeumys* of the Santa Cruz.[10] The upper molars of *Scotaeumys* (Scott, 1905, Pl. 68, fig. 22) could have been derived from those of *Scotamys*, but this would have involved a reversal in the direction in which the evolution of *Scotamys* had evidently been proceeding. Scott states that in P_4 of *Scotaeumys* (the only lower tooth known) there is an anterior third lamina. However, he indicates a distinct change in pattern of the upper molars with wear. From this, it would appear that *Scotamys* is appreciably more advanced in its hypsodonty than is *Scotaeumys*. *Scotamys* is therefore probably too specialized in its own direction to be ancestral to *Scotaeumys*. On the other hand, *Perimys* could have descended from *Scotamys* if the posterior cingulum of M^{1-2} were eliminated and the incisor shortened. P^4 of *Perimys* could be derived from that of *Scotamys* by an emphasis of the separation between the paracone and the anteroloph. This latter would result in the reversal of the drainage of the valley, and the formation of a buccal, rather than a lingual, cleft in partly worn teeth. In P_4, elimination of the anterior cleft, not a persistent feature in *Scotamys*, would give a *Perimys*-like pattern. *Scotamys*, then, could be a collateral ancestor of *Scotaeumys* of the Santa Cruz, and perhaps, but probably not, an actual ancestor of *Perimys* of the Colhué-Huapí and Santa Cruz. *Prolagostomus* and *Pliolagostomus* are at present of unknown ancestry, although descent from *Scotamys*, or from a form generally similar to it, is not impossible. The relationships, then, might be as shown in Figure 11.

Landry (1957a, p. 59) refers *Scotamys* to the "Cephalomyidae," although from his text (*op. cit.*, p. 54) it is obvious that he feels there are suggestions of relationship to *Perimys*. We do not differ greatly from him on this point, but we feel that the

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[10] Landry's account of the taxonomic history of *Scotamys* (1957a, p. 54) is somewhat confused. He states that it was considered to be a cephalomyid by Ameghino and Loomis. However, Ameghino had died before the genus was described, and Loomis, as stated, referred it to the Chinchillidae.

similarities to *Perimys* are indicative of phylogenetic relationships, and that the similarities to *Cephalomys* are indicative of the close approach of the two distinct lines in the Deseadan. Landry, combatting an early idea of Ameghino's that *Perimys* was directly ancestral to *Lagostomus*, has also separated some of the earlier chinchillids as a family, the Perimyidae, on the following grounds: cheek teeth with less appressed laminae, and with folds opening lingually on upper molars and labially on upper premolars; ventral maxillary zygomatic root not anterior to dorsal maxillary zygomatic root; masseteric ridge on mandible strongly developed (*op. cit.*, p. 59). As regards these characters, we may observe: 1), that *Scotamys*, which on other grounds would be a "perimyid," has the fold in the upper premolar opening in the same direction as in the molars; and 2), that the ventral maxillary zygomatic root is just as far anterior to the dorsal root (the upper portion of the preorbital bar) in *Perimys* as it is in the living forms (Scott, 1905, Pl. 68, fig. 4, and original specimens). We are thus left with the more open folds and the masseteric ridge as the characters of the new family. As noted above, the masseteric ridge, or crest, is considerably less prominent in *Perimys* than in *Scotamys*, which suggests it was undergoing reduction through time. The folds in the upper cheek teeth of *Prolagostomus*, which Landry places in the Chinchillidae, are not as tightly appressed as in the living forms. It would seem that narrowing of the flexi and flexids was progressive in the family. *Perimys* may well have been, in these respects, a persistently primitive form, and may prove referable to a

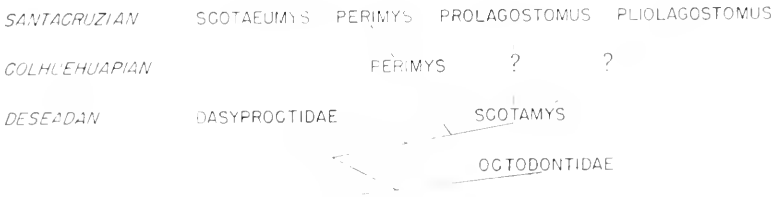

Fig. 11. Tentative phylogeny of the Oligocene and early Miocene Chinchillidae.

distinct subfamily when the phylogeny is better known, but we do not think that recognition of a family Perimyidae is at present helpful.

TABLE 2

Tooth measurements (in mm.) of *Scotamys antiquus*

UPPER TEETH

		M.N.H.N. No. 1903-3-8 left	M.N.H.N. No. 1903-3-47 right
P^4	anteroposterior	2.53*	2.70*
	width anteroloph	2.57*	2.21*
	width posterior lobe	1.73*	1.64*

		M.N.H.N. No. 1903-3-9 left	M.N.H.N. No. 1903-3-10 left	M.N.H.N. No. 1903-3-11 left
$M^{1 \text{ or } 2}$	anteroposterior	2.58*	2.49*	2.20*
	width protoloph	2.33*	2.41*	2.53*
	width metaloph	2.15*	2.18*	2.41*

		M.N.H.N. No. 1903-3-12 right	M.N.H.N. No. 1903-3-13 left
M^3	anteroposterior	2.84*	2.68*
	width protoloph	2.12*	2.61*
	width metaloph	2.23*	2.38*

		M.N.H.N. No. 1903-3-72 left	M.N.H.N. No. 1903-3-71 left	M.N.H.N. No. 1903-3-14 right
I^1	anteroposterior	2.19	2.07	2.25
	transverse	1.40	1.60	1.48

LOWER TEETH

		Type A.C.M. No. 3063 left	M.N.H.N. No. 1903-3-4 left	M.N.H.N. No. 1903-3-5 left	M.N.H.N. No. 1903-3-6 right
P_4	anteroposterior	2.62	2.68*	2.45*	2.97*
	width metalophid	1.74	1.75*	1.86*	1.41*
	width hypolophid	2.75	2.58*	2.38*	2.29*

			M.N.H.N., various specimens, M_1 and M_2						
			left				right		
			No. 1903-3-66	No. 1903-3-68	No. 1903-3-67	No. 1903-3-65	No. 1903-3-62	No. 1903-3-63	No. 1903-3-64
M_1	anteroposterior	2.64	2.77*	2.49*	2.15*	2.76*	2.53*	2.25*	2.23*
	width metalophid	2.38	2.48*	2.57*	2.40*	2.56*	2.63*	2.48*	2.43*
	width hypolophid	3.08	2.45*	2.56*	2.52*	2.73*	2.99*	2.73*	2.74*
M_2	anteroposterior	2.78							
	width metalophid	2.62							
	width hypolophid	2.85							

		M.N.H.N. No. 1903-3-7 right
M_3	anteroposterior	2.09*
	width metalophid	2.20*
	width hypolophid	2.08*

		Type A.C.M. No. 3063	M.N.H.N. No. 1903-3-80	M.N.H.N. No. 1903-3-79
I_1	anteroposterior	1.98	1.98	1.90
	transverse	1.52	1.50	1.51

* = Maximum diameter of tooth.

Family DASYPROCTIDAE Smith 1842

Cephalomyidae Ameghino 1897.

Two previously described Deseadan genera are here referred to this family, *Cephalomys* Ameghino and *Litodontomys* Loomis, and there is a third unnamed form that appears to belong with them. There has been much uncertainty concerning the position of *Cephalomys* and a reëvaluation of its affinities leads to certain changes in the content of superfamilies, not only as envisaged by others (e.g. Simpson, 1945) but also as envisaged by ourselves at the stage of this investigation reported by Wood (1955).

Ameghino, in establishing the family Cephalomyidae, stated that "On ne peut les placer dans aucune des familles connues de preference aux autres . . . Ils présentent un assemblage de caractères propre aux *Eriomyidae* [=Chinchillidae], *Caviidae*, *Echinomyidae* [=Echimyidae], *Hystricidae*, etc." (1897c, p. 494). At that time and subsequently, Ameghino regarded them as the basal stock for the Hystricomorpha (*sensu lato*). Loomis (1914, p. 186) put *Cephalomys* in the Chinchillidae, as ancestral to *Perimys* of the Santa Cruz.[11] Miller and Gidley (1918, p. 445) placed *Cephalomys* and *Litodontomys* in their subfamily Octodontinae (our Octodontidae plus Ctenomyidae) of the family Echimyidae. L. Kraglievich (1940a, p. 441) considered the Cephalomyidae to have been ancestral to the Eocardiidae and, through them, to the Caviidae and Hydrochoeridae. Simpson's

[11] Landry (1957a, p. 54) states that Ameghino and Loomis placed *Cephalomys* in the Caviidae and that Simpson referred it to the Chinchillidae. However, Ameghino never considered it as anything but the type of his family Cephalomyidae, Loomis referred it to the Chinchillidae, and Simpson accepted Ameghino's Cephalomyidae.

classification (1945, p. 94) placed them in a similar position. We formerly referred them to the Capromyidae (*in* Wood, 1955). Landry (1957a, pp. 54 and 59), considers the Cephalomyidae to be a basal family of the Chinchilloidea, from which he excludes *Dasyprocta*. It appears to us that almost every allocation except the right one, or so we now think, has been made.

There are no very striking resemblances between *Cephalomys* and the Cavioidea in general, or the Eocardiidae in particular, other than those common to most of the South American rodents. Some similarities exist in the general outlines of worn teeth, but the details of the tooth structure of *Cephalomys* are very different from those of *Eocardia* (cf. figures given here with those in Scott, 1905, Pl. 69). The resemblance to *Perimys,* pointed out by Loomis and by Landry, is definite, but again is most prominent in worn teeth, and is largely confined to the upper molars. The reversal of pattern between worn upper premolars and molars is present in both of these genera, however, and this is of interest and is discussed below. The cheek teeth are far more advanced than those of the contemporary octodontids and echimyids. Now that unworn teeth are available, it has become apparent, as pointed out below, that there is great similarity, although not identity, in the dentition between *Cephalomys* and *Neoreomys* of the Santa Cruz, which we think indicative of affinity, and this is supported by what is known of skull structure. Since Scott's study (1905) of the Santacruzian rodents, the view that *Neoreomys* and apparently related genera — *Scleromys* and *Olenopsis* — were capromyids or myocastorids has been rather generally held. Accepting this, without more ado we considered *Cephalomys* and, tentatively, *Litodontomys* to be capromyids. Further, noting the close resemblance in cheek tooth structure between *Cephalomys* and the contemporary chinchillid *Scotamys* Loomis, we transferred the Capromyidae from the Octodontoidea of Simpson's classification to the Chinchilloidea (Wood, 1955). It would now appear that our acceptance of *Neoreomys* as a capromyid and the allocations based on this acceptance were in error.

We had noted the replacement of dm_4^4 by P_4^4 in *Neoreomys,* a difference from the Capromyidae, in which, as in post-Deseadan Echimyidae, there is no such replacement, but had supposed that retention of the milk teeth in the family had come about in post-

Santacruzian time.[12] However, reinforcing this difference, there is also a cranial character that sets *Neoreomys* sharply apart from the Capromyidae. In the latter group there is a process from the supraoccipital (the lateral process of Tullberg, 1899, p. 69) that projects downward parallel and anterolateral to the paroccipital process, from which it is separated by a narrow notch. This process is very large in *Myocastor* and of more modest dimensions in the other capromyids. It also occurs in echimyids, ranging in size from incipient to small, and in erethizontids. The structural base for such a process is present in Santacruzian (*Sciamys*, Scott, 1905, Pl. 67, fig. 9) and Recent octodontids, and in abrocomids and ctenomyids, in which a strip from the supraoccipital extends down to a point above the attachment for the stylohyal but does not form a process. In the Deseadan *Platypittamys*, however, so far as can be determined from the crushed material, there is not even a rudiment of such a strip. This suggests that the strip — and the process that could arise from it — was not a part of the original caviomorph heritage but arose independently more than once. The primitive octodontids could have given rise to groups with and without this character, and the possibility of its later rise in other groups cannot be excluded. Landry (1957a, pp. 74-75) correctly points out that this feature is widespread and sporadic among rodents. In one very young specimen of *Erethizon* seen by us the "process" starts as an independent ossification, separate from the supraoccipital. The complete absence in *Neoreomys* of even the rudiment of a supraoccipital strip (see Scott, 1905, Pl. 54, figs. 6, 6c), not to mention a lateral process, coupled with replacement of dm^4_4, however, would appear to exclude this form from the Capromyidae. The latter family, as probable echimyid derivatives, should be returned to the superfamily Octodontoidea.[13] The combination of lateral process and unreplaced dm^4_4 so neatly reinforces other characters that suggest a close relationship between the Echimyidae and the Capromyidae that it is almost a pity to have to introduce a note of caution.

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[12] The supposedly Santacruzian *Paramyocastor* Ameghino (1904) is actually from the Pliocene Hermosan (J. L. Kraglievich, personal communication).

[13] We are greatly indebted to Drs. Ernest E. Williams, Karl Koopman and Samuel B. McDowell for their kindness in pointing out to us the important lack of a lateral process in *Neoreomys*.

Rodents being what they are, however, we are compelled to observe that the two characters do not always go together in the Caviomorpha. *Elasmodontomys* has a lateral process second only to *Myocastor* in point of size, yet its milk molars are shed,[14] a feature that scarcely admits it to either the Capromyidae or the Echimyidae.

Neoreomys and *Cephalomys* being excluded from the Capromyidae, the question of their familial position comes to the fore. Fortunately we do not have far to seek for an answer, no farther in fact that the work of Scott, who (1905, pp. 387-399) very clearly pointed out the many resemblances of *Neoreomys* to *Dasyprocta* and *Cuniculus*. Quite obviously, he felt that *Neoreomys* could almost equally as well be referred to the Dasyproctidae as to the Capromyidae. Following the hint contained in his work, and in agreement with Miller and Gidley (1918, p. 447) and Winge (1924, pp. 66. 77), we now refer *Neoreomys* and its relatives to the Dasyproctidae.

Scott's work, moreover, contains a further hint of interest in this connection: ". . . . the likenesses of *Neoreomys* to the *Dasyproctidae* and *Dinomyidae* are also very suggestive and indicate that this genus is not far removed in structure from some earlier and more generalized form, which was the common ancestral stock of several distinct families" (1905, p. 387). We are in complete agreement with Scott that *Neoreomys* suggests some degree of relationship between Dasyproctidae, Cuniculidae and Dinomyidae. With Schaub (*in* Stehlin and Schaub, 1951, pp. 369-370), and Landry (1957a, pp. 44, 57-58), we now believe that these families should be removed from the Cavioidea of Simpson's classification, thus limiting that superfamily to the Eocardiidae, Caviidae and Hydrochoeridae. We agree with Schaub that the Cuniculidae and Dinomyidae should be associated with the Chinchillidae, and to these we would add the Dasyproctidae, which he left as *incertae sedis* together with the "Cephalomyidae" (Schaub, 1953a, pp. 396-397). The West Indian *Elasmodontomys* group may also be included here, at least

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[14] *"Heptaxodon"* is in fact based on young individuals of *Elasmodontomys* with dm $^{4}_{4}$. The fine material now available, much of it obtained since Anthony's work on these forms, includes enough of the growth stages to relieve all doubt on this head. This question will be discussed in a forthcoming study of West Indian rodents by Mr. Clayton E. Ray.

provisionally. For this assemblage the earliest available name is Chinchilloidea L. Kraglievich 1940. We agree with Schaub, Stirton (1947), Landry (1957a) and Fields (1957) that the extinct Eumegamyinae belong in the Dinomyidae and not in the *Elasmodontomys* group.

Landry (1957a, pp. 57-59) groups the Myocastoridae (including *Neoreomys*), Cuniculidae (including *Dasyprocta*), Dinomyidae, Octodontidae and the *Elasmodontomys* group in the Octodontoidea. As we have indicated, we consider *Neoreomys* to be a dasyproctid. *Eumysops*, which Landry refers to the Myocastoridae,[15] is an echimyid. We feel that the distinction between the Cuniculidae and Dasyproctidae is sufficient to justify their familial separation, and that, as we have just indicated, they should be referred to the Chinchilloidea, while *Myocastor* surely belongs with the Echimyidae and Capromyidae in the Octodontoidea. The Chinchillidae, as represented by *Scotamys*, and the Dasyproctidae, as represented by *Cephalomys*, are very similar in most details of crown structure in the Deseadan. Both forms have molars in which the structural details are rather shallow, in the former somewhat shallower than in the latter. This, we suspect, foreshadows a marked difference between later representatives of these two rapidly diverging families. In the Dasyproctidae, the evolutionary trend was toward the preservation and increase of crown complexity, the crown growing down toward the root, as it were. Chinchillid molar evolution proceeded in almost precisely the opposite direction, eliminating all the minor features of the cheek tooth crown, deepening only the clefts between the lobes.

Cephalomys, in view of its resemblance to *Neoreomys* and to the contemporary chinchillid *Scotamys*, seems surely to be a member of this group, but its exact position within the superfamily is uncertain. As is emphasized below, the upper molars of *Neoreomys* and *Cephalomys* are not identical; they differ in the structure of the neoloph and in the extent of enamel deposition. There are also differences in the skull and mandible, which are generally, but not entirely, due to *Cephalomys* being the more primitive. Although the two forms are, we believe, related,

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[15] A deduction from the position occupied by the genus in L. Kraglievich's list (1934, p. 30) of Argentinian Pliocene rodents (Landry, pers. comm.).

they are most certainly not ancestor and descendant. In fact, *Cephalomys* cannot at present be brought into direct relationship with any later rodents, which is rather curious in view of its great abundance in the Deseadan. For the moment it can only be regarded as representing a very successful although short-lived phylum. *Litodontomys* may be related to the type species of *Olenopsis* although this is uncertain. The third Deseadan form, represented only by an isolated upper cheek tooth in the Ameghino Collection, was, on this slender evidence, perhaps close to the Santacruzian *Scleromys*, and may conceivably, therefore, have something to do with the ancestry of this form. The only known Colhué-Huapí form possibly referable to the Dasyproctidae is represented by an isolated upper molar intermediate in some respects between those of *Neoreomys* and *Scleromys*. Divergence was clearly under way during the Deseadan, but presumably had not begun very long previously. The phylogeny of these forms was certainly complex. We undoubtedly know only a small fraction of the forms that once existed.

It will be evident that in a situation such as this taxonomic assignments can only be tentative. There is no available evidence that any of the Santacruzian and earlier forms are members of the Cuniculidae. There is a possibility that some of them may be dinomyids. Very recently, Fields (1957) has published a valuable paper on late Miocene rodents, especially Dinomyidae, from Colombia. He refers the species of this family represented among his material to *Scleromys* (in which he includes *Lomomys*) and to *Olenopsis*, the type species of which are Santacruzian. There is no question as to the familial position of the Colombian species, but we feel some uncertainty as to the generic references. As pointed out below under *Litodontomys*, there is doubt as to whether the Santacruzian species of *Olenopsis* is congeneric with the Colombian one described by Fields. We reserve judgment, pending further knowledge of the type species of both genera. The Colhuehuapian material (including Stirton's 1953, p. 611, record of teeth of *Scleromys*? from Colombia) is so fragmentary as to permit no certainty as to familial position. Continued recognition of the family Cephalomyidae for the reception, primarily, of one seemingly aberrant genus is hardly warranted. Our present, very tentative, conception of affinities within this very complex and little understood group is shown in Figure 12.

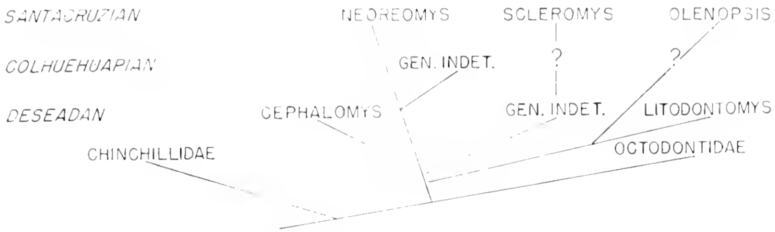

Fig. 12. Tentative phylogeny of the Oligocene and early Miocene Dasyproctidae.

Cephalomys Ameghino, 1897

Cephalomys Ameghino 1897c, p. 494. Loomis 1914, pp. 186-188; Stehlin and Schaub 1951, p. 61; Schaub, *in* Stehlin and Schaub 1951, pp. 245-246.
Orchiomys Ameghino 1897c, p. 495.
Asteromys Ameghino 1897c, p. 495; 1902b, p. 37 (in part, not including type species).

Type species. Cephalomys arcidens Ameghino 1897.

Referred species. Cephalomys plexus Ameghino 1897.

Type species of synonym. Orchiomys prostans Ameghino 1897.

Distribution. Deseadan, Patagonia.

Emended diagnosis. Teeth high-crowned but rooted, with unilateral hypsodonty, particularly in upper molars; no cement on crowns; crown pattern of unworn cheek teeth essentially resembling that of *Neoreomys*, also basically similar to that of *Platypittamys* but with P_4^4 much more advanced than in latter; pattern disappearing fairly rapidly with wear, much less persistent than in *Neoreomys;* enamel interrupted on lingual and anterior sides of lower teeth and buccal and posterior sides of upper teeth after considerable wear; rostrum shorter than in *Platypittamys,* narrower than in *Neoreomys*; fossa for M. massetericus medius pars anticus present on lateral surface of rostrum but smaller than in *Neoreomys*; infraorbital foramen very large, larger than in *Neoreomys*; mandibular condyle low, nearly on level of cheek teeth.

The synonymy is discussed below under the species.

DENTITION

All the cheek teeth of this genus are divided into two lobes. In the upper molars, these lobes unite, after wear, on the buccal side of the crown; in the lowers, at the center of the tooth. The molars are made up of five cross crests above and four below, but the valleys between the members of the anterior and posterior sets of crests are shallow and evanescent.

Several specimens in the Amherst, Buenos Aires, Chicago and Paris collections show unworn or essentially unworn cheek teeth, from which the details of the pattern can be determined for nearly all of the teeth.

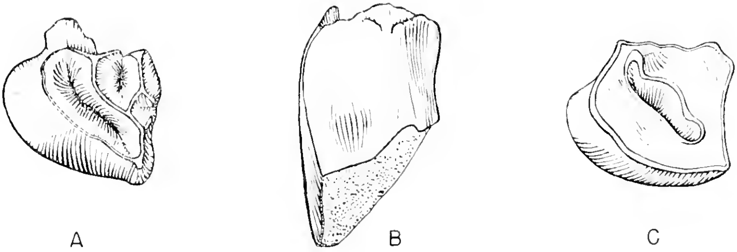

Fig. 13. ***Cephalomys arcidens*** Ameghino, LP⁴ x 5. *A* and *B*, crown and posterior views of A.C.M. no. 3122; *C*, crown view of A.C.M. no. 3064.

Two unworn and two little worn P⁴ are available: A.C.M. no. 3122 (Fig. 13A and B), C.N.H.M. nos. P15241 and P14652 (Fig. 14A) and M.N.H.N. no. 1903-3-23. These agree closely in essentials. There is a long narrow blade extending across the anterior and lingual sides of the crown to unite posterointernally with the straight, transverse posterior margin of the tooth. In the middle of the buccal side is a large cusp that sends a curved crest posterad to the posterior margin. A little distance anterior to the point of junction, a short oblique ridge runs anteroexternally between this crest and the posterior margin, isolating a shallow, posteromedian fossette on three of the teeth. The interpretation of this structure seems clear. The large, curving anterior and internal crest is certainly the anteroloph plus protocone; the large buccal cusp is the paracone; and the crest curving posteriorly from it is a protoloph that has lost contact with the protocone. The transverse, posterior crest may be interpreted as the posteroloph with the metacone incorporated in its external portion, precisely as in *Platypittamys* and *Deseadomys*. The short, oblique crest connecting the posteroloph and the protoloph appears to be the serial equivalent of the corresponding additional crest (neoloph) of the molars (see below) rather than a metaloph. A hypocone, as such, is not differentiated and there is no trace of a hypoflexus. P^4 of the contemporary chinchillid *Scotamys*, which is a basically similar tooth, has a very shallow hypoflexus. This suggests that the hypocone may have been slightly differentiated, or that a tendency existed toward its differentiation, in the common ancestry, perhaps to the extent seen in *Platypittamys*. The Santacruzian *Scleromys*, which has a deep hypoflexus and a well defined hypocone in P^4, also suggests that this was the case and that, furthermore, divergence took place among these forms, *Cephalomys* and *Neoreomys* obliterating, the Santacruzian *Scleromys* accentuating the hypoflexus. According to Fields' figures (1957), the Colombian species he refers to *Scleromys* agree in this respect with *Cephalomys* and *Neoreomys*. However, his figures indicate that P^4 in his forms is more molariform than in *Cephalomys*.

Minor variations in pattern occur in all specimens. In M.N.H.N. no. 1903-3-23, which is very slightly worn, there are irregularities in the buccal margin of the paracone, not indicated in the other specimens. The paracone of the unworn C.N.H.M. no. P15241 is broad and quadrilateral, instead of being a thin blade. There is a clearly marked depression on its top, surrounded by ridges of thick enamel and floored with a thin veneer of enamel. There are three buttresses of enamel running down the buccal margin of the cusp, which would give its outer border a fluted pattern if the tooth were slightly worn. There are two small knobs on the posterior face of A.C.M. no. 3122. These differences in the details of the crown (seen also in the unworn molars) are not considered to have any taxonomic significance. Variation of this sort (which would be considered of specific or even generic value in brachyodont teeth) is a very common feature in the portions of the crown pattern of extremely hypsodont teeth that have not taken part in the increased hypsodonty, and is of no taxonomic significance whatever (Wood, 1940, p. 300), though it may give clues to the phylogeny of the animals concerned.

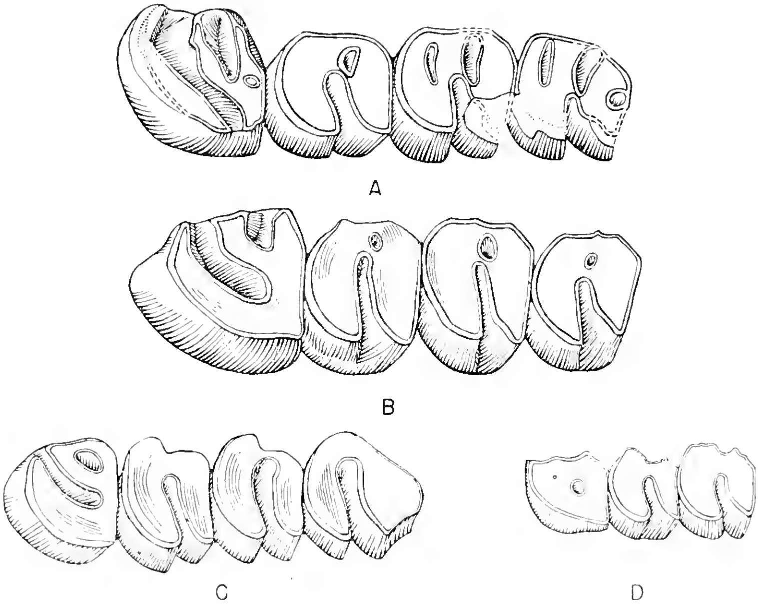

Fig. 14. *Cephalomys,* upper cheek teeth, x 5. *Cephalomys arcidens* Ameghino. *A*, LP^4-M^3, C.N.H.M. no. P 14652; *B*, LP^4-M^3, A.C.M. no. 3099 (M^3 reversed from right side of same specimen). *Cephalomys* sp. *C*, LP^4-M^3, A.C.M. no. 3109. *Cephalomys plexus* Ameghino. *D*, LP^4-M^2, A.C.M. no. 3085.

The first development during wear of P^4 is the isolation of a small lake between the knobs on the posterior surface, when these are present (Fig. 14A). Further wear produces a trident-like pattern (Fig. 14B), and then eliminates all the pattern except for the valley behind the protocone-anteroloph blade, which remains as a lake reaching almost to the roots (Fig. 13C). The sequence of pattern changes with wear (at least in *C. arcidens*) is as follows:

1. elimination of minor irregularities and formation of posterior lake (Fig. 14A);
2. elimination of posterior lake and development of trident pattern (Fig. 14B);
3. conversion of posterior external valley to a lake (Fig. 14C);
4. elimination of posterior external lake (Fig. 13C);
5. conversion of anterior valley to a lake (Fig. 13C);
6. interruption of enamel on posterior face.

In *Cephalomys plexus*, it seems that there may be variability in the sequence, with some specimens agreeing with that listed above (Fig. 14D), whereas in others stage 6 precedes stages 4 and 5 (Fig. 22B), as is also true in *Cephalomys* sp. (Fig. 14C).

The upper premolars of the dasyproctid *Cephalomys* and of the chinchillid *Scotamys* are very similar, differing only in that the latter apparently lacks a neoloph, and has an internal opening of the paraflexus. Superficially, they appear to be quite different from those of the early octodontids, yet closer inspection reveals that all the ingredients for them are represented in P^4 of *Platypittamys* and *Deseadomys*. To convert premolars of this type into the *Cephalomys-Scotamys* P^4 would require only the posterior growth of the protocone, loss of contact between the paracone and the protocone, and a posterior shifting of the lingual end of the paracone crest as the protocone shifted to the rear. This paracone shift might have been facilitated by capture of an incipient mure of the type seen in *Deseadomys* (Fig. 4).

An entirely unworn left upper molar (probably M^3) of *C. plexus*, M.N.H.N. no. 1903-3-3, reveals every detail of the crown (Fig. 15A). Four crests are present, the third crest running obliquely to the posteroloph in the more buccal part of its course. This crest we take to be the lingual part of the metaloph plus a diagonal neoloph crossing the metaflexus. The protoloph, lingual part of the metaloph, neoloph and the buccal part of the posteroloph are the highest parts of the crown, and are practically at the same level, the anteroloph being slightly lower, especially buccally. The lingual portion of the posteroloph is considerably lower and is bowed posteriorly at the occlusal surface, though not at a lower level of the crown. At the posteroexternal angle of the tooth, and somewhat below the level of the rest of the crown, is a small cuspule, from which a short crestlet runs antero-lingually. By comparison of this tooth with the slightly worn first or second upper molars of *C. arcidens* shown in Figures 15B and C, this cusp would appear to be the metacone, and the crestlet running from it to be the last stage in the degeneration of the buccal part of the metaloph. In the specimens shown in Figures 15B and C, the metaloph is complete and five crests are present. This may be a specific character, but is probably an individual variant, since, in upper molars of *Neoreomys australis* (Fig. 17A), and especially in M^3, the metaloph exhibits various stages of disintegration. The neoloph in *Cephalomys* has split the metafossette into two parts, the posterior one (which may be termed the lingual neofossette) being large, irregularly trumpet-shaped, but decreasing rapidly in size with depth. Only a moderate degree of wear would eliminate both parts of the metafossette entirely, and no suggestion of the presence of the neoloph would remain. The parts of the metafossette are worn away in all other available material except C.N.H.M. no. P14652, where the lingual neofossette is preserved on M^3 (Fig. 14A).

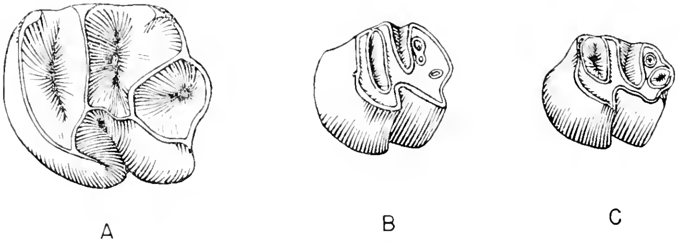

Fig. 15. *Cephalomys*, unworn and little worn upper molars. *Cephalomys plexus* Ameghino. *A*, LM^3, M.N.H.N. no. 1903-3-3, x 10. *Cephalomys arcidens* Ameghino. $LM^{1 \text{ or } 2}$, x 5; *B*, M.N.H.N. no. 1903-3-22; *C*, M.N.H.N. no. 1903-3-20.

This peculiar development of a diagonal neoloph directed anterointernally might at first glance seem to separate *Cephalomys* widely from all other caviomorphs. However, investigation of unworn teeth of various members of the suborder shows that it is by no means a unique feature, appearing in several forms as an individual variation. For example, it is also present in some specimens of *Erethizon dorsatum epixanthum* (Fig. 1D). In *Coendou brandti* we have seen the neoloph extending to the hypocone. Landry figures an interesting case in *Dasyprocta fuliginosa* (1957a, Pl. 5, fig. a) in which the neoloph seems to have split into two parts, one diagonal and one transverse, and we have seen the same thing in *D. aguti.* Evidently this part of the upper molars of caviomorphs is quite unstable.

The angulations at the ends of the neoloph on M.N.H.N. no. 1903-3-3 would be eliminated by wear about the same time the lingual neofossette was lost (Fig. 15A). The great depths of the hypoflexus, mesoflexus and paraflexus are strikingly apparent, the hypoflexus being the deepest, followed by the mesoflexus and paraflexus in that order. The anteroloph and protoloph unite at the buccal margin of the tooth a short distance below the apex of the crown so that the parafossette is isolated soon after wear begins. The protoloph and metaloph (or its vestige) unite considerably farther down, the mesofossette becoming isolated about the time the lingual neofossette disappears (cf. A.M.N.H. no. 29558 or C.N.H.M. no. P14652, Fig. 14A), or later (Fig. 16A). The mure is slightly angulate, but shows no thickening that would suggest the presence of a mesocone.

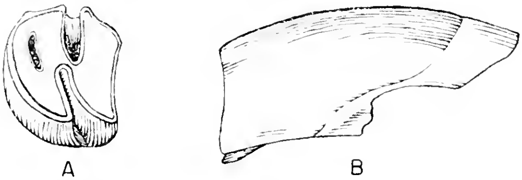

Fig. 16. *Cephalomys arcidens* Ameghino. A.C.M. no. 3160, LM$^{1\text{ or }2}$, x 5; *A*, crown, and *B*, anterior views.

In addition to giving us the crown pattern of an upper molar of a member of this genus, these teeth are interesting because of the similarity — apart from the neoloph — to the unworn molars of *Neoreomys* (Fig. 17A). In the latter, there is also a fifth crest, but this seems to be a normal neoloph, a development from the posterolophid, as in *Protosteiromys*, since it is connected at both ends with that crest, and has no connections whatever with the hypocone. There is a good metacone in *Neoreomys,* which is sometimes partially isolated from the lingual part of the metaloph as in *Cephalomys*, and which thus looks like part of a mesoloph, which it certainly is not. This difference between the manner of development of the fifth crest in *Cephalomys* and *Neoreomys* merely emphasizes the great plasticity of rodent cheek tooth patterns, and the fact that variants may (and generally do) arise in a wide variety of different manners. Perhaps this discrimination of minor types of neoloph variation may seem to be ultra-fastidious but one of the difficulties in unraveling rodent evolution has been the tendency to overlook such differences in origin of a pattern, or to assume that these differences are of no phylogenetic significance. The development of a neoloph, of various types, seems to be characteristic of the caviomorphs, and to distinguish them from the hystricomorphs, where the fifth crest appears to be a mesoloph.

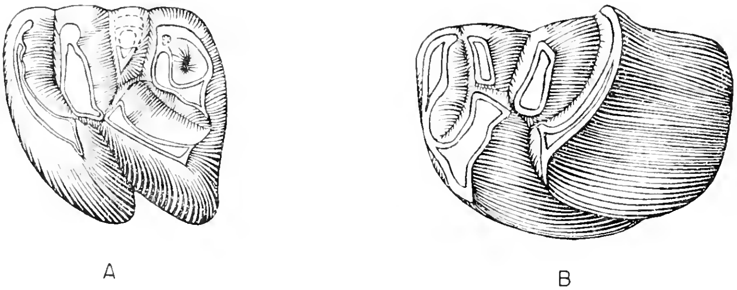

Fig. 17. *Neoreomys australis* Ameghino. C.N.H.M. no. P 13164, x 5; *A*, LM^2; *B*, LM_2.

The primary difference in pattern between the premolars and the molars is that, in the latter, the hypocone is a large and independent element, which it is not in the premolar. This presumably means that the teeth represent specializations of something like those of *Platypittamys*, and that, in the premolar, the protocone grew backward along the lingual margin of the tooth, taking over the functions of both protocone and hypocone in the molars. An additional difference is that the main valley of the premolar is deeper buccally than lingually, so that, with wear, it opens on the buccal side of the tooth, as in chinchillids.

With wear, the molars pass through the following stages:

1. crown formed of anteroloph, protoloph, metaloph or remnant, posteroloph and neoloph, the last dividing the metafossette into two parts (Figs. 15B-C);
2. paraflexus converted to a parafossette (Fig. 14A);
3. elimination of all parts of metafossette;
4. mesoflexus converted to mesofossette (Fig. 14A);
5. elimination of parafossette (Fig. 14B);
6. interruption of enamel on buccal surface (Fig. 14B);
7. elimination of mesofossette;
8. interruption of enamel on posterior surface (Fig. 14C).

Fig. 18. *Cephalomys arcidens* Ameghino. RP$_4$ x 5. *A*, A.C.M. no. 3108; *B*, M.N.H.N. no. 1903-3-19.

The little worn lower premolar (Figs. 18A, 19A, and 19E) shows a pattern rather distinct from that of the lower molars. The trigonid consists of a metaconid, a protoconid and an anteroconid. All of these elements are exceedingly narrow and compressed on the unworn surface, showing little or no suggestion of separate cusps. The protoconid curves forward at its buccal end, and the anteroconid extends straight forward, so that, in unworn or partly worn teeth, there is an anterior lobule (Fig. 18A) giving this tooth a distinctive appearance. Various specimens show notable variation in the anteroconid, which is in part intraspecific (Figs. 18A, 18B, 19A, *C. arcidens*) and is in part associated with the fact that two distinct species are represented. In the unworn P$_4$ of *C. arcidens* the tip of the anteroconid is connected with the anterolophid, whereas in unworn *C. plexus* it stands free (A.C.M. no. 3113, Fig. 19E, and M.A.C.N. nos.

A 52-103, and A 52-106). The talonid in slightly worn teeth consists of a single lobe, connected diagonally with the middle of the metalophid. This diagonal crest arises from the central part of the talonid. Unworn teeth, however, show that the lingual margin of the talonid is actually subdivided into two crests, the hypolophid and the posterolophid. The division extends neither very far across the tooth nor very far down the crown. The entoconid is considerably higher than the posterior cingulum. The enamel over the latter is very thin, sometimes appearing almost not to have been deposited. The apparent pinching at the waist of A.C.M. no. 3108 (Fig. 18A) is due to the lower part of the crown being buried in the jaw. If this tooth were fully erupted, the outline would presumably be the same as that shown in Figures 18B and 19A. The crown pattern is so shallow and so rapidly worn away that there is really no sequence in its loss.

All three lower molars show essentially the same pattern, which may be very clearly seen in M_{1-2} of M.N.H.N. no. 1903-3-2 (Fig. 19B) and in M_3 of A.C.M. nos. 3162 and 3113 (Figs. 19C and E). This pattern is obviously the same as that of *Neorcomys* (Fig. 17B). Again there is variation among the specimens referred to the two species of the genus. The anterolophid extends across the anterior face of the tooth, reaching the lingual margin of the crown, uniting with the metaconid either at or a short distance below the level of the crown. It gives the appearance of having been prevented from growing forward by the presence of another tooth in front, whereas the absence of such a tooth permitted forward growth in the premolar. The anterofossettid is quite ephemeral, though not as short-lived as the metafossettid of P_4. The hypolophid curves slightly to the rear, swinging forward to join the metaconid a short distance below the crown surface. In the crown view of an unworn tooth, the entoconid appears to have its relationships with the trigonid rather than with the talonid (Figs. 19C, E). However, the valley between this crest and the metaconid is actually much deeper than that between it and the rest of the talonid. The latter consists of a long lobe, believed to be formed of the hypoconid and posterolophid. In *C. arcidens*, the posterolophid is incipiently subdivided near its lingual margin in one specimen (Fig. 19C), in a manner that might be the initial stage in the development of an additional lobe. The roots have not yet formed on these unworn third molars, though they probably soon would have developed since they have formed on the second molars of the same specimens.

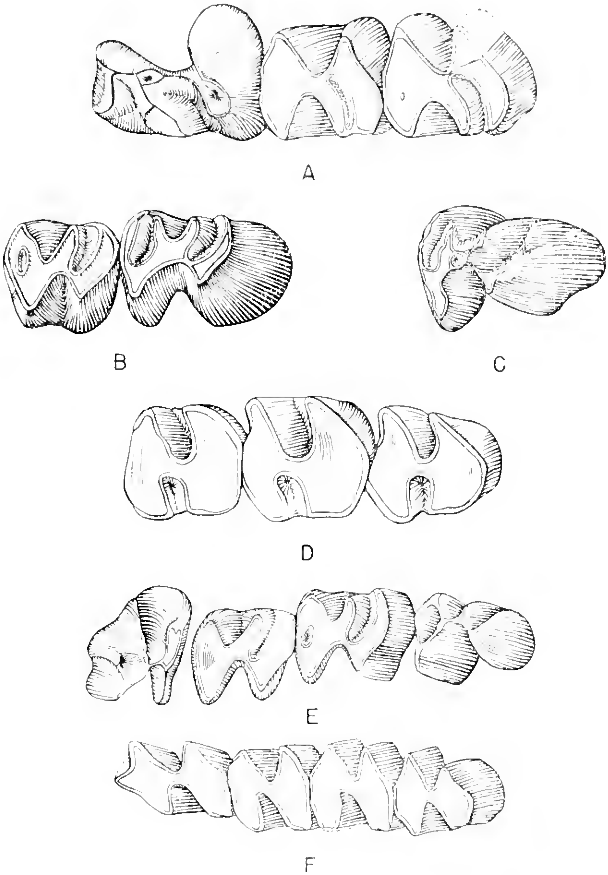

Fig. 19. *Cephalomys*, lower cheek teeth, x 5. *Cephalomys arcidens* Ameghino. *A*, RP$_4$-M$_2$, A.C.M. no. 3161; *B*, LM$_{1-2}$, M.N.H.N. no. 1903-3-2; *C*, LM$_3$, A.C.M. no. 3162; *D*, RM$_{1-3}$, A.C.M. no. 3078. *Cephalomys plexus* Ameghino. *E*, LP$_4$-M$_3$, A.C.M. no. 3113; *F*, RP$_4$-M$_3$, A.C.M. no. 3006.

In another specimen of *C. arcidens* (A.C.M. no. 3144), there is a slightly more worn M_3. In this tooth, though damaged, the metaconid and anterolophid have nearly united lingually. In *C. plexus* they may (A.C.M. no. 3113, Fig. 19E) or may not (e.g. M.A.C.N. no. A 52-103) be united lingually on unworn teeth. The entoconid is shorter, on the crown surface, in A.C.M. no. 3144 than in the previously described specimens, and the talonid is broken. The valley between the metaconid and entoconid is 5.0 mm. deep at the lingual edge of the tooth, extending within 0.6 mm. of the base of the enamel on the crown. The roots are formed in this tooth, so that the crown height can be determined to have been approximately 5.6 mm. on the lingual side and 7.5 mm. on the buccal side.

The sequence of loss of crown pattern in the lower molars is as follows:

1. wear to produce a flat surface with loss of minor irregularities;
2. conversion of the anteroflexid (in *C. arcidens*) to a lake, as in unworn *C. plexus* (Fig. 19E);
3. loss of the anterofossettid (Fig. 19A);
4. conversion of hypoflexid to a lake (Fig. 19A);
5. loss of hypofossettid;
6. interruption of enamel on anterior face (Fig. 19D);
7. conversion of mesoflexid to a lake;
8. interruption of enamel on lingual face.

This sequence of events is based on *C. arcidens*. There may be slight differences in the sequence in *C. plexus*, but they are not very significant. In general, through stage 6, each tooth is about one stage ahead of the next one behind it.

Four specimens in the Amherst and two in the Ameghino collections show dm_4. There is a certain amount of variation in the anterior part of the crown, which is not unusual among rodents (Figs. 20A, B). The talonid seems to be similar to that of the permanent teeth, except that the valley between the entoconid and the posterolophid is as deep as any other valley in the crown. The talonid is connected to the center of the straight metalophid. Anterior to this is what seems to be a tripartite anteroconid, connected to the protoconid or to the protoconid and metaconid. There are two buccal, one anterior, and four lingual valleys. The tooth is replaced after M_1 has reached wear stage

3 or 4, and M_2 wear stage 2 or 3, and very shortly after M_3 has come into use.

The crowns of all the teeth were covered by a complete enamel cap, even though it was removed very quickly by wear. That on the upper surface of the talonid of P_4 was so thin as to appear absent (Fig. 19E). Its thinness in this specimen cannot be due to wear, however, unless the wear was against the roots of dm_4, since we personally removed the roots from over this part of the crown in A.C.M. no. 3113.

The enamel extends to varying distances down the sides of different parts of the crown of the cheek teeth, due to the asymmetric development of hypsodonty. It is interrupted, after the tooth is about half worn down, along the anterior faces of the lower molars (Figs. 19D, F). Before this level is reached, the thickness of the enamel is considerably reduced by interdental wear (Fig. 19A).

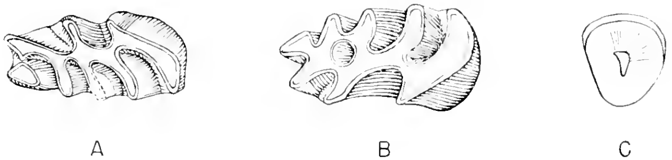

Fig. 20. *Cephalomys arcidens* Ameghino, lower teeth, x 5. *A*, Rdm_4, A.C.M. no. 3013; *B*, Ldm_4, A.C.M. no. 3011; *C*, cross-section of RI_1, anterior view, A.C.M. no. 3155.

The enamel is next lost on the posterointernal corner of the entoconid, beginning with M_1. This occurs much earlier in *C. plexus* (Fig. 19F) than in *C. arcidens*. A layer of cement is deposited around the basal portions of the crown, particularly in *C. plexus*, which sometimes makes it difficult to determine the exact points at which the interruptions occur. In the upper molars, since the teeth are high-crowned lingually and low-crowned buccally, the initial point of loss of enamel is the buccal surface of M^1, followed in turn by M^2 and M^3. The enamel is then lost on the posterior faces of the same teeth. Before the level of no enamel is reached, the buccal enamel becomes considerably thinned, which is obviously not due to interdental wear.

These interruptions are certainly primarily due to non-deposition, and not to interdental wear, as may be seen by looking at the anterior or posterior faces of slightly worn teeth (Fig. 16B), where the uneven ends of the enamel may be seen on the intra-alveolar portions of the teeth. Conditions appear to be identical with those described for the Lagomorpha (Wood, 1940, pp. 356-357). After the portion of the tooth with interrupted enamel has reached the occlusal surface, however, interdental wear becomes quite prominent, and the shapes of the teeth may change considerably and quite rapidly, due to the wear of the enamel of one tooth against the dentine of the adjacent tooth (H. E. Wood, 1938).

The crowns of the teeth are quite high, the height in unworn upper premolars and M_3 reaching twice their maximum diameter.

The difference in pattern between slightly worn lower premolars and molars is believed to be due to two factors: 1) the anterolophid of P_4 extends anterad, whereas in the molars it is squeezed parallel to the metaconid; and 2) the entoconid of P_4 is closely united with the posterolophid, on the wear surface as well as farther down the crown. However, the difference in pattern between both upper and lower premolars and the molars indicates that the molarization of the premolars in this, as well as in other Deseadan genera in which the premolars are known, occurred at a time when the molars had already acquired the main elements of their pattern, while the premolars were relatively simple. It would therefore be in accord with the derivation of *Cephalomys* from something quite similar to *Platypittamys*.

The lower incisor has a nearly flat but gently curved anterior face (Fig. 20C). The enamel face bears a series of fine lines, nearly parallel to the long axis of the tooth. The enamel extends over about a third of the lingual side and about half the buccal side of the tooth. The incisors are relatively short and narrow in proportion to the size of the cheek teeth. The pulp cavity is roughly triangular in outline.

No upper incisors are present in the jaws, but two such incisors are apparently associated. They appear to be similar to the lower incisors, but have not been figured because of the lack of positive association. The course of the alveolus is shown in M.A.C.N. no. A 52-89. It is curved to about the same extent as in *Neoreomys*, but does not extend as far posteriorly, ending a short distance behind the maxillo-premaxillary suture and thus well in front of the anterior root of the zygoma. Its posterior extremity descends farther ventrally, however, than in the Santa Cruz form.

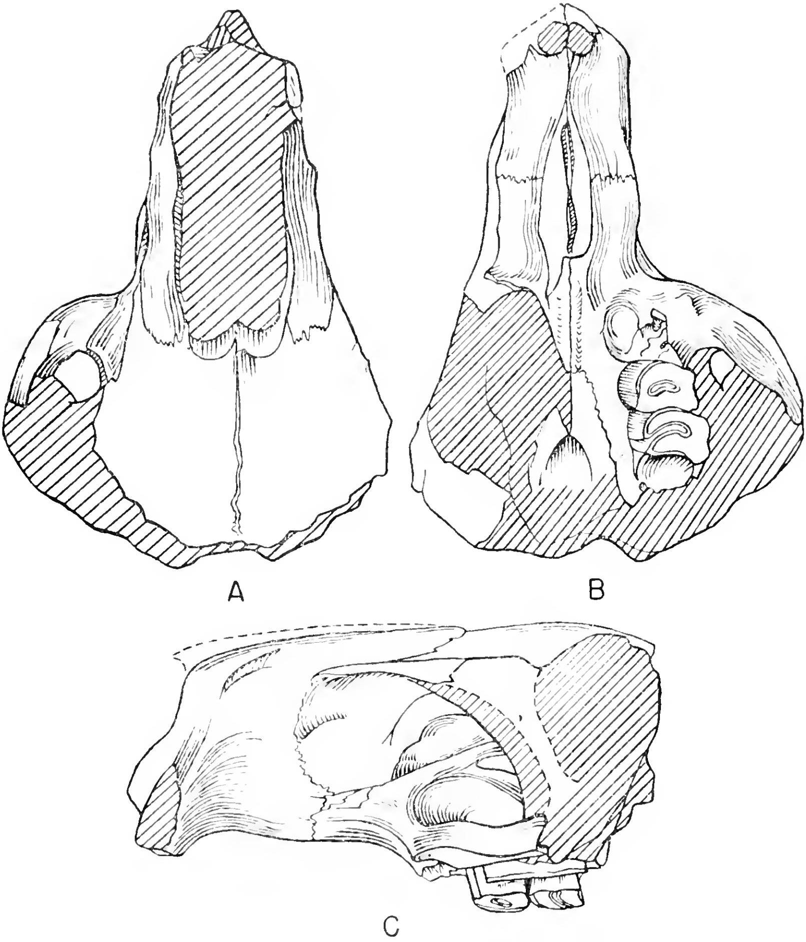

Fig. 21. *Cephalomys arcidens* Ameghino. Facial region of skull, M.A.C.N. no. A 52-89; *A* dorsal, *B* ventral, *C* right lateral view, x 2. Crosshatching indicates matrix; position of infraorbital foramen shown in dashed outline in *C*.

Skull and Mandible

Various specimens, M.A.C.N. no. A 52-89, A.C.M. nos. 3066, 3085, 3091, 3099, 3274 and A.M.N.H. no. 29558, combine to furnish some information concerning the skull. By far the most complete of these is M.A.C.N. no. A 52-89, consisting of the greater part of the facial region. This is the "skull" mentioned by Ameghino in his original description (1897c, p. 494) and the following account is largely based on it.

The rostrum (Fig. 21) is relatively narrow and nearly parallel-sided; it is shorter, but otherwise rather similar to that of *Platypittamys,* and decidedly narrower than the rostrum of *Neoreomys.* The nasals are missing. They extended as far posteriorly as in *Neoreomys,* and the suture between them and the frontals is nearly as transverse; the only notable difference between the two forms in this area is that the frontal in *Cephalomys* sends forward a small wedge between the premaxillary and the nasal. The position of the suture relative to the dorsal root of the zygoma was clearly very similar in both. The frontals are extremely flat, even those parts above the orbits not curving downward to any marked extent. The maxillo-frontal suture, transverse in *Neoreomys,* is here almost longitudinal in direction, due to a narrow triangular projection from the frontal that runs forward between the premaxillary and maxillary. Posterior to this projection, the edge of the frontal shows a somewhat ribbed ventral surface, which suggests the sutural area for the lachrymal. If this indication is correctly interpreted, the size and relations of the latter bone must have been much as in *Neoreomys.* Behind this supposed sutural surface, the upper margin of the orbit is more sharply excavated than in *Neoreomys.* In all probability a postorbital process was present, as in Caviomorpha generally, but the specimen ends at a point just anterior to where this structure would begin.

The premaxillary is similar in general to that of *Neoreomys.* Anteriorly, it sends forward a thin median projection in advance of the incisor alveoli, a feature barely indicated in the Santa Cruz form. The dorsal process is stout, and extends back almost as far as the level of the fronto-nasal suture. The lateral surface of the bone, in decided contrast to *Neoreomys,* is not involved in the masseteric fossa on the side of the rostrum. The ventral surface is about as wide, proportionately, as in *Neoreomys*, the expansion of the rostrum in the latter having taken place in the dorsal portion, evidently *pari passu* with the forward extension of the masseteric fossa. The incisive foramina are wide, much wider than in *Neoreomys*, and lie together in a fossa that deepens posteriorly in its maxillary portion, the posterior wall sloping sharply posteroventral to the palate. The fossa extends back almost to the level of P^4 and slightly beyond that of the anterior root of the zygoma (Fig. 22B). Precisely similar conditions do not appear to exist in any Santa Cruz rodents.

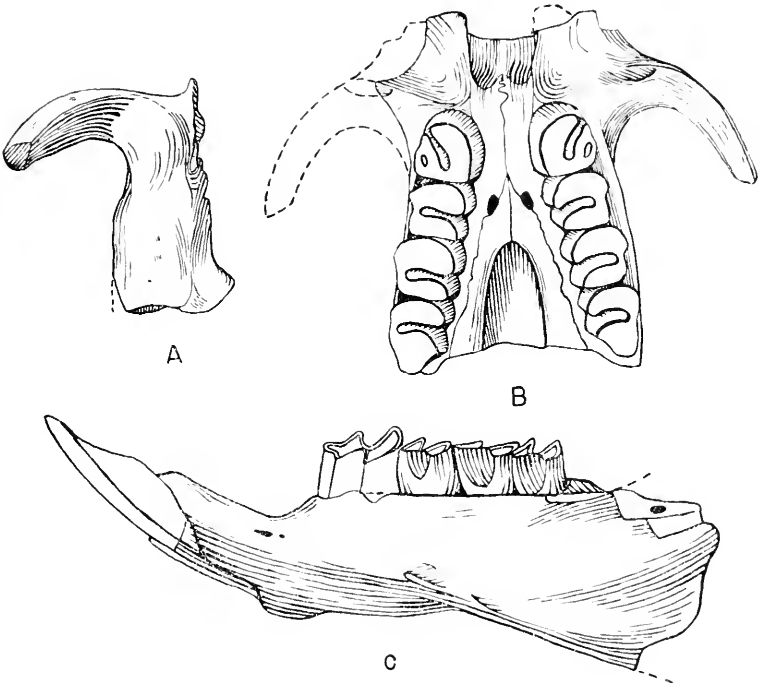

Fig. 22. *Cephalomys*. *A*, *Cephalomys plexus* Ameghino, dorsal view of left maxilla, A.C.M. no. 3085; *B*, *Cephalomys* sp., ventral view of palate, A.C.M. no. 3109 (detail between tooth rows restored from A.C.M. no. 3091, *C. plexus*), x 3. *C*, *Cephalomys arcidens*, lateral view of mandible, A.C.M. no. 3058 (parts in outline from A.C.M. no. 3005, *C. plexus*), x 2.

The palate is very compressed, being narrowest between the premolars and gradually widening (Fig. 22B), as in *Myocastor* and *Olenopsis?* (Fields, 1957, Fig. 15). The posterior widening is much more marked than in *Neoreomys* but less so than in *Perimys*. A deep notch, extending as far forward as the middle (*C. arcidens*) or even the front (*C. plexus*) of M^2, marks the posterior border of the palate. Such a deep notch is not present in *Neoreomys* nor in any other Santa Cruz rodent figured by Scott except *Stichomys* (Scott, 1905, Pl. 65, fig. 17); there is no posterior median projection of the palate. The palatine extends parallel to the margin of this notch, its anterior limit being near the front of M^1 (Figs. 21B, 22B). The posterior palatine foramina lie very close to the midline beside the anterior tip of the palatines, which they may indent very slightly (Fig. 22B). In this, they differ from *Neoreomys*, in which the foramina notch the palatines so deeply "as to be almost entirely enclosed in them" (Scott, 1905, p. 394).

The greater part of the zygomasseteric region is preserved, and what is missing may be inferred with confidence from what is present (Figs. 21-22). The anterior root of the zygoma is somewhat variable in size in some specimens of *C. arcidens*, extending from well in front of P^4 to a point external to M^1, but in some of *C. plexus* not extending behind P^4. The ventral surface of the arch is gently concave, with a sharply crested external margin and a rounded internal one that becomes less pronounced posteriorly. Anterointernally there is a small but clearly defined ventral projection, on the posterior slope of which is a very slightly roughened area, prominent in some specimens of *C. plexus*, that is set off a little from the surrounding bone. It seems very likely that this marks the place of origin of the tendon of M. masseter superficialis. M. masseter lateralis clearly originated from the concave under surface of the arch, and M. masseter medialis, pars posticus, probably had its origin along the medial border. The relations of these portions of the muscle mass would appear to have been essentially similar to those of *Chinchilla* (Wood and White, 1950, pp. 552-554, Figs. 2-3). The dorsal side of the ventral root is very robust, arching strongly upward from front to back. Its posterior surface passes medially into a raised area on the side of the maxillary above P^4-M^1. The arch is preserved to a point opposite M^2 in M.A.C.N. no. A 52-89, and at its posterior extremity the dorsal margin begins to turn upward, thus marking the beginning of the ventral part of the lateral wall of the infraorbital foramen (Fig. 21C). In *Neoreomys* the upturn begins opposite M^1. The fenestra, therefore, was relatively larger in the Oligocene form than in the Miocene one, a fact of some interest, as will appear. The infraorbital nerve and blood vessels evidently ran forward medial to the raised area on the side of the maxillary, where there is a groove (Fig. 22A), and reached the rostrum via the ventral part of the infraorbital foramen. The lateral surface of the rostral portion of the maxilla is occupied by the masseteric fossa mentioned above, which extends anteriorly as far as the maxillo-premaxillary suture (Fig. 21C). Within the fossa, the naso-lachrymal canal is large and prominent, similar in general to that of *Neoreomys* and *Dasyprocta*. Dorsally, the fossa is roofed, as in most caviomorphs, by a thin lateral extension from the upper part of the maxillary, which progressively increases in width posteriorly. This extension is broken off at the level of the naso-frontal suture, but obviously it continued downward and backward to join the upturned part of the zygomatic portion of the maxillary and thus formed, together with the lachrymal, the lateral wall of the infraorbital foramen (Fig. 21C). The fossa clearly served for the reception of M. masseter medialis, pars anticus.

Wood (1949, pp. 13, 49-50) has suggested that enlargement of the infraorbital foramen did not accompany but preceded the forward migration of the anterior portion of the deep masseter to the rostrum. Conditions in *Platypittamys*, in which there is a foramen of moderate size, much smaller than in other caviomorphs, and no indication of a fossa in the side of the rostrum, certainly appear to indicate that this was the case. *Cephalomys* is clearly a more advanced form. As noted above, the infraorbital foramen of *Cephalomys* is relatively larger than that of the later *Neoreomys*. Despite this, the fossa in the rostrum is smaller, extending anteriorly to the maxillo-premaxillary suture, whereas that of the Santa Cruz form extends far on to the premaxillary (Scott, 1905, Pl. 64, fig. 6a). It seems evident that the part of the masseter that had its origin in the fossa in *Cephalomys* must have been smaller than the corresponding part in *Neoreomys*. As in *Platypittamys*, it is therefore probable that enlargement of the foramen preceded, or at least more than merely kept pace with, the forward migration of the muscle. This is not the only interesting inference to be drawn from the available facts. *Platypittamys*, in which the masseter had not begun, or at most had just begun, to pass off the ventral surface of the zygoma, is an octodontid; *Cephalomys*, in which the migration is in full progress, is a dasyproctid. It would therefore appear that in the ancestral caviomorph stock: 1) there was an infraorbital foramen of moderate proportions; 2) M. masseter medialis, pars anticus, was of protrogomorph type; 3) this combination provided the structural basis for the acquisition of the caviomorph zygomasseteric structure; and 4) the advanced stages of this structure were acquired independently in the various groups that rapidly diverged from the ancestral stock. It is now, we believe, virtually certain that the resemblances between caviomorphs and hystricomorphs in zygomasseteric structure are the result of parallel evolution.

Several mandibles, one or two quite complete, are known. The ventral part of the mandible is broadened, as in *Cavia, Cuniculus, Neoreomys, Dasyprocta* and *Lagostomus*, but is quite different from the conditions in *Chinchilla, Coendou* or *Erethizon*. This thickening is lateral to the roots of the cheek teeth, and is apparently related to the development of a more efficient insertion for the masseter. The lower incisor lies on the lingual side of the roots of the cheek teeth, its posterior end being below or nearly below M_3. The diastema is rather short. The mental foramen is high on the ramus, nearly at the alveolar border of the diastema, and well forward of the cheek teeth. There is some uncertainty as to the coronoid process. M.A.C.N. no. A52-104, *C. plexus*, the specimen figured by Ameghino, shows a thin ridge of bone running from a point external to the posterior half of M_3 to the base of the condyle and scarcely rising to the level of the molars. There is no trace of an elevation on the ridge, although a small process could have been broken off. Loomis (1914, p. 191, Fig. 121) figures and describes a small coronoid. His figure was apparently based on A.C.M. no. 3005, *C. plexus*, but this specimen is now broken off behind M_3. A.C.M. no. 3058, *C. arcidens* (Fig. 22C), suggests that a coronoid may have been present. The mandibular foramen is large.[16] The condyle is oval,

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[16] Ameghino shows a minute foramen beneath the mandibular foramen, within the pterygoid fossa. Examination of the figured specimen (M.A.C.N. no. A 52-104) does not support this. The jaw is cracked in this region, and the supposed foramen appears to be a local enlargement within the crack. Other specimens show no foramen in this position.

laterally compressed, faces dorsally, and is but little above the level of the cheek teeth. Below it, and continuing from its posterior margin, is a delicate right-angled process. The structure of this part of the mandible is rather different from that of *Neoreomys*,[17] in which the condyle is higher. Although the angle is broken off in all available material, the beginning of it is present in A.C.M. no. 3059, showing it to have been inflected. The symphysis is very extensive, running the entire length of the receding chin, as in *Erethizon*, but is rather corrugated, indicating a relatively firm union of the two mandibles. This varies between the species. The geniohyal pit is very weak. Near the anterior end of the masseteric fossa is a pit for the attachment of the masseter. The chin region bears a considerable number of nutritive foramina, as in *Eutypomys* (Wood, 1937a, Pl. 29).

SPECIES

The species of *Cephalomys* are not as readily distinguishable as would appear at first glance. Due to their hypsodonty, the details of the tooth pattern are rapidly lost with wear, and only the generic pattern remains. A few possible characters have been mentioned above. Ameghino's distinctions were based largely on size. Initially we thought that three species were represented. However, on plotting the greatest length against the greatest width for each tooth, two size groups appeared. These are quite separate except for one individual, initially referred to *C. plexus* (A.C.M. no. 3109, a palate with all eight cheek teeth; Figs. 14C, 22B, Table 6), which falls in the smaller group for P^4, occupies an intermediate position as regards M^{1-2}, although somewhat nearer the smaller group, and falls in the larger group for M^3. A few other specimens that appear to be intermediate in size are clearly very old individuals of the larger species, *C. arcidens*, the small size being due to the fact that the widest parts of the crown have been worn away. The statistical analysis for the larger species, *C. arcidens* (Tables 3-4) shows that it is a homogeneous population (V usually in the range 6-10). This is true even

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[17] While on the subject of the jaw of *Neoreomys*, we may mention that this genus does not possess the "wide, shelflike masseteric ridge extending back along the angular process" (Landry, 1957a, p. 45) which might be expected of it if it were closely related to *Myocastor*. *Neoreomys* is actually very much like *Dasyprocta* in this respect, the ridge in both being of modest proportions.

though the measurements of maximum tooth diameter, maximum extra-alveolar diameter, and diameter of wear surface were lumped (Tables 3-4). An analysis of two of the three types of measurements taken separately and all three lumped (Table 3) showed that their means and standard deviations coincided within the overlap of their standard errors. Similar investigation of the less numerous, smaller species, *C. plexus* (Table 5) showed about the same situation for the lower teeth, but gave extreme variation in the upper teeth (with the SD reaching 20 per cent of the mean, and V reaching 22.07) when A.C.M. no. 3109 was included. When this specimen was excluded, the statistics of the upper teeth of *C. plexus* correspond with those of the other sets of teeth. It is therefore concluded that there are two valid species, *C. arcidens* and *C. plexus*, and that A.C.M. no. 3109 is an anomalous individual that requires separate treatment. Its measurements are given in Table 6.

Regression lines were computed for the length, x, versus metalophid width, y, of M_2. These gave regression coefficients for the two species which showed no significant difference, the only distinction in the regression lines being the size of the species. The regression coefficients are: *C. arcidens*, $b_{yx} = .658$, $b_{xy} = .667$; *C. plexus*, $b_{yx} = .765$, $b_{xy} = .703$.

It might be worth mentioning that the coefficient of variation (V) of *Cephalomys* is much greater than that computed for brachyodont rodent teeth (particularly a series on members of the Paramyidae), which is certainly related to the much greater hypsodonty of *Cephalomys* and the corresponding inability to measure with certainty the maximum diameters, except on isolated teeth.

As indicated, the variation in tooth measurements is partly due to wear. The widest point of the tooth is near the middle, vertically. Therefore, old individuals show smaller measurements of maximum transverse width than do younger ones. Very young individuals also show smaller measurements if the teeth are in jaws, since the widest point may be within the alveoli. In the anteroposterior measurement, there is extensive interdental wear after the enamel is interrupted, and the teeth become markedly shortened with further use. Processes of this sort, together with long-continued growth, rather than tooth growth anywhere except at the base of the crown, are, we feel certain, the basis for the anomalous results reported by Fields (1957, pp. 354-355) for late Miocene dinomyids.

The possibility has been considered, and can by no means be ruled out, that these two groups represent the two sexes. In general, however, sexual size differences among rodents do not appear to be as great as the differences between these two groups. Moreover, it would seem reasonable to expect more nearly equal representation of the two sexes in a sample of this magnitude than is the case with the two size groups.

It seems probable to us that these differences are of taxonomic significance and that two forms are present. The presence of the unusual individual, A.C.M. no. 3109, rather complicates the picture, in that it shares size features with both groups. This could be explained as merely an extreme in the variation of either group except for the statistical studies. It might also be a hybrid, if specific crosses were possible in *Cephalomys*. The possibility also exists that A.C.M. no. 3109 is an isolated representative of a third species, occupying a different habitat from that in which the other two species lived and were buried.

CEPHALOMYS ARCIDENS Ameghino 1897

Figs. 13, 14A-B, 15B-C, 16, 18, 19A-D, 20 and 21

Cephalomys arcidens Ameghino 1897c, p. 494; 1906, p. 414, Fig. 292; Loomis 1914, pp. 189-190, Figs. 118-119; Schaub, *in* Stehlin and Schaub 1951, Fig. 396, p. 246.

Cephalomys prorsus Ameghino 1903a, p. 95, Fig. 11, p. 98, Figs. 14, 16, p. 99 (in part, not including the type).

Orchiomys prostans Ameghino 1897c, p. 495.

Syntypes. M.A.C.N. no. A 52-88, right and left palatal fragments with P^4-M^3, left mandible with P_4-M_3 and root of I; M.A.C.N. no. A 52-89, facial region of skull with alveoli of R and L I, alveoli of LP^4, M^3 and LM^{1-2}. M.A.C.N. no. A 52-88, Ameghino's figured specimen, is here designated as lectotype.

Type of Orchiomys prostans. M.A.C.N. no. A 52-96, fragment of right mandible with posterior part of dm_4, M_{1-2}.[18]

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[18] Ameghino (1897c, p. 495) referred to the two complete teeth as the fourth and fifth molars, i.e. as P_4-M_1, which is certainly not the case. Earlier (1896, 1897b), he had declared that the Deseadan rodents had five lower cheek teeth, a statement that he soon corrected (1897c, p. 494, footnote), declaring that he had based it on a specimen in which the anterior part of the milk molar was preserved together with the corresponding premolar. The type of ***O. prostans*** may have been the specimen in question, with "anterior end of the milk molar" being a lapsus for posterior end, and M_1 mistaken for P_4; certainly there is no other specimen now in the Ameghino Collection on which the error could possibly have been based.

Hypodigm. The types listed above, and an additional series of good specimens: six in the Ameghino Collection, twenty-eight in Amherst, twelve in the Muséum National d'Histoire Naturelle, three in Chicago Natural History Museum, six in The American Museum of Natural History, five in the Yale Peabody Museum and two in the Museum of Comparative Zoology. The more important of these are mentioned in the account of the morphology or identified in the figure captions. In addition there are numerous isolated first and second molars and incisors that have not been used in the statistical investigation.

Horizon and localities. Deseadan. The Muséum National specimens are from La Flecha, Santa Cruz; those in the Amherst, Chicago, Yale, Museum of Comparative Zoology and American Museum collections are from Cabeza Blanca, Chubut. Ameghino gave no localities for his specimens, but to judge from their appearance, it is probable that all of them are from Cabeza Blanca. One lot of isolated teeth in the Ameghino Collection, M.A.C.N. no. A 52-97, has an accompanying label reading "Gran yacimiento del Pyroterio — Río Chico," which surely indicates this locality.

TABLE 3

Comparison of measurements (in mm.) for occlusal diameter and maximum diameter of lower cheek teeth of *C. arcidens*

	N	M	SD	V
P_4 anteroposterior				
diameter of occlusal surface	24	4.33±.06	.31±.04	7.16±1.03
maximum diameter of crown	12	4.45±.09	.30±.06	6.74±1.38
Total, all specimens	37	4.38±.05	.32±.04	7.31± .85
width hypolophid				
diameter of occlusal surface	14	3.24±.09	.32±.06	9.88±1.87
maximum diameter of crown	16	3.46±.12	.47±.08	13.58±2.40
Total, all specimens	34	3.38±.07	.42±.05	12.43±1.51
M_1 width hypolophid				
diameter of occlusal surface	10	3.07±.04	.12±.03	3.91± .87
maximum diameter of crown	17	3.12±.08	.32±.05	10.26±1.76
Total, all specimens	29	3.10±.05	.26±.03	8.39±1.10
M_3 width metalophid				
diameter of occlusal surface	10	3.00±.06	.19±.04	6.33±1.42
maximum diameter of crown	10	3.16±.08	.26±.06	8.23±1.84
Total, all specimens	24	3.11±.05	.24±.03	7.72±1.11

Statistics not run on specimens where measurement was "greatest extra-alveolar diameter," since in all cases there were fewer than 10 specimens.

TABLE 4

Tooth measurements (in mm.) of *Cephalomys arcidens*

		N	Observed Range	M	SD	V	Lectotype, M.A.C.N. no. A 52-88
P^4-M^3		7	12.6-14.2	13.6			
P^4	anteroposterior	20	3.16-4.29	3.63±.06	.26±.04	7.16±1.13	3.61
	width, protoloph	15	2.87-3.71	3.38±.06	.25±.05	7.40±1.35	
	width, metaloph	15	3.09-4.80	3.55±.06	.25±.05	7.04±1.29	4.80†
M^1	anteroposterior	16	2.53-3.32	3.08±.05	.20±.04	6.49±1.15	3.32
	width, protoloph	14	2.97-4.29	3.25±.04	.16±.03	4.92±.93	4.07†
	width, metaloph	14	2.71-3.37	3.03±.05	.18±.03	5.94±1.12	
M^2	anteroposterior	12	2.83-3.36	3.06±.05	.18±.04	5.88±1.20	3.28
	width, protoloph	10	3.25-4.62	3.45±.04	.12±.03	3.48±.78	4.39†
	width, metaloph	10	2.96-3.58	3.20±.07	.21±.05	6.56±1.47	
M^3	anteroposterior	9	2.58-3.23	2.94			3.19
	width, protoloph	8	2.86-4.29	3.18			4.12†
	width, metaloph	8	2.22-3.27	2.74			
I^1	anteroposterior	3	2.45-2.90	2.61			
	transverse	3	1.79-2.20	1.95			
P_4-M_3		5	14.9-17.5	15.6			
P_4	anteroposterior	37	3.67-4.92	4.38±.05	.32±.04	7.31±.85	4.50
	width, metalophid	20	2.53-3.57	3.19±.06	.27±.04	8.46±1.34	
	width, hypolophid	34	2.04-4.23	3.38±.07	.42±.05	12.43±1.51	2.90†
M_1	anteroposterior	26	2.62-3.88	3.22±.05	.25±.03	7.76±1.08	2.90
	width, metalophid	21	2.74-3.52	3.12±.05	.25±.04	8.01±1.24	3.01†
	width, hypolophid	29	2.43-3.63	3.10±.05	.26±.03	8.39±1.10	
M_2	anteroposterior	22	2.96-3.66	3.30±.04	.21±.03	6.36±.96	3.10
	width, metalophid	22	3.00-3.73	3.35±.04	.21±.03	6.27±.95	3.24†
	width, hypolophid	14	2.99-3.77	3.35±.06	.23±.04	6.87±1.30	
M_3	anteroposterior	22	2.67-3.63	3.02±.06	.26±.04	8.61±1.30	2.67
	width, metalophid	24	2.70-3.67	3.11±.05	.24±.03	7.72±1.11	2.70†
	width, hypolophid	14	2.40-3.27	2.74±.07	.25±.05	9.12±1.72	
I_1	anteroposterior	13	1.96-2.60	2.19±.06	.21±.04	9.59±1.88	
	transverse	15	1.72-2.35	1.99±.05	.20±.04	10.05±1.83	
dm_4	anteroposterior	2	4.70-4.78	4.74			
	width, hypolophid	3	2.25-2.30	2.28			

Means computed on all measurements ; other statistics only when N>9.

Diagnosis. Largest known species of the genus (Tables 3-4); anteroconid of P_4 a rounded enlargement in middle of anterolophid when unworn. In addition, several possible differences based on one or two individuals have been mentioned above in the description of the genus.

Ameghino's reference of two specimens of this species to *Cephalomys prorsus* (a synonym of *C. plexus*) was probably a lapsus. The specimens in question — M.A.C.N. no. A 52-94, a mandible, and M.A.C.N. no. A 52-95, an isolated P_4 and dm_4 — fall within the size range of *C. arcidens,* and this is evident not only from our very large series but also from the much smaller one that was available to Ameghino. M.A.C.N. no. A 52-94 is, in fact, approximately the same size as the lectotype of *C. arcidens.* "*Orchiomys prostans*" was based on a young individual of *C. arcidens,* in which M_1 is at stage 3 and M_2 at stage 2. The lectotype of *C. arcidens* happened to be an old individual with M_1 at stage 6 and M_2 at stage 5. Ameghino did not visualize the differences resulting from wear; his identification of M_{1-2} of "*O. prostans*" as P_4-M_1 may indeed have prevented him from doing so.

This is the most abundant Deseadan mammal (Loomis, 1914, p. 189), being represented by over 100 individuals, counting isolated teeth, in the collections we have studied. In the unworn P_4, the anteroconid is connected primarily with the middle or the lingual part of the metalophid. This may be its only connection (A.C.M. no. 3161, Fig. 19A and no. 3162), or there may be another one with the protoconid (A.C.M. no. 3108, Fig. 18A). The enamel, as already pointed out, is interrupted on the anterior face of the lower molars (Fig. 19D) and the buccal and posterior faces of the upper molars after considerable wear. There do not appear to be any other interruptions.

CEPHALOMYS PLEXUS Ameghino 1897

Figs. 14D, 15A, 16E-F and 22A

Cephalomys plexus Ameghino 1897c, p. 494; 1906, p. 421, Fig. 314; Loomis, 1914, pp. 190-191, Figs. 120-122; Stehlin and Schaub, 1951, Fig. 76, p. 61; Schaub, *in* Stehlin and Schaub, 1951, p. 245, Fig. 394.

Cephalomys prorsus Ameghino, 1899, p. 560, Fig. 6; 1902b, p. 37; 1902d, p. 425, Fig. 6; 1903a, p. 82, Fig. 1, p. 96, Fig. 12, pp. 122-123, Figs. 41-42; Schaub, *in* Stehlin and Schaub, 1951, Fig. 395, p. 245.

Cephalomys prosus [*sic*] Loomis 1914, pp. 191-192, Figs. 123-124 (lapsus for *C. prorsus* Ameghino).

Asteromys prospicuus Ameghino 1897*c*, p. 495.
Asteromys annectens Ameghino 1902b, p. 37.

Syntypes. M.A.C.N. no. A 52-99, portion of right maxillary with P^4-M^3; M.A.C.N. no. A 52-100, portion of left maxillary with P^4-M^3; M.A.C.N. no. A 52-101, portion of right mandible with P_4-M_2; M.A.C.N. no. A 52-102, portion of left mandible with P_4-M_2. M.A.C.N. no. A 52-99, the only one of the series subsequently figured by Ameghino, is here designated as the lectotype.

Types of synonyms. Cephalomys prorsus. M.A.C.N. no. A 52-103, portion of right mandible with P_4 not yet fully erupted and M_{1-3}.[19] *Asteromys prospicuus.* M.A.C.N. no. A 52-107, four isolated upper molars, one LM^3, one $LM^{1 \text{ or } 2}$, one $RM^{1 \text{ or } 2}$ and one fragment. LM^3, the only tooth that actually comes within the size range given by Ameghino, is hereby designated as the lectotype. *Asteromys annectens.* M.A.C.N. no. A 52-108, portion of the left mandible with I, P_4-M_3, and M.A.C.N. no. A 52-109, palate with R and L P^4-M^3; M.A.C.N. no. A 52-108 is here designated as the lectotype.

Hypodigm. The types listed above and a series of good additional specimens, three in the Ameghino collection, seventeen in Amherst, one in the Muséum National d'Histoire Naturelle, one in Chicago Natural History Museum, two in The American Museum of Natural History and four in the Yale Peabody Museum. As in the case of *C. arcidens*, there are, in addition, numerous isolated teeth.

Horizon and localities. Deseadan. The Muséum National specimens are from La Flecha, Santa Cruz; those in the Amherst, Chicago, Yale and American Museum collections are from Cabeza Blanca, Chubut. Again, as in the case of *C. arcidens*, it is probable that Ameghino's specimens were obtained at Cabeza Blanca.

Diagnosis. Approximately two-thirds the size of *C. arcidens* (Table 5); apex of anteroconid of P_4 distinct from anterolophid when unworn.

Cephalomys "prorsus" was distinguished from *C. plexus* on the basis of slightly smaller size and on the following structural

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[19] *C. prorsus* was formally proposed as new by Ameghino in 1902b, p. 37, and the diagnosis there given was based on this specimen and on M.A.C.N. nos. A 52-104 and A 52-105. Previously, however, he had described and figured M_3 of M.A.C.N. no. A 52-103 under this name (1899, p. 560, Fig. 6). The earlier account is sufficient to date the name from 1899 and to fix the type as M.A.C.N. no. A 52-103.

TABLE 5

Tooth measurements (in mm.) of *Cephalomys plexus*

		N	Observed Range	M	SD	V	Lectotype M.A.C.N. no. A 52-94
P^4-M^3		4	7.50-9.60	8.91			
P^4	anteroposterior	10	2.10-2.90	2.45±.08	.26±.06	10.61±2.37	2.40
	width, protoloph	5	1.90-2.96	2.30			
	width, metaloph	9	2.12-3.04	2.68			2.89†
M^1	anteroposterior	13	1.82-2.45	2.24±.05	.18±.04	8.04±1.58	2.02
	width, protoloph	12	1.97-2.74	2.40±.08	.26±.05	10.83±2.21	2.70†
	width, metaloph	7	1.72-2.57	2.07			
M^2	anteroposterior	11	2.03-2.72	2.23±.06	.20±.04	8.97±1.91	2.10
	width, protoloph	11	2.07-2.98	2.48±.08	.25±.05	10.08±2.15	2.51†
	width, metaloph	6	1.88-2.40	2.21			
M^3	anteroposterior	11	1.72-2.28	1.96±.05	.15±.03	7.65±1.63	1.91
	width, protoloph	11	1.82-2.46	2.16±.07	.22±.05	10.19±2.17	2.28†
	width, metaloph	5	1.36-1.88	1.63			
P_4-M_3		4	9.65-11.68	10.57			
P_4	anteroposterior	9	2.45-3.53	2.90			
	width, metalophid	4	1.74-2.63	2.20			
	width, hypolophid	9	1.81-3.10	2.28			
M_1	anteroposterior	12	2.04-2.76	2.41±.06	.22±.04	9.13±1.86	
	width, metalophid	7	1.96-2.85	2.30			
	width, hypolophid	12	1.89-2.82	2.29±.08	.26±.05	11.35±2.32	
M_2	anteroposterior	10	2.20-2.63	2.38±.05	.15±.03	6.30±1.41	
	width, metalophid	10	2.05-2.51	2.31±.05	.16±.04	6.93±1.55	
	width, hypolophid	5	2.30-2.36	2.33			
M_3	anteroposterior	11	1.68-2.50	2.14±.07	.22±.05	10.28±2.19	
	width, metalophid	11	1.71-2.31	2.11±.05	.17±.04	8.06±1.72	
	width, hypolophid	7	1.32-1.96	1.77			
I_1	anteroposterior	6	1.44-1.57	1.52			
	transverse	6	1.16-1.39	1.28			

† = Greatest extra-alveolar diameter.

Means computed on all measurements; other statistics only when N>9.

TABLE 6

Tooth measurements (in mm.) of *Cephalomys* sp., A.C.M. no. 3109

		Left	*Right*
P^4-M^3		11.0	
P^4	anteroposterior	2.42	2.40
	width, protoloph	2.53	2.27
	width, metaloph	2.86	2.51
M^1	anteroposterior	2.33	2.42
	width, protoloph	2.99	2.89
	width, metaloph	2.33	2.47
M^2	anteroposterior	2.39	2.55
	width, protoloph	2.82	2.78
	width, metaloph	2.37	2.44
M^3	anteroposterior	3.10	3.19
	width, protoloph	2.89	2.76
	width, metaloph	2.09	2.33

characters: 1) anterior lobe of lower molars more compressed anteroposteriorly and more pointed at the extremities, 2) posterior lobe of lower molars with a more convex posterior face, and 3) upper molars with small, isolated enamel fossettes. The difference in size is not significant. The first two features are due in part to age and in part to individual variation; specimens structurally intermediate exist, even in the Ameghino Collection. Item 3) has no significance whatever, being entirely an age character; these fossettes may also be seen in Ameghino's syntype series of *C. plexus*.

"*Asteromys prospicuus*" was not, of course, contrasted with *C. plexus* by Ameghino, and the only character he gave to separate it from *Asteromys punctus* was the small size of the upper molars, 1.6 to 1.8 mm. in length. Since *A. punctus* was based on a mandible, no real basis for comparison existed. The syntypes of "*A. prospicuus*" are upper molars of *Cephalomys* at stage 5. Their sizes (length of LM^3 1.8, of LM^{1-2} 2.0, and of $RM^{1 \text{ or } 2}$ 2.4 mm.) are within the range of *C. plexus* and there can be no doubt as to the synonymy.[20]

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[20] In the same labeled box with the molars of *A. prospicuus* was another upper tooth, M.A.C.N. no. A 52-87 (described here on p. 376), that is very different from the syntypes and does show some resemblance in crown structure to the lower molars of *A. punctus*, although much lower-crowned. This tooth may have decided Ameghino that he was dealing with an *Asteromys*, but it cannot be selected as the lectotype and the other molars excluded from the species. It is over 3 mm. in length, and this is too great a difference from the measurements given by Ameghino to be attributed to the cruder measuring devices and optical aids available in 1897.

"*Asteromys annectens*" was described as being transitional between *Asteromys* and *Cephalomys*. In reality, the syntypes are indistinguishable from *C. plexus* either in size or in structure. In the lectotype mandible, M_{1-2} are at stage 4, and M_3 at stage 2. P^4 is at stage 2, M^{1-2} at stage 5, and M^3 at stage 4.

The differences, other than size, separating *C. plexus* from *C. arcidens* are difficult to detect. The distinction in the anteroconid of P_4 can be seen only in unworn teeth. With wear, there are interruptions of the enamel at the posterointernal corners of the lower molars, which occur before the interruptions on the anterior face (Fig. 19F). In the upper cheek teeth there is some variation. In most specimens, the enamel is interrupted first along the buccal side and subsequently along the posterior face, as in the anomalous specimen, A.C.M. no. 3109 (Fig. 14C). In one specimen, A.C.M. no. 3085 (Fig. 14D), which is at the lower limit of the size range, the interruption appears to take place at a much later stage in the wear, as indicated by the difference in pattern of P^4. In this specimen, however, the enamel along the buccal and posterior margins of the teeth is considerably thinner than elsewhere.

LITODONTOMYS Loomis 1914

Litodontomys Loomis 1914, p. 193.

Type species. *L. chubutensis* Loomis 1914.

Distribution. Deseadan, Patagonia.

Emended diagnosis. Cheek teeth high-crowned, cement present in flexids, enamel not extending to bases of teeth on anterior and lingual faces; P_4 not molariform, elongate; para- and metaflexids shallow (obliterated by wear on only known specimen), mesoflexid not as deep as hypoflexid, converting to fossettid with deep wear.

LITODONTOMYS CHUBUTENSIS Loomis 1914

Fig. 23

L. chubutensis Loomis 1914, p. 194, Fig. 127.

Type. A.C.M. no. 3086, fragmentary right mandible with I, P_4-M_3.

Hypodigm. Type only.

Horizon and locality. Deseadan, Cabeza Blanca, Chubut.

Diagnosis. As for the genus; for measurements see Table 7.

The teeth are evidently not typically brachyodont, as Loomis believed, but are fairly well along the road toward high crowns. They appear low, however, due to the excessive wear that they have undergone. This interpretation is based on the fact that cement is present, that the enamel is interrupted on the anterior and lingual sides of the teeth, and that there is a considerable difference in the crown height of M$_1$ and P$_4$, on the one hand, and M$_3$, on the other. In many respects, this form appears to us to be one of the more specialized of the Deseadan rodents. The hypoflexids are directed just posterad of the mesoflexids.

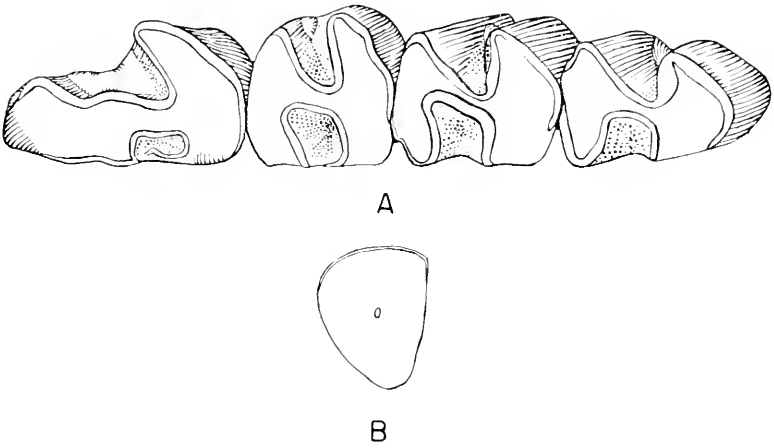

Fig. 23. *Litodontomys chubutensis* Loomis, type, A.C.M. no. 3086, x 10. *A*, RP$_4$-M$_3$; *B*, cross-section of RI$_1$, anterior view.

The premolar has what appears to be a simple talonid (although a shallow metaflexid or -fossettid may have been present originally) connected with an anteroposteriorly expanded trigonid by an ectolophid that widens near its anterior end (Fig. 23A). The mesoflexid is considerably smaller than the hypoflexid, both trigonid and talonid sending arms along the lingual margin of the tooth, which meet, closing off a cement-filled mesofossettid at the present stage of wear. The hypoflexid is much larger, and extends low down on the side of the tooth, as a broad, open embayment. It is partially blocked by a low cingulum, and is partially filled with cement. Enamel is absent over the anterior face of the tooth and from the lingual surface of the talonid, in both cases obviously due to original non-deposition near the base of a high-crowned tooth (Wood, 1940, pp. 356-357), and not due to interdental wear (H. E. Wood, 1938). The free end of the enamel plate on the lingual margin of the tooth apparently is embedded in the dentine.

The molars are made up of two nearly equal lobes, although the talonid is somewhat the larger in each case. The flexids are of more nearly the same size than in P_4, though the hypoflexids are somewhat larger than the mesoflexids in each case. In M_1, both flexids are nearly filled with cement. The mesoflexid is closed, as in P_4, by arms from the internal cusps, whereas the hypoflexid appears to slope to the base of the tooth, being filled with cement. Enamel is absent along the anterior and lingual faces of the tooth and the lingual part of the posterior face.

The mesoflexid of M_2 appears to be of about the same depth as that of M_1 of this specimen. Since the tooth is less worn than M_1, this means that the mesoflexid was actually shallower. The hypoflexid is quite deep. The lingual fold extends as a groove down the side of the tooth, the cingulum closure not being quite at the lingual margin of the valley. Enamel is missing from that part opposite the enamel-bearing portion of M_1 and is present on that part opposite the enamel-free section. It is also missing on part of the lingual border of the talonid, as in geomyoids (Wood, 1937b). A peculiar feature is the apparent encirclement of the free end of the posterior enamel plate by dentine.

M_3 is more elongate and narrower than the other molars, so that the two flexids are wider (especially at their open ends) than in the anterior molars. This is partly due to the lesser amount of wear on this tooth. The enamel has only just been interrupted on the anterior face of the tooth, but is broadly absent on the lingual face of the talonid. The lingual side of the tooth is grooved, as in M_2, but the mesoflexid does not seem to be dammed. This is not certain, however, due to the cement filling. The hypoflexid contains little cement, and is not dammed except at the very base of the crown, where there is a prominent cuspule. The absence of cement here is very possibly due to its removal during preparation.

Loomis' statement (1914, p. 193) that the folds are narrowest at the margin of the teeth and expand toward the center is true of the mesoflexids, due to their having been dammed by the cingular outgrowths of the trigonid and talonid, but is definitely not true of the hypoflexids.

A section of the right lower incisor is associated with this specimen as well as a fragment of the mandible. The tooth is egg-shaped in cross section, with a round, wide, enamel-covered anterior face and a tapering posterior side (Fig. 23B). The lingual margin is nearly straight. The enamel extends about a third of the way around the lateral surface and about a fifth of the distance around the lingual face. The enamel is smooth, and is rather thin. The pulp cavity is very small and is essentially circular near the tip of the tooth. The tooth is quite long, with a large radius of curvature.

The affinities of *Litodontomys* appear to be with the Dasyproctidae, but its position within the family is uncertain. There are some similarities to *Cephalomys* in the cheek teeth and in the incisor, and also in crown height and the tendency toward non-deposition of enamel, but there are also differences. The premolar outlines are very different, for example, and *Cephalomys* lacks cement. There are resemblances to the type material of *Olenopsis*[21] that may indicate some degree of relationship. P_4 of *O. uncinus* agrees in general outline, and, what is more important, in the presence of cement at the base of the crown and in the hypoflexid. The mesoflexid has been converted into a mesofossettid, very possibly in much the same manner as in *Litodontomys*. It is not likely that the two forms stood in an ancestor-descendant relationship. *Olenopsis uncinus* has a more

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[21] The type species, *O. uncinus* Ameghino from the Santa Cruz, was based on three syntypes: M.A.C.N. no. A 17, a fragmentary left mandible with the base of I, dm_4-M_2 (M_2 unerupted); M.A.C.N. no. A 1613, an isolated RP_4; and M.A.C.N. no. A 1614, an isolated Ldm^4 (Ameghino 1889, pp. 145-146. Pl. 6, figs. 14-16). M.A.C.N. no. A 17 is unfortunately not to be found in the Ameghino Collection. M.A.C.N. no. A 1613 has a deposit of cement. M.A.C.N. no. A 1614 lacks all trace of this substance and agrees very closely with dm^4 of *Neoreomys*, to which it may well be referable. Fields (1957, p. 325), in his description of the material he identifies as *Olenopsis aequatorialis* and places in the Dinomyidae, states that there is no evidence of cement in the teeth of that form, which raises the question as to whether or not this species is correctly referable to ***Olenopsis***.

persistent crown pattern and the enamel was more extensive and differently distributed. In addition to the metafossettid, there are three small anterior fossettids, possibly remnants of a large anterior fossettid with an irregular floor or with spurs of enamel projecting into it, and a long, narrow metafossettid. The enamel extends down to the roots everywhere except along the posterior two-thirds of the lingual face, whereas in *Litodontomys* it is incomplete anteriorly as well. The two genera may or may not have had a common, pre-Deseadan ancestry, but the resemblances between them at least suggest some degree of affinity. There are no particular resemblances between *Litodontomys* and the material Fields described as *Olenopsis aequatorialis.*

Table 7

Tooth measurements (in mm.) of *Litodontomys chubutensis*, A.C.M. no. 3086

P_4	anteroposterior	3.21	M_2	anteroposterior	2.21
	width, metalophid	1.21*		width, metalophid	2.08*
	width, hypolophid	1.90*		width, hypolophid	2.03*
M_1	anteroposterior	1.97	M_3	anteroposterior	2.27
	width, metalophid	1.85*		width, metalophid	1.71*
	width, hypolophid	2.09*		width, hypolophid	1.59*
I_1	anteroposterior	1.88			
	transverse	1.44			

?DASYPROCTIDAE gen. et sp. indet.

Fig. 24

M.A.C.N. no. A 52-113, an isolated, unworn upper cheek tooth, presumably from Cabeza Blanca, Chubut.

This tooth shows a very high degree of unilateral hypsodonty, comparable to that of *Cephalomys.* It differs from that genus and from *Litodontomys* in the distribution of the enamel, which persists evenly all around the tooth as far as the beginning of the roots. Fields' figures of the Colombian material referred by him to *Scleromys* suggest a similar distribution of enamel (Fields, 1957, Figs. 10, 14). The protocone and hypocone are approximately subequal and sharply angulate internally. They are separated by a prominent hypoflexus that progressively diminishes and disappears about half way down the crown. The protocone-anteroloph crest curves forward and outward, losing altitude progressively, so that the extremity is far below the level of the apex of the paracone. The paraflexus deepens lingually, and would convert to a long, narrow parafossette. Protoloph and mure form a curving crest connecting the paracone and hypocone. Opposite the protocone, there is a short blunt projection that, with wear, would unite the two crests at this point. The paracone is joined to the external part of the posteroloph by a gently curving crest that bears two minute cuspular elevations. Protoloph, mure, posteroloph and this external crest isolate a large, deep fossette. From the external crest, opposite the second cuspular elevation, a prominent spur projects into this valley. A slight swelling is present on the outer surface of the mure. The region of the hypocone is the highest part of the unworn crown. No trace of cement is present.

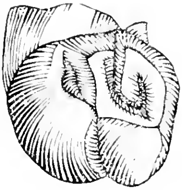

Fig. 24. ?Dasyproctidae, gen. et sp. indet. Left upper cheek tooth, M.A.C.N. no. A 52-113, x 6.

We are in some doubt as to whether this tooth should be interpreted as P^4 or as a molar. It agrees in outline with P^4 of Santacruzian *Scleromys* as figured by Scott, but not with Fields' (1957) referred material. It differs from both in the presence of the large spur in the posterior valley. This structure appears to be a remnant of a metaloph, the swelling on the mure representing the aborted inner end of the crest. So molariform a premolar would be decidedly exceptional in the Deseadan. If the spur and swelling be regarded as a metaloph in process of formation, then such a mode of origin would be exceptional for P^4 among caviomorphs. Agreement with the upper molars of Santacruzian *Scleromys* is close. These teeth lack the metaloph entirely, and, since this is clearly a secondary condition, the structure in M.A.C.N. no. A 52-113 could be regarded as indicating a molar in process of losing this crest. This we believe to be the more likely interpretation. It is supported by the structure of the only known Colhuehuapian dasyproctid, also an isolated upper molar (M.A.C.N. no. A 52-163),[22] in which the metaloph is interrupted by a deep notch in its outer half.

We believe that this specimen is probably a dasyproctid. It is clearly distinct from *Cephalomys* and there is no basis for reference to *Litodontomys.* As regards the even distribution of enamel on the crown, it is more normal, with respect to the later members of the family, than either of its contemporaries. The tendency toward loss of the metaloph suggests affinities with the Santacruzian *Scleromys* rather than with *Neoreomys,* in which complete loss of this crest occurs only on M^3, where it is represented merely by a small metacone behind the paracone (Scott, 1905, Pl. 65, figs. 1-2). M.A.C.N. no. A 52-113 shows no indication of a neoloph, however. This structure does occur in the Santacruzian *Scleromys,* as is revealed by a minute remnant of the floor of the neofossette in M^1 of M.A.C.N. no. A 10142 and by the presence of a neofossette in M^3 of M.A.C.N. no. A 4361. (The isolated Colhuehuapian molar, in which the neoloph and neofossette are fully developed and the metaloph is in process of reduction, demonstrates that these are neofossettes and not metafossettes.) If M.A.C.N. no. A 52-113 was in the ancestral line leading to the Santacruzian *Scleromys,* then a neoloph must have arisen in post-Deseadan time. This is conceivable, but more and better material is clearly needed before any conclusion can be reached.

TABLE 8

Tooth measurements (in mm.) of M.A.C.N. no. A 52-113

Anteroposterior	3.10†
Greatest width	3.83†
Height, buccal side	2.80
Height, lingual side	over 6.4

† = Greatest extra-alveolar diameter.

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[22] This tooth is one of Ameghino's two syntypes of *Luantus initialis* (see below, p. 365).

Superfamily CAVIOIDEA L. Kraglievich 1930
Family EOCARDIIDAE Ameghino 1891

Two cavioid genera, *Asteromys* Ameghino and *Chubutomys* gen. nov., that differ rather strikingly from each other, occur in the Deseadan. So different are they that we once thought that *Chubutomys* should be considered as an aberrant dasyproctid. Study of the Colhuehuapian and Santacruzian material in the Ameghino Collection, however, has revealed that there are two clear-cut groups within the Eocardiidae, one typified by *Luantus*,[23] the other by *Eocardia* and *Schistomys*. *Asteromys* is clearly referable to the first of these, and *Chubutomys* is as certainly an early representative of the second; both these genera possess small, ephemeral mesofossetids, a typical eocardiid character. The two groups may be distinguished as follows:

LUANTINAE subfam. nov. Cheek teeth mesodont to hypsodont; hypoflexus and hypoflexid extending approximately half way across crowns; external fossettes and internal fossettids relatively persistent; metalophid lost on M_{2-3} of later forms; enamel extending equally far down all sides of cheek teeth; no cement.

Distribution. Deseadan to Santacruzian, Patagonia.

Genera. Asteromys Ameghino 1897, Deseadan; *Luantus* Ameghino 1899, Colhuehuapian to Santacruzian.

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[23] Ameghino, subsequent to his description of the Colhuehuapian *L. initialis* (1902c, pp. 114-115), consistently referred *Luantus* to the Capromyidae (Myocastoridae of his usage). *L. initialis* was based on two syntypes, a portion of a left ramus with the base of the incisor and P_4-M_2 (M.A.C.N. no. A 52-164), and an isolated right upper molar (M.A.C.N. no. A 52-163) — not a premolar, as he supposed. The latter represents a hitherto unknown dasyproctid and as such has been briefly referred to above (p. 364), but it clearly has nothing to do with the jaw fragment, which we designate as the lectotype of the species. The two specimens were presumably picked up and packed together, a circumstance that Ameghino all too frequently considered to be sufficient proof of natural association. There is a general resemblance between the lower molars of the Santacruzian species of *Scleromys* and those of *Luantus*, but the latter retains the metalophid in M_1 and has a short, typically eocardiid incisor that does not extend back beyond M_2. Scott (1905, p. 388), evidently on the basis of the lectotype jaw, placed *Luantus* with *Eocardia* and *Schistomys*, an assignment followed by Simpson (1945, p. 94) and Landry (1957a, p. 43). There can be no doubt that this is the correct position of the genus, although we cannot agree with Landry that "a form only a little less specialized than *Luantus* . . . may have been the common ancestor of the Superfamilies Octodonoidea, Cavioidea, and possibly Chinchilloidea" (*op. cit.*, p. 44). The Deseadan *Asteromys* is such a less specialized form, and it is unmistakably a cavioid. Schaub *(in* Stehlin and Schaub 1951, p. 369) considers that *Luantus* is widely separated from the Eocardiidae, and should be referred to the "Acaremyinae" (1953a, p. 399) because the second and third inner "synclinals" of the lower cheek teeth are united. This condition, which is due to loss of the metalophid in M_{2-3}, we cite as a character of the new subfamily Luantinae. We, too, regard it as a character of importance, though we cannot agree that it requires the removal of *Luantus* from the Eocardiidae.

EOCARDIINAE. Cheek teeth hypsodont to hypselodont; hypoflexus and hypoflexid, after slight wear, extending more than half way across crowns; external fossettes and internal fossettids becoming shallow and ephemeral; metalophid retained; enamel of crowns not extending equally far down all sides of cheek teeth, and lacking, after slight wear, on external sides and antero- and posteroexternal corners of uppers, on internal sides and antero- and posterointernal corners of lowers; cement present in some later forms on sides of crowns and in hypoflexus and hypoflexid.

Distribution. Deseadan to Santacruzian, Patagonia.

Genera. Chubutomys gen. nov., Deseadan; *Eocardia, Schistomys, Phanomys*[24] Ameghino 1887, Santacruzian.

Both in the luantines and in the eocardiines with rooted teeth, the hypoflexus and hypoflexid decrease in extent toward the base of the crown and disappear entirely before the root is reached. The known luantines may well have formed a direct phyletic series. *Luantus* has not hitherto been recorded from the Santa Cruz proper, but there are from this horizon two good specimens, a right mandible (M.A.C.N. no. A 2018) and a palate (M.A.C.N. no. A 2025), and a number of isolated teeth in the Ameghino Collection that are certainly referable to the type species, *L. propheticus* Ameghino 1898.[25] The type specimen of this species was found in the Pinturas, or *Astrapothericulus*, beds, supposed by Ameghino to be older than the Santa Cruz. Examination of the scanty, and fragmentary, Pinturas fauna reveals, however, that there is really no good evidence for con-

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[24] This is a very poorly known genus. The syntypes of *P. mixtus*, the type species, are not now in the collections of the Museo de La Plata, and must be presumed lost. Material in the Ameghino Collection described later by Ameghino (1889, p. 217, Pl. 10, figs. 12-25) agrees well with the brief original description. Unfortunately, these "neosyntypes" (M.A.C.N. no. A 2022) are all isolated teeth, as are the syntypes of *P. vetulus* Ameghino (M.A.C.N. no. A 2024). The best specimen *of P. mixtus*, the maxillary fragment with P^4-M^2 figured in 1889 (Pl. 10, fig. 21) and in 1906 (Fig. 313), cannot be found in the collection. The available material shows that *Phanomys* is a valid form with rooted molars but with cement; hypoflexid and distribution of enamel are as in *Eocardia* and *Schistomys. Hedymys*, also described by Ameghino in 1887, is a *nomen vanum* (see below).

[25] P_4 and M_3 of M.A.C.N. no. A 2018 are so similar to the types of Ameghino's *Eocardia prisca* and *Luantus propheticus* as to show that these species were based on RM_3 and RP_4, respectively, of one species, perhaps even of one individual. The former has line priority, which we disregard. *Luantus propheticus* was described by Ameghino as the type species of the genus, and the fact that *Eocardia prisca* was described two lines above would have been an altogether inadequate reason for violating common sense and presenting a new combination. *B. prisca* is here relegated to the synonymy of *L. propheticus*.

sidering it to be anything but a Santacruzian local fauna. The palate, M.A.C.N. no. A 2025, a young specimen with dm^4-M^3 preserved, reveals a very interesting feature of *Luantus* that must be recorded here. M^2 has a swelling in the center of the posteroloph, which on M^3 becomes a minute fossette, partially open posteriorly on the left side. This is a rudimentary neofossette, the first stage in the formation of a neoloph such as occurs in various caviomorphs and it is of the greatest interest to find a tendency toward this condition occurring in the family. This specimen has been figured by Scott (1905, Pl. 68, fig. 27) and by Ameghino (1906, Fig. 311, p. 419). The former figure is very inaccurate, and shows neither the swelling nor the minute fossette; the latter shows the swelling but not the minute fossette and errs in depicting the enamel as missing from the outer face of M^1. Scott called the specimen "*Eocardia* sp. (referred to *Hedymys integrus*)" while Ameghino labeled it "*Hedimys integrus*," and thereby hangs another lengthy footnote.[26]

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[26] *Hedymys integrus* (Ameghino, 1887, p. 14; 1889, pp. 217-218 — the unjustified emendation to *Hedimys* dates from 1894, p. 331) was based on a single upper molar, measuring 3 mm. in length and breadth, with a large internal and two small external roots, a deep hypoflexus and no enamel on the external face. The tooth was evidently only moderately worn since it measured 6 mm. high on the internal side and 4 mm. on the external. The type is not now in the Museo de La Plata and is almost certainly lost. From the description, it is clear that the specimen was an eocardiine, but beyond that it is impossible to go. *Hedymys integrus* Ameghino 1887 is a *nomen vanum* in the fullest sense of that useful term. Scott (1905, p. 472) stated that in his opinion the type was a milk molar of *Eocardia*, but there is no real evidence for this view. In the Ameghino Collection, however, the palate, M.A.C.N. no. A 2025 is labeled as "*Hedimys integrus* tipo." This label, and others like it purporting to identify the types of species described in 1887, has an interesting history. After Ameghino's resignation from the staff of the Museo de La Plata in 1888, he was denied access to the collections by Moreno, the Director. Consequently, he had no opportunity to compare Santacruzian specimens obtained at a later date with those he had described in his paper of 1887. It then became his custom to label as types (and his concept of a type was not that now current) specimens in his own collection that he had referred, without benefit of direct comparison, to species described in that publication, frequently selecting material figured in his great work of 1889. The present specimen was not there figured, and it is difficult to understand why he made the identification, because the teeth considerably exceed the measurements he gave for *H. integrus*. How thoroughly Ameghino had come to base his conception of *Hedymys* on this newly established "type" is shown by his subsequent description of "*Hedimys*" *gracilis* (1906, Fig. 312, p. 420 — the figure caption is the only mention in his writings of this species although it is not there stated to be new). "*H.*" *gracilis* was based on two isolated cheek teeth, M.A.C.N. no. A 4481, an upper molar (designated P^4 by Ameghino) and dm$_4$. The upper molar is here designated as the lectotype; the dm$_4$ is probably referable to *Eocardia*. The molar is smaller than any of the cheek teeth of the new "type" of *H. integrus* and agrees with them in pattern, allowing for the difference in wear, but the measurements (L. 3.0, W. 2.5 mm.) do not suffice to separate it from the real type (now lost) of *H. integrus*. The degree of wear is almost exactly the same as in this lost specimen (external height 6.0, internal 3.3 mm.), however, and this reveals that "*H.*" *gracilis* is not *H. integrus*, since Ameghino's description of the latter stresses the absence of enamel on the outer face and makes no mention of fossettes on the grinding surface, whereas there is enamel and there are fossettes on the lectotype of *gracilis*. The species must be listed as *Luantus gracilis* Ameghino.

The absence of eocardiines in the Colhuehuapian is certainly an accident of collecting; the family is very rare prior to the Santa Cruz, being represented by only three identifiable specimens from the earlier deposits. The Colhuehuapian *Archaeocardia* is not an eocardiid. The two proposed species, "*Palaeocardia*" *mater* Ameghino 1902c and *Archaeocardia mustersiana* Ameghino 1904, both fall into the synonymy of the echimyid *Protacaremys prior* Ameghino 1902 (Patterson and Kraglievich ms.). Simpson (1945, p. 94) inadvertently credits *Archaeocardia* to Ameghino. The name was proposed by Cossmann in 1902[27] to replace *Palaeocardia* Ameghino 1902 *nec* Hall 1867. The hypselodont *Eocardia* and *Schistomys*, both adequately known from Scott's work, are the only common eocardiids. Both forms, and also the rooted *Phanomys*, may well have been derived from *Chubutomys*. The phylogeny of the family may be tentatively expressed as shown in Figure 25.

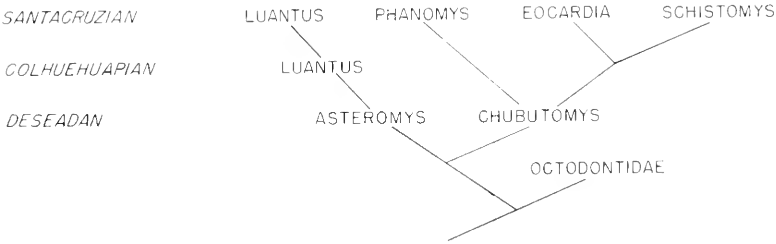

Fig. 25. Tentative phylogeny of the Eocardiidae.

Subfamily LUANTINAE

Asteromys Ameghino

Asteromys Ameghino, 1897c, p. 495; 1898, p. 176. Loomis, 1914, pp. 194-195 (in part). Stehlin and Schaub, 1951, p. 244.

Type species. *A. punctus* Ameghino, 1897.

Distribution. Deseadan, Patagonia.

Emended diagnosis. Cheek teeth mesodont, considerably lower-crowned than in *Luantus initialis*; P_4 not molariform, anterior

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[27] In an unsigned footnote on page 176 of the Revue Critique de Paléozoologie, sixième année.

face with deep vertical groove, minute fossettid on side of ectolophid, mesoflexid large, widely open internally; metalophid present on molars; M_{2-3} not notably larger than P_4-M_1.

ASTEROMYS PUNCTUS Ameghino
Fig. 26

A. punctus Ameghino, 1897c, p. 495; 1906, p. 412, Fig. 287. Stehlin and Schaub, 1951, Fig. 390, p. 244.

Type. M.A.C.N. no. A 52-110, fragment of right ramus with base of I, P_4-M_3, part of anterior root of dm_4.

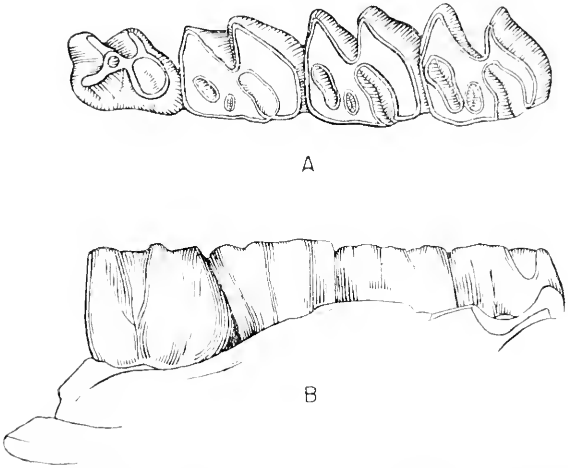

Fig. 26. *Asteromys punctus* Ameghino. RP_4-M_3, type, M.A.C.N. no. A 52-110. *A*, crown, *B*, labial view, x 5.

Hypodigm. Type only.

Horizon and locality. Deseado formation; evidently Cabeza Blanca, Chubut.

Diagnosis. As for the genus; for tooth measurements see Table 9.

The cheek teeth are moderately high-crowned and exhibit a strong degree of unilateral hypsodonty. The enamel is continuous all around the crowns. P_4 differs somewhat from those of other Deseadan rodents. It is less curved and hence exhibits a lesser degree of unilateral hypsodonty than the molars. The crown tapers toward the apex both transversely and anteroposteriorly; the maximum area of grinding surface would not be attained until wear had proceeded about half way down the crown. The upper portion of M_1 curves forward over the obliquely sloping upper part of the posterior face of the premolar, so that with wear the relative proportions of the two teeth would change considerably (Fig. 26). The talonid of P_4 is essentially molariform, the only difference being that the metaflexid is shallower; the hypolophid arises near the center of the tooth and is directed slightly posteriorly, thus suggesting that it may have arisen anterior to the primary posterior crest as in the specimen of *Sciamys* referred to above (p. 297). The trigonid is very different from that of the molars. The anterior face is deeply grooved and the groove extends back between the protoconid and metaconid, which thus appear as though situated at the ends of crests that diverge from the ectolophid. Immediately behind the point of divergence, there is a minute fossettid on the inner side of the ectolophid. The differences from the trigonid of P_4 of *Platypittamys* are striking but apparently not profound. The divergent crests running to the protoconid and metaconid appear to be merely the two wings of the anterolophid, here deeply concave due to the anterior groove, and the inner wall of the minute fossettid is best interpreted as a rudimentary metalophid connected, again due to the presence of the groove, to the metaconid wing of the anterolophid. The crown elements present in both thus appear to be comparable. In *Luantus*, the anterior groove has been eliminated, the short anterolophid is transverse and the metalophid is at first small and freely projecting (*L. initialis*), later becoming larger and uniting with the inner extremity of either the anterolophid or the hypolophid (*L. propheticus*). The hypoflexid extends about half way across the crown and persists nearly to the root. The mesoflexid is very large, wide above and tapering downward; it persists for about two-thirds of the height of the crown. The metaflexid is a mere nick in the rim of the shallow metafossettid basin.

The molars are very similar in size, a notable difference from *Luantus*, in which $M_{2\text{-}3}$ are larger than P_4-M_1. The only apparent structural difference within the series is the greater depth of the metaflexid in M_3, which is not entirely due to the difference in wear. The protoconid and hypoconid form sharp external angles and the lingual border is very straight in all. The metalophid is present and complete on all molars, whereas in *Luantus initialis* it is interrupted on M_2 (M_3 unknown) and in *L. propheticus* absent on M_{2-3}. The hypoflexid extends approximately half way across the crown, diminishing in size and ending near the roots. The metaflexid is the deepest of the internal folds, and the others, if present at all, must have been ephemeral. The minute mesofossettid is the smallest and shallowest of the fossettids, as in all eocardiids. The parafossettid is considerably larger and somewhat deeper, and the metafossettid is the largest and deepest of the three. The metaconid is a large cusp and the metalophid unites with its posterior extremity. In *Luantus initialis*, the inner extremity of the metalophid appears to have lost its connection with the metaconid and to have become secondarily enlarged on M_2.

The incisor is small in comparison with the size of the cheek teeth, and there is not much difference between the two diameters. The anterior face is gently convex. The tooth lies ventromedial to the cheek tooth row, relatively lower than in later forms, and evidently did not extend posteriorly beyond M_2. The internal face of the horizontal ramus is gently shelving above the incisor, as in other eocardiids. The lateral surface of the mandible is not preserved in this specimen and is incomplete in the lectotype of the Colhuehuapian *Luantus initialis*. It is fortunately preserved in one of Ameghino's specimens of *L. propheticus*, which reveals a typically eocardiid structure.

Ameghino placed *Asteromys* in his family Cephalomyidae, which he regarded as broadly ancestral to all caviomorphs, and indeed to all rodents. In 1898, he shot very close to the mark with his statement that the genus ". . . parece ser el antecesor de los cavinos" (1898, p. 176). By 1906, however, he appears to have receded from this conclusion for we find him making comparisons between *Asteromys* and *Alactaga*. Later authors, misled by the upper cheek teeth erroneously referred to "*A. prospicuus*" by Loomis, have placed the genus in the Erethizontidae (as "Acaremyinae"). There can be no doubt whatever that Ameghino's views of 1898 were very nearly correct; *Asteromys* is unquestionably the most primitive known cavioid. It is equally clearly a member of the Luantinae, and none of its known features would seem to bar it from the ancestry of *Luantus*.

The contemporary, and much higher-crowned, *Chubutomys* shows that the eocardiid dichotomy began in pre-Deseadan time, but it is nevertheless probable that in *Asteromys* we have a comparatively little-modified descendant from the common ancestry. The lower molars are of the usual, four-crested, early caviomorph type. Apart from the higher crowns and the reduction of the mesoflexid-mesofossettid, a striking familial character that was presumably established early in the history of the group, there is no important structural difference from the molars of *Platypittamys*. The premolar, as Wood (1949, p. 20) has pointed out, is advanced over that of *Platypittamys* in talonid structure, and is superficially different in the trigonid, as noted above. These differences appear to be relatively trivial. The premolars of Santacruzian octodontids, especially the lowers, were extraordinarily variable in superficial detail (Patterson and Kraglievich ms.). Within *Sciamys principalis*, P_4 may or may not possess a grooved anterior face and a mesolophid and a fossettid on the side of the ectolophid, the talonid may or may not be molariform, and all combinations of these characters occur at random. If earlier octodontids were similarly variable — and it may be noted that the premolars of the two known specimens of *Platypittamys* are far from being exactly similar — derivation of the ancestral eocardiids from an octodontoid stem is altogether likely.

As stated elsewhere in this paper, caviomorphs do not possess, nor were they derived from forms possessing, a mesolophid in the lower molars. The "mesolophid" of P_4 of certain specimens of *Sciamys principalis* was an independently acquired premolar character. It crops up as one of a number of variants resulting from the essentially random variation of the talonid crestlets, which differ in position and in attachments to each other and to the metaconid, protoconid and ectolophid.

TABLE 9
Tooth measurements (in mm.) of *Asteromys punctus*, M.A.C.N. no. A 52-110.

I_1	anteroposterior	1.52
	transverse	1.45
P_4	anteroposterior	3.50†
	transverse	2.51†
M_1	anteroposterior	2.97
	transverse	2.58†
M_2	anteroposterior	3.10
	transverse	2.77†
M_3	anteroposterior	3.17†
	transverse	2.30†

† = Greatest extra-alveolar diameter.

Subfamily EOCARDIINAE

CHUBUTOMYS gen. nov.

Type species. *C. simpsoni* sp. nov.

Distribution. Deseadan, Patagonia.

Diagnosis. Cheek teeth much higher-crowned than in *Asteromys*, approaching hypselodonty, higher than in *Cephalomys* and *Litodontomys;* lower molars with hypoflexids extending across approximately two-thirds of crown diameter; enamel interrupted after wear on anterior face and posterointernal corner of teeth, more persistent on internal sides than in later eocardiines; cement absent.

CHUBUTOMYS SIMPSONI[28] sp. nov.

Fig. 27

Type. A.M.N.H. no. 29557, fragment of left ramus with M_{2-3}.

Hypodigm. Type only.

Horizon and locality. Deseado formation; Cabeza Blanca, Chubut, Argentina.

Diagnosis. As for the genus; for tooth measurements see Table 10.

The teeth are very high-crowned. As in *Cephalomys*, the enamel extends to variable distances down the sides of the teeth,

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[28] Named for Dr. George Gaylord Simpson, leader of the Scarritt Patagonian Expeditions and finder of the type.

so that it is interrupted after wear on the anterior face (beginning at the lingual side) and at the posterointernal corner. The large hypoflexid, dividing the teeth into two equal halves, extends about two-thirds of the way across the crown. At the lower levels of the crown, this fold gradually becomes shallower, disappearing just above the roots, as in the luantines and in other eocardiines with rooted cheek teeth. The anterofossettid is a narrow oval, diagonally placed on the crown and extending well down into the tooth. On M_3, the posterior end of the metaflexid still opens lingually. On M_2, it had just been converted to a metafossettid, which also extends deep into the crown. No trace is present of the ephemeral mesofossettid, the smallest and shallowest of the folds in all eocardiids. The buccal tips of the protoconid and hypoconid are partially separated from the rest of the tooth by faint vertical furrows (Fig. 27), which Scott (1905, p. 462) observed in *Eocardia,* and which also occur, although not constantly, in *Luantus.*

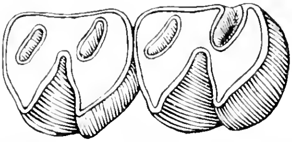

Fig. 27. *Chubutomys simpsoni* gen. et sp. nov. LM_{2-3}, type, A.M.N.H. no. 29557, x 5.

Enough of the bone is present on the lateral side of the ramus fragment to reveal the presence of a rather weak masseteric crest of eocardiid type.

There are several points of resemblance to *Scotamys*: the ephemeral nature of the lingual flexids; the linguad extension of the hypoflexid; and the disposition of the enamel. Among other features, however, the two genera differ in that the hypoflexid is shallower, the antero- and metafossettids persist longer, and there is no cement in *Chubutomys.* There are also resemblances to *Cephalomys* and *Litodontomys,* but the present form is more hypsodont and the crown is divided into two lobes by the hypoflexid instead of by that fold and the mesoflexid, which disappears quickly in *Chubutomys*. As in *Neoreomys*, the hypoflexid becomes progressively more anterior in position as the root is approached and the outline of the tooth becomes less elongate and more quadrangular.

These various similarities to other high-crowned caviomorphs are merely such as would be expected to occur among forms that had diverged from a common ancestry not long prior to the Deseadan. The several characters in which *Chubutomys* resembles the eocardiines seem definitely to indicate close affinity. The obviously small and ephemeral mesoflexid-mesofossettid, already worn away in the type specimen, the very high crowns, the very extensive hypoflexid, the general shape of the crowns, and the sharply angulate protoconids and hypoconids with their tendency toward constriction of the tips by faint vertical furrows — all these present a combination of characters typical of this subfamily. The distribution of enamel is more extensive internally than on the corners. The bearing of *Chubutomys* and other high-crowned Deseadan forms on the time of origin and initial radiation of the Caviomorpha is discussed in the concluding section.

TABLE 10

Tooth measurements (in mm.) of *Chubutomys simpsoni*, A.M.N.H. no. 29557.

M_1	anteroposterior	3.42
	width metalophid	2.65
	width hypolophid	2.80
M_2	anteroposterior	3.58
	width metalophid	2.73
	width hypolophid	2.65

EOCARDIIDAE gen. et sp. indet.

Fig. 28

A.C.M. no. 3054, RM^3, figured by Loomis (1914, Fig. 129) as M_2 of *Asteromys prospicuus* Ameghino. Cabeza Blanca, Chubut.

M.A.C.N. no. A 52-87, R dm^4 (the tooth, referred to above, p. 357, that was in the same box with the syntypes of "*Asteromys prospicuus*"). Presumably Cabeza Blanca, Chubut.

The Amherst specimen (Fig. 28) has a wear facet at only one end, showing that it cannot have been M_2, as Loomis supposed. There was a single internal root, indicating that the tooth is an upper. The lack of divergence of the roots and the rather high crown suggest that it is a permanent tooth. We consider it most probably to be M^3. The tooth is elongate, quite high-crowned, despite considerable wear, and shows marked unilateral hypsodonty. The parafossette is larger and deeper than either the mesofossette or the metafossette. Of the three, the mesofossette is the smallest and the metafossette is the shallowest, and hence the most ephemeral. There is a partial dam across the parafossette, so that it might be split into two fossettes briefly at the right stage of wear. These characters combine to suggest eocardiid affinities.

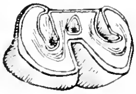

Fig. 28. Eocardiidae gen. et sp. indet. RM^3?, A.C.M. no. 3054, x 5.

M.A.C.N. no. A 52-87 lacks the posteroloph and is not quite complete externally. It is not as worn as the Amherst tooth — the paraflexus is still open — but is very similar in structure. There is also one large internal root and two small external ones. We suspect this tooth to be dm^4.

These two teeth certainly represent the same form. The fact that they agree with the lower molars of *Asteromys punctus* in possessing a similar complete investment of enamel inclines us to suspect that they may possibly be referable to that species. Certainty, of course, can only come with discovery of more complete material.

TABLE 11

Tooth measurements (in mm.) of Eocardiidae indet.

	A.C.M. no. 3054, RM^3	M.A.C.N. no. A 52-87, dm^4?
Anteroposterior	3.05	—
Width protoloph	1.70	1.91
Width metaloph	1.73	—

Superfamily ERETHIZONTOIDEA Simpson 1945
Family ERETHIZONTIDAE Thomas 1897
Subfamily ERETHIZONTINAE Thomas 1897

The New World porcupines are represented in the Deseadan by various isolated teeth that indicate the presence of one genus, *Protosteiromys* nov., with two species. These fragmentary remains reveal that the typical, rather simple molar pattern of the family was then already fully established; in this character there has been almost no subsequent change. The Recent erethizontids are rather distinct in their myology, serology and lice from the remaining caviomorphs, and there are considerable differences between the Santacruzian representatives of the family and other contemporary forms in the structure of the skull and the postcranial skeleton. The skull structure of the Colhuehuapian erethizontids, so far as known, is generally similar to that of the Santacruzian ones. It seems likely that the cranial and postcranial specializations characteristic of the family were already under way by Deseadan time. At the least, it would be unsafe to assume that the similarity in molar structure between the erethizontids and the earliest octodontids and echimyids indicated that the Erethizontidae had diverged from the ancestral stock only slightly prior to the Deseadan.

PROTOSTEIROMYS gen. nov.

Type species. Eosteiromys medianus Ameghino 1903.

Distribution. Deseadan, Patagonia.

Diagnosis. Molars lower-crowned than in later forms other than *Eosteiromys:* upper molars with four main crests, rudimentary neoloph; mesoflexus shallower than in *Eosteiromys;* hypocone on same anteroposterior line as protocone on $M^{1\text{-}3}$; lower molars with four crests, antero- and metafossettids nearly or fully formed.

The taxonomic history of this genus is rather confused. In 1901 Ameghino (pp. 76-78) gave a faunal list of the Santacruzian including *Steiromys principalis* and *S. annectens,* and indicated that the Coendidae (=Erethizontidae), to which he referred them, were present in the Colhué-Huapí (=*Colpodon* beds). The following year (1902c, p. 110), he described *Eosteiro-*

mys homogenidens, nov. gen., nov. sp., from the Colhué-Huapí, but marked it as having been mentioned in the 1901 paper, which was not the case. A year later (1903a, p. 129), Ameghino discussed *Eosteiromys homogenidens* and *E. uniformis* from the Colhué-Huapí, and *E. medianus* from the Deseado (=*Pyrotherium* beds). Although he did not describe *E. medianus* as new in this paper, his brief discussion and figure (Fig. 51) are sufficient to date the species from this paper. The next year (1904, p. 249), he formally described *E. medianus* as a new species from the Deseado, referring it with some doubt to the Colhuehuapian *Eosteiromys*, and cited his previous reference of 1903. This confusion was no fault of Ameghino's, but was the result of papers being published in different journals. Also in 1904, he described *Parasteiromys uniformis*, nov. gen., nov. sp., from the Colhué Huapí, referring back to the 1903 paper where he had figured and described it as *Eosteiromys uniformis*.

In view of this rather confused situation some comment on the Colhuehuapian erethizontids is necessary. Three genera have been recorded: *Eosteiromys*, *Parasteiromys* and *Steiromys*. The first of these is a relatively primitive form, but little advanced over *Protosteiromys*, and with a non-molariform P^4. *Parasteiromys* was originally diagnosed by possession of P^3, reduction of the mure (resulting in continuity of the meso- and hypoflexus), and the presence of a neofossette. The type specimen of *P. uniformis* is a very young individual in which dm^4-M^1 are preserved, not P^4-M^1 as Ameghino supposed. The evidence for a tooth anterior to dm^4 consists of the perforations in the maxilla shown in his figure and interpreted as alveoli (1903a, pp. 126-7, Fig. 47). At the same time, he stated that a fifth upper cheek tooth also occurred in young individuals of *Steiromys detentus*, presumably on similar evidence. Whatever these perforations may be, and they are probably vascular, they are not alveoli. Similar ones occur in young Recent erethizontids and in these no cheek tooth anterior to dm^4 is ever present. A neofossette occurs in several erethizontids, and is fully as well developed in the Santacruzian *Steiromys duplicatus* as it is in the type of *P. uniformis*. The reduction of the mure scarcely seems to be a character of generic significance, and we therefore refer *uniformis* to *Steiromys*. The species *Steiromys axiculus*, *S. tab-*

ulatus and *S. nectus*, the last two synonyms of the first, represent a new and very distinct genus, *Hypsosteiromys* (Patterson, 1958a), also with a non-molariform P^4.

The Deseadan species, *medianus*, is generically distinct from the forms from the Colhué-Huapí. Direct comparison with the type of *E. homogenidens* reveals that the latter has a considerably deeper mesoflexus, and a hypocone more external in position on M^{1-2}. We therefore have no alternative but to propose a generic name and have selected *Protosteiromys*. A second, and more primitive species, *P. asmodeophilus,* is described below.

This genus may be characterized as including very low-crowned erethizontids with the four principal crests of the upper molars usually still quite distinct and with incipient division of the posteroloph to form a neoloph. In the lower molars, the fossettids are already nearly or quite formed. Variability in homologous teeth is considerable, as in later forms, which warns against too rigid a reliance on diagnoses based on one or two specimens.

The upper premolar is unfortunately unknown, but there is no reason to doubt that only three crests, the anteroloph, protoloph, and posteroloph, were present. This tooth is not yet molariform in the Colhuehuapian *Eosteiromys homogenidens,* in which a small fossette in the posteroloph marks the rudiment of a fourth crest.

Five isolated upper molars are known: Ameghino's type of *medianus*; A.C.M. no. 3014, described by Loomis (1914); and three specimens in the Muséum National d'Histoire Naturelle. All are referred to *P. medianus*. The type upper molar, $M^{1 \text{ or } 2}$ (Fig. 30A), is a little wider than long, and shows a slight degree of unilateral hypsodonty; there is a wear facet at each end. The protocone and anteroloph form a curving, lunate, crest that extends almost to the paracone, only a very shallow paraflexus intervening. The protocone is connected to the anterior end of the short mure by a well developed isthmus, the protoloph continuing externally from this point in a very gentle curve, convex forward. A slight terminal swelling marks the position of the paracone. The thin, straight and nearly transverse metaloph arises at the posterior end of the mure, both loph and mure diverging from the anterior arm of the hypocone. A very shallow metaflexus intervenes between the metaloph and the anteriorly curving external extremity of the posteroloph. Both para- and metaflexus would be converted to fossettes with very little additional wear. The mesoflexus is deeper and it is doubtful if a mesofossette would ever have developed. All three flexi are rather shallow relative to the height of the crown. The protocone is moderately elongate anteroposteriorly, more so than in most erethizontids. Probably in correlation with this, the hypocone is decidedly internal in position, on the same anteroposterior line as the protocone. Posterointernally, it is produced into a thin, prominent crest. The hypoflexus is widely open in the unworn or little worn crown but rapidly decreases in size upward, due to the forward slope of the anterior face of the hypocone. It extends for approximately half the height of the internal face of the tooth. On the anterior slope of the external half of the posteroloph there is a small, fifth crest, the neoloph, which has isolated, with the posteroloph, two small neofossettes, a minute external one and a slightly larger internal one. This crest is further discussed below (p. 391).

The other first or second molars (Fig. 30B) differ from the type, and among themselves, in a few respects. Only one small neofossette is isolated by the posteroloph and the neoloph, the anteroloph may be less curved and the paraflexus and metaflexus slightly deeper. If we may judge from *Steiromys*, in which the molars show a considerable degree of variability in these features, such minor differences have no taxonomic significance.

The last molar is represented by M.N.H.N. no. 1903-3-15, (Fig. 30C), a practically unworn specimen. As in M^3 of all erethizontids, the hypocone is more buccad in position than the protocone. The protocone is not united with the protoloph; spurs from the protocone and the lingual end of the protoloph approach each other but would not have united until a considerably more advanced stage of wear had been reached. This feature also occurs in some specimens of *Hypsosteiromys*, and may crop up in molars of *Steiromys* and the Recent forms. Anteroloph and protoloph are united buccad, an advanced feature not found in the other specimens. The metaloph is not connected to the hypocone. The neoloph is rudimentary and the neofossette very small.

Five lower molars (Figs. 31, 32) are also known, of which three are of appropriate size for *P. medianus* and are accordingly referred to that species. The remaining two, which differ from the rest in large size, relative narrowness and other features, constitute the hypodigm of *P. asmodeophilus* described below. As in later erethizontids, the lower molars are relatively broad compared to their length. The four lophids are very distinct, stout and narrowing rapidly toward their summits, as are those of the upper molars. When unworn they tend to have a delicate appearance, which is rapidly lost with wear. The cusps are almost indistinguishable from the crests, only a few traces remaining in *P. medianus*. The hypolophid and posterolophid are united lingually to isolate the metafossettid, even in unworn teeth. The anterofossettid is similarly isolated in the type of *P. asmodeophilus;* in the other available teeth a slight and shallow notch intervenes between the anterolophid and metalophid. The mesoflexid is the deepest of the lingual folds. Only after great wear, if at all, would a mesofossettid be formed. The hypoflexid is deeper than the mesoflexid and extends into the crown surface for slightly over a third of the total width of the tooth. A thin, prominent spur extends anteroexternally from the site of the hypoconid, but, in contrast to some later forms, there is no corresponding spur from the site of the protoconid. There is no trace in the anterofossettid of any cuspules or crestlets, such as may occur in later forms (cf. *Steiromys duplicatus,* Scott, 1905, Pl. 66, fig. 2a).

The upper and lower molars of this earliest known erethizontid genus show no particular resemblance to those of the Hystricidae, in which the unworn crowns have massive, tuberculate and closely appressed crests (Friant, 1935, p. 231).

Protosteiromys seems clearly to be related to *Eosteiromys* of the Colhuehuapian and to *Steiromys* of the Colhuehuapian and Santacruzian, to which it may well have been directly ancestral. The Colhuehuapian *Hypsosteiromys* is sufficiently specialized to suggest that its ancestry may have been distinct in the Deseadan. The only known later Tertiary form is the relatively gigantic *Neosteiromys bombifrons* Rovereto from the Pliocene of Catamarca, the largest known erethizontid (condylobasal length 151 mm.); this was probably a descendant of *Steiromys.* The living erethizontids appear readily derivable from an ancestor such as *Protosteiromys.* This form, then, as far as known, may be considered as representing essentially the basal stock of the Erethizontidae, as indicated in the phylogenetic chart of the Oligocene and Miocene members of the family (Fig. 29).

Fig. 29. Tentative phylogeny of the Oligocene and early Miocene Erethizontidae.

PROTOSTEIROMYS MEDIANUS (Ameghino)

Figs. 30-31

?*Eosteiromys medianus* Ameghino, 1903a, Fig. 51[29], p. 129.

***Eosteiromys medianus* Ameghino, 1904, p. 249; 1906, p. 413, Fig. 288; Loomis, 1914, p. 196, Fig. 130; Schaub, *in* Stehlin and Schaub, 1951, pp. 40-41, Fig. 38.**

Type. M.A.C.N. no. A 52-111, $RM^{1 \text{ or } 2}$.

Hypodigm. Type and the following specimens: A.C.M. no. 3014, $LM^{1 \text{ or } 2}$ (*not* right, as Loomis stated); M.N.H.N. nos. 1903-3-83, $LM^{1 \text{ or } 2}$; 1903-3-84, broken $LM^{1 \text{ or } 2}$; 1903-3-15, unworn LM^3; 1903-3-16, $LM_{1 \text{ or } 2}$; 1903-3-17, $RM_{1 \text{ or } 2}$; 1903-3-85, $RM_{1 \text{ or } 2}$.

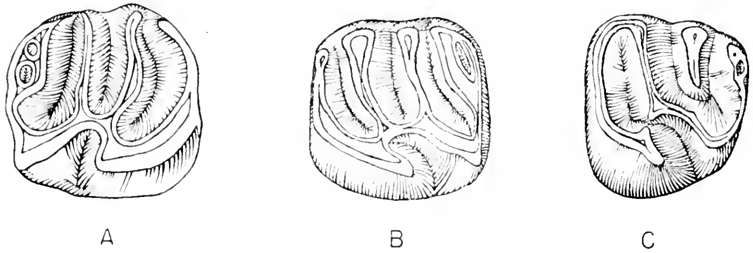

Fig. 30. *Protosteiromys medianus* (Ameghino). Upper molar teeth x 5. *A*, RM^1, type, M.A.C.N. no. A 52-111; *B*, $LM^{1 \text{ or } 2}$, A.C.M. no. 3014; *C*, LM^3, M.N.H.N. no. 1903-3-15.

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[29] Ameghino's figure is actually about four times natural size, and not three times as stated. It is inaccurate as regards shape and in showing one fossette too many at the rear of the tooth. Loomis' figure of A.C.M. no. 3014 is likewise inaccurate in shape and in most details of crown structure.

Horizon and localities. Deseado formation; the Amherst specimen is from Cabeza Blanca, Chubut; the Muséum National d'Histoire Naturelle specimens are from La Flecha, Santa Cruz. Ameghino (1904, p. 249) stated that the type was from the "pyrotheriense del Deseado." This was the Ameghinos' designation, variously written as "Deseado," "Río Deseado" or "Sur del Deseado," for the La Flecha locality.

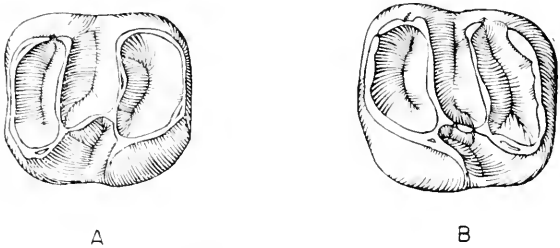

Fig. 31. *Protosteiromys medianus* (Ameghino). Lower molar teeth x 5. *A*, LM_1, M.N.H.N. no. 1903-3-16; *B*, RM_2, M.N.H.N. 1903-3-17.

Diagnosis. Smaller and relatively slightly higher-crowned than *P. asmodeophilus* (Table 12); lower molars shorter relative to width, fossettids thus more compressed anteroposteriorly, metalophid and hypolophid slightly convergent buccad.

PROTOSTEIROMYS ASMODEOPHILUS[30] sp. nov.

Fig. 32

Type. C.N.H.M. no. 15061, $RM_{1\text{ or }2}$.

Hypodigm. Type and M.N.H.N. no. 1903-3-18, a worn and broken tooth, perhaps RM_3.

Horizon and locality. Deseado formation, La Flecha, Santa Cruz.

Diagnosis. Larger than *P. medianus* (Table 12); crowns of same actual height as in *P. medianus* and hence proportionately lower; fossettids, particularly the metafossettid, rounder and less compressed anteroposteriorly; mesoflexid with sides slightly divergent rather than slightly convergent lingually, lingual ex-

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[30] The type was found in the laboratory in matrix surrounding a femur of *Asmodeus osborni* Ameghino.

tremity deeper; central portion of ectolophid less oblique; no trace of distinct cusps.

In every character except the complete incorporation of the cusps into the crests, this species is more primitive than *P. medianus*. An early trend in dental evolution in the Erethizontidae was toward rather wide lower molars. Nearly every point in which *P. asmodeophilus* differs from *P. medianus* reflects a tooth that is relatively narrower in this diameter.

TABLE 12

Tooth measurements (in mm.) of *Protosteiromys*

P. medianus

	Type M.A.C.N. no. A 52-111 RM$^{1 \text{ or } 2}$	A.C.M. no. 3014 LM$^{1 \text{ or } 2}$	M.N.H.N. no. 1903-3-83 LM$^{1 \text{ or } 2}$	M.N.H.N. no. 1903-3-15 LM^3	M.N.H.N. no. 1903-3-84 LM$^{1 \text{ or } 2}$
anteroposterior	5.21	4.70*	4.48*	4.25*	ca. 4.63
width protoloph	5.48	5.00*	5.07*	4.81*	
width metaloph		4.75*	4.92*	4.09*	
height of crown, protocone	3.01	2.80	worn	2.77	

	M.N.H.N. no. 1903-3-16 LM$_{1 \text{ or } 2}$	M.N.H.N. no. 1903-3-85 RM$_{1 \text{ or } 2}$	M.N.H.N. no. 1903-3-17 RM$_{1 \text{ or } 2}$
anteroposterior	4.88*	5.19*	5.18*
width trigonid	4.51*	4.62*	4.62*
width talonid	4.58*	4.84*	4.93*
height of crown, protoconid	2.47	worn	2.44

P. asmodeophilus

	Type C.N.H.M. no. P 15061 RM$_1$ or$_2$	M.N.H.N. no. 1903-3-18 RM$_3$?
anteroposterior	6.75*	ca. 7.20
width trigonid	5.52*	ca. 4.45
width talonid	5.60*	5.01*
height of crown, protoconid	2.50 (unworn)	2.47 (worn)

The referred specimen is somewhat narrower than the type. As in M_3 of *Hypsosteiromys*, the trigonid is appreciably narrower than the talonid, which is the chief reason for identifying this tooth as M_3, since the break at the rear of the tooth makes it impossible to determine whether or not there was a wear facet there. The anterofossettid is still a little open lingually, in contrast to the closed condition in the type.

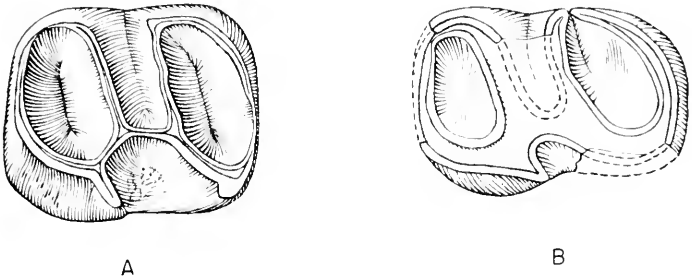

Fig. 32. *Protosteiromys asmodeophilus* sp. nov. Lower molar teeth x 5. *A*, $RM_{1\text{ or }2}$, type, C.N.H.M. no. P 15061; *B,* RM_3, M.N.H.N. no. 1903-3-18.

CAVIOMORPHA indet.

A single left lower molar (A.C.M. no. 3039, Cabeza Blanca, Chubut) cannot be allocated to any of the described forms. It is high-crowned but rooted, comparable to *Cephalomys* and *Litodontomys* and of about the same size as *L. chubutensis* and *C. plexus*. It does not have any cement, and the enamel is continuous around the crown almost, if not quite, to the roots. There is a hypoflexid that extends about half way across the crown, buccal to which is a small mesofossettid (Fig. 33A). Neither

Fig. 33. Caviomorpha, gen. et sp. indet. x 5. *A,* left lower molar, A.C.M. no. 3039; *B*, $LM^{3?}$, M.N.H.N. no. 1903-3-21.

antero- nor metafossettid is present. This form is clearly distinct from all described species in the uniform extension of enamel and the persistence of the mesofossettid. It shows some resemblance to the tooth described above (p. 362) as Dasyproctidae indet., to which it may conceivably be related.

An isolated upper molar (M.N.H.N. no. 1903-3-21, La Flecha, Santa Cruz; Fig. 33B) appears to represent still a different structural type. There are three transverse crests, although a small anteriorly directed crestlet from the posteroexternal corner suggests the last remnant of a metaloph. There is a continuous ridge of enamel around the margin of the tooth, so that the buccal valleys were fossettes from the start. In the reduction to three crests, this tooth is reminiscent of the lower molars of *Deseadomys,* but no such reduction occurs in the uppers referred to that form. In addition, the present tooth is much too high-crowned to be referred to the Echimyidae. It is possible that the animal represented by this molar may also be a dasyproctid. The degree of hypsodonty is also comparable to that occurring in *Cephalomys* and *Litodontomys,* and the absence of a metaloph and the presence and direction of the short spur running from the metacone are reminiscent of conditions in the unworn upper molar of *Cephalomys plexus* (cf. Fig. 15A). There is a slight elevation near the middle of the posteroloph and another postero-internal to the protoloph on the mure. These two elevations occupy positions comparable to those occupied by the two ends of the neoloph in *C. plexus.*

It is obviously inadvisable to name either of these forms until material is available that would permit their relationships to be better understood. They clearly show how very far we are from a complete knowledge of the Deseadan rodents.

TABLE 13

Tooth measurements (in mm.) of Caviomorpha, indet.

	M.N.H.N. no. 1903-3-21 LM^3?	A.C.M. no. 3039 $RM_{1 \text{ or } 2}$
anteroposterior	2.75*	2.06
anterior width	2.10*	1.91*
posterior width	2.00*	1.94*

DISCUSSION

BEARING OF THE RODENTS ON THE AGE OF THE DESEADAN

The Deseado is sufficiently older than the Colhué-Huapí so that all genera of rodents, and practically all genera of other mammalian groups, are different in the two horizons. If the criteria on which these South American rodent genera are based are comparable to the criteria distinguishing their contemporaneous North American relatives, the gap between the Deseado and Colhué-Huapí is much greater, for example, than that between the early Oligocene Chadronian at Pipestone Springs, Montana, and the middle Oligocene Brulé of the "Oreodon Beds" of South Dakota. Of the seven rodent genera from Pipestone, *Prosciurus, Ischyromys* and *Paradjidaumo* are represented in the Brulé; *Titanotheriomys* probably is; and *Adjidaumo* is found in contemporaneous deposits not in South Dakota. This leaves *Pseudocylindrodon* and *Cylindrodon* as the only rodent genera present at Pipestone but not in the "Oreodon Beds," and the former is represented only by a single specimen. This comparison suggests that the gap between the Deseado and the Colhué-Huapí may represent most of the Oligocene.

Since, however, no rodents are known from South America earlier than the Deseadan, we are convinced (as pointed out below) that they reached that continent during the long post-Mustersan hiatus. Once members of this order reached the relatively virgin field of South America, they certainly underwent a very rapid initial radiation, and this would have lasted until the rodents had occupied most of the available niches. Therefore, such an evolutionary development would have involved less time than a similar amount of evolution in North America, where the niches were already filled.

Intercontinental correlations would be greatly aided if we knew the detailed derivation of the Caviomorpha. Of the known possible ancestors, however, we believe *Rapamys* to be the most probable candidate (see below). This rodent, known from the late Eocene Duchesnean of North America, could be distantly ancestral to all the Deseadan rodents. If so, the morphologic change was certainly much greater than that between the Deseadan and Colhuehuapian rodents, being on the subordinal or familial rather than the generic level. Of course, if the argument for rapid post-Deseadan evolution, outlined above, is valid, that for rapid pre-Deseadan evolution would be even more so.

A combination of these lines of reasoning would suggest that the Deseadan is early Oligocene, but probably not earliest Oligocene, being perhaps contemporaneous with typical Chadron in North America; the Colhuehuapian is perhaps early Whitneyan.

If the Deseadan caviomorphs were not derived from *Rapamys* or a close relative, all other known possible ancestral forms would be middle Eocene or earlier. Such an ancestry would allow the age of the Deseadan to be shifted back toward the beginning of the Oligocene, but probably not as far as into the late Eocene. Therefore, no matter what the ultimate source of the Caviomorpha, it would seem probable that we are here dealing with an early Oligocene fauna. Schaub (*in* Stehlin and Schaub, 1951, p. 41) has expressed a comparable opinion.

The Relationships of the Deseadan Rodents to Later Forms and to Each Other

The problem of the relationships of these rodents is a twofold one. On the one hand, is the question of their affinities to each other and to those that follow them in time; on the other, is the broader question of the origin of the indigenous Neotropical rodent fauna as a whole.

The second part of the first question — the relationships of Deseadan to later forms — has been gone into in the discussions on the preceding pages. We believe that it has been satisfactorily demonstrated that *Platypittamys* is very near the direct line of the Octodontidae and is structurally very close to the ancestry of all the rest of the fauna except *Protosteiromys;* that the two species of *Deseadomys* are essentially ancestral to the *Adelphomys* group of the Echimyidae; that *Cephalomys* and *Litodontomys* may be referable to the Dasyproctidae, although their precise relationships to later members of the family cannot be decided at present; that *Scotamys* is a broadly ancestral member of the Chinchillidae; that *Asteromys* and *Chubutomys* are ancestral members of the two subfamilies of the Eocardiidae; and that *Protosteiromys* is on or very near the direct line of the Erethizontidae.

It would appear at first glance, therefore, that the Deseadan rodent fauna was highly diverse, almost as much so as later ones. Representatives of seven families and of all four of the recognized superfamilies are present. In point of fact, however, this heterogeneity is to an extent an artifact of taxonomy that tends to mask the essential homogeneity of these forms. These animals are widely separated in the scheme merely because a vertical classification best expresses the fact that the Deseadan forms can be traced forward into groups that subsequently become highly distinct from each other. That the ancestors of the various later groups were still close to each other structurally as well as genealogically is rather vividly demonstrated by the differences of opinion concerning the relationships of *Cephalomys*, which of course resulted from this similarity.

Wood (1949) has pointed out that the molars of all indigenous South American rodents suggest derivation from forms with four transverse crests above and below — the pattern shown by the early Octodontidae and Echimyidae. Winge (1887) had much earlier advanced a similar opinion, and it would also appear that Ameghino, with his customary insight, had implicitly recognized this—witness the repeated use of *Acaremys* as a basis for comparison in his descriptions of the early forms. Scott (1905, pp. 387-388) also entertained an essentially similar opinion, but without mentioning *Acaremys* specifically. We believe that the present study goes far towards establishing the validity of this view. Except for *Protosteiromys* and *Cephalomys*, every Deseadan rodent, of which the original upper molar crown pattern can be made out, conforms fully with the four-crested pattern. The lower molars of all are or may be presumed to be four-crested, save only *Deseadomys loomisi.*

There is no suggestion in any of these forms that the crests were surmounted by numerous small cuspules. Where an evolutionary sequence can be traced, rodents that have such a pattern can be shown to have been related (just as in the Proboscidea) to earlier forms whose crests were made up by ridges connecting the basic tribosphenic cusps. This is true for the cuspidate Recent *Dasyprocta, Myoprocta* and *Cuniculus* (Landry, 1957a, p. 47) which contrast with the crested Miocene *Neoreomys* among the Caviomorpha, for the Geomyoidea and for some murids. Such cuspules are present in the Hystricidae, but the phylogeny of this family is essentially unknown. We therefore disagree completely with Landry's statement (*op. cit.*, p. 48) that the "low-crowned teeth of erethizontids and echimyids are specialized and derived from [the] early cuspy tooth type" found in "low-crowned, primitive hystricids, which I believe to be close to the original tooth type in the Hystricomorpha." (Incidentally, his reference at this point to pl. 1, d, which does not exist, probably refers to pl. 2, a, which is a hystricid.) Landry's whole concept of dental evolution appears to us to be completely erroneous and based on a series of misconceptions and misinterpretations. He observes the presence of teeth with a multiplicity of cusps in a variety of late Tertiary and Recent caviomorphs and hystricomorphs and states that the pattern of cross crests and folds does not appear until after some wear. He believes that "this breaking up of the crown into a number of cuspules may have been a fundamental adaptation to the propalinal grinding of hystricomorph teeth" (*op. cit.*, p. 88), and he concludes that "such an arrangement suggests at once that the cusps are primitive and the infolded pattern derived" (*op. cit.*, p. 85). As he recognized, this observation is not original; it has led various observers to draw the now thoroughly discredited ultimate conclusion, namely that rodent teeth (or placental teeth) were derived from teeth of multituberculates, a conclusion in which Landry does not concur (*op. cit.*, p. 89). In fact, he states (*op. cit.*, p. 90) that he believes "that this multiplication in cusps is connected with the adaptation to propalinal grinding." It may or may not be true that a multiplicity of cusps is correlated with an adaptation to propalinal grinding, but it certainly cannot be assumed that such a multiplicity was inherited from a common ancestral "hystricomorph" stock. Furthermore, Landry has provided no evidence in support of his conclusion regarding the primitive nature of a multiplicity of cusps, except to state that "If a structure occurs in a group in many different lines, we assume that it was derived from the basal members of that group unless there is other evidence that it arose through parallelism in the different lines. Almost exactly the same pattern of change with wear as that of hystricids is found in the New World genera *Cuniculus* and *Dasyprocta* . . ." (*op. cit.*, p. 85). A little later, however, he states that "The same general folded type of tooth appears in many lines of rodents not particularly related to each other: beavers, theridomyids, eomyids, rhizomyids, cylindrodonts, as well as porcupines, and unless we assume, as do Stehlin and Schaub (1951) and Schaub (1953), that all these diverse rodents came from a common source, we must believe that the infolded crown arose through convergence in the different lines" (*op. cit.*, p. 87). Nowhere does Landry offer any explanation as to why the presence of cuspules in several forms is a more significant indication of relationship than is the presence of a folded crown, and the only conclusion we can reach, from a careful study of his paper, is that his opinion that the multicusped crowns are primitive derives from his conviction that all hystricomorphous rodents are specially related and that the Hystricidae are among the more primitive members of the group. Whether or not these last two statements are correct (and we doubt both of them), all evidence of mammalian dental evolution is opposed to the primitiveness of multicuspidation. When he states that "the intermediate stage between such a tritubercular tooth [as that of late Paleocene species of *Paramys*] and the teeth of hystricomorphs should show a multiplication of cusps tending toward the condition seen in the unworn teeth of *Atherurus*" (*op. cit.*, p. 90), he is indicating a lack of familiarity with the known facts of mammalian dental evolution.

The exceptions to the general rule that all Deseadan rodent molars are four crested require discussion. We believe that in *Protosteiromys* the forward shift of the metaloph and the derivation of as large a neoloph as is present might require a considerable lapse of time. The Erethizontidae may have been the first group to diverge from the ancestral stock, the split perhaps going back to the late Eocene. The differences in the skull and skeleton between the Santa Cruz erethizontids and remaining contemporary caviomorphs support this point of view, as does the fact that the Recent Erethizontidae are myologically rather distinct from the remaining caviomorphs. Moody and Doninger (1956, pp. 52-53) report that the Erethizontidae appear to be as distinct serologically from the other caviomorphs they tested (*Cavia* and *Dasyprocta*) as either is from the Hystricomorpha (*sensu stricto*), and they suggest the possibility that the erethizontids had been independent since they split off from the Paramyidae, and that, therefore, a separate suborder is needed for this family. Vanzolini and Guimarães (1955a, p. 30; 1955b, p. 346) point out that the Erethizontidae are parasitized by an isolated stock of trichodectid Mallophaga, suggesting that they are very distantly related to other caviomorphs. Although there can be little question that the erethizontids were separated from the other members of the Caviomorpha at an early date, we feel that serologic and parasitologic evidence is difficult to evaluate, and that, at least for the time being, it is advisable to consider that the erethizontids are merely an early offshoot of the central caviomorph stock.[31]

The structure of the upper molars of *Cephalomys* has been discussed above (p. 333). Derivation from the four-crested pattern seems certain and the loss of the metaloph and the shift of the neoloph anterointernally probably required no longer a time than origin of the neoloph in the erethizontids.

The presence of only three crests in the lower molars of some early echimyids and the incomplete development of the fourth crest (metalophid) in others is at first glance perplexing. However, this is certainly a case of secondary suppression of the metalophid. The structural sequence *Platypittamys—Deseadomys arambourgi — D. loomisi* shows how such reduction took place. The metalophid is an unstable crest in a variety of later caviomorphs.

The premolars of the Deseadan genera are basically similar, uppers to uppers, lowers to lowers, and are notably less complicated (and therefore, we believe more primitive) than the molars (this would certainly be the case also in those forms, *Protosteiromys*, *Chubutomys*, and *Deseadomys loomisi*, whose premolars are not yet known), something that is by no means true of all later forms. P^4 is throughout much shorter than the molars and three-crested, the metaloph being absent or minute. Two types of P^4

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[31] Fields (1957, p. 351) has very tentatively suggested the possibility of a relationship between the Erethizontidae and the Dinomyidae, pointing out certain resemblances between the two in the auditory region and in the fusion of cervical vertebrae. We are not certain as to the significance of the auditory region (Fields' figures show differences as well as resemblances), and such characters as molar structure and the absence of any trace of a lateral process in dinomyids argue against close relationship. Ray (1958, p. 8), in a study of cervical fusion in dinomyids and erethizontids, questions this feature as an indication of close relationships between the two families.

occur. In the first, represented by *Deseadomys* (and probably *Protosteiromys*) the protoloph and metaloph were joined by a mure, as in the molars, as well as being joined lingually through what seems to be a hypocone. In the second, represented by *Scotamys* and *Cephalomys,* there is no mure and the combined anteroloph and protocone sweep around the inner face of the tooth to join the posteroloph posterointernally. *Platypittamys* combines the features of both and shows how each could have arisen from a common ancestral form. The difference is not fundamental, in fact the anteroloph becomes separated in later dasyproctids. It seems likely that a division into comparable structural types occurred in lower premolars, but the details are not clear.

Landry (1957a, p. 87-88) argues that a study of the pattern of the deciduous teeth can give us valuable clues to the "conditions which were present in the ancestral teeth . . ., since the milk dentition, being more or less transient, might not be so much affected by the selection pressures which were operating to change the permanent dentition. However, we cannot accept all the conditions found in the milk teeth as primitive, because there is always the possibility that the milk dentition has been subject to selective pressures of its own and has evolved special characters in response to them. . . ." We are in complete agreement with this last statement, and feel that a study of the milk teeth, while very important in understanding the evolution of the milk teeth, has little or no bearing on the ancestral condition in the permanent teeth. We therefore must conclude that the presence of cuspules on "the unworn milk premolar of *Coendu* . . . strongly reminiscent of an unworn cheek tooth of *Dasyprocta* or *Atherurus*" is merely an interesting observation and cannot be considered evidence "that the surface of the primitive hystricomorph cheek tooth was made up of a series of small cuspules. . . ." (*op. cit.*, p. 88).

Having briefly recapitulated the evidence demonstrating the essential morphologic unity of the dentitions of the Deseadan rodents, it is now necessary to do the same for the degrees of their divergence. It is at once obvious that a very distinctive group is that formed by *Scotamys*, *Cephalomys*, and *Litodontomys,* representatives of the Chinchillidae and Dasyproctidae.

The first two genera share nearly every dental feature, have a distinctive P^4 and are either hypsodont or hypselodont. They thus stand sharply apart from the rest, which is of course the warrant for brigading them in the same superfamily, a step taken in a preceding section. *Chubutomys,* representing the Eocardiinae, is close morphologically to the lower-crowned luantine, *Asteromys.* The other brachyodont to mesodont genera fall into two groups. The erethizontids, even this early, stand well apart (Wood, 1949, p. 5), certainly as much as do the contemporary chinchilloids; they are essentially modern as regards their molars. The cavioids do not have a P^4 of the chinchilloid type, and *Asteromys* and *Chubutomys* reveal that the basic four-crested pattern was present in the lower molars, at least, of the early representatives. We are strongly inclined to believe that the cavioids arose from the octodontid stock subsequent to the divergence of the chinchilloids, and that both of these separated somewhat later than did the erethizontoids. Our conception of the relationships and phylogeny is graphically shown in Figure 34.

Differentiation of the echimyids, the octodontids and the eocardiid *Asteromys* would appear to be relatively slight and could have been accomplished in a very small fraction of a geologic epoch. The time required for the evolution of the hypselodont to sub-hypsodont Deseadan chinchilloids and of the hypsodont eocardiid *Chubutomys* is another matter. Ordinarily, it would be assumed that hypselodonty and hypsodonty such as that exhibited by *Scotamys* and *Chubutomys*, respectively, must have required considerable time for its evolution. Such an assumption would not be a safe one in the present instance, however. When the rodents reached South America, they found a vast area over which to spread and an almost virgin adaptive zone with niche after niche open to exploitation. The situation was ideally suited to radiation, and the population structures were in all probability such as to permit the most rapid evolutionary rates. Under such conditions, the acquisition of hypsodonty presumably does not take long, and it is entirely possible that the initiation of the caviomorph diversification may have taken place as recently as late Eocene time. That the rodents were still a rapidly evolving group in the Deseadan is revealed

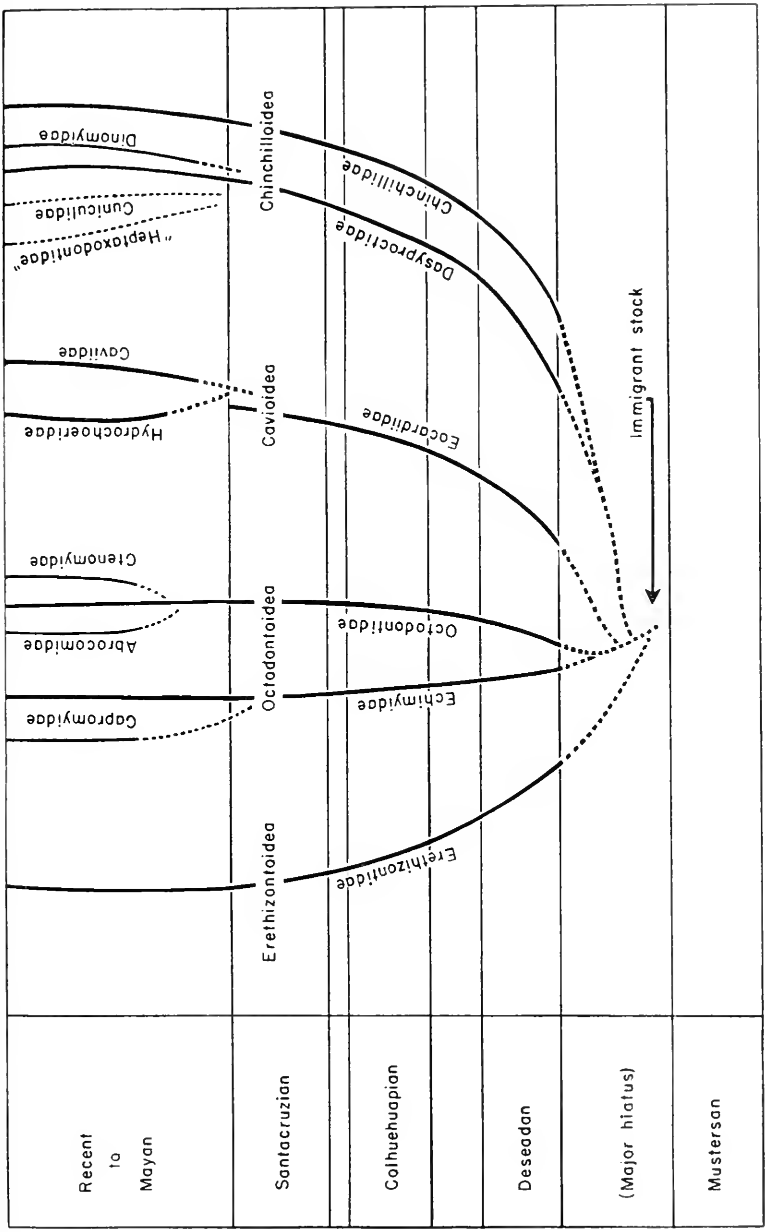

Fig. 34. Diagram illustrating the geologic ranges of the families of caviomorph rodents and our concept of their relationships.

by the considerable degree of advance that took place in all lines between Deseadan and Colhuehuapian time. The parallel case of late Pliocene and Pleistocene evolution of hypsodonty in the microtines can be cited in this connection. This point of view is a considerable contrast to that of Landry, who considers that the absence of any paramyids, as well as theridomyids and hystricids, in South America "suggests the possibility that no known rodent is ancestral to the hystricomorphs and that their intercontinental dispersal may have taken place considerably before the time usually postulated, perhaps as far back as the Early Paleocene" (1957a, pp. 81-82). This is, naturally, a possibility, but the hypothesis involves the assumption that pre-Deseadan rates of evolution in caviomorphs were extremely slow, and for this we see no evidence. Furthermore, as pointed out in more detail below, it also requires us to believe that in the Paleocene a relatively advanced group of rodents was in existence in the Northern Hemisphere, and that this group then disappeared from that hemisphere to be replaced (or displaced) in the early Eocene by the less advanced paramyids. This we regard as unlikely in the extreme.

The Origin of the Deseadan Rodents

The relative uniformity of the Deseadan caviomorphs leaves little doubt that the entire South American stock represents a development from a single invasion. A number of problems still remain to be considered, however. These are: (1) from what region did the ancestors of the caviomorphs come; (2) at what time did the invasion occur; and (3) what group of rodents was ancestral to the caviomorphs. These questions will be discussed in order.

The similarities between South American and African rodents tempted many authors to derive the former from the latter by a direct transatlantic invasion via a land bridge. Current opinion seems practically unanimous that there could not have been direct connection between Africa and South America, either by bridge or by former continental juxtaposition, at any time when rodents could have utilized it, and that therefore the immediate source of the South American rodents must have been North

America (see for example Lavocat, 1951a, 1951b, p. 72; Schaub, 1953a, p. 391; Simpson, 1950, p. 375; Wood, 1950).[32] Landry (1957a, p. 91) suggests that the ancestral caviomorphs may have reached South America by way of the Greater Antilles, and thus ultimately be of North American derivation. On present evidence, this route is nearly (though not quite) as logical a postulate as the alternative route through the then Central American archipelago. Landry's second hypothesis, that "hystricomorph" rodents reached the Antilles in the Paleocene is not a necessary part of his migration route hypothesis, and is discussed in more detail below. Viret (1955, pp. 1563-1564) is more cautious on the whole problem, and concludes: "Le problème du peuplement de l'Amérique du Sud par les Rongeurs reste une énigme qui ne peut être résolue dans l'état actuel de nos connaissances."

Simpson (1950, p. 375) and Wood (1950) have discussed the question of arrival of rodents over a land bridge or by rafting. Both reached the conclusion that the rodents must have entered South America by the latter method, because both interpreted the evidence as showing that the invasion took place in the latter part of the Eocene, a time at which no other mammals entered South America from North America, with the possible exception of the primates. We fully agree with this conclusion. Recently, however, Schaub has suggested that the source of the Caviomorpha is to be found in rodents with a *Theridomys*-like tooth pattern that reached South America in the Eocene, Paleocene, or even earlier (1953a, p. 393). Lavocat (1956, p. 55) goes part way with Schaub, suggesting that the similarities between the Caviomorpha and the Hystricomorpha (or Nototrogomorpha and Palaeotrogomorpha) could be explained on the assumption that the two groups were remnants of a homogeneous Paleocene

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[32] That the ancestral South American rodents might have been transported by natural rafts directly from Africa to South America, or, contrariwise, the ancestral hystricomorphs (*sensu stricto*) from South America to Africa, in the latter part of the Eocene are views seldom advanced. We do not take either possibility very seriously, particularly not the former. Hystricomorphs (*sensu stricto*) do not appear to be raft-prone: they have failed to reach such islands as Madagascar and the Philippines proper, not to mention New Guinea and the continent of Australia. We wish to point out, however, that, in the light of current knowledge of the paleontology and zoogeography of the Rodentia, raftings of this sort are the only alternatives left to those who insist on direct caviomorph-hystricomorph relationships. Otherwise, as we indicate below, there seems to be no escape from the conclusion that the ancestors of the South American rodents lived in North America during the latter part of the Eocene, and that, in this continent at that time, they could only have been protrogomorphs and, in all probability, paramyids.

rodent population of the Northern Hemisphere that had penetrated South America and Africa. On the other hand, he had previously concluded (1951a, p. 38) that any resemblances between New and Old World forms must be pure parellelism. Landry (1957a, pp. 90-91) strongly supports the caviomorph-hystricomorph distribution as indicative of a Paleocene radiation. In view of the weight of this continued support for close relationships between South American and Old World forms, the problem of the time of origin of the caviomorphs must be reconsidered.

There was certainly an early immigration from North America to South America, in late Cretaceous and/or early Paleocene time, which provided the ancestors of most of the indigenous South American Tertiary mammalian fauna (Simpson, 1950, pp. 368-373). These immigrants may well have reached the continent by rafting (Darlington, 1957, p. 364; Patterson 1958b, pp. 11-13). This, apparently, would be the source envisioned by Schaub and Landry, although, as already mentioned, Landry (1957a, p. 91) hedges a bit by suggesting that perhaps the "hystricomorphs" reached the Greater Antilles in the Paleocene, but did not reach South America until early Oligocene. Lavocat specifically suggests (1956, p. 55) that, after making such a Paleocene invasion, the rodents could well have lived in parts of South America whose Tertiary history is still unknown. Although this is undoubtedly a hypothetical possibility, it does not seem at all probable to us, for several reasons. There are actually three problems to be discussed here: whether there could have been any rodent invasion much before the end of the Eocene; whether there could have been an invasion by any Paleocene rodents (Lavocat, 1956, p. 55); or whether there could have been an invasion by Paleocene theridomyids. Establishment of the improbability of any one of these would establish the improbability of any of the others.

Since the Deseadan rodents are, as pointed out above, a closely related stock, and since they were at this time near the beginning of a rapid differentiation which continued through Colhuehuapian into Santacruzian time, it seems to us almost certain that there was a single common ancestor of the Deseadan rodents which existed not too long before Deseadan time. All previous history of South American rodents must have involved a relatively small amount of evolutionary progress, with little or no adaptive radiation.

No trace of a rodent has been found in the Paleocene Río Chico of Patagonia, in the Paleocene Itaborai fauna of southern Brazil, or in the Eocene Casamayoran and Mustersan of Patagonia. It could be supposed that these animals might have been living in northern South America during the earlier part of the Tertiary, but we regard this as extremely unlikely. The Pleistocene faunal history of South America and the Recent faunal history of Australia reveal what happens when forms fitted for life in a given adaptive zone are suddenly confronted by invaders higher in the scale of evolutionary progress that happen to be fitted for the same zone; the forms lower in the scale do not linger long and the invaders spread with the greatest rapidity. Had any rodents reached South America before late Eocene time, we believe it to be essentially axiomatic that their descendants would have swept all before them within their adaptive zone, which was then only marginally occupied (by polydolopids, groeberids, typotheres and hegetotheres), and would surely have put in an appearance in Patagonia. Moreover, we see only one probable explanation, other than their recent arrival in South America, for the sudden burst of the rodents just before Deseadan time. This would be the rapid development of new structures that enabled them to compete much more successfully with their non-rodent rivals. The only such structures of which we are aware would be the multilophate cheek teeth and the enlargement of the masseter muscle and its expansion through the infraorbital foramen. While we believe that such changes did take place in the latter part of the Eocene, their development at this time in the ancestors of the caviomorphs, had these been in the continent at a much earlier date, would establish that these ancestors were non-hystricomorphous in teeth and masseter; would eliminate the possibility that any Old World hystricomorph-like rodent had any special relationship with them; and, we believe, would lead by a process of elimination to our interpretation of the late Eocene caviomorph ancestor as being a paramyid or sciuravid. It appears to us, however, virtually certain that rodents did not reach South America until after the close of the Mustersan, which, according to the best recent estimate (Simpson, 1940), is approximately of mid-Eocene age. They therefore arrived sometime during a great hiatus in South American faunal history — the gap in our knowledge that extends from Mustersan to Deseadan, from approximately mid-Eocene to early Oligocene. The precise time of their arrival within this interval cannot now be determined.

Rejection of the possibility of a Paleocene rodent invasion of South America requires consideration of the time of origin and of early geographic radiation of the rodents. This is something about which virtually nothing is known, except that rodents do not become numerous until the early Eocene and that only a single earlier species, *Paramys atavus,* is known from the late Paleocene (Jepsen, 1937). How much earlier the rodents were in existence we do not know. Wilson (1951) has argued that the order, as such, probably arose about late Paleocene time, agreeing with Jepsen (1949) that the abrupt replacement of multituberculates by rodents at the beginning of the Eocene argues against the latter having been in existence for more than a short time previously. We believe that if rodents had entered South America in the Paleocene they would surely have been widespread in North America at that time and hence would be represented in our collections from that continent, as well as from the Eocene of South America. This, of course, is arguing from negative evidence, and anyone who wishes to hold contrary views is free to do so. However, it is surely unwarranted to conclude that such a hypothetical group of rodents were so much more highly specialized than any of the known early Eocene rodents that they must have been hystricomorphous, and to assume, further, that they acquired a world-wide (or nearly world-wide) distribution is piling hypothesis upon hypothesis, and is logically indefensible. We do not wish to argue the question as to the date of the separation of the rodents from the insectivores, or as to the rates of pre-Eocene rodent evolution, because we know of no new evidence bearing on these subjects.

The possibility of a theridomyid having reached South America in the Paleocene, as envisioned by Schaub (1953a, p. 393), has additional arguments against it. As Viret has observed (1955, p. 1564, footnote 1), the *Theridomys*-pattern was not present, even in Europe, in the Paleocene. As pointed out above, we believe that we can trace the development of five-crested caviomorphs from four-crested ones, and not vice versa. If we are correct in this interpretation, the theridomyids again could not have been ancestral to the Caviomorpha, and we should have to rely for ancestors on four-crested or incipiently four-crested North American forms, of which a number are known. Our arguments on this point are involved in the whole question of the basic pattern of rodent teeth and the primitive stock of the rodents, which are discussed below. But we feel very strongly that, whatever the Paleocene rodents were like, they had not yet attained the complexity of structure that would permit them to be called theridomyids, or indeed to be referred to any currently recognized groups except the Paramyidae.

We therefore feel that the most probable explanation of the known history of South American rodents is that they arrived, by island-hopping, from North America, sometime in the latter part of the Eocene.

ANCESTRY OF THE CAVIOMORPHA

Having attempted to answer the questions as to the geographic source of the Caviomorpha and the time of their arrival in South America, we come to the question of the group of rodents that gave rise to them.

Stehlin and Schaub (1951) have presented a major and exceedingly valuable study of the development of the cheek teeth in rodents, which we will discuss more fully below. But, on the basis of this study, Schaub has strongly supported the Theridomyidae as being the ancestral stock of all multi-crested rodents. We have tried to show above that the ancestral caviomorphs were not pentalophate, as is *Theridomys*, but tetralophate, and that the development of a fifth crest, when it occurs, is a strictly local phenomenon in South America. It would be advisable, however, to review in this connection the possible origins of each of the known Deseadan rodents.

As indicated above, *Platypittamys* must be very close to the basic type from which all the rest of the caviomorphs were derived. It clearly could not be descended from the Theridomyidae, but shows numerous structural similarities to such North American rodents as an undescribed lowest Eocene paramyid and the Duchesnean *Rapamys*, as far as the latter is known. The pattern of the teeth (particularly of P^4) of *Descadomys* is very different from that of the Theridomyidae. Without exerting what we consider to be an excessive strain on the imagination, the only known source from which it could ultimately have been derived would be a paramyid or sciuravid. *Descadomys* shows no close relationships to any Old World forms, and particularly not to the theridomyids or to *Phiomys*. It would be possible to imagine its descent from such forms, by the loss or fusion of crests, but there is no evidence for this and it seems clear to us that derivation was from the octodontids as represented by *Platypittamys*. It is therefore much simpler and more reasonable to assume the ultimate derivation of *Descadomys* from North American paramyid ancestors.

Landry (1957a, p. 94) states, "Wood's proof that South American hystricomorphs could not be related to Old World hystricomorphs consists entirely of reasons why the teeth of *Platypittamys* could not be derived from those of the theridomyids." There really *was* a little more to the story, but leaving this aspect of the matter aside we must point out that, in 1949, derivation of Hystricomorpha (*sensu lato*) from the theridomyids was a hypothesis very much to the fore and Wood had no choice but to discuss it. The idea is still current — in greatly expanded form (cf. Stehlin and Schaub, 1951) — and we still think it necessary to discuss it. As we have shown above, the third crest in caviomorph upper molars is a metaloph, and, as may be seen from Stehlin and Schaub's figures (16, 21, 26, 29) showing portions of the sequence (which we believe to be phylogenetic or nearly so) running from *Paramys* to *Decticadapis* to *Adelomys* to *Theridomys*, the third crest in theridomyids is a mesoloph. The considerable superficial resemblance notwithstanding, the two molar types are quite different, despite Landry's remark (*op. cit.*, p. 95) that "A comparison . . . shows that exactly the same elements are present in both. . . . The only difference is in the assignment of names to them." As regards the Hystricomorpha (*sensu stricto*), we suspect the third crest of the upper molars to be a mesoloph. Hystricomorph history is very poorly known, however, and since this homology has not yet been proven phylogenetically, the possibility still exists that the third and fourth crests of hystricomorph molars and of such caviomorph molars as possess five crests may be comparable. Even if this should prove to be the case, it would not affect the evidence indicating that the fifth crest of caviomorphs came into existence after arrival of the group in South America, and thus quite independent of its origin in the Hystricomorpha. We may state our full agreement with Landry — and with Lavocat before him — as concerns his observation that the sciurognath type of jaw characteristic of the Theridomyidae tends to bar the family from the hystricomorph — and caviomorph — ancestry.

Cephalomys could likewise have been ultimately derived from a North American Eocene paramyid, perhaps something like *Rapamys*, through intermediate stages similar to *Platypittamys*. In view of the pattern of P^4, it would seem almost certain that it was not descended from forms with quadrilophate upper premolars. This would eliminate most forms that have been suggested as being the ancestral stock, and particularly the theridomyids (Fig. 35A), which have a completely molariform upper premolar. The theridomyids also show no particular similarity in the structure of P_4. The presence of a mesoloph in the theridomyid upper teeth is a notable difference from the pattern of *Cephalomys*. The patterns of the lower molars are similar in a very general way in the two groups, but by no means sufficiently so to indicate special relationships. The pattern of dm_4 appears rather similar at first glance, but it is not identical. The posterolophid and hypolophid of the two seem closely comparable. The mesolophid in *Theridomys* (Fig. 35B) lies well behind the anterior part of the tooth, and the metalophid is connected with both ends of the anterolophid whereas in *Cephalomys* (Figs.

Fig. 35. Cheek teeth of *Theridomys* x 5. *Theridomys rotundidens* Schlosser, LP^4-M^3, Munich no. 1879–xv–182 a-d; *B*, *Theridomys speciosus* Schlosser, Rdm_4-M_1, Munich no. 1879–xv–183 a-b.

20A, B) there appears to be no mesolophid, and the three anterior cusps, presumably derived from the anterolophid, connect with the middle of the metalophid. Although these are rather notable differences, how much weight should be attached to them is uncertain, due to our general lack of knowledge of the evolution of rodent deciduous molars. *Scotamys*, which, as has already been shown, is fundamentally similar to *Cephalomys*, is also derivable from the octodontids. The same applies to the two cavioids, *Asteromys* and *Chubutomys*.

Protosteiromys, as already noted, is the only Deseadan form that shows any appreciable similarity to the theridomyids, and much of the resemblance is due to the presence of a neoloph, giving an incipient five-crested pattern. Even if the similarities in tooth pattern had originated in the same way, which, with Friant (1936b), we do not believe, it would still be simpler to postulate an origin of *Protosteiromys* from the Octodontidae, rather than to assume that one Deseadan rodent originated from an Old World group while the others had a different ancestry. Since the last crests to develop, the neoloph (fourth crest) in *Protosteiromys* and the mesoloph (third crest) in the theridomyids, are not homologous, we believe the octodontid relationship to be the only possible one. These arguments, of course, would have no weight with anyone who adopts Landry's point of view that "the pattern of the occlusal surface of almost any tooth *could* be derived from any other" (1957a, p. 89), but this does not appear to us to detract from the validity of our argument. Since the Old World theridomyids must, it would seem, be ruled out of the caviomorph ancestry, the only possible source of this ancestry is some North American rodent, unless, with Landry, one prefers hypothetical ancestors with hypothetical molar structure, or fancies transatlantic rafting. Such an ancestral form would have reached South America from North America by island-hopping. Since all the South American forms could hardly have been derived from anything else, and since it seems virtually certain that the Deseadan forms were derived from a single source, this appears to be the only logical interpretation of the available data. The similarities between the Hystricomorpha and the Caviomorpha must then be parallelisms. We feel very strongly that parallelism is a dominant character of rodent evolution, and particularly of rodent dental evolution (Wood, 1937b, 1947, 1950), and that very similar structures may appear over and over again within the order. Lavocat (1956) argues this same point of view. For all these reasons, we do not feel that any known theridomyid, or any ancestral rodent which was sufficiently advanced so it would be called a theridomyid, could be ancestral to the Caviomorpha, and the possibility of such relations between theridomyids and hystricomorphs (*sensu stricto*) also seems to be ruled out.

The resemblances of the thryonomyids and petromurids to certain caviomorphs have been cited as indicative of relationships. As pointed out by Wood (1950), if there were a close relationship, which is most unlikely, it would indicate that the African forms more probably had a South American ancestry, rather than vice versa. Landry (1957b) has recently demonstrated that the petromurids do not resemble the octodontids to any significant extent.

There are only two known groups of North American rodents that could be ancestral to the Caviomorpha, on the basis of their tooth structure.[33] These are the Sciuravidae and the Paramyidae. The Sciuravidae show a basic four-crested pattern that could have been ancestral to that of the Caviomorpha. There are a number of variant types within the sciuravids, which have not been thoroughly studied. But none of the known material shows any suggestion of an enlargement of the infraorbital foramen, and none that we have seen suggests the inflected angle of the hystricognath type found in caviomorphs. For the present, at least, we regard the sciuravids as a possible source for caviomorphs, but not a probable one.

The review of the Paramyidae, in progress by Wood, has revealed that a four-crested pattern develops within this family from a basic tribosphenic ancestral type. Structures of this sort

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[33] Landry (1957a, pp. 88-89) objects to the use of dental anatomy in studying rodent evolution, pointing out that different students have interpreted tooth structures and tooth relationships differently, which is, of course, equally true for characteristics of the other parts of the animals. He objects to "the notion that by demonstrating that a certain tooth *could* be derived from another, we demonstrate that it *was* so derived. . . . Proof that one tooth pattern was derived from another requires corroborative evidence from the study of other structures, or a series of intermediate stages. Particularly is this true in the study of rodents, where the same tooth pattern has evolved again and again in different lines" (*op. cit.*, p. 89). Having made this statement, he then proceeds to ignore it over and over again in his discussion of hypothetical evolutionary trends in other structures where parallelism is just as complex as it is in tooth patterns.

have arisen several times within the family in different lines, in each of which the temporal sequence is sufficiently complete so that it is obvious that this is what was taking place. In one line, leading through *Reithroparamys* to the Duchesnean *Rapamys*, acquisition of this dental pattern is associated with an enlargement of the infraorbital foramen. Unfortunately, the known material of *Rapamys* is very fragmentary, and it is impossible to be sure of the exact size of the foramen. Nothing is known of the structure of the angle in the genus, although, as pointed out by Landry (1957a, p. 82), the angle of *Reithroparamys* suggests an incipient stage toward a hystricognath jaw. Therefore, all that can be stated with certainty is that *Rapamys* seems to be closer to the caviomorph type than does any other currently known North American rodent. An undescribed earliest Eocene paramyid in the Amherst College collections, represented by a partial skull, a jaw, and fragments of the skeleton, has some similarities to the Deseadan rodents, particularly in the pattern of P^4. The infraorbital foramen is that of a typical paramyid, but the angle appears to be arising lateral to the incisive alveolus, making this a hystricognath paramyid. It is possible that this form may bear some relationship to the caviomorph ancestry.

Geographically, then, we believe that the Caviomorpha were derived ultimately, and perhaps directly, from North American rodents, which, taxonomically, would be referred to the Paramyidae. The sequence is, of course, far from complete. The South American rodents were not descended from immigrants from Wyoming, but rather from rodents that lived in some part of Middle America or southeastern United States, regions from which the Eocene mammalian faunas are essentially unknown. When and if these are discovered, we feel that they will include paramyids, probably related to *Rapamys*, which will show a number of pre-caviomorph specializations. The discovery of sciuravids at Guanajuato, Mexico (Fries, Hibbard and Dunkle, 1955), suggests that there are deposits of the critical age in this area that may eventually produce additional rodents that will help to solve this important problem.

PROBLEMS OF RODENT PHYLOGENY

The discussion above on the origin of the caviomorphs appears logical to us on the basis of our ideas as to rodent evolution. Not everyone is in agreement with these, and we must therefore explain why our opinions differ from those of some other students.

Stehlin and Schaub (1951) present a detailed analysis of rodent tooth patterns and their interrelationships. This work was unfinished by Stehlin at the time of his death in 1941, and was completed, with signed sections and unsigned insertions within brackets, by Schaub. Both authors have an unsurpassed background of study on fossil rodents, so that it is with some hesitation that we express our serious objection to a number of points they raise.

One of the main points of this major contribution, and the one of chief concern for the present study, is Stehlin's concept of a "*Theridomys-Trechomysplan*" in molar structure. This "plan" is believed by him to have been structurally derivable from the "trigonodonten Grundplan," represented by such forms as *Marmota*, and to have been structurally capable of giving rise to a wide variety of derivatives. The pattern found in the early Eocene rodents referred by us to the Paramyidae is not considered by him to represent the primitive rodent tooth pattern, in spite of its being the pattern of the earliest known members of the order, and in spite of the fact that it shows considerable similarity to the *Marmota* pattern. Nor is the paramyid structure considered to be intermediate between the "trigonodonten Grundplan" and the "*Theridomys-Trechomysplan*," which leaves practically no known forms occupying such a position. Evidently considered as close structurally (Verwandten) to *Theridomys* are various African and European forms (*Phiomys*, *Sciuromys*, etc.) and *Eosteiromys* (including our *Protosteiromys*) and "*Parasteiromys*." The morphological derivates of the "*Theridomys-Trechomysplan*" include a wide variety of groups: Hystricidae, Thryonomyidae and Bathyergidae, all the Caviomorpha of this paper (derivable morphologically, it would seem, via the Erethizontidae), Castoridae and Eutypomyidae, Rhizomyidae and Spalacidae — to give but a partial list.

It must be emphasized that, as Stehlin states (*op. cit.*, p. 351), this is a morphological study pursued essentially without reference to taxonomy and with but little reference to relative ages of the forms concerned. The work is in fact an undertaking carried out partially, but only partially, along the lines of what Davis (1949, p. 65) has dubbed the neoclassical school of comparative anatomy, although without reference in the bibliography to works of any of the chief exponents of this school, e.g., Naef, Kälin. It is no deprecation of the methodology characteristic of this approach to state that, in our opinion, its application, as partially carried out by Stehlin, to a single system of an order notorious for the parallelism that has occurred within it is not at this time very helpful. The "*Theridomys-Trechomysplan*" is a morphological abstraction that has, we believe, a limited phylogenetic — and also morphologic — application, and may well contribute to future misunderstanding. As Stehlin himself emphasizes, only an acquaintance with more than one structural system of a group through time can place our knowledge of taxonomy and phylogeny on a sound basis. For this very reason we are inclined to regard the inclusion of all forms that appear to show four or five transverse crests on their cheek teeth, whatever other variations may occur in the rest of their anatomy, among the structural derivatives of this "plan" as being a step away from a classification based on phylogeny and back toward a convenient pigeon-holing with no basis in the evolution of the rodents.

A rather large part of our objection to Stehlin's procedure is nomenclatural. To label this morphologic abstraction the "*Theridomys-Trechomysplan*" is, we believe, dangerous. To do so is to apply terms relevant in one frame of reference, the phylogenetic-taxonomic, to another that is admittedly non-taxonomic. Although it may not have been Stehlin's intention, no one can read this paper without feeling that there are at least implications that the arrangement in accordance with this "plan" is a phylogenetic one. This point of view has since been expressly adopted by Schaub (1953a, p. 394 *et seq.*), and the usage has spread to at least one standard reference work (Grassé and Dekeyser, 1955).

In neo-classical comparative anatomy, if it is to serve its purpose, interpretations (in this case anything that smacks of formal taxonomy) must be rigidly excluded from the methodological process and introduced only in the terminal interpretive phase. That the "*Theridomys-Trechomysplan*" was derived from the "trigonodonten Grundplan" is a reasonable assumption from the viewpoint either of neoclassical comparative anatomy or of interpretive phylogeny, but to assume that it is itself a single entity from either viewpoint is hardly warranted. Nor does it appear to us to be reasonable to assume that all the lower Eocene rodents are highly specialized and that none of the primitive ones appear until considerably later. Neither does it seem reasonable to assume that a family, whose known distribution is restricted to Europe, gave rise to a wide variety of forms living in all the rest of the world. At the very least, this is contrary to what has been observed in other orders of mammals. Without entering into a detailed neoclassical comparative anatomical analysis of rodent molars with "Aussen- und Innenantiklinalen und- synklinalen," it would seem to us that any such analysis should surely postulate, or at least entertain the possibility of, an ancestral stage ("plan") without a fifth crest; and that, in the interpretive phase of the work, the possibility that various forms with this crest may have passed independently through such a stage should be carefully considered.

If the "trigonodonten Grundplan," with anterior and posterior cingula, protoloph and metaloph, but no mesostyle or mesoloph (Stehlin and Schaub, 1951, Fig. 1) gave rise to the "*Theridomys-Trechomysplan*," it would seem almost (though perhaps not quite) necessary to assume that a four-crested pattern preceded the five-crested one. At the very least, a primitive four-crested stage should be considered as an alternative possibility to the postulate that the four-crested pattern is a specialization formed by reduction from a five-crested one.

This is one point where we feel that the "*Theridomys-Trechomysplan*" has been transferred from a morphologic to a phylogenetic concept by Stehlin and Schaub. For example, dealing with *Deseadomys* ("*Asteromys*"), they state: "Dass schon in der Deseadoformation Sudamerikas stark spezialisierte Formen vorliegen, beweist *Asteromys prospicuus*. . . . Die brachyodon-ten Zähne besitzen nur noch drei Aussensynklinalen; es fehlt anscheinend, wie bei *Acaremys*, die vierte" (*op. cit.*, p. 60).

The transformation of one type of rodent tooth into another has clearly occurred independently on numerous occasions. For example, the change from brachyodont to mesodont or hypsodont teeth can be followed independently in the Geomyidae, Heteromyidae, Eomyidae, Theridomyidae, Sciuravidae, and Cricetidae, to name but a few cases, and the same was true, we believe, for the Caviomorpha. In each case, the original, low-crowned members of the group have rounded, plump cusps, or distinct traces of cusps, with a minimum of connecting crests. In each case, subsequent evolution accentuates the crests, giving rise to rather similarly appearing multi-crested forms. As far as we are able to interpret the evolutionary picture of the rodents, these animals represent a number of lines that evolved, independently, from ancestors that were primarily cuspate. On the basis of the time of occurrence of the earliest members of these groups, the ancestors must be sought not later than late Eocene for the geomyids, heteromyids, cricetids and caviomorphs; not later than middle Eocene for the eomyids and theridomyids; and not later than earliest Eocene for sciuravids. This, again, suggests to us that these various groups have developed independently of each other.

We believe that the early Eocene paramyids are the most primitive known rodents. The data supporting this point of view will be included in the review of the Paramyidae in preparation by Wood. Unfortunately, most published illustrations of the teeth of primitive paramyids are inadequate, but a few good ones are available (Stehlin and Schaub, 1951, Figs. 16, 17, 156, 157, 305, 306, 465 and 466). Within the Paramyidae, a series of lines can be traced, leading to greater specialization and gradual development of lophate teeth. Some of these lines we believe can be considered to lead to other, and more advanced, families (*Paramys* — *Decticadapis* — *Adelomys* — *Theridomys; Paramys* — *Sciuravus; Paramys* — later paramyids — sciurids; etc.), whereas others were doubtless sterile offshoots. But we believe that this early and middle Eocene radiation of the Paramyidae provided the source for the subsequent evolution of the rodents.

It is in the lack of allowance for the known parallelism that is found among the rodents, it seems to us, that Stehlin's analysis fails of being a completely neo-classical one, just as it is admittedly not a phylogenetic one. And it is here that the employment of the term "*Theridomys-Trechomysplan,*" rather than a descriptive, non-committal name, introduces an unnecessarily complicating nomenclatural factor. This term is associated with a well-known phylogenetic hypothesis (derivation of Hystricomorpha *sensu lato* from the Theridomyidae) that should never have been introduced into the morphological analysis. This phylogenetic hypothesis would be applicable at the very most only in part (Theridomyidae-Hystricomorpha *sensu stricto*), and even so limited an application as this now seems unlikely, since Lavocat has clearly indicated that this cannot be a true phylogenetic series for some of the Old World Hystricomorpha, and he has recently (1956, p. 54) suggested that the Theridomyidae are related to no known rodents except the Pseudosciuridae. We further believe that the analysis of the differences between the theridomyid and caviomorph cheek teeth given here destroys the validity of the "*Theridomys-Trechomysplan*" as a non-phylogenetic concept also, certainly so far as it applies to the caviomorphs.

The somewhat critical tone of part of the foregoing should not be interpreted as an expression of our opinion concerning Stehlin and Schaub's work as a whole. The volume is one of the most useful publications on rodents that has ever appeared, and will, we believe, rank with Tullberg as a classic that must always be consulted, particularly by anyone interested in rodent teeth. The clear and lucid descriptions, the magnificent figures and the stimulating taxonomic discussions by Schaub ensure for it a great and enduring value.

Part of our difference of opinion with Stehlin and Schaub over the primitive nature of the Paramyidae lies in the interpretation of the anterior end of the lower molars. This will be discussed at length by Wood in his forthcoming review of the Paramyidae, but we believe that the paraconid was lost before the first appearance of any rodents in the fossil record. There is, in the paramyids, a weak crest along the anterior face of the lower molars. This might be the last remnant of the paraconid-protoconid crest, or it might be a neomorph, but there certainly is no paraconid. When a cusp appears at the anterior end of lower molars later on in rodent history, we believe that it is clearly a neomorph, best called an anteroconid. This is the structure Schaub (1953b, pp. 8-9 and Figs. 11-12) calls a paraconid, and which he considers an important indication that Oligocene squirrels are the most primitive known rodents.

The recent discussion of ''hystricomorph'' relationships by Landry (1957a) falls into an entirely different category. This starts out as a comparative-anatomical study of rodents that have been classified as hystricomorphs at one time or another, and concludes, on the basis of a number of similarities of various kinds, that they are related. The resemblances exist, and in the absence of a fossil record would indeed justify retention of the Old and New World forms in one suborder. As matters stand, however, we are compelled to differ and to regard the resemblances as due to parallelism, not to special affinity in the sense of derivation from a common ancestral stock that was already ''hystricomorph.'' Furthermore, we have to take exception to some of Landry's reasoning.

We cannot accept his view that structures appearing late in evolutionary history, such as the multicusped pattern of the molar teeth in some groups, are primitive. When a specialized character, which he considers as basic for the ''Hystricomorpha,'' does not occur in some early members of the group, he considers that these members have secondarily reverted to the primitive rodent condition, a hypothesis requiring a degree of evolutionary reversal which appears improbable. For example, Landry considers the loss of the entepicondylar foramen to be a basic character for the ''Hystricomorpha,'' stating that ''. . . the fact that the entepicondylar foramen is almost never found in hystricomorphs indicates that it was lost early in the history of this group'' (Landry, 1957a, p. 20). He adds that the only form he knows that had such a foramen was the Pliocene *Lagostomopsis*, in which L. Kraglievich found it in 14 out of 16 specimens. This he interprets as meaning that the lost entepicondylar foramen was reacquired by *Lagostomopsis*, and subsequently lost once more by its descendants. In this connection, however, he overlooked Wood's record (1949, p. 29) of the presence of this foramen in *Platypittamys*, which we consider as evidence that the foramen was present in the basic caviomorph stock, and independently lost in a number of lines. It should be emphasized that this form is the only pre-Santacruzian caviomorph for which we have any knowledge of the postcranial skeleton. As another example, Landry considers that fusion of the upper ends of the tibia and fibula "may have been present in ancestral hystricomorphs" (p. 19), overlooking the fact that there is no evidence of such fusion in *Platypittamys,* nor in the Santacruzian *Neoreomys* and *Steiromys* (Scott, 1905, pp. 397, 415). Having decided that a proximal fusion of the tibia and fibula may have been present in the ancestral "hystricomorphs," and accepting that this may be a fossorial character, he suggests that the ancestral "hystricomorphs" may have been fossorial animals. He then states that the fossorial bathyergids possess some primitive rodent characters, such as a separate scaphoid and lunar, and that therefore they may be modified descendants of the ancestral "Hystricomorpha" (*op. cit.,* pp. 19-20). This we think is somewhat tenuous. His arguments in favor of the primitive nature of a multiplicity of cusps, of the value of the milk teeth in determining the primitive nature of the molar pattern, of a secondary decrease in hypsodonty in the teeth of the Bathyergidae, and his refusal to accept reasonably well documented evolutionary lines as being indicative of what really happened, seem to us to reflect a basic unfamiliarity with the fossil record and with the methods of study of fossils, without which no classification can hope to achieve a firm phylogenetic base.

Landry is unwilling to accept the results of detailed phylogenies of rodents based on tooth structure, stating ". . . it is nevertheless true that where one observer sees similarities in teeth, another sees differences. The matter is so subjective that I believe that classifications of rodents based on similarities of the occlusal surface of the teeth are useless" (*op. cit.*, p. 89), and he cites the fact that the same type of tooth pattern has evolved many times in the rodents. He is perfectly willing, however, to accept the evidence of structures where there is, and presumably always will be, no actual evidence of evolutionary sequence, such as the sacculus urethralis in the penis (*op. cit.,* pp. 16-17).[34] He believes that the presence of multiple cuspules in isolated instances among modern "hystricomorphs" is a clue to the ancestral pattern, but that the underlying structure of the teeth is not. He believes the structure of the angular process but not that of the infraorbital foramen to be fundamental; e.g., he places the Bathyergidae in the Hystricomorpha and eliminates the Pedetidae. He believes that the histologic structure of the incisor enamel is important, except presumably for such forms as *Pedetes* that do not fit his classification. He considers the fact that there are spines on the penis or a forward opening of the pterygoid fossa in "hystricomorphs" as indicative of relationship among these forms, but disregards these characters when they occur in non-hystricomorphous rodents (e.g. a forward opening of the pterygoid fossa in geomyoids), or passes over the absence of one of them in a group regarded as "hystricomorph" (e.g. lack of a forward opening of the pterygoid fossa in Ctenodactylidae). The evidence from auditory ossicles that he advances has been discussed above (p. 292). He believes that cranial foramina are worthless in rodent classification because there is considerable variability as to which nerves and blood vessels follow which paths, whereas this fact may well indicate that the cranial foramina and their contents are potentially very useful although at present poorly understood. In other words, in spite of his protestations to the contrary, we feel that Landry is setting up a key classification instead of a phylogenetic one. This is justifiable when the phylogenetic data are not available, and is justifiable as an adjunct to the use of data from phylogeny, but is not warranted when it is contrary to the data from the study of fossil rodents, as is the case with Landry's proposed classification. Finally, it seems to us, Landry is guilty, on a number of occasions, of assuming that a particular condition held true for the hypothetical ancestral "hystricomorphs,"

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[34] We fully share Landry's interest in the remarkable distribution of the sacculus urethralis within the Rodentia, although we are unable to see quite eye-to-eye with him regarding the over-riding importance he attributes to it as a proof of the unity of Hystricomorpha (*sensu lato*). We note its occurrence in the Bathyergidae and the presence of a vestige (or rudiment?) of it in the Ctenodactylidae, groups which, with Lacovat, we would exclude from the Hystricomorpha (or Palaeotrogomorpha). Landry does not mention Pocock's finding (1922, pp. 412, 425) that the sacculus is lacking in *Lagostomus* — presumably a secondary loss, since it is present in *Chinchilla*. This absence so shocked Dathe, another student of this curious little structure, that he was almost prepared (1937, p. 54) to read *Lagostomus* out of the Hystricomorpha (*sensu lato*).

and then of using these assumed ancestors in an attempt to demonstrate the truth of some of his other hypotheses. Perhaps we do him an injustice here, but repeated reading of his work gives us this impression. A quotation from Landry succinctly illustrates our objections to his method of approach: "The usual procedure [in dealing with South American fossil rodents] seems to be to sort out the fossils into categories already set up on the basis of the morphology of the living forms, a procedure that is likely to be misleading" (*op. cit.*, p. 36). We agree heartily with this statement, which we feel describes precisely what he has done.

CLASSIFICATION OF RODENTS

This paper was first written toward the end of a period in which there had been growing dissatisfaction with the then prevalent division of rodents into Sciuromorpha, Myomorpha, and Hystricomorpha, but during which no one had attempted to solve the problems of the overall relationships of rodents, due to the obvious complexity of the problem. Simpson's classification (1945) was essentially an effort to retain the simplicity of the tripartite classification, even though he recognized its serious disadvantages. Subsequently, however, there has appeared a series of important papers suggesting basic modifications in rodent classification, particularly those by Lavocat (1951b, 1955 and 1956), Schaub (1953a and 1953b), Viret (*in* Grassé and Dekeyser, 1955), and Wood (1954 and 1955). Since there are several different approaches to the problem of rodent classification represented by these works, it would be well to analyze them briefly in order to explain the position that we adopt below.

If anything is clear about rodent evolution, it must be that the order has been a numerous and successful one ever since the early Eocene. Circumscribed in their evolutionary potentiality by their possession of gnawing incisors, groups of them have evolved time after time along parallel lines. Lavocat (1956) stresses this point. Parallelism, in fact, can be detected within the order as far back as the early Eocene. It is therefore always dangerous to assume that there is a special relationship between two geographically separated forms, or groups, merely because of a similarity in certain structures.[35] If the similarity amounts to practical identity, especially if the structures are slightly unusual, additional use may perhaps be made of these features as a basis for classification. But, even here, care must be used. In the study of rodent tooth patterns, for example, unworn teeth must be used wherever possible, as has been stressed by numerous authors, but there must also be a proper understanding of the significance of the structures that occur.

We do not believe that there is a touchstone for the taxonomy of rodents. No one structure (teeth, jaw muscles, angle of the jaw, baculum, or male reproductive tract) is a sure criterion for determining relationships; all available characteristics must be weighed before we can be certain that we have obtained a correct picture. Here again, Lavocat (1956) has expressed an essentially identical opinion, as has Landry (1957a) also. However, a study of living forms, representing the end stages of evolution, can never in itself give a complete picture of the relationships involved. The only way in which relationships can be demonstrated positively is by tracing the evolution of all forms through an adequate series of intermediate stages. This is far from having been accomplished as yet, which is why there are still disagreements on the classification of the order. Nevertheless, whenever a phylogeny can be established for any portion of the order, it serves as an aid in understanding the overall phylogeny; it demonstrates that some of the potential phylogenies, based on living forms, are exceedingly unlikely to have been the true ones.

Many students have expressed dissatisfaction with the neo-Brandtian classification as given by Simpson (1945), and have suggested rather extensive modifications of it, of one sort or another, a development cheerfully anticipated by Simpson himself. A few voices, however, have been raised in support of Brandt's concepts of 1855, or Tullberg's modification thereof of 1899, one of which is represented by Landry's views (1957a)

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[35] Landry (1957a, pp. 33-36) discusses the importance of parallelism, remarking that it "implies that the structural similarities independently acquired in two forms are genetically related, although I have never seen this expressly stated" (Landry, 1957, p. 33). However, a number of previous authors (e.g. Haas and Simpson, 1946, p. 336; Moody, 1953, p. 107; Simpson, 1945, p. 9; 1949, pp. 181-183; Wood, 1937b, p. 175) have discussed this subject and have expressly stated that parallelism may be due to corresponding mutations of identical genes.

as to the unity of the "hystricomorphs." That we are unable to share these views should by now be evident.

Schaub has recently (1953a) presented a reclassification of the "Hystricomorpha," in which he proposes a suborder Pentalophodonta, consisting of all forms that have five-crested cheek teeth or which he believes to have been derived from ancestors having five crests. This includes two infraorders, the Palaeotrogomorpha, or Old World forms, and the Nototrogomorpha, or New World ones. His Infraorder Nototrogomorpha is the same as our Suborder Caviomorpha, the difference in taxonomic rank between the two being unimportant. But Schaub's grouping of the Nototrogomorpha and Palaeotrogomorpha into the suborder Pentalophodonta indicates his conviction, with which we cannot agree, that all pentalophate rodents are descended from the Theridomyidae. For this reason, we have continued to use Caviomorpha since it does not indicate any special relationship of Old and New World "hystricomorphs," which we feel is an important point to stress at the present stage of our knowledge. As Lavocat points out (1956), any classification, such as Schaub's, which is based on a single character or a single associated group of characters, becomes a key rather than a classification.

Viret (in Grassé and Dekeyser, 1955, pp. 1526-1564) discusses fossil rodents and their classification. In this article, he reaches what seems to be an extreme version of Schaub's classification, with three suborders: the Pentalophodonta of Schaub, the Myodonta of Schaub and an assemblage simply called Non-Pentalophodonta for the reception of the rest, namely the Sciuroidea, the Aplodontoidea (including what Wood calls the Ischyromyoidea), the Eomyoidea of Stehlin and Schaub, the Gliroidea, the Geomyoidea and the Ctenodactyloidea. We are reasonably sure that the non-pentalophodonts are not a natural group.

Kretzoi (1943) divided rodents into two suborders: the Idioglires with trituberculate teeth, including the Sciuridae, Gliridae and Paramyidae, and the Euglires with quadrituberculate teeth, including all other rodents. This classification is not very useful, even from the point of view of establishing a key to the rodents.

Lavocat (1951a, pp. 72-73) divided the rodents into three divisions, Atypognathes, Hystricognathes and Sciurognathes, basically following Tullberg, but adding the Atypognathes for what Wood (1937a) included in the Ischyromyoidea. He did not elaborate on their arrangement. He stated (p. 72) that the structure of the mandible would seem to be more basic than that of the infraorbital foramen, since the latter is more subject to adaptation. But he also stated that his arrangement would tend to admit the possibility that there were numerous parallel groups independently derived from the Ischyromyoidea. On the basis of a subsequent discussion by Lavocat (1956), we feel that we are in very close agreement with him on general principles of rodent classification as well as on most of the major criteria. We do not think, however, that current evidence warrants belief that the jaw structure is any more fundamental than that of any other part of the animal. In other words, we do not see why there should not have been parallelism in the jaw structure as well as in anything else. The variable condition in the Paramyidae would have permitted either type of jaw structure to evolve one or more times. In addition, we feel that the use of the terms Hystricognathes, with two subdivisions Orthohystricognathes for the group we call Caviomorpha and Parahystricognathes for the Old World forms, implies a real relationship between the groups, which we cannot accept. In this lack of belief in a real relationship between the two (other than the derivation of both ultimately from the Paramyidae), we are supported by Lavocat himself (1951b, p. 38), although he later (1956, p. 55) suggested the possibility that the two groups were related through special Paleocene ancestors, as others have also done.

Landry (1957a) does not precisely spell out his ideas of classification above the superfamily level. He accepts, however, the three-fold division of the order into Sciuromorpha, Myomorpha and Hystricomorpha (pp. 1-2), although he feels there is more justification for subdividing the Myomorpha, at least, than the Hystricomorpha (p. 3). He believes that the shape of the angle of the jaw is a very fundamental character, separating the sciurognaths from the hystricognaths. He does not specify that these are taxonomic entities, but his work carries that implication. He follows a neo-Brandtian system, including all the hystricognaths in the Hystricomorpha, instead of separating the

Bathyergidae, as did Tullberg.[36] Landry apparently was unaware of the similarity of his views to those of Lavocat (1951a), since he makes no reference to that work. As indicated at various points above, there are a number of bases on which we disagree with his conclusions. Some are factual. Many of these have been pointed out in the text. Some rest on interpretation of the data. Primarily, however, our differences stem from different methods of approach. Landry relies to a very heavy extent on the comparative anatomy of living rodents. This is not unreasonable, since complete specimens of living rodents are available, whereas most fossil rodents are represented only by scraps. The fragmentary nature of the fossil material explains why so much paleontological work consists of discussions of tooth anatomy and the relationships it suggests. Admittedly, no study limited to the teeth can ever give a complete picture of rodent evolution, but, on the other hand, a correct phylogeny of the rodents must be in accord with the evidence of dental evolution, as well as with the evidence from other points of view. We feel very strongly that any classification, to be meaningful, must reflect the phylogeny of the forms involved. Since we disagree strongly with Landry's conclusions as to the direction of tooth evolution in the hystricomorphous rodents, we can only conclude that the other resemblances he cites, when he is correct, are the results of parallelisms between the Old and New World groups. This means either that the Hystricomorpha and Caviomorpha have a common Paleocene ancestor, distinct from the Paleocene ancestor of the other rodents (as, in fact, is postulated by Schaub, 1953a, p. 393, and by Landry, 1957a, p. 91), which we do not believe, or that the Paleocene ancestors of these forms, and of all other rodents, were paramyids, which we do believe. As pointed out above, we cannot accept the Paleocene invasion of South America by "hystricomorphs," so we fall back on the conclusion that the Hystricomorpha and Caviomorpha have derived those characters, which they hold in common, independently and subsequent to their geographic separation. This is extreme parallelism. We

[36] A recent study of the bathyergid *Heterocephalus* emphasizes the very isolated position of this family within the order, the authors concluding that the results of their investigation indicate that the bathyergids have "myomorph" and "hystricomorph" features, but "point even more emphatically towards a complete severance of the bathyergids from all three subordinal groups of recent Rodentia" (Hill, Porter, Bloom, Seago and Southwick, 1957, p. 511).

believe it took place in the rodents. We believe, with Landry, that this means that the common ancestors of the two groups were closely related. We differ with him, however, in that we are convinced that these common ancestors must have been characterized by an assemblage of characters such that they could not have been included in either the Caviomorpha or the Hystricomorpha, and that they must have been members of the group variously called Protrogomorpha (Wood, 1937a) or Ischyromyoidea (Simpson, 1945).

Lavocat (1956, pp. 52-53) raises objections to the Suborder Sciuromorpha as used by Wood (1955), suggesting that the Sciuridae are so distinct from the ancestral stock in every respect except their tooth pattern that the ancestral stock itself should be retained as the Suborder Protrogomorpha. This we feel is a reasonable suggestion. Lavocat raises a number of other questions in regard to Wood's classification. His views seem very logical to us, whether or not we are in complete accord with the end results. Logically followed out they would result in a classification of the rodents in which only three suborders (Protrogomorpha, Myomorpha, and Caviomorpha) would contain more than three families; one suborder (Hystricomorpha) would contain three families; four suborders (Theridomorpha, Castorimorpha and perhaps two new groups, one for the Gliroidea and another for the Anomaluridae and Pedetidae) would contain two families; and three suborders (Sciuromorpha, Bathyergomorpha and a new group proposed but not named by Lavocat for the Ctenodactylidae) would contain a single family each. Under this reshuffling, or indeed under most published rearrangements of the order, the Caviomorpha, however named or ranked, becomes the largest of the major divisions of rodents, containing between 11 and 14 families, depending upon individual judgment as to whether such assemblages as the tuco-tucos and the nutrias merit familial rank. The reason is of course obvious: caviomorphs were the only group of rodents to occupy a whole continent for a very long period of time free from the competition of any other rodents. That an arrangement such as the above might best express the actual evolution of rodents is by no means impossible. It raises, however, questions concerning the classification of the order. Would it be more useful, for practical purposes and to assist in the understanding of the phylogeny, 1), to establish 11 suborders, several containing a dozen or fewer known genera; 2), to establish three suborders for the groups of considerable size (Protrogomorpha, Myomorpha and Caviomorpha), leaving all other rodents in isolated superfamilies; or, 3) to abandon suborders for the time being and use the superfamily as the unit? We think that the second of these might be the most accurate expression of current knowledge, but might prove the most confusing to the non-specialist. The last has been suggested by Simpson (*in litt.*, to Wood, dated March 22, 1954) and strongly concurred in by Ellerman (*in litt.*, to Wood, dated June 20, 1955). This would, however, in our opinion create practical difficulties in the treatment of a large and obviously natural group such as the Caviomorpha. We are in any event convinced of the utter futility of trying to continue brigading the rodents into Brandt's classical Sciuromorpha, Myomorpha and Hystricomorpha. As the early phylogeny of rodents becomes better known it may once again become possible to reduce the number of independent groups, by demonstrating relationships between two or more of the now isolated late Tertiary and Recent assemblages, possibly including ancestral forms which are now, perhaps, included in the Protrogomorpha. This time, however, has obviously not yet come.

SUMMARY

The rodents of early Oligocene Deseadan age, the earliest known from South America, are described. They are shown to represent early stages in the evolution of all the superfamilies and about half of the families of South American rodents.

The South American "Hystricomorpha" are referred to a separate suborder, the Caviomorpha, which is believed to have originated and evolved in South America.

The arrival of rodents in South America is discussed. It is concluded that they came from North America, in the latter part of the Eocene, and that, at the time of arrival, they were protrogomorphs and very probably paramyids.

It is pointed out that parallelism occurs in dental evolution of the rodents, and arguments are presented against the Stehlin-

Schaub concept of a "*Theridomys-Trechomysplan*" as the starting point for all pentalophate rodents.

The Paramyidae, as represented particularly in the early Eocene (Wasatchian) species of *Paramys*, are considered to be the most primitive known rodents, and to be either the actual or the structural ancestors of all later forms.

Comments are made on various recent proposals for the classification of the rodents, and the suggestion is made that there may be eleven or more independent groups, of subordinal rank. Forcing all rodents into the classic Sciuromorpha, Myomorpha and Hystricomorpha now seems impossible.

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THE TYPES OF CORBICULIDAE AND SPHAERIIDAE (MOLLUSCA: PELECYPODA) IN THE MUSEUM OF COMPARATIVE ZOOLOGY, AND A BIO-BIBLIOGRAPHIC SKETCH OF TEMPLE PRIME, AN EARLY SPECIALIST OF THE GROUP

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With Eight Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May, 1959

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The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

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No. 4 — The Types of Corbiculidae and Sphaeriidae (Mollusca: Pelecypoda) in the Museum of Comparative Zoology, and a Bio-bibliographic Sketch of Temple Prime, an Early Specialist of the Group

By Richard I. Johnson

INTRODUCTION

The importance of the collection of Corbiculidae and Sphaeriidae in the Museum of Comparative Zoology may be attributed largely to the efforts of one man, Temple Prime. In 1895, at the age of sixty-three, Prime presented this museum with the collection he had begun when but a lad of nineteen and a student of Louis Agassiz. The collection includes the types of most of the species he described. The figured holotypes were generally marked with a cross in ink. The number of primary types that he acquired from his contemporaries is impressive.

As originally planned, this paper was to be a bio-bibliographic sketch of Temple Prime including a list of his papers on recent Mollusca, and a complete list of the species he described (with the location and number of the holotype specimens); and it was intended to figure those types which had not previously been illustrated. The original plan will account for the inclusion of several species which would otherwise seem outside the scope of this work.

However, as work progressed it seemed wise to include all of the types in the Museum of Comparative Zoology which belong in the Corbiculidae and Sphaeriidae. Thus, we have included a number of species of Corbiculidae described by G. P. Deshayes from the Hugh Cuming collection, paratypes of which were sent to Prime. The holotypes are now in the British Museum (Natural History). Many of these have never been figured. But rather than figure the paratypes sent to Prime, we have illustrated holotypes or lectotypes from the British Museum, thereby avoiding inadvertently stealing the primary types from that institution.

In addition to the Prime collection, the Museum of Comparative Zoology now has the E. W. Roper collection of Sphaeriidae which was acquired when a change of policy in the Boston Society of Natural History (now Museum of Science) caused that institution to give up most of its study collections. While not containing a great number of types, this collection is extensive and rich in series.

To make the Museum of Comparative Zoology collection even more valuable, it now contains a remarkable set of types from the Musée Heude in Shanghai. These specimens formed the basis of R. P. Heude's work on the mollusks of the Province of Nanking and include types of almost every species of *Corbicula* that he described. They were purchased by R. T. Abbott in 1946 while he was in China with the United States Navy.

BIOGRAPHICAL SKETCH OF TEMPLE PRIME

Temple Prime was born on September 14, 1832, at 1 Battery Place, New York City, in the same room where the inventor Robert Fulton died. On his father's side he was from "good old New England stock." Through his mother he was descended from Governor Bowdoin of Massachusetts, one of whose daughters married Sir John Temple — first British Consul under the administration of President Washington. Prime's mother died when he was but eight years old. In 1855 his father, Rufus, bought a farm in Huntington, Long Island, New York, which became the family seat. When Rufus died in 1885, Temple and his sister Cornelia made it their permanent home. There were no direct descendants since neither ever married, and their brother was killed in the Civil War.

Young Temple began his education in New York City at the school of Monsieur Peugnet, one-time officer under Emperor Napoleon. Temple's father was a great admirer of Napoleon. Temple was subsequently sent to Geneva, Switzerland, to study, and then to Professor Block's Institute in Saxony, Germany, where he had as a classmate Prince Hohenlohe who was later to become governor of Alsace-Lorraine. Needless to say, Prime came to know several languages with great fluency. When he was sixteen years old, Prime returned to the United States and studied under the private tutelage of a Reverend Mr. Harwood of Hell Gate, New York. At eighteen he entered Harvard College where he studied at the School of Science under Louis Agassiz. This was before Agassiz founded the Museum of Comparative

Zoology. At the age of nineteen he described his first new species of mollusk in the Proceedings of the then flourishing Boston Society of Natural History. (The Society's collection of mollusks was later deposited in the Museum of Comparative Zoology.)

For a time Prime went to Holland as Secretary of the American Legation at The Hague under August Belmont where he remained until a change of administration removed his superior. On his return to the United States he entered Columbia Law School. Upon graduation he read law in the office of Judge Samuel Blanchford, but he never practiced professionally. During these years he was constantly writing papers in his chosen field of malacology, as well as works on genealogy and French history.

When traveling with his sister, Cornelia, in Europe during the Franco-Prussian war of 1870-71, they left Paris on one of the last trains to leave that city before the outbreak of the Commune. They inadvertently spoke in German and were arrested at Aumale as spies. They were released only upon proof of American citizenship.

Prime was very active in the local affairs of Huntington, New York. He was a trustee of numerous charities and societies as well as president of several business enterprises. He was especially interested in the Historical Society of Brooklyn, New York, and took a primary role in founding the Soldiers' and Sailors' Memorial Building, at Huntington — a tribute to the dead of the Civil War. At the present time it houses the public library.

It is said that, as a youth, Prime was a brilliant member of New York and Newport Society, being sought after because of his ready wit and rare powers of conversation. However, he grew taciturn with the years for at the time of his death on February 25, 1903, he was thus described by the Hon. Townsend Scudder in his funeral oration: ". . . an austere man, a man of few words but of sincere purposes; of lofty ideals, of grim determination. He was blunt and outspoken, but he thought before he spoke, and his actions were ever the result of mature reflection. He did not speak to make you feel good, he spoke to give you the information you sought."

At the time of this writing, Townsend Scudder was ninety-three, and understandably did not remember this event at which he spoke; however, Miss Mary Theresa Scudder generously contributed the following interesting remarks from her recollections.

"The eulogies (in the Memorial Service) are factual and true. I remember when I was a high-school student seeing Temple Prime walking through the assembly room, a tall slender figure with a thin aristocratic face. Temple Prime was a man of probity, brusque and terse in speech, but a gentleman.

"The Prime house in the east end of the town of Huntington still exists, an attractive, gracious house. The rooms were not large, the furniture was good, and the rooms were simple and uncluttered. The fireplaces in all the rooms were used to heat the house with wood, and candles were used for lighting. Across the street there was a little house painted red, which Temple had for his library and study. (It was still extant in 1956.) The estate ran for a mile or more through fields and woods to great hay lots where there was a big hay 'barracks.' Always there were beautiful horses.

"After her brother's death Miss Prime continued his charities and also helped boys and girls through college. [Miss Scudder was among those aided, and she wrote concerning this:] Every fall she gave me a check of $100.00 which almost paid my tuition at Mount Holyoke College, where I majored in Zoology. Upon graduation she gave me a six-weeks' summer session at the Biological Laboratory in Cold Spring Harbor. Thereafter, for years, this scholarship appeared annually in the prospectus of the Biological Laboratory of the Brooklyn Institute of Arts and Sciences as the Temple Prime Scholarship in honor of a great conchologist."

Prime's privately printed "Catalogue of the species of Corbiculadae in the Collection of Temple Prime, now forming part of the collection of the Museum of Comparative Zoology" has been an invaluable aid in locating his types. One of his original labels has been reproduced on Plate 2, figure 2. The number in the upper left hand corner refers to the catalogue where every species of each genus bears a numeral. When the species is represented by several lots the number is followed by a letter to distinguish them from one another.

In many cases it has been possible to locate the holotype since it is either the figured or measured specimen, and usually marked with a cross. In those instances where we could not be certain which specimen was regarded as the type we have selected lectotypes. In the Sphaeriidae, with few exceptions, we have avoided doing this, since it seems advisable to allow a subsequent reviser of this difficult group to bear this responsibility.

It will be noted that a number of previously published *nomina nuda* have been included when associated with Prime's name. This was done to facilitate the determination of the validity of these names should they appear in the literature or on specimens in collections.

The Museum of Comparative Zoology has most of Prime's types. About a dozen are in the British Museum (Natural History), and a few are in other American institutions. Many of Prime's types are figured here for the first time.

Prime was a careful worker and during the course of his life described some one hundred and sixty-seven species. He was not afraid to admit his own errors. Maturity and access to greater series of specimens led him to place in synonymy more than sixty of his own names. Certainly this is a great credit to him, as are his carefully prepared and usually well illustrated monographs. He was also ahead of his time in his emphasis on authentic material. As a result, there was in his collection type material received from Deshayes, and many other of his contemporaries.

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This project was originally conceived many years ago by R. A. McLean, but upon his appointment to the Academy of Natural Sciences of Philadelphia, the preliminary work was turned over to R. W. Foster, who in 1947 encouraged the present author to assume the task.

Thanks are due to the following for the loan of type material: Dr. H. A. Rehder, United States National Museum; Dr. R. T. Abbott, Academy of Natural Sciences of Philadelphia; Dr. W. K. Emerson, American Museum of Natural History. Special thanks are due to the late Guy L. Wilkins of the British Museum (Nat. Hist.), who when confronted with an impossibly long request for information and material immediately set to the task of supplying our wants. Mr. I. C. J. Galbraith and Mr. S. P.

Dance have cheerfully carried on and supplied us with photographs and the loan of valuable type material.

It is also a pleasure to thank Miss M. T. Scudder for her delightful recollections of the Prime family.

Most gratefully, thanks go to Drs. W. J. Clench, R. D. Turner, and M. E. Champion for suffering many interruptions in their own research, to help with advice and labor to make the present work possible. Finally, I wish to thank my wife who kindly helped prepare the manuscript for press.

Several photographs are reproduced by courtesy of the Trustees of the British Museum (Natural History), including: Plate 2, figure 2; Plate 3, figures 1-3; Plate 4, figure 1; Plate 5, figures 1-3. All others were photographed by F. White, staff photographer for the Biological Laboratories, Harvard University.

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Notes on the Species of *Cyclas* found in the United States. Proc. Boston Soc. Nat. Hist., **4**: 271-286, text figures (March-April).

1854. Descriptions of Three New Species of *Pisidium*. Ann. Lyceum Nat. Hist. New York, **6**: 64-66, pl. 1, figs. 1-3 (March).

On the Identity of *Cyclas elegans* Adams, with *Cyclas rhomboidea* Say. Ann. Lyceum Nat. Hist. New York, **6**: 66-67 (March).

1857. Notes on some American Species of *Cyclas* described by Lamarck, Say, Rafinesque, and Linsley. Part 1, Lamarck and Say, p. 1-4. The Hague (privately printed).

1859. List of the Known Species of *Pisidium*, with their Synonymy. Ann. Lyceum Nat. Hist. New York, **7**: 94-103 (March). (Also reprinted and repaged: 1-10.)

1860. Descriptions of New Species of *Cyrena* and *Corbicula* in the Cabinet of the Academy of Natural Sciences of Philadelphia. Proc. Acad. Nat. Sci. Philadelphia, **12**: 80 (February).

Description of Two New Species of the Genus *Batissa*, with Notes on that Genus. Ann. Lyceum Nat. Hist. New York, **7**: 112-115 (April). (Also reprinted and repaged: 1-4.)

Check List of the Shells of North America. Cyclades by Temple Prime. Smithson. Misc. Coll., **2**: Art. 6, pt. 7: 1-2 (June). (Also reprinted on a single sheet.)

Synonymy of the Cyclades, a Family of Acephalous Molluska. Part 1. Proc. Acad. Nat. Sci. Philadelphia, **12**: 267-301 (June). (Also reprinted and repaged: 1-37.)

Descriptions of New Shells from the Collection of Hugh Cuming, Esq. Proc. Zool. Soc. London, **28**: 319-323 (June). (Also reprinted and repaged: 1-4.)

Synonymy of the Species of *Cyrenella*, a Genus of Mollusca Belonging to the Family of the Lucinidae. Proc. Boston Soc. Nat. Hist., **7**: 345-347 (October).

Synonymy of the Known Species of *Rangia*, a Genus of the Family Mactracea. Proc. Boston Soc. Nat. Hist., **7**: 347-348 (October). (Also reprinted and repaged with the preceding: 1-4.)

1861. Note sur quelques espèces peu connues des genres *Batissa, Cyrena, Corbicula* et *Sphaerium*. Journal de Conchyliologie, **9**: 38-43, pl. 2 (January).

Synonymy of the Cyclades, a Family of Acephalous Mollusca. Part 2. Proc. Acad. Nat. Sci. Philadelphia, **13**: 25-33 (January). (Also reprinted and repaged: 39-47.)

Descriptions of New Species of *Cyrena, Corbicula* and *Sphaerium*. Proc. Acad. Nat. Sci. Philadelphia, **13**: 125-128 (June).

Notes on the *Cyrena salmacida* and the *Cyrenella americana* of Morelet. Ann. Lyceum Nat. Hist. New York, **7**: 314-315, pl. 6 (June).

Diagnosis d'espèces nouvelles. Journal de Conchyliologie, **9**: 354-356 (October).

Description of Three New Species of Mollusca of the Genus *Sphaerium*. Proc. Acad. Nat. Sci. Philadelphia, **13**: 414-415 (December).

1861-1862. Monograph of the Species of *Sphaerium* of North and South America. Proc. Acad. Nat. Sci. Philadelphia, **13**: 402-410 (December); *ibid.*, **14**: 28-36 (February). (Also reprinted and repaged: 1-19.)

1862. Descriptions of Three New Species of Shells Belonging to the Family of Cyclades. Proc. Zool. Soc. London, 1862: 2-3 (January [June]).

Descriptions of Two New Species of Shells. Proc. Boston Soc. Nat. Hist., **8**: 273-274 (February).

Descriptions of Two New Species of Mollusca of the Genus *Corbicula*. Ann. Lyceum Nat. Hist. New York, **7**: 480-481, text figs. (February).

Description of a New Species of Mollusca of the Genus *Venus*. Ann. Lyceum Nat. Hist. New York, **7**: 482-483, text fig. (February).

Description d'espèces nouvelles des genres *Glauconome, Cyrena, Batissa* et *Corbicula*. Journal de Conchyliologie, **10**: 383-390, pls. 13-14 (October).

1863. Catalogue of the Species of Corbiculadae[1] Contained in the Collection of Temple Prime. New York: 1-18 (privately printed).

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[1] T. Prime usually spelt the family name Corbiculadae.

1864. Description d'une nouvelle espèce de *Corbicula*—*C. angasi*. Journal de Conchyliologie, **12**: 151-152, pl. 7, fig. 6 (April).

1864-1867. Notes on the Species of the Family Corbiculadae with Figures. Ann. Lyceum Nat. Hist. New York, **8**: 57-92, 39 text figs. (June 1864); *ibid.*, **8**: 213-237, text figs. 40-66 (April 1866); *ibid.*, **8**: 414-416, text figs. 67-69 (April 1867).

1865. Description of a New Species of Mollusca of the Genus *Glauconome*. Ann. Lyceum Nat. Hist. New York, **8**: 107-108, text fig. (May).

Monograph of American Corbiculadae (recent and fossil). Smithson. Misc. Coll., No. 145, **7**, Art. 5: i-xi + 1-80, 86 text figs. (December).

1866. Notes on Species of the Family Corbiculadae, with figures. Ann. Lyceum Nat. Hist. New York, **8**: 213-237 (April).

1867. Notes on the Classification of the Corbiculadae, etc. Ann. Lyceum Nat. Hist. New York, **8**: 418-427, 6 text figs. (April).

1869. Catalogue of the Recent Species of the Family Corbiculadae. American Journal of Conchology, **5**: 127-187 (October). [The bibliography of this paper was reprinted and repaged: 1-11.]

On the Names Applied to *Pisidium*, a Genus of Corbiculadae. Ann. Lyceum Nat. Hist. New York, **9**: 276-279 (December).

List of the Species of Mollusca Found in the Vicinity of North Conway, New Hampshire. Ann. Lyceum Nat. Hist. New York, **9**: 280-281 (December).

1870. Notes on Species of the Family Corbiculadae, with Figures. Ann. Lyceum Nat. Hist. New York, **9**: 298-301, figs. 70-72 (March).

Report on the Mollusca of Long Island, N.Y., and of its Dependencies. Ann. Lyceum Nat. Hist. New York, **9**: 377-407, 6 text figs. (June). (With Sanderson Smith.)

1872. Notes on Specimens of Corbiculadae in the Cabinet of the Jardin des Plantes at Paris, and on the Authorship of the Encyclopédie Méthodique. Ann. Lyceum Nat. Hist. New York, **10**: 188-190, text fig. (May).

Catalogue of the Family Cyrenellidae. American Journal of Conchology, **7**: 251. ("Reprinted from the Proc. Boston Soc. Nat. Hist., 1860, **7**, and rearranged in accordance with the plan of the catalogues issued in this series." [Tryon]).

1878. Description of a New Species of *Corbicula*, with Notes on Other Species of the Corbiculadae Family. Bull. Mus. Comp. Zool., **5**: 43-46, pl. 2 (July).

Notes on the Anatomy of Corbiculadae (Mollusca), and a translation from the Danish of an Article on the Anatomy of *Cyclas* (*Sphaerium*) by Jacobsen. Bull. Mus. Comp. Zool., **5**: 47-54, pl. 3 (July).

1884. Description of a New Species of *Sphaerium*. Proc. United States Nat. Mus., **7**: 102-103 (July).

1895. Catalogue of the Species of Corbiculadae in the Collection of Temple Prime, now forming part of the Collection of the Museum of Comparative Zoology at Cambridge, Massachusetts. New York: 1-62 (privately printed).

There is also an unpublished manuscript in the M.C.Z. entitled "Identification of Certain Species of Corbiculadae" [1896].

A LIST OF THE RECENT SPECIES OF CORBICULIDAE AND SPHAERIIDAE IN THE MUSEUM OF COMPARATIVE ZOOLOGY, INCLUDING A COMPLETE LIST OF THE RECENT MOLLUSCA DESCRIBED BY TEMPLE PRIME, WITH THEIR ORIGINAL REFERENCE AND TYPE LOCALITIES

The following list is arranged alphabetically by species, giving the original author, the original genus, the year and place of publication of its original description, the type locality and collector (in parenthesis), reference to the first figure of a type if not originally figured, the kind of type material — holotype or paratype, etc. — the MCZ or other number, and the source by which it came to this museum.

All locality data, in brackets, contained in this report are additions to already published records and have been obtained from original labels.

ABBREVIATIONS

ALNHNY —Annals of the Lyceum of Natural History of New York.
AJC —American Journal of Conchology.
BJNH —Boston Journal of Natural History.

BM (NH) —British Museum (Natural History).
J. de Conch.—Journal de Conchyliologie.
MCZ —Museum of Comparative Zoology.
PANSP —Proceedings of the Academy of Natural Sciences of Philadelphia.
PBSNH —Proceedings of the Boston Society of Natural History.
PZS —Proceedings of the Zoological Society of London.

Smithsonian Misc. Coll. No. 145 — Monograph of American Corbiculadae (*sic*) (Recent and Fossil), by Temple Prime.

NOTE: The British Museum (Nat. Hist.) numbers are made up of the date on which they are catalogued. The final number refers to the specific specimen.

abditum Haldeman, *Pisidium*: 1841, PANSP, p. 53 (Springs in Lancaster County, Pennsylvania) 6 Cotypes MCZ 19806 from S. S. Haldeman ex Prime collection.

abyssorum 'Stimpson' Sterki, *Pisidium*: 1898, Nautilus, **11**, p. 124 (Region of the Great Lakes, in deep water. — Lake Michigan; Racine, Wisconsin, dredged, Geo. T. Marston [Cotypes MCZ 112570 ex E. W. Roper coll'n.]; different places on the Michigan side, partly from a depth of 24 meters; Pine Lake, Michigan, dredged; Green Lake, Wisconsin dredged; from stomachs of White Fish, Lake Michigan, all sent by B. Walker).

acuminata Prime, *Cyclas*: 1852, PBSNH, **4**, p. 155 (Lake Superior, L. Agassiz) Cotypes MCZ 19430. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

acuta Prime, *Cyrena:* 1861, J. de Conch., **9**, p. 355; *ibid.*, **10**, p. 387, pl. 14, fig. 1 (Central America) Holotype MCZ 176951.

acutum Pfeiffer, *Pisidium:* 1841, Archiv für Natur., **7** (1), p. 230 (Aus einem kleinen Bache in der Aue bei Kassel [Germany]) Cotypes MCZ 19928 ex Prime coll'n.

adamsi 'Prime' Stimpson, *Pisidium:* 1851, Shells of New England, p. 16. New name for *Cyclas nitida* Mighels and Adams, preoccupied. See under: *nitida* Mighels and Adams, *Cyclas*.

adunca Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 1, fig. 3 (rivière de Kien-p'ing-hien) Paratypes MCZ 167279 ex Musée Heude.

aequata 'Shepard' Prime, *Cyclas:* 1860, PANSP, p. 287 [*nomen nudum*]. Listed as a synonym of *Sphaerium rivicola* Lamarck.

aequilaterale Prime, *Cyclas:* 1852 BJNH, **6**, p. 366, pl. 12, figs. 23-25 (Augusta, Maine, Prime [Cotypes MCZ 19784]; Groton, Massachusetts, Lewis [Cotypes MCZ 19785]; Hudson River, New York, Ingalls; Herkimer County, New York, Lewis [Cotypes MCZ 19786]).

aequilateralis Deshayes, *Cyrena:* 1854 [1855] PZS, **22**, p. 20 (Cayenne rivulets). The specimen figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 19, fig. 114 is not a type as "this specimen was purchased by the British Museum (Nat. Hist.) in 1842" (Wilkins). There are two Cotypes of this species in the Cuming collection. The largest is, here selected, Lectotype British Museum (Nat. Hist.) 1956.12.3.1, Pl. 7, fig. 6. Paratype MCZ 176948 from H. Cuming ex Prime coll'n. Prime considered the original locality to be in error, and suggested Mazatlan, Mexico, as being more accurate.

affinis Deshayes, *Cyrena:* 1854, PZS, **22**, p. 16 (Australia, H. Cuming) Measured Holotype British Museum (Nat. Hist.) 1956.12.3.26, Pl. 5, fig. 3; also Paratype 1956.12.3.27. Not figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*. Paratype MCZ 176886 from H. Cuming ex Prime coll'n.

africana Krauss, *Cyrena:* 1884, Die Sudafrikanischen Moll., p. 8, pl. 1, fig. 8 (In flumine Gauritz, provincia Zwellendam Cape Province, South Africa, Krauss) 1 Paratype MCZ 154182 from Krauss ex C. B. Adams coll'n.

agrensis Prime, *Corbicula:* 1860, PANSP, p. 268 [*nomen nudum*]; 1861, PANSP, p. 128: 1864, ALNHNY, **8**, p. 75, fig. 24 (Agra, India) Holotype MCZ 176921.

alata 'Leach' Prime *Cyclas:* 1869, Amer. Jour. Conch., **5**, p. 152 [*nomen nudum*]. Listed as a synonym of *Sphaerium corneum* Scopoli.

albula Prime, *Cyclas:* 1852, PBSNH, **4**, p. 155 (Lake Superior, Agassiz) Cotypes MCZ 19704, J. G. Anthony coll'n. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

altile 'Anthony' Prime, *Pisidium:* 1852, BJNH, **6**, p. 353, pl. 11, figs. 10-12 (Canadaigua Lake, New York, T. Prime; Miami Canal, near Cincinnati, Ohio, J. G. Anthony) Cotypes MCZ 19797 from J. G. Anthony ex Prime coll'n. [Is *Pisidium compressum* Prime, *teste* Prime.]

amazonica 'Anthony' Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 299 (Amazon River, Brazil, from the stomach of a fish) Holotype MCZ 175641, Pl. 6, fig. 4.

americana 'Christofori and Jan' Prime, *Cyclas:* 1862, PANSP, p. 36 [*nomen nudum*].

ammiralis Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 298, fig. 10 (Saigon, Cambodia) Holotype MCZ 176922; 2 Paratypes in British Museum (Nat. Hist.).

amplum 'Ingalls' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 94 [*nomen nudum*]. Listed as a synonym of *Pisidium abditum* Haldeman.

angasi Prime, *Corbicula:* 1864, J. de Conch., **12**, p. 151, pl. 7, fig. 6 (Murray River, South Australia) Lectotype, here selected, MCZ 176917. [It cannot be determined which specimen was figured.] Pl. 7, fig. 1.

angelicum Rowell, *Pisidium:* 1867, Proc. California Acad. Sci., **3**, p. 353 (Angel Island, [San Francisco Bay, California]) Cotype MCZ 112554, ex E. W. Roper coll'n.

anglicana Prime, *Cyrena:* 1860, PANSP, p. 275. New name for *Cyrena obtusa* Forbes, 1836, *non* Roemer 1835. [Fossil.]

angulatum Prime, *Pisidium:* 1860, PZS, **28**, p. 322 (Valparaiso, [Chile]). The type was in the Cuming coll'n and should be in the British Museum (Nat. Hist.). It could not be located there in 1952. Idiotypes MCZ 19854 from Coquimbo, Chile. [Is *Pisidium chilense* Deshayes, *teste* Prime.]

anomala Deshayes, *Cyrena:* 1854 [1855] PZS, **22**, p. 21 (Bay of Caraccas, Peru [Caraques Bay, near Quito, Ecuador]) Measured Holotype British Museum (Nat. Hist.) 1957.6.25.8. Paratype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 19, fig. 109. Another Paratype, MCZ 143090, has been figured by Prime 1865, Smithsonian Misc. Coll. No. 145, p. 30, fig. 24.

aquilina Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 2, fig. 12 (les canaux le long du Fleuve-Bleu, entre Tchen-kiang et Nanking) 2 Paratypes MCZ 167284, ex Musée Heude.

arctata Deshayes, *Cyrena:* 1854 [1855] PZS, **22**, p. 20 ([Lake] Maracaibo [Venezuela] H. Cuming) Lectotype, here selected, British Museum (Nat. Hist.) 1956.12.3.28, Pl. 5, fig. 2; also Paratypes BM (NH) 1956.12.3.29-30. Not figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, since he could not locate the types; 16 Paratypes MCZ 176878 from H. Cuming ex Prime coll'n. One of the latter was figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 16, fig. 10, but it cannot be determined which specimen was figured.

arcuatum Prime, *Pisidium:* 1852, BJNH, **6**, p. 364, pl. 12, figs. 14-16 (Brattleboro, Vermont, Ingills) Cotype MCZ 165567. [Is *Pisidium abditum* Haldeman, *teste* Prime.] [Fossil.]

astronomica Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 2, fig. 7 (Canaux de Chang-hai, vers la limite extrême de l'influence de la marée) 3 Paratypes MCZ 167260 labeled Ts'ingp'ou, ex Musée Heude.

aurea Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 41 (La rivière Siang, province de Hou-nan) 2 Paratypes MCZ 167305 ex Musée Heude; 1 Paratype MCZ 154844 presented to A. Morelet by R. P. Heude ex E. W. Roper coll'n.

aurea Prime, *Cyclas:* 1852, PBSNH, **4**, p. 159 (Lake Superior) [Agassiz?] Holotype MCZ 19437. Figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 35, fig. 26. He questions the accuracy of the type locality. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

aurea Prime, *Truncatella:* 1853, Bermuda Pocket Almanac for 1852, p. 55 (Bermuda) [*nomen nudum*].

bahamensis Clench, *Byssanodonta:* 1938, Bull. Mus. Comp. Zool., **80**, no. 14, p. 535, pl. 2, fig. 6 (½ mile due east of Arthurstown, Cat Island, Bahamas) Holotype MCZ 107726.

barbadenae Prime, *Sphaerium:* 1861, PANSP, p. 415 (Barbados) Cotypes MCZ 73918. Figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 53, fig. 53. [It cannot be determined which specimen was figured.]

baronialis Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 300 (Port Morton [Morton Bay] Australia) Holotype MCZ 176936, Pl. 8, fig. 6.

baudonianum de Cessac, *Pisidium:* 1855, Bull. Soc. Nat. et Archéol. Creuse, **2**, p. 4 ([Department of] Creuse, France) 5 Cotypes MCZ 19926 ex Prime coll'n. [*Teste* Prime 1869, the author was unable to locate the original publication in which this species was described.]

bengalica Deshayes, *Corbicula:* 1854, Cat. Conchifera in British Museum (Nat. Hist.), p. 224; 1854 [1855] PZS, **22**, p. 344 (Bengal, H. Cuming). The type figured by Prime 1866, ALNHNY, **8**, p. 220, fig. 52, is, here selected Lectotype MCZ 176920 from H. Cuming ex Prime coll'n.

bensoni Prime, *Pisidium:* 1895, Cat. of Prime Shells in MCZ, p. 61 [*nomen nudum*]; new name for *Pisidium parvulum* Benson, itself a *nomen nudum*.

bensonii Deshayes, *Corbicula:* 1854, Cat. Conchifera in British Museum (Nat. Hist.), p. 223; 1854 [1855] PZS, **22**, p. 345 (Bengal from Benson, collection of H. Cuming) Lectotype British Museum (Nat. Hist.) 1956.12.3.31, Pl. 6, fig. 1; also Paratype (single valve) BM(NH) 1956.12.3.32; 3 specimens MCZ 176918 from Benson, probably from the original lot.

bermudensis Prime, *Bulimus:* 1853, Bermuda Pocket Almanac for 1852, p. 55 [*nomen nudum*].

bermudensis Prime, *Cerithium:* 1853, Bermuda Pocket Almanac for 1852, p. 55 [*nomen nudum*].

bermudensis Prime, *Cytherea:* 1853, Bermuda Pocket Almanac for 1852, p. 55 [*nomen nudum*].

bermudensis Prime, *Pupa:* 1853, Bermuda Pocket Almanac for 1852, p. 55 [*nomen nudum*].

bermudensis Prime, *Succinea:* 1853, Bermuda Pocket Almanac for 1852, p. 55 [*nomen nudum*]. *non Succinea bermudensis* Godet, 1860.

bernardiana Prime, *Cyrena:* 1861, PANSP, p. 126; 1864, ALNHNY, **8**, p. 83, fig. 33 (New Caledonia) Holotype MCZ 176882.

bezauriana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 1, fig. 5 (Les environs de Fou-tcheou-fou [Province of Fou-kien China], Vicomte G. de Bezauré) 4 Paratypes MCZ 167291 ex Musée Heude.

bilineata Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 6, fig. 33 (La rivière Hia-yu-fang qui debouche dans le Fleuve-Bleu en amont de Tong-lieou) 3½ Paratypes MCZ 167293; 2 Paratypes MCZ 154843 presented to A. Morelet by R. P. Heude ex E. W. Roper coll'n.

blandiana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 71, fig. 18 (Montes Laos, Cambodia) Holotype MCZ 176919.

bonnafauxianum de Cessac, *Pisidium:* 1855, Bull. Soc. Nat. et Archéol. Creuse, **2**, p. 6 (Department of Creuse, France) 2 Cotypes MCZ 19931 ex Prime coll'n. [*Teste* Prime 1869, the author was unable to locate the original publication in which this species was described.]

borealis Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 48 (Le petit affluent, rive gauche de la Han, au-dessous de Fan-tch'eng, Hou-pé) 5 Paratypes MCZ 167292 ex Musée Heude.

brunea Prime, *Corbicula:* 1860, PANSP, p. 269 [*nomen nudum*]; 1861, PANSP, p. 126; 1864, ALNHNY, **8**, p. 67, fig. 13 (Seamander River, [Tasmania]) Holotype MCZ 176924.

brunnea Prime, *Cyrena:* 1860, PZS, **28**, p. 321 (Hab. ?, H. Cuming) Holotype British Museum (Nat. Hist.) 1952.8.20.32. Pl. 4, fig. 1.

bulbosa 'Anthony' Prime, *Cyclas:* 1853, PBSNH, **4**, p. 283 (Arkansas) Holotype MCZ 19436. [Is *Sphaerium stamineum* Conrad, *teste* Prime.]

burgundiacum 'Billié' Prime, *Pisidium:* 1866, AJC, **5**, p. 166 [*nomen nudum*]. Listed as a synonym of *Pisidium amnicum* Jenyns.

californiensis Prime, *Cyrena:* 1860, PANSP, p. 276. New name for *Cyrena subquadrata* Deshayes, 1854, *non* Sowerby 1836.

calyculata C. B. Adams, (*non* Draparnaud) *Cyclas:* 1841, American Jour. Sci., **40**, p. 277 (Middlebury, Vermont) Cotypes MCZ 176958 ex C. B. Adams coll'n. See under: *pellucida* 'Prime' Stimpson, *Cyclas.*

canariense Shuttleworth, *Pisidium:* 1852, Mittheilungen Naturforsch. Gesell. [Bern], p. 146 (Teneriffa, Canaries) Cotypes MCZ 19936 from Shuttleworth ex Prime coll'n.

cantatoria Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 36 (Les petits ruisseaux de Kien-té-hein, partie sud du territoire) 6 Paratypes MCZ 167300 ex Musée Heude.

cardissa, Prime, *Cyclas:* 1852, PBSNH, **4**, p. 160 (Fresh Pond, Cambridge [Massachusetts] Cotypes MCZ 19521; Salem [Massachusetts]). Is *Sphaerium securis* Prime, *teste* Prime.

castanea Morelet, *Cyrena* (*Corbicula*): 1865, J. de Conch., **13**, p. 288: 1875, Series Conchyliologiques, No. 4, p. 362, pl. 15, fig. 4 (Cochinchine) 1 Cotype MCZ 176925 from Morelet ex Prime coll'n. 3 Idiotypes MCZ 87989 (Canton, China) from Morelet ex E. W. Roper coll'n.

castanea Prime, *Cyclas:* 1852, PBSNH, **4**, p. 159 (Wabash River [Illinois] S. S. Haldeman) Cotypes MCZ 19460. [Is *Sphaerium fabilis* Prime, *teste* Prime.]

chemnitziana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 60, fig. 5 (China?) Holotype MCZ 152913. [Is *Corbicula largillierti* Philippi; *teste* Prime.]

cheniana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 27 (Les torrents et ruisseaux sablonneux de Kouang-té-tcheou) 3 Paratypes MCZ 154848 presented to A. Morelet by R. P. Heude ex E. W. Roper coll'n.

chilina Prime, *Cyrena:* 1867, ALNHNY, **8**, p. 418 (Chile) Holotype MCZ 176883, Pl. 6, fig. 6.

chinensis 'Férussac' *Cyrena:* 1869, AJC, **5**, p. 149 [*nomen nudum*].

cicer Prime, *Pisidium:* 1854, ALNHNY, **6**, p. 64, pl. 1, fig. 1, a, b, c, (Washington County, New York, Ingalls) Cotypes MCZ 19798. [Is *Pisidium compressum* Prime, *teste* Prime.]

citrinum Normand, *Sphaerium:* 1854, Cyclades Dépt. du Nord, p. 1 (l'Escaut [River] à Valenciennes [France]) 4 Cotypes MCZ 19555 from Normand ex Prime coll'n.

clenchii Johnson, *Corbicula:* (new name for *Corbicula squalida* Heude 1888, *non* Deshayes 1855) see under: *squalida* Heude, *Corbicula.*

cochinensis Hanley, *Cyrena:* 1858, PZS, **26**, p. 543 (Cochin [China]) Idiotype figured by Prime, 1866, ALNHNY, **8**, p. 236, fig. 66; 6 Idiotypes MCZ 119016 ex Prime coll'n.

coerulea Prime, *Cyclas:* 1852, PBSNH, **4**, p. 161 (Clay pit near Fresh Pond, Cambridge, Massachusetts) Cotypes MCZ 19495. [Is *Sphaerium partumeium* Say, *teste* Prime.]

colombeliana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 3, fig. 14 (Canaux des districts de Li-yang, Yi-hing) 3 Paratypes MCZ 167298 ex Musée Heude.

colonialis Prime, *Corbicula:* ALNHNY, **8**, p. 416 (Java) Holotype MCZ 135633, Pl. 8, fig. 4.

colorata Prime, *Cyrena:* 1865, Smithsonian Misc. Coll'n. No. 145, p. 30, fig. 23 (New Providence, B.W.I.) Holotype MCZ 143091.

compressa Prime, *Batissa:* 1860, PZS, **28**, p. 320 (Borneo, Cuming) Holotype British Museum (Nat. Hist.) 1952.8.20.20, Pl. 8, fig. 5.

compressum Prime, *Pisidium:* 1852, PBSNH, **4**, p. 164; 1852, ALNHNY, **5**, p. 219, pl. 6; 1852, BJNH, **6**, p. 356, pl. 11, figs. 13-15 (Fresh Pond, Cambridge, Massachusetts) Cotypes MCZ 19789. [It cannot be determined which specimen was first figured.]

conica Heude, *Corbicula:* 1880, Conch, Fleuv. Nanking, pt. 10, pl. 3, fig. 16 (La rivière qui passe par la ville de Kein-ping-hien) 3 Paratypes MCZ 167271 ex Musée Heude.

conica var. b, Heude *Corbicula:* 1880, Conch, Fleuv. Nanking, pt. 10, pl. 3, fig. 16 b. (La rivière qui passe par la ville de Kein-ping-hein) 4 Paratypes MCZ 167265 ex Musée Heude.

consanguinea Prime, *Corbicula:* 1867, ALNHNY, **8**, p. 417 (India) Holotype MCZ 152901. [Is *Corbicula trigona* Deshayes, *teste* Prime.]

consanguineum Prime, *Pisidium:* 1865, Smithsonian Misc. Coll. No. 145, p. 76, fig. 86 (Retiro, Monte Verde and Catalina de Guarra, Cuba) Cotypes MCZ 19938.

constricta 'Anthony' Prime, *Cyclas:* 1853, PBSNH, **4**, p. 274 ([Miami Canal, near Cincinnati] Ohio) Cotypes MCZ 19511. [Is *Sphaerium transversum* Say, *teste* Prime.]

consularis Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 300 (Malacca) Holotype MCZ 152911, Pl. 6, fig. 5.

contortum Prime, *Pisidium:* 1854, ALNHNY, **6**, p. 65, pl. 1, fig. 2 a-c. (Pittsfield, Massachusetts, Shurtleff) Cotypes MCZ 19942. [Sub-fossil.]

contractum Prime, *Sphaerium:* 1865, Smithsonian Misc. Coll. No. 145, p. 48, fig. 46 (Big Prairie Creek and Greer's Creek, Alabama) Cotypes MCZ 19512. [Is *Sphaerium transversum* Say, *teste* Prime.]

convexa Deshayes, *Corbicula:* 1854, [1855] PZS, **22**, p. 342 (Central America [Mazatlan, Mexico] Cuming). The Cotype from Deshayes figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 3, fig. 1, is, here selected, Lectotype MCZ 143099.

cooperianum Prime, *Sphaerium:* 1869, AJC, **5**, p. 152 [*nomen nudum*].

corbiculaeformis Prime, *Cyrena:* 1860, PANSP, p. 80 (Cochin in Malabar) Holotype Academy of Natural Sciences of Philadelphia 54893. [Is *Velorita cochinensis* Hanley, *teste* Prime.]

corbiculoides Deshayes, *Batissa:* 1854, PZS, **22**, p. 14 (New Guinea, Jukes, coll'n of H. Cuming). The specimen figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena,* pl. 6, fig. 21 is not a type. "This figure was from a 'Rattlesnake' specimen registered in 1856" (Wilkins). Lectotype, here selected, British Museum (Nat. Hist.) 1957.6.25.4, Pl. 3, fig. 2. Paratype MCZ 119015 from H. Cuming ex Prime coll'n.

cordieriana Heude, *Corbicula:* 1880, Conch, Fleuv. Nanking, pt. 10, pl. 2, fig. 2 (Le district de Kouen-chan) 3 Paratypes MCZ 167266, ex Musée Heude.

corsa 'Charpentier' Prime, *Cyclas:* 1860, PANSP, p. 290, [*nomen nudum*]. Listed under the synonymy of *Sphaerium brochonianum* Bgt.

costaricense Prime, *Sphaerium:* 1885, Proc. United States Nat. Mus., **7**, p. 102 (Lake Yuriria, West Costa Rica, W. M. Gabb, ex W. H. Dall) Lectotype United States Nat. Mus. 37251, Pl. 7, fig. 4. Paratypes MCZ 215490.

crassior Schepman, *Batissa albertisii:* 1919, Nova Guinea, Zool., **13**, p. 185, pl. 6, fig. 8 (New Guinea: Bivak Island; Kampong above Dumas River, Lorenz River, Van Weel's Camp) 1 Cotype MCZ 40866 from Lorenz River, ex Zoological Museum of Australia.

crocea Lewis, *Cyclas:* 1854, PBSNH, **5**, p. 25 (Otsego [Cotypes MCZ 19522 from Lewis ex Prime coll'n.] and Schuyler's Lake in Otsego County and in Little Lakes, Herkimer County, New York).

crosseana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 72, fig. 10 (Philippines) Holotype MCZ 135635. [Is *Corbicula cumingii* Deshayes, *teste* Prime.]

cruciatum Sterki, *Pisidium:* 1895, Nautilus, **8**, p. 97, pl. 2, figs. 1-6, 13, 13a (Tuscarawas River, New Philadelphia, Ohio) Cotypes MCZ 88390 ex E. W. Roper coll'n.

cubense Prime, *Sphaerium:* 1865, Smithsonian Misc. Coll. No. 145, p. 58, fig. 60 (Catalina de Guantanamo, Punta de la Jaula [Cotypes MCZ 73914] and Esperanza [Cotypes MCZ 73913] Cuba).

cubensis Prime, *Cyrena:* 1860, PANSP, p. 277. New name for *Cyclas maritima* D' Orbigny, preoccupied.

cumingi Prime, *Glauconome:* 1863, J. de Conch., **10**, p. 384, pl. 14, fig. 4 (Malacca). Prime says this species is in the collections of Jay and Cuming as well as his own. His own types could not be located. ''Not in British Museum (Nat. Hist.)'' (Wilkins). The American Museum of Natural History, New York City has a single lot of this species which is undoubtedly the Jay type though someone has credited it to the Constable coll'n. Amer. Mus. Nat. Hist. 31551.

cumingii Deshayes, *Corbicula:* 1854, Cat. Conchifera in British Museum, p. 228 (Insula Luzon, Philippinarum, Cuming). The Cotype from Cuming figured by Prime, 1866, ALNHNY, **8**, p. 218, fig. 46 is here selected, Lectotype MCZ 187468.

cychkolzii 'Bientina' Prime, *Cyclas:* 1869, AJC, **5**, p. 162 [*nomen nudum*].

cyprinaeformis Prime, *Cyrena:* 1861, PANSP, p. 125; 1864, ALNHNY, **8**, p. 89, fig. 37 (Northern Australia) Holotype MCZ 176891.

cyreniformis Prime, *Corbicula:* 1860, PZS, **28**, p. 321; 1861, J. de Conch., **9**, p. 41, pl. 2, fig. 5 (Hab. ?) Holotype British Museum (Nat. Hist.) 1952.8.20.33.

debrixiana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 4, fig. 23 (Le torrent de Ning-kouo-hien) 3 Paratypes MCZ 167270 ex Musée Heude.

deformis H. F. Carpenter, *Sphaerium:* 1889, Nautilus, **3**, p. 22; *ibid.*, **16**, p. 18 (Tiogue Reservoir, Coventry, Rhode Island) Cotypes MCZ 34595 from H. F. Carpenter ex H. M. Winkley coll'n.

delandii 'Férussac' Prime, *Cyrena:* 1869, AJC, **5**, p. 149 [*nomen nudum*].

delavayana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 50 (Ruisseaux à Pak-hoy, province du Kouang-tong, M. l' abbé Delavay) 2 Paratypes MCZ 167286 ex Musée Heude.

delessertiana Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 299 (Smyrna, Asia Minor and [the Pyramids] Egypt) Holotype MCZ 72987 from the latter locality. [Is *Corbicula fluminalis* Deshayes, *teste* Prime.]

depressum 'Pfeiffer' Prime, *Pisidium:* 1866, AJC, **5**, p. 175 [*nomen nudum*].

detruncata Prime, *Cyclas:* 1852, PBSNH, **4**, p. 155 (Schuylkill River, Pennsylvania) Holotype MCZ 19509. [Is *Sphaerium transversum* Say, *teste* Prime.]

difficilis Prime, *Corbicula:* 1863, Cat. Corbiculadae in Prime coll'n., p. 4 [*nomen nudum*]; 1864. ALNHNY, **8**, p. 62, fig. 7 (Africa Septentrionalis) Holotype MCZ 72895. [Is *Corbicula fluminalis* Deshayes, *teste* Prime.]

diminuta Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 2, fig. 11 (La rivière de Nanking) 3½ Paratypes MCZ 167278 ex Musée Heude.

distorta Prime *Cyclas:* 1852, PBSNH, **4**, p. 158 (Ohio, Adams, Agassiz) Cotype MCZ 19439. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

ducalis Prime, *Corbicula:* 1862, PBSNH, **8**, p. 274; 1866, ALNHNY, **8**, p. 225, fig. 58 (Java) Holotype MCZ 135629.

dulchurchiensis? [*sic*] Prime, *Cyrena:* 1860, PANSP, 278 [*nomen nudum*].

duplicatum Pfeiffer, *Pisidium:* 1841, Archiv. für Natur., **7** (1) p. 230 (In einem Teiche auf dem Gipfel des Basaltberges bei Burghausungen, 4 Stunden von Kassel [Germany]) 6 Cotypes MCZ 19919 ex Prime coll'n.

dupuyanum Normand, *Pisidium:* 1854, Cyclades Dépt. du Nord, p. 5, (les fossés des marais à Valenciennes [France]) 4 Cotypes MCZ 19940 ex Prime coll'n.

eburnea 'Anthony' Prime, *Cyclas:* 1853, PBSNH, **4**, p. 279 (Arkansas) Cotypes MCZ 19496 ex Prime coll'n. [Is *Sphaerium partumeium* Say, *teste* Prime.]

elegans Prime, *Batissa:* 1862, J. de Conch., **9**, p. 385, pl. 13, fig. 1 (Hab.?) Holotype MCZ 176943. [Is *Batissa jayana* Lea, *teste* Prime.]

elegans C. B. Adams, *Cyclas:* 1840, BJNH, **3**, p. 330, pl. 3, fig. 11 (Swamp, Weybridge, Vermont, K. Prescott: Burlington, Vermont) Cotypes MCZ 136001 ex C. B. Adams coll'n.

elevata Haldeman, *Cyclas:* 1841, PANSP, p. 53 (no locality given). Prime says the Holotype is in the Academy of Natural Sciences of Philadelphia, and consists of one valve presumably from Florida. ½ Idiotype MCZ 19498 labeled "Alabama" ex Prime coll'n. This specimen was figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 44, fig. 40.

elliptica 'Férussac' Prime, *Cyclas:* 1869, AJC, **5**, p. 162 [*nomen nudum*].

elongata Prime, *Batissa:* 1860, PZS, **28**, p. 320 (New Caledonia) Holotype British Museum (Nat. Hist.) 1952.8.20.26, Pl. 2, fig. 1.

emarginata Prime, *Cyclas:* 1852, PBSNH, **4**, p. 156 (Lake Superior, Agassiz); 1865, Smithsonian Misc. Coll. No. 145, p. 43, fig. 38, Holotype MCZ 19441. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

episcopalis Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 300, fig. 72 (Cambodia). Prime described this species from specimens in the collection of Arthur Morelet. Cotypes MCZ 152917 ex E. W. Roper coll'n.

equilaterale Prime, *Pisidium:* [misprint of Prime] see under: *aequilaterale* Prime, *Pisidium.*

erans 'Lewis' Prime, *Cyclas:* 1869, AJC, **5**, p. 162 [*nomen nudum*].

erosa Prime, *Corbicula:* 1861, PANSP, p. 126; 1866, ALNHNY, **8**, p. 213, fig. 40 (Cambodia) Holotype MCZ 176928. [Is *Corbicula lydigiana* Prime, *teste* Prime.]

euphratica 'Bronn' Prime, *Cyrena:* 1869, AJC, **5**, p. 149 [*nomen nudum*].

exquisita Prime, *Cyrena:* 1867, ALNHNY, **8**, p. 417 (Chepo River near Panama, New Granada) Holotype MCZ 176955. [Is *Cyrena radiata* Hanley, *teste* Prime.]

fabalis Prime, *Cyclas:* 1852, PBSNH, **4**, p. 159 (Lake Superior, Agassiz); 1865, Smithsonian Misc. Coll. No. 145, p. 40, fig. 33. Holotype MCZ 19455.

fallax Deshayes, *Cyrena:* 1854, PZS, **22**, p. 15 (Philippine Islands; Australia, H. Cuming) Holotype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 10, figs. 41, 42. British Museum (Nat. Hist.) 1956.12.3.3, also Paratype BM(NH) 1956.12.3.4; Paratype MCZ 176887 from Australia, from H. Cuming ex Prime coll'n.

fallax Sterki, *Pisidium:* 1896, Nautilus, **10**, p. 20 (Tuscarawas River and Sugar Creek, Ohio) Cotypes MCZ 88389 from the former locality ex E. W. Roper coll'n.

fenouilliana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 24 (Le lac de Yun-nan-fou, province du Yun-nan, M. l' abbé Fenouil) 1 Paratype MCZ 167276 ex Musée Heude.

ferroense Mörch, *Pisidium:* 1837, Catalogue Conchlyorum quae reliquit Suenson [Hafniae], p. 43 (Faroe Islands, Denmark) 2 Cotypes MCZ 19933 ex Prime coll'n. [The author was unable to locate the publication in which this species was described.]

ferruginea Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 38 (Un torrent dans le district de Ts'ing-yang) 2½ Paratypes MCZ 167298 ex Musée Heude.

ferrugineum Prime, *Pisidium:* 1852, PBSNH, **4**, p. 162; 1852, BJNH, **6**, p. 362, pl. 12, figs. 8-10 (Salem and Cambridge, Massachusetts) Cotypes MCZ 17839 labeled ''Massachusetts.''

flava Prime, *Cyclas:* 1852, PBSNH, **4**, p. 155; 1853, *ibid.*, p. 284 (Sault Ste. Marie, Lake Superior, Agassiz); 1865, Smithsonian Misc. Coll. No. 145, p. 43, fig. 39. Holotype MCZ 19442. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

flava Prime, *Cyrena:* 1860, PZS, **28**, p. 320 (Hab.?) Holotype British Museum (Nat. Hist.) 1952.8.20.30, Pl. 7, fig. 5. Paratype BM(NH) 1952.8.20.31.

floridana Conrad, *Cyrena:* 1846, PANSP, p. 23, pl. 1, fig. 1 (Tampa Bay, Florida). The Cotype from Conrad figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 28, fig. 21, is, here selected, Lectotype MCZ 143092 ex Prime coll'n.

fluitans Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 47 (La Houai supérieure, branche de Lieou-ngan-tegeou) 4 Paratypes MCZ 167274 ex Musée Heude.

fluminea 'Bosc' Prime, *Cyclas:* 1869, AJC, **5**, p. 162 [*nomen nudum*].

fluminea 'Férussac' Prime, *Cyclas:* 1869, AJC, **5**, p. 149 [*nomen nudum*].

fluminea Müller, *Tellina:* 1774, Verm. Terr. & Fluv., **2**, p. 206 (In arena fluviali Chinae). A cotype has been figured: 1926, Proc. Mal. Soc. London, **17**, p. 100, pl. 9, fig. 2a-d. 1 Cotype MCZ 152926 from University of Copenhagen ex Prime coll'n.

fluviatilis 'Bosc' Prime, *Cyclas:* 1869, AJC, **5**, p. 162 [*nomen nudum*].

fortis Prime, *Batissa:* 1860, PZS, **28**, p. 320 (New Caledonia). The Cotype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 5, fig. 16, is here selected, Lectotype British Museum (Nat. Hist.) 1952.5.20.24.

fortis Prime, *Cyrena:* 1861, J. de Conch., **9**, p. 355; 1862, *ibid.*, **10**, p. 387, pl. 14, fig. 2 (Republica Aequatoriana [Ecuador]) Holotype MCZ 176908.

fossarum 'Krynicki' Prime, *Cyclas:* 1869, AJC, **5**, p. 152 [*nomen nudum*]. Listed as a synonym of *Sphaerium corneum* Scopoli.

fou-kiensis Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 1, fig. 6 (Des environs de Fou-tcheou-fou, Mgr. Gentili, vicomte G. de Bézaure) 2½ Paratypes MCZ 167297 ex Musée Heude.

fragilis 'Deshayes' Sowerby, *Cyrena:* 1875 [in] Reeve, Conch. Iconica, **20**, *Cyrena*, pl. 17, fig. 98 (No locality, H. Cuming). Since either type could be the one figured a lectotype British Museum (Nat. Hist.) 1956.2.3.5 is, here selected. Paratype BM (NH) 1956.12.3.6. Paratype MCZ 176942 from H. Cuming ex Prime coll'n. Previous to Sowerby's description, this was a nude name listed by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 22 as a synonym of *Cyrena mexicana* Sowerby.

furcata 'Rafinesque' Prime, *Cyclas:* 1853, PBSNH, **4**, p. 281 (Ohio?) Holotype MCZ 19435 ex Prime coll'n. Subsequently referred to as *fuscata*. [Is *Sphaerium stamineum* Conrad, *teste* Prime.]

fuscata Prime, *Batissa:* 1860, PZS, **28**, p. 319 (Hab.? H. Cuming). The Holotype is figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 4, fig. 11, British Museum (Nat. Hist.) 1952.8.20.16.

fuscata Prime, *Cyclas:* see under *furcata* 'Rafinesque' Prime, *Cyclas*.

galatheae 'Rheinhardt' Mörch, *Cyrena* (*Corneocyclas*): 1850, Cat. Conch. Kierulf, p. 32, pl. 2 (in Insulis Nicobar, Fl. Galatheae) 1 Paratype MCZ 176895 from Kierulf ex Prime coll'n.

gallicana Prime, *Cyrena* 1860, PANSP, p. 279. New name for *Cyrena compta* Deshayes 1857, *non* Deshayes 1854.

gentiliana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 1, fig. 5 (les environs de Fou-tcheou-fou, province du Fou-kien, Mgr. Gentili) 3 Paratypes MCZ 167273 ex Musée Heude.

germana Prime, *Cyrena:* 1867, ALNHNY, **8**, p. 417 (Panuco River, Tampico, Mexico) Holotype MCZ 176944, pl. 8, fig. 2.

gigantea Prime, *Batissa:* 1860, ALNHNY, **7**, p. 112 (Hab.?) Holotype in Jay coll'n. American Museum of Natural History, New York City, 31427. "All that remains in the appropriate tray is an unnumbered ligament." (W. K. Emerson, 1957.)

gigantea Prime, *Cyclas:* 1852, PBSNH, **4**, p. 157 (Pennsylvania); 1853, *ibid.*, **4**, p. 282 (Tuscarora Creek, Franklin Co. Penn., Haldeman. [Cotypes MCZ 19406] Cassadaga Creek, [Chautauqua Co.] N.Y., Redfield). It seems obvious that Prime had only the former lot in his possession when he made the original description. [Is *Sphaerium simile* Say, *teste* Prime.]

globulosum Gassies, *Pisidium:* 1855, Act. Soc. Linn. Bordeaux, **20**, p. 348 (des fontaines calcaires du environs d'Agen, [France]) 1 Cotype MCZ 19907 ex Prime coll'n.

globulus 'Jonas' Prime, *Corbicula:* 1860, PANSP, p. 269 [*nomen nudum*]. Listed as a synonym of *Cyrena cuneata* Jonas.

gracilis Prime, *Batissa:* 1860, PZS, **28**, p. 319 (Hab.?). The type figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 6, fig. 20, is, here selected, Lectotype, British Museum (Nat. Hist.) 1952.8.20.25.

gracilis Prime, *Corbicula:* 1860, PANSP, p. 270 [*nomen nudum*]; 1862, J. de Conch., **10**, p. 389, pl. 14, fig. 7 (Java) Holotype MCZ 135628.

gracilis Prime, *Cyclas:* 1852, PBSNH, **4**, p. 156 (Ohio, Adams) 3 Cotypes MCZ 177107. [Is *Sphaerium transversum* Say, *teste* Prime.]

grande 'Whittemore' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 98 [*nomen nudum*]. Listed as a synonym of *Pisidium variabile* Prime.

grateloupianum Normand, *Pisidium:* 1854, Cyclades Dépt. du Nord, p. 4 (les fossés du marais de Bourlain, à Valenciennes [France]) 4 Cotypes MCZ 19866 ex Prime coll'n.

gravis Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 4, fig. 20 (la rivière de Kien-p'ing-hien) 3 Paratypes MCZ 167295 ex Musée Heude.

grilloana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 6, fig. 34 (les torrents du Koué-tché-hien, dans le Tché-tcheou-fou) 3 Paratypes MCZ 167302 ex Musée Heude.

gryphaea Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 28 (La petite rivière de Ti-kang, district de Fan-tcha'ng dans le T'ai-p'ing-fou, rive droite du Fleuve-Bleu) 2 Paratypes MCZ 167257 ex Musée Heude.

gubernatoria Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 298, fig. 71 (Saigon, Cambodia) Holotype British Museum (Nat. Hist.) 1893.2.4.1408, Pl. 6, fig. 2, also Paratype BM(NH) 1893.2.4.1409 collection of A. Morelet.

gundlachi Arango, *Pisidium:* 1865, [in] Poey, Repertorio Fisico-Natural de la Isla de Cuba, pp. 88 [*nomen nudum*] 4 Cotypes MCZ 19851. Arango, 1879, Cont. Fauna Mal. Cubana, p. 143 lists this species as a synonym of *Pisidium consanguineum* Prime.

hammalis 'Férussac' Prime, *Corbicula:* 1869, AJC, **5**, p. 137 [*nomen nudum*].

hammalis 'Rafinesque' Prime, *Cyclas:* 1869, AJC, **5**, p. 162 [*nomen nudum*].

harfordianum Prime, *Pisidium:* 1866, AJC, **5**, p. 169 (Mendocino County, California) [*nomen nudum*].

hendersoni Sterki, *Sphaerium:* 1906, Nautilus, **20**, p. 69 (Crow Creek, 25 miles N.E. of Greeley, Weld County, Colorado) Cotypes MCZ 10405, ex J. Henderson.

herminii 'Wäld' [*Welwitsch*] Prime, *Sphaerium:* 1866, AJC, **5**, p. 168 [*nomen nudum*] listed as a synonym of *Pisidium casertanum* Bourguignat. Described as *Pisidium herminii* 'Welwitsch' by Clessin, 1877, [in] Martini & Chemnitz, Conch. Cabinet, **9**, pt. 3, Cycladeen, p. 61, pl. 7, figs. 12-14.

idahoense Roper, *Pisidium:* 1890, Nautilus, **4**, p. 85 (Old Mission, Northern Idaho, H. Hemphill) Cotypes MCZ 88393 ex E. W. Roper coll'n.

ignobilis Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 32 (La petite rivière qui draine le lac de Peng-tse-hien, au pied des montagnes) 2 Paratypes MCZ 167287 labeled "Tong-lieou" ex Musée Heude. 2 Paratypes MCZ 154840 from Heude to Morelet ex E. W. Roper coll'n.

imperialis Prime, *Corbicula:* 1870, ALNHNY, **9**, p. 299 (Pondicherry, India) Holotype 176915. [Is *Corbicula fuscata* Lamarck, *teste* Prime, in MS.]

inaequilateralis Prime, *Corbicula:* 1861, PANSP, p. 128; 1864, ALNHNY, **8**, p. 80, fig. 30 (Africa) Holotype MCZ 72898.

incertum Normand, *Pisidium:* 1854, Cyclades, Dépt. du Nord, p. 6 (fossés des marais à Valenciennes, Condé, etc. [France]) 3 Cotypes MCZ 19922 ex Prime coll'n.

inconspicuum Prime, *Sphaerium:* 1860, PZS, **28**, p. 322, 1861, J. de Conch., **9**, p. 43, pl. 2, fig. 7 (Lycia, Asie Mineure). Prime stated that the type was in the Cuming collection. The author located the original card on which the specimen had been glued at the British Museum (Nat. Hist.) in 1952, but the shell was missing.

indigotina Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 4, fig. 21 (La rivière de King-hien dans le Ning-kouo-fou) 2 Paratypes MCZ 167258 ex Musée Heude. 2 Paratypes MCZ 154814 from Heude to Morelet ex E. W. Roper coll'n.

inflata Prime, *Batissa:* 1860, PZS, **28**, 320 (Nicobar). The Holotype British Museum (Nat. Hist.) 1952.8.20.17 was figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 4, fig. 10.

inflata Deshayes, *Cyrena* (*Anomala*): 1854 [1855] PZS, **22**, p. 23 (Panama, H. Cuming). Holotype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 8, fig. 29 as *panamensis* Prime. British Museum (Nat. Hist.) 1956.12.3.7. "This specimen has Deshayes' exact measurements and has *inflata* pencilled in one valve" (Wilkins). Paratype BM(NH) 1956.12.3.8. 1 Paratype MCZ 176952 from H. Cuming ex Prime coll'n. *Cyrena inflata*, preoccupied by Philippi 1851, was changed to *Cyrena panamensis* Prime, 1869, PANSP, p. 283.

ingloriosa Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 4, fig. 19 (La rivière de Kein-p'ing-hien) 3 Paratypes MCZ 167289 ex Musée Heude.

inornata Prime, *Cyclas:* 1852, PBSNH, **4**, p. 159 (Illinois, Haldeman) Holotype MCZ 19431. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

insignis Deshayes, *Batissa:* 1854, PZS, **22**, p. 13 (Calamana, Island of Luzon, Philippine Islands, H. Cuming). The largest type figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 3, fig. 7 is, here selected, Lectotype British Museum (Nat. Hist.) 1956.12.3.9; also Paratype BM (NH) 1956.12.3.10. Paratype MCZ 19007 from H. Cuming ex Prime coll'n.

insularis Prime, *Corbicula:* 1867, ALNHNY, **8**, p. 414, fig. 67 (Formosa) Holotype MCZ 152900.

iodina Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 46 (La Houai moyenne) 1 Paratype MCZ 167268 ex Musée Heude.

iridinea Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 39 (Un torrent du district de Ts'ing-yang) 3 Paratypes MCZ 154849 from Heude to Morelet ex E. W. Roper coll'n.

islandica 'Férussac' Prime, *Cyrena:* 1869, AJC, **5**, p. 149 [*nomen nudum*].

jamaicense Prime, *Pisidium:* 1865, Smithsonian Misc. Coll. No. 145, p. 70. New name for *Cyclas pygmaea* C. B. Adams 1849 *non* Koch & Dunker 1837.

japonica Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 68, fig. 15 (Japan) Holotype MCZ 152904. [Is *Corbicula orientalis* Deshayes, *teste* Prime.]

japonicum Pilsbry & Hirase, *Pisidium:* 1908, PANSP, **60**, p. 35, fig. 1 (Akkeshi, Kushiro, Yesso, Japan) Paratypes MCZ 44761 ex Hirase.

jayana Prime, *Glauconome:* 1861, J. de Conch., **9**, p. 354; *Ibid.*, **10**, p. 383, pl. 14, fig. 5 (Australia, collection of Prime, Cuming and Jay). The type lot could not be located in the MCZ. Lectotype, here selected, in Jay coll'n, American Museum of Natural History, New York, 31537, Pl. 5, fig. 5.

jayanum 'Gassies' Prime, *Pisidium:* 1854, ALNHNY, **7**, p. 99 [*nomen nudum*] listed as a synonym of *Pisidium henslowianum* Jenyens.

jayanum Prime, *Sphaerium:* see under, *jayensis* Prime, *Cyclas.*

jayensis Prime, *Cyclas:* 1852, PBSNH, **4**, p. 157 (Lake Superior, Agassiz) Smithsonian Misc. Coll. No. 145, p. 46, fig. 43 as *Sphaerium jayanum.* This figured specimen, is here selected, Lectotype MCZ 19646. [Is *Sphaerium partumeium* Say, *teste* Prime.]

jayensis Lea, *Cyrena:* 1834, Trans. American Phil. Soc., **5**, p. 108 pl. 17, fig. 52; 1834, Observations on Genus *Unio*, **1**, p. 220, pl. 17, fig. 52 (Batavia?, J. C. Jay) 1 Paratype MCZ 176905 from I. Lea ex Prime coll'n.

jeannoti Normand, *Sphaerium:* 1854, Cyclades, Dépt. du Nord, p. 2 (près d' Avesnes) [France] M. Jeannot) 1 Cotype MCZ 19562 ex Prime coll'n.

kirkii Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 66, fig. 12 (Mozambique, Central Africa) Holotype in Isaac Lea coll'n., United States National Museum 122441.

kurtzii Prime, *Pisidium:* 1852, PBSNH, **4**, p. 162; 1852, BJNH, **6**, p. 361, pl. 12, figs. 5-7 (Charleston, South Carolina, Lt. Kurtz) Cotype MCZ 19830. [Is *Pisidium abditum* Haldeman, *teste* Prime.]

laevis Prime, *Cyrena:* 1861, PANSP, p. 125; 1866 ALNHNY, **8**, p. 233, fig. 64 (Borneo) Holotype MCZ 176907. [Is *Cyrena nitida* Deshayes, *teste* Prime.]

lamarckiana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 69, tig. 16 (Montes Laos, Cambodia) Holotype MCZ 176916.

lapicida Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 30 (habite deux rivières qui sortent de la chaîne s'etendent le long du

Fleuve-Bleu, de Tong-lieou à P'eng-tse) 2 Paratypes MCZ 167269 labelled Kien-té-hien ex Musée Heude; 2 Paratypes MCZ 154837 from Heude to Morelet ex E. W. Roper coll'n.

largillierti Philippi, *Cyrena:* 1844, Zeitschr. für Mal., **1**, p. 163; 1847, Abbild. und Besch. neuer Conch., **2**, p. 75, pl. 1, fig. 1 (China in flumine Yang-tse-kiang, Largilliert) 2 Cotypes MCZ 152932 from Largilliert ex Prime coll'n.

larnaudieri Prime, *Corbicula:* 1862, ALNHNY, **7**, p. 480, text fig. (Siam) Holotype MCZ 176934.

lauta Deshayes, *Cyrena:* 1854, PZS, **22**, p. 15 (Hab.?, H. Cuming). Lectotype, here selected, British Museum (Nat. Hist.) 1956.12.3.11, Pl. 4, fig. 3; also Paratype BM(NH) 1956.12.3.12; Paratypes MCZ 176904 from H. Cuming ex Prime coll'n.

leana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 68, fig. 14 (Japan). Holotype United States National Museum No. 122429 Isaac Lea coll'n. Paratype MCZ 152910 ex Prime coll'n.

leleciana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. **10**, pl. 2, fig. 10 (La rivière de Nanking) 3 Paratypes MCZ 167272 ex Musée Heude.

lenticularis Deshayes, *Batissa:* 1854, PZS, **22**, p. 14 (Philippine Islands, H. Cuming) Lectotype, here selected, British Museum (Nat. Hist.) 1956.12.3.13, figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 1, fig. 2; also Paratype BM(NH) 1956.12.3.14; Paratype MCZ 57001 from H. Cuming ex Prime coll'n.

lenticularis Normand, *Cyclas:* 1844, Notice Cyclades de Valenciennes, p. 8, figs. 7-8 (la forêt de Raismes, dans les fossés, mais principalement dans les mares des chemins) 8 Cotypes MCZ 19903 ex Prime coll'n.

lermondi Sterki, *Pisidium:* 1913, Nautilus, **26**, p. 138 (Duck Pond, Warren, Maine, N. W. Lermond) Cotypes MCZ 20082 ex V. Sterki.

leviuscula Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 64, fig. 9 (Cochin-China) Holotype MCZ 176931.

lilycashense F. C. Baker, *Sphaerium:* 1898, Nautilus **12**, p. 65 (Lily-cash Creek, Joliet, Illinois, J. H. Handwerk) 2 Cotypes MCZ 165537 ex E. W. Roper coll'n.

limosum Gassies, *Pisidium:* 1849, Tableau Méthod. et Des. Moll. de l'Agenais, p. 206, pl. 2, figs. 10-11 (fontaine de Chantilly, près Pecau [Lot-et-Garonne, France]) 6 Idiotypes MCZ 19899 from Agen, France ex Prime coll'n.

linneana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 70, fig. 17 (Montes Laos, Cambodia) Holotype MCZ 176930.

littoralis 'Férussac' Prime, *Cyclas:* 1865, Smithsonian Misc. Coll. No. 145, p. 54 [*nomen nudum*]. Listed as a synonym of *Sphaerium modioliforme* Anton.

loe-hensis Kruimel, *Corbicula:* 1918, [In] Abendanon, Geol. en Geog. doorkruisingen van Midden-Celebes, **4**, p. 1645, pl. 27, figs. 2-3 (Süd-Ost-Kuste der grossen Insel Loeha in Towuti-See, Sud-Ost-Celebes, Abendanon) 3 Paratypes MCZ 77752 ex Zoological Museum, Amsterdam, Netherlands.

lucidum Sterki, *Pisidium:* 1923, Nautilus, **37**, p. 19 (a roadside pool at Buena Vista, Chaffee Co., Colorado) Cotypes MCZ 83805 ex J. Henderson.

lutea Morelet, *Cyrena* (*Corbicula*)*:* 1862, Rev. et Mag. de Zöol., (2) **14**, p. 481 (China). The Cotype figured by Prime, 1864, ALNHNY, **8**, p. 61, fig. 6, is here selected, Lectotype MCZ 187463.

lydigiana Prime, *Corbicula:* 1861, J. de Conch., **9**, p. 355; *Ibid.*, **10**, p. 388, pl. 114, fig. 8 (Siam) Holotype MCZ 176929.

mactraeformis Prime, *Cyrena:* 1860, PANSP, p. 281. New name for *Cyrena mactroides* Deshayes 1854, *non* Roemer, 1835.

mactroides Deshayes, *Cyrena:* 1854 [1855], PZS, **22**, p. 17 (Hab.? H. Cuming) Holotype British Museum (Nat. Hist.) 1956.12.3.33, Pl. 3, fig. 3. Not figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, since he mentions in the index that he could not locate the type. Paratype MCZ 176903 from H. Cuming ex Prime coll'n. See previous entry.

maculata Morelet, *Cyclas:* 1851, Testacea Novissima insulae Cubanae et Americae Centralis, pt. 2, p. 25 (Vivit in paladibus Yucatanensis) Cotypes MCZ 47199 ex Prime coll'n.

mahalonensis Kruimel, *Corbicula:* 1918 [in] Abendanon, Geol. door-kruisingen van Midden-Celebes, **4**, p. 1644, pl. 27, fig. 4 (Mahalona See, Sud-Ost Celebes, Abendanon) 2 Paratypes MCZ 53501 ex Zoological Museum, Amsterdam, Netherlands.

mainese Sterki, *Pisidium walkeri:* 1898, Nautilus, **12**, p. 79 ([South Branch, Caribou River Woodland] near Caribou, Maine, O. O. Nylander) Cotypes MCZ 20612 and 165569 ex O. O. Nylander.

malaccensis Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 343 (Malacca, H. Cuming). The Cotype figured by Prime, 1864, ALNHNY, **8**, p. 65, fig.

10 is, here selected, Lectotype MCZ 152921 ex H. Cuming. This is the earliest figure of one of the types.

manchurica 'A. Adams,' Prime *Corbicula:* 1895, Cat. Corbiculadae in MCZ, p. 21 (Japan) Cotype MCZ 152929 from Adams, *fide* H. Crosse [*nomen nudum*]. No description of this species could be located.

manhattensis Prime, *Venus* (*Gemma*)*:* 1862, ALNHNY, **7**, p. 482, text figs. (The State of New York, in the East River, and at Greenport, Long Island, J. Jay, A. A. Gould, S. Smith, T. Prime) Cotype MCZ 219259 ex Gould type coll'n (localities not separated). Idiotypes MCZ 73310 from Huntington Harbor, Long Island ex Sanderson Smith. The Prime and Jay lots could not be located.

masapensis Kruimel, *Corbicula:* 1918, [in] Abendanon, Geol. en Geog. doorkruisingen van Midden-Celebes, **4**, p. 1645, pl. 27; fig. 1 (Masapi-See, Sud-Ost Celebes, Abendanon) 3 Paratypes MCZ 53502 ex Zoological Museum, Amsterdam, Netherlands.

maxima Prime, *Corbicula:* 1860, PZS, **28**, p. 321 (Hab.?, H. Cuming). I could not locate the type at the British Museum in 1952; however, a type was figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 15, fig. 78. While the correct original reference is given, the species is mistakenly credited to Deshayes.

mediocris Prime, *Corbicula:* 1862, ALNHNY, **7**, p. 481, text figs. (Hab.?) Holotype MCZ 152912. [Is *Corbicula occidens* Benson, *teste* Prime].

meridionale Prime, *Sphaerium:* 1861, PANSP, p. 414; 1865, Smithsonian Misc. Coll. No. 145, p. 55, fig. 54 (Panama) Holotype MCZ 73986.

meridionalis Prime, *Cyrena:* 1865, Smithsonian Misc. Coll. No. 145, p. 19, fig. 14 (Payta, Peru) Holotype MCZ 176877.

minervae Prime, *Sphaerium:* 1895, Cat. Corbiculadae in MCZ, p. 45 (River Ouse, Cumberland Co., Tasmania) Cotype MCZ 19569 [*nomen nudum*].

minor Prime, *Batissa:* 1860, PZS, **28**, p. 320 (Feejee Islands, H. Cuming) Holotype British Museum (Nat. Hist.) 1952.8.20.19, figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 3, fig. 8 a-b.

minor Prime, *Corbicula:* 1860, PANSP, p. 271 [*nomen nudum*]; 1861, PANSP, p. 127; 1864, ALNHNY, **8**, p. 80, fig. 29 (Hab.? Australia) Holotype MCZ 176926.

minor Mighels and Adams, *Cyclas:* 1842, BJNH, **4**, p. 39, pl. 4, fig. 2 (Weybridge, Vermont; Portland, Maine) Lectotype MCZ 19827 selected by Johnson, 1949, Occ. Papers on Mollusks, **1**, No. 14, p. 227 from the former locality.

minutum Sterki, *Pisidium medianum:* 1899, Nautilus, **13**, p. 11 ([Hackett's Mill Brook, Caribou River, Woodland] Aroostook Co., Maine, O. O. Nylander) Cotypes MCZ 20621 ex V. Sterki. The following other localities are given for this variety: Mohawk, New York, J. Lewis; Hess Lake, Michigan, L. H. Streng; 24 meters off New York Point, Lake Michigan, B. Walker; Blue Lake, Michigan, R. J. Kirkland.

mirabile 'Whittemore' Clessin, *Pisidium:* 1877, [in] Martini & Chemnitz, Conch. Cabinet, **9**, pt. 3, Cycladeen, p. 49, pl. 6, figs. 1-3 (near Waltham, Massachusetts) 9 Paratypes MCZ 20002 ex Whittemore. [Is *Sphaerium partumeium* Say, *teste* Prime.]

mirabilis Prime, *Cyclas:* 1852, PBSNH, **4**, p. 157 (Georgia, Haldeman) Cotype MCZ 19494. [Is *Sphaerium partumeium* Say, *teste* Prime.]

mirum Sterki, *Pisidium:* 1923, Nautilus, **37**, p. 20 (mostly from the vicinity of Silver Lake [Colorado], J. Henderson) Cotypes MCZ 83804 ex J. Henderson.

modesta Prime, *Cyclas:* 1852, PBSNH, **4**, p. 159 (Pennsylvania, Haldeman); 1853, *Ibid.*, **4**, p. 284. Cotypes MCZ 19433. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

mörchiana Prime, *Cyrena:* 1866, ALNHNY, **8**, p. 232, fig. 63 (Hab.? [Philippines]) Holotype MCZ 176900.

moltkiana Prime, *Corbicula:* 1878, Bull. MCZ, **5**, p. 43, pl. 2, fig. 2a-c (Sumatra). The two type specimens are in the University of Copenhagen, Denmark.

montana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 26 (Les minces filets d'eau qui descendent de la chaîne de collines que sépare les lacs du T'ai-p'ing-fou) 5 Paratypes MCZ 167288 ex Musée Heude.

moreletiana Prime, *Corbicula:* 1867, ALNHNY, **8**, p. 416 (Cambodia) Holotype MCZ 187461. [Is *Corbicula lydigiana* Prime, *teste* Prime.]

mulleriana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 59, fig. 3 (Fuh-Chau River, China) Holotype MCZ 152903. [Is *Corbicula fluminea* Deshayes, *teste* Prime.]

murilloi Clench, *Musculium:* 1939, Mem. Soc. Cubana Hist. Nat., **13**, no. 5, p. 286, pl. 36, fig. 1 (Soacha, Dept. Cundinamarca, Colombia, J. Bequaert) Holotype MCZ 91374.

nicaraguana Prime, *Cyrena:* 1869, AJC, **5**, p. 146. New name for *Cyrena solida* Philippi 1847, *non* Dunker 1843.

nitens Philippi, *Cyrena:* 1844, Zeitschr. für Mal., 1, p. 164; 1847, Abbild. und Besch. neuer Conch., **2**, p. 76, pl. 1, fig. 4 (China in flumine Yangtsee-king, Largilliert) 1 Cotype MCZ 152933 ex Largilliert.

nitida Mighels and Adams, *Cyclas:* 1852, BJNH, **6**, p. 352, pl. 11, figs. 1-3 (Norway, Oxford Co., Maine) Lectotype MCZ 19783, selected by Johnson, 1949, Occ. Papers on Mollusks, 1, No. 14, p. 227. *Non Cyclas nitida* Jenyns 1832. [Is *Pisidium adamsi* 'Stimpson' Prime.]

nitida Deshayes, *Cyrena:* 1854 [1855], PZS, **22**, p. 23 (Borneo, H. Cuming) measured Holotype British Museum (Nat. Hist.) 1956.12.3.34, Pl. 4, fig. 4; also Paratype BM(NH) 1956.12.3.35; 4 Paratypes MCZ 176902 from H. Cuming ex Prime coll'n.

nobilis Gould, *Cyclas:* 1855, PBSNH, **5**, p. 229 (San Pedro, California, Dr. Webb) Lectotype, here selected, MCZ 19475; this specimen was figured by Prime, 1865, Smithson. Misc. Coll. No. 145, p. 41, fig. 35.

notata Prime, *Corbicula:* 1860, PANSP, p. 271 [*nomen nudum*]; 1861, *ibid.*, p. 127 (Philippines) Holotype MCZ 135632. [Is *Corbicula cumingii* Deshayes, *teste* Prime.]

notatum Prime, *Pisidium:* 1852, BJNH, **6**, p. 365, pl. 12, figs. 20-22 (Greenwich, Washington County, New York, Ingalls) Cotypes MCZ 19833. [Is *Pisidium abditum* Haldeman, *teste* Prima.]

novaezelandiae Prime, *Pisidium:* 1862, PZS, **28**, p. 3; 1864, ALNHNY, **8**, p. 92, fig. 39 (as *P. novzealandicum*) (New Zealand, Prime and Cuming) Cotype MCZ 19935. The type in the H. Cuming coll'n at the British Museum (Nat. Hist.) could not be located in 1952. It is difficult to say which specimen is the one figured by Prime.

noveboracense Prime, *Pisidium:* 1854, ALNHNY, **6**, p. 65, pl. 1, fig. 3a-c; (as *novi emboraci*) 1859, ALNHNY, **7**, p. 100 (Washington County, New York, Ingalls [Cotypes MCZ 19838]; Herkimer County, New York, Lewis [Cotypes MCZ 19837]) [Is *Pisidium abditum* Haldeman, *teste* Prime.]

nucleous 'Moricand' Prime, *Pisidium:* 1852, BJNH, **7**, p. 388 [*nomen nudum*].

nylanderi Sterki, *Pisidium pauperculum:* 1898, Nautilus, **11**, p. 125 (Partridge Lake, in the thoroughfare between Partridge and Long Lakes, in Long Lake, Square Lake, all in Maine. . . . O. O. Nylander; White Pond, New Jersey, Pilsbry & Rhodes) Cotypes MCZ 165514 from O. O. Nylander ex Boston Soc. Nat. Hist.; 1 Cotype MCZ 20623 labeled "from the type lot."

oblonga Deshayes, *Cyrena:* see under *similis* Deshayes, *Cyrena.*

oblonga Prime, *Glauconome:* 1865, ALNHNY, **8**, p. 107, text fig. (Singapore). The type could not be located at the MCZ. Types were also said to be in the Cuming Coll'n now in the British Museum (Nat. Hist.), and the C. M. Wheatley coll'n formerly at Union College and now at the Schenectady Museum, Schenectady, New York, but the curators could not locate these types in 1956.

obscura Prime, *Cyrena:* 1860, PZS, **28**, p. 321 (New Granada [old name for Colombia]). Figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**; *Cyrena*, pl. 9, fig. 33, 2 Cotypes British Museum (Nat. Hist.) 1952.8.20.28-29. The two specimens are about the same size and it could not be determined which had been figured.

obscurum Prime, *Pisidium:* 1852, PBSNH, **4**, p. 161 (Ohio, Adams). Although Prime said the types were in the C. B. Adams coll'n, they could not be found. [Is *Pisidium abditum* Haldeman, *teste* Prime.]

obsoleta Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 343 (Uruguay, H. Cuming). Figured by Prime, 1861, J. de Conch., **9**, p. 41, pl. 2, fig. 4. It is impossible to be sure which of the types Prime figured from the specimens in either the MCZ or British Museum (Nat. Hist.). Therefore, the Cotype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 16, fig. 85 is, here selected, Lectotype British Museum (Nat. Hist.) 1956.12.3.15; also Paratype BM(NH) 1956.12.3.16. 4 Paratypes MCZ 176912 from H. Cuming ex Prime coll'n.

obtruncata Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 1, fig. 2 (La rivière de Ning-kouo-fou) 2 Paratypes MCZ 167285 ex Musée Heude; 2 Paratypes MCZ 154842 from Heude to Morelet ex E. W. Roper coll'n.

occidens 'Benson' Deshayes, *Corbicula:* 1854, British Mus. Cat. Conchifera, p. 223 (India; loco Sikkim dicto, Moredabad, Bengal, Cuming coll'n). The Cotype sent to Prime by H. Cuming labeled "Bareilly, Bengal, India" which Prime figured, 1866, ALNHNY, **8**, fig. 51, is, here selected, Lectotype MCZ 187449.

occidentale Newcomb, *Pisidium:* 1863, Proc. California Acad. Nat. Sci., **2**, p. 94 ("Ocean House," San Francisco, California, J. Rowell) 2 Cotypes MCZ 88392 from J. Rowell ex E. W. Roper coll'n.

occidentalis 'Prime' Lewis, *Cyclas:* 1856, PBSNH, **6**, p. 2. New name for *Cyclas ovalis* Prime, 1853 *non* Férussac 1807. [Prime's own correction of the name was not published until 1860, PANSP, p. 295.]

olivacea Carpenter, *Cyrena:* 1855, Cat. Mazatlan Shells in British Mus., p. 114 (Mazatlan, Mexico). Figured by Prime 1865, Smithsonian Misc. Coll. No. 145, p. 17, fig. 12. 6 Cotypes MCZ 176906 from H. Cuming ex Prime coll'n. [It cannot be determined which, if any, of this lot was the one figured.]

orbicularia 'Barrett,' Linsley, *Cyclas:* 1845, American Jour. Sci., **48**, p. 276 [*nomen nudum*] 8 Cotypes MCZ 19493 ex Prime coll'n.

ordinaria Prime, *Cyrena:* 1865, Smithsonian Misc. Coll. No. 145, p. 19, fig. 15 South America) Holotype MCZ 176880. [Is *Cyrena meridionalis* Prime, *teste* Prime.]

ovalis Prime, *Corbicula:* 1860, PZS, **28**, p. 321; 1861, J. de Conch., **9**, p. 42, pl. 12, fig. 6 (Hab.?). Holotype British Museum (Nat. Hist.) 1956.12.3.38.

ovalis Prime, *Cyclas:* 1853, PBSNH, **4**, p. 276 (Oswego and Greenwich, New York, Ingalls; Columbus, Ohio, J. G. Anthony); 1865, Smithsonian Misc. Coll. No. 145, p. 41, fig. 34. Cotypes MCZ 177105 from J. G. Anthony ex C. B. Adams coll'n. *Non Cyclas ovalis* Férussac 1807, changed to *Cyclas occidentalis* 'Prime' Lewis, 1856, PBSNH, **6**, p. 2.

ovatum 'Lewis' Prime, *Sphaerium:* 1869, AJC, **5**, p. 163 [*nomen nudum*].

oviformis Deshayes, *Cyrena:* 1854, PZS, **22**, p. 16 (Basilan, Philippine Islands; Port Essington [Australia] H. Cuming). Measured Holotype, from the latter locality and here restricted, British Museum (Nat. Hist.) 1956.12.3.36, Pl. 5, fig. 1, also Paratype BM(NH) 1956.12.3.37. Paratype MCZ 176885 also from Port Essington from H. Cuming, ex Prime coll'n.

pallida 'De Charpentier' Prime, *Cyclas:* 1860, PANSP, p. 291 [*nomen nudum*]. Listed as a synonym of *Sphaerium elevatum* Haldeman.

pallidum Gassies, *Pisidium:* 1855, Actes de la Société Linnéenne de Bordeaux, **20**, p. 43 (les fossés d'eau vive a Pourretet Saint-Marcel près d'Agen, au Sud [France]) 6 Cotypes MCZ 19730 labeled "Agen" from Gassies ex Prime coll'n.

palustre 'Lewis' Prime, *Pisidium:* 1869, AJC, **5**, p. 173 [*nomen nudum*]. Listed as a synonym of *Pisidium variable* Prime.

panamensis Prime, *Cyrena:* 1860, PANSP, p. 280. New name for *Cyrena inflata* Deshayes 1853, *non* Philippi 1851.

papyracea Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 6, fig. 35 (Les petits ruisseaux des montagnes du Koué-tché-hien) 6 Paratypes MCZ 167301 ex Musée Heude.

parasiticum 'Parreyss' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 100 [*nomen nudum*]. Listed as a synonym of *Sphaerium ferrugineum* Krauss.

parisiense Prime, *Sphaerium:* 1860, PANSP, p. 296. New name for *Cyclas transversa* 'Lev.' Grateloup 1855, *non* Say 1821 [fossil].

parva Prime, *Corbicula:* 1860, PANSP, p. 272. New name for *Cyrena ovalina* Deshayes 1857, *non* Deshayes 1854 [fossil].

parvula Prime, *Corbicula:* 1860, PANSP, p. 272 [*nomen nudum*] (India); 1861, *Ibid.*, p. 127; 1864, ALNHNY, **8**, p. 76, fig. 25. Holotype MCZ 152916.

parvula Prime, *Velorita:* 1867, ALNHNY, **8**, p. 418; 1878, Bull. MCZ, **5**, pl. 2, fig. 4, a-e (Hab.?) Holotype MCZ 119020.

parvulum Prime, *Sphaerium:* 1865, Smithsonian Misc. Coll. No. 145, p. 57, fig. 28 (Hamacao, Puerto Rico) Cotypes MCZ 73917.

patella Gould, *Cyclas:* 1850, PBSNH, **3**, p. 292; 1852, [in] Wilkes, United States Exploring Expedition, **12**, p. 426, pl. 36, fig. 527 (Oregon, at Wallawalla and Vancouver) Paratypes MCZ 19476 from Gould ex Prime coll'n.

pauperculum Sterki, *Pisidium:* 1896, Nautilus, **10**, p. 64 (Massachusetts: Winchester, E. W. Roper; New York: Mohawk, Herkimer County, Erie Canal, E. W. Roper, A. Bailey, Dr. Jas. Lewis; Hudson River, R.F.C. Stearns; Pennsylvania: Philadelphia, in different waters, M. Schick; New Jersey: White Pond, dredged, Pilsbry and Rhoads; Michigan: Ann Arbor, High Island Harbor in Lake Michigan, B. Walker [Cotypes MCZ 112571]; East Saginaw, Pine Lake, dredged, B. Walker; Grand Rapids, L. H. Streng; Wisconsin: Fox River, G. T. Marston; Minnesota: Clearwater and Mississippi Rivers, Heath Lake, H. E. Sargent.)

pellucida 'Prime' Stimpson, *Cyclas:* 1851, Shells of New England, p. 16. A new name for *Cyclas calyculata* Adams, 1843 [in] Thompson's History of Vermont, p. 168 *non* Draparnaud 1805. See under: *calyculata* Adams, *Cyclas.*

perezeii 'Villa' Prime, *Cyclas:* 1860, PANSP, p. 293 [*nomen nudum*]. Listed as a synonym of *Sphaerium lacustre* Fér.

perplexa Prime, *Corbicula:* 1865, Smithsonian Misc. Coll. No. 145, p. 75, fig. 84 (South America) Holotype MCZ 143094. [Is *Corbicula limosa* Deshayes, *teste* Prime.]

pexata Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 57, fig. 1 (Fuhchan River, China) Holotype MCZ 152931. [Is *Corbicula primeana* Morelet, *teste* Prime.]

pfeifferiana Prime, *Corbicula:* 1867, ALNHNY, **8**, p. 417 (China) Holotype MCZ 152902. [Is *Corbicula fluminea* Deshayes, *teste* Prime.]

pictum 'de Cessac' Prime, *Pisidium :* 1866, AJC, **5**, p. 170 [*nomen nudum*]. Listed as a synonym of *Pisidium henslowianum* Jenyns.

pisidiiformis Prime, *Corbicula:* 1866, ALNHNY, **8**, p. 215, fig. 42 (Siam) Holotype MCZ 176933. [Is *Corbicula lydigana* Prime, *teste* Prime.]

placida Deshayes, *Cyrena:* 1854 [1855], PZS, **22**, p. 19 (Hab.?, H. Cuming [Port Curtis, South Australia]). The measured Holotype was figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 18, fig. 106. British Museum (Nat. Hist.) 1956.12.3.17, also Paratype BM(NH) 1956.12.3.19. Paratype MCZ 176889 from H. Cuming ex Prime coll'n.

planum 'Pfeiffer' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 101 [*nomen nudum*]. Listed as a synonym of *Pisidium casternanum* Bgt.

plenum 'Lewis' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 97 [*nomen nudum*]. Listed as a synonym of *Pisidium abditum* Haldeman.

politum Sterki, *Pisidium:* 1895, Nautilus, **9**, p. 75 (small swamp nr. New Philadelphia, Ohio [Cotypes MCZ 165550 from Sterki ex E. W. Roper coll'n.]; Philadelphia, Pennsylvania, Morris Schick; Grand Rapids, Michigan, L. H. Streng; Joliet, Illinois, J. S. Ferris; Clearwater Lake and Dallas Lake, Minnesota, H. E. Sargent.)

polychromatica Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 29 (La rivière du district de Ts'ing-yang qui débouche dans le Fleuve-Bleu a Ta-t'ong, dans la partie de son cours qui draine le lac de Mé-keng) 5 Paratypes MCZ 167263 ex Musée Heude.

ponderosa Prime, *Batissa:* 1862, PBSNH, **8**, p. 273; 1866, ALNHNY, **8**, p. 231, fig. 62 (New Caledonia) Holotype MCZ 119014. [Is *Batissa fortis* Prime, *teste* Prime.]

ponderosa Prime, *Cyclas:* 1852, PBSNH, **4**, p. 157 (Lake Superior, Agassiz); 1853, *ibid.*, p. 282. Cotype MCZ 19407. [Is *Sphaerium simile*, Say *teste* Prime.]

ponderosa Prime, *Cyrena:* 1860, PANSP, p. 80; 1864, ALNHNY, **8**, p. 88, fig. 36 (Philippine Islands) Holotype MCZ 176893.

porcellanea Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 3, fig. 17 (La rivière de Ningh-kouo-fou) 2 Paratypes MCZ 167277, ex Musée Heude.

portentosa, var. *a* Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 36, fig. 31 (la rivière qui s'écoule au nord des collines du district de Kien-té, en drainant le lac de Tong-lieou) 2½ Paratypes MCZ 167281 ex Musée Heude.

portoricense Prime, *Sphaerium:* 1861, PANSP, p. 415 (Puerto Rico); 1865, Smithsonian Misc. Coll. No. 145, p. 56, fig. 57. Cotype MCZ 73916.

praeterita Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 40 (Le lac P'o-yang) 2 Paratypes MCZ 167306 ex Musée Heude.

presseplicata Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, figs. 42 (La rivière de San-ho, district de Ho-fé, avant son entrée dans le lac Teh'ao) 4½ Paratypes MCZ 167304 ex Musée Heude.

primei Morelet, *Cyrena* (*Batissa*)*:* 1862, Rev. et Mag. de Zool., (2) **14**, p. 480 (Che Fou, in Chinâ boreali). The Cotype figured by Prime 1864, ALNHNY, **8**, p. 58, fig. 2 is, here selected, Lectotype MCZ 187474.

probum, Sterki, *Pisidium:* 1923, Nautilus, **37**, p. 18 (Roaring Fork, above Aspen, Pitkin Co., Colorado, J. Henderson) Cotypes MCZ 83808 ex J. Henderson.

prolongata Prime, *Corbicula:* 1861, J. de Conch., **9**, p. 356; 1862, *Ibid.*, **10**, p. 389, pl. 14, fig. 6 (Australia) Holotype MCZ 152909.

protexta Conrad, *Cyrena:* 1895, Cat. Corbiculadae in MCZ, p. 20 [*nomen nudum*]. Listed as a synonym of *Cyrena floridana* Conrad.

proxima Prime, *Cyrena:* 1864, ALNHNY, **8**, p. 85, fig. 34 (Siam) Holotype MCZ 176879. [Is *Cyrena bernardiana* Prime, *teste* Prime.]

proximum 'Alder' Prime, *Sphaerium:* 1869, AJC, **5**, p. 163 [*nomen nudum*].

pumilum Sterki, *Pisidium subrotundum:* 1916, Annals Carnegie Museum, **10**, p. 460 (Danvers, Massachusetts, H. W. Winkley) Cotypes MCZ 34673 ex H. W. Winkley coll'n.

punctatum Sterki, *Pisidium:* 1895, Nautilus, **8**, p. 99, pl. 2, figs. 7-12 (Ohio; Tuscarawas River, Bear Run [Cotypes MCZ 112563 ex E. W. Roper coll'n]; tributary to the Mahoning River, Portage County; emptying into the Cuyahoga River [Lake Erie and St. Lawrence drainage]).

punctifera Guppy, *Cyclas:* 1867, Ann. Mag. Nat. Hist., (3) **19**, p. 160, text fig.; 1867, Proc. Sci. Assoc. Trinidad, p. 137 (Pond at St. Ann, near Port of Spain, Trinidad) 4 Paratypes MCZ 19852 from Guppy ex Prime coll'n.

purpurea Prime, *Corbicula:* 1863, Cat. Corbiculadae in Prime Coll'n, p. 4 [*nomen nudum*]; 1864, ALNHNY, **8**, p. 77, fig. 26 (Tigris River, Iraq) Paratypes MCZ 176933. The figured Holotype MCZ 176914 is from Antioch, Syria. [Is *Corbicula fluminalis* Deshayes, *teste* Prime.]

pusilla 'Parreyss' Philippi, *Cyrena:* 1847, Abbild. und Besch., neuer Conch., **2**, p. 78, pl. 1, fig. 7 (Pars superior fluminii Nili) 4 Paratypes MCZ 154143 from Parreyes ex C. B. Adams coll'n. 6 Paratypes MCZ 72899 ex Prime coll'n.

pygmea C. B. Adams, *Cyclas:* 1849, Contributions to Conchology, No. 3, p. 44 (Jamaica) Cotypes MCZ 19849 ex Prime coll'n. Cotypes MCZ 155588 ex C. B. Adams coll'n. *Non* Koch and Dunker 1837, name changed to *Pisidium jamaicense* Prime.

quercus 'Lewis' Prime, *Cyclas:* 1869, AJC, **5**, p. 163 [*nomen nudum*].

quilonensis 'Benson' Prime, *Corbicula:* see under *quilonica.*

quilonica Benson, *Corbicula:* 1860, Ann. Mag. Nat. Hist., (3) **6**, p. 260 (Quilon, Madras, India). The Cotype figured by Prime [as *quilonensis*] 1866, ALNHNY, **8**, p. 224, fig. 56, is, here selected, Lectotype MCZ 187460.

radiata 'Parreyss' Philippi, *Cyrena:* 1846, Abbild. und Besch. neuer Conch., **2**, p. 78, pl. 1, fig. **8** (Ramus albus Nili, Bahr-el-abiad, [Sudan]) 6 Paratypes MCZ 154144 from Parreyss ex C. B. Adams coll'n.

radiata Hanley, *Cyrena:* 1844, PZS, **12**, p. 159 (Central America). An Idiotype was figured by Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 13, fig. 7. 2 Cotypes MCZ 176946 from Hanley ex J. G. Anthony coll'n.

randolphi Roper, *Pisidium:* 1896, Nautilus **9**, p. 99 (Seattle, Washington) 2 Cotypes MCZ 135513 ex E. W. Roper coll'n.

rathouisiana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 4, fig. 22 (Le torrent de Ninh-kouo-hien) 2½ Paratypes MCZ 167264 ex Musée Heude.

recluzi Prime, *Cyrena:* 1860, PANSP, p. 276. New name for *Cyrena cordiformis* Recluz 1853, *non* Deshayes 1824.

regalis Prime, *Cyrena:* 1865, Smithsonian Misc. Coll. No. 145, p. 18, fig. 13 (South America ? [Muertos Island, Gulf of Uraba, Colombia]) Figured Holotype MCZ 176894.

regulare Prime, *Pisidium:* 1852, BJNH, **6**, p. 363, pl. 12, figs. 11-13 (Miami Canal, nr. Cincinnati, Ohio, Anthony) Cotypes MCZ 19832. [Is *Pisidium abditum* Haldeman, *teste* Prime.]

regularis Prime, *Corbicula:* 1860, PANSP, p. 273 (Deccan River, Australia, H. Cuming) [*nomen nudum*]; 1860, PZS, **28**, p. 321 (Deccan, India, H.

Cuming). Figured by Sowerby, [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 15, fig. 76. Holotype British Museum (Nat. Hist.) 1952.8.20.35. The latter locality is the correct one.

regularis Prime, *Cyrena:* 1861, PANSP, p. 126 (Hab. ?) [Java]); 1864, ALNHNY, **8**, p. 90, fig. 38. Holotype MCZ 176892. [Is *Cyrena eximia* Dunker, *teste* Prime.]

resartum 'Ingalls' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 94: [*nomen nudum*]. Listed as a synonym of *Pisidium abditum* Haldeman.

retusum Prime, *Pisidium:* 1860, PZS, **28**, p. 322 (Honduras) Lectotype MCZ 19848, Pl. 8, fig. 1.

rhomboidea Prime, *Corbicula:* 1860, PANSP, p. 273 [*nomen nudum*]; 1861, PANSP, p. 127 (Malacca); 1864, ALNHNY, **8**, p. 66, fig. 11, Holotype MCZ 152905.

roperi Sterki, *Pisidium:* 1898, Nautilus, **12**, p. 77 (Higginbotham's Spring near Joliet, Illinois, Ferris & Handwerk)Cotypes MCZ 112560 ex E. W. Roper coll'n. This species was also found at other localities.

rosacea Prime, *Cyclas:* 1852, PBSNH, **4**, p. 155 (Schuylkill River, Pennsylvania) Smithsonian Misc. Coll. No. 145, p. 50, fig. 48. Holotype MCZ 19523. [Is *Sphaerium securis* Prime, *teste* Prime.]

roseum Scholtz, *Pisidium:* 1843 [In] Schlesien's L. U. Wasser Moll. syst. geordnet und bescher. [Breslau], p. 140, (Schneegruben,[near Agnetendorf, Riesen Gebirge, Upper Silesia, Poland]) 5 Cotypes MCZ 19915 ex Prime coll'n.

rotunda Prime, *Corbicula:* 1860, PANSP, p. 80 (Surinam River [Dutch Guiana]) Holotype MCZ 176913, Pl. 8, fig. 3.

rotundatum Prime, *Pisidium:* 1852, PBSNH, **4**, p. 164; 1852, BJNH, **6**, p. 357, pl. 11, figs. 19-21 (Lake Superior, Agassiz) Cotypes MCZ 19844. [Is *Pisidium ventricosum* Prime, *teste* Prime.]

rubellum Prime, *Pisidium:* 1852, PBSNH, **4**, p. 163 (Lake Superior, Agassiz) The types were in the Boston Soc. Nat. Hist., but they have been lost. [Is *Pisidium abditum* Haldeman, *teste* Prime.]

rubrum 'Lewis' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 97 [*nomen nudum*]. Listed as a synonym of *Pisidium abditum* Haldeman.

rugosa 'Whittemore' Prime, *Cyclas:* 1869, AJC, **5**, p. 103 [*nomen nudum*].

ryckholtii Normand, *Cyclas:* 1844, Notice Cyclades de Valenciennes, p. 7, figs. 5-6 (les eaux tranquilles des forêts de Raismes et Vicoigne [Valenciennes, Somme, France]) 5 Cotypes MCZ 19560 ex Prime coll'n.

sabulicola 'Krynicki' Prime, *Cyclas:* 1869, AJC, **5**, p. 157 [*nomen nudum*]. Listed as a synonym of *Sphaerium rivicola* Lamarck.

salculosa 'Charpentier' Prime, *Cyclas:* 1860, PANSP, p. 291 [*nomen nudum*]. Listed as a synonym of *Sphaerium fabalis* Prime.

sancta-georgiensis Prime, *Helix:* 1853, Bermuda List, p. 55 [*nomen nudum*]. Listed as a synonym of *Polygyra apressa* Say by Verrill, 1902, Trans. Conn. Acad. Sci., **11**, p. 732, text figs. on p. 730, fig. 75,d,e,f.

sandysii Prime, *Bulimus:* 1853, Bermuda List, p. 55 [*nomen nudum*].

sayana Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 71, fig. 19 (Philippines) Holotype MCZ 135631.

scaldiana Normand, *Cyclas:* 1844, Notice Cyclades de Valenciennes, p. 5, figs. 1-2 (l'Escaut [River] à Valenciennes [Somme] France) 5 Cotypes MCZ 19554 ex Prime coll'n.

scholastica Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 5, fig. 25 (Les ruisseaux du district de Suen-tchen, dans le Ning-kouo-fou, région des montagnes) 6 Paratypes MCZ 167282 ex Musée Heude.

scutellatum Sterki, *Pisidium:* 1896, Nautilus, **10**, p. 66 (Pine Lake, 5-10 meters; Lake Michigan, off New York Point, 24 meters, also from the stomachs of white fish of Lake Michigan, B. Walker. Later . . . fresh specimens in lots from different places in Michigan) Cotypes MCZ 112552 from Hess Lake, Newayago Co., Michigan ex E. W. Roper coll'n.

securis Prime, *Cyclas:* 1852, PBSNH, **4**, p. 160; 1852, ALNHNY, **5**, p. 218, pl. 6 (Fresh Pond and in Meadows, Cambridge, Mass.) Cotypes MCZ 19516; 1853, PBSNH, **5**, p. 276. (Groton, Mass., Lewis; Vermont, Adams.)

semisulcata Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 343 (Victoria River, Australia, H. Cuming) Holotype British Museum (Nat. Hist.) 1956.12.3.19, Pl. 3, fig. 1. "The specimen figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 16, fig. 84 is not the type" (Wilkins). Paratype MCZ 143096 from Cuming ex Prime coll'n. labeled, "South America." "With regards to the *Corbicula semisulcata* Desh., with the habitat New Holland, Australia, of which I have received authentic specimens from Mr. Cuming. . . . I am convinced that the habitat is incorrect, from the fact that it has a sinus, a peculiarity confined to the Corbiculadae of this continent," (Prime, 1865, Smithson. Misc. Coll. No. 145, p. 6.)

septentrionale Prime, *Pisidium:* 1895, Cat. Corbiculadae in Prime coll'n. in MCZ, p. 61 (Umea, Lapland) Cotypes MCZ 19934 [*nomen nudum*].

septentrionale Sterki, *Pisidium fallax:* 1898, Nautilus, **12**, p. 78 (Pine and Mountain Rivers on south shore of Lake Superior, B. Walker; Clear Water River, Minn., H. E. Sargent; Little Madawaska River at New Sweden, Aroostook River, Caribou, Maine, O. O. Nylander) Cotypes MCZ 69981 from the latter locality ex N. W. Lermond coll'n.

sharperei Prime, *Cyprina:* 1861, PANSP, p. 32. New name for *Cyprina globosa* Sharpe 1850, *non* Deshayes 1849. (Fossil.)

siamensis Prime, *Cyrena:* 1861, PANSP, p. 126; 1864, ALNHNY, **8**, p. 86, fig. 35 [as *Cyrena siamica*] (Siam) Holotype MCZ 176884.

simile Prime, *Pisidium:* 1865, Smithsonian Misc. Coll. No. 145, p. 69, fig. 74 (Guadeloupe, British West Indies) Cotypes MCZ 19850.

similis Prime, *Batissa:* 1860, ALNHNY, **7**, p. 112; 1866, *Ibid.*, **8**, p. 229, fig. 60 (Nicobar Islands) Holotype MCZ 119006.

similis Deshayes, *Cyrena:* 1854, PZS, **22**, p. 16 (Manila, Philippines, H. Cuming) "No specimen available from the Cuming coll'n. Deshayes, 1854, Cat. Conchifera in B. M., p. 245 gives *C. oblonga* Deshayes, 1854, PZS, **22**, p. 341, as a synonym of *C. similis.* The Holotype of *oblonga* has exactly the measurements given for *similis* so perhaps the Cuming label was never altered" (Wilkins). The Holotype of *oblonga* Deshayes British Museum (Nat. Hist.) 1956.6.25.3 figured here as Plate 6, figure 3, is, here selected, as Lectotype for *Cyrena similis*, since it probably served as type for both species. 3 Paratypes MCZ 176899 labeled Borneo from H. Cuming ex Prime coll'n. The name *similis* was preoccupied for *Cyrena* by Gray [in] Griffith and Pidgeon, 1834, Mollusca and Radiata, arranged for Baron Cuvier, pl. 20, fig. 2, and *oblonga* by Quoy and Gaimard [in] d'Urville, 1835 Voyage du "Astrolabe" Zool., **2**, p. 517. We therefore propose the name *Cyrena wilkinsii* for this species.

simplex Prime, *Cyclas:* 1852, PBSNH, **4**, p. 159 (Illinois, Haldeman); 1853, *Ibid.*, **4**, p. 284, (Fox River, Illinois, Haldeman) Holotype MCZ 19432. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

singleyi Sterki, *Pisidium:* 1898, Nautilus, **11**, p. 112 (Drift from Guadeloupe River, Comal Co., Texas, J. A. Singley; Itzlan Creek, Guadalajara, Mexico) Cotypes MCZ 135508 from the latter locality ex E. W. Roper coll'n.

sinuatum Bourguignat, *Pisidium:* 1851, J. de Conch., **2**, p. 421; 1852, *Ibid.*, **3**, p. 49, pl. I, figs. 6-10 (Amances, près Vendeuvre-sur-Barse, Aube [France]) Idiotype MCZ 19901 from Dept. of Oise, from Bourguignat ex Prime coll'n.

sinuosa Deshayes, *Cyrena:* 1854 [1855] PZS, **22**, p. 18 (River Paningbang, Java, H. Cuming) Lectotype British Museum (Nat. Hist.) 1957.6.25.6. Pl. 4, fig. 2. The specimen figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 7, fig. 26 is not a type "unless Sowerby made it a trifle smaller [larger] and left out some of the erosion marks" (Wilkins). 2 Paratypes MCZ 176898 from H. Cuming ex Prime coll'n.

solida Normand, *Cyclas:* 1844, Notice Cyclades de Valenciennes, p. 6, figs. 3-4 (l'Escaut canalisé à Valenciennes [Somme, France]) 6 Cotypes MCZ 19556 ex Prime coll'n.

solida Philippi, *Cyrena:* 1847, Abbild. und Besch. neuer Conch., **2**, p. 78, pl. 1, fig. 9 (Nicaragua, Largilliert; California, ex auct. mercatoris Hamburgensis) 2 Cotypes MCZ 152935 ex Largilliert. "The figured type was from California, so these specimens are *C. radiata* Hanley" (J. P. E. Morrison). *Non* Dunker 1843, changed to *Cyrena nicaraguana* Prime 1869.

solidula Prime, *Batissa:* 1862, PZS, p. 3; 1864, ALNHNY, **8**, p. 82, fig. 32 (Hab.? [Java]) Holotype MCZ 176910. [Is *Batissa jayana* Lea, *teste* Prime.]

solidula Prime, *Corbicula:* 1860, PANSP, p. 273 [*nomen nudum*]; 1861, *Ibid.*, p. 127; 1864, ALNHNY, **8**, p. 81, fig. 31 (Hab. ?) Holotype MCZ 152907.

solidula Prime, *Cyclas:* 1852, PBSNH, **4**, p. 158 (Ohio, Adams, Agassiz); 1865, Smithsonian Misc. Coll. No. 145, p. 36, fig. 27 Holotype MCZ 19438. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

somersetii Prime, *Helix:* 1853, Bermuda List, p. 55 [*nomen nudum*].

soriniana Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 49 (Ruisseau des montagnes dans la province de Kouang-tong, M. l'abbé Sorin) 2 Paratypes MCZ 167280 ex Musée Heude.

sphaerica Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 7, fig. 37 (Ruisseaux du Kien-té hien sud) 2½ Paratypes MCZ 167299 ex Musée Heude; 2 Paratypes MCZ 154845 from Heude to Morelet ex E. W. Roper coll'n.

sphaerica 'Anthony' Prime, *Cyclas:* 1853, PBSNH, **4**, p. 275, text fig. (Black River, Loraine Co., Ohio) Cotypes MCZ 19524.

sphaerica Prime, *Cyrena:* 1861, J. de Conch., **9**, p. 354; *Ibid.*, **10**, p. 386, pl. 13, fig. 2 (Hab.?) Holotype MCZ 176901.

sphaericula Prime, *Batissa:* 1860, ALNHNY, **7**, p. 155 [*nomen nudum*]; 1862, PZS, **22**, p. 2 (Panimbang River, near Pardana, Java) Holotype MCZ 17691. [Is *Batissa jayana* Lea, *teste* Prime.]

sphaericum Sterki, *Pisidium:* 1912, Nautilus, **26**, p. 8 (Westbrook, Maine, A. H. Norton; Saco, Maine, H. M. Winkley [Cotypes MCZ 34662]; Lynnfield, Mass., H. M. Winkley).

splendidulum Sterki, *Pisidium:* 1898, Nautilus, **11**, p. 113 (Barren Brook, Caribou, Aroostook Co., Maine, O. O. Nylander [Cotypes MCZ 20616 ex V. Sterki]; Saco, Maine, H. W. Winkley; Old Orchard, Maine, J. B. Henderson; Grand Rapids, Michigan, L. H. Streng [Cotypes MCZ 112574]; Potomac River, Washington, D.C.)

splendidum 'Parreyss' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 102 [*nomen nudum*] "Is a *Nucula,*" (Prime).

squalida Deshayes, *Corbicula:* 1854, [1855] PZS, **22**, p. 342 (Hab.? [Philippines], H. Cuming). The Cotype figured by Prime 1866, ALNHNY, **8**, p. 218, fig. 47 is, here selected, Lectotype MCZ 187443 ex H. Cuming.

squalida Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 43 (Les lacs de Mé-keng, Tong-lieou, sur la rive droite et sur la rive gauche, le lac Teh'ao et ses dépendences) 2 Paratypes MCZ 167303 from le lac Teh'ao ex Musée Heude. Since this name is preoccupied by Deshayes, 1854, we propose the name *Corbicula clenchii.*

stabileii 'Schmidt' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 97. [*nomen nudum*]. Listed as a synonym of *Pisidium castertanum* Bourguignat.

staminea Conrad, *Cyclas:* 1834, Amer. Jour. Sci., **25**, p. 342, pl. 1, fig. 5 (small streams in South Alabama) Holotype Acad. Nat. Sci. Phila. 10186. Paratype MCZ 19434 ex Prime coll'n. The Paratype is figured by Clench and Turner, 1956, Bull. Florida State Mus., **1** (3), pl. 6, fig. 5.

steenbuchi Moller, *Cyclas:* 1842, Naturhist. Tidsskrift, **4**, p. 93 (Greenland). Figured by Prime 1878, Bull. MCZ, **5**, p. 45, pl. 2, fig. 1, a-e. 2½ Cotypes MCZ 19845 ex Prime coll'n.

sterkianum Pilsbry, *Pisidium:* 1897, PANSP, **49**, p. 291, pl. 6, figs. 1-4 ("Prado" Montevideo, Uruguay) Cotypes MCZ 78076 ex B. Walker.

stimpsoniana Prime, *Corbicula:* 1866, ALNHNY, **8**, p. 222, fig. 54 (Hab.?) Holotype MCZ 152908.

strengi Sterki, *Pisidium:* 1902, Nautilus, **15**, p. 126 (Perch Lake, Michigan, L. H. Streng and Dr. Kirkland; Reed Lake [Cotypes MCZ 154927 ex

Grand Rapids Public Mus. coll'n.] and Little Bostwick Lake, Michigan; Base Lake, Indiana, L. E. Daniels; Meyer's Lake, Ohio, V. Sterki; Little Lakes, New York, J. Lewis).

striatella Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 344 (Pondicherry [India], H. Cuming). It is doubtful if the specimen figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 11, fig. 49 is a type, since it is from Hanley. The largest Cotype, therefore, is, here selected, Lectotype, British Museum (Nat. Hist.) 1956.12.3.20, Pl. 7, fig. 3, also Paratype BM(NH) 1956.12.3.21, 5 Paratypes MCZ 152920 from H. Cuming ex Prime coll'n.

striatella 'Férussac' Prime, *Cyclas:* 1865, Smithsonian Misc. Coll. No. 145, p. 54 [*nomen nudum*]. Listed as a synonym of *Sphaerium modioliformia* Anton.

strictum Normand, *Sphaerium:* 1854, Cyclades, Dépt. du Nord., p. 3 (habits les fossés do forêts de Raismes et de Vicoigne, et ceux des marais d'Hélesmes [France]) 1 Cotype MCZ 19516 labeled "France," ex Prime coll'n.

sublobata Deshayes, *Cyrena:* 1854, PZS, **22**, p. 18 (Hab.? [New Caledonia], H. Cuming) Holotype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 10, fig. 39 [40]. British Museum (Nat. Hist.) 1956.12.3.22. "Some of the erosion pits have been left out" (Wilkins). Also Paratype BM(NH) 1956.12.3.23. 5 Paratypes MCZ 176898 (labeled Louisiade Archiapelago) from H. Cuming ex Prime coll'n.

subquadrata Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 45 (La Houai moyenne [Hong-tse]) 4 Paratypes MCZ 167262 ex Musée Heude. 2 Paratypes MCZ 154839 from Heude to Morelet ex E. W. Roper coll'n.

subradiata 'Kerr' Prime, *Corbicula:* 1861, PANSP, p. 127; 1864, ALNHNY, **8**, p. 75, fig. 23 (Agra, India) Holotype MCZ 152914.

subrotundum Sterki, *Pisidium:* 1906, Nautilus, **20**, p. 19 (New England, Anticosti Island to Michigan. Jupiter River, Anticosti Id., Albany River, Ontario, W. McInnes ed., both sent by J. F. Whiteaves; 'Vineyard," Pawtuxet, R. I., J. F. Perry; several places in Aroostook Co., Maine [Mud Lake, West Manland], O. O. Nylander, [Cotypes MCZ 20615 ex O. O. Nylander]; Pine River, Marquette Co., and Oswald Lake, Michigan, B. Walker; . . .)

subtransversum Prime, *Sphaerium:* 1860, PZS, **28**, p. 322(Tobasco, Mexico, H. Cuming) Holotype British Museum (Nat. Hist.) No. 1952.8.20.41

figured by Sowerby, [in] Reeve, 1875, Conch. Iconica, **20**, *Sphaerium*, pl. 4, fig. 38.

sulcatina Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 345 (Hab.?, H. Cuming). The Cotype figured by Prime, 1864, ALNHNY, **8**, p. 79, fig. 28 [China] is, here selected, Lectotype MCZ 187458 ex H. Cuming, since it precedes, Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 14, fig. 70.

sulcatum 'Parreyss' Prime, *Pisidium:* 1859, ALNHNY, **7**, p. 95 [*nomen nudum*]. Listed as a synonym of *Pisidium amnicum* Muller.

sulculosa 'Charpentier' Prime, *Cyclas:* 1860, PANSP, p. 300 [*nomen nudum*]. Listed as a synonym of *Sphaerium fabale* Prime.

sumatrensis 'Férussac' Prime, *Cyclas:* 1869, AJC, **5**, p. 164 [*nomen nudum*].

sumatrensis Prime, *Glauconome:* 1862, J. de Conch., **9**, p. 384, pl. 14, fig. 3 (Sumatra) Lectotype, here selected, MCZ 176956. 3 Paratypes British Museum (Nat. Hist.) 1952.8.20.38-40.

tenellum Gould, *Pisidium:* 1850, [in] Agassiz, Lake Superior, p. 245 (Fort William, Michipicotin, Ontario). In comparison to *Pisidum dubium* Say, Gould says, "They are smaller, more elevated, less sulcated, and the hinge is less robust. I had designed to apply to them the specific name *P. tenellum*, but unfortunately the specimens were mislaid before I could examine them with sufficient care to give the characters with the requisite precision." Idiotype MCZ 19828, ex Prime coll'n.

tenuis Prime, *Cyclas:* 1852, PBSNH, **4**, p. 161 (small stream in the vicinity of New Bedford, Mass.); 1853, *Ibid.*, **4**, p. 285 (Mass., Stimpson; Androscoggin River, Maine, Girard); 1865, Smithsonian Misc. Coll. No. 145, p. 47, fig. 44. "It was discovered some years since by Mr. Girard, from whom I obtained my specimens." 1 Cotype MCZ 19474, from Girard ex Prime coll'n. [Is *Sphaerium occidentale* Prime, *teste* Prime.]

tenuistrata Prime, *Corbicula:* 1860, PZS, **28**, p. 322 (Hab.? H. Cuming); 1861, J. de Conch., **9**, p. 40, pl. 2, fig. 3. The type was figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 15, fig. 80. Holotype British Museum (Nat. Hist.) 1952.8.20.34.

tenuistrata Prime, *Cyclas:* 1852, PBSNH, **4**, p. 156 (Tennessee). Prime states: (1853, PBSNH, **4**, p. 272) "Besides the specimen I possess (Alabama, Ingalls, Idiotype MCZ 19429), I have seen but one other, which was kindly sent to me for description by Prof. C. B. Adams." Holotype MCZ 177106 ex C. B. Adams coll'n. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

terveriana Dupuy, *Cyclas:* 1849, Cat. Extram. Galliae Test. No. 87; 1852, Moll. de France, p. 674, pl. 29, fig. 9. (les mares des environe d'Auch, à la Boubée et a la Hourre, Dépt. de Gers, France) 5 Cotypes MCZ 19558 ex Prime coll'n. [Specific locality not mentioned.]

tetragonum Normand, *Pisidium:* 1854, Cyclades, Dépt. du Nord, p. 5 (Habite les fossés des marais à Valenciennes, . . . aussi dans la forêt de Raismes) 3 Cotypes MCZ 19925 from Valenciennes ex Prime coll'n.

thermale Dupuy, *Pisidium:* 1849, Cat. Extram. Galliae Test. No. 238 (les eaux thermales dans les Pyrénées, à Bagneiures de Bigorre, . . . à Cauterets, près de la Raillere et de Mahourat [Dépt. de Creuse, France]) 2 Cotypes MCZ 19900 ex Prime coll'n. [Specific locality not mentioned.]

titicacense Prime, *Pisidium:* 1895, Cat. Corbiculadae in MCZ, p. 55 (Lake Titicaca, Peru) Cotypes MCZ 19853 [*nomen nudum*].

towutensis Kruimel, *Corbicula:* 1918 [in] Abendanon, Geol. en Geog. doorkruisingen van Midden-Celebes, **4**, p. 1645, pl. 27, fig. 5 (Towuti-See, Sud-Ost-Celebes, Abendanon) 2 Paratypes MCZ 53503 ex Zoological Museum, Amsterdam, Netherlands.

trapezoideum Sterki, *Pisidium:* 1896, Nautilus, **9**, p. 125 (Michigan: many places in the Upper and Lower Peninsula; Southern Minnesota; Pedan River, Canada; Philadelphia, Pa.; Adamsville, New Jersey [Cotypes MCZ 112579 ex E. W. Roper coll'n]; Comal Co., Texas).

triangularis Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 345 (Hab.?, H. Cuming). Not figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*. Lectotype, here selected, British Museum (Nat. Hist.) 1957.6.25.22, Pl. 7, fig. 2; 1 Paratype MCZ 176923, from H. Cuming ex Prime coll'n.

tribunalis Prime, *Cyrena:* 1869, AJC, **5**, p. 148 [*nomen nudum*]; 1870, ALNHNY, **9**, p. 300 ([Tecames River], Ecuador) Holotype MCZ 176888, Pl. 5, fig. 4.

trigona Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 344 (Pondicherry [India], H. Cuming). The cotype sent to Prime by Cuming, and figured, 1866, ALNHNY, **8**, p. 221, fig. 53 is, here selected, Lectotype MCZ 152922, since it precedes Hanley & Theobald, 1866, Conch. Indica, p. 60, pl. 155, fig. 7 and Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 11, fig. 43.

triquetra Deshayes, *Batissa:* 1854, PZS, **22**, p. 13 (Philippine Islands; Australia, H. Cuming). The cotype sent to Prime by Cuming from the Philippine Islands and figured, 1866, ALNHNY, **8**, p. 230, fig. 61 is, here selected, Lectotype MCZ 119013 since it precedes the type figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena*, pl. 2, fig. 3. Paratypes British Museum (Nat. Hist.) 1957.6.25.18-19.

tumida Deshayes, *Corbicula:* 1854 [1855], PZS, **22**, p. 343 (Borneo, H. Cuming). The Cotype sent to Prime by Cuming and figured, 1866, ALNHNY, **8**, p. 219, fig. 50 is, here selected, Lectotype MCZ 187444. Since it precedes the type figured by Sowerby, [in] Reeve 1875, Conch. Iconica, **20**, *Cyrena*, pl. 17, fig. 92.

tumida Prime, *Cyrena:* 1860, PANSP, p. 286. New name for *Cyrena angulata* Deshayes 1854, *non* Roemer 1835.

ultramontanum Prime, *Pisidium:* 1865, Smithsonian Misc. Coll. No. 145, p. 75, fig. 85 (Canoe Creek, California) Cotypes MCZ 19847.

uncinulata Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 2, fig. 13 (Canaux des districts de Li-yang, Yi-hing) 2 Paratypes MCZ 167290 ex Musée Heude. 1 Paratype MCZ 154847 from Heude to Morelet ex E. W. Roper coll'n.

unioniformis Prime, *Batissa:* 1860, PZS, **28**, p. 319 (Hab.? H. Cuming) Holotype British Museum (Nat. Hist.) 1952.8.20.18 figured by Sowerby, [in] Reeve 1875, Conch. Iconica, **20**, *Cyrena*, pl. 3, fig. 9. Idiotype MCZ 176909 from the Fiji Islands. [Is *Batissa violacea* Deshayes, *teste* Prime.]

variabile Prime, *Pisidium:* 1852, PBSNH, **4**, p. 163; 1852, BJNH, 6, p. 351, pl. 11, figs. 7-9 (Fresh Pond, Cambridge, Mass.) Cotypes MCZ 19805.

varians 'Carpenter' Prime, *Cyrena:* 1865, Smithsonian Misc. Coll. No. 145, p. 22 [*nomen nudum*]. Listed as a synonyn of *Cyrena mexicana* Sowerby.

variegata Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 8, fig. 44 (La Houai moyenne) 2 Paratypes MCZ 167256 ex Musée Heude.

variegata D'Orbigny, *Cyrena:* 1835, Mag. de Zool., **5**, p. 44 "Synopsis Terr. et Fluv. Moll. Amer. Mérid." (flumina repub. Uruguayensis orientalis, nec non Paranaense flumen, a provincia Buenos Ayres ad Missionum provinciam); 1846, Voyage Amer. Mérid., p. 567, pl. 82, figs. 15-17. 1 Paratype MCZ 143097 from D'Orbigny (former locality) *fide* H. Cuming ex Prime coll'n.

veatleyii C. B. Adams, *Cyclas:* 1849, Cont. to Conch., p. 44 (Jamaica) Cotype MCZ 73920 from Adams ex Prime coll'n.

venezuelensis Prime, *Cyclas:* 1860, PANSP, p. 294 [*nomen nudum*]. Listed as a synonym of *Sphaerium maculatum* Morelet. Later, Prime, 1865, Smithsonian Misc. Coll. No. 145, p. 54, listed this name under *Sphaerium modioliforme* Anton.

ventricosa Prime, *Corbicula:* 1860, PANSP, p. 274 [*nomen nudum*]; 1865, Smithsonian Misc. Coll. No. 145, p. 3. Listed as a synonym of *Corbicula convexa* Deshayes.

ventricosa Deshayes, *Cyrena:* 1854, PZS, **22**, p. 16 (Philippine Islands. Australia, H. Cuming) Holotype figured by Sowerby [in] Reeve, 1875, Conch. Iconica, **20**, *Cyrena,* pl. 9, fig. 35, British Museum (Nat. Hist.) 1956.12.3.24; also Paratype BM(NH) 1956.12.3.25; 1 Paratype MCZ 176897 (Philippines) from H. Cuming ex Prime coll'n.

ventricosum Prime, *Pisidium:* 1851, PBSNH, **4**, p. 68; 1852, BJNH, **6**, p. 355, pl. 11, figs. 16-18 (small stream running out of Fresh Pond, Cambridge, Mass.) Cotypes MCZ 19814.

venustula Prime, *Corbicula:* 1864, ALNHNY, **8**, p. 73, fig. 21 (Manilla, Philippine Islands) Holotype MCZ 135636. [Is *Corbicula cumingii* Deshayes, *teste* Prime.]

vermontana Prime, *Sphaerium:* 1861, PANSP, p. 128 (Vermont, C. B. Adams); 1865, Smithsonian Misc. Coll. No. 145, p. 42, fig. 37 (Lake Champlain and Memphremagog) Holotype MCZ 19440. [Is *Sphaerium striatinum* Lamarck, *teste* Prime.]

vicina Heude, *Corbicula:* 1880, Conch. Fleuv. Nanking, pt. 10, pl. 3, fig. 15 (La rivière de San-ho, district de Ho-fé, Lu-tcheon-fou) 4 Paratypes MCZ 167259 ex Musée Heude.

vintaense Call, *Sphaerium:* 1886, Proc. Davenport [Iowa] Acad. Nat. Sci., **5**, p. 8, fig. 4 (Lake in the Vinta Mountains, Utah, elevation 10,500 feet) Holotype MCZ 4859 ex R. E. Call coll'n.

violacea Prime, *Corbicula:* 1860, PANSP, p. 274 (Hab.?) [*nomen nudum*]; 1861, PANSP, p. 128 (Hab.?) Measured specimen, here selected, Lectotype MCZ 152899. [Is *Corbicula trigona* Deshayes, *teste* Prime.]

viridante 'Morelet' Prime, *Sphaerium:* 1865, Smithsonian Misc. Coll. No. 145, p. 57, fig. 59 (Pointe à-Pitre, Guadeloupe) Cotypes MCZ 73919. It cannot be determined which is the figured specimen.

vulgaris Prime, *Corbicula:* 1866, ALNHNY, **8**, p. 223, fig. 55 (Hab.?) Holotype MCZ 152906. [Is *Corbicula largillierti* Deshayes, *teste* Prime.]

walkeri Sterki, *Pisidium:* 1895, Nautilus, **9**, p. 75 (Kent County, Michigan, B. Walker; Utica, Michigan; Grand Rapids, Michigan, L. H. Streng; Columbia, Pa., B. Walker; Mohawk, New York, in E. W. Roper's coll'n, from E. R. Mayo [Cotypes MCZ 112551]; Clearwater and Mississippi Rivers, Minn., H. E. Sargent).

watsoni Paiva, *Pisidium:* 1866, J. de Conch., **14**, p. 340, pl. 9, fig. 3 (Madeira) Paratypes MCZ 20023 ex le Baron de Castello de Paiva.

wilkinsii Johnson, *Cyrena:* (new name for *Cyrena similis* Deshayes 1854, *non* Gray 1834) see under: *similis* Deshayes, *Cyrena.*

winkleyi Sterki, *Musculium:* 1909, Nautilus, **23**, p. 66 (Old Orchard, Maine; Danvers, Massachusetts, H. W. Winkley). Sterki selected the former place as the type locality. Cotypes MCZ 84751, ex H. W. Winkley coll'n. Specimens from the latter locality also ex H. W. Winkley are MCZ 34745.

woodiana Lea, *Cyrena:* 1834, Trans. American Phil. Soc., **5**, p. 110, pl. 18, fig. 55; 1834, Obs. Genus *Unio*, **1**, p. 222, pl. 18, fig. 55 (Canton [China], W. W. Wood). An Idiotype MCZ 152936 was figured by Prime, 1866, ALNHNY, **8**, p. 227, fig. 59.

zeteki Pilsbry, *Polymesoda:* 1931, Nautilus, **44**, p. 85, pl. 7, fig. 2-2a (near Chamá, Panama, J. Zetek) 5 Paratypes MCZ 81073 ex J. Zetek.

zonatum Prime, *Pisidium:* 1852, PBSNH, **4**, (Fresh Pond, Cambridge, Mass.); 1852, BJNH, **6**, p. 364, pl. 12, figs. 17-19. Cotypes MCZ 19831. [Is *Pisidium abditum* Haldeman, *teste* Prime.]

zonatum Prime, *Sphaerium:* 1860, PANSP, p. 301 (New Zealand) [*nomen nudum*].

PLATE 1

Portrait of Temple Prime taken from his own copy of his complete works on Mollusca. This volume is now in the library of the Museum of Comparative Zoology.

Temple Prime

PLATE 1

PLATE 2

Fig. 1. *Batissa elongata* Prime. New Caledonia. Holotype BM (NH) 1952.8.20.26 (Natural size).

Fig. 2. An original Prime label. The number in the upper left hand corner is a reference to his "Catalogue of the species of Corbiculadae in the collection of Temple Prime, now forming part of the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts" published in 1895.

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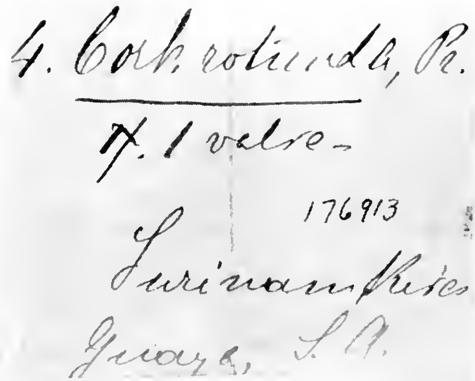

4. Cork. rotunda, Rv.

7. 1 valve

176913

Surinam River

Guiana, S. A.

2

PLATE 2

PLATE 3

Fig. 1. *Corbicula semisulcata* Deshayes. Victoria River, Australia. Holotype BM (NH) 1956.12.3.19 (2 x).

Fig. 2. *Batissa corbiculoides* Deshayes. New Guinea. Lectotype BM (NH) 1957.6.25.4 (Natural size).

Fig. 3. *Cyrena mactroides* Deshayes. Hab.? Holotype BM (NH) 1956.12.3.33 (Slightly reduced. Actual length 98 mm.).

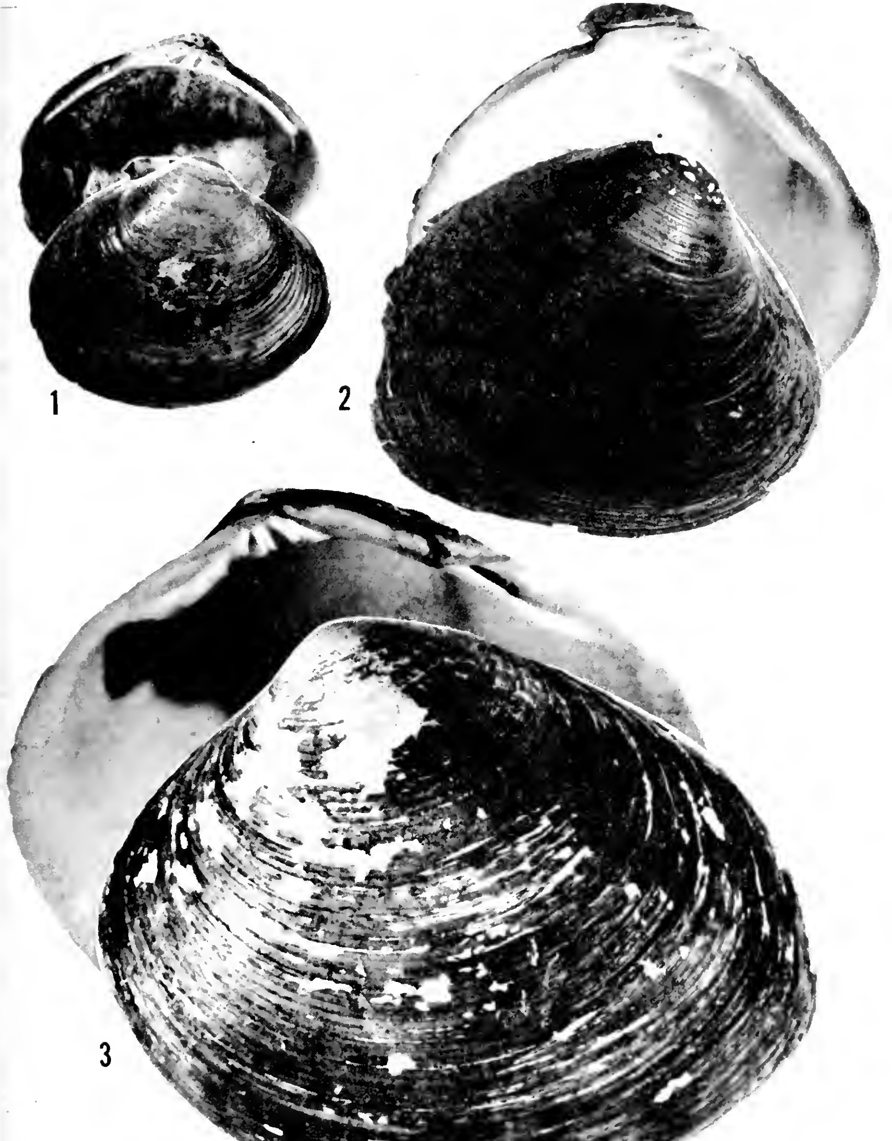

PLATE 3

PLATE 4

Fig. 1. *Cyrena brunnea* Prime. Hab.? Holotype BM (NH) 1952.8.20.32 (Natural size).

Fig. 2. *Cyrena sinuosa* Deshayes. Paningbang River, Java. Lectotype BM (NH) 1957.6.25.6 (About ¾ natural size. Actual length 71 mm.).

Fig. 3. *Cyrena lauta* Deshayes. Hab.? Lectotype BM (NH) 1956.12.3.11 (About ⅘ natural size. Actual length 68 mm.).

Fig. 4. *Cyrena nitida* Deshayes. Borneo. Holotype BM (NH) 1956.12.3.34 (About ¾ natural size. Actual length 74 mm.).

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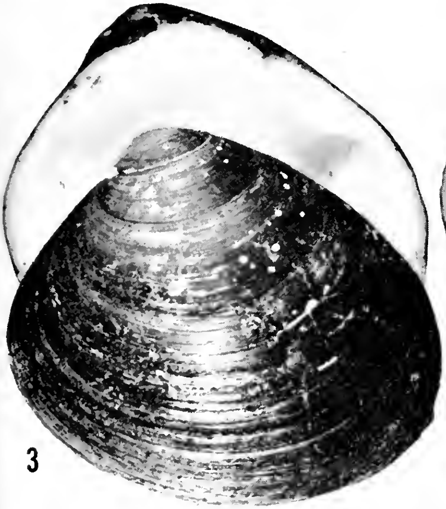

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PLATE 4

PLATE 5

Fig. 1. *Cyrena oviformis* Deshayes. Port Essington [Australia]. Holotype BM (NH) 1956.12.3.36 (Natural size).

Fig. 2. *Cyrena arctata* Deshayes. [Lake] Maracaibo [Venezuela]. Lectotype BM (NH) 1956.12.3.28 (Slightly enlarged. Actual length 30 mm.).

Fig. 3. *Cyrena affinis* Deshayes. Australia. Holotype BM (NH) 1956.12.3.26 (About ⅘ natural size. Actual length 55 mm.).

Fig. 4. *Cyrena tribunalis* Prime. [Tecames River], Ecuador. Holotype MCZ 176888 (About ⅘ natural size. Actual length 55 mm.).

Fig. 5. *Glauconome jayana* Prime. Australia. Lectotype American Museum of Natural History, New York, 31537 (About 1½ x. Actual length 65 mm.).

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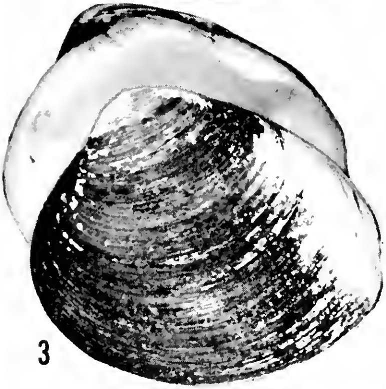

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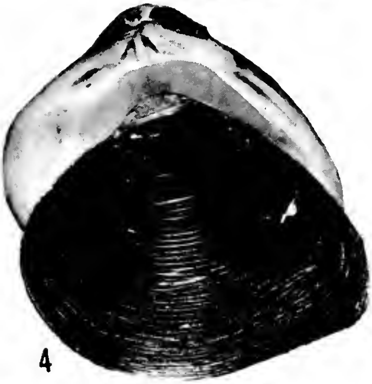

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PLATE 5

PLATE 6

Fig. 1. *Corbicula bensonii* Deshayes. Bengal. Lectotype BM (NH) 1956.12.3.31 (2 x).

Fig. 2. *Corbicula gubernatoria* Prime. Saigon, Cambodia. Holotype BM (NH) 1893.2.4.1408 (2 x).

Fig. 3. *Cyrena similis* Deshayes. Manila, Philippines. Holotype BM (NH) 1956.6.25.3 (Natural size).

Fig. 4. *Corbicula amazonica* 'Anthony' Prime. Amazon River, Brazil. Holotype MCZ 175641 ($1\frac{1}{2}$ x. Actual length, 16 mm.).

Fig. 5. *Corbicula consularis* Prime. Malacca. Holotype MCZ 152911 ($1\frac{1}{2}$ x. Actual length 17 mm.).

Fig. 6. *Cyrena chilina* Prime. Chile. Holotype MCZ 176883 ($1\frac{1}{4}$ x. Actual length 52 mm.).

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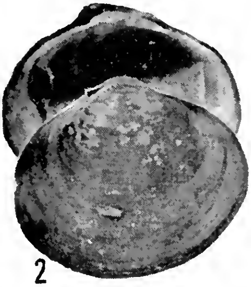

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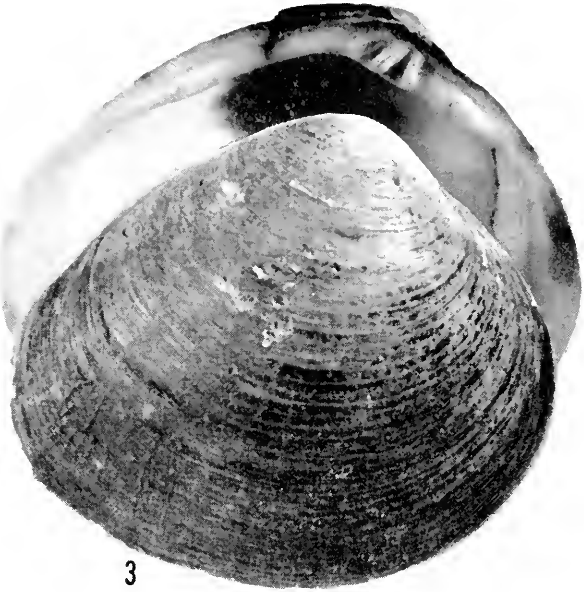

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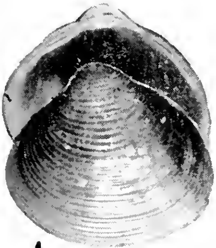

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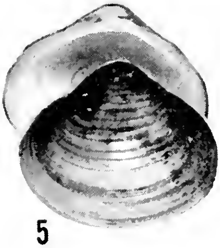

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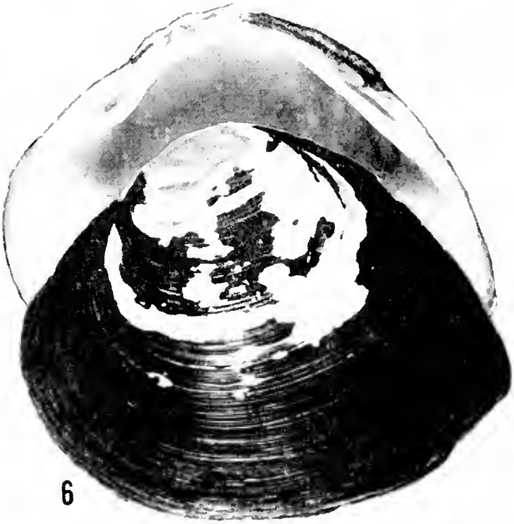

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PLATE 6

PLATE 7

Fig. 1. *Corbicula angasi* Prime. Murray River, South Australia. Lectotype MCZ 176917 (5 x).

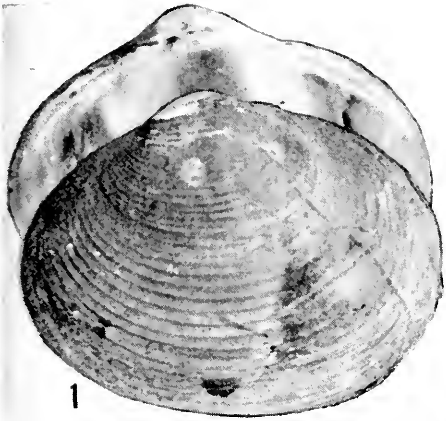
Fig. 2. *Corbicula triangularis* Deshayes. Hab. ? Lectotype BM (NH) 1957.6.25.22 (2 x).

Fig. 3. *Corbicula straitella* Deshayes. Pondicherry [India]. Lectotype BM (NH) 1956.12.3.20 (1½ x. Actual length 19 mm.).

Fig. 4. *Sphaerium costaricense* Prime. Lake Yuriria, West Costa Rica. Lectotype United States National Museum 37251 (6 x).

Fig. 5. *Cyrena flava* Prime. Hab.? Holotype BM (NH) 1952.8.20.30 (1½ x. Actual length 45 mm.).

Fig. 6. *Cyrena aequilateralis* Deshayes. Cayenne [Mazatlan, Mexico]. Lectotype BM (NH) 1956.12.3.1 (About 1⅖ x. Actual length 30 mm.).



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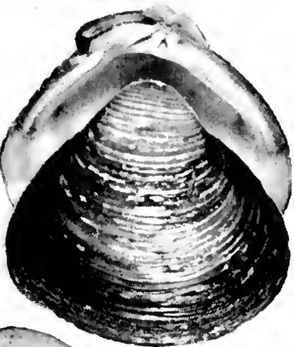

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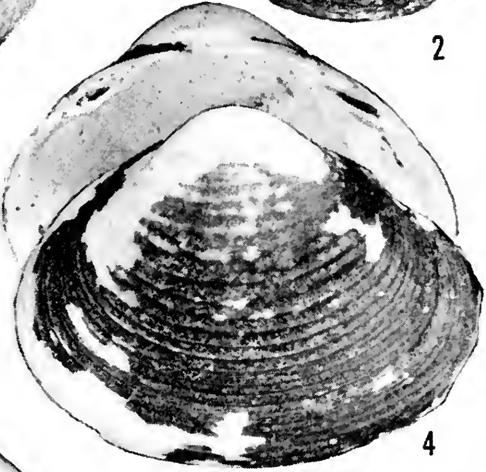

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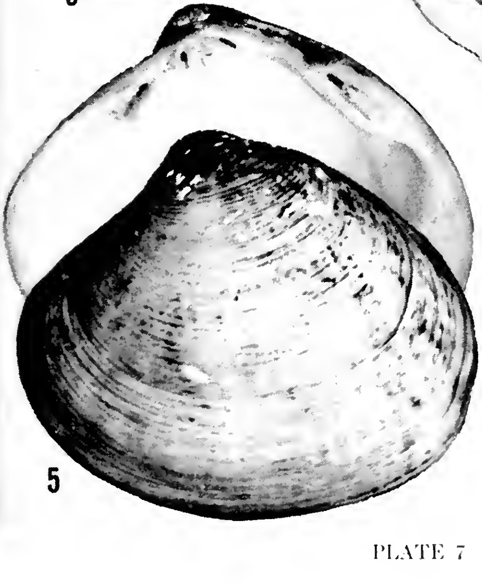

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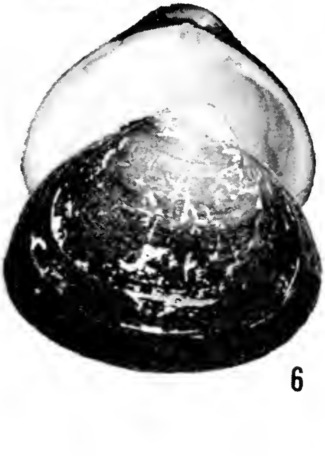

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PLATE 7

PLATE 8

Fig. 1. *Pisidium retusum* Prime. Honduras. Lectotype MCZ 19848 (13 x. Actual length 3.25 mm.).

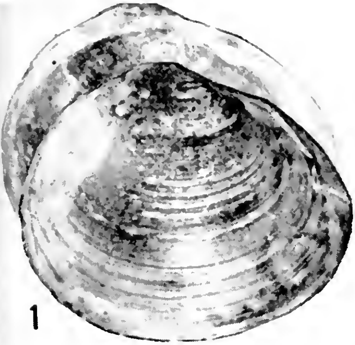
Fig. 2. *Cyrena germana* Prime. Panaco River, Tampico, Mexico. Holotype MCZ 176944 (About $1\frac{2}{5}$ x. Actual length 43 mm.).

Fig. 3. *Corbicula rotunda* Prime. Surinam River [Dutch Guiana]. Holotype MCZ 176913 (5 x).

Fig. 4. *Corbicula colonialis* Prime. Java. Holotype MCZ 135633 ($1\frac{1}{2}$ x. Actual length 23 mm.).

Fig. 5. *Batissa compressa* Prime. Borneo. Holotype BM (NH) 1952.8.20.20 ($\frac{4}{5}$ natural size. Actual length 68 mm.).

Fig. 6. *Corbicula baronialis* Prime. Port Morton [Morton Bay] Australia. Holotype MCZ 176936 ($1\frac{3}{5}$ x. Actual length 17 mm.).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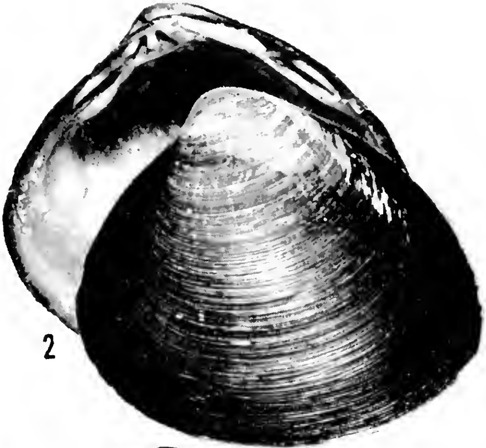
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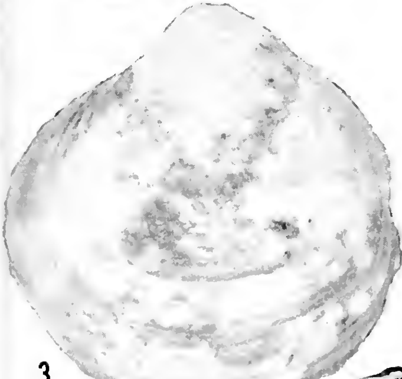
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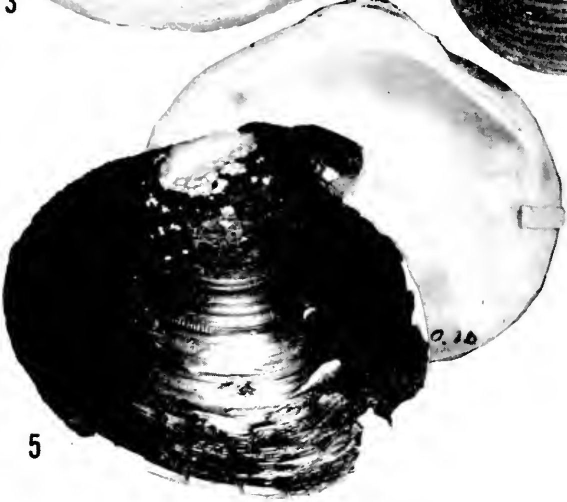

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PLATE 8

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 120, No. 5

STUDIES ON THE ANT FAUNA OF MELANESIA
V. THE TRIBE ODONTOMACHINI

By Edward O. Wilson
Biological Laboratories, Harvard University

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May, 1959

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AT HARVARD COLLEGE

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BREVIORA (octavo) 1952 — No. 109 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 38 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 22 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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STUDIES ON THE ANT FAUNA OF MELANESIA

V. THE TRIBE ODONTOMACHINI

By Edward O. Wilson
Biological Laboratories, Harvard University

With Two Plates

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No. 5 — *Studies on the Ant Fauna of Melanesia*
V. The Tribe Odontomachini[1]

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The odontomachine fauna of Melanesia is the largest and most diversified of any comparable area of the world. Eighteen species of *Odontomachus* and five of *Anochetus* are known from New Guinea alone. The evolutionary history of *Odontomachus* seems to have pursued a pattern common for the Formicidae in this part of the world: initial colonization from southeastern Asia, followed by extensive radiation on New Guinea and concurrent penetration by some of the more successful stocks into outer Melanesia and Australia.[2] Three species, *aciculatus*, *cephalotes*, and *saevissimus*, appear to have begun a secondary expansion out of New Guinea across the Moluccas; *cephalotes* has in addition entered Queensland. The Papuan species of *Anochetus* are for the most part peculiar to this region, with no clear affinities to any known Oriental or Australian stocks. It is uncertain whether they have been derived ultimately from early invaders from southeastern Asia, as is the case with most precinctive *Odontomachus* species.

The *Odontomachus saevissimus* group is the largest and most varied odontomachine species group in Melanesia. Of the eleven species found on New Guinea, two (*malignus*, *papuanus*) are closely related to or conspecific with widespread Oriental species; the remaining nine are truly precinctive. *O. malignus* is unusual among the odontomachines, and Melanesian ants generally, in its preference for littoral habitats. Possibly as a result of this exceptional ecological distribution, it is one of the most widely dispersed of all Indo-Australian ants, ranging from Sarawak in the west to Aru and Santa Cruz in the east.

New Caledonia is occupied by only two odontomachine species, *Odontomachus simillimus* and *Anochetus graeffei*. Both of these species very likely have been introduced onto the island by

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[1] Previous parts of this series were published in the Bulletin of the Museum of Comparative Zoology, 118:101-153, and 119:303-371 (1958).

[2] Wilson, E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. Evolution, in press.

man, since they are widespread in other parts of the Pacific, and on New Caledonia occur mostly in disturbed habitats.

The author wishes to express his gratitude to the following persons for making possible the examination of many of the critical type specimens: W. Forster, Zoologische Staatssammlung, Munich; D. Guiglia, Museo Civico di Storia Naturale, Genoa; G. E. J. Nixon, British Museum (Natural History): E. S. Ross, California Academy of Sciences, San Francisco; E. Taylor, Oxford University Museum.

The Genus ODONTOMACHUS Latreille

List of the Melanesian and Moluccan *Odontomachus*, Arranged in Species Groups and Including New Synonymy.

Group of *O. saccrissimus* Fr. Smith

angulatus Mayr
animosus Fr. Smith
emeryi Mann
gressitti Wilson
imperator Emery
latissimus Viehmeyer
linae Donisthorpe
malignus Fr. Smith
    = *Odontomachus tuberculatus* Roger
montanus Stitz
opaculus Viehmeyer
papuanus Emery
    = *Odontomachus papuanus* var. *concentricus* Emery
rufithorax Emery
saccrissimus Fr. Smith
    = *Odontomachus imperator* var. *tauerni* Stitz
    = *Odontomachus transversostriatus* Donisthorpe

Group of *O. simillimus* Fr. Smith

aciculatus Fr. Smith
    = *Odontomachus ruficeps cephalotes* var. *verticillatus* Stitz
aeneus Emery
cephalotes Fr. Smith

= *Odontomachus ruficeps cephalotes* var. *cruenta* Emery
= *Odontomachus ruficeps cephalotes* var. *fusca* Emery
= *Odontomachus ruficeps cephalotes* var. *ternatensis* Forel
= *Odontomachus ruficeps cephalotes* var. *tamensis* Stitz
= *Odontomachus ruficeps* subsp. *aruanus* Karawajew
= *Odontomachus ruficeps cephalotes* var. *longitudinalis* Donisthorpe

simillimus Fr. Smith (*haematoda auct. part.*)
= *Odontomachus haematodus* var. *fuscipennis* Forel

Group of *O. tyrannicus* Fr. Smith

nigriceps Fr. Smith
= *Odontomachus angulatus* subsp. *praefectus* Forel

testaceus Emery
= *Odontomachus gulosus* Emery
= *Odontomachus gulosus* var. *nubila* Emery
= *Odontomachus nigrifrons* Donisthorpe

tyrannicus Fr. Smith
= *Odontomachus tyrannicus* var. *obsolescens* Donisthorpe

Key to the ODONTOMACHUS *Species of Melanesia and the Moluccas, based on the Worker Caste*[1]

1. Extraocular furrow not demarcated posteriorly, the posterior declivity of the ridge sloping evenly and without a break into the occipital zone (see Fig. 3, upper); exceptionally slender species, with heads either entirely blackish brown or else bearing a distinct infuscation in the frontal area, thus contrasting with a predominantly yellow or light reddish brown gaster (*tyrannicus* group) 2

   Extraocular furrow demarcated posteriorly by a distinct secondary rise between it and the occipital zone (see Fig. 3, lower); stouter species, never showing the above color combination 4

2. Entire head, alitrunk, and petiole blackish brown, contrasting sharply with the gaster, which is light reddish brown

   tyrannicus Fr. Smith

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[1] Two morphological terms pertaining to the head and used in the key and subsequent descriptions need definition. The *ocular ridge* is the transverse welt bearing the eye; the two ocular ridges arise at the anterior margins of the compound eyes and converge obliquely and posteriorly toward the midline of the head (see Fig. 3). The *extraocular furrow* is the trench-like depression just posterior to the ocular ridge in species of the *sacrissimus* and *simillimus* groups; this term is not used to refer to any finer sculptural details such as rugae or striae. The standardized measurements used have already been defined in an earlier paper (Bull. Mus. Comp. Zool., 116:355, 1957).

Body of a different color 3

3. Entire head blackish brown; the remainder of the body testaceous, with local infuscations on the gaster *nigriceps* Fr. Smith

At most only the central portion of the head dark in color, and this area ranges from light brown to blackish brown; the remainder of the body testaceous, with local infuscations on the gaster *testaceus* Fr. Smith

4. Central portion (disc) of first gastric tergite striate 5

Entire first gastric tergite completely smooth or partly shagreened 7

5. Much of body surface showing pronounced metallic reflections *aeneus* Emery

Body surface completely lacking metallic reflections 6

6. Sculpturing of first gastric tergite in addition to central striae consisting chiefly of either coarse shagreening or striation; if the latter, then the individual striae are strongly curved and many run longitudinally for variable distances *cephalotes* Fr. Smith

Sculpturing of first gastric tergite consisting of striae that are at most slightly curved and always transverse *aciculatus* Fr. Smith

7. Most of the pronotum, including all of its dorsal surface exclusive of the anterior "neck," completely lacking striae, its surface either shagreened or smooth and shining 8

Most or all of the pronotum covered by striae; in occasional specimens a limited transverse strip may lack striae and be smooth and shining, but in these individuals the greater part of the pronotum is still striate 12

8. Occiput bearing distinct tumosities on either side of the median line of the head one-third the distance from the median line to the occipital corners; color uniformly yellowish orange *malignus* Fr. Smith

Occiput lacking tumosities; color other than described above 9

9. Posterior border of basal portion of petiolar spine viewed exactly from the side strongly convex, contrasting markedly with the weakly convex anterior border (Fiji Islands) *angulatus* Mayr

Posterior border of basal portion of petiolar spine viewed exactly from the side only weakly convex, appearing very similar in this respect to the anterior border (New Guinea) 10

10. Seen exactly from the side, the anterior face of the petiolar node forms an angle of 120°-130° with the dorsal node face (for a similar condition, see drawing of *papuanus* in Fig. 1) *latissimus* Viehmeyer

Seen exactly from the side, the anterior face of the petiolar node forms an angle of approximately 100° with the dorsal node face (see drawing of *imperator* in Fig. 1) 11

11. Extraocular furrows at least partly striate; head and gaster black, alitrunk and petiole red *rufithorax* Emery

Extraocular furrows completely lacking striae; body uniformly dark reddish brown *imperator* Emery

12. Striae covering almost the entire dorsum of the head 13

Striae covering at most the interocular depression and parts of the ocular ridge and extraocular furrow, and strongly developed only in the interocular depression 15

13. Entire body concolorous blackish brown (widespread over all Melanesia and the Moluccas) *simillimus* Fr. Smith

Head, alitrunk, and petiole dull dark reddish yellow; gaster dark reddish brown (New Guinea only) 14

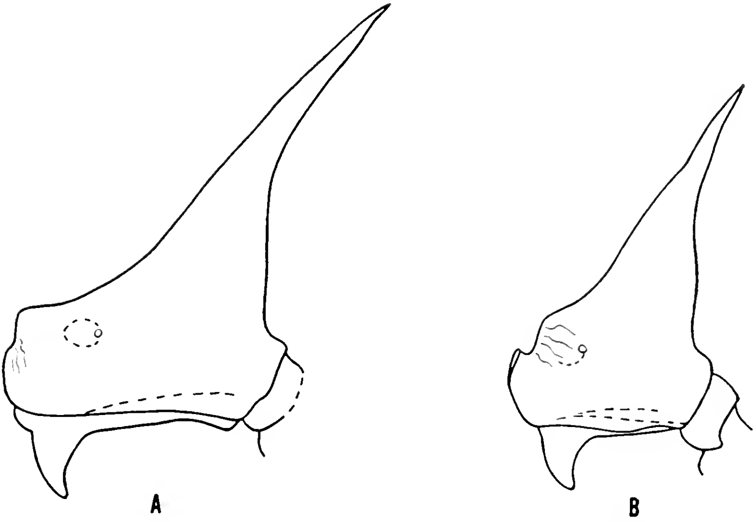


Fig. 1. Side views of petioles of worker syntypes of *Odontomachus imperator* Emery (*A*) and *O. papuanus* Emery (*B*); based on specimens in the Emery Collection, Genoa.

14. Mesepisternum completely smooth and shining except for the anterior sixth of its length, which is vertically striate; smaller species, HW of unique type 2.08 mm (Manokwari, Neth. New Guinea) *animosus* Fr. Smith

Mesepisternum completely covered by dense vertical striae; larger species, HW of syntype examined 2.64 mm (Sepik Watershed, N-E. New Guinea) *montanus* Stitz

15. Extraocular furrows partly striate, although occasionally the striae are very feeble and limited to the inner one-fifth of the furrows 16

Extraocular furrows completely smooth and shining 18

16. Head, alitrunk, and petiole light reddish brown; gaster medium reddish brown . . . *linae* Donisthorpe (*partim*)

Body concolorous dark to blackish brown 17

17. Striae limited to upper fifth of extraocular furrows; anterior and anterodorsal faces of petiolar node grading into one another through an even curve without any sign of an intervening angle *papuanus* Emery (*partim*)

Striae covering approximately the upper half of the extraocular furrow; anterior and anterodorsal petiolar node faces meeting in a distinct angle of about 100° *opaculus* Viehmeyer

18. Anterodorsal surface of petiole, exclusive of the spine, transversely striate; color of head and alitrunk yellowish to light reddish brown, with the possible exception of the mesonotum, which is occasionally (in *gressitti*) medium to dark reddish brown 19

Either the anterodorsal surface of the petiole is completely smooth, or the color of the head and alitrunk is dark reddish brown, or both 20

19. Head, alitrunk, and petiole uniformly light reddish brown; larger species, HW of two specimens examined 2.52-2.54 mm *linae* Donisthorpe (*partim*)

Either head, mesonotum, and gaster dark reddish brown, contrasting with the yellowish brown alitrunk (exclusive of mesonotum) and petiole (Central Highlands of New Guinea), or body concolorous yellowish brown, the mesonotum a shade darker than the rest (Guadalcanal); smaller species, HW of two type specimens 2.16 mm *gressitti* Wilson

20. Posterior face of petiole, extending from the tip of the spine to the posterior peduncle, evenly concave when viewed from the side *saevissimus* Fr. Smith (*partim*)

Lower half of posterior face of petiole appearing distinctly convex when viewed from the side 21

21. Mesepisternum almost completely smooth; body and antennae dark reddish brown, legs yellowish brown (New Guinea) *papuanus* Emery

Mesepisternum completely striate; coloration not as above 22

22. Head and gaster dark reddish brown; alitrunk and petiole light yellowish red, with the mesonotum lightly infuscated (Solomon Islands) *emeryi* Mann

Gaster medium reddish brown, only slightly darker than the alitrunk (head color unknown) (New Ireland variant) *saevissimus* Fr. Smith (*partim*)

ODONTOMACHUS ACICULATUS Fr. Smith
(Fig. 4, no. 12)

Odontomachus aciculatus Fr. Smith, 1863, J. Proc. Linn. Soc. London, Zool., 7:19, worker. Type locality: Misol. Mayr, 1876, J. Mus. Godeff. Hamburg, 12:86; worker. Donisthorpe, 1940, Entomologist, 70:109; worker.
Odontomachus cephalotes var. *aciculatus*, Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, 4:428, worker, dist.
Odontomachus ruficeps var. *aciculata*, Emery, 1911, Gen. Ins., 118:115.
Odontomachus ruficeps cephalotes var. *verticillatus* Stitz, 1912, Sitzber. Ges. Nat. Freunde Berlin, 9:501-503, figs. 5, 6, worker. Type locality: New Guinea (*ex* Kaiserin-Augustafluss Exped.). NEW SYNONYMY. (Syntype examined — MCZ.)

Material examined. NEW GUINEA: *verticillatus* syntype.

ODONTOMACHUS AENEUS Emery

Odontomachus aeneus Emery, 1910, Nova Guinea, 5(4) Zool.: 534, worker. Type locality: Wendèsi, Neth. New Guinea.

Known from only the unique type worker. This species should be easily distinguished from all other Melanesian *Odontomachus* through its remarkable metallic coloration: "La tête est bronzée avec des reflets violacés, le corselet est de la même teinte, mais plus foncée, le pétiole et le gastre noir-bronze, les pattes sont brun foncé."

ODONTOMACHUS ANGULATUS Mayr

Odontomachus angulatus Mayr, 1866, Sitzber. Akad. Wiss. Wien, 53:500, fig. 10, worker. Type locality: Ovalau, Fiji Islands. Mann, 1921, Bull. Mus. Comp. Zool., 64:427, fig. 11, queen, ecology, distribution.

Material examined. FIJI ISLANDS: Nadarivatu, Viti Levu (W. M. Mann); Vunidawa, Viti Levu (N. L. H. Krauss); Andubangda, 300-500 m., Ovalau (E. C. Zimmerman).

ODONTOMACHUS ANIMOSUS Fr. Smith
(Fig. 4, no. 3)

Odontomachus animosus Fr. Smith, 1860, J. Proc. Linn. Soc. London, Zool., 4 (suppl.): 102-103, worker. Type locality: Dory (Manokwari), Neth. New Guinea. Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10:461. (Holotype examined — Oxford University Museum.)

Through the courtesy of Mr. Ernest Taylor of Oxford University I have recently had the opportunity to study the unique type of this most enigmatic of *Odontomachus* species. *O. animosus* proves to be a very distinct species belonging to the *saevissimus* group. In petiole shape and general habitus it is convergent (or annectant) to the species of the *simillimus* group, in particular *simillimus* itself, and may in fact represent a true phylogenetic link between the two groups. Unfortunately, I have been unable to find any more material of this species in recent collections. Below is a brief redescription of the holotype.

Holotype worker. HW 2.08 mm, HL 3.08 mm, SL 3.09 mm, PW 1.19 mm, distance from the basal line of the petiolar node to the tip of the petiolar spine 1.34 mm, distance from the posterior margin of the petiolar spiracle to the tip of the spine 1.21 mm. Shape of petiole similar to that of *O. papuanus* Emery, differing in that the anterodorsal face of the node seen from the side forms an almost perfectly straight line from the spine itself to the anterior collar, thus lacking the rounded angle that separates the anterior and dorsal faces in other members of the *saevissimus* group (*animosus* shares this character with some species of the *simillimus* and *tyrannicus* groups; see Fig. 4). Entire dorsal surface of head striate, the striae becoming feeble in the occipital region. Ocular ridge striate posterior to the eye, smooth anterior to it. Sides of head ventral to the inner border of the eye, including the ventral half of the extraocular furrow, smooth and shining. Pronotum, mesonotum, and propodeum covered by dense transverse striae. Anepisternum vertically striate; katepisternum almost completely smooth and shining. Anterior face of petiolar node very faintly and transversely striate; remainder of node smooth and shining. Gaster entirely smooth and shining. Coloration uniformly yellowish brown (but the specimen is undoubtedly faded; Frederick Smith described it in 1860 as "ferruginous").

ODONTOMACHUS CEPHALOTES Fr. Smith
(Fig. 4, no. 11)

Odontomachus cephalotes Fr. Smith, 1863, J. Proc. Linn. Soc. London, Zool., 7:19, worker. Type locality: Ceram. Crawley, 1922, Ann. Mag. Nat. Hist., (9)9:441, fig. 6; redescription of holotype.

Odontomachus ruficeps subsp. *cephalotes*, Emery, 1911, Nova Guinea, 9(2) Zool.: 250-251, diagnosis, variation, distribution.

Odontomachus ruficeps cephalotes var. *cruenta* Emery, 1911, *ibid.*, p. 251, worker, queen. Original localities: Merauke and Etna Bay, Neth. New Guinea. NEW SYNONYMY.

Odontomachus ruficeps cephalotes var. *fusca* Emery, 1911, *ibid.*, p. 251, worker. Type locality: Merauke, Neth. New Guinea. NEW SYNONYMY.

Odontomachus ruficeps subsp. *cephalotes*, Forel, 1911, Sitzber. Bayer. Akad. Wiss., (1911), p. 252, worker, variation.

Odontomachus ruficeps cephalotes var. *ternatensis* Forel, 1911, *ibid.*, p. 252, worker. Type locality: Ternate. NEW SYNONYMY.

Odontomachus ruficeps cephalotes var. *tamensis* Stitz, 1912, Sitzber. Ges. Nat. Freunde Berlin, 9:503, fig. 7, worker. Type locality: Tami Islands, N-E. New Guinea. NEW SYNONYMY.

Odontomachus ruficeps subsp. *aruanus* Karawajew, 1925, Konowia, 4:295, fig. 14, worker. Type locality: Wammar Island, Aru Archipelago. NEW SYNONYMY.

Odontomachus ruficeps cephalotes var. *longitudinalis* Donisthorpe, 1940, Entomologist, 73:108-109, fig. 1, worker. Type locality: Camp Nok, Waigeo, 800 m. NEW SYNONYMY. (Syntype examined — MCZ.)

Material examined. WAIGEO: Camp Nok: (*longitudinalis* Donisthorpe syntype). NETH. NEW GUINEA: Merauke (MCZ). PAPUA: Karema, Brown R. (Wilson, nos. 545. 553, 579); Bisianumu, 500 m. (Wilson, no. 615). N-E. NEW GUINEA: Sepalakambang, 1920 m., Saruwaged Ra. (E. J. Ford). AUSTRALIA: several series from various localities in North Queensland (MCZ).

Taxonomic note. This species shows considerable variation in several external characters. The sculpturing of the first gastric tergite usually consists of whorled, coarse striae, but in a minority of series from Queensland the striae are replaced by heavy shagreening. The pattern of pronotal sculpturing is also very variable. The petiolar node varies in shape from a form resembling that of *O. papuanus* to one resembling that of *O. simillimus*. The body color is typically blackish brown but is occasionally replaced locally by a lighter reddish brown.

Ecological notes. At Karema a colony was found nesting in a small rotting log on the floor of primary lowland rain forest. Workers from other colonies were found at the same locality foraging in leaf litter during the day.

ODONTOMACHUS EMERYI Mann, n. status
(Fig. 4, no. 5)

Odontomachus imperator subsp. *emeryi* Mann, 1919, Bull. Mus. Comp. Zool., 63:303, fig. 12, worker, queen, male. Type locality: Maliali, Florida, Solomon Islands. (Syntypes examined — MCZ.)

Material examined. SOLOMON ISLANDS: Maliali, Florida (syntypes); Fulakora, Santa Isabel (syntypes); Torokina R., Bougainville (B. D. Valentine); Kokure, 690 m., Bougainville (E. J. Ford); Boku, Bougainville (Ford).

Taxonomic notes. This species is very similar to the widespread *O. saevissimus* of western Melanesia and in fact may be no more than a geographic variant of it. *Emeryi* differs in its distinctive coloration and convex posterior border of petiolar node. A single worker of *saevissimus* from New Ireland appears to be both geographically and morphologically intermediate. It has a petiolar node like that of *emeryi*, but the body coloration is typical of *saevissimus*. Unfortunately, the head of this interesting specimen is missing.

Ecological notes. Mann made the following observations on the type colonies: "They were in dense forest; the nests were in the ground among the roots of trees and contained large numbers of workers. The workers are less active than *haematoda* [= *simillimus*] and not as aggressive." E. J. Ford, Jr., collected winged queens from a nest at Kokure on June 12, 1956.

ODONTOMACHUS GRESSITTI Wilson, n. sp.
(Fig. 4, no. 8)

Diagnosis. A small, slender species belonging to the *saevissimus* group and most closely resembling *papuanus* Emery. It differs from *papuanus* by its distinctive coloration, presence of transverse striae on the anterodorsal face of the petiolar node, and more slender petiolar spine. It bears a superficial resemblance to *linae* Donisthorpe but differs markedly from that species in its smaller size, distinctive coloration, and "*papuanus*-type" petiolar node.

Holotype worker. HW 2.16 mm, HL 3.48 mm, SL 3.43 mm, PW 1.35 mm, length of petiolar node 1.00 mm, distance from posterior margin of petiolar spiracle to tip of petiolar spine 1.42 mm.

Cephalic striae entirely limited to frontal lobes and interocular depression; remainder of head entirely smooth and shining. Entire alitrunk transversely striate, the striae becoming very weak in the center of the pronotum and even failing entirely in a limited area just 1.32 mm posterior to the anterior margin of the pronotal "neck." Entire anterodorsal and lateral faces of petiolar node, exclusive of the spine and most of its supporting cone, transversely striate. Gaster completely smooth and shining.

Head and gaster dark reddish brown. Pronotal "neck," posterior margin of pronotum, entire mesonotum, and propodeal dorsum posterior to the level of the propodeal spiracles medium reddish brown. All of these areas contrast with the remainder of the alitrunk and the petiole, which are a much lighter shade of brownish yellow.

Type locality. Nondugl, 1750 m., Ahl Valley, N-E. New Guinea (J. L. Gressitt). The single worker from this locality has been returned to Dr. Gressitt for deposit in the B. P. Bishop Museum, Honolulu.

Paratype worker. A single worker from Gold Ridge-to-Suta (Jonapau), 1100 m., Guadalcanal (Gressitt) has been determined as this species. It differs from the holotype in its overall much lighter coloration (body light brownish yellow, the pronotal neck and mesonotum a shade darker than the rest), slightly thicker petiolar spine, and presence of numerous oblique hairs on the spine and cone (standing hairs completely lacking in holotype). Further collecting may show the Solomons form to rank as a distinct species. The single Solomons specimen has been deposited in the Museum of Comparative Zoology.

ODONTOMACHUS IMPERATOR Emery
(Fig. 1A)

Odontomachus imperator Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova. (2)5:429, pl. 1, fig. 1, worker. Type locality: Andai, near Manokwari, Neth. New Guinea. (Lectotype examined — Emery Coll.)

Through the courtesy of Dott. Delfa Guiglia, I have been able to examine a syntype worker, which, with her permission, is herein designated as lectotype.

Lectotype worker. HW 2.59 mm, HL 4.20 mm, SL 4.20 mm, PW 1.55 mm, petiolar node length 1.13 mm, distance from the level of the basal line of the petiolar node to the tip of the petiolar spine 1.55 mm. Striae of the head limited to the transverse depression just anterior to the ocular ridge, and not extending onto the ridge itself; remainder of head smooth and shining. Anterior "neck" of pronotum transversely striate, remainder of pronotum smooth and shining. Entire mesonotal and propodeal surfaces transversely striate, the mesonotal striae much more feeble than those on the propodeum, becoming obsolescent anteriorly and medially. Anepisternum striate; katepisternum striate only along its dorsal margin, the remainder of its surface smooth and shining. Petiolar node and gaster entirely smooth and shining. Body uniformly dark reddish brown, appendages medium reddish brown.

ODONTOMACHUS LATISSIMUS Viehmeyer

Odontomachus latissimus Viehmeyer, 1913, Arch. Naturges., 79A(12):31, fig. 5, worker. Type locality: Sattelberg, N.-E. New Guinea.

Known from type material only.

ODONTOMACHUS LINAE Donisthorpe, n. status
(Fig. 4, no. 6)

Odontomachus saevissimus var. *linae* Donisthorpe, 1940, Entomologist, 73:107, worker, queen. Type locality: Mt. Lina, 1200 m., Cyclops Mts., Neth. New Guinea. (Syntype examined — MCZ.)

Material examined. NETH. NEW GUINEA: Mt. Lina (syntype). N-E. NEW GUINEA: Kumur, 1000 m., upper Jimmi Valley (J. L. Gressitt).

Taxonomic notes. The only observable difference between this species and *opaculus* Viehmeyer is in the color characters cited in couplet 16 of the key. But the two forms have widely overlapping ranges and occur at similar elevations. The wisest course for the present would seem to be to treat them tentatively as distinct biological species.

The Kumur specimen differs from the syntype cited in its weaker body sculpturing. Striae are very feeble in the center of the pronotum and completely lacking from the extraocular furrows and mesopleural centers.

ODONTOMACHUS MALIGNUS Fr. Smith
(Figs. 3; 4, no. 9)

Odontomachus malignus Fr. Smith, 1859, J. Proc. Linn. Soc. London, Zool., 3:144, worker. Type locality: Aru. Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, 4:429; distribution. Kutter, 1934, Mitt. Schweiz. Ent. Ges., 15:472. Donisthorpe, 1940, Entomologist, 73:107, redescription of holotype.

Odontomachus tuberculatus Roger, 1861, Berl. Ent. Zeitschr., 5:28-30, worker. Type locality: unknown. NEW SYNONYMY (provisional). Donisthorpe, 1940, Entomologist, 73:107, worker.

Odontomachus malignus subsp. *tuberculatus*, Mann, 1919, Bull. Mus. Comp. Zool., 63:305-306, fig. 13, worker.

Material examined. SANTA CRUZ: Graciosa Bay (W. M. Mann). Emery (1887) records this species from Sarawak, Celebes, and New Guinea (Sorong), while Kutter (1934) records it from Jacquinot Bay, on the southern coast of New Britain.

Taxonomic note. Roger's *tuberculatus* is probably conspecific with *malignus*. The only difference that can be gleaned from the original description is in the orientation of the mesonotal striation, which is said to be horizontal in *malignus* and longitudinal in *tuberculatus* (Mann, 1919). However, the distinction is doubtful. In Mann's single nest series of "*tuberculatus*" from Santa Cruz the orientation of mesonotal striae actually varies widely, from longitudinal to oblique.

Ecological notes. This species, which ranges from Borneo to the Santa Cruz Islands, appears to be a normal inhabitant of the littoral zone. Mann says of his Solomons collections, "I found this species only once, at Graciosa Bay, where workers were moving in and out of the crevices of a large block of coral on the beach. Mr. Harry Hall, who brought me specimens from Simoli on South Malaita, states that he found it nesting there under the same conditions." According to Kutter (1934), H. Hediger found workers of *malignus* at Jacquinot Bay, New Britain, foraging 100 meters out in the intertidal zone during low tide! These individuals were running among the coral rocks and far from the normal foraging ranges of other ant species.

ODONTOMACHUS MONTANUS Stitz, n. status
(Fig. 4, no. 7)

Odontomachus imperator var. *montanus* Stitz, 1923, Sitzber. Ges. Nat. Freunde Berlin, p. 116, worker. Type locality: Lordberg, middle Sepik region, N-E. New Guinea. (Syntype examined — MCZ.)

Known from type material only.

ODONTOMACHUS NIGRICEPS Fr. Smith

Odontomachus nigriceps Fr. Smith, 1860, J. Proc. Linn. Soc. London, Zool., 4 (suppl.): 103, pl. 1, fig. 9 (this figure is also referred to by Smith as *O. saevissimus*). Type locality: Dory (Manokwari), Neth. New Guinea. Mayr, 1876, J. Mus. Godeff. Hamburg, 12:85, distribution. Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10:461, worker.

Odontomachus angulatus subsp. *praefectus* Forel, 1911, Sitzber. Akad. Wiss. Munich, p. 251, worker. Type locality: New Guinea. (Holotype examiued — Zoologische Staatssammlung, Munich.) NEW SYNONYMY.

Material examined. PAPUA: Kokoda, 350 m. (L. E. Cheesman); Dobodura (P. J. Darlington).

Taxonomic notes. This species is closely related to *testacea* Emery, from which it can be distinguished by its distinctive coloration and much denser body pilosity. The two species occur together at Dobodura.

The holotype of *O. angulatus* subsp. *praefectus* Forel is a typical worker of *nigriceps.* It has relatively convex anterior and posterior nodal borders, resembling the Kokoda specimen rather more closely than workers from Dobodura. There is no evident reason for Forel's decision to associate it with *angulatus* Mayr, a widely dissimilar member of the *saevissimus* group.

ODONTOMACHUS OPACULUS Viehmeyer, n. status

Odontomachus imperator subsp. *opaculus* Viehmeyer, 1912, Abh. Zool. Anthrop. Mus. Dresden, 14:6, fig. 6, worker. Type locality: Torricelli Mts., 640 m., N.-E. New Guinea. (Syntype examined — MCZ.)

Material examined. NETH. NEW GUINEA: Wendèsi-Majosi (S. Issiki). N.-E. NEW GUINEA: Torricelli Mts. (syntype).

Taxonomic note. A single worker examined from Wendèsi-Majosi differs from the *opaculus* syntype in its larger size (HW 2.77 mm vs. 2.32 mm), different orientation of pronotal striae (concentric vs. straight-transverse), and feebler striation within the extraocular furrow.

ODONTOMACHUS PAPUANUS Emery, n. status
(Fig. 1B)

Odontomachus rixosus var. *papuanus* Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, (2)5:429, worker. Type locality: Aru. (Syntype examined — Emery Coll.).

Odontomachus papuanus var. *concentricus* Emery, 1897, *op. cit.*, 38:557, worker. Type locality: Moroka, Papua. NEW SYNONYMY (provisional).

Material examined. NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: lower Busu River (Wilson, nos. 901, 923); Bulolo, 730 m. (E. J. Ford); Sattelberg-Maroruo, 800-900 m. (Wilson, no. 724); Maroruo, 900 m. (Wilson, no. 729); Nganduo, 1000 m. (Wilson, no. 733); Ebabaang, 1300-1400 m. (Wilson, no. 828); Wamuki, 800 m. (Wilson, no. 850). ARU: syntype worker.

Taxonomic notes. O. papuanus is closely related to the Oriental species *virosus* Fr. Smith, differing chiefly in its longer petiolar spine and more rounded apical mandibular teeth. Its recognition here as a distinct species is a provisional measure only. Significant geographic variation occurs within the range of *papuanus* on New Guinea. Workers from the lowlands (Maffin Bay, lower Busu River) are smaller and lighter in color than those from the mountains of the Huon Peninsula. The syntype from Aru is light in color but as large as the montane New Guinea workers.

Ecological notes. This species has been collected in both primary lowland rain forest and primary and secondary mid-mountain rain forest on New Guinea. Workers were found foraging singly on the ground during both the day and night. At the Busu River, a nest was found on a steep forested hillside. It consisted of a single shaft, five centimeters wide, extending horizontally into the soil beneath a tree root for a distance of approximately 45 centimeters. The colony was a small one, containing a single queen and about twenty workers, and may have been incipient.

ODONTOMACHUS RUFITHORAX Emery, n. status

Odontomachus imperator subsp. *rufithorax* Emery, 1910, Nova Guinea, 5(4)Zool.: 534, worker. Original localities: "Tawarin" and "Timena," Neth. New Guinea.

Known from type material only.

ODONTOMACHUS SAEVISSIMUS Fr. Smith
(Fig. 4, no. 4)

Odontomachus saevissimus Fr. Smith, 1858, Cat. Hym. Brit. Mus., 6:80, pl. 5, fig. 10, worker. Type locality: Ceram. Fr. Smith, 1860, J. Proc.

Linn. Soc. London, Zool., 5(suppl.): pl. 1, fig. 9, queen. Mayr, 1867, Tijdschr. Ent., 10:47, worker, distribution. Karawajew, 1925, Konowia, 4:290-292, fig. 12, worker, queen, male. (Holotype examined — BMNH.)

Odontomachus imperator var. *tauerni* Stitz, 1923, Sitzber. Ges. Nat. Freunde Berlin, p. 116, worker. Type locality: Ceram. (Syntype examined — MCZ.) NEW SYNONYMY.

Odontomachus transverso-striatus Donisthorpe, 1941, Trans. Roy. Ent. Soc. London, 91:53, worker. Type locality: Mt. Baduri, 300 m., Japen I., Neth. New Guinea. (Holotype examined — BMNH.) NEW SYNONYMY.

Material examined. MOLUCCAS: Ceram (holotype; syntype of *tauerni*). NETH. NEW GUINEA: Japen I. (*transversostriatus* holotype); Doormanpad (W. C. van Heurn). N-E. NEW GUINEA: Korop, 1300 m., Upper Jimmi Valley (J. L. Gressitt). NEW BRITAIN: St. Paul's, 350 m., Bainings Mts. (Gressitt). NEW IRELAND: "Camp Bishop," 12 km. up Kait River, 240 m. (E. J. Ford) (tentative determination; see below).

Taxonomic notes. This is one of the most widespread of the Papuan-based *Odontomachus*. Mayr (1867) records it from Celebes, while as noted elsewhere the form *emeryi* Mann may be nothing more than a geographic variant from the Solomon Islands. Notable geographic variation is shown in the sculpturing of the mesepisternum. Workers from New Guinea have katepisterna completely striate and the anepisterna smooth except for feeble striation along the dorsal and posterior margins. A single worker examined from the offshore island of Japen has essentially similar sculpturing, except that on the katepisternum striation is confined to the posterior margin. Workers from more peripheral localities both to the east and west (Ceram, New Britain, New Ireland) have completely striate mesepisterna. Thus geographic variation in this character appears to exhibit a concentric "central-peripheral" pattern. A single headless worker from New Ireland differs from other material in having heavier alitruncal sculpturing and a convex posterior border of petiolar node, in these characters approaching the Solomons form *emeryi*. Future collecting may show that *saevissimus* and *emeryi* are connected by other morphologically intermediate populations and hence must be considered conspecific. If so, then alitruncal sculpturing and coloration clearly show discordant patterns of geographic variation.

ODONTOMACHUS SIMILLIMUS Fr. Smith
(Fig. 4, no. 10)

Odontomachus simillimus Fr. Smith, 1858, Cat. Hym. Brit. Mus., 6:80, pl. 5, figs. 8, 9, queen. Original localities: Fiji Islands, Ceylon.

Odontomachus haematodus, div. auct. (*nec Formica haematoda* Linné, 1758, Syst. Nat., 10th ed., 1:582).

Odontomachus haematodus var. *fuscipennis* Forel, 1913, Zool. Jahrb. Syst., 36:19, worker, queen, male. Original localities: Peradeniya, Ceylon; Bahsoemboe, Sumatra. NEW SYNONYMY.

Material examined. MOLUCCAS: Amboina (H. Smith). NETH. NEW GUINEA: Doormanpad (W. C. van Heurn); Biak I. (G. E. Bohart). N-E. NEW GUINEA: Goroka, 1600 m., Asaro Valley, Central Highlands (J. J. H. Szent-Ivany); Mt. Misim (H. Stevens); Wareo; Nadzab (Wilson, no. 1100); Bubia (N. L. H. Krauss); lower Busu River (Wilson, no. 944); Finschhafen (Wilson); Bolingbangeng, 900-1000 m. (Wilson, no. 728); Zingzingu, 1200 m. (Wilson, no. 763). PAPUA: China Strait (W. J. Eyerdam); Dobodura (P. J. Darlington); Laloki R., near Port Moresby (Wilson, no. 528). NEW BRITAIN: St. Paul's, Bainings Mts., Gazelle Pen. (J. L. Gressitt). NEW IRELAND: "Camp Bishop," 12 km. up Kait R., 240 m. (J. L. Gressitt). SOLOMON ISLANDS: Kungana Bay, Rennell (M. Willows, Jr.); Bellona I. (Willows). SANTA CRUZ: Vanikoro (Willows). NEW HEBRIDES: Vila, Efate (N. L. H. Krauss); Aore I. (W. L. Nutting); Ratard Plantation, near Luganville, Espiritu Santo (Wilson). FIJI ISLANDS: numerous series from throughout the islands, from Viti Levu to the Lau Archipelago, collected chiefly by W. M. Mann. This species is also widespread through Micronesia and Polynesia.

Taxonomic note. W. L. Brown (pers. commun.), who is currently studying the New World species of *Odontomachus*, informs me that the true *O. haematodus* is probably a species indigenous to the Amazon-Orinoco Basins and not conspecific with the Pacific *simillimus*. According to Linné's original description, *haematodus* possesses the following color characters: "Abdomen nigricans . . . Pedes flavi . . . Corpus nigrum." The Melanesian species identified here as *simillimus* (the next oldest name applicable to Indo-Australian populations) has medium brown legs and dark brown head and alitrunk.

Ecological notes. In eastern New Guinea *simillimus* is common everywhere in clearings and second-growth forest. Colonies apparently nest in the soil, and workers can be found foraging in leaf litter during both day and night. At the Laloki River in Papua a colony was found nesting in accumulated soil and vegetable debris in the primary fork of a tree a little less than two meters from the ground. Near Luganville, in the New Hebrides, a large colony, containing alate queens and males, was found in early January beneath a rotting log on the floor of lowland rain forest.

ODONTOMACHUS TESTACEUS Emery, n. status
(Fig. 4, no. 2)

Odontomachus tyrannicus var. *testacea* Emery, 1897, Ann. Mus. Civ. Stor. Nat. Genova, 38:557, worker. Type locality: "Haveri," New Guinea. (Syntype examined — Emery Coll.)

Odontomachus gulosus Emery, 1902, Természetr. Füz., 25:160, worker. Type locality: Sattelberg, N-E. New Guinea. NEW SYNONYMY. (Syntype examined — Emery Coll.)

Odontomachus gulosus var. *nubila* Emery, 1911, Nova Guinea, 9(2)zool.: 250, worker. Type locality: Etna Bay, Neth. New Guinea. NEW SYNONYMY (provisional).

Odontomachus nigrifrons Donisthorpe, 1940, Entomologist, 73:106, worker. Type locality: Hollandia, Neth. New Guinea. NEW SYNONYMY. (Syntype examined — BMNH.)

Material examined. NETH. NEW GUINEA: Hollandia (*nigrifrons* Donisthorpe syntype). N-E. NEW GUINEA: lower Busu River (Wilson, nos. 904, 944); Lae (N. L. H. Krauss); Boana, 1100 m. (Wilson, no. 1115); Finschhafen (N. G. L. Wagner); Lambaeb, 900 m., Saruwaged Ra. (E. J. Ford); Foria River to Zingzingu, ca. 1000 m. (Wilson, no. 757); Zingzingu, 1200 m. (Wilson, no. 761); Gemeheng, 1300 m. (Wilson); Tumnang, 1450-1600 m., a single male (Wilson). PAPUA: Dobodura (P. J. Darlington); Karema, Brown R. (Wilson, no. 595); Bisianumu, 500 m. (Wilson, nos. 607, 623; J. L. Gressitt).

Taxonomic note. Workers from the Huon Peninsula have a paler ground color than those from Papua, and their cephalic and gastric patches are reduced to faint infuscations. They include the type specimens of Emery's synonymous form *gulosus*.

Ecological notes. Many nests of this species were found by the author during his field studies in New Guinea. In most cases they had been excavated in the soil and were marked externally by a single wide, vertical entrance shaft surrounded by a ring of coarse pellets of excavated earth. Often they were located between the buttresses of forest trees. At Karema a single colony was in the rotting center of a branch of a fallen tree, in a terminal portion raised off the ground. At Bisianumu a dealate queen was found isolated with five eggs in a cell under the bark of a rotting log. Mature colonies contain several hundred workers. Alate queens and males were taken in a nest at Karema on March 10, 1955, and a lone male was collected at light at Tumnang on April 14, 1955. The workers are unusually aggressive and capable of delivering a shocking sting. These traits, combined with the large size of the workers, make them among the most formidable ants to be found anywhere in the world.

ODONTOMACHUS TYRANNICUS Fr. Smith
(Fig. 4, no. 1)

Odontomachus tyrannicus Fr. Smith, 1859, J. Proc. Linn. Soc. London, Zool., 3:455, worker. Type locality: Aru. Viehmeyer, 1912, Abh. Zool. Anthrop. Mus. Dresden, 14:6. *Nec Odontomachus tyrannicus* Fr. Smith, 1861, J. Proc. Linn. Soc. London, Zool., 6:44, pl. 1, fig. 4 (see *O. gladiator* Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10:467).

Odontomachus tyrannicus var. *obsolescens* Donisthorpe, 1940, Entomologist, 73:106-107, worker, male. Original localities: Kokoda, Papua; Camp Nok, Waigeo. NEW SYNONYMY. (Syntypes examined — MCZ.)

Material examined. WAIGEO: Camp Nok (syntypes). NETH. NEW GUINEA: Mamberamo River (W. C. van Heurn). N-E. NEW GUINEA: Finschhafen (2 series; N. G. L. Wagner, E. S. Ross); Lambaeb, 900 m., Saruwaged Ra. (E. J. Ford); Sattelberg, 660 m. (Wilson, no. 722); Sattelberg-Marorno, 800-900 m. (Wilson, no. 724); Bolingbangeng-Ngandno, 960-1000 m. (Wilson, no. 731). PAPUA: Mt. Lamington (C. T. McNamara); Bisianumu, 500 m. (Wilson, nos. 659, 667). NEW BRITAIN: St. Paul's, 350 m., Bainings Mts., Gazelle Pen. (J. L. Gressitt); Ti, Nakanai Mts. (Ford).

Taxonomic note. The depth of pronotal striation varies greatly, as noted by Donisthorpe in his description of var. *obsolescens,* but this variation is apparently non-geographic. Both extremes as well as intermediates are included in material from a single locality, Finschhafen.

Ecological note. This species was relatively common in second-growth forest along the native trail between Sattelberg and Nganduo. Both in this area and at Bisianumu, Papua, workers were found foraging on the ground during the day. A note accompanying van Heurn's Mamberamo series (MCZ) states that this collection was made from a small colony nesting in the soil beneath a fallen palm trunk.

The Genus *ANOCHETUS* Mayr

List of the Melanesian and Moluccan Species, Arranged into Species Groups and Including New Synonymy

Group of *A. cato* Forel

cato Forel
  = *Anochetus cato* var. *subfasciatus* Mann
  = *Odontomachus rossi* Donisthorpe
isolatus Mann
seminiger Donisthorpe
splendens Karawajew

Group of *A. chirichinii* Emery

chirichinii Emery
fricatus Wilson

Group of *A. graeffei* Mayr

graeffei Mayr
  = *Anochetus amati* Karawajew
  = *Anochetus minutus* Karawajew
  = *Anochetus punctiventris* Mayr
  = *Anochetus punctiventris* subsp. *oceanicus* Emery

Group of *A. variegatus* Donisthorpe

variegatus Donisthorpe

Incertae Sedis

filicornis (Wheeler)

Key to the ANOCHETUS *Species of Melanesia and the Moluccas, based on the Worker Caste*

1. Masticatory border of mandible with a prominent blunt tooth located at midlength; dorsolateral propodeal corners tuberculate; dorsal margin of petiolar node concave when node is viewed anteroposteriorly . . . 2

Masticatory border of mandible lacking a prominent tooth at midlength; dorsolateral propodeal corners rounded or obtusely angulate; dorsal margin of petiolar node convex to acute in anteroposterior view . . . 3

2. Central portion of pronotum striate and subopaque; dorsolateral corners of petiolar scale forming angles of 80° or more . . . *fricatus* Wilson

Central portion of pronotum completely smooth and shining; dorsolateral corners of petiolar scale drawn out into spine-like processes of which the apices form angles of 60° or less . . . *chirichinii* Emery

3. Central portion of pronotum coarsely rugose and subopaque; propodeum angulate when viewed from the side; petiolar scale broad and moderately convex in anteroposterior view; anterior half of first gastric tergite often punctate . . . *graeffei* Mayr

Central portion of pronotum smooth and shining; propodeum rounded in side view; petiolar scale narrowed dorsally, its crest strongly convex to acute; anterior half of first gastric tergite always completely smooth and shining . . . 4

4. Intercalary tooth of apical mandibular fork located on the inner border of the ventral tooth about two-thirds the distance from the angle of the fork to the tip of the ventral tooth (position of the median tooth is measured from the center of its base); petiolar scale tapering dorsally into a spine . . . *variegatus* Donisthorpe

Intercalary tooth of apical mandibular fork located on the inner border of the ventral tooth about half way between the angle of the fork and the tip of the ventral tooth; petiolar scale tapered somewhat dorsally but not forming a spine . . . 5

5. Cephalic striae covering most of the dorso-central surface of the head as well as the frontal area . . . *cato* Forel

Cephalic striae limited to the area between the frontal carinae (*isolatus* superspecies) . . . 6

6. Head and alitrunk black, gaster and appendages yellowish brown (Waigeo) . . . *seminiger* Donisthorpe

Head and alitrunk at most dark reddish brown, gaster and appendages dark yellowish brown to reddish brown . . . 7

7. Head and alitrunk dark reddish brown, petiole and gaster dark yellowish brown (eastern Solomons and Santa Cruz) . . . *isolatus* Mann

Head and alitrunk light yellowish brown, petiole and gaster light reddish brown (Aru) . . . . *splendens* Karawajew

ANOCHETUS CATO Forel
(Fig. 2)

Anochetus Cato Forel, 1901, Mitt. Zool. Mus. Berlin, 2(1, b); 6, worker. Type locality: Lowon Valley, near Ralum, New Britain.

Anochetus cato var. *subfasciatus* Mann, 1919, Bull. Mus. Comp. Zool., 63:301, worker, queen, male. Type locality: Malapaina I., Three Sisters Group, Solomons. (Syntypes examined — MCZ.) NEW SYNONYMY.

Odontomachus rossi Donisthorpe, 1947, Ann. Mag. Nat. Hist., (11)14:186-187, worker, queen. Type locality: Maffin Bay, Neth. New Guinea. *Nec Anochetus rossi* Donisthorpe, 1949, *op. cit.*, (12)1:747. (Syntypes examined — CAS, MCZ.) NEW SYNONYMY.

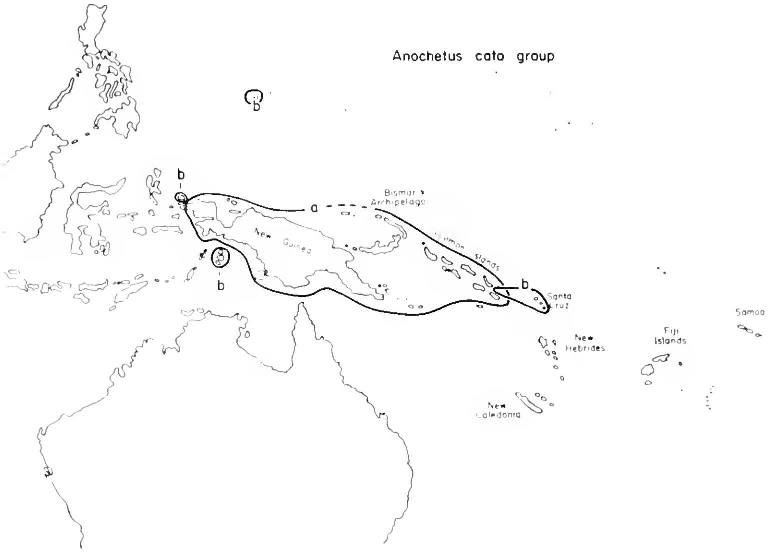


Fig. 2. Maximum known distributions of species of the *Anochetus cato* group. *a*, *cato*, New Guinea to Solomon Islands; *b*, *isolatus*, eastern Solomons and Santa Cruz; *b′*, *splendidulus*, Palau; *b″*, *seminiger*, Waigeo; *b‴*, *splendens*, Aru.

Material examined. NETH. NEW GUINEA: Maffin Bay (syntypes of *Odontomachus rossi* and one additional nest series).

N-E. NEW GUINEA: Bolingbangeng-Nganduo, 900-1000 m., alate queen (Wilson, no. 731). PAPUA: Bisianumu, 500 m. (Wilson, nos. 659, 660, 667). NEW BRITAIN: Keravat, 60 m., Gazelle Pen. (J. L. Gressitt). SOLOMONS: Rendova; Malapaina; Fulakora, Santa Isabel; Pawa, Ugi; Auki, Malaita; Wai-ai, San Cristoval (all W. M. Mann).

Taxonomic notes. The available material of this species shows noteworthy geographic variation in color, which can be outlined as follows. *New Britain and Rendova:* body and appendages concolorous reddish yellow. *Ugi:* body medium reddish brown, legs yellowish brown. *San Cristoval:* body dark reddish brown, legs yellowish brown. *Malapaina and Santa Isabel:* body very dark reddish brown, nearly black, the legs medium brown. *Malaita:* body and appendages intermediate in shade between the San Cristoval and Malapaina-Santa Isabel series. *Bisianumu, Papua:* body very dark reddish brown, almost black, legs yellowish to medium brown. *Bolingbangeng, N-E. New Guinea:* head, alitrunk, and petiole very dark reddish brown, almost black, gaster somewhat lighter in shade, appendages medium brown. *Maffin Bay, Neth. New Guinea:* head very dark reddish brown, almost black, alitrunk medium to moderately dark reddish brown; petiole and gaster contrasting dark yellowish brown; legs light reddish brown.

Of particular interest is the possibility revealed in the above data of the existence of graded inter-island variation in the eastern Solomons. As more material becomes available from over its entire range, this species should prove an especially fruitful subject for a thorough analysis of geographic variation.

Ecological notes. At Bisianumu a small colony of this species was found nesting in a large, "passalid-stage" log on the floor of second-growth foothills rain forest. Workers from other nests were found foraging on the forest floor during the daytime. On Rendova, Mann (1919) also found a colony nesting in a rotting log, presumably in lowland rain forest. Winged queens were collected in a nest on September 9, 1944, at Maffin Bay by Dr. E. S. Ross.

ANOCHETUS CHIRICHINII Emery

Anochetus Chirichinii Emery, 1897, Természetr. Füz., 20:597, pl. 15, figs. 46, 47, worker. Type locality: Hansemann Mts., N-E. New Guinea. (Syntype examined — Emery Coll.)

Material examined. N-E. NEW GUINEA: Hansemann Mts., near Madang (syntype); Nadzab (Wilson, nos. 1088, 1101, 1107); lower Busu River (Wilson, nos. 999, 1051, 1112).

Ecological notes. The collections so far recorded indicate that *A. chirichinii* is relatively abundant in both rain forest and monsoon forest. At the Busu River and Nadzab, workers were encountered on several occasions foraging during the day on the forest floor. A male tentatively determined as *chirichinii* was collected at light on May 16, 1955, at the Busu River.

ANOCHETUS FRICATUS Wilson, n. sp.

Diagnosis. Closely related to *A. chirichinii* Emery, differing primarily in the following characters:

(1) In *fricatus* the entire pronotum is covered by longitudinal striae, and its surface is subopaque. In *chirichinii* striae are limited to the declivitous surfaces and posterior margin of the pronotum, and the entire central portion of the sclerite is smooth and shining.

(2) In *fricatus* the striae of the central portion of the cephalic dorsum extend all the way back to the occipital border; in *chirichinii* they reach only to within about 0.09 mm of it.

(3) In *fricatus* the posterolateral corners of the petiolar node are much less attenuated than in *chirichinii,* forming a blunt angle of 80° or more (as opposed to 60° or less in *chirichinii*).

(4) The body pilosity of *fricatus* is considerably denser overall than in *chirichinii.* When the mesonotum is seen in exact side view the number of hairs projecting beyond its dorsal margin is 15-19 in the *fricatus* types and 5-10 in the Museum of Comparative Zoology series of *chirichinii.*

Holotype worker. HW 1.06 mm, HL 1.22 mm, SL 1.00 mm, CI 87, SI 94, PW 0.58 mm, petiole height 0.36 mm.

Worker paratype variation. HW 1.02-1.12 mm, HL 1.17-1.30 mm, SL 0.98-1.10 mm, CI 85-87, SI 94-98, PW 0.56-0.62 mm, petiole height 0.33-0.35 mm.

Material examined. PAPUA: Karema, Brown River (type locality), holotype and two paratype workers (Wilson, no. 541). N-E. NEW GUINEA: Bubia, a single paratype worker (Wilson, no. 683).

Ecological note. The holotype nest series was collected from a large rotting log on the floor of primary lowland rain forest.

ANOCHETUS GRAEFFEI Mayr

Anochetus Graeffei Mayr, 1870, Verh. zool.-bot. Ges. Wien, 20:961, worker. Type locality: Upolu, Samoa.

Anochetus punctiventris Mayr, 1878, *op. cit.*, 28:15-16, worker. Type locality: Calcutta area, India. NEW SYNONYMY. (Syntype examined — Emery Coll.)

Anochetus punctiventris subsp. *oceanicus* Emery, 1897, Természetr. Füz., 20:597, worker. Original localities: Friedrich-Wilhemshafen (Aitape), N-E. New Guinea. NEW SYNONYMY. (Holotype examined — Emery Coll.)

Anochetus amati Karawajew, 1925, Konowia, 4:285, fig. 8, queen. Type locality: Wammar I., Aru Archipelago. NEW SYNONYMY (provisional).

Anochetus minutus Karawajew, 1925, *ibid.*, pp. 288-289, fig. 10, worker, queen. Type locality: Segamat, Johore, Malaya. NEW SYNONYMY (provisional).

Anochetus minutus, Yasumatsu, 1940, Annot. Zool. Jap., 19:313, fig. 2, worker, distribution.

Material examined. N-E. NEW GUINEA: Aitape (*oceanicus* Emery holotype); Didiman Creek, Lae (Wilson, no. 690). SOLOMON ISLANDS: Maravo Lagoon, New Georgia (W. M. Mann); Auki, Malaita (Mann); Wainoni Bay and Pamua, San Cristoval (Mann). NEW HEBRIDES: Ratard Plantation, Luganville, Espiritu Santo (Wilson, no. 332). FIJI ISLANDS: Lasema, Vanua Levu (Mann); Somo Somo, Taviuni (Mann). NEW CALEDONIA: Chapeau Gendarme (Wilson, no. 62); Mt. Mou (Wilson); "S.E. New Caledonia" (N. L. H. Krauss). This species is found through large parts of southeastern Asia, Melanesia, Polynesia, and Queensland. Very probably it has been distributed through part of this range through the inadvertent agency of man.

Taxonomic notes. During the course of the present study the author has examined large amounts of Asian, Melanesian, and Australian material determined by earlier specialists variously as *graeffei* and *punctiventris*, without being able to distinguish two species on the basis of Mayr's original diagnostic characters or any other characters. There appears to be but a single relatively variable species. In particular, sculpturing of the first gastric tergite, traditionally stressed in earlier descriptions, varies gradually from smooth and shining (extreme "*graeffei*" form) to coarsely punctate and subopaque ("*punctiventris*" form). The same conclusion has been reached with respect to the supposed distinction between *punctiventris* and its subspecies *oceanicus*. A few differences observed between types of the two forms in the Emery Collection, involving, especially, total size and petiolar node shape, are connected in other series by intergradient forms.

A. amati Karawajew was described without reference to *A. graeffei*, but its characters seem to fit the latter species in detail. *A. minutus* Karawajew was compared with *amati* in the original description; it is supposedly distinguished from that species by its smaller size and proportionately shorter mandibles. There seems to be no reason to suppose that it is anything more than an infraspecific variant of *graeffei*.

Ecological notes. Both the author's New Guinea and New Hebrides collections consist of stray workers taken during the day from the floor of lowland rain forests. At Chapeau Gendarme, New Caledonia, a small colony was found nesting beneath a rock in a clearing.

ANOCHETUS ISOLATUS Mann, n. status
(Fig. 2)

Anochetus cato subsp. *isolatus* Mann, 1919, Bull. Mus. Comp. Zool., 63:302, fig. 11, worker, male. Type locality: Graciosa Bay, Santa Cruz. (Syntypes examined — MCZ.)

Material examined. SANTA CRUZ: Graciosa Bay (syntypes). Mann also recorded this species from Malapaina, Three Sisters Group, Solomons, on which island it occurs sympatrically with the closely related *A. cato* Forel.

Taxonomic note. A. isolatus forms with *A. splendens* (Aru), *A. seminiger* (Waigeo), and *A. splendidulus* (Carolines), the "*isolatus* superspecies," i.e., a tightly-knit group of cognate forms which seem sufficiently well differentiated to be good biological species, but which are completely allopatric in distribution. Actually, treatment of these four forms as species must be considered arbitrary until evidence is obtained of non-intergradation in areas of overlap, if indeed such areas exist at all.

The range of the *isolatus* superspecies forms a nearly complete circle around that of the related species *cato*. Brown (Quart. Rev. Biol., 32:271, 1957) has suggested that this unusual pattern may have resulted from the replacement of *isolatus* in New Guinea, Bismarck Archipelago, and western Solomons by the more recently evolved *cato.*

ANOCHETUS SEMINIGER Donisthorpe
(Fig. 2)

Anochetus seminiger Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)9:170, worker. Type locality: Camp Nok, 800 m., Waigeo.

Known only from type material. See discussion under *A. isolatus* Mann.

ANOCHETUS SPLENDENS Karawajew

Anochetus splendens Karawajew, 1925, Konowia, 4:289, fig. 11, queen. Type locality: Wammar I., Aru Archipelago.

Known from type material only. See discussion under *A. isolatus* Mann.

ANOCHETUS VARIEGATUS Donisthorpe, n. status

Anochetus cato var. *variegatus* Donisthorpe, 1938, Ann. Mag. Nat. Hist., (11)1:597, worker. Type locality: Mt. Nomo, south of Mt. Bougainville, Neth. New Guinea. (Syntype examined — MCZ.)

Material examined. NETH. NEW GUINEA: Mt. Nomo (syntype). N-E. NEW GUINEA: Didiman Creek, Lae (Wilson, no. 711).

Taxonomic note. The Lae specimens differ from the MCZ syntype in having cephalic striae limited to the area between the frontal carinae; in the type, striae extend laterally beyond the carinae to a point midway between the carinae and the compound eyes, and posteriorly to within 0.20 mm of the anteriormost point of the occipital border. The Lae specimens also have somewhat more acute petiolar spines.

Ecological notes. At Lae, two workers were found during early evening foraging on the lower part of a tree trunk at the edge of rain forest.

Species Inquirendae

ANOCHETUS FILICORNIS (Wheeler)

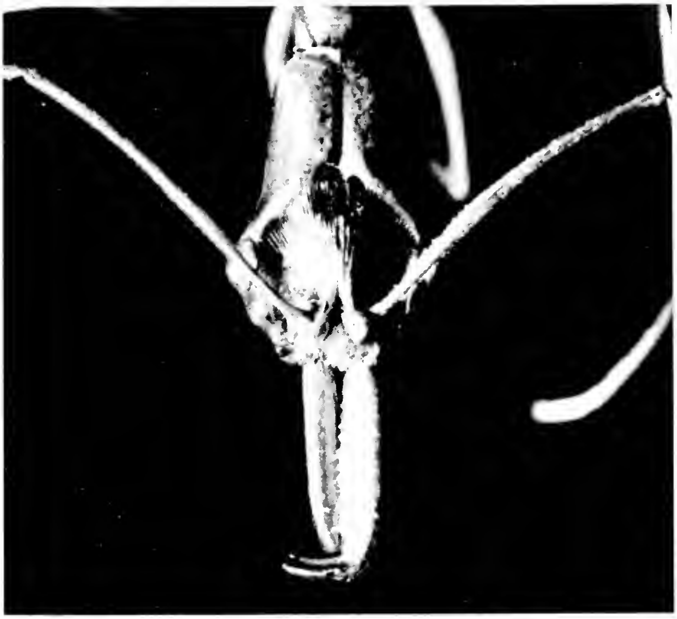
Myrmapatetes filicornis Wheeler, 1929, Amer. Mus. Novitates, no. 349: 6, fig. 3, male. Type locality: Larat I., Tanimbar. (Holotype examined — MCZ.)

Anochetus filicornis, Brown, 1953, Breviora, Mus. Comp. Zool., no. 18: 2.

Brown's assignment of this species to *Anochetus* is probably correct. However, its affinities to other known Papuasian species of the genus remain problematical. The holotype is similar in size to the males of the largest known New Guinea species *A. cato* Forel and *A. isolatus* Mann, but it differs widely from these in its much larger eyes and proportionately broader head and in details of petiolar and genitalic structure.

PLATES

Fig. 3. Heads of the worker caste of two species of *Odontomachus*. *Above, O. testaceus* Emery, Finschhafen; *below, O. malignus* Fr. Smith, Graciosa Bay, Santa Cruz.



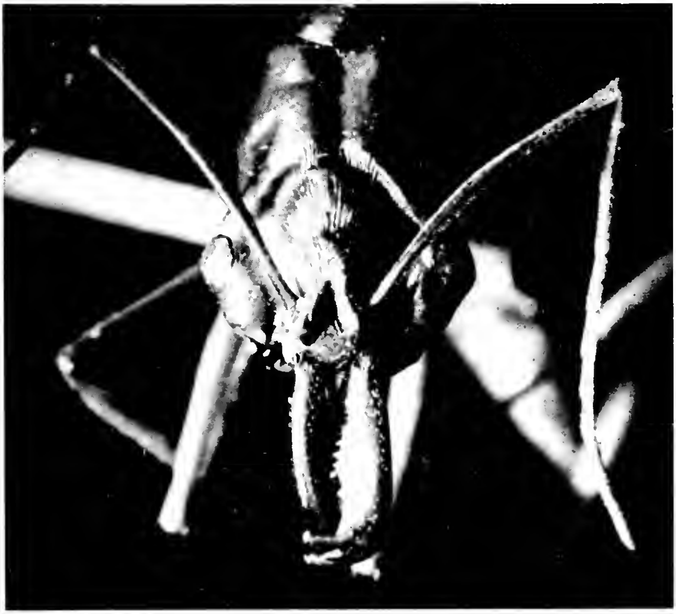


Fig. 4. Lateral view of worker petioles of various Melanesian *Odontomachus*. (1) *tyrannicus* Fr. Smith, Finschhafen, N.-E. New Guinea; (2) *testaceus* Emery, Finschhafen; (3) *animosus* Fr. Smith, holotype from Manokwari, Neth. New Guinea; (4) *saevissimus*, Doormanpad, Neth. New Guinea; (5) *emeryi* Mann, syntype from Maliali, Solomon Islands; (6) *linae* Donisthorpe from Cyclops Mts., Neth. New Guinea; (7) *montanus* Stitz, syntype from Lordberg, N.-E. New Guinea; (8) *gressitti* Wilson, holotype from Nondugl, N.-E. New Guinea; (9) *malignus* Fr. Smith, Graciosa Bay, Santa Cruz; (10) *simillimus* Fr. Smith, Luganville, Espiritu Santo, New Hebrides; (11) *cephalotes* Fr. Smith, Bisianumu, Papua; (12) *aciculatus* Fr. Smith, syntype of synonymous *verticillatus* Stitz.

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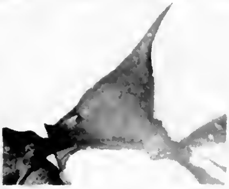

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