WITH THE AUTHOR'S COMPLIMENTS

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A review of the genus *pelusios* Wagler in southern Africa (Pleurodira : Pelomedusidae)

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ABSTRACT

Analysis of variation in 429 specimens of *Pelusios* from southern Africa (south of Latitude 8°S) largely confirms the taxonomic arrangement proposed by Laurent (1964; 1965), but better diagnostic characters are indicated for several forms. The recognition of *P. rhodesianus* as a full species by Raw (1978) is confirmed by the sympatry of this taxon with *P. castaneus* at Lake St Lucia.

A sample of 50 *P. bechuanicus* is compared with sympatric and parapatric populations of *P. subniger* and *P. rhodesianus*. A northern race of *P. bechuanicus* is described from the Upemba National Park in the Shaba Province of Zaire.

Samples of *P. castaneus* from Madagascar and the Seychelles seem to be indistinguishable from *P. castaneus castanoides* of eastern Africa, but the type specimen of *P. c. seychellensis* (Siebenrock) may represent a distinct population (its precise locality of origin is unknown).

P. williamsi Laurent appears to be conspecific with *P. castaneus* and this taxon is sympatric with *P. rhodesianus* at Entebbe, Uganda.

INTRODUCTION

In the last comprehensive revision of the genus *Pelusios*, Loveridge (1941) recognised only four species, i.e. *P. adansonii* (Schweigger), *P. gabonensis* (Duméril), *P. subniger* (Lacépède) and *P. sinuatus* (A. Smith). Müller & Hellmich (1954) subsequently reinstated *P. niger* (Duméril & Bibron) as a valid species.

In 1956 Laurent revived *P. castaneus* (Schweigger) from the synonymy of *P. subniger* and described two new species from Zaire, *P. nanus* and *P. carinatus*, but Wermuth & Mertens (1961) rejected these findings without discussion.

Laurent (1964) subsequently resurrected *P. bechuanicus* FitzSimons from the synonymy of *P. subniger* on the basis of a single Angolan specimen. In 1965 he presented additional evidence to support his previous taxonomic decisions, also describing a new species *P. williamsi*, a subspecies of it (*P. w. lutescens*) and a new giant subspecies of *P. castaneus* (*P. c. chapini*). Laurent revived the taxa *derbianus* (Gray) and *rhodesianus* Hewitt as races of *P. castaneus*.

Mitchell & Steyn (1967) recorded *P. bechuanicus* from the Okavango River in South West Africa (Namibia), but Mertens (1971) treated this taxon as a race of *P. castaneus*, a species that he had finally recognised in 1969.

Wood (1974) recognised *P. nanus* as a full species, but believed that *P. bechuanicus*, *P. carinatus*, *P. castaneus* and *P. williamsi* were all geographic variants of *P. subniger*.

Wermuth & Mertens (1977) placed *P. nanus* as a subspecies of *P. adansonii* and recognised *P. castaneus* and *P. carinatus* as full species, but treated *P. bechuanicus* and all Laurent's races of *P. castaneus* as synonyms of *P. castaneus* (although *castanoides* Hewitt was treated as a synonym of *P. subniger*).

In a review of the genus *Pelusios* in Natal, Raw (1978) reported populations of *P. rhodesianus* from Durban and Zululand, treating this taxon as a full species because of its sympatry with *P. castaneus* in Zululand.

Bour (1978) made a good case for the application of the name *P. castaneus castaneus* to the West African populations previously included under *P. c. derbianus* and he erected the name *P. c. kapika* for the Malagasy populations.

MATERIALS AND METHODS

This review is concerned with the populations of *Pelusios* found south of Latitude 8°S., including Angola, the Shaba Province of Zaire, Zambia, Malawi, southern Tanzania, South West Africa (Namibia), Botswana, Zimbabwe, Moçambique, South Africa and Swaziland: 429 specimens from this region were examined. Small samples from other parts of Africa, Madagascar and the Seychelles were examined for comparative purposes.

The nomenclature of epidermal shields and bones of the shell follows Zangerl (1969). Vertebral shields were stripped from many specimens in order to check neural patterns, which could not be detected on X-rays. Neurals are numbered from the front 1 to 8 and are referred to in the text as N1 to N8. Names used for head shields are indicated in Fig. 2. The standard measurements are mostly those employed by Laurent (1964; 1965), but some different head measurements were used. The carapace was measured between blocks with a white-face tape; epidermal shields were measured with dial calipers.

Under 'Localities' for each taxon, literature citations are listed alongside the museum catalogue numbers for specimens which I have examined (or have been provided with data). The following abbreviations are used for author's names: Blgr = G. A. Boulenger; Brdly = D. G. Broadley; Laur. = R. F. Laurent; Lov. = A. Loveridge. In the lists of material examined, countries (or provinces, within South Africa) are listed from north to south and from west to east in a given latitude, localities are in alphabetical order within countries (or provinces).

The material examined is listed under the following institutional prefixes:

AM	Albany Museum, Grahamstown, South Africa
AMNH	American Museum of Natural History, New York, U.S.A.
BM	British Museum (Natural History), London, England
CM	Carnegie Museum, Pittsburgh, U.S.A.
DSP	FitzSimons' Snake Park, Durban, South Africa
EBM	Estaçao de Biologia Maritima, Inhaca Island, Moçambique
IRScNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
JPT	J. P. Tello Collection, Maputo, Moçambique
LCFM	La-Chaux-de-Fonds Musée d'Histoire Naturelle, Switzerland
MBL	Museu Bocage, Lisboa, Portugal (recently destroyed)
MHNP	Muséum Nationale d'Histoire Naturelle, Paris, France
MMK	McGregor Museum, Kimberley, South Africa
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NM	Natal Museum, Pietermaritzburg, South Africa
NMBO	Nasionale Museum, Bloemfontein, South Africa
NMSR	National Museum, Bulawayo, Zimbabwe
NMW	Naturhistorisches Museum, Vienna, Austria
QVMS	Queen Victoria Museum, Salisbury, Zimbabwe *
SMF	Senckenbergische naturforschende Gesellschaft, Frankfurt-am-Main, Germany
TM	Transvaal Museum, Pretoria, South Africa

UM Umtali Museum, Umtali, Zimbabwe*
USNM National Museum of Natural History, Washington, U.S.A.

If more than one specimen is catalogued under the same number, the number of specimens is shown in parentheses after the institutional catalogue number.

On the distribution maps, the solid symbols denote specimens examined during the course of this study, or for which data have been supplied by various colleagues; open symbols indicate literature records.

CHARACTER ANALYSIS

A plethora of taxonomic characters has been employed by previous workers on the genus *Pelusios*. The majority of these were examined, but many of the ratios based on proportions of the epidermal shields of head, carapace and plastron proved to be too variable to provide useful diagnostic characters.

1. Neural pattern

In his *Catalogue of the Chelonians*, Boulenger (1889) stated that in the Pleurodira the neural series rarely contains more than seven bones, but he illustrated the neural pattern of a *Sternothaerus derbianus* (= *P. c. castaneus*) with a continuous series of eight neurals. He also indicated that in this suborder a single 'pygal' (= suprapygal) is present and that in none of the Recent forms does it make contact with the neurals.

The first author to note a reduction in the number of neural bones in *Pelusios* was Hewitt (1933), who illustrated a paratype of *P. sinuatus leptus* with only five neurals, N1 failing to contact the nuchal and N5, N7 and N8 being absent. He recorded a Zululand specimen of *P. sinuatus zuluensis* with a continuous series of seven neurals.

Broin (1969) illustrated the variation in neural arrangement in nine Recent and fossil specimens of *P. sinuatus* (including the type of *P. rudolphi* Arambourg). N1 fails to contact the nuchal in two fossil specimens, N5 is reduced or absent in five, N6 is missing in one and N7 and N8 are absent in all specimens.

During the course of the present study, neural patterns were checked in 136 specimens and the variation may be summarised as follows:

P. nanus: One specimen from Chitau, Angola, has eight neurals, N8 being reduced in size and meeting N7 at a point (Fig. 1A); three other specimens from Angola and Zambia lack N8. N1 is narrowed anteriorly, meeting the nuchal at a point or narrowly separated from it.

P. subniger: The usual arrangement (20 specimens) is eight neurals forming a continuous series, but separated from the single suprapygal (Fig. 11). Three specimens from Kariba Lake and Hartley have two superposed suprapygals (Fig. 1B) and two others from Que Que and Mpika District lack N8 (Fig. 1C).

P. bechuanicus bechuanicus: All 13 specimens have a continuous series of 8 neurals, separated from the single suprapygal (Fig. 12). In two specimens N1 is reduced in size and does not contact the nuchal (Fig. 1D). In one specimen N8 is transversely divided near the posterior tip.

* Collections now held at the National Museum, Bulawayo.

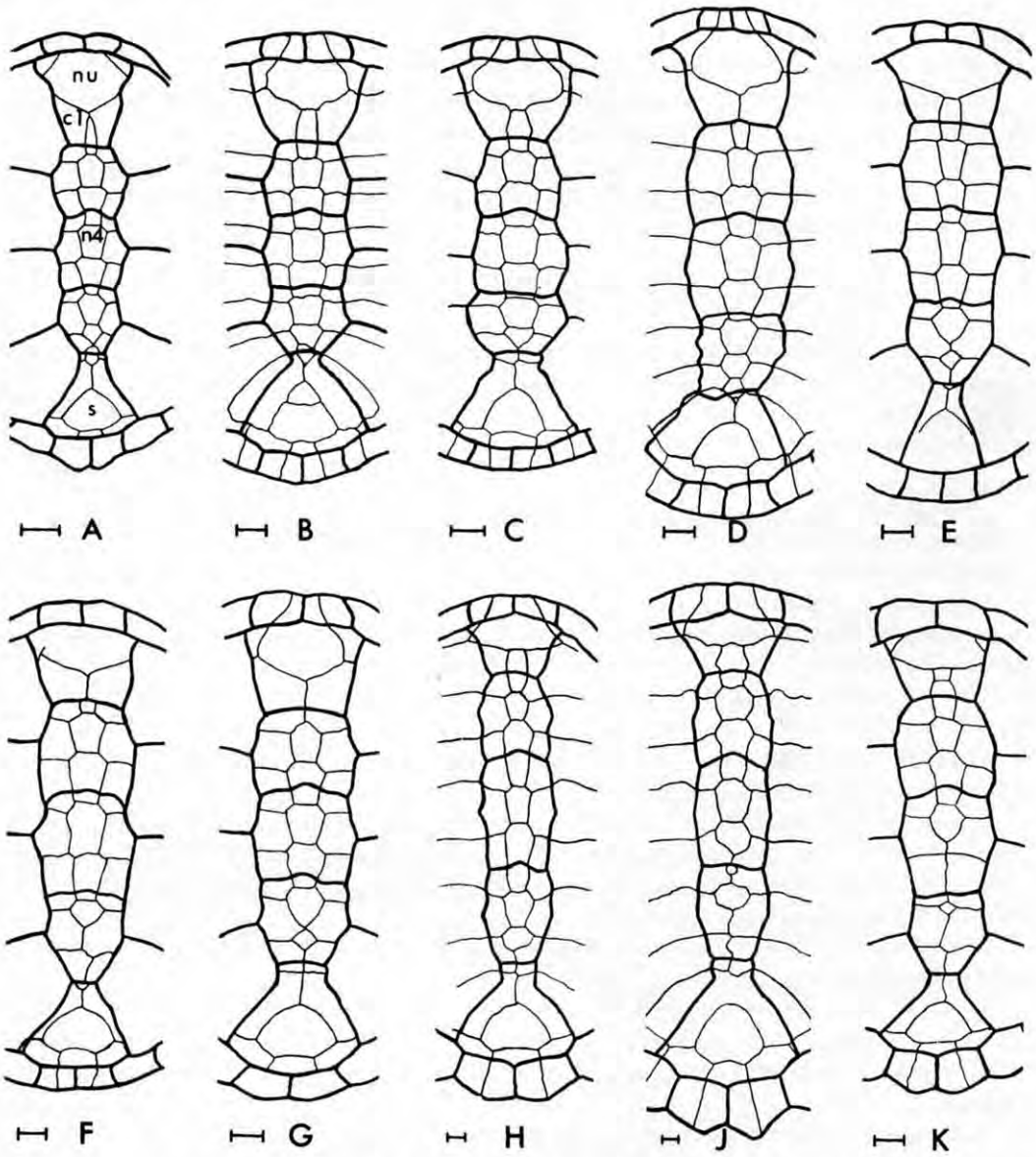


Fig. 1. Neural patterns in *Pelusios*: A. *P. nanus* — AMNH 50757 Chitau, Angola; B. *P. subniger* — UM 850 Lake Kariba; C. *P. subniger* — AM 5432 Mpika District, Zambia; D. *P. b. bechuanicus* — UM 29159 north Botswana; E. *P. rhodesianus* — AMNH 50752 Chitau, Angola; F. *P. castaneus castanoides* — UM 27828 Tando, Mocambique; G. *P. castaneus castanoides* — TM 52160 Lake St. Lucia, Kwazulu; H. *P. sinuatus* — UM 12076 Fishan, Lundi River, Zimbabwe; J. *P. sinuatus* UM 5278 Bumi Confluence, Lake Kariba, Zimbabwe; K. *P. sinuatus* — AM 5432 Mpika District, Zambia. Thin lines indicate sutures between bones; thick lines indicate sulci between epidermal shields. Key to bones: c= costal; n= neural; nu = nuchal; s = suprapygal. The horizontal lines equal 1 cm to scale.

P. bechuanicus upembae: The holotype agrees with the typical form in neural pattern. A paratype (MRAC 11460) has an elongate N8 which is transversely divided.

P. rhodesianus: All 28 specimens examined (including 4 from Entebbe, Uganda) have 8 neurals, but in MRAC 16962 N8 is fused with the left costals. In AMNH 50732 and NMSR 2625 N7 and N8 are reduced in size and isolated; in AM 5432 N8 is isolated. In all five specimens from Kwazulu and Durban N8 is elongate and contacts the suprapygal; a similar arrangement is found in 3 out of 5 Zimbabwean specimens, but only one out of 7 Zambian specimens (Fig. 13). N8 is separated from the suprapygal in all specimens from Angola (2: Fig. 1E), Zaire (4) and Moçambique (1). The suprapygal is fused with costal 8 (left) in UM 33033.

P. castaneus castaneus: Four specimens from Senegal, Ghana and Nigeria all agree with the 'West African' specimen illustrated by Boulenger (1889: Fig. 47), having a continuous series of 8 neurals, separated from the suprapygal.

P. castaneus williamsi: A topotype (TM 16433) has a continuous series of 8 neurals, N8 elongate and only narrowly separated from the suprapygal. A paratype (UM 33165) is similar, but lacks N1.

P. castaneus lutescens: A paratype (CM 62248) lacks N1, N8 is reduced in size and well separated from the suprapygal.

P. castaneus castanoides: Eight specimens from KwaZulu and Moçambique have 5 to 7 neurals, well separated from both nuchal and suprapygal, N1, N7 and N8 being reduced in size or absent (Fig. 1F, G). Six Malawi specimens have only 5 neurals (Fig. 14), like the single Malagasy specimen checked for this character. Three Seychelles specimens have 7-8 neurals, but with N1, N7 and N8 usually vestigial.

P. sinuatus: The neural pattern was checked in fifty specimens. Most of them have 6 or 7 neurals, with N8 always absent and N7 often reduced or absent (Fig. 1H). N1 occasionally fails to reach the nuchal (Fig. 15), but it is absent only in UM 32996 from Zambia. Specimens from the Luangwa Valley northwards to Lake Tanganyika have 5 or 6 neurals, with N5 usually reduced in size (Fig. 1J) or absent, leaving N6 isolated (Fig. 1K).

The neural patterns in the seven southern forms of *Pelusios* are summarised as follows:

P. nanus: 7-8 neurals, N1 tapered and meeting the nuchal at a point, N8 reduced or absent.

P. subniger: 8 neurals.

P. bechuanicus bechuanicus: 8 neurals.

P. bechuanicus upembae: 8 neurals.

P. rhodesianus: 8 neurals, N8 often elongate and in contact with the suprapygal.

P. castaneus castanoides: 5 to 7 neurals, with N1, N7 and N8 always reduced in size or absent.

P. sinuatus: 5 to 7 neurals, N8 always absent, N7 frequently absent, N5 sometimes absent, N1 absent in only one out of fifty specimens.

2. Median protuberences on vertebral shields

Hatchlings of *P. sinuatus* have a pronounced vertebral keel on the carapace which gradually disappears with growth, but many adults retain distinct median posterior pro-

tuberances on vertebrals 3 and 4 (Fig. 15). Hewitt (1927; 1931; 1933) used the presence of these 'vertebral knobs' in his diagnoses of the races *zuluensis* and *leptus*, but their retention in adults is spasmodic even within populations and is without taxonomic significance (Pl. IV).

P. bechuanicus hatchlings have a moderate vertebral keel and posterior median protuberences on vertebrals 3 and 4 are well marked in subadult specimens, including the type (FitzSimons, 1935: Pl. xi). All traces of the vertebral keel are lost in large adults.

P. rhodesianus and *P. castaneus* hatchlings have a poorly marked vertebral keel and few adults have 'vertebral knobs'; vertebral 4 is the shield most likely to bear a posterior protuberence.

P. nanus and *P. subniger* show little indication of a vertebral keel at any stage.

3. Shape of posterior marginals

The serrated posterior carapace of *P. sinuatus* has been utilised as a diagnostic character by many workers from Siebenrock (1903) to Loveridge (1941), but the marginals are only sharply serrate in young and subadult specimens, they are usually sinuate in adults, but may be smoothly rounded. The posterior marginals may also be somewhat upturned, a feature used by Hewitt (1931) in the diagnosis of his subspecies *zuluensis*.

In the other five species under consideration the posterior margin of the carapace is smoothly rounded. An exception is a *P. nanus* with the posterior pair of marginals produced, separated by a notch (Fig. 1A).

4. Shape of the upper jaw (beak) at symphysis

Gray (1863; 1870) and Boulenger (1889) used the shape of the beak as a major diagnostic character, i.e. hooked in *niger*; bicuspid in *sinuatus* (but including *P. rhodesianus* and *P. castaneus* material) and smooth in *nigricans* (= *P. subniger*). The differences found in southern African material are as follows:

Beak strongly bicuspid	..	*P. rhodesianus; P. castaneus*
Beak weakly bicuspid	..	*P. sinuatus*
Beak smooth	.. .. ..	*P. nanus; P. subniger; P. bechuanicus*

5. Shape of parietal crest on skull

In a series of *P. subniger* skulls the parietal crest shows no trace of a lateral flange, whereas the flange is well developed in skulls of *P. bechuanicus*, *P. rhodesianus* and *P. sinuatus*, it also appears to be present in *P. niger* (Boulenger, 1889: Fig. 46).

6. Axillary shield

The presence of an axillary shield in *Pelusios sinuatus* has previously been mentioned only by Hewitt (1927), it is apparently absent in all other species of *Pelusios*. A discrete axillary is absent in hatchling *P. sinuatus*, but it appears with the development of the plastral hinge and it is clearly defined in all specimens with a carapace length exceeding 70 mm (Fig. 15).

7. Falciform scales on forelimb

Siebenrock (1903) noted that two rows of falciform scales are present on the forelimbs of most species in the genus, but are not present in *S. nigricans* (= *P. subniger*). Hewitt (1933: Pl. ix, Fig. 5) described and illustrated these transversely elongate scales in *P. rhodesianus* and Laurent (1956) used the character to distinguish this species (under the name

P. castaneus) from *P. subniger*, but there is considerable variation.

Falciform scales on the forelimb are usually well developed in *P. rhodesianus* and *P. castaneus*, moderately developed in *P. bechuanicus* and usually poorly developed in *P. subniger* (except in Malagasy material) and *P. sinuatus*. There is no indication of falciform scales on the forelimb of *P. nanus* (Laurent, 1956: Pl . iv, Fig. 4).

8. Supralabial shield between postocular and masseteric shields (Fig. 2)

Rendahl (1939a) noted that in Seychelles material *S. nigricans* (= *P. subniger*) has the postocular separated from the subtympanal (= masseteric) shield by a rectangular shield (= supralabial), whereas in *S. castaneus* the postocular makes contact with the subtympanal shield above a small triangular shield. Rendahl (1939b) subsequently noted that in *S. sinuatus* the postocular was again separated from the subtympanal shield by a relatively large shield.

The condition in southern African populations with respect to postocular/masseteric contact and the presence or absence of a supralabial shield is as follows:

P. nanus: Supralabial present, but postocular and masseteric may make contact above it.

P. subniger: Supralabial always present (36 specimens), postocular and masseteric usually well separated.

P. bechuanicus bechuanicus: Supralabial present in 8; present/absent in 1; absent in 2 (Fig. 2A-C).

P. bechuanicus upembae: Supralabial present in the type specimen (Fig. 2D) and paratypes.

P. rhodesianus: Supralabial absent in 18; present/absent in 3; present in 5, but the postocular and masseteric may make contact above it.

P. castaneus castanoides: Supralabial absent in 5; present in 1. Supralabial may be present or absent in Malagasy and Seychelles material, if present the postocular and masseteric are usually in contact above it. (Rendahl, 1939a: Fig. 14C).

P. sinuatus: Supralabial present, postocular and masseteric usually well separated. (Rendahl, 1939b: Fig. 5).

9. Number of mental barbels

In the Neotropical pelomedusid genus *Podocnemis* most species have two mental barbels, but two have a single barbel (Williams, 1954b). In the Afrotropical/Malagasy genera *Pelomedusa* and *Pelusios* there are two barbels in all taxa except *P. bechuanicus bechuanicus*, which usually has three (Fig. 2B). One aberrant specimen of *P. rhodesianus* (UM 9716) has four barbels. Occasional specimens lack one or both barbels, apparently due to injury, but the bases of the barbels can usually be detected. The barbels vary in length, but tend to be longest in *P. sinuatus*.

10. Scalation of chin posterior to tomium

Vaillant (1891), with reference to Malagasy material, found that the narrow space between the tomium and the mental barbels is granular in *S. nigricans* (= *P. subniger*), but covered by a transverse series of polygonal shields in *S. castaneus*. Rendahl (1939a) confirmed and illustrated the difference between the two species with material from the Seychelles. Loveridge (1941) and Laurent (1956) believed such differences to represent

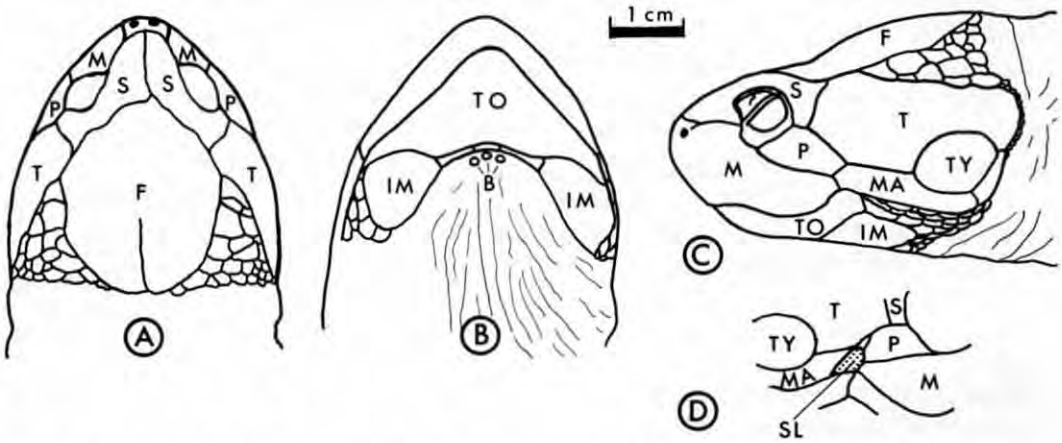


Fig. 2. Head shields of *P. bechuanicus*: A-C. dorsal, ventral and left lateral views of head of *P. b. bechuanicus* UM 20165 Thamalakane River, Botswana; D. right lateral view of head of *P. b. upembae* (type) TM 38178, to show position of supralabial. Key: B = mental barbels; F = frontal; IM = inframandibular; M = maxillary; MA = masseteric; P = postocular; S = supraocular; SL = supralabial (stippled); T = temporal; TO = tomium; TY = tympanum.

individual variations, but there are significant interspecific differences in the development of a series of elongate scales bordering the tomium between the large inframandibular scales (Fig. 2B), i.e.

P. nanus: About five well developed shields.

P. subniger: Granular or slight development of shields (feebly developed polygonal shields may also be present in Malagasy specimens — Siebenrock, 1906).

P. bechuanicus: Elongate processes from the large inframandibular scales meet on the midline: these may be fragmented.

P. rhodesianus: A series of well developed scales.

P. castaneus castanoides: A series of well developed scales.

P. sinuatus: Feeble development of elongate scales, followed by a granular area.

11. Scales on nape

Vaillant (1891) noted that in live Malagasy specimens *S. nigricans* (= *P. subniger*) had prominent cervical scales on the neck, whereas those of *S. castaneus* were flattened. No such difference has been observed in the course of the present study, but *P. bechuanicus* does differ from all other species in its finely granular cervical scalation (like shagreen). At the other extreme, *P. nanus* has relatively larger flat cervical scales than any other species.

12. Carapace length (Fig. 3)

Gibbons (1967) found that in southwestern Michigan maximum size of the painted turtle *Chrysemys picta* is affected by the habitat. River turtles are primarily carnivorous and attain the largest size, while marsh turtles are largely herbivorous and have a small maximum size. Habitat seems to affect the maximum size of African terrapins in a similar way. Northern populations of *Pelomedusa subrufa* inhabit temporary pans and seasonal swamps,

attaining a maximum carapace length of about 200 mm: southern populations, free of competition from *Pelusios*, are able to occupy rivers and other permanent water bodies and attain a maximum length of 325 mm (Hewitt, 1935).

The six species of *Pelusios* under consideration range in maximum size from 120 mm (*P. nanus*) to 465 mm (*P. sinuatus*: Witte, 1952). Unfortunately we know little of the ecology of the dwarfed species *P. nanus*.

P. subniger, like the northern populations of *Pelomedusa subrufa*, inhabits seasonal pans and swamps and does not seem to exceed 200 mm in carapace length.

P. rhodesianus attains a maximum carapace length of 255 mm (Laurent, 1965; *P. c. chapini* is reported to attain 380 mm, perhaps due to inclusion of *P. bechuanicus upembae* material). This species appears to inhabit swamps and weed-choked dams.

P. castaneus castanoides reaches a length of 230 mm (NMW —, Majunga, Madagsar)

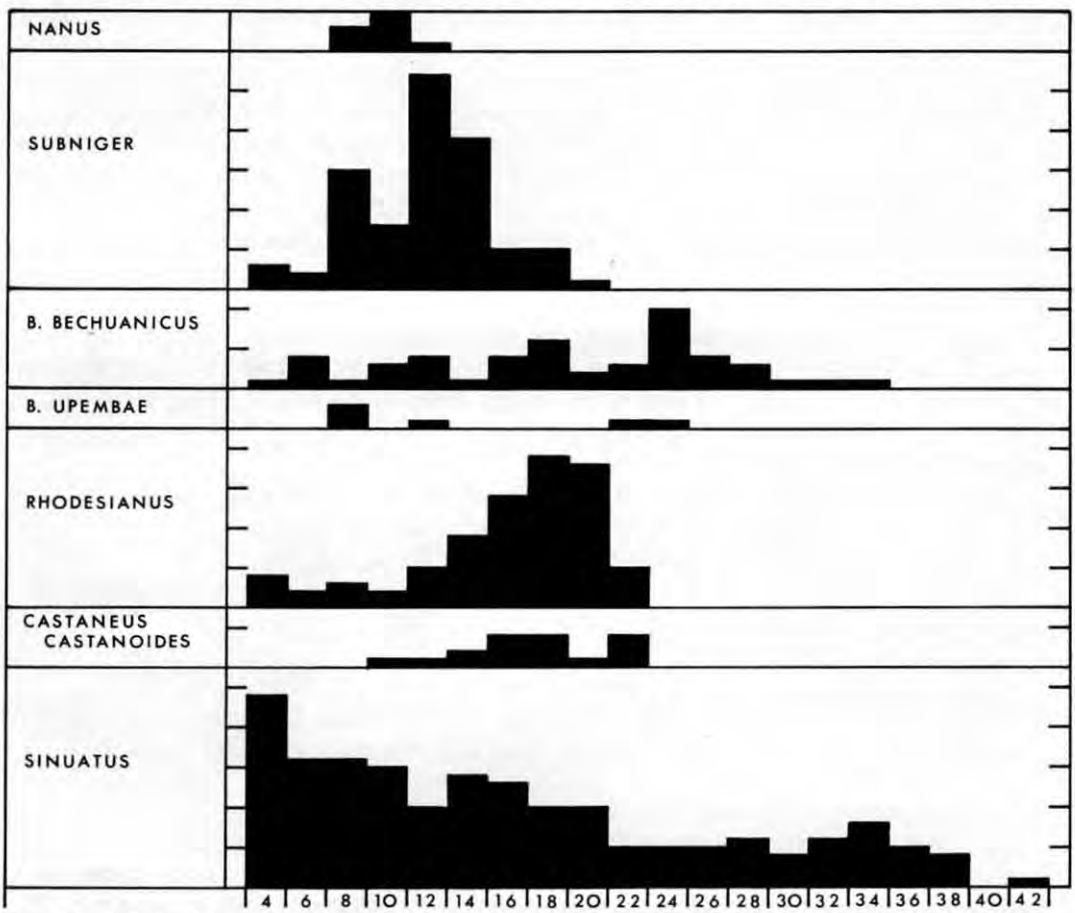


Fig. 3. *Pelusios:* histograms to show number of specimens in each carapace length size class for southern African populations. The horizontal scale is in centimetres, e.g. class 4 = 30 to 49 mm. Divisions on the vertical (frequency) scale indicate five specimens.

and seems to inhabit stagnant lakes and swamps at low altitudes.

P. bechuanicus bechuanicus attains a carapace length of at least 330 mm. Its distribution is restricted to the crystal clear waters of the Okavango system, including the upper Zambezi and upper Kafue Rivers. It is marginally sympatric with *P. rhodesianus*.

P. sinuatus is known to attain a carapace length of 465 mm in Lake Tanganyika (Witte, 1952) and specimens exceeding 300 mm are common in large lakes and rivers. Individuals from small rivers and dams may not exceed 200 mm in maximum length. This species often occurs in turbid water and above the Victoria Falls it inhabits muddy backwaters which are shunned by *P. bechuanicus*.

13. Colour of carapace

The true colour of both carapace and plastron may be obscured by either mineral deposits (Siebenrock, 1906) or algal growth. Mineral deposits are presumably formed while a terrapin is aestivating in mud, they affect both carapace and plastron, being evenly distributed, hard and often polished. Black, carbon-like deposits coat specimens from some areas, for example *P. rhodesianus* from Durban and *P. castaneus williamsi* from Kaimosi, the type locality. Laurent (1965) described this taxon as having the carapace black and the plastron largely black, but in fact they are naturally brown and yellow respectively. In some parts of Zimbabwe (Mazoe; Inyanga) specimens of *P. rhodesianus* have a red-brown lateritic deposit on carapace and plastron. Mineral deposits are often betrayed on subadult specimens by recent growth rings at the periphery of epidermal shields, these show the true colouration, not yet obscured by mineral deposits.

Algal growth affects only the carapace and is important in strongly aquatic species. *P. sinuatus* usually has the carapace more or less obscured by soft green algae, whereas *P. castaneus* and *P. rhodesianus* may have a rough scabrous coating of brown algae.

P. nanus, *P. subniger* and *P. bechuanicus* seem to remain largely free of both mineral deposits and algal growth.

The *natural* carapace colouration of the six southern African species is as follows:

P. nanus: Dark brown, sometimes with radiating streaks of black.

P. subniger: Dark brown to yellow-brown.

P. bechuanicus: Uniform black or with irregular narrow yellow-brown bands across lower ends of pleurals 2 and 3.

P. rhodesianus: Uniform black.

P. castaneus castanoides: Yellow-brown to blackish-brown on African mainland; chestnut brown to blackish on Pemba Island, Madagascar and Seychelles (sometimes mottled).

P. sinuatus: Uniform black; rarely dark brown with fine black radiating lines.

14. Colour pattern of plastron (Plate I)

The distinctive plastron pattern of *P. sinuatus* has been used as a diagnostic character by Rendahl (1939b), Loveridge (1941) and subsequent authors, while Laurent (1956) used plastron colouration to distinguish *P. rhodesianus* (as *P. castaneus*) from *P. subniger*. The *natural* plastron colour patterns encountered in southern African taxa are shown in Plate I and may be summarised as follows:

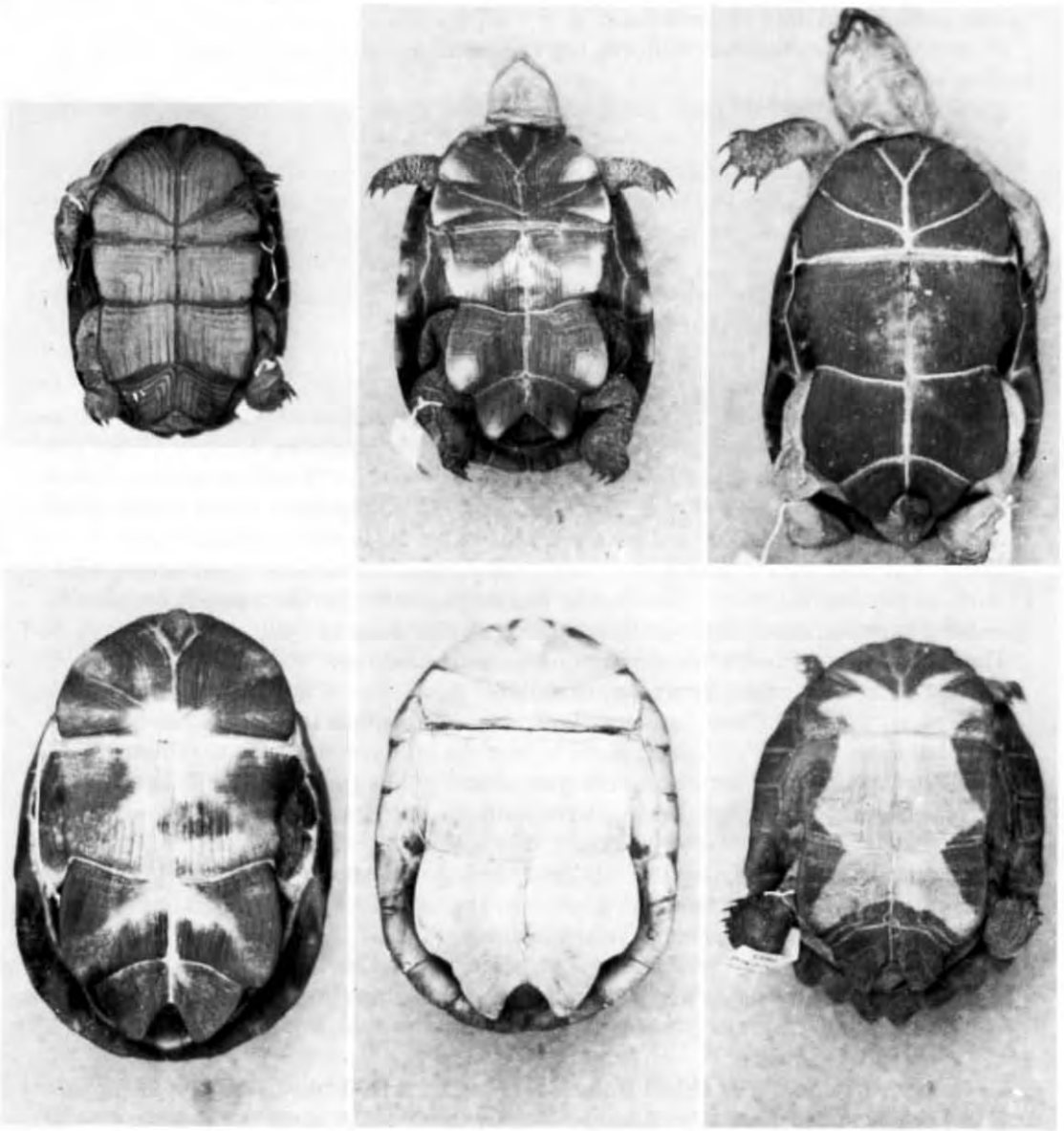


Plate I. *Pelusios:* plastral colour patterns. A. *P. nanus* — CM 5970 Chitau, Angola; B. *P. subniger* UM 19172 Kwaai River, Botswana; C. *P. b. bechuanicus* — UM 20165 Thamalakane River, Botswana; D. *P. rhodesianus* — UM 48 Lochinvar, Kafue River, Zambia; E. *P. castaneus castanoides* — AM — Lake Chilwa, Malawi; F. *P. sinuatus* — UM 32996 Chipangali, Zambia.

P. nanus: yellow, with a little blackish at periphery.

P. subniger: usually with a symmetrical yellow and brown/blackish pattern, each shield yellow mesially and dark towards the sulci.

P. bechuanicus bechuanicus: uniform black, sometimes with yellow patches along the median sulci.

P. bechuanicus upembae: black, with some yellow along the median sulci (Plate III), especially in subadults.

P. rhodesianus: usually black with irregular yellow patches mesially, sometimes uniform yellow (2 Zimbabwean specimens) or uniform black.

P. castaneus castanoides: uniform yellow, or with a little black on the anterior peripheral sulci.

P. sinuatus: yellow mesially with an angular black peripheral pattern; sometimes with one or two narrow black forward-directed chevrons mesially.

15. Colour pattern of head

Rendahl (1939a) noted that the vermiculate head pattern of *S. castaneus* helped to distinguish this species from *S. nigricans* (= *P. subniger*) in the Seychelles. Laurent (1956) also used this character to separate *P. rhodesianus* (as *P. castaneus*) with head finely vermiculate from *P. subniger* with head uniform brown in Zaire. He subsequently found that Angolan specimens of *P. rhodesianus* do not have vermiculate heads (Laurent, 1964).

The symmetrical yellow head pattern of *P. bechuanicus bechuanicus* (FitzSimons, 1935: Pl. xi) is an excellent diagnostic character for this taxon, but the northern race *P. bechuanicus upembae* has similar head markings to parapatric *P. rhodesianus.*

The head patterns recorded in southern Africa are as follows:

P. nanus: black with light brown vermiculation.

P. subniger: usually uniform brown, sometimes spotted with black. UM 30428 has black vermiculation.

P. bechuanicus bechuanicus: black with symmetrical yellow markings (Pl. II, left).

P. bechuanicus upembae: light brown above, uniform or with yellow vermiculation, yellow laterally.

P. rhodesianus: Northern populations (Zaire, northern Angola, Zambia and Malawi) — brown/yellow vermiculation. Southern populations (southern Angola and Zambia, south to Natal) — uniform brown, becoming yellow laterally.

P. castaneus castanoides: black with fine yellow vermiculation (Pl. II, right).

P. sinuatus: black with light brown or yellow vermiculation (Pl. IV).

16. Colour of neck and limbs

P. subniger may be distinguished from the other southern forms by its grey/black skin colour. This character was used to distinguish the species from *P. castaneus* in the Seychelles by Rendahl (1939a). *P. castaneus castanoides* is the only taxon in which the outer surfaces of the limbs are yellow.

Skin colouration in the southern African species is as follows:

P. nanus: skin yellow, outer surfaces of limbs dark brown.

Plate II. *Pelusios:* lateral head markings in live specimens. Left, *P. bechuanicus bechuanicus* juvenile from Victoria Falls (photo: D. K. Blake); Right, *P. castaneus castanoides* from Ntambeni Pan, Kwa-Zulu (photo: E. Moll).

P. subniger: skin grey/black, outer surfaces of limbs black.
P. bechuanicus bechuanicus: skin pale grey, outer surfaces of limbs and claws grey.
P. bechuanicus upembae: skin yellow, outer surfaces of limbs and claws yellow-brown.
P. rhodesianus: skin pale yellow, outer surfaces of limbs grey-brown.
P. castaneus castanoides: skin yellow, outer surfaces of limbs yellow.
P. sinuatus: skin olive/yellow, outer surfaces of limbs grey.

17. Colour of iris

Vaillant (1891) found that live specimens of *S. castaneus* from western Madagascar had a fine silver line encircling the pupil, whereas in *S. nigricans* (= *P. subniger*) from eastern Madagascar the iris was uniform brown. Rendahl (1939a) also found this character to be diagnostic for the two species in the Seychelles.

In live material from Zimbabwe, the iris is grey with silver flecks and a silver ring encircling the pupil in *Pelomedusa subrufa*, *Pelusios subniger*, *P. rhodesianus* and *P. sinuatus* (Pl. IV). The iris is uniform dark brown in a ♀ *P. b. bechuanicus* from Victoria Falls.

18. Ratio: Interorbital width/supraocular sulcus (Fig. 2)

This ratio featured prominently in the key to the genus prepared by Boulenger (1889) and was also employed by Loveridge (1941) to separate *P. sinuatus* from his composite '*P. subniger*'. Analysis of this character in southern African populations (Fig. 4A) indicates great variation, so that it could only be used to separate the blunt-headed *P.bechuanicus* from the relatively long-snouted *P. sinuatus*.

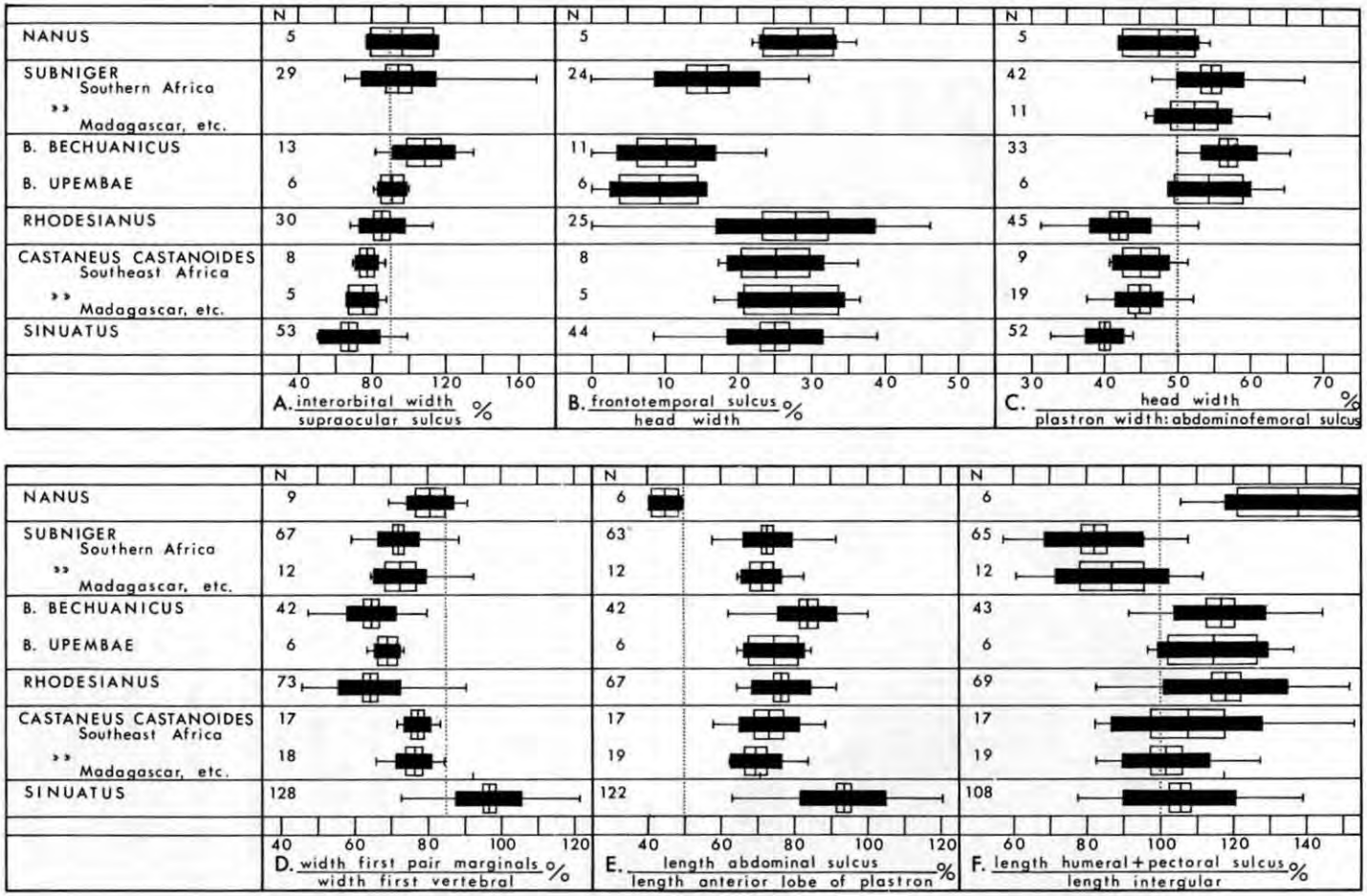
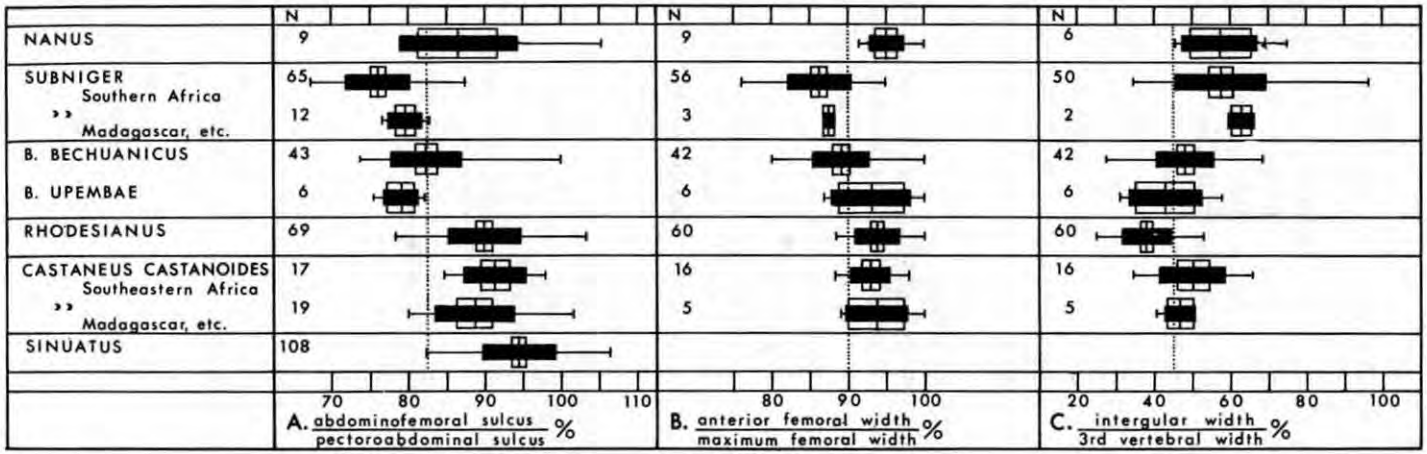


Fig. 4. *Pelusios:* variation in southern African populations for the following ratios: A. Interorbital width/supraocular sulcus; B. Frontotemporal sulcus/head width; C. Head width/plastron width at abdominofemoral sulcus. D. Width first pair of marginals/width first vertebral; E. Length of abdominal sulcus/length of anterior lobe of plastron; F. Length of humeral + pectoral sulcus/length of intergular. The horizontal line indicates the range; the vertical line indicates the mean; the solid rectangle indicates one standard deviation on each side of the mean and the hollow rectangle indicates twice the standard error on each side of the mean.



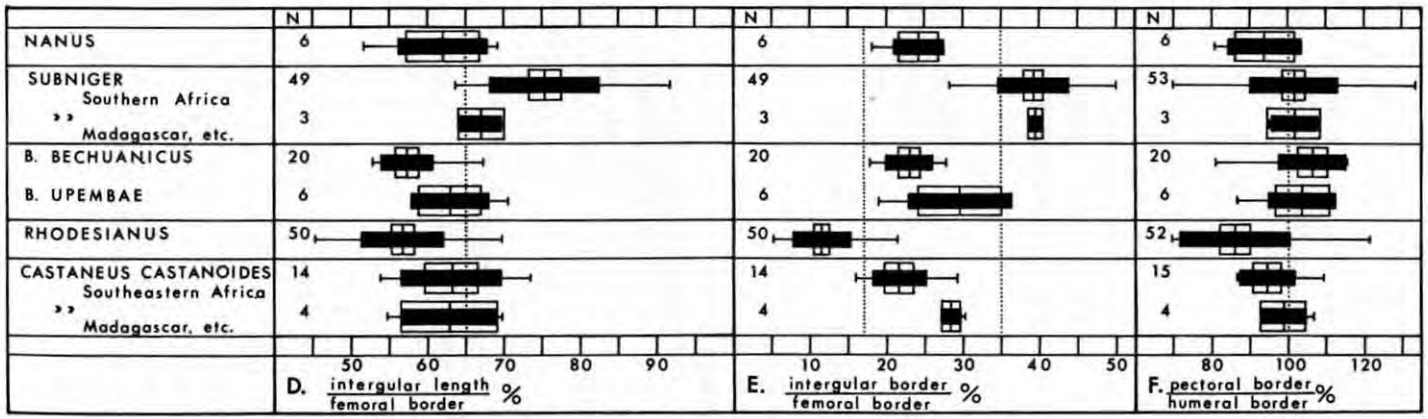


Fig. 5. *Pelusios:* Variation in southern African populations for the following ratios: A. Plastron width at abdominofemoral sulcus/pectoroabdominal sulcus; B. Anterior femoral width/maximum femoral width; C. Intergular width/third vertebral width; D. Intergular length/femoral border; E. Intergular border/femoral border; F. Pectoral border/humeral border. Conventions as in Fig. 4.

19. Ratio: Frontotemporal sulcus/head width (Fig. 2)

Gray (1863; 1870) used the scalation of the temporal region as a diagnostic character for the separation of his sections (or subgenera) *Tanoa* and *Notoa*. His illustration of the *Tanoa* arrangement is based on a Port Natal specimen, one of two which Gray had previously (1855) assigned to *S. castaneus*, but now called *S. sinuatus*: they are in fact *P. rhodesianus*. In this case there is a long sulcus between the frontal and temporal (the 'tympano-frontal suture' of Boulenger, 1907a), which is *ca.* 42% of the head width. In the section *Notoa*, based on a Malagasy specimen of *S. subniger*, there is only a short sulcus between frontal and temporal (9% of head width), followed by a wedge-shaped group of small shields. Vaillant (1891), Siebenrock (1906) and Rendahl (1939a) also used the scalation of the temporal region to distinguish *S. castaneus* from *S. nigricans* (= *P. subniger*).

This is an extremely variable character, but Fig. 4B indicates some average differences. *P. bechuanicus* can be separated from all other species except *P. subniger* on the basis of its very short frontotemporal sulcus.

20. Ratio: Head width/plastron width at abdominofemoral sulcus

This ratio was used by Laurent (1956; 1965) to distinguish *P. rhodesianus* (as *P. castaneus*) from *P. subniger*. Fig. 4C indicates that on the African mainland this ratio will usually separate *P. rhodesianus* and *P. castaneus* from sympatric *P. subniger* and *P. bechuanicus*, but it is a poor diagnostic character in the Madagascar/Seychelles region.

21. Ratio: Width of first pair of marginals/width of first vertebral

This very useful character was first employed by Gray (1855), but was ignored by subsequent workers until introduced into a key for Zambian forms (Broadley, 1971). In *P. sinuatus* the first pair of marginals are subequal (usually more than 85%) to the anterior margin of the first vertebral in width, in the other five species they are usually less than 85% of the width of the first vertebral (Fig. 4D).

A check on extralimital material shows that in West Africa typical *P. castaneus* (= *P. derbianus* auct.) has wide first marginals (well illustrated by Gray, 1855: Pl. xx and Villiers, 1958: Fig. 215) as does the type of *P. c. seychellensis* (Siebenrock).

The narrowest first vertebrals occur in near-topotypic populations of *P. rhodesianus*.

22. Ratio: Length/width of third vertebral

Hewitt (1933) used this character in his diagnosis of *P. sinuatus leptus*. Fig. 6 demonstrates the allometric growth in this character, but the third vertebral is always longer than wide in adults of *P. sinuatus*.

23. Ratio: Abdominal sulcus/anterior lobe of plastron

A relatively long abdominal suture was used to distinguish *S. sinuatus* from *S. nigricans* by Siebenrock (1903) and Nieden (1913), but the latter author noted that the latter measurement did not exceed that of the anterior lobe of the plastron in specimens less than 200 mm in carapace length. This ratio (Fig. 4E) was the primary character in the key to the genus compiled by Loveridge (1941).

P. nanus (together with the extralimital species *P. adansonii* and *P. gabonensis*) has an abdominal sulcus less than half as long as the anterior lobe of the plastron, together with a poorly developed plastral hinge.

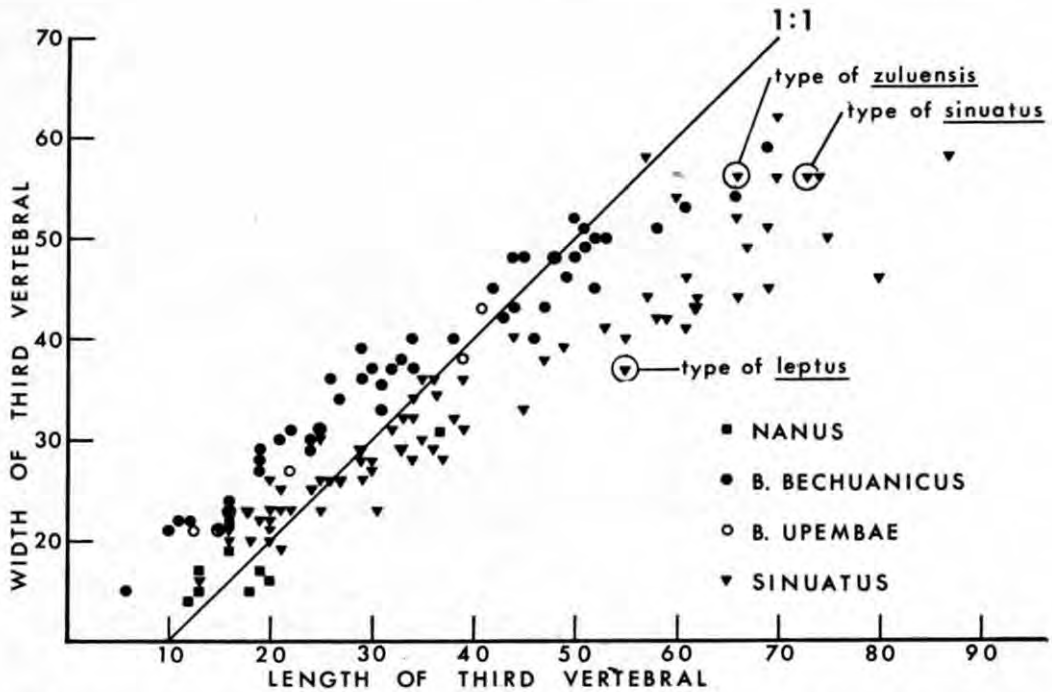


Fig. 6. *Pelusios:* Scatter diagram showing length versus width of third vertebral in *P. nanus*, *P. bechuanicus* and *P. sinuatus*. The latter species shows marked allometric growth in this shield.

The remaining species all have an abdominal sulcus more than half the length of the anterior lobe of the plastron and in large specimens of *P. sinuatus* it may be as long or even longer (Fig. 7) due to allometric growth.

Raw (1978) claimed that in Natal *P. rhodesianus* could be distinguished from *P. castaneus* because the anterior lobe of the plastron is flat, not rounded and recurved at the margins. This character is variable in all species, especially *P. sinuatus*.

24. Ratio: Humeral + pectoral sulcus/intergular length

This ratio was used by Laurent (1956; 1965) to distinguish *P. rhodesianus* (as *P. castaneus*) from *P. subniger*. In southern Africa *P. subniger* usually has the intergular longer than the humeral + pectoral sulcus, whereas these proportions are reversed in *P. nanus*, *P. rhodesianus* and *P. bechuanicus* (Fig. 4F). *P. castaneus* cannot be separated from *P. subniger* on the basis of this character.

25. Ratio: Plastron width at abdominofemoral sulcus/pectoroabdominal sulcus

This ratio was used by Laurent (1956) in his separation of *P. rhodesianus* (as *P. castaneus*) from *P. subniger*. Fig. 5A indicates that this ratio effectively separates *P. subniger* from *P. rhodesianus* and *P. castaneus* wherever they are sympatric, but allopatric populations of

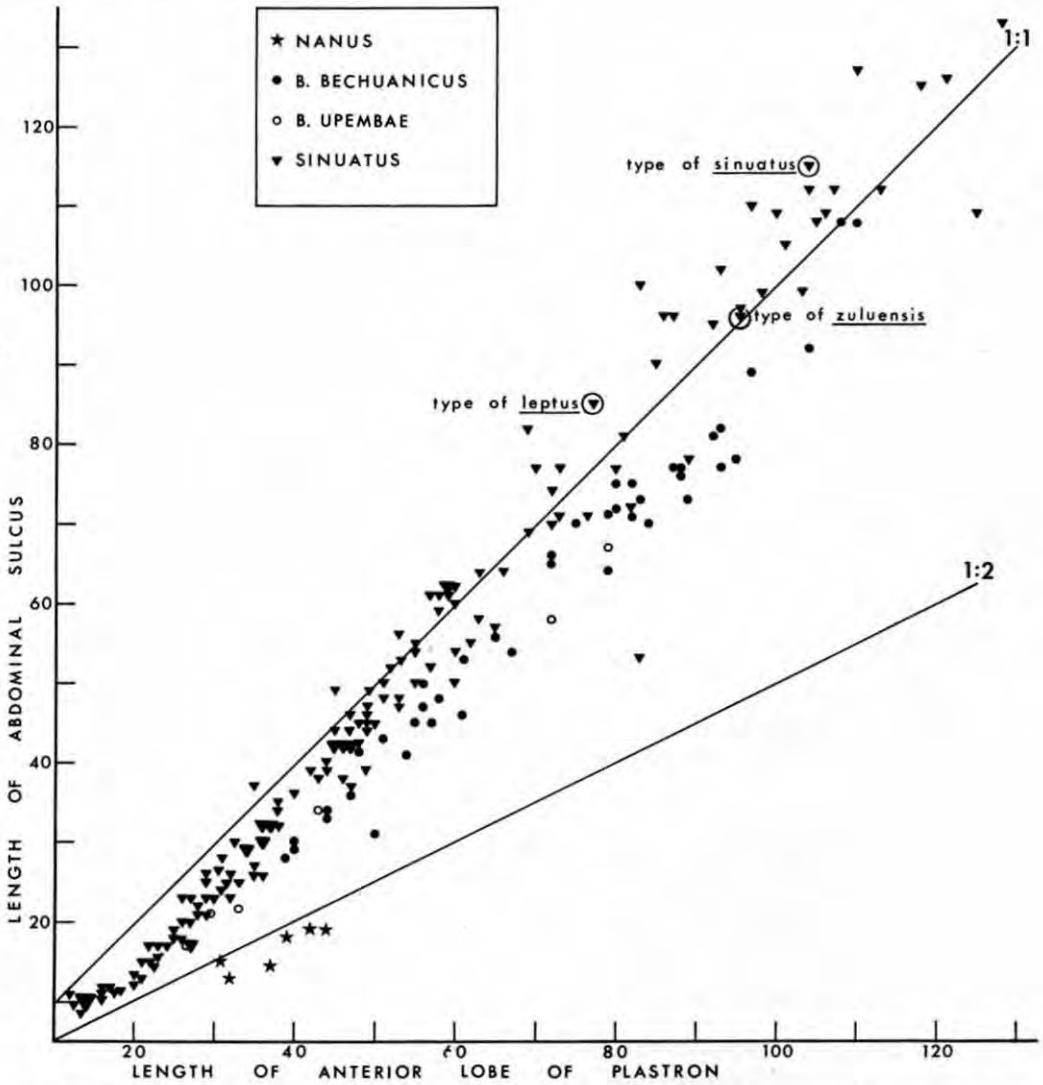


Fig. 7. *Pelusios:* Scatter diagram showing abdominal sulcus versus length of anterior lobe of plastron in *P. nanus*, *P. bechuanicus* and *P. sinuatus*. The latter species shows allometric growth in this ratio.

P. rhodesianus in Angola and *P. castaneus castaneus* in West Africa show some overlap and *P. bechuanicus* is also intermediate in this character.

The high ratio shown by *P. sinuatus* is due to the posterior constriction of the anterior lobe of the pastron at the level of the axillary shields, combined with the absence of any abdominofemoral constriction.

26. Ratio: Anterior femoral width/maximum femoral width

This ratio was introduced by Laurent (1964), but not used in his 1965 review of the genus. It specifically measures the abdominofemoral constriction and Fig. 5B indicates that it will usually separate *P. subniger* from *P. nanus*, *P. rhodesianus* and *P. castaneus*, but *P. bechuanicus* is intermediate.

27. Ratio: Intergular width/third vertebral width

This ratio was used by Laurent (1965) in his analysis of variation in *P. rhodesianus* (as *P. castaneus*) in Zaire and Rwanda, but in his Fig. 11 showing similar data for *P. williamsi*, the vertical scale has obviously been wrongly calibrated. Analysis of variation in southern African taxa shows a clear separation of *P. rhodesianus* from *P. subniger* and *P. nanus*; *P. b. bechuanicus* and *P. castaneus castanoides* are intermediate (Fig. 5C).

Raw (1978) drew attention to the narrow intergular in Natal specimens of *P. rhodesianus*. He states that it is not 'diamond-shaped', whereas Hewitt (1927) emphasised the 'diamond-shaped' gular of the type of *P. rhodesianus*, contrasting it with the 'pear-shaped' intergular of *P. castaneus* as illustrated by Siebenrock (1906). Most *P. rhodesianus* have a moderate to narrow lozenge-shaped intergular, but the range of variation includes the form illustrated by Raw (1978: Fig. 3).

28. Ratio: Intergular length/femoral border

Laurent (1965) used this ratio in his diagnosis of *P. williamsi*, but the vertical scale in his Fig. 10 is obviously wrongly calibrated, as the same data appear in Fig. 12, which is apparently correct.

The data for the southern African taxa is illustrated in Fig. 5D. *P. subniger* is readily distinguished from *P. bechuanicus* and *P. rhodesianus*, but overlaps *P. castaneus castanoides* to some extent.

29. Ratio: Intergular border/femoral border

This ratio was presented in graphical form by Laurent (1965: Fig. 9) to demonstrate differences between *P. niger*, *P. rhodesianus* (as *P. castaneus*) and *P. c. castaneus* (as *P. c. derbianus*), but southern African material of *P. rhodesianus* would plot among the *derbianus*, suggesting that the vertical scale is wrongly calibrated. Data for southern African populations are analysed in Fig. 5E, which highlights the narrow intergular border of *P. rhodesianus* and the very broad one of *P. subniger*.

Laurent (1965: Fig. 19) also plotted intergular border against gular border when trying to separate his new taxon *chapini* from *P. rhodesianus*, but it is difficult to measure these small shields accurately because of wear on their outer edges. Laurent noted dimorphism in the width of the intergular border, but at least some of the specimens with a wide intergular border are actually *P. bechuanicus upembae*.

30. Ratio: Pectoral border/humeral border

This ratio was used by Boulenger (1889) as a key character to separate *S. derbianus* from *S. nigricans*. Siebenrock (1903) and Rendahl (1939a) have pointed out that the great variability makes it a poor taxonomic character. Data for southern African taxa (Fig. 5F) shows that its only possible use might be in separating headless shells of *P. bechuanicus* from

P. rhodesianus, although there is a considerable overlap.

Laurent (1965) also plotted the pectoral sulcus against both humeral sulcus and width of third vertebral in his analysis of variation in *P. castaneus* (including *P. rhodesianus*), but there is great variation within populations and considerable overlap of data for the taxa concerned. When similar data were plotted for southern African populations, the only clear feature was that the pectoral suture averaged longest in *P. castaneus castanoides*.

31. Size of eggs

There is a consistent difference in egg size between *P. bechuanicus bechuanicus* (38 to 39 × 23 mm) and *P. rhodesianus* (33 to 34 × 20 mm), two species which are sympatric over a considerable area. This character should be checked for other taxa.

32. Karyotype

Killebrew (1975) has illustrated the karyotypes of *Pelomedusa* and three species of *Pelusios*, but locality data for the specimens are not given, so the data given for *P. castaneus* could belong to *P. rhodesianus*. The other two species checked were *P. subniger* and *P. sinuatus*. The karyotypes are uniform in chromosome number (2N = 34), arm lengths and morphology.

ATTRIBUTION OF NAMES

Pelusios subniger, the type species of the genus, was initially given the vernacular name *La Noiratre* by Lacépède in 1788 and was formally named *Testudo subnigra* by him in the following year. The type is in the Paris Natural History Museum (MNHN 8366), the type locality is unknown, but Bour (1978) has restricted it to Tamatave, Madagascar. Most early references to this taxon appear under the name *Pelusios* (or *Sternothaerus*) *nigricans* Donndorff.

Emys castanea was described by Schweigger in 1812, based on a young (74 mm carapace length) specimen, previously described (but not named) by Daudin (1801) as a 'Tortue brun marron', lacking locality data. The specimen was formerly in Daudin's private collection and is now lost (Bour, 1978). The redescription of '*Sternotherus castaneus*' by Duméril & Bibron (1835) was based on a Malagasy specimen, but Bour (1978) has pointed out that the brief descriptions of Daudin (1801) and Schweigger (1812) agree better with *Pelusios* material from the Gulf of Guinea, especially with regard to the extensive brown peripheral patches on the plastron. He has consequently applied the name *P. castaneus castaneus* to the West African form (with *derbianus* Gray as a synonym), which does have a chestnut-coloured carapace. Bour (1978) has proposed a new name *P. castaneus kapika* for the Malagasy populations.

Sternotherus sinuatus was described by Andrew Smith in 1838 from 'rivers to the north of 25° south latitude' (here restricted to the Crocodile-Marico confluence, northern Transvaal). The type is in the Royal Scottish Museum, Edinburgh (RSM 1859.13.1684) and has been redescribed and illustrated by FitzSimons (1937), who drew attention to various discrepancies in Smith's original figures. Various data provided by FitzSimons (1937) have been used in the species analysis.

Sternothaerus nigricans seychellensis was described by Siebenrock in 1906 on the basis of a single specimen from the Seychelles, *not* Gloriosa Island as indicated by Loveridge

(1941), Wermuth & Mertens (1961; 1977) and Laurent (1965). I have examined the type specimen, No. 13247 in the Naturhistorisches Museum, Vienna, and it differs in several respects from the *P. castaneus* populations of East Africa, Pemba Island, Madagascar and the islands of Mahé and La Digue. The carapace and plastron are black, not brown and yellow respectively as is usual in eastern populations of *P. castaneus*. The first pair of marginals are very wide (as in *P. sinuatus*), 92 per cent of the width of the first vertebral anteriorly. This name has priority over *castanoides* Hewitt 1931 for the eastern race of *P. castaneus*, but it may represent a valid taxon restricted to one of the Seychelles Islands which has not been sampled since Prof. Brauer collected the type. I have examined the specimen from Gloriosa Island listed by Stejneger (1893), now USNM 20954, and it is a *P. subniger*.

Pelusios sinuatus zuluensis Hewitt 1927, was based on a series of specimens from the Umsinene River, Zululand. He distinguished this subspecies from the typical form on the basis of the well developed median protuberances on vertebrals 3 and 4 and the upturned posterior marginals. The holotype (NMBO 609) and paratype (NMBO 610) are in the Nasionale Museum, Bloemfontein, and data for them have been provided by Dr. S. W. P. de Waal. This taxon is considered a synonym of *P. sinuatus*.

Pelusios nigricans rhodesianus was also described by Hewitt in 1927, based on a series of specimens from Mpika District, Zambia, that was apparently sympatric with 'typical *P. nigricans*' (= *P. subniger*). He noted that his new form resembled *P. n. castaneus*, but differed in its 'somewhat diamond-shaped intergular'. The holotype and four paratypes in the Albany Museum (dry shells) all bear the same catalogue number AM 5432. The holotype had most of the shields of the carapace burnt during a fire at the Albany Museum in 1941, but the plastron is only slightly damaged and can readily be identified with Plate xxi, Fig. 2, in Hewitt, 1927. The holotype has a continuous series of eight neural bones (Fig. 13) and the name is applicable to the blackish form with a narrow or lozenge-shaped intergular which is sympatric with *P. castaneus* in Zululand.

The precise type locality is unknown, but the collector published an account of his observations of game in Zambia (Knowles Jordan, 1959) and it seems likely that the type of *P. rhodesianus* was obtained southeast of Lake Bangweulu or possibly on the Chambeshi River.

Pelusios nigricans castanoides was described by Hewitt in 1931, based on a single large female (TM 13433) from Lake St. Lucia, Zululand (locality data from label and catalogue entry: Hewitt's reference to Richard's Bay in the original description seems to be an error, he indicated that the locality was St. Lucia Lake in his key to the genus). The characters employed by Hewitt to separate this form from *P. nigricans castaneus* (*sensu* Siebenrock, 1906) are variable ones, but with the application of the name *castaneus* to the West African form with eight neurals by Bour (1978), *castanoides* becomes available for the eastern race with the neurals reduced.

P. bechuanicus was briefly diagnosed by FitzSimons in 1932 and more fully described and illustrated in 1935. The type specimen (TM 14688) is subadult and the only valid diagnostic character mentioned by FitzSimons is the symmetrical yellow head markings. The new taxon was compared only with *P. sinuatus*. Adequate topotypic material of *P. bechuanicus*

is now available to confirm the validity of this species.

P. sinuatus leptus was described by Hewitt in 1933 from an adult shell collected at Isoka in northeastern Zambia by E. Knowles Jordan. The subspecies was distinguished from the typical form on the basis of its narrow vertebral shields (Fig. 6 & 15), reduction in number of neural bones and strong development of conical vertebral protuberances, especially on vertebral 4. Hewitt's assertion that this form was adapted for terrestrial life seems to be without foundation.

Unfortunately the holotype (AM un-numbered) differs from the paratypes in having a fully developed fifth neural (reduced or absent in four paratypes); it is also aberrant in having 13 marginals on the right side. The skeletal carapace illustrated in Hewitt, 1933, Pl. ix, Fig. 1, is now missing. The surviving paratypes are AM 5432 (Mpika District), AM 5794 (Isoka) and AM 6696 (Luangwa Valley).

P. nanus was described by Raymond Laurent in 1956, based on a ♀ holotype from Dilolo, Haut Lualaba, in the Katanga (= Shaba) Province of Zaire, and nine paratypes from southeastern Zaire. One paratype (MRAC 7836) was examined during the present study.

P. castaneus kapika was described by Roger Bour in 1978, the holotype (MNHN 1929-238) originating from Sambirano delta, Diégo Suarez, Madagascar. It seems doubtful whether the Malagasy populations of *P. castaneus* can be distinguished from those of the east African mainland, here referred to *P. castaneus castanoides* Hewitt.

KEY TO THE GENUS *PELUSIOS* IN SOUTHERN AFRICA (EXCLUDING JUVENILES WITH CARAPACE LENGTH <70 mm)

1a. Sulcus between abdominals less than half length of anterior lobe of plastron (Fig. 10); plastron hinge weakly developed .. .. *nanus*

1b. Sulcus between abdominals more than half length of anterior lobe of plastron; plastron hinge strongly developed 2

2a. An axillary shield present (Fig. 15); posterior width of first pair of marginals usually more than 85% of anterior width of first vertebral; posterior margin of carapace usually serrated or sinuate; plastron yellow with a symmetrical black angular peripheral pattern (Pl. IF) .. .. *sinuatus*

2b. No discrete axillary shield present; posterior width of first pair of marginals usually less than 85% of anterior width of first vertebral; posterior margin of carapace smoothly rounded; plastron black to brown and/or yellow, without a black angular peripheral pattern 3

3a. Head width usually more than half plastron width at abdominofemoral sulcus; tip of beak not bicuspid; postocular usually separated from masseteric shield by a quadrilateral supralabial; falciform scales on anterior face of forelimb poorly to moderately developed 4

3b. Head width usually less than half plastron width at abdominofemoral sulcus; tip of beak bicuspid; postocular and masseteric shield usually in contact; a series of transversely elongate falciform scales on forelimb 6

4a. Carapace brown; shields of plastron yellow mesially, brown to black at sulci, forming a symmetrical pattern (Pl. IB); skin of neck and limbs grey-black; intergular usually longer than humeral + pectoral sulcus and more than 65% length of femoral border; intergular border usually more than 35% length of femoral border .. .. *subniger*

4b. Carapace black; plastron uniform black or yellow/brown along median sulci; skin of neck and limbs grey or yellow-brown; intergular usually shorter than humeral + pectoral sulcus and less than 65% length of femoral border; intergular border usually less than 35% length of femoral border 5

5a. Mental barbels 3; head above black with distinct yellow symmetrical pattern (Pl. II, left) nape and outer faces of limbs dark grey; range Okavango basin .. .. *bechuanicus bechuanicus*

5b. Mental barbels 2; head above light brown, uniform or with fine yellow vermiculation, nape and outer faces of limbs yellow-brown; range Upemba basin .. .. *bechuanicus upembae*

6a. Eight neurals, the first always in contact with nuchal; intergular rhomboidal, its border usually less than 15% of femoral border; carapace black; plastron black, or yellow mesially, rarely uniform yellow; head with yellow vermiculation in the Congo basin, uniform brown above in southern populations; skin on outer faces of limbs grey-brown .. .. *rhodesianus*

6b. Five to seven neurals, the first (if present) never in contact with nuchal; intergular pentagonal or pyriform, its border usually more than 15% of femoral border; carapace yellow to brown, uniform or with black blotches; plastron yellow, uniform or with some peripheral sulci black, especially on anterior lobe of plastron; head with brown and yellow vermiculation; skin on outer faces of limbs yellow .. .. *castaneus castanoides*

SYSTEMATIC ACCOUNT

PELUSIOS NANUS Laurent

Fig. 1A, 10; Pl. IA.

Pelusios derbianus (not Gray) Schmidt, 1933: 3.

Sternothaerus nigricans (not Donndorff) Monard, 1937: 148 (part).

Pelusios subniger (not Lacépède) Witte, 1952: 12 (part) & 1953: 19 (part).

Pelusios nanus Laurent, 1956, *Annls. Mus. r. Congo belge* Sér. 8vo, 48: 31, Pl. iv, Fig. 2-4. Type locality: Dilolo, Shaba Province, Zaire. Laurent, 1964: 25; 1965: 4 & 26; Broadley, 1971: 45, Pl. ii; Wood, 1974: 303.

Pelusios adansonii (not Schweigger) Wermuth & Mertens, 1961: 286 (part)

Pelusios adansonii nanus Wermuth & Mertens, 1977: 116.

Diagnosis. A dwarfed species (maximum carapace length 120 mm) with anterior lobe of plastron more than twice length of abdominal sulcus and weakly developed hinge. Forelimbs without falciform scales. Vertebrals without keels. Top of head vermiculate. First neural narrowed anteriorly, eighth reduced or absent.

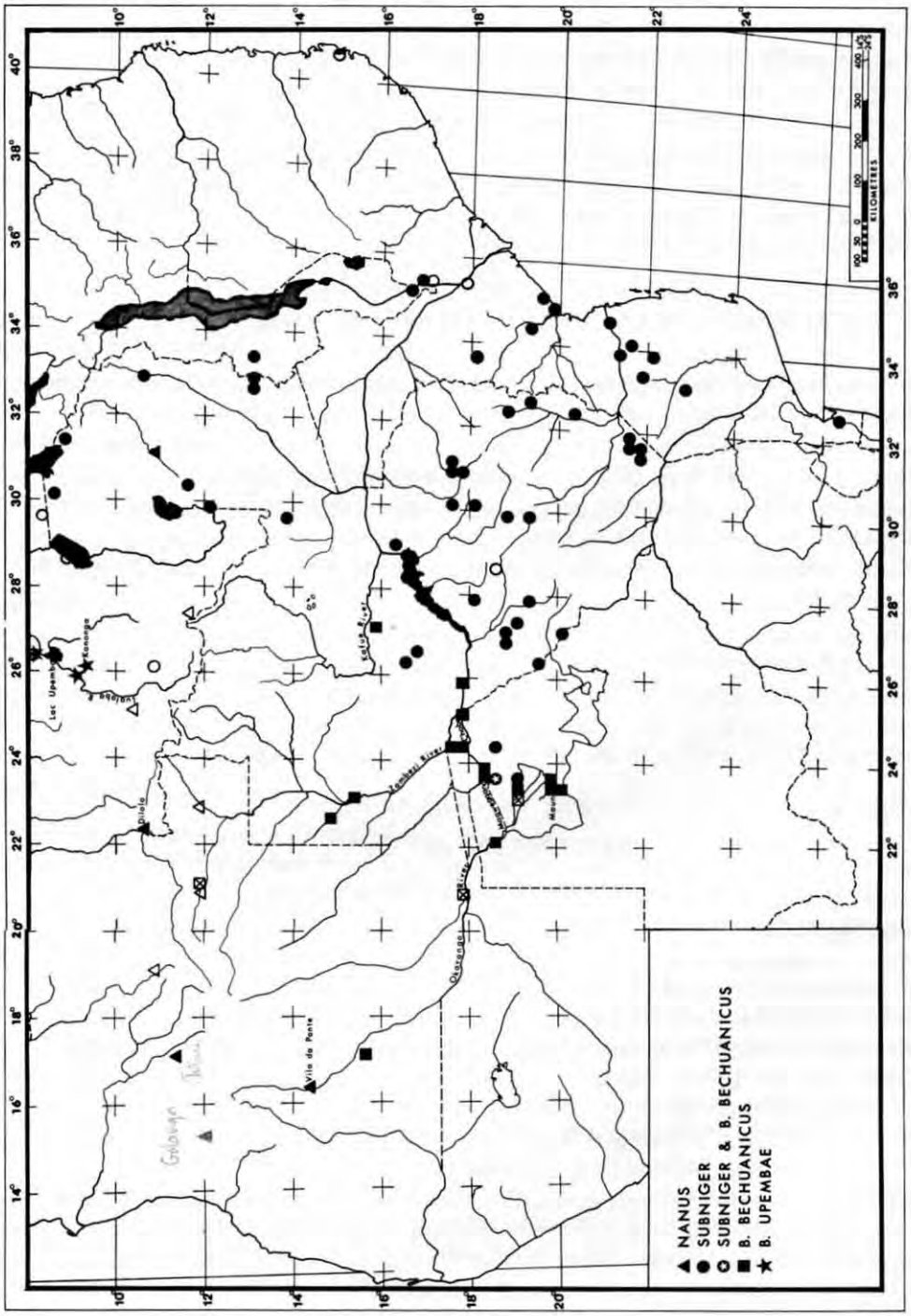


Fig. 8. Distribution of *P. nanus*, *P. subniger* and *P. bechuanicus* in southern Africa.

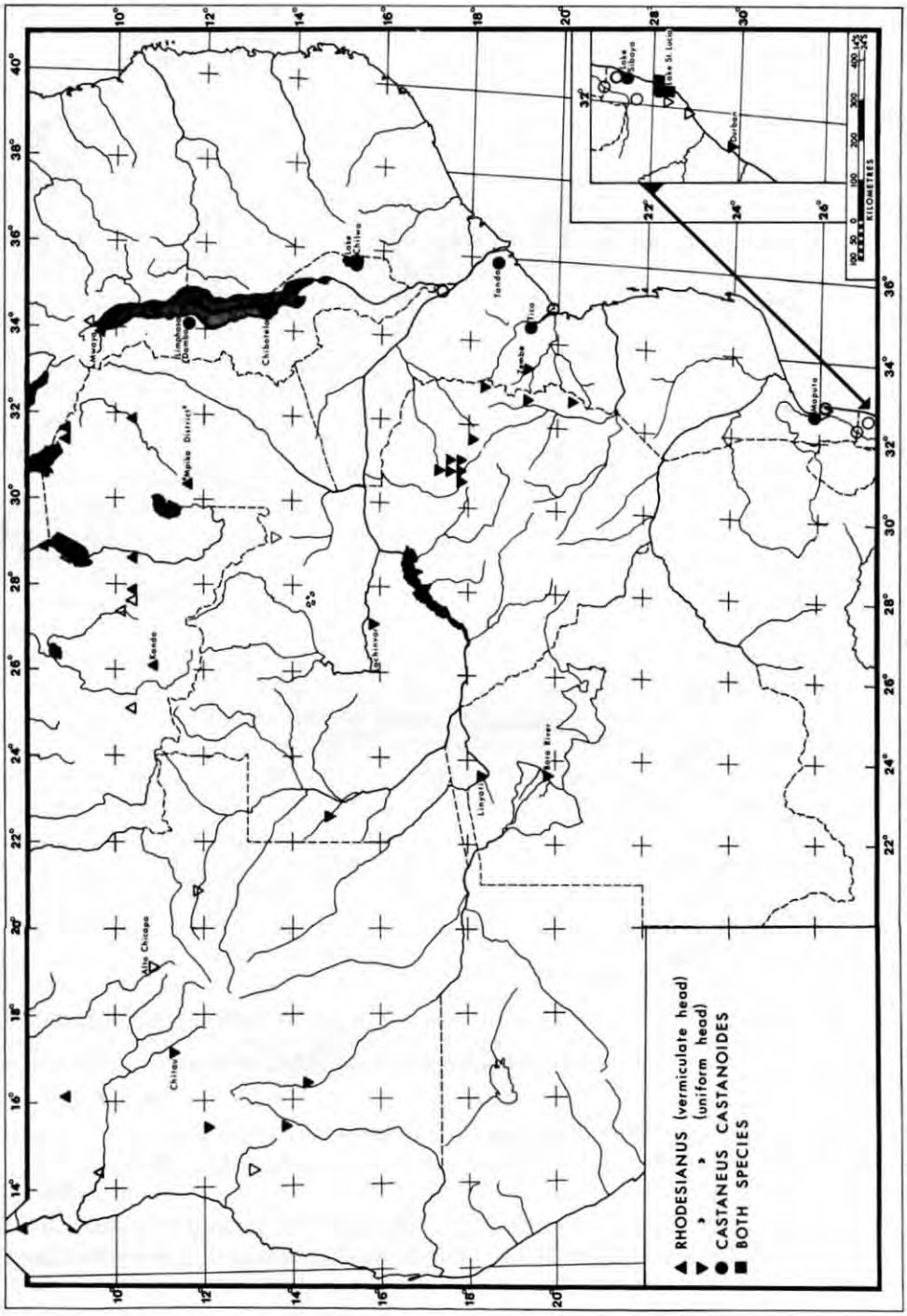


Fig. 9. Distribution of *P. rhodesianus* and *P. castaneus castanoides* in southern Africa.

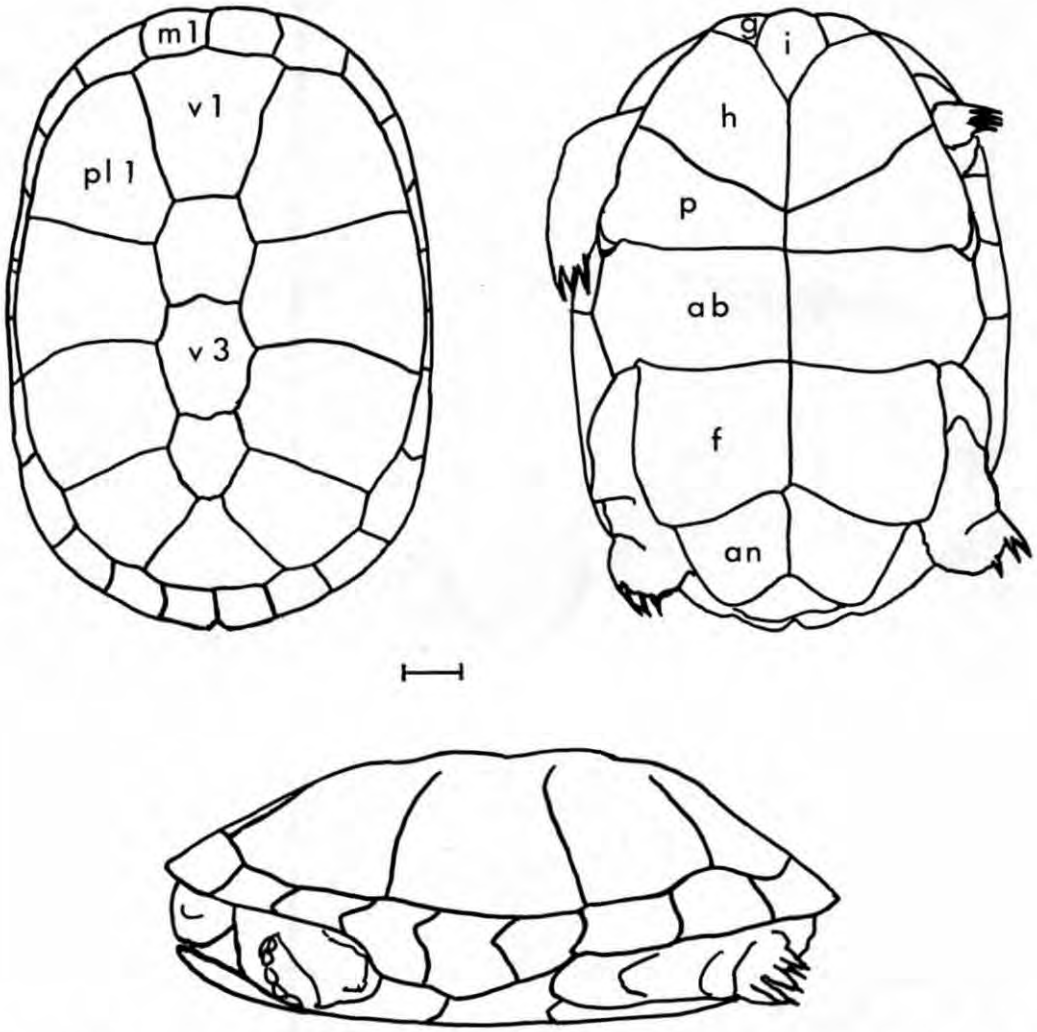


Fig. 10. *P. nanus:* dorsal, ventral and lateral views of the shell of CM 5970 Chitau, Angola. Key to epidermal shields: ab = abdominal; an = anal; f = femoral; g = gular; h = humeral; i = intergular; m = marginal; p = pectoral; pl = pleural; v = vertebral. The horizontal line equals 1 cm to scale.

Description. Head black with brown vermiculation, skin of neck and limbs yellow, outer faces of limbs dark brown. Carapace brown, sometimes streaked with black; bridge black; plastron yellow, margined with black.

Head moderate with blunt snout; beak not bicuspid; frontotemporal sulcus long; supralabial present. Tomium separated from two mental barbels by a transverse series of about five scales. No development of falciform scales on forelimb.

Carapace oval, rather elongate in male, with a notch between the twelfth marginals, which may project (Fig. 1A); vertebrals with little trace of a median keel, third vertebral wider than long in subadults, longer than wide in adults; first pair of marginals between 70 and 85% anterior width of first vertebral; lateral marginals not keeled; growth rings on carapacial shields well marked.

Plastron with anterior lobe more than twice the length of the abdominal sulcus, hinge weakly developed; intergular and pectoral sulcus both short in relation to humeral sulcus; intergular pyriform; posterior lobe of plastron only slightly constricted at abdomino-femoral and femoroanal sulci. Epidermal shields with well-defined growth rings.

Neural bones 7 or 8, the first narrowed anteriorly and barely contacting the nuchal, the eighth reduced in size (Fig. 1A) or more commonly absent.

The largest specimen examined has a carapace length of 113 mm (AMNH 50757 Chitau, Angola). Laurent (1956) recorded a ♀ of 119 mm from Kanzenze, Zaire.

Distribution. Moist savannas along the southern edge of the Congo Basin from Angola eastwards to northern Zambia. One specimen has been recorded from Vila da Ponte on the Cubango (Okavango) River to the south of the South Equatorial Divide (Wellington, 1955) (Fig. 8).

Localities. ANGOLA: Alto Chicapa (Laurent, 1964); Cazombo (Laurent, 1964); Chitau (Schmidt, 1933; Laurent, 1965) AMNH 50757, 50760; CM 5970; UM 33262; Lac Calundo (Laurent, 1964); Vila da Ponte, Kuvangu River (Monard, 1937) LCFM 961. ZAIRE (SHABA PROVINCE): Dilolo (Witte, 1953; Laurent, 1956, 1964) MRAC 7834/6 (paratype); Kanzenze (Witte, 1953; Laurent, 1956); Katibili, Lake Tanganyika (Witte, 1952; Laurent, 1956) BM 1953.1.11. 45-6; Lubumbashi (Witte, 1953; Laurent, 1956). ZAMBIA: Chambeshi-Lukulu Confluence (Broadley, 1971) NMSR 3958.

Discussion. Wermuth & Mertens (1977) placed this taxon as a subspecies of *P. adansonii*, but the two species are very different, especially in the carapace. That of *P. adansonii* is depressed, broadened posteriorly, with a median keel on vertebrals 3 and 4 and no N1. The dwarfed *P. nanus* has a narrow carapace with no trace of a vertebral keel and N1 is always present and distinctively narrowed anteriorly. The colouration is also quite different. *P. adansonii* has a yellow carapace with an attractive pattern of brown spots, the plastron being uniform yellow. *P. nanus* has a dark brown carapace which may be streaked with black, the plastron yellow with peripheral black markings.

The two taxa are widely separated geographically and there appear to be no grounds for considering them conspecific.

PELUSIOS SUBNIGER (Lacépède)

Fig. 1B-C, 11; Pl. IB.

Testudo subnigra Lacépède, 1789, *Hist. nat. Quadrup. ovip. Serpens*, 2; Synops méthod: 175, Fig. 13. Type locality unknown, but restricted to Tamatave, Madagascar by Bour (1978).

Testudo nigricans Donndorff, 1798, *Zool. Beitr.*, 3: 34. No locality.

Sternothaerus leachianus Bell, 1895, *Zool. J. Lond.*, 2: 306, Pl. 15. No locality.

Sternothaerus nigricans Peters, 1882: 8; Bocage, 1896: 97; Tornier, 1896: 7; Boulenger,

1907a; 6 (part); 1907b: 482; Chubb, 1908: 220; 1909a: 592; 1909b: 34; Cott, 1935: 973; Rendahl, 1939a: 304, 322, Fig. 11-12.

Sternothaerus nigricans nigricans Siebenrock, 1906: 35, Pl. v, Fig. 19.

Pelusios nigricans Hewitt, 1927: 375; Pitman, 1934: 307 (part).

Pelusios nigricans nigricans Hewitt, 1931: 466.

Sternothaerus Derbianus (not Gray) Witte, 1933: 47.

Pelusios subniger Loveridge, 1941: 489 (part); 1953: 162 (part); Witte, 1953: 19 (part); Laurent, 1956: 37, Pl. v, Fig. 2 & 4; Sweeney, 1960: 47 (part); Wermuth & Mertens, 1961: 291 (part); Broadley, 1962: 792; Laurent, 1965: 28; Broadley, 1971: 45, Fig. 3; Stevens, 1974: 11; Blake & Broadley, 1974: 314; Wermuth & Mertens, 1977: 118 (part); Broadley & Blake, 1979: 5.

'Lower Shire Pelusius' Mitchell, 1946: 20.

Diagnosis. A small to moderate sized species (maximum carapace length 200 mm) with anterior lobe of plastron less than twice length of abdominal sulcus and strongly developed hinge. No axillary shield. First pair of marginals usually less than 85% anterior width of first vertebral; posterior margin of carapace rounded. Head large, usually more than half width of plastron at abdominofemoral sulcus, where it is strongly constricted; beak not bicuspid; postocular always separated from masseteric shield by a quadrilateral supralabial. Intergular usually longer than humeral + pectoral sulcus and more than 65% length of femoral border; intergular border usually more than 30% length of femoral border. Usually two mental barbels. Carapace brown, shields of plastron yellow mesially, brown/black at sulci; skin of neck and limbs grey/black. Usually eight neurals, separated from suprapygal.

Description. Head brown, usually uniform, sometimes with black spots, rarely vermiculate; skin of neck and limbs grey/black. Carapace brown; bridge yellow and brown; shields of plastron yellow mesially, dark brown towards sulci.

Head large with blunt snout, beak not bicuspid; frontotemporal sulcus short, supralabial always present, separating postocular from masseteric shield. Tomium bordered by granular skin, two mental barbels. Falciform scales on forelimb poorly developed or absent.

Carapace oval (♂♂) to subcircular (♀♀), vertebrals not keeled, the third vertebral usually wider than long throughout life; first pair of marginals usually 65 to 80% of anterior width of first vertebral; lateral marginals not keeled; growth rings on carapacial shields moderately well marked.

Plastron with anterior lobe always longer than (but never twice the length of) abdominal sulcus, hinge well developed; intergular usually longer than humeral + pectoral sulcus and more than 65% of femoral border, pectoral sulcus short (rarely absent); intergular subpentagonal; posterior lobe of plastron strongly constricted at abdominofemoral and femoroanal sulci. Epidermal shields with well marked growth rings.

Neural bones normally eight, forming a continuous series and in contact with the nuchal, but separated from the suprapygal. There are occasionally two superposed suprapygals (Fig. 1B) or the eighth neural may be absent (Fig. 1C). In the skull, the parietal crest lacks a lateral flange.

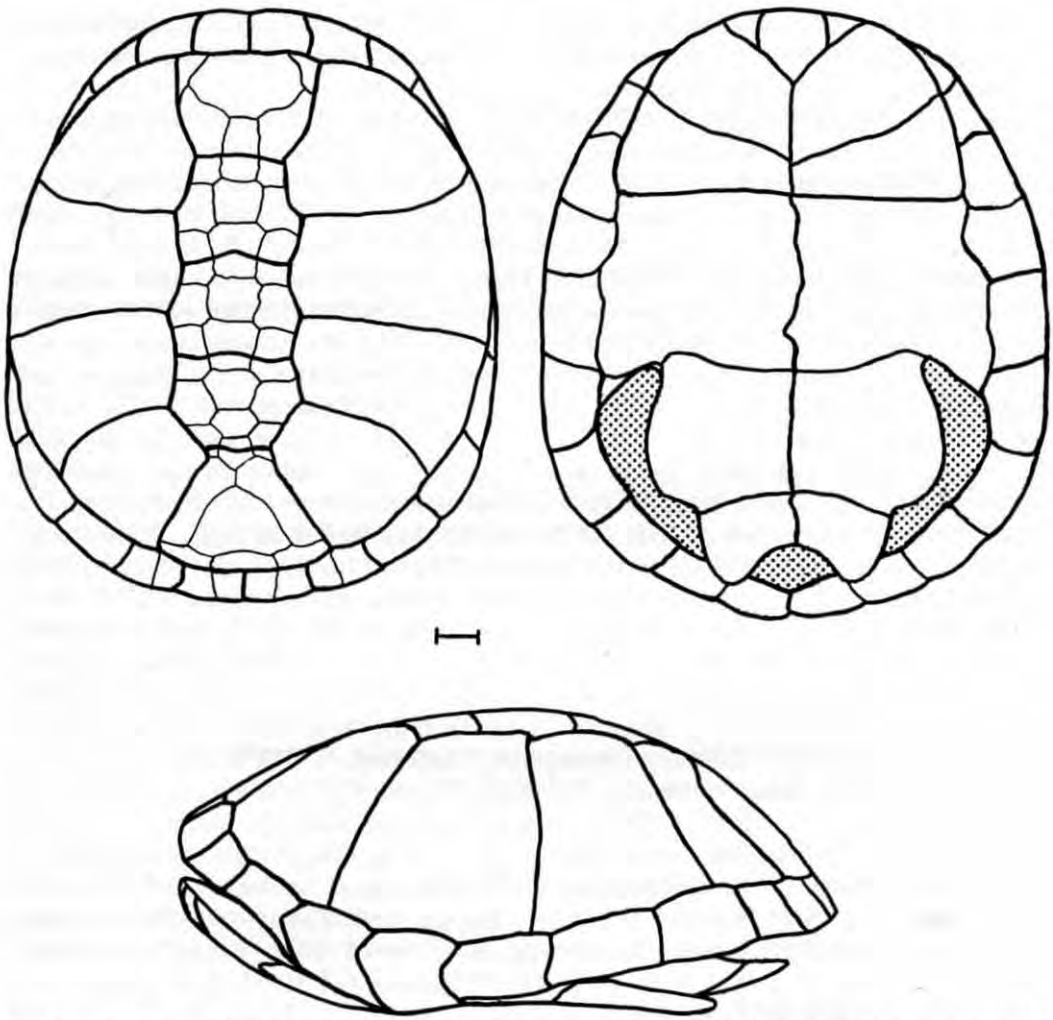


Fig. 11. *P. subniger:* dorsal, ventral and lateral views of the shell of UM 849♀ Lake Kariba. Thin lines indicate sutures between bones; thick lines indicate sulci between epidermal shields. The horizontal line equals 1 cm to scale.

The largest specimen examined has a carapace length of 195 mm (IRScNB 4477a Mbala, Zambia).

Distribution. Eastern Africa from Burundi (Laurent, 1956) and Tanzania to southern Moçambique, west to the Shaba Province of Zaire, Zambia and northern Botswana (Fig. 8), also Madagascar, Gloriosa Island, Seychelles and Mauritius. Laurent (1965) has recorded a specimen from Ethiopia (MCZ 5985), which requires verification. I have examined the 'Pretoria' specimen (MCZ 41943) listed by Loveridge (1941) and Laurent (1965): it was formerly TM 4803 and the original catalogue entry indicates that it was presented on 14

July 1911 by the National Zoological Gardens, locality "Pretoria?" and originally identified as *P. sinuatus* (juvenile). As this species has not subsequently been found in the Transvaal, this doubtful record should be rejected.

Localities. ZAIRE (SHABA PROVINCE): Kando (Witte, 1933; Laur., 1956); Kikondja (Witte, 1933; Laur., 1956); Lukonzolwa (Laur., 1956); Musosa (Witte, 1953; Laur., 1956). ZAMBIA: Alala Plateau (Blgr., 1907a) BM 1906.11.22.2; Bilibili Hot Springs, Kalomo NMSR 3150; Buleya, Mweru-Wantipa (Laur., 1956) IRScNB 4414; Chipangali UM 6574; Chiwale (Pitman, 1934) AM—; Kalikali Dam UM 6575; Kaluwa (Laur., 1956); Lake Kariba, Lufua Confluence MRAC 80-12-R-2; Luangwa Valley AM 5144; Lulimala River (Pitman, 1934) AM —; Mbala (= Abercorn, Laur., 1956) IRScNB 4477 (3); Mpika District (Hewitt, 1927) AM 5432 (3); NMK —; Mulilo AM 6876; Mwesi Stream, Kalomo NMSR 2628. MALAWI: Chiromo (Sweeney, 1960) AM — (2); Kasungu National Park UM 25462; Nsanje (= Port Herald: Loveridge, 1953a; Sweeney, 1960) MCZ 51100. BOTSWANA: Khwai River UM 19172, 20168; Maitengwe River MCZ 157066; UM 33026; Ngamiland TM 45987; Tamasanka Pan UM 19522; Tsotsoroga Pan TM 46229. ZIMBABWE: Gonarezhou National Park — Ntabambomvu Hills UM 32967; Nyala Pan 32987, 32995; Malugwe Pan AMNH 118725; MNHP 1980-983; UM 19625, 20214, 20269, 33036 and Naivasha Pan UM 33170; Gwaai Forest Reserve (Teakland) UM 32966, 32985-6, 33024; Gwamayaya River (Chubb, 1908, 1909a, 1909b); Gwelo River (Chubb, 1908, 1909a, 1909b) BM 1908.5.14.1; Hartley UM 3181-2, 9708-10; Kapiri Salt Pan, Lusulu UM 10572; 10 km E of Kariba QVM (mounted); Lake Kariba UM 849-50, QVM (mounted, ex Charara Confluence); Mazoe UM 9711; Mupudzi River, Umtali UM 14517; Ngamo Pans (Brdly., 1962) UM 1151; Odzi UM 29960; Que Que UM 9720; Sabi Experimental Station UM 3871, 3901; Salisbury District MRAC 80-12-R-1; UM 33138; 15 km W of Salisbury UM 3162; Sinoia to Hartley TM 50060; Wankie National Park — Lavingi Pan UM 20370 and Mukwa Pan UM 29586. MOCAMBIQUE: Banhinhe Swamp TM 29316; Beira (Blgr., 1907b; Rendahl, 1939a) BM 1907.4.29. 9-10; UM 9712; Caia (Cott, 1935); Chambajojo UM 30428; Lake Banamana JPT 526; Lake Nhamapanza UM 30426; Mabunguere UM 30427; Mahicas UM 28345; Maputo River TM 39918; Mhanda Mountain UM 9714; Mossuril (Peters, 1882; Bocage, 1896; Tornier, 1896); Pande II UM 28842; Savane UM 9713; Tica TM 48703; UM 11337; Zimbiti TM 12758; Zinave JPT 1172. LOCALITY UNKNOWN: MCZ 41943 ("Pretoria").

Extralimital material examined:

MADAGASCAR: no precise locality NMW 19084 (2)-5; Majunga SMF 7936; Tamatave NMW 1806-7; SMF 7937. GLORIOSA ISLAND: USNM 20954. SEYCHELLES (MAHE ISLAND): SMF 33051; TM 49339; UM 33056.

PELUSIOS BECHUANICUS BECHUANICUS FitzSimons

Fig. 1D, 12; Pl. IC, II (left).

Sternothaerus nigricans (not Donndorff) Monard, 1931: 109 & 1937: 148 (part).

Pelusios bechuanicus FitzSimons, 1932, *Ann. Transv. Mus.* 15: 37. Type locality: Thamalakane River at Maun, Botswana. FitzSimons, 1935: 306, Pl. xi; Laurent, 1964: 27; Mitchell & Steyn, 1967: 24; Broadley, 1971: 47; Blake & Broadley, 1974: 314; Broadley

& Blake, 1979: 5.

Pelusios subniger (not Lacépède) Loveridge, 1941: 489 (part); Wermuth & Mertens, 1961: 291 (part).

Pelusios castaneus bechuanicus Mertens, 1971: 28.

Pelusios castaneus (not Schweigger) Wermuth & Mertens, 1977: 116.

Diagnosis. A large species (maximum carapace length 330 mm) with anterior lobe of plastron less than twice length of abdominal suture and strongly developed hinge. No axillary shield. First pair of marginals less than 85% anterior width of first vertebral; posterior margin of carapace rounded. Head very large, 50 to 65% of width of plastron at abdominofemoral sulcus, where it is constricted; beak not bicuspid; postocular usually separated from masseteric shield by a supralabial. Intergular usually shorter than humeral + pectoral sulcus and less than 65% of femoral border; intergular border less than 30% of femoral border. Usually three mental barbels. Carapace black; plastron largely or entirely black; skin of neck and limbs yellowish, but grey on outer faces of limbs. Eight neurals, separated from suprapygal.

Description. Head black with symmetrical yellow markings, which are sharply contrasting in juveniles (Pl. II, left); skin of neck and limbs yellowish, outer faces of limbs grey. Carapace black, uniform or with irregular yellow-brown patches across the lower ends of pleurals 2 and 3; bridge black; plastron black, with a little yellow along the median sulci.

Head very large, with blunt snout, beak not bicuspid; frontotemporal sulcus very short, supralabial usually present. Tomium bordered posteriorly by a series of elongate scales linking the large inframandibular scales, followed by three mental barbels. Falciform scales on forelimb moderately developed.

Carapace ovate, expanded posteriorly; vertebrals moderately keeled in hatchlings and posterior median protuberances on vertebrals 3 and 4 persist in subadults, no trace of a vertebral keel in adults. Third vertebral wider than long in juveniles, usually as long as wide in adults; first pair of marginals usually 55 to 75% of anterior width of first vertebral; lateral marginals obtusely keeled in subadults, smooth in adults; growth rings on carapacial shields poorly defined or absent.

Plastron with anterior lobe always longer than (but never twice the length of) abdominal sulcus, hinge well developed; intergular usually shorter than humeral + pectoral sulcus and less than 65% of femoral border, pectoral sulcus short (rarely absent); intergular subpentagonal; posterior lobe of plastron constricted at abdominofemoral sulcus. Epidermal shields usually without growth rings.

Eight neural bones, separated from the suprapygal. In two specimens first neural fails to contact nuchal (Fig. 1D). The parietal crest of the skull bears a strong lateral flange.

The largest specimen examined has a carapace length of 330 mm (TM 39401 Sangwali, Caprivi, Namibia.

Distribution. The greater Okavango basin, from the Cubango/Okavango River in the west to the Kafue Flats in the east (Fig. 8). The latter area was formerly a lake that drained southwest via the Nanzhila and Sichifula Rivers into the Zambezi; the latter river is still intermittently connected with the Okavango via the Chobe River and Magwegqana (Selinda spillway).

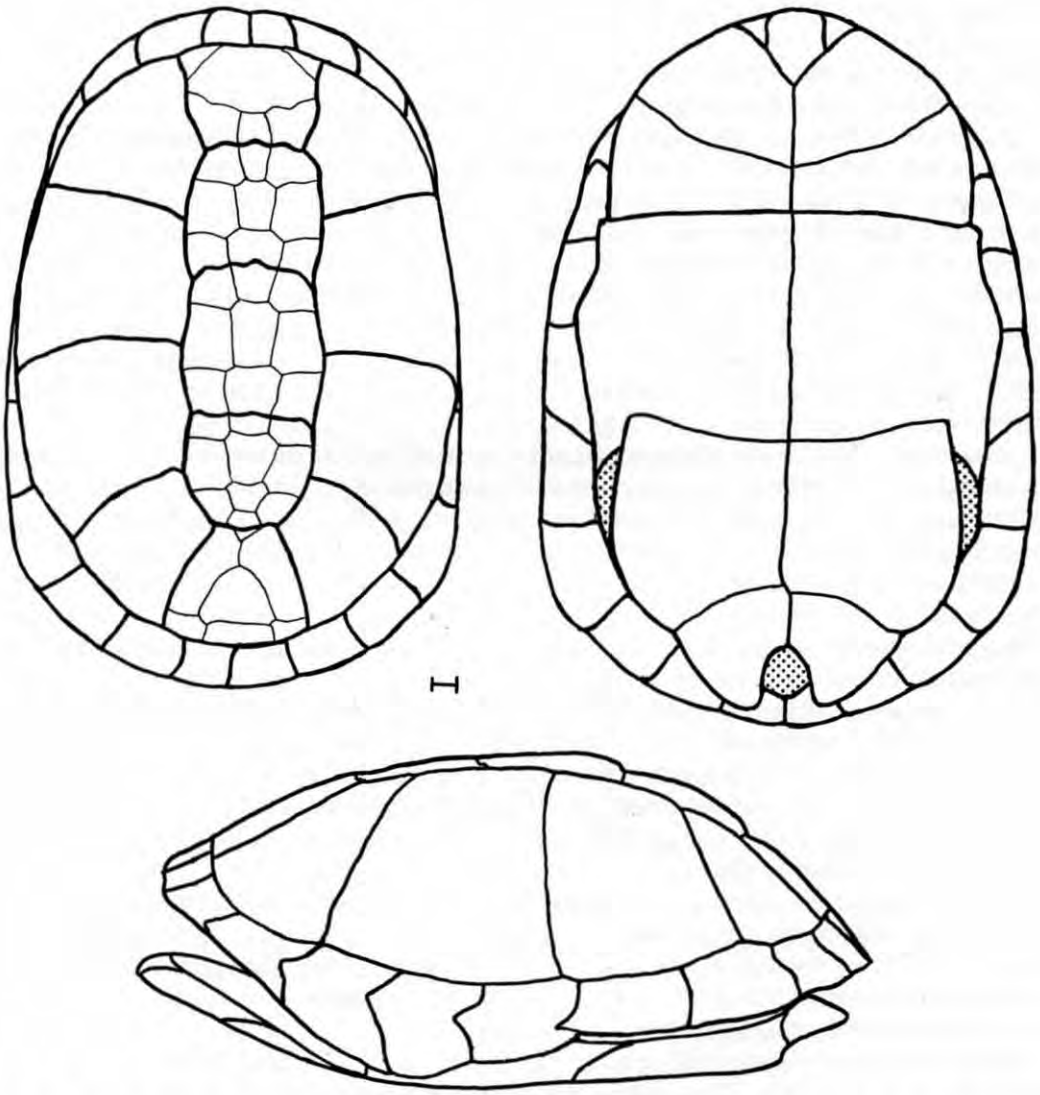


Fig. 12. *P. bechuanicus bechuanicus:* dorsal, ventral and lateral views of the shell of UM 32984 Kasane, Botswana. Conventions as in Fig. 11.

Localities. ANGOLA: Chimporo Marsh (Monard, 1931, 1937) LCFM 289; Chonga River (Laur., 1964). NAMIBIA: Kabuta TM 22620, 22624; Kapaku (Mitchell & Steyn, 1967); Lake Liambezi TM 45994; Linyanti Swamp TM 39407-10; Lisikili-Mulapo TM 44253; Mukuvi (Mitchell & Steyn, 1967); Sangwali TM 39400-6. BOTSWANA: no

precise locality UM 29157; Chobe River UM 5275; Kasane UM 10749, 16374, 22338, 32984; Kwando River UM 33317; Maun on Thamalakane River (FitzSimons, 1932, 1935) TM 14688 (type), 31126, UM 12938; 10 km S of Maun MCZ 157065; MRAC 79-14-R1; UM 20162-5; 10 km E of Maun TM 34937-41; Moremi Wildlife Reserve UM 33435; Sepopa UM 16191; Zibadianja UM 29150. ZIMBABWE: Victoria Falls UM 20218, 33422 + 1 live. ZAMBIA: Kalabo UM 10673, 10677, 15594; Livingstone Game Park UM 9718; Lochinvar, Kafue Flats (Brdly, 1971) UM 761; Upper Zambezi River (Brdly, 1971) UM 9719.

PELUSIOS BECHUANICUS UPEMBAE subsp. nov.

Fig. 2D; Pl. III.

Pelusios derbianus (not Gray) Witte, 1933: 67 (part).

Pelusios subniger (not Lacépède) Witte, 1953: 19 (part).

Pelusios castaneus rhodesianus (not Hewitt) Laurent, 1965: 30 (part).

Holotype ♀ TM 38178, Kanonga River, tributary of the right bank of the Fungwe River (695 m), Upemba National Park, Shaba Province, Zaire. Collected by G.-F. de Witte, 13-27 September 1947. Paratypes: MRAC 5157 Nyonga; MRAC 5160, 11459-60 Kikondja; MRAC 11951 Bukama — all localities on the Lualaba River, Shaba Province.

Diagnosis. A subspecies of *P. bechuanicus* distinguished from the typical form by having two mental barbels instead of three, and by the colouration of the head, which is yellow-brown, uniform or with fine yellow vermiculation, instead of black with symmetrical yellow markings. The two adult specimens have a carapace that is more depressed than is usual in the typical form (carapace height/length 38,0 and 41,3% compared with 37,0 — 48,6: $\bar{X} = 43{,}0\%$ in the typical form). This form is most readily distinguished from sympatric *P. rhodesianus* by the finely granular skin on neck and throat.

Description (paratype variations in parentheses). Head uniform yellow-brown above (with brown and yellow vermiculation), yellow below, skin of neck, limbs and claws yellow-brown. Carapace and bridge black, plastron black with extensive yellow patches mesially (Pl. III).

Head very large, 64,6% (48,9-54,7) of plastron width at abdominofemoral sulcus; snout blunt, interorbital width 97,6% (80,7-100,0) of supraocular sulcus; beak not bicuspid; frontotemporal sulcus very short, 7,1% (0-15,5) of head width; supralabial present (Fig. 2D). Tomium bordered by elongate processes from the large inframandibular scales which meet on the midline (broken up in the paratypes), followed by two mental barbels. Falciform scales on forelimb moderately to well developed.

Carapace ovate, expanded posteriorly; vertebrals smooth. Third vertebral slightly longer than wide (Fig. 6); first pair of marginals 73,3% (63,3-71,4) of anterior width of first vertebral; lateral marginals smooth; no trace of growth rings on carapacial shields (present in paratypes).

Plastron with abdominal sulcus 80,6% (64,2-84,8) length of anterior lobe; hinge well developed; humeral + pectoral suture 114,7% (96,8-136,8) length of intergular, which is 58,6% (58,5-70,5) length of femoral border; pectoral sulcus half the length of humeral

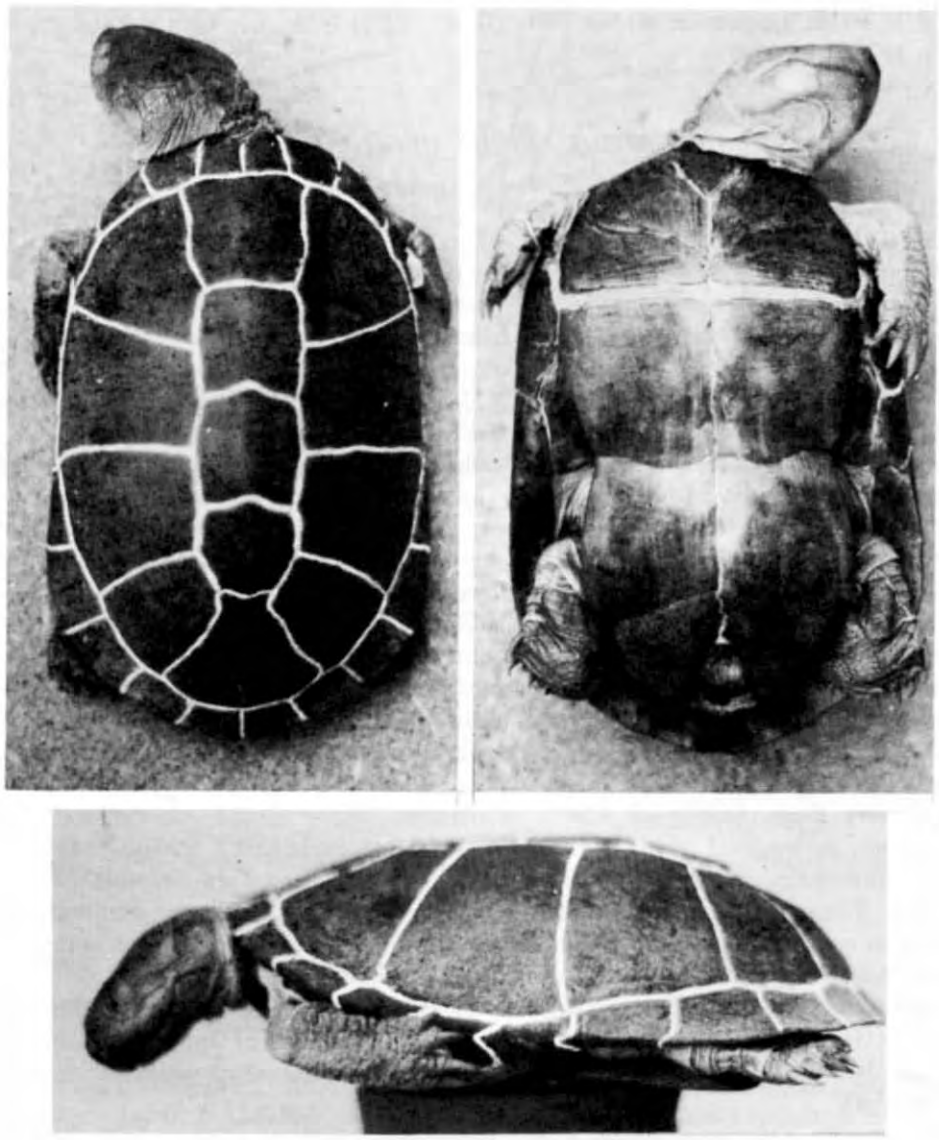


Plate III. *P. bechuanicus upembae*: dorsal, ventral and lateral views of the type, TM 38178.

sulcus (equal in the largest paratype); intergular tear-shaped; posterior lobe of plastron constricted at abdominofemoral sulcus, 87,8% (86,8-100) of maximum femoral width. Growth rings on epidermal shields ill-defined.

Eight neural bones, separated from the suprapygal.

The carapace of the holotype is 221 mm long and 141 mm wide, with a shell height of 84 mm; the head is 51 mm wide. The largest paratype (MRAC 5160) is 230 mm long and 158 mm wide, with a shell height of 95 mm; the head is 45 mm wide.

Discussion. The type specimen originates from a tributary of the Fungwe River which empties into the complex of Upemba lakes bordering the Lualaba River, a major tributary of the Congo. The paratypes also come from the Upemba Basin. That this large deep-water species should be represented in the Congo Basin by a taxonomically distinguishable population is not surprising. The reason that it has not been recognised earlier could be that many large specimens in museum collections are dry shells lacking skulls, for the big head is the best diagnostic character of *P. bechuanicus*.

Laurent (1965: 25) drew attention to discontinuous variation in the width of the intergular border in some populations of *P. rhodesianus* (including *chapini*), but did not examine the specimens personally. Laurent noted that all the Katanga specimens with a wide intergular border came from the Lualaba River and they are now made paratypes of *P. bechuanicus upembae*. The Lower Congo and northern Zaire samples still await examination. Some of the other specimens with a wide intergular border are probably *P. bechuanicus*, particularly the very large ones assigned to *chapini* by Laurent. All the material in the Brussels and Tervuren collections should be checked for the presence of additional material of *P. bechuanicus*.

PELUSIOS RHODESIANUS Hewitt

Fig. 1E, 13; Pl. ID.

Sternothaerus castaneus (not Schweigger) Gray, 1855: 52 (part).

Sternothaerus sinuatus (not A. Smith) Gray, 1863: 193, Fig.; 1870: 78, Fig.; Boulenger, 1889: 194 (part); Bocage, 1895: 4; Blgr., 1902: 15; Monard, 1937: 148.

Sternothaerus Derbianus (not Gray) Strauch, 1890: 102; Bocage, 1895: 3.

Sternothaerus nigricans (not Donndorff) Boulenger, 1907a: 6 (part); Nieden, 1913: 59 (part).

Pelusios nigricans rhodesianus Hewitt, 1927, *Rec. Albany Mus.* 3: 375, Fig. 1a-c, Pl. xxi, Fig. 2-3. Type locality: Mpika District, Zambia. Hewitt, 1933: 47, Pl. ix, Fig. 5; Loveridge, 1933: 210; Pitman, 1934: 307.

Pelusios sinuatus sinuatus (not A. Smith) Schmidt, 1933:3.

? *Pelusios derbianus* (not Gray) Mertens, 1938: 430.

Pelusios subniger (not Lacépède) Loveridge, 1941: 489 (part); Müller & Hellmich, 1954: 72 (part); Wermuth & Mertens, 1961; 291 (part).

Pelusios castaneus (not Schweigger) Laurent, 1964: 26; Blake & Broadley, 1974: 314; Wermuth & Mertens, 1977: 116 (part)

Pelusios castaneus rhodesianus Laurent, 1965: 30; Broadley, 1971: 47, Pl. iii.
Pelusios rhodesianus Raw, 1978: 291, Fig. 3; Broadley & Blake, 1979: 5.

Diagnosis. A medium-sized species (maximum carapace length ? 255 mm), with anterior lobe of plastron less than twice length of abdominal suture and strongly developed hinge. No axillary shield. First pair of marginals less than 85% anterior width of first vertebral; posterior margin of carapace rounded. Head relatively small, less than half width of plastron at abdominofemoral sulcus, where it is not or but feebly constricted; beak bicuspid; postocular usually in contact with masseteric shield, rarely separated by a supralabial. Carapace black; plastron black and/or yellow, without forming a geometric pattern; skin of neck and limbs yellowish, but grey-brown on outer faces of limbs. Eight neurals, often in contact with the suprapygal.

Description. Head brown with yellow vermiculation in northern specimens, brown above and yellow laterally in southern specimens; skin of neck and limbs yellowish, outer faces of limbs grey-brown. Carapace and bridge uniform black, plastron uniform black, with irregular yellow patches mesially or uniform yellow (a few Zimbabwean specimens).

Head small, with moderate snout; beak bicuspid; frontotemporal sulcus long, supralabial usually absent, or small with postocular and masseteric in contact above it. Tomium bordered posteriorly by a transverse row of enlarged scales, followed by two mental barbels. Falciform scales on forelimb well developed (Hewitt, 1933: Pl. ix, Fig. 5).

Carapace ovate, expanded posteriorly; vertebrals feebly keeled in subadults, with a posterior median protuberance often persisting on vertebral 4 of adults. Third vertebral wider than long in juveniles and most adults, slightly longer than wide in some adults (including the type specimen); first pair of marginals usually 55 to 75% of anterior width of first vertebral; lateral marginals smooth; growth rings and radiating ridges on carapacial shields usually clearly defined.

Plastron with anterior lobe always longer than (but never twice the length of) abdominal sulcus, hinge well developed; intergular usually shorter than humeral + pectoral sulcus and less than 65% of femoral border, pectoral sulcus much shorter than humeral sulcus (25-75%); intergular rhomboidal; posterior lobe of plastron not constricted at abdominofemoral sulcus. Epidermal shields usually with well defined growth rings and radiating ridges.

Neural bones 8 (eighth absent only in one Shaba specimen MRAC 16962), first always making good contact with nuchal, eighth often in contact with suprapygal; seventh and eighth neurals occasionally reduced in size and isolated.

The largest specimen examined has a carapace length of 222 mm (DSP 85 Durban Bluff, Natal). A specimen from Victoria Nyanza measures 255 mm (NMW —). Laurent (1965) has quoted a maximum length of 380 mm for his *P. c. chapini* from northeastern Zaire, but it is possible that the largest specimens are in fact *P. bechuanicus upembae*, judging by the remarks of Witte (1966).

Distribution. Central and southeastern Africa from northern Zaire and Uganda south to Angola, northern Botswana, Zimbabwe and central Moçambique, with apparently relict populations in KwaZulu and at Durban, Natal (Fig. 9).

Localities. ANGOLA: no precise locality MBL 2388; Ambriz (Bocage, 1895) MBL

2300; Chitau (Schmidt, 1933; Laur., 1965) AMNH 50751-3; CM 5971; Cubal (Mertens, 1938); Dundo (Laur., 1964); Duque de Bragança (Bocage, 1895) MBL 2384; Galanga MBL 2297; Lac Calundo (Laur., 1964); Mucoso, Cuanza River (Müller & Hellmich, 1954); Rio Cuce (Bocage, 1895) MBL —; Rio Cuillo (Bocage, 1895) MBL 2302; Vila da Ponte (= Kuvangu: Monard, 1937) LCFM 382. ZAIRE (SHABA PROVINCE): Kando (Witte, 1933; Laur., 1965) MRAC 16962-5; UM 33392; Kasenga (Laur., 1965) MRAC 7445; Kundelungu Plateau (= Upper Lofoi: Laur., 1956, 1965) MRAC 19117-8; UM 33391; Lofoi River (Laur., 1965); Lukafu (Witte, 1933; Laur., 1965); Lukonzolwa (Laur., 1965); Mpala (Witte, 1953); Pweto (Laur., 1965) MRAC 2001. ZAMBIA: Bwela Flats, Chinsali (Hewitt, 1933; Pitman, 1934) BM 1932.12.13.236; Fwambo BM 49.12.20.10-11; Kalabo (Brdly, 1971); Lochinvar, Kafue Flats (Brdly, 1971: Pl. iii) NMSR 2624-7; UM 47-50; Mbala (= Abercorn) IRScNB 4477D, 4478 (2); Mpika District (Hewitt, 1927) AM 5432 (5, including holotype); Msofu River (Blgr, 1907a); Nyamkolo (Lov., 1933; Pitman, 1934; Laur., 1965) MCZ 30015. TANZANIA: Mwaya (Lov., 1933; Laur., 1965) MCZ 30014; north shore of Lake Nyasa (Nieden, 1913). NAMIBIA (CAPRIVI): Linyanti Swamps TM 39411. BOTSWANA: Boro River, Okavango Swamps TM 43076. ZIMBABWE: Eastern Highlands Tea Estates, Inyanga UM 33013, 33667; Garamapudzi River, Mazoe AM —; Lake McIlwaine UM 30227, 33033; Marandellas UM 21654; 'Mashonaland' NM 108; Mazoe (Blgr., 1902) BM 1902.2.12.2-3; Musinziwi River, Mount Silinda UM 944; Mupudzi River, Umtali UM 14516; Norton UM 33042, 33385; Salisbury UM 9615-6, 33038. MOCAMBIQUE: Zembe, Chimoio District UM 9717. KWAZULU: Lake St. Lucia TM 52341-2, 52477-8; Mtubatuba (Raw, 1978); Mtunzini (Raw, 1978); Ukwakwa-Tabor TM 52479. NATAL: Durban (Gray, 1855, 1863, 1870; Blgr., 1889; Strauch, 1890; Hewitt, 1927; Raw, 1978) BM 62.12.4.3.(2); DSP 85-7; NM 107; UM 33621; 'South Africa' BM 78a.

Discussion. It may be possible to make a case for dividing this species into northern and southern races on the basis of head colouration. Laurent (1956), with material from Zaire, Rwanda and Burundi, observed that the head is vermiculated with yellow and brown, whereas the head of *P. subniger* is uniform brownish. He subsequently found that some Angolan specimens have the head blackish brown above and lighter on the sides and below (Laurent, 1964). The distribution of the two types of head colouration is indicated in Fig. 9. The division almost follows the South Equatorial Divide (Wellington, 1955: Fig. 1), with the following exceptions. In Angola, the southern plain-headed phase extends north of the watershed to Chitau and Alto Chicapa. Three specimens from Kando, Zaire, have the vermiculate head markings largely obscured, particularly on top of the head, and might be classed as intermediate in head markings. The specimen from Mwaya, Tanzania (south of the watershed) has coarse yellow vermiculation on the head. The type series of *P. rhodesianus* consists of dry shells, but the assumed type locality lies north of the watershed, so if subspecies were recognised the northern form would be the typical race. No other diagnostic characters are apparent and there may prove to be more intergrading populations along the watershed, so subspecies of *P. rhodesianus* are not recognised in this study.

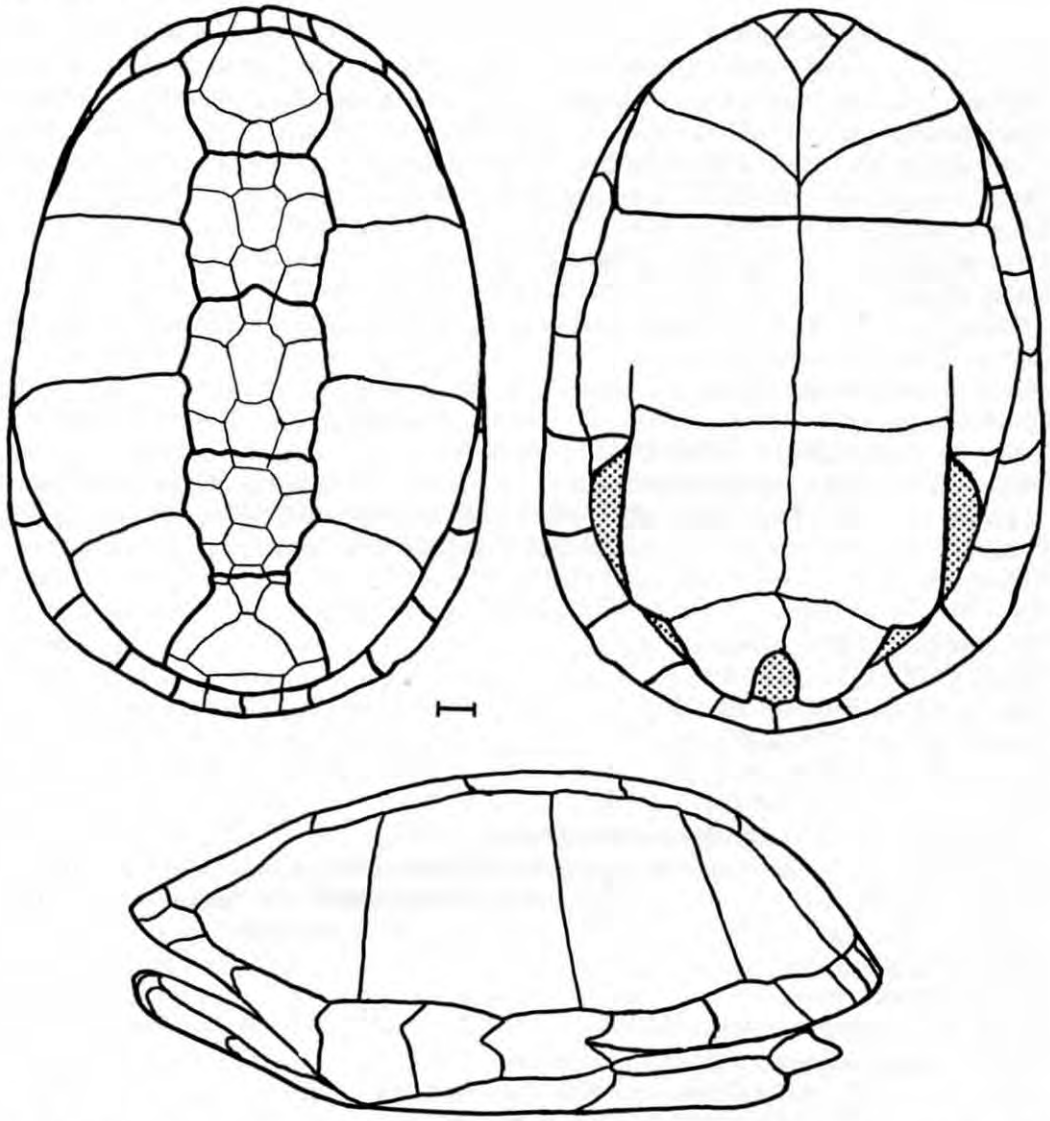


Fig. 13. *P. rhodesianus:* dorsal, ventral and lateral views of the shell of AM — Mpika District, Zambia (holotype). Conventions as in Fig. 11.

PELUSIOS CASTANEUS CASTANOIDES Hewitt

Fig. 1F-G, 14; Pl. IE, II (right).

Sternothaerus nigricans castaneus (not Schweigger) Siebenrock, 1906: 35, Pl. v, Fig. 18.

Pelusios castaneus castanoides Hewitt, 1931, *Ann. Natal Mus.*, 6: 463, Pl. xxxvi, Fig. 1-2.

Type locality: Lake St. Lucia estuary, KwaZulu.

Sternothaerus derbianus (not Gray) Cott, 1935: 973.

Pelusios subniger (not Lacépède) Loveridge, 1941: 489 (part) & 1953a: 162 (part); Sweeney, 1960: 47 (part); ? Pooley, 1965: 54; Wermuth & Mertens, 1977: 118 (part).

'Chilwa Pelusius' Mitchell, 1946: 20.

Pelusios castaneus castaneus (not Schweigger) Laurent, 1965: 29; Bruton & Haacke, 1975: 30; Raw, 1978: 290, Fig. 2.

Pelusios castaneus (not Schweigger) Mertens, 1969: 31, Fig. 2; Wermuth & Mertens, 1977: 116 (part).

Pelusios sinuatus (not A. Smith) Stevens, 1974: 11 (part); Dudley, 1978: 96.

Diagnosis. A medium-sized form (maximum carapace length 230 mm), with anterior lobe of plastron less than twice length of abdominal suture and strongly developed hinge. No axillary shield. First pair of marginals less than 85% anterior width of first vertebral; posterior margin of carapace rounded. Head moderate, less than half width of plastron at abdominofemoral sulcus, where it is feebly constricted; beak bicuspid; postocular usually in contact with masseteric shield, rarely separated by a supralabial. Carapace olive, blackish-brown or yellowish; plastron yellow, usually with a little black on anterior peripheral sulci; skin of neck and limbs yellow. Five to seven neurals, well separated from both nuchal and suprapygal, neurals 1, 7 and 8 being reduced in size or absent.

Description. Head blackish-brown with fine yellow vermiculation (Pl. II, right); skin of neck and limbs yellow. Carapace yellow-brown to blackish brown, bridge yellow with blackish sulci, plastron yellow with a little black on anterior peripheral sulci.

Head moderate, with moderate snout; beak bicuspid; frontotemporal sulcus long; supralabial usually absent, or small with postocular and masseteric in contact above it (Rendahl, 1939a: Fig. 14C). Tomium bordered posteriorly by a transverse row of enlarged scales, followed by two mental barbels. Falciform scales on forelimb well developed.

Carapace ovate, expanded posteriorly; vertebrals without keels, but a posterior median protuberence usually noticeable on vertebral 4. Third vertebral wider than long in sub-adults and most adults, slightly longer than wide in some adults; first pair of marginals about 72 to 82% of anterior width of first vertebral; lateral marginals smooth; growth rings on carapacial shields usually visible.

Plastron with anterior lobe always longer than (but never twice the length of) abdominal sulcus, hinge well developed; intergular usually shorter than humeral + pectoral sulcus, pectoral sulcus shorter than humeral sulcus (50-90%); intergular pyriform; posterior lobe of pastron only slightly constricted at abdominofemoral sulcus. Epidermal shields usually with clear growth rings.

Neural bones 5-7, Nos. 1, 7 and 8 reduced in size or absent.

The largest specimen examined is a female with a carapace length of 223 mm (UM 33390 Lake Chilwa, Malawi), but a specimen from Majunga, Madagascar (NMW —) measures 230 mm.

Localities. MALAWI: Chibotela (Lov., 1953a; Sweeney, 1960) AMNH 67850; Lake Chilwa (Mitchell, 1946; Sweeney, 1960; Stevens, 1974; Dudley, 1978) AM — (4); UM 33390; Limphasa Dambo, Nkhata Bay UM 32990. MOCAMBIQUE: Beira (Cott, 1935);

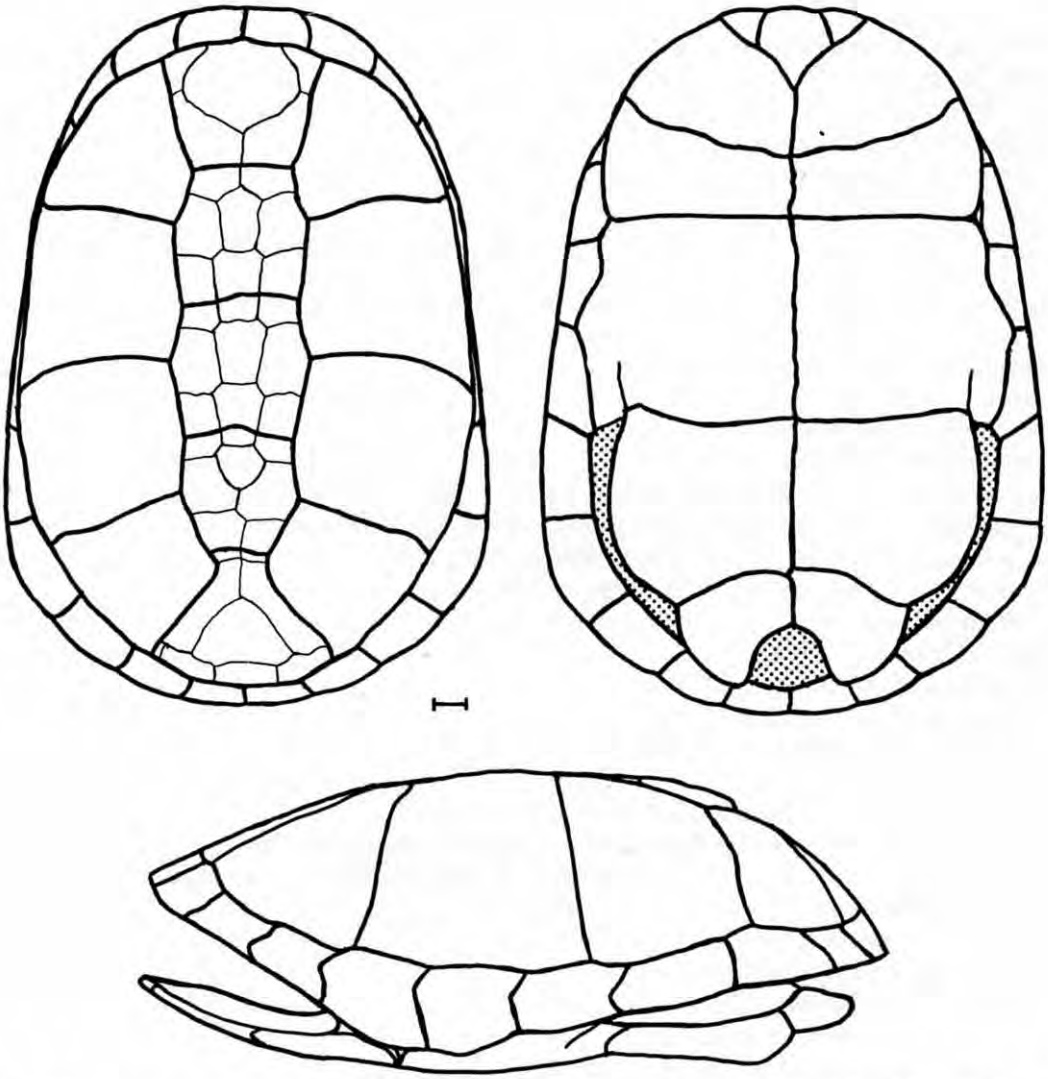


Fig. 14. *P. castaneus castanoides:* dorsal, ventral and lateral views of the shell of UM 33390 Lake Chilwa, Malawi. Conventions as in Fig. 11.

Charre (Cott, 1935); Inhaca Island (EBM —); Maputo NMW 19053; Tando UM 27828; Tica (Live at Tica Zoo). KWAZULU: Charter's Creek TM 52543; Lake St. Lucia (Hewitt, 1931; Bruton & Haacke, 1975) TM 13433 (type), 52160; Lake Sibaya (Bruton & Haacke, 1975) TM 45644, 48318; Mapelane TM 52544; ? Mkuzi Game Reserve (Pooley, 1965); Monzi (UM 33634); ? Ndumu Game Reserve (Pooley, 1965); Ntambeni Pan (Bruton & Haacke, 1975) Photo: E. Moll (Pl. II right); "Zululand" LR 1038.

Extralimital material examined. PEMBA ISLAND: NKW 19054 (2); SMF 60858. MADAGASCAR: no precise locality SMF 7931-2; 6 km S of Ambanja USNM 149819; Diego Suarez NMW 19081 (2); Majunga NMW 1805, 19076 (2), 19077-80 + 1 uncatalogued; SMF 7933-5; UM 33166. SEYCHELLES: AM 1417; BM 74.8.7.1 (La Digne Island); TM 49338 (Mahé Island).

Material of other subspecies examined

PELUSIOS CASTANEUS CASTANEUS (Schweigger)

SENEGAL: Dakar CM 24785. GUINEA-BISSAU: Bissau MBL 2391 (2). GHANA: no precise locality UM 33495. NIGERIA: no precise locality AM 7282; Nko BM 1974. 3014. SAO THOMÉ ISLAND: MBL 2298-9.

PELUSIOS CASTANEUS LUTESCENS Laurent

ZAIRE: Vitshumbi, Lake Edward CM 62248 (paratype).

PELUSIOS CASTANEUS WILLIAMSI Laurent

KENYA: Kaimosi, Kagamega Forest TM 16433; UM 33165 (paratype).

PELUSIOS SINUATUS (A. Smith)

Sternothaerus sinuatus A. Smith, 1838, *Ill. Zool. S. Afr., Rept.* Pl. i. Type locality: 'Rivers to the north of 25° south latitude' (here restricted to the Crocodile/Marico Confluence, N. Transvaal), South Africa. Peters, 1882: 8; Boulenger, 1889: 194 (part); Günther, 1894: 618; Bocage, 1896: 97, Mocquard, 1899: 219; Boulenger, 1905: 251; 1907a: 6; Siebenrock, 1903: 193; Rendahl, 1939b: 2.

Sternotherus dentatus Peters, 1848, *Arch. Anat. Physiol.*: 494. No locality.

Sternothyrus subniger (not Lacépède) Günther, 1864: 306.

Pelusios sinuatus Hewitt, 1927: 371, Pl. xxi, Fig. 1; ? Power, 1927: 411; Loveridge, 1933: 208; Pitman, 1934: 307; Hewitt, 1935: 345; FitzSimons, 1937: 261, Pl. x; 1939: 19; Loveridge, 1941: 502; 1953a: 163; 1953b: 140; Laurent, 1956: 38; Sweeney, 1960: 48; Wermuth & Mertens, 1961: 291 (part); Broadley, 1962: 792; Pooley, 1965: 54; Bourquin *et al.*, 1971: 21; Broadley, 1971: 47; Stevens, 1974: 11 (part); Blake & Broadley, 1974: 311; Dudley & Stead, 1976: 25; Wermuth & Mertens, 1977: 118; Jacobsen, 1978: 19; Pienaar, 1978: 217; Raw, 1978: 289; Broadley & Blake, 1979: 5.

Pelusios sinuatus zuluensis Hewitt, 1927, *Rec. Albany Mus.* 3: 371, Pl. xx. Type locality: Unsinene River, Zululand. Hewitt, 1931: 465; Mertens, 1937: 5.

Pelusios sinuatus sinuatus Hewitt, 1931: 462, 465, Pl. xxxvi, Fig. 3; Pienaar, 1966: 131, Pl. 52; Switak, 1971: 9, 37.

Pelusios sinuatus leptus Hewitt, 1933, *Occ. Pap. Rhod. Mus.* 1 (2): 45, Pl. ix, Fig. 1 & 2. Type locality: Isoka, Zambia. Pitman, 1934: 307.

'Nyasa Pelusius' Mitchell, 1946: 20.

Diagnosis. A large species (maximum carapace length 465 mm), with anterior lobe of plastron subequal in length to abdominal suture (shorter in large adults) and strongly developed hinge. An axillary shield (Fig. 15) present in all specimens exceeding 70 mm in

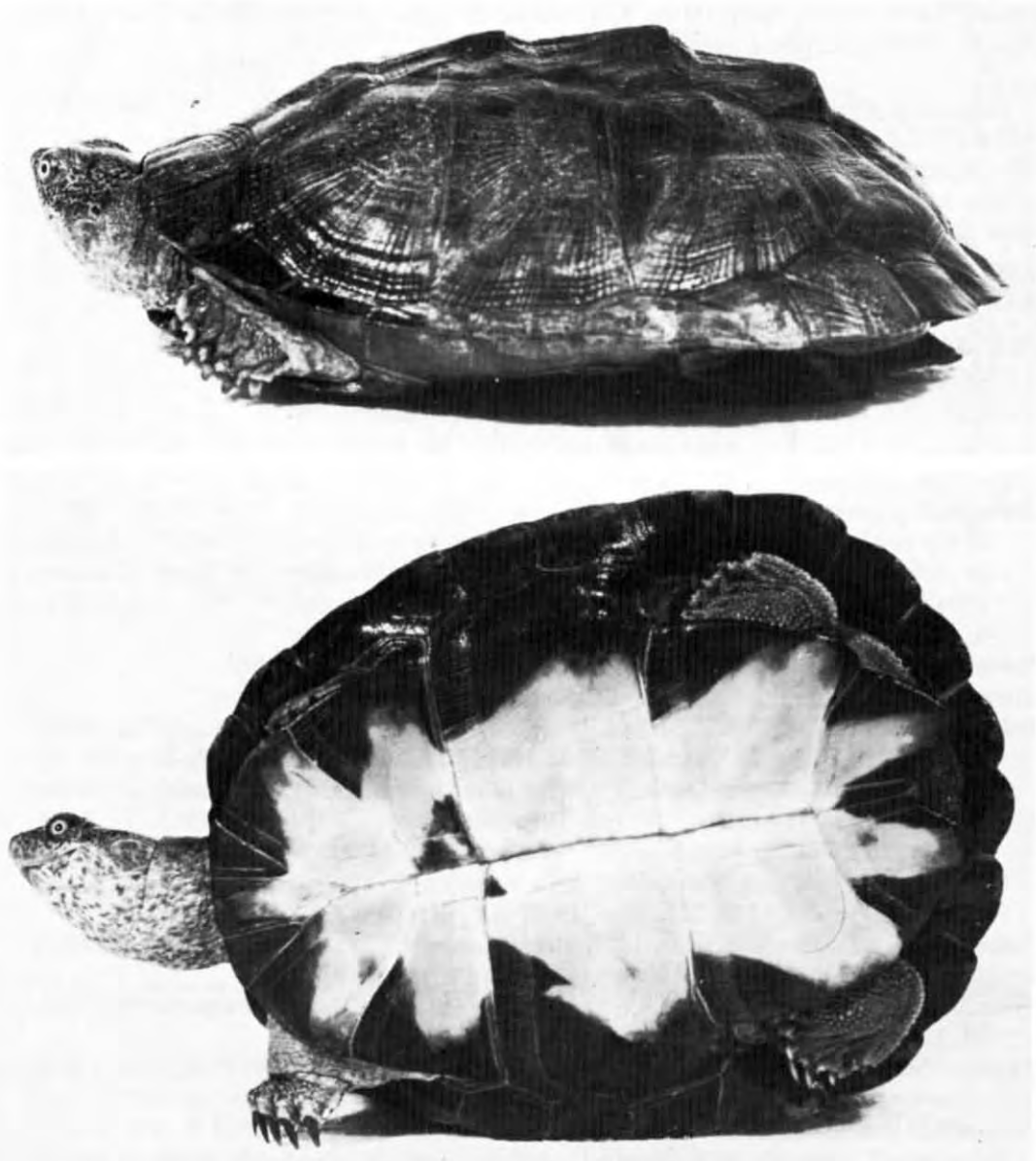


Plate IV. *Pelusios sinuatus:* lateral and ventral views of a live topotype from the Limpopo River, Transvaal/Botswana border. Carapace length 10 cm. Photos: J. D. Visser.

carapace length. First pair of marginals more than 85% of anterior width of first vertebral; posterior margin of carapace usually serrated or sinuate. Plastron yellow with a symmetrical black angular peripheral pattern (Pl. IF, IV lower).

Description. Head blackish brown with yellow or brown vermiculation (Pl. IV upper); skin of neck and limbs pale olive-grey, outer faces of limbs dark grey. Carapace and bridge uniform black (rarely dark brown), plastron yellow with sharply defined black angular peripheral pattern. Sometimes (especially in Kwazulu specimens) there are several black chevrons mesially (Rendahl, 1939b, Fig. 3). Hatchlings have the plastron mottled salmon pink and grey.

Head relatively small, 35 to 45% of plastron width at abdominofemoral sulcus; snout rather pointed, beak bicuspid; frontotemporal sulcus long; supralabial always present. Tomium bordered by a row of feebly enlarged scales, separated by granular skin from a pair of mental barbels. Falciform scales on forelimb poorly developed.

Carapace ovate, expanded posteriorly: vertebrals strongly keeled in subadults, often persisting in adults as posterior median protuberances on vertebrals 2, 3 and 4 (Pl. IV upper). Third vertebral wider than long in subadults, much longer than wide in adults (Fig. 6); first pair of marginals subequal in width to first vertebral (85 to 105%); lateral marginals keeled; growth rings on carapacial shields usually distinct.

Plastron with anterior lobe longer than abdominal sulcus in subadults, but shorter in most adults (Fig. 7); hinge well developed; intergular usually subequal to or shorter than humeral + pectoral sulcus; intergular an elongate pentagonal; posterior lobe of plastron not constricted at abdominofemoral sulcus. Epidermal shields usually with clear growth rings.

Neural bones 5-7, N1 sometimes fails to reach the nuchal, N5 may be reduced in size or absent, leaving N6 isolated, N7 is often reduced in size or absent; N8 is always absent, so that the last two pairs of costal bones are in median contact.

The largest specimen examined has a carapace length of 388 mm (UM 33040 Lake Malombe, Malawi), but much larger specimens occur in Lake Tanganyika, reaching a maximum of 465 mm (Witte, 1952).

Distribution. East Africa from Somalia south to the Kwazulu, extending westwards to Lake Tanganyika and Victoria Falls (Fig. 16). Known fossil from the Lower Pleistocene of Tchad and Lake Turkana (Broin, 1969).

Localities. TANZANIA: Kala (Witte, 1952); Kasanga (Nieden, 1913); Lake Rukwa (Nieden, 1913); Mbanja (Lov., 1942) MCZ 48020-5; Rovuma River (Nieden, 1913). ZAMBIA: Chipangali UM 6576, 32996-9, 33028, 33037; Chipata TM 22232; Hore Bay, Lake Tanganyika BM 89.7.24.1; Isoka (Hewitt, 1933) AM — (holotype of *P. s. leptus*), 5794; Kalikali Dam UM 9141; Kalimba, Munyamadzi River (Hewitt, 1933; Pitman, 1934) BM 1932.12.13.235; Luangwa Valley (Hewitt, 1933; Laurent, 1956) AM 6696; UM 17528; Mfuwe, Luangwa River UM 6577; Mpika District (Hewitt, 1927) AM 5432; Mpulungu (Witte, 1952); Ngoma, Kafue River (Brdly, 1971) UM 23853; Petauke (Blgr, 1907a; Pitman, 1934); Songwe, Livingstone NMSR 3151; UM 762. MALAWI: Chimwala, Shire River (Lov., 1953b); Lake Malombe UM 33031, 33040; Liwonde National Park (Dudley & Stead, 1976); Mangochi (= Fort Johnston: Sweeney, 1960) BM 1926.5.8.56; NMSR

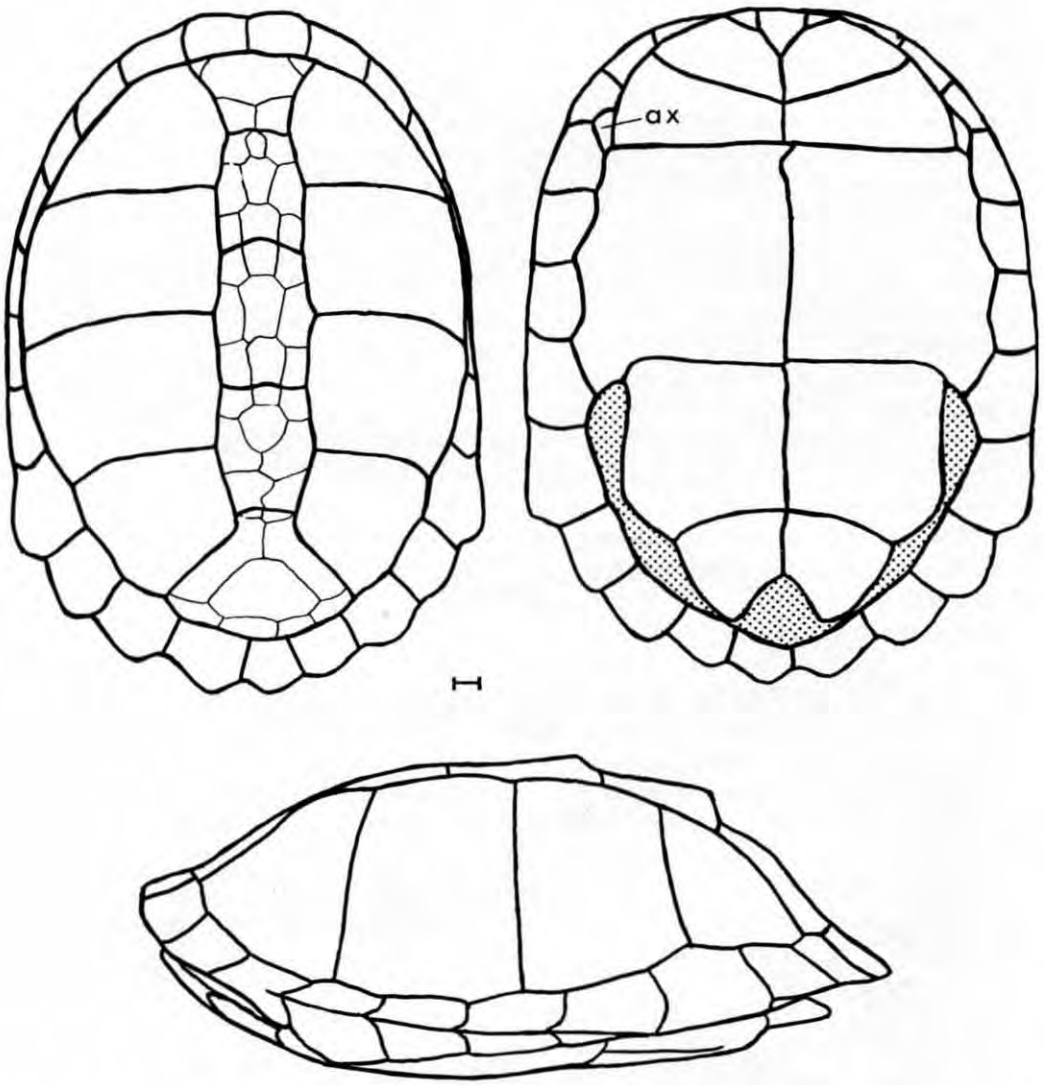


Fig. 15. *P. sinuatus:* dorsal, ventral and lateral views of the shell of AM — Isoka District, Zambia (holotype of *P. s. leptus* Hewitt). Conventions as in Fig. 11; ax = axillary shield.

4851; TM 21483-4; Matope, Shire River UM 25461; Monkey Bay (Sweeney, 1960); Mtimbuka (Lov., 1953a); Murchison Falls (Gray, 1863, 1870; Günther, 1864; Blgr., 1889; Lov., 1953a) BM 63.12.4.3; Yua, northern Lake Nyasa BM 1926.5.8.57; "Zomba" (Günther, 1894) BM 93.10.26.1. ZIMBABWE: Birchenough Bridge (FitzSimons, 1939) TM 18734;

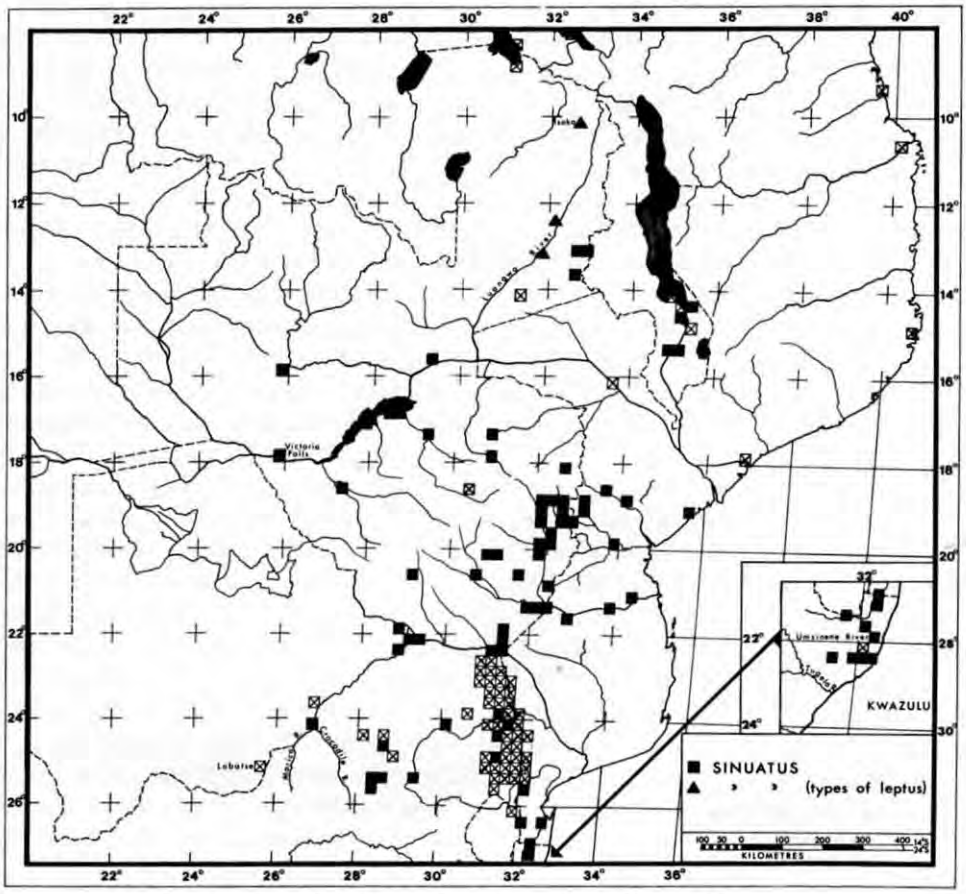


Fig. 16. Distribution of *P. sinuatus* in southern Africa.

Buffalo Bend Pan, Gonarezhou Nat. Park UM 19623; Chimwara Ranch, Gwaai River (Brdly, 1962) NMSR 3700-1; Chipinda Pools, Lundi River UM 32969; Deve River, Karoi UM 17944; Devuli Ranch UM 17193; Devure Bridge UM 28295-6, 33002-3; Fishan, Lundi River UM 12076; Hot Springs, Melsetter UM 6310; Inyangombe River, Inyanga UM 23682; Irisvale, Nsese River NMSR 3899-900, 4944; NMW 24842; 25 km W of Kariba NMSR 582; Lake Kariba NMSR 3984; Lake Kariba/Bumi Confluence UM 5278; Lake Kariba/Mwenda Confluence UM 32970; Lake Kyle MRAC 79-14-R3; UM 3178-9, 10340-1, 20049; Lake McIlwaine UM 32975; Limpopo River NMSR 3987; Mabalauta Field Stn, Nuanetsi River UM 12343; Machinawa Pan, Gonarezhou Nat. Park UM 19621; Majinji Pan, Nuanetsi UM 20247; Mana Pools UM 4850, 33029-30, 33039; Maranke T.T.L., Umtali UM 3177, 20048, Marodzi River, Mazoe AM —; 'Mashonaland' BM 96.4.17.3; Matusadona National Park UM 33097, 33386-8,33547; Mupudzi River, Umtali UM 10763; Musaswi River, Chipinga UM 9799; Ngesi Dam (4 live); Nuanetsi River at Moçambique border QVMS/R 556; Nyamashato River, Umtali NMSR 3898; Nyanadzi-

Odzi Confl. UM 33094-5; Nyayesi River, Inyanga UM 30401, 31638; Odzi UM 33096; Old Umtali UM 10332; Pesu River, Sengwe T.T.L. UM 20233; Razi Dam, Chibi UM 23540; Ruware, Ndanga UM 5867; Sabi-Lundi Confluence NMSR 1210; UM 19622, 28368; MRAC 79-14-R2; Sabi-Tsungwesi Confl. UM 5856; Salisbury District (Lov., 1941); Samalema Gorge, Nuanetsi River UM 32976; Shinda, Umtali UM 33004; Tuli Safari Area UM 33494; 15 km S of Tuli UM 3180; Umtali UM 11311, 21532; Victoria Falls UM 31929, 32980; Zimunya T.T.L., Umtali UM 33032. MOCAMBIQUE: Alves de Lima UM 30430; JPT (2); Boror (Peters, 1882); Chemezi NMSR 3157; Chicamba Dam UM 10343; Estatuane UM 30431-5; Inhambane (Peters, 1882); Maputo Game Reserve TM 39919; Massangena, Save River TM 29212; UM 29268; Mkurrumbane UM 30429; JPT (1); Mossuril (Peters, 1882); Nhameruza UM 29131; Plaine du Zambèze (Mocquard, 1889); Pungwe River at Gondola/Gorongoza pontoon UM 5905; Quelimane (Peters, 1882); 10 km SSE of Ressano Garcia UM 30436-42; Revue River (Lower bridge) UM 27585; Samo, Pungwe River UM 8801; Tete (Peters, 1882); Zinave, Save River UM 28346, 30443; JPT (5). BOTSWANA: Achilles Farm TM 42759;? Lobatsi (Power, 1927); Notuani-Limpopo Confluence (Siebenrock, 1903; Lov., 1941); 5 km W of Zelu Hill UM 11255. TRANSVAAL: Chalonis Farm TM 15076; Crocodile/Marico Confluence (A. Smith, 1838; FitzSimons, 1937) RSM 1859. 13.1684 (holotype of *S. sinuatus*); Gravelotte (Hewitt, 1931, 1933); Hammanskraal AM 7361; TM 24638; Koedoespoort (Hewitt, 1927, 1931) TM 12735; Kruger National Park (Pienaar, 1966; 1978; Switak, 1971); Letaba River, near Rubber Vale (Hewitt, 1935) TM 14920-1; Loskop Dam TM 27447; Malta Farm (Hewitt, 1931) TM 12736; Mawobje Creeks, near Letaba Camp (Mertens, 1937); Naboomspruit (Hewitt, 1931) TM 13434, 16014; Ravenscourt Farm, Pilgrim's Rest TM 45750; Timbavati Nature Reserve TM 42754; Vaalwater, Waterberg (Lov., 1941). SWAZILAND: Tshaneni (Photos: J. D. Visser). ZULULAND: Black Umfolozi River (Mertens, 1937); Dingaanstad TM 34493; Hluhluwe Game Reserve (Bourquin *et al.*, 1971); Lake Teza TM 50138; Mkuzi Game Reserve (Pooley, 1965); Mkuzi-Umbombo TM 46019; Mzinyeni Pan, Pongola UM 31499-500, 31515; Ndumu Game Reserve (Pooley, 1965) TM 29125, 34682-4; St. Lucia Village TM 46238; Tete Pan TM 47979-81, 48005, 48262; Umfolozi Game Reserve (Bourquin *et al.*, 1971); Umfolozi Station (Blgr, 1905); Unsinene River (Hewitt, 1927, 1933) NMBO 609-610 (holotype & paratype of *P. s. leptus*); White Umfolosi Nature Res. TM 34611.

EVOLUTIONARY TRENDS

Williams (1954a) has suggested that small lateral mesoplastra are primitive for the Pelomedusidae, as this condition is found in all known Cretaceous pelomedusids. This means that large mesoplastra in median contact is a secondarily derived condition in *Pelusios*, associated with the development of the plastral hinge.

Pelusios rusingae from the Miocene of Rusinga Island, Victoria Nyanza, is the earliest known representative of the genus (Williams, 1954a). It belongs to the *P. gabonensis* group, in which the anterior lobe of the plastron is more than twice the length of the abdominal sulcus and the mesoplastra are tapered medially. In *P. rusingae* the mesoplastra are strongly

tapered both anteriorly and posteriorly, so that they barely make contact. In *P. gabonensis* the mesoplastra make good median contact, but are tapered on both sides, forming oblique sutures with both hyo- and hypoplastra. *P. adansonii* and *P. nanus* have the mesoplastra tapered medially only posteriorly, so that they form a straight transverse hinge with the hyoplastra. *P. nanus* differs from *P. adansonii* in shape of carapace and plastron, lack of keels on the third and fourth vertebral shields, median vertebrals longer than broad in adults, neural pattern and smaller size.

The *P. subniger* group includes those species in which the anterior lobe of the plastron is less than twice the length of the abdominal sulcus and the mesoplastra are not tapered, having straight transverse sutures with both hyo- and hypoplastra.

The neural pattern seems to be a useful indicator of evolutionary trends, despite considerable intraspecific variation. There appears to be a tendency to strengthen the carapace by reduction of neurals from both ends of the series until they are completely eliminated and all the costals make median contact. This ultimate development is well shown by the Australasian chelid genus *Chelodina*, in which one species *C. oblonga* is isolated in the south-west corner of Australia and has 5 to 8 neurals (with reductions at both ends of the series), while six other species completely lack neurals (Burbridge, Kirsch & Main, 1974).

The type of *Pelusios rusingae* has a continuous series of eight neurals, making good contact with the nuchal anteriorly, but separated from the suprapygal posteriorly (Williams, 1954a: Pl. i). This appears to be the ancestral condition in the genus. A few specimens of the *P. gabonensis* group have been checked for neural arrangement, but although all three species usually have 7 or 8 neurals, in *P. gabonensis* and *P. adansonii* it is N1 that is lost, whereas *P. nanus* retains an N1 that is narrowed anteriorly and has N8 reduced or absent.

In the *P. subniger* group, *P. subniger* usually retains the primitive neural pattern, the only exceptions in a series of 25 are three which have two superposed suprapygals and two which lack N8. *P. bechuanicus* also retains the primitive pattern, but in two out of 15 specimens N1 is reduced and fails to contact the nuchal.

P. rhodesianus shows a departure from the primitive pattern in that N8 tends to be elongate, often contacting the suprapygal. However, a few specimens have N7 and N8 reduced in size and isolated, a pattern that is found in *P. carinatus* and is apparently ancestral to those found in *P. sinuatus*, in which there are 5 to 7 neurals, N8 always absent and N7 and N5 often reduced or absent; N1 is sometimes reduced, but rarely absent. The extreme reduction to 5 or 6 neurals with N5 reduced or absent is found in the holotype of *P. rudolphi* (a synonym of *P. sinuatus*) and two topotypes dated 3,75 to 1,8 million years B.P. from Omo, north of Lake Turkana, Ethiopia (Broin, 1969).

In *P. castaneus* there may be a stepped cline in neural arrangement. The typical form of West Africa retains the primitive pattern. In a paratype of *P. c. lutescens* (from north-eastern Zaire) N1 is absent and N8 reduced, leading up to the condition found in *P. c. castanoides*, with 5 to 8 neurals, N1, N7 and N8 all reduced or absent. *P. c. williamsi* does not quite fit into the pattern, as two Kaimosi (type locality) specimens agree with *P. rhodesianus* in having an elongate N8, almost contacting the suprapygal, but one of them lacks N1.

ECOLOGY

The most primitive Recent species in the genus, *P. gabonensis*, inhabits the evergreen forests of west and central Africa, but is replaced by *P. nanus* in moist savannas and forest/savanna mosaic along the southern rim of the Congo/Zaire Basin.

P. subniger inhabits pans and other temporary bodies of water in southeastern Africa, in this respect resembling *Pelomedusa subrufa* (Wood, 1973). Many specimens show extensive fire damage to the carapace. It feeds on aquatic insects, frogs and tadpoles.

In Zimbabwe, *P. rhodesianus* seems to favour quiet weed-choked backwaters of dams, as at Lake McIlwaine, where it was encountered during the removal of Water Hyacinth (*Eichornia crassipes*). In Zambia and Zaire this species inhabits extensive swamps. B. L. Mitchell collected a series of *P. rhodesianus* (with one *P. b. bechuanicus*) at Lochinvar on the Kafue Flats. His field notes record "On the night of 12 Sept 1958 the first rain of the season fell in thunder showers (estimated10 mm). On the following morning, I picked up 33 turtles walking about in the grassland. My Game Guards collected others to eat. I presumed that the rain had stimulated the turtles to come ashore to oviposit. I do not believe that they had been buried in the soil during the preceding dry weather". (*N.B.* there is only one ♂ among the series of 8 specimens now available).

P. castaneus seems to inhabit marshes and swamps, burying itself in the mud if these dry out and emerging again when the rains break (Loveridge, 1936: 223, Pl. ii). UM 32990 from Limphasa Dambo was caught while swimming at night in a shallow pool where many amphibians were breeding: the upper surface of the carapace shows clear evidence of extensive fire damage sustained while the terrapin was shallowly buried in a dry swamp. In Lake Chilwa these terrapins inhabit a large, very shallow, extremely muddy, weed-choked, brackish lake, where they feed largely on large pulmonate snails (Mitchell, 1946) and also the floating water lettuce (*Pistia striatoides*) (Dudley, 1978).

P. b. bechuanicus is a large 'deep water' terrapin restricted to the clear waters of the greater Okavango system on the Kalahari sands. Many of the specimens from the Thamalakane River were caught in fish nets.

P. sinuatus is the largest species and it inhabits all the river systems of eastern Africa, attaining its largest size in Lakes Tanganyika and Malawi. In the latter lake it feeds almost entirely on a large pulmonate snail with a shell about 50 mm long (Mitchell, 1946). This species is heavily preyed upon by the crocodile (*Crocodylus niloticus*). This species overlaps the range of *P. bechuanicus* above Victoria Falls, but in this situation *P. sinuatus* seems to be restricted to lagoons and muddy backwaters where large game animals drink. *P. carinatus* is apparently the ecological equivalent of *P. sinuatus* in the Congo Basin.

BREEDING

Remarkably little information on breeding in *Pelusios* is available and it is surprising to find that much of it relates to *P. bechuanicus*. The eggs of these terrapins are relatively thin-shelled.

A 170 mm ♀ *P. subniger* laid about 8 eggs in an aquarium during Feb/Mar (several were broken and eaten by other terrapins).

A *P. b. bechuanicus* with a carapace length of 239 mm laid 21 eggs in moist soil at Linyanti, Caprivi, on 16 October before being collected (TM 39410). A 330 mm ♀ from Sangwali, Caprivi (TM 39401) contained 48 eggs measuring 39 x 23 mm on 8 October. A 245 mm ♀ from Kalabo, Zambia (UM 10677), contained 28 eggs measuring 38 x 23 mm. A 265 mm ♀ from the Kafue Flats, Zambia (UM 761) contained 32 eggs measuring 35 to 38 x 21 to 23 mm (B. L. Mitchell, *in litt.*).

A *P. rhodesianus* from Linyanti Swamps, Caprivi (TM 39411) contained eggs measuring 33 x 21 mm on 11 October. A 199 mm ♀ from the Kafue Flats (UM 47) contained 14 eggs measuring 33 to 37 x 22 to 23 mm in mid-September (Mitchell, *in litt.*). A 170 mm ♀ from Mupudzi River, Zimbabwe (UM 14516), contained 13 eggs measuring 33 x 20 mm in November. A 139 mm ♀ from Norton laid 11 eggs of similar size in captivity during April/May and then died (now UM 33385).

Two captive *P. castaneus castanoides* from Lake Chilwa, Malawi, each laid 25 eggs at the end of September (Mitchell, 1946). These measured 30 to 33 x 21,5 to 23 mm (Mitchell, *in litt.*).

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