A COMPARATIVE STUDY OF DEGENERATION OF THE POSTERIOR LIMBS AND GIRDLES OF SOME *SCELOTES* SPECIES.

by

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INTRODUCTION

Aim and Scope

The genus *Scelotes* was instituted by Fitzinger in 1826 and is represented by nineteen species and subspecies in Southern Africa (Fitzsimons, 1943). Valuable contributions have been made to our knowledge of the Lacertilia by pioneers such as Gadow (1881), Cope (1892), El-Toubi (1938), King (1964) and Tiedeman et al. (1975) who investigated the osteology and myology. Essex (1927), Stokely (1947), Lande (1978) and Leonard (1979) dealt with the evolution of limb loss and pelvic girdle degeneration in the lizards, and especially in the skinks. Van der Klaauw (1948), Snyder (1952; 1954) and Gans (1962; 1966; 1973) studied the ecology and behaviour of limbless tetrapods, while De Witte and Laurent (1943) and Greer (1970) contributed to our knowledge on the systematics of the skinks.

Partial or complete loss of limbs and degeneration in the pelvic arch have possibly evolved independently in a variety of tetrapods. The genus *Scelotes* exhibits a full range of degeneration - from fully pentadactyle tetrapodous forms to limbless species. The question arises: Can a general pattern of devolution be observed in this genus? Although many of the *Scelotes* species have already been described, it will here for the first time be attempted to compare the different stages of degeneration as exhibited in this genus.

A major objective of this work will, therefore be to analyze the pattern of degeneration in *Scelotes*. Firstly, the osteology of the pelvic girdle and hindlimbs of the *Scelotes* species will be described and, secondly, these structures will be compared.

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Thirdly, an attempt will be made to graphically reflect the major trends associated with limb regression by employing morphometric data obtained from the limited number of specimens available.

PROCEDURE (MATERIAL AND METHODS)

Specimens for study purposes were obtained from Dr. C.J. Leonard, Mr. J. Visser, The South African Museum (S.A.M.) and the Transvaal Museum (T.M.). Morphometric data were obtained as follows:

(1) The specimens were dried with Whatman filter paper and then weighed on a Sartorius toploading balance to the nearest 0,5gram.

(2) Measurements of the limb-, and snout-eye-lengths were made with a micrometer eyepiece attachment on a Vickers dissecting microscope.

(3) The diameters of the head were measured with a N.S.K. vernier caliper.

(4) The length from the tip of the snout to the cloaca (snout to vent length) as well as that of the tail was made by making use of a cotton thread.

A male *S. inornatus inornatus* specimen was anaesthetized with ether and fixed in Bouin's fluid for six days. Afterwards the scales in the pelvic region were removed, and this region was placed in von Ebner's solution to decalcify. After eight weeks this region was dehydrated, cleared in

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terpineol, embedded in paraffin wax and serially sectioned at twelve micron. Finally the sections were stained according to Heidenhein's Azan method (Azocarmine + aniline blue + Gold Orange G.)(Romeis, 1948).

One specimen of each species was preserved in formalin (10%) and $Mg(CO_3)_2$ or 70% in ethanol. Then they were stained according to Wassersug's Alizarin Red-S and Alcian Blue staining technique (1976). Cartilaginous elements stained blue, while osseous elements stained red.

One specimen of *S. mira* and one *S. brevipes* were kept alive for observations of their behaviour.

Drawings of the girdles and limbs were made by using a camera lucida attachement to a Zeiss microscope.

	S. capensis	*S. mira*	*S. limpopoensis*	*S. alberti*	*S. caffer*	*S. kasneri*	*S. bipes sexlineatus*	*S. bipes*	*S. bidigittatus*	*S. gronovii*	*S. brevipes*	*S. inornatus inornatus*	*S. anguia*
Number of specimens	6	3	10	1	10	1	1	12	1	15	2	9	9
Number of stained specimens	1	1	1	0	1	0	1	1	1	1	1	1	1
Number of sectioned specimens	0	0	0	0	0	0	0	0	0	1	0	1	0

TABLE 1 LIST OF SPECIMENS EXAMINED

4./........

ACKNOWLEDGEMENTS

I am indebted to various individuals and institutions, without whose assistance this work would not have been completed. To them I wish to extend my gratitude: Prof J.H. Skinner and Dr. C.J. Leonard for their supervision, constructive criticism and the use of their personal collection of publications; Mr. John Visser, the South African Museum and the Transvaal Museum for providing specimens for research; and Dr. D. Kotze and her husband, Dr. T.J. van Wyk Kotze, for their assistance with the interpretation of the morphometric data.

I wish to thank Martin Hendricks, Merle McOmbring and Ronnie Lakey for helping with the research, and Neil Heideman and Fadli Wagiet for their constructive suggestions. I am also grateful to Valerie Christians for doing the typing of this manuscript.

Finally I would like to thank the Council for Scientific and Industrial Research for rendering financial assistance.

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SCELOTES CAPENSIS

THE PELVIC GIRDLE

Three paired endochondral bones, namely the pubis, ischium and ilium form the pelvic girdle. The pubes and ischia form the ventral part of the girdle and delimit a heart-shaped thyroid (pubo-ischiadic) fenestra, while the posterodorsally directed ilia articulate with the sacrum (Figs. 1 + 2).

An acetabulum is present at the junction of the three pelvic elements. No distinct sutures between the three bones could be observed in the adult specimen examined.

The Pubes

Each pubis broadens posterolaterally towards the acetabulum where it joins the other pelvic elements. From this junction the pubes are directed anteromedially so that they approach and join each other at the cartilaginous pubic symphysis. A separate, more or less rhomboid-shaped cartilage, the epipubis, is wedged into the anterior part of the pubic symphysis.

The external border of the pubis gives rise to a blunt downwardly curved, posteromedially directed process, at a point approximately a quarter of its length from the acetabulum. Stokely (1947) named it the pectineal process, whereas Tiedeman et al. (1975) called it the processus praepubis. The pubic foramen (Stokely, 1947) or obturator foramen (El-Toubi, 1938), situated just posteriorly to the pectineal process, provides passage for the obturator nerve.

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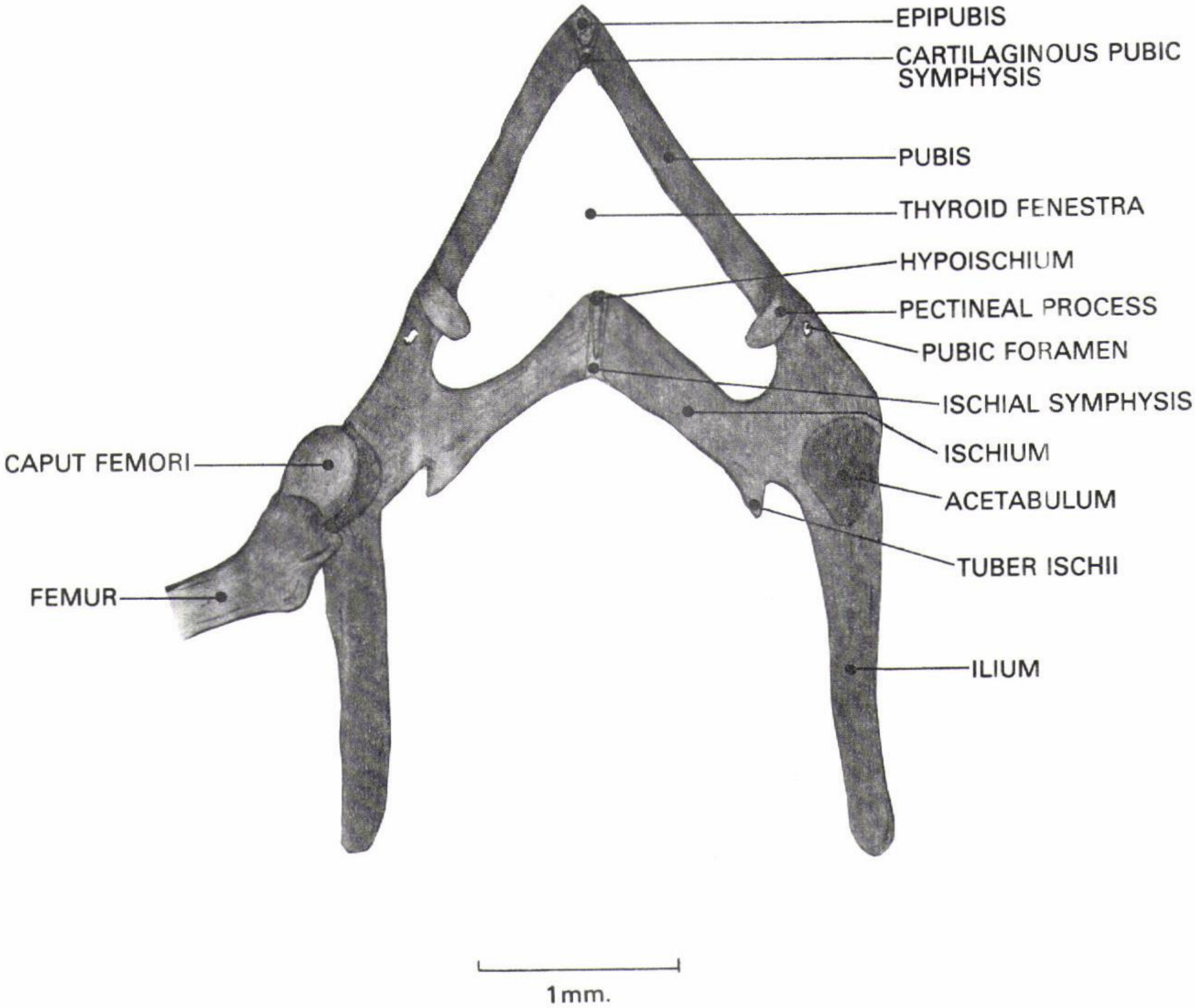

FIG. 1

S. capensis
VENTRAL VIEW OF THE
PELVIC GIRDLE

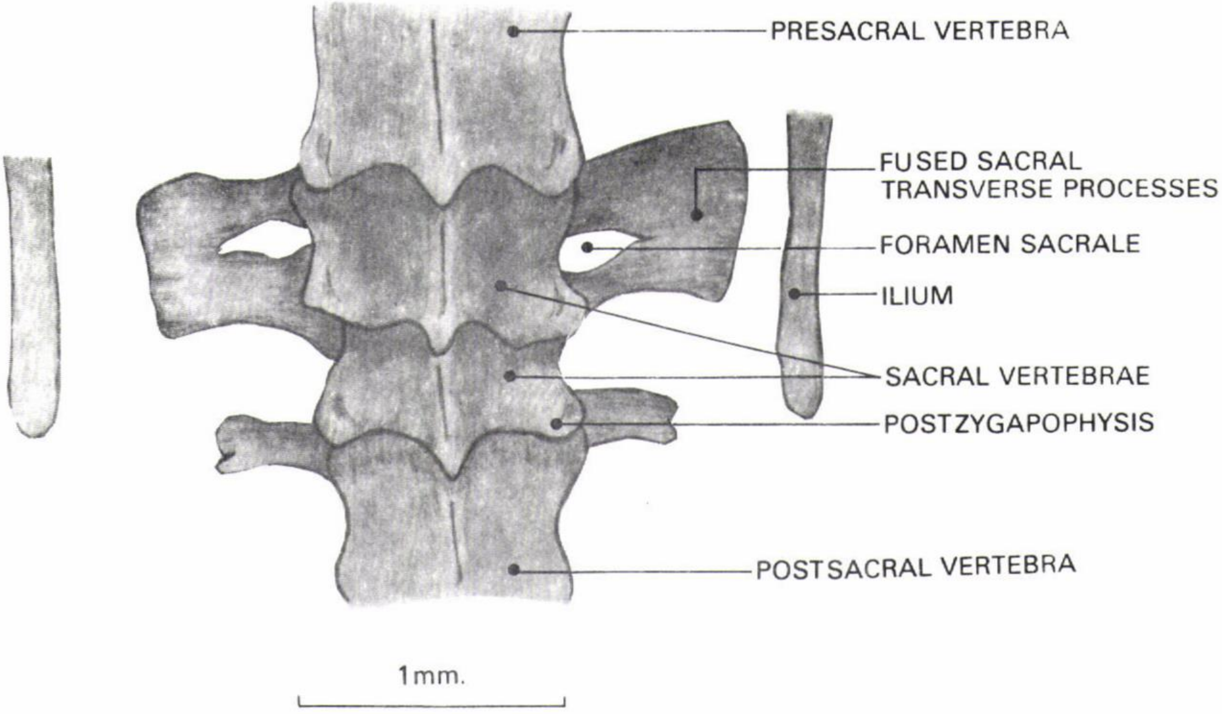

FIG. 2

S. capensis
DORSAL VIEW OF
THE SACRUM

The Ischia

Of the three pelvic elements the ischium is the shortest and broadest. Whereas the pubis and ilium are essentially cylindrical bones, the ischium is a blade-like structure. From the acetabulum the ischium projects ventromedially to the well-developed, cartilaginous ischial symphysis.

A distinct rod-shaped hypoischium is present between the ischia. Camp (1923) suggested that the hypoischium is a posterior continuation of the symphyseal ligament which starts at the anterior point of the pubes as the epipubis. Mehnert (1891) in his embryological studies, however, reasoned that there is no developmental relationship between the ligament and the calcareous epipubis and hypoischium. According to Parker and Haswell (1963), the hypoischium in *Lacerta* passes backwards from the ischial symphysis and supports the ventral wall of the cloaca. This is, however, not the case in *S. capensis*, the hypoischium being a very short rod.

On its posterior border, nearer to the acetabulum, the ischium gives rise to a posterolaterally directed process, the tuber ischii.

The Ilia

The ilia are the elements by means of which the pelvic girdle articulates with the sacrum. From the acetabulum the ilium radiates posterodorsally and the inner surface of the central third of the bone forms a synovial joint with the fused transverse processes of the sacrum. The posterior third of the ilium projects beyond the transverse processes of the sacral vertebrae.

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The ilium is broader than the pubis, though not as broad as the ischium. The cross-sectional shape of the ilium varies along its length. The portion nearer to the acetabulum is essentially cylindrical, but the bone flattens posterodorsally.

THE SACRUM

As in most Lacertilia the sacrum consists of two fused vertebrae modified to articulate with the ilium. In *S. capensis* the forty-fourth and forty-fifth vertebrae form the sacrum. Each bears a pair of strong transverse processes. Researchers differ on whether these are transverse processes or pleurapophyses (i.e. transverse processes formed by the fusion of sacral ribs to their vertebrae). El-Toubi (1947), Kamel (1951), Holder (1960) and Hofstetter and Gasc (1969) are of the opinion that these processes are pleurapophyses. They, however, base their assumptions mainly on studies of adult specimens, and did not study the embryonic condition in much detail.

If the Lacertilia possess sacral ribs, there should be separate centres of ossification for these elements and these would be expected in the embryonic condition. If there are no ribs, we would not expect to find different ossification centres in the embryonic condition, nor would sutures of separation of the ribs from the centra persists in the young of the lizards. Moodie (1907) in his embryological studies found no separate centres of ossification. In a later work (1909) he again referred to this view, but he suggested that studies of chondrification might indicate the presence of sacral ribs. He did not, however, employ this method.

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The Lacertilia occupy a special place among all other known reptiles in that they do not have any sacral ribs. Research workers as Mahendra (1950) and Romer (1956) also maintain that there are no sacral ribs in lizards. The lateral projections of the centra should therefore rather be considered as transverse processes.

The two sacral vertebrae in *S. capensis* are fused at the centra, the zygapophyses, neural arches and the lateral tips of the transverse processes. A foramen sacrale separates the two transverse processes on each side. Each ilium forms a diarthrosis with the fused transverse processes.

THE HINDLIMBS

The hindlimb is pentadactyle.

The Femur

The femur, the stoutest and longest element of the hindlimb, is essentially a cylindrical bone, moderately expanded proximally and distally.

Proximally the bone has a caput femori which fits into the acetabulum. The femur also exhibits proximally three trochanters. Distally the bone bears two asymmetrical condyles, a larger lateral one separated by a shallow intercondylar fossa from the smaller mesial one. The articular surface of the lateral condyle is divided into two facets. The tibia articulates with the smaller condyle and with the mesial facet of the larger one while the fibula is in contact with the lateral facet of the lateral condyle only (Fig. 3).

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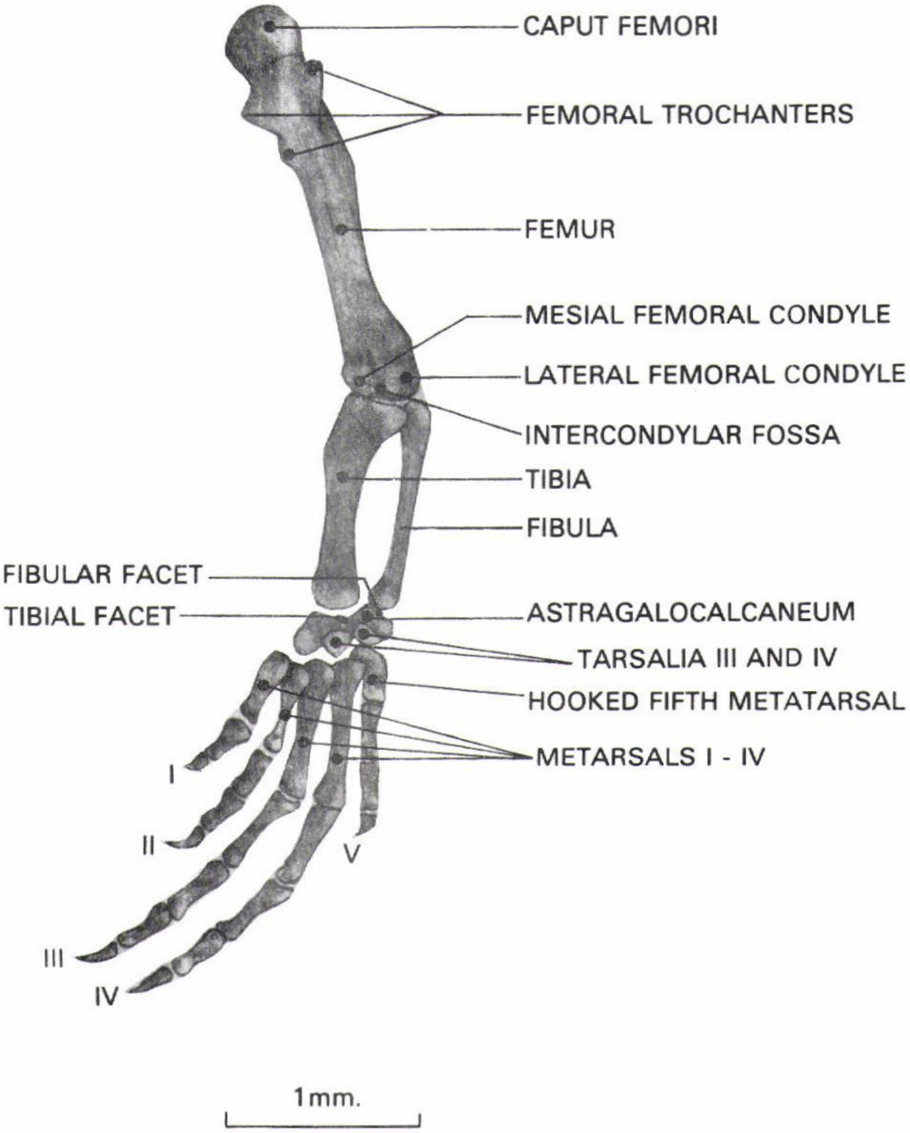

FIG. 3

S. capensis
DORSAL VIEW OF THE
LEFT HINDLIMB

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The Crus (Tibia and Fibula)

Of these two epipodials the medial tibia is the stouter one. It broadens proximally to form a flat articular surface for the mesial condyle and the inner facet of the lateral femoral condyle. That part of this expanded portion adjoining the fibula also articulates with the fibula. Distally the tibia also broadens to accommodate the tibial facet of the astragalo=calcaneum.

The slender fibula broadens proximally and distally and is markedly concave towards the tibia. Proximally it articulates with the lateral femoral condyle and the tibia whereas distally it articulates withthe fibular facet of the astragalocalcaneum.

The Tarsus

Three elements make up the tarsus, namely the proximal astragalocalcaneum and two distal tarsals. The large astragalocalcaneum represents the fused astragalus and calcaneum (Russel and Rewcastle, 1979). The astragalus itself consists of the fused intermedium, tibiale and centrale, while the calcaneum represents the fibulare (Hughes, 1968).

There are two distal tarsals of which the lateral one is the larger. They represent the third and fourth tarsalia (Hughes, 1968).

The Metatarsus and Digiti

The foot consists of five toes with a phalangeal formula (Tiedeman, et al. 1975) of $\frac{2:\ 3:\ 4:\ 4:3}{\mathrm{I:II:III:IV:V}}$.

Metatarsals I to V are relatively simple with III and IV being the longest. The fifth metatarsal has a peculiar hooked shape. This hooked metatarsal consists of a fused distal tarsal V and the fifth metatarsal (Sewertzoff, 1931 and Holmgren, 1933).

The five small distal phalanges all bear claws.

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SCELOTES MIRA

THE PELVIC GIRDLE

The pelvic girdle also consists of three paired endochondral bones, namely the pubis, ischium and the ilium, the former two delimiting a heart-shaped thyroid fenestra (Fig. 4).

A well-developed acetabulum is present at the junction of the three pelvic elements.

The Pubes

Each pubis is a fairly straight bone broadening posterolaterally to join the other pelvic elements at the acetabulum. It differs from the pubis of *S. capensis* in the following respects:

(1) A pubic symphysis is not present. A cartilaginous rhomboid-shaped epipubis is, however, situated between the anterior tips of the pubes without contacting these.

(2) The anterior border of the somewhat tapered pectineal process of *S. mira* is more or less convex in contrast to the blunt, anteriorly concave, pectineal process of *S. capensis*.

The Ischia

The short broad ischium which is directed ventromedially from the acetabulum, differs from that of *S. capensis* in the following ways:

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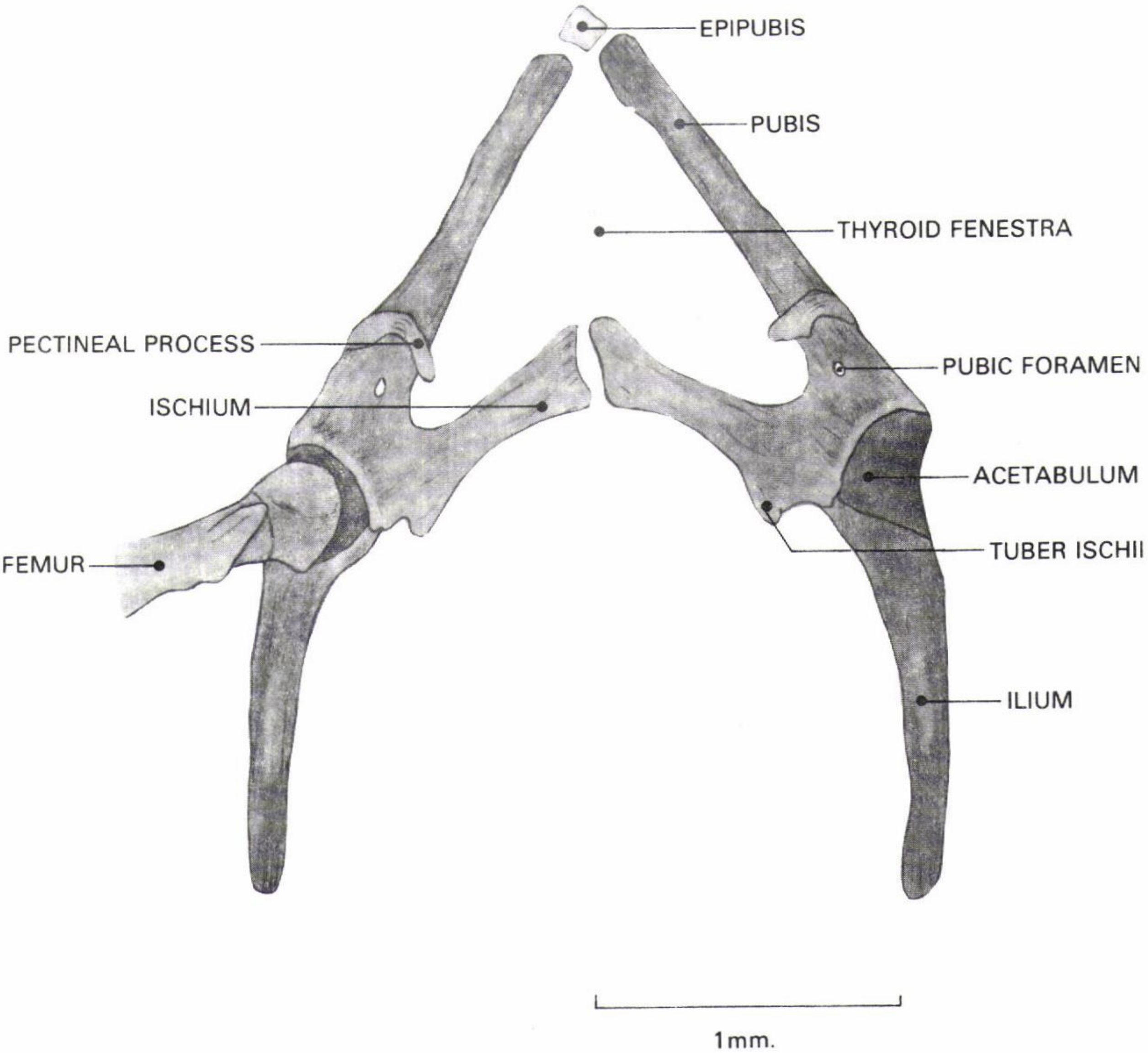

FIG. 4

S. mira
VENTRAL VIEW OF
THE PELVIC GIRDLE

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(1) The two ischia are not synchondrotically joined as in *S. capensis*. A gap filled with connective tissue separates the medial tips of the ischia so that there is no ischial symphysis as in *S. capensis*.

(2) A hypoischium between the ischia is absent.

(3) The posterolaterally directed tuber ischii of *S. mira* is blunter and shorter.

The Ilia

The posterodorsally directed ilia articulate with the sacrum. The ilium of *S. mira* is slightly curved inwards, whereas in *S. capensis* the ilium is a rather straight element with the distal portion curved slightly outwards.

THE SACRUM

The sacrum (Fig. 5) is situated further posteriorly, being formed by the fused forty-seventh and forty-eight vertebrae.

THE HINDLIMBS

The hindlimb of *S. mira* is also pentadactyle (Fig. 6).

The Femur

This is the longest and stoutest element of the hindlimb and articulates with the pelvic girdle by means of the caput femori which fits into the acetabulum. It differs from the femur of *S. capensis* in the following respects:

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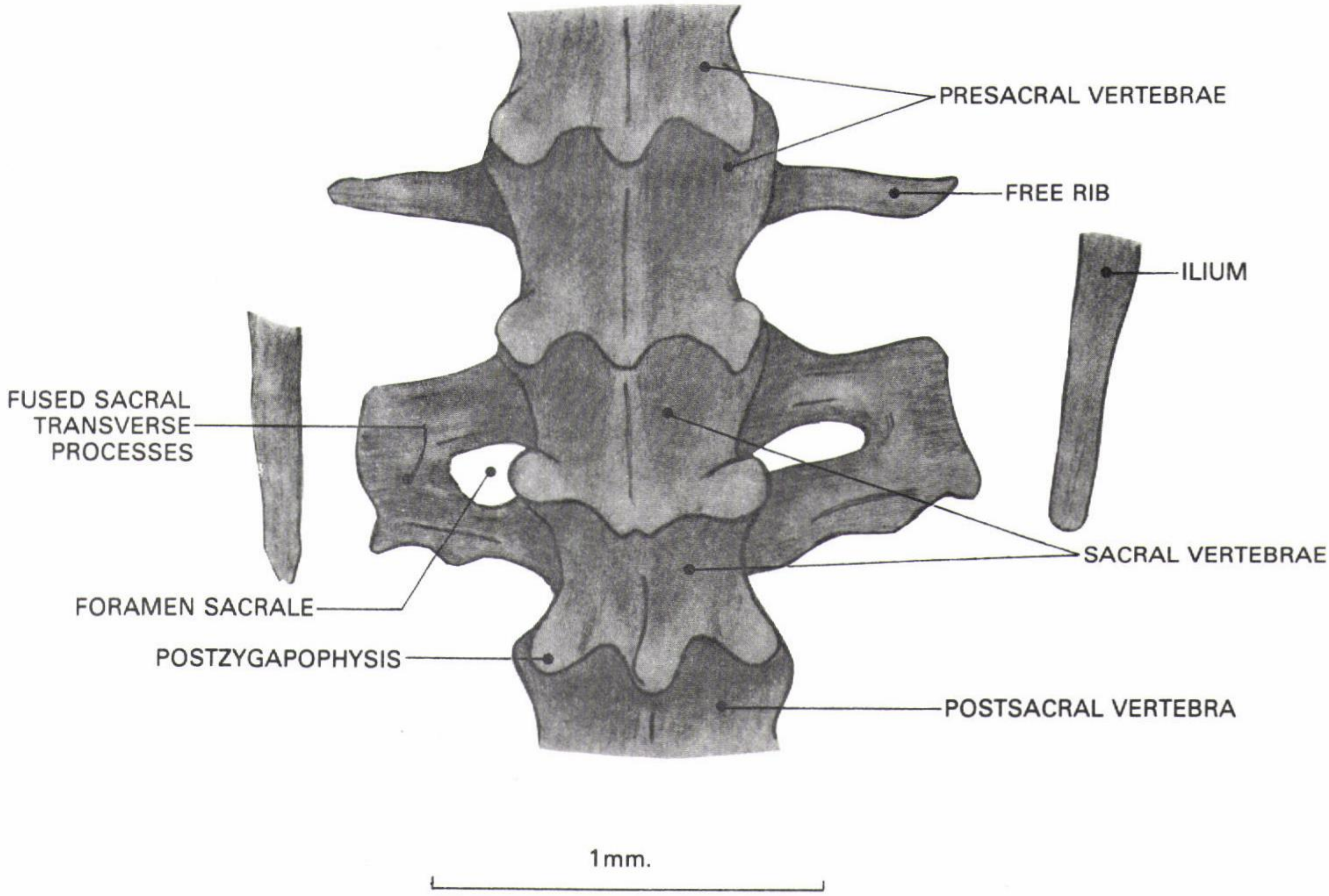

FIG. 5

S. mira
DORSAL VIEW
OF THE SACRUM

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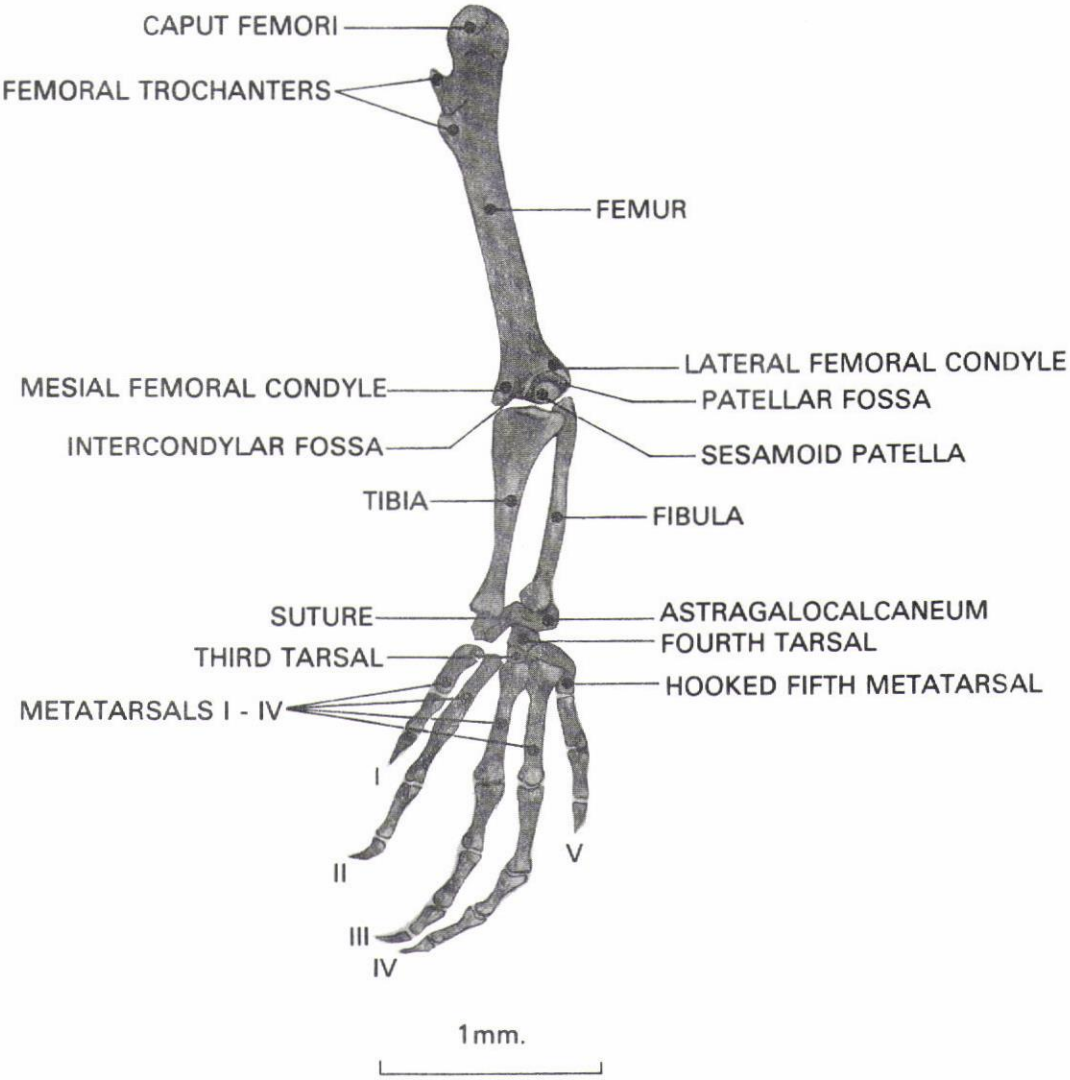

FIG. 6

S. mira
DORSAL VIEW OF
THE LEFT HINDLIMB

(1) The proximal portion of the femur in *S. mira* exhibits only two trochanters.

(2) The lateral femoral condyle is markedly larger than the mesial condyle.

(3) On the lateral femoral condyle of *S. mira* a sesamoid bone, comparable to the patella of mammals, is present in a patellar fossa.

(4) Separate facets on the lateral femoral condyle could not be distinguished in the adult specimen examined.

The Crus

The stouter tibia is greatly expanded proximally to articulate with the mesial condyle as well as with part of the lateral femoral condyle.

The slender fibula articulates proximally with part of the lateral femoral condyle and also with the adjacent proximal portion of the tibia. Distally the tibia and fibula articulates with the astragalocalcaneum.

The Tarsus

The tarsus comprises three elements as in *S. capensis*. In *S. mira*, however, a distinct suture is present where the astragalus is fused with the calcaneum. The fourth distal tarsal is larger than tarsal III.

The Metatarsus and Digiti

No marked difference is present between the pes of *S. capensis* and that of *S. mira*. The latter also has a phalangeal formula of: $\frac{2:\ 3:\ 4\ :\ 4:3}{\mathrm{I:II:III:IV:V}}$.

SCELOTES LIMPOPOENSIS

THE PELVIC GIRDLE

The normal three paired endochondral bones make up the pelvic girdle, joining one another at the acetabulum (Fig. 7).

The Pubes

The pubis of *S. limpopoensis* differs as follows from that of *S. capensis*:

(1) The pectineal process tapers medially in *S. limpopoensis*.

The Ischia

The blade-like ischium does not differ markedly from that in *S. capensis*. It differs from that in *S. mira* as follows:

(1) A well-developed cartilaginous ischial symphysis is present between the ischia.

(2) The hypoischium is also present.

The Ilia

The ilium is rather straight and the distal portion curves slightly outwards.

THE SACRUM

Vertebrae forty-seven and forty-eight fuse to form the sacrum (Fig. 8).

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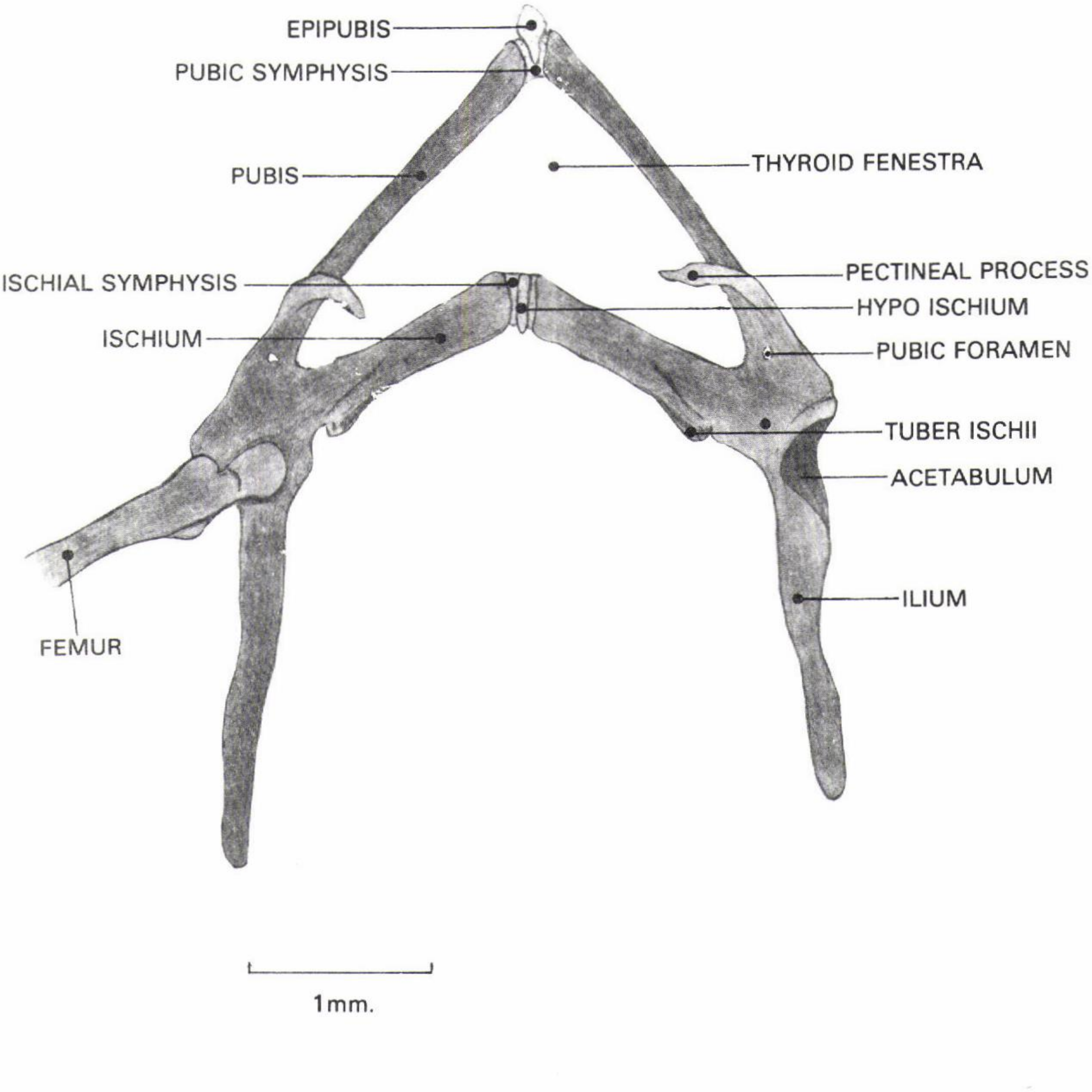

FIG. 7

S. limpopoensis
VENTRAL VIEW OF THE
PELVIC GIRDLE

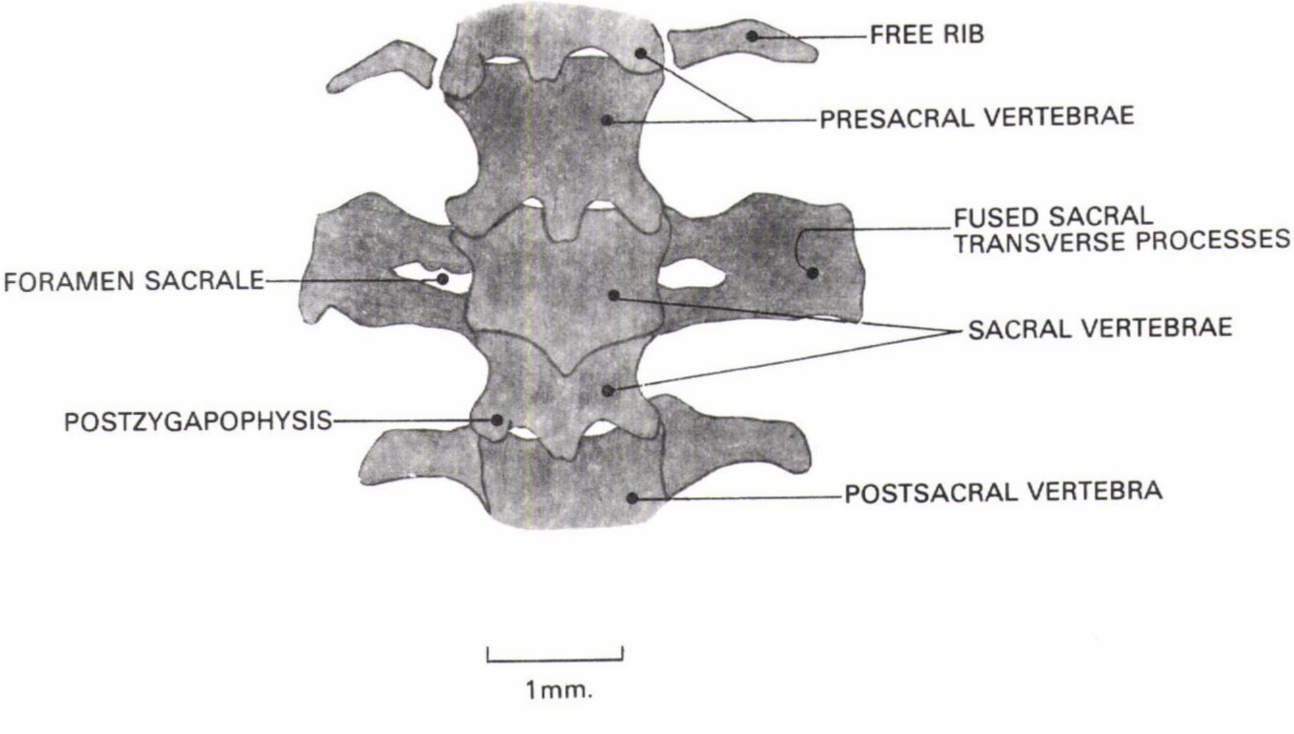

FIG. 8

S. limpopoensis
DORSAL VIEW OF
THE SACRUM

THE HINDLIMBS

The hindlimb of *S. limpopoensis* is tetradactyle (Fig. 9).

The Femur

The stoutest and longest element of the hindlimb, the femur, differs from that of *S. capensis* as follows:

(1) In *S. limpopoensis* the femur exhibits proximally only two trochanters.

(2) Separate facets on the lateral femoral condyle could not be distinguished in the specimen examined.

The Crus

The expanded proximal portion of the stouter tibia contacts the mesial condyle as well as part of the lateral femoral condyle.

Proximally the slender fibula articulates with part of the lateral femoral condyle and also with the adjacent proximal portion of the tibia. Distally the two epipodials are not in contact with each other. Both, however, articulate with the astragalocalcaneum.

The Tarsus

The astragalocalcaneum and two distal tarsals make up the tarsus. In *S. limpopoensis* a suture marking the line of fusion of the astragalus and calcaneum was distinct in the astragalocalcaneum of the specimen examined.

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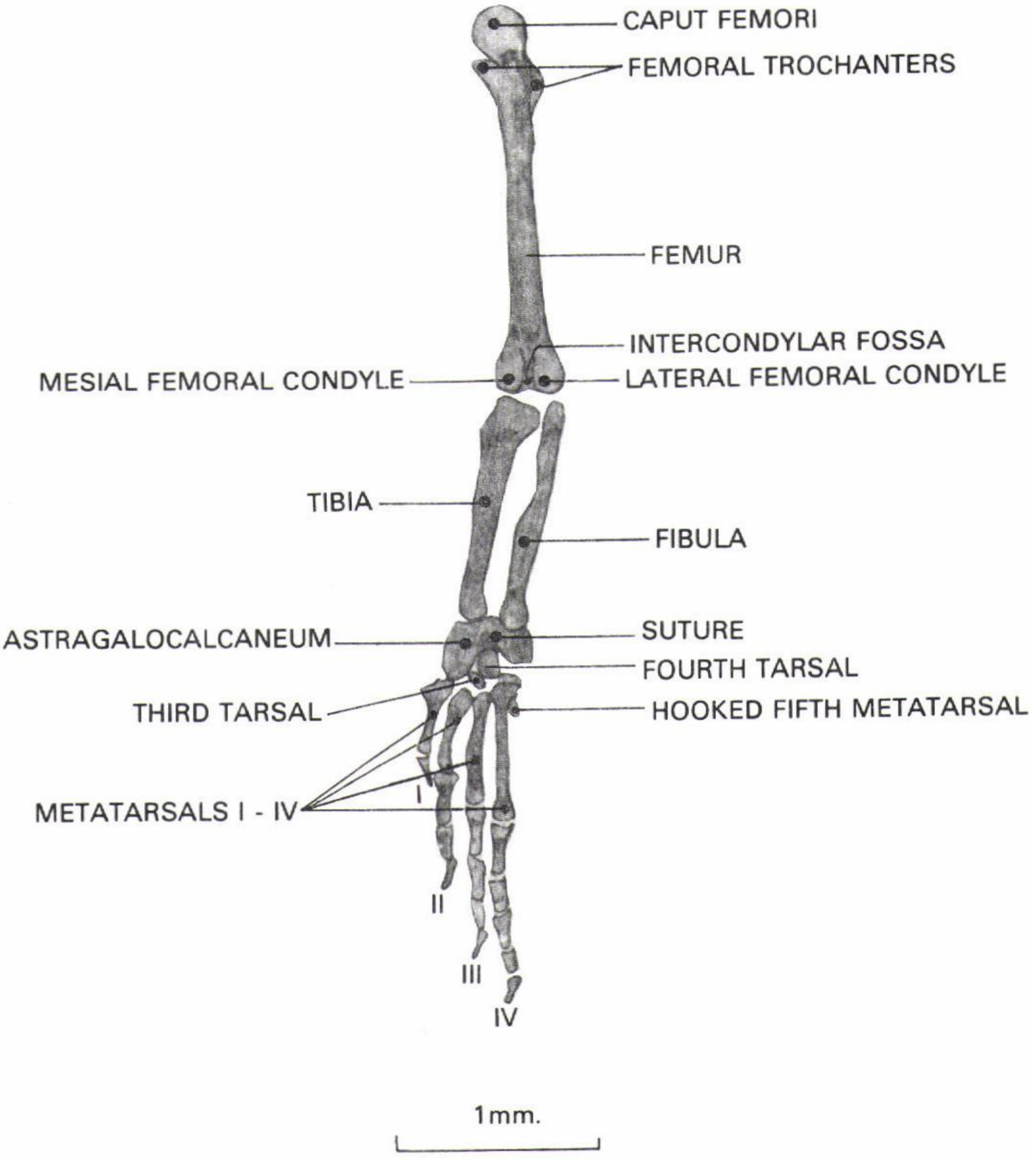

FIG. 9

S. limpopoensis
DORSAL VIEW OF THE
LEFT HINDLIMB

The Metatarsus and Digiti

The four digits present in the pes are digitalia I; II; III and IV. The hooked fifth metatarsal is present, but bears no phalanges, consequently the fifth digit is absent.

Digit IV is the longest one and in contrast to *S. capensis*, where the fourth digit bears only four phalanges, it bears five phalanges. Digit I has only one phalanx.

The phalangeal formula is $\frac{1:\ 3:\ 4\ :\ 5:0}{\mathrm{I:II:III:IV:V}}$.

SCELOTES CAFFER

THE PELVIC GIRDLE

The pelvic girdle (Fig. 10) is essentially similar to those of the previously described specimens except that it is relatively smaller.

The Pubes

The pubis is a fairly narrow bone which broadens towards the acetabulum. The pubis of *S. caffer* differs from that in *S. capensis* in the following ways:

(1) A gap separates the two pubes as in the case of *S. mira.*

(2) The epipubis is not in contact with the pubes. Moreover it consists of two small pieces of cartilage lying at the level of the tips of the pubes.

(3) The pectineal process is a very short, blunt process curving inwards from the external border of the pubis.

The Ischia

The broad ischium radiates ventromedially from the acetabulum. It differs from the ischium of *S. capensis* as follows:

(1) The two ischia are separate.

(2) A hypoischium is absent.

(3) The syndesmotic ischial joint lies nearer to the pubic joint.

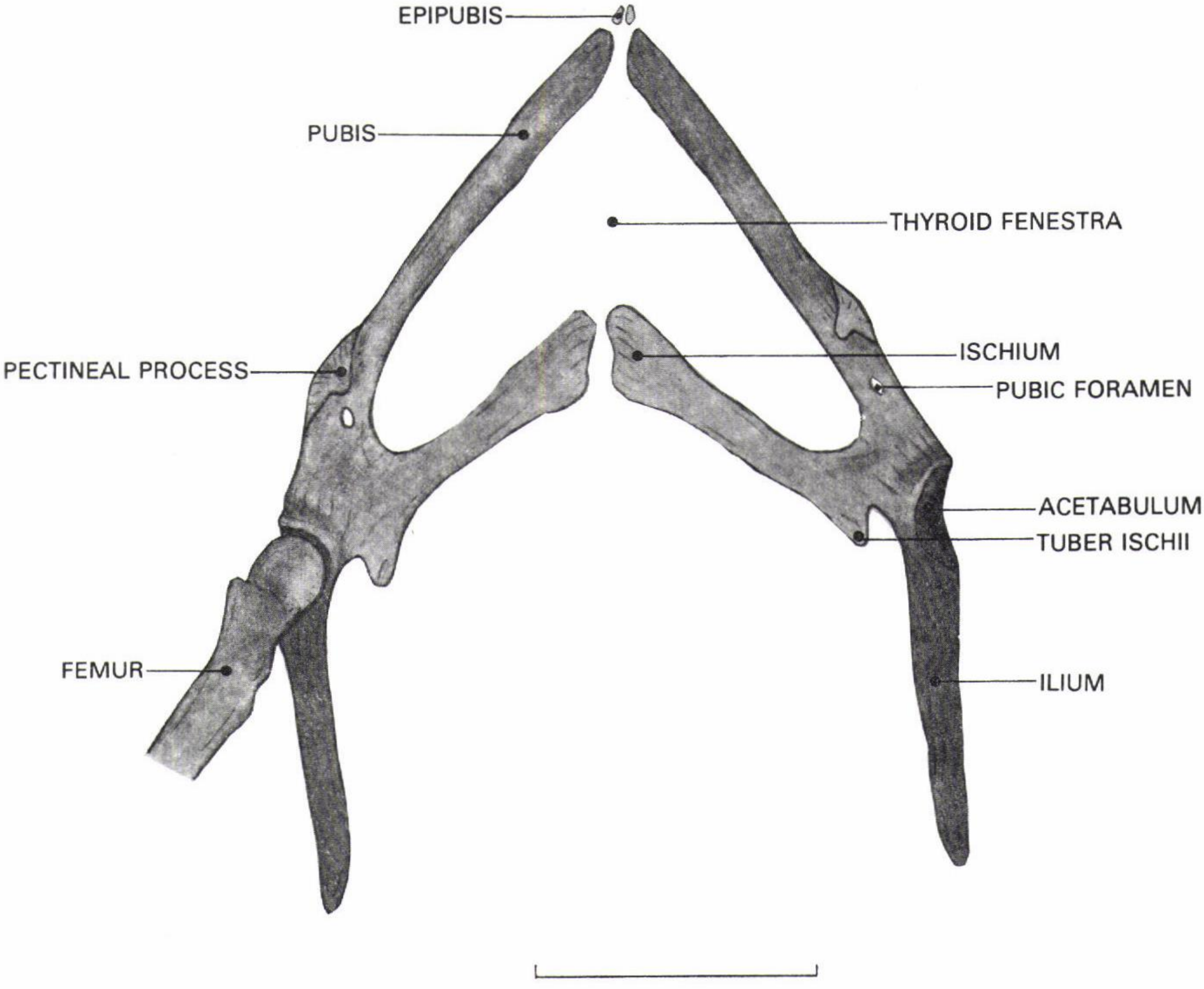

FIG. 10

S. caffer
VENTRAL VIEW OF THE
PELVIC GIRDLE

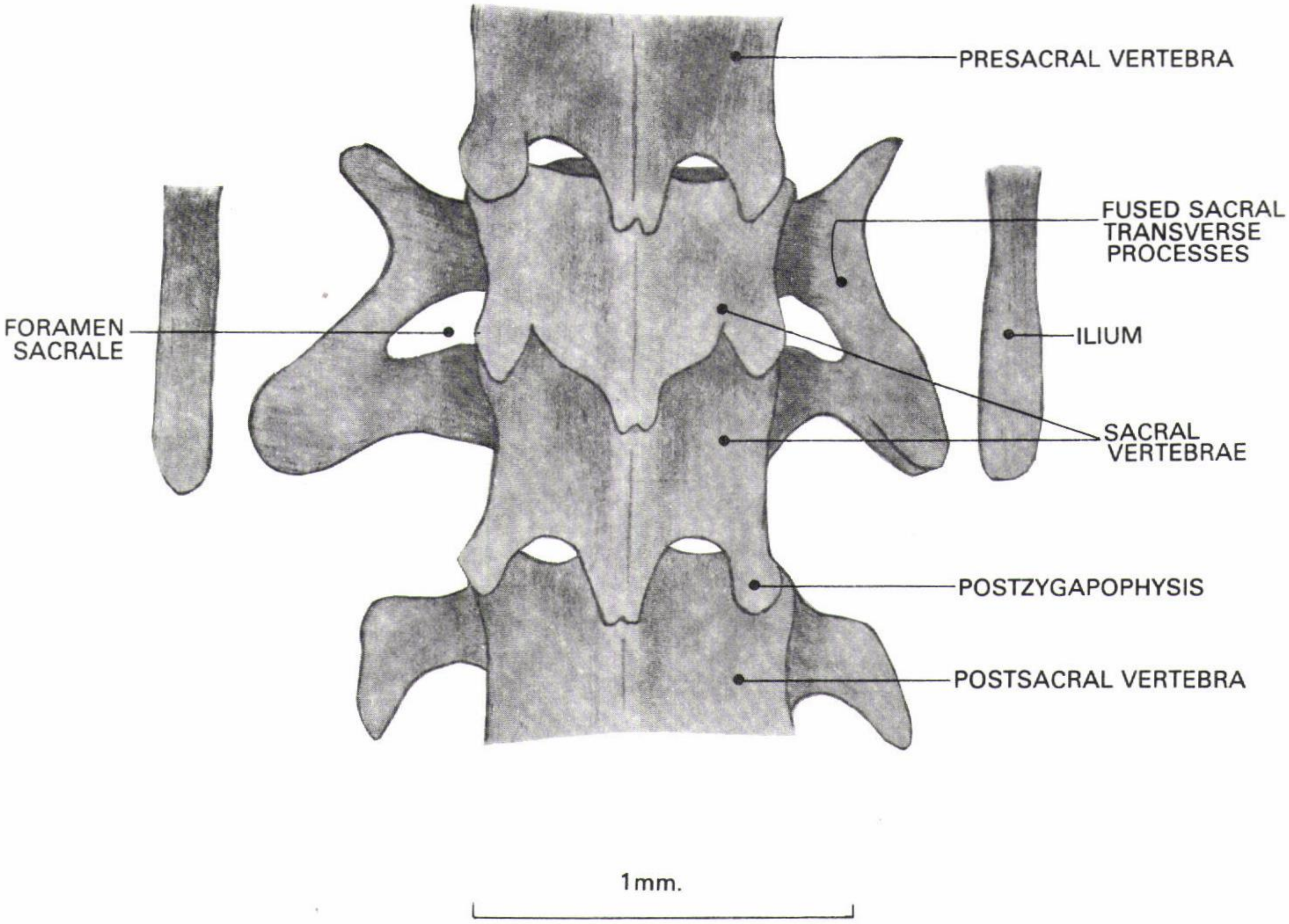

FIG. 11

S. caffer
DORSAL VIEW OF
THE SACRUM

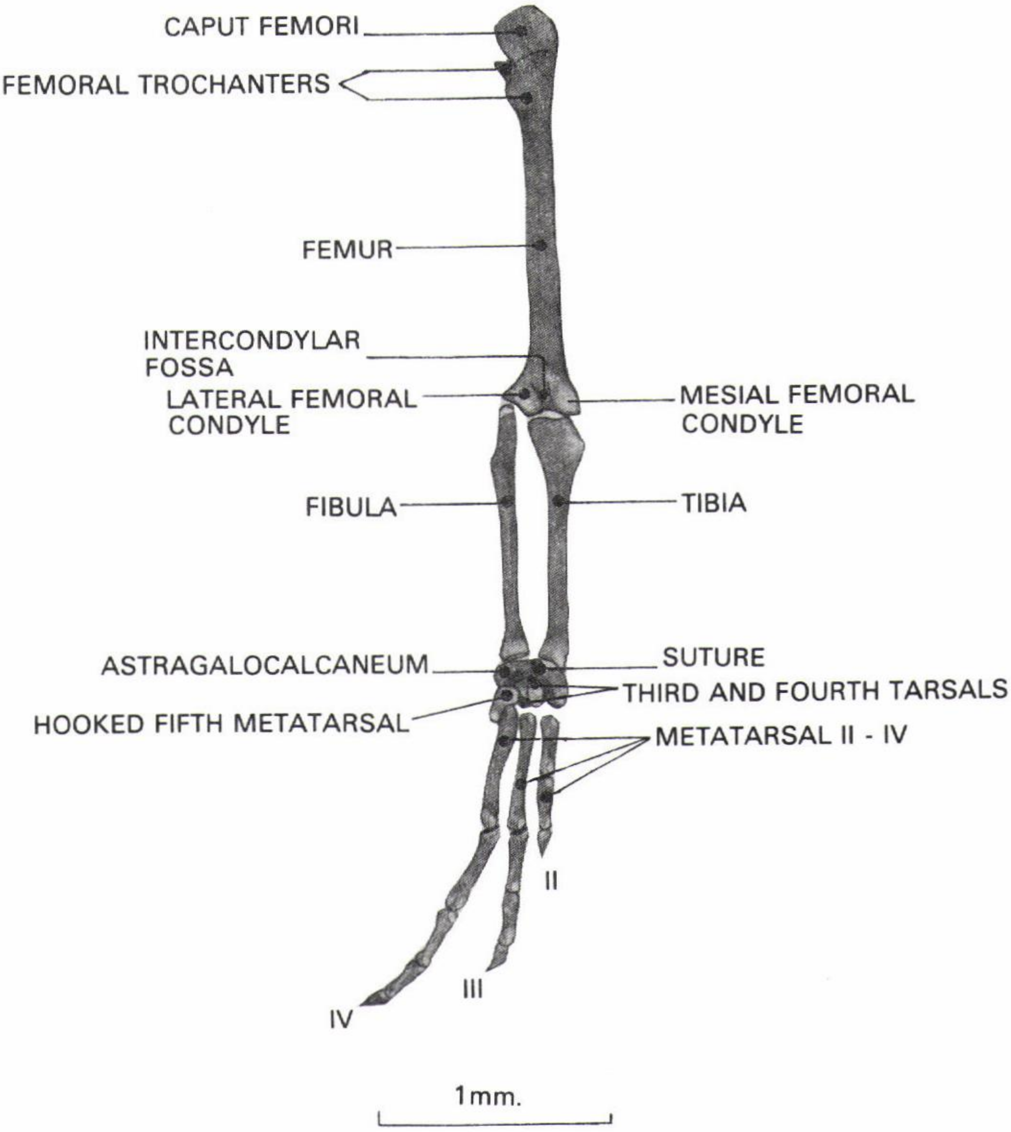

FIG. 12

S. caffer
VENTRAL (FLEXOR) VIEW OF
THE LEFT HINDLIMB

(2) Proximally there is no contact between the tibia and fibula.

The Tarsus

In the astragalocalcaneum there is a suture which marks the line of fusion of the astragalus and the calcaneum. The hooked fifth metatarsal is closely associated with the tarsal elements.

The Metatarsus and Digiti

Only three digits are present in the pes of *S. caffer*. Digits I and V are absent. No phalanges are borne on the hooked fifth metatarsal. In *S. limpopoensis* the first digit has only one phalanx, therefore it is possible to assume that this digit was the second to have degenerated.

Metatarsals II to IV are relatively simple, the third and fourth being the longest. The fifth metatarsal is smaller than that of *S. capensis*, but also hooked.

The phalangeal formula of the pes of *S. caffer* is $\frac{0:\ 2:\ 2\ :\ 4:0}{0:II:III:IV:V}$.

SCELOTES BIPES

THE PELVIC GIRDLE

The paired pubes, ischium and ilium form the pelvic girdle (Fig. 13). In *S. bipes* the pelvic girdle is smaller than *S. capensis* clearly demonstrating the tendency of miniaturization of girdles and limbs in degenerate species.

The Pubes

The pubis differs from that of *S. capensis* as follows:

(1) The pubic symphysis is absent.

(2) No epipubis could be observed between the anterior tips of the pubes. The cartilages at the tips of pubes are probably unossified termini of the bones.

(3) The pectineal process is a very short process, curving inwards from the external border of the pubis and tapered at its medial end.

In the alizarin Red-S-stained specimen (S.A.M. 44035) the ligament extending from the pectineal process to the medial tip of the ischium, namely the pubo=ischiadic ligament, was especially distinct.

The Ischia

The ischium of *S. bipes* differs from that of *S. capensis* as follows:

(1) There is no ischial symphysis.

(2) There is no hypoischium between the ischia.

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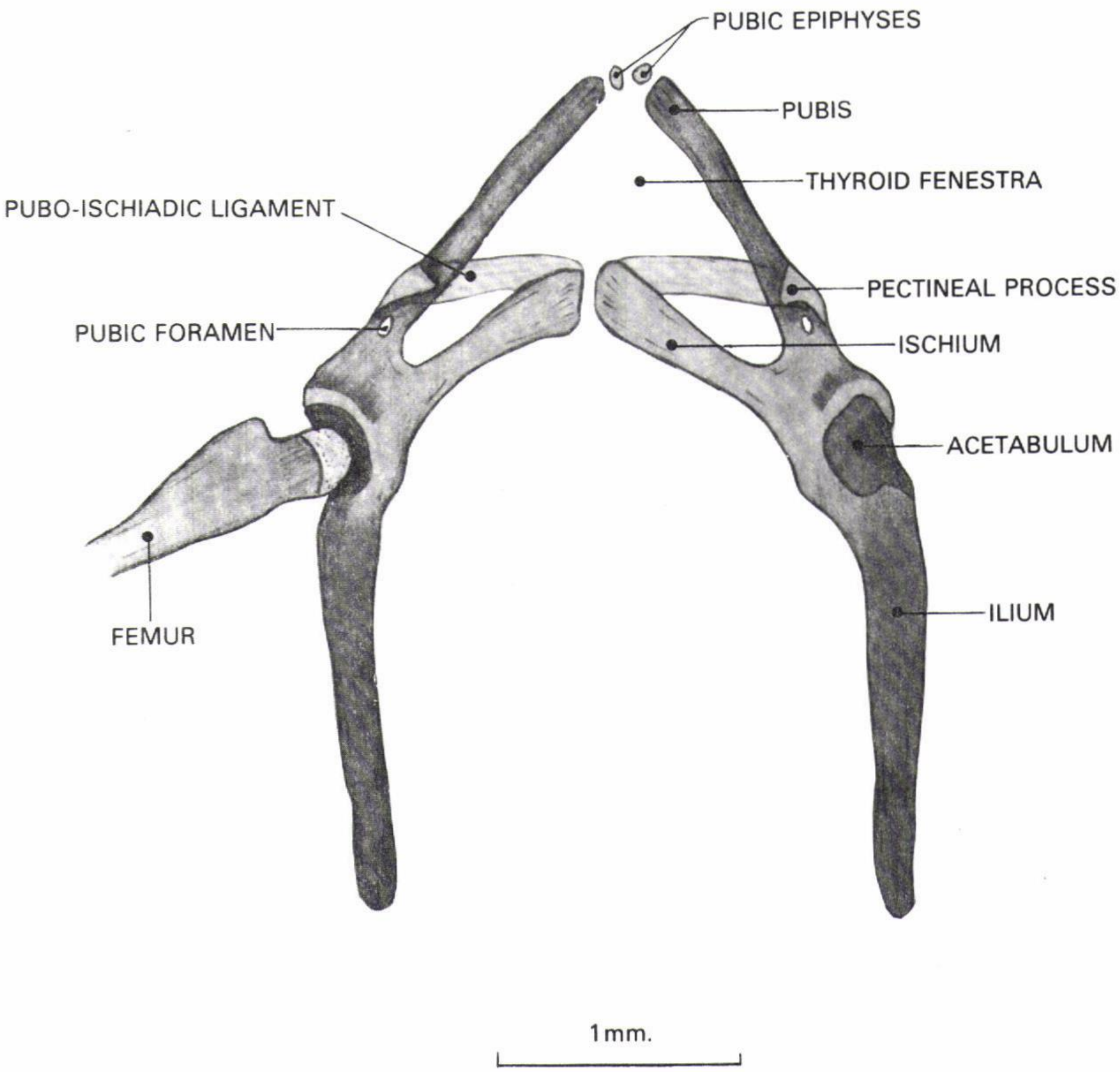

FIG. 13

S. bipes
VENTRAL VIEW OF
THE PELVIC GIRDLE

34./.......

(3) The posterior border of the ischium does not form a tuber ischii.

(4) The ischial joint consisting of connective tissue,lies nearer to the pubic joint.

The Ilia

There is no marked difference between the ilium of *S. capensis* and that of *S. bipes*, except that this element is much more slender in the latter.

THE SACRUM

The small sacrum (Fig. 14) lies relatively far back and is formed by the fused fifty-second and fifty-third vertebrae. There seems to be a closer association between the ilium and the fused transverse processes of the sacral vertebrae.

THE HINDLIMBS

The hindlimb of *S. bipes* is didactyle (Fig. 15).

The Femur

The long and stout femur of *S. bipes* differs as follows from that of *S. capensis*:

(1) Proximally the femur exhibits only one trochanter.

(2) Distally only one femoral condyle, facilitating articulation with the crus, is present.

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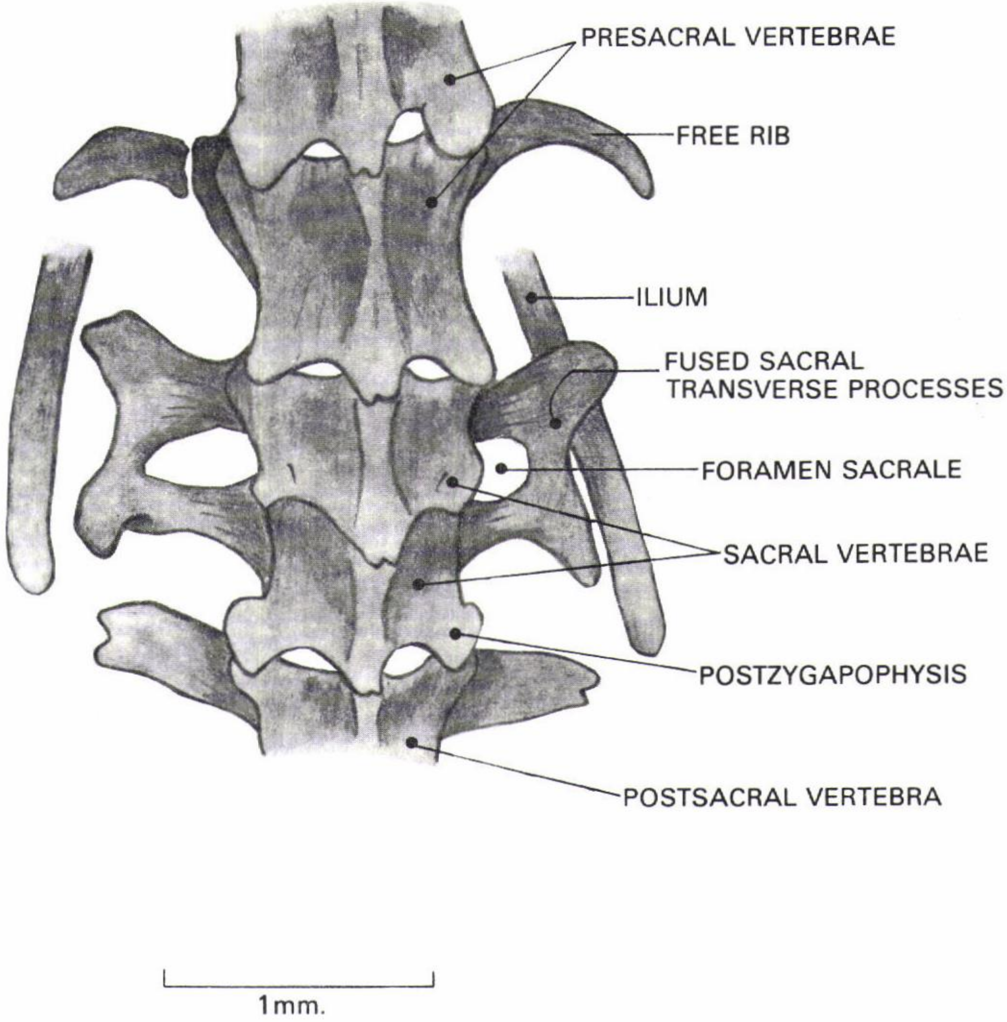


FIG. 14

S. bipes
DORSAL VIEW OF
THE SACRUM

The Crus

Proximally the slender fibula is in contact with the much stouter tibia.

The Tarsus

A suture on the astragalocalcaneum marking the fusion of the astragalus and the calcaneum is quite distinct in the specimen examined. Three distal tarsal elements are present, namely tarsalia III and IV and metatarsal V.

Judging from its position, the third distal tarsal element probably represents a remnant of the hooked fifth metatarsal of *S. capensis* and should therefore be called a metatarsal.

The Metatarsus and Digiti

Two digits, namely digitalia III and IV, are present. The first and fifth digits are absent, and taking the phalangeal formula of *S. caffer* into consideration, as well as the position of the two remaining digits, it is most likely that it is the second digit which is absent, therefore the phalangeal formula of the pes of *S. bipes* is $\frac{0:0:\ 2\ :\ 3:0}{0:0:\mathrm{III}:\mathrm{IV}:\mathrm{V}}$.

38./.......

SCELOTES BIDIGITTATUS

THE PELVIC GIRDLE

The pelvic girdle is made up of the usual three paired endochondral elements. The sutures which mark the junction of the three bones were distinct in the specimen examined (Fig. 16).

The Pubes

The contrasting characters between the pubes of *S. bidigittatus* and *S. capensis* are as follows:

(1) *S. bidigittatus* lacks a cartilaginous pubic symphysis and epipubis; the two pubes are syndesmotically connected.

(2) The pectineal process in *S. bidigittatus* is directed anteriorly while in *S. capensis* it projects posteromedially.

The Ischia

The broad ischium of *S. bidigittatus* differs from its counterpart in *S. capensis* as follows:

(1) No cartilaginous ischial symphysis is present, although the two ischia are syndesmotically connected.

(2) A hypoischium between the ischia is absent.

(3) The syndesmotic ischial joint lies nearer to the pubic joint than in the case of *S. capensis*.

39./..........

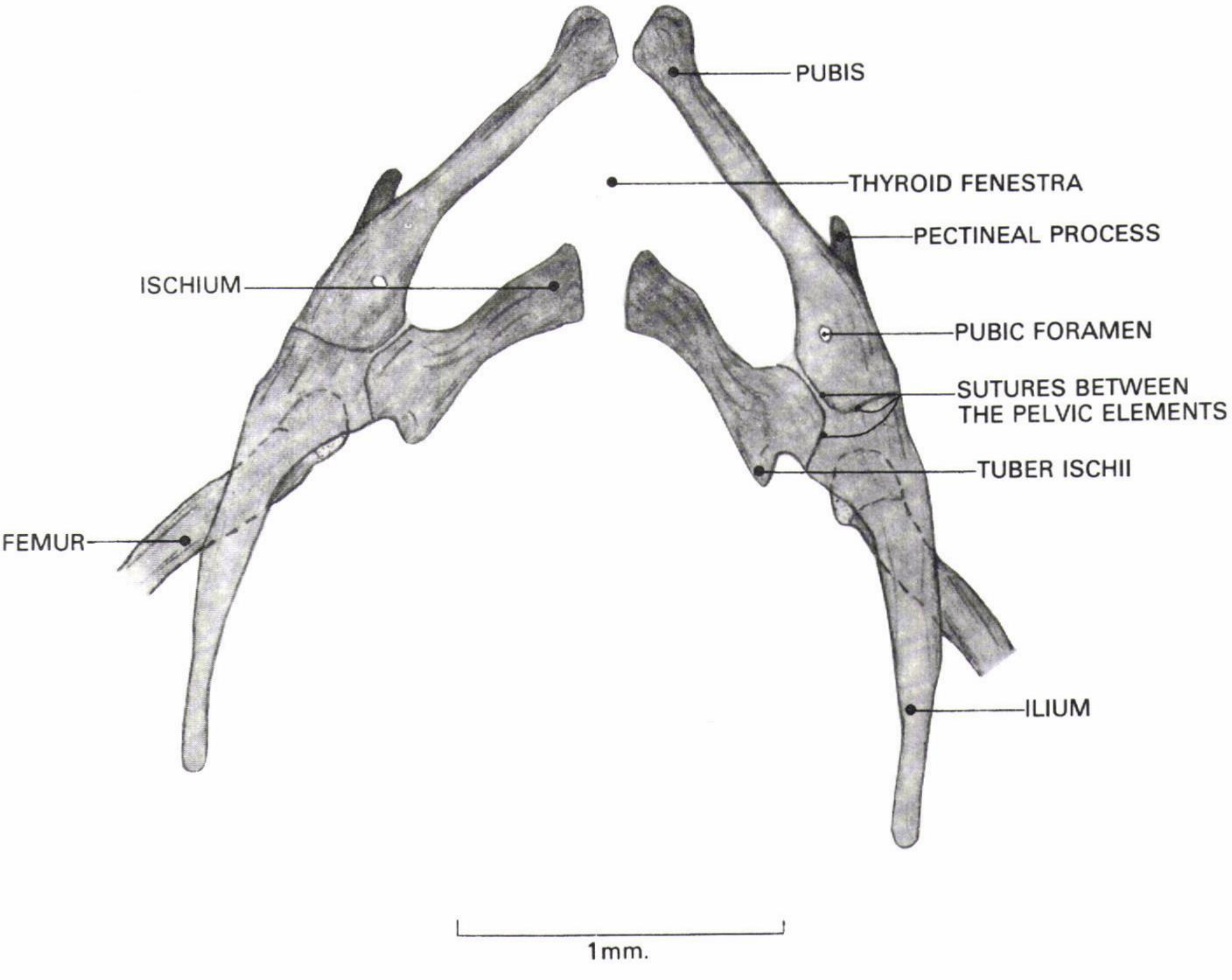


FIG. 16

S. bidigittatus
DORSAL VIEW OF THE
PELVIC GIRDLE

40./.....

The Ilia

Whereas in *S. capensis* the posterior tip of the ilium curves outwards, it curves inwards in the case of *S. bidigittatus.*

THE SACRUM

In *S. bidigittatus* the sacrum is made up of three vertebrae, namely the fifty-second, fifty-third and fifty-fourth (Fig. 17). The fifty-fourth vertebra is a caudal vertebra becoming functionally a sacral one (Hoffstetter and Gasc, 1969). The left transverse process of the first sacral vertebra is not fused with that of the second, the latter being fused with the transverse process of the third sacral vertebra. On the right-hand side the transverse processes of the first two sacral vertebrae are fused while that of the third sacral remains unattached.

THE HINDLIMB

The hindlimb of *S. bidigittatus* is didactyle (Fig. 18).

The Femur

The longest and stoutest element of the hindlimb, the femur, differs from that in *S. capensis* in the following respects:

(1) Proximally it exhibits only one trochanter.

(2) The distal portion of the femur is not divided into femoral condyles, consequently there is no intercondylar fossa.

41./........

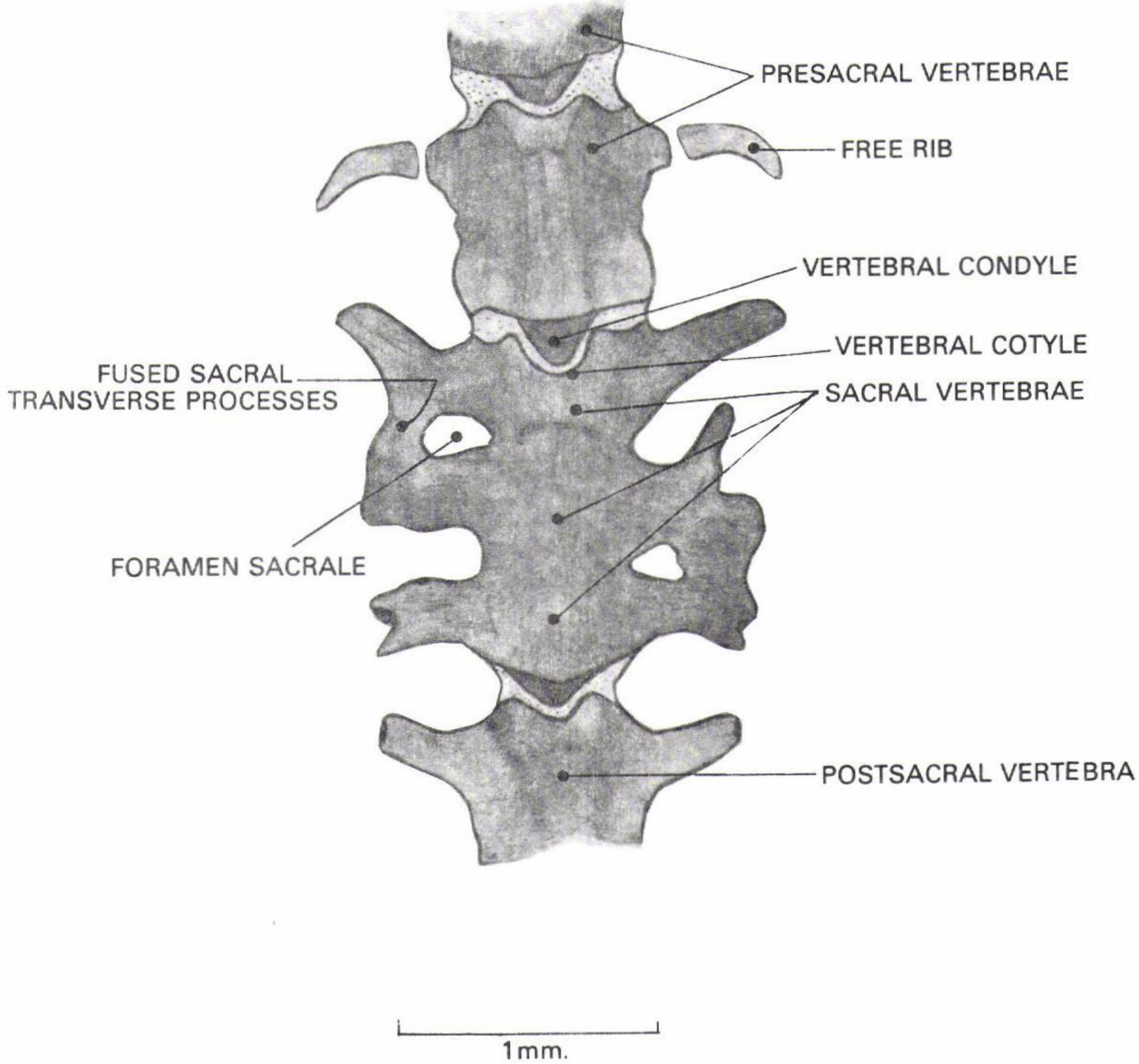


FIG. 17

S. bidigittatus
VENTRAL VIEW OF
THE SACRUM

42./....

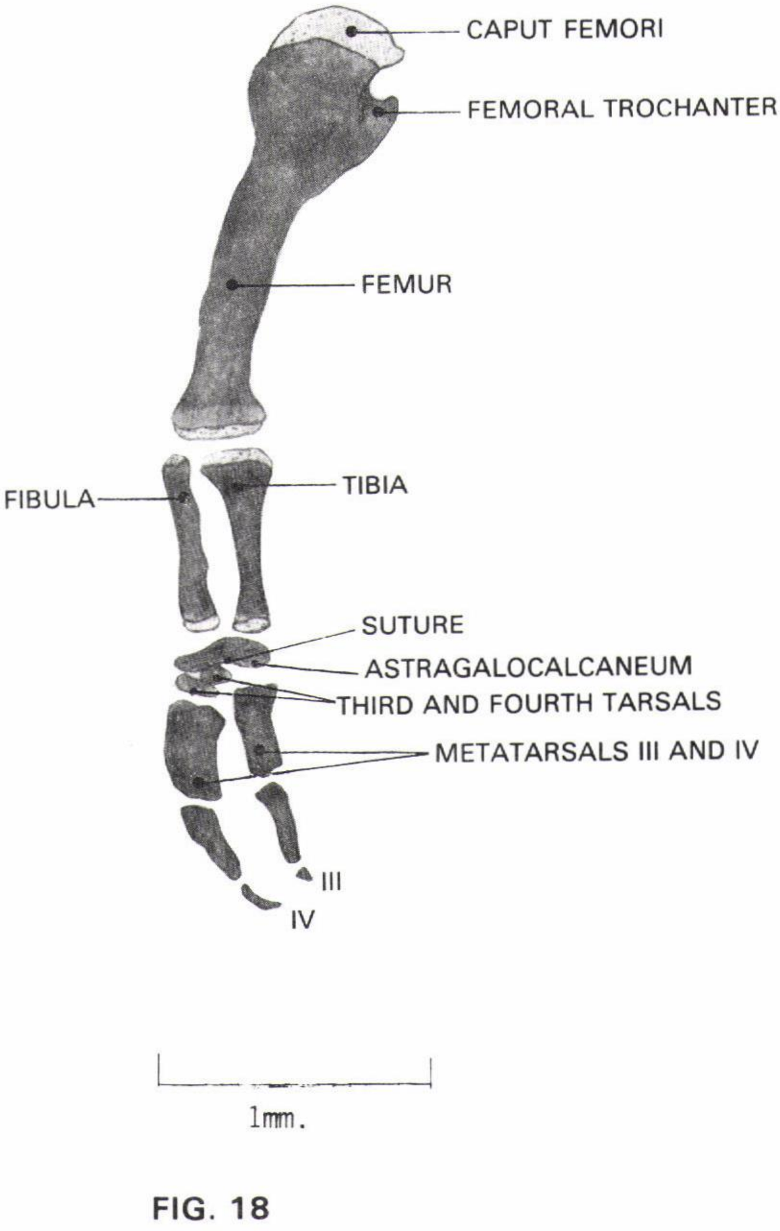


FIG. 18

S. bidigittatus
VENTRAL VIEW OF THE
LEFT HINDLIMB

43./.........

The Crus

The crus of *S. bidigittatus* differs from that of *S. capensis* in that:

(1) The length of the two epipodials relative to that of the femur is smaller in the case of *S. bidigittatus*.

(2) There is not a marked difference in stoutness between the tibia and fibula, the tibia being nearly as thin as the fibula.

(3) Proximally there is no contact between the tibia and fibula.

The Tarsus

Three elements, namely the astragalocalcaneum and distal tarsalia III and IV make up the tarsus.

The Metatarsus and Digiti

Digitalia III and IV make up the pes. The fourth metatarsal is the stouter of the two and it bears only two phalanges, therefore the phalangeal formula is $\frac{0:0:\ 2\ :\ 2:0}{0:0:\mathrm{III}:\mathrm{IV}:0}$.

SCELOTES GRONOVII

THE PELVIC GIRDLE

Although much smaller than in *S. capensis* the pelvic girdle still consists of the usual three paired endochondral elements (Fig. 19).

The Pubes

The differences between the pubis of *S. gronovii* and that of *S. capensis* are as follows:

(1) No cartilaginous pubic symphysis is present. The two pubes are syndesmotically connected.

(2) An epipubis is also absent.

(3) The pectineal process is directed anteromedially whereas in *S. capensis* it is directed posteromedially.

The thin pubo-ischiadic ligament could be discerned in the alizarin-stained specimen (S.A.M. 43540).

The Ischia

The ischium of *S. gronovii* differs as follows from that of *S. capensis*:

(1) A cartilaginous ischial symphysis is absent but a syndesmosis exists between the two ischia.

(2) The hypoischium is not present.

45./......

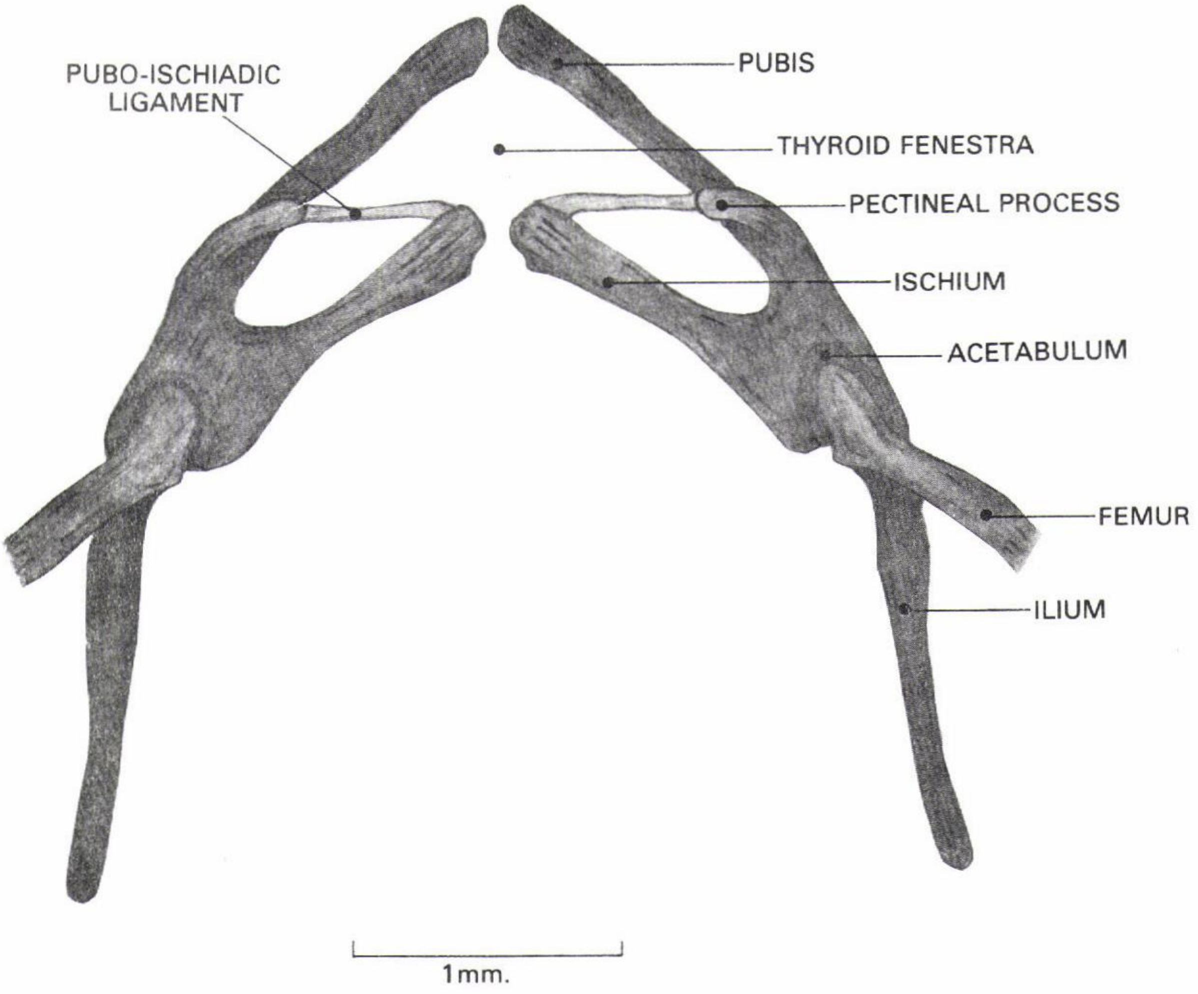


FIG. 19

S. gronovii
VENTRAL VIEW OF THE
PELVIC GIRDLE

46./.........

(3) The posterior border of the ischium in *S. gronovii* does not form a tuber ischii.

(4) The ischial joint lies much nearer to the pubic joint.

The Ilia

No marked difference is present between the ilia of *S. gronovii* and *S. capensis*.

THE SACRUM

Vertebrae fifty-one and fifty-two fuse to form the sacrum (Fig. 20).

THE HINDLIMB

The hindlimb of *S. gronovii* is monodactyle (Fig. 21).

The Femur

This is the stoutest and longest element of the hindlimb and is distinguishable from that of *S. capensis* in the following respects:

(1) Proximally only one trochanter is present.

(2) The distal end is not divided into femoral condyles.

47./.......

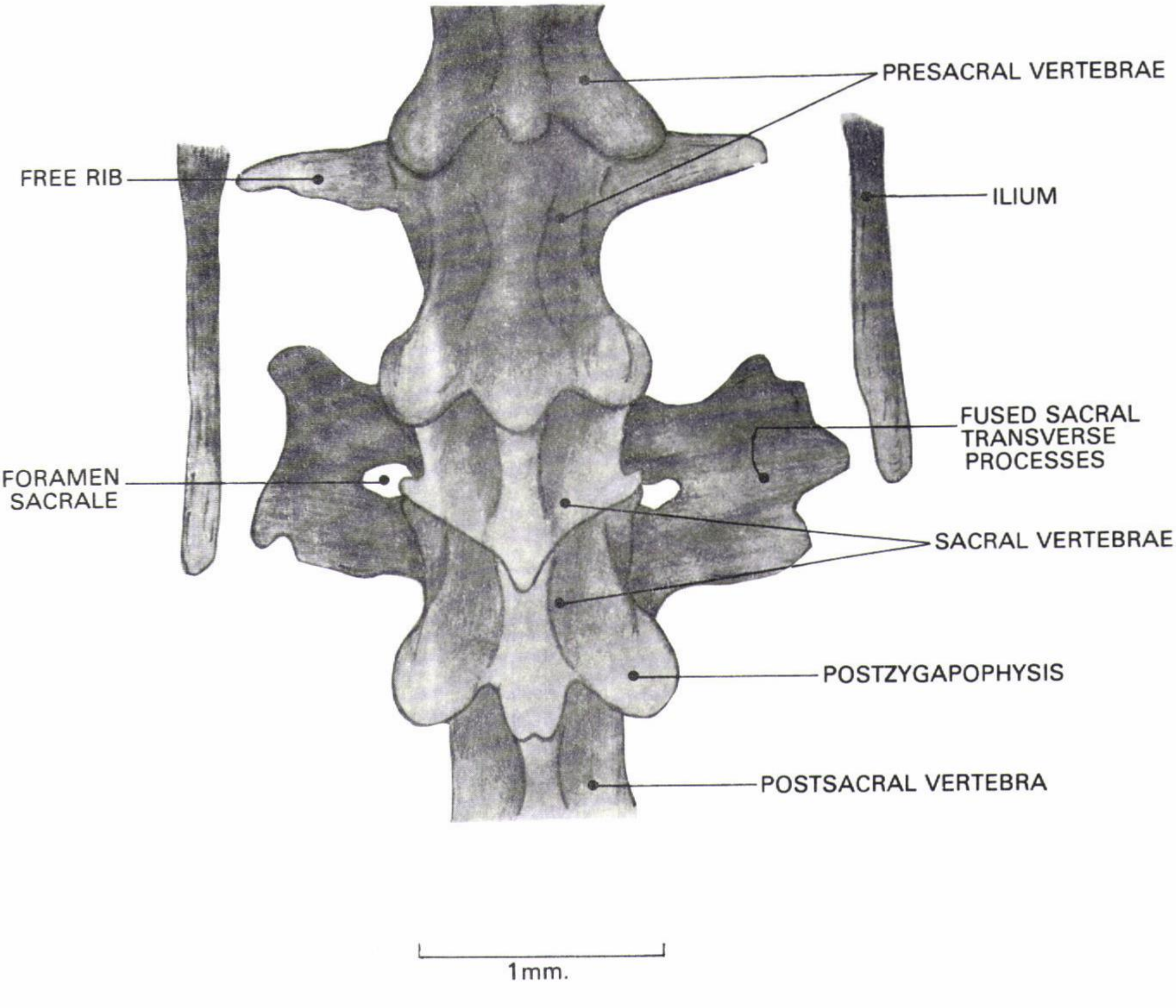


FIG. 20

S. gronovii
DORSAL VIEW OF
THE SACRUM

48./......

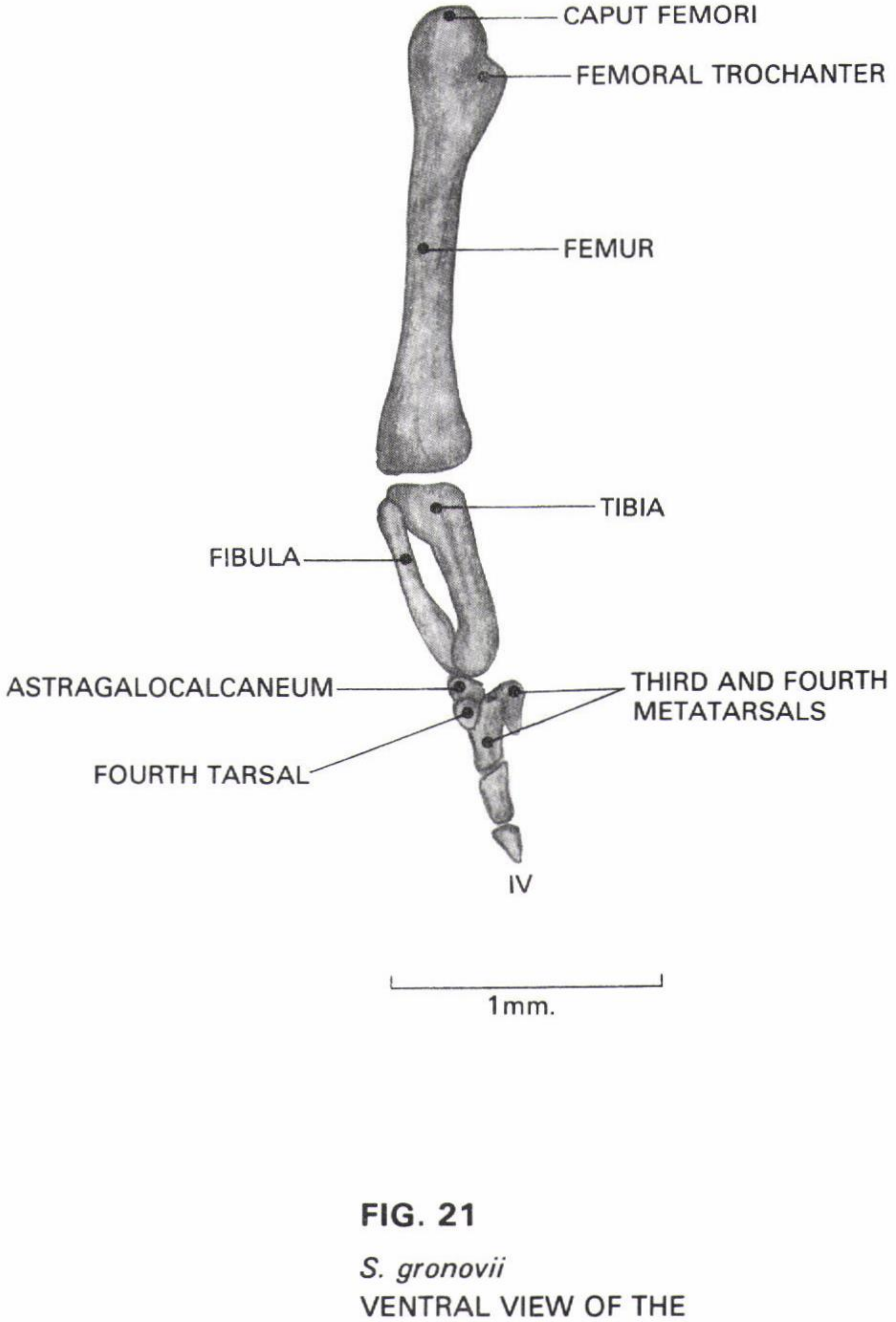


FIG. 21

S. gronovii
VENTRAL VIEW OF THE
LEFT HINDLIMB

The Crus

The crus of *S. gronovii* is different from that of *S. capensis* in the following ways:

(1) The length of the epipodials relative to the length of the femur is much smaller than in the case of *S. capensis*.

(2) The proximal portion of the slender fibula does not articulate with the femur, but is only in contact with the broad expanded proximal portion of stouter tibia.

(3) Distally thefibula and tibia are also in contact.

The Tarsus

Only two tarsals elements are present - a much reduced astragalocalcaneum and probably the fourth distal tarsal since the third tends to be smaller (cf. Figs. 3, 6, 9, 12, 15, 18 & 21).

The Metatarsus and Digiti

The pes is made up of only one digit, probably the fourth one. The third digit is represented only by a reduced metatarsal III on the medial side of the metatarsal IV.

The phalangeal formula is $\frac{0:0:\ 0\ :\ 2:0}{0:0:III:IV:0}$.

SCELOTES BREVIPES

THE PELVIC GIRDLE

The paired pubis and ischium no longer delimit a heart-shaped thyroid fenestra (Fig. 22), as the two halves of the pelvic girdle are separated by a large gap.

The Pubes

The distinguishable characters between the pubes of *S. brevipes* and *S. capensis* are as follows:

(1) The angle at which the pubes approach each other is much larger in the case of *S. brevipes*.

(2) No cartilaginous pubic symphysis is present in *S. brevipes*, instead a very large gap separates the two pubes. However, they are still connected by means of connective tissue.

(3) An epipubis is absent. A small piece of cartilage is present at the tip of the pubis. This probably represents an epiphysis.

(4) The pectineal process is short and curves inwards from the external border of the pubis.

The Ischia

The short ischium of *S. brevipes* differs from that of *S. capensis* in the following respects:

(1) It is much thinner relative to the other pelvic elements than is the case in *S. capensis*.

51./.....

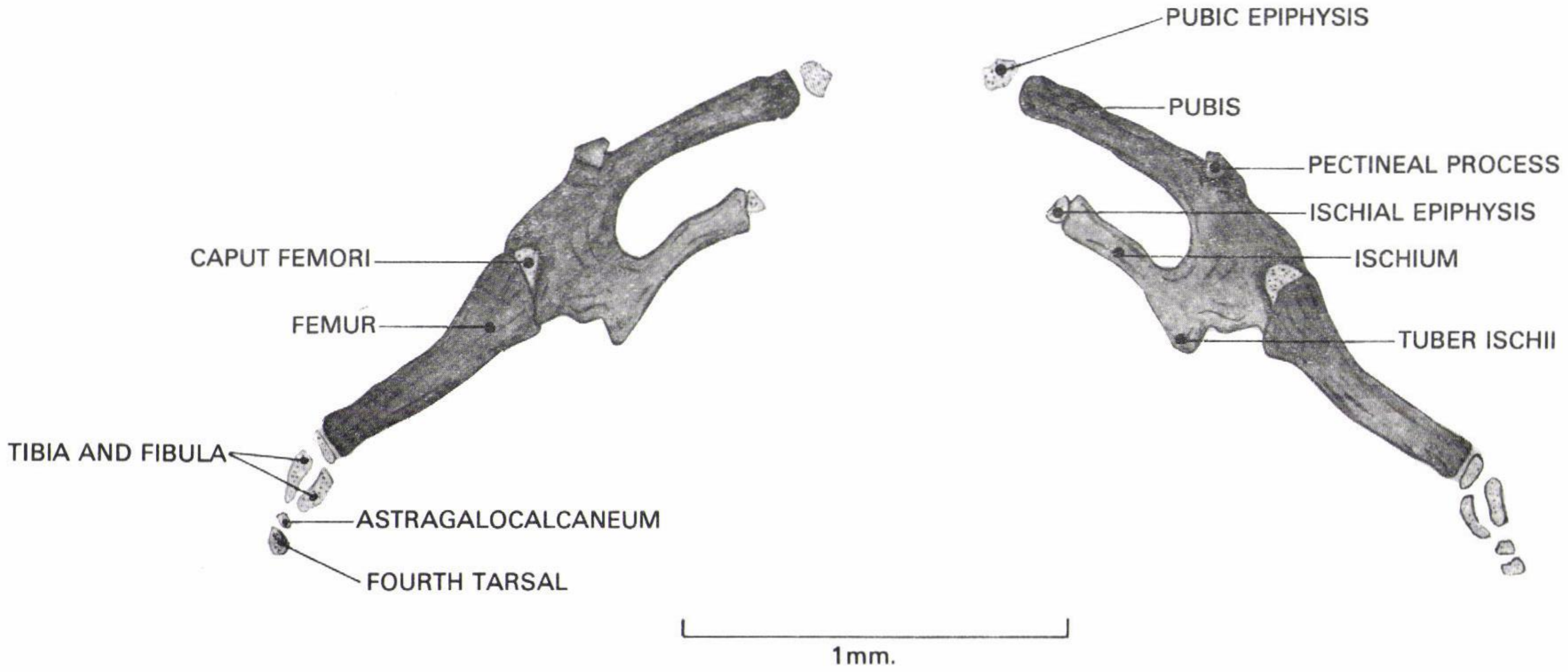


FIG. 22

S. brevipes
VENTRAL VIEW OF THE
PELVIC GIRDLE AND THE HINDLIMBS

(2) A large gap spanned by connective tissue separates the ventromedial tips of the ischia, there being no cartilaginous ischial symphysis in *S. brevipes*.

(3) The free tips of the ischia lie much nearer to the anterior tips of the pubes.

The Ilia

The thin ilium projects posterodorsally from the acetabulum.

THE SACRUM

The relatively more posteriorly situated sacrum is formed by the fused fifty-fourth and fifty-fifth vertebrae.

THE HINDLIMB

The hindlimb of *S. brevipes*, although much reduced (Fig. 22), is still externally visible.

The Femur

The femur is the only osseous element of the hindlimb. A caput femori is present on its proximal expanded portion, whereas no femoral condyles can be distinguished distally.

53./........

The Crus And The Distal Hindlimb Elements.

The tibia and fibula are represented by two small cartilaginous elements, more or less equal in size.

Distally only two cartilaginous elements are present. According to their positions, the proximal one could probably represent the astragalocalcaneum and the distal one the fourth distal tarsal rather than a separate astragalus and calcaneum.

SCELOTES INORNATUS INORNATUS

THE PELVIC GIRDLE

A big gap occurs between the two degenerate halves of the pelvic girdle (Fig. 23). At the junction of the three pelvic elements no sutures between them could be seen neither is there a trace of an acetabulum. However, the sutures which mark the junction of the three pelvic elements could be discerned in the juvenile specimen examined (Fig. 24).

The Pubes

The differences between the pubis of *S. inornatus inornatus* and that of *S. capensis* are as follows:

(1) In the adult specimen examined, the pubis of *S. inornatus inornatus* is smaller than the ischium.

(2) The angle of approach of the two pubes is much larger than in *S. capensis*.

(3) Neither pubic symphysis nor an epipubis is present in *S. inornatus inornatus*. The cartilages at the tips of the pubes probably represent epiphyses. The two elements are completely separated.

The Ischia

The ischium of *S. inornatus inornatus* differs from that of *S. capensis* in that:

(1) An ischial symphysis is absent. A large gap separates the ischia, which are also completely separated.

55./......

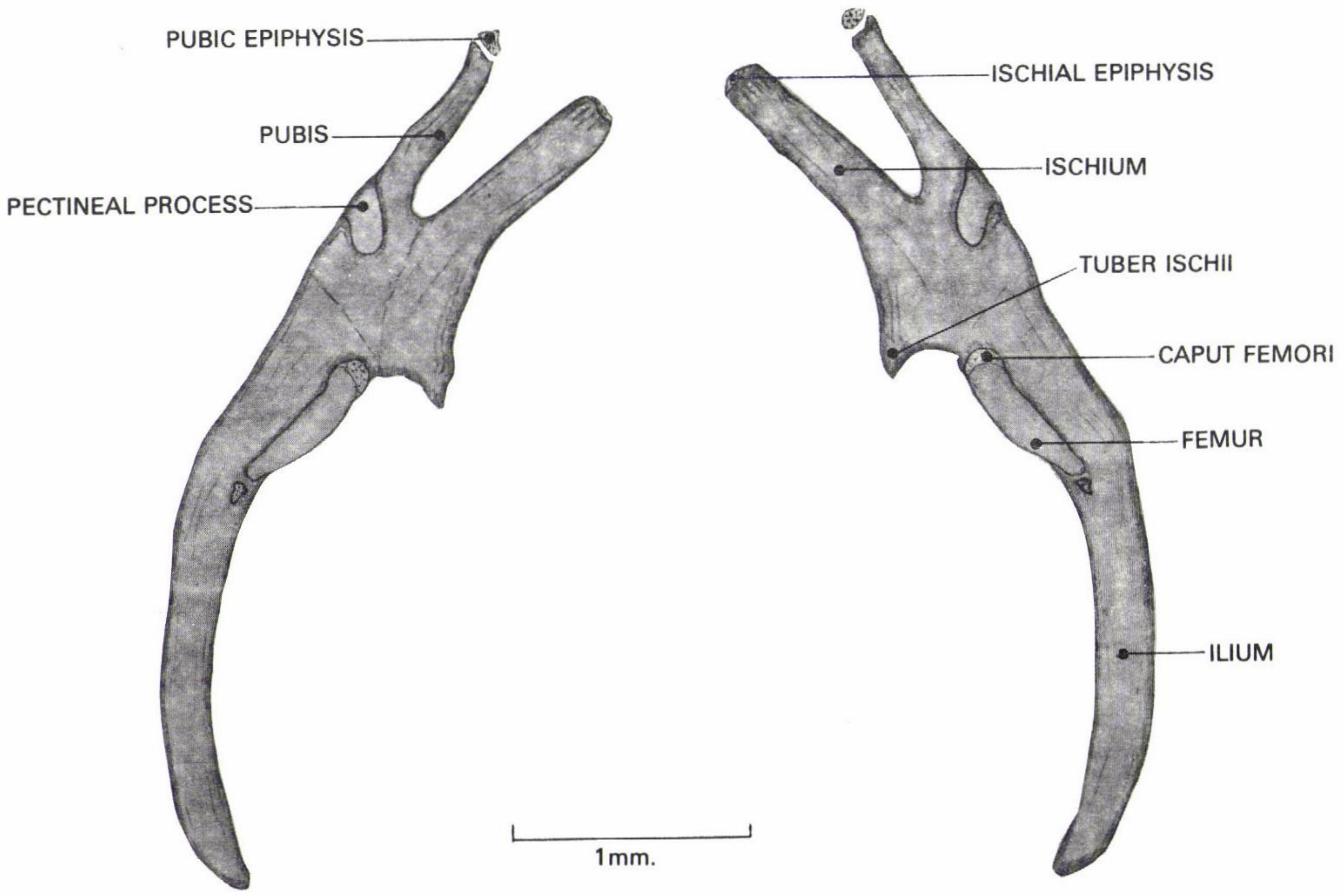


FIG. 23

S. inornatus inornatus
VENTRAL VIEW OF THE
PELVIC GIRDLE AND HINDLIMB

(2) A hypoischium is absent.

(3) The free tips of the ischia lie very near to the tips of the pubes.

The Ilia

Except for relative size, there is no marked difference between the ilia of *S. inornatus inornatus* and *S. capensis*.

THE SACRUM

The sacrum is made up of the fused fifty-second and fifty-third vertebrae (Fig. 25).

THE HINDLIMB

S. inornatus inornatus is externally limbless. A much reduced hindlimb (Fig. 23) is, however, present beneath the skin.

The Femur

The small osseous, relatively featureless femur abuts against the ilium. Proximally a cartilaginous caput femori is still present.

The Distal Elements Of The Hindlimb

These elements are represented by a single small piece of cartilage lying at the distal tip of the femur (Fig. 23).

58./......

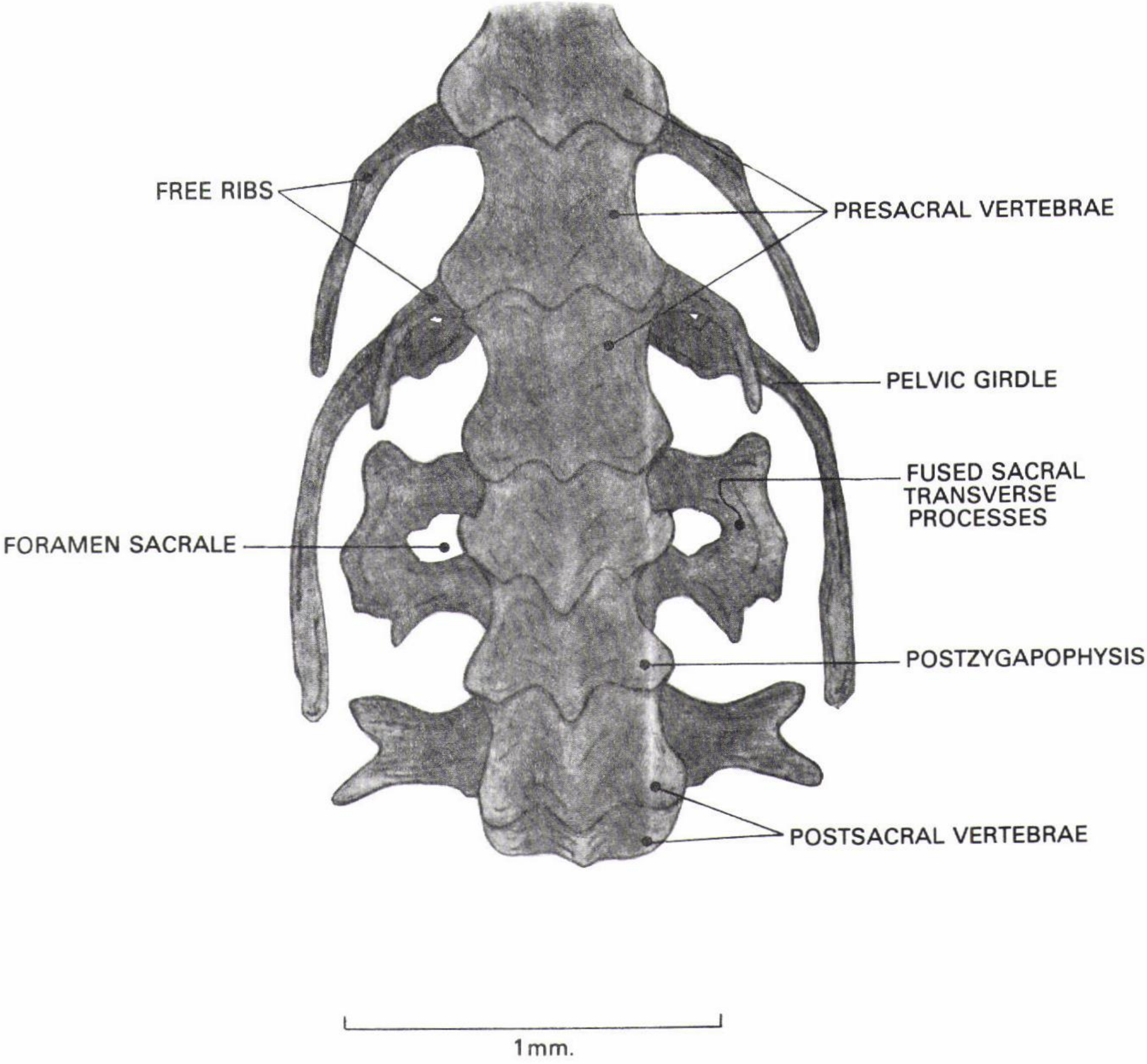


FIG. 25

S. inornatus inornatus
DORSAL VIEW OF THE
SACRAL REGION

SCELOTES ANGUINA

THE PELVIC GIRDLE

The two halves of the pelvic girdle are widely separated, although not as widely as in *S. inornatus inornatus*. An acetabulum at the junction of the three pelvic elements is absent (Fig. 26).

The Pubes

The pubis of *S. anguina* differs from that of *S. capensis* as follows:

(1) The angle at which the pubes approach each other is much larger than in *S. capensis*.

(2) A cartilaginous pubic symphysis is absent in *S. anguina*, the two pubes being completely separate.

(3) In *S. anguina* the external border of the pubis does not form a pectineal process.

The Ischia

The medially directed ischium of *S. anguina* differs as follows from that of *S. capensis*.

(1) The cartilaginous ischial symphysis is not present, instead a gap separates the ischia. The two ischia are completely separated.

(2) A hypoischium is absent.

(3) The posterior border of the ischium does not bear a tuber ischii.

60./........

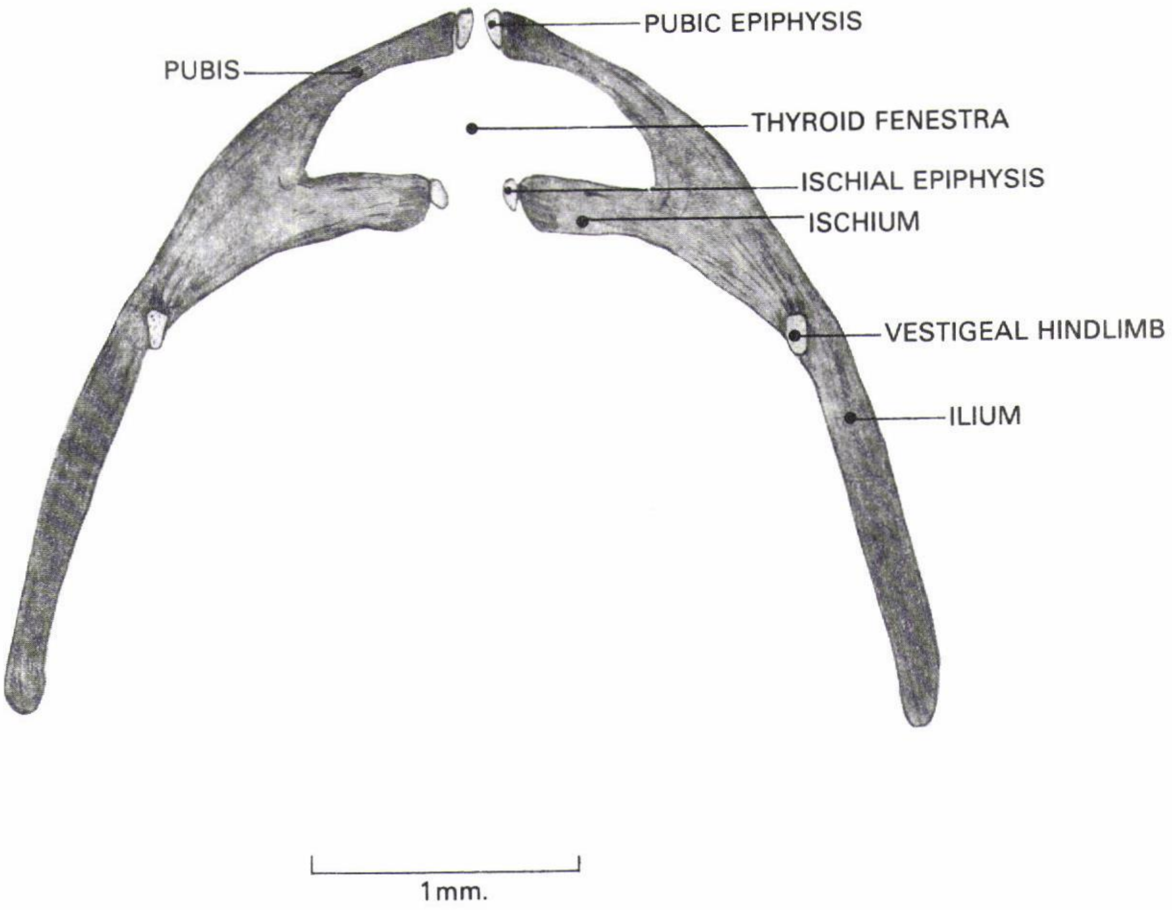


FIG. 26

S. anguina
VENTRAL VIEW OF THE
PELVIC GIRDLE AND VESTIGEAL HINDLIMBS

61./.........

The Ilia

The ilium is the longest element of the pelvic girdle, and does not differ markedly from that of *S. capensis*.

THE SACRUM

The sacrum (Fig. 27) is relatively further anteriorly situated, being formed by the fused forty-seventh and forty-eighth vertebrae.

THE HINDLIMB

S. anguina is externally limbless. The only remnant of the hindlimb is a small piece of cartilage lying next to the ilium under the skin (Fig. 26).

62./.....

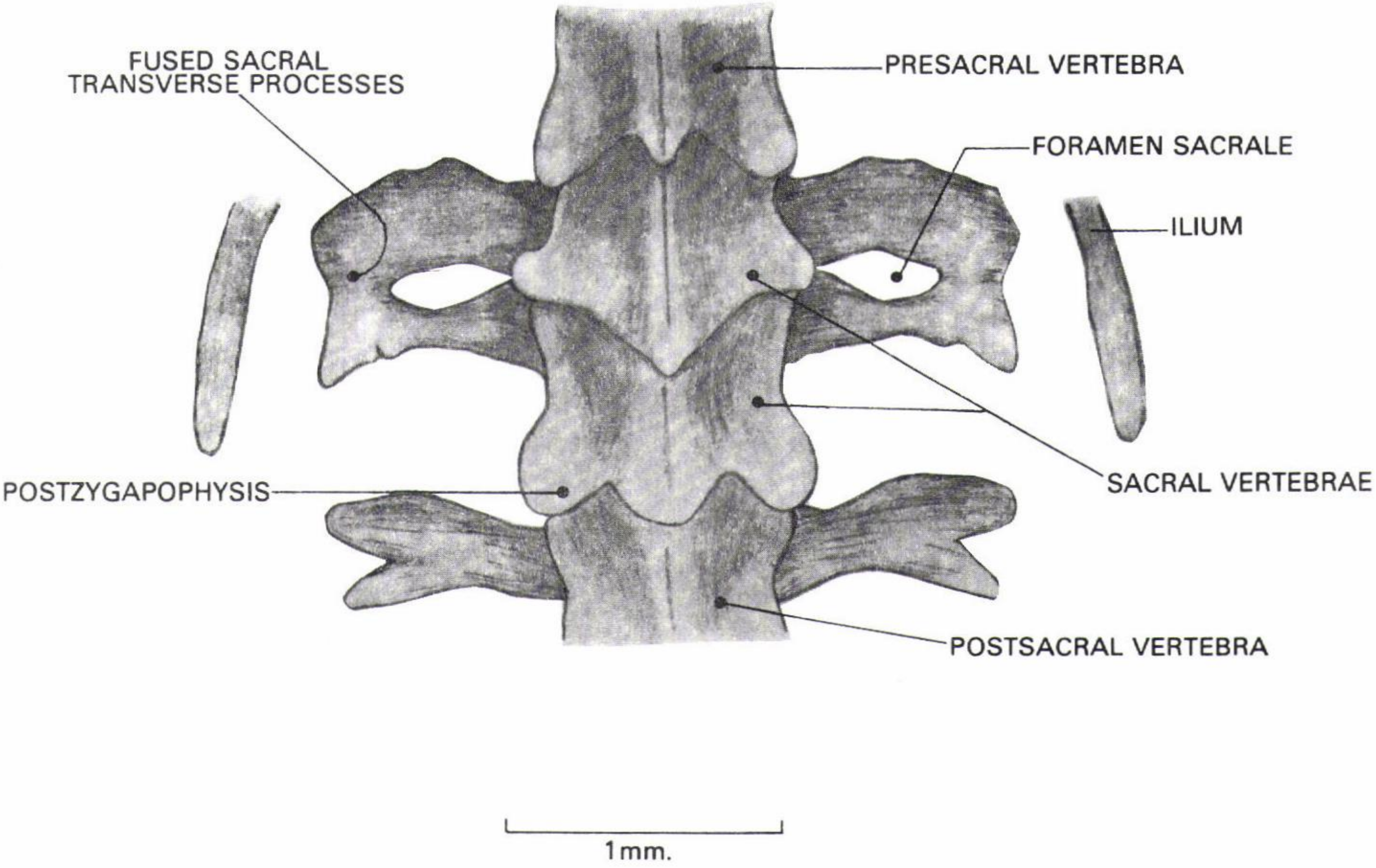


FIG. 27

S. anguina
DORSAL VIEW OF
THE SACRUM

	Epipubis	Cartilaginous Pubic Symphysis	Pectineal Processes	Ischial Symphysis	Hypoischium	Tuber Ischii	Acetabulum	Number Femoral Trochanters	Number Femoral Condyles	Number Elements in Crus	Crus- Bony or Cartilaginous	Number of Tarsal Elements	Number of Digits	Externally Visible Limbs
S. capensis	P	P	P	P	P	P	P	3	2	2	B	3	5	P
S. mira	P	A	P	A	A	P	P	2	2	2	B	3	5	P
S. limpopoensis	P	P	P	P	P	P	P	2	2	2	B	3	4	P
S. caffer	P	A	P	A	A	P	P	2	2	2	B	3	3	P
S. bipes	A	A	P	A	A	A	P	1	1	2	B	3	2	P
S. bidigittatus	A	A	P	A	A	P	P	1	1	2	B	3	2	P
S. gronovii	A	A	P	A	A	A	P	1	1	2	B	3	1	P
S. brevipes	A	A	P	A	A	P	P	1?	0	2	C	2	0	P
S. inor. inor.	A	A	P	A	A	P	A	0	0	1?	C	0	0	A
S. anguina	A	A	A	A	A	A	A	0	0	0		0	0	A

P = Present
B = Bony

A = Absent
C = Cartilaginous

TABLE II TRENDS IN THE *SCELOTES* SPP.

MORPHOMETRIC STUDIES

General

Morphometric data were obtained as set out in the section under procedure. The data on the mass were not taken into consideration, because the specimens used were preserved either in alcohol or formalin for up to fifteen years. The mass of each of these specimens would therefore not be a true reflection of the mass of the living animal. Skinks possess powers of causal autotomy. Tails are commonly autotomised and then regenerated with the result that tail length may vary greatly even within a species. Limbless soil crawlers such as *Acontias* have a relatively long trunk to facilitate soil penetration, consequently the tail tends to shorten (Leonard, 1979). The snout to vent length, being of major functional importance, can therefore be used as a better basis for comparative studies. The data on the vent to tail length were, because of this, not considered for the graphs. All the data of snout to vent length, tail length, hindlimb length, snout to eye length, diameter of the head, and the mass, are set out in Appendix I.

Six graphs were constructed:

Graph I - scatterdiagram depicting the relationship between hindlimb length and snout to vent length.

Graph II - scatterdiagram depicting the relationship between hindlimb length and snout to eye length.

Graph III - Scatterdiagram depicting the relationship between snout to vent length and diameter of the head.

65./.......

Graph IV - scatterdiagram depicting the relationship between hindlimb length and diameter of the head.

Graph V - scatterdiagram depicting the relationship between snout to vent length and snout to eye length.

Graph VI - a bar graph relating the hindlimb length as a percentage of snout to vent length and plotted against the species of *Scelotes* arranged in order of hindlimb degeneracy.

The data of the juvenile specimens of *S. caffer* (S.A.M. 44595; S.A.M. 4321; S.A.M. 18170; S.A.M. 6092 and S.A.M. 18052 #2), *S. bipes* (S.A.M. 44599; S.A.M. 44547 and S.A.M. 1961 #2) and *S. gronovii* (S.A.M. 44517 # 2; S.A.M. 44517 #3; S.A.M. 44517 #4; S.A.M. 44548 #2 and S.A.M. 44548 # 3) were also included in graph VI. The average values obtained when these data are included, are slightly higher than when only the data of the mature specimens are used.

The data of juvenile specimens will not give a true reflection of evolutionary trends within a species, because these specimens are still growing and have not yet reached mature proportions. The data are, however, included in all the graphs to indicate the effect they have on the average values of a species. Lande (1978) and Leonard (1979) based their conclusions mainly on data of mature specimens.

When conducting a morphometric analysis, the sample size should be as large as possible. Although the number of *Scelotes* specimens measured was small, certain trends are revealed by the graphs.

66./.....

Results

Leonard (1979) stated that limb regression is correlated with an increase in snout to vent length. This elongation is demonstrated by the graphs. The morphometric studies were undertaken mainly to investigate this statement.

A conclusive statistical analysis cannot be executed with the limited number of specimens, but the graphs do indicate certain patterns. The hindlimb length is plotted against the snout to vent length (Graph I), and for a given body length the hindlimbs are shorter in more degenerate species (cf. for example *S. gronovii* and *S. limpopoensis*). The different species form definite clusters. In the case of *S. gronovii, S. bipes* and *S. caffer* two different clusters are formed in each species. The clusters in the smaller snout to vent range are formed by the data on juvenile specimens. A certain amount of overlapping is present between the species (e.g. between *S. gronovii*, and *S. bipes*). This is not surprising, because one expects some overlap within a single genus.

Russel Lande (1978) used snout to eye lengths as constants in his morphometric studies. In response to this it was attempted to establish whether there is a relation between hindlimb length and snout to eye length (Graph II). More or less the same distribution as in graph I was obtained, indicating that there is a fair amount of increase in snout to eye length with degeneracy in the hindlimbs. Overlapping of the different groups again occur as for example between the groups of *S. capensis* and *S. limpopoensis*.

67./......

Since the species investigated are soil-crawlers, the question arises whether there is a correlation between the body length and the diameter of the head. This was investigated in graph III. No definite groupings could be obtained as in the previous two graphs. These skinks use the head to force through the soil. Therefore one finds that there is a complete overlap of species such as *S. limpopoensis* (tetradactyle) and *S. gronovii* (monodactyle). For a given body length the diameter of the head will not differ much between a pentadactyle species and a degenerate species.

If the hindlimb length is plotted against the diameter of the head, as in graph IV, a pattern again emerges. Although there is much overlapping between *S. limpopoensis* and *S. capensis*, as well as between *S. bipes* and *S. gronovii,* the species are again arranged in clusters. There is a clear distinction between species such as *S. capensis* and more degenerate species such as *S. gronovii*. For a given value of diameter of the head, the hindlimb length is smaller in more degenerate species. One can assume with a fair amount of certainty that the diameter of the head stays more or less constant with hindlimb degeneracy. The rate of hindlimb degenera=tions is faster than the rate of changes occuring in the diameter of the head.

Is there a correlation between body length and snout to eye length? This was investigated and set out in graph V. No definite groupings can be observed and much overlapping is present. As the body length increased with hindlimb degeneracy, there is an increase in snout to eye length as well.

For a given body length, therefore the snout to eye length will not differ much between a pentadactyle species and a more degenerate species.

The hindlimb lengths of the species were expressed as percentages of their snout to vent lengths, and plotted against these species in order of hindlimb degeneracy (Graph VI).

If only the data of the mature specimens are taken into account, the tendency for body length to elongate correspondingly with increasing degeneracy in the hindlimb, is shown on this graph. The hindlimb length is a lower percentage of the body length in species with lost digits - the percentage being the lowest in the monodactyle *S. gronovii* and highest in the pentadactyle *S. capensis*. There is also a gradual decrease in the percentage from *S. capensis* to *S. gronovii*.

If the data of the juvenile specimens are included, the average values are slightly higher (cf. *S. caffer* and *S. bipes*). The value of *S. caffer* is then also higher than that of the tetradactyle *S. limpopoensis*. In juvenile specimens the hindlimb - to body length ratio is higher than that of adult specimens, therefore the discrepancies in the results when their data are included.

Although the number of specimens does not permit a conclusive statistical analysis, the tendency for a correlated increase in body length with hindlimb degeneracy is effectively shown on the graphs. Parameters such as diameter of the head and snout to eye lengths also depict some relation with hindlimb degeneracy.

69./.......

SCATTERDIAGRAMS RELATING THE DIFFERENT BODY PROPORTIONS IN SOME *SCELOTES* SPECIES.

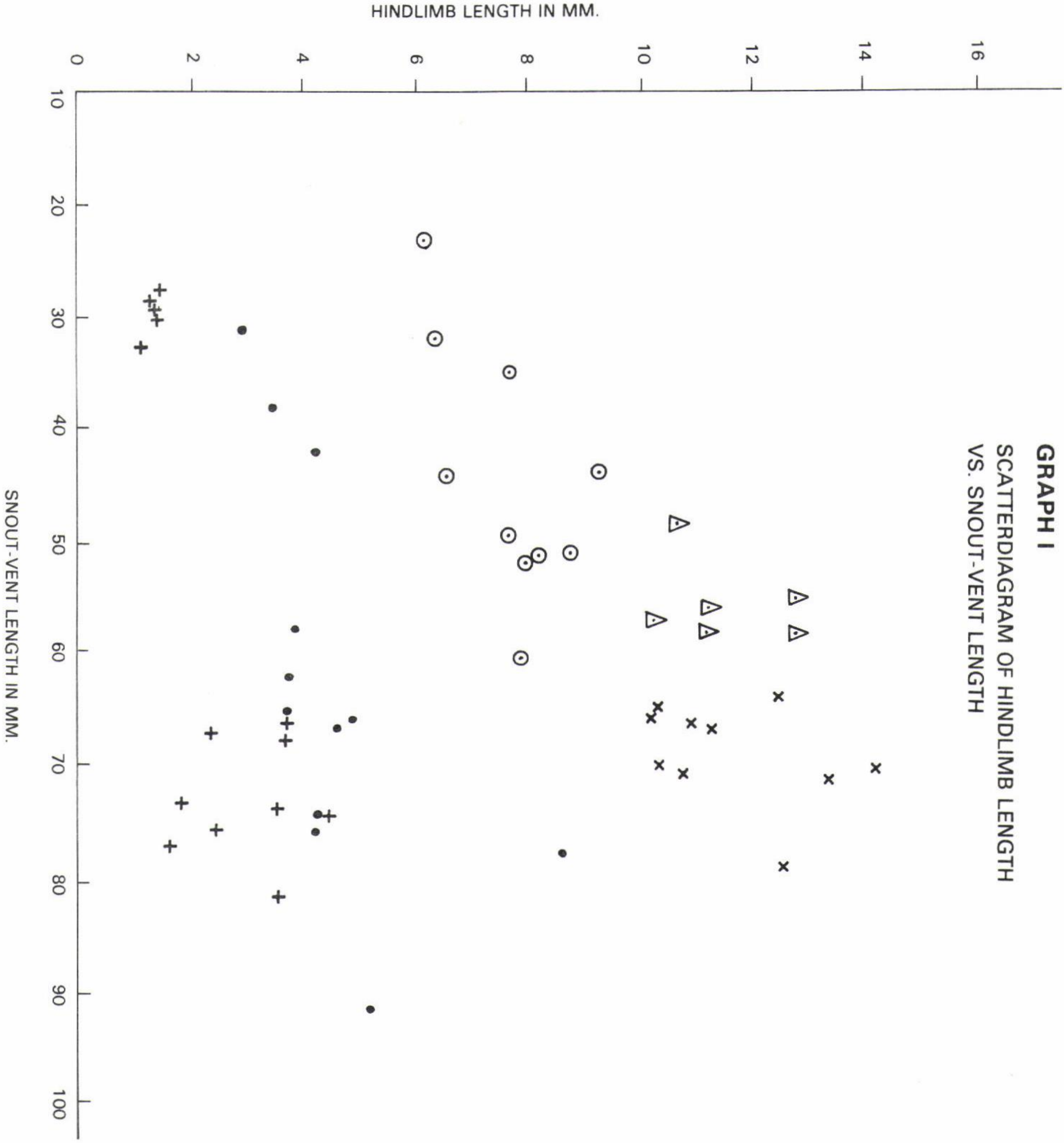
Because of the small number of specimens available, it serves no purpose to statistically analyze the morphometric data obtained. Graphs I, II and VI show the tendency of the body to be longer in more degenerate species. Although a cluster analysis could not be executed (too few specimens), the scatterdiagrams show the tendency for definite groups to be formed.

KEY TO THE GRAPHS I - V

Δ - *S. capensis*
x - *S. limpopoensis*
ϴ - *S. caffer*
• - *S. bipes*
\+ - *S. gronovii*

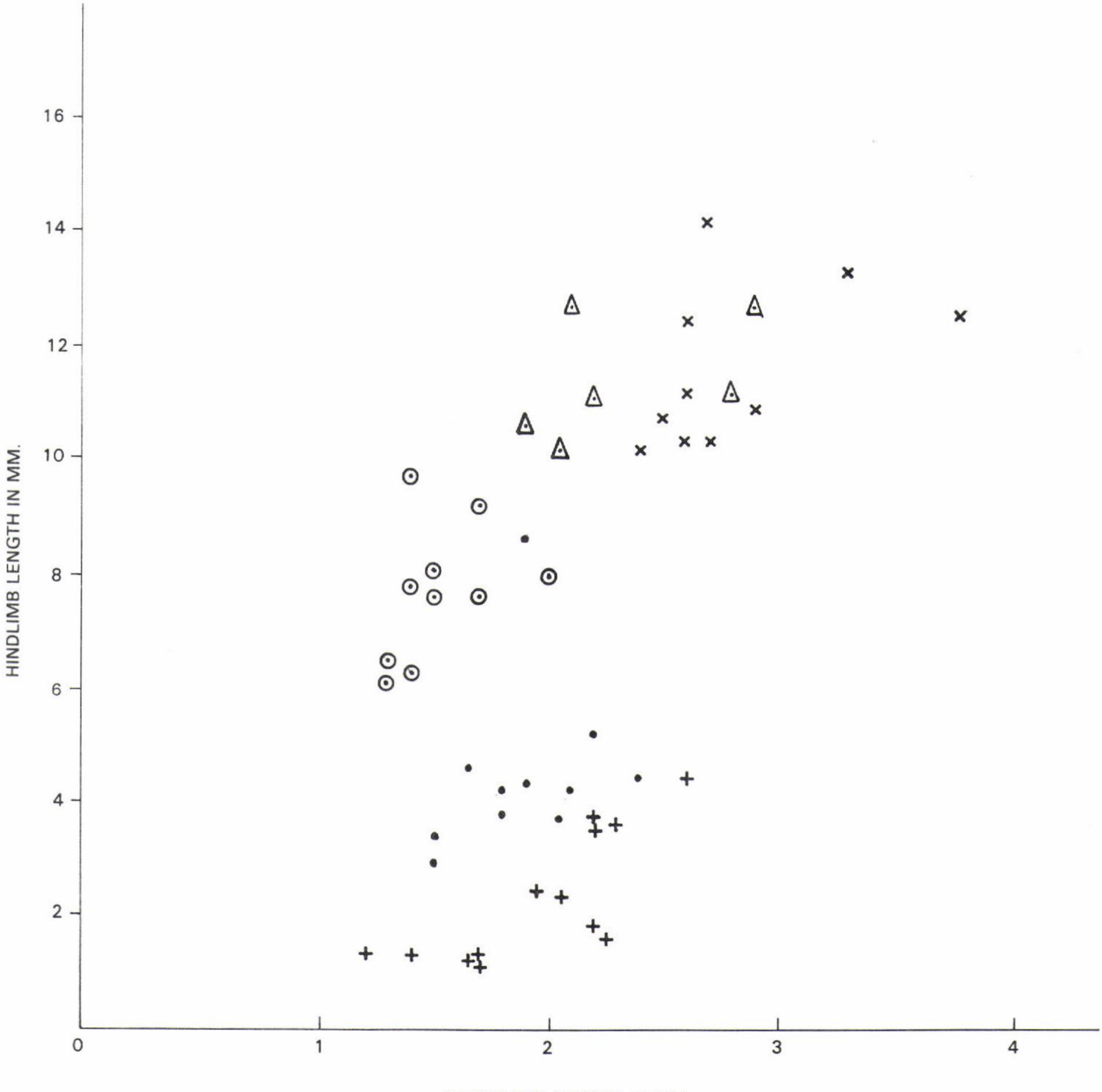
KEY TO GRAPH VI

░ - average value of mature specimens only
▥ - average value when juveniles are included.



GRAPH I

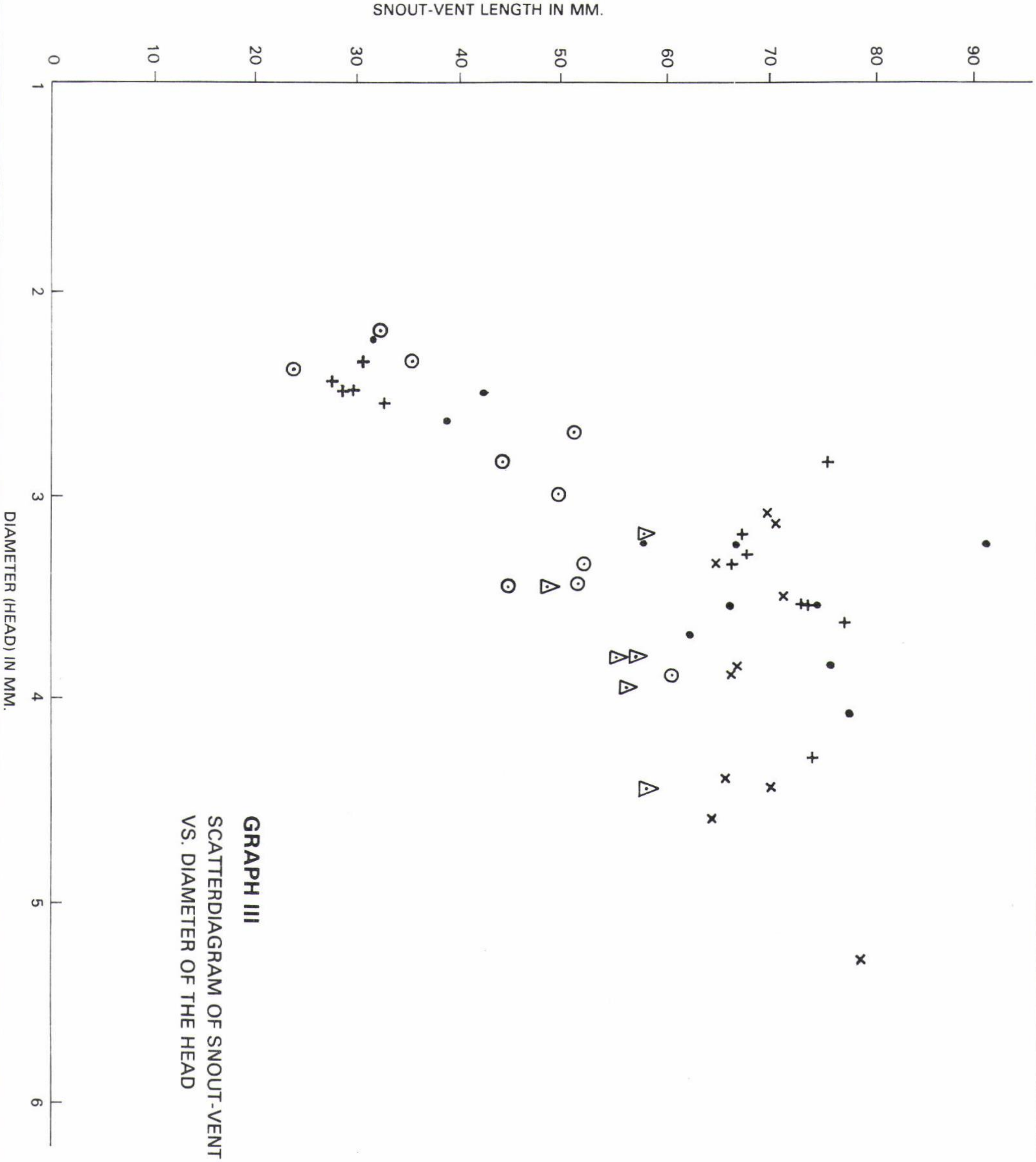
SCATTERDIAGRAM OF HINDLIMB LENGTH
VS. SNOUT-VENT LENGTH



GRAPH II

SCATTERDIAGRAM OF HINDLIMB LENGTH
VS. SNOUT-EYE LENGTH

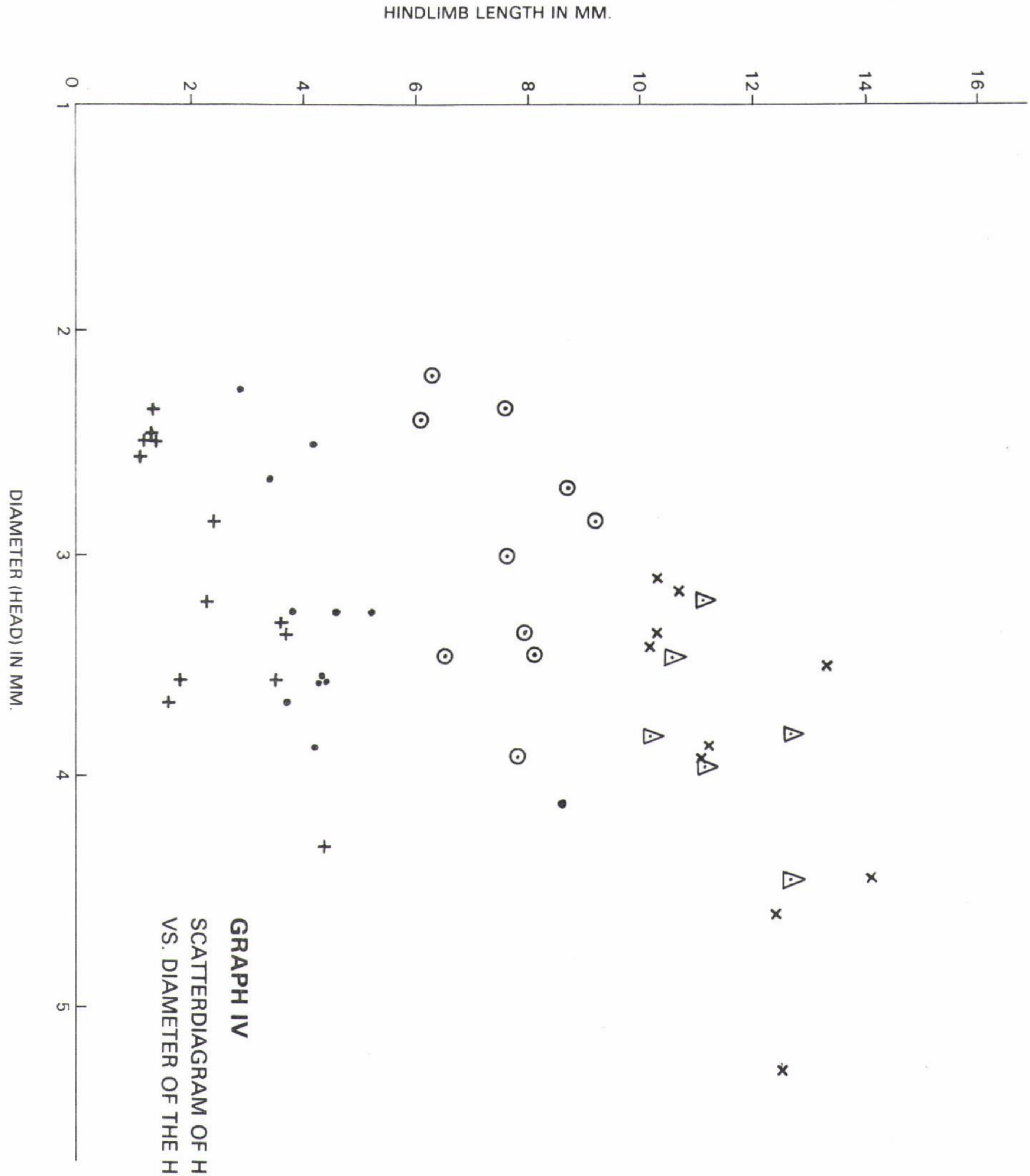
72./........



GRAPH III

SCATTERDIAGRAM OF SNOUT-VENT LENGTH
VS. DIAMETER OF THE HEAD

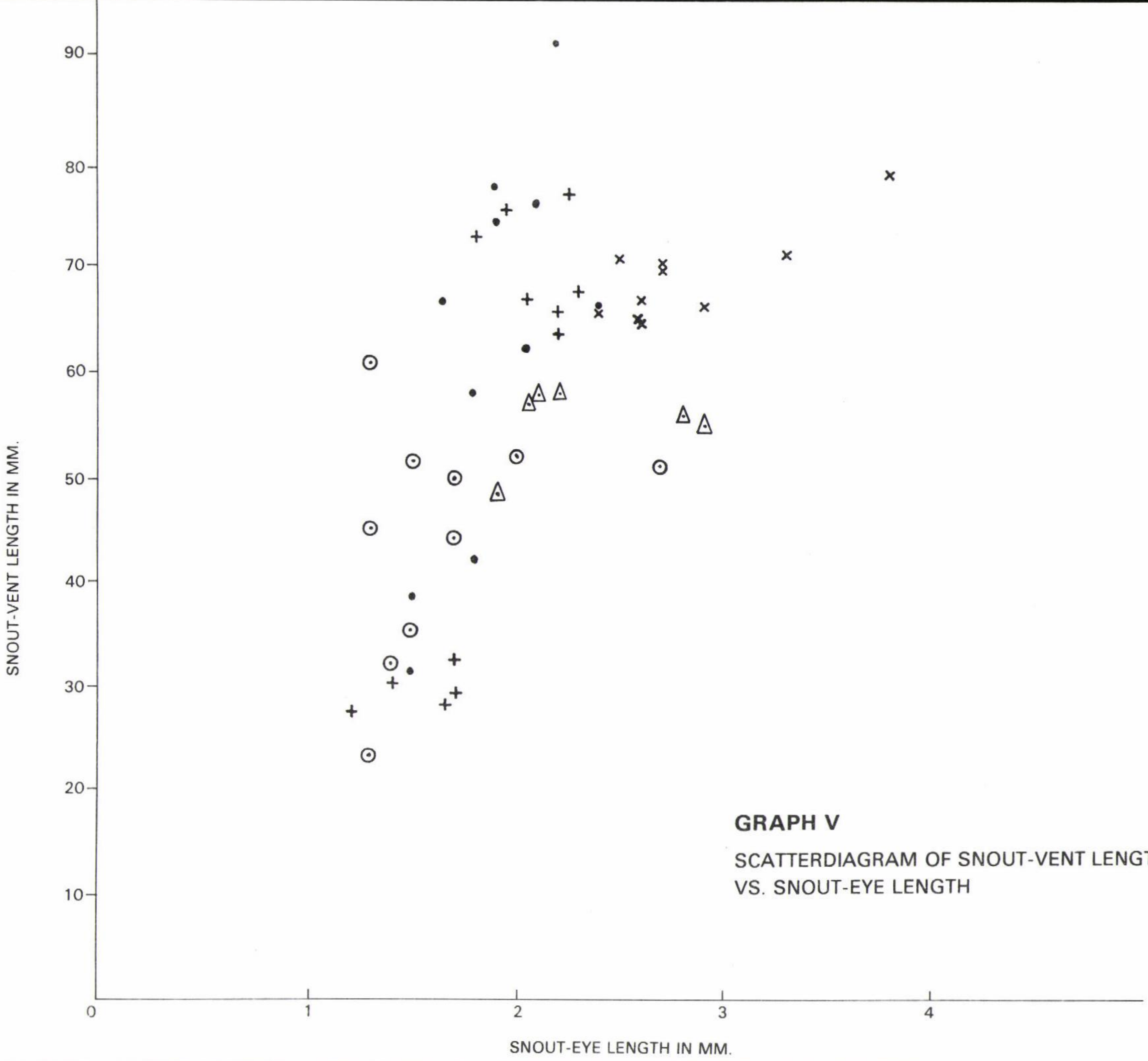
73./........



GRAPH IV

SCATTERDIAGRAM OF HINDLIMB LENGTH
VS. DIAMETER OF THE HEAD

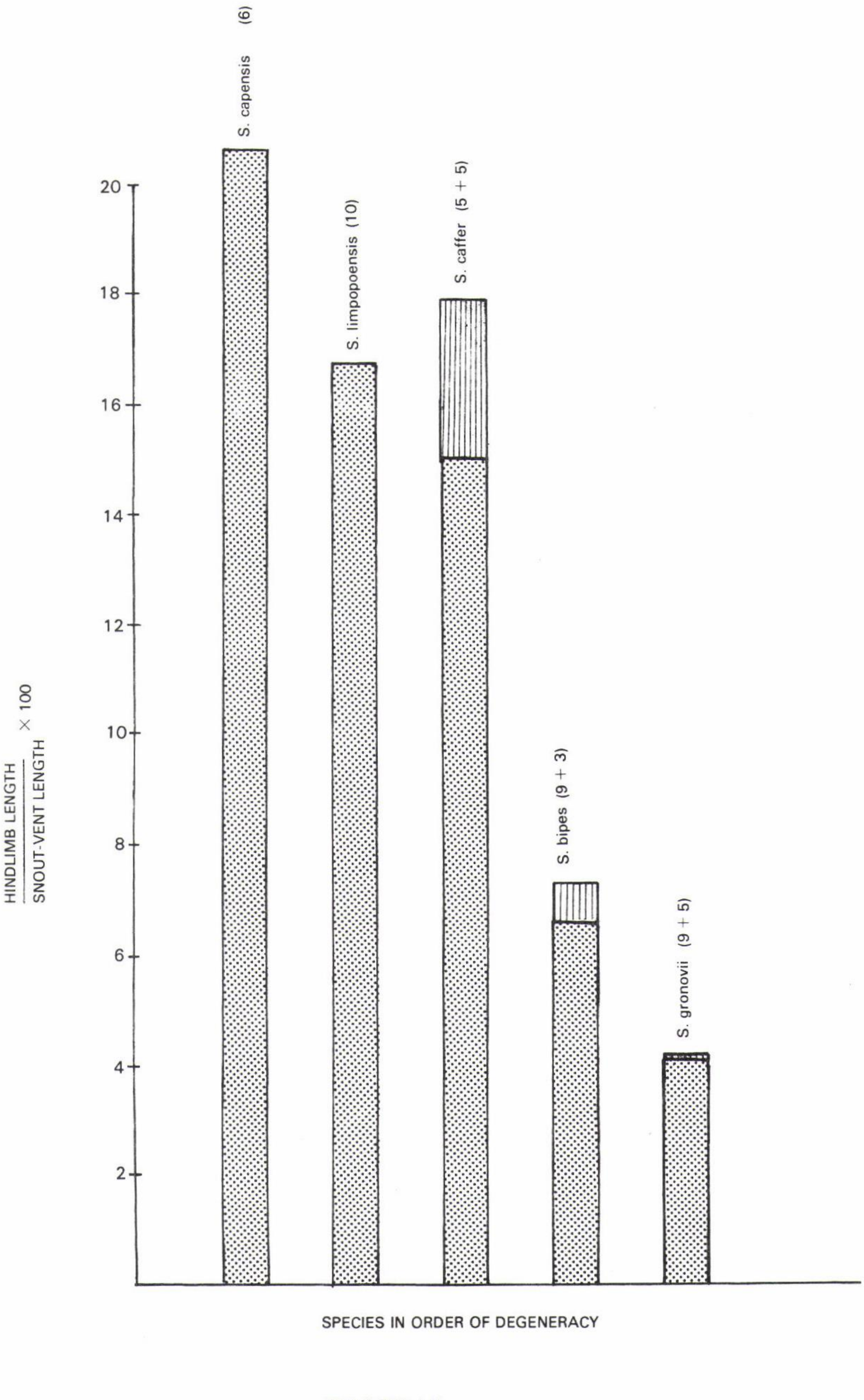
74 ./.........



GRAPH V

SCATTERDIAGRAM OF SNOUT-VENT LENGTH
VS. SNOUT-EYE LENGTH

75../........



GRAPH VI

$\frac{\text{HINDLIMB LENGTH}}{\text{SNOUT-VENT LENGTH}} \times 100$

VS.

SPECIES

DISCUSSION

Much work has been done on the pelvic region of degenerate skinks by researchers such as Cope (1892), Essex (1927), Sewertzoff (1931) and Tiedeman et al. (1975). They worked on species of different genera, and did pioneer work in explaining the different degenerative trends.

The genus *Scelotes* is represented by nineteen species and subspecies in Southern Africa (Fitszimons, 1943). The species in this genus range from fully limbed to completely limbless forms, exhibiting small degrees of degeneration between the different stages. As the earlier researchers based their conclusions mainly on extreme forms, a study of a genus where devolution of the pelvic region is represented by a series such as in *Scelotes*, will shed light on this subject. A major objective of this work is therefore to analyze the different trends associated with pelvic degeneration in the genus *Scelotes*.

Several questions regarding the evolutionary significance of this degeneration may be asked:

(1) What are the general degenerative trends and tendencies? In what sequence are structures reduced and lost? Can a general pattern of degeneration be observed?

(2) What are the implications of these trends? What are the relation=ship between these trends and the mode of life of the species? Are these changes of any functional significance for the animal?

Only the osteology of the pelvic girdle and hindlimbs of the *Scelotes* species was investigated. Although this will give us a fairly good account of what the evolutionary tendencies of degeneration are, a study of the myology of the pelvic region will help in giving us a more complete picture of degenerative trends in the genus.

TRENDS OF DEGENERATION IN *SCELOTES* SPECIES

The degeneration of limbs and girdles follows a fairly fixed pattern (cf. Table II). There are general trends which can be listed as follows:

(1) Elongation of the body (i.e. snout to vent length).

(2) The loss of the cartilaginous pubic and ischial symphyses.

(3) Miniaturization and reduction of the pelvic girdle.

(4) Tendency of the ischial joint to shift nearer to the pubic joint.

(5) Miniaturization and eventual loss of the hindlimbs.

Cope (1892) did valuable work on the Lacertilia but he stated, rather unfortunately, that the disappearance of the pubis and ischium precedes the loss of the hindlimb. In the *Secoltes* species examined, it was found that, although there is evidence of reduction in the pelvic girdle of the degenerate species, the pubis and ischium are still present in externally limbless forms. This is in line with the findings of Sewertzoff (1931) and Lande (1978). The former found that in the limb the distal elements are the first to be lost, so that there is more or less a distal to proximal sequence of degeneration.

(1) Elongation of the body

Gans (1975) observed that elongation of the body is the first evolutionary step towards a serpentiform locomotion.

The elongation of the body creates problems regarding the organs and their arrangements in the body, for example that of the viscera (Bellairs, 1969). These problems must have been effectively overcome if we take into consideration the large variety of skinks inhabiting this niche (Gans, 1968).

In his comprehensive work on limb regression in certain skinks, Leonard (1979) stated that the cross-sectional area of such an animal becomes reduced relatively to the length of the body. This would effectively minimize the energy utilized by the animal during subterrestrial locomotion (Gans, 1975), enhancing "the animal's effeciency as a burrower" (Leonard, 1979, p. 281).

As the vertebral column is an integral part of the body, it would be duly affected by body elongation. The vertebrae are shorter but wider in degenerate species (Leonard, 1979). For the degenerate species to move effectively by lateral undulation it is necessary for the body axis to be flexible so that many flexures can be formed over the length of its body. Shorter vertebrae would undoubtedly decrease the rigidity of the vertebral column.

Body elongation is a direct consequence of an increased number of body metameres. This is demonstrated by the position of the sacral vertebrae. There is a general tendency for the sacrum to be situated more posteriorly in reduced limbed and limbless species of *Scelotes*. An exception to this general trend is in the case of the limbless *S. anguina*, where the sacrum lies in a position similar to that of the pentadactyle *S. capensis*. A study of the phylogeny of *S. anguina* may possibly explain this anomaly.

This elongation is demonstrated on graphs I to VI. In these diagrams the trend for elongation of the body in *Scelotes* species is rather distinct, the ratio of snout-vent length to hindlimb length being higher in the species with more degenerate limbs. This further strengthens the assumption of Leonard (1979), that there is a correlation between hindlimb degeneracy and body length.

In a fully limbed lizard, for example *Mabuya capensis,* both axial and appendicular systems contribute towards the animal's locomotion (Leonard, 1979). Such an animal moves forward by pushing its feet against the sub=stratum, thereby creating a thrust propelling the body forward. The axial musculature is responsible for lateral undulating movement of the body particularly that part between the pectoral and pelvic girdles. These oscillations increase the step length of the animal. This phenomenon was also seen in *S. mira* (personal observation).

In studying the locomotion of *S. bipes bipes, S. gronovii* and *S. brevipes*, Leonard (1979) found that these skinks move by lateral undulation and that progression by concertina movement could not be induced in these species. Lateral undulation involves continuous progression, so that no part of the body is stationary during locomotion (Gans, 1974). As the more degenerate *Scelotes* species do not use their limbs to create a posteriorly directed thrust, they need pressure points (such as grass stems, pebbles, walls of their tunnels, etc.) against which the body can push to create forward motion. These points are called *points d' appui.* Skinks with degenerate limbs mainly occupy subterrestrial environment (Camp, 1923). It is therefore understandable that the longer the body of the skink, the more points it can contact.

80./......

In the studies undertaken, I have only made use of the snout to vent length. The data on tail lengths are less reliable, since the tails of some of the specimens examined were in various stages of regeneration as a result of caudal autotomy, while in others, parts of the tails were missing. The snout to vent length and especially the number or presacral vertebrae, however, indicate the tendency for the body of degenerate *Scelotes* species to elongate. The elongation also precedes the loss of the hindlimbs.

(2) Loss of the cartilaginous pubic and ischial symphyses.

Fürbringer (1870) argued that the loss of the pubic and ischial symphyses sometimes occurs before the onset of hindlimb degeneration. The condition in *S. mira* seems to support this conclusion. *S. capensis* has a pubic and ischial symphysis, while it is absent in *S. mira*. The condition in *S. limpopoensis*, however contradicts this conclusion. *S. limpopoensis* which is tetradactyle, refutes Fürbringer's assumption, because it has well-developed pubic and ischial symphyses. This phenomenon again illustrates that evolution is a random process.

An effect of the loss of symphyses is that the two halves of the pelvic girdle are separated by a gap which becomes progressively wider in those *Scelotes* species with more degenerate limbs. In all the stained specimens, except in *S. inornatus inornatus* and *S. anguina*, the two halves of the girdle are either firmly connected by means of a synchondrotic symphysis or in various degrees of firmness by means of a syndesmotic connection. In these two species the two halves are not joined as in the other cases, thus increasing flexibility of the body axis in the pelvic region.

In the midline, between the pubes and between ischia, pieces of cartilage respectively named the epipubis and hypoischium, are present. A epipubis is present in *S. capensis, S. mira, S. limpopoensis* and *S. caffer*.

81./.....

In some of the other degenerate species pieces of cartilage are present at the tips of the pubes. Since the epipubis is that cartilage situated in the median line (Camp, 1923), the cartilages at the tips of the pubes should rather be regarded as the epiphyses of the bones concerned. Mehnert (1891) regarded the tips of the pubes and ischia as the origins of the epipubis and hypoischium respectively, while Camp (1923) advocated that these structures are calcified portions of the symphyseal ligament extending in the median line from the pubes to the ischia. Embryological research can throw light on this problem. The rod-like hypoischium is present in *S. capensis* and *S. limpopoensis* only.

Loss of the cartilaginous pubic and ischial symphyses, the epipubis and the hypoischium are clear indicators of degeneration in the pelvic girdle of *Scelotes* species and points the way towards a complete reduction of the said girdle.

(3) Miniaturization and reduction of the pelvic girdle.

Another interesting feature of degeneration in the *Scelotes* species is that miniaturization of the pelvic girdle precedes external limb loss. Measurements of the elements of the girdle have not been undertaken, but the diagrams of the girdles illustrate this point.

It must be borne in mind that evolution is a natural, and therefore a random process, and a precise pattern of reduction is not always adhered to. A general pattern of devolution in the *Scelotes* species can, however, be observed. Different rates of reduction occur in the three pelvic elements:

82./.....

(a) The Pubes

The anteromedially directed pubis shows the most obvious degeneration in the series described.

In the series from the pentadactyle to the limbless species, the pubis becomes progressively shorter and narrower to the point where it is actually shorter than the ischium in *S. inornatus inornatus* (Fig. 23). One would expect that it would be much shorter in *S. anguina* (with more degenerate hindlimbs) but this is not the case, the pubis being longer than the ischium (Fig. 26). Although a study of the phylogeny of this species might throw some light on this problem, it again shows the randomness of evolution.

There is also a general trend for the angle of approach of the two pubes to become larger in the *Scelotes* species with reduced hindlimbs. This enlargement is quite evident in the case of *S. brevipes* (Fig. 22). The enlargement of the angle is a possible consequence of the loss of the pubic symphysis. It has the effect of the two halves of the pelvic girdle becoming curved structures. If the pelvic girdle follows the curvature of the body, not being a structure spanning across the body, it will not hinder effective flexion of the trunk in the pelvic region. Tiedeman et al. (1975) recorded that the remnants of the pelvic girdle are curved in the case of *Acontias*, a highly degenerated skink.

The pectineal process shows a tendency to become shorter and blunter as limbs become more degenerate. In *S. anguina* it is completely absent.

The pectineal process provides attachment for the pubo-ischiadic ligament which serves as attachment for some of the muscles of the hindlimb (Tiedeman, et al. 1975). With the reduction and loss of the hindlimbs, these muscles atrophy and the pubo-ischiadic ligament subsequently loses its function. This ligament also disappears (Tiedeman et al. 1975) and consequently the pectineal process becomes redundant.

(b) The Ischia

The blade-like ischium becomes progressively narrower in the series described. The tuber ischii is absent in several species, but is surprisingly well-developed in the limbless *S. inornatus inornatus*.

(c) The Ilia

In the *Scelotes* species it is the ilium which exhibits the greatest stability in form and structure of the three pelvic elements, the reduction of the ilia being slower than that of the pubis or ischium.

The ilium is the element of the pelvic girdle which is bound to the sacrum. In all the *Scelotes* species examined it retains its contact with the vertebral column. Tiedeman et al. (1975), in fact argued that the ilium becomes more firmly attached to the sacral transverse processes in skinks with more reduced pelvic girdles.

The circumstances that the degeneration of the ilium is slower than the rest of the pelvic bones, strengthens the theory that this is the main element present in the hind girdle of skinks with vestigeal pelvic girdles.

84./......

Stokely (1947), working on the girdles of *Anniella pulchra* and *Acontias percivali*, argued that the vestigeal pelves present in these species be regarded as ilia.

(4) The tendency for the ischial joint to lie nearer to the pubic joint.

The tendency for the ischia to approach the pubes, is linked with the miniaturization of the pelvic girdle and the loss of the hindlimbs.

We would expect the appendicular muscles to atrophy as the limbs degenerate. On the other hand the axial musculature hypertrophies (Leonard, 1979). The burden of providing attachment for the limb muscles is then removed from the pelvic girdle. Not having to cope with these muscles and the pubo-ischiadic ligament, the tendency would be for the two halves of the pelvic girdle to become more compact units, resulting in a reduction of the distance between ischium and the pubes. In his work on different skinks, Tiedeman et al. (1975) also observed this forward shifting of the ischia.

This shift in position is also evinced in the pectineal process of the pubis. In *S. capensis* the pectineal process is directed posteromedially while it projects anteriorly in *S. bidigittatus*. The ischium and the pectineal process are the points of attachment for the pubo-ischiadic ligament, and a shift in the position of the ischium will require a corresponding change in orientation of the pectineal process.

The forward shifting of the ischium, together with the fact that the pubis becomes smaller than the ischium (as in *S. inornatus inornatus*), strengthens

85./......

the assumption of Tiedeman et al. (1975) that the vestigeal pelvic girdle of a completely limbless skink, *Acontias meleagris* consists of an ilium and ischium only.

(5) Miniaturization and eventual loss of the hindlimbs

Miniaturization and loss of the hindlimbs are probably the most obvious manifestations of degeneration in the *Scelotes* species examined. Loss of hindlimb elements takes place in a distal to proximal sequence.

Loss of hindlimbs is directly correlated to the habitat occupied by these skinks. Burrowing through the soil, a denser medium than air, limbs would be a hindrance to forward progression and energetically very costly (Leonard, 1979). In the subterrestrial environment of the *Scelotes* species, selection pressures would be for a streamlined body.

The small hindlimbs of *S. brevipes*, *S. bipes and S. gronovii* are pressed against the body during lateral undulation (Leonard 1979). Sometimes on the ground, though, these rudimentary appendages "strut perfunctorily" (Leonard, 1979, p. 267).

Loss of phalanges heralds the start of digit degeneration. The lateral digits are the first to be lost. In the tetradactyle *S. limpopoensis*, digit V is absent. This is followed by the loss of digit I as in *S. caffer*. Lande (1978) reasoned that the digits which develop last, are likely to be lost first. Porter (1972) found that digits I and V are the last to develop in *Lacerta vivipara*. Sewertzoff (1931) and Tiedeman et al. (1975) concluded that the third and fourth digits are the last to remain. The monodactyle *S. gronovii* has only the fourth digit remaining.

86./.......

In *S. brevipes* digits are absent, but two distal cartilaginous hindlimb elements are present which I regard as tarsal elements. The crus of *S. brevipes* is cartilaginous, but two epipodials can still be discerned.

Although externally limbless, both *S. inornatus inornatus* and *S. anguina* retain a remnant of the hindlimb beneath the skin. In the case of *S. anguina* the vestige is extremely minute (Fig. 26).

In conclusion it may be stated that, although much and valuable work has already been done on degeneration as a whole, many aspects remain vague. Embryological and phylogenetic research may shed light on these problems. It must also be remembered that any animal is a compromise structure and to be successful in an evolutionary sense, it will have to overcome a variety of environmental hurdles. While the studies in osteology will give a general outline of degeneration associated with a shift towards a subterrestrial environment, investigations of the animal's myology, physio= logy, reproduction, etc., will evidently supply a more complete picture of the animal's adaptation to its habitat.

87./......

SUMMARY AND CONCLUSIONS

1 — 6

(1) The genus *Scelotes* exhibits a full range of pelvic girdle and hindlimb degeneration; from forms which have miniaturized, pentadactyle hindlimbs, to those which are externally limbless.

(2) Reduction of the pelvic girdle and hindlimbs are correlated with the subterrestrial habitat occupied by these skinks.

(3) Elongation of the body is the first step towards a serpentiform locomotion, the latter being mainly lateral undulation in *Scelotes*.

(4) There is a corresponding increase in body length with degeneration of the hindlimb.

(5) Species with degenerate limbs have more, but shorter presacral vertebrae.

(6) Reduction of the pelvic girdle precedes external limb loss.

(7) The loss of the cartilaginous pubic and ischial symphyses is the first manifestation of reduction in the pelvic girdle.

(8) The three pelvic elements degenerate at different rates.

(9) In the series the pubis exhibits the most pronounced rate of reduction of the pelvic bones.

(10) The angle of approach of the two pubes becomes progressively larger in the series.

88./....

14, 15, 16, 17

(11) The two halves of the pelvic girdle become structures following the curvatures of the body.

(12) The distance between the pubis and the ischium gets shorter, so that each half of the pelvic girdle becomes a more compact unit.

(13) The reduction of the ilium is much slower than that of the pubis and ischium.

(14) In a subterrestrial environment limbs would be a hindrance to forward progression and energetically very costly for the animal. Selection pressures in this environment favour the loss of limbs.

(15) Loss of hindlimb elements occurs in a distal to proximal sequence, the digits being the first to be lost.

(16) The lateral digits are the first to be lost. Digit IV is the only one present in the monodactyle *S. gronovii*.

(17) The crus and tarsus of the small, externally visible hindlimb of *S. brevipes* are cartilaginous, pointing the way towards eventual loss of these elements.

(18) Both *S. inornatus inornatus* and *S. anguina* retain a vestige of the hindlimb beneath the skin.

(19) In brief, the invasion of a subterrestrial habitat creates problems for a fully limb skink, consequently selection pressures favour a streamlined body. Limb loss and the corresponding pelvic girdle degeneration are regarded as adaptive responses for soil crawling.

89./....

APPENDIX I

Morphometric data of some *Scelotes* species.

SNOUT-VENT LENGTH - length of the body from the tip of the snout to the cloacal opening.

VENT-TAIL LENGTH - length of the tail from the cloacal opening to the posterior extremity.

SNOUT-EYE LENGTH - length of the head from the tip of the snout to the anterior border of the eye.

DIAMETER (HEAD) - diameter of the portion of the head immediately behind the eyes.

S.A.M. - South African Museum.

T.M. - Transvaal Museum

90./.......

	Snout-vent Lenght (mm)	Vent-tail Length (mm)	Hindlimb Length (mm)	Forelimb Length (mm)	Snout-eye Length (mm)	Diameter (Head) (mm)	Mass (GM)
S.A.M 18689	57,0	55,0	10,2	5,7	2,05	3,8	1,00
S.A.M 18688	58,2	51,9	12,7	6,2	2,1	4,45	1,00
S.A.M. 18546 # 1	58,0	37,5	11,1	5,1	2,2	3,2	1,00
S.A.M. 18546 # 2	56,0	Part of tail broken off	11,2	5,7	2,8	3,95	1,00
S.A.M. 44644	55,0	34,0	12,7	6,6	2,9	3,8	1,00
S.A.M. 18546 # 2	48,5	Part of tail broken off	10,6	5,9	1,9	3,45	1,00

APPENDIX I A *SCELOTES CAPENSIS*

	Snout-vent Length (mm)	Vent-tail Length (mm)	Hindlimb Length (mm)	Forelimb Length (mm)	Snout-eye Length (mm)	Diameter (Head) (mm)	Mass (GM)
S.A.M 44615	45,0	Part of tail broken off	7,3	4,4	2,45	3,6	1,00

APPENDIX I B *SCELOTES MIRA*

S.A.M. 17481	45,0	Part of tail broken off	6,05	2,9	1,95	2,45	0,50

APPENDIX I C *SCELOTES ALBERTI*

S.A.M. 44508	110,0	Part of tail broken off	11,6		3,1	5,7	4,00

APPENDIX I D *SCELOTES KASNERI*

	Snout-vent Length (mm)	Vent-tail Length (mm)	Hindlimb Length (mm)	Forelimb Length (mm)	Snout-eye Length (mm)	Diameter (Head) (mm)	Mass (GM)
T.M. 33751	71,0	44,0	10,7	3,15	2,5	3,15	2,00
T.M. 37977	70,5	76,0	14,1	3,2	2,7	4,45	3,00
T.M. 36681	66,0	Part of tail broken off	10,15	2,4	2,4	3,4	2,00
T.M. 37978	64,5	66,5	12,4	2,7	2,6	4,6	2,00
T.M. 38217	79,0	61,0	12,5	3,2	2,9	3,9	4,00
T.M. 41706	66,5	54,5	10,9	3,1	2,9	3,9	2,0
T.M. 42884	71,5	Part of tail broken off	13,3	3,7	3,3	3,5	3,00
T.M. 12885	67,0	50,5	11,2	3,05	2,6	3,85	2,00
T.M. 46991	70,0	68,5	10,3	3,4	2,7	3,1	2,00
T.M. 48547	65,0	Part of tail broken off	10,3	3,2	2,6	3,35	1,00

APPENDIX I E *SCELOTES LIMPOPOENSIS*

	Snout-vent Length (mm)	Vent-tail Length (mm)	Hindlimb Length (mm)	Forelimb Length (mm)	Snout-eye Length (mm)	Diameter Length (mm)	Mass (GM)
S.A.M. 18052 # 1	60,6	33,0	7,8	3,1	1,4	3,9	1,0
S.A.M. 17960	52,0	Part of tail broken off	7,95	3,05	2,0	3,35	1,0
S.A.M. 18052 # 2	51,5	65,0	8,1	3,3	1,5	3,45	1,0
S.A.M. 2413	51,0	32,5	8,7	2,8	1,4	2,7	0,5
S.A.M. 17973	44,5	42,5	6,5	2,55	1,3	3,45	0,5
S.A.M. 44595	44,0	53,5	9,2	3,2	1,7	2,85	0,5
S.A.M. 4321	32,0	31,0	6,3	2,4	1,4	2,2	0,5
S.A.M. 18170	35,0	43,0	7,6	2,55	1,5	2,35	0,5
S.A.M. 6092	49,7	Part of tail broken off	7,6	2,65	1,7	3,0	0,5
S.A.M. 18052 # 2	23,3	29,2	6,1	2,3	1,3	2,4	0,5

APPENDIX I F *SCELOTES CAFFER*

	Snout-vent Length (mm)	Vent-tail Lenght (mm)	Hindlimb Length (mm)	Snout-eye Length (mm)	Diameter (Head) (mm)	Mass (GM)
S.A.M. 2037	67,0	40,5	4,6	1,65	3,25	1,0
S.A.M. 2050	66,5	65,0	4,4	2,4	3,55	1,0
S.A.M. 1459	74,5	40,5	4,3	1,9	3,55	1,5
S.A.M. 44084	78,0	62,0	8,6	1,9	4,1	2,0
S.A.M. 44546	62,5	47,0	3,7	2,05	3,65	1,00
S.A.M. 43859	92,0	69,0	5,2	2,2	3,25	1,5
S.A.M. 44035	65,5	49,5	3,7			1,0
S.A.M. 1987	76,2	48,4	4,2	2,1	3,85	1,5
S.A.M. 44599	38,5	25,0	3,4	1,5	2,65	0,5
S.A.M. 1961 # 1	58,0	47,0	3,8	1,8	3,25	1,00
S.A.M. 44547	31,4	Part of tail broken off	2,9	1,5	2,25	0,5
S.A.M. 1961 # 2	42,2	15,4	4,2	1,8	2,5	0,5

APPENDIX I G *SCELOTES BIPES*

	Snout-vent Length (mm)	Vent-tail Length (mm)	Hindlimb Length (mm)	Snout-eye Length (mm)	Diameter (Head) (mm)	Mass (GM)
S.A.M. 44548 # 1	73,5	Part of tail broken off	1,8	2,2	3,55	1,0
S.A.M. 44616	68,0	Part of tail broken off	3,6	2,3	3,3	1,0
S.A.M. 44515	76,0	49,0	2,4	1,95	2,85	1,0
S.A.M. 44517 # 1	77,5	19,5	1,6	2,25	3,65	1,0
S.A.M. 43243	66,5	42,0	3,7	2,2	3,35	1,0
S.A.M. 44516	67,5	43,0	2,3	2,05	3,2	1,0
S.A.M. 43991	74,0	72,5	3,5	2,2	3,55	1,5
S.A.M. 43990	74,5	65,0	4,4	2,6	4,3	2,0
S.A.M. 43540	82,0	43,5	3,5			1,59
S.A.M. 44517 # 2	32,6	16,1	1,1	1,7	2,55	
S.A.M. 44517 # 3	28,7	17,2	1,2	1,65	2,5	
S.A.M. 44517 # 4	30,4	16,3	1,35	1,4	2,35	
S.A.M 44548 # 2	29,5	16,5	1,3	1,7	2,5	
S.A.M. 44548 # 3	27,8	17,9	1,35	1,2	2,45	

APPENDIX I H : *SCELOTES GRONOVII*

	Snout-vent Length (mm)	Vent-tail Length (mm)	Snout-eye Length (mm)	Diameter Length (mm)	Mass (GM)
S.A.M. 44594	66,0	Part of tail broken off	2,6	3,35	1,0
S.A.M. 44893	57,5	37,0	2,4	3,85	1,0
S.A.M. 9047	53,5	Part of tail broken off	1,95	2,65	0,5
S.A.M. 3952	64,5	Part of tail broken off	2,2	3,4	0,5
S.A.M. 4228	59,0	Part of tail broken off	2,25	2,9	0,5
S.A.M. 4950	69,0	50,5	2,3	3,3	1,5
S.A.M. 5043	63,0	Part of tail broken off	1,7	3,15	1,0
S.A.M. 1448	45,0	43,0	1,9	2,65	0,5

APPENDIX II *SCELOTES ANGUINA*

REFERENCES

BELLAIRS, A D'A (1969). The Life of Reptiles. Weidenfeld and Nicolson, London.

CAMP, C L (1923). Classification of the lizards. Bull. Amer. Mus. Nat. Hist., 48 (11) : 289-481.

COPE, E D (1892). On degenerate types of scapular and pelvic arches in the Lacertilia. J. Morph., 7 (2) : 223-244.

DE WITTE, G F and R Laurent (1943). Contribution a la systematique des formes dégradées de la famille des Scincidae apparentées au genre *Scelotes* Fitzinger. Mém. Mus. Roy. d'Hist. Nat. Belgique, 2me sér., fasc 26 : 1-44.

EL-TOUBI, M R (1938). The Osteology of the Lizard *Scincus scincus* (Linn.). Bull. Fac. Sci. Cairo Univ., 14 : 30-38.

EL-TOUBI, M R (1947). Sacral Ribs of Lacertilia. Nature, Lond., 159 (4036) : 342.

ESSEX, R (1927). Studies in reptilian degeneration. Proc. Zool. Soc. Lond., 59 : 879-945.

FITZSIMONS, V F (1943). The Lizards of South Africa. Trans. Mus. Mem., No. 1 : 175-205.

*FÜRBRINGER, M (1870). Die Knochen und Muskeln der Extremitäten bei den Schlangenähnlichen Sauriern. Leipzig vi + 135p. Wilhelm Engelmann.

GADOW, H (1881). Beiträge zur Myologie der hinteren Extremität der Reptilien. Gegenb. Morph. Jahrb 7 (3) : 22-466.

GANS, C (1962). Terrestrial locomotion without limbs. Amer. Zool. 2 : 167-182.

GANS, C (1966). Locomotion without limbs, Natural History, 75 : 10-41.

GANS, C (1968). Relative success of divergent pathways in Amphisbaenian specialization. Amer. Nat., 102 : 345-362.

GANS, C (1973). Locomotion and burrowing in limbless vertebrates. Nature (London), 242 (5397) : 414-415.

GANS, C (1974). Biomechanics, An approach to vertebrate biology. J P Lippincott. Philadelphia.

GANS, C (1975). Tetrapod limblessness : evolution and functional corollaries. Amer. Zool. 15 : 455-467.

GREER, A E (1970). A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool., 139 : 151-184.

HOFFSTETTER, R and J -P Gasc (1969). Vertebrae and ribs of modern reptiles. In Biology of the Reptilia, I. (C Gans, A d'A Bellairs and T S Parsons, eds.). Academic Press. London and New York, 201-310.

HOLDER, A (1960). The comparative morphology of the axial skeleton in the Australian Gekkonidae. Zool. Journ. 64 : 300-335.

HOLMGREN, N (1933). On the origin of the tetrapod limb. Acta Zool. Stokh. 14 : 185-295.

HUGHES, B (1968). The tarsus of rhynchocephalian reptiles. J. Zool. Lond., 156 : 457-481.

KAMEL, A H (1951). Sacral ribs of Lacertilia. Nature, 168 (4276) : 660-661.

KING, D (1964). The osteology of the water skink, *Lygosoma (Sphenomorphus) quoyii*. Aust. J. Zool. 12 : 201-216.

LANDE, R (1978). Evolutionary mechanism of limb loss in tetrapods. Evolution 32 : 73-92.

LEONARD, C J (1979). A functional morphological study of limb regression in some Southern African species of Scincidae (Reptilia : Sauria). Ph.D. Diss. Univ. Cape Town.

MAHENDRA, B C (1950). The osteology of the Indian house-gecko, *Hemidactylus flaviridis* Rüppel. Proc. Zool. Soc. Bengal. 3 (1) : 49-64.

MEHNERT, E (1891). Untersuchungen über die Entwicklung des Os hypoischium (Os cloacae ant.) Os epipubis und Ligamentum medianum pelvis bei den Eidechsen. Morph. Jahrb., XVII : 123-143.

MOODIE, R L (1907). The sacrum of the Lacertilia. Biol. Bull., 13 : 84-93.

MOODIE, R L (1909). The morphology of the vertebrate sacral rib. Anat. Anz., 34 (15) : 361-364.

PARKER, T J and W A Haswell (1963). A textbook of Zoology. Macmillan & Co (London), II.

PORTER, K R (1972). Herpetology. W B Saunders Co. Philadelphia. 542pp.

REWCASTLE, S C (1980). Form and function in lacertilian knee and mesotarsal joints - a contribution to the analysis of sprawling locomotion. J. Zool. Lond., 191 : 147-170.

ROMEIS, B (1948). Mikroskopische Technik. R. Oldenbourg. München.

ROMER, A S (1956). The Osteology of the Reptiles. Univ. of Chicago Press.

RUSSEL, A P and S C Rewcastle (1979). Digital reduction in *Sitana* (Reptilia : Agamidae) and the dual roles of the fifth metatarsal in lizards Can. J. Zool., 57 : 1129-1135.

*SEWERTZOFF, A N (1931). Morphologische Gesetzmässigkeiten der Evolution. Studien über die Reduktion der Organs der Wirbeltiere. Zool. Jahrb. abt. F. Ant., 53 (4) : 611-700.

SNYDER, R C (1952). Quadrupedal and Bipedal locomotion of lizards. Copeia 2 : 64-70.

SNYDER, R C (1954). The anatomy and function of the pelvic girdle and hindlimbs in lizard locomotion. Amer. J. Anat., 95 (1) : 1-45.

STOKELY, P S (1947). Limblessness and correlated changes in the girdles of a comparative morphological series of lizards. Amer. Midl. Nat., 38 : 725-754.

TIEDEMAN, M and F Tiedeman (1975). Vergleichend anatomische Untersuchungen ans Schulter und Beckengürtel verschiedener südafrikanischer Skinkarten mit besonderer Berücksictigung von Reduktionserscheinungen. Zoologica, 43 : 1-70.

VAN DER KLAAUW, C J (1948). Ecological studies and reviews. Ecological Morphology. Leiden, E J Bril |Ser. D| Bibliotheca Biotheoretica, IV (2).

WASSERSUG, R J (1976). A procedure for differential staining of cartilage and bone in whole formalin fixed vertebrates. St. Tech., 51 (2) : 131-134.

* - not seen in the original.