A FUNCTIONAL MORPHOLOGICAL STUDY

OF

LIMB REGRESSION

IN

SOME SOUTHERN AFRICAN SPECIES OF SCINCIDAE
(REPTILIA:SAURIA)

BY

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OF

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ABSTRACT

How and why did limblessness evolve in certain skinks? These questions are explored in certain species of the Scincidae (from southern Africa) that vary in the degree of limb reduction. This regression series consists of *Mabuya capensis* (with normal, pentadactyle limbs), *Riopa sundevallii* (with miniaturized, pentadactyle limbs), three species of the genus *Scelotes* (*bipes*, *gronovii* and *brevipes* - with vestigial hindlimbs varying in the degree of degeneration) and, finally, *Acontias meleagris* (without any trace of limbs).

The osteology and the myology of the locomotor apparatus are described for all members of this regression series with special reference to the axial system which has in the past received but scant attention compared with the appendicular apparatus. Qualitative and morphometric data are used to construct morphoclines that are correlated with limb reduction. Numerous morphological trends and tendencies support the conclusion that the axial system hypertrophies as the appendages degenerate.

The patterns of locomotion are also described for all members of the regression series. Furthermore, an ethocline, that links the limbed and limbless extremes, is postulated. Even in quadrupedal skinks the dominant appendicular system may be assisted by axial flexures that increase stride length. As limbs degenerate, appendicular progression is phased out while axial progression increases in importance.
In this regression series such morphological and behavioural transformations are associated with some form of underground existence. Consequently, the hypothesis, that limbless axial progression adapts these skinks for soil-crawling, is investigated and confirmed.

The evolution of limblessness among skinks may be partially explained in terms of the following factors. Firstly, a slender, elongated soil-crawler enjoys the selective advantage (over a stout, long limbed skink) of requiring only a narrow (therefore, energetically less costly) tunnel for progression. Consequently, entry into an underground adaptive zone is likely to create selective pressures that favour axial progression. Secondly, the primitive functional overlap of axial and appendicular systems is protoadaptive for change. In quadrupedal skinks a weak axial component serves the dominant appendicular system by increasing stride length. But such a functional overlap creates the potential for the phasing out of the appendicular system as the axial system is phased in.
ACKNOWLEDGEMENTS

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I am deeply grateful to Professor Carl Gans of the University of Michigan (U.S.A.) for the contribution he has made to my education and also for editorial suggestions that have substantially improved the text. My wife and I unite in thanking Mrs Mabel Gans for helping to make our stay in Ann Arbor pleasantly memorable. I also thank Professor Herb Rosenberg of the University of Calgary for supervising the E.M.G. experiments.

* For "Graph X.Y." read "Fig.X.Y." here and in the rest of the text.
Then I thank my wife, Sylvia, for her constant support, encouragement and general assistance.

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1. INTRODUCTION

1. GENERAL

The paradox of limblessness among the Tetrapoda has fascinated man since time immemorial. The first book of the Bible contains a reference to limb loss by snakes (Genesis III:14); while elsewhere in the Old Testament a sage comments on the awe-inspiring wonder of serpentine locomotion (Proverbs XXX:19). Although limb loss is usually associated with the Ophidia, undoubtedly the most diverse and successful group of limbless Tetrapoda, many other lower tetrapods lack functional limbs. In this category are fossil and living amphibiaans (Auffenberg, 1962), about 130 species of amphisbaenians (Gans, 1974) and many families of lacertilians (Gans, 1975; Presch, 1975).

Partial or complete loss of limbs occurs with surprising frequency among lizards. It probably evolved independently in several saurian families such as the Anniellidae, Anguidae, Pygopodidae, Anelytropsidae, Dibamidae, Scincidae, Gerrhosauridae and Teiidae (Sewertzoff, 1931; Stokely, 1947; Waters, 1969; Gans, 1975 and Presch, 1975). Even in the family Scincidae itself, the trend towards limblessness probably occurred independently many times (Camp, 1923; and Greer, 1970a and b); the same is probably true of the Anguidae (Gans, 1975). In the words of Camp (1923, p. 351): "Reduction of feet, limbs and girdles seems to be a fashionable course of devolution among autarchoglossine lizards. This process has
occurred independently in many diverse groups, and seems to be rapidly going on at present among otherwise normal genera and species of scincs in widely separated parts of the world".

An interesting aspect of limb regression among saurians is that not only are some lizards totally limbless, but that a full spectrum of limb regression ranging from quadrupedal to apodous forms, are found. In contrast with snakes, which are usually totally without appendages and only rarely exhibit tiny vestiges of hind-limbs (Gasc, 1966; Bellairs, 1972), living saurians show many morphological "intermediate stages" en route to complete limblessness. Thus Camp (1923, p. 354) could write: "It is, of course, possible to arrange degradational series of living forms showing gradual degeneration of limbs, one toe at a time. Whether such a series illustrates the actual course of devolution does not concern us here". Such a series attracted the attention of a large number of comparative morphologists whose work chiefly involved documenting morphological variations in limb and girdle structure.

The phenomenon of limb reduction is especially common in the family Scincidae (Camp, 1923; Stokely, 1947 and Greer, 1970a and b). Several closely related species belonging to a single scincid genus (such as *Scelotes* or *Chalcides*) may be pentadactyle quadrupedal, bipodous or even apodous. This wide range in the condition of the locomotor apparatus, in probably closely related species, render the Scincidae ideal material for the study of appendicular degeneration.
2. DEFINITION OF THE PROBLEM

This investigation explores the questions how and why did limb regression occur in some African members of the family Scincidae. The "how" part of the question, in context of the synthetic theory of evolution, implies explaining how a quadrupedal animal could gradually evolve, through many intermediate stages, into a limbless one, and nevertheless still retain the ability to perform its vital locomotor activities. This analysis has been carried out on two levels: the morphological and the behavioural.

Morphological analysis entails comparison of the locomotor apparatus among members of a series of skinks exhibiting limb regression. Similarities in structure are attributed to a common scincid heritage. Differences will be scrutinized more carefully and an explanation for them will be sought in terms of adaptation to different modes of locomotion. A major objective of the morphological analysis will be to construct a morphocline (if possible) of the locomotor apparatus linking limbed and limbless skinks.

The behavioural analysis entails investigating how locomotor behaviour changes with limb regression. This entails description of the locomotion of a sample of skinks including species with normal limbs, with reduced limbs and without limbs. Again, those aspects appearing to provide clues as to how the apodous condition evolved will be stressed. In brief, can a morphocline and a correlated ethocline be established for aspects of the locomotor apparatus and behaviour of a group of skinks exhibi-
ting a spectrum of limb regression from a normal limbed to a totally limbless condition?

The "why" aspect of the question is concerned with determining the underlying mechanisms of selection responsible for limb reduction and loss. Natural selection produces adaptation. In this context adaptation may be defined as a "correlation to the advantage of the organism between structure, function and environment". In skinks appendicular degeneration is associated with a fossorial or semi-fossorial mode of life (Camp, 1923; FitzSimons, 1943; Waters, 1969 and Greer, 1970a and b). Locomotion in a more or less subterranean habitat imposes mechanical demands somewhat different from those to which terrestrial animals are exposed. Do these different mechanical demands provide selective advantage for some of the changes in locomotor behaviour and anatomy associated with limb loss?

3. PROBLEM IN HISTORICAL CONTEXT

3.1 GENERAL

Studies of the locomotor apparatus and of locomotor behaviour have usually proceeded independently. Investigation into the anatomy of partially or completely limbless lizards started early in the last century, whereas analyses of locomotor behaviour are mainly products of the present one.

3.2 LIMB REGRESSION

Joh. Müller (1831) utilizes morphology in a major review of
the classification of a wide selection of limbless vertebrates, including caecilians, partially or completely limbless lizards, amphisbaenians and burrowing snakes. He illustrates and briefly describes a skull and a few ribs and parasternalia of *Acontias meleagris*. He notes that the skinks, *Seps (= Chalcides) tridactylus* and *Acontias meleagris* possess parasternalia, which distinguish them not only from snakes but from other limbless lizards such as *Pseudopus oppellii*, *Anguis fragilis* and *Ophisaurus ventralis*.

Fürbringer (1869) gives a detailed account of the osteology and the myology of the girdles and appendages of a series of lizards belonging to the family Anguidae, Pygopodidae and a few Scincidae (e.g. *Acontias meleagris* and *Acontias niger = Acontias plumbeus*, Broadley and Greer, 1969). His main conclusion is that loss of limbs involves the diminution, transformation or even loss of bones and muscles. He concludes that such reduction starts with the most distal elements and then proceeds proximally. The problem of limb reduction is also considered in his major work on the pectoral osteology and myology published in 1900.

In his analysis of a series of lizards with reduced limbs (including the skinks *Chalcides lineatus* and *Evesia monodactyla*), Cope (1892b) concludes: (i) that the reduction of an appendage starts with the distal elements and then proceeds in a proximal direction and (ii) that in contrast to other lizards the anterior limbs have a tendency to persist longer in the Teiidae and the "Amphisbaenidae".
Krieg (1919) carefully analyzes the proportions of the shoulder girdles of normal limbed and reduced limbed lizards. The latter category is represented by a skink, *Chalcides tridactylus* and an anguid, *Anguis fragilis*, while *Lacerta serpa* and another skink serve as lizards with normal limbs. Krieg concludes that extreme variability and asymmetry are symptomatic of degeneration and that the reduction of the shoulder girdle is distinct from that of the sternum.

Camp (1923) stresses that the reduction and the loss of limbs never occur among the Ascalobota but only among the Autarchoglossa, which have a more complex hypaxial body musculature (including a M. rectus superficialis) which he surmises permits more extensive tail and body movements. In addition, he points out that loss or reduction of limbs are usually associated with burrowing or grass dwelling habitats. Furthermore, the most extreme degeneration has taken place in those lizards most specialized for a subterranean existence.

Essex (1927) studies (i) the osteology of degenerate girdles and limbs in lizards and burrowing snakes (including species of *Acontias* and of *Scelotes*) and (ii) the geographical distributions, especially of those South African forms with reduced limbs. (iii) In addition, he records speculation about "the method of degenerative evolution".

An investigation of the ontogeny and anatomy of a series of reduced limbed lizards led Sewertzoff (1931) to several important conclusions. An increase in the number of presacral vertebrae could be correlated with a decrease in limb size.
As lizards became more snake-like, the number of body segments presumably increased and sacral vertebrae developed from more caudal somites. His ontogenetic studies led him to postulate two types of reduction viz.: rudimentation ("negative Archaalaxis") and complete reduction ("Aphanisia"). "Rudimentation" implies that an organ becomes reduced in size when compared with the ancestral condition either diminishing in size throughout its ontogeny and/or when the terminal stages in its ontogeny are eliminated. "Aphanisia" or total reduction implies that the total loss of an element leading ultimately to the disappearance of its Anlage from the embryo.

Stokely (1947) describes the osteology of a series of lizards showing gradual reduction of limbs and girdles. His reduced limbed forms are chiefly from the family Scincidae "with supplementation from observations made on some Anguidae, Pygopodidae, Lacertidae and Anniellidae". Although his descriptions are confined to the appendicular skeleton he does correlate an increase in the number of presacral vertebrae with limb regression. In addition, he discusses a few theories on the origin of limblessness.

In a series of brief articles, Gasc (1965, 1967a&b, and 1968) deals with aspects of the postcranial skeleton, myology and locomotion of serpentine squamates.

Waters (1969) sought convergent or parallel modifications for locomotion without limbs in several independent lines of functionally limbless lizards and a snake. His study was especially detailed for the trunk vertebrae and musculature. He con-
cludes: "Functionally limbless grass dwelling lizards and snakes do not share a common or convergent suite of vertebral and muscular features which distinguishes them from limbed forms. However, a suite of parallel modifications does appear on comparison of limbed and limbless allies in selected taxa, particularly in the vertebrae" (Waters, 1969, p. 172).

The pattern of limb bud development in species with reduced limbs has been studied extensively by Raynaud and various collaborators. Raynaud (1969 and 1973) provides English summaries of these studies. Raynaud et al. (1973 and 1976) report on the relationship between the somites and limb bud formation in three species of *Scelotes* with greatly reduced limbs.

Gans (1975) deals with the evolution and functional corollaries of limblessness. He concludes that only bodily elongation is universally associated with limb loss in diverse lines of tetrapods. He suggests that elongation may have arisen to permit the organism to pass through narrow crevices. Furthermore, such elongation would protoadapt these animals to acquire lateral undulation as a new mode of locomotion. Such a new pattern of progression would render the total loss of limbs possible.

In the teiid genus, *Bachia*, the hindlimbs undergo more rapid degeneration than the front limbs (Presch, 1975). This condition is similar to that of some amphibiaenians (Gans, 1975). It is in sharp contrast with the condition in some other squamates, which have vestiges of hindlimbs persisting even after
front limbs are no longer present (Bellairs, 1972).

M and F Tiedemann (1975) a husband and wife team, submitted doctoral dissertations on the osteology and myology of the limbs, the pectoral and the pelvic girdles of a series of African skinks exhibiting appendicular degeneration. In their series *Mabuya quinquetaeniata margaritifer* was chosen as an example of a normal limbed skink, *Ablepharus wahlbergii* as a species with small, though pentadactyle limbs, *Scelotes bipes* or *Scelotes bidigittatus* as a bipodous form and *Acontias meleagris* as a limbless skink. They state the aims of their investigation as follows: "Diese anatomischen Untersuchungen wollen und können nicht die Ursachen der besonders bei Scincidae auftretenden Extremitäten-reduktionen ergründen, sondern haben die Aufgabe, eine genaue Darstellung der myologischen und osteologischen Situation der Extremitätengürtel der vier verschie denen Skinkarten zu geben und dabei jene Gesetzmäßigkeiten au zuzeigen, denen die Reduktion der Gürtel bzw. Extremitäten auf Grund funktioneller Veränderungen unterliegen".

The present study had progressed for almost two years before the work of Tiedemann came to my attention. Although there is some overlap in material and theme, there are major differences of emphasis and approach. The Tiedemanns purposely avoid questions concerning the causes of limb loss; such questions are central in the present study. They provide a detailed description of the appendicular skeleton and musculature, but they ignore the axial system, the sole locomotor apparatus of limbless skinks. This investigation emphasizes the hypertrophy of the body axis associated with appendicular degeneration. As pre-
vious studies lack a functional dimension, the present project considers changes in locomotor behaviour associated with limb reduction.

In brief, the previous studies on limb regression may be characterized as:

(i) investigating a heterogeneous collection of partially or completely limbless lizards from several independent lines (notable exceptions being the more recent works of Tiedemann & Tiedemann, 1975 and Presch, 1975);

(ii) being strictly morphological in approach with the emphasis falling mainly on the osteology of the degenerating limbs and girdles;

(iii) ignoring functional considerations almost entirely;

(iv) emphasizing the phenomenon of limb loss as devolution, degeneration or loss of elements while ignoring the concomitant increase in the complexity of other elements, for instance, the axial skeleton and musculature (a notable exception being Gans, 1975).

In contrast the present study attempts:

(i) to reduce the heterogeneity of the animals studied by confining the investigation to members of the single family, Scincidae from southern Africa;

(ii) to broaden the scope of the morphological aspect of the study to encompass the entire locomotor apparatus (not merely the degenerating limbs and girdles);
(iii) to include a functional analysis of the locomotion of the skinks under investigation;

(iv) to look beyond the mere degeneration of limbs and girdles to the hypertrophy of the axial skeleton and musculature which adapts these reduced limbed skinks for locomotion in subterranean habitats.

This investigation is confined to African members of the family Scincidae, on the assumption that the more closely related compared animals are, the greater the probability that differences in the structure and the performance of their locomotor organs will reflect ecological and behavioural adaptations (Gambaryan, 1974). This assumption is supported by Waters (1969) who found that no common suite of convergent traits characterize all limbless squamates. However, within closely related groups (e.g. families) specific trends could be detected.

Previous work contains much osteology, somewhat less myology, almost all confined to the degenerating appendicular system. Thus a clear picture of the atrophying limbs and girdles can be constructed, but the rest of the locomotor apparatus is usually disregarded. As the appendicular system atrophies, the axial system hypertrophies (Gans, 1975). The present study will record changes in the body axis correlated with partial or complete limb loss.

Previous studies lacked a functional dimension; the present one attempts to correlate anatomical, behavioural and ecological data. In the skinks under consideration limb regression
is invariably associated with a fossorial or semi-fossorial mode of life (FitzSimons, 1943; Greer 1970a and b). What functional demands do such a habitat impose on the organism? What changes occur in mode of locomotion and locomotor anatomy?

3.3 LOCOMOTOR BEHAVIOUR

Howell (1944) gives a concise and semi-popular account of lacertilian locomotion in a study devoted mainly to mammalian locomotion.


Urban (1964 and 1965) attempts to quantify differences in the locomotor patterns of various species of quadrupedal lizards belonging to the family Teiidae and of a single species from the Iguanidae.

Gray (1968) reviews previous studies on lacertilian locomotion and gives an interesting interpretation of the biomechanics of the pectoral girdle.

The contribution of lateral bending of the body axis to lacertilian locomotion is considered by Daan and Belterman (1968) who studied the locomotion of several lizards including the skinks, *Chalcides ocellatus* (with slightly miniatu*
rized limbs) and *Tiliqua scincoides* (with normal limbs). They distinguish two types of movements of the body axis: traveling waves and standing waves. The former is associated with limb regression while the latter occurs in quadrupedal lizards.

Peterson (1973) in an unpublished Ph.D. thesis deals with the adaptation of the shoulder girdle for aboreal locomotion in chameleons and agamid lizards. This is one of the few works in which an attempt is made to analyze the biomechanics of the shoulder girdle.

In his comprehensive review of locomotion in lower tetrapods, Sukanov (1974, p. 111) summarizes the state of knowledge as follows: "Studies on the locomotion of lower tetrapods are, for the most part inadequate. Specific works are extremely few and do not give a comparative picture of locomotion in the different groups of amphibians and reptiles. The majority of works are of 'incidental character', mentioning the particular specialities of motion for this or that form." He describes the locomotion of some eight species of lizards including the skink *Eumeces schneideri*. He confines himself to locomotory behaviour and does not consider the anatomical bases of movement at all.

With the exception of a three-paged article by Rathor (1970) no specific works on the locomotion of limbless skinks have been traced. Many papers incidently mention the serpentine wiggings of functionally limbless lizards (cf. FitzSimons, 1943; Waters, 1969). Weidemann (1932) does, on the other
hand, briefly describe the locomotion of the anguids *Ophisaurus* and *Anguis* in a study devoted mainly to the locomotion of snakes. So also Gray (1946) in a study on serpentine progression illustrates (without further description) lateral undulation in *Ophisaurus*.

Daan and Belterman (1968) describe travelling waves in the body axis of *Ophisaurus*. In other words, though limbless anguids have received some attention, not a single detailed account of limbless locomotion in skinks could be traced.

A more considerable literature is devoted to the locomotion of another group of limbless squamates, the snakes (Mosauer, 1932 and 1935; Gray, 1946; Gray and Lissman, 1950; Gans, 1960, 1962, 1966a & b and 1974). The information acquired for this group will be employed to assist with the analysis of the locomotion of limbless skinks. The amphisbaenians, another group of highly specialized reptiles, are mainly limbless. Their locomotion and adaptations to a fossorial mode of existence have been described by Gans (1960, 1968, 1969 and 1978).

In brief, previous studies have either dealt with anatomy or locomotion; very rarely with both. In the present work a combination of approaches is adopted. Anatomical and behavioural data will be correlated in a biomechanical analysis. Some hypotheses generated will be tested experimentally.
4. TAXONOMIC CONSIDERATIONS

The present study is confined to the family Scincidae in order to increase the homogeneity of the group under investigation and to reduce problems due to different phylogenies (Gans, 1963). Such problems can be limited but not entirely eliminated because of the vastness, great diversity and global distribution of this family. A brief survey of the systematics of the Scincidae will serve to place this study into a taxonomic context.

Greer (1970a and b) provides a recent and comprehensive taxonomic survey of the Scincidae with special reference to African taxa. He divides the Scincidae into the four subfamilies, Scincinae, Acontinae, Feylininae and Lygosominae.

The Scincinae, comprised of at least 30 genera and 180 species, is considered to be the most primitive subfamily of skinks, from which the other three subfamilies evolved independently (Greer, 1970a). The centre of diversity and abundance of this group is subsaharan Africa; the group is less abundant in Asia, absent from the Australian region and represented in the New World only by the widely distributed genus Eumeces and the partially limbless Neoseps reynoldsi (Telford, 1959).

Trends towards the loss of limbs have occurred independently in several scincine genera (Greer, 1970a). Several genera contain not only species with normal limbs, but also those displaying various degrees of limb reduction.

The subfamily Acontinae (Greer, 1970a) is confined to southern
Africa with an isolated population in south eastern Kenya. This group is completely limbless and highly adapted to a subterrestrial existence. It comprises the 3 genera: *Acontiotophiops lineatus* (1 species), *Acontias* (7 species, Broadley and Greer, 1969) and *Typhiosaurus* (8 species, Broadley, 1968).

The Feylininae include four species confined to central and west Africa as well as the Principe Islands. Like the Acontinae, this group is entirely limbless and highly adapted to a subterranean existence.

The Lygosominae consisting of at least 50 genera and well over 600 species, is regarded by Greer (1970a) as the most advanced subfamily of skinks. The skinks of this subfamily occur on all the continents and are especially abundant in the Australian region. The vast majority can be regarded as normal limbed; however, about 1% of the species are partially or completely limbless (Greer, 1970a).

In brief, the widely distributed, diverse family Scincidae, includes two subfamilies (Acontinae and Feylininae) of completely limbless lizards. Several scincine genera apparently developed the trend towards limblessness independently; while partially or completely apodous forms are relatively rare among the Lygosominae.

The scincine genus *Sceiotes*, which will receive special attention, manifests a complete spectrum of limb reduction from fully tetrapodous to apodous species. The main features of limb reduction in the southern African members of this genus
is summarized in the table below:

<table>
<thead>
<tr>
<th>Species of <em>Scelotes</em> (after FitzSimons, 1943)</th>
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<tr>
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<tr>
<td><em>capensis</em> (A Smith, 1849)</td>
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<td><em>àlberti</em> (Hewitt, 1929)</td>
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<td><em>limpopoensis</em> (FitzSimons, 1930)</td>
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<td><em>caffer</em> (Peters, 1861)</td>
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<td><em>angolensis</em> (Bocage, 1866)</td>
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<td><em>bipes sexlineatus</em> (Harlan, 1824)</td>
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<td><em>bipes bipes</em> (Linnaeus)</td>
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<td><em>bidigittatus</em> (FitzSimons, 1930)</td>
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<td><em>gronovii</em> (Daudin, 1802)</td>
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<td><em>brevipes</em> (Hewitt, 1910)</td>
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<tr>
<td>inornatus inornatus (A Smith, 1849)</td>
<td>0</td>
</tr>
<tr>
<td>inornatus mossambicus (Peters, 1882)</td>
<td>0</td>
</tr>
</tbody>
</table>

5. **CHOICE OF ANIMALS**

Two considerations influenced the choice of species for detailed study: firstly, the availability of living specimens for the behavioural studies and secondly, the aim to have the most important phases in the regression series represented. The following animals were chosen for detailed study:

5.1 *Mabuya capensis* (Gray, 1830) - subfamily Lygosominae - is selected as it is a readily available terrestrial skink with normal limbs.

5.2 *Acontias meleagris* (Linnaeus) - subfamily Acontinae - is a fairly large, readily obtainable and totally limbless skink specialized for a subterranean mode of life.

5.3 Living specimens of *Scelesotes bipes bipes* (bipodous, didactyle), *S. gronovii* (bipodous, monodactyle) and *S. brevipes* (with bud-like hindlimbs) were available for behavioural studies.
5.4 *Riopa sundevallii* (A Smith, 1849) - subfamily Lygosominae - is included as a tetrapodous skink with slightly reduced limbs as it was not possible to obtain living tetrapodous species of *Scales*. Thus *R. sundevallii* serves as a skink exhibiting an initial stage of limb degeneration.

The limbless Peylininae are omitted from detailed consideration because living specimens are difficult to obtain and they are superficially similar to the more abundant and diverse Acontinae.

Previous studies were criticized for lumping together partially or completely limbless forms from different lines (families) and treating them as if they formed a single series. This investigation attempts to increase the homogeneity of the material by focussing attention on some African members of the family Scincidae. Such an approach presumably has two advantages. Firstly, members of this family are assumed to have a fairly homogeneous genetic background. Secondly, limb loss in skinks is always associated with the acquisition of a subterranean habitat. For lizards in general appendicular degeneration is associated either with subterranean or with grass-dwelling habitats (Camp, 1923). These contrasting niches are likely to exert different selective forces (cf. Gans, 1975). Consequently, as limb regression in these skinks is invariably associated with invasion of a subterranean habitat, greater homogeneity in the selective pressures, which induce limb reduction, is expected. These two assumptions (homogeneous genetic background and
uniform selective pressures) are accepted at this stage as working hypotheses. If they are justified one would expect to find clear morphoclines and ethoclines linking the limbed and limbless polarities.

6. TECHNIQUES

6.1 CINEMATOGRAPHY AND FILM ANALYSIS

Lizard locomotion is usually far too rapid for its details to be observed with the unaided eye. Consequently, direct observation must be supplemented by medium to high-speed cinematography depending on the rapidity of the behaviour being investigated.

Gans (1963) and Sukanov (1974) both emphasize the importance of recording the behaviour of animals under natural conditions. The disadvantages of filming animals under laboratory conditions include:

(a) the use of animals that have been kept for some time in captivity in confined cages;

(b) the artificial nature of the substrate;

(c) the confined space within which the animal is expected to move (Sukanov, 1974).

Practical reasons as well as several advantages justify filming under laboratory conditions. In the present case the work was done thousands of miles from the natural home of the animals studied. Advantages include:
(a) better control over the intense lighting required for high-speed photography (Gans, 1963);

(b) the substrate is constant, without natural irregularities;

(c) a runway with a grid provides the animal with a straight but scaled pathway, thus facilitating analysis of speed changes during a run;

(d) a pair of mirrors (one on each side of the runway and inclined at an angle of about 55°) facilitate the simultaneous recording of a dorsal as well as two lateral views.

The following films were taken with a Canon Super 8 camera at the camera speeds of 18, 24 or 40 frames per second with either strobe or movie light illumination:

(a) *Mabuya capensis* (5 specimens) moving along a marked runway as described above;

(b) *Riopa sundevallii* (2 specimens) moving along the same runway;

(c) *Acontias meleagris* (5 specimens) moving:

   (i) on smooth glass covering a grid;

   (ii) into dry sand;

   (iii) over a polythene covered pegboard;

   (iv) in between two heavy strips of wood placed parallel to each other to simulate a deep furrow with parallel sides.

(d) *Scelotes bipes* (2 specimens), *Scelotes gronovii* (3 spe-
imens) and *S. brevipes* (2 specimens) were also filmed under conditions (i) to (iv) described for *Acontias meleagris*.

In all 18 rolls of 50 ft. super 8 colour movie film was taken for analysis. After viewing the films at reduced speed, certain sections were selected for the following types of detailed analysis:

6.1.1 Gait analysis in the case of quadrupedal lizards.
6.1.2 Lateral bending of the body axis.
6.1.3 Sequential drawing of selected frames.

6.1.1 *GAIT ANALYSIS*

The technique of gait analysis has a lengthy history which is summarized by Sukanov (1974) and Gambaryan (1974). In brief, it is a method for recording, comparing and classifying the actions of the limbs of quadrupedal animals.

The first step in gait analysis is the construction of a gait diagram on graph paper prepared in the following way. Sets of four horizontal rows are assigned to each of the four feet. Vertical lines 0.5 cm. apart represent successive motion picture frames and hence equal intervals of time. The section of film selected for detailed analysis is viewed a single frame at a time. Before advancing a frame, the position of each foot is recorded. If a particular foot is in contact with the ground then the area on the graph paper assigned to that particular foot and frame is lined or shaded. If the foot makes no contact the corresponding areas is left unshad
ded. By recording for each frame the position of each of the limbs, a gait diagram is constructed. Such a diagram reflects clearly the sequence and duration of limb contact with the substrate (see Figs. V.15 & 19).

From a gait diagram the following variables of tetrapodous locomotion can be deduced or calculated: Footfall patterns, the support formula, duration of support (i.e. limbs in contact with the substrate), duration of transport (limbs out of contact with the substrate) and the sequence and rhythm of limb action. Hildebrand (1966), Sukanov (1974) and Zug (1972) have devised schemes for determining the gait formula.

6.1.2 LATERAL BENDING

To facilitate the analysis of lateral bending during the locomotor cycle, 15 films were taken from above perpendicular to the axis of progression of the animals. Natural markings of the animal or specific dots painted on its skin were employed as points of reference during analysis. An unsuccessful attempt was made to use x-ray cinematography to record the movements of the vertebral column during locomotion. In these small skinks clear images of the skeletal parts could not be obtained.

6.1.3 SEQUENTIAL FRAMES

Enlargements of single frames were obtained in two ways:
(i) by tracing the projected images of particular frames;
(ii) by making photomicrographs of individual frames through
a Carl Zeiss compound microscope fitted with a Zeiss camera attachment which in turn is connected to a photoelectric exposure measuring device and a Leica M3 camera.

6.2 ELECTROMYOGRAPHY

An Acontias plumbeus was anaesthetized by covering the animal with crushed ice for about 5 minutes. The electrodes were prepared (from 316 stainless steel wire insulated with teflon and marketed by the Medwire Corporation) according to the technique described by Basmajian and Stecko (1962). The electrodes were implanted with the aid of a hyperdermic syringe in a locality where one would be fairly certain of striking a particular muscle mass. After the final series of electromyograms were recorded, the electrodes were left in position so that their exact location could be determined by dissection. After implantation the electrodes were soldered to a multiwire cable composed of teflon coated silver wires. This cable was attached to the animal by a strip of velcro. The wires of this cable was then connected to the preamplifier cables by a multipin connector. The preamplifier cable was linked to a Tektronix Model 26A2 with 4 differential amplifiers set at a frequency range of between 100 Hertz to 3 Kilohertz. The signal from the preamplifier was led to a Honeywell 117 amplifier. From here the signal was led to a T-connector with one arm linked to a Gould Brush 481 Chart Recorder and the other arm joined to a Honeywell Model 5600 Tape Recorder and Oscilloscope.
6.3 ANATOMICAL TECHNIQUES

For the anatomical aspects of the study the following techniques were employed:

6.3.1 X-ray photographs of around 180 specimens of skinks, mainly from the collection of the South African Museum (S.A.M.), were used to determine vertebral counts and to gain an overall picture of the postcranial osteology of those specimens not readily available. Johnson (1955) discusses the merits and limitations of this technique. See Table III.2 for a list of the specimens x-rayed.

6.3.2 Several cleared and stained whole preparations were made mainly according to the procedure outlined by Wassersug (1976). Appendix IA lists these specimens.

6.3.3 To facilitate close examination of isolated skeletal elements such as vertebrae and ribs, skeletons of Mabuya, Acontias and Scolotes were cleaned using the Antiformin technique as described by Mahoney (1962, p. 344).

6.3.4 Gross muscular anatomy was investigated by means of dissections under a stereomicroscope. The stain formulated by Bock and Shear (1972) facilitated this operation by staining individual muscle fibres.
6.3.5. Dissection was supplemented by microscopic study of serial sections of the following specimens:

(a) *A. melagris* - series of transverse sections ten microns thick of the anterior third of the body;

(b) *M. capensis* - (i) a complete series of sections of the entire trunk, 15 microns; (ii) a series of frontal sections 20 microns thick of the anterior half of the body; (iii) a series of sagittal sections 25 microns thick of the anterior half of the body;

(c) *R. sundevallii* - sections of the trunk and tail of a juvenile specimen. The anterior and posterior parts of the body were microtomised into transverse sections 15 microns thick, while frontal sections of 20 microns were prepared from the mid-trunk region;

(d) *S. bipes bipes* - 10 micron transverse sections of the anterior third of the body;

(e) *S. gronovii* - transverse sections 10 microns thick of the entire trunk, except for a small mid-trunk segment.

After skinning and partially eviscerating these specimens, they were decalcified in Ebner's solution, embedded in tissue wax (with a melting point of about 52°C), sectioned se-
rially and stained in Heidenhein's Azan stain (Humason, 1962, pp. 149-151).

These sections were utilized to determine details of muscle attachment and fibre orientation as well as to provide a rough estimate of the relative physiological cross-section of certain axial muscles. As the fibres of the axial muscles have a more or less longitudinal orientation, in transverse sections some are cut almost perpendicularly to their axes of extension. The ratio between the cross-sectional area of a particular muscle mass to the total cross-sectional area of the body was estimated by taking sequential photomicrographs of the serial sections, making enlarged prints, cutting out the printed area (i.e. the image of the transverse section of the body, or a particular muscle) and then determining its area with the aid of a planimeter. The percentage of the total cross-sectional area occupied by a particular muscle mass could then be calculated. A minimum of 10 photographs were used for the calculation of each ratio.
6.4 MORPHOMETRIC TECHNIQUES

The smaller external dimensions of the specimens, such as body diameter and limb length were determined with the aid of vernier calipers, while bigger dimensions, such as snout to vent length or tail length, were usually measured with a ruler or measuring tape. The individual vertebrae were measured through a dissecting microscope fitted with an ocular micrometer scale (100 divisions per cm.). Care was taken to minimize errors of parallax.
II. BODY PROPORTIONS

1. REGRESSION OF LIMBS

It seems useful first to explore some changes in the dimensions of the body associated with limb reduction, to summarize the pattern of appendicular degeneration and to define terms employed to categorize this phenomenon.

The overall pattern of limb regression is well established for skinks through the investigations of Förbringer (1869), Cope (1892b), Essex (1927), Sewertzoff (1931) and Stokely (1947); hence this aspect is summarized but briefly. Starting with a normal-limbed quadrupedal skink such as *M. capensis*, the initial stages of appendicular degeneration involve miniaturization of the appendages as seen in *Riodia sundevalli* and *Scelotes capensis*. The limbs remain pentadactyle but have become smaller relative to the trunk and are referred to here as "miniaturized limbs". The next phase involves loss of one or more of the distal digits of the relatively small limbs. *S. angolensis* and *S. caffer* illustrate this phase of degeneration. They have four small limbs but these are no longer pentadactyle as one or more digits have been lost. This shall be called the "tetrapodous-reduced" condition. In skinks the front limbs are lost before the hind ones, so that several species exist in which a pair of hindlimbs varying in the degree of reduction is present (e.g. *S. bipes sexlineatus, S.g. bipes, S. gronovii, S. brevipes*). The term "bipodous" is reserved for this two-limbed condition. Finally, after all
external traces of the hindlimbs have disappeared, the animal becomes limbless or apodous (e.g. all the Acontinae as well as S. arenicola and S. anguina).

Both normal limbs and miniaturized limbs are pentadactyle but they vary in relative size. In order to establish an empirical criterion for differentiating between these two types, the sum of the lengths of the limbs on the one side of the body was plotted against snout to vent length for a sample of 105 skinks (Fig. II.1 and Table II.1).

Although the sample of normal-limbed lizards is small (35), it includes at least one set of data points for each of the species of Mabuya catalogued by FitzSimons (1943). The regression line for the normal-limbed quadrupedal lizards is well separated from that of the specimens with miniaturized limbs (represented by specimens of R. sundevallii, S. capensis, S. mira, S. arnoldi as well as Chalcides ocellatus; Fig. II.1). In the normal-limbed group the sum of the lengths of two limbs on the one side of the body constitute on the average 65% of the snout to vent length. The corresponding figure for the miniaturized limbed forms is 34% (see Table II.1). A value of 50% which lies midway between these two averages, has arbitrarily been chosen as the dividing line between the two categories. A normal-limbed lizard is thus defined as one having four pentadactyle limbs, the cumulative lengths of which on the one side of the body constitute more than 50% of the snout to vent length of that animal. M. capensis clearly falls into this category. A lizard with miniaturized limbs
Fig. II.1 Scatter diagram in which the snout to vent length of the body is plotted against the sum of the lengths of the limbs on one side of the body. See Table II.1 for a summary of the data used.
<table>
<thead>
<tr>
<th>Group</th>
<th>Sample Size</th>
<th>Snout to Vent Length in mm.</th>
<th>Sum of Limb Lengths on one side in mm.</th>
<th>Correlation Coefficient</th>
<th>Limb Lengths % Snout to Vent Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal limbed</td>
<td>35</td>
<td>73.8</td>
<td>48.0</td>
<td>0.85203</td>
<td>65</td>
</tr>
<tr>
<td>Miniaturized limbed</td>
<td>21</td>
<td>80.8</td>
<td>27.5</td>
<td>0.73474</td>
<td>34</td>
</tr>
<tr>
<td>Tetrapodous reduced</td>
<td>28</td>
<td>71.6</td>
<td>15.5</td>
<td>0.51208</td>
<td>22</td>
</tr>
<tr>
<td>Bipodous</td>
<td>21</td>
<td>56.2</td>
<td>4.9</td>
<td>0.02490</td>
<td>9</td>
</tr>
</tbody>
</table>

Table II.1 Summary of data on which Fig.II.1 is based
has four pentadactyle limbs but the sum of their lengths on one side of the body constitutes less than 50% of the snout to vent length of the animal. *Riopa sundevallii* clearly belongs in this category.

It is also interesting to note that the correlation coefficient between the limb lengths and snout to vent lengths is quite high (around 0.85) in the normal-limbed lizards. This correlation drops as degeneration proceeds (Table II.1). This suggests that in the normal-limbed group selection operates co-jointly on limb and on snout to vent lengths. Such a condition is to be expected, as there are functional relationships among intergirdle span, the location of the centre of gravity and the size of the limbs required to lift the body clear of the substrate. As limbs undergo reduction this functional linkage is broken. Selection pressures favouring further reduction in limb size or a change in snout to vent length then operate independently.

Five categories of skinks are then recognized for descriptive purposes:

(a) Normal-limbed quadrupedal skinks with the cumulative lengths of their four pentadactyle limbs equal to or greater than the snout to vent length.

(b) Skinks with miniaturized limbs with the cumulative lengths of the four pentadactyle limbs less than or equal to the snout to vent length.

(c) Tetrapodous-reduced skinks with four limbs, each with
Fig. II.2A & B. An anterior view of the left forelimb of *Mabuya capensis* (A) and *Riopa sundevallii* (B).
Fig. II. 2c&d. Camera lucida sketch of a fully stretched hind limb of *Mabuya capensis* (C) and *Riopa sundevallii* (D)
FIG. II.2E. A HINDLIMB OF FOUR BIPODOUS AND ONE EXTERNALLY LIMBLESS (arenicola) SPECIES OF Scelotes IN LATERAL VIEW.
one or more digits missing.

(d) Bipodous skinks without front limbs but with two vestigial hindlimbs.

(e) Limbless skinks.

Limbs of specimens belonging to categories a, b and d are illustrated in Figures II.2(A to E). The diminishing size of the limbs relative to the snout-vent length is illustrated for the species considered in detail in graph, Fig. II.3A. In addition changes in the intra-limb proportions are also summarized. As degeneration proceeds there is a tendency for the distal portions of a limb to occupy a relatively smaller percentage of its total length (Fig. II.3B).

The manus of *M. capensis* (Fig. II.2A) has a phalangeal formula of $2_1, 3_1, 4_1, 5_1, 3$ which agrees with that of normal-limbed skinks, such as *Sphenomorphus quoyii* (King, 1964), *Euamenes schneideri* (Sewertzoff, 1931) and *M. quinquetaeniata margaritifer* (Tiedemann & Tiedemann, 1975; El-Toubi, 1938) does, on the other hand, report the presence of an extra phalanx in each fifth finger of *Scincus scincus*. In *R. sundevalli* this formula is $2_1, 3_1, 4_1, 4_1, 3_1$ (Fig. II.2C). Although the limb of this species is much reduced in overall size compared with *M. capensis* (Fig. II.3A), it has lost, in addition, a single phalanx of the fourth finger. In the tetrapodous-reduced limbed *S. angolensis* the phalangeal formula for the minute anterior limbs is $0_0, 2_0, 2_0, 2_0, 0_0$. Thus, these limbs have even fewer phalanges than do those of *Chalcides sepoides*, *Ophiomorus tridactylus* and *Seps tridactylus* (Sewertzoff, 1931).
FIG. 11.3A: THE LENGTH OF THE PECTORAL LIMB (DOTS) AND THE PELVIC LIMB (TRANSVERSE LINES) AS A PERCENTAGE OF THE SNOOT TO VENT LENGTH FOR SKINKS VARYING IN THE DEGREE OF LIMB REDUCTION.
FIG. 11.3B. VARIATION IN THE LENGTH OF THE STYLOPODIUM (BACK), THE ZEUPOPODIUM (CROSS-HATCHED) AND THE ACROPODIUM (DOTTED) EXPRESSED AS A PERCENTAGE OF THE TOTAL LIMB LENGTH AND MEASURED IN CLEARED, ALIZARINE-STAINED SPECIMENS.
The pes of *M. capensis* has a phalangeal formula of 2, 3, 4, 5, 4 (Fig. II.2C). Again this formula is typical for the normal-limbed skinks described by Sewertzoff (1931), King (1964) and Tiedemann and Tiedemann (1975). In the miniaturized limbed *Riopa sundevallii* the formula is 2, 3, 4, 5, 3 (Fig. II.2D).

Once more, much reduction in size is accompanied by the loss of a single element from the fifth toe. The formula for *S. angolensis* is 0, 2, 3, 3, 0. The phalangeal formulae for the bipodous species of *Scelotes* in order of degeneration are:

- *bipes sexlineatus*: 0, 0, 2, 4, 0
- *bipes bipes*: 0, 0, 2, 3, 0
- *gronovii*: 0, 0, 0, 2, 0
- *brevipes*: 0, 0, 0, 1, 0 (see Fig. II.2E).

These phalangeal formulae support the thesis of Sewertzoff (1931) that an organ undergoing degeneration is first miniaturized and then there follows a progressive subtraction of the terminal stages of ontogenetic development. Thus the sequence of degeneration appears to be the reverse of the sequence whereby the normal adult structure is formed.

It is interesting to note that *S. brevipes*, whose tiny limb rudiment comprises around 2% of the total snout to vent length, still retains cartilaginous vestiges of the tibia and fibula as well as a pes consisting of two cartilaginous elements (probably a tarsal element and the fourth metatarsal - Fig. II.2E). Even more interesting is the condition in *S. areni*
cola, where, although all external traces of limbs are lost, tiny vestiges of hindlimbs are concealed beneath the skin (Fig. II.2E).

Even in normal-limbed skinks the forelimbs are smaller than the hind ones. Furthermore, the forelegs of skinks degenerate more rapidly than their hindlegs. Consequently, in all bipodous forms the hindlimbs persist though the front ones have disappeared completely. This trend is shared by all reduced-limbed scincomorph lizards. In contrast, among the Teiidae, and some Amphisbaenia, the anterior limbs have a tendency to persist longer (Presch, 1975; Gans, 1975).

As the limbs atrophy, the dimensions of the trunk also change.

2. ELONGATION

Gans (1975) concludes that bodily elongation is the only common denominator associated with limb-loss or limb-reduction among lower tetrapods. By elongation is meant that the animal is long in proportion to its breadth or transverse diameter. Graph II.4, in which snout to caudal tip length is plotted against diameter for a series of 324 skinks, confirms this conclusion. Although the diameters and total snout to tail tip lengths of the animals range widely (Table II.2), for any given diameter the reduced limbed forms are longer.

Though the regression lines for the normal and miniaturized limbed specimens overlap, the regression line for the bipodous forms lies between that for the limbed and the limbless
Fig. II.4. Scatter diagram of maximum body diameter against snout to caudal tip length in a series of skinks belonging to diverse genera. See Table II.2 for summary of data. A regression line is included for each of the five categories:

A Normal limbed skinks (△)
B Skinks with miniaturized limbs (▴)
C Skinks with tetrapodous reduced limbs (+)
D Bipodous skinks (x)
E Limbless skinks (○)
<table>
<thead>
<tr>
<th>Group</th>
<th>Sample Size</th>
<th>Maximum Diameter in mm. mean</th>
<th>Maximum Diameter in mm. standard deviation</th>
<th>Total Length mean</th>
<th>Total Length standard deviation</th>
<th>Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal limbed</td>
<td>87</td>
<td>12.5</td>
<td>4.0</td>
<td>163.9</td>
<td>44.2</td>
<td>0.66289</td>
</tr>
<tr>
<td>Miniaturized limbed</td>
<td>34</td>
<td>11.4</td>
<td>4.1</td>
<td>153.5</td>
<td>39.5</td>
<td>0.81855</td>
</tr>
<tr>
<td>Tetrapodous reduced</td>
<td>101</td>
<td>7.4</td>
<td>3.0</td>
<td>141.7</td>
<td>48.8</td>
<td>0.73623</td>
</tr>
<tr>
<td>Bipodous</td>
<td>28</td>
<td>4.3</td>
<td>1.0</td>
<td>118.0</td>
<td>25.3</td>
<td>0.72631</td>
</tr>
<tr>
<td>Apodous</td>
<td>74</td>
<td>6.3</td>
<td>2.4</td>
<td>166.6</td>
<td>60.5</td>
<td>0.85639</td>
</tr>
</tbody>
</table>

Table II.2
Fig. II.5. Scatter diagram of maximum body diameter against snout to vent length for a series of skinks belonging to diverse genera. Symbols and regression lines as given in Fig. II.4. See Table II.3 for summary of data.
<table>
<thead>
<tr>
<th>Group</th>
<th>Sample Size</th>
<th>Diameter of Trunk in mm.</th>
<th>Snout to Vent Length in mm.</th>
<th>Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mean</td>
<td>standard deviation</td>
<td>mean</td>
</tr>
<tr>
<td>Normal limbed</td>
<td>99</td>
<td>12.7</td>
<td>3.9</td>
<td>69.7</td>
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<tr>
<td>Miniaturized limbed</td>
<td>42</td>
<td>11.4</td>
<td>4.0</td>
<td>80.0</td>
</tr>
<tr>
<td>Tetrapodous reduced</td>
<td>123</td>
<td>7.3</td>
<td>2.9</td>
<td>77.6</td>
</tr>
<tr>
<td>Bipodous</td>
<td>38</td>
<td>4.3</td>
<td>1.0</td>
<td>67.8</td>
</tr>
<tr>
<td>Apodous</td>
<td>77</td>
<td>6.2</td>
<td>2.4</td>
<td>128.1</td>
</tr>
</tbody>
</table>

Table II.3
species. After accepting that elongation is associated with limb reduction and loss, the question arises how is elongation achieved?

Elongation could occur in three ways:

(a) The entire body (both trunk and tail) may become proportionally longer.

(b) The snout to vent distance may increase relatively more.

(c) The tail length may increase relatively more.

Which of these three patterns occurs in skinks?

First let us compare the normal-limbed and the limbless extremes. In the majority of skinks with normal limbs (including the genera Carlia, Ctenotus, Leioplisma, Sphenomorphus and a sample of some 20 species of Mabuya) the tail length is much greater than the snout-vent length. However, in some quadrupedal skinks the tail length has been drastically reduced (see Fig. II.7). In specialized limbless skinks, on the other hand, the tail is usually short and has a diameter almost equal to or only slightly less than that of the trunk. Broadley (1968) reports that the tail of 545 specimens, comprising the eight species of the genus Typhlosaurus, ranges from 11.9% to 20.5% of the total length. Seven species of Acontias (763 specimens examined) had a tail length ranging from 11.1% to 21.6% of the total length (Broadley, 1969). The tail of Feylinia "is relatively short, comprising approximately one-third of the total length" (Greer, 1970a). The following data were obtained from four specimens lodged in
Comparison of the limbed and limbless extremes leads to the following conclusions: Most normal limbed skinks have long tapering tails which average well over 50% of the total length. The tail of specialized limbless skinks is invariably short, less than 25% of total length in Acontinae and less than 35% in Feylininae.

As normal-limbed skinks usually have long, slender, tapering tails while the specialized limbless skinks have much shorter and stouter tails, two hypotheses are implied:

(a) The elongation associated with the reduction of limbs among skinks involves mainly an increase of the snout to vent distance.

(b) As snout to vent distance increases the tail becomes shorter and stouter.

These two generalizations definitely hold true for the Acontinae and Feylininae. Do these two trends also apply to other lines of scincids manifesting limb-reduction? To answer this

<table>
<thead>
<tr>
<th>Species</th>
<th>Museum Number</th>
<th>A= Snout to Vent Length</th>
<th>B= Tail Length</th>
<th>A+B%</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Feylinia c. currui</em></td>
<td>F.M.N.H. 26336</td>
<td>240</td>
<td>110</td>
<td>69</td>
</tr>
<tr>
<td><em>Feylinia c. currui</em></td>
<td>F.M.N.H. 3991</td>
<td>94</td>
<td>36</td>
<td>72</td>
</tr>
<tr>
<td><em>Feylinia polylepis</em></td>
<td>F.M.N.H. 120967</td>
<td>143</td>
<td>43</td>
<td>77</td>
</tr>
<tr>
<td><em>Feylinia polylepis</em></td>
<td>F.M.N.H. 120968</td>
<td>150</td>
<td>62</td>
<td>71</td>
</tr>
</tbody>
</table>
Fig. II.6. Snout to vent length as a percentage of the snout to caudal tip length. The dot indicates the average % for the number of specimens indicated in brackets. The straight line indicates the standard deviation.
question two approaches were followed. Firstly for a hetero-
genous sample of 339 reduced and normal-limbed skinks, the
snout to vent length was plotted against maximum body diame-
ter (Graph II,5). Then secondly, species belonging to the
same genus and which show varying degrees of limb reduction
are compared (Graph II.7). Graph II.5 (see also Table II.3)
is based on slightly more data points than Graph II.4 (see
also Table II.2), because specimens showing signs of caudal
autotomy were disregarded in the latter. Comparison of these
two graphs shows that the regression lines for the five cate-
gories of limb reduction are much more sharply separated in
Graph II.5. Snout to vent elongation apparently accompanies
limb reduction, and is more important than caudal elongation.
Further confirmation for this conclusion is reflected in a
plot of the ratio of snout-vent to total length for the five
categories of limb reduction (Fig. II.6). Limb reduction is,
accompanied by an elongation of the trunk which thus occupies
a greater percentage of the total body length. As this in-
crease is modest for the intermediate categories (Fig. II.6),
changes in body proportions of species belonging to the same
genus and showing varying degrees of limb reduction were also
examined (Fig. II.7). Figure II.7 related intra-generic va-
riations in snout to vent length (as a percentage of the to-
tal body length) to the degree of limb reduction. The value
for normal-limbed skinks are given at the top of the graph.
Note that the animals fall into a cluster with long tails
distinct from a second group with much reduced tails. Limb
reduction most probably occurred independently in the genera
Chalcides, Lerista, Scelotes and Ophiomorus; yet in each of these lines greater limb-degeneration is associated with an elongation of the snout to vent region. The limbless Acontinae show the most extreme elongation of the trunk.

In brief, both approaches, that of looking at a larger heterogeneous sample of skinks and that of looking at smaller intra-generic samples lead to the conclusions that elongation accompanies limb reduction and that in skinks such elongation is mainly confined to the trunk. Skinks thus differ markedly from some other reduced-limbed lizards, such as cordylids and species of the genus, Tetradactylus, in which limb reduction is accompanied by an enormous elongation of the tail. Further consideration of the functional meaning of such differences is deferred to the discussion (Chapter VI.6.5).

If elongation were confined mainly to the trunk, one would expect the trunk elongation ratio (snout to vent length over maximum diameter) to increase as limb degeneration proceeds. This is indeed the case (Fig. II.8 and Table II.4). The standard deviation of the ratio is modest for most of the categories of limb-reduction, except for the limbless group for which it is very large.

To determine whether an increase in the trunk elongation index is also accompanied by a reduction in tail size as reflected by a high relative snout-vent length, these two indices were plotted (Fig. II.9). The regression lines for the five categories of limb reduction as well as the low correlation
NORMAL LIMBED SKINKS

---

**Chalcides**

- C. ocellatus (5), C. polylepis (1)
- C. sepoide (7), C. guntheri (2)
- C. tridactylus (1), C. de listi (3)
- C. mauritanicus (1)

**Lerista**

- L. distinguenda (2), L. timida (1)
- L. bougainvilli (1), L. bipes (2)

**Scelotes**

- S. arnoldi (3), S. astrolabi (2), S. capensis (2)
- S. eqellii (3), S. limpopoensis (1), S. mira (2)
- S. alberti (2), S. angolensis (4)
- S. caffer (5)

- S. bipes (4), S. gronovii (5), S. brevipes (5)

- S. anguina (14), S. arenicola (4)
- S. bicolor (1), S. inornatus (2)

**Ophiomorus**

- O. tridactylus (2)

- O. puntatissimus (3)

---

**Fig. II.7.** Snout to vent length as a percentage of the total length for diverse normal limbed skinks (105 specimens; ••••••••••), and for four genera varying in the degree of limb reduction; species with miniaturized limbs (----), with tetrapodous reduced limbs (-----), bipodous species (———), limbless species (———). The average and range are reflected.
coefficient (Table II.4) suggest that there is no simple relationship between these two indices in this heterogenous sample of skinks. Normal-limbed skinks include a specialized short-tailed group ($A_1$) and long-tailed ones ($A_2$) which are in the majority. Both groups share a low trunk elongation ratio. The limbless skinks also fall into two classes: those with short tails (to the right of regression line E) and those with moderately long tails (to the left of regression line E).

The suggested pattern of changes in body proportion associated with limb regression follows. The ancestral animal probably had:

(a) a low trunk elongation ratio (Evidence: this is a common trait shared by the normal-limbed skinks, Figs. II.8 and II.9);

(b) a long tapering tail (i.e. belonged to group $A_1$ in Fig. II.9 rather than $A_2$) because the reduced-limbed skinks all have moderately long tails (almost 50% of total body length - Fig. II.6).

During the initial stages of limb regression:

(a) elongation is confined mainly to the snout to vent length (Figs. II.6, II.7 and II.8);

(b) the length of the tail probably remains more of less static, i.e.

(i) the tail is not drastically elongated because it is usually slightly less than 50% of the total
<table>
<thead>
<tr>
<th>Categories of Limb Reduction</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apodous</td>
<td>(74)</td>
</tr>
<tr>
<td>Bipodous</td>
<td>(28)</td>
</tr>
<tr>
<td>Tetrapodous-reduced</td>
<td>(101)</td>
</tr>
<tr>
<td>Miniaturized limbed</td>
<td>(34)</td>
</tr>
<tr>
<td>Normal limbed</td>
<td>(87)</td>
</tr>
</tbody>
</table>

Fig. II.8. The snout to vent length over maximum diameter plotted against the 5 categories of limb reduction. The number in brackets indicated the sample size. The dot indicates the average value of the elongation index while the lines indicate the standard deviation.
length in the intermediate forms (Figs. II.6, II. 7 and II.8);

(ii) the tail is not drastically shortened for there exists a cluster of limbless forms to the left of regression line E (Fig. II.9);

(iii) the tail is bulky and of only slightly less diameter than the trunk.

Finally, further elongation of the trunk accompanied by shortening of the tail could account for the origin of Acontinae and Feylinae clustered to the left of regression line E in Fig. II.9. The functional significance of these changes is discussed below (Chapter VI).
Fig. II.9  Two ratios are plotted against each other for a series of diverse scincid genera.

See Tab.II.4 (p.56) for a summary of the data.
<table>
<thead>
<tr>
<th>Group</th>
<th>Sample Size</th>
<th>Snout to Vent Length % Total Length</th>
<th>Snout to Vent Length Maximum diameter</th>
<th>Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mean</td>
<td>standard deviation</td>
<td>mean</td>
</tr>
<tr>
<td>Normal limbed</td>
<td>87</td>
<td>42.6</td>
<td>9.9</td>
<td>5.6</td>
</tr>
<tr>
<td>Miniaturized limbed</td>
<td>34</td>
<td>51.6</td>
<td>5.5</td>
<td>7.3</td>
</tr>
<tr>
<td>Tetrapodous reduced</td>
<td>101</td>
<td>55.2</td>
<td>6.6</td>
<td>11.0</td>
</tr>
<tr>
<td>Bipodous</td>
<td>28</td>
<td>55.8</td>
<td>6.3</td>
<td>15.3</td>
</tr>
<tr>
<td>Apodous</td>
<td>74</td>
<td>75.2</td>
<td>13.5</td>
<td>20.7</td>
</tr>
</tbody>
</table>

Table II.4
III. LOCOMOTOR APPARATUS: OSTEOLOGY

1. GENERAL

The postcranial skeleton comprises the vertebral column, ribs, parasternalia, girdles and limbs. All play a direct or indirect role in the process of locomotion. The main objectives of this section are:

(a) to provide a descriptive survey of the postcranial skeletons of members of a scincid regression series;
(b) to look for trends and tendencies associated with limb regression.

Although partially or completely limbless skinks employ their heads for burrowing, craniological adaptations will not be considered here (see Leonard, 1978 for a review of this aspect of the problem). Special attention is devoted to the body axis which is neglected or ignored by previous investigators.

2. VERTEBRAL COLUMN AND RIBS

2.1 GENERAL

Hoffstetter and Gasc (1969) provide a comprehensive survey of descriptive papers dealing with the structure of lacertilian vertebrae and ribs together with an extensive bibliography. The vertebral column of skinks has received repeated attention since the report of Müller (1831) which illustrates and briefly describes a few trunk vertebrae of Acontias meloagris.
FIG. III.1 A PHOTOGRAPH OF AN ALIZARINE STAINED SPECIMEN OF AN ADULT M. capensis ILLUSTRATING THE TRUNK VERTEBRAE AND RIBS IN DORSAL VIEW (A); AND A CONTACT PRINT OF A JUVENILE SPECIMEN MADE FROM AN X-RAY NEGATIVE.
Siebenrock (1895) provides a comprehensive, comparative account of the axial skeleton of about thirty species of skinks, gerrhosaurids and anguids. Sewertzoff (1931) comments on the increase in vertebral number among skinks with reduced limbs. El-Toubi (1938) and King (1964) describe the axial skeletons of *Scincus scincus* and *Lygosoma quoyii* respectively. Stokely (1947) gives vertebral counts for several skinks. Camp (1923) refers to the description of the skeleton of *Voeltzkowia mira* by Rabanus (1911).

This chapter is primarily concerned with differences in the structure of ribs and vertebrae of skinks exhibiting limb regression. To highlight these changes, the two extremes, namely the normal limbed *M. capensis* and the limbless *A. meleagris* will be described first. The conditions in the reduced limbed species of the genera *Riopa* and *Soelotes* will then be investigated to ascertain whether morphoclines can be established between the two extremes.

2.2 **MABUYA CAPENSIS** (Fig. III.1A & B)

2.2.1 **GENERAL**

The vertebral column of *Mabuya* consists of 26 presacral vertebrae, two fused sacral elements and 40 to 50 caudal vertebrae.

The vertebral column of *Mabuya*, like that of the limbed lizards in general, can be divided into cervical, dorsal, sacral and caudal regions (Romer, 1956). In mammals the thoracic (rib-bearing) region is differentiated from the ribless lumbar
Fig. III.2  A lateral view of the atlas and axis of *Mabuya capensis* (A) and *Acontias meleagris* (C). Also an anterior view of the atlas of *M. capensis* (B) and *A. meleagris* (D).
region which lies anterior to the sacrum. In Mabuya there is no ribless region anterior to the sacrum, though the last four presacral ribs are relatively shorter.

2.2.2 CERVICAL REGION (Figs. III.1, III.21)

Those vertebrae in the neck region which either lack ribs or have ribs that fail to reach the sternum are classified as cervical vertebrae (Hoffstetter and Gasc, 1969). In Mabuya, as in all quadrupedal scincomorph lizards, there are eight cervical vertebrae (Hoffstetter and Gasc, 1969).

2.2.2.1 Atlas (Figs. III.2A & B)

The nearly ring-shaped atlas is composed of a ventral intercentrum, and two lateral neurapophyses. Distinct sutures indicate the joints between the ventral margins of the neurapophyses and the intercentrum. The latter bears a short median downwardly directed spine on its mid-ventral surface (hypapophyses, Evans, 1939). The base of each neurapophysis is stout, while its dorsal portion flattens into a thin lamina of bone which arches over the spinal cord but fails to reach that of the opposite side. Thus, there is no neural spine; instead, a narrow gap separates the upper tips of the two neural arch laminae. The widened basal portion bears a lateral ridge which appears to be serially homologous with the synapophysis found on the more posterior rib-bearing vertebrae. This ridge provides an attachment area for cervical muscles. The ventrocranial region of the atlas forms a concave surface which articulates with the reniform occipital
Fig. III.3 The third postcranial vertebra of *M. capensis* (A) and *A. meleagris* in lateral view.
condyle of the skull. Its caudoventral region is also concave to accommodate an diarthrosis with the odontoid process of the axis. Prezygapophyses are absent, while the vestigial postzygapophyses are non-articulating.

2.2.2.2 Axis (Figs. III.2A & B)
The axis is the largest vertebra in the cervical series (see Graph III.13). On its cranioventral aspect there is a prominent odontoid process onto which the base of the atlas rotates while the tip of this process is in syndesmosis with the mediodorsal, concave surface of the occipital condyle. The neurapophyses meet mediodorsally to form a wide triangular spinal crest, the apex of which is directed anteriorly. A pair of atrophied prezygapophyses projects slightly beyond the anterior surface of the neurapophyses, while the prominent postzygapophyses are functional. Two median hypapophyses project downwards from the ventral surface of the axis, and a prominent lateral process extends from the anterior ventrocranial surface of the neurapophysis. The posterior axial hypapophysis is the largest in the cervical series (Fig. III.13).

2.2.2.3 Typical Cervical Vertebra (Fig. III.3)
The first three cervical vertebrae do not bear ribs; the next five do. The ribs are short anteriorly and become progressively longer posteriorly along the column so that the ribs borne on the 8th vertebra almost reach the sternum. The synapophyses articulate with the ribs and are more promi-
Fig. III.4. Mid-trunk vertebrae of *Acontias meleagris* (A & B) and *Mabuya capensis* (C & D), in ventral view (B & D) and in dorsal view (A & C).
ment in the neck region than in the rest of the trunk and provide attachment areas for the massive cervical musculature. The first three ribless vertebrae bear prominent projecting processes, probably serial homologues of the synapophyses, to which muscles attach. All trunk vertebrae posterior to the atlas and axis are typically procoelous and have functional prezygapophyses as well as postzygapophyses.

2.2.3 DORSAL VERTEBRAE (Figs. III.4 & III.5)

The cervical region is followed by eighteen dorsal vertebrae which resemble each other closely although they may vary in size. Typical examples of trunk vertebrae are illustrated in dorsal (Fig. III.4C), ventral (Fig. III.4D), anterior (Fig. III.5A), posterior (Fig. III.5B) and lateral (Fig. III.5C) views.

2.2.4 SACRUM (Fig. III.6)

The sacrum consists of two vertebrae modified to articulate with the ilium. Each bears a pair of strong pleurapophysis (i.e. transverse processes formed by the precocious fusion of sacral ribs to their vertebrae). The two sacral vertebrae are fused at the zygapophyses, neural arches, centra and the tips of the pleurapophyses. On each side a large foramen sacrale separates adjacent pleurapophyses. A diarthrosis separates each ilium from a sacral pleurapophysis (Fig. III.27C).

2.2.5 CAUDAL VERTEBRAE (Fig. III.7)

*Mabuya capensis* has 40 to 50 caudal vertebrae that gradually diminish in size inside the tapering tail (Fig. III.1B). Caudal
Fig. III.5. Trunk vertebrae of *Mabuya capensis* (A, B & C) and *Acontias meleagris* (D, E & F) in anterior view (A & D), in posterior view (E & F) and in lateral view (C & F).
vertebrae differ from dorsal vertebrae in several respects. They lack free ribs, but each side of a vertebra bears a long transverse process. According to Hoffstetter and Gasc (1969) these processes are essentially of vertebral origin. All caudal vertebrae, except for the proximal three and some of the most distal vertebrae, bear vertebral chevrons that are Y-shaped and composed of two ventromedially fused haemapophyses. All vertebral processes become smaller towards the tip of the tail. The five most anterior pygal vertebrae lack autotomy splits. Each post-pygal vertebra has an irregular fracture plane which passes anterior to the base of the transverse processes.

2.2.6 INTERCENTRAL JOINTS

Longitudinal sections through vertebral column of *Mabuya capensis* document that the intervertebral joints cannot be described as synovial joints because they lack synovial cavities. Instead, a thin pad of connective tissue links successive vertebrae thus forming an amphiarthrodial joint that conforms to the shape of the condyle and cotyle. Although it is often suggested that the intercentral joints of lizards are diarthroses (Moffat, 1973; Waters, 1969), *Lacerta vivipara* also lacks synovial joints (Winchester and Bellairs, 1977).

2.2.7 RIBS (Figs. III.1, III.21)

The first three cervical vertebrae of *Mabuya* lack ribs, the next three bear short stout ribs that are distally widened into forks of calcified cartilage (Fig. III.21), and the se-
FIG. III.6  THE SACRUM OF MABUYA CAPENSIS IN DORSAL VIEW (A) AND IN VENTRAL VIEW (B). THE PELVIC GIRLDE OF ACONTIAS MELEAGRIS: THE RIGHT ONE IN MEDIAL VIEW (C) AND THE LEFT ONE IN LATERAL VIEW (D). NOTE THE ASYMMETRY.
venth and eighth cervical ribs are long and slender but just fail to contact the sternum. The next three pairs of ribs are joined to the sternum by means of rods of calcified cartilage (Fig. III.21). These sternal ribs are followed by two pairs of ribs joined to the mesosternum. A single pair of ribs unite with a complete parasternal chevron. The remaining twelve pairs do not extend into the ventral body wall. The next eight pairs of ribs, after supporting the dorsal and lateral aspects of the body wall, terminate in claws of calcified cartilage while the posterior four pairs of ribs preceding the sacrum shorten abruptly terminating in the dorsal body wall (Fig. III.1).

Each rib is unicipital or holocephalous (Hoffstetter and Gasc, 1969) and has an ovate head with a shallow depression serving as an articular surface. The head articulates with a synapophysis of a vertebra by means of a synovial joint. The shape and degree of lateral extension of the synapophyses vary along the length of the vertebral column. In the cervical region these processes are longer blades of bone (Fig. III.13), flattened in a transverse plane; along the trunk they are shorter and almost hemispherical (Fig. III.5). The sternal ribs of *Mabuya* may be divided into a bony costovertebral segment, a cartilaginous intercostal segment, and finally, a sternocostal segment linked to the sternum or mesosternum. The intercostal segments of the first pair of poststernal ribs are fused with a parasternal chevron. The intercostal cartilages of the more posterior ribs terminate in the lateral ventral abdominal wall as hook-like claws of calcified cartilage.
Fig. III.7. Caudal vertebrae of *Mabuya capensis* in lateral view (A) and a caudal vertebra of *Acontias meleagris* in dorsal view (B).
The costovertebral segments support the body wall dorsally and laterally in most of the trunk region. This segment is, however, shorter in the presternal ribs and the four ribs preceding the sacrum.

2.3 ACONTIAS MELEAGRIS

2.3.1 GENERAL

In contrast with the normal limbed Mabuya capensis, Acontias meleagris is totally limbless though vestiges of a pectoral and a pelvic girdle still remain (Figs. III.26 & III.6C). Its vertebral column is composed of around 78 precaudal vertebrae and 20 to 25 caudal vertebrae (Table III.2). In contrast to the condition shown by Mabuya, Acontias shows a marked increase in the number of precaudal vertebrae and an almost equally striking reduction in the number of caudal vertebrae.

The vertebral column of Acontias manifests less regional differentiation than does that of Mabuya. The vertebrae and ribs are more uniform, consequently cervical and sacral subdivisions of the vertebral column are no longer unambiguously demarcated.

The caudal region can be distinguished from a precaudal one, by the presence of fused transverse processes instead of free ribs. All the precaudal vertebrae, with the exception of the atlas and the axis, bear a pair of free ribs. Occasionally, even the axis bears a minute pair of ribs.
FIG. 111,8 A MID-TRUNK LEFT RIB (IN ANTERIOR VIEW) OF Mabuya capensis (A), Riopa sundevallii (B); Scelotus gronovii (C); AND Acontias meleagris (D). NOTE THAT IN THE PARTIALLY OR COMPLETELY LIMBLESS SPECIES THE RIBS ARE THICKER RELATIVE TO THEIR LENGTH.
There is no direct contact between any of the ribs and the supposed vestige of the sternum. Consequently, the posterior limits of the cervical region cannot be unequivocally delimited. The first 10 vertebrae bear hypapophyses. The atlas, axis and cervical vertebrae resemble closely those of *Mabuya* and are therefore illustrated without repeating a description (Figs. III.2, III.3, III.4 & III.5).

The sacral region is no longer distinctly marked off from the rest of the vertebral column. The last two vertebrae of the precaudal series are not fused nor do they bear pleurapophyses; instead they bear free ribs which are only slightly shorter than those of the preceding vertebrae (Figs. III.6C & D). The sacral region often manifests asymmetry. In the specimen illustrated, for example, the vestigial pelvic girdle is syndesmotically joined to a single rib on the one side and to two ribs on the other (Figs. III.6C & D). No sharp differences exist between the two "sacral" vertebrae which grade into the "presacral" series. In brief, subdivision of the vertebral column is based essentially on the position of the girdles. When the girdles are regressed they loose their direct linkage to the axial skeleton and it becomes difficult to delimit the cervical and sacral subdivisions on classical criteria. Other proposed criteria show so much interspecific variation that they cannot be applied consistently (Hoffstetter and Gasc, 1969).

The midtrunk vertebrae of *Acontias* (Figs. III.4A & B and also III.5D, E, F) are similar in basic structure to the trunk ver-
FIG. III.9. CONTACT PRINT OF AN X-RAY OF *A. meleagris* TO ILLUSTRATE THE VERTEBRAL COLUMN AND RIBS.
tebrae of Mabuya (Figs. III.4C & D and also III.5A, B, C). There are, however, marked differences in the proportions of the different parts. These differences are briefly mentioned here, but will then be subjected to a morphometric analysis for all the species investigated. In Acontias the zygapophyses are larger and extend outwards further than in Mabuya; the neural spines appear to be shorter; and the central length appears to be relatively less (Figs. III.4 & III.5).

2.3.2 CAUDAL VERTEBRAE (Fig. III.7B)

The tail of Acontias meleagris is composed of around 21 vertebrae (see Table III.2) which bear large tapering, posterolaterally directed transverse processes (Fig. III.7B). The latter are largest in the anteriormost tail vertebrae and become progressively smaller in a posterior direction. The Y-shaped haemapophyses are located intervertebrally starting from between the third and fourth caudal vertebrae. From the 9th to 15th tail vertebrae distinct autotomy fracture gaps are present in the neural arches and the base of the transverse processes. The zygapophyses of the first eleven caudal vertebrae are in articular contact, while the vestigial zygapophyses in the last ten vertebrae are separated by a gap.

2.3.3 RIBS (Figs. III.9, III.6 & III.8)

All the precaudal vertebrae with the exception of the atlas and usually the axis, bear free ribs. Hence, 76 to 77 pairs of movable ribs are present in A. meleagris. In some specimens (5 out of 9 alizarine preparations) of Acontias meleagris
even the axis carries a pair of small rib-like structures that lie in series with the rest of the ribs, but do not contact the synapophyses of the second vertebra directly. The ribs borne by the third, fourth and fifth vertebrae are shorter than the rest but become progressively longer as one passes in a posterior direction - consequently the last ribs of the series are only slightly shorter than the ribs borne by the 6th vertebra.

The last two pairs of free ribs found in the region of the vestigial pelvic girdle are also relatively shorter than the ones preceding it (Fig. III.6). Thus, the anteriormost three or four pairs of ribs and the last two pairs of ribs are slightly shorter than the rest. All the remaining ribs are similar in size and structure but may be divided into ribs with complete parasternal chevrons and ribs that terminate freely in the ventrolateral margin of the trunk. The eighth or ninth vertebra normally bears the first ribs that attach to a complete parasternal chevron, while last chevron articulates with the thirty-fifth to thirty-eighth vertebra. The starting and terminating points of contact with the parasternalia differ among specimens of Acontias meleagris. In addition, incomplete portions of parasternalia lie in front of the first and behind the last complete parasternal chevrons.

Thus, on the basis of their relationship to the parasternalia the ribs may be divided into

(a) preparasternal ribs consisting of 6-8 pairs located in front of the first complete parasternal chevron (the
first 3 or 4 pairs are short but become progressively longer and reach the normal length well before the end of the series);

(b) the parasternal ribs which contact a variable number of complete parasternal chevrons (usually 27 to 31); and

(c) the postparasternal ribs which terminate in the ventrolateral margins of the body wall, excepting for the shortened last two pairs.

Each parasternal rib consists of a proximal bony vertebrocostal portion (which follows the curve of the body wall), connected to a cartilaginous intermediate segment that curves sharply forwards and inwards in the ventral wall of the body to join with a parasternal chevron composed of calcified cartilage (Fig. III.26). In the pre- and postparasternal ribs the costovertebral segment bears, at its distal end, a short intermediate segment which terminates in the ventrolateral margin of the body wall as a hook-like claw of cartilage.

The ribs follow the curve of the body and extend backwards and downwards from their articulations with the vertebrae. Proximally each rib bears a cup-like holocephalous head which forms a synovial joint with a synapophysis of a vertebra (Hoffstetter and Gasc, 1969). Each rib of Acontias bears two prominent processes, the posterodorsally directed pseudotuberculum (Hoffstetter and Gasc, 1969) and a smaller anterolaterally directed one (Fig. III.8).
FIG. III,10. A DORSAL VIEW OF THE VERTEBRAL COLUMN OF *Riopa sundevallii*. A PHOTOGRAPH OF AN ALIZARINE PREPARATION FROM WHICH THE LIMBS AND GIRDLES HAVE BEEN REMOVED.
2.4 RIOPA SUNDEVALLII

The vertebral column of *R. sundevallii* is composed of eight cervical vertebrae, 29 dorsal and two fused sacral vertebrae and more than 27 caudal vertebrae. The last number cannot be given more precisely, since the eight x-rayed and two alizarine stained specimens examined all showed signs of caudal autotomy. The first six cervical vertebrae each bear a single ventral hypapophysis, excepting for the axis which bears two. The haemapophyses start between the second and third caudal vertebrae, while the first autotomy fracture plane is located in the fourth or fifth vertebrae.

The main features of the ribs may be summarized as follows:

<table>
<thead>
<tr>
<th>Position of Vertebrae</th>
<th>Nature of Ribs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 - 3</td>
<td>None present.</td>
</tr>
<tr>
<td>4 - 6</td>
<td>Short ribs terminate in forked cartilaginous processes.</td>
</tr>
<tr>
<td>7 - 8</td>
<td>Long pre sternal ribs.</td>
</tr>
<tr>
<td>9 - 11</td>
<td>Sternal ribs joined to the sternum by a costosternal segment (Fig. III.22).</td>
</tr>
<tr>
<td>12 - 13</td>
<td>Mesosternal ribs.</td>
</tr>
<tr>
<td>14 - 15 or 16</td>
<td>Parasternal ribs i.e. joined to 2 (Fig. III.22) or 3 complete parasternal chevrons.</td>
</tr>
<tr>
<td>16 or 17 - 33</td>
<td>Ribs terminating in the ventrolateral margin of the body wall and bearing tapering claw-like processes.</td>
</tr>
<tr>
<td>Position of Vertebrae</td>
<td>Nature of Ribs</td>
</tr>
<tr>
<td>----------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>34 - 37</td>
<td>Progressively shorter and confined to the dorsal body wall. Not terminating in claw-like cartilaginous processes.</td>
</tr>
<tr>
<td>38 - 39</td>
<td>Fused pleurapophyses on sacral vertebrae.</td>
</tr>
<tr>
<td>40 and those behind</td>
<td>Prominent transverse processes, but no free ribs on caudal vertebrae.</td>
</tr>
</tbody>
</table>
FIG. III. 11. DORSAL (A) AND LATERAL (B) VIEWS OF AN Scelotes bipes sexlineatus TO ILLUSTRATE THE TRUNK VERTEBRAE AND RIBS
2.5 **SCELOTES BIPES BIPES**

*Scelotes bipes bipes* usually has 50-51 precaudal, two fused sacral and between 40 and 50 caudal vertebrae. Since the ninth vertebra bears the first pair of ribs to reach the sternum, the usual eight cervical vertebrae are present. The first seven of these each bears a single medioventral hypapophysis excepting for the axis which bears two. The anterior-most haemapophysis occurs between the third and fourth caudal vertebrae. The first autotomy plane is visible in the fifth caudal vertebra. Some specimens of this species have an "incipient rib" joined by means of connective tissue with the synapophysis of the third vertebra. The main features of the ribs may be summarized as follows:

<table>
<thead>
<tr>
<th>Vertebrae</th>
<th>Ribs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 - 2</td>
<td>None.</td>
</tr>
<tr>
<td>3</td>
<td>&quot;Incipient rib&quot;.</td>
</tr>
<tr>
<td>4 - 8</td>
<td>Progressively longer ribs but none with forked tips; instead these terminate in blunt cartilaginous processes.</td>
</tr>
<tr>
<td>9 - 10</td>
<td>Sternal ribs.</td>
</tr>
<tr>
<td>11 - 21 or 22</td>
<td>Bear 11 to 12 pairs of paraster nal chevrons (Fig. III.23).</td>
</tr>
<tr>
<td>22 or 23 - 49</td>
<td>Terminate freely in claw-like portions of cartilage.</td>
</tr>
<tr>
<td>50 - 52</td>
<td>Progressively shorter in region of pelvic girdle.</td>
</tr>
<tr>
<td>53 - 54</td>
<td>Sacrum with fused pleurapophyses.</td>
</tr>
<tr>
<td>55 - 100</td>
<td>Caudal vertebrae with prominent transverse processes and with</td>
</tr>
</tbody>
</table>
haemapophyses but without free ribs.

2.6 **SCELOTES BREVIPES**

This species has around 51 presacral, and two fused sacral vertebrae (Table III.2). It is noteworthy that the ribs of the eighth vertebra are joined to the sternum, hence by definition there are only seven cervical vertebrae. The first six of these bear hypapophyses (as usual two on the axis and one on the rest). The transverse process of the first caudal vertebra is slightly forked. The series of haemapophyses start between the second and third caudal vertebrae, while the first autotomy fracture plane occurs on the fifth. The caudal vertebrae become progressively smaller posteriorly so that the last few are merely minute cylinders of bone.

The main features of the ribs may be summarized as follows:

<table>
<thead>
<tr>
<th>Sequence of Vertebrae</th>
<th>Nature of Ribs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 - 3</td>
<td>None present.</td>
</tr>
<tr>
<td>4 - 7</td>
<td>Presternal ribs which become progressively longer and terminate as unforked rods of cartilage.</td>
</tr>
<tr>
<td>8 and 9</td>
<td>Sternal ribs which articulate with a reduced sternum (Fig. III.25).</td>
</tr>
<tr>
<td>10 - 18+</td>
<td>9 or more pairs of parasternal ribs which articulate with parasternal chevrons (Fig. III.25).</td>
</tr>
<tr>
<td>19+ - 49</td>
<td>Postparasternals terminating in the ventrolateral margin of the body wall as hook-like claws of cartilage (cf. Fig. III.25).</td>
</tr>
<tr>
<td>Sequence of Vertebrae</td>
<td>Nature of Ribs</td>
</tr>
<tr>
<td>-----------------------</td>
<td>---------------</td>
</tr>
<tr>
<td>50 and 51</td>
<td>Shorter ribs lacking an intermediate segment.</td>
</tr>
<tr>
<td>52 - 53</td>
<td>Fused to sacral vertebrae as prominent pleurapophyses.</td>
</tr>
<tr>
<td>54 - 103</td>
<td>The caudal vertebrae bear fused transverse processes instead of free ribs.</td>
</tr>
</tbody>
</table>

2.7 COMPARISON

The ribs of *Acontias meleagris* (Fig. III.8) differ from those of *M. capensis* in several respects. They are more numerous, more uniform and of smaller radius. Limb regression is accompanied by the multiplication of body segments hence both vertebrae and ribs are more numerous. The more anterior vertebrae tend to acquire ribs in reduced limbed species. In normal limbed skinks and the majority of quadrupedal lizards the first three vertebrae are ribless, the next three bear short ribs that are distally widened into forks of cartilage and the final two cervical vertebrae bear long and slender ribs (Fig. III.21). In *Acontias meleagris* the third postcranial vertebra bears a pair of short ribs while a pair of bony nodules ("incipient" ribs") are sometimes associated with the axis. Hoffstetter and Gasc.,1969 incorrectly refers to ",,...the first rib which is borne by the fourth vertebra..." in *Acontias meleagris* (p. 254). In some bipodous specimens of *Sselotes* an "incipient rib" is associated with the third vertebra. However, such an anterior shift of the rib bearing region is not confined to skinks with reduced limbs. A few normal limbed skinks also have ribs asso-
associated with the third vertebrae (Hoffstetter and Gasc, 1969).

While the ribs of *Mabuya* (Fig. III.1B) exhibit much variation in size and structure, those of *Acontias* are much more uniform (Fig. III.9). Ribs bearing forked cartilaginous processes are present in *Mabuya* and *Riopa* but other members of the regression series lack them. With the exception of *Acontias* in which the last two precaudal vertebrae bear free ribs, the sacrum has prominent fused pleurapophyses in the rest of the regression series. The sacrum of *Mabuya* is preceded by four pairs of ribs that become progressively shorter as they approach the sacrum (Fig. III.1B); only two pairs of shorter ribs are present in the bipodous *Scelotes* (Fig. III.11), while in *Acontias* none are markedly shorter (Fig. III.9). This suggests that the ribs become more uniform as limbs regress.

In correlation with the degeneration of the sternum the number of sternal ribs diminishes as limbs regress, but there is a reciprocal increase in the number of parasternal chevrons and more ribs articulate with the latter. Thus *Mabuya* usually has three pairs of true sternal ribs plus two pairs of mesosternal ribs, but only one pair of parasternal ribs (Fig. III.21). For the bipodous *Scelotes* the corresponding figures are two pairs of sternal ribs, no mesosternal ribs and around 12 pairs of parasternal ribs (Figs. III.23, III.24 and III.25), while in *Acontias meleagris* sternal and mesosternal ribs are lacking but 27 to 31 pairs of parasternal ribs are present.

The ribs of the limbless *Acontias* have a smaller and more uni=
Fig. III.12. The number of presacral vertebrae for diverse skinks exhibiting limb regression.

Normal limbed species

- Mabuya species (11 species/60 specimens)
- Scincus affricanus (1)
- Eumeces schneideri (1)
- Ischnura rugosa (1)
- Tiliqua gigas (1)
- Tiliqua scincoides (1)

Range

Species with miniaturized limbs

- Rhipso undevallii (10)
- Chalcides simonyi (1)
- C. ocellatus (1)
- Soeotes capensis

Range

Tetrapodous species

- C. sepoides (2)
- S. caffer (5)
- Ophiomorus tridactylus (1)
- C. tridactylus (1)
- C. striatus (1)

Range

Bipodous species

- S. bipes seclinata (1)
- S. bipes bipes (4)
- S. gromovii (5)
- S. brevipes (4)

Range

Apodous species

- S. anguina (5)
- S. inornatus (1)
- S. arenicola (3)
- Typhlomaus mimicus (3)
- Acantias melagris (10 specimens)
- Acantias (other species 23 specimens)
- Typhlomaus species (3 species/6 specimens)

Range
## Data From Literature

### Table III.1

<table>
<thead>
<tr>
<th>Species</th>
<th>Condition of Limbs</th>
<th>Number of Presacral Vertebrae</th>
<th>Caudal Vertebrae</th>
<th>Source of Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lygosoma smaragdinum</td>
<td>N=(normal)</td>
<td>26</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>Lygosoma quoyi</td>
<td>N</td>
<td>26</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>Mabuia multifasciata</td>
<td>N</td>
<td>26</td>
<td>48</td>
<td></td>
</tr>
<tr>
<td>Mabuia striata</td>
<td>N</td>
<td>26</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>Eumeces schneideri</td>
<td>N</td>
<td>29</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td>Egernia whitii</td>
<td>N</td>
<td>26</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>Tiliqua scincoides</td>
<td>N</td>
<td>37</td>
<td>27</td>
<td>Siebenrock (1895)</td>
</tr>
<tr>
<td>Tiliqua gigas</td>
<td>N</td>
<td>37</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>Trachysaurus rugosus</td>
<td>N</td>
<td>35</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Chalcides simonyi</td>
<td>M=(miniaturized)</td>
<td>37</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Chalcides tridactylus</td>
<td>T-R=(tetrapodous reduced)</td>
<td>61</td>
<td>53</td>
<td></td>
</tr>
<tr>
<td>Scincus officinalis</td>
<td>N</td>
<td>27</td>
<td>33</td>
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**Data From Literature** (cont.)

<table>
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<th>Caudal Vertebrae</th>
<th>Source of Information</th>
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</thead>
<tbody>
<tr>
<td>Scincus officinalis</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Eumeces schneideri</td>
<td>N</td>
<td>30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lygosoma punctulatum</td>
<td>T-R</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chalcides ocellatus</td>
<td>M</td>
<td>39</td>
<td></td>
<td>Sewertzoff (1931)</td>
</tr>
<tr>
<td>Chalcides sepoides</td>
<td>T-R</td>
<td>48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ophiomorus tridactylus</td>
<td>T-R</td>
<td>52</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seps (=Chalcides) tridactylus</td>
<td>T-R</td>
<td>61</td>
<td></td>
<td>El-Toubi (1938)</td>
</tr>
<tr>
<td>Scincus officianalis</td>
<td>N</td>
<td>27</td>
<td></td>
<td>King (1964)</td>
</tr>
<tr>
<td>Lygosoma quoyii</td>
<td>N</td>
<td>26</td>
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</table>
### DATA From Literature (cont.)

<table>
<thead>
<tr>
<th>Species</th>
<th>Condition of Limbs</th>
<th>Number of Presacral Vertebrae</th>
<th>Caudal Vertebrae</th>
<th>Source of Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eumeces anthracinus</td>
<td>N</td>
<td>26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ablepharus boutonii</td>
<td>N</td>
<td>27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eumeces skiltonianus</td>
<td>N</td>
<td>28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachymeles schadenbergii</td>
<td>M</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachymeles gracilis</td>
<td>T-R</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chalcides ocellatus</td>
<td>M</td>
<td>37*</td>
<td></td>
<td>Stokely (1947)</td>
</tr>
<tr>
<td>Chalcides sepoides</td>
<td>T-R</td>
<td>46*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chalcides tridactylus</td>
<td>T-R</td>
<td>58</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Chalcides striatus</td>
<td>T-R</td>
<td>59</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Acontias percivali</td>
<td>A</td>
<td>76</td>
<td></td>
<td>*</td>
</tr>
</tbody>
</table>

* - Note the differences in vertebral counts for the same species reported by Sewertzoff (1931) and Stokely (1947).
List of Species in which the vertebrae were counted using:
(a) X-rayed material

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Condition of Limbs</th>
<th>Number of Precaudal Vertebrae</th>
<th>Caudal Vertebrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mabuya acutilabris</td>
<td>8</td>
<td>N</td>
<td>26+2</td>
<td>41</td>
</tr>
<tr>
<td>M. binotata</td>
<td>4</td>
<td>N</td>
<td>26+2</td>
<td>38</td>
</tr>
<tr>
<td>M. capensis</td>
<td>14</td>
<td>N</td>
<td>26+2</td>
<td>46-54</td>
</tr>
<tr>
<td>M. maculibabris</td>
<td>4</td>
<td>N</td>
<td>26+2</td>
<td>54-55</td>
</tr>
<tr>
<td>M. occidentalis</td>
<td>2</td>
<td>N</td>
<td>26+2</td>
<td>46+</td>
</tr>
<tr>
<td>M. quinquetaemata</td>
<td>3</td>
<td>N</td>
<td>26+2</td>
<td></td>
</tr>
<tr>
<td>M. sulcata</td>
<td>5</td>
<td>N</td>
<td>26+2</td>
<td>48</td>
</tr>
<tr>
<td>M. varia</td>
<td>6</td>
<td>N</td>
<td>26+2</td>
<td></td>
</tr>
<tr>
<td>M. variegata</td>
<td>6</td>
<td>N</td>
<td>26+2</td>
<td></td>
</tr>
<tr>
<td>Riopa sundevallii</td>
<td>8</td>
<td>T-R</td>
<td>37+2</td>
<td>27+</td>
</tr>
<tr>
<td>Scelotes capensis</td>
<td>3</td>
<td>M</td>
<td>43+2</td>
<td>44+</td>
</tr>
</tbody>
</table>

S.A.M. 18546
### TABLE III. 2

List of Species in which the vertebrae were counted using:

(a) X-rayed material

<table>
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<th>Species</th>
<th>No.</th>
<th>Condition of Limbs</th>
<th>Number of Precaudal Vertebrae</th>
<th>Caudal Vertebrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scelotes caffer</td>
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<td></td>
</tr>
<tr>
<td>S.A.M. 18052</td>
<td></td>
<td>T-R</td>
<td>48+2</td>
<td>45+</td>
</tr>
<tr>
<td>&quot;</td>
<td></td>
<td>T-R</td>
<td>50+2</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td></td>
<td>T-R</td>
<td>50+2</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td></td>
<td>T-R</td>
<td>50+2</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td></td>
<td>T-R</td>
<td>50+2</td>
<td></td>
</tr>
<tr>
<td>Scelotes bipes</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M. 1459</td>
<td></td>
<td>B-(bipodous)</td>
<td>50+2</td>
<td>42</td>
</tr>
<tr>
<td>S.A.M. 2037</td>
<td></td>
<td>B</td>
<td>50+2</td>
<td></td>
</tr>
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<td>S.A.M. 2050</td>
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<td>B</td>
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<tr>
<td>Scelotes gronovii</td>
<td>3</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>S.A.M. 1982</td>
<td></td>
<td>B</td>
<td>50+2</td>
<td>49-50</td>
</tr>
<tr>
<td>S.A.M. 1982</td>
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<td>B</td>
<td>51+2</td>
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<td>S.A.M. 1983</td>
<td></td>
<td>B</td>
<td>50+2</td>
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</tr>
</tbody>
</table>
### List of Species in which the vertebrae were counted using:

(a) X-rayed material

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Condition of Limbs</th>
<th>Number of Precaudal Vertebrae</th>
<th>Caudal Vertebrae</th>
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<tbody>
<tr>
<td><strong>Scelotes inornatus</strong></td>
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</tr>
<tr>
<td><strong>Scelotes anguina</strong></td>
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</tr>
<tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot; &quot;</td>
<td></td>
<td>A</td>
<td>47+2</td>
<td>29A</td>
</tr>
<tr>
<td>&quot; &quot;</td>
<td></td>
<td>A</td>
<td>47+2</td>
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</tr>
<tr>
<td>&quot; &quot;</td>
<td></td>
<td>A</td>
<td>47+2</td>
<td></td>
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<tr>
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<td>&quot; &quot;</td>
<td></td>
<td>A</td>
<td>46+2</td>
<td></td>
</tr>
<tr>
<td><strong>Scelotes arenicola</strong></td>
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<tr>
<td>S.A.M. 2840</td>
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<td>A</td>
<td>52+2</td>
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</tr>
<tr>
<td>S.A.M. 2873</td>
<td></td>
<td>A</td>
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<tr>
<td>S.A.M. 2821</td>
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<td>A</td>
<td>52+2</td>
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</tr>
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<td><strong>Acontias meleagris lineatus</strong></td>
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<td><strong>Acontias lineatus orangensis</strong></td>
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<td>S.A.M. 16150</td>
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<td>A</td>
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</tr>
<tr>
<td>&quot;</td>
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<td>83</td>
<td>24-25</td>
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### TABLE III, 2
List of Species in which the vertebrate were counted using:

(a) X-rayed material

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<th>Number of Precaudal Vertebrae</th>
<th>Caudal Vertebrae</th>
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<tbody>
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<td>18579</td>
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<tr>
<td>S.A.M.</td>
<td>18136</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acontias plumbeus occidentalis</td>
<td>4</td>
<td>A</td>
<td>85</td>
<td>19</td>
</tr>
<tr>
<td>S.A.M.</td>
<td>19828</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M.</td>
<td>15990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M.</td>
<td>14772</td>
<td></td>
<td></td>
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<tr>
<td>S.A.M.</td>
<td>19811</td>
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<td></td>
<td></td>
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<tr>
<td>Acontias meleagris</td>
<td>3</td>
<td>A</td>
<td>78</td>
<td>20</td>
</tr>
<tr>
<td>C 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>No.</td>
<td>Condition of Limbs</td>
<td>Number of Precaudal Vertebrae</td>
<td>Caudal Vertebrae</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----</td>
<td>--------------------</td>
<td>------------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Acontias plumbeus gracilicauda</td>
<td>3</td>
<td>A</td>
<td>71</td>
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<td>S.A.M. 467</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>S.A.M. 18316</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>S.A.M. 18316</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>2</td>
<td>A</td>
<td>77</td>
<td>19</td>
</tr>
<tr>
<td>S.A.M. 43512</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M. 43511</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acontias lineatus</td>
<td>3</td>
<td>A</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td>S.A.M. 18057</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M. 18057</td>
<td></td>
<td></td>
<td>78</td>
<td>24</td>
</tr>
<tr>
<td>S.A.M. 18057</td>
<td></td>
<td></td>
<td>77</td>
<td></td>
</tr>
<tr>
<td>Acontias typhlosaurus</td>
<td>1</td>
<td>A</td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>S.A.M. 16150</td>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table III.2

List of Species in which the vertebrae were counted using:

(a) X-rayed material

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Condition of Limbs</th>
<th>Number of Precaudal Vertebrae</th>
<th>Caudal Vertebrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typhlosaurus lineatus</td>
<td>3</td>
<td>A</td>
<td>83</td>
<td>16</td>
</tr>
<tr>
<td>S.A.M. 19704</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M. 19716</td>
<td></td>
<td>A</td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>S.A.M. 18657</td>
<td></td>
<td>A</td>
<td>86</td>
<td>16</td>
</tr>
<tr>
<td>Typhlosaurus gariepensis</td>
<td>1</td>
<td>A</td>
<td>84</td>
<td>20</td>
</tr>
<tr>
<td>S.A.M. 11232</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Typhlosaurus vermis</td>
<td>2</td>
<td>A</td>
<td>107</td>
<td>20</td>
</tr>
<tr>
<td>U.W.C. unnumbered</td>
<td></td>
<td>A</td>
<td>103</td>
<td>24</td>
</tr>
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<td>Typhlacontias ngamiensis</td>
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<td>A</td>
<td>66</td>
<td>24</td>
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<td>S.A.M. 508</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.A.M. 2 unnumbered</td>
<td></td>
<td>A</td>
<td>64</td>
<td></td>
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<td></td>
<td></td>
<td>A</td>
<td>69</td>
<td></td>
</tr>
</tbody>
</table>
List of Species in which the vertebrae were counted using:

(b) Alizarine stained and cleared specimens.

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Condition of Limbs</th>
<th>Number of Precaudal Vertebrae</th>
<th>Caudal Vertebrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. capensis</td>
<td>8</td>
<td>N</td>
<td>26</td>
<td>usually more than 46 vertebrae</td>
</tr>
<tr>
<td>R. sundevallii</td>
<td>2</td>
<td>M</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>S. angolensis</td>
<td>1</td>
<td>T-R</td>
<td>50 (approx.)</td>
<td></td>
</tr>
<tr>
<td>F.M.N.H. 142794</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. bipes sexlineatus</td>
<td>1</td>
<td>B</td>
<td>55+2</td>
<td>around 40</td>
</tr>
<tr>
<td>S. bipes bipes</td>
<td>2</td>
<td>B</td>
<td>51+2</td>
<td></td>
</tr>
<tr>
<td>S. Gronovii</td>
<td>2</td>
<td>B</td>
<td>51+2</td>
<td></td>
</tr>
<tr>
<td>S. brevipes</td>
<td>4</td>
<td>B</td>
<td>51+2</td>
<td></td>
</tr>
<tr>
<td>S. arenicola</td>
<td>1</td>
<td>A</td>
<td>52+2</td>
<td></td>
</tr>
<tr>
<td>A. meleagris</td>
<td>1</td>
<td>A</td>
<td>77</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>3</td>
<td>A</td>
<td>78</td>
<td>21-23</td>
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<tr>
<td>&quot;</td>
<td>1</td>
<td>A</td>
<td>79</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>1</td>
<td>A</td>
<td>80</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>1</td>
<td>A</td>
<td>81</td>
<td></td>
</tr>
</tbody>
</table>
form radius than do those of quadrupedal skinks of equivalent mass (Figs. III.1B and III.9). Although the radii of the ribs have diminished, they nevertheless are thicker and stronger in reduced limbed forms (Fig. III.8). Each trunk rib of *Acontias* bears a strongly developed dorsocaudal projection called a pseudotuberculum (Hoffstetter & Gasc, 1969). The ribs of *Mabuya* and of the intermediate members of the regression series lack such projections.

2.8 VERTEBRAL NUMBER

Higher numbers of trunk vertebrae in species showing regressed limbs represent a well documented phenomenon (Siebenrock, 1895; Camp, 1923; Sewertzoff, 1931; Stokely, 1947; Romer, 1956; Hoffstetter and Gasc, 1969). Table III.1 summarizes data from the older literature while Table III.2 reflects the vertebral counts for a further 136 specimens of diverse skinks. Figure III.12 relates the presacral vertebral counts to the degree of limb reduction. Three aspects are emphasized. Firstly, the increase is confined mainly to the precaudal region (cf. Table III.2 and Fig. II.6). Secondly, in the reduced limbed species there is much greater inter- and intra-specific variation in vertebral number (Fig. III.12). Finally the correlation between the degree of limb loss and vertebral number is not absolute even in a single genus.

When comparing the limbed and limbless extremes, one notes that *Acontias* has about three times the number of precaudal vertebrae and less than half the number of caudal vertebrae than
does *Mabuya* (Table III.2). Fewer caudal vertebral counts were made than precaudal ones because of the frequency of caudal autotomy and the difficulty in obtaining accurate counts of the minute posterior vertebral vestiges. Even the long-tailed *Scoleotes brevipes* only has around 50 caudal vertebrae and falls within the range of normal limbed skinks. These facts provide a morphological explanation for the conclusion drawn from morphometry that elongation in skinks is mainly confined to the trunk region (Fig. III.6).

The reduced limbed skinks evince greater variation in their presacral vertebral counts than do their quadrupedal counterparts (Fig. III.12). For example, the vertebral counts for a random sample of 60 specimens of *Mabuya*, representing 11 species, was invariably 26. On the other hand, 10 alizarine stained specimens of the single species *Acontias meleagris* had 77 to 81 vertebrae. Furthermore, 14 specimens of bipodous *Scelotes* species had 50 to 55 vertebrae. In other words, the normal limbed species are characterized by great inter- and intra-specific stability while the reduced limbed skinks are much more variable.

Although there is an unambiguously positive relationship between limb reduction and vertebral multiplication, this correlation is not absolute even for members of the same genus. The limbless *S. arenicola* has only 54 presacral vertebrae while the tetrapodous *Chalcides tridactylus* has 61 (Gasc, 1967). Four specimens of *S. arenicola* have 52 presacral vertebrae plus a
sacrum of two fused vertebrae (personal observation). Furthermore, although this animal is externally limbless, it does have vestigial hindlimbs hidden beneath its skin. A glance at Fig. III.12 will show that even within the genus Scelotes the reciprocal relationship between limb regression and vertebral number is not a strict one. Although there is a general increase in vertebral number as one passes down the regression series, there are also many anomalies (even in this small sample of Scelotes species). For example, the limbless S. anguina has 47 or 48 presacral vertebrae while the bipodous species with the best developed limbs, S. bipes sexlineatus (see also Table III.2), has the highest vertebral count of all (55). Thus, it is not surprising that bipodous species show an almost zero correlation between limb length and snout to vent length (Table II.1).

Although the mode of presacral numbers is 26 for normal limbed skinks (Hoffstetter and Gasc, 1969) the range extends from 26 to just under 40 (Fig. III.12). Tiliqua and Tachysaurus, which occupy a position at the upper extreme of this range are gar- guantuan skinks that have normal limbs. Perhaps their unusually high vertebral counts may be related to their extraordinary massiveness.

To summarize, there is a clear though fluctuating correlation between limb reduction and an increase in the number of presacral vertebrae. The latter is stable both intra- and interspecifically in normal limbed forms and fluctuates widely in species with reduced limbs.
Fig. III.13. Intracolumnar variation of the dimensions in the presacral vertebrae of *Mabuya capensis*
2.9. MORPHOMETRIC COMPARISON

The vertebrae of limbed and limbless skinks are similar in fundamental morphology. However, there are differences in the relative dimensions of the constituent parts of the vertebrae. These variations are explored for precaudal vertebrae on two levels. In order to obtain an overall picture of intracolumnar variations in measurements, the length, width and height of each individual vertebra in the body axis were taken for a single specimen of each of the following species: *M. capensis*, *R. sundevallii*, *S. brevipes* and *A. meleagrīs* (Figs. III.13, III.14, III.15 and III.16). Measurements that disclosed distinct trends in this morphological series were then explored more fully using larger samples.

Two measurements of vertebral length are reflected in these graphs:

(a) Zygapophysial length (ZL), i.e. the greatest sagittal distance from the anterior margin of the prezygapophyses to the posterior margin of the postzygapophysis of the same vertebra (Fig. III.4A).

(b) Central length (CL) - the mid-ventral length of the centrum from the lip of the cotyle to the lip of the cotyle of the succeeding vertebra. The total length of the cotyle is not reflected in this measurement (Fig. III.4B).

If the specialized atlas-axis complex is omitted from consideration, vertebral length measured in these two ways are well correlated; their curves rise and fall almost parallel to
Fig. III.14. Intracolumnar variations in vertebral dimension of the presacral vertebrae of *Riopa sundevallii*. 
each other (Figs. III.13 to III.16). Furthermore, in each of the postatlanatal vertebrae the zygapophysial length is greater than the central length.

In *M. capensis* the vertebral length rapidly increases behind the head, waxes more slowly in the mid-trunk region, reaches a peak value in the posterior third of the trunk and diminishes over the last six or so presacral vertebrae (Fig. III.13).

In *A. meleagris*, on the other hand, vertebral length increases gradually over the first 20 or so postcranial vertebrae to reach a plateau involving the next 50 or so vertebrae before diminishing over the last 10 or fewer precaudal vertebrae (Fig. III.16).

Two differences emerge from this comparison of limbed and limbless extremes. Firstly, the magnitude of increase appears to be greater in the limbed forms. Secondly, whereas the vertebral length of the limbed forms reaches a peak and then declines towards the sacrum, that of the limbless *Acontias* is characterized by a mid-trunk plateau occupied by vertebrae of uniform length (cf. Figs. III.13 and III.16).

The intermediate species in our regression series appear to display a less extensive plateau (Figs. III.14, III.15 and III.16). In order to determine whether these two divergent patterns hold for the entire regression series, I calculated the central length of each vertebra as a percentage of the total snout to vent length for 16 well-cleared alizarine stained specimens. These data illustrate two trends which apparently form a mor=
Fig. III.15. Intracolumnar variation in the dimensions of presacral vertebrae in *Scelotes brevipes*. (For most lines the dimensions of every fifth vertebra are plotted.)
phocline (Graph III.17). Firstly, the range of vertebral length declines as limbs are lost. Secondly, the extent of the plateau formed by vertebrae of uniform length increases with limb reduction. In brief, as limbs regress the trunk vertebrae not only become more numerous but also shorter and more uniform in length.

Vertebral width was measured in three ways:

(a) **Prezygapophysial width (PW)**

The maximum width of a vertebra from the lateral margin of the left prezygapophysis to the lateral margin of the right prezygapophysis (Fig. III.4A).

(b) **Waist width (WW)**

The minimum width of a vertebra from its left interarticular ridge (= margo lateralis) to its right interarticular ridge (Fig. III.4B).

(c) **Synapophysial width (SW)**

The maximum width from the left synapophysis to the right synapophysis (Fig. III.4B).

In *M. capensis* the synapophysial width is the greatest transverse dimension throughout the cervical region. More posteriorly both synapophysial and prezygapophysial width decline and remain more or less equal for most of the trunk before flaring outwards again immediately in front of the sacrum. *A. meleagris* shows a different pattern. The prezygapophysial width is the greatest transverse dimension in vertebrae posterior to the fourth or fifth postcranial one. In most of the anterior half of the body prezygapophysial width is exceeded in magnitude only
Fig. III.16. Intracolumnar variation in the dimensions of the precaudal vertebrae of Acontias meleagris.
by the zygapophyssial length. In the posterior half of the body
prezygapophyssial width declines more or less in parallel with
the synapophyssial width which is always smaller excepting in
the first 4 or 5 vertebrae (Fig. III.16). In brief, the limb-
less form displays extreme hypertrophy of zygapophyssial width.

The width dimensions of vertebrae may now be explored for a
larger sample of skinks in terms of three indices:

(a) \[
\frac{\text{prezygapophysial width}}{\text{transverse diameter of the body in the same plane}} \times \frac{100}{1} \quad \text{(Fig. III.18)}
\]

(b) \[
\frac{\text{prezygapophysial width}}{\text{waist width of the same vertebra}} \times \frac{100}{1} \quad \text{(Fig. III.19)}
\]

(c) \[
\frac{\text{zygapophysial length}}{\text{prezygapophysial width}} \times \frac{100}{1} \quad \text{(Fig. III.20)}
\]

To accommodate the great fluctuation in the number of presacral
vertebrae evinced by the regression series (Fig. III.12), as
well as the different patterns of intracolumnar variation in
width dimensions (Figs. III.13 to III.16), these indices were
calculated for five roughly equivalent positions (A, B, C, D
and E) in a vertebral column. These positions are defined for
the members of the regression series in Figure III.18.

The first index (a) examines the relationship between maximum
vertebral width and transverse diameter for a morphological se-
ries (Fig. III.18). The data are based on measurements of 35
vertebral columns. The ratio is highest for the Acontinae and
lowest for species of the genus \textit{Mabuya}. The tetrapodous and
bipodous species of \textit{Scelotes} occupy an intermediate position
suggesting that this ratio exhibits a morphocline between limbed
Fig. III.17. Intracolumnar variation in central length recorded for each vertebra as a percentage of the snout to vent length for the species of skinks named in the graph. The number of specimens on which a line is based is given in brackets. The vertical lines indicate the range of a particular point.
and limbless extremes.

The increase in this ratio for the posterior region of the body in *Mabuya* and *S. capensis* is due to the increase in transverse width of the last presacral vertebrae accompanied by a marked decrease in trunk diameter. The steady decline in this ratio over the posterior three-quarters of the trunk in the Acontinae is due largely to a steady decline in the width of the vertebrae posteriorly to the anterior quarter of the body (Fig. III.16). In the bipodous specimens the decline is slight and confined to the posterior quarter of the body. It has been shown that limb regression is accompanied by elongation, that is, a decline in transverse diameter relative to body length (Fig. II.8). Such reduction in body diameter does not involve a proportionate reduction in vertebral width, on the contrary the latter increases, hence the sharp difference in the width indices for the regression series (Figs. III.18 and 19).

Whereas the first index highlights the relation between vertebral and body width, the second compares the maximum and minimum widths of a vertebra. It indicates the extent to which the prezygapophyses flare beyond the narrowest diameter of a vertebra. Even a glance at Figure III.4 leaves the impression that the zygapophyses flare further outwards in *Acontias* than in *Mabuya*. Graph III.19 confirms this impression. Although the ratio varies along the length of the vertebral column it is always very much higher in *Acontias* than in other members of the regression series. However, although the curve for *Scelotes* and, to a lesser extent, for *Riopa sundevallii* occupies an in-
POSITIONS OF VERTEBRAE MEASURED IN VARIOUS SPECIES:

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mabuya capensis (12)</td>
<td>-5</td>
<td>10</td>
<td>15</td>
<td>20</td>
<td>LAST PERSA-CRAL VERTEBRA</td>
</tr>
<tr>
<td>Scelotes capensis (4)</td>
<td>-5</td>
<td>13</td>
<td>21</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>BIPODOUS SPECIES OF Scelotes (5)</td>
<td>5</td>
<td>15</td>
<td>25</td>
<td>35</td>
<td></td>
</tr>
<tr>
<td>Acontias meleagris (14)</td>
<td>5</td>
<td>20</td>
<td>35</td>
<td>50</td>
<td></td>
</tr>
</tbody>
</table>

**FIG. III. 18.** COMPARISON OF THE MAXIMUM WIDTH OF A VERTEBRA WITH THE DIAMETER OF THE BODY IN THE SAME PLANE AT FIVE PLACES IN THE TRUNK FOR THE SPECIMENS NAMED ABOVE. THE VERTICAL LINES INDICATE RANGE FOR THE LIMBED AND THE LIMBLESS EXTREMES.
termediate position, both fall well within the range of values for *M. capensis*. Thus no clear trend can be inferred. Graph III.17 implies that the vertebrae of reduced limbed forms become shorter while Graphs III.18 and III.19 indicate that their width becomes greater.

To test these generalizations the index

\[
\frac{\text{zygapophysial length}}{\text{zygapophysial width}} \times \frac{100}{1}
\]

was calculated and plotted in Graph III.20 for a regression series. In the anterior and posterior regions of the trunks the values do not form the expected morphocline. In the mid-trunk region, however, the expected morphocline is shown. In other words, only in the mid-trunk region are the vertebrae of reduced limbed forms very much shorter and wider than those of their normal limbed counterparts.

2.10 SUMMARY OF TRENDS AND TENDENCIES

As limbs degenerate, the vertebral columns of skinks show the following trends and tendencies:

(a) There is an increase in the number of precaudal vertebrae (Fig. III.12).

(b) The inter- and intra-specific variation in the number of precaudal vertebrae becomes greater (Fig. III.12).

(c) The vertebrae become relatively shorter, i.e. they occupy a smaller percentage of the total snout to vent length (Fig. III.17).
Comparison of the maximum and minimum widths of a particular vertebra for a regression series of skinks named in the graph. The vertical lines indicate the range for the limbed and limbless extremes.
(d) The majority of the trunk vertebrae (with the exception of the anteriormost and posteriormost ones) become uniform in length (Fig. III.17).

(e) The prezygapophysial width increases relative to the body diameter (Fig. III.18) and, to a lesser extent, also increases relative to the "waist width" (Fig. III.19).

(f) The mid-trunk vertebrae become shorter and wider (Fig. III.20).

(g) Vertebral height declines relative to the other vertebral dimension in the regression series (Figs. III.13 to III.16).

(h) More of the anterior vertebrae bear hypapophyses (Figs. III.13 to III.16).

(i) The synapophyses, though still prominent, are overshadowed in partially or completely limbless species, by the extension of the prezygapophyses (Figs. III.13 to III.16).

(j) The intercentral joints are amphiarthroses in Mabuya while those of Acontias and Scelotes are diarthroses.

As limbs atrophy, ribs show the following trends and tendencies:

(a) As the number of presacral vertebrae increases so does the number of ribs.

(b) The second and third vertebrae tend to acquire ribs in reduced limbed skinks.

(c) As the body diameter becomes reduced the ribs form arches of smaller radius.

(d) The ribs are relatively thicker in reduced limbed forms (Fig. III.8).
Fig. III.20. The ratio between zygapophyial length and zygapophyial width for a regression series of skinks using the same codes as in graph III.19. A, B, C and E is defined in graph III.18.
(e) Ribs are more uniform in size and structure in reduced limbed skinks resulting in a more uniform trunk profile (Figs. III.9, III.10 and III.11).

(f) As limbs regress there is less regional differentiation (Figs. III.1, III.9, III.10 and III.11).

(g) The Acontinae are unique in that their ribs bear prominent pseudotubercula (Fig. III.8).
3. PECTORAL GIRDLE

3.1 GENERAL

Several comprehensive surveys of the anatomy of the pectoral girdle of lizards have been published (Parker, 1868; Fürbringer, 1875, 1900; Cope, 1892(a), (b); Howell, 1936; Lecuru, 1968, 1969). A number of monographs on scincid osteology include descriptions of the pectoral girdle (Siebenrock, 1895; El-Toubi, 1938; King, 1964). The pectoral girdles of certain species of reduced limbed or limbless skinks have been described by Rathke (1853), Fürbringer (1869), Cope (1892(b)), Krieg (1919), Essex (1927), Sewertzoff (1931), Stokely (1947) and Tiedemann and Tiedemann (1975).

The ontogeny of the lacertilian pectoral girdles has received somewhat less attention (Parker, 1868; Van Gelderen, 1922). Limb bud formation in reptiles with normal and vestigial limbs was investigated by Raynaud (1972).

While the morphology of the pectoral girdle has been investigated often, its biomechanical role in locomotion has hardly been considered at all. Two works touch on this problem. Gray (1968) attempts a functional analysis of the operation of the shoulder girdle in the light of what was known about its morphology and Peterson (1973) in an unpublished thesis deals with the biomechanical adaptations of aboreal lizards.

This section provides a brief descriptive survey of the pectoral girdles of *M. capensis*, *Riopa sundevillii*, *Scelotes bipes bipes*, *Sceletes gronovii* and *Sceletes brevipes*. The girdles of
these species have not been described previously. The vesti-
gial girdles of *Acontias meleagris* are briefly reconsidered be-
due to inconsistencies in previous descriptions (Rathke, 1853; 
Fürbringer, 1869; Essex, 1927 and Tiedemann and Tiedemann, 
1975).

Special attention is paid to joints between the various elements 
as these are important for a biomechanical analyses. Finally, 
trends associated with limb regression will be sought.

3.2 **MABUYA CAPENSIS**

The shoulder girdle of *Mabuya capensis* is essentially similar 
to that of normal limbed skinks and for that matter to those of 
quadrupedal lizards in general (Fig. III.21). The girdles are 
comprised of paired endochondral units, the scapulocoracoids, 
and also of several dermal elements such as the paired clavi-
cles and the unpaired interclavicle (Romer, 1956). Though the 
 sternum is strictly speaking part of the axial skeleton, it is 
functionally associated with the shoulder girdle and is, thus, 
considered here.

3.2.1 **SCAPULOCORACOID** (Fig. III.21, SOC)

Each scapulocoracoid is a skeletal plate composed of two ele-
ments, the scapula and the coracoid. These elements are fused 
in the region of the glenoid cavity. As each of these two ele-
ments has a bony part and a cartilaginous portion, the entire 
scapulocoracoid may be divided along its dorso-ventral axis in-
to a suprascapula, an infrascapula or scapula proper, a cora-
Fig. III.21. The right half of the pectoral girdle of *Mabuya capensis* in lateral view.

ACP - Acromial process; CLV - clavicle; CVR - cervical ribs; EPC - epicoracoid;
FRSC - foramen supracoracoideum; FSC - fenestra supracoracoidea; FSS - fenestra suprascapularis; GLC - glenoid cavity; INCL - interclavicle; IS - infrasculapula;
MSC - mesoscapulum; MSS - mesosternum; PRC - procoracoid; PRS - proscapulum;
SFCS - semifenestra coraco-scapularis; SOC - scapulocoracoid; SRB - sternal ribs;
SS - suprasculapula; STN - sternum.
coid and an epicoracoid (Lecuru, 1968 and see Figs. III.21 and III.22).

3.2.1.1 Suprascapula (Fig. III.21)

The uppermost portion of the scapulocoracoid, the suprascapula is a curved cartilaginous plate lodged against the axial musculature at the posterior extremity of the cervical region. It is edged with thin delicate cartilage which progressively thickens and becomes calcified toward the infrascapula. Anteroventrally the suprascapula bears the acromial process which forms a cap over the tip of the vertical clavicular rod, to form a syndesmosis (Fig. III.21). The suprascapula unites with the infrascapula on either side of the fenestra scapularis (Lecuru, 1968) also called Fenestra suprascapularis (Tiedemann and Tiedemann, 1975). The medial and lateral surfaces of the suprascapula provide attachment for the muscles that suspend the scapulocoracoid from the rib cage.

3.2.1.2 Infrascapula (Fig. III.21)

The scapula proper or infrascapula is a flat bony plate of varying thickness. From the very thick basal part in the region of the glenoid cavity, two thick pillars of bone radiate upwards and forwards, one posterior (the proscapulum) and the other anterior (mesoscapulum, Lecuru, 1968) to the fenestra suprascapularis. The arms of the bone thus have a V-shaped appearance (Fig. III.21). These thick areas of bone would be able to resist compression in an upwards and an anterior direction. The infrascapula fuses with the coracoid synchondrosis.
cally in the younger animals. This joint may become obliterated as the animal matures. The two bones join at an angle slightly more than 90° so that the scapula lies in a vertical plane while the coracoid has a more horizontal orientation following the ventral curvature of the thorax. Besides forming the upper support of the glenoid cavity, the infraspinata also provides attachment for important axillary muscles such as M. subscapularis and the scapulohumeralis (Howell, 1936).

3.2.1.3 Coracoid (Fig. III.21)

The coracoid of living reptiles actually corresponds to the procoracoid of primitive fossils and is not homologous to the mammalian process of that name (Romer, 1956). The term coracoid together with its subdivisions such as the procoracoid and the epicoracoid, are adopted from the previous literature (Fürbringer, 1900; Lecuru, 1968) as topographical terms which do not necessarily imply homology with similarly named structures in primitive mammals. In Mabuya it is a more or less oval plate lying in a horizontal plane. There is a strong bony region which completes the glenoid cavity ventrally and anteriorly. From here two arms of bone reach forward forming a C-shaped structure behind the fenestra supracoracoidea (Tiedemann and Tiedemann, 1975; also called the coracoid fenestra, Lecuru, 1968; fenestra coracoidea principalis, Fürbringer, 1900).

The bony arm above fenestra supracoracoidea together with its cartilaginous prolongation is often termed the procoracoid. The fenestra supracoracoidea is closed by a membrane. The foramen supracoracoideum, an opening for the nervus supracoracoi-
deus together with blood vessels, is lodged between the last named fenestra and the glenoid cavity. This opening is regarded as a very constant feature of the coracoid (Fürbringer, 1900 and Lecuru, 1968). A cranial, membrane-spanned embayment between the scapula and the coracoid is called the semifenestra coraco-scopularis.

3.2.1.4 *Epicoracoid* (Fig. III.21)

Epicoracoid is cartilagenous and lies medial to the fenestra suprascoracoidea and to the glenoid cavity. Its posteromedial edge fits into a sulcus coracoideus sterni with which it forms a diarthrosis.

3.2.1.5 *Suspension of scapulocoracoid*

The scapulocoracoid is linked to the body axis in four ways:

(a) Muscles from the suprascapula run to ribs and vertebrae.
(b) Muscles from the body axis overlap the scapulocoracoid before attaching to the proximal extremity of the humerus.
(c) A diarthrosis joins the posteriomedial edge of each epicoracoid and the sulcus coracoideus sterni.
(d) An acromial process forms a syndesmotic link between the suprascapula and the upper extremity of the clavicle which in turn is linked to the body axis by means of several muscles.

3.2.2 *CLAVICLE* (Fig. III.21)

The paired clavicles constitute the anteriormost elements of
the shoulder girdle. Each bone consists of a vertical rod and a curved horizontal plate. The upper tip of the vertical rod forms a pivot joint with the acromial process of the suprascapula. The base of this rod curves medially into a horizontal plate with a thick and smooth anterior margin while the posterior one is rough and thin. In the ventral midline the right and left horizontal plates meet beneath the anterior tip of the interclavicle to form a very dense syndesmotic joint between these three bones. A tough membrana episterno-claviculares spans the gap between the posterior edge of the horizontal plate and the transverse arms of the interclavicle.

3.2.3 INTERCLAVICLE = EPISTERNUM (Fig. III.21)

In ventral view the interclavicle is cruciform. Its arms lie almost entirely in a horizontal plane though distally they curve gently following the contours of the body. The four arms are more or less equally long. The tip of the anterior arm forms a syndesmotic union with the upper medial areas of the clavicles while the caudal tip of the posterior arm is in syndesmosis with the medioventral surface of the sternum. These longitudinal arms of the interclavicle, therefore, keep the sternum and clavicles fixed relative to each other, while the lateral arms provide for the origin of muscles such as M. episterno-cleido-hyoideus. In addition, the membrana episterno-clavicularis extends between the lateral arms of the interclavicle and the horizontal plates of the clavicles, while the membrana sterno-episternalis extends from the lateral arms of the interclavicle to the sternum.
3.2.4  **STERNUM (= PRESTERNUM)** (Fig. III.21)

The sternum is functionally linked with the shoulder apparatus. The presternum (= sternum proper) is a shield-shaped plate of calcified cartilage located medioventrally behind the scapulo-coracoids. Its anterolateral margins are deeply grooved into sulci coracoidei sterni (= sulci articulares coracoidei) bordered by an upper labium internum and a lower labium externum. The posteromedial margin of the epicoracoid fits into this deep sulcus to form a synovial coracosternal joint. The posterolateral margins of the sternum are in contact with three pairs of sternal ribs while posteromedially it is joined to a mesosternum.

3.2.5  **MESOSTERNUM (= XIPHISTERNUM - Färbringer, 1900)** (Fig. III.21)

The mesosternum is roughly O-shaped, attached to the posteromedial edge of the sternum and to two pairs of ribs. Its oval opening is closed by a membrane.

3.2.6  **PARASTERNUM**

A single pair of fused parasternal chevrons is located behind the mesosternum and it articulates with a single pair of ribs.

3.3  **RIOPA SUNDEVALLII** (Fig. III.22)

The shoulder girdle of *Riopa sundevallii* is similar in basic morphology to that of *Mabuya*. However, the two species differ in the nature of the joint between the clavicle and suprascapula. In *Riopa* the vertical rod of the clavicle no longer articu-
Fig. III.22. Ventral view of the left pectoral girdle, the sternum and the parasternum of *Riopa sundevallii*. 
lates with a cap-like projection; instead it terminates in a mass of connective tissue associated with an antero-ventral, thin area of the suprascapula. A delicate rod of cartilage touches the lateral surface of the clavicle near the tip (Fig. III.22). Behind the mesosternum two or three parasternal chevrons articulate with the post mesosternal ribs (contrast with one pair in *Mabuya*).

### 3.4 BIPODOUS *SCELOTES*

Although the bipodous species of *Sceiotes* lack front limbs, they nevertheless possess shoulder girdles containing the full complement of bones, but these are greatly miniaturized. Much variation and asymmetry characterize their girdles (cf. Krieg, 1919).

#### 3.4.1 SCAPULOCORACOIDS (Figs. III.23, III.24 and III.25)

Each scapulocoracoid, though relatively small, is still differentiated into a suprascapula, an infrascapula, a coracoid and an epicoracoid. Minute muscles attach to the cartilaginous suprascapula to suspend the scapulocoracoid from the body axis. The infrascapula and coracoid are fused into a ribbon of bone which varies in thickness, but lacks distinct fenestrae in *S. bipes* and *S. gronovii*. *S. brevipes* does have fenestrae (Fig. III.25). As front limbs are absent there is no trace of a glenoid cavity. Both Fürbringer (1900) and Lecuru (1968) consider the foramen supracoracoideum to be diagnostic for the coracoid. As this foramen occurs in *Sceiotes*, the presence of a bony coracoid is inferred. Each cartilaginous epicoracoid articulates
Fig. III.23. A ventral view of the pectoral girdle and parasternum of *Scelotes bipes bipes*
with the sternum via a reduced sulcus coracoideus sterni by means of a dense syndesmosis. The scapulocoracoids are only slightly curved as they no longer follow the curvature of the thorax towards the ventral midline of the body, but instead they terminate against the craniolateral margins of the sternum (Figs. III.23, III.24 and III.25).

3.4.2 CLAVICLES (Figs. III.23 to 25).

The bony clavicular plates still form a syndesmotic joint in the ventral midline of the thorax. Their posterior margins are smoother than in the normal limbed *Mabuya* with exception of those of *S. brevipes* (Fig. III.25) which retains the rough and serrated posterior edge. The vertical processes of the clavicles no longer articulate with a distinct acromial process, but instead are in extensive syndesmotic contact with the anterior margin of the suprascapula and infrascapula. Again *S. brevipes* has the more conservative clavicular-scapular joint (Fig. III.25).

3.4.3 INTERCLAVICLE (Figs. III.23 to 25)

The interclavicle is fairly cruciform in *S. brevipes* but even here the longitudinal arms are relatively short, hence the clavicles have moved much nearer to the sternum. In *S. bipes* and *S. gronovii* the lateral arms are flattened into bony plates which fill most of the gap between the sternum and the clavicles. The interclavicles are in broad syndesmotic contact with the sternum and clavicles. The *S. gronovii* illustrated (Fig. III.24) is unusual in that the interclavicle appears to be
Fig. III.24. A ventral view of the pectoral girdle and parasternum of *Scelotes gronovii*.
paired. Although the anterior arms of the interclavicle still overlap the clavicle, its posterior arms terminate in front of the sternum.

3.4.4 STERNUM (Figs. III.23 to 25)

The reduced sternum usually articulates with only two pairs of ribs instead of three pairs as is found in quadrupedal skinks. In addition the mesosternum has disappeared completely. As already mentioned, the sulcus coracoideus sterni is reduced and transformed into a syndesmotic joint with the epicoracoid. The interclavicle no longer overlaps the ventral surface of the sternum, instead it is in broad syndesmotic articulation with the anterior surface of the sternum.

3.4.5 PARASTERNALIA (Figs. III.23 to 25)

The number of parasternal chevrons range from about nine to twelve pairs followed by a few parasternal vestiges. In *S. bi­pes* and *S. gronovii* each segmental pair of parasternalia are fused to form a complete arciform parasternal chevron (Figs. III.23 and 24). In *S. brevipes* fusion is less complete and parasternal chevrons resemble inverted V's (Fig. III.25).

3.5 ACONTIAS MELEAGRIS (Fig. III.26)

In each of the nine alizarine-stained specimens examined the pectoral girdles are represented by a pair of vestigial scapulocoracoids. The latter are orientated obliquely posteriorly and inwards below the first and second pairs of ribs.
FIG. III.25 THE LEFT PECTORAL GIRDLE AND THE PARASTERNUM OF SCELOTES BREVIPE IN VENTRAL VIEW.
FIG. III.26 THE PECTORAL GIRDLE OF *ACONTIAS MELEAGRIS*, (A) PHOTOGRAPHED IN SITU FROM ALIZARINE-STAINED SPECIMEN; (B) CAMERA-LUCIDA DRAWING OF ISOLATED LEFT SCAPULOCORACOID
(borne by the 3rd and 4th vertebrae). The posteromedial extremities almost meet ventral to the trachea but remain separated by a narrow gap spanned by a strong interconnecting ligament. On the basis of the muscle associated with this vestige, Rathke (1853) suggested that it may represent the scapula only. Five out of the nine shoulder girdles examined, had at least one side differentiated into three regions. These probably correspond to a suprascapula of calcified cartilage, a bony scapula (plus coracoid?) and an epicoracoid of calcified cartilage. Hence, this element probably represents a vestige of the entire scapulocoracoid. The series of shoulder girdles of *Acontias* species illustrated by Essex (1927) appear to confirm this interpretation. However, Essex also describes clavicles in certain specimens of *Acontias meleagris* but these were not observed in my specimens.

3.6 TRENDS AND TENDENCIES

As limbs regress the pectoral girdle shows the following trends and tendencies:

(a) The shoulder girdle apparatus is miniaturized. In the bi- and apodous *Scelotes* all the elements of the pectoral girdle are still present though they are greatly reduced in size. The limbless *A. meleagris* has lost the dermal components of the shoulder girdle but still retains a vestigial scapulocoracoid.

(b) Asymmetry and much variation characterize the reduced girdles (cf. Krieg, 1919; Figs. III.23 and 24).
(c) The degree of limb loss is not strictly correlated with the degree of girdle reduction. For example, of the three bipodous skinks illustrated, *S. brevipes* has the smallest limbs, yet its girdle is the least reduced (cf. Figs. III. 23 to 25).

(d) The joints between the girdle elements lose their mobility as limbs are reduced.

(e) The longitudinal arms of the interclavicle become shorter during limb reduction while its transverse arm becomes broader. Consequently, the clavicles move closer to the sternum (Figs. III.22 to 25).

(f) The dermal components of the pectoral girdle disappear before the endochondral constituents.

(g) Limbed skinks have a well developed presternum and mesosternum associated with five pairs of ribs; in the bipodous *Scelotes* there is no trace of a mesosternum and only two pairs of ribs are associated with the presternum. In *Acontias meleagris* no distinct sternum is present though the anteriormost element in the parasternal series is usually homologised with the sternum. Even so, these elements do not articulate with any ribs.

(h) As the sternum degenerates, the parasternum becomes more extensive (cf. Figs. III.21 to 25).

(i) The vestigial shoulder girdle appears to shift forward as limbs regress. Normal limbed lizards have 8 cervical vertebrae, in *Scelotes brevipes* there are only seven, while
in *A. meleagris* the vestigial scapulocoracoid is found in the region of the third and fourth vertebrae.

(j) In *Acontias* the vestigial girdle appears to act as an *inscriptio tendinea* of the hypaxial musculature immediately behind the head (cf. Tiedemann and Tiedemann, 1975).

3.7 PRELIMINARY FUNCTIONAL INTERPRETATION

In normal limbed lizards the girdles seem to perform several biological roles. For example, it links the front limbs to the body axis, it provides attachment for certain cervical and trunk muscles, and it covers and protects vital viscera such as the heart. As front limbs are lost, the locomotor functions fall away, but these elements may still play a protective role and provide attachment for muscles of the body wall as in *Scelotes*, while in *Acontias* only the last function is retained.
4. PELVIC GIRDLES

The pelvic girdle of *Mabuya capensis* consists of three paired bones - the ilium, ischium and pubis (Fig. III.27B). These three bones radiate from the acetabulum where their boundaries are demarcated by sutures (Fig. III.27B). The ilium projects posterodorsally and its inner surface forms a synovial joint with the pleurapophyses of the sacrum (Fig. III.27C). The pubis, on the other hand, extends anteromedially in a more or less horizontal plane to meet its partner in the midline of the belly. (Fig. III.27B). The ischium stretches ventromedially to unite with its partner in the ventral midline at the ischial symphysis (Fig. III.27A).

The pelvic girdle shows the following tendencies associated with limb regression:

(a) Miniaturization of the girdle is the first step in the process of degeneration (cf. Figs. 27A to D).

(b) The projection of the ischia are more oblique in reduced limbed skinks; consequently the thyroid fenestra becomes smaller (cf. Figs. III.27A-D).

(c) The symphyses weaken in *Scelotes* (Fig. III.27D) and disappear in *Acontias* (Fig. III.6C & D).

(d) Even in the externally limbless *S. arenicola* the three pelvic bones are still distinct (Fig. III.27D).

(e) On the other hand, in the totally limbless *A. meleagris* only a rod-like pelvic vestige remains (Fig. III.6C & D).
FIG. III.27 A

THE PELVIC GIRDLE OF MABUYA CAPENSIS:
(A) A TRANSVERSE SECTION AT THE LEVEL of the ACETABULUM;
(B) A POSTEROVENTRAL VIEW of the ENTIRE GIRDLE;
(C) A TRANSVERSE SECTION THROUGH THE SACRO-ILIAC JOINT.
(D) PELVIC GIRDLE OF SCELOTES BREVIPES IN VENTRAL VIEW:
(E) PELVIC GIRDLE OF SCELOTES BIPES IN VENTRAL VIEW:
(F) PELVIC GIRDLE OF RIOPA SUNDEVALII IN VENTRAL VIEW.
IV. Locomotor Apparatus: Myology

1. General

The muscular and skeletal systems are intimately associated with each other and together form two major components of the locomotor apparatus (Romer, 1956). From the previous section it is clear that limb regression is accompanied by marked modifications of the postcranial skeleton. This section explores the parallel modifications of the axial musculature.

Special attention is focused on the axial musculature for several reasons. Firstly, whereas the appendicular muscles atrophy with partial or complete reduction of limbs, the axial muscles are present in both limbed and limbless forms. Secondly, the hypertrophy of the axial skeleton as documented in the previous chapter leads one to expect positive development of the axial musculature, which in limbless skinks is exclusively responsible for progression. Thirdly, these muscles have been neglected in previous studies.

The absence of studies on the axial muscles of skinks is a major reason for this investigation. Fürbringer (1869) deals in detail with the osteology and myology of the degenerating shoulder girdles of several lizards including species of skinks. Tiedemann and Tiedemann (1975) undertook a similar study on four species of skinks which form a regression series. But as Camp (1923) points out "Fürbringer (1869), when investigating the anatomy of degenerating limbs, unfortunately paid little attention to the much more significant changes..."
in the body muscles in limbless lizards" (pp. 380-81). Gans (1962) expressed the need for a study on the axial musculature as follows: "It is regrettable that we lack any careful comparative studies of the myological changes in the trunk musculature of a series of species approaching the limbless condition" (p. 173). Waters (1969) also comments on the paucity of works dealing with the trunk muscles of reduced limbless lizards. Gasc (1968, p. 137) noted that histological techniques are indispensable for a thorough study of the axial musculature. Hence, the present study is based on serial sections as well as on dissections.

Waters (1969) reviews the earlier works dealing with reptilian muscles. Consequently, only those publications specifically concerned with the musculature of skinks or those found useful in the present study are mentioned. Camp (1923) provides a thorough study of the rectus abdominis system as well as a review of Maurer's investigations (1869 and 1898) on the embryology and comparative anatomy of the hypaxial musculature. Smirnowsky (1930) describes the respiratory muscles of a number of lizards including the skinks Eumeces schneideri and E. septemtaeniata. His description of the muscles of the lateral body wall proved very useful. Nishi (1938) and Vallois (1922)* are credited with providing the most definitive classical accounts of the epaxial musculature. Hence two systems of terminology are found in the literature. The terminology of Nishi (1938) is adopted for the epaxial muscles.

* Original not seen.
Olson (1936) describes the epaxial muscles of *Iguana* and provides reconstructions of homologous muscles in fossil amphibians and reptiles. The accounts on cervical muscles by Evans (1939) and Van der Heever (1976) also proved useful. Nash and Tanner (1970) describes some of the axial muscles of the skinks, *Eumeces gilberti* and *E. skiltonianus*. Gasc in a series of papers (1965, 1967a, 1968 and 1977) considers aspects of the axial musculature of partially or completely limbless reptiles. In this description the scheme of subdivisions as outlined by Romer (1956) and Guibè (1970) is followed.

As the axial musculature is often composed of overlapping sheets or slips of muscles that are intergrown and not separated by distinct epimysia (Waters, 1969), its detailed description is very complicated. On the other hand, larger groups of muscles such as the transversospinalis system are clearly distinguishable. Consequently, this analysis characterizes the larger groups of muscles in the regression series before considering details such as fibre arrangement, attachment, number of segments spanned by constituent sheets or slips of muscles. The questions addressed are: Have any of these clearly definable muscle groups hypertrophied? Have any undergone reduction or change in position? How are the observed changes related to trends observed in the skeleton?

2. MUSCLE GROUPS

Romer (1956) classifies reptilian axial muscles as follows:
DEFINITIONS

3.1  EPAXIAL MUSCULATURE (Fig. IV.1)

The trunk muscles of fishes are clearly divisible into an epaxial group located above the horizontal septum and a hypaxial group situated below this septum (Romer, 1956). Traces of this division are retained by reptiles in which the epaxial musculature is comprised of three longitudinal bands of muscle found on either side of the vertebral column (Nishi, 1938). These bands are: the transversospinalis system, the longissimus system and the iliocostalis system (Fig. IV.1).

3.1.1  TRANSVERSOSPINALIS SYSTEM (Fig. IV.1)

The paraspinal columns of the transversospinalis system lie on either side of the neural spines along the entire length of the vertebral column (Olson, 1936). Though its subdivisions are sometimes poorly delimited by epimysia (Waters, 1969), the system as a whole is clearly demarcated as it is housed in an osseofibrous canal, the transversospinalis compartment (cf. Jonsson, 1970). The muscle system is bounded medially
by the neural spines and the longitudinal interspinal fascia, ventrally it rests on the neural arches, laterally it is bordered by the medial intermuscular septum (Waters, 1969; dorsal septum, Olson, 1936), and dorsally it is covered by the dorsal fascia (Fig. IV.1).

3.1.2 LONGISSIMUS SYSTEM (Fig. IV.1)

The longissimus system is a muscular band that lies lateral to the transversospinalis system on either side of the body. The longissimus is housed in a fascious canal, the longissimus compartment (cf. Jonsson, 1970) that is formed by the lateral intermuscular septum (Waters, 1969) that passes from the vertebra below and around the longissimus to fuse with the dorsal fascia. This fascia curves over the muscle and joins the medial intermuscular septum, which separates the transversospinalis and the longissimus compartments (Fig. IV.1).

3.1.3 Iliocostalis System (Fig. IV.1)

The iliocostalis differs from the transversospinalis and the longissimus systems in several respects. Firstly, instead of being almost oval in cross-section, it is a broad, thick sheet of muscle which extends alongside the longissimus in the dorsolateral flanks of the trunk. Secondly, it is not enclosed in a distinct fascial compartment, thus it is not as clearly demarcated especially distally, as are the other two epaxial components. Its proximal margin joins the dorsal fascia as well as a small portion of the lateral intermuscular septum in the region where these two sheets intersect. Medially, the
FIG. IV.1 A & B. DIAGRAMMATIC CROSS-SECTION OF Mabuya capensis (A) AND Scelotes bipes BASED ON MICROSCOPIC SLIDES. DOR, DORSAL FASCIA; ISS, INTERSPINAL SEPTUM; LIS, LATERAL INTERMUSCULAR SEPTUM; LNGC, LONGISSIMUS COMPARTMENT; MIS, MEDIAL INTERMUSCULAR SEPTUM; TRSC, TRANSVERSOSPINALIS COMPARTMENT.
FIG. IV.1c. DIAGRAMMATIC CROSS SECTION OF *Acontias meleagris*

A1A2 LATERAL SPREAD OF TRANSVERSOSPINALIS SYSTEM.
B1B2 LATERAL SPREAD OF LONGISSIMUS SYSTEM.
C1C2 DIAMETER.
CIRCUMFERENTIAL SPREAD: U OF TRANSVERSOSPINALIS, V OF LONGISSIMUS, W OF ILIOCOSTALIS, X OF OBLIQUUS ABDOMINIS EXTERNUS, Y OF VENTRAL RECTUS MUSCULATURE.
iliocostalis partially overlaps, but remains distinct from, the underlying hypaxial musculature. By contrast, its distal end is intimately interwoven with the M. obliquus abdominis superficialis.

In brief, the epaxial musculature of the entire regression series is composed on each side of two columnar masses, the transversospinalis and the longissimus systems. These are housed in distinct osseofibrous or fibrous canals, while the third group forms a thick sheet along the dorsolateral flanks of the trunk with its distal margin closely interwoven with the hypaxial muscles (Fig. IV.1A and B).

3.2 HYPAXIAL MUSCULATURE (Fig. IV.1)

The hypaxial musculature is composed of several superimposed sheets of muscle which constitute the lateral and ventral walls of the trunk. These layers of muscle are interrupted by the pectoral and pelvic girdles (Romer, 1956). In quadrupedal lizards thoracic and abdominal subdivisions can be distinguished, associated with variation in the structure of the ribs (Guibè, 1970).

For the morphometric analysis, the hypaxial musculature is treated as a single unit with the exception of the M. rectus abdominis. The latter is treated differently for two reasons. Firstly, it is clearly demarcated in serial sections by fasciae which extend on either side from the M. transversus abdominis (Fig. IV.1). Secondly, Camp (1923, p. 385) suggests that the rectus musculature is an indispensable requisite for
limb reduction. This idea, which seems doubtful, has found its way into subsequent literature. For example, Gorman (1975, in the 15th edition of the Encyclopaedia Britannica vol. 16, p. 286), asserts that after limb loss has occurred: "Such lizards propel themselves entirely by lateral undulations emanating from highly complicated ventral abdominal muscles". If this statement were true, one would expect the ventral rectus abdominis to hypertrophy with limb regression. Therefore, the cross-sectional area of this muscle will also be determined for the regression series.

4. MORPHOMETRIC ANALYSIS

4.1 RELATIVE CROSS-SECTIONAL AREA

Graph II.5 illustrates that as limbs degenerate there is a concomitant reduction in the maximum trunk diameter. The vertebrae of reduced limbed species are, however, wider than those of their normal-limbed counterparts (Fig. III.18). Let us explore how this reduction in transverse diameter affects the relative cross-sectional areas of the body wall and the visceral space. Any cross-section is comprised of the body wall (consisting mainly of muscle and skeleton) and the visceral cavity (housing the viscera)(Fig. IV.1). Reduction in cross-sectional area, characteristic of reduced limbed skinks, must therefore, involve either a decrease in the transverse area of the body wall or a diminution of the transverse area occupied by the visceral cavity or a combination of both. In order to determine which of these three alternatives pertain
FIG. IV.2, THE RELATIVE AREA OCCUPIED BY BODY WALL AND VISCERAL SPACE BASED ON 120 AREA DETERMINATIONS (SEE APPENDIX IV.A)
the following indices were calculated from planimeter determinations of areas occupied by specific regions in enlarged photographs of serial sections:

(i) \( \frac{\text{Area occupied by visceral cavity in the photograph} \times 100}{\text{Area of entire cross-section of the body in the same photograph}} \)

(ii) \( \frac{\text{Area of photograph occupied by the body wall} \times 100}{\text{Area of entire transverse section in the same photograph}} \)

These two ratios are complementary (their sum should equal 100) but all three areas were measured and both ratios were calculated to compare the values obtained (see Appendix IV.A).

With limb regression there is an increase in the transverse area occupied by the body wall and a decline in that of the visceral cavity (Fig. IV.2). In other words the body wall hypertrophies steadily at the expense of the visceral space. (This comparison does not take elongation into account.) Having established that the body wall is better developed in partially or completely limbless skinks, let us examine the relative contributions of the epaxial and hypaxial musculature to the body wall by means of the following indices:

(i) \( \frac{\text{Area epaxial musculature}}{\text{Area of body wall in the same photograph}} \times 100 \)

(ii) \( \frac{\text{Area of hypaxial musculature}}{\text{Area of body wall}} \times 100 \)

The sum of these complementary ratios equalled 100 within a fraction of 1 (see Appendix IV.A).

Since the vertebrae constitute a large part of each cross-
FIG. IV.3 RELATIVE AREA OCCUPIED BY EPAXIAL AND HYPAXIAL MUSCULATURE BASED ON 120 AREA DETERMINATIONS. (SEE APPENDIX IV.A)
section, their areas are also reflected in Graph IV.3. On the other hand, the relatively small sections of the ribs were included in the area determined for the hypaxial musculature. As limbs regress the epaxial musculature hypertrophies relative to the hypaxial musculature (Fig. IV.3).

Having established that the epaxial group has hypertrophied, the question arises to what extent does each of its three components contribute to this increased development? The following index was employed:

\[
\frac{\text{Area occupied by each of the epaxial components}}{\text{Area occupied by the entire body wall}} \times 100
\]

(see Appendix IV. A). No simple trends are obvious. There is a steady but modest increase in the development of the iliacostalis down the regression series (Fig. IV.4). There is a marked increase in the sum of the areas of the transversospinalis and longissimus systems. When these two are considered separately no simple trends are obvious (Fig. IV.4). There seems to be a trend for the transversospinalis to increase in development down the regression series, but *R. sundevallii* does not fit into such a pattern (Fig. IV.4). Similarly the longissimus appears to hypertrophy down the regression series; however, this muscle is not as well developed in the limbless *Acontias* as in the bipodous *Scelotes*. Two distinct trends appear to occur. Whereas *Scelotes* maximizes the development of the longissimus system with only moderate increase in the transversospinalis, *Acontias* on the other hand, appears to develop both systems to an almost equal degree.
It is interesting to note that Graph III.19 corroborates the interpretation given above. In Graph III.19 *Acontias* is well separated from the rest of the regression series by having vertebrae with wide flaring zygapophyses and narrow vertebral waists. Such vertebrae could accommodate relatively large transversospinalis compartments. Thus, whereas *Scelotes* maximized the development of its longissimus system at the expense of the transversospinalis and the longissimus systems, *Acontias* maximizes to an almost equal degree the development of all three systems.

The relative cross-sectional area of the ventral rectus musculature is expressed by the index

\[
\frac{\text{Area of rectus musculature}}{\text{Area of body wall}} \times \frac{100}{1}
\]

As limbs regress the contribution of the rectus musculature to the body wall declines (Fig. IV.5).

4.2 LATERAL SPREAD

The operation of a muscle depends not only on its physiological cross-section but also on its position relative to the lever or levers it operates. The transversospinalis and longissimus systems act on the vertebral column. The distance separating them from the vertebral column will influence the mechanical advantage of the lever system. Hence indices reflecting the lateral spread of the transversospinalis and iliocostalis were determined. Figure IV.1C defines the measurements used in the calculation of these indices (also see Appendix IV.B).
Fig. IV.4 The area occupied by the three components of the epaxial musculature relative to the area of the entire body wall X 100. (See appendix IV.A)
They reflect the lateral spread of the muscle system in question relative to the diameter of the body in the midtrunk region. The nearer a muscle extends to the lateral surface of the body the larger the index. Figure IV.6 shows that as the limbs regress, the lateral spread indices increase, for both the transversospinalis and the longissimus systems. As limbs degenerate the positions of these muscles shifts laterad. The biomechanical implications of such change in relative position will be discussed in Chapter VI.6.

4.3 CIRCUMFERENTIAL SPREAD

The maximum trunk diameter of the specimens in our regression series varies a great deal (Fig. II.5). Therefore it should be useful to measure the development of the various muscles in a way independent of the animal's diameter or cross-sectional area.

This was done by determining the angle over which the superficial extremities of certain muscles spread as illustrated in Figure IV.1C. The circumferential spread of the transversospinalis, longissimus, iliocostalis, obliquus abdominis externus and the rectus abdominis is reflected in Graph IV.7.

As limbs regress the circumferential spread of:

(a) the epaxial group increases;
(b) the superficial hypaxial musculature declines;
(c) the transversospinalis system increases;
(d) the longissimus group waxes;
(e) the iliocostalis system shows no unambiguous trend;
FIG. IV.5. THE RELATIVE DEVELOPMENT OF THE M. RECTUS ABDOMINIS SUPERFICIALIS IN A REGRESSION SERIES OF SKINKS.
(f) the superficial portions of the M. obliquus abdominis superficialis decline;

(g) M. rectus abdominis (medianus and superficialis only) steadily declines.

There is thus an unequivocal trend for the epaxial groups to spread over a larger portion of the lateral circumference of the body with the concomitant decline in the spread of the superficial hypaxial musculature.

Thus in *Mabuya* the iliocostalis is a broad thin sheet covering the dorsolateral aspect of the trunk while the M. obliquus abdominis externus covers most of the lateral and ventrolateral areas (Fig. IV.1). In *Acontias* on the other hand, as a result of the expansion of the transversospinalis and longissimus groups, the iliocostalis now occupy a lateral position while the M. obliquus abdominis has retreated to the ventrolateral aspect of the trunk.
Fig. IV. 6. Comparison of the lateral spread index of the transversospinalis and longissimus systems in a regression series. The measurements are defined in Fig. IV. 1c. Each column reflects the mean for a minimum of 25 slides.
(See Appendix IV.B)
5. DESCRIPTION OF TRUNK AXIAL MUSCULATURE

5.1 GENERAL

The axial musculature of the mid-trunk region is described in detail for *M. capensis* and *A. meleagris*. Two specimens of the much larger *A. plumbeus* were also available for dissection, hence whenever the generic name *Aontias* is employed it refers to these two species. Attention is confined to the mid-trunk region because the axial musculature is either partially or completely segmented. Hence the anatomy of the mid-trunk region is repeated for much of the body. Moreover, these muscles appear to be mainly responsible for locomotion (Fig. VI.3). Consequently, specializations of the cervical and caudal regions are not considered. Instead of describing all the trunk muscles of each animal in turn, homologous muscle groups are first defined, then described in *Mabuya* and in *Aontias*. Differences are noted and the intermediate groups (*Riopa* and *Saelotes*) examined to establish whether specific trends can be detected.

5.2 TRANSVERSOSPINALIS SYSTEM

This long, medium column of muscle is continuous on either side of the vertebral column, adjacent to the neural spines, starting from the posterior margin of the skull and extending almost to the tip of the tail (Olson, 1936; Guibè, 1970). It is housed in an osseofibrous canal, the transversospinalis compartment (Fig. IV.1) which is bounded medially by the neural spines, neural arches and interspinal fascia (Fig. IV.1).
FIG. IV. 7.

TRANSVERSE SECTIONS OF Acontias meleagris (C); Scelotes bipes sexlineatus (B); AND Mabuya capensis (A); SUPERIMPOSED WITH THE MID-SAGITTAL PLANES AND THE CENTRAL POINTS (CP) ALIGNED IN ORDER TO COMPARE THE CIRCUMFERENTIAL SPREAD OF THE SUPERFICIAL AXIAL MUSCLES. AROUND THE CROSS SECTIONS THE CIRCUMFERENTIAL SPREADS OF THE VARIOUS MUSCLES ARE ILLUSTRATED GRAPHICALLY

ILC, ILIOCOOSTALIS SYSTEM;
LNG, LONGISSIMUS SYSTEM
TRS, TRANSVERSOSPINALIS SYSTEM.
Its superficial surface is covered by the dorsal fascia which in turn is joined by the medial intermuscular septum running from interarticular ridges of the vertebrae (Fig. IV.1).

The medial part of the muscular column is covered by a series of segmental, imbricating tendons (usually described as points of insertion) while the lateral part of the column is fleshy (Fig. IV.9A). Behind these segmental tendons of insertion the muscle fibres are complexly intergrown.

This intergrown mass of fibres can be differentiated, not on the basis of distinct epimysia (Waters, 1969), but on the grounds of fibre direction and points of attachment of these fibres, into three superimposed components: the M. semispinalis et spinalis, the M. multifidus and M. interneuralis (Nishi, 1938; Waters, 1969; Guibè, 1970). The layering of these three groups of partially intergrown muscles is very complex. The anterior portion of the overlapping M. semispinalis et spinalis reach the surface of the muscular column. They cover completely the deeper M. multifidus. The short segmental Mm. interneuralis lie deepest, adjacent to the neural arches and spines of the vertebrae.

The M. semispinalis et spinalis (= M. articulo-spinalis dorsi, Vallois, 1922; per Guibè, 1970) is composed of two intimately intergrown muscles only distinguishable by their different fibre directions and points of origin (cf. Waters, 1969). The semispinalis component links a zygapophysis to a neural spine (Mosauer, 1935); the spinalis component links neural spines
FIG. IV. 8A.  THE SUPERFICIAL AXIAL MUSCULATURE OF *Mabuya capensis* IN LATERAL VIEW.

EMC,  M. episterno-cleidomastoideus;
IAR,  M. interarticularis superior;
IEB,  M. intercostalis externus brevis;
IEL,  M. intercostalis externus longus;
ILC,  M. iliocostalis;
IMY,  intermyoseptal muscle;
INI,  M. intercostalis internus;
INN,  M. interneuralis;
LAT,  M. latissimus dorsi;
LNG,  M. longissimus dorsi;
LNGC, longissimus compartment;
LNGT, tendon of M. longissimus dorsi;
MSP,  M. spinalis;
MUL,  M. multifidus;
MYS,  myoseptum;
NSP,  neural spine;
OAES, M. obliquus abdominis externus superficialis;
OAI,  M. obliquus abdominis internus;
OOM,  origin of M. multifidus;
OSM,  origin of the semispinalis;
OSN,  origin of M. spinalis;
PEC,  M. pectoralis;
RLA,  M. rectus lateralis;
RME,  M. rectus medianus;
SCD,  M. subcostalis dorsalis;
SCL,  superior costal ligament;
SMP,  M. spinalis et semispinalis;
SPC,  M. sphincter colli;
TAB,  M. transversus abdominis;
TAD,  tendon from anterodorsal aspect of neural spine;
TCSMP, common tendon of the M. spinalis et semispinalis;
TNA,  tendon on posterior aspect of neural arch;
TRAP,  M. trapezius;
TRS,  transversospinalis system;
TRSC, transversospinalis compartment;
VER,  vertebra.
FIG. IV. 8A. THE SUPERFICIAL AXIAL MUSCULATURE OF *Mabuya capensis* IN LATERAL VIEW
FIG. IV.8B  DIAGRAM TO ILLUSTRATE THE MUSCLES ASSOCIATED WITH THE RIBS OF Mabuya capensis. (SEE FIG IV.8A FOR ABBREVIATIONS).

FIG. IV.8C  DIAGRAM TO ILLUSTRATE THE LAYERING AND VARYING FIBRE DIRECTIONS OF SOME OF THE HYPAXIAL MUSCLES ASSOCIATED WITH THE RIBS OF Mabuya capensis. (SEE FIG. IV.8A FOR ABBREVIATIONS).
that are several segments apart (Mosauer, 1935).

The M. multifidus (= M. spino-articularis dorsi, Vallois, 1922; per Guibé, 1970) lies deep to the M. semispinalis et spinalis and is much shorter than the latter, spanning only two or three segments.

The Mm. interneurales (Guibé, 1970) are short segmental muscles lying against and linking successive vertebrae. They usually occur between the axis and the posterior caudal region where they are intergrown with the M. extensor caudae medialis (Olson, 1936). They are partially homologous with the Mm. intervertebrales of Mosauer (1935) and are sometimes subdivided into Mm. interspinales (linking successive neural spines), Mm. interarcuales (joining successive neural arches) and (connecting successive zygapophyses) Mm. interarticulares (cf. Olson, 1936). The skinks dissected for this study have only two distinct groups of muscles, sagitally disposed muscle slips attaching to the entire margins of the neural spines and neural arches, the Mm. interneurales (cf. Guibé, 1970) and a second group of distinct muscles which interconnect successive posterior zygapophyses, the Mm. interarticulares superiores (cf. Mosauer, 1935).

5.2.1 TRANSVERSOSPINALIS SYSTEM IN M. CAPENSIS

5.2.1.1 General

The transversospinalis column can be exposed by slitting the fascia dorsi directly over the transversospinalis compartment. Care must be taken not to cut the imbricating tendons which
run backwards, from the posterodorsal aspects of the neural spines. These tendons gradually descend into the medial portion of the muscle with the result that its lateral margin remains fleshy and fused with the medial intermuscular septum (Fig. IV.9A).

5.2.1.2  *M. semispinalis et spinalis* (Fig. IV.9A & B)

Although the overlapping, anterior tendons of insertion of these muscles are segmented, the muscular column shows no further signs of segmentation. The *M. semispinalis et spinalis* are also intergrown with the result that they can only be distinguished on the basis of different fibre directions and separate points of attachment. Although muscle fibres of the individual slips are fused, in each slip the *M. spinalis* mainly originates from a tendon that arises from the anterodorsal summit of a neural spine (Fig. IV.9A, TAD). Each slip of the *M. semispinalis* originates more ventrally from a postzygapophysis and the intermuscular septum in front of such a postzygapophysis (Fig. IV.9A, OSM). The tendon which extends forward over two segments from the anterodorsal aspect of the neural spine widens into a straplike, parasagittally disposed tendon with fibres of the *M. multifidus* originating from its inner surface (Fig. IV.9A, OOM) while the fascicles of the *M. spinalis* arises from its outer surface (Fig. IV.9A, OSN). The pinnate *M. spinalis* lies in a parasagittal plane (Fig. IV.9A, MSP). The fleshy part of this muscle is almost two segments long and inserts onto the common anterior tendon which joins the posterodorsal surface of a neural spine about two-and-a-half
FIG IV. 9. THE MAIN EPAXIAL MUSCLES OF *Mabuya capensis* IN DORSAL VIEW (A) AND IN SEMI-DIAGRAMMATIC TRANSVERSE SECTION (B) (SEE FIGURE IV.8A FOR ABBREVIATIONS).
segments anterior to the point where the muscle fibres originate (Fig. IV.9A, TCSMP). Some fibres of the M. spinalis are fused with those of the underlying M. multifidus. The M. semispinalis has a fleshy origin from a postzygapophysis and the adjacent intermuscular septum (Fig. IV.9A, OSN). The fibres of a particular slip are intergrown with those of preceding and succeeding slips. The fibres lie in a more or less frontal plane, pass over about two-and-a-half vertebral segments before joining the spinalis on the common anterior tendon (Fig. IV.9A, TCSMP). The M. semispinalis et spinalis plus its tendons are five segments long. In *Mabuya quinque­taeniata* this muscle is five metameres long (Gasc, 1967b).

5.2.1.3 *M. multifidus* (Fig. IV.9A & B)

The multifidus is a paraspinal muscle about two segments long lying deep to the M. spinalis and in turn concealing two slips of the M. interneuralis (Fig. IV.9A, MUL). It originates from the medial side of the cranially directed tendon which arises from the anterodorsal apex of a neural spine (Fig. IV.9A, OOM). The fibres of the M. multifidus run medially deep to the next cranial tendon and fuse to the outer surface of a short but broad tendon which extends posteriorly from the entire posterior edge of a neural spine and a neural arch (Fig. IV.9A, TNA). This tendon is about half-a-segment long. The fibres of a M. interneuralis attach to its inner surface while the fibres of the M. multifidus attach to its outer surface (Fig. IV.9A, TNA).

5.2.1.4 *M. interneuralis* (Fig. 9A; INN)

The segmental M. interneuralis originates above a postzygapophysis and inserts onto the inner surface of tendon, TNA (Fig. IV. 9A).
FIG. IV 9c. Diagram to illustrate the rectus musculature of *Mabuya capensis* in ventral view. The supporting skeletal elements are outlined in dots and on the left side portions of the *Mm. rectus medianus* and the *obliquis abdominis externus superficialis* are excised to expose the *M. rectus internus* and the *M. rectus lateralis.*
5.2.1.5 *M. interarticularis superior* (Fig. IV.9A)

The frontally disposed segmental *M. interarticularis superior* lies deep to the *M. semispinalis* and interconnects two successive postzygapophyses (Fig. 9A, IAR). The fleshy caudal attachment arises from the craniodorsal surface of a postzygapophysis and attaches in association with a tendon to the caudodorsal surface of the next anterior postzygapophysis (Fig. IV.9A, IAR).

5.2.2 TRANSVERSOSPINALIS SYSTEM IN ACONTIAS

5.2.2.1 General

The transversospinalis system is exposed by slitting the dorsal fascia between the medial intermuscular septum and the neural spines, taking care not to cut the underlying imbricating tendons of insertion onto the neural spines (Fig. IV.10A, DOF, TCSMP).

5.2.2.2 *M. semispinalis et spinalis* (Fig. IV.10, SMP)

Although the overlapping tendons of insertions of the *M. semispinalis et spinalis* are attached to the neural spines, there are no further signs of segmentation as the overlapping muscle fascicles are intergrown (Fig. IV.10, TCSMP). Despite complex interfusion of muscle fascicles individual units can be recognized (Fig. IV.10, SMPU). Each of these arises in association with two converging tendons. The upper wider, straplike tendon arises from the anterodorsal summit of a neural spine (Fig. IV.10A, TAD). Fibres of the *M. multifidus* arise from its inner surface (Fig. IV.10A, MUL) while the *M. spinalis* is
FIG. IV, 10A. THE AXIAL MUSCULATURE OF *Acontias meleagris* AS SEEN IN RIGHT, LATERAL VIEW. THIS DRAWING IS BASED ON A SERIES OF DISSECTIONS SUPERIMPOSED ONTO A SKELETAL OUTLINE DRAWN FROM A CLEARED, ALIZARINE-STAINED SPECIMEN. TO FACILITATE INTERPRETATION OF THE SKETCH EACH MUSCULAR UNIT IS ILLUSTRATED IN ISOLATION WITH BOTH THE SUPERFICIAL AND DEEP MUSCLES REMOVED. THE PARTS LABELLED a TO e REPRESENT PORTION OF THE SEGMENTAL M. SEMISPINALIS ET SPINALIS SUPERFICIAL TO A SINGLE SEMISPINALIS ET SPINALIS UNIT.

AOAES, Anterior attachment of OAES;
DOF, dorsal fascia;
IAR, M. interarticularis superior;
IEB, M. intercostalis externus brevis;
IEL, M. intercostalis externus longus;
ILC, M. iliocostalis;
IMY, intermyoseptal muscle;
INN, M. interneuralis;
ISS, interspinal septum;
LEC, M. levator costae;
LIS, lateral intermuscular septum;
LNG, M. longissimus dorsi;
LNGC, longissimus compartment;
LNGU, longissimus unit;
MIS, medial intermuscular septum;
MUL, M. multifidus;
MYS, myoseptum;
NSP, neural spine;
OAES, M. obliquus abdominis externus superficialis;
OSN, origin of a M. spinalis slip;
RAS, M. rectus abdominis superficialis;
SCD, M. subcostalis dorsalis;
SCV, M. subcostalis ventralis;
SMP, M. semispinalis et spinalis;
SMPU, semispinalis et spinalis muscular unit;
TAB, M. transversus abdominis;
TAD, anterodorsal tendon;
TCSMP, common tendon of the M. semispinalis et spinalis;
TLNG, tendon of the M. longissimus;
TNA, tendon on the posterior margin of the neural arch;
TRS, transversospinalis system;
TRSC, transversospinalis compartment;
TUC, M. tuberculocostalis;
TV ventral anterior tendon;
VER vertebra.
FIG. IV. 10B SEMI-DIAGRAMMATIC TRACING OF A CROSS-SECTION THROUGH THE TRUNK OF *Acontias meleagris* TO ILLUSTRATE THE *in situ* RELATIONSHIPS OF THE MUSCLES SHOWN IN FIG. IV.10A. (SEE LATTER FOR ABBREVIATIONS.)
associated with its outer surface and also partially intergrown with M. multifidus as well as the M. semispinalis (Fig. IV.10A, GSN). The pinnate fibres of the M. spinalis portion lie in a more or less parasagittal plane adjacent to the neural spines. They pass craniad over about four segments before fusing with the common semispinalis et spinalis tendon (Fig. IV.10A, TCSMP). The M. semispinalis originates from the lower much narrower tendon (Fig. IV.10A, TV), the medial intermuscular septum and the upper surface of a postzygapophysis. Its pinnate fibres lie in a more or less frontal plane and are medially intergrown with those of M. spinalis. The fibres of both components span approximately four segments before fusing with the common tendon of the M. semispinalis et spinalis. This common tendon passes over three segments free of muscle before fusing with the posterodorsal aspect of the neural spine (Fig. IV.10A, TCSMP). This long common tendon is held in position by connective tissue sheets emanating from its medial and lateral sides.

Each M. semispinalis et spinalis unit is thus approximately seven vertebral segments long in A. meleagris. This confirms the findings of Gasc (1967a). The M. semispinalis et spinalis as a whole consist of overlapping units which lie in the transversospinalis compartment deep to the dorsal fascia and superficial to the Mm. multifidi and the Mm. intervertebrales.

5.2.2.3 M. multifidus (Fig. IV.10A; MUL)

The M. multifidus lies deep to the M. spinalis and it in turn conceals the M. interneuralis. It is approximately two seg-
ments long. Posteriorly it arises from the medial surface of the converging tendons (Fig. IV.10A, TAD & TV) described in connection with the M. semispinalis et spinalis. After originating from the inner surface of the converging tendons, for the length of one segment the fibres run medially between the opening of the next anterior set of converging tendons to insert onto the outer surface of a strong tendon emanating from the entire posterior margin of a neural spine and arch (Fig. IV.10, TNA). The M. interneuralis attaches to the inner surface of this tendon (Fig. IV.10, INN) while the M. multifidus attaches to its outer surface (Fig. IV.10, MUL).

The M. multifidus thus originates from a tendon associated with the anterodorsal summit of a neural spine and attaches to a short broad tendon projecting from the posterior margin of the neural spine arch and the neural spine of the third vertebra anterior to its origin.

5.2.2.4 Mm. interneurales (Fig. IV.10, INN)

The segmental Mm. interneurales are well developed in Acontias. Their fibres originate from the concavity of the neural arch anterodorsal to its postzygapophysis and insert onto a broad, strong tendon which emanates from the entire posterior margin of the neural arch as well as the neural spine and extends backward for approximately the length of half a vertebra. While the M. interneuralis attaches to the inner surface of this tendon (Fig. IV.10, TNA) the M. multifidus inserts on its outer surface.
5.2.2.5 *M. interarticularis superior* (Mosauer, 1935)

Each *M. interarticularis superior* is a segmental muscle linking two successive postzygapophyses (Fig. IV.10, IAR). The posterior attachment to the anterodorsal surface of a postzygapophysis is fleshy while a tendon which runs forward from about the middle of the muscle is associated with the next cranial postzygapophysis. While the Mm. interneurales are parasagittally disposed the Mm. interarticulares lie in a frontal plane.

5.2.3 COMPARISON

The overall organization of the transversospinalis system is similar in the entire regression series. The subdivisions - M. semispinalis et spinalis, M. multifidus, M. interneuralis and M. interarticularis superior - are easily recognizable in all members of the series.

There are, however, striking differences in the degree of development and the number of segments spanned by elements of this muscular system. In the reduced limbed species these muscle systems show a greater cross-sectional area (Fig. IV.4), wider lateral spread (Fig. IV.6) and greater circumferential spread (Fig. IV.7). The transversospinalis system is not only hypertrophied in terms of its transverse bulk but its length also increases by the multiplication of the number of presacral metameres (Fig. III.12).

Furthermore, whereas the M. semispinalis et spinalis spans approximately five metameres in *Mabuya*, it spans about seven

In *Acontias* the origin of the M. semispinalis et spinalis is associated with a pair of converging tendons (Fig. IV.10, TAD & TV) which resembles the tendinous arcade which Mosauer (1935) described in snakes. Waters (1969) also describes a ventral tendon in *Ophisaurus*. In *M. capensis* no ventral tendon was observed.

Comparison of the transversospinalis system in the regression series leads to the following conclusions:

(a) The basic subdivisions of the system are retained by all members.

(b) The system usually hypertrophies in reduced limbed forms.

(c) The system develops from a greater number of metameres in reduced limbed forms.

(d) The M. semispinalis et spinalis spans slightly more segments in the limbless *Acontias* than in *Mabuya*.

5.3 M. LONGISSIMUS DORSI

5.3.1 GENERAL

The longissimus system lies between the M. transversospinalis and the M. iliocostalis. It is separated from the former by the medial intermuscular septum and from the latter by the lateral intermuscular septum. These intermuscular septa fuse with the dorsal fascia to form a fibrous canal, the longissimus compartment around the longissimus system (Fig. IV.10B, LNGC). The M. longissimus extends along almost the entire
length of the trunk and along most of the tail (Olson, 1936). Slips originate from the ilium, prezygapophyses, the medial intermuscular septum. Anteriorly the system starts on the posterior surface of the skull as the M. longissimus cervico-capitis (Guibè, 1970).

5.3.2 *M. LONGISSIMUS IN M. CAPENSIS* (Fig. IV.9A; LNG)

The longissimus system is housed in the longissimus compartment lateral to the transversospinalis system and medial to the iliocostalis system which partially overlaps it. Posteriorly the muscle originates from the ventral surface of a prezygapophysis and the medial intermuscular septum (especially at its ventral and dorsal extremities). The fibres run craniolaterally over approximately 3 segments and insert pinately on a short forked tendon (Fig. 9A; TLNG). The shorter lateral arm of this tendon fuses with the lateral intermuscular septum almost immediately. The medial arm is longer and runs forward before fusing with the dorsal fascia as a wide circumferential tendon which is more or less equidistant from the medial and the lateral intermuscular septa. The lateral portion of the muscle in the region of the tendon is the only part that is clearly segmented. The fibres of the deeper portions are intergrown.

5.3.3 *M. LONGISSIMUS IN ACONTIAS* (Fig. IV.10A; LNGU, LNGC)

The longissimus system is exposed by carefully slitting the dorsal fascia over the longissimus compartment. Immediately beneath this fascia and partially attached to it are a series
of Y-shaped tendons with the two arms of the Y running forward in such a way that the upper arm fuses broadly with the inside of the dorsal fascia while the shorter lateral arm fuses with the lateral intermuscular septum (Fig. IV.10A, TLNG) directly opposite a point of origin of a portion of the M. iliocostalis.

The base of the Y forms a tendon that descends into the column of muscle with the result that its lateral surface near the tendons is segmented, while the deeper layers of the muscular column show no segmentation. The fibres which converge pinately onto this tendon arise 6 to 8 segments further back from the medial intermuscular septum and the anteroventral surface of a prezygapophysis as well as from a strong aponeurosis covering the intercostal muscles at the base of the longissimus compartment.

The fleshy part of the muscle extends over five to six segments while the Y-shaped tendon is about two segments long. The entire muscles span about eight vertebrae. (This confirms the findings of Gasc, 1967b).

5.3.4 COMPARISON

The longissimus system is easily recognizable in all members of the regression series. Partially or completely limbless skinks differ from normal limbed ones in the following respects:

(a) The relative cross-section area of the muscle is greater in skinks with reduced limbs (Fig. IV.4),

(b) The muscle columns are positioned nearer to the lateral
margins of the trunk (Fig. IV.6).

(c) The muscle has a greater circumferential spread (Fig. IV.7).

(d) The muscle develops from a greater number of trunk metameres.

(e) The muscle spans about three segments in *M. capensis* but about seven to eight in *Acontias*.

(f) The Y-shaped tendon is longer and better developed in *Acontias*.

5.4 ILIOCOSTALIS SYSTEM

5.4.1 GENERAL

The iliocostalis system is the lateralmost component of the epaxial musculature. This thin but wide layer of muscle occupies the dorsolateral aspects of the trunk, and lies immediately deep to the skin and lateral to the lateral intermuscular septum. Unlike the other epaxial groups, it is not housed in a distinct compartment; instead a very thin continuation of the dorsal fascia is fused with its superficial surface. Hence, Waters (1969) states that it is not covered by the dorsal fascia. Unlike the other members of the epaxial group this muscle is interrupted posteriorly by the ilium. The posteriormost fibres originate from the craniodorsal edge of the ilium. The muscle extends forward as far as the atlas (Guibè, 1970). Laterally, slips of this continuous sheet of muscle interdigitate with slips from the *M. obliquus externus superficialis* to insert directly on the ribs or to insert via myosepta.
5.4.2 **ILIOCOSTALIS IN M. CAPENSIS** (Fig. IV.8A; ILC)

The iliocostalis forms a wide tract of muscle that lies laterally to the longissimus. The posteriormost fibres originate from the ilium. Most of the fibres, however, originate from the lateral intermuscular septum (Fig. IV.9A, ILC) at the level of the lateral tendon of the longissimus, pass cranial and ventrolateral over approximately four segments before attaching onto the posterior surface of a rib or a myoseptum near the origin of the M. obliquus abdominis externus superficialis. The lateral parts of the muscle differentiate into short segmental slips before inserting onto a myoseptum. The rest of the muscle forms an unsegmented sheet (Fig. IV.8A; ILC).

Although the fibres run over three to four segments from origin to insertion, they are usually interrupted more or less midway by an upper margin of a myoseptum (Fig. IV.9A, MYS). Such myosepta provide surfaces of attachment, mainly for the medial segmental M. intercostalis externus so that only their distal edges are free to interrupt the fibres of the overlying M. iliocostalis (Fig. IV.8B, MYS & IMY).

The latter is covered by the skin and it in turn conceals the medial portion of the M. intercostalis externus as well as the origins of the slips of the M. obliquus abdominis externus (Fig. IV.8A, ILC).

5.4.3 **ILIOCOSTALIS SYSTEM IN ACONTIAS** (Fig. IV.10A, ILC)

As a result of the hypertrophy of the transversospinalis and longissimus systems the M. iliocostalis occupies a lateral
rather than a dorsolateral position along the trunk (Fig. IV. 10A & B). The fibres of this sheet of muscle run obliquely forwards and downwards following the curve of the body over seven to eight segments. They arise from the lateral intermuscular septum at the level of the insertion of the longissimus and insert onto a myoseptum or rib seven to eight segments cranial to their point of origin. Three or four segments from its point of origin the fibres are usually interrupted by a distal margin of a myoseptum (Fig. IV.10A, MYS).

5.4.4 COMPARISON

Although the iliocostalis is not housed in distinct fibrous compartments such as the transversospinalis and the longissimus, it can be readily recognized in the entire regression series where its fibres usually extend from the lateral intermuscular septum to a rib.

With limb regression this muscle system manifests the following trends:

(a) There is a steady increase in its cross-sectional area (Fig. IV.4).

(b) As a result of the hypertrophy of the transversospinalis and longissimus systems, the iliocostalis acquires a more lateral orientation in reduced limbed skinks (cf. Fig. IV.1 & IV.7).

(c) In reduced limbed skinks the iliocostalis system develops from more metameres.
(d) In partially or completely limbless skinks the muscle units span more segments. For example, in *Mabuya* the muscle spans three to four segments while, in *Acontias* it spans seven to eight segments (Fig. IV.10A).

5.5 M. OBLIQUUS ABDOMINIS EXTERNUS

5.5.1 M. OBLIQUUS ABDOMINIS EXTERNUS IN M. CAPENSIS
(Fig. IV.8A)

The larger portion of the M. obliquus abdominis externus superficies is exposed by removal of the skin. Its segmental slips partially overlap like the tiles of a roof. Its upper extremity is interwoven and partially hidden by the lateral margin of the M. iliocostalis while the first two segments are also partially covered by the M. lattissimus dorsi (Fig. IV.8A; OAES). After attaching to a rib via a myoseptum located deep to and proximal to the attachment of a slip of the M. iliocostalis associated with the same myoseptum, the fibres run in a posteroventral direction following the curvature of the trunk, over approximately three segments to insert onto the abdominal intermuscular septum which is continuous with the fascia covering the belly. The muscle begins in the area of the thorax associated with the first sternal rib while it terminates via an aponeurosis onto the lateral process of the pubis and the pubo-ischiadic ligament.

In the thoracic region the M. obliquus abdominis externus is subdivided into two layers - an internal layer (M. obliquus externus profundus) confined to the thoracic region and a more superficial layer (M. obliquus externus superficialis) which occupies both thoracic and abdominal regions (Guibè, 1970; Smirnowski, 1930).
5.5.2 *M. OBLIQUUS ABDOMINIS EXTERNUS IN ACONTIAS*  
(Fig. IV.10A & B; OAES)

The *obliquus abdominis externus* muscle is not differentiated into a superficial and a deep layer, instead it forms a narrow sheet, located immediately deep to the skin between the *M. longissimus* and the *M. rectus abdominis*. In *Acontias* the muscle occupies a ventrolateral rather than a lateral position (cf. Fig. IV.10A & B). Anteriorly the muscle attaches to the caudoventral edge of a myoseptum of a rib deep to the attachment of a slip of the *iliocostalis* (Fig. 10A; AOAES).

From its attachment onto the rib the fibres of the *M. obliquus abdominis externus* run obliquely posteriorly and ventrally following the curve of the body. They pass over 4 to 5 segments before attaching to an aponeurosis (approximately one segment long). The latter attaches to the inside of the skin and to the fascia which covers the *M. rectus superficialis* while further forward the aponeuroses are attached to parasternal chevrons.

5.5.4 *COMPARISON*

(a) As a result of the hypertrophy - especially circumferential spread of the epaxial muscles - the *M. obliquus abdominis externus* occupies a more ventrolateral position in reduced limbed or limbless skinks in which it is also less well developed (Fig. IV.7).

(b) Even in normal limbed skinks the *M. obliquus abdominis externus profundus* is weakly developed and confined to
the thoracic region (cf. Smirnowski, 1930; Guibè, 1970). A profundus subdivision is not present in the limbless Acontias.

5.6 M. RECTUS ABDOMINIS

5.6.1 GENERAL

The ventral abdominal wall between the pelvic and pectoral girdles is usually comprised largely of the M. rectus abdominis. It is much better developed and subdivided in M. aapen-sis than other members of the regression series. There is some confusion about the number of subdivisions comprising the rectus group. According to Camp (1923) there are four subdivisions in autarchoglossine lizards, namely the M. rectus profundus, the M. rectus medianus, the M. rectus lateralis and the M. rectus internus. Nishi (1938) recognizes only three components, namely the M. rectus medianus, the M. rectus lateralis and the M. rectus internus. Waters (1969) describes the four subdivisions as defined by Camp, but qualifies his description of the M. rectus medianus and the M. rectus profundus as follows: "The two muscles are closely applied to one another. The plane of separation is very delicate and difficult to locate, in fact unconvincing" (p. 58). Guibè (1970) states without further elaboration that there are usually three subdivisions.

In M. aapensis three distinct muscles were identified: (a) a M. rectus lateralis, (b) a M. rectus internus and (c) a third muscle which conforms to Camp's definition of the M. rectus profundus. Thus a M. rectus medianus (sensu Camp)
does not appear to be differentiated. Even careful examination of serial sections did not reveal any layering of the profundus group. In conclusion, though *M. capensis* is a member of Camp's Autarchoglossa its rectus musculature is composed of three (and not four) subdivisions. This leaves us with a terminological problem. Nishi (1938) called the entire third portion of the rectus group, the M. rectus medianus while Camp (1923) split it further and reserved the name medianus for a subdivision of this third layer which "...develops by splitting from the main Rectus profundus at an early stage and it seems usually to maintain its individuality because of its connections and functions as a skin muscle... intimately connected with the skin over the whole belly and aiding in locomotion by its pull on the ventral scales" (p. 378).

*M. capensis* lack a M. rectus medianus (*sensu* Camp, 1923) but it has an undifferentiated median rectus group, the rectus medianus (*sensu* Nishi). This third muscle group will be called the M. rectus medianus (*sensu* Nishi).

5.6.2 *RECTUS ABDOMINIS IN M. CAPENSIS* (Figs. IV.8A; IV.1A; IV.9C)

In *M. capensis* this group of muscles comprises three distinct subdivisions: M. rectus lateralis, the M. rectus internus and the M. rectus medianus (*sensu* Nishi).

5.6.2.1 *M. rectus medianus* (*sensu* Nishi, 1938; Fig. IV.9C)

A sheet of muscle on either side of the ventral midline and
extending from the pelvic girdle up to the sternum constitutes the M. rectus medianus. A narrow median gap filled with connective tissue, the linea alba lies between the right and left bands. The muscle fibres are oriented in a longitudinal direction and interrupted by about 6 or 7 tendinous insertions. The entire ventral surface of the muscle is covered by a strong fascia which is continuous with the abdominal intermuscular septum, which is in turn suspended from the M. transversus abdominis (Fig. IV.1A). Posteriorly, the M. rectus is attached to the ischium in three ways. Medially the superficial fascia thickens to form a tendon which is attached to the ischiadic symphysis. Some fibres originate from the pubo-ischiadic ligament and others from the ventral surface of the pubis itself (Fig. IV.9C). Anteriorly, the muscle inserts on the entire lateral margin of the mesosternum deep to the articulation of the mesosternal ribs (Fig. IV.9C). Each longitudinal straplike muscle is thus secured anteriorly and posteriorly by elements of the girdles, medially by the connective tissues of the linea alba and laterally its superficial fascia fuses with the lateral abdominal intermuscular septum. This septum is suspended from a longitudinal aponeurosis of the M. transversus abdominis (Fig. IV.1A). This muscle is thus suited to provide support for the viscera that lie deep to it.

5.6.2.2 M. rectus internus (Fig. IV.9C)

The M. rectus internus is located below the pubis and deep to the M. rectus medianus (山口 Nishi). The fibres of the for-
mer converge from the inside of the lateral process of the pubis toward the linea alba up to about five vertebral lengths in front of the pubic symphysis (Fig. IV.9C). Each muscle forms a triangle with its base attached to the pelvic girdle and its apex on the linea alba. The muscle fibres originate from the inside of the lateral process of the pubis and the pubo-ischiadic ligament while some of the posteriormost fibres are intergrown with the M. rectus medianus (sensu Nishi). The fibres pass craniad and mediad from the pelvic girdle to insert onto the linea alba (Fig. IV.9C). This arrangement of fibres suggests two possible functions. If both right and left portions of the muscle were to contract simultaneously, the pelvis would be stabilized. Unilateral contraction could cause rotation of the pelvis so that the acetabulum moves forward on the contracting side. The synovial joint between the ilium and sacrum would permit such rotation (Fig. III.27C).

The unsegmented M. rectus lateralis lies for most of its length deep to the M. obliquus abdominis externus superficialis and lateral to the abdominal intermuscular septum to which it is also attached (Fig. IV.9C). Posterior to the axilla its fibres emerge from behind the M. obliquus abdominis externus superficialis and run medially over the M. pectoralis to insert into a sheet superficial fascia which covers the M. pectoralis (Fig. IV.8A & 9C). Posteriorly the M. rectus lateralis fuses with the M. rectus medianus and these two then arise from the pubo-ischiadic ligament and the ventral surface of the ischium (Fig. IV.9C).
5.6.3 **M. RECTUS ABDOMINIS SUPERFICIALIS IN ACONTIAS**

The much reduced rectus musculature of *Acontias* is represented by a pair of narrow, thin longitudinal sheets of muscle, the M. rectus superficialis (Camp, 1923). The latter lies in the ventral wall of the body, deep to the skin and a superficial fascia and on either side of a wide linea alba. The distal margin of the M. obliquus abdominis externus overlaps its lateral edge. Neither a M. rectus lateralis nor a M. rectus internus occur.

The fibres of the M. rectus superficialis lie in an antero-posterior plane. They are frequently interrupted, often into segmental slips. Behind the parasternal region these slips attach to tendinous inscriptions and the superficial fascia. In the anterior third of the body some fibres pass deep to the parasternalia while others are attached to them. The deep surface of the muscle is covered by a strong peritoneal fascia.

Posteriorly, each sheet of muscle originates from the ventro-medial tip of a vestigial pelvic girdle element located on either side of the body (Fig. III.6). Anteriorly, the muscle terminates on the ventrocaudal tip of a rudimentary scapulo-coracoid. The ventral surfaces of both sheets are covered by a tough, continuous superficial fascia which passes laterad deep to the costal cartilages to join the aponeurosis of the M. transversus abdominis on either side of the body. An aponeurosis from the M. obliquus abdominis externus also fuses with the superficial fascia.
As the linea alba is relatively wide and the M. rectus superficialis is comparatively narrow, the ventral mid-line of the body is free of muscle fibres. The tough skin and superficial fascia appear to support the viscera.

5.6.4 COMPARISON

(a) Although skinks are members of the Autarchoglossa, the rectus musculature of *M. capensis* has three instead of four subdivisions (cf. Camp, 1923).

(b) With limb regression the rectus musculature atrophies. In the first place there is a reduction in the subdivisions (medianus, lateralis and internus) are represented in *Mabuya*, *Riopa* and *Scelotes* while only one (M. rectus superficialis) persists in *Acontias meleagris*. Secondly, the cross-sectional area and circumferential spread of this muscle declines (Figs. IV.5; IV.7).

(c) In reduced limbed species, on the other hand, the muscles develop from a greater number of metameres.

5.7.1 M. INTERCOSTALIS EXTERNUS IN M. CAPENSIS

The M. intercostalis externus is exposed by the removal of the M. iliocostalis and the M. obliquus abdominis externus. It is differentiated into two parts. The M. intercostalis externus brevis with fibres one segment long and the M. intercostalis externus longus with fibres that span two segments (Fig. IV.8B).

Near the distal ends of the ribs a M. intercostalis externus
brevis have the same fibre direction as a longus component but it only spans a single segment (Fig. IV.8B). Between two successive ribs these fibres fill the intercostal spaces (superficial to the M. intercostalis internus; Fig. IV.8C) from the head of the ribs right up to their distal ends but proximal to the costal cartilages. The fibres arise on the posterior surface of one rib and pass in a posteroventral direction to attach on the anterior surface of the next posterior rib. The muscle is much thicker proximally where its fibres also acquire a more or less anteroposterior orientation. In the proximal region the muscle fibres do not only insert on successive ribs but the larger portion inserts on prominent myosepta which run obliquely backwards from the surfaces of the ribs (Fig. IV.8B, IMY). The iliocostalis fibres are interrupted by and attach to parts of the same myosepta. The thick fleshy portion of the muscle is covered by the M. iliocostalis and is intergrown with it. Waters (1969) considers the fibres spanning the myosepta to be part of the M. iliocostalis.

According to Smirnowsky (1930) the M. intercostalis externus longus is especially well developed in the trunks of skinks where it serves as a substitute for the M. obliquus abdominis profundus which is absent in this family. The fibres of the M. intercostalis externus longus originate from an aponeurosis deep to the attachment of the M. obliquus abdominis externus superficialis and the M. iliocostalis. The fibres are directed posteroventrally. They cross the next posterior rib before inserting onto the base of a rib near to its costal cartilage (Fig. IV.8B). The last slip of this series is at=
tached to the processus lateralis pubis.

5.7.2 M. INTERCOSTALIS EXTERNUS IN ACONTIAS (Fig. IV.10)

The M. intercostalis externus of Acontias is concealed by the M. iliocostalis and the M. obliquus abdominis externus. Its proximal part is covered by the M. longissimus (Fig. IV.10A; IEB). At least four subdivisions of the muscle can be distinguished: M. intercostalis externus brevis, M. intercostalis externus longus, M. levator costae and the M. tuberculo-costalis. The last two are differentiated from the proximal portions of the intercostal muscles near the costal heads (cf. Waters, 1969).

The M. intercostalis externus brevis extends between successive ribs and its fibres are one segment long. The fibres arise on the posterior surface of one rib or its myoseptum (Fig. IV.10A; IEB). The more distal fibres pass ventrad and caudad to attach on the anterior face of the next successive rib or its myoseptum. The more proximal fibres have similar points of attachment but run in a nearly straight anteroposterior direction.

The superficial, proximal fibres are intergrown with those of the overlying M. iliocostalis. Waters (1969) regards these fibres spanning the myosepta as part of the iliocostalis system (Fig. IV.10; IMY).

The M. intercostalis externus brevis fills the intercostal space medially up to the vertebral column and distally up to the tip of the rib excluding its costal cartilage. In M.
*Capensis* the fleshiest portion of the muscle is located medially, in *Acontias* the thickest portion of the muscle has a more lateral location (cf. Figs. IV.8B & IV.10A; IMY).

The M. intercostalis externus longus consists of a series of narrow slips which extend from the base of a myoseptum over the next posterior rib before attaching to the rib next in sequence, next to the costal cartilage. Its fibre direction is similar to that of the brevis; the only difference being that it spans two, instead of one, intercostal spaces (Fig. IV.10A; IEL).

The proximal portion of M. intercostalis externus seems to differentiate into a M. levator costae (cf. Mosauer, 1935), which according to Nishi (1938), is a derivative of the M. intercostalis externus (Waters, 1969). These short stocky muscles lie in series directly ventral to the longissimus. The thick tendons of origin of the M. levator costae contribute to the floor of the longissimus compartment (Fig. IV.10B; LEC) and are joined by connective tissue to the lateral intermuscular septum. Each muscle arises from a broad tendon attached to the caudoventral surface of a prezygapophysis. The fibres run from the ventral surface of the tendon laterad and caudad to attach onto the lateral surface of the proximal third of the rib articulating with the next posterior vertebra. This attachment is mainly fleshy but is also associated with a tendon. Fibres of the M. levator costae attach onto the upper surface of this tendon and fibres of the M. intercostalis externus attach to its lower surface. Distal to
this area of attachment a prominent myoseptum arises. The latter provides attachment for M. intercostalis externus, M. obliquus abdominis externus and the M. iliocostalis (Fig. IV.10A; MYS).

In the regression series, the ribs of Acontias are unique in that they possess pseudotubercula (Hoffstetter and Gasc, 1969). A series of cylindrical muscles, the Mm. tuberculocostales (Gasc, 1968) is associated with these projections. Each muscle originates via a short tendon from a pseudotuberculum, it passes caudad to attach onto the next posterior rib just distal to the costovertebral joint. On contraction this muscle will tend to swing the rib forward (Fig. IV.10A & B; TUC).

5.7.3 COMPARISON

(a) The intercostalis externus develops from more metameres in reduced limbed skinks.

(b) In the trunk region of both limbed and limbless forms it is differentiated into the brevis and longus portions.

(c) In M. capensis the thick fleshy part of the muscle is located proximally stretching between the upper third of the ribs and its myosepta. Here its superficial fibres are intergrown with the iliocostalis. In Acontias, on the other hand, this fleshy part as well as the myosepta occupy a lateral position.

(d) The proximal portion of the muscle in Acontias is differentiated into a M. levator costae and a M. tuberculo-costalis. Such subdivisions were not observed in the
the trunk of *M. capensis*.

5.8.1 *M. INTERCOSTALIS INTERNUS IN M. CAPENSIS*

This segmental muscle lies deep to and is merely differentiated from the *M. intercostalis externus* by the direction of its fibres (Fig. IV.8B & C; INI). These fibres are one segment long and extend from the anterior surface of a rib to the posterior surface of the next anterior rib. The fibres run diagonally between the two ribs. They start distal to the myoseptum and extend right to the distal end of a rib. Deep to this muscle are the *M. obliquus internus*, the *M. transversus abdominis* and the peritoneum; superficial to it are the *M. intercostalis externus*, the *M. obliquus abdominis externus*.

5.8.2 *M. INTERCOSTALIS INTERNUS IN A. MELEAGRIS*

*A. Meleagris* lacks a segmental muscle corresponding to the *M. intercostalis internus*. It is interesting to note that the limbed anguid *Gerrhonotus* has a *M. intercostalis internus*, but that the limbless anguid *Ophisaurus ventralis* lacks it (Waters, 1969).

Although there are no segmental slips of the *M. intercostalis internus*, there are muscular slips spanning two intercostal spaces. Their fibres lie in the direction (obliquely forward and downwards) expected of internal intercostal muscles. These muscles originate from the inner surface of a rib near the origin of the *M. transversus abdominis* and the adjacent internal fascia. Their fibres pass ventrad and craniad deep to a rib before inserting onto the posteroverentral tip of a rib and also onto its costal cartilage. Each muscle slip is thus two segments long. It is called a *M. subcostalis ventralis*.
It lies superficial to the M. transversus abdominis and the M. obliquus abdominis internus and deep to the ribs and the M. intercostalis externus (Fig. IV.10; SCV).

5.9 M. SUBCOSTALIS DORSALIS (Waters, 1969)

5.9.1 GENERAL

Mm. retractentes costarum (Smirnowski, 1938); Mm. intercostales interni longi dorsales (Nishi, 1938); M. retrahens costarum (Guibè, 1970); and Mm. intercostales interni dorsalis longi (Guibè, 1970).

It is a thin sheet of muscle that lines the dorsolateral aspect of the visceral cavity superficial to the peritoneum and deep to the proximal halves of the ribs.

5.9.2 M. SUBCOSTALIS DORSALIS IN MABUYA CAPENSIS (Fig. IV.1A & 8B)

In M. capensis the M. subcostalis dorsalis is a thin, continuous sheet that lies superficial to the peritoneum in the dorsolateral region of the trunk. It originates aponeurotically from the ventrolateral surface of the centra. The fibres run craniad and ventrolaterad, inside the curvature of the body wall, to insert onto the posteromedial face of a rib about two vertebrae anterior to its point of origin.

The points of insertion of the M. subcostalis dorsalis interdigitate with the common points of origin of the M. obliquus abdominis internus and the M. transversus abdominis (Fig. IV.1A & 8B).

5.9.3 MUSCULUS SUBCOSTALIS DORSALIS IN ACONTIAS (Fig. IV.10B)

In Acontias the condition of the M. subcostalis dorsalis is similar to that in M. capensis. It forms a continuous sheet
in the dorsolateral roof of the visceral space, stretching from approximately the 7th vertebra to the vestigial pelvic girdle. The muscle arises from a broad aponeurosis attached to the vertebral centra and is continuous with the peritoneum. The fibres run craniad and laterad for approximately two intercostal spaces before inserting onto the inner surface of a rib and the adjacent internal fascia (= peritoneum) (Fig. IV. 10A & B; SCD).

5.10.1 M. TRANSVERSUS ABDOMINIS IN M. CAPENSIS (Fig. IV.1A)

In M. capensis the transversus abdominis is a thin sheet of muscle lying immediately outside the peritoneum in the ventrolateral part of the trunk where it forms the deepest layer of muscle. It is sandwiched between the peritoneum and the M. obliquus abdominis internus. It lines the distal halves of the ribs. The fibres of the M. transversus abdominis originate from approximately the middle of the inner surface of a rib and also from the peritoneum associated with this region. At its point of origin fibres of the M. transversus abdominis interdigitates with those of the M. subcostalis dorsalis (Fig. IV.1A). The fibres of the former extend almost straight ventrad following the internal curvature of the body wall (Fig. IV.8C; TAB). The sheet of muscle extends anteriorly up to the scapulocoracoid and posteriorly almost up to the level of the acetabulum. In the pectoral region the muscle inserts via a strong aponeurosis along the entire lateral margin of the sternum and the mesosternum. Posterior to the mesosternal region the ventral aponeurosis appears to split into a deep
and a superficial layer. The former is continuous with the peritoneum and lies deep to the M. rectus medianus (sensu Ni- shi). The latter passes through the abdominal intermuscular septum and runs right across the belly as a strong superficial fascia, which joins the corresponding muscular sheet on the opposite side of the body. In other words, the aponeuroses of the two sheets of transversus abdominis muscles form a supporting sling across the belly.

5.10.2 TRANSVERSUS ABDOMINIS IN ACONTIAS (Fig. IV.10A & B)

The arrangement of the M. transversus abdominis is essentially similar to the condition in Mabuya. These two sheets of muscle form the deepest layers in the ventrolateral region of the trunk. Each starts in the region of the vestigial scapulocoracoid, to which a few fibres are attached, and extends backwards up to the rudimentary pelvic girdle to which it is also connected. The muscle originates from the inner face of the upper half of the ribs and runs ventrad and mediad.

The sheets as a whole can be differentiated into two regions. In the region of the parasternalia, the ventral muscle fibres are almost twice as long as in the more posterior area and the thick internal aponeurosis runs up to the margin of the linea alba before fusing with the superficial aponeurosis. Behind the parasternal chevrons the aponeurosis is not only continuous with the peritoneum but it is also continuous with the abdominal intermuscular septum as well as with the superficial fascia which runs across the belly. The muscle is very thin in Acontias, only one to two fibres thick.
5.11.1 M. OBLIQUUS ABDOMINIS INTERNUS IN MABIYA CAPENSIS
(Fig. IV.8C & B)

The M. obliquus abdominis internus is a thin sheet of muscle superficial to and largely contiguous with the M. transversus abdominis (Fig. IV.8C). It differs from the latter in fibre direction and points of insertion. It originates from the inner surface of the ribs slightly ventral to the insertion of the M. subcostalis dorsalis and from the outer surface of the internal fascia (peritoneum) lining the body cavity.

In the trunk region the fibres run ventrad and craniad over roughly three segments (these fibres are more or less parallel with those of the M. intercostalis internus - its distal aponeurosis also pass through the abdominal intermuscular septum together with the aponeurosis of the M. transversus abdominis) to fuse with the ventral superficial fascia.

5.11.2 M. OBLIQUUS ABDOMINIS INTERNUS IN ACONTIAS

In Acontias the M. obliquus abdominis internus is approximately one fibre layer thick and contiguous with the M. transversus abdominis. Its relationships and attachments are similar to those of the last named muscle and also like those of its homologue already described for M. capensis.

6. SUMMARY OF TRENDS AND TENDENCIES

The overall organization of the mid-trunk axial musculature is similar in the entire regression series. Consequently, there is usually little doubt about the homology of the muscle groups compared. These similarities, which are assumed
to reflect a common scincid heritage, are not emphasized as much as the differences which could indicate adaptive changes. The biomechanical implications of such changes will be explored in Chapter VI.

The differences observed in the axial musculature may be classified into several categories. Firstly, homologous muscle groups may differ in bulk or degree of development. Secondly, they may change their position relative to the vertebral column. Thirdly, they may change in length and structure. Fourthly, some muscle may disappear and finally "new" muscles may differentiate.

Ideally the bulk of a muscle should refer to its mass or its total volume. In this study some transverse dimension of the muscle is employed in comparisons of relative development. It must be emphasized, however, that because the axial muscles are either partially or completely segmental and because the number of precaudal segments increases with limb reduction, these muscles are usually composed of more metameres in limbless forms. This longitudinal hypertrophy applies to all the axial muscles discussed below.

The following trends and tendencies with regard to the relative bulk of muscle groups were noted for the regression series. As limb regress:

(a) there is a decline in the cross-sectional area of the trunk relative to its length (Fig. II.4 & 5) mainly at the expense of the visceral space while the body wall
actually hypertrophies (Fig. IV.2);

(b) the relative cross-sectional area of the epaxial musculature increases while that of most of the hypaxial musculature declines (Fig. IV.3);

(c) the relative hypertrophy of the three subdivisions of the epaxial musculature varies among the genera (Fig. IV.4);

(d) the relative cross-sectional area (Fig. IV.5) and circumferential spread (Fig. IV.7) of the ventral rectus musculature wanes;

(e) the dorsoventral spread of the obliquus abdominis declines (Fig. IV.7).

Changes in the size of muscle groups influence the spacing around the axial skeleton. As limbs regress:

(a) the epaxial muscle increases its circumferential spread into the lateral regions of the trunk, restricting the dorsoventral spread of the obliquus abdominis (Fig. IV.7);

(b) the longissimus shifts nearer to the lateral margin of the trunk (Fig. IV.6);

(c) the iliocostalis shifts from dorsolateral into a more ventrolateral position (Figs. IV.1A to C & IV.7);

(d) the iliocostalis displaces the M. obliquus abdominis into a more ventrolateral position (Figs. IV.3A & 10A; OAES);

(e) the fleshy part of the M. intercostalis externus and contiguous parts of the iliocostalis which span successive segmental myosepta; both muscles shift from a dorsolateral
ral position to one that is due lateral (cf. Figs. IV.8A & 10A; IMY).

The more striking structural trends and tendencies of the muscles described will now be considered:

(a) Transversospinalis system

While the other subdivisions resemble each other closely, the M. spinalis et semispinalis tends to elongate slightly. It is five segments long in *Mabuya* and seven segments long in *Acontias*.

(b) Longissimus system

In *Acontias* the longissimus system lies nearer to the lateral margin of the trunk (Fig. IV.6) and the length of its slips increases from about 3-4 segments in *Mabuya* to 7-8 in *Acontias*.

(c) Iliocostalis system

The iliocostalis, which has shifted into a lateral position, also tends to increase in length. It spans 3-4 metameres in *M. capensis* and 7-8 in *A. meleagris*.

A major modification of the three subdivisions of the epaxial musculature is their increase in length so that the constituent elements span more vertebral segments. This tendency is confirmed by Gasc (1967) and Waters (1969) for partially or completely limbless lizards while Auffenberg (1962) suggests that in ophidian evolution there is a tendency for serial homologues to fuse thus increasing the length of the muscle units.
As limbs regress, certain axial muscles disappear. Thus *Acontias* lacks a M. rectus internus, a M. rectus lateralis and a M. intercostalis internus. The first two muscles are only weakly developed in *Scelotes*.

Functionally distinct axial muscles such as the M. levator costae and the M. tuberculocostalis have developed in *Acontias* at the proximal ends of the ribs. The first named muscle is derived from M. intercostalis externus (Nishi, 1938 and Waters, 1969). According to Waters (1969) tuberculocostalis muscle is probably derived from the M. intercostalis externus. The functional significance of the "new" muscles will be discussed in Chapter VI.
V. LOCOMOTION

1. GENERAL

Locomotion refers to the act of moving from one place to another. In its simplest form it involves merely the displacement of an animal's centre of gravity; in its more complicated form it comprises both shifting of the centre of gravity and at the same time maintaining equilibrium (Howell, 1944, p. 217).

Vertebrates display two types of locomotion: axial and appendicular (Zug, 1969). In axial progression propulsion is produced by flexing of the body axis (i.e. vertebral column, ribs and axial musculature), while in appendicular locomotion the limbs (or fins) produce the propulsive thrust required for progression.

The locomotion of *M. capensis* is predominantly appendicular; that of the apodous *A. meleagris* is exclusively axial. How could a shift occur from the one mode of locomotion to the other with the intermediate stages maintaining an adequate degree of locomotory proficiency? More specific questions that require answers are: Is there an axial component in the quadrupedal locomotion of *Mabuya*? Does the axial component increase as limbs become miniaturized as in *Riopa sundevalli*? Do the vestigial limbs of the bipodous *Scelotes bipes*, *S. gronovii* and *S. brevipes* make a contribution to propulsion? Which of the four recognized categories of limbless locomotion are displayed by *Acontias meleagris*?

The locomotion of *A. meleagris* is described first because it is exclusively axial and because it could indicate what trends and
tendencies should be sought in the rest of the regression series.

2. LOCOMOTION OF *A. meleagris*

2.1 GENERAL

No account of the locomotion of limbless skinks, beyond cursory remarks about its serpentine resemblances (FitzSimons, 1943; Waters, 1969; Tiedemann & Tiedemann, 1975) could be traced. Wielemann (1932) briefly analyzed the locomotion of the limbless anguids, *Ophisaurus* and *Anguis* in a study devoted mainly to the locomotion of snakes. As snakes are by far the most successful limbless tetrapods, much attention has been devoted to the analysis of their progression (Mosauer, 1933, 1932a & b; Gray, 1946; Gray and Lissmann, 1950; Gans, 1962, 1966a & b, 1970; Gans and Mendelssohn, 1972). The locomotion of the amphisbaenians, a highly specialized group of limbless reptilian burrowers, has been analyzed by Gans, 1960, 1968, 1969 and 1978).

The caecilians, a group of limbless amphibian burrowers, have received some attention (Gaymer, 1971; Gans, 1973a). Raveshky (1960) provides a general mathematical model for the analysis of limbless locomotion. Only the work of Daan and Belterman (1968) treats in any detail the role of lateral bending in sau- rian locomotion.

*A. meleagris* is a limbless burrower which spends most of the day below the surface of loose sandy soil. From spring to autumn it is frequently found beneath stones in the Western Cape (Tiedemann & Tiedemann, 1975) where scores of specimens were collected. This animal roams above the soil at night. It has been observed crossing tarred roads at night. Laboratory ani-
mals also emerge from their sandy hiding places when the lights are turned off, but wriggle back into the soil when the lights are turned on.

It would be extremely difficult to record the locomotor behaviour of these animals in their natural habitat. Consequently, they were filmed under a variety of special conditions where they were either partly or completely exposed. Films recorded under the following conditions were analyzed:

(i) *A. meleagris* wriggling on smooth glass or polythene placed over a black grid;

(ii) the animal progressing over a smooth polythene covered grid provided with flexible *points d'appui*;

(iii) the animal wriggling on smooth glass with a few scattered brass weights to serve as *points d'appui*;

(iv) the organism penetrating dry sand.

2.2 WRIGGLING ON A SMOOTH SURFACE

2.2.1 REASONS FOR ANALYSIS

When a specimen of *A. meleagris* is placed on a smooth surface the animal wrinkles rapidly by throwing its body into a series of S-shaped or reversed S-shaped curves. Despite this energetic activity, the animal hardly moves forward at all but remains almost stationary relative to the substrate. Mosauer (1931) allowed snakes to wriggle on smooth surfaces in order to demonstrate that serpentine progression is strictly dependent upon the presence of projections from the surface of the substrate (*points d'appui*) against which the animal's body must push.
Only in the presence of such projections can the animal glide forward smoothly.

A detailed analysis of wriggling on a smooth surface is undertaken on the assumption that the absence of points d'appui would elicit from the animal stereotyped undulatory behaviour relatively unmodified by its response to projections in the environment. During such innately controlled lateral bending a maximum or near to maximum amplitude is likely to be reached as the animals "searches" for projections against which to push. An additional value of this type of analysis is that it would allow us at a later stage to determine how the pattern of undulation changes in response to differently placed points d'appui. Consequently, on the assumption that the movements on a smooth surface are stereotyped and innate, such motion will be analyzed with reference to the nature, number, shape, dimensions, rate and direction of propagation of the lateral oscillations observed.

2.2.2 DEFINITIONS (Fig. V.1)

Waves of lateral bending commence immediately behind the head and pass posteriorly along the length of the body (Fig. V.2). The term "wave" has two distinct meanings when referring to animal locomotion (Blight, 1977). Firstly, the term may refer to the actual series of lateral curvatures of the body as illustrated in Fig. V.2. Such bends shall be called body waves (cf. Daan and Belterman, 1968). Secondly, the term "wave" may refer to the path of oscillation of any given point on the body relative to the medium through which the animal moves. This type of wave shall be called point waves. The latter is obtained by
FIG. V.1. DIAGRAM OF A FLEXED Acontias meleagris TO ILLUSTRATE SOME OF THE TERMS DEFINED IN THE TEXT.
constructing a trajectory of a specific point on the body relative to the substrate through one or more locomotory cycles.

The "axis of a body wave" is defined as the straight line drawn between the tip of the snout and the tip of the tail (Fig. V.1). "Amplitude" refers to the maximum perpendicular displacement of the columnar line from the axis of the body wave (Fig. V.1).

In the case of a point wave the axis of progression is used as the plane from which maximum departure is measured. In Figure V.1 three alternate flexures are shown. Those above the axis, the crests are called left flexures while those below the axis, the troughs are called right flexures.

In the vocabulary of harmonic motion the concept of wave-length is very important. It is defined as the distance between successive points of equal phase in wave motion; thus the wave length may be measured from crest to crest, trough to trough or, as in Figure V.1, from successive points in the same phase and intersecting the axis.

When an *Acontias* is undulating on glass the wave length varies during the oscillatory cycle and the number of alternating flexures fluctuate from one to three. Consequently, the concept, flexure-length is more useful for the present analysis. "Flexure-length" is defined as the distance along the axis of the body wave between two successive points which intersect this axis (Fig. V.1). It thus corresponds to half a wave-length measured specifically along the axis of the wave.

An "oscillatory cycle" in this context is defined as the series of undulatory changes between successive states of similar cur-
vature. Figure V.2 illustrates such a cycle in which the first and last tracings are more or less in the same state of curvature.

2.2.3 CATEGORIES

Even prior to detailed analysis the wriggling behaviour on glass seemed to fall into two categories. Firstly, there was the slower pattern in which a wave of lateral flexure appeared to pass along the length of the body leaving the impression of an S-shaped or reversed S-shaped pattern. Then secondly, a much more rapid series of panic wriggles in which the two ends of the body seemed to be brought much nearer to each other, leaving the dominant impression of the body being thrown into C-shaped and reversed C-shaped curves. Both of these patterns will be analyzed.

2.2.3.1 Slow Wriggling Motion

Figure V.2 illustrates an oscillatory cycle of this type. A single right crest is marked with a white dot to facilitate observation of its caudad displacement during the cycle which took around 0.75 seconds. Note that the number of alternate curves fluctuates between one and three. There are never more than three alternate flexures (Right-Left-Right or Left-Right-Left) when the animal oscillates on glass. In the three-flexure state, the anteriormost bend develops behind the head while the posteriormost one wanes in the region of the tail.

After having examined the overall pattern of undulation on a smooth surface, changes in the various parameters of body curvature will now be considered in more detail. In Figure V.3A tracings 1, 4, 7, 10, 13 and 16 (from Fig. V.2) are superimposed
**FIG. V.2.** _Actias meleagris_ Wriggling slowly on glass. Successive tracings are 1/24th of a second apart. Note the caudal passage of the flexure marked with a white dot.
with the axis of the body wave as well as the tip of the tail aligned. This allows one to view changes in body curvature for equal intervals of an oscillatory cycle relative to the tail as a fixed point and the axis of the body wave as a fixed plane. Figure V.3A illustrates the following facts:

(i) A flexure starts behind the head and is propagated caudad down the length of the animal.

(ii) The amplitude of curvature varies during an oscillatory cycle. It increases in the anteriormost right lateral bend up to and including tracing 10; thereafter, it declines abruptly in tracings 13 and 16. The growth and decline of alternate flexures for a full cycle are illustrated in Graph V.4.

(iii) The alternate flexures are propagated backwards in phase. In tracings 1 and 13 the initial growth and propagation of the anteriormost right flexure is accompanied by the posterior displacement and growth of the alternate left flexure and the disappearance of the posteriormost right flexure. As the one flexure waxes its alternate partner wanes. Graph V.4 illustrates the reciprocal relationship between alternate flexures through time.

(iv) The right and left alternate flexures are asymmetrical. The amplitude of the right curves reach a much greater magnitude than those of the left ones. This unexpected finding may be related to the way in which the animal enters the soil. During entry it invariably curves to one side hence the need for a bigger "pushing wave" towards the opposite side.
(v) There is a reciprocal relationship between the cumulative magnitude of the amplitudes and the length of the axis of the body wave. When the sum of the amplitudes reaches a maximum, the length of the line connecting the snout to tail tip is the shortest. This relationship is explored more fully in Graph V.5 as it promises to provide a convenient indicator of the degree of lateral bending. In the fully stretched animal the snout and tail tips reach their maximum separation. Such a fully stretched phase does not occur in these oscillatory cycles. As the animal bends, snout and tail tip approach each other as shown in Graph V.5. The reciprocal relationship illustrated by the latter provides justification for employing the length of the axis of the body wave as an indicator of the degree of lateral bending.

(vi) Flexure length waxes and wanes together with amplitude. See Figure V.4 for a graphical illustration of this relationship.

(vii) As amplitude and flexure length increase over the larger part of an oscillatory cycle, the displacement of a crest of a wave can be analyzed into two components, one posterior and the other lateral. The posterior component is parallel with the axis of the body wave. The lateral component varies in direction. As the flexure waxes the lateral component is directed away from the axis, whereas, while the wave wanes the lateral component is directed towards the axis.

(viii) The average speed at which the crest is displaced back=}
FIG. V.4. THE CHANGES IN FLEXURE LENGTH AND AMPLITUDE OF THE BODY FLEXURES OF AN *Acontias meleagris* WRIGGLING SLOWLY ON GLASS.
wards is around 22 cm/sec or nearly one body length per second.

Figure V.3A, on which the analysis given above is based, illustrates changes in body flexures when the tip of the tail is kept stationary and the body axis is confined to a single plane. In reality both the tip of the tail and the body axis move relative to the substrate. Figure V.3B illustrates the same series of flexural changes relative to the substrate. The body flexures still pass caudad, and are asymmetrical; the amplitude and flexure length grow to a maximum and then diminish in the caudal region. The big difference, however, is that the tip of the snout and the tail oscillate relative to the substrate. Note as well that although the substrate is too smooth for forward movement, friction between the ventral surface of the animal and the substrate does allow a small measure of lateral displacement and rotation of the entire animal.

2.2.3.2 Rapid Wriggling (Fig. V.5)

Figure V.5 illustrates fluctuations in amplitude and flexure length through a few oscillatory cycles. Comparison of this figure with V.4 illustrates the similarities and differences between the two modes of wriggling. Rapid and slow wriggles resemble each other in the caudad progression of the waves as well as in the rise and fall of flexure length and amplitude. There are, however, several important differences.

There is, firstly, a difference in the rate of propagation of the body flexures. During rapid wriggling a single body flexure takes between 0.3 and 0.4 seconds to travel along the en-
tire length of the body; this interval is less than one half of that of the slower pattern of wriggles.

A second difference is that the body flexures are propagated so rapidly that no distinct three flexure phase was recorded when filming at 24 frames per second.

A third difference is that the right and left flexures are more symmetrical during rapid wriggling. In Figure V.4 the right flexure is much larger than the left one; in Figure V.5 they are more or less equal. Under normal conditions rapid wriggling probably enables these animals to escape from a particular area without diving into the soil. On the other hand, the asymmetrical pattern may be associated with rapid entry into soil.

The activities described above lead one to the following conclusions. In the absence of points d'appui the stereotyped pattern of behaviour is to throw the body into a series of waves which travel caudad. These grow to maximum amplitude and flexure length behind the mid-trunk region before waning in the caudal region. These flexures are termed "travelling waves" (sensu Daan and Belterman, 1968). In brief, the stereotyped locomotory pattern of Acontias conforms to a series of travelling waves.

2.3 PROGRESSION IN PRESENCE OF POINTS D'APPUI (Figs. V. 7 & 8)

When wriggling on glass or polythene, the body waves slip backwards over the smooth surface with hardly any forward progression by the animal. To test the effect of the presence of points d'appui on the locomotor behaviour of Acontias, the animal was placed on a smooth polythene covered grid with rows of flexible rubber projections two centimetres apart. If the animal
FIG. V.5  FLUCTUATIONS IN AMPLITUDE AND FLEXURE LENGTH OF A RAPID WRIGGLING Acontias meleagris.
pushed against any of the thin rubber rods, they would bend indicating where force was applied. This behaviour of the animal on the grid was filmed and analyzed.

How do these points d'appui affect the behaviour of the animal? Firstly, they permit the animal to progress relative to the substrate (Fig. V.7&8). Secondly, the body waves no longer slip freely over the substrate; instead they may even remain stationary relative to certain rubber projections against which they push (Fig. V.7). In other words, as the body flexures travel towards the tail, they engage the rubber projections, which prevents their backward slippage, hence the body is propelled forwards as the waves of curvature propagate backwards. This type of progression is called horizontal undulatory movement (Mosauer, 1931); serpentine wriggling (Mosauer, 1931) or simply lateral undulation (Gray, 1946; Gans, 1962).

Two essential requirements for lateral undulation are: the cranio-caudal propagation of lateral flexures on the part of the animal; and on the part of the environment, points d'appui prevent or at least limit slippage of these travelling waves in a direction normal to the lateral surface of the animal.

A comparison of Figures V.3A and V.8 shows that, though the magnitude of the lateral flexures differ, in the absence or in the presence of points d'appui, similar travelling waves are involved. Such waves of curvature travel backwards along the body axis, but in the presence of suitable points d'appui they remain stationary relative to the substrate (Figs. V.7&9). Under conditions of zero slip these flexures "stand" relative to the substrate while the rest of the body moves forward relative to
FIG. V.6 THE RELATIONSHIP BETWEEN LENGTH OF AXIS OF BODY WAVE \[ \frac{\text{SUM OF AMPLITUDES}}{\text{STRETCHED LENGTH}} \] % AND \[ \frac{\text{SUM OF AMPLITUDES}}{\text{STRETCHED LENGTH}} \] % Total Stretched Length
the substrate.

Gray and Lissmann (1964) discuss the importance of "slippage" in lateral undulation. This concept is defined by the following formula:

\[
\% \text{ slip} = 100 \frac{(V_w - V_x)}{V_w}
\]

where:

- \(V_w\) = velocity of backward propagation of a lateral flexure relative to the head (or tail or any other convenient point of reference in the body axis);
- \(V_x\) = velocity of progression of the animal relative to the substrate. Ideally, the progression of the centre of gravity should be the reference point. For the sake of convenience either the tip of the snout or the tip of the tail or the midpoint of the body is used as a point of reference.

When *Acontias* wriggles on a smooth surface such as glass or polythene, \(V_x\) is almost zero (Fig. V.3B); not quite zero because friction between the skin of the wriggling animal and the substrate does result in a small measure of random displacement (Fig. V.3B). The "percentage slip" is, therefore, almost 100% - i.e. the body flexures slide over the substrate without pushing the animal forward.

At the other extreme, when the velocity of propulsion of the animal relative to the substrate (\(V_x\)) is equal to the velocity of the backward propagation of the waves of curvature along the body axis (\(V_w\)), there is no slippage. The body flexures then remain stationary relative to the substrate. These three fact-
Acontias melagris progressing slowly by lateral undulation on a smooth grid with flexible points d'appui.

FIG. V.7.
ors are in perfect correlation. If there is zero slip, then the body waves "stand" relative to the substrate and the speed of propagation of a body flexure is equal to (but opposite to) the speed of propagation of the animal as a whole relative to the substrate.

The essential requirement for zero slip is that those portions of the body axis in force transmitting contact with the ground move tangentially to their own surface. In other words, the substrate must be capable of resisting (without deformation) the forces inducing displacement of the body perpendicular to its own surface. If this condition is not met, certain parts of the body also move at velocity, \( V_n \) (Gray and Hancock, 1955) normal to the surface (Fig. V.9). The animal then no longer glides simply tangentially to its lateral body surface, instead there are additional oscillations perpendicular to its path of travel (Fig. V.9). In the caudal region (c) there is no component \( V_n \) hence the flexure "stands" relative to the substrate. In the mid-trunk region (M), there is a component \( V_n \) and the flexure slips relative to the substrate until it engages rubber Rod RR. Because of the wasted movement \( V_n \) in the mid-trunk region the head is moved forward only about 27 mm while the tail simultaneously progresses about 31 mm during the three seconds illustrated in Figure V.9. Consequently, a second way of expressing the conditions under which zero slip occurs is to say that width of the tract of the animal should not be greater than the diameter of the animal's body (Gray and Lissmann, 1964).

Mosauer (1932, p. 584) describes lateral undulation under condition of zero or near to zero slip as follows: "Every point of the snake's body and tail faithfully follows the path taken
by the head and neck, so that the snake seems to flow gracefully through grass and shrubs like a water course in its narrow, winding bed". Hertel (1968, p. 183) writes in a similar vein: "The snake describes a 'snaking line' with its head, and the body follows this line over its entire length. The path laid out acts like a river bed between the banks of which the snake moves without leaving them".

On the polythene grid an Acontias cannot form a "snaking line", instead its flexures slide over the smooth substrate until they engage a rubber projection. The degree of slippage is largely dependent on the nature of the terrain in which the animal moves (Gray and Lissmann, 1964).

At this point a brief digression, to discuss different ways in which the terms "travelling" and "standing" waves are employed in the literature dealing with limbless locomotion, may be useful. For example, Hildebrand (1974) refers to the flexures formed by snakes as "standing waves" since they stand relative to the substrate, after having engaged particular points d'appui. From the discussion above it should be clear that whether a wave remains stationary relative to the substrate or not, depends on the nature of the terrain and not on the kinds of waves formed by the animal. In Figure V.2 waves travelling along the body axis slip over the substrate. In Figure V.9, on the other hand, flexures generated in the same way stand, at least partially, relative to the substrate. In this paper "travelling waves" refer to flexures that travel along the length of the body axis; and "standing waves" refer to lateral bends of the body confined to a few fixed (nodal) points along the body axis (Daan and Belterman, 1968).
FIG. V.9. SUPERIMPOSED TRACINGs (INTERVAL 0.5 SEC) OF AN Acontias meleagris MOVING BY LATERAL UNdULATION. NOTE THAT THE POSTERIOR FLEXURE "STANDS" RELATIVE TO points d'appui A & B, WHILE SLIPPAGE OCCURS IN THE ANTERIOR MOST FLEXURE.
FIG. V.10. TRAJECTORIES OF THREE POINTS ON THE BODY OF AN UNDULATING Acontias melaeagris. NOTE THE ALMOST SINUSOIDAL POINT WAVE FORMED BY THE TAIL; THE SNOUT TIP PERFORMS EXPLORATORY OSCILLATIONS; THE MID-POINT OF THE BODY ALSO FORMS ALMOST SINUSOID OSCILLATIONS UNTIL THE ANIMAL CHANGES THE DIRECTION OF PROGRESSION AND STRETCHES MORE FULLY.
Forward propulsion can be caused by lateral undulation provided the resistance to slippage acting normal to the body surface ($R_N$) is greater than the resistance offered along the axis of the body ($R_L$) (cf. Gray and Hancock, 1955). Consequently, the two essential requirements for lateral undulation are:

(a) the animal must be able to generate travelling waves along its body axis; and

(b) the environment must impede the slippage of these waves in a direction perpendicular to the body surface i.e. $R_N > R_L$.

Under ideal conditions of zero slippage the travelling waves will appear to "stand" relative to the substrate.

2.4 PROGRESSION IN DRY SAND

Thus far the locomotor behaviour of Acontias has been described for highly artificial substrates. Does the animal progress by lateral undulation below soil? This question was explored by filming the animal's behaviour as it entered a pile of dry sand just deep enough to cover its body completely. Because of the lack of cohesiveness among the soil particles, as the animal burrowed into the soil it formed a temporary tunnel defined by its outline and as it progressed the tunnel collapsed behind it leaving a clear furrow.

The sinuous outline of the furrow formed in this way indicates that the animal moves forward below this soil by lateral undulation with but slight slippage (Fig. V.11).
FIG. V.11. FOUR SUPERIMPOSED TRACINGS OF *Acontias meleagris* PROGRESSING THROUGH A PILE OF SAND BY LATERAL UNDULATION (INTERVAL 4 SECONDS).
When snakes are placed in a parallel walled channel, they change their mode of progression to concertina movement (Gray, 1946). *A. meleagris* does likewise when placed in a parallel walled chamber with a smooth floor (Fig. V.13).

The body is flexed into a number of curvatures of relatively short radius. The crests of some of these flexures are pushed firmly against the parallel walls thus creating regions of stationary contact (Figs. V.12&13). Behind such areas of static contact, the body may be pulled forward into curves; while in front of such areas existing curvatures may be extended (Figs. V.12&13). This alternate extending and folding of the body has led to the name "concertina movement" (Gans, 1974). When new flexures establish stationary contact, old ones may be extended with the result that portions of the body progress in a stop-start manner.

As all segments of the body do not move forward continuously, there is loss of momentum by those regions in stationary contact. Consequently, concertina movement is relatively slow and inefficient (Gans, 1974, and see Table V.1).

Although both concertina movement and lateral undulation employ lateral bending of the body axis and though the former may be derived from the latter (Gans, 1974); they differ in several respects. Firstly, the kinds of body flexures formed are different. During lateral undulation travelling waves are propagated caudad. During concertina movement discrete lateral flexures are formed. These curvatures are folded and extended rather than propagated. Secondly the *points d'appui* are located diffe-
**FIG. V.12.** AN _Acontias meleagris_ PERFORMING CONCERTINA MOVEMENTS. THE CHANNEL IS 19MM WIDE. THE SHADED PARTS ARE AREAS OF STATIC CONTACT. THE TIME INTERVAL BETWEEN SUCCESSIVE TRACINGS IS 0.5 SEC.
<table>
<thead>
<tr>
<th>Diameter of specimen mm</th>
<th>Length of specimen mm</th>
<th>Width of channel mm</th>
<th>Speed in cm per sec.</th>
<th>Speed in body length per second</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.0</td>
<td>202</td>
<td>25</td>
<td>0.6</td>
<td>0.03</td>
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<tr>
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<td>0.02</td>
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<td>7.7</td>
<td>210</td>
<td>19</td>
<td>0.4</td>
<td>0.02</td>
</tr>
<tr>
<td>5.5</td>
<td>159</td>
<td>37</td>
<td>0.3</td>
<td>0.02</td>
</tr>
<tr>
<td>6.5</td>
<td>214</td>
<td>37</td>
<td>0.4</td>
<td>0.02</td>
</tr>
</tbody>
</table>

Table V.1  Speed of progression of five different specimens of *Acontias meleagris* moving in channels of varying width.
IN TRACING 3 & 4 THE SNOUT MOVES FORWARD

EXTENSION OF ANTERIOR FLEXURES PUSHES SNOUT FORWARD

POSTERIOR FLEXURES PROVIDE STATIC CONTACT

TRACING 1 & 2
TAIL MOVES FORWARD
SNOUT TIP PROVIDES STATIC CONTACT

FLEXURE IN THIS REGION PULLS TAIL TIP FORWARD

FIG. V.13. SUPERIMPOSED TRACINGS OF Acontias meleagris PERFORMING CONCERTINA MOVEMENTS IN A 22 MM CHANNEL (INTERVAL 0.5 SEC).
rently. They are applied to the arms of the body waves in undulatory movements, and to the crests of the curvatures in concertina movement in tunnels. Thirdly, and this is very important, during lateral undulation momentum can be maintained as all the parts of the body slide forward together; during concertina movement parts of the body must be static.

Lateral undulation is not possible in a parallel walled chamber as there are no points d'appui to prevent the posterior slip of waves of curvature travelling down the body axis. A novel strategy is adopted, the crests of a few flexures are pushed firmly against the parallel walls thus immobilizing a portion of the animal's body. Behind this static region waves of lateral curvatures pass forward (instead of backwards as in lateral undulation). Furthermore, in front of the region of static contact the body is merely extended - the bends are straightened without the crest of the curvature exhibiting much travelling.

In brief, concertina movement differs from lateral undulation in the following respects:

(a) discrete flexures rather than travelling waves are formed;
(b) it has an obligatory phase of static contact;
(c) forces are transmitted to the environment via the crests rather than the arms of the lateral curvatures in tunnels.

Concertina movement is likely to be resorted to only when conditions are unsuitable for lateral undulation.
2.6 SUMMARY

(a) The limbless *A. meleagris* relies exclusively on axial locomotion.

(b) Of the four modes of apodous locomotion generally recognized (Gans, 1962), *Acontias* exhibits lateral undulation and concertina movement.

(c) Lateral undulation is the dominant means of progression.

(d) The essential requirements for this mode of locomotion are:
   
   (i) a body axis capable of propagating travelling waves;
   
   (ii) a lateral body wall capable of bearing stress resulting from pushing against points d'appui;
   
   (iii) resistance offered to progression along the body axis ($R_L$) must be less than the aggregate resistance preventing slippage normal to the body axis ($R_N$).

(e) The relationship between these behavioural characteristics and the morphological features of the animal will be discussed in Chapter VI.

3. LOCOMOTION OF *M. capensis*

3.1 GENERAL

As this investigation is concerned with the transition to limbless locomotion, a detailed analysis of appendicular progression is beyond its scope. Three aspects of quadrupedal locomotion will be treated briefly: the step cycle of an individual limb, interlimb co-ordination and finally, the co-ordination between the limbs and the body axis. The last of these three aspects
is the most important, because only as the body axis assumes
greater responsibility for progression, can the appendages de-
generate (Gans, 1975). Consequently, it is important to ascer-
tain the role of the body axis in normal quadrupedal locomotion.
In this connection two questions must be answered. What con-
tribution does the body axis make to quadrupedal locomotion?
How are limb movements related to body flexures during a loco-
 motory cycle?

3.2 STEP CYCLE OF AN INDIVIDUAL LIMB

In M. capensis the limbs support the body (i.e. lifts it more
or less clear of the ground when walking or trotting) and they
generate propulsive forces. Usually the entire trunk is lift-
ed more or less clear of the substrate, and only the tip of the
long tapering tail is dragged over the ground. In a specimen
with a short autotomized tail, however, the entire tail was
held erect well clear off the substrate as the animal moved
forward. The tail acts to counter-balance the influence of
gravity on the trunk (Gray, 1968). Much more is known about
the kinematics of mammalian step cycles than that of lizards
(Alexander, 1977, p. 168; Sukanov, 1974). In lacertilians
the analysis is complicated by three factors. The limbs of li-
 zards oscillate with their stylopodia in a more or less hori-
zontal plane, while the acropodia swing in a more or less ver-
tical plane, with the result that the limb executes much more
complicated movements than the pendulum-like swing executed
by a mammalian limb. Furthermore, the limbs are small and exe-
cute their movements very rapidly.

The step cycle of Mabuya conforms to the patterns described for
FIG. V,14. A Locomotor Cycle of *Mabuya capensis* with Dots Painted on the Mid-Line of Its Trunk, Made from Motion Picture Tracings 1/24 Sec Apart. Limbs in Transport are Lightly Stippled.
several species of lizards by Snyder (1949, 1952, 1954 & 1962). The propulsive forces are supplied mainly by the much larger hindlimbs (Fig. II.3A). The movements executed by both hind and front limbs are similar. A propulsive stroke begins, when the pes or manus contacts the substrate in a plantigrade position, with the stylopodium drawn far forward. Propulsion is generated by the retraction and rotation of the stylopodium, and the straightening of the entire leg (Fig. V.14) to provide the final propulsive thrust before the foot leaves the ground. The recovery (transport) phase begins as soon as the foot is lifted clear off the ground; the limb is then swung forward in an "over-arm fashion" (Snyder, 1954) before being placed back onto the substrate for the start of the next propulsive stroke (Fig. V.14).

During a step cycle the stylopodia oscillate in a more or less horizontal plane while the acropodial elements for much of the cycle occupy a more or less vertical position. This sprawled posture (Romer, 1956) simplified equilibrium control (Grillner, 1975, p. 256) as the points of support (manus and pes) are further lateral from the centre of gravity than in mammals (Gray, 1968). The sprawling arrangement is, however, mechanically less efficient than the mammalian one (Howell, 1944; Snyder, 1952; Hildebrand, 1974).

3.3 INTERLIMB CO-ORDINATION

Although individual limbs execute complex and superficially stereotyped oscillations, for progression all four limbs and the body axis must probably move in a co-ordinated manner to ensure the efficient transmission of propulsive forces and the
maintenance of equilibrium. Interlimb co-ordination is ordinarily presented in gait diagrams that indicate the duration and sequence of foot contact during locomotory cycles.

Three examples of gait diagrams are given (Figs. V.15A, B & C). These reflect the footfall patterns and duration of support for two specimens of *M. capensis* moving at varying velocities. The latter as well as other relevant parameters are listed in Table V.2.

3.4 LATERAL BENDING (Figs. V.14 & 16)

*M. capensis* bends its body axis rhythmically during appendicular locomotion (Fig. V.14). These curvatures occur in both trunk and tail. As the caudal flexures play only an indirect role in propulsion, they will not be considered further.

The lateral undulations of the trunk are co-ordinated with limb action. As a limb swings forward the trunk becomes convex on the side of the forward swinging limb; as a limb swings backward the trunk becomes concave on the side of the backward swinging limb (Fig. V.14).

Daan and Belterman (1968) relate such lateral flexures to girdle rotation. They argue that lateral bending causes the pectoral and pelvic girdles to rotate in a horizontal plane and that such girdle rotation adds to the angle over which the limb is displaced and thereby adding to the stride length. Figure V.17 illustrates how the presumed contribution of girdle rotation may be measured. Table V.2 gives examples of the such measurements for *M. capensis*. Such estimates are based on the assumption that the girdles are linked to the body axis in such
FIG. V.15 A, B & C. GAIT DIAGRAM OF *Mabuya capensis*. Parameters of locomotion are reflected in Table V.2. $\frac{1}{24}$ sec. Each complete cycle is numbered with a capital Roman numeral. LH, left hind limb; LF, left forelimb; RF, right forelimb; RH, right hindlimb.
### Table V.2 Parameters of locomotion in *Mabuya capensis*

<table>
<thead>
<tr>
<th>GAIT DIAGRAM</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter</td>
<td>13</td>
<td>13</td>
<td>10</td>
</tr>
<tr>
<td>Snout to Vent Length (S.V.L.) (mm)</td>
<td>71</td>
<td>71</td>
<td>67</td>
</tr>
<tr>
<td>Number of Cycles</td>
<td>3</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Number of Frames</td>
<td>33</td>
<td>36</td>
<td>34</td>
</tr>
<tr>
<td>Distance Covered (cm)</td>
<td>10.2</td>
<td>23.3</td>
<td>20.5</td>
</tr>
<tr>
<td>Time Taken (sec.)</td>
<td>1.4</td>
<td>1.5</td>
<td>1.4</td>
</tr>
<tr>
<td>Speed (cm per sec.)</td>
<td>4.9</td>
<td>15.5</td>
<td>14.6</td>
</tr>
<tr>
<td>Speed (S.V.L.)</td>
<td>0.69</td>
<td>2.18</td>
<td>2.18</td>
</tr>
<tr>
<td>Stride Length of Front Limbs (mm)</td>
<td>32</td>
<td>51</td>
<td>28</td>
</tr>
<tr>
<td>Stride Length of Hind Limbs (mm)</td>
<td>33</td>
<td>51</td>
<td>30</td>
</tr>
<tr>
<td>Stride Rate (per sec.)</td>
<td>2.1</td>
<td>4.6</td>
<td>4.2</td>
</tr>
<tr>
<td>Duration of contact of stride with substrate (mean)</td>
<td>LH</td>
<td>78%</td>
<td>61%</td>
</tr>
<tr>
<td></td>
<td>LF</td>
<td>72%</td>
<td>66%</td>
</tr>
<tr>
<td></td>
<td>RF</td>
<td>72%</td>
<td>69%</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>72%</td>
<td>63%</td>
</tr>
<tr>
<td>% of stride that front foot= fall follows the hind foot=</td>
<td>42%</td>
<td>41%</td>
<td>47%</td>
</tr>
<tr>
<td>fall on the same side</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Gait:
(a) Sukanov, 1974  
(b) Hildebrand, 1966

---

S.V.L. = Snout Vent Length  
LH = Left Hindlimb  
LF = Left Frontlimb  
RH = Right Hindlimb  
RF = Right Frontlimb  
STW = Slow Trotlike Walk  
SWT = Slow Walking Trot  
MWT = Moderate Walking Trot
a way that lateral bending and girdle rotation must occur together. However, the anatomy of these systems suggest a much more flexible linkage. The shoulder girdle is suspended from the body axis by a muscular sling: without any skeletal joints being involved. In addition, the scapulocoracoid, which bears the forelimb, can rotate between the clavicle and the sternum (see Fig. III.21). The scapulocoracoid is not only articulated in a way that would permit intragirdle rotation, it is also supplied with muscles (M. sternocoracoideus internus profundus et superficialis) which are suitably located to bring about such rotation. Gray (1968) suggests that such intragirdle rotation is common among quadrupedal lizards (with the exception of the Chamaeleontidae - but see Peterson, unpublished Ph.D. thesis, who states that in chamaeleons the shoulder girdle oscillates from front to rear). The pelvic girdle articulates directly with the vertebral column via the sacral pleurapophyses by means of synovial joints (Fig. III.27C). Thus, this linkage between vertebral column and girdle elements is also movable. Moreover, the Mm. rectus internus and rectus lateralis (which are absent in the limbless Acontias) are well situated either to stabilize or to rotate the pelvic girdle relative to the vertebral column (see Chapter IV.5.6.2).

As the vertebral column of Mabuya flexes only weakly, intragirdle rotation (i.e. rotation due to action of intrinsic musculature of the girdle rather than flexure of the vertebral column) probably plays a significant role in increasing stride length. Consequently, the pattern of girdle rotation suggested by Daan and Belterman (1968) is probably an oversimplification, as it ignores the flexible nature of the connection between
FIG. V.16 TRACINGS OF THE MID-LINE OF THE TRUNK TOGETHER WITH THE DOTS PAINTED ON THE ANIMAL FOR A SINGLE LOCOMOTOR CYCLE OF Mabuya capensis. THE POSITIONS OF THE LIMBS ARE ALSO INDICATED SCHEMATICALLY. INTERVAL $\frac{1}{2}\text{sec}$. 
girdles and the vertebral column as well as those anatomical features that permit intragirdle rotation.

How do the axial flexures of Acontias compare with those of Mabuya? The amplitude of the body flexures are very much higher in Acontias than in Mabuya where they are usually only a fraction of the animal's diameter (Fig. V.14); in Acontias these flexures are always greater than and usually many times greater than the body diameter (Fig. V.2). The weak flexures of Mabuya do not show clear cranio-caudal displacement and, therefore, approximate "standing waves" (sensu Daan and Belterman, 1968). In Acontias, on the other hand, the body flexures travel caudad and are called "travelling waves" (sensu Daan and Belterman, 1968). These authors state: "In any case, only standing waves seem to occur in animals with strongly developed limbs. The functional contribution of standing waves is that they allow the limbs to cover a larger stride. They appear to be inappropriate to provide propelling forces like those furnished by travelling undulations; the propelling force is exerted by the limbs" (p. 265). These authors claim that typical standing waves, with nodes in the region of the shoulder and hip girdle, are displayed by the newt, Triturus, while Lacerta viridis displays: "Standing waves, with a slight travelling tendency: nodes not as clearly developed as in the newt; especially the shoulder node trends to be blurred..." (p. 265). The flexures of M. capensis are likewise not "pure standing waves". A measure of travelling does appear to take place but it is not as obvious as in Acontias (cf. Fig. V.14 & 16) and maximum bending is usually localized somewhere between the pectoral and pelvic girdles (Fig. V.16).
FIG. V.17. DIAGRAM TO ILLUSTRATE HOW THE CONTRIBUTION OF LATERAL BENDING TO STRIDE LENGTH IS ESTIMATED. TWO TRACINGS ARE SUPERIMPOSED: ONE SHOWING THE BEGINNING OF FOOT CONTACT WITH THE SUBSTRATE AND THE OTHER THE VERY END OF CONTACT. $\alpha$ IS THE ANGLE THROUGH WHICH THE LOCAL BODY AXIS SWINGS DURING FOOT CONTACT WHILE $\beta$ IS THE ANGLE THROUGH WHICH THE PROXIMAL END OF THE LIMBS SWINGS THROUGH ITS PROPULSIVE PHASE.
Snout to Vent Length (mm) & 71 & 71 & 67 & 71 & 71  \\[-0.5em]
Diameter (mm) & 13 & 13 & 10 & 13 & 13  \\[-0.5em]
Time (sec.) & 0.17 & 0.17 & 0.17 & 0.21 & 0.21  \\[-0.5em]
Speed (cm per sec.) & 20 & 19.2 & 13.2 & 9.6 & 7.5  \\[-0.5em]

| Pelvic Girdle |  \( \alpha \) | 20° | 26° | 18° | 20° | 15°  \\[-0.5em]
| Girdle |  \( \beta \) | 87° | 83° | 76.5° | 71° | 76°  \\[-0.5em]
|  \( \beta - \alpha \) | 67° | 57° | 58° | 51° | 51°  \\[-0.5em]

| Stride Length of CHL | 38 & 56 & 32 & 37 & 30  \\[-0.5em]
| Stride Length of ILF | 37 & 54 & 30 & 40 & 28  \\[-0.5em]
| Forward Displacement of Snout Tip (mm) | 25 & 24 & 9 & 20 & 20  \\[-0.5em]

| Pectoral Girdle |  \( \alpha \) | 7° | 20° | 25° | 0° | 12°  \\[-0.5em]
| Girdle |  \( \beta \) | 93° | 87° | 107° | 86° | 78°  \\[-0.5em]
|  \( \beta - \alpha \) | 87° | 67° | 82° | 86° | 66°  \\[-0.5em]

CHL = Contralateral Hindlimb  
ILF = Ipsilateral Frontlimb

Table V.3 Girdle rotation in *Mabuya capensis* (2 specimens)
The differences in wave pattern between *Mabuya* and *Acontias* can be explained largely on the basis of osteological and, to a lesser degree, myological differences between these two animals. In *Acontias* a long chain of around one hundred vertebrae, of more or less uniform length, is interconnected by means of synovial cotylo-condylar joints. The vestigial girdles hardly interrupt the uniformity of this chain; this arrangement is likely to enhance the passage of travelling waves. In contrast, the seventy to eighty vertebrae of *M. capensis* are subdivided into a short trunk consisting of only twenty-eight vertebrae and a long tapering tail composed of forty to fifty vertebrae. Furthermore, the precaudal vertebrae vary greatly in length, their intercentral joints are amphiarthroses, and they show regional differentiation to accommodate the girdles; an arrangement likely to limit the formation and to inhibit the smooth propagation of body flexures.

Furthermore, the *M. rectus abdominis lateralis* (absent in *Acontias*) extends from the pelvic girdle to the pectoral region along the ventrolateral margins of the trunk (Fig. IV.9C). Contraction of this muscle is likely to cause mid-trunk flexures.

In brief, the contrasting wave patterns are probably related to anatomical differences rather than differences in the mechanism of wave generation; and the distinction between travelling and standing waves should be seen as a useful metaphor rather than two distinct categories.
3.5 SUMMARY

(a) In *M. capensis* the limbs are responsible for support and propulsion.

(b) Some variation of the trot seems to be the most common gait.

(c) Weak body flexures contribute to stride length and possibly girdle rotation.

(d) The girdles are, however, linked to the vertebral column in a way permitting independent movement.

(e) The weak flexures of *M. capensis* usually reach a low maximum amplitude between the pelvic and pectoral girdles and may, therefore, be described as "standing waves, with a slight travelling tendency" (cf. Daan and Belterman, 1968, p. 265).

4. LOCOMOTION OF *Riopa sundevallii*

*Riopa* has miniaturized pentadactyle limbs (Fig. II.2B, D & 3A). It either oscillates these in the normal manner (Fig. V.18) during locomotion above ground or may press them against the side of its body while wriggling into or through soil.

The limbs are far too small to lift the entire trunk off the substrate. Still the tiny anterior limbs appear to contribute towards lifting the thoracic, cervical and head regions clear off the ground. The belly and most of the tail remains in continuous contact with the substrate. In other words, the limbs of *Riopa* have lost the role of supporting the trunk during locomotion.
FIG. V.18. A Locomotor Cycle of *Riopa sundevallii*. Dots are painted on the mid-line of the trunk and the limbs in transport are lightly stippled.
However, the feet still act as areas of high frictional contact with the substrate and the retraction of the miniaturized limbs still help to thrust the body forward assisted by lateral flexures of the body axis.

Gait diagrams (Figs. V.19A, B & C) illustrate the pattern and duration of limb contact with the substrate at three different speeds of progression. There is, however, a complication regarding the phase of limb contact, because there appears to be a phase of active thrust and a phase of passive contact. In Riopa the limbs no longer support the body, hence they can rest passively on the ground without upsetting the equilibrium of the animal. Although these two phases in limb contact could be observed, it was difficult to determine the exact moment of shift from passive to active contact, hence gait diagrams (Figs. V.19A, B & C) show total contact only. Daan and Belterman (1968) described a similar "dragging phase" for Chalcides ocellatus, a skink with slightly miniaturized limbs.

Some of the important parameters of locomotion not reflected in the gait diagram are tabulated in Table V.4.

In Riopa the amplitude of body flexures is higher than in Mabuya (c.f. Figs. V.16 & 20). The contribution of lateral bending to girdle rotation is around 50° and the latter contributes almost 50% to the stride length; in Mabuya the contribution of lateral bending is less than 30° and it contributes less than 35% to the stride length (Table V.3).

Minimal bending occurs when a pair of limbs is more or less mid-way through a stride while maximum flexure occurs in such
FIG.V.19 GAIT DIAGRAMS OF *Riopa sundevallii* PARAMETERS OF LOCOMOTION ARE REFLECTED IN TABLE V.4. EACH COMPLETE LOCOMOTOR CYCLE IS NUMBER WITH A CAPITAL ROMAN NUMERAL.
<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter (mm)</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Snout to Vent length (S V L) in mm</td>
<td>56</td>
<td>56</td>
<td>56</td>
</tr>
<tr>
<td>Number of locomotor cycles</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Number of frames</td>
<td>12</td>
<td>36</td>
<td>42</td>
</tr>
<tr>
<td>Distance covered</td>
<td>3.7</td>
<td>8.8</td>
<td>2.7</td>
</tr>
<tr>
<td>Time taken</td>
<td>0.3</td>
<td>0.9</td>
<td>1.05</td>
</tr>
<tr>
<td>Speed (cm per case)</td>
<td>12.3</td>
<td>9.7</td>
<td>2.6</td>
</tr>
<tr>
<td>Speed S L V</td>
<td>2.1</td>
<td>1.73</td>
<td>0.46</td>
</tr>
<tr>
<td>Stride length of Front limbs</td>
<td>35</td>
<td>25</td>
<td>14</td>
</tr>
<tr>
<td>Stride length of Hind limbs</td>
<td>38</td>
<td>33</td>
<td>18</td>
</tr>
<tr>
<td>Stride Rate (per sec)</td>
<td>3.3</td>
<td>3.3</td>
<td>0.9</td>
</tr>
<tr>
<td>Duration of contact with substrate</td>
<td>LH 66%</td>
<td>77</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>LF 66%</td>
<td>66</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>RF 66%</td>
<td>83</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>RH 66%</td>
<td>83</td>
<td>90</td>
</tr>
</tbody>
</table>
% of Stride that front footfall follows the ipsilateral hind footfall

Gait (Hildebrand, 1966)  MFWT  SWT  VSW

<table>
<thead>
<tr>
<th></th>
<th>50</th>
<th>44</th>
<th>45</th>
</tr>
</thead>
</table>

TABLE V.4 Some parameters of locomotion in *Riopa sundevallii*. (See text for explanation and Table V.2 for abbreviations).
FIG. V.20 SEQUENTIAL TRACINGS OF THE TRUNK MID-LINE OF A MOVING *Riopa sundevallii* SUPERIMPOSED WITH THE SNOUT TIP AND THE TAIL AlIGNED SO THAT MOVEMENT RELATIVE TO THE SUBSTRATE IS NOT SHOWN BUT ONLY THE CAUداد DISPLACEMENT OF BODY FLEXURES. (INTERVAL $\frac{1}{40}$ SEC.)
a way that the body is concave on the side of the limb that is further forward and convex on the side of the body with the backward limb. This is especially so in the pelvic region.

In *Riopa* the crests of the body flexures travel in a cranio-caudal direction (Fig. V.20). The tendency to form travelling waves is stronger in *Riopa* than in *Mabuya* (cf. Figs. V.16 & 20) but the amplitude of these travelling waves are modest compared to those of *Acontias* (Fig. V.21) or those of *Sceletes* (Fig. V.22).

The importance of the axial system for locomotion is highlighted by the fact that the animal can wriggle through shallow sand with its limbs addorsed to its body.

SUMMARY

(a) The limbs have lost their supportive role.

(b) However, they still act as points of high frictional contact with the substrate and probably contribute to propulsive thrust.

(c) As the animal enters soil the limbs are pressed against the body and it relies exclusively on axial undulation for progression.

(d) The amplitudes of the body flexures are higher than in *Mabuya capensis* but much lower than in *Sceletes* or *Acontias*.

(e) The body flexures of *Riopa* are weak travelling waves.

(f) In conclusion, the initial stages of limb reduction, as typified by *Riopa sundevallii*, is characterized by a
FIG. V.21 *Scolotes gronovii* WIRGGING RAPIDLY ON GLASS. THE HEAD IS NUMBERED IN SUCCESSIVE TRACINGS.
strong mixture of axial and appendicular behaviour, so that compared with *M. capensis*, its axial system contributes relatively more and its appendages relatively less to progression.

5. **LOCOMOTION OF *Scelotes***

5.1 **GENERAL**

The locomotor behaviour of three species (*Scelotes bipes*, *S. gronovii* and *S. brevipes*) was filmed and analyzed. They progress by lateral undulation above (Fig. V.22) and below the surface of soil (Fig. V.23). No concertina movements could be induced, in anyone of these three species, by placing them into a parallel walled channel, even though this procedure was regularly successful with *A. meleagris* (see Chapter V.2.5 and Fig. V.15).

5.2 **WRIGGLING ON GLASS**

Figure V.21 illustrates a specimen of *S. gronovii* wriggling on glass. The animal is prone to execute very rapid panic movements. It is also much more flexible than *A. meleagris* (Fig. V.2 & 4); consequently, the body is frequently thrown into a coil which is then propagated caudad. Despite its vigorous activity the animal does not progress when suitable *points d'appui* are lacking; instead only slight random displacement, probably due to friction between the glass and the animal's belly, occurs.

5.3 **SOIL PENETRATION BY *Scelotes brevipes***

Although *S. brevipes* still has a pair of minute pelvic limb buds
FIG. V.22. *Scolelepis b. bipes* Progressing by lateral undulation on a peg-board. Tracings taken from a movie-film and 0.25 sec apart were superimposed to illustrate that a single flexure with its anterior and posterior arms engaging a *point d'appui* each, is the minimum requirement for progression by lateral undulation. Note that in tracing 4, loss of contact with C is accompanied by contact with point A.
(Figs. II.2E), these do not contribute to propulsion. The animal progresses entirely by lateral undulation.

Figures V.23A & B illustrate S. brevipes entering a pile of dry sand after moving across a pane of glass covering a grid. A single (20 gm) brass weight is provided as point d'appui. The animal uses its tail to push against the weight shifting it backwards. This illustrates the importance of the tail as a propulsive organ. In the animal the tail forms an important part (almost 50%) of the undulatory surface (Fig. II.6).

The portion of the body in contact with the smooth glass slips a great deal. In the absence of points d'appui, Vn (as defined in Chapter V.2.3) is predictably large.

While pushing against the weight with its tail the animal penetrates the soil by rapidly oscillating its head from side to side.

The undulations of the animal's body below the surface of the soil produce a furrow which indicates its path of progression. Before the tail loses contact with the weight, a flexure, which pulls the posterior part of the body into the sand, is formed beneath the soil (Fig. V.23B).

The anterior and posterior arms of the flexure slip slightly in the direction of force application. Hence, the direction of slippage indicates the direction in which the arms push. Note that as the caudal surface of the anterior arm pushes in the direction $F_{aa}$, the posterior arm pushes in direction $F_{pa}$. The co-ordinated action of the anterior and the posterior flexure arms on the pegboard (Fig. V.22) and beneath sand (Fig. V.
FIG. V.23A. THE ENTRY OF DRY SAND BY A *Scelotes brevipes* MOVING FROM A GLASS COVERED GRID, NOTE SLIP-PAGE IN THE ABSENCE OF *points d'appui* AND THE PUSH EXERTED BY THE TAIL (DISPLACING A 20 g WEIGHT).
**FIG. V.23B** *Sceletotes brevipes* PROGRESSING BY LATERAL UNDULATION IN DRY SAND. NOTE THAT THE ANTERIOR ARM OF THE ANTERIORMOST BODY FLEXURE PUSHES IN THE DIRECTION $F_{AA}$ WHILE THE POSTERIOR ARM PUSHES IN THE DIRECTION $F_{PA}$. 
23) suggests that to understand the kinetics of lateral undulation, one must look at the force application of both an anterior and a posterior arm of a body flexure. This point can be illustrated best by referring to the force application diagrams of investigators who studied ophidian locomotion.

Mosauer (1932) illustrates the forces acting on a point d'appui and their translation into progression in the following diagram.

There is agreement with Mosauer on the following points:

(a) C presses against P normal to the surface of the body.

(b) S is the equal and opposite reaction to C.

(c) F, which causes progression, should act along the longitudinal axis of the animal.

However, the origin of force R is not explained. Forces C and S cannot have a resultant acting at right angles to it, hence force R is essential for the derivation of F; but where does R come from?
Hildebrand (1974) illustrates the dilemma of the single arm cum single point d'appui mode of analysis.

The thrust of the snake against an object \( (F_t) \) results in an equal but opposite force \( (F_0) \) which can be resolved into a lateral component \( (F_1) \) and a forward component \( (F_f) \). Although \( F_f \) acts in the overall direction of progression by the snake as a whole, the actual propulsive force must act along the coils of the snake or in Mosauer's terminology along the longitudinal axis of the snake.

The problem becomes, how can a resultant force which acts along the longitudinal axis of the body, in the direction of actual motion be derived; or alternatively how can the force \( R \) in the diagram of Mosauer be derived?

The action of the anterior and the posterior flexure arms suggest a solution to this problem along the following lines:

(a) The basic propulsive unit is a body flexure comprised of:
   (i) an anterior arm,
(ii) a crest, and
(iii) a posterior arm (Figs. V.22 & 23B).

(b) Active bending occurs in the crest of the flexure (Gray, 1968, pp. 191-3) with the result that the flexure arms wax and wane (Fig. V.24).

(c) The anterior and posterior arms of the flexure act as stiff levers which transmit the forces developed in the crest to points d'appui.

(d) The generation of forces in the crest involves two processes:

(i) As a result of musculature contraction on one side of the body (C_a) segment 3 (which represents one or more vertebrae together with its ribs and the body wall it supports) is flexed into the anterior arm of a flexure;

(ii) Simultaneous contraction on the opposite side of the body (C_b) causes segment 5 to be drawn into the crest of a wave (Fig. V.24).

(e) In the absence of points d'appui the crest slips backwards (Figs. V.24 & V.2).

(f) In the presence of suitable points d'appui, the posterior arm exerts thrust F_pa and the anterior arm thrust, F_aa (Figs. V.24 & V.23B).

(g) F_aa and F_pa results in a forward thrust along the body axis.

This interpretation implies that the axial muscles contract almost simultaneously on both sides of a crest. E.M.G. records indicate that such simultaneous contractions occur in an undulating animal (Fig. VI.3).
POSTERIOR FLEXURE ARM

REPRESENTS ONE OR MORE VERTEBRAE

CREST

ANTERIOR FLEXURE ARM

JOINT

FIG. III.24 SIMPLIFIED, SCHEMATIC ILLUSTRATION OF THE PROPOSED MECHANISM OF FLEXURE TRAVEL. SEE TEXT FOR THE EXPLANATION.

Foa

Foa
5.4 SUMMARY

(a) *S. b. bipes*, *S. gronovii* and *S. brevipes* progress by lateral undulation.

(b) Concertina movement could not be induced.

(c) The vestigial hind limbs of *S. b. bipes* and *S. gronovii* still go through the motions of walking though their contribution to propulsive thrust is probably minimal.

(d) In the presence of suitable points d'appui and below the soil these limbs are adpressed to the body, while the animal undulates.

(e) Propulsive force along the longitudinal axis of the animal is the resultant of the interaction of the forces exerted by both an anterior and a posterior arm of a flexure against its separate points d'appui.

6. COMPARISON

Although the locomotion of *M. capensis* is predominantly appendicular, there is a distinct, though weak, axial component which contributes to girdle rotation and hence stride length (Table V.3). As these flexures are weak it is difficult to state whether they are "standing" or "travelling waves" (sensu Daan and Belterman, 1968). In the tail the waves travel quite clearly, while in the trunk they show a slight tendency to travel. But, as pointed out by Peterson (unpublished thesis): "The analogy of behavioural waves with physical waves is, in fact, a loose one" (p. 227).

The miniaturized pentadactyle limbs of *Riopa* have reduced
thrusting power and no longer lift the entire trunk clear off the substrate. Axial undulations are stronger than in *M. capensis* and make a larger contribution to propulsive thrust. These flexures travel caudad along the trunk and tail. In other words, the appendicular system has become weaker and the axial system has increased in importance.

The three species of *Scoleotes* studied progress by lateral undulation, though the vestigial limbs sometimes strut perfunctorily. These animals are very flexible. This is due in part to their relatively long stout tails which form an integral part of their undulatory length. Concertina movement could not be induced.

*A. meleagris* employs two methods of axial progression, lateral undulation and concertina movement. Its trunk comprises about 80% of its undulatory length. The animal switches readily to concertina movement when placed in a parallel walled chamber, while this behaviour could not be induced in the other functionally limbless members of the regression series. This behavioural deviation on the part of *Acontias* is perhaps related to anatomical deviations from the rest of the regression series. Graph III.19 shows that the narrow "waisted" vertebrae with widely flaring zygapophyses of *A. meleagris*, differ significantly from those of the rest of the regression series; while Figure IV.4 shows that *A. meleagris* has an unusually well developed transversospinalis system. The widely flaring vertebrae and strong transversospinalis column (with its short segmental interneural and multifidus musculature) adapt the animal for the formation of the numerous curvatures of short radius required for concertina movement.
The patterns of locomotor behaviour shown by members of the regression series suggest the following ethocline. Quadrupedal skinks have a dual system of locomotion; both axial and appendicular. Initially the axial system is weak and it contributes to stride length and, therefore, the efficiency of the appendicular system. As limbs regress, the propulsive role of the appendages decreases and to compensate the propulsive role of axial undulations increases.

Thus, the gradual degeneration of limbs is accompanied by a gradual hypertrophy of the axial system; concomitantly, on the behavioural level, the gradual decline of appendicular propulsion is accompanied by a gradual increase in the undulatory capacity of the body axis.
VI. DISCUSSION : ADAPTIVE SIGNIFICANCE

1. General

A major objective of this section is to integrate the data presented in Chapters II-V. To facilitate description, one may consider body proportions, osteology, myology, and locomotion separately, but in the living, moving organism these aspects form an integrated whole, a form-functional complex (Bock and von Wahlert, 1965). Several levels of integration are aimed at. What are the anatomical bases of the changes in body proportions recorded in Chapter II? What are the biomechanical implications of observed osteological (Chapter III) and myological (Chapter IV) trends and tendencies? How are these related to changes in locomotor behaviour? Such integration of structural and behavioural information is often referred to as a functional interpretation (cf. Davis, 1949, p. 66). Functional systems have evolved in response to selection pressure imposed by the environment. This interdependence of form, function and environment is covered by the concept, adaptation (Davis, 1949).

2. Concept of Adaptation

Adaptation is a fundamental and unique attribute of all living organisms (Allee, et al., 1949). "The study of adaptation is the central theme of biology, although its generality sometimes remains unrecognized" (Gans, 1974, p. V). Williams (1966, p. 258) even goes as far to suggest that the study of adaptation is important enough "to warrant a special branch
of biology for its investigation". This speciality, he sug­
gests, should be called teleonomy. "Its first concern with a biological phenomenon would be to answer the question: 'What is its function?'. An initial assumption might be, in Pittendrigh's words, that 'some feature of the organism - morphological, physiological, or behavioural... serves some proximate end (food getting, escape, etc.) that the observer believes he can discern fully by direct observation without reference to the history of the organism'."

As the term "adaptation" refers to extremely complex pheno­mena manifested by the vast variety of living organisms adopting diverse strategies to survive in a multitude of hab­itats, it is not surprising that the term is "plagued with ambiguity" (Dobshansky, 1968) and that there is no generally accepted or acceptable definition of adaptation or adapted­ness (Stern, 1970).

We are concerned with presenting limb regression in skinks as a case study of adaptation, hence will not get involved in the polemics surrounding some definitions. Intuitively one feels that the phenomenon is too complex to be summarized by a brief definition, general enough to cover all the mani­festations of the phenomenon, but at the same time precise and concise.

The approach adapted here is to select a definition suita­ble for our purpose and to briefly justify the choice.

There are several biological definitions of adaptation (Bock and von Wahlert, 1965; Dobshansky, 1968; Stern, 1970; De Beer,
1972). We are not concerned with "physiological adaptation", i.e. change in an organism as a result of exposure to certain environmental conditions which make it react more effectively to these conditions (e.g. tanning of human skin in the presence of intense light). We are not concerned with "sensory adaptation", i.e. change in the excitability of a sense organ as a result of continuous stimulation. We are not even concerned with "universal adaptation" (Bock and von Wahlert, 1965, pp. 283-4.

We are, however, concerned with "evolutionary adaptation", meaning the longterm hereditary adjustment of a species to a particular set of environmental conditions (Bock and von Wahlert, 1965, p. 285). Henceforth the term adaptation will refer to "evolutionary adaptation" only.

Stern (1970) has pointed out that definition of the term "adaptation" is complicated by the fact that this noun is commonly used in three quite different semantic situations:

(a) "Adaptation" may refer to a trait or feature possessed by an organism or population. For example, Abercrombie et al. (1951) defines adaptation as follows:

"Any characteristic of living organisms which, in the environment they inhabit, improves their chances of survival and ultimately of leaving descendants, in comparison with the chances of similar organisms without the characteristic; natural selection therefore tends to establish adaptations in a population".
An adaptation to a particular feature of the environment is an adaptation because it reduces destruction by that particular feature. An adaptation to a particular activity of an organism (e.g. flying) means simply a characteristic which makes possible or improves performance of that activity without necessarily being measured in terms of survival, though usually that is implied.

(b) The term "adaptation" may refer to a state of being adjusted to an environment. For example, Jepsen et al. (1949, p. 449) defines adaptation as a "Correlation, in a way useful to the organism, between structure, function, and environment".

(c) "Adaptation" may also refer to the process whereby the traits in (a) or the state in (b) above is achieved. Discussion of adaptation as a process is deferred to the next chapter. In this one attention will be focussed on adaptive traits and the state of adaptedness.

The definition of Jepsen et al. (1949) is adopted here because it can be applied readily to our data. This definition implies a consonance or adjustment between three factors:

(a) morphology (= form, structure, anatomy, etc. - in this case of the locomotor apparatus)

(b) function (= behaviour, activity, physiology - in this
(c) environment (= habitat, surroundings - in this case those features of the environment that influence locomotion).

During limb regression there is an interrelated shift in each of these three factors. On the morphological level as the limbs and girdles atrophy the axial skeleton and musculature hypertrophies (Chapters III and IV). On the behavioural level there is a shift from a dominantly appendicular mode of locomotion to an exclusively axial means of progression. As far as the shift in habitat is concerned, the limbed skinks are terrestrial; the partially or completely limbless skinks are largely subterranean (Camp, 1923; FitzSimons, 1943).

3. Rationale
As pointed out by Stern (1970) a large problem in determining the adaptive value of most characteristics is that there are no alternative states with which to make comparison. The regression series of skinks lends itself to the comparative method. Limb reduction is invariably associated with a fossorial mode of life. The question arises what special demands are imposed by such a subterranean habitat? Next we ask, in what ways do the locomotor anatomy and behaviour deviate from that of the typical quadrupedal condition? The form-functional deviations are then compared with the habitat demands to determine whether any of the deviations appear to hold advantages for the organism in the new environment.

This mode of analysis is employed to determine the adaptive value of limb regression, elongation of the body axis, and the biomechanical features of the body axis.
<table>
<thead>
<tr>
<th>Conditions of Limbs</th>
<th>Normal-limbed</th>
<th>Reduced-limbed and limbless</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factors</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>Mainly terrestrial</td>
<td>Mainly subterrestrial</td>
</tr>
<tr>
<td>Mode of locomotion</td>
<td>Appendicular with some assistance from lateral bending of the body axis.</td>
<td>Axial - especially lateral undulation and also Concertina Movement in Acontias.</td>
</tr>
<tr>
<td>Morphology</td>
<td>Pentadactyle limbs, short trunk and usually a long tail.</td>
<td>Limbs partially or completely lost; trunk elongated and tail usually shortened.</td>
</tr>
</tbody>
</table>

Table VI.1 General trends associated with limb regression
4. Limb regression

The process of limb loss is a gradual one; millions of years are required for their complete degeneration (Lande, 1977). Living skinks illustrate many stages in this process of appendicular degeneration. The limbs are first miniaturized as seen in *Riopa sundevallii* (Fig. II.2C & D) and *Scelotes capensis*. Then there follows further miniaturization (Fig. II.2E) accompanied by the loss of elements starting with the digits (Fig. II.2E). In skinks the hind limbs persist longer than the front ones. Even after external traces of limbs are lost, vestiges of hind limbs may still persist beneath the skin as in *S. arenicola* (Fig. II.2E). Finally, as in the Acontinae, even internal traces of limbs are lost. Rudimentary girdles do persist after the limbs have disappeared completely. As limbs degenerate the body axis elongates to take over the locomotory functions.

Of what adaptive significance is limb loss? This problem can be analysed into the following questions: What functions do limbs perform in terrestrial locomotion? Considering the fact that limb loss is associated with the invasion of a subterranean habitat, in these skinks the next question is: Can limbs perform similar functions in a fossorial environment? What characteristics of a subterranean habitat would demand reduction or loss of limbs?

During normal quadrupedal locomotion above the surface of the soil, the limbs perform a number of tasks. Firstly, they may lift the trunk clear off the substrate so that only the pos-
terior region of the long tapering tail is dragged over the ground. This elevation of the trunk reduces wear of its ventral surface and also reduces the sliding friction acting opposite to the direction or progression. The manus and pes, on the other hand, are covered by rough scales which are likely to enhance frictional contact with the substrate. These points of high friction diminish the tendency for the feet to slip when propulsive forces are transmitted to the substrate (Badoux, 1964; Gray, 1968). After having thrust the body forward relative to a limb, the latter is swung forward during a recovery stroke. The cyclical movements of the limbs, according to a rather stereotyped pattern, are essential for normal progression (Gray, 1968). The swinging appendages as well as the forward progressing body cleaves through air, which offers minimal resistance to their movements.

The tasks performed by the limbs during normal quadrupedal progression may, consequently be listed as follows:

(a) They reduce friction between the body and the substrate by supporting it during progression.

(b) They transmit propulsive forces to the substrate via feet adapted for high frictional contact.

(c) The limbs oscillate backwards (during the propulsive stroke) and forward (during the recovery stroke).
(d) The limbs must maintain equilibrium during their movements, i.e. "the projection of the centre of gravity must fall in an optimally stable point between the moving points of support and be maintained within rather narrow limits. In order to accomplish this a whole set of different compensating mechanisms has evolved that enables the animal to counteract various types of unexpected perturbations" (Grillner, 1975, p. 248).

Are any of these tasks normally performed by limbs relevant in a subterranean habitat?

In a subterranean environment it is impossible for the limbs to lift the body free of the substrate as soil envelopes the animal. Furthermore, if limbs were to be employed in the normal way they would have to be swung anteriorly through the dense soil, an energetically very costly process. In other words, if limbs are not utilized as digging instruments, they loose their usefulness in a subterranean environment and can no longer perform the tasks outlined above.

Normal limbed skinks have been observed to scratch into the soil with the aid of their limbs. However, they usually press their appendages against their bodies as they enter soil or pass through other crevices. It is not uncommon for a lizard to adpress its forelimbs to the body as the anterior half of the trunk enters a crevice while its hindlimbs still continue to perform propulsive movements. However, when the hindlimbs reach the crevice, they stop moving and are pressed against the body which progresses further by lateral bending of the trunk.
The limbs of skinks are not only ineffective as propulsive organs in a fossorial environment, but their presence is probably a hindrance in at least three ways. Their presence disrupts stream-lining of the body which becomes important in a medium such as soil which offers much resistance to progression. Furthermore, the presence of limbs would increase the effective cross-sectional area of the body hence the width and energetic cost of tunnel creation (Gans, 1960). Finally, the habit of adpressing the limbs against the lateral surface of the body is likely to impede undulation, the alternative propulsive mechanism.

Williams (1966) has emphasized that the concept of adaptation should not be invoked unnecessarily. He would exclude regressed structures, which were formerly useful, from this category. In specialized fossorial skinks, however, the limbs are not only useless but actually a hindrance. Hence their loss is advantageous to the organism and, therefore, by definition adaptive. The gradual loss of limbs would facilitate a smooth transition from appendicular to an axial mode of locomotion. For limb regression is always accompanied by elongation of the body axis (Gans, 1975).
5. **Elongation**

Gans (1975) has shown that elongation is universally associated with limb reduction in lower tetrapods. What are the anatomical bases of elongation? Of what adaptive significance is it? Elongation involves a relative increase in length as well as a reduction in cross-sectional area. Each of these two will first be discussed separately.

In skinks the lengthening of the body is confined mainly to the precaudal region (Figs. II.5, II.6, II.7 and II.8). What is the anatomical basis of this lengthening? The number of precaudal trunk metameres have increased. The majority of normal limbed skinks have 26 presacral vertebrae (metameres), and this number seems to be very stable for several genera (Table III.1 and III.2 and also Fig. III.12). On the other hand, correlated with limb regression is a marked increase in the number of precaudal metameres (Fig. III.12). The maximum number of precaudal vertebrae recorded to date in a skink is 107 (in the limbless *Typhlosaurus vermis*).

Although the general correlation of an increased number of metameres with limb regression is beyond dispute, there is no strict correlation between the degree of limb loss and the number of precaudal vertebrae; instead it fluctuates intra- as well as intergenerically. Even intraspecific fluctuations occur (Fig. III.12). This suggests instability; as if selection for the maintenance of a particular precaudal vertebral number is not strong. The contrasting stability in this number for normal limbed skinks indicate that here
stabilizing selection is operative.

Lande (1978) in a paper dealing with limb loss in lower tetrapods also compares limb and body lengths. He found a "few discrepancies" in the ordering of the species in relative body length. He proposed a statistical solution: "There is an interesting explanation for the discrepancies in the ordering of the relative body lengths in the figures. They are probably due to allometric growth of the body relative to the skull." An alternative explanation is suggested here. There is only a general, but not an absolute relationship, between elongation and the degree of limb loss. Thus in Figure III.12 we see that several species of bipodous Scelotes have more precaudal vertebrae than several limbless species of the same genus.

On the other hand, in the normal limbed Mabuya for a sample of 11 species and 60 specimens the number of precaudal vertebrae is 26. In the reduced limbed species even smaller samples evince much more variation even on the intraspecific level (See Fig. III.12). This suggests that in the normal-limbed Mabuya a strong stabilizing selective force operates to keep constant the presacral vertebral number, and hence the intergirdle span. In other words, there is a functional link between the limbs and the body axis in quadrupedal skinks. This demanded co-ordinated change. Gradual elongation permits the body axis to assume responsibility for locomotion and renders limbs superfluous. Once the functional link between limbs and trunk is disrupted, selection can
operate independently on the limbs and on the number of trunk metameres. Consequently, even in closely related species, limb reduction may have progressed slightly further in one while lengthening may have progressed further in another. At this stage selection may also operate on the non-locomotory role of limbs. For example, vestigial hind limbs may play a role in mating activities (cf. Bellairs, 1972; Gasc, 1967b).

Thus far we have confined our remarks to the lengthening of the trunk; but what of the tail? It was suggested in Chapter II that elongation in skinks is confined mainly to the trunk (Fig. II.5) that in intermediate forms the tail remains moderately long (Fig. II.7) but that it is relatively short in the specialized Acontinae (Fig. II.7). If these suggestions are correct then it implies that the multiplication of metameres should be confined exclusively to the trunk region. This is the case (See Table III.2). In the relatively long tailed intermediate skinks, there is no indication of an increase in the number of caudal metameres (Table III.2).

Elongation involves not only the lengthening of the trunk but also a concomitant reduction in the transverse area of the animal. The cross-sectional area is not only reduced but it tends to become uniform along the entire length of the trunk (cf. Figs. III.1, III.9). Such a reduced and more or less uniform cross-section is likely to enhance the
animal's efficiency as a burrower. When tunnelling through soil, the soil particles have to be displaced or compressed. The quantity of energy required to accomplish this is "proportional to some function of the diameter of the tunnel" (Gans, 1975, p.462). More energy is required to create a wider tunnel. Hence if the animal were to present a small, smooth cross-sectional area without projections such as limbs, a reduced amount of energy would be required by it to move through soil. In the absence of limbs the animal progresses by lateral undulation, i.e. by lateral bending of its trunk (See Chapter V). The body wall pushes against points d'apui while the axial musculature generates these propulsive forces. Consequently, the animal seems faced with conflicting demands. On the one hand, reduction in its cross-sectional area will reduce the amount of energy required for tunneling; on the other hand, a strong body wall is required to generate and to transmit adequate propulsive forces. What anatomical solutions were devised for these conflicting requirements?

These conflicting demands are resolved by reducing the transverse area of the body at the expense of the visceral space (Fig. IV.2). The epaxial musculature of the body wall hypertrophies at the expense of the hypaxial (Fig. IV.3). As the epaxial musculature expands over the lateral aspect of the trunk (Fig. IV.7) the hypaxial musculature, with the possible exception of the M. intercostalis externus, is reduced. In other words the conflicting demands are resolved by reducing the visceral space while simultaneously increasing the
FIG. VI.1 THE ARRANGEMENT OF THE VISCERA RELATIVE TO THE VERTEBRAL SEGMENTS IN *Mabuya capensis* AND *Acontias meleagris*. (See figures III.1 & III.9 for trunk profiles of these animals)
contribution of the epaxial muscles at the expense of certain hypaxial muscles. It will be shown below that the hypaxial musculature generate the muscular effort required for lateral undulation. It will also be shown that the hypaxial musculature, which atrophies, have a reduced role in supporting the viscera.

On the assumption that even in a normal limbed skink the visceral space is utilized fully without leaving the utilized room, it follows that reduction of the visceral space would require compacting or repacking of the viscera. Only a limited amount of compacting is presumably possible. Redistribution of the viscera is the more important process. (Fig. VI.I). Redistribution of the viscera can only occur along the longitudinal axis of the body. The overall volume of the visceral cavity cannot be reduced too much - what is lost in a transverse plane must be added in a longitudinal plane. It is interesting to note that Typhlosaurus vermis which has the lowest transverse diameter among the skinks also has the most elongated trunk.

It is, therefore, suggested that a reduction in the cross-sectional area of the trunk must of necessity be accompanied by a lengthening of the trunk region. Hence, in skinks with partially reduced limbs reduction of body diameter is accompanied by snout-to-vent lengthening.

The scincid evolutionary pathway with regard to elongation appears to be the following:
(a) The plesiomorphous condition appears to be similar to that of *M. capensis*, i.e. the animal is stout, short-trunked and has a long tapering tail.

(b) To decrease the investment of energy required for soil penetration, the transverse diameter of the body and the limbs must be reduced.

(c) If the reduction in diameter occurs mainly at the expense of the visceral space – elongation of this space, hence the trunk, must occur. Therefore the trunk lengthens.

(d) This lengthening of the trunk enhances its capacity to perform lateral undulation and also increases the intergirdle span, thus further decreasing the utility of the limbs. Hence appropriate mutations and selection could lead to their further reduction and eventual elimination.

(e) Initially, the long tail probably assists with lateral undulation and becomes stouter to fulfil this function (cf. *R. sundevallii* and *Scelotes* species).

(f) Further reduction in transverse diameter may result in further elongation of the trunk at the expense of the tail so that a thick walled trunk becomes the main locomotor organ and the tail becomes reduced in length (cf. Fig. II.7 where intrageneric reduction of limbs is correlated with a reduction in tail length).

In specialized limbless skinks the trunk serves as a container for the viscera as well as the major portion of the locomotor apparatus.

There is, however, a second pathway evinced by partially or
completely limbless lizards belonging to other families. The limbless *Ophisaurus apodus* (Aguidae) has a long tail, around 60% of the body length (Gasc, 1967b). In the cordylid *Chamaesaura anguina* (with four reduced, didactyle limbs) the tail occupies 78% of the total length (Gasc, 1967b and another specimen 73% of the total length (FitzSimons, 1943). In the bipodous *C. macrolepsis* the tail occupies 72% of the body length (FitzSimons, 1943). Especially in the cordylids limb reduction appears to be accompanied by elongation of the tail. This is directly opposite to the condition in skinks. What is the explanation for these contrasting trends?

Limb loss adapts skinks for a subterrestrial environment; anguids and cordylids occupy grassy habitats (FitzSimons, 1943; Waters, 1969). The degeneration of the limbs prevent their becoming entangled in grass. Motion is very rapid and smooth in these "sweepslange" ("whip-snakes") which progress with their vestigial limbs adpressed to their bodies (FitzSimons, 1943).

Do differences in their habitats explain the contrast in their tail lengths? The long tails of the anguids and cordylids make a major contribution to the undulating length of the animal (Gasc, 1967b). In the cordylids the tail constitutes more than 70% of the undulating length; by contrast in the Acontinae this figure is less than 25%. There are obvious advantages in having the tail as the major propulsive unit. It does not contain any viscera that is flexed during lateral bending. It is composed (ignoring the large quantities of fat) mainly of vertebrae and muscles,
the basic components of any locomotory apparatus. As viscera are not involved but only axial metameres it should be ontogenetically less complicated to elongate the tail compared with the trunk where the enclosed viscera are also affected. A long muscular tail might well be proto-adapted to take over the locomotory functions after the partial or complete loss of limbs. The question now arises why did the African skinks not exploit the locomotory potential of their tails?

In the first place, the compressing or compacting of soil during tunnelling would probably require more energy for animals of equal cross-sectional area, than would the pushing aside of flexible blades of grass. Consequently, the reduction of transverse diameter is a much more crucial requirement in burrowers than in grass-tuft-dwellers. However, if reduction occurs at the expense of the visceral space then the latter has to be accommodated along the longitudinal axis.

In the second place, an arrangement where a slightly flexible trunk pushes grass aside while a long flexible muscular tail provides the propulsive power will be less effective in a subterranean habitat. The propulsive power required for compacting soil is best applied close to the head. It is less effective to have the propulsive power concentrated in the tail and then transmitted to the tip of the snout if the trunk must also be long, thin and flexible. Much energy could be wasted or special modifications would be needed to prevent buckling (cf. Gans, 1960).
In brief, the specialised scincid burrowers of Southern Africa may be short-tailed (a) because extreme reduction of the transverse diameter demands the lengthening of the visceral cavity and (b) because it is advantageous to have the propulsive forces generated as near to the digging snout as possible. In intermediate members of the regression series the tail undergoes only slight shortening (Fig. II.7) but becomes almost as bulky as the rest of the trunk. Here it apparently makes a significant contribution to the total undulating length of the animal. This interpretation is corroborated by the following:

(a) Burrowing snakes usually have shorter tails than non-burrowers (Hoffstetter and Gasc, 1969). The specialized fossorial Amphisbaenia also have relatively short tails (Gans, 1974).

(b) Gans (1976) has shown that in uropeltids the anterior trunk muscles are physiologically adapted to cope with burrowing.

The evidence mentioned above all point to a reduced importance of the tail as an undulating propulsive organ in some burrowers.

Of what functional significance is elongation? Firstly, the reduction in cross-sectional area reduces the energy investment required for tunnelling (Gans, 1975). Secondly, there is a particular mass of abdominal viscera and this has to be packed in a longer tube. Thirdly, elongation allows the use of lateral undulation, and thus the reduction of limbs (Gans 1975).
Lateral undulation requires that the animal be sufficiently long and flexible to transmit a series of travelling waves along its trunk. This lengthening of the trunk, and hence increased flexibility, is achieved by the multiplication of trunk metameres.
6. Biomechanical Analysis

6.1 General

We have shown in Chapter VI.4 that in most subterranean environments the limbs of skinks are not only useless but probably even represent a hindrance to progression. As limbs regress the body axis elongates and assumes responsibility for locomotion. Several trends and tendencies in osteology (Chapter III), myology (Chapter IV) and behaviour (Chapter V) are correlated with appendicular degeneration. These trends will now be subjected to a biomechanical analysis to determine their adaptive significance.

During locomotion propulsive forces are generated by the body and transmitted to the environment. Appendicular and axial locomotion differs in respect of the body parts involved in force generation and also the mode of its transmission to the substrate. In quadrupedal skinks limbs are mainly responsible for force generation and transmission to the substrate. In limbless skinks, on the other hand, the body axis generates the propulsive forces and transmits them to the environment along the entire body axis (Fig VI.2). In intermediate forms, such as *Riopa sundevallii* the role of the body axis is on the increase while the role of the limbs is on the decline. However, both the axial and the appendicular systems are, however, functional.
Why develop axial locomotion in a fossorial habitat? In normal limbed skinks lateral bending of the body makes only a minor contribution to progression. If appendages are useless and even disadvantageous in a fossorial habitat, the body axis is protoadapted to assume responsibility for locomotion. (This assumption will be fully discussed in the next chapter when considering the evolution of limblessness). In other words, the body axis is the only alternative locomotor apparatus potentially available to skinks, and lateral undulation the concomitant alternative mechanism (Gans, 1975).

Besides being the only viable alternative, the body form required by lateral undulation would also meet certain demands imposed by a subterranean habitat. Firstly, lateral undulation requires a slender, flexible body axis. This functional demand can be met by reducing the cross-sectional area of the trunk and by increasing its length. A consequence of such elongation is to reduce the energetic cost of tunnelling. Secondly, for progression to occur by lateral undulation, resistance offered to motion along the body axis (\(R_L\)) must be less than the resistance offered perpendicular to the body surface (\(R_N\)) i.e. \(R_N > R_L\) (Gray, 1953). An animal enveloped in a temporary tunnel below the soil has all its flexure arms (Fig. V.23B) pushing against resistant soil like a fish swimming in water. In an underground habitat there is never a shortage of points d'appui.
Accepting that the body axis takes over progression in a subterranean environment, the question arises how is the primitive scincid pattern modified to accommodate this derived mode of locomotion? What anatomical features would enhance axial locomotion? The basic requirements for this type of locomotion are:

(a) a long flexible body axis capable of forming travelling waves (Fig. V.2);
(b) a small cross-sectional area to keep $R_L$ as low as possible;
(c) muscles capable of generating powerful travelling waves along the body axis;
(d) a body wall strong enough to transmit propulsive force to the environment.

Any anatomical feature that promotes one or more of these general requirements will be interpreted as being adaptive. Those features which appear to form distinct morphoclines in the regression series will be assessed in terms of these requirements.

6.2 Significance of osteological trends.

As limbs degenerate the precaudal portion of the vertebral column evinces the following changes:

(a) The number of presacral vertebrae increases (Fig. III.12).
(b) They become shorter relative to the snout-vent length (Fig. III.17).
(c) Their length becomes more uniform along the column (Fig. III.17).

(d) The cotylo-condylar intercentral joints are amphiarthroses in Mabuya, and diarthroses in Acontias and Scelotes.

(e) The width of the zygapophyses increases relative to body diameter (Fig. III.18) and relative to the length of the vertebrae (Fig. III.20).

Features (a), (b) and (d) would enhance the flexibility of vertebral column. Not only have the number of vertebral levers increased, they are shorter and their intercentral joints have become more mobile.

Regional differentiation of the vertebral column in quadrupedal skinks is probably due to the influence of gravity and the presence of girdles which must be linked to the body axis. The trunk of such an animal may be divided into three regions. A cervical region cantilevered from the shoulder girdle, a trunk region spanned between the two girdles and finally a tail cantilevered from the pelvic girdle. When the body is supported by limbs, these regions must resist the tendency of gravity to cause bending in a vertical plane.

In a limbless skink almost the entire body rests on the substrate, girdles are vestigial, hence the influence of gravity is decreased. Moreover, propulsion is effected by travelling waves passing down the entire column. Uniformization of central length is likely to promote the smooth passage of such waves.
Bone muscle systems may be regarded as machines which transmit force from one place to another (Hildebrand, 1974). Any input force applied to a machine is designated as an in-force ($F_i$) and any output force derived from a machine is called an out-force ($F_o$) (Hildebrand, 1974). During progression propulsive forces, generated by the locomotory muscles and transmitted to the environment, are the out-forces. The in-forces, on the other hand, refer to the propulsive reaction elicited from the environment.

While muscles are responsible for the generation of the out-forces, bones act as levers to transmit both the in- and out-forces. Each force is spaced from a fulcrum (i.e. a movable joint) by a segment of a lever called a lever-arm. The in-lever arm ($L_i$) extends from the fulcrum to the point of application of the in-force ($F_i$) and the out-lever arm ($L_o$) extends from the fulcrum to the point of application of the out-force ($F_o$). The product of a force times its lever arm is called a turning force, or moment, or torque ($T$).

If one makes a number of simplifying assumptions such as that the joints in the system or the flexing tissue offer no resistance to motion, then, when a lever system is in equilibrium:

$$F_i L_i = F_o L_o \quad (1) \quad (cf. \ Hildebrand, \ 1974).$$
FIG. VI.2 DIAGRAM OF A PORTION OF THE BODY AXIS OF ACONTIAS MELEAGRIS, SHOWN AS A THREE DIMENSIONAL LEVER SYSTEM. EACH OF THE EPAXIAL MUSCLES IS REPRESENTED BY A PATTERN CODE AND THE APPROXIMATE ORIGIN AND INSERTION OF EACH ARE SHOWN: (A) IN LATERAL VIEW; and (B) IN DORSAL VIEW.

- $F_i$, In-force or reaction to resistance offered by point d'appui;
- $F_o$, out-force exerted by body against point d'appui;
- $L_i$, in-lever arm;
- $L_o$, out-lever arm shown for the M. longissimus and for the M. iliocostalis only.
Fi is the reaction elicited from the environment by the action of the body. It is explained by Newton's third law which states: "For every action there must be an equal but opposite reaction" (Gray, 1968, p. 5).

In quadrupedal skinks Fi is transmitted to the body axis from the substrate via the feet, limbs and girdles. In the limbless Acontias on the other hand, this reaction is transmitted from the points d'appui via the body wall and the ribs to the vertebral column. In other words, the crucial difference is that in limbed skinks normally no Fi is exerted against the ribs of the trunk while in limbless skinks Fi is exerted exclusively against the ribs and body wall (Fig. VI.2).

Furthermore, as soil offers more resistance to progression than air, it follows that when undulating through soil relatively large in-forces must be elicited from the environment. Consequently, a soil-crawling skink must be adapted to elicit and to withstand Fi of great magnitude. From (1) it follows that

\[ F_i = \frac{F_0 L_0}{L_i} \]  

This formula implies that Fi can be increased by increasing F0 and L0 and by decreasing Li. The osteological and myological trends manifested by partially or completely limbless skinks will now be examined in the light of these requirements.
In an undulating skink, $L_i$ is the perpendicular distance from the point on the body wall where $F_i$ is applied to the mechanical axis of the vertebral column. The mechanical axis refers to a hypothetical line drawn through the longitudinal axis of vertebral centra so that it passes through the centres of the cotylo-condylar joints (cf. Gasc, 1976). This single line can effectively replace the bone when its movements are being considered (Warwick et al., 1973).

Ribs mediate as in-lever arms that withstand bending and compression. They must, therefore, be adapted to withstand in-forces of great magnitude and it is beneficial to the animal, according to formula (2), to keep $L_i$ as low as possible. As limbs regress the ribs:

(a) become more numerous;
(b) form arches of smaller radii;
(c) are thicker in a transverse plane (Fig. III.8A-D);
(d) become more uniform in size;
(e) articulate on more massive synapophyses.

These changes have numerous beneficial consequence for an undulator. The strengthening of the body wall will be enhanced by (a), (c) and (e). There are now more ribs located closer to each other (as a result of the shortening of the vertebrae) and they are strengthened in a transverse plane to withstand the shearing effect of $F_i$ (Fig. VI.2). The medial displacement of the rib is prevented by the strong superior costal ligament and $F_i$ is communicated to the vertebral column via strong
Features (b) and (d) give the body a more uniform and streamlined profile, they reduce its cross-sectional area and they promote its flexibility; in addition, they have two important mechanical consequences; they reduce the in-lever arm (as required by formula (2)), and they reduce the magnitude of the torsional forces around the mechanical axis.

The latter is a major problem of undulators especially when $F_i$ is applied well below the level of the mechanical axis of the vertebral column. The incoming forces will tend to twist the vertebrae around their longitudinal axis. In reduced limbed skinks one effect of the much enlarged zygapophysial joints is to counteract torsion. In snakes additional articulatory surfaces (viz. zygosphenes and zygantra) also assist. Ribs of smaller radius will reduce the torque of these torsional forces (Fig. VI.2, $F_i \times L_i$).

When skinks perform undulatory movements, travelling waves pass along the body axis towards the tail (Fig. V.2). Such waves can only be formed by the sequential lateral flexion of the vertebral column with the ribs communicating the wave of curvature to the body wall. Thus, $F_o$ must be generated by muscles attached in such a way that they can cause lateral bending of the vertebral column.
6.3 Significance of Myological Trends

On morphological grounds the epaxial musculature seems to be the most likely candidate. It links vertebrae to other vertebrae or to ribs. Furthermore, as limbs regress they hypertrophy at the expense of the visceral space (Fig. IV.3) and at the expense of the hypaxial musculature (Fig. IV.3). Moreover, their lateral spread (Fig. IV.6) and their circumferential expansion (Fig. IV.7) are likely to improve their orientation for lateral bending of the vertebral column.

Simultaneous recordings of muscle activity by electromyography and of undulatory movements by cinematography reveal unequivocal activity in the epaxial muscles during lateral undulation (Fig. VI.3). Electrodes placed next to each other, one in the transversospinalis or longissimus system and the other in the iliocostalis system indicate activity in phase during an undulatory cycle.

Morphological considerations as well as limited electromyographical data indicate that the following muscles are active during lateral undulation.

(a) M. semispinalis et spinalis (confirmed by electromyography);

(b) M. longissimus dorsi (confirmed by electromyography);

(c) M. iliocostalis (confirmed by electromyography);
FIG. VI.3 ELECTROMYOGRAMS SHOWING THE ACTIVITY IN CERTAIN EPAXIAL MUSCLES OF AN Acontias plumbeus UNDULATING RAPIDLY ON A SMOOTH METAL SURFACE (SEE CHAPTER 1.6.2). THE RIGHT AND LEFT ELECTRODES ARE IMPLANTED AT THE SAME LEVEL. NOTE THE PERIODIC "ACTIVITY" OF THESE MUSCLE ASSOCIATED WITH UNDULATORY BEHAVIOUR.
(d) that portion of the M. intercostalis externus or iliocostalis which span successive myosepta;

(e) to a lesser extent the M. obliquus abdominus externus superficialis.

As limbs regress there is a tendency for (a), (b) and (c) to increase in relative cross-sectional area (Fig. IV.4), hence in strength. The total torque produced by these muscles is a product of the magnitude of the forces they generate times the out-lever arms ($L_0$). An $L_0$ is, of course, the perpendicular distance from the point of attachment of each of these muscles to the mechanical axis of the vertebral column.

The semispinalis component of the transversospinalis group arises from the upper surface of a postzygapophysis and from the inner surface of the medial intermuscular septum (Fig. IV. 9A + 10A). Its $L_0$ is, consequently, the perpendicular distance from its point of attachment on the postzygapophysis or medial intermuscular septum to the mechanical axis. This lever arm increases as limbs regress, for then zygaphysial width becomes greater (Fig. III.18).

The M. longissimus arises from the outer surface of the medial intermuscular septum and the ventrocranial surface of a prezygapophysis. Thus in reduced limbed skinks its point of origin is further from the mechanical axis for the reason given in the previous paragraph (Fig. II.18).
The Y-shaped tendons insert onto the inner surface of the dorsal fascia and the lateral intermuscular septum. These points of insertion are situated relatively further from the mechanical axis in reduced limbed skinks because of the lateral spread (Fig. IV.6) and the circumferential expansion (Fig. IV.7) of the epaxial musculature in these animals. Consequently, $L_0$ for these muscles are relatively larger in reduced limbed skinks. The anterior attachment can, however, be stabilized so that flexion is caused at the vertebra from which the muscle originates.

Fibres of the ilioscostalis originate from the lateral intermuscular septum and insert onto a rib 7 to 8 segments cranial to its point of origin. As limbs regress this muscle is displaced laterad (Fig. IV.1A,B,C). In the limbless Acontias this muscle inserts on the ventral half of a vertebral rib, consequently its lever arm is only slightly less than half of the diameter of the animal. As in the case of the longissimus, the anterior attachment of the muscle may be stabilized and the posterior one moved.

In brief, all the multisegmental units of the epaxial musculature have shifted their points of insertion laterad, relative to the limbed counterparts, consequently they have increased their $L_0$ and leverage for lateral bending. Herein lies the biomechanical significance of the changes reflected in graphs IV.6 and IV.7.
There is also a tendency for the epaxial muscles to elongate as limbs regress, with the result that in limbless forms the muscle spans more segments than in the case of their limbed allies (cf. Auffenberg, 1962). Such chains of overlapping muscles are likely to promote the smooth passage of travelling waves (Gasc, 1976). This arrangement results in near to fifty epaxial muscles crossing the joints between two successive mid-trunk vertebrae (Table VI.2), a situation which complicates the detailed analysis of lateral bending.
<table>
<thead>
<tr>
<th>Name of Epaxial Muscles</th>
<th>Number of slips in pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. interneurales</td>
<td>1</td>
</tr>
<tr>
<td>M. interarticularis superior</td>
<td>1</td>
</tr>
<tr>
<td>M. multifidus</td>
<td>2</td>
</tr>
<tr>
<td>M. semispinalis et spinalis</td>
<td>6</td>
</tr>
<tr>
<td>M. longissimus</td>
<td>±7</td>
</tr>
<tr>
<td>M. iliocostalis</td>
<td>±7</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>±24 pairs</strong></td>
</tr>
</tbody>
</table>

Table VI.2 The number of muscular units crossing a mid-trunk vertebral joint in *Acontias meleagris*
Although the epaxial muscles are the prime force generators for lateral undulation, certain hypaxial muscles are suited in attachment and fibre direction to make a contribution as well. One of the most important of these is the intermyoseptal fibres fused with the M. intercostalis externus ventral and the iliocostalis dorsal to it. These intermyoseptal fibres are present in the entire regression series. In _M. capensis_ they are located right next to the vertebral column (Fig. IV. 8B; IMY); in the limbless _Acontias_ they are displaced laterad so that they span the ventral, instead of the upper half, of a pair of ribs (Fig. IV.10; IMY). These longitudinal fibres could exert longitudinal pull on successive ribs near to the lateral margin of the body, thus giving them a very favourable leverage (large \( L_0 \)) for flexing the body axis. To bring about vertebral flexure, however, the vertebro-costal joint must be stabilized during contraction of the intermyoseptal muscles. This requirement could explain the presence of the M. levator costae and the M. tuberculo-costalis which occur in the limbless _Acontias_ and have no counterpart in the quadrupedal _M. capensis_.

Stabilization of the costo-vertebral joint is not only induced by the intermyoseptal muscle slips, but also by the iliocostalis which inserts onto ribs or their myosepta. Its contraction would tend to pull the shaft of a rib backwards. Contraction of the M. tuberculo-costalis and M. levator costae would tend to pull a rib forward.
In limbless skinks the somewhat reduced M. obliquus abdominis externus runs from its insertion on a myoseptum obliquely backwards and downwards (Fig. IV.10A). This fibre direction indicates that on contraction the pull of the muscle can be resolved into two components: one ventrad and the other caudad. The latter can contribute to lateral bending.

In brief, as limbs degenerate, the epaxial muscles, which generate out-forces, hypertrophy and acquire more lateral points of insertion to improve $L_o$; the rib becomes strengthened and more numerous to transmit large $F_i$; and their reduced size diminishes $L_i$.

7. Summary

(a) Limb loss and the concomitant elongation of the trunk adapts skinks for subterranean soil-crawling.

(b) As soil offers much more resistance to progression than air, the cross-sectional area of the body must be reduced. This occurs at the expense of the visceral cavity in the transverse plane; in compensation the visceral space is extended longitudinally, hence the trunk instead of the tail actively elongates; contrasting with the condition in reduced limbed grass-dwellers.

(c) Elongation is achieved by the multiplication of trunk metameres in which the vertebrae are shorter, wider and of almost uniform length; and the ribs become stronger, of shorter radius and uniform.
(d) In a fossorial habitat limbs become less effective as generators and transmitters of propulsive forces.

(e) Appendages will actually impede efficient progression by disrupting the streamlining of the body, by increasing the effective cross-sectional area of the body, and by impeding lateral undulation of the body axis when the limbs are adpressed against it. Consequently, limb loss is adaptive.

(f) The gradual loss of limbs permit a transition from an appendicular mode of locomotion to an exclusively axial one.

(g) Features of the skeleton (coupled with the hypertrophy of the epaxial musculature) that adapt the body axis to act as an efficient undulatory lever system in a fossorial environment are:

(i) more numerous vertebrae as well as the development of synovial intervertebral joints to improve the flexibility of the body axis;

(ii) wider zygapophyses displacing laterally the medial intermuscular septum to accommodate a bulkier transversospinalis system and to increase its leverage as a vertebral flexor;

(iii) stronger and more numerous ribs separated by shorter intercostal spaces strengthen the body wall letting it transmit and withstand propulsive forces (Fig. III.8).
(iv) the shorter radius of the ribs reducing the cross-sectional area of the body, hence the energetic cost of tunnelling. It also reduces the in-force lever arms ($L_i$).

(v) uniformity of the ribs creating a smooth stream-lined trunk.

(h) The hypertrophied epaxial musculature acquire insertions that increase their $L_0$, and their effectiveness as producers of undulatory waves.

(i) Long epaxial muscles overlapping a larger number of segments in reduced limbed skinks promote the smooth passage of travelling waves.
VII. EVOLUTION OF LIMBLESSNESS

1. STATEMENT OF PROBLEM:
Can a plausible theory for the evolution of limblessness in skinks be constructed from the anatomical and behavioural data presented in Chapters II to V? This question has two aspects. The first concerns the reconstruction of a plausible evolutionary pathway linking the limbed and the limbless extremes. What intermediate stages are involved in the acquisition of limblessness? The second concerns the mechanism of evolutionary change. Why did limbless skinks evolve? Of what selective value were the initial changes en route to limblessness?

Before attempting to answer these questions, a more fundamental matter must be considered; the assumptions upon which this analysis is based. There are assumptions concerning the phylogenetic interrelationships of the animals studied and then there are assumptions concerning the meaning or interpretation of the data.

2. ASSUMPTIONS
The animals studied may be arranged on the basis of the degree of limb reduction into the following sequence:

\[ M. \text{capensis} \rightarrow R. \text{sundevallii} \rightarrow S. \text{bipes bipes} \rightarrow S. \text{gronovii} \rightarrow S. \text{brevipes} \rightarrow A. \text{meleagris} \]

This is, however, a morphological series and not a phylogenetic one.
The probable phylogenetic interrelationships among these animals are summarized in Figure VII.1. This cladogram reflects the views of Greer (1970a) who infers from morphological and distributional data that the Scincinae is the most primitive scincid subfamily and that it was independently ancestral to the Lygosominae, Acontinae and the Feylininae. The exact points of divergence are not known. Although our knowledge of the genealogy of these skinks is incomplete, the various species probably represent parallel lines of evolution within a monophyletic group.

The following assumptions are made:

2.1 Members of the regression series have all evolved from a broadly homogeneous scincine ancestral group ($A_1$).

2.2 They are the survivors of parallel lineages ($A_2$).

2.3 The partially or completely limbless species have evolved in response to similar selection pressures that adapt them for soil-crawling ($A_3$).

2.4 The rate of evolution probably differed in the various lineages ($A_4$).

These assumptions are embraced in Maslin's "principle of heterochronic parallelism: "Related forms possess the potentiality for the development of identical clines, and under similar environmental conditions identical clines may develop at different times or in separate geographical areas". (Maslin, 1952, p. 62).

From the assumptions that the partially or completely limbless
FIG. VII. 1  DENDOGRAM TO ILLUSTRATE PROBABLE PHYLOGENETIC RELATIONSHIPS OF SKINKS BELONGING TO THE REGRESSION SERIES. BROKEN LINES INDICATE THAT GENEALOGICAL DETAILS ARE UNCERTAIN.
skinks have evolved in parallel lineages from a common ancestral stock ($A_1$) in response to similar environmental demands or opportunities ($A_2$), one may deduce that the parallel transformations in anatomy and behaviour are likely to follow broadly similar lines. Combine the last deduction with the assumption that the rates of evolution differ ($A_4$) in the parallel lineages and it follows that the parallel lines could have survivors that reflect different stages of evolution in the broad process of limb regression among skinks. In the words of Maslin (1952) "...morpho-clines are partially or entirely identical to the chrono-clines from which they are derived" (p. 52).

When members of the regression series show consistent morpho-clines these are interpreted as a record of the changes involved in the evolution of limblessness among skinks.

3. EVOLUTIONARY PATHWAY

3.1 GENERAL

The aim of this section is to reconstruct a plausible evolutionary pathway for the acquisition of limblessness among skinks. For a hypothetical sequence of evolutionary changes to be plausible, it must satisfy the following conditions:

(a) it must be supported by a consistent morphocline;

(b) it must allow for gradual change;

(c) the innovative steps must be selectively advantageous.
3.2 DIRECTION OF CHANGE

It is generally assumed in the literature that limbless lizards evolved from normal limbed quadrupedal ancestors (Fürbringer, 1869; Cope, 1892; Camp, 1923; Essex, 1927; Sewertzoff, 1931; Stokely, 1947; Waters, 1969; Presch, 1975; Gans, 1975). This assumption is not only strongly supported by ontogenetic evidence (Sewertzoff, 1931; Lande, 1977) but it is also the most parsimonious hypothesis available.

3.3 DEGREE OF CHANGE

Although *M. capensis* and *A. meleagris* belong to the same family, the differences between them may be described as macroevolutionary. Macroevolution refers to phenotypic transformations that are so large, that they occur over periods of time that are long with respect to generation times and consequently they have a multigenic basis (Salthe, 1975). In connection with the time aspect, "millions of years are required for complete loss of external traces of limbs" (Lande, 1977, p. 89).

In connection with the degree of "phenotypic transformations", the great differences in body proportions (Chapter II), in osteology (Chapter III), in myology (Chapter IV) and in locomotor behaviour (Chapter V) have already been documented. Instead of merely summarizing these differences here, let us examine the kinds of changes that have occurred.

3.4 KINDS OF CHANGES

The transformations associated with limb regression may be divided into the following categories:
3.4.1 GRADUAL DEGENERATION OF LIMBS AND GIRDLES

The process of limb loss is a gradual one starting with miniaturization of the limbs followed by a roughly distal-to-proximal sequence of loss of constituent limb bones. The pattern for the girdles appear to be similar. For example, *Scelotes bipes*, *S. gronovii* and *S. brevipes* have a complete, miniaturized pectoral girdle, though there is no trace of anterior limbs in these species.

In the Scincidae there exists an impressive morphocline of partially limbless skinks (Fürbringer, 1869; Cope, 1892b; Camp, 1923; Essex, 1927; Sewertzoff, 1931; Stokely, 1947; Waters, 1969; Lande, 1977 and Chapter II of this study). The completeness of the morphocline suggests that appendicular degeneration occurred gradually. Such gradual reduction of limbs is likely to prolong their functional utility during the transition from appendicular to axial locomotion. Although the progressive atrophy of limbs received repeated attention, the equally impressive transformation of the axial system was largely ignored.

3.4.2 HYPERTROPHY OF THE AXIAL SYSTEM

As appendages atrophy, the body axis hypertrophies in essentially two ways. Firstly, the number of precaudal metameres (i.e. vertebrae, ribs, segmental muscles, etc.) increases (c.f. Fig. III.12). Secondly, the body wall of the trunk occupies a relatively larger percentage and the visceral space a relatively smaller percentage of any cross-section (Fig. IV.2).
The multiplication of metameres appears to be confined to the trunk. In the apodous Acontinae the tail is very short, less than 25% of the total length while in a regression series of species belonging to the genus *Scolotes* reduction in tail length appears to accompany limb reduction (Fig. II.7). In partially or completely limbless skinks, the tail usually becomes almost as stout as the trunk, thus creating a fairly uniform undulatory length to which the caudal region makes a significant contribution (Fig. V.23A).

The increase in the number of trunk metameres is accompanied by a decrease and a uniformization of their cross-sectional area. This elongation of the precaudal region enhances its flexibility, improves its streamlining and permits the longitudinal spread of the viscera (as discussed more fully in Chapter VI.5).

The body wall is strengthened as limbs regress (Fig. V.2). A large number of small, strong ribs support the body wall of partially or completely limbless skinks. In addition, there is differential development of the axial musculature. The epaxial musculature which is responsible for lateral bending (Fig. VI.3) hypertrophies while the hypaxial musculature is generally reduced (Fig. IV.3). The epaxial musculature spread further laterad along the circumference of the body thus enhancing their orientation for causing lateral bending (as already discussed more fully in Chapter VI.). In addition they also span more segments which are of relatively small and uniform length (Fig. III.17), thus creating the anatomical conditions for the smooth passage of travelling waves.
Although there are striking differences in the axial systems of the limbed and limbless extremes, these differences appear to involve two processes: (a) multiplication of trunk metameres; and (b) differential growth. The first process accounts for the remarkable lengthening of the trunk and the second process for the changes in portion of the different subunits of the system (as discussed in Chapter VI).

The genetic bases of these transformations are unknown. Moreover, a large number of genes are probably involved, rendering detailed analysis beyond the capacity of even modern computer techniques (Salthe, 1975). The ontogenetic mechanisms, on the other hand, appear to be relatively straightforward and to involve well-documented processes such as polymetamerism (Gregory, 1951; De Beer, 1958) and differential growth (Thompson, 1917; Huxley, 1932).

Are there no "evolutionary novelties" involved in the transition to limblessness? Mayr (1960, p. 351) defines this concept as follows: "Tentatively, one might restrict the designation 'evolutionary novelty' to any newly acquired structure or property which permits the assumption of a new function."

The body axis of limbless skinks becomes exclusively responsible for locomotion. The axial system shows differential hypertrophy to cope with its new function by increasing the size of its epaxial musculature and by decreasing the relative cross-sectional area of constituent metameres; but structurally there seems to be nothing unequivocally new. Bony projections such as the pseudotubercula found on the ribs of
Acontias, or muscles such as the M. tuberculocostalis and the M. levator costae could possibly be categorized as evolutionary novelties. But, on the whole, the major differences between limbed and partially or completely limbless skinks emanate from changes in relative proportions of body parts, the multiplication of trunk metameres and the co-ordinate response of other body parts to such changes. The acquisition of limblessness conforms to the dictum, "nature is prodigal in variety, though niggard in innovation".

On the morphological level, the gradual regression of limbs is accompanied by the hypertrophy of the body axis; on the behavioural level, there is a correlated shift from predominantly appendicular locomotion to exclusively axial progression.

3.4.3 BEHAVIOURAL CHANGE

The following ethocline is proposed for the regression series:

(a) A primitive phase, typified by M. capensis, in which the animal relies mainly on its limbs for propulsive thrust but weak lateral flexures of its axial system contribute to stride length.

(b) A "tetrapodous reduced phase" as exemplified by Riopa sundevallii follows. The animal depends on both axial undulation and the action of its miniaturized limbs for progression above the soil. For sandswimming body undulations suffice.

(c) The bipodous species of Scelotes progress by lateral un-
dulation though their vestigial hind limbs perform per-
functory strutting movements. The stout tails of these
animals may form up to almost half of their undulatory
length.

(d) The limbless *A. meleagris* relies exclusively on axial
locomotion and it is capable of progression by lateral
undulation and concertina movements. Its stout tail ma-
kes only a minor contribution to its undulatory length.

In conclusion, a smooth transition from appendicular to axial
locomotion is possible, because even in the primitive quadru-
pedal condition there appears to be a weak axial component
with the potential to become accentuated and intensified as
limbs gradually regress. The gradual degeneration of limbs
are then accompanied by a gradual hypertrophy of the body axis
which becomes increasingly responsible for progression by la-
teral undulation.
4. SEQUENCE OF CHANGE

The main transformations involved in the acquisition of limblessness among skinks appear to be (a) the gradual reduction of limbs; (b) the increase in the number of trunk metameres; (c) the reduction of cross-sectional area; (d) reduction in caudal length; (e) the hypertrophy of the epaxial musculature; (f) changes in the relative magnitudes of ribs and vertebrae and (g) on the behavioural level, a gradual shift from appendicular to axial locomotion. Can a specific sequence of changes be inferred from the data recorded in Chapters II to V?

The behavioural shift is straightforward in broad perspective; the sequence of morphological changes underlying this ethocline is less clear. Two impressions dominate the picture. The one is the co-ordinated nature of the changes; and the other, the varying rates of change in different parts of the body. For example, one can with justification generalize that as limbs are reduced the number of trunk metameres increase (Fig. III.12). But this reciprocal relationship between appendicular atrophy and trunk hypertrophy is not a strict one even for the presumably closely related species of the genus Scelotes. Thus, an externally limbless species such as S. anguina has fewer presacral vertebrae (around 47) than the bipodous S. bipes, S. gronovii and S. brevipes (which have between 51 and 55 presacral vertebrae; Table III.2).

Similar discrepancies are evident in the structure of the pectoral girdle. The pelvic limbs of S. brevipes are more redu-
ced than those of either *S. bipes* or *S. gronovii* (Fig. III.2E); yet the pectoral girdle is less degenerate in the former (cf. Figs. III.23 to 25). These examples indicate that even in presumably closely related species, the rate of change in different parts of the body may be out of step. Hence the quest for a detailed sequence of changes is likely to be at best highly speculative.

Although the correlation between changes in different parts of the body is less than one, the morphoclines recorded give the impression of a series of co-ordinated, adaptive transformations in response to some form of underground existence (Camp, 1923; Greer, 1970a; Tiedemann and Tiedemann, 1975).

Soil is likely to impose a negative selective influence on both limb size and cross-sectional area. Limbs not only become useless for propulsion in a subterranean habitat, but in addition, they are likely to disrupt the streamlining of the body (Chapter VI.4). Furthermore, the energetic cost of soil-crawling can be greatly reduced by decreasing the cross-sectional area of the animal (Gans, 1975). Which is likely to have occurred first, the miniaturization of limbs or the reduction of cross-sectional area?

Although the diminution of limbs is also likely to reduce cross-sectional area, it is more likely that the reduction of body diameter preceded drastic limb reduction. The reasons for this conclusion are as follows. If the animal was to become more slender, the energetic cost of soil-crawling would not only be reduced but the body axis would be rendered more
flexible, hence enhancing its potential for axial progression. Consequently, the reduction of cross-sectional area is of immediate selective value in two ways: it reduces the energetic cost of soil-crawling and creates a slender trunk with enhanced potential for lateral bending.

But if the animal is to increase its capacity for lateral bending, its body wall must hypertrophy and consequently reduction of cross-sectional area must be at the expense of the visceral space (Fig. IV.2). To compensate for loss of space in a transverse plane the trunk must lengthen (Fig. II.5). If lengthening is achieved by the multiplication of trunk metameres (Fig. III.12), then flexibility is further enhanced as the trunk is composed of a longer chain containing a greater number of vertebral levers. While the trunk is elongating the tail may make a significant contribution to the undulatory length (Fig. V.23A).

Figure II.7 suggests that as limbs degenerate in species for each of five genera, the tail is reduced. Furthermore, the highly specialized limbless Feylininae and Acontinae have short tails (less than 35% and 25% of the total length respectively). This condition contrasts sharply with that of partially or completely limbless anguids (Gasc, 1973), gerrhosaurids and cordylids (FitzSimons, 1943) in which the tail appears to elongate. An explanation for these differences is given in Chapter VI.5. Here it is emphasized that the tail makes a significant contribution to lateral undulation in intermediate species. On the other hand, extreme reduction in
cross-sectional area accompanied by hypertrophy of the body wall is likely to impose pressures for the further lengthening of the trunk. A much elongated trunk would not only accommodate the staggered viscera (Fig. VI.1) but also reach an adequate undulatory length rendering a long tail superfluous.

5. EVOLUTIONARY MECHANISM:

5.1 GENERAL

After having summarized the co-ordinated morphological and behavioural changes associated with limb regression, the question of the underlying evolutionary mechanisms may be explored.

Evolution is a dual process involving, in the first place, the production of genetic variability (through mutation, recombination and chance events); and, in the second place, ordering of such variability by natural selection (Mayr, 1978). Of these two steps the first is beyond the scope of this study; the second is considered in some detail. Although the mechanisms underlying the morphological changes associated with limb regression involve the multiplication of trunk metameres, as well as negative and positive allometric growth, nothing is known about the genetic basis of these changes (See Lande, 1977).

Limb regression among skinks appears to adapt these animals for some form of underground existence (chapter VI). Furthermore, partial or complete loss of limbs has occurred indepen-
dently in different scincid lineages (Camp, 1923; Greer, 1970 a). These two generalizations raise the question, why have skinks become subterrestrial so frequently? The answers to this question will be discussed with reference to:

5.2 Ecological opportunities offered by a subterranean habitat.

5.3 Protoadaptation.

5.2 ECOLOGICAL OPPORTUNITIES

Reptiles are primarily adapted to life above ground, consequently invasion of a subterranean habitat poses special problems for these animals; for their locomotor apparatus (Gans, 1968; 1975); for their cranial morphology (de Villiers, 1939; Brock, 1941; Leonard, 1978); for their olfactory organs (Stebbins, 1943; Pratt, 1948; Parsons, 1970); for their eyes (Walls, 1942; Underwood, 1970); for their auditory organs (Toerien, 1963; Baird, 1970; Wever and Gans, 1972) for their respiratory mechanism (Pough, 1969; Pough, 1971) and for the arrangement of their viscera (Bellairs, 1969; Gans 1975).

Despite these restrictions imposed by a subterranean habitat, the latter has been invaded repeatedly by diverse lines of tetrapods, suggesting that the subterranean niche offers special ecological opportunities for those tetrapods that can adjust to its restrictions. The benefits of an underground existence have been discussed by Gans, 1968, and 1974 and may be summarized as follows:
(a) Underground microhabitats are often more stable than terrestrial ones. For example, the microclimate of a tunnel is buffered by the surrounding soil (Gans, 1974 p. 117). The humidity in tunnels are often higher than at the surface. Withers (in press) states that Scelesotes and Acontias are probably unable to thermoregulate in the field, their preferred body temperature is lower than that of Mabuya and they are more susceptible to dehydration death.

(b) A variety of small insects, insect larvae and worms inhabit the upper layers of the soil. Animals adapted to soil-crawling would have access to these food resources (Wallwork, 1970).

(c) As soil is opaque it provides a good hiding place from many larger predators (Gans, 1974). Even normal limbed skinks tend to hide in soil or leaf-litter when disturbed, while away from their normal sheltering spots (Brookes, 1967).

(d) Tetrapods constitute a very small fraction of soil fauna (Wallwork, 1970), hence subterranean habitats are relatively empty as far as this group is concerned. Where a niche exists vacant, some species is likely to fill it, even if considerable structural modifications are involved in the process (Allee et al., 1949 p. 663)
In brief, a subterranean habitat offers many ecological opportunities to tetrapods that can cope with its special demands. Several lines of skinks have coped (Camp, 1923; Greer, 1970a). They have even undergone drastic reduction or loss of limbs to adapt them for soil-crawling (chapter VI). The presence of appropriate protoadaptations permit such drastic transformations.

5.3 PROTOADAPTATIONS

The term "protoadaptation" (Gans, 1974) is preferred to the older term, "preadaptation" because the latter has numerous shades of meaning (de Beer, 1972) which are inappropriate in this context. By "protoadaptation" is meant that an organism is by its peculiarities predisposed to take advantage of a certain type of environment (cf. Huxley, 1942, p. 450). This concept implies that a new adjustment develops out of pre-existing features. The concept embraces not only morphology but also function. The definition of preadaptation of Bock and von Wahlert (1965, p. 201) may be paraphrased as follows: A structure is said to be protoadaptive for a new function if its present form which enables it to discharge its original function also enables it to assume a new function whenever the need for that function arises. In other words, protoadaptation permit smooth transitions by providing an overlap between "old" and "new" functions.

A quadrupedal skink (such as *M. capensis*) has a dual system of locomotion. Although mainly its limbs are responsible for propulsion, lateral flexures of the body axis assist the
limbs by increasing stride length (Chapter V. 3.4). Such lateral curvatures, though initially weak and in support of the appendicular system, are protoadaptive, because they have the potential, after accentuation and intensification, of being transformed into travelling waves required for progression by lateral undulation. Starting from a condition in which both systems are present, a gradual intensification of axial undulations accompanied by a gradual reduction of limbs could ensure a smooth (or at least a non-disruptive) shift from appendicular to axial locomotion. The difficulty of explaining the selective value of a feature before it becomes fully functional is thus eliminated (Davis, 1949; Mayr, 1960); for initially lateral bending of the trunk was probably enhanced by natural selection to increase stride length (i.e. in the service of appendicular progression).

However, the presence of an axial component in support of the dominant appendicular system provides the necessary functional overlap that creates the potential for the former to wax while the latter wanes.

Such protoadaptation establishes the potential for change, but what caused the actual shift? The answer appears to be the invasion of a subterranean adaptive zone. Sheltering in leaf-litter or in the upper layers of soil is important in the lives of many quadrupedal skinks (Brookes, 1967; FitzSimons, 1943). They use the upper layers of the soil for hiding
(Brookes, 1967; Rose, 1950), for hibernating and possibly for behavioural thermoregulation (see Withers - in the press). In other words, the upper layers of the soil often form a marginal habitat even for quadrupedal skinks, and consequently, they are exposed, for at least a fraction of the lives, to some of its selective demands.

The shift to an underground habitat may have been caused by either or both of the following factors in combination. Firstly, in a variable population, those variants slightly better adapted to conditions below the soil (e.g. slightly elongated) may have remained underground to exploit the subterranean habitat. Secondly, in the face of changes above ground (e.g. in temperature or humidity), the more stable underground habitats may have provided a retreat to conditions nearer to the optimum. Consequently, selection would favour those variants slightly better adapted for coping with the demands imposed by an underground environment. The entry into an underground adaptive zone due to these or other causes, would subject the "pioneer invaders" to intense selection pressure to adjust to the demands of the subsoil environment (See Chapter VI). Consequently the stage would be set for hyperadaptation (Nicholson, 1960 p. 507) or postadaptation (Bock and von Wahlert, 1965).

Hyperadaptation refers to the improvement of an adaptation beyond the minimum level necessary for the maintenance of a species in a particular environment (Nicholson, 1960 p. 507). It is the process by which the initial protoadaptations are
improved and the animal finds "better and better solutions" (Lewontin, 1978), in this case, to the "problems" of soil-crawling.
VIII. SUMMARY AND CONCLUSIONS

1.0 GENERAL

Correlated trends in the morphology, behaviour and habitat of those skinks belonging to the regression series permit the following general conclusions:

1.1 As the limbs and girdles gradually atrophy, the body axis hypertrophies. (Chapters II to IV).

1.2 As appendicular locomotion declines in importance, there is a reciprocal shift to axial progression. (Chapter V).

1.3 Limb regression, which in skinks is correlated with a switch from a mainly terrestrial to a largely sub-terrestrial habitat, is probably an adaptive response to soil-crawling (Chapter VI).

The evidence, which substantiates these conclusions, is summarized below.

1.1.1 ATROPHY OF LIMBS AND GIRDLES

1.1.1.1 The wide spectrum of limb reduction displayed by living skinks implies that limb regression is a gradual process that starts with the miniaturization of the appendages, followed by a distal-to-proximal loss of appendicular elements. Such gradual degeneration is likely to prolong the functional utility of the appendicular system, as the axial system progressively assumes responsibility for locomotion.
1.1.1.2 The pectoral and pelvic girdles, like the limbs, undergo miniaturization before any loss of elements occurs (Figs. III: 21-27; Figs. III: 6 C & D).

1.1.1.3 Much variation and even asymmetry characterize the degenerating girdles (cf. Figs. III: 21-26).

1.1.1.4 Furthermore, even in the genus Scelotes, the degree of girdle degeneration is not in exact step with the degree of limb reduction. For example, S. brevipes have smaller limb vestiges than either S. bipes or S. gronovii, yet its pectoral girdle is less degenerate. This observation points to the danger of employing a single feature for arranging these skinks in a series from "primitive" to "advanced."

1.1.1.5 Devolution of the appendicular system is accompanied by anagenesis of the axial system.

1.1.2 HYPERTROPHY OF THE BODY AXIS

1.1.2.1 The trunk elongates as limbs regress. There is a reduction in the cross-sectional area and a relative lengthening of the snout to vent length (Chapter II.2).

1.1.2.2 Trunk elongation is accomplished by an increase in the number of precaudal metameres. (Chapter II.2.8)

1.1.2.3 The reciprocal relationship between the number of trunk vertebrae (as an index of the number of metameres) and the degree of limb reduction is not absolute even for presumably closely related species.
belonging to the genus *Scelotes*. (Fig. III.12).

1.1.2.4 Furthermore, reduced limbed skinks appear to show greater intrageneric and intraspecific variation in vertebral counts than their normal limbed counterparts. (Fig. III.12).

1.1.2.5 As limbs regress trunk *vertebrae* undergo the following changes in proportion:

(a) they occupy a smaller percentage of the snout to vent length (Fig. III.17);

(b) their length becomes more uniform along the column (Fig. III.17);

(c) they become wider relative to body diameter (Fig. III.18);

(d) the mid-trunk vertebrae become shorter and wider (Fig. III.20).

1.1.2.6 The trunk intercentral joints lack synovial cavities in *M. capensis*; such cavities are present in *A. meleagris* and *S. gronovii*.

1.1.2.7 These changes in vertebral proportions and intercentral joints enhance the flexibility of the body axis and increase the areas of attachment as well as the lever-arms of the epaxial musculature (Chapter VI. 6.2).

1.1.2.8 In partially or completely limbless skinks, the ribs are more numerous, more uniform and stronger, but of smaller radius than those of their quadrupedal
counterparts (Figs. III.8 A-D). The great number of ribs separated by shorter intercostal spaces (cf. Fig. III.17) strengthens the body wall which transmits propulsive thrust to the substrate during axial progression (Chapter VI.6).

1.1.2.9 As limbs regress the parasternalia become more numerous (Figs. III. 21-26). The parasternalia co-extend with the elongated lungs (Fig. VI. 1). The increase in the number of parasternalia is probably related to the greater importance of the ventral body wall in the respiration of subterrestrial skinks (See Pough, 1969 & 1971).

1.1.2.10 The reduction of the cross-sectional area of the trunk relative to its length (Fig. II.5), occurs, in partially or completely limbless members of the regression series, at the expense of the visceral space while the body wall actually hypertrophies (Fig. IV.2) to cope with its increased role in progression (Chapter VI.6.2).

1.1.2.11 During appendicular devolution the axial muscles show the following trends:

(a) the cross-sectional area of the epaxial musculature increases relative to that of the hypaxial musculature (Fig. IV.2).

(b) the transversospinalis and longissimus systems spread nearer to the sides of the trunk (Fig. IV.6)
(c) the epaxial musculature spreads along the dorsolateral circumference of the trunk, thus restricting the hypaxial muscles to the ventrolateral aspects of the trunk (Fig. IV.7).

(d) the cross-sectional area (Fig. IV.5) and the circumferential spread (Fig. IV.7) of the rectus musculature decline as limbs regress, suggesting that Camp (1923) over-estimated the pro-toadaptive value of these muscles in limb regression.

(e) the epaxial muscles tend to span a larger number of segments in reduced limbed skinks (Chapter IV.5.2.3; 5.3.4 and 5.4.4).

1.1.2.12 The importance of the epaxial muscles for axial progression is strongly suggested by its hypertrophy during limb regression (Fig. IV.2 and IV.7) and is confirmed for A. plumbeus by electromyography (Fig. 6.3).

1.1.2.13 Although, there is a tendency for epaxial musculature to hypertrophy in the regression series; the degree of development of the three main subdivisions of the epaxial musculature vary in the different genera (Fig. IV.4).

1.1.2.14 To summarize the reduction of the appendicular system concurs with the hypertrophy of the axial system. Anagenetic changes include the multiplication of trunk metameres; the increase in the development
of the epaxial musculature at the expense of the hypaxial musculature.

1.2 ETHOCLINE

1.2.1 In the quadrupedal *M. capensis* the limbs are the most important propulsive organs. However, a weak axial component serves to increase stride length (Chapter V.3.4).

1.2.2 In *R. sundevallii* the axial component is more prominent than in *M. capensis* (cf. Figs. V.16-20) while the miniaturized limbs are less important. Both axial and appendicular components are used for progression above the soil (Fig. V.18).

1.2.3 The bipodous species of *Scelotes* (*bipes, gronovii* and *brevipes*) progress by lateral undulation above and below the soil. Above the soil the vestigial hind limbs may strut perfunctorily. (Chapter V.5).

1.2.4 The limbless *Acontias* relies exclusively on axial progression; either lateral undulation or concertina movement or a combination of both (Chapter V.2).

1.2.5 In brief, the approximately reciprocal relationship between appendicular atrophy and axial hypertrophy is correlated on the behavioural level with a shift from appendicular to axial locomotion. These transformations are associated with entry, into a subterranean adaptive zone.
1.3 ECOLOGICAL SHIFT

1.3.1 The partially or completely limbless members of the regression series have adopted some form of underground existence. A subterranean habitat seems to characterize reduced limbed and limbless skinks (Camp, 1923; Essex, 1927; Stokely, 1947; Rose, 1950; Tiedemann and Tiedemann, 1975).

1.3.2 When theorizing about the evolution of limblessness among skinks, the correlated morphological, ethological and ecological transformations, seen in the regression series, must be explained.

2.0 EVOLUTION OF LIMBLESSNESS

The following hypotheses are proposed in partial explanation of the evolution of limblessness:

2.1 Limb regression and the reciprocal hypertrophy of the axial system adapt skinks for soil-crawling (Chapter VI).

2.1.1 A primary problem presented by soil to an animal crawling through it, is the high resistance it offers to tunnelling.

2.1.2 Consequently, a stream-lined body profile with a small cross-sectional area is demanded to minimize the high energetic cost of soil deformation and compaction.

2.1.3 If an alternative locomotory system were available, the reduction or elimination of the sprawling limbs would contribute to the reduction of the cross-sectional area.
2.1.4 Axial locomotion requires a body axis that is highly flexible. Flexibility is enhanced by an elongated, slender body.

2.1.5 As at least some of the key requirements for axial locomotion coincide with the demands of soil crawling (e.g. both require a slender, elongated body), the shift to axial progression is interpreted as an adaptive "solution" to the "problem" of high resistance offered by soil to progression.

2.1.6 However, such an adaptive shift is only possible in the presence of suitable protoadaptations, adequate variability and appropriate selection pressures.

2.2 Primitive quadrupedal skinks were protoadapted for limb reduction because they possessed a dual system of locomotion.

2.2.1 Axial and appendicular functions overlap even in modern quadrupedal skinks such as *M. capensis* in which weak flexures of the vertebral column aid the dominant appendicular system by increasing stride length (Chapter V. 3.4).

2.2.2 Starting with such an overlap, a phasing out of the appendicular system accompanied by a phasing in of the axial system (as suggested by the ethocline) would permit a viable transition from limbed to limbless locomotion.
2.2.3 Although such an overlap together with the usual variability that characterize populations create the potential for change, natural selection provides the impetus for such transformation.

2.3 The impetus for the initial shift from appendicular to axial locomotion is provided by entry into an underground adaptive zone.

2.3.1 Selection pressure may have been directed at improving the capacity of protoadapted skinks to exploit the ecological opportunities of an underground existence (See Chapter VII.4.2).

2.3.2 On the other hand, skinks may have been "driven" underground by unfavourable conditions (e.g. temperature or humidity) above ground, while these conditions remained more stable and nearer the optimum underground.

2.3.3 Even a combination of these and other factors may have been responsible for entry into an underground habitat.

2.4 Elongation of the trunk probably constitutes one of the initial morphological changes.

2.4.1 Elongation of the body axis characterizes all partially or completely limbless tetrapods (Gans, 1975).

2.4.2 Elongation increases the functional potential of the axial system thus permitting the phasing out of appendages.
2.4.3 Elongation permits a reduction in the cross-sectional area of the trunk with the consequent reduction in the energetic cost of tunnelling.

2.4.4 Although only slight elongation may initially have pushed the animal in the direction of axial locomotion, hyperadaptive elongation probably concurred with further drastic limb reduction. This interpretation is supported by the large spectrum of vertebral counts and stages in limb reduction (Fig. III. 12 & Fig. II.2).

2.5 The rates of reduction or hypertrophy of the various subdivisions of the locomotor apparatus (such as limbs, girdles, the vertebral column, parasternalia, etc.) are not in exact consonance even for presumably closely related species belonging to the genus Scelotes.

2.5.1 For example, *S. brevipes* has smaller vestiges of limbs than either *S. bipes* or *S. gronovii* but its pectoral girdle is more conservative (cf. Figs. III.24-26).

2.5.2 Although broad trends are associated with limb regression, detailed changes occur at different rates; and the degenerating or hypertrophying structures show much more variation than their homologues in quadrupedal skinks.

2.6 The change to soil crawling involves adaptive compromises.

2.6.1 For example, soil-crawling requires a small cross-sectional area; axial progression demands a strong axial system (body wall).
2.6.2 Therefore, reduction of the cross-sectional area can only occur at the expense of the visceral space; while the body wall actually hypertrophies (Fig. IV.2).

2.6.3 Consequently, the trunk must elongate to provide a longer tube for the viscera.

2.6.4 Hence elongation among skinks appear to be confined to the trunk.

2.6.5 Although the bipodous *Scelotes* have tails as long as or slightly longer than their precaudal length, there is no evidence of multiplication of caudal vertebrae.

2.6.6 The specialized Acontinae and Feylininae on the other hand, have short tails (less than 25% and 35% of the body length, respectively).

2.6.7 Thus soil crawling skinks appear to contrast sharply with reduced limbed grass-tuft-dwellers in which there are significant caudal elongation.

2.6.8 A tentative explanation for this difference is discussed in Chapter VI.5.

2.7 Although the genetic mechanisms underlying the transition from quadrupedalism to limblessness among skinks are unknown, the ontogenetic bases of these changes are:

(a) multiplication of trunk metameres; and

(b) positive and negative allometric growth.
2.8 In brief, the primitive functional overlap of axial and appendicular systems creates the potential for change; the entry into an underground adaptive zone provides the impetus for such change. The relatively high density of soil places a premium on reducing the effective cross-sectional area of the animal. But an elongated, streamlined body axis is required for effective undulatory progression as well. Consequently, the switch to axial progression and the correlated partial or complete loss of limbs, in this scincid regression series, are interpreted as adaptations to soil-crawling.
REFERENCES


APPENDIX I.A: LIST OF ALIZARINE STAINED SPECIMENS:

- *M. capensis* .......... 12 specimens
- *R. sundevallii* .......... 2 specimens
- *Scelotes b. bipes* ...... 3 specimens
- *Scelotes b. sexlineatus* . 1 specimen
- *Scelotes grońovi* ..... 3 specimens
- *Scelotes brevipes* ...... 6 specimens
- *Scelotes arenicola* .... 1 specimen
- *Acontias meleagris* .... 9 specimens
APPENDIX IV.A

Photographs of serial sections (each number under the heading Section Number represents one serial section) were cut into the portions listed below. For each such portion three plamimeter readings in cm² are given (with the exception of TOT and BW). For illustrations of the portions listed below see Figs. IV. 1A-C:

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CALCULATIONS FOR M. CAPENSIS:

\[
\frac{VS}{TOT} = 50.4\% \\
\frac{EP}{BW} = 18.9\% \\
\frac{TRS}{EP} = 30.6\% \\
\frac{REC}{BW} = 4.8\% \\
\frac{BW}{TOT} = 49.7\% \\
\frac{HP}{BW} = 74.6\% \\
\frac{LNG}{EP} = 30.1\% \\
\frac{VER}{BW} = 6.5\% \\
\frac{ILC}{EP} = 39.8\% \\
\]

APPENDIX IV.A: MABUYA CAPENSIS.
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**Calculations for R. Sundevallii:**

\[
\frac{\text{VS}}{\text{TOT}} = 42.5\% \\
\frac{\text{EP}}{\text{BW}} = 21.4\% \\
\frac{\text{TRS}}{\text{EP}} = 24.9\% \\
\frac{\text{REC}}{\text{BW}} = 3.8\% \\
\frac{\text{BW}}{\text{TOT}} = 57.5\% \\
\frac{\text{HP}}{\text{BW}} = 70.1\% \\
\frac{\text{LNG}}{\text{EP}} = 37.8\% \\
\frac{\text{VER}}{\text{BW}} = 8.5\% \\
\frac{\text{ILC}}{\text{EP}} = 38.8\% \\
\]

**Appendix IV.A: RIOPA SUNDEVELLLII**
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**CALCULATIONS FOR S. B. SEXLINEATUS:**

\[ \frac{VS}{TOT} = 40.5\% \]
\[ \frac{EP}{BW} = 31.1\% \]
\[ \frac{TRS}{EP} = 25.8\% \]
\[ \frac{REC}{BW} = 1.7\% \]

\[ \frac{BW}{TOT} = 59.4\% \]
\[ \frac{HP}{BW} = 62.7\% \]
\[ \frac{LNG}{EP} = 44.3\% \]

\[ \frac{VER}{BW} = 6.3\% \]
\[ \frac{ILC}{EP} = 30.2\% \]

**APPENDIX IV.A : SCLOOTES BIPES SEXLINEATUS**
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APPENDIX IV.A: ACONTIAS MELEAGRIS.
Calculations for *A. Meleagris*:

\[
\frac{VS}{TOT} = 34.4\% \\
\frac{EP}{BW} = 33.6\% \\
\frac{TRS}{EP} = 33.7\% \\
\frac{REC}{BW} = 1.5\%
\]

\[
\frac{BW}{TOT} = 65.6\% \\
\frac{HP}{BW} = 50.8\% \\
\frac{LNG}{EP} = 37.4\% \\
\frac{VER}{BW} = 15.6\% \\
\frac{ILC}{EP} = 29.2\%
\]

Appendix VI.A: *Acontias Meleagris*. 
APPENDIX IV.B

The LATERAL SPREAD of the TRANSVERSOSPINALIS SYSTEM (TRS) and the LONGISSIMUS SYSTEM (LNG) relative to the maximum DIAMETER (DIAM) of serial sections. The measurements are defined in Figure IV.1C. An ocular micrometer scale was used for the measurements.
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