
by

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PREFACE

The research described in this thesis was carried out during candidature for the Degree of Doctor of Philosophy at the University of Sydney and is my own work except where appropriate acknowledgement is given. Parts I, II and IV are entirely new but certain sections of Part III, particularly those relating to the Gekkonidae, are an expansion and complete reassessment of work previously published (Holder, 1960) and have involved not only a re-examination of the material used in the early paper but also the incorporation of new additional material from North America.

During leave of absence from candidature I was engaged in postgraduate research and lecturing at the University of London, England, where I published papers and notes in collaboration with Professor A. d'A. Bellairs, St. Mary's Hospital Medical School (Holder & Bellairs, 1962, 1963a, b; Moffat & Bellairs, 1964).
# CONTENTS

## SUMMARY

PART I ... GENERAL INTRODUCTION .......................................................... 1

PART II .. VERTEBRAL COLUMN OF LEIOPELMAN

1. INTRODUCTION ....................................................................................... 11

2. MATERIAL & METHODS ....................................................................... 28

3. VERTEBRAL DEVELOPMENT .................................................................. 30

4. ADULT VERTEBRAL COLUMN .. Leiopelma archeyi 47

.. L. hochstetteri 50

5. DISCUSSION ......................................................................................... 53

PART III .. VERTEBRAL COLUMN OF THE GEKKOTA

1. INTRODUCTION .. GENERAL .................................................................. 78

.. HISTORY OF CLASSIFICATION OF THE GEKKOTA 81

.. CLARIFICATION OF NOMENCLATURE ................................................. 90

2. MATERIAL & METHODS ....................................................................... 96

3. VERTEBRAL NUMBERS ....................................................................... 101

4. VERTEBRAL MORPHOLOGY .. GENERAL ........................................... 108

5. INTERNAL MORPHOLOGY OF THE VERTEBRAL COLUMN .............. 112

6. REGIONAL MORPHOLOGY

.. ATLAS ................................................................................................. 124

.. AXIS ................................................................................................. 135

.. POSTAXIAL PRESACRAL VERTEBRAE .................................................. 141

. .. Geckos and Xantusia

. .. Third, Fourth, Fifth & Sixth Cervical Vertebrae 141

. .. Dorsal or Trunk Vertebrae ............................................................. 146

. .. Lumbar Vertebrae ........................................................................... 152

. .. Pygopods ....................................................................................... 153

. .. SACRUM ......................................................................................... 160

. .. POSTSACRAL OR CAUDAL VERTEBRAE ........................................ 173

. .. SUBCENTRAL FORAMINA ............................................................... 194

(ii)
7. DISCUSSION.. AMPHICOELY AND PROCOELY IN THE
GEKKOTA

.. MECHANICS OF INTERCENTRAL
JOINTS

PART IV .. PHYLOGENETIC SIGNIFICANCE OF VERTEBRAL
CHARACTERISTICS IN AMPHIBIANS AND REPTILES

ACKNOWLEDGEMENTS

REFERENCES

PLATES following p. 301

APPENDIX .. THE CONCEPT OF PRIMITIVENESS
AND ITS BEARING ON THE PHYLOGENETIC CLASSIFICATION OF THE
GEKKOTA.

(iii)
SUMMARY

The development and adult internal morphology of the vertebral column of the rare endemic New Zealand frog, *Leiopelma*, are described and it is concluded that the persistent notochord and absence of synovial intercentral joints found only in this genus and in the North American genus *Ascaphus* are ancestral conditions retained in living forms. The so-called transverse processes in *Leiopelma* are all pleurapophyses because they consist in part of rib elements which are detectable during early development if not in adults. The urostyle of *L. archeyi* develops from a subchordal rod of cartilage or hypochord formed from the perichordal tube of the first five postsacral vertebrae together with the first four pairs of postsacral neurapophyses. The vertebral morphology of *Leiopelma* and *Ascaphus* does not suggest that these genera are closely related.

The external and internal morphology of the vertebral column are described in juvenile and adult members of the Gekkota whose two recognised families, the Gekkonidae and Pygopodidae, occur together only in Australasia. It is concluded that the notochordal state of the centra, the absence of synovial intercentral joints and the presence of trunk intercentra in amphicoelous and procoelous gekkotans and the amphicoelous state of the centra in most geckos are persistent ancestral conditions. The phylogenetic significance of various other vertebral characteristics in squamate reptiles is also discussed. The mechanics of various types of intercentral joints in the Squamata are considered on the basis of their morphological characteristics.
Consideration is given to the homologies of various characteristics of the axial skeleton of amphibians and reptiles. Cervical and trunk intercentra and caudal chevron bones in the Gekkota are considered to be serially homologous despite differences in their modes of development and adult form. The single rib head of geckos is claimed to be syncephalous. The single centrum of living amphibians and most reptiles has different types of homology, while similar states of the osseous centra may be associated with different states of their unossified components. Homologous character-states may also be primitive or advanced.

In the Appendix, the different aspects of primitiveness and their bearing on the determination of phylogenetic relationships are discussed and a recent classification of the Gekkonidae (Kluge, 1967a) is reviewed. Phylogenetic relationships within the Gekkota are deduced from the occurrence in the Pygopodidae and the three subfamilies of geckos of the primitive states of seventeen morphological characters. The account of gekkonid inter-relationships given here differs from that proposed by Kluge. Consideration is also given to recent claims that the Xantusiidae should be transferred from the Scincomorpha to the Gekkota and it is concluded that there are no grounds at present for doing so.
In the ontogeny of vertebrates the original component of the axial skeleton is the notochord. In fishes this structure may be retained in adults as the main element of support as in the living crossopterygian, *Latimeria* (Millot & Anthony, 1958) and in dipnoans and chondrosteans (Romer, 1962) or it may be replaced to varying degrees by cartilaginous or bony vertebral elements as in other fishes. The main function of the axial skeleton in fish is to serve as an incompressible elastic rod counteracting the rhythmic contractions of the segmentally arranged trunk muscles used in swimming (Gasc, 1967b; Schmalhausen, 1968).

In terrestrial vertebrates the axial skeleton consists of bony vertebrae whose rigid centra partly or completely replace the notochord. The axial skeleton in these animals is required to support the weight of a body no longer buoyed up by water but is sufficiently flexible in most lower tetrapods to allow the extreme lateral bending required by the gait of sprawling animals (Szarski, 1962). In birds and mammals, the notochord is completely replaced during embryonic stages by the bony centra (Romanoff, 1960, Fig. 350; Dawes, 1930; Sensenig, 1949) which have essentially the same structure within each of these classes irrespective of differences in body form and mode of progression. In birds the articular surfaces of the centra are usually heterocoelous (saddle-shaped) and the axial skeleton of the trunk is strengthened in response to the mechanical requirements of flight and its flexibility is greatly reduced by vertebral fusion.
(Bellairs & Jenkin, 1960). Mammalian centra are acoelous (= amphiplatyan) and are joined together by tough, fibrocartilago

ginous intervertebral discs whose nucleus pulposus is the only

remnant of the notochord. Complex intervertebral muscles and

ligaments as well as the articulating processes of adjacent verte-

brae strengthen the mammalian column (Slijper, 1946) and its

flexibility in most cases has changed from the horizontal to the

vertical plane (Daan & Belterman, 1968).

In amphibians and reptiles the notochord may persist with-

out interruption in adults so that the centra are of the noto-

chordal amphicoelous type or it may be replaced during develop-

ment so that the adult centra are acoelous, procoelous or

opisthocoelous depending on their shape (Fig. 1:1). Variation

in the structure of the centrum among amphibians and reptiles

often appears to be independent of differences in body form and

mode of progression. Thus differently shaped centra occur in

closely related animals whose bodies are highly specialised for

the same type of locomotion, viz. the Anura which have procoelous,

opisthocoelous or notochordal amphicoelous vertebrae (Noble, 1931).
Conversely, similarly shaped centra are found in various amphi-

bians and reptiles which differ greatly in body form: for example,

notochordal amphicoelous centra occur in some frogs and urodeles

(Noble, 1931), in Sphenodon and the majority of gekkonid lizards
(Romer, 1956) and in the trunk of some turtles (Remane, 1936).
All other living reptiles, apart from the Chelonia, have pro-

coelous vertebrae (Hoffstetter & Gasc, 1969).

In the Chelonia, which are a very ancient and conservative

group despite their diversity of habitat (Bellairs, 1957), the
Figure 1:1

Principal types of vertebral centra found in amphibians and reptiles. Sagittal section, diagrammatic, modified from Romer (1956).

A. Solid amphicoelous;
B. Notochordal amphicoelous;
C. Acoelous, platycoelous, amphiplatyean or biplanar;
D. Procoelous;
E. Opisthocoelous.
form of the trunk vertebrae is greatly modified by their fusion to the rigid carapace while the articulations of the cervical vertebrae are complex to allow mobility and withdrawal of the head (Hoffstetter & Gasc, 1969). In other reptiles and in amphibians, whose vertebral columns are flexible at least as far back as the sacrum, notochordal amphicoely has often been regarded as primitive.

The concept of primitiveness has two aspects which are not always clearly separated (see also Appendix). The first is that one form of an organ more closely resembles the ancestral condition (i.e. is more primitive) than other forms of the same organ. The second aspect, which does not necessarily follow from the first, is that those animals in which the organ is in its more primitive state more closely resemble their ancestral stock (i.e. are more primitive) than related animals in which the organ has been modified. As evolutionary changes in the same organ may proceed at different rates in related stocks, and different organs evolve at different rates in the same stock (Mayr, 1965), it is necessary to compare and assess many characters in order to decide which of two related stocks is the more primitive. Whether many characters have been assessed or not, however, notochordal amphicoely in living tetrapods has been thought to represent the retention of an ancestral condition from which all other conditions of the centrum have evolved and for this reason has often been the main criterion for considering ascaphid frogs (Noble, 1924, 1931) and gekkonid lizards (Boulenger, 1885; Camp, 1923) to be the most primitive living members of the respective orders.

The primitiveness of notochordal amphicoely in living tetra-
pods has not always been accepted. Inger (1967) considered it to be secondary in the Ascaphidae and Cope (1900), Underwood (1954), Romer (1956) and Kluge (1967a) regarded it as "degenerate" rather than primitive in the Gekkonidae. This possibility, that notochordal amphicoely in the Ascaphidae and Gekkonidae is not a persistent ancestral condition but has evolved secondarily, has not been thoroughly investigated. It is known, however, that the well developed notochord of living lungfishes is secondary: fossil dipnoans had solid amphicoelous vertebral centra like most other fishes (Millot & Anthony, 1958). In view of the wide phylogenetic gaps between dipnoan fishes, anuran amphibians and gekkonid lizards, it would be possible for the persistent notochord to be primitive in one group and secondary in another.

For many years the classification of lower tetrapods has been based to a large extent on vertebral morphology. Extensive ossification of the centrum and the presence of articular processes on adjacent vertebrae help to distinguish early amphibians from ancestral and contemporary rhipidistian fishes (Schmalhausen, 1968, p. 71-2; Szarski, 1962; Romer, 1966). Reduction of the intercentrum to a small ventral wedge is one feature by which the earliest reptiles are distinguished from amphibians (Baird, 1964; Carroll, 1969c), the pleurocentrum forming the body of the vertebra as in all other amniotes. The relative sizes of the pleurocentrum and intercentrum have been used in the classification of labyrinthodonts to the extent that many groups are named on this basis, e.g. the Diplomeri, Embolomeri, Rhachitomi, Schizomeri, Stereospondyli and Neorhachitomi (Romer, 1947, 1966). Other amphibian categories named on the basis of vertebral morphology
are the Lepospondyli, whose spool-shaped centra consisted of single pieces of bone without sutures, in contrast to the temnospondylous and anthracosaurian labyrinthodonts whose centra consisted of pleurocentra and intercentra (Romer, 1966). Vertebral morphology is of secondary importance in the classification of reptiles. Although amphicoely and procoely of the centrum have been used to classify gekkonid lizards (e.g. by Boulenger, 1885; Noble, 1921), the main criteria at most supra-generic levels are structural features of the skull (Romer, 1956).

As the classification of vertebrates should be, as far as possible, consistent with their phylogenetic relationship to one another (Simpson, 1961), a clear understanding of the criteria used to decide these relationships is essential. Many vertebrates are known only as fossils whose hard parts alone have been preserved, so that the only facts known about them concern the skeleton and those soft parts which have left their impressions in bones. Various assumptions can be made concerning other characters by comparison with living forms but extreme care must be taken that the assumptions are justifiable. In any case, assumed characters cannot replace observed characters in the determination of relationships.

The use of assumed developmental characteristics to classify fossil vertebrates is fallacious in two respects: there can be no proof that the assumptions are justified and it is well known that among living vertebrates structurally similar organs and animals often develop in very different ways. Nevertheless, Romer's (1945) scheme of amphibian classification was largely based on the assumption that fossil vertebrae developed in the
same way as structurally similar vertebrae in living forms. Thus he described the lepospondylous vertebra (or 'husk vertebra') as a single structure, often spool-shaped with a notochordal perforation, whose centrum forms directly by the deposition of bone around the embryonic notochord without preformation in cartilage and which is found in urodeles and apodans as well as many small Palaeozoic amphibians. In contrast, Romer described the apsidospondylous vertebra (or 'arch vertebra'), which primitively consisted of pleurocentra and intercentrum, as being laid down as cartilage blocks or arches and then ossified to a greater or lesser degree. This type of vertebra, he claimed, was inherited directly from crossopterygian fishes, was characteristic of the labyrinthodonts and persists today in frogs and all amniotes.

In a later edition of "Vertebrate Paleontology" (1966) Romer deleted all reference to development from his description of lepospondylous and apsidospondylous vertebrae and in 1968 abandoned the term Apsidospondyli altogether as anurans are no longer believed to show traces of the presence of central 'arch' elements somewhat comparable to the situation in labyrinthodonts. Anurans are now classified with urodeles and apodans in the Lissamphibia (Parsons & Williams, 1963) on grounds other than vertebral structure with the result that almost all other amphibians fall naturally into the Lepospondyli or the Labyrinthodontia depending on the structure of the centrum (Romer, 1968).

The lack of justification for assuming that fossil vertebrae developed in the same way as structurally similar vertebrae in living forms is well illustrated by the Palaeozoic Lepospondyli whose origins and interrelationships are unknown (Romer, 1968,
1969) but which have been considered by Schmalhausen (1968) and others to be ancestral to modern urodeles and apodans. In the absence of statements to the contrary, the assumption that the centra of lepospondyls ossified directly as perichordal cylinders of bone (Romer, 1945; Baird, 1965; Olson, 1965; Schmalhausen, 1968) seems to have been based solely on their structural similarity to the centra of urodeles which develop this way (Mookerjee, 1930). In illustrations such as those of Baird (1965), Brough & Brough (1967a & b) and Gregory, Peabody & Price (1956), however, lepospondylous centra closely resemble in general form the notochordal amphicoelous centra of two groups of living reptiles, namely Sphenodon and gekkonid lizards, which are known to be preformed in cartilage (Howes & Swinnerton, 1901; Werner, 1971). Furthermore, the similarity between microsaurian lepospondyls and contemporary stem reptiles was so marked that the microsaurian genus Tuditanus (=Eosauravus) was mistaken for a reptile by Baird (1958) and Peabody (1959) while the romeriid genus Cephalerpeton was once thought to be a microsaur (see Baird, 1965). In these circumstances it seems equally possible for lepospondylous vertebrae to have ossified directly or to have been preformed in cartilage. In any case, knowledge of the development of lepospondylous vertebrae is not necessary for the understanding of lepospondyl relationships because, as Szarski (1962) has emphasised, a difference in ontogenetic development can never be considered proof of a lack of affinity between structurally similar organs or structurally similar animals.

Many misconceptions concerning the structure and development of vertebrae were dispelled by Devillers (1954) and Williams (1959a) who entirely rejected Gadow's nomenclature and theory
regarding vertebral evolution and development in tetrapods. The theory that all vertebrae except those of elasmobranchs arise as four pairs of arcualia homologous with the vertebral primordia of teleost fishes was first proposed by Gadow (Gadow & Abbott, 1895; Gadow, 1897) and later expanded into book form (Gadow, 1933) and influenced almost all work on vertebral development for more than fifty years. In general, subsequent summaries of the original literature on vertebral development in tetrapods have accepted Gadow's hypotheses with reservations (e.g. Goodrich, 1930; Remane, 1936; Romanoff, 1960; Gasc, 1961; Jollie, 1962). Some authors, however, have accepted them without question (e.g. Nelsen, 1953; Von Huene, 1954) while others (e.g. Hamilton, 1952; Patten, 1958) avoid any reference to Gadow's nomenclature.

According to Gadow's theory, the vertebrae of different groups of tetrapods were believed to develop from various combinations of the basiventralia, basidorsalia, interventralia and interdorsalia and, in consequence, were not considered mutually homologous. Szarski (1962) emphasised that, even if vertebrae did develop as Gadow and his followers maintained, the conclusion that they were therefore not homologous would be false, because organs which are surely homologous sometimes develop in closely affiliated species in very different ways. Williams (1959a) showed, however, that the four pairs of discrete arcualia do not occur in tetrapods and emphasised the basic similarity of vertebral development: the recombination of the caudal half of one sclerotome with the cranial half of the following one produces an intersegmental centrum in all living tetrapods.

On the basis of the apparent homology of the vertebral
centra of living tetrapods, Williams (1959a) concluded that the centrum of living amphibians, whose ancestry is uncertain, is a pleurocentrum like that of amniotes whose homology with the pleurocentra of labyrinthodont amphibians can be traced in the fossil record. Estes (1965) has suggested, however, that the centrum of modern amphibians might be an intercentrum like the single centrum of fossil stereospondyls and that its intercentral nature would be shown by its movement during development from an original midsegmental position to its final intersegmental position in the adult. Although such movement has not been mentioned in existing descriptions of amphibian vertebral development (e.g. Ridewood, 1897; Mookerjee, 1930, 1931, 1936; Mookerjee & Das, 1939; Smit, 1953; Lawson, 1966; Wake, 1970), the possibility remains that the centrum of modern amphibians could be an intercentrum.

From the foregoing outline of the use of vertebral morphology and development in establishing phylogenetic relationships among tetrapods, it is clear that several basic problems which have been debated for many years still await solution. New data from studies in comparative morphology, functional anatomy and embryology could clarify this situation, especially as the material available for the present study includes unique animals restricted to Australia and New Zealand.

The present study includes a description of vertebral structure and development in the rare endemic New Zealand frog, Leiopelma, and a comparative description of the vertebrae of the Gekkota whose two recognised families, the Gekkonidae and Pygopodidae, occur together only in Australasia. New evidence is
given concerning two major problems pertaining to tetrapod vertebrae, namely the phylogenetic significance of notochordal centra among lower tetrapods and the question of vertebral homology.
PART II — THE VERTEBRAL COLUMN OF LEIOPELMA

INTRODUCTION

Only two genera of living frogs, *Ascaphus* Stejneger, 1899 from North America and *Leiopelma* Fitzinger, 1861 from New Zealand, are known to possess notochordal amphicoelous vertebrae in adult stages. In other anurans the notochord is discontinuous if not entirely absent from the adult vertebral column and the joints between adjacent centra are synovial joints which may be procoelous, opisthocoelous or amphicoelous in shape (Fig. 1:1), the last named having a free intervertebral disc. In some frogs such as the Ranidae and Brevicipitidae the shape of the centrum varies in different parts of the vertebral column (Noble, 1922). Various aspects of vertebral structure and development in anurans with synovial intercentral joints have been described by many authors including Cope (1866), Gadow (1897, 1901, 1933), Ridewood (1897), Schauinsland (1906), Beddard (1907), Nicholls (1916), Gillies & Peberdy (1917), de Gaay Fortman (1918), Noble (1922, 1924, 1931), Mookerjee (1931), Ramaswami (1933), Zaharesco (1935), Mookerjee & Das (1939), Al-Hussaini (1941), Hodler (1949 a,b), Smit (1953), Stokely & List (1955), de Silva (1956). Much of the earlier work on anuran vertebrae has been reviewed by Remane (1936), Devillers (1954) and Griffiths (1959a, 1963).

The only investigations concerned specifically with the vertebrae of ascaphids appear to be Ritland's (1955) account of the external and internal morphology of the adult vertebral column of *Ascaphus*, van Dijk's (1960) discussion of the number of verte-
brae contributing to the urostyle in this genus and E.M. Stephenson's (1952, 1960) descriptions of the external features of the vertebrae of the three species of *Leiopelma*. There appears to be no detailed account, however, of the internal morphology of the adult vertebral column in *Leiopelma* or of vertebral development in either of these two genera.

As various characteristics of the adult vertebral column or its ontogenetic development have been used to determine relationships among frogs, it is relevant to review briefly in this context the taxonomic history of the Anura (= Salientia). Until comparatively recently most authors regarded the shape of the adult centrum as an important classificatory criterion, among the earliest to do so being Blanchard (1885) who classified frogs in two groups with opisthocoelous and procoelous vertebrae respectively. Nicholls (1916) recognised that the sacral vertebra also varies in shape and defined the Aglossa and four tribes within the Phaneroglossa as follow:

**Aglossa.** Sacral vertebra always fused with coccyx; presacral vertebrae seven (or fewer), opisthocoelous; with ribs in development.

**Phaneroglossa.**

I. Opisthocoela. Sacral vertebra biconvex, free from coccyx; presacral vertebrae eight, opisthocoelous; with ribs.

  Includes but one family, the Discoglossidae.

II. Anomocoela. Sacral vertebra ankyloed to coccyx or articulating therewith by a single condyle; vertebrae procoelous (rarely opisthocoelous); without ribs.
Includes a single family, the Pelobatidae.

III. Procoela. Sacral vertebra free, articulating with the coccyx by a double condyle; vertebrae uniformly procoelous.

Includes the Bufonidae, Hylidae, and Cystignathidae.

IV. Diplasiocoela (= Fimisternia). Sacral vertebra biconvex, eighth vertebra biconcave; the first seven vertebrae procoelous.

Includes the Ranidae and Engystomidae.

Noble (1922) criticised a number of characters which had been used earlier to classify the Anura such as dentition and various characteristics of the skull, pectoral girdle and vertebral column, and maintained that the five groups were not as circumscribed as Nicholls (1916) had believed. Nevertheless Noble (1922) considered that, of all the characters which had been fully investigated, those of the vertebral column were the most important, and his modification of Nicholls' classification is summarised as follows:

Sub-Order I. -- Opisthocoela. Presacral vertebrae opisthocoelous; ribs present at some stage in development.

Families Pipidae and Discoglossidae.

Sub-Order II. -- Anomocoela. Sacral vertebra procoelous, ankylosed to coccyx or if free with only a single articular condyle for coccyx (except in Pelodytes); presacral vertebrae eight, uniformly procoelous (rarely opisthocoelous); without ribs at any stage in development.

Family Pelobatidae.
Sub-Order III. -- Procoela. Sacral vertebra free, procoelous, with double condyle for coccyx; presacral vertebrae eight to five, procoelous; without ribs.

Families Bufonidae, Hylidae, Brachycephalidae.

Sub-Order IV. -- Diplasiocoela. Sacral vertebra biconvex with double condyle for coccyx; eighth vertebra biconcave, preceded by seven procoelous vertebrae; without ribs.

Families Ranidae, Brevicipitidae.

In 1924 Noble recognised that Leiopelma and Ascaphus have amphicoelous vertebrae, having previously (1922) considered the latter to be opisthocoelous, and in 1931 erected a fifth sub-order, the Amphicoela, for these two genera for which he had already (1924) erected the family "Liopelmidae". With some other modifications made in 1931 such as the inclusion of the fossil family "Palaeobatrachidae" in the Procoela and of the Polypedatidae in the Diplasiocoela, the classification outlined above became widely accepted and, as recently as 1957, was used by Brattstrom as a basis for the discussion of anuran phylogenetic relationships, while Goin & Goin (1962) adopted it with almost no further modification.

According to Ramaswami (1933) and Griffiths (1959a, 1963) the vertebral characters used by Nicholls (1916) and Noble (1922, 1931) are not always indicative of anuran inter-relationships owing to their variability. Intrafamilial, intrageneric and, in some cases, intraspecific variation with respect to the shape of the presacral intervertebral joints has been reported by Boulenger
(1908), Mookerjee (1932), Ramaswami (1933), Parker (1934), Griffiths (1959a, 1963) and Holman (1963b) as well as by Nicholls (1916) and Noble (1922) themselves. Griffiths (1959b, 1963) maintained that synovial intercentral joints in the Anura are formed by the invasion of an arc of connective tissue into the intervertebral cartilage and that the shape of the joint depends on the angle of penetration of this arc, thus intimating that variation in the shape of these joints involves no great morphological change. The form of the coccygeal joint can also vary, being monocondy lar or bicondylar in different members of the Pelobatidae (Boulenger, 1897; Gadow, 1901; Nicholls, 1916; Noble, 1926a; Taylor, 1941; Zweifel, 1956; Griffiths, 1963). The joint between the sacral and presacral vertebrae can be fused as in Philautus (Griffiths, 1959a) which had nevertheless been placed by Noble (1931) in the diplasio-coelous Polypedatidae. As the use of the term "amphicoelous" to describe the vertebrae of the Ascaphidae has also been questioned (Ritland, 1955; E.M. Stephenson, 1960, 1961), it would appear that the Opisthocoela alone, of the five suborders recognised by Noble (1931), represent a valid taxonomic unit when defined exclusively on the basis of Noble's vertebral characteristics (Griffiths, 1963).

Having demonstrated that the vertebral articulation patterns used by Nicholls (1916) and Noble (1922, 1931) are unsatisfactory characters for the determination of anuran relationships, Griffiths (1963) proposed that the number of presacral vertebrae and the shape of the centrum in transverse section can be used instead as primary characters in the diag-
nosis of major categories of frogs. According to Griffiths (op. cit.), the nine presacral elements of the Ascaphidae sets them unequivocally apart from all other salientian families in which the number is eight. Even in animals with vertebral fusions, which happen occasionally in the Ascaphidae (E.M. Stephenson, 1952, 1960; Ritland, 1955) and frequently in some non-ascaphid frogs such as Rana (Zaharesco, 1935; Al-Hussaini, 1941; Dasgupta & Grewal, 1968), the number of vertebral elements can be determined from the arrangement of the spinal nerves (Griffiths, 1963).

The three different types of adult centrum recognised by Griffiths (1963) are the ectochordal centrum found in the Ascaphidae and Rhinophrynidae which consists of a bony cylinder enclosing a persistent notochord, the stegochordal condition found in the Pipidae, Pelobatidae and Discoglossidae in which the centra are flattened dorsoventrally and lie dorsally to the degenerated notochord, and the holochordal centrum of all other anurans which is cylindrical and solid. Griffiths defined these three types of centrum in terms of their ontogeny as well as their adult structure and pointed out that ectochordy represents an intermediate stage in the development of holochordy and that the stegochordal condition arises in two ways, either by the restriction of ossification to the dorsal region of a cartilaginous perichordal tube as in the Pipidae and Pelobatidae, or by restriction of chondrification as well as ossification to the dorsal region of a fibrous perichordal tube as in the Discoglossidae. At metamorphosis the ventral part of the perichordal tube, whether it is fibrous or cartilaginous, together with the
notochord, begins to degenerate.

Many other characters besides the number and shape of the vertebral centra and the presence of ribs have been used in attempts to determine anuran inter-relationships, the number of characters used and the emphasis placed on any one character varying according to the author concerned. Among these non-vertebral characters are the tongue, hyolaryngeal apparatus, osteology and myology of the head, skeletal elements of the limbs, structure and development of the dorsal and ventral elements of the pectoral girdle, musculature of the thigh, genital system, breeding behaviour and larval characters. The bearing of these characters on anuran relationships has been discussed by various authors including Griffiths (1959a, 1963), Griffiths & Carvalho (1965), Inger (1967) and Kluge & Farris (1969). New data have been accumulating in recent years from cytotaxonomical investigations (Duellman & Cole, 1965; Cole, 1966, 1971a & b; Morescalchi 1966, 1967, 1968a,b,c; Cole, Lowe & Wright, 1968; E.M. & N.G. Stephenson, 1970; Cole & Zweifel, 1971) and new methods, namely various forms of numerical taxonomy have been used to interpret morphological data in attempts to determine anuran phylogenetic relationships (Inger, 1967; Kluge & Farris, 1969).

In order to determine the course of evolution within a group such as the Anura, and hence to classify the members of this group in a manner consistent with their evolutionary history, it is necessary to assess which characteristics (= character-states, Kluge & Farris, 1969) are primitive and which are advanced within this group (see Appendix). The recognition of
such states in the Anura has been more difficult than in most other terrestrial vertebrates for a number of reasons. Prior to 1960, comparatively few fossil frogs have been described and the earliest forms known, such as Notobatrachus and Eodiscoglossus from the Jurassic (Reig, 1957; Melendez, 1957) and Boxenopoides and Saltenia from the Cretaceous (Haughton, 1931; Reig, 1959), already possessed the major skeletal characteristics of living frogs and therefore give no indication as to the origins of the Anura. Although Protobatrachus massinoti, renamed Triadobatrachus by Kuhn, 1962, a tailed amphibian from the Lower Triassic, was considered by Piveteau (1937) and Watson (1940) to have been ancestral to the Jurassic Anura, some other authors such as Hecht (1960, 1962) doubted whether "Protobatrachus" had any connection with the evolution of frogs.

Because so little fossil evidence was available regarding the origins, not only of the Anura, but also of the Urodela and Apoda, many different theories have been put forward to explain the evolutionary relationships of the modern Amphibia (see Parsons & Williams, 1963, for review). For many years the most commonly held view was that urodeles, and in some cases the Apoda as well, had a different origin from the Anura, but there was little agreement as to the ancestral groups concerned. Those suggested included dipnoan and crossopterygian fishes (Holmgren, 1933, 1949, 1952; Jarvik, 1942, 1968) as well as lepospondyl and labyrinthodont amphibians (Romer, 1945; Gregory, Peabody & Price, 1956; Schmalhausen, 1968). In 1959 a different view was put forward by Eaton who derived both the Anura and Urodela from labyrinthodonts and only the Apoda from the Lepospondyli. The
current view is that all three living amphibian orders arose from a common ancestor (Parker, 1956a; Szarski, 1962; Parsons & Williams, 1963). To express this relationship Parsons & Williams revived Gadow's (1901) term "Lissamphibia" but neither these authors nor the majority of later ones including Romer (1966, 1968) were able to cite a probable lissamphibian ancestor among the Amphibia of the Palaeozoic. In consequence, information from fossil amphibians has played a negligible part in the classification of the Anura and those character-states which have been considered primitive or advanced within this group have been assessed on the basis of comparisons among living forms (e.g. Inger, 1967; Kluge & Farris, 1969).

As the Anura are structurally very different from all other vertebrates, comparisons between them are often of little assistance in the determination of primitive anuran character-states. Also, although frogs closely resemble one another in general body form, they nevertheless exhibit considerable variability, even in organ systems such as the vertebral column which plays an important part in locomotion. In addition to the variation already noted with respect to the shape of the joints between adjacent centra, anomalies resulting in bilateral asymmetry may occur in the cervical and sacral regions (Marelli, 1928; Noble, 1931; Zahasesco, 1935; Ritland, 1955; Holman, 1963a and others) and the number of vertebrae can vary within a single genus, e.g. Rana in which eight to ten presacral and one post-sacral vertebrae have been reported (Bourne, 1884; Howes, 1886; Zahasesco, 1935). Although fusion of adjacent vertebrae appears to be rare in some genera such as Ascaphus (Ritland, 1955), it
is not uncommon in others such as *Rana* (Zaharesco, 1935; Al-Hussaini, 1941; Dasgupta & Grewal, 1968). In *Rana cyanophylctis* vertebral fusions, which may or may not involve structural alterations of the two or more vertebrae involved (Grewal & Dasgupta, 1967), are governed by a single dominant gene and are correlated with increased temperature tolerance during embryonic stages (Dasgupta & Grewal, 1968). As anurans also show considerable variability with respect to other characters (see Griffiths, 1963), some of which is attributable to heterochrony (E. M. Stephenson, 1960, 1961; N. G. Stephenson, 1965; Jacobson, 1968), comparative studies within the Anura themselves may not show which state of a character is the most primitive within this group.

Further difficulties arise from the fact that the Anura have two morphologically distinct stages in their life history, even in forms such as *Anhydrophryne* from South Africa and *Leiopelma* from New Zealand which emerge from the egg as miniature tailed frogs (Hewitt, 1919; Archey, 1922; N.G. Stephenson, 1951b; E.M. Stephenson, 1961). The larva or tadpole occupies an entirely aquatic environment whereas the metamorphosed frog lives in an environment which in most cases is at least partially terrestrial. Therefore the evolution of the Anura has involved responses to selection pressures in two different environments inhabited consecutively by each individual animal, so that the evolutionary trends of larvae as well as adults must be considered in determining anuran relationships. The necessity for this is clearly demonstrated by the indistinguishability of larval *Megalophrys montana* and *M. parva* which are distinct as adults.
(Boulenger, 1908) and the close similarity of adult *Phyllobates tamarancae* and *P. latinasus* which are extremely different in their larval stages (Dunn, 1924). The existence of larval stages in amphibians also complicates the interpretation of fossils as some fossils may represent the morphologically different larval stages of others, e.g. the "Phyllospondyli" are now known to be larval labyrinthodonts (Romer, 1966, 1968) but, in the absence of an adequate series of fossils at different developmental stages, an ontogenetic relationship of this type might not be recognised.

In view of the difficulties outlined above regarding the recognition of character-states which are primitive in the Anura, either because they are ancestral states retained in living forms or states which have departed least from ancestral conditions (see Appendix), it is hardly surprising that the evolutionary history of this group is still a subject for debate. In recent years, however, the fossil history of the Anura has become better known. More fossil frogs are now known from the Jurassic and Cretaceous, many of which are relatively complete skeletons (Hecht & Estes, 1960; Casamiquela, 1961, 1966; Reig, 1961; Hecht, 1963; Estes, 1964; Nevo, 1956, 1968), and in some cases the fossils in a single deposit are so numerous as to permit population studies (Nevo, 1968). Additional information has also accumulated on the anuran fauna of the Tertiary which is now known from the works of Hinsche (1941) Kuhn (1941), Taylor (1941), Friant (1944), Schaeffer (1949), Spinar (1952, 1963, 1966, 1967a & b), Zweifel (1956), Tiien (1960), Holman (1963a), Estes & Wassersug (1963) and Vergnaud-Graziini (1966). As some
Mesozoic and Tertiary anurans so closely resemble living forms that they can be placed in Recent families and, in the case of some Tertiary forms, even in Recent genera, it is evident that the Anura had already undergone a large part of their evolution into existing families by the end of the Triassic. In these circumstances it is possible to determine evolutionary trends within some families such as the Pipidae (Nevo, 1968), bearing in mind, however, that character-states which appear to be primitive in a family are not necessarily primitive in the Anura as a whole.

More is known regarding the structure of *Triadobatrachus massinoti* from Hecht's (1962) and Griffiths' (1963) re-examinations of the unique type specimen, but there is still disagreement about its nature and affinities. Griffiths (1963) agreed with Piveteau (1937) and Watson (1940) regarding its anuran affinities, but questioned Piveteau's belief that it was a terrestrial animal directly ancestral to the anurans of the Jurassic. According to Griffiths (1956, 1963), *T. massinoti* was, from a structural point of view, a partly metamorphosed tadpole and should therefore be compared, not with adult stages of living anurans, but with tadpoles undergoing metamorphosis. As Griffiths (1963) pointed out, *T. massinoti* may have been a sexually mature aquatic animal structurally intermediate between tailed amphibians and anurans, or it may have been in the process of metamorphosing into an adult frog comparable to those living today. Griffiths favoured the latter view which, if it is correct, suggests that the ancestors of frogs may have diverged as early as the Palaeozoic. According to Hecht (1962) however, the amount of ossification of
the skeleton of _T. massinoti_ suggests that it was in fact adult.

Among the many different amphibians which have been considered ancestral to frogs are two small, closely related Carboniferous forms, _Amphibamus grandiceps_ and _Miobatrachus romeri_ (Watson, 1940). Although Watson considered them to belong to the now defunct "Phyllospondyli", Gregory (1950) and Carroll (1964) have shown that they are rhachitomous labyrinthodonts belonging to the family Dissorophidae. Gregory (1950) reduced _Miobatrachus romeri_ Watson, 1940 to a synonym of _Amphibamus grandiceps_ Cope, 1865 and cast doubt on the affinities of this genus with anurans but Griffiths (1963) maintained that too many amphibamid features suggest anuran trends for the group to be summarily dismissed from consideration as the ancestral stock. More recently Bolt (1969) has proposed another ancestor, not only of the Anura, but of all three groups of living amphibians (i.e. the Lissamphibia) which is also a rhachitomous labyrinthodont and which Bolt considered to be so closely related to the Dissorophidae that he erected for both groups the superfamily Dissorophoidea. Bolt named this Lower Permian fossil _Doleserpeton_ annectens and considered that it not only possesses no characters which would debar it from protolissamphibian status, which also applies to many other Palaeozoic amphibians, but that it also has three positive features suggestive of relationship to lissamphibians: (i) nearly monospondylous vertebrae, (ii) pedicellate teeth (*sensu* Parsons & Williams, 1963) and (iii) bicuspid teeth. Although it would thus appear that the Lissamphibia arose from rhachitomous labyrinthodonts belonging to or closely related to the Dissorophoidea, the problem of the
divergence of the three living orders still remains. Nevertheless, by reference to labyrinthodonts in general and the Disso-rophoidea in particular as well as to fossil and living frogs it should now be possible to establish with some measure of confidence which states of skeletal characters are the most primitive in living anurans. In order to determine evolutionary relationships within the Anura it is necessary to refer to as many characters as possible whose primitive states can be determined, even when their corresponding advanced states are known to have arisen more than once in parallel (cf. gekkonid lizards -- Appendix).

The aspects of anuran inter-relationships which are relevant to the present investigation concern the affinities of Ascaphus and Leiopelma with one another and with other frogs. Various aspects of the taxonomic history of these two genera were discussed by N.G. Stephenson (1951b), E.M. & N.G. Stephenson (1957), E.M. Stephenson (1961), Metter (1968) and Fawcett & Smith (1971) and the main points are summarised as follow. In 1923 Fójerváry erected the family Ascaphidae for the type genus alone. In 1924 Noble removed both Ascaphus Stejneger, 1899 and Leiopelma Günther, 1868 laps. cal. = Leiopelma Fitzinger, 1861 from the Discoglossidae and erected for them the family "Liopelmidae", justifying his use of this name instead of Fójerváry's Ascaphidae by the fact that "Leiopelma" is the older generic name. Although Metter (1968) claimed that Ascaphidae is the correct name for the family containing these two genera according to Article 23 of the International Code of Zoological Nomenclature, Fawcett & Smith (1971) requested the International Commission of Zoological
Nomenclature for official recognition of the family-group name Leiopelmatidae Mivart 1869. These authors pointed out recent doubts raised by Kuhn (1967) concerning the phylogenetic relationships between Ascaphus and Leiopelma and maintained that the name Ascaphidae should therefore not be dealt with officially at the present time. Until this matter is decided, it seems advisable to retain the name Ascaphidae in the present investigation as this has been the most frequently used name for many years (see Fawcett & Smith, 1971).

Ascaphus and Leiopelma are widely accepted as belonging to a family distinct from all other living frogs because they share more character-states with one another than with any other anuran. The states emphasised by Noble (1931) were (i) the amphicoelous condition of the vertebrae and (ii) the presence of two tail-wagging muscles in the tail-less adult, namely the pyriformis and the caudalipubo-ischio-tibialis. Subsequent authors have drawn attention to other shared characteristics such as (iii) the presence of nine presacral vertebrae in contrast to other living frogs in which the maximum number is eight (N.G. Stephenson, 1951b; E.M. Stephenson, 1952; Griffiths, 1963), (iv) the presence of discrete ribs in adult stages in contrast to most other frogs in which rib elements are distinguishable from the transverse processes of the vertebrae only during developmental stages if at all, (v) the presence of an "uncinate process" on the bony proximal portion of the rib of the third vertebra which also occurs in some leptodactylids such as Neobatrachus (E.M. Stephenson, 1952, 1960; Ritland, 1955; N.G. Stephenson, 1965), (vi) posterior cardinal veins, which occur
in larval frogs and urodeles, and occur together with the posterior vena cava in adult Leiopelma and Ascaphus as well as in some adult urodeles, Bombina, Discoglossus and some Alytes (Howes, 1888; E. M. & N.G. Stephenson, 1947; Szarski, 1951), (vii) the absence, as in all urodeles, of middle ear elements such as tympanum and stapes (Noble, 1931; E. M. Stephenson, 1951, 1955), (viii) the presence in Ascaphus and some Leiopelma of a procoracoid centre of ossification in the pectoral girdle (E. M. Stephenson, 1952, 1960; Ritland, 1955), (ix) the existence of a cartilaginous epipubis in the pelvic girdle which occurs in only one other anuran, namely Xenopus (Noble, 1931; de Villiers, 1934b; E. M. Stephenson, 1952, 1960; Ritland, 1955) and (x) the presence in Ascaphus and Leiopelma of the articular bone in the lower jaw (de Villiers, 1934a; E. M. Stephenson, 1951) in addition to the mandibular elements present in other frogs, namely the dentary and prearticular (Noble, 1931). If, as is generally believed, most of these points of resemblance between Ascaphus and Leiopelma represent primitive character-states within the Anura, it would appear that these two genera are the most primitive living frogs in that they have diverged least from the ancestral anuran stock. Further support for this contention is provided by the presence of additional primitive character-states in one genus or the other, such as the well developed abdominal ribs of Leiopelma, traces of which also appear in the discoglossid Bombina but which are absent from Ascaphus (Noble, 1931; E. M. Stephenson, 1952, 1960).

It cannot be assumed, however, that genera which are
primitive with respect to many characteristics are necessarily primitive in all. For example, the extreme specializations of *Ascaphus* for copulation and larval development in swiftly flowing mountain streams as exemplified by the presence of an intro-mittent organ in adult males and of large sectorial lips in tadpoles almost certainly represent advanced conditions in the Anura generally (Noble, 1931), especially as the tadpoles of other frogs living in mountain torrents have similar but not the same structural modifications. Also, the retention in *Ascaphus* and *Liopelma* of a number of character-states which are primitive in the Anura is not in itself indicative of their close relationship to one another as these primitive states could have been retained independently in these two genera.

The present investigation of the internal morphology and ontogenetic development of the vertebral column of *Liopelma* has been undertaken in order to ascertain the extent to which it resembles the column of *Ascaphus* as described by Ritland (1955) and to determine if possible whether the ectochordal centra (*sensu* Griffiths, 1963) and uninterrupted notochord of adult ascaphids are persistent ancestral conditions as believed by Noble (1924, 1931), E. M. Stephenson, (1952), Griffiths (1963), Kluge & Farris (1969) and others or secondarily derived from the holochordal condition as postulated by Inger (1967).
MATERIAL AND METHODS

Twelve specimens of developing Leiopelma archeyi were available for investigation in the form of transverse, longitudinal or approximately horizontal serial sections cut at 10 or 12 μ and stained in van Gieson's stain, Masson's Trichrome or Heidenhain's Azan. As this material had already been sectioned, it was not possible to stage the embryos by reference to tables of development such as Shumway's (1940) table for Rana pipiens or Nieuwkoop & Faber's (1956) table for Xenopus laevis. They were therefore given the arbitrary stage numbers 2 to 9 to indicate increasing age. Stages 2 to 5 were intra-capsular embryos, Stage 6 was hatching while Stages 7, 8 and 9 were tailed froglets fixed one, two and three weeks after hatching respectively.

Five serially sectioned specimens of developing Leiopelma hochstetteri were also available, all cut transversely at 10μ, but because they had been used in the experiments described by N. G. Stephenson (1955), their ages with respect to hatching were unknown. As the youngest specimen of L. hochstetteri was clearly less advanced in its development than the youngest specimen of L. archeyi, it was called Stage 1, while two other specimens which appeared overall to be about the same age as the oldest L. archeyi were regarded as Stage 9H. These specimens were stained in Mallory's Triple Stain.

The adult material examined included a specimen of L. archeyi, male, snout-vent length 27mm, and a specimen of L. hochstetteri, male, snout-vent length 34mm. The vertebral
columns of these two animals were serially sectioned horizontally at 10µ and 12µ respectively and stained in Mallory's Triple Stain and Masson's Trichrome.

Selected sections through developing and adult vertebrae were photographed using a Zeiss Photomicroscope, while the vertebrae of *L. archeyi*, Stages 4, 6, 7, 8 and 9 are also illustrated by contour reconstructions using the method described by Pusey (1939). The magnification of all illustrations is shown by the accompanying horizontal or vertical line.
VERTEBRAL DEVELOPMENT

Leiopelma archeyi

Stage 2, T.S. (Pl. 1). The notochord is almost uniform in cross sectional area throughout the trunk and is more dorsoventrally depressed anteriorly than posteriorly. There appears to be only one elastic notochordal sheath, contrary to Mookerjee's (1931) contention that a two-layered sheath is universal in the Anura, and the notochordal tissue itself is diffuse and vacuolated, the layer of cells underlying the notochordal sheath being the notochordal epithelium.

The relationships of the posterior region of the skull and the most anterior vertebra or atlas are not clear owing to the diffuse nature of the sclerotogenous mesenchyme in this region. Further posteriorly the neurapophyses are forming between consecutive spinal nerve ganglia. The more anterior neurapophyses are cartilaginous while the more posterior elements are still procartilaginous. Each neurapophysis is dorsolaterally situated on the notochord, extending laterally to meet the myotome and dorsally as far as the ventral margins of the adjacent ganglia. Further dorsally beside each ganglion is an aggregation of mesenchymatous cells which are connected to the dorsal extremity of the neurapophysis, while the region dorsal to the ganglion between the spinal cord and the myotome is filled with loose mesenchyme. The surface of the notochord between and beneath the bases of the neurapophyses is invested by a thin layer of squamous cells which forms the perichordal tube.

Situated distally to the myotomes adjacent to the third
vertebra are large vessels, the anterior lymph hearts, which at this stage are widely separated from the developing axial skeleton.

**Stage 3, T.S. (Pls. 2, 3).** The notochord is oval and depressed in cross section from the basis cranii to the tenth vertebra, gradually increasing in size posteriorly so that its cross sectional area in the tenth vertebra is approximately four times that in atlas. Posterior to the tenth vertebra the notochord becomes cylindrical and even larger so that its cross sectional area in the anterior tail is approximately eight times that in atlas.

Fourteen pairs of neurapophyses are present. Their cartilaginous bases extend for a short distance anteriorly and posteriorly along the lateral surfaces of the perichordal tube in the anterior trunk and along its dorsolateral surfaces further posteriorly. The arch pedicels of the first twelve vertebrae are slender, subcylindrical structures curving around the spinal cord, and the procartilaginous apices of each pair of neurapophyses are widely separated from one another above the spinal cord. The arch pedicels of the thirteenth and fourteenth vertebrae extend only a short distance above the notochord to terminate laterally to the spinal cord. Cells from the dorsal extremities of the myotomes are contributing to the apices of the neurapophyses. A short distance below the apex of each neurapophyses of the second to the ninth vertebrae there are procartilaginous processes extending a short distance anteriorly and posteriorly from the arch. Only the posterior processes are present on the atlas and both pairs of processes are absent
from the tenth and following vertebrae. These processes represent the developing zygapophyses and only those of the first three vertebrae are joined together by procartilage at this stage, those of the more posterior vertebrae being connected by diffuse bands of mesenchyme.

On the neurapophyses of the second to the tenth vertebrae there is a laterally directed transverse process whose apex is mesenchymatous. On some vertebrae, particularly the second, third, seventh and tenth, the unchondrified material is clearly a separate element from the transverse process and is therefore a rib, those of the third vertebra lying against the mesial surfaces of the anterior lymph hearts. Both transverse processes and ribs are lacking on atlas and vertebrae eleven to fourteen.

The perichordal tube of the first ten vertebrae has increased in thickness to become a sheath of squamous cells several cells thick, and is slightly thicker ventrally than dorsally to the notochord. Further posteriorly the outer limits of the perichordal tube are ill-defined, at first laterally then also ventrally to the notochord. In the regions between consecutive vertebrae the notochord is enclosed only by the perichordal tube but between the atlantal neural arch and the occipital arch of the skull there are also strong cartilaginous connections attached to the lateral surfaces of the perichordal tube.

Occupying much of the space between consecutive neurapophyses at the level of the transverse processes are the ganglia of the spinal nerves. The only spinal nerve lacking a ganglion is the first which lies between the atlantal arch and the skull and consists of the ventral root only. At this stage the ganglia
of nerves two to fourteen vary little in size while those of the more posterior nerves gradually become smaller. The origins of the dorsal and ventral roots in the spinal cord are in almost the same transverse plane as the ganglia, and the spinal nerves pass ventrally on either side of the notochord.

Stage 4, late intracapsular embryo, L.S. (Fig. 2:1; Pl. 4). The apices of the neurapophyses of the first ten vertebrae lie close together but have not fused, while those of the eleventh vertebra are still widely separated from one another. The arch pedicels are slender and subcylindrical and are orientated vertically to the notochord when seen in side view. The atlantal neural arch is the largest in the column and, dorsally to the spinal cord, is widely separated from the skull. The regional variation in the size of the neural arches and the notochord is illustrated in Figure 2:1.

All the neural arches as far back as the tenth vertebra are joined together by bands of procartilage lying dorsolaterally to the spinal cord and representing the zygapophyses. The zygapophyseal joints have not yet appeared, but the position of the atlanto-occipital joint is shown by a layer of younger cartilage which extends laterally and posteriorly from the surface of the notochord between the bases of the atlantal neural arch and the occipital region of the chondrocranium.

Regional variation has occurred in the sizes of the spinal nerve ganglia, the largest being those of nerves three, four and eleven, and the smallest those of nerves seven and eight.

The ventral part of the perichordal tube is of uniform
Figure 2:1
thickness from the chondrocranium to the ninth vertebra but, from the tenth to the thirteenth vertebra, its thickness ventrally to the notochord has increased owing to squamous cell hyperplasia.

Stage 5, later intracapsular embryo, T.S. and oblique H.S. (Pl. 4). The notochord still has its greatest cross sectional area in the anterior tail, in the twelfth and thirteenth vertebrae where it is almost circular in section. It gradually becomes smaller and more depressed in the more anterior vertebrae and posterior skull but further anteriorly in the basis cranii it is compressed slightly to become subcircular again in section. Posterior to the thirteenth vertebra the notochord tapers gradually to the end of the tail.

A sheath of squamous cells comprising the perichordal tube now invests the notochord throughout the vertebral column. It has chondrified by the deposition of matrix similar to that in the neural arches. In the specimen sectioned transversely the increase in thickness of the ventral part of the perichordal tube begins towards the posterior end of the tenth vertebra and reaches its maximum in the twelfth vertebra. In the thirteenth vertebra the thickness of the perichordal tube is reduced laterally to the notochord as well as ventrally so that the notochord of the fourteenth vertebra is invested by a uniformly thin sheath of squamous cells.

Fourteen pairs of neurapophyses are present, the first ten of which are fused together mid-dorsally. In contrast to the arch pedicels which are subcylindrical, the dorsal laminae
of the arches are broader plates of cartilage which form a partial roof over the neural canal. The cartilaginous arch bases of the first nine vertebrae lie laterally to the notochord from which they are separated by the perichordal tube, and consecutive arch bases almost meet one another so that the intervertebral region is very short. In the tenth and following vertebrae the arches lie dorsolaterally to the notochord and the distance between consecutive arches increases. In this region, unlike the more anterior trunk, there is cartilaginous continuity between consecutive arch bases in the form of a band of cartilage attached to the dorsolateral surface of the perichordal tube. These tracts of cartilage extend posteriorly from the fourteenth pair of neurapophyses, varying slightly in thickness at irregular intervals. They are present as far back as the eighteenth pair of spinal nerves (Pl. 4F) after which they diminish and disappear.

In the specimen sectioned transversely, only the second, third, fourth, tenth and eleventh vertebrae have clearly defined ribs, those of the second, third and fourth vertebrae being at least partly chondrified while those of the tenth and eleventh are mesenchymatous. There is no fusion in this specimen between the ribs of adjacent vertebrae.

In the specimen sectioned horizontally there are clearly defined ribs attached to the apices of the transverse processes of the third to the eleventh vertebrae inclusive. Those of the third, fourth and fifth vertebrae are cartilaginous, the right rib of the eighth vertebra is cartilaginous proximally and procartilaginous distally while the remaining ribs consist entirely
of procartilage. The right rib of the third vertebra is deeply notched to enclose the anterior lymph heart and is separate from the rib of the fourth vertebra. On the left side of the body the ribs of the third and fourth vertebrae are fused together and the combined rib encloses the lymph heart. In the posterior region of the body the largest rib elements are those of the tenth vertebra, suggesting that this is to be the sacral vertebra. At this stage, however, the ilia of the pelvic girdle are still widely separated from the vertebral column (Pl. 4 F).

Stage 6, at hatching, T.S. and L.S. (Figs. 2:2, 2:3; Pls 5, 6). In the specimen sectioned transversely the cross sectional area of the notochord gradually increases from front to back, reaching its maximum in the ninth, tenth and eleventh vertebrae and there appears to be little change in its cross sectional area in the following two vertebrae. The notochord is laterally compressed to a small degree within the basis cranii, becoming circular in cross section in the first three vertebrae. In the following eight vertebrae it is slightly depressed dorsoventrally while that of the more posterior tail is squarish in outline. In the specimen which was sectioned longitudinally, the notochord gradually increases in size from its anterior extremity just behind the hypophysis to the level of the fourteenth vertebra.

The perichordal tube of the first ten vertebrae of both specimens is of uniform thickness along the vertebral column and is slightly thicker ventrally than it is dorsally to the notochord. The ventral thickening of the perichordal tube which begins at the posterior end of the tenth vertebra and
Figure 2:2

Contour reconstructions of vertebrae 1 - 5 of _L. archeyi_ at hatching (Stage 6). First vertebra from posterior aspect, vertebrae 2 - 5 in anterior view. The procartilaginous ribs of the 5th vertebra are shown in coarse stipple.

*dr*, dorsal root of spinal nerve; *nab*, base of neural arch; *nal*, lamina of neural arch; *nap*, neural arch pedicel; *nca*, neural canal; *ncc*, notochordal canal; *occ*, occipital condyle; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis; *r*, rib; *sq*, spinal nerve ganglion; *sn1-4*, spinal nerves 1 - 4; *trp*, transverse process; *vr*, ventral root of spinal nerve.
Figure 2:3

Contour reconstructions from anterior aspect of the 6th vertebra and vertebrae 9 - 13 of *L. archeyi* at hatching (Stage 6). The procartilaginous ribs of the 6th vertebra are shown in coarse stipple. The mesenchymatous ribs of vertebrae 9 - 13 were too indistinct in outline for reconstruction.

*i1*, ilium; *na*, neural arch; *nab*, base of neural arch; *nal*, lamina of neural arch; *nca*, neural canal; *nc',* notochordal canal; *nc',* notochordal sheath; *pct*, perichordal tube; *pre*, prezygapophysis; *r*, rib; *scr*, subchordal rod; *sg*, ganglion of spinal nerve; *sn7-14*, spinal nerves 7 - 14.
reaches its maximum in the thirteenth vertebra is increased at this stage by the metaplasia of chondrified squamous cells into hyaline cartilage in which the cells are subspherical and the matrix more abundant. This subchordal rod of cartilage occupies the full width of the notochord and is chondrified as far as the posterior end of the thirteenth vertebra. The dorsal and lateral regions of the perichordal tube which lie between the arch bases and the subchordal rod of the thirteenth vertebra are thin and membranous. In the fourteenth vertebra the subchordal rod also becomes membranous and diffuse and disappears towards the posterior end of this vertebra.

In the specimen sectioned transversely, fourteen pairs of neurapophyses are present. Except for the fourth, and the eleventh to the fourteenth pairs, they are fused together dorsally to the spinal cord for a short distance near the posterior end of the arch. The arch bases of the first four vertebrae are attached laterally to the perichordal tube while those further posteriorly are more dorsolaterally placed with respect to the notochord. The tracts of cartilage extending back from the arch bases of the fourteenth vertebra disappear a short distance behind the vent at approximately the level of the sixteenth pair of spinal nerves so that the notochord in the remainder of the regressing tail is surrounded by a thin membranous perichordal tube. In the longitudinally sectioned specimen, none of the fourteen pairs of neurapophyses had fused together.

Transverse processes occur on all vertebrae with the exception of the atlas and the fourteenth vertebra and in many cases have clearly defined rib elements attached
to them. The ribs of the third vertebra are cartilaginous and are curved so that they lie against the mesial and ventral surfaces of the anterior lymph hearts, while those of the tenth vertebra are represented by condensations of mesenchyme attached to the transverse processes. At this stage the ilia are growing anteriorly and dorsally towards the vertebral column. Although the anterior ends of the ilia are level with the eleventh vertebra at this stage, the greater size of the tenth vertebra and its ribs than the eleventh vertebra and its ribs suggests that the former is the sacral vertebra. This is supported by the fact that the anterior ends of the ilia are procartilaginous and evidently in a state of rapid elongation.

The spatial relationships of the components of the spinal nerves with one another and the adjacent vertebrae are the same as in earlier stages: the dorsal and ventral nerve roots, the ganglia and the spinal nerves passing ventrally beside the vertebrae all lie in approximately the same transverse plane and the ganglia lie in approximately the same horizontal plane as the transverse processes.

Stage 7, one week after hatching, T.S. and L.S. (Fig. 2:4). Although the two specimens representing this stage hatched and were fixed at the same time, the longitudinally sectioned specimen is more advanced in its vertebral development than the one sectioned transversely. As they also differ in other respects they are described separately.

In the specimen sectioned transversely the notochord gradually increases in size posteriorly as far as the fifteenth
Figure 24: Contour reconstructions of vertebrate 1-12 of T. Archeyi one week after hatching (Stage 7).
vertebra. It is slightly compressed in the basis cranii and the first three vertebrae, is slightly depressed in the remaining vertebrae and is somewhat irregular in cross sectional outline. The perichordal tube is slightly thinner dorsally to the notochord than it is ventrally while its lateral surfaces are covered by the cartilage of the neural arch bases except for a narrow region between adjacent vertebrae. The ventral thickening of the perichordal tube to form the subchordal rod begins in the tenth vertebra, has partly changed into hyaline cartilage in the twelfth to the fourteenth vertebrae and disappears in the region of the fifteenth vertebra between the fifteenth and sixteenth pairs of spinal nerves.

Fifteen pairs of neurapophyses are present in this specimen, the more anterior eleven of which are fused together middorsally. The neurapophyses of the twelfth vertebra lie close together above the spinal cord without fusing while those of the thirteenth, fourteenth and fifteenth vertebrae consist of the arch pedicels only, and these diminish in size posteriorly. Joint cavities are forming in the cartilaginous zygapophyseal bars connecting the first three vertebrae, those connecting the third to the eleventh vertebrae being undivided although the position of the joint is clearly defined. Posterior to the eleventh vertebra there are no zygapophyseal connection between consecutive neural arches.

Transverse processes are present on all vertebrae except the atlas and the last three in the column. Cartilaginous ribs are attached to the transverse processes of the third, fourth and fifth vertebrae, those of the fourth vertebra instead of the
third as is usual in *Leiopelma* being deeply notched to enclose the anterior lymph hearts. The ribs associated with the sixth, seventh and twelfth vertebrae are procartilaginous or mesenchymatous while the remaining vertebrae lack separate rib elements. The pleurapophyses of the eleventh vertebra are connected to the ilia of the pelvic girdle by broad bands of connective tissue, thus demonstrating that the eleventh vertebra is the sacral vertebra in this specimen instead of the tenth as is usual in *Leiopelma* (E. M. Stephenson, 1952, 1960).

A synovial cavity has begun to form in the posterolateral regions of the atlanto-occipital joint, the more medial region of the joint on either side of the continuous notochord remaining undivided.

In the specimen which was sectioned longitudinally, the tenth vertebra is the sacral vertebra, a total of fourteen pairs of neurapophyses are present, the first ten of which are fused together mid-dorsally, and the ribs of the third vertebra are notched to enclose the anterior lymph hearts. The somewhat more advanced state of vertebral development in this specimen is shown by the presence of joint cavities in all the zygapophyseal bars connecting the first ten vertebrae, there being no zygapophyseal connections between the more posterior neural arches, the somewhat greater extent of the synovial cavity in the atlanto-occipital joint, and the onset of perichondral ossification of the vertebrae. Ossification begins on the neural arches at the level of the transverse processes but does not extend to the ends of these processes or to the bases or the laminae of the arches.
Stage 8, two weeks after hatching, T. S. (Fig. 2:5).
Perichondral ossification of the vertebrae is more advanced than in Stage 7, extending further down the neural arches towards their bases and further dorsally onto the arch laminae. The synovial cavities between the zygapophyses are more extensive with the postzygapophyses overlying the prezygapophyses of the following vertebrae. The neurapophyses of the eleventh vertebra as well as those of the more anterior vertebrae are fused together mid-dorsally.

Of the two specimens at this stage which were available for investigation, one had fourteen and the other fifteen pairs of neurapophyses. In the latter, the sacrum is anomalous in that the right transverse process of the tenth vertebra and the left process of the eleventh vertebra support the pelvic girdle (Fig. 2:5). In the former the sacrum appears to consist of only the tenth vertebra but, unlike the latter in which the transverse processes supporting the girdle are in contact with the ilia, the transverse processes and ilia of this specimen are widely separated from one another. It would thus appear that this specimen is also anomalous in that development of the sacrum has been retarded relative to the rest of the column.

Stage 9, three weeks after hatching, T. S. (Figs. 2:6, 2:7; Pls 7,8). There are fourteen pairs of neurapophyses of which the first twelve are fused together mid-dorsally, the thirteenth are widely separated dorsally to the spinal cord and the fourteenth consist of low arch pedicels. Further posteriorly the bars of cartilage lying along the dorsolateral surfaces of the perichordal tube are irregularly thickened and end just behind
Figure 2:5

Anomalous sacrum comprising the 10th & 11th vertebrae in a specimen of *L. archeyi* two weeks after hatching (Stage 8). Contour reconstructions from anterior aspect.

Third and fourth vertebrae of *L. archeyi* three weeks after hatching (Stage 9). Contour reconstructions from posterior aspect.

*nab*, base of neural arch; *nca*, neural canal; *ncc*, notochordal canal; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis.
Contour reconstructions of vertebrae 7 - 13 in *L. archeyi* three weeks after hatching (Stage 9). 8th and 13th vertebrae in posterior view, remainder from anterior aspect.

the sixteenth pair of spinal nerves. At this stage there is cartilaginous continuity between all the neural arch bases on each side of the body as a result of fusion between consecutive arches on the dorsolateral surface of the perichondral tube. The perichondral tube itself has the same configuration in the presacral region as it did in Stage 7.

The notochord is slightly compressed from side to side in the basis cranii, the nine presacral vertebrae and the anterior end of the tenth or sacral vertebra, increasing gradually in cross sectional area from front to back. Within the posterior end of the sacral vertebra the cross sectional area of the notochord is suddenly reduced to less than half its value at the anterior end of the vertebra as a result of centripetal growth of the neural arch bases and subchordal rod. Maximum constriction of the notochord occurs in the twelfth vertebra behind which it gradually expands to become only slightly smaller at the end of the subchordal rod than in the anterior end of the sacral vertebra. Within this region of notochordal constriction the appearance of the notochordal sheath and notochordal tissue also change, the sheath being corrugated and thickened due to constriction, and the notochordal tissue more dense due to an accumulation of non-cellular material. In the presacral vertebrae and in the tail posterior to the end of the subchordal rod, the notochord and its sheath appear the same histologically as at the onset of vertebral development.

The subchordal rod is now composed entirely of hyaline cartilage and gradually narrows from the posterior end of the sacral vertebra to its posterior end just behind the vent, at
the level of the sixteenth pair of spinal nerves. In the eleventh and twelfth vertebrae the subchordal rod has fused on either side of the notochord to the ventral surfaces of the neural arch bases while the arch bases of the thirteenth and fourteenth vertebrae and the following bars of cartilage are still separated from one another and the subchordal rod by the perichordal tube. In the region of the tail posterior to the end of the subchordal rod the perichordal tube is of almost uniform thickness around the notochord and is apparently fibrous in nature.

Synovial joints are present between the postzygapophyses of the first to the ninth vertebrae and the prezygapophyses of the second to the tenth vertebrae, posterior to which there are no zygapophyses. Their articular surfaces are flat in end view and are inclined upwards and outwards from the midline at an angle of approximately 45° to the horizontal. The synovial joint between atlas and the occipital condyles is not yet complete and is traversed by the unconstricted notochord.

There are no discrete rib elements present at this stage owing to their fusion to the transverse processes of the vertebrae. As discrete ribs have been found at some stage of development in association with all vertebrae bearing transverse processes, the latter are more correctly described as pleurapophyses. The pleurapophyses of the third vertebra are deeply notched to enclose the anterior lymph hearts which are covered dorsally by the cartilaginous suprascapulæ of the pectoral girdle. The pleurapophyses of the tenth or sacral vertebra lie dorsally to the ilia of the pelvic girdle to which they are attached by
ligaments. The ilia extend anteriorly beyond this point to reach the level of the pleurapophyses of the ninth vertebra but are not joined to them.

The spinal ganglia are more ventral in position at this stage, lying between the pedicles of the neural arches below the level of the pleurapophyses. The relative positions of the dorsal and ventral nerve roots, the ganglia and the spinal nerve trunks are also changing in different parts of the body. The result is that the nerve roots, particularly towards the sacrum, come to lie some distance anteriorly to the ganglia to which they belong. The relationship of the nerves to the vertebrae is described below in the section on adult stages. Sixteen pairs of spinal nerves are present at this stage, the most posterior of which lie laterally to the posterior end of the subchordal rod.

**Leiopelma hochstetteri**

*Stage 1, T.S.*

In this specimen, the youngest of all the available specimens of *Leiopelma*, the spinal cord is flanked dorsolaterally by the neural crest and laterally by the somites which have not yet begun to differentiate into myotomes and sclerotomes. The notochord lying between the spinal cord and the subnotochord has a single sheath and the same histological characteristics as in *L. archeyi*.

*Stage 9H, T.S.*

Of the two oldest available specimens of *L. hochstetteri*, one was sectioned completely and the other only as far back as the anterior end
of the eighth vertebra. These two specimens are a little more advanced than the oldest available specimen of *L. archeyi* (Stage 9) with respect to perichondral ossification in that the layer of bone on the neural arches is somewhat thicker and extends further dorsally towards the apices and further ventrally towards the bases of the neurapophyses. The transverse processes have also ossified as far as their junction with the associated ribs.

In some other respects, vertebral development in these specimens of *L. hochstetteri* is less advanced than in *L. archeyi* Stage 9. In the partially sectioned specimen the first four pairs of neurapophyses are unfused while in the other specimen, which has thirteen pairs of neurapophyses in all, the apices of the first ten pairs lie close together above the spinal cord but remain unfused. The eleventh, twelfth and thirteenth pairs of arches are more widely separated mid-dorsally. Ribs are still detectable as distinct elements from the transverse processes of the vertebrae, those of the third and fourth vertebrae being cartilaginous and fused to the transverse processes. The more posterior ribs are procartilaginous or mesenchymatous, including the ribs of the tenth vertebra which appears by virtue of its size to be the sacral vertebra although it is still widely separated from the ilia of the pelvic girdle. There is slight constriction of the notochord within the eleventh and twelfth vertebrae but its histological appearance remains unchanged. The subchordal rod consists of hyaline cartilage for the greater part of its length but it has not yet fused to the bases of the postsacral neural arches.
With respect to the joints developing between atlas and the occipital condyles and between the zygapophyses of consecutive vertebrae, these two specimens of *L. hochstetteri* are comparable with the Stage 9 specimen of *L. archeyi*.
ADULT VERTEBRAL COLUMN

*L. archeyi*, H.S. (Figs. 2:8, 2:9; Pl. 9).
Thirteen pairs of neurapophyses are present in this specimen of which the first nine are presacral, the tenth is sacral and the eleventh, twelfth and thirteenth are fused to the anterior dorsal surface of the urostyle. The first eleven pairs of arches are fused together mid-dorsally and, with the exception of the sacral vertebra, the perichondral bone of the arch laminae is fused as well as the inner core of hyaline cartilage. The neural arch of the sacral vertebra remains unossified mid-dorsally. The arches of the twelfth and thirteenth vertebrae are separate mid-dorsally but fused together on either side of the neural canal dorsally and ventrally to the thirteenth pair of spinal nerves. The arches of the first ten vertebrae articulate by means of zygapophyses and are also connected by strong sheets of collagenous connective tissue. A similar connective tissue sheet joins the atlantal arch to the occipital arch of the skull but there is no zygapophyseal connection between these two arches which are widely separated from one another. Zygapophyses are also absent posterior to the sacrum. The tenth and eleventh arches are widely separated and the eleventh, twelfth and thirteenth arches are considerably smaller than those of the more anterior vertebrae.

With the exception of atlas and the twelfth and thirteenth vertebrae, all the neural arches bear pleurapophyses, those of the presacral and sacral vertebrae being ossified perichondrally for the greater part of their length and cartilaginous at their
Composite horizontal section of vertebral column and posterior skull of adult *L. archeyi* in ventral view, showing relationship of spinal nerves, ganglia and ventral nerve roots to spinal cord, neural arches and urostyle. As the urostyle lies ventrally to the ependymal tube, its position is indicated by a heavy broken line. Only the anterior and posterior ends of the urostyle are shown. Diagrammatic, scale approximate.

ac, auditory capsule; alh, anterior lymph heart; e, ependyma; et, ependymal tube; fj, foramen jugulare; g, ganglion; ms, marrow space; napV4, neural arch pedicel of 4th vertebra; oa, occipital arch; plp, pleurapophysis; rV3, rib of 3rd vertebra; sc, spinal cord; snl, sn9, sn13, 1st, 9th & 13th spinal nerves; splp, sacral pleurapophysis; u, urostyle; V1, V12, 1st & 12th vertebrae; vr, ventral nerve root; VII - X, cranial nerves. Bone, solid black; cartilage, coarse stipple.
distal extremities. Most of them have also undergone endochondral ossification but the marrow spaces do not extend as far distally as the layer of perichondral bone so that the ends of the processes retain a core of hyaline cartilage. In those pleurapophyses with a suture in the perichondral bone between the rib element and the transverse process, namely those of the third and fourth vertebrae, the marrow cavities do not extend out beyond the level of the sutures. In each case, endochondral ossification of the pleurapophyses appears to have progressed outwards from the neural arch rather than originating from separate ossification centres within the pleurapophyses. The pleurapophyses of the eleventh vertebra are much smaller than those of the more anterior vertebrae and consist almost entirely of perichondral bone.

From the occiput to the twelfth vertebra the neural canal enclosed by the neural arches contains the spinal cord which tapers gradually posteriorly as it gives off successive spinal nerves of which there are thirteen pairs in all. The spinal cord itself does not extend further posterior than the twelfth vertebra but its investing membranes and the lining of the spinal canal or ependyma continue back between the thirteenth pair of neuapophyses and along the dorsal surface of the urostyle to its posterior extremity. The most anterior spinal nerve on each side has neither ganglion nor dorsal root but its ventral root is in two parts lying close together, one behind the other. The following twelve pairs of nerves have dorsal and ventral roots as well as ganglia although the ventral roots of the second pair resemble those of the first in having two components arising from the spinal cord. The roots and ganglia of the third pair of nerves
lie in approximately the same transverse plane but further posteriorly the distance between the origins of the nerve roots in the spinal cord and the ganglia to which they belong becomes greatly increased. Maximum displacement is found in the case of the eleventh nerve whose ganglion lies between the tenth and eleventh vertebrae and whose roots leave the spinal cord anteriorly to the ninth vertebra.

The bodies of the presacral and sacral vertebrae, often referred to as centra, are largely cartilaginous, the only bone present being the perichondral and endochondral bone of the neural arch bases which extend almost to the ventral surface of the column and the thin layer of perichondral bone covering the dorsal and ventral surfaces of the vertebral bodies. The term "centrum" is avoided in the present context as anuran vertebral bodies are structurally very different from those of amniotes which are also called centra (see Part IV). All the cartilage within and between consecutive vertebrae is hyaline cartilage, the perichondral tube of chondrified squamous cells present in developmental stages having disappeared. From the arrangement of the cartilage cells and matrix within the vertebrae, which is more clearly seen in the specimen of *L. hochstetteri* than in this specimen of *L. archeyi*, it is evident that much of the cartilage of the presacral vertebral bodies belongs to the bases of the neurapophyses. The cartilage between adjacent vertebrae appears to have arisen as a result of hyperplasia of the perichondral tube in the ends of adjacent vertebral bodies which has become hyaline like the arch bases. Unlike the neural arch bases, however, whose growth has not constricted the notochord
to any extent, growth of the cartilage in the ends of the vertebrae has constricted the notochord to a slender thread.

The notochord together with its sheath is still continuous from the posterior region of the basis cranii to the anterior end of the urostyle ventral to the eleventh pair of neurapophyses. It is continuous through the atlanto-occipital joint, lying very close to the ventral surface of the joint, and contains fibrous cartilage in the base of the skull, the joint region and the anterior end of atlas. In the middle of atlas, as in the following eight vertebrae, it is unconstricted and extends almost to the dorsal and ventral surfaces of each vertebral body. In these vertebrae it has essentially the same histological appearance as in earlier stages. In the sacral vertebra the notochord is constricted to a considerable extent and has changed histologically to appear fibrous and non-cellular. In this form and with little further constriction the notochord passes back into the anterior end of the urostyle but it terminates here owing to the presence of the adjacent marrow space. No vestige of the notochord remains further posteriorly; the urostyle has ossified perichondrally and endochondrally for almost its entire length, the single cavity within it being a marrow space in endochondral bone, not the notochordal canal. The only parts of the urostyle which are still cartilaginous are the most anterior portion of the urostyle where it joins the body of the sacral vertebra and its most posterior extremity where it still appears to be growing.

L. hochstetteri, H.S. (Fig. 2:9; Pl. 9). Of the thirteen neural arches present in this specimen, the tenth
Posterior vertebrae and anterior end of urostyle of adult *Leiopelma* in horizontal section showing the structure of the sacral vertebra and the relationships between the notochord, the bases of the neural arches and the intervertebral cartilage.

A. *L. archevi*, ♂, snout-vent length 27 mm.
B. *L. hochstetteri*, ♂, snout-vent length 34 mm.

hc, hyaline cartilage;  ivc, intervertebral cartilage;
ms, marrow space; nc, notochord; ncs, notochordal sheath;
f, nutritive foramen; pb, perichondral bone; snab, base of sacral neural arch; u, urostyle; V7 – V11, 7th to 11th vertebrae.
is sacral, the eleventh belongs to an additional postsacral vertebra and the twelfth and thirteenth are fused to the anterior end of the urostyle. Zygapophyseal joints connect the first to the eleventh arches, there being no zygapophyseal connections between the atlantal arch and the occipital arch of the skull or between the arches posterior to the eleventh vertebra. The two halves of the first twelve arches are joined together mid-dorsally by hyaline cartilage which, except for that of the tenth vertebra, is enclosed in a thin layer of perichondral bone, while the two halves of the thirteenth arch are separate from one another.

Pleurapophyses are borne by the second to the twelfth vertebrae inclusively, those of the presacral and sacral vertebrae possessing cartilaginous distal portions which, except for those of the ninth vertebra, are fused to their transverse processes. The distal cartilaginous rib elements of the ninth vertebra are connected to their transverse processes by ligaments. The bases of the pleurapophyses contain marrow spaces continuous with those in the neural arches but in the pleurapophyses of the third and fourth vertebrae which have sutures in their perichondral bone, the marrow spaces do not extend into the ribs. The pleurapophyses of the eleventh and twelfth vertebrae are ossified to the tip.

As in _L. archeyi_, there are thirteen pairs of spinal nerves of which only the first pair lacks dorsal roots and ganglia. The relationship of the nerves to their roots and ganglia and to the spinal cord, and the transition from spinal cord to ependymal tube in the region of the twelfth neural arch are also similar in the two specimens.
Except for the sacral and immediately postsacral regions, the relationships of the neural arch bases to the intervertebral cartilage and the internal structure of the vertebral bodies including the conformation of the notochord are the same in *L. hochstetteri* as in *L. archeyi*. The similarities and differences between these two frogs in the structure of their posterior presacral, sacral and postsacral vertebrae are illustrated in Fig. 2:9. The body of the sacral vertebra in both cases consists in part of the bases of the neural arches but, unlike the presacral vertebrae, the mesial surfaces of the arch cartilages do not lie close to the surface of the notochordal sheath. These elements are separated from one another by a region of cartilage which is hyaline like that of the arch bases but which appears, like the hyaline intervertebral cartilage, to have formed as a result of metaplasia and hyperplasia of the perichordal tube. Like the intervertebral cartilage also, and unlike the cartilages of the arch bases, the cartilaginous core of the sacral vertebra has strongly constricted the notochord within it. In *L. archeyi* the bases of the sacral neural arches contribute to the body of the vertebra but in *L. hochstetteri* the arches are separate from the dorsal regions of the vertebral body, and further ventrally where they join the latter they project laterally from the surface of the column. In both frogs the sacral neural arches are smaller in horizontal section than those of the presacral vertebrae, and are proportionally much smaller in *L. hochstetteri* than in *L. archeyi*. 
DISCUSSION

From the foregoing description of the development and adult structure of the vertebral column of *Leiopelma archeyi* and *L. hochstetteri* as well as from E. M. Stephenson's (1952, 1960) accounts of the external morphology of the vertebrae of all three species of *Leiopelma*, it is evident that individual variation in vertebral characteristics is not uncommon. Embryos of the same age may be at somewhat different stages of vertebral development as shown by the closure or otherwise of the neurapophyses, the proximity of the ilia of the pelvic girdle to the vertebral column and the extent of perichondral ossification while the structure of the column can also vary in the number of presacral vertebrae (nine or ten), the number of vertebrae modified to support the ilia and the number of postsacral vertebrae which are free or are incorporated into the anterior end of the urostyle. Variation also occurs in the ribs of the more anterior vertebrae in that those of the third, fourth or both may be forked and fusion can occur between these ribs on either side of the body. As this range of variability was observed in the comparatively few specimens available for the present investigation, it is often difficult to be certain which embryonic and adult features are characteristic of species and which are due to individual variation. Also some developmental stages were not represented, notably the early intracapsular stage between Stages 1 and 2 exhibiting the sclerotomic precursors of the vertebrae, and sub-adult stages more than three weeks old. Consequently it was not possible to determine the cellular density of the sclerotomes or the presence or absence
of a sclerocoel (see Wake, 1970), nor was it possible to observe the onset of endochondral ossification in the neural arches or ossification of the perichordal tube as illustrated in \textit{L. hochstetteri} by E. M. Stephenson (1960) or later stages in the formation of the cranio-vertebral joint and urostyle which apparently occur after the completion of metamorphosis. Despite these limitations, however, it is possible to compare the adult vertebral columns of \textit{Leiopelma} and \textit{Ascaphus} with one another and with non-ascaphid anurans as well as a number of features of vertebral development in \textit{Leiopelma} and non-ascaphids.

\textit{Leiopelma} and \textit{Ascaphus} are unique among living anurans in that they retain an uninterrupted notochord and lack synovial joints between the bodies of adjacent vertebrae throughout life (E. M. Stephenson, 1952, 1960; Ritland, 1955). Although some other frogs such as \textit{Rana temporaria} retain these characteristics for some two years after metamorphosis, synovial cavities form during the third year and the notochord is subsequently entirely lost from the ends of the vertebrae (Mookerjee, 1931). In Griffiths' (1963) terminology, the vertebrae of \textit{Leiopelma} and \textit{Ascaphus} are ectochordal in that the fully formed vertebral body is a hollow bony cylinder enclosing the persistent notochord while the vertebrae of \textit{Rana} are holochordal because the notochord is ultimately resorbed so that the body of the vertebra becomes a solid cylinder of bone. The term amphicoelous has also been used to describe the vertebrae of \textit{Ascaphus} and \textit{Leiopelma} but its accuracy has been questioned by E. M. Stephenson (1952, 1960) and Ritland (1955) on the grounds that the vertebrae of these frogs are structurally very different from the notochordal amphicoelous
vertebrae of some other vertebrates. This point as well as the use of the term centrum as applied to anuran vertebrae is discussed in the section on vertebral homologies (Part IV).

In *Leiopelma* the bodies of adult presacral vertebrae consist of the perichordal tube together with the bases of the neural arches which cover its lateral surfaces. Although Ritland (1955) described the laterally situated endochondrally ossified regions of the vertebral bodies in *Ascaphus* as centra, a comparison between his illustrations of the vertebrae in end view with his horizontal sections shows that these ossified regions are the arch bases as in *Leiopelma*. In both genera the notochord is moniliform in shape and its extreme constriction between consecutive vertebrae results from hyperplasia of the perichordal tube in this region to form the intervertebral cartilage. Although the mid-vertebral regions of the notochord appear unconstricted, a comparison between the width of the notochord in the eighth and ninth vertebrae of a tailed froglet of *L. archeyi* three weeks after hatching (Fig. 2:7) and that in a sexually mature specimen (Fig. 2:9) shows that some mid-vertebral constriction occurs as well.

Despite the overall similarity between *Leiopelma* and *Ascaphus* in the internal morphology of their presacral vertebrae, there are also differences between them. The neural arch bases of *Ascaphus* (Ritland, *op. cit.*, Fig. 3, Pl. 1) contain considerably more endochondral bone than those of *Leiopelma* (Fig. 2:9) including *L. hochstetteri* which, according to E. M. Stephenson (1960), has the most heavily ossified skeleton of all three species of *Leiopelma*. The notochord, on the other hand, is more strongly
constricted intervertebrally in *Leiopelma* than in *Ascaphus* and differs histologically in the two genera. In *Leiopelma* the notochord is fibrous only where it is strongly constricted between consecutive vertebrae, the tissue within the unconstricted mid-vertebral portions consisting of vacuolated notochordal cells, but in *Ascaphus* the fibrous cord is continuous throughout the vertebral column, forming a fibrous core through the middle of the vacuolated notochordal tissue in the centre of each vertebra.

Until recently it was generally accepted that the ectochordal centra and continuous notochord in *Ascaphus* and *Leiopelma* are ancestral conditions retained in living forms (Noble, 1924, 1931; E. M. Stephenson, 1952; Griffiths, 1963; Kluge & Farris, 1969). Inger (1967), however, postulated that ectochordal centra have been secondarily derived from the holochordal condition as a result of neoteny. He pointed out the reduced ossification of the skeleton in some species of ascaphids, namely of *Leiopelma* as described by E. M. Stephenson (1960), and considered the holochordal condition to be primitive because most lepospondylous amphibians had holochordal vertebrae. According to Inger, the only evidence for the primitive nature of ectochordy is its appearance as an early ontogenetic state in many frogs.

Contrary to Inger's (1967) contention, the available evidence points to the primitiveness within the Anura of the notochordal state of the vertebrae of *Leiopelma* and *Ascaphus*. The sequence in which organs appear during the ontogeny of an animal does not constitute evidence for the early or late appearance of these organs during the animal's evolutionary history as organs which are known to have arisen relatively late in phylogeny
often appear early in ontogeny and vice versa (de Beer, 1958). The state of the vertebrae of the Lepospondyli is also irrelevant as the Anura are generally considered to have evolved from labyrinthodonts, either independently or together with the Urodela and Apoda (see Romer, 1968). A current view is that all three orders of living amphibians evolved from labyrinthodonts belonging to the Dissorophoidea (Bolt, 1969).

Within the Amphibia as a whole, persistence of an uninterrupted notochord in the adult vertebral column is more primitive than its partial or complete absence because an uninterrupted notochord was inherited by labyrinthodonts from their rhipidistian ancestors (Romer, 1966). In any smaller group within the Amphibia such as the Anura, the presence of an uninterrupted notochord in adult stages may be this original amphibian character-state retained in living forms or it may have arisen secondarily as a result of neoteny, especially as heterochrony appears to be widespread among frogs (E. M. Stephenson, 1960, 1961; N. G. Stephenson, 1965; Jacobson, 1968).

Pre-anuran fossils do not resolve this point because only one extinct amphibian is known which is structurally intermediate between Palaeozoic tailed amphibians and the Anura, namely Triadobatrachus massinoti. Contrary to the opinion of most authors including Piveteau (1937, 1955) and Watson (1940) who considered T. massinoti to have been adult, Griffiths (1956, 1963) claimed that it was an immature animal comparable to living frogs during metamorphosis. There is also uncertainty as to the structure of its vertebrae. According to Piveteau (1937) they are cylindrical, amphicoelous, with a medial constriction, and
separated from one another by a lens of cartilage. Griffiths (1963) re-examined the specimen and described its vertebral column as a chain of bony, spool-shaped centra, pierced by a persistent notochord, and without any evident emargination on either their anterior or posterior borders. The difference between these two descriptions concerns the continuity or otherwise of the notochord throughout the column and the nature of the material between consecutive vertebrae. From Piveteau's (1937, 1955) photographs of the fossil, it is clear that ball and socket joints are not present between consecutive vertebrae and that the ends of the vertebral bodies, particularly those lying between the ilia of the pelvic girdle, contain conical plugs of matrix (see also Hecht, 1962). Whether this matrix has replaced notochordal tissue or cartilage is unknown. From Piveteau's photographs it is impossible to decide whether the vertebrae of *T. massinoti* were solid, holochordal elements joined together by imperforate lenses of intervertebral cartilage or whether they were hollow and ectochordal with the notochord strongly constricted between the vertebrae by the intervertebral cartilage as in *Ascaphus* and *Leiopelma* or unconstricted as in some apodans and urodeles (see Mookerjee, 1930; Hilton, 1948; Lawson, 1966; Wake, 1970).

Even if the structure of the vertebrae of *T. massinoti* could be determined with certainty, its bearing on the vertebral morphology of living frogs is questionable. In the first place, although *T. massinoti* is structurally intermediate in many of its skeletal characteristics between Palaeozoic amphibians and the Anura, it was not necessarily ancestral to the Anura (cf. the
relationship between the Jurassic Ardeosauridae and the Recent Gekkonidae -- Appendix, p. 8). Therefore it cannot be assumed that the various types of vertebrae found in living frogs have necessarily evolved from that found in *Triadobatrachus*. In the second place, if Griffiths' (1956, 1963) contention that *T. massinoti* was an immature animal is correct, it cannot be assumed that the condition of its vertebrae is primitive in the Anura although this may be the case. It is the state of the vertebrae in the adult animal which shows the stage reached by this animal in the evolution of vertebral structure in the group to which the animal belongs. In any case, as the amount of bone in the skeleton of *T. massinoti* is comparable to that in adult anurans rather than metamorphosing stages where the skeleton is still largely cartilaginous (see Parker, 1881), it would appear that *Triadobatrachus* was in fact an adult animal representing an early stage in the evolution of the Anura.

Fossil frogs belonging to the genus *Notobatrachus* from the Jurassic of Patagonia (Reig, 1957) provide some evidence for the primitiveness of notochordal vertebrae in the Anura. According to Reig, the vertebrae of *Notobatrachus* have the same form as those of *Leiopelma* and *Ascaphus*; he described biconcave centra and unossified intercentra (i.e. intervertebral cartilages) while his figures 6 and 7 show the presence of a slender notochordal canal in the ends of the vertebrae. Although it cannot be assumed that *Notobatrachus* was directly ancestral to any group of living frogs, including *Leiopelma* and *Ascaphus* with which some authors consider it to be congeneric (e.g. Griffiths, 1963), the existence of a persistent notochord in its vertebrae and the
absence of ball and socket articulations between them demonstrate that the type of vertebral construction found in *Leiopelma* and *Ascaphus* is not a recently acquired condition but existed in the earliest known members of the Anura.

Although the structure of the vertebrae in adult *Leiopelma* and *Ascaphus* bears a superficial resemblance to that found in immature stages of other living frogs with holochordal vertebrae such as *Bufo melanosticus* and *Rana temporaria*, the differences between them are significant (see also Ritland, 1955). In metamorphosing *B. melanosticus* and *R. temporaria* only 9mm and 12mm respectively in total length the ball and socket joint between the vertebrae has already begun to develop, the notochord consists only of notochordal tissue and is of uniform width in horizontal sections except for the narrow region between the vertebrae where it is constricted by the ring of intervertebral cartilage (Mookerjee, 1931, Pl. 15 Fig. 8, Pl. 16 Fig. 12). In adult *Ascaphus* and *Leiopelma* there is no sign of an incipient joint within the intervertebral cartilage, the constricted portions of the notochord are fibrous and its relatively unconstricted portions occur only in the centres of the vertebrae. Therefore the state of the vertebrae in adult *Ascaphus* and *Leiopelma* is not the same state as that found in juvenile *Bufo* and *Rana* and consequently cannot be considered neotenic compared with the adult condition in the last named genera.

In some families of frogs such as the Australian Leptodactylidae, the procoelous holochordal vertebrae do not develop by the invasion of an arc of connective tissue into the intervertebrae cartilage as in *Bufo* and *Rana* (Mookerjee, 1931) but
by the fusion of a free intervertebral disc to the posterior end of the preceding vertebra (N. G. Stephenson, 1965). Stephenson maintained that within the Leptodactylidae heterochronous changes have been responsible for many of the morphological differences used to distinguish genera and species and that all stages are found in adult leptodactylids from the completely free intervertebral disc condition to the completely fused procoelous state found in Cyclorana australis. A similar range of structure was described by N. G. Stephenson (1965) in other parts of the leptodactylid skeleton. For example, the skull of adult Glauertia russelli is similar in structure to that of juvenile C. australis in that it is largely cartilaginous and the bony elements are small, delicate structures which in many cases are widely separated from one another, whereas the skull of adult C. australis is heavily ossified with extensive surface sculpturing and many elements are broad plates of bone with extensive sutures between them. If adult Leiopelma and Ascaphus were neotenic compared with other frogs such as Rana temporaria in the way that Glauertia russelli is neotenic compared with Cyclorana australis, one would expect this to be evident in their cranial morphology. In fact, the amount of bone in the skull of Leiopelma hochstetteri (E. M. Stephenson, 1951, Fig. 16) and Ascaphus truei (Noble, 1931, Fig. 81) is of approximately the same order as that found in R. temporaria (Marshall, 1951, Figs. 7, 8).

Although it is possible that the presence of an uninterrupted notochord and the absence of ball-and-socket joints in the vertebral columns of Leiopelma and Ascaphus could have resulted from some form of heterochrony other than overall neoteny (see
de Beer, 1958), the similarity between L. archeyi and L. hochstetteri in the states of these characters despite heterochronus changes in other parts of the skeleton (see E. M. Stephenson, 1960) suggests that the internal morphology of the vertebral column of Leiopelma is not affected by heterochrony. Furthermore, although the vertebrae of Ascaphus as illustrated by Ritland (1955) are more heavily ossified than those of Leiopelma, constriction of the notochord is no greater than in Leiopelma.

From the foregoing discussion it is evident that the presence of an uninterrupted notochord and the absence of ball-and-socket joints in the vertebral columns of Leiopelma and Ascaphus are not secondarily derived conditions resulting from neoteny as postulated by Inger (1967) but ancestral conditions which have been retained in living forms and which are therefore primitive character-states within the Anura. Whether the type of vertebra found in these two genera could have been ancestral to all other types of anuran vertebrae, however, remains to be seen. The ontogenetic changes required to derive the type of holochordal vertebrae found in Bufo and Rana (see Mookerjee, 1931) are the invasion of the intervertebral cartilage by an arc of connective tissue to form the ball and socket joints and more extensive ossification to obliterate the notochord within the vertebra. Atrophy of the notochord and ventral portions of the perichordal tube, including the presacral subchordal cartilage in Xenopus (Mookerjee, 1931; Smit, 1953) produces the stegochordal condition (see also Griffiths, 1959b, 1963). From Mookerjee's (1931) account and the present description of vertebral develop-
ment in *Leiopelma* it is clear that the critical stages in ontogeny which determine the adult state of the vertebrae in these frogs occur during or immediately after metamorphosis, even in frogs like *Rana temporaria* which take several more years to complete development. It is not possible to comment here on the possible course of evolution of the holochordal procoelous vertebrae of the Leptodactylidae because, although it is known that the condyles of the vertebrae are formed by the fusion of free intervertebral discs (N. G. Stephenson, 1965), other aspects of the ontogeny of leptodactylid vertebrae are unknown. According to Griffiths (1959b, 1963), the free disc condition in the Megophryinae and some members of the Criniinae is not the developmental precursor of procoelous or opisthocoelous vertebrae but is the end product of a particular type of vertebral development.

Two other aspects of vertebral development and adult structure in *Leiopelma* require further discussion, namely the occurrence of ribs and the construction of the sacrum and urostyle. The presence of ribs in association with the third and fourth vertebrae of *Ascaphus* and *Leiopelma* has long been recognised (Noble, 1931; E. M. Stephenson, 1952, 1960; Ritland, 1955) but the laterally directed processes without sutures borne by other vertebrae are usually described as transverse processes or diapophyses, thus implying that they consist entirely of outgrowths from the neural arches. From the present study it is clear that all these processes including those of the sacral vertebra, whether or not they possess a suture in adult stages, are formed in part from cells originating outside the vertebra and are therefore pleurapophyses (see Cligny, 1899a,b; Hoffstetter, 1939b; Smit,
1953). N. G. Stephenson (1965) pointed out that the terminal cartilaginous epiphyses of the pleurapophyses which are found in leptodactylids as well as many other frogs including *Ascaphus* and *Leiopelma* presumably represent the cartilaginous sternal (i.e. distal) portions of the ribs of other tetrapods.

According to Piveteau (1937), the forked ribs of the third vertebra in *Ascaphus* and *Discoglossus* enclose the anterior lymph hearts. Ritland (1955) disagreed with Piveteau and claimed that the large ribs of the third and fourth vertebrae, either or neither of which may be forked, provide origins for muscles inserting on the scapula and suprascapula of the pectoral girdle. In *Leiopelma* the forked ribs also have muscles attached to them but they are also closely associated from early stages with thin-walled vessels which are usually empty of cellular material but sometimes contain erythrocytes. These vessels are evidently the anterior lymph hearts described by Piveteau (1937) and the occasional presence of erythrocytes in them is explained by the ability of lymph vessels to return extravasated erythrocytes to the blood vascular system (Le Gros Clark, 1965). In early embryos the dorsal components of the pectoral girdle are widely separated from the ribs and lymph hearts but by the third week after hatching, i.e. during metamorphosis, the suprascapular has grown over the ends of the ribs so that each lymph heart is enclosed in a channel whose floor and inner wall are formed by the two rami of the rib and whose roof is the suprascapula (Pl. 7C).

The urostyle of adult anurans represents the proximal region of the postsacral (caudal) axial skeleton after atrophy of the embryonic or larval tail during metamorphosis. Its struc-
ture and development in a variety of frogs have been described by many authors including Ridewood (1897), Gadow (1897), Schauinsland (1906), Mookerjee (1931), Mookerjee and Das (1939), Hodler (1949b), E. M. Stephenson (1952), Smit (1953), Stokely & List (1955), van Dijk (1960) and Griffiths (1963), many of whom have given comprehensive reviews of the previous literature. The main points of disagreement regarding the structure of the urostyle concern the number of vertebral elements contributing to its formation and their relationship with the hypochord. Both these points can be clarified with respect to Leiopelma, bearing in mind that the situation in other frogs, particularly those with stegochordal presacral vertebrae, is not necessarily the same.

In the past there were basically three opinions regarding the construction of the urostyle. It was considered to result from the fusion of as many as twelve vertebrae (Gadow, 1897, 1933; Romer, 1945, 1962, 1966) or from the fusion of three longitudinal, unsegmented strips of cartilage (Noble, 1931; Shumway, 1942). The third school of thought now appears to be correct, that the urostyle of anurans consists in part of an unsegmented rod which lies ventrally to the notochord and which eventually fuses with several anterior post-sacral neural arches (Mookerjee, 1931; MacBride, 1932; Mookerjee & Das, 1939; Smit, 1953; Stokely & List, 1955; Griffiths, 1963).

In developing Leiopelma archeyi the ventral component of the urostyle is a rod of cartilage formed from the ventral part of the postsacral perichordal tube which has increased in thickness due to hyperplasia of the chondrified squamous cells compris-
ing it and their subsequent metaplasia into hyaline cartilage. It occupies the full width of the notochord and, towards the end of metamorphosis, fuses with the bases of the postsacral neural arches and the tracts of cartilage connecting them. The ventral component of the urostyle of *Ascaphus* is formed in the same way, as a rod of cartilage within the perichordial tube (Baton, 1959). In the trunk of *Xenopus laevis* tadpoles there is also a subchordal rod of cartilage which forms from the ventral region of the perichordial tube but it is resorbed together with the notochord during metamorphosis. (Ridewood, 1897; Mookerjee, 1931; Smit, 1953).

The question arising here is whether the subchordal rod of cartilage in the postsacral region of *Leiopelma* and *Ascaphus* should be described as a hypochord. According to Mookerjee (1931), the rod of cartilage in the trunk of *Xenopus* is not homologous with the hypochord in the tail because the latter is not part of the perichordial tube but a separate structure fused to its ventral surface. A separate hypochord has been described in a number of other anurans and, according to Mookerjee & Das (1939), its relationship with the perichordial tube varies in different species. In *Rana afghana*, *Microhyla rubra*, *Rhacophorus maculatus* and *Xenopus laevis* there lies between the membranous ventral portion of the perichordial tube and the cartilaginous hypochord a continuous band of hyaline cartilage which subsequently degenerates together with the notochord when the hypochord fuses with the postsacral neural arches and the dorsal region of the perichordial tube to form the urostyle. According to Mookerjee & Das (op. cit.), the band of hyaline cartilage is absent in other anurans such as *Bominaeom igneus* so that the hypochord rests directly on the
membranous perichordal tube while in others again such as *Rana temporaria* and *Bufo melanosticus* the entire perichordal tube in the region of the urostyle chondrifies but remains distinct from the hypochord even when subsequent ossification of the urostyle is well advanced (Mookerjee, 1931, Pl. 15 Fig. 10; Mookerjee & Das, 1939, Fig. 12B). The separate identity of the hypochord in the pelobatid, *Megophrys major*, is particularly clear because metamorphosing stages of this frog have approximately 17 ossified caudal vertebrae of which the most anterior four are attached to the dorsal surface of the cartilaginous hypochord (Griffiths, 1956, 1963).

Although the separate identity of the hypochord is usually established from its manner of origin during ontogeny, this seems to be as variable as the later relationship of the hypochord with the overlying perichordal tube. From the works of Mookerjee (1931) and Smit (1953) it appears that the hypochord of *Rana temporaria*, *Bufo melanosticus*, *Bombinator igneus* and *Xenopus laevis* originates as a longitudinal condensation in the subvertebral mesenchyme which subsequently chondrifies. Stokely & List (1955) described the hypochord in *Pseudacris nigrita* during metamorphosis as an ossified rod-like process but concluded that the exact origin of the hypochord during ontogeny has yet to be determined. Griffiths (1963) described the hypochord of *Megophrys major* as a posterior, ventral outgrowth of the first postsacral intervertebral body and implied that it arises in this manner in all anurans. Despite this diversity of opinion and the diversity it suggests regarding the origin of the hypochord in different members of the Anura, it would appear that the separate hypochord in many species has
no counterpart in Leiopelma and Ascaphus whose subchordal rod of cartilage is part of the perichordal tube. Nevertheless the subchordal rod of Leiopelma and Ascaphus may be considered homologous with the hypochord of other anurans since they are both rods of cartilage which lie ventrally to the postsacral notochord and constitute the ventral component of the urostyle. According to Szarski (1962) organs which have the same structure and the same location in relation to neighbouring organs are homologous although they may develop in very different ways.

The number of postsacral vertebral segments involved in the formation of the urostyle has also been debated, largely because discrete caudal vertebrae are rarely found in anurans. To date, Megophrys major described by Griffiths (1956, 1963) appears to be the only exception in that metamorphosing stages have approximately seventeen ossified caudal vertebrae of which the first four contribute to the urostyle. In embryonic and recently hatched Leiopelma archeyi there are usually fourteen pairs of neurapophyses in all, less often fifteen. As the tenth pair is usually sacral and the specimens with fifteen pairs had the eleventh vertebra modified to support the pelvic girdle, it would appear that four pairs of postsacral neurapophyses are normally present during developmental stages. In the adult specimen of L. archeyi examined, only three pairs of postsacral neurapophyses were present, which suggests that the tiny fourth pair belonging to the fourteenth vertebra had been indistinguishably incorporated into the urostyle. According to E. M. Stephenson (1952) no more than three postsacral vertebrae are normally found in developing L. hochstetteri while her illustration of a
common condition of the anterior urostyle of adults (op. cit., Fig. 2) shows only two postsacral arches. Three pairs of post-sacral neurapophyses were present in the adult *L. hochstetteri* examined here but this specimen was atypical in possessing a free postsacral vertebra. In these circumstances it would appear that *L. archeyi* normally has one more neural arch on the anterior end of the urostyle than *L. hochstetteri* and that in both species the most posterior arch is indistinguishable in adults.

In view of the small size of the most posterior pair of neurapophyses, the number of arches recognisable during developmental stages of *Leiopelma* may not represent the total number of vertebral segments incorporated into the urostyle. The total number of segments can be determined, however, from the relationship between the subchordal rod of hyaline cartilage and the spinal nerves. In late intracapsular and hatching stages of *L. archeyi* the anterior and posterior limits of the rod are ill-defined but, by three weeks after hatching, at a stage comparable to late metamorphosis in other frogs, it terminates abruptly just behind the vent. As the specimen at this stage examined here had a total of fourteen neural arches, the tenth of which was sacral, and the subchordal rod began immediately behind the sacral vertebra and terminated in the region of the sixteenth pair of spinal nerves, it is evident that the most anterior five postsacral vertebrae formed the urostyle and that the fifth of them lacked a neural arch. The dorsal components of this vertebra are the posterior extensions of the tracts of cartilage situated dorso-laterally to the notochord and connecting the bases of the more
anterior postsacral arches. Whether the urostyle of *L. hochstetteri* also comprises five vertebrae could not be determined from the material available.

According to van Dijk (1960), the eleventh, twelfth, thirteenth and possibly the anterior half of the fourteenth vertebra contribute to the formation of the urostyle in *Ascaphus*. Van Dijk based this conclusion on the relationships of the coccygeal lymph hearts and the origin on the urostyle of the *pyriformis* muscle in an adult specimen and a larva with well developed hind limbs. He also claimed that Ritland's (1955) identification of a thirteenth spinal nerve in *Ascaphus* suggests the participation of the eleventh, twelfth and thirteenth vertebrae in its urostyle. From this investigation of *Leiopelma* it is seen that the number of spinal nerves associated with the anterior end of the urostyle in fully metamorphosed frogs can show the minimum number of vertebrae present but gives no indication of the total number involved. In embryonic *L. archeyi* the spinal cord and its associated nerves are present throughout the tail but in adults all but the most anterior three postsacral nerves have been resorbed and the spinal cord posterior to the last of the persistent nerves, i.e. the thirteenth, is reduced to a slender ependymal tube extending along the dorsal surface of the urostyle to its posterior extremity. As each spinal nerve lies anterior to the vertebra of the same number, the presence of the thirteenth spinal nerve in adult *L. archeyi* gives no indication that the fourteenth and fifteenth vertebrae are present in the urostyle.

Van Dijk (1960) commented on the extreme elongation of the urostyle in *Ascaphus* behind the thirteenth spinal nerve and con-
cluded that the thirteenth vertebra extends almost as far as the position at which the fifteenth should lie due to posterior movement of both the ischiopubic region of the pelvic girdle and the posterior end of the urostyle relative to the sacrum. Similar elongation of the urostyle also occurs in *Leiopelma archeyi* but in this case it applies to the fifteenth vertebra. In the specimen three weeks after hatching which was sectioned transversely at 10µ, it was calculated that all five urostylar vertebrae were the same length, i.e. 0.27mm. It was also calculated that the presacral column in this specimen measured 2.62mm and was therefore almost twice as long as the urostyle. As the urostyle of the adult *L. archeyi* sectioned horizontally was the same length as the presacral column, i.e. 6.8mm, it is clear that the urostyle has not only increased in length by almost 5.5mm to become five times its original length but has also grown much more rapidly than the presacral column. As the proportions of the anterior end of the urostyle in postmetamorphic *Leiopelma* do not seem to alter with age (see E. M. Stephenson, 1960, Fig. 3), most of the elongation of the urostyle takes place at its posterior end in the region of the fifteenth vertebra. Moreover, the presence of cartilage at the posterior end of the urostyle of adult *Leiopelma* shows that its growth may continue after sexual maturity.

According to van Dijk (1960), the backward migration of the end of the urostyle and the ischiopubic region of the pelvic girdle rather than a forward migration of the sacro-iliac articulation accounts for much of the forward slope of the ilia in *Ascaphus* and therefore a primitively vertical pelvic girdle would
have articulated with a sacrum not more than two vertebrae further back than at present. From the ontogenetic development of the pelvis and sacrum in Leiopelma, it is clear that backward migration of the posterior parts of the pelvis and urostyle in postmetamorphic stages accounts for the disproportionately long pelvic girdle in adult frogs compared with non-anuran amphibians, living and extinct (see Smith, 1927; Hilton, 1945-47; Wake, 1963; Romer, 1966), but plays no part in determining the position of the sacrum. This is determined during metamorphosis, before the posterior end of the urostyle is clearly defined, by the growth of the ilia towards the vertebral column, the sacral vertebra being the one whose pleurapophyses are induced to enlarge by the proximity of the anterior ends of the ilia (see also Ridewood, 1897). The growth of the ilia in an antero-dorsal direction is demonstrated by the movement of their anterior extremities from a position below and behind the pleurapophyses of the eleventh vertebra in hatching stages (Fig. 2:3) to a position slightly above and in front of the pleurapophyses of the ninth vertebra three weeks after hatching, the tenth vertebra by this stage having become the sacrum (Fig. 2:7). As the acetabula are situated ventrally to the thirteenth vertebra in both these stages, the posterior migration of the ischiopubic region characteristic of later stages has not yet begun, so that the increase so far in the length of the ilia is due entirely to the growth of their anterior ends in an antero-dorsal direction.

Slight changes in the rate and direction of growth of the ilia and of the more posterior pleurapophyses of the vertebral column during this period could account to a large extent for
the different positions of the sacrum in anurans and the different numbers of vertebrae comprising it. Another factor which may alter the position of the sacrum is a shift of the entire pelvic girdle anteriorly or posteriorly along the body as indicated by the position of the acetabulum during early metamorphosis. Developmental changes of this nature can not only explain the variability of the presacral and sacral regions within species (see Ridewood, 1897) but can also account for the different numbers of presacral and sacral vertebrae which are typical of different species and which vary between the nine presacrals and one sacral normally found in *Ascaphus* and *Leiopelma* (E. M. Stephenson, 1952; Ritland, 1955) to the six presacrals and three sacrals of the brachycephalid *Oreophrynella quelchii* (Noble, 1931). Although occasional specimens of *Leiopelma, Ascaphus* and some other frogs such as *Xenopus* have one more than the number of presacral vertebrae typical of the species concerned (Hodler, 1949b; E. M. Stephenson, 1952; Ritland, 1955), it is generally agreed that the overall evolutionary trend in the Anura is towards further shortening of the presacral column as a result of forward migration of the sacroiliac articulation (Gadow, 1901; Green, 1931; Ramaswami, 1933; Ritland, 1955).

Although anterior migration of the sacro-iliac articulation in the Anura can result from an anterior shift in the position of the pelvic girdle and/or anterior growth of the ilia, it is apparent that only the first of these alternatives could have led to reduction of the presacral column in the ancestors of the Anura. Among the Palaeozoic rhachitomous labyrinthodonts belonging to the Dissorophoidea, which are currently considered to contain the ancestors of the three living amphibian orders (Bolt, 1969), the
number of presacral vertebrae varied between eighteen and twenty-six and the pelvic girdle had the robust, plate-like construction and the vertical ilium characteristic of early amphibians (Watson, 1940; Gregory, 1950; Carroll, 1964; Bolt, 1969). As relative changes in the rate of elongation of a vertical ilium would not alter its position on the vertebral column, variation in the number of presacral vertebrae in the Dissorophoidea must have resulted from shifts in the position of the entire girdle. The pelvic girdle of the Triassic pro-anuran Triadobatrachus massinoti is structurally intermediate between those of the Dissorophoidea and the Anura in that approximately six caudal vertebrae are present instead of a urostyle, the acetabula lie below the eighteenth vertebra, the fifteenth and possibly the sixteenth vertebrae are sacral and the ilia, although directed anteriorly, are shorter and stouter than those of adult frogs (see Piveteau, 1937; Hecht, 1962). Although it is not certain whether T. massinoti was a sexually mature adult or a metamorphosing juvenile (see p. 22), it is evident from the relative positions of the sacral ribs, the anterior ends of the ilia, the caudal vertebrae and the acetabula that posterior migration of the ischio-pubic region has not taken place and that the position of the sacrum has been determined little if at all by anterior growth of the ilia.

The sacral vertebra of living anurans varies considerably in external form, not only in the nature of its articulations with the presacral vertebra and the urostyle (see Griffiths, 1963) but also in the shape of its pleurapophyses which may be of almost uniform width throughout their length as in Rana (Noble, 1931; Ramaswami, 1933), or slightly expanded as in Leiopelma and Ascaphus
(E. M. Stephenson, 1952, 1960; Ritland, 1955) or broadly expanded distally as in other anurans including Scaphiopus and Xenopus (Noble, 1931). According to E. M. Stephenson (1952, 1960) the sacral vertebra of Leiopelma appears to be unique in the Anura because the bony neural arches are joined together dorsally and ventrally by cartilage and the vertebra as a whole is narrower from front to back than the presacral vertebrae. The sacral vertebra of Ascaphus as described by Ritland (1955) is fully ossified and of normal size comparable to that of Discoglossus. In horizontal section the sacral vertebra of Ascaphus (Ritland, 1955, Fig. 3A) resembles the presacral vertebrae in that the mesial surfaces of the neural arch bases lie close to the surface of the unconstricted notochord, whereas horizontal sections of Leiopelma (Fig. 2:9) show the arch bases to be widely separated from the surface of the notochord which has become greatly constricted by hyperplasia of the perichordal tube within the vertebra. Whether the marked difference seen here between the sacral vertebrae of L. archeyi and L. hochstetteri is of normal occurrence could not be determined from the material available but, of these two specimens, the sacral vertebra of L. archeyi more closely resembles the presacral vertebrae in the size of the arch bases and their relationship to the perichordal tube than does the sacral vertebra of L. hochstetteri.

From E. M. Stephenson's (1952, 1960) descriptions and illustrations of the sacral vertebra in Leiopelma, its failure to fuse ventrally appears to be due to the absence of a centre of ossification between the arch bases like those of the more anterior vertebrae. However, the atlas also lacks a mid-ventral centre of ossification (E. M. Stephenson, 1960, Fig. 3), yet this vertebra
becomes enclosed in bone in later stages, apparently due to ventral growth and subsequent fusion of the bone of the neural arches. As the sacral vertebra fails to ossify dorsally and ventrally even in comparatively aged specimens in which the mid-dorsal cartilage has calcified (E. M. Stephenson, 1960), it would appear that the persistence of cartilage mid-dorsally and mid-ventrally in this vertebra has not resulted simply from delayed development of the vertebra but has instead been selected for because of its functional significance. It probably serves as a shock-absorber to reduce jarring of the axial skeleton during salterial locomotion, especially as the ligamentous connection between the ilia and the sacral pleurapophyses appears to be a firm one (E. M. Stephenson, 1952). According to Ridewood (1897), a close connection between the ilia and sacrum such as that found in "the frog" (presumably Rana sp.) is rare in anurans, the majority of which have considerable mobility of the ilia relative to the sacrum, especially those genera with broadly expanded sacral pleurapophyses. In terrestrial anurans, mobile sacro-iliac articulations would act as shock-absorbers but in some aquatic forms such as Pipa and Xenopus the extreme mobility of these joints is an adaptation to allow rapid elongation of the body to dilate the pharynx for the rapid engulfment of food (Willem, 1939).

The final point to be made here is that the vertebral morphology of Ascaphus and Leiopelma is not indicative of close relationship between them. Although the persistence of a continuous notochord in adult stages and the absence of synovial joints between the bodies of consecutive vertebrae are character-states found only in these two genera of anurans, they have been shown
already to be character-states inherited from the ancestors of the Anura and could therefore have persisted independently in distantly related genera. Although the moniliform configuration of the notochord is similar in *Ascaphus* and *Leiopelma*, it results from greater constriction between vertebrae than within them due to centripetal growth of the intervertebral cartilage, and centripetal growth of the intervertebral cartilage also occurs in other anurans which acquire synovial intervertebral joints such as *Rana temporaria* (Mookerjee, 1931). Other vertebral characteristics, on the other hand, such as the continuous fibrous core of the notochord in *Ascaphus* (see Ritland, 1955) and the structure of the sacral vertebra in *Leiopelma* (p. 75; E. M. Stephenson, 1952, 1960), as well as other differences between the two genera reported by Noble (1931), E. M. Stephenson (1951), N. G. Stephenson (1951b) and Stephenson, Robinson & Stephenson (in preparation), strongly suggest that *Ascaphus* and *Leiopelma* are not sufficiently closely related to be placed in the same family. In view of the number of character-states shared by *Ascaphus* and *Leiopelma* which appear to be primitive states in anurans generally (Noble, 1931; de Villiers, 1934a, b; Pusey, 1943; E. M. & N. G. Stephenson, 1947; N. G. Stephenson, 1951b; Szarski, 1951; E. M. Stephenson, 1952, 1955, 1960; Ritland, 1955; Griffiths, 1963), it would appear that these two genera are both relics of ancient but otherwise independent groups within the Anura.
PART III — THE VERTEBRAL COLUMN OF THE GEKKOTA

INTRODUCTION

GENERAL

In addition to the comparative works of Cope (1892), Camp (1923) and Hoffstetter & Gasc (1969), papers which describe the vertebrae of geckos include those of Calori (1861), Ficalbi (1883), Siebenrock (1893), Gadow (1897), Noble (1921), Mahendra (1950), Underwood (1954), El-Toubi & Khalil (1955), N. G. & E. M. Stephenson (1956), Ganguly & Mitra (1958), Kluge (1962b, 1967a), Hoffstetter (1946b, 1964) and Werner (1961, 1965, 1967, 1971). The vertebral column of pygopods has been described by Stokely (1947), Parker (1956b) and Underwood (1957a).

The Gekkonidae are unique among the Lacertilia in that both amphicoelous and procoelous genera occur within this one family. Amphicoely is by far the more common condition but intercentra are typically present throughout the vertebral column in both amphicoelous and procoelous forms. It has long been considered, by Boulenger (1885), Camp (1923) and others, that the Gekkonidae include the most primitive of living lizards because of their vertebral structure. Romer (1956) considered that the Nyctisauria (Gekkonidae and Pygopodidae) vie with the Iguania (Iguanidae, Agamidae and Chamaeleontidae) for position as the most primitive of living lizards but, following Underwood's (1954) contention that amphicoely in geckos is secondary, placed the Iguania first in his scheme of classification.
Cope (1900) appears to have been the first to regard amphicoely in geckos as a degenerate condition but gave no reasons for this belief. Underwood's (1954) conclusion that amphicoely is secondary followed from his classification of geckos largely on ophthalmological characters, but he later (1955) rescinded this conclusion because of the amphicoely of Triassic squamates. Kluge (1967a) criticised Underwood's change of opinion, pointing out that the Triassic Squamata were not true lizards, and used the procoely of the Upper Jurassic Ardeosauridae as evidence for the primitiveness of procoely among the Gekkonidae. Hoffstetter & Gasc (1969) strongly opposed Kluge's view on several grounds: Bavarisaurus, contemporary with the Ardeosauridae and probably a gekkonid, was amphicoelous; Gonatodes, the most primitive member of the predominantly procoelous sphaerodactyline geckos, is amphicoelous; the similarity between the vertebrae of Sphenodon and those of amphicoelous geckos is too striking to suggest a secondary origin for gekkonid amphicoely. Hoffstetter & Gasc also maintained that, if procoely were the primitive condition in lizards, all procoelous vertebrae would be of a single type.

In addition to the configuration of the central articulation, several other characters of gekkonid vertebrae are generally accepted as primitive. The centra are short and broad (Camp, 1923); the atlantal neurapophyses are frequently unfused (Mahendra, 1950; Underwood, 1955); there are paired foramina containing blood vessels in the vertebral centrum (Camp, 1923; Mahendra, 1950); in some geckos the dorsal ligament attaching each rib to the neural arch has been described as fibrocartilaginous, cartilaginous
or even ossified, and has therefore been considered to represent a reduced tuberculum (Noble, 1921; N. G. & E. M. Stephenson, 1956).

Some of these characters are shared by the Pygopodidae which are now recognised as the closest living relatives of the geckos. However, the internal structure of their procoelous vertebrae has never been described, and the external morphology of their vertebrae has been described only in the more common genera (Stokely, 1947; Parker, 1956b; Underwood, 1957a). In view of the morphological specialization of pygopods in association with their limbless habit, some vertebral characters will undoubtedly have evolved in association with this habit. Others, if shared only by geckos, would provide additional evidence of relationship and may help to resolve the problem as to whether amphicoely or procoely is the primitive vertebral state in living lizards.

The Xantusiidae have been described by Camp (1923, Hoffstetter 1962) and others as very similar to procoelous geckos in the structure of their vertebrae and have recently been included by Hoffstetter (1962) and Savage (1963) within the Gekkota. However, the xantusiid vertebral column has never been described in detail. Although only one specimen from this North American family was available to me for the present study, an adult specimen of *Xantusia vigilis*, and therefore no conclusions can be drawn regarding the family as a whole, a description of its vertebral morphology compared with that of geckos and pygopods could give some indication of its affinity or otherwise with the Gekkota.
HISTORY OF CLASSIFICATION OF THE GEKKOTA

In recent years four families of living lizards have been placed with the Gekkonidae in the Infra-order Gekkota, namely the Pygopodidae, Xantusiidae, Dibamidae and Anelytropsidae. As it is doubtful whether the last three families are as closely related to the Gekkonidae as the Pygopodidae appear to be, it is necessary to review the evidence for grouping any of these families with geckos in the Gekkota.

The family Gekkonidae used to be considered by Boulenger (1885), Noble (1921) and others to contain only those lizards with notochordal amphicoelous vertebrae. The only amphicoelous lizard not included in the Gekkonidae was the Madagascan genus *Uroplatus* Duméril, 1805, (= *Uroplates* Gray, 1825) for which Boulenger (1884) erected the family Uroplatidae on the basis of its slender clavicle, minute interclavicle and fused nasal bones. According to Smith (1933), Loveridge (1947) and Romer (1956), however, the supposedly distinctive features of *Uroplatus* are found in other geckos and this genus should therefore be included in the Gekkonidae. Kluge (1967a) also placed *Uroplatus* in the Gekkonidae, in his subfamily Gekkoninae.

The possession of procoelous vertebrae has been the main criterion, apart from the presence of eyelids, for regarding the Bublepharidae as a separate family from all other geckos. Boulenger (1883) erected the family for those geckos with eyelids, procoelous vertebrae and a single parietal bone in the skull and in 1885 placed within it the following genera: *Psilodactylus* Gray,
1864 (given the nom. nov. Hemitheconyx by Stejneger, 1893, due to homonymy -- see Wermuth, 1965), Eublepharis Gray, 1827 and Coleonyx Gray, 1845. He made no comment on the vertebrae of Sphaerodactylus Wagler, 1830 and included this genus in the Gekkonidae. Noble (1921) described the procoelous vertebrae of Sphaerodactylus as agreeing in detail with those of the eublepharids Lepidoblepharis and Lathrogecko, and but slightly different from those of Coleonyx and proposed that Sphaerodactylus should be withdrawn from the Gekkonidae and grouped instead with Coleonyx in the Eublepharidae. According to Noble (op. cit.), a morphogenetic sequence exists from amphicoelous Gonatodes through Lathrogecko and Lepidoblepharis to Sphaerodactylus, these four Central American genera being more closely related to one another than to Coleonyx or to other geckos. He pointed out that procoely had probably arisen in this series independently from similar changes in other series, yet suggested that in all probability the Eublepharidae had a polyphyletic origin and, instead of being a very ancient group as hitherto believed, they may be a very recent assemblage. Parker (1926), referring to these Central American forms as "Eublepharids", clearly doubted the validity of their inclusion in this family, but agreed that these genera form a natural group. (The genus Lathrogecko Ruthven, 1916, is no longer valid, having been synonymised by Parker (op. cit.) with Lepidoblepharis Peracca, 1897.) Camp (1923) included Coleonyx as well as Sphaerodactylus and its allies among the Gekkonidae, made no mention of the Eublepharidae as a separate family, and considered that the transition from amphicoely to procoely involves little morphological change. Underwood (1954), however, continued to regard the Euble-
pharidae as a separate family containing Coleonyx, Bublepharis, Hemitheconyx, Aelurosscalabotes Boulenger, 1885, and Holodactylus Boettger, 1893, all of which have procoelous vertebrae, true eyelids, and united parietales. He erected a new family, the Sphaerodactylidae, for those geckos with procoelous vertebrae but possessing paired parietales and a spectacle over the eye like amphicoelous geckos. Romer (1956) proposed that all geckos should be included in the Gekkonidae because the supposedly distinctive procoelous forms appear to include two distinct groups of genera, typified by Bublepharis and Sphaerodactylus respectively.

The present position is that all living geckos are placed in the Family Gekkonidae which is divided into four subfamilies, the Bublepharinae, Diplodactylinae, Gekkoninae and Sphaerodactylinae. These subfamilies were erected by Kluge (1967a) on the basis of 18 characters, 13 of them skeletal, which were coded into two or more character-states and weighted according to whether they were primitive or advanced in order to delimit natural assemblages of genera. Kluge concluded that his subfamilies are natural assemblages since they are consistent with current zoo-geographical concepts.

According to Kluge (op. cit.), these four subfamilies each have a characteristic geographical range. The Bublepharinae are distributed circumglobally but discontinuously, all five genera being widely separated from one another. The Diplodactylinae are restricted to Australia, New Zealand and neighbouring small islands. The Sphaerodactylinae are found only in Central America, northern South America and the islands of the Caribbean whereas the Gekkonii-
nae occur on continents and islands throughout the world, the 50° latitude being the approximate limit of their north-south range.

The Pygopodidae are a small family of legless lizards consisting at present of only six recognised genera: *Aprasia* Gray, 1839, *Delma* Gray, 1831, *Lialis* Gray, 1835, *Ophidiocephalus* Lucas & Frost, 1897, *Pletholax* Cope, 1864 and *Pygopus* Merrem, 1820. *Pygopus lepidopodus* was the first pygopod to be described (as *Bipes lepidopodus* Lacêpède, 1804) and was usually classified by early authorities together with other elongated lizards with reduced limbs (see Lynn & Komorowski, 1957). The Family Pygopodidae was erected by Gray (1845) for *Pygopus* and *Delma*, *Aprasia* and *Lialis* being placed in separate families, the Aprasiidae and Lialisidae respectively. Most later authors, however, including Cope (1900), Kinghorn (1923, 1926) & Underwood (1957a & b), recognise only one family, the Pygopodidae.

This family is restricted in its distribution to the Australian region. *Pygopus* and *Delma* are widely distributed over the Australian mainland and *P. lepidopodus* is found in Tasmania as well (Kinghorn, 1926). *Lialis burtonis* is widely distributed in New Guinea, the islands of Torres Straits, Australia and Tasmania, whereas *L. jicari* is restricted to New Guinea and some of the neighbouring islands (Kinghorn, 1924, 1926). *Aprasia* is restricted to South and West Australia, *Pletholax* to south-western Australia and *Ophidiocephalus* Lucas and Frost, 1897 is known only from one specimen, the holotype of *O. taeniatus* from Charlotte Waters in Central Australia.

Opinion has differed greatly in the past over the affinities
of the Pygopodidae with other lizards. Cope (1864) included Pygopus and Lialis in his tribe Leptoglossa along with the Teiidae, Lacertidae and Scincidae on the basis of their simple premaxillary but doubted the relationships of Aprasia because of its apparent similarity to Anniella. Boulenger (1884, 1885) considered that the Pygopodidae resemble scincs only in superficial appearance and are most similar to geckos in the structure of the skull, and placed them immediately after the geckos in his (1885) scheme of classification. In 1900, Cope relocated the Pygopodidae with the Zonuridae, Anguidae and Xenosauridae in the Superfamily Diploglossa, a "somewhat heterogeneous" assemblage occupying a position between the Pachyglossa (Agamidae and Iguanidae) and the Leptoglossa (Teiidae, Xantusiidae, Lacertidae, Gerrhosauridae, Scincidae, Acontiidae, Dibamidae and Anelytropidae), having the papillose tongue and proximally simple clavicle of the former and the cruciform interclavicle and distinctive petrous bone of the latter. Camp (1923) based his classification of lizards largely on osteological and muscular characteristics and separated them into two divisions, the Autarchoglossa and the Ascalabota, in which the rectus superficialis muscle is present or predominantly absent respectively. Thus the geckos which lack this muscle and the pygopods which possess it were widely separated in Camp's scheme of classification. According to Camp, the M. rectus superficialis is essential in the locomotion of limbless lizards and the evolution of forms possessing the muscle from stocks which have lost it would be impossible. Underwood (1957a) pointed out, however, that the rectus superficialis may be present or absent even in different genera of a single family, namely the Agamidae, that its loss is almost certainly secondary, and suggested that geckos
and pygopods arose from a stock of terrestrial lizards which possessed _rectus superficialis_ muscles. Kluge (1967a) discounted the importance of these muscles in the determination of saurian relationships, not only because of their peculiar distribution among modern groups of lizards, but also because of their developmental plasticity as described by Maurer (1896, 1898).

Hebard & Charipper (1955a & b) considered that the distribution of the adrenal cortical cells and their nuclei in _Pygopus_ and _Lialis_ is very similar to that in geckos and unlike that in anguids, but found a similar pattern of these cells in the scincomorphan families Dibamidae, Xantusiidae and Scincidae as well as in the Gekkonidae and Pygopodidae. According to Gabe (1970), the position of the nuclei in the interrenal cells (i.e. the adrenal cortical cells) is so variable that it cannot be used as a distinguishing characteristic. Thyroid morphology does not appear to have any obvious bearing on gecko-pygopod relationships either, as it varies to some extent in different pygopods (Lynn & Komorowski, 1957; Lynn, 1967) and resembles only one gecko, _Uroplatus_, of the 57 genera Lynn examined.

With respect to some other morphological characteristics, however, modern opinion favours Boulenger's (1885) conclusions that the Pygopodidae are more closely related to the Gekkonidae than to any other group of living lizards. According to Shute & Bellairs (1953), the extreme development of the lip of the cochlear limbus described by them is found only in geckos and pygopods, while Miller (1966a) described the cochlear ducts of pygopods and geckos as remarkably similar to one another and unrelated to those of any other group. Baird (1970) also pointed out that, except for
Aprasia which shows a high degree of fossorial adaptation in its aural anatomy, the structure of the internal ear in geckos and pygopods is essentially the same. McDowell & Bogert (1954) described the similarity in scalation, post-cloacal sacs and bones, eyes, tongues and skulls and maintained that the most definite indications of gecko-pygopod affinity are to be seen in the braincase. These authors also maintained that the procoelous vertebrae of pygopods are similar to those of procoelous geckos and most unlike those of anguinomorphs.

Romer (1956) accepted the close relationship of the Pygopodidae with the Gekkonidae to the extent that he placed only these two families in his infraorder Nyctisauria (= Gekkota) of the suborder Lacertilia. Underwood (1957a) assessed more than 40 examples of morphological similarity between geckos and pygopods and placed them together in his infraorder Gekkota. N. G. Stephenson (1961), unlike most other authors, was able to examine a range of juvenile and adult specimens of the four more common genera of pygopods, namely Pygopus, Delma, Lialis and Aprasia, as well as an adult of the rare genus Pletholax and confirmed that their hyobranchial apparatus and skulls are gecko-like in general form and in the elements present.

Underwood (1957b) considered from preliminary observations that Dibamus is probably related to geckos and pygopods and, in another paper (1957a) tentatively included the limbless Dibamidae and Anelytropsidae with the Pygopodidae in his superfamily Pygopodoidea. Hoffstetter (1962) questioned the inclusion of the Anelytropsidae as these lizards have osteoderms (see Camp, 1923) which are characteristic of the Scincomorpha rather than the
Gekkota. Miller (1966a, b & c) considered the anatomy of the probably degenerate cochlear duct in *Dibamus* and *Anelytropsis* to be so similar that these genera probably belong to the same family but their relationship to other groups of lizards cannot be established from cochlear duct anatomy alone. These genera also resemble one another closely in the structure of their caudal vertebrae (Etheridge, 1967) which are most like the caudal vertebrae of scincs. Gasc (1968) investigated the osteology and myology of *Dibamus* and concluded that, although the Dibamidae resemble the Gekkota in possessing several archaic characteristics, they are extremely distinctive squamates of ancient origin. Gasc emphasised this by erecting for them a new suborder Dibamia.

The Xantusiidae are a small family of secretive lizards with a disjunct distribution in Central America and the Western United States (Savage, 1963). Camp (1923) considered this family to be characterised by procoelous vertebrae with extremely small gekkonid condyles, squarish centra, and tiny persistent intercentra fused with the condylar balls, almost exactly as in the procoelous gecko *Coleonyx* but that the family cannot be placed among the Gekkota as their musculature, ventral squamation and tongue are autarchoglossid in nature. Camp maintained, however, that they appear to be the most primitive group in the Autarchoglossa as the third branchial arch is nearly complete and a free intermedium is present in the carpus. Other more recent authors including Malan (1946), McDowell & Bogert (1954) and Saint Girons (1970) have noted similarities between the Xantusiidae and the Gekkota, not all of which exist (see Bellairs & Boyd, 1950; Underwood, 1957b; Savage, 1963). Although Hoffstetter (1962) and
Savage (1963) included the Xantusiidae with geckos and pygopods in the infraorder Gekkota, other authors such as Miller (1966a) and Baird (1970) on the basis of inner ear morphology and Etheridge (1967) on the basis of the structure of the caudal vertebrae considered the affinities of the Xantusiidae to lie more with scincomorphans than gekkotans. As Hoffstetter's (1962) grounds for transferring the Xantusiidae to the Gekkota from the Scincomorpha with which they are classified at present (Romer, 1956; Bellairs, 1969) included similarity of vertebral structure, it is necessary to consider the extent of this similarity and its significance with respect to xantusiid relationships (see Appendix).
CLARIFICATION OF NOMENCLATURE

To avoid confusion regarding the identity of the lizards used in this study, it is necessary to clarify the nomenclature used for several genera.

The status of various geckos has been reviewed during the last ten years but not all of the proposed changes have been widely accepted. Chrapliwy, Smith & Grant (1961) reviewed in detail the taxonomic history of Gehyra Gray, 1834, and Peropus Wiegmann, 1835, and concluded on the basis of their digital lamellae that they are both valid genera, the former containing three species: G. australis Gray, 1845, G. marginata Boulenger, 1887 and G. oceanica (Lesson), 1830, and the latter containing ten species including Peropus variegatus (Duméril & Bibron), 1836. Wermuth (1965), however, recognised both oceanica and variegatus as belonging to the genus Gehyra. Mitchell (1965b) rejected Chrapliwy, Smith & Grant's proposed separation of Gehyra and Peropus but considered on osteological grounds that oceanica and australis are part of an Indo-Australian species group derived independently of other Australian geckos currently referred to Gehyra. Mitchell retained Gehyra (sensu stricto) for the Indo-Australian forms and suggested that the endemic Australian species belong in the genus Dactyloperus Fitzinger, 1843, but deferred final decision pending the examination of additional Indo-Australian species.

The names Heteronota Gray, 1845, and Lucasius Kinghorn, 1929, were changed by Wermuth (1965) to Heteronotia nom. nov. and Lucasium nom. nov. because of preoccupation. Kluge (1967b) transferred Lucasium damaeum (Lucas & Frost), 1896, to the genus
Diplodactylus Gray, 1832, but regarded the species as a very distinct member of the stenodactylus group within this genus. Gonatodes fuscus (Hallowell), 1855, was reduced by Vanzolini (1968a) to a subspecies of G. albogularis (Duméril & Bibron), 1836. According to Wermuth (1965), Phyllodactylus Güntheri Boulenger, 1885, is a synonym of P. marmoratus (Gray), 1844, but Kluge (1967a) considered it to be a separate species. Wermuth also regarded Coleonyx brevis Gray, 1845, as a subspecies of C. variegatus (Baird), 1858, but Kluge (1962b, 1967a) recognised both these species as valid. Chrapliwy, Smith & Grant's (1961) proposal that the generic names of the New Zealand geckos Hoplodactylus Fitzinger, 1843, and Naultinus Gray, 1842, should be changed to Naultinus Gray, 1842, and Naultinulus nom. nov. respectively was strongly opposed on several grounds including priority by Myers (1961) and subsequent authors such as Wermuth (1965) and Kluge (1967a,b) have retained the older names as clarified by Smith (1933). Cogger (1964) confirmed that the South African genus, Afroedura Loveridge, 1944, is distinct from the Australian genus, Oedura Gray, 1842. Where there is any doubt as to the justification for a change in nomenclature as indicated by a lack of agreement between authors or the admitted distinctiveness of a species such as Lucasium damaeum (Kluge, 1962a, 1967b), the older name is retained here.

Dixon and Kluge (1964) erected the genus Crenadactylus for those Australian geckos with forked terminal phalanges, namely Phyllodactylus ocellatus (Gray), 1845, Diplodactylus bilineatus Gray, 1845, and Ebenavia horni Lucas & Frost, 1895. The genus Ebenavia now contains only the type species, E. inunguis Boettger, 1878, which is restricted to Madagascar and the Mascarenes (Wermuth,
1965).

Underwood (1954) divided the genus *Gymnodactylus* Spix, 1825, (sensu Boulenger, 1885) into four groups on the basis of pupil form, retaining *Gymnodactylus* (sensu stricto) for the South American species and reviving *Phyllurus* Schinz, 1822, for the Australasian species including *P. platurus* (Shaw), 1790, *P. cornutus* (Ogilby), 1892, and *P. milii* Bory de St. Vincent, 1825. Although the form of the pupil is no longer recognised as a reliable criterion for classifying geckos (Kluge, 1964, 1967a), Wermuth (1965) erected the subgenus *Underwoodisaurus* of the genus *Gymnodactylus* Spix for those Australasian members of the genus which have a vertical, unlobed but straight-edged pupil and designated *Gymnodactylus milii* (Bory) as the type species. According to Wermuth the genus *Phyllurus* Schinz should be restricted to the two species *platurus* and *cornutus* which resemble one another closely, especially in the form of their characteristic, flat tails. Kluge (1967a), however, recognised four species of *Phyllurus*, namely *platurus*, *cornutus*, *sphyrrurus* and *milii* without reference to Wermuth's (1965) subgenus *Underwoodisaurus* and noted (p. 22) that *P. milii* is the member of the genus most closely related to *Nephrurus* Gunther, 1876. As the position of *milii* is still not clear, it will be retained here for the sake of convenience in the genus *Phyllurus*.

With the exception of *Ophioseps* and *Paradelma*, there have been no major changes in the nomenclature of pygopods since Kinghorn's (1926) review. As the position of *Ophioseps* has been the subject of much confusion and that of *Paradelma* is still in doubt, it is pertinent to review the systematic position of both these genera.
Ophioseps du Bocage, 1873, is now considered to be synonymous with Aprasia Gray, 1839, but, until comparatively recently, its affinities both with Aprasia and with the Pygopodidae have been much debated. Boulenger (1887), referring to the genus as Ophiopsisepseps, considered that it is "probably the type of a distinct family" rather than a connecting link between lizards and snakes as suggested by du Bocage. Jensen (1900) maintained that Ophiopsisepseps (= Ophioseps) nasutus du Bocage, 1873 is related to the Scincidae but is sufficiently different from them to merit a separate family and, following Boulenger's (op. cit.) suggestion, erected for it the Family Ophiopsisepidae. Angel (1920) recognised this family and further confused matters by placing within it his genus Typhioseps from Siam, which has since been removed to the Scincidae in the synonymy of Ophioscincus Peters, 1874 (Romer, 1956).

In 1923, Kinghorn transferred Ophioseps repens Fry, 1914 to the genus Aprasia and stated that all the supposed Ophioseps spp. which he was able to examine, including Fry's type, really belong to the genus Aprasia but, lacking the genotypic specimen of O. nasutus du Bocage, 1873, Kinghorn left this species in the genus Ophioseps. In a later paper (1926) Kinghorn retained the generic status of Ophioseps for O. nasutus but questioned Jensen's (1900) figures showing its skull structure and considered again that its external features and general appearance tended to place it in the pygopod genus Aprasia. McDowell & Bogert's (1954) views regarding the affinities of Ophioseps and Aprasia contained discrepancies (see Underwood, 1957b) while Romer (1956) and Underwood (1957a) placed both these genera in the Pygopodidae. Parker (1956b)
eventually resolved the problem. He examined the holotype of *O. nasutus* and could decipher or measure sufficient characters to make it virtually certain that the species involved was the same one which Gray had previously named *Aprasia pulchella*. Much of the confusion surrounding *Ophioseps* seems to have arisen from Jensen's (1900) use of juvenile specimens which he identified as *O. nasutus*. Parker re-examined these specimens and identified them as *Aprasia striolata striolata* Lütken, 1863, so that the genus *Ophioseps* is now completely synonymous with *Aprasia*.

Apart from *Ophioseps*, the only other genus in Kinghorn's (1926) review of the Pygodopidae whose status has since been questioned is *Paradelma nom. nov*. The genus *Cryptodelma* (sp. *nigriceps*) was founded by Fischer (1882) on a single withered specimen. A second species, described by Günther (1876) as *Delma orientalis*, was recognised by Boulenger (1885) as *Cryptodelma orientalis*. Kinghorn (1926) examined numbers of specimens which agreed entirely with Fischer's description of *C. nigriceps* but which could not be distinguished from *Pygopus schraderi* Boulenger 1913, and felt obliged on these grounds to transfer *C. nigriceps* to the genus *Pygopus* and to place *P. schraderi* in the synonymy of that species. With the consequent lapse of the genus *Cryptodelma*, the remaining species, *C. orientalis*, was placed by Kinghorn (op. cit.) in the genus *Paradelma nom. nov*. Roman (1956) listed *Paradelma* Kinghorn, 1926 as a synonym of *Delma* Gray, 1831, but gave no reasons for doing so. N. G. Stephenson (1961) pointed out that preanal pores occur only in *Pygopus* and *Paradelma* and, although *Delma* lacks these pores, it stands very close to *Pygopus* compared with other genera. According to Stephenson, the similarity
between *P. lepidopodus* and *D. fraseri* in the structure of the skull and girdles makes it hard to envisage a further genus between them, which would yet be comparable in distinctiveness to *Lialis*, *Pletholax* and *Aprasia*. 
MATERIAL AND METHODS

The lizards listed below were used for the study of the vertebral column. The generic and specific names used have been adopted after consulting Boulenger (1885-1887), Zeitz (1920), Kinghorn (1923, 1924, 1926), Waite (1929), Smith (1933), Loveridge (1934, 1947), Underwood (1954), Parker (1956b), Cogger (1957, 1964), Chrapliwy, Smith & Grant (1961), Myers (1961), Kluge (1962a & b, 1963a & b, 1965, 1967a & b, 1968), Storr (1963), Savage (1963), Dixon & Kluge (1964), Mitchell (1965b), Wermuth (1965) and Vanzolini (1968a & b). Differences of opinion regarding the status of various genera and species and changes in the nomenclature of the geckos as published by Holder (1960) have already been discussed in the previous section. The localities given below indicate the places where the material was collected rather than the distribution of the species.

Family GEKKONIDAE

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<tr>
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<td>D. vittatus Gray, 1832</td>
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Lucasium damacum (Lucas & Frost), 1896
Nephrurus asper Günther, 1876
N. levis De Vis, 1886
Oedura lesueurii (Duméryl & Bibron), 1836
O. marmorata Gray, 1842
O. monilis De Vis, 1888
Phylloactylus marmoratus (Gray), 1845
Phyllurus cornutus (Ogilby), 1892
P. milii Bory de St Vincent, 1825
P. platurus (Shaw), 1790
Rhynchoedura ornata Günther, 1867

Africa
Afroedura transvaalica (Hewitt), 1925

Jamaica
Aristelliger praesignis (Hallowell), 1857
Gonatodes albobularis (Hallowell), 1855
Sphaerodactylus parkeri Grant, 1939

New Guinea
Gekko vittatus Houttuyn, 1782

New Hebrides
Lepidodactylus lugubris (Duméryl & Bibron, 1836

New Ireland
Hemidactylus garnotii Duméryl & Bibron, 1836

New Zealand
Hoplodactylus duvaucelii (Duméryl & Bibron), 1836
H. pacificus (Gray), 1842
Naultinus elegans Gray, 1842

Norfolk Island
Phylloactylus Güntheri Boulenger, 1885

Solomon Islands
Lepidodactylus guppyi Boulenger, 1884.
L. woodfordii Boulenger, 1887
United States of America

Coleonyx brevis Stejneger, 1893
C. variegatus (Baird), 1858

Family PYGOPODIDAE

Australia

Aprasia pulchella Gray, 1839
Delma fraseri Gray, 1831
D. tincta De Vis, 1888,
Lialis burtonis Gray, 1835
Pletholax gracilis Cope, 1864
Pygopus lepidopodus (Lacépède), 1804
P. nigriceps (Fischer), 1882

New Guinea

Lialis burtonis Gray, 1835
L. jicari, Boulenger, 1903

Family XANTUSIIDAE

Xantusia vigilis Baird, 1859

Specimens of the above species were prepared as
Alizarin transparencies using a modified version of Williams' (1941) technique and were dissected under a Zeiss Opton binocular microscope with epi- and sub-illumination. The specimens were transferred from pure glycerine to water for examination to eliminate the optical distortion caused by the glycerine and to render the ligaments slightly opaque, thus facilitating their dissection. Although uncalcified cartilage does not stain red with Alizarin as do bone and calcified cartilage, it could readily
be seen in water owing to its distinctive appearance.

Longitudinal frozen sections were made from Alizarin-stained anterior cervical, mid-trunk and caudal vertebrae of immature and adult *Phyllurus platurus*, *P. milii*, *Coleonyx variegatus*, *Delma fraseri*, *Pygopus lepidopodus* and *Lialis burtonis* and from adult specimens of *Sphaerodactylus parkeri*, *Aprasia pulchella* and *Xantusia vigilis*. Anterior and mid-trunk vertebrae were dissected from the Alizarin transparency of *Pletholax gracilis*, washed in water to remove the glycerine, dehydrated, blocked in wax, serially sectioned longitudinally at 10 μ, then stained with Light Green. Although this material stained extremely poorly owing to its prior maceration, the structural components of the vertebrae could be determined by means of phase contrast microscopy.

Serial longitudinal sections 10 μ thick were also cut through mid-trunk vertebrae of adult *Oedura lesueurii*, *Phyllurus platurus*, *Coleonyx variegatus*, *Delma fraseri*, *Pygopus lepidopodus* and of sub-adult and adult *Lialis burtonis* and through the anterior five vertebrae of *D. fraseri*. Serial transverse sections were cut at 10 μ through mid-trunk vertebrae of sub-adult *L. burtonis*, an entire hatchling specimen of *O. lesueurii*, the trunk of juvenile *Aristelliger praesignis* and the sacrum of an adult *O. lesueurii*. The head and cervical vertebrae of embryonic *O. marmorata* and *Gehyra variegata* were sectioned transversely at 8 μ while the remainder of the latter specimen was sectioned transversely at 10 μ. Transverse and longitudinal serial sections at 10μ were cut through caudal vertebrae of juvenile and adult specimens of
O. lesueurii. With the exception of Pletholax gracilis, these serial sections were stained with Heidenhain's azan, Mallory's triple stain or Ehrlich's haematoxylin and eosin.

This range of sectioned material was used to study the internal morphology of the centrum and intervertebral region, the atlas-axis complex, rib attachment, the plane of caudal fracture and the blood vessels in the subcentral foramina. Representative sections are illustrated as photomicrographs or as semidiagrammatic line and stipple drawings. The text figures of the internal and external morphology of the vertebrae and ribs were drawn freehand from sections and dissected alizarin transparencies respectively. The proportions of the text figures were verified and the magnification of all illustrations was determined using stage and eyepiece micrometers.

In addition to the material listed above, there were also available for comparative purposes preserved adult specimens, a dried adult skeleton and an alizarin transparency of a hatchling Sphenodon punctatus as well as alizarin transparencies of a number of lizards belonging to the Agamidae, Scincidae, Lacertidae and Anguidae, and snakes belonging to the Elapidae and Typhlopidae. Comparative material in the form of serial sections comprised embryonic and postnatal stages of the lacertid Lacerta vivipara and the anguid Anguis fragilis sectioned transversely and longitudinally, as well as transversely sectioned mid-trunk vertebrae of the typhlopid snake Typhlops nigrescens.
Vertebral counts were made on 130 Australian geckos, representing 12 genera and 21 species, and are presented in Table I. For purposes of comparison, counts taken on 26 non-Australian geckos representative of nine genera and 12 species are presented in Table II. The genera are placed in the subfamilies to which they were allocated by Kluge (1967a).

The presacral count throughout the available material was typically 26, with a range of 25 - 28. Two species, Phyllurus cornutus and P. platurus, have a typical count of 25, while of nine Phylloleptodactylus marmoratus, five had 27 presacral vertebrae and the remaining four had 28.

The presacral series has been arbitrarily divided into cervical and dorsal series on the basis of rib structure. The term 'cervical' is often considered to be synonymous with 'presternal' but will not be so regarded here. Eight presternal vertebrae were found in every gecko examined but only the anterior six are classified as cervical because, as Camp (1923) pointed out, the ribs of the eighth vertebra in lizards may join with the sternum, and those of the seventh and eighth vertebrae resemble the dorsal ribs more closely than those of the vertebrae preceding them. This is particularly obvious in the majority of geckos in which the ribs of the fourth, fifth and sixth vertebrae are structurally very different from those of the seventh and eighth.
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<tr>
<th>Species</th>
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<th>Vertebral count</th>
<th>Cervical vertebrae</th>
<th>Total cervical vertebrae</th>
<th>Dorsal and caudal vertebrae</th>
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130
The first three cervical vertebrae of geckos are normally devoid of ribs, although incomplete rib elements were present on the third vertebra of 27 specimens. Only one species, *Phylodactylus marmoratus*, typically bore a pair of reduced ribs on the third cervical vertebra. The fourth, fifth and sixth vertebrae without exception bore a pair of normal ribs.

The lumbar vertebrae are those immediately presacral vertebrae whose ribs are either lacking or reduced. In the material examined, the number of lumbar vertebrae varied from one to three.

The sacral count was found to be typically two, except in the genus *Nephrurus*. Six of the eight specimens of this genus had three sacral vertebrae, one specimen had two and the remaining specimen had four. Three of the 33 *Phyllurus platurus* also possessed three sacral vertebrae.

The pygal vertebrae, i.e. those anterior caudals devoid of fracture planes, were usually five in number, although four pygals seem typical of *Nephrurus levis* and *Phyllurus mili*, and four, five or six pygals may occur in *Hemidactylus frenatus*. Four pygal vertebrae are also found occasionally in other species including the New Zealand geckos *Hoplodactylus* and *Naultinus* described by N. G. & E. M. Stephenson (1956).

An exact evaluation of the postpygal vertebrae could not be made as many of the specimens had lost at least part of the tail by autotomy. Consequently, the postpygal vertebral count has not been tabulated. In those specimens with a complete tail,
### Table II. Vertebral counts on non-Australian geckos and *Xantusia vigilis*

<table>
<thead>
<tr>
<th>Species</th>
<th>Total specimens</th>
<th>Specimens with a particular vertebral count</th>
<th>Presacral</th>
<th>Total cervical</th>
<th>Anterior cervicals devoid of ribs</th>
<th>Pairs of cervical ribs</th>
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</table>

Total: 26
the postsacral (caudal) count was approximately thirty. In specimens which had undergone autotomy there was usually a completely regenerated tail whose axial skeleton consisted of a cartilaginous tube.

Twenty-two caudal vertebrae were present in the only specimen of *Nephrurus asper* with a complete tail. This tail was very short, being only one-sixth of the total length of the animal. *N. asper* was the only gecko in which caudal fracture planes were entirely absent and whose tail was incapable of autotomy.

**Xantusia**

The number of vertebrae in the different regions of the body of *Xantusia vigilis* are given in Table II and fall within the range shown by geckos. According to Savage (1963), there are usually 28 presacral vertebrae in the Xantusiidae, the range being 26 - 29, three cervicals (anterior vertebrae without ribs) and four or five pygals.

**Pygopods**

Vertebral counts were made on 35 Australian pygopods, representing five of the six known genera, and are presented in Table III. For comparative purposes the eight specimens of *Lialis* from New Guinea are listed separately in Table IV.

Although individual pygopods vary in their number of presacral vertebrae, each genus appears to have a characteristic range. There were 106 - 120 in *Aprasia*, 80 - 92 in *Lialis*,...
75 - 82 in Pygopus, 52 - 58 in Delma and 47 in the single specimen of Pletholax. The presacral series in pygopods has not been divided into cervical and dorsal series because all the presacral ribs are similar in structure and there is considerable individual variation in the number of ribs, if any, attached to the sternum in the genera where such attachment occurs, namely Pygopus and Delma.

In Pygopus and Pletholax the one or two vertebrae immediately in front of the sacrum bear ribs which are incomplete in some respect. For the sake of convenience, these vertebrae are described as lumbar.

The sacrum of pygopods may consist of one or two vertebrae whose ribs are modified to support the pelvic girdle. Two sacral vertebrae where both pairs of ribs articulate with the ilium commonly occur in Delma and were found in one specimen of Aprasia. In the other genera, a sacrum consisting of two vertebrae was abnormal in that a rib of one or both vertebrae did not articulate with the girdle.

The pygal vertebrae in most lizards are those anterior caudals which lack fracture planes and the postpygals are completely divided by them. In pygopods the pygal and postpygal series are difficult to delimit as the more anterior fracture planes only partly divide their vertebrae and it is not possible to determine solely from the skeleton whether a partly divided vertebra is capable of autotomy. In view of this difficulty, the pygal series in pygopods is defined here in accordance with general practice as those anterior caudal vertebrae which com-
<table>
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<tr>
<th>Species</th>
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<th>Specimens with a particular vertebral count</th>
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<th>Presterial</th>
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+Very young animal in which all but the first few caudal vertebrae were still uncalcified.

*Abnormal in that one rib of one or both sacral vertebrae was not modified for support of the pelvic girdle.
pletely lack fracture planes. The widest variation in pygal counts was found in *Delma* with one to three pygals and *Pygopus* with three to five; *Lialis* varied least in that 20 out of 21 specimens had two pygals. By definition there were two pygal vertebrae in *Pletholax* but none of the more posterior caudals was completely divided and the tail was incapable of autotomy.

The full complement of caudal vertebrae was present in few of the pygopods examined: the majority had lost part of the tail through autotomy. Two *Delma fraseri* with complete tails had 102 and 106 caudal vertebrae; in four *Pygopus lepidopodopus* the range was 104 - 114, while five *Lialis burtonis* had a range of 72 - 82 caudal vertebrae. In the single specimen of *Pletholax*, from which the end of the tail had been lost, there were 86 caudals and in the three specimens of *Aprasia*, all with incomplete tails, there were 44 - 56 caudal vertebrae. According to Romer (1956), the caudal vertebrae in pygopods may number 45 - 80 while Etheridge (1967) found 119 in a specimen of *Delma fraseri*.

Parker (1956b) found a correlation in *Aprasia repens* between the number of presacral vertebrae and the mean normal temperature for December in the places where his animals were collected. Assuming that development takes place during the summer, Parker suggested that this correlation may be the result of development at different temperatures. Fox (1948) found from experiments that the number of scale rows in the garter snake, *Thamnophis elegans atratus*, increases with the temperature at which development takes place and warned against the assumption that meristic variation in natural populations is necessarily genetically controlled. The number of body annuli in *Amphisbaena*
Alba increases with developmental temperature according to
Vanzolini (1968c) who suggested, in contrast to Fox, that tem-
perature influences the number of body annuli through selection,
pleiotropic mechanisms determining at the same time some physio-
logical adaptive character and the number of somites. According
to Alexander and Gans (1966), the number of body annuli in
Amphisbaena is directly related to the number of somites which
is known to be very sensitive to changes in environmental tem-
perature. Meristic characters in fishes, such as the number of
fin rays and vertebrae, are often thermoplastic: higher counts
can result from raising or lowering the temperature during the
critical period of development (Tåning, 1946, 1950, 1952; Lindsey,
1954). Visible light intensity also affects the number of ver-
tebrae in Salmo gairdneri, but only during the pre-eyed stage of
development (MacCrimmon & Kwain, 1969).

Of the pygopods examined personally, many had no precise
locality data. Nevertheless sufficient information was available
in the case of Lialis burtonis to allow comparison between
Australian and New Guinean members of the species. The Australian
animals had a mean presacral count of 87.6, with a range of 81 -
92, while the mean for the New Guinean specimens was 85.6, range
80 - 92. Clearly, from these figures, there is no correlation in
Lialis burtonis between the number of presacral vertebrae and
latitude. However, as there is considerable variation in summer
temperatures within the range of this species in Australia and
New Guinea, and as no estimate of the developmental temperature
is possible due to the absence of particular locality data, the
possibility remains that there may be temperature plasticity in
### TABLE IV

Vertebral Counts on New Guinean Pygopods

<table>
<thead>
<tr>
<th>Species</th>
<th>Total specimens</th>
<th>Specimens with a particular vertebral count</th>
<th>Presacral</th>
<th>Presternal</th>
<th>Anterior presacrales devoid of ribs</th>
<th>Lumbar</th>
<th>Sacral</th>
<th>Pygal</th>
<th>Partly divided postpygals</th>
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* Abnormal in that one rib of each sacral vertebra was not modified to support the pelvic girdle.
the number of presacral vertebrae in this species and in other pygopods as well. As Parker (1956b) pointed out, precise information is needed on breeding seasons and developmental temperatures before such a thermoplastic effect can be established with certainty.
According to Camp (1923), the centrum of geckos is broad and squarish in ventral outline with a median, waist-like constriction. With the exception of the two species of Coleonyx examined, C. variegatus and C. brevis, all the geckos examined here agree with this description, their centra varying only slightly in size and shape in different parts of the body. In Coleonyx, however, regional variation is more conspicuous: the cervical centra are short and broad in ventral outline whereas those of the mid-trunk are appreciably longer and narrower. The lumbar centra are the largest in the column, being squarish in ventral outline like the cervical centra, after which there is a rapid reduction in overall size through the two sacral and four or five pygal vertebrae.

The vertebrae of pygopods have long been described as procoelous with a large, rounded condyle situated posteriorly on the centrum and, with the exception of Pletholax whose mid-trunk vertebrae are long and narrow, they are squarish in ventral outline with a median, waist-like constriction like those of most geckos. The most anterior centra are somewhat larger than those of the trunk but otherwise there is little variation in the size and shape of the centra throughout the precaudal region of the body.

Intercentra are present throughout the vertebral column of amphicoelous and procoelous geckos and Xantusia. Despite Hoffstetter & Gasc's (1969) statement that intercentra are absent in the trunk region of pygopods, a complete series of intercentra
is also found in *Pygopus* and *Lialis*. The atlantal and axial intercentra are fused to their vertebrae in adults while the more posterior ones are usually visible as discrete elements. The intercentra of *Delma*, *Pletholax* and *Aprasia* do not extend throughout the vertebral column but are restricted to the most anterior presacral vertebrae and to the tail where, as is usual in lizards, they take the form of haemal arches or chevron bones. In *Delma* some of the anterior intercentra are separate or only partially fused to their vertebrae whereas there are no free intercentra in the precaudal column of *Aprasia* and *Pletholax*. It appears, at least in *Delma*, that intercentra are truly absent from the trunk rather than fused to an adjacent centrum. In one adult *Delma* there were nine anterior intercentra and the ninth, in contrast to the seventh and eighth which were relatively large and fused to their centra, was a very slender discrete element.

Howes & Swinnerton (1901) described a stage in the embryonic development of *Sphenodon* when intercentra are absent from the trunk following dedifferentiation of the primary procartilaginous intercentra and before the appearance of the secondary intercentra which ossify directly in the subvertebral fibrous tissue. The primary intercentra of the most anterior vertebrae and those of the tail, however, are retained throughout life. Werner (1971) described this phenomenon in embryonic geckos and it would appear that it also occurs in the pygopod, *Pygopus lepidopodus*. A very young specimen of *P. lepidopodus*, in which none of the neural arches had fused together in the mid-dorsal line, possessed the first four intercentra as discrete elements but, from the fifth
presacral vertebra to the fourth caudal, there was no sign of ossified intercentra. However, it must be recognised that the primary intercentra may have been present in the trunk of this animal as there was no way of distinguishing cartilaginous intercentra from intervertebral cartilage in alizarin transparencies.

According to Camp (1923) the intercentra of Coleonyx and Xantusia fuse to the condyles of the centra. No such fusion has been observed in any of the procoelous lizards examined here: the intercentrum between adjacent vertebrae is attached to the intervertebral cartilage lying ventrally to the condyle of the preceding vertebra. When fusion occurs between centra and intercentra it takes place along the ventral margin of the centrum where it joins the intervertebral cartilage.

With the exception of atlas and the posterior caudal vertebrae, the consecutive neural arches of geckos and pygopods articulate with one another by means of zygapophyses whose facets are flat or slightly curved in end view (Figs. 3:9D, 3:10B; 3:17A). Those of the prezygapophyses face upwards and inwards towards the midline while those of the postzygapophyses face down and outwards. The zygapophyses of Xantusia resemble those of geckos and pygopods except that the atlantal postzygapophyses articulate with the axial prezygapophyses. In none of these lizards are there additional articulations between adjacent neural arches in the form of zygosphenes and zygantra which occur in some other lizards and in snakes. These additional points of articulation are often found in long-bodied reptiles where they serve to strengthen the column and at the same time limit dorso-ventral flexure (Romer, 1956) but, according to Camp (1923), they are not found
in any limbless lizard.

The neural spines of geckos, pygopods and *Xantusia* are inclined posteriorly throughout the column with the exception of the axial spine, which projects anteriorly and posteriorly over the ends of the axial neural arch, and the last pygal spine which in some geckos is vertical. The variation in the size and shape of the neural spines in different parts of the body is discussed below.
Geckos and pygopods

With respect to the internal morphology of their vertebral centra, amphicoelous and procoelous geckos and the entirely procoelous Pygopodidae closely resemble one another in that the notochord is retained in adult stages. Those differences which do occur between the centra of gekkotans are mainly concerned with the relative size of the notochord and the ways in which it diminishes with age.

The vertebrae of amphicoelous geckos (Fig. 3:1A, B) are characterised by their biconcave centra and continuous notochord. Each centrum is the major supporting element of the vertebra and is hollowed at both ends into funnel-shaped depressions which are connected through the middle of the vertebra by the notochordal canal. The centra are joined together by a ring of fibrocartilage which merges with the calcified cartilage at the ends of the bony centra. These rings of intervertebral cartilage are present throughout the column, the most anterior one occurring between the axis and the third cervical vertebra (Fig. 3:5A, B). The moniliform notochord, extending without interruption from the axis to the tail, has its smallest diameter mid-vertebrally in the region of the chordal plate and its greatest diameter intervertebrally within the ring of intervertebral cartilage. Thus the funnel-shaped depressions in the ends of the centra contain notochordal tissue, so that only the "rims" of the "funnels" are attached to the intervertebral cartilage. It would appear that
Mid-trunk vertebral centra of geckos in sagittal section, showing transition from amphicoely to procoely.

A. Phyllurus platurus, juvenile;
B. P. platurus, adult;
C. P. milii, juvenile;
D. P. milii, adult;
E. Sphaerodactylus parkeri, adult.

A and B are amphicoelous, C, D and E are procoelous geckos. The broken lines drawn across the notochord indicate the ends of the centra.

c, condyle; cc, chordal cartilage; cct, calcified cartilage; eb, endochondral bone; ic, intercentrum; ivc, intervertebral cartilage; nc, notochord; ncs, notochordal sheath; pb, perichondral bone; rcc, region of maximum chordal constriction.
the notochord has this moniliform configuration because ossification of the centrum begins mid-vertebrally and proceeds anteriorly and posteriorly to the ends of the centrum, the outward growth of the notochord ceasing as the surrounding perichordal tissue (in this case cartilage) becomes ossified (see Werner, 1971).

Only five of the 36 species of geckos examined were procoelous. These were Coleonyx variegatus and C. brevis from North America, Sphaerodactylus parkeri from Jamaica of which only one adult specimen was available for examination and two Australian species, Carphodactylus laevis and Phyllurus mili. In these five species the centra are pierced throughout their length by the chordal canal which continues without interruption through the intervertebral region, at least in juvenile and early adult stages (Figs 3:1C, D, E; 3:2A). The condition in adult Carphodactylus is the same as that found in juvenile P. mili as illustrated in Fig. 3:1C. In each of these procoelous species a discrete intercentrum lies between adjacent centra as in amphicoelous forms. The main difference between this type of procoelous centrum and the amphicoelous centra of other geckos is one of shape; each centrum has a cup-shaped depression or cotyle anteriorly and a rounded condyle posteriorly so that adjacent vertebrae together form a ball-and-socket articulation.

According to Kluge (1967a) there is a tendency towards procoely in Australian geckos other than Carphodactylus and Phyllurus, namely Crenadactylus, Diplodactylus and Oedura. In the species of these genera examined here, however, the centra were amphicoelous because no difference in shape existed between the anterior and posterior ends of the centra.
Figure 3:2

Procoelous mid-trunk centra of *Coleonyx* (Fam. Gekkonidae) and *Xantusia* (Fam. Xantusiidae) in sagittal section.

A. *Coleonyx variegatus*, sub-adult;
B. *C. variegatus*, adult;
C. *Xantusia vigilis*, adult.

c, condyle; cart, uncalcified cartilage; cc, chordal cartilage; cct, calcified cartilage; eb, endochondral bone; ic, intercentrum; ivc, intervertebral cartilage; ms, marrow space; nc, notochord; ncs, notochordal sheath; pb, perichondral bone.
The type of procoely found in adult *Carphodactylus laevis* is minimal in that it involves a slight convexity of the posterior end of the centrum and a correspondingly slight concavity of the anterior end, while the notochord retains the moniliform configuration characteristic of amphicoelous geckos. In all the other procoelous geckos examined, the notochord was constricted to a greater or lesser extent in adult stages. The sites of chordal constriction in procoelous geckos are the ends of the centra, mainly within the condyle and to a smaller degree in the anterior end of the centrum just behind the concavity. As a result of constriction within the vertebra, the intervertebral chordal diameter is reduced. In immature specimens chordal constriction is comparatively slight (Fig. 3:2A) or absent altogether (Fig. 3:1C) but it increases with age. In *Phyllurus mili* the notochord is almost uniform in diameter in adults (Fig. 3:1D) and does not appear to diminish further after sexual maturity. In *Coleonyx*, on the other hand, which also attains sexual maturity with a continuous notochord, chordal constriction continues in adult stages so that the notochord of older specimens is reduced within the condyle to thin strands of the chordal sheath (Fig. 3:2B). It is not known whether chordal constriction continues in a similar manner in adult *Sphaerodactylus* but in none of the geckos examined was the notochord interrupted at any point other than the ends of the centrum.

The centra of pygopods also contain notochordal tissue. In juveniles (Figs 3:3A, 3:4A), just as in amphicoelous and procoelous geckos, the notochord is continuous throughout the verte-
Figure 3:3

Procoelous mid-trunk centra of *Pygopus* and *Delma* (Fam. Pygopodidae) in sagittal section, showing reduction of notochord.

A. *Pygopus lepidopodus*, juvenile;  
B. *P. lepidopodus*, young adult;  
C. *P. lepidopodus*, adult;  
D. *Delma fraseri*, sub-adult;  
E. *D. fraseri*, adult.

c, condyle; cart, uncalcified cartilage; cc, chordal cartilage; cct, calcified cartilage; eb, endochondral bone; ic, intercentrum; ivc, intervertebral cartilage; ms, marrow space; nc, notochord; ncs, notochordal sheath; pb, perichondral bone; rcc, region of maximum chordal constriction.
bral column, being severed only at the atlanto-occipital joint. With increasing age the notochord becomes discontinuous but the rate and manner of its reduction vary in the different genera. *Pygopus* attains sexual maturity with no further interruption of the notochord (Fig. 3:3B) whereas the closely related genus *Delma* loses its chordal continuity by the time it is adult (Figs 3:3D, E). The notochord is also discontinuous in adult *Lialis* (Fig. 3:4B), *Aprasia* (Fig. 3:4C) and *Pletholax* (Fig. 3:4D). However, as it was not possible to establish whether the single available specimen of *Pletholax* was recently matured or comparatively old, the possibility remains that this genus may retain an uninterrupted notochord in early adult stages. The continued reduction of the notochord in adult pygopods is well illustrated by *Pygopus* in which the chorda is progressively resorbed from the ends of the centra (Fig. 3:3C) until in relatively old specimens it is entirely absent, having been replaced by endochondral bone.

In *Pygopus* and *Lialis* the notochord is reduced in the same way as in procoelous geckos, by progressive constriction within the ends of the centra while remaining intact midvertebrally. In *Delma, Aprasia* and *Pletholax*, on the other hand, the notochord is not only constricted in the ends of the centra but is also interrupted midvertebrally by the deposition of bone within the chordal canal. In *Delma* this midvertebral interruption of the notochord follows its loss from the condyle (Figs 3:3D, E) whereas in *Aprasia* the notochord is interrupted midvertebrally while it is still continuous between adjacent centra (Figs 3:4C). Although the notochord of *Pletholax* (Fig. 3:4D) is reduced within the ends of the centra to remnants of the chordal sheath, it is clear from
**Figure 3:4**

Procoelous mid-trunk centra of *Lialis*, *Aprasia* and *Pletholax* (Fam. Pygopodidae) in sagittal section, showing reduction of notochord.

A. *Lialis burtonis*, juvenile;
B. *L. burtonis*, adult;
C. *Aprasia pulchella*, adult;
D. *Pletholax gracilis*, adult.

c, condyle; cart, uncalcified cartilage; cc, chordal cartilage; cct, calcified cartilage; eb, endochondral bone; ic, intercentrum; ivc, intervertebral cartilage; ms, marrow space; nc, notochord; ncs, notochordal sheath; pb, perichondral bone; rcc, region of maximum chordal constriction.
the extent of midvertebral ossification that the sequence in this genus is the same as that found in Aprasia. Early stages in the deposition of midvertebral chordal bone as seen in Delma (Fig. 3:3E) show that it begins in the cartilaginous chordal plate.

The chordal plate of geckos and pygopods is situated within the chordal canal towards the middle of the centrum and consists of large vacuolated cells embedded in a small amount of matrix (Pls 10A, 11). In sections of Alizarin stained vertebrae it was found to be calcified like the cartilage in the ends of the centra as demonstrated by its affinity for Alizarin, provided that the stain had penetrated the vertebra deeply enough during preparation. The chordal cartilage of Sphenodon, which also has notochordal amphicoelous vertebrae, has a somewhat different histological appearance in that it is composed mainly of matrix in which are embedded small circular cells with a conspicuous rounded nucleus (Howes & Swinnerton, 1901). At least in hatchlings, the chordal cartilage of Sphenodon is not calcified as demonstrated by its lack of affinity for Alizarin, even when excised from an Alizarin transparency and restained.

As in Sphenodon (Howes & Swinnerton, 1901) and Lacerta laevis (Werner, 1961), the chordal cartilage of geckos and pygopods in endochondral in origin and is apparently formed by the differentiation of notochordal tissue. There is no invasion of cartilage from outside the notochordal canal as demonstrated by the intact nature of the surrounding notochordal sheath (see also Werner, 1971). Unlike Sphenodon, however, in which the chordal
sheath is of uniform thickness throughout the centrum (Howes & Swinnerton, 1901), the chordal sheath of geckos and pygopods is much thicker towards the ends of the centra than in the region of the chordal plate. In procoelous gekkotans, this difference in the thickness of the sheath is most obvious in juveniles in which chordal constriction is minimal. Underlying the chordal sheath is the chordal epithelium, a single layer of cells in a thin matrix which merges with the chordal cartilage. Although the chordal epithelium appears to be a thin layer of cartilage similar to the chordal plate, it is not possible to determine from wax sections of decalcified material whether the chordal epithelium is calcified, and it is too thin to be detected in frozen sections taken from Alizarin transparencies. In Sphenodon the chordal sheath is underlain by a structureless cuticle or tunica chordae, which according to Howes & Swinnerton (1901), appears to represent the chordal epithelium and which passes into the faces of the chordal plates whose superficial portions resemble the tunica in their staining properties.

In adult Delma (Fig. 3:3E, Pl. 11C, D) the notochordal sheath is discontinuous in the middle of the centrum and bone is present within the chordal cartilage. The onset of ossification has not been seen so it is not known whether it originates from a separate ossification centre within the chordal cartilage, without prior perforation of the chordal sheath, or whether osteoblasts pass into the chordal cartilage from the surrounding centrum following perforation of the sheath. There was one marrow space in the chordal bone of Delma which communicated at only one point with the marrow spaces in the surrounding centrum.
Figure 3:5

Centra of axis and third cervical vertebra of geckos in sagittal section, showing smaller degree of chordal reduction in the cervical region than in the trunk (cf. Fig. 3:1).

A. *Phyllurus platurus*, juvenile;
B. *P. platurus*, adult;
C. *P. milii*, juvenile;
D. *P. milii*, adult;
E. *Sphaerodactylus parkeri*, adult.

A and B are amphicoelous, C, D and E are procoelous geckos. The broken lines drawn across the notochord indicate the ends of the centra.

*axhs*, axial hypapophyseal spine; *c*, condyle; *cart*, uncalcified cartilage; *cc*, chordal cartilage; *cct*, calcified cartilage; *eb*, endochondral bone; *icax*, axial intercentrum; *icCe3*, intercentrum of third cervical vertebra; *ivc*, intervertebral cartilage; *nc*, notochord; *ncs*, notochordal sheath; *od*, odontoid process; *pb*, perichondral bone.
The remnants of the chordal sheath in this region are not displaced but are resorbed after they have been surrounded by bone. Lying in front of the chordal bone and behind it, within the chordal canal, is a layer of cartilage with large, irregular lacunae which stains most densely where it joins the bone. As this cartilage resembles the original chordal cartilage histologically and is also of endochondral origin as indicated by the enclosure of the edges of the chordal sheath in bone, it should also be regarded as chordal cartilage. The growth of bone anteriorly and posteriorly along the chordal canal as seen in Aprasia (Fig. 3.4C) and Pletholax (Fig. 3.4D) would thus appear to follow the progressive chondrification of notochordal tissue to form chordal cartilage.

In procoelous geckos and pygopods whose notochord is no longer continuous between adjacent centra, the ends of the chordal canal sometimes contain cartilage. In some cases, as in the anterior vertebrae of adult Delma (Fig. 3.7D), this cartilage is calcified like the cartilage in the ends of the centrum where it joins the intervertebral cartilage but in others such as Pletholax the matrix is relatively abundant and calcification does not seem to have occurred. As this cartilage is not always present in all the vertebrae of a single animal, being absent for example from some trunk vertebrae in adult Delma (Pl. II C), and is not present unless the chordal sheath has been perforated, it would appear to be of perichondral origin, unlike the intervertebral chordal cartilage occurring in the posterior tail of geckos which is of endochondral origin (Werner, 1971).
Figure 3:6

Centra of axis and third cervical vertebra of Coleonyx (Fam. Gekkonidae) and Xantusia (Fam. Xantusiidae) in sagittal section, showing the smaller degree of chordal reduction in the cervical than the dorsal region of Coleonyx (cf. Fig. 3:2) and the absence of the notochord in Xantusia.

A. Coleonyx variegatus, sub-adult;
B. C. variegatus, young adult;
C. Xantusia vigilis, adult.

axhs, axial hypophyseal spine; c, condyle; cart, uncalcified cartilage; cc, chordal cartilage; cct, calcified cartilage; eb, endochondral bone; icax, axial intercentrum; icCe3, intercentrum of third cervical vertebra; ivc, intervertebral cartilage; ms, marrow space; nc, notochord; ncs, notochordal sheath; od, odontoid process; pb, perichondral bone.
When the mid-trunk vertebrae of Delma, Aprasia and Pletholax are compared with the most anterior centra in the column (Figs 3:7D, 3:8C, D), it is seen that the amount of chordal bone is approximately the same in these two regions of the body. Constriction of the notochord within the ends of the centra, on the other hand, is more advanced in the middle of the trunk than it is in the more anterior and posterior regions of the column, not only in these three genera, but in all procoelous geckos and pygopods (Figs 3:1-3:8). In those animals with a continuous notochord the convexity of the condyle depends on the degree of chordal constriction, so that the largest condyles are also found on the mid-trunk vertebrae (e.g. Figs 3:3A, B; 3:7A, B). Those animals which had lost their chordal continuity between adjacent centra showed little variation in the size of the condyle throughout the presacral series (e.g. Figs 3:4B, 3:8B). In those gekkotans in which the procoelous condition was least well developed, namely Carphodactylus and juvenile Phyllurus miliis, the trunk vertebrae had recognisable condyles (Fig. 3:1C) but the cervical centra differed only slightly from the amphicoelous condition (Fig. 3:5C). The pygal vertebrae of juvenile and adult procoelous gekkotans usually had a more or less well developed condyle but those of Carphodactylus and juvenile P. miliis had none and were therefore amphicoelous.

The sequence of mid-dorsal closure of the neural arches, seen in hatchlings, also begins in the mid-trunk region. A similar situation is also seen in hatchling Sphenodon in which the two halves of the neural arches of the middle of the body are
Centra of axis and third vertebra of *Pygopus* and *Delma* (Fam. Pygopodidae) in sagittal section, showing the smaller degree of notochordal reduction in this region than in the trunk (cf. Fig. 3:3).

A. *Pygopus lepidopodus*, juvenile;
B. *P. lepidopodus*, adult;
C. *Delma fraseri*, sub-adult;
D. *D. fraseri*, adult.

*axhs*, axial hypapophyseal spine; *c*, condyle; *cart*, uncalcified cartilage; *cc*, chordal cartilage; *cct*, calcified cartilage; *eb*, endochondral bone; *icax*, axial intercentrum; *icCe3*, intercentrum of third cervical vertebra; *ivc*, intervertebral cartilage; *ms*, marrow space; *nc*, notochord; *ncs*, notochordal sheath; *od*, odontoid process; *pb*, perichondral bone; *rcc*, region of maximum chordal constriction.
closer together than those of the neck, sacrum and tail, although none of the arches in this specimen had fused. With respect to the intercentra of *Sphenodon* (Howes & Swinnerton, 1901), loss of the primary intercentra and their subsequent replacement by secondary intercentra also begin in the trunk. The early development of axial structures, however, such as the differentiation of the notochord and somites, proceeds in a posterior direction in reptiles as in vertebrates generally (Strahl, 1883; Peter, 1904; Defaure & Hubert, 1961; Zehr, 1962; Yntema, 1968). In birds (Romanoff, 1960, pp. 924-948), internal differentiation of the notochord and development of the vertebrae begin anteriorly and proceed towards the tail. Although, in some birds, thoracic ossification centres may appear at the same time as those of the anterior cervical vertebrae, the cranio-caudal gradient is established a few days later (Romanoff, *op. cit.*, Fig. 349). Among mammals, the human embryo (Sensenig, 1949) resembles geckos and pygopods in that closure of the neural arches and involution of the notochord spread rostrally and caudally from the thorax. What has caused this change from the rostro-caudal gradient seen in earlier stages does not appear to be known.

All geckos and pygopods, irrespective of the shape of their centra or the state of the notochord, have non-synovial intercentral joints. Between amphicoelous centra the intervertebral tissue is in the form of a cartilaginous ring fused to the adjacent centra, while in procoelous gekkotans it takes the form of a cup which is perforated by the notochordal canal in those animals with a continuous intervertebral notochord. Contrary to the opinion of Hoffstetter & Gasc (1969), there is
no morphological evidence that the amphicoelous intervertebral joints of geckos function as though they were procoelous or that those of Sphenodon are functionally opisthocoelous. The thick peripheral cartilage described by Hoffstetter & Gasc as making a strong rim which is fixed to the circular edge of the centrum is in fact the ring of intervertebral cartilage, while the anterior "cartilage", described as especially well developed in the centre of the cavity, resembling a condyle, must, from its position, be the intervertebral region of the notochord.

The intervertebral cartilage is extremely fibrous, particularly in procoelous forms (Pls 11A-C, 12A-D) and is thus very different from the hyaline cartilage investing the articulating surfaces of joints such as the zygapophyses (Pl. 10B) which have a synovial cavity (see also Werner, 1971). In some sections of procoelous gekkotan vertebrae which have lost the notochord from the intervertebral region there appears to be a joint cavity between adjacent centra (Pl. 11B) but this is an artefact caused by shrinkage during preparation; separation is rarely complete and strands of cartilage cross the space between the centra. In contrast to geckos and pygopods, most other procoelous squamates such as the blind snake Typhlops nigrescens have a synovial joint between adjacent centra (Pl. 12E), the only known exception being Xantusia vigilis (vide infra).

At the beginning of the postpygal series of autotomous vertebrae in pygopods and procoelous geckos there is a marked reduction in the size of the condyle accompanied by a marked increase in the thickness of the intervertebral cartilage so that the reduced condyles of the anterior postpygal vertebrae
Figure 3:8

Centra of axis and third vertebra of *Lialis*, *Aprasia* and *Pletholax* (Fam. Pygopodidae) in sagittal section, showing the smaller degree of notochordal reduction in this region than in the trunk (cf. Fig. 3:4).

A. *Lialis burtonis*, juvenile;
B. *L. burtonis*, adult;
C. *Aprasia pulchella*, adult;
D. *Pletholax gracilis*, adult;

*axhs*, axial hypapophyseal spine; *c*, condyle; *cart*, uncalcified cartilage; *cc*, chordal cartilage; *cct*, calcified cartilage; *eb*, endochondral bone; *hsCe3*, hypapophyseal spine of third cervical vertebra; *icax*, axial intercentrum; *icCe3*, intercentrum of third cervical vertebra; *ivc*, intervertebral cartilage; *ms*, marrow space; *nc*, notochord; *ncs*, notochordal sheath; *od*, odontoid process; *pb*, perichondral bone.
no longer fit into the concavities of the following centra. Further posteriorly the condyles disappear altogether (Fig. 3:22). The condyles also disappear in Pletholax which is incapable of autotomy (Fig. 3:22D) but the thickening of the intervertebral cartilage, like that in geckos such as Phyllurus platurus whose fracture planes are restricted to the first two or three postpygal vertebrae (Fig. 3:22B), is less marked than in the tails of other gekkotans which can undergo autotomy at any point in the postpygal tail. In those animals whose notochord is continuous between adjacent centra, namely juveniles, Carphodactylus, Phyllurus milii, Sphaerodactylus and Aprasia and in some adult Coleonyx and Pygopus, all but the most anterior postpygal vertebrae have essentially the same type of notochordal amphicoelous articulation as the trunk and tail vertebrae of most geckos. In adult Delma and Lialis and in older specimens of Pygopus and Coleonyx where the notochord has been lost from the ends of the centra, the acoelous ends of adjacent caudal centra are joined together by an unperforated mass of intervertebral cartilage. The presence of non-synovial joints in the autotomous region of the tail, as distinct from the precaudal region of the body, may not be uncommon in lizards as it also occurs in the lacertid Lacerta vivipara (Pl. 12G) in which the presacral vertebrae articulate by means of synovial joints.

Xantusia

There were no remnants of the notochord visible in the centra of Xantusia vigilis, either in the cervical vertebrae (Fig. 3:6C) or those of the trunk (Fig. 3:2C), although a small
indentation in the surface of condyles of trunk vertebrae indicated its former position. The condyles were comparable in size and shape to those of procoelous geckos and pygopods which had lost the notochord from the intervertebral region and showed little variation throughout the precaudal series. The condyles of the postpygal vertebrae became smaller posteriorly and were soon lost so that most of the caudal centra were acoelous, being joined together by a thick disc of intervertebral cartilage.

At no point in the vertebral column of Xantusia vigilis was there a joint cavity between adjacent centra, so that the centra of this lizard articulate in the same way as those procoelous geckos and pygopods. Unfortunately, however, it was not possible to determine how and when the notochord is lost from the centra of Xantusia as only one adult specimen was available for study. In other non-gekkotan lizards such as Lacerta vivipara and Anguis fragilis, of which a large series of embryonic and neonatal stages was available, the notochord together with its poorly defined sheath is completely resorbed soon after birth while the centrum is still largely cartilaginous, at approximately the same time as the synovial cavities appear between adjacent centra. The notochord is lost from the ends of the centra shortly before birth, largely through centripital growth of the cartilage in the condyle.
REGIONAL MORPHOLOGY

ATLAS (Figs 3:9 - 3:15)

Atlas is a ring-shaped vertebra consisting of the paired neural arches and intercentrum of the first vertebra, the atlantal centrum having been incorporated into axis as its odontoid process or dens epistrophei. The neurapophyses are united to the intercentrum by uncalcified cartilage in embryonic and juvenile stages but in adults these elements are fused together to form a bony ring. In a juvenile specimen of Phyllurus platurus a strong ligament, as well as the cartilage, was found to connect the intercentrum to the neurapophyses (Fig. 3:9B). In adult Hemitractus frenatus the components of atlas fuse intimately but a thin ligament lies ventrally across the suture (Fig 3:9A).

Mahendra (1950) maintained that the connection in H. flaviviridis is by means of a ligament only but in the New Zealand geckos, Hoplodactylus and Naultinus, the atlantal elements fuse together (N. G. & E. M. Stephenson, 1956). Stokely (1947) described the atlas of Aprasia repens as consisting only of the neurapophyses, making no mention of the intercentrum which, according to Romer (1956), forms the ventral part of the atlantal ring in all but the most primitive fossil reptiles and in mammals.

The atlantal intercentrum usually bears a median ventral spine whose size varies in different species and, to some extent, within species. Among the Australian geckos it may be a knob, a spine or a laterally compressed blade, but in most cases it is relatively small. In many of the other geckos examined, particularly in Aristelliger (Fig. 3:11A), the atlantal hypapophyseal
Figure 3:9

Cervical vertebrae and ribs of geckos.

A. Hemidactylus frenatus, adult, anterior view of atlas;
B. Phyllurus platurus, juvenile, posterior view of atlas;
C. Gehyra variegata, adult, dorsal view of first four cervical vertebrae;
D. Phyllurus platurus, adult, anterior view of sixth cervical vertebra and right rib.

abs, atlantal hypapophyseal spine; ansp, axial neural spine; arr, anterior ramus of distal rib element; cart, uncalcified cartilage; cct, calcified cartilage; cf, costal facet; cn, centrum; co, canal which encloses odontoid process; cpv, costal process of vertebra; dl, dorsal costal ligament; fa, facet which articulates with axis; fo, facet which articulates with occipital condyle; hl, horizontal ligament; ic, intercentrum; l, ligament; nap, neural arch pedicel; nat, atlantal neurapophyses; nca, neural canal; ncc, notochordal canal; nsp, neural spine; oc, occipital region of skull; pre, proximal rib element; prr, posterior ramus of distal rib element; prz, prezygapophysis; pz, postzygapophysis; rh, rib head; sc, spinal cord; sut, suture; vlc, branch of ventral costal ligament to centrum; vli, branch of ventral costal ligament to intercentrum.
spine is very large. Among the pygopods, *Lialis* (Fig 3:15A) and *Delma* (Fig 3:14B) usually have a long spine on the atlantal intercentrum which may extend anteriorly and posteriorly to form a blade. *Aprasia* (Fig 3:14C) has no atlantal hypapophyseal spine and *Pygopus* (Fig 3:14A) either has none or, if a spine is present, it is in the form of a low knob as in *Pletholax* (Fig 3:15B).

On their anterior surfaces the intercentrum and the bases of the arch pedicels together bear a semicircular facet, covered with hyaline cartilage, for articulation with the single occipital condyle of the skull (Fig 3:9A). In a similar position on their posterior surface these elements bear a similar facet for articulation with the odontoid process of axis and the anterior face of the axial intercentrum (Figs 3:9B, 3:10A). Connecting the atlantal neurapophyses to one another, just above these facets, is a broad transverse ligament which divides the canal enclosed by atlas into a dorsal neural canal and a smaller ventral canal for the odontoid process. A similar ligament occurs in the New Zealand geckos (N. G. & E. M. Stephenson, 1956), in the snakes, *Typhlops jamaicensis* (Evans, 1955) and *Cylindrophis rufus* (Williams, 1959b), and is apparently of widespread occurrence since, according to Williams, the head joint of *C. rufus* is typical of the usual squamate condition. The function of the transverse ligament is clearly to prevent dorsal deflection of the odontoid process and resultant injury to the spinal cord.

The atlantal neurapophyses failed to fuse dorsally above the spinal cord in 17 of the 36 species of gecko examined (Figs 3:9A, B, C), among which were representatives of the Diplo-
dactylinae, Gekkoninae and Bublepharinae (sensu Kluge, 1967a). Lack of fusion in this region has also been recorded for Uroplatus fimbriatus (Siebenrock, 1893) and Hemidactylus flaviviridis (Mahendra, 1950), and has already been described in Hoplodactylus and Naultinus by N. G. & E. M. Stephenson (1956) and in Coleonyx by Kluge (1962b). In the Australian diplodactyline genus, Nehrurus, only immature specimens show this lack of fusion; the adult atlas is completely roofed over although a suture may be present. This condition also occurs in Phyllurus milii whereas in P. platurus and P. cornutus the atlantal neurapophyses remain separate throughout life. Other Australian diplodactyline geckos in which there was a tendency towards fusion of the atlantal neurapophyses were Diplodactylus strophurus, D. tessellatus, D. vittatus, Oedura lesueurii and O. marmorata. Two species of Australian gekkonines, namely Crenadactylus ocellatus and Phylloodactylus marmoratus, also have the fused condition. Of the non-Australian geckos, fusion was found to occur in the gekkonines Gekko vittatus, Hemidactylus garnotii, Phylloodactylus guntheri and all three species of Lepidodactylus and in the sphaerodactyline species Gonatodes albogularis and Sphaerodactylus parkeri. Fusion also occurred in the eublepharine, Coleonyx brevis, but not in C. variegatus. Mid-dorsal fusion of the atlantal neurapophyses is found only in adult geckos; in immature stages they are separate.

According to Mahendra (1950), the unfused condition of the atlantal neural arch is primitive in lizards. Underwood (1954) considered this view to be untenable as unfused atlantal neurapophyses are apparently characteristic of amphicoelous geckos, but in 1955 he reversed his opinion, stating that he regarded
the unfused condition as a primitive character among geckos. The significance of this character within the Gekkonidae seems to be questionable, however, as both the fused and unfused conditions are not only found in at least three of the four subfamilies, the Bublepharinae, Diplodactylinae and Gekkoninae, but occur even within genera, viz Hemidactylus and Coleonyx. The unfused condition of adults may represent a neotenic state since, according to Stephenson (1960), neotony is widespread among Australian geckos, except that it does not appear to be correlated with neotony of the skull. Carphodactylus, Phyllurus platurus and P. cornutus have unfused atlantal neurapophyses, yet these are large geckos like Nephurus and the posterior roofing of the adult skull is comparable in all these forms. Conversely, some of the genera with markedly neotenic skulls compared with adult Nephurus have fused atlantal neurapophyses.

The atlantal neurapophyses of adult pygopods are usually fused mid-dorsally with complete obliteration of the suture (Fig 3:10A) although occasionally in Pygopus they are found to be separate. In juveniles they are more often separate but even in very young specimens of Lialis they are intimately fused with no suture. According to Underwood (1957a) the atlantal neurapophyses of Delma, Pygopus and Lialis remain paired whereas those of Aprasia pulchella are fused together, while Stokely (1947) described the atlantal arches of A. repens as dorsally united. It appears that, in general, the atlantal neural arch closes earlier in pygopods than in geckos as the fused condition was found among juveniles, but growth of the arches towards the midline apparently continues in Pygopus after sexual maturity has
Figure 3:10

Anterior vertebrae and ribs of pygopods.

A. *Delma fraseri*, sub-adult, posterior view of atlas;
B. *Pygopus lepidopodus*, adult, anterior view of sixth vertebra;
C. *Lialis burtonis*, adult, biramous ribs of fifth and sixth, undivided ribs of fourth and seventh vertebrae.

*ahs*, atlantal hypapophyseal spine; *arr*, anterior ramus of distal rib element; *awp*, anteroventral process of rib head; *cart*, uncalcified cartilage; *cct*, calcified cartilage; *cf*, costal facet; *cn*, centrum; *co*, canal which encloses odontoid process; *cpv*, costal process of vertebra; *dl*, dorsal costal ligament; *dre*, distal rib element; *fa*, facet which articulates with axis; *hl*, horizontal ligament; *ic*, intercentrum; *ica*, atlantal intercentrum; *nap*, neural arch pedicel; *nat*, atlantal neurapophyses; *nca*, neural canal; *ncc*, notochordal canal; *nsp*, neural spine; *pre*, proximal rib element; *prr*, posterior ramus of distal rib element; *prz*, prezygapophysis; *pz*, postzygapophysis; *V4-V7*, ribs of fourth to seventh vertebrae; *v1c*, branch of ventral costal ligament to centrum; *vli*, branch of ventral costal ligament to intercentrum.
been reached as both the fused and unfused conditions were found in adult specimens.

Unfused atlantal neurapophyses also occur in non-gekkotan lizards, having been observed in a scinc *Tiliqua scincoides*, a lacertid *Lacerta vivipara*, an anguid *Anguis fragilis* and an agamid *Amphibolurus muricatus*. In the 14 species of the agamid genera *Amphibolurus* and *Tympanocryptis* examined by Mitchell (1965a) the atlantal neurapophyses were also unfused and in most species were widely separated from one another. In these circumstances it would appear that a lack of fusion of the two halves of the atlantal neural arch above the spinal cord may not be uncommon in lizards.

The atlantal neural spine is poorly developed in geckos and pygopods, even where the atlantal neurapophyses are fused. Among the geckos with a fused arch the spine was best developed in *Gonatodes albogularis* where it took the form of a very low, narrow ridge. In *Carphodactylus laevis* and several specimens of *Hemidactylus frenatus*, in which the arch was not fused, the medial edges of the separate neurapophyses extended dorsally into very low spines. An atlantal neural spine is often present in *Lialis*, *Pletholax* and *Pygopus*, taking the form of a low knob or longitudinal ridge situated mid-way along the arch, but was absent from *Aprasia* and *Delma*.

The base of each atlantal arch pedicel of adult geckos, close to its junction with the intercentrum, often bears a laterally directed process. In *Gonatodes*, *Sphaerodactylus* (Fig 3:12B), *Hemidactylus* (Figs 3:9A, 3:11B) and *Coleonyx* (Fig 3:13A) it takes
the form of a well developed, slightly oblique ridge and in one specimen of *Lepidodactylus* was a small pointed spine. In other adult geckos such as *Oedura* (Fig 3:12A) and *Phyllurus platurus* (Fig 3:9B) there is no distinct process in this position. These processes serve for the attachment of muscles and are considered here to be serially homologous with the rib-bearing costal processes of the more posterior vertebrae, even though, in geckos, they have not been observed to bear ribs. The terms parapophysis, diapophysis or synapophysis are not used here to describe the costal process of the vertebra (cf. Holder, 1960) because they imply that the head of the rib is a capitulum, a tuberculum or both fused together. The nature of the rib head in gekkotans is discussed later in Part IV.

Among the pygopods, *Lialis* has atlantal costal processes in the form of conspicuous spines or ridges. In *Pletholax* (Fig. 3:15B) and in some specimens of *Delma* (Fig. 3:14B) they were large knobs while in other *Delma* and in some *Pygopus* and *Aprasia* the costal processes were comparatively small. Other specimens of *Pygopus* (Fig. 3:14A) and *Aprasia* (Fig. 14C) completely lacked atlantal costal processes. There appears to be no correlation in pygopods or in geckos between the size of these processes and the age of the animal.

It appears that large atlantal costal processes, particularly those of *Lialis*, should more accurately be termed pleurapophyses to imply that they incorporate rib material because three specimens of *L. burtonis* were found to have paired atlantal ribs. These ribs were bony in the two adult animals and cartilaginous in the juvenile and in each case were intimately fused to
their vertebrae, their existence being shown by a suture across their bases. In one adult (Fig. 3:15A) both proximal and distal rib elements were present, the latter in the form of a small bony nodule fused to the end of the pleurapophysis. In all three animals ribs were present on axis as well as the most posterior presacral vertebrae so that ribs were present throughout the precaudal series. Ribs were present on the first two vertebrae of eusuchians such as _Prolacerta_ (Piveteau, 1955, p. 551) and the fossil rhynchocephalian _Champsosaurus_ (op. cit., p. 570) so it is probable that a complete series of precaudal ribs was characteristic of the early lepidosaurs (Romer, 1956, p. 283). In geckos and most pygopods only the costal processes remain, the ribs having disappeared, but in some pygopods, notably _Lialis_, the large atlantal paraphyses may be derived in part from costal elements which are distinct in embryonic stages but which later become indistinguishably fused to the vertebra.

The atlantal neural arch of geckos (Figs. 3:9C, 3:11, 3:12A, B, 3:13A) and of pygopods (Figs 3:14, 3:15) is widely separated both from the skull and from the axial neural arch and does not articulate with the latter. These spaces are covered over by thin sheets of connective tissue. The spacing of the anterior cervical elements together with the lack of articulation between the axial and atlantal neural arches permits freedom of movement of the atlas on the odontoid process of axis.

Each atlantal neurapophysis in most geckos and in the pygopods _Lialis_ and _Pletholax_ bears a horizontal, posteriorly curved process on the angle formed by the stout arch pedicel
Cervical vertebrae of geckos in lateral view.

A. *Aristelliger praesignis*, juvenile;
B. *Hemidactylus frenatus*, adult.

_ahs_, atlantal hypapophyseal spine; _arr_, anterior ramus of distal rib element; _axhs_, axial hypapophyseal spine; _cn_, centrum; _cpv_, costal process of vertebra; _dl_, dorsal costal ligament; _drb_, bifurcated distal rib element; _ica_, atlantal intercentrum; _icax_, axial intercentrum; _ivc_, intervertebral cartilage; _nap_, neural arch pedicel; _nat_, atlantal neurapophyses; _ns_, neurocentral suture; _nsp_, neural spine; _od_, odontoid process; _pre_, proximal rib element; _prr_, posterior ramus of distal rib element; _prz_, prezygapophysis; _pz_, post-zygapophysis; _rh_, rib head; _scf_, subcentral foramen; _vlc_, branch of ventral costal ligament to centrum; _vli_, branch of ventral costal ligament to intercentrum.
and the thin dorsal lamina. The zygapophyses are found in this position on the following vertebrae and for this reason the processes on the atlantal arch are considered to be serially homologous with the following postzygapophyses. The atlantal postzygapophyses are small in *Aprasia* and most *Delma* but occasionally in *Delma* they are quite prominent, pointed spines. In *Pygopus* they take the form of low ridges or knobs. Adult *Nephrurus* was the only gecko found to lack large atlantal postzygapophyses, these processes being represented by low, horizontal ridges. In immature stages, however, they were the well developed structures typical of the adults of other genera. In pygopods there appears to be no correlation between the size of the processes and the age of the animals.

The atlas of *Xantusia vigilis* (Fig. 3:13B) resembled in many respects the first vertebra of geckos and pygopods. The atlantal intercentrum was fused to the neurapophyses, but with a distinct suture, and its hypapophyseal spine took the form of a large, longitudinal blade. The laminae of the neural arch were widely separated mid-dorsally as in many geckos and a transverse ligament connected the bases of the arch pedicels across the canal enclosed by the atlas. The costal processes were large, blunt processes on the neural arch pedicels, just above their junction with the intercentrum, and the neural arch itself was widely separated from that of axis.

However, unlike geckos and pygopods, the atlantal postzygapophyses of *Xantusia* articulated with the prezygapophyses of axis. Each atlantal postzygapophysis was greatly elongated compared with those of the more posterior vertebrae, was much larger
than the atlantal postzygapophyses of geckos and pygopods, and bore an articular facet on its mesial surface. Unlike the more posterior zygapophyseal facets which were inclined no more than 45° to the horizontal, these facets were orientated vertically, thus allowing dorsoventral flexion but limiting lateral flexion and rotation of atlas with respect to axis.

The atlas-axis complex in lizards has been reviewed or described in general terms by a number of authors including Remane (1936), Romer (1956) and Hoffstetter & Gasc (1969). It has also been described or figured in members of various families including the Scincidae (El-Toubi, 1938), Agamidae (El-Toubi, 1947a; George, 1956), Iguanidae (Evans, 1939; Blanc, 1965), Amphibianidae (Zangerl, 1945) and the Anniellidae (Barrows & Smith, 1947). The atlantal postzygapophyses are often illustrated overlying the anterior margin of the axial neural arch (e.g. Romer, 1956, Fig. 121c, f; Hoffstetter & Gasc, 1969, Fig. 44 AI, AII) in a position which would theoretically allow articulation between the arches. The atlantal postzygapophyses of *Sphenodon* occupy a similar position but Hoffstetter & Gasc stated that there is no zygapophyseal articulation with axis and personal inspection has confirmed this. According to Hoffstetter & Gasc, the atlas of lizards resembles that of *Sphenodon*. There are few specific references in the literature, however, to the presence or absence of articulation between the atlantal and axial neural arches of lizards. One is by Evans (1939) who described tiny atlantal postzygapophyses articulating with correspondingly small axial prezygapophyses in *Iguana* sp. while George (1956) described anteriorly directed prezygapophyses on the axial neural arch of the agamid
Figure 3:12

Cervical and dorsal vertebrae of geckos in lateral view.

A. Oedura le sueurii, adult, presternal vertebrae;
B. Sphaerodactylus parkeri, adult, atlas, axis and third cervical vertebra;
C. Gonatodes albogularis, adult, sixth cervical and first dorsal vertebrae.

ahs, atlantal hypapophyseal spine; axhs, axial hypapophyseal spine; c, condyle; cct, calcified cartilage; cpv, costal process of vertebra; dl, dorsal costal ligament; drb, bifurcated distal rib element; dre, distal rib element; hs, hypapophyseal spine; ivc, intervertebral cartilage; l, ligament; nsp, neural spine; od, odontoid process; pr, bony process; pre, proximal rib element; prz, prezygapophysis; pz, postzygapophysis; rh, rib head; rr, rudimentary rib; scf, subcentral foramen; vlc, branch of ventral costal ligament to centrum; vli, branch of ventral costal ligament to intercentrum.
**Uromastix hardwickii** for articulation with the atlas.

Examination of several non-gekkotan lizards has shown that a joint may be present in this position in some members of a family and absent from others. In the Australian agamids *Amphibolurus muricatus* and *Moloch horridus* the atlantal postzygapophyses and axial prezygapophyses are stout processes bearing large facets for articulation whereas in other Australian agamids *Tympanocryptis* sp. and *Amphibolurus adelaidensis* the processes are smaller and non-articulating. Articulating facets are also present in the British lacertid *Lacerta vivipara* but are absent from the British anguid *Anguis fragilis* and the Australian scincs *Tiliqua scincoides* and *Hinulia* sp. Moving joints between the neural arches of atlas and axis may be regarded as a primitive characteristic in living lizards since they occurred in cotylosaurs such as *Seymouria* (Gasc, 1961, Fig. 1) and *Diadectes* (Evans, 1939) and in early mammal-like reptiles (Kemp, 1969) and are retained today in the Chelonia, the only surviving members of the Anapsida, whose atlas-axis complex has changed little from that of the earliest known chelonians of the Triassic (Romer, 1956; Hoffstetter & Gasc, 1969). These joints are also found in living crocodilians, the only surviving archosaurs (Hoffstetter & Gasc, 1969). The atlas-axis complex as a whole in cotylosaurs, mammal-like reptiles, chelonians and crocodilians is more primitive than that of lizards in that the atlantal centrum is exposed ventrally rather than modified to form the odontoid process of axis. The phylogenetic significance of the articulations between the atlantal and axial neural arches in lizards is problematical, however, as they may not only be
present or absent in different genera within a family but also in different species of the same genus.
AXIS (Figs 3:5 - 3:9, 3:11 - 3:15)

The axis is a compound structure consisting of the paired neurapophyses, centrum and intercentrum of the second vertebra together with the atlantal centrum modified to form its odontoid process (or dens epistrophei). In juveniles these elements are joined together by uncalcified cartilage but in adults they are fused and the sutures lost. The atlantal centrum is attached to the dorsal half of the anterior face of the axial centrum and to the dorsal surface of the axial intercentrum and its narrow anterior portion constitutes the odontoid process on which the atlas rotates. Overlying the anterior and lateral surfaces of the odontoid process is a layer of hyaline cartilage for articulation with the atlas. This cartilage is thickened at the anterior end of the dens, providing a cushion for articulation with the occipital condyle of the skull.

In embryonic specimens the notochord extends unbroken through the dens into the occipital region of the skull but is later constricted and severed within the dens as the latter becomes rounded for articulation with the occipital condyle. This is the only point throughout the vertebral column at which the notochord is severed in amphicoelous geckos, the procoelous geckos Carphodactylus laevis, Phyllurus milii and Sphaerodactylus parkeri and in juvenile Coleonyx and pygopods. It extends to the tip of the dens in juvenile Pygopus (Fig. 3:7A) and almost to the tip in sub-adult Coleonyx (Fig. 3:6A) in which the components of the axis are still separate elements. A small depression may persist on the anterior surface of the dens, indicating the position of the
nootochord before it was severed.

With increasing age the part of the notochord situated in the narrow anterior part of the atlantal centrum is replaced by cartilage, then by bone. In some geckos and pygopods, for example Coleonyx and Pygopus (Figs 3:6B, 3:7B), the notochord of the dens is apparently constricted to a thread before being replaced by cartilage, while in others such as Phyllurus (Fig. 3:5) and Lialis (Fig. 3:8A) the replacing cartilage appears to grow back within the chordal canal, incorporating the odontoid chordal cartilage within it.

In amphicoelous geckos (Fig. 3:5B) and Carphodactylus the notochord is lost only within the dens itself: the wide posterior portion of the atlantal centrum retains the notochord surrounded by its sheath. In Phyllurus milii and Sphaerodactylus the notochord is lost from the entire atlantal centrum but persists in the axial centrum (Fig. 3:5D, E). This condition is also found in some adult Coleonyx (Fig. 3:6B) and Pygopus (Fig. 3:7B) in which the notochord is still continuous between axis and the third vertebra, but in older specimens and in adult Lialis (Fig. 3:8B) which have lost their chordal continuity, most of the notochord in the axial centrum has disappeared. Loss of the axial notochord in Delma, Aprasia and Pletholax is apparently caused also by the ossification of the chordal cartilage which occurs in the third and following vertebrae of the column (Figs 3:7D; 3:8C, D).

Mahendra (1950) described in Hemidactylus flaviviridis a peculiar prominent process projecting forwards from the dorsal
Figure 3:13

Cervical vertebrae of *Coleonyx* (Fam. Gekkonidae) and *Xantusia* (Fam. Xantusiidae) in lateral view.

A. *Coleonyx variegatus*, adult, first five cervical vertebrae;

B. *Xantusia vigilis*, adult, first five cervical vertebrae.

Intervertebral cartilage not shown.

 ahhs, atlantal hypapophyseal spine; arr, anterior ramus of distal rib element; axhs, axial hypapophyseal spine; c, condyle; cct, calcified cartilage; cn, centrum; cpv, costal process of vertebra; dl, dorsal costal ligament; drb, bifurcated distal rib element; ezs, epizygapophyseal spine; icCe3, intercentrum of third cervical vertebra; nap, neural arch pedicel; nat, atlantal neurapophyses; nsp, neural spine; pro, proximal rib element; prr, posterior ramus of distal rib element; prz, prezygapophysis; pz, postzygapophysis, rh, rib head; rr, rudimentary rib; scf, subcentral foramen; sut, suture; vlc, branch of ventral costal ligament to centrum; vli, branch of ventral costal ligament to intercentrum.
part of the \textit{dens}. This process in geckos and pygopods, and also in \textit{Sphenodon} (Howes & Swinnerton, 1901), is the \textit{dens} itself: the narrow anterior portion of the atlantal centrum of which it is an integral part. In some other amniotes such as the monotreme \textit{Ornithorhynchus} and in cynodonts and tritylodonts (mammal-like reptiles) the \textit{dens} is a neomorphic process distinct from the atlantal centrum which is distinguishable as a separate element in embryos and constitutes the anterior part of the body of axis (Jenkins, 1969).

The axial intercentrum is the largest in the column (Figs 3:5 - 3:8) and is usually produced ventrally into a hypapophyseal spine to which are attached subvertebral muscles and ligaments. In geckos this process is usually a prominent median ridge, knob or blunt spine and in the pygopods \textit{Lialis} and \textit{Delma} it takes the form of a large, median blade. In \textit{Aprasia}, \textit{Pletholax} and most \textit{Pygopus} it is a low knob or ridge, while in other specimens of \textit{Pygopus} it is absent altogether. There is often an accessory process lying on each side of the median spine so that from the ventral aspect the axial intercentrum is seen to bear three posteriorly directed processes.

Mahendra (1950) described two hypapophyses on the axis of \textit{Hemidactylus flaviviridis}, the anterior one belonging to the odontoideum and the posterior to the centrum of the axis. In fact, the hypapophysis belonging to the odontoideum is the atlantal intercentrum which is attached to the atlantal neurapophyses, and the hypapophysis lying ventrally to the odontoideum belongs to the axis. The second hypapophysis described by Mahendra may possibly be the intercentrum of the third cervical vertebra which
has become fused to the posterior end of the axial centrum. Although no such fusion of the third intercentrum has been noted by the present author in any gecko, it was found in one pygopod, a specimen of *Aprisia pulchella*. In adult pygopods which lack free intercentra in the precaudal column, namely *Aprasia* (Fig. 3:14C) and *Pletholax* (Fig. 3:15B), the third intercentrum is normally fused to the anterior edge of its own centrum.

The axial costal processes are usually in the form of a ridge on the base of the arch pedicel, sloping up and back and extending ventrally onto the centrum. Its position is ascertained from juveniles (Fig. 3:11A) in which the neurocentral suture is still visible. These processes are particularly prominent in the geckos *Sphaerodactylus* (Fig. 3:12B), *Lepidodactylus* and *Hemidactylus* (Fig. 3:11B) and the pygopods *Lialis*, *Delma* (Fig. 3:14B) and *Pletholax* (Fig. 3:15B) but are entirely absent from *Aprasia* (Fig. 3:14C).

Axial ribs have not been seen in geckos but do occur in pygopods. They were present in two specimens of *Delma fraseri*, in seven *Lialis burtonis*, three of which possessed atlantal ribs as well, and in one specimen of *Pygopus lepidopodus* (Fig. 3:14A). In general, the axial ribs consisted only of the proximal bony portion which was either ankylosed to the costal process of the vertebra or connected to it by a ligament, but in some cases the ventral cartilaginous portion was present as well. In one specimen of *Lialis* (Fig. 3:15A), in which the atlas also bore proximal and distal rib elements, both the proximal and distal portions of the axial ribs were ossified and the rib heads articulated with the costal processes in the same way as the more posterior ribs.
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of the column. According to Underwood (1957a), the most anterior pair of ribs is borne by the third vertebra in *Delma*, *Pygopus* and *Lialis* and by the fourth vertebra in *Aprasia*, and Hoffstetter & Gasc (1969) considered the limbless burrowing lizard *Dibamus* to be unique among the Sauria in having small free ribs on the axis. It appears, however, that axial and even atlantal ribs may not be uncommon among pygopods.

The axial neurapophyses are fused mid-dorsally and extend into a large neural spine which projects anteriorly and posteriorly over the ends of the arch and which is almost always taller than those of the following cervical vertebrae. In very young specimens the whole of the dorsal edge of the spine is capped with cartilage but, with increasing age, the cartilage becomes restricted to the posterior end of the spine which eventually becomes completely ossified.

The anterior edge of each axial neurapophysis may bear a small process lying in the plane of the arch or projecting laterally for a short distance. These processes are reduced and non-articulating prezygapophyses. Among the geckos they are most pronounced in *Carphodactylus*, *Phyllurus* and *Coleonyx* (Fig. 3:13A) but are absent from *Nephrurus*, *Crenadactylus*, *Rhynchoedura* and the three Jamaican forms. The New Zealand geckos (N. G. & E. M. Stephenson, 1956) and *Hemidactylus flaviviridis* (Mahendra, 1950) also have reduced axial prezygapophyses. Among the pygopods these processes are usually absent or very small but in one specimen of *Lialis* they were well developed spines.

Projecting posteriorly from the axial neural arch of all pygopods, just dorsally to each postzygapophysis, is a prominent
spine to which epaxial muscles are attached (Figs 3:14, 3:15). A similar spine is found in this position in some colubrid and crotalid snakes and was given the name spizygaphyseal spine by Auffenberg (1963). The spines become smaller on the more posterior vertebrae but may occur as far back as the fifth vertebra in some specimens of *Pygopus* and *Delma*. Epizygaphyseal spines were found in only one gecko, *Coleonyx* (Fig. 3:13A), and were very small compared with those of pygopods.

In *Xantusia vigilis* the components of the axis were fused together and the sutures obliterated (Fig. 3:13B). Unlike adult geckos and pygopods, the axial centrum of this lizard contained no vestiges of the notochord (Fig. 3:6C). The hypapophyseal spine was a large median blade with a smaller longitudinal ridge on either side of it while the costal processes of axis were prominent ridges which appeared to extend ventrally onto the centrum. Each axial prezygapophysis was a short, anteriorly directed process bearing an articular facet on its outer surface for articulation with the postzygapophyses of atlas (see p.131).
Figure 3.14

Anterior four vertebrae of pygopods in lateral view.

A. *Pygopus lepidopodus*, adult;
B. *Delma fraseri*, adult;
C. *Aprasia pulchella*, adult.

Intervertebral cartilage not shown.

ahs, atlantal hypapophyseal spine; avp, antero-ventral process of rib head; axhs, axial hypapophyseal spine; c, condyle; cct, calcified cartilage; cn, centrum; cpv, costal process of vertebra; dl, dorsal costal ligament; dre, distal rib element; ezs, epizygapophyseal spine; hsCe4, hypapophyseal spine of fourth vertebra; icCe3, intercentrum of third vertebra; nap, neural arch pedicel; nat, atlantal neurapophyses; nsp, neural spine; od, odontoid process; pre, proximal rib element; prz, prezygapophysis; pz, postzygapophysis; rh, rib head; rr, rudimentary rib; scf, subcentral foramen; vlc, ventral costal ligament or branch thereof to centrum; vli, branch of ventral costal ligament to intercentrum.
POSTAXIAL PRESACRAL VERTEBRAE

In this section, the geckos and Xantusia are described separately from the Pygopodidae. This is because their presacral vertebral columns are divisible into cervical, dorsal and lumbar series depending on the structure of the ribs, whereas the presacral ribs of the limbless pygopods differ little in structure and are present on all but the most anterior vertebrae of the series. Furthermore, the factors influencing the morphology of limbless lizards differ greatly in many respects from those affecting limbed forms and comparisons between pygopods and other limbless lizards can more readily be made if the pygopods are described separately.

**Geckos and Xantusia**

**Third, Fourth, Fifth and Sixth Cervical Vertebra (Figs 3:9, 3:11 - 3:13)**

Geckos and Xantusia resemble one another closely in the structure of their remaining cervical vertebrae. In any one animal these vertebrae are basically identical in structure, differing only in the ribs associated with them. Low costal processes in the form of oblique ridges are present on the third cervical vertebra of some genera and are particularly well developed in Conatodes albogularis, Aristelliger praesignis, Hemidactylus frenatus and occasionally in the three species of Phyllurus. When ribs are present on the third vertebra (Figs. 3:12A & B, 3:13) they are rudimentary and most frequently appear on only one side of the body. They usually consist only of the proximal bony shaft
which is either fused to the costal process or attached to it by a ligament or a band of cartilage. When the distal portion of the rib is present it is in the form of a small cartilaginous rod fused to the end of the proximal shaft. It is sometimes calcified but never bifurcated. A pair of ribs occurs occasionally on the third vertebra of *Oedura lesueurii*, *Gehyra variegata*, *Gekko vittatus*, *Lepidodactylus woodfordii* and *Coleonyx variegatus* and was present in the single specimens of *Sphaerodactylus parkeri*, *Coleonyx brevis* and *Xantusia vigilis*. All nine specimens of *Phyllolepidus marmoratus* available for study had a reduced pair of ribs on the third cervical vertebra.

The fourth, fifth and sixth cervical vertebrae bear paired ribs (Figs 3:9D; 3:11, 3:12A, C; 3:13), each of which has a single head articulating with its costal process. The costal processes are borne mainly by the neural arch pedicles but are seen to extend ventrally onto the centrum in those young specimens whose neurocentral sutures are still visible (Fig. 3:11A). A ligamentous band connects the head of the rib to the neural arch above the articulation and a similar ligament joins the rib ventrally to the intercentrum with a smaller branch to the centrum.

The ribs of the fourth, fifth and sixth vertebrae increase in length rostrocaudally but never meet the sternum. Each rib consists of a proximal bony portion attached to the vertebra and a distal cartilaginous portion joined to the proximal shaft. In most genera this distal piece is bifurcated. *Nephrurus asper*, *N. levis*, *Carphodactylus laevis* and *Phyllurus milii* are exceptions, for in these lizards none of the cervical ribs is divided; the distal portion of the rib in each case consists of a simple rod
of cartilage. This undivided condition of the cervical ribs was also found in one of the 33 specimens of *Phyllurus platurus*. In some genera, namely *Diplodactylus* and *Rhynchoedura*, and occasionally in *P. platurus*, the ribs belonging to the fourth vertebra may bear an undivided distal portion while those of the fifth and sixth vertebrae are bifurcated. The ribs of the sixth vertebra of *Naultinus* have single, slender, elongated cartilaginous portions while those of the more anterior ribs are forked (N. G. & E. M. Stephenson, 1956). The type of bifurcation seen here in the cervical ribs of geckos and *Xantusia vigilis*, where only the distal portion of the rib is divided, differs from that in the Egyptian gecko *Tarentola annularis* in which the proximal shafts of the cervical ribs are forked with a small undivided distal rib element at the end of each ramus (El-Toubi & Khalil, 1955, Fig. 2). Bifurcated cervical ribs also occur in other lizards such as *Lacerta simonyi* (Siebenrock, 1894) and *L. vivipara* (personal observation).

In addition to the differences between species of gecko in the occurrence of bifurcated cervical ribs, there is also variation in the relative size of the two rami among those species which have forked ribs. In the Jamaican genera *Aristelliger*, *Gonatodes* (Fig. 3:12C) and *Sphaerodactylus*, and in *Hemidactylus* (Fig. 3:11B), *Lepidodactylus, Coleonyx* (Fig. 3:13A) and *Xantusia* (Fig. 3:13B) the rami are broadly expanded and almost equal in size, whereas in the other genera examined the anterior ramus is considerably longer than the posterior one, the ratio increasing in the more posterior cervical ribs. The ratio is greatest in the third rib of *Phyllurus platurus* (Fig. 3:9D) where the anterior ramus may be as much as six times longer than the posterior one.
Figure 3:15

Anterior vertebrae of pygopods in lateral view.

A. **Lialis burtonis**, adult, first three vertebrae;

B. **Pletholax gracilis**, adult, first four vertebrae.

Intervertebral cartilage not shown.

**ahs**, atlantal hypapophyseal spine; **axhs**, axial hypapophyseal spine; **c**, condyle; **cpp**, costal process of vertebra; **dl**, dorsal costal ligament; **dre**, distal rib element; **ezs**, epizygapophyseal spine; **hsCe3**, **hsCe4**, hypapophyseal spines of third and fourth vertebrae; **icCe3**, intercentrum of third vertebra; **nsp**, neural spine; **od**, odontoid process; **pre**, proximal rib element; **prz**, prezygapophysis; **pz**, postzygapophysis; **rh**, rib head; **rr**, rudimentary rib; **scf**, subcentral foramen; **vlc**, ventral costal ligament or branch thereof to centrum; **vli**, branch of ventral costal ligament to intercentrum.
Both the proximal and distal portions of the cervical ribs increase in length rostrocaudally to give an overall increase in rib length.

In most of the geckos examined the proximal shafts of the cervical ribs are smooth, but in *Nephrurus asper* and *Phyllurus milii* there is a pronounced knob or flange projecting from the anterior edge of each shaft a short distance from the rib head. The function of these processes is obscure.

Calcification of the distal portions of the cervical ribs is of common occurrence in adult geckos as noted also by N. G. & E. M. Stephenson (1956) in *Naultinus* and *Hoplodactylus*, and also occurs in *Xantusia*. No calcification occurs in newly hatched juveniles but gradually takes place during the subsequent growth of the animal. The anterior ramus tends to be the more heavily calcified of the two and calcification of the distal portion as a whole is more marked in the more posterior cervical ribs. At no time do they ossify; they remain cartilaginous, though they may be heavily calcified in comparatively old specimens.

The anterior cervical intercentra of geckos and *Xantusia* are larger than those of the trunk and each of them is prolonged ventrally into a hypapophyseal spine (Figs 3:11; 3:12, 3:13). They decrease in size posteriorly to become small, smooth oval elements similar to those of the trunk. In the Australian geckos none of the cervical intercentral spines is very large and the first dorsal intercentrum is smooth. In *Gonatodes*, *Aristelliger* and *Hemidactylus* the cervical intercentra bear very long hypapophyseal spines and smaller spines are present on the anterior dorsal
intercentra. Hoffstetter & Gasc (1969) noted that the presence of hypapophyseal spines on the cervical intercentra of geckos distinguishes the amphicoelous vertebrae of these lizards from those of *Sphenodon* while various authors including Johnson (1955), Dowling (1959) and Bogert (1964) have referred to the form of the hypapophyses in classifying snakes. When using these processes to show relationships among squamates, however, it should be recognised that their size and shape depend at least in part on the stresses caused by the muscles and ligaments attached to them (Murray, 1936) and that hypapophyses are entirely lacking in chicks which have developed under paralysis (Murray & Drachman, 1969).

The cervical neural arches, excluding the atlantal arch, generally lie close together in adult geckos to form a continuous shield above the spinal cord. Exceptions to this were found in *Heteronotia, Lepidodactylus, Gehyra* (Fig. 3:9C) and *Hemidactylus garnotii* in which there is a considerable space mid-dorsally between the successive arches which is covered over by a thin sheet of connective tissue. In juvenile specimens generally, the cervical neural arches are more widely spaced than they are in adults. The cervical neural spines usually differ somewhat in shape from those of the more posterior vertebrae: apart from the atlas and axis, the remaining cervical spines are often rounded dorsally, in contrast to the triangular or trapezoid spines of the trunk.
Dorsal or Trunk Vertebrae (Figs 3:12, 3:16)

The vertebrae of the dorsal region or trunk of geckos and Xantusia typically bear paired ribs consisting, like those of the cervical vertebrae, of proximal and distal portions. The proximal part of the rib is bone while the distal or sternal part is always cartilaginous and usually heavily calcified. The term "sternal" is more appropriately applied to those ribs connected to the sternum but is frequently used also to denote the distal portions of all the ribs of the column.

The ribs of the seventh and eighth vertebrae, i.e. the first two pairs of ribs in the dorsal series, are long slender structures curving around the body so that their distal extremities are ventral in position but are not united with the sternum (Fig. 3:12A, C). The distal portions of these ribs are short cartilaginous rods which are always single undivided structures and which are uncalcified in juvenile specimens and often heavily calcified in adults. The distal portions of the following four or five pairs of ribs unite with the pectoral girdle, the more anterior two or three pairs directly with the sternal plate while the posterior two pairs unite to form the xiphisternum (N. G. Stephenson, 1960; Kluge, 1962b).

In the Jamaican geckos (Fig. 3:12C) and in Hemidactylus, Gehyra and Lepidodactylus there is a thin, triangular bony blade extending posteriorly from the proximal portion of the ribs of the seventh vertebra. This process may be large, small or absent in Coleonyx and was not present in Xantusia. It is among these lizards that the most marked difference exists between the proximal shafts of the cervical and dorsal ribs. The proximal shafts of the
Figure 3:16

Nineteenth vertebrae of adult geckos in lateral view, showing correlation between size of crest of neural spine (i.e. area of neural spine attached to sub-dermal fascia) and length of presacral column. The diagram above each vertebra is a plan of the neural spine in dorsal view, the crest being cross-hatched.

A. *Phyllophactus guntheri*, presacral column = 58 mm;
B. *Phyllurus platyrus*, 59 mm;
C. *Gebyra oceanica*, 60 mm;
D. *Phyllurus mili*, 64 mm;
E. *Gekko vittatus*, 66 mm;
F. *Nephrurus asper*, 77 mm;
G. *Carphodactylus laevis*, 83 mm;
H. *Phyllurus cornutus*, 90 mm.

c, condyle; cf, costal facet; cn, centrum; dla, point of attachment of dorsal costal ligament; ic, intercentrum; la, crest of neural spine; nap, neural arch pedicel; nsp, neural spine; prz, prezygapophysis; pz, postzygapophysis; scf, subcentral foramen; vla, point of attachment of ventral costal ligament.
cervical ribs are short and broadly expanded for the attachment of the bifurcated distal portion whereas the ribs of the dorsal series are typically long slender structures curving around the body. In view of this difference and the inconstancy of size and occurrence of the process in Coleonyx, this triangular process on the first pair of dorsal ribs appears to indicate a state transitional between the ribs of the cervical and dorsal series.

Romer (1956) maintained that the rib structure seen in seymouriamorphs such as Seymouria and Kotlassia can reasonably be regarded as a primitive reptilian pattern and that the proximal portion of the cervical ribs, with the exception of the atlantal pair, is expanded, presumably for the origin of the serratus and levator scapulae muscles. The expansion of the cervical ribs in some geckos is comparable to the condition in the seymouriamorphs so that there may have been broad cartilaginous processes (which do not readily fossilize) attached to the cervical ribs of seymouriamorphs as there are in geckos. On the eighth and ninth (anterior dorsal) ribs of Kotlassia there are posteriorly directed bony processes (Romer, 1956, fig. 137) which are similar to those seen in some geckos. Thus it would appear that the anterior dorsal ribs of seymouriamorphs as well as some geckos show a condition transitional between the short expanded cervical ribs and the longer, more cylindrical ribs of the dorsal series.

Mahendra (1935b, 1950) described delicate, backwardly projecting processes which he called "uncinate processes" on the ribs of the fourth, fifth, sixth and in some cases the seventh vertebrae of Hemidactylus flaviviridis. If the condition of the anterior ribs of H. flaviviridis is comparable to that of H. frenatus and
H. garnotii, then the first three "uncinates" are cartilaginous and belong to the distal portion of the rib while the fourth "uncinate", on the rib of the seventh vertebra, is a bony flange on the proximal part of the rib. Furthermore, there is no suture between any of the processes and its accompanying rib, even in juvenile specimens in which the neurocentral sutures are still present. If the "uncinate" processes arise as separate structures in geckos as they do in birds (Bellairs & Jenkin, 1960), they must fuse with their ribs at an early stage in development. There is no indication of "uncinate" processes on the ribs of the eighth or subsequent vertebrae.

The term "uncinate" cannot be used indiscriminately to describe processes on ribs, as N. G. & E. M. Stephenson (1956) pointed out. Uncinate processes are typically associated (for example, in birds & Sphenodon) with the proximal portion of the sternal and poststernal ribs, not with the distal portion of the cervical ribs where the so-called "uncinates" are found in the majority of geckos. Only in Gonatodes, Aristelliger, Sphaerodactylus, Lepidodactylus, Hemidactylus, Gebyra and Coleonyx of the 21 genera examined was there found an "uncinate process" in its typical position on the proximal part of the rib, and even here it is still presternal. Until developmental studies can clarify the situation, it seems undesirable that the term "uncinate" should be applied to these processes in geckos. It is more probable that the bifurcated cervical ribs serve for the attachment of muscles and that the processes on the fourth pair of ribs in some genera indicate a state transitional between the cervical and dorsal ribs as described above.
The poststernal ribs end freely in the body wall, the more anterior of them terminating midventrally close behind the xiphisternum. They shorten rostrocaudally so that the more posterior ribs in the dorsal series terminate in the dorsal body wall only a short distance from the vertebral column. In some genera the decrease is gradual while in others it is to some degree abrupt in the region of the twentieth presacral vertebra. There tends to be little mobility in these posterior dorsal ribs since the respiratory movements of the body wall occur more in the anterior part of the trunk.

No traces of abdominal ribs (gastraliala) have been detected in any of the geckos examined or in Xantusia although, according to Mahendra (1950), such ribs are present in the superficial parts of the rectus muscle of Hemidactylus flaviviridis. Cartilaginous inscriptive ribs are found in other lizards, however, such as the Iguanidae (Etheridge, 1965).

The ribs of the dorsal series, like those of the cervical region, articulate by means of a single rib head with the costal process of the vertebra. In adult specimens it is not possible to ascertain the exact position of the costal process on the vertebra owing to the disappearance of the neurocentral suture but embryonic or juvenile specimens of Phyllurus, Gehyra, Dedura, Nephrurus, Crenadactylus, Hemidactylus, Lepidodactylus and Aristelliger showed the costal processes of the trunk vertebrae to be situated on the neural arch alone (Pl. 10). In juvenile Coleonyx variegatus, however, the costal processes in the trunk extended down onto the centrum.

Dorsal to the articulation is a ligament connecting the
shaft of the rib to the neurapophysis below the level of the zygapophyses. There is sometimes a small tubercle on the neurapophysis and another on the rib at the points of attachment of the dorsal costal ligament. Although Noble (1921) described this structure in *Sphaerodactylus* as a cartilaginous or fibrocartilaginous band and N. G. & E. M. Stephenson (1956) described it as distinctly bony in sections of the New Zealand gecko *Hoplodactylus pacificus*, it was found to be entirely fibrous in all the geckos examined in the present study, including specimens of *Sphaerodactylus* and *Hoplodactylus*. Ventral to the rib joint there is another ligament attaching the shaft of the rib to the centrum. In the anterior part of the dorsal series there is a transition between the type of rib attachment pertaining to the cervical series and that of the more posterior trunk. A change takes place in the relative size of the two branches of the ventral ligament: in the cervical region the main part of the ventral costal ligament is attached to the intercentrum whereas in the anterior dorsal region the branch of the centrum becomes the major one while the branch to the intercentrum gradually disappears altogether. At the beginning of the dorsal series of some geckos there is also a sudden (Fig. 3:12C) or a gradual (Fig. 3:12A) increase in the length of the dorsal ligament, its insertions moving higher up the neural arch and further out along the rib. In others there is little increase in the length of the dorsal costal ligament: its insertions lie close to the rib articulation throughout the trunk (Fig. 3:16).

The neural spines of the dorsal region are fairly constant in size and shape with the occasional exception of the spine be-
longing to the seventh (first dorsal) vertebra which may be stouter than those of the adjacent vertebrae. The greatest development of the first dorsal neural spine was found in *Gonatodes* (Fig. 3:12C).

Except in the genera *Carphodactylus* and *Phyllodactylus* the neural spines of the remaining dorsal vertebrae are low relative to the size of the vertebrae. In all the material examined, with the exception of *Carphodactylus*, *Gekko*, *Phyllurus* and *Nephrurus*, the spines in this region are approximately triangular in lateral view, the longest side of the triangle forming the dorsal edge of the spine and the apex flattened or rounded where it joins the subdermal fascia. The neural spines of *Phyllodactylus*, though tall, are triangular in side view with the crest or area of attachment to the subdermal fascia occupying only the apex of the spine. In the other genera mentioned above, the neural spines are trapezoid, their dorsal edges forming a horizontal surface. Fig. 3:16 shows the major variations in the size and shape of the neural spines and their crests among geckos.

Romer (1956) suggested that the relative length (i.e. height) of the neural spines within a given group of reptiles may be correlated exponentially with the absolute size of the animal, presumably in relation to the accessory supporting function of the spines. The largest gecko examined was *Phyllurus cornutus* which has relatively low neural spines with large crests. *Carphodactylus*, which is somewhat smaller than *P. cornutus*, also has large crests but also has very tall neural spines. *Phyllodactylus Güntheri* is smaller than *Carphodactylus* but it too possess tall neural spines. The crests in this species, however, are comparatively small.
Hence it seems that, in the available material at least, the area of the crest rather than the height of the spine may be correlated with the size of the animal. The correlation appears to be valid only in species whose adult presacral column exceeds 60 mm in length. In species smaller than this the size of the crest seems to be constant relative to the size of the vertebra.

Lumbar Vertebrae

As mentioned in the section on vertebral numbers, the lumbar vertebrae are defined here, for the sake of convenience, as those vertebrae immediately preceding the sacrum which are devoid of any discernible rib elements or whose ribs are reduced in some respect. Tables I and II show that the number of lumbar vertebrae in geckos varied between one and three. There was one lumbar vertebra in Xantusia vigilis.

A lumbar rib may be reduced in one or more of the following ways:

(i) it may occur on only one side of the body;
(ii) it may lack a normal connection with its vertebra. That is, there is no clearly defined rib head articulating with the costal process and the ligaments lying above and below the articulation are absent. Instead, the rib head may be ankylosed to the costal process or joined to it by a single ligament or a band of cartilage.
(iii) it may consist only of the proximal bony portion which may be normal in size and shape, lacking only the distal cartilaginous part, or it may be reduced to a small knob or splint of bone.
In general, the vertebra immediately in front of the sacrum is devoid of ribs. In specimens with three lumbar vertebrae there may be rib elements on the first two vertebrae of the series and in such cases the ribs of the second vertebra are almost always reduced further than those of the first. Only two exceptions, both Phyllurus platirus, were found to these generalizations. One specimen had ribs on both lumbar vertebrae so that there was no break in the presacral rib series and the ribs of the second lumbar vertebra were larger than those of the first. In the other specimen ribs were present on the first and third lumbar vertebrae but not on the second.

Postaxial Presacral Vertebrae of Pygopods

(Figs 3:10, 3:14 - 15, 3:17)

In pygopods generally all the postaxial presacral vertebrae bear ribs consisting of a bony proximal portion and a distal cartilaginous portion. In juveniles the distal rib elements are uncalcified but in adults they may become heavily calcified although they do not ossify. The ribs of the third vertebra of pygopods usually extend for some distance around the body, especially in animals which also have axial ribs. Aprasia was the only genus which lacked normal ribs on the third vertebra: they were either very short structures which sometimes lacked the distal cartilaginous portion or were absent altogether (Fig. 3:14C).

The distal portions of most of the presacral ribs are slender, undivided cylinders of cartilage, short on the more anterior ribs and lengthening posteriorly. Biramous anterior
centrum and neural canal? ᵇ, vertebral costal ligament. svl, subvertebral ligament; syv, synovial cavity? ᵇ, venous from subc, subcancellous foramen; sg, spinous ganglion; sn, spinal nerve; pzb, postzygapophysis; i ᵇ, infratrb. head; sc, spinous canal; nsp, neural spine; pz, process; pzz, prezygapophysis; can, ncs, notochordal sheath; ns, neurocentral sutures; mal, neural arch lamina; nq, neural arch pedicle; nca, neural vertebral cartilage; vc, joint capsule; m, marrow space; ver, vertebral cartilage; hc, hyaline articular cartilage; lvc, fibrous intervertebral cartilage; cc, costal facet; dc, dorsal costal art, artery to neural canal? αvp, antero-ventral process of art, articular surface of bone, endochondral and perichondral, solid block.

and subcancellous foramina.

A. Midline region IV region of chordal cartilage 

B. Midline of centrum in region of chordal cartilage

Intermediate joint.

and zygapophyseal joints and the non-synovial

A. Anterior region of centrum showing synovial costal

Oblique transverse section.

Mid-trunk vertebrae of subadult lizard 

Figure 3:17
ribs do occur, however, in *Aprasia*, *Lialis* (Fig. 3:10C), *Pletholax* and *Pygopus* but their number and position vary considerably. They were present in most of the specimens of *Lialis burtonis* examined, usually on the fifth vertebra and less often on the fourth and sixth. In one specimen of *Aprasia* the sixth to the tenth vertebrae bore paired biramous ribs while another specimen had biramous ribs only on the fifth vertebra. The variation in the occurrence of biramous anterior ribs in pygopods as well as their structure suggests that they merely represent a state transitional between the most anterior ribs whose distal portions are directed posteriorly and the ribs behind them whose distal elements curve anteriorly.

*Pygopus* and *Delma* are the only genera in which ribs connect with the sternum and in both genera there is variation in the number which do so and the vertebrae to which they belong. In *P. lepidopodus* and *D. fraseri* the first vertebra to bear a sternal rib is usually the seventh, while in the single specimens of *P. nigriceps* and *D. tincta* examined it was the sixth. The eighth vertebra may have a sternal rib in both these genera and in some cases the sternum bears cartilaginous processes which are clearly distal rib elements but which are not connected to the main part of the rib.

Each rib articulates with a costal process on the vertebra which, in the more anterior vertebrae, lies partly on the neural arch and partly on the centrum, its position being ascertained from juveniles in which the neurocentral suture is still visible. Further posteriorly the costal processes tend to be more dorsal in position. In *Delma* the costal processes in the trunk are borne only by the neural arch but in *Lialis* (Fig. 3:17A), *Pygopus* and
Aprasia they continue to overlie the neurocentral suture. A strong ligament connects the dorsal surface of the rib head to the neural arch, often inserting onto well developed bony processes (Fig. 3:17B). The ventral ligament attaching the rib to the vertebra is branched in the anterior column of Pygopus, Delma and Lialis one branch inserting on the intercentrum and the other onto the centrum (Figs 3:14A & B, 3:15A). In the trunk of Lialis and Pygopus, where the intercentra lack hypapophyseal spines, and of Delma whose seventh and subsequent presacral vertebrae usually lack intercentra, the ventral ligament inserts on the centrum alone. In Aprasia and Pletholax, which lack discrete intercentra even in the neck (Figs 3:14C, 3:15B), the ventral ligament is undivided and inserts only on the centrum throughout the presacral column. In all the pygopods examined as alizarin transparencies or serial sections, both the dorsal and the ventral ligaments appeared to be completely fibrous.

Projecting anteroventrally from the rib head in pygopods is a well developed process for muscle attachment (Fig. 3:10B). It is present on all the presacral ribs with the exception of the first one or two pairs. Camp (1923) illustrated this process in Lialis as well as similar but posteriorly directed processes in Amphisbaena and the anguid, Ophisaurus. According to Zangerl (1945), the process faces caudally in most amphisbaenids, rarely cranially as in Rhineura. Underwood (1957b) described in the Typhlopidae an anterodorsally directed process from the rib head which he considered to be characteristic of snakes. In the Australian typhlopid, Typhlops nigrescens, and in the Australian elapid snakes, Demansia olivacea and Notechis scutatus, all of
which were examined personally, the process from the rib head is posterodorsally inclined. According to Hoffstetter & Gasc (1969), the muscle process from the rib head (pseudotuberculum) of limbless lizards is usually posterodorsal in position, although another anteroventral process is often present as well. These authors regard the Pygopodidae as remarkable in having only the latter process, which is placed anteroventrally and directed obliquely inward. To call this process a pseudotuberculum seems inappropriate, however, in view of its anteroventral position on the rib head.

There is no interruption in pygopods in the rib series of the posterior trunk, unlike geckos in which the vertebra in front of the sacrum usually lacks ribs. Only two genera of pygopods, *Pletholax* and *Pygopus*, possess lumbar vertebrae, whose ribs are usually reduced to the same extent and in the same manner on both sides of the body in that they lack their distal cartilaginous portions. In *Pletholax* the single pair of lumbar ribs articulated normally with the vertebra but in *Pygopus lepidopodus* the ribs were fused to the vertebra, with or without loss of the suture. Of the two lumbar vertebrae in *Pygopus nigriceps*, the anterior pair articulated normally whereas the second smaller pair had ankylosed to the vertebra. In Lialis, Delma and Aprasia there are no lumbar vertebrae: the last presacral vertebra bears a pair of complete ribs which are little shorter than the more anterior ribs and which articulate normally with the vertebra. According to Hoffstetter & Gasc (1969), the number of lumbar vertebrae in lizards (those lacking free ribs) has no systematic value at the familial level and there appears to be no general
correlation between this character and the presence of absence of hind limbs. Among pygopods, however, there is correlation between the presence of lumbar ribs and fusion of the sacral ribs to their vertebrae. In Delma, Aprasia and Lialis, in which the posterior presacral ribs are complete and articulate normally, the sacral ribs following them almost always articulate freely with their vertebra. In Pygopus, whose posterior presacral ribs are reduced and fused to their vertebra, the sacral ribs are also fused.

The postaxial neural spines of most pygopods are triangular in side view and inclined posteriorly so that the longest side of the triangle forms the dorsal edge of the spine and the crest or area of attachment to the subdermal fascia occupies its apex. In Pletholax the neural spines are trapezoid in lateral view so that their dorsal edges are horizontal. In no pygopod are the spines very tall, although they are somewhat taller in Lialis and Pygopus than in Delma and Pletholax, and in Aprasia they are so low that they barely extend above the level of the neural arch. The neural spines of Aprasia are also notched at the tip although the neurapophyses are otherwise completely fused together. A similar notch is found at the posterior edge of the neural arch of the blind snake Typhlops nigrescens which lacks neural spines in the trunk and is probably associated in both these reptiles with poor development of the neural spine.

Towards the end of the presacral series in Lialis, Pygopus and Delma the neural spines increase somewhat in height and also extend anteriorly to become more or less trapezoid in side view, and these larger spines are also found on the sacral and anterior
pygal vertebrae. In *Pletholax* there is a slight increase in height only but in *Aprasia* there is no change in the size and shape of the neural spines in the region of the cloaca. The height of the neural spines in pygopods and their increase in size near the cloaca may depend to some extent on the overall size of the animal (see Romer, 1956, p. 226) as both these characteristics are most conspicuous in the two largest species, namely *Lialis burtonis* and *Pygopus lepidopodus*. They are less obvious in those species which are intermediate in size, namely *L. jicari*, *P. nigriceps*, *Delma fraseri*, *D. tincta* and *Pletholax gracilis* and are virtually absent from the smallest species, *Aprasia pulchella*.

Intercentra are present throughout the vertebral column of *Pygopus* and *Lialis* but are restricted to the most anterior vertebrae and tail in *Delma*, *Aprasia* and *Pletholax*. All the postaxial intercentra of *Lialis* are free elements, those of the third to the sixth vertebrae in adults bearing hypapophyseal spines in the form of median blades which are longest on the third intercentrum (Fig. 3:15A) and progressively smaller on the more posterior intercentra. In juveniles the hypapophyses are proportionally smaller and extend only as far as the fourth vertebra. The remaining precaudal intercentra are smooth. The postaxial intercentra of adult *Pygopus* are normally free (Fig. 3:14A) but occasionally the third and fourth fuse with their centra and, in apparently aged specimens, fusion of the intercentra may extend as far back as the ninth vertebra. The hypapophyseal spines of *Pygopus* are smaller than in *Lialis*, taking the form of low knobs on the first five or six intercentra in adults and the first four in juveniles,
and may be absent altogether. In Delma the intercentra extend only as far as the sixth vertebra or rarely the ninth and are either free elements or partly fused to their vertebrae, the more anterior of them bearing well developed hypapophyseal spines (Fig. 3:14B). Aprasia and Pletholax have no free presacral intercentra but the presence of these elements in the neck is indicated by small hypapophyseal spines on the first four or five vertebrae, usually towards the anterior edge of the centrum. In one specimen of Aprasia, however, the third vertebra bore two hypapophyseal spines, one at the anterior and the other at the posterior edge of the centrum, while the fourth vertebra bore one spine posteriorly. It appears that in this specimen the fourth and fifth intercentra have fused, not with their own centra behind them, but with the centrum in front. This type of fusion is rare in the Gekkota but is characteristic of the cervical intercentra of scincid and anguimorphan lizards, the Amphisbaenia and snakes (Hoffstetter & Gasc, 1969).
SACRUM

Geckos (Figs. 3:18, 19A, Pl. 13A)

In the majority of geckos two vertebrae are modified for the support of the pelvic girdle. According to Romer (1956) two sacral vertebrae were typical of eosuchians and rhynchocephalians and occur in all lizards with well developed limbs. Three sacral vertebrae are found occasionally, however, in Phyllurus platurus and seem to be typical of Nephrurus levis, occurring in four of the five specimens examined. Four sacrals were present in one specimen of N. asper.

Each sacral vertebra bears a pair of large processes, usually described as transverse processes, which consist of two distinct portions: a proximal bony shaft projecting from the neural arch and a distal cartilaginous portion fused to the proximal shaft. The cartilaginous portions of the sacral processes on each side of the body fuse into a single mass which is attached by ligaments to the ilium of the pelvic girdle.

There has been considerable controversy in the past regarding the nature of the sacral 'transverse processes' in lizards, but the current opinion is that they are ribs which have fused to their vertebrae and should therefore be called pleurapophyses (Hoffstetter & Gasc, 1969). Owen (1851) pointed out the ambiguity of the term transverse process, which implies an outgrowth from the vertebra itself, and used the term pleurapophysis for all ribs, freely articulating and fused. Cligny (1899a, b) and Hoffstetter (1939b) restricted the term to those ribs which are embryologically distinct and later fused. Moodie (1909) considered that a study
Sacral vertebrae of geckos.

A. *Gonatodes albogularis*, adult, dorsal view;
B. *Phyllostomus marmoratus*, juvenile, ventral view of abnormal sacrum.

fdc, fused distal cartilaginous portions of sacral ribs; ic, intercentrum; ivc, intervertebral cartilage; ns, neurocentral suture; nsp, neural spine; Pls, first pygal vertebra incorporated into sacrum; plp, pleurapophysis; pr, process on pleurapophysis of second sacral vertebra; pre, proximal rib element; prz, prezygapophysis; pz, postzygapophysis; S₁, S₂, first and second sacral vertebrae; sut, suture.
of the stages of chondrification may indicate the presence of sacral ribs in lizards although, in an earlier paper (1907), he denied their presence. El-Toubi (1947b) and Kamel (1951, 1952) reported the undoubted presence of sacral rib elements in the agamid *Agama stellio* and the scinc *Chalcides ocellatus* respectively. Nevertheless some other authors, including Mahendra (1950) and Romer (1956), maintained that lizards have no sacral ribs.

Kamel (1951, 1952) described the sacral region of the scinc, *Chalcides ocellatus*, in embryos 14mm to 45mm in length and found that the sacral ribs are quite distinct and separate from the transverse processes, each rib being a compound one formed from a dorsal (proximal) rib rudiment and a ventral (distal) rib rudiment which fuse early in the connective tissue stage. According to Kamel, the sacral rib chondrifies and unites with the transverse process of the first sacral vertebra and to that of the following vertebra as well and articulates with the ilium. According to Kamel's description, the transverse processes of the two sacral vertebrae are long and form the greater part of the length of the sacral processes: only the distal portion of each sacral pleurapophysis is costal in origin.

Sacral ribs are also present in geckos and consist of proximal and distal elements which fuse to the vertebra during early embryonic stages. However, the construction of the gekkonid pleurapophyses differs considerably from that described by Kamel in *Chalcides ocellatus*. Direct evidence for the occurrence and structure of the sacral ribs in geckos comes from two juvenile specimens of *Nephrurus, N. asper* (Fig. 3:19A) and *N. levis*, and from a juvenile specimen of *Phyllodactylus marmoratus* with an
abnormal sacrum (Fig. 3:18B). In the two specimens of *Nephrurus*

faint sutures were present on the proximal bony shafts of all four

and three pairs of pleurapophyses respectively. The parts of the

pleurapophyses lying distally to the sutures thus constitute the

sacral ribs. The specimen of *Phyllopectylus* had a small piece of

bone attached to the inner surface of the distal cartilaginous

mass on one side of the body, anteriorly to the first pleurapo-

ophysis. There can be little doubt that this element is the proxi-

mal part of a rib which, owing to the abnormal development of the

sacrum, has not become connected to its vertebra.

Thus the sacral ribs of geckos consist of proximal bony

and distal cartilaginous portions like the more anterior presacral

ribs. The proximal portion forms the greater part of the bony

shaft of the pleurapophyses while the distal portions of the ribs

on each side of the body fuse together to form the mass of carti-

lage apposing the ilium. Calcification of this cartilage often

takes place in adult geckos and there is usually a calcification

centre to correspond with each of the sacral pleurapophyses. As

in the case of the presacral ribs, the distal cartilage of the

sacral ribs does not ossify.

Fusion of the sacral ribs of geckos to their vertebrae must

normally occur during early stages of embryonic development, in

most cases no later than the cartilaginous stage, because sutures

between the ribs and vertebrae are so rarely found, even in hatch-

lings. In the youngest specimen examined, a serially sectioned

embryo of *Gebyra variegata* whose notochord was still continuous

between the odontoid process and the skull but whose vertebrae

and ilium were already undergoing ossification, there still remained
a vestige of the suture between the sacral rib and the vertebra (Pl. 13A). In Sphenodon fusion of the sacral ribs to their vertebral takes place much later than it does in geckos. In juvenile specimens with advanced perichondral ossification of the vertebrae, there is still a distinct suture between each sacral rib and its neural arch and centrum. Fusion of the distal cartilaginous portions of consecutive sacral ribs occurs in Sphenodon as in geckos. Examination of Kamel's (1952) illustrations of the developing sacrum of Chalcides ocellatus suggests that the sacral pleurapophyses of this specie are similar to those of geckos and Sphenodon. Kamel's dorsal and ventral rib rudiments appear to be the distal cartilaginous portions of the first and second sacral ribs, the proximal shafts apparently fusing to the neural arch much earlier in development, before the onset of chondrification. (see also Werner, 1961, 1971).

Although the number of sacral vertebrae varies in geckos, the most anterior is almost invariably the largest. The body of the second vertebra is somewhat smaller but, when there are only two sacral vertebrae, the pleurapophyses are always expanded distally and may closely approximate the size of the first pair of pleurapophyses. In Phyllurus platyrurus, the pleurapophyses of the second and third sacral vertebrae in those specimens with three sacrals are expanded to a less marked degree than the second pair of sacral pleurapophyses in those specimens with only two sacral vertebrae. In the specimens of Niphurus with three sacrals, the second and third pairs of pleurapophyses are considerably expanded though not as greatly as the first pair, while in the specimen of N. asper with four sacrals the pleurapophyses of the fourth verte-
bra of the series are hardly expanded at all, being merely joined
to the distal cartilages of the preceding pleurapophyses by a
cartilaginous band. The other two specimens of *N. asper* had three
sacral vertebrae, but in both animals one or both of the
pleurapophyses of the first pygal were joined to the distal car-
ilage of the sacral pleurapophyses by a ligament (Fig. 3:19A).

Moodie (1907) implied that the most anterior sacral verte-
bra of lizards, by reason of its size, represents the original
element for support of the pelvis. Whether or not such a sugges-
tion can be verified, it is at least probable that the additional
vertebra incorporated into the sacrum of geckos, in excess of the
number typical of the species concerned, comes from the pygal
series. In all four specimens with an increased sacral count
(one *Nephrurus asper* and three *Phyllurus platurus*), the additional
pair of pleurapophyses closely resembled those of the pygal verte-
brae. In the other two *N. asper* the pygal pleurapophyses attached
to the sacrum were curved anteriorly while the unattached pleura-
pophyses extended laterally in the normal way. Possibly the third
sacral vertebra typical of *Nephrurus* has been recruited from the
caudal series in a like manner, particularly as the pygal count
in *N. levis* is typically four instead of five as in other geckos.
Nevertheless an interdependence of sacral and pygal numbers can-
not be accepted without reservation as four pygals sometimes occur
in other species in conjunction with two sacrals, and in the New
Zealand genera two sacral and four pygal vertebrae commonly occur

Fusion of the bony shafts of consecutive sacral pleurapop-
hyses occurs in a number of gekkonid genera. The more common con-
dition is that found in Phyllurus, Oedura, Sphaerodactylus, Aristelliger and Coleonyx in which the shafts fuse just before they join the mass of distal cartilage and often have a suture between them. Juveniles of these genera do not have the fused condition. Adult Nephurus and the single specimens of Carphodactylus and Gonatodes (Fig. 3:18A) showed considerable fusion of the shafts while juvenile N. asper (Fig. 3:19A) had the fused condition typical of adult Phyllurus. Only in N. asper did this juvenile fusion occur and it increases with age. In the remaining genera the ends of the bony shafts often lie very close together but do not fuse.

There is a tendency in some genera for the sacral centra to fuse in adulthood with reduction of the intercentrum between them. Some constriction of the notochord occurs in such vertebrae so that in amphicoelous forms the concave ends of the centra tend to be flattened. The intercentra lying between the sacral vertebrae may fuse with the margins of the adjacent centra but usually they remain as small discrete elements attached loosely over the suture. In the genus Nephurus, which usually has more than two sacral vertebrae, the tendency towards fusion is greatest between the first two vertebrae of the series. In the single adult specimen of Gonatodes (Fig. 3:18A) and in adult Nephurus, not only had the centra fused, but the dorsal laminae of the neural arches were also fused and the suture was partly obliterated. In juvenile Nephurus the arches were still separate dorsally but the zygapophyses were reduced. According to Hoffstetter & Gasc (1969), fusion of the sacral centra, neural arches and ends of the pleurapophyses is usual among lizards with fully developed limbs.
Figure 3:19

Sacral and caudal vertebrae of geckos showing costal components of pleurapophyses.

A. *Nephrurus asper*, juvenile, ventral view of sacrum;
B. *Phyllurus platurus*, juvenile, ventro-lateral view of pygal and postpygal vertebrae.

cart, bridge of uncalcified cartilage between first and second haemal spines; *cn*, centrum; *cpv*, costal process of vertebra; *dre*, distal rib element; *fdc*, fused distal cartilaginous portions of sacral ribs; *frp*, fracture plane; *ha*, haemal arch; *ic*, intercentrum; *ivc*, intervertebral cartilage; *l*, ligament; *ncc*, notochordal canal; *ns*, neurocentral suture; *P₁* first pygal vertebra; *PP₁*, first postpygal vertebra; *pre*, proximal rib element; *prz*, prezygapophysis; *pz*, postzygapophysis; *r*, rib; *S₁*, first sacral vertebra; *scf*, subcentral foramen.
The second pair of sacral pleurapophyses varies in shape among geckos. In most of the Australian genera examined the bony proximal portion of the second pair of pleurapophyses is smooth and more or less conical, the base of the cone lying against the distal cartilage (Fig. 3:19A). Occasionally in Australian forms, and more often in the non-Australian genera, there is a large, thin, triangular process on the posterior edge of the bony shaft (Fig. 3:18A). In none of the geckos examined was there any suggestion of a state transitional between the smooth shaft and the shaft with a large process: the process was either very well developed or entirely absent. It was present in all the species examined of the following genera: Heteronotia, Gehyra, Phyllo-

lodactylus, Hemidactylus, Gekko, Lepidodactylus, Aristelliger,

Afroedura, Gonatodes, Sphaerodactylus and Coleonyx. Of these genera, only the first four have Australian representatives. In all the non-Australian genera examined, with the exception of Hoplodactylus and Nautinus from New Zealand, the process was present. Cogger (1964) considered the process to be significant in distinguishing the African genus Afroedura from the Australian genus Oedura as it is present in the two species he examined of the former and absent from all five species of the latter. It is also present in the Indian house-gecko, Hemidactylus flaviviridis (Mahendra, 1950), Gekko gekko (Etheridge, 1967) and the Egyptian geckos, Stenodactylus sthenodactylus, Tropidocolotes tripolitanus, T. steudneri, Ptyodactylus hasselquistii, Hemidactylus turcica Tarentola mauritanica and T. annularis (El-Toubi & Khalil, 1950, 1955). The thin, triangular process on the second sacral pleura-
pophysis of Coleonyx variegatus and C. brevis is fenestrated and,
according to Kluge (1962b), the six species of *Coleonyx* show various stages of erosion of the foramen to a lateral notch.

Of the geckos listed above as possessing a triangular process on the second sacral pleurapophysis, *Gonatodes* and *Sphaerodactyulus* belong to the Sub-family *Sphaerodactylinae*, *Coleonyx* to the Bublepharinae and the remainder to the Gekkoninae (*sensu* Kluge, 1967a). All the Australian geckos which lack the process together with the New Zealand genera *Hoplodactylus* and *Naultinus* which also lack it belong to Kluge's sub-family Diplodactylinae. In all, 25 genera of geckos of the 82 acknowledged by Kluge (1967a) are known either to possess or lack the process. As all the genera lacking it, and only these genera belong to the Diplodactylinae, it appears to be a character of sub-familial importance among geckos (see Appendix).

The presence of a process on the posterior edge of the second sacral pleurapophyses is not limited to geckos as it is also found in numerous Agamidae, a few Iguanidae, in the gerrhosaurs *Chamaesaura* and, in rudimentary form, in some Lacertidae (Hoffstetter & Gasc, 1969). It also occurred in the Jurassic rhynchocephalian families Sphenodontidae and Pleurosaauridae (Hoffstetter, 1955a; Cocude-Michel, 1963) but is absent from modern *Sphenodon*. It was present in the Triassic squamate, *Macrocnemus* (Peyer & Kuhn-Schnyder, 1955; Fig. 7, p. 585) but was absent from the Jurassic gekkotan, *Eichstättisaurus* (Cocude-Michel, 1963) and the Triassic gliding squamate *Icarosaurus* (Colbert, 1966). The function of the process is a matter for conjecture as it does not contact the ilium in lizards (Hoffstetter & Gasc, 1969) or in rhynchocephalians (Cocude-Michel, 1963, Figs.) but it may pro-
vide an increased surface for the insertion of muscles and strengthen the sacrum as a support for the pelvic girdle.

The pelvic girdle of geckos is attached to the sacral pleurapophyses by means of ligaments, the main one of which inserts on the iliac crest and on the cartilaginous extremities of the sacral pleurapophyses as well as on the distal portions of their bony shafts. This ligament thus has a small insertion on the ilium and a large one on the sacral pleurapophyses. Other smaller ligaments serve to attach the more anterior parts of the iliac blade to the sacrum. The cartilage of the pleurapophyses probably serves not only for the insertion of ligaments but also as a cushion between the sacrum and the pelvic girdle.

*Xantusia vigilis*

The sacrum of *Xantusia vigilis* had essentially the same form as that of geckos. It consisted of two vertebrae, the first of which was slightly larger than the second with respect to both the body of the vertebra and its pleurapophyses. A suture was present between the fused centra but the intercentrum had disappeared, probably through fusion to one centrum or the other. The zygapophyseal connection between the neural arches was also strongly fused. The bony shafts of the pleurapophyses on each side of the body were fused together distally as in some geckos, e.g. *Phyllurus*, and the second pair of pleurapophyses had no posterior process on their bony shafts (see also Savage, 1963, Fig. 2).
Pygopods (Fig. 3:20)

One sacral vertebra seems to be characteristic of pygopods with the possible exception of Delma and Aprasia. Two unfused sacral vertebrae, both bearing a pair of ribs modified to support the pelvic girdle, were found in four of the eight available specimens of D. fraseri, in the single specimen of D. tincta and in one of the three specimens of Aprasia pulchella. In the other genera, a sacrum consisting of two vertebrae was abnormal in that one rib of one or both vertebrae was not modified to support the girdle.

Stokely (1947) stated that there are no sacral ribs in Aprasia repens but that the transverse processes are plainly visible. According to Parker (1956b), however, the first two of the three sacral vertebrae which this author considered to be characteristic of the genus Aprasia bear free ribs, while those of the third vertebra are knob-like and fused to the centrum, articulating directly with the posterodorsal corner of the ilium. In the specimens of Aprasia pulchella examined here there were only one or two sacral vertebrae (Fig. 3:20A) all the ribs of which articulated freely with their vertebrae. In no instance did the posterodorsal corner of the ilium articulate with a rib and the most anterior postsacral (caudal) pleurapophysis in each case was comparatively long and rather pointed.

The sacral ribs of Lialis almost always articulate freely with the costal process of the vertebra (Fig. 3:20B) and, as in Aprasia pulchella, the dorsal and single ventral ligaments are present. Occasionally, however, one or both of the sacral ribs of Lialis fuse to the vertebra, with or without obliteration of
Figure 3:20

Sacral vertebrae and ribs of adult pygopods in lateral view.

A. Aprasia pulchella
B. Lialis burtonis with freely articulating sacral rib. The part of the distal cartilaginous element between the points » and « is often absent.
C. Partially fused sacral rib of L. burtonis showing variation in form of rib elements.
D. Pletholax gracilis.
E. Delma fraseri.
F. Pygopus lepidopodus.

avp, antero-ventral process of rib head; cart, uncalcified cartilage; c, condyle; cct, calcified cartilage; dl, dorsal costal ligament; dre, distal rib element; fdc, fused distal cartilaginous portions of sacral ribs; ic, intercentrum; nsp, neural spine; plp, pleurapophysis; ppr, posterior process of rib head; pre, proximal rib element; prz, prezygapophysis; pz, postzygapophysis; rh, rib
vl, ventral costal ligament.
the suture, although the ligaments may be retained in a reduced form in those cases where the suture is particularly clear (Fig. 3:20C). Both sacral ribs articulate freely in those specimens of Delma with one sacral vertebra and, in those possessing two sacral vertebrae, the ribs of the first vertebra at least are movable. Occasionally both ribs of the second vertebra are movable as well (Fig. 3:20E) but more often one or both of these are fused. The sacral ribs of Pygopus are intimately fused to the vertebra, usually with loss of the suture and ligaments (Fig. 3:20F). There is sometimes a suture across the base of the pleurapophysis, however, and a greatly reduced dorsal costal ligament may be present as well, but freely articulating ribs have not been seen in this genus, not even in animals with an abnormal sacrum consisting of two vertebrae. The single specimen of Pletholax examined resembled Pygopus in having one sacral vertebra to which the ribs were intimately fused (Fig. 3:20D).

The presence in any one genus of ribs which articulate freely or are fused to their vertebrae appears to bear no relationship to an animal's age. Thus the free ribs characteristic of Lialis are found in juveniles and adults while the fused condition can occur in immature animals in which the neuro-central sutures are still visible. Similarly, in Pygopus, sutures may be absent from the pleurapophyses of young specimens but present in adults.

The sacral ribs of pygopods consist of a proximal bony shaft and a distal cartilaginous portion like the presacral ribs. The proximal shaft is shorter and stouter than those of the trunk, especially in Lialis and Pygopus which normally have only one sacral vertebra and in Pletholax. In Delma and Aprasia the one
or two sacral ribs on each side of the body are shorter but only slightly stouter than the presacral ribs. The anteroventrally directed process characteristic of the ribs of the trunk in pygopods is sometimes present on the sacral rib head in *Lialis*, and may be accompanied by another posteriorly directed process which has no counterpart on the ribs of the trunk (Fig. 3:20B). In some *Lialis*, however, as in the other genera, both these processes for muscle attachment are absent.

The distal cartilaginous portion of the rib is usually expanded to some extent to meet the ilium of the pelvic girdle, with the exception of those specimens of *Delma* and *Aprasia* with two sacral vertebrae. In these animals the distal rib elements are of the same diameter as the bony shafts and those on at least one side of the body are fused together (Fig. 3:20B). In those specimens of *Delma* and *Aprasia* with one sacral vertebra, and in *Pygopus* and *Pletholax*, the distal element is a little broader than the bony shaft and is flattened or grooved where it meets the ilium. The distal element in *Lialis*, on the other hand, is usually broadly expanded (Fig. 3:20C) and in many specimens took the form of a large, thin, tri-radiate sheet of cartilage whose two outermost rami are sometimes joined together to enclose a large fenestra (Fig. 3:20B). The cartilaginous portion of the sacral ribs may become calcified in adult pygopods but does not ossify. In all pygopods the sacral ribs are attached to the ilia of the pelvic girdle by means of ligaments.

In general, the number of sacral vertebrae, the size and shape of the sacral ribs and their degree of fusion to their vertebrae are fairly constant in each pygopod genus. Nevertheless, there
is more inter- and intra-generic variation in these characters in pygopods than in geckos, doubtless because the sacrum is not required to be a rigid support for the reduced girdle and hind limbs. There is no apparent correlation, however, between the form of the sacrum and the amount of reduction described by N.G. Stephenson (1961) in the pelvic girdle and hind limbs in the different genera, nor do Pygopus and Delma, considered by Stephenson to be more closely related to one another than to other genera, resemble one another more than other pygopods in the structure of the sacrum. The presence of two sacral vertebrae in Delma and Aprasia may indicate the retention of an ancestral character, as two sacral vertebrae are typically found in lizards with fully developed limbs, but this cannot be taken for granted as Delma (with Pygopus) is most similar to geckos on other osteological grounds (N.G. Stephenson, 1961) while Aprasia is in many respects the most modified in association with its burrowing habit (Mitchell, 1958). Furthermore, one of the two sacral vertebrae sometimes found in other pygopods is clearly the last presacral or the first caudal vertebra, one of whose ribs is somewhat modified to support the ilium while the other is normal for the series to which the vertebra belongs. This condition has probably arisen through slightly different rates of growth and differentiation on the two sides of the body. In short, apart from the correlation already noted (p. 157) between the states of the sacral ribs and the ribs of the most posterior presacral vertebra, variation in the structure of the sacrum of pygopods between genera and within genera appears to be unrelated to variation in other parts of the skeleton.
POSTSACRAL OR CAUDAL VERTEBRAE

(Figs 3:19B, 3:21 - 22, Pl. 13 B, C)

The caudal vertebrae of most geckos and pygopods can be divided into two regions -- the pygal and postpygal series. The pygal vertebrae lie immediately behind the sacrum and are short and broad like the presacrals. They have no fracture planes as they serve, at least in geckos, for the attachment of the caudo-femoral muscles (Furieri, 1956), and the posterior portions of the kidneys, the cloaca and the hemipenes in males are found in this part of the body. Although some authors such as Remane (1936) and Hoffstetter & Gasc (1969) have used the term "pygal" to refer to those anterior caudal vertebrae which lack chevron bones, the term is used here in its more usual sense to refer to the anterior, non-autotomous vertebrae of the caudal series (see N. G. & E. M. Stephenson, 1956; Werner, 1965). The postpygal vertebrae, at least at the beginning of the series, are divided into two parts by planes of fracture.

In geckos, with the exception of *Nephrurus asper* (vide infra), the pygal vertebrae are usually five in number, although four or six pygals are found occasionally (see Tables I and II). Mahendra (1950) recorded five pygals in *Hemidactylus flaviviridis*, Kluge (1962b) recorded four or five in various species of *Coleonyx* and Calori (1861) illustrated six pygal vertebrae in *Platydactylus guttatus*. Only in the Australian species *Nephrurus levis* and in the New Zealand genera are the pygal vertebrae typically four in number.
Nephrurus asper was the only gecko examined in which the vertebrae of the tail were not divisible into pygal and postpygal series, as none of the vertebrae in the extremely short tail possessed a fracture plane. In this species, all the caudal vertebrae decrease sharply in length and breadth. The anterior five are similar to the pygal vertebrae of other geckos while the remaining 17 vertebrae are devoid of neural spines and pleurapophyses. Chevron bones, however, are present in the greater part of the tail, the most posterior being that of the 17th caudal vertebra. The neural arches of the first nine caudal vertebrae articulate by means of zygapophyses while the ninth vertebra has reduced and non-functional postzygapophyses. The last 13 vertebrae are small cylinders of bone, completely devoid of processes, which are joined together only by the intervertebral cartilage.

In all the other geckos examined there were fracture planes in at least the most anterior two postpygal vertebrae. There are fracture planes in all but the most posterior caudal vertebrae of those species whose tails gradually become narrower posteriorly, whereas species with a distinct constriction visible externally between the pygal and postpygal regions, e.g. those geckos with flattened leaf-like tails, have only two or three fracture planes which lie in the region of the constriction. Species noted to have this condition are Nephrurus levis and the three examined species of Phyllurus. When autotomy occurs in these geckos the whole of the postpygal region is lost, except occasionally for the most anterior postpygal vertebra. According to Siebenrock (1893), Uroplatus fimbriatus also has only two fracture planes which usually divide the eighth and ninth caudal vertebrae, unlike
Phyllurus and Nephrurus levis where the first divided vertebra is the fifth or sixth.

Etheridge (1967) maintained that restriction of autotomous ability to a few vertebrae near the base of the tail in lizards is an ontogenetic phenomenon which involves progressive ossification of the fracture planes from the posterior end of the tail forwards, resulting in fusion of the two halves of the vertebrae. He claimed that the tails of sub-adult animals contain vertebrae in all stages of fusion, the most anterior postpygals showing the least amount. It is doubtful whether this explanation applies to all adult lizards whose fracture planes are restricted to a few anterior postpygal vertebrae because, in juveniles of at least one species of gecko with this condition, namely Phyllurus platurus, the first three postpygal vertebrae were completely divided while the more posterior vertebrae showed no sign of division. Whether fracture planes are present at an earlier stage in the development of this species is not known. In other geckos such as Ptyodactylus hasselquistii and Hemidactylus turcicus in which most of the caudal vertebrae are divided (Werner, 1965) the fracture planes are present from the beginning of vertebral development and represent the original intersegmental boundary which has remained unossified (Werner, 1971). According to Etheridge (1967) the complete or partial loss of fracture planes is an advanced condition which has probably arisen several times in lizards, the more primitive condition being the presence of fracture planes in all the vertebrae of the postpygal series. According to Werner (1965, 1968), restriction of the fracture planes to the base of the tail has probably arisen several times even within the Gekkonidae.
In the Pygopodidae, all of the genera examined except *Pletholax* are capable of caudal autotomy. In the autotomous genera the caudal vertebrae are divisible into pygal and post-pygal series but, unlike geckos in which the pygal vertebrae completely lack fracture planes and at least the most anterior postpygals are completely divided, there is a transitional region in the tails of pygopods consisting of at least one vertebra whose fracture plane is incomplete. The most anterior plane of fracture is represented by a vertical slit in each side of the neural arch, about half way along the arch just behind and above the pleurapophyses. In the following vertebra the slit is larger, extending further up the neural arch and in some cases partially or completely dividing the centrum as well. Vertebrae whose centra are completely divided appear to be able to break autotomously even though the neural arch may not be completely divided mid-dorsally. The variation seen in pygopods in the number of pygal vertebrae which by definition completely lack fracture planes and are therefore incapable of autotomy, as well as the variation in the number of partly divided postpygal vertebrae are shown in tables III and IV.

The only pygopod examined here which was incapable of autotomy was the single specimen of *Pletholax gracilis*. In this animal there were no lines of cleavage in the cleared skin of the tail and no complete fracture planes in the vertebrae. Apertures were present in the neural arch pedicels of the third caudal vertebra but, although they enlarged slightly in the more posterior vertebrae, they did not extend further than the sides of the arches. The end of the tail had been lost from this specimen but not through autotomy as the last (86th) caudal vertebra was complete,
Figure 3:21

Third caudal vertebra of *Pygopus lepidopodus*, adult, in ventrolateral view showing caudal ribs and haemal arch elements.

\(c\), condyle; \(cct\), calcified cartilage; \(cpv\), costal process of vertebra; \(ha\), haemal arch; \(hap\), haemal arch pedicel; \(hsp\), haemal spine; \(ic\), intercentrum; \(psz\), prezygapophysis; \(pz\), postzygapophysis; \(r\), rib; \(sci\), subcentral foramen; \(sut\), suture.
the break having occurred between the vertebrae with the inter-
vertebral cartilage splitting off the following centrum. Autot-
tomy can occur in some lizards whose vertebrae completely lack
fracture planes, e.g. the "glass-snake", Ophisaurus, whose caudal
vertebrae are so thin that they break more readily than they dis-
articulate (Cope, 1892). The caudal vertebrae of Pletholax,
however, are comparatively robust and separate from one another
in the intervertebral region rather than break through the verte-
brae themselves.

Each fracture plane in geckos and pygopods divides the
vertebra into approximately equal parts, passing behind the pleura-
pophyses or through the posterior parts of their bases (Figs 3:19B,
3:22). In Xantusia vigilis, in which all but the terminal post-
pygal vertebrae were autotomous, the fracture planes of the more
anterior postpygal vertebrae were situated further forward in the
vertebra than in geckos and pygopods so that the anterior portions
of these vertebrae were approximately half the length of the
posterior portions. In these anterior postpygals in Xantusia the
fracture planes divided the pleurapophyses into a smaller anterior
portion and a slightly larger posterior portion but the broadly
spatulate posterior portions figured diagrammatically by Savage
(1963) were not present. In the more posterior tail of X. vigilis
the vertebrae were divided into approximately equal parts and the
fracture planes passed through the posterior part of the pleura-
pophyseal bases. Detailed accounts of the external morphology of
the caudal vertebrae of lizards belonging to several families
including the Gekkonidae, Pygopodidae and Xantusiidae were given
by Werner (1965) and Etheridge (1967).
The nature of the split in the autotomous centra of geckos and pygopods which retain the notochord, at least mid-vertebrally, differs somewhat from the condition seen in other pygopods such as old *Pygopus lepidopodus* and in *Xantusia vigilis* from which the midvertebral notochord has disappeared. In all of these lizards the neural arch is in two parts which are either in contact as in most geckos or widely separated laterally as in pygopods (Fig. 3:22), while in *X. vigilis* the two parts of the arch were in contact but a large foramen pierced each side of the arch just in front of the fracture plane. The two parts of the centrum are also separate in those forms which lack the notochord midvertebrally, the apposing surfaces consisting entirely of bone, but in those geckos and pygopods which retain the notochord midvertebrally, only the peripheral ossified region of the centrum is divided. The chordal cartilage together with the surrounding notochordal sheath remains intact (Pl. 1B, C) except in the event of autotomy when it splits into two approximately equal portions.

The fracture planes in the caudal vertebrae of lizards are not structures in themselves but interfaces or zones of discontinuity between the adjacent halves of the vertebrae. In general, recent authors recognise this and describe the fracture planes as splits in the vertebrae (see Werner, 1961, 1964, 1967, 1971; Moffat & Bellairs, 1964) but some people have regarded them as morphological entities. Gadow (1897, 1901, 1933), Slotopolosky (1922), El-Toubi & Khalil (1955) and Vorontsova & Liosner (1960) described them as cartilaginous septa whereas Woodland (1920), who disagreed with Gadow's description, considered them to be non-cellular hyaline sheets. As recently as 1967, Etheridge described the caudal fracture planes of lizards as septa of cartilage
Figure 3:22

Autotomous and non-autotomous caudal vertebrae of adult geckos and pygopods in lateral view.

A. Oedura lesueurii, 10th caudal (total 24);
B. Phyllurus platurus, 8th caudal (total 31); the most anterior postpygal vertebra lacking a fracture plane;
C. Pygopus lepidopodus, 20th caudal (total 110);
D. Pletholax gracilis, 20th caudal (total 84+);
E. Delma fraseri, 20th caudal (total 106);
F. Lialis burtonis, 20th caudal (total 80).

A and B are geckos; C, D, E, and F are pygopods. B. and D are non-autotomous vertebrae; A, C, E and F are autotomous.

ap, aperture in neural arch; cart, uncalcified cartilage; cct, calcified cartilage; cn, centrum; frp, fracture plane; ha, haemal arch; hsp, haemal spine; iva, intervertebral cartilage; nsp, neural spine; plp, pleurapophysis; prz, prezygapophysis; pz, postzygapophysis; scf, subcentral foramen.
or connective tissue. A small quantity of connective tissue may be present within the autotomy split in various lizards (Quattrini, 1954; Werner, 1967, 1971) and in some forms, e.g. *Lacerta vivipara*, is continuous with the connective tissue septa in the perivertebral adipose tissue and caudal musculature (Pratt, 1946; Moffat & Bellairs, 1964). In the geckos described by Werner (1971), on the other hand, there appears to be no direct connection between the connective tissue within the autotomy split and the septa in the surrounding soft tissues as the periosteum of the vertebra bridges the split. These differences may be associated with the mode of development of the fracture planes which apparently occurs in various ways and at different stages in the ontogeny of different lizards. According to Werner (1961, 1971) the two parts of the autotomous vertebrae of the geckos *Ptyodactylus*, *Hemidactylus* and *Sphaerodactylus* are separate at all stages of development from their initial appearance as two half sclerotomes whereas the fracture planes of *Lacerta vivipara*, according to Moffat & Bellairs (1964), develop after birth and appear to arise as the result of invasion of the partly ossified vertebra by vascular connective tissue.

Compared with some lizards such as the iguanid *Anolis carolinensis* whose autotomous centra are reduced midvertebrally to a single layer of bone (Cox, 1969), the divided centra of geckos, pygopods and *Xantusia vigilis* are subcylindrical structures whose midvertebral diameter is little less than that of the ends of the centra (Fig. 3:22). This appears to be the most usual type of autotomous centrum in lizards as it is also found in the geckos described by Woodland (1920) and Werner (1967, 1971), in the
lacertids *Lacerta vivipara* (Pratt, 1946; Quattrini, 1954; Moffat & Bellairs, 1964) and *Takydromus tachydromoides* (Fukada & Ishihara, 1967), in the scinc *Lygosoma laterale* (Cox, 1969) and in the anguid *Anguis fragilis* (personal observation). The presence of subcylindrical divided centra in *Sphenodon* (Howes & Swinnerton, 1901) as well as the Jurassic rhynchocephalians *Homoeosaurus* and *Sapheosaurus* (Price, 1940; Cocude-Michel, 1963) suggests that this was probably the original type of autotomous centrum in lepidosaurs.

The ability of lizards and *Sphenodon* to undergo autotomy depends not only on the presence of vertebral fracture planes but also on the complex segmental arrangement of the other tissues of the tail, namely the scalation, dermis, muscles and adipose tissue (Woodland, 1920; Ali, 1941, 1950; Boring, Chang and Chang, 1948; Quattrini, 1952a & b, 1953, 1954; Furieri, 1956). Furthermore, the presence of segmental sphincters in the caudal artery which minimise blood loss when the tail breaks is apparently unique to the tails of autotomous lizards (Woodland, 1920). According to Ali (1941) they are not found in *Sphenodon*. Although Morgan (1901), Gadow (1933), Pratt (1946) and Weiner & Smith (1965) implied that autotomy is an advanced condition in lizards, having arisen several times in different phylectic lines, other authors such as Etheridge (1967) and Hoffstetter & Gasc (1969) considered it to be a primitive condition among lepidosaurs which has been lost independently in different lines. Caudal autotomy is evidently of great antiquity among reptiles as indicated by the presence of fracture planes in the caudal vertebrae of the Permian ctylosaurs *Captorhinus* and *Labidosaurus* (Price, 1940) but whether the Lepido-
sauria inherited autotomy from cotylosaurs or evolved it independently is problematical as fracture planes are absent in the few eosuchians whose tails are known Romer (1956). Etheridge (1967), however, considered it unlikely that the capacity for midvertebral caudal autotomy could ever be regained once it had been lost because, despite its obvious selective value in a great variety of lizards, it is not found in the Agamidae where caudal fracture occurs intervertebrally.

In general, those lizards which have lost the capacity for autotomy appear to have lost all the structural characteristics associated with it. This is apparently true of the gecko Neophurus asper as well as chamaeleons and varanids (Ali, 1948, 1949) in which the caudal vertebrae lack fracture planes, the skin lacks lines of cleavage and the caudal musculature is not segmented but is continuous throughout the tail. In the pygopod Pletholax gracilis the caudal skin and musculature are unsegmented and the vertebrae do not readily break in two although vestiges of the fracture planes are present in the neural arches. However, for autotomy to be lost in lizards it is not necessary for all the structural characteristics associated with it to be lost simultaneously: ossification of the fracture planes as described by Etheridge (1967) would effectively reduce if not entirely inhibit autotomy without any further modification of the tail. In these circumstances autotomous ability could be regained, either by the return of the fracture planes or by the acquisition of a different type of vertebral fragility. In descendants of a lizard such as Iguana iguana in which the fracture planes are all obliterated only in adults (Etheridge, 1967), the fracture planes could reappear as a result
of neoteny whereby the adult stage of the descendant structurally resembles juvenile stages of the ancestor. Autotomy lost and regained in this way would escape detection, however, unless both the ancestral and descendant conditions were available for comparison. In another iguanid, Anolis carolinensis, in which only the anterior autotomous vertebrae have fracture planes (Cox, 1969), the midvertebral region of each postpygal centrum is weakened by a reduction in its dorsoventral thickness so that the centrum and neural arch in this region together form a thin-walled cylinder of bone which breaks in the event of autotomy. Although it is not known whether midvertebral attenuation of the caudal centra is common in iguanids, many of which are not autotomous (Hoffstetter & Gasc, 1969), this type of vertebral fragility appears to be a secondary condition which allows autotomy to occur in the absence of fracture planes. Although it appears unlikely, as Etheridge (1967) pointed out, that midvertebral autotomy can be regained after all the interdependent structural characteristics of the autotomous tail have been lost, a loss of autotomy involving only the fracture planes in the vertebrae need not be irreversible.

After autotomy in geckos and pygopods, as in most other lizards, a new tail develops which, when fully grown, resembles the original tail in size and shape but differs from it in several other respects. The differences include a lack of segmentation and the absence of vertebrae and spinal cord, innervation of the regenerate being by means of spinal nerves from the tail stump which grow back into the new tail (Hughes & New, 1959). Although Ganguly & Mitra (1958) described slender, rod-like vertebrae in
the regenerated tail of *Hemidactylus flaviviridis*, other authors including Woodland (1920), Hughes & New (1958) and Werner (1967) have described the regenerated axial skeleton of geckos including *H. flaviviridis* as an unsegmented tube of cartilage enclosing the ependymal tube which grows from the severed end of the spinal cord. In pygopods the cartilage tube is usually uncalcified although it may be slightly calcified in *Aprasia*, *Delma* and *Lialis* at its junction with the terminal part-vertebra of the original tail stump. In all the adult geckos examined with regenerated tails, the cartilaginous tube was calcified anteriorly. Only in the two species of *Hemidactylus*, *H. frenatus* and *H. garnotii*, was the tube calcified throughout its length and here, as in *H. flaviviridis* (Woodland, 1920) and *H. turcicus* (Werner, 1967), only the inner and outer surfaces of the tube were calcified.

Ossification of the regenerated axial skeleton has not been observed in geckos or pygopods although, according to Vorontsova & Liosner (1960), it can occur in lizards. If the bone fragment of the Permian lizard-like cotylosaur *Araeoscelis* is part of a regenerated caudal axial skeleton as proposed by Vaughn (1955), then tail regeneration as well as caudal autotomy is of great antiquity in reptiles.

The anterior caudal vertebrae of geckos and pygopods lack articulating ribs but bear well developed pleurapophyses on the neural arch pedicels. There may be a suture across the base of the pleurapophysis (Fig. 3:21) or near its tip or, in some cases, both sutures may occur on the same pleurapophysis (Fig. 3:193) indicating the presence of both the proximal and the distal rib elements. Very occasionally in pygopods the distal rib element
is cartilaginous but, in general, the pygal pleurapophyses of geckos and pygopods are completely ossified. Sutures on the pygal pleurapophyses may occur on adult as well as juvenile pygopods but in geckos they have been observed only in juveniles. The sutures usually take the form of an irregular line of discontinuity in the bone but, in one specimen of *Lialis*, the most anterior caudal rib on each side was joined to its vertebra by a thin layer of uncalcified cartilage, indicating a state transitional between the freely articulating ribs of the sacrum and trunk and the fused ribs typical of the caudal series.

The question whether caudal ribs occur in lizards has been debated for many years. Cligny (1899a & b) regarded the laterally directed processes on the caudal vertebrae of lizards as pleurapophyses whose costal component forms the major part of each process and is often recognisable in embryonic stages while Goodrich (1930) considered that the caudal transverse processes of amniotes in general consist partly of rib material. El-Toubi & Khalil (1950, 1955) described caudal ribs on one side of the body in the Egyptian geckos *Ptyodactylus* and *Tarentola*, while some New Zealand geckos have distinct caudal ribs on both side of the body (N. G. & E. M. Stephenson, 1956). In each of these geckos the ribs were distinguishable on the most anterior four caudal vertebrae. Other authors have described the laterally directed processes on the caudal vertebrae of geckos as transverse processes, thus implying that they arise solely from the neural arch (Siebenrock, 1893; Wellborn, 1933; Kluge 1962; Etheridge, 1967) while Romer (1956) stated that caudal ribs has not been reported in lizards generally. Hoffstetter & Gasc (1969) were non-committal: they supposed from
El-Toubi & Khalil's (1950) description of small terminal rib elements in geckos that the caudal transverse processes of lizards are essentially vertebral in origin but noted that this is contrary to the situation in Sphenodon where these processes are clearly the result of fusion of caudal ribs and are thus true pleurapophyses. They also pointed out that this interpretation does not agree with the embryological studies of Emelianov (1936), according to whom the lateral processes of the caudal vertebrae of Lacerta, Ophisaurus and Anguis consist almost entirely of ribs which fuse to their vertebrae during embryonic stages.

Although it cannot be assumed that the caudal transverse processes of all lizards are mainly costal in origin because they are so in Anguis, Ophisaurus and Lacerta, the presence of a suture across the bases of the processes occasionally in geckos and more often in pygopods suggests that the processes consist largely of fused ribs in the Gekkota as well. The variability in the occurrence of detectable caudal ribs in the Gekkota as well as in the position of the sutures suggests that fusion of the proximal and distal rib elements with one another and with their vertebrae is not strictly confined to a particular stage of their differentiation and growth. The absence of sutures in the majority of specimens would result from fusion at an early stage, probably before the onset of ossification. In any case, whether a caudal rib comprises the whole process or only part of it, it clearly represents in a reduced form the well developed and movably articulating caudal ribs of ancestral tetrapods.

Occasionally in pygopods the pleurapophyses of the first
caudal vertebra are slightly notched at their tips. Salle (1881) described the forked pleurapophyses in the cloacal region of snakes and snake-like lizards as lymphapophyses as their rami partially enclose and protect the posterior lymph hearts, and pointed out that the lymph hearts of *Lialis* are very small. In some limbless squamates such as the snakes and amphisbaenids (Hoffstetter & Gasc, 1969) and the anniellid lizard, *Anniella* (Coe & Kunkel, 1906), the lymphapophyses are deeply forked. In other lizards such as the anguids, *Anguis* and *Ophisaurus*, the bifurcation is comparatively shallow while the legless Teiidae and some apodous members of the Scincidae lack lymphapophyses (Hoffstetter & Gasc, 1969). In view of the rarity of notched pygal pleurapophyses in the pygopods examined here, the generalization of Romer (1956) and Hoffstetter and Gasc (1969) that lymphapophyses are absent from the Pygopodidae is accepted.

In the tails of geckos, pygopods and *Xantusia vigilis*, as in lizards generally, there are Y-shaped haemal arches or chevron bones. In those forms with a full complement of intercentra throughout the body, namely the geckos and *Xantusia* and the pygopods, *Lialis* and *Pygopus*, the haemal arch pedicels are usually attached to the intercentra (Fig. 3:19B) which may be in two sub-equal parts, but are sometimes attached separately to the intervertebral cartilage with a small, thin intercentral element lying between them (Fig. 3:21). In the other pygopods, which lack intercentra in the trunk, the haemal arch pedicels rest separately on the intervertebral cartilage, and are sometimes partly fused to the anterior margin of the following centrum.

Although the caudal chevrons of geckos and pygopods are
attached to the vertebral column in an intervertebral position, they are distinct from the intercentra rather than outgrowths from them as implied by Hoffstetter and Gasc (1969). According to Werner (1971), each caudal chevron in geckos develops from two arch pedicels which are preformed in cartilage and grow ventrally to join together below the caudal artery and vein, the intercentrum itself being a membrane bone which becomes coossified with the arch bases. The haemal arches of pygopods also arise separately from the intercentra in those forms with a complete series of intercentra as shown by specimens of *Lialis* in which rudimentary haemal arch pedicels representing the first chevron bone may take the form of slivers or nodules of bone suspended in connective tissue a short distance from the intercentrum to which they belong. The independent origin of the arch and intercentrum may also be inferred from situations where the arch bases and the intercentra are attached separately to the intervertebral cartilage (Fig. 3:21). Whether the haemal arches as well as the basal intercentral elements should be regarded as components of the caudal intercentra in geckos and pygopods is a question which concerns the homologies of all the intercentra in the column. For this reason discussion of this point is deferred to Part IV where the question of vertebral homologies is discussed.

The position of the first chevron is variable, especially in those pygopods with variable numbers of pygal vertebrae and of partly divided anterior postpygals. Unlike turtles and crocodilians in which the position of the first chevron is a sexual character (Romer, 1956), geckos and pygopods appear to show no sexual
dimorphism regarding the position of the first chevron although its form seems to be sex dependent in some species (vide infra). In geckos, which normally have five pygal vertebrae, the first chevron usually lies between the third and fourth vertebrae of the series, i.e. belongs to the fourth pygal. In Phyllurus platurus, however, the first chevron usually belongs to the fifth pygal in those specimens with two sacral and five pygal vertebrae and to the fourth pygal in specimens with three sacrals and four pygals. The position of the first haemal arch in Oedura lesueurii seems to vary independently of the sacral and pygal counts: it may belong to the third of fourth pygal vertebra although the sacral count is always two. In all the specimens of Nephurus examined the most anterior haemal arch elements belonged to the fourth caudal vertebra irrespective of the sacral count which was two, three or four. Among the pygopods, Lialis burtonis showed the least variation: in sixteen of the twenty specimens available for examination of the posterior region of the body the first chevron belonged to the third caudal vertebra. In Aprasia, Pygopus and Delma whose non-autotomic and partly divided vertebrae are more variable in number, the most anterior haemal arch elements may belong to the second, third or fourth caudal vertebra.

Variation in the form of the first chevron appears in some species to be related to its position, that is, to its proximity to the sacrum. In Aprasia pulchella, for example, the most anterior chevron of one specimen belonged to the second caudal vertebra and consisted of two small nodules of bone representing the arch bases; in another specimen it belonged to the third caudal and took the form of two separate, slender arch pedicels; in the third
specimen the first chevron belonged to the fourth caudal vertebra and was a complete arch prolonged ventrally into a haemal spine. Similarly in Lialis burtonis the first chevron is usually a complete arch when it belongs to the third caudal vertebra but consists of very small pedicel rudiments when it occasionally belongs to the second. The size of this chevron, particularly when it lies close to the sacrum, is probably limited by adjacent soft structures such as the posterior extremities of the kidneys and, in males, the hemipenes and their retractor muscles. Most of the species examined were represented by too few specimens for any sexual dimorphism to be evident in the size of the first chevron but in Lialis burtonis and Oedura lesueurii, represented by 20 and 32 specimens respectively, some dimorphism appears to exist. Of the 16 L. burtonis whose first chevron belonged to the third caudal vertebra, all eight females and five of the males had a complete arch while the remaining three males had comparatively short, unjoined pedicels. Similarly in O. lesueurii the first chevron was a complete arch in all the females whether it belonged to the third or fourth caudal vertebra, but was often reduced in males when it belonged to the third caudal. In Phyllurus platurus (33 specimens), on the other hand, there appears to be no difference between males and females in the form of the first chevron which is a complete arch whether it belongs to the fourth or the fifth caudal vertebra. The second chevron in all the geckos and pygopods examined was a complete arch, irrespective of its position in the tail.

Chevron bones in the form of arches are usually prolonged ventrally into more or less cylindrical haemal spines whose termi-
nal portions are almost always of cartilage (Figs 3:19B, 3:21, 3:22A - C, E - F) which often calcifies (Fig. 3:21, 3:22A) but rarely ossifies. In Pletholax, however, all the haemal spines were completely bony (Fig. 3:22D) and, especially in the anterior tail, were broadly spatulate rather than cylindrical with their concave surfaces directed dorsally. The most anterior haemal spines of some geckos and pygopods are joined together by a strong ligament or by a band of cartilage representing the conjoined distal portions of the spines (Figs 3:19B, 3:21). This junction of the spines may be a modification to increase the rigidity of the pygal region, and hence to protect the cloaca and associated organs in the event of autotomy, but does not necessarily serve this purpose as the first two haemal spines are joined by a ligament in Pletholax gracilis and by a cartilage bridge in Nephurus asper, yet both these species are incapable of autotomy. In Nephurus levis and the three species of Phyllurus, whose fracture planes occur only in the more anterior postpygal vertebrae, the haemal arch preceding the first fracture plane of adult specimens is enlarged and its spine is fused to the spine in front of it, usually by cartilage (Fig. 3:19B) and only rarely by fusion of the bony shafts of the spines. Similar junction of the last pygal and the first postpygal haemal spines was also found in the single specimens of Carphodactylus laevis and Rhynchoedura ornata but, as these two specimens had lost their original tails at the level of the first fracture plane, the presence or absence of fracture planes in the rest of the tail could not be determined. Among the other geckos examined, whose tails have fracture planes in all but the terminal postpygal vertebrae, conjoined haemal spines were found in only five specimens: one of the 32 specimens of Oedura
lesueurii and four of the five adult specimens of Coleonyx.

Among autotomous pygopods, junction of the first two haemal spines is usually found in adult Delma, Pygopus and Lialis but has not been observed in Aprasia. In Delma and most Pygopus the spines are joined by a ligament. Occasionally in Pygopus (Fig. 3:21) and almost always in Lialis the spines are joined by cartilage which is often heavily calcified. Occasional specimens of Lialis have the first three haemal spines joined by a bridge of cartilage. Owing to the presence of partly divided centra in the anterior tail of pygopods, it was not possible to ascertain whether the conjoined haemal spines immediately precede the most anterior fracture plane which is capable of autotomous breakage as is the case in some geckos. In most cases the vertebra to which the more posterior of the joined spines belongs is only partly divided by its fracture plane.

The neural spines of the anterior pygal vertebrae of geckos and pygopods are similar in size and shape to those of the sacrum and posterior trunk. In most of the geckos described above as having conjoined haemal spines, namely Nephurus levis (but not N. asper), the three species of Phyllurus, the two species of Coleonyx and the single specimens of Carphodactylus laevis and Rhynchoedura ornata, the neural spine of the last pygal vertebra is enlarged and directed vertically, unlike the more anterior pygal neural spines which are less robust and posteriorly inclined. The body of the last pygal vertebra and its pleurapophyses are not enlarged but continue the trend for rostrocaudal reduction in size shown by the more anterior pygal vertebrae. Enlargement of the last pygal neural spine and of the first postpygal chevron bone
together with junction of its haemal spine with the one in front of it would strengthen the base of the tail considerably and suggests that autotomy normally occurs through the most anterior fracture plane in all of these geckos, whether or not there are fracture planes in the more posterior postpygal vertebrae. In other geckos which are known to be capable of autotomy through any part of the postpygal tail, e.g. *Gehyra variegata* (Cogger, 1967, Pl. 9; Bustard, 1968) *Heteronotia binoei* (Worrell, 1963, Pl. 14 - banded phase; Bustard, 1970, Pl. 33) and *Oedura lesueurii* (personal observation of living specimens), there is no such strengthening of the tail base.

There is no enlargement of the pygal neural spines in pygopods. Instead, in the transitional region where the fracture planes are incomplete, especially in *Lialis* and *Pygopus* which have comparatively large neural spines, there is a rapid reduction in the rostrocaudal length of the spines so that they become restricted to the posterior halves of the neural arches behind the planes of fracture. A similar reduction in the size of the neural spines also occurs in the anterior postpygal region of geckos and *Xantusia*. There is no sudden reduction in their height; they become gradually smaller posteriorly together with the other processes of the caudal vertebrae.

Stokely (1947) described double neural spines on the autotomous vertebrae of *Aprasia repens* which are comparatively more conspicuous than those of the more anterior vertebrae. In all the lizards examined here, however, including *Aprasia pulchella*, there is only one neural spine on the autotomous vertebrae, situated at the posterior end of the arch (Fig. 3:22 A, B). Stokely may
have regarded as neural spines the somewhat raised edges of the autotomy cleft through the neural arch, particularly in the more posterior caudal vertebrae which have lost their true neural spine. Duplication of caudal neural spines has been reported in other lizards such as Dipsosaurus, Anolis and Lacerta (Cope, 1892) but from personal observation of Lacerta vivipara it is clear that only the more posterior spine is the true neural spine. The more anterior of the two spines, situated approximately half way along the arch, comprises the lips of the autotomy cleft which are closely applied to one another and elongated dorsally into a sharp spine. Hoffstetter and Gasc (1969) used the term dorsal paraseptal apophyses to describe the two halves of this spine in view of the inaccuracy of the more common term, secondary neural spine.
SUBCENTRAL FORAMINA

(Figs 3:11 - 19, 3:21 - 22, Pls 10, 14)

The postatlantal centra of geckos, pygopods and Xantusia are perforated by a pair of subcentral foramina. In geckos these foramina are ventral in position, lying on either side of the midline about half way along the centrum (Fig. 3:16, 3:18B) and have been described in living forms by Mahendra (1935a, 1950), N. G. & B. M. Stephenson (1956), Kluge (1962b) and Werner (1971) and in fossil species of the extant genus Aristelliger by Hecht (1951).

The subcentral foramina of the pygopods examined here are also situated approximately half way along the ventral surface of the centrum although, according to Stokely (1947, fig. 1b), those of Aprasia repens are more anteriorly placed about one third of the way along the centrum. In Delma the subcentral foramina lie close to the ventral mid-line as in geckos but in the other pygopods examined they are more variable in position, either lying close to the mid-line or at some distance from it on the ventrolateral surface of the centrum. Both these conditions are seen in Pygopus, Lialis and Aprasia, sometimes within the same animal. In Pletholax the position of the subcentral foramina varied widely in different parts of the body. They lay close to the ventral mid-line in the anterior and posterior thirds of the presacral column and in the sacral and pygal regions where the centra are squarish in ventral outline but in the middle of the presacral region, where the centra are longer and more slender, they were laterally placed behind the costal processes. Some of these mid-trunk foramina appeared to lie at the neurocentral boundary while others were placed further dorsally on the side of the vertebra and clearly entered the base
of the neural arch. Some vertebrae had two pairs of foramina, a pair in each of these positions. The subcentral foramina of *Xanthusia vigilis* were smaller than those of geckos and pygopods and were more anterior in position, lying only one fourth of the way along the ventral surface of the centrum. In geckos, pygopods and *Xanthusia* the only centrum throughout the vertebral column which lacks foramina is the atlantal centrum which has been incorporated into the axis vertebra as its odontoid process.

Each subcentral foramen opens into a canal which passes through the centrum to the side of the notochord where this is present, is continuous with the marrow spaces in the centrum and opens by means of a second foramen into the neural canal (Fig. 3:17B, Pl. 10A). According to Camp (1923) the subcentral foramina of lizards are arterial foramina but in the geckos and pygopods examined here the foramina were found to contain veins carrying blood away from the spinal cord. Veins were also found in this position in the Israeli gecko, *Ptyodactylus hasselquistii*, by Werner (1971). The arteries of the spinal cord are branches of the segmental arteries and enter the neural canal through the spaces between adjacent neural arches (or intervertebral foramina) alongside the spinal nerves (Fig. 3:17A). The nature of these vessels was determined from serial sections of the geckos *Gehyra variegata*, *Oedura lesueurii* and *Coleonx variegatus* and the pygopods *Pygopus lepidopodus* and *Lialis burtonis* and was confirmed in *P. lepidopodus* by dissection of a freshly killed animal whose heart had been injected with India ink.

The presence of paired foramina in the centrum of reptilian vertebrae appears to be a character of some antiquity. Possibly
the oldest reptile known to possess them was the problematic reptile from the upper Permian described by Parrington (1956) who considered this animal to be a representative of a very early radiation of the diapsids but was unable to identify it further from the available fragments. The foramina in this reptile were laterally placed on the centrum and, according to Parrington, were probably nutritive and may have been concerned with the persistent notochord. Paired subcentral foramina are also present in the sacral and pygal vertebrae of adult *Sphenodon* and it was established from dissection of two preserved adult specimens that the apertures in the sacral vertebrae, which are larger than those in the tail, contain two blood vessels, a vein and an artery. The latter vessel is a very fine branch of a segmental artery from the dorsal aorta, a larger branch of which appeared to enter the neural canal between adjacent neural arches. Examination of a dried skeleton showed that subcentral foramina are absent from the trunk of adult *Sphenodon* but they are present in juveniles prepared as alizarin transparencies. No blood vessels could be detected in the foramina of this macerated material. According to Howes and Swinnerton (1901), the paired apertures in the centrum of *Sphenodon* embryos are regions of incomplete ossification. Two pairs of subcentral foramina are present in the anterior postpygal vertebrae of adult *Sphenodon*, one pair on each side of the plane of fracture, while the apertures in the more posterior caudal centra are variable in number and position.

The presence of subcentral foramina is generally regarded as a primitive characteristic in the Squamata. Camp (1923) considered them to be primitive in lizards while Mahendra (1935c)
regarded them as primitive in snakes as well. They are nevertheless of widespread occurrence in squamates and may be present in some and absent from other members of the same family. Families of lizards in which they have been reported include the Amphisbaenidae (Camp, 1923; Zangerl, 1945), the Iguanidae (Blanc, 1965), the Xenosauridae and the Anguidae (Barrows & Smith, 1947). Of the Australian material examined personally they were present in Amphibolurus barbatus, A. muricatus and A. adelaidensis and absent from Tropidocryptis lineata and Moloch horridus (Fam. Agamidae), present in Rhodora vittatopunctata and absent in Lygosoma verreauxi, Hinulia monttrois, Sphenomorphus quoyi and Saiphos aequale (Fam. Scincidae). (The last three genera were listed by Romer, 1956, as synonyms of Lygosoma). They are also present in the British anguid, Anguis fragilis. Subcentral foramina have been observed in several families of snakes by Mookerjee & Das (1933), Mahendra (1935c, 1936), Dunn & Tihen (1944), Hoffstetter (1946c), Sood (1948), Evans (1955), Liss (1958, 1966), Hoffstetter & Gayraud (1964) and Thireau (1967, 1968). According to Hoffstetter & Gayraud (1964) several foramina pierce the vertebrae of snakes and occupy rather precise positions while Hoffstetter & Gasc's (1969) observation that the subcentral foramina are usually paired and only rarely in the form of a single median aperture suggests that these foramina are normally found in ophidian vertebrae. In view of the widespread occurrence of subcentral foramina in the Squamata, their presence in the Gekkota would appear to have little phylogenetic significance.

The development of the subcentral foramina of squamates does not appear to have been described although Mookerjee & Das
(1933) suggested that, after the formation of the blood vessels in *Typhlops braminus*, the developing centrum fails to ossify at these points. Although the embryonic material available for the present study was inadequate for a description of early stages of vertebral development in the Gekkota, there was available a large series of serially sectioned embryos of the anguid *Anguis fragilis* and the lacertid *Lacerta vivipara*. In neither of these lizards was there any sign of subcentral foramina or central canals during early stages of vertebral development, not even in centra which were entirely cartilaginous (Pl. 14A, C). Soon after the onset of perichondral ossification of the centrum, however, an endochondral ossification centre appears on either side of the notochord and through the marrow cavity so formed a vein is seen to pass from the neural canal to the subcentral foramina (Pl. 14B, D). From Werner's (1971) illustrations of vertebral development in *Ptyodactylus hasselquistii*, it is clear that the venous canals in this gecko arise in a similar manner (op. cit. Figs 23, 30, 32). According to Le Gros Clark (1965), the vascularization of cartilage bones occurs in the following way: after the onset of perichondral ossification, an active and highly vascular ingrowth from the deeper osteogenic layer of the periosteum pushes its way into the bone, eroding the calcified cartilaginous matrix to do so, and carrying with it the osteoblasts which will lay down endochondral bone. In *Anguis* and *Ptyodactylus* the veins so formed and the foramina through which they pass persist in adult stages but in *Lacerta* they are lost during postnatal stages with the result that the adult centrum lacks subcentral foramina. Whether transient venous canals occur in the developing centra of other
lizards whose adult centra lack subcentral foramina is apparently not known but the presence of these apertures in adult *Anguis* and *Ptyodactylus* and their absence in adult *Lacerta* appear to be due to relatively minor differences in the development of the vertebral column and its associated blood vessels rather than to inherent differences in their morphology.

According to Mahendra (1935c), the position of the sub-central foramina of the gecko, *Hemidactylus*, and of other squamates coincides very well with the position of the intersegmental blood vessels in Goodrich's (1930) diagrams of the sclerotogenous (op. cit., fig. 62c) and early cartilaginous stages (op. cit., fig. 62d) of developing amniote vertebrae. Mahendra suggested that the apertures are intersegmental in position, representing in the adult animal the sclerotomic segmentation of earlier stages. However, as the central canals of such diverse lizards as the gekkonid, *Ptyodactylus hasselquistii*, the anguid, *Anguis fragilis*, and the lacertid, *Lacerta vivipara*, appear comparatively late in development, long after the sclerotomic components of the vertebra have fused together, it cannot be assumed that they mark the site of the original intersegmental boundary.
DISCUSSION

AMPHICOELY AND PROCOELY IN THE GEKKOTA

The procoelous vertebrae found in two Australian geckos, *Carphodactylus laevis* and *Phyllurus milii*, closely resemble those of *Sphaerodactylus parkeri* from Jamaica and *Coleonyx variegatus* and *C. brevis* from North America and are not far removed from the amphicoelous condition. In all of these procoelous geckos the notochord extends without interruption from the axis vertebra to the tail, at least in juvenile and early adult stages, and discrete intercentra are present throughout the vertebral column.

The procoelous centra of pygopods are also notochordal in adult stages but only *Lialis* and *Pygopus* have a full complement of intercentra. Like amphicoelous and procoelous geckos, *Pygopus* reaches adulthood without any interruption of the notochord posterior to the axis whereas *Lialis*, *Delma*, *Aprasia* and possibly *Pletholax* appear to lose their chordal continuity by the time they are sexually mature. Geckos and pygopods also resemble one another in the structure of their intervertebral cartilage which is undivided by a synovial cavity even in animals which have completely lost the notochord from the intervertebral region. Thus, contrary to the opinion of Hoffstetter & Gasc (1969), the Gekkonidae and Pygopodidae resemble one another very closely in vertebral structure. This similarity augments the many other points of resemblance between geckos and pygopods considered by Shute & Bellairs (1953), McDowell & Bogert (1954), Underwood (1957a), N. G. Stephenson (1961) and others to be indicative of the close
relationship of these two families, especially as none of the particular points of resemblance between their vertebrae, namely notochordal adult centra, non-synovial intercentral joints and free intercentra in the trunk, is known to occur in any other squamates except the Xantusiidae. In other lizards such as *Anguis fragilis* and various species of *Lacerta* (von Ebner, 1892; Goette, 1897; Manner, 1899; Cligny, 1899b and personal observation) and in several genera of snakes (von Ebner, 1892; Goette, 1897; Manner, 1899; Cligny, 1899b; Brünauer, 1910; Sood, 1948; Gasc, 1967b) a joint cavity forms between consecutive procoelous centra and the notochord within the centrum is resorbed during pre-adult stages.

The relationship between notochordal amphicoelous and procoelous vertebrae in squamate reptiles is best illustrated by reference to their ontogeny and phylogeny. During early stages of vertebral development in reptiles generally (see Schauinsland, 1906; Remane, 1936) the centra are essentially of notochordal amphicoelous construction in that the notochord is continuous throughout the vertebral column and the intervertebral tissue takes the form of a ring enclosing the notochord between the ends of consecutive centra. In *Sphenodon* and most geckos this type of centrum is retained in adult stages whereas in adult stages of other squamates and crocodiles the vertebrae have become procoelous.

The ontogeny of the procoelous condition in reptiles has been described in different ways depending on whether chordal constriction occurs within the intervertebral tissue or within the centrum itself and whether the intervertebral tissue retains its identity or becomes incorporated into one or both of the adjacent centra. According to some early workers including von Ebner
(1892), Goette (1897) and Schauinsland (1906) the notochord in various non-gekkotan squamates is constricted within the intervertebral tissue which becomes fused to the posterior end of the preceding centrum to form its condyle. Camp (1923) considered that procoelous gekkonid vertebrae are probably formed in a similar manner while some later authors such as Remane (1936) and Romer (1956) maintained that all procoelous lacertilian vertebrae develop this way. According to Romer, the intervertebral disc becomes rounded and attached to the sheath of the centrum anterior to it as a condylar ball. A similar condition is thought to exist in chelonians (see Remane, 1936) except that the line of division occurs in the middle of the intervertebral body so that part of it becomes fused to the preceding centrum and part to the following one. According to Balfour (1885), the intervertebral cartilage of reptiles in general becomes thickened and gradually constricts the notochord and soon becomes divided into two parts which form the articular faces of two contiguous vertebrae.

The procoelous centra of crocodiles, on the other hand, are said to develop in quite a different manner (see Schauinsland, 1906; Remane, 1936) in that the intervertebral tissue becomes the cartilaginous intervertebral disc and the condyle forms as a result of growth of the centrum itself. Goodrich (1930) maintained that, in procoelous reptiles generally, the central cartilage develops greatly posteriorly and eventually completely obliterates the notochord intervertebrally, the bulk of this posterior region of the centrum forming the convexity of the adult vertebra.

From the foregoing brief summary of past opinions regarding the ontogeny of procoelous reptilian vertebrae, it is clear that
each interpretation has been applied, directly or indirectly to squamate procoely in general. From the present study and the work of Werner (1971) it is seen that procoelous vertebrae in the Gekkota develop in essentially the manner described by Goodrich (1930), as a result of differential growth of the posterior end of the centrum. The cartilage of each centrum grows out posteriorly to form the condyle, without at first constricting the notochord, and is subsequently invaded by endochondral ossification from the body of the centrum. This is the stage reached by adult Carphodactylus and juvenile Phyllurus milii, Coleonyx and Pygopus. Subsequent growth of the condyle in a posterior direction is accompanied by its growth centripitally with the result that the diameter of the notochord is reduced within the condyle, while a similar but less marked constriction occurs in the anterior end of the centrum. As a result of these constrictions in the ends of adjacent centra the diameter of the notochord within the intervertebral cartilage is reduced, while the constriction in the anterior end of the centrum also allows the formation of the concave socket for articulation with the preceding condyle. This is the stage reached by adult P. milii, and Sphaerodactylus, sub-adult Coleonyx and Pygopus and juvenile Lialis. Posterior and centripetal growth of the condyle continues, increasing the convexity of the condyle and further constricting the notochord within it as seen in recently matured Coleonyx and Pygopus and sub-adult Lialis, until the notochord is reduced to a thread consisting of remnants of the chordal sheath as found in older specimens of Coleonyx. In older specimens of Pygopus and in adult Lialis the notochord has been resorbed from both ends of the centrum and in apparently aged specimens of Pygopus has been
lost altogether. In addition to the reduction of the notochord in the ends of the centrum in Delma, Aprasia and Pletholax, but not apparently in Pygopus or Lialis, the notochord is also lost midvertebrally as a result of ossification beginning in the chordal cartilage. In Aprasia and apparently Pletholax as well, midvertebral interruption of the notochord precedes its interruption in the ends of the centrum whereas in Delma the notochord is lost from the ends of the centrum prior to its interruption midvertebrally.

This comparative account of the ontogeny of procoelous gekkotan vertebrae, shown diagrammatically in Fig. 3:23, demonstrates that the procoelous condition develops in the same way in geckos and pygopods and that the differences found between the procoelous centra of different genera depend on the stage they reach in this ontogenetic sequence, i.e. on the extent of notochordal reduction, at the time of sexual maturity and on the extent to which chordal reduction continues during adult life. The intervertebral cartilage, instead of constricting the notochord within it and fusing to the preceding centrum to form its condyle as postulated by Camp (1923), retains its identity throughout development as an undivided layer of fibrous cartilage joining adjacent centra. The most noticeable change it undergoes is in its shape. In early stages, before the onset of chordal constriction, it is in the form of a ring enclosing the notochord as in amphicoelous geckos but later, as the condyle grows posteriorly and the notochord decreases in diameter, it becomes a concavo-convex layer joining the condyle to its socket. The fact that no intervertebral synovial cavity exists in procoelous gekkotans
Vertebral region prior to ossification of chondral cartilage.

Figure 3:22. Morphogenetic stades in ontogeny and evolution of procoelous vertebral centra in
the gekkota.

Figure 3:1 - 3:4, are as follows:

Phases found in gekkota of different ages, some of which are illustrated in
mediolateral section, diagrammatic. Intercentra not shown. The

Centra in a are amphiocodynamics, remainder procoelous. Centra in p are non-procoelous, remainder

P. Prognosis, old adult? (acro xenota, adult)
B1. Pterohex, adult
D. Aporesta, adult
D1. Rhine, adult
C. P. mitriform, adult; spinerectocylus, adult
B. Carinocylus, adult; phylogenetic, juvenile, adult
A. Amphicoelous geckos, juvenile, a adult
which have entirely lost the notochord from the ends of the centra may be due to the development of this condition comparatively late in life, at a time when the intervertebral tissue is no longer able to differentiate into the hyaline cartilage normally found on the opposing surfaces of moving joints. Although nothing is known regarding vertebral development in the Xantusiidae, the presence of a small pit on the condyle and the absence of an intercentral synovial cavity in adult *Xantusia vigilis* suggest that, in this family too, the notochord may remain continuous between consecutive vertebrae until comparatively late in development.

A significant feature of the ontogeny of procoelous vertebrae in the Gekkota is that it begins late in embryonic life (see also Werner, 1971) at a time when the procoelous condition in other squamates is already well established (see Goette, 1897; Schauinsland, 1906; Brüner, 1910). Reduction of the notochord within the condyles of procoelous gekkotan vertebrae occurs during pre-adult and adult stages whereas in other squamates this process is virtually complete by the time of hatching. Whether the sequence of events in the ontogeny of non-gekkotan squamate vertebrae is essentially the same as that in the Gekkota, or whether the original intervertebral tissue forms the condyle as described by Goette (1897), Schauinsland (1906), Remane (1936) and others, remains to be seen. Nevertheless, in embryos of *Lacerta vivipara* and *Anguis fragilis* examined personally, the distinctive histological appearance of the condyle compared with the body of the centrum appears to be due to the fact that the condyle is the most actively growing region of the centrum.
From a phylogenetic point of view, the amphicoelous condition of the centrum, as found today in *Sphenodon* and most Gekkonidae, used to be regarded as the more primitive condition from which the procoelous conditions found in other reptiles have evolved (Boulenger, 1885; Gadow, 1901; Camp, 1923; Remane, 1936). According to some other authors, however, namely Cope (1900), Underwood (1954), Romer (1956) and Kluge (1967a), procoely is the more primitive condition in squamate reptiles and the amphicoelous condition found in most geckos is secondary or degenerate. Cope (1900) gave no reasons for his opinion that amphicoely is secondary in geckos while Underwood's (1954) conclusion to this effect, which was subsequently withdrawn in view of the amphicoely of Triassic lizards (Underwood, 1955), followed from his classification of geckos on ophthalmological grounds. Romer's (1956) reason for regarding gekkonid amphicoely as secondary was because most workers believe it to be so (*op. cit.*, p. 255). Kluge (1967a) pointed out in his classification of the Gekkonidae that the Triassic reptiles referred to by Underwood (1955), i.e. *Kuehneosaurus* (Robinson, 1962) and *Macrocnemus*, *Tanystropheus* and *Askeptosaurus* (Kuhn-Schnyder, 1954), were not ancestral to modern lizards but constituted a separate radiation of squamates, thereby implying that their amphicoely has no bearing on the amphicoely of most living geckos.

Kluge (1967a) regarded the procoelous centra of eublepharine geckos (which include *Coleonyx*) as the primitive condition from which the amphicoelous condition found in most other living geckos has evolved. The basis for this conclusion was Kluge's assumption that the procoelous Upper Jurassic Ardeosauridae were directly
ancestral to the Eublepharinae which he considered in turn to be ancestral to all other living geckos. The procoelous centra found in some other non-eublepharine geckos were considered by Kluge to have evolved secondarily from the amphicoelous condition. Because Gonatodes possesses more primitive character-states than any other member of the Sphaerodactylinae and has amphicoelous centra, Kluge maintained that the procoelous condition found in all other sphaerodactyline genera has evolved secondarily. The procoely found in one gekkonine genus, Ebenavia from Madagascar, he considered to be secondary because all other gekkonines are amphicoelous. According to Kluge, the Diplodactylinae are all amphicoelous except for Carphodactylus, Crenadactylus, Diplodactylus, Oedura and Phyllurus in which "there is a tendency towards procoely"; unlike all other procoelous geckos, these diplodactyline genera do not attain "the typical saurian form" of the centrum. To explain these evolutionary sequences Kluge suggested that the amphicoelous condition found in the majority of the geckos could have been derived from the procoelous type by arrested development and retention of the embryonic form. According to Kluge, the tendency toward procoely, as exhibited by some diplodactyline genera, could have evolved secondarily by suppression of the neotenic process, or it might simply be a reflection of the primitive genetic background of the subfamily.

A general assessment of Kluge's (1967a) method of classifying the Gekkonidae and his conclusions regarding their interrelationships is given in the Appendix where it is pointed out that there are no grounds for assuming that the Upper Jurassic Ardeosauridae were ancestral to any group of living geckos and that his contention that the Eublepharinae were directly ancestral
to the Diplodactylinae and therefore indirectly ancestral to the Gekkoninae and Sphaerodactylinae was based on false premises. Of the five diplodactyline genera considered by Kluge to show a tendency towards procoely, only *Carphodactylus laevis* and *Phyllurus mili** of the geckos examined in the present investigation were found to be even slightly procoelous. Moreover, it has been shown already that the centra of various procoelous geckos belonging to the Eublepharinae, Sphaerodactylinae and Diplodactylinae closely resemble one another and those of pygopods but differ considerably from the procoelous centra of non-gekkotan lizards. Indeed, in view of the variation seen in the ancestral form of the centrum in different families of lizards (Camp, 1923), it is questionable whether a "typical" procoelous centrum can be said to exist in the Lacertilia. Heterochrony (de Beer, 1958) and neoteny in the broad sense have played an important part in gekkonid evolution (N. G. & E. M. Stephenson, 1956; N. G. Stephenson, 1960) but there is no evidence that neoteny has been responsible for the evolution of amphicoely from procoely in these lizards. On the contrary, the available evidence points to the primitiveness of amphicoely in the Gekkota and the parallel evolution of procoely in different lineages.

There seems to be no doubt that notochordal amphicoely of the centrum and a complete series of discrete intercentra were the original states of these characters in reptiles, as discrete intercentra and pleurocentra and a continuous notochord were characteristic of the labyrinthodont amphibians from which the reptiles evolved (Romer, 1966). Among early reptiles notochordal amphicoely and a complete series of intercentra were characteristic
of the Cotylosauria or stem reptiles and also occurred in the
pelycosaurian ancestors of the mammal-like reptiles as well as
the eosuchian ancestors of other lepidosaurs and the Archosaurus
(Romer, 1956; Carroll, 1969a, b & c). The Permian genus,
Araeoscelis, considered by Williston (1910, 1914) to be an ance-
stral lizard, also had notochordal amphicoelous vertebrae and inter-
centra, but this reptile is now considered to be a captorhinomorph
cotylosaur (Vaughn, 1955).

Within the Lepidosauria, there was a trend in the Eosuchia
towards loss of the notochord so that many forms had solid, acoelous
centra (Romer, 1956) but, as far as is known, no eosuchian was
procoelous. In Prolacerta the centra were shallowly biconcave
but pits in the articular faces of the centra indicated the pre-
sence of the notochord (Camp, 1945). The Rhynchocephalia, which
descended from the Eosuchia (Romer, 1968) were for the most part
amphicoelous (Romer, 1956) although there was a rapid trend to-
wards planar (or acoelous) centra in the Triassic Rhynchosauria
(Hoffstetter, 1955a). Only one family of rhynchocephalians, the
Upper Jurassic Sapheosauridae, had procoelous vertebrae (cf.
Hoffstetter & Gasc, 1969, p. 243) in which the condyles, according
to Hoffstetter (1955a), were exactly the same as those of living
procoelous geckos. Of the relatively unspecialised and very con-
servative Sphenodontidae, living Sphenodon has retained the noto-
chordal amphicoelous state of the centrum and intercentra to the
present day (Hoffstetter, 1955a; Hoffstetter & Gasc, 1969).

In the Squamata, which also evolved from the Eosuchia
(Romer, 1968), the only forms known definitely to have notochordal
amphicoelous centra are living geckos and fossil geckos ascribed
to living genera. From most descriptions of fossil squamates it cannot be established with certainty whether centra described as amphicoelous or biconcave were or were not notochordal, although in some forms which have been described as acoelous, it is clear that the centra did not enclose a continuous, unconstricted notochord.

Some Triassic reptiles may be classified as squamates or eosuchians depending on one's definition of a lizard (see Robinson, 1967; Romer, 1968). Tarlo (1968) reviewed the taxonomic history of these Triassic forms and placed them in the Squamata but, in contrast to Kuhn (1963), placed them in different orders from the Sauria (= Lacertilia) which have living representatives. Askeptosaurus was specialised for a marine existence, Macrocnemus was an unspecialised, apparently littoral reptile while Tanystropheus, with its bizarre long neck, may have been semi-aquatic (Peyer & Kuhn-Schnyder, 1955; Tarlo, 1967). All of these reptiles had biconcave centra lacking intercentra in the trunk (Kuhn, 1952; Peyer & Kuhn-Schnyder, 1955). Two other Triassic reptiles, Keuhneosaurus (Robinson, 1962) and Icarosaurus (Colbert, 1966), differed from the preceding genera in that they had a fully movable quadrate and were therefore true lizards (Romer, 1968). They were both highly specialised for gliding flight despite their early appearance in squamate history and had platycoelous (= acoelous) and amphicoelous vertebrae respectively but without trunk intercentra (Robinson, 1962; Colbert, 1966). Considering the diversity of these genera, there was evidently a widespread trend in Triassic squamates towards loss of the trunk intercentra. Whether there was an equally widespread trend towards loss of the notochord cannot be determined from the literature as Keuhneosaurus, whose
centra were first described by Robinson (1962) as "platycoelous" and later as "weakly amphicoelous" (Robinson, 1967), is the only Triassic squamate which apparently lacked a continuous notochord.

The oldest squamates known to have had procoelous vertebrae come from the Upper Jurassic and were thus more or less contemporary with the only known procoelous rhynchocephalians. By the Upper Jurassic, most of the larger suprafamilial groups of living lizards were recognisable but the families had not yet acquired their modern characteristics (Hoffstetter, 1964, 1967). Although no squamates are known between the Triassic and the Upper Jurassic and the relationships of many of the Upper Jurassic lizards are not yet clear (Hoffstetter, 1964, 1967; Romer, 1968), it appears that procoely was already of general occurrence in the Autarchoglossa (Scincomorpha and Anguimorpha) at that time whereas the contemporary Ascalabota (Gekkota and Iguania) contained some amphicoelous and some procoelous forms as they do today (Hoffstetter, 1967).

The Gekkota of the Upper Jurassic have been described by Cocude-Michel (1963) and Hoffstetter (1953, 1962, 1964, 1966) and, according to Hoffstetter (1964), form three distinct groups. Ardeoarosaurus, Richstaettisaurus (= Broilisaurus) and Yabeinosaurus form a natural group (Family Ardeoarosauridae) which, on the basis of skull structure, definitely belongs to the Gekkota. At least two of these genera, Ardeoarosaurus and Yabeinosaurus, are known to have had procoelous vertebrae (Hoffstetter, 1964, 1966) but there appears to be no record of the presence of free trunk intercentra in any of them. The second group, represented by the single genus Bavarisaurus from the same horizon as the Ardeoarosauridae (Hoffstetter & Gasc, 1969), was placed tentatively in the Gekkonoidea by
Hoffstetter (1964) on the basis of its vertebral characters, namely the relatively short amphicoelous vertebrae with free intervertebral intercentra throughout the trunk. Although Hoffstetter (1964) was unable to confirm the absence of condyles on the centra of *Bavarisaurus*, he considered them to be amphicoelous because they were typically gekkonoidean in lateral view. In a later publication (Hoffstetter & Gasc, 1969), the vertebrae of this lizard were described as "clearly amphicoelous", the source cited for this information being Hoffstetter's above-mentioned 1964 paper. The third group of Upper Jurassic lizards tentatively ascribed by Hoffstetter (1964) to the Gekkota was represented by the poorly known genus, *Palaeolacerta*. This genus had some features in common with the Ardeosauridae and *Bavarisaurus* but was separated from them by Hoffstetter (1964) because its amphicoelous centra were elongated and free intercentra were present only in the neck and anterior trunk. Although Hoffstetter (1964) considered that *Bavarisaurus* and *Palaeolacerta* could be included in the Ardeosauridae if this family were redefined, he also acknowledged that they may not in fact belong to the Gekkota but may instead have been proto-iguanians with amphicoelous vertebrae.

More recent fossil geckos whose vertebrae are known include the Tertiary genus, *Gerandogekko*, and the Pleistocene subfossil, *Macrophelsuma*, both of which had amphicoelous vertebrae (Hoffstetter, 1964b), and the late Pleistocene or sub-Recent forms placed in the Recent genus, *Aristelliger*, whose amphicoelous centra had a deep conical hollow in each end (Hecht, 1951). Free trunk intercentra were not described in these forms.
The last-named genus of fossil squamates appears to be the only one whose amphicoelous centra have been described in sufficient detail to be recognised as notochordal like the centra of living geckos. Although centra described as having flat ends (i.e. biplanar, amphiplatyean, platycoelous or aceloelous centra), such as those found in some eosuchians and rhynchocephalians, were relatively solid structures which either lacked the notochord entirely or retained it in a greatly reduced form (cf. Prolacerta -- Camp, 1945), the centra of Triassic and Jurassic squamates which have been described as "amphicoelous" or "biconcave" may have been hollow and notochordal like those of Sphenodon and most living geckos or solid like the "weakly amphicoelous" centra of Triassic Kuehneosaurus. In these circumstances the "amphicoely" of Triassic squamates is not evidence for the primitiveness of notochordal amphicoely in living squamates (cf. Underwood, 1955; Hoffstetter & Gasc, 1969), especially as none of the known Triassic forms is likely to have been close to the ancestry of any of the living Squamata (Romer, 1966; Kluge, 1967a). Nor is there any justification for using the amphicoely of Jurassic Bavarisaurus as an argument for the primitiveness of notochordal amphicoely in the living Gekkonidae (cf. Hoffstetter & Gasc, 1969). The centra in this genus were only assumed to have been amphicoelous and there is no evidence as to whether they were notochordal, yet the presumed amphicoely of Bavarisaurus was one of the reasons why Hoffstetter (1964) tentatively placed this genus in the Gekkonoida.

Procoelous centra in the Squamata may also be notochordal, as in some living members of the Gekkota, or solid like those of living non-gekkotan squamates, but it is not known which of these
conditions existed in the Jurassic Ardeosauridae. In any case, the procoely of the Ardeosauridae is not evidence for the primitiveness of procoely in living geckos (cf. Kluge, 1967a), even though this family definitely belonged to the Gekkonoidea on the basis of its skull structure, as the Ardeosauridae may have been advanced geckos in some respects, despite their early appearance in the history of the Gekkota (see also Appendix). In short, bearing in mind the fact that notochordal amphicoely was the original state of the centrum in the Reptilia, existing descriptions of the centra of fossil squamates are of no assistance in determining whether the notochordal amphicoely of the Gekkonidae is the original reptilian condition retained in living forms or a similar condition which has evolved secondarily within the Squamata.

In order to determine whether notochordal amphicoely or procoely is the more primitive state of the centrum in living squamates, it is necessary to compare the amphicoelous and procoelous centra of living lepidosaurs with one another and with the original notochordal amphicoelous condition of early fossil reptiles. Hoffstetter & Gasc (1969) pointed out that if procoely were the more primitive condition in the living Squamata, all procoelous squamate vertebrae would be of a single type. They reasoned that, because the procoelous joints found in some geckos differ from those in other living squamates (Werner, 1961, 1967), procoely in squamates must therefore be a secondary phenomenon. Among reptiles generally, the procoely of squamates is clearly secondary since notochordal amphicoely was the original state of the centrum in reptiles, but it does not follow that procoely is
also secondary to notochordal amphicoely within the Gekkonidae. As the procoel of pygopods and geckos develops much later in ontogeny than the procoel of other squamates, so that gekkotan procoelous vertebrae are notochordal in adult stages, it is possible that the notochordal amphicoelous condition found in most geckos could have evolved from gekkotan notochordal procoel as a result of neoteny (see Kluge, 1967a) especially as neoteny is a common phenomenon in the Gekkonidae (N. G. Stephenson, 1960). According to Kluge, only the procoel of eublepharine geckos is primitive; the procoelous conditions found in some members of the Gekkoninae, Diplodactylinae and Sphaerodactylinae he regarded as having evolved independently from gekkonid amphicoely.

If the Eublepharinae were ancestral to all other living geckos and the amphicoely of the latter evolved from the procoel of the former by neoteny as suggested by Kluge (1967a), one would expect non-eublepharine geckos to be neotenic compared with the Eublepharinae. In fact, this is not so. At least two eublepharine genera, Coleonyx (Kluge, 1962b, fig. 1) and Psilodactylus (now Hemitheconyx -- Wermuth, 1965) (Wellborn, 1933, p. 157, fig. 4), closely resemble many non-eublepharine geckos (Wellborn, 1933, figs.; N. G. Stephenson, 1960) in the extent to which the jaw suspension and occiput are exposed dorsally, yet these geckos are neotenic in their skull structure compared with some amphicoelous Australian forms, particularly Nephrurus asper, in which the posterior region of the skull is roofed over by the broadly expanded parietal and supratemporal bones (N. G. Stephenson, 1960). Phyllurus milii is believed to be closely related to Nephrurus (Kluge, 1967a, p. 22) and is neotenic in its skull structure com-
pared with at least two species of this genus, namely *N. asper* and *N. levis* (personal observation), both of which are amphicoelous, yet *P. miliii* has procoelous vertebrae. *Carphodactylus laevis* is also procoelous but is comparable to *N. levis* in the extent to which the back of the skull is roofed over by the parietals and supratemporalis (N. G. Stephenson, 1960). Thus it would appear that neoteny has no bearing on the shape of the centrum in geckos.

If amphicoely had evolved from procoely within the Gekkonidae, one would also expect the amphicoelous centra of geckos to differ from those of *Sphenodon*, the only surviving non-squamate lepidosaur. On the contrary, the centra of amphicoelous geckos are strikingly similar to those of *Sphenodon*, not only with respect to their ossified components but in the anatomy of their soft parts as well. According to Werner (1971), the notochord of amphicoelous geckos closely resembles that of *Sphenodon* as described by Howes & Swinnerton (1901) in the differentiation and structure of its sheath, the mid-vertebral chordal plate and, in the posterior tail, the intervertebral chordal cartilage as well. The trunk intercentra of geckos and *Sphenodon* are membrane bones or secondary intercentra, unlike the primary intercentra of the neck and tail which are preformed in cartilage (Werner, 1971), while the intervertebral tissue consists of a ring of fibrous cartilage fused to the adjacent centra and enclosing the notochord which has its greatest diameter in this region. The structural resemblance between the centra of amphicoelous geckos and *Sphenodon* is even more obvious when these reptilian centra are compared with the notochordal amphicoelous centra of some living amphibians
(see Goodrich, 1930, fig. 58; Ritland, 1955). There are slight differences between the centra of Sphenodon and amphiocelous geckos such as the presence of an intervertebral chordal vesicle in the former which is absent from geckos (Werner, 1971). Also the chordal sheath of Sphenodon is of uniform thickness and is underlain by a structureless tunica chordae (Howes & Swinnerton, 1901) in contrast to the chordal sheath of geckos which is thicker intervertebrally than in the middle of the centrum and is underlain by the cellular chordal epithelium. However, these differences are comparatively minor, especially when it is recalled that the ancestors of Sphenodon and the Gekkonidae probably diverged no later than the early Mesozoic (see Romer, 1968).

The common ancestors of the Rhynchocephalia and Squamata are known largely on the basis of their skull morphology to have been members of the Eosuchia which evolved in turn from captorhinomorph cotylosaurs (Romer, 1966, 1968; Carroll, 1969b) and it is widely accepted that Sphenodon inherited its notochordal amphiocelous from these ancestral groups because the Sphenodontidae evolved from generalised eosuchians near the beginning of the Triassic, retained many eosuchian characteristics and have survived with very little change to the present day (Romer, 1956, 1966; Hoffstetter & Gasc, 1969). Since amphiocelous living geckos not only have the same type of bony centrum as Sphenodon, eosuchians such as Youngina (Romer, 1956) and captorhinomorphs such as Paleothrys (Carroll, 1969c) and Araeoscelis (Vaughn, 1955) but also share with Sphenodon the same structural features of the notochord, intervertebral cartilage and intercentra, there can be no reasonable doubt that the Gekkonidae as well as Sphenodon
have inherited their notochordal amphicoelous from their distant cotylosaurian ancestors.

Thus the notochordal amphicoelous state of the centrum found in most living geckos and *Sphenodon* is the primitive (= original) state of the centrum in the Lepidosauria because it is the ancestral state retained in living forms (see Appendix). From this ancestral state all other states of the centrum within the Lepidosauria have evolved, including the different types of procoely found in living squamates. The type of procoely found in the Gekkota is more primitive than that of other squamates because, unlike the latter, it is notochordal in adult stages and has therefore departed less from the ancestral condition. Similarly, because procoelous geckos and the pygopods, *Pygopus* and *Lialis*, have discrete intercentra throughout the vertebral column, the vertebrae of these gekkotans are more primitive than those of *Delma*, *Apasia* and *Pletholax* which lack trunk intercentra. Therefore, of all living squamates, the Gekkota have the most primitive vertebrae because the centra are notochordal and intercentra are usually present in the trunk and, within the Gekkota, the vertebrae of most geckos are the more primitive because they are also amphicoelous.

Further evidence for the primitiveness of notochordal centra in living squamates, as distinct from amphicoelous or procoelous, lies in the fact that this type of centrum is found in the Pygopodidae as well as the Gekkonidae. Unlike all geckos, however, the Pygopodidae are snake-like lizards which have undergone many structural modifications to become limbless (see Underwood, 1957a; N. G. Stephenson, 1961) such as complete loss of the fore limb
except for a tiny vestige of humerus, extensive reduction of the
hind limb and pelvic girdle and a considerable increase in the
number of presacral vertebrae. Despite the fact that the main
skeletal elements concerned with locomotion in limbless reptiles
are the vertebral column and ribs (Gasc, 1957b), the centra of
pygopods have essentially the same external shape and internal
structure as those of procoelous geckos. It is therefore evident
that the notochordal centra of the Gekkota represent a very stable
character which has persisted in pygopods despite the high selec-
tion pressures their ancestors must have endured to become snake-
like in body form and way of life.

Within the Gekkota, procoely was once considered to be of
primary importance in classification (see pp. 81-83) with the
result that all geckos known to be procoelous were placed in the
Eublepharidae, irrespective of their affinities with amphicoelous
forms which were all placed in the Gekkonidae (Noble, 1921).
Today, when all living geckos are grouped into four subfamilies
within the Family Gekkonidae on the basis of various morphological
similarities besides the shape of the centrum (Kluge, 1967a & b;
Vanzolini, 1968a & b; Appendix), amphicoely and procoely are no
longer of primary importance in the classification of geckos
inter se.

Of the 82 genera of geckos recognised by Kluge (1967a),
15 were described by him as procoelous. Of these 15 genera,
five belong to the Eublepharinae, four to the Sphaerodactylinae,
five to the Diplodactylinae and one to the Gekkoninae. With the
exception of the Eublepharinae which are all procoelous (see also
Underwood, 1954), each of these subfamilies contains at least one
genus which is amphicoelous. The majority of the Diplodactylinae and Gekkoninae are amphicoelous and, although Underwood (1954) described all five sphaerodactyline genera, including Gonatodes, as procoelous, this genus is now known to be amphicoelous as well (Kluge, 1967a; Vanzolini, 1968b; personal observation). As the closest relatives of the procoelous members of each of these three subfamilies are amphicoelous members of the same subfamily, it is clear that procoely has evolved independently in each of these groups. Furthermore, as the Eublepharinae have various characteristics which are primitive in the Gekkonidae, including eyelids which are shared by no other living geckos (see Appendix), this subfamily could not have evolved from any other group of modern procoelous geckos. Therefore procoely has arisen independently in the Eublepharinae as well.

Thus the procoelous state of the centrum has arisen at least four times within the Gekkonidae. As the disjunct, worldwide distribution of the five eublepharine genera indicates the former existence of some ancient, more generally dispersed group (Boulenger, 1885; Kluge, 1967a) and at least two of these genera, Coleonyx and Bublepharis, closely resemble one another in their pattern of colouration as well as their structure (Boulenger, 1885), it is more reasonable to conclude that the ancient, widely dispersed ancestors of the modern Eublepharinae were procoelous than to regard procoely as having arisen comparatively recently in each of the five living genera.

The Sphaerodactylinae, on the other hand, are distributed in an entirely different manner from the Eublepharinae, being a completely Neotropical group restricted to the islands and main-
land of the Caribbean region and the northern half of South America (Underwood, 1954; Kluge, 1967a; Vanzolini, 1968b). Although Vanzolini (1968b) considered that the Sphaerodactylinae are probably an old group which branched off from the general gekkonid stock at a stage no longer represented by any living species and exhibits a mild case of mosaic evolution rather than a morphogenetic sequence as suggested by Noble (1921), it is evident from the restricted distribution of this small subfamily and the continued existence of an amphicoelous genus within it that procoely has evolved more recently in the Sphaerodactylinae than in the Eublepharinae.

Procoely in the Diplodactylinae is of still more recent origin. Kluge (1967a) divided the Diplodactylinae into two tribes, the Diplodactylini containing Diplodactylus, Oedura, Rhynchoedura and Crenadactylus and the Carphodactylini, which he considered to be the more primitive tribe, containing the remaining genera including the two New Zealand forms, Hoplodactylus and Naultinus, as well as the Australian genera, Nephrurus, Phyllurus and Carphodactylus. The two species within the Carphodactylini which are known to be procoelous are Carphodactylus laevis and Phyllurus mili, both of which exhibit early stages in the evolution of procoely compared with Coleonyx and Sphaerodactylus. Neither the procoely of Carphodactylus laevis nor that of Phyllurus mili is far removed from the amphicoely of most other geckos, although that of P. mili is a little further advanced because the notochord is reduced in diameter within the ends of the centra. Although the systematic position of P. mili requires clarification (see p. 92 and Kluge, 1967a, p. 22), it is improbable
that this species will be found to be closely related to the monotypic genus, Carphodactylus, especially as Kluge (1967a) noted its similarity to Nephurus which it resembles in its external features as well as various osteological characteristics (personal observation). If Carphodactylus and Phyllurus miliii do not prove to be so closely related that they could have inherited their procoely from a common ancestor, they must have acquired their procoelous conditions independently of one another.

A somewhat different situation exists in the Diplodactylini. Kluge (1967a) described Diplodactylus, Crenadactylus and Oedura as showing a "tendency towards procoely" similar to that in Carphodactylus and Phyllurus but the species showing this tendency were not named. Although none of the specimens of Diplodactylus michaelensi, D. strophurus, D. tessellatus, D. vittatus, Crenadactylus ocellatus, Oedura lesueurii, O. marmorata or O. monilis examined personally showed any convexity of the posterior ends of their centra, it is nonetheless possible that other species of these genera may do so, in which case the closest relatives of the procoelous species would be amphicoelous species within the same genera. If several examples of intra-generic procoely are found to exist in the Diplodactylini, the number of times procoely will have arisen in this tribe will be no less than the number of otherwise amphicoelous genera in which it occurs. An evolutionary trend of this nature would suggest that the genetic potential for procoely, at least in the Diplodactylini, may be more widespread than its expression.

The Gekkoninae are the largest subfamily of living geckos (58 genera -- Kluge, 1967a) and the most widely distributed,
occurring on islands and continents throughout the tropical and temperate regions of the world, yet within this subfamily only one genus, the monotypic Malagasy genus Ebenavia, has been described as procoelous (Kluge, 1967a). As the closest relatives of Ebenavia are amphicoelous members of the currently widespread Gekkoninae, this example of procoely is evidently more recent in origin than that of the ancient Bublepharinae. However, although Kluge (1967a) described the centra of Ebenavia as exhibiting a "typical procoelous condition" unlike that in the Diplodactylinae, nothing is known of the internal morphology of its centra. As the exact affinities of Ebenavia with other gekkonines do not appear to be known either, and the fauna of Madagascar and the Mascarenes is unique and archaic in many respects (Darlington, 1957), there is no way at present of assessing more accurately the relative antiquity of Ebenavia's procoely within the Gekkonidae.

In contrast to the Gekkonidae, the Pygopodidae are a very small family of gekkotans restricted to the Australasian region and comprising only six recognised genera, five of which are known to be procoelous. The sixth genus is Ophidiocephalus which is known only from the holotype. As all pygopods are limbless and the five more common genera, except for Pygopus and Delma which appear to be closely related, are very distinct from one another (N. G. Stephenson, 1961), it would appear that the Pygopodidae have existed as a separate group for a very long time. Although it is theoretically possible for this family to have inherited its procoely from an early group of procoelous geckos, namely the ancestors of the Bublepharinae, it seems more reasonable to postulate that procoely arose independently in the Pygopodidae,
especially as it has arisen independently at least once in each of the four living subfamilies of geckos. When other characteristics are assessed for the determination of phylogenetic relationships within the Gekkota (see Appendix), it is apparent that the procoely of pygopods is of independent origin.

Despite the evolution of procoely within the Gekkota on at least five separate occasions, the procoelous centra of geckos and pygopods have essentially the same structure and the same mode of ontogenetic development. The fact that Delma, Aprasia and Pletholax have acquired during their evolutionary history an additional method of reducing the notochord apart from constriction in the ends of the centra, i.e. midvertebral ossification beginning in the chordal cartilage, has no bearing on the evolution of procoely which depends on changes in the ends of the centra. If adult centra only of geckos and pygopods are compared with one another, they are seen to form a morphogenetic sequence with respect to the growth of the condyle, leading from the notochordal amphicoelous condition found in most geckos to the procoelous condition in Lialis and Delma in which the notochord is absent from the ends of the centra at maturity. This morphogenetic sequence tends to be confused, however, by the fact that the ontogenetic development of procoely in the Gekkota continues during adult stages so that several adult animals from the same species, e.g. Pygopus lepidopodus, can vary widely in the extent of notochordal reduction in the ends of the centra. Nevertheless it is evident that, of all the procoelous conditions seen in the Gekkota, the procoely of Carphodactylus is closest to amphicoely in that the centra are only slightly convex posteriorly and the
notochord has the moniliform configuration characteristic of amphicoelous geckos. Thus the transition from amphicoely to procoely within the Gekkota has involved only a very slight morphological change (see Camp, 1923), the immediate cause of which is evidently a change in the relative growth rates of the ends of the centra. The factors which have brought about this change in the growth of the centrum and those which have accelerated the growth of the condyle in gekkotans with more advanced procoely than that of *Carphodactylus* are not yet known.

When the evolutionary sequence from amphicoely to procoely in the Gekkota is compared with the ontogenetic sequence in a single animal such as *Pygopus lepidopodus*, it is seen that these two sequences involve the same succession of morphological changes culminating, in relatively old *P. lepidopodus*, in complete resorption of the notochord from within and between the centra (Fig. 3:23 A - F). Although it remains to be seen whether a similar sequence of morphological changes also occurs in the ontogeny of non-gekkotan procoelous vertebrae or has occurred in the evolution of non-gekkotan procoely, it is evident that notochordal procoely as found in the Gekkota could not have given rise to the solid type of procoelous centrum found in other squamates without a major heterochronous change in vertebral development, resulting in complete resorption of the notochord soon after hatching. As procoely has evolved on at least five separate occasions in the Gekkota alone, it seems reasonable to suggest that it has also evolved directly from notochordal amphicoely at least once again in other squamates.
MECHANICS OF INTERCENTRAL JOINTS

In the literature describing the vertebral column of reptiles which has been accumulating for more than a century, by far the greater numbers of papers are concerned with the phylogenetic rather than the functional significance of vertebral characteristics. Among the comparatively small number of authors concerned with vertebral function were Troxell (1925) who described the mechanics of the intervertebral joints of crocodiles, Rockwell, Evans & Pheasant (1938) who reviewed vertebral structure in relation to function from fish to man, and several recent authors including Gans (1962) and Gasc (1965, 1967a, b) who were concerned with the relationships of the vertebral column, ribs and associated musculature in limbless reptiles.

According to Gasc (1967b), who described the axial skeleton and musculature in a number of limbless squamates including the gekkotan *Pygopus*, the centra of all procoelous squamates articulate by means of diarthroidal (i.e. synovial -- Mathews, 1967) ball-and-socket joints. In a later publication (Hoffstetter & Gasc, 1969) it was claimed that the notochordal amphicoelous centra of most geckos are functionally procoelous while those of *Sphenodon* were claimed to be functionally opisthocoelous. Now that procoelous gekkotans are known to resemble amphicoelous geckos and *Sphenodon*, and to differ from other squamates, in having notochordal non-synovial joints between their centra, while old specimens of *Pygopus* and the xantusiid *Xantusia vigilis* have non-synovial procoelous intercentral joints which lack a persistent notochord, it is necessary to consider how differently constructed vertebrae
articulate with one another.

In vertebrates generally, the joints between the centra can be classified from a functional point of view into two main categories, freely movable diarthroses and amphiarthroses which are joints of limited motion (see Mathews, 1967; Moss, 1971). Among living forms which are generally considered to have the diarthroidal condition are many urodele and most anuran amphibians whose intercentral joints may be procoelous or opisthocoelous ball-and-socket joints or biconcave joints with a free intervertebral disc (Goodrich, 1930; Noble, 1931; Wake, 1965, 1970), the majority of squamate reptiles with procoelous vertebrae, and the Crocodilia whose second sacral vertebrae is biconcave and first caudal vertebra is biconvex in an otherwise procoelous column (Troxell, 1925; Romer, 1956). The cervical vertebrae of chelonians and birds also articulate by means of diarthroses, those of birds being heterocoelous (Bellairs & Jenkin, 1960) while those of chelonians vary greatly in shape (Romer, 1956).

In all other living vertebrates, moving joints between consecutive centra are amphiarthroses. All mammals have fibro-cartilaginous intervertebral discs which connect the flat or acoelous surfaces of the vertebrae and which contain a remnant of the notochord in the form of the nucleus pulposus (Dawes, 1930; Rockwell, Evans & Pheasant, 1938; Badoux, 1969). In many fishes, urodeles and apodans, most gekkonid lizards and in Sphenodon the rims of the deeply biconcave centra are joined together by a ligamentous or cartilaginous ring while a large proportion of the interior of the joint and the ends of the centra is occupied by the notochord (Howes & Swinnerton, 1901; Goodrich, 1930;
Mookerjee, 1930; Noble, 1931; Romer, 1956; Lawson, 1963; Wake, 1970; Werner, 1971). In some other urodèles (Goodrich, 1930; Wake, 1970) and in two genera of frogs, *Ascaphus* (Ritland, 1955) and *Leiopelma* (Part II), the biconcave bony vertebrae are joined together by a double cone of cartilage containing a more or less constricted portion of the notochord. Amphiarthroses between procoelous vertebrae occur in some geckos, all pygopods and at least one member of the Xantusiidae, *Xantusia vigilis*, the intervertebral material in these squamates being a concavo-convex layer of fibrous cartilage which may be unperforated or perforated by a notochord of variable diameter.

The structure and mechanics of diarthroses in mammals have been investigated in considerable detail (see Walmsley, 1928; Gardner, 1950; Barnett, Davies & MacConaill, 1961; Le Gros Clark, 1965). In its simplest form a mammalian diarthrosis consists of the cartilage covered surfaces of two bones which are separated from one another by an enclosed space or bursa containing viscous synovial fluid, while the wall of the bursa has two layers, an inner synovial membrane and a tough outer fibrous sheath. In the so-called synovial joints of some lower vertebrates such as lungfish the cartilage between the bones is not completely divided by the joint cavity, while in others such as the synovial joints of *Sphenodon* and some other reptiles, the outer layer of the bursa consists of connective tissue but is not a true fibrous capsule (Barnett et al., 1961). Although little appears to be known of the detailed structure of diarthroidal intercentral joints in amphibians and reptiles, they probably operate in essentially the same way as the diarthroses of mammals in which the articular
cartilages are lubricated by the synovial fluid and their freedom of movement is limited by the shape of the articulating surfaces, the bursa of the joint and the associated ligaments and muscles (Barnett et al., 1961; Le Gros Clark, 1965). The stresses produced in this type of joint, by muscle action as distinct from the force of gravity, are mainly shearing stresses within the synovial fluid in which, because of its viscosity or internal friction, successive layers of molecules move in relation to one another. As the layer of molecules adhering to the surface of each cartilage is stationary with respect to that cartilage and the viscosity of synovial fluid is mainly due to long-chain molecules of a complex mucopolysaccharide, hyaluronic acid, which increases in viscosity with lower rates of shear, wear and tear on the cartilages is minimal and freedom of movement is maximal under almost all conditions. Diarthroses thus have a high degree of mechanical efficiency (Barnett et al., 1961) and, as intercentral joints, would greatly increase the overall potential flexibility of a vertebral column compared with amphiarthroidal intercentral joints.

When considering the mechanics of amphiarthroses dealing with stresses in a solid rather than a fluid medium. A vertebral column with amphiarthroidal intercentral joints may be regarded as a rod of alternating rigid regions which are resistant to distortion, i.e. the vertebrae, and plastic intervertebral regions which change in shape when an external force alters the spatial relationship of consecutive vertebrae. The forces or stresses produced within the intervertebral material during its deformation may be compression, tension or shear (see Ference, Lemon
& Stephenson, 1956). From a mechanical point of view, the simplest type of intercentral amphiarthrosis appears to be that found in mammals where the ends of the centra are relatively flat and bending of the vertebral column causes compression of one side of the intervertebral disc and tension in the other (Rockwell, Evans & Pleasant, 1938). From their morphological characteristics, it would appear that the deeply biconcave vertebrae of most geckos and Sphenodon articulate in essentially the same way, the principal stresses evoked in the intervertebral material being compression and tension on opposite sides of the joint (Fig. 3:24).

Hoffstetter & Gasc (1969, p. 206) claimed that the joints between the deeply biconcave centra of Sphenodon are functionally opisthocoelous because the shape of the cartilage at the posterior end of the centrum is thick at the periphery, making a strong rim which is fixed to the circular edge of the centrum, while the anterior cartilage is especially well developed in the centre of the cavity to resemble a condyle. In amphicoelous geckos, on the other hand, these authors maintained that the arrangement of the cartilages seems to be the reverse, producing a condition resembling procoely. Later in the same work (p. 300), Hoffstetter & Gasc stated that the cartilaginous intervertebral material in Sphenodon provides a weak ball-and-socket joint allowing a better distribution of the compressive stresses than in a purely amphicoelous joint, but at no point did they state their evidence for these conclusions, merely implying (p. 301) that they were based on observations of living animals.

The morphological evidence available from the literature and from the preserved, alizarin treated, dried or sectioned
Figure 3:24

Intercentral joint between notochordal amphicoelous centra as found in *Sphenodon* and most geckos. Diagrammatic.

A. Joint at rest,

B. After a change of $\theta^\circ$ in the angle of inclination between the centra about the axis YZ.

C, compression; *cn*, centrum; *ivc*, intervertebral cartilage; *nc*, notochord; *ncs*, notochordal sheath; *T*, tension.
material examined in the present investigation throws serious
doubt on the existence of functional procoely or opisthocoely
in modern amphicoelous reptiles. In an adult dried vertebral
column of *Sphenodon* which was broken in several places, the ring
of intervertebral cartilage did not divide but, together with
the intercentrum, remained partially attached to the more posterior
centrum. Nor was there any sign of division in the intervertebral
cartilage of amphicoelous geckos or juvenile *Sphenodon* prepared as
alizarin transparencies. There was no suggestion in Howes &
Swinnerton's (1901) account and illustrations of sectioned verte-
brae of *Sphenodon*, nor is there any histological evidence in
amphicoelous geckos (Pl. 12A, B), of a functional ball-and-socket
joint between the vertebrae. Indeed, considering that the radius
of the notochord in the intervertebral region of *Sphenodon* (Howes
& Swinnerton, 1901, Pl. 1 fig. 15) and in amphicoelous geckos
(Fig. 3:1) is approximately equal to the thickness of the inter-
vetebral cartilage enclosing it, approximately one quarter of
the transectional area of the intervertebral joint is occupied by
the notochord. That is to say, a large proportion of the region
between consecutive centra which is occupied by the condyle in
most procoelous gekkotans (Figs 3:1 - 3:4) and other squamates is
occupied by the notochord in these amphicoelous reptiles. In these
circumstances, it is hard to imagine how part of the intervertebral
cartilage could be especially well developed in the centre of the
cavity at one end or the other of a structurally amphicoelous centrum
to resemble the condyle of a ball-and-socket joint. When the str::
involved in the articulation of procoelous amphiarthroses are con-
sidered as well, it would appear most improbable that the structura-
ally amphicoelous intercentral joints of *Sphenodon* and most geckos
could be functionally procoelous.
The procoelous centra of some geckos, all known pygopods and at least one xantusiid, Xantusia vigilis, are joined together, by an undivided layer of intervertebral cartilage and in many cases by the notochord as well, both of which restrict freedom of movement between the centra compared with the diarthrodial intercentral joints of other squamates. As the state of the vertebrae in these lizards varies from a condition only slightly removed from notochordal amphicoely, as seen in some juvenile gekkotans and adult Carphodactylus where the condyle is only slightly convex and the intervertebral notochord is unconstricted, to the condition seen in Xantusia vigilis and old specimens of Pygopus lepidopodus, in which the notochord has been completely resorbed and the condyle is subspherical while its socket is approximately hemispherical, it is evident that amphiarthrodial ball-and-socket joints can function over a wide range of shape and structure. In Fig. 3:25 an attempt is made to compare diagrammatically these two extreme conditions as well as an intermediate state as found, for example, in adults of the gecko Phyllurus mili. Although these diagrams are greatly oversimplified, in that they take no account of the fact that the proportions of the vertebrae and the shape of the intercentral joints vary in different animals as well as in different parts of the same animal, they nevertheless permit some general conclusions to be drawn.

As movement of the vertebrae relative to one another is controlled by the muscles and ligaments associated with the vertebral column as well as by the joints between the centra and neural arches, it is reasonable to assume that a bend in the
Diagrammatic comparison of three procoelous joints occurring in the Gekkota, showing the effects on joints of varying curvature of the same change of $\varphi$ in the inclination of the vertebrae about different points on the long axis of the column at rest.

A. Condyle slightly convex, i.e. its centre of curvature, X, lies some distance in front of the posterior surface margin, p, of the centrum, eg. many juvenile gekkotans and adult Carphodactylus.

B. Condyle hemispherical, i.e. its centre of curvature, X, lies in the same plane as the posterior surface margin of the centrum, eg. adult Phyllurus milli.

C. Condyle subspherical, socket hemispherical. Centre of curvature, X, of condyle is posterior to the posterior surface margin, p, of the centrum, eg. adults of most pygopods, Colenonyx, Sphaerodactylus. Although the extreme condition as found in Xantusia and old Pygopus entirely lacks the notochord, a remnant of the sheath is shown here because some gekkotans with well developed condyles retain the notochord intervertebrally.

I. Joints at rest.

II. Rotation of posterior centrum about centre of curvature, X, of condyle, resulting in maximum shear between the condyle and socket and minimal distortion of the intervertebral cartilage, which has not been drawn in the interests of clarity.

III. Rotation of posterior centrum about Y, the mid-point between the condyle and socket, resulting in a relatively high degree of compression and tension in the intervertebral cartilage on opposite sides of the joint and minimal displacement of the notochord.

IV. Rotation of posterior centrum about Z, which lies in the transverse plane mid-way between the posterior surface margin, p, of one centrum and the anterior surface margin, a, of the following centrum. This results in minimal displacement of the surfaces of the centra but the amount of shear or of compression and tension varies with the convexity of the condyle, shear being greatest in C and compression and tension being greatest in A.

The fine stippled line in II, III, and IV shows the position of the socket at rest, as indicated in I, while a shows the resting position of the anterior surface margin of the more posterior centrum. $a_1$, $a_2$, and $a_3$ show the new position of $a$ after the vertebrae have changed their angle of inclination. c, condyle; cn, centrum; nc, notochord; ncs, notochordal sheath.
column will approach as nearly as possible a smooth curve, i.e. all the accessory structures as well as the centra and inter-central material will be displaced as little as possible from their positions at rest. State IV of the joints shown in Figure 3:25 most closely approaches this state of minimum displacement, at least with respect to the surfaces of the centra and the intervertebral cartilage, while State I shows the joints at rest. As a concavo-convex joint does not permit one vertebra to change its angle of inclination with the next one without producing at least a slight shearing force within the intervertebral material, it is not possible to show diagrammatically the alignment of consecutive centra when compression and tension are the only stresses involved. State III shows an approximation to this state, i.e. an hypothetical alignment of consecutive centra when the degree of compression and tension is relatively high and the degree of shear is relatively low. When State III is compared with State II, which shows an hypothetical alignment of the centra when the force evoked in the intervertebral material is a shearing force, it is evident that distortion of the notochord increases with the amount of shear involved, irrespective of the shape of the condyle. When the three joints in State IV are compared with one another, it is seen that compression and tension on opposite sides of the joint are maximal and shear is minimal where the condyle is only slightly convex, while, conversely, the greater the convexity of the condyle, i.e. the more closely it approaches a sphere, the greater is the shear and the smaller the amount of compression and tension in the intervertebral material between the condyle and its socket with the same change in the angle of inclination between the centra. In these circumstances, the
functional advantage of resorption of the notochord from the region between strongly procoelous centra is self-evident: a continuous longitudinal structure such as the notochord interferes with shearing stresses in the intervertebral cartilage which result in the sliding of consecutive layers of the cartilage on one another (see Ference et al., 1956). Where shear is minimal and the intervertebral cartilage is distorted mainly by compression and tension on opposite sides of the joint, a notochord of large diameter can remain within the joint without hindering its operation.

Of these three amphiarthroidal ball-and-socket joints, joint A has the least convex condyle; i.e. the condyle with the greatest radius of curvature, and therefore has the smallest distance between Y, the mid-point between the condyle and socket, and Z, which is in the transverse plane midway between the surface margins of the centra. Rotation about Y causes least displacement of the intervertebral notochord, while rotation about Z causes least surface displacement of the centra. If the radii of curvature of the condyle and socket are produced to infinity, so that the condyle and socket no longer exist, Y and Z coincide. Changes in the angle of inclination of the centra about this common axis require no compromise regarding the displacement of the notochord and the surfaces of the centra; the vertebral column bends in this relatively plastic intervertebral region in the same way as any other rod acted on by an external force, with compression and tension on opposite sides of the bend (Ference et al., 1956). As this is the type of intercentral joint found in Sphenodon and those geckos which also have
notochordal amphicoelous vertebrae (Fig. 3:24), it would appear
that Hoffstetter & Gasc (1969) were mistaken in regarding these
vertebrae as functionally opisthocoelous and procoelous respec-
tively.

The foregoing discussion of the mechanics of
constructed intercentral joints, particularly those found in the
Gekkota, is a general outline based solely on morphological data
and concerns only the joints themselves. Many other factors in-
fluence the way in which an intercentral joint functions in parti-
cular circumstances, including the number, size and disposition
of the associated muscles and ligaments, the size and shape of
the centra and intercentral joints and of the neural arches and
their joints in different parts of the body, the force of gravity
and type of locomotion. Although direct measurements using living
animals and techniques such as X-ray cinematography are necessary
to establish how joints actually function under natural conditions,
it is clear that both diarthroidal and amphiarthroidal inter-
central joints can function effectively despite considerable
differences in body form, since both types of joint occur in
limbless and tetrapod squamates. The intervertebral joints of
limbless reptiles, for example, which are dependent on the vertebral
column and ribs for locomotion, may be freely articulating diarthro-
oses as in snakes (Gasc, 1967b) or the strongly procoelous amphiar-
throses of pygopods, where the flexibility of the joint itself
appears to be severely limited by the attachment of a subspherical
condyle to a hemispherical socket. Therefore it is to be expected
that other characteristics of the vertebrae and of the periverte-
bral soft tissues compensate in some measure for the difference in
flexibility of the two types of joint.
PART IV --- THE PHYLOGENETIC SIGNIFICANCE OF VERTEBRAL CHARACTERISTICS

Any discussion of the phylogenetic significance of the characteristics of organisms requires an understanding of homology and the so-called laws of evolution whether they are referred to directly or not. Although these topics have been discussed at length by numerous authors including Btkin & Livingston (1947), Zangerl (1948), Remane (1956), de Beer (1958), Rensch (1959), Simpson (1961), Szarski (1962), Gans (1969) and Kluge (1971) so that the limitations of the laws of evolution are now generally recognised, there is still an element of vagueness associated with the concept of homology. This vagueness stems largely from a failure by some authors (e.g. Zangerl, 1948; Abercrombie, Hickman & Johnson, 1951; Kluge, 1971) to distinguish between at least two of the three basic components of the concept, namely the definition of homology, the criteria used to detect it, and its application in biological reasoning.

It is often stated or implied (e.g. by Kluge, 1971) that Darwin in his Origin of Species was responsible for the so-called evolutionary definition of homology. According to Szarski (1962) this definition states that those characters are called homologous which give evidence of the common ancestry of their bearers. In fact, Darwin (1859, p. 434) was quite clearly applying Owen's (1843) definition which states that an homologous organ or homologue is the same organ in different animals under every variety of form and function. Where Darwin differed from Owen was in ascribing the presence of the same organ in different
animals to a relationship by descent instead of by Divine Creation.

The criteria used for the recognition of homologues were listed by Etkin and Livingston (1947), Remane (1956) and Szarski (1962), the principal criteria being mutual location in different organisms, particular structure and connection by intermediate states of the organ. In some instances, the third of the principal criteria, as well as the accessory criteria listed by Szarski (1962), presuppose that the phylogenetic relationships of the organisms concerned are already known. According to Zangerl (1948), however, the identification of homologues serves only one purpose: it provides a method for the determination of phylogenetic relationships. Gans (1969) commented on the apparently circular reasoning involved in this situation and concluded that a phylogenetic criterion for homology may be applied as long as the phylogeny being used is not one that is derived from the particular characteristic studied. According to Gans (1969), an established phylogeny is tested each time a new character is found which can be subjected to analysis.

In the present investigation several characteristics of vertebrae have already been shown to be homologous but have not been described as homologous because of the confusion outlined above. Instead, these characteristics (or character-states, sensu Kluge, 1967a; Kluge & Farris, 1969) have been described in Owen's (1843) terminology as the same character-state occurring in different organisms. For example, the notochordal amphicoelous state of the centrum in Sphenodon and most geckos is homologous because of particular structure (see p. 216) while the procoelous
state of the centrum in other geckos and the Pygopodidae is also homologous on the basis of particular structure and connection by intermediates. (see p. 204). From these two examples it is seen that an homologous state occurring in a number of organisms is not necessarily primitive in the taxon to which the organisms belong: notochordal amphicoely is primitive in the Gekkota but procoely in this taxon is an advanced state which has evolved on at least five separate occasions in parallel (see p. 224). De Beer (1958) described homology of the latter type as latent homology, since parallel evolution of the same advanced state may be regarded as evidence of genetic affinity, even though the state itself was not present in the common ancestor. Latent homology is evidently of widespread occurrence in the Gekkota, since the advanced state of many characters is morphologically the same state in all members of the Gekkota which possess it (Appendix, p. 31), and is probably of widespread occurrence in other organisms as well. It is therefore clear that homology alone is not sufficient for the determination of phylogenetic relationships. It is also necessary to determine whether homologous states are primitive or advanced within the taxa concerned.

Some homologies of reptilian vertebrae are relatively easily recognised. Since the vertebrae are formed during development from the posterior half of one sclerotome and the anterior half of the following sclerotome like the vertebrae of birds and mammals (Williams, 1959a), the vertebrae of all amniotes are intersegmental in position and therefore homologous according to the criterion of mutual location. Moreover, because the evolution of amniote vertebrae can be traced back through the fossil record to the
rhachitomous labyrinthodonts of the Palaeozoic and their rhipidistian ancestors in which the body of the vertebra consisted of intercentral and pleurocentral elements (Romer, 1966, 1968), it is evident that the amniote centrum is homologous with the paired pleurocentra of rhipidistians and labyrinthodonts (Williams, 1959a; Carroll, 1969c) on the basis of connection by intermediate conditions.

Williams (1959a) also considered the intercentra of living reptiles to be homologous with the intercentra of fossil forms but Werner (1971) considered, on the basis of differences in their embryonic development, that the trunk intercentra of Sphenodon and gekkonid lizards are not serially homologous with the cervical intercentra, thereby implying that either the cervical or the trunk intercentra are not homologous with the intercentra of fossil forms. According to Howes & Swinnerton (1901) and Werner (1971), the intercentra in the trunk of Sphenodon and gekkonid lizards are membrane bones or secondary intercentra which replace the cartilaginous primary intercentra during development, whereas the cervical intercentra are the primary cartilaginous elements which have ossified. It was most strongly emphasised by Szarski (1962), however, that differences in mode of development do not constitute evidence for the absence of homology, while Le Gros Clark (1965) pointed out that perichondral or membranous ossification plays a considerable part in the development of bones which are preformed in cartilage. From Howes & Swinnerton's (1901) and Werner's (1971) accounts, it is evident that the difference between the cervical and trunk intercentra of Sphenodon and geckos is a relatively minor one involving the disappearance, probably by metaplasia into intervertebral cartilage, of the
cartilaginous intercentra of the trunk prior to the onset of membranous ossification. In the pygopod *Pygopus*, which has a complete series of intercentra in adult stage, ossification of the trunk intercentra occurs later in development than ossification of the cervical intercentra (see p. 109), while in adults of the closely related genus *Delma*, ossified intercentra are absent from all but the most anterior presacral vertebrae (p. 159). Although the presence of cartilaginous primary intercentra in pygopods could not be determined, it is possible that the ossification of intercentra whose cartilaginous components have already disappeared during development represents a stage in the loss of trunk intercentra during the evolution of lepidosaurs.

The homology of the haemal arches or chevron bones in reptiles with those of rhipidistians and labyrinthodonts is readily determined from their particular structure and their mutual location which is always in association with intercentra (= hypocentra) when these elements are present (Williams, 1959a). Opinion differs, however, regarding the serial homology of these elements in living lepidosaurs with the more anterior intercentra of the neck and trunk. According to Hoffstetter & Gasc (1969), the entire chevron is an intercentrum in reptiles generally, whereas Werner (1971) distinguished in geckos between the arch itself which is preformed in cartilage and the basal transverse bar which is a membrane bone like the intercentra of the trunk. That Werner himself was uncertain as to the serial homology of chevron bones with the trunk intercentra of geckos is shown by his preference for Williams's non-committal term, ventral arches, over Howes & Swinnerton's expression, primary intercentra. In
pygopods with a complete series of intercentra, namely Lialis and Pygopus, the most anterior haemal arch may consist of rudimentary arch pedicels suspended in connective tissue some distance from the intercentrum to which they belong. They may also take the form of a complete arch whose pedicels are fused to a basal intercentrum as in geckos or attached separately to the intervertebral cartilage on either side of the intercentrum (p. 187). The existence of haemal arch elements at some distance from the vertebral column suggests that these arches in pygopods may be formed, at least in part, from material outside the vertebral column itself, i.e. from exogenous material, like the costal components of pleurapophyses. Unlike pleurapophyses, however, which often have sutures showing the presence and the extent of the costal component, there appears to be no record of similar sutures on the chevron bones of terrestrial vertebrates, living or extinct. Indeed, so far as it can be determined, the nearest approximation to such a state is the condition seen in Pygopus and Lialis where the arch pedicels are sometimes separate from the intercentrum. In these circumstances, the most satisfactory explanation for the situation found in the Gekkota and Sphenodon is that the cartilaginous elements attached ventrally to the intervertebral cartilage, whether they are transient or permanent, and the perichondral or membrane bone associated with them, together constitute the intercentra or hypocentra. These elements are serially homologous throughout the body irrespective of differences in development and adult form.

A component of the axial skeleton of reptiles whose homology has been debated for many years is the proximal end of the rib or rib head in geckos. In many early reptiles such as the
corylosaur Kotlassia (Romer, 1956, fig. 138) each rib had two heads, a tuberculum which articulated with a diapophysis on the base of the neural arch and a capitulum which articulated with a parapophysis on the intercentrum. According to Romer (1956), the single rib head of modern squamates probably consists of the capitulum and tuberculum which have fused together. Some other authors including Noble (1921) and N. G. & E. M. Stephenson (1956) believed the dorsal ligament of geckos to be a reduced tuberculum and the head of the rib a capitulum, while McDowell (1967) considered the single rib head in all squamates to be a tuberculum.

Recent evidence has shown that in some lizards holocephaly of the trunk ribs has arisen in the manner postulated by Romer (1956), by fusion of the capitulum and tuberculum to produce a syncephalous condition. In Varanus (Hoffstetter & Gasc, 1969, and personal observation) the cervical ribs are dichcephalous (bicipital or two-headed) and articulate with two distinct facets on the vertebra. In the anterior trunk the tubercular and capitular facets of the rib join together, while the diapophyseal and parapophyseal facets on the vertebra also join to produce one long narrow facet or synapophysis which gradually shortens to become hemispherical in the posterior trunk. A similar condition is found in Sphenodon in which the first pair of ossified ribs (belonging to the fourth vertebra) has two heads, the more posterior cervical and anterior dorsal ribs are sub-bicipital and the ribs of the posterior trunk are unicipital or holocephalous. However, the origin of holocephaly in Varanus by fusion of the capitulum and tuberculum cannot be taken as evidence in itself that the holocephalous condition has arisen in this way in all squamates.
If the original radiation of squamates occurred while the ribs were still dicocephalous, holocephaly in different groups could take any one of the three forms described above.

The only evidence which has been put forward in support of the capitular nature of the rib head in geckos is that the dorsal costal ligament, which occupies a similar position to the tuberculum of primitive reptiles, is sometimes cartilaginous or bony and is therefore a reduced tuberculum. Although chondrification of the dorsal ligament was described by Noble (1921) in several gekkonid genera including *Sphaerodactylus* and *Gonatodes*, it has not been described by other authors and was not found in any of the geckos examined here (which also included *Sphaerodactylus* and *Gonatodes*), either in serial sections or in Alizarin transparencies in which cartilage is easily detected by its resilient texture and transparent, granular appearance. Ossification of the dorsal costal ligament in geckos is apparently of rare occurrence. It was not found in any of the material examined here which included specimens of *Hoplodactylus* and was presumably absent from N. G. & E. M. Stephenson's (1956) Alizarin stained specimens as these authors remarked on the presence of ossified ligaments only in sectioned material. In any case, the ossification of a ligament cannot be taken as evidence that the ligament is a vestigial bony structure because tendons and ligaments can ossify in response to extreme mechanical stress in the form of tension (Murray, 1936). Similarly, the small bony tubercle on the neural arch of some geckos at the point of attachment of the dorsal costal ligament (Fig. 3:16) is not necessarily a vestigial diaphysis. Much of the surface sculpturing of bones occurs during development at the points of attachment of tendons,
muscles and ligaments in response to repeated stresses brought about by muscle action (Murray, 1936; Murray & Drachman, 1969), either by ossification of the bases of tendinous structures (van der Klaauw, 1963) or by a thickening of the bone itself (Frazzetta, 1968). Moreover, the deposition of collagen fibres to form ligaments also occurs in response to tension, in this case on indifferently arranged connective tissue (Le Gros Clark, 1965). In the absence of tensions caused by muscle action during development, as in experimental paralysis of the embryo chick, ligaments and tendons fail to develop normally and are either atrophied or absent (Murray & Drachman, 1969). Therefore the dorsal costal ligament associated with holocephalous ribs of geckos cannot be considered homologous with the tuberculum of dicocephalous ribs, especially as small costal ligaments were found in the present investigation to occur in cervical region of Sphenodon where the ribs are two-headed or sub-bicipital.

The suggestion that the rib head is a tuberculum in squamates generally was put forward by McDowell (1967) on the grounds that the vertebro-costal joint, although dorsoventrally elongated, is not traversed by the vertebral artery but lies entirely dorsal to it, and that intercentra when present have no connection with the rib. McDowell's use of the position of the vertebral artery to establish the nature of the rib head in squamates is open to question. In some other vertebrates such as birds the vertebral arteries occur in the cervical region (Romanoff, 1960) and can therefore have no bearing on the form of the trunk ribs, yet the trunk ribs are dicocephalous (Bellairs & Jenkin, 1960; Ede, 1964). In at least one squamate with dicocephalous cervical ribs, namely
Varanus, the vertebral artery does not lie between the capitular and tubercular articulations because, although the facets on the rib heads and vertebra are quite distinct, there is no vertebrocostal canal between the two joints. As it is functionally impossible for a blood vessel to pass through a single, movable articulating joint as suggested by McDowell (1967), the absence of the vertebral artery from the vertebrocostal joint of a holoccephalous rib has no bearing on the homology of the rib head.

McDowell's (1967) statement that the intercentra of squamates have no connection with the ribs does not apply to geckos in which the more anterior ribs are joined to the cervical intercentra by the ventral costal ligament. Although this ligament occupies a similar position to the capitulum of some early reptiles in that it inserts onto the intercentrum or the centrum, the arguments given above against the tubercular nature of the dorsal costal ligament apply equally well against the capitular nature of the ventral ligament. The similarity in position between these ligaments and the two heads of dicocephalous ribs is probably because they serve similar functions in strengthening the attachment of the rib to the vertebra and limiting its dorsoventral mobility. In reptiles with dicocephalous cervical and trunk ribs such as crocodiles (Hoffstetter & Gasc, 1969) and in birds, both of these functions are effected by the two rib heads, each of which acts as a buttress for the other.

The third hypothesis, that holocephaly of the gekkonid rib has arisen as a result of fusion of the capitulum and tuberculum to produce a syncephalous condition, has no evidence to support it among living geckos as all the ribs are holoccephalous. The
position of the costal facet on the vertebra is irrelevant because, although it is normally borne by the neural arch, it often extends onto the centrum as well, particularly in the cervical region. In some other reptiles which have dicocephalous ribs, the diapophysis is borne by the neural arch but the parapophysis can vary greatly in position, even in the same animal (see Romer, 1956; Hoffstetter & Gasc, 1969).

The evidence for syncephaly of gekkonid ribs is found in fossils. According to Romer (1956) there was a strong tendency in all cotylosaurs beyond the seymouriamorph level, at which all the ribs were dicocephalous, for the parapophysis and diapophysis to come closer together in the posterior trunk while remaining distinct in the neck. According to Romer (op. cit.), this trend was continued in early lepidosaurs: although clearly two-headed ribs were present in some eousuchians such as Prolacerta (see also Camp, 1945), most early lepidosaurs had holocephalous ribs with two more or less distinct articular facets. As the trend towards syncephaly of the ribs, especially in the posterior trunk, was already well established in the Cotylosauria and Eosuchia, which contained the ancestors of the Rhynchocephalia and Squamata, and was continued in fossil rhynchocephalians and Sphenodon as well as some living lizards, it seems improbable that any other group of lizards such as the Gekkonidae could acquire the holocephalous condition in any other way. According to Hoffstetter (1964), the most anterior cervical ribs of the Upper Jurassic lizard Bavarisaurus were two-headed and the more posterior ribs holocephalous. If this lizard was in fact an early gecko as Hoffstetter (1964) and Hoffstetter & Gasc (1969) believed, rather
than a lizard with iguanid affinities as postulated by Cocude-Michel (1963), it provides direct evidence that the trend towards syncephaly was also continued by the Gekkonoidea. The presence of only holocephalous ribs in another Jurassic lizard, Ardeosaurus (Cocude-Michel, 1963), which comes from the same horizon as Bavarisaurus (Hoffstetter & Gasc, 1969) and is considered definitely to belong to the Gekkonoidea (Hoffstetter, 1964), does not reduce the possibility that living geckos have syncephalous ribs as the trend towards fusion of the capitulum and tuberculum could have progressed at different rates in the two groups.

According to Szarski's (1962) criteria for the recognition of homology, the syncephalous state of the ribs of geckos is established through connection by intermediate states in fossil reptiles between the dicocephalous and holocephalous conditions, while syncephaly of the trunk ribs in Varanus is determined from the existence of intermediate states within the same animal. As all the freely articulating ribs of geckos are holocephalous, the Gekkonidae are more advanced with respect to this character than other lizards such as Varanus in which the most anterior ribs are two-headed. If, however, the dorsal costal ligament in geckos had been a reduced tuberculum and the rib head a capitulum as postulated by Noble (1921) and N. G. & E. M. Stephenson (1956), the state of the rib head in the Gekkonidae would not only have been more primitive than that of other lizards but also more primitive than the states found in many eusuchians and cotylosaurs, because separate capitular and tubercular components would have been present throughout the presacral column. In these circumstances, the state of the rib head would have been of comparable
antiquity with the notochordal amphicoelous state of the centrum found in most geckos (see Part III, Discussion). The importance of antiquity in determining the primitiveness of character-states and the importance of a correct assessment of primitiveness in the elucidation of phylogenetic relationships are discussed in the Appendix.

Various other characteristics of gekkotan vertebrae which have been considered significant in determining the relationships of geckos and pygopods within the Squamata are discussed in Part III of the present work. The phylogenetic significance of amphicoelous and procoelous centra, non-synovial intercentral joints and the persistence of the notochord in the vertebrae of adult gekkotans is dealt with at length in the Part III Discussion, while characteristics of the external morphology of the vertebrae and ribs are discussed in the appropriate parts of the section on Regional Morphology. Among these characteristics are the fused or unfused state of the atlantal neurapophyses (p.126), the presence or absence of a synovial joint between the atlantal postzygapophyses and the axial prezygapophyses (p.132), the presence or absence of a triangular process on the pleurapophyses of the second sacral vertebra (p.167), the ability to undergo caudal autotomy (p.180), the presence of fracture planes in the majority of caudal vertebrae or in restricted regions of the tail (p.175), the structure of vertebrae capable of autotomous breakage (p.182) and the presence or absence of subcentral foramina in the vertebrae of adults (p.196). Some of these characteristics have been used in the Appendix to determine the evolutionary history of the Gekkota inter se and to examine the possibility that the Xantusii-
dae may be more closely related to geckos and pygopods than to other members of the Scincomorpha with which they are classified at present.

It remains now to consider the question of homology between the vertebrae of living amphibians and those of amniotes, a subject which has been debated for many years and still awaits solution despite Devillers' (1954) and Williams' (1959a) rejection of Gadow's (1897, 1933) nomenclature and theory concerning the evolution of tetrapod vertebrae. Although Wake (1970) discussed this problem at some length, referring in particular to work published since Williams' (1959a) paper, several points merit further discussion.

Wake (1970) agreed with Williams (1959a) that the vertebrae of living amphibians are homologous with those of amniotes because they alternate with the primary segments of the body but he questioned Williams' conclusion from this that the amphibian centrum is a pleurocentrum like that of amniotes. The intersegmental position of the vertebrae in all terrestrial vertebrates is shown by the origins of the myocommata and, in amniotes, also by the recombination of half sclerotomes from adjacent segments early in vertebral development. The absence of a sclerocoel in all three orders of living amphibians and the paucity of sclerotomic tissue in anurans and urodeles (Wake, 1970) show that amphibians differ from amniotes in the early stages of vertebral development but do not affect the homologies of the adult vertebrae (see Szarski, 1962). Before considering the possible homology of the centrum of living amphibians with the intercentrum or pleurocentra of labyrinthodonts, however, it is necessary to
consider what is described as the centrum in different groups of living tetrapods.

The components of the vertebrae of living tetrapods are identified in embryonic or juvenile animals because in most adult vertebrae they have either been resorbed or are indistinguishably fused together. The innermost component of the developing vertebral column is the notochord whose homology in different groups is evident from its position in the body and its histological characteristics. The perichordal tube is homologous for the same reasons, as it is a sheath of squamous cells enclosing the notochord (see Pls. 2-8, 10; Wake, 1970; Werner, 1971). In most amniotes, each neurapophysis of the cartilaginous vertebra is connected by a neurocentral suture to another element which in turn rests on the perichordal tube, and the ventral part of the vertebra lying between the two neurocentral sutures is described as the vertebral body or centrum. Although most authors agree by implication if not by direct statement that the perichordal tube or primary centrum (see Werner, 1971) is homologous in different groups of tetrapods (e.g. Mookerjee, 1936; Williams, 1959a; Wake, 1970; Werner, 1971), opinion differs regarding the identity in amniotes of the region of the vertebra lying between the perichordal tube and the so-called neurocentral suture, i.e. the secondary centrum. According to Howes & Swinnerton (1901) and Ganguly & Mitra (1958) this region in *Sphenodon* and geckos respectively is a lateral outgrowth from the perichordal tube, and Mookerjee (1936) and Williams (1959a) considered this to be so in all amniotes. Goette (1897), Schauinsland (1906) and Werner (1971), on the other hand, described the secondary centrum of
various amniotes including geckos and *Sphenodon* as the base of the neural arch which acquires a suture after it has been laid down as a single element resting on the perichondral tube.

The cartilaginous vertebrae in developmental stages of many living amphibians have no sutures comparable to the neuro-central sutures of reptiles and mammals and in this respect they resemble the cartilaginous vertebrae of one other group of amniotes, namely birds. The neural arches at this stage of development in birds and most amphibians rest on the perichondral tube or, in some urodeles, directly on the notochordal sheath (Part IV; Marcus & Blume, 1926; Piiper, 1928; Mookerjee, 1930, 1931, 1936, 1939; Williams, 1959a; Wake, 1970). During subsequent ossification of the vertebra, separate endochondral ossification centres occur adjacent to the notochord as well as in the neural arches of all amniotes including birds, while perichondral bone forms from a midventral centre on the vertebra which is separate from the perichondral bone of the arches (Williams, 1959a; Romanoff, 1960; Werner, 1971). Because of its manner of ossification, the vertebral body or centrum of birds as well as reptiles and mammals is considered to be a combination of primary and secondary centra.

In amphibians the patterns of perichondral and endochondral ossification are highly variable, but in general the centrum is thought to consist only of the primary centrum or perichondral tube and the bone resulting from its partial or complete perichondral and/or endochondral ossification, together with any bone which may be formed from endochondral ossification of cartilage within the notochordal canal (see Griffiths, 1963; Wake, 1970). From Wake's account it would appear that secondary centra which can
be identified as distinct bodies of cartilage or endochondral bone are absent from living amphibians.

At this point it may be recalled that the purpose of determining whether the part of the vertebra called the centrum is the same part and therefore homologous in different groups of living tetrapods is to assist in the determination of their phylogenetic relationships. One method of determining whether superficially different organs are homologous is by the existence of intermediate states of that organ either in living forms or in fossils. As the only parts of vertebrae which are preserved as fossils are the ossified components and nothing can be known regarding their membranous or cartilaginous precursors in ontogenetic development, the only practicable method of comparing the components of living and fossil vertebrae is by reference to bony elements which are separated from one another by sutures. The homology of vertebral sutures is relatively easy to establish. The neurocentral sutures of living amniotes are homologous with those of labyrinthodonts because they occupy the same position on the vertebra, lying between the dorsal elements which roof the neural canal and the ventral elements which enclose or replace the notochord. This homology is also evident from the existence of sutures in the same position in fossil tetrapods which are intermediate between Palaeozoic labyrinthodonts and living amniotes. The elements lying dorsally to the sutures are the neurapophyses while the ventral elements in each vertebral segment, irrespective of the number present in a particular animal, constitute the centrum (see also Panchen, 1963, 1967). The absence of neurocentral sutures from many living amphibians,
presumably from all stages of their development (Wake, 1970),
does not mean that the regions of the vertebra which are homo-
logous with the neurapophyses and centra of labyrinthodonts are
also absent, but it does prevent their identification.

Wake (1970) claimed that Williams' (1959a) report of a
neurocentral suture in young specimens of *Leiopelma hochstetteri*
is the only recorded instance of such a feature in living amphi-
bians. Although it is clear from the present investigation that
the cartilaginous vertebrae of *L. hochstetteri* and *L. archevi*
(Pls 1 - 7) have no neurocentral sutures comparable to those
found in amniotes such as gekkonid lizards (see Werner, 1971,
Figs 31, 35), even after the onset of perichondral ossification
of the neural arches, E. M. Stephenson's (1960) Figure 3d of a
young postmetamorphic specimen of *L. hochstetteri* shows quite
clearly that neurocentral sutures are present in later stages.
Each vertebra in this specimen, except for the atlas and the
sacral vertebra, had a midventral centre of ossification which
was widely separated from the bone of the neurapophyses. The
notable difference between the neurocentral sutures of geckos
and *Leiopelma* is that the former are present in the cartilage of
the vertebra, appearing soon after the onset of chondrification
(Werner, 1971, Fig. 23), and persist after the rest of the ver-
tebra has ossified (*op. cit.*, Figs 37, 38), whereas the neuro-
central sutures of *Leiopelma* are superficial and their appearance
coincides with the appearance of the central ossification centre
at a stage when ossification of the arches is comparatively well
advanced. As separate midventral ossification centres, in this
case paired, have also been described in *Xenopus laevis* (Bernasconi,
1951), while Mookerjee (1931, Pl. 16 fig. 14) recorded a neuro-
central suture in the cartilage as well as the perichondral bone
of a trunk vertebra of *Bufo melanosticus* about two years old, it
would appear that neurocentral sutures may not be uncommon in
anuran vertebrae although the time of their appearance varies.
Therefore the vertebrae of some anurans, like those of amniotes,
can be shown to consist of a ventral centrum and dorsal neuro-
pophyses because these elements are separated by sutures at some
stage during development.

The question whether the centrum of living amphibians is
a pleurocentrum like that of amniotes as claimed by Williams
(1959a) or an intercentrum as postulated by Estes (1965) cannot
be determined at the present time because the evolutionary history
of the modern orders is too poorly known from fossils (see also
Wake, 1970). There appears to be no doubt, however, that the
Amphibia evolved from crossopterygian fishes belonging to the
Rhipidistia and that the Reptilia, the forerunners of all other
amniotes, evolved from amphibians (Szarski, 1962; Romer, 1966,
1968; Carroll, 1969b, c). As the earliest amphibians such as
*Pholidogaster* and the *Rhipidistia* had protorhachitomous vertebrae
in which the elements lying ventrally to the neural arches were
Westoll, 1970), it is reasonable to accept that the vertebrae of
all other amphibians and those of amniotes evolved originally from
vertebrae of this type. In contrast to amniotes, whose centrum
is clearly a pleurocentrum because intermediate states are found
in fossils as well as some living reptiles, the single centrum
of living amphibians could be a pleurocentrum which lacks ossified
intercentra as in most amniotes, or an intercentrum which lacks ossified pleurocentra as in Palaeozoic stereospondylous labyrinthodonts, or a combination of both these elements.

Estes (1965) accepted the possibility that the centra of living amphibians might be an intercentrum and explained the apparent anomaly of an intersegmental intercentrum in terms of its movement during development from an original midsegmental position in embryos to an intersegmental position in adults. As no such movement has ever been recorded in descriptions of amphibian vertebral development, Estes' reasoning would lead to the conclusion that amphibian centra are pleurocentra. Another explanation for the existence of intersegmental intercentra, which does not depend on embryological evidence whose admissability is questionable (see Szarski, 1962), was offered by Panchen (1963, 1967) in an attempt to determine in labyrinthodonts the position of the myocommata and hence the intersegmental boundaries whose theoretical positions were functionally unsatisfactory if one accepted William's (1959a) contention that the labyrinthodont pleurocentrum is homologous with the amniote centrum and the intercentrum with the amniote intervertebral disc. Panchen suggested that the entire centrum of labyrinthodonts is homologous with the centrum of amniotes, the oblique division between the pleurocentra and intercentrum of rhachitomes moving posterodorsally in the temnospondyl line leading to stereospondyls whose centra are intercentra, and anteroventrally in the anthracosaurian line leading to seymouriamorphs and reptiles whose centra are predominantly if not entirely pleurocentra. In the ancestors of living amphibians, the oblique division could have moved in
either direction, or it may have been lost entirely as a result of fusion between the intercentrum and pleurocentra. If, as Bolt (1969) has suggested, all living amphibian orders evolved from labyrinthodonts belonging to the Dissorophoidea in which the main component of the centrum was a pleurocentrum, it could be that the Lissamphibian centrum is mainly if not entirely a pleurocentrum like that of amniotes after all.

It has usually been accepted that similarity in the shape of a single centrum signifies the same type of centrum in various groups of vertebrates. For example, the centra of various fishes, _Leiopelma_ and _Ascaphus_, various urodeles, apodans and fossil reptiles, _Sphenodon_ and most geckos have all been described as amphicoelous because in all of these vertebrates the centra are biconcave (Goodrich, 1930; Noble, 1931; Robinson, 1962, 1967; Romer, 1956). In the case of many fossil forms, e.g. Triassic squamates, it is impossible to determine from the literature whether the centra were solid structures or whether they enclosed a continuous notochord (see p. 210). Among the living forms listed above, the vertebrae are described as amphicoelous because the osseous centra have a deep conical depression in each end and enclose a persistent notochord, but the state of the centrum is not the same state in all these forms because the notochord may be strongly constricted between consecutive vertebrae by the intervertebral cartilage as in some urodeles, _Ascaphus_ and _Leiopelma_, or unconstricted as in many fishes, _Sphenodon_ and most geckos (see also McBride, 1931; E. M. Stephenson, 1952, 1960; Ritland, 1955). There are also different types of procoely in amphibians and reptiles. In the Anura the condyle is formed from
the intervertebral cartilage, either in situ or as a separate element which becomes fused to the centrum in front of it (Mookerjee, 1931; Griffiths, 1963; N. G. Stephenson, 1965), while the condyle in the Gekkota, if not in all reptiles, is a posterior outgrowth of the centrum itself. Different types of procoely also exist within the Reptilia: the procoelous centra of the Gekkota are notochordal and articulate by means of non-synovial intercentral joints while those of other living reptiles are non-notochordal and articulate by synovial joints.

From the foregoing discussion, it is evident that the same organ in different organisms, in this case the vertebral centrum in living tetrapods, can have more than one type of homology. Also the terms used to describe similar states of centra such as their shape may apply to the osseous centrum but take no account of differences in the morphology of their soft parts. Even when it can be shown that the state of a skeletal element is homologous in different organisms because of the particular structure of its ossified and unossified components, this state may be primitive or advanced in the taxon concerned, e.g. the notochordal amphicoelous and the notochordal procoelous states of the centrum in the Gekkota. In these circumstances, recognition that an organ or a state of that organ is homologous in different organisms is insufficient in itself for determining the phylogenetic relationships of the organisms concerned. The particular nature of the homology and its primitive or advanced nature within the taxon concerned must also be recognised, and require much detailed study for their elucidation.
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PLATE 1

Mid-trunk vertebra of an early intracapsular embryo of Leiopelma archeyi (Stage 2) in transverse section. Van Gieson.

nab, base of neural arch; nc, notochord; ncs, notochorda sheath; pct, perichordal tube; sg, spinal ganglion.
Anterior vertebrae of an intracapsular embryo of *Leiopelma archeyi* (Stage 3) in transverse section. Azan.

A. Region between bases of atlantal neurapophyses and occipital region of chondrocranium.

B. Atlas

C. Second vertebra showing relationship between neurapophysis, mesenchymatous rib and anterior lymph heart.

D. Posterior region of neural arch base of second vertebra showing its relationship to the perichordal tube and notochord.

E. Third vertebra showing relationship between neurapophysis, mesenchymatous rib and anterior lymph heart.

F. Seventh vertebra with mesenchymatous rib. Note migration of cells, indicated by the arrow, from the dorsal extremity of the myotome to the dorsal region of the neurapophysis.

*alh*, anterior lymph heart; *my*, myotome; *n*, neurapophysis or neural arch; *nab*, base of neural arch; *nal*, lamina of neural arch; *nc*, notochord; *ncs*, notochordal sheath; *pct*, perichordal tube; *r*, rib.
PLATE 3

Posterior vertebrae of an intracapsular embryo of *Leiopelma archeyi* (Stage 3) in transverse section, showing increase in size of notochord. Azan.

A. Intervertebral region between eighth and ninth vertebrae. Note mesenchymatous zygapophyseal bar.
B. Tenth vertebra with mesenchymatous rib.
C. Eleventh vertebra.
D. Twelfth vertebra.

nc, notochord; pct, perichordal tube; r, rib; sg, ganglion of 9th spinal nerve; zb, zygapophyseal bar. The arrow in C shows the migration of cells from the myotome to the neura-pophysis.
Axial skeleton of late intracapsular embryos of *Leiopelma archeyi*.

A. Atlanto-occipital joint forming in a Stage 4 embryo, L.S. Azan.

B. Procartilaginous zygapophyseal bar between fourth and fifth vertebrae in a Stage 4 embryo, L.S. Azan.

C. Tenth vertebra with mesenchymatous rib in a stage 5 embryo, T.S. Azan. Double arrow indicates the cells migrating from the myotome to the neuropophysis.

D. Eleventh vertebra with mesenchymatous rib and mid-ventral hyperplasia of perichordal tube in a Stage 5 embryo, T.S. Azan.

E. Cartilaginous zygapophyseal bar between fifth and sixth vertebrae in a Stage 5 embryo, oblique H.S. Masson.

F. Posterior trunk and anterior tail of a Stage 5 embryo, oblique H.S. Masson.

*a*, atlas; *bc*, basis cranii; *cart*, cartilaginous tract along dorsolateral surface of notochord; *il*, ilium; *na*, neural arch; *nc*, notochord; *occ*, occipital condyle; *pct*, perichordal tube; *r*, rib; *sc*, spinal cord; *sgl1*, *sgl8*, ganglia of 11th and 18th spinal nerves; *snl3*, 13th spinal nerve; *zb*, zygapophyseal bar. The single arrow in A, B and E points anteriorly.
PLATE 5

Anterior and posterior vertebrae of *Leiodelma archeyi* at hatching (Stage 6) in transverse section. Azan.

A. Cartilaginous rib of third vertebra showing its relationship with the transverse process of the neural arch and the anterior lymph heart.

B. Intervertebral region between second and third vertebrae.

C. Cartilaginous rib and transverse process of fourth vertebra.

D. Mesenchymatous rib of tenth vertebra.

E. Mesenchymatous rib of eleventh vertebra.

F. Posterior region of eleventh vertebra through anterior region of subchordal rod.

alhb, anterior lymph heart; n, neurapophysis or neural arch; nab, base of neural arch; nc, notochord; pct, perichordal tube; r, rib; trp, transverse process.
PLATE 6

Urostylar and post-urostylar regions of Leiopelma archeyi at hatching (Stage 6) in transverse section. Azan.

A. Twelfth vertebra with mesenchymatous rib and subchordal rod.

B. Thirteenth vertebra with mesenchymatous rib and subchordal rod.

C. Fourteenth vertebra showing maximum height of neural arches and diffuse nature of perichordal tube.

D. Axial skeleton posterior to vent showing diffuse perichordal tube and tracts of cartilage on dorso-lateral surfaces of notochord.

cart, cartilage; nab, base of neural arch; nal, lamina of neural arch; nc, notochord; ncs, notochordal sheath; r, rib; scr, subchordal rod.
PLATE 7

Anterior and posterior vertebrae of *Leiopelma archeyi* three weeks after hatching (Stage 9) in transverse section. Azan.

A. Developing atlanto-occipital joint.

B. Zygaphyseal joint between third and fourth vertebrae.

C. Anterior lymph heart lying between pleurapophysis of third vertebra and suprascapula.

D. Pleurapophysis of sixth vertebra showing rib fused to transverse process.

E. Tenth or sacral vertebra in plane of pleurapophyses

F. Ligamentous connection between sacral pleurapophysis and ilium.

G. Posterior end of sacral vertebra just anterior to subchordal rod.

*a*, atlas; *ahl*, anterior lymph heart; *il*, ilium; *nah*, base of neural arch; *nc*, notochord; *occ*, occipital condyle; *pb*, perichondral bone; *pct*, perichondral tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis; *r*, rib; *sc*, spinal cord; *scp*, suprascapula; *snab*, base of sacral neural arch; *splp*, sacral pleurapophysis; *trp*, transverse process.
Urostylar region of *Leiopelma archevi* three weeks after hatching (Stage 9) in transverse section. Azan.

A. Eleventh vertebra showing fusion of subchordal rod to neural arch bases and constriction of notochord.

B. Thirteenth vertebra.

C. Subchordal rod and tracts of cartilage on dorso-lateral surfaces of notochord posterior to 14th pair of spinal nerves.

D. Posterior end of subchordal rod immediately anterior to 16th pair of spinal nerves.

E. Axial skeleton of tail immediately posterior to end of subchordal rod and 16th pair of spinal nerves.

cart, cartilage; nab, base of neural arch; nc, notochord; ncs, neurocentral suture; pct, perichordal tube; sc, spinal cord; scr, subchordal rod; sgl3, ganglion of 13th spinal nerve.
Vertebræ of adult Leiopelma in horizontal section.


B. Mid-trunk vertebrae of L. hochstetteri. Masson. Only the right side of the column is shown.

C. Mid-vertebral and intervertebral regions of the notochord in the trunk of L. archeyi. Mallory.


E. Atlanto-occipital joint of L. hochstetteri, showing fibrous cartilage in the notochordal canal in the anterior end of atlas and the basis cranii. Masson.

F. Cartilaginous posterior extremity of urostyle of L. archeyi. Mallory.

a, atlas; cart, cartilage; ivc, intervertebral cartilage; ms, marrow space; nab, base of neural arch; nc, notochord; ncs, notochordal sheath; occ, occipital condyle; pb, perichondral bone; snab, base of sacral neural arch; u, urostyle; V5, V8, 5th and 8th vertebrae. The arrow accompanying each figure points anteriorly.
Vertebrae of newly hatched *Oedura lesueurii* in transverse section. Azan.

A. Fourth cervical vertebra through middle of centrum and posterior portions of vertebrocostal joints.

B. Mid-trunk vertebra through anterior half of centrum and anterior margins of rib heads.

cc, chordal cartilage; cf, costal facet on neural arch; cn, centrum; dr, dorsal root of spinal nerve; n, neuropophysis or neural arch; nc, notochord; ncs, notochordal sheath; nps, neuropaiphyseal suture; ns, neurocentral suture; pb, perichondral bone; pct, perichondral tube; prz, prezygapophysis; pz, postzygapophysis; rh, rib head; sc, spinal cord; sg, spinal ganglion; v, vein; vl, ventral costal ligament.
PLATE 11

Procoelous centra of adult gekkotans in sagittal section.
Mallory.

A. **Coleonyx variegatus.**
B. **Lialis burtonis.**
C. **Delma fraseri.**
D. **Delma fraseri.** Enlargement of an adjacent section to that in C, showing communication between the marrow space of the chordal bone and one in the surrounding centrum.

\( c, \) condyle; \( cc, \) chordal cartilage; \( eb, \) endochondral bone; \( ic, \) intercentrum; \( ivc, \) intervertebral cartilage; \( ms, \) marrow space; \( nc, \) notochord; \( ncs, \) notochordal sheath; \( pct, \) perichordal tube. The arrow accompanying each figure points anteriorly.
PLATE 12

Intercentral joints of gekkotan and non-gekkotan squamates.

A. Intervertebral cartilage between trunk centra of adult Oedura lesueurii (Fam. Gekkonidae) lateral to notochord. L.S. Azan.

B. Intervertebral cartilage ventral to notochord between trunk centra of adult O. lesueurii. S.S. Azan.

C. Non-synovial procoelous intercentral joint in trunk of adult Coleonyx variegatus (Fam. Gekkonidae). S.S. Mallory.

D. Non-synovial procoelous intercentral joint in trunk of sub-adult Lialis burtonis (Fam. Pygopodidae). S.S. Mallory.

E. Synovial procoelous intercentral joint in trunk of adult Typhlops nigrescens (Fam. Typhlopidae). T.S. Mallory.

F. Intervertebral cartilage ventral to notochord in autotomous region of tail of adult O. lesueurii. S.S. Azan.

G. Non-synovial procoelous intercentral joint between autotomous caudal vertebrae of juvenile Lacerta vivipara (Fam. Lacertidae). S.S. Azan.

C, condyle; cc, chordal cartilage; cct, calcified cartilage; hc, hyaline articular cartilage; ivc, intervertebral cartilage; ms, marrow space; nc, notochord; ncs, notochordal sheath; pct, perichondal tube; svl, subvertebral ligament. The arrows accompanying the longitudinal and sagittal sections point anteriorly.
PLATE 13

Sacral and autotomous caudal vertebrae of geckos. Azan.

A. Pleurapophysisis of first sacral vertebra of embryonic Gehyra variegata. T.S. The double arrow indicates the disappearing suture between the rib and the neural arch.

B. Plane of caudal fracture in newly hatched Oedura lesueurii, showing the undivided state of the chordal cartilage, notochordal sheath and the cartilage of the surrounding centrum. The layer of perichondral bone is discontinuous. S.S.

C. Plane of caudal fracture in adult Oedura lesueurii. S.S. The notochordal sheath, and the chordal cartilage and cartilaginous perichondral tube, both of which are calcified, have ruptured during preparation. The surrounding bone of the centrum was already divided, as demonstrated by the presence of connective tissue, indicated by double arrows, within the cleft.

cc, chordal cartilage; cn, centrum; frp, fracture plane; ms, marrow space; nc, notochord; ncs, notochordal sheath; ns, neurocentral suture; pb, perichondral bone; pct, perichordal tube; splp, sacral pleurapophysisis. The single arrows accompanying the s
PLATE 14

Vertebrae of early and late embryos of non-gekkotan lizards showing the absence of subcentral foramina from cartilaginous centra and their presence in ossified centra. Azan.

A. Cartilaginous vertebrae of *Lacerta vivipara* (Fam. Lacertidae). Oblique H.S.

B. Ossified vertebra of *L. vivipara*. T.S.

C. Cartilaginous vertebrae of *Anguis fragilis* (Fam. Anguidae). Oblique H.S.

D. Ossified vertebra of *A. fragilis*. T.S.

cc, chordal cartilage; cn, centrum; nab, base of neural arch; nc, notochord; ns, neurocentral suture; r, rib; scf, subcentral foramen; v, vein.
APPENDIX

THE CONCEPT OF PRIMITIVENESS AND ITS BEARING
ON THE PHYLOGENETIC CLASSIFICATION OF THE GEKKOTA *

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Synopsis

The different aspects of primitiveness and their bearing on the determination of phylogenetic relationships are discussed and Kluge's (1967a) Higher Taxonomic Categories of Gekkonid Lizards and their Evolution is reviewed.

The evolutionary history of the four subfamilies of geckos and the Pygopodidae is proposed as follows. Subsequent to the divergence of the Gekkonidae and Pygopodidae, the Eublepharinae diverged from the ancestral stock of the other three gekkonid subfamilies. A less likely possibility is also recognized, that the Pygopodidae and non-eublepharine geckos may have arisen from a common stem distinct from the Eublepharinae. After the ancestral non-eublepharine stock had become world-wide in distribution, a group in or near Australasia became sufficiently distinct to be classified today as the Diplodactylinae and another group in northern Africa or Neotropical America evolved into the Sphaerodactylinae. The groups of non-eublepharine geckos which remained after the appearance of the Diplodactylinae and Sphaerodactylinae and which have not become sufficiently distinct from one another to be classified in separate subfamilies are the Gekkoninae. This account of relationships within the Gekkonidae differs from that proposed by Kluge.

Consideration is also given to recent claims that the Xantusiidae should be transferred from the Scincomorpha to the Gekkota and it is concluded that there are no grounds at present for doing so.
TABLE OF CONTENTS

Introduction ................................................. 1
The concept of primitiveness .............................. 4
Criteria for the determination of primitive
    character-states ..................................... 7
Evolution of the Gekkonidae and Pygopodidae ....... 26
Affinities of the Xantusiidae ............................ 42
Acknowledgements ......................................... 50
References ................................................. 51
Introduction

A clear understanding of primitiveness is an essential prerequisite for the determination of phylogenetic relationships and hence for any classification which is intended to be consistent with these relationships, irrespective of the nature of the data employed or the methods used to process them. In the past, almost all the data used in zoological classification were morphological data concerning organs and organ systems (see Boulenger, 1885, 1887; Camp, 1923; Kluge, 1967a & b; Vanzolini, 1968a & b re lizards) and their relative importance as indicators of relationship was assessed in the light of their antiquity, their stability despite changes in body form, and the possibility that they may be the result of special adaptation or parallel or convergent evolution (see Simpson, 1961; Mayr, 1965). Although such value judgements by the taxonomist have been criticised for being subjective (see Sokal & Sneath, 1963), many of the phylogenies worked out on the basis of such reasoning have since been supported in the light of more extensive fossil records (Mayr, 1965).

In recent years, new data bearing on the relationships of animals have been accumulating from biochemical and cytological investigations (see Leone, 1964). Among the studies in these fields relating to lizards are the works of Werner (1956), Pennock, Tinkle & Shaw (1968), Gorman, Huey & Williams (1969), Cole (1970, 1971a & b) and Gorman, Wilson & Nakanishi (1971). New methods for processing the data used in zoological classification have also been developed and consist of various forms of numerical taxonomy, including quantitative phyletics,
which involve the use of electronic computers for the sorting of character complexes and the grouping of organisms into taxa (see Sokal & Sneath, 1963; Camin & Sokal, 1965; Crovello, 1967; Kluge & Farris, 1969). These new data and techniques will no doubt contribute greatly to the development of phylogenetic classifications provided that they are not expected to replace the older data and methods but are used instead in conjunction with morphological data and long-standing basic principles of evolutionary deduction.

The most comprehensive enquiry into the phylogenetic relationships of the Gekkota in recent years was Kluge's (1967a) Higher Taxonomic Categories of Gekkonid Lizards and their Evolution which involved the examination of 18 characters, 16 of which were morphological, in 82 genera of geckos. As some of the characters used by Kluge are still too poorly known in geckos generally to be used to determine their inter-relationships and some of his methods and conclusions require re-examination, it is necessary to review his paper in some detail. Before doing so, however, the meanings of the terms classification, taxonomy, phylogeny and primitive must be clearly recognised.

According to Simpson (1961), zoological classification is defined as the ordering of animals into groups (or sets) on the basis of their relationships, that is, of associations by contiguity, similarity or both and taxonomy is the theoretical study of classification, including its bases, principles, procedures and rules so that the subjects of classification are organisms and the subjects of taxonomy are classifications.
Both classification and taxonomy are also used to express the end results of these processes (Sokal & Sneath, 1963). Phylogeny, on the other hand, is defined as evolutionary history (Abercrombie, Hickman & Johnson, 1951).

The relationship between phylogeny and classification has been discussed at length by many authors including Simpson (1945, 1961), Blackwelder (1967) and Mayr (1969). Blackwelder pointed out that evolution has given rise to the organisms being classified, that the sequence of forms which gave rise to a particular species represents the phylogeny of that species, and that some of the characteristics of the organisms have resulted from phylogeny because they have been inherited from an ancestor which possessed the same characteristics. He emphasised, however, that phylogeny can never be known but can only be inferred from the degrees of similarity between organisms and for this reason cannot be regarded as a basis of classification. But classification, like the detection of phylogenetic relationships, is based on the degrees of similarity between organisms. Provided that the similarities used in classification are due to common ancestry, the classification will be consistent with the evolutionary history of the organisms concerned, if only in the sense that it expresses their inter-relationships in very general terms. As classification is essentially a tool "to provide a convenient, practical means by which zoologists may know what they are talking about and others may find out" (Simpson, 1945), it should be as stable as possible despite increasing knowledge about the organisms classified. A classification intended to be consistent with
phylogenetic relationships will be most stable if the similarities on which it is based are the result of descent from a common ancestor, and for the recognition of such similarities a clear understanding of the nature of primitiveness is essential.

The Concept of Primitiveness

The different aspects of primitiveness are frequently confused (see Sporne, 1956; Cain & Harrison, 1960; Simpson, 1961; Sokal & Sneath, 1963). In the first place, primitiveness is always relative: a characteristic or organism which is primitive in one lineage or taxon is not necessarily primitive in another. (A taxon was defined by Simpson (1961) as a group of organisms recognised as a formal unit at any level of a heirarchic classification). For example, those organs which are in a primitive state with respect to the Gekkonidae are not necessarily primitive with respect to the Squamata, and primitive geckos are not necessarily primitive squamates.

Simpson (1961) defined the usage of the terms primitive and specialised (= advanced, sensu Kluge, 1967a) with respect to the characteristics of taxa, lineages and phylogenies as follows: Within a taxon, the characteristics (= character-states, sensu Kluge, 1967a) of the common ancestry are primitive and others are more or less specialised in proportion to their departure from the ancestral condition. Within a single lineage, characteristics occurring earlier are more or less primitive and those appearing later more or less specialised in proportion to their times of appearance. Within a phylogeny (which is
divided into taxa and consists of branching lineages) characteristics of any one common stem are more primitive than different characteristics of its descendent branches; within single branches they are more primitive or more specialised in accordance with less or more departure from the stem condition.

In practice, as an extant taxon comprises the living representatives of one or more lineages, a character-state is considered to be primitive if it is either the ancestral state retained in the living forms, in which case it is the original state of the character within the taxon, or is less modified from this ancestral state (i.e. less advanced or specialised) than other states of the character within the taxon. The distinction between primitive (= original) and primitive (= less advanced) character-states is important, not only for establishing the phylogenetic relationships of the taxon inter se, but also for determining its relationship to other taxa.

The concept of primitiveness as applied to organisms is open to several interpretations (see Sokal & Sneath, 1963) and is therefore meaningless unless the terms of reference are clearly specified. One interpretation is that an organism is more primitive than other members of the same taxon because it more closely resembles their ancestral stock with respect to the states of particular characters, which is another way of saying that these characters are in a more primitive state in this organism than in other members of the taxon (vide supra). An organism is also considered to be primitive if it possesses more primitive character-states than any other single member
of the taxon and therefore bears a greater overall resemblance to the ancestral stock than the rest of the taxon. This is the usual connotation of primitiveness when organisms are described as primitive without any qualification of the term, e.g. primitive geckos, primitive squamates. Although such an organism may represent an ancient lineage within the taxon, i.e. one which arose at an early stage in the history of the taxon, it does not follow that this lineage is ancestral to other members of the taxon as it may have arisen with other character-states which are not primitive in the taxon as a whole.

The bearing of these different aspects of primitiveness on the phylogenetic relationships of geckos was not adequately taken into account by Kluge (1967a) whose method of classifying the Gekkonidae inter se was based on quantitative phyletics (or numerical cladistics), the branch of numerical taxonomy in which quantitative methods are used to infer phylogenetic relationships among living organisms whose ancestry cannot be determined from the fossil record (Camin & Sokal, 1965; Kluge & Farris, 1969). As various aspects of numerical taxonomy including phyletics (or cladistics) have been described and criticised by many authors including Cain & Harrison (1960), Sokal & Sneath (1963), Mayr (1964, 1965), Camin & Sokal (1965), Watson, Williams & Lance (1966), Blackwelder (1967), Inger (1967), El-Gazzar, Watson, Williams & Lance (1968), Kluge & Farris (1969) and Colless (1971), only Kluge's (1967a) methods and conclusions regarding the classification of geckos need to be considered here.
Criteria for the Determination of Primitive Character-states

The data considered by Kluge (1967a) to show the primitiveness of character-states were grouped by him into four categories, or criteria of primitiveness. His First Criterion for regarding a character-state as primitive in living geckos is its similarity to the state of the character in fossil forms presumed to be related to the ancestors of the modern group. His other three criteria which are those used in quantitative phyletics allow the primitiveness of a character-state to be determined in the absence of fossil evidence (see Wagner, 1961; Kluge & Farris, 1969), by comparing living geckos with other living squamates and with one another. On the basis of the Rule of Parsimony (see Camin & Sokal, 1965; Kluge & Farris, 1969) whereby it is assumed that the more widely a character-state occurs among related taxa, the less likely it is due to multiple parallel evolution (Kluge, 1967a), a character-state was considered by Kluge (op. cit.,) to be primitive in the Gekkonidae if it is universal or frequent in other squamate families or subfamilies (2nd Criterion of Primitiveness) or in the Gekkonidae themselves (3rd Criterion). According to the Fourth Criterion, those character-states which are confined to the Gekkonidae and occur in those geckos with the largest number of primitive features as determined by one or more of the first three criteria are also considered to be primitive.

The fossil forms cited by Kluge (1967a) in connection with his first criterion of primitiveness were not the ancestors
of squamates in general or of the Gekkonoidea in particular (the Gekkonoidea being all geckos, living and extinct), but were instead a single family of Upper Jurassic lizards, the Ardeosauridae, which are currently placed within the Gekkonoidea (Hoffstetter, 1964). By the late Jurassic, most of the larger suprafamilial groups of living lizards, namely the Scincomorpha, Anguimorpha and Iguania as well as the Gekkonoidea, were already strongly differentiated (Hoffstetter, 1953, 1967) and there had previously been considerable radiation of highly specialised squamates during the Triassic (Kuhn-Schnyder, 1954; Robinson, 1962; Hoffstetter, 1962; Colbert, 1966; Tarlo, 1967, 1968). In view of the evident diversity of squamates during the Triassic and Jurassic and the fortuity of fossilization, it cannot be assumed that the Ardeosauridae were the only geckos in existence during the Upper Jurassic and therefore directly ancestral to the living Gekkonidae (cf. Kluge, 1967a, p. 35, 51). Nor can it be assumed that they were necessarily more primitive than other geckos, living or extinct, in their structural characteristics including the procoelous state of their vertebrae (op. cit., p. 35, 36). On the contrary, as the genus Bavarisaurus (Fam. Bavarisauridae -- Hoffstetter, 1964) from the same horizon as the Ardeosauridae was probably also a gekkonoid (Hoffstetter & Gasc, 1969) yet differed from the Ardeosauridae in various structural features including the apparent amphicoely of their vertebrae (Hoffstetter, 1964), it is not improbable that both of these families were in some respects advanced groups of geckos despite their early appearance in the history of the Gekkonoidea.
In order to determine from the fossil record which character-states are primitive in a modern group of lizards it is necessary to refer, not only to fossil members of this group which may have had a mixture of primitive and advanced character-states like modern members, but also to earlier groups of reptiles containing the ancestors of the lacertilian group under investigation. Although the immediate squamate ancestors of the Gekkonoidea are not yet known, it is now accepted that the ancestors of the Squamata (and Rhynchocephalia) were members of the Eosuchia which in turn evolved from cotylosaurs (Romer, 1966, 1968). A character-state which occurred in any one of these ancestral groups and was directly inherited by the Gekkonidae is automatically a primitive character-state within the Gekkonidae, irrespective of whether it was a primitive or advanced condition within a particular ancestral group and irrespective of the number of living forms which still retain it. Such a character-state is not merely similar to those occurring in fossil forms (Kluge, 1967a, p. 15 -- 1st criterion of primitiveness) but is exactly the same character-state as one of those occurring in an ancestral group, and is primitive in the Gekkonidae because it is the original state of the character from which all other states within this family have evolved. Moreover, this primitive (= original) character-state in geckos can also be the primitive (= original) state of the character in other reptiles arising from the same ancestral group.

Wilson (1965) and Inger (1967) used the term unique to describe a character-state which has arisen only once in phylo-
geny and which has never been temporarily reversed in any of the lineages possessing it, and maintained that unique character-states, provided that they can be identified, serve as extremely reliable indicators of phylogenetic relationships. It is important to realise that a unique character-state is not necessarily primitive in a particular taxon: the primitive or advanced nature of a unique state depends on the stage in the evolutionary history of the taxon at which the state appeared. Provided that this unique state arose prior to the origin of the taxon, however, it is automatically primitive within this taxon.

In view of the fragmentary fossil record of early squamates, it is not possible to tell whether a character-state which apparently arose for the first time in these forms appeared only once and is therefore unique or several times in parallel. The greater the antiquity of a character-state, however, the greater is the probability that it is in fact unique. For example, a character-state which was present in the earliest reptiles, was inherited by eotherians and later by the earliest known squamates and rhynchocephalians and is also present in geckos is almost certainly unique and is therefore of considerable importance in establishing the phylogenetic relationships of the Gekkonidae, not only in them, but with other lizards as well. Camp (1923) also stressed the importance of character-states of great antiquity (or high palaeotelic value) because they reveal relationships which might otherwise be obscured by a high degree of specialization in the states of other characters.
For the recognition of unique character-states among living organisms whose ancestry cannot be determined from the fossil record, Inger (1967) put forward four criteria. The first and fourth of these, which referred respectively to the absence of obvious selective differences between the states of a character and to unusual developmental patterns, were rejected by Kluge & Farris (1969) on the grounds that they are not sufficiently objective. Inger's second and third criteria referred respectively to the occurrence of the state in many taxa of the group being studied and to the low variability of the state within these taxa. From these criteria it is clear that Inger was attempting to establish, not the uniqueness of character-states, which is absolute, but their relative primitiveness within a particular taxon (cf. the criteria used in quantitative phyletics for determining the primitiveness of character-states -- Kluge & Farris, 1969). In practice, however, the term unique can be used, not in its strict, absolute sense, but in a relative sense to describe a character-state which has arisen only once within a particular taxon. Such a unique advanced state within that taxon will be a primitive state in all smaller groups possessing it within the taxon concerned.

The determination of the primitiveness of character-states in living organisms from a comparison of these organisms with one another is based on the following assumption: if the same character-state occurs in two or more species or groups of species (genera, families, etc.) of living organisms it is assumed to have been inherited from a common ancestor unless there is evidence to show that it has arisen independently in
these taxa as a result of parallel evolution. This assumption is the basis of all systems of classification intended to be consistent with phylogenetic relationships among living organisms whose ancestors cannot be observed directly, either as living forms or fossils, and is the principle of Parsimony (see Camin & Sokal, 1965; Kluge & Farris, 1969) on which Kluge's second and third criteria of primitiveness were based. It does not deny the existence or minimise the importance of parallel evolution as suggested by Inger (1967) but is instead the only practicable method for detecting parallelisms which, according to Rensch (1959), are very common evolutionary phenomena and which may be caused by similar hereditary factors including parallel mutation and/or by parallel selection acting on homologous or analogous characters.

Kluge's (1967a) explanation of the Rule of Parsimony, that the more widely a character-state occurs in related taxa the less likely it is due to multiple parallel evolution, and therefore his second and third criteria of primitiveness, lose sight of a well-known evolutionary phenomenon; the extent to which a character-state is widespread in a living taxon depends, not only on the stage in the evolutionary history of the taxon at which the state appeared, but also on the rate of evolution and extinction in the lineage possessing this state compared with other lineages with other states (see Mayr, 1965). Thus character-states which occur in comparatively few members of a taxon may nevertheless be primitive. Conversely, an advanced character-state may be of widespread occurrence within the taxon, especially if it arose soon after the appearance of the
taxon and is therefore almost as ancient within this taxon as the primitive state from which it evolved. Although this advanced state is primitive compared with other more advanced states within the taxon, it does not follow that all states of the character which are found in fewer members of the taxon than this state have necessarily evolved from it as assumed in quantitative phyletics. Because of this assumption, a character-state can be primitive according to the second of Kluge's criteria and advanced according to the third or vice versa. Obviously at least one of these criteria must be giving an incorrect assessment of primitiveness.

The validity of Kluge's (1967a) fourth criterion of primitiveness is even more dubious. In the first place, as its terms of reference are conclusions based on one or more of the first three criteria, any errors inherent in these criteria or arising from their application will automatically invalidate conclusions based on the fourth criterion. Moreover, although it may be true that the probability of a character-state's being primitive increases very rapidly with the increase in the number of primitive character-states with which it is correlated (Sporne, 1954; Kluge, 1967a, p. 15) it is not necessarily true that the state concerned is primitive and therefore a valid indicator of phylogenetic relationships. Unless the primitiveness of a character-state as determined by this criterion can be supported by other evidence, e.g. from the fossil record, the character concerned should not be chosen as a basis for evolutionary classification.

The characters assessed by Kluge (1967a) according to
his fourth criterion of primitiveness were the ability to vocalise, the number of eggs laid and the distribution of escutcheon scales. Kluge himself admitted that the first and second of these characters are poorly documented in the literature and that his own conclusions regarding them were based on cursory observations. Too little is known at present of the detailed morphology of the laryngeal region and epidermal glands in lizards for vocal ability and escutcheon scales to be used as reliable characters in the determination of phylogenetic relationships. Kluge's contention that escutcheon scales have evolved from preanal organs in geckos contradicts the earlier opinions of Noble & Klingel (1932) and Taylor & Leonard (1956) that the reverse is true in these and other lizards, while Maderson & Chiu (1970) postulated that glandular scales and preanal organs have evolved independently from unspecialised epidermis. Maderson & Chiu (1970) also pointed out that macroscopically similar epidermal glands in geckos may represent parallel adaptive trends involving different parts of the epidermis so that great care should be exercised in using glandular structures in systematic investigations. The number of eggs laid is also of doubtful validity as an indicator of relationship. According to Tinkle, Wilbur & Tilley (1970), the two distinct reproductive strategies (i.e. early-maturing, multiple-brooded versus late-maturing, single-brooded) found in eight families of non-gekkotan lizards bear no relation to their taxonomic arrangement. Furthermore, there is a significant positive correlation between the number of eggs laid at a time (i.e. clutch size) and age at first reproduction, and between
clutch size and snout-vent length at maturity. In these circumstances, the laying of one egg by the sphæroidactyline geckos, considered by Kluge (1967a) to be a diagnostic feature of this subfamily, would appear to have little phylogenetic significance, especially as the sphæroidactyline genus _Lepidoblepharis_ contains the smallest of all known Recent lizards and the Sphaerodactylinae as a whole are small geckos (see Vanzolini, 1968b).

With respect to bony characters which exist in fossils, Kluge was not consistent in his reasons for considering some states primitive and others advanced. He considered the presence of the splenial and angular bones in the lower jaw and the supratemporal bone in the skull to be more primitive than their absence because this was the conclusion drawn by Romer (1956) regarding squamates in general. Mainly because of their occurrence in the Ardeosauridae, Kluge considered the following character-states to be primitive, the states he considered advanced being shown here in parentheses: development of the premaxilla from two (one) centres of ossification, paired (fused) nasals, and the procoelous (amphicoelous) state of the vertebral centra. He considered a single parietal to be more primitive in geckos than paired parietales because a single parietal is found in almost all adult non-gekkonid lizards and was also present in the Ardeosauridae. A single frontal was considered to be more primitive than paired frontals because the fused state is of almost universal occurrence in the living Ascalabota apart from the Xantusiidae, the paired condition in some ardeosaurids being attributed to the preadult stage of
development of these particular fossils (see Hoffstetter, 1964). The presence of the squamosal bone was considered more primitive than its absence, apparently because of its widespread occurrence within the Gekkonidae.

The same structural elements do not reappear once they have been lost in phylogeny (Szarski, 1962) although analogous organs may be acquired which serve a similar function (cf. the dorsal fins of fishes, ichthyosaurs and whales). As the angular, splenial, supratemporal and squamosal bones were present in presquamate groups of reptiles (Romer, 1956), Kluge (1967a) was correct in regarding the presence of these bones in living geckos as primitive character-states within the Gekkonidae. At this point it should be mentioned that, although a single temporal bone has usually been identified as the supratemporal (see Stephenson, 1961), it has also been called a tabular (McDowell & Bogert, 1954) or a squamosal (Underwood, 1957; Kluge, 1962). As a comparative embryological study is required to determine whether a single temporal bone is in fact a supratemporal (not a tabular according to Romer, 1956) or a squamosal in non-subtlepharine gekkotans as well as the Eublepharinae, Kluge's (1967a) contention that it is always the squamosal is provisionally accepted.

Because the roofing bones of the skull were paired in cotylosaurs, eosuchians and other early lepidosaurs and are also paired in some living lizards, the paired condition should be regarded as the primitive (=original) state of these bones in the Squamata (Romer, 1956; Robinson, 1962). However, owing to the widespread occurrence of heterochrony in the Gekkonidae...
(Stephenson, 1960), the possibility must be recognised that the paired state of these bones in some living geckos may have been secondarily derived from the fused state as a result of neoteny. The premaxillae are paired in Nephrurus, Phyllurus and Carphodactylus but they are partially fused in some other Australian diplodactylines (sensu Kluge, 1967a) such as Oedura lesueurii whose skulls are neotenic compared with the above genera (Stephenson, 1960), so that the paired state of the premaxillae in these geckos is clearly more primitive than the fused state. According to Kluge, the genera he assigned to the Diplodactylinae and Eublepharinae have paired premaxillae at hatching which may fuse later, whereas the premaxilla is single in the Gekkoninae and Sphaerodactylinae at the time of hatching.

Fusion of the nasals and parietals is apparently found only in adults, judging by Kluge's emphasis on adulthood with respect to these characters, and is found in comparatively few genera. Fused nasals were reported in some of his gekkonine genera while fused parietals occur in the five eublepharine genera and a few members of the Gekkoninae. A single frontal, on the other hand, is almost universal in geckos and, at least in Australian forms, fusion is well advanced at the time of hatching. In a juvenile specimen of Nephrurus levis figured by Stephenson (1960) the frontals were completely fused, while in newly hatched Oedura lesueurii (personal observation) the frontals are fused for the greater part of their length and unfused for only a short distance anteriorly. In some other geckos fusion apparently occurs later in development: Lygodactylus capensis has paired frontals at hatching (Brock, 1932) and a single frontal in adulthood
(Kluge, 1967a). Other geckos again such as *Pachydactylus maculosa* (Brock, 1932) and the forms cited by Kluge (1967a) retain the paired condition in adult stages.

From the variation seen in living geckos in the distribution of the paired and fused states of the different skull roofing bones and the variation in the stage of ontogeny at which fusion occurs, it is clear that heterochrony (de Beer, 1958) has contributed to the cranial evolution of geckos. Neoteny in the broad sense, which is only one of eight possible types of heterochrony is recognised by de Beer, has also been an important factor in gekkonid evolution (Stephenson & Stephenson, 1956; Stephenson, 1960, 1961). In these circumstances, the paired state of any of the skull roofing bones in living geckos may represent a persistent ancestral condition in some forms and a secondarily derived condition in others. For the sake of parsimony, however, it should be regarded as primitive, irrespective of the number of genera possessing it, unless there is evidence to show that it has arisen secondarily, especially as the most primitive hyobranchial skeleton found in living geckos is found in only two genera.

Contrary to Kluge's (1967a) opinion that procoely of the vertebral centra in eublepharine geckos is more primitive than the amphicoelous condition found in most other living geckos and his contention that the procoely of some non-eublepharine geckos has been secondarily derived from the amphicoelous condition, all the available evidence points to the primitiveness of amphicoely. As this evidence is presented
in detail elsewhere (Moffat, MS) and is intended for publication in due course, it will suffice here to summarise the main points. Notochordal amphicoelous centra were characteristic of the earliest reptiles or Cotylosauria (Vaughn, 1955; Fox & Bowman, 1966; Romer, 1966; Carroll, 1969) and also occurred in the pelycosaurian ancestors of the mammal-like reptiles and in ichthyosaurs as well as in the Eosuchia which contained the ancestors of other lepidosaurs and the Archosauria (Romer, 1956). This type of centrum is thus the original state of the centrum in reptiles and was inherited from the Eosuchia by the Rhynchocephalia, including the relatively un specialised and conservative Sphenodontidae of which Sphenodon is the only living representative (Romer, 1966; Hoffstetter & Gase, 1969). As the notochordal amphicoelous centra of geckos are strikingly similar to those of Sphenodon with respect to their soft anatomy as well as their bony components (see Howes & Swinnerton, 1901; Werner, 1971), especially when they are compared with the notochordal amphicoelous centra of some living amphibians (see Goodrich, 1930, fig. 58; Ritland, 1955), there can be little reasonable doubt that the Gekkonidae as well as Sphenodon have inherited their notochordal amphicoely from their distant cotylosaurian ancestors.

The remaining six characters used by Kluge (1967a) to classify the Gekkonidae are membranous, cartilaginous or delicate bony structures which do not usually fossilise. The states he considered primitive are the presence of true mobile eyelids (v. a brille or spectacle), the absence (v. presence) of a calcified sac in the postcranial endolymphatic apparatus,
significantly more than 14 (v. approximately 14) scleral ossicles and the presence (v. absence) of cloacal sacs and bones. In common with Camp (1923), Romer (1956) and Stephenson & Stephenson (1956), Kluge regarded a hyobranchial skeleton consisting of three complete arches as primitive in lizards and reduction of the hyoid and second branchial arches as advanced conditions. As the hyobranchial skeleton of reptiles, which serves for the attachment of throat and tongue muscles, represents part of the gill-bearing visceral skeleton of fishes (Romer, 1956), the most primitive condition of this apparatus in any group of reptiles is that which most closely resembles the piscine condition. Kluge's contention that three complete arches in the Gekkonidae are found only in Coleonyx and not also in Naultinus as described by Stephenson & Stephenson (1956) may stem from the recent confusion over the nomenclature of the New Zealand geckos (see Chrapliwy, Smith & Grant, 1961; Myers, 1961) although Kluge himself used the more generally accepted names used by Smith (1933) and Wermuth (1965). It is also possible that Naultinus varies intragenerically with respect to the state of the second visceral arch.

Bellairs & Boyd (1947) and Bellairs (1948) considered the possibility that the eyelids found in some geckos have evolved from extrabrillar fringes with loss of the brille or spectacle (Smith, 1935, 1939) and concluded that the reverse has occurred: that a brille has evolved independently in snakes and in several families of lizards including the Gekkonidae as a result of fusion of the primordia of the true eyelids. Postcloacal sacs and bones are found in some pygopods and xantusiids
as well as in geckos (McDowell & Bogert, 1954; Underwood, 1954, 1957). According to Kluge (1967a), post-cloacal sacs occur in both sexes but post-cloacal bones occur only in male geckos and personal observation has shown these bones to be present only in male pygopods as well, the only exception being *Pletholax* which had conspicuous testes but no post-cloacal bones. Thus the available evidence supports Kluge's contention that the presence of post-cloacal bones as well as eyelids are primitive character-states in the Gekkonidae.

Whether the absence of calcified postcranial endolymphatic sacs is more primitive in geckos than their presence is problematical. Calcareous material is produced by the endolymphatic apparatus of all classes of vertebrates (Whiteside, 1922) and calcified postcranial endolymphatic sacs occur in some iguanids (e.g. *Anolis*) and the Xantusiidae as well as many geckos (Camp, 1923). Moreover, there is some evidence that calcified sacs occur only in females (Kluge, 1967a, pl. 5, figs. 2,3) and that their calcification is seasonal and associated with egg-shell formation (Ruth, 1918). As Kluge himself admitted that nothing is known of the detailed structure of the endolymphatic apparatus in geckos or of the existence of uncalcified postcranial sacs in geckos which lack calcified sacs, it seems inadvisable to use this character for gekkonid classification.

Kluge's (1967a) only reason for regarding a scleral ossicle count in the low- to mid-twenties as the primitive state of this character in the Gekkonidae appears to be that this is the number of ossicles found in the more primitive *eublepharines, Aeluroscalabotes* and *Eublepharis* (op. cit., p. 24).
From his own data and discussion, however, as well as from the presence of 14 scleral ossicles in eosuchians (Underwood, 1970), it is clear that the primitive number in geckos is 14 or thereabouts. According to Gugg (1939), the number of scleral ossicles shows little variation about 14 in living lepidosaurs, i.e. squamates and Sphenodon, but he did not examine any of the indigenous Australian geckos placed by Kluge in the Diplodactylinae. There are 14 or 15 ossicles per eye in pygopods (Underwood, 1957) and in the Xantusiidae (Savage, 1963) and 13-17 (usually 14) in Kluge's Group I of the Gekkoninae and 12-15 (usually 14) in the genera he placed in the Sphaerodactylinae while some members of the eublepharine genus Coleonyx were also listed as having 14 scleral ossicles. The higher numbers of ossicles found in other eublepharine genera (15-25), Group II of the Gekkoninae (15-28) and the Diplodactylinae (21-40) show considerably more inter- and intra-generic variation and should be regarded as advanced conditions which may have arisen independently in these three groups.

In short, four of the 18 characters used by Kluge (1967a) to classify the Gekkonidae, namely vocalization, the number of eggs laid, escutcheon scales and the postcranial endolymphatic apparatus, are too poorly known at present to be used in the phylogenetic classification of geckos. The remaining 14 characters are sufficiently well documented for their primitive states within the Gekkonidae to be determined but, with respect to the frontal and parietal bones of the skull, the number of scleral ossicles and the form of the vertebral centrum, the states claimed here to be primitive among geckos were regarded by
Kluge as advanced.

Moreover, in order to determine which of several states of a character is the most primitive, it is necessary to consider all the available evidence. As the nature and quantity of this evidence vary with different characters depending on their antiquity, their presence in fossils and their distribution among living forms, no predetermined formula such as that used in quantitative phyletics can be relied upon to give a true assessment of primitiveness. On the contrary, it is necessary to analyse each character separately in the light of the evidence which specifically applies to it. Also, an assessment of primitiveness which is based on a comparison of living organisms is not necessarily less significant than another based on fossil evidence (cf. Kluge, 1967a, p. 15). For example, the primitiveness of eyelids in the Squamata is virtually indisputable since the squamate brille or spectacle consists of modified eyelids and the evolutionary sequence from eyelids to brille can still be seen in some lacertids and scincs; the movable "eyelids" of some forms with a brille are modified extrabrillar fringes (Bellairs & Boyd, 1947; Bellairs, 1948).

Finally, when ordering genera into larger taxa according to the occurrence of various character-states, their occurrence should be described by reference to these genera and not to the taxa to be erected. Kluge (1967a) deliberately described the distribution of character-states in subfamilies of geckos which he subsequently defined on the basis of this distribution for simplicity's sake, rather than repeat the numerous generic names
for each character-state under discussion (op. cit., p. 8), the only genera cited in connection with each character being those with the less common state. The presentation of data only in this form limits their re-examination by other workers, especially as there is a discrepancy between Kluge's Table 1 and his Appendix 1 in the numbers of genera placed in the Diplodactylinae and the Gekkoninae. It is also conducive to circular argument, an obvious example being as follows: character-states are primitive within the Gekkonidae because they occur in the more primitive geckos, particularly the Eublepharinae (op. cit., p. 19, 33), yet these geckos are considered to be the most primitive because they possess the greatest number of primitive character-states (op. cit., p. 21, 45). Clearly, any phylogenetic classification based on such reasoning requires re-examination.

Despite the foregoing criticisms of Kluge's methods and his conclusions regarding the primitiveness of various character-states in geckos, his four subfamilies appear on the whole to be natural assemblages in that the members of each group appear to be more closely related to one another than to the members of any other group. The Eublepharinae and Sphaerodactylinae are generally accepted as natural assemblages (Boulenger, 1885; Underwood, 1954; Vanzolini, 1968a & b) while subsequent work by Kluge (1967b) and the occurrence of the triangular process on the pleurapophyses of the second sacral vertebra (vide infra) support Kluge's (1967a) contention that the Gekkoninae and Diplodactylinae are also natural groups within the Gekkonidae. The reason why these four subfamilies appear to be natural assemblages is that Kluge (1967a, p. 41) grouped his 82 genera
of geckos on the basis of the greatest number of shared or unshared character-states and the least number of parallelisms. That is, he classified the Gekkonidae according to the degrees of similarity or dissimilarity among them on the understanding that the more closely two forms resemble one another, the more closely they are related by descent. For such a classification a correct assessment of the primitiveness within the Gekkonidae of the character-states employed is not essential.

A correct assessment of the primitive or advanced nature of character-states within the Gekkonidae is most essential, however, in order to establish that the four subfamilies are indeed natural assemblages and to determine their phylogenetic relationships with one another and with other squamates. Although it is not possible here with the data available to verify the generic composition of each subfamily, it is possible to demonstrate that Kluge's (1967a) conclusions regarding the evolutionary history of the subfamilies are unacceptable. Kluge summarised his views as follow: The Diplodactylinae appear to have been derived directly from the most primitive subfamily, the Eublepharinae, whereas the Gekkoninae probably evolved from a considerably more advanced form. According to Kluge, the gekkonid subfamily Sphaerodactylinae is the most advanced, and it appears to have been derived from the evolutionary stock that gave rise to the Gekkoninae.

In the following reassessment of the phylogenetic relationships of the four subfamilies of geckos, two other families are considered as well, namely the Pygopodidae and the Xantusiidae. The Pygopodidae are the closest living relatives
of the Gekkonidae as shown by the fact that they have many morphological features in common (McDowell & Bogert, 1954; Underwood, 1957; Stephenson, 1961), some of which are advanced character-states within the Squamata which are shared by no other living lizard. Such a state is the extreme development of the lip of the cochlear limbus of the inner ear (Shute & Bellairs, 1953). The position of the Xantusiidae, on the other hand, is much less certain although some authors such as McDowell & Bogert (1954), Hoffstetter (1962) and Savage (1963) have suggested that this family should also be included with the Gekkonidae and Pygopodidae in the Infraorder Gekkota.

Evolution of the Gekkonidae and Pygopodidae

Fourteen of the characters used by Kluge (1967a) in his classification of the Gekkonidae are also used here to determine the evolutionary history of the Gekkota (i.e. the Gekkonidae and Pygopodidae). The states of these characters which are claimed here to be primitive in the Gekkonidae are also primitive in the Gekkota because they are ancestral states retained in living forms. Only three other characters are sufficiently well known to be used to determine gekkotan inter-relationships, namely the rectus superficialis muscle, limbs and the triangular processes on the pleurapophyses of the second sacral vertebra. According to Camp (1923), pygopods have the rectus superficialis whereas geckos do not. As this muscle is present in crocodiles, Sphenodon and many squamates including all limbless forms in which it is essential for locomotion, its absence from other squamates is regarded as a secondary condition (Camp, 1923;
Underwood, 1957). Thus, within the Gekkota, the presence of this muscle in the Pygopodidae is more primitive than its absence from the Gekkonidae. Although Camp (1923) named only seven genera of geckos as lacking the *rectus superficialis*, he considered it to be absent from all geckos. In view of the extreme thinness of the ventral body wall in these lizards through which the viscera are often clearly visible (e.g. Carr, 1964, pp. 138-9), it is evident that the ventral abdominal musculature is greatly reduced. In contrast, the ventral body wall of pygopods is opaque and relatively thick (personal observation) and the *rectus superficialis*, according to Camp (1923), forms a broad ribbon on each side of the mid-line. In these circumstances Camp's contention that the *rectus superficialis* is absent from geckos generally is accepted as correct.

The presence of limbs is more primitive than their partial or complete absence because four well developed limbs were present in the ancestors of the Squamata. The triangular processes on the pleurapophyses of the second sacral vertebra as described by Holder (1960) and Cogger (1964) are found in members of the Bublepharinae, Gekkoninae and Sphaerodactylinae but not in pygopods or, as far as is known, in the Diplodactylinae. According to Holder (1960), these processes are found in the gekkonine genera *Heteronota* (=Heteronotia - see Wermuth, 1965), *Peropus* (=Gehyra - see Mitchell, 1965; Wermuth, 1965), *Phyllodactylus*, *Hemidactylus*, *Gekko*, *Lepidodactylus*, *Aristelliger* and *Afroedura* and in the sphaerodactyline genera *Sphaerodactylus* and *Gonatodes* but were absent from all the diplodactyline genera she examined. They are also present in the gekkonines *Stenodactylus*,
Tropiocolotes, Ptyodactylus and Tarentola (El-Toubi & Khalil, 1950, 1955) and in the eublepharine Coleonyx (Kluge, 1962). As sacral pleurapophyseal processes are also found in various living non-gekkotan lizards (Hoffstetter & Gasc, 1969) as well as some Triassic squamates (Peyer & Kuhn-Schnyder, 1955) and Jurassic rhynchocephalians (Hoffstetter, 1955; Cocude-Michel, 1963), their presence is considered here to be a primitive character-state within the Gekkota.

The occurrence in the Pygopodidae and the four sub-families of geckos of the primitive states of these 17 characters within the Gekkota is shown in Table II. Table I shows the occurrence of these states in the different genera of pygopods as this information is scattered in the literature. From Table II, two facts about the Gekkota are obvious, namely that few characteristics clearly distinguish one group of gekkotans from another and that parallel evolution has occurred many times. The presence of the rectus superficialis and the absence of walking legs distinguish the Pygopodidae from the Gekkonidae while the presence of eyelids, by definition, distinguishes the Eublepharinae from all other members of the Gekkota. The only other character-states which appear to be confined to particular groups of gekkotans are the presence of the sacral pleurapophyseal processes in the Eublepharinae, Gekkoninae and Sphaerodactylinae and the absence of these processes from the Diplodactylinae and Pygopodidae. Unfortunately, however, the state of this character could not be determined in all genera of geckos so that the possibility remains that some members of the Eublepharinae, Gekkoninae and Sphaerodacty-
or absence of the primitive state of a character in each genus.

and -I- symbols denote respectively the known presence and absence in these genera, as shown by the symbol -I-. The +I+ genera may be taken as granted. The fact that it has not been described in these genera is shown by the symbol 0. The 0 genera are those of limbless lizards, so that its presence in the other three superfamilies must only be pointed out.

Although Camp (1923) described the presence of the rectum cases.

were obtained from personal examination of atherizitans from D. atherizitans. and sciatric pleurothallia in all the genera, vertebral centra and sciatric pleurothallia in all the genera, the splenial and angular bones in Pterodactylus and the shape of the processes and pleurothallia the shape of the second vesticular arch and Pterodactylus, the state of the postclavicular bones in D. atherizitans, the number of sciatric ossicles in D. atherizitans (1944), Underwood (1957), and Stepheson (1967). Data not given from the works of Camp (1923), Kühnert (1926), and Dowell (1929).

The presence or absence of these characters is known in the gekkonideae, but these data are given in Table I. The taxonomic characters are those of characters whose occurrence was confirmed by the most part of research, even though not entirely confirmed by the research.
### TABLE I

**OCCURRENCE OF PRIMITIVE GEKKOTAN CHARACTER-STATES IN THE PYGOPODIDAE**

<table>
<thead>
<tr>
<th>Character-state</th>
<th>Pygopus</th>
<th>Delma</th>
<th>Lialis</th>
<th>Aprasia</th>
<th>Pletholax</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eyelids</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4 limbs</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Rectus superficialis</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>muscle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sacral pleuraphyseal</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>processes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Postcloacal bones</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Approx. 14 scleral</td>
<td>+(15)</td>
<td>+(16)</td>
<td>+(14)</td>
<td>+(14)</td>
<td>+(14)</td>
</tr>
<tr>
<td>ossicles</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paired premaxillae in</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paired nasals in adults</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-*</td>
<td>+</td>
</tr>
<tr>
<td>Paired frontals in</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paired parietals in</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Squamosal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Supratemporal</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Splenial</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Angular</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Continuous hyoid arch</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>0**</td>
<td>0**</td>
</tr>
<tr>
<td>Continuous 2nd visceral</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0**</td>
<td>-</td>
</tr>
<tr>
<td>arch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphicoely***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* Partially fused at least (Stephenson, 1961).
** Not known because specimens were damaged in this region.
*** Adult pygopod vertebrocentra are procoelous with a persistent notochord and have non-synovial joints between them like procoelous geckos (Holder, 1960; Moffat, MS).
Table II

With the exception of the states of the premaxillae in the Diplodactylinae and of the rectus superficialis muscle and sacral pleurapophyseal processes in geckos generally, the occurrence in the four subfamilies of geckos of the primitive character-states listed in Table II was determined from Kluge (1967a). Data regarding the premaxillae in the Diplodactylinae were obtained from Kluge (1967b) and the occurrence of the rectus superficialis and sacral pleurapophyseal processes in the Gekkota is discussed in the text. The occurrence of all 17 primitive states in the various genera of pygopods is given in Table I.

The total number of genera given for each subfamily of geckos was taken from Kluge’s (1967a) Table 1 showing the numbers of scleral ossicles found in the different genera, not from his Appendix I listing the material from which all osteological data were obtained and which listed 13 diplodactyline and 51 gekkonine genera. As Kluge cited individual genera and species in his text only in connection with the less common states of characters in each subfamily, it is possible that the numbers of genera listed here in Table II as having the more common conditions may not always be correct.

The headings 'P' and 'A' refer respectively to the presence or absence of the primitive state of each character while the numerals refer to the number of genera in each group which possess or lack this state. The symbol 'O' means that the presence or the absence of a primitive character-state has not been reported to occur in a group; where all the genera in a group have not been described with respect to a character-state (as indicated by *** it is possible that some of the undescribed genera may possess or lack the state concerned. With respect to the occurrence of paired premaxillae in adult eublepharines, the symbols 'P' and 'A' are used instead of numerals to show that the primitive state is present in some and absent from other genera in this group. As Kluge (1967a) was concerned with the state of the premaxillae at hatching, the distribution of the paired condition in adults could not be determined numerically.

Although the absence of the primitive state of a character implies the presence of that character, no attempt is made here to states may have arisen.
<table>
<thead>
<tr>
<th>Primitive character-state</th>
<th>Phrynopodidae</th>
<th>Eublepharinae</th>
<th>Gekkoninae</th>
<th>Diplodactylineae</th>
<th>Sphaeroactylineae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>A</td>
<td>P</td>
</tr>
<tr>
<td>Eyelids</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4 limbs</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>58</td>
</tr>
<tr>
<td>Rectus superficialis muscle</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Sacral pleurophyseal processes</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Postcloacal bones***</td>
<td>4</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td>c.14 scleral ossicles per eye</td>
<td>5</td>
<td>0</td>
<td>1*</td>
<td>4</td>
<td>56</td>
</tr>
<tr>
<td>Paired premaxillae in adults***</td>
<td>0</td>
<td>5</td>
<td>P</td>
<td>A</td>
<td>0</td>
</tr>
<tr>
<td>Paired nasals in adults</td>
<td>4</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>43</td>
</tr>
<tr>
<td>Paired frontals in adults***</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Paired peristals in adults</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>57*</td>
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<tr>
<td>Squamosal</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>55</td>
</tr>
<tr>
<td>Supratemporal</td>
<td>0</td>
<td>5</td>
<td>3*</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Splantal</td>
<td>4</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>56</td>
</tr>
<tr>
<td>Angular</td>
<td>0</td>
<td>5</td>
<td>4</td>
<td>1*</td>
<td>1</td>
</tr>
<tr>
<td>Continuous hyoid arch***</td>
<td>3</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>58</td>
</tr>
<tr>
<td>Continuous 2nd visceral arch***</td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Amphicoely</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>57</td>
</tr>
</tbody>
</table>

* Primitive character-state is present in some species and absent from other species of at least one of these genera.

** As Stephenson & Stephenson (1956) described the 2nd visceral arch of Naultinus as uninterrupted whereas Kluge (1967a) described it as interrupted, there would appear to be intrageneric variation in Naultinus with respect to this character.

# Pairstals paired at sexual maturity although fusion may occur later in some genera.

## According to Kluge (1967a), *Phyllurus*, *Carphodactylus*, *Cophodactylus*, *Diplodactylus* and *Oedura* all show a tendency toward procoely. All the representatives of these genera examined by Holder (1960), however, were described as amphicoelous with the exception of one species of *Phyllurus*, *P. milli*, which had notochordal procoelous vertebrae. Subsequent re-examination of this material has confirmed these findings except for *Carphodactylus laevis* which was found to have centra which are very slightly convex posteriorly (Moffat, MS). In these circumstances, it would appear that intrageneric variation with respect to the shape of the centrum may be widespread in the Diplodactylineae.

*** Presence or absence of primitive character-state not known for all genera of geckos and/or pygopods.

+ Fusion of premaxillae may be partial or complete, the variation in some cases being intrageneric (Kluge, 1967b).
linae may also lack sacral pleurapophyseal processes.

Whether or not the Diplodactylinae prove to be distinguishable from all other geckos by their lack of sacral pleurapophyseal processes, this subfamily appears to be distinct from the Gekkoninae because, apart from the sacral processes, the Gekkoninae have three primitive and five advanced character-states which are absent from the Diplodactylinae and the Diplodactylinae have two primitive states which are absent from the Gekkoninae. The Diplodactylinae also appear to be distinct from the Sphaerodactylinae because, apart from the sacral processes, the Sphaerodactylinae have one primitive and four advanced states which are not shared by the Diplodactylinae and the Diplodactylinae have four primitive and one advanced states which are absent from the Sphaerodactylinae. In contrast, the distribution of character-states shown in Table II does not distinguish between the Gekkoninae and Sphaerodactylinae. As all eight primitive character-states and 11 of the 12 advanced states found in the Sphaerodactylinae also occur in the Gekkoninae and the only advanced state not found in the Gekkoninae, namely the discontinuous hyoid arch, occurs in only one of the five sphaerodactyline genera, there is no justification for regarding the Sphaerodactylinae as a separate subfamily from the Gekkoninae on the basis of the data in Table II. The evidence for the validity of the Sphaerodactylinae as a separate subfamily involves characters such as the scalation of the digits, the supraciliary scales and folds, sexual dichromatism, sexual dimorphism in ventral pholidosis, the morphology of the inner ear and adult body size (see Vanzolini, 1968b) but too little
is known of the occurrence of different states of these characters in geckos generally for a clear distinction to be drawn between the Sphaeroedactylinae and Gekkoninae. Indeed, one of the genera placed by Kluge (1967a) in the Gekkoninae, namely Pristurus, may belong instead to the Sphaeroedactylinae.

According to Kluge himself (op. cit., p. 33), there are many similarities between Pristurus and the Sphaeroedactylinae which include diurnal or shade activity, sexual dichromatism, the presence of "eyelids" (i.e. superciliary folds or extra-billary fringes - see Bellairs & Boyd, 1947), simple undilated digits as in Gonatodes, small adult size and the absence of preanal organs. As Kluge considered that the splenial had not been lost in parallel by Pristurus and the Sphaeroedactylinae, he clearly regarded these two groups as closely related. A close relationship between the Neotropical Sphaeroedactylinae and Pristurus of north-east Africa and south-west Asia (see Romer, 1956, p. 542) is not surprising since some groups of endemic New World gekkonine genera are more closely related to Old World gekkonines than they are to one another (Kluge, 1967a; Vanzolini, 1968b). However, if Pristurus has more characteristics in common with the Sphaeroedactylinae than the Gekkoninae and if the available evidence suggests that these similarities have not arisen in parallel, this genus must be transferred to the Sphaeroedactylinae even though such a change would extend the geographical distribution of the Sphaeroedactylinae to include north-east Africa and south-west Asia and would also suggest that this subfamily arose in the Old World rather than in Neotropical America as is generally believed to be the case.
(see Werner, 1961; Vanzolini, 1968b). For the present purpose, however, namely the determination of evolutionary relationships between subfamilies of geckos and pygopods, Pristurus is retained in the Gekkoninae even though it is clearly recognised this genus and possibly others may be transferred from one subfamily to another and that the character-states used by Kluge (1967a) to define gekkonid subfamilies may be augmented or changed in the light of further knowledge.

The second fact about the Gekkota which is self-evident in Table II, namely that parallel evolution has been of widespread occurrence in their evolution, is clearly demonstrated by the co-existence of the primitive state and an advanced state of 11 of the 17 characters in at least two groups within the Gekkota. As the advanced state of each character (e.g. the absence or fused state of bony elements and procoely of the vertebral centrum) is morphologically the same state in all groups in which it occurs, even when it has arisen in parallel in two or more groups, it may also have arisen in parallel in two or more groups where it is not accompanied by the primitive state. It is for the purpose of detecting parallelisms of the latter type that as many characters as possible should be used in the determination of phylogenetic relationships. However, if an advanced character-state can be shown to have arisen only once within the Gekkota so that it is unique within this group, it is important as the primitive state of the character for determining gekkotan relationships inter se although it has no bearing on relationships between the Gekkota and non-gekkotan lizards. As all groups within the Gekkota possessing such a
unique advanced state must have inherited it from the same source, it follows that this state of the character is more primitive than any other state in the groups possessing it although it is an advanced state in the Gekkota as a whole. The distribution of character-states which are primitive in the Gekkota can eliminate some evolutionary sequences such as the evolution of non-eublepharine geckos from the Eublepharinae (*vide infra*) but, unless it can eliminate all but one sequence, the distribution of unique advanced states is also required to show that a particular sequence is correct. As none of the advanced states of the 17 characters used here can be shown to be unique and the distribution of primitive states as shown in Table II permits more than one sequence consistent with these data, the relationship of geckos and pygopods cannot be determined precisely.

As all the character-states listed in Table II are primitive in the Gekkota because they are ancestral states retained in living forms, it follows that all of these states must have been present in the immediate common ancestor of geckos and pygopods. Three of these primitive states, namely the continuous hyoid arch, the squamosal and paired nasals, are of no help in determining relationships within the Gekkota because they occur in all four sub-families of geckos as well as in pygopods. The distribution of the other 14 primitive states among the five groups of living Gekkota is summarised in Figures 1A & 1B which show the two most parsimonious phylogenies of the Gekkota (*sensu* Kluge & Farris, 1969) which are consistent with the available data.
the Sphenodactylinae.

Primitively character-state present in the Diphyodactylinae and gekkonoids but not in
the Diphyodactylinae.

Primitively character-state present in the Sphenodactylinae and gekkonoids but not in
geckos.

Geckos, superficially was lost independently in the Eublepharinae and non-eublepharines
in which the eyes have evolved into a slit. In this case, the rectus
fig. 1. By the non-eublepharine geckos and pygopodids, a common stock

which the eyes have evolved into a slit has evolved independently in
the Pygopodidae and non-eublepharine geckos. In

had been lost, in which case the eyes have evolved into a slit is independent in
fig. 1. All geckos are shown arising from a common stock in which the rectus
superficially

of time involved in their evolution.

Five groups (cf. Kluge, 1974a, 1974b) or to indicate either the relative or the absolute
age of these groups. No attempt is made to show the relative advancement of these
primitive character-states listed for each group are those states which are absent from
in which the five groups of living gekkonoids could have diverged from one another. The
on the data in Table II and consistent with the primitive of parsimony, aligning the order

Dramamatic representations of the two possible phylogenies of the gekkonidae

Figure 1
As the Sphaerodactylinae cannot be distinguished from the Gekkoninae using the data in Table II the former group is omitted temporarily from the following discussion. From the distribution of primitive character-states in the other four groups, it is clear that none of these groups in its present form could have been ancestral to any other because each group retains at least one primitive state which is not present in any other group. For example, as the Gekkoninae and Diplodactylinae retain primitive character-states such as paired parietals and amphicoelous vertebrae which are absent from the Bubalepharinae, neither the Gekkoninae nor the Diplodactylinae could have evolved from the Bubalepharinae (cf. Kluge, 1967a). Nor could the Gekkoninae have evolved from the Diplodactylinae as the latter lack sacral pleurapophyseal processes, the primitive number of scleral ossicles, paired frontals and the angular, all of which occur in at least some members of the Gekkoninae. The possibility of direct evolutionary sequences between any other two of these four groups can be ruled out in a similar manner, by reference to the appropriate primitive character-states.

The distribution of primitive character-states in the Bubalepharinae, Diplodactylinae, Gekkoninae and Pygopodidae does not rule out the possibility that each of these groups may have arisen independently from the same ancestral stock, especially as many advanced states in the Gekkota are known to have evolved in parallel. If these four groups did arise independently, all of their advanced character-states must have arisen in parallel, including the loss of the rectus superficialis muscle and the transformation of eyelids into a brille. The rectus superficialis
would have been lost on at least three separate occasions, once in each group of geckos, while the brille would have appeared at least three times, once each in the Gekkoninae, Diplodactylinae and Pygopodidae. To accept such a phylogeny, however, would be to ignore one of the basic tenets of evolutionary deduction, namely the principle of parsimony whereby the same character-state occurring in two or more groups of organisms is assumed to have been inherited from a common ancestor unless there is evidence to the contrary. In view of the widespread occurrence of parallel evolution in the Gekkota, the principle of parsimony is applied here only to those characters whose advanced states do not appear to have arisen in parallel within this group, namely the \textit{rectus superficialis} and the eye-covering (see Table II). Nor is there any suggestion that the loss of the primitive states of these characters and their replacement by advanced states is correlated with body form. The brille occurs in geckos and pygopods and the \textit{rectus superficialis} is retained in many tetrapod non-gekkotan lizards as well as in limbless forms. However, from the distribution of the primitive and advanced states of these two characters in the Eublepharinae, Diplodactylinae, Gekkoninae and Pygopodidae, it is clearly impossible for the advanced states of both characters to have arisen only once within the Gekkota.

If the \textit{rectus superficialis} was lost only once so that its absence is a unique state within the Gekkota, it follows that the Gekkonidae arose from a common stem distinct from the Pygopodidae and that eyelids must have been lost on at least two occasions, once in non-eublepharine geckos and again in pygopods
(Fig. 1A). On the other hand, if true eyelids were lost and the brille acquired only once within the Gekkota, it follows that non-eublepharine geckos and pygopods must have evolved from a common stem distinct from the Eublepharinae and that the *rectus superficialis* was lost independently in eublepharine and non-eublepharine geckos (Fig. 1B). In the absence of data on characters other than those used here, the only way to choose between these alternative evolutionary sequences would be to establish that either the absence of the *rectus superficialis* or the presence of the brille is a unique state within the Gekkota.

Among lizards in general, the *rectus superficialis* is present in some families and absent from others and, within the Family Agamidae, is present or absent in different genera (Camp, 1923; Underwood, 1957) so that this muscle has clearly been lost several times within the Lacertilia. As it also shows considerable variability in its development (Maurer, 1896, 1898; Camp, 1923), there would appear to be no restriction on its loss on more than one occasion within the Gekkota.

The loss of true eyelids has also occurred several times in the Lacertilia as shown by their absence from several families apart from the Gekkonidae and Pygopodidae and by the existence of a morphological series from eyelids to brille in some lacertids and scincs (Walls, 1942; Bellairs & Boyd, 1947; Bellairs, 1969). In all snakes, too, the eyelids have evolved into a brille (Walls, 1942; Bellairs & Boyd, 1947; Bellairs, 1948, 1969). Although the brilles of geckos and pygopods do not appear to resemble one another more closely than those of other lizards
in their morphological characteristics (Bellairs & Boyd, 1947; Underwood, 1957), geckos and pygopods do share another characteristic associated with the eye which does not appear to have been described in any other lizards and is absent from snakes (Cogger, 1967). This characteristic is the practice of wiping the eye with the broad, fleshy tongue which has been described or illustrated in geckos and pygopods by Smith (1952), Mitchell (1958), McPhee (1959), Worrell (1963), Bustard (1963, 1965, 1970), Carr (1964) and Cogger (1967) and it is no doubt of considerable advantage to pygopods and non-eublepharine geckos which lack eyelids and a nictitating membrane to keep the eyes free from dust, especially as vision is a major sense in the Gekkota, many of which are most active in dim light (Underwood, 1970).

It was thought at first that if this eye-licking behaviour could be shown to exist only in those gekkotans possessing a brille, it could reasonably be regarded as having evolved in association with the brille. In these circumstances it would be most improbable that both the brille and eye-licking behaviour could have evolved on more than one occasion within the Gekkota, so that the brille could be regarded as a unique as well as an advanced state within this group. This argument breaks down, however, when it is recognised that eublepharine geckos can also lick their eyes. Bustard (1963, 1965) reported the occurrence of eye-licking in Coleonyx variegatus and it has also been elicited in Eublepharis macularius in conditions simulating a dust storm (Maderson, 1971). Therefore it is clear that the ability to pass the tongue high up the side of the head and over the eyes must have existed in
the Gekkota prior to the appearance of the brille.

From the foregoing discussion, it is evident that neither the brille nor the absence of the *rectus superficialis* muscle can be described from the information available as a unique character-state within the Gekkota. Therefore, on the basis of the distribution of primitive character-states within the Gekkota, the two alternative relationships between geckos and pygopods as shown in Figures 1A & B appear equally probable. The more conservative of these alternatives, that the Bouplepharinae and non-bouplepharine geckos arose from a common stem distinct from the Pygopodidae (Fig. 1A), is accepted provisionally because it does not require any alteration to the existing classification of the Gekkota. The alternative evolutionary sequence as illustrated by Figure 1B in which the non-bouplepharine geckos are shown to be more closely related to the Pygopodidae than to the Bouplepharinae would necessitate the elevation of the Bouplepharinae to familial status and the restriction of the Family Gekkonidae to include only the Diplodactylinae, Gekkoninae and Sphaerodactylinae and such a change in classification is not justified by the present state of knowledge of gekkotan relationships. Further knowledge regarding the distribution of primitive and advanced states of other characters which are as yet poorly known in gekkotans generally, such as the visual cells and accessory structures of the eye (see Underwood, 1970), the inner ear and glandular scales (see Vanzolini, 1968b) as well as cytological, biochemical and serological characters may demonstrate conclusively which, if either, of these evolutionary sequences is correct.
It is now relevant to consider the inter-relationships of the non-eublepharine geckos, including the Sphaerodactylinae. It has already been shown that the Diplodactylinae could not have evolved from the Gekkoninae in their present form or vice versa because each of these groups retains primitive character-states which are not present in the other. For the same reason, neither the Gekkoninae nor the Diplodactylinae could have evolved from the Sphaerodactylinae, nor could the Sphaerodactylinae have evolved from the Diplodactylinae. Although the Sphaerodactylinae cannot be distinguished from the Gekkoninae using the data in Table II and would therefore appear to have evolved from the Gekkoninae as they exist today, Vanzolini (1968b) pointed out that sphaerodactyline geckos have undergone mosaic evolution with respect to other characters which show relationships within this group and regarded the Sphaerodactylinae as an old group of geckos which branched off the general gekkonid stock at a stage no longer represented by any living species. Therefore none of the existing subfamilies of non-eublepharine geckos can be considered ancestral to any other.

From the distribution of primitive character-states as summarised in Figures 1A & B, it is seen that one of three evolutionary sequences could have given rise to the Gekkoninae, Diplodactylinae and Sphaerodactylinae. The three groups may have arisen independently from the ancestral non-eublepharine stock, or the Gekkoninae and Sphaerodactylinae may have evolved from a common stock (with sacral pleurapophyseal processes and c. 14 scleral ossicles) distinct from the Diplodactylinae in which these processes were lost and the ossicle number in-
creased, or the Gekkoninae and Diplodactylinae may have evolved from a common stock (with post-cloacal bones and splenial) distinct from the Sphaerodactylinae which lost these bones. It is most improbable that the Diplodactylinae and Sphaero-
dactylinae evolved from a common stock distinct from the Gekkoninae because none of the character-states listed in Table II occurs only in these two groups and they are both comparatively small groups which are very different in other morphological characteristics (see Kluge, 1967a & b; Vanzolini, 1968b) and which are restricted and widely separated in their geographical distribution (vide infra). Although the second of these alternative evolutionary sequences appears at first to be the most probable because the Sphaerodactylinae and Gekkoninae share more primitive and advanced character-states than any other two non-eublepharine subfamilies, this sequence can be confirmed only by establishing that a unique advanced gekkotan character-state occurs only in these two groups. As no advanced gekkotan character-state is known to fulfil these requirements, it is also possible that the Diplodactylinae, Gekkoninae and Sphaerodactylinae evolved independently from the same ancestral stock.

From the distribution of character-states as shown in Table II, it is seen that the Gekkoninae have more primitive states (12) and more advanced states (14) than either the Diplodactylinae (with 10 primitive and 10 advanced states) or the Sphaerodactylinae (with 8 primitive and 12 advanced states). Therefore, of these three subfamilies, the Gekkoninae are not only the most variable but are also closest to the ancestral
non-eublepharine stock because they retain the greatest number of primitive character-states. The Gekkoninae are also by far the largest group numerically (58 genera) and the most widespread, occurring on islands and continents throughout the world between the 50° latitudes (Kluge, 1967a) while the Diplodactylinae comprise 14 genera restricted to the Australasian region and the Sphaerodactylinae currently consist of only five genera restricted to Neotropical America (Kluge, op. cit., 1967b; Vanzolini, 1968b). Although the Diplodactylinae and Sphaerodactylinae are small groups compared with the Gekkoninae, their restricted distribution suggests that they are not the living representatives of formerly larger, more widespread groups (cf. the Bublepharinae - Boulenger, 1885; Kluge, 1967a) but have instead undergone the major part of their evolution in the regions where they are found today.

The evolutionary history of the Diplodactylinae, Gekkoninae and Sphaerodactylinae which best explains the distribution of character-states in these three groups, as well as their differences in size and geographical distribution, is as follows. The ancestral stock of the existing non-eublepharine geckos radiated throughout most of the world between the 50° latitudes, replacing most of the Bublepharinae whose present discontinuous world-wide distribution indicates the former existence of a large and widespread group. In the process of radiating into many different habitats in different parts of the world, different groups of non-eublepharine geckos retained and lost different combinations of primitive character-states and acquired different combinations of advanced states.
In or near Australasia, one of these groups became sufficiently different from other non-eublepharine geckos to be classified today as a separate group, the Diplodactylinae. On the other side of the world, in northern Africa or Neotropical America, another group with a different combination of primitive and advanced states evolved into the existing Sphaerodactylinae. The groups of non-eublepharine geckos which remained after the appearance of the Diplodactylinae and Sphaerodactylinae, and which have not become sufficiently different from one another to be placed in separate taxa, were the earliest members of the Gekkoninae.

This evolutionary history of the Diplodactylinae, Gekkoninae and Sphaerodactylinae is believed to be correct because it offers a satisfactory explanation for the known data concerning these groups. It explains why the Gekkoninae are the most widespread geographically and the most numerous in terms of genera. It accounts for the fact that the Gekkoninae are at the same time the most variable among themselves and the most similar to ancestral forms with respect to the distribution of character-states. It explains the obviously widespread occurrence of parallel evolution in these three subfamilies (see Table II) and the absence of advanced character-states which are universally present in two groups and absent from the third and which might therefore be unique states among non-eublepharine geckos (cf. the absence of the rectus superficialis and the presence of the brille with respect to gecko-pygopod relationships). Moreover, if the Sphaerodactylinae and Diplo- dactylinae evolved from two different groups within a widespread
and variable ancestral stock, it is not necessary to establish the relative antiquity of these two subfamilies. Whether they arose at the same time or at different times in geological history does not affect the inter-relationships of living non-eublepharine geckos and for this reason the three subfamilies are shown in Figures 1A & B arising from the same point. The subfamily Gekkoninae, on the other hand, is only as old as the more recent of the other two subfamilies, since this group represents all the non-eublepharine geckos which remained after the divergence of the Diplodactylinae and Sphaerodactylinae.

Affinities of the Xantusiidae

It remains now to consider whether the Xantusiidae can be included with geckos and pygopods in the Infra-order Gekkota as proposed by McDowell & Bogert (1954), Hoffstetter (1962) and Savage (1963). Although no final statement regarding xantusiid relationships can be given here as it requires a detailed comparison between the Xantusiidae and all other living lizards, it is relevant to consider the circumstances which would justify transferring the Xantusiidae from the Scincomorpha to the Gekkota and to discuss the extent to which xantusiids, geckos and pygopods resemble one another.

The tetrapod Gekkonidae and the limbless Pygopodidae are placed together in the Gekkota, not only because they have many more character-states which are not apparently correlated with body form in common with one another than with any other group of lizards, including the extreme development of the cochlear limbus which is found only in these two families (Shute & Bellairs, 1953), but also because none of the character-
states shared by either of these families and non-gekkotan lizards (e.g. imbricate scales in pygopods and most non-gekkotan families) suggests relationship with a particular non-gekkotan group. Having established that the Gekkonidae and Pygopodidae resemble one another so closely that they may be considered to have arisen from a common ancestral stock which was shared by no other group of living lizards, it is then possible to determine the course of evolution within the Gekkota from the distribution of character-states which are primitive in the Gekkota and of others which may be unique and advanced within this group.

If the Xantusiidae are to be placed in the Gekkota as well, it is necessary to show that this family has more character-states in common with either the Gekkonidae or the Pygopodidae than with any other family in the Infra-order Scincomorpha, i.e. the Teiidae, Scincidae, Lacertidae or Cordylidae (=Zonuridae) with which the Xantusiidae are classified at present (Romer, 1956; Bellairs, 1969). The presence in the Xantusiidae and either the Gekkonidae or the Pygopodidae of character-states which are primitive (=original) in the Squamata as a whole is not in itself indicative of close relationship as such states have been inherited from the ancestors of all living lizards. On the other hand, the presence only in these families of one character-state which is unique as well as advanced within the Squamata would establish beyond question that these three families are more closely related to one another than to any other living lizards. In practice, however, it is often difficult to determine whether one state of a character (e.g. of the preanal pores, postcranial endolymphatic apparatus and vocalization in geckos) is more
primitive than another and it is rarely possible to establish conclusively that a character-state is unique as well as advanced in a particular group of lizards (e.g. the brille in geckos and pygopods). It is for these practical reasons that two groups are considered to be closely related to one another if they have many character-states in common, in the hope that at least one of these states is advanced in squamates generally and has not arisen in parallel in the two groups.

The data used in the following discussion of the distribution of character-states in the Xantusiidae and the Gekkota as currently defined have been compiled from the works of Camp (1923), Bellairs & Boyd (1947, 1950), Shute & Bellairs (1953), McDowell & Bogert (1954), Romer (1956), Stephenson & Stephenson (1956), Underwood (1957, 1970), Stephenson (1961), Kluge (1962, 1967a & b), Savage (1963), Hoffstetter & Gasc (1969) as well as from the present author's study of the vertebral morphology of these lizards (Holder, 1960; Moffat, MS). Three character-states have been considered erroneously to be characteristic of the Xantusiidae and geckos, namely the production of only two eggs at ovulation and the absence of the pineal (or parietal) foramen and the angular bone in the lower jaw (McDowell & Bogert, 1954). It is now known that the Xantusiidae produce from one to nine offspring at a time and possess both the pineal foramen and the angular bone (Savage, 1963) and that the angular bone is also present in some geckos (Kluge, 1962, 1967a).

Character-states which are shared by the Xantusiidae and the Gekkota and which, in some cases, have been regarded as evidence of their close relationship fall into three categories:
character-states which are primitive in the Squamata, those which are advanced in the Squamata and those whose primitive or advanced nature is uncertain. The occurrence of 33 primitive character-states in these lizards is shown in Table III in which the data concerning the Eublepharinae and non-eublepharine geckos are given separately because of the possibility that the latter group may be more closely related to the Pygopodidae than to the Eublepharinae.

With the exception of the post-cloacal bones (vide infra), all the character-states listed in Table II as primitive in the Gekkota are also primitive in the Squamata because they were inherited from the ancestors of the Squamata. Of the additional character-states listed in Table III, the majority are primitive in the Squamata because they also occurred in fossil groups containing the ancestors of the Squamata (see Romer, 1956). Non-synovial joints between adjacent vertebral centra, which occur in xantusiids and pygopods as well as in geckos as described by Holder (1960), are considered to be more primitive than the synovial intercentral joints of other lizards because the former are characteristic of the notochordal amphicoelous vertebrae of geckos and Sphenodon and were undoubtedly present in the earliest fossil reptiles as well. Direct communication between the duct of Jacobson's organ and the choanal groove in the superficial palate is considered to be more primitive than the absence of such communication because the former condition is also found in Sphenodon and the latter condition in other squamates arises from the former during ontogeny (Bellairs & Boyd, 1950). The broad, flat tongue with no more than a slight terminal notch
The presence of the primitive state of a character within a group, whether or not other members of the group have an advanced state of the same character, is shown by the symbol '+'. The symbol '-' denotes the absence of a primitive state from all members of a group while the 'A' symbol indicates that the primitive state is known to be absent from some members of a group but may be present in others.
TABLE III

OCCURRENCE OF PRIMITIVE SQUAMATE CHARACTER-STATES IN
GECKOS, PYGOPODS AND XANTHUSIIDS.

<table>
<thead>
<tr>
<th>Character-state</th>
<th>Eublepharinae</th>
<th>Non-eublepharine geckos</th>
<th>Pygopodidae</th>
<th>Xantusiidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paired premaxillae in adults</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Paired nasals in adults</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Paired frontals in adults</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Paired parietals in adults</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Paired vomers in adults</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ectopterygoid (=transpalatine)</td>
<td>+</td>
<td>A</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Lachrymal bone</td>
<td>+</td>
<td>A</td>
<td>-</td>
<td>+***</td>
</tr>
<tr>
<td>c. 14 scleral ossicles</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Jugal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Palatochoananate bony palate</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Pinnae foramen</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Supratemporal</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Squamosal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Upper temporal arch</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Postorbital arch</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Arterial foramen in stapes</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>A</td>
</tr>
<tr>
<td>Eyelids</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Duct of Jacobson’s organ in direct communication with choanal groove</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Splenial</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Angular</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Tongue broad, undivided</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Uninterrupted hyoid arch</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Uninterrupted 2nd visceral arch</td>
<td>+</td>
<td>+</td>
<td>A</td>
<td>-</td>
</tr>
<tr>
<td>Sacral pleuraphysyal processes</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>A</td>
</tr>
<tr>
<td>Autotomy</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>*Amphicoely</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>*Notochordal centra in adults</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>A</td>
</tr>
<tr>
<td>*Non-synovial joints between</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>. adjacent centra</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>*Complete series of intercentra</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Centra squarish in ventral outline</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Zygaphysyal joint between atlas 6 &amp; axis</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Rectus superficialis muscle</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>4 limbs</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

Total number of primitive character-states in each group 25 25 19 23

*Character-state not found in other lizards
**Partly fused to prefrontal (Savage, 1963)
found in xantusiids, geckos and pygopods is also considered to be primitive compared with the deeply forked tongues of some other lizards (Bellairs, 1969), especially as the tongue of *Sphenodon* is also broad, flat and undivided (personal observation).

Of the 33 primitive squamate character-states listed in Table III, 28 occur in geckos (25 in the Eublepharinae and 25 in non-eublepharine geckos), 19 in pygopods and 23 in the Xantusiidae. Although the Xantusiidae more closely resemble ancestral lizards than do pygopods because they retain a greater number of these primitive character-states, this does not mean that they are more closely related than pygopods to geckos which, of these three groups of lizards, are most similar to the ancestral stock. Of the 19 primitive states in the Pygopodidae, only the *rectus superficialis* is not also found in geckos. Of the 23 primitive states in the Xantusiidae, five are absent from geckos and, of the 28 primitive states present in geckos, ten are absent from the Xantusiidae. Although the distribution of primitive character-states suggests that geckos and pygopods diverged from one another at a later stage in evolutionary history than the Xantusiidae diverged from their common ancestor, it is necessary to consider other character-states which are not primitive in squamates in order to determine their inter-relationships. The fact that the Xantusiidae and the Gekkota resemble one another in their vertebral structure is not indicative of close relationship (cf. Hoffstetter, 1962; McDowell & Bogert, 1954) because, although these lizards are the only living forms known to possess non-synovial intercentral joints and a complete
series of intercentra, these primitive states could have been retained independently in two groups more closely related to other lizards than to one another.

A number of character-states which are known to be advanced in the Squamata also occur in xantusiids, geckos and pygopods such as a brille, a single premaxilla, absence of the splenial bone, a discontinuous second visceral arch and proocoelous vertebrae. Although each of these advanced states appears to be present in all members of the Xantusiidae (Savage, 1963), none of them is a unique state which arose once in the common ancestor of the Xantusiidae and the Gekkota because, in each case, the corresponding primitive state exists in the Gekkota. Nor is it possible for the Xantusiidae to have inherited these advanced states from the Gekkota because the Xantusiidae retain primitive character-states which are absent from all living gekkotans (see Table III). As a similar argument applies to advanced character-states which are universally present in the Gekkota but co-exist with the primitive state in the Xantusiidae (e.g. the absence of the pineal foramen), it is evident that advanced character-states which occur in the Xantusiidae and the Gekkota and whose corresponding primitive states exist in either of these groups must have evolved in parallel.

Character-states whose primitive or advanced nature in the Squamata has not yet been demonstrated and which are known to occur only in the Xantusiidae and the Gekkota include the distinctive morphology of the base of the braincase and the presence of post-cloacal bones (McDowell & Bogert, 1954; Underwood, 1957). Underwood (1957), however, considered the absence of post-cloacal sacs (with which the post-cloacal bones
are intimately associated) to be a secondary condition in lizards generally, i.e. that the presence of these structures is primitive in the Squamata, because the development of a special organ and its later disappearance are bound to influence associated organ systems such as nerves, muscles and blood-vessels.

From the foregoing discussion of character-states which are shared by the Xantusiidae and the Gekkota, it is evident that no conclusions can be drawn regarding xantusiid affinities from these character-states alone. Other character-states, however, which occur in only one of these two groups and which, in some cases, can be shown to be advanced states in the Squamata as a whole do give some evidence regarding the relationships of the Xantusiidae. For example, the extreme development of the lip of the cochlear limbus of the inner ear, which is considered to be an advanced condition in squamates, is found only in geckos and pygopods, there being no limbic lip in the family Xantusiidae, which is generally regarded as having affinities with the Gekkonidae (Shute & Bellairs, 1953). According to Miller (1966), the cochlear duct anatomy of xantusiids shows this group to be closely related to the Scincidae but with enough differences to merit their separate familial status. Baird (1970) described the internal ear of Xantusia as basically like that of scincs and maintained that the scincid and gekkonid conditions have both departed significantly from the typical lacertilian condition as found, for example, in the Teiidae. The superficial palate of the Xantusiidae, in which the ectochoanal cartilages are so greatly enlarged that they overlap in the mid-line, is advanced compared with the superficial palates of most lizards.
including geckos, pygopods, lacertids, teiids and scincs in which each ectochoanal cartilage passes backwards and ventrally between the vomer and the palatal process of the maxilla and supports the choanal fold (Bellairs & Boyd, 1950). The Xantusiidae are also advanced compared with some other lizards with an upper temporal arch in that the upper temporal fenestra is closed by the juxtaposition of the postorbitalfrontal and squamosal bones with the parietal, and in this respect resemble the Cordylidae (Romer, 1956; Savage, 1963). According to Etheridge (1967), the caudal vertebrae of the Xantusiidae are structurally intermediate between those of scincs and lacertids.

In short, as the presence in the Xantusiidae and the Gekkota of primitive squamate character-states is not in itself indicative of relationship and as all the known advanced states shared by these two groups have arisen in parallel, there are no grounds at present for transferring the Xantusiidae to the Gekkota as proposed by McDowell & Bogert (1954), Hoffstetter (1962) and Savage (1963). On the contrary, the resemblance between the Xantusiidae and various families in the Scincomorpha with respect to other advanced squamate character-states suggests that the Xantusiidae are rightly placed in the Scincomorpha. As pointed out earlier, however, the final answer to this question must await a detailed comparison between the Xantusiidae and non-gekkotan lizards.
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