

## THE COMPARATIVE MORPHOLOGY OF THE AXIAL SKELETON IN THE AUSTRALIAN GEKKONIDAE

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(Communicated by Dr N. G. STEPHENSON, F.L.S.)

(With 9 text-figures)

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### INTRODUCTION

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 typically persist throughout the column in both the amphicoelous and procoelous forms. It has long been considered, because of their vertebral structure, that geckos include the most primitive of living lizards. Boulenger (1885) and Camp (1923) both placed the amphicoelous geckos first in their schemes of classification. Underwood (1954) proposed a classification of geckos using such ophthalmological characters as the presence of an eyelid or a spectacle and the exact form of the pupil as criteria of primary importance, and suggested that in geckos 'the procoelous condition is primitive and the amphicoelous condition secondary'. Romer (1956) maintained that the Iguania and the Nyctisauria (Gekkonidae and Pygopodidae) contest for the position of the most primitive of the living Lacertilia, but he did place the Infraorder Iguania first in his classificatory scheme. He expressed the view that the geckos, though specialized in the structure of the skull and feet 'are thought to be degenerate in vertebral structure but are nevertheless archaic in nature'.

The earliest definitive lizards, however, had amphicoelous vertebrae, there being considerable radiation of these forms during the Triassic. Underwood noted this in a subsequent publication (1955) and withdrew his earlier view. Thus procoely in lizards is still generally accepted as having evolved from amphicoely, there being no evidence that the reverse has taken place. Nevertheless the procoelous condition could have arisen more than once during lacertilian evolution, particularly as it is generally agreed that the morphological change involved is only small.

It is essential when classifying a group of animals that the criteria accepted as homologous throughout a group should in fact be so. Amphicoely and procoely are basic criteria in the classification of several vertebrate groups, so that the components of the axial skeleton in amphicoelous and procoelous forms must be clearly recognized.

The present study of the vertebral column of geckos has been undertaken in an attempt to clarify the problem as far as the Lacertilia are concerned, and to discover whether or not there is any indication of 'degeneracy' in gekkonid amphicoely.

#### MATERIAL AND METHODS

The following geckos were used for the study of the vertebral column. The generic and specific names used have been adopted after consulting Boulenger (1885, 1887), Zietz (1920) and Loveridge (1934).

#### AUSTRALIA

- Carphodactylus laevis* Günther, 1897
- Diplodactylus michaelsoni* Werner, 1910
- D. strophurus* (Duméril & Bibron), 1839
- D. tessellatus* (Günther), 1875
- D. vittatus* Gray, 1832
- Ebenavia horni* Lucas & Frost, 1895
- Hemidactylus frenatus* Duméril & Bibron, 1836
- Heteronota binoei* Gray, 1845
- Lucasius damaeus* (Lucas & Frost), 1896
- Nephurus asper* Günther, 1876
- N. laevis* De Vis, 1886
- Oedura lesueurii* (Duméril & Bibron), 1836
- O. marmorata* Gray, 1842
- O. monilis* De Vis, 1888
- Peropus oceanicus* (Lesson), 1828
- P. variegatus* (Duméril & Bibron), 1836
- Phyllodactylus 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), 1856
- Gonatodes fuscus* (Hallowell), 1855
- Sphaerodactylus parkeri* Grant, 1939

#### NEW GUINEA

- Gekko vittatus* Houttuyn, 1782

#### NEW HEBRIDES

- Lepidodactylus lugubris* (Duméril & Bibron), 1836

#### NEW IRELAND

- Hemidactylus garnoti* Duméril & Bibron, 1836

## NEW ZEALAND

*Hoplodactylus duvaucelii* (Duméril & Bibron), 1836*H. pacificus* (Gray), 1845*Nautilinus elegans* Gray, 1845

## NORFOLK ISLAND

*Phyllodactylus güntneri* Boulenger, 1885

## SOLOMON ISLANDS

*Lepidodactylus guppyi* Boulenger, 1884*L. woodfordii* Boulenger, 1887

Specimens of the above species were prepared as alizarin transparencies and were dissected under a Zeiss Opton binocular microscope with epi- and sub-illumination. Although uncalcified cartilage does not stain red as do bone and calcified cartilage, it could be detected readily owing to its distinctive appearance. 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.

Longitudinal frozen sections were made of cervical and dorsal vertebrae of *Phyllurus platurus*, *P. milii* and *Sphaerodactylus parkeri* which had been alizarin stained, in order to compare the procoelous and amphicoelous conditions.

Transverse and longitudinal serial sections at 10  $\mu$  thickness were cut through the caudal vertebrae of juvenile and adult specimens of *Oedura lesueurii* to examine the plane of caudal fracture.

An entire juvenile specimen of *O. lesueurii* was sectioned transversely at 10  $\mu$ . The sacrum of an adult *O. lesueurii* was cut transversely at 10  $\mu$ , while dorsal vertebrae of the same specimen were sectioned longitudinally, again at 10  $\mu$ . Serial sections at 8  $\mu$  were cut transversely through the head and cervical vertebrae of an embryonic *O. marmorata* and *Peropus variegatus*, the remainder of the latter specimen being sectioned transversely at 10  $\mu$ . This range of sectioned material was used in the study of the components of the intervertebral region, the atlas-axis complex, rib-attachment, the chordal cartilage and the foramina in the centrum. Representative sections from these series have been drawn from photomicrographs or from direct observation in order to illustrate points described in the text. The remaining figures are free-hand drawings whose proportions have been checked by careful measurement.

## THE VERTEBRAL COLUMN

## General

The vertebrae of amphicoelous geckos (Fig. 1A, B) are characterized by their biconcave centra, by the continuous notochord, and by the discrete intercentra in the inter-

FIG. 1.—Medial section of the centra of dorsal vertebrae, showing the 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, inter-centrum. ivc, intervertebral cartilage. nc, notochord. ncs, notochordal sheath. pb, perichondral bone. rec, region of maximum chordal constriction.

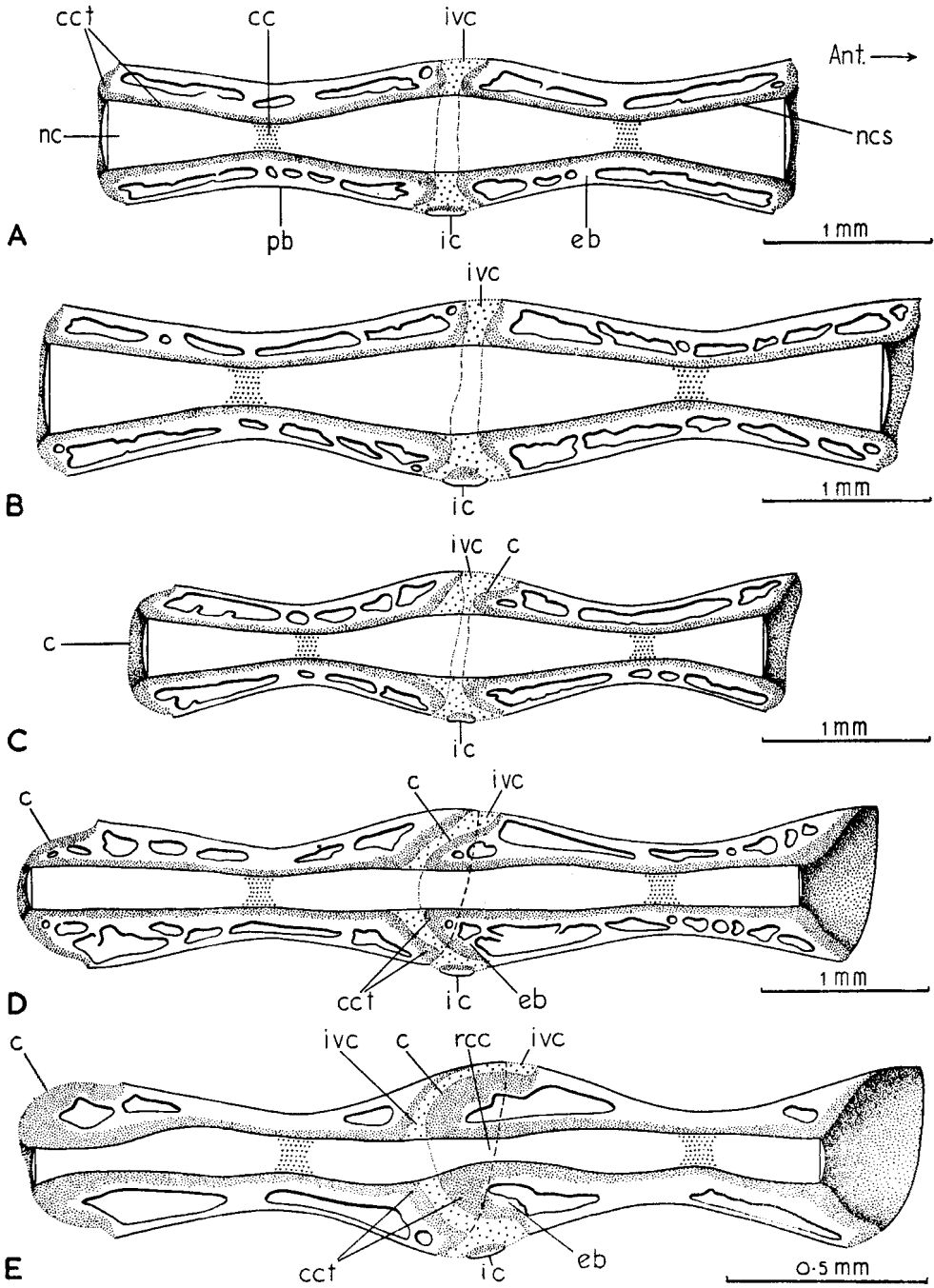


FIG. 1.

vertebral region. Each centrum is the major supporting element of the vertebra ; it is short and broad, and is hollowed at both ends into funnel-shaped depressions which are connected through the vertebra by the notochordal canal. This type of notochordal amphicoelous centrum was characteristic of primitive reptiles, and was retained during the Triassic in ichthyosaurs and in some early lepidosaurs, viz. *Eosuchia* and *Rhynchocephalia*. It exists today only in the rhynchocephalian *Sphenodon*, most geckos, and in the trunk vertebrae of turtles (Romer, 1956).

Procoelous centra were to be found in the *Eusuchia* before the end of the Mesozoic, were present in pterosaur presacra and are characteristic of nearly all Squamata (Romer, 1956). They are also present in the cervical and caudal regions of some chelonians, although their number varies as does their occurrence.

The vertebrae of amphicoelous geckos 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 first occurring between the axis and the third cervical vertebra. The moniliform notochord, extending without interruption from the axis to the tail, has its smallest diameter midvertebrally 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 intervertebral cartilage. Fused to the ventral surface of this cartilage is an oval plate of bone, the intercentrum.

Only two of the 34 species of geckos examined were procoelous. One of these was the Jamaican gecko *Sphaerodactylus parkeri*, of which only one specimen (adult) was available, and the other was the Australian species *Phyllurus milii*. In both species the short, broad centra are pierced throughout their length by the chordal canal, which continues without interruption through the intervertebral region (Fig. 1C, D, E). A discrete intercentrum lies ventrally between adjacent centra. In possessing these characters the vertebrae of *S. parkeri* and *P. milii* are identical with those of amphicoelous geckos. The difference between this type of procoelous centrum and the amphicoelous centra of other geckos is mainly one of shape. In both species each centrum has a cup-shaped depression anteriorly and a rounded condyle posteriorly, so that neighbouring vertebrae together form a ball-and-socket articulation. The greater part of the condyle consists of calcified cartilage, with a core of endochondral bone which is indistinguishable from that of the centrum.

The tissue lying between the procoelous centra of *S. parkeri* and *P. milii* consists of a cup-shaped layer of cartilage fused to the adjacent centra and pierced by the chordal canal. There is no articular cavity between the centra in these procoelous geckos, just as there is none in the amphicoelous forms. Constriction of the notochord occurs largely within the condyle, and is most noticeable in the dorsal vertebrae of *S. parkeri* (Fig. 1E). It also occurs to a smaller degree in the anterior region of the centrum just behind the cup-shaped depression. As a result of the constriction within the vertebra, the intervertebral chordal diameter is reduced compared with amphicoelous forms.

FIG. 2.—Medial section of the centra of axis and the third cervical vertebra, showing the lesser extent of procoely in the cervical region compared with the dorsal region.

- 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.

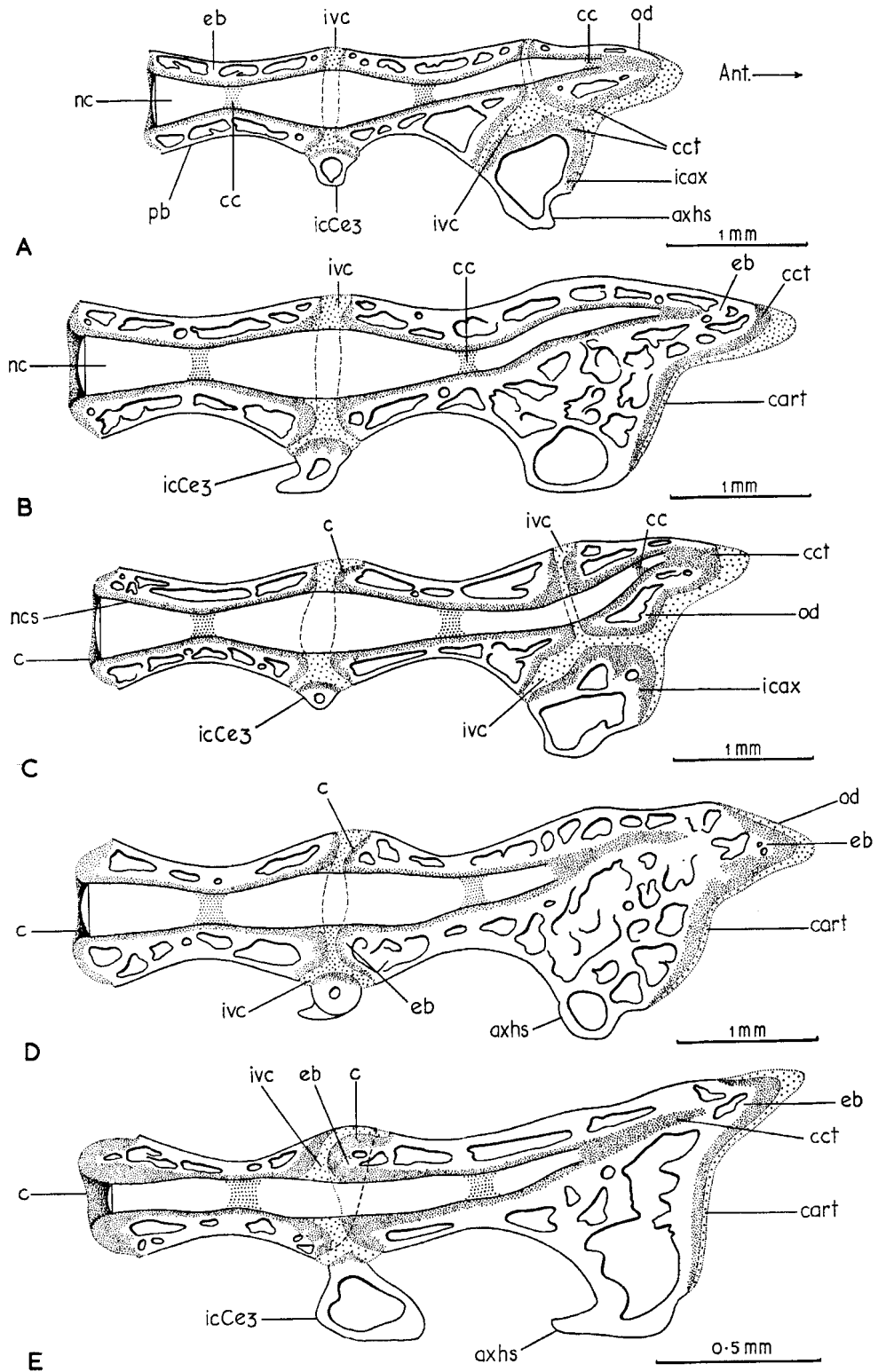


FIG. 2.

Camp (1923) stated that the condyles of gekkonid procoelous vertebrae fuse ventrally with the intercentra. This does not apply either to *S. parkeri* or to *P. milii* in which the intercentra are quite separate from the condyles, and are attached as in amphicoelous forms to the intervertebral cartilage. Intercentra have also been observed in procoelous lizards other than the geckos. They occur in the Xantusoidea whose centra are like those of the amphicoelous geckos except for the development of a cup-and-ball articulation (Camp, 1923). In the agamid *Uromastix aegyptia* six separate and successive intercentra are present in the cervical region (El-Toubi, 1949), the first forming the ventral part of the atlas ring. They gradually decrease in size posteriorly and are described by El-Toubi as possessing distinct sutures with the centra. Discrete intercentra are also noted by the present author to occur in several genera of pygopods.

In neither of the two procoelous species examined is procoely developed to the same extent in all the vertebrae of the column. In both species the mid-dorsal vertebrae show the greatest development of the procoelous condition, there being a gradual decrease in the size of the condyle and its corresponding cup in the more anterior and posterior regions of the column (Figs 1, 2). In *S. parkeri* all the vertebrae from the axis to the end of the pygal region bear a well-developed condyle, with the exception of the two sacral vertebrae which are intimately fused. The cervicals and pygals of adult *P. milii* on the other hand differ only very slightly from the amphicoelous condition; the condyles are very small and chordal constriction is slight.

Procoely is not developed to the same extent in juvenile *Phyllurus milii* as it is in adults. In the dorsal region the condyles are small and chordal constriction has not yet begun (Fig. 1c, d). The cervical condyles are even smaller (Fig. 2c, d), while the pygal vertebrae are amphicoelous. Postpygal vertebrae were present on only one adult specimen of *P. milii* and were amphicoelous.

It is apparent that the vertebrae of *Sphaerodactylus parkeri* represent an early stage in the development of procoely in that they retain the intervertebral notochord and intercentra. *Phyllurus milii*, with its smaller condyles and greater intervertebral chordal diameter, represents an even earlier stage in the transition from amphicoely to procoely.

Mahendra (1950) stated that the vertebral column of geckos is unique among lizards in closely resembling *Sphenodon* in many of its characteristics, among which he noted the notochordal amphicoelous vertebrae, the intercentra and the chordal plates. In the geckos, as in *Sphenodon*, each chordal plate is situated midvertebrally in the notochordal canal; it is cartilaginous tissue consisting in geckos of large, vacuolated cells embedded in a small amount of hyaline matrix, whereas in *Sphenodon* the cartilage is composed mainly of matrix in which are embedded small circular cells with a conspicuous rounded nucleus (Howes & Swinnerton, 1901). In both groups the chordal plate is endochordal in origin, and is probably formed by the differentiation of chordal tissue. The chordal sheath remains intact throughout the column, but in geckos it is very much thicker intervertebrally than it is around the chordal plate. In *Sphenodon* the chordal sheath is of uniform thickness, and lying internally to it is a structureless cuticle, except in the region of the chordal plates. This cuticle is the *tunica chordae*, which appears to represent the chordal epithelium. The *tunica* passes into the faces of the plates whose superficial portions stain correspondingly with it (Howes & Swinnerton, 1901). In geckos there is no modification of the chordal epithelium to form a *tunica chordae*; the epithelium is retained into adulthood.

With the exception of the atlas and the posterior caudal vertebrae, the neural arches articulate by means of zygapophyses, which lie close to the body of the vertebra. The facets are slightly curved in end view (Fig. 3d). In no gecko is there any indication of an additional articulation by means of zygosphenes and zygantra, such as occur in some of the other lacertilian groups and in the Ophidia.

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

#### *Vertebral Numbers*

Vertebral counts made on 130 Australian geckos, representing 12 genera and 21 species are presented in Table I. For purposes of comparison, counts taken on 21 non-Australian geckos representative of eight genera and ten species are presented in Table II.

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 *Phyllodactylus marmoratus*, five have 27 presacral vertebrae and the remaining four have 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 'presterneal', but will not be so regarded here. Eight presternals were found in every gecko examined, but only the anterior six are classified as cervical for, 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.

The first three cervical vertebrae are normally devoid of ribs, although incomplete rib elements were present on the third cervical of 25 specimens. Only one species, *Phyllodactylus 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 varies from one to three.

The sacral count was found to be typically two, except in the genus *Nephruroides*. 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 predominantly five in number, although four pygals seem typical of *Nephruroides laevis* and *Phyllurus milii*, and four, five or six pygals may occur in *Hemidactylus frenatus*. Four pygal vertebrae are also found occasionally in other species.

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, the postsacral count was approximately 30. In specimens which had undergone autotomy, there was usually a completely regenerated tail whose axial skeleton consisted of a cartilaginous tube.

Twenty-two postsacral vertebrae were present in the only specimen of *Nephruroides asper* with a complete tail; this tail was very short, being only one-sixth of the total length of the animal. *N. asper* is the only species in which caudal fracture planes are completely absent, and whose tail is therefore incapable of autotomy.

#### *Atlas (Figs 3 and 4)*

The atlas consists of the paired neural arches and the intercentrum of the first vertebra, the atlantal centrum having been incorporated into the axis as the odontoid process.



TABLE I.—Vertebral counts on Australian geckos

Species	Total specimens	Specimens with a particular vertebral count	Presacral	Total cervical	Anterior cervicals devoid of ribs	Pairs of cervical ribs	Lumbar	Sacral	Pygal
<i>Carphodactylus laevis</i>	1	1	27	6	3	3	3	2	4
<i>Diplodactylus michaelsoni</i>	1	1	26	6	2	3.5	3	2	5
<i>D. strophurus</i>	2	2	26	6	3	3	2	2	5
<i>D. tessellatus</i>	1	1	26	6	3	3	3	2	5
<i>D. vittatus</i>	4	2	26	6	3	3	2	2	5
		2	26	6	3	3	3	2	5
<i>Ebenavia horni</i>	2	2	26	6	3	3	2	2	5
<i>Hemidactylus frenatus</i>	16	10	26	6	3	3	1	2	5
		1	26	6	3	3	1	2	4
		1	26	6	3	3	1	2	6
		1	26	6	2	3.5	1	2	4
		1	25	6	3	3	1	2	6
		2	27	6	3	3	2	2	4
<i>Heteronota binoei</i>	4	4	26	6	3	3	1	2	5
<i>Lucasius damaeus</i>	1	1	26	6	2	3.5	2	2	5
<i>Nephruerus asper</i>	3	1	26	6	3	3	2	3	Nil
		1	26	6	3	3	2	4	Nil
		1	26	6	2	3.5	2	3	Nil
<i>N. laevis</i>	5	2	25	6	3	3	2	3	4
		1	25	6	3	3	3	3	4
		1	26	6	3	3	2	3	4
		1	26	6	3	3	3	2	4
<i>Oedura lesueurii</i>	32	23	26	6	3	3	1	2	5
		2	26	6	3	3	2	2	5
		1	26	6	2	3.5	1	2	5
		1	26	6	2	3.5	1	2	4
		1	26	6	2	3.5	2	2	5
		1	26	6	2	4	1	2	5
		1	26	6	2	3.5		Abnormal	
		1	25	6	3	3	1	2	5
		1	27	6	3	3	1	2	4
<i>O. marmorata</i>	1	1	26	6	3	3	1	2	5
<i>O. monilis</i>	1	1	26	6	3	3	2	2	4
<i>Peropus oceanicus</i>	2	2	26	6	3	3	1	2	5
<i>P. variegatus</i>	3	1	26	6	3	3	2	2	4
		1	26	6	2	4	2	2	5
		1	25	6	3	3	2	2	5
<i>Phyllodactylus marmoratus</i>	9	4	28	6	2	4	2	2	5
		2	27	6	2	4	1	2	5
		1	27	6	2	4	1	2	6
		1	27	6	2	4		Abnormal	
		1	27	6	2	4	2	2	5
<i>Phyllurus cornutus</i>	3	3	25	6	3	3	2	2	5
<i>P. milii</i>	5	3	26	6	3	3	2	2	4
		2	26	6	3	3	3	2	4
<i>P. platurus</i>	33	20	25	6	3	3	2	2	5
		3	25	6	3	3	2	2	4
		1	25	6	3	3	2	3	4
		3	25	6	3	3	3	2	5
		2	25	6	2	3.5	2	3	4
		1	26	6	3	3	3	2	4
		3	26	6	3	3	2	2	5
<i>Rhynchoedura ornata</i>	1	1	27	6	3	3	2	2	5
	130								

TABLE II.—*Vertebral counts on non-Australian geckos*

Species	Total specimens	Specimens with a particular vertebral count	Presacral	Total cervical	Anterior cervicals devoid of ribs	Pairs of cervical ribs	Lumbar	Sacral	Pygal
<i>Afroedura transvaalica</i> .	1	1	27	6	3	3	3	2	4
<i>Aristelliger praesignis</i> .	1	1	26	6	3	3	1	2	5
<i>Gekko vittatus</i> .	3	1	26	6	3	3	1	2	5
		1	26	6	3	3	2	2	5
		1	26	6	2	4	1	2	5
<i>Gonatodes fuscus</i> .	1	1	26	6	3	3	1	2	5
<i>Hemidactylus garnoti</i> .	5	4	26	6	3	3	1	2	5
		1	26	6	3	3	1	2	4
<i>Lepidodactylus guppyi</i> .	1	1	26	6	3	3	1	2	5
<i>L. lugubris</i> .	1	1	26	6	3	3	1	2	5
<i>L. woodfordii</i> .	6	4	26	6	3	3	1	2	5
		1	26	6	2	3.5	1	2	5
		1	26	6	2	4	1	2	5
<i>Phyllodactylus güntheri</i> .	1	1	27	6	3	3	1	2	5
<i>Sphaerodactylus parkeri</i> .	1	1	26	6	2	4	1	2	5
	21								

The neurapophyses are united to the intercentrum by uncalcified cartilage in embryonic, juvenile and adolescent forms, but in adults these elements usually fuse together to form a bony ring. In a juvenile specimen of *Phyllurus platurus* it was found that a strong ligament, in addition to the cartilage, connected the intercentrum to the neurapophyses (Fig. 3B). In adult *Hemidactylus frenatus* the components of the atlas fuse intimately, but there is a thin ligament lying ventrally across the suture (Fig. 3A). Mahendra (1950) maintained that in *H. flaviviridis* the connection is by means of a ligament only, while in the New Zealand geckos (Stephenson & Stephenson, 1956) the atlantal elements fuse.

Anteriorly the intercentrum and arch pedicels together bear a semicircular facet for articulation with the single occipital condyle, while in a comparable position on the posterior surface is the articular facet serving the odontoid process. Investing both these facets is a thin layer of uncalcified cartilage. The cavity enclosed by the atlas is divided horizontally, by a strong ligamentous band connecting the neurapophyses, into a dorsal neural canal and a ventral canal into which fits the odontoid process (Fig. 3A, B).

The atlantal intercentrum usually bears a median ventral spine, which varies in its development in different species and, to a large extent, within species. In the Australian forms 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. 4A), the atlantal hypapophyseal spine is very large.

The atlantal neurapophyses fail to fuse dorsally in many species, a condition believed by Mahendra (1950) to be primitive (Fig. 3A, B, c). Underwood (1954) considered this view to be untenable, since the condition occurs largely in amphi-coelous geckos. However, in 1955 Underwood reversed his opinion, stating that he

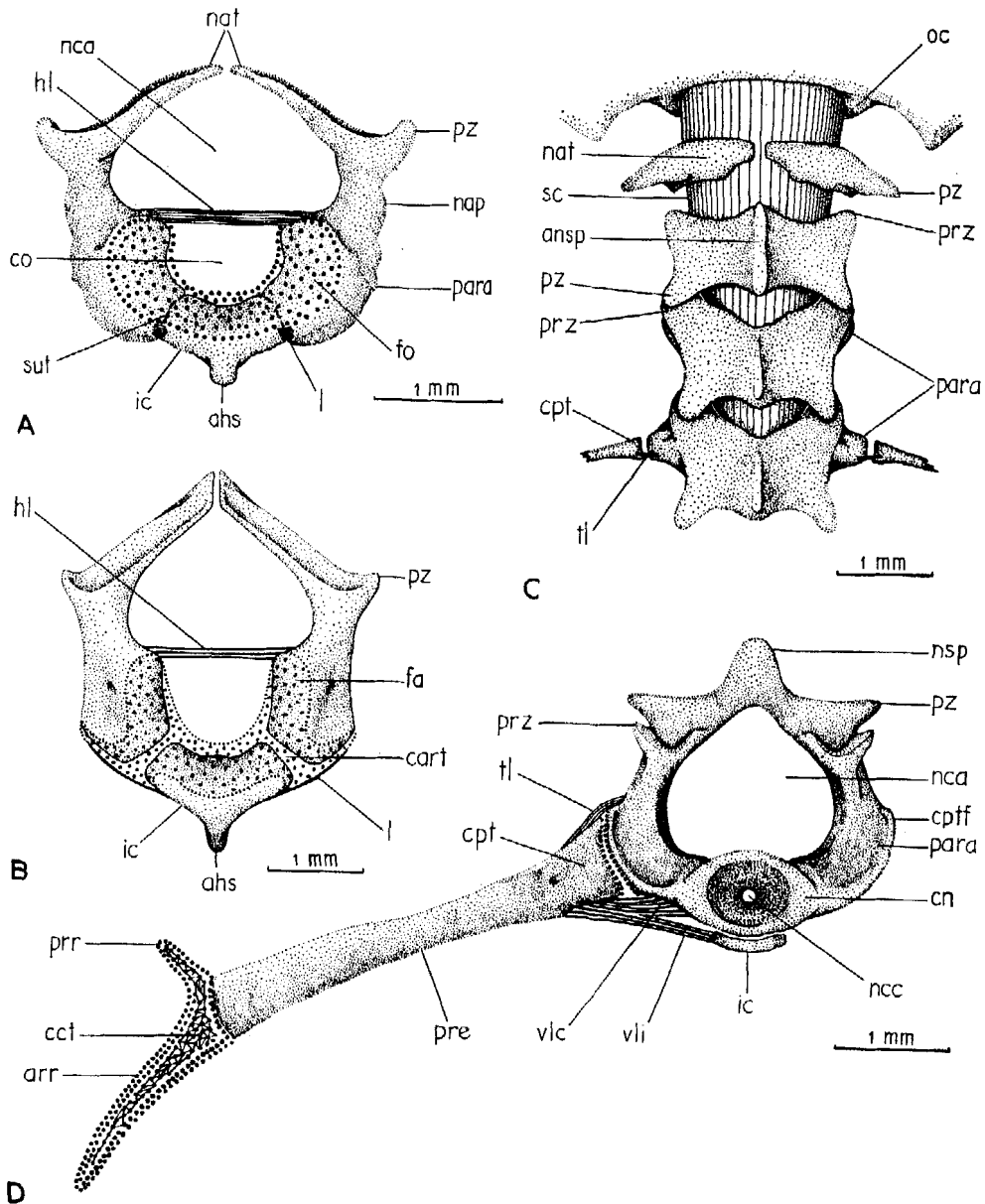


FIG. 3.—Cervical vertebrae.

A. *Hemidactylus frenatus* adult, anterior view of atlas.

B. *Phyllurus platurus* juvenile, posterior view of atlas.

C. *Peropus variegatus* adult, dorsal view of first four cervical vertebrae.

D. *Phyllurus platurus* adult, anterior view of sixth cervical vertebra.

ahs, atlantal hypapophyseal spine. ansp, axial neural spine. arr, anterior ramus of cervical rib. cart, uncalcified cartilage. cct, calcified cartilage. cn, centrum. co, canal which encloses odontoid process. cpt, capitulum of rib. cptf, capitular facet. 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 neural apophyses. nca, neural canal. ncc, notochordal canal. nsp, neural spine. oc, occipital region of skull. para, parapophysis. pre, proximal rib. prr, posterior ramus of cervical rib. prz, prezygapophysis. pz, postzygapophysis. sc, spinal cord. sut, suture. tl, tubercular ligament. vlc, branch of ventral ligament to centrum. vli, branch of ventral ligament to intercentrum.

then considered the paired atlantal neurapophyses to constitute a primitive character. Lack of fusion in this region has also been recorded in *Hoplodactylus* and *Nautinus* (Stephenson & Stephenson, 1956). In the Australian genus *Nephruirus*, only immature specimens exhibit 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 neurapophyses remain separate throughout life. Other Australian geckos in which there was a tendency for fusion of the atlantal neurapophyses were *Diplodactylus strophurus*, *D. tessellatus*, *D. vittatus*, *Ebenavia horni*, *Oedura lesueurii*, *O. marmorata* and *Phyllodactylus marmoratus*. Of the non-Australian geckos, fusion was found to exist in *Gekko vittatus*, *Hemidactylus garnoti*, *Phyllodactylus guintheri*, *Gonatodes fuscus*, *Sphaerodactylus parkeri* and all three species of *Lepidodactylus*. Fusion of the atlantal neurapophyses occurs only in adult specimens; during the immature stages the arches of all species remain separate.

In those geckos with fused atlantal neurapophyses, there is little, if any, development of a neural spine. It was best developed in *Gonatodes fuscus*, where it took the form of a very low, narrow ridge. In *Carphodactylus laevis* and several specimens of *Hemidactylus frenatus*, in which the atlantal arch is not fused, the separate neurapophyses extend dorsally into very low spines.

In most geckos the atlantal neurapophyses bear a horizontal, posteriorly-curved process situated at the angle formed by the stout arch pedicel and the plate-like dorsal lamina. It is in this position on the subsequent vertebrae that the zygapophyses lie, and on this basis the processes on the atlas are here considered to be serially homologous with the following postzygapophyses. There is no articulation between the atlantal and axial neural arches (Figs 3c, 4). Adult *Nephruirus* alone lack large atlantal postzygapophyses, these processes being represented by low horizontal ridges. In immature stages however, they are the well-developed structures typical of the adults of other genera.

The atlantal arch pedicels of most geckos are swollen just above their junction with the intercentrum (Figs 3A, 4B). In *Gonatodes*, *Sphaerodactylus* and *Hemidactylus* there is a well-developed ridge in this position, and in one specimen of *Lepidodactylus woodfordii*, a small pointed spine. These processes serve for the attachment of ligaments and muscles and are considered here, although they have never been observed to bear ribs, to be serially homologous with the parapophyses of the other vertebrae. Ribs have been found on the first two vertebrae of fossil rhynchocephalians, and it is probable that in early lepidosaurs, ribs were present on every vertebra to the proximal caudal region (Romer, 1956). In the geckos, only the parapophyses on the vertebrae remain, the ribs having disappeared.

#### *Axis* (Figs 2, 3, 4 and 5)

The axis is a compound structure consisting not only of paired neurapophyses, a centrum and intercentrum, but incorporating the atlantal centrum as well (Fig. 2). The atlantal centrum (odontoid process or *dens epistrophei*) is attached anteriorly to the axial centrum and intercentrum, and forms a peg on which the atlas rotates. In adult specimens the components of the axis are intimately fused, but in juvenile or even more adolescent specimens they are joined together by cartilage. The odontoid process widens posteriorly, so that the bulk of it overlies the large axial intercentrum.

In embryonic specimens the notochord extends unbroken through the *dens* into the occipital region of the skull. It is later constricted and severed within the *dens* as the latter becomes rounded to form a condyle. This is the only point throughout the length of the column of amphicoelous geckos, and of the procoelous species *Sphaerodactylus parkeri* and *Phyllurus milii*, at which the notochord is interrupted. In juvenile and even more adolescent geckos, the part of the chordal canal situated in the narrow anterior portion of the odontoid process becomes obliterated by cartilage,

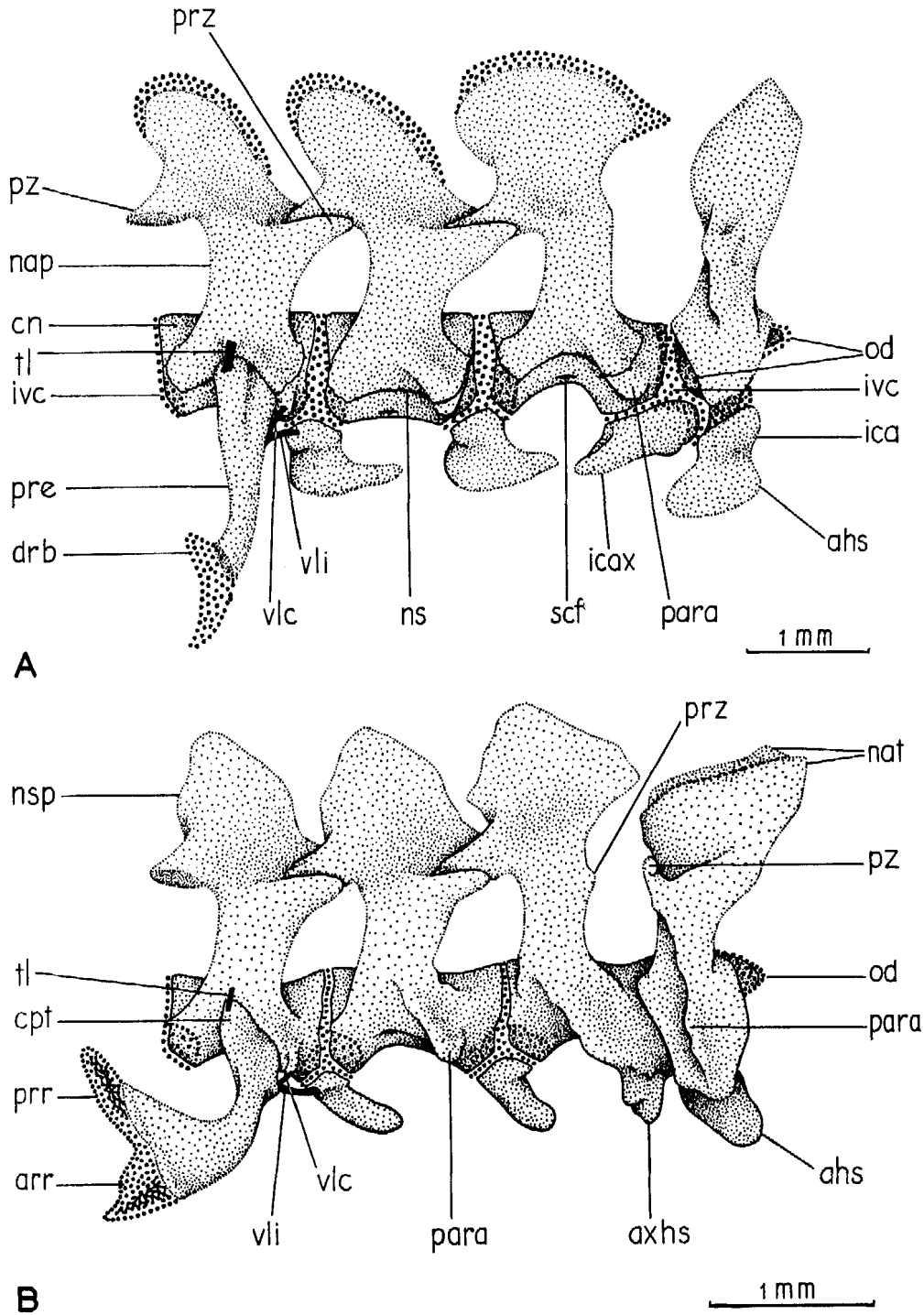


FIG. 4.

into which is incorporated the odontoid chordal cartilage (Fig. 2A, C). At this stage a small depression on the anterior surface of the process indicates the position of the notochord before it was severed. In adult specimens a core of endochondral bone has formed in the anterior part of the *dens* (Fig. 2B, D, E); only the wide posterior portion of the *dens* retains true notochordal tissue surrounded by the chordal sheath. Mahendra (1950) described in *Hemidactylus flaviviridis* 'a peculiar prominent process projecting forwards from its (the odontoid process's) dorsal portion'. This process is in fact the narrow anterior portion of the odontoid process of which it is an integral part. Overlying the anterior and lateral surfaces of the *dens* and the anterior face of the axial intercentrum is a layer of resilient cartilage forming a smooth surface on which the atlas articulates. This cartilaginous layer is thin except on the anterior extremity of the *dens*, where it is thickened to provide a cushion for articulation with the occipital condyle.

Although the axial centrum is somewhat broader than those of the following cervical vertebrae, its structure is essentially the same. In amphicoelous genera it contains persistent notochord which is continuous with that of the odontoid process and third cervical vertebra. Piercing the centrum ventrally is a pair of small foramina for the passage of blood vessels. The posterior surface is concave in all the amphicoelous specimens examined. There is no process, similar to that described by Mahendra (1950) in *Hemidactylus flaviviridis*, to articulate with the third vertebra except in the procoelous species *Sphaerodactylus parkeri* and *Phyllurus milii*.

The axial intercentrum is the largest in the column (Figs 2A, C; 4A). In adult specimens it is fused, together with the odontoid process, to the anterior surface of the centrum (Fig. 2B, D, E). It is usually produced ventrally into a prominent hypapophyseal spine, ridge, or knob to which are attached subvertebral muscles and ligaments. There is only one such hypapophysis on the axis. Mahendra (1950) described two hypapophyses in *Hemidactylus flaviviridis* 'the anterior one belonging to the ontoideum and the posterior to the centrum of the axis', but such a condition is not possible in normal individuals. The hypapophysis belonging to the ontoideum is the atlantal intercentrum which is attached to the atlantal neuropophyses. The hypapophysis lying ventrally to the ontoideum belongs to the axis. The second axial 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 of the specimens examined.

Each axial arch pedicel frequently bears a low ridge or parapophysis sloping up and back, close to its junction with the centrum (Fig. 4). In *Sphaerodactylus*, *Hemidactylus* and *Lepidodactylus* the parapophyses are prominent and knife-edged, while in a juvenile specimen of *Aristelliger praesignis* they were seen to extend ventrally onto the centrum. In no gecko has the axis been noted to bear ribs.

The anterior edge of the axial neuropophyses may bear a small process lying in the plane of the arch or projecting laterally for a short distance (Figs 4B, 5A). These processes are reduced and non-functional prezygapophyses; they are most pronounced in *Carphodactylus* and *Phyllurus* and are absent from *Nephurus*, *Ebenavia*,

FIG. 4.—Lateral view of cervical vertebrae.

A. *Aristelliger praesignis* juvenile.

B. *Hemidactylus frenatus* adult.

*ahs*, atlantal hypapophyseal spine. *arr*, anterior ramus of cervical rib. *axhs*, axial hypapophyseal spine. *cct*, calcified cartilage. *cn*, centrum. *cpt*, capitulum of rib. *drb*, bifurcated distal rib. *ica*, atlantal intercentrum. *icax*, axial intercentrum. *ivc*, intervertebral cartilage. *nap*, neural arch pedicel. *nat*, atlantal neuropophyses. *ns*, neurocentral suture. *nsp*, neural spine. *od*, odontoid process. *para*, parapophysis. *pre*, proximal rib. *prp*, posterior ramus of cervical rib. *prz*, prezygapophysis. *pz*, postzygapophysis. *scf*, subcentral foramen. *tl*, tubercular ligament. *vlc*, branch of ventral ligament to centrum. *vli*, branch of ventral ligament to intercentrum.

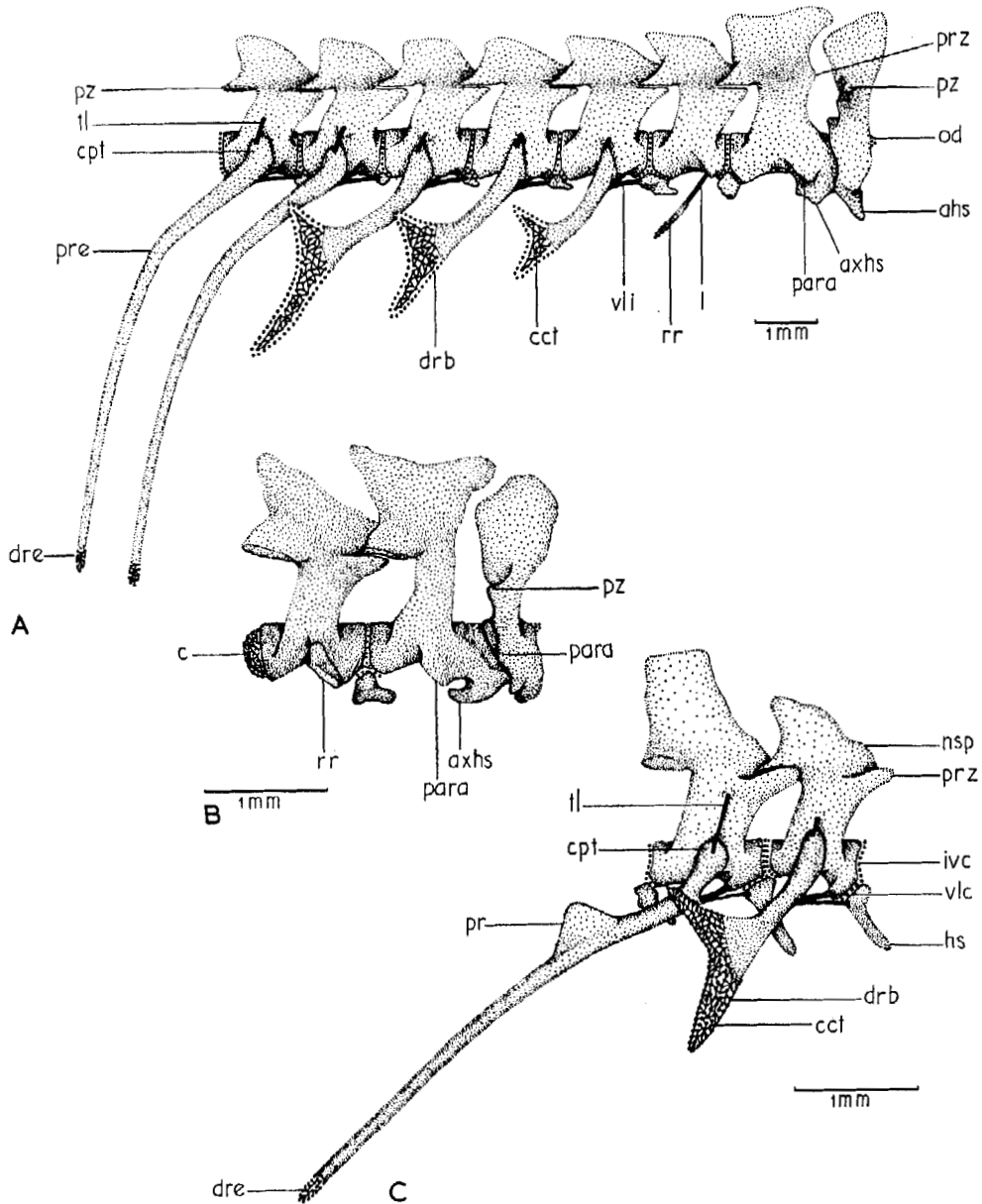


FIG. 5.—Lateral view of cervical and dorsal vertebrae.

A. *Oedura lesueurii* adult; presternal vertebrae.

B. *Sphaerodactylus parkeri* adult; atlas, axis and third cervical vertebra.

C. *Gonatodes fuscus* adult; sixth cervical and first dorsal vertebrae.

ahs, atlantal hypapophyseal spine. axhs, axial hypapophyseal spine. c, condyle. cct, calcified cartilage. cpt, capitulum of rib. drb, bifurcated distal rib. dre, distal rib. hs, hypapophyseal spine. ivc, intervertebral cartilage. l, ligament. nsp, neural spine. od, odontoid process. para, parapophysis. pr, bony process. pre, proximal rib. prz, prezygapophysis. pz, postzygapophysis. rr, rudimentary rib. tl, tubercular ligament. vlc, branch of ventral ligament to centrum. vli, branch of ventral ligament to intercentrum.

*Rhynchoedura* and the three Jamaican forms. The New Zealand geckos (Stephenson & Stephenson, 1956) and *Hemidactylus flaviviridis* (Mahendra, 1950) also have reduced axial prezygapophyses.

The axial neurapophyses of adult geckos are fused mid-dorsally and are prolonged into a large neural spine. This spine is almost always taller than those of the following cervical vertebrae, and takes the form of a longitudinal blade projecting anteriorly and posteriorly over the ends of the arch. The neural arches of the axis and atlas are frequently quite widely separated from one another, so that the reduced and modified zygapophyses are incapable of articulation (Figs 3c, 4). In addition, the atlantal neurapophyses are frequently widely separated from the skull. These spaces are devoid of cartilage, but are covered over by thin sheets of connective tissue. Such spacing of the anterior cervical elements together with the lack of articulation between the atlantal and axial neural arches permits greater freedom of movement of the atlas on the odontoid process.

#### *Third, Fourth, Fifth and Sixth Cervical Vertebrae* (Figs 3, 4 and 5)

The remaining cervical vertebrae are basically identical in structure, differing only in the ribs associated with them. Low parapophyses in the form of diagonal ridges are present on the third cervical vertebra of some genera, and are particularly well developed in *Gonatodes fuscus*, *Aristelliger praesignis*, *Hemidactylus frenatus* and occasionally in the three species of *Phyllurus*. When ribs are present on the third cervical vertebra they are rudimentary, and most frequently appear only on one side of the body (Fig. 5A). They usually consist only of the proximal bony shaft which is attached to the vertebra 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 cervical of *Oedura lesueurii*, *Peropus variegatus*, *Gekko vittatus*, *Lepidodactylus woodfordii* and was present in the single specimen of *Sphaerodactylus parkeri* examined (Fig. 5B). All nine specimens of *Phyllodactylus marmoratus* available for study had paired, reduced ribs on the third cervical vertebra.

The fourth, fifth and sixth cervical vertebrae bear paired ribs (Figs 3D, 4, 5A). Each rib has a single head which articulates with the parapophysis of the neural arch. A ligamentous band connects the head of the rib to the neural arch just above the articulation. Ventral to the articulation is a similar ligament joining the shaft of the rib to the intercentrum, with a smaller branch to the anterior margin of the centrum. The three pairs of ribs increase in length rostrocaudally but never meet the sternum.

Each rib consists of a bony proximal portion attached to the vertebra, and a distal cartilaginous part joined to the proximal shaft. In most genera this distal piece is bifurcated. *Nephurus*, *Carphodactylus* and *Phyllurus milii* are exceptions, for in these forms none of the cervical ribs is bifurcate; the distal portion of the rib in each case consists of a single 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 bifurcate. In *Nautilinus* (Stephenson & Stephenson, 1956), the cartilaginous process on the rib of the sixth vertebra is a single, slender, elongate structure, whereas those of the more anterior ribs are forked.

Not only are there differences between species in the occurrence of forking in the cervical ribs, but there is also variation in the relative size of the two rami composing them. In the Jamaican genera *Aristelliger*, *Gonatodes* (Fig. 5c) and *Sphaerodactylus*, and in *Hemidactylus* (Fig. 4B) and *Lepidodactylus* the rami are large and almost



equal in size, whereas in the other genera examined the anterior ramus is considerably longer than the posterior one, the ratio progressively increasing in the more posterior cervical ribs. The ratio is greatest in the third cervical rib of *Phyllurus platurus* (Fig. 3D), where the anterior ramus may be as much as six times as long as the other. Both the proximal and the distal portions of the cervical ribs increase in size rostro-caudally to give an overall increase in rib length.

In the Jamaican geckos (Fig. 5C) and in *Hemidactylus*, *Peropus* and *Lepidodactylus* there is a thin, triangular, bony blade extending posteriorly from the proximal portion of the ribs of the seventh vertebra (first of the dorsal series). It is in these forms that the most marked difference exists between the proximal shafts of the cervical and dorsal ribs. The former are short and broadly expanded for the attachment of the distal bifurcated process, whereas the ribs of the dorsal series are typically long slender structures curving round the body. The triangular process on the first pair of dorsal ribs appears to indicate a transitional state 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'. 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 the 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. It would appear then 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 (1935 b, 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 cervical ribs of *H. flaviviridis* is comparable to that in *H. frenatus* and *H. garnoti*, then the first three 'uncinates' are cartilaginous, belonging 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 so that fusion must have occurred while the sternal rib and the 'uncinate' were still sclerotogenous or procartilaginous tissue. In the case of the fourth pair of ribs, fusion could have occurred no later than the cartilaginous stage. There is no indication of 'uncinate processes' on the ribs of the eighth or following vertebrae.

The term 'uncinate' to describe these processes cannot be used indiscriminately, as Stephenson & Stephenson (1956) point out. Uncinate processes typically arise from the proximal portion of the sternal and poststernal ribs, not from the distal cartilaginous portion of the cervical ribs where the so-called 'uncinates' are found in the majority of geckos. Only in *Aristelliger*, *Gonatodes*, *Sphaerodactylus*, *Lepidodactylus*, *Hemidactylus* and *Peropus* of the 20 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' be applied to these processes in geckos. It is more likely that the bifurcated cervical ribs have been modified in this way for the attachment of muscles, and that the process on the fourth pair of ribs in some genera indicates a transitional state between the cervical and dorsal ribs, as is described above.

In *Nephurus asper* and *Phyllurus milii* there is a pronounced knob on the anterior

edge of the proximal portion of the cervical ribs. In the other species examined the proximal shaft is smooth; the function of the knobs is at present obscure.

Calcification of the distal portions of the cervical ribs is of common occurrence in adult geckos, as noted also by Stephenson & Stephenson (1956) in *Naultinus* and *Hoplodactylus*. No calcification occurs in newly-hatched juveniles, but gradually takes place during the subsequent growth of the animal. The anterior ramus, if either, is the more heavily calcified of the two, and calcification of the distal portion as a whole is more marked in the posterior pair than it is in those preceding. At no time do they ossify; they remain cartilaginous, though they may be very heavily calcified in fully adult specimens.

In all the cervical vertebrae, except the atlas, there is a pair of small foramina in the centrum for the passage of blood vessels. In one specimen of *Phyllurus platurus* there were apertures in the neural arch pedicels and in the axial intercentrum as well. The occurrence of these foramina is discussed below in a separate section.

The cervical intercentra are typically larger than those in the rest of the pre-pygial region, and each is prolonged ventrally into a hypapophyseal spine (Figs 4, 5). They decrease in size posteriorly to become small, flat, oval elements similar to those of the dorsal region. In the Australian genera, none of the cervical intercentral spines is very large, and the first dorsal intercentrum is flat. In *Gonatodes*, *Aristelliger* and *Hemidactylus* the cervical intercentra bear very long hypapophyseal spines, and smaller spines are present on the anterior dorsal intercentra.

The cervical neural arches, excluding the atlantal arch, generally lie close together in adult specimens to form a continuous shield above the spinal cord. Exceptions to this were found in *Heteronota*, *Lepidodactylus*, *Peropus* (Fig. 3c) and *Hemidactylus garnoti* in which there is a considerable space mid-dorsally between the successive arches, which is covered over by a thin connective tissue sheet. 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 with the triangular or trapezoid spines of the dorsal region.

#### *Dorsal Vertebrae (Figs 5 and 6)*

The vertebrae of the dorsal region typically bear paired, articulated 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 is usually heavily calcified. The term 'sternal' is more appropriately applied to those ribs connected with the sternum, but it is frequently used also to denote the distal portion of all the ribs in the column.

The ribs of the seventh and eighth vertebrae, i.e. the first two pairs of ribs in the dorsal series, are long, curving round the body so that their distal extremities are ventral in position, but are not united with the sternum (Fig. 5A, c). The distal processes of these ribs are short cartilaginous rods which are always single, non-bifurcate structures; they are not calcified in juvenile specimens, but are often heavily calcified in adults. The distal portions of the following three to six pairs of ribs unite with the sternum, the more anterior ones directly with the sternal plate and those behind with the xiphisternum. There is considerable generic variation in the number of ribs connected independently with the sternal plate and in the number joined to form a xiphisternum.

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 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 in some degree abrupt in the region of the twentieth presacral

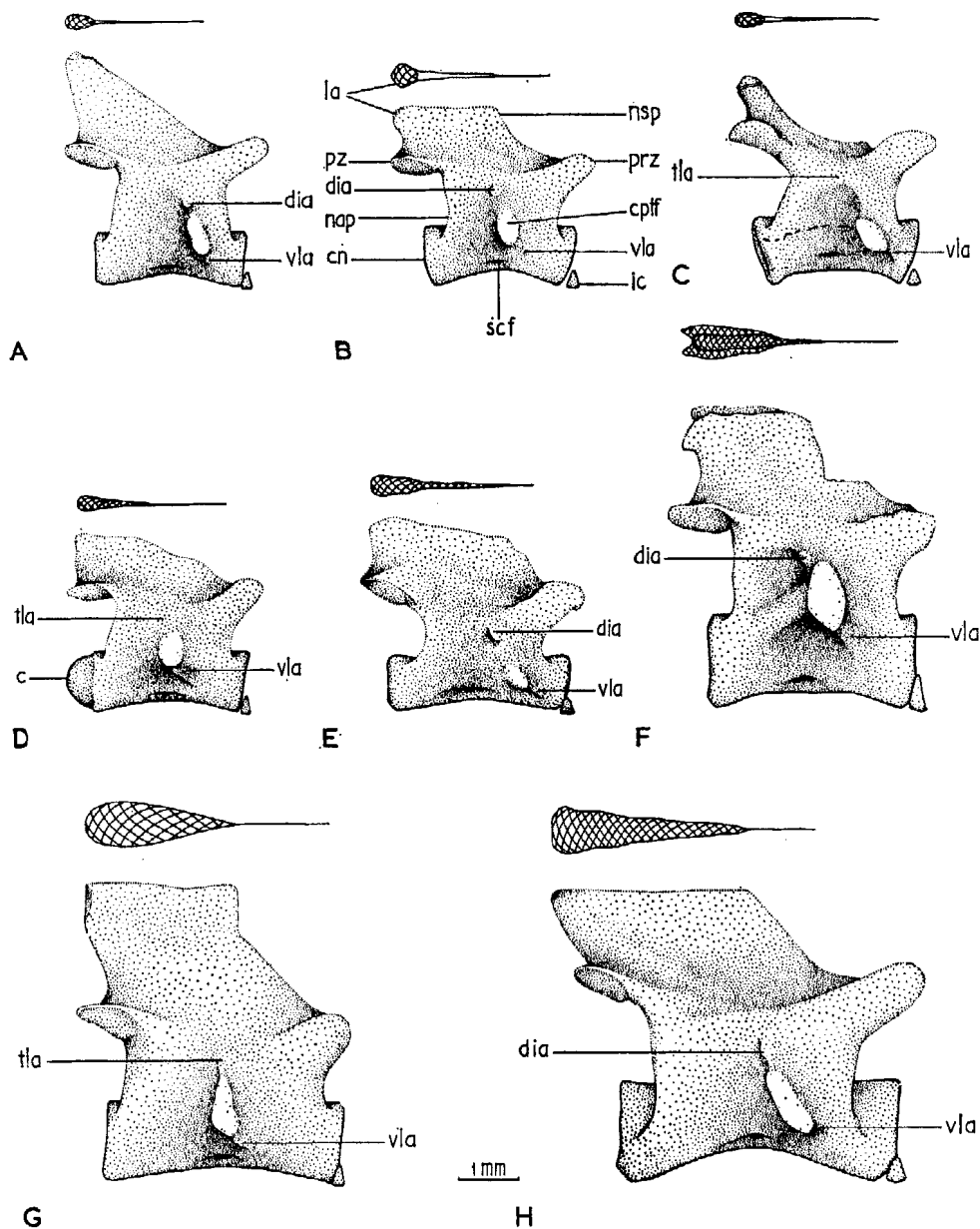


FIG. 6.—Nineteenth vertebrae of adult geckos, showing correlation between size of crest and length of presacral column. The diagram above each vertebra is a plan of the neural spine in dorsal view.

- A. *Phyllodactylus guntheri*, presacral column = 58 mm.
- B. *Phyllurus platurus*, 59 mm.
- C. *Peropus oceanicus*, 60 mm.
- D. *Phyllurus mitii*, 64 mm.
- E. *Gekko vittatus*, 66 mm.
- F. *Nephurus asper*, 77 mm.
- G. *Carphodactylus laevis*, 83 mm.
- H. *Phyllurus cornutus*, 90 mm.

c, condyle. cn, centrum. cptf, capitular facet. dia, diapophysis. ic, intercentrum. la, crest. nap, neural arch pedicel. nsp, neural spine. prz, prezygapophysis. pz, postzygapophysis. scf, subcentral foramen. tla, point of attachment of tubercular ligament. vla, point of attachment of ventral ligament.

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 (gastralia) have been detected in any of the geckos examined, although according to Mahendra (1950), such ribs are present in the superficial parts of the *rectus* muscle of *Hemidactylus flaviviridis*.

The ribs of the dorsal series, like those of the cervical region, articulate by means of a single head with the parapophysis of the vertebra. As with the cervical vertebrae, the parapophyses of the dorsal series arise from the neural arch, although in some genera they appear to extend onto the centrum. It is not possible to ascertain the exact position of the parapophyses in adult material but juvenile or embryonic specimens of *Phyllurus*, *Peropus*, *Oedura*, *Nephrurus*, *Ebenavia*, *Hemidactylus*, *Lepidodactylus* and *Aristelliger* showed the parapophyses to be situated on the neural arch alone.

Dorsal to the articulation there is a ligament connecting the shaft of the rib to the neurapophysis, below the level of the zygapophyses. There is sometimes a small tubercle, or diapophysis on the neurapophysis at the point of attachment of this dorsal ligament. Ventral to the articulation there is a ligament connecting 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 region of the trunk (Fig. 5A, c). The insertions of the dorsal ligament move higher up the neural arch and out along the rib shaft respectively, while a change takes place in the relative importance of the two branches of the ventral ligament. In the cervical region the main part of the ventral ligament is attached to the intercentrum, whereas in the anterior dorsal region the branch to the centrum becomes the major one, and the branch to the intercentrum gradually disappears altogether.

The lacertilian rib is typically holocephalous, and Romer (1956) maintained that the head of the rib probably consists of the fused tuberculum and capitulum. Such an interpretation is doubted in the case of the New Zealand geckos, in which a ligamentous band was found to connect the shaft of the rib to the neural arch (Stephenson & Stephenson, 1956). This band, when sectioned, was found to be distinctly bony. Noble (1921) found a cartilaginous or fibrocartilaginous band in *Sphaerodactylus*, a cartilaginous band in *Lathrogecko*, *Lepidoblepharis* and the neotropical species of *Gonatodes*, and a ligament in all the other lacertilians he examined. Both Noble and the Stephensons believe that this dorsal ligament is a reduced tuberculum and the head of the rib the capitulum.

The neural spines of the dorsal region are fairly constant in size and shape, with the occasional exception of the spine belonging 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 fuscus* (Fig. 5c).

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 for the insertion of muscles and ligaments. The neural spines of *Phyllodactylus*, though tall, are triangular in lateral view, with the crest or ligament attachment area 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. 6 indicates the major variations in the size and shape of the neural spines and their crests.

Romer (1956) suggested that the relative size 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 has very tall neural spines. *Phyllodactylus güntheri* is smaller again, but it too possesses tall neural spines. The crests in this species however are comparatively small. Hence it seems that, in the available material at least, the size of the ligament insertion, rather than the size of the spine as a whole, may be correlated exponentially with the absolute size of the animal. This correlation appears to be valid only in those species whose adult presacral column exceeds 60 mm. In species smaller than this, the size of the ligament insertion seems to be constant relative to the size of the vertebra.

Lying ventrally between successive centra of the dorsal region are discrete intercentral elements, which are oval plates of bone attached to the intervertebral cartilage. The intercentra of the dorsal region are typically flat, unlike the more anterior cervical intercentra which bear a hypapophyseal spine. Only in *Gonatodes*, *Aristelliger* and *Hemidactylus* were there hypapophyseal spines on the intercentra belonging to the dorsal vertebrae; they occur on the first few intercentra of the series, and decrease in size posteriorly so that the more posterior intercentra are the typical flat discs of bone.

#### *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 varied between one and three.

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 the vertebra; that is, there is no clearly defined rib-head articulating with the parapophysis, and the ligaments lying above and below the articulation are absent. Instead the rib element may be ankylosed to the parapophysis 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 splint or knob of bone.

In general the vertebra immediately before 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. In such cases the ribs of the second vertebra are almost always reduced further than those of the first. Only two exceptions, both *Phyllurus platyrus*, 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 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.

#### *Sacrum* (Figs. 7 and 8)

In the majority of geckos two vertebrae are modified for the support of the pelvic girdle. According to Romer (1956) two sacral vertebrae are typical of eosuchians and rhynchocephalians and occur in all lizards with well-developed limbs. In *Phyllurus platyrus*, however, occasional specimens have three sacral vertebrae. Three sacrals seem typical of *Nephurus laevis*, occurring in four out of five specimens examined, while four sacrals were present in one specimen of *N. asper*.

Each sacral vertebra bears a pair of large processes, usually referred to 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 proxi-

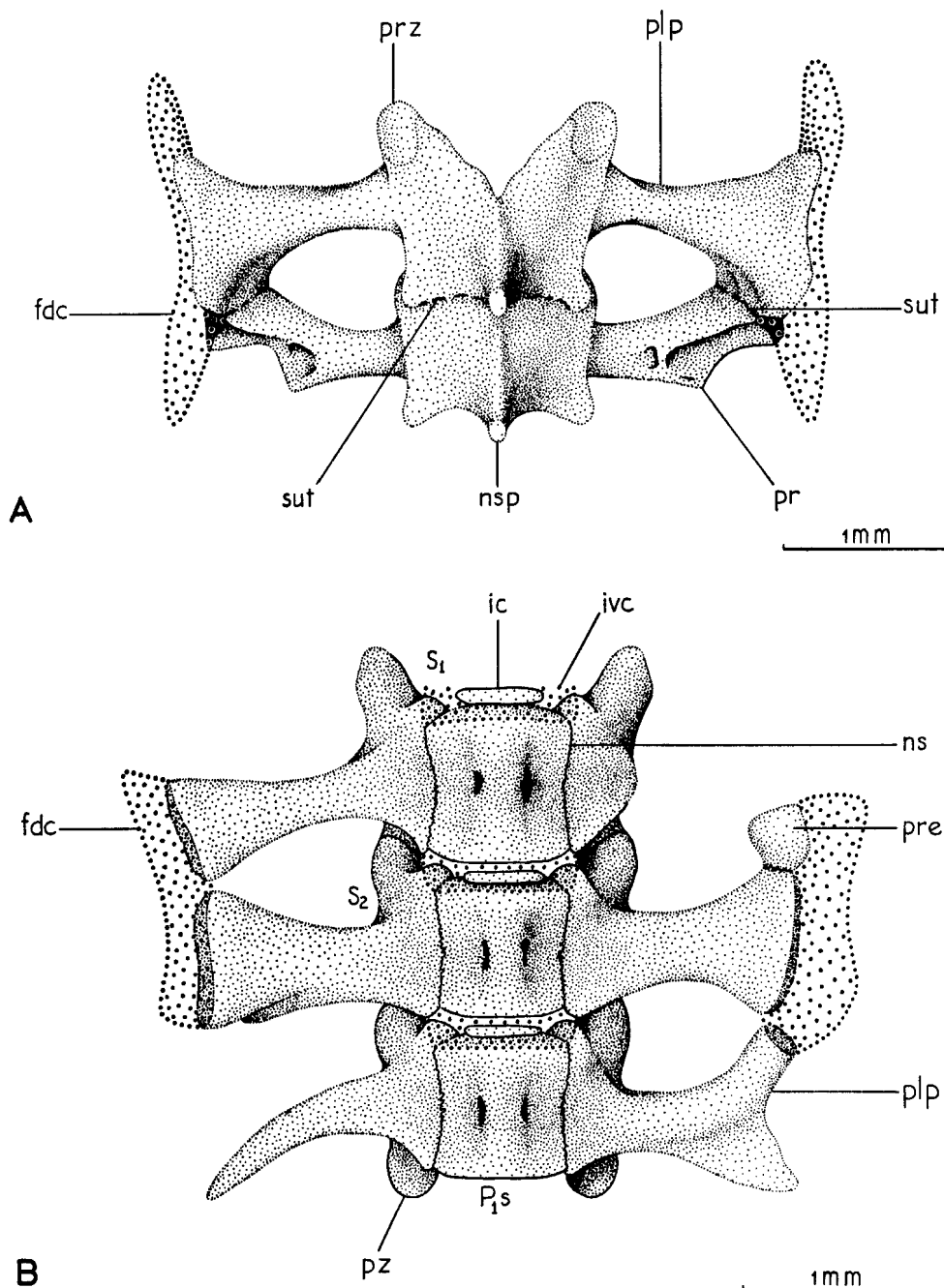


FIG. 7.—Sacral vertebrae.

A. *Gonatodes fuscus* adult, dorsal view.B. *Phyllodactylus 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. *plp*, pleurapophysis. *p1s*, first pygal vertebra incorporated into sacrum. *pr*, process on pleurapophysis of second sacral vertebra. *pre*, proximal rib element. *prz*, prezygapophysis. *pz*, postzygapophysis. *s1*, *s2*, sacral vertebrae. *sut*, suture.

mal shaft. The cartilaginous portions of the sacral processes on each side of the column fuse into a single mass which takes the form of a large expanded blade.

There has been considerable controversy in the past regarding the nature of the sacral 'transverse processes' in the Lacertilia, but the current opinion is that they consist of fused parapophyses and rib elements and should therefore be termed 'pleurapophyses'. Moodie (1907) maintained that 'there are no sacral ribs in modern lizards. The ilia are always attached directly to the transverse processes of the two sacral vertebrae'. However, in a subsequent paper (1909), Moodie considered that a study of the stages of chondrification may indicate the presence of sacral ribs, and El-Toubi (1947) and Kamel (1951) reported the undoubted presence of sacral rib elements in *Agama stellio* and *Chalcides ocellatus* respectively. Nevertheless some recent workers, including Mahendra (1950) and Romer (1956), still maintain that lizards have no sacral ribs.

Kamel (1951), describing the sacral region of *Chalcides ocellatus* in embryos varying in length from 14 to 45 mm., found that 'sacral ribs are quite distinct and separate from the transverse processes. Each rib is a compound one formed from a dorsal (proximal) rib rudiment and a ventral (distal) rib rudiment which fuse early in the connective tissue stage'. The sacral rib chondrifies and unites with the transverse process of the first sacral vertebra. Kamel maintains that this rib fuses to the transverse process of the following vertebra as well and articulates with the ilium. According to Kamel's description, the transverse processes (or more accurately, parapophyses) from 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 fusing to the vertebra during early embryonic stages. However, the construction of the gekkonid pleurapophyses differs considerably from that described by Kamel (1951) in *Chalcides ocellatus*. Direct evidence for the occurrence and structure of the sacral ribs in geckos comes from two juvenile specimens of *Nephurus* (*N. asper* (Fig. 8A) and *N. laevis*) and from a juvenile specimen of *Phyllodactylus marmoratus* with an abnormal sacrum (Fig. 7B). In the two specimens of *Nephurus* faint sutures were present on the proximal bony shaft of all four and three pairs of pleurapophyses respectively. The portions of the pleurapophyses lying distally to these sutures thus constitute the sacral ribs. The specimen of *Phyllodactylus* 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 pleurapophysis. There is little doubt that this element is the proximal portion of a rib which, owing to the abnormal development of the sacrum, has not become connected to its vertebra.

It is apparent then that sacral ribs occur in geckos, and that they consist of proximal bony and distal cartilaginous portions like the more anterior presacral ribs. The proximal portion of each rib constitutes the greater part of the bony shaft of the sacral pleurapophyses, while the distal portions of the ribs on each side of the body fuse together to form the mass of cartilage apposing the ilium. Calcification of this cartilage often takes place in adult geckos, and there is usually a calcification centre to correspond to 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 gekkonid sacral ribs to their vertebrae must occur during the early stages of embryonic development, in most genera no later than the cartilaginous stage, since sutures between rib and vertebra are so rarely found, even in newly hatched specimens. In the youngest specimen examined, a serially sectioned embryo of *Peropus variegatus* whose notochord was still continuous between the odontoid process and the skull, there was no sign of a suture between the sacral rib and the vertebra. Yet in juvenile geckos the three components of the innominate bone of the pelvis are clearly distinguishable from one another, even though perichondral ossification is well advanced. In *Sphenodon* fusion of the sacral ribs to their vertebrae

takes place much later than it does in geckos. In juvenile specimens with advanced perichondral ossification there is still a distinct suture between each sacral rib and its neural arch and centrum. Fusion of the distal cartilaginous portions of the sacral ribs takes place in *Sphenodon* (Howes & Swinnerton, 1901), as it does in geckos.

Although the number of sacral vertebrae varies in the geckos, the most anterior is almost invariably the largest in both size of the body of the vertebra and the size of the pleurapophyses. 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 platurus*, 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 *Nephrurus* 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 vertebra in 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 of these one or both of the pleurapophyses of the first pygal were joined to the distal cartilage of the sacral pleurapophyses of the same side by a ligament.

Moodie (1907) implies that the more anterior sacral vertebra of lizards, by reason of its size, represents the original element for the support of the pelvis. Whether or not such a suggestion can be verified, it is at least very 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 vertebrae. In the other two *N. asper* the pygal pleurapophyses attached to the sacrum were curved anteriorly, while the unattached pleurapophysis extended laterally in the normal manner. Probably the third sacral vertebra typical of *Nephrurus* has been incorporated from the caudal series in a like manner, particularly as the pygal count in *N. laevis* is typically four, instead of five as in other geckos. Nevertheless an interdependence of sacral and pygal numbers cannot be accepted without reservation, since 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 (Stephenson & Stephenson, 1956).

Fusion of the bony shafts of consecutive sacral pleurapophyses occurs in a number of gekkonid genera. The more common condition is that found in *Phyllurus*, *Oedura*, *Sphaerodactylus* and *Aristelliger*, in which the shafts fuse just before joining the mass of articular cartilage, and often have a suture between them. Juveniles of these species do not have the fused condition. Old specimens of *Nephrurus* and the single specimens of *Carphodactylus* and *Gonatodes* (Fig. 7A) showed considerable fusion of the shafts, while juvenile *N. asper* (Fig. 8A) have the fused condition typified by *Phyllurus*, *Oedura*, *Sphaerodactylus* and *Aristelliger*. Only in *N. asper* did this juvenile fusion occur, and it appears to increase with age. In the remaining genera the pleurapophyses on each side 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 the reduction of the intercentrum between them. Some constriction of the notochord occurs in such vertebrae, and in amphicoelous forms the concave faces of the centra tend to be flattened. The intercentra lying between the sacral vertebrae may fuse with the margins of adjacent centra, but usually they remain as small, discrete elements, attached loosely over the suture. In the genus *Nephrurus*, which usually possesses more than two sacral vertebrae, the tendency for fusion is greatest between the first two vertebrae of the series. In the single adult specimen of *Gonatodes* (Fig. 7A) and in adult *Nephrurus*, not only have the centra fused, but the neural



arches are also fused and the suture is partially obliterated. In juvenile *Nephurus* the arches were still separate dorsally, but the zygapophyses were reduced.

The second pair of sacral pleurapophyses varies in shape among the geckos. Two distinct conditions have been recorded so far, and it appears that only one of them occurs in each genus. In the majority of Australian genera 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 cartilaginous blade (Fig. 8A). 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. 7A). The function of the processes is a matter for conjecture, but they probably provide a greater surface for the insertion of muscles, and may strengthen the sacrum as a support for the pelvic girdle. There was no indication in any of the geckos examined, of a transitional state between the smooth shaft and the shaft with a large process; the process was either very well developed or absent altogether. It was present in *Heteronota*, *Peropus*, *Phyllodactylus*, *Hemidactylus*, *Gekko*, *Lepidodactylus*, *Aristelliger*, *Gonatodes*, *Sphaerodactylus* and *Afroedura*. Of these genera, only the first four have Australian representatives. All the non-Australian genera examined, with the exception of *Hoplodactylus* and *Nautilinus* from New Zealand, possessed the thin projecting plate on the posterior border of the second sacral pleurapophysis, and it is also present in the Indian house-gecko *Hemidactylus flaviviridis* (Mahendra, 1950).

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. It is probable that the cartilage of the pleurapophyses serves not only for the insertion of ligaments but also as a cushion between the sacrum and the pelvic girdle.

#### *Postsacral (Caudal) Vertebrae (Fig. 8)*

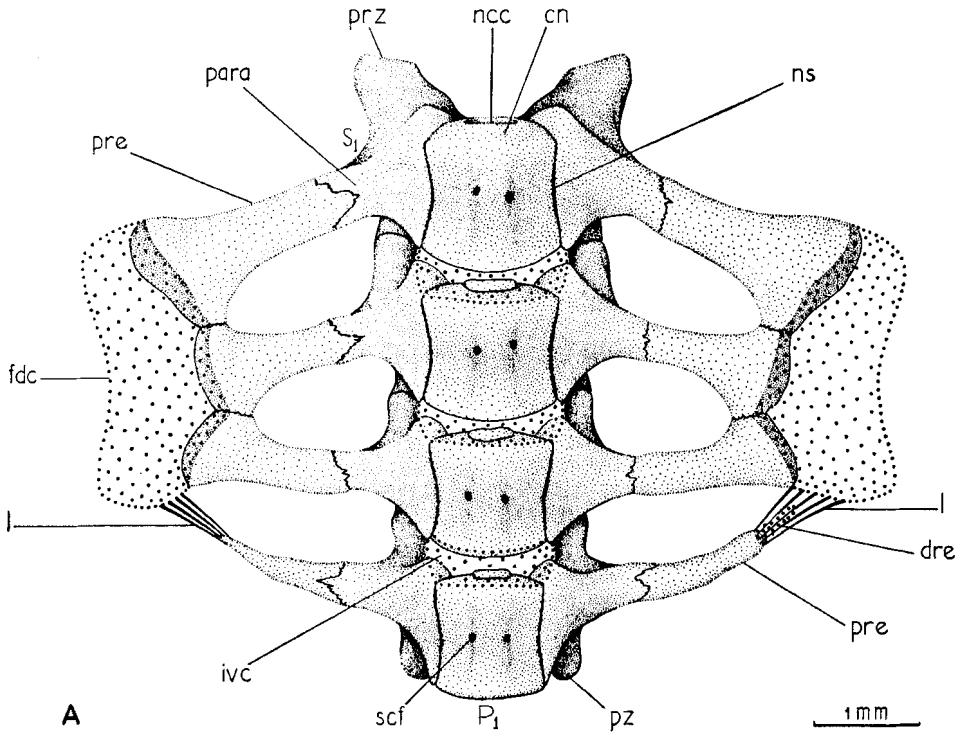
The caudal vertebrae in most geckos can be divided into two distinct regions—the pygal and the postpygal series. The pygal vertebrae lie immediately behind the sacrum; they are short and broad like the presacrals and contain no fracture planes; they serve to protect the cloaca in the event of autotomy and to support the basal region of the tail. The postpygal vertebrae typically contain the fracture planes; they gradually become elongated and their processes become smaller, until in the posterior part of the tail the processes are so small as to become virtually non-functional. *Nephurus asper* was the only species in which the tail did not consist of pygal and postpygal regions, 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 species, while the remaining 17 are devoid of neural spines and pleurapophyses. The neural arches of the first nine caudal vertebrae articulate by means of zygapophyses; the ninth vertebra has reduced and non-functional postzygapophyses.

FIG. 8.—Sacral and caudal ribs.

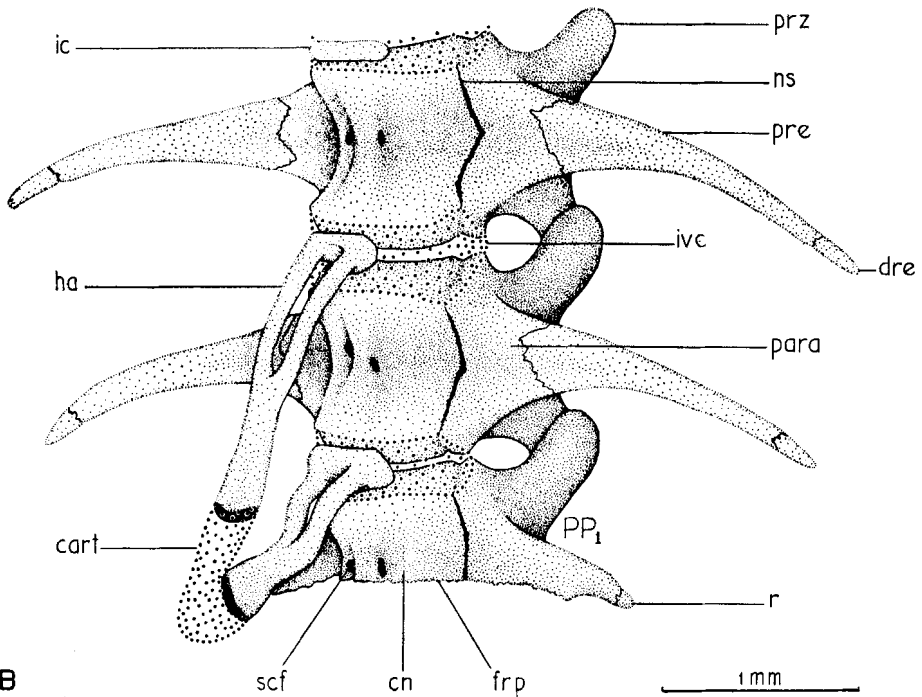
A. *Nephurus asper* juvenile, ventral view of sacrum.

B. *Phyllurus platurus* juvenile, ventro-lateral view of pygal and postpygal vertebrae.

*cart*, uncalcified cartilage. *cn*, centrum. *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. *para*, parapophysis. *p<sub>1</sub>*, first pygal vertebra. *pp<sub>1</sub>*, first postpygal vertebra. *pre*, proximal rib element. *prz*, prezygapophysis. *pz*, postzygapophysis. *r*, rib. *scf*, subcentral foramen. *s<sub>1</sub>*, first sacral vertebra.



A



B

FIG. 8.

The remaining 13 vertebrae are small cylinders of bone, completely devoid of processes, and are joined together only by the intervertebral cartilage.

The pygal vertebrae in the geckos examined, apart from *Nephurus asper*, are usually five in number, although four or six pygal vertebrae occur occasionally (see Tables I and II). Mahendra (1950) records five pygals for *Hemidactylus flaviviridis*. Only in the Australian species *Nephurus laevis* and *Phyllurus milii* and in the New Zealand genera are the pygal vertebrae typically four in number.

Throughout the material examined, again excluding *Nephurus asper*, there were fracture planes present in at least two of the postpygal vertebrae. There are septa in all the postpygal 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 possess this condition are *Nephurus laevis* and the three species of *Phyllurus*. When autotomy occurs in these cases the whole of the postpygal region is lost, except occasionally for the most anterior postpygal vertebra. This arrangement appears to be a specialized condition peculiar to these geckos. In *Sphenodon* and in the Permian reptiles discussed by Price (1940), caudal autotomy may occur in any of the postpygal vertebrae, and this condition would no doubt be recognized as the primitive one.

Each fracture plane passes through the middle of the vertebra, through or behind the pleurapophyses, and posteriorly to the paired subcentral foramina; it completely divides the vertebra into two halves. According to Woodland (1920), complete division of the postpygal vertebrae also occurs in *Hemidactylus flaviviridis*. In this gecko the vertebral cleavage planes are marked by simple septa of a hyaline matrix bordered by connective tissue, which traverse and separate into segments the entire substance of the tail, with the exception of the spinal cord, nerves and blood-vessels.

The vertebrae of the gekkonid tail lack articulating ribs, but bear well-developed pleurapophyses on the neural arch pedicels. A number of specimens, representing several species, were observed to have a suture across these processes. The 'transverse processes' are therefore not wholly derived from the neural arch, as their name implies, but are composed of rib elements as well and should therefore be known as pleurapophyses. Several juvenile specimens had two faint sutures across each pygal pleurapophysis (Fig. 8b), indicating that both the proximal and distal rib elements were present in each process. In the other specimens with caudal ribs, including a juvenile specimen of *Oedura lesueurii* that was sectioned transversely, only a small rib element at the end of each pleurapophysis could be detected.

Romer (1956) stated that no ribs are reported as present in the tail of lizards, even though El-Toubi and Khalil (1950) noted the presence of caudal ribs in the Egyptian geckos *Tarentola* and *Ptyodactylus*. In these animals the ribs occurred only on one side of the body, the combined rib and process from the vertebra being equal in length to the corresponding undivided process on the opposite side. The New Zealand geckos *Hoplodactylus* and *Naultinus*, described by Stephenson & Stephenson (1956), possess a bilateral disposition of caudal ribs. Although it cannot be determined, even from juvenile specimens, whether a single rib element on each pygal pleurapophysis is serially homologous with the proximal or distal portion of the presacral ribs, it is at least certain that it represents, as a vestige, the well-developed caudal ribs found in ancestral tetrapods.

The caudal intercentra typically bear Y-shaped chevron bones or haemal arches. The most anterior chevron bone may be a complete arch produced ventrally into a spine, which may or may not be tipped with cartilage, or it may consist of two parallel shafts, the haemal arch pedicels, which have failed to fuse together. These shafts are always completely bony and are sometimes very short. In nearly all the specimens

in which the first chevron bone was a complete arch, it was more slender and often shorter than the following one.

The first of the haemal arch elements usually lies between the third and fourth pygal vertebrae, but variation in the location of this first arch occurs within and between species. In *Phyllurus platurus* the first chevron tends to lie between the fourth and fifth pygal vertebrae in those specimens in which there are two sacral and five pygal vertebrae, and between the third and fourth in those specimens with three sacrals and four pygals. The position of the first chevron in *Oedura lesueurii* seems to vary independently of the sacral and pygal counts; it may be between the second and third, or third and fourth, pygal vertebrae, whereas the sacral count is always two. In *Nephruroides*, the first chevron was found invariably between the third and fourth pygals even though the sacral count was occasionally two or four instead of the typical three. In the specimen with four sacral vertebrae, the first chevron consisted of a pair of bony nodules on the intercentrum.

In adult specimens of two of the genera examined, *Phyllurus* and *Nephruroides*, the two haemal arches preceding the first fracture plane were joined together (Fig. 8B). The connection was achieved by a bridge of cartilage, consisting of the conjoined cartilaginous processes of the two haemal spines. Very occasionally the bony shafts themselves are fused together. Only four other specimens had the last pygal and the first postpygal haemal spines connected by cartilage:—one of the 32 specimens of *Oedura lesueurii*, the single specimens of *Carphodactylus laevis*, *Sphaerodactylus parkeri*, and *Rhynchoedura ornata*. This junction of the spines may be a modification to increase the rigidity of the pygal region, and hence to protect the cloaca, in the event of autotomy. Since the condition occurs largely among those species which lose the whole of the postpygal region when autotomy takes place, it may be that there is more strain on the pygal region in these forms than there is in species whose tail can break through any one of the postpygal vertebrae.

In addition to the junction of the last pygal and the first postpygal haemal spines in *Phyllurus* and *Nephruroides*, further strength is imparted to the pygal region by the enlarged neural spine of the last pygal vertebra. Neither the body of the vertebra nor the pleurapophyses are in any way enlarged; in fact, they continue the trend for reduction in size posteriorly shown by the more anterior pygal vertebrae. But, whereas the more anterior pygal neural spines slope posteriorly as usual, the one immediately preceding the first plane of fracture is vertical and much stouter than those before it. The haemal arch immediately preceding the first plane of autotomy, i.e. the first postpygal chevron bone, may also be enlarged.

In all the geckos examined, apart from *Nephruroides asper*, the postpygal vertebrae rapidly elongate, and their neural spines, pleurapophyses and zygapophyses become smaller, so that in the end of the tail the vertebrae consist of long, narrow cylinders of bone joined together by elongated tubes of intervertebral cartilage. The chevrons persist as well-developed processes farther posteriorly than the other processes of the vertebrae, although they do not reach the extremity.

After autotomy a new tail is regenerated, but it differs in many ways from the original tail. One of the most important differences is that the regenerate completely lacks vertebrae, the axial skeleton being a tube of cartilage surrounding the spinal cord. In all the specimens with regenerated tails, the cartilaginous tube was calcified anteriorly at its junction with the last half vertebra of the column. Only in *Hemidactylus* was the tube found to be calcified throughout its length, and as in *H. flaviviridis* (Woodland, 1920), only the inner and outer surfaces of the tube were calcified.

#### *Subcentral Foramina* (Figs 6, 7, 8 and 9)

Situated midventrally on the centrum of geckos, on either side of the midline, is a pair of small foramina. Such foramina were present in all the specimens examined

personally, and have also been recorded in the Indian house-gecko *Hemidactylus flaviviridis* (Mahendra, 1935 a, 1950), and in the New Zealand geckos *Hoplodactylus* and *Nautilinus* (Stephenson & Stephenson, 1956). The only centrum throughout the column to lack the paired foramina is the atlantal centrum, which has become modified as the odontoid process of the axis. Each aperture in the remaining vertebrae leads to a canal which pierces the body of the centrum, passing to the side of the chordal canal, and opening by a second foramen into the neural canal. Serial sections of

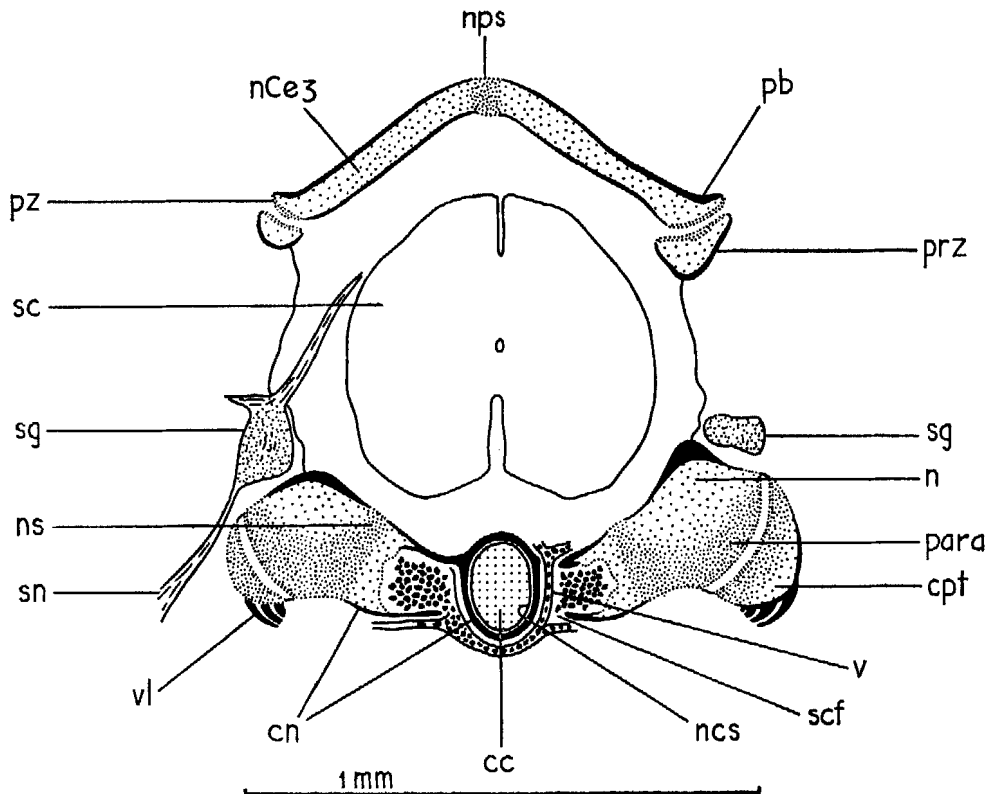


FIG. 9.—*Oedura lesueurii* juvenile, T. S. fourth cervical vertebra.

cc, chordal cartilage. cn, centrum. cpt, capitulum of rib. n, neurapophysis. nCe3, neurapophysis of third cervical vertebra. ncs, notochordal sheath. nps, neurapophyseal suture. ns, neurocentral suture. para, parapophysis. pb, perichondral bone. prz, prezygapophysis. pz, postzygapophysis. sc, spinal cord. scf, subcentral foramen. sq, spinal ganglion. sn, spinal nerve. v, vein, vl, ventral ligament.

embryonic *Peropus variegatus* and juvenile and adult *Oedura lesueurii* (Fig. 9) show that veins pass from the neural canal into the centrum and emerge ventrally from the subcentral foramina. The arteries supplying the spinal cord enter the neural canal alongside the spinal nerves, passing through the space between adjacent neural arches.

The occurrence of foramina in the vertebral centrum is not restricted to the Gekkonidae; similar apertures have been recorded in a number of reptilian groups. Possibly the oldest reptile known to have apertures in the centrum was the problematic reptile from the Upper Permian described by Parrington (1956), who was not able to name the animal from the available fragments, but who nevertheless considered it to be a representative of a very early radiation of the diapsids. The foramina in

this reptile were laterally placed on the centrum. At the time, Parrington described them as 'probably nutritive and may have been concerned with the persistent notochord'.

Camp (1923) described a pair of apertures in the centrum of the Pygopodidae, Amphisbaenidae and Xantusiidae as well as in the Gekkonidae, and maintained that these apertures undergo reduction in the more advanced groups of lizards. Foramina have also been found in the centrum of the Typhlopidae. Mookerjee & Das (1933) described a single aperture in *Typhlops braminus* near the anterior margin of the centrum. According to these authors, branches of the vertebral artery anteriorly and of the dorsal aorta posteriorly enter the neural canal via the apertures in the centra, instead of passing through the intervertebral spaces along with the spinal nerves. Mookerjee & Das stated that the mode of development of the foramina was not known, but suggested that after the formation of the artery supplying blood to the body of the vertebra, the ossifying centrum failed to constrict the vessel, leaving an unossified space for it to pass through the body of the vertebra to the spinal cord. In the Australian species, *Typhlops nigrescens*, as observed personally, there is a pair of foramina in the centrum. Zangerl (1945) noted the presence in the Amphisbaenidae of paired foramina situated ventrolaterally in the anterior half of the centrum, but did not suggest their function. In a juvenile specimen of *Sphenodon* which was available for investigation, it was noted that there is a pair of apertures in the centrum in the same position as those of the geckos; those in the sacral vertebrae particularly are very large, and together occupy a large proportion of the ventral surface of the centrum. Howes & Swinnerton (1901) stated that the apertures in juvenile *Sphenodon* are the regions where the cartilaginous expansions of the centrum are being absorbed during ossification. There is no mention by these authors of blood vessels passing through the foramina.

Additional apertures have been found in the vertebrae of a number of geckos, occurring ventrally in the bases of the pleurapophyses of the sacral and pygal vertebrae. Specimens from the following species are noted to possess these apertures:—*Ebenavia horni*, *Oedura marmorata*, *Peropus variegatus*, *Phyllurus platurus* and *Lepidodactylus lugubris*. Additional foramina were also present in the axial arch pedicels and intercentrum of one specimen of *Phyllurus platurus*. The function of the additional apertures in the vertebrae of geckos is a matter for conjecture, particularly as they occur only in occasional specimens.

#### AMPHICOELY AND PROCOELY IN THE GEKKONIDAE

Two facts arising from this study of the gekkonid vertebral column help to clarify the relationship between amphicoelous and procoelous geckos. The first is that an Australian species, *Phyllurus milii*, is found to be procoelous whereas the other species of the same genus are amphicoelous; the second is that the procoelous vertebrae of *P. milii* and those of the Jamaican species, *Sphaerodactylus parkeri*, resemble one another very closely, and are not far removed from the amphicoelous condition.

In both these procoelous forms the notochord extends without interruption from the odontoid process of the axis to the tail, just as it does in the amphicoelous geckos, and discrete intercentra are present throughout the column. The procoelous geckos differ from the amphicoelous forms in possessing a rounded condyle on the posterior end of the centrum. It is evident that there is no great morphological change involved in the transition from amphicoely in geckos to the type of procoely seen in *P. milii* and *S. parkeri*.

When the vertebrae of *Phyllurus milii* and *Sphaerodactylus parkeri* are compared with one another and with the most closely related amphicoelous geckos available, namely *P. platurus* and *P. cornutus*, it is evident that they form an evolutionary sequence. The type of procoely found in *P. milii* is not as advanced as that of *S. parkeri*, and is important as an intermediate procoelous stage. This, of course, does

not imply a close relationship between *Phyllurus milii* and *Sphaerodactylus parkeri*. On the grounds of distribution and other morphological features a close relationship is very unlikely. Nevertheless it does appear that procoely has arisen in the same way in both forms, although the condition is less advanced in *P. milii* than it is in *S. parkeri*.

Several theories have been propounded in the past to explain the transition from amphicoely to procoely in reptiles. Goodrich (1930) maintained that 'in reptiles with procoelous vertebrae the central cartilage develops greatly posteriorly, and eventually completely obliterates the notochord intervertebrally. The bulk of this posterior region of the centrum forms the convexity of the adult vertebra'. Both *Phyllurus milii* and *Sphaerodactylus parkeri* appear to have achieved procoely in this way, except that they have not lost the intervertebral notochord. The stages by which procoely has evolved in these geckos are probably as follow.

The cartilage of the centrum grows out posteriorly to form a condyle, without at first constricting the notochord. As the condyle increases in size it is invaded by endochondral ossification from the body of the centrum, and begins to constrict the notochord within it, while a similar but less marked constriction is occurring in the anterior end of the centrum. The constriction in the ends of the vertebra itself results in the reduction of the chordal diameter within the ring of intervertebral cartilage, while the anterior constriction also allows the formation of the bowl-shaped concavity which articulates with the condyle. Procoely in *P. milii* and *S. parkeri* is thus achieved without the loss of the intervertebral notochord and without any apparent change in the nature and function of the intervertebral cartilage.

The most noticeable feature of the procoelous vertebrae of *Phyllurus milii* and *Sphaerodactylus parkeri*, apart from the presence of the intervertebral notochord, is the fact that chordal constriction occurs within the vertebra itself. Constriction of the notochord *intervertebrally* is apparently dependent on its prior constriction *intravertebrally*.

Camp (1923) suggested that 'the differences between procoelous and amphicoelous geckos probably include the elimination of the intercentral chorda by the constriction and thickening of the intervertebral disc (intervertebral cartilage), which becomes reduced, rounded, and attached anteriorly to form a small condylar ball'. Romer (1956) expressed a similar view. This theory in no way applies to *Phyllurus milii* or *Sphaerodactylus parkeri*, since in these forms the procoelous condition of the vertebrae coexists with a continuous notochord and with the apparently unaltered intervertebral cartilage.

Although it is generally accepted today that procoely in lizards has evolved from amphicoely, it has been suggested only recently that in geckos the reverse is true, i.e. that procoely gave rise to amphicoely (Underwood, 1954; Romer, 1956). Underwood's suggestion that procoely in geckos is the ancestral condition, and that amphicoely is secondary to it, was the logical outcome of his proposed classification of geckos based largely on ophthalmological characters. Investigation of the vertebral morphology of geckos fails to support this proposal, since the amphicoelous condition shows no sign of being secondary or degenerate. On the contrary, the evidence points to the primitive nature of gekkonid amphicoely. As Underwood (1955) later pointed out when retracting his initial view, there was considerable radiation of amphicoelous definitive lizards during the Triassic, long before the fixation of the procoelous condition.

Today, of all the geckos which constitute the widely distributed gekkonid group, only a small minority are procoelous. Underwood (1954) lists only ten genera as being procoelous out of a total of more than 70 genera. Of the ten procoelous genera, five have a strictly New World distribution on the islands and mainland of the Caribbean area, one genus extending into Peru. These five genera Underwood grouped together on the basis of eye and vertebral structure, into the Family Sphaerodactylidae

of the Superfamily Gekkonoidea (= Gekkota). The other five procoelous genera together have a much wider distribution, ranging completely round the world, between the equator and the northern temperate zone. Underwood (1954) grouped these last five genera in the Family Eublepharidae of the Superfamily Gekkonoidea, using ophthalmological characters as well as procoely to distinguish them. Boulenger's (1885) Family Eublepharidae of the Lacertilia Vera included three procoelous genera, of which two, *Eublepharis* and *Coleonyx*, were also placed by Underwood in his family of the same name. Boulenger considered that the extraordinary distribution of so few representatives of this small family indicates the former existence of some ancient, more generally dispersed group. This group was probably procoelous since the existing forms resemble one another so closely, not only structurally but in the pattern of coloration as well.

Nevertheless it does not follow from this that procoely antedated amphicoely in geckos. Camp (1923) in his classification of the lizards, attempted to evaluate characters with regard to their reliability as indicators of primitiveness. He assigned comparative rank (palaeotelic value) to 34 characters, and considered that a group with few characters of high antiquity may be regarded as more ancient than a group with more characters of lesser palaeotelic value. The first two characters listed in decreasing order of palaeotelic value are (1) three complete branchial arches, and (2) vertebrae amphicoelous. The most primitive of living geckos described to date are believed on osteological grounds to be the New Zealand genera *Hoplodactylus* and *Nautilinus* which have, among other primitive features, two of the three branchial arches reaching the skull and amphicoelous vertebrae (Stephenson & Stephenson, 1956). In *Nautilinus* two complete arches reach the skull. The only other gecko with a hyobranchial skeleton comparably primitive with that of *Nautilinus* is *Coleonyx* which is procoelous.

It is possible that the ancestors of *Coleonyx* and related genera evolved procoelous vertebrae while retaining the primitive condition of the branchial apparatus, and subsequent evolution has led to the reduction of this apparatus in the majority of genera in both the procoelous and the ancestral amphicoelous groups. The New Zealand genera and *Coleonyx* would then be the modern geckos closest to the ancestral gekkonid stock, and of the two, the New Zealand genera would be the closer because of their amphicoely.

The group of geckos including *Sphaerodactylus* and related genera *Lepidoblepharis* and *Gonatodes* is described by Underwood (1954) as being procoelous. Noble (1921) however implies that *Gonatodes* is amphicoelous, and personal examination of *Gonatodes fuscus* confirms this. Despite the difference in the shape of the centrum, these three genera are closely related on other morphological grounds.

Noble maintains that a natural series commences with *Gonatodes*, leads through *Lathrogecko* and *Lepidoblepharis* to *Sphaerodactylus*, and that this series represents an actual morphogenetic sequence. The more important changes which occur in this series are the change in the vertebrae from amphicoelous to procoelous, and the loss of most of the intercentra. The genus *Sphaerodactylus* has the most advanced type of procoely in the group. The eighteenth vertebra of *S. macrolepis* illustrated by Noble has no intercentrum, nor has it an aperture in the condyle for the chordal canal. Yet one species, *S. parkeri* which was examined personally, not only retains the entire complement of intercentra, but also has the uninterrupted notochord diagnostic of notochordal amphicoelous geckos. It is obvious that no conclusions can be drawn regarding the position of *S. parkeri* in the scheme put forward by Noble until more information is available. Nevertheless the restricted distribution of the sphaerodactyline geckos, together with the existence of a series leading from amphicoely to procoely, points to the relatively recent evolution of procoely in this group.

The newly discovered example of gekkonid procoely is found in the Australian species, *Phyllurus milii*. As long as the species *milii* is recognized as one of the genus



*Phyllurus*, this example of procoely, in contradistinction to those of Noble (1921), is intrageneric. The other two species of *Phyllurus*, *P. cornutus* and *P. platurus*, also restricted to Australasia, are amphicoelous, and there is no other example of procoely among the Australian geckos. Examination of the external features and the osteology in general of *P. milii* has raised a doubt as to whether this species rightly belongs to the genus *Phyllurus*, but whether it does or not, the position regarding procoely remains unchanged. The closest relatives of this species, whether they are the other two species of *Phyllurus* or not, are amphicoelous Australian geckos. The type of procoely seen in *P. milii* is only slightly removed from amphicoely, so that it may be concluded that the evolution of procoely in this species has occurred most recently of all.

It is apparent then that procoely is not only secondary to amphicoely, but that it has evolved at least three times during the history of the geckos. It apparently evolved first in the ancestors of *Coleonyx* and related genera, which are commonly consigned to a separate family, the Eublepharidae. Procoely in the sphaerodactyline geckos appears to have evolved more recently, since a series still exists between amphicoelous and procoelous genera within this group. The most recent of all the cases of gekkonid procoely seems to be that exemplified by *Phyllurus milii*, which is one procoelous species within an otherwise amphicoelous genus.

The procoelous vertebrae of *Phyllurus milii* and *Sphaerodactylus parkeri* are very simple examples of procoely and may represent early stages in the development of the more advanced procoelous condition of other lizards, but it seems most unlikely that there has been a direct evolutionary line between procoelous geckos and other lacertilian groups. It seems more reasonable to assume that the three cases of procoely found to date among the Gekkonidae have not only evolved separately from one another, but are also independent of the procoelous condition in other lizards.

It has been a practice in the past to regard procoely as a major character in the classification of geckos. Procoelous forms have been considered distinct from the amphicoelous geckos despite any relationships they may have had with the latter. Noble (1921) for example, considered that the procoelous vertebrae of *Sphaerodactylus* agree in detail with those of *Lepidoblepharis* and *Lathrogecko*, which he termed eublepharids, but differ slightly from those of *Coleonyx*. He maintained that the genus *Sphaerodactylus* 'should no longer be ranged with the gekkonids, but should be grouped with *Coleonyx* in the Eublepharidae' and 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, even if a conservative one'. The Eublepharidae would then include the small group now represented by *Coleonyx* and related genera, which are widely dispersed and morphologically very similar, as well as the procoelous sphaerodactyline geckos which are restricted in distribution and still retain a closely related amphicoelous form. Noble considered that *Gonatodes*, which is amphicoelous, is more closely related to these procoelous sphaerodactyline geckos than to any other gekkonid, yet he upheld the placing of the procoelous genera among the Eublepharidae, leaving *Gonatodes* in the Gekkonidae.

If the family Eublepharidae is to be retained, it should contain only *Coleonyx* and related genera. Romer (1956) however proposed that all geckos should be placed in one family, the Gekkonidae, since the supposedly distinctive features of the Uroplatidae and Eublepharidae are not as marked as hitherto believed. Until conclusive evidence is found to support the subdivision of the geckos into separate families, it seems wisest to consign them all to the one family, the Gekkonidae.

The discovery that procoely has apparently evolved at least three times during the evolution of geckos, and that on two occasions its evolution has been relatively recent, makes it necessary to reconsider amphicoely as a character of primary importance in the classification of lizards. Within the Gekkonidae, it appears that at the specific and generic levels, amphicoely and procoely cannot be used as major distin-

guishing characters regardless of other morphological relationships. Despite its procoely, the species *Phyllurus milii* is more closely related to other amphicoelous Australian geckos than it is to *Coleonyx* or the sphaerodactyline geckos. So also are the procoelous sphaerodactyline genera more closely related to amphicoelous forms than they are to procoelous *Coleonyx*. At the familial level, however, amphicoely retains the palaeotelic importance Camp (1923) assigned to it. The Gekkonidae as a family are predominantly amphicoelous, and the only amphicoelous lizards belong to this family. Not only do the amphicoelous vertebrae of geckos retain the uninterrupted notochord, but at least two procoelous forms, *Phyllurus milii* and *Sphaerodactylus parkeri* do so as well. The apparent lack of profound morphological change in the transition from amphicoely to procoely among geckos means that procoely may not be used alone to distinguish subfamilial groups, but it does mean that the palaeotelic weight of notochordal amphicoely when applied to the Gekkonidae as a family, retains its importance. Despite the occurrence of procoely in some geckos, the vertebrae of the Gekkonidae are the most primitive of all lizards.

The structure and distribution of geckos suggest on the whole that these lizards form a very old, if not the most ancient group of living lacertilians. In vertebral morphology alone there are a number of characters accepted as primitive which, when assessed together, lead to this conclusion. 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 is fibrocartilaginous, cartilaginous or even ossified, and is considered to represent a reduced tuberculum (Noble, 1921; Stephenson & Stephenson, 1956). These characters together with the predominance of notochordal amphicoely, indicate the ancient nature of the Gekkonidae.

#### ACKNOWLEDGMENTS

To Dr N. G. Stephenson of the Department of Zoology, University of Sydney, I am deeply grateful for ungrudging advice and criticism, and for the loan of much of the necessary material. Thanks are also due to Dr B. Macmillan of the School of Public Health and Tropical Medicine, Mr H. G. Cogger of the Australian Museum, Miss A. G. C. Grandison of the British Museum (Natural History), Mr R. A. S. Barnard, lately of the Department of Zoology, University of Sydney, Mr D. Havenstein, lately of the Department of Geology, University of Sydney, and to the many people who have helped to supply material. I am indebted furthermore, to Professor P. D. F. Murray for his helpful suggestions.

During the preparation of this paper the author has received a stipend from the University of Sydney Research Grant.

#### SUMMARY

1. The systematic position of Gekkonidae is considered, and the need for careful assessment of basic criteria such as amphicoely and procoely is stressed.

2. The procoelous centra of *Phyllurus milii* and *Sphaerodactylus parkeri* are similar to one another and to those of amphicoelous geckos in possessing a continuous notochord, interrupted only at the atlanto-occipital joint, and the full complement of intercentra, but differing from amphicoelous forms in that they bear a rounded condyle posteriorly.

3. Tables of vertebral counts made on 151 geckos, representing 20 genera and 31 species are given.

4. The laterally projecting processes on the atlantal neurapophyses are considered to be serially homologous with the postzygapophyses of following vertebrae; the low processes on the arch pedicels are regarded as parapophyses.

5. The axial neurapophyses bear parapophyses and reduced prezygapophyses.

6. Rudimentary ribs may occur on the third cervical vertebra. The ribs of the fourth, fifth and sixth vertebrae usually bear cartilaginous processes inappropriately termed 'uncinate processes'. The triangular bony process on the proximal portion of the ribs of the seventh vertebra of some genera, also inappropriately termed an 'uncinate process', is considered to represent a state transitional between the ribs typical of the cervical and dorsal series. Presence of sacral and caudal ribs is confirmed.

7. Ribs normally are attached to the vertebra by means of an articulation between rib head and parapophysis of neural arch, and two ligaments, one above and one below the articulation. Dorsal ligament is considered to be homologous with the tuberculum, and rib head with capitulum.

8. In most geckos fracture planes occur in all postpygal vertebrae. Geckos with a distinct constriction in the tail at junction of pygal and postpygal series, have fracture planes only in this region; *Nephruroides asper* has no fracture planes at all. Last two conditions may be regarded as specialized.

9. In geckos with a constricted tail, the last pygal neural spine is enlarged, and the two chevrons immediately preceding the first fracture plane are joined together by a bridge of cartilage.

10. No great morphological change is required for transition from amphicoely to procoely in geckos, and amphicoely is regarded as ancestral to procoely. Procoelous vertebrae of *Phyllurus milii* and *Sphaerodactylus parkeri* are only slightly removed from the amphicoelous condition. There is no evidence of degeneracy in the vertebral column of amphicoelous geckos; living Gekkonidae as a whole are regarded as an ancient lacertilian group.

11. Procoely is considered to have arisen at least three times in the Gekkonidae—first, in ancestors of *Coleonyx* and related forms; second, in the series leading to *Sphaerodactylus*; and third in the Australian species *Phyllurus milii*. Probable course of evolution of procoely in geckos is described.

12. Arguments are presented against placing all procoelous geckos in one subgroup, the Eublepharidae, regardless of affinities with amphicoelous forms. Nevertheless amphicoely, in relation to geckos as a whole, is considered to retain the palaeotelic weight ascribed to it by Camp (1923).

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