

**Article XI.—CLASSIFICATION OF THE LIZARDS**

BY CHARLES LEWIS CAMP

## CONTENTS

	PAGE
INTRODUCTION.....	290
HISTORY OF SAURIAN CLASSIFICATION.....	291
SELECTION OF NAMES.....	295
OUTLINE OF CLASSIFICATION ADOPTED.....	296
SYNOPSIS OF CHARACTERS.....	297
REVIEW OF TAXONOMY AND PALEONTOLOGY.....	301
DISCUSSION OF THE PHYLOGENY.....	331
EVALUATION OF PALEOTELIC CHARACTERS.....	337
1. The Branchial Arches.....	339
2. Saurian Vertebrae.....	343
3. The Skull Arches.....	345
4. The Tabulare Question.....	346
5. Degeneration of Extremities and Girdles.....	351
6. The Lungs.....	355
7. Fusion of Median Skull Elements.....	356
8. The Prevomer.....	356
9. The Hemipenes.....	358
10. The Number of Cervical Ribs.....	359
11. The Postfrontal and Postorbital.....	360
12. The Lacrymal.....	362
13. The Mandibular Teeth.....	363
14. The Palatal Teeth.....	365
15. The Interclavicle.....	366
16. The Clavicle.....	368
17. The Throat Musculature.....	369
18. The Tongue.....	374
19. The Lower Jaw.....	375
20. The Caudal Chevrons.....	376
21. The Os Intermedium.....	376
22. The Body Musculature.....	377
22a. The Parasternum and Its Relations to the Xiphisternum and Sternum.....	386
23. The Epipterygoid.....	393
24. The Palate.....	394
25. The Pineal Foramen.....	394
26. The Dermal Scutes.....	395
27. The Squamation.....	398
27a. The Femoral Pores.....	401
28. The Shoulder Musculature.....	403
29. The Elevation of the Skull.....	404
30. The Os Hypoischium.....	405

	PAGE
31. The Patellar Sesamoids.....	408
32. The Sternal Fontanelles.....	409
33. The Scapulo-coracoid Emarginations and Fenestræ.....	411
34. The Endolymphatic Glands.....	414
DISCUSSION.....	414
RÉSUMÉ.....	416
Summary of Classification.....	416
Summary of Morphological Points.....	419
BIBLIOGRAPHY.....	422

### INTRODUCTION

The present paper is an attempt to define more fully the structural relationships of the Sauria. The views here expressed are the result of a correlation of previous investigation with certain efforts of my own touching upon morphology and paleontology, and the effort is made to furnish a more perfect historical and taxonomic picture, which, it is hoped, will aid studies and emphasize in outline certain developmental tendencies in a group which seems to be almost unequalled in the interesting number of convergent and parallel forms it comprises.

I have recently undertaken to determine the range of variation of the muscular system in the lizards and hope to publish the results of this work. Findings in myology thought to be of value in a taxonomic sense are included in the present paper.

After examination of the muscles of almost all parts of the body among representative adaptive and taxonomic types some features of the superficial body and throat musculature are believed to be indicative of relationship. The throat region exhibits complex "patterns" developed similarly in most of the superfamilies. These patterns result from an interdigitation of differently directed layers and bundles. In general, the style of the pattern cannot be considered as adaptive, though the size of various bundles comprising the pattern, their insertion on skin, mid-ventral raphe or hyoid, may be very directly so.

In addition, a series of thirty-odd characters has been selected, and a check made of the distribution of each among the families of the sub-order.

The material has been obtained mainly from the collections of the Department of Herpetology of the American Museum and my thanks are especially due to Miss Mary C. Dickerson, Dr. G. K. Noble, and Mr. Karl P. Schmidt for their generous interest, valuable counsel and the loan of important specimens for dissection.

Furthermore, Dr. Noble has permitted the use of a series of carefully cleared specimens including many geckos, a xantusid, an iguanid

and a teiid, which have proven useful in the osteological study of these small forms.

I am indebted to Drs. Thomas Barbour and Joseph Grinnell for loan of specimens from the collections under their charge.

A survey of the paleontological evidence as to the derivation of the Sauria and the history of the sub-groups has been thought indispensable, and this review has been extended by a study of Cretaceous, Eocene and Oligocene material from the collections of the Department of Palæontology of the American Museum and made available for my use through the kindness of Dr. W. D. Matthew and Mr. Walter Granger.

The late Professor Williston's manuscripts and well-known papers have been of the greatest help in allocating fossil genera and determining the nature of supposedly primitive characters among recent lizards.

The present work has been done under the supervision of Dr. W. K. Gregory and is due primarily to his inspiration. The author wishes both to properly acknowledge this and to thank him for his patience and his faithful interest in the slow growth of these results.

It is pleasant to record that the work leading up to the present paper and to other projects now in hand, dealing with the myology and adaptive radiation of the Sauria, has been made possible only through the generous facilities placed at my disposal in The American Museum of Natural History by its president, Professor Henry Fairfield Osborn. And I should also wish to acknowledge with warmest thanks the courtesy of the authorities of the University of California and Miss Annie M. Alexander who have kindly furnished the funds for concluding this research.

Most of the drawings are due to the excellent skill of Mrs. E. L. Beutenmüller. The plates have been lettered by Mr. William Belanske.

#### HISTORY OF SAURIAN CLASSIFICATION

Cope's synopsis of 1864 marked a turning point in knowledge of saurian relationships. Before this time a score of schemes had been proposed based chiefly upon the obvious characters of physiognomy, feet and limbs, tongue, squamation, and habits. The pre-Copeian period is in part reviewed in the first volume of Duméril and Bibron's '*Erpétologie Générale*,' 1834. Early systems which have contributed to present views are those of Brongniart (1800), Duméril (1807), Cuvier (1817), Merrem (1820), Latreille (1825), Gray (1825), Fitzinger (1826), Wagler (1830), Duméril and Bibron (1834-1854), Wiegmann (1834), Gray (1845), and Stannius (1856).

Cope's researches leading up to his first summary of results (1864) involved a consideration of many details of the osteology for the first time examined among lizards. His scheme formed the basis of Boulenger's conservative arrangement (1884) employed in the second edition of the British Museum Catalogue (1885-1887). Cope enlarged the field again in 1892 in a paper that formed the systematic basis of his 'Crocodilians, Lizards and Snakes of North America,' 1900,—a great body of morphological fact, considered from the taxonomic standpoint.

Baur, Boulenger, Fürbringer, Gadow, Williston, Stejneger, and many others cited in the text are well known for important recent contributions.

Boulenger (1884 et seq.) has not employed names for groups of lizards higher than the family. Gill (1886) in a review of Boulenger's system has attempted to supply superfamily divisions based on characters employed by Boulenger. Stejneger (1907) has in part followed the nomenclature of Gill.

The latest views of Cope (1900) are based on his own system of 1864 with modifications. He regards the serpents as related to the amphisbæniæ, the Xenosauridæ as related to the geckos and the geckos as degraded "in the characters of their vertebræ, for [he does] not believe this character to be of primitive origin." I have taken exception to these views, but I should support his arguments that the chameleons are modified agamidæ and that the pygopodids are diploglossids.

Cope recognized nine suborders (or superfamilies?) of the Sauria including twenty-four families. Certain ambiguities, for example, the double allocation of the Anniellidæ, make it impossible to determine just what were some of Cope's final opinions. The work (1900), unfortunately, had to be edited and published posthumously. The arrangement was:

Squamata (Subclass)	Helodermatoidea
Ophidia (Order)	Helodermatidæ
Pythonomorpha	Diploglossa
Sauria	Zonuridæ, Pygopodidæ, Anguidæ,
Rhiptoglossa (Suborder)	Xenosauridæ
Chamæleontidæ	Leptoglossa
Pachyglossa	Teiidæ, Xantusiidæ, Lacertidæ,
Agamidæ, Iguanidæ	Gerrhosauridæ, Scincidæ, Acon-
Nyctisaura	tiidæ, Dibamidæ, Anelytropi-
Eublepharidæ, Geckonidæ	dæ
Uroplatoidea	Annulati
Uroplatidæ	Anniellidæ, Euchirotidæ, Amphis-
Thecoglossa	bænidæ, Trogonophidæ
Varanidæ	



Cope regarded his *Pachyglossa* as ancestral to the *Rhaptoglossa*, *Nyctisaura*, and *Diploglossa*, and the latter as giving rise to the *Thecoglossa*, *Leptoglossa* and *Annulati*.

Fürbringer (1900) coincidentally with Cope proposes the following scheme:

Order Lacertilia

Suborder Lacertilia vera

Gens *Nyctisaura* s. *Geckonomorpha*

Fam. *Geckonidæ*, *Eublepharidæ*

Gens *Pygopodomorpha*

Fam. *Pygopodidæ*

Gens *Leptoglossa* s. *Autosauromorpha*

Superfam. *Scinco-Lacertæ*

Fam. *Scincidæ*, *Anelytropidæ*, *Dibamidæ*, *Gerrhosauridæ*, *Lacertidæ*

Superfam. *Teji*

Fam. *Tejidæ*, *Xantusiidæ*

Gens *Diploglossa* s. *Anguimorpha*

Superfam. *Zonuri*

Fam. *Zonuridæ*

Superfam. *Angues*

Fam. *Anguidæ*

Fam. *Anniellidæ*

Superfam. *Helodermates*

Fam. *Helodermatidæ*

Superfam. *Xenosauri*

Fam. *Xenosauridæ*

Gens *Pachyglossa* s. *Eunota* s. *Iguanomorpha*

Fam. *Telerpetidæ* (uncertain), *Iguanidæ*, *Agamidæ*

Gens *Gecko-Chamæleontes* s. *Uroplatimorpha*

Fam. *Uroplatidæ*

Suborder *Platynota* s. *Varano-Dolichosauria*

Gens *Varanomorpha*

Fam. *Varanidæ*

Gens *Dolichosauromorpha*

Fam. *Aigialosauridæ*

Fam. *Dolichosauridæ*

Suborder *Mosasauria*

Gens *Mosasauromorpha*

Fam. *Mosasauridæ*

Suborder *Amphisbænia*

Gens *Amphisbænomorpha*

Fam. *Amphisbænidæ*

"(vielleicht mit den Subfamilien *Chirotinæ*, *Trogonophinæ*, s. *Amphisbænidæ oxyuræ* und *Amphisbæninæ* s. *Amphisbænidæ amblyuræ*)."

Suborder *Chamæleontia*

Gens *Chamæleontomorpha*

Fam. *Chamæleontidæ*

He regards the geckos as primitive. His views are derived chiefly from a study of the shoulder girdle apparatus, and other parts of the anatomy are not extensively considered.

Gadow (1901) reviews the characters employed by Cope and Boulenger and adopts the following system:

- Subclass
  - Pythonomorpha
    - Order I Dolichosauri
    - Order II Mosasauri
  - Subclass
    - Sauria
      - Order I Autosauri or Lacertilia
        - Suborder I Geckones
          - Geckonidæ (Geckoninæ, Eublepharinæ, Uroplatinæ)
        - Suborder II Lacertæ
          - Group I. Agamidæ, Iguanidæ, Xenosauridæ, Zonuridæ, Anguidæ, Helodermatidæ, Lanthanotidæ, Anniellidæ
          - Group II. Xantusiidæ, Tejidæ, Amphisbænidæ
          - Group III. Scincidæ, Gerrhosauridæ, Lacertidæ, Anelytropidæ, Dibamidæ (uncertain)
          - Group IV. Varanidæ
        - Suborder III Chamæleontes
          - Chamæleontidæ
      - Order II Ophidia

Gadow regards the Pygopodidæ as too obscure for a place in the system, the Chamæleontidæ as of unknown origin, the geckos as an independent and very old branch of the saurians, and the Iguanidæ and Anguidæ as closely related in somewhat the way Boulenger (1884) has suggested.

Williston (1904) has outlined a system and has lately (in manuscript) briefly reviewed the characters that support it:

- Order Squamata (Lepidosauria)
  - Suborder Sauria (Lacertilia)
    - Superfamily Platynota
      - Family Varanidæ
        - Dolichosauridæ
        - Aigialosauridæ
    - Superfamily Mosasauria
      - Family Mosasauridæ
    - Superfamily Kionocrania (true lizards)
      - Superfamily Amphisbænia
      - Superfamily Rhiptoglossa
  - Suborder Serpentes (Ophidia)

Williston's contribution seems especially valuable for its carefully drawn perspective of the relations of the mosasaurs.

## SELECTION OF NAMES

I have in most cases followed suggestions of Stejneger (1907, p. 49) in applying names to groups higher than the superfamily. New names proposed are as follows, fossil groups being indicated by a dagger.

Scincomorpha (Section)	†Megalaniinae
†Ardeosauridae	†Saniwinæ
Feyliniidae <sup>1</sup>	Zonurinae
Anelytropsidae	Chamæsaurinae
Varaninae <sup>2</sup>	

Groups recharacterized and placed under old names or emended names are:

Ascalabota (Division)	Autarchoglossa (Division) Cont.
Gekkota (Section)	†Euposauridae
Iguania (Section)	Platynota (Subsection)
Autarchoglossa (Division)	Diploglossa (Subsection)
Xantusioidea	Pygopodoidea
Scincoidea	Anguioidea
Lacertoidea	†Glyptosauridae
Anguimorpha (Section)	Zonuroidea

First usage of the names employed is indicated in the following list.

## Suborder Sauria

1802—MacCartney, in Ross' 'Transl. Cuvier's Lect. Comp. Anat.,' I, tab. III. [cf. Gill, 1900].

## Division Ascalabota

1820—Merrem, 'Tentamen Syst. Amphib.,' p. 9 (*Ascalabotæ*).

## Section Gekkota

1825—Latreille, 'Fam. Nat. du Règne Animal,' p. 96 (*Geckotii*).

## Section Iguania

1825—Latreille, *loc. cit.*, p. 95 (*Iguanii*).

## Section Rhiptoglossa

1834—Wiegmann, 'Herp. Mex.,' p. 6 (*Rhiptoglossa*)

<sup>1</sup>The Feyliniidae replaces the Anelytropsidae named for *Anelytrops* preoccupied (cf. Boulenger, 1887, p. 431). The Anelytropsidae includes only the genus *Anelytropsis*.

<sup>2</sup>The Varanidae I consider as covering the fossil and recent species placed in the genus *Varanus* by Fejérváry (1918). The Megalaninae is substituted for the Megalanidae of Fejérváry (*loc. cit.*). The Saniwinæ is proposed for the North American Eocene genera *Saniwa* Leidy and *Thinosaurus* Marsh.

## Division Autarchoglossa

- 1830—Wagler, 'Nat. Syst. der Amphibien,' p. 152  
(Autarchoglossa; omits *Heloderma* and *Varanus*)

## Section Scincomorpha, new name

- (=Leptoglossa Cope, Proc. U. S. Nat. Mus., 1900, p. 201 (*nec*  
Wiegmann, *loc. cit.*), omits Annulata.)

## Section Anguimorpha

- 1900—Fürbringer, Jenaische Zeitschrift, XXXIV, p. 621 (Diploglossa s.  
Anguimorpha, omits Platynota and Mosasauria).

## Subsection Platynota

- 1836—Duméril and Bibron, 'Erpétologie Gén.' III, p. 437 (Platynotes,  
includes *Heloderma*).  
1890—Baur, Science, November 7, 1890 (Platynota, includes *Helo-*  
*dermatoidea*).

## Subsection Diploglossa

- 1864—Cope, Proc. Acad. Nat. Sci., Phila., XVI, p. 227.

## OUTLINE OF CLASSIFICATION ADOPTED

Suborder **SERPENTES**Suborder **SAURIA**Division **Ascalabota**Section **GEKKOTA**

- †Family Ardeosauridæ
- Family Gekkonidæ
- Family Uroplatidæ

Section **IGUANIA**

- Family Iguanidæ
- Family Agamidæ

Section **RHIPTOGLOSSA**

- Family Chamæleontidæ

Division **Autarchoglossa**Section **SCINCOMORPHA**

- Superfamily Xantusioidea
  - Family Xantusiidæ
- Superfamily Scincoidea
  - Family Scincidæ
  - Family Anelytropsidæ
  - Family Feyliniidæ
  - Family Dibamidæ

- Superfamily Lacertoidea
  - Family Gerrhosauridæ
  - Family Lacertidæ
  - Family Teiidæ
- Superfamily Amphisbænoidea
  - Family Amphisbænidæ
- Section ANGUIMORPHA
  - †Family Euposauridæ
- Subsection Platynota
  - Superfamily Varanoidea
    - Family Varanidæ
      - †Subfamily Saniwinæ
      - †Subfamily Megalaninæ
    - †Family Dolichosauridæ
    - †Family Aigialosauridæ
  - Superfamily Mosasauroidæ
    - †Family Mosasauridæ
- Subsection Diploglossa
  - Superfamily Pygopodoidea
    - Family Pygopodidæ
  - Superfamily Anguioidea
    - †Family Glyptosauridæ
    - Family Helodermatidæ
    - Family Anguidæ
    - Family Xenosauridæ
    - Family Anniellidæ
  - Superfamily Zonuroidea
    - Family Zonuridæ
      - Subfamily Zonurinae
      - Subfamily Chamæosaurinae

#### SYNOPSIS OF CHARACTERS

- I. Rectus superficialis rarely present; usually more than four transverse rows of ventral scales over each body segment; scales with wide free margin ("deciduous"), when imbricate; hemipenes calyculate.... Division ASCALABOTA.
- A. Vertebrae amphicœlous; or procœlous with small condyles and persistent intercentra; centra short, equal in width at both ends and constricted medially; tongue fleshy and non-extensile; postorbital arch incomplete or absent; six cervical vertebrae; Mylohyoideus anterior in a single layer..... Section GEKKOTA.
1. Skull arches absent; clavicle usually more or less expanded and often perforate, or with appearance of having been perforate; interclavicle rhomboid, cruciform, or reduced to a longitudinal bar; nasals separate; body muscles well-developed; Rectus abdominis extensive; Mylohyoideus strong and not overlapped by Constrictor colli..... GEKKONIDÆ.

2. Skull arches absent; clavicle simple; interclavicle minute; nasals fused; body muscles greatly reduced; Rectus abdominis limited; Mylohyoideus weak and largely overlapped by Constrictor colli.

## UROPLATIDÆ.

- B. Vertebrae always procœlous with large condyles and no intercentra; centra short, conical; tongue fleshy and non-extensile; skull arches complete; six cervical vertebrae; Mylohyoideus anterior usually in two layers.

## Section IGUANIA.

3. Dentition pleuro-homodont; Mylohyoideus anterior usually with posteriorly directed superficial portion, with transverse or anteriorly directed principal portion, and no profound portion... IGUANIDÆ.
4. Dentition hyper-acrodont, usually heterodont; Mylohyoideus anterior with anteriorly directed or transverse principal portion, with posteriorly directed profound portion, and no superficial bundle.

## AGAMIDÆ.

- C. Vertebrae always procœlous with large condyles and no intercentra; centra elongate, cylindrical; tongue vermiform and extensile; skull arches complete; three cervical vertebrae; Mylohyoideus anterior in two layers, arranged as in the Agamidæ..... Section RHIPTOGLOSSA.
5. Nasal bones not bounding nasal apertures; epipterygoid absent, clavicles rudimentary or absent; interclavicle absent; feet zygodactylous, grasping; body muscles weak; Rectus abdominis reduced..... CHAMÆLEONTIDÆ.
- II. Rectus superficialis always present; less than four transverse rows of ventral scales to each body segment; scales with narrow free margin when imbricate; hemipenes usually falcated or plicate..... Division AUTARCHOGLOSSA.
- D. Tongue scaly or with oblique plicæ; hemipenes usually laminate; clavicles, when present, usually dilated, often perforate, and sometimes hook-shaped; interclavicle, when present, usually cruciform; osteoderms, when present, compound on the ventral surface of the body; tooth replacement usually directly successive by intrusion of new tooth into hollow base of old; teeth rarely conical and recurved; caudal chevrons, when present, always intercentral or slightly post-intercentral.

## Section SCINCOMORPHA.

6. Vertebrae of primitive procœlous type as in procœlous geckos; intercentra persistent as small scale-like elements; Rectus lateralis closely attached to belly scales; dorsal scales granular; ventral scales usually squarish, non-imbricate; femoral pores present; no parasternum..... XANTUSIOIDEA.
- (a.) Osteoderms absent on body; supra-temporal fenestra closed by union of squamosal and parietal bones; Mylohyoideus without superficial anterior bundle..... XANTUSIIDÆ.
7. Vertebrae of normal procœlous type with large condyles and tapering centra; no intercentra; Rectus lateralis usually not closely attached to belly scales; scales, imbricate, cycloid, or cycloid-hexagonal; no femoral pores; rudiments, at least, of a parasternum.

## SCINCOIDEA.

- (b.) Skull arches always present; pectoral girdle complete; premaxillaries usually not fused; Mylohyoideus with a superficial anterior bundle; osteoderms present. . . . . SCINCIDÆ.
- (c.) No skull arches; caudal chevrons present (?); no traces of a pectoral girdle<sup>1</sup>; premaxillary single (?); osteoderms present; interorbital septum and epipterygoids present (?).  
ANELYTROPSIDÆ.
- (d.) No skull arches; caudal chevrons present; rudiments of a pectoral girdle; premaxillary single; osteoderms present; interorbital septum and epipterygoids present; Mylohyoideus without anterior superficial bundle. . . . . FEYLINIDÆ.
- (e.) No skull arches; no caudal chevrons; rudiments of a pectoral girdle; premaxillary double; no osteoderms; no interorbital septum or epipterygoids; Mylohyoideus with anterior superficial bundle. . . . . DIBAMIDÆ.
- 8. Vertebrae of normal procœlous type with large condyles and tapering centra; no intercentra; Rectus lateralis attached closely to belly scales; dorsal scales granular or imbricate; ventral scales usually squarish and non-imbricate; femoral pores present; parasternum rarely present. . . . . LACERTOIDEA.
- (f.) Osteoderms present; supratemporal fossa roofed over; Mylohyoideus with an anterior superficial bundle.  
GERRHOSAURIDÆ.
- (g.) Osteoderms absent; supratemporal fossa roofed over; Mylohyoideus with an anterior superficial bundle. . . . LACERTIDÆ.
- (h.) Osteoderms absent; supratemporal fossa open; Mylohyoideus without anterior superficial bundle. . . . . TEIIDÆ.
- 9. Vertebrae with broad flat centra and wide condyles, no neural spines; no intercentra; Rectus lateralis attached closely to belly scales; dorsal scales granular when present; body usually without scales; no parasternum. . . . . AMPHISBÆNOIDEA.
- (i.) Osteoderms absent; no skull arches; no interorbital septum; no epipterygoids; pre-maxillary single; extra-columella enormous. . . . . AMPHISBÆNIDÆ.
- E. Tongue smooth or papillate; hemipenes flounced; clavicles simple; osteoderms, when present, simple, and often corresponding in extent with the horny scales; tooth replacement usually alternate; teeth frequently conical, pointed and recurved; caudal chevrons often attached centrally.  
Section ANGUIMORPHA.
- 10. Vertebrae highly developed, procœlous, with short, constricted centra; condyles very large and with a flange; seven or more cervical vertebrae; nasals elongate, fused; premaxillaries elongate; lower jaw with a median transverse sutural joint; caudal chevrons pediculate and articulated to the median portion of each centrum; no osteoderms; scales granular; no parasternum.

Subsection PLATYNOTA.

<sup>1</sup>Fide, Cope, 1892a: I have not seen representatives of this family.





- (7) Skull arches both absent; subpleurodont; five bones in mandible; osteoderms present, non-tuberculate; no interclavicle or sternum; no interorbital septum.  
ANNIELLIDÆ.
- (8) Skull arches both present; pleurodont; six bones in mandible; osteoderms present over skull, ornamented with minute tubercles; interclavicle anchor-shaped; an interorbital septum.....XENOSAURIDÆ.
- (9) Skull arches both present; pleurodont; six bones in mandible; osteoderms present over skull and body, imbricate and simple as in Anguidæ but with many minute tubercles.....†GLYPTOSAURIDÆ.
- (10) Postorbital arch present; supratemporal arch absent; subpleurodont; osteoderms present, non-imbricate, nodular, and slightly tuberculate; interclavicle a longitudinal splint; an interorbital septum.  
HELODERMATIDÆ.
- (n.) Vertebral centra tapering, not constricted; condyles never as wide as the centra; ribs without muscular processes; femoral or preanal pores present; no Geniomyoideus muscle; no Mylohyoideus anterior superficialis; tooth replacement successive.....ZONUROIDÆ.
- (11) Skull arches both present; dentition pleurodont.  
ZONURIDÆ.
- (d). Body and limbs normal; osteoderms and zygosphenes sometimes present; two rows of ventral scales over each body segment; no parasternum.  
ZONURINÆ.
- (e). Body serpentiform; limbs reduced; no osteoderms; no zygosphenes; one row of ventral scales over each body segment; a large parasternum.....CHAMÆSAURINÆ.

## REVIEW OF TAXONOMY AND PALEONTOLOGY

### Suborder **SERPENTES**

Brain-case completely bony anteriorly; rami of lower jaw never united by suture; no urinary bladder (Cope, 1900); no pectoral girdle; elements of lower jaw reduced; usually one dorsal temporal element articulating with the quadrate.

In totality of characters the serpents approach the anguimorphine lizards (p. 359). The hemipenes have a similar texture; the brain-case is bony beneath the frontals in *Varanus* and *Heloderma*; the vertebræ of the Varanoidea are similar in shape (cf. Figs. 25, 26) to those of *Python* and sometimes develop a zygosphenes and zygantrum as in the serpents (pp. 322 and 345); the caudal chevrons are universally central in position

in the Platynota and the snakes; in some limbless *Diploglossa* (p. 376) they are anchylosed to the centra in the same way as in the serpents. The number of transverse ventral scale rows (p. 400) corresponds to the body segments, there being in the Typhlopidae, Glauconiidae, Leptotyphlopidae, and Uropeltidae, as in the saurian *Autarchoglossa*, two rows to every segment. In all other serpents there is only a single ventral scale for each pair of ribs.

The throat muscles of *Typhlops congestus* (cf. Fig. 53) show typical saurian arrangements, there being a considerable interdigitation of the Geniohyoideus with the Mylohyoideus anterior; a reflected anterior superficial bundle of the Mylohyoideus anterior as in many autarchoglossid lizards; and a very typically placed Cervicomandibularis. All these features are absent in *Sphenodon* and apparently in the Chelonina and crocodiles and the second is unknown in most of the Ascalabota. I am inclined to think the anterior mandibular (Intermaxillaris) muscle is the same as what I have called the Geniomyoideus of the *Diploglossa* (p. 373).

Maurer (1896) states that the *Transversus abdominis* is absent in the serpents. I have found it, however, in *Typhlops* and in *Diadophis*.

A tabulare is present in most ophidians but is absent in the Typhlopidae, Glauconiidae, and Uropeltidae.

Ophidian remains are not known from formations earlier than the Cretaceous and are fairly common in the Eocene.

### Suborder SAURIA

Brain-case never completely bony anteriorly; rami of lower jaw usually united by suture; a urinary bladder; not more than two sacral vertebrae, no sacral ribs (Moodie, 1907); usually an ectepicondylar, never an entepicondylar foramen (Williston, 1914); pectoral girdle usually present; articular and prearticular always fused; quadrate streptostylic; usually two dorsal temporal elements articulating with the quadrate.

Fossil reptiles referred by Williston, Nopcea (1908), and others to the Sauria, but otherwise *incertae sedis*, occur in the Upper Jurassic<sup>1</sup> (*Saurillus* Owen, 1885,—vertebrae procelous, dermal scutes present, Lydekker, 1888); Upper Cretaceous (*Coniasaurus* Owen, cf. Nopcea,

<sup>1</sup>Under the name *Eifelosaurus triadicus*, Jaekel (1904) has described and figured a reptile with lizard-like habitus from the Triassic. This is apparently a terrestrial form with amphicoelous vertebrae, weakly double-headed ribs, short, stout, curved femora, short, broad, body and broad tail. Parasternal ribs are present. There is no skull and an allocation with the Sauria is problematical (cf. von Huene, 1910a).

provisionally placed with the Dolichosaurs; *Saurospondylus* Seeley, referred by Woodward and Sherborn to the genus *Dolichosaurus*,—an allocation questioned by Nopcsa; *Tylosteus* Cope, cf. Hay 1901, p. 477); Eocene (*Enigmatosaurus* Nopcsa [for *Thaumastosaurus* de Stefano, 1903, preoccupied], *Naocephalus* Cope, cf. Nopcsa); and Pleistocene (*Notiosaurus* Owen, *Patricosaurus*, Seeley, cf. Nopcsa).

#### Division **ASCALABOTA**

The geckos, iguanoids, and chameleons are distinguished by simplicity of body musculature, tongue and hemipenial texture, and by peculiar, apparently primitive, characters of squamation. The *Rectus superficialis*, a ventral muscle covering the *Pectoralis* in limbed forms, is absent except in a few agamids. Other trunk muscles are reduced or absent (pp. 377–385). Except in the chameleons the tongue is broad, thick and papillate and is not divided into anterior and posterior portions. The hemipenes lack flounces and plicæ and are of simple texture covered with fine calyculi. There is generally little or no correspondence between the segmentation of the body and the ventral scales. The latter are usually small and rarely number less than four (p. 400) over each segment. The scales when imbricate are easily separated from the skin owing to their loose basal attachment (Fig. A).<sup>1</sup> Osteoderms are rarely present and then apparently in a primitive diffuse state (pp. 395–397). A parasternum occurs in some forms and attains a peculiar development in the arboreal *Uroplates* and *Chamæleon* (pp. 386 and 390). The caudal chevrons are always attached intercentrally (p. 376). The intermedium is curiously enough almost universally absent or fused with the ulnare (pp. 376–377). The patella ulnaris is usually bony (p. 408). An enlarged endolymphatic system is frequently exhibited (p. 414).

This complex group includes many most highly specialized arboreal types, a few exceedingly primitive terrestrial “relicts,” and some forms of aquatic and semi-aquatic habit, but no highly modified burrowers or snake-like, grass-dwelling genera. There is no apparent tendency for the reduction of limbs and girdles. The loss of limbs together with the necessary specialization of body musculature required by a snake-like or a burrowing, worm-like habitus, is never accomplished. Many arboreal tendencies not found in other groups are shown. Sucking laminae are sometimes developed on the toes (*Gekkota* and *Iguania*). The tail is occasionally prehensile in *Gekkota* and *Iguania* and usually so in the

<sup>1</sup>In some of the Ceylonese agamids (*Cophotis* and *Ceratophora*) the dorsal scales are imbricate and strongly anchored but have the appearance of being enlarged tubercles.

*Rhoptoglossa*. In the *Uroplatidæ*, the lateral tail-fringe functions in a most peculiar way as a prehensile apparatus.

The known fossils seem to include the oldest form assignable to the *Sauria*. This is *Paliguana whitei* Broom, from the Triassic of South Africa.

*Paliguana* is apparently a true lacertilian, although Watson (1914), who has examined the specimen, is not sure of this, and Boulenger (1918a), considers it "problematical." *Paliguana* can scarcely be related to any of the families I have included within the *Autarchoglossa*.

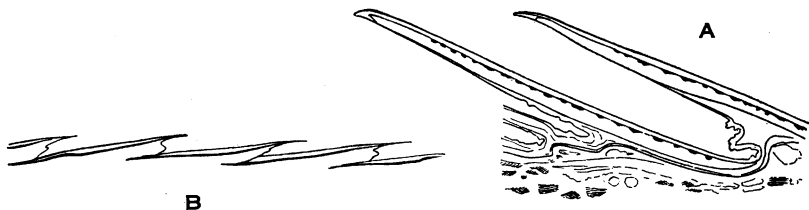


Fig. A. Longitudinal section through the dorsal scales of *Geckolepis polylepis*, adult,  $\times 30$ , after Schmidt (1906-1915, Pl. xxv, fig. 16).

The scales are loosely embedded in the skin in the manner generally found among the *Ascalabota*.

Fig. B. Longitudinal section through the dorsal scales of *Voeltzkowia mira*,  $\times 22$ , after Schmidt (1910, text-fig. S, p. 626).

The points of Broom's illustrations and description which strike me most forcibly are: the large size of the quadrate approached in certain geckos and agamids, and not closely in the *Iguanidæ*; the small, short squamosal (impression preserved) such as occurs only in the *Iguanidæ* and *Agamidæ*; the narrow space between quadrate and jugal, a relation seen only in the *Ascalabota*, but seldom as exaggerated as here; and the lack of prolonged posterior processes of the parietals, also indicating marked separation from autarchoglossid forms. What is suggested by the little-known teeth would point to gekkonoid affinities, which, of course, the large size of the postorbital arch would negative.

The better-known features would indicate a position among the primitive *Ascalabota* with resemblances to the *Iguania* (*Iguanidæ*+*Agamidæ*) closer than to the geckos.

### Section *Gekkota*

This group includes the *Gekkonidæ*, *Uroplatidæ*, and the Jurassic *Ardeosauridæ*. Some of its living members retain the most primitive features of squamation, vertebræ, and branchial apparatus known among lizards.

In most of the genera the vertebræ are amphicœlous and retain the chorda in the intervertebral spaces. A few non-related groups of species are proœlous, having become so secondarily (p. 343). The so-called Eublepharidæ are one of these groups; the sphærodactyloids are another (cf. Noble, 1921).

When proœlous the centra still retain the typical geckonid, short, squarish ventral outline and the condyle is never enlarged (cf. Figs. 3-4). Also, the intercentra remain (pp. 343-344) as fused elements. The tongue is always fleshy and non-extensile and sometimes is decorated with elongate, ribbon-like lappets which develop from the basal villose papillæ. In the recent families no skull arches are ever present; the squamosal is presumably absent; the jugal remains, and there is a strong postfronto-jugal ligament. As in most lizards, there are six cervical vertebræ.

The Mylohyoideus anterior is disposed in a fanwise way, much more markedly so in the Uroplatidæ than in the Gekkonidæ, and develops but a single layer. The Pectoralis, as in many Ascalabota, is extensive, sending a slip to the pelvis in some forms; this may be connected with active arboreal use of the limbs, and the requirements for control of lamellate, sucking digital extremities.

The eyes are usually extremely large with vertical pupils and covered with an immobile transparent eyelid, but in a few genera the eyelids are moveable (*Ælurosaurus*, *Ptenopus*, *Eublepharis*, *Coleonyx*, and *Psilodactylus*).

The interclavicle is rhomboid, cruciform or further reduced; it never becomes a horizontal bar. Osteoderms are rarely present and usually lie diffusely scattered without relation to the superincumbent horny scales (Fig. 83). Dermal cranial ossifications seldom occur; the soft skin usually lying quite free from the skull. Teeth are never present on the palate so far as known. The lacrymal is crowded inside the orbit. The elements of the lower jaw are reduced to five by fusion of the angular and subangular in the Uroplatidæ; in the Gekkonidæ it is the angular and prearticular which join. No pineal foramen; proximal belly of Biceps brachii simple (reduced to a single tendon in *Uroplates*); quadrate relatively large, simple; skull elevated; enlarged endolymphatic sacs frequently present.

Among the exclusively arboreal forms of this group the body often becomes depressed; compression never occurs. A lateral fringe is sometimes developed among the most highly depressed types, and this may extend to the limbs and tail (cf. *Ptychozoon* and *Uroplates*), and to the

feet as a webbing (cf. *Rhacodactylus* and *Ptychozoon*). The claws tend to be reduced in some of the excessively lamellate geckos, and in a simple-toed form (*Chondrodactylus*) are entirely lost.

#### Family †*Ardeosauridæ*

No fossil geckos are known from the Tertiary but von Meyer (1860) has excellently described and figured an important form, *Ardeosaurus brevipes*, from the Lithographic stone of Eichstätt. The age is Tithon, a formation which has been lately assigned to the Jurassic, but some question this and would place it in the Cretaceous.

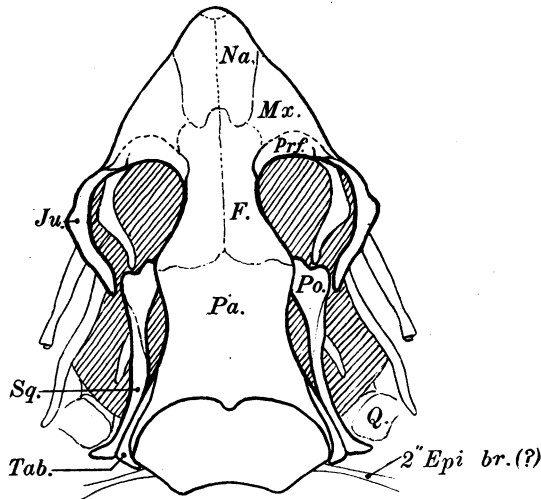


Fig. C. Skull of *Ardeosaurus brevipes*, dorsal view,  
 × 4, after von Meyer (1860, Pl. XIII, Fig. 5).

The sutures on the rostrum are doubtful.

Leydekker (1888) has assigned *Ardeosaurus* to the Rhynchocephalia. Nopcsa (1908) calls the genus a "scincoid," without stating reasons. The small reptile is unquestionably a lacertilian as von Meyer supposed it to be. The position of the tabulare and squamosal, the shape of these elements and their relations to the streptostylic quadrate prove this (Fig. C). The broad parietals, narrow supratemporal fenestræ, large depressed vertebræ, paired frontals and elongate squamosal will not allow an inclusion with the Iguania or the Teiidae. The large size of the vertebræ, lack of dermal skull plates, osteoderms, enlarged postfrontals, and the incomplete postorbital arch separate *Ardeosaurus* most decidedly from the Xantusoidea, Scincoidea, Lacertidae and Gerrhosauridae and the Anguimorpha.

The only existing lizards which show the following combination of characters, to be seen in *Ardeosaurus*, are the geckos:—

Vertebrae broad, depressed and at least one-fifth of the body width; parietals broad and flat; nasals and frontals paired, parietals united; postfrontals small; postorbitals small or absent; jugal small, nearly straight and not joined to the postfrontal; hyoid arch (or possibly the second epibranchial) joined to the paroccipital process; six cervical vertebrae; (two cervical ribs preserved); tabulare exposed dorsally; humerus apparently without foramina; no osteoderms or secondary cranial ossifications.

The differences which establish the Ardeosauridae as a separate family of the Gekkota, perhaps ancestral to the geckos, include:—

Presence of a supratemporal arch and fenestra; an elongate squamosal; a pineal foramen; orbits small, and but little wider than distance across frontals; rostrum pointed. The tail was autotomous by transverse fission of the vertebral centra as in many lizards and geckos, and the fission as indicated by skin impressions in the fossil has left a basal stump shaped much like that of certain geckos. There are no evidences of scales although the outline of the body is preserved. The limbs were short and stout; the neck thick; the body short and much broader than the base of the tail.

The ventral surfaces of the vertebrae and the shape of the vertebral condyles, if present, are not seen on the specimen.

### Section *Iguania*

Vertebrae always procelous with short tapering centra (moderately elongate in some Agamidae) and large condyles; tongue as in the Gekkota but never with long, basal filaments, more extensile in the Agamidae; six cervical vertebrae; the skull arches always present; of normal form or slightly produced posteriorly and upward (*Chamaeleolis*, *Phrynosoma*); Mylohyoideus anterior usually in two layers, well separated or, in some Iguanidae, consisting merely of differently directed fibers,—*Holbrookia*, *Callisaurus*, and *Uma* constitute the only known exceptions (p. 370); Pectoralis sometimes with an abdominal portion strongly developed; eyes small or moderate, normal, never with connivent or transparent, immobile lids, pupil circular; interclavicle usually T-shaped or still further reduced, cruciform in certain Agamidae (p. 369); osteoderms never developed on the body but a dermal cranial ossification takes place in some iguanids (cf. *Amblyrhynchus*) and obscures the supratemporal fenestra in the highly advanced species, *Phrynosoma* (*Anota*)

*m'callii* (cf. Bryant, 1911); the postfrontal is frequently absent in this group and possibly also in the chameleons (p. 361); the lacrymal is present in the usual position in the Iguanidæ and is frequently absent in Agamidæ (p. 362); a few pterygoid teeth occur in many Iguanidæ, they are absent in the Agamidæ (p. 365); the clavicles are always present though reduced in the Agamidæ, and are usually simple, though in some iguanids they have retained a perforation (p. 369); the lower jaw is normal, but the splenial is small in Agamidæ (cf. *Rhaptoglossa*) (p. 375); the pineal foramen is rarely absent and undergoes a forward migration in certain species (p. 394) (cf. *Rhaptoglossa*); the proximal belly of the Biceps brachii is complex, being usually composed of a fleshy belly and two or more tendinous parts (cf. pp. 403-404); the skull is often elevated, doubtless being secondarily so in connection with the compression of the body; the quadrate is relatively shorter than in the Gekkota; a proscapular process is usually present in the Iguanidæ (p. 411) and is absent in all known agamidæ with the exception of *Lophura*; enlarged endolymphatic sacs are present in *Anolis sagræ* (p. 414).

In the arboreal members of this group, compression of the body always seems to occur. This tendency reaches its highest expression in the *Rhaptoglossa*. Coincidentally with compression, a strong fold, ridge or series of dermal rays frequently develops along the mid-dorsal line and the claws become specially compressed sharp-pointed, and decurved; those of terrestrial forms are depressed, and have stumpy points, while the horny axis is weaker and the gristly "sole" is heavier than in the arboreals (cf. W. J. Schmidt, 1916, p. 392). In a general way this is true throughout the lizards but the claws of chameleons are peculiarly modified owing to the scansorial form of the feet; and the arboreal autarchoglossids never acquire such perfect climbing tools as do the non-lamellate (and, to be sure, most of the lamellate) ascalabotids.

In the arboreal Iguania the ceratobranchials of the third arch are joined and produced, sometimes extending ventrally to beyond the middle of the sternum. This is part of a mechanism used to dilatate the throat fan frequently present in tree-living forms of this group but unknown elsewhere. The habit of "displaying the gorget," which is often brilliantly colored, is associated with a rapid, emotional play of colors in the skin occurring in certain arboreal forms and in these alone. This is carried to highest attainment in the peculiarly arboreal *Rhaptoglossa*.

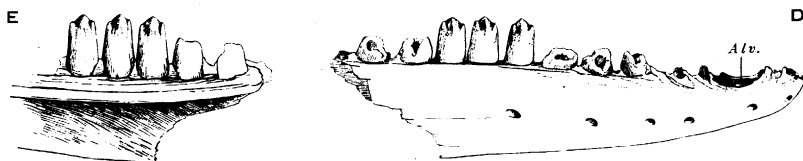
The genus *Chalarodon* of Madagascar is certainly an iguanid. The combination of characters of dentition, pattern of throat musculature, and presence of a proscapular process demonstrates this.



Fossil evidence is not absolutely lacking to show the antiquity of the Iguania. *Paliguana* and *Chamops* appear close to what we should expect of stem forms. Tertiary genera from the Eocene of Europe (Quercy) and of North America (Bridger) are possibly referable. *Proiguana* Filhol (1877, cf. de Stephano, 1903) and *Agama galliæ* Filhol seem the most certain. *Iguanavus* Marsh (1872), "*Chamæleo*" *pristinus* and *Palæo-chamæleo europeus* de Stephano are problematical.

### †*Chamops*

There is a specimen referred to *Chamops* and consisting of a portion of a right dentary with several teeth, in the American Museum (No. 988, Dept. Paleont., Laramie Cretaceous, Ceratops Beds, Converse County, Wyoming). The teeth in this fragment agree well with Marsh's description and figures (1892) of *Chamops segnīs* based on an upper maxillary tooth row. Boulenger (1892, 1918a) and Williston (manuscript) have included the latter in the Teiidae. Hay (1901) considers it an iguanid.



Figs. D and E. Portions of right dentary with teeth of *Chamops*,  $\times 4$ , Dept. Vert. Pal., A. M. N. H. No. 988, Laramie Cretaceous.

Fig. D. Outer (buccal) view. Fig. E. Inner (lingual) view.

The teeth are thecodont and set in alveoli (*Alv.*), but are more exposed on the inner than the outer aspect of the jaw. This condition may precede both the highly pleurodont and the hyper-acrodont series of modern lizards.

Marsh's specimen differs from the teiids in having a strictly homodont type of dentition and our specimen seems to agree in this particular. Also the trilobate teeth are not developed anteriorly in the teiids and even in the posterior teeth the lateral cusps are not so large as in *Chamops*. The teeth (Figs. D, E) seem to be closest among living lizards to those of certain non-specialized Iguanidae (cf. *Crotaphytus collaris*), agreeing with these in the swollen base, ratio of height to diameter of crown, form of cusps, in homodonty, and in the fact that a line drawn through the summit of the crowns is straight. They differ in being pleuro-thecodont rather than strictly pleurodont, and they are more completely exposed externally than in recent iguanids.

We may not consider *Chamops* an iguanid on account of lack of definite characters but feel that among living lizards it is most closely

related to that stock. In tooth insertion it seems to partially bridge the wide gap between pleurodont and hyper-acrodon Ascalabota (Iguanidæ and Agamidæ and Rhiptoglossa).

The trilobate teeth of generalized iguanids and agamids and the Rhiptoglossa do not differ materially in form. In the two latter groups such a high degree of acrodonity is attained, coupled with a slicing, shear-like motion of the mandible, that the tooth shafts have come into view more on the outside than the inside of the dentary. To account for this extraordinary digression by closely related groups is a difficulty perhaps best hypothecated by regarding the thecodont or pleuro-thecodont type of tooth insertion seen in Jurassic Euposauridæ and the Cretaceous *Chamops* as a slight advance upon the typically thecodont condition of the Permian *Aræoscelis*. It is obvious that the stage illustrated by *Chamops* would more easily lead, on the one hand, to typical pleurodonity and, on the other, to acrodonity, than the derivation of the highly developed agamid type of acrodonity from iguanid pleurodonity or vice versa (cf. p. 363).

#### †“*Chamæleo pristinus*”

A portion of a right dentary with several teeth of a highly acrodon agamoid type from the Bridger Eocene was redescribed and figured by Leidy (1873) as a rhiptoglossid under the name *Chamæleo pristinus*. This form was also considered by Hay (1901) to be a chameleon. There seems nothing, however, to prevent it from representing equally well a true agamid of the *Calotes* type. After comparison of Leidy's figures with *Calotes* and with *Chamæleon gracilis* and *Chamæleon vulgaris*, I can distinguish no diagnostic peculiarities in the parts preserved in the fossil, between teeth of any of these forms, and therefore prefer to place “*Chamæleo pristinus*” among the Ascalabota as either an agamid or chamæleontid.

#### Section **Rhiptoglossa**

Vertebræ procœlous with elongate cylindrical centra and large condyles; tongue vermiform, highly extensile; only three cervical vertebræ; two skull arches always present and produced posteriorly and upward; pterygoid not in contact with quadrate; no retroarticular process on the lower jaw; Mylohyoideus anterior in two layers corresponding exactly with those in the Agamidæ.

Family **Chamæleontidæ**

Feet zygodactylous, grasping; clavicles reduced or absent; inter-clavicle absent; nasal bones not bounding nasal apertures; epipterygoid absent.

Pectoralis never with an abdominal portion; body muscles reduced; sterno-hyoid muscles enlarged; eyes large, covered with lids which are connivent except for a pin-hole-like opening becoming a horizontal slit when the animal is at rest; no osteoderms but with dermal cranial and pelvic ossifications in *Brookesia*; postfrontal absent; lacrymal present in the usual position; no pterygoid teeth; splenial absent; pineal foramen very small and located between the frontals; vomers generally fused; os tabulare present; a complete parasternum; proximal belly of Biceps brachii reduced to a single tendon as in *Uroplates*; no os hypischium.

Cope is the only herpetologist who has ventured to regard the Rhiptoglossa as related to the Agamidæ. From additional evidence now obtainable I think Cope's view can be supported. The chameleons, remarkably specialized as they are, show no primitive characters (with the very doubtful exception of the development of a "pro-atlas," cf. Baur, 1886c, and the presence of a rib on the third cervical vertebra) that are not common to the Iguania. There are but few even of the most extraordinary specializations of chameleons which are not at least approached by certain of the arboreal Ascalabota: Geckos (*Phyllurus*) sometimes show an incipient zygodactyly; *Uroplates* wholly resembles the Rhiptoglossa in the loss of body musculature and development of hoop-like parasterna; certain arboreal iguanids (*Anolis*, *Polychrus*, *Chamæleolis*) parallel them in independent mobility of the eyes, diverticulate lung structure,<sup>1</sup> anterior position of the pineal foramen, and casque-shaped head; their great power of color change is equalled if not exceeded by the agamid, *Calotes*. Agamids, generally, share with them the highly important characters, detailed elsewhere, of dentition, hemipenes, composition of lower jaw, and pattern of throat musculature. Agamids also frequently have the prevomers fused and tend to elongate and narrow the vertebral centra (Figs. 5 and 7), and to reduce the clavicle, the inter-clavicle, the epipterygoid, the tabulare, and the splenial. In the higher agamids the Cervicomandibularis is absent as in the Rhiptoglossa. No lizards except the Iguania and Rhiptoglossa develop highly compressed arboreal forms.

<sup>1</sup>Beddard (1907) and Methuen and Hewitt (1915) have shown that in some chameleons the lung diverticuli are weakly or not at all developed. Milani (1894) illustrates the strongly diverticulate lung of the iguanid *Polychrus*.

The characters outlined by Boulenger (1887, p. 437) are the most important which have been employed to separate the *Rhaptoglossa* from other lizards. Of these, the first three are shiftings of lacertilian skull elements probably accompanying extreme compression of the body and casque-like development of the head. The fourth (presence of a supratemporal bone [tabulare] as a nodule) rather proves, than otherwise, close association with the true lacertilians, and would not hinder connection with the Agamidæ. The fifth has been spoken of; it is doubtless also connected with bodily compression as the conditions in agamids would indicate. The sixth and seventh (structure of feet and tongue) are highly adaptive features not known in similar degree elsewhere. Connected with the peculiar functioning of the tongue and development of an enormous sternohyal musculature arising in the mid-sternal region, the neck has been shortened and stiffened, either by the dropping out of three vertebræ, or else by the shifting forward of the shoulder girdle a corresponding number of segments.

There would seem few or no objections from morphological or distributional viewpoints against deriving the chameleons from highly developed agamids at the beginning of the Tertiary.

The fossil record shows no undoubted chameleons; all those so described are jaw fragments and can equally well be placed with the Agamidæ.

#### Division **AUTARCHOGLOSSA**

*Rectus superficialis* always present; hemipenes usually falcated or plicate; less than four, and usually only two, rows of ventral scales to each body segment; scales, when imbricate, with narrow free margin and firmly attached to the skin (cf. Fig. B); osteoderms frequently present and never entirely diffuse (Figs. 84-98). A parasternum often occurs and attains considerable extent only in the burrowing forms (p. 387); caudal chevrons attached intercentrally or centrally; intermedium sometimes present; epipterygoids occasionally absent; patella ulnaris rarely bony. The tongue is variously developed but is like the *Ascalabota*, only in the *Zonuridæ*.

None of the high arboreal specializations of the *Ascalabota* ever appear in this terrestrially inclined group. There are no digital or caudal lamellæ, no prehensile tails, no excessive flattening or compression of the body. On the other hand remarkable subterranean and snake-like modifications are frequently acquired.

The body musculature is more complex even in the limbed forms than in the Ascalabota (pp. 377-385) and the belly musculature, specially developed, seems usually to help along the action of the limbs in walking. This allows the limbs to gradually disappear, on occasion, without hindrance to locomotion. The limbs may act as an encumbrance in the case of burrowing or grass-dwelling forms. They appear to dwindle only in correlation with such habitats.

The most advanced burrowing types sometimes lose the pectoral girdle completely, develop a complete dermal covering over the eye and ear, lose the skull arches, the interorbital septum, the epipterygoid, the median skull sutures, and gain body musculature of greatly increased complexity,—sometimes with specially developed skin layers and sets of bundles running from ribs to skin so arranged as to allow both backward or forward motion, underground and on the surface. The tail always becomes very short in the burrowers and the caudal chevrons shorten and in an extreme case (*Dibamus*) are entirely absent. The extra-columella, in absence of a tympanum, may greatly enlarge as in the *Amphisbænidae* to function from the side of the jaws and face (cf. Figs. F, G). Such an arrangement may serve as a microphonic device to detect noisy insectivorous prey such as termites.

In the limbless grass-inhabiting forms, the profound developments seen in the burrowers do not occur. The skull arches are never lost (except in *Pygopodidae*, p. 345); the skull elements reduced in the burrowers remain as normal; the girdles remain; the body musculature gains in extent in various ways but not as in the burrowers. There is never a large *Cervicomandibularis* muscle developed to swing the head, as in burrowers. Only the normal *Scalares* (skin slips) are developed and never extra sets. The tail always becomes very long and brittle and the caudal chevrons sometimes fuse with the centra. The eye remains normal and the ear does not close (*Ophiodes striatus* has a closed ear and may be an exception).

The snakes appear to have arisen from anguimorphid, grass-living lizards. The burrowing snakes (*Typhlopidae* and allied families) parallel the burrowing lizards in many profound ways and would seem to be derived from autarchoglossid stock for that reason and because of the paleotelic characters they hold in common with the *Anguimorpha* (p. 301).

#### Section **Scincomorpha**

Tongue scaly or with oblique plicæ (pp. 374-375); hemipenes laminate; clavicles when present usually dilatated, often perforate and sometimes hook-shaped (Figs. 78-80); osteoderms when present com-

pound (except dorsally in Gerrhosauridæ) and ventrally not corresponding in extent with the horny scales (pp. 395-397); tooth replacement often directly successive by intrusion of new tooth into hollow base of old (p. 364); caudal chevrons, when present, always intercentral or slightly post-intercentral (p. 376); teeth usually hollow, cylindrical, obtusely pointed or rarely (Teiidæ) broader and with small lateral cusps.

The tongue, osteodermal, tooth, and clavicular structures separate this group more widely from the Anguimorpha than external appearances might indicate. Another point of distinction is to be found in the simplicity of the throat musculature as detailed under the various superfamilies. The primary throat musculature is obscured in the burrowing members of this group, and not elsewhere (cf. *Anniella*, and *Typhlops*), by supergrowth of the terminal fascia of the Cervicomandibularis which is actively used in turning the head while burrowing. In *Feylinia* and *Dibamus* the terminal fascia entirely covers the throat and the muscle extends a great way down the body. In the amphisbænians certain processes of the lower jaw (cf. Peters, 1882) are provided for the attachment of this muscle.

Degenerative tendencies in the group appear to be first to lose the hind limbs (except in *Neoseps* and in the Dibamidæ where the hind limbs, present only in the male, appear to be used as claspers) and then the fore limbs (p. 354), but, while the pectoral girdle may in extreme cases entirely fail, rudiments of the pelvis always remain. In the girdle itself the clavicular parts are the first to disappear. Degenerate forms are found in all families except the Lacertidæ and Xantusiidæ.

#### Superfamily **XANTUSIOIDEA**

Vertebræ procœlous with extremely small geckonoid condyles, squarish centra, and tiny, persistent intercentra fused with the condylar balls (Fig. 8); hemipenes peculiar (cf. Cope, 1900, p. 541); *Rectus lateralis* closely attached to the ventral scales as in lacertoids; *Mylohyoideus* with a few large interdigitating bundles; ventral scales usually squarish, non-imbricate as in lacertoids and some other autarchoglossids; dorsal scales granular; femoral pores present; no parasternum.

#### Family **Xantusiidæ**

Vertebræ almost exactly as in the procœlous gecko *Coleonyx* (cf. Figs. 4 and 8); supratemporal fenestra closed by union of squamosal and parietal bones; clavicles dilatated and perforated; interclavicle cruciform; *Mylohyoideus* without superficial anterior bundle; a few fibers of *Genioglossus* run to the skin partly on the body simulating the *Genio-*

myoideus muscle of the Anguioidea; no osteoderms; dermal skull-roof present; parietals distinct.

The presence of an archaic type of vertebræ would indicate a position among the Gekkota were it not for the assemblage of purely autarchoglossid characters in the musculature, ventral squamation, and tongue. The group is an isolated one and should be placed as the most primitive of the Autarchoglossa on the basis of the geckonoid characters, and by reason of the nearly complete third branchial arch (p. 339) and the free intermedium (p. 377). Were it not for the intermediate position and relationships of this family, one could derive the Scincomorpha and Anguimorpha from iguanoid stock, as Cope has done.

#### Superfamily **SCINCOIDEA**

Vertebræ procelous with large condyles, tapering centra and no intercentra (Figs. 10, 11); Rectus lateralis not closely fused with the ventral scales; Mylohyoideus simple and usually with many regularly interdigitating bundles; scales cycloid or rhombo-cycloid, strongly imbricate; no femoral pores; rudiments, at least, of a parasternum.

Filhol (1882) refers his *Cadurcosaurus sawagei* to the scincs. The form was described on a lower jaw with an enlarged posterior crushing tooth. *Dracænosaurus croizeti* Gervais (1859) is a similar genus from the Oligocene and has been placed with the scincoids by Lydekker (1888). The identification of jaw fragments such as these is questionable.

A scincoid lizard, *Didosaurus mauritanicus* Günther, has been described from a marsh deposit on the island of Mauritius. The locality is referred by Nopcsa (1908) to the Pliocene, but the fauna is certainly not older than Pleistocene and contains remains of recently exterminated animals.

*Didosaurus* has resemblances to the scincs in the structure of the mandible, the short teeth, the closure of the Meckelian sulcus beneath the internal border of the coronoid, the pattern of the scale-plates on the fused frontals, and the shape of the vertebræ. Resemblances to *Cyclodus* which Gadow mentions, do not seem close on account of the number of teeth, twice as great as in *Cyclodus*.

#### Superfamily **LACERTOIDEA**

Vertebræ as in Scincoidea; Rectus lateralis closely fused with the ventral scales; Mylohyoideus as in Scincoidea; ventral scales usually squarish, sometimes non-imbricate; dorsal scales granular or imbricate; femoral pores present; a parasternum in some of the Teiidae.

The characters of the Gerrhosauridæ are intermediate between those of the typically teioid members of this family and the Scincidæ.

The ventral scales of *Gerrhosaurus* are imbricate and cover osteoderms of compound nature similar to those of the scincoids (Figs. 88, 89). In the Lacertidæ osteoderms are absent on the body and remain as a dermal covering over the skull. In the Teiidæ there are no traces of osteoderms even on the skull.

A number of fossil lizards have been referred to the genus *Lacerta*. Of these the best established is *Nucras*, an existing African lacertid which has been found enclosed in Oligocene amber from East Prussia (cf. Klebs, 1910, and Boulenger, 1891a, 1920). On Boulenger's authority, the Upper Eocene *Lacerta mucronata* Filhol (1877; cf. de Stephano, 1903), is close to the living species *agilis*.

Lartet (1851), Pomel (1853), and others have described fossil species of *Lacerta* from Miocene, Pliocene, and Pleistocene formations of Europe. Many of the determinations seem based on too scanty material (cf. Nopcsa, 1908).

Ambrosetti (1887), and Rovereto (1914) have examined remains of large teiids, close to the living genus *Tupinambis*, from Oligocene and Pliocene localities in Argentina. The systematic determinations are quite convincing.

#### Superfamily **AMPHISBÆNOIDEA**

Vertebræ with broad, flat centra and wide condyles (Fig. 9), sub-central arterial foramina present as in geckonids and pygopodids; no neural spines, no intercentra; Rectus lateralis attached closely to the belly scales and greatly extended, reaching the dorsal mid-line in some forms; dorsal scales granular or tubercular when present; skin usually naked; no parasternum; preanal pores present.

#### Family **Amphisbænidæ**

No osteoderms; no skull arches; no interorbital septum; no epipterygoids; pre-maxillaries single; extra-columella enormous (Figs. F, G).

The rudimentary pelvis resembles that of degenerate scincomorphs and is not like that of limbless anguimorphs. The tongue and hemipenes also show scincomorph affinities. The skull and cervical vertebræ are remarkably specialized and the complexity of the body musculature is greater than that of other Squamata except the burrowing snakes, *Typhlops*, which greatly resemble the amphisbænians in this adaptational particular. The Cervicomandibularis is enormous, as in other burrowing



scincomorphs but not as in the degenerate subterranean anguimorphs and the burrowing snakes, where it is small or moderate. The tail is exceptionally short even for a burrowing lizard but caudal chevrons (lost in the Dibamidæ) are still present. A spade-like development of the tail is sometimes seen with enlarged frictional tubercles in *Rhineura*, as in the uropeltid serpents. External limbs are present only in the single genus *Bipes*. The pectoral girdle is entirely wanting in some forms. The teeth vary in the subfamilies from pleurodont to acrodont and the number of annuli over each body segment becomes reduced to one in some of the Old World forms and apparently becomes doubled again in *Trogonophis* (pp. 399-400).

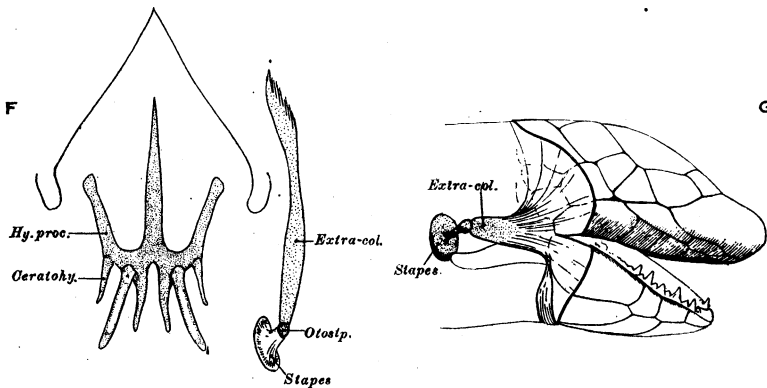


Fig. F. Hyoid apparatus and enlarged extra-columella of embryo of *Amphisbæna cæca*,  $\times 15$ , A. M. N. H. No. 13146.

A small ceratohyal (*Ceratohy.*) remains and its location proves that an extended basihyal process (*Hy. proc.*) is present as in teiids. No direct continuity between the tip of the extra-columella and the hyoid is thought possible.

Fig. G. Extra-columella *in situ* of the amphisbænid *Rhineura floridana*,  $\times 4$ , A. M. N. H. No. 5724.

Functional significance of the enlarged extra-columella is indicated by its attachments to the fascia extending into the spongy tissue surrounding the jaw.

The resemblances to the degenerate Teiidæ are for the most part secondary but are nevertheless indicative of ancestral relationship to that family, as is also the fact that the anterior process of the basi-hyal is exceptionally long, as it is in all known teiids (cf. Fig. F).

The locomotory and burrowing habits are exceptional, the double sets of Scapulae (which are so developed also in *Typhlops*) permitting movements forward or backward with equal facility (Fig. 40).

The great morphological variation and scattered distribution of this group as well as its isolated position as one of the most highly modified

lacertilians lead one to expect the antiquity which is indicated by the fossil record.

Close relatives of *Rhineura* are found in the Oligocene of North America (White River) along with numerous other genera, represented by vertebræ and skulls, one of which (*Hyporhina* Baur) shows a persistent postorbital arch (cf. Baur, 1893 and Douglass, 1908).

### Section **Anguimorpha**

Tongue smooth or papillate; hemipenes flounced and often pocketed or repand (p. 358); clavicles always present and simple; osteoderms, when present, never compound and usually corresponding in extent with the horny scales; teeth frequently conical, pointed, recurved, and, except in Zonuridæ, without lateral cusps, with alternate replacement and with shafts more solid than in the Scincomorpha; caudal chevrons often attached to the middle of the centra; no parasternum except in *Chamæsaurosa*.

The throat musculature is complex (cf. Figs. 54-61), except in the Zonuridæ, where it has iguanoid resemblances. In the burrowing members (and in the serpents) the Cervicomandibularis does not enlarge. This has doubtless to do with the fact that the construction of the lower rami (loosely articulated anteriorly) does not favor such a method of moving the head while burrowing.

In degradational forms the fore limbs are first lost and the clavicles seem to maintain a slower rate of reduction (pp. 352 and 354) than the scapulo-coracoid and sternum.

Degenerate forms are not found among the Platynota, Helodermatidæ, and Xenosauridæ.

Fossil remains perhaps referable to this group have been discovered in the Upper Jurassic and were described by Lortet (1892) as the Euposauridæ.

### Family †**Euposauridæ**

A nearly complete and finely preserved skeleton of *Euposaurus thiollieri* Lortet (1892, Pl. VI), shows saurian characters quite satisfactorily in the absence of a lower quadrato-jugal bar, the lacertilian pes (cf. Boulenger, 1893), the six cervical vertebræ, double sacral articulation, and the single-headed ribs.

On the basis of pleurodont dentition, absence of supratemporal fossæ; and non-dilatation of the clavicles, Boulenger considers that the characters approximate those of the Anguidæ.

The teeth do not appear to be strictly pleurodont and are possibly not at all so. Some, in Lortet's figure, are set in sockets, while a few appear to have broken through the lingual walls of the alveoli to lie as pleurodont teeth do. The teeth are small, pointed, and slightly recurved at the extreme tip. The skull roof appears to be covered with secondary encrustation, a feature which should place this family among the Autarchoglossa as might also the combination of extremely short propodials with very long metapodials in the hind limb, and the elongate, narrow, lacertid-like body. The clavicles appear to be simple, but are not certainly so. This would allow a reference with the Anguimorpha about as Boulenger has suggested.

If the other species referred by Lortet to *Euposaurus* can be so considered, as may appear doubtful, the family had attained considerable radiation in respect to length of body, limbs, and feet, and size of head, a differentiation not to be unexpected among any group of Ascalabota but scarcely found in this form among the Autarchoglossa. It might be recalled that a secondary dermal skull-roof does occasionally occur among living iguanids. Williston (manuscript) placed the Euposauridæ in his serial order between the Gekkonidæ and Agamidæ. I should allow this family a provisional situation in the Anguimorpha.

The family characters seen on Lortet's specimens include:

Teeth thecodont or subpleurodont; cranial ossifications present roofing over the supratemporal fenestræ; frontals fused; orbits large, directed dorsally and with a posterior emargination; quadrate bones narrow; clavicles simple (?); no parasternum (?); vertebræ broad, depressed (?).

#### Subsection **Platynota**

Seven or more cervical vertebræ; dorsal vertebræ of highly modified procelous type (Figs. 22-26); centra short, cylindrical, or tapering; condyles very large and with flanges well-developed; caudal chevrons pediculate and articulated (rarely fused) near the middle of each centrum; no transverse suture in the caudal centra; nasals elongate, fused; premaxillaries elongate; lower jaw with median transverse sutural joint or a well-developed joint (Mosasauroidæ); a parietal foramen; no osteoderms or bony skull plates; dorsal scales granular, (rhomboid on some parts in *Varanus* and in the aigialosaurs, dolichosaurs, and mosasaurs, cf. Nopcsa, 1903).

Superfamily **VARANOIDEA**

Centra depressed; condylar surfaces but little apparent in ventral view; clavicles and interclavicles present<sup>1</sup>; a lacertilian sacrum; digits with claws and without hyperphalangy; sclerotic ring cartilaginous.

Family **Varanidæ**

Postorbital arch usually incomplete<sup>2</sup>; frontals divided; seven cervical vertebræ; dentition subpleurodont; limbs normal, ambulatory; propodials elongate.

The existing species form a peculiarly isolated group with the following outstanding characters; tongue smooth, slender, elongate, extensile, deeply forked, and sheathed posteriorly as in the serpents; Mylohyoideus anterior concealed beneath the extensive Mylohyoideus posterior and the fascia of the Geniohyoideus and Cervicomandibularis which are specially developed in connection with the median mandibular joint; interclavicle anchor-shaped; hyoid arch broken at the basi-cerato-hyal joint, as in some *Diploglossa*; ventral scales small in comparison with those of other autarchoglossids; epipubis double.

The living species, despite considerable radiation in habitat, are very conservatively modified, being now placed within the one genus *Varanus*. The food habits are carnivorous or moluscivorous. Aquatic, subaquatic, terrestrial, and thoroughly arboreal forms are included. The extinct members form a long line of descent since the Lower Eocene. The early forms seem extremely like the living genus, and the Old World members, forty-one species in all, occurring in Eocene, Oligocene, Miocene, and Pliocene formations, are referred by Fejérváry (1918) without exception to the living genus, *Varanus*.

The North American Eocene genera differ from the known Old World stock in characters that may be recapitulated here.

†**Saniwinæ**, new subfamily

To include *Saniwa* Leidy (1870) and *Thinosaurus* Marsh (1872) from the Lower and Middle Eocene of North America (Huerfano, Wasatch, and Bridger formations).

Dorsal vertebræ resembling recent *Varanus* but not so short and with a less-marked precondylar constriction (cf. Figs. 24, 25); condyles not relatively as broad as in Varaninæ; a zygosphenal articulation is present in *Thinosaurus*, less marked in some species, and absent in *Saniwa*.<sup>3</sup>

<sup>1</sup>Perhaps lacking in Dolichosauridæ.

<sup>2</sup>Some recent Varanidæ are known to develop a complete jugal arch as a variant (Fejérváry, 1918).

<sup>3</sup>Gilmore in a recent paper (1922, Proc. U. S. Nat. Mus.) states that the type specimen of *Saniwa* has small zygosphenes and zyganchra. Forms related to *Saniwa* and represented in the American Museum collections appear to have no zygosphenal articulations. Gilmore finds that the type skull of *Saniwa* is very like *Varanus*.

A single tooth, referred by Leidy to *Saniwa ensidens*, is varanoid; being conical, recurved, sharp-pointed, smooth and thick-walled, but differs from typical *Varanus* in its "rhomboidally oval" base.

The caudal chevrons are articulated as in the Platynota generally.

The other known Varanidæ may be divided as follows:

†**Varaninæ**, new subfamily

To include *Varanus*, and possibly all the Old World Tertiary forms (excepting the Megalaninæ).

Mid-dorsal vertebræ short, with pronounced precondylar constriction; condylar surfaces scarcely apparent in direct ventral view; condyles relatively larger than in the Saniwinæ; no zygosphenes and zyganthrum.

†**Megalaninæ**, new subfamily

To include the Megalanidæ of Fejérváry (1918),—Pleistocene ?, Australia.

Mid-dorsal vertebræ very short, broad; an extremely pronounced precondylar constriction; condylar surfaces not greatly apparent in direct ventral view, condyles broader than in Varaninæ; a zygosphenes and zyganthrum (Fig. 26).

The vertebræ of the Saniwinæ, as well as what is known of the teeth, point to characters in this group more like those of less specialized anguimorphs. The gigantic megalanians may be considered as the most highly developed terrestrial branch of the Platynota.

Family †**Aigialosauridæ**

This family, known only from the Lower Cretaceous (Neocomion) of Europe, includes the following genera (Nopcsa, 1903): *Aigialosaurus* Kramberger, *Carsosaurus* Kornhuber, *Opetiosaurus* Kornhuber, ? *Meso-leptos* Cornalia.

The skeleton and squamation resembles that of *Varanus* in some detail but there is a complete postorbital arch, the frontals are fused, the dentition as in the mosasaurs is subthecondont, large pterygoid teeth are present, and the limbs are shortened and the feet broadened, doubtlessly in connection with subaquatic habits.

Boulenger (1891a, 1893) regarded this group, with the dolichosaurs, as ancestral to all other lizards, mosasaurs, and serpents. Kramberger (1892) held similar views. Dollo (1892, 1904) considers the aigialosaurs as derived from true lizards near the Varanidæ and as ancestral to both Dolichosauridæ and Mosasauridæ. Nopcsa (1903) reaches the same

conclusions, apparently independently. Williston (1904) also adopts this opinion, emphasizing the varanoid affinities of the aigialosaurs and dolichosaurs. I hold this view, and regard the presence of the annectant Aigialosauridæ as grounds for denying rank higher than that of a superfamily to the mosasaurs.

#### Family †**Dolichosauridæ**

This family is distinguished from the Varanidæ and Aigialosauridæ by the presence of thirteen cervical vertebræ and in the relatively small, short skull, small, short limbs, elongate, serpentiform body and tail, possible lack of clavicles and interclavicles, and lack of preacetabular pubis. The dentition, as in *Varanus*, is subpleurodont; the frontals are separate, and a postorbital arch is present.

The group is known only from the Cretaceous of Europe, and includes under the authority of Nopcsa (1903), the genera *Dolichosaurus* Owen, *Acteosaurus* von Meyer, *Pontosaurus* Kramberger, and *Adriosaurus* Seeley.

The so-called "ophidian" characters of the aquatic dolichosaurs (cf. Nopcsa, 1908) are paralleled in many other non-related lizards (cf. p. 345). Of these characters the small skull, zygantral articulations, cylindrical body, and reduction of extremities do not of themselves indicate serpent relationship; nor does the elongate neck, since we cannot tell whether or not the cervical vertebræ of snakes have been increased above those of lizards (cf. Janensch, 1906). The paleotelic characters held in common with the Serpentes are those of platynotine lizards in general. Furthermore, it is difficult to see how a group so highly modified in body form could be ancestral to the mosasaurs.

#### Superfamily †**MOSASAUROIDEA**

Postorbital arch complete; seven cervical vertebræ; centra cylindrical; condylar surfaces directed posteriorly; dentition subthecondont; clavicles and interclavicles greatly reduced or absent; limbs paddle-shaped, without claws and with hyperphalangy; sclerotic ring bony.

Three, perhaps four, adaptive types of mosasaurs are recognized (Williston, manuscript). These include: (1) surface, swimming forms "with elongate trunk composed of as many as thirty-five dorsals, the tail with pronounced subterminal dilatation, zygosphenes, a well ossified carpus and only slight hyperphalangy,"—*Mosasaurus* and *Clidastes*; (2) deep sea forms "with proportionally shorter neck, less elongated trunk with but twenty-one vertebræ, a more uniformly flattened tail, less well-

ossified carpus and tarsus and greater hyperphalangy,"—*Platecarpus*; (3) "a diving type, with more elongated head, heavy cartilaginous protections for the ears, a relatively short neck, body with but twenty-two vertebrae, a longer and much flattened tail, almost entirely cartilaginous mesopodials and highly developed hyperphalangy,"—*Tylosaurus*; and (4) possibly a littoral, molluscivorous genus, *Globidens* Gilmore (1912), in which the teeth were rounded and rugose.

In *Globidens* the replacing teeth are pointed before they become functional. In *Varanus niloticus*, a cancrivorous and molluscivorous monitor with rounded teeth, the teeth in the young are pointed (cf. K. P. Schmidt, 1919).

The osteology of the mosasaurs has been studied extensively. Far more material has been handled than of any group of recent lizards. Yet, curiously enough, disagreement still prevails regarding their descent and place in the system.

The history of this controversy has been reviewed by Baur (1892) Williston (1898), Nopcsa (1903), and Dollo (1904). Those who have favored varanoid relationship of the mosasaurs and have generally regarded them as something less than a division of the Squamata separate from lizards are: Cuvier; Goldfuss, Owen, Marsh, Baur (1892, 1895, 1896), Merriam (1894), Williston (1898, 1904), Nopcsa (1903, 1908), and Versluys (1907).

Those who have considered varanoid relationships as questionable or distant are: Cope (1869, 1878, 1895*a*, 1895*b*, 1896*a*), Boulenger (1891*a*, 1893), Dollo (1892), Kramberger (1892), Osborn (1899), Fürbringer (1900), Gadow (1901), and Fejérváry (1918). Von Huene (1910) is non-committal.

Osborn writes (1899, p. 187): "Besides the secondary degenerate adaptation to marine life shown in the girdles and appendicular skeleton, there are certain fundamental differences in the basioccipitals (p. 170) and ribs (p. 176), in fact in all parts of the skeleton. These differences . . . do not even justify the assertion that the Varanidæ and Mosasaurs sprang from a common stem."

The basioccipital processes are less developed in *Varanus* than in any other lizards I have examined with the exception of the specialized Uroplatidæ. This is a feature apparently correlated with the strength and degree of tendinous insertion of the long subcervical muscles. The process is absent in some varanids, present as a small tubercle in others, and may be further developed as a considerable swelling. From its variability in the Varanidæ I should not be inclined to regard its presence in Mosasaurs as grounds for distinct separation.

A point is made of the *Sphenodon*-like tendencies of the ribs in *Tylosaurus*. This, it is shown, is most apparent in their shape and curvature, in the position of the diapophyses of the dorsal ribs, and in the general form of the chest.

The ribs in both *Varanus* and *Tylosaurus* are flattened. The curvature, as shown by a skeleton of *Varanus* at hand, and by placing the disarticulated ribs directly upon a photograph of the ribs of *Tylosaurus*, lying in place as they were found, is almost exactly the same in the two genera. The expansion of the anterior dorsal ribs is shown almost equally in *Varanus* and in *Tylosaurus*. In the most anterior dorsal rib of *Tylosaurus*, there seems to be no more vertical flattening than in the specimens of *Varanus* at hand. The rib differences cannot be considered a strong objection to varanoid relationships.

The form of the chest depends largely upon the correctness of Dr. McGregor's restoration of the sternum. If the ten anterior dorsal ribs had a sternal connection as shown in the restoration, profound divergence from the usual lacertilian condition would be indicated. No sternal rib connections are actually seen on the specimen but the direction of the anterior five dorsal ribs, at least, would suggest sternal attachment for these. The posterior five cartilaginous ventral rib-ends may well have lain free in ventral intercostal muscles, as in many lizards, and the comparatively small sternum may not really provide attachment for so many ribs. The specimen as it lies shows no marked departure from lacertilian conditions in relative position of sternum and cartilaginous ribs.

The form of the axis and the two rounded anterior intercentra are considered by Osborn to represent primitive features in the skeleton. The number and position of the elements of the axis and the lack of fusion of the axial intercentrum are the same in *Varanus* and the Mosasaurs. Can the rounded form of the intercentrum be considered primitive? If the ring-shaped intercentrum of *Varanus* represents the element occurring in the amphiœlous geckos and many other lizards, as should be unquestionably the case, and if we may consider the gekkonid condition as primitive on the basis of its close resemblance to certain Permian Cotylosaurs (p. 343), (and also owing to the fact that in geckos the intercentra persist and are half-ring-shaped throughout the dorsal region), we may certainly consider the half-ring-shaped centra of other lizards as of primitive shape and should hesitate to regard the mosasauroid condition as anything but a secondary development.

Followers of Baur, Williston, and Nopcsa will perhaps be surprised to find that Fejérváry (1918) is not inclined to regard the Aigialosauridæ



as intermediate between the Varanidæ and the mosasaurs. Williston (1904) holds that "there are no more striking examples of evolution presented in all vertebrate paleontology than that of the aquatic mosasaurs of the Upper Cretaceous, through the semi-aquatic aigialosaurs of the Lower Cretaceous, from the terrestrial varanoids of the lowermost Cretaceous or Upper Jura." Fejérváry retorts: "I must doubt of so striking a transformation taking place in comparatively so short a time," and adopts the Osborn-Fürbringer conception of separate origin of varanids and mosasaurids. All this in the face of the fact that among the thousands of specimens of mosasaurs so far collected not a single one has been taken below the Upper Cretaceous! It is curious that Fejérváry's long, slow evolution of the mosasaurs has left us no trace.

I am inclined to retain the mosasaurs as a superfamily of the Platygota as Baur has done. This is suggested by the shape and position of the skull elements, the teeth, the median mandibular joint, the vertebræ, the shape of the interclavicle when present, the formula of the scapulo-coracoidal fenestræ, the central pediculate articulation of the caudal chevrons, the lack of osteoderms, cranial plates, and parasternum, the lingual furrows in the prevomerine bones, and the shape of the scales.

#### Subsection **Diploglossa**

Six cervical vertebræ; dorsal vertebræ of normal procœlous type (except in Pygopodoidea); centra not constricted in front of condyles; no condylar flange; proximal belly of Biceps brachii often with a posterior tendon and an anterior fleshy portion, the opposite of what usually occurs (p. 404); caudal chevrons central and pediculate only in the Glyptosauridæ, otherwise when central (limbless Anguidæ and the Anniellidæ) ankylosed to the centra as in the Serpentes; osteoderms present in all families except the Pygopodidæ, never compound, and sometimes (Glyptosauridæ, Xenosauridæ and slightly in Helodermatidæ) ornamented with tubercles; dorsal scales imbricate except in the Helodermatidæ and Xenosauridæ.

Most of the footless members of this group are grass-living, practically non-burrowing forms, such as are rarely developed among scincimorphs (cf. *Tetradactylus*).

The girdles are never profoundly reduced except in the Anniellidæ and in a few Pygopodidæ. In these, closed eyes and ears, and shortened tails point to a burrowing habitus. *Anniella* shows close similarities to the Anguidæ, and especially to *Gerrhonotus*, as expressed in the pattern of the mylohyoid, the hemipenes, and in other characters determined by Baur (1894) and Coe and Kunkel (1906).

The Pygopodidæ and Helodermatidæ include the only non-burrowing forms, except the geckos, that lose the supratemporal arch. A hypoischial cartilage is generally present (pp. 405–406). In the degenerate *Pygopus* it divides, half going with each of the well-separated ischii. The same phenomenon occurs in the degenerate anguid, *Ophiodes*; this may occur in the serpents but is unknown in other groups of lizards.

#### Superfamily **ANGUIOIDEA**

Vertebral centra tapering, not constricted medially; condyles not nearly as wide as the centra except in *Ophisaurus* where the condyles are varanoid, but where there is no precondylar constriction as in the Varanoidea; ribs in *Ophisaurus* with a dorsal muscular process but no ventral process; no femoral or preanal pores; a geniomyoid muscle (p. 373) such as occurs in no other lizard with possible exception of *Xantusia*; teeth solid; tooth replacement alternate (pp. 363–364).

This superfamily has many superficial resemblances to the Scincoidea, but scarcely any of the paleotelic characters common to that group, being more specialized in hemipenial texture, pattern of throat musculature, osteodermal structure, fusion of skull elements, variations in position of caudal chevrons, variation in tooth replacement, and other features.

The pattern of the throat musculature indicates close affinity between the families Anguidæ, Anniellidæ, and Xenosauridæ. The Helodermatidæ are included because of the presence of a Geniomyoideus muscle, and because of their relationship to the Glyptosauridæ,—true anguoids which are in some characters intermediate between the Anguidæ and Helodermatidæ.

The greater number of species of the two latter are distributed in southwestern North America. The Anniellidæ and Xenosauridæ are monotypical and confined to that region.

Fossil genera referable to the Anguidæ include forms from the Miocene of Europe. Some of these closely resemble recent *Ophisaurus*. The best known is *Propseudopus fraasii* Hilgendorf (1885) described from a complete skeleton taken at Steinheim. The ribs have a dorsal tuberculum-like process as in *Ophisaurus*, the skull, teeth, and osteoderms are also similar to *Ophisaurus*. The generic distinction rests upon the greater number of teeth on the prevomers.

Hilgendorf includes von Meyer's *Pseudopus*, from the Oligocene of Bonn (later described under the name *Pseudopus moquintius* by Boettger, *Paleontographica*, Band XXIV), with his genus *Propseudopus*.

Some of the species of "*Anguis*" noticed by Lartet (1851) from Sansan are described as having obtuse teeth as in *Ophisaurus*. Gervais (1859) has redescribed two of Lartet's species.

Gerhardt (1903) has studied a lower jaw with teeth from the Lower Miocene of Ulm and refers the genus to *Ophisaurus*.

#### Family †*Glyptosauridae*

The lizards of this Tertiary group are characterized by their osteoderms of the simple anguoid type, imbricate on the body, and minutely embossed with small enamel-covered tubercles. Scutes of this nature in connection with a skull fragment were first described by Gervais (1859) under the name *Placosaurus rugosus*. This material was found in the Upper Eocene of Sainte Aldegarde. Other European remains described by Gervais (*Varanus margariticeps*), Filhol (1877, *Plestiodon cadurcensis*; 1894, *Necrodasyus galliæ*), de Stephano (1904, *Diploglossus cadurcensis*) and Leenhardt (1906) are all regarded by Boulenger (1919b) as *Placosaurus*. All are from the Eocene.

Boulenger had the opportunity of studying photographs of the skull of *Placosaurus*, which Leenhardt described, and pronounced the fossil a helodermatid. The absence of a squamosal (supratemporal) arch would separate *Placosaurus* from the American forms, *Glyptosaurus* and *Xestops* (cf. Marsh, 1871, 1872). All known parts of the skeleton of *Placosaurus*, the teeth and the osteoderms, are so similar in the American genera, however, that I am inclined to think a squamosal arch may eventually be found in *Placosaurus*. Depéret (1917) suggests resemblances between the European and American genera.

Douglass (1903, 1908) has described and illustrated portions of skulls of *Helodermoides* and *Glyptosaurus*. He says that a supratemporal arcade is present in his skull of *Glyptosaurus* but the figure does not show this important point satisfactorily. The bone called squamosal by Douglass is evidently the median element (tabulare). Cope (1884) states that both arches occur in *Peltosaurus*. His type specimen does not show this but another fragment of *Peltosaurus* figured by Douglass (1908) illustrates part of the squamosal in place.

The American Museum collections contain considerable material representing this group of lizards. Skeletal and skull fragments, jaws with teeth, and osteoderms, are included of each of the four genera, *Glyptosaurus* (Eocene), *Xestops* (Eocene), *Helodermoides* (Oligocene), and *Peltosaurus* (Oligocene).

Among nine or more portions of crania collected at various localities only one shows the squamosal arch. This specimen consists of the skull, jaws and scutes of *Xestops* (A. M. N. H. No. 5168) from the Wasatch Eocene of Clark's Fork Basin. The skull has been crushed flat but after preparation indicates the disarticulated bones of the temporal region with remarkable clearness (Figs. 103, 109). Characters seen on this and other specimens which establish distinctions of family rank between this group and the *Helodermatidæ* include:

- (1) Presence of a supratemporal arch and fenestra.
- (2) Separation of prefrontal and postfrontal above orbit.
- (3) Postfrontal and postorbital entirely distinct.
- (4) Pediculate caudal chevrons on the centra (Fig. 101).
- (5) A pineal foramen (very small in *Xestops*, absent in *Peltosaurus*).
- (6) Imbricating osteoderms on the body.
- (7) Teeth on the pterygoid, palatine, and prevomerine bones.
- (8) Parietals united by suture (fused in *Peltosaurus*).
- (9) Transverse processes of first caudal vertebra arising from the entire length of the centrum as in *Gerrhonotus* (cf. Figs. 99-101).
- (10) Jugal with an angular process (Fig. 107).
- (11) Frontals fused (separate in *Helodermoides*?).
- (12) Teeth highly pleurodont with cylindrical, solid shafts and blunt, highly wrinkled crowns, as in some *Anguidæ* (Figs. H and I).

Except for the unfused parietals the above characters would allow inclusion with the *Anguidæ*. There are, however, distinctions which will not permit this:

- (1) The great extent of the patches of teeth on the pterygoids and palatines.
- (2) The massive rectangular jugal, somewhat as in *Heloderma*.
- (3) The extremely large tabulare, exposed dorsally as in *Heloderma*.
- (4) The great length of the slender squamosal which extends forward nearly to the jugal.
- (5) The corresponding reduction of the postorbital.
- (6) The embossed tuberculate osteoderms slightly suggesting *Heloderma* (cf. Figs. 94-98, 104, 105), in ornamentation.
- (7) Quadrate peculiar in having a broad, thin, semicircular internal wing (Fig. 110).
- (8) Lower jaw massive; curved posteriorly as in *Heloderma* (Fig. 106).
- (9) Meckelian sulcus completely covered (Fig. 112).
- (10) Splenial extensive posteriorly (Fig. 112).
- (11) Angular with extensive external surface covering the surangular as a thin plate somewhat as in *Gerrhonotus* (Fig. 107).
- (12) Paroccipital a separate element as figured by Leydig (1872, pp. 26 and 41, Pl. III, fig. 33) for *Lacerta agilis* (Fig. 109).

I think it desirable to reestablish the family *Glyptosauridæ* (Marsh, 1872) to include the genera *Glyptosaurus* Marsh, *Xestops* Cope (for *Oreosaurus* Marsh preoccupied), *Peltosaurus* Cope, *Helodermoides* Douglass, and probably also *Placosaurus* Gervais.

Many of the characters mentioned above indicate that the group is intermediate between the Anguidæ and Helodermatidæ.

Some of the observations of Cope (1884) on *Peltosaurus* may be extended to *Glyptosaurus* and *Xestops*. Thus, in the latter, the pre-maxillaries are undivided, constituting a separation from the Scincidæ; inferior crests are present on the frontal plate as in *Ophisaurus* and many other Anguimorpha; there is a straight frontoparietal suture and the parietals are extended posteriorly.

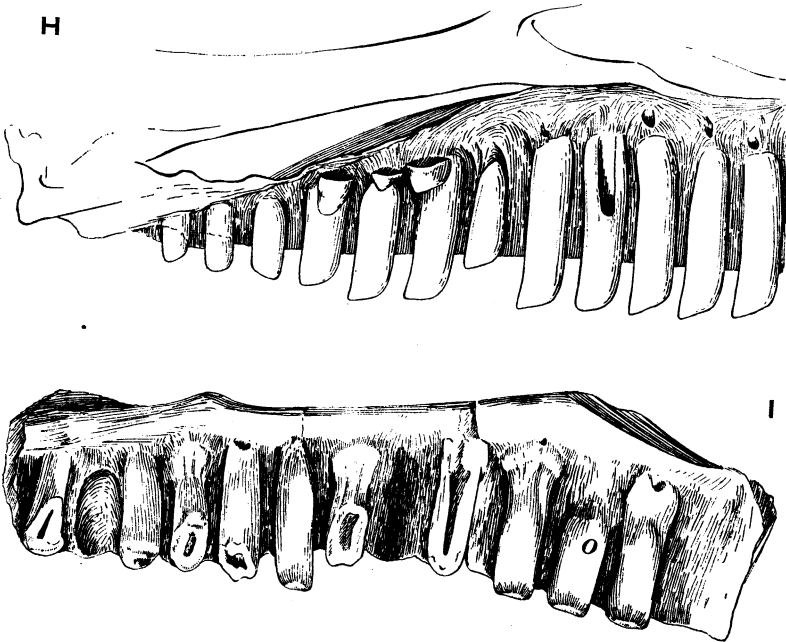


Fig. H. Portion of left maxillary with teeth of *Gerrhonotus scincicauda scincicauda*,  $\times 6$ , A. M. N. H. No. 595.

The small replacement teeth do not enter the bases of the old shafts but lie outside them as in most Anguimorpha. The shafts are semi-solid and chisel-shaped. Similar features are seen in the glyptosaurid, *Xestops* (Fig. I), where an old shaft (O) is seen, which indicates by erosion at the base that a replacement bud has occupied a position comparable with that seen in *Gerrhonotus*.

Fig. I. *Xestops* sp.?,  $\times 1\frac{1}{2}$ , Dept. Vert. Pal., A. M. N. H. No. 5175.

#### Superfamily PYGOPODOIDEA

Vertebral centra short, cylindrical, slightly constricted medially as in the Gekkota; condyles large, nearly as wide as the centra (Fig. 13); ribs with a long, ventral muscular process (Fig. 17); teeth solid; preanal pores present; no Geniomyoideus; no Mylohyoideus anterior superficialis.

This is an isolated group with some apparently primitive features in the vertebræ and throat musculature (p. 370) and with anguoid and zonuroid convergences.

#### Family **Pygopodidæ**

Skull arches both lacking; pleurodont or pleurothecodont; only three or four bones in the mandible (p. 375); no osteoderms; eyelids immobile, transparent; only one series of transverse scales to each body segment; Rectus superficialis as in *Chamæsauro* (p. 380).<sup>1</sup>

Jensen (1901), following the suggestion of Boulenger (1885–1887), and after study of additional specimens of the Australian *Ophioseps* Bocage, established the family Ophiopsisepidæ to include that genus. Werner (1912) has referred the form to the Pygopodidæ, a course approved by Fry (1914) and Zietz (1921). Fry evidently considers the genus distinct from *Aprasia* but comparison of Jensen's plate with figures of *Aprasia pulchella* given by McCoy (1885–1890, II, Pl. CLXI, fig. 1) show very close resemblances between the two genera.

*Aprasia* and *Ophioseps* are especially interesting as examples of burrowing forms developed in a limbless family which includes both subterranean and surface-living types. In *Pygopus* and *Lialis* the tail is extremely long and brittle, the ear is exposed and there is no enlargement of the rostral and nasal plates. Although the Horn Expedition Reports state *Lialis* to be a burrower I am assured by Mr. A. S. Le Souëf that the lizard is a surface dweller and that it catches and swallows other surface-living lizards. *Pygopus lepidopus*, from observations of Werner (cited in Brehm's 'Tierleben'), appears to be a climber; the only limbless lizard known to have this habit. *Delma impar* (cf. Lucas and Le Souëf, 1909, p. 219) is probably at least a partial subterranean with much shorter tail and slightly enlarged rostral plate. In *Aprasia pulchella* the tail is still shorter and blunter, the rostrum extended, and the ear completely closed. A specimen is stated by McCoy to have been "turned up by a plough in a field." *Ophioseps nasuta* is a highly specialized pygopodid. According to Jensen's figures the postfrontal is absent and the dentition is reduced to two very small teeth on each side in the extremely weak dentary. The fore part of the skull is expanded as in the burrowing snakes, Typhlopidae. The parietals are elongate and fused. *Ophioseps repens* Fry represents the most extreme burrowing habitus developed among the Pygopodidæ with a tail less than a third of

<sup>1</sup>Peculiar postcloacal bones have been seen in *Lialis* (Fürbringer, 1869). Carlsson (1887) finds them also in *Pygopus* and figures them as furnishing attachment to some of the median subcaudal muscles. There would seem the remote possibility that these bones represent the ossa cloacæ of certain geckos.

the total length and the anterior head plates much broadened. The shoulder girdle has not been investigated.

We should accordingly surmise that the Pygopodidæ are of considerable antiquity, both on account of their morphological peculiarities as a whole and because of the development of a radiation quite unique in a single family of limbless lizards.

The Pygopodidæ have not been found beyond the limits of the Australian-New Guinean-Tasmanian region. Ángel (1920) has referred a Siamese genus, *Typhloseps*, to the "Ophiopsisepidæ." This lizard appears to be a scincoid possibly near or identical with *Isopachys*, described by Lönnberg (1916) from the same vicinity.

#### Superfamily ZONUROIDEA

Vertebrae as in the limbed anguoids; ribs without muscular processes; femoral or preanal pores present; no geniomyoid muscle; no Mylohyoideus anterior superficialis; teeth cœlodont; tooth replacement successive. The osteoderms when present are of the highly developed type found in other diploglossids, especially in *Gerrhonotus* and *Ophirosaurus*. The throat musculature, while not primitive, is of a simpler type than in other diploglossids except the Pygopodidæ (cf. Figs. 55-61). Resemblances with the Ascalabota in details of tongue and hemipenial structure, in the pattern of the throat musculature, and in the teeth, are closer than those shown by any other anguimorphs.

#### Family Zonuridæ

Skull arches both present; dentition pleurodont; six bones in the lower jaw; interclavicle cruciform with tendency to be widened; osteoderms usually present and non-tuberculate. A rudimentary zygosphenal articulation appears and the skull is roofed over in *Zonurus*. The Geniohyoideus is divided in that genus as in the Iguanidæ. In *Chamæsaurosa*, the Geniohyoideus is not divided and the Rectus superficialis is arranged as in the Pygopodidæ and is free from the skin as in that group; also, as in the Pygopodidæ, there is only one transverse scale row over each segment of the body.

#### DISCUSSION OF THE PHYLOGENY

In attempting to determine the phylogeny, attention has been directed: (1) to the fossil record, (2) to the comparative morphology of the living genera, and (3) to the geographic distribution.

The systematic groups are established primarily on the basis of universally distributed and mutually exclusive characters. The phylo-

geny demands consideration not only of these but of certain archaic features, such as persistence of chorda in the vertebræ, which may be distributed so as to have relatively little systematic value.

In estimating the value of characters supposed to have a bearing on the phylogeny, I have been guided: (1) by the distribution of such characters in paleontological sequences, (2) by the time of appearance in the ontogeny, (3) by the possible vestigial or non-functional nature of the structure in the adult, and (4) by the degree of complexity of the structure, indicating with reasonable assurance whether or not reversion may have taken place. These points are considered in the review which occupies the remaining pages of this paper. The order in which these characters are treated is intended to illustrate the order of their relative phylogenetic importance or **PALEOTELIC VALUE**. The sum total of such characters in any given form or group is an index of the relative primitiveness, or **PALEOTELIC WEIGHT**, of that form or group. The approximate **PALEOTELIC WEIGHT** of each family is illustrated in the phylogenetic chart (p. 333), where the black columns of greatest height indicate the greatest degree of evolutionary development, greatest loss of primitive characters, and the least **PALEOTELIC WEIGHT**. Such a scale serves as a check, preventing the derivation of any group having a large sum total of primitive heritage from another group with less of such a total.

An example will immediately present itself. Cope (1900, p. 206) derives the gekkos (*Gekkota* = *Nyctisaura*) from the group to which the iguanids and agamids are referred. By placing the emphasis on the tooth character which Cope has employed this appears plausible, but after comparison of *Gekkota* and *Iguania* in total reserve of heritage, such a step seems unjustified (cf. p. 304).

After determining what derivations cannot reasonably be established, I have endeavored to gain some idea of interfamily relationships by examination of characters common to two or more families. This method meets with the usual difficulties that one character may join, let us say, families A and B, another A and C, and another B and C, leaving us as much in the dark as before concerning the true descent. Consequently, where there is conflicting evidence, an attempt has been made to find two or more characters of practically universal distribution among the groups in question. This procedure has been adopted for still higher groups, with results as indicated in the accompanying chart.

Another line of evidence which cannot well be set aside is the matter of distribution (cf. Gadow, 1901; Palacký, 1899). In some cases this



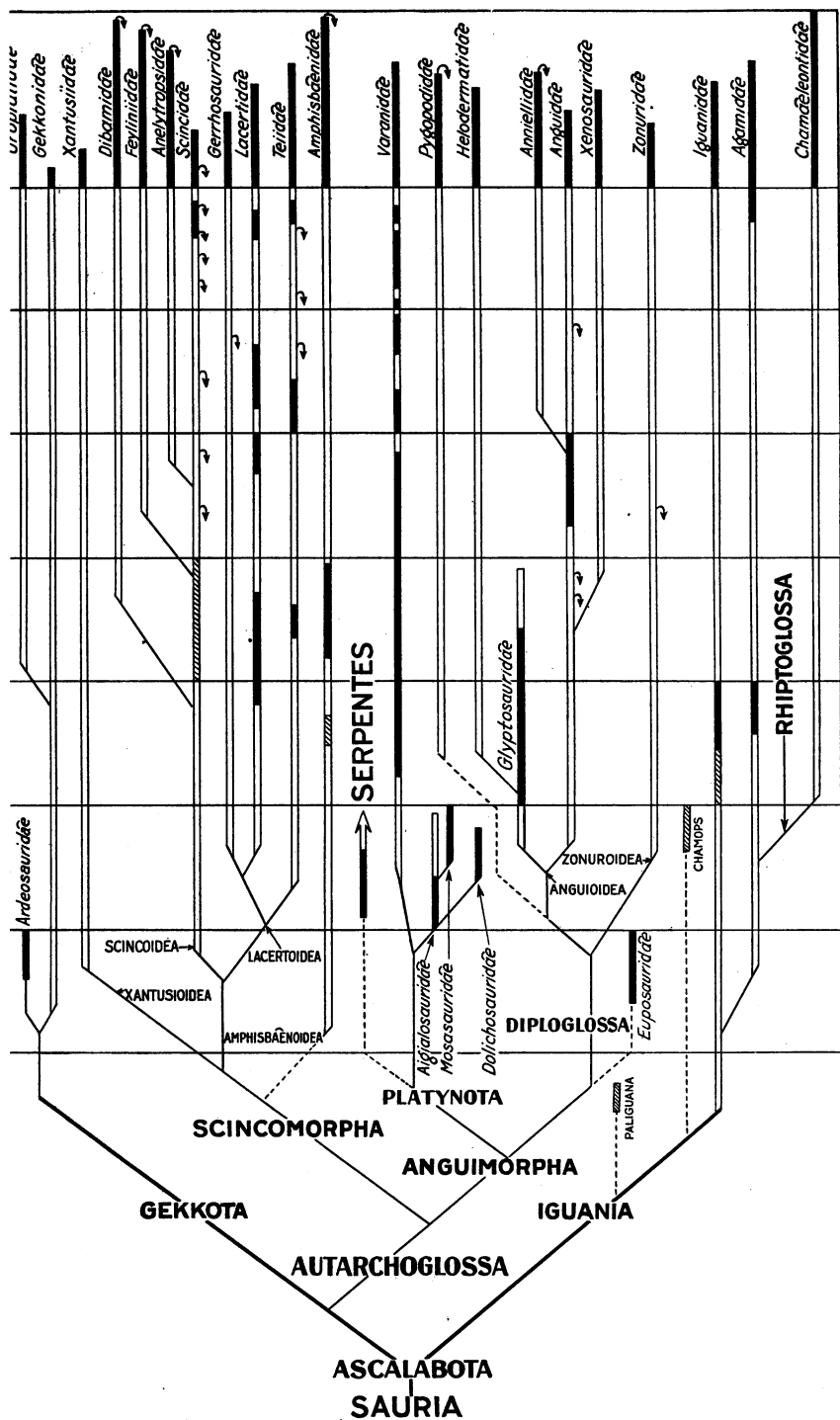


Chart Illustrating the Phylogeny and Classification of the Families of Lizards.

Heavy black columns under the space marked "Recent" indicate the relative specialization of each family. Retention of primitive characters and paleontologic weight is greatest in those groups having the lowest columns. The fossil record includes only well authenticated genera (heavy black) and fairly certain (cross-lined) references. Many fossil genera are omitted altogether as of unsatisfactory status. Dotted lines denote uncertain relationship; downwardly directed arrows, limbless families and groups of species.

gives important supplementary data as to the relationships and antiquity of groups.

Most of the "primitive" families (here so called) are of wide distribution. The Gekkonidæ and Scincidæ are cosmopolitan. The Anguidæ holarctic and South American. The Iguanidæ are scattered, related forms) cf. p. 308), occurring in Madagascar, the Fiji and Friendly Islands, and the Western Hemisphere. Supplantation of this group by the Agamidæ has doubtless occurred in most parts of the Old World. The Amphisbænidæ, known abundantly from the Oligocene of temperate North America, occur at present throughout the tropics except in Australasia, most Oceanic Islands, the Oriental region, and Madagascar. The Amphisbænidæ, distributionally an ancient group, have acquired an extreme degree of specialization, obscuring much of what appears to have been a relatively primitive heritage. Other groups have the distributional facies of relicts—the Helodermatidæ in Borneo and southwestern America,—the Xantusiidæ in southwestern America and the West Indies.

Some families of seemingly intermediate age on the basis of structure are restricted to the Old or New World exclusively, such being in the Old World: the Gerrhosauridæ (Africa and Madagascar); Lacertidæ (Africa and Eurasia); Varanidæ (tropical Asia and Australasia, and Africa); Zonuridæ (southern and eastern Africa); Agamidæ and Chamæleontidæ (Africa, Madagascar, and southern Asia, eastward into India); and the Teiidæ in the New World. Boulenger (1920) expresses the possibility of derivation of the Lacertidæ from unknown Old World teiids and subsequent supplantation of the latter.

Three of the more recent families occurring in Asia are absent from Australia—Lacertidæ, Anguidæ, and Chamæleontidæ. Those absent from Madagascar but occurring in Africa are the Lacertidæ, Varanidæ, Anguidæ, Zonuridæ and Agamidæ. Many locally distributed families are presumably so because of recent origin. We might place in this category the Uroplatidæ, possibly derived from less specialized geckos in Madagascar; the local, burrowing scincoids, independent families of which seem to have arisen in Mexico, in Africa and in the East Indies; the burrowing anguroid, *Anniella*, of California; the non-primitive Xenosauridæ of extremely local central Mexican distribution.

Temperature exerts an important control over the distribution. Anguids are rare in the tropics but range far northward and higher in the Alps and the Sierra Nevada than other lizards. The varanids, geckos and gerrhosaurids are tropical and subtropical. The amphisbænids

are almost exclusively tropical—partly, perhaps, because of soil conditions or food supply.

What appear to represent archaic members of primitive groups (*Phyllurus* and *Nephrurus* among the Gekkonidæ, and *Trachysaurus*, *Tiliqua*, and *Egernia* among the Scincidæ) occur in Australia. The New Zealand geckos, *Naultinus* and *Hoplodactylus* are perhaps primitive in the arrangement of the femoral pores. Other cases of peripheral distribution of ancient forms (cf. Matthew, 1915, pp. 288–292) are rare. The recent African range of *Nucras*, a generalized lacertid, also found in Oligocene Amber of Prussia, is significant (cf. Boulenger, 1920); also the African and Australian dispersal of primitive anguimorphs, the Zonuridæ and Pygopodidæ.

After trying to establish the relationships on the basis of universally distributed characters, it has proved instructive to ascertain the “tendencies of evolution” among the chief groups. Some of these apparent tendencies are listed in the sections devoted to group characters, and the matter deserves remark.

I have divided the Sauria into two main divisions partly on the basis of the presence or absence of an extensive muscle—derived from the Rectus and frequently connected with the ventral scales,—partly on certain hemipenial characters worked out by Cope thirty years ago and used by him in the definition of less extensive groups, and partly on characters of lepidosis. In the Ascalabota the muscle in question is absent and no other muscles take its place. In all limbed Autarchoglossa, it is present. In all Ascalabota, which includes about half the known species of lizards, no snake-like or limbless forms of any kind are developed. Among the Autarchoglossa, limbless or practically limbless forms are present in no less than ten different families. Apparently a latent “tendency” is here present which may be preserved under certain requirements of habitat. This particular “tendency” is correlated with the presence of a certain muscle. The muscle seems to be useful in pulling the body over the ground as the limbs cease to be functional. To take another case: many permanently arboreal lizards are developed among both of the divisions just considered. In the Autarchoglossa not a single arboreal form shows any pronounced modifications in body form or in the shape of the digits. K. P. Schmidt has illustrated (1919, Pl. XXIII, fig. 2) an African bark-living lacertid (*Holaspis*) that has gained a slightly flattened form and Boulenger (1917, p. 232) describes another lacertid (*Platyplacopus*) which has developed specialized distal phalanges probably in correlation with the habit of living in the tops of tall grass.

But these are minor matters in comparison with the profound changes which accompany permanent arboreal life among the Ascalabota. Here we have the following conditions. Arboreal Gekkota, which are usually bark-dwelling and cling close to the broader surfaces of trees, often exhibit unusually flattened bodies and sometimes have lateral fringes and webbed feet; truly compressed forms are unknown in this group. The permanently arboreal Iguania are all compressed and this condition is carried to an extreme in the *Rhiptoglossa*. *Draco* is slightly depressed but here is a volant as well as arboreal habitus. Both the Gekkota and the Iguania develop laminate sucking digits—the arboreal *Autarchoglossa* never develop them. The histology of these structures is similar in the two groups of Ascalabota.

The chart (p. 333), is intended to exhibit the phylogeny as far as the various families. The conventional synopsis of classification is usually thought of as being dichotomous. A true phylogeny is of course not necessarily so. It might be considered undesirable to give equal rank to subdivisions such as the *Autarchoglossa* and *Ascalabota* where one group is apparently derived from the other and not from a common stem. The same argument would hold for the *Serpentes* and *Sauria*, and for the *Rhiptoglossa* and *Iguania*. It is obvious that groups held to be equal or dichotomous on the basis of classification may not have had an equal extent of geologic history, and when it is intended to illustrate this history simultaneously with the classification some difficulties present themselves. The agreement between classification and phylogeny is seldom exact and allowances must be made for artificiality on both sides.

It may also be objected that in the chart the *Iguania* are more widely separated from the Gekkota than their order in the synopsis would indicate. This difficulty will be avoided if one thinks of the chart as rolled into a cylinder with the main stem of the *Iguanidæ* near that of the *Gekkonidæ*. The linear arrangement of the families is intended in some degree to express relationships which cannot be shown in the branching scheme.

Thus in the linear arrangement, the *Xantusiidæ* are placed near the *Gekkonidæ*, to which they show some affinity, and in the branching scheme they retain their place among the *Scincomorpha*, where the greater number of their characters would place them. So also the *Zonuridæ* occupy a position next to the *Iguanidæ* on the basis of common retention of certain characters.

The extent of the paleontologic record is indicated in black. The almost continuous record of the rather specialized *Platynota* far into the Cretaceous forces us to extend many of the other less specialized

groups back to beyond this point. There are no records of true Sauria from the Permian but the supposedly ancestral form *Aræoscelis* is known to be of that age. The Sauria constitutes an entirely natural and diversified group and appears to have arisen in the Permian from a stem perhaps related to Williston's *Aræoscelis*. This ancestral form should have a fair proportion of the following characters:

Vertebrae with centra cylindrical, not tapering, biconcave, and with thin, half ring-shaped intercentra.

Teeth thecodont or pleurothecodont.

Postfronto-squamosal arch short and massive. Postfrontal and postorbital present.

Postorbital arch (jugal) broad, short, and erect. Skull elevated.

Two dorsal temporal elements adjoining the quadrate.

Median bones of skull-roof not united.

Teeth present on the pterygoid, palatine, and vomerine bones.

A parasternum.

A proatlas (?).

An os intermedium.

A pineal foramen.

Pterygoids separated on the mid-line.

Ribs slightly double-headed. The third cervical with ribs.

Lacrymal exposed externally as part of lower anterior border of orbit.

Scapula narrow at base.

Coracoids plate-like and shallowly emarginate anteriorly.

Clavicle broadened toward the mid-line.

Interclavicle a subrhombic plate.

An epipterygoid.

Osteoderms, if present, compound or diffuse.

#### EVALUATION OF PALEOTELIC CHARACTERS

An attempt has been made to assign some comparative rank (paleotelic value) to each of the following characters, those first treated being thought the older, hence the more important in determination of the phylogeny. A form having even a few characters of high antiquity may be considered more ancient than one having many characters of lesser paleotelic value. High specialization in a group may obscure an archaic position that can only be traced by recognition of satisfactorily primitive characters. By employment of such a scale as here introduced, an estimate of the PALEOTELIC WEIGHT of various groups may be ascertained. By such an estimate we may detect, even in the presence of secondary specialization, the relative antiquity of highly modified forms. The characters enumerated are subsequently discussed following the order of the list which is intended to indicate their relative phylogenetic value, assigned after consideration of the points mentioned in the preceding section.

- 1.—Three complete branchial arches.
  - 1a.—Some remnants of third arch remaining.
- 2.—Vertebrae amphicelous.
  - 2a.—Procelous condyle small.
  - 2b.—Zygosphenal and zygantral articulations not developed.
  - 2c.—A continuous series of half-ring-shaped free intercentra in cervical and dorsal region.
  - 2d.—Intercentra persistent but fused to the procelous condyles.
- 3.—Two complete skull arches.
- 4.—Os tabulare (Williston) present.
- 5.—Pentadactyl limbs and girdles complete.
  - 5a.—Eyes well developed and with sclerotic plates, eyelids free.
- 6.—Lungs equally developed on both sides and simple.
- 7.—Premaxillaries, nasals, frontals, and parietals unfused.
- 8.—Prevomerine bones paired.
- 9.—Hemipenes not flounced or laminate.
- 10.—Third cervical vertebra with ribs.
- 11.—Postfrontal present.
- 12.—Lacrymal present.
- 13.—Pleuro-celo-homodont dentition.
- 14.—Teeth present on palate.
- 15.—Rhomboid or cruciform interclavicle.
- 16.—Expanded non-perforate clavicle.
- 17.—Mylohyoideus anterior in one layer, with many regularly spaced interdigitations with the Geniohyoideus, and scarcely separable from the Mylohyoideus posterior.
- 18.—Tongue broad, fleshy, and smooth or papillate.
- 19.—Six separate elements in lower jaw.
- 20.—Caudal chevrons attached intercentrally.
- 21.—Os intermedium present and separate in the carpus.
- 22.—A Rectus lateralis present.
  - 22a.—A parasternum.
- 23.—Epipterygoid (Columella cranii) present.
- 24.—Pterygoids separate.
- 25.—Pineal foramen present and located between the parietals.
- 26.—Osteoderms compound.
- 27.—Several rows of belly scales over each body segment; sometimes with a few larger dorsal tubercles.
- 28.—Proximal belly of Biceps brachii simple.
- 29.—Skull elevated.
- 30.—Os hypischium not present.
- 31.—No bony patellar sesamoids.
- 32.—Sternum without fontanelles.
- 33.—Scapulo-coracoid emarginations and fenestræ present.
- 34.—No endolymphatic sacs.

I have reviewed the distribution of each character discussed in order to bring out systematic points and to indicate the gaps in our knowledge.

## 1.—THE BRANCHIAL ARCHES

Cope (1892) was the first to point out the significance of modification of the branchial arches among lizards. Sauvage (1878), Parker (1880), and Van Bemmelen (1887) made pioneer discoveries. Supplementary work has been done by Gaupp, Gadow (1888), Beddard (1905*b*, 1907), Zavattari (1908), Fürbringer (1919), Hewitt (1920), and Noble (1921). I have examined twenty-six genera in various families (Figs. 27–38).

*Coleonyx* (Gekkonidæ) is the only genus so far known in which three complete arches still persist (cf. Fig. 27; Cope, 1892, Fig. 7 [Fig. 8 erroneous]; Noble, 1921, Fig. 3A). The third arch here appears to be functionless, being unconnected with the muscles in its dorsal half (second epibranchial) and lying as a thin flexible cartilage just dorsal to the muscles, Sternohyoideus and Constrictor colli. The second ceratobranchial is attached to the dorsal surface of the Sternothyroideus.

In most lizards the third arch has been either entirely lost or is well reduced. A few geckos (*Lepidoblepharis*, *Gonatodes*, *Lathrogecko*, *Psilodactylus*) and xantusids (*Xantusia*, *Lepidophyma*) have the third arch nearly complete, with only a slight break between the two halves.

Both second epibranchials and second ceratobranchials are said or known to be present in the following genera:

Gekkonidæ: *Coleonyx* (2 species), *Sphærodactylus*, *Lepidoblepharis*, *Lathrogecko*, *Gonatodes*.

Iguanidæ: *Iguana* (some others according to Fürbringer).

Agamidæ: *Uromastix* (some others according to Fürbringer).

Xantusidæ: *Xantusia* (2 species), *Lepidophyma*.

Lacertidæ: *Nucras*, *Lacerta*, *Algiroides*.

Scincidæ: *Trachysaurus*, *Tiliqua*, *Egernia*, *Scincus*, *Lygosoma*, *Eumeces*, *Macroscincus*, *Chalcides*, *Liolepisma*, *Mabuya trivittata*.

Zonuridæ: *Zonurus*, *Pseudocordylus* (?), *Chamæsauro*.

The second epibranchial is apparently absent and the second ceratobranchial is still present in the following:

Gekkonidæ: *Aristelliger*, *Platydictylus mauritanicus* (Ficalbi, 1880).

Iguanidæ: Most of the genera, including *Chalarodon*.

Agamidæ: Most of the genera (absent in *Amphibolurus*, rudimentary in *Chlamydosaurus*, Beddard, 1905*b*).

Teiidæ: *Bachia intermedia*.

Amphisbænidæ: *Chirotes*, *Amphisbæna*.

In the arboreal iguanids and agamids this section of the arch plays an important role in the support of the throat fan and is sometimes greatly elongated (cf. Bell, 1825 and von Geldern, 1919).

The second epibranchial is present and the second ceratobranchial is absent in the following:

Gekkonidæ: *Homopholis*, *Pachydactylus*, *Platydictylus guttatus*.

Uroplatidæ: *Uroplates fimbriatus*.

Gerrhosauridæ: *Gerrhosaurus* (3 species), *Zonosaurus*.

Teiidæ: *Tupinambis*.

Helodermatidæ: *Heloderma*.

Anguidæ: *Gerrhonotus scincicauda*.

All traces of the third arch are lost in:

Gekkonidæ: *Paragonatodes*, *Hemidactylus*, *Gehyra*.

Pygopodidæ: *Lialis*, *Pygopus*.

Chamæleontidæ: *Chamæleon*.

Scincidæ: *Acontias*.

Feyliniidæ: *Typhlosaurus*.

Dibamidæ: *Dibamus* (hyoid arch also wanting).

Amphisbænidæ: *Rhineura*.

Varanidæ: *Varanus*.

Anguidæ: *Ophisaurus*, *Anguis*.

Xenosauridæ: *Xenosaurus*.

Anniellidæ: *Anniella* (hyoid arch also totally wanting).

Extreme reductions are found in the terminal and specialized forms of the phyletic system.

The degree and point of attachment of the third and first arches to the skull may be of some significance but the circumstances are not all clear. There appear to have been migrations of the point of contact.

The second epibranchial is connected with the skull in the most primitive forms,—*Coleonyx* and many other Gekkonidæ, *Uroplates*, *Xantusia*, *Lepidophyma*, *Trachysaurus*, *Gerrhosaurus*, and *Gerrhonotus*—being attached to the paroccipital in *Coleonyx* and *Thecadactylus*, in *Gonatodes*, *Lepidoblepharis*, *Lathrogecko*, *Sphærodactylus*, and *Lepidophyma*, and to a tubercle on the exoccipital in *Trachysaurus*, *Tiliqua*, *Egernia*, and *Gerrhosaurus*.

Attachments of the hyoid (first arch) to the skull are known in a number of ascalabotids, in *Gerrhosaurus*, *Lacerta* and *Gerrhonotus*, and possibly in *Amphisbæna*. The latter case depends upon interpretation and may be left for the moment in order to follow the ontogeny of the



hyoid as investigated and reviewed by Versluys (1898 and 1904, cf. Gregory, 1913).

The reptilian ear bones (columella auris), consisting of the stapes and extra-columella and the various parts and processes appertaining thereto<sup>1</sup> have usually been considered as modifications of the cervical extremity of the hyoid arch. This derivation has been traced in embryos of *Sphenodon* (Howes and Swinnerton), in *Sceloporus* (Kingsley), in *Gekko verticillatus*, *Platydactylus mauritanicus*, and *Lacerta agilis* (Versluys, 1904). Rice (1920) explains that "the preponderance of evidence strongly favors the interpretation of the columella as a unit structure with otostapes and hyostapes in direct genetic relation to one another . . . that the otic capsule, columella auris, and hyoid arch are all parts of a 'continuous stroma' of undifferentiated early embryonic tissue." The primary relation of the tip of the hyoid to the ossicula auditus becomes modified in the adult form in primitive lizards by dorsal migration or looping of the remaining portion of the hyoid extremity which finally forms a close union with the paroccipital process of the opisthotic bone. This post-primary cervical union occurs only in certain ascalabotid lizards and in *Sphenodon*. It is known in many geckos including *Coleonyx* (2 species), *Gekko verticillatus*, *Platydactylus mauritanicus*, *Pachydactylus bibroni*, *Uroplatus fimbriatus*, *Uromastix spinipes*, and *U. acantherinus* (cf. Versluys, 1898, Figs. 5, 6, 8, 18, and 23). It represents a stage of evolution in which the primary connection of hyoid with extra-columella has just been lost. Its ontogenetic similarity in the Gekkota and in *Uromastix* is strengthened by the presence and attachments of the Stylohyoideus. This muscle (cf. Versluys, 1898, Figs. 9, 15, 17, and 23), morphologically a part of the posterior edge of the Mylohyoideus posterior, arises from the extremity of the epihyal. Its embryology in geckos shows that the fundamental origin is upon the tip of the epihyal where the latter joins the interhyal cartilage. When the epihyal moves dorsalwards to reach the paroccipital process the muscle is carried with it finally to arise in this unusual position.

In *Lacerta agilis* and other autarchoglossids (cf. Versluys, 1904, pp. 132, 133) there is no stylohyoid muscle. The epihyal does not lose its connection with the elongate interhyal and a ligament comes to take the place of the latter establishing a loose connection with the paroccipital process, a union which persists into post-embryonic life. The condition in the Ascalabota is more primitive than the union found in *Lacerta*

<sup>1</sup>Versluys finds that in geckos the foot plate develops independently of the capsule, but as a part of it in other lizards.

*agilis*. *Gerrhosaurus zechi* (Fig. 32) has a closer union than *Lacerta*; *Gerrhonotus* has a loose connection. *Amphisbæna* has been said to have a persistent connection of the hyoid with the skull. This is a matter worthy of attention.

The conditions found in the *Amphisbænidae* are most anomalous (cf. Versluys, 1898, Figs. 66, 68, and 69). In *Amphisbæna alba* (A. M. N. H. 8747) an extremely long, cartilaginous rod-like "extra-columella" lies in articulation with a short, relatively broad and mobile stapes and runs forward across the quadrate in a deep groove to the labial side of the dentary as far as the region of the submaxillary gland. If this element represents the epihyal, as Fürbringer (1919) would have it, the *Amphisbænidae* retain the most primitive connection known in adult reptiles. This view, as Versluys himself grants (1904), is open to considerable doubt.

I have found an "extra-columella," undoubtedly homologous with that noted by Versluys, in *Amphisbæna fuliginosa*, in *Rhineura floridana* and in the unhatched embryo of *Amphisbæna cæca*. In *Rhineura* the element is bony, and very much shorter than in *Amphisbæna* (cf. Figs. F, G, and Versluys, *loc. cit.*). It fastens to the expanded distal extremity of the elongate stapes by strong ligaments and lies imbedded in the handle of a Y-shaped fascia running beneath the rictus to the areas of spongy tissue under the upper and lower lips. It is so arranged that vibrations received through this tissue must be transmitted directly to the mobile stapes. It might be considered simply as an enlarged extra-columella functioning in an unusual way in absence of a tympanum.

In an embryo of *Amphisbæna cæca* (Fig. F) the extra-columella is enormous, extending as a thick cartilaginous band, in the position of the rod-like structure of *Amphisbæna alba*, forward to the spongy tissue beneath the lower labials. The union with the abbreviated stapes is a mobile articulation and a small cartilaginous element (Fig. F, *Otostp.*) is intercalated. This nodule would represent the outer segment of the so-called otostapes of normal lizards (cf. Versluys, 1904, Fig. 10) if we could consider the elongate external rod as a true extra-columella.

What is the evidence in favor of such a view? (1) No connection of any kind was observable in our embryo between the extra-columella and the process representing the hyoid (first arch). (2) A true ceratohyal is present in this embryo (Fig. F, *ceratohy.*) in the position occupied in the *Teiidae*. The main portion of the hyoid in adult *amphisbænians* seems to represent the elongate process of the basihyal of the *teiids*. (3) This small ceratohyal in normal posterior position would presum-

ably never have had a connection with the forward tip of the extra-columella as would be necessary on the supposition that the extra-columella is a remnant of the epihyal. Such a connection would be unlikely owing to relations of neighboring muscles and ligaments. (4) The extra-columella in *Rhineura*, although bony, is of much more typical extra-columellar form and would scarcely be mistaken, as the homologous rod-like element in *Amphisbæna* has been, for a part of the undifferentiated epihyal. The outer ear of amphisbænians is not a degenerate structure but a highly specialized one in which the extra-columella transmits vibrations from the side of the head and lower jaw instead of from the tympanum in the usual way. This may account for the extraordinary change in the form of the extra-columella and indicate that we are not dealing with a part of the hyoid in such an exceedingly primitive and unsaurian position.

## 2.—SAURIAN VERTEBRÆ

What appears to be the most primitive type of vertebral column found among the Sauria occurs in many of the Gekkota (e.g., *Gekko verticillatus*, *Phyllodactylus*, *Pachydactylus*, *Hemidactylus*, *Tarentola*, *Gehyra* and *Uroplatus* (cf. Siebenrock, 1893). Here the centra are bi-concave and the cervical intercentra (hæmopophyses) are similar to and directly continuous with the intercentra of the dorsolumbar region as far posteriorly as the sacrum (cf. Baur, 1886a). The intercentra including those of the atlas and axis vertebræ are thin, half-ring-shaped bones (cf. Figs. 1-2) usually separate from the centra (quite strongly fused in *Thecadactylus rapicauda*), and furnishing attachment for the long sub-vertebral ligament and some of the subcervical axial musculature. The conditions are similar to those found in *Aræoscelis*, *Sphenodon*, *Dimetrodon*, *Trimerorhachis*, *Seymouria*, and many other primitive reptiles. All lizards except the ampicæous gekkonids have procæous vertebræ.

The transition from ampicæous to procæous conditions involves no profound change. Early stages in procæous lizards are similar to those in ampicæous geckos and in *Sphenodon*, and somewhat different from crocodile (Goette, 1894). In the adult the chief difference, according to Goette, between the ampicæous geckos and the procæous lacertids and anguids is that in the former the intervertebral rings do not entirely pinch off the chorda (cf. also Schauinsland, 1906).

Goette (1894, 1897) did not recognize the importance in geckos of the intercentrum, which was discovered later by Baur. The differences

between procœlous and amphicœlous geckos probably include the elimination of the intercentral chorda by the constricting and thickening of the intervertebral disc which becomes reduced, rounded, and attached anteriorly to form the small condylar ball. The condyles fuse ventrally with the intercentra, which, in higher forms, become indistinguishable. The subvertebral ligament comes to insert at the point of fusion of each intercentrum with its condyle. In the procœlous gecko, *Coleonyx variegatus*, and in *Xantusia vigilis* (cf. Figs. 4 and 8), the intercentra may still be found as fused, bony, scale-like elements, and the centra are like those of amphicœlous geckos except for the development of a cup-and-ball articulation.

Noble (1921), in a discussion of the relationships of certain groups of geckos, considers the amphicœlous condition as primitive on comparative grounds. *Aræoscelis*, a supposed Permian ancestor of the Squamata, has amphicœlous vertebræ not unlike those of the geckos, with "persistent intercentra" (Williston, 1914, Fig. 1 and manuscript).

The degree of enlargement and specialization of the procœlous condyle is an important index of the amount of specialization in the various families (Figs. 1-26). The initial advance from the most primitive gekkonid condition is seen in the lower iguanid and scincomorph genera. The amphisbænids are similar to *Ophisaurus* and the Eocene varanid *Saniwa* in broadening of the condyle; while the most advanced saurian stage is seen in the Pleistocene and recent Platynota where the extremely large condyles are set off by a waist-like constriction of the centrum. A sharp flange is raised at the periphery of the flattened articular surface and that surface itself is turned dorsally so as to be almost concealed in direct ventral view.

In the chameleons and pygopodids, special developments are indicated (cf. Figs. 7, 13 and 17). The latter retains gekkonid characters, apparently, in the broad, squarish, ventral outline, the median constriction of the centrum, and the persistence of well-developed subcentral foramina in the median position. The large condyle would indicate a position well above that of the modern geckos. The chamæleontid type is elongate, narrow and cylindrical.

The size of the intervertebral canals, large in the Gekkota and Xantusiidæ, undergoes reduction in the more advanced groups. The paired subcentral foramina, present in geckos, pygopodids, and amphisbæniæns (cf. Figs. 1-4, 8, 9 and 13) appear less frequently among the Scincomorpha and are absent in the higher anguimorphs and in the chameleons.

Some families develop a zygosphenal articulation supplementing the ordinary zygapophyseal type. Although this supplementary articulation is characteristic of snakes it occurs, so far as I know, in no snake-like lizard. It is present in the large iguanids, including *Dipso-saurus* and *Sauromalus*, and, as a rudiment, in *Crotaphytus* (cf. Cope 1892, pp. 199-209). It is known to be absent in the iguanids, *Anolis*, *Polychrus* (Boulenger, 1891a, p. 113), *Sceloporus*, and *Phrynosoma*. It is present among the Lacertidæ and Teiidæ (large in *Tupinambis*; absent or extremely rudimentary in *Bachia*); and occurs among the Varanidæ in the Megalaninæ and in the North American Eocene genus *Saniwa* where it is small. It is present among the Mosasauridæ and Dolichosauridæ. It is small in *Zonurus*.

Development of the zygosphenæ and zyganthrum appears to be a result of enlargement of the bony area of the vertebræ, and especially of the forward part of the neural arch, until interference with the base of the arch of the next forward vertebra takes place.

Boulenger, largely on the strength of this character, suggests placing *Thinosaurus*, of the North American Eocene, with the Teiidæ and not with the Varanidæ. Other characters of the vertebræ of *Thinosaurus* and the related *Saniwa* indicate varanid relationships. (Cf. Figs. 23-26.)

Presence of zygosphenæ and zyganthrum alone cannot be taken to show affinity with the serpents. Secondary formation seems to be the rule.

### 3.—THE SKULL ARCHES

Two normal skull arches (cf. Figs. 106-108) are present in all non-burrowing forms with the exception of the Gekkonidæ and Uroplatidæ, the Varanidæ, the Pygopodidæ and the Helodermatidæ. It is not possible to account for the loss of arches in these families on adaptational grounds.

In all permanently subterranean forms the head becomes bullet-like, with partial and often total loss of arches and more solid union of other skull elements. This occurs in all the limbless autarchoglossid burrowers but not in the limbless grass-living members of the same group, including the scincomorph *Tetradactylus*, the anguimorphine *Ophisaurus*, *Anguis*, and *Chamæsauro*.

The relationship of the Squamata to other orders of reptiles and especially to the Rhynchocephalia is a problem intimately concerned with the correct identification of the bones of the temporal arches. The homologies in lizards and *Sphenodon* of the four elements of the cotylosaurian skull, lying in the temporal region above and lateral to the

quadrate, have been variously interpreted and speculated upon; yet no concord is in sight as to what the two elements usually present in lizards really are.

Baur (1889), Williston (1914), and Watson (1914) essentially agree that the streptostylic condition of the Squamata arose not from the "diapsid" modern Rhynchocephalian by dropping out of the lower arch but by emargination from the ventral side of a broad, unfenestrated lateral arch or plate. The presence of a quadratojugal embryonic connection (cf. Broom, 1903b) is not at present regarded as strong evidence against the emargination hypothesis. Baur could show no very convincing evidence for his view. Watson regarded the condition in *Pleurosaurus* as ancestral. In *Pleurosaurus* the postorbital (= ? postorbital + postfrontal) is massive and in connection with the jugal extends posteriorly to form a broad lateral temporal arch, unfenestrated and scarcely emarginate below. A small quadratojugal and "squamosal" are present in about the position seen in *Sphenodon*.

Watson thinks it possible that the quadratojugal in the primitive state, such as in *Pleurosaurus*, could have retreated upwards as emargination progressed and the quadrate became free. The "*Pleurosaurus* theory" would leave us with an outer quadratojugal and an inner squamosal in the typical lizard. One chief objection of course is the late geologic occurrence of the "Acrosauria" including *Pleurosaurus*, and the fact that highly developed true lizards (Euposauridae) occur with them in the Jurassic. Another difficulty is the wide difference between the appearance of the quadratojugal in the primitive state, in Cotylosaurs, Pelycosaurs, and in *Pleurosaurus*, as a lower lateral element, and the supposed "quadratojugal" of lizards, an upper lateral bone often with a strong process reaching the parietal, and with practically no extension downwards over the quadrate.

#### 4.—THE TABULARE QUESTION

Williston (1917, p. 68 and manuscript) believes that the Squamata arose at an earlier date than the Rhynchocephalia, and without close relationship to that group, from forms represented in the Lower Permian of Texas by his genus *Aræoscelis* and possibly also by *Kadaliosaurus* Credner (1889). The forms represented by *Aræoscelis* are described as "very slender, arboreal or leaping, hollow-boned reptiles. . . . The broad temporal region is formed apparently of a single bone, here identified as the squamosal. The quadrato-jugal is absent. The dermo-supra-occipital is apparently large. [Tabulare present.] Lacrimal vestigial or

absent. A parietal foramen. All cranial bones paired. Palatal bones with teeth. . . . Vertebræ amphicœlous with persistent intercentra. Cervical ribs, at least, single headed, the dorsal more or less dichocœphalous. Coracoid and scapula closely fused. Humerus with both entepicondylar and ectepicondylar foramina, . . . the earliest definitely known reptile with a single upper temporal vacuity, bounded as in lizards, and a fixed quadrate." (Cf. Williston, 1914.)

Williston (1917, p. 66) derives the Squamata with the Ichthyosauria directly from the Cotylosauria and unites the two former under the name Parapsida because of supposed similarity of origin of the temporal openings in these orders. The upper temporal fenestra he believed to have arisen "by the primitive separation of the postorbito-squamosal arcade from the parietal" and the lower fenestra, by emargination of the squamosal, from a condition such as that seen in *Aræoscelis*. An important point is that in the Parapsida "an additional temporal bone was retained long after it was lost in other [reptilian] groups." This is the so-called tabulare present according to Williston in some lizards, in the Ichthyosauria, and in *Aræoscelis*.

In *Aræoscelis*, what is considered to be the tabulare, forms the posterior boundary of the superior temporal opening and lies superficially between the squamosal, parietal, and paroccipital, adjoining also the antero-dorsal end of the quadrate. Few would question this homology, but the identity of the true tabulare with the inner temporal bone in lizards is a contention which only Williston and Broom (1913) have been bold enough to support.

The relations of the inner element to adjacent parts in lizards, mosasaurs, ichthyosaurs, and other forms engaged Baur (1886*b*, 1889, 1892, 1894, 1895, 1896) and Cope (1895*a*, 1895*b*, 1896) in a long controversy. Baur (1886*b*, 1886*c*) originally regarded the outer element in lizards as the squamosal, the inner as the supratemporal. In 1889 he considered the outer to be the quadratojugal and the inner the squamosal. The single element present in geckos he thought represented the quadratojugal (1889). Later (1894) he further modified the terminology calling the upper outer element the prosquamosal because of confusion in the employment of the term supratemporal and restricting the quadratojugal to the lower outer element not considered as present in the Sauria.

Cope stoutly maintained his view that the inner element represents the paroccipital, a bone which has been shown (Leydig, 1872) to be separately present in certain forms along with Cope's "paroccipital." Cope (1895) calls the outer element of lizards the supratemporal and

believes it to be homologous with the similarly placed (median) element in ichthyosaurs. The lower outer element (quadratojugal of Baur) in ichthyosaurs and *Sphenodon* he terms the zygomatic.

Beddard (1905a) notes the presence of still a third "bone" adjoining the end of the paroccipital process of certain lizards (*Uromastix*, *Lacerta*, *Heloderma*). He calls this supratemporal 2. Fortunately "supratemporal 2" has been long since disposed of by Versluys (1898, 1904) who shows it to be essentially a cartilaginous epiphysis on the tip of the paroccipital process formed partly *in situ* and largely from the columellar and epihyal cartilages which extend dorsally to form paroccipital connections that persist in certain forms (cf. p. 341). Versluys notes the "epiphysis" in the Gekkonidæ and in *Uromastix*, *Agama*, *Calotes*, *Amphibolurus*, and *Draco*; in *Iguana*, *Phrynosoma*, and *Polychrus*; in *Trachysaurus*, *Gerrhosaurus*, *Tupinambis*, *Heloderma*, *Varanus*, and *Zonura*. It appears to be absent in *Mabuya*, *Lygosoma*, *Ophisaurus*, and *Anguis*.

It might appear profitable to compare the conditions in lizards with those found in ichthyosaurs and especially with the thalattosaurs. Unfortunately, the temporal region of the latter is still imperfectly known. In *Thalattosaurus alexandrae*, Merriam (1905) regards two temporal elements as questionably present and calls the inner one the squamosal, the outer prosquamosal. The relations appear similar to those of lizards if we accept von Heune's view of the matter (1910a, 1912). Merriam did not succeed in discovering the quadratojugal but thought he could see indications of its presence. Von Heune apparently favors omitting the quadratojugal, and thinks he can recognize in the temporal region an outer "squamosal" (prosquamosal of Merriam), an inner supratemporal, and an element lying between the two which may represent a backward prolongation of the very large postfronto-orbital or a part of the supratemporal (=squamosal of Merriam).

It would seem very highly improbable to say the least that the outer dorsal element ("prosquamosal") in thalattosaurs can represent the quadratojugal, as would be necessary on Watson's view, providing the thalattosaurs are streptostylic. If they prove to have a lower quadratojugal it would be impossible for the upper bone to represent that element, and this makes it seem that in either case the "*Pleurosaurus* theory" as far as it relates to the quadratojugal is untenable.

In the relatively primitive ichthyosaur *Cymbospondylus petrinus*, Merriam (1908) recognized three bones in the temporal region. An inner squamosal, an upper and outer supratemporal, and a lower quadrato-



jugal. On Watson's view we should have to believe that the quadratojugal of ichthyosaurs, in lizards, takes the place of Merriam's supratemporal. This seems unlikely.

Comparison of the occiput of *Cymbospondylus* with a disarticulated (and reassembled) skull of the pelycosaur *Diopeus leptocephalus* Cope would indicate that the element omitted in the phylogeny of the ichthyosaurs was the supratemporal. The remaining elements on this view would be a dorsal and inner tabulare, an upper, outer squamosal, and a lower quadratojugal. This returns to Williston's interpretation of the parapsid evolution and agrees with his "*Aræoscelis* theory" as to the origin of the lizard temporal elements.

Professor Gregory formerly favored the interpretation that Watson (1914) gives of the inner bone regarding it as squamosal. But he was inclined to doubt the advisability of calling the outer element quadratojugal and preferred to leave the outer element in lizards unnamed as an "X bone" (cf. Schmidt, K. P., 1919, Fig. 10).<sup>1</sup> Siebenrock has called it the paraquadrato. The views and synonymies of other investigators have been given by Baur, Thyng (1906), von Huene (1910b), Broom (1913), Watson, Methuen and Hewitt (1915), and Versluys (1919).<sup>2</sup>

Cope (1895a) and Williston consider the inner element in lizards as the one present in snakes. This would seem probable also from the facts outlined below regarding degeneration of the outer element in *Heloderma*. Both elements appear to be absent in the Uropeltidæ (Williston, MS., cf. Boulenger, 'Cat. Snakes,' I, p. 138).

Baur (1896) regarded the upper element in *Sphenodon* as the united squamosal (= tabulare) and prosquamosal (= squamosal). The topography and relationships of the single element present in *Sphenodon* would support this view. There is, however, not the slightest embryological ground for it at present. The results of Howes and Swinnerton (1903) and of Shauinsland (1903) show that the "squamosal" arises as a unit and that the flattened hook-shaped projection adjoining the end of the paroccipital process seems never to be separate from it. I am not sure that the ontogeny can give us a decisive answer to this question since even such recently united bones as the paired prevomers and the postfrontals and postorbitals are fused in the embryo of *Lygosoma* (cf. Siebenrock, 1892 and Pearson, 1921).

The shape and position of the two temporal bones are constant enough in lizards to enable us to be fairly certain of their identity in the

<sup>1</sup>After reviewing the subject and suggesting many points Professor Gregory now adopts the present view.

<sup>2</sup>Thyng, Versluys, and von Huene all regard the outer lacertilian element as the true mammalian squamosal.

group. I follow Williston and Broom in designating the inner as the tabulare (cf. Figs. 103, 106-109, and Text-Fig. C), reserving the name squamosal for the main posterior element of the supra-temporal arch.

The identification of the tabulare in geckos and in *Anniella* might be questioned because, with absence of the supra-temporal arch, there remains only a single element in place of the two (squamosal and tabulare) found in all lizards where skull arches persist. Which of these two bones the one in geckos represents is a difficulty that can be partly surmounted by examination of the analogous case in *Heloderma*. In this form, as in geckos, the supra-temporal bar is absent, but a small triangular rudiment of the squamosal remains alongside a large tabulare in normal position. The squamosal has been reduced to less than half the size of the tabulare, reversing the usual situation, and the tabulare remains apparently unchanged despite the reduction of the temporal arch. It would seem that in geckos also a reduction of the squamosal must have accompanied the reduction of the arches and that the bone remaining is the tabulare (cf. Fig. C) as its relations with the large (internal-posterior) head of the quadrate also would indicate (cf. Baur, 1889). There might still remain the question as to whether there actually has been a reduction and elimination of the supra-temporal arch in geckos or whether the conditions seen are a result of overgrowth of the parietal and fusion of that bone with the arch, thus eliminating the supra-temporal arcade. This is apparently what is about to occur in *Xantusia*, where both squamosal and tabulare are still present. If the outer element, squamosal, were to disappear in *Xantusia*, we should have exactly the conditions obtaining in geckos. But should the tabulare in *Xantusia* disappear, gekkonid conditions could not exist without great corresponding reduction and shifting of the squamosal.

The known distribution of the tabulare in lizards is as follows:—

Gekkota: Present in †*Ardeosaurus* (Fig. C), in *Pachydactylus*, *Hemidactylus*, *Gehyra*, *Tarentola*, *Sphærodactylus*, *Coleonyx*, *Uroplates* (cf. Siebenrock, 1893), and probably in most, if not all, other geckos as a small element.

Iguania: Very small in *Ctenosaura* and *Sauromalus*; present in *Iguana* (Beddard, 1905a) and *Conolophus* (Baur, 1896); a mere nodule in two species of *Anolis*; partly fused with squamosal in *Crotaphytus c. baileyi*; partly fused with parietal in *Calotes versicolor*; large in *Uromastix* (Beddard, 1905a) but concealed beneath the parietal process of the squamosal. According to Siebenrock (1895b) *Moloch* is the only agamid in which the element is lacking.

**Rhiptoglossa:** Present in *Chamæleon* as small element extending posteriorly inside the backwardly prolonged base of the squamosal; reduced to a vestige in *Brookesia* (cf. Siebenrock, 1893a, Pl. 1, fig. 4, s.t.); absent in *Rhampholeon* (Methuen and Hewitt, 1915).

**Scincomorpha:** Small in *Tiliqua* and *Egernia*; questionably present in *Acontias* (Gervais, 1853); present in *Voeltzkowia* (Rabanus, 1906-1915), in *Lygosoma*, *Mabuya*, *Eumeces*, and *Chalcides* (Siebenrock, 1892); a slender element in *Lacerta* and *Gerrhosaurus* (2 species); large in *Tejus* (cf. Hoffman, 1890) and *Tupinambis*; questionably present in some amphisbænians, cf. *Lepidosternon* (Gervais, 1853), *Amphisbæna* (= *Blanus cinerea*, Bedriaga 1884); absent in *Agamodon* (Peters, 1882) and in *Amphisbæna alba* (Williston, 1918, Fig. 4A).

**Anguimorpha:** Large in *Gerrhonotus* (Siebenrock, 1892); short and broad in *Ophisaurus*; large in *Anniella*; large, trihedral, and pointed in *Heloderma horridum* and in the †*Glyptosauridæ*; large in *Varanus* and †*Mosasaurus* (Cope, 1895a), †*Clidastes*, and †*Platycarpus* (= squamosal of Zittel); apparently fused with squamosal in *Zonurus*.

The os tabulare is regarded as a primitive saurian element which undergoes reduction and obliteration in a few of the higher Iguania and Diploglossa and in some of the extreme, burrowing amphisbænians.

##### 5.—DEGENERATION OF EXTREMITIES AND GIRDLES

Reduction of feet, limbs, and girdles seems to be a fashionable course of devolution among autarchoglossine lizards. This process has occurred independently in many diverse groups, and seems to be rapidly going on at present among otherwise normal genera and species of scincs in widely separated parts of the world. Its investigation has naturally attracted a large number of students whose work has chiefly involved the examination of the morphological variations in limb structure.

On the morphological side, Fürbringer's summary (1869), of the osteological and myological structure of the limbs of some fifty-eight snake-like genera, is the most important contribution available. Cope (1892b), Fürbringer (1900), and Max Müller (1900) have investigated the reduction of the girdles in a number of forms, the former adding taxonomic views which differ generically from the system adopted by Boulenger. Cope following Gray (1845) regards as generic within the Scincidæ each grade of limb and foot reduction "so long as the characters are constant," admitting, however, the primary divisions of Boulenger. Boulenger's system seems the more natural and is widely adopted.

There is no case of the acquisition of complete limbs from a limbless or partly limbless progenitor in the whole of vertebrate history. This is a reasonably certain corollary of Dollo's law. We must proceed on the assumption at least that all limbless or partially limbed lizards have had fully limbed ancestors among their own kind, that in cases where a so-called degradational series exists such a series at least illustrates the probable stages of descent, and that in the cases where such a series is found within a single species the evolution of the end-stage must have been comparatively rapid admitting that the life-term of such a species is relatively short.<sup>1</sup>

We may fairly assume that total loss of limbs and girdles is entirely secondary—this is all the more certain since such conditions occur in reptiles only among the more advanced Ophidia. Total loss of the shoulder girdle among lizards is said to occur among the following forms:—

Scincoidea—Anelytropidae: *Anelytropis papillosus*, Cope (1892b, p. 237).

Amphisbænoidea—*Anopsibæna kingii* Smalian, (1885), *Amphisbæna occidentalis*, Cope (*loc. cit.*, p. 241); *Rhineura floridana*, idem; *Cephalopeltis scutigera*, Müller (1900, p. 34); *Lepidosternon sphenorhynchum*, Peters (cited, in Müller, 1900); cf. also Fürbringer (1900, p. 261).

It has frequently been stated that *Anniella* has no trace of a shoulder girdle (cf. Cope, 1892a; Baur, 1894; Fürbringer, 1900, and Coe and Kunkel, 1906). A small cartilaginous element is present, however, in connection with several sets of muscles (cf. Figs. 70–72) and this element, if it represents a further evolution of the stages seen in *Ophisaurus* and *Anguis*, *Pygopus*, etc., must be the clavicle. In anguimorphs, the clavicle is not reduced as rapidly as the scapulo-coraco-sternoid complex; and in *Ophisaurus* (Müller, 1900, Fig. 4) the clavicle is partly cartilaginous. The muscles bear out the view that the element is the clavicle but it is possible, of course, that shiftings of insertion have occurred during degeneration.

Lönnberg (1916, Fig. 6) has given an interesting skiogram of the Siamese scinc *Isopachys gyldestolpei*, and finds a rudimentary pelvis but no shoulder girdle. I am inclined to think that a small cartilaginous, splint-like shoulder girdle would not, if present, be shown in his picture for two reasons. (1) The direction in which the photo was taken (dorsal view) would show a lateral element only as a small dot. (2) Even

---

<sup>1</sup>Born (1883) finds external, rudimentary forelimbs present in young embryos of *Anguis fragilis*, a genus totally limbless in the adult stage.

the presumably heavy parasternum, developed in all known subterranean scincs, appears only very faintly in the photo.

Boulenger (1887, 1912) has included as one of the family characters of the Dibamidæ, "no rudiments of the sternal apparatus." In a specimen at hand (A. M. N. H. No. 1264, ♀) of *Dibamus novæguineæ* there are present small bones connected with the most anterior parasternal chevron (which doubtless represents the sternum, cf. p. 390). These bones lie deep within the anterior fibers of the Obliquus externus profundus and are connected to this muscle by special slips (Fig. 75). There is also a serratus muscle running from the elements in question to the first thoracic rib. This relation, together with the similarity in appearance to *Feylinia*, which is not quite so far advanced (cf. Fig. 73), makes it seem that the rudiments present in *Dibamus* are the scapulo-coracoids.

When looking over such illustrations as those of Fürbringer (1900, Pl. XIII), Müller (1900), Rabanus (1906-1915), and Figs. 68, 73 and 75 of the present paper, in comparison with embryonic conditions as figured by Goette (1877) and Bogoljubsky (1914), one cannot fail to be struck by the marked resemblances of the extreme degenerative series to the early embryonic stages in such elements as the sternum and scapulo-coracoid. In *Blanus strauchii* for example (Fürbringer, Fig. 104), the sternal remnants are in the shape of two small cartilaginous discs quite separate on either side of the mid-line (cf. Bogoljubsky, 1914, Fig. 8). The united scapulo-coracoids are largely cartilaginous and quite widely separated medially. The interclavicle appears last in embryology and disappears first. The clavicle is the next in turn each way in scincomorphs. The sternum disappears before the scapulo-coracoids and appears later in the embryo; before final reduction it takes on the form of a parasternal chevron and at the final end-stages may resemble such fragments as are seen in the embryology of the salamanders (cf. Goette, 1877, Fig. 57).

Krieg (1919) after study of the shoulder girdle in seventy to eighty cleared specimens of *Lacerta serpa* and normal *Chalcides*, in comparison with degenerate *Chalcides tridactylus* and *Anguis fragilis*, decides that the intensity of variation in the bony elements is twice as great in *Anguis* as in the normal forms and that asymmetry develops frequently in the degenerates and rarely in the fully limbed genera. He regards extreme variation and asymmetry as symptoms of degeneration.

So far as known, vestiges, at least, of a pelvis, are always present in lizards.

Cope (1892b) has given results to show divergent tendencies of degeneration in different families:—

(1) Anterior limbs have disappeared more generally than the posterior in the Diploglossa and Pygopodidæ.

(2) The limbs incline to degenerate and disappear more nearly *pari passu* in the Scincoidea. (Anterior limbs persist in *Voeltzkowia* and posterior limbs are larger in *Neoseps*.)

(3) The anterior limbs have a tendency to persist longer in the Teiidæ and Amphisbænidæ (cf. Figs. 68 and 74).

Fürbringer's results (1869) show that there is no causal connection between the degeneration of a limb bone and the degeneration of the muscles inserting upon it. The muscle may lose its attachment and cease to function or be entirely reduced before the bone has disappeared, or the muscle may remain after the bone disappears. In degenerating limbs, the muscles, however, keep quite closely their original relations till the very last and usually disappear with the bone to which they are functionally attached.

It is apparent that few if any clues as to how or why special conditions have been brought about can be obtained from morphological study of degenerating parts. It seems that we should attempt to gather new facts from a comparative study of the special development of the trunk musculature to serve the needs of the changing habitus and habitat of the animal. The basis for such a work may be found in Smalian's classic 'Anatomie der Amphisbæniden' (1885).

It is, of course, possible to arrange degradational series of living forms showing gradual degeneration of limbs, one toe at a time. Whether such a series illustrates the actual course of devolution does not concern us here. It is useful to know that full degeneration has taken place only in the most advanced types of burrowing lizards whose extraordinary development of body musculature, skull modifications, closure of ear, shortening of tail and loss of caudal chevrons, degeneration of lungs on one side, and loss of functional eyes, eyelids, sclerotic plates and osteoderms show in the most obvious way an extreme degree of specialization in connection with permanent subterranean life habits.

Such modifications in habitus have often obscured the heritage to such an extent that determination of original relationship becomes difficult. Even now we can but hint at the ancestry of the pygopodids and amphisbænids by emphasis of such conservative characters as tongue structure, form of vertebræ, pattern of throat musculature, and hemipenial texture.

High degree of convergence in habitus has frequently occasioned lumping of subterranean forms apparently of widely different ancestry. Most painstaking search for paleotelic characters will be necessary to correct this.

#### 6.—THE LUNGS

In limbed and in some limbless Squamata the lungs are developed equally on both sides. Butler (1895) has investigated the lungs in no less than fifty-nine species of snakes, belonging to nine different families, and in twenty-one species of lizards, including the following examples:—

Scincidæ: *Acontias meleagris*, *Acontias monodactylus*, *Scelotes bipes*.

Teiidæ: *Ophiognomon abendrothii*.

Amphisbænidæ: twelve species.

Pygopodidæ: *Pygopus lepidopus*, *Lialis burtoni*.

Anguidæ: *Anguis fragilis*, *Ophisaurus apus*, *Ophisaurus ventralis*.

Coe in Coe and Kunkel (1906) has studied the lungs of the anguroid *Anniella pulchra* and Bedriaga (1884) has examined certain typhlopine, rhinophine and calamarine serpents. Both Butler and Coe have checked the earlier work of Cope (1894 and 1900) and the results obtained show that in all forms except the Amphisbænidæ the left lung is the one to be reduced. In the Amphisbænidæ alone is the right lung reduced or absent. This would surely indicate that the Amphisbænidæ are not directly related to any known existing forms of limbless Squamata.

Milani (1894) distinguishes four degrees of differentiation of the lung structure in lizards. In the first or "Sphenodon-type," found in certain scincs and teiids, the lungs are simple alveolar-walled sacs without septa and differing from the Amphibia only in the specialization of the trachea. In the "Lacerta-type" found in *Gekko verticillatus*, *G. vittatus*, *Tarentola mauritanica*, *T. annularis*, *Gymnodactylus platurus*, *Thecadactylus rapicauda*, *Hemidactylus turcicus*, *Calotes jubatus*, *Tiliqua*, *Lacerta ocellata*, *L. agilis*, *L. viridis*, and *Zonurus giganteus* there are a number of septa dividing a portion of the lungs into small internal chambers. This type is developed from the first by enlargement of some of the alveolar walls and is not essentially different from the first. The "Iguana-type" is still more highly specialized by marked extension and enlargement of the less numerous septa. This type is found in a number of iguanids and agamids. The lungs of *Heloderma* and *Phrynosoma* approach but do not attain the typical development of this type. The "Varanus-type" is by far the most highly modified of all with long internal bronchi and a spongy internal reticular network much as in mammals. The "avian" lungs of *Uroplatus* and *Polyehrus* have the

finger-like processes characteristic of some chameleons (cf. Methuen and Hewitt, 1915). Internal septa are developed as in the "Iguana-type." In *Amphisbæna* and *Anguis* the internal structure is simple.

#### 7.—FUSION OF MEDIAN SKULL ELEMENTS

In *Aræoscelis* (Williston, 1914, Fig. 3*B*) all the median skull elements are paired. This condition also obtains in a few geckos, *Phyllurus* (cf. Cope, 1892*a*).

The premaxillaries are paired only in some Gekkonidæ and in the Scincidæ.

The nasals are paired in all forms except the Uroplatidæ; the chamæleontid, *Brookesia*; the Varanidæ; Aigialosauridæ; Mosasauridæ (?)<sup>1</sup>; and Feyliniidæ.

The frontals are separate in the Ardeosauridæ, in some Gekkonidæ, some Scincidæ, in the Feyliniidæ, Gerrhosauridæ, some Lacertidæ, the Amphisbænidæ, Varanidæ, Dolichosauridæ, Helodermatidæ, some Anguidæ, and in the Anniellidæ.

The parietals are paired only in some Gekkonidæ, and in the Uroplatidæ and Xantusiidæ. There is a partial suture, according to von Huene (1910*b*), in *Tylosaurus dyspelor*. Some Glyptosauridæ appear to have a suture.

The primitive nature of unfused paired skull elements is usually acceded to in accordance with the fossil evidence. Méhely inclines to the view, however, that embryonic or post-embryonic paired conditions may prevail in descendants of a series of ancestors with fused elements, thus upsetting any scheme based on progressive fusion and non-disjunction of once fused elements (cf. p. 404). Whatever may happen, it is certain that the point of least fusion occurs just where we might expect it should *a priori*—that is among the geckos, and that end-branches of the phylogeny have the greatest extent of fusion of skull elements.

The chameleons, iguanids and agamids, helodermatids, varanids and teiids, and certain of the burrowing degenerates have the greatest amount of fusion. The amphisbænids are relatively primitive in this as in vertebral characters.

#### 8.—THE PREVOMER

Broom (1914) considers the mammalian vomer as represented in reptiles by the parasphenoid and thinks that the so-called lacertilian "vomers" are homologous with the "dumb-bell bone" of *Ornitho-*

<sup>1</sup>Von Huene (1910*b*) states that isolated, small nasals are present in *Tylosaurus*.



*rhynchus* and with a similar bone in certain bats. He has named the lizard "vomer" the prevomer, a designation lately accepted by Williston and by Watson. Whether or not the mammalian vomer represents the parasphenoid does not discount the value of Broom's demonstration of fundamental difference between the so-called "vomers" of reptiles and the true mammalian vomer. Consequently it seems advisable to adopt Broom's terminology.

Cope (1892a) states that the "vomers" of lizards are separate in all forms except *Chamæleon*. This is incorrect. The prevomers are completely fused in the scincs *Lygosoma*, *Chalcides*, and *Ablepharus*, and partially so in many other scincs, gerrhosaurids, lacertids, and anguroids (Siebenrock, 1892, 1894). They are quite separate in the primitive scincs *Trachysaurus* and *Tiliqua*, in *Tupinambis*, the *Amphisbænidae*, *Zonurus*, and *Varanus*. They are rarely fused in iguanids (*Crotaphytus c. baileyi*) and are not known to be fused in other groups with the exception of the *Agamidae* (cf. Siebenrock, 1895b) and *Chamæleontidae* where they are generally united. Boulenger (1887) states that they are single in the latter group. Cope (1900, p. 209) refutes this and at this date states the "vomer" to be paired in chameleons. Siebenrock (1893a) after careful examination of *Chamæleon vulgaris* determined the "vomer" to be "entschieden unpaarig." Cuvier and Brühl (1888) regard it as paired, Blanchard, Parker (1881) and Born as unpaired. Parker's figures show that the "vomer" in the specimens he had of *Chamæleon vulgaris* and *C. pumilus* was partly divided. A specimen of *Chamæleon* in the Department of Comparative Anatomy of the American Museum has traces of a median suture in the prevomer. Another unidentified skull has no suture. Specimens at hand of *Chamæleon vulgaris* and *C. gracilis* have a single median element occupying the usual position of the lacertilian "vomer" and separated from the premaxilla and palatines by definite sutures.

Lying on either side of the "vomer" in the carefully prepared skull of *Chamæleon vulgaris* are delicate triangular elements underlying Jacobson's organ. These lateral bones are apparently broken away in the rough skeleton of *C. gracilis* which shows, after preparation, an unpaired median prevomer. Possibly these lateral elements represent the "maxillo-palatines" of Cope, but this does not seem very likely. They appear to be cartilage bones identifiable with the cornu trabeculæ of Parker (1881).

Siebenrock (1893a) considers the "vomer" to be absent in *Brookesia* and from his figures I should regard it as fused with the inferior spine of

the premaxillary. Methuen and Hewitt (1915) record the absence of the "vomer" in *Brookesia* and *Rhampholeon*.

There is little question but that the prevomer of the chameleons represents the fused "vomeres" of other lizards and was originally a double element. It seems also that the differences in descriptions of the chameleon prevomer are due in no small part to actual variations in different species and individuals.

#### 9.—THE HEMIPENES

The external form of the copulatory organs or hemipenes of the Sauria would appear from the recorded investigations of Cope (1896b) to have an important bearing on the phylogeny and classification. No illustrations for the lizards accompanied the terminology of Cope and it might be helpful to compare his descriptions with figures given by Gray (1870, *Varanus*), Leydig (1872, Pl. ix, fig. 118, *Anguis*; figs. 125 and 126, *Lacerta agilis*), Fleischmann (1902, Pl. viii, figs. 1 and 7, *Platy-dactylus guttatus*; figs. 2 and 6, *Anguis*), and Coe and Kunkel (1906, Pl. xlv, figs. 30–32, *Anniella*).

Cope's view was that "the higher Sauria have the parts modified as in the serpents by the presence of calyculi. Such are characteristic of the Rhiptoglossa and Pachyglossa (= Iguania). The Nyctisaura (= Gek-kota) possess the same feature. The Diploglossa, Helodermatoidea, and Thecaglossa (= Varanoidea) have the organ flounced, the flounces often pocketed or repand on the margin. In the Leptoglossa (= Scincomorpha) we have laminæ only; in the Teiidae mostly transverse and in the Scincidae mostly longitudinal. In various genera terminal papillæ are present. The organ may be simple or bifurcate or merely bilobate." In the Zonuridae there are still traces of calyculi. In the Xantusiidae and Xenosauridae, the form is peculiar. All the groups included in my Ascalabota have calyculate hemipenes; all those in the Autarchoglossa, with the exceptions noted, have the organ flounced or laminate. In the Serpentes, calyculi, spines and flounces are present in varying degree. The spinous character is a decided similarity to the Anguimorpha.

Fleischmann has shown that the hemipenes originate in both snakes and lizards in the same way from the ectoderm of the lateral corners of the cloacal lips.

Cope's statement that the organs are calyculate in the "higher Sauria" does not exactly fit his phylogenetic scheme (1900), where he considers the calyculate forms, Pachyglossa (= Iguania), as ancestral. He is again forced to regard the close resemblances of serpents to the

anguimorphine lizards as due to convergence (p. 196) because of his preconceived idea of separation between the "Pythonomorph" and saurian lines (p. 180). I cannot regard the Serpentes as anything but highly modified anguimorphine lizards near the platynotid stock. The detailed hemipenial resemblances in addition to similar characters in the vertebræ, skull, teeth, and tongue in varanids and ophidians,—the similar reductions of the body segments in certain autarchoglossids and in the serpents, and the details of the throat musculature would seem to preclude any possibility of convergence, especially since the many characters separating the lizards and true snakes are not much beyond the range of differences found among certain snake-like lizards. Among such characters may be included: absence of temporal arches, jugals, squamosals, lacrymals, postoptics, and epipterygoids; and reduction of bones in the lower jaw.

#### 10.—THE NUMBER OF CERVICAL RIBS

Lizards may be said to have, typically, six or eight cervical vertebræ, depending on the way they are counted. I should consider all vertebræ whose ribs ever attain a connection with the sternum, to be dorsal. Since the elongate rib of the so-called eighth "cervical" sometimes has a sternal connection (Fig. 68) and since the seventh "cervical" is so obviously a pair to it, there may be some advantage in considering six the typical number. Cope and Siebenrock regard the number as eight.

All lizards as far as known have six cervicals except *Varanus* and the Mosasauroids (Platynota) which have seven, the allied Dolichosaurs which have thirteen, and the Chamæleontidæ which have only three. The number in many limbless forms, of course, is not ascertainable. These forms usually have three anterior cervicals without ribs, as in most lizards, and it may be well to consider the number in all such forms as six. This will provide a comparative basis for rib-counts.

In the following table those genera followed by a letter (C) are given on the authority of Cope (1892a). It may be noted that families and genera (Gekkonidæ, Scincidæ), considered primitive on other grounds, have greater numbers of cervical ribs than do groups of less paleotelic weight (Agamidæ, Chamæleontidæ).

Four cervical ribs:

Gekkonidæ: *Coleonyx*, *Phyllodactylus* (2 species), *Pachydactylus*.

Scincidæ: *Egernia*, *Trachysaurus*, *Tiliqua*.

Three cervical ribs:

Gekkonidæ: *Gehyra*, *Phelsuma*, *Thecadactylus*, *Gonatodes*, *Lathrogecko*, *Lepidoblepharis*, *Sphærodactylus*.

Iguania: *Uromastix*, *Sceloporus* (C) 2 species, *Phrynosoma*, *Crotaphytus* (2 species), *Holbrookia*.

Scincomorpha: *Xantusia*, twenty species of Scincidæ according to Siebenrock (1895a), *Gerrhosaurus*, *Lacerta*, *Cnemidophorus* (C), *Tupinambis*, *Bachia*, *Amphisbæna*, *Rhineura* (C).

Anguimorpha: *Gerrhonotus* (C), *Ophisaurus*, *Anguis*, *Heloderma*, *Zonurus*.

Two cervical ribs:

Iguania: *Calotes versicolor*, twenty-nine species of Agamidæ according to Siebenrock (1895b), *Norops*, *Xiphocercus*, *Anolis*, *Iguana*, *Sauromalus*, *Dipsosaurus* (C), *Callisaurus*, *Chalarodon*.

One cervical rib: *Draco formosus*, (?) *Chamæleon gracilis*.

No cervical ribs: *Chamæleon vulgaris*.

The only lizards I have noted which bear ribs on the third (first post-axial) vertebra are the primitive geckos, *Coleonyx*, *Phyllodactylus*, and *Pachydactylus*; the primitive Australian scincs, *Egernia*, *Trachysaurus* (cf. Werber, 1895) and *Tiliqua*; and a species of *Chamæleon*. The latter case is remarkable but not strictly comparable with the others and probably not indicative of primitiveness since it may be due to ex-calcation of the more anterior vertebræ.

Professor Osborn (1899, p. 179) states that the third cervical of *Tylosaurus* bears "a small rib, which is not preserved." The appearance of the cervical diapophyses in varanoids and other lizards, however, may be deceptive and the evidence should be conclusive before allowing the mosasaurs an extraordinary number of ribs. I have found only two cervical ribs in our skeletons of *Varanus*.

#### 11.—THE POSTFRONTAL AND POSTORBITAL

We are indebted to Siebenrock for accurate observations upon the osteology of lizards. Data from his papers are credited by the letter (S).

Some confusion prevails concerning the disposition of the post-frontal and postorbital in lizards. By tracing through a series of forms in the Scincidæ (*Lygosoma*) where fusion sometimes occurs, it is found (S., 1895b) that in this group the postorbital grows smaller and is finally absorbed by the postfrontal. On the other hand, if Beddard (1905a) is correct in his recognition of an anterior postfrontal in *Uromastix*, the large element present in the Agamidæ is the postorbital. An examination of the analogous case in *Iguana* and *Sauromalus* shows that here also the larger element is the postorbital, as its relations with the squamosal would further indicate.

In existing Gekkota the single element present, as shown by its relations to the frontal, the parietal, and the postorbital ligament, is the postfrontal.

We have then the following relations:—

Gekkota: postfrontal only. In *Ardeosaurus* the single bone present (Fig. C, *Po*) may represent the fused postfrontal and postorbital.

Iguania: postorbital large; postfrontal small (*Iguana*, *Sauromalus*, *Uta thalassina*, *Uromastix spinipes*) or absent (*Crotaphytus collaris* and most Agamidæ, S, 1895b).

Rhaptoglossa: it is impossible to say what the single bone present represents.

Xantusiidæ: anterior postfrontal and posterior postorbital both large and separate in *Lepidophyma* (Duméril and Bibron, 1870); fused into a single broad postfronto-orbital (*Xantusia vigilis*, *X. riversiana*).

Scincidæ: median postfrontal large, lateral postorbital moderate (*Chalcides simonyi*, S, 1892); postfrontal large, postorbital small (*Mabuya multifasciata*, *Ablepharus*, *Lygosoma quoyi*, S, 1892); postfrontal large, postorbital absent (most Scincidæ, including many species of *Lygosoma*).

Gerrhosauridæ: a small anterior postfrontal and a large posterior postorbital excluded from the orbit, (S, 1892).

Lacertidæ: postfrontal and postorbital of about equal size and separated by a longitudinal suture (*Lacerta dugesii*, *L. ocellata*, *L. viridis*, *L. agilis*, *L. muralis*, *L. oxycephala*, *L. mosorensis*, *Algiroides*, *Acanthodactylus*, *Ophiops*, S, 1894) or a single, fused postfronto-orbital (*Lacerta simonyi*, *L. galloti*, *L. atlantica*, *L. vivipara*, *Tachydromus*, *Psammodromus*, *Eremias*, S, 1894).

Teiidæ: postfrontal a small anterior element, postorbital long, slender, and extending far posteriorly along the squamosal (*Tupinambis*); the elements are fused in *Cnemidophorus* (Cope, 1892a).

Amphisbænidæ: postorbital only, in *Amphisbæna alba* (Williston, 1918); both elements absent in *Agamodon* (Peters, 1882), in *Blanus cinereus* (Bedriaga, 1884), and in *Amphisbæna fuliginosa*, *Lepidosternon* and *Trogonophis wiegmanni* (Gervais, 1853).

Anguimorpha: postfrontal and postorbital separate and of nearly equal size (Anguidæ, Glyptosauridæ and Aigialosauridæ, Nopcsa, 1903) (cf. Figs. 103, 106–108); fused (Varanidæ and Mosasauridæ, Baur, 1892); separate but postfrontal much smaller (Zonuridæ); postfrontal present and in contact with prefrontal, no postorbital (*Heloderma*, *Lialis*); neither postfrontal nor postorbital (*Ophioseps*, Jansen, 1901).

In the Xantusiidæ, Gerrhosauridæ, and the Lacertidæ, the supra-temporal fenestra is entirely closed by the backward growth of the post-orbitals. In the Scincidæ (*Mabuya*), this occurs by backward prolongation of the postfrontals.

By the relations and variations of these elements we may distinguish the following groups of lizards: Gekkota, Iguania, Rhiptoglossa, Scincidæ, Xantusiidæ+Lacertidæ+Gerrhosauridæ, Varanidæ+Mosa-sauridæ, Anguidæ+Glyptosauridæ, *Heloderma*+*Lialis*.

## 12.—THE LACRYMAL

The lacrymal in lizards is small, when present, and surrounds or lies externally to the lacrymal canal at the antero-inferior margin of the orbit (cf. Gregory, 1913, 1920, p. 131).

The primitive state of the lacrymal in parapsids is probably that illustrated in *Aræoscelis* (Williston, 1914, p. 135, and Fig. 3A), where it is already small but still apparent externally as a short bar between the prefrontal and jugal. This is its position in the primitive orbital ring of the stegocephalians and cotylosaurs (Gregory, 1920, Figs. 12, 14, 18, 33, 34, etc.). In some lizards (cf. Teiidæ and some Iguanidæ) a condition similar to that in *Aræoscelis* is maintained; in others (Varanidæ and Helodermatidæ) there is a shortening and thickening of the bone. In the Gekkonidæ the lacrymal is crowded within the orbit and lost to view externally. I have not been able to discover the element in *Xantusia vigilis* (it is slightly fused with the prefrontal in *X. riversiana*), nor in the Scincidæ, Feyliniidæ, Gerrhosauridæ, Lacertidæ, Amphisbænidæ, and Zonuridæ. Cope (1892a) states that in the Scincidæ it has fused with the prefrontal and this may have occurred among certain other groups (cf. *Lacerta*) where the lacrymal tubercle seems to be present on the prefrontal.

In a skull of *Chamæleon gracilis* at hand, the lacrymal is certainly present as a long, thin, external element. In the related genus *Brookesia* it appears from Siebenrock's figures (1893a) to be absent.

In the Agamidæ it is often small and is absent (Siebenrock, 1895b) in: *Draco*, *Sitana*, *Lyriocephalus*, *Calotes versicolor*, *C. mystaceus*, *Agama sanguinolenta*, *A. pallida*, *A. hispida*, *Phrynocephalus*, *Amphibolurus* and *Uromastix*.

What little we know, accordingly, of the distribution of the lacrymal appears not specially significant. Its characteristic shape has been lost in *Heloderma* and *Varanus* and obscured in the geckos and in those families where fusion has occurred. Small elements such as the lacrymal and intermedium are not of great importance in the phylogeny because of their sporadic disappearance and fusion.

## 13.—THE MANDIBULAR TEETH

There has been no uniformity of opinion as to what kind of tooth-insertion is oldest in the Sauria. *Aræoscelis* is described as having thecodont or proto-thecodont teeth, subconical (solid?), nearly homodont, and simple—without accessory cusps (Williston, 1914, p. 118–119). In the Eocene of North America we find both acrodont and pleurodont types of dentition. In the Phosphates of Quercy (Eocene-Oligocene), both types are present. Boulenger, basing his views doubtless on the conditions in the Rhynchocephalia, considers acrodonty as primordial in lizards. Cope regards the acrodont and pleurodont series of parallel value and expresses the view (1900, p. 206) that the *Pachyglossa* (Iguanidæ and Agamidæ) are “probably ancestral to the other superfamilies. The dentition of the Agamidæ is quite identical with that of many of the Rhynchocephalia, and with that of the chameleons as well. It is a modification of the primitive rhizodont dentition which prevailed during the Permian.”

The teeth of the Jurassic Euposauridæ are not certainly pleurodont (cf. p. 319). Those of *Chamops* from the Laramie Cretaceous are not typically so (cf. p. 309). It would seem from what we know of the record, that thecodonty has preceded both pleurodonty and acrodonty in the saurian line. It also appears from comparative evidence and from the embryology that thecodonty or pleurodonty has in every case preceded acrodonty. Siebenrock (1895b) shows that the developing tooth in *Agama* goes through a pleuro-thecodont stage. Carlsson's results (1896) are also interpreted in this way. It seems probable that the transitions such as seen in Teiidæ, Varanidæ, Helodermatidæ, and Amphisbænidæ are developing in the direction of acrodonty rather than pleurodonty. All the more so since in the subpleurodont, advanced, limbless scincs and anguids this would be most likely owing to undoubtedly recent development from pleurodont ancestors. Some forms of *Ophisaurus* (cf. *O. harti*, Boulenger, 1899a) have a subacrodont, pythonomorph dentition like that of *Anguis* (cf. Leydig, 1872). The typical dentition of *Ophisaurus* is subpleurodont. The dentition of the limbed anguids is pleurodont (cf. Figs. H, I).

If we regard the thecodont dentition of *Aræoscelis* as primitive we should consider the pleurodont condition as developed from it by breaking down of the lingual alveolar walls and lengthening of the tooth crown, which becomes a hollow, cylindrical shaft.

The highly acrodont teeth of the Agamidæ and Chamæleontidæ may have arisen directly from a thecodont type by atrophy and shorten-

ing of the base and coincident replacement of the alveolar cups by infilling of mandibular bone or, as seems less likely, by such modifications directly from pleurodonty as might be illustrated in many stages among various living forms.

We may, therefore, question the advisability of Cope's view of the primitive status of the agamids. It is among the Agamidæ that some of the most specialized types of lizards are developed. The relations of this family to the chameleons seem not distant and it can also be demonstrated that there is scarcely anything primitive in the structure of the chameleons. It is among the Agamidæ that the most heterodont types of Saurian dentition occur and this again would make it appear that the acrodont series cannot be considered primitive.

Another feature which marks the hyperacrodonty of *Sphenodon* and the Agamidæ and Chamæleontidæ as a highly specialized condition is the failure to develop replacement teeth in the adult. Harrison (1901) has shown that in *Sphenodon* there are no replacement teeth developed after the first five dentitions of the embryo. Röse (1893) finds that there is no succession or shedding even in the young of chameleons. He did not study the embryos. Carlsson (1896) discovers a succession in embryos of *Calotes* but mentions none beyond the embryonic stages. She does, however, state that the persistence of an enamel organ into late life is a resemblance to the pleurodont lizards not to be seen in *Chamæleon*. Woerdeman (1919), without knowledge of the results of Carlsson, and after study of snakes and many pleurodont lizards, found old embryos of *Calotes* to represent "das einzige Reptil gewesen we ich die Alternierung nicht auffinden konnte."

When the teeth become worn or broken away in the hyperacrodont lizards, enamel is sometimes deposited upon the edges of the mandibles (cf. *Uromastix* and *Sphenodon*) which then take on a masticatory beak-like function.

Succession occurs throughout life among pleurodont lizards. In the most highly developed types of pleurodonty such as occur among the Iguania and Scincomorpha, the teeth are hollow, thin-walled cylinders which receive the replacement teeth into their bases (cf. Leydig, 1872). Among the more solid toothed anguimorphs this occurs only in the Zonuridæ. Even in *Gerrhonotus* (Fig. H), which is quite typically pleurodont, the new teeth lie outside the old. There is evidence of similar replacement in the Eocene Glyptosauridæ (Fig. I). Among the subacrodont anguimorphs, the replacement is strictly alternate.



## 14.—THE PALATAL TEETH

Pterygoid teeth are present in many Iguanidæ, Scincidæ, Gerrhosauridæ, primitive Lacertidæ, Glyptosauridæ, Cretaceous Platynota, Anguidæ, and in some Teiidæ (cf. Boulenger, 1885–1887, and 1920; Cope, 1892a, Siebenrock, 1892). Genera of Iguanidæ with such teeth are given in Boulenger 1885: [*Crotaphytus*, 1 species with, 1 species without, *Sauromalus hispidus*], *Dipso-saurus*, *Ctenosaura*, *Brachylophus*, *Cyclura*, *Hoplocercus*, *Metopoceros*, *Iguana*, *Conolophus* (in young), *Amblyrhynchus*, *Phymaturus*, some *Uraniscodon*, *Tropidurus*, most *Leiocephalus*, *Saccodira*, *Liolaemus*, *Ctenoblepharis*, *Stenocercus roseiventris*, *Stenocercus cupreus*, *Hoplurus*, *Chalarodon*, *Pristidactylus*, *Liosaurus*, *Urostrophus*, most *Enyalius*, *Enyalioides*, *Ophryoessa*, *Basiliscus*, *Læmanctus*, *Corythophanes*, *Polychrus*, *Tropidodactylus*, most *Anolis*, *Xiphocercus*, *Chamæleolis*.

Among Scincomorpha having pterygoid teeth those listed by Siebenrock (1892 and 1894) are: *Mabuya multifasciata* (2 teeth), *Eumeces schneideri* 6, *Gerrhosaurus nigrolineatus* 5, *Zonosaurus* 6, *Algiroides* 2 to 3, *Tachydromus* 3 to 4, *Eremias* 5 to 6, *Lacerta muralis* 6 to 7, *L. oxycephala* 6 to 7, *L. atlantica* 6 to 8, *L. viridis* 8 to 10, *L. agilis* 10 to 12, *Psammodromus* 10 to 12, *L. galloti* 12 to 14, *L. simonyi* 13 to 16, *L. ocellata* 16 to 20,—genera with more than eight teeth having several rows.

Anguimorpha with pterygoid teeth are: the Aigialosauridæ, the Mosasauridæ, *Heloderma*, *Lanthanotus*, the Glyptosauridæ, *Gerrhonotus*, and *Ophisaurus*.

Hilgendorf (1885) figures prevomerine teeth in *Pseudopus pallasii* (= *Ophisaurus apus*) and notes that there are a greater number of such teeth present in his fine specimen of *Propseudopus fraasii* from the upper Miocene of Steinheim. Prevomerine teeth occur in a specimen of *Ophisaurus* at hand (2 to 3 on each side). *Ophisaurus*, having the most dentigerous palate of all living lizards, is the only recent genus known to have prevomerine teeth (cf. Brühl, 1875–1888). They are present in the Eocene diploglossids, the Glyptosauridæ.

The palate appears to be toothless in the Gekkonidæ, Uroplatidæ, Pygopodidæ, some Iguanidæ, the Agamidæ, Chamæleontidæ, Xantusiidæ, some Scincidæ (*Trachysaurus*, *Tiliqua*, and *Egernia*), the Anelytropsidæ and Dibamidæ, some Lacertidæ (*Ophiops*), some Teiidæ, the Amphisbænidæ, most Anguidæ (including some species of *Gerrhonotus*, all known *Diploglossus*, *Ophiodes*, and *Anguis*), the Annielliidæ, Xenosauridæ, and in the Zonuridæ.

The Iguanidæ without palatal teeth, according to Boulenger (1885) are: [*Crotaphytus c. baileyi*], *Callisaurus*, *Holbrookia*, *Phrynosoma*, *Uta*, *Sceloporus*, *Urocentron*, *Strobilurus*, some *Uraniscodon*, some *Leiocephalus*, *Helocephalus*, *Stenocercus marmoratus*, *S. torquatus*, *S. humeralis*, *S. varius*, *S. moestus*, *Scartiscus*, *Diplolæmus*, some *Anolis*, *Norops*.

I should consider the simple presence of teeth on the palate as paleotelic. Such teeth would seem to be ancestral owing to lack of development in secondary lines of descent, and prevalence of teeth in greater numbers in certain more ancient forms. One may not, however, regard the distribution of such teeth as of paleotelic significance owing to the likelihood of dropping out, development and migration of cutaneous tooth buds from one bone to another in the course of recent phylogeny.

#### 15.—THE INTERCLAVICLE

The classic view of Gegenbaur (1865), supported by the paleontological and to a considerable extent by modern embryological evidence, is that the clavicle and interclavicle are secondary "derm-bones" of later origin than the so-called primary shoulder girdle. Goette (1877) did not accept this theory believing that the clavicle in lizards arises as a part of the cartilaginous scapulo-coracoid anlage. Bogoljubsky (1914) reconciles the embryological history in lizards at least partially with Gegenbaur's conclusions, showing that the clavicle is not preformed in cartilage and develops for the most part independently and originally in close connection with the skin. The interclavicle develops from the median ends of the clavicular fundaments as a paired structure (Goette and Bogoljubsky). According to the latter, it takes on very early in *Lacerta* the broadened rhomboid form comparable with the shape found in certain Permian amphibians, *Palæohatteria*, and some of the cotylosaurs.

We know nothing of the condition of the interclavicle in the ancestral Squamata. In *Proterosaurus* it is represented as in Fig. 76. It reaches its highest development among the stegocephalous Amphibia as a rhombic plate. It disappears rather early in mammalian history. It is not present in the birds. From its distribution we have reason to believe that reduction of various parts of the interclavicle is taking place in the Sauria. Such reductions seem to have occurred locally among the Gekkota, almost universally among the Iguania, and also in other groups.

In the Gekkonidæ, a subrhomboid plate-like form appears in some genera. Such a form obtains in the amphi-celous *Gehyra* and *Gonatodes*; and in the procelous *Coleonyx*. In the apparently more advanced

*Lathrogecko*, and *Sphærodactylus* (cf. Noble, 1921) a sub-cruciform shape is attained; in *Phyllodactylus* as well. In *Paragonatodes* further reduction takes place and a splint-like longitudinal element remains. In *Uroplates* only a nodule occupies the position of the interclavicle.

Among the Iguanidæ most forms have a typically T-shaped or anchor-shaped element of possible derivation from the cruciform shape. In *Phrynosoma* (Fig. 45) this is reduced by elimination of the lower bar. In the Agamidæ (cf. Siebenrock, 1895b), great variation occurs. The two primitive genera *Liolepis* and *Uromastix* retain the cruciform shape. In *Phrynocephalus* this has been apparently transformed into an anchor. In *Draco*, *Sitana*, *Lyriocephalus*, *Gonocephalus*, *Acanthosaura*, *Calotes*, *Japalura*, *Charasia*, *Amphibolurus*, an arrowhead is found similar to that seen in *Xantusia* (Fig. 69). *Agama* has a small T-shaped element, *Moloch* a plate.

The interclavicle is considerably reduced in *Draco*, *Sitana*, *Lyriocephalus*, *Gonocephalus*, *Japalura*, *Charasia*, and in most species of *Agama* and *Phrynocephalus*. It is altogether absent in the Chamæleontidæ.

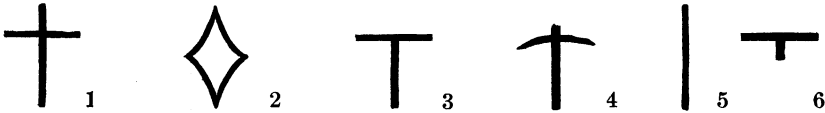


Fig. J. Various types of saurian interclavicles.

According to Boulenger, in the Xantusidæ alone among the limbed scincomorphs is a T-shaped form present. *Xantusia vigilis* and *X. riversiana*, however, have a cruciform shape (Fig. 69) characteristic of all fully limbed scincomorphs. In *Chalcides lineatus* this form is retained; in the limbless *Evesia* (*Acontias monodactylus*) only a longitudinal bar remains (Cope, 1892b, Fig. 9), this is the condition in the teiids *Ophiognomon* and *Bachia* (Fig. 68); in *Chirotes*, the only amphisbænian with limbs, there is no interclavicle.

Among the Anguimorpha, all the limbed Anguidæ and all the Zonuridæ have the cruciform shape. In the Helodermatidæ, the interclavicle is reduced to a thin, longitudinal rod, and in the Varanidæ, Aigialosauridæ and Xenosauridæ to an anchor-shaped element. The interclavicle appears to be absent in the Dolichosauridæ and in most of the Mosasauridæ. Among the limbless Anguidæ, *Ophisaurus ventralis* and "*Pseudopus pallasii*" retain a T-shaped form with the lower bar reduced. *Anguis fragilis* has but a variable nodule remaining, sometimes cruciform (cf. Krieg, 1919). In the embryo of *Anguis* the cruciform

shape persists (Goette, 1877). According to Cope (1892b), in *Ophiodes striatus* conditions are similar to *Ophisaurus pallasii* but with a broad separation between sternal plate and interclavicle; in "*Dopasia*" *gracilis* and in the Pygopodidæ, the interclavicle is wanting.

The interclavicle in Sauria is connected with certain muscles of the neck and shoulder (Figs. 63-67). The attachments of these muscles seem directly responsible for its cruciform shape in many groups (Fig. J1). This, it would appear, is a modification of a still more ancient condition (Fig. J2) retained by certain geckos. The action of the deltoid and pectoralis muscles would presumably account for the hollowing out of the four sides of the rhomb. The retention of the arms is due to the attachments by fascia of the extremely heavy sternohyoid and sternothyroid muscles serving the head. Reductions of the cruciform interclavicle to the forms indicated in Figs. J3, J4, J5, and J6 are all seen in various groups. And it seems likely that these further reductions have all been derived from a cruciform condition (cf. Fürbringer, 1900).

#### 16.—THE CLAVICLE

The clavicle as known in *Aræoscelis* (Williston, 1914, Pl. iv, fig. L) is expanded toward the mid-line and imperforate. Similar conditions are seen in the primitive Australian scinc, *Trachysaurus* (cf. Werber, 1865), where the expansion is carried to a higher development. In *Trachysaurus* and in the nearly related *Tiliqua* and *Egernia* more or less perforation sometimes occurs in the broadened end. Many of the geckos have broadly expanded perforate clavicles and whenever the clavicle is rod-shaped in the geckos it seems to bear trace of a former breadth and perforation (cf. Noble, 1921, Figs. 4 and 5).

These conditions among primitive groups lead me to believe that broadly expanded, non-perforate clavicles are ancestral among modern Sauria and that simple rounded clavicles have been shaped from these.

The origin of the peculiarly reflected portion of the Clavodeltoideus should be understood (Figs. 63-67) when examining the correlated morphological conditions. This muscle passes over the anterior edge of the clavicle from the dorsal side, arising on the ventral border of the bone in the broadly expanded autarchoglossid types. The perforation occurs under the belly of this muscle and may be concerned with the action of the muscle. Further development of the muscle, as in the case of the interclavicle, apparently means reduction of the clavicle, first to a hook-like form, then to a bar.

In *Uroplates* the clavicle is elongate and simple. In the Iguanidæ it is usually simple, but two known genera (*Basiliscus* and *Læmanctus*) have retained or regained a loop-shaped form (Boulenger, 1885). The Agamidæ have a simple and delicate bone which is hook-shaped in *Lyriocephalus* and broadened laterally in *Liolepis* and *Moloch* (cf. Siebenrock, 1895b). In the chameleons clavicles are absent or rudimentary in the adult but "fairly well developed" in the embryo (Broom, 1906).

In all limbed and many limbless Scincomorpha, the clavicle is dilatated and frequently perforate or hook-shaped. The latter form constitutes an apparent advance from the perforate condition occurring in the Teiidæ which rarely (*Tretioscincus* and *Scolecosaururus* Cope, 1892a) have simple clavicles. Goette (1877) finds in the embryo of *Cnemidophorus* a perforate clavicle which later develops a hook-shape typical of the Teiidæ. In the Scincidæ and Gerrhosauridæ, the element is unusually broad and generally perforate. In Lacertidæ, narrower and always perforate.

In the Anguimorpha, the clavicle is always simple (Fig. 81). It is absent only in certain mosasaurs and in the dolichosaurs.

Among the limbless Scincomorpha, the clavicles always disappear before the scapulo-coracoids (cf. Müller, 1900, Figs. 7, 8 and 9; Cope, 1892b, Pl. XIII, fig. 12). In the Anguimorpha the clavicle seems to persist after all the other elements have vanished (cf. Figs. 70-72 with Figs. 73 and 75). In final stages of reduction both scapulo-coracoid and CLAVICLE become cartilaginous but retain characteristic muscle connections. In many cases (Amphisbænidæ, *Acontias*, Anguidæ), the course of reduction can be followed through various stages in related forms (cf. Müller and Cope, *loc. cit.*).

#### 17.—THE THROAT MUSCULATURE<sup>1</sup>

In *Sphenodon*, the Chelonia, the Crocodilia, and the urodele Amphibia, the Mylohyoideus anterior and posterior are present as a continuous superficial layer (Fig. 38). In the Squamata this sheet is interrupted by interdigitation of the Geniohyoideus where the latter arises upon the median ventral border of the lower jaw. In the Sauria differences in number and size of the interdigitating bundles are noticeable among the various superfamilies. All the lizards have at least one interdigitating bundle separating the Mylohyoideus anterior and posterior. Many of the families have a number of regularly spaced bundles inter-

<sup>1</sup>I have not been able to employ systematically the extensive morphological studies of Zavattari (1910) on the reptilian throat musculature.

lacing at definite intervals with the Mylohyoideus anterior. In most cases the lesser number of bundles is associated with certain complexities, undoubtedly secondary, in the form and divisions of the Mylohyoideus. Also the lesser number is usually present in those groups where wide separation, in space and in direction of fibers, occurs between Mylohyoideus anterior and posterior. This leads one to suppose that primitive saurian conditions are represented by a number, eight or more, of small, equal, regularly distributed interdigitating bundles of the Geniohyoideus and Mylohyoideus and by scarcely any separation between the anterior and posterior parts of the latter muscle.

Families in which these supposedly ancestral features remain are the:

Gekkonidæ: *Coleonyx variegatus*, Fig. 42.

*Gekko verticillatus*, Fig. 62.

Scincidæ: *Trachysaurus rugosus*, Fig. 49.

Gerrhosauridæ: *Gerrhosaurus zechi*, Fig. 52.

Lacertidæ: *Lacerta ocellata*, Fig. 50.

Teiidæ: *Tupinambis nigropunctatus*, Fig. 51.

In the specialized gekkonid *Uroplatus* the Mylohyoideus anterior is very thin and aponeurotic. Its fibers run strongly fanwise and are concentrated at their origin, allowing few or no parts of the Geniohyoideus to insert through them. The Mylohyoideus posterior in each case is extremely thin and degenerate with fibers directed obliquely backward and largely covered superficially by a broad portion of the median terminus of the constrictor colli which extends forward to the hyoid corpus. It is widely separated from the Mylohyoideus anterior. Some similarities are shown to the diploglossids, *Pygopus* and *Lialis* (cf. Figs. 43 and 56).

The Iguania and Rhyptoglossa, with a few explicable exceptions, have the Mylohyoideus anterior in two layers. The fibers of the superficial layer in the Iguanidæ are directed transversely or obliquely backward (cf. Figs. 44 and 45). The fibers of the principal (profound) layer run transversely and obliquely forward from their origin. The superficial layer is developed from an anterior slip and never interdigitates with the Geniohyoideus. The principal layer represents the usual Mylohyoideus anterior of the Gekkota, and interdigitates by from one to six small bundles with the Geniohyoideus. In the iguanids, *Callisaurus*, *Uma*, and *Holbrookia*, alone, is the superficial layer absent. In these genera it is still amalgamated with the principal layer. Various stages of separation may be seen in the genera *Sceloporus*, *Chalarodon*, and

*Phrynosoma*. Further separation appears to occur in *Leiocephalus*, *Crotaphytus*, and *Dipsosaurus*. In *Anolis*, *Polychrus*, and *Basiliscus*, the superficial bundle is weak but well separate. In the "Cyclura group" comprising the genera *Iguana*, *Amblyrhynchus*, *Ctenosaura*, *Brachylophus*, *Sauromalus*, and *Cyclura*, the superficial bundle is very specialized and consists of definitely directed fibers not connected with the skin. Detailed resemblances are present in this group which I have outlined in manuscript and which will not be repeated here. Suffice it to say that the group appears to be a natural one, on the basis of the musculature with close resemblances prevalent between *Sauromalus* and *Cyclura*, and *Ctenosaura* and *Brachylophus*.

There is some evidence (e.g., number of cervical ribs) to show that *Holbrookia*, *Crotaphytus*, *Phrynosoma*, and *Sceloporus* are relatively primitive iguanids. If so regarded, we may perhaps consider the conditions of the throat muscles as primordial in these and related genera. This would be expected from the simplicity of the Mylohyoideus in *Holbrookia*, *Callisaurus*, and *Uma* and high number of interdigitations in some of these genera. Simple conditions are also present in *Chalarodon*, *Crotaphytus*, *Phrynosoma*, and *Sceloporus*. *Dipsosaurus*, *Uta*, and *Leiocephalus* possess closer resemblances to the *Cyclura* group than do the genera just mentioned.

Eight representative genera of agamids examined exhibit two layers in the Mylohyoideus anterior. It is evident from the relations with the Geniohyoideus that the superficial (principal) layer in the agamids and chameleons represents the profound (principal) layer in the iguanids, and that the profound layer is not present in the latter group. The superficial (principal) layer has the same direction as the profound (principal) layer in Iguanidæ, being transverse or anteriorly oblique. The profound layer is directed transversely and obliquely backward in both agamids and chameleons (cf. Figs. 46 and 47).

Among the agamid genera examined, *Liolepis belliana* appears to be the most generalized. Here the profundus is thin, restricted, and almost indistinguishable; there are four strong interdigitations with the Geniohyoideus and direct continuity persists between Mylohyoideus anterior and posterior. In *Agama colonorum* and *Physignathus lesueurii* the profundus is more advanced and the intersecting portion of the Geniohyoideus is smaller. In *Amphibolurus muricatus* the profundus is exceptionally broad and there are only two interdigitating bundles. In *Calotes* and *Japalura* a wide separation of anterior and posterior occurs with specialization of the former. In *Draco* there are many

singular features including the presence of a *Depressor labii inferioris* innervated by the mylohyoid nerve and unique among lizards so far as I know. There is but a single interdigitating slip and a considerable interspace is developed as in *Calotes*, *Amphibolurus*, and *Japalura*.

*Uromastix* has an extent and separation of parts almost exactly the reverse of what occurs in the cycluran iguanids.

Apparently in both agamids and iguanids a tendency is evinced for development of certain masticatory specializations. This involves separation of the fibers of the *Mylohyoideus* anterior apparently for pressure forward and upward, and backward and upward of the tongue upon the palate. The end result accomplished appears to be the same in the more specialized members of both families, but the derivation of the muscle fibers in the mechanism evolved is not identical and the direction of each resulting layer and bundle of the *Mylohyoideus* anterior becomes opposite in the two families (cf. Figs. 44 and 45 with Fig. 46).

It should be emphasized that the relations and appearance of the two layers of the *Mylohyoideus* anterior in *Chamæleon* are like those in the Agamidæ and not at all like any other lizards. This strengthens much other evidence of community in these two groups. In *Chamæleon gracilis* (Fig. 47), the *Mylohyoideus* posterior has vanished to a mere shred, and the area of the *Constrictor colli* is greatly extended forward beneath the posterior end of the *Mylohyoideus* anterior.

Among the Scincomorpha (except in amphisbænians) no great modifications of the throat muscles are found. An anterior cutaneous slip of the *Mylohyoideus* anterior is developed in the Scincidæ, Dibamidæ, Gerrhosauridæ, and Lacertidæ, but is lacking in the Xantusiidæ, Feyliniidæ, and Teiidæ (cf. Figs. 48-52).

The Amphisbænidæ are unique in pattern of throat musculature. The *Cervicomandibularis* has a broad insertion and, as in all strong burrowers, is enormously developed to act as a powerful depressor and lateral adductor of the head. The forward extension of *Mylohyoideus* posterior, likewise the longitudinal raphe in the *Constrictor colli* and the anterior separation of two parts of the *Cervicomandibularis*, recall the conditions in *Varanus* (cf. Figs. 40 and 54).

In the Varanidæ very peculiar modifications arise apparently in connection with the sutural break in the lower jaw. The *Mylohyoideus* posterior is specially developed and strong. It extends far forward over the nearly concealed *Mylohyoideus* anterior, and seems to be so placed as to exert a powerful action in swallowing and in pulling together the angles of the jaw. The *Constrictor colli*, a swallowing muscle, is enor-



mous and is divided into dorsal and ventral halves by a longitudinal raphe. The Geniohyoideus and Cervicomandibularis are both specially developed and by their pull would tend to spread the jaws when the mouth is open. The Cervicomandibularis in two divisions is attached to the lower jaw on the ventral side by a superficial fascia and profound supplementary tendons, controlling both halves of each ramus (cf. Fig. 54.)

The Anguioidea are distinguished by the possession of an anterior mandibular muscle similar to the Intermaxillaris of serpents and developed, as shown in *Gerrhonotus*, as a cutaneous attachment of the forward part of the Genioglossus. I have called this muscle the Genio-myoideus (cf. Figs. 58-61). It is present in all the Anguidæ, Xenosauridæ, and Anniellidæ I have examined and reaches its maximum development in *Heloderma*. It is absent in the Zonuridæ.

The Anguioidea are further differentiated by the presence of an anterior superficial reflected bundle of the Mylohyoideus anterior similar to that found in the cycluran iguanids. The pattern of the throat muscles of *Anniella pulchra nigra* and of *Gerrhonotus scincicauda webbi* is complex and almost identical; and equally close resemblances are seen between *Celestus costatus* and *Ophiodes striatus*. *Ophisaurus anguis* and *Anguis fragilis* are similar to each other and somewhat different from both *Ophiodes* and *Gerrhonotus*.

The Zonuridæ represent a moderately advanced stage in comparison with the Scincomorpha and Gekkota but a less complex type than other Anguimorpha (cf. Figs. 55 and 57). The Mylohyoideus is simple and undivided but the geniohyoid interdigitation is much restricted in both *Zonurus* and *Chamæsauro*. In *Zonurus* as in the Iguania the Geniohyoideus is divided, the median half inserting on the mid-ventral raphe and the external half in the usual position on the mandible (cf. Figs. 44, 45 and 55). In *Chamæsauro* the Geniohyoideus is single.

The Mylohyoideus, a breathing muscle in urodeles and Chelonia, has become highly specialized in certain lizards for masticatory and cutaneous functions.<sup>1</sup> In some groups the muscle is degenerate, but still shows signs of former specialization. In the strictly herbivorous forms, *Amblyrhynchus*, *Uromastix*, *Iguana*, *Dipsosaurus*, and *Sauromalus*, a thickening and increase of mass has occurred which has not apparently affected the pattern characteristic of the groups to which these lizards belong.

<sup>1</sup>In absence of a secondary palate (cf. p. 394) the Mylohyoideus anterior probably also serves to hold the tongue (floor of mouth in Varanidæ) closely up against the palate in order to allow the passage of air through the naso-pharyngeal canals during respiration.

## 18.—THE TONGUE

The shape and particularly the texture of the tongue have long been considered diagnostic of various groups of saurian families. Further investigations have upheld the importance of these features. Miss De Rooÿ (1915, Fig. 1) has illustrated certain examples of tongues among the Gekkota, Iguania, Scincomorpha, and Anguimorpha. Göppert (1903) figures others and shows the exact relation of the shape of the tongue to the fleshy and bony parts of the roof of the mouth.

The histological significance of the texture of the tongue in the major groups of lizards may be determined upon examination of the results of Seiller (1891, 1892). The papillæ of the *Ascalabota* and *Diploglossa* are delicate structures, developed apparently to give more surface for the epidermal glands which cover them as a continuous sheath of unspecialized glandular tissue. The papillæ of the *Scincomorpha* have produced a toughened, non-glandular tip, the glandular surfaces being restricted to the bases of the scale-like papillæ. The glands in *Lacerta* are of a more highly specialized type than those of *Anguis* and *Pseudopus*, making derivation of the papillate from the laminate and scaly forms improbable. Holl (1888) shows sections of the tongue in *Lacerta* similar to those Seiller has figured.

The broad, fleshy, partly smooth, partly papillate tongues of geckos and iguanids would seem histologically the least specialized and probably the more ancient type. It is impossible to regard the varanid and ophidian deeply bifid, sheath-based, tubular condition as anything but specialized. The tongue in these forms is highly extensile and functions externally as a tactile organ. Various stages illustrating the steps leading up to such a highly modified state may be seen in certain forms (*Lacertidæ*, *Teiidae*, and *Anguidæ*) where the tongue functions both as a masticatory and as an external tactile organ. On this view the original, slightly nicked tip of the *Ascalabota* has become drawn out into two rather sharp points, the tongue surface has become smooth, thin, and folded to allow greater extensile capacity, the basihyal segment of the hyoid arch becomes more elongate, loosely articulated with the corpus, and in *Varanus* even separated from the rest of the hyoid apparently to allow more freedom of motion of the entire branchial apparatus.

The structure of the chameleon tongue comprises highly modified muscles, bones, and ligaments strictly comparable throughout with those of other lizards, and there is nothing to prevent the complex from having been acquired from an agamoid type of throat musculature (cf. Gandolfi, 1908). The highly extensile tongue has apparently been developed in

connection with the sloth-like movements of this extreme, arboreal, insectivorous type. The curious mechanism has been carefully studied by Kathariner (1895) and by Dewèvre (1895) who do not agree as to the *modus operandi*. The "pneumatic" theory of Dewèvre is not thoroughly acceptable since Germershausen (1913) has shown that many chameleons do not possess the laryngeal air sac necessary under his argument. (Cf. Fig. 47.)

#### 19.—THE LOWER JAW

Certain of the elements of the reptilian lower jaw (cf. Gregory, 1913) are fused or absent in many families of lizards (cf. Figs. 107 and 112). Cope (1892a) has stated that the angular fuses with the articular (=articular+prearticular) in the Gekkonidæ, Feyliniidæ, *Acontias*, the Anniellidæ, and Amphisbænidæ. Bedriaga (1884) finds only four elements in *Blanus cinereus*.<sup>1</sup> Baur (1894) recognizes five elements in *Anniella*—"the articular and supra-angular being ossified." Coe and Kunkel (1906) support the observations of Baur. The splenial is small or absent in Agamidæ and absent in Chamæleontidæ; being well-developed in other families. In the Chamæleontidæ the dentary enlarges to take the place of the splenial. The articular, prearticular, and surangular have fused in the advanced chamæleontid *Brookesia* (cf. Siebenrock, 1893a, Pls. I and II). In *Xantusia* but three bones remain, "the articular [=articular+prearticular] angular, and surangular are coössified, and the splenial and dentary."

According to Boulenger (1885, p. 239) the mandible consists of only four bones in the Pygopodidæ, "the angular, surangular, and articular [=articular+prearticular] having coalesced." Only three elements remain in *Ophioseps*, Jensen (1901).

In the Uroplatidæ (cf. Siebenrock, 1893b, Pl. XIV) only five bones are present, the articular and prearticular, and the surangular and angular being fused.

In some Lacertidæ (cf. Siebenrock, 1894) the splenial is exceptionally large.

The articular and prearticular are fused in all adult lizards I have examined or seen figured. They are separate in the Cotylosauria and Pelycosauria, and in the embryo of *Sceloporus* (Kingsley, 1905).

Fusion between the prearticular and surangular seems to be an age character in *Lygosoma* and *Tupinambis*, and we cannot naturally attach as much phylogenetic importance to fusions as to such absence and reduction as occur in the subterranean forms and in the agamids and chameleons.

<sup>1</sup>Apparently there are only three in *Agamodon*, Peters (1882).

## 20.—THE CAUDAL CHEVRONS

Caudal chevrons are intercentral (cf. Boulenger, 1891, p. 114, 115) in most lizards including all the Ascalabota, most of the Scincomorpha, and the more primitive Anguimorpha. The intercentral position is unquestionably the original one. In the Anguimorpha alone is there any strong tendency for central attachment and in this group such union always seems to occur by progressive anterior migration of the chevron base (intercentrum).

In the teiid, *Tupinambis*, there is an apparent tendency toward central attachment by posterior migration (cf. Boulenger, *loc. cit.*, Fig. 4) but the attachment itself has not yet been developed. In the degenerate scincomorph, *Dibamus*, chevrons are absent.

In the less specialized Anguimorphs, *Zonurus*, *Gerrhonotus*, and *Heloderma*, intercentral attachment still occurs with a tendency to forward migration (cf. Figs. 99–101). In *Ophisaurus*, *Anguis*, and *Anniella* the chevrons are fused centrally as they are in the Serpentes. In *Xenosaurus*, *Chamæsauro*, and *Lialis* they are unfused and intercentral. Among the Glyptosauridæ, the Eocene forms (cf. Fig. 101) have a posterior central attachment, the Oligocene *Helodermoides* possibly a more advanced central situation. For this reason and because of the highly specialized body scutes and fused frontals, I do not derive *Heloderma* directly from the known Glyptosauridæ. Among all the Platyota nearly mid-central attachments occur. *Varanus*, *Saniwa*, *Thinosaurus*, and *Tylosaurus* are alike in having such a location and in the pediculate articulation of the chevrons.

## 21.—THE OS INTERMEDIUM

The intermedium is always small and frequently absent in the Sauria. It seems to be sporadically present among primitive families but is entirely absent as far as known in the Gekkota. Its loss seems usually to occur through fusion with the neighboring ulnare which sometimes provides a pocket for its reception. It is large in *Sphenodon* and in many fossil reptiles, including *Aræoscelis* (Williston, 1914, p. 128 and Fig. 2F).

It appears only in scattering genera for the most part, but what is known of its distribution seems significant—namely that families (except the gekkonoids) considered primitive in other respects all have some genera with an ossified intermedium present as a separate element in the adult. Cope (1892a, p. 196) indicates that the intermedium was present in all genera at his disposal (*Phyllodactylus*, *Coleonyx*, *Anolis*, *Dipsosaurus*, *Sauromalus*, *Crotaphytus*, *Sceloporus*, *Phrynosoma*, *Gerrho-*

notus, *Cnemidophorus*, *Xantusia*, and *Eumeces*). I have examined all these except *Dipso-saurus*, *Cnemidophorus*, and *Eumeces* with results as indicated below.

The intermedium is present in:

Xantusiidæ (*Xantusia vigilis*, Noble, 1921, p. 15); Scincidæ (*Tiliqua*, A. M. N. H., *Eumeces schneideri*, cf. Siebenrock, 1895a, p. 33, *Chalcides ocellatus*, Born, 1880); Lacertidæ (all species examined by Born, 1876, and Siebenrock, 1894); Teiidæ (*Tupinambis nigropunctatus*, A. M. N. H., *Tejostejuexin* and *Ameiva vulgaris* Born, 1876); Helodermatidæ (*Heloderma*, A. M. N. H., cf. also Troschel, 1853); Anguidæ (*Gerrhonotus*, A. M. N. H. 9159); Zonuridæ (*Zonurus giganteus*, A. M. N. H.).

In some Gerrhosauridæ (cf. *Zonosaurus*, Siebenrock, 1895, Fig. 8) the intermedium appears to be joined by suture to the ulnare. In the following genera it is fused with the ulnare or absent entirely: according to Hoffmann (1890) in *Phyllodactylus lesueuri*, *Lygosoma*, *Seps chalcides*, and *Draco viridis*; according to Siebenrock (1893b) in *Uroplates*, (1895a) in most Scincidæ, including most species of *Chalcides*, and certain Gerrhosauridæ and Anguidæ.

I have found it lacking in *Coleonyx* and many other gekkonoids, in the scincs *Trachysaurus* and *Egernia*, in the degenerate teiid *Bachia* (Fig. 68a), in *Varanus*, in *Xenosaurus*, in the iguanids *Crotaphytus*, *Anolis*, *Sceloporus*, *Phrynosoma*, *Sauromalus*, *Cyclura*, and *Iguana*, in the agamid *Calotes*, and in *Chamæleon gracilis* and *C. vulgaris*.

Brühl (1875–1888) in copying a figure of Born (1876) wrongly interprets one of the palmar sesamoids of *Chamæleon* as an intermedium. This error has gained a place in subsequent literature, although Born himself (1880) has called attention to it. Born also reports the intermedium in *Gonocephalus dilophus*.

Born (1876) derives the *Chamæleon* foot from that of other lizards. Stecker (1877) thinks this improbable and believes that *Chamæleon* represents the primitive type from which others have been modified. He finds the intermedium present in the very young embryo of *Chamæleon senegalensis* as a tiny cartilage. There seems nothing but this obscure evidence to support Strecker's opinion.

## 22.—THE BODY MUSCULATURE

The Rectus abdominis muscle in autarchoglossid lizards can usually be subdivided into four parts (cf. Maurer, 1896). Of these only two are generally present in the Ascalabota (cf. Schneider, 1879; Gadow, 1882). These parts comprise (cf. Figs. 40, 62–66, 68, and 75): (1) the Rectus

profundus or main median portion of the Rectus, segmented, in contact on each side with the Obliquus externus profundus and homologous anteriorly with the substernal longitudinal muscles; (2) the Rectus medianus, segmented, often intimately connected with the skin over the whole belly and aiding in locomotion by its pull on the ventral scales; (3) the Rectus lateralis, unsegmented, and forming the lateral continuation of the Rectus medianus; (4) the Rectus internus, unsegmented, arising on the pubis and passing forwards sometimes as far as the sternum and dorsal to the Rectus profundus. The first and last subdivisions need not further concern us. The medianus and lateralis may together be called the Rectus superficialis and as such have an important bearing on taxonomy and saurian evolution.

The Rectus lateralis is found only in lizards. According to Maurer (1898) it arises in the embryo of *Lacerta* as the lateral portion of the superficial layer of the Rectus abdominis. The muscle may usually be recognized by its position alongside the Rectus medianus and profundus and between the Obliquus externus superficialis and the median portion of the Obliquus externus profundus (cf. Figs. 63 and 64). It is unsegmented and in the limbed *Autarchoglossa* may be distinguished by the fact that it passes ventrally over the superficial surface of the Pectoralis to insert into the skin beneath the shoulder girdle or near the axilla. It is sometimes continuous by fascia, below the Pectoralis, with the sterno-cleido-mastoid and sterno-hyoid muscles. It is often closely joined to the skin and seems in these cases to function very strongly in jerking the body forward, assisting the limbs (*Lacertidæ*, *Teiidæ*). It is absent as a separate muscle in the limbless lizards, here being fused indistinguishably with the Rectus medianus to form the Rectus superficialis.

The Rectus medianus is comparable with the Rectus superficialis so-called of *Sphenodon* and in lizards the fibers join the parasternal bars, when the latter are present, in the same way as in *Sphenodon*. The Rectus medianus develops in *Lacerta* (Maurer, *loc. cit.*) by splitting from the main Rectus profundus at an early stage and it seems usually to maintain its individuality because of its connections and functions as a skin-muscle. It gives off the unsegmented Rectus lateralis extending out between the Obliquus externus superficialis and the Obliquus externus profundus. It is covered superficially by the terminal fibers or fascia of the Obliquus externus superficialis. It arises on the pubis and passes forward only to the sternum. It receives upon its dorsal surface the scalares bundles arising on the tips of the ribs. These bundles

are absent in the Iguania and Rhiptoglossa and are usually reduced in the Gekkota. Here they join the inscriptions of the Rectus profundus.

The parasternum develops on the ventral surface of the Rectus superficialis and the true ribs, in order to join the parasternal bars, are usually forced (as in *Sphenodon*) to pass up through the fibers of the Rectus profundus.

In the limbed Autarchoglossa the Rectus superficialis is divided into median and lateral portions; in the limbless forms the two parts cannot be separated and the whole muscle continues as a band on each side as far forward as the terminus of the sterno-cleido-mastoid and sterno-hyoid muscles, from which it is separated by an inscription or by the presence of the reduced sternum or clavicle (cf. Figs. 40 and 75). In the highly subterranean Scincoidea the Rectus superficialis becomes reduced to a narrow strip on each side hidden beneath the overgrowth of the enormous Obliquus externus superficialis. In the degenerate teiids and the Amphisbænidae it is attached to the skin (cf. Figs. 40 and 68). In the grass-inhabiting, surface-terrestrial, limbless anguids it is broadened and almost inseparably joined with the ventral scales. In the Pygopodidae and Chamæosauridae, it is developed as a broad ribbon on each side of the mid-line and is not closely connected with the skin.

I have not been able to find any trace of the Rectus superficialis in any of the ascalabotids examined, with the exception of three genera of terrestrial Agamidae (*Uromastix*, *Physignathus*, and *Liolepis*) where the Rectus lateralis continues forward over the Pectoralis (cf. also Sanders, 1872, and Fürbringer, 1875). I have seen it in all the Autarchoglossids investigated, including representatives of all families except the Anelytropsidae.

It is absent in the following genera:

#### Gekkota

*Ptyodactylus* (Gadow, 1882), *Thecadactylus rapicauda*, *Gekko verticillatus*, *Coleonyx variegatus*, *Hemidactylus brookii*, *Uroplates fimbriatus*, and *Platydictylus japonicus* (Sanders, 1870).

#### Iguania

*Uma notata*, *Chalarodon madagascarensis*, *Crotaphytus collaris baileyi*, *Crotaphytus wislizenii*, *Phrynosoma hernandesi*, *Phrynosoma coronatum* (Sanders, 1874), *Sceloporus magister*, *Uta thalassina*, *Dipsosaurus dorsalis*, *Sauromalus hispidus*, *Amblyrhynchus cristatus*, *Basiliscus vittatus*, *Anolis cuvieri*, *Polychrus marmoratus*, *Enyalius rhombifer*, *Enyalioides heterolepis*, *Stenocercus boettgeri*, *Liolaemus multiformis*, *Leiocephalus*

*carinatus* (and, according to Gadow [1882], in *Iguana* and *Ophyroessa*); in the agamids, *Amphibolurus muricatus*, *Lophura amboinensis*, *Japalura swinhonis*, *Calotes versicolor*, and *Draco formosus* (cf. also Lafrenz, 1914).

### Rhaptoglossa

*Chamæleon gracilis*, *Chamæleon vulgaris*.

The Rectus superficialis is present in the following:

### Iguania

*Uromastix hardwickii* (cf. Fürbringer, 1875), *Physignathus lesueurii*, and *Liolepis belliana* (cf. Sanders, 1872).

### Scincomorpha

*Xantusia riversiana*, *Trachysaurus rugosus*, *Dasia smaragdinum*, *Plestiodon quinquelineatum*, *Chalcides ocellatus*, *Chalcides sepoides*, *Chalcides tridactylus*, *Acontias meleagris*, *Feylinia currori*, *Dibamus novæguineæ*, *Gerrhosaurus zechii*, *Lacerta ocellata*, *Tupinambis nigropunctatus*, *Bachia intermedia*, *Cnemidophorus* sp.?, *Amphisbæna alba*, *Rhineura floridana*.

### Anguimorpha

*Varanus nuchalis*, *Lialis burtoni*, *Pygopus lepidopus*, *Heloderma suspectum*, *Xenosaurus grandis*, *Gerrhonotus scincicauda webbiai*, *Ophisaurus apus*, *Anguis fragilis*, *Ophiodes striatus*, *Anniella pulchra nigra*, *Zonurus giganteus*, and *Chamæsauro macrolepis*.

There are other body muscles reduced or absent among the Ascalabota and present in the Autarchoglossa. Of the Intercostales ventralis (part of Int. internus), the special slips (Scalares) which run downward into the Rectus are absent in all iguanids and agamids I have examined and in the chameleons; they are never so greatly developed in geckos as in autarchoglossids and are absent in *Uroplates*. The Intercostales externi longi, constituting those parts of the Intercostales externi which skip over the ribs, are absent in all iguanids and most agamids and in chameleons, but are often present in geckos. The Obliquus externus profundus is absent or reduced in iguanids, in some agamids, and is absent in chameleons and in *Uroplates*.

The Intercostales externi longi, present in all the Autarchoglossa, are most powerfully developed in the limbless forms where the ribs are used for walking and burrowing.

Fürbringer (1869), when investigating the anatomy of degenerating limbs, unfortunately paid little attention to the much more significant



changes in the body muscles in limbless lizards. He recognized no subdivisions of the Rectus abdominis except those in *Pseudopus* (= *Ophisaurus*); he distinguished the Rectus lateralis under the name Suprapectoralis as Rüdingen had done (cf. Fürbringer, 1875).

Schneider (1879) was apparently the first to appreciate the important variations of the body muscles of the Sauria. He drew up an outline of classification based upon muscle characters but too few facts were at his disposal for the expression of any significant generalizations. He recognized the absence of the Scalares in the Iguanidæ, Agamidæ (Chamæleontidæ?) and in the gekkonid *Platydictylus*; he noticed the great reduction of the Rectus in chameleons without knowing of the almost equal reduction in *Uroplatus*; and he commented upon the decreasing number of myocomata in the Rectus abdominis of certain iguanids and especially among agamids.

Gadow (1882) described certain divisions of the Rectus including the Rectus lateralis (the latter he observed to be absent in the genera *Ptyodactylus*, *Iguana*, *Ophryoesa*, *Polychrus*, *Phrynosoma*, and *Chamæleon*). His view of the innervations and "visceral" origin of the muscle and of the nature of the Rectus internus have been shown by Maurer to be incorrect but he noticed the important variations of the Rectus superficialis.

Maurer (1896, 1898) has most thoroughly studied the body muscles of certain reptiles and amphibians both from comparative and embryological points of view. The conclusions he reaches regarding the origin of the various layers present in lizards are important enough to warrant summary here.

The ventral body musculature in reptiles is innervated segmentally by the ventral branches of the spinal nerves. The Rectus itself is formed from the more dorsal layers and cannot be considered "visceral musculature," as Gadow and Schneider have stated. There is no genetic basis for Müller and Huxley's divisions—the episkeletal and hyposkeletal musculature—the more logical distinction is between the dorsal musculature innervated by dorsal branches of the spinal nerves and the ventral musculature with which we are dealing.

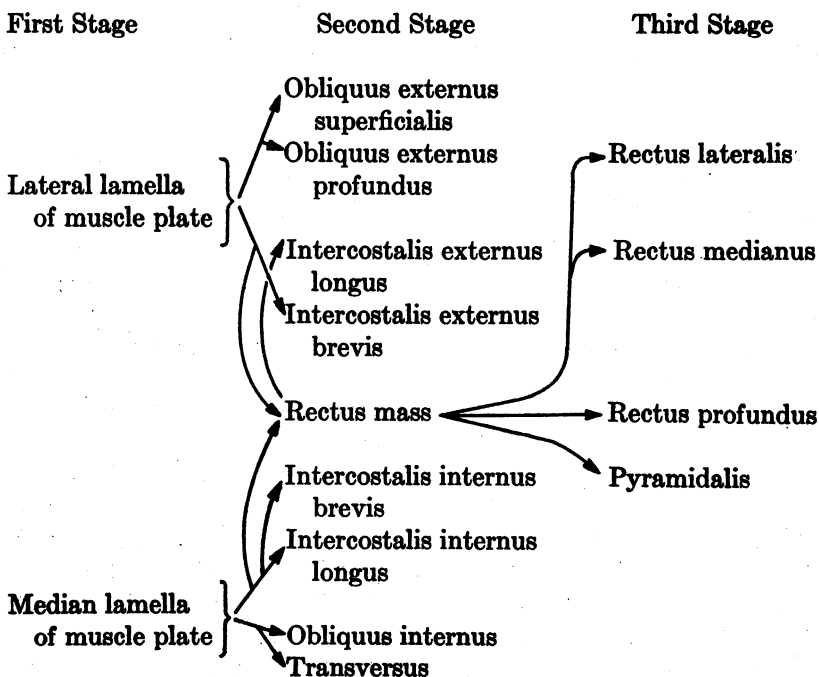
The ventral musculature arises from the ventral half of the mesodermic muscle plates, and these at a very early stage develop two layers of primordial muscle cells supposedly corresponding to the two layers of side muscles found in fish and in *Cryptobranchus*.

The outside layer develops into the entire group of muscles lying over the ribs, including the Intercostalis externus. The inside layer forms

the Intercostalis internus, the Obliquus internus and the Transversus, as had already been suspected from comparative data. The Rectus develops from both layers during their growth downward around each side of the body. The layers which contribute to it are shown in the following diagram.

### THE EMBRYOLOGICAL DEVELOPMENT OF THE RECTUS ABDOMINIS

#### EMBRYO OF *Lacerta agilis*



# THE COMPARATIVE MORPHOLOGY OF THE RECTUS ABDOMINIS

## RAMI VENTRALES OF NERVI SPINALES

*Chamaeleon*  
(Ascalabotid)

*Lacerta*  
(Autarchoglossid)

*Sphenodon*

Crocodile

*Triturus*

Primary Layers  
As in *Cryptobranchus*  
and embryo  
*Lacerta*

Obliquus externus	Rectus profundus (weak in adult, strong in larva)	Rectus profundus	Pyramidalis (= Rectus internus Gadow)	Pyramidalis	Sometimes absent
Obliquus internus	Rectus superficialis (strong in adult, weak in larva)	Truncocaudalis (a swimming muscle)	Rectus profundus	Rectus profundus (sometimes absent)	Rectus abdominis
		Rectus superficialis	Rectus superficialis	Rectus medialis	Absent
				Rectus lateralis	Absent

# RAMI VENTRALES OF NERVI SPINALES

384

It is apparent from Maurer's results that the *Rectus superficialis* is a morphologically widespread and embryologically precocious muscle. Its absence in *Ascalabota* cannot well be due to the primitiveness of that group but more probably to the fact that all forms in the group except certain primitive agamids have lost the muscle, while it remains and develops in the *Autarchoglossa*. This would seem to imply that the pro-Sauria may have carried the body close to the ground and that this mode of locomotion has been correlated with the development of "slinking" musculature in the belly-wall.

Lizards today which retain this mode of locomotion retain the musculature, while the group that seems to have early adopted arboreal life has apparently lost the musculature in question and carries the body more stiffly and sometimes held up off the ground. Even the thoroughly terrestrial and non-lamellate geckos carry the body well elevated. Depressed geckos are mostly arboreal. Compressed Iguania are all arboreal and carry the body elevated. Depressed Iguania are always terrestrial but generally elevate the body when running in contrast to the scincs, lacertids, teiids, and anguids, where the belly usually remains in closer contact with the earth.

Whatever has happened, it seems clear that the method of locomotion attained by the *Autarchoglossa* preserves a key system of highly developed body muscles opening up a treasure-chest of possibilities when opportunity for preservation of a worm-like burrowing, or a limbless, snake-like, grass-living, habitus is afforded by the environment. Time and again in various parts of the world scincs, teiids, and anguids appear to have gone off on such a course, lost the limbs and girdles in varying degree, and developed even more highly, and in a number of different ways, sets of muscles already present in their more normal ancestral forms. The ascalabotids constitute half of the entire lizard population of the world. They have never developed limbless, burrowing genera and seemingly cannot do so on account of the arboreal specializations and reductions in their locomotory musculature.

If for any reason whatever the limbs should degenerate in geckos and iguanians the lizards would find themselves helpless; if, however, such a thing happened in a scincoid or anguimorph (as indeed it seems to be happening in frequent instances) the creature finds itself still capable of locomotion, and if grass-land or humus-soil environments happen to be at hand, such limb reduction may become favorable.

## 22a.—The Parasternum and its Relations to the Xiphisternum and Sternum

The parasternum, constituting the so-called abdominal ribs, seems to be developed separately from the sternum chiefly among arboreal and in burrowing genera. It reaches a maximum extent among the subterranean Scincoidea (Fig. 75). It also appears in a slight degree among all known surface-living terrestrial Scincoidea, and, so far as known among the Anguimorpha,<sup>1</sup> only in the Chamæosaurinæ. It is most highly specialized in certain burrowing Teiidae (Fig. 68). I have recognized it in the Uroplatidae, a few iguanids, the Chamæleontidae, the Scincidae, the Feyliniidae, and the Dibamidae, in a teiid, *Bachia*, and in the zonurid, *Chamæsauro*. It has not previously been noted in the Dibamidae and Zonuridae. Stannius (1856) has mentioned the presence of abdominal ribs in *Platydictylus guttatus*. I have not found the parasternum in any of the gekkonid genera at my disposal.

In the Iguanidae "abdominal ribs" are present according to Boulenger in the terrestrial genera, *Hoplocercus*, *Ctenosaura* (1 pair), *Cyclura* (1 pair), *Hoplurus*, *Chalarodon*, and *Liosaurus*, and in the arboreal genera *Iguana* (1–2 pairs), *Leiocephalus*, *Scartiscus*, *Urostrophus*, *Anisolepis*, *Enyalius*, *Enyalioides*, *Polychrus*, *Tropidodactylus*, *Norops*, *Anolis*, *Xiphocercus*, and *Chamæleolis*.

Siebenrock (1895a) notes the "costæ abdominalis" in *Chalcides tridactylus* (9 complete pairs), *C. mionecton* (5 pairs), *Ablepharus pan-nonicus* (4 pairs) and from one to three pairs in the rest of the scincid genera he examined. "Den Gerrhosauriden und Anguiden fehlen sie ganzlich."

Rabanus (1906–1915) figures sixteen pairs of parasternalia in the scincid, *Voeltzkowia mira*.

The number of parasternal ribs present in various genera is indicated below. Comparisons are given in order to illustrate the progressive increase in the number of parasternal ribs in series of autarchoglossine forms having a progressively burrowing habitus.

	Habitat	Digits	Parasternal Ribs
Ascalabota			
<i>Uroplates fimbriatus</i>	Arboreal	5	13
<i>Chalarodon madagascarensis</i>	Terrestrial	5	3
<i>Brachylophus fasciatus</i>	Arboreal (?)	5	2

<sup>1</sup>It should be noted that both *Lialis* and *Anniella* and other snake-like anguids lack parasternal ribs in spite of their degenerate habitus. This may lend additional support to the view that the Pygopodidae are diploglossids.

	Habitat	Digits	Parasternal Ribs	
<i>Cyclura</i>	Terrestrial	5	1	
<i>Ctenosaura</i>	Terrestrial	5	1	
<i>Iguana</i>	Arboreal	5	2	
Anoline iguanids (Cope, 1892a)	Arboreal	5	4-5	
Polychrine iguanids (Cope, 1892a)	Arboreal	5	7-10	
<i>Chamæleon vulgaris</i>	Arboreal	5	11	
	Habitat	Digits	True Ribs After Sieben- rock (1895a)	Parasternal Ribs
<b>Autarchoglossa</b>				
<b>Scincomorpha</b>				
<i>Trachysaurus rugosus</i>	Surface terrestrial	5	32	7
<i>Tiliqua scincoides</i> (Beddard, 1904b)	Surface terrestrial	5	34	7
<i>Ablepharus pannonicus</i> (Siebenrock, 1895a)	?	5	28	4
<i>Chalcides ocellatus</i>	Surface terrestrial	5	37	2
<i>Chalcides mionecton</i> (Siebenrock, 1895a)	Burrowing?	4	44	5
<i>Chalcides sepoides</i>	Burrowing	3-4	?	14
<i>Chalcides tridactylus</i>	Burrowing	3	58	9 <sup>1</sup>
<i>Voeltzkowia mira</i> (Rabanus, 1906-15)	Burrowing	0	?	14-17
<i>Acontias niger</i> (Fürbringer, 1900)	Burrowing	0	?	23
<i>Acontias meleagris</i>	Burrowing	0	?	23
<i>Typhlosaurus auranticus</i> (Fürbringer, 1900)	Burrowing	0		27
<i>Feylinia currori</i>	Burrowing	0		35+ <sup>2</sup>
<i>Bachia intermedia</i>	Burrowing	3-4 (cf. Fig. 68)		13
<i>Chamæsauro macro- lepis</i>	Surface terrestrial	1-2		9

<sup>1</sup>Carlsson (1887) has counted fifteen in this species.<sup>2</sup>Some irregular pieces (cf. also Müller, 1900 and Rabanus, 1906-15, who find the same number).

Schneider (1879) was perhaps the first to demonstrate, by the muscular connections, the different nature of what he called the true ribs and the belly ribs in *Anolis* and *Polychrus*, but he believed the condition here to be unlike that in the Chamæleons.

Gadow (1882) taking into account the absence of the Rectus considers the abdominal ribs of *Anolis* and *Chamæleon* "fully homologous" and takes issue with Schneider on this point. But Gadow did not distinguish the belly ribs from the true ribs; in other respects I should confirm his view.

Fürbringer's opinion of the so-called abdominal ribs of certain lizards was stated in 1900 (p. 249) about as follows: The abdominal or metasternal ribs following the sternum show various relations—they either end freely at different distances from the ventral mid-line, or they are bound together only by ligaments, or they join more or less intimately in the mid-line by their long terminal cartilages (abdominal ribs). . . . Sometimes these are cartilaginous sometimes calcareous. Also, ossified and partly independent abdominal ribs may form what might be thought to be a rudimentary parasternalia. Abdominocostalia still both united to the ribs and separated from them can be found together in the same animal. I have no definite views regarding these conditions and consider further accurate investigation necessary to decide the question (translation).

After this time Beddard (1904a, 1904b, 1906) published some accounts of supposedly special conditions in the Australian scincs *Tiliqua* and *Trachysaurus*, and believed that in these forms he could demonstrate the presence of a definite parasternum comprising the free lateral "abdominal ribs" overlapping at certain points the cartilaginous tips of the dorsal ribs lying in the deeper musculature.

He makes it clear, however, that he does not mean to extend the term parasternum to include all the so-called mid-ventral abdominal ribs but only those free lateral ribs included in the two special cases mentioned. Concerning the case in *Trachysaurus* where a pair of true ribs meet and fuse in the mid-line a little way behind the sternum, he says (1906): "These true ribs meet and fuse superficially and exactly resemble the succeeding abdominal ribs, so far as the median region is concerned. This, however, can invalidate no homology, for . . . the remaining pieces of cartilage so entirely overlap so considerable a portion of the true ribs that they [the cartilages?] cannot possibly be regarded as the equivalent of their [the cartilages?] median ventral extremities, which, indeed, themselves reach to within a millimetre or two of the



ventral middle line." Earlier than this he states (1904b): "It is to my mind possibly a matter for further inquiry as to how far the median ventral region of the post-sternal ribs which actually meet each other behind the sternum may not be actually a parasternum fused with true ribs." Williston (1916, p. 187) regards with favor this suspicion, saying: "We know of no fossil form in which the anterior or any dorsal ribs met or even approached each other in the middle or behind" the median coracoids. And Williston carries these observations to the logical inference that with the support of other paleontological evidence the sternum itself may be regarded as derived from such a parasternal apparatus as is represented in *Ophiacodon*.

It is of importance, therefore, to determine the morphology of the parasternum in lizards and to try and decide the question left open by Fürbringer as to whether all mid-ventral rib elements can be considered as true parasternalia. I think that the following summary of evidence will lead to the definite answer that in all cases both mid-ventral and free lateral parts of the abdominal ribs, when present, should be regarded as portions of a true parasternum.

We shall consider the following points in respect to the mid-ventral elements: (1) Their relations to surrounding soft tissues; (2) their relations to the true ribs; (3) their relations to the so-called xiphisternal rods and to the sternum; (4) their distribution and relations during development in a series of progressively degenerating species of a single genus; (5) comparisons with *Sphenodon*, crocodile, and more ancient forms.

(1)

In the following discussion of the myological relations of the parasternum, the muscle names proposed by Maurer (1896) are employed (cf. p. 377). The Rectus, it should be remembered, is almost absent in the chameleons and in Uroplates, so that the true relations appear only at the extreme posterior part of the abdomen where the Rectus is present. With this in mind we may say that the parasternum in lizards INVARIABLY lies ventral to the main Rectus profundus in the tissue between that muscle and the median terminal fascia of the Obliquus abdominis superficialis. The muscle sheet developed as the superficial layer of the Rectus abdominis, i.e. Rectus superficialis, is the muscle most closely attached to the median parasternum and fibers of the fascia of the superficial obliquus usually insert upon it (cf. Figs. 68 and 75). It must be emphasized that the parasternum never lies ventral to the superficial obliquus nor dorsal to the Rectus profundus. The first relation would allow a strictly dermal

origin which has probably not occurred (p. 392). The second would imply primitive association with the ribs, which is undoubtedly erroneous.

In autarchoglossid lizards, but not in *Sphenodon*, the lateral portion of the Rectus superficialis extends outward over the surface of the Obliquus abdominis profundus, the Intercostalis externus longus, and the extremities of the true ribs; and the ends of the true parasternal bars may extend out into this Rectus lateralis to overlap the terminal cartilaginous rib ends in the way noted by Beddard in the Australian scincs. I have seen this also in *Chalcides sepoides* and such a situation does not appear to be common.

The parasternal bars in lizards usually correspond exactly with the inscriptions of the Rectus and are never more numerous except where the Rectus is absent. Also, it is important to note, the parasternum never extends forward over the sternum and xiphisternum although the Rectus lateralis, in which it is sometimes developed, often does so.

(2)

The parasternal chevrons always correspond in position to the ribs but rarely extend caudalwards as far as do the dorsal ribs. Only in *Chamaeleon* and *Uroplatus* does this occur but even here the most posterior parasternal bars never gain a pleural articulation. The parasternal bars usually join the cartilaginous rib-ends directly, but connections are frequently lacking in the posterior region, are often anomalous and misplaced, and in cases where the parasternum extends laterally into the Rectus lateralis, the rib-tips may join the bars medially.

The parasternum of lizards does not therefore appear to be either primitively or ontogenetically related to the ribs. This is exactly what appears in the embryology of *Sphenodon* (cf. Schauinsland, 1903).

(3)

There is however a very specific relation of the parasternal bars to the xiphisternum and possibly also to the sternum. The position in the muscles is identical if we may accept Maurer's view that the sternocosto-coracoid muscles are certainly the disconnected, forward continuations of the Rectus profundus. These longitudinal muscles lie immediately dorsal to the sternum and represent that anterior continuation of the Rectus above the sternum which is found in the urodeles. Also, as the sternum and xiphisternum degenerate, in the limbless lizards, they gain more and more the appearance of the parasternal chevrons so that in some extreme degenerates (cf. *Dibamus*, Fig. 75; *Feylinia*, Fig. 73) the resemblance is nearly perfect. Furthermore, when anomalies occur

in the attachments of the sternum and xiphisternum to the ribs, the contiguous parasternal bars may show close affiliation with parts of the xiphisternal apparatus. Such a case is illustrated (Fig. 68). Here a true, highly modified parasternal bar, (P), has been made over on one side into a xiphisternal rod while its opposite half remains in normal condition. A parasternal element is apparently used to help "balance" assymetry in the xiphisternal apparatus and close serial homology of the structure is indicated.

## (4)

Further support for the theory of the independence of the parasternum in lizards may be obtained from a comparative study of the conditions in a group of closely related degenerating scincs. Such a series is available in the genus *Chalcides* (cf. Table, p. 387). Here are a number of closely related forms, some of which are progressively modified in many ways in correlation with burrowing habits. The parasternum in the more advanced burrowers is much more extensive than in the fully limbed surface forms. We may be quite sure that in at least the majority of such lizards the parasternum is undergoing development rather than degeneration. Slight turning back might, to be sure, occur in some cases anywhere along the line, but if we handle three species we can be sufficiently certain that at least one of these will give us the conditions we require—namely a progressively developing structure rather than a degenerating one. Now in all of the stages (represented by species of the genus *Chalcides*) which we have examined, *C. ocellatus*, *C. sepioides*, and *C. tridactylus*, and in many other limbed and limbless scincs, the posterior chevrons, supposedly the developing parts of the parasternum, are not fully or not at all connected with the ribs. This can scarcely mean anything else than that the parasternal elements arise near the mid-line NOT FROM THE SKIN but in the connective tissue immediately ventral to the Rectus superficialis at a distance from the rib-ends which they join only later. This is all we need show, after consideration of the evidence given under other headings, to demonstrate (even in the absence of direct embryological data for lizards) that the parasternum of the Sauria is similar to that of *Sphenodon*.

## (5)

In *Sphenodon*, the parasternum is bony; it is sometimes so in lizards. It lies in the superficial layer of the Rectus and beneath (dorsal to) the tendinous fascia of the Obliquus abdominis externus; it does so in lizards. It extends outward laterally beyond the rib-ends with which it

connects; it occasionally does the same in lizards. It arises separately from the ribs as a mid-ventral structure developed in the subcutaneous connective tissue (cf. Voeltzkow, 1902); it arises apparently in this manner in lizards. The parasternum in crocodiles and in *Sphenodon* is similar in all its relations except that, as in the lizards, the chevrons of the crocodile correspond to the metamerism of the body while, in *Sphenodon*, they are twice as numerous (Voeltzkow, *loc. cit.*, Daiber, 1921).

This significant difference between the condition in *Sphenodon* and in the Sauria seems to involve the question of the origin of the parasternum itself. Voeltzkow and Döderlein (1902), Williston (1916), and many others call attention to the fact that the parasternum in the more ancient fossil amphibians and reptiles is often less localized than in recent forms. In the *Cotylosauria* and *Theropleura* (Williston, *loc. cit.*) and *Ophiacodon* (Williston and Case), and in *Kadaliosaurus* Credner (1889), the parasternalia consist of a multitude of small bars or segments of bars, lying as a series of closely set chevrons, numbering six to each pair of true ribs. Even more numerous than this are the transverse elements of the plastron in the amphibian *Melanerpeton*. In crocodiles, dinosaurs, birds (*Archæopteryx*), Pterosaurs and lizards, on the other hand, the number of parasternal bars is reduced to one for every body segment. Howes and Swinnerton (1903) determine that each parasternal bar of *Sphenodon* arises as a number of separate fragments. These become fixed in the adult so that each chevron normally consists of three segments. We would therefore surmise that the arrangement in *Sphenodon* represents a slightly less advanced stage than in lizards and that the parasternum is tending to disappear among lizards, especially in the Anguimorpha, where neither an extreme aquatic habitus (*Mosasauroidæ*) nor an extreme burrowing one (*Anniellidæ*) have succeeded in redeveloping it.

Our conclusion would be that the sternum and xiphisternum are modified parasternal structures originally represented as mid-ventral, serially homologous parasternalia quite separate from the ribs. Some embryological evidence does not support this view. Goette (1877), in lizards, and Schauinsland (1903), in *Sphenodon*, find that the sternum arises in connection with the ribs. Goette considered the sternum of the salamanders, which arises in the way we should expect on the parasternal hypothesis, to be non-homologous with the "costal sternum" of amniotes. But Rathke (1853) viewed the saurian sternum as non-costal, and Bogoljubsky (1914) has found good evidence for this in early embryos of *Lacerta* where, as in salamanders, the sternal anlage are separate from

the ribs, arising as a paired clump of cells on the mid-line and developing independently for a time.

Hanson (1919) has reviewed and added significant results which support the non-costal theory of the origin and the universal homology of the tetrapod sternum. But he goes so far as to regard the copula of the pectoral girdle in Elasmobranchs as a true sternum and presents evidence to show the common origin of the scapulo-coracoid and sternum, while considering the parasternal structures as something apart.

Most of Hanson's evidence comes from the field of mammalian embryology. His comparisons of conditions in reptiles and amphibians are largely based on adult and highly specialized forms and even these scarcely show his contention that the scapulo-coracoid and sternal apparatus are of similar origin. He does not refer to the investigations of Bogoljubsky (1914) who clearly demonstrates that in *Lacerta* the sternum arises much later than the scapulo-coracoid and quite separately from that structure.

### 23.—THE EPIPTERYGOID

The epipterygoid (columella cranii) is of interest because of its reduction or absence in burrowing forms, its reduction in some Agamidæ, and its complete absence in the chameleons.

It is totally lost in a few extreme subterraneans (Dibamidæ, Boulenger, 1887; Amphisbænidæ, Cope, 1892a). In *Anniella*, Cope denies its presence; Baur (1894) discovered it; Coe and Kunkel (1906) claim to have recognized it but do not show it in their figures.

Stannius (1856) found it absent in the chameleons. Dollo (1884) thought he had discovered it in *Chamæleon vulgaris*, but Siebenrock (1892) thinks that the bone Dollo saw was the orbitosphenoid. In a skeleton of *Chamæleon vulgaris* at hand prepared by Frič, the orbitosphenoid can be traced in its usual lacertilian position within the membrane closing the brain-case in front of the paroccipital. No trace of an epipterygoid can be seen.

In connection with the question of relationship of the chameleons to the agamids, it is noteworthy that the only limbed lizards (non-burrowers) in which the epipterygoid is greatly reduced are *Lyriocephalus*, *Phrynocephalus*, and certain other Agamidæ (Siebenrock, 1895 b).

In the Scincoidea the epipterygoid is met dorsally by a long, descending process from the parietal. A pocket in the dorsal surface of the pterygoid receives its base.

## 24.—THE PALATE

A united palate formed by contact of the pterygoids in the mid-line is found only among the Scincidæ (Boulenger, 1887) and Agamidæ where the condition is doubtless secondary. The primitive scincs *Trachysaurus*, *Tiliqua*, and *Egernia* have the pterygoids well separated. The agamids *Gonocephalus godeffroyi*, *Calotes cristatellus*, and *C. versicolor* have the pterygoids in contact (Siebenrock, 1895b). The pterygoids are separate in *Aræoscelis* (Williston, 1914).

It is interesting to note the investigations of Göppert (1903) who illustrates how closely the fleshy and bony parts of the palate reflect the shape of the tongue in lizards and in birds. Here no true secondary palate is present and the tongue serves to close the naso-pharyngeal passages during respiration. In *Varanus* and in the Serpentes where the tongue is attenuate, the floor of the mouth appears to serve the required function. In *Varanus* and possibly in the mosasaurs (cf. Baur, 1892a and Williston, 1898, Pl. XII) grooves which appear to accommodate the tongue are present anteriorly in the prevomerine bones. Accordingly the tongue in the mosasaurs must have been long and forked as in *Varanus*.

## 25.—THE PINEAL FORAMEN

The presence or absence and position of the pineal (parietal) foramen may indicate certain evolutionary tendencies. The foramen is usually pierced between the parietals but, in the Iguania and Rhipitoglossa, where these bones are constricted posteriorly it sometimes migrates forward to lie in the fronto-parietal suture (*Iguana*, *Cyclura*, *Basiliscus*, *Corythophanes*, *Xiphocercus*, *Norops*—Boulenger, 1890; most Agamidæ—Siebenrock, 1895b), or entirely within the frontal (*Dipso-saurus*—Cope, 1892a; *Sitana ponticeriana*, *Gonocephalus kuhlii*—Siebenrock, *loc. cit.*; *Uromastix spinipes*—Beddard, 1905b, *Chamæleon* and *Brookesia*—Siebenrock, 1893a).

There is no foramen in the recent Gekkota including *Coleonyx* and *Uroplates*; in the agamid *Liolepis belliana* (Siebenrock, 1895b); in the scincomorphs *Xantusia*, *Cnemidophorus*, *Tupinambis*, and the Amphisbænidæ; and *Voeltzkowia mira* and *Zonosaurus madagascariensis* (W. J. Schmidt, 1909). In *Cicigna* and *Cordylosaurus* (Hoffmann, 1890) the foramen is lacking. In *Gerrhosaurus* the opening is closed but a clear space is present at its former location. The foramen is also absent in many of the Diploglossa including the Pygopodidæ, *Heloderma*, †*Peltosaurus*, *Anguis*, and *Anniella*. It is very small in the Eocene glyptosauroids, *Xestops* (Fig. 103) and *Glyptosaurus*, and is present in the Jurassic gecko, *Ardeosaurus*.

W. J. Schmidt (1909) has investigated the structure of the pineal organ in many lizards and reviews most of what is known on the subject. He finds the organ reduced and the eye lacking in the *Gekkota*, in *Zonosaurus*, and in *Voeltzkowia mira*. The loss of the foramen is accompanied by a loss of the eye in every known case except in *Gerrhosaurus* and *Anniella* (Coe and Kunkel, 1906). In the latter the eye may "function" through the transparent parietals.

In the *Iguanidæ* and *Agamidæ* the eye is optically imperfect and lacks a nerve connection. Similarities between *Draco* and *Chamæleon* have been noted. In both the eye is extremely small and degenerate and the foramen is minute.

In the *Scincidæ* and *Lacertidæ* a nerve sometimes remains in the adult. The size of the foramen has no relation to the size of the eye in the latter group. Those who would relate functional significance of the eye with size of the foramen in fossil forms should note this.

Nowikoff (1910) believes that the eye is an organ of protection since, he claims, it is not developed in animals which are of large size, which are nocturnal, or which live out of harm's way in the tops of trees (*Draco* and *Chamæleon*). This theory is likely to be discountenanced. Experimental evidence so far is negative. Nowikoff finds the eye non-functional in the *Varanidæ*—the lens being filled with dark pigment.

It is suggestive that in certain *Scincidæ* and in *Amblyrhynchus*, where a heavy skull covering of dermal bone occurs, the foramen still persists. This may mean that the eye retains some function as an optical organ in these forms.

## 26.—THE DERMAL SCUTES

The systematic importance of the differences in structure of the bony plates underlying the horny scales in certain lizards was first appreciated by Duméril and Bocourt (1870). No satisfactory investigation of the comparative morphology and histology of these structures appeared however until the recent work of Otto (1909), the further investigations of Stehli (1910), and the extraordinary researches of W. J. Schmidt (1910, 1912, 1913, 1914, 1915).

Otto developed some interesting systematic views based almost wholly upon his idea of the evolution of the various types of structure of the bony plates and their relation to the horny scales. He considered the conditions found in geckos (cf. Fig. 83) illustrative of the most advanced stage; that of *Zonurus* (Fig. 90) the most primitive. All degrees of intermediate structure were noted between these two extremes (Figs.

84-98). His theory of the direction of evolution of the bony scales is apparently supported by conditions observed in regenerated tails of scincs and in embryonic stages of *Anguis*. In these he thought he could distinguish a more "primitive" (more *Zonurus*-like) type of scute structure and arrangement. On the basis of these observations he places *Zonurus* and *Pseudopus* (*Ophisaurus*) in a family opposite the Scincidæ and he regards the genus *Anguis* as a sort of link between the two. After an examination of the evidence we shall reconsider these views.

The bony dermal scutes found in lizards are developed just under the pigment zone in the uppermost layer of the cutis (Krauss, 1906). They arise from mesenchymatic cells and the epidermis is wholly unconcerned with their formation (Stehli). They are now known in the Scincidæ, Anelytropidæ, Feyliniidæ, Gerrhosauridæ, Helodermatidæ, Anniellidæ, Anguidæ, Zonuridæ, and in a few geckos having been observed in *Tarentola mauritanica*, "*Platydictylus murorum*," and *Gekko verticillatus* by Cartier in 1872 (cf. Ficalbi, 1880); by Wiedersheim (1875) in *Phyllodactylus*; by Todaro in "*Ascalabotes*," and by W. J. Schmidt (1915) in *Geckolepis*.<sup>1</sup>

In *Tarentola* Otto finds very little correlation (none on some parts of the body) between the distribution of the small, regularly placed bony ossicles (Fig. 83) and the horny epidermal scales above them. Otto believes that he gets a more definite relation between the bony plates and the scales in the young stages of *Tarentola* but his illustration (Fig. 27) of this point is not convincing. Also on the regenerated tail of *Tarentola*, where we should expect to find phylogenetically the more primitive conditions, a horny scale defines a definite area of bony plates. But these differences seem so slight as not to appear significant.

Among the Scincidæ, Otto studied scales from various parts of the body in the genera *Scincus*, *Gongylus*, *Seps*, *Lygosoma*, *Mabuya*, and *Acontias*. In all these (cf. Figs. 84-87), bony plates are found beneath each scale but the peripheral limits of the bony scutes and the horny scales never exactly coincide, and the tubercles in each scute are so arranged as to form a mosaic-like structure of from two to many small parts. In the scales taken from the large plates under the jaw and in the cloacal region (Fig. 84) a "complex" condition is apparently reached approximating that found in the geckos. Great similarity exists in the form of scales from identical parts of the body in the various genera of scincs studied, and considerable differences obtain among the scales on different parts of the same body. Otto considers the "primi-

<sup>1</sup>Osteoderms are developed only over the skull in the Lacertidæ, Xantusiidæ, Xenosauridæ, and in some Iguanidæ. In the Xenosauridæ they are minute, nodular, and on a small scale resemble those seen in *Heloderma* (Fig. 98).



tive" stages to be represented by the dorsal caudal scutes in Scincidæ "while those on the head show a more complicated form."

"These conditions must bring us to the conclusion that both in *Ascalabotes* which still have a double scale covering as well as in the Brevilingues [=Scincomorpha], there existed primitively a close relationship between the horny and bony structures."

Schmidt shows (Figs. 88-89) that the bony scaling in the ventral plates of the Gerrhosauridæ, as in the Scincidæ, does not exactly correspond to the form of the horny scales, and that a tendency to develop a mosaic pattern is present in this family as well as in the Scincidæ. Schmidt also believes that the simpler pattern found dorsally in *Gerrhosaurus* is more advanced than that of the Scincidæ. This would reverse the phylogeny of Otto. Stehli supports Otto's opinion chiefly on embryological evidence.



Fig. K. Imbricating osteoderms of the simple type. *Gerrhosaurus nigrolineatus*, dorsal scutes,  $\times 10$ , after Schmidt (1913a, Fig. G1, p. 83).

This is the most advanced stage found among scincomorphs and corresponds with the conditions seen in the Anguimorpha.

Otto finds in *Anguis* a stage still simpler than in the scincs. Here (cf. Fig. 92) the mosaic pattern of the bony scutes becomes almost completely obliterated and the relation of each scute to the overlying scale is more exact. In *Zonurus* and *Pseudopus* (Figs. 90, 91 and 93) the outline of the bony scute conforms exactly to that of the horny scale and the scute itself is a heavy solid piece without apparent pattern. This is Otto's most "primitive" stage. Exactly similar conditions are found in sculptured scutes of the North American Eocene Glyptosauridæ, tending to corroborate other evidence that these lizards are diploglossine (cf. Figs. 94-97). In *Heloderma* an exact relation of bony and horny elements is maintained although the scales are reduced to bead-like knobs. I think this shows that we are not dealing with a primitive condition in the osteodermal Diploglossa but with the maximum development of the bony derm that is known among lizards. We may well believe that the more generalized condition of geckos is primitive though we cannot prove it any more than Otto can demonstrate his own opposite contention.

Obliteration of osteoderms proceeds *pari passu* with profound subterranean life and has apparently occurred in the Dibamidæ. In the Anelytropsidæ and Anniellidæ the scutes are reduced, apparently by vacuolization (cf. Coe and Kunkel, 1904), but retain their group characteristics.

## 27.—THE SQUAMATION

As long ago as 1888 Boulenger had convinced himself "that in some cases, the aberrant scaling of the reproduced tail is a reversion to an ancestral form." Examples shown were the regenerated tails of a "Geissosaurine," teiid, *Gymnophthalmus*, in which the scaling was that hexagonal type of the "Cercosaurine" teiids rather than the normal cycloid form, and of an anguid, *Ophisaurus*, in which the scalation took the cycloid form of the related genus *Anguis* rather than the normal rhomboid type.

Werner (1896) in a study of the squamation of the regenerated tail in comparison with that of the embryo found support for Boulenger's discovery in the fact that in certain geckos having rows of larger tubercles on the tail the reproduced tail developed the uniform granular scaling found both on the embryo and in certain other geckos believed to be more primitive on account of the non-laminate condition of their toes.<sup>1</sup>

Werner's investigations indicate that the uniform granular lepidosis is the most primitive condition in the geckos. This view is held on other grounds by Sokolowsky (1899), by Barbour (1921) for the genus *Sphaerodactylus*, and by W. J. Schmidt (1906–1915) who demonstrates the probability that in the few cases in which dorsal, imbricating scales have been developed in geckos (*Geckolepis*, *Teratoscincus*, *Teratolepis*, and others) such squamation is secondary, since the lizards in which it occurs are widely separated genetically and, for the most part, geographically.

Judging from Schmidt's figures and descriptions, and from specimens I have handled, the imbricate scales of geckos do not essentially differ from the imbricating scales of other ascalabotids including the Iguanidæ and Agamidæ. In all these there is a long "free-margin" and the scales "stand out" and are not so firmly anchored in the flesh as are the imbricating scales apparently of all the Autarchoglossa (cf. Figs. A–B).

We are therefore probably dealing with a most primitive type of squamation in the uniform granular covering of many Ascalabota. Whether this is ever developed secondarily in higher groups need not specially concern us. The important fact seems to be that the ventral parts in the Ascalabota possess a lepidosis consisting of either granular or very small imbricate scales and that the number of these for every

---

<sup>1</sup>Tornier (1897) takes exception to Boulenger's theory on the grounds: (1) that in many lizards, i.e., Iguanidæ, Agamidæ, Zonuridæ, Lacertidæ, Gerrhosauridæ, certain Gekkonidæ (and certain Scincidæ), the scaling of the reproduced tail is normal; (2) that some geckos (*Pachydactylus*) seem to show an advanced rather than a reversional type of scaling in the outgrowing tail; (3) that the hexagonal, keeled scales of "Geissosaurine" regenerated tails are more advanced than the cycloid type which he regards as primitive. Boulenger's wording "in some cases" covers the first two objections, and Tornier, in the third count, does not explain why *Ophisaurus* should take on a "less advanced" cycloid form of scaling.

segment of the body is greater (except in *Sphærodactylus*, *Leiocephalus* and *Sceloporus magister* and probably in *Geckolepis* and *Teratoscincus*) than in the Autarchoglossa.

Smalian (1885) noticed that among amphisbænians the New World forms, *Amphisbæna fuliginosa* and *Anopsibæna kingii*, have two annuli corresponding to each body segment (I have found this to be the case also in *Amphisbæna alba* and *Rhineura floridana*), while in the Old World *Blanus cinereus* there is only one; and in *Trogonophis wiegmanni*, an African acrodont genus, there are two dermal segments to each rib. *Trogonophis*, however, is fundamentally different from the New World forms for each segment of the skin is innervated by a separate nerve (Rami lateralis of ventral branches of spinal nerves). May we consider the double or the single annulus as primitive?—the acrodont or the pleurodont series? Whatever may be the views as to the New World forms, it seems evident that the African *Trogonophis* is developed from a singly annulate type such as *Blanus*. The nerve distribution would show this and I believe that here we have an exception to what seems to be the usual rule of progressive skin metamerism, and increasingly close correspondence of ventral scale rows and body segmentation in the higher forms.

Stehli (1910) discovered that in certain snakes a single row of scales corresponds to one body segment, that in scincs and anguids there are two scale rows for every rib, and that in the geckos he studied there is no segmental arrangement of the scales. He came to the conclusion that among reptiles the segmental order is the original order, with the necessary corollary that the horny scales, when in correspondence with the segmentally arranged bony scutes, represent a more primitive condition than the diffused type found in geckos. He supports this conclusion with the observations of Hase who demonstrated a segmental arrangement of scales in bony fishes and ganoids. For his paleontological evidence he goes to *Aëtosaurus*, where the bony plates are, to be sure, segmentally arranged. *Aëtosaurus*, he thinks, represents the primitive condition one should expect to find among ancestral lizards. If all this is so we have genuine support for the conclusions of Otto (p. 395) in regard to the evolution of the bony scales of lizards. And we must dismiss our scheme of phylogeny and regard the serpents, zonurids, and anguids, and some limbless lizards as primitive, and the normal scincs and geckos as more advanced or more degenerate. If Stehli's evidence holds we must overrule the data of Werner, Sokolowsky, and W. J. Schmidt regarding lacerilian squamation, and we must believe with Maurer and Gegenbaur that the granular geckonid condition is degenerate.

Stehli would regard those forms having a single row to each segment as more primitive than those with two rows as he states in his conclusions (p. 795). This would involve the derivation of the normal zonurids from the degenerate *Chamæsauroidea*, the normal teiids from the worm-like *Bachia*, and many other equally startling cases.

I have counted the number of transverse scale rows on the belly, in correspondence with each body segment, in the following lizards:

Ascalabota (Approximate): *Thecadactylus rapicauda*—8; *Coleonyx variegatus*—6; *Sphærodactylus macrolepis*—2; *S. cinereus*—2; *Chalarodon madagascarensis*—12; *Iguana tuberculata*—6; *Sceloporus magister*—2-3; *Leiocephalus carinatus*—2; *Enyalius rhombifer*—4; *Chamæleon gracilis*—5.

Autarchoglossa: *Xantusia riversiana*—2; *Trachysaurus rugosus*—2; *Feylinia currori*—2; *Dibamus novæ-guinæ*—2; *Gerrhosaurus zechi*—2; *Lacerta ocellata*—2; *Tupinambis nigropunctatus*—2; *Cnemidophorus* sp.?—2; *Bachia intermedia*—1 (cf. Fig. 68); *Amphisbæna alba*—2; (*Amphisbæna fuliginosa*)—2; *Rhineura floridana*—2; (*Anopsibæna kingii*—2)<sup>1</sup>; (*Blanus cinereus*—1)<sup>1</sup>; (*Trogonophis wiegmanni*—2)<sup>1</sup>; *Varanus nuchalis*—3; *Pygopus lepidopus*—1; *Lialis burtonii*—1; *Hemiderma suspectum*—2; *Xenosaurus grandis*—2; *Gerrhonotus scincicauda*—2; *Ophiodes striatus*—2; *Anniella pulchra*—2; *Zonurus grandis*—2; *Chamæsauroidea macrolepis*—1; *Typhlops congestus*—2 (ophidian); *Diadophis* sp.?—1 (ophidian).

The facts appear to be that in the Ascalabota the scaly covering when imbricate is as figured by W. J. Schmidt (1906-1915, Pl. xxv, fig. 15) for *Geckolepis*. The scales are not so firmly anchored and have a longer free border than in the Autarchoglossa. Also that in the Ascalabota there are usually several (more than four) transverse ventral scale rows to each segment of the body, whereas, in the Autarchoglossa there are usually two and never more than three.

The best evidence seems to show that the most primitive features of the squamation of lizards are: (1) uniform granular scales on all parts of the body; (2) imbricating scales, when present, with a wide free-margin; (3) transverse rows of ventral scales not in correspondence with each pair of ribs; (4) osteoderms composed of many small, diffuse granules (cf. Figs. 82-83). All these features are represented only in the Ascalabota. The frequency of the lesser number of ventral skin segments aligns itself with the frequency of attachments of the specially

---

<sup>1</sup>After Smalian (1885).

developed layers of the rectus muscle concerned with serpentiform or worm-like terrestrial locomotion.

### 27a.—The Femoral Pores

Gland-like organs, of which the femoral, preanal, inguinal and anal pores are the external orifices, appear in the following families (cf. Boulenger, 1885–1887, Werner, 1895, and Schaefer, 1902):—

Ascalabota: Gekkonidæ, Iguanidæ, Agamidæ.

Autarchoglossa: Xantusiidæ, Gerrhosauridæ, Lacertidæ, Teiidæ, Amphisbænidæ, Pygopodidæ, Zonuridæ.

They are absent in:—

Ascalabota: Uroplatidæ, Chamæleontidæ.

Autarchoglossa: (Scincimorpha) Scincoidea; (Anguimorpha) Anguidæ, Xenosauridæ, Anniellidæ, Helodermatidæ, and Varanidæ.

They occur universally only in the Xantusiidæ, Gerrhosauridæ and Zonuridæ. They are distributed among twenty-nine of the fifty-two genera of gekkonids recognized in Boulenger's Catalogue. Among the Iguanidæ they appear chiefly in the North American genera and in the Fijian *Brachylophus*, being absent in the Mascarine and South American forms except *Enyalioides*, *Ctenoblepharis*, *Liolaemus*, *Phymaturus*, *Amblyrhynchus*, and *Conolophus*.

Among the Agamidæ all the Australian genera and species except *Chelosania* possess the organs and they are present among representatives of this family elsewhere only in *Uromastix* and *Liolepis*.

The pores are present in the males in all genera of the Teiidæ except *Monoplocus*, *Callopistes*, *Leposoma*, *Loxopholis*, *Pholidobolus*, and *Macropholidus*.

All the Lacertidæ except the genus *Aporosaura* have pores in both sexes. In *Tachydromus* the pores are inguinal.

In the Amphisbænidæ the pores are represented in all genera except *Rhineura*, *Lepidosternon*, and *Trogonophis*.

The pygopodid genera *Pygopus*, *Cryptodelma*, and *Lialis* retain preanal pores. The burrowing forms *Delma*, *Pletholax*, *Aprasia*, and *Ophioseps*, lack them.

In the Autarchoglossa the pores are usually restricted to a single row. Among the Ascalabota several rows or patches may be present as in the New Zealand geckos *Naultinus* and *Hoplodactylus* (cf. Fisher, 1883, Abhandl. Naturwiss. Vereins. Bremen, VII, Pl. xvi, fig. 3). In *Thecadactylus australis*, from the islands of Torres Straits, a subtriangular patch of eighteen pores is said to occur in the males, whereas in the

American species, *rapicauda*, referred to the same genus, there are no pores.

This interesting, patch-like arrangement in the Australian and New Zealandian geckos would seem to be a primitive condition retained in these forms. The Australian and North American distribution of *Iguania* having femoral pores, together with the presence of so-called "false pores" in certain extra-Australian agamids, might lead one to suppose that secondary development in the phylogeny does not occur, but such a conclusion would scarcely be in line with what we know of the histological structure of the incipient pores of certain agamids and *Varanidæ*.

Tölg (1903) has described and figured the supposedly secondary papillæ of *Agama inermis* and *Agama stellio*, and makes it plain that these organs may be considered as true, incipient pores. That they cannot so well be regarded as vestiges follows from their occurrence on the belly of *Agama stellio*. Tölg also finds them in the inguinal region of *Varanus griseus* (cf. K. P. Schmidt, 1919, p. 488). He regards the papillæ as representing the first stages in the development of the usual, more deeply invaginated and glandular epidermal organs. He finds what he considers an intermediate stage in *Lacerta muralis* var. *maior*.

That the glands may undergo histological differentiation in some groups is indicated by the results of Cohn (1904) who discovers a, very highly developed type of femoral organ in *Cnemidophorus lemniscatus*.

Félizet (1911) has shown that the glands arise in the embryo of *Lacerta* as pockets in the profound layers of the epidermis.

Duvernoy, Wagler (1830), and Johannes Müller first noted the glandular nature of the femoral organs. The histology has been investigated by Leydig (1872), Schaefer (1902), Cohn (1904), Tölg (1903), Félizet (1911), and others. Félizet remarks upon the similarities with the mammalian sebaceous gland: "La glande fémorale de l'adulte présente une évolution identique à celle de la peau ou plutôt à celle d'une glande sebacée. . . tout comme les cellules des glandes sebacées (les cellules) se rapportent à deux types." This was also partly the view of Meissner (1832), Leydig, and Schaefer, and many later workers. Tölg objects to it considering the "secretion" in the adult as the cellular modified form of the horny layer of the epidermis, a point which Félizet's observations do not seem to contradict. Tölg further states: "Wir haben es also, wenn wir die Verhältnisse nochmals überblicken; in den Femoralorganen mit scharf begrenzten Teilen der Oberhaut zu tun, die sich von dieser nur dadurch unterscheiden, dass sich hier der Ver-

hornungsprozess mit einer besonderen Intensität, aber nicht periodisch wie in der Haut abspielt, sondern einen mehr regelmässigen, stetigen Verlauf nimmt. Den Beziehungen der Femoralorgane zu einem umfangreichen lymphraum kann ich keine besondere Bedeutung beimessen."

The last sentence is in reference to the view of Maurer who believed that the proximity of lymph spaces indicated a similarity to the musk glands of crocodiles. Eggeling (1914) evidently regards the pores as paleotelic and relates them to the callous patches developed in male newts during the breeding season. Such a view appears improbable.

The glands are seemingly of functional significance and not vestigial or rudimentary structures, as might appear from their erratic distribution in some groups. In most geckos they occur only in the males. This is also true of certain teiids and of the iguanid *Phymaturus*.

Meissner (1832) studied the structures in many genera, observing that the pores were often greatly enlarged in the males. Otth (1833) confirmed this by observation of captive *Lacerta*, finding that enlargement occurred during the breeding season. Without recognizing the structure as being glandular, he regarded the pores as an accessory copulatory mechanism. It has been subsequently noted that the organs are passive in both sexes during the greater part of the year and that active secretion occurs only in the males at the time of breeding. This indicates a sexual function, the nature of which is not definitely known. Observations of Collin de Plancy (1877) and others on the mode of copulation would suggest that the waxy secretion may serve to maintain closer adhesion during the embrace.

Conclusions are that the femoral organs, functionally of some importance, are sometimes secondarily developed in the Ascalabota. Varying degrees of complexity in different forms tend to show how this might happen. Less complete localization of the pores in certain geckos may signify primitiveness of those forms; and the complete absence in certain groups and universal presence in others is of systematic interest.

## 28.—THE SHOULDER MUSCULATURE

Fürbringer (1900) in his great work on the reptilian pectoral girdle has investigated the shoulder musculature in a number of lizards. None of the systematic points he discusses seem of more significance than the variation in form of the proximal belly of the Biceps brachii (cf. pp. 421–425 and Pl. XIII, figs. 127–132).

Progressive specializations and reductions occur in this muscle which seem to be of evolutionary consequence.

The primitive condition appears to be represented in all Gekkonidæ examined, in most Scincidæ, and in a gerrhosaurid (*Hemidactylus*, *Gekko*, *Tarentola*, *Ptychozoon*, *Lygosoma*, *Gongylus*, *Zonosaurus*). In these the proximal belly is simple, undivided, and fleshy throughout.

In what Fürbringer calls the "next stage" a small tendon of origin appears alongside the proximal fleshy bundle. Such a condition obtains in the scincomorphs *Trachysaurus*, *Lacerta*, *Ameiva*, and *Tupinambis* and in the genus *Zonurus*. In *Varanus* this tendon has become enlarged and the fleshy belly reduced and directed somewhat backward. In the Iguania,—*Phrynosoma*, *Liolepis* and *Uromastix*, a division of the tendon into two or more parts occurs. Finally a total reduction of the fleshy belly appears and the biceps comes to have a long tendinous origin—*Uroplates*, *Iguana*, *Phrynosoma* (according to Rüdingen), *Stellio*, *Calotes*, *Chamæleon*, and *Heloderma* (cf. Shufeldt, 1890).

I have checked this character and find that in the primitive gecko, *Coleonyx variegatus*, the tendinous band between the two bellies of the biceps is scarcely wider than an inscription; that in *Gerrhosaurus zechi* the proximal belly is completely fleshy as in many scincoids; that the conditions in *Gerrhonotus*, *Zonurus*, and *Xenosaurus* are very similar, and different from other forms (cf. Figs. 64–65). In these three diploglossids a small tendon of origin is developed posteriorly instead of anteriorly to the fleshy proximal belly and this tendon is separate well down into the distal belly of the biceps. In the third stage along with *Liolepis*, *Uromastix*, etc., I should place *Brachylophus fasciatus* which has not completely lost the fleshy proximal bundles. My observations on *Uroplates*, *Calotes*, and *Phrynosoma* agree with those of Fürbringer.

#### 29.—THE ELEVATION OF THE SKULL

Boulenger (1920) in a monographic study of the Lacertidæ, in which the paleontology as well as the comparative structure and taxonomy is considered, outlines certain evolutionary modifications that he believes can be determined in this family. First among these tendencies are listed reduction of palatal teeth and FLATTENING and weaker ossification of the skull. Méheley (1907), likewise in a review of the Lacertidæ, adopts a system diametrically opposed to that of Boulenger and regards those forms with elevated skulls as derived from the flat-skulled types. To do this, however, Méheley is forced to obtain palatal teeth from absence of teeth, parietal foramina from forms in which these do not exist, normal eyelids from genera in which a transparent disc has been developed, non-denticulate from denticulate ear-openings, normal digits



from digits elongate and compressed, nostrils pierced in the center of the nasal from nostrils enclosed between two or more plates, and striated from spotted types of coloration (in opposition to the views of Eimer, Cope, and Gadow as to the origin and history of the color pattern in the Lacertoidea. (Cf. Boulenger, *loc. cit.*)

In the Lacertidæ at least we choose to conclude with Boulenger that the elevated type of skull is primitive. It is probable that this also holds true in the Scincidæ where certain Australian forms, in certain other respects primitive (*Trachysaurus*), have a relatively elevated type of skull. In *Trachysaurus* the inner (orbital) angle of the jugal approaches 90°. In the anguimorph Eocene family, the Glyptosauridæ, this is also the case (cf. Douglass, 1908, p. 278, Fig. 2; also Figs. 103, 106, 107 of the present paper).

The elevated skull is possibly developed secondarily in some Iguania and in the Rhiptoglossa (cf. *Amblyrhynchus*, *Uromastix*, and some other agamids, and the chameleons).

### 30.—THE OS HYPOISCHIUM

A cartilaginous or calcareous os hypoischium occurs as far as known in all genera of limbed lizards except certain geckos, the Xantusiidæ, a single iguanid *Chalarodon*, most Scincidæ, and the Rhiptoglossa. I have found it absent in cleared or alcoholic specimens of the following: *Hemidactylus*, *Phyllodactylus*, *Lepidoblepharis barbouri*, *Coleonyx variegatus*, *Lathrogecko xanthostigma*, *Gonatodes annularis*, *Chalarodon madagascarensis*, *Xantusia vigilis*, *X. riversiana*, *Chamæleon vulgaris*, *C. dilepis*, *Egernia cunninghami*, *Dopasia smaragdinum*, and *Plestiodon quinquelineatus*. Siebenrock (1893b) has noted its absence in *Brookesia* and *Chamæleon*, and states it to be universally absent in the Scincidæ.

Gadow (1882b) has failed to find the bone in *Phrynosoma cornutum* but it is present in all western species of *Phrynosoma* according to Bryant (1911).

The element has been seen in the following genera. Where no authority is cited, I am responsible for the examination.

Gekkonidæ: *Sphærodactylus macrolepis* (Noble, 1921, p. 11, Fig. 6B, "rudimentary or wanting"), *Coleonyx variegatus* (Noble, *loc. cit.*), *Pachydactylus maculatus* (idem, "extremely long"). *Thecadactylus*, *Gehyra*, *Phyllodactylus*, and *Gekko verticillatus*, *Gekko* (Mehnert, 1891), *Platydictylus mauritanicus* (Ficalbi, 1880).

Uroplatidæ: *Uroplates fimbriatus* (Siebenrock, 1893b,—the bone is triangular in shape and extends farther posteriorly, in a specimen at hand, than Siebenrock has figured it).

Iguanidæ: *Holbrookia maculata approximans*, *Crotaphytus collaris baileyi* (both ♂ and ♀, but stronger in the ♂), *Iguana tuberculata* (Hoffman, 1890), *Iguana delicatissima* (Gadow, 1882b), *Amblyrhynchus cristatus*, *Brachylophus fasciatus*, *Sauromalus hispidus*, *Basiliscus amboinensis* (Hoffmann, loc. cit.), *Polychrus marmoratus* (idem), *Anolis sagræ*, *Norops auratus*, *Xiphocercus heterodermus*.

Agamidæ: *Japalura swinhonis*, *Agama plica* (Hoffmann, 1890), *Gonocephalus subcristatus* (Mehnert, 1891), *Liolepis guttata* (idem), *Calotes versicolor*, *Draco formosus*; and in the following listed by Siebenrock (1895b): *Charasia*, *Phrynocephalus*, *Amphibolurus*, *Lophura*, *Uromastix*, *Moloch*, *Sitana*, *Lyriocephalus kuhlii*, and *Acanthosaura*.

Scincidæ: *Trachysaurus rugosus*, absent in *Tiliqua* according to Werber, 1865.

Gerrhosauridæ: *Gerrhosaurus*.

Lacertidæ: All forms examined by Siebenrock (1894) including *Lacerta*, *Algiroides*, and *Acanthodactylus* (cf. also Mehnert, 1891).

Teiidæ: *Ameiva surinamensis* (Mehnert, 1891), *Ameiva vulgaris* (Gadow, 1882b), *Tupinambis nigropunctatus*.

Varanidæ: *Varanus niloticus*, *V. exanthematicus*, *V. nuchalis*, *V. bivittatus* (Hoffmann, 1890), *V. salvator* (Mehnert, 1891).

Pygopodidæ: *Pygopus lepidopus* (Cope, 1894b, Pl. XIII, fig. 3b and c, [=Hypogastroid].) The cartilage is totally divided, one half attaching to each of the widely separated halves of the ischio-pubis. If we knew the ontogeny of this interesting condition it might be found to support Mehnert's conception of the paired origin of the hypoischial cartilages.

Helodermatidæ: *Heloderma suspectum*.

Xenosauridæ: *Xenosaurus grandis*.

Anguidæ: *Gerrhonotus scincicauda webbiai*, *G. imbricatus* (Siebenrock, 1895a), *Ophiodes striatus* (Fürbringer, 1869—here, with separation of the much reduced ischii the symphysis has been lost but the Y-formed "Cartilago cloacalis" still remains joined to each ischium in the usual way. Cf. also Cope, 1892b, Pl. XIII, fig. 2b).

Zonuridæ: *Zonurus giganteus*, *Chamæsauro macrolepis* (Cope, 1894b, Pl. XIII, fig. 1b—very large in comparison with rest of pelvis and apparently degenerating at a slower rate.)

The shape is usually elongate and pointed (Fig. L1), often with a split at the distal extremity (Fig. L2) where the tips curve around the insertions of the Mm. Transversus perinei, and sometimes (Fig. L3) arising from each ischium. Rarely is the bone short and rectangular (Fig. L4) (cf. *Uroplates*).

The os hypoischium, discovered in *Phrynosoma* by Spring and Lacordaire (1842), has been studied by Mehnert (1891) and Wiederheim (1872) in connection with other pelvic median elements at one time supposed to represent the phylogenetically oldest portion of the girdle. The late appearance of the os hypoischium, derived, according to Mehnert, from the ischium, and of the os epipubis which arises from the pubis in a similar manner, would seem to discredit the view that these elements represent primitive parts present in *Protopterus*. It is also claimed that no developmental relation exists between the ligamentum medianum (symphyseal ligament) and the end bones, epipubis and hypoischium. The ligamentum medianum develops as a muscular septum and later obtains a secondary pelvic connection.

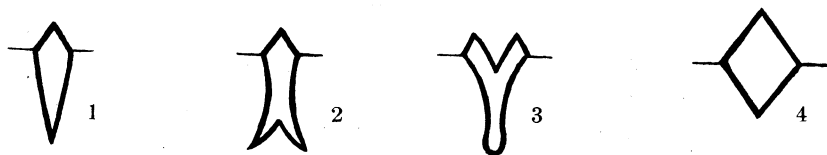


Fig. L. Various types of the os hypoischium.

In adult material the hypoischium has every appearance of being a posterior continuation of the symphyseal ligament but according to Mehnert the whole hypoischial structure (os hypoischium and ligamentum hypoischium) is a direct outgrowth of the median posterior portion of the primordial ischial cartilage.

Mehnert's figures (Pl. VIII, figs. 3 and 4) do not clearly show all points of his contention. It would appear very probable that the so-called perichondrial tissue of the developing cartilaginous anlage of ischium and hypoischium (Fig. 4) is represented by the medial so-called hypoischium of an earlier stage (Fig. 3) and that the origin of this tissue may well be the medial ends of the ischii (Fig. 2). There really appears to be no embryological ground for the statement that the os hypoischium originates in two parts since, as Mehnert admits and illustrates (Fig. 4), the center of ossification arises in the perichondrial tissue as a single cartilaginous element separate from the ischii. It never becomes a true bone in lizards, and its distribution might better be accounted for on the view that the element is only an epiphysial calcareous deposition in the ligamentum hypoischium than that we are dealing with a more primitive degenerating element as Mehnert would suggest. This lessens the paleontologic value of the structure and prevents us from regarding the

distribution in *Menobranchus* and *Didelphys* as indicative of primitiveness, or as offering homology with the lizard bone.

The ligamentum hypoischium, universally present in limbed lizards, lies between the median termini of the large transverse perineal muscles which constrict the base of the tail. A chondrification or calcification frequently occurs in this ligament and may extend along the entire ligamentum medianum as far as the pubis (cf. Wiedersheim, 1892; also Bryant, 1911, Figs. A and B, and Siebenrock, 1895*b*, Figs. 32, 34, 38). There is often a suture or foramen at the basal end of the hypoischial bone which would indicate a separate center of calcification for the os hypoischium as Mehnert has found.

The os hypoischium is absent in *Sphenodon*, and also, so far as known, in the extinct reptilia and amphibia. It is apparently a neomorph in lizards; develops early in the phylogeny; is not represented in most primitive geckos though occasionally developed in that family; is absent in the relatively primitive xantusids and in most scincids and possibly has been lost in *Chamæleon* owing to reduction of the Mm. Transversus perinei.

The Varanidæ alone among lizards is the anterior representative of the os hypoischium, the epipubic bone, paired.

### 31.—THE PATELLAR SESAMOIDS

The patella ulnaris lies in the tendon of insertion of the triceps which rides over the end of the humerus to reach the olecranon. It is partly bony in most of the Ascalabota and cartilaginous in most Autarchoglossa. When cartilaginous it merges insensibly into the fibers of the triceps tendon. It would seem possible that its weaker development in the latter group is associated with use of the belly muscles for purposes of locomotion. Unfortunately, for this theory, however, the element is bony in the scincs, *Tiliqua* and *Trachysaurus*, (cartilaginous in *Egernia*), and in *Tupinambis*.

Fürbringer (1900, pp. 443-444, 459, Pl. xv, figs. 147-158) is not inclined to regard its form and distribution as of great significance in lizards. He found the patella ulnaris in all the forms he examined, it being bony or partially so in the ascalabotids, *Hemidactylus*, *Gekko*, *Ptychozoon*, *Uroplates*, *Phrynosoma*, and *Calotes*,—and in *Lacerta*; and cartilaginous (faserknorpelige) in the autarchoglossids, *Lygosoma*, *Zonosaurus*, *Zonurus*, *Ameiva*, and *Varanus*,—and in *Chamæleon* and *Brookesia*.

Cope (1892a) has found the patella tibialis only in *Varanus*. It is also present and bony in *Tiliqua*, *Trachysaurus*, and *Gerrhosaurus*, and I have seen it bony in no other forms. It seems to be neomorphic and the ulnar patella is doubtless of like nature in the bony state.

A peculiar bony fibular interarticular sesamoid is sometimes developed in the internal femero-fibular ligament lying beneath the broad insertion tendon of the Rectus femoris in which the patella tibialis develops. This element is present in *Crotaphytus*, *Sauromalus*, *Iguana*, *Cyclura*, *Chamæleon vulgaris*, *Egernia*, *Trachysaurus*, *Tiliqua*, *Gerrhosaurus*, and *Tupinambis*. It is double in *Egernia*. It seems to be present, along with a bony patella, in the dolichosaur *Opetiosaurus* (Nopcsa, 1903). Banchi (1900) has named this bone the parafibula. He finds it in *Lacerta ocellata*, *Varanus arenarius*, *Chamæleon vulgaris*, *Platydactylus mauritanicus* and *Gongylus occellatus*. He regards it as a primitive element, the remnant of a third metapodial, because of its large size and separate development in the embryo.

### 32.—THE STERNAL FONTANELLES

Sternal fenestræ are present in most of the families of lizards exclusive of the Anguimorpha, where they have never been found. A single fontanelle occurs in most Iguanidæ, most Scincoidea, and Lacertoidea, and in the amphisbænoid *Chirotos*. *Xantusia vigilis* has a very small double fenestra (cf. Fig. 69). In a few Iguanidæ the opening is divided by a median strip of cartilage and in all known Agamidæ having a perforate sternum, the fontanelles are double.

In the following synopsis the capital letters in parentheses refer to Cope (1892), and Siebenrock (various papers).

#### NO FONTANELLES:—

Gekkota: *Phyllodactylus tuberculatus* (C), *Gonatodes atricucularis* (Noble, 1921), *Paragonatodes dickersoni* (idem), *Lepidoblepharis barbouri* (idem), *Platydactylus guttatus* (Calori, 1861), *Hemidactylus ovalensis* (Gegenbaur, 1865), *Gonatodes annularis*, *Gehyra*, *Lathrogecko xanthostigma*, *Coleonyx variegatus*, *Uroplates fimbriatus* (S).

Iguania: *Læmanctus longipes* (Parker, 1868), *Chalarodon madagascarensis*, *Sauromalus* (C), *Crotaphytus wislizenii* (C), *Polychrus* (C), *Lyriocephalus* (Boulenger 1885), *Lophura* (S), *Moloch* (Boulenger, 1885, states that the sternum has a longitudinal median suture. In specimens examined by Siebenrock, 1895, this was not observed).

Anguimorpha: *Gerrhonotus multicarinatus* (C), *Gerrhonotus scincicauda*, *Anguis fragilis* (C), *Ophisaurus ventralis* (C), *Dopasia gracilis*

(C), *Ophiodes striatus* (C), *Xenosaurus grandis*, *Heloderma suspectum* (Shufeldt, 1890), *Delma fraseri* (Müller, 1900), *Pygopus lepidopus* (C), *Varanus bengalensis* (Parker, 1868), *Tylosaurus dyspeltor* (Osborn, 1899), *Clidastes dispar* (Fürbringer, 1900, after Marsh), *Zonurus cordylus* (Fürbringer, 1900), *Chamæsauro macrolepis* (C).

Rhoptoglossa: *Brookesia* (S), *Chamæleon quilensis* (Methuen and Hewitt, 1914), *C. demaranus* (idem), *C. ventralis* (idem), *C. brevicornis* (idem), *C. lateralis* (idem), *C. dilepis* (idem), *C. vulgaris* (Gegenbaur, 1865), *C. gracilis*.

Scincomorpha: *Plestiodon aldrovandi* (Gegenbaur, 1865), *Trachysaurus rugosus* (idem), *Mabuya multifasciata* (S), *Gongylus ocellatus* (Müller, 1900), *Chalcides lineatus* (C), *Evesia monodactyla* (C), *Tiliqua nigrolutea* (Parker, 1868), *Egernia*, *Zonosaurus ornatus* (S), *Propus vermiformis* (C), *Blanus cinereus* (Müller, 1900).

#### A SINGLE MEDIAN FONTANELLE:—

Iguanidæ: *Phrynosoma* (many species, Bryant, 1911), *Iguana tuberculata* (Parker, 1868), *Anolis carolinensis* (C), *A. sagræ*, *Dipsosaurus dorsalis* (C), *Crotaphytus collaris* (C), *Sceloporus undulatus* (C), *S. spinosus* (C).

Scincomorpha: *Eumeces obsoletus* (C), *E. fasciatus* (C), *Lygosoma quoyi* (S), *L. tæniolatus* (S), *L. sundevallii* (S), *Mabuya striata* (S), *Chalcides mionecton* (S), *Gerrhosaurus nigrolineatus* (S), *Lacerta agilis* (Gegenbaur, 1865), *L. simonyi* (S), *L. muralis* (S), *L. oxycephala* (S), *L. mosorensis* (S), *Ophiops* (S), *Acanthodactylus* (S), *Eremias* (S), *Cnemidophorus tessellatus* (C), *C. sexlineatus* (C), *Bachia intermedia*, *Chirotus canaliculatus* (Parker, 1868).

#### TWO FONTANELLES:—

Iguanidæ: Some species of *Holbrookia* (specimens prepared by Miss M. C. Dickerson and described by her in MS.).

Agamidæ: *Gonocephalus kuhlii* (S), *Agama atra* (S), *Lirolepis beliana* (S), *Grammatophora barbata* (Gegenbaur, 1865), *Agama stellio* (Calori, 1859b), *Physignathus lesueurii* (Beddard, 1905b). *Calotes jubatus* (Boulenger, 1912), *Calotes versicolor*.

Scincimorpha: *Xantusia vigilis*, *Ablepharus pannonicus* (S. Here there is a small anterior and a larger posterior fontanelle, the latter being partially divided), *Lacerta muralis* var. *cærulea* (S).

Siebenrock (1895b) finds the sternal fontanelles much larger in the young of certain agamids. He explains this on the assumption that the fontanelles are formed directly by incomplete union of the two halves

of the embryonic sternum, basing this idea on Goette's observations (1877). Bogoljubsky (1914), however, has shown that the openings arise by resorption of the mesenchymatous and cartilaginous median parts after complete union of the sternal halves. It seems probable that the fontanelles are sometimes of secondary development, possibly in connection with certain relations of the Pectoralis musculature. Their non-appearance in the Anguimorpha and rather uniform distribution in some other groups give them a systematic value.

### 33.—THE SCAPULO-CORACOID FENESTRÆ

Fenestræ are present in the coracoid and anteriorly between the coracoid and scapula in most lizards. Usually these are enclosed anteriorly by the cartilaginous coracoidal and scapular borders<sup>1</sup>; sometimes they are simply open emarginations. A membranous window usually closes each fenestra (cf. Figs. 64–69).

The most lateral of these openings, lying entirely within the scapula, occurs notably in the Iguanidæ and Scincidæ. Its presence results in the formation of the proscapular process, present in the Gekkonidæ and Iguanidæ, in the agamid *Lophura*, in many Scincidæ, in the teiids, *Cnemidophorus* and *Ameiva*, and in the anguid *Celestus striatus* (cf. Cope, 1892a).

The scapulo-coracoid fenestra is almost universal among fully limbed lizards but is represented in *Heloderma*, some varanoids, the mosasaurs, and a few other forms simply by an emargination and is absent in *Uroplatus* and *Chamæleon*.

The first, and most lateral, coracoidal fenestra is also widely distributed, being absent so far as known only in *Heloderma*, some dolichosaurs and mosasaurs, and *Chamæleon* among the limbed forms. The second, and most medial, fenestra is irregularly distributed as indicated in the following table where X indicates the presence of a closed fenestra and E of an emargination.

<sup>1</sup>The so-called "epicoracoids" and suprascapula of lizards are remains of the cartilaginous embryonic scapulo-coracoidal plate (cf. Goette, 1877, and Broom, 1906). The anterior coracoid (=epicoracoid or procoracoid) of theromorphous reptiles (=epicoracoid of *Ornithorhynchus*) is not to be confused with the "epicoracoid" of lizards. The bony coracoid of lizards, *Sphenodon*, and the cotylosaur, *Seymouria*, may represent both anterior and posterior coracoidal elements of theromorphs.

	SCAPULAR	SCAP.-CORACOID	1" CORACOID	2" CORACOID
<b>GEKKOTA</b>				
<i>Platydictylus muralis</i> (Calori, 1859a)	E?	X	X	X
<i>Platydictylus mauritanicus</i> (Ficalbi, 1880)	E	X	X	X
<i>Hemidactylus oualensis</i> (Gegenbaur, 1865)	X	X	X	X
<i>Gekko verticillatus</i> (Boulenger, 1912)	?	X	X	X
<i>Gonatodes atricucullaris</i> (Noble, 1921)	E	X	X	O
<i>Paragonatodes dickersoni</i> (idem)	E	X	X	X
<i>Lepidoblepharis barbouri</i> (idem)	E	X	X	O
<i>Sphærodactylus macrolepis</i> (idem)	E	X	X	O
<b>IGUANIA</b>				
<i>Chalarodon madagascarensis</i>	X	X	X	O
<i>Iguana tuberculata</i> (Parker, 1868)	X	X	X	X
<i>Læmanctus longipes</i> (idem)	O	E	X	O
<i>Sauromalus hispidus</i>	X	X	X	X
<i>Sauromalus varius?</i>	X	X	X	X
<i>Cyclura</i>	X	X	X	X
<i>Crotaphytus collaris</i>	X	X	X	X
<i>Crotaphytus wislizenii</i>	X	X	X	X
<i>Grammatophora barbata</i> (Gegenbaur, 1865)	O	X	X	O
<i>Stellio cordylinus</i> (Parker, 1868)	O	E	X	O
<i>Liolepis belliana</i> (Siebenrock, 1895b)	O	X	X	O
<i>Agama atra</i> (idem)	O	X	X	O
<i>Gonocephalus kuhlîi</i> (idem)	O	X	X	X
<i>Lyriocephalus scutatus</i> (idem)	O	E	X	O
<i>Lophura</i> (Salverda, cited by idem)	X	X	X	?
<i>Moloch horridus</i> (idem)	O	E	X	O
<i>Calotes versicolor</i>	O	X	X	O
<i>Calotes jubatus</i> (Boulenger, 1912)	O	X	X	O
<b>RHIPTOGLOSSA</b>				
<i>Brookesia superciliaris</i> (Siebenrock, 1893a)	O	E?	O	O
<i>Chamæleon vulgaris</i> (Gegenbaur, 1865)	O	O	O	O
<i>Chamæleon gracilis</i>	O	O	O	O
<b>SCINCOMORPHA</b>				
<i>Xantusia vigilis</i>	O	X	X	O
<i>Trachysaurus rugosus</i> (Gegenbaur, 1865)	X <sup>1</sup>	X	X	X
<i>Plestiodon aldrovandi</i> (idem)	O	X	X	O
<i>Cyclodus [Tiliqua] nigrolineatus</i> (Parker, 1868)	X	X	X	O
<i>Egernia whitei</i> (Siebenrock, 1895a)	X	X	X	O
<i>Mabuia multifasciata</i> (idem)	X	X	X	O
<i>Mabuia striata</i> (idem)	X	X	X	O
<i>Lygosoma moco</i> (idem)	X	X	X	O
<i>Lygosoma ornatum</i> (idem)	X	X	X	O

<sup>1</sup>This occurs only on the right side in one of our specimens and is absent in Parker's figure (1868).



SCINCOMORPHA (*continued*)

<i>Lygosoma smithii</i> (idem)
<i>Albepharus pannonicus</i> (idem)
<i>Chalcides mionecton</i> (idem)
<i>Chalcides tridactylus</i> (Krieg, 1919)
<i>Zonosaurus ornatus</i> (Siebenrock, 1895a)
<i>Gerrhosaurus flavigularis nigrolineatus</i>
<i>Lacerta agilis</i> (Gegenbaur, 1865)
<i>Lacerta simonyi</i> (Siebenrock, 1894)
<i>Lacerta serpa</i> Krieg, 1919)
<i>Lacerta viridis</i> (Calori, 1859a)
<i>Tupinambis nigropunctatus</i>
<i>Bachia intermedia</i>
<i>Chirotes canaliculatus</i>

## ANGUIMORPHA

<i>Carsosaurus</i> (Nopcea, 1903)
<i>Dolichosaurus</i> (Nopcea, 1908)
<i>Plioplatecarpus marshii</i> (Dollo, 1882)
<i>Platecarpus coryphæus</i> (Williston, 1892)
<i>Platecarpus ictericus</i> (idem)
<i>Clidastes velox</i> (idem)
<i>Clidastes westii</i> (idem)
<i>Tylosaurus dyspeler</i> (idem)
<i>Psammosaurus scincus</i> (Parker, 1868)
<i>Monitor dracæna</i> (Parker, 1868)
<i>Varanus niloticus</i>
<i>Varanus griseus</i> (Boulenger, 1912)
<i>Heloderma suspectum</i>
<i>Xenosaurus grandis</i>
<i>Gerrhonotus imbricatus</i> (Siebenrock, 1895a)
<i>Anguis fragilis</i> (Goette, 1877)
<i>Zonurus griseus</i> (Sauvage, 1872)
<i>Zonurus giganteus</i>

SCAPULAR	SCAP.-CORACOID	1" CORACOID	2" CORACOID
X	X	X	O
X	X	X	O
O	X	X	X
O	X	X	O
O	X	X	O
O	X	X	O
O	E	X	O
O	E	X	O
O	E	X	O
O	E	X	O
O	X	X	X
O	X	X	X
O	O	O	O
O	E	X	X
O	E	O	O
O	E	O	O
O	E	X	X
O	X	X	X
O	X	X	X
O	E	X	X
O	E	O	O
O	X	X	O
O	X	X	O
O	X	X	O
O	X <sup>2</sup>	X <sup>2</sup>	O
O	X	X	O

The almost universal presence of the scapulo-coracoid fenestra is suggestive of a paleotelic nature. Fürbringer (1900) is even led to think that the parts are comparable with those found in the salamanders. This view has some support from the embryological side. Bogoljubsky (1914) finds that, in the Lacertidæ and especially in the Gekkonidæ, the scapulo-coracoid and chief coracoid fenestræ develop very early,

<sup>1</sup>A trace of a lateral coracoid fenestra is present (cf. Osborn, 1899).<sup>2</sup>United in adult, separate in embryo (cf. *Ophisaurus*, Sauvage, 1878).

even before the sternum joins the ribs. This does not confirm the results of Goette (1877) who thought he found the early stages in *Cnemidophorus* to be "*Sphenodon*-like," nor does it agree with what we know of the fossil record. The Permian *Aræoscelis*, a supposed ancestor of the Sauria, appears to have had an unfenestrated scapulo-coracoid. Broom (1906) believes that the lacertilian girdle is "merely a highly specialized modification of the *Sphenodon* type."

The relations of the two chief fenestræ to the Supracoracoideus and Scapulohumeralis anterior muscles is illustrated in Fig. 67.

#### 34.—THE ENDOLYMPHATIC GLANDS

Endolymphatic glands (Aquæductus vestibuli, Wiedersheim, 1876), extending posteriorly beyond the limits of the skull, are known in many Ascalabota including most of the Gekkota and the iguanid *Anolis sagræ* (A. M. N. H.). They are also found in *Xantusia vigilis* (A. M. N. H.), their phylogenetic importance lying in the fact that they are, so far as known, present only in this one family of the Autarchoglossa; a circumstance that strengthens evidence, from the vertebræ and hyoid, of the primitive nature of the Xantusiidæ and their more than superficial affiliation with the Ascalabota. (Cf. Fig. 43).

Ruth (1918) has given a plausible reason for the sporadic and variable occurrence of the glands. He finds an increased functional activity in certain Philippine geckos during pregnancy and especially at the time when the egg-shell is forming. After the eggs are laid the gland is exhausted and one conclusion is that the calcium secreted is poured into the blood stream to furnish material for the calcareous shells of the eggs. It is thought that a more usual function in amphibians and reptiles is to provide for growth of bone, while the original use would seem to have been to supply the calcareous otoliths of the equilibrating system.

The secretion of the glands crystalizes as Aragonite according to Physalix, but in geckos Ruth has shown it to be amorphous until exposed to the air (cf. Calori, 1861).

#### DISCUSSION

The systematic arrangement should be a carefully considered compromise between the differences as they exist in living forms and the distance of phylogenetic separation of the groups. The arrangement subserves convenience to some extent and cannot express all the relationships.

There is a constant tendency for multiplication of super-groups on the basis of great morphological differences and wide separation of living forms. For the sake of "consistency" in respect to morphological, and too often cænotelic, differences, species are raised to genera, genera to families, superfamilies to suborders, until finally classification will almost cease to express relationship as indicated by paleontologic evidence.

The true phylogeny is based not upon cænotelic differences, however great, but strictly upon the distribution of related conservative features such as primitive and vestigial structures, tendencies for certain types of modification to occur, similar ontogenies, and the paleontological record.

If, for the sake of "consistency" in respect to morphological divergence, we should place the pygopodids into a separate "gens" as Fürbringer has done, we should, to be "consistent," elevate the Anniellidæ, the Feyliniidæ, and the Dibamidæ.

If we should elevate the Chamæleontidæ, we should do the same with the Uroplatidæ which have evolved along the same lines, and with the Amphisbænidæ which have gone as far in a different direction. Instead of recognizing the number of larger groups of equal rank outlined by Fürbringer (1900) I have tried to arrange a system more illustrative of the phylogeny and have ventured to consider the lizards as divided into two main branches differing in lepidosis, in muscular, hemipenial, possibly in visceral, characters (cf. Cope, 1900, p. 450), and in the frequency of appearance of different tendencies of development in each line of descent. The origin of these groups seems to have been concerned with an early divergent habitus involving adaptive capabilities rather closely circumscribed by the respective morphological equipment. This equipment appears in the Ascalabota to have been perfected along lines connected with the requirements for arboreal life habits, and in the Autarchoglossa to have improved in correlation with terrestrial conditions of habitat. It seems that long association and accommodation of organism to habitat has resulted in adjustments so balanced in each group that tendencies for the more profound secondary modifications, arising in connection with arboreal life in the Ascalabota, never appear in the terrestrial group (Autarchoglossa) even among those genera which are exclusively arboreal in habit. Whereas, in the Ascalabota, profound secondary modifications for terrestrial life never occur even among the many forms which are highly terrestrial (cf. Cope, 1900, p. 201). Only the Autarchoglossa are able to fulfill the morphological requirements for advanced subterranean life although opportunities for

such development must always be gratuitously open to the terrestrial, temporarily burrowing *Ascalabota*. Only the latter group has been able to accept the opportunities afforded at the top of the scale of arboreal requirements, although for the arboreal *Autarchoglossa* such situations must be continually at hand.

In accordance with the evidence it seems that certain descent lines may carry tendencies to change in ways in which a neighboring series of forms cannot be modified. It would appear that identical characters do often "crop out" separately in one stock and that a related group may be wholly incapable of such deviation. The incapacity of geckos, iguanians, and chameleons to develop burrowing, limbless, terrestrial forms seems to be due to lack of a certain important ventral locomotory muscle, the *Rectus superficialis*, developed in the scincs, lacertids, teiids, anguids, and all other members of the *Autarchoglossa*, many of which have limbless representatives. In the latter group, mutations involving reduction of limbs may become favorable for existence of the animal in an unoccupied habitat. In the *Ascalabota* such mutations would leave the creature without effective means of locomotion.

## RÉSUMÉ

### SUMMARY OF CLASSIFICATION

It is proposed to divide the Sauria into two main groups, the *Ascalabota* and *Autarchoglossa*. The first of these includes the geckos, iguanids, agamids, and chameleons.

The geckos are considered as primitive, chiefly on account of the persistence of chorda in their vertebræ, the universal presence of dorso-lumbar intercentra, and the occasional complete or nearly complete third branchial arch.

The iguanids and agamids are related to the geckos on characters of the hemipenes, musculature, and squamation. *Holbrookia* and other North American iguanids are regarded as primitive, *Iguana*, *Cyclura*, *Sauromalus*, *Dipsosaurus*, and *Amblyrhynchus* as central, and *Basiliscus* and *Anolis* as offshoots of the latter group on the characters of throat musculature, number of cervical ribs, presence of femoral pores, and dentition. *Chalarodon* of Madagascar is an iguanid as shown by the dentition, throat musculature, and presence of a proscapular process. The Fijian *Brachylophus* is closely related to *Ctenosaura* and *Cyclura* on the basis of details of the throat musculature, and number of abdominal parasterna. *Liolepis* and *Uromastix* are considered primitive agamids in respect to throat musculature, structure of interclavicle,

and presence of a *Rectus superficialis* muscle. *Agama*, *Physignathus*, and *Amphibolurus* are central and *Calotes*, *Japalura*, and *Draco* derived from them. Some characters of the Agamidæ are more primitive than those of iguanids, but the dentition and frequent absence and reduction of skeletal and muscular parts place them on a higher level than the Iguanidæ.

The chameleons are offshoots of agamid stock.

The family Xantusiidæ is intermediate between the first group (Ascalabota) and the second (Autarchoglossa). The trunk vertebrae still retain an intercentrum and are of geckonoid shape; the third branchial arch is nearly complete. Skull characters, the presence of a *Rectus lateralis* muscle, and the exact relation of the ventral scales to the body segments relate the group most closely to the scincs, teiids, and especially to the lacertids. The interclavicle of *Xantusia* is cruciform and dermal skull ossifications are present.

The Xantusiidæ, Scincoidea, and Lacertoidea, with the possible inclusion of the Amphisbænidæ, form a separate group, Scincomorpha, distinct from the Anguimorpha, the latter comprising the Platynota, anguioids, and zonurids. The differences between these two groups concern the structure and relations of the ventral osteoderms, the greater complexity of the throat musculature in Anguimorpha, the texture of the tongue and hemipenes, as well as tendencies in the evolution of tooth replacement, the place of attachment of the caudal chevrons and the failure of a parasternum in the degenerate forms.

Degenerate Scincomorpha tend to develop a burrowing habitus recognized in the anatomical features; short tail, closed eyes, and ears, degeneration of limb girdles, enormous increase in complexity of body musculature, increase in the Cervicomandibularis muscle, increased parasternum, inflation of cranium; final loss of skull arches; inter-orbital septum, epipterygoids, caudal chevrons, and osteoderms.

Degenerate Anguimorpha are frequently surface-living, apparently grass-inhabiting forms which greatly increase the tail, retain the skull arches and other cranial elements, retain a more simple body musculature complete girdles, osteoderms, and functional eyes.

Further indication of the scincomorph relationship of the amphisbænians is found in the teioid form of the hyoid of the embryo of *Amphisbæna*. No special relationship with degenerate teiids or other degenerate lizards or with serpents can be expected, although the body musculature parallels that of the burrowing snakes, Typhlopidae. The throat musculature is unique but nearest that of *Varanus*.

The Mosasauroidæ are regarded as derived from varanoid stock through the Aigialosauridæ. The Dolichosauridæ, on account of the great number of their cervical vertebræ, reduction of limbs, and elongation of body, are believed to be a side branch and not ancestral.

The Platynota are related to the Diploglossa in hemipenial and dental characters, the ligamentary, symphyseal attachment of the lower jaws, formula of the scapulo-coracoid fenestræ, attachment of the caudal chevrons, structure of the skull arches, and lack of femoral pores.

The Pygopodoidea are considered as diploglossids rather than geckonids because of tongue texture, relation of ventral scaling to body segmentation, presence of a Rectus superficialis muscle, nondeciduate, imbricating scales and the relations of the os hypoischium to the degenerating pelvis in *Lialis* and *Ophiodes*. The adaptive radiation and morphological separation of this group indicates antiquity. The anguoids include the Helodermatidæ, Anguidæ, Anniellidæ, and Xenosauridæ on the basis of presence of a unique muscle in the throat. *Heloderma* is related to the Anguidæ through the Eocene and Oligocene family Glyptosauridæ.

The Anniellidæ are close to *Gerrhonotus* in structure of throat musculature and hemipenes. *Ophiodes* resembles *Celestus* in the former respect. *Gerrhonotus* and *Ophisaurus* are not as closely related as the latter is to *Anguis*.

*Xenosaurus* is specialized in throat musculature and loss of the third branchial arch, and is neither intermediate between the Anguidæ and Iguanidæ, nor related to the Gekkonidæ. It is related to and probably derived from the anguids.

The Zonuridæ are not related to the Iguanidæ except as they retain the tongue and, partially, the hemipenial structure of the Ascalabota. They have the key characters of the Autarchoglossa and are included in the Anguimorpha on account of their simple clavicles and the structure of their osteoderms.

The Serpentes are believed to have arisen from anguimorphid lizards.

*Paliguana* Broom of the Triassic is regarded as a lizard.

*Ardeosaurus* von Meyer of the Jurassic constitutes the type of a new family related to the gekkos.

*Chamops* Marsh of the Cretaceous is believed to be related to the Iguanidæ and Agamidæ and to be intermediate between them in tooth emplacement.

The Tertiary Glyptosauridæ should be retained as a distinct family including *Placosaurus* of the Eocene of France.

The Eocene genera *Thinosaurus* Marsh and *Saniwa* Leidy are varanids as far as the shape of their vertebræ and teeth will permit us to judge.<sup>1</sup>

#### SUMMARY OF MORPHOLOGICAL POINTS

Complete branchial arches and attachments of the first arch (hyoid) to the paroccipital process are regarded as primitive characters in lizards. The Amphisbænidæ are not primitive in this respect. The extra-columella in the Amphisbænidæ is functionally enlarged probably for subterranean audition and does not represent a detached portion of the epihyoid.

The rib processes in the Amphisbænidæ, *Ophisaurus*, and *Lialis* are secondary muscle attachments and do not represent the primitive tuberculum.

Amphicœlous vertebræ, separate intercentra and the presence of sub-central arterial foramina are primitive characters. Zygosphepal articulations are secondary and do not of themselves show relationships between groups higher than the family. The form of the centra and the articular condyles has a systematic value.

The two dorsal temporal elements of the primitive lizard skull are regarded as the tabulare (inner) and squamosal (outer). Relationships with thalattosaurs and ichthyosaurs are closer in this respect than with *Sphenodon*. The single element present in geckos and other lizards in which the supratemporal arch is absent is considered the tabulare.

Remains of the shoulder-girdle are present in the Anniellidæ and Dibamidæ. The degenerating girdle in scincomorphs tends to first loose the clavicle and interclavicle. In anguimorphs, the scapulo-coracoids and interclavicles are the first to disappear. Many stages of extreme degeneration in scincomorphs correspond to early stages in the ontogeny of the pectoral girdle and sternum.

Paired skull elements are the primitive condition. After fusion all traces of separation are soon lost in the embryo (cf. Siebenrock, 1892) so that it seems unlikely that reversion can occur.

The prevomers of *Chamæleon* are often fused and sometimes paired.

Retention of ribs on the anterior cervical vertebræ is regarded as primitive. Articular facets on the cervical diapophyses are not a safe indication of the presence of corresponding ribs.

The postfrontal tends to be reduced in the Ascalabota, the post-orbital in the Autarchoglossa. There are exceptions. In the Scincimorpha the postfrontal sometimes enlarges to secondarily close the supratemporal fenestra. This does not occur in the Anguimorpha.

<sup>1</sup>Gilmore (1922, Proc. U. S. Nat. Mus.) has recently described the skull and skeleton of *Saniwa* and finds it to be remarkably similar to *Varanus*.

Thecodont dentition is considered ancestral to the present day, highly developed pleurodont and acrodon types.

Palatal teeth are best developed in the anguroids and are not known to be secondarily produced, though they are frequently increased in number and extent of area.

The interclavicle and clavicle undergo progressive reduction in various descent lines.

The throat musculature is regarded as an important index to the degree of specialization and the relationships of certain families one to another.

The glands on the surface of the papillate tongues of the Ascalabota and Anguimorpha are less specialized than those of the scaly-tongued Scincomorpha. This leads us to regard the former condition as primitive.

The elements of the lower jaw undergo fusion and reduction in specialized groups.

The caudal chevrons tend to migrate forward to the centra in the Anguimorpha, having done so in the Platynota, the Glyptosauridæ, the Anniellidæ, and in *Ophisaurus*, but retaining the primitive intercentral position in the Helodermatidæ, Pygopodidæ, Zonuridæ, Xenosauridæ, and in *Gerrhonotus*.

The presence of a separate os intermedium is regarded as primitive. Its absence or fusion is of little significance.

The superficial layer of the rectus is regarded as a primitive crawling muscle. Its presence in certain primitive agamids tends to show this and its absence in all other Ascalabota is considered secondary and possibly concerned with the arboreal tendencies of the group.

The body musculature as a whole is most highly modified in burrowing, worm-like forms and least developed in permanent arboreals, especially in *Uroplates* and *Chamæleon*.

The sternum is homologous in salamanders and lizards, and is formed of the anterior portions of the parasternal bars. The xiphisternum has a similar origin. Neither are they products of the ribs or the coracoids.

The parasternum is homologous in lizards, *Sphenodon*, and reptiles and amphibians. In lizards it attains a closer correspondence with the body segmentation than in early reptiles and *Sphenodon*.

Closure of the palate is secondary in lizards and is not related to the mammalian condition.

There is some anatomical evidence to show that the pineal eye may still be functional in the Scincoidea and some Anguioidea. It is certainly



non-functional as a visual organ in most other lizards. Size of the foramen is not always a safe index to the size and functional ability of the eye.

Diffuse and compound osteoderms are regarded as primitive, solid and simple osteoderms covered by a single horny scale as specialized.

Granular lepidosis and non-correspondence between ventral scale-rows and internal metamerism is considered more primitive than exact correspondence between external and internal segmentation.

The femoral organs are pseudo-glands proliferating modified epidermal cells. The secretion may serve the male to hold more firmly during copulation. Secondary development seems to occur in the Agamidæ.

## BIBLIOGRAPHY

- AMBROSETTI, J. B. 1887. 'Observaciones sobre los Reptiles Fosiles Oligocenos de los Terrenos Terciarios Antiguos del Paraná.' Bol. Acad. Nac. Cienc. Cordoba (Argentina), X, pp. 409-426.
- ANGEL, F. 1920. 'Sur un Saurien nouveau de la famille des Ophiopsisepidés.' Bull. Mus. Nation. d'Hist. Nat., Paris, XXVI, pp. 4-6. [*Typhloseps*, new genus.]
- BANCHI, A. 1900. 'Rudimenti di un terzo elemento scheletrico (Parafibula) nella gamba di alcuni rettili.' Monit. Zool. Ital., XI, pp. 231-243.
- BARBOUR, T. 1921. '*Sphærodactylus*.' Mem. Mus. Comp. Zoöl., XLVII, pp. 217-278, Pls. I-XXVI.
- BAUR, G. 1886a. 'The Intercentrum of Living Reptilia [and Mammalia].' Amer. Nat., XX, pp. 174-175.
- 1886b. 'Über die Homologien einiger Schädelknochen der Stegocephalen und Reptilien.' Anat. Anzeiger, I, 1886, pp. 348-350.
- 1886c. 'Osteologische Notizen über Reptilien.' Zoolog. Anzeiger, IX, pp. 685-690 [Proatlas noted in *Chamæleon*].
1889. 'On the Morphology of the Vertebrate Skull.' Journ. Morph., III, pp. 467-474.
- 1892a. 'On the Morphology of the Skull in the Mosasauridæ.' Idem, VII, pp. 1-22, Pls. I-II.
- 1892b. 'Bemerkungen über die Osteologie der Schläfengegend der höhern Wirbelthiere.' Anat. Anzeiger, X, pp. 315-330.
1893. 'The Discovery of Miocene [Oligocene] Amphisbæniæans.' Amer. Nat., XXVII, pp. 998-999.
1894. 'The Relationship of the lacertilian genus *Anniella*, Gray.' Proc. U. S. Nation. Mus., XVII, pp. 345-351.
1895. 'Cope on the Temporal Part of the Skull and on the Systematic Position of the Mosasauridæ. A Reply.' Amer. Nat., XXIX, pp. 998-1002.
1896. 'The Paroccipital of the Squamata and the Affinities of the Mosasauridæ once more. A Rejoinder to Prof. E. D. Cope.' Idem, XXX, pp. 143-147, Pl. iv.
- BEDDARD, F. E. 1904a. "'Abdominal Ribs" in Lacertilia.' Nature, LXX, p. 6.
- 1904b. 'On the Presence of a Parasternum in the Lacertilian Genus *Tiliqua*, and on the Parasternal Ribs in that Genus.' Proc. Zoöl. Soc. London, 1904, pp. 154-157.
- 1905a. 'Some Notes on the Cranial Osteology of the Mastigure Lizard, *Uromastix*.' Idem, pp. 2-9.
- 1905b. 'A Contribution to the Anatomy of the Frilled Lizard (*Chlamydosaurus kingii*).' Idem, pp. 9-22.
1906. 'Exhibition of, and remarks upon, a dissected specimen of the Lizard *Trachysaurus rugosus* showing abdominal ribs.' Idem, pp. 376-377.
1907. 'Contributions to the Knowledge of the Systematic Arrangement and Anatomy of certain Genera and Species of Squamata.' Idem, pp. 35-68.
- BEDRIAGA, J. VON. 1884. *Amphistæna cinerea* Vand. und *A. Strauchi* v. Bedr. Erster Beitrag zur Kenntniss der Doppelschleichen.' Archiv. für Naturgeschichte, L, Band I, pp. 23-77, Pl. iv.

- BELL, T. 1825. 'Observations on the structure of the throat in the genus *Anolis*.' Zoölog. Journ., II, pp. 11-14, Pl. II. [Also in Ann. Sci. Nat., VII, 1826, pp. 191-195.]
- BOGOLJUBSKY, S. 1914. 'Brustbein- und Schultergürtelentwicklung bei einigen Lacertilien.' Zeitschrift für Wiss. Zool., CX, pp. 620-666, Pls. XVII-XXI.
- BORN, G. 1876. 'Zum Carpus und Tarsus der Saurier.' Morphol. Jahrb., II, pp. 1-26, Pl. I.
1880. 'Nachträge zu Carpus und Tarsus.' Idem, VI, pp. 49-78, Pl. I.
1883. 'Eine frei hervorragende Anlage der vorderen Extremität bei Embryonen von *Anguis fragilis*.' Zoolog. Anzeiger, VI, pp. 537-539.
- BOULENGER, G. A. 1884. 'Synopsis of the Families of existing Lacertilia.' Ann. Mag. Nat. Hist., (5) XIV, pp. 117-122.
- 1885-1887. 'Catalogue of the Lizards in the British Museum (Natural History).' 2nd Ed., I-III. 8 vo. London.
1888. 'On the Scaling of the Reproduced Tail in Lizards.' Proc. Zoöl. Soc. London, 1888, pp. 351-353.
1890. 'On the Distinctive Cranial Characters of the Iguanoid Lizards allied to *Iguana*.' Ann. Mag. Nat. Hist., (6) VI, pp. 412-414.
1891. 'Notes on the Osteology of *Heloderma horridum* and *H. suspectum*, with Remarks on the Systematic Position of the Helodermatidæ and the Vertebræ of the Lacertilia.' Idem, 1891, pp. 109-118.
1893. 'On some newly-described Jurassic and Cretaceous Lizards and Rhynchocephalians.' Ann. Mag. Nat. Hist., (6) XI, pp. 204-210.
- 1899a. 'On a Collection of Reptiles and Batrachians made by Mr. J. D. La Touche in N. W. Fokien, China.' Proc. Zoöl. Soc. London, 1899, pp. 159-172. [Description of *Anguis*-like teeth of *Ophisaurus harti*.]
- 1899b. 'Exhibition of, and remarks upon, a specimen of the Bornean Lizard *Lanihanotus borneensis*.' Idem, pp. 596-597.
1912. 'Reptilia and Batrachia.' In 'A Vertebrate Fauna of the Malay Peninsula.' xiii+294 pp., Map. 8 vo. London.
1917. 'A Revision of the Lizards of the Genus *Tachydromus*.' Mem. Asiatic Soc. Bengal, V, pp. 207-235, Pls. XLVI-XLVII.
- 1918a. 'Considerations sur les affinités et la dispersion géographique des Lacertides.' Comptes Rendus Acad. Sci. Paris, CLXVI, pp. 594-598.
- 1918b. 'Les Lézards Héloclermatides de l'Eocene supérieur de la France.' Idem, pp. 889-893.
1920. 'Monograph of the Lacertidæ.' I, x+352 pp., 8 vo. London.
- BRONGNIART, A. 1800. 'Essai d'une classification naturelle de Reptiles avec la description et la figure de plusieurs espèces.' Bull. Soc. Philom. Paris, II, pp. 81-82, 89-91.
- BROOM, R. 1903a. 'On the skull of a true lizard (*Paliquana whitei*) from the Triassic beds of South Africa.' Rec. Albany Museum, I, No. 1, pp. 1-3, Pl. I.
- 1903b. 'On the Development of the Pterygo-quadrate Arch in the Lacertilia.' Journ. Anat. Physiol., XXXVII, pp. 107-111.
1906. 'Note on the lacertilian shoulder girdle.' Trans. S. African Philos. Soc., XVI, part 4, pp. 373-375.
1913. 'On the Squamosal and related Bones in the Mosasaurs and Lizards.' Bull. Amer. Mus. Nat. Hist., XXXII, pp. 507-508.

1914. 'Croonian Lecture: On the Origin of Mammals.' *Philos. Trans. Roy. Soc. London*, CCVI (B), pp. 1-48, Pls. i-vii.
- BRÜHL, C. B. 1875-1888. 'Zootomie aller Thierklassen für lernende nach Autopsien, skizzirt.' I, 1875, Pls. i-LXXX, II, 1888, Pls. LXXXI-CLX.
- BRYANT, H. C. 1911. 'The Horned Lizards of California and Nevada of the Genera *Phrynosoma* and *Anota*.' *Univ. Calif. Publ. Zoöl.*, IX, pp. 1-84, Pls. i-ix.
- BUTLER, G. W. 1895. 'On the Complete or Partial Suppression of the Right Lung in the Amphisbænidae and of the Left Lung in Snakes and Snake-like Lizards and Amphibians.' *Proc. Zoöl. Soc. London*, 1895, pp. 691-712, Pl. xl.
- CALORI, L. 1859a. 'Sulla Riproduzione di una Doppia Coda nelle Lucertole e sullo Scheletro del *Platydictylus muralis* Duméril e Bibron.' *Mem. Accad. Sci. Inst. Bologna*, X, pp. 357-368, Pls. xix-xx.
- 1859b. 'Sullo Scheletro dello *Stellio vulgaris* Daudin.' *Idem*, pp. 369-376, Pls. xxi-xxiii.
1861. 'Sulle Tracheloliti ed Oftalmoliti osservate in alcuni Gecchidi e sullo Scheletro del *Platydictylus guttatus* Cuv.' *Idem*, XII, pp. 149-157, Pl. i.
- CARLSSON, A. 1887. 'Untersuchungen ueber Gliedmassen—Reste bei Schlagèn.' *Bihang K. Svenska Vet.-Akad. Handl.*, XI, No. 11, [1886], pp. 1-38, Pls. i-iii.
1896. 'Ueber den Zahnersatz bei *Agama colonorum*.' *Anat. Anzeiger*, XI, pp. 758-766.
- CASE E. C., WILLISTON, S. W., AND MEHL, M. G. 1913. 'Permo-Carboniferous Vertebrates from New Mexico.' *Carnegie Inst., Wash., Publ. No.* 181, pp. 1-81. [Chap. V, Description of a nearly complete skeleton of *Ophiacodon* Marsh, pp. 37-59.]
- COE, W. R., AND KUNKEL, B. W. 1904. 'The Reproductive Organs of the Limbless Lizard *Anniella*.' *Amer. Nat.*, XXXVIII, pp. 487-490.
1906. 'Studies on the California Limbless Lizard, *Anniella*.' *Trans. Conn. Acad.*, XII, part 1, pp. 1-55 [of reprint], Pls. xli-xlviii, [I. Habits and Visceral Anatomy.—W. R. Coe. II. External Anatomy and Skeleton.—B. W. Kunkel. III. Urogenital Organs.—W. R. Coe and B. W. Kunkel. IV. Brain and Pineal Apparatus.—B. W. Kunkel.]
- COHN, L. 1904. 'Die Schenkeldrüsen des *Cnemidophorus lemniscatus* Daud.' *Zoolog. Anzeiger*, XXVII, pp. 185-192.
- COLLIN DE PLANCY, V. 1877. 'L'Accouplement et la Ponte chez les Lézards de France.' *Bull. Soc. Zool. France*, 1877, II, pp. 325-358, Pl. vi.
- COPE, E. D. 1864. 'On the Characters of the higher Groups of Reptilia Squamata—and especially of the Diploglossa.' *Proc. Acad. Nat. Sci. Phila.*, [XVII], 1864, pp. 224-231.
1869. 'On the Reptilian Orders Pythonomorpha and Streptosauria.' *Proc. Boston Soc. Nat. Hist.*, XII, pp. 250-266.
1878. 'Professor Owen on the Pythonomorpha.' *Bull. U. S. Geol. Geog. Survey, Hayden*, IV, pp. 299-311.
1884. 'The Vertebrata of the Tertiary Formations of the West.' *Rept. U. S. Geol. Survey Territories (Hayden)*, III, pp. xxiv+1009, Pls. i-lxxvii.

1887. 'The Origin of the Fittest. Essays on Evolution.' xix+467 pp., 8 vo. New York.
- 1892a. 'The Osteology of the Lacertilia.' Proc. Amer. Philos. Soc., XXX, pp. 185-222, Pls. II-VI. [Many of the figs. are wrongly captioned. For corrections cf. substitute pages, idem, No. 139, December, 1892.]
- 1892b. 'On Degenerate Types of Scapular and Pelvic Arches in the Lacertilia.' Journ. Morph., VII, pp. 223-244, Pl. XIII.
1894. 'On the Lungs of the Ophidia.' Proc. Amer. Philos. Soc., XXXII, pp. 217-224, Pls. XI-XVI.
- 1895a. 'Baur on the Temporal Part of the Skull, and on the Morphology of the Skull in the Mosasauridae.' Amer. Nat., XXIX, pp. 855-859, Pl. XXXI.
- 1895b. 'Reply to Dr. Baur's critique on my paper on the Paroccipital bone of the Scaled Reptiles and the Systematic Position of the Pythonomorpha.' Idem, pp. 1003-1005.
- 1896a. 'Criticism of Dr. Baur's rejoinder on the homologies of the paroccipital bone, etc.' Idem, XXX, pp. 147-149.
- 1896b. 'On the Hemipenes of the Sauria.' Proc. Acad. Nat. Sci. Phila., [XLVIII], 1896, [1897], pp. 461-467. [Abstract in Amer. Nat., XXX, pp. 945-946.]
1900. 'The Crocodilians, Lizards, and Snakes of North America.' Ann. Rept. U. S. Nation. Mus., 1898 [1900], part 2, pp. 151-1294, Pls. I-XXXVI.
- CREDNER, H. 1888. 'Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. Siebenter Theil. *Palaeohatteria longicaudata* Cred.' Zeitschrift. Deutsch. Geol. Gesell., Jahrg. 1888, pp. 487-560, Pls. XXIV-XXVI [text-fig. 19, *Proterosaurus*].
1889. 'Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. Achter Theil. *Kadaliosaurus priscus* Cred.' Idem, Jahrg. 1889, pp. 319-342, Pl. xv.
- CUVIER, G. L. C. F. D. 1817. 'Le Règne Animal distribué d'après son organisation, . . .' I-III. 8 vo. Paris.
- DAIBER, M. 1921. 'Das Bauchrippensystem von *Sphenodon (Hatteria) punctatus* Gray.' Anat. Anzeiger, LIII, pp. 371-382, Pls. I-II.
- DEPÉRET, C. 1917. 'Monographie de la Faune de Mammifères Fossiles du Ludien Inférieur d'Euzet-les-Bain (Gard).' Ann. Univers. Lyon, (N.S.) I, fasc. 40, viii+288 pp., 25 Pls.
- DE ROOÿ, N. 1915. 'The Reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria.' xiv+384 pp. 8 vo. Leiden.
- DE STEFANO, G. 1903. 'I Sauri del Quercy appartenenti alla Collezione Rossignol.' Atti Soc. Ital. Sci. Nat. Mus. Civ. Milano, XLII, pp. 382-418, Pls. IX-X.
- DEWÈVRE, L. S. 1895. 'Le Mécanisme de la projection de la Langue chez le Caméléon.' Journ. d'Anat. Physiol., XXXI, pp. 343-360.
- DOLLO, L. 1882. 'Note sur l'Ostéologie des Mosasauridae.' Bull. Mus. Roy. d'Hist. Nat. Belgique, I, pp. 55-74, Pls. IV-VI.
1884. 'Notes Erpétologiques. I. Le Caméléons sont des Lacertiliens kionocrânes.' Zoolog. Anzeiger, VII, pp. 547-548.

1894. 'Nouvelle Note sur l'ostéologie des Mosasauriens.' Bull. Soc. Belge Géol. Paléon. d'Hydrol., VI, pp. 219-259, Pls. III-IV.
1904. 'L'Origine des Mosasauriens.' Idem, XVIII, pp. 217-222.
- DOUGLASS, E. 1903-1904. 'New Vertebrates from the Montana Tertiary.' Ann. Carnegie Mus., II, pp. 145-199. [*Helodermoides tuberculatus*, new genus and species, pp. 160-161.]
1908. 'Some Oligocene Lizards.' Idem, IV, pp. 278-285.
- DUMÉRIL, ANDRÉ M. C. 1804. 'Traite élémentaire d'Histoire naturelle.' 1 vol., Paris [2nd Ed. 2 vols. 1807].
- DUMÉRIL, ANDRÉ M. C., AND BIBRON, G. 1834-1854. 'Erpétologie Générale ou Histoire Naturelle complète des Reptiles.' I-IX vols. and atlas of 109 Pls., 8 vo. Paris. [Vols. VII-IX with collaboration of Auguste Duméril.]
- DUMÉRIL, AUGUSTE, AND BOCOURT, F. 1870. 'Études sur les Reptiles et les Batraciens.' In 'Mission Scientifique au Mexique.' Recherches Zoologiques, part 3, Chap. I, Chéloniens, Crocodiles et Sauriens, pp. 1-494, Pls. I-XXIX.
- EGGELING, H. VON. 1914. 'Zur Phylogenie der sogenannten Schenkelporen.' Jenaische Zeitschrift, LI, pp. 124-162.
- FEJÉRVÁRY, G. J. DE. 1918. 'Contributions to a Monography on fossil Varanidæ and Megalanidæ.' Ann. Mus. Nat. Hungarici, XVI, pp. 341-467, Pls. I-II.
- FÉLIZET, J. 1911. 'Recherches sur les Glandes Fémorales de *Lacerta muralis*.' Journ. d'Anat. Physiol., XLVII, pp. 333-370, Pls. XI-XII.
- FICALBI, E. 1880. 'Osteologia del Platidattilo mauritanico.' Atti Soc. Toscana Sci. Nat. Pisa, Mem., V, pp. 287-330, Pls. XIII-XIV.
- FILHOL, H. 1877. 'Recherches sur Les Phosphorites du Quercy. Étude des Fossiles qu'on y rencontre et spécialement des Mammifères.' Ann. Sci. Géol. Hébert, VIII, pp. 1-340, Pls. I-XXIX.
1882. 'Description d'un genre nouveau de Reptile fossile.' Bull. Soc. Philomath. Paris, (7) VI, p. 127. [*Cadurcosaurus sauvagei*, new genus and species.]
1894. 'Observations concernant Quelques Mammifères fossiles nouveaux du Quercy.' Ann. Sci. Nat., XVI, pp. 129-150.
- FITZINGER, L. I. 1826. 'Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften . . .' [6] + 66 pp., 1 Pl. 4to. Vienna.
- FLEISCHMANN, A. 1902. 'Morphologische Studien über Kloake und Phallus der Amnioten.' Morphol. Jahrb., XXX, pp. 539-581, Pl. VIII.
- FRY, D. B. 1914. 'On a Collection of Reptiles and Batrachians from Western Australia.' Rec. W. Australian Mus. and Art Gallery, I, pp. 174-210, Pls. XXVII-XXVIII.
- FÜRBRINGER, M. 1869. 'Die Knochen und Muskeln der Extremitäten bei den Schlangenähnlichen Sauriern.' Inaug. Dissert. Berlin. Leipzig: Wilh. Engelmann, pp. 1-58 [issued again in 1870 with 7 Pls.]. 4to.
1875. 'Zur vergleichenden Anatomie der Schultermuskeln.' Theil III, Chap. IV, Saurier und Crocodile. Morphol. Jahrb., I, pp. 636-816, Pls. XXIII-XXVII.

1900. 'Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln.' *Jenaische Zeitschrift.*, XXXIV, pp. 215-718, Pls. XIII-XVII.
1919. 'Über das Zungenbein der Reptilien.' *Bijdragen Tot de Dierkunde k. zoolog. genootschap. Amsterdam, Feest-nummer für Kerbert*, pp. 195-212.
- GADOW, H. 1882a. 'Untersuchungen über die Bauchmuskeln der Krokodile, Eidechsen und Schildkröten.' *Morphol. Jahrb.*, VII, pp. 57-100, Pl. I.
- 1882b. 'Beiträge zur Myologie der hinteren Extremität der Reptilien.' *Idem*, pp. 329-466, Pls. XVII-XXI.
1888. 'On the Modifications of the First and Second Visceral Arches, with especial reference to the Homologies of the Auditory Ossicles.' *Philos. Trans. Roy. Soc. London*, CLXXIX B, pp. 451-485, Pls. LXXI-LXXIV.
1896. 'Evolution of the Vertebral Column of the Amphibia and Amniota.' *Idem*, CLXXXVII B, pp. 1-57.
1901. 'Amphibia and Reptiles.' *The Cambridge Natural History*, VIII, [2nd Ed. 1909], xiii+668 pp. 8vo. London.
- GANDOLFI, H. 1908. 'Die Zunge der Agamidæ und Iguanidæ.' *Zoolog. Anzeiger*, XXXII, pp. 569-580.
- GEGENBAUR, C. 1865. 'Untersuchungen zur vergleichenden Anatomie der Wirbelthiere.' II, Ab. 1. *Schultergürtel der Wirbelthiere*, vi+135 pp., 3 Pls. 4to. Leipzig.
- GELDERN, C. E. VON. 1919. 'Mechanism in the Production of the Throat-Fan in the Florida Chameleon, *Anolis carolinensis*.' *Proc. Calif. Acad. Sci.*, (4) IX, pp. 313-329.
- GERHARDT, K. 1903. '*Ophisaurus ulmensis* n. sp. aus dem Unteriocän von Ulm a. D.' *Jahresber. Vereins Vaterl. Naturkunde Württemberg*, 1903, pp. 67-71.
- GERMERSHAUSEN, G. 1913. 'Anatomische Untersuchungen über den Kehlkopf der *Chamæleonen*.' *Sitzungsber. Gessell. Naturfor. Freunde, Berlin*, pp. 462-535.
- GERVAIS, P. 1853. 'Recherches sur l'osteologie de Plusieurs espèces d'Amphibien et Remarques sur la Classification de ces Reptiles.' *Ann. Sci. Nat.*, (3) XX, pp. 293-312, Pls. XIV-XV.
1859. 'Zoologie et Paléontologie Françaises.' 2nd Ed., 543 pp. and atlas, 12 pp., 84 Pls. 4to. Paris.
- GILL, T. 1886. 'The classification of the Lizards.' *Ann. Rept. Smithson. Inst.*, 1885 [1886], part 1, pp. 797-801.
1900. 'The earliest use of the names Sauria and Batrachia.' *Science*, (2) XII, p. 730.
- GILMORE, C. W. 1912. 'A New Mosasauroid Reptile from the Cretaceous of Alabama.' *Proc. U. S. Nation. Mus.*, XLI, pp. 479-484, Pls. XXXIX-XL. [*Globidens alabamaensis*, new genus and species.]
- GOETTE, A. 1877. 'Beiträge zur vergleichenden Morphologie des Skelet-systems der Wirbelthiere.' *Archiv für Mikros. Anat.*, XIV, pp. 502-620, Pls. XXX-XXXIII [Contains only part 1, on the shoulder girdle and sternum].
1894. 'Über die Zusammensetzung der Wirbel bei den Reptilien.' *Zoolog. Anzeiger*, XVII, pp. 359-363.

1897. 'Über den Wirbelbau bei den Reptilien und einigen anderen Wirbelthieren.' Zeitschrift. Wiss. Zool., LXII, pp. 343-394, Pls. xv-xvii.
- GÖPPERT, E. 1903. 'Die Bedeutung der Zunge für den sekundären Gaumen und den Ductus nasopharyngeus. Beobachtungen an Reptilien und Vögeln.' Morphol. Jahrb., XXXI, pp. 311-357, Pls. xii-xv.
- GRAY, J. E. 1825. 'A Synopsis of the Genera of Reptiles and Amphibia, with a Description of some new Species.' Annals of Philosophy (Thompson), (N.S.) X, pp. 193-217.
1845. 'Catalogue of the Specimens of Lizards in the Collection of the British Museum.' xxviii+289 pp. 12 mo. London.
1870. 'On the Claspers of Male Lizards (Sauri).' Ann. Mag. Nat. Hist., (4) VII, pp. 283-286.
- GREGORY, W. K. 1913. 'Critique of Recent Work on the Morphology of the Vertebrate Skull, Especially in Relation to the Origin of Mammals.' Journ. Morph., XXIV, pp. 1-42.
1920. 'Studies in Comparative Myology and Osteology; No. IV. A Review of the Evolution of the Lacrymal Bone of Vertebrates with Special Reference to that of Mammals.' Bull. Amer. Mus. Nat. Hist., XLII, Art. 2, pp. 95-263, Pl. xvii.
- HANSON, F. B. 1919. 'The Ontogeny and Phylogeny of the Sternum.' Amer. Journ. Anat., XXVI, pp. 41-91, Pls. i-xii.
- HARRISON, H. S. 1901. 'The Development and Succession of Teeth in *Hatteria punctata*.' Quart. Journ. Micros. Sci., (N.S.) XLIV, pp. 161-213, Pls. x-xii.
- HAY, O. P. 1901. 'Bibliography and Catalogue of the Fossil Vertebrata of North America.' Bull. U. S. Geol. Surv., No. 179, pp. 1-868.
- HEWITT, J. 1920. 'Note on the So-called Second Branchial Arch in Lizards.' Trans. Roy. Soc. S. Africa, VIII, part 2, pp. 91-93.
- HILGENDORF, F. 1885. 'Die Steinheimer Gürtelchse *Propseudopus Fraasii*.' Zeitschrift. Deutsch. Geol. Gesell., XXXVII, pp. 358-378, Pls. xv-xvi.
- HOFFMANN, C. K. 1890. 'Dr. H. G. Bronn's Klassen und Ordnungen des Thierreichs, wissenschaftlich dargestellt in Wort und Bild.' VI Band, III Abt. Reptilien (II Eidechsen), pp. 443+1399, Pls. XLIX-CVII. 8vo. Leipzig.
- HOLL, M. 1888. 'Zur Anatomie der Mundhöhle von *Lacerta agilis*.' Sitzungsber. der Math. Natur. Classe der Akad. Wiss., Wien, XCVI, pp. 161-169, 1 Pl.
- HOWES, G. B., AND SWINNERTON, H. H. 1903. 'On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*; with remarks on the Egg, on the Hatching and on the Hatched Young.' Trans. Zoöl. Soc. London, XVI, pp. 1-86, Pls. i-vi.
- HUENE, F. VON. 1910a. 'Über einen echten Rhynchocephalen aus der Trias von Elgin, *Brachyrhinodon Taylora*.' Neuen Jahrb. für Mineral. Geol. u. Paläon., Jahrg. 1910, Band. II, pp. 29-62.
- 1910b. 'Ein ganzes *Tylosaurus*-Skelett.' Geol. Palaeon. Abhandl. (N.F.) VIII (= XII), Heft VI, pp. 297-314, Pls. xli-xlii.



1912. 'Der Zweite Fund des Rhynchocephalen *Brachyrhinodon* in Elgin.' Neuen Jahrb. Mineral. Geol. Paläon., Jahrg. 1912, Band I, pp. 51-57, Pls. iv-v.
- JAEKEL, O. 1904. 'Über ein neues Reptil aus dem Buntsandstein der Eifel.' Zeitschrift. Deutsch. Geol. Gesell., LVI, Briefliche Mitteilungen, pp. 90-94. [*Eifelosaurus triadicus*, new genus and species.]
- JANENSCH, W. 1906. 'Über *Archæophis proavus* Mass. eine Schlange aus dem Eocan des Monte Bolca.' Beitr. zur Paläon. und Geol. Österreich-Ungarns und des Orients, XIX, pp. 1-133 [of reprint], Pls. i-ii.
- JENSEN, A. S. 1901. 'Om *Ophiopsis nasutus* Du Bocage og dens Stilling i Reptiliernes System.' Videnskab. Meddel. Nat. Forening, Kjøbenhavn, (6) II, pp. 317-328, Pl. iii.
- KATHARINER, L. 'Anatomie und Mechanismus der Zunge der Vermilinguer.' Jena-ische Zeitschrift, XXIX, pp. 247-270, Pl. iii.
- KINGSLEY, J. S. 1905. 'The Bones of the Reptilian Lower Jaw.' Amer. Nat., XXXIX, pp. 59-64.
- KLEBS, R. 1910. 'Über Bernsteineinschlüsse in allgemeinen und die Coleopteren meiner Bernsteinsammlung.' Schrift. Phys.-Oek. Gesell. Königsberg in Pr., LI, pp. 217-242. [Lizards in amber.]
- KRAMBERGER, GORJANOVIĆ-K. 1892. '*Aigialosaurus*, eine neue Eidechse a. d. Kriedeschiefern der Insel Lesina, mit Rücksicht auf die bereits beschriebenen Lacertiden von Comen und Lesina.' Glasnik. Soc. Hist. Nat. Croatica, VII, pp. 74-106, Pls. iii-iv.
- KRAUSS, F. 1906. 'Der Zusammenhang zwischen Epidermis und Cutis bei den Sauriern und Krokodilen.' Archiv für Mikros. Anat., LXVII, pp. 319-363, Pls. xxxiii-xxiv.
- KRIEG, H. 1919. 'Beiträge zur Rudimentierungsfrage nach Beobachtungen an *Anguis fragilis*, *Chalcides tridactylus* und *Lacerta serpa*.' Archiv für Entwicklungsmech., XLV, pp. 571-601, Pl. xxii.
- LAFRENTZ, K. 1914. 'Die Flughaut von *Draco volans*, ihr Bau, ihre Entwicklung und Function, nebst Bemerkungen über die Bedeutung der Kehlsäcke.' Zoolog. Jahrb., Abt. Anat. u. Ont., XXXVIII, pp. 593-642, Pls. xxxvii-xxxviii.
- LARTET, E. 1851. 'Notice sur la Colline de Sansan, suivie d'une Récapitulation des diverses Espèces d'Animaux Vertébrés Fossiles, . . .' Annuaire du Depart. du Gers, Année 1851, pp. 1-46 [of reprint], 1 Pl.
- LATREILLE, P. A. 1825. 'Familles naturelles du Règne Animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres.' 570 pp. 8vo. Paris.
- LEENHARDT, F. 1906. 'A propos des Edentés fossiles de France.' Bull. Soc. Geol. France, (4) VI, p. 176.
- LEIDY, J. 1873. 'Contributions to the Extinct Vertebrate Fauna of the Western Territories.' Rept. U. S. Geol. Surv. Terr., Hayden Survey, I, pp. 1-358, Pls. i-xxxvii.
- LEYDIG, F. 1872. 'Die in Deutschland lebenden Arten der Saurier.' vii+262 pp., 12 Pls. 4to. Tübingen.
- LÖNNBERG, E. 1916. 'Lizards.' In 'Zoölogical Results of the Swedish Zoölogical Expeditions to Siam.' K. Svenska Vet.-Akad. Handl., (N.F.) LV, No. 4, part 2, pp. 1-12. [Skiagram of *Isopachys gyldestolpei*.]

- LORTET, L. 1892. 'Les Reptiles fossiles du Bassin du Rhone.' Archiv Mus. d'Hist. Nat. Lyon, V, pp. 1-139, Pls. I-XII.
- LUCAS, A. H. S., AND LE SOUËFF, W. H. DUDLEY, 1909. 'The Animals of Australia. Mammals, Reptiles and Amphibians.' xi+327 pp. 8 vo. London.
- LYDEKKER, R. 1888. 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History).' Part I. xxviii+309 pp. 8 vo. London.
- MARSH, O. C. 1871. 'Notice of some new Fossil Reptiles from the Cretaceous and Tertiary Formations.' Amer. Journ. Sci., (3) I, pp. 447-459.
1872. 'Preliminary Description of New Tertiary Reptiles. Part I.' Idem, (3) IV, pp. 298-309.
1892. 'Notice of New Reptiles from the Laramie Formation.' Idem, (3) XLIII, pp. 449-453.
- MATTHEW, W. D. 1915. 'Climate and Evolution.' Ann. N. Y. Acad. Sci., XXIV, pp. 171-318.
- MAURER, F. 1896. 'Die ventrale Rumpfmuskulatur einiger Reptilien. Eine vergleichend-anatomische Untersuchung.' Festschrift für Gegenbaur, Band I, pp. 183-256, Pls. I-IV.
1898. 'Die Entwicklung der ventralen, Rumpfmuskulatur bei Reptilien.' Morphol. Jahrb., XXVI, pp. 1-60, Pls. I-III.
- MCCOY, F. 1885-1890. 'Prodromus of the Zoölogy of Victoria; or figures and descriptions of the living species of all classes of the Victorian indigenous animals.' 2 vols. 4to. Melbourne and London.
- MÉHELÿ, L. VON. 1907. 'Archæo- und Neo-lacerten.' Ann. Mus. Nat. Hungarici, V, pp. 469-493.
- MEHNERT, E. 1891. 'Untersuchungen über die Entwicklung des Os hyposichium (Os cloacæ aut.), Os. epipubis und Ligamentum medianum pelvis bei den Eidechsen.' Morphol. Jahrb., XVII, pp. 123-143, Pl. VIII.
- MEISNER, C. F. 1832. 'De Amphibiorum quorundam Papillis Glandulisque Femoralibus.' 30 pp., 1 Pl., 4to. Basel.
- MERREM, B. 1820. 'Versuch eines Systems der Amphibien.' xv+191 pp. 8 vo. Marburg. [Alternate pages identically numbered and in Latin under the title Tentamen Systematis Amphibiorum.]
- MERRIAM, J. C. 1894. 'Ueber die Pythonomorphen der Kansas-Kreide.' Palaeontographica, XLI, pp. 1-39, Pls. I-IV.
1905. 'The Thalattosauria, A Group of Marine Reptiles from the Triassic of California.' Mem. Calif. Acad. Sci., V, No. 1, pp. 1-50, Pls. I-VIII.
1908. 'Triassic Ichthyosauria with Special Reference to the American Forms.' Mem. Univ. Calif., I, No. 1, pp. 1-196, Pls. I-XVIII.
- METHUEN, P. A., AND HEWITT, J. 1915. 'A Contribution to our Knowledge of the Anatomy of the Chamæleons.' Trans. Roy. Soc. S. Africa, IV, pp. 89-104.
- MEYER, H. VON. 1860. 'Reptilien aus dem Lithographischen Schiefer des Jura in Deutschland und Frankreich.' In 'Zur Fauna der Vorwelt,' IV, pp. 1-142, Pls. I-XXI, Frankfurt am Main.
- MILANI, A. 1894. 'Beiträge zur Kenntniss der Reptilienlunge.' Zoolog. Jahrb. Anat. Physiol., VII, pp. 545-589.
- MIVART, ST. G. 1867. 'Notes on the Myology of *Iguana tuberculata*.' Proc. Zoöl. Soc. London, 1867, pp. 766-797.
1870. 'On the Myology of *Chamæleon parsonii*.' Idem, 1870, pp. 850-890.

- MOODIE, R. L. 1907. 'The Sacrum of the Lacertilia.' *Biolog. Bull.*, XIII, pp. 84-93.
- MÜLLER, K. H. M. [1900.] 'Die Reduktion des Brustschultergürtels der Saurier bis zum völligen Verluste desselben.' *Inaug. Dissert.* Leipzig: Hesse and Becker. 1-42 pp., 1 Pl. 8 vo.
- NOBLE, G. K. 1921. 'The bony Structure and phyletic Relations of *Sphærodactylus* and allied lacertilian Genera, with the Description of a new Genus.' *Amer. Mus. Novitates*, No. 4, pp. 1-16.
- NOPCSA, F. 1903.. 'Über die Varanus-artigen Lacerten Istriens.' *Beitr. zur Paläon. und Geol. Österreich-Ungarns und des Orients*, XV, pp. 31-42, Pls. v-vi. [Abstract in *Geol. Mag.*, (4) X, pp. 119-121. Critical remarks by Dollo in *Bull. Sci. France et Belgique*, XXXVIII, pp. 137-139.]
1908. 'Zur Kenntniss der fossilen Eidechsen.' *Idem*, XXI, pp. 33-62, Pl. III.
- NOWIKOFF, M. 1910. 'Untersuchungen über den Bau, die Entwicklung und die Bedeutung des Parietalauges von Sauriern.' *Zeitschrift für Wiss. Zool.*, XCVI, pp. 118-207, Pls. III-VIII.
- OSBORN, H. F. 1899. 'A Complete Mosasaur Skeleton, Osseous and Cartilaginous.' *Mem. Amer. Mus. Nat. Hist.*, I, pp. 167-188, Pls. XXI-XXIII.
- OTTH, A. 1833. 'Ueber die Schenkelwarzen der Eidechsen.' *Tiedemann und Treviranus Zeitschrift. Physiol.*, V, pp. 101-104.
- OTTO, H. 1909. 'Die Beschuppung der Brevilinguier und Ascalaboten.' *Jenaische Zeitschrift.*, XLIV, pp. 193-252, Pl. IX.
- PALACKÝ, J. 1899. 'Die Verbreitung der Eidechsen.' *Zoolog. Jahrb., Abt. Syst. Geog. u. Biol.*, XII, pp. 247-285.
- PARKER, W. K. 1868. *A Monograph on the Structure and Development of the Shoulder-girdle and Sternum in the Vertebrata.* xi+237 pp., 30 Pls. 4to. London.
1880. 'On the Structure and Development of the Skull in the Lacertilia. Part I. On the Skull of the Common Lizards (*Lacerta agilis*, *L. viridis*, and *Zootoca vivipara*).' *Philos. Trans. Roy. Soc. London*, CLXX, pp. 595-640, Pls. XXXVI-XLV.
1881. 'On the Structure of the Skull in the Chameleons.' *Trans. Zoöl. Soc. London*, XI, part 3, pp. 77-105, Pls. xv-xix.
- PEARSON, H. S. 1921. 'The Skull and Some Related Structures of a Late Embryo of *Lygosoma*.' *Journ. Anat.*, LVI, part 1, pp. 20-43.
- PETERS, W. 1882. 'Über eine neue Art und Gattung der Amphibænoiden, *Agamoden anguliceps*, mit eingewachsenen Zähnen, aus Barava (Ostafrika) und über die zu dem Trogonophides gehörigen Gattungen.' *Sitzber. Akad. Wiss. Berlin*, Jahrg. 1882, Hlbnd. I, pp. 579-584, Pl. x.
- POMEL, A. 1853. 'Catalogue Méthodique et Descriptif des Vertébrés Fossiles découverts dans le Bassin hydrographique supérieur de la Loire, et surtout dans la Vallée de son Affluent principal d'Allier.' 193 pp. 8vo. Paris.
- RABANUS, K. 1906-1915. 'Über das Skelett von *Voeltzkowia mira* Bttgr. Ein Beitrag zur Osteologie der Eidechsen.' In *Voeltzkow, 'Reise in Ostafrika,' Band IV, Anatomie und Entwicklungsgeschichte*, pp. 279-330, Pls. xx-xxiii.
- RATHKE, H. 1853. 'Ueber den Bau und die Entwicklung des Brustbeins der Saurier.' 26 pp. 4to. Königsberg.

- RICE, E. L. 1920. 'The Development of the Skull in the Skink, *Eumeces quinelineatus* L. I. The Chondrocranium.' Journ. Morph., XXXIV, pp. 119-220, Pls. I-XII.
- RÖSE, C. 1893. 'Ueber die Zahnentwicklung vom *Chamaeleon*.' Anat. Anzeiger. VIII, pp. 566-577.
- ROVERETO, C. 1914. 'Los Estratos Araucanos y sus Fósiles.' Anales Mus. Nac. Hist. Nat. Buenos Aires, XXV, pp. 1-247, Pls. I-XXXI.
- RUTH, E. S. 1918. 'A Study of the Calcium Glands in the Common Philippine House Lizard.' Philippine Journ. Sci., XIII (B), pp. 311-317, Pls. I-II.
- SANDERS, A. 1870. 'Notes on the Myology of *Platydictylus japonicus*.' Proc. Zool. Soc. London, 1870, pp. 413-426.
1872. 'Notes on the Myology of *Lirolepis belli*.' Idem, 1872, pp. 154-183.
1874. 'Notes on the Myology of the *Phrynosoma coronatum*.' Idem, 1874, pp. 71-89.
- SAUVAGE, H. E. 1878. 'Étude sur le Membre Antérieur du Pseudope de Pallas.' Ann. Sci. Nat., (6) VII, Art. 15, pp. 1-13, Pl. xx.
- SCHAEFER, F. 1902. 'Ueber die Schenkeldrüsen der Eidechsen.' Archiv für Naturgeschichte, LXVIII, Band I, pp. 27-64, Pls. III-IV.
- SCHAUINSLAND, H. 1903. 'Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere. I. *Sphenodon*, *Callorhynchus*, *Chamaeleo*.' Zoologica, XVI, pp. 1-98, Pls. I-XXXI. [Cf. also Archiv für Micros. Anat., LVII, 1900, pp. 747-867, Pls. XXXII-XXXIV. Reviewed by Gaupp, Zoolog. Centralblatt., VIII, 1901, No. 179; and by Fürbringer, Morphol. Jahrb., XXXI, 1903, pp. 628-630.]
1906. 'Die Entwicklung der Wirbelsäule nebst Rippen und Brustbein.' Handb. Vergl. u. Experiment. Entwickl. Wirbelthiere, III, Teil II, pp. 339-572.
- SCHMIDT, K. P. 1919. 'Contributions to the Herpetology of the Belgian Congo based on the Collection of the American Museum Congo Expedition, 1909-1915. Part I. Turtles, Crocodiles, Lizards and Chameleons.' Bull. Amer. Mus. Nat. Hist., XXXIX, pp. 385-624, Pls. VII-XXXII.
- SCHMIDT, W. J. 1906-1915. 'Beobachtungen an der Haut von *Geckolepis* und einigen anderen Geckoniden.' In Voeltzkow, 'Reise in Ostafrika,' Band IV, Anatomie und Entwicklungsgeschichte, pp. 331-351, Pls. XXIV-XXV.
1909. 'Beiträge zur Kenntniss der Parietalorgane der Saurier.' Zeitschrift. Wiss. Zool., XCII, pp. 359-426, Pl. XIX.
1910. 'Das Integument von *Voeltzkowia mira* Bttgr. Ein Beitrag zur Morphologie und Histologie der Eidechsenhaut.' Idem, XCIV, pp. 605-720, Pls. XXII-XXIV.
1912. 'Studien am Integument der Reptilien. I. Die Haut der Geckoniden.' Idem, CI, pp. 139-258, Pls. VIII-XII.
- 1913a. 'Studien am Integument der Reptilien. III. Über die Haut der Gerrhosauriden.' Zoolog. Jahrb., Abt. Anat. u. Ont., XXXV, pp. 75-104, Pls. I-IV.
- 1913b. 'Studien am Integument der Reptilien. IV. *Uroplatus fimbriatus* (Schneid.) und die Geckoniden.' Idem, XXXVI, pp. 377-464, Pls. XXXIII-XXXVI.
1914. 'Studien am Integument der Reptilien. V. Anguiden.' Idem, XXXVIII, pp. 1-102, Pls. I-VI.

1916. 'Studien am Integument der Reptilien. VII. Bau und Entwicklung der Eidechsenkrallen.' *Zoolog. Jahrb., Abt. Anat. u. Ont.*, XXXIX, pp. 385-484, Pls. xxiii-xxvii.
- SCHNEIDER, A. 1879. 'Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere.' viii + 164 pp., Pls. i-xvi. 4to. Berlin.
- SEILLER, R. F. VON. 1891. 'Ueber die Zungendrüsen von *Anguis*, *Pseudopus* und *Lacerta*. Ein Beitrag zur Kenntniss der einzelligen Drüsen.' *Archiv für Mikros. Anat.*, XXXVIII, pp. 177-264, Pls. x-xiii.
1892. 'Die Zungendrüsen von *Lacerta*.' *Festschrift für R. Leuckart*, pp. 250-258, Pls. xxv-xxvi.
- SHUFELDT, R. W. 1890. 'Contributions to the Study of *Heloderma suspectum*.' *Proc. Zool. Soc. London*, 1890, pp. 148-244, Pls. xvi-xviii.
- SIEBENROCK, F. 1892. 'Zur Kenntniss des Kopfskelettes des Scincoiden, Anguiden und Gerrhosauriden.' *Annalen des K. K. Naturhist. Hofmus. Wien*, VII, Heft III, pp. 163-196, Pls. xi-xii.
- 1893a. 'Das Skelet von *Brookesia superciliaris* Kuhl.' *Sitzungsber. der Math. Natur. Classe der Akad. Wiss. Wien*, CII, Abt. I, pp. 71-118, Pls. i-iv.
- 1893b. 'Das Skelet von *Uroplates fimbriatus* Schneid.' *Annalen des K. K. Naturhist. Hofmus. Wien*, VIII, Hefts III-IV, pp. 517-536, Pl. xiv.
1894. 'Das Skelet der *Lacerta simonyi* Steind. und der Lacertidenfamilie überhaupt.' *Sitzungsber. der Math. Natur. Classe der Akad. Wiss. Wien*, CIII, Abt. I, Hefts I-X, pp. 205-292, Pls. i-iv.
- 1895a. 'Zur Kenntniss des Rumpfskeletes der Scincoiden, Anguiden und Gerrhosauriden.' *Annalen des K. K. Naturhist. Hofmus. Wien*, X, Heft I, pp. 17-40, Pl. iii.
- 1895b. 'Das Skelet der *Agamidæ*.' *Sitzungsber. der Math. Natur. Classe der Akad. Wiss. Wien*, CIV, Abt. I, Hefts I-X, pp. 1089-1196, Pls. i-vi.
- SMALIAN, C. 1885. 'Beiträge zur Anatomie der Amphibænen.' *Zeitschrift. für Wiss. Zool.*, XLII, pp. 125-202, Pls. v-vi.
- SOKOLOWSKY, A. 1899. 'Über die äussere Bedeckung bei Lacertilien. Ein Beitrag zur Phylogenie der Lacertilien.' 56 pp., 1 Pl. Zurich. [Critical review by Werner in *Zoolog. Centralblatt*, VI, pp. 415-418.]
- SPRING, A., AND LACORDAIRE, J. T. 1842. 'Notes sur quelques points de l'organisation du *Phrynosoma Harlanii* Saurien de la famille des Iguaniens.' *Bull. Acad. Roy. Sci. Bruxelles*, IX, part 2, pp. 192-209, Pl. i.
- STANNIUS, H. 1856. 'Handbuch der Anatomie der Wirbelthiere.' Zweites Buch: 'Zootomie der Amphibien.' In Siebold and Stannius, 'Handbuch der Zootomie.' Teil II. 'Die Wirbelthiere,' 2nd Ed. 270 pp. 8 vo. Berlin. [The first edition, 1846, does not contain the systematic views presented here.]
- STECKER, A. 1877. 'Zur Kenntniss des Carpus und Tarsus bei *Chamaeleon*.' *Sitzungsber. der Math. Natur. Classe der Akad. Wiss. Wien*, LXXV, Abt. I, pp. 7-17, Pls. i-ii.
- STEHLI, G. 1910. 'Ueber die Beschuppung der Reptilien.' *Jenaische Zeitschrift*, XLVI, pp. 737-800, Pl. xxviii.

- STEJNEGER, L. 1907. 'Herpetology of Japan and adjacent Territory.' Bull. U. S. Nation. Mus., No. 58, pp. xx+577, 35 Pls.
- THYNG, F. W. 1906. 'Squamosal Bone in Tetrapodous Vertebrata.' Proc. Boston. Soc. Nat. Hist., XXXII, pp. 387-425, Pls. xxxix-xlii.
- TÖLG, F. 1905. 'Beiträge zur Kenntniss drüsenartiger Epidermoidalorgane der Eidechsen.' Arbeiten Zoolog. Inst. Wien, XV, pp. 119-154, Pls. i-iii.
- TORNIER, G. 1897. 'Über Schwanzregeneration und Doppelschwänze bei Eidechsen.' Sitzungsber. Gesell. Naturfor. Freunde, Berlin, 1897, pp. 59-64.
- TROSCHEL, F. H. 1853. 'Ueber *Heloderma horridum* Wiegman.' Archiv für Naturgeschichte, XIX, Band I, pp. 294-315, Pls. xiii-xiv. [Also published under the title "Symbolae de Helodermate horrido Wiegman." 12 pp. 4to. Bonn., 1851.]
- VAN BEMMELEN, J. F. 1888. 'Beiträge zur Kenntniss der Halsgegend bei Reptilien. I. Anatomischer Theil.' Bijdragen Tot de Dierkunde k. zoolog. genootschap. Amsterdam, XVI, pp. 101-146, Pls. i-ii.
- VERSLUYS, J. 1898. 'Die mittlere und äussere Ohrsphäre der Lacertilia und Rhyncycephalia.' Inaug. Dissert. Giessen. Jena: Gustav Fisher, pp. 1-247, Pls. i-viii. [Also in Zoolog. Jahrb., Abt. Anat. u. Ont., V.]
1904. 'Entwicklung der Columella auris bei den Lacertilern. Ein Beitrag zur Kenntniss der schalleitenden Apparate und des Zungenbeinbogens bei den Sauropsiden.' Zoolog. Jahrb., Abt. Anat. u. Ont., XIX, pp. 107-188, Pls. viii-xi.
1907. 'Eene bijzonderheid van de onderkaak der *Mosasauria* in aanleg reeds bij *Varanus* aanwezig is.' In Verslag. Wetenschap. Vergader. Nederland. Dierkund. Vereen., Tijdschrift. Ned. Dierk. Vereen., (2) X, Afl. 4, pp. xxviii-xxxix. [The imperfect joint in the lower jaw of *Mosasauria* is indicated in *Varanus*.]
1919. 'Über die Phylogenie der Schläfengruben und Jochbogen bei den Reptilia.' Sitzungsber. Heidelberger Akad. Wiss., Jahrg. 1919, Abh. 13, pp. 1-29 [of reprint].
- VOELTZKOW, A., AND DÖDERLEIN, L. 1902. 'Beiträge zur Entwicklungsgeschichte der Reptilien. III. Zur Frage nach der Bildung der Bauchrippen.' In Voeltzkow, 'Reisen in Madagaskar,' Band II. Abhandl. Senckenberg. Naturfor. Gesell. Frankfurt A. M., XXVI. 1. 'Ontogenie der Bauchrippen,'—A. Voeltzkow, pp. 315-326; Pl. xxx; 2. 'Das Gastralskelett (Bauchrippen oder Parasternum) in phylogenetischer Beziehung,'—L. Döderlein, pp. 329-336, Pl. xxxi.
- WAGLER, J. 1830. 'Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel. Ein Beitrag zur vergleichenden Zoologie.' vi+354 pp., 2 Pls. 8 vo. München, Stuttgart and Tübingen.
- WATSON, D. M. S. 1914. 'Pleurosauros and the Homologies of the Bones of the Temporal Region of the Lizard's Skull.' Ann. Mag. Nat. Hist., (8) XVI, pp. 84-95, Pl. vi.
- WERBER, A. 1865. 'Beiträge zur vergleichenden Anatomie der Scincoiden, spec. der Genera *Cyclodus* und *Trachysaurus*.' Berichte. Verhandl. Nat. Gesell. Freiburg, I. B., Band III, Heft 1, pp. 33-50, Pl. i.
- WERNER, F. 1895. 'Ueber sekundäre Geschlechts unterschiede bei Reptilien.' Biol. Centralblatt, XV, pp. 125-140.

1896. 'Über die Schuppenbekleidung des regenerierten Schwanzes bei Eidechsen.' Sitzungsber. der Math. Natur. Classe der Akad. Wiss. Wien, CV, Abt. I, pp. 123-146, Pls. I-II.
- 1911-1912. 'Reptilia.' In Schulze, 'Das Tierreich. Ein Zusammenstellung und Kennzeichnung der rezenten Tierformen.' 27 Lieferung; Chamæleontidæ. xii+52 pp., 1911. 33 Lieferung; Eublepharidæ, Uroplattidæ, Pygopodidæ. x+33 pp., 1912. 4to. Berlin.
- WIEDERSHEIM, R. 1876. 'Zur Anatomie und Physiologie des *Phyllodactylus europæus* mit besonderer Berücksichtigung des Aquæductus vestibuli der Ascalaboten im Allgemeinen. Zugleich als zweiter Beitrag zur Inselfauna des Mittelmeeres.' Morphol. Jahrb., I, pp. 495-534, Pls. XVII-XIX.
1892. 'Die Phylogenie der Beutelknochen. Eine entwicklungsgeschichtlich-vergleichend anatomische Studie.' Zeitschrift für Wiss. Zool., Suppl., LIII, pp. 43-66, Pls. VI-VII.
- WIEGMANN, A. F. A. 1834. 'Herpetologia Mexicana.' Pars I. vi+54 pp., 10 Pls. Folio. Berlin.
- WILLISTON, S. W. 1898. 'Mosasaurs.' In Univ. Geol. Surv. Kansas, IV, Paleontology. Part 5, pp. 83-221, Pls. X-LXXII.
1904. 'The Relationships and Habits of the Mosasaurs.' Journ. Geol., XII, pp. 43-51.
1914. 'The Osteology of Some American Permian Vertebrates.' Contrib. Walker Mus., Univ. Chicago, I, pp. 107-162.
- 1916a. 'The Osteology of Some American Permian Vertebrates. II.' Idem, pp. 165-192.
- 1916b. 'Synopsis of the American Permian Carboniferous Tetrapoda.' Idem, pp. 193-236.
1917. 'The Phylogeny and Classification of Reptiles.' Idem, II, pp. 61-71.
1918. 'The Evolution of Vertebræ.' Idem, pp. 75-85.
- WOERDEMAN, M. W. 1919. 'Beiträge zur Entwicklungsgeschichte von Zähnen und Gebiss der Reptilien.' Archiv für Mikros. Anat., XIX, Abt. I, pp. 104-244, Pls. IV-X. [Also in, Werken Genootschap ter bevordering Natuur-, Genees- en Heelkunde Amsterdam, (2) VIII, 1916, pp. 377-382.]
- ZAVATTARI, E. 1908. 'Materiali per lo Studio dell'Osso Ioide dei Sauri.' Atti Reale Accad. Sci. Torino, XLIII, pp. 1-10 [of reprint], 1 Pl.
1910. 'Muscoli Ioidei dei Sauri in Rapporto con i Muscoli Ioidei degli altri Vertebrati.' Part I, Mem. Reale Accad. Sci. Torino, (2) LX, pp. 351-392, Pl. LX. Part 2, idem, XLI, pp. 55-134, Pl. LXI.
- ZIETZ, F. R. 1921. 'Catalogue of Australian Lizards.' Rec. S. Australian Mus., I, pp. 181-228.

Figs. 1-7. VERTEBRÆ OF ASCALABOTA; ventral view of mid-dorsal vertebræ, the eighth forward from the sacrum.

Figs. 1-4. Gekkonidæ. The centra are squarish in ventral view and retain intercentra, ITC, and subcentral foramina. The condylar ball in the procœlous forms is small.

Figs. 5-6. Iguania. The centra taper, the intercentra and subcentral foramina are lost and the condylar ball is enlarged.

Fig. 7. Rhiptoglossa. The elongation of the cylindrical centra has proceeded beyond the point reached in the Agamidæ, Fig. 5.

Fig. 1. *Thecadactylus rapicauda*, A. M. N. H. No. 6474. The intercentrum, ITC, is partly fused with the posterior end of the amphiœlous centrum.

Fig. 1a. End view of the half-ring-shaped intercentrum.

Fig. 2. *Tarentola cubana*, A. M. N. H. No. 22727. The intercentrum, ITC, is loosely joined to the amphiœlous centrum.

Fig. 3. *Sphærodactylus macrolepis*, A. M. N. H. No. 22729.

Fig. 4. *Coleonyx variegatus*, A. M. N. H. No. 2541.

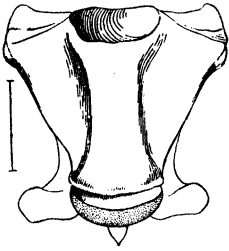
Figs. 3 and 4. Procœlous geckos in which the scale-like intercentrum remains fused to the small condyle.

Fig. 5. *Calotes versicolor*, Skel. in Dept. Herpetol., A. M. N. H.

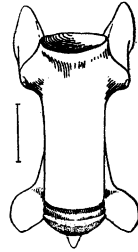
Fig. 6. *Sauromalus hispidus*, A. M. N. H. No. 5675.

Fig. 7. *Chamæleon gracilis*, A. M. N. H. No. 11608.





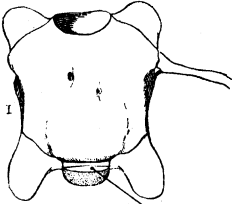
6



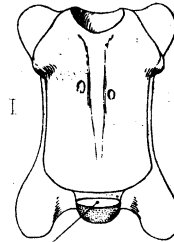
7



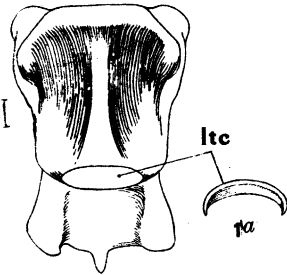
5



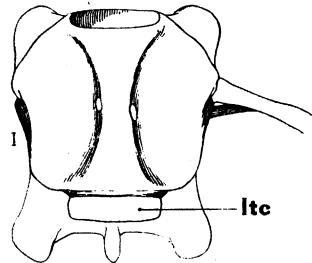
3



4



1



2

Figs. 8-12. VERTEBRÆ OF SCINCOMORPHA; ventral view of mid-dorsal vertebræ, the eighth forward from the sacrum.

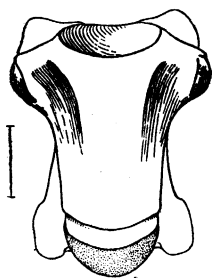
Fig. 8. *Xantusia vigilis*, A. M. N. H. No. 9204. (Cf. Fig. 4, *Coleonyx*.)

Fig. 9. *Amphisbæna alba*, A. M. N. H. No. 8747.

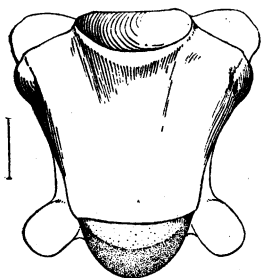
Fig. 10. *Tupinambis nigropunctatus*, A. M. N. H. No. 2246.

Fig. 11. *Trachysaurus rugosus*, Skel. in Dept. Herpetol., A. M. N. H.

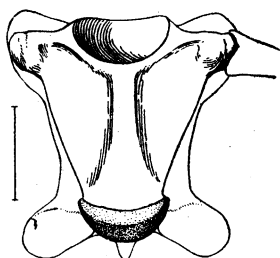
Figs. 2-4 and 8 drawn from specimens prepared by Dr. G. K. Noble.



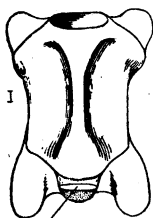
12



11

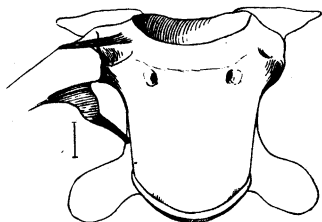


10



lto

8



9

Figs. 13-21. VERTEBRÆ AND RIBS OF ANGUIMORPHA, ventral view. Mid-dorsal vertebræ, the eighth forward from the sacrum.

Fig. 13. *Lialis burtonii*, A. M. N. H. No. 30.

Fig. 14. *Ophisaurus* sp.?, Skel. in Dept. Comp. Anat., A. M. N. H.

Fig. 15. *Gerrhonotus scincicauda scincicauda*, A. M. N. H. No. 595.

Fig. 16. Left rib of *Gerrhonotus*, dorsal view, showing ligaments of attachment and lack of muscular processes.

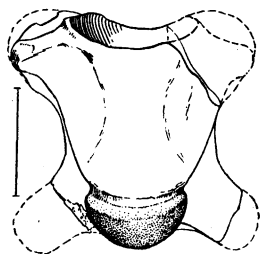
Fig. 17. Right rib of *Lialis*, dorsal view, showing ventral process of attachment of subvertebral muscles.

Fig. 18. Right rib of *Amphisbæna* showing posterior process for attachment of dorsal muscles (cf. Fig. 9).

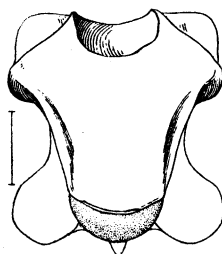
Fig. 19. Right rib of *Ophisaurus* showing posterior process for attachment of dorsal muscles (cf. Fig. 14).

Fig. 20. Mid-dorsal vertebra of a glyptosaurid, Dept. Vert. Pal., A. M. N. H. No. 5109, Wind River, Lower Eocene.

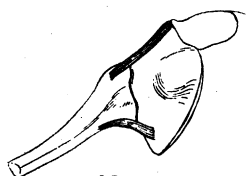
Fig. 21. *Heloderma* sp.?, Skel. in Dept. Comp. Anat., A. M. N. H.



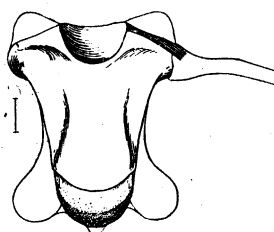
20



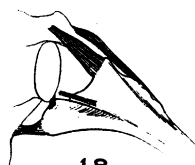
21



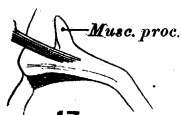
16



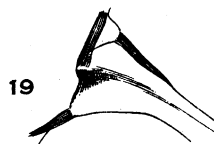
15



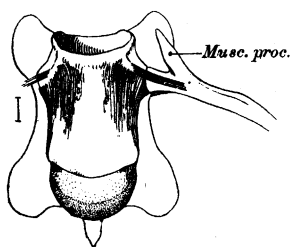
18



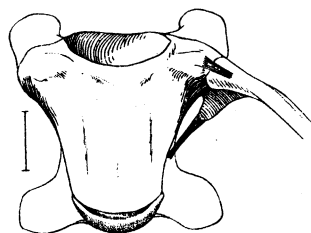
17



19



13



14

Figs. 22-26. MID-DORSAL VERTEBRÆ OF PLATYNOTA.

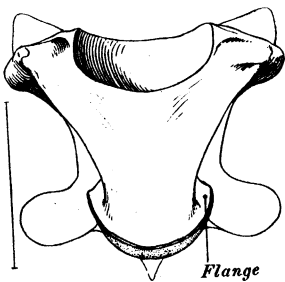
Fig. 22. *Clidastes westii*,  $\times \frac{1}{2}$ , after Williston (1898, Pl. LIII, fig. 2).

Fig. 23. *Thinosaurus* sp.? Dept. Vert. Pal., A. M. N. H. No. 6057.

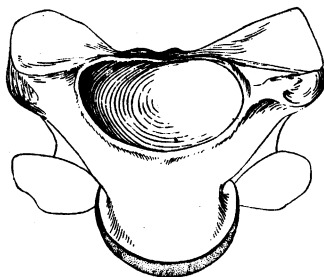
Fig. 24. *Saniwa* sp.?, Dept. Vert. Pal., A. M. N. H. No. 6056. █

Fig. 25. *Varanus niloticus*, Skel. in Dept. Herpetol., A. M. N. H.

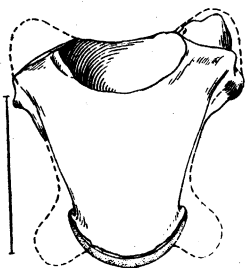
Fig. 26. *Megalanina prisca*,  $\times \frac{1}{6}$ , after Fjéjéváy (1918, Fig. 34d, p. 458, from an original figure by R. Owen).



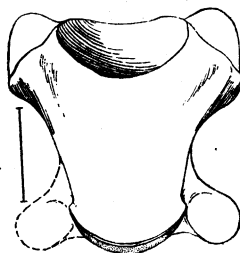
25



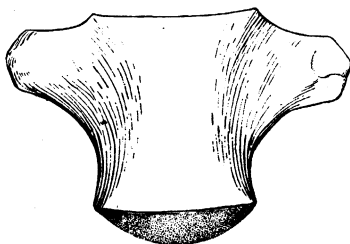
26



23



24



22

Figs. 27-31. HYOID APPARATUS OF ASCALABOTA.

Fig. 27. *Coleonyx variegatus*,  $\times 4\frac{1}{2}$ , A. M. N. H. No. 2538. The three arches are complete, the first and third being connected with the paroccipital process. All parts are cartilaginous with exception of the second arch.

Fig. 28. *Uroplates fimbriatus*,  $\times 1\frac{3}{4}$ , A. M. N. H. No. 2235. The second epibranchial remains as a short cartilage connected with a posterior slip of the Hyoglossus muscle. The epihyal is joined to the paroccipital process.

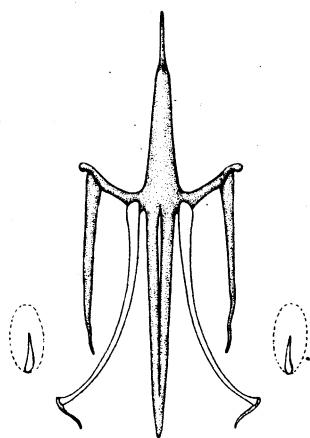
Fig. 29. *Brachylophus fasciatus*,  $\times 2\frac{1}{4}$ , A. M. N. H. No. 17701. The second ceratobranchial is enlarged, as in many Iguania, for support of the throat fan. The second epibranchial is absent.

Fig. 30. *Calotes versicolor*,  $\times 2\frac{1}{4}$ , A. M. N. H. No. 2147. This agamid is similar to the arboreal iguanids in form of the hyoid but the ceratohyal is relatively more reduced.

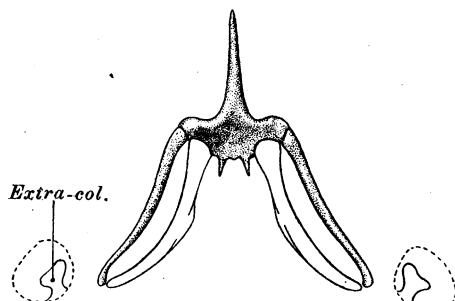
Fig. 31. *Phrynosoma hernandesi*,  $\times 2\frac{1}{4}$ , A. M. N. H. No. 583. Shows extreme reduction for an iguanian.

*Ceratobr.* = Ceratobranchial  
*Ceratohy.* = Ceratohyal  
*Extra-col.* = Extra-columella

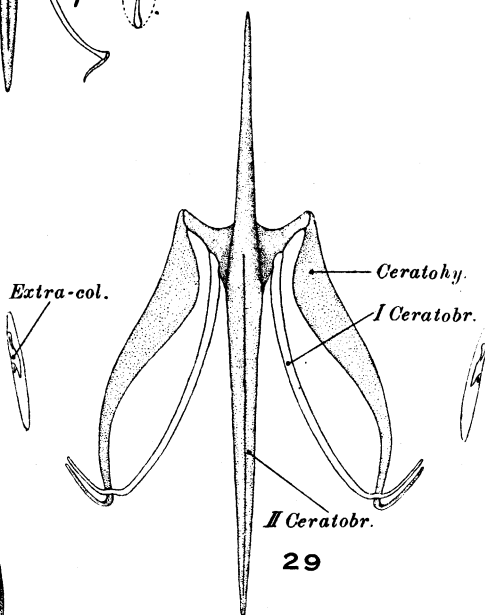




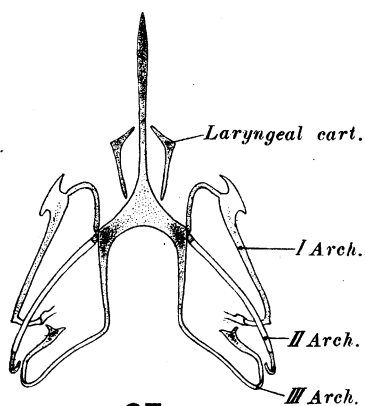
30



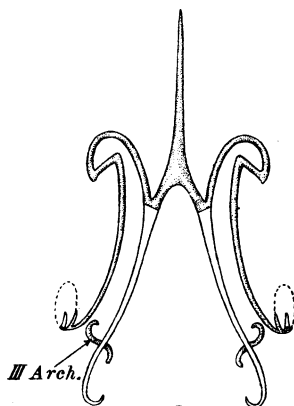
31



29



27



28

Figs. 32-37. HYOID APPARATUS OF AUTARCHOGLOSSA.

Fig. 32. *Gerrhosaurus zechi*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 10721. Hyoid and first branchial arches attached to the paroccipital. Second epibranchial attached to the exoccipital.

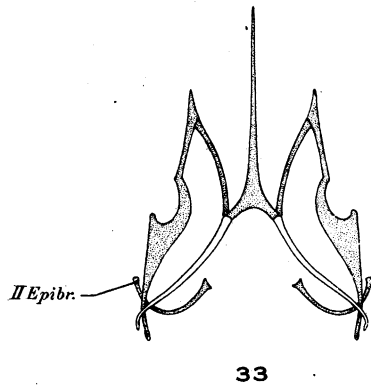
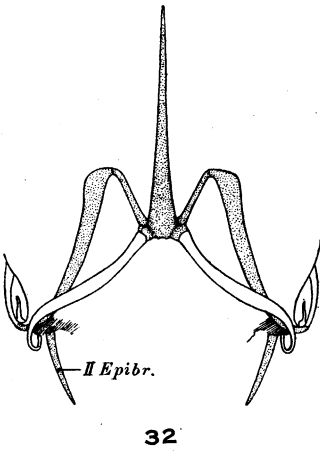
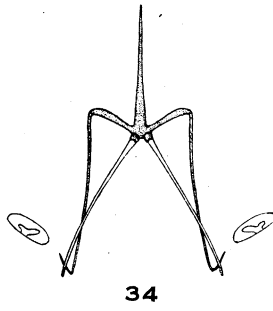
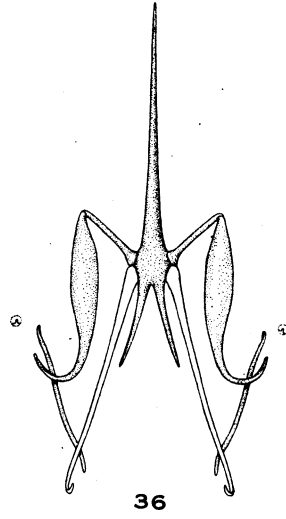
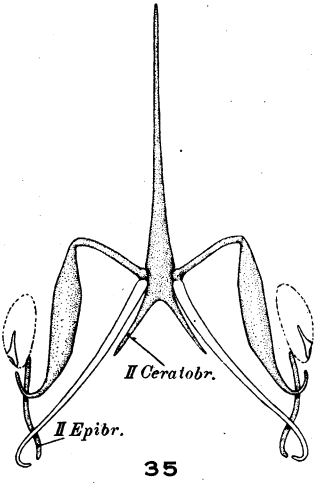
Fig. 33. *Gerrhonotus scincicauda webbi*,  $\times 2$ , A. M. N. H. No. 9159. Hyoid and second branchial arches loosely attached to the paroccipital process.

Fig. 34. *Xenosaurus grandis*,  $\times 2$ , A. M. N. H. No. 19381. No elements of the third arch remain.

Fig. 35. *Zonurus giganteus*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 8736.

Fig. 36. *Chamæsauro macrolepis*,  $\times 4$ , A. M. N. H. No. 2398. Showing close resemblance to *Zonurus*.

[Fig. 37. Omitted by author.]



Figs. 38-41. THROAT MUSCLES OF REPTILIA, for comparison with those of lizards.

Fig. 38. *Sphenodon punctatus*,  $\times .85$ , after Ruge (Festschrift für Gegenbaur, III, 1897, Figs. 61, p. 324), checked with a specimen in the Dept. Invert. Zoöl., A. M. N. H. The Mylohyoideus is in a single continuous layer and entirely underlies the Geniohyoideus. There is no Cervicomandibularis.

Fig. 39. *Crocodylus americanus*,  $\times .65$ , A. M. N. H. No. 19866. The Mylohyoideus is arranged as in *Sphenodon*. There is no Cervicomandibularis.

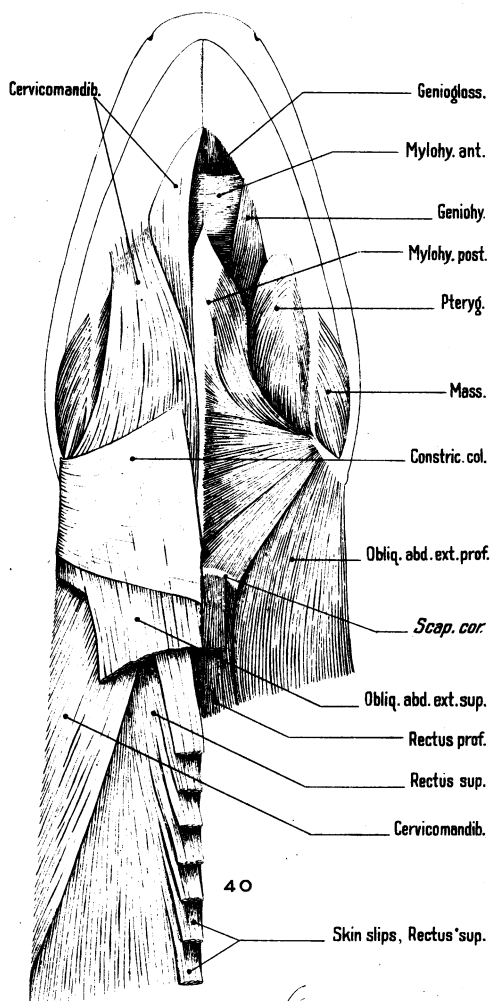
Fig. 40. *Amphisbæna alba*,  $\times 2$ , A. M. N. H. No. 8747. This lizard, though highly specialized, shows the typically saurian interdigitation of the Geniohyoideus with the Mylohyoideus, the separation of the latter into anterior and posterior portions and the presence of a Cervicomandibularis.

In comparison with other lizards the following points may be noted. The Cervicomandibularis is extensive. This muscle pulls the head sideways and downward as the animal forces its way through the soil. The muscle is greatly developed in all permanently subterranean lizards as are usually the body muscles shown here,—Obliquus abdominis externus superficialis which attaches closely to the skin over nearly the whole body; Obliquus externus profundus which extends forward to gain an attachment to the head; Rectus superficialis which sends slips to the skin to facilitate backward locomotion.

Fig. 41. *Chelydra serpentina*,  $\times 1$ , A. M. N. H. No. 22716. The Mylohyoideus does not interdigitate with the Geniohyoideus, and there is no Cervicomandibularis.

#### Abbreviations for Figs. 38-61

CERVICOMANDIB. = Cervicomandibularis. CONSTRIC. COL. = Constrictor colli. DEP. MANDIB. = Depressor mandibularis. EPIBR. = Epibranchial. GENIOGLOSS. = Genioglossus. GENIOMY. = Genio-myioideus. GENIOHY. = Geniohyoideus. HY. = Hyoid arch. HYOGLOSS. = Hyoglossus. INTERMAX. = Intermaxillaris. MASS. = Masseter. MYLOHY. ANT. PRINCIP. = Mylohyoideus anterior principalis. MYLOHY. ANT. PROF. = Mylohyoideus anterior profundus. MYLOHY. ANT. SUP. = Mylohyoideus anterior superficialis. MYLOHY. POST. = Mylohyoideus posterior. OBLIQ. ABD. EXT. PROF. = Obliquus abdominis externus profundus. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. OMOHY. = Omohyoides. RECTUS PROF. = Rectus profundus. RECTUS SUP. = Rectus superficialis. SCAP. COR. = Scapulo-coracoid. SPHINC. GLANDULÆ. = Sphincter glandulæ. STERNOCLEIDOM. = Sternocleidomastoideus. STERNOHY. = Sternohyoides. STERNOTHY. = Sternothyreoides. STYLOHY. = Stylohyoideus (posterior part of Mylohyoideus posterior).



40

N. Mylohy. V

Mylohy.

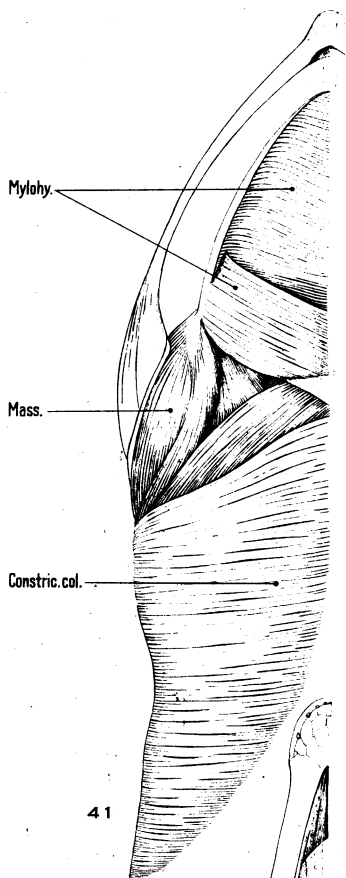
Dep. mandib.

N. VII

N. IX

Constrictor col.

38



41

Mylohy.

Sphinct. glandulae.

Glossophary. innerv.

Constrictor col.

39

Figs. 42-47. THROAT MUSCLES OF ASCALABOTA.

Fig. 42. *Coleonyx variegatus*,  $\times 2\frac{3}{4}$ , A. M. N. H. No. 2538 (cf. Fig. 62). The Gekkonidæ resemble the scincomorphs in the great number of interdigitations of the Mylohyoideus anterior with the Geniohyoideus, perhaps a primitive feature.

Fig. 43. *Uroplates fimbriatus*,  $\times 1$ , A. M. N. H. No. 2235. A specialized gecko-noid (Uroplatidæ). All the muscles are excessively thin.

Fig. 44. *Brachylophus fasciatus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 17701. An iguanid, of the *Cyclura-Ctenosaura-Iguana* group, showing the well-separated, superficial bundle of the Mylohyoideus anterior characteristic of that division of the family. The Cervicomandibularis is absent in this genus.

Fig. 45. *Phrynosoma hernandesi*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 583. Shows the Mylohyoideus anterior superficialis as scarcely separable from the Mylohyoideus anterior principalis, a feature of the genera *Holbrookia*, *Callisaurus*, *Uma*, *Chalarodon*, *Crotaphytus*, and, to a lesser extent, of *Uta* and *Sceloporus*.

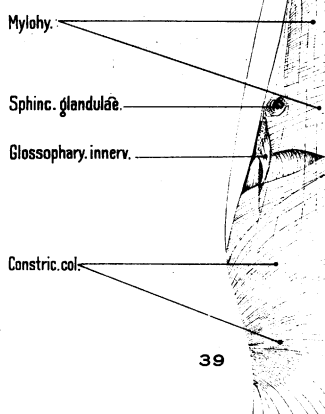
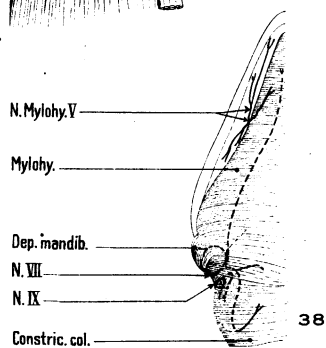
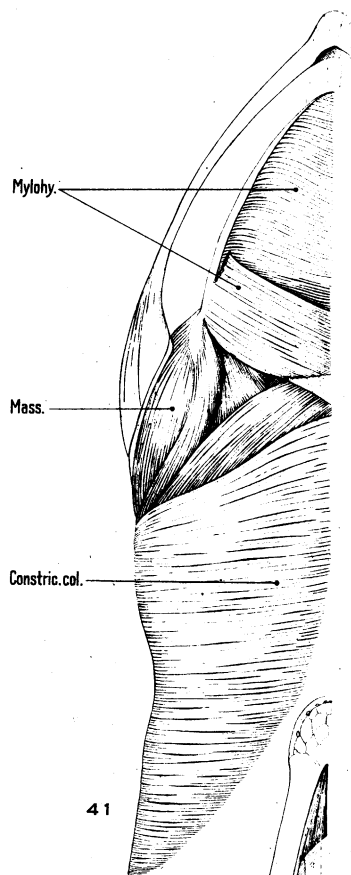
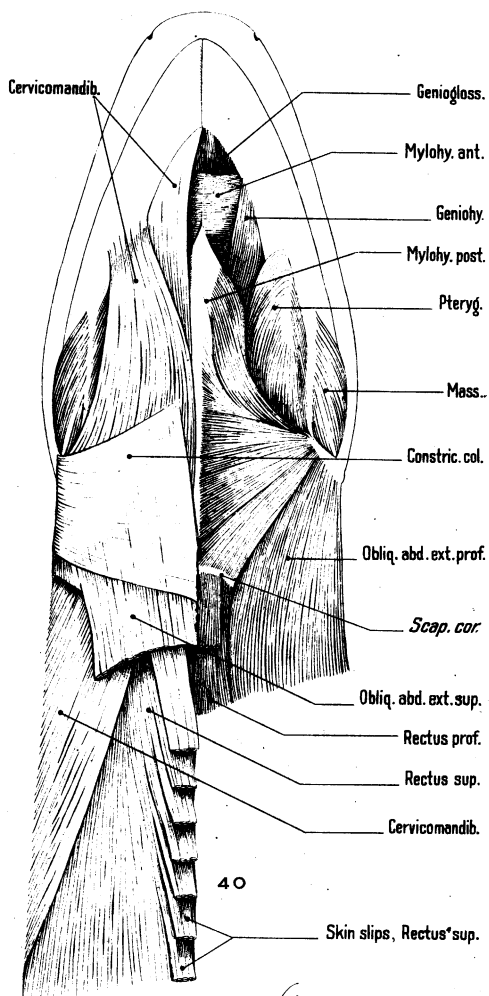
Fig. 46. *Calotes versicolor*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 2147 (cf. Fig. 47).

Fig. 47. *Chamaeleon gracilis*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 11313.

Chameleons and agamids differ from other lizards in having an internal layer, the Mylohyoideus anterior profundus, lying dorsal to the Mylohyoideus anterior principalis. The latter always interdigitates with the Geniohyoideus lateralis. The Mylohyoideus anterior superficialis is absent in agamids and chameleons. The Cervicomandibularis is absent in the highly arboreal agamids and in the chameleons, and in both, the Mylohyoideus posterior runs obliquely forward over the Mylohyoideus anterior.

Features apparently peculiar to chameleons are the forward extension of the Constrictor colli, the great breadth of the Mylohyoideus anterior principalis, and the reduction of the Mylohyoideus posterior.

For abbreviations see p. 448.



Figs. 42-47. THROAT MUSCLES OF ASCALABOTA.

Fig. 42. *Coleonyx variegatus*,  $\times 2\frac{3}{4}$ , A. M. N. H. No. 2538 (cf. Fig. 62). The Gekkonidæ resemble the scincomorphs in the great number of interdigitations of the Mylohyoideus anterior with the Geniohyoideus, perhaps a primitive feature.

Fig. 43. *Uroplates fimbriatus*,  $\times 1$ , A. M. N. H. No. 2235. A specialized gekkonoid (Uroplatidæ). All the muscles are excessively thin.

Fig. 44. *Brachylophus fasciatus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 17701. An iguanid, of the *Cyclura-Ctenosaura-Iguana* group, showing the well-separated, superficial bundle of the Mylohyoideus anterior characteristic of that division of the family. The Cervicomandibularis is absent in this genus.

Fig. 45. *Phrynosoma hernandesi*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 583. Shows the Mylohyoideus anterior superficialis as scarcely separable from the Mylohyoideus anterior principalis, a feature of the genera *Holbrookia*, *Callisaurus*, *Uma*, *Chalarodon*, *Crotaphytus*, and, to a lesser extent, of *Uta* and *Sceloporus*.

Fig. 46. *Calotes versicolor*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 2147 (cf. Fig. 47).

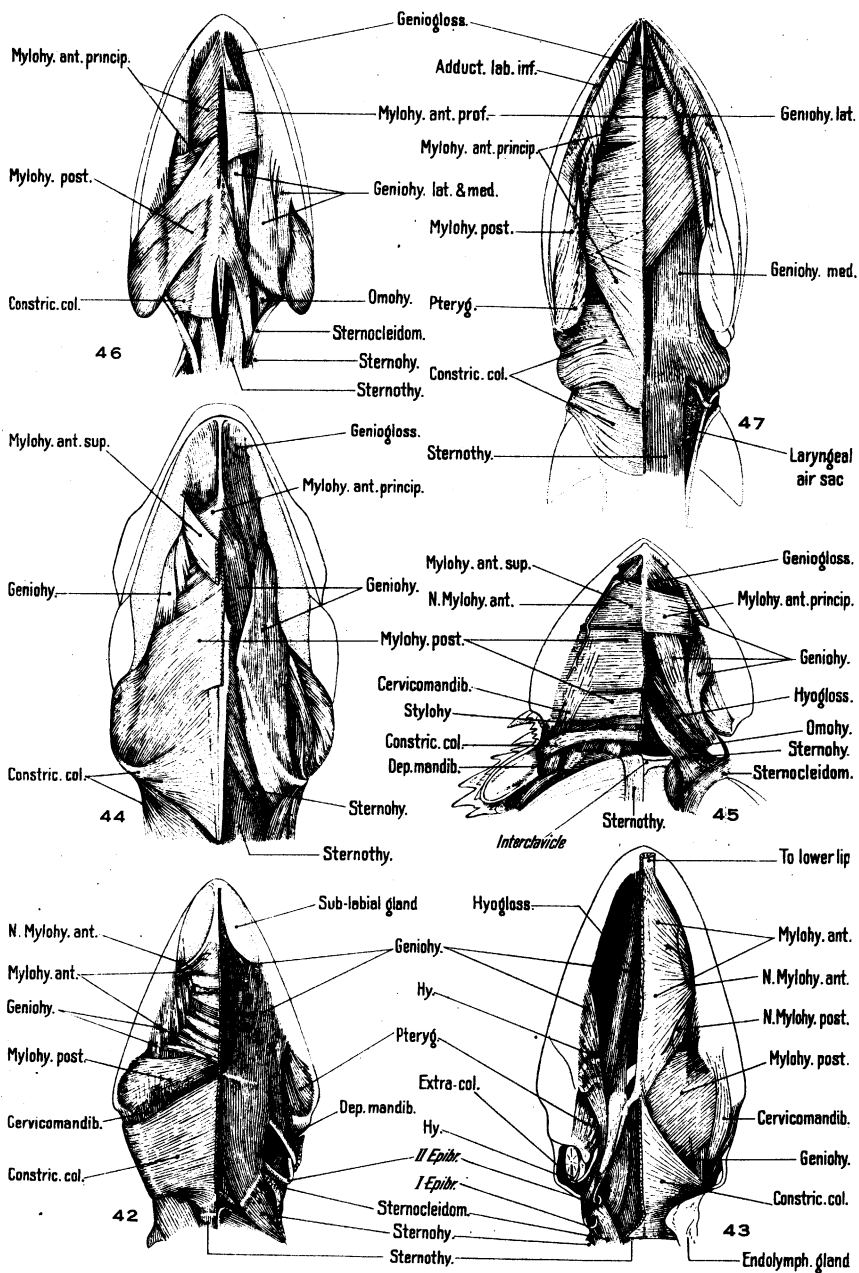
Fig. 47. *Chamæleon gracilis*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 11313.

Chameleons and agamids differ from other lizards in having an internal layer, the Mylohyoideus anterior profundus, lying dorsal to the Mylohyoideus anterior principalis. The latter always interdigitates with the Geniohyoideus lateralis. The Mylohyoideus anterior superficialis is absent in agamids and chameleons. The Cervicomandibularis is absent in the highly arboreal agamids and in the chameleons, and in both, the Mylohyoideus posterior runs obliquely forward over the Mylohyoideus anterior.

Features apparently peculiar to chameleons are the forward extension of the Constrictor colli, the great breadth of the Mylohyoideus anterior principalis, and the reduction of the Mylohyoideus posterior.

For abbreviations see p. 448.





Figs. 48-52. HYOID MUSCLES OF SCINCOMORPHA.

Fig. 48. *Xantusia riversiana*,  $\times 2$ , No. 7072, Mus. Vert. Zoöl. The Cervico-mandibularis is very broad as in *Coleonyx*; otherwise the arrangement of the muscles is not geckoidean.

Fig. 49. *Trachysaurus rugosus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 2046.

Fig. 50. *Lacerta ocellata*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 1731.

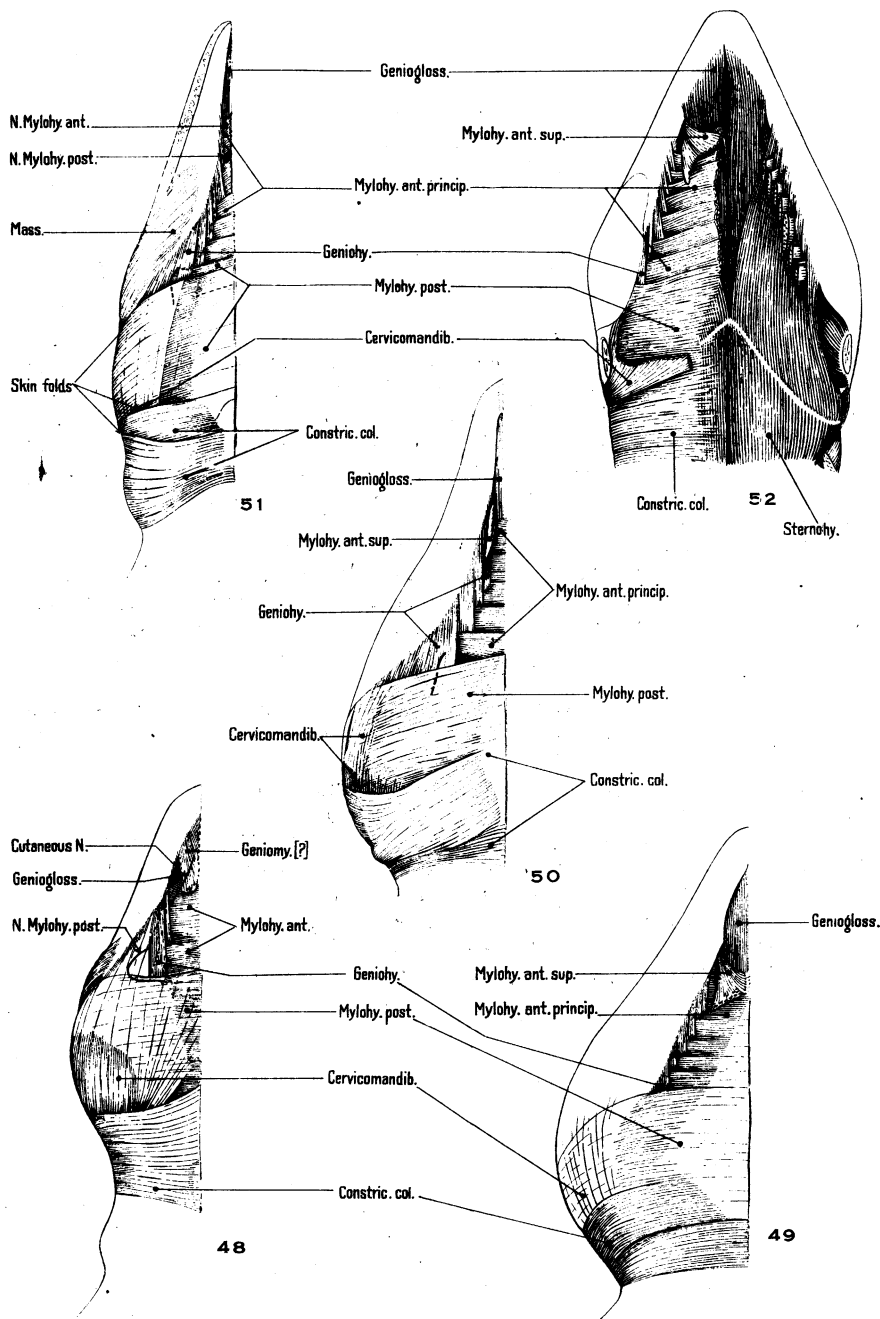
Fig. 51. *Tupinambis nigropunctatus*,  $\times .8$ , A. M. N. H. No. 1932.

Fig. 52. *Gerrhosaurus zechi*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 10721.

Typical scincomorphid characters are the large number of regular and closely placed interdigitations of the Mylohyoideus anterior and posterior, the directly transverse fibers of these muscles, and their unbroken continuity. Resemblances are closest between the scinc, *Trachysaurus*, the lacertid, *Lacerta*, and the gerrhosaurid, *Gerrhosaurus*. Each of these has a small reflected anterior slip of the Mylohyoideus anterior.

The skin folds on the throat of *Tupinambis* join the edges of the muscles along the lines indicated.

For abbreviations see p. 448.



Figs. 53-57. THROAT MUSCLES OF ANGUIMORPHA AND SERPENTES.

Fig. 53. *Typhlops congestus*,  $\times 3$ , A. M. N. H. No. 11664. This burrowing snake has saurian resemblances in the presence of a typical Cervicomandibularis, an interdigitation of Geniohyoideus, and Mylohyoideus with consequent separation of the latter into anterior and posterior portions. In addition there is a reflected portion of Mylohyoideus anterior. The Intermaxillaris may represent the Geniomyoideus of the Anguioidea (cf. Figs. 58-61).

Fig. 54. *Varanus nuchalis*,  $\times .8$ , A. M. N. H. No. 620. The Constrictor colli is divided by a longitudinal raphe. This is known elsewhere only in *Blanus cinereus* (cf. Smalian, 1885). Other features in common with the Amphisbænidæ are the forward continuation of Mylohyoideus posterior, the deeply set Mylohyoideus anterior, and the division of the anterior tendons of the Cervicomandibularis into two parts (cf. Fig. 40).

The Geniohyoideus, Mylohyoideus posterior and Cervicomandibularis are peculiarly arranged, apparently to act upon the sutural articulation across the middle of the lower jaw.

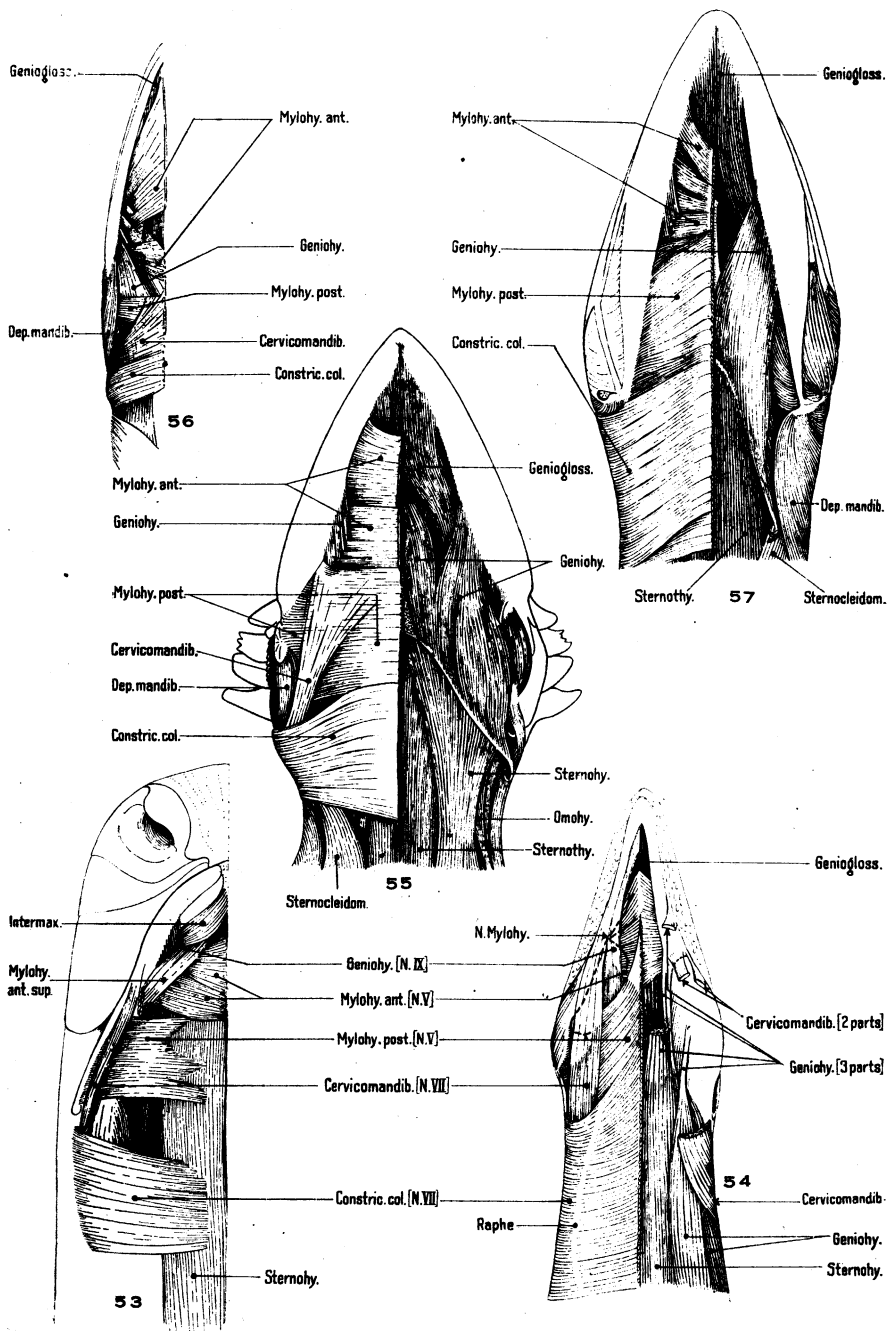
Fig. 55. *Zonurus giganteus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 8736.

Fig. 56. *Lialis burtonii*,  $\times 2$ , A. M. N. H. No. 30.

The arrangement is peculiar and suggests that seen in *Uroplates*. Differences between *Lialis* and *Chamæsaura* are not great enough to prohibit relationship with the Diploglossa which other points in the structure suggest.

Fig. 57. *Chamæsaura macrolepis*,  $\times 3$ , A. M. N. H. No. 2398. Similarities between these two genera include restriction of the interdigitating portion of the Geniohyoideus, lack of separation of parts of the Mylohyoideus.

For abbreviations see p. 448.



Figs. 58-61. THROAT MUSCLES OF THE ANGUIOIDEA, a well-united group on the basis of the throat musculature. A peculiar feature is the presence of the Genio-myioideus, a superficial derivative of the Genioglossus. A character uniting *Gerrhonotus*, *Anniella*, and *Xenosaurus* is the division of the Mylohyoideus into four distinct parts.

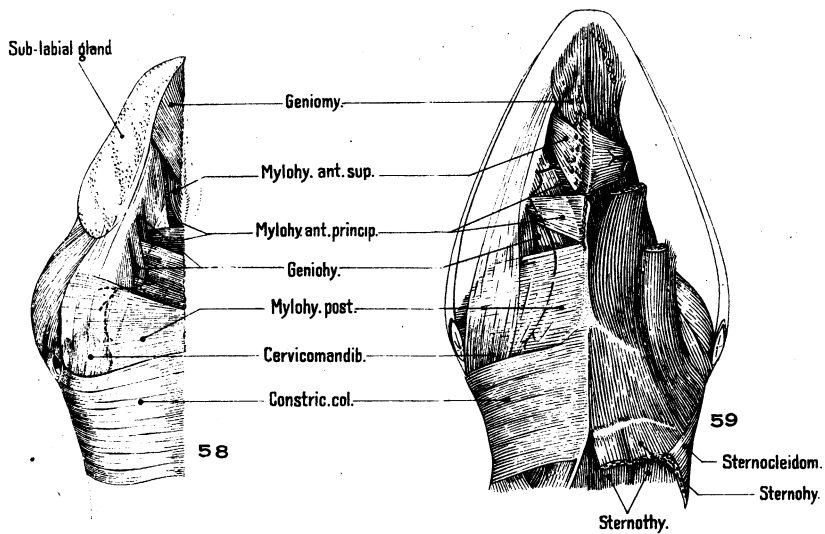
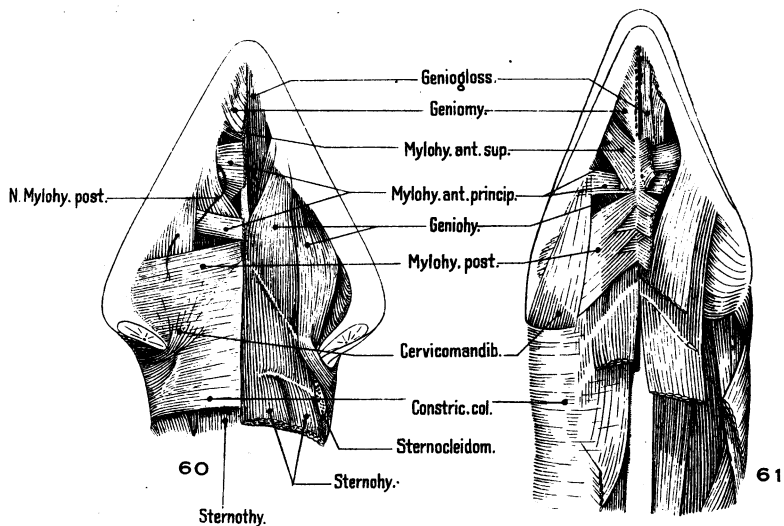
Fig. 58. *Heloderma suspectum*,  $\times .8$ , A. M. N. H. No. 804.

Fig. 59. *Gerrhonotus scincicauda webbiai*,  $\times 1.8$ , A. M. N. H. No. 9159.

Fig. 60. *Xenosaurus grandis*,  $\times 1.8$ , A. M. N. H. No. 19381.

Fig. 61. *Anniella pulchra nigra*,  $\times 4\frac{1}{2}$ , A. M. N. H. No. 20426.

For abbreviations see p. 448.



Figs. 62, 63. COMPARISON OF SUPERFICIAL BODY MUSCULATURE OF AN ASCALATBOID AND AN AUTARCHOGLOSSID; shows also pattern of throat musculature in the Gekkonidæ (cf. Figs. 42-47). The muscles of the shoulder girdle of a scincomorph, *Gerrhosaurus*, a lizard with a cruciform interclavicle and perforated clavicle, are drawn for comparison with those of an anguimorph, *Xenosaurus* (Figs. 64-65), a form with T-shaped interclavicle and simple clavicles.

Fig. 62. *Gekko verticillatus*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 1812.

CERVICOMANDIB. = Cervicomandibularis. CONSTRIC. COL. = Constrictor colli. GENIOHY. LAT. = Geniohyoideus lateralis. GENIOHY. MED. = Geniohyoideus medialis. MYLOHY. ANT. = Mylohyoideus anterior. MYLOHY. POST. = Mylohyoideus posterior. PECT. = Pectoralis. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS PROF. = Rectus profundus. STERNOCLEIDOM. = Sternocleidomastoideus. STERNOHY. = Sternohyoideus. STERNOTHY. = Sternothyreoides.

Fig. 63. *Gerrhosaurus zechi*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 1721.

CLAVODELT. = Clavodeltoideus. COR. BRACH. LONG. = Coracobrachialis longus. RECTUS LAT. = Rectus abdominis lateralis. SCAP. HUM. ANT. = Scapulohumeralis anterior. Other abbreviations as in Fig. 62.



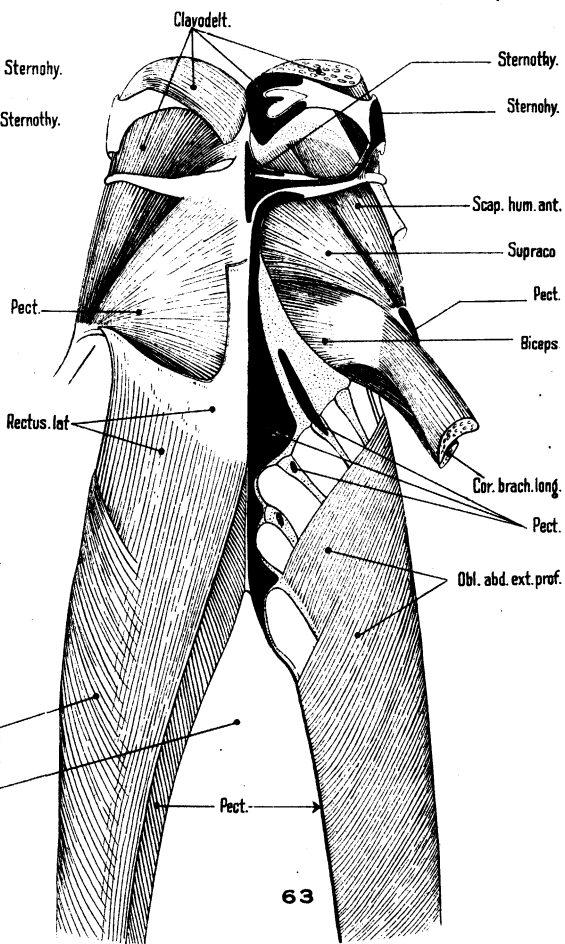
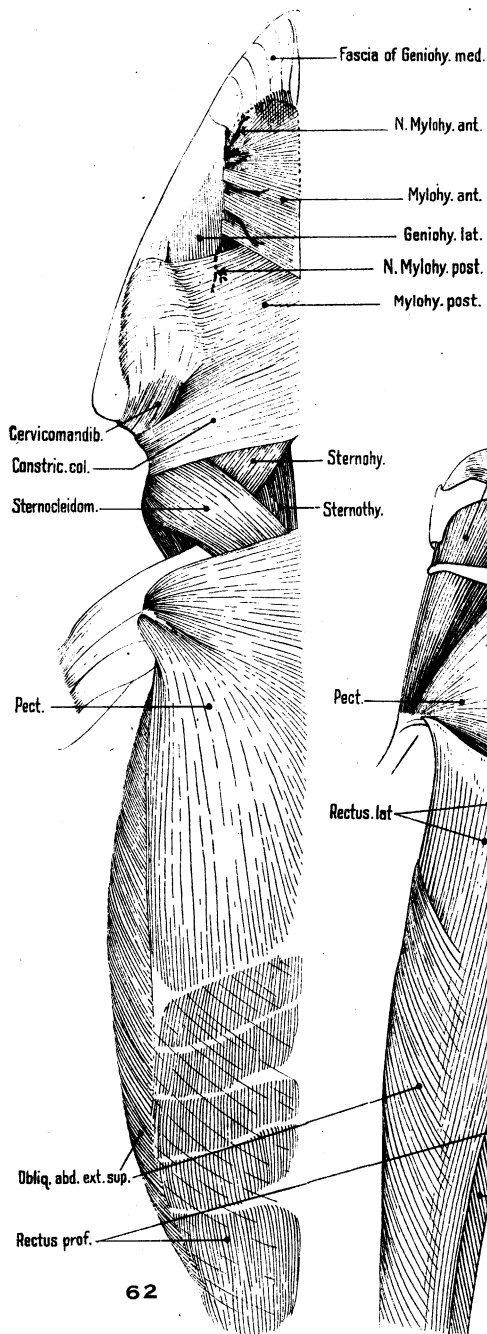
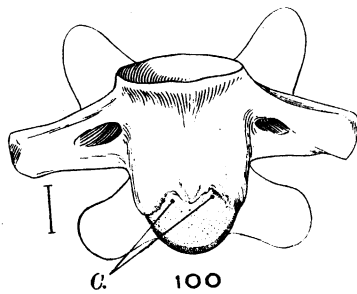
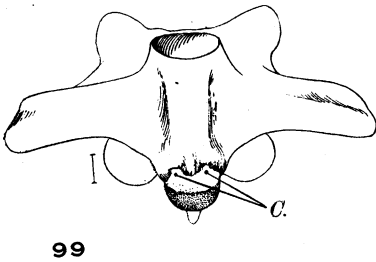
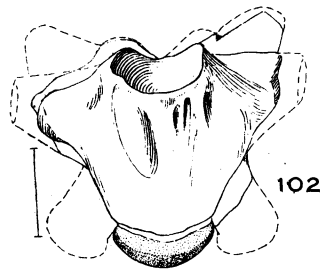
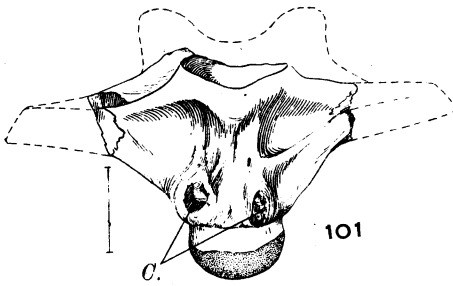
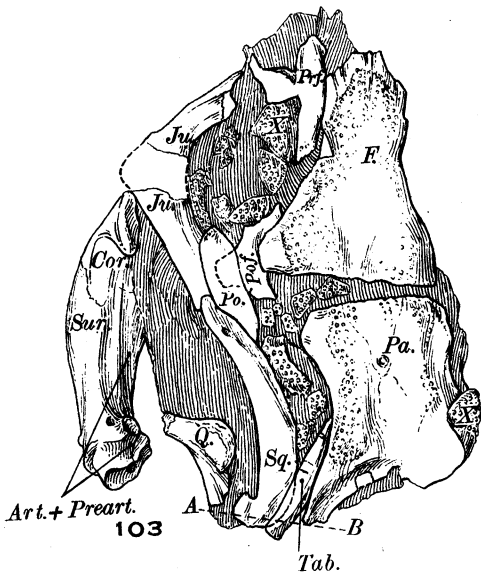


Fig. 64. Ventral shoulder and body muscles surrounding the shoulder girdle in the anguimorph *Xenosaurus*. Compare with Figs. 63 and 65-67.

*Xenosaurus grandis*,  $\times 4\frac{3}{4}$ , A. M. N. H. No. 19381.

CLAVODELT.=Clavodeltoideus. COR. BRACH. BREVIS.=Coracobrachialis brevis. OBLIQ. ABD. EXT. PROF.=Obliquus abdominis externus profundus. OBLIQ. ABD. EXT. SUP.=Obliquus abdominis externus superficialis. PECT.=Pectoralis anterior. PECT. ABD.=Pectoralis abdominis. RECT. MED.=Rectus abdominis medialis. RECT. LAT.=Rectus abdominis lateralis. SCAP. DELT.=Scapulodeltoideus. STERNOHY.=Sternohyoideus. STERNOHY.=Sternothyreoideus. SUPRACOR.=Supracoracoideus.



Figs. 106, 107. RECONSTRUCTION OF SKULL OF *Xestops*, based chiefly on specimen figured in Fig. 103. The shape of other bones is seen on the following specimens: Dept. Vert. Pal., A. M. N. H. No. 5113, prefrontal, lacrymal<sup>1</sup>; A. M. N. H. No. 5175, jugal, maxillaries, premaxillary, tooth row, and occiput; A. M. N. H. No. 5176, sutures in lower jaw (cf. Fig. 112). A superciliary bone was probably present but has not been recognized in our material. Comparison should be made with a figure of *Glyptosaurus* by Douglass (1908).

Fig. 106. Dorsal view,  $\times 1.2$ .

Fig. 107. Lateral view,  $\times 1.2$ .

---

<sup>1</sup>Presence indicated by a groove in the prefrontal.

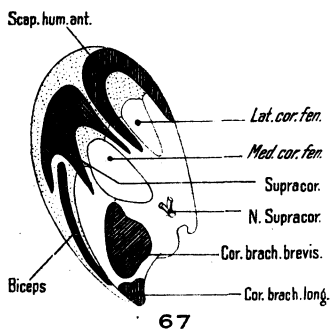
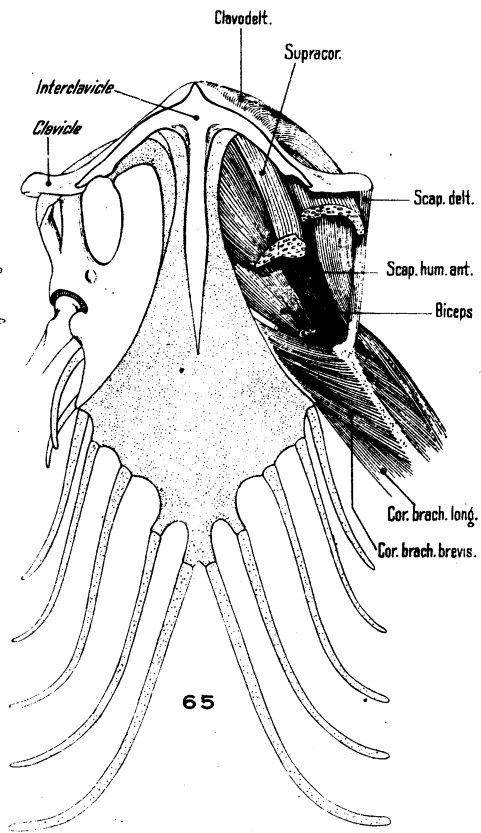
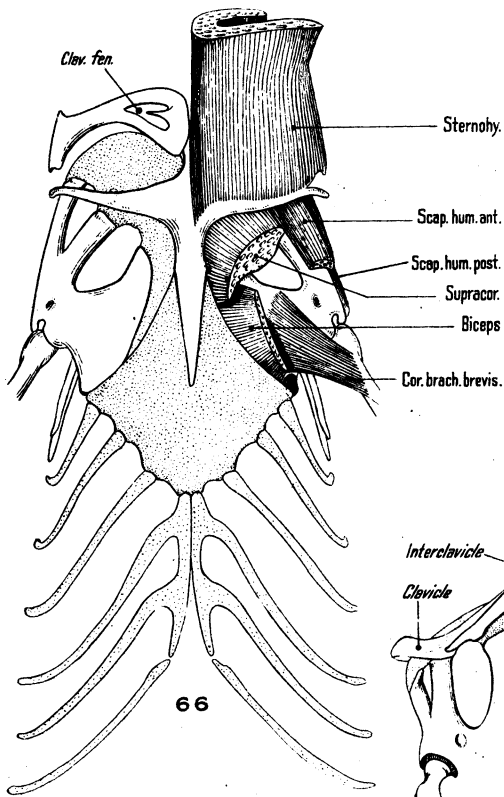


Fig. 68. Shoulder girdle and parasternum of the degenerate teiid, *Bachia intermedia*,  $\times 14$ . Bones and cartilages are drawn from a specimen, A. M. N. H. No. 22731, prepared by Dr. G. K. Noble. Muscles are added from a dissection of A. M. N. H. No. 22730. Ventral view. Four segments omitted in the mid-dorsal region.

The clavicles retain the hook-shaped form characteristic of teiids. The cartilage closing the scapulocoracoid fenestra anteriorly is reduced to a ligament. The sternum is greatly reduced, and contains a large fontanelle.

The xiphisternum is asymmetrical and shows its serial homology with the parasternum by the circumstance that the anterior parasternal wing on the right side has developed into a xiphisternal rod (P).

The parasternum is greatly specialized in connection with body muscles used in terrestrial locomotion and has no union with the rib at its posterior end on the right side.

The segmentation of the skin corresponds with the metamerism of the body.

Fig. 68a. Left forefoot of A. M. N. H. No. 22731,  $\times 16\frac{1}{2}$ .

The carpals are reduced to five. The last metacarpal (IV) is cartilaginous, the fifth is absent.

PALM. SES. = Palmar sesamoids. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS PROF. = Rectus profundus. RECTUS SUP. = Rectus superficialis (= Rectus lateralis + Rectus medianus) closely joined to skin, along with the wings of the parasternum.

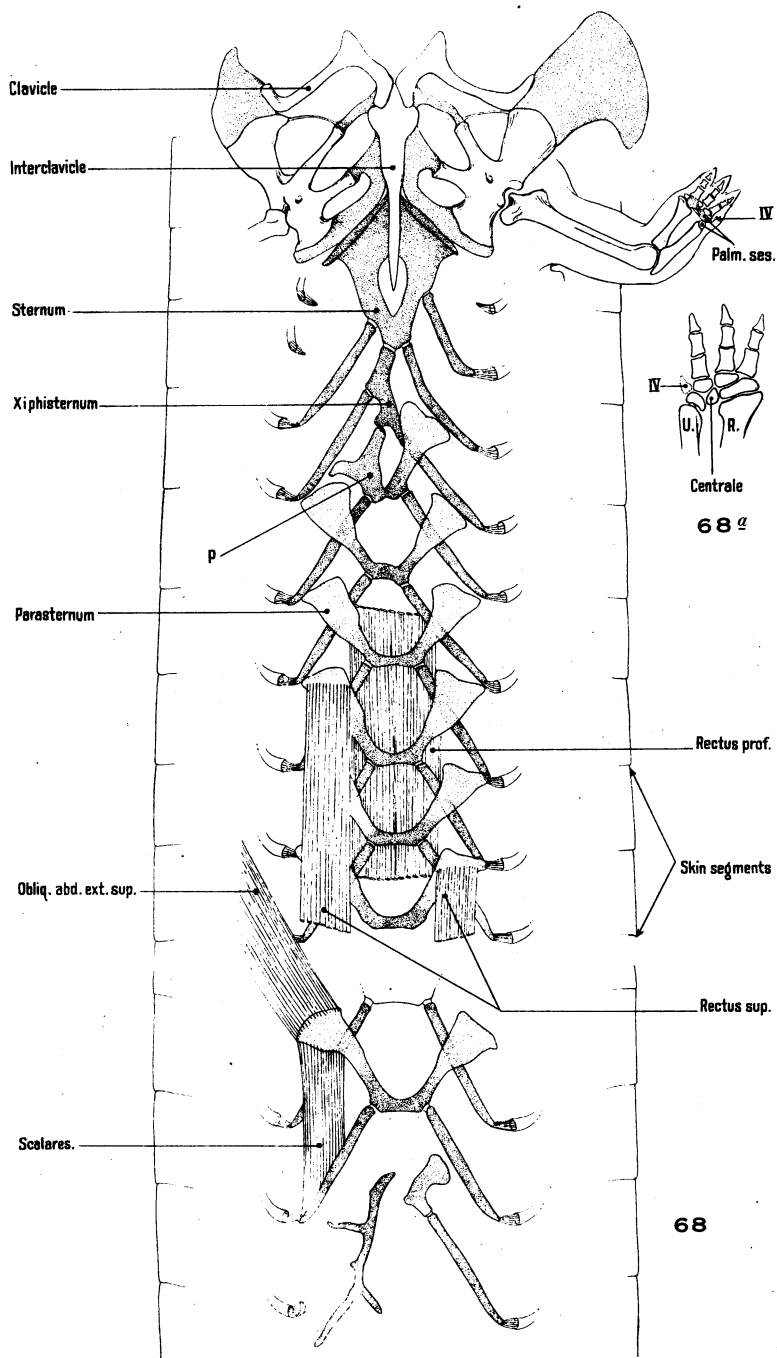


Fig. 69. Shoulder girdle of *Xantusia vigilis*,  $\times 15$ , A. M. N. H. No. 9204, prepared by Dr. G. K. Noble. The interclavicle is cruciform and the clavicles are perforate. There are two small sternal fontanelles. The supracoracoid foramen is enormous. The formula of the scapulo-coracoidal fenestræ is OXXO.



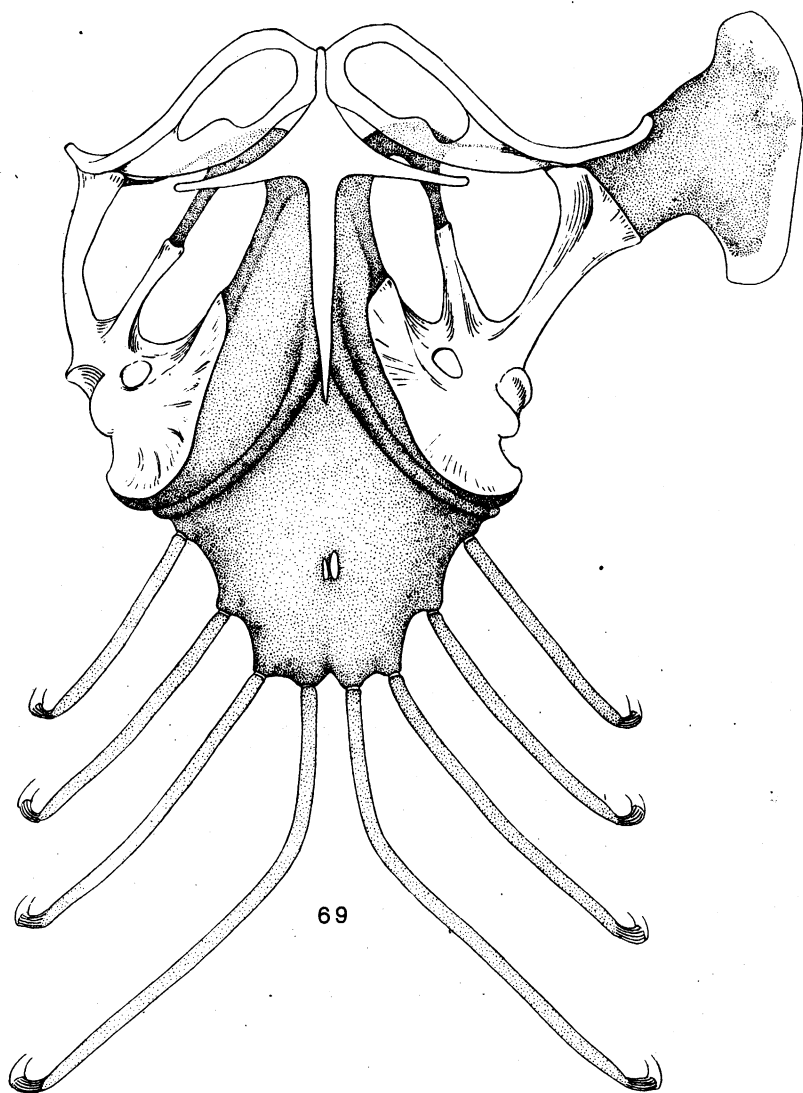


Fig. 70. Cartilaginous shoulder girdle of the degenerate anguioïd, *Anniella pulchra nigra*,  $\times 10$ , A. M. N. H. No. 20426, left clavicle from the side.

Fig. 71. Both clavicles, direct ventral view of the same.

Fig. 72. Muscles adjoining the shoulder girdle of the same.

OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS SUP. = Rectus superficialis. STERNOCLEIDOM. = Sternocleidomastoideus. STERNOHY. = Sternohyoideus. STERNOTHY. = Sternothyreoides.

Fig. 73. Shoulder girdle of the degenerate scincoïd, *Feylinia currorii*,  $\times 10$ , after Rabanus (1906-1915, Pl. xxiii, fig. 33). The clavicles are disappearing, the scapulocoracoid remains. The sternum is reduced to a small median parasternal-like cartilage (cf. Fig. 75).

Fig. 74. Right half of the pelvis of a degenerate teiid, *Bachia intermedia*,  $\times 22$  (same specimen as Fig. 68a).

The hind limbs in the teiids and amphisbænids tend to disappear more rapidly than the forelimbs. In this example, the ilium is fused with the ischium, the pubis and epipubis are separate, the femur is relatively large, the tibia and fibula are much reduced, and the hind foot is represented by a single bone, probably the fibulare.

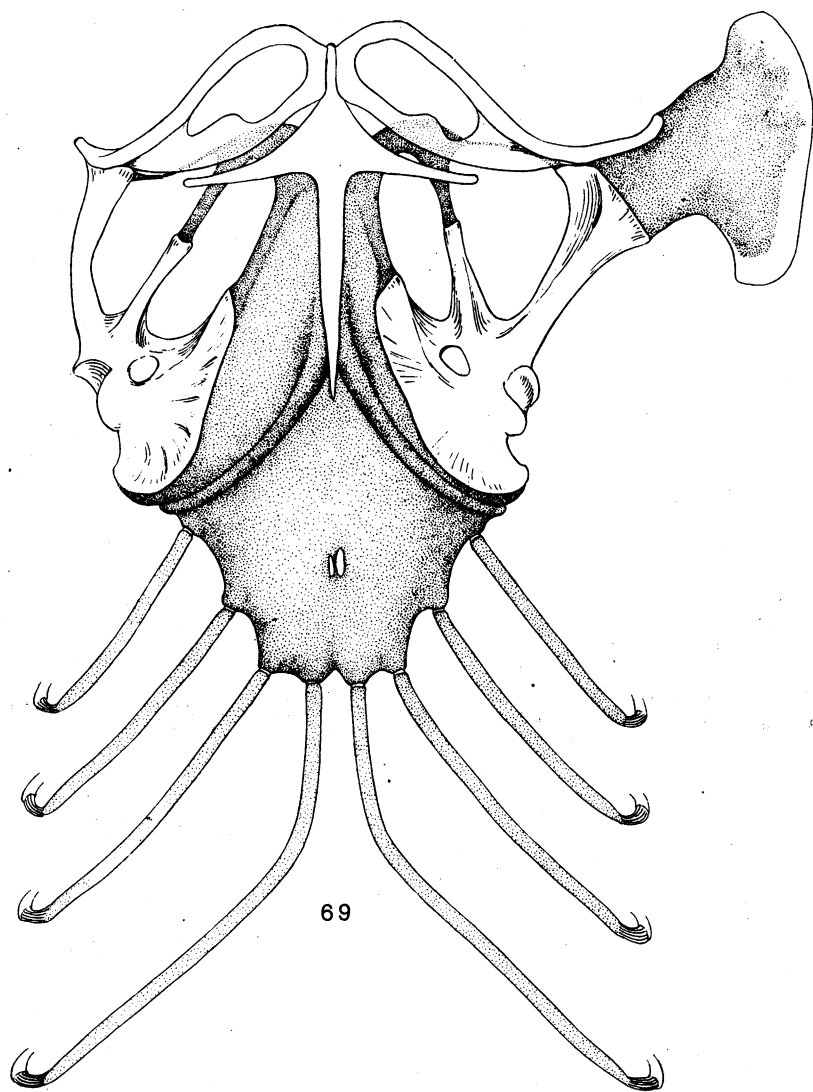


Fig. 70. Cartilaginous shoulder girdle of the degenerate anguroid, *Anniella pulchra nigra*,  $\times 10$ , A. M. N. H. No. 20426, left clavicle from the side.

Fig. 71. Both clavicles, direct ventral view of the same.

Fig. 72. Muscles adjoining the shoulder girdle of the same.

OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS SUP. = Rectus superficialis. STERNOCLEIDOM. = Sternocleidomastoideus. STERNOHY. = Sternohyoideus. STERNOTHY. = Sternothyreoideus.

Fig. 73. Shoulder girdle of the degenerate scincoid, *Feylinia currorii*,  $\times 10$ , after Rabanus (1906-1915, Pl. xxiii, fig. 33). The clavicles are disappearing, the scapulocoracoid remains. The sternum is reduced to a small median parasternal-like cartilage (cf. Fig. 75).

Fig. 74. Right half of the pelvis of a degenerate teiid, *Bachia intermedia*,  $\times 22$  (same specimen as Fig. 68a).

The hind limbs in the teiids and amphisbænids tend to disappear more rapidly than the forelimbs. In this example, the ilium is fused with the ischium, the pubis and epipubis are separate, the femur is relatively large, the tibia and fibula are much reduced, and the hind foot is represented by a single bone, probably the fibulare.

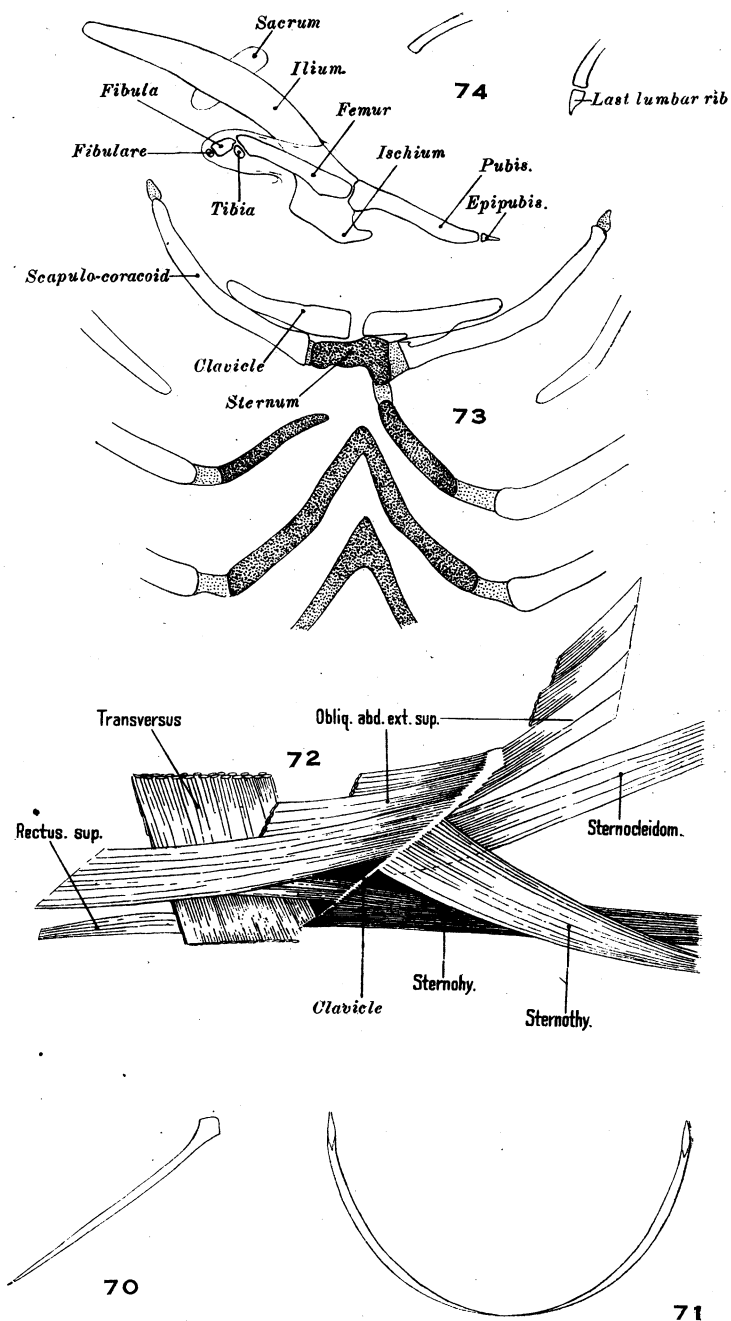
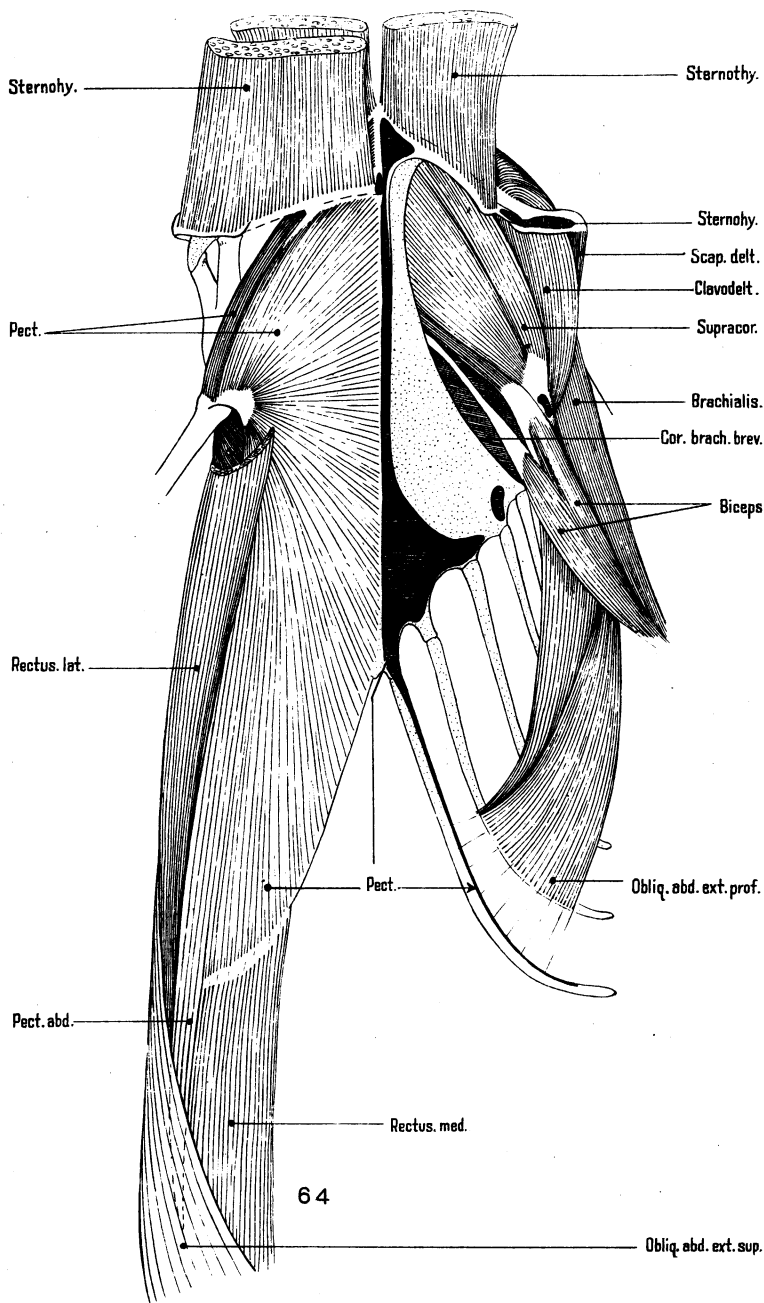


Fig. 75. Shoulder girdle of the degenerate scincoid, *Dibamus novæ-guineæ*,  $\times 22$ , A. M. N. H. No. 1264.

The scapulocoracoids are small, partly bony, and connected to the tip of the first dorsal rib by a muscle which probably represents the Serratus. The sternum has almost the exact shape of the parasternal chevrons which succeed it. The Rectus profundus lies dorsal to the parasternum and the Rectus superficialis lies ventral to it in the usual way. The posterior parasternal chevrons are omitted.

The Transversus is present but is not shown. The Scapulae join the skin on each alternate segment with the Rectus superficialis.

INTERCOST. EXT. BREVIS = Intercostalis externus brevis. INTERCOST. EXT. LONG. = Intercostalis externus longus. INTERCOST. INT. BREVIS = Intercostalis internus brevis. OBLIQ. ABD. EXT. PROF. = Obliquus abdominis externus profundus. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS PROF. = Rectus profundus. RECTUS SUP. = Rectus superficialis. SCAP. COR. = Scapulocoracoid.



Figs. 65-66. VENTRAL SHOULDER MUSCULATURE IN *Gerrhosaurus* AND *Xenosaurus* to show the relations of the muscles to the excavated parts and the processes of the bony elements. Compare with Figs. 63 and 64.

Fig. 65. *Xenosaurus grandis*,  $\times 3\frac{7}{8}$ , A. M. N. H. No. 1938.

COR. BRACH. LONG. = Coracobrachialis longus. SCAP. HUM. ANT. = Scapulohumeralis anterior. SUPRACOR. = Supracoracoideus. Other abbreviations as in Fig. 64.

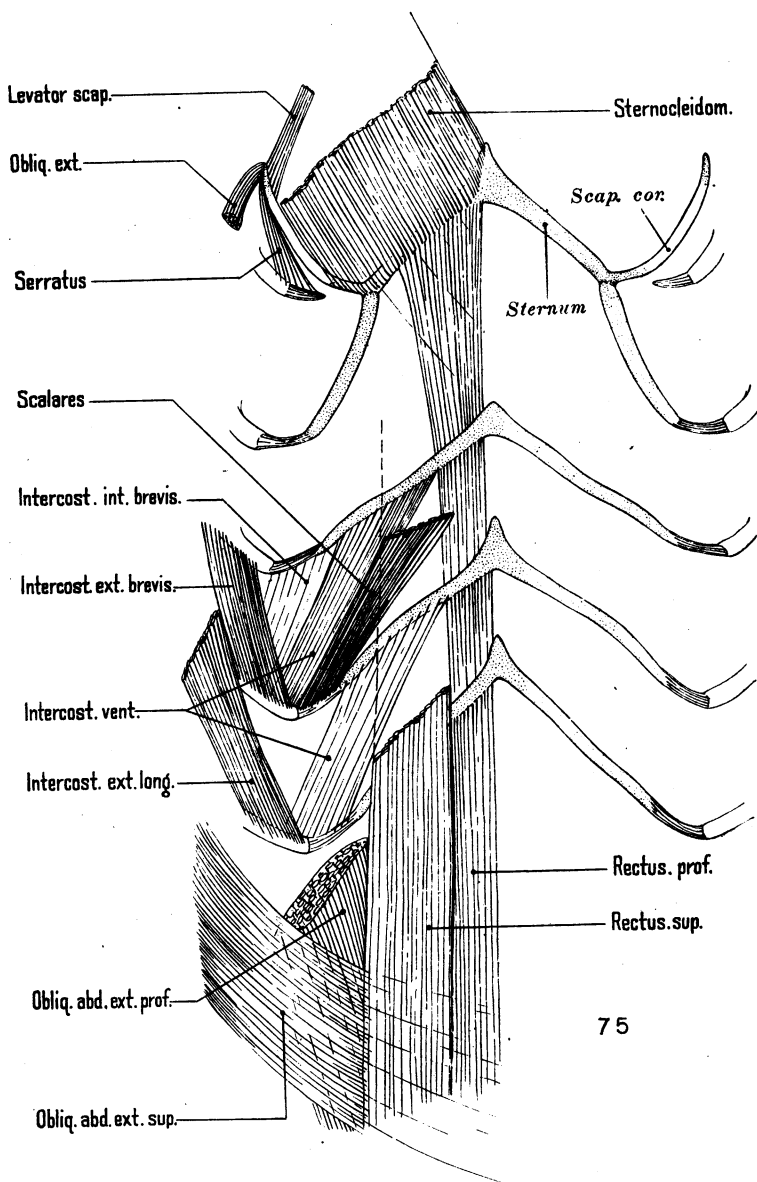
Fig. 66. *Gerrhosaurus zechi*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 10721.

SCAP. HUM. POST. = Scapulohumeralis posterior. Other abbreviations as in Figs. 64 and 65.

Fig. 67. CORACOID OF *Gerrhosaurus*,  $\times 1\frac{1}{2}$ , showing relations of muscle insertions to the coracoideal fenestræ.

LAT. COR. FEN. = Lateral (1'') coracoidal fenestra. MED. COR. FEN. = Median (2'') coracoidal fenestra.





Figs. 76-81. A SERIES SHOWING MODIFICATIONS OF THE CLAVICLE IN VARIOUS LIZARDS (cf. Figs. 62-75). Ventral views, left clavicle.

Fig. 76. Interclavicle and end of left clavicle of *Proterosaurus speneri*, after Credner (1888, Fig. 19, p. 520).

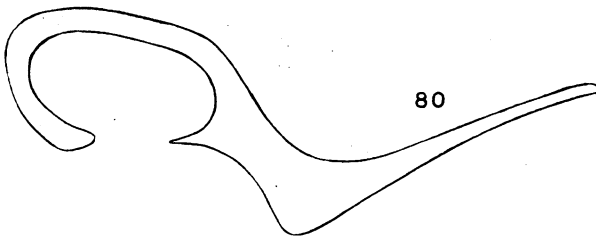
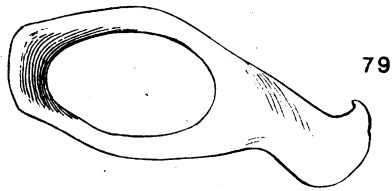
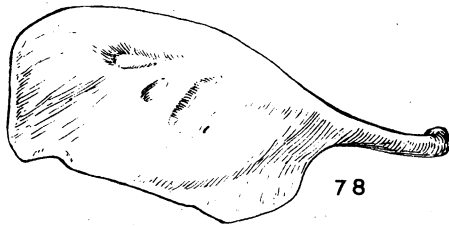
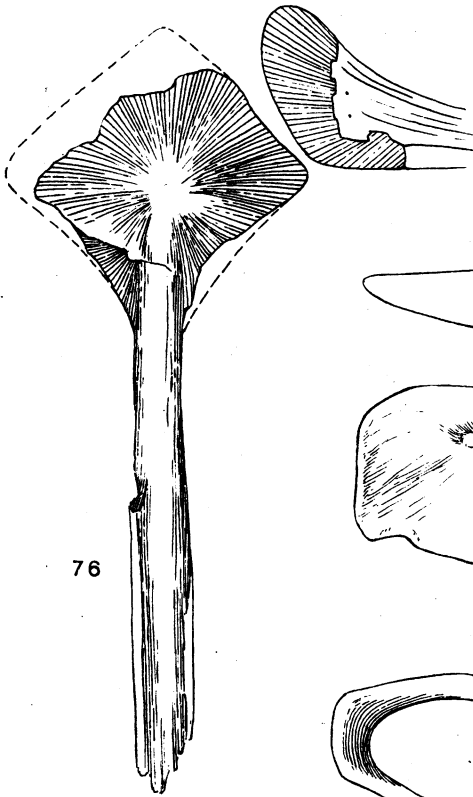
Fig. 77. *Aræoscelis*,  $\times 2\frac{1}{4}$ , after Williston (1914, Fig. 4, L).

Fig. 78. *Trachysaurus rugosus*,  $\times 3$ , Skel. in Dept. Herpetol., A. M. N. H.

Fig. 79. *Lacerta simonyi*,  $\times 4\frac{1}{2}$ , after Sibenrock (1894, Pl. IV, fig. 24).

Fig. 80. *Lacerta serpa*, after Krieg (1919, Fig. 1, p. 574).

Fig. 81. *Zonurus giganteus*,  $\times 3$ , Skel. in Dept. Herpetol., A. M. N. H.



Figs. 82-98. OSTEODERMS OF LIZARDS. Figs. 84-89, Scincomorpha. Figs. 90-98, Anguimorpha.

The osteoderms are on a higher plane of development in the Anguimorpha than in the Scincomorpha. The ventral scutes of the Anguimorpha appear never to be compound; those of Scincomorpha are always so. Some approach to geckonoid conditions (Fig. 83) is seen in the scines (Fig. 84). The least developed scutes of the Anguimorpha (Figs. 90 and 92) show a slight advance upon the most specialized scutes of the Scincomorpha (Figs. 87 and 89). The most highly specialized scutes are those of the Glyptosauridae and Helodermatidae (Figs. 94-98). The least specialized are apparently the diffuse scutes of the cotylosaur, *Pantylus*, and of the gecko, *Tarentola* (Figs. 82-83). The position of the horny scales covering the scutes is indicated in many of the figures.

Fig. 82. *Pantylus*,  $\times 2$ , after Williston (1916a, Fig. 30, p. 175).

Fig. 83. *Tarentola mauritanica*, ventral scales and scutes, after Otto (1909, text-fig. 19, p. 234).

Fig. 84. *Scincus officinalis*, scute from right side of cloaca, after Otto, (1909, text-fig. 5, p. 210).

Fig. 85. *Gongylus* [*Chalcides*] *ocellatus*, scute from dorsal surface of tail, after Otto (1909, text-fig. 9, p. 218).

Fig. 86. *Scincus officinalis*, scute from the cervical region, after Otto (1909, text-fig. 4, p. 209).

Fig. 87. *Lygosoma tenue*, scute from the cervical region, after Otto (1909, text-fig. 13, p. 225).

Figs. 88-89. *Gerrhosaurus nigrolineatus*, after Schmidt (1913a, Figs. D=88, ventral, C=89, dorsal, p. 80),  $\times 3$ .

Figs. 89a and b. *Zonosaurus madagascariensis*,  $\times 10$ , after Schmidt (1913a, Figs. M<sub>2</sub> dorsal, M<sub>3</sub> ventral).

Fig. 90. *Zonurus cordylus*, mid-dorsal scute and scale, after Otto (1909, text-fig. 1, p. 204).

Fig. 91. *Zonurus cordylus*, mid-dorsal scute, after Otto (1909, Pl. ix, fig. 1).

Fig. 92. *Anguis fragilis*, mid-dorsal scute, after Otto (1909, text-fig. 2, p. 207).

Fig. 93. *Gerrhonotus liocephalus*, dorsal scute,  $\times 8$ , after Schmidt (1914, Pl. vi, fig. 68).

Fig. 94. *Xestops*, scute from the body,  $\times 1\frac{1}{4}$ , Dept. Vert. Pal., A. M. N. H. No. 5175.

Fig. 95. *Glyptosaurus*, scute from the body,  $\times 1\frac{1}{4}$ , Dept. Vert. Pal., A. M. N. H. No. 5113, Bridger Eocene.

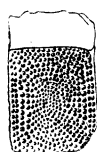
Fig. 96. *Glyptosaurus*, scute from the head,  $\times 1\frac{1}{4}$ , Dept. Vert. Pal., A. M. N. H. No. 5109.

Fig. 97. *Placosaurus rugosus*, scute from the head,  $\times .8$  after Gervais (1859, Atlas, Pl. LXIV, fig. 2a).

Fig. 98. *Heloderma horridum*,  $\times 4$ , A. M. N. H. No. 7216.



94



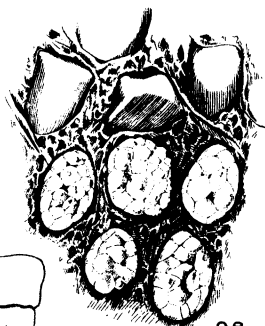
95



96



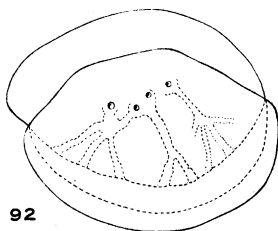
97



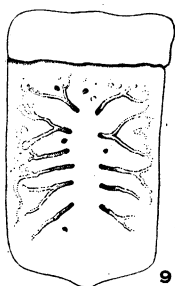
98



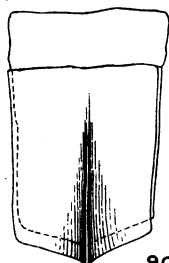
93



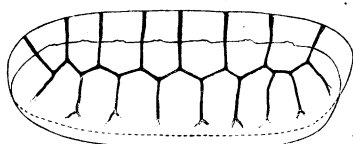
92



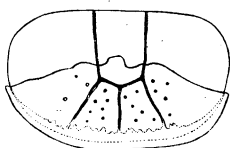
91



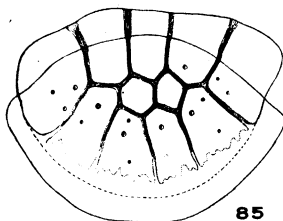
90



86



87



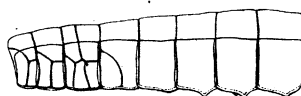
85



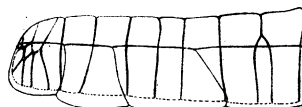
89<sup>a</sup>



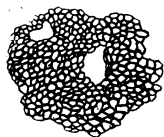
89<sup>b</sup>



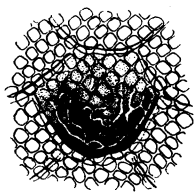
89



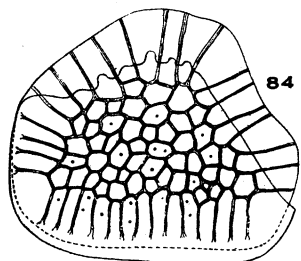
88



82



83



84

Figs. 99-105. SKULLS AND VERTEBRÆ OF GLYPTOSAURIDÆ, AND VERTEBRÆ OF OTHER ANGUIOIDS.

Fig. 99. First caudal vertebra of *Gerrhonotus scincicauda scincicauda*,  $\times 6\frac{1}{2}$  A. M. N. H. No. 595. The transverse processes arise from the whole length of the centrum as in the Glyptosauridæ. The chevrons are attached intercentrally at *C*.

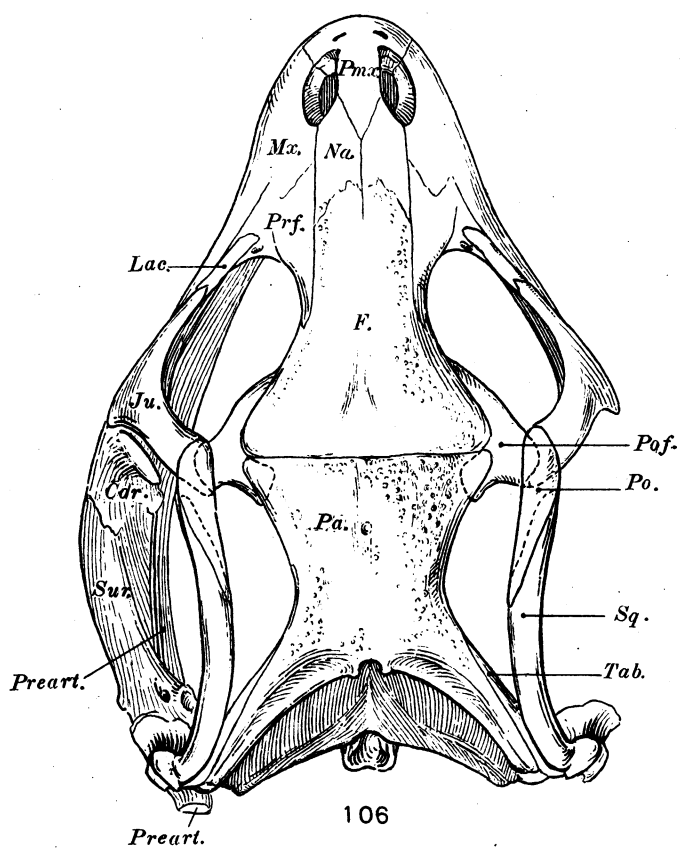
Fig. 100. First caudal vertebra of *Heloderma* sp.?,  $\times 3\frac{1}{2}$ , Skel. in Dept. Comp. Anat., A. M. N. H. The transverse processes arise from the anterior two-thirds of the centrum. The chevrons are attached intercentrally at *C*.

Fig. 101. *Xestops*, Dept. Vert. Pal., A. M. N. H. No. 5175. The transverse processes arise from the whole length of the centrum as in *Gerrhonotus*. The chevrons are attached centrally at *C*.

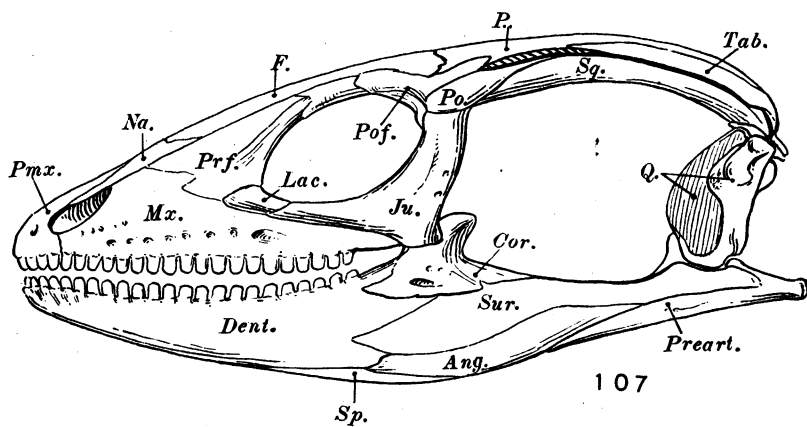
Fig. 102. *Xestops*,  $\times 1$ , Dept. Vert. Pal., A. M. N. H. No. 5175. Mid-dorsal vertebra, ventral view for comparison with Figs. 15, 20, and 21.

Fig. 103. Skull of *Xestops*,  $\times 1$ , Dept. Vert. Pal., A. M. N. H. No. 5168. Dorsal view. The skull is crushed flat. The disarticulated bones lie nearly in position showing the correct relation of the Frontals (*F.*), Parietals (*Pa.*), Prefrontal (*Prf.*), Postfrontal (*Pof.*), Postorbital (*Po.*), Jugal (*Ju.*), Squamosal (*Sq.*), Quadrate (*Q.*), and the posterior end of the lower jaw. (Cf. Figs. 106-110.)

Figs. 104-105. *Placosaurus rugosus*. Top of skull of type specimen showing same kind of osteoderms (Figs. 104-105) as in *Glyptosaurus* and on the side of the head in *Xestops* (Fig. 103, *X*), after Gervais (1859, Atlas, Pl. LXIV, figs. 2-2a).



106



107

Figs. 108-112. SKULL OF THE ANGUID, *Gerrhonotus*, AND PORTIONS OF SKULLS OF GLYPTOSAURIDÆ, for comparison with Figs. 106, 107.

Fig. 108. Top of skull of *Gerrhonotus scincicauda scincicauda*,  $\times 2$ , A. M. N. H. No. 595. Superciliare omitted. General similarities to *Xestops* are shown. The heavy secondary covering of bony scales is preserved on the right side.

Fig. 109. Section of quadrato-parietal region of *Xestops* through line A-B, Fig. 103,  $\times 3$ . The squamosal has a basal expansion resting upon the head of the quadrate. The paroccipital is separate from the exoccipital and its posterior extremity (*Parocc.*) lies beneath the tabular-parietal suture. The exoccipital bears a dorsal groove for the reception of the tabulare. There is a muscular excavation on the posterior border of the parietal. The quadrate is rotated out of position due to crushing.

Fig. 110. Postero-internal view of quadrate of same specimen as Fig. 109,  $\times 3$ . The broadened internal "wing" is represented in *Heloderma* by a slight ridge and is absent in *Gerrhonotus*.

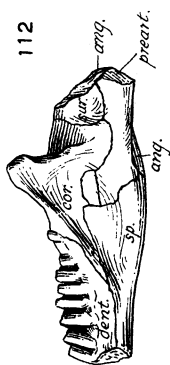
Fig. 111. Anterior portion of lower left dentary, internal view of *Xestops*,  $\times 2\frac{1}{2}$ . Dept. Vert. Pal., A. M. N. H. No. 5175. The direction of the teeth at the symphysis, the highly pleurodont character of the semi-solid teeth, and the wrinkling of the blunt crowns are shown. The teeth are firmly attached to the dentary for nearly their whole length.

Fig. 112. Sutures on internal face of middle of lower jaw of a glyptosaurid,  $\times 1$ , Dept. Vert. Pal., A. M. N. H. No. 5176, Wasatch Eocene. The Meckelian sulcus is closed. The splenial is large. The elements are all suturally distinct.

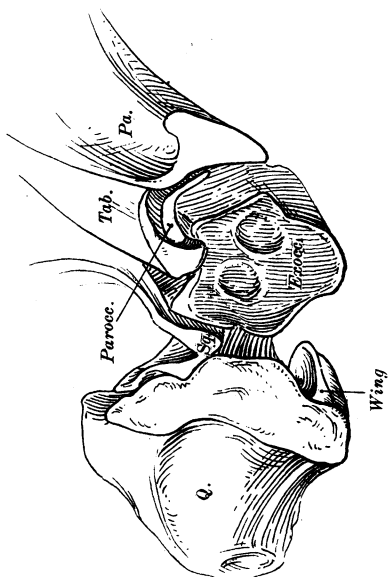




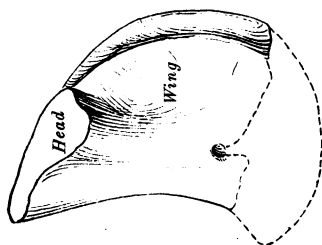
111



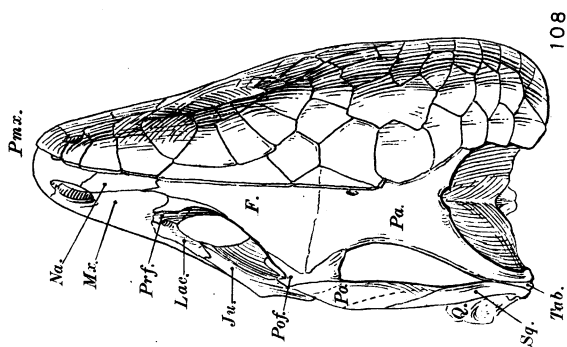
112



109



110



108

