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LIEUWE DIRK BOONSTRA

THE GIRDLES AND LIMBS OF THE PRISTEROGNATHID THEROCEPHALIA

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THE GIRDLES AND LIMBS OF THE PRISTEROGNATHID THEROCEPHALIA

By

LIEUWE DIRK BOONSTRA

South African Museum, Cape Town

(With 50 text-figures and one Plate)

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INTRODUCTION

In the *Tapinocephalus* zone of the Karoo the oldest Therocephalia known are well represented. The Therocephalia form the main component of the carnivores, the only other carnivores being the very large anteosaurs represented by five genera and a few small to medium-sized Gorgonopsia represented by 10 genera, of which 30 specimens are known in all.

The Therocephalia are represented in the *Tapinocephalus* zone by the families Pristerognathidae, Lycosuchidae, Scylacosauridae and Scaloposauridae. Of these the pristerognathids are the dominant family and are well represented in numbers of specimens as well as in the number of distinct species. Hitherto 16 genera with 28 species have been described. Most of the specimens consist of partly preserved snouts, with good complete skulls few in number. Of the postcranial skeleton little is known, for only rarely are some of the postcranial

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bones preserved and then mostly associated with cranial parts difficult to classify.

In this paper I present an account of the girdle and limb material in the South African Museum mostly collected by myself since 1928.

This collection includes material which necessitates the establishment of the following new genus and species.

ZINNOSAURUS new genus

Type-species: Zinnosaurus paucidens.

Diagnosis: A medium-sized pristerognathid with the dental formula i.5, c.1, pc.2; the incisors are fairly weak and well spaced and the postcanines are weak and lie far apart; the postcanines situated on a thin lappet of the maxilla clearly demarcated from the general maxillary surface. Scapula with a well-developed flange-like process on its posterior border immediately above the glenoid for the scapular head of the triceps. The glenoid widely open and facing much laterally. Humerus with greatly expanded epicondyles, thin and sheet-like. Femur with broadly oval caput and strong thickened internal trochanter.

Affinities: Nearest relative *Glanosuchus.*

Zinnosaurus paucidens new species

(Figs. 1, 19, 28, 46*d* and 46*e*)

Holotype. S.A.M. 12185, skull with lower jaw, scapulo-coracoid, humeri, ends of femora.

Locality: Meyerspoort, Beaufort West, South Africa.

Horizon: High *Tapinocephalus* zone, Lower Beaufort Beds, Karoo.

I have great pleasure in naming this new genus after H. Zinn, who has, as techinical assistant, accompanied me on numerous collecting trips in the *Tapinocephalus* zone.

The scapulo-coracoid, humeri and ends of femora of the holotype are described in the appropriate sections of this paper.

Material

In the South African Museum catalogue 219 specimens of pristerognathids from the *Tapinocephalus* zone are listed. Of these only the following 37 specimens have parts of the girdles and limbs preserved. Taken together one gets a good idea of the family character of these structures.

The material studied consists of the following specimens listed in the order of the date of acquisition by the South African Museum collection.

S.A.M. 4335. *Pristerognathus* sp. Beaufort West. High? *Tapinocéphalus* zone. Coll. Whaits 1916? Incomplete coraco-scapulae, distal and proximal ends of a humerus and the proximal halves of an ulna and radius. No skull.

S.A.M. 5018. *Pristerognathus* sp. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton 1916. Two incomplete ilia, proximal and distal halves of two femora and of two humeri, proximal ends of tibiae, radii and ulnae. No skull.

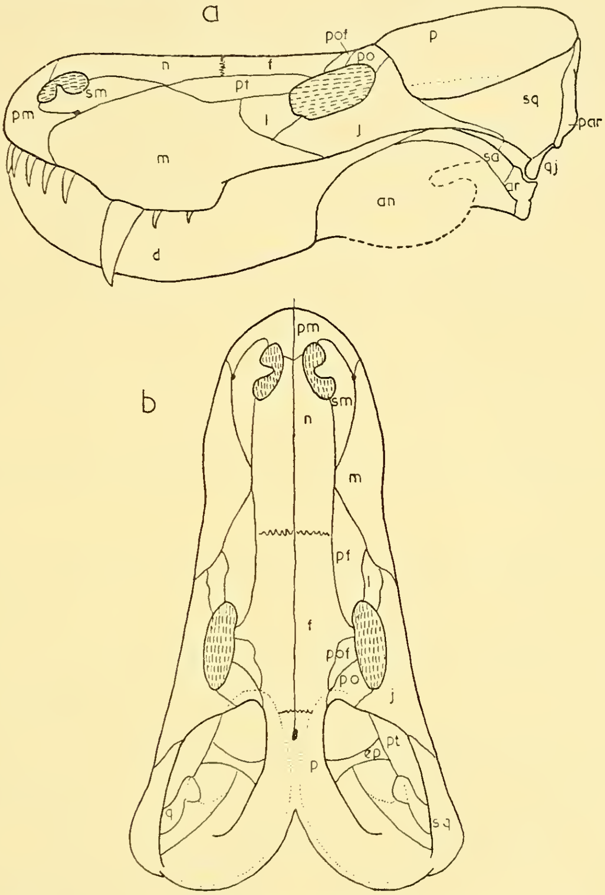

Fig. 1. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. Type $\times \frac{1}{3}$. Skull. *a*, lateral. *b*, dorsal.

S.A.M. 9005. *Scymnosaurus major*. Holotype. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1929. Interclavicle with proximal parts of both clavicles, distal ends of both humeri, complete radius and ulna, associated with a good anterior half of the skull.

S.A.M. 9084. *Scymnosaurus ferox*. Rietkuil, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1929. A coracoid, proximal and distal ends of a humerus and proximal ends of an ulna and radius associated with a good skull.

S.A.M. 11458. *Pristerognathus* sp. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Avenant 1939. An interclavicle, proximal ends of clavicles, parts of coracoids, poor ends of femur, humerus, radius, ulna. No cranial material.

S.A.M. 11459. *Scymnosaurus* sp. Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Marais 1939. Part of carpus and tarsus associated with a poor snout.

S.A.M. 11557. *Scymnosaurus* sp. Die Cypher, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1940. A scapula, humerus, femur, interclavicle, clavicle, radius, and partial manus. Without skull.

S.A.M. 11558A. *Scymnosaurus?* Die Cypher, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1940. A pair of well-preserved ischia.

S.A.M. 11695. *Scymnosaurus* sp. Seleryfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Jooste 1946. A coraco-scapula, interclavicle, clavicles and humerus. With good anterior half of skull.

S.A.M. 11794 *Cynariognathus* sp. Seleryfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Jooste 1947. Imperfect pelvis, femora, humeri, epipodials and manus. With a poor skull.

S.A.M. 11888. *Therioides cyniscus*. Holotype. Vindragersfontein. Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1948. Parts of pectoral girdle, humerus, radius, ulna and part of manus associated with a nearly complete skull.

S.A.M. 11934. *Pristerognathus?* Steenboksfontein, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1951. Distal end of femur and proximal ends of tibia and fibula. Without cranial association.

S.A.M. 11936. *Pristerognathoides* sp. Bosluiskraal, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1951. Proximal and distal end of a femur associated with a snout.

S.A.M. 11942. *Ptomalestes avidus*. Holotype. Steenboksfontein, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1951. Part of pectoral girdle, humeri, ulnae and radii associated with a good skull.

S.A.M. 11957. *Scymnosaurus* sp. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Le Roux 1923. Acetabular parts of ischium and pubis and proximal end of femur. Without skull.

S.A.M. 12051. *Alopecognathus* sp. Rietfontein, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Fourie 1957. Part of scapula, proximal end of humerus, proximal and distal ends of femur, ends of radii and ulna and part carpus, tibia and fibula and a complete pes associated with a snout.

S.A.M. 12102. *Pristerognathoides* sp. Kalkkraal. Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957. Most of the pectoral girdle, ends of humerus, ulna and radius associated with a complete skull.

S.A.M. 12112. *Pristerognathus?* Skoppelmaaikraal, Laingsburg. Low *Tapinocephalus* zone. Coll. Botes 1957. Part of ilium, proximal end of humerus and other fragments without any skull parts.

S.A.M. 12118. *Scymnosaurus* sp. Palmietfontein of Kruidfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957. Proximal end of femur, part scapula.

S.A.M. 12185. *Zinnosaurus paucidens* gen. et spec. nov. Meyerspoort, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Part coraco-scapula, one complete humerus and one proximal half, proximal and distal end of femur and proximal end of ulna and radius and distal end of radius associated with a good skull.

S.A.M. 12193. *Scymnosaurus* sp. Fortuin of Dalajalon, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Fairly complete pectoral girdle, humerus, ulna and radius associated with piece of jaw containing teeth.

S.A.M. 12204. *Pristerognathoides* sp. Plaatjiesrivier, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Fairly complete pectoral girdle, humerus, ulna and radius associated with the posterior third of a skull.

S.A.M. 12262. *Scymnosaurus* sp. Seleryfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Jooste 1959. Femur, radius, ulna and manus.

S.A.M. K218. *Alopecognathus* sp. Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. Weathered pelvis.

S.A.M. K233A and B. *Alopecognathus* sp. Palmietfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. Two incomplete pectoral girdles.

S.A.M. K223C. *Pristerognathoides* sp. Palmietfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. A ncarly complete pelvic girdle associated with a skull.

S.A.M. K227. *Pristerognathus* sp. Louisrus of Dalajalon, Beaufort West. *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Two ilia found in association with a poor snout.

S.A.M. K231. *Alopecognathus angusticeps* Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Boonstra and Gow 1959. The major part of an articulated skeleton articulated to a skull.

S.A.M. K234. *Pristerognathus* sp. Palmietfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. Part of pelvis associated with a snout.

S.A.M. K238A. *Pristerognathus?* Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. A pelvis and pes.

S.A.M. K245A. Pristerognathid? Rietfontein of Vlakfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. A pelvis and part of the pes.

S.A.M. K306. *Pristerognathus* sp. Kranskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1960. Distal and proximal ends of two femora.

S.A.M. K317. *Pristerognathus* sp. Bulwater, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Gow 1960. Proximal and distal ends of femur with parts of skull.

S.A.M. K339. *Alopecognathus* sp. Klipbanksfontein, Beaufort West. *Tapinocephalus* zone. Coll. Boonstra and Zinn 1962. Incomplete pectoral girdle associated with anterior two-thirds of a skull.

S.A.M. K352. *Scymnosaurus* sp. Skoppelmaaikraal, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1962. Femur (isolated).

S.A.M. K353. *Scymnosaurus* sp. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1929. Proximal end of a large femur.

Historical

Hitherto little was known of the postcranial skeleton of the Pristerognathidae.

In 1929 Broom published a figure of the shoulder girdle of *Pristerognathus minor* as seen in ventral view. Broom does not state on what specimen this restoration was based and I have not been able to trace the specimen. In the sequel I am reproducing figures (fig. 2) of the pristerognathid pectoral girdle drawn from a model I have carved out of a rectangular block of plaster which has enabled me to be quite sure that the lateral, anterior and ventral views are really at right angles to each other. My ventral view differs considerably from that given by Broom, particularly in the disposition of the scapulo-coracoid.

In 1932 Broom published as a front view of the pelvis of a therocephalian (possibly *Pristerognathus minor*) what is in fact a ventral view, but again I have not been able to trace the specimen on which the drawing was based.

The specimen on which Seeley founded *Theriodesmus phylarcus*, from the *Endothiodon* zone, has by some recent compilators been referred to the Pristerognathidae. Comparison with the pristerognathid material described in this paper shows that *Theriodesmus* is not a therocephalian at all, but really a gorgonopsian.

General Morphology

Pectoral Girdle (fig. 2)

This general account is compiled from facts derived from 18 specimens representing 6 pristerognathid genera described in the systematic part of this paper. The material as a whole is not well preserved and in even the best specimens the constituent bones have been displaced relative to each other and distorted mostly by dorso-ventral compression. The reconstructions presented here in semi-diagrammatic form have been drawn from a composite model carved out in a block of plaster.

As in all primitive reptiles the pectoral girdle is composed of 11 bones—one unpaired and five paired, but in no case is the cleithrum preserved and its presence is only indicated by the facet on the scapula to which it was applied. There is no ossified sternum.

The girdle consists of two sets of bones—replacement and dermal bones. The replacement bones, forming the so-called scapular girdle, form a scapulo-coracoid composed of a dorsal plain blade-like scapula, lying practically vertically but curving slightly round the thorax, and a ventral antero-posteriorly elongated coracoidal plate, composed of a large precoracoid and a smaller posterior coracoid, curving gently inwards towards the middle line. The pair of scapulo-coracoids are held in position relative to each other by their connexion

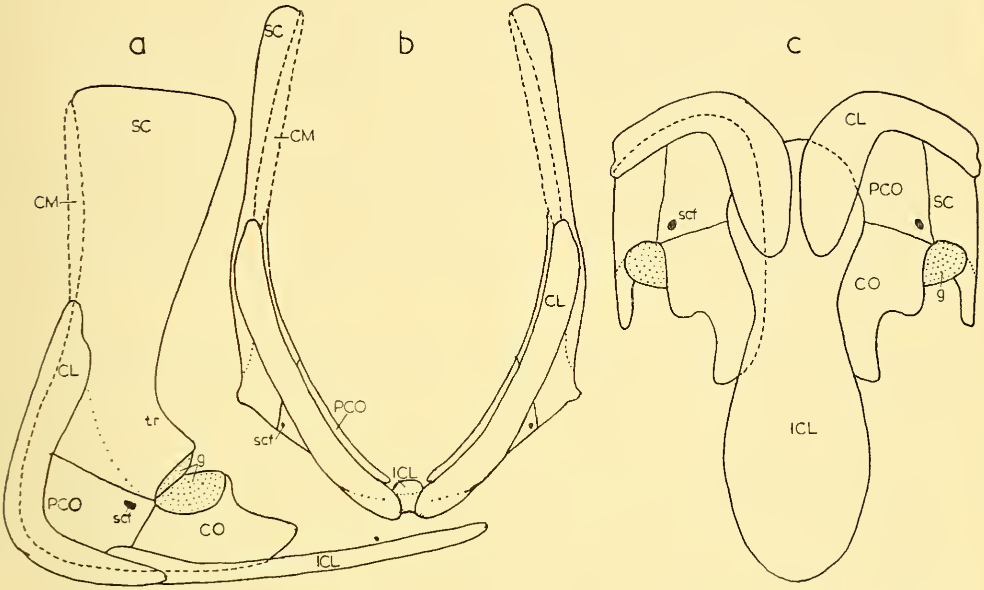

FIG. 2. Diagrams of the pristerognathid pectoral girdle drawn from a model based on a number of specimens. *a*, lateral. *b*, anterior. *c*, ventral.

CO—coracoid (posterior). CL—clavicle. CM—cleithrum. g—glenoid. ICL—interclavicle. PCO—precoracoid (anterior). SC—scapula. scf—foramen supracoracoideus. tr—origin of the scapular head of the m. triceps (in *Zinnosaurus* the origin is from a distinct tubercle).

with the clavicular girdle of dermal bones consisting of an unpaired medially disposed interclavicle and a pair of bracing clavicles. Ventrally the coracoidal plate rests on the upper face of the interclavicle. Ventrally the spatulate end of each clavicle curves below around the anterior end of the interclavicle to fit into an oval hollow on the under face of this bone. Dorsally the stem of the clavicle sweeps upwards externally of the anterior end of the precoracoid and the lower part of the scapula and is then applied to the anterior edge of the scapular blade. Here it meets the cleithrum which is in all probability a splint-like bone applied to the upper anterior scapular edge.

On the posterior border of the scapulo-coracoid, at the junction of the scapular and the coracoid, lies the simple, antero-posteriorly shortened, glenoid cavity. The glenoid has a dorsal scapular facet which faces ventro-posteriorly and but slightly externally, and a ventral coracoid facet which faces dorso-externally and slightly posteriorly. The nature of the glenoid cavity prevents the humerus from assuming any appreciable downward disposition and also limits an anterior disposition, but it can be freely directed upwards and backwards.

The area of origin of the scapular head of the triceps muscle from the postero-lateral surface of the scapula above the glenoid is very indistinct, except in one specimen, the type of the new genus *Zinnosaurus*, where a prominent tubercle is developed very similar to that present in the anteosaurian dino-cephalian genus, *Eccasaurus*. On the anterior edge of the scapula there is no indication of an incipient acromion process. The scapula blade is flat with no indication of any spine.

The precoracoid takes no part in the formation of the glenoid cavity and just enters into its anterior rim. Immediately anterior to this lies the foramen supracoracoideus. The anterior extent of the precoracoid is great, forming a large surface for the origin of the m. supra-coracoideus. Above the precoracoid lies the thin anterior plate of the scapula from whose outer face the m. scapulo-humeralis originates.

The coracoid is a smaller but more heavily built bone than the precoracoid, with a large strong glenoid facet. There is no special process as in the pelycosaurs for the origin of the coracoidal head of the triceps and this head was probably absent.

The clavicle of the pristerognathids is very distinctive, differing greatly from both that of the more primitive pelycosaurs and of the other contemporary therapsids. It is peculiar in that the ventral spatulate end curving round to the under face of the interclavicle is sharply bent backwards and extends far posteriorly along the under face of the interclavicle. The dorsally sweeping stem is also relatively stronger.

The interclavicle is a long, well-developed bone with the anterior spatulate end rounded in outline, not much expanded laterally and curving upwards only very slightly. In these features it differs markedly from the interclavicle in both pelycosaurs and the other therapsid contemporaries.

The cartilaginous sternum presumably lay above the spatulate posterior end of the interclavicle and extending to the coracoids.

Humerus (fig. 3)

A dozen fairly complete humeri and numerous proximal and/or distal ends are available for study, but bad preservation due to both erosion and post-mortem deformation makes it difficult to get a good picture of the nature of the pristerognathid humerus. It is particularly difficult to determine the angle subtended by the proximal and distal ends and thus the rotation on the shaft.

The pristerognathid humerus varies from a fairly light bone with moderately expanded ends and a fairly long and slender shaft to a moderately heavy bone with greatly expanded ends and a short thickened shaft. The rotation of the ends on the shaft apparently varies from 10° to 25°.

The proximal surface has the processus medialis and processus lateralis indistinctly demarcated from the caput which is narrowly oval in outline. The facet of the caput curves a little on to the dorsal surface of the humerus. The delto-pectoral crest is fairly weak and this subsides into the shaft without continuing as an oblique ridge in the direction of the entepicondylar foramen.

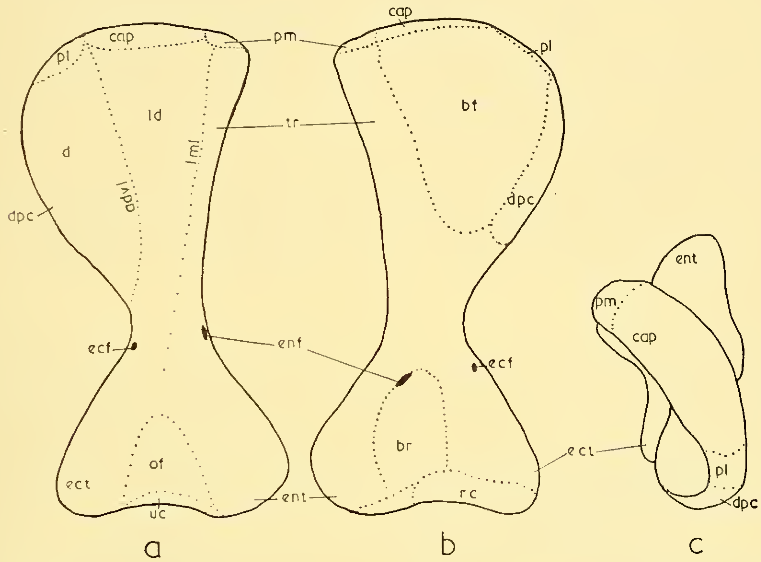

FIG. 3. Diagrams of the pristerognathid humerus. *a*, dorsal. *b*, ventral. *c*, proximal.

advl—anterior dorso-ventral line. bf—bicipital fossa. br—origin of the m. brachialis. cap—caput humeralis. d—insertion of the m. deltoideus. dpc—delto-pectoral crest. ect—ectepicondyle (radial). ecf—ectepicondylar foramen. ent—entepicondyle (ulnar). enf—entepicondylar foramen. ld—insertion of the m. latissimus dorsi. lml—latero-medial line. of—fossa for olecranon (trochlear). pl—processus lateralis. pm—processus medialis. rc—radial condyle or capitellum. tr—origin of the medial head of the triceps. uc—ulnar condyle.

The bicipital fossa is deep with a strong rounded posterior rim whose posterior face forms a rectangular area for the origin of the medial head of the triceps.

The proximo-dorsal surface of the humerus is divided by the anterior dorso-ventral line (ADVL) into two parts. Anteriorly (preaxially) to this line lies the roughly triangular surface for the insertion of the m. deltoideus. On the surface posterior (postaxially) of the ADVL there is a weak oblique latero-median line (LML). Anterior to this line the area of insertion indicates a strong m. latissimus dorsi. Posterior to the LML a well-developed rectangular area indicates the origin of a strong medial head of the m. triceps.

Distally the epicondyles are usually moderately developed, except in *Zinnosaurus*, where the epicondyles have widely expanded thin flanges of bone. In this genus the ectepicondyle, which is fused to a well-developed supinator flange, forms a widely expanded thin sheet of bone. A rounded foramen pierces the supinator-ectepicondylar flange obliquely. The entepicondyle in this form forms an extensive distal sheet of bone indicating well-developed flexors.

Distally the condyles are weakly developed. This is particularly so in the case of the radial condyle whose articulatory face lies practically wholly distally with hardly any ventral surface and no indication of a ventral bulbous swelling (capitellum) as is present in most of the contemporary therapsids. On the dorso-distal surface the trochlear fossa is shallow, which is related to the virtual absence of an olecranon on the ulna.

The elbow joint in the pristerognathids thus differs markedly from that of the other therapsids.

The distal position of the distal humeral condyles makes a more upright dispostion of the limb possible. With the weak development of the olecranon a deep trochlear fossa is not necessary for the extension of the epipodial.

Ulna and Radius (fig. 4)

The pristerognathid ulna has its proximal end greatly expanded. Proximally the lateral corner is developed into a short but thickened olecranon with a rugose surface for the reception of the m. triceps. The sigmoid face for the reception of the humerus is shallow but the coronoid process is well developed. Dorsally the sigmoid rim is concave to receive the head of the radius, and the sigmoid face of the ulna and the proximal face of the radius form a common articulatory facet for the reception of the humerus. This facet is shallow and, the humerus having hardly a capitellum, the elbow joint forms a poor hinge joint.

The sigmoid face of the ulna lies on the proximal end of the bone and the coronoid process on the medial edge is also proximally situated, so that in the elbow joint the propodial and epipodial meet end-on without the ulna curving round the distal end of the humerus.

Carpus and Manus (fig. 4)

The proximal row of carpals consists of three elements—a robust radiale, a lighter elongated ulnare and a small laterally compressed intermedium. A pebble-like pisiforme lies laterally of the ulna-ulnare articulation.

In the middle row there are two centrals—one lying between the radiale and the first and second distals, the central one lying wedged in between the ulnare and radiale and distally articulated with the third distal.

There are four distals—the fourth and fifth are fused and articulate with the fourth and fifth metacarpals.

The metacarpals are well developed—the first is very short and looks very much like the first phalanx, the second is nearly twice as long as the first, the third about $2\frac{1}{2}$ times as long, the fourth 3 times as long and the fifth just over 3 times as long. The phalangeal formula is 2, 3, 3, 3, 3. The proximal phalanges are all fairly short and robust and there is no indication of any further reduction. The ungual phalanges carried talon-like claws and have a ventral thickening proximally.

The first digit is the shortest, then come the second and fifth of equal length, then the third and fourth which are again of equal length.

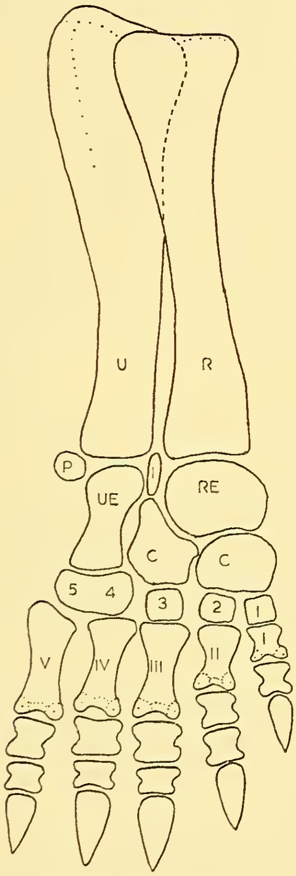

FIG. 4. Diagram of the pristerognathid epipodial and manus in dorsal view.

C_1, C_2—centrals. I—intermedium. P—pisiforme. R—radius. RE—radiale. U—ulna. UE—ulnare. 1–5—distals. I–V metacarpals.

The purchase of the forefoot on the ground is thus more meso-post-axonic than pre-axonic.

The digits as a whole are short and the metacarpals and carpus in comparison long. The manus can be considered semi-digitigrade.

Pelvic Girdle (fig. 5)

Pelves are not well represented and this account is compiled from half a dozen specimens representing four genera.

The pelvis is much lower than the pectoral girdle and the pubo-ischiadic plate shorter than the interclavicle, but longer than the coracoidal plate.

The three bones of each side are not firmly ankylosed and the junction between the two sides is weak between the pubis but stronger at the ischiadic keel.

The acetabulum is large and nearly circular in outline; all three bones take part, with the ilium contributing about half. The acetabulum faces mainly outwards; it is shallow, with strong rims for the attachment of the joint capsule

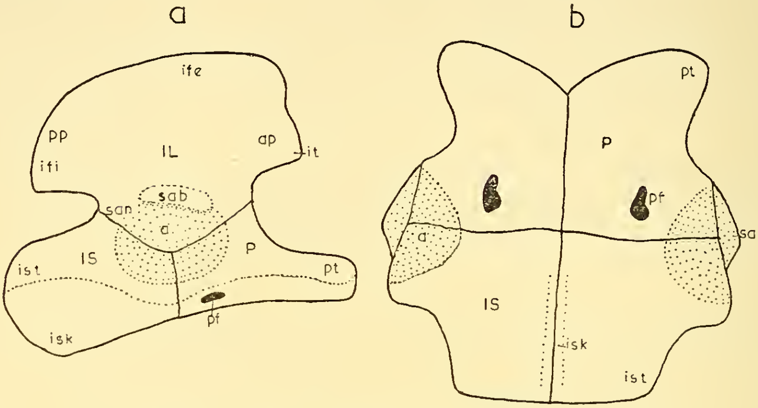

FIG. 5. Diagram of the pristerognathid pelvis. *a*, lateral. *b*, ventral.

a—acetabulum. ap—anterior process of the iliac blade. ife—area of origin of m. ilio-femoralis. ifi—area of origin of m. ilio-fibularis. it—area of origin of m. ilio-tibialis. IL—ilium. IS—ischium. isk—ventral keel of the ischia. ist—ischial tuber. P—pubis. pf—pubic foramen. pp—posterior process of the iliac blade. pt—pubic tuber. sab—supra-acetabular buttress. san—supra-acetabular notch.

and ligaments. Dorsally lies a strong supra-acetabular buttress formed by the ilium, overhanging the acetabulum and forming the main attachment of the joint capsule. At the dorso-posterior corner of the acetabulum, just posterior to the buttress, lies the supra-acetabular notch.

At the level of the iliac buttress the iliac blade is antero-posteriorly expanded to form a high anterior and a somewhat lower posterior process. In most specimens the anterior process is much shorter than the posterior process, but in two specimens the lower corner of the anterior process is prolonged to form a long but weak process. In the other specimens there is an indication of this process. More and better-preserved specimens may prove that this elongation is normal for the family. The outer face of the iliac blade is both dorso-ventrally as well as antero-posteriorly convex. In antero-dorsal direction runs a shallow groove and near the dorsal edge in a vertical line with the posterior end of the buttress there is also a slight hollow. One can thus speak of an undulating surface. There is no eversion of either anterior or posterior edges. The areas of origin of the ilio-fibularis, ilio-femoralis and ilio-tibialis are thus indefinitely determinable.

The ischium in its acetabular part is massive and forms here, the strongly thickened postero-ventral segment of the strong acetabular rim. From here it tapers posteriorly and forms a thickened upper edge but without a distinct ischial tuber. Extending medially the ventral surface is flattened anteriorly but just behind the junction with the pubis it carries a strong and prominent ventral keel.

The pubis in its acetabular part is fairly massive and here forms a fairly strong acetabular rim. From here it tapers anteriorly and forms a thickened lateral edge but without a marked pubic tuber. The ventral surface of the pubis is fairly flat. Just medial to the acetabular rim, near its posterior edge, lies a well-developed pubic foramen.

The pubo-ischiadic plate is broad and large as in the pelycosaurs, the antero-posterior dimension of the pubis being relatively larger than in other therapsids and both anterior and posterior pelvic openings broad and not V-shaped as in other therapsids; but the posterior opening is incipiently V-shaped because of the ischial keel.

Femur (fig. 6)

The pristerognathid femur is represented in 20 specimens of 5 separate genera. Ten femora are fairly complete and there are a couple of dozen poor to good distal and proximal ends unconnected and usually lacking a shaft.

The femur, always longer than the humerus, is a fairly light bone with only slightly expanded ends and with a long, fairly slender shaft. There is a considerable twist on the shaft so that the proximal head and the distal condyles subtend an angle of 30°–40°. The distal preaxial condyle lies a little further ventrally than the postaxial distal condyle and a little proximal of its fellow.

The preaxial border is more concave than the postaxial border due to the femoral head being directed somewhat preaxially.

Proximally the caput femoris is terminal but somewhat preaxially directed; it is antero-posteriorly elongated, thick, preaxially with a rounded edge; postaxially it tapers and curves gently towards the external trochanter, into which it flows. In its thickened preaxial part the caput is convex and rounded in its postaxial part. The caput femoris is much smaller than the acetabulum.

The external trochanter forms the proximo-postaxial rounded corner of the femur; it flows with a rounded curve into both the caput and the postaxial edge.

On the dorsal proximal surface lies a well-developed ridge near the preaxial border of the femur; it lies parallel to the preaxial border and commencing from the caput runs for a short distance distally and then fades away. This ridge serves as the area of insertion of the m. pubo-ischio femoralis internus. Between this ridge and the external trochanter lies the area of insertion of the m. ilio-femoralis.

On the ventral proximal surface a sharp, prominent longitudinal ridge is developed. Lying in the middle of the bone, it commences a short distance distally of the caput and extends distally for a variable distance to fade away into the general ventral face of the shaft. This ridge is the only part of the primitive Y system of adductor ridges preserved in the pristerognathids and represents an internal trochanter.

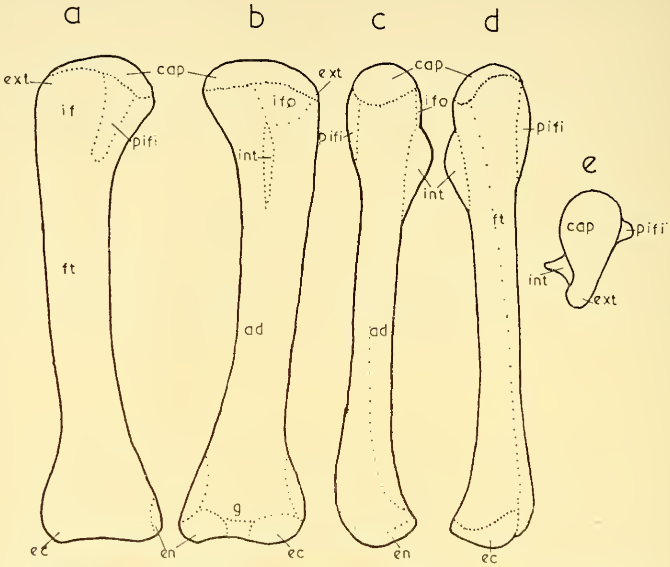

Fig. 6. Diagrams of the pristerognathid femur. *a*, dorsal. *b*, ventral. *c*, anterior. *d*, posterior. *e*, proximal.

ad—insertion of adductor muscle. cap—caput femoris. ec—ectocondyle. en—entocondyle. ext—external trochanter (major). ft—origin of m. femoro-tibialis. g—origin of the gastrocnemius. if—insertion of the m. ilio-femoralis. int—internal trochanter. ifo—intertrochanteric fossa. pifi—ridge on which is inserted the m. pubo-ischio-femoralis internus.

Between the internal and external trochanters lies a relatively small intertrochanteric fossa.

The distal condyles lie terminally facing very slightly ventrally and are well modelled. The intercondylar sulcus is very shallow. Dorsally the intercondylar fossa is very shallow, but ventrally the gastrocnemic fossa is quite well developed.

Tibia, Fibula and Pes (fig. 7)

The posterior epipodial and pes are not as well represented in the material at my disposal as the corresponding structures of the forelimb.

The posterior epipodial is longer than the anterior one, as we have already seen is also the case in regard to the propodial.

Both tibia and fibula are lightly built, slender bones, lighter and slenderer than the radius and ulna. In both epipodials the pairs of bones are approximately of equal length. Proximally the tibia and fibula form a common terminal articular facet to meet the femoral condyles end on. Distally the tibia articulates with a rounded face on the astragalus and the fibula with an elongated facet on the proximal end of the calcaneum.

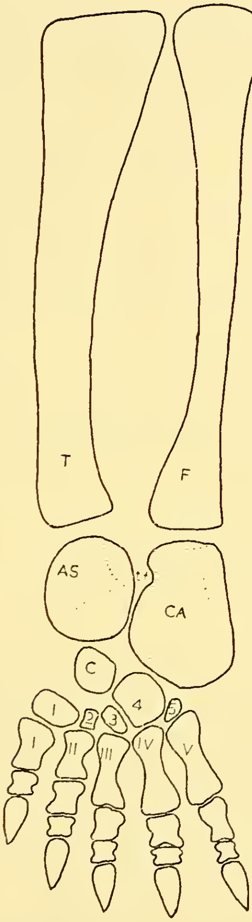

FIG. 7. Diagram of the pristerognathid epipodial and pes in dorsal view. AS—astragulus. CA—calcaneum. C—central. F—fibula. T—tibia. tf—tarsal foramen. 1–5—distals. I–V—metatarsals.

As in pelycosaurs and therapsids generally the pristerognathid tarsus has a pair of proximal elements—an astragalus and a calcaneum.

The astragalus is a robust, roughly ovoid bone with a rounded face for articulation with the tibia; laterally it has an elongated facet articulating with the calcaneum and distally a curved facet facing the centrale.

The calcaneum is a larger but more lightly built bone. It is a sheet of bone, thickened proximally to form an elongated facet for the reception of the fibula and with a thickened medial edge abutting against the astragalus, but notched for the passage of the penetrating tarsal vessels, and thickened distally where it carries a facet to receive the fourth distal carpal. There is no indication of a tuber-like heel.

One fairly small centrale is present. There are five distal tarsals, but in one specimen the small fifth distal is fused to the large fourth distal as is usual in therapsids.

The fourth distal is always large; the third and second distals, when well developed, have flattened upper faces and are roughly squarish in outline; the first distal is usually large, articulating with both first and second metatarsals, but in one specimen it is a small, pebble-like bone.

The first metatarsal is a short, fairly squat bone, the second, also short, has a more constricted shaft; from the third to the fifth the metatarsals become progressively longer with well-expanded ends.

The digits are, as in the manus, short, with the phalangeal formula 2, 3, 3, 3, 3. The first phalanx in all the digits is usually fairly long, but in one specimen that of the first digit and in another that of the fifth digit is greatly shortened, being disc-like without a constricted waist.

The second phalanx of the second to the fifth digits is short with a constricted waist.

The terminal phalanges are long, curving, claw-like. The first digit is short and the other four of about equal length. The purchase of the hind foot thus lies in the postaxial part of the foot.

Systematic Descriptions of Specimens

A. PECTORAL GIRDLE

Alopecognathus (figs. 8–10)

The specimen 12051 includes a scapular blade; K339 has a nearly complete scapula; K223A and K223B each consists of a fairly complete girdle, but both lack the scapular blades and the upper part of the clavicles and have undergone distortion and displacement of the constituent elements; K231 includes a nearly complete girdle, but is distorted by dorso-ventral compression. In the accompanying figures the distortion has been corrected and the symmetry restored. In none of these is the cleithrum preserved.

The girdle is a structure of considerable size; high, broad, with its ventral element—the interclavicle—long. The scapula, as restored, is dorsally directed or is tilted slightly backwards and curved slightly to follow the contour of the thorax. The area of origin of the scapular head of the triceps is indistinct—there is no ridge, mound or tubercle. The coracoidal plate is long, but in two specimens the anterior edge of the procoracoid is concave, whereas in the other it forms an even convex curve. The clavicles have a long, posteriorly directed ventral spatulate end in two specimens, whereas in another this part of the clavicle is quite short. The interclavicle is large, with a rounded anterior

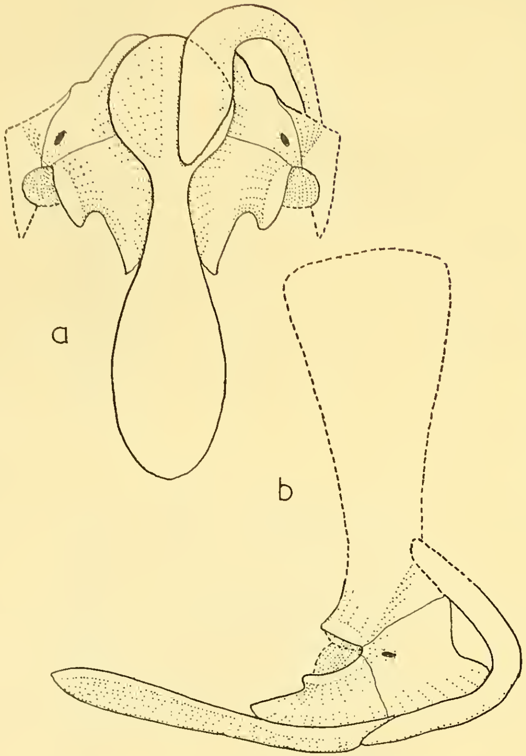

Fig. 8. *Alopecognathus angusticeps* ? S.A.M. K223A. $\times\frac{1}{3}$. Pectoral girdle. *a*, ventral. *b*, lateral.

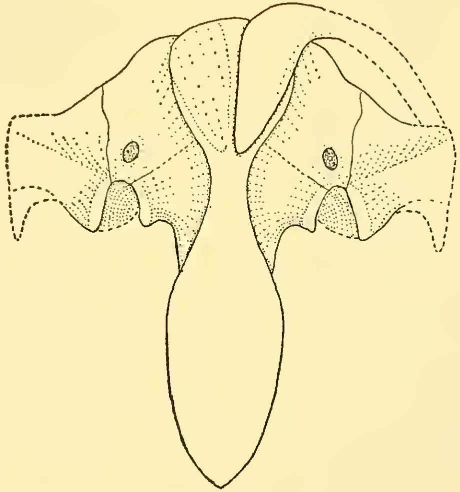

Fig. 9. *Alopecognathus angusticeps* ? S.A.M. K223B. $\times\frac{1}{3}$. Pectoral girdle in ventral view.

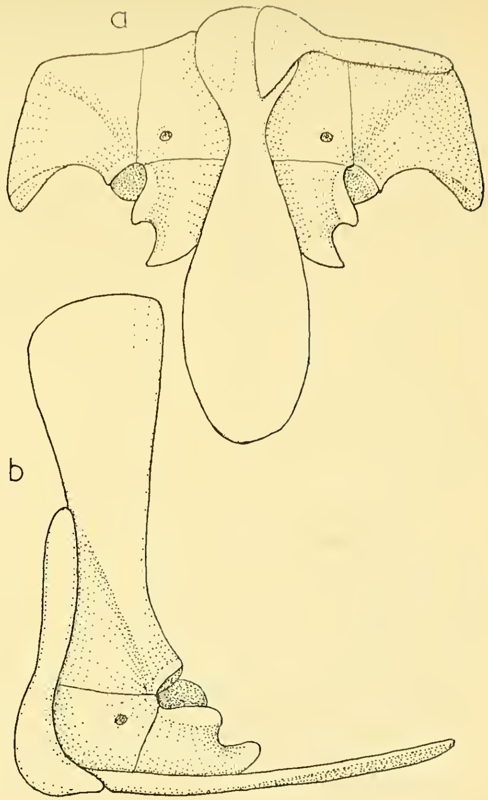

Fig. 10. *Alopecognathus angusticeps*. S.A.M. K231 $\times\frac{1}{3}$. Pectoral girdle. *a*, ventral. *b*, lateral.

expansion and a long broad posterior spatula joined by a fairly narrow neck at the level of the posterior coracoids.

Priesterognathoides (figs. 11 and 12*a*)

In 12102 the right half of the pectoral girdle is preserved together with an incomplete interclavicle and parts of the left half of the girdle. The girdle is partially disarticulated but only slightly distorted in its fall backwards when the soft tissues decomposed.

In 12204 a disarticulated girdle has a good scapula, coracoid, procoracoid, interclavicle and the ventral spatulate ends of the clavicles.

The scapula is apparently tilted somewhat backwards and shows a marked curvature around the thorax. No origin of the triceps can be determined and there is definitely no tubercle. The coracoid is short, but the procoracoid well developed. The interclavicle is very similar to that of *Alopecognathus*.

Pristerognathus (fig. 12*b* and *c*)

In 4335 there are a pair of incomplete scapulo-coracoids. The coracoid is short and the procoracoid well developed. No scar or tubercle for the scapular

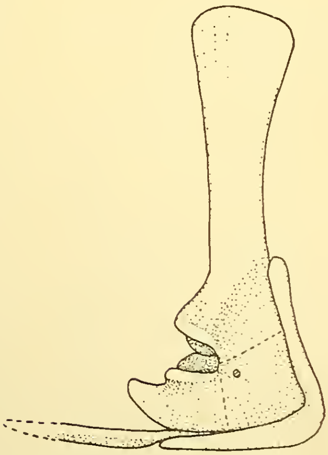

FIG. 11. *Pristerognathoides sp.* S.A.M. 12102. × $\frac{1}{3}$. Pectoral girdle in lateral view.

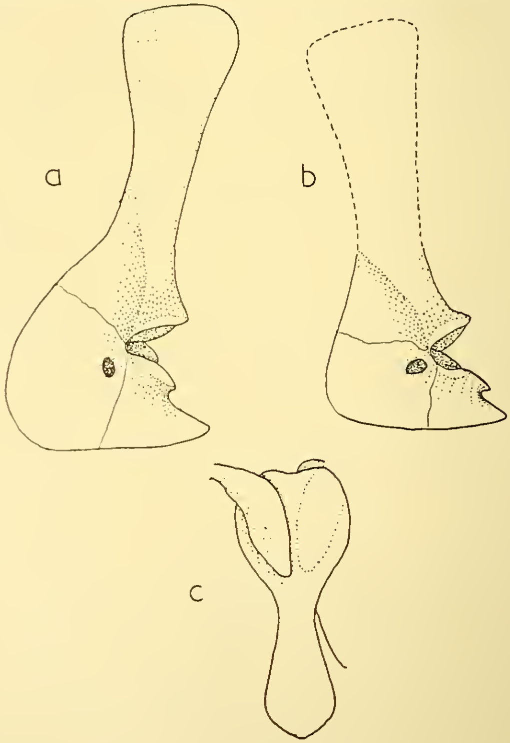

FIG. 12. Pectoral girdles. × $\frac{1}{3}$. *a*, *Pristerognathoides* sp. S.A.M. 12204 in lateral view. *b*, *Pristerognathus* sp. S.A.M. 4335 in lateral view. *c*, *Pristerognathus* sp. S.A.M. 11458 in ventral view.

head of the triceps can be traced. In 11458 there is a good interclavicle which has a large anterior expansion, but the posterior spatula is only slightly expanded. The ventral spatulate ends of the clavicles extend well posteriorly. The procoracoid extends anteriorly of the interclavicle.

Scymnosaurus (figs. 13–17)

Five specimens have parts of the pectoral girdle preserved. 8034 and 12193 have a well-preserved coracoid each. Both are massive, and that of 12193 is probably of *S. major*. In the type specimen of *S. major* (9005) there are the anterior two-thirds of a large interclavicle and the ventral spatulate ends of both clavicles, which, though massive, have relatively a short posterior extent. In 11557 there are a disarticulated scapula, interclavicle and clavicle. The scapula is robust but short; the glenoid facet faces much posteriorly and laterally; the facet for the cleithrum is clearly shown, but the origin of the scapula head of the triceps is from the smooth postero-lateral surface just above the glenoid.

A left clavicle is stoutly built; the dorsal end clasping the anterior border of the scapula is expanded and strong. The ventral spatulate end is large and extends far posteriorly along the circular head of the interclavicle. Both the articulating surface of the clavicle as well as the hollowed face on the inter-

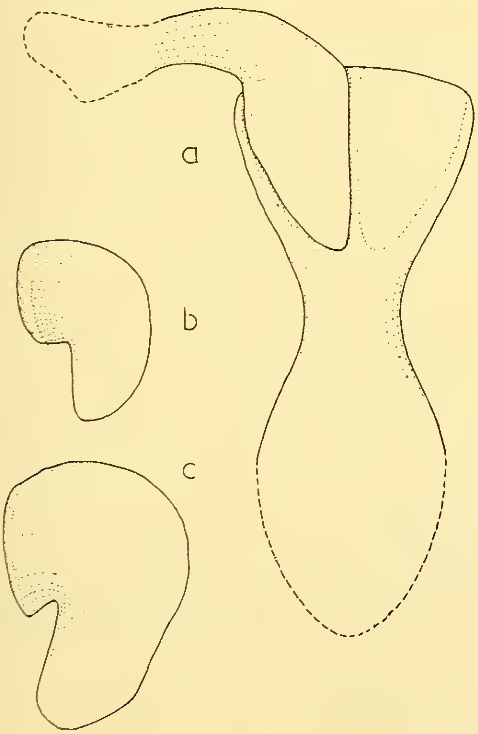

FIG. 13. Bones of pectoral girdles. × $\frac{1}{3}$. *a*, *Scymnosaurus major*. S.A.M. 9005. Type. Ventral view of interclavicle and clavicle. *b*, *Scymnosaurus ferox*. S.A.M. 9084. Right coracoid in ventral view. *c*, *Scymnosaurus* sp. S.A.M. 12193. Right coracoid in ventral view.

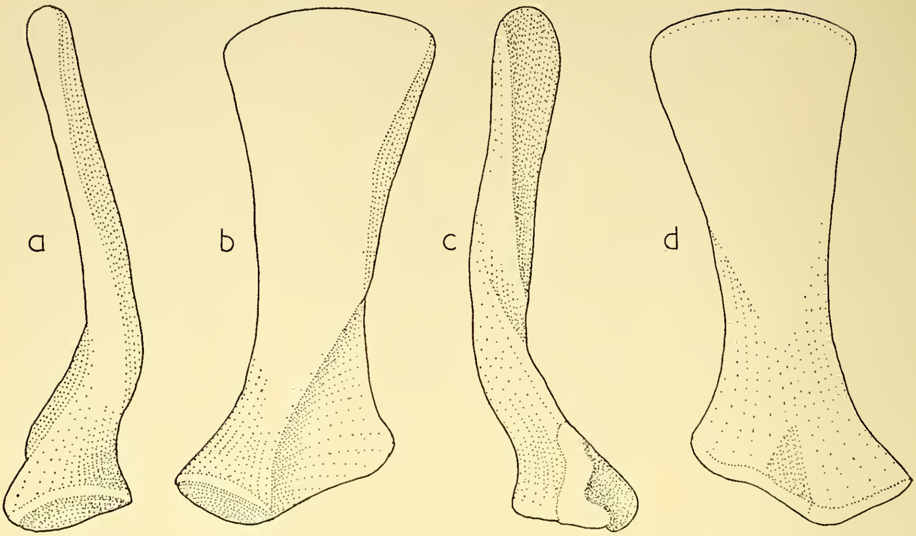

Fig. 14. Right scapula of *Scymnosaurus* sp. S.A.M. 11557. × ⅓. *a*, posterior. *b*, lateral. *c*, anterior. *d*, internal.

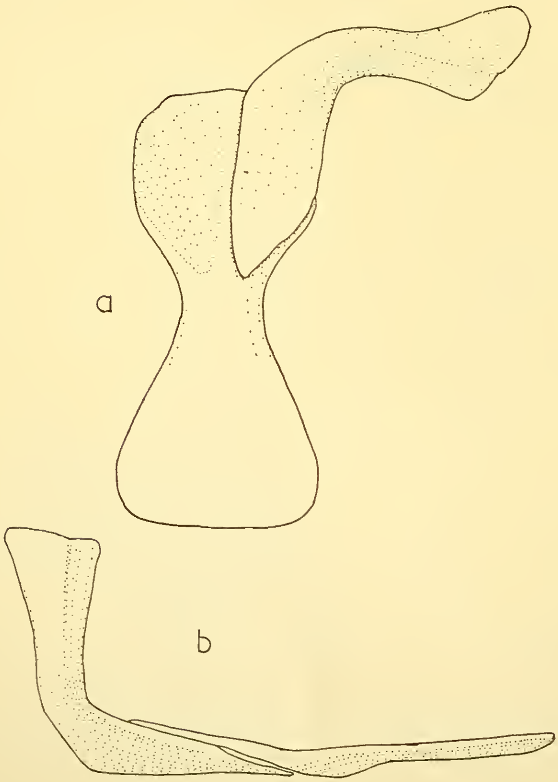

Fig. 15. *Scymnosaurus* sp. S.A.M. 11557. × ⅓. Clavicle and interclavicle. *a*, ventral. *b*, lateral.

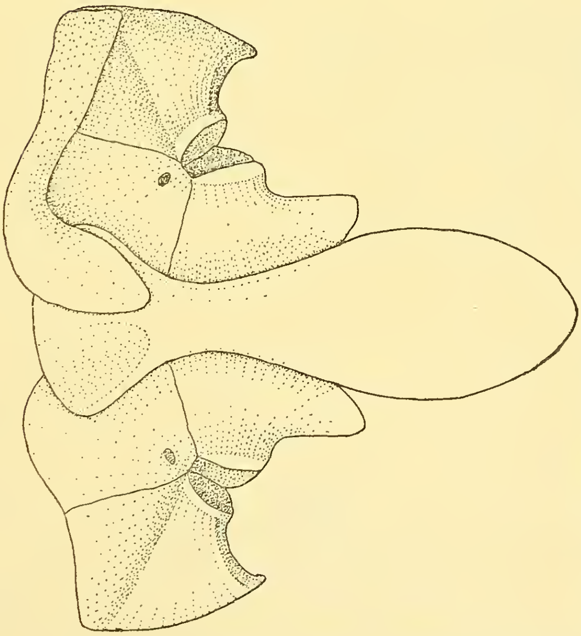

Fig. 16. *Scymnosaurus* sp. S.A.M. 11695. $\times\frac{1}{3}$. Ventral view of pectoral girdle.

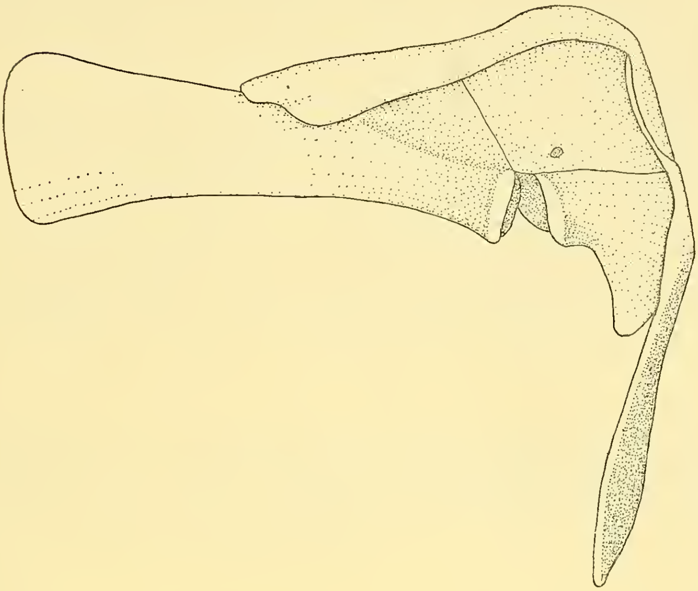

Fig. 17. *Scymnosaurus* sp. S.A.M. 11695. $\times\frac{1}{3}$. Lateral view of pectoral girdle.

clavicle bear longitudinal striae, and the backward movement of the clavicle is limited by a thickened border on the clavicle which abuts against the anterior edge of the interclavicle. The dorsal stem of the clavicle and its ventral spatulate end subtend what is nearly a right angle.

The anterior end of the interclavicle is large and nearly circular in outline, and a strong median ridge separates the two facets for the clavicles. The posterior end is greatly expanded but short, and is remarkably lightly built.

In 11695 there is a fairly complete shoulder girdle, but with the constituent bones displaced and distorted by dorso-ventral pressure. The anterior head of the interclavicle and ventral spatula of the clavicle are both relatively smaller than in 11557, and the dorsal stem of the clavicle is longer and more slender, with a bifurcated end. The scapular blade is fairly tall but is relatively lightly built.

Therioides (fig. 18)

In 11888, the holotype specimen, much of the pectoral girdle is preserved, but here again disarticulation and distortion have made reassembly and restoration of symmetry, as shown in the figures, difficult. The girdle is very like

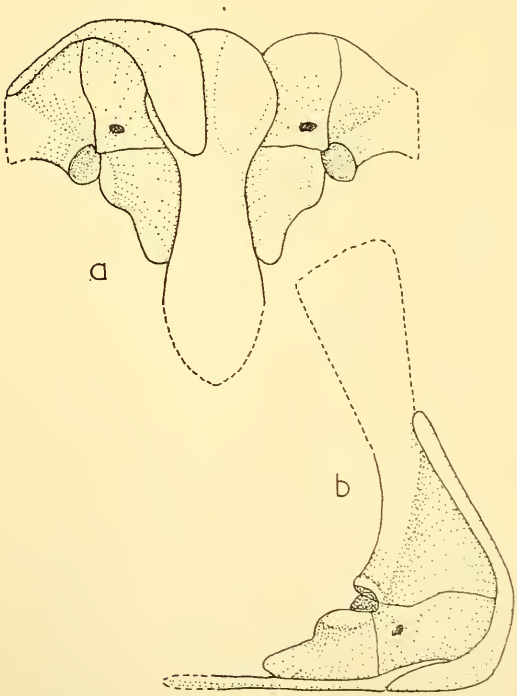

Fig. 18. *Therioides cyniscus*. Pectoral girdle. S.A.M. 11888. Type. $\times\frac{1}{3}$. *a*, ventral. *b*, lateral.

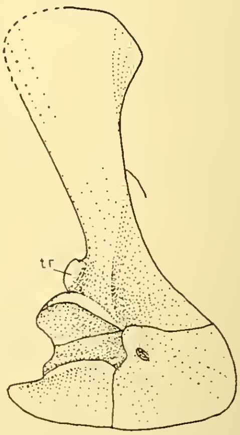

Fig. 19. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. Type. $\times\frac{1}{3}$. Lateral view of scapulo-coracoid.

that in *Alopecognathus*, but smaller and of a lighter build, with a proportionately large anterior expansion of the interclavicle.

Zinnosaurus paucidens gen. et spec. nov. (fig. 19)

In 12185, the holotype specimen, there is a well-preserved right scapulo-coracoid without scapular blade, and a left scapular blade. This scapulo-coracoid differs very markedly from all those hitherto considered. The scapular blade has its upper anterior part expanded and on this outer face lies a facet for the upper end of the cleithrum; lower down the cleithrum is applied to the anterior edge of the scapula.

Immediately above the upper rim of the glenoid there lies a process on the posterior face of the scapula for the origin of the scapular head of the triceps. This process forms a strong, prominent flange of bone, laterally compressed and dorso-ventrally elongated.

The glenoid is a widely open cavity facing largely outwards. Both its dorsal scapular rim and ventral coracoidal rim are sharp and prominent. Anteriorly there is no rim on the procoracoidal border of the glenoid so that in its anterior movement the head of the humerus would ride in a broad groove.

The procoracoid extends far anteriorly.

B. HUMERUS

Alopecognathus (fig. 20)

In 12051 there is a good, apparently undistorted, proximal half of a humerus. In K231 both humeri are preserved but both are quite obviously distorted and in the figures I have tried to correct the distortion. The result is not very convincing and the two humeri have quite distinctive outlines.

In 12051 the central part of the caput quite definitely flows over onto the dorsal surface and this would obviously affect the nature of the shoulder joint

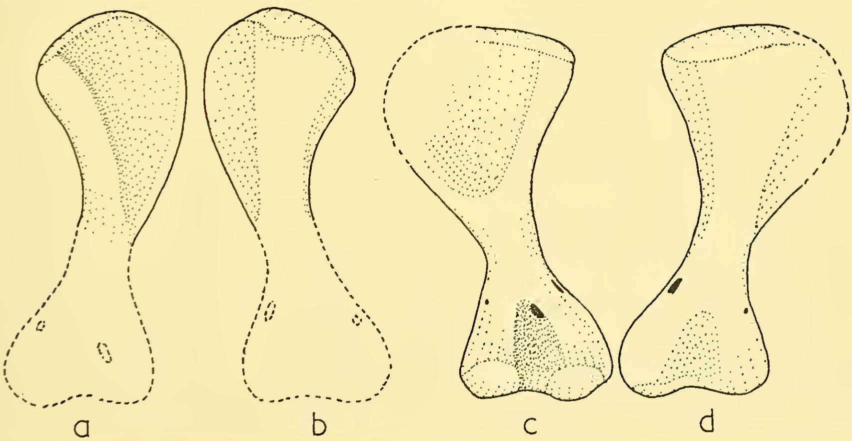

FIG. 20. *Alopecognathus angusticeps*. Humerus. × $\frac{1}{3}$. S.A.M. 12051 : *a*, ventral. *b*, dorsal. S.A.M. K231 : *c*, ventral. *d*, dorsal.

as the humerus would tend to be directed more horizontally. In K231 the caput is terminal. In 12051 the delto-pectoral crest is weak with little indication of the pectoralis insertion, and the processus medialis, caput and processus lateralis flow into one another.

In K231 the distal condyles are mostly terminal with only a little extension onto the ventral face. Both supra-trochlear fossa and brachialis fossa are deeply excavated. The radial condyle is not developed into a rounded capitellum.

Cynariognathus (fig. 21*a*)

In 11794 both humeri are imperfectly preserved. The bone is lightly built and the distal condyles mostly terminal without a bulbous capitellum.

Pristerognathoides (figs. 21*b*, *c* and *d* and 22)

In 5018 both humeri are incompletely preserved and in 12204 is a fairly good left humerus. In other specimens, e.g. 12102, only poorly preserved humeral ends are present. In 5018 the humerus is long, with both ends well expanded and the shaft slender. The caput, mainly terminal, curves slightly onto the dorsal surface. The distal condyles are a little ventral of terminal, and the capitellum is moderately swollen. I have not been able to locate an ectepicondylar foramen. In 12204 the ulnar condyle is separated from the olecranon fossa by a well-developed ridge which would appear to limit the extension of the epipodial. The delto-pectoral crest is weak and the area for the insertion of the deltoideus small.

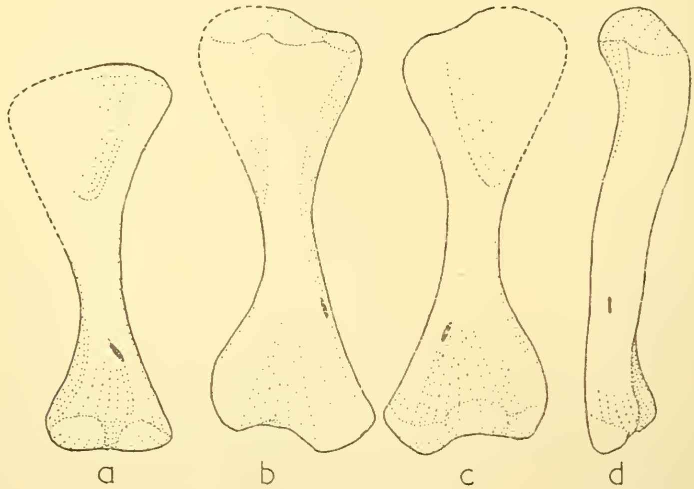

FIG. 21. Humerus. $\times\frac{1}{3}$. *Cynariognathus* sp. S.A.M. 11794. *a*, ventral. *Pristerognathoides* sp. S.A.M. 5018. *b*. dorsal. *c*, ventral. *d*, posterior.

Pristerognathus

A number of humeral ends of *Pristerognathus* are poorly preserved and warrant no description except to state that the humerus is very similar to that of *Pristerognathoides*—but smaller.

Ptomalestes (fig. 23)

In 11942, the holotype, both humeri are preserved. I am including figures of both the right and left humerus which show how much they have suffered from post-mortem distortion. If the distortion is corrected the humerus would be a fairly robust bone, moderately long with well-expanded proximal and

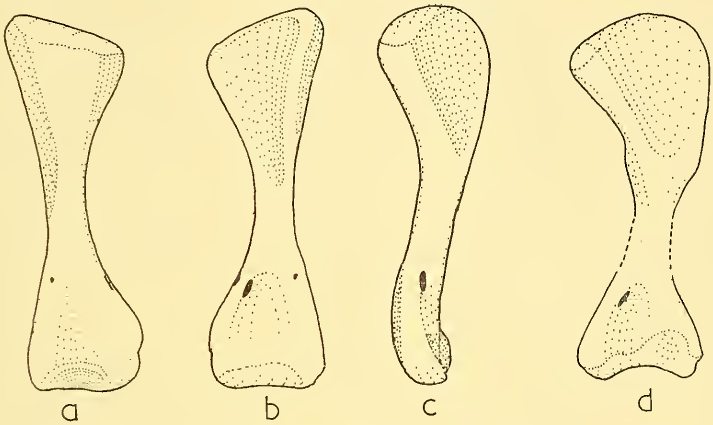

FIG. 22. Humerus. *Pristerognathoides* sp. S.A.M. 12204. ×⅓. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, S.A.M. 12102, ventral.

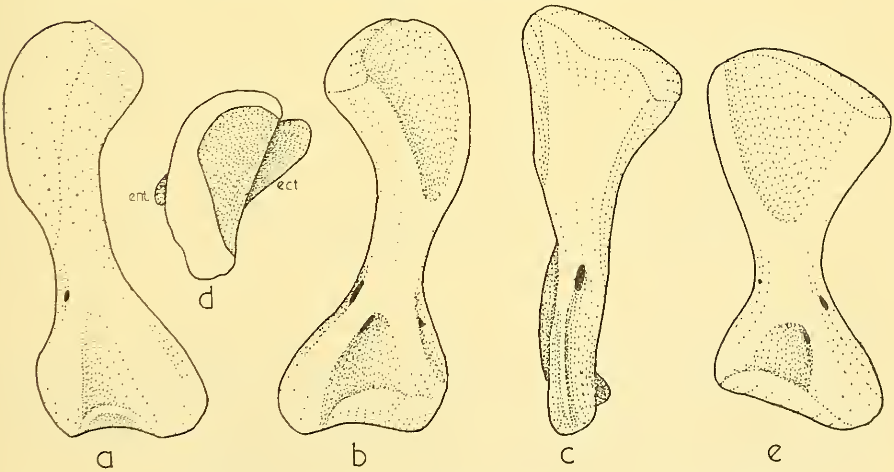

FIG. 23. Humerus. *Ptomalestes avidus*. S.A.M. 11942. Type. ×⅓. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, proximal. *e*, ventral of right humerus.

distal ends and a fairly short shaft; both caput and distal condyles are terminal, with the capitellum weak and little ventrally placed. A ridge separates the ulnar trochlea from the shallow supra-trochlear fossa.

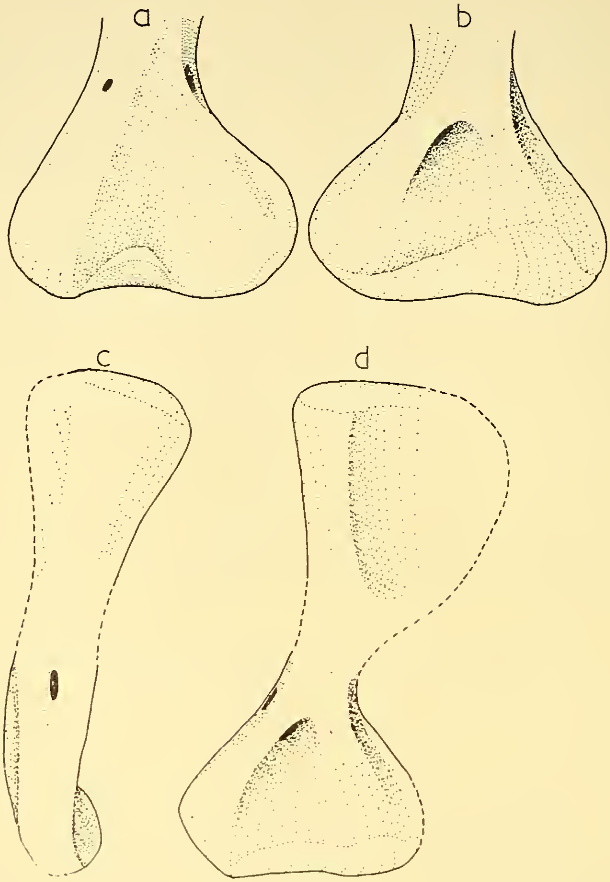

FIG. 24. Humeri. $\times \frac{1}{3}$. *Scymnosaurus major*. S.A.M. 9005. Type. *a*, dorsal. *b*, ventral. *Scymnosaurus ferox*. S.A.M. 9084. *c*, posterior. *d*, ventral.

Scymnosaurus (figs. 24–26)

Of this genus I have two very well preserved distal ends, and one good complete humerus, which I believe to be undistorted, and this specimen must be taken to give us the best idea of the pristerognathid humerus as represented by the largest genus of this family of primitive Therocephalia.

In 9005, the type specimen of *Scymnosaurus major*, the good distal humeral end is, considering the bulk of the animal, only moderately robust. The epi-

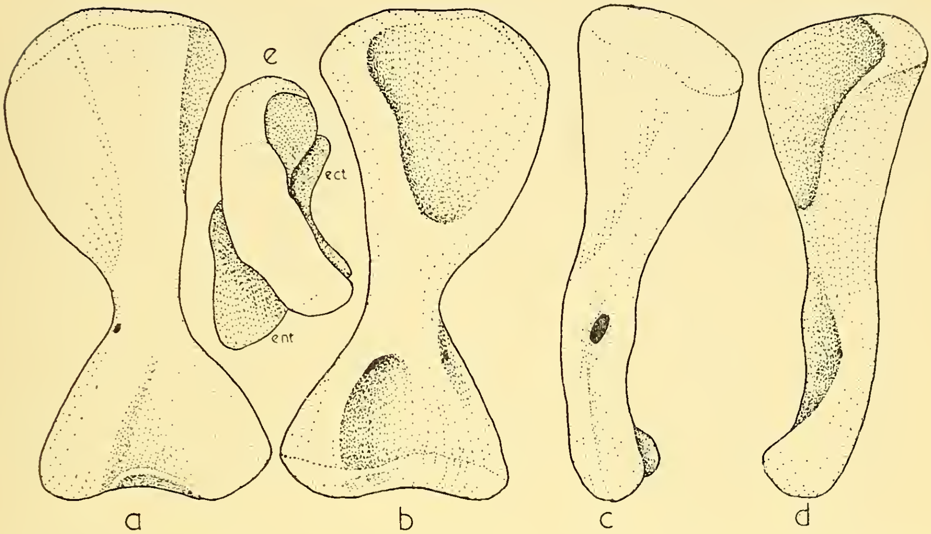

FIG. 25. *Scymnosaurus* sp. S.A.M. 11557. × ⅓. Humerus. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, anterior. *e*, proximal.

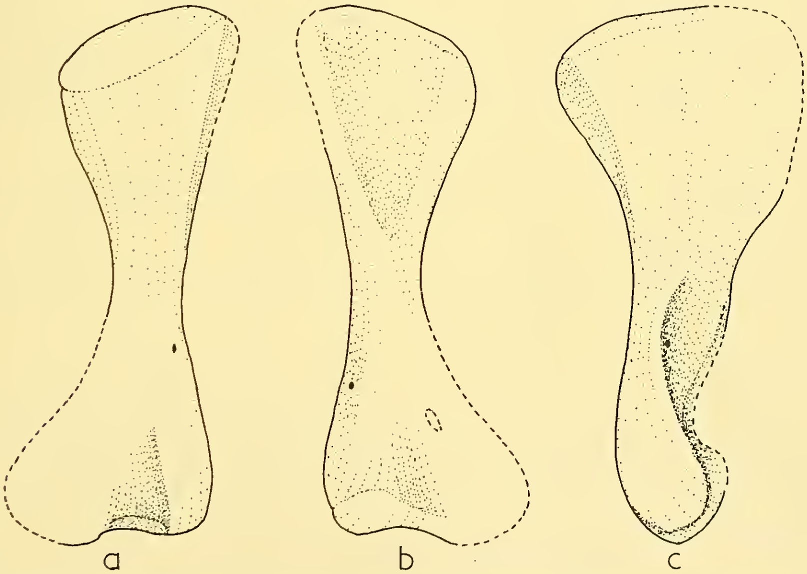

FIG. 26. *Scymnosaurus* sp. S.A.M. 11695. × ⅓. Humerus. *a*, dorsal. *b*, ventral. *c*, anterior.

condylar expansions are modest, with the confluent supinator flange and ectepicondyle slightly more prominent than the entepicondylar edge. The condyles lie chiefly terminal. The radial condyle forms only a weak capitellum, which only slightly enters the ventral surface. The ulnar condyle forms a shallow trochlea, which dorsally has a ridge separating it from the very shallow supra-trochlear fossa hardly functioning as an olecranon fossa. Ventrally there is hardly a coronoid fossa, but the large oval entepicondylar foramen opens into a deep hollow bounded postaxially by a strong rounded ridge. The distal epicondylar edges are strong but not much expanded and their rugose surfaces give a strong origin for the flexors and extensors. In 9084, which is smaller and lighter, being a humerus of the less bulky *Scymnosaurus ferox*, the ectepicondylar flange is more expanded and curves downwards to form a deep groove. In 11557, which is most probably also of *Scymnosaurus ferox*, there is a well-preserved left humerus. Its terminal distal condylar face is less rounded than in 9084 and has no capitellum to speak of, and in its postaxial part it is concave instead of convex, indicating the presence of considerable joint cartilege. Its ectocondyle is without the flange present in 9084. Its supratrochlear fossa is deeper than in 9084 with a strong preaxial border.

11557 is the only *Scymnosaurus* humerus with a good proximal two-thirds preserved. Ventrally the bicipital fossa is deep and well demarcated from the surface of the short shaft. The delto-pectoral crest is fairly strong but the pectoralis insertion is not localized but diffuse. The postaxial border of the bicipital fossa is formed by a robust rounded ridge which on its postaxial face gives a strong face for the origin of the medial humeral head of the triceps. Dorsally both the anterior dorso-ventral line and latero-medial line are moderately developed and the areas of insertion of the deltoideus, latissimus dorsi and both the scapulo-humeralis anterior and posterior are well developed.

Proximally the caput is terminal with only a slight extension onto the dorsal surface; it is a very flat oval and flows evenly into both the processus medialis and lateralis.

The incomplete humerus of 11695 shows a greater twist on the shaft but is otherwise very similar to that of 11557.

Therioides (fig. 27)

The one humerus known in the type, 11888, is fairly short with moderately expanded ends but otherwise shows no special features to distinguish it from those of the other medium-sized pristerognathids so far described.

Zinnosaurus gen. et spec. nov. (fig. 28)

In the type material (12185) there are a practically complete right humerus and the proximal half of the left humerus. Both have suffered from distortion. I am including figures of the right humerus with the distortion corrected.

The caput is strap-shaped but in its middle part tends to overflow slightly onto the dorsal face. The processus medialis and processus lateralis flow gently into the caput. The delto-pectoral crest is long, with its proximal edge thin and its distal end somewhat thickened for the reception of the pectoralis.

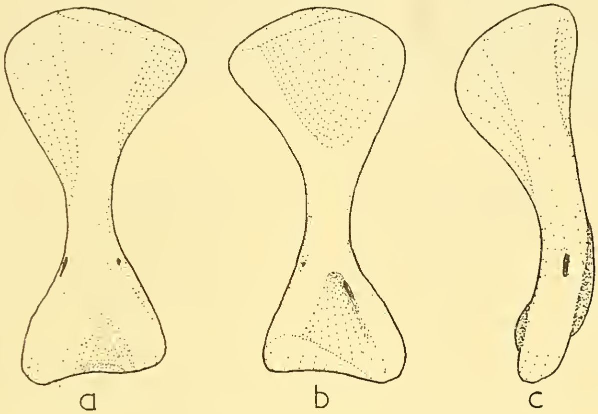

FIG. 27. *Theroides cyniscus*. S.A.M. 11888. Type. ×⅓. Humerus. *a*, dorsal. *b*, ventral. *c*, posterior.

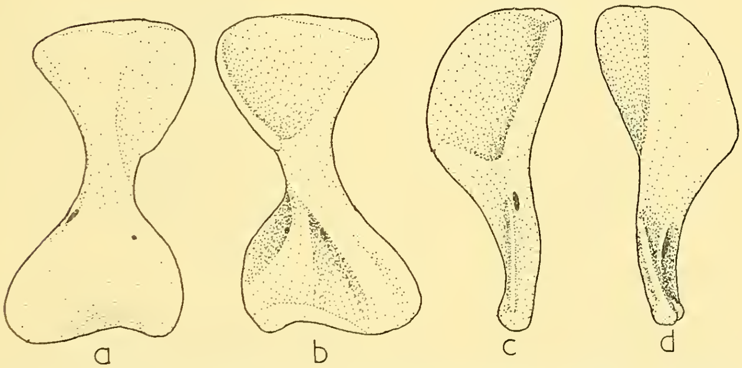

FIG. 28. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. ×⅓. Right humerus with distortion corrected. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, anterior.

The distal end is greatly expanded. This expansion is mainly due to the development in both epicondyles of thin sheets of bone. This is particularly so in the ectepicondyle, where the confluent supinator process and the epicondyle form an extensive antero-ventrally sweeping sheet of bone.

The distal condyles are terminal with very little capitellar development, but the ulnar condyle is quite well developed with a dorsal ridge separating it from the very shallow supra-trochlear depression.

C. THE LOWER FORELIMB AND FOREFOOT

Alopecognathus (fig. 29)

In 12051 proximal and distal ends of both ulnae and radii and one good carpus are preserved.

Proximally the head of the radius fits into the concave sigmoid rim of the ulna so that its facet lies nearly as far proximally as that of the sigmoid facet of the ulna which is also situated terminally. The olecranon is robust but does not extend proximally as a process.

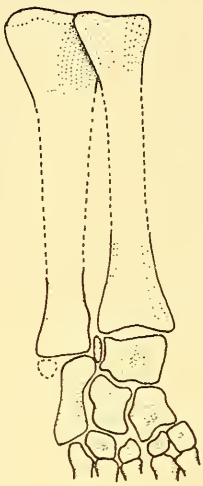

Fig. 29. *Alopecognathus angusticeps.* S.A.M. 12051. $\times \frac{1}{3}$. Epipodial and carpus.

Fig. 30. *Cynariognathus* sp. S.A.M. 11794. $\times \frac{1}{3}$. Right epipodial and partial manus.

In the carpus the radiale is a stout bone roughly rectangular in outline. A longitudinal ridge separates a larger preaxial dorsal face from a smaller postaxial face. Distally a ridge separates the facets for the two centrals.

The intermedium is a laterally flattened small bone wedged in between radiale and ulna and ulnare.

The ulnare is a long element with expanded ends and a long constricted waist. Its proximal facet is much smaller than the distal ulnar facet.

Both centralia are well-developed bones, each articulating with a pair of distals.

There are four distals—the fused fourth and fifth articulating with the fourth and fifth metacarpals.

Only the proximal ends of the five metacarpals are preserved.

Cynariognathus (fig. 30)

In 11794 both anterior epipodials are preserved but the preservation is not very good. Both the ulna and radius are lightly built and the ulna has no olecranon process. In the figure the proximal ends of the two bones are shown as lying next to each other but in life the proximal head of the radius is applied to the edge of the sigmoid cavity of the ulna so that the two bones have their proximal facets forming a confluent articulating face. The radial facet meets the capitellum and in extension the ulna rides on the trochlear facet of the humerus.

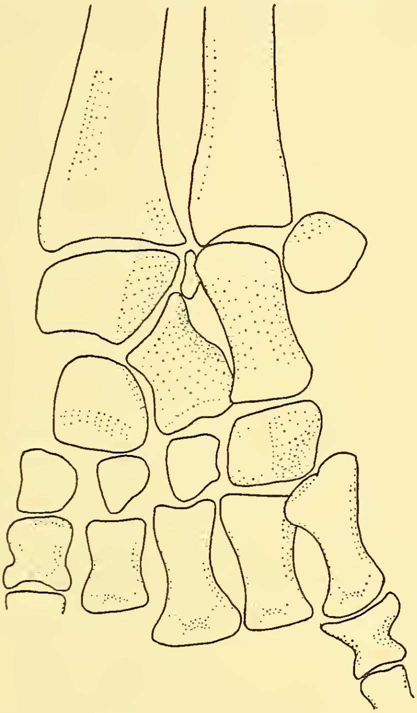

FIG. 31. *Pristerognathoides* ? S.A.M. K357. Nat. size. Partial manus.

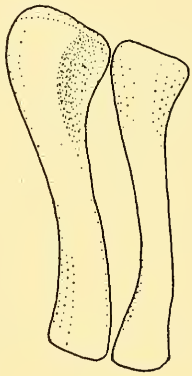

FIG. 32. *Ptomalestes avidus*. S.A.M. 11942. Type. ×⅓. Epipodial.

Only the right manus is in part preserved—the digits are missing.

In the carpus 9 bones are preserved. The proximal row consists of a long slender ulnare shaped somewhat like a metacarpal, a large laterally compressed intermedium and a short, broad radiale with distally two well-developed concave facets for the two centralia.

The two centrals are well-developed bones of irregular shape each with a good facet for articulation with the radiale.

There are four distalia; the first three articulate with the first three metacarpals, whereas the fourth articulates with both the fourth and fifth metacarpals.

Of the five metacarpals the last three have only their proximal ends preserved. They are short, with well-expanded ends. No. 1 is small and light, and from the second to the fifth they increase rapidly in size so that No. 5 is quite a strong element.

Pristerognathoides (fig. 31)

In a number of specimens ulnae and radii are preserved, exceptionally complete but mostly represented by proximal and distal ends. They call for little comment, except that in all these there is no definite olecranon process, and that proximally the two facets form a confluent terminal articulating face for the humeral condyles.

FIG. 33. *Scymnosaurus major* $\times \frac{1}{3}$. Epipodial of S.A.M. 9005. Type. Carpus of S.A.M. 12193.

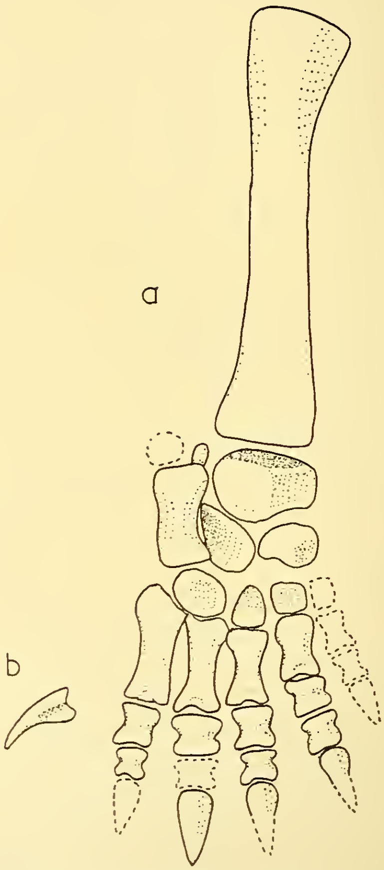

FIG. 34. *Scymnosaurus* sp. S.A.M. 11557. $\times \frac{1}{3}$. *a*, radius and manus in dorsal view. *b*, lateral view of no. IV terminal phalanx.

In K357 there is a good carpus with all five metacarpals present. Here the intermedium is a weak element and articulating with the ulna and ulnare there is a well-developed pebble-like pisiforme. The ulnare is elongate, the radiale robust, and the two centrals well developed. There are four distals, with the fourth articulating with both the fourth and fifth metacarpal.

The first two metacarpals are short, squat bones and the other three much longer, with the fifth the longest. The proximal phalanx of the fifth digit has its proximal end greatly expanded.

Ptomalestes (fig. 32)

In the type specimen of *Ptomalestes* (11942) both anterior epipodials are preserved. Both the radius and ulna are lightly built and the ulna has no distinct olecranon process. In the figure the proximal head of the radius is shown moved out of its articulation with the proximal end of the ulna.

Scymnosaurus (figs. 33–35)

In this genus the epipodial, carpus and manus are represented by some very good specimens.

The epipodial in the type specimen of *Scymnosaurus major* (9005) is represented by a well-preserved left ulna and radius (a mirror image is shown in the figure). In 9084 there are good proximal ends of the right ulna and radius in articulation. In 11557 there is a good radius, in 12193 proximal and distal ends of both ulna and radius and in 12262 a good complete radius and ulna.

In all these specimens the olecranon process of the ulna extends little proximally of the sigmoid face, and the proximal head of the radius lies anteriorly (morphologically dorsally) of the proximal end of the ulna and fits securely against the sigmoid edge forming a confluent articulating face for the feeble capitellum and the shallow trochlea of the humerus.

The carpus is preserved in part or nearly complete in 12193, 11459, 11557 and in 12262.

In 12193 the radiale is a robust bone; in dorsal view oval in outline with a convex dorsal and proximal face; concave distally for the first centrale and with a convex facet for the second centrale; ventrally it has a deep oblique groove.

The ulnare has its dorsal face with an outline like that of a metacarpal. Ventrally it has a longitudinal groove and its preaxial edge is convex in contrast to the dorsal concave preaxial edge.

The two centrals are robust; the first is nearly circular in outline with a penetrating foramen near its preaxial edge. The proximal central has its postaxial edge deeply concave, facing the concavity of the ulnare, thus forming a passage for the vessels penetrating the carpus.

Of the distal carpals only the proximal parts are preserved with the fourth distal strongly developed.

In 11459 the two centrals, distals together with metacarpals 1, 2 and 3, and the proximal phalanx of the second digit are preserved. The first central has a groove and a penetrating foramen near its preaxial border. The metacarpals increase in length from 1 to 3.

In 11557 there is a nearly complete carpus, but the manus is incomplete with the preserved bones partly displaced and disarticulated. In the figure

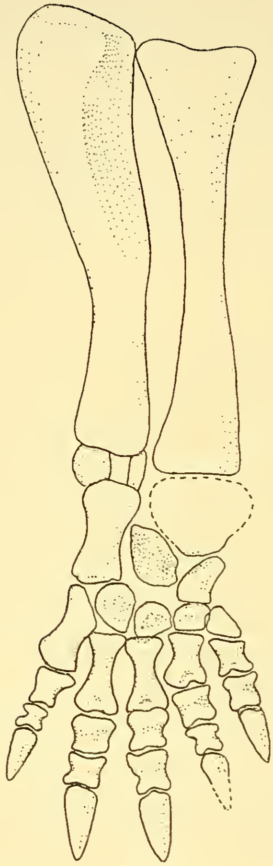

Fig. 35. *Scymnosaurus* sp. S.A.M. 12262. $\times \frac{1}{3}$. Epipodial and manus in dorsal view.

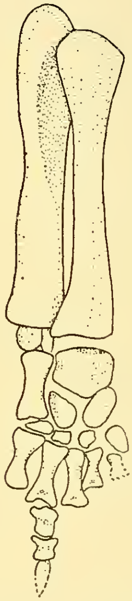

Fig. 36. *Theriodes cyniscus.* S.A.M. 11888. Type. $\times \frac{1}{3}$. Dorsal view of epipodial and partial manus.

the constituent bones are shown in natural relation. The radiale is fairly robust, with a flattish face for the radius; its dorsal surface shows two faces—the preaxial face nearly rectangular and the postaxial face more squarish, meeting at an angle of about 130°; the facet for the first central is slightly concave and for the proximal central convex.

The ulnare is elongated, with a dorsal outline resembling that of a metacarpal.

The intermedium is a small, laterally compressed bone. The first central has a depression near its preaxial border and the proximal central is hollowed out near its proximal wedge-like end.

The first distale is missing, numbers 2 and 3 lie proximally to their respective metacarpals and the large fourth articulates with both the fourth and fifth metacarpals.

The first metacarpal is missing; from number 2 to 5 the metacarpals increase in length with the fifth about $1\frac{1}{2}$ times the length of number 2.

The phalangeal formula is 2, 3, 3, 3, 3, 3. The ungual phalanges are curved, narrow, pointed and claw-like. The others are short, broad and squat, with well-expanded ends.

In 12262 the forefoot is very well preserved and is complete except that part of the radiale and the tip of the ungual phalanx of the second digit have been lost in transit from the field. The general structure is as in all the pristerognathids described above, viz. carpal formula 3, 2, 4 plus an ulnar pisiforme, and phalangeal formula 2, 3, 3, 3, 3. The fourth and fifth metacarpals articulate with the large fourth distal carpal; the metacarpals increase in length in postaxial direction and the distal ends of the third and fourth are particularly well modelled, with a dorsal trochlear fossa and well-rounded distal corners. The third and fourth digits are the longest and strongest; the first digit is relatively weak and the fifth strong. The weight is thus carried somewhat more postaxially than preaxially.

Therioides (fig. 36)

In the type specimen (11888) much of the right forefoot is preserved. The carpus is complete; the last four metacarpals are present but only the second digit is completely preserved.

The structure is typically pristerognathid but the metacarpals are relatively long and slender.

D. PELVIC GIRDLE

Alopecognathus (fig. 37)

In K218 a fairly large pelvis is preserved. This is, however, badly weathered and all that can be determined is that the pelvic plate is large with a distinct ischial keel and that the outer face of the ilium is convex.

In K231 most of a fairly large pelvis is preserved, but with the edges of the ilia incomplete. The pelvic plate is long and broad with both ischium and pubis strong; just more than half is contributed by the ischium; the ilium is large, with its length nearly as long as the ventral plate (91%). The pelvis is low and long, with the height 79 per cent of the length.

The ilium is not completely preserved on either side, but the two sides are complementary so that the figure could be compiled fairly accurately. The antero-posterior length of the iliac blade is great but its supra-acetabular height moderate; the height is a little more than half the length (52%). The posterior process of the iliac blade is long but fairly low, whereas the anterior process is fairly short but high; although its ventral corner apparently has a long, low elongation.

The outer face of the iliac blade is in general convex both antero-posteriorly as well as dorso-ventrally. The m. ilio femoralis (gluteus) thus originated from a convex area whereas in tetrapods this area is usually concave. The supra-acetabular ridge is strong. The ilium forms more than half of the acetabulum.

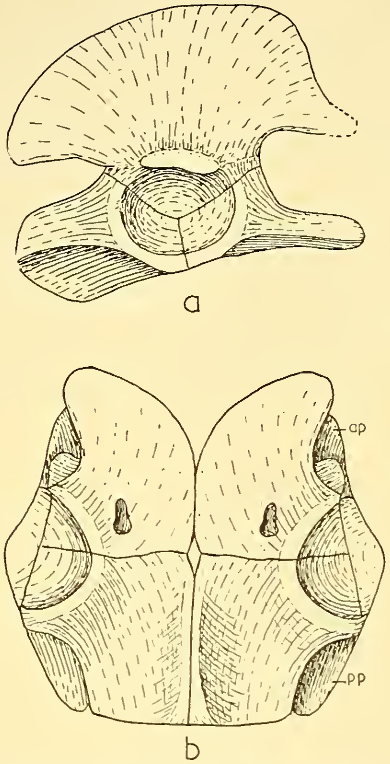

FIG. 37. Pelvis of *Alopecognathus angusticeps*. S.A.M. K231. $\times\frac{1}{3}$. *a*, lateral view. *b*, ventral view.

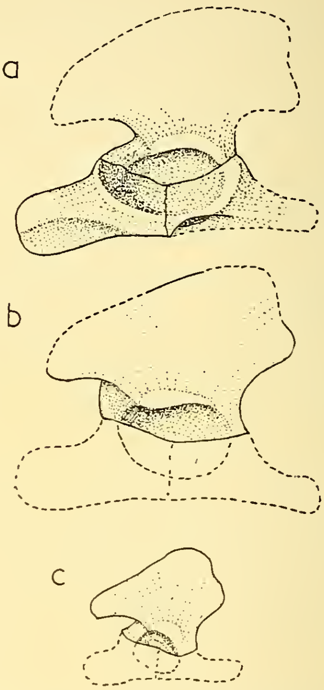

FIG. 38. Lateral views of pelves. $\times\frac{1}{3}$. *a*, *Cynariognathus* sp. S.A.M. 11794. *b*, *Pristerognathoides* ? S.A.M. 5018. *c*, *Pristerognathus*? S.A.M. K227.

The pubis is massive in its acetabular part, with a strong dorso-lateral edge, terminating in a moderate pubic tuber somewhat outwardly directed. The two pubes form a weak symphysis. A fairly large foramen pierces the bone near its posterior edge just medial to the strong acetabular rim. The ischium is longer than the pubis: its acetabular part is strongly developed and its rounded dorso-lateral edge ends in a moderate tuber. The two ischia form a strong symphysis which develops a strong medial keel.

The acetabulum is large and faces mainly outwards.

Cynariognathus (fig. 38*a*)

In 11794 there are preserved, of the right half of the pelvis, the acetabular proximal parts of the three constituent bones, whereas on the left there are a fair ischium and the proximal part of the pubis. The iliac blade is not preserved. Although of lighter build, the pelvis is essentially as in *Alopecognathus*. The pubic foramen is large.

Pristerognathoides (figs. 38*b* and 39)

In 5018 the two ilia are partly preserved and the figure incorporates features of both sides. The ilium is very similar to that of *Alopecognathus*, however its outer face, though also convex, is less so than in *Alopecognathus*.

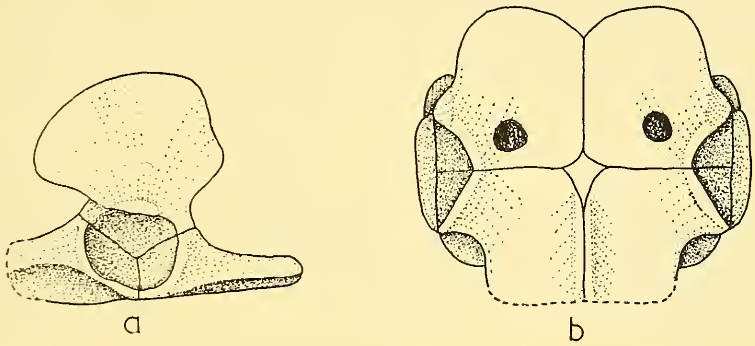

FIG. 39. Pelvis of *Pristerognathoides* sp. S.A.M. K223C. × ⅓. *a*, lateral. *b*, ventral.

In K233C the pelvis lacks only the posterior ends of the ischia. The pelvis is fairly low but quite long, the height being 75 per cent of the length as reconstructed. The blade of the ilium is both low and very short, the height being 74 per cent of the length. The outer face of the iliac blade is peculiar. It is not hollowed out as is usual in all other therapsids, but cannot be described as convex either. Dorso-anteriorly there is a pronounced bulge separating two hollows so that the surface can be described as undulating. The anterior process is short but high, with its anterior edge cut back at the level of the anteriorly hollowed-out area.

The posterior process is also short but much lower than the anterior process.

The supra-acetabular ledge is strong.

Both ischia and pubes are robust in their acetabular parts, with strong circum-acetabular borders. Anteriorly the pubis has a broad, thin anterior edge with the outer corner showing little of a pubic tuber. The pubic foramen is large but the symphysis is weak. The ischia form a fairly strong ventral keel. In its pubic part the pelvis has a flat floor, which in its ischial part becomes shallowly V-shaped.

Pristerognathus (fig. 38*c*)

In K227 there is a pair of beautifully preserved ilia. Much smaller than the ilia in the forms so far described, these ilia are nevertheless very similar. The undulating outer face is clearly shown; the anterior process is high, with its anterior edge notched; the posterior process is relatively longer and lower. The supra-acetabular height of the ilium is about two-thirds of the length of the iliac blade.

In K238A there are a partial ilium and most of a pair of ischia.

Scymnosaurus

Of this genus only the acetabular parts of an ilium and a pubis which indicate a moderately robust pelvis with an acetabulum of moderate size directed outwards are preserved (11957).

In 11558A a pair of good ischia are preserved.

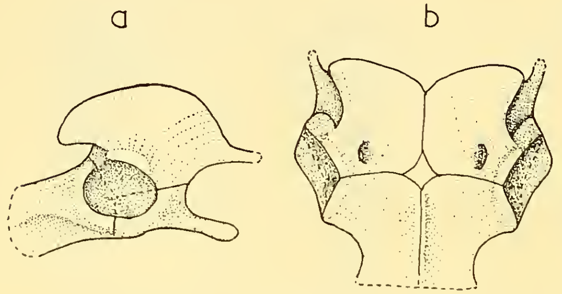

Fig. 40. Pelvis of a pristerognathid. S.A.M. K245A. $\times\frac{1}{3}$. *a*, lateral. *b*, ventral.

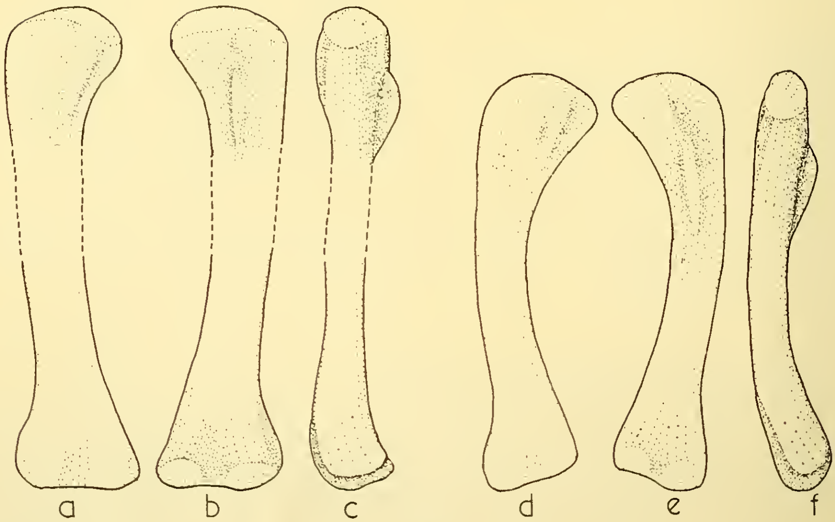

Fig. 41. Femora. $\times\frac{1}{3}$. *Alopecognathus* sp. S.A.M. 12051. *a*, dorsal. *b*, ventral. *c*, anterior. *Cynariognathus* sp. S.A.M. 11794. *d*, dorsal. *e*, ventral. *f*, anterior.

An unidentified pristerognathid (fig. 40)

In K245A there is a good pelvis, basically as in the above described forms, but the ilium is rather peculiar, with a long, low process directed anteriorly.

E. FEMUR

Alopecognathus (fig. 41*a*, *b* and *c*)

In 12051 a proximal and two distal femoral ends are preserved. The ends are moderately expanded, shaft fairly strong, somewhat dorso-ventrally flattened, and fairly straight.

The well-rounded caput, although terminal, is directed somewhat pre-axially. The external trochanter is not prominent and is situated well proximally. The pubo-ischio femoralis internus ridge is well developed, not near the anterior border. The internal trochanter forms a sharp ridge. The inter-trochanteric fossa is small and shallow.

In K231 both femora are present and, although badly preserved, are essentially similar to that figured here.

Cynariognathus (fig. 41*d*, *e* and *f*)

In 11794 both femora are preserved, but are both somewhat weathered and distorted. The curvatures in the figures on the long axis are thus artificial. The ridge forming the internal trochanter is long and not so far proximally situated.

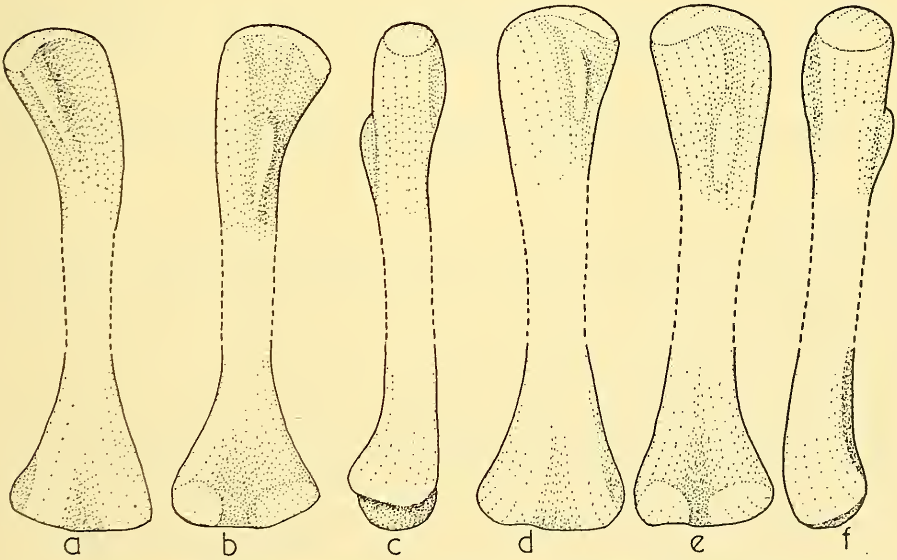

FIG. 42. Femora. $\times \frac{1}{3}$. *Pristerognathoides* sp. S.A.M. 5018. *a*, dorsal. *b*, ventral. *c*, anterior. S.A.M. 11936. *d*, dorsal. *e*, ventral. *f*, anterior.

Pristerognathoides (figs. 42 and 43)

The femur in this genus is represented by the distal and proximal ends of both femora in 5018 and K306 and one femur in 11936.

In 5018 the internal trochanter forms a long ridge extending on to the shaft, but it does not extend far proximally, so that the intertrochanteric fossa is long. The pubo-ischio femoralis internus ridge is low. The distal end is well expanded. In 11936 the femur is more robust.

In K306 the right femur is a larger, heavier bone than the left and is certainly not of the same individual and may be of a different species. The distal ends are only moderately expanded.

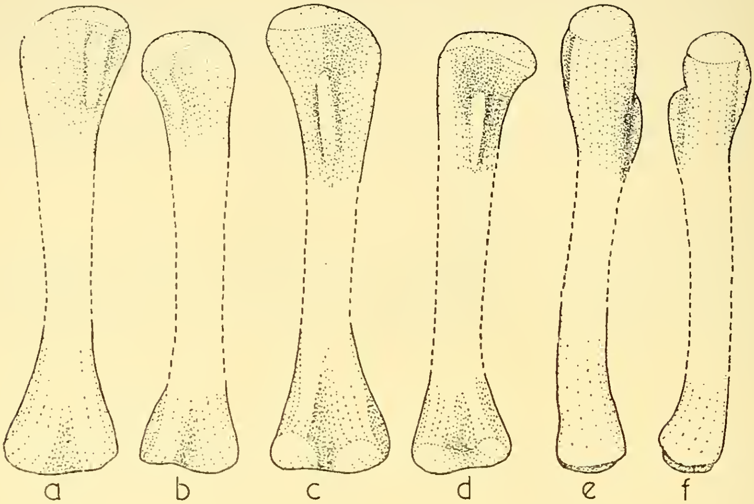

Fig. 43. Femora. × ⅓. *Pristerognathoides* sp. S.A.M. K306. Right: *a*, dorsal. *c*, ventral. *e*, anterior. Left: *b*, dorsal. *d*, ventral. *f*, anterior.

Pristerognathus

In this genus the femur is represented by poor ends. In K317 the internal trochanter forms a short, thickened ridge proximal to which lies a long, deep inter-trochanteric fossa.

Scymnosaurus (figs. 44, 45, 46*a*, *b* and *c*, 47)

In this genus the femur is fairly well represented. In 11557 there is a good, well-preserved femur, in 11597 a proximal end, in 12118 a proximal end, in 12193 a distal and proximal end, and in 12262 and K352 a poorly preserved but nearly complete femur.

In the three complete femora there is a greater amount of twist or rotation of the two ends on the shaft relative to each other than in the femur of all the other pristerognathids as hitherto described. This twist or rotation is an anticlockwise or postaxial movement of the proximal expansion in relation to the distal end. The result is that the caput, though terminal, is directed somewhat dorsally, whereas in the hitherto described forms this direction runs somewhat anteriorly.

Another difference is that the pubo-ischio femoralis internus ridge in *Scymnosaurus* lies on the morphological anterior edge of the bone and not some-

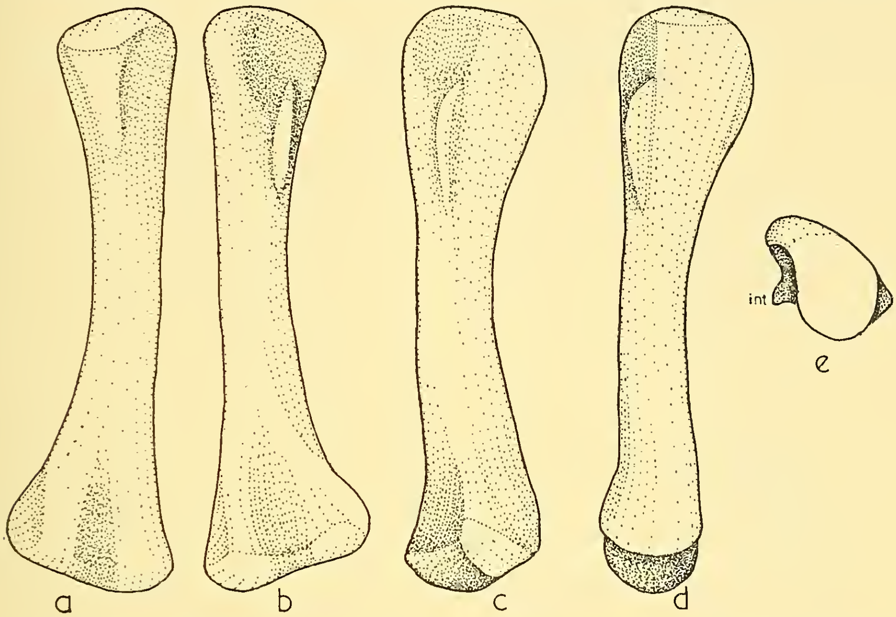

FIG. 44. Left femur of *Scymnosaurus* sp. S.A.M. 11557. × ⅓. *a*, dorsal. *b*, ventral (projection onto plane of distal condyles). *c*, ventral (projection onto the plane of the ventral face of the proximal end). *d*, anterior. *e*, proximal.

what away from this edge onto the dorsal surface. The straight, long axis of 11557 is normal whereas the downward curvature of the proximal end in both 12262 and K352 would appear to be due to post-mortem distortion. The internal and external trochanters are as in the already described Pristerognathids.

K353 consists of an isolated, well-preserved proximal end of a large femur which may be that of *Scymnosaurus major*. Although it has an internal trochanter and pubo-ischio femoralis internus ridge as in the other pristerognathid femora, both these structures are feebly developed and appear to be out of proportion to the size of the bone.

Zinnosaurus (fig. 46*d* and *e*)

In 12185 a proximal and distal femoral end is preserved. The caput is well rounded and somewhat anteriorly directed. The internal trochanter forms a robust ridge. The external trochanter is weak and the inter-trochanteric fossa short but deep.

The pubo-ischio femoralis internus ridge is very weak; it forms the anterior border of the bone and runs into the anterior edge of the caput.

F. THE LOWER HIND LIMB AND PES

Alopecognathus (figs. 48 and 49*a*)

In 12051 the left epipodial and pes are completely preserved and in K231 both epipodials and an incomplete pes.

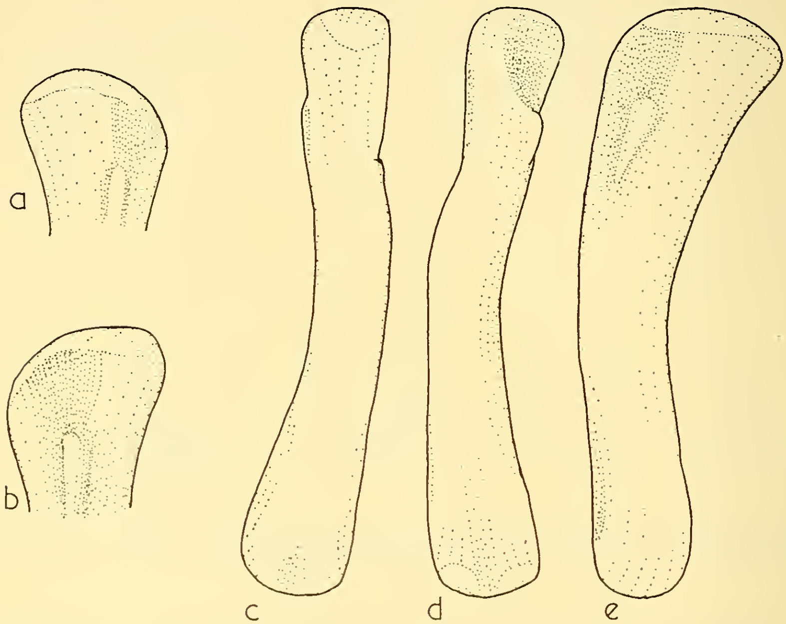

FIG. 45. Femora. × ⅓. *Scymnosaurus* sp. S.A.M. 11957. *a*, ventral. *Scymnosaurus* sp. S.A.M. 12118. *b*, ventral. *Scymnosaurus major*. S.A.M. 12262. *c*, dorsal. *d*, ventral. *e*, anterior.

The tibia is stout proximally with a well-developed facet for the femur. The fibula is much slenderer and curved to give a wide spatium interosseum. The proximal facet of the fibula is terminal and not applied to the outer corner of the femoral condyle but end-on.

The astragalus is a robust, rounded bone with a convex facet for the tibia.

The calcaneum is a large but lightly-built flat bone thickened proximally at the facet for the fibula. Preaxially it is notched for the passage of the intertarsal vessels.

The central is quite small.

There are five distals. The first is large and articulates with both first and second metatarsals. The fourth is the largest whereas numbers 2, 3 and 5 are small.

The metatarsals increase in length from number 1 to 5.

The digital formula is 2, 3, 3, 3, 3, with the fourth the longest, but due to the short phalanges all the digits are short. The ungual phalanges are curved and carried sharp claws.

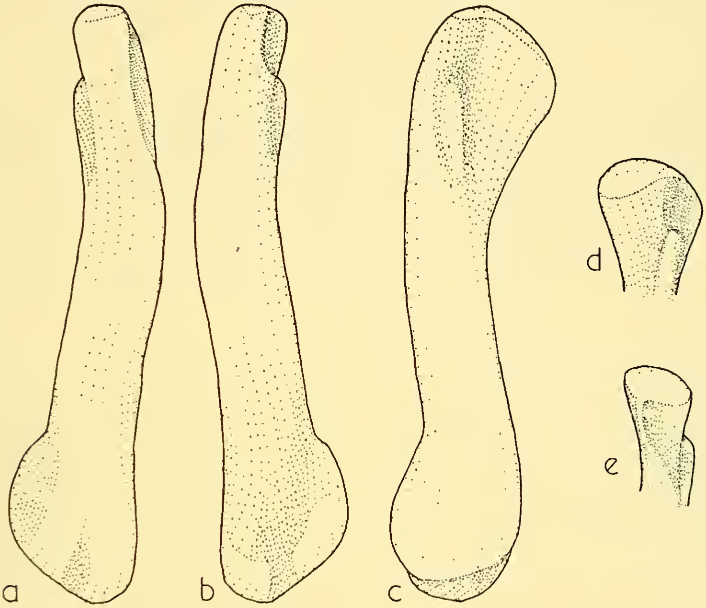

FIG. 46. Femora. $\times \frac{1}{3}$. *Scymnosaurus major* ? S.A.M. K352. *a*, dorsal. *b*, ventral. *c*, anterior. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. *d*, ventral surface of proximal end. *e*, anterior face of proximal end.

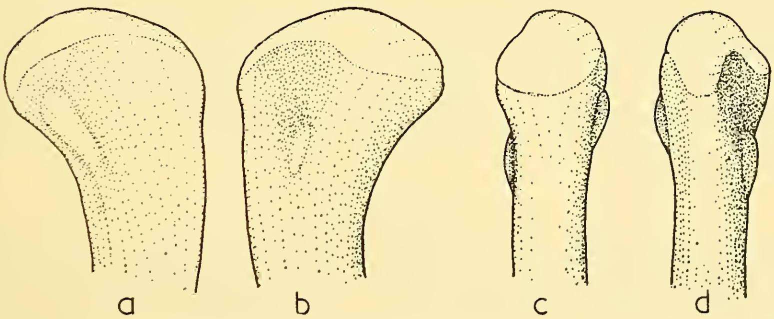

FIG. 47. *Scymnosaurus major* ? S.A.M. K353. $\times \frac{1}{3}$. Proximal end of femur. *a*, dorsal. *b*, ventral. *c*, anterior. *d*, posterior.

Cynariognathus (fig. 49*b*)

In 11794 a somewhat crushed tibia and fibula are preserved, with features as shown in the figure. Distal to the tibia lies a bony element of quite intricate shape, not at all like the astragalus preserved in *Alopecognathus* and probably is not this bone at all.

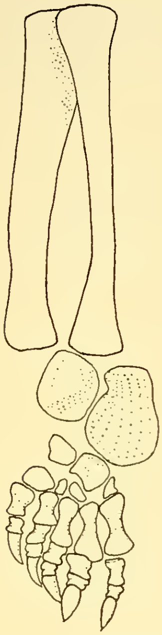

Fig. 48. Epipodial and pes of *Alopecognathus*. S.A.M. 12051. × ⅓.

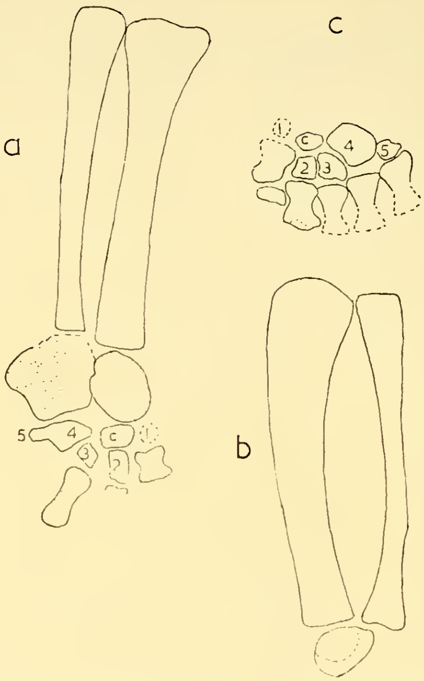

Fig. 49. Epipodials and pes. × ⅓. *a*, *Alopecognathus angusticeps*. S.A.M. K231. *b*, *Cynariognathus* sp. S.A.M. 11794. *c*, *Scymnosaurus* sp. S.A.M. 11459.

Fig. 50. Pes of a pristerognathid. S.A.M. 245A. × ⅓.

Scymnosaurus (fig. 49*c*)

In 11459 part of a pes is preserved. I have identified a small central. Distals 2 and 3 are small, 4 is much larger, and 5 is still a small, separate element. Parts of all five metatarsals are present. Number 1 digit has a very short first phalanx.

Discussion

It would be of interest to compare the girdles and limbs of the pristerognathid Therocephalia with those of the other therapsids of the *Tapinocephalus* zone. Unfortunately these structures in the contemporary therapsids are inadequately known. Only in the Dinocephalia have they been adequately described, and in the Dromasauria two specimens have these structures preserved. Of the Gorgonopsia, they have been described in one genus. Of the Dicynodontia nothing has as yet been published. Of the other therocephalian families represented in this zone, a shoulder girdle of a lycosuchid has been figured, of the Akidnognathidae a manus, and of the Scaloposauridae a brief account has been given of parts of a hind limb.

I have in recent years collected some gorgonopsians and dicynodonts from the *Tapinocephalus* zone in which parts of the girdles and limbs are preserved.

As soon as these specimens have been prepared a comparative discussion will be presented.

Summary

Descriptions are given of the girdles and limbs of the pristerognathid Therocephalia from the *Tapinocephalus* zone of the Karoo. The descriptions are based on 37 specimens in the South African Museum which have parts of the girdles and limbs preserved. Taken together this material gives a good idea of the family character of these structures. A new genus and species of pristerognathid therocephalian, *Zinnosaurus paucidens*, is described.

Acknowledgements

The specimens collected in recent years were obtained on Museum collecting trips, which were in part financed by the C.S.I.R. For these grants we are grateful.

Some of the later specimens have been prepared for study by Mr. C. Gow, to whom our thanks are due.

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A. Photograph of a habitat group with life-sized models modelled by the author and exhibited in a diorama in the South African Museum. *Scymnosaurus* feeding on *Brachypareia*.

B. Photograph of life-sized models made by the author and exhibited as a habitat group in the South African Museum. The Therocephalians (l. to r.) *Pristerognathoides*, *Therioides* and *Alopecognathus* feeding on a cadaver of *Moschops*.

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SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July* 1958, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:
Euplonia capensis (Smith) Brown, 1955: 259.
When misidentified as another species:
Plonia natalensis (*non* West), Jones, 1956: 18.
When another species has been called by the same name:
[*non*] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).

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