On the Shoulder Girdle of the
Mammalian Subclass Allotheria

By MALCOLM C. McKENNA

INTRODUCTION

The mammalian subclass Allotheria consists of a single extinct order, the Multituberculata. The allotheres were a highly successful side branch of the early mammals or possibly even therapsid reptiles, depending on what one chooses for mammalian criteria. Allotheres are regarded as mammals in the present paper. They first appeared in the record in the late Jurassic and made their last known appearance in the earliest Eocene of North America. During this long span they spread throughout the Holarctic Region, but there are no known remains from any of the southern continents. Many genera are known, representing several basic types, but the evidence of these is almost wholly dental in nature. The skull is known in four genera, but significant information has been obtained from only two, *Ptilodus* and *Taeniolabis*. Allotheres are best known from the North American Paleocene, in which remains of their distinctive jaws and dentitions are notably abundant and varied. The allotherian dentition and some details of the jaw and maxillary regions have been treated extensively by Simpson (1928a, 1929), Jepsen (1940), and Clemens (in preparation). The skull has been interpreted most thoroughly by Simpson (1937).

The hind limb of a Paleocene allothere, *Eucosmodon*, has been described by Simpson and Elftman (1928). They found that "the femur had unusual freedom of motion in all directions, but in the normal standing position of the animal it was nearly horizontal, inclined forward,

outward, and slightly downward. The angle between the femur and tibia could never have exceeded 90° in life and was usually considerably less—the leg could not be straightened and the crus was usually drawn well backward and could be made almost parallel with the upper limb. Normally the tibia and fibula would thus be directed backward, inward, and downward. The foot, as clearly shown in its almost completely known osteology, is unusually primitive. It is pentadactyl and plantigrade, of grasping type with partially opposable hallux. The digits are strong, the functional length formula $3 > 4 = 2 > 5 = 1$. The terminal phalanges carried claws of moderate size, somewhat compressed transversely."

The allotherian shoulder girdle has been known previously from a single poorly preserved scrap of a right scapulocoracoid of *Djadochtatherium* from the late Cretaceous of Mongolia. A fragmentary scapula and a supposed interclavicle from the Lance formation of Wyoming were once referred to this subclass by O. C. Marsh, but Marsh's identification has not been accepted.

Recently two extensive collections of late Cretaceous small vertebrates from the Lance formation have been made in the United States by the University of California Museum of Paleontology and by the American Museum of Natural History. In addition to the many specimens of jaws and dentitions of Cretaceous mammals that were secured (Clemens, in preparation), a number of isolated bones of the skeletons have been collected. Additional undescribed skeletal elements have been found in the Peabody Museum of Natural History among the many specimens from the Lance formation collected for O. C. Marsh. More than a dozen fragmentary mammalian scapulae and scapulocoracoids have been identified in these three major collections of Lance mammals. The scapulae and scapulocoracoids represent a variety of types, mostly therian, but two agree in essentials with the few useful details preserved on the *Djadochtatherium* scapulocoracoid and are therefore referred with reasonable certainty to the Allotheria. Both of the fragmentary allotherian scapulocoracoids recently identified are distinctly mammalian in aspect, but differ from unspecialized scapulae of adult therians, including a number of Cretaceous therians, in that the lower part of the blade of the scapula does not extend anterior to the scapular spine.

I am indebted to Drs. E. L. Simons and P. Robinson for the loan of specimens from the collections at the Peabody Museum of Natural History, Yale University, and to Dr. J. C. Moore for help with the collections in the Department of Mammalogy in the American Museum

of Natural History. Drs. E. H. Colbert, R. Estes, M. K. Hecht, S. B. McDowell, Jr., and B. Schaeffer have contributed stimulating comments. The illustrations were prepared by Mr. Chester Tarka.

The following abbreviations are used:

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History
A.M.N.H.:M., Department of Mammalogy, the American Museum of Natural History
U.C.M.P., University of California (Berkeley), Museum of Paleontology
Y.P.M., Peabody Museum of Natural History, Yale University

ORIENTATION

If one attempts to describe or compare scapulocoracoids of therapsids, monotremes, multituberculates, and therians, the problem of orientation looms large. Which direction is anterior? Is there a medial component to this direction or that one? What was the true anatomical position of the shoulder girdle? Was it a yoke around the neck? Was it placed against the rib cage? Has author A illustrated his material at the same orientation as author B?

The three multituberculate scapulocoracoids discussed in this paper have been described as though the principal orientations of important anatomical structures are anterior, posterior, ventral, dorsal, lateral, and medial. In reality such is almost certainly not the case, but much printers' ink is saved if terms such as "posterodorsolateral" are kept at a minimum. The orientation that seems the most practical for the multituberculate scapulocoracoids under discussion is that in which the scapular spine projects laterad. The description can be written consistently, and I hope clearly, in that orientation. Once the anatomy is in mind, the reader can mentally rotate the specimen to any desired orientation.

DJADOCHTATHERIUM

Figure 1

MATERIAL: A.M.N.H. No. 20440, various parts of the skeleton, including a fragmentary right scapulocoracoid.

LOCALITY: Djadochta, Outer Mongolia.

AGE: Late Cretaceous.

DESCRIPTION AND COMMENTS: The scapulocoracoid of *Djadochtatherium* is known from a single poorly preserved fragment reported by Simpson (1928b, pp. 10, 11, fig. 7F). At the time of description, the specimen was covered by a tenacious quartzitic matrix common to nearly all

Fɪɢ. 1. Unretouched photographs of the fragmentary right scapulocoracoid of *Djadochtatherium matthewi* (A.M.N.H. No. 20440), a late Cretaceous multituberculate from *Djadochta*, Outer Mongolia. *Upper left:* "Lateral" view. *Upper right:* "Medial" view. *Lower left:* Glenoid fossa. *Lower right:* "Posterior" view. All × 4.

specimens from the same locality. It has recently become possible to remove some of this matrix and thus to permit certain additional observations. Simpson stated that the relationship of glenoid cavity to blade is exactly that of higher mammals and fundamentally unlike that in monotremes. In addition to Simpson's comments, to which the reader is referred, it may be noted that, if the coracoid projected pos-

teroventromedially as in *Oligokyphus* and monotremes, the scapula would have to have been rotated nearly 180 degrees, with the spine medially (costally) situated and the humerus projecting forward as well as ventrolaterad. The coracoid projected anteroventromedially as in adult therians and may have curved mediad to come in contact with the sternum as in embryonic *Trichosurus* (Broom, 1897; Watson, 1917), *Pseudocheirus* (Broom, 1899, pp. 756–757), *Petrogale* (Broom, 1899, pp. 757–758), *Dasyurus* (Broom, 1912), and *Didelphis* (Hanson, 1920, pp. 330–331, pl. 1; McCrady, 1938, p. 163). The scapulocoracoid of *Djadochtatherium* was therefore not part of an anterodorsally projecting yoke around the neck as in *Oligokyphus* (as interpreted by Kühne, 1956) and monotremes, but was placed farther back as in therians. Further, the anteroventromedial projection of the true (posterior) coracoid makes it unlikely that an anterior coracoid was present.

Simpson did not mention the scapular spine, although the base of the acromion is indicated on his figure of the lateral view. Additional preparation has freed part of the acromion and spine from the enclosing matrix, but details are still obscure. A large projection representing the base of the acromion occupies the center of the lateral face just above the glenoid fossa. From the anterior part of this projection the scapular spine runs up to join the (actual) anterior border of the blade, but this part of the spine is heavily damaged. The posterior base of the acromion is either hollowed out by a deep fossa, heavily damaged, or both. This last feature is not present in the American allotherian scapulocoracoids. Anterior to the scapular spine there is no supraspinous fossa on the lateral face of the blade, except possibly a small area just above the (presumed) fused suture with the large coracoid bone.

The coracoid, of which the actual length is unknown because of breakage, possesses a rather flat lateral face near its coalescence with the scapula. It is therefore inferred that part of the supracoracoid (coracohumeralis) musculature probably took its origin from this area in the adult more or less as in foetal *Didelphis* (Cheng, 1955, pp. 442–443) and adult *Zaglossus* (Allen, 1912, p. 270) and *Tachyglossus* (McKay, 1894, p. 308). If so, however, it is not necessarily established that the part involved is m. supraspinatus (m. coracohumeralis profundus of Howell, 1936). The medial face of the coracoid is continuous with the anterior part of the medial face of the scapula. M. supraspinatus may have extended onto the scapula in this area. Posterior to the acromion, part of the infraspinous fossa is preserved, but its characters are obscure. It is not possible to say whether it housed an infraspinatus division of m. supracoracoideus and a small m. teres minor as in therians

(except certain talpids, *fide* Howell, 1937b, p. 458) or simply a large m. teres minor (m. infraspinatus of authors prior to Howell, 1937a) as in monotremes.

On the medial (costal) face of the scapula there are two low ridges similar to those of A.M.N.H. No. 58850 from the American Cretaceous. The more anterior of these extends from the edge of the glenoid fossa up the scapula for about 4 mm., at which point it curves to the rear and loses its identity. The more posterior of the crests connects the posteromedial corner of the glenoid fossa with the axillary border. Both crests are rather weak and could be partly the result of differential crushing or erosion, but, in view of their similarity to crests in the same positions in the much better preserved American material, I believe they are true anatomical features. If this view is correct, these small crests presumably separated small anterior divisions of m. subscapularis (derived from dorsal premuscular anlage).

The axillary border of the scapula broadens to form a triangular face just above the posterior border of the glenoid fossa. This face meets the lateral face at nearly a right angle along a ridge running from the posterolateral corner of the glenoid fossa to the posterior base of the acromion. The boundary of the posterior triangular face with the posterior part of the medial (costal) face of the scapula is less well defined. M. subscapularis probably occupied part of or nearly all the triangular posterior face as well as the posterior part of the medial (costal) face, but it seems doubtful that it extended to the lateral face. The dorsal extent of the triangular face is not known. Its triangular shape may be caused by unrecognized breakage along its lateral edge.

LANCE TYPE 1

Figure 2

MATERIAL: A.M.N.H. No. 58850, a fragmentary right scapulocoracoid.

LOCALITY: U.C.M.P. No. V-5620, approximately 1700 feet above the base of the Lance formation, Niobrara County, Wyoming.

AGE: Latest Cretaceous.

DESCRIPTION AND COMMENTS: This is a very small scapulocoracoid which in most details is closely comparable to the scapula of *Djadochtatherium*. There is no close similarity to an assortment of Cretaceous therian scapulae at hand. The latter are generally little different from those of primitive living therians and will be described elsewhere.

The glenoid fossa is more rounded than in *Djadochtatherium* and is crudely teardrop-shaped in outline. The lateral lip projects farther

FIG. 2. Retouched photographs of A.M.N.H. No. 58850, a fragmentary right scapulocoracoid of a small multituberculate here designated Lance Type 1, U.C.M.P. locality V-5620, Lance formation, late Cretaceous, Lance Creek, Wyoming. *Upper left:* "Lateral" view. *Upper right:* "Posterior" view. *Lower left:* Glenoid fossa. All × 8.

laterad than in *Djadochtatherium*. As is the scapulocoracoid of the latter genus, the coracoid is firmly fused to the scapula in the adult, but the position of the former suture is not known. The coracoid is broken, so that there is no direct information concerning its length. It is a large and important structure, however, just as it is in *Djadochtatherium*, and it projected anteroventromediad.

The scapular spine is continuous with the base of the acromion. In contrast to the damaged scapula of *Djadochtatherium*, the spine is fairly well preserved, although the acromion itself is apparently missing lateral to its base. The base of the acromion is situated about midway between the axillary and coracoid borders of the scapula, about 1.3 mm. above the lateral rim of the glenoid fossa, an advance towards therians over the condition exhibited by *Cynognathus* and *Oligokyphus*. From there the spine rapidly approaches the coracoid (actual anterior) border of the

blade. About 3.0 mm. above the lateral rim of the glenoid fossa the spine actually forms the anterior limit of the bone.[1] On the lower part of the scapula the blade therefore does not extend farther forward than the spine except for a small area near the coracoid. In this latter area the supracoracoid (coracohumeralis) musculature probably still originated mainly from the coracoid. Probably a small part of the supracoracoid musculature extended up onto the base of the acromion, somewhat as in *Ornithorhynchus* (see Wilson and McKay, 1893, p. 380), but the main part of this muscle mass appears to have lain anterior and medial to the scapulocoracoid bone, more or less as in foetal *Didelphis* (Cheng, 1955, pp. 442–443) and adult *Zaglossus* (Allen, 1912, p. 270) and *Tachyglossus* (McKay, 1894, p. 308).

The infraspinous fossa was well developed, but its posterior border is damaged. It is not possible to say whether it was occupied principally by a large m. teres minor as in monotremes, or by both m. infraspinatus and m. teres minor as in almost all therians.

The medial (costal) face of the scapula bears a prominent anterior fossa which is continuous with the medial face of the coracoid, suggesting that m. supraspinatus (derived from ventral premuscular anlage) rather than m. subscapularis (derived from dorsal premuscular anlage and associated with m. teres major, according to Cheng, 1955, p. 456) occupied the fossa. This fossa evidently occupied most of the vertebral end of the blade as well, but near the glenoid fossa it is limited posteriorly by a low ridge. Posterior to this ridge are a groove and then a second ridge which marks the posteromedial border of the scapula near the glenoid fossa. Neither the groove nor its limiting ridges appear to have extended very far up the blade.

As in *Djadochtatherium,* there is a broad triangular area above the glenoid fossa at the posterior end of the scapula. The dorsal part of the lateral edge of the area is damaged, so that the exact shape of the posterior face is not known. It may have been nearly as extensive as in Lance Type 2, extending laterad as the posterior and posteromedial surface of a lamina posteriorly limiting the infraspinous fossa. M. subscapularis probably occupied this area (see Wilson and McKay, 1893, pp. 381–383; McKay, 1894, pp. 310–314; Cheng, 1955, p. 465), and possibly extended around onto the posterior part of the medial face near the glenoid fossa.

---

[1] In *Cynognathus,* a cynodont therapsid, there is a small extension of the blade at the extreme vertebral end of the scapulocoracoid anterior to the outturned spine. This area is missing from all three known allotherian scapulocoracoids as well as from those of *Oligokyphus.*
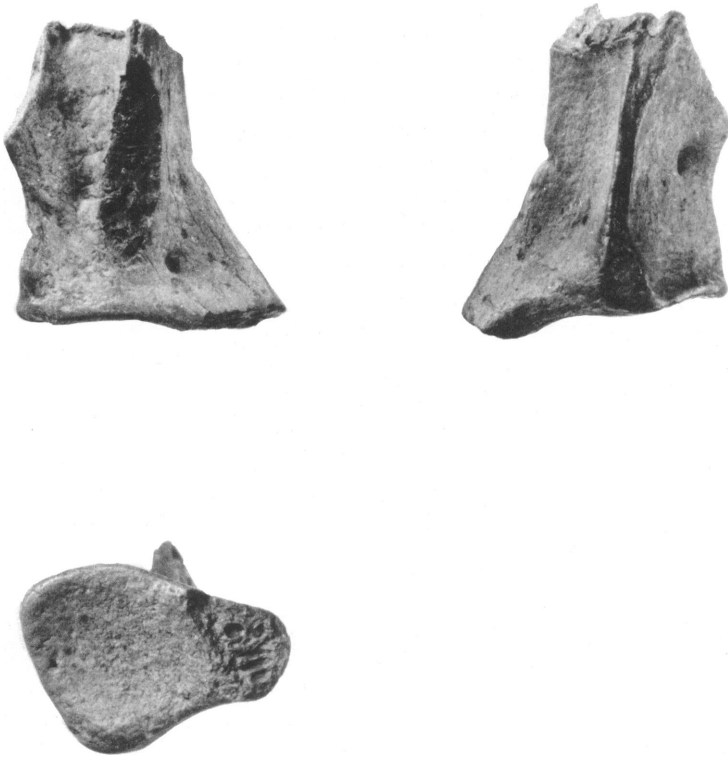
FIG. 3. Unretouched photographs of Y.P.M. No. 16501, a fragmentary right scapulocoracoid of a large multituberculate here designated Lance Type 2, Lance formation, late Cretaceous, Lance Creek, Wyoming. *Upper left:* "Lateral" view. *Upper right:* "Medial" or "posteromedial" view. *Lower left:* Glenoid fossa. All × 4.

LANCE TYPE 2

Figure 3

MATERIAL: Y.P.M. No. 16501, framentary right scapulocoracoid.

LOCALITY: Lance formation, Lance Creek, Wyoming; exact stratigraphic position and geographic location uncertain.

AGE: Latest Cretaceous.

DESCRIPTION AND COMMENTS: This specimen represents an animal of about the same size as *Djadochtatherium*. The anteroventromedially projecting coracoid has been broken away, presumably near the position of its fusion with the scapula. The nature of the break suggests that the coracoid was quite large and was completely fused to the scapula at the time of breakage; otherwise there would not be a clean fracture so

close to the position of the point of coalescence. The scapular spine is broken away at its distal end. Near the point where the spine becomes the (actual) anterior edge of the scapula there is a break which has resulted in the loss of the vertebral end of the blade. It is not possible to say whether the blade extended a short distance in front of the spine at the extreme vertebral end of the blade as it does in *Cynognathus*.

The glenoid fossa is shaped somewhat like that of Lance Type 1, but is a little less elongate and has a straighter posterior border. The latter makes nearly a right angle with the posterior ends of both adjoining borders and between them projects as a lip which ventrally limits the posterior face. As in Lance Type 1 and *Djadochtatherium*, the curvature of the glenoid fossa appears to have continued onto the posterior surface of the coracoid, a prototherian[1] and reptilian feature that occurs in foetal *Trichosurus* (Broom, 1897, p. 514) but not in adult marsupials. The head of the humerus probably articulated almost entirely with the scapula, however, in much the same way as Broom (*ibid.*) has stated for foetal *Trichosurus*.

The scapular spine is continuous with the base of the acromion. It begins about 1.5 mm. above the lateral border of the glenoid fossa, near the middle of the lateral face of the scapula. From there it runs upward, merging with the (actual) anterior edge of the scapula near the broken edge of the blade. Anterior to the spine there is a small area the distal end of which was continuous with the lateral face of the coracoid. Part of the supracoracoid musculature probably occupied this area and may have extended up onto the base of the acromion,

---

[1] In adult monotremes the coracoid plays a greater part in articulation with the humerus than does the scapula. In two half-grown specimens of *Tachyglossus setosa* seen (A.M.N.H.: M. Nos. 65831 and 65842) the suture between the coracoid and scapula is still present. It crosses the dorsal half of the glenoid fossa and is reminiscent of the shoulder joint of mammal-like repiles. In a somewhat younger specimen of *Tachyglossus aculeatus* (A.M.N.H.: M. No. 35679) the condition is the same. The shoulder joint of *Ornithorhynchus* may, however, be different. The osteology collection of the Peabody Museum of Natural History, Yale University, possesses a half-grown *Ornithorhynchus* skeleton in which the sole proximal contact of the humerus is with the posterior coracoid bone. The scapulocoracoid suture is entirely proximal to the glenoid fossa and has not yet been obscured by fusion of the two bones. The scapula itself does not enter into the shoulder joint. A.M.N.H.: M. No. 150101 is a somewhat older specimen of *Ornithorhynchus anatinus* than the young Yale specimen. Though not yet full-sized, the scapulocoracoid suture has fused. The specimen is young enough, however, to permit the location of the former suture to be traced locally. It seems to have crossed the proximal part of the glenoid fossa. If this is true, the scapula may come to occupy part of the glenoid fossa by the time growth is completed. The contribution to the glenoid fossa may be considerably less in the case of the scapula of adult *Ornithorhynchus* than it is with adult *Tachyglossus*.

but probably no farther. A foramen penetrates the scapula just anterior to the distal end of the base of the acromion. Posterior to the spine is an infraspinous fossa similar to that of Lance Type 1. The fossa is deep, but its posterior border is broken, and its actual extent is unknown other than near the glenoid fossa. It may have been limited posteriorly by a lamina resulting from lateral extension of the upper part of the posterior face of the scapula. A foramen penetrates the floor of the fossa at the point where the upper part of the blade has broken away. Whether m. teres minor or an infraspinatus division of the supracoracoid musculature was the principal occupant of this fossa is not known.

The remaining two faces may be designated the medial and posterior faces, although their true orientation is not precisely known. If the coracoid projected anteroventrad only, then both faces would have a medial component, but it seems more probable that the coracoid projected anteroventromedially rather than merely anteroventrad and that in this orientation the posterior face of the scapula is homologous with the posterior faces of the scapulae of *Djadochtatherium* and Lance Type 1. If this orientation is correct, the long axis of the glenoid fossa runs posterolaterad and the "lateral" face of the scapula in reality faces somewhat anterolaterad.

The medial face is continuous with the medial face of the coracoid as in the other specimens, which again suggests that m. supraspinatus extends into the area. Above the coracoid it is hollowed out as a fossa and is terminated by anterior and posterior right angles with the base of the scapular spine and the posterior face, respectively. A small foramen is present in the deepest part of the fossa.

The posterior face is quite broad and evidently extended much farther up the scapula than in *Djadochtatherium* or Lance Type 1. Its great width and dorsal extent make the term "blade" a misnomer when applied to this specimen. A horizontal cross section of the scapula just above the glenoid fossa would be nearly triangular. Above that it would be ∩ shaped. A large foramen penetrates the posterior face 3.7 mm. dorsal to the posterior border of the glenoid fossa. The posterior face turns somewhat posteromediad near the dorsal broken edge of the specimen. The face is probably the true subscapular fossa, occupied by m. subscapularis. There is no evidence to indicate that m. subscapularis extended forward onto any part of the medial face of the scapula.

CAMPTOMUS PROBABLY A CRETACEOUS MARSUPIAL

In 1889 O. C. Marsh of Yale University published the first of several

papers in which he described and figured the type specimens of most of the mammalian species, both real and supposed, known from the Lance formation of northeastern Wyoming. In this first paper he described (p. 87) and figured (pl. 5, figs. 1, 2) a scapula which he made the type of *Camptomus amplus*. In the legend for plate 5 (p. 92) Marsh stated that the specimen depicted on plate 5, figures 3 and 4, was an interclavicle and provisionally referred it to the same species. In the same legend he stated that the astragalus depicted on plate 5, figures 18–20, was that of *Camptomus amplus* and that the calcaneum depicted on plate 5, figures 21–23, was apparently of the same individual. In the text (p. 87) Marsh simply stated that the additional remains were found *with* (italics mine) the scapula but that the association of the various remains may be accidental. The locality was not given, but Lull (1915, p. 345) stated that the locality was Hatcher's locality no. 1. Lull gave the location of locality no. 1 on his map (*ibid.*, figs. 1 and 2), but Lull's map has proved to be rather unreliable. In any event, the locality is at the top of Beecher's section, published by Lull (*ibid.*, p. 334, fig. 3) and may lie north of Peterson's Quarry, as indicated on Lull's map. There is a chance that Hatcher's locality no. 1 is the same as one of the principal sites found by the University of California expedition in 1957 (U.C.M.P. locality V-5711) and extensively excavated by the Museum of Paleontology of the University of California and by the American Museum of Natural History in the period 1957–1960. Unfortunately, however, there can be no proof of these suppositions. The large size of the remains makes it very unlikely that any of them was recovered from an anthill, and the nature of occurrence of bones at blowouts like U.C.M.P. V-5711 is such that it is very doubtful that the remains were actually associated in the field, even though the astragalus and calcaneum are clearly allotherian and probably belong to the same species.

In the first decade after Marsh's description of *Camptomus,* Lydekker (1889, pp. 1264–1266), Dollo (1889, p. 676), Lemoine (1889, p. 240, fig. 1), Osborn (1891, pp. 8 ff.), Ameghino (1893, and Obras Completas, 1918, vol. 10, p. 563), Zittel (1893, pp. 68, 73, fig. 44), Trouessart (1898, p. 1256), and Woodward (1898, p. 252) all mention the genus. Lemoine, Trouessart, and Woodward accepted Marsh's identifications. Lydekker, Dollo, and Osborn saw monotreme affinities because of the separate coracoid[1] and the presence of an interclavicle (*fide* Marsh).

---

[1] The posterior (true) coracoid of adult monotremes fuses to the scapula. The anterior coracoid is a separate bone which is in contact with the interclavicle, clavicle, and posterior coracoid but does not fuse to them.

Zittel spoke of the unfused coracoid and placed marsupials, mono-tremes, multituberculates, and all other Mesozoic mammals in a sub-class Eplacentalia. Ameghino, however, was of the opinion that the scapula and interclavicle were those of a reptile, a viewpoint close to that of Simpson 35 years later. Ameghino claimed that, if he were right, the argument based on *Camptomus* for monotreme affinities of the Mul-tituberculata collapsed.

During the first quarter of this century *Camptomus* was accepted as a multituberculate by all authors who bothered to mention it at all. Broom (1914, p. 125) accepted Marsh's identification of the interclavi-cle and agreed that it probably belonged to a multituberculate. He noted the separate coracoid indicated by the coracoid facet of the type scapula and theorized that, "Any animal which had an interclavicle like the one figured [by Marsh] must have had a large coracoid artic-ulating with the sternum and even if we did not know that an inter-clavicle of this type had been found we could have predicted that any animal which had a large coracoid articulating with the sternum was likely to have an interclavicle." Broom used this dubious argument to bolster his opinion that the Allotheria were related to the Prototheria. Much of Broom's thesis depended on other supposed evidence which proved to be erroneous even while Broom's paper was in press (see note by Walter Granger *in* Broom, 1914, p. 134; and Simpson, 1928b, pp. 11-12).

Simpson (1928a, p. 167; 1928b, pp. 11-12) accepted the association of the interclavicle with the type scapula of *Camptomus* (Marsh himself said only that they were provisionally associated) but doubted that the other fragments described by Marsh (astragalus and calcaneum) be-longed with the supposedly associated shoulder girdle elements. Simp-son believed that the newly found scapulocoracoid fragment of *Djadoch-tatherium* showed that Marsh was probably incorrect in referring the *Camptomus* fragments to a multituberculate. Simpson did not actually say that *Camptomus* was a reptile, but that he believed it to be so is clear enough. *Camptomus* has been banished from the mammal classification ever since.

Y.P.M. No. 11769 (fig. 4), type of *Camptomus amplus* Marsh, 1889, is a mammalian scapula with a spine projecting laterad from the middle of the blade, a feature thus far known only in therians. There are two additional *Camptomus* scapulae in the collections of the American Mu-seum of Natural History (A.M.N.H. Nos. 55990 and 55992). A second, larger form is represented by A.M.N.H. No. 55991, a fragmentary scapula otherwise nearly identical with the type of *C. amplus*.

FIG. 4. Unretouched photographs of Y.P.M. No. 11769, type of *Camptomus amplus* Marsh, 1889, fragmentary right therian scapula with facet for the coracoid, Hatcher's quarry no. 1, Lance formation, late Cretaceous, Lance Creek, Wyoming. *Upper left:* "Lateral" view. *Upper right:* "Posterior" view. *Lower left:* Glenoid fossa and coracoid facet. All × 4.

The coracoid is clearly a separate ossification in Y.P.M. No. 11769 and A.M.N.H. No. 55991, however, a fact that must be accounted for. Although almost no fully adult therian mammals living at the present time possess a large, separately ossified coracoid bone, the coracoid does persist as such a structure until very late in ontogeny in at least some individuals of a number of therian types and has actually been found in adults of a few living genera. Parker (1868, p. 204, pl. 23, fig. 21) figured and briefly mentioned a shoulder blade of an adult *Myrme-*

TABLE 1

Separate Coracoids in Late Stages of Ontogeny in Some Marsupials

	Condition of Coracoid	Stage in Ontogeny
DIDELPHIDAE		
Didelphis m. marsupialis, A.M.N.H.: M. No. 42881, British Guiana	Suture; left coracoid beginning to fuse to scapula	Half-grown male; no sagittal crest; M^3 and M_4 not fully erupted; deciduous teeth still present
Chironectes panamensis, A.M.N.H.:M. No. 148720, Costa Rica	Fused, but former suture can be traced locally	Young adult female; three young in pouch
Metachirus sp., A.M.N.H.:M. No. 97321, Rio Tocantins, Brazil	Suture; right coracoid beginning to fuse to scapula	Half-grown male; trace of sagittal crest; M^3 and M_4 not fully erupted; deciduous teeth still present
PHALANGERIDAE		
Phalanger ursinus, A.M.N.H.:M. No. 30596, northeast Celebes	Suture; large coracoid	Adult male
Phalanger orientalis, A.M.N.H.:M. No. 80934, Wetar I., Indonesia	Fused, but former suture can be traced locally; large coracoid	Adult female
Phascolarctos cinereus, A.M.N.H.:M. No. 65611, Queensland	Suture	Adult male
Shoinobates v. minor, A.M.N.H.:M. No. 65379, Queensland	Suture fusing	Adult female
PHASCOLOMIDAE		
Phascolomis u. tasmaniensis. A.M.-N.H.: M. No. 65623, Tasmania	Suture	Pouch young; cheek teeth barely erupted and barely worn; skull length, 80 mm.
Phascolomis u. tasmaniensis, A.M.-N.H.: M. No. 65621, Tasmania	Suture fusing	Young adult male, age unknown
Phascolomis u. tasmaniensis, A.M.-N.H.: M. No. 65624, Tasmania	Suture	Young adult male, age unknown
MACROPODIDAE		
Petrogale xanthopus, A.M.N.H.:M. No. 35642, locality unknown (zoo)	Suture	Half grown; M^3_3 not fully erupted; M^4_4 in capsules; sex not recorded
Thylogale s. stigmatica, A.M.N.H.:M. No. 65137, Queensland	Suture	Young male; M^4_4 not erupted; deciduous teeth present
Aepyprymnus rufescens, A.M.N.H.:M. No. 65282, Queensland	Suture fusing	Young female; M^3 and M^4_4 formed but not in place; deciduous blades present

cophaga in which the scapula and coracoid are separate. Lydekker (1893) found the same condition in an adult *Bradypus*. Howes (1887, 1893) observed that a suture may occur between the coracoid[1] and scapula in young lagomorphs (*Lepus*, four and seven weeks after birth), rodents (*Sciurus*, juvenile), edentates (*Bradypus*, juvenile; *Choloepus*, half grown), and primates (*Homo*, 14–15 years). Ameghino (1908) extended the list of edentates in which the phenomenon is known. Curiously, neither Howes (1893) nor Ameghino (1908) listed a single member of the Marsupialia, the one living therian order most likely to display the feature. Howes(1887, p. 192) had previously stated that the coracoid process was small in most marsupials, and this statement was apparently accepted by later students. Table 1 shows the results of a casual survey of recent marsupial skeletons in the collections of the Department of Mammalogy of the American Museum of Natural History. In the course of this work genus after genus was found in which the coracoid does not fuse to the scapula until well after the cheek teeth are in use. In two marsupials, *Phalanger* and *Phascolarctos*, separate coracoids were observed in individuals in which P_3^3 and M_4^4 were in use. These individuals are perhaps exceptional, but they demonstrate that the coracoid may remain separate in adult marsupials some 70 million years after the end of Cretaceous time. The small amount of evidence gathered to date indicates that further work will show that the coracoid fuses to the scapula rather late in ontogeny in a variety of therians and that in particular this phenomenon is fairly general in edentates and marsupials. One need not be a literal-minded Haeckelian to suspect that the coracoid remained as an ossification distinct from the scapula in at least some adult Cretaceous therians, such as *Camptomus*. The type specimen of *Camptomus* (Y.P.M. No. 11769) and A.M.N.H. Nos. 55990–55992 may therefore be regarded as therian without question and marsupial with great probability. *Camptomus* is probably a synonym of one of the Lance marsupial genera. The new material will be described elsewhere.

THE INTERCLAVICLE

Figure 5

    Marsh's identification of the interclavicle rests on the fact that it is a median structure, that it evidently possessed a long posterior process,

---

[1] Howes believed that there are two coracoid ossifications in a number of therians, corresponding to the coracoid and anterior coracoid (epicoracoid of Cuvier) of mammalian ancestors. Broom (1889, 1912) and various subsequent authors appear to have satisfactorily shown that one of these is an epiphysis and the other is the true (or posterior) coracoid.

FIG. 5. Unretouched photographs of a possible allotherian interclavicle (Y.P.M. No. 10639), probably from Hatcher's locality no. 1 (?U.C.M.P. locality V-5711), Lance formation, late Cretaceous, Lance Creek, Wyoming. *Above:* Ventral view. *Center:* Anterior view. *Below:* Dorsal view. All × 4.

and that the lateral wings at its anterior end bear elongate facets for the reception of a pair of bones, presumably the clavicles. Marsh's identification is probably correct.[1] Among the Lance vertebrates, how-

---

[1] Watson (1917, pp. 46–49, fig. 25) has suggested that the interclavicle may be represented in marsupials by the omosternum. This subject might well be investigated more fully.

ever, only *Champsosaurus,* the crocodilians, various lizards, and the mammals are likely to have had an interclavicle approximating the one discussed by Marsh. If correctly identified, Marsh's specimen would have to belong to a very young champsosaur if referable to that group. The crocodile interclavicle is always a long, sword-shaped bone which is not comparable to Marsh's specimen in detail. Teiid and varanid lizard interclavicles like those of *Tupinambis* and *Varanus* may have lateral processes at the anterior end for contact with the clavicles but are generally smaller and more slender than Marsh's specimen. The latter, if that of a lizard, would have to belong to a rather large species. It does not resemble the interclavicle of *Polyglyphanodon.* A feature of the Cretaceous specimen which occurs in none of the various types of interclavicles examined is the crudely paired system of foramina that penetrates the bone. There are two compound lateral foramina and one median foramen on what is interpreted as the ventral side of the bone. These meet in a series of interconnecting passages within the bone. A pair of foramina on the dorsal surface connect with these passages, and a third, unpaired lateral foramen appears to do so as well. Symmetry is not well developed.

If the specimen is truly an interclavicle (or omosternum), it may well belong to a large multituberculate such as *Meniscoëssus,* or possibly even to a large marsupial. It is approximately the right size to be referable to *Camptomus,* but it could equally well belong with a multituberculate such as that represented by the scapula called Lance Type 2. Further speculation is useless at present.

DISCUSSION

Three scapulocoracoids recovered from Cretaceous sediments permit certain conclusions concerning the shoulder girdle of the mammalian subclass Allotheria. An interclavicle described by O. C. Marsh may be referable to the Allotheria as well, but its affinities are still uncertain. Three specimens do not represent adequately the whole subclass, but insofar as can be determined in this study the allotherian shoulder girdle possesses the following distinctive attributes.

1. The spine is located at the front of the scapula and projects laterad. The scapular blade does not extend anterior to the spine on the lower (known) part of the scapula, although it may near the (unknown) vertebral border. There is no supraspinous fossa on the lateral side of the scapula other than a small area next to the coracoid.

2. The coracoid is a large bone, more or less like a bar, which projects

anteroventromedially, not posteroventromedially as in the posterior cora-
coid of monotremes. The exact extent of the coracoid is not known. It is
not possible to say whether, or not, it touched the sternum as in certain
foetal marsupials. The coracoid contributes to the glenoid fossa, but the
amount of this contribution is not known, because a scapulocoracoid su-
ture has not been observed. The orientation of the coracoid and the
glenoid fossa indicates that the shoulder girdle was not a yoke around
the neck as in monotremes or as interpreted for *Oligokyphus* but was situ-
ated lateral to the anterior ribs. In this orientation the humerus was
probably still carried at about the same angle as in cynodonts; it still pro-
jected somewhat laterad, in agreement with the orientation of the femur
as elucidated by Simpson and Elftman (1928). The anteroventromedial
orientation of the true (posterior) coracoid suggests that the anterior
coracoid bone was absent.

3. A division of the supracoracoid (coracohumeralis) musculature
(from ventral premuscular anlage) and not of the subscapular and teres
major musculature (from dorsal premuscular anlage) appears to occupy
the anterior part of the medial face of the scapula. It is derived from the
same source as m. supraspinatus of other mammals, but may not neces-
sarily be homologous with m. supraspinatus. It could be a parallel devel-
opment. The lack of an extension of the scapular blade anterior to the
spine on the lower part of the scapula evidently permits this ventral mus-
cle to transfer the site of its origin from the coracoid up onto the *medial*
face of the scapula, thus restricting the dorsally derived m. subscapularis
to more posterior parts of the scapula. A similar medial position of the in-
fraspinatus occurs in adult *Tachyglossus* and *Zaglossus* and in foetal *Didel-
phis* and has been suggested for adult *Oligokyphus* (Kühne, 1956). Such a
position may well be general in foetal therians, but the subject has not
been investigated.

AFFINITIES

The affinities of the Allotheria have been in doubt since the first speci-
mens of *Plagiaulax* were described by Falconer more than 100 years ago.
A comprehensive analysis of the question has been prepared by Simpson
(1937). The latest survey of the question is by Ride (1957). Thus far, the
problem of the degree of relationship to the remaining mammalian sub-
classes has not been completely solved by the skulls, jaws, or hind limb
recovered to date from late Cretaceous or early Tertiary sites. What is re-
quired now is the finding of better Jurassic or even early Cretaceous
material. Knowledge of the condition of the shoulder girdle at the close

of Cretaceous time adds valuable data to the evidence previously accumulated, but even the new evidence is not conclusive in itself. The shoulder girdle is generally a conservative complex, however, and in this case demonstrates similarities to foetal therians and advanced therapsids which may be meaningful.

Among the Therapsida, *Oligokyphus* and *Cynognathus* possess scapulocoracoids significantly similar to the allotherian scapulocoracoids discussed here. *Cynognathus* (see especially Romer, 1922a, pl. 33) possesses an acromion, a rather ventrally projecting posterior coracoid, a reduced anterior coracoid, and a trough-shaped infraspinous fossa.[1] The latter lies between the laterally projecting anterior edge of the blade (spine) and a similarly projecting lamina at the rear of the blade. At the vertebral end of the blade a second anterior edge is present medial to the outturned spine, a foreshadowing of the therian condition which unfortunately cannot be demonstrated at present in allotherians because of damage to all three available specimens. In comparable features, almost all that is required to transform the scapulocoracoid of *Cynognathus* into an allotherian scapulocoracoid is a reduction in the over-all size, a fusion of the posterior coracoid to the scapula and a swinging of the former around to become an anteroventromedian projection, an aborting of the ossification of the anterior coracoid or its fusion insensibly to the scapula or coracoid, and the undercutting of the acromion. These are all minor changes and continue trends leading up to *Cynognathus*.

The lower half of the scapulocoracoid of *Oligokyphus* has been interpreted by Kühne (1956). The vertebral half is unknown. The anterior edge of the known part of the blade turns sharply laterad to form the spine. The acromion is undercut, an advance over *Cynognathus*. The anterior edge of the blade does not extend forward beyond the base of the acromion. Behind the spine is a trough-shaped infraspinous fossa. Both coracoids are present. The posterior coracoid is suturally connected to the scapula but fuses to it in some specimens, presumably old ones. The anterior coracoid is suturally attached to the posterior coracoid and perhaps to the scapula, although this latter point is not clear. The posterior coracoid projects ventromediad. Like *Cynognathus*, *Oligokyphus* is notably

---

[1] The muscle originating from this fossa in therapsids is universally called m. infraspinatus, a designation that stems from comparisons with a homologous muscle of monotremes as interpreted by Wilson and McKay (1893) and McKay (1894). But "m. infraspinatus" of monotremes has been shown by Howell (1937a) to be m. teres minor, a muscle of dorsal derivation. M. infraspinatus is derived from the ventral premuscular anlage and is probably restricted to the Mammalia. In embryonic *Didelphis* (Cheng, 1955, p. 435) the potential teres minor occupies the infraspinous fossa prior to the invasion by the potential infraspinatus at stage III (6.0 mm. in crown to rump length).

advanced towards the therian condition, but both genera also show simi-
larities to monotremes.

Cheng (1955) has discussed the developing shoulder girdle of *Didelphis*
in detail. When the embryo has attained about 6.0 mm. in crown to
rump length, the supraspinous fossa still has not formed. The acromion
projects laterad from the anterior edge of the blade (*ibid.*, p. 431, fig. 7)
and is undercut. The true coracoid still projects posteroventromediad. A
slightly larger embryo (*ibid.*, pp. 439, 440, figs. 11, 12) of 7.5 mm. in
crown to rump length shows that a new anterior edge of the scapula has
formed *before* the spine has begun to grow laterad, which can be inter-
preted in several ways: Either the old anterior edge gives rise to a new
anterior projection and then the former grows laterad as the spine, or the
spine is not the homologue of the old anterior edge of the vertebral half
of the scapula. I prefer to think that both the spine and the new anterior
edge are outgrowths of the old anterior edge of the vertebral half of the
blade and that arguments over homology in this case are meaningless.
What happens is clear enough.

In foetal *Didelphis* the coracoid comes to project ventromediad by the
time the crown to rump length has reached 12.0 mm., but by that time
the supraspinous fossa is well formed. Insofar as comparison here is
meaningful, such a condition is in contrast to that in adult allotheres. The
latter possess an anteroventromedially projecting coracoid but have not
developed a supraspinous fossa on the lateral face of the scapula. A re-
semblance of these foetal stages of *Didelphis* to adult *Cynognathus* and *Oli-
gokyphus* is about as great as to the allotheres discussed in this paper. It
seems probable that the resemblances to allotheres shown by the *Didelphis*
embryos are evidence of common ancestry from animals with a shoulder
girdle at the cynodont stage of development.

The three living genera of the subclass Prototheria are placed in a sin-
gle order, the Monotremata, despite great anatomical differences be-
tween *Ornithorhynchus* and the other two genera. The ancestry of the Pro-
totheria is unknown other than a few Pleistocene fossils which yield no
significant information. Opinions concerning affinities range from Greg-
ory's (1947) view that the Prototheria are essentially neotenic marsupials
to Howell's (1937a) view that the Prototheria are of reptilian origin but
are not derived from any known therapsid because of the reduction in
that group of the anterior coracoid bone. A truly thorough study of pro-
totherian embryology would doubtless go far towards an answer to the
problem.

The shoulder girdle of monotremes is clearly of reptilian origin, but
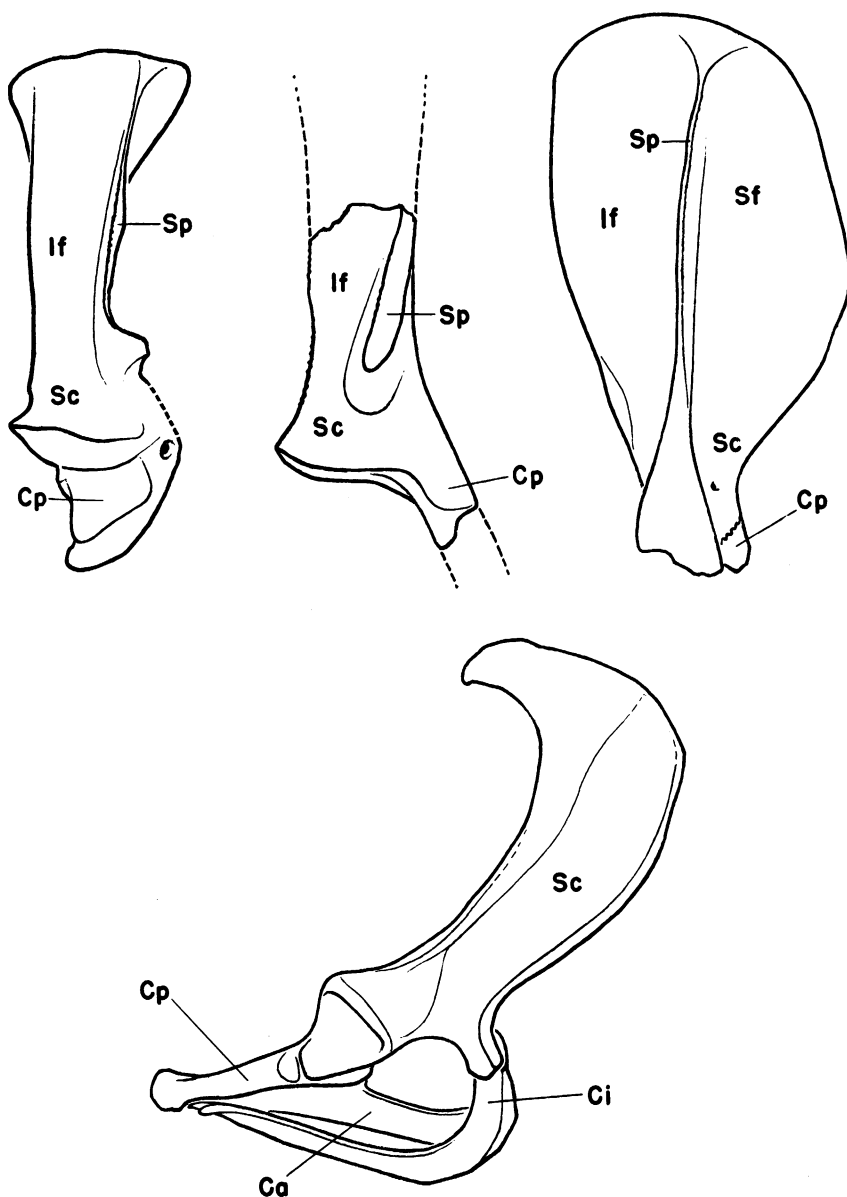there is such an overlay of habitus characters that the adult scapulocora-

Fig. 6. Diagrammatic lateral views of some major types of mammalian and therapsid scapulocoracoids. *Upper left: Cynognathus,* a cynodont therapsid. *Upper center:* Lance Type 1, an allotherian (multituberculate). *Upper right: Didelphis,* a therian mammal. *Below: Ornithorhynchus,* a prototherian (monotreme). *Abbreviations:* Ca., anterior coracoid; Ci., clavicle and interclavicle; Cp., posterior coracoid; If., infraspinous fossa; Sc., scapula; Sf., supraspinous fossa; Sp., spine.

coid is unlike that of any other vertebrate in detail. The cynodonts, allo-
theres, and even therians all possess a trough-like infraspinous fossa pos-
terior to a laterally projecting spine. The lateral face of a monotreme
scapulocoracoid is essentially flat. The acromion of all three monotremes
projects forward, not laterad. It could even be argued that there is no
spine in monotremes; what has been taken for the homologue of the spine
may only be homologous with the anterior edge of the developing scapula
of a stage III *Didelphis* embryo (6.0 mm. in crown to rump length; see
Cheng, 1955, fig. 9). Prior to the development of the spine and new an-
terior edge, in all three monotreme genera the posterior coracoid projects
posteroventromediad. As Howell has noted, the retention of a large an-
terior coracoid is not a special similarity to therapsids. Whatever the ori-
gin of monotremes, either marsupial neoteny or remote derivation from
the Reptilia, the adult shoulder girdle of *Ornithorhynchus, Tachyglossus,* and
Zaglossus is not significantly similar to that of the Theria or known Allo-
theria. The adult shoulder girdle does not indicate close relationship of
the subclasses Allotheria and Prototheria (fig. 6).

From the evidence of the shoulder girdle, and that complex only, the
Mesozoic and early Cenozoic subclass Allotheria appears to have orig-
inated from cynodont therapsids in the first half of the Mesozoic era. The
subclass Allotheria appears to be more closely related to the mammalian
subclass Theria than to the subclass Prototheria, but the closest relatives
of all appear to be the cynodont therapsids. The shoulder girdle supports
the thesis that the Mammalia, as currently classified, are polyphyletic.

SUMMARY

The Allotheria constitute a nominally mammalian subclass consisting
of a single order, the Multituberculata. The known chronologic range of
the Allotheria is long: late Jurassic to early Eocene. The shoulder girdle
is known from only three scapulocoracoids, only one of which was un-
questionably associated with remains of the dentition. An interclavicle
may be referable to the Allotheria, but only with considerable doubt. The
allotherian shoulder girdle differs significantly from that of the subclasses
Theria and Prototheria. Similarities to cynodont therapsids and to foetal
marsupials suggest that the Allotheria originated either from cynodonts
or from early mammals still possessing a shoulder girdle at the cynodont
level of organization.

REFERENCES

AMEGHINO, F.
    1893.   Les premiers mammifères. Relations entre les mammifères diprotodontes

éocènes de l'Amerique du Nord et ceux de la République Argentine. Rev. Gen. Sci., Paris, vol. 4, pp. 77–81, 5 figs. Reprinted with Spanish translation in Obras Completas, vol. 10, art. 85, pp. 548–567, figs. 1–5, Buenos Aires, 1918.

1908.   El arco escapular de los desdentados y monotremos y el origen reptiloide de estos dos grupos de mamíferos. An. Mus. Nac. Buenos Aires, ser. 3, vol. 10, pp. 1–91. Reprinted in Obras Completas, vol. 17, art. 151, pp. 295–382, figs. 1–60, Buenos Aires, 1934.

ALLEN, G. M.
1912.   *Zaglossus*. Mem. Mus. Comp. Zool., Harvard College, vol. 40, no. 5, pp. 253–307, pls. 1, 2.

BROOM, R.
1897.   On the existence of a sterno-coracoidal articulation in a foetal marsupial. Jour. Anat. Physiol., London, vol. 31, pp. 513–515, 1 fig.
1898.   A contribution to the development of the common phalanger. Proc. Linnean Soc. New South Wales, ser. 2, vol. 13, pp. 705–729, pls. 22–25.
1899.   On the development and morphology of the marsupial shoulder girdle. Trans. Roy. Soc. Edinburgh, vol. 39, pt. 3, pp. 749–770, pls. 1, 2.
1902.   On the early condition of the shoulder girdle in the polyprotodont marsupials *Dasyurus* and *Perameles*. Jour. Linnean Soc. London, Zool., vol. 28, pp. 449–454, pl. 41.
1912.   The morphology of the coracoid. Anat. Anz., vol. 41, pp. 625–631, figs. 1–16.
1914.   On the structure and affinities of the Multituberculata. Bull. Amer. Mus. Nat. Hist., vol. 33, pp. 115–134, figs. 1–9, pls. 11, 12.

CHENG, CZE-CHING
1955.   The development of the shoulder region of the opossum, *Didelphis virginiana*, with special reference to musculature. Jour. Morph., vol. 97, no. 3, pp. 415–471, figs. 1–20.

COPE, E. D.
1888.   The Multituberculata monotremes. Amer. Nat., vol. 22, p. 259.

DOBSON, G. E.
1882–1890.   A monograph of the Insectivora, systematic and anatomical. London, J. Van Voorst, pts. 1–3 (all), iv + 172 pp., 28 pls.

DOLLO, LOUIS
1889.   Mammifères crétacés. Rev. des Questions Sci., Soc. Sci. Bruxelles, vol. 26, pp. 674–676.

FLOWER, W. H.
1885.   An introduction to the osteology of the Mammalia. Third edition, revised with the assistance of Hans Gadow. London, the Macmillan Co., xii + 383 pp., 134 figs.

FRIANT, M.
1954.   Sur les affinités du *Plagiaulax*, mammifère mésozoique. Proc. Zool. Soc. London, vol. 124, pp. 501–507, figs. 1–7.

GIDLEY, JAMES WILLIAMS
1909.   Notes on the fossil mammalian genus *Ptilodus*, with descriptions of new species. Proc. U. S. Natl. Mus., vol. 36, pp. 611–626, figs. 1–9, pl. 70.

GREGORY, WILLIAM KING
1910.   The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1–524,

figs. 1–32.

1915.   Present status of the problem of the origin of the Tetrapoda. Ann. New
         York Acad. Sci., vol. 26, pp. 317–383, figs. 1–15, pl. 4.

1918.   Second note on the evolution of the coracoid elements in reptiles and
         mammals. *Part VI of* Gregory, W. K., and C. L. Camp, Studies in com-
         parative myology and osteology. No. III. Bull. Amer. Mus. Nat. Hist.,
         vol. 38, art. 15, pp. 545–552, figs. 14–16.

1947.   The monotremes and the palimpsest theory. *Ibid.,* vol. 88, art. 1, pp. 1–
         52, figs. 1–17, pls. 1, 2.

GROSS, WALTER
1954.   Zur Phylogenie des Schultergürtels. Paläont. Zeitschr., vol. 28, pt. 1,
         no. 2, pp. 20–40, figs. 1–10.

HANSON, F. B.
1919.   The coracoid of *Sus scrofa.* Anat. Rec., vol. 16, pp. 197–202, figs. 1–6.
1920.   The problem of the coracoid. *Ibid.,* vol. 19, pp. 327–345.

HOWELL, A. BRAZIER
1937a.   Morphogenesis of the shoulder architecture. Part V. Monotremata.
         Quart. Rev. Biol., vol. 12, no. 2, pp. 191–205, figs. 1–4.
1937b.   Morphogenesis of the shoulder architecture. Part VI. Therian Mam-
         malia. *Ibid.,* vol. 12, pp. 440–463.

HOWES, G. B.
1887.   The morphology of the mammalian coracoid. Jour. Anat. Physiol., vol.
         21, pp. 190–198.
1893.   On the coracoid of the terrestrial Vertebrata. Proc. Zool. Soc. London,
         pp. 585–592, figs. 1, 2.

JEPSEN, G. L.
1940.   Paleocene faunas of the Polecat Bench formation, Park County, Wyo-
         ming. Part I. Proc. Amer. Phil. Soc., vol. 83, no. 2, pp. 217–341, figs.
         1–22, pls. 1–5.

KUHNE, W. G.
1956.   The Liassic therapsid *Oligokyphus.* London, British Museum (Natural His-
         tory), x + 149 pp., 66 figs., 12 pls.

LEMOINE, VICTOR
1889.   Considérations générales sur les vertébrés fossiles des environs de Reims
         et spécialement sur les mammifères de la faune cernaysienne. Compte-
         Rendu Séances du Congr. Internatl. Zool., 1889, pp. 233–279, figs. 1–8.

LULL, R. S.
1915.   The mammals and horned dinosaurs of the Lance formation of Niobrara
         County, Wyoming. Amer. Jour. Sci., vol. 40, pp. 319–348, figs. 1–5.

LYDEKKER, R.
1889.   Paleozoology, Vertebrata. *Part 3 of* Nicholson, H. A., and R. Lydekker,
         A manual of paleontology for the use of students, with a general intro-
         duction on the principles of paleontology. Third edition, revised. Edin-
         burgh and London, vol. 2, pp. i–xiv, 889–1474, figs. 813–1354.
1893.   Note on the coracoidal element in adult sloths, with remarks on its homol-
         ogy. Proc. Zool. Soc. London, pp. 172–174, 1 fig.

McCRADY, EDWARD, JR.
1938.   The embryology of the opossum. Amer. Anat. Mem., no. 16, pp. 1–233,
         figs. 1–66, pls. 1–3.

McKay, W. J. S.
  1894. The morphology of the muscles of the shoulder-girdle in monotremes. Proc. Linnean Soc., New South Wales, vol. 9, pp. 263–360, pls. 20–23.
Marsh, O. C.
  1889. Discovery of Cretaceous Mammalia. Amer. Jour. Sci., vol. 38, app., art. 11, pp. 81–92, pls. 2–5.
Osborn, H. F.
  1891. A review of the Cretaceous Mammalia. Proc. Acad. Nat. Sci. Philadelphia, pp. 124–135, 8 figs.
Parker, W. K.
  1868. A monograph on the structure and development of the shoulder-girdle and sternum in the Vertebrata. London, the Royal Society, xii + 237 pp., 6 figs., 30 pls.
Ride, W. D. L.
  1957. The affinities of *Plagiaulax*. Proc. Zool. Soc. London, vol. 128, pt. 3, pp. 397–402, fig. 1.
Romer, Alfred S.
  1922a. The locomotor apparatus of certain primitive and mammal-like reptiles. Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 517–606, figs. 1–7, pls. 27–46.
  1922b. The comparison of the mammalian and reptilian coracoids. Anat. Rec., vol. 24, pp. 39–47, fig. 1.
  1944. The development of tetrapod limb musculature—the shoulder region of *Lacerta*. Jour. Morph., vol. 74, pp. 1–41, figs. 1–18.
Shrivastava, R. K.
  [MS.] Anatomie comparée du muscle deltoide et son innervation dans la série des mammifères. Theses présentées a la Faculté des Sciences de l'Université de Paris. 1960. Unpublished doctoral thesis.
Simpson, G. G.
  1928a. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London, British Museum (Natural History), x + 215 pp., 56 figs., 12 pls.
  1928b. Further notes on Mongolian Cretaceous mammals. Amer. Mus. Novitates, no. 329, pp. 1–14, figs. 1–7.
  1929. American Mesozoic Mammalia. Mem. Peabody Mus., Yale Univ., vol. 3, pt. 1, pp. i–xvi, 1–171, figs. 1–62, pls. 1–32.
  1937. Skull structure of the Multituberculata. Bull. Amer. Mus. Nat. Hist., vol. 73, pp. 727–763, figs. 1–9.
Simpson, G. G., and H. O. Elftman
  1928. Hind limb musculature and habits of a Paleocene multituberculate. Amer. Mus. Novitates, no. 333, pp. 1–19, figs. 1–6.
Skinner, J. H.
  1959. Ontogeny of the breast-shoulder apparatus of the South African lacertilian, *Microsaura pumila pumila* (Daudin). Ann. Univ. Stellenbosch, vol. 35, sect. A, no. 1, pp. 5–66, figs. 1–28.
Trouessart, E. L.
  1898. Catalogus mammalium tam viventium quam fossilium. Nova editio. Paris, fasc. 4, pp. 665–1264.

WATSON, D. M. S.
    1917. The evolution of the tetrapod shoulder girdle and forelimb. Jour. Anat., vol. 52, pp. 1–62, figs. 1–27.
    1931. On the skeleton of a bauriamorph reptile. Proc. Zool. Soc. London, pp. 1163–1205, figs. 1–27.
WEBER, MAX
    1927. Die Säugetiere. Jena, Gustav Fischer, vol. 1, Anatomischer Teil, xvi + 444 pp., 316 figs.
WILSON, J. T., AND W. J. STEWART MCKAY
    1893. On the homologies of the borders and surfaces of the scapula in monotremes. Proc. Linnean Soc., New South Wales, ser. 2, vol. 8, pp. 377–388, pl. 21.
WOODWARD, A. S.
    1898. Outlines of vertebrate paleontology for students of zoology. Cambridge, Cambridge University Press, xxiv + 470 pp., 288 figs.
ZITTEL, K. A.
    1893. Handbuch der Palaeontologie. I Abteilung. Palaeozoologie. Munich and Leipzig, R. Oldenbourg, vol. 4, Vertebrata (Mammalia), xii + 799 pp., 590 figs.