

THE POSTCRANIAL SKELETON OF THE LATE TRITYLODONT BIENOTHEROIDES

by

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ABSTRACT

The text is a description of the postcrania belonging to the latest tritylodont *Bienotheroides*. A correlation is also made between this taxa, other tritylodonts, and primitive mammals. There appears a incipient supraspinatus fossa on the scapula that is evidence that the relationship between mammals and tritylodonts is even more intimate than previously envisioned.

INTRODUCTION

The Tritylodontia is a family of extremely advanced theriodonts that appears in the Late Triassic and Early Jurassic. According to previous descriptions, there is only one other genus in addition to *Bienotheroides* that exists in the Middle Jurassic, this being the European *Stereognathus*.

Bienotheroides from Sichuan Province is a tritylodont from the late stage of the Jurassic and coexists with the sauropod dinosaur *Mamenchisaurus* produced from the Upper Xiaximiao Formation. Its stratigraphic position is 150-200m above the basal boundary of the upper conchostracan beds in the Upper Xiaximiao Formation. Based upon other fossil taxa, the age of the Upper Xiaximiao Formation is Middle Jurassic (Gu, 1976) to early Late Jurassic (Dong, 1980).

Advanced mammalian characters manifested in the Tritylodontia are also clearly noticeable in their postcranial skeleton. An extremely good description has been made of the European *Oligokyphus* (Kühne, 1956), as well as several accounts made of *Bienotherium* from Yunnan Province (Young, 1947); however, this is the first discovery of a relatively complete postcranial skeleton from the later stages, warranting an additional description.

The material described is compiled from among three individuals: V4734 is the type specimen of *Bienotheroides wanhsienensis*. The skull, attached to four cervical vertebrae, has been published on previously (Young, 1982; Sun, 1984). The specimen was produced by the Hamachong Shiliang Production Brigade of Gaoliang Commune in Wan County, Sichuan Province. A second specimen, V7905, is the anterior half of an individual produced from Nanjiangcuijia Gou in Sichuan. Specimen V7906 is an incomplete individual produced by a production brigade of the Hongqi Commune at Tangjiahe, Wancang County, Sichuan.

These three individuals all belong to *Bienotheroides* based upon diagnoses of the skulls. Because the skulls of V7905 and V7906 have still not been properly prepared and studied, it is not possible to assign them to different species, or to provide separate descriptions within this text.

1. Vertebrae

Material: V4734: cervical vertebrae 1-4; V7905: 5 individual cervical and anterior thoracic vertebrae; V7906: 11 presacral vertebrae.

Atlas and Axis:

These are identical to several cynodonts and mammals. On specimen V4734 the atlas and axis are fused, with the atlas only preserving the centrum. The unit is shaped as a slightly dorsoventrally compressed cube with the suture between the atlas-axis clearly distinguished at the ventral aspect, where it is situated at the center of the square.

It differs from the mammalian condition, because the tritylodontids still maintain a well-developed atlas centrum. Also, the development of the odontoid process is slightly inferior to those of extant mammals; similar to *Morganucodon*; and particularly similar to that of *Oligokyphus*. The anterior margin of the *Bienotherodes* atlas centrum is expanded laterally on both sides resulting in the odontoid process not

being as distinguishable as on either *Oligokyphus* or *Morganucodon*.. The facet for the atlas arch is an expanded crecentric face (F.at.a.) and there is an oblique surface at the ventral side of the odontoid process that is contiguous with the facet for the atlas intercentrum (F.a.i.). At the posterior surface there is a broad and shallow sulcus that serves as a corridor for the spinal cord. Apart from the damaged neural spine, the remainder of the axis is complete. On *Galesaurus* the ventral surface of the axis body is dumbbell shaped with its medially convex anterior margin contiguous with a rhomboid-shaped intercentrum. On specimen V4734 it is possible to observe the axis ventral surface, the anterior margin of which is laterally convex and articulates with the atlas. Based upon an inference of its length, it appears as though a rhomboid-shaped intercentrum should be present. The suture, however, is difficult to distinguish.

The axis is also displayed as a transversely broadened form with the length of the axis centrum noticeably smaller than that of the atlas centrum, thereupon also suggesting the possibility of an axis intercentrum. This is also a noticeable primitive character compared to mammals. Mammals, in general, with the exception of the Monotremata, have an axis much larger than the atlas, and as the size of the atlas centrum is greatly reduced, only the odontoid process alone is preserved (Jenkins, 1971).

Although the neural arch of the axis is incomplete, it is clearly broadened with the length of the basal section equivalent to the length of the centrum. Both sides of the dorsal aspect each possess a foramen for muscular attachment. The postzygopophyses are situated at the posterior margin's lateral angle and are not developed very well. The transverse process on the left side is completely preserved, situated laterally at the center of the centrum, extended posterolaterally, and is short and thick.

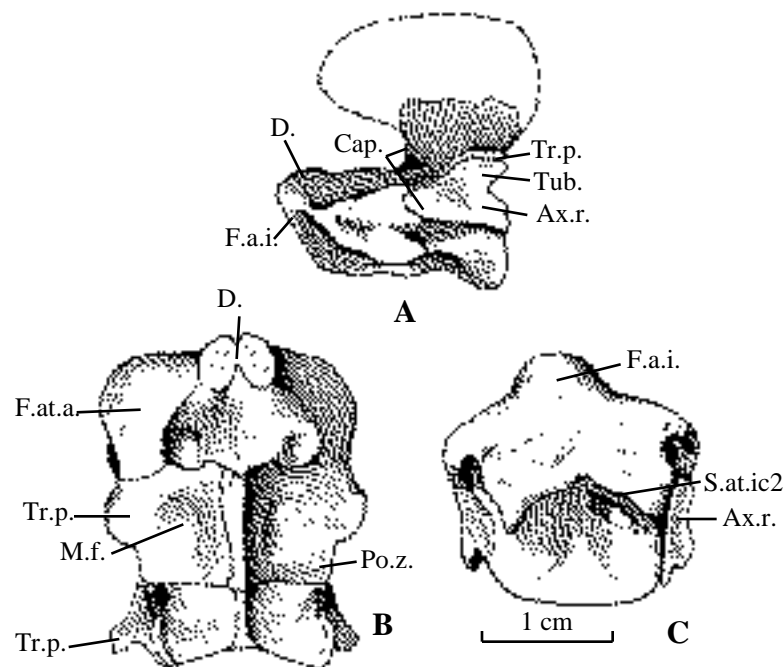


Figure 1. Cervical vertebrae of *Bienotheroides* (V4734).
 A. Lateral view of atlas and axis. B. Dorsal view of first three anterior cervicals.
 C. Ventral view of atlas and axis.

Specimen 7905 has a centrum compressed upon the dorsal side of the interclavicle, with a total of Specimen V4734 maintains the third and fourth cervical vertebrae articulated with the atlas-axis. The fourth cervical vertebra is rather greatly reduced, but morphologically is generally consistent with that of the preceding vertebra. The third cervical vertebra is also short, and appears to be the same breadth as the axis. The length of the neural arch is shorter than that of the axis, the right side has been crushed into the

ventral surface of the axis, and the neural spine has been broken off. The distance between the anterior and posterior zygopophyses has also been reduced. The structure of the transverse processes is consistent with that of the axis, being also extended posterolaterally and positioned low. The neural arch is expanded laterally, which is identical to *Megazostrodon rudnerae* (Jenkins and Parrington, 1976). five dorsal vertebrae. The first only preserves a transverse process and the ventral section of the centrum. The morphology of these vertebrae are generally consistent with the third and fourth cervical vertebrae of specimen V4734, only the neural spine is beginning to become well developed. Particularly noteworthy is the pedicle on the most posterior vertebrae, which is beginning to become medially reduced, such that the distance between the left and right zygopophyses is shortened and the neural spine is noticeably increased in height. The transverse processes on this string of vertebrae are all very well developed, are clearly longer than those on specimen V4734, and have extremely robust terminal ends. The breadth of the centrum is still greater than the length. Extremely thick and large parapophyses may be observed from the ventral aspect that are positioned very much toward the ventral side. The lateral surfaces have an appearance identical to *Megazostrodon*.

Regarding specimen V7905, although this string of vertebrae has been crushed upon the dorsal surface of the clavicle and long shaft of the interclavicle, it is possible from the ventral aspect to observe a short and thick cervical rib articulated to the ends of the transverse process; hence, the interpretation of these being the posterior cervical vertebrae appears to be more appropriate. Although the last vertebra is incompletely preserved, it is clearly morphologically different from the anterior vertebrae and should be considered the first thoracic vertebra based upon the observation of its lateral side.

Specimen V7905 possesses eleven dorsal vertebrae; these are preserved in three sequences and are all accompanied by very well-developed ribs at their lateral sides. At the extreme anterior end, the first sequence contains two dorsal vertebrae preserved with the left radius-ulna. The second sequence contains five dorsal vertebrae and the third sequence contains four dorsal vertebrae. Undoubtedly, these three sections are from an articulated vertebral column, and although there has been some loss between them, the damage is not extensive. Compared to the preceding cervical vertebrae, these dorsal vertebrae are notably larger, but careful consideration of specimens V7905 and V7906 indicate the size of their humerus and scapula to be identical, such that the reason specimen 7906 has larger dorsal vertebrae should not be the result of individual variation.

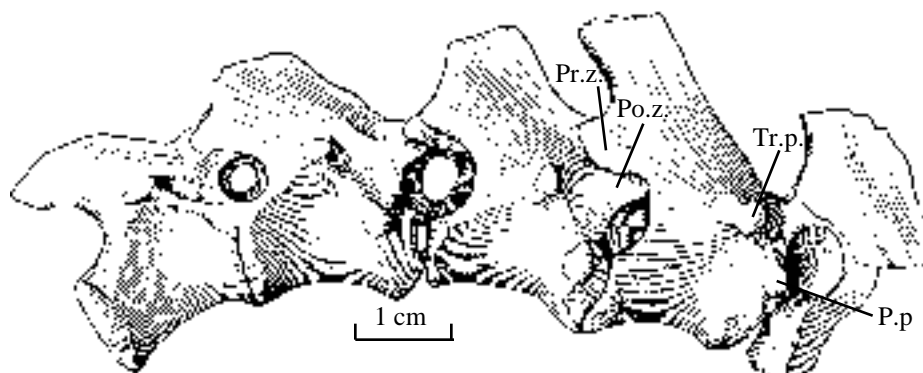


Figure 2. Lateral view of view dorsal vertebrae of *Bienotheroides* (V7906).

There are no complete neural spines preserved on the vertebrae, but the remnants are inclined posteriorly, with their degree of inclination increasing posteriorly. The breadth of the neural arches is also progressively reduced. The positions of the transverse processes and parapophyses are ascended more than on the cervical vertebrae. Seven vertebrae of the anterior two sequences each maintain two relatively well-preserved dorsal ribs attached to them with their position and distance of projection consistent. Only the two posterior dorsal vertebrae have alterations in which the transverse processes are directed slightly posteriorly, and the parapophyses directed slightly dorsally. It may therefore be observed that these seven

vertebrae represent the anterior dorsal vertebrae. The pre- and post-zygopophyses are all well articulated with each other.

The most posterior section's vertebrae are not exceptionally preserved as the left and right ribs have been crushed overlapping them. From a dorsal perspective, the neural arches are even more narrow and long, and the neural spine is even more posteriorly inclined. Naturally, they should still be assigned as dorsal vertebrae.

Material: V4734 left axial rib; V7905 most posterior cervical and first thoracic rib; V7906 several dorsal ribs.

There may be observed on specimen V4734 at the ventral surface of the axis a small triangular-shaped bone projecting from the lateral side of the axis. Undoubtedly, this is an axial rib. The rib is triangular in shape and the tuberculum is tightly abutted to the ventral surface of the transverse process. The capitulum is extended straight to the anterior margin of the axial centrum concealing the parapophysis of the axis. The posterior section of the rib has been lost, but it is estimated that the loss is not much.

There are two short and robust bones on specimen V7905 at the right side of the cervical vertebra's ventral surface. The proximal ends are still articulated to the transverse processes, but there is a slight space between them and the parapophyses. These represent the cervical ribs of *Bienotherium*. The presence of cervical and axial ribs illustrates that this taxa still preserves primitive reptilian characters.

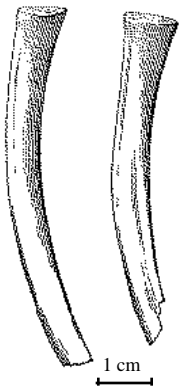


Figure 3.
Ribs of
Bienotheroides
(V7906)

The posterior section of the V7905 cervical rib is inclined to lie upon a relatively long dorsal rib. This should be considered the first thoracic rib due to its extended shape which stretches from the left side of the first dorsal vertebra to the last vertebra on this specimen. The rib head is extended but is still not bifurcated, being similar to specimen 7374 and 7376 of *Oligokyphus* as described by Khüne (1956). The anterior surface of the rib is smooth and glossy while the posterior surface maintains a depression. The distal end is not preserved.

Additionally, specimen V7906 possesses two ribs that have been separated (Figure 3). The rib heads are not extended and are moncapitate. Their width is comparable to the other ribs and should represent posterior dorsal ribs. The curvature of the ribs is not great. No ribs display a complete and well-preserved distal end.

Material: V7905 left and right clavicle, interclavicle, left and right presternum, left and right scapula, left and right corocoid. Preservation is quite complete with each element articulated in natural position. V7906: left scapula, corocoid

This element is sigmoid shaped with a length of 55mm. The proximal ends are flat, even, and slightly inflated. The left and right clavicles are connected to form a slightly arc-shaped plate. The dorsal section articulates with the interclavicle at a point that is depressed medially. There is a slight rotation along the curvature at the distal third of the element that causes the posterior margin of the proximal end to rotate into the anterior margin of the distal end. Distally it becomes narrow and thick.

The interclavicle is formed as a T-shape that is identical to that of *Morganucodon*. The discrepancies that occur between this specimen and *Morganucodon* consist of the proximal end of this element being flat and straight and not projected anteriorly. From the ventral surface, the entire transverse beam of the interclavicle is covered by the closure of the left and right clavicle. This also deviates from the condition of *Morganucodon*. There is a pair of small projections at the anterior quarter of the interclavicle shaft, which is a feature not observed on *Morganucodon*. *Bienotheroides* has a transverse beam 40mm in length, compared to the 10mm length of the posterior shaft. The terminal end of the posterior shaft is slightly broadened. This is unlike the morphology of an echidna monotreme (Figure 5).

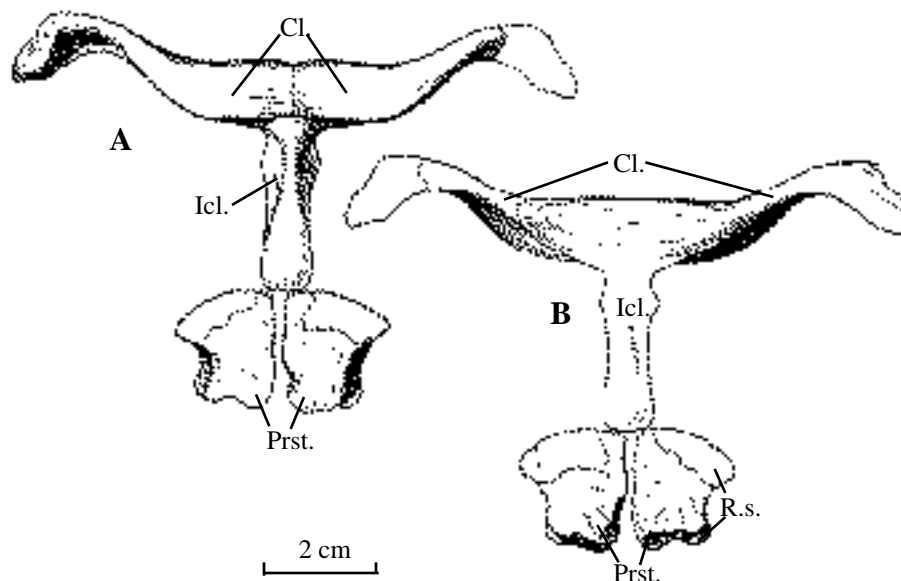


Figure 4. Dermal shoulder girdle of *Bienotheroides* (V7905).
A. Ventral view. B. Dorsal view.

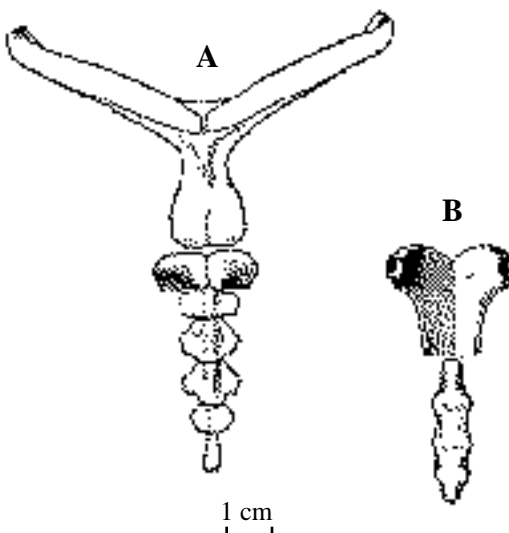


Figure 5. A. Ventral view of *Echidna* dermal shoulder girdle and sternum.
B. Dorsal view of *Oligokyphus* sternum and presternum (from Kühne, 1956)

The shape of the presternum is nearly square with a morphology similar to *Oligokyphus*. There is a 2mm gap between the left and right presternum illustrating a connection by cartilage when the animal was living. The anterior margin is broadened. The anterolateral angle and posterolateral angle both maintain nodes for the attachment of ribs. The dorsal surface is slightly concave. Posteriorly the sternum has not been preserved.

The tritylodontid shoulder girdle and sternum are extremely similar to those of the monotremes. The Echidna interclavicle differs in that the terminal end has become inflated into a heart shape, and the presternum is thicker and shorter.

Regardless of whether or not *Oligokyphus* is still the earliest mammal, there are no complete scapula preserved, and of those scapula that are preserved, all consist of proximal ends. Therefore, comprehension of this element is limited.

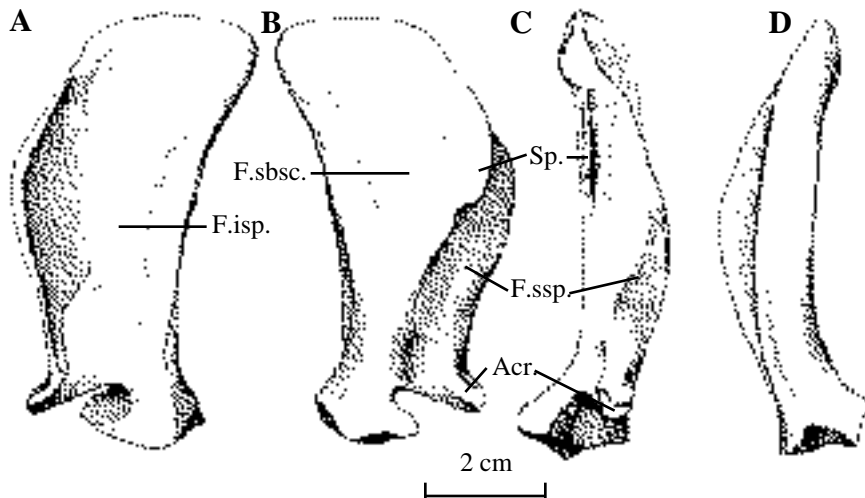


Figure 6. Left scapula of *Bienotheroides* (V7905).
A. Lateral view. B. Medial view. C. Anterior view. D. Posterior view.

Bienotheroides specimen V7905 possesses a relatively complete scapula with a length of 82mm. Its greatest breadth is at the center of the scapular blade. It is similar to the *Cynodontia* and *Oligokyphus* with the cranial and caudal borders strongly laterally recurved. The infraspinatus fossa lying between these two borders is extremely deep and extends directly to the lower region of the scapular spine. It appears as though the *m. infraspinatus* would have been perfectly well developed.

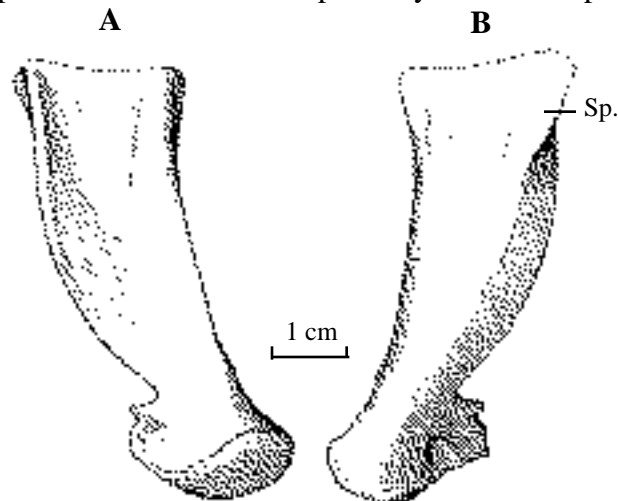


Figure 7. Left scapula of cf.? *Cynognathus* (cf.? *Diademodon*) (from Jenkins, 1971; Fig. 17)
A. Lateral view. B. Medial view

Particularly noteworthy is a characteristic point on specimen V7905 where on the medial side of the scapula at the anterior section of the vertebral margin there is a small protuberance that extends anteroventrally and attenuates at the center of the scapula blade. Consequently, there is the appearance of a secondary anterior margin on the scapula blade. Moreover, there is a fossa formed between the lateral side and the original anterior margin of the scapula. Clearly this fossa may be correlated to the supraspinatus fossa existing on mammals. On specimen V7906 the vertebral margin of the scapula has been lost, but it is still possible to observe the same presence of the supraspinatus fossa and the small blade-like projection that exists on specimen V7905. The structure of the supraspinatus fossa has been considered to be absent on the theriodonts (Romer, 1922). In his description of the cynodont scapula-corocoid, F.A. Jenkins (1971) does not mention the supraspinatus fossa, although in his figure 17 B there appears to be a similar fossa situated at the same position, but not as well developed as on *Bienotheroides*. Therefore, the current authors believe that on certain advanced cynodonts an incipient supraspinatus fossa is present.

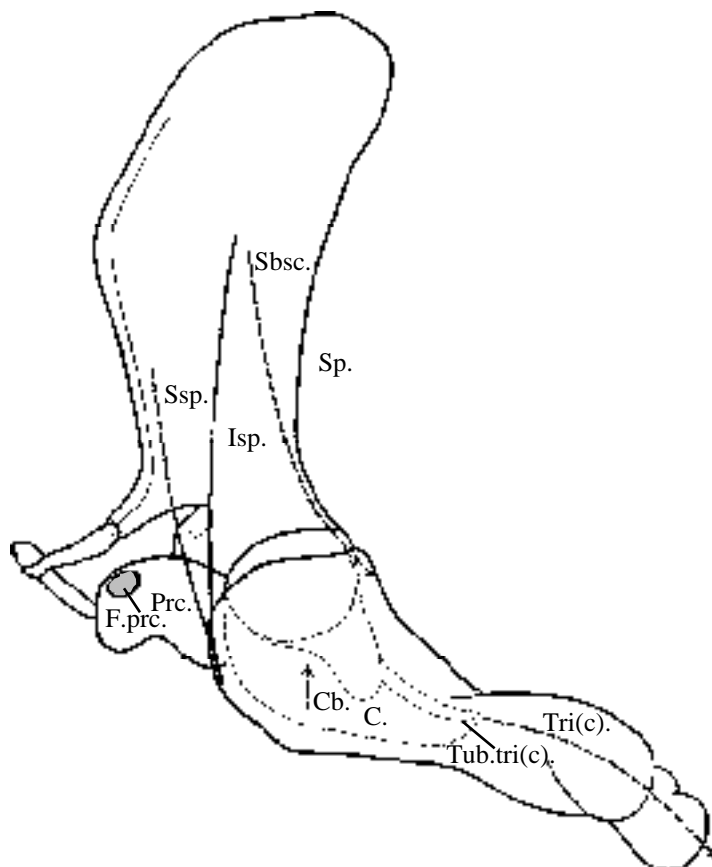


Figure 8. Lateral view of reconstruction of *Bienotheroides* shoulder girdle.

The *Bienotheroides* scapula has an anterior margin that is strongly laterally inflected into the form of a broken wing and is somewhat similar to the scapula of mammals. This margin exists as a spine that is extended ventrally with its terminal end projecting to become the acromion. The position of the acromion is relatively low and equivalent to that on *Oligokyphus*. The terminal ends of the acromion are incomplete on both scapulas of V7905. On specimen V7906 the lower section of the scapular spine is united with the acromion and extended anteriorly strongly and evenly. At the surface of the large section on the medial side of the scapula there is a shallow triangularly shaped depression, undoubtedly to facilitate the attachment of the m. subscapularis. Because this triangle's apex is only extended to the midsection of the scapula, the m. subscapularis ascension point differs from that of the mammals by not extending to the basal section of the scapula. The proximal end of the scapula on both specimens is similar to the general

cynodont condition; the glenoid is extremely thickened, pointed, and thin anteriorly, while also rotated both posteriorly and laterally.

Both the left and right coracoids are preserved on specimen V7905; however, their preservation is neither good nor complete, and neither are well articulated to the scapula. The right coracoid plate is preserved relatively well, but the procoracoid is incomplete, with the majority of the suture between the two observable, as only the dorsal section has been obliterated. The relationship between the coracoid plate and the scapula is not revealed. The dorsal aspect of the coracoid maintains a strong projection that combines with the scapula supraglenoid buttress to compose the glenoid fossa. The coracoid is extremely similar to those of the cynodonts, as the posterior section has an extremely long upward projection that clearly indicates the coracoid head of the m. triceps is still preserved. Differing from the coracoids of the cynodonts is the presence of a shallow sulcus on the lateral surface. However on specimen V7905, the lateral surface is level, or even slightly projected. Therefore, the morphology of the m. coracobrachialis attachment region differs from that of the cynodontia. Although the left coracoid and scapula are preserved together, they exist in a shifted position such that their relationship is not very clear. The plate is internally reflected such that the interpretation of their arrangement is concealed. The ventral margin of the coracoid plate is compressed into the medial side of the proximal scapula. The procoracoid of this side is comparatively complete and illustrates a relatively clear suture between its posterior surface and the coracoid. There exists a foramen that should represent the procoracoid foramen. This foramen is not only small, it is also dorsally situated and is moreover placed distantly from the procoracoid-coracoid suture. The coracoid of V7906 is clearly more robust than that of specimen V7905, with a clearly illustrated depression at the anteroventral side of the lateral surface. The attachment position for the m. coracobrachialis is comparatively more posteriorly placed. Although the procoracoid of *Bienotheroides* has been more reduced than those of the cynodonts, it is still a relatively large skeletal element. From observing its condition of preservation it is very possible to establish this element's position where it connected to the scapula margin, being exactly like *Cynognathus*. In contrast, the procoracoid of *Morganucodon* has been even more greatly reduced such that there is only an extremely small relationship to the margin of the scapula.

Jenkins (1971) believed the m. supraspinatus did not exist on the Cynodontia for the principle reason that the proximity of the clavicle and relatively large procoracoid obstructed the passage of the m. supracoracoideus from beneath the clavicle to the medial side of the scapula. He suggested that either a corridor must open to permit the passage of this muscle, the procoracoid must be reduced, or the acromion-clavicle articulation must be shifted dorsally to facilitate the presence of this muscle.

The acromion on the Chinese specimen is not very high, but compared to that of the Cynodontia is much more well developed; moreover, it is situated much further anteriorly. The procoracoid is not extremely reduced, however its relative point of articulation with the scapula ventral to the acromion has been rotated posteromedially. In this manner, there has been created an aperture between the acromion and the attachment region for the m. supracoracoideus. The attachment region for this muscle is clearly situated medially to the acromion-clavicle articulation. The m. supracoracoideus is thereby able to migrate without the slightest impedance to the medial supraspinous fossa at the scapular blade's medial aspect. The existence of a supraspinatus, therefore, clearly does not present a problem.

It is regrettable that the vertebral margin on the *Oligokyphus* scapula is not preserved, as it is not possible to discern whether or not there is a presence of a supraspinatus fossa. Kühne, however, deduced that the m. supraspinatus had already occurred on *Oligokyphus*, based upon muscle attachment traces at the terminal end of the acromion.

M.C McKenna (1961) made a brief description of a scapula coracoid belonging to the possible marsupial *Camptomus*. Based upon observations of the figures provided, the structure of this region on *Camptomus* is extremely similar to the therian condition. In spite of the dorsal section being damaged, it is still possible to observe the presence of the completely well-developed supraspinatus fossa at the center of the scapula. Undoubtedly, this animal's m. supraspinatus and m. infraspinatus were already clearly

bifurcated and extended along both sides of the scapula spine. The coracoid is still a separate skeletal element, but has been rotated medially to the scapula's anteroventral aspect, and is very closely linked to the scapula. The glenoid is ventrally directed. The morphology of the ventral scapula and lateral coracoid is almost identical to the Theria, with the only difference being the coracoid has not reduced its coracoid process to the same degree.

Hence, it is possible to distinguish three probable phases of shoulder girdle development from the Cynodontia to the mammalian condition:

I. The anterior and posterior margins of the scapula blade are strongly reflected laterally and there is a well-developed infraspinatus fossa. The acromion begins to form. The association of the procoracoid with the scapula at the region ventral to the acromion occupies the aperture between the clavicle and scapula-coracoid. The coracoid and procoracoid are relatively large. The procoracoid is an element composing the glenoid fossa. The m. supracoracoideus only intrudes upon the lateral surface of the scapula. The coracoid head of the m. triceps is well developed. The relatively primitive cynodonts are situated at this phase.

II. At the anterior section of the scapula, on the medial surface, there appears a small protuberance extended anteroventrally, and the supraspinatus fossa exists. The acromion has already clearly evolved. The scapular section ventral to the acromion tends to have become reduced. The procoracoid has become diminished. The center of the glenoid fossa is also contracted. The m. supracoracoideus has begun to encroach upon the medial side of the scapula ventrally from the clavicle (supraspinatus fossa). The coracoid head of the m. triceps still exists. *Bienotherioides* and possibly some advanced members of the Cynodontia belong to this model.

III. The scapula spine has become extremely well developed at the center of the scapula's lateral surface. The procoracoid has become lost. The coracoid has also become greatly reduced and reflected medially to the anteroventral side. The glenoid fossa is ventrally directed. The m. supraspinatus and m. infraspinatus have become well separated. The coracoid head of the m. triceps has possibly become simplified. *Camptomus*, as described above, may possibly be a representative of this phase.

Cheng Cze-ching (1955) described several embryonic developmental phases of the Marsupialia. Through this contrast it may be observed that phases III, IV, and V of Cheng are astonishingly similar to the three phases described above, such that paleontological conclusions are apparently consistent with embryological studies.

Forelimb material: V7905; right humerus, right ulna, radius, right forefoot; 7906; left humerus, left ulna, radius.

V7905 preserves only the right humerus with a certain amount of damage at the proximal and distal ends. Its morphology is fundamentally consistent with that of the other Tritylodontia and advanced cynodonts, with both ends extremely expanded. The breadth at the laterodistal condyle is a little over half the total length of the humerus. The two ends are rotated about the humeral axis at an approximately 45° angle. The humeral head has been damaged such that it is difficult to determine the morphology. The condyles are not well developed. The deltopectoral crest is extremely well developed. The ectepicondular foramen has been lost. The entepicondular foramen is present.

Specimen 7906 possesses a left humerus that has been damaged at the medial side of the distal end. From the perspective of the entire bone, this element is clearly longer and more gracile than V7905, rather like *Bienotherium*. Several muscle attachment points may be distinguished. The proximal width is smaller than 7905 and the two ends are twisted about the humeral axis at a larger angle than V7905. The humeral head is very well separated and slightly spherically shaped. The greater and lesser tuberosities are also not well developed. The m. supraspinatus, m. infraspinatus, and m. subscapularis should be divided and situated at appropriately opposite positions on the greater and lesser trochanters. The terminal point for the

m. pectoralis is at the medial side of the deltopectoral crest's ventral margin. The terminal point for the m. deltoideus is at the lateral side of the deltopectoral crest. There exists a long and shallow canal on the face of the deltopectoral crest's lateral side that should be the commencement point for the m. brachialis. A section has been lost at the proximal medial side. There is a medially projected protuberance approaching the center of the humerus. This protuberance has a slightly concave dorsal surface that clearly represents the attachment for the m. triceps. The distal condyle of the humerus is projected as an extremely well-developed sphere. The tuberosity for the m. supinator is relatively distinct.

The radius is preserved in its natural state together with the ulna. The difference between this specimen, *Oligokyphus*, and *Morganucodon* lies in the bone shaft being straight and even, with nearly no sigmoid curvature. The shaft is relatively gracile with both ends inflated. The proximal end is an obliquely inclined elliptical concave face, however, the articular surface is not completely preserved. Descending from the facet for the articulation with the radial notch of the ulna is a ventrally extended ridge bearing a tuberosity that is similar to the Cynodontia, *Oligokyphus*, and *Morganucodon*. It was interpreted by F.A. Jenkins as being the attachment point for a radio-ulnar interosseous ligament as well as for forearm flexor muscles. The distal end of the radius is flat, even, and wider than the proximal end.

The ulna is baton-shaped. Both sides of the shaft are flat and even with no alteration in breadth. The olecranon is extremely well formed. From the olecranon's apex a level surface extends anteriorly directly to the radial notch and gradually attenuates as further downward it is replaced by a flat edge that bifurcates the ulnar shaft into two faces. Distally from the olecranon on both the medial and lateral sides exist shallow troughs facilitating the attachment of the flexor and extensor muscles. Although the preservation of the proximal articular surface is not ideal, several facets may be vaguely distinguished. The entire articulation region is combined to form a rhombic-shaped structure. On the medial side and lying obliquely is the sigmoid notch and the ulnar condyle, or trochlea, that articulates with the humerus. At the anterior angle of the rhombus is the radial condyle lying at the anterior section of the sigmoid notch. The distal angle of the rhombus is an extended concave surface, being the facet for the articulation with the radius. At the anterior angle's lateral surface there is a ridge extending distally, directly to the ulna's distal end, thereupon becoming the angle at the anterior margin connecting the lateral and medial surfaces. The anterior margin is therefore much narrower than the posterior margin.

Among the Cynodontia, only *Thrinaxodon*, *Diademodon*, and *Exaeretodon* preserve skeletal elements of the carpal region. There are no records of the carpus of either *Oligokyphus* or early mammals. Specimen V7905 preserves a relatively complete carpus beneath the radius and ulna. These authors believe it preserves its natural morphology.

Among the four proximal carpals, the radiale is the largest and occupies the medial half of the radius. It is semicircular in shape; its midpoint is indented with the indented surface directed to the center of the carpus. *Diademodon* (Jenkins, 1971) illustrates an identical radiale, only its position has been shifted.

The intermedium is positioned at the lateral half of the distal radius. Its proximal end is slightly inflated and possesses an articular surface for contact with the radius. Its distal end is also expanded. The intermedium is positioned between the ulnare and radiale, such that these three carpals are aligned linearly.

The proximal face of the ulnare is 4 mm from the distal end of the ulna and rectangular in shape with its length greater than its width. Its dorsal surface is relatively level but its medial constriction is not conspicuous. The distal end possesses an articular surface.

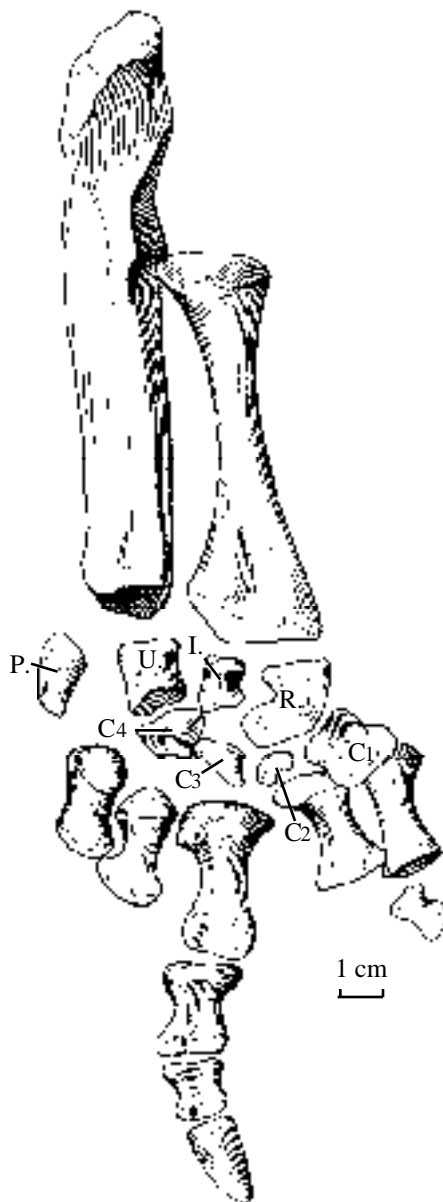


Figure 10. Dorsal view *Bienotheroides* right forelimb (V7905).

The pisiform is crescentic and separated from the ulnare by 2-3 mm. Its lateral margin is more even and straight than its medial margin and its dorsal surface is flat and level. The pisiform exists universally in the Synapsida as it maintains a relationship to muscle attachment.

The distal section of the carpus maintains four carpals: Distal carpal I is associated with the radiale such that the margins of both these elements articulate naturally to compose a crescentic form that represents the medial margin of the carpus. It is a relatively large element that is trapezoid in configuration. Its proximal end occupies one half of the distal radiale and its distal end articulates with the first metacarpal. Distal carpal II is extremely small, lenticularly shaped, and is situated between the radiale and the second metacarpal. This is similar to *Exaeretodon*. Distal carpal III and IV are mutually connected and each positioned at the anterior region of the third and fourth metacarpal. Distal carpal V is not preserved and the presence of a centrale is unobservable. The structure of the *Bienotheroides* carpus is identical to that of the Mammalia, as its pisiform is well developed, the centrale has been reduced, and the intermedium has

moved to the lower region of the radius. The first and fourth distal carpals are extremely large while the second and third distal carpals are extremely small, particularly the third. The inflated terminal end of the radius as well as the robust nature of the radiale and first distal carpal illustrates the weight of the forearm was stressed along the medial line.

There are five well-preserved metacarpals, moderate in length, and unlike the extended manner observed in *Morganucodon*. The difference in length among each of the metacarpals is not great: I, 15 mm; II, 16 mm; III, 18 mm; IV, 16mm; V, 14 mm. Among them MC I and II are clearly slightly smaller and more gracile. During plantation the five digits should have been unified in direction as there is no indication that the thumb is separated. The proximal ends of the metacarpals are broadened and thickened, and the distal ends are broadened.

At the time of its preservation specimen V7905 possessed a complete foot. Unfortunately, throughout the course of collection and preparation, phalanges have become lost or damaged, such that only the middle digit is currently preserved. The third digit maintains the basic mammalian pattern: short and broad dorsally, ventrally flat and straight, proximal and distal ends expanded, and terminal phalanx spade shaped.

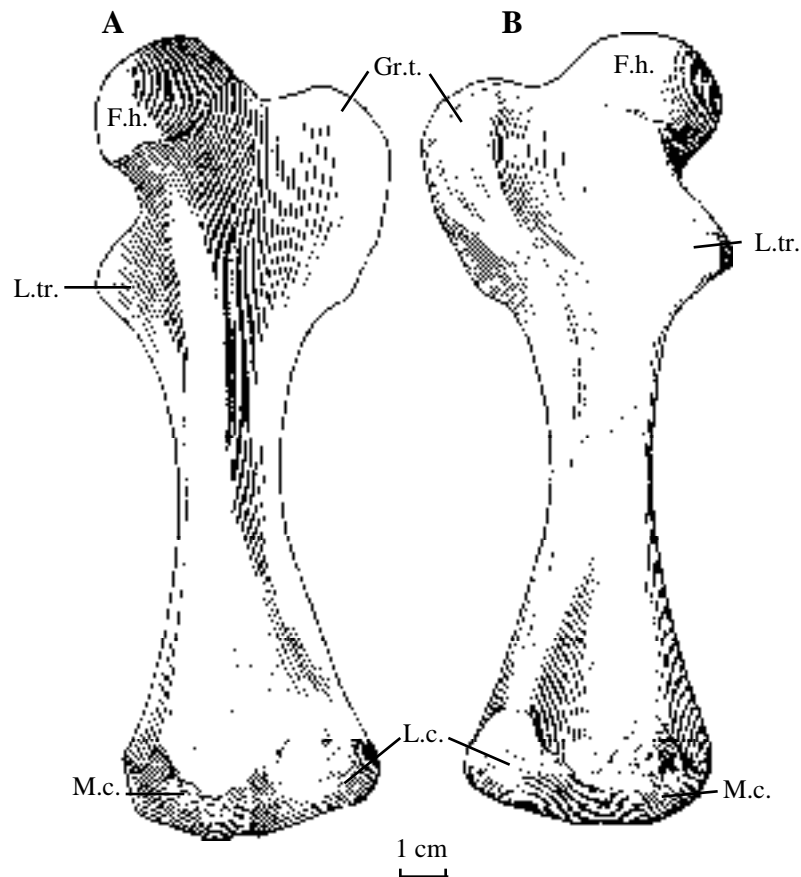


Figure 11. Left femur of *Bienotheroides* (V7905).
A. Dorsal view; B. Ventral view.

The basic morphology of the femur is extremely close to *Bienotherium* and *Oligokyphus*, being slightly sigmoid shaped. Compared to the Cynodontia, the femoral head, greater trochanter, and lesser trochanter are separated even more. The femoral head is nearly spherical in shape, medially projected, and slightly dorsally directed. Due to the completeness of the femur it is possible to observe the articulation

with the acetabulum from the medial aspect. The greater trochanter is situated lateral to the femoral head and slightly dorsally reflected. Its dorsolateral aspect and ventral aspect each have a ridge extending distally that attenuates anteriorly on the shaft, but posteriorly extends along the lateral aspect of the shaft directly to the lateral condyle. The level surface between the two ridges should be the terminal point for the musculature originating from the dorsal section of the ilium's lateral side. The distal end of the femur lacks any diagnostic projections. Ventrally, the two condyles are relatively well developed.

DISCUSSION

Within the evolutionary phase of the transition from advanced theriodont to Mammalia, the position of the Tritylodontia provides food for thought. The postcranial skeleton of the Tritylodontia is demonstrated to be of a shockingly similar nature to that of the primitive mammals, as manifested by such aspects as the shoulder, the structure of the pelvic girdle, the well-developed elbow projection, and the morphology of the atlas-axis. However, their skull still maintains primitive cynodont characters such as the absence of a dentary squamosal contact and the structure of the ear region, in addition to maintaining extremely specialized characters such as the tritylodont dentition and the functional ability for bilateral occlusion. As a result, when discussions arise regarding the origin of the Mammalia, attention is not aroused toward the tritylodonts as they have only been considered a side branch that arose from the traversodont cynodonts (Crompton and Jenkins, 1979; Hopson and Barghusen, 1984). At the time the senior author of this text advanced work upon the skull of *Bienotheroides* (1984), she was also influenced by this mode of thought, which caused her to reject careful consideration to the morphologically similar characters between the Tritylodontia and Mammalia.

Most recently, T.S. Kemp (1984) made the controversial suggestion that the Tritylodontia was a sister group to the Mammalia. He enumerated certain advanced skull characters of the Tritylodontia as the basis for his argument, such as the appearance of a lateral wing of the prootic, the loss of the prefrontal and post orbital, the absence of a dorsal process of the premaxilla to separate the nares, the structure of the palate, as well as multi-rooted molars, and other characters. The current authors genuinely do not agree the aforementioned characters are synapomorphies uniting the Tritylodontia and Mammalia; however, based upon the post-cranial description in the prior text, and particularly based upon the presence of the supraspinatus fossa, it must, at minimum, be demonstrated that the relationship between the tritylodontia and mammalia must be advanced further than previously visualized.

Concurrently, with regard to this concept, Kemp suggested the relationship between the Monotremata and therian mammals is closer than to the metatherian mammals. It is still not possible for the current authors to accept this point.

The Monotremata are united by several extremely derived as well as several extremely primitive characters, causing them to be completely isolated from the extant Mammalia. As their scapula and shoulder girdle are very close to the Tritylodontia, it has thereupon been believed that they developed isolated and independently during the extremely early period of mammalian history (Kühne, 1956).

The current authors believe that through a correlation to the Tritylodontia, the distance between the monotremes and mammalia may perhaps be even further, as not the slightest trace of a supraspinatus fossa is observable on the scapula of the monotremes. To the contrary, and at the same time preserved on the theriodont reptiles (directly from the anterior margin of the scapula) at the posterior surface there appears a unique second scapula spine creating a difficulty in the comprehension of monotreme spinatus muscle distribution. From the perspective of a well-developed supraspinatus fossa, the ancestral relationship between the Cynodontia, Tritylodontia, and Mammalia is closer than to the Monotremata.

T.S. Kemp considered the monotremes and mammals to be a monophyletic group with the most significant synapomorphy lying perhaps in the appearance of three ear ossicles. In this respect, however the transformation of the jaw articulation to the middle ear could have arisen independently within each

branch (Crompton and Sun, 1985). Consequently, it is not possible to utilize these characters as synapomorphies uniting the Mammalia and Monotremata.

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