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Postcranial skeleton of a brachyopoid (Amphibia, Temnospondyli) from the Triassic of Mendoza (Argentina)

CLAUDIA A. MARSICANO

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Fairly complete postcranial remains collected by Bonaparte in 1963 in Cerro Cacheuta, Mendoza Province (Argentina) are described in detail. The remains are referred to the Superfamily Brachyopoidea on account of the distinctive architecture of the clavicular dorsal process. The presence of longitudinal ridges on the neural spines and presumably the lack of posterior displacement of the neural spines are considered autapomorphies of the species from Mendoza. The presence of well developed pleurocentra and the lack of conspicuous parapophyses, which are also absent in the Jurassic chigutisaurid *Siderops kehli*, characterize the material described.

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Key words: Amphibia, Temnospondyli, Brachyopoidea, Triassic, Argentina.

KNOWLEDGE of the postcranial skeleton of Mesozoic temnospondyls is generally poor. Very few complete descriptions have been published, especially in comparison with those of skulls. Within the Brachyopoidea (Brachyopidae + Chigutisauridae, *sensu* Warren & Black, 1985) only the postcranial skeleton of the Jurassic chigutisaurid *Siderops kehli* from Australia is fairly complete and fully described (Warren & Hutchinson, 1983). Besides this, some isolated remains found in association with skulls are known (e.g. Woodward, 1909; Shishkin, 1966; Welles & Estes, 1969; Cosgriff, 1974; Chernin, 1977).

In 1963, complete postcranial remains were collected by Dr J. Bonaparte in Cerro Cacheuta (Mendoza Province). Bonaparte assigned this material to *Pelorocephalus mendozensis* Cabrera and briefly described some of the bones (Bonaparte, 1978; figs 97, 99). The remains were found disarticulated in two different concretions (PVL3462 and PVL3468), one of which (PVL3462) included a fragment of occiput (Bonaparte, pers. comm.); this fragment could not be located by the author. The skull in Bonaparte's fig. 97 was found at a different locality from the postcranial remains and obviously belongs to a different specimen. A description of a postcranial skeleton from a nearby locality was presented by Rusconi (1951), who assigned it to a new brachyopoid species, *Chigutisaurus tunuyanensis*. This skeleton, however, was later identified as a thecodont (Reig, 1961). Rusconi (1951) also described some isolated postcranial remains from the same area as representing a new trematosaurian taxon, *Icanosaurus rectifrons*, but later Bonaparte (1978) considered *I. rectifrons* a junior synonym of *P. mendozensis*. Part of this last-mentioned material is apparently lost, like other remains referred to the new taxa *Chigutisaurus tenax* and *Chigutisaurus cacheutensis* by Rusconi (1951, 1955). Some postcranial remains (fragments of a humerus, ribs and vertebrae) were mentioned by Cabrera (1944) in his description of the holotype of *P. mendozensis*, but their poor preservation prevents any comparison. Therefore the skeletons collected by Bonaparte in 1963 and subsequently briefly

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described (Bonaparte, 1978) are the only fairly complete postcranial remains from South America referable to a brachyopoid. The only brachyopoids represented in the levels from which this postcranial remains have been collected belong to the family Chigutisauridae. However, at least two chigitisaurid taxa might be represented based on cranial remains currently been reviewed by the author. Thus the present material is referred only at familial level. In this paper a detailed comparative description of those postcranial remains is given. No difference except size could be found between the sets of bones coming from the two concretions.

Description

Superfamily BRACHYOPOIDEA Säve-Söderbergh 1935

Family CHIGUTISAURIDAE Rusconi 1951

Material. PVL3468 (Paleontología de Vertebrados, Instituto M. Lillo), an incomplete postcranial skeleton; PVL3462, an almost complete postcranial skeleton.

Locality. Southern side of Cerro Cacheuta, Cacheuta, Mendoza Province.

Horizon. Cacheuta Formation, Carnian-Norian (Kokogian & Mancilla, 1989).

Vertebral column and ribs

Neural arches (Fig. 1). All arches described belong to the presacral region of the vertebral column, according to the inclination of the transverse processes by comparison with those of *Siderops kehli* (Warren & Hutchinson, 1983).

Each transverse process extends at an angle a little larger than 90° from the body of the arch. The dorsal surface of each process inclines forward, increasing the slope in its anteroventral part, whereas the ventral surface is gently concave. Beneath this ventral surface the pleurocentra articulate. The diapophyses appear to be either missing or damaged. Possibly, like *Siderops*, these structures were mostly cartilaginous and have been lost (Warren & Hutchinson, 1983).

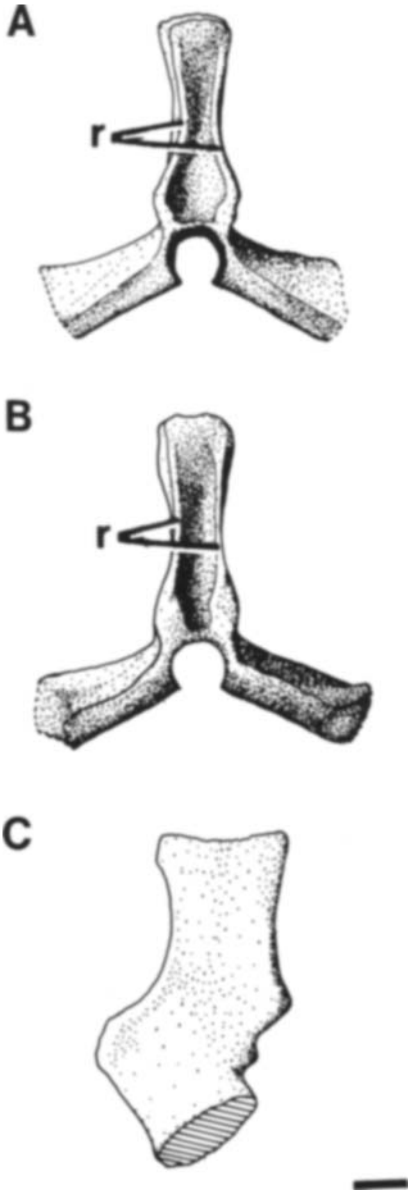

Fig. 1. **Brachyopoid, presacral neural arch PVL3462. A, anterior, B, posterior, C, lateral view. r, ridge. Scale = 1 cm.**

The neural spine is fairly high, more than half the total height of the neural arch. In section it is laterally compressed and its upper surface appears to be of unfinished bone. The neural spine is positioned above the transverse processes, rather than being displaced posteriorly.

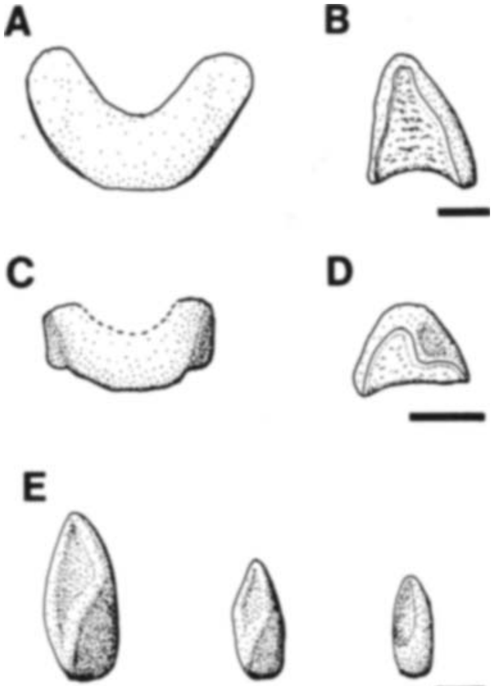

Fig. 2. Brachyopoid, presacral intercentrum PVL3468. A, anterior, B, lateral view. ?postsacral intercentrum PVL3468 in C, anterior and D, lateral views. E, pleurocentra PVL3462 in anterodorsal view. Scale = 1 cm.

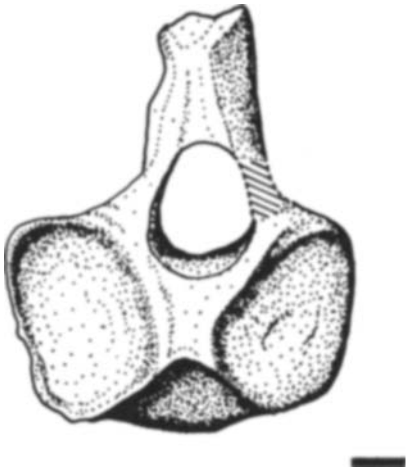

Fig. 3. PVL3462 atlas in anterior view. Scale = 1 cm.

The prezygapophyses are well developed. They are elongated and get thinner upwards. Each prezygapophysis continues into a ridge that runs along the anterior surface of the neural spine. The postzygapophyses are prominent and are located at the base of the neural spine. Like the prezygapophyses, they turn into a ridge along the posterior surface of the spine.

The cross section of the neural canal shows that it was bordered ventrolaterally by a pair of longitudinal ridges which partially constricted its ventral opening.

Intercentra (Fig. 2A–D). All the examined intercentra are similar in size, although they differ in form. Anteriorly, they are crescentic and become more flattened posterad. In anterior view their dorsal surfaces are less curved than their ventral ones, so that the central region of each intercentrum is relatively thicker than the ends. All the surfaces, except those of the concave ventral strip, were probably finished in cartilage because they are of unfinished bone. None of the intercentra has conspicuous parapophyses. The parapophyses lack the distinct rim around the facet seen in some other temnospondyl intercentra.

Among the remains numbered PVL3468 two intercentra different from those previously mentioned were collected (Fig. 2C-D). They are smaller and have two distinct features: 1. the intercentra have a rim around the parapophyses; 2. the middle part of their posterior edge is sharply projected towards the ventral region. Possibly these intercentra correspond to vertebrae from the anterior part of the tail, instead of the trunk, because their projected ventral edge could be the tail muscle insertion site. However, known caudal intercentra are usually flattened ventrally.

Pleurocentra (Fig. 2E). The pleurocentra, which are well developed, vary in size and form but even so it is possible to establish a common configuration. They are rounded with their proximal portion somewhat pointed. Each pleurocentrum has an anterodorsal facet for articulation with the neural arch, an anterior facet and a posteroventral area. All surfaces of the pleurocentra are of unfinished bone. The anterodorsal facet is somewhat concave whereas the anterior one is flattened. In contrast the posteroventral area is convex. De-

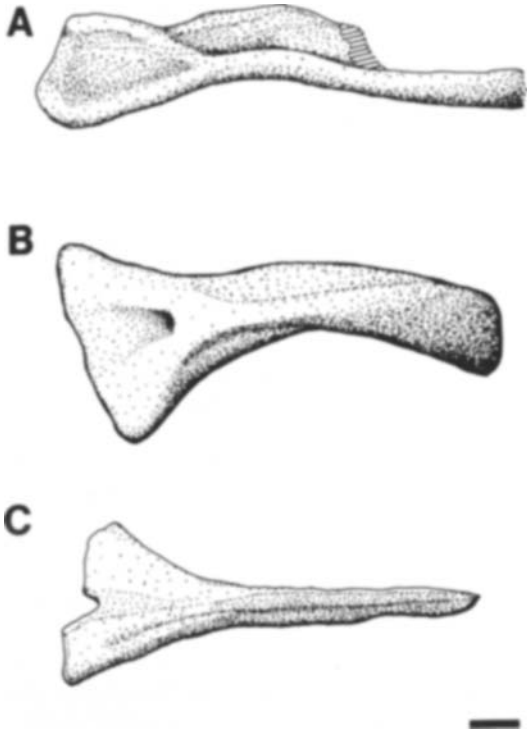

Fig. 4. A, PVL3468 presacral rib; B, PVL3462 sacral rib and C, PVL3462 postsacral rib. All in anterodorsal view. Scale = 1 cm.

crease in size of pleurocentra is accompanied by a reduction in size of the anterodorsal facet and in the distinctness of the anterior facet.

Atlas (Fig. 3). Only the anterior part of the atlas is preserved. It has two circular facets for the exoccipital condyles. Each facet is round, concave and faces anterolaterally. The neural arch is fused to the centrum. In cross section, the neural spine is somewhat laterally compressed. The neural canal is well developed and circular. Like the neural spines of the other vertebrae, it has two ridges that run along its anterior and posterior surfaces.

Ribs (Fig. 4). Among all the ribs collected, it is possible to establish three different types: presacral ribs, sacral ribs and postsacral ribs. The presacral ribs are single-headed but have well developed tubercular and capitular areas. Each rib has an uncinate process which ends abruptly at the point where the rib turns downwards. All the distal ends of this type of rib are broken. Probably these ribs continued in a distal expansion as in other temnospondyl ribs (Howie, 1970; Warren & Hutchinson, 1983; Dutuit, 1976). The sacral rib is wide and flattened. Its proximal end is strongly built and expanded, forming a single head. This head is clearly divided into a ventral capitular area and a dorsal tubercular area. On the anterodorsal surface of the rib there is a thick uncinate process that gradually disappears towards the distal end of the rib. The distal end is also expanded. In this type of rib there is a single foramen on the most distal part of the anterodorsal surface of the head. Only the postsacral ribs are clearly double-headed because of the presence of a distinct notch between the capitular and tubercular articular areas. The uncinate process is a thin crest that runs along the shaft. The distal end is not expanded.

Pectoral girdle

Interclavicle (Fig. 5). The dorsal surface only of the interclavicle has been partially preserved. Part of its posterior half is lost leaving a cast of its ornamented ventral surface visible on the sediment.

The interclavicle has a diamond shape, with the anterior half of the diamond a little smaller than the posterior one. All the projections are rounded except the posterior one which is quadrangular and has strong ridges on its dorsal surface. The cast on the sediment shows that the interclavicle has its ventral surface covered with coarse ridge-and- groove ornamentation which radiates from a point just posterior to the line of maximum width. The dorsal surface has an elongated depressed zone on its anterior half, just anterior of the line of maximum width. The clavicular facets of the interclavicle are covered by sediment.

Clavicle (Fig. 6). Left and right dorsal processes only are preserved. In lateral view, each process is sigmoid. The process is tall and forms a right angle with the ventral plate. In posterior view it is broadly grooved for the cleithrum and the posterolateral edge is extended as a ridge.

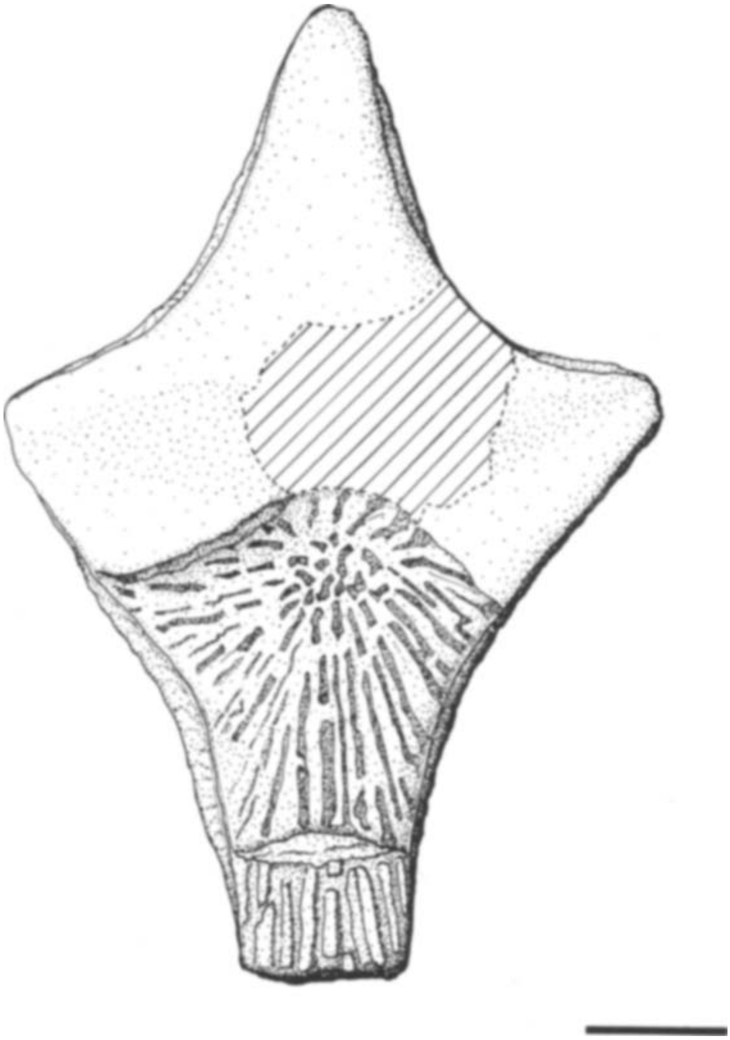

Fig. 5. PVL3468 interclavicle in dorsal view. Scale = 3 cm.

Scapulocoracoid (Fig. 7). Both scapulocoracoids are preserved, but they are broken along their anterior borders. The scapular blade is tall and laterally flattened as is the coracoid blade which is expanded anteroposteriorly. Between the coracoid blade and the supraglenoid buttress there is a large supraglenoid foramen open ventrally. This means that, at least ventrally, the scapulocoracoid was finished in cartilage.

Forelimb

Humerus (Fig. 8). The humerus, as in other temnospondyls, has its proximal and distal ends twisted almost at right angles to one another. It is a slender bone with smooth surfaces. In anterior view, the supinator crest rises from a well developed deltoid process. Ventrally, a depressed zone posterior to the deltoid process is developed. Probably, this muscle scar corre-

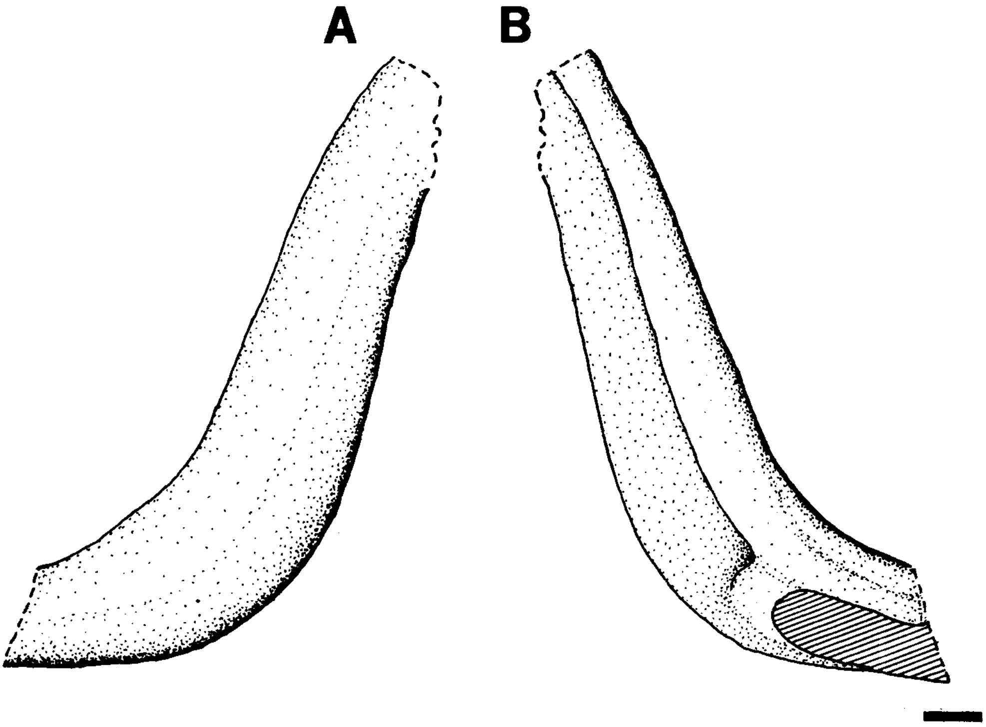

Fig. 6. PVL3462 left clavicle dorsal process in A, external and B, internal views. Scale = 1 cm.

sponds to the insertion 'du grand pectoral' described for the Triassic metoposaurid from Madagascar, *Metoposaurus ouazzoui* (Dutuit, 1976, p.140-141).

Radius (Fig. 9). The radius has an almost straight shaft, flattened in its medial portion. Both distal and proximal ends are a little expanded and were finished in cartilage. A low ridge lies longitudinally on the posterior surface. On the anterior surface a short ridge, formed by a distal thinning of the shaft, is visible.

Pelvic Girdle

Ilium (Fig. 10). The ilia are well preserved. The distal portion is anteroposteriorly expanded, and shows a marked posterior slope. The acetabulum is well developed with a rim around its dorsolateral border. This rim is thicker dorsally so that the acetabulum faces somewhat downwards. There is a recess behind the posterior border of the acetabulum. The shaft of the ilium is unusually slender and tall, and two diagonal ridges run along its external surface.

Ischium (Fig. 11). Both ischia are articulated in the midline. They are damaged with the anterior and posterior ends having been lost. The bone gets thinner posteriorly, and its lateral border is strongly convex. The facet for the ilium articulation slopes anteroventrally.

Hindlimb

Femur (Fig. 12). Like the other limb bones described, the femora are lightly built. Dorsally, the distal end of each femur has a longitudinal ridge. Between this ridge and the anterior border of the femur there is a triangular depression. This depression has a similar position to the 'gouttière dorsal externe' of *Metoposaurus ouazzoui* (Dutuit, 1976, p.156).

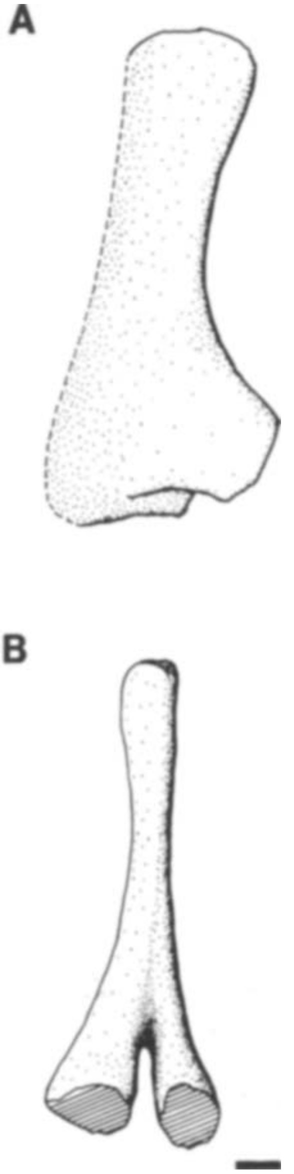

Fig. 7. **PVL3462 right scapulocoracoid in A, internal and B, posterior views. Scale = 1 cm.**

In ventral view, the fourth trochanter is barely present, like the ventral adductor crest.

Tibia (Fig. 13A-D). This is a slender bone with an expanded proximal end. It is concave both in ventral and anterior aspects. The proximal and distal ends are poorly ossified with the result that they have not developed articular processes.

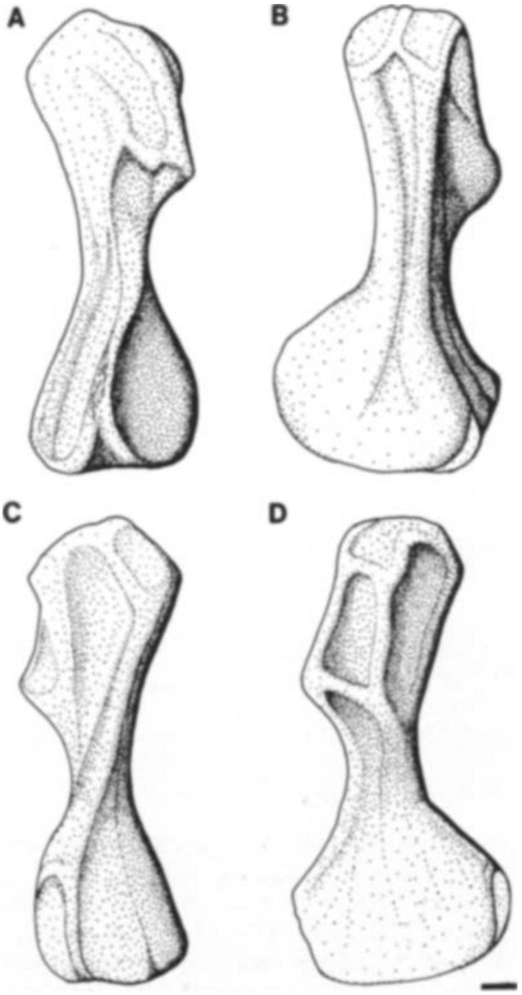

Fig. 8. **PVL3462 right humerus in A, dorsal; B, anterior; C, ventral and D, posterior views. Scale = 1 cm.**

Fibula (Fig. 13E-H). The fibula is a flattened bone with its distal end more expanded than the proximal one. The anterior border is strongly concave while the posterior one is nearly straight. On its distal medioventral surface there is a triangular scar. Like the tibia, the ends of this bone lack well developed articular facets.

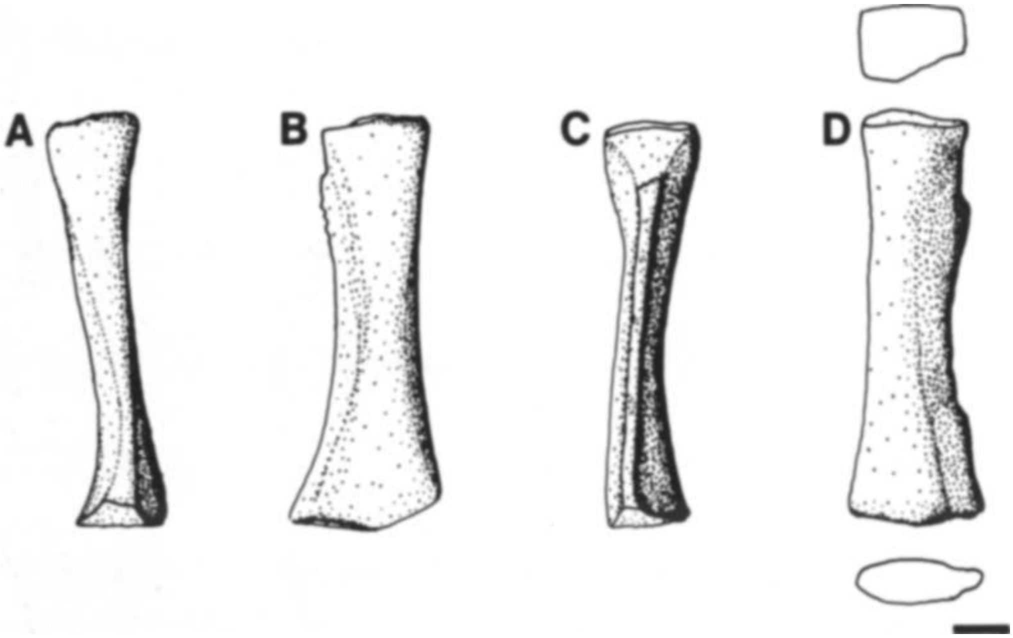

Fig. 9. PVL3462 left radius in A, dorsal; B, anterior; C, ventral and D, posterior views. Scale = 1 cm.

Comparisons

Warren & Hutchinson (1983), in their study of the Jurassic chigutisaurid *Siderops kehli*, described different clavicles with dorsal processes intact. These authors could arrange them systematically, taking into consideration several groups diagnosed by cranial character states. Although the polarity of the different states recognized in the clavicular architecture was not considered by these authors, the configuration of the dorsal processes was used as an identification tool. The shape of the clavicular dorsal processes from Mendoza agrees almost exactly with those described for *Siderops* as well as with the configuration presumably present in brachyopids (Warren & Hutchinson, 1983). Based on this evidence and considering that the taxa represented in the same levels belong to the family Chigutisauridae, the material is referred to the Chigutisauridae, a monophyletic taxon included within the Brachyopoidea (Warren & Black, 1985). For this reason the material will be compared mainly with brachyopoids, but other temnospondyl taxa will be included where appropriate.

The vertebral structure of the brachyopoids is well know only in *Siderops*. In other brachyopoids, e.g. *Hadrokkosaurus bradyi* (Welles &

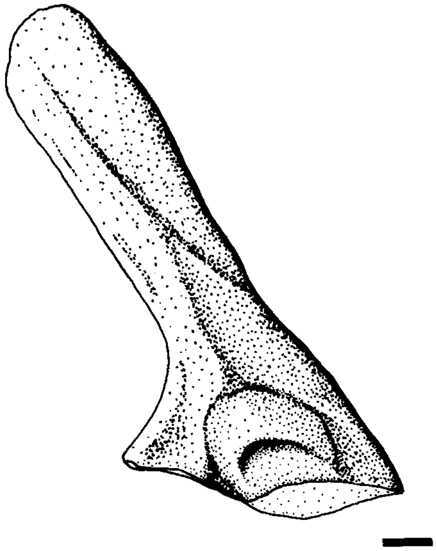

Fig. 10. PVL3468 right ilium in external view. Scale = 1 cm.

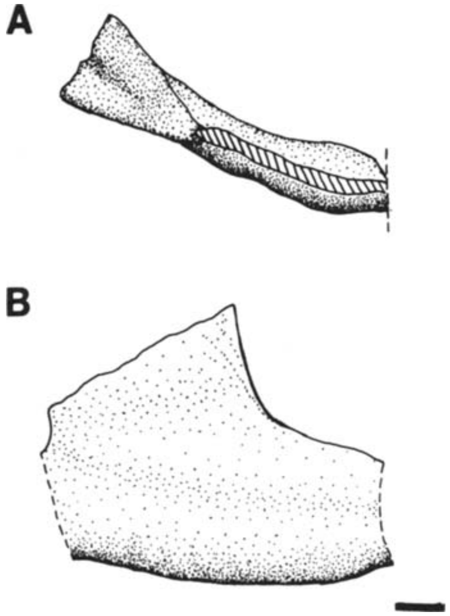

Fig. 11. PVL3462 left ischium in A, lateral and B, posterior views. Scale = 1 cm.

Estes, 1969), *Batrachosuchus* sp. UCMP 42856 (Welles & Estes, 1969), ?*Batrachosuchus* sp. DMSW B-140 (Watson, 1956), *Batrachosuchus concordi* (Chernin, 1977), *Batrachosuchoides lacer* (Shishkin, 1966) and *Blinasaurus townrowi* (Cosgriff, 1974) only the atlas and some intercentra were described. The atlas of *Hadrokkosaurus bradyi* and *Batrachosuchus* sp. UCMP 42856 have a notochordal groove that is absent in the atlas from Mendoza. In the description given by Watson (1956) for ?*Batrachosuchus* sp. DMSW B-140, the articular facets are 'separated by a rather wide, slightly hollowed and pitted surface', unlike the condition present in the atlas from Mendoza. In all known brachyopid atlantes the articular facets are rounded and in most of them the centrum is dorsoventrally short. In the atlas from Mendoza, like that of *Siderops*, the articular facets are more elongated and the centrum deeper dorsoventrally. *Siderops* and the species from Mendoza, however, differ from one another in the relative size of the neural canal and the lack of a hollow between the articular facets in the latter. A hollow in a similar position is also

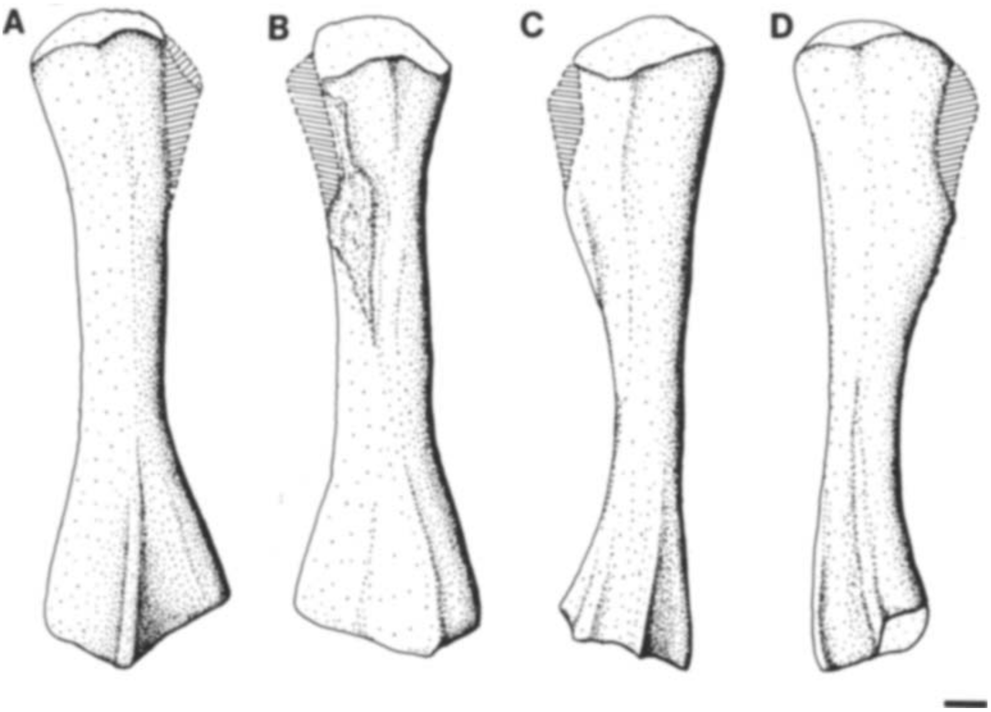

Fig. 12. PVL3462 right femur in A, dorsal; B, anterior; C, ventral and D, posterior views. Scale = 1 cm.

known in the brachyopid *Batrachosuchoides lacer* (Shishkin, 1966).

Important differences in the structure of the neural arches exist between *Siderops* and the brachyopoid from Mendoza, some of them already noted by Warren & Hutchinson (1983). The neural spines are much taller and more compressed than those of *Siderops*. They are

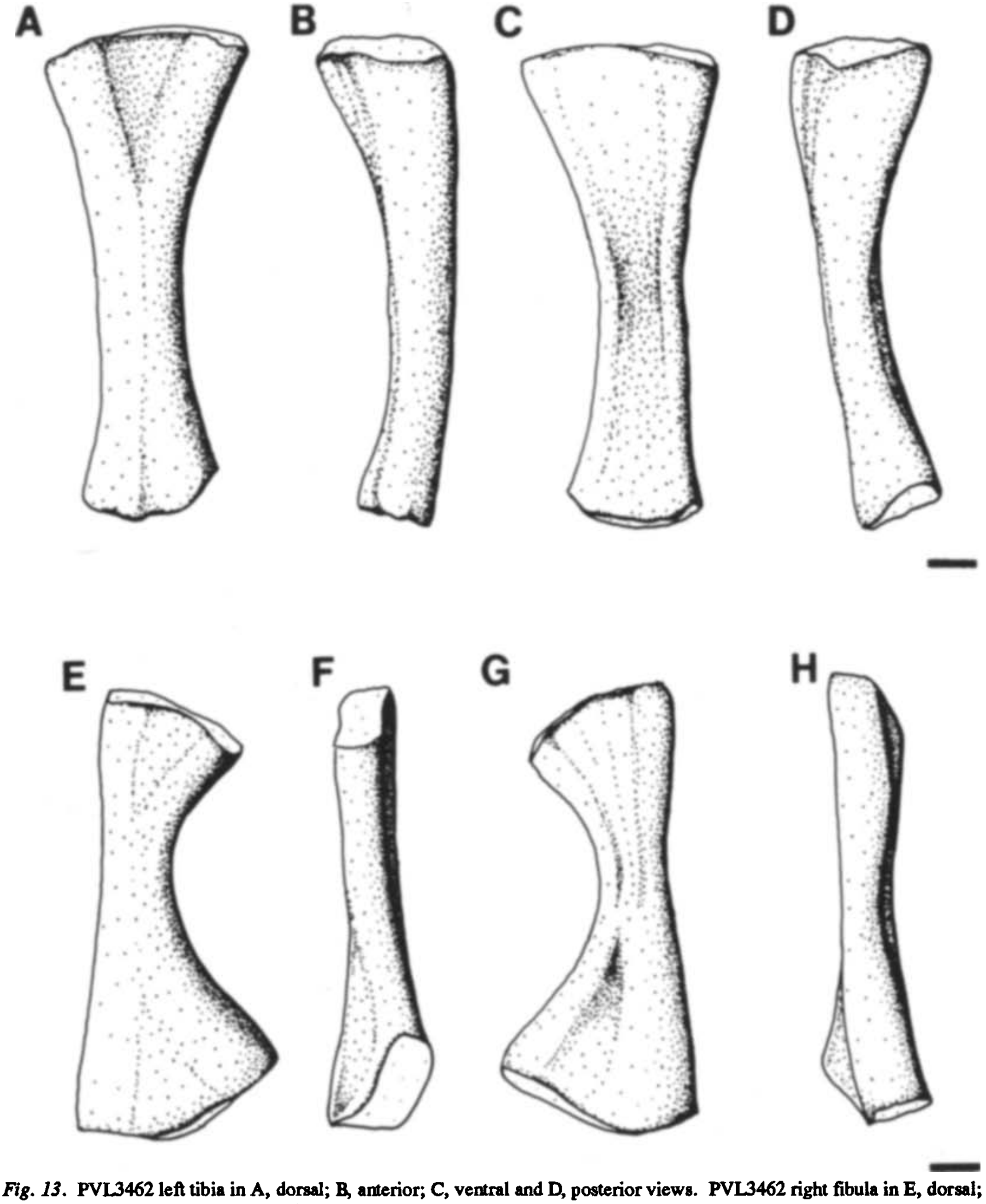

Fig. 13. PVL3462 left tibia in A, dorsal; B, anterior; C, ventral and D, posterior views. PVL3462 right fibula in E, dorsal; F, anterior; G, ventral and H, posterior views. Scale = 1 cm.

not posteriorly displaced, are strongly ridged and have the neural canal more ventrally closed than does *Siderops*. When considering neural arches of the same region of the vertebral column, these features also distinguish the neural spines from Mendoza from those of other families of Triassic temnospondyls, like the Trematosauridae (Nilsson, 1943), Capitosauridae (Howie, 1970; Watson, 1958), Metoposauridae (Dutuit, 1976) and Lydekkerinidae (Watson, 1919).

The vertebral intercentra are very similar to those of *Siderops* in their general shape, especially in that the ventral region of each intercentrum is thicker than the ends and in the lack of conspicuous parapophyses. In other Triassic temnospondyls whose intercentra are known, the parapophyses are well developed and have a rim around the articular facet as, for example, Trematosauridae (Nilsson, 1943), Capitosauridae (Howie, 1970; Watson, 1958), Rhytidosteidae (Howie, 1972; Cosgriff & Zawiskie, 1979) and Brachyopidae (Cosgriff, 1974; Shishkin, 1966).

The presence of well developed pleurocentra in the Mendoza species is unique within Brachyopoidea, although well developed pleurocentra have been described for many Triassic temnospondyls, e.g. Rhytidosteidae (Howie, 1972; Cosgriff & Zawiskie, 1979), Trematosauridae (Nilsson, 1943), Metoposauridae (Dutuit, 1976), Capitosauridae (Watson, 1958; Howie, 1970), Rhinesuchidae (van Hoepen, 1913) and Kourerpetontidae (Olson & Lammers, 1976).

The ribs are very similar to those of other Mesozoic temnospondyls (Warren & Hutchinson, 1983; Howie, 1970, 1972; Dutuit, 1976), although the sacral ribs have a foramen on the anterodorsal surface of the head that is absent in other brachyopoids. A similar foramen was described by Howie (1972) for sacral (?) ribs of the rhytidosteid *Rewana quadricuneata* but it is in a different position on the rib head.

The interclavicle from Mendoza is very similar to that of *Siderops* in general shape and in the position of the centre of ossification. In the latter two taxa, the centre of ossification of the interclavicle is posterior to the widest part of the bone as in metoposaurids (Warren, pers. comm.). It is not possible to observe the clavicular areas, which prevents more detailed comparisons. Cosgriff (1974) described two interclavicles of the brachyopoid *Blinasaurus townrowi*, but they differ in shape and in the position of the centre of ossification from that of Mendoza. In *Blinasaurus wilkinsoni* (Watson, 1956), as in *B. townrowi*, the centre of ossification is more anterior than it is in the interclavicle from Mendoza. The scapulocoracoids resemble those of *Rewana* (Howie, 1972) and *Siderops* (Warren & Hutchinson, 1983), especially in the open supraglenoid foramen, although the shaft is thicker in the latter two.

In the pelvic girdle, the ischia have a similar shape to those of Triassic temnospondyls in general, with left and right ischia nearly joined in the midline. Conversely, the ilium is strikingly different having a relatively tall and slender shaft. A similar condition was observed in *Mastodonsaurus giganteus* (von Huene, 1922), *Lydekkerina huxleyi* (Watson, 1919) and *Metoposaurus ouazzoui* (Dutuit, 1976). Also, the dorsal process of the ilium resembles that of metoposaurs in being unexpanded anteroposteriorly (Warren, pers. comm.). The acetabular portion has a well developed posterior slope and a somewhat ventrally directed acetabulum. This last condition is not observed in other Mesozoic temnospondyls.

Brachyopoid forelimb bones are poorly known. Humeri were described in *Hadrokkosaurus bradyi* (Welles & Estes, 1969), *Batrachosuchus* sp. UCMP 42856 (Welles & Estes, 1969) and *Siderops*. Other forelimb bones are known in *Batrachosuchus concordi*, but their identification remains doubtful (Chernin, 1977). The humeri from Mendoza, as noted by Warren & Hutchinson (1983), are fairly similar to those of *Siderops*. They share a relatively smooth surface, a discrete pointed deltopectoral crest and a symmetrically fanned-out distal portion. When comparing the other brachyopoid humeri mentioned with those from Mendoza the main differences are the relatively shorter shafts and well developed supinator processes in the former. The radius from Mendoza was compared with those known in other Triassic temnospondyls (Howie, 1970, 1972; Dutuit, 1976). Only the metoposaur *Metoposaurus ouazzoui* (Dutuit, 1976) radius resembles the one from Mendoza. Both are lightly built without developed muscle scars and projections, and also share a similar ridge on their posterior surface.

Hindlimb bones, like the forelimb ones, are poorly known in brachyopoids. Two brachyopoid femora have been described, one for the brachyopid *Blinasaurus townrowi* (Cosgriff, 1974) and another for the chigutisaurid *Siderops kehli* (Warren & Hutchinson, 1983). The former has a better developed adductor crest (= adductor ridge in Cosgriff, 1974) and projecting fourth trochanter than in the femur from Mendoza and lacks the dorso-distal ridge and triangular scar present in this specimen. The femur in *Siderops* is poorly preserved so that it is difficult to compare it with that from Mendoza. However, their shafts are similarly slender. When the femur from Mendoza was compared with those of other Mesozoic temnospondyls (von Huene, 1922; van Hoepen, 1913; Watson, 1919, 1958; Howie 1970, 1972; Dutuit, 1976) some resemblance to that of *Metoposaurus ouazzoui* is evident. They resemble one another in the slenderness of the shaft, the degree of development of the adductor crest and fourth trochanter, and the presence of a muscle scar on the dorsal surface of the distal end.

The other hindlimb bones, tibia and fibula, are unknown in brachyopoids and, like the femur, these hindlimb bones are more similar to those of *Metoposaurus ouazzoui* (Dutuit, 1976) than to those of other temnospondyls.

Conclusions

Although the Temnospondyli (*sensu* Romer, 1947; apart from the loxommatids) have been recognized as a monophyletic group by Smithson (1982), recent works have pointed out its paraphyletic condition (Milner, 1988, 1990; Cannatella & de Queiroz, 1989). Besides, the phylogenetic relationships among most temnospondyl subgroups and their strict monophyly are still to be demonstrated. In spite of this situation, some attempts to reassess the relationships among those subgroups have been recently carried out (Gardiner, 1983; Warren & Black, 1985; Milner, 1990). These authors have presented a scheme of relationships mostly based on cranial characters probably because the postcranial characters are simply not known or are suspected of convergent evolution.

Tentatively, the postcranial remains from Mendoza are assigned to the Brachyopoidea, as proposed by Warren & Black (1985), on account of the distinctive architecture of the clavicular dorsal processes in this taxon (Warren & Hutchinson, 1983), and within it to the family Chigutisauridae.

The lack of conspicuous parapophyses on the intercentrum is a character state present in the taxon from Mendoza and the Jurassic chigutisaurid from Australia *Siderops kehli*. This feature is not present in any other Mesozoic temnospondyl, including those brachyopids in which the intercentra are known. This suggests a close relationship between both taxa but it also could be a synapomorphy of chigutisaurids. As *Siderops* is the only chigutisaurid whose vertebral structure is known, apart from the studied specimen, no choice can be made between these two hypotheses.

Conversely, ossified pleurocentra are present in the material from Mendoza but not in *Siderops*, although most of the skeleton of the latter is well preserved. Well developed pleurocentra occur in many Palaeozoic and Mesozoic temnospondyls and this has been considered a plesiomorphic character state. However, the poor knowledge of the vertebral structure in other brachyopoids prevents the polarity evaluation of this character state at the level of the current analysis.

The presence of longitudinal ridges on the anterior and posterior surfaces of the neural spines characterizes the taxon from Mendoza. No other known temnospondyl, including other brachyopoids, exhibits this character state and thus it is considered an autapomorphy of this taxon.

Many Triassic and Jurassic temnospondyls have their neural spines posteriorly displaced in respect to the transverse processes. This condition is not present in the material from Mendoza which has the spines lying at the same level as the transverse processes. This character state appears to be unique at least within Brachyopoidea, and presumably is another autapomorphy of the taxon from Mendoza.

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