The postcranial skeleton of *Boreogomphodon* (Cynodontia: Traversodontidae) from the Upper Triassic of North Carolina, USA and the comparison with other traversodontids

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ABSTRACT

Postcranial remains of *Boreogomphodon* from the Upper Triassic of North Carolina are described and compared with those of other known traversodontid cynodonts. The postcranial skeleton of *Boreogomphodon* is characterized by four sacral ribs, simple ribs lacking costal plates, the extension of the scapular neck below the acromion process, a short scapular facet on the procoracoid, a concave anterior margin of the procoracoid, humerus entepicondyle with smooth corner, and the presence of a fifth distal carpal. Four types of ribs are identified within traversodontids: 'normal' form, tubercular rib, costal plate, and Y-shaped rib. Fossorial behavior is ~~inferred~~ suggested for traversodontids with elaborate costal plates. Within Traversodontidae, the procoracoid tends to decrease in size~~.~~; ~~The~~ the anterior process of the iliac blade extends anteroventrally to different degrees in different taxa, which facilitates

Comentario [L1]: I think it would be better if you state which is the relevant feature: “a long scapular neck ventral to the acromion process”

Comentario [L2]: I do not think that the brief discussion presented here allows you to infer a fossorial behavior for these forms. I suggest you tone this down.

Comentario [L3]: This is not clear enough to me. If this is a phylogenetic trend, you could say something like: “Within Traversodontidae, more derived forms tend to present a relatively smaller coracoid”. If it is not a phylogenetic trend, then you could say: “Within Traversodontidae, several taxa show a comparatively small procoracoid” or “Most traversodontids have a relatively small procoracoid”, depending on the case.

retraction of the femur~~.~~ ; and ~~The~~ the limb bones show allometric growth in terms of length and width.

Keywords *Boreogomphodon*, Traversodontidae, Cynodontia, postcranial skeleton

INTRODUCTION

Cynodontia is a diverse and important therapsid group and a key component as it includes living mammals. During the Early Triassic, eucynodonts diverged into two clades, Cynognathia and Probainognathia. The former includes many taxa with buccolingually (transversely) expanded postcanine teeth whereas the latter, a clade mostly represented by sectorial-toothed members, gave rise to mammaliaforms by the Late Triassic (Hopson & Kitching 2001; Liu & Olsen 2010). One subclade of Cynognathia, Traversodontidae, is characterized by the structure of its labiolingually expanded postcanines with ellipsoid to rectangular crown ~~in~~ outline, and a deep occlusal basin in the upper postcanines. The lower postcanines are quadrangular in outline usually showing an anteriorly positioned transverse crest (Liu & Abdala 2014). Traversodontidae ~~This~~ is the most successful Triassic cynodont group in terms of their specific diversity and individual abundance (Abdala & Ribeiro 2010; Liu & Abdala 2014).

Boreogomphodon jeffersoni was originally described after a left maxilla with postcanine teeth from the Tomahawk Creek Member of the Vinita Formation (Carnian) in the Richmond Basin of the Newark Supergroup, Chesterfield County, Virginia (Sues

& Olsen 1990). Later many cranial remains and a few postcranial bones from the same locality were referred to this species (Sues & Hopson 2010; Sues & Olsen 1990). *Plinthogomphodon herpetairus* was named ~~for~~ on the basis of the cranial remains of a small cynodont preserved in the gut content of a partial skeleton of the archosaur *Postosuchus alisonae* from the “Lithofacies Association II” (Upper Triassic: Norian) of the Deep River basin of the Newark Supergroup in North Carolina (Sues & Hopson 2010; Sues et al. 1999). Later, Liu and Sues (2010) suggested that *Plinthogomphodon* might prove to be a subjective junior synonym of *Boreogomphodon* although there are slight differences in the structure of the lower gomphodont postcanines. Additional traversodontid ~~materials~~remains, including cranial and well-preserved postcranial elements, from the Pekin Formation (upper Carnian or lower Norian) of Merry Oaks Quarry, Triangle Brick Company, Chatham County, North Carolina were tentatively referred to *Boreogomphodon jeffersoni* (Liu & Sues 2010). However, a more secure ~~T~~taxonomic identification of the latter materials will have to await completion of a detailed study on the skull and mandible remains~~of the latter~~. ~~These materials also include many well-preserved postcranial bones.~~

Traditionally, research has been focused on the cranial morphology of therapsids, and the study of the postcranial skeleton was largely neglected. Only a few postcranial characters ~~were~~ have been used in phylogenetic analyses, and coding of postcranial characters is unavailable for most species (Huttenlocker et al. 2015; Kammerer et al. 2013; Liu & Olsen 2010) and this is also the case for traversodontid cynodonts (Liu & Abdala 2014). Recent studies of traversodontids, however, have paid more attention to the postcranial skeleton. Description of traversodontid postcranial skeletons have been produced for *Exaeretodon argentinus* (Bonaparte 1963), *Pascualgnathus polanskii* (Bonaparte 1966), *Massetognathus pascuali* (Jenkins 1970b), *Luangwa drysdalli* (Kemp 1980a), *Menadon besairiei* (Kammerer et al. 2008), *Andescynodon mendozensis* (Liu & Powell 2009), *Protuberum cabralensis* (Reichel et al. 2009), and *Massetognathus ochagaviae* (Pavanatto et al. 2015). In this paper, we ~~will~~ describe the postcranial bones ~~of~~ referred to *Boreogomphodon* from Pekin Formation of North Carolina and review the variation of postcranial features among Traversodontidae.

Material: NCSM 20698, skull with lower jaws, most of the postcranial skeleton; NCSM 20711, skull with lower jaws, anterior part of the postcranial skeleton including ~27 nearly continuous vertebrae; NCSM 21370, skull with lower jaws, and partial postcranial skeleton including nearly complete left forelimb.

DESCRIPTION

Axial skeleton

A nearly complete vertebral column is preserved in NCSM 20698 and include about 27 mostly articulated vertebrae. The total number of presacral vertebrae is probably 24 and there are four sacrals.

Comentario [L4]: Is this number ok? Please check that you are not referring to NCSM 20711.

Cervical series. It is difficult to distinguish between cervical and dorsal vertebrae in non-mammaliaform cynodonts due to the presence of cervical ribs. Brink (1954) differentiated cervicals from dorsals based on the presence of the tallest neural spine on the first thoracic vertebra and identified five cervicals in *Thrinaxodon*. Jenkins's (1971) identification of cervical and dorsal vertebrae is based on the shift in the orientation of the zygapophyses and transverse processes and the change in the structure of the neural spine. He identified seven cervicals in *Thrinaxodon* and *Cynognathus*, the same number as in mammals (Jenkins, 1971). Neither set of criteria can be applied to the material under study here and thus the number of cervicals remains uncertain.

The following description is based on the cervical vertebrae of NCSM 20711 (Fig. 1). No proatlas or atlas can be identified. The centra of the second (axis), third and fourth cervicals are broken, with only the right sides partially preserved. The fifth centrum shows only the anterior end. However, their neural spines are well-preserved. The axis centrum is almost ~~seven~~ 7 mm long, ~~two~~ 2 mm longer than the centra of the following centra. The axial neural spine is a broad blade with a strongly concave dorsal margin, as in *Menadon besairiei* (Kammerer et al. 2008). However, it is slightly different in the convex rather than concave posterior half of the neural spine. The axial neural spine is approximately 10 mm long. Transversely, it is thin through the middle portion, but it is increased in thickness anteriorly and posteriorly, ending in a tuberosity. *Menadon* and *Boreogomphodon* have the only completely known axial neural spines of traversodontids.

The neural spine of the third cervical (C3) is canted posteriorly behind the posterior process of the axial spine, with a height equal to the posterior margin of the axial neural spine. Thus, it is proportionately taller than that of *Menadon besairiei* (Kammerer et al. 2008). On the fourth through seventh cervicals the neural spines are tall, narrow, and slightly canted posteriorly. The neural spines on the third through fifth cervical abruptly

Comentario [L5]: You said that in NCSM 20698 the vertebrae are mostly articulated whereas in NCSM 20711 they are inferred to be nearly continuous. So, why not use NCSM 20698 for the description? Please include a sentence explaining. It could be something like: "The following description is based on the cervical vertebrae of NCSM 20711, as they are better preserved/more clearly observable than the articulated elements in NCSM 20698".
Additionally, you should state the rationale for suggesting that the cervical vertebrae of NCSM 20711 are nearly continuous.

Comentario [L6]: The photograph provided is very difficult to understand. As it is, the bones are not easily identifiable. I strongly encourage the authors to also include a line drawing with their interpretation of the specimen.

Comentario [L7]: None of the features described below can be observed in fig. 1. From fig. 1, it seems that the axis neural spine of *Boreogomphodon* is not completely preserved and, if it were, then it is very different from that of *Menadon* (see Kammerer et al. 2008: fig. 6). If you are using a different specimen of *Boreogomphodon* to base your comparisons and descriptions, you must illustrate it.

Comentario [L8]: This is not completely true. There are unpublished specimens with complete axis neural spines of other traversodontids, too. Maybe you could change this sentence for something like: "Up to know, the only published traversodontid specimens with completely known axial neural spines belong to *Menadon* and *Boreogomphodon*".

Comentario [L9]: Please, label this structure in fig. 1.

Comentario [L10]: Cervical 6 and 7 are not present in fig. 1 (as stated in the epigraph). You should provide illustrations.

taper toward the apex and are triangular in lateral view. The neural spines on the sixth and seventh vertebrae are distinctly taller than the preceding ones. The transverse processes of the third and fourth cervicals are stout and directed posterolaterally and ventrally.

Comentario [L11]: This is not clearly observed in cervical 5 in fig. 1 (it is covered by another bone). Please check if this is correct.

Comentario [L12]: These are not represented in fig. 1. You should provide illustrations.

Comentario [L13]: Please, label this structures in fig. 1. As it is, I cannot recognize them.

The second (axis) through fifth cervical ribs are preserved in NCSM 20711. In lateral view, each rib is a short curved rod, which is directed posteroventrally. Each rib is approximately 7 mm in length, slightly longer than the corresponding centra. Vertebral articulations of the ribs are not exposed.

Dorsal series. Based on the structure of the posterior ribs, the dorsal vertebral column in traversodontid cynodonts is either relatively undifferentiated (e.g., *Exaeretodon* sp., Bonaparte 1963) or divided into a “thoracic” and “lumbar” region (e.g., *Pascualgnathus polanskii*, Bonaparte 1966). The ribs are poorly preserved in known specimens of *Boreogomphodon*, therefore no assessment of any division in the dorsal column is possible.

In NCSM 20698, 14 dorsal vertebrae are exposed and form the basis for the following description (Figs. 2, 3). The centrum is amphicoelous, approximately circular in cross-section, and slightly constricted at mid-length. Its ventral surface is smooth without a keel. There are no intercentra. The anteroposterior length of the centrum measures approximately 5 mm for each of the anterior dorsal vertebrae and slightly increases posteriorly, reaching 6 mm for the more posterior dorsal vertebrae except for last three, where it is 5.3 mm.

Comentario [L14]: You stated that this specimen includes 27 mostly articulated vertebrae. Please specify which vertebral number would these 14 purported dorsal elements represent. Also provide the rationale for your identification of these vertebrae as dorsal elements (you stated above that it was impossible for you to identify the last cervical from the first dorsal vertebrae).

In lateral view, the neural arch joins the centrum along an irregular suture. The pedicles are incised anteriorly and posteriorly to form vertebral notches, of which the latter are invariably more deeply incised. No anapophyses are present~~s~~. The transverse processes are reduced into small bulges on the pedicles. Their positions vary along the dorsal column: anteriorly, the processes arise from the anterior half of the pedicles, close to the prezygapophyses, but, on the last three dorsals, they arise from the pedicles at a point adjacent to the postzygapophyses.

The articular facets of the prezygapophyses face mainly medially and slightly dorsally against the ventrally and laterally directed of the postzygapophyses. The prezygapophyses are thin blades that extend slightly beyond the level of the anterior margin of the centrum. The postzygapophyses extend posteriorly from the base of the neural spine beyond the posterior margin of the centrum. The neural spines remarkably decrease in height posteriorly. They shift to the posterior end~~s~~ of the neural arches and extend posteriorly beyond the posterior rim of the centrum and above the prezygapophyses of the succeeding vertebra. ~~In all, t~~The posterior dorsal vertebrae are featured by a nearly flat dorsal surface not including the neural spine (Fig. 2C, D).

The dorsal ribs articulate with costal foveae on the anterior dorsal vertebrae in *Massetognathus* and *Menadon* (Jenkins 1970b; Kammerer et al. 2008), which are intervertebral in position. The situation in *Boreogomphodon* is not clear-cut. The ribs lack any structural specialization. The length of anterior dorsal ribs is approximately 33 mm in NCSM 20711, whereas the length of an isolated rib is approximately 20 mm in NCSM 21370 (both specimens have similar skull length).

Comentario [L15]: Maybe you could also say that there is no structure on the vertebra that could suggest an intervertebral articulation of the ribs.

Sacral series. ~~The s~~Sacral vertebrae are those ~~is defined on the basis of the contact of~~

~~its~~ whose rib contact ~~with~~ the medial surface of the iliac blade. No ilium is preserved in the material under study. In *Thrinaxodon* and *Cynognathus*, the sacral centra are similar in length to those of the lumbar region, but tend to be narrower and more constricted at the middle (Jenkins 1971). Following this criterion, four sacral vertebrae are identified in NCSM 20698 (Fig. 3). The transverse processes and the zygapophyses of the first sacral vertebra are more slender than those of the last dorsal vertebra. The zygapophyseal facets are nearly parallel to the parasagittal plane.

The first left sacral rib and second right sacral rib are still articulated with the centra. The first sacral rib is wider than the last dorsal rib, whereas the latter appears to be wider than the second sacral rib. The second right sacral rib is approximately 6 mm long and has a distinctly expanded distal end. One isolated element (sr3? in Fig. 3) is identified as a sacral rib with an expanded distal end. It is 7 mm long, 4 mm wide proximally, and 6 mm wide distally. Posteriorly, there is another sacral rib (sr4?), which is more slender than the anterior ones. As on the sacral ribs in other cynodonts, the capitulum and tuberculum are confluent but the sacral ribs are not fused to the corresponding vertebrae.

Caudal series. Three anterior caudal vertebrae are exposed in ventral view in NCSM 20698. Their centra each are approximately 4 mm long.

Pectoral girdle

Most elements of pectoral girdle are preserved in NCSM 20711 (Fig. 4), including the left clavicle, left scapula, the interclavicle, and the coracoids. The left procoracoid and coracoid are firmly connected along a serrated suture whereas the incomplete right

Comentario [L16]: In fig. 4 epigraph, you should provide a colour key. Also, in the abbreviations it says “insertion of d-t min, insertion for deltoideus plus teres minor muscle complex”, instead it should say: “d-t min, insertion for deltoideus plus teres minor muscle complex”. Additionally, the abbreviation “f cor” should be replaced for “f prc” as in the image.
In Fig. 4E, the labels “prc (cor)” and “prc (s)” lack a line pointing to the bone.

procoracoid is ~~free~~isolated. Most elements are also preserved in NCSM 20698, but only the left scapula and right procoracoid are well exposed.

Scapula. The scapula is relatively small. In NCSM 20698 (Fig. 4B-D), it is 20 mm tall, compared to a humerus length of 29 mm. The scapula is bowed laterally and has a narrow, elongate blade that has a narrow but deep fossa on its lateral surface. This fossa mainly extends from the dorsal part of the blade to about the midpoint of the blade. This is the site of origin for the deltoid and teres minor muscles, as reconstructed by Kemp (1980).

The posterior border of the scapula extends close to the edge of the glenoid as a clearly defined crest, although at the base it is merely a low ridge and not a free flange as along the anterior border. The anterior flange extends only for about two thirds of the dorsal portion of the scapular blade, ending above the scapular base. The dorsal part of this flange is a thin sheet of free-standing bone. The acromion process extends in a position similar to that of *Luangwa* or *Menadon* (Kammerer et al. 2008; Kemp 1980a). The scapula is constricted and elongate between the acromion process and the glenoid portion, and this constriction is more pronounced than in *Massetognathus* (Jenkins, 1970b) and *Exaeretodon* (Bonaparte 1963; Jenkins 1970b).

The base of the scapula bears a slightly convex semicircular glenoid facet. The articular surface is rough, indicating an extensive cartilaginous covering in life. It faces posterolaterally as well as ventrally.

Procoracoid. The procoracoid is identified by the presence of a procoracoid foramen. A bone in NCSM 20698 is identified as a right procoracoid in lateral view (Fig. 4E). It

Comentario [L17]: Neck?

Comentario [L18]: What do you mean by “dorsal part of the flange”? Please clarify.

Comentario [L19]: Is? The acromion process does not seem to be very well developed or projected.

Comentario [L20]: You mean the neck of the scapula?

differs from the procoracoid ~~corresponding bone in~~of other known traversodontids ~~procoracoid~~ in the presence of an acute anterior tuberosity.

The bone is an ax-shaped plate (Fig. 4A, E). The procoracoid foramen is close to the concave anterodorsal border of the bone. The articular surface for the scapula forms an obtuse angle to the anterodorsal border. The dorsal edge is short, and the procoracoid does not participate in the formation of the glenoid.

Anterior to the foramen is a shallow fossa for attachment of part of the supracoracoid muscle. An anteriorly directed ridge, which is more prominent in NCSM 20698, separates the supracoracoid origin from the remainder of the lateral surface of the procoracoid. Ventral to this ridge, a crescentic depression faces anteroventrally and probably represents the origin of the biceps brachii muscle. The ventral margin of this fossa forms a sharp, strongly convex keel. The procoracoid is reconstructed as protrud~~e~~ing~~s~~ anteriorly far beyond the procoracoid-scapula contact, it forms~~ing~~ a swollen terminal tuberosity, adding the area for the attachment of biceps and possible coracobrachialis.

Coracoid. The coracoid contacts the procoracoid in NCSM 20711 (Fig. 4A). It is larger than the procoracoid. Although not preserved in articulation with the scapula, i~~I~~ts robust anterodorsal margin would have ~~contacts~~ contacted the supraglenoid buttress above and ~~forms~~ formed the coracoid portion of the glenoid. The posterodorsal margin of the coracoid is concave. The posterior end forms a slightly elongated process, which is incomplete but probably terminated in a turbercle for the origin of the coracoid head of the triceps. The ventral side of the lateral surface of the coracoid is indented to form

Comentario [L21]: Please label this structure in fig. 4.

Comentario [L22]: Please label this structure in Fig. 4E. I think that this structure is out of focus in the illustration, you should try to replace it.

Comentario [L23]: Please label this in the figure. I do not recall such a tuberosity to be present in the procoracoid of other cynodonts; if this is the case (check), it would be interesting to point this out.

a shallow fossa for the origin of the coracobrachialis muscle. The fossa extends onto the posteroventral corner of the lateral surface of the procoracoid.

Comentario [L24]: Please represent and label this in the figure.

Clavicle. The lateral half of the clavicle is a slender rod that is directed dorsolaterally. The medial half consists of a gradually expanding spatulated plate, which is directed medially and horizontally (Fig. 4A). The long axes of the medial and lateral portions intersect at an angle of about 150˚. The medial plate is bordered by rather sharply defined edges. The posterior edge becomes distinct from the clavicular shaft at approximately the midpoint of the clavicular shaft where the shaft has its greatest curvature. The anterior edge is set off from the clavicular shaft more abruptly. This gives the medial plate a slightly asymmetrical appearance. The medial plate of the left clavicle is articulated to the anteroventral concavity of the interclavicle. The clavicular facet for the acromion on the distal end is not well exposed but it contacts the left scapula.

Interclavicle. The interclavicle is similar to that of *Thrinaxodon* (Jenkins 1971). It is cruciform with a long posterior ramus and a short transverse bar (Fig. 4A). The anterior triangular part is slightly convex, and the anterior and lateral ridges are not distinct. The concavities defined by the anterior and lateral ridges are shallow, and the left one is in contact with the medial end of the clavicle. The posterior rectangular portion of the interclavicle is nearly flat except for a low but distinct posterior ridge in the center. The posterior margin is slightly expanded transversely.

Comentario [L25]: But you draw them in the line drawing. Please check for consistency.

Forelimb

The forelimb is preserved in NSCM 20698, 20711 and 21370, including two articulated hands. The articulated hands are rare among traversodontids and have only been reported in *Exaeretodon* (Bonaparte 1963). The bones of NCSM 21370 are better ossified than those in the other two specimens. NCSM 21370 includes a nearly complete left hand, in which a set of nine carpals and most of the phalanges are preserved. The following description is mainly based on this specimen.

Comentario [L26]: You should state that when you describe structures not visible in NCSM 21370, it will be made explicit and the specimen number provided.

Humerus. The humerus is essentially similar to that in most traversodontid cynodonts except *Exaeretodon* (Bonaparte 1963) (Fig. 5). The width of its proximal end, measured from the lesser tuberosity to the region of the greater tuberosity, equals approximately one third of the total length of the humerus. The maximum width across the epicondyles is about 45% of the humerus length (Table 1); this ratio is greater than 50% in *Exaeretodon* (Bonaparte 1963).

Comentario [L27]: You figure NCSM20698 in fig 5A-D. If you base the following description on this specimen please make that clear (you just said that most descriptions were from NCSM 21370).
There is something wrong with the images in this figure, it is like bones have been not properly cropped and some sections were missing. There is also a whitish line around the figured bones.

The proximal half of the humerus is composed of two planes, the deltopectoral crest and the shaft, which intersect along the broad bicipital groove at an angle of around 105°. The shaft is short and triangular in cross-section. The planar distal half of the humerus is triangular in dorsal view. The proximal and distal articular ends of the humerus are well ossified as in other large-sized cynodonts, differing from those of the similar-sized *Thrinaxodon* (Jenkins 1971). The rounded humeral head is at the center of the strap-shaped surface of the proximal end. Its boundary is not obvious because the articular surface is confluent with the lesser tuberosity medially and with the proximal margin of the deltopectoral flange laterally. The greater tuberosity is hard to discern. The lesser tuberosity is set apart from the head by a slight depression across the strap-shaped proximal articular surface. The broad deltopectoral flange amounts to

Comentario [L28]: What do you mean by “shaft” here? It seems that this word is not used here in the same sense than in the previous sentence. Are you referring to the “non expanded” portion of the diaphysis? Please clarify.

Comentario [L29]: Expanded?

Comentario [L30]: Please include more references regarding large cynodonts.

nearly half the total length of the humerus. It is thin and flat, but becomes thicker towards the junction with the shaft. The free margin of the flange curves distinctly ventrally. The dorsal bony ridge on the dorsal side extending across the flange in other cynodonts is evident although it is not as clearly preserved.

Arising from the robust ectepicondylar region, a thin supracondylar flange extends proximally as well as somewhat dorsally. Its anterior margin is straight, not curved. The ectepicondylar foramen does not open on the dorsal surface, but a concave fossa appears to be present on the ventral surface of the proximal side of the flange, in particular, on the right humerus of NCSM 20711. It indicates that the ectepicondylar foramen is closed. The long, oval entepicondylar foramen is enclosed by a stout bar of bone, which arises from the entepicondylar region and continues to the deltopectoral flange (Fig. 5E).

The capitulum is bulbous and contributes to the thickness of the ectepicondylar region. Its articular surface is entirely confined to the ventral aspect of the humerus where its surface is confluent with those of the trochlea and ectepicondyle. A bulbous ulnar condyle lies between the capitulum and the entepicondyle, which is only slightly smaller than the capitulum. A shallow, narrow groove represents the trochlea. The dorsoventral principal axis of this groove is slightly oblique as in *Massetognathus* (Jenkins 1970b). The ulnar condyle is well developed and contacted the sigmoid notch of the ulna. The thickness of ectepicondylar region is much greater than that of entepicondylar region. The entepicondyle is a stout process but less dorsally developed and thus continuous with the posterior margin, as in *Exaeretodon*, contrasting with the

Comentario [L31]: You use the word “shaft” with two different meanings. Please check this for clarity.

Comentario [L32]: Please provide references and mention the other cynodonts in which this structure is visible.

Comentario [L33]: Please label this in fig 5. According to the figure, this structure is observable in NCSM 20698 but broken in NCSM 21370. Please, make explicit which specimen you are describing.

Comentario [L34]: It should also be visible in fig 5A. Please include a label.

Comentario [L35]: Please check this sentence, it seems that you say that the trochlea is ventral.

Comentario [L36]: Medial?

angular shaped entepicondyle of *Luangwa* and *Pascualgnathus* (Bonaparte 1963; Bonaparte 1966; Kemp 1980a).

Radius. –The radii are articulated with the ulnae in all specimens (Fig. 6). The radius is a sigmoid bone with expanded proximal and distal ends. The distal half of the shaft is curved posteriorly and slightly medially to facilitate its crossing over the anterior aspect of the ulna. The proximal articular facet is oval or nearly semicircular, with a nearly straight edge along the posteromedial side. The facet forms a shallow concavity sloping medially. On the posterolateral aspect of the proximal end a protuberance bears a facet for articulation with the ulna. A flange or ridge for insertion of the biceps brachii is not evident on the radii of NCSM 20698 and this region is not exposed in NCSM 21370. The distal end of the radius is triangular in outline, expanding gradually toward the distal articular facet. Along the anterolateral side of the rim is a tuberosity for contact with the distal end of the ulna.

Comentario [L37]: Please refer to the figure in the text and include labels of the described structures in the figure.

Ulna. The ulna is a sigmoid bone with an anteroposteriorly expanded proximal end (Fig. 6C, E). In lateral view, its shaft is narrow, with the distal end evenly expanded mediolaterally and the proximal end expanded primarily anteriorly. An olecranon process is absent. As preserved, the semilunar notch is a relatively shallow, slightly concave facet with a rather straight posterior margin and a nearly semicircular anterior margin. This facet is inclined mainly medially.

Comentario [L38]: Please include more references to the figure in the text and include labels of the described structures in the figure.

The ulnar flange on the medial side of the shaft for the interosseous ligament (Jenkins 1970b) is not well exposed. The radial notch is represented by a fossa on the medial side of the anterior surface, immediately distal to the sigmoid facet. The posterior surface of the ulna is smooth.

Carpus. Nine carpals have been identified, including the ulnare, intermedium, radiale, two centralia, and four distal carpalia; at least one distal carpal is missing. The ulnare is a stout bone, longer than wide in anterior and posterior view. It is constricted between its proximal and distal ends and the medial edge is longer than the lateral edge in plantar view. Its proximal end articulates not only with the distal end of the ulna but also the intermedium. The thickness of the bone is greater dorsally than ventrally so that the bone is nearly triangular in lateral view. The distal surface bears a small facet for articulation with the fourth and fifth distal carpal; the medial surface bears a deep groove for the reception of the lateral centrale (c2). The intermedium is a small rounded bone and only exposed in dorsal view (Fig. 6D–E). It underlies the ulna and lies between the radius and the ulnare. It could contact the lateral centrale and possible radiale distally when completely ossified. The radiale is stout, with an irregular quadrangular shape, and is best exposed in ventral view. Its proximal surface is a rounded facet for articulation with the radius. It contacts two centralia with anteromedial (dorsomedial) and anterolateral (dorsolateral) facets; and distally it touches the distal carpal 2 (Fig. 6D, E). This was likely the original relationship in life because the same pattern is observed in both NCSM 20698 and 21370. No pisiform is present. Medial centrale (c1) is rectangular, with its proximodistal length shorter than those of the other axis. Lateral centrale (c2) is a flat, nearly square bone. The medial and part of its ventral surface are covered by the radiale, so this bone is exposed as a small triangle in ventral view (Fig 6B). Its distal end articulates with distal carpals 3 and

Comentario [L39]: You should mention that the oleocraneon process is very low.

Comentario [L40]: If you think that this is not a completely ossified specimen you should state possible reasons (e.g., juvenile). If this is not the case, isn't it possible that the intermedium does not completely ossify in *Boreogomphodon*?

Comentario [L41]: Refer to the figure

4. Although only distal carpals 2 to 4 are preserved, there were probably five in total because distal carpal 1 is present in all cynodont manus described (Bonaparte 1963; Jenkins 1971; Kemp 1980b). All distal carpalia are somewhat nodular. The third and fourth distals have the same size, and both are slightly larger than the second and much larger than the fifth.

Metacarpal. Four metacarpals are preserved in NCSM 21370. All five metacarpals are preserved in NCSM 20698 but the fifth is incomplete. The metacarpals are elongate and dumbbell-shaped and vary only in shaft length, with IV>III>II>I. In ventral view, the metacarpals appear nearly symmetrical, their proximal ends flaring somewhat less laterally than the distal ends. The proximal articular facet of each metacarpal is gently convex, whereas the distal facet is flat.

Phalanges. In NCSM 21370, the fourth and fifth digits have three phalanges, whereas in NCSM 20698, the first digit has two phalanges, the second digit has at least two phalanges, and the third digit has three phalanges (Fig. 6A, F). The inferred digital formula of the manus is 2-3-3-3-3. The phalanges are more slender than those of *Exaeretodon* and *Cynognathus* (Jenkins 1971) and flat in lateral view. Proximal phalanges are elongate and dumbbell-shaped with the articular ends similar in size and approximately the same in proportions. They are moderately constricted at mid-length. Penultimate phalanges are also elongated and dumbbell-shaped and approximately the same in proportions, but the proximal articular end is slightly wider than the distal one. The mid-length constriction is much narrower than on the proximal phalanges. The articular surface for the ungual phalanx is concave. The fourth and fifth ungual

Comentario [L42]: Please improve the quality of fig 6. The phalanges are difficult to observe.

Comentario [L43]: This is not clearly visible in the figure.

phalanges are slender, tapering cones (Fig. 6A). The proximal articular facet is convex in ventral view. The first and third ungual phalanges are short and obtuse (Fig. 6F).

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Comentario [L44]: I do not understand what you mean by "obtuse" phalange. Please rephrase.

Pelvis Girdle

The left ischium in NCSM 20698 is the only element of the pelvis girdle that could be studied (Fig. 7). The ischium is composed of a proximal head and a ventromedially enlarged plate. Its acetabular surface is oval, concave, and occupies the anterolateral surface of the head. The articular facets for the ilium and pubis are convex. The ischium is slightly constricted below the head, forming a short neck with the plate. The ischial plate is fan-shaped, with an expanded distal part. The dorsal margin of the plate is mediolaterally expanded by a ridge extending from the middle of the lateral acetabular rim to the posterodorsal corner of the plate. The dorsal surface is smooth without an obvious groove. The portion of the plate below the ridge is thin. The posterior edge of the plate is short and straight. Anteroventrally there is the long ischial symphysis. The anterior edge of the ischium is smoothly concave, forming the posterior border of the obturator foramen. The anteroventral corner has no evidence of contact with the pubic plate; this suggests the specimen is not an adult.

Comentario [L45]: Fig. 7A is out of focus. Please correct.

Comentario [L46]: This ridge is not clearly observed in the figure. Is it very faint? Please check.

Comentario [L47]: The posterior edge of the ischium figured is broken. Despite this, it appears to be convex in lateral view, not straight. Please check.

Comentario [L48]: This is not observable in Fig. 7A-B. Please check that this is correct; from the picture, it does not seem to be the case to me.

Comentario [L49]: Is there any other evidence that this is not an adult specimen? There is a possibility that the pubic-ischial plate contact is not completely ossified even in adult specimens.

Hindlimb

The hindlimb is known in NCSM 20698. It includes the incomplete left femur, the left tibia, the proximal half of the left fibula, the nearly complete right fibula, and the articulated right pes. An articulated pes has only been reported in *Exaeretodon* (Bonaparte 1963) and NHMUK R9391, possibly *Scalenodon* (see discussion) (Jenkins 1971).

Femur. The femur is exposed in ventral and anteromedial views (Fig. 7A,C). It has a moderately slender shaft and expanded articular end. The femur is straight except proximally where the shaft strongly turns dorsomedially. Due to the dorsal bowing of the proximal end of the shaft the head, which is bulbous and almost hemispherical, is reflected medially. The head bears rough texture typical of bone supporting a cartilaginous cap. There is a crest connecting the head with the major trochanter, resulting in a semicircular outline for the proximal end of the femur (Fig. 7C).

Comentario [L50]: The femur is also figured in B. Please check the epigraph of figure 7, part B is not properly described.

A deep intertrochanteric fossa lies on the ventral surface between the head and major trochanter and represents the insertion of the pubo-ischio-femoralis externus muscle. Distal to the fossa, the minor trochanter ~~a prominent flange~~ extends distally along the ventral side of the shaft. It is a prominent flange~~the minor trochanter,~~ which extends for about 6 mm and gradually merges into the bone at about mid-shaft. Distal to ~~this flange~~the minor trochanter, the anterior and the ventral surfaces of the femur are clearly separated, rather than confluent as in *Cynognathus* (Jenkins 1971). In cross-section, the shaft is nearly oval at mid-length; its thickness from the extensor to flexor surface is about 3.2 mm and its transverse width is 4.8 mm.

Con formato: Color de fuente: Automático

Comentario [L51]: I do not completely understand. What do you mean by separated? Is there a crest? Does this has to do with a triangular cross-section of the diaphysis? Please clarify.

Tibia. The left tibia is articulated to the proximal half of the fibula. It is almost only exposed in posterior view. The shaft of the tibia is flat and bowed medially. The proximal and distal ends are expanded mainly laterally so that the lateral margin is concave and the medial margin is slightly convex. Due to the poor ossification, the facets on the proximal articular end are not clearly defined. The lateral margin of this end is thicken and protuberant. The distal end terminates in a convex oval facet set at a right angle to the long axis of the shaft.

Comentario [L52]: Please refer to the figure.

Fibula. The fibula has a slender shaft with expanded ends and is bowed laterally. The proximal articular end is poorly ossified. The shaft is narrow proximally but gradually expands anteroposteriorly distally. The distal articular surface is oval in outline and convex. It contacts the concave articular surface formed by the calcaneum and astragalus.

Comentario [L53]: Please, refer to the figure.

Tarsus. The shape, number and proportion of the tarsus elements (Fig. 7D) are similar to those in an unidentified cynodont from the Manda beds of Tanzania (NHMUK R9391) (Jenkins 1971).

Comentario [L54]: References to the figure should be included along the text.

The calcaneum is distoproximally elongate, but, in contrast to NHMUK R9391, its distal head is slightly narrower than the proximal tuber calcis. A separate element seems present between the calcaneum and the astragalus. Based on the comparison with NHMUK R9391, it is identified as a process of the calcaneum. This stout process is about half of the width of the calcaneum and covers the astragalus ventrally. The sustentaculum tali lies dorsal and distal to the proximal facet for the astragalus, and distinct calcaneal sulcus separates them. The calcaneum is constricted distally to form an articular surface exclusively for the cuboid.

Comentario [L55]: The description of the astragalus is very important as there are only a few published. However, the features you mention are not observed in the photograph and are not represented in the line drawing. I strongly encourage you to provide a close-up of the astragalus and a more detailed drawing with all these structures labeled.

The exact shape of the astragalus is unknown because it is covered by the calcaneum. It looks like a curved sausage in ventral view. Its anterior edge is concave with the distal end articulating with the navicular. The medial edge is slightly convex in a dorsomedial direction.

Comentario [L56]: Please, re-phrase. A "curved sausage" is not the proper terminology. Please consider that there are very different kinds of sausages around the word =)

The navicular (centrale) is an irregular oval element. Its plantar surface is nearly flat or slightly convex. It proximally articulates with the astragalus and distally with the first, second, and third distal tarsalia (ento-, meso- and ectocuneiforms) and probably with the fourth distal tarsal (cuboid) as well.

There are four distal tarsalia—entocuneiform, mesocuneiform, ectocuneiform, and cuboid (from medial to lateral). The entocuneiform is nearly rectangular but its distal side is slightly wider than the proximal side. Distally it articulates with metatarsal I and apparently laterally with metatarsal II. The mesocuneiform, the smallest of the tarsalia, is wedge-shaped. Distally it articulates with metatarsal II and proximally it has a short contact with the navicular. The ectocuneiform is triangular in outline and articulates distally with metatarsal III. The cuboid is smaller than the entocuneiform and similar to the navicular in size and shape. Distally it articulates with metatarsal IV and possibly V, laterally with the ectocumeiform and possibly the navicular, and proximally with the calcaneum.

Metatarsal. Four metatarsals are present but the distal end of the metatarsal I is missing. Metatarsals II, III, and IV are nearly similar in size and shape. Their distal ends are wider than the proximal ends and the bones have slightly constricted shafts. The distoproximal lengths are: II, 5.4 mm; III, 6.2 mm; IV, 6.0 mm.

Comentario [L57]: Refer to the figure.

Phalanges. Only a few phalanges are preserved, so the digital formula is unknown. In contrast with NHMUK R R9391 (Jenkins 1971), the proximal phalanges are long and dumbbell-shaped with a median constriction. The lengths of these elements are close to those of the metatarsals.

Comentario [L58]: Refer to the figure.

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COMPARISON AND DISCUSSION

The traversodontids are a diverse group with skull sizes ranging from a few centimeters to more than 40 cm (Liu 2007). They are highly variable in the shape of postcanine teeth, which provided most of the diagnostic characters. The postcranial elements also show considerable variation among traversodontids. Here we summarize the postcranial features from previous studies and personal observation.

Comentario [L59]: Please include a reference.

Axial skeleton

Vertebral column. The number of vertebrae is poorly known in traversodontids due to poor preservation and/or insufficient preparation. The number of presacral vertebrae is 28 in *Exaeretodon argentinus* and *E. riograndensis* (Bonaparte 1963; Oliveira et al. 2007), possibly 26 (>23) in *Massetognathus pascuali* (Jenkins 1970b), at least 16 in *Protuberum cabralensis* (Reichel et al. 2009), and ~24 (>20) in *Boreogomphodon*. Among presacral vertebrae, seven cervicals are identified in the former two species as well as in *Thrinaxodon* and *Cynognathus* (Jenkins, 1971), as much as in most extant mammals, event tough cervical vertebrae in traversodontids, as well as in all non mammaliaform cynodonts with known cervical series, have cervical ribs. In mammals, the dorsal vertebral column is divided into thoracic, with articulated ribs, and lumbar series lacking articulated ribs. Two series are also recognized in some cynodonts based on rib morphology (Jenkins 1970b, 1971). Because the rib morphology of the dorsal series varies among traversodontids, no common criterion is applicable. The sacral vertebrae are defined on the basis of their rib contact with the medial surface of the iliac blade. The number of sacral vertebrae varies from six or seven in *Exaeretodon*

Comentario [L60]: Please provide a reference.

Comentario [L61]: Please provide references.

Comentario [L62]: Please provide references.

(Bonaparte 1963; Oliveira et al. 2007), three or four in *Pascualgnathus* (Bonaparte 1966) (Fig. 8C), six in *Massetognathus pascuali*, although the last ribs do not directly link to the iliac plate (Jenkins 1970b), four in *Andescynodon* (Liu & Powell 2009), and possibly four in *Boreogomphodon*. Based on the current view of phylogenetic relationships (Liu & Abdala 2014), the common ancestor of traversodontids should have four sacral vertebrae. A traversonodontid should have more than 20 presacrals including 7 cervicals.

Comentario [L63]: Please explain the rationale for this generalization. Maybe you could say something like: “According to the presacral vertebral count in known traversodontids, it is inferred that the presence of more than 20 presacrals is characteristic of traversodontids”

Ribs. The ribs are normally simple in synapsids, but complex ribs appear in cynodonts. Special types of rib morphology evolved in traversodontid cynodonts, with different types coexisting in the same individual.

The cervical ribs are simple, their lengths increase backwards in *Exaeretodon* (Bonaparte 1963). The dorsal ribs in Traversodontidae can be divided into four basic types (Fig. 8). Type I, ‘normal’, in which the rib is a slender shaft with a slightly expanded proximal end (Fig. 8A). All ribs of *Exaeretodon*, *Boreogomphodon* and the anterior dorsal ribs of *Massetognathus* belong to this type, which is likely represented in all traversodontid species. Type II, tubercular rib, with ~~protuberences~~protuberances on the dorsal border of the rib (Fig. 8B), only documented in *Protuberum* (Reichel et al. 2009). Type III, rib modified as costal plate, displaying a complex morphological gradient, and in which the anteroposterior width of the plate and the shaft distal to the plate are variable in the same individual (Fig. 8C). This type is present in *Andescynodon*, *Pascualgnathus*, *Luangwa*, *Menadon*, *Traversodon*, and *Protuberum* (Barberena 1981; Bonaparte 1966; Kammerer et al. 2008; Kemp 1980a; Liu & Powell

Comentario [L64]: This is very specific. I do not understand the purpose of this sentence.

2009; Reichel et al. 2009). It is also present in the basal cynodonts *Thrinaxodon* and the basal Cynognathia *Cynognathus*, *Diademodon* and trirachodontids. The presence of this rib type is considered plesiomorphic in traversodontids (Crompton 1955; Jenkins 1971). Compared to *Thrinaxodon* and trirachodontids (NMQR3521), the distal end of the costal plate does not form a double-layered recurved surface. Type IV, fused rib with a Y-shaped distal end (Fig. 8D), ~~. It is~~ only known as the posterior dorsal ribs of *Massetognathus* (Jenkins 1970b; Pavanatto et al. 2015).

The anterior dorsal ribs of traversodontids do not bear costal plate as in *Cynognathus*, *Diademodon* and trirachodontids, whereas the posterior dorsal ribs are represented by costal plate in most genera, except *Massetognathus*, *Exaeretodon*, and *Boreogomphodon*. The posterior dorsal ribs are generally shorter than the anterior dorsal ribs, but the transformation in length is smooth in most species and no clear differentiation on thoracic and lumbar region can be made possible other than in *Massetognathus*. Jenkins (1971, p55) identified the first lumbar vertebra in *Thrinaxodon* on the basis of the loss of a rib shaft distal to the costal plate. In traversodontids with type III ribs, this criterion can be applied (e.g., Kemp 1980).

Generally, the sacral ribs have similar length and distal expansion to connect with the iliac blade. However, in *Massetognathus pascuali,* the first sacral ribs (Jenkins, 1970b: fig. 2A, S1) has similar shape as the last lumbar, and the last sacral rib (Jenkins, 1970b: fig. 2A, S6) is too short to contact the iliac blade (Jenkins 1970b). The first sacral rib has more expanded distal end than remaining ones. The caudal ribs are synostosed to the vertebrae and their shafts direct posterolaterally.

NHMUK R9391 from the Manda Formation is associated with bones of the probainognathian *Aleodon* and the traversodontid *Scalenodon*. This specimen only features type III ribs (Fig. 8E). These ribs are essentially similar to the posterior dorsal ribs of *Andescynodon* and *Pascualgnathus*. Because this kind of ribs is unknown in Probainognathia, it is considered here as more likely representing *Scalenodon angustifrons*.

Jenkins (1971) reviewed the epaxial muscles in reptiles and mammals, associating the costal plates in cynodonts with well-developed iliocostalis muscle. He suggested two functions for them. The first is about locomotion. The coastal plates provided larger insertional area for attachment of the muscle; and assisted the lateral flexure of the vertebral column. The second function is provision of intrinsic strength to the vertebral column by the imbrication of successive ribs. He connected this function with the reinforcement of lumbar region of mammals, which promote the ability of transmit thrust force. Kemp (1980) analyzed function of the costal rib in *Luangwa*. He suggested that *Luangwa* has no lateral movement of the vertebral column because vertebral column is effectively rigid in this plane. He proposed two advantages: the first one is maintenance of the momentum; the second one is the improvement on the maneuverability. However, the curled skeletons of *Thrinaxodon* such as BP/1/2776 indicate the presence of a considerable lateral movement of the vertebral column even it has the costal plates.

In mammals, ~~xenarthrae~~ xenarthry is perhaps ~~are~~ an adaptation for fossorial behavior (Gaudin & Biewener 1992). Expanded ribs may increase the stability of the

Comentario [L65]: I do not understand the purpose of this sentence.

vertebral column, and are common character in fossorial mammals (Jenkins 1970a). Evidence showed that *Thrinaxodon* and *Trirachodon*, both with costal plates and anapophyses, are burrow-making animals (Damiani et al. 2003; Groenewald et al. 2001). The anapophyses are associated to type III ribs in all known traversodontids; this perhaps ~~suggested~~ suggests a fossorial behavior for these species. In *Massetognathus*, the zygapophyseal facets on posterior dorsals are oriented at angles of around 45˚ but the anapophyses are absent. So ~~both~~ the bending in both lateral and dorsoventral directions is permitted. The posterior process on posterior dorsal ribs maintains the tendency of reinforcement of lumbar region but reduced to a lighter structure to acquire higher mobility. Although the ribs of *Protuberum* are special in the tubercles on dorsal side, the basic pattern is the same as that of other traversodontids with type I ribs. In *Protuberum*, ~~The~~ the posterior dorsal ribs have larger costal plates than other traversodontids; they overlap each other to form a connected plate. This is the most rigid vertebral column in this group, ~~improved~~ improving the protection of inner ~~organisms~~organs. The proximal tubercles possibly are homologous to the ridges on the costal plates of other cynodonts. The tubercles perhaps indicate one defensive structure on the surface. On the other hand, the s~~S~~imilar sized *Exaeretodon* ~~adapted~~ adopted another strategy as~~,~~ their ribs are reduced to normal costal type I. Perhaps only *Boreogomphodon* has ~~the~~ a truly lumbar region in all known traversodontids. The lumbar vertebrae, and possibly all dorsals, can rotate in sagittal and horizontal planes, indicating that the vertebral column was able to bend~~ing~~ laterally and dorsoventrally. The lumbar vertebrae are more massive than thoracic vertebrae, similar to mammals

Comentario [L66]: You should provide evidence to support this statement. If not, you should re-phrase this in a more speculative manner.

Comentario [L67]: Include reference.

~~too~~.

Shoulder girdle

Interclavicle and clavicle. The interclavicle and the clavicle are known only in *Exaeretodon argentinus* (Fig. 9A,B; Bonaparte, 1963: fig.16), *Massetognathus pascuali* (Fig. 9C,D; Jenkins 1970a: fig. 5) and *Boreogomphodon* (Figs. 4~~, 9~~); the clavicle is also reported in *Andescynodon* (Liu & Powell 2009) and *Pascualgnathus* (Bonaparte 1966). As in *Thrinaxodon* (Jenkins, 1971), the interclavicle is cruciate with an elongate posterior ramus in *Boreogomphodon* and *Massetognathus*. In *Exaeretodon*, it is laterally expanded with a short posterior ramus, so the width is close to the length. No notable difference between traversodontid species has been observed for the clavicle.

Scapulocoracoids. Other than *Boreogomphodon*, the scapulocoracoids were reported in *Andescynodon* (Liu & Powell 2009), *Exaeretodon* (Bonaparte 1963), *Luangwa* (Kemp 1980a), *Massetognathus* (Jenkins 1970b; Pavanatto et al. 2015), *Menadon* (Kammerer et al. 2008), *Pascualgnathus* (Bonaparte 1966) and *Traversodon* (von Huene 1935-42)(Fig. 10).

Comentario [L68]: Please include more references to the figures in this section.

In *Cynognathus* and *Diademodon*, the scapula does no constrain below the acromion process and the anteroposteriorly shorter place lies above the acromion process (Jenkins, 1971: fig. 17; Fig 10A-D). In Traversodontidae, the scapular blade constrains below the acromion process, forming an anteroposteriorly short neck (Fig. 10), that provides extra space for the insertion of the supracoracoideus muscle. Kemp~~s~~ (1980) described the acromion process of *Luangwa* as more reflected laterally than that of *Diademodon*-*Cynognathus*. This condition is represented in all traversodontids with well-preserved scapula. The acromion process is reconstructed very high in the scapula of *Pascualgnathus* (Bonaparte 1966), however that portion of the bone is poorly preserved in the specimen and here is interpreted as part of the scapular flange based on personal observation.

The procoracoid participates into the glenoid in *Luangwa* and *Pascualgnathus*; it reaches but does not participate in the glenoid in *Massetognathus*, *Menadon*, and perhaps *Andescynodon*; and it is far from the glenoid in *Exaeretodon*, *Boreogomphodon*, and *Traversodon*.

The shape of the procoracoid is variable within this group. The ventral margin of procoracoid is confluent with that of coracoid, forming a convex flange in *Andescynodon*, *Massetognathus*, *Menadon*, possible in *Boreogomphodon*, and *Pascualgnathus*; while it is roughly straight in *Luangwa*. The anterior margin of the procoracoid is convex in *Luangwa*, and *Menadon* as in *Cynognathus* and *Diademodon*, nearly straight or slight concave in *Andescynodon*, *Boreogomphodon*, and perhaps *Exaeretodon* and *Massetognathus*.

The procoracoid foramen is close to the articular surface with the scapula in this group, while it lies in the anterior corner of the bone, far from the articular surface with the scapula in *Cynognathus* (Fig 10A, B). It is closer to the articular surface with the coracoid than the anterior margin in *Luangwa*, *Massetognathus* (contra Jenkins 1970b: fig. 6), and *Menadon* whereas it is closer to the anterior margin of the bone in *Exaeretodon* (PVL 2554) and *Boreogomphodon*.

The coracoid is irregularly quadrilateral or approximately triangular in outline in traversodontids and~~. I~~ its posterior process ends in a tuberosity. The tuberosity is short and mainly ventral to the glenoid in *Luangwa*, *Traversodon*, and possibly *Exaeretodon*; but long and distinctly posterior to the glenoid in *Andescynodon*, *Pascualgnathus*, *Massetognathus*, and *Menadon*. The dorsal margin of the coracoid in the medial side is shorter than that of the procoracoid in *Luangwa* and possible *Pascualgnathus*, nearly equal in *Massetognathus* and *Menadon*, and is longer in *Boreogomphodon* and perhaps in *Andescynodon*.

Forelimb

Comentario [L69]: Please include more references to the figures in this section.

Humerus. The humeri are preserved in many species. The basic shape is the same in this group ~~as~~ than in *Cynognathus* or *Diademodon* (Fig. 11). The proximal half of the humerus is roughly triangular in most species, while it is roughly trapezoid in *Exaeretodon* for the development a flange on the posteromedial surface. The articular surface is confluent medially with the lesser tuberosity and laterally with the proximal margin of the deltopectoral flange. The lesser tuberosity is well-developed in *Luangwa* than other species. The deltopectoral crests reflect laterally in different degrees but this part is easily deformed during fossilization, and it is uncertain how much of the differences are due to the deformation.

The relative width of the humerus varies with the length (Table 1). Among t~~T~~he basic functions of the bones are the support of the body against gravity and to attach the muscles. The diameter (width) of ~~the~~ a supporting bone ~~like~~as the humerus should increase with the increase of length; this is ~~showed~~ shown by the positive ~~allometric~~

Comentario [L70]: In the epigraph of this table the meaning of PW/L and DW/L is missing and should be added.

Comentario [L71]: Please provide references.

Comentario [L72]: Why? Please explain and/or provide reference.

allometry of the proximal width (PW), the distal width (DW), and the sum of the shaft minimum width in anteroposterior and dorsoventral directions (S1+S2) relative to the length (L) (Fig. 12). The scaling is close to 1.2 other than the one related to the distal width. The regression function for L (Y) to S1+S2 (X) is: $Y=5.7695X^{0.833}$ ($R^2=0.984$). In the mammalian humerus, the scaling for the least circumference to the length is 0.76 for all mammals, 0.83 for small mammals under least squares regression (Christiansen 1999). Here, the sum of S1 and S2 can be used as a lineal approximation of the least circumference, so this scaling (0.83) can be compared with that of small mammals. This scaling ($l\propto d^{0.83}$) is ~~middle~~ intermediate between geometric similarity (isometry: $l\propto d$) and elastic similarity ($l\propto d^{0.67}$), far from stress similarity ($l\propto d^{0.5}$). It shows that the humeral growth strategy is similar to that of small mammals. The point of *Luangwa* appears to be an outlier; indicating ~~a sl~~that its shaft is slenderer than the normal humerus (Fig. 12).

Comentario [L73]: This figure is not easy to understand. I strongly recommend that you include labels for the axes.

Comentario [L74]: Please provide reference.

Comentario [L75]: This is not clearly identified in fig. 12. It would be great if you could reference each dot to a taxon.

Ulna and radius. As the humerus, the ulna and the radius are robust in large specimen and slender in small specimens. The inter-specific difference is distinct on the proximal side of the ulna (Fig. 13). The ossified olecranon process is absent in all but *Exaeretodon*, in which the relative length of the olecranon is about fifteen percent of remaining portion of the ulna (MACN 18063, PVL 2467) (Bonaparte 1963). The length of the ulna is about 68% of the humerus in two specimens of *Boreogomphodon*, this ratio~~s~~ in *Exaeretodon*, *Massetognathus*, and *Pascualgnathus* ~~are~~ is greater than 76% (Table 2). If the olecranon part is excluded, the ratio in *Exaeretodon* (PVL2467) is similar to that of *Boreogomphodon*.

Comentario [L76]: In the epigraph of fig 13 you refer to *Exaeretodon besairiei* but this is not a currently recognized taxon. Please check.

Comentario [L77]: You should make explicit which ratio you are referring to. Is it humerus/ulna or ulna/humerus?

Manus. The manus is only known in *Boreogomphodon* and *Exaeretodon*. Most carpals are identified in both species, except for the fifth distal carpal in *Exaeretodon*, and the pisiform in *Boreogomphodon*. The pisiform is a large element in *Thrinaxodon*~~,~~ and *Diademodon* (Jenkins, 1971, p127), but smaller in *Exaeretodon*. Even if this bone was ossified in *Boreogomphodon*, it should be too small to be observed. Besides *Boreogomphodon*, a separate fifth distal carpal is only known in one specimen of *Thrinaxodon* among non mammaliaform cynodonts (Jenkins 1971; Parrington 1933). When present, the fifth is the smallest of the distal carpals. It is lost or fused in *Exaeretodon*. The digital formula of *Exaeretodon* is 2-3-3-3-3; whereas the preserved elments in *Boreogomphodon* are 2-1-3-3-3~~.~~. Because *Cynognathus*, *Diademodon*, *Cricodon* also have this digital formula, it is safe to infer this formula presents in all cynognathians, including *Boreogomphodon* (Crompton 1955).

Comentario [L78]: Reference to figure and Bonaparte, 1963

Comentario [L79]: Which one? Please clarify.

Pelvis

The pelvis was described in *Andescynodon* (Liu & Powell 2009), *Exaeretodon* (Bonaparte 1963), *Luangwa* (Kemp 1980a), *Massetognathus* (Jenkins 1970b; Pavanatto et al. 2015), *Menadon* (Kammerer et al. 2008), *Pascualgnathus* (Bonaparte 1966) and NHMUK R9391 (Jenkins 1971) (Fig. 14).

Comentario [L80]: *Pascualgnathus* is not properly spelled in the epigraph of fig. 14. In fig 14, the bone in the lower right corner is not identified by a letter and is not included in the epigraph.

The ilium in tranversodontids is clearly different from that of *Cynognathus* or *Diademodon* (Jenkins 1971). The dorsal (vertebral) margin is nearly straight or slightly concave rather than convex in all well-preserved ilia. In a trirachodontid (NMQR 3521), this part looks still convex (Fig. 14H). The angle between the ventral margin ~~on~~ of the anterior and posterior processes of the iliac blade is around 120° in NHMUK R9391 and *Pascualgnathus*, about 150˚ in *Andescynodon*, *Luangwa*, *Massetognathus*, and *Menadon*, nearly 180˚ in *Exaeretodon*; so the neck between the blade and the base is narrower and more obvious in NHMUK R3521 and *Pascualgnathus*~~.~~. In *Cynognathus* and *Diademodon*, the neck is wide and short as *Massetognathus*; but in a trirachodontid (NMQR 3521), the neck is narrow and pronounced as in *Pascualgnathus* (Fig. 14H). The ventral margin of the anterior process of the blade is nearly parallel to the dorsal margin, the anterior part of the blade is narrowly rounded and somewhat spoon-shaped other than in *Exaeretodon*, in which the anterior part is widely rounded and ax-shaped. The anterior process is short in *Scalenodon* (less than the diameter of the acetabulum), relatively long in *Pascualgnathus* (between 1 to 1.5 times of the diameter of the acetabulum), and long in other species. The posterior process is long in all known species other than *Exaeretodon*, in which its length is less than the diameter of the acetabulum.

Comentario [L81]: Please clarify to which taxon you are referring to.

Comentario [L82]: Refer to the figure.

Comentario [L83]: Provide proportion for consistency.

The lateral surface of the blade is concave ~~to form~~forming a fossa, which lies mainly on the anterior process. The anterior process in *Luangwa* and *Massetognathus* features a lateral reflected ventral margin (Kemp, 1980; Liu, pers. obs: PVL 4442) that enhance the fossa on the anterior process. With the ~~modification~~ shape of iliac blade of *Exaeretodon*, the center of the fossa is close to the anterior margin of the blade than in other taxa. The ilio-femoralis (gluteal) muscle origins on the lateral surface of the iliac blade. Jenkins (1971) did not observe muscle markings on the lateral surface of iliac blade in *Cynognathus*, he suggested the muscle origin on the fossa anterodorsal to the acetabulum, whereas Kemp (1980) suggested this muscle occupies most of the lateral

Comentario [L84]: Provide reference.

surface of the iliac blade in *Luangwa*. We interpret this fossa as the origin for ilio-femoralis muscle. With the extension of the anterior process, and the anterior position of the fossa as in *Exaeretodon*, the muscle is disposed more horizontally and increases the volume, with results in an increased retraction force on the femur.

One problem about the ilium is its original body position. In Jenkins' (1970: fig. 10, 11~~)~~ reconstruction), the ventral margin of the posterior process of the iliac blade in *Massetognathus* is nearly horizontal. This placement is probably reconstructed following the conditions represented in *Thrinaxodon* (AMNH 2228) and *Diademodon* (USNM 23352), in which the pelvis is preserved in situ. Meanwhile, Bonaparte (1963: fig. 21) reconstructed the iliac blade more posteriorly inclined in *Exaeretodon*; Bonaparte (1966: fig. 15) and Kemp (1980: fig. 13) represented the ilium anteriorly inclined in *Pascualgnathus* and *Luangwa*, respectively. The exact original position of the ilium is difficult to ~~know~~infer, but the axis of the attaching points of the ribs on the blade should form some degree with the horizontal following the transition of the position of sacral vertebrae (Fig. 14).

Comentario [L85]: There is something strange with this sentence. Please check and rephrase.

Based on the reconstructed posture, the anterior part of the pubis extends anteriorly beyond the anterior margin of the acetabulum in *Scalenodon*, *Andescynodon*, and *Pascualgnathus*, and ventral to the acetabulum without reaching its anterior margin in *Luangwa*, *Massetognathus*, *Menadon* and *Exaeretodon*. The pubis generally is ventrally and medially directed, but is almost medially directed in *Luangwa*. The diameter of the obturator foramen is similar to the diameter of the acetabulum in *Scalenodon*, *Andescynodon*, *Pascualgnathus*, and *Massetognathus*, smaller in

Exaeretodon~~,~~ and perhaps larger in *Luangwa*.

Hindlimb

As major supporting bones, the diameters of the femur, the tibia, and the fibula increase with their length, so they are slender in small specimens and more massive in large ones.

Comentario [L86]: I strongly encourage the authors to include a table with the measurements.

Femur. The basic structure of the femur in traversodontids is similar to that of *Cynognathus* (Fig. 15). The robust major trochanter generally is confluent with the head forming a semicircular outline to the proximal side of the bone. A notch separates the head from the trochanter major in *Andescynodon*, *Massetognathus pascuali* (Jenkins, 1971: fig. 7) (Fig. 15D, F) but not in *M. ochagaviae* (Pavanatto et al., 2015: fig. 7). The notch could be the result of poor ossification or preservation at least in *Andescynodon*. Kemp (1980) described the major trochanter of *Luangwa* as extending further proximally than in the femur of *Cynognathus-Diademodon*; however, the position of the major trochanter is similar for them and is slightly more distally and laterally than most tranversodontids (Jenkins, 1971: fig.48). The minor trochanter is mostly directed posteriorly and slightly medially in *Boreogomphodon*, *Massetognathus*, *Pascualgnathus*, *Scalenodon angustifrons*, and *Traversodon*; but is directed strongly medially in *Andescynodon*, *Exaeretodon*, and *Luangwa*, although in the latter taxon could be accentuated by deformation.

Comentario [L87]: In the epigraph of fig. 15 *Pascualgnathus* is wrongly spelled.

Pes. The tarsus is well preserved in *Scalenodon* (NHMUK R9391), *Boreogomphodon* (NCSM 20698), and *Exaeretodon* (PVL 2554). Seven tarsals ~~as mammals~~ are counted in former two species as in mammalas, whereas one more is present in *Exaeretodon* ~~the~~

Comentario [L88]: Provide reference.

~~latter~~ (Bonaparte 1963; Jenkins 1971). The first is the shortest metatarsal in all cases. The digital formula ~~perhaps~~ is interpreted as 2-3-3-3-3 for all species of this group.

Comentario [L89]: This statement is a bit ambitious in my opinion as there is not enough data to support such a generalization. I suggest that you tone that down.

CONCLUSION

In summary, the postcranial skeletons of traversodontids have the following common features: 20-30 presacral vertebrae including 7 cervicals and at least 4 sacrals; interclavicle cruciate with an elongate posterior ramus; scapula constrains on the base below the acromion process, forming a neck; iliac dorsal margin nearly straight or slightly concave; major trochanter of femur robust; manus and pes digital formula 2-3-3-3-3. They also show variation in different species. The variation is most distinctive in axial skeleton, then, in the pelvis and pectoral girdle, and a little in limb. The vertebrae mainly differ in the number of sacral vertebrae, the presence of the anapophyses and the angle of zygophyseal facets. The ribs in most species preserve the primitive morphology of *Diademodon* and trirachodontids while the ridge on costal plates is reduced. The structure of ribs is further reduced in some species like *Boreogomphodon*, *Massetognathus*, and *Exaeretodon*; but is complicated in *Protuberm*. The acromion process and the neck below are developed in this group, but the extension of the neck only occurred in *Boreogomphodon*. The major transformation in shoulder girdle is the diminution of the procoracoid size. The anterior process of the iliac blade extends anteroventrally ~~extends~~ in this group, and ~~their~~ the iliac neck is less pronounced than in the primitive member ~~like~~ *Pascualgnathus*; the posterior process shows no distinct change other than the shortening in *Exaeretodon*. The structure of the limb bones is relatively uniform, and the robustness of the limb bones is directly related to their size.

The relative uniformity of the structures indicates ~~the~~ similar ~~locomotion~~ locomotory strategies in this group. The humerus still moves in a horizontal plane, and the femur is half-erect. The locomotory force is mostly generated by the hind limb. The anterior position of the iliac blade enables more efficient rotation of the femur in nearly erect gait. The vertebral column is rigid but permits bending in most species, more flexible in derived forms. The pelvis connects the hind limbs to the trunk, a strong connection is required especially in large sized animals, resulting in the extension of the iliac blade and the increase of sacral vertebrae and ribs in large size groups like *Exaeretodon*.

Comentario [L90]: You had not discussed and probed this conclusion.

Comentario [L91]: You had not discussed and probed this conclusion.

As stated ~~anteriorly~~previously, specimen NHMUK R9391 represents a traversodontid with primitive features, such as its morphology of the ilium and the ribs. Two genera, *Scalenodon* and *Mandagomphodon*, have been referred to Traversodontidae ~~from~~ on the basis of materials ~~of~~ from the Manda Formation (Crompton 1972; Hopson 2014; Liu & Abdala 2014). Within their named species, *S. angustifrons* is far more basal than other species; accepted the correlation of skull and postcranial features, NHMUK R9391~~this specimen~~ could be referred to *S. angustifrons*.

Comentario [L92]: This is interesting but this conclusions seems to be unrelated to your work. You should specifically discuss this in a previous section and provide the adequate context for your conclusion.

Comentario [L93]: There are several problems with the figures/tables/epigraphs: (1) many of the photographs are out of focus, (2) the bones are not properly cropped, (3) there are dark and clear lines and spots surrounding the bones, (4) the lettering (position and order) is not consistent among the different figures, (5) some labels are lacking a line pointing to the referred structure, (6) some structures are not labeled and not properly visible due to the small size and/or lack of focus of the figured elements, (7) some abbreviations are not present in the epigraphs or are wrongly cited, and (8) some genera are misspelled in the epigraphs.
Please check carefully all the figures and tables for these and other problems.

Institutional abbreviations

AMNH	American Museum of Natural History, New York, NY, USA
BP	Evolutionary Studies Institute, University of the Witwatersrand,

	Johannesburg, South Africa
MACN	Museo Argentino de Ciencias Naturales ‘‘Bernardino Rivadavia’’, Buenos Aires, Argentina
NCSM	North Carolina State Museum, Raleigh, NC, USA
NHMUK	Natural History Museum, London, UK
NMQR	National Museum, Bloemfontein, South Africa
PVL	Colección de Palaeontología de Vertebrados, Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina
USNM	National Museum of Natural History, Washington D.C., USA

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