The Osteology of South American Camelids

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### DESCRIPITIVE OSTEOLOGICAL ATLAS OF SOUTH AMERICAN CAMELIDS

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For the consideration of our colleagues who are interested in Andean zooarchaeology or paleozoology, we submit this essay prepared by our students: Victor Raul Pacheco Torres, Alfredo Altamirano Enciso, and Enma Guerra Porras, entitled: "The Osteology of South American Camelids."

In the publication "On the Laboratory of Paleo-ethnozoology" (1976) we wrote the following:

During a time of confusion and contradictions in Andean Archaeology, the Laboratory of Paleoethnozoology originated as a center of specialized study of the fauna of the Central Andes and its center of influence. The founding of this laboratory is not a matter of imitation, nor of simply establishing one more laboratory in Peru. It is a natural consequence of the progress of a scientific archaeological investigation. The archaeologist can no longer work alone, much less with empty hands. He needs the assistance of specialists from the natural sciences, as well as those of the social sciences, from computer analysis, and from the specialized laboratories of biologists and physical chemists.

Many people have seen Peru as an inexhaustible mine for exploitation. For centuries the archaeological deposits were removed, finding their way into museums and private collections, especially in the West. Our national organizations, unfortunately, did nothing to impede this. Recently the same thing was occurring with samples of plants and animals; others have thus benefited from the lack of state control.

More recently our criteria for control have been substantial and effective. One manner of defending our cultural and natural resources is precisely to think about and to give life to the centers of investigation. We established the Laboratory of Paleoethnozoology in 1975. We invited visiting professors to collaborate in its organization, and we asked the support of Dr. Aurelio Malaga Alba, who accepted the directorship of the Laboratory, an office which he has held ad-hocorem to date.

The orientation of work in archaeology with natural resources, the interaction of man with his environment, etc., follows the theoretical orientation of Kent Flannery. After my return from the United States in 1968, my interest was in the archaeological remains of animals and plants, the latter recovered by means of the technique of flotation. Through the use of this
technique and with faunal collection, by 1972 we already had a small comparative collection which increases each year. The University of San Marcos relies on this important center, and on our obligation to continue increasing and enlarging its services.

The collections of prehistoric fauna came principally from Junin. The modern collections, for the most part camelids, came from Instituto Veterinario de Investigaciones Tropicales y de Altura in La Raya, an important National Center of South American camelids endorsed by the University of San Marcos.

By working in this Laboratory of Paleoethnozoology and by studying its collection, the authors of this present manual have developed this important work which undoubtedly will be an excellent book of reference. It is a product of three earnest young students who have established both interest and vocations in archaeology.

This first publication will be the object of much criticism. I hope that it will be so. In such a case, science will benefit.

Ramiro Matos M.
Introduction

South American camelids entered this continent between one and three million years ago, migrating from North America. During this time, the camelids became adapted to a dry environment and, more recently, to one characterized by high altitudes. The adaptation was brought about by means of the development of locomotive and feeding mechanisms suitable for areas of scarce plant resources, such as that of the puna or the altiplano (high plain), with its rocky ground and seasonal snow cover. These physiological mechanisms evolved as the product of the relation between the phylogenetic history of the camelids and the requirements of their environment.

At present there are four principal camelids: the llama, the alpaca, the vicuña, and the guanaco. The four are very similar in morphology. In fact, it is now possible to hybridize them with various levels of success.

Because of such a high degree of similarity, caused by similar adaptation and their ability to interbreed with some success, it has been very difficult to distinguish, osteologically, the bones of each variety of camelid. This difficulty is especially manifest macroscopically.

Less difficult, but still problematic, is the similarity between bones of camelids and those of the other ungulates that are similarly adapted, such as the cervids (e.g., the white-tailed deer Odocoileus virginianus, or the taruga, Hippocamelus antisensis). This similarity stems from the fact that they have developed convergent mechanisms that permit the animals of the sierra to adapt to similar environmental requirements. This fact is reflected in an osteological similarity.

Our purpose in this manual is to provide the field investigator with a handy reference for the identification of the osseous remains of camelids and allow that investigator to easily distinguish the remains of a camelid from those of the other animals with which they may be confused. One may apply this manual to the remains of any one of the four varieties of camelid.

This manual may be used by range managers, biologists, archaeologists, and public officials dedicated to the protection and propagation of these valuable animals, as well as by investigators of animal science and veterinary medicine. For example, the expert in animal management frequently encounters osseous remains of animals victimized by predators or killed by other means. He may use this manual to determine if the faunal remains belong to camelids so that he might change pasture areas or take measures against the predators.

In a similar manner, the biologist needs to evaluate how the food web functions within a particular ecological zone.
Given that the vicuña and the guanaco are animals threatened by extinction, and given the increase in illegal hunting, this manual would provide those officials charged with carrying out conservation laws a way to determine if remains found in the field belong to a camelid or to some other animal. This would serve not only to provide evidence in a court prosecution, but also to permit the taking of effective measures against such illegal hunting practices in the future.

The archaeologist's problems are somewhat different because often he has, even in the best circumstances, only a partial skeleton. More frequently, he has to identify animals represented by mere fragments of bones. It is hoped that the inclusion of various keys to diagnostic elements will help him in his work.

This manual can be used with the most effectiveness if the specimen is at hand. It is also recommended that whoever uses it familiarize himself with each one of the illustrated bones and the keys to diagnostic elements. This familiarity will improve the process of identification.

In the description of the diagnostic elements (including tubercles, fossae, foramina, crests, general forms, etc.), the emphasis has been placed, through the illustrations, on those elements which serve to distinguish efficiently the camelids from other large animals. In those cases in which a diagnostic feature might be variable, the variation is indicated in the text. The numbers in parenthesis in the text refer to the features numbered in the figures and usually are of special importance.

The manual has been prepared using a large collection of camelid skeletons in the Paleoethnozoology Laboratory of the University of San Marcos, academic program of Veterinary Medicine, Lima, Peru. That collection was largely prepared through the efforts of previous investigators and, without their activities, this manual would not exist.

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Notes

1. "Success" is measured in terms of the proportion of live births to the total number of births.

Three million years before present (b.p.) represents a likely date for the start of a major faunal interchange between North and South America. However, the date of the emergence of the Panamanian land bridge is uncertain, and there are records of minor faunal migrations between continents for much of the Pliocene (i.e., back to thirteen million years b.p.; see Marshall et al. 1979:275).

2. Later on we hope to publish a manual about methods to distinguish the bones of the four species of camelids from one another.
Note: ( ) indicates translator's comments for clarification in English.

The Skull (Figure 1)

The mastoid foramen of the occipital is very large; however the diameter varies considerably and it tends to become narrower in the guanaco. The tympanic bulla (18) is compressed antero-posteriorly, its quadrangular and oblique form is oriented forward and toward the axial axis. The edge of the paramastoidal apophysis (the most ventral part of the bulla) is at the same level as the occipital condyles (19).

The zygomatic arch (17) is formed in the South American camelid when the zygomatic process of the temporal inserts like a wedge between the two branches of the molar (6): the orbicular and the zygomatic. The facial crest of the molar is little pronounced and does not extend as far as the upper maxillary. The supraorbital notch, located over the orbital foramen, can be found closed or open (in the guanaco).

In most of the individuals there exists a lacrimal fenestra in front of the orbital foramen. This fenestra is not present in our samples of vicuñas but appears as a frontal-maxillary articulation.

The permanent dental formula is:

\[ I^1_3 \quad C^1_1 \quad P^2_1 \quad M^3_3 \]

In the upper maxillary, the premolars are in front of the infraorbital foramen. The upper molars are slightly more posterior than the lowers; the molars, of the selenodont type, possess four cusps except for the third lower molar which has five cusps. Upon emerging, these cusps wear out. The lower fourth premolar customarily appears with six tubercles arranged in three rows of two tubercles each. In the palate of the adult the choanas (posterior nares) reach to the level of molar three.

The Mandible (Figure 2)

The mandible contains a reduced angular process which generally is oriented medially toward the main axis of the skull. The mandibular foramen has a lip which partially covers it. The coronoid process is very high.
Figure 1. Skull of a 9-year-old *Lama glama* (A-118) male. Top: Left lateral view. Bottom: Ventral view.
The Osteology of South American Camelids

The Mandible

1. Coronoid process
2. Masseteric fossa
3. Molars
4. Canine
5. Incisors
6. Mental foramen
7. Body of mandible
8. Mandibular angle
9. Angular process
10. Mandibular condyle

Figure 2. Mandible of a Lama alama (A-118) male. Right lateral view.

The Vertebral Column (Not Illustrated)

C-7 T-12 L-7 S-5 C-11-17
(7 cervical vertebrae, 12 thoracic, 7 lumbar, 5 sacral, and 11 to 17 caudal vertebrae)

Cervical Vertebrae (Figure 3)

In the cervical vertebrae there is evident dominance of the length over the other measurements, except in the first (atlas) and in the seventh. The vertebral body ((centrum)) has a ventral crest with a posterior tubercle which is less marked in the sixth and seventh vertebrae. The second ((the axis)) through the sixth cervicals contain transverse canals ((vertebroarterial canals)) in the interior of the vertebral foramen ((neural arch)) for the vertebral artery. The dorsal spinal process is very reduced and appears only in the extreme anterior of each vertebra. The transverse processes are winged and slightly curved toward the dorsal face; in the axis they are curved toward the ventral face.
CERVICAL VERTEBRAE

1. Posterior articulating facet
2. Transverse process
3. Ramus of the transverse process
4. Spinous process
5. Body or centrum
6. Ventral process
7. Anterior articulating process

Figure 3. Two cervical vertebrae of a 9-year-old Lama pacos (A-114) male. Left: Sixth cervical vertebra, right side. Right: Third cervical vertebra, right side.

The Atlas (Figure 4)

This is the vertebra where the greatest dimension of the vertebral foramen may be seen. The anterior articular cavity is not separated by a notch or groove (between the two dorsal facets) as occurs in cervids. A moderate ventral crest is present; the transverse process is winged, slanting antero-posteriorly from above to below, with the transverse foramen (or alar canal) exiting on the posterior dorsal surface.
The Osteology of South American Camelids

THE ATLAS

1. Dorsal arch
2. Articulating facets for the occipital condyles
3. Ventral tubercle
4. Transverse process or wing
5. Intervertebral foramen
6. Ventral arch
7. Cotyloid process
8. Alar fossa
9. Transverse foramen
10. Posterior articulating facets
11. Intervertebral canal
12. Alar canal
13. Ventral arch (for the odontoid process of the axis)

The Axis (Figure 5)

The transverse process is winged and slightly curved below. The spinal process originates anteriorly and increases slightly in height as it progresses posteriorly, without extending to the two posterior articulating facets; the posterior end of this spinal process is expanding.

Cervical Vertebra No. 6: The ventral processes ((the costellar processes)) and the two posterior rami of the transverse processes (actually these are the postero-ventral costellar processes) appear to elevate this vertebra on four feet.

Cervical Vertebra No. 7: The body ((centrum)) is shorter, broader, and more compressed dorso-ventrally than the other cervicals. The dorsal spinal process is always anterior, but is shorter and bears a heavier tubercle on the anterior end. The transverse foramen may or may not be present; the transverse process is more anterior than in the other cervical vertebrae.

Thoracic Vertebrae (Figure 6)

The vertebral centrum or body is much shorter than in the cervical vertebrae; all of the vertebrae are similar in size, with a ventral crest which is very sharp-edged in the more anterior thoracic vertebrae. The spinous process is rectangular, very high, and curved backward in the first vertebrae. In the most posterior vertebrae, it becomes more quadrangular, more vertical, and smaller in size. The dorsal arch has intervertebral articulating facets (the anterior facets face up, the posterior facets face down), except on the first thoracic vertebra where the anterior articulating facet is found in the transverse process.

In the fourth and fifth thoracic vertebrae the two small posterior inter­vertebral articulating facets move together; at times they fuse into one single facet, then in the following vertebra they may continue to be two separate facets. In the anterior facets, the transverse processes begin to form a border which serves to narrow the small articulating faces so that in the tenth, eleventh, and twelfth vertebrae, the articulation is of the engaging type and will not slip.

Lumbar Vertebrae (Figure 7)

In all lumbar vertebrae, the centra are almost of the same length and are a little larger than those of the thoracic vertebrae. The seventh lumbar is a little smaller and is more compressed dorso-ventrally. The spinous processes are quadrangular and, all together, are inclined slightly forward. The articulating processes are found very close to the linea media ((dorsal half-line of the antero-posterior row)), and the anterior articulating process possesses a concave facet antero-posteriorly and dorsal-ventrally, giving the appearance of being a little hole or pit with a posterior border that limits the entrance of the posterior process of the vertebra which precedes it. The transverse processes are very long and, in general, more than double the length of the same vertebra, except in the first lumbar where it is less than double.
THE AXIS

1. Anterior articulating process
2. Intervertebral canal
3. Spinous process
4. Transverse process
5. Centrum
6. Odontoid process
7. Ventral process
8. Postzygapophyses

Figure 6. Thoracic vertebrae of a Lama pacos (A-114) male (top), and the third thoracic vertebra shown in its lateral view (bottom left), anterior view (bottom middle), and posterior view (bottom right).
LUMBAR VERTEBRAE

Figure 7. Left lateral view of lumbar vertebrae. The numbers correspond to the vertebra number.

The Sacrum (Figure 8)

The lateral crests of the sacrum become narrower posteriorly but without joining themselves to a central crest as occurs in cervids. The sacral aperture (passage) is very triangular. The ventral part of the articulating surface (the pleurapophysis) of the sacrum has a postero-ventral prolongation. The sagittal crest (spine) of each sacral vertebra is independent, low, and becomes increasingly heavy toward the posterior end. The fifth sacral vertebra usually is not completely fused with the anterior vertebra.

Caudal Vertebrae (Not Illustrated)

A clear predominance of the vertebral centrum or body is noted in the caudal vertebrae, with a reduction of all of the processes. From front to back, the vertebrae do not diminish as much in length as they do, gradually, in thickness.
THE SACRUM

A. Articulating processes of the sacrum
B. Dorsal sacral foramina
C. Wing
D. Ventral sacral foramina
E. Articulating surface for the ilia (pleurapophysis)

Figure 8. Sacrum of a Lama pacos. Top left: Dorsal view. Top right: Ventral view. Bottom: Lateral view.
Ribs (Figure 9)

There are twelve pairs of ribs: seven sternal and five a-sternal. The size, breadth, and angle of the body are quite variable. The body is wider in its sternal end than in the vertebral end, a feature that is more conspicuous in the first to the sixth ribs. The breadth of the sternal end is more convex, anteroposteriorly, in the third, fourth, and fifth ribs, diminishing in the last rib where it is quite flat.

The length of the ribs increases gradually from the first to the seventh rib, and decreases in the same manner in the a-sternal (costal) ribs. The costal groove is always posterior; it is encountered in the sternal end in the first rib and in the vertebral end in the rest; it is not marked in the eleventh rib and it disappears in the twelfth.

The nutrient foramen is found in the middle of the costal groove. The costal angle is very open in the first ribs, closing progressively until the fifth and decreasing by degrees until the last rib. The head is composed of two convex articulating facets in order to articulate between two thoracic vertebrae. The anterior face is more convex than the posterior, the difference being more marked on the first to the fifth ribs. In the seven remaining ribs the diminution of the shape of the articulating facets is evident. The tubercle is large in the first two ribs, convex from forward to back in the first two ribs, changing to be clearly concave in effect across the third to the ninth ribs. In the tenth and eleventh ribs the tubercles are very small, flat, and they move very close to the head, becoming fused in the twelfth rib.

The neck is thick, uniform, and short in the first ribs, but it increases progressively until the fifth rib where it continues more or less constant to the ninth, decreasing later until it almost disappears in the twelfth rib.

Figure 9. The ribs of a Lama pacos (A-114) male. Left: Right side of the first rib, medial view. Center: Second rib, medial view. Right: Eleventh rib, posterior view.
The Sternum (Figure 10)

The sternum is formed by six sternebrae. It has the form of a small canoe, flattened anteriorly and posteriorly, and cylindrical in its middle portion, with the dorsal face concave in the longitudinal direction. The first and second sternebrae are flattened dorso-ventrally, being more depressed in the anterior end than in the posterior. The first sternebra is less wide in the anterior end than in the posterior. The rest of the sternebrae are of a uniform thickness, except for the sixth which is thinner and which is more compressed on its posterior end than on the anterior. The first sternebra, viewed from above, is concave transversely. Ventraly, in the second, third and fourth sternebrae, a slight longitudinal groove is evident; dorsally in the third and fourth sternebrae are slight longitudinal crests.

The Scapula (Figure 11)

The scapula is a bone of a triangular contour with the infraspinous fossa more developed than the supraspinous fossa. The spine is elevated, its border curved, and it continues distally with the acromion which projects to a height which extends well above the glenoid cavity. The neck is thicker posteriorly than anteriorly. The anterior border of the scapula is a sharp crest; the posterior border is thick and flattened and projects deeper at the subscapular fossa. The tuberosity of the scapula (the coracoid process) is thick, rough, and furrowed and does not extend to the glenoid cavity on the anterior border. The coracoid process has a short lip which faces toward the interior (medially).

The Humerus (Figure 12)

The body of the humerus is compressed laterally in its proximal metaphysis (diaphysis or shaft) and is irregularly cylindrical in its distal end. The circumferential contour of the proximal end, viewed from above, is pentagonal. The lateral and medial tuberosities form two sharp and parallel furrows separated by a tubercle or prominence. Both tuberosities, viewed from the side, are at the same level and are well above the head of the humerus. The deltoid tuberosity is prominent with a lip which is directed backward. Distally the lateral border of the olecranon fossa is more projecting and thicker than its opposite (when viewed from the medial side). Distally and anteriorly, the medial condyle is demonstrably larger than the lateral condyle; the lateral epicondyle is thicker than the medial epicondyle. The distal metaphysis (diaphysis or shaft) presents a single nutrient foramen which tends to be on the lateral side.
1. Body or sternum center  
2. Fourth sternebra  
3. Fifth sternebra  
4. Sixth sternebra  
5. First sternebra  
6. Second sternebra  
7. Third sternebra  
8. Manubrium  
9. Articulating rib facets  
10. Xiphoid process

**Figure 10.** Sternum of a 55-month-old *Lama pacos* (A-275) female. Left: Ventral view. Center: Dorsal view. Right: Lateral view.
Figure 11. Right side of a scapula from a 5-month-old *Lama pacos* (A-219) male. Left: Lateral view. Right: Distal view.
Figure 12. Right humerus of a 11-month-old *Lama pacos* (A-292) male.
Radius-Ulna (Figure 13)

The radius-ulna is long and largely fused together in the adult, evidenced by the interosseous space left only at the proximal and distal ends. The radius-ulna is generally compressed antero-posteriorly. Proximally, the articular surface for the humerus consists of two facets; the facet on the lateral side is slightly larger and higher compared with the one on the medial side and in relation to the anterior border. The two facets are divided by a single axial elevation. Distally, in the anterior view of the radius, two sharp and parallel crests are presented, the lateral being the larger. The distal articular surface is composed of three facets for the carpals; the lateral and medial articular facets are almost of the same width and both are wider than the central facet. The medial facet extends farther to the posterior and also extends farther distally than the lateral facet.

The Pelvis (Figure 14)

In juveniles the iliac crest is curved and even, but in adults it becomes more vertical, more rugose and uneven, and its ventral point is inclined some 45° outward. On its internal surface the iliac wing (ilium) possesses the articular surface for the sacrum which is posterior to andchiefly superior to the pelvis wing.

In the external view of the pelvic wing, the females have a pronounced concavity. In the dorsal border of the same part of the pelvic wing, the males possess a crest. Structurally, in the female, the pelvis allows an enlargement of the pelvic cavity. The body of the ilium is extended lengthwise, is laterally compressed, and is more extended in the female than in the male.

The acetabular arm of the ischium in camelids possesses a high crest which terminates in the superior side or end of the obturator foramen. The symphysis branch or arm is flat, and its internal border forms an angle of a clear vertex in the females while in the male it looks like an inverted keel in which the apex of the angle is curved.

The pubic symphysis ramus and the acetabular ramus of the pubis are very concave, giving the ventral part of the pelvis a very deep appearance; the acetabular ramus may present a pronounced blunt elevation and be very concave transversely. This ramus is quite perpendicular to the pubic symphysis, causing the anterior end of this symphysis to be at the same level as the anterior border of the acetabulum.

The acetabulum is a fossa produced by the union and fusion of the three pelvic bones. It is not totally fused, as a posterior and internal entry opens into the obturator foramen; its internal sides constitute a smooth articular surface, except in the center where it is rough and generally is not separated by a projecting border. Anterior to the foramen are two lateral-ventral depressions for the tendons of the rectus femoris muscle; the external is better developed than the internal. The border of the obturator foramen adjoining the acetabulum comes very close to the acetabulum in camelids.
THE RADIUS-ULNA

1. Anconeal process
2. Olecranon
3. Semilunar notch
4. Glenoid cavity of the radius
5. Distal end of the radius
6. Body of the radius
7. Radius
8. Ulna
9. Distal end of the ulna

Figure 13. Right radius-ulna of an immature Lama pacos (A-293) female. Left: Anterior view. Top: lateral view. Also shown is the radius of an adult Lama pacos (A-249) female. Middle: Lateral view, proximal end. Bottom right: Carpal view of distal epiphysis seen from below.
Figure 14: Pelvis of a 45-month-old *Lama glama* (A-282) male. Top: Ventral view. Bottom: Dorsal view.
The Femur (Figure 15)

The femur is the long bone of the thigh. In its proximal end, the head is at the level of the greater trochanter which has a rugged and uniform border and ((posteriorly)) a sharp oblique crest which runs toward the lesser trochanter ((with an angle of about 45°)). The lesser trochanter is situated more over the medial side than over the posterior side; it is quite prominent and is oriented slightly forward.

A posterior crest stands out clearly in the diaphysis. This crest originates on the lesser trochanter and is directed obliquely below and outward until it connects with the lateral and medial epicondylar crests a few centimeters below the proximal half. The nutrient foramen is situated in the middle of the posterior face of the diaphysis and in the medial border of the crest.

In the anterior distal end of the femur we encounter a trochar and an epitrochlear fossa. Two condyles separated by an intercondylar fossa occur posteriorly; the lateral condyle is larger than its opposite, and the intercondylar fossa is slightly oblique. The internal border of the lateral condyle possesses an oblique groove.

The Patella (Figure 16)

The patella is a short bone of oval form; its posterior articular surface is rectangular, smooth, and concave from top to bottom but convex transversely. Its distal end is more prominent; viewed anteriorly, it is very convex and rugged.

The Tibia (Figure 17)

The tibia is a long, slightly curved bone and, except for the crest, its shaft is compressed antero-posteriorly. Viewed from above, the proximal surface is triangular; the posterior angles are the medial condyle and the lateral condyle. The anterior end is an isolated tuberosity of triangular form also, which posteriorly joins the crest. Each of the condyles forms an articular facet; the lateral condyle is larger and more square in form.

The fibula is only a spinous process located underneath the lateral condyle and is found only in some adults.

Proximally and anteriorly, the shaft has a crest whose lateral side is very concave, forming a fossa.

The nutrient foramen is always posterolateral and is situated about one-fifth of the total length from the proximal end.

The view of the distal end shows two long parallel depressions, slanting and separated by a prominence. Laterally there is a sulcus (or fibular groove) and two articulating facets for the lateral malleolus. The two prominences on the anterior edge of the distal end are larger than those of the posterior border; the central prominence is larger or equal in size to the medial one.
Figure 15. Right femur of a 9-year-old Lama pacos (A-278) female. Left: Anterior view. Center: Medial view. Right: Lateral view.
Figure 16. Patella of a 9-year-old *Lama pacos* (A-114) male. Left: Left side shown in its anterior, posterior, and lateral views (clockwise from left). Right: Right side, also shown in its anterior, posterior, and lateral views.
Figure 17. Left tibia of a 9-month-old (A-287) *Lama pacos* female, shown in anterior, lateral, posterior, and superior (or top) views. Also shown is the inferior or distal view of a tibia belonging to a different camelid, A-277.
The Metacarpal (Figure 18)

The metacarpal is a long bone which is compressed antero-posteriorly. The shaft, viewed from the posterior side, has a long, deep groove whose borders are quite parallel. A central line stands out on the anterior surface running distally from a proximal anterior process to the distal cleft which separates the two condyles.

The proximal end, seen from above, consists of two quite ovoid articular facets. The medial facet is itself subdivided by a ridge which produces two smaller facets, the posterior being the smaller.

The distal end of the metacarpal consists of two articulating condyles separated by a central cleft. The sagittal crest of each condyle is blunt and runs down the center of the condyle from the midpoint to the posterior border, dividing it into two symmetrical sides situated at the same level; these crests are smooth on the anterior half.

The Metatarsal (Figure 18)

The proximal surface of the metatarsal consists of four articular elements: a posterior elevated extension and three horizontal articulating facets. The two most anterior facets are the larger in size and are shaped like two beans. The medial facet is at a slightly more elevated level than the lateral facet. The third facet, which articulates with the first tarsal, is medial and very small.

The diaphysis presents a posterior fusiform groove and a smaller concavity than that of the metacarpal; the two nutrient foramina are lodged in the middle of the groove. As in the metacarpal, the external (lateral) edge of the groove is sharper and more prominent than the internal edge. The distal end of the metatarsal consists of two articulating condyles similar to those of the metacarpal except that the sagittal crests are of smaller elevation.

The Carpal Bones (Figure 19)

The carpals include seven small, short bones arranged in two rows; those of the first (superior) row are greater in height than those of the second, lower row. In their proximal end, the first row of carpals together form a generally horizontal plane with their dorsal surfaces which articulates with the radius-ulna.

First Row (Upper): Scaphoid (No. 2); Lunar (No. 4); Cuneiform (No. 3); and the accessory carpal, the Pisiform (No. 1).

Second Row (Lower): First carpal, the Trapezoid (No. 6); second carpal, the Magnum (No. 5); and third carpal, the Unciform (No. 7).

The scaphoid and cuneiform are cubical, of similar size, and larger than the central carpal, the lunar, which is fastened like a wedge between them. The cuneiform supports the pisiform, the accessory carpal, which projects from a small articular protuberance on the posterior surface of the cuneiform.

The carpal bones in the second row increase in size progressively from the medial face to the lateral.
Figure 18. Posterior, proximal, and distal end views of the metacarpal (left, middle-top, and center) and of the metatarsal (right, middle-bottom, center) of a Lama pacos. Note that the distal end views for both the metacarpal and the metatarsal are identical.
The Osteology of South American Camelids

THE CARPAL BONES

1. Accessory carpal, pisiform
2. Scaphoid
3. Cuneiform
4. Central carpal, lunar
5. Third carpal, magnum
6. Second carpal, trapezoid
7. Unciform
8. Radius-ulna
9. Metacarpal

Figure 19. Carpal bones of a Loma pacos (A-101) female.
The Tarsal Bones (Figure 20)

The tarsals include six bones of quite different structures. The calcaneum is well compressed laterally and has a projecting edge almost in the middle of its medial face in order to articulate with the astragalus. In the anterior edge of the calcaneum's distal end there is a smooth articular prominence for the lateral malleolus, and in the same distal end there is an articular face for the fourth tarsal, the cuboid.

The astragalus is a bone with many rounded surfaces and of a rather regular form with two trochleae: one proximal and one distal with their corresponding crests. A fossa is situated anteriorly between both trochleae, separating them. Posteriorly, the astragalus is very convex and articulates with the calcaneum.

The first tarsal is cubic and very small; the third tarsal has the form of a drum. Both bones articulate proximally with the navicular and distally with the metatarsal. The fourth tarsal is an irregular cuboid form with a posterior process. Its superior medial face adjoins the navicular and it has articular facets for all of the tarsal bones except for the first tarsal; it also has a facet for the metatarsal.

The Phalanges (Figure 21)

The camelids have two toes on each of their legs. The first phalanx is a long bone of larger size in the foreleg than in the rear leg. The proximal articular surface of the first phalanx is similar to a concave semi-circle, antero-posteriorly, with a small central posterior groove. The distal articular surface is a condyle with its anterior edge situated at a lower level than the posterior edge.

The second phalanx differs from the first in that it is smaller and has no mortise or groove in its ventral posterior surface. On the other hand, the posterior crest is more proximal than the dorsal crest, and it is more proximal than on the same surface of the first phalanx. The second phalanx has both a thicker body and a broader posterior articular surface in the foreleg than in the rear leg.

The third phalanx is a short bone of a pyramid type with a concave posterior articular surface. Ventrally it is flattened and dorsally it is a sharp-edged curve. In the forefoot it is less high and it is broader than in the rear foot. The sides of the third phalanx possess many holes for blood veins; most of these holes are on the internal side.
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THE TARSAL BONES (Right)

Anterior  Lateral  Posterior

Astragalus  Calcaneus  Astragalus  Calcaneus

Tibia

Metatarsal

1. Third tarsal, entocuneiform
2. Central tarsal, navicular
3. Lateral malleolus, fibulare
4. Fourth tarsal, cuboid
5. First tarsal

Figure 20. Tarsal bones of a Lama pacos (A-114) male.
Figure 21. Right phalanges of a 9-year-old *Lama pacos* (A-114) male.
The Osteology of South American Camelids

Table of Ages for Camelids
((Based on Tooth Eruption and Morphology))
By Alfredo Altamirano E.

DENTAL MORPHOLOGY OF MANDIBLE OF ONE SIDE:

<table>
<thead>
<tr>
<th>AGE</th>
<th>dP3</th>
<th>dP4</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 days</td>
<td>I Pre (B)</td>
<td>1P, 1P, 1P</td>
<td>2P (A)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 month</td>
<td>I Pre (B)</td>
<td>1P, 1P, 1P</td>
<td>2P (A)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 months</td>
<td>I Pre (C)</td>
<td>3P</td>
<td>2P (A)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 months</td>
<td>I Pre</td>
<td>3P</td>
<td>2P (B, A)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9 months</td>
<td>I Pre</td>
<td>3P</td>
<td>2P (C, B)</td>
<td>1P (A)</td>
<td></td>
</tr>
<tr>
<td>1 year</td>
<td>I Pre</td>
<td>3P</td>
<td>2P (A, A)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 years</td>
<td>I Pre</td>
<td>3P</td>
<td>2P (adult, C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 years</td>
<td><strong>--</strong></td>
<td>3P</td>
<td>2P</td>
<td>2P (B, A)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>P4</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 years</td>
<td>I Pre</td>
<td>2P, 2P, 2P (adult, C)</td>
<td></td>
</tr>
<tr>
<td>5 years</td>
<td>I Pre</td>
<td>2P, 2P, 2P (with a small additional loph)</td>
<td></td>
</tr>
<tr>
<td>7 years</td>
<td>I Pre</td>
<td>2P, 2P, 3P</td>
<td></td>
</tr>
<tr>
<td>8 years</td>
<td>I Pre</td>
<td>2P, 2P, 3P</td>
<td></td>
</tr>
<tr>
<td>9 years</td>
<td>--</td>
<td>2P, 2P, 3P</td>
<td></td>
</tr>
<tr>
<td>14 years</td>
<td>--</td>
<td>2P, 2P, 3P</td>
<td></td>
</tr>
<tr>
<td>16 years</td>
<td>I Pre</td>
<td>2P, 2P, 3P</td>
<td></td>
</tr>
</tbody>
</table>

A = Dentition exceedingly young, unerupted
B = Dentition young, erupted from the mandible to a medium height, compared with the adult
C = Dentition in mature state without wear
Pre = Signifies premolar dentition
P = Number of parts, single or double cusps, or lophs to the tooth

(Altamirano's permanent dental formula:

\[
\frac{1-1-2-3}{3-1-1-3}
\]

Incisors are not included on this chart)

(* dP4 is tri-cusped at birth and is replaced by a permanent unicusped premolar in adulthood.

** When P4 pushes out the dP4, the dP3 is sometimes caught and taken out with it (hole resorbed), and sometime remains. The dP3 is unicusped at birth, is generally lost by age 1 year, and is not replaced by a permanent tooth. Dental formula for infants:

\[
\frac{1-0-2-0}{3-0-1-0}
\]
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