

UNIVERSIDAD DE GUADALAJARA

CENTRO UNIVERSITARIO DE CIENCIAS BIOLÓGICAS Y
AGROPECUARIAS

DIVISIÓN DE CIENCIAS BIOLÓGICAS Y AMBIENTALES



*“Stegomastodon (Mammalia, Proboscidea) from the Pliocene of
Jalisco, Mexico and the Species-Level Taxonomy of
Stegomastodon”*

TRABAJO DE INVESTIGACIÓN

QUE PARA OBTENER EL TÍTULO DE

LICENCIADO EN BIOLOGÍA

PRESENTA:

RICARDO HERNÁN AGUILAR ALONSO

Las Agujas, Zapopan, Jalisco; Octubre de 2012



Universidad de Guadalajara
Centro Universitario de Ciencias Biológicas y Agropecuarias

Coordinación de Carrera de la Licenciatura en Biología

COORD. BIOL. 187/2012

C. RICARDO HERNÁN AGUILAR ALONSO
PRESENTE

Manifestamos a usted, que con esta fecha, ha sido aprobado su tema de titulación en la modalidad de **Investigación y Estudios de Posgrado** opción: **Seminario de Investigación**, con el título "**Stegomastodon (Mammalia, Proboscidea) from the Pliocene of Jalisco, Mexico and the Species-Level Taxonomy of Stegomastodon**", para obtener la Licenciatura en Biología.

Al mismo tiempo le informamos, que ha sido aceptado como director(a) de dicho trabajo a **Biol. Margarito Mora Núñez**.

Sin más por el momento, aprovechamos para enviarle un cordial saludo.

A T E N T A M E N T E
"PIENSA Y TRABAJA"

Las Agujas, Nextipac, Zapopan, Jal., 25 de septiembre, del 2012.


DRA. TERESA DE JESÚS ACEVES ESQUIVIAS
PRESIDENTE DEL COMITÉ DE TITULACIÓN



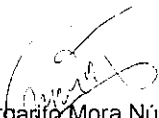

M.C. VERÓNICA PALOMERA AVALOS
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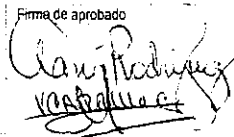
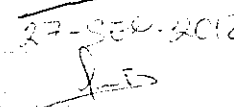
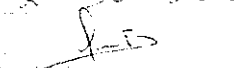
Dra. Teresa de Jesús Aceves Esquivias.
Presidente del Comité de Titulación.
Licenciatura en Biología.
CUCBA.
Presente

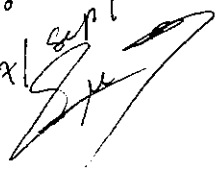
Nos permitimos informar a usted que habiendo revisado el trabajo de titulación, modalidad Investigación y estudios de posgrado, opción Seminario de investigación con el título: "Stegomastodon (Mammalia, Proboscidea) from the Pliocene of Jalisco, Mexico and the Species-Level Taxonomy of Stegomastodon" que realizó el pasante Ricardo Hernán Aguilar Alonso con número de código 093615689 consideramos que ha quedado debidamente concluido, por lo que ponemos a su consideración el escrito final para autorizar su impresión.

Sin otro particular quedamos de usted con un cordial saludo.

Atentamente
Guadalajara, Jalisco a 25 de septiembre de 2012


Margarito Mora Núñez
Director del trabajo

Nombre completo de los Sinodales asignados por el Comité de Titulación	Firma de aprobado	Fecha de aprobación
Dr. Aarón Rodríguez Contreras		Sep 27, 2012 27/sep/12
MC. Victoria Carrillo Camacho Dr. Sergio Guerrero Vázquez		27-SEP-2012 27/sep/12
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V. BO
27/sep/2012


STEGOMASTODON (MAMMALIA, PROBOSCIDEA) FROM THE PLIOCENE OF JALISCO, MEXICO AND THE SPECIES-LEVEL TAXONOMY OF *STEGOMASTODON*

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Abstract—We describe a nearly complete skeleton of the gomphotheriid proboscidean *Stegomastodon primitivus* Osborn from the Pliocene (Blancan) of Lago de Chapala, Jalisco, Mexico. This skeleton documents important differences between the postcranial of North American *Stegomastodon* and the gomphotherid postcranial from South America assigned to *Cuvieronius*, *Haplomastodon* and *Stegomastodon* that include features indicative of more graviportal limbs (especially the forelimb) in North American *Stegomastodon*. This strengthens the case against referring any South American gomphotherid fossils to *Stegomastodon*; *Nottomastodon* and *Haplomastodon* are the valid generic names for these fossils. *Stegomastodon* is known only from North America, and ranges from early Blancan (~4 Ma) to early Irvingtonian (~1.2 Ma) in age. Its fossils form a chronomorphocline that can be assigned to three species: early Blancan *S. primitivus*, primarily late Blancan *S. mirificus* (Leidy) and early Irvingtonian *S. aftoniae* (Osborn).

INTRODUCTION

In North America, one of the last gomphotheres was *Stegomastodon*, a genus known from Blancan and Irvingtonian (Pliocene-early Pleistocene) localities, primarily in the United States. Despite the fact that Leidy (1859) described the first diagnostic specimen of *Stegomastodon*, relatively little has been published on the postcranial osteology of the genus except for incomplete information provided by Gidley (1926) and Osborn (1936). Here, we describe the nearly complete skeleton of a *Stegomastodon* from Jalisco, Mexico. This specimen was briefly mentioned and identified by Alberdi et al. (2002) and Lucas (2003) as *Stegomastodon* and described in part by Alberdi et al. (2009). It is cataloged as MPG-PD-001 in the collection of the Museo de Paleontología de Guadalajara in Guadalajara, Mexico.

LOCALITY

In southern Jalisco, south of Guadalajara, Lake Chapala (Lago de Chapala) is the largest natural freshwater lake in Mexico (Fig. 1). Located in the inner graben of the Chapala rift basin, more than 600 m of Pliocene-Pleistocene sediments are exposed in and on the northern flank of Lake Chapala. These strata yield an extensive assemblage of late Pleistocene (Rancholabrean) mammals as well as a few records of Blancan and Irvingtonian(?) mammals (see reviews by Rufolo, 1998 and Lucas, 2008). The *Stegomastodon* skeleton described here (Fig. 2) was found on the exhumed floor of Lake Chapala.

This *Stegomastodon* skeleton (MPG-PD-001) was discovered near Santa Cruz de la Soledad at UTM zone 13, 692479E, 2245494N (datum NAD 27). It was found as a nearly articulated skeleton with some disaggregation of elements (especially of the manus and pes) (Fig. 2; Alberdi et al., 2009, fig. 2). It was located in light olive gray calcareous clay on the exhumed floor of Lago de Chapala. Alberdi et al. (2009) provided a more detailed description and photographs of the *Stegomastodon* locality.

Most of the fossil mammals from the floor of Lake Chapala are of late Pleistocene (Rancholabrean) age (Downs, 1958; Rufolo, 1998; Lucas, 2008). However, the skeleton of *Stegomastodon* from near Santa Cruz de la Soledad is older, of Blancan age. We advocate this age assignment because of the primitive molar morphology of this *Stegomastodon*, much like that of Blancan members of the genus (Lucas, 2003). The youngest North American *Stegomastodon* are of Irvingtonian age and have a much more advanced molar morphology (Lucas et al., 1998, 1999, 2011; Morgan and Lucas, 2011; Pasenko and Lucas, 2011).

Nevertheless, Alberdi et al. (2009) reported a 14C AMS date of

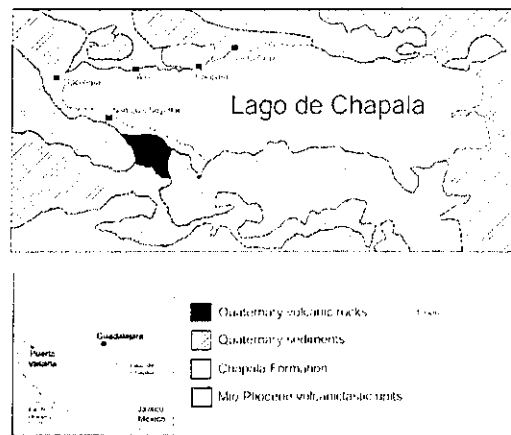


FIGURE 1. Geologic map around Lake Chapala (modified from Rufolo, 1998, fig. 3). The *Stegomastodon primitivus* skeleton described here was found near Santa Cruz.

27,910 ± 270 years BP for a sample of molar enamel from MPG-PD-001, concluding it is late Pleistocene in age. However, not only is this date much younger than the age of any other North American *Stegomastodon* (the youngest is early Irvingtonian, about 1.2 Ma; Morgan and Lucas, 2011), but the molar morphology of MPG-PD-001 is that of an early Blancan (about 3–4 Ma) *Stegomastodon* (see below and Lucas, 2003, 2008). Therefore, we conclude that the date reported by Alberdi et al. (2009) is much too young and not the age of the *Stegomastodon* described here, which is Pliocene (Blancan).

TAXONOMY

Key features of taxonomic significance of the MPG proboscidean skeleton are: (1) the skull is elephantoid in outline, meaning it is tall in the region of the frontals and parietals; (2) it has long, relatively straight tusks that lack enamel; (3) no lower tusks are present; (4) the mandibular symphysis is relatively short and tall; (5) the m3 has five lopheids and double trefoils; and (6) m3 length = 200 mm, width = 88 mm. These

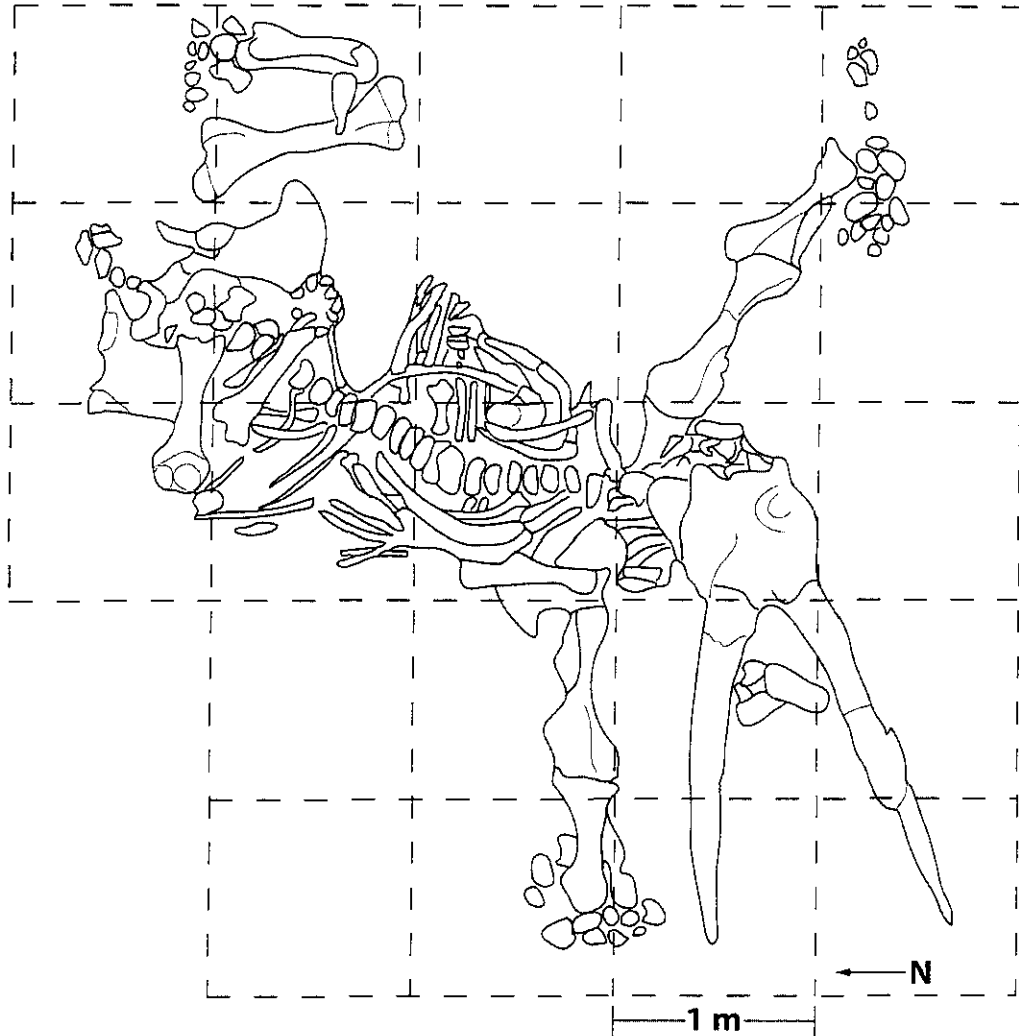


FIGURE 2. Quarry map of the *Stegomastodon primitivus* skeleton from Lake Chapala.

features justify assigning the fossil to *Stegomastodon* (cf. Osborn, 1936; Kurtén and Anderson, 1980; Lambert and Shoshani, 1998). The presence of only five m3 lophids, the relatively simple trefoiling and size support assignment to *Stegomastodon primitivus* (= *S. rexroadensis* of Woodburne, 1961).

Clearly, the genus *Stegomastodon* is in need of taxonomic revision. In North America, we provisionally recognize three species – a primitive early Blancan species (*S. primitivus*), a more derived late Blancan species (*S. mirificus*) and the most derived species, Irvingtonian *S. afoncae* (see below). The Jalisco *Stegomastodon* belongs to the most primitive species, so we assign it to *S. primitivus*. This indicates the fossil is of early Blancan age, ~3–4 Ma (Lucas et al., 2011).

OSTEOLOGY

We illustrate (Figs. 2–27), present measurements (Appendix) and describe the *Stegomastodon* skeleton from Jalisco. The skeleton consists of an incomplete skull with essentially complete tusks and an incomplete M3, hyoid elements, both dentaries with a complete left m3 and an incomplete right m3, the atlas, axis, 28 thoracic/lumbar vertebrae, sacrum, seven caudal vertebrae, sternbrae, 19 rib pairs, left and right scapulae, left humerus, incomplete right humerus, left and right radius/ulna, nearly complete left and right manus, pelvis, right femur, incomplete left femur, both tibiae, complete right fibula and incomplete left fibula, and nearly complete left and right pes. Alberdi et al. (2009) provided a brief descrip-

tion of this skeleton but only illustrated some cranio-dental and pedal elements. They did, however, provide metric data. All of our postcranial measurements (Appendix, Figs. 29-30) follow measurement protocols based on Dutrow (1980; also see Agenbroad, 1994).

Skull, Lower Jaws and Dentition

The face (maxillae, frontals, part of parietals) and upper tusks are all that remain of the skull and they have been dorso-ventrally flattened (Figs. 2, 3A, C-D). The face appears to be "tall" (though this is accentuated by flattening) with a long sulcus for the nasal opening between the tusk alveoli, which are slightly divergent. This gives the skull an elephantoid profile, as in other *Stegomastodon* (Gidley, 1926; Osborn, 1936). It is important to note, though, that compression of the skull and tusks in the sediment in part may account for the nearly straight tusks and the facial profile. The tusks (Fig. 3) are nearly straight (slight curved), lack enamel and have a maximum length of 155 cm.

The incomplete left M3 is preserved and has at least four lophs and weak double trefoils (Fig. 4A-B). The dentary fragments with left m3 (Fig. 4C-F) document a lack of lower tusks and a relatively short, nearly vertical (convex anterior) symphyseal profile. The incomplete left m3 has 5 lophs and weakly developed double trefoils. The m3 length = 200 mm and maximum width = 88 mm, very much within the range of measurements of Blancan *S. "vexroadensis"* (= *S. primitivus*, see below) from Kansas (Woodburne, 1961, table 4). The teeth and lower jaw closely resemble other specimens assigned to *Stegomastodon primitivus* (cf. Osborn, 1936; Woodburne, 1961) and we assign the Jalisco *Stegomastodon* skeleton to that species (also see Lucas, 2003, 2008).

Hyoid

Five hyoid elements are preserved within the Jalisco *Stegomastodon* skeleton. Two appear to be part of a stylohyal (Fig. 5A-B), two are thyrohyals (Fig. 5D-E), and the fifth may be the basihyal (Fig. 5C). The stylohyal appears to have a blunt-tipped, flange like superior ramus with a dorsally expanded end. The base of the posterior ramus is thicker than the base of the inferior ramus. The posterior ramus (Fig. 5A) is a long, thin, flattened, slightly curved bone with a pointed distal tip. The basihyal (Fig. 5C) is a rod of bone with expanded ends. Both thyrohyals (Fig. 5D-E) also have rod-like distal ends. The hyoid complex of *Stegomastodon* does not appear to differ significantly from that of *Elephas* (e.g., Shoshani and Marchant, 2001).

Vertebrae

Of the cervical vertebrae, only the atlas and axis were recovered. The atlas vertebra (Fig. 6A-B) has a round, doughnut-shaped articular surface flanked by short, triangular transverse processes. Distinct transverse foramina are present at the bases of the transverse processes. The centrum is short and has a small keel ventrally. The dorsal tuberosity is low and blunt.

The axis vertebra (Fig. 6C-D) has a centrum that is circular in articular view and a short, blunt odontoid process. The neural canal is tall and covered dorsally by a thick, wide neural arch.

Of the thoracic vertebrae, two are pathologic and fused (Fig. 6E-F). These vertebrae have long, posteriorly inclined neural spines with antero-posteriorly expanded distal tips. The centra are antero-posteriorly short and proximo-distally tall with a nearly circular in cross section, but the two are fused by an extensive mass of exostosis most visible in lateral view (Fig. 6F).

The lumbar vertebrae (Figs. 7-8A-I) have antero-posteriorly short, nearly circular centra that lack rib facets. Most of the centra have low, ventral keels and concave (waisted) lateral surfaces. The neural arches are low, with short, posteriorly-inclined neural spines that end with expanded, rugose distal tips.

The sacrum (Fig. 8I) consists of four vertebrae, which are distinct, square (anterior) to rectangular (posterior) centra connected by two plate-

like alar processes. Lateral to each centrum are antero-posteriorly oval transverse foramina.

The caudal vertebrae (Figs. 9-11) have short, round centra with concave ventral aspects. Their neural arches are low with short, blunt neural spines. The transverse processes are flat, wing-like flanges of bone that rapidly decrease in size posteriorly.

Sternebrae and Ribs

The sternum (Fig. 12) consists of three sternebrae: (1) a proximal manubrium (Fig. 12A-B), broken near the distal end, which is a proximally rugose, nearly cylindrical bone (antero-posteriorly flattened) with a convex distal articulation for the mesosternum; (2) the mesosternum (Fig. 12A, C), a similarly nearly cylindrical bone (antero-posteriorly flattened) with a convex rugose, proximal end and a nearly flat posterior end for articulation with the xiphosternum; and (3) the xiphosternum (xiphoid process) (Fig. 12A, D-E), a short, wedge-shaped bone with a flat proximal end and a concavo-convex distal end. The ribs (Figs. 3B, 13) of the Jalisco *Stegomastodon* are long, arcuate bones very similar to those of other proboscideans (e.g., Göhlich, 1998, figs. 86-87, pl. 7, fig. 10).

Scapulae

The scapulae (Fig. 14) are not complete, missing portions of the blade edges. These bones are broadly triangular in lateral (or medial) view with a pronounced, wide, concave glenoid fossa. The scapular spine is thick at the glenoid, and thins dorsally. The acromion process is large, similar to the blunt flange seen in *Gomphotherium* (Göhlich, 1998, fig. 89). The metaacromion process is also a large, triangular flange that projects from the acromion process at an ~45° angle. The suprascapular fossa is long and concave, and much narrower than the subscapular fossa. The dorsal edge of the scapula is long, rugose and thickened.

Forelimb

Long bones

The humerus is a long, pillar-like bone essentially of equal width at its proximal and distal ends (Fig. 15A-D). The humeral head is low and rounded, well separated from the greater tuberosity by a long, concave bicipital groove. Note that the greater tuberosity extends little, if at all, proximal to the head. The deltoid ridge is a thick flange of bone. The distal end has moderately broad epicondyles and a hinge-like distal articular surface in which the trochlea is larger than the capitellum.

The ulna is much larger than the radius, and the bones are not fused (Fig. 15E-I). The olecranon fossa is shallow, and the supracondyloid ridge is large, extending proximally about one-third of the length of the shaft. The proximal end of the ulna has a tall, rugose olecranon process. The semilunar notch is a broad, concave articular surface. The radial notch is much smaller. The ulna shaft is slightly constricted relative to the expanded distal end, which has a concavo-convex styloid process.

The radius (Fig. 15E-J) has a concave, ovoid proximal articular surface for the humerus. The thin shaft has a prominent anterior ridge thickens distally to a thick, blunt distal end with a hinge-like distal articular process (styloid process).

Manus

The manus is disarticulated but largely complete (Figs. 16-19). It does not differ much morphologically from that of *Gomphotherium*, as described and illustrated in detail by Göhlich (1998, p. 133-154, figs. 96-124, pls. 9-13), and that of *Haplomastodon*, described and extensively illustrated by Ferretti (2010, p. 695-700, figs. 14-16). Therefore, we do not describe the manus in detail, though we illustrate it and provide measurements (Appendix). However, we do note that the manus of the Jalisco *Stegomastodon* (Fig. 16) is relatively much shorter and broader



FIGURE 3. *Segomastodon primitivus* from Jalisco, Mexico. Cast of skeleton on exhibit, skull and tusks. A. Cast of skeleton in anterior view. B. Cast of rib cage in left lateral view. C-D. Skull in C, anterodorsal and D, anterolateral views. E-F. Tusks in E, anterior and F, posterior views. Lower right scale bar applies to E-F.

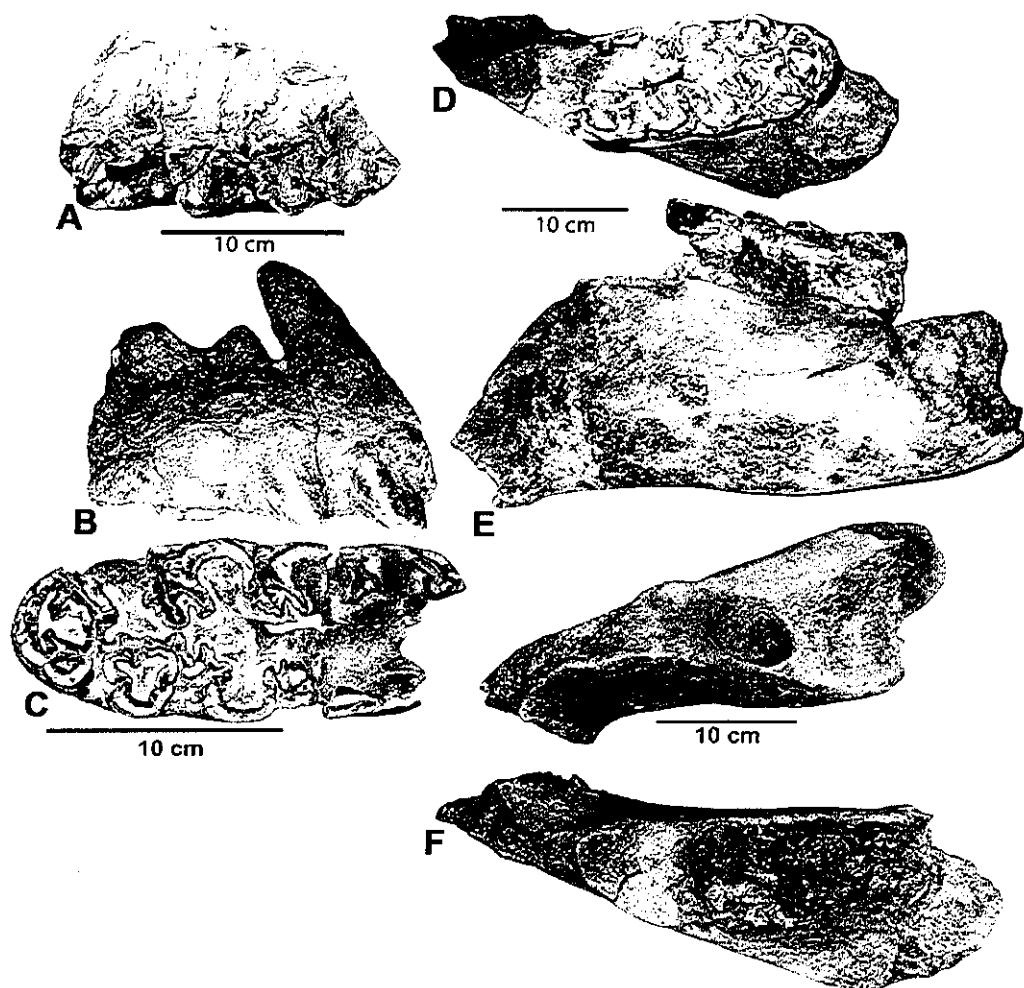


FIGURE 4. *Stegomastodon primitivus* from Jalisco, Mexico. Molars and mandible. A-B, Isolated right M3 in A, occlusal and B, labial views. C, Left m3 in occlusal view. D-E, Left dentary in D, occlusal and E, labial views. F, Paired dentaries in occlusal view. Scale bars: A-B, upper left, C, lower left, D-E, upper right, F, lower right.

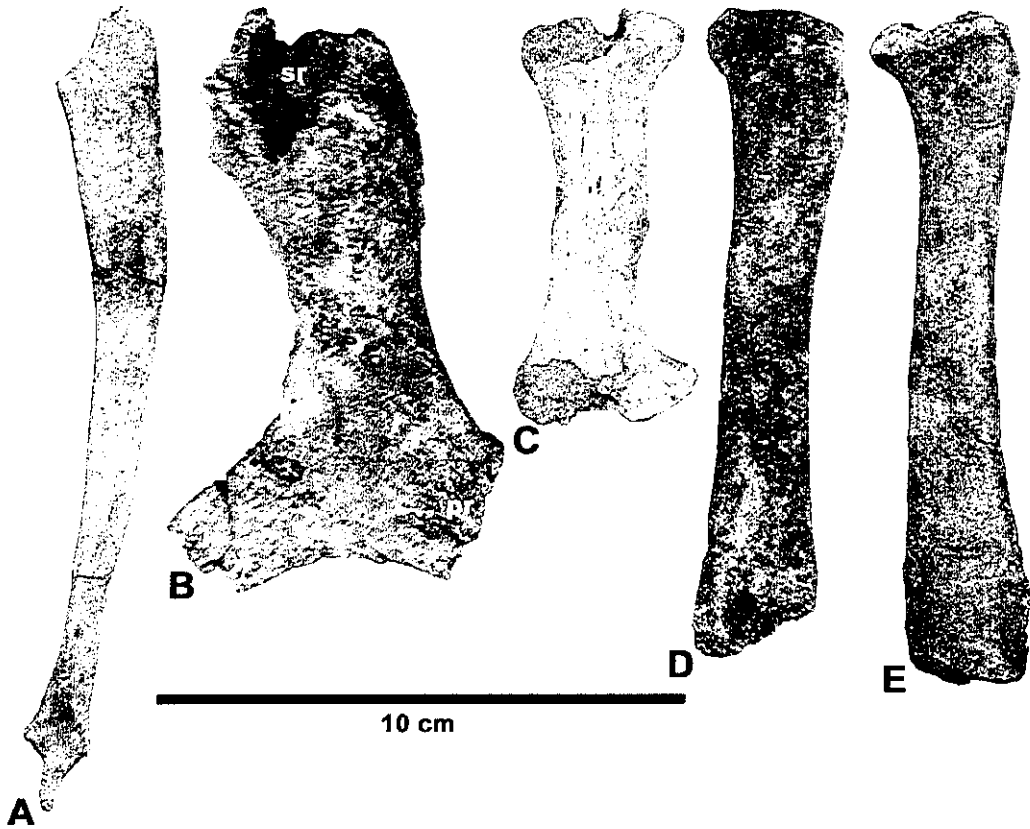


FIGURE 5. *Stegomastodon primitivus* from Jalisco, Mexico. Hyoid bones: A-B, Stylohyal fragments. C, Basihyal? D-E, Thyrohyals. Abbreviations: ir, inferior ramus; pr, posterior ramus; sr, superior ramus.

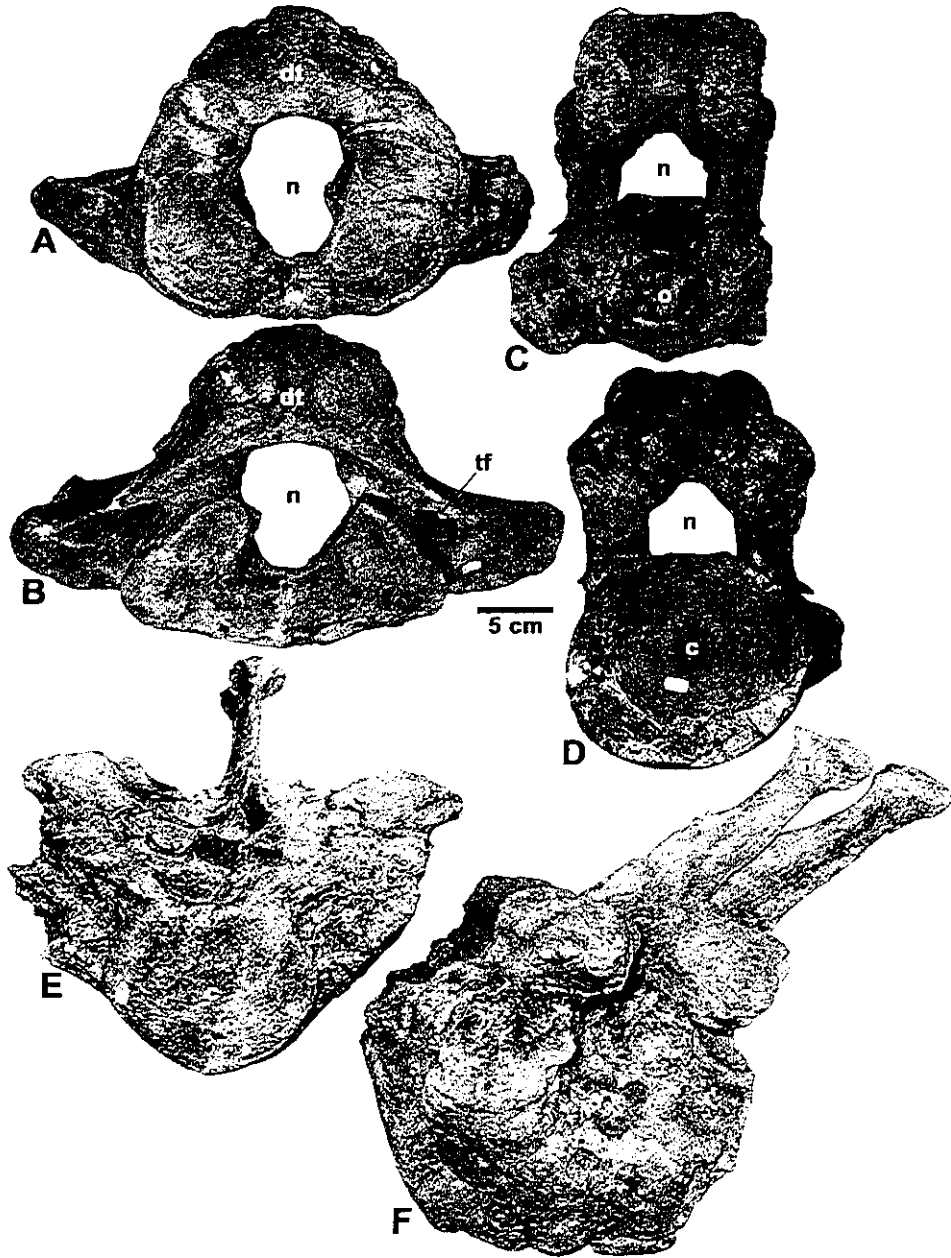


FIGURE 6. *Segomastodon primitivus* from Jalisco, Mexico. Cervical and thoracic vertebrae. A-B, Atlas in A, anterior and B, posterior views. C-D, Axis in C, anterior and D, posterior views. E-F, A pair of fused, pathologic thoracic vertebrae in E, anterior and F, left lateral views. Abbreviations: c, centrum; dt, dorsal tuberosity; e, exostoses; n, neural canal; ns, neural spine; o, odontoid process; tf, transverse foramen.

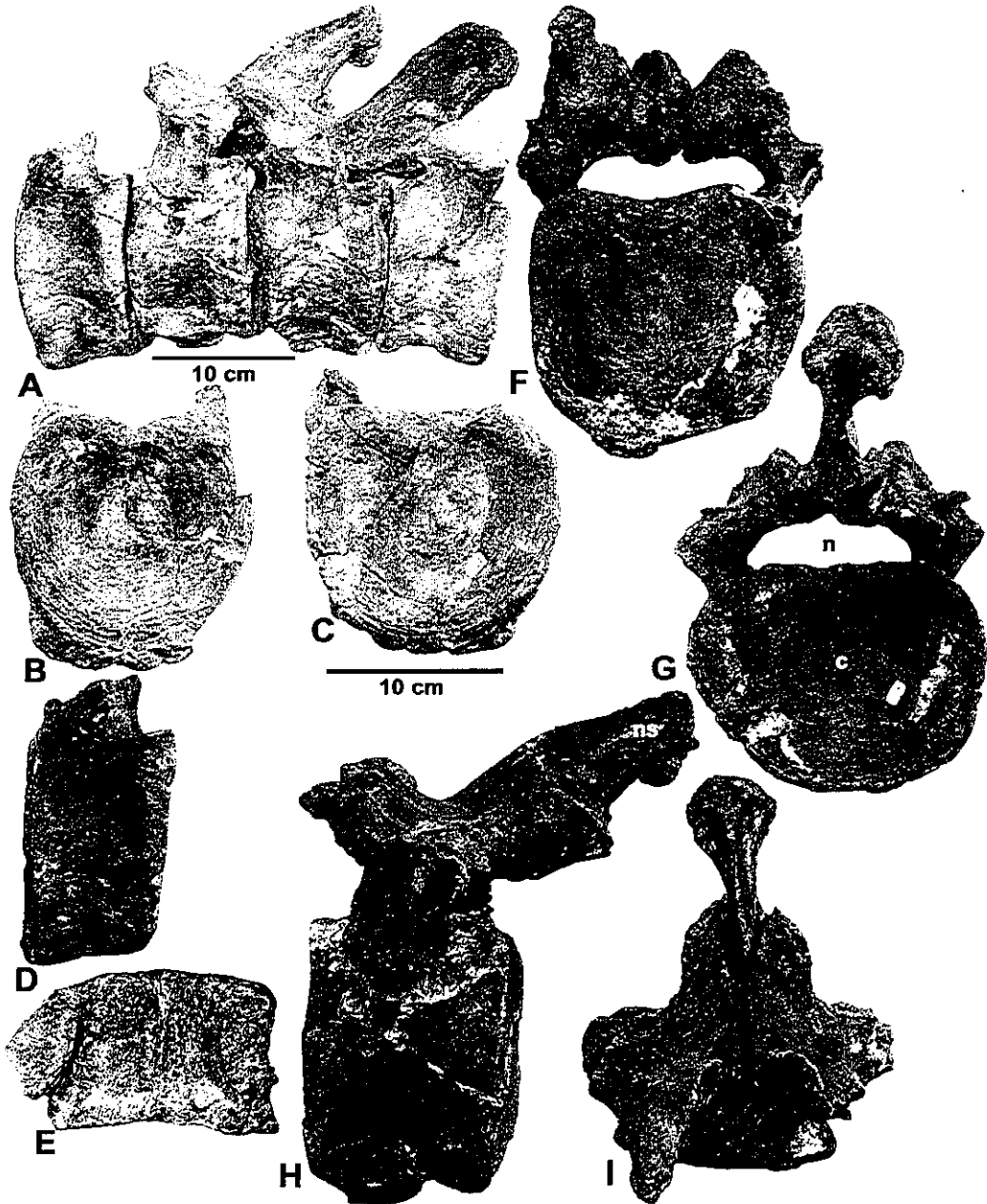


FIGURE 7. *Segomastodon primitivus* from Jalisco, Mexico. Lumbar vertebrae. A, Lumbar vertebrae 1-4 in articulation in ventrolateral view. B-E, Lumbar vertebra 1 in B, anterior, C, posterior, D, left lateral and E, ventral views. F-I, Lumbar vertebra 2 in F, anterior, G, posterior, H, left lateral and I, dorsal views. Scale bars: A, upper and B-I, lower. Abbreviations same as in Figure 6.

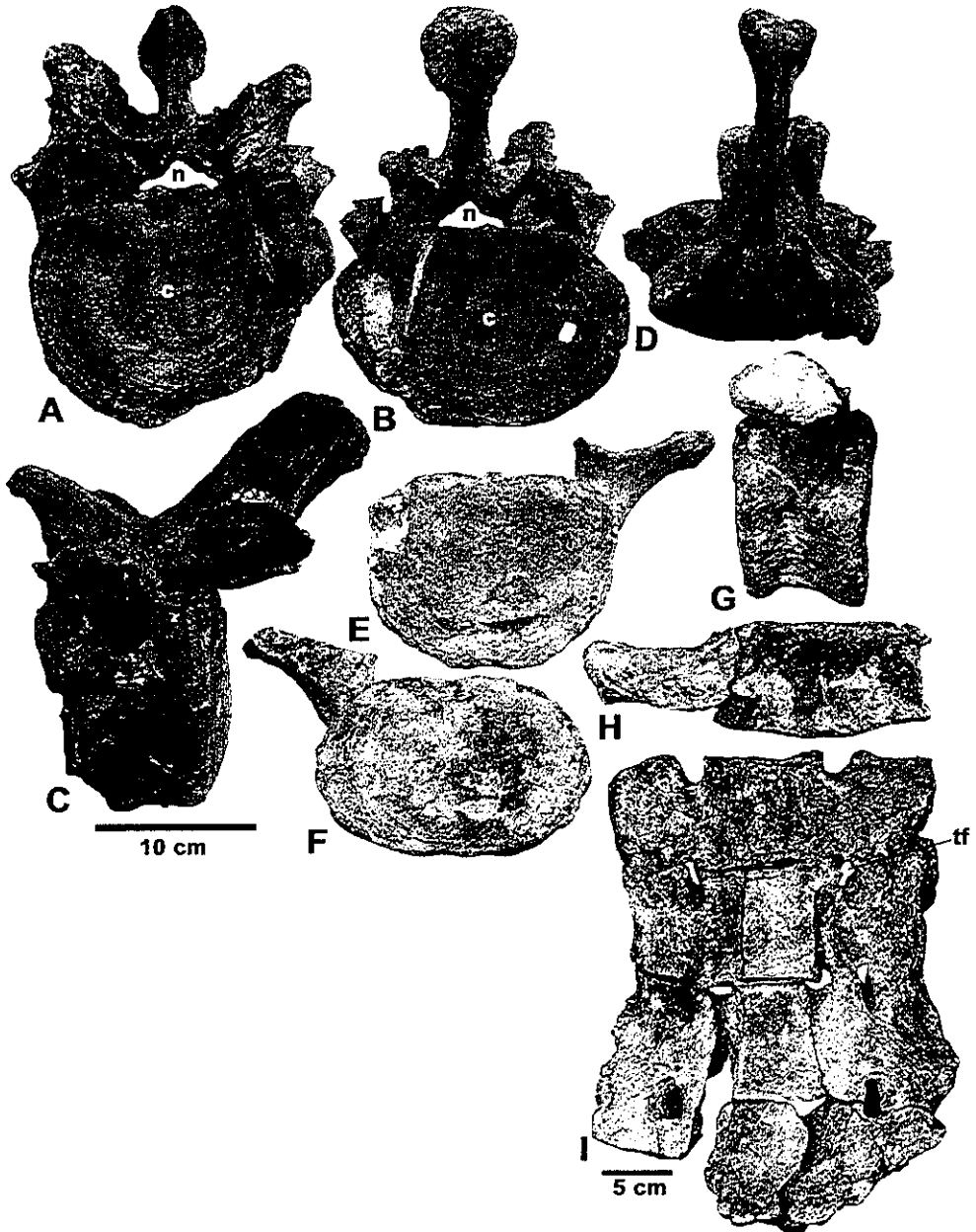


FIGURE 8. *Segomastodon primitivus* from Jalisco, Mexico. Lumbar and sacral vertebrae. A-D, Lumbar vertebra 3 in A, anterior, B, posterior, C, left lateral and D, dorsal views. E-H, Lumbar vertebrae 4 in E, anterior, F, posterior, G, left lateral and H, ventral views. I, Sacrum in ventral view. Abbreviations: a, alar process; c, centrum; n, neural canal; tf, transverse foramen.

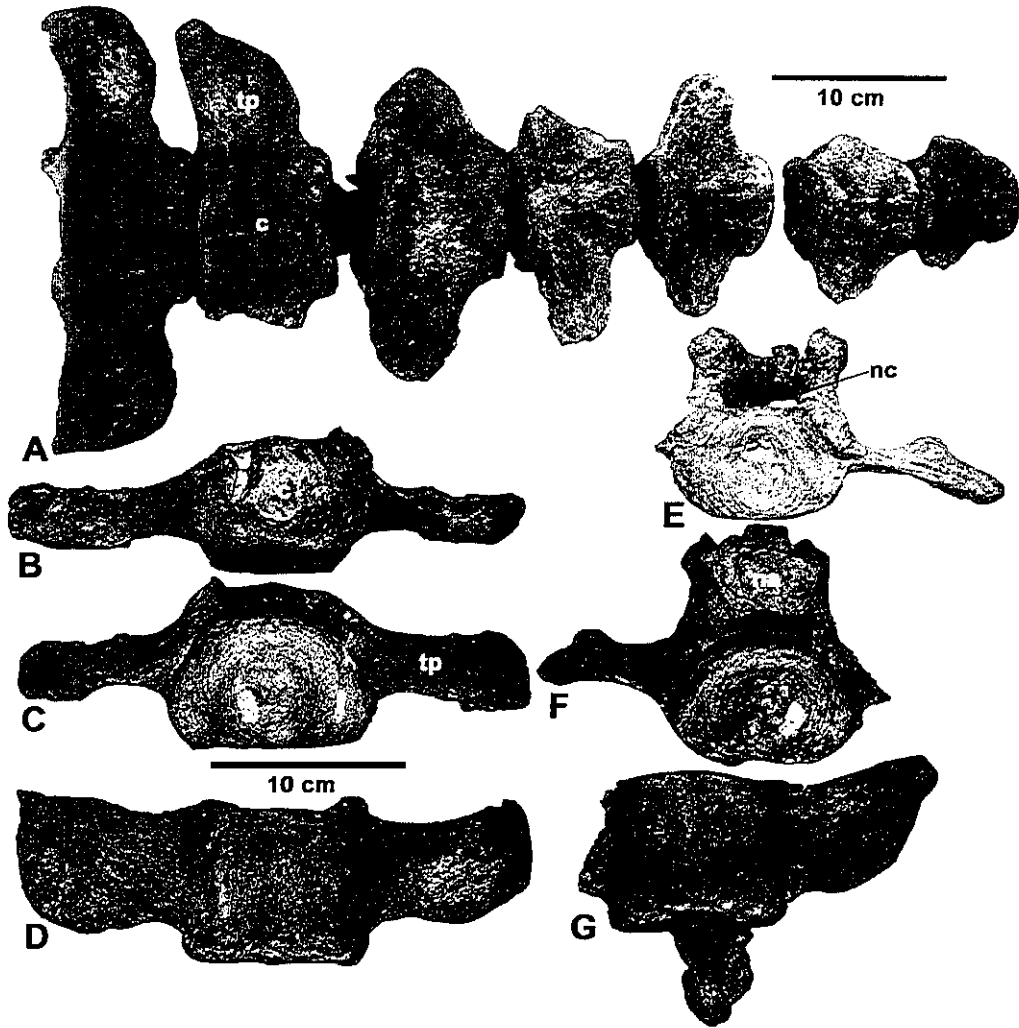


FIGURE 9. *Segomastodon primitivus* from Jalisco, Mexico. Caudal vertebrae. A. Caudal vertebrae 1-7 in articulation in ventral view. B-D, Caudal vertebra 1 in B, anterior, C, posterior and D, ventral views. E-G, Caudal vertebra 2 in E, anterior, F, posterior and G, ventral views. Abbreviations: c, centrum; na, neural arch; nc, neural canal; tp, transverse process.

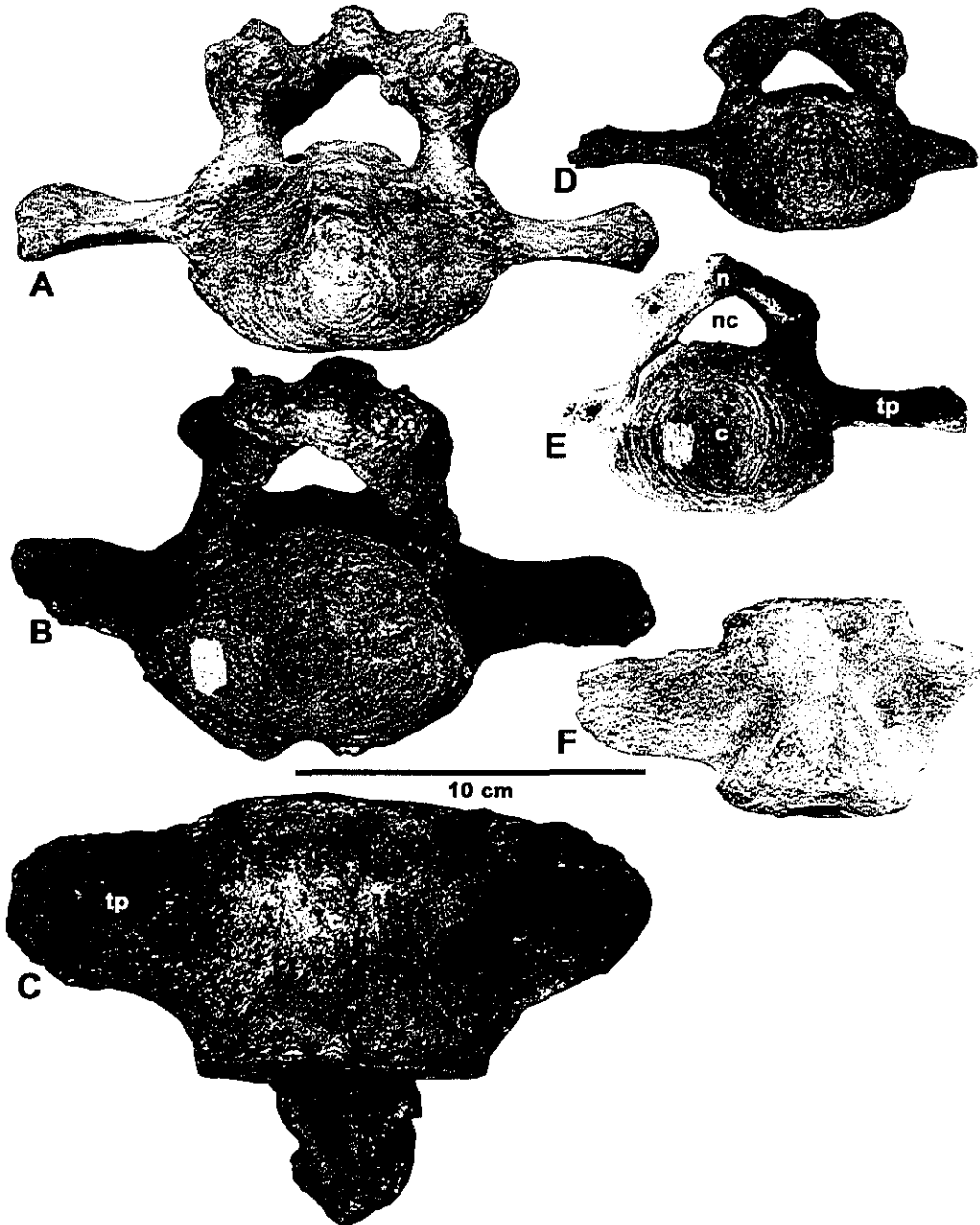


FIGURE 10. *Segomastodon primitivus* from Jalisco, Mexico. Caudal vertebrae. A-C, Caudal vertebra 3, A, anterior, B, posterior and C, ventral views. D-F, Caudal vertebra 4, D, anterior, E, posterior and F, ventral views. Abbreviations same as in Figure 9.

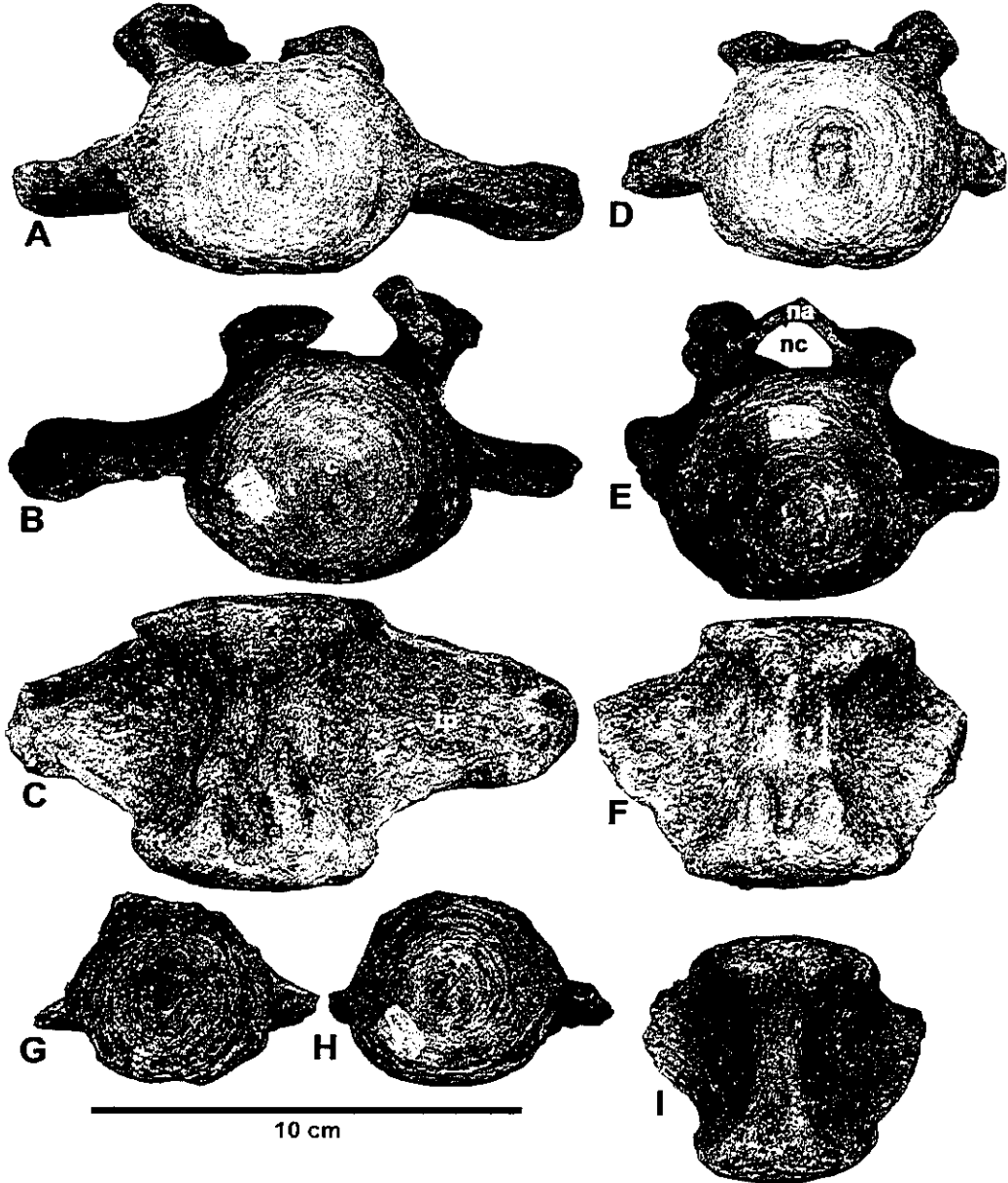


FIGURE 11. *Siegomastodon primitivus* from Jalisco, Mexico. Caudal vertebrae. A-C, Caudal vertebra 5, A, anterior, B, posterior and C, ventral views. D-F, Caudal vertebra 6, D, anterior, E, posterior and F, ventral views. G-I, Caudal vertebra 7, G, anterior, H, posterior and I, ventral views. Abbreviations same as in Figure 9.

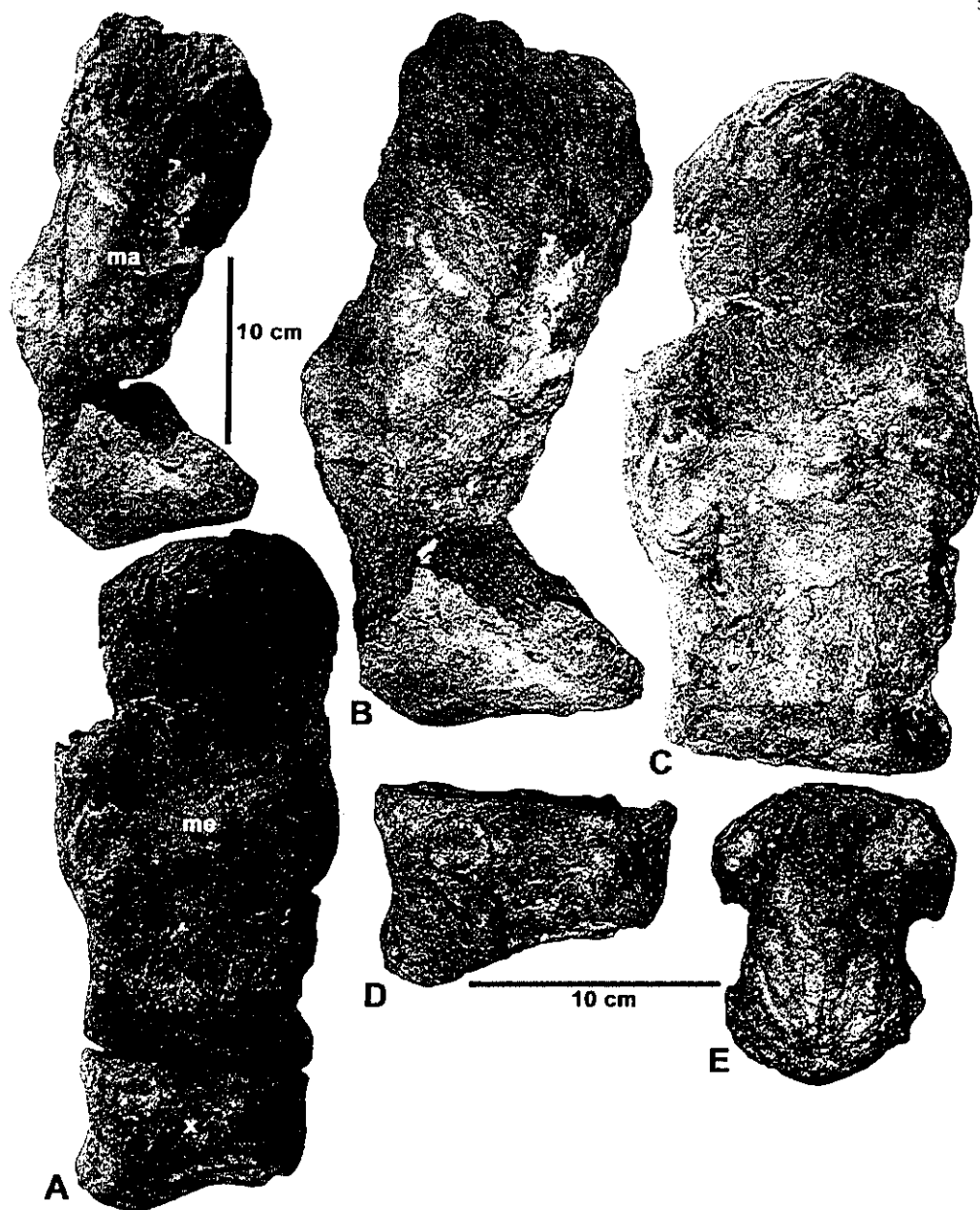


FIGURE 12. *Segomastodon primitivus* from Jalisco, Mexico. Sternebrae. A, Sternum in articulation in right lateral view. B, Manubrium in right lateral view. C, Mesosternum in right lateral view. D-E, Xiphosternum in D, right lateral and E, distal views. Scale bars: A, left and B-E, right. Abbreviations: ma, manubrium; me, mesosternum; x, xiphosternum

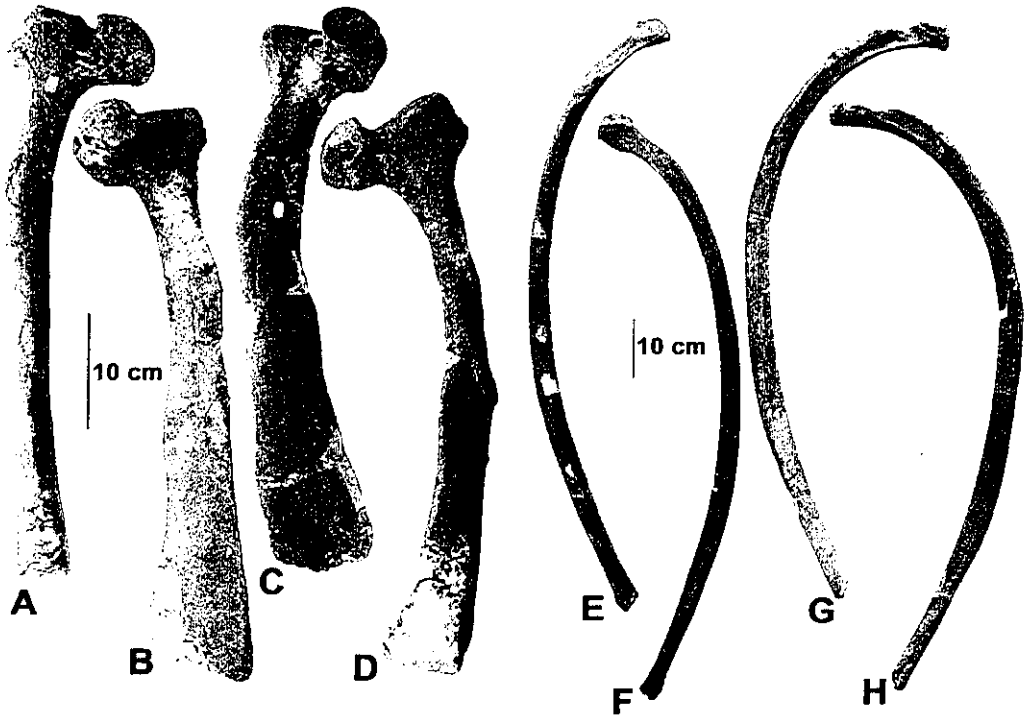


FIGURE 13. *Stegonastodon primitivus* from Jalisco, Mexico. Ribs. A-D, First ribs, right in A, anterior and B, posterior views and left in C, posterior and D, anterior views. E-H, Left abdominal ribs in E, G, posterior and F, H, anterior views. Scale bars. A-D, left and E-H, right.

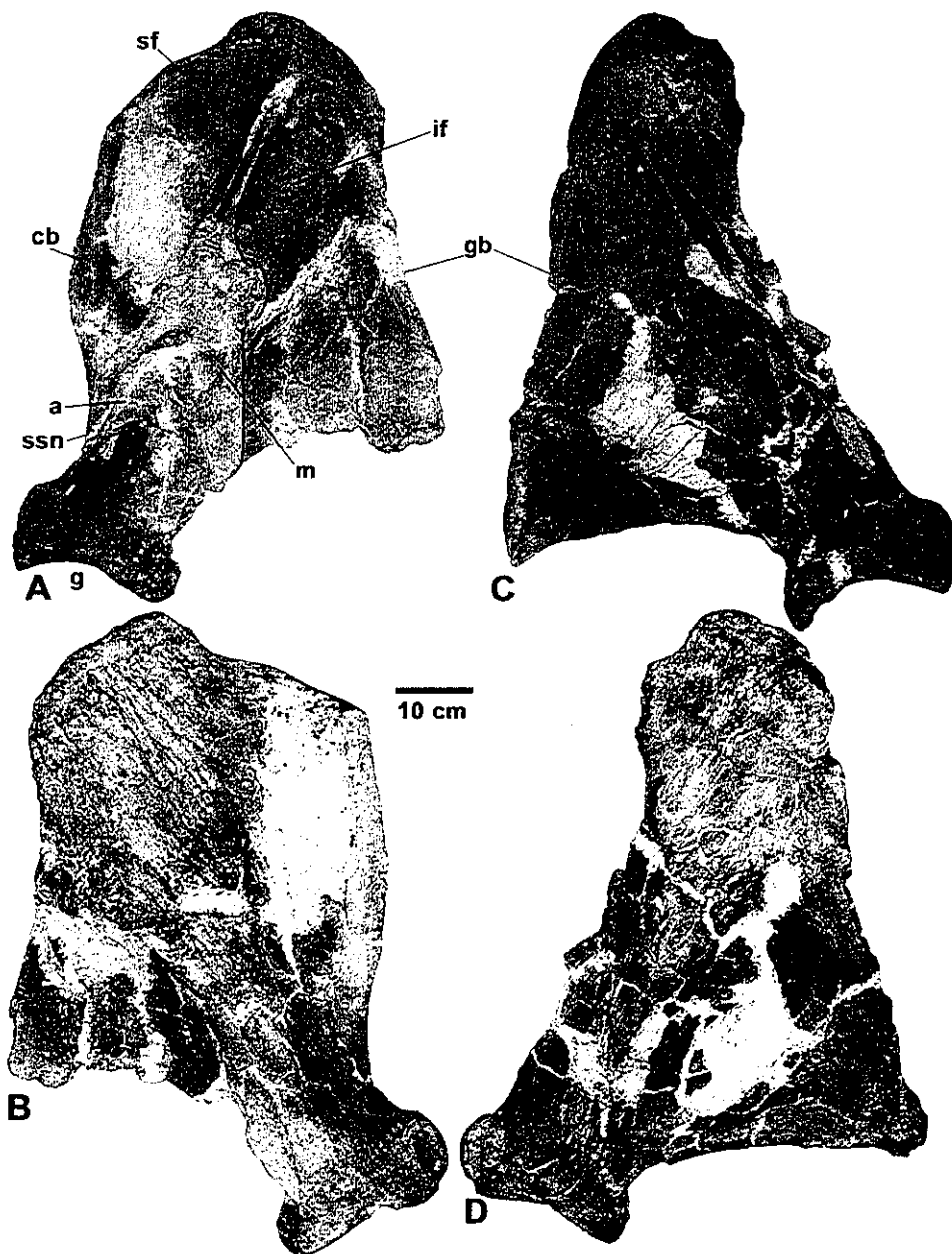


FIGURE 14. *Siegonastodon primitivus* from Jalisco, Mexico. Scapulae. A-B, Left scapula in A, lateral and B, medial views. C-D, Right scapula in C, lateral and D, medial views. **Abbreviations:** a, acromion process; cb, cranial border; g, glenoid fossa; gb, glenoid border; if, infraspinous fossa; m, metacromion process; sf, supraspinous fossa; ssn, suprascapular notch.

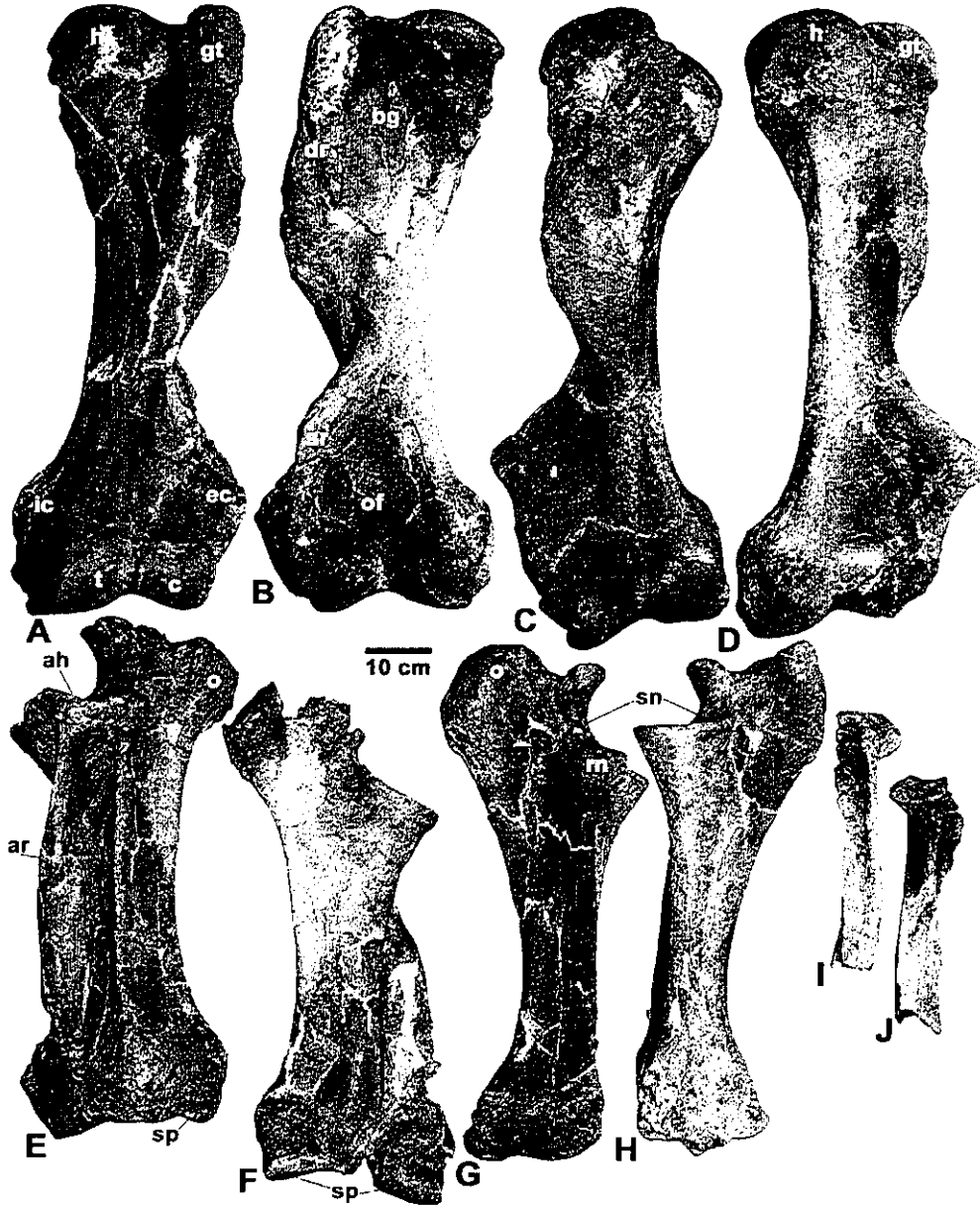


FIGURE 15. *Segonastodon primitivus* from Jalisco, Mexico. Long bones of the forelimb. A-B, Left humerus in A, anterior and B, posterior views. C-D, Right humerus in C, anterior and D, posterior views. E-F, Left ulna and radius in E, lateral and F, medial views. G-H, Right ulna in G, lateral and H, medial views. I-J, Right radius in I, lateral and J, medial views. **Abbreviations:** ah, articular surface for humerus; ar, anterior ridge; bg, bicipital groove; c, capitellum; dr, deltoid ridge; ec, external condyle; gt, greater tuberosity; h, head; ic, internal condyle; o, olecranon process; of, olecranon fossa; rn, radial notch (lesser sigmoid notch); sn, semilunar notch (greater sigmoid notch); sp, styloid process; t, tuberculum.

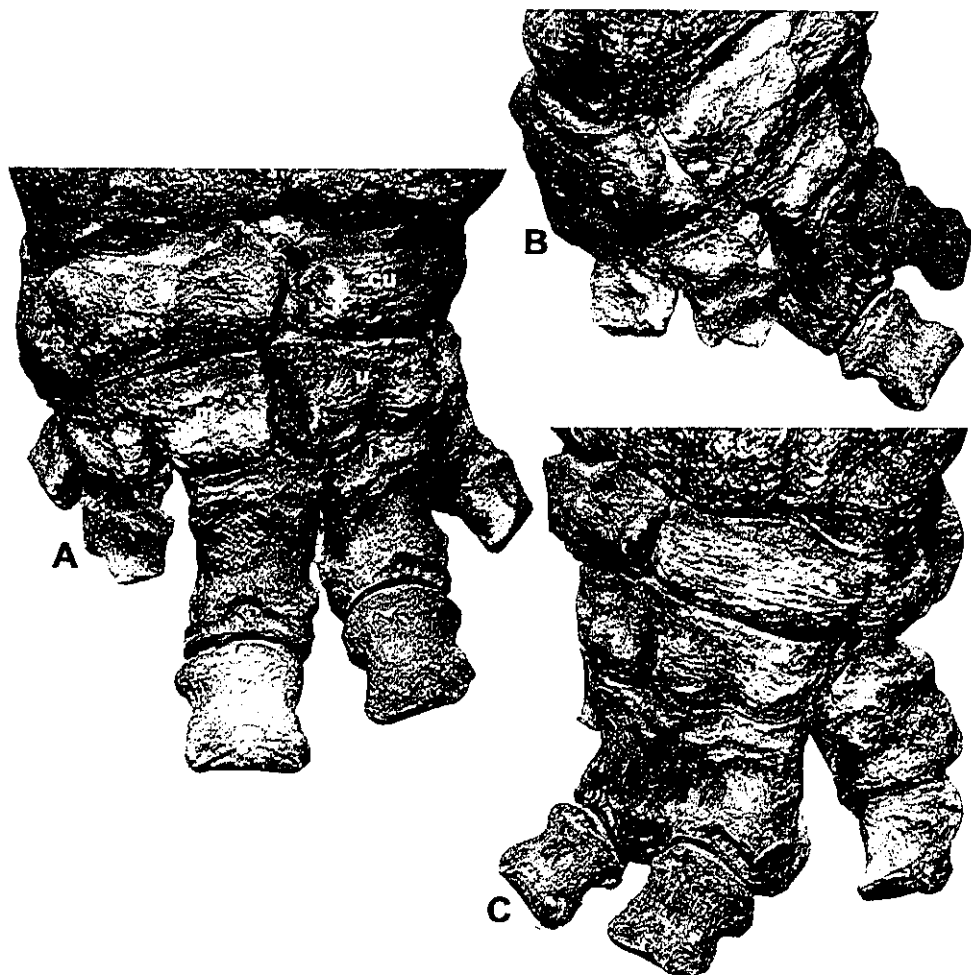


FIGURE 16. *Stegomastodon primitivus* from Jalisco, Mexico. Left manus in A, anterior, B, medial and C, lateral views. Abbreviations: cu, cuboid (pyramidal); l, lunar; m, magnum; s, scaphoid; u, unciform.

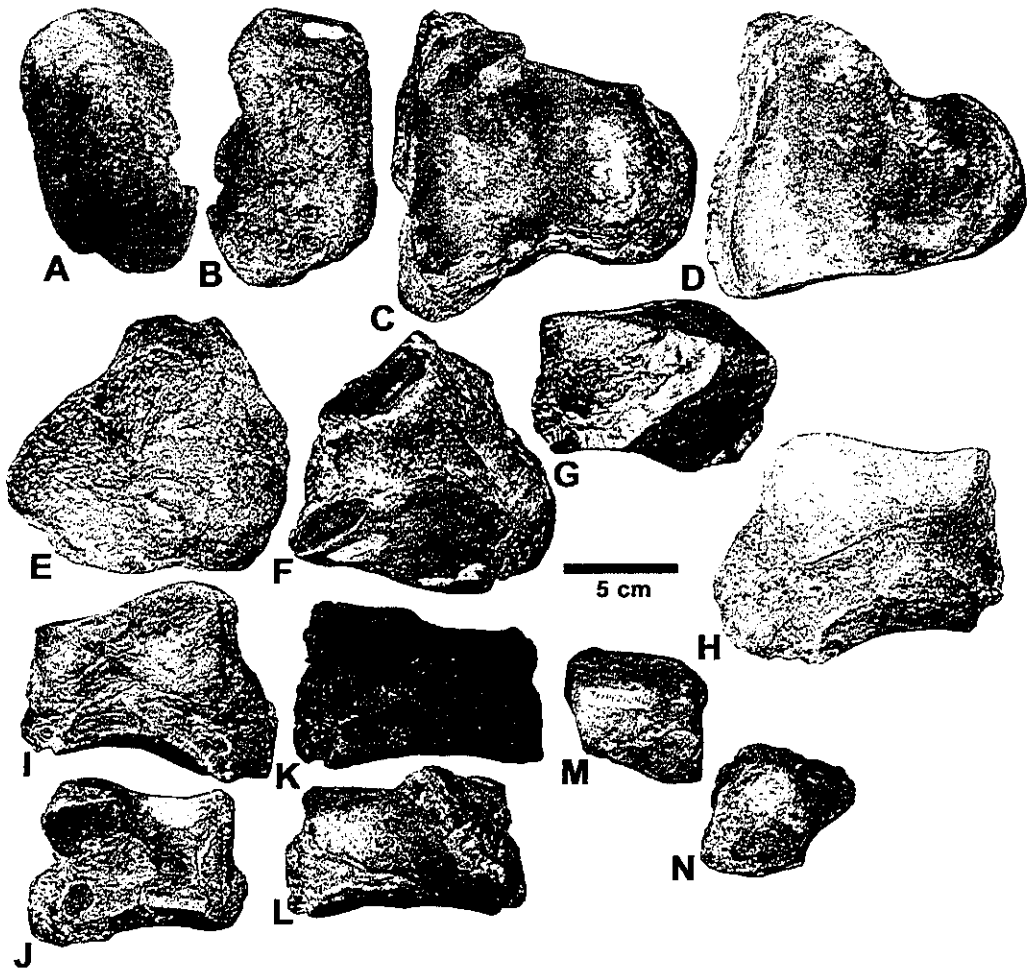


FIGURE 17. *Segomastodon primitivus* from Jalisco, Mexico. Carpals: A-B, Left pisiform in A, lateral and B, medial views. C-D, left lunar in C, dorsal and D, ventral views. E-F, left scaphoid in E, lateral and F, medial views. G-H, Unciform in G, lateral and H, medial views. I-J, Left magnum in I, lateral and J, medial views. K-L, Left trapezoid in K, lateral and L, medial views. M-N, Trapezium in M, medial and N, ventral views

than that of *Gomphotherium* (Göhlich, 1998, fig. 96) and even slightly so with respect to *Haplomastodon* (Ferretti, 2010, fig. 14A). This is most readily seen in some of the relatively broader carpals of *Stegomastodon*, such as the lunar (Fig. 17C-D), a relatively shorter and broader bone than the same bone in *Gomphotherium* (Göhlich, 1998, fig. 100) or *Haplomastodon* (Ferretti, 2010, fig. 15D-H).

Pelvis

The pelvis of the Jalisco *Stegomastodon* (Fig. 20) is a large, rugose and arcuate bone. The ilium is thickened dorsally so that its iliac crest is rugose. The auricular surface projects anteriorly to a large, tongue-shaped and rugose flange that is the cranial margin of the ilium. The cranial margin of the iliac crest is much shorter, more blunt and thinner. The acetabular border is a low, blunt ridge dorsal to the acetabulum, which is a relatively shallow and circular articular surface. The pubes and ischia are incomplete, so the obturator foramen is not complete, though it appears to be subtriangular in outline, widening distally. The proximal portions of the pubis and ischium are thick and rod-like.

Hindlimb

Long bones

The femur (Fig. 21) is a long, pillar-like bone, as is characteristic of all large proboscidean femora. The femoral head projects proximally and is ball-like without a significant pit for the ligamentum teres. The neck is short and confluent with the shaft. The greater trochanter is a rugose and thick flange, with a long, concave trochanteric fossa medial to it on the posterior surface. There is no lesser trochanter present and no third trochanter present. The shaft expands distally to a distal end with an internal tuberosity that is a prominent flange of bone, a much less pronounced external tuberosity and two slightly convex condyles. The internal condyle is much larger than the external condyle, and the intercondylar notch is narrow and deep. The trochlea is broad and shallow.

The patella (Fig. 22G-H) is a wide, round and rugose bone with a long, triangular distal process. The proximal process is short and rounded, and the concave articular surfaces are well defined.

The tibia (Fig. 22A-D) is relatively short and robust. The intercondylar spine is low and blunt, between slightly concave internal (larger) and external (smaller) condyles. The internal tuberosity is rounded and blunt, whereas the external tuberosity is a more pronounced, thick flange of bone. The tibial tubercle is a broad, triangular, rugose projection on the anteroproximal face of the bone that is confluent distally with a low, rugose tibial crest. On the posterior face of the tibia, the popliteal ridge extends about half the length of the shaft. The proximal fibular facet is a broad, concave and rugose area just distal to the external tuberosity. The thick, trihedral shaft expands distally to a blunt distal end that has a broad, nearly flat astragalar facet lateral to a blunt malleolus. The distal facet for the fibula is slightly convex and rugose.

The fibula (Fig. 22E-F) is a long, thin bone with expanded proximal and distal ends. The head is angled with a nearly flat articular surface for the tibia. Its medial aspect has a concave proximal tibial facet. The shaft is concave medially, and nearly flat laterally. The distal end is a rugose triangular flange with a broad, rounded malleolus separated from a flat distal articular facet.

Pes

The pes is nearly complete but disarticulated (Figs. 23-27). It is very similar to the pes of *Gomphotherium* (Göhlich, 1998, p. 163-182, figs. 135-161, pls. 16-18) and *Haplomastodon* (Ferretti, 2010, p. 705-706, fig. 19) except it is relatively broader and shorter. Therefore, we do not provide a detailed description of the pes of the Jalisco *Stegomastodon*, but we do include metrics (Appendix).

COMPARISON

We compare the osteological features of *Stegomastodon primitivus*

from Jalisco to those of the proboscideans "*Stegomastodon*" from Argentina (Cabrera, 1930); *Cuvieronius* from Bolivia (Boule and Thevenin, 1920); *Mammut* and *Mammuthus* from the USA (Olsen, 1972); *Haplomastodon* from Ecuador (Hoffstetter, 1952; Ferretti, 2010); and *Stegomastodon* from the USA (Gidley, 1926; Osborn, 1936).

The skull and tusks of the Jalisco *Stegomastodon* are greatly distorted; they have been flattened in a dorso-ventral plane. The skull fragment preserved (little more than part of the face with the external nares and tusk alveoli) does not differ from that of *Stegomastodon* from the United States (Gidley, 1926, pl. 34; Osborn, 1936, fig. 642). Alberdi et al. (2009, p. 244) drew attention to the "divergent but not curved" tusk alveoli, as the nearly straight (not divergent) anterior portion of the premaxilla, and a central depression or fissure in the sagittal plane of the Jalisco skull as characters also seen in South American "*Stegomastodon*." However, these features are also present in *Stegomastodon* from the USA (e.g., Osborn, 1936, fig. 642) and thus of no taxonomic significance.

Much has been made of the supposed taxonomic significance of the presence (or absence) of the transverse foramina in the atlas vertebra in South American gomphotheres (e.g., Hoffstetter, 1950, 1952; Simpson and Paulo Couto, 1957). Nevertheless, this feature is variable in *Haplomastodon* samples (Simpson and Paulo Couto, 1957; Ficcarelli et al., 1993, 1995) and therefore of no taxonomic significance. The atlas of the Jalisco *Stegomastodon* does have transverse foramina. It, and the axis, do not appear to differ much from those vertebrae in *Haplomastodon* (Hoffstetter, 1952, fig. 48; Simpson and Paulo Couto, 1977, fig. 6, pls. 12-15; Ferretti, 2010, fig. 9), *Cuvieronius* (Boule and Thevenin, 1920, pl. 7, figs. 1-2) and the Argentine "*Stegomastodon*" (Cabrera, 1930, figs. 17-18, pl. 36) except that the atlas of *Stegomastodon* has a relatively smaller dorsal tuberosity of the dorsal arch (also see Ferretti, 2010). We see no obvious difference in the other vertebrae between the Jalisco *Stegomastodon* and the South American gomphotheres.

The scapula of the Jalisco *Stegomastodon* is essentially identical to that of *Stegomastodon* from Arizona, USA, illustrated by Gidley (1926, pls. 38-39). It differs from the scapula of *Haplomastodon* (Hoffstetter, 1952, fig. 56; Ferretti, 2010, fig. 12a-c) in having a much more prominent metacromion process and a relatively larger supraspinous fossa. In these features the scapula of North American *Stegomastodon* is more similar to that of *Gomphotherium* (Göhlich, 1998, fig. 89). A very large metacromion process is also seen in the scapulae of *Mammut* and *Mammuthus* (Olsen, 1972, fig. 11). The relatively large supraspinous fossa appears to be unique to *Stegomastodon* and may be diagnostic of the genus.

The humerus of the *Stegomastodon* from Jalisco is also indistinguishable from the *Stegomastodon* humerus from Arizona illustrated by Gidley (1926, pl. 36, figs. 1-3). It differs from the humerus of *Haplomastodon* (Hoffstetter, 1952, fig. 57A; Ferretti, 2010, fig. 2d-g), *Cuvieronius* (Boule and Thevenin, 1920, fig. 15, pl. 8, figs. 2-3) and *Gomphotherium* (Göhlich, 1998, pl. 8, fig. 2) in having a low and blunt lesser tuberosity. In the latter gomphotheres the lesser tuberosity is a long flange that extends well proximal to the humeral head. The short, blunt lesser tuberosity of the humerus in *Stegomastodon* is more similar to that feature in *Mammut* and *Mammuthus* (Olsen, 1972, figs. 12-14). The humerus of "*Stegomastodon*" from Argentina (Cabrera, 1930, figs. 20, 32) also has a proximally extended lesser tuberosity as in *Haplomastodon* and *Cuvieronius*, different from the humerus of North American *Stegomastodon*.

The radius-ulna of the Jalisco *Stegomastodon* does not differ significantly from that of the *Stegomastodon* from Arizona illustrated by Gidley (1926, pl. 36, figs. 2-3). However, the ulna of *Stegomastodon* does differ from those of *Haplomastodon* (Hoffstetter, 1952, fig. 57B; Simpson and Paulo Couto, 1957, pl. 16, figs. 2-3; Ferretti, 2010, fig. 13h-i), *Cuvieronius* (Boule and Thevenin, 1920, fig. 18, pl. 8, figs. 4-6), *Gomphotherium* (Göhlich, 1998, figs. 92-93) and the Argentine "*Stegomastodon*" (Cabrera, 1930, fig. 21) in having a blunt, less-produced and less deflected (laterally) olecranon process. The short-blunt olecranon process is present in *Mammut* (Olsen, 1972, fig. 14), but



FIGURE 18. *Siegomastodon primitivus* from Jalisco, Mexico. Metacarpals. A, Articulated left metacarpals. B-C, Metacarpal I in B, anterior and C, posterior views. D-E, Metacarpal II in D, anterior and E, posterior views. F-G, Metacarpal III in F, anterior and G, posterior views. H-I, Metacarpal IV in H, anterior and I, posterior views. J-K, Metacarpal V in J, anterior and K, posterior views. Scale bars: A, upper and B-K, lower.

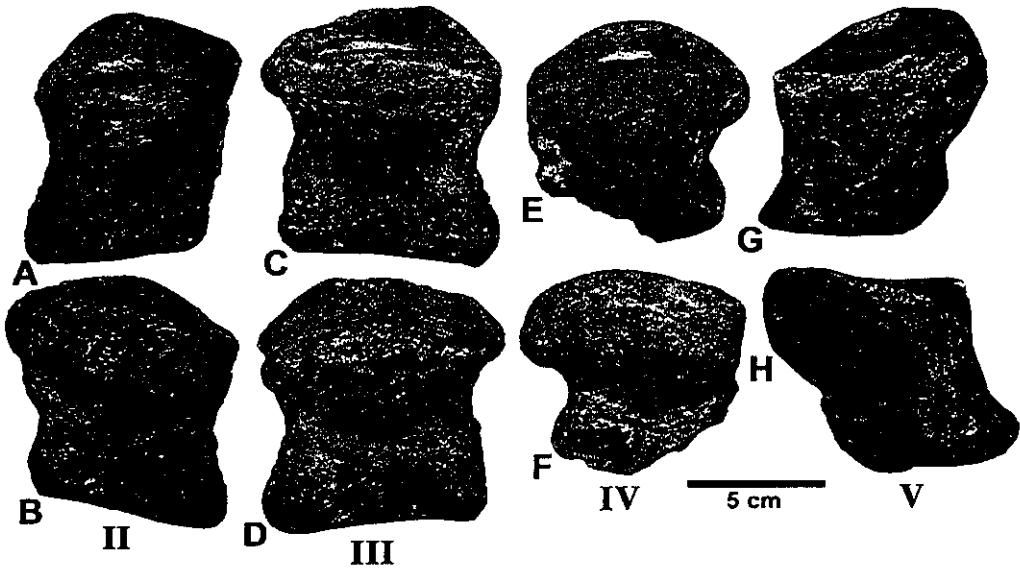


FIGURE 19. *Segomastodon primitivus* from Jalisco, Mexico. Manual phalanges. A-B, Digit II phalanx in A, anterior and B, posterior views. C-D, Digit III phalanx in C, anterior and D, posterior views. E-F, Digit IV phalanx in E, anterior and F, posterior views. G-H, Digit V in G, anterior and H, posterior views.

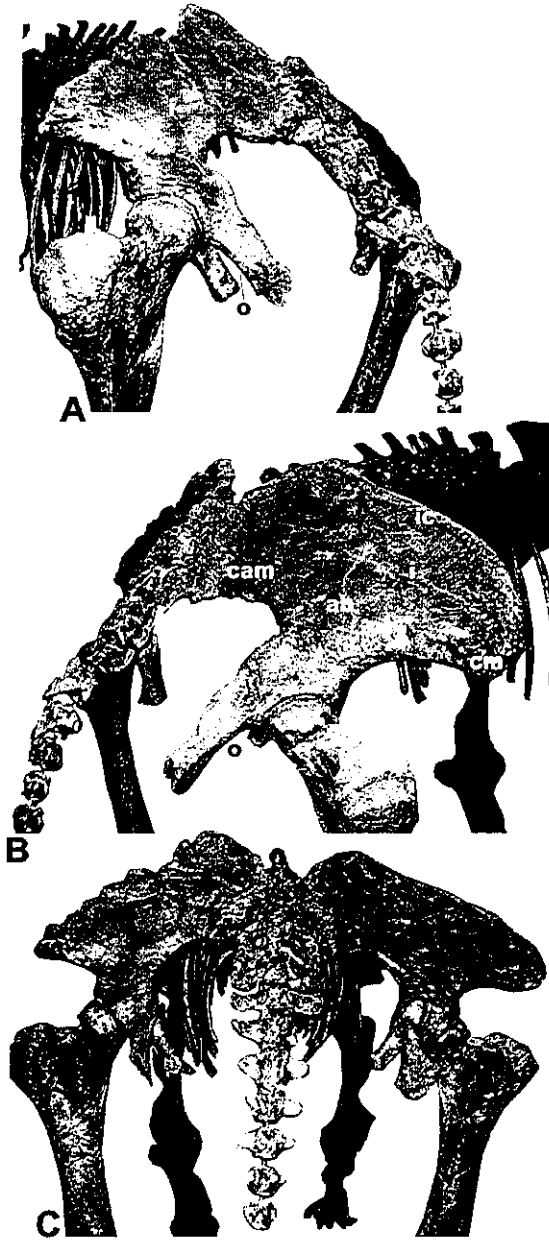


FIGURE 20. *Stegomastodon primitivus* from Jalisco, Mexico. Cast of pelvic girdle on exhibit. Pelvic girdle, proximal hindlimbs, and caudal series in A, left posterolateral, B, right posterolateral and C, posterior views. Abbreviations: a, acetabulum; ab, acetabular border; cam, caudal margin; cm, cranial margin; i, ilium; ic, iliac crest; is, ischium; o, obturator foramen; p, pubis.

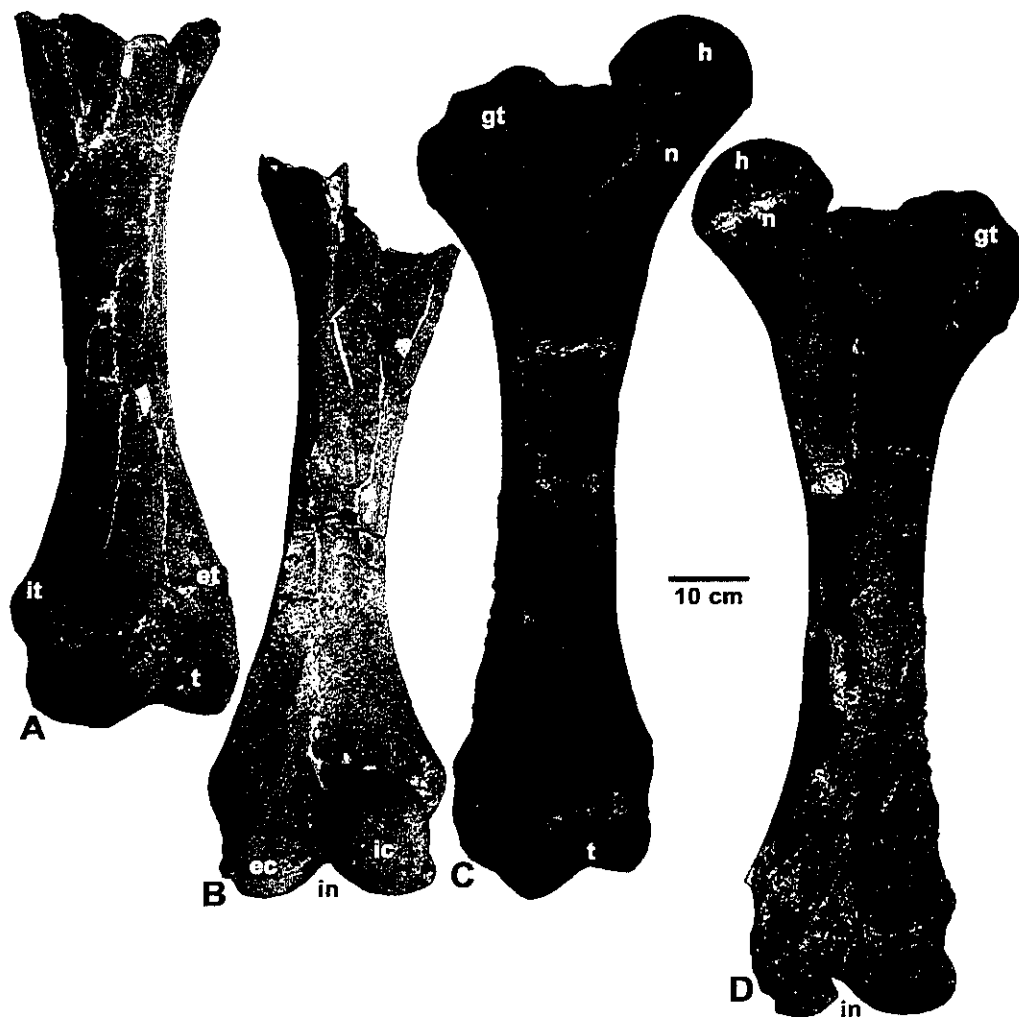


FIGURE 21. *Stegomastodon primitivus* from Jalisco, Mexico. Femora. A-B, Left femur missing proximal end in A, anterior and B, posterior views. C-D, Right femur in C, anterior and D, posterior views. **Abbreviations:** ec, external condyle; et, external tuberosity; gt, greater trochanter; h, head; ic, internal condyle; in, intercondylar notch; it, internal tuberosity; n, neck; t, trochlea.

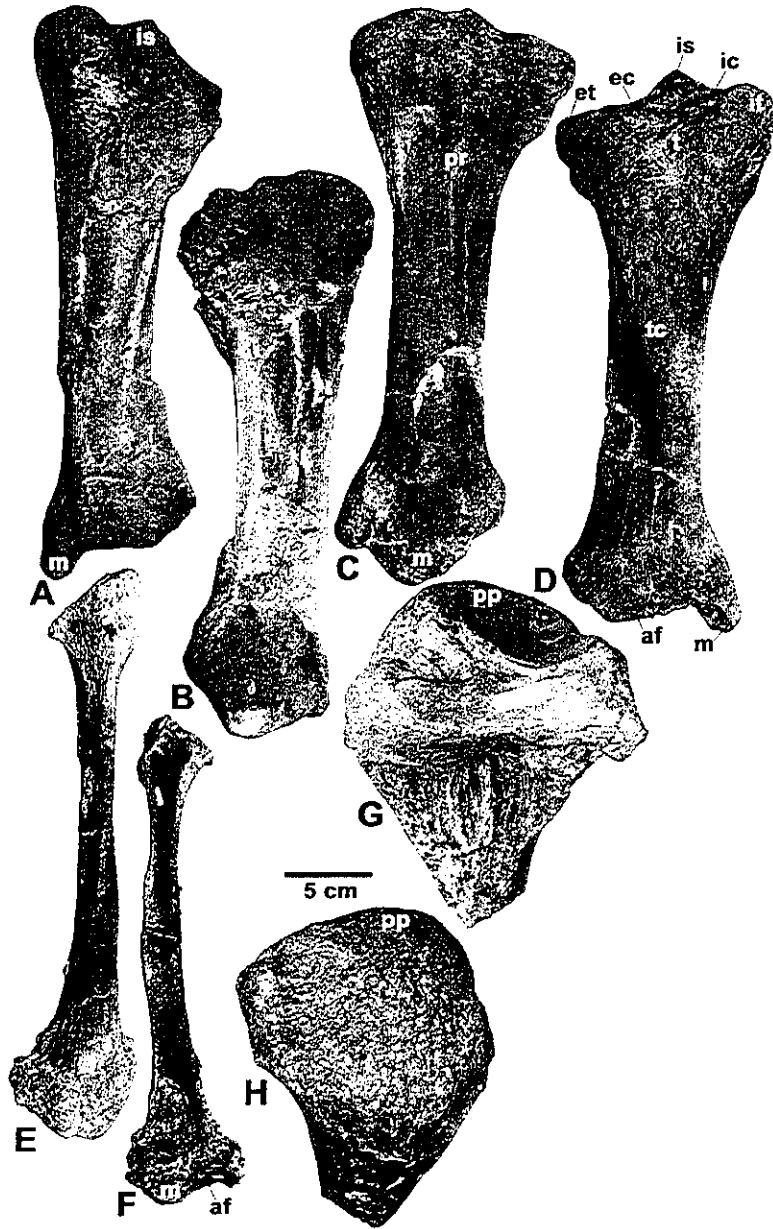


FIGURE 22. *Stegomastodon primitivus* from Jalisco, Mexico. Tibiae, fibulae and patella. A-B. Left tibia in A, anterior and B, posterior views. C-D. Right tibia in C, anterior and D, posterior views. E-F. Right fibula in E, lateral and F, medial views. G-H. Distal end of left fibula in G, medial and H, lateral views. Abbreviations: af, astragalar facet; ec, external condyle; et, external tuberosity; ic, internal condyle; is, intercondylar spine; it, internal tuberosity; m, malleolus; pp, proximal process; pr, popliteal ridge; pt, proximal tibial facet; t, tibial tubercle; te, tibial crest.

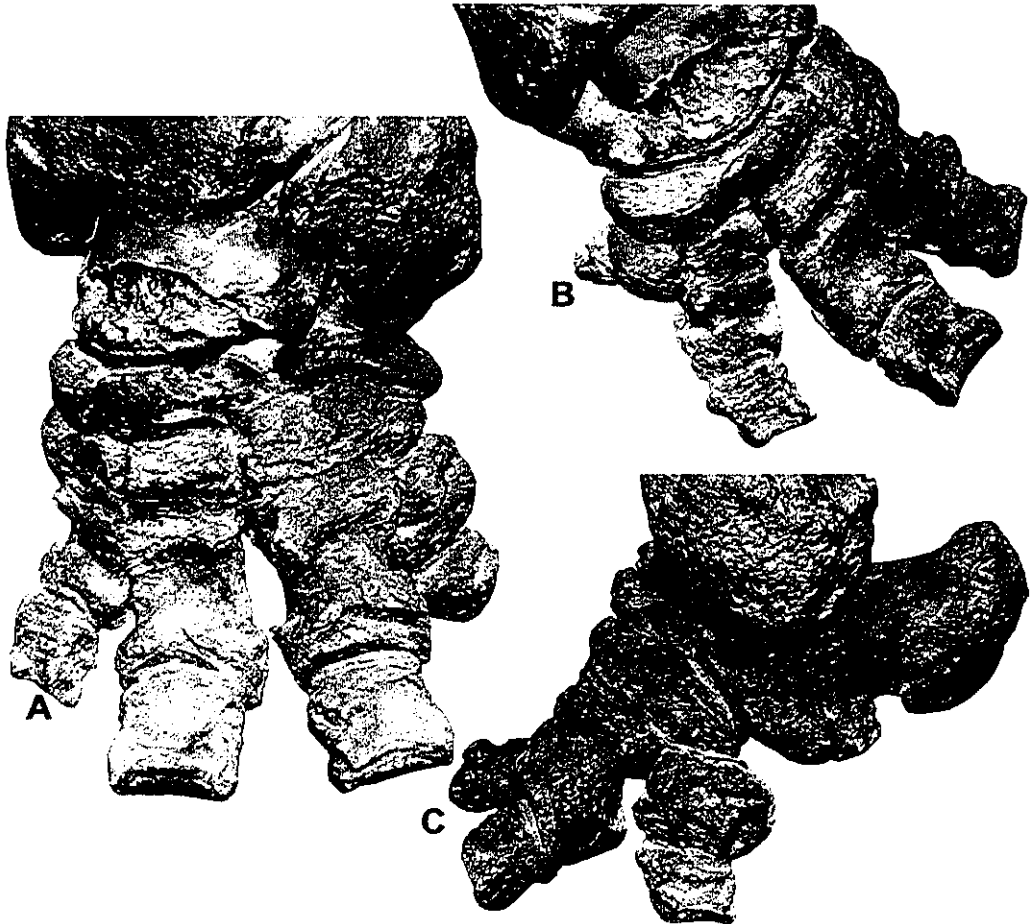


FIGURE 23. *Segomastodon primitivus* from Jalisco, Mexico. Left pes in A, anterior, B, medial and C, lateral views.

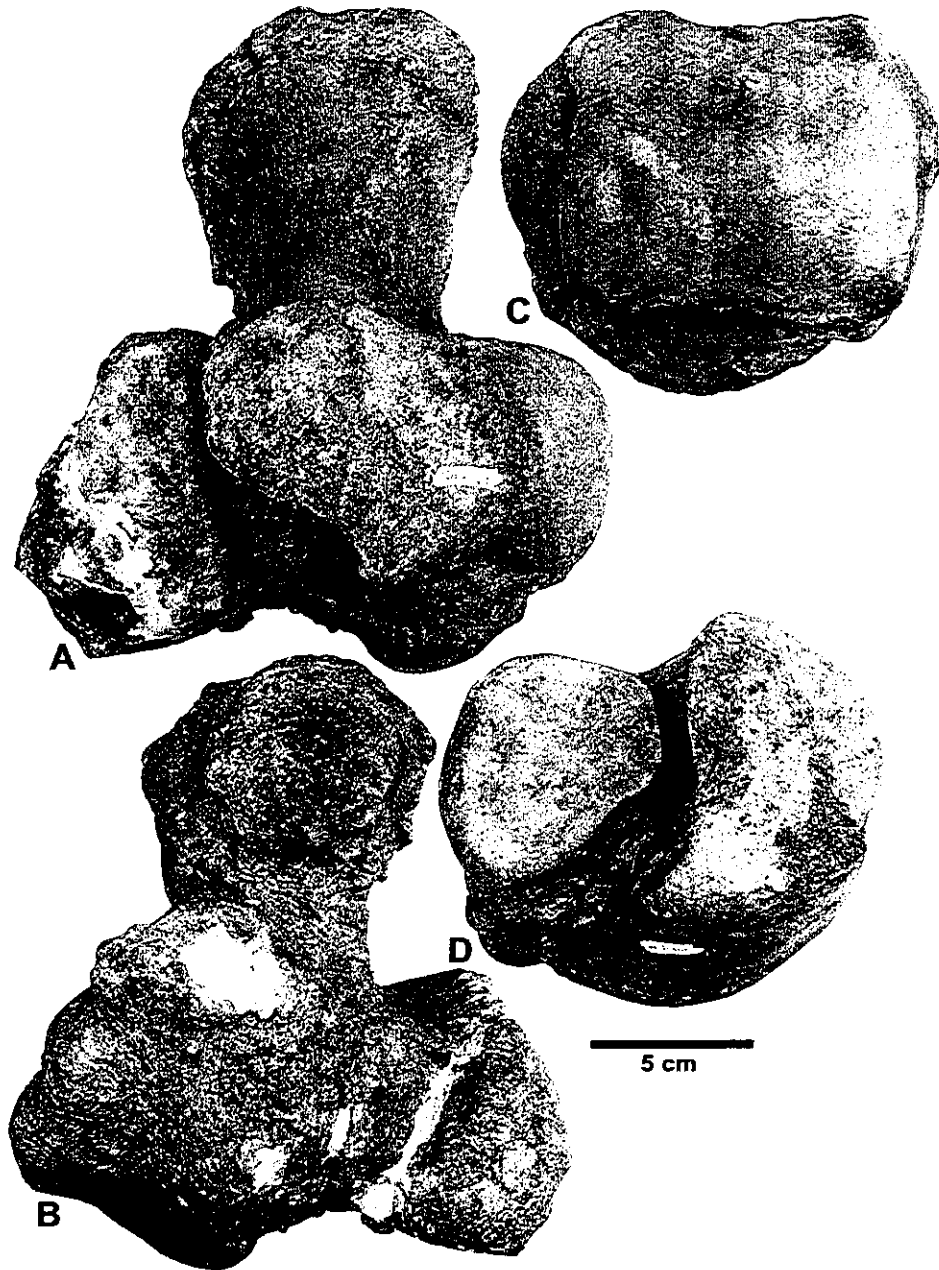


FIGURE 24. *Stegomastodon primitivus* from Jalisco, Mexico. Astragalus and calcaneum A-B, Left calcaneum in A, anterior and B, posterior views C-D, Left astragalus in C, dorsal and D, ventral views.

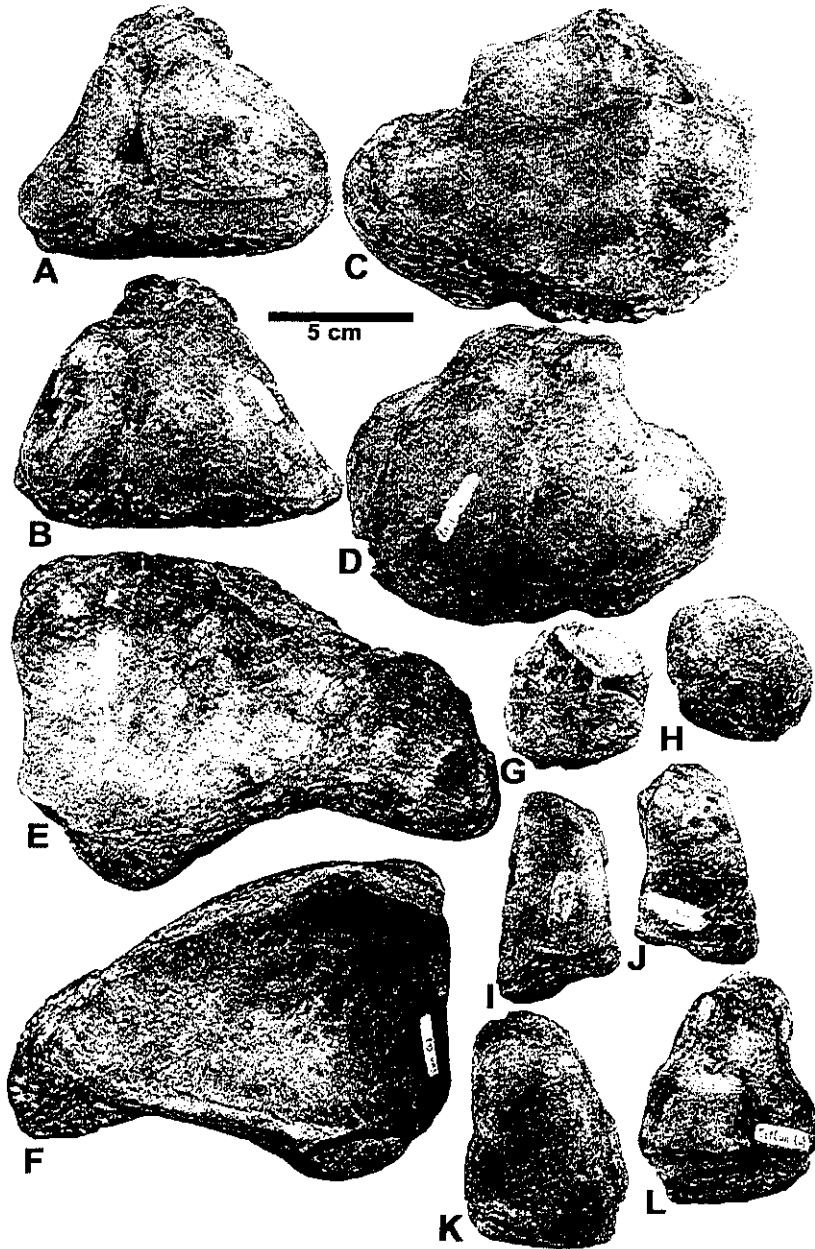


FIGURE 25. *Stegomastodon primitivus* from Jalisco, Mexico. Tarsals. A-B, Left cuboid in A, dorsal and B, ventral views. C-D, Left navicular in C, dorsal and D, ventral views. E-F, Left cuneiform in E, dorsal and F, ventral views. G-H, Left endocuneiform G, dorsal and H, ventral views. I-J, Left mesocuneiform I, dorsal and J, ventral views. K-L, Left ectocuneiform in K, dorsal and L, ventral views.

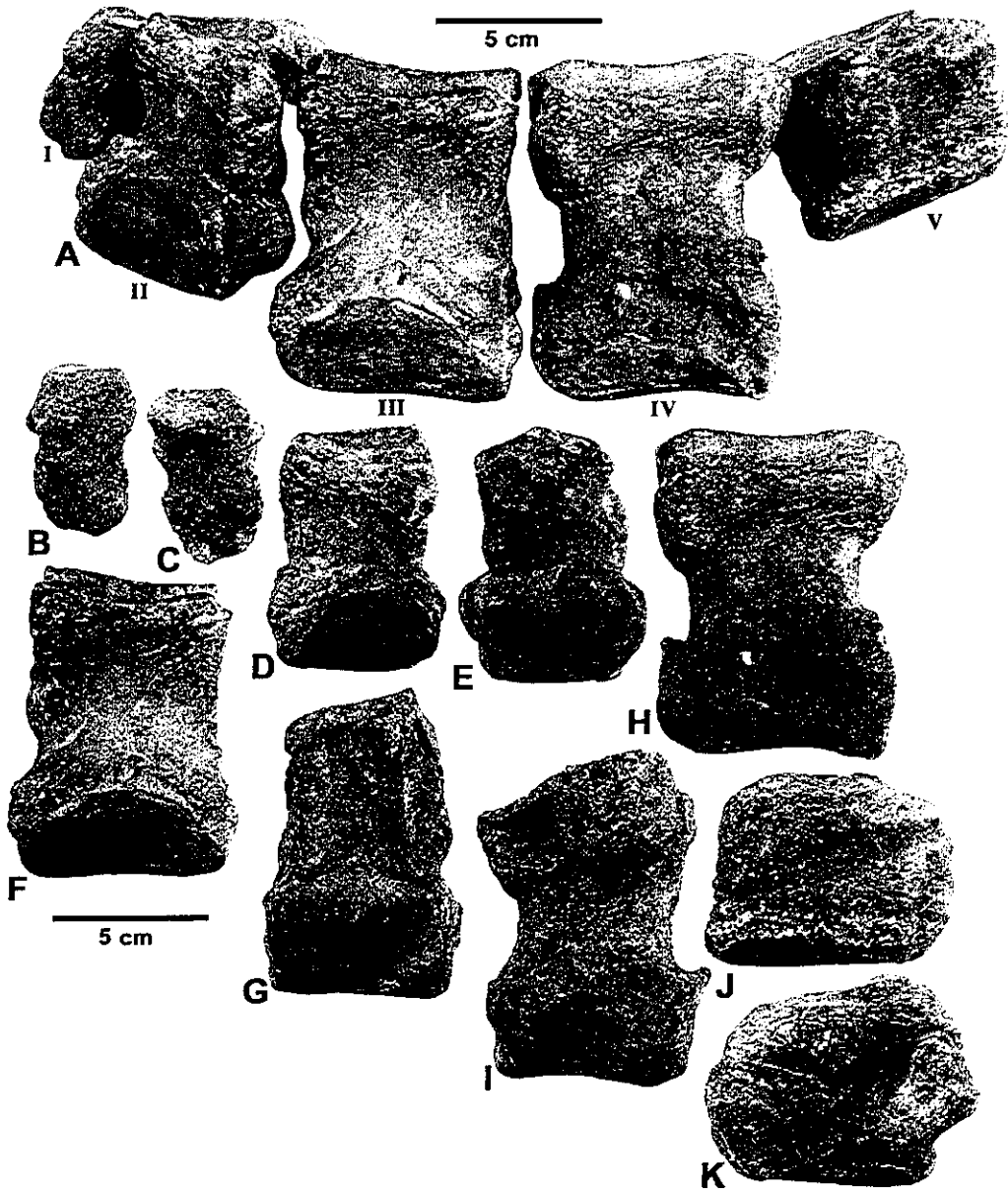


FIGURE 26. *Stegomastodon primitivus* from Jalisco, Mexico. Metatarsals. A, Articulated left metatarsals in anterior view. B-C, Left metatarsal I in B, anterior and C, posterior views. D-E, Left metatarsal II in D, anterior and E, posterior views. F-G, Left metatarsal III in F, anterior and G, posterior views. H-I, Left metatarsal IV in H, anterior and I, posterior views. J-K, Left metatarsal V in J, anterior and K, posterior views. Scale bars: A, upper and B-K, lower.

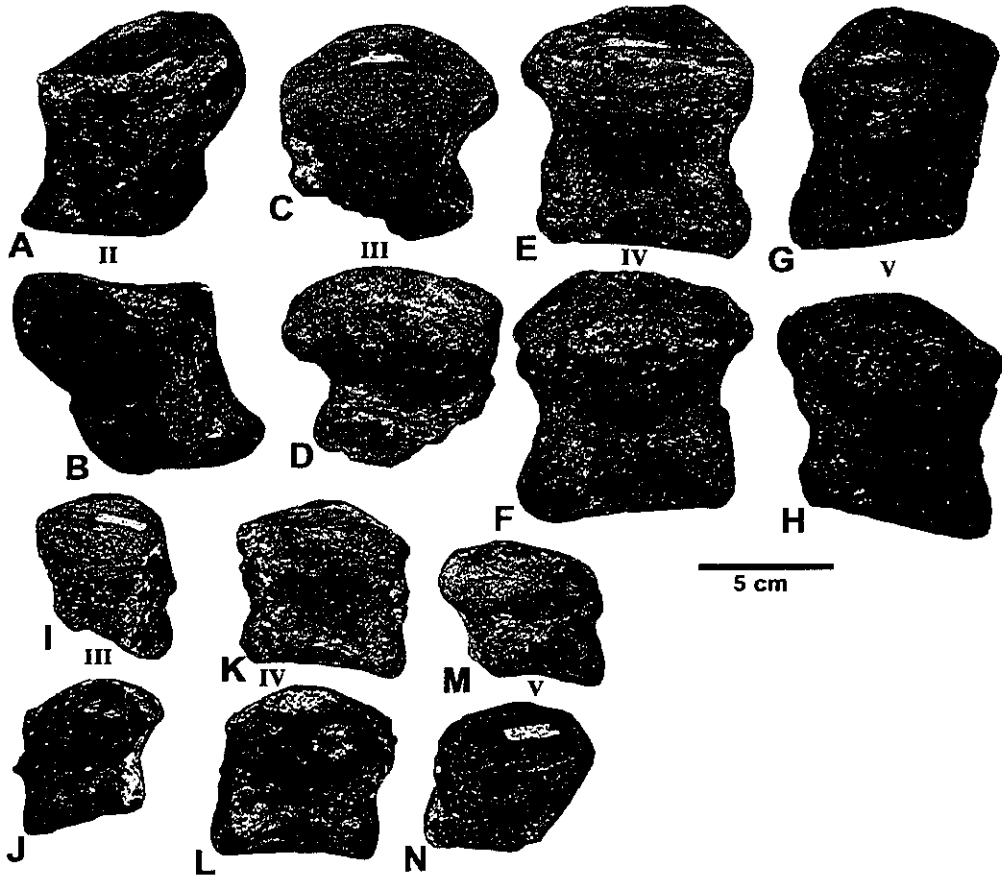


FIGURE 27. *Segomastodon primitivus* from Jalisco, Mexico. Pedal phalanges. A-B, Left digit II phalanx in A, anterior and B, posterior views. C-D, Left digit III phalanx in C, anterior and D, posterior views. E-F, Left digit IV phalanx in E, anterior and F, posterior views. G-H, Left digit V in G, anterior and H, posterior views. I-J, Right digit III phalanx in I, anterior and J, posterior views. K-L, Right digit IV phalanx in K, anterior and L, posterior views. M-N, Right digit V phalanx in M, anterior and N, posterior views.

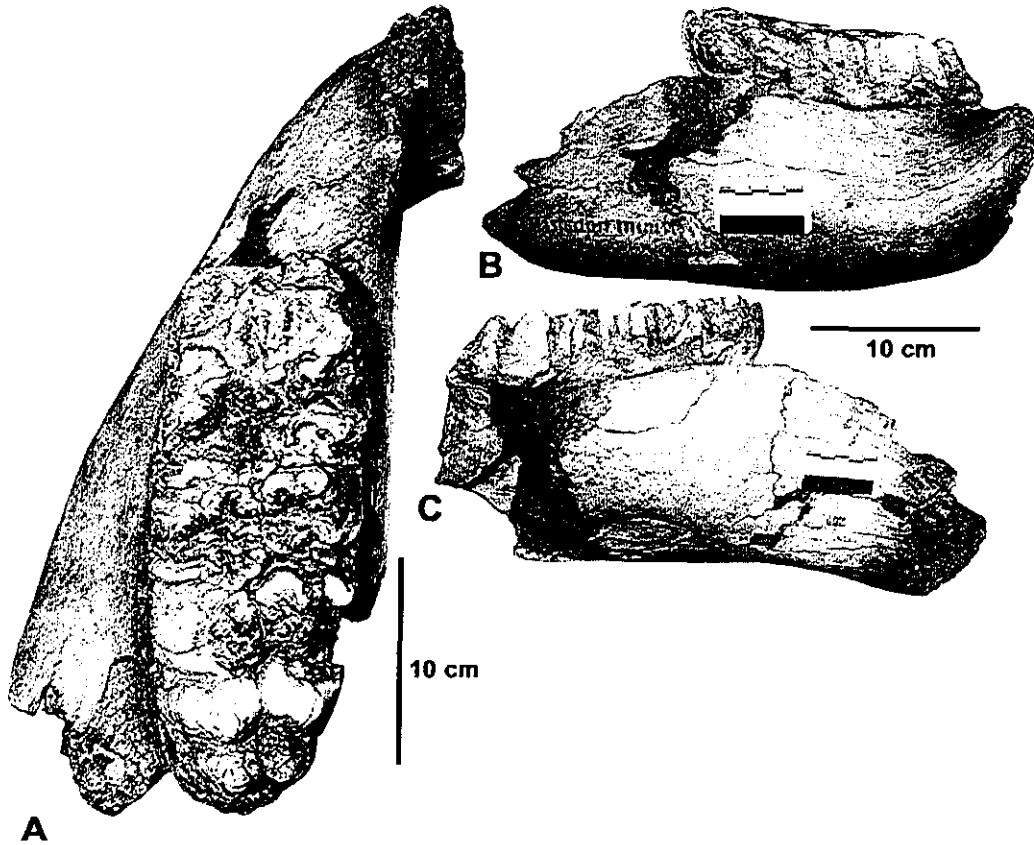


FIGURE 28. *Stegomastodon mirificus*, USNM 209, holotype left dentary in A, occlusal, B, labial and C, lingual views.

Mammuthus has a vertically oriented flange-like olceranon process (Olsen, 1972, fig. 14) distinct from the gomphothere ulnae. The manus of the Jalisco *Stegomastodon* is relatively broad and short compared to those of *Cuvieronius* (Boule and Thevenin, 1920, fig. 30), *Haplomastodon* (Ferretti, 2010) and *Gomphotherium* (Göhlich, 1998).

The pelvis of the Jalisco *Stegomastodon* resembles that of the Arizona *Stegomastodon* (Gidley, 1926, pl. 33) but has a much more cranially convex and thick, rugose iliac crest than do the gomphotheres *Haplomastodon* (Hoffstetter, 1952, fig. 51; Ferretti, 2010, fig. 20), *Cuvieronius* (Boule and Thevenin, 1920, fig. 20) and *Gomphotherium* (Göhlich, 1998, fig. 126). The pelvis of *Mammuthus* (Olsen, 1972, figs. 24-28) also has a rounded, convex cranial end to its iliac crest.

The pillar-like femur of the Jalisco *Stegomastodon* with its large, thick greater trochanter is like that of *Stegomastodon* from Arizona (Gidley, 1926, pl. 39, fig. 3). This femur is similar to that of *Haplomastodon* (Hoffstetter, 1952, fig. 58A; Simpson and Paulo Couto, 1957, pl. 16, fig. 1; Ferretti, 2010, fig. 18a-e) but differs from the femur of *Cuvieronius* (Boule and Thevenin, 1920, figs. 23-24, pl. 9, fig. 2) and the Argentine "*Stegomastodon*" (Cabrera, 1930, figs. 22, 33-34), which have a relatively smaller greater trochanter and a head on a relatively long neck that projects proximally. These latter femora are more similar to those of

Mammut and *Mammuthus* (Olsen, 1972, fig. 25) than to *Stegomastodon*.

The patella, tibia and fibula of the Jalisco *Stegomastodon* do not appear to differ significantly from those bones in other gomphotheres, such as *Cuvieronius* (Boule and Thevenin, 1920, fig. 27, pl. 9, figs. 5-8), *Stegomastodon* (Gidley, 1926, pl. 39, fig. 1) and the Argentine "*Stegomastodon*" (Cabrera, 1930, figs. 23, 35). The pes does not appear to differ significantly from that of *Cuvieronius* (Boule and Thevenin, 1920, fig. 31), *Haplomastodon* (Ferretti, 2010) and *Gomphotherium* (Göhlich, 1998) except in being relatively broader and shorter.

The postcranial differences between North American *Stegomastodon* and the South American gomphotheres *Cuvieronius*, *Haplomastodon* and the Argentine "*Stegomastodon*" suggest a greater degree of graviportality in *Stegomastodon* than in those gomphotheres (cf. Gregory, 1912; Smith and Savage, 1956). There is some quantitative confirmation of this by comparing the intermembral index (radius length + humerus length/tibia + femur length \times 100) of the Jalisco *Stegomastodon*, which is 93, to that of *Haplomastodon*, which, based on data in Ferretti (2010), is \sim 82. This means the forelimb of *Stegomastodon* is relatively longer than it is in *Haplomastodon*. The more massive, pillar-like limbs (especially the forelimbs) of *Stegomastodon* thus identify it as a more graviportal gomphothere than were the South American gomphotheres.

NO *STEGOMASTODON* IN SOUTH AMERICA

Cabrera (1930) first assigned some South American gomphothere fossils to *Stegomastodon*. There was subsequent debate about this assignment. Recently, Alberdi et al. (2002, 2004, 2007), Prado et al. (2003) and Prado and Alberdi (2008) have endorsed the concept of only two South American gomphothere genera, *Cuvieronius* and *Stegomastodon* (= *Haplomastodon*). At issue is the important conclusion as to whether there was one immigration of gomphotheres to South America (then there would be no true *Stegomastodon* in South America) or two immigrations, one of *Cuvieronius* and one of *Stegomastodon*.

Several workers have questioned the presence of *Stegomastodon* in South America, including Osborn (1936), Savage (1955), Madden (1984), Webb (1992), Ferretti (2008, 2010) and Lucas and Alvarado (2010). The Jalisco *Stegomastodon* skeleton strengthens this case, as it demonstrates several features of the postcranium (especially of the fore- and hindlimbs, see above) in which the Argentine "*Stegomastodon*" fossils differ substantially from North American *Stegomastodon* and instead resemble *Haplomastodon* and *Cuvieronius*. Like Ferretti (2008) and Lucas and Alvarado (2010) we advocate using the name *Notiomastodon* for the Argentinean fossils that Cabrera (1930) originally (and we believe erroneously) assigned to *Stegomastodon*. The South American gomphotheres are thus a Plio-Pleistocene evolutionary radiation of *Cuvieronius hyodon* in the Andean Cordillera and its descendants *Notiomastodon* and *Haplomastodon* in the Brazilian tropical lowlands and the Argentine pampas.

SPECIES-LEVEL TAXONOMY OF *STEGOMASTODON*

Pohlig (1912) coined the name *Stegomastodon* for Leidy's (1859) *Mastodon mirificus*. The holotype of the genotypic species *S. mirificus* includes USNM 209, a left dentary fragment with m3 (Fig. 28). This specimen documents diagnostic features of the genus – the brevisrostrine lower jaw lacking tusks and the m3 with six lophs that show relatively complex (at least double) trefoils. Osborn (1936, p. 667-684) provided the last detailed review of the genus *Stegomastodon*, to which he assigned eight species. Here, we briefly review these species, and others that have been assigned to the genus.

Stegomastodon chapmani

Hays' (1834) species *Mastodon chapmani* was based on part of an upper molar crown with three lophs that have a complex enamel pattern (Hays, 1934, pl. 22, figs. 3-4; Osborn, 1936, fig. 637). The type has long been lost (Osborn, 1936, p. 669), and its collecting locality is unknown. Although Osborn (1924, 1926, 1936) referred the tooth fragment to *Stegomastodon*, it is not diagnostic of the genus and could, indeed, belong to another gomphothere genus such as *Gomphotherium* or *Cuvieronius*. We therefore regard *Mastodon chapmani* as a *nomen dubium* (*nomen vanum*) best forgotten.

Stegomastodon mirificus

Leidy's (1859) type of *Mastodon mirificus* (Fig. 28) was said to be from the "Loup Fork of Platte River," Nebraska, which according to Hay (1924, p. 100) was probably near Seneca in Thomas County, and Osborn (1936) assigned it an early-middle Pleistocene age. The species *S. mirificus* is the oldest valid species of the genus (and the type species), so it is the name most commonly used for a species of *Stegomastodon*. Indeed, Kurtén and Anderson (1980) considered *S. mirificus* to be the only valid species of the genus (but see below). Particularly significant for understanding morphology and variation in *S. mirificus* is the population from the Blanco Cita Canyon locality in Texas described by Savage (1955). We consider *S. mirificus* to encompass most known *Stegomastodon* specimens. This species has cheek teeth that wear to double trefoils, second molars with rudimentary fourth lophs/lophids and third molars with 6-7 lophs/lophids.

Stegomastodon successor

The type of *Mastodon successor* Cope, 1892, is an incomplete lower jaw with left m2-3 from the Blanco Formation of West Texas (Cope, 1893, pls. 16-17; Osborn, 1936, fig. 641). The m3 has six lophs, and the worn crown of m2 has complex trefoils. Meade (1945) documented the sample of *Stegomastodon* from the Blanco Formation and noted (p. 525) that the holotype of *S. mirificus* falls within the range of variation of the Blanco *Stegomastodon*. Based on this, Savage (1955) regarded *S. successor* as a junior subjective synonym of *S. mirificus*. We concur.

Stegomastodon aftoniae

Calvin (1909) described a single M3 from the lower Pleistocene ("Altonian") of Iowa that he compared to *Stegomastodon mirificus* (the locality is Irvingtonian; Skinner and Libbard, 1972). Osborn (1924) coined the new species *S. aftoniae* for this molar, which has seven lophs and a talonid plus a complicated enamel pattern. Thus, Osborn (1924, 1936) regarded *S. aftoniae* as the most advanced (and geologically youngest) species of *Stegomastodon*. However, some specimens of *S. mirificus* (= *S. successor*, *S. texanus*) from the late Blancan of Texas overlap the size and morphology of the holotype of *S. aftoniae*.

The possibility that a derived, geologically young (Irvingtonian) species of *Stegomastodon* can be recognized merits consideration. For example, the *Stegomastodon* palate from the Irvingtonian Tortugas Mountain gravel pit in southern New Mexico (Lucas et al., 1999, 2000) displays a derived morphology not unlike that of *S. aftoniae*. *S. aftoniae*, the most derived species of *Stegomastodon*, has very complex trefoils, a fourth loph/lophid on the second molar and 7 lophs/lophids on the third molars.

Stegomastodon texanus

Osborn (1924) coined a second species of Blanco Formation *Stegomastodon* for a skull with tusks and mandible with worn m3s. Meade (1945), in his review of the Blanco Formation *Stegomastodon*, concluded that the sample represents a range of variation that suggests one species, so he synonymized *S. successor* and *S. texanus*. We agree with this conclusion, as did Savage (1955). Thus, *S. successor* and *S. texanus* are synonyms of *S. mirificus* (cf. Savage, 1955).

Stegomastodon barbouri

Osborn (1924) created a "subgenus" *Morrillia* for *Tetralophodon barbouri* from the Pliocene of Nebraska. Tobien (1973, p. 243-246) reviewed in detail the status of *Morrillia barbouri* (also see Osborn, 1936, p. 377-379) and concluded that *Morrillia barbouri* is definitely a *Stegomastodon* and likely *S. mirificus*. We agree, and thus regard it as a synonym of *S. mirificus*.

Stegomastodon arizonae

Gidley (1926) named *Stegomastodon arizonae* for a partial skeleton (includes a skull and lower jaws) from the late Blancan Curtis Ranch local fauna of southeastern Arizona. Pasenko and Lucas (2011) review the record of Arizona *Stegomastodon* (and other gomphotheres) to conclude that *S. arizonae* is a junior subjective synonym of *S. mirificus*.

Stegomastodon priestleyi

Hay and Cook (1930) named *Gomphotherium priestleyi* for a lower molar fragment from a gravel pit near Frederick, Oklahoma. Osborn (1936) regarded the locality as Pliocene and assigned *G. priestleyi* to *Stegomastodon*. While this generic assignment may be correct, the holotype tooth fragment of *S. priestleyi* is too incomplete to be diagnostic of a species of the genus. Therefore, we regard *S. priestleyi* as a *nomen dubium* (*nomen vanum*).

Stegomastodon primitivus

Osborn (1936, p. 726) named *Stegomastodon primitivus* for a palate that is part of a quarry sample of *Stegomastodon* found near Ainsworth, Nebraska, referred to the medial Blancan Sand Draw fauna (Skinner and Hibbard, 1972). Osborn diagnosed the species by its relatively primitive molar morphology of five lophi/lophids and relatively little trefoiling. However, as Savage (1955, p. 66) noted, the morphology of the *S. primitivus* sample described by Osborn (1936) overlaps that of the late Blancan Cita Canyon and Blanco Formation samples assigned to *S. mirificus*. Savage (1955) thus expressed skepticism about the validity of *S. primitivus*. However, we regard *S. primitivus* (= *S. rexroadensis*) as the most primitive species of *Stegomastodon* characterized by cheek teeth with relatively simple trefoils, second molars with three lophi/lophids and third molars with 5-6 lophi/lophids.

Stegomastodon rexroadensis

Woodburne (1961) named the new species *Stegomastodon rexroadensis* for teeth from the medial Blancan Rexroad fauna of Kansas. The teeth of *S. rexroadensis* have simple trefoils and the molars have 5+ lophi/lophids. They are thus indistinguishable from those of *S. primitivus*, but Woodburne (1961, p. 84) distinguished the species by the smaller lower jaw of *S. rexroadensis*. Woodburne (1961, p. 88) thus referred to Savage (1955, p. 66), who noted that one of the jaws of *S. primitivus* is unusually large for the dentition. However, this statement only applies to one jaw of *S. primitivus* (F:AM [American Museum of Natural History, Friek Collection] 24985); the other jaws in the *S. primitivus* quarry sample from Nebraska are much smaller (they contain deciduous teeth: Osborn, 1936, fig. 676, p. 728). Significantly, Woodburne (1961, p. 88) noted that only one mandible of *S. rexroadensis* (UMMP 33366) is measurable, but he reported no metrics than can be compared to those of the quarry sample of *S. primitivus*. Instead, he reported symphyseal lengths of the Rexroad specimen (115 mm), which overlap those of specimens he assigned of *S. mirificus*. We conclude instead that jaw size is variable among *Stegomastodon* and clearly is influenced ontogenetically, if not by other factors (sexual dimorphism?, epigenetics?) not relevant to taxonomic distinctions. Therefore, we consider *S. rexroadensis* to be a junior subjective synonym of *S. primitivus*.

Summary

There have been two extreme approaches to the species-level taxonomy of *Stegomastodon* represented by Osborn (1936) and by Kurtén and Anderson (1980). Osborn (1936) recognized seven valid species and arranged them in the morphocline *S. primitivus* → *S. successor* → *S. mirificus* → *S. chapmani* → *S. texanus* → *S. arizonae* → *S. affoniae*. In contrast, Kurtén and Anderson (1980) assigned all *Stegomastodon* to one species, *S. mirificus*.

There is extensive morphological overlap and polymorphism in the entire sample of North American *Stegomastodon*, but it is possible to construct a chronomorphocline from the *Stegomastodon* sample that allows recognition of three successive species that do temporally and morphologically overlap, but that can be distinguished. This is similar to the taxonomy of North American *Mammuthus* in which the chronomorphocline *M. meridionalis* (or *M. huxi*) → *M. imperator* → *M. columbi* recognizes three distinct morphotypes that nonetheless grade into each other and temporally overlap. The most primitive species of *Stegomastodon*, *S. primitivus* Osborn (= *S. rexroadensis* Woodburne) is early Blancan in age. The type of *S. mirificus* is from a site of unknown age in Nebraska; however, most specimens of this species are late Blancan. The type of *S. affoniae* is from the early Irvingtonian of Iowa (Osborn 1924).

We view the evolution of *Stegomastodon* as the development of a derived, grazing gomphothere. The tall, elephantid-like skull directly above the short, robust lower jaw suggests a powerful vertical bite of the relatively broad and increasingly complex, grinding cheek teeth. The relatively graviportal limbs of the Jalisco *Stegomastodon* support the idea of a large quadruped covering long distances in open country, much like other large savannah-adapted proboscideans. Thus, *Stegomastodon* was likely a grazer, and it is no coincidence that its disappearance in North America during the early Irvingtonian is almost coeval with the appearance of a more effective grazer, *Mammuthus*.

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APPENDIX-MEASUREMENTS OF JALISCO *STEGOMASTODON*

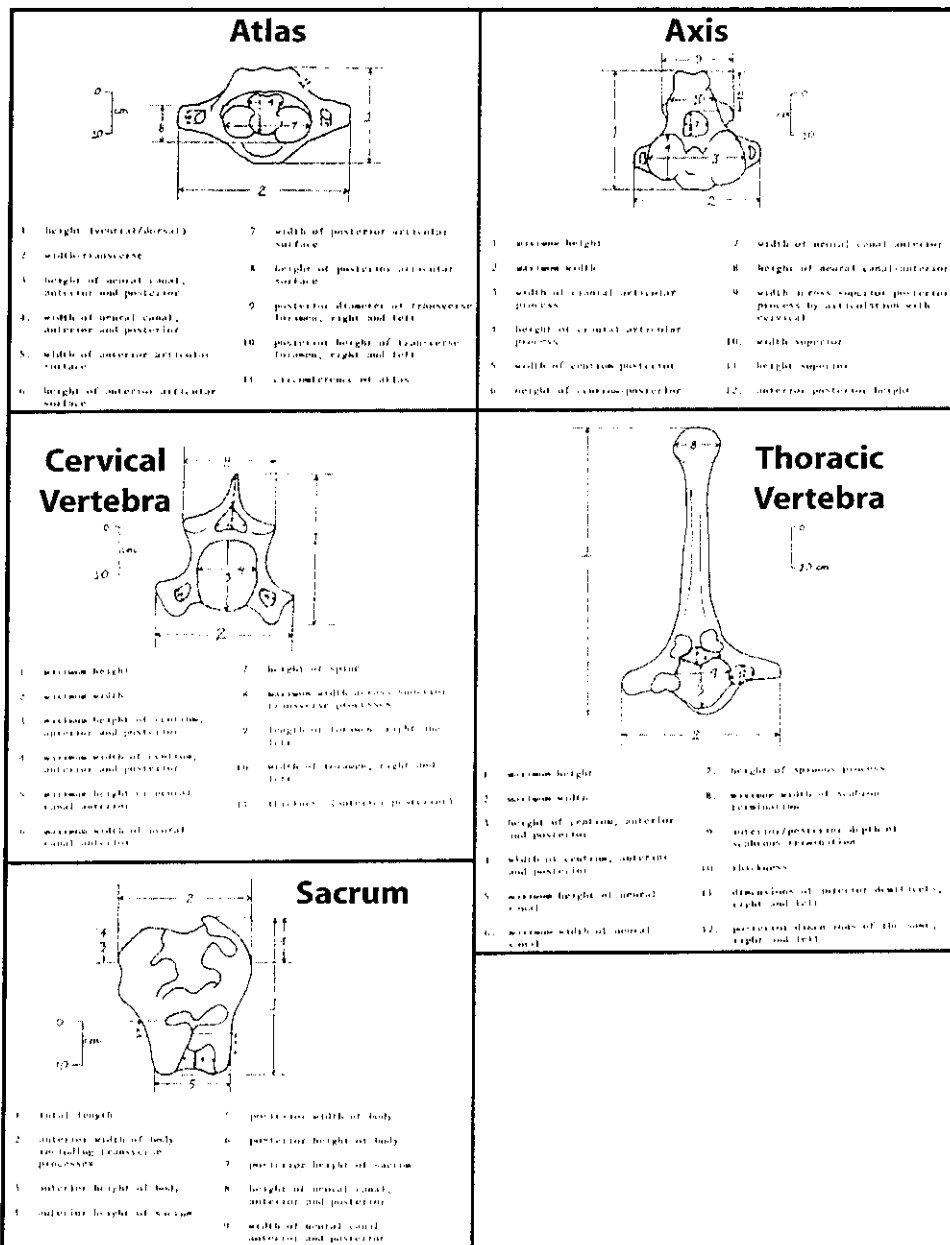


FIGURE 29. Measuring protocol 1, from Dutrow (1980).

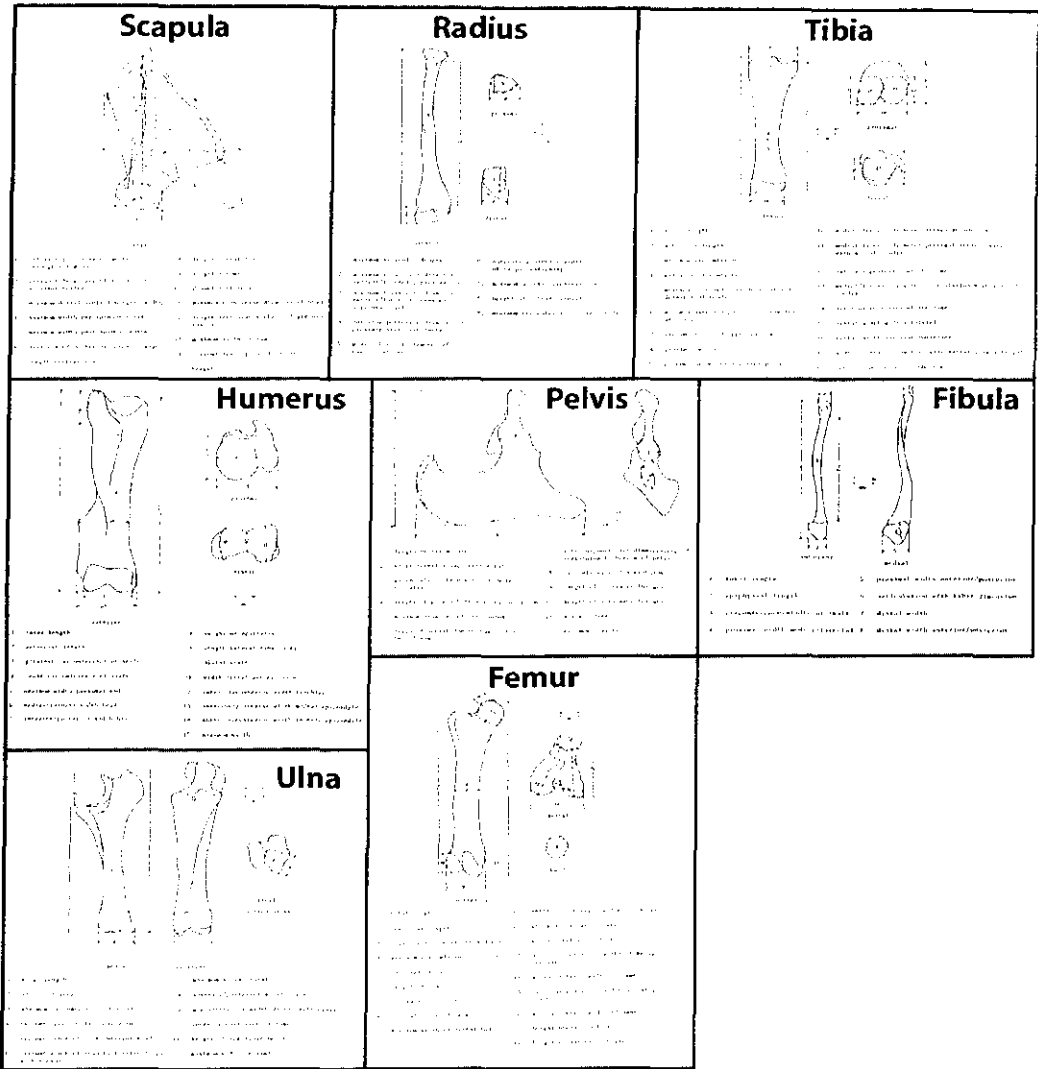


FIGURE 30. Measuring protocol 2. from Dutrow (1980).

Atlas		Patella	
1. 271 mm	7. 228 mm	1. 160 mm	4. 134 mm
2. 435 mm	8. 121 mm	2. 154 mm	5. 115 mm
3. Ant = 114 mm;	9. L = 26 mm;	3. 142 mm	
Post = 122 mm	R = 23 mm		
4. Ant = 79 mm;	10. L = 27 mm;		
Post = 71 mm	R = 25 mm		
5. 210 mm	11. 900 mm		
6. 146 mm			
Axis		Right Fibula	
1. 285+ mm	7. 75 mm	1. 652 mm	5. 77 mm
2. 200+ mm	8. 105 mm	2. 525 mm	6. W = 60 mm;
3. 192+ mm	9. 180 mm	3. 60 mm	H = 56 mm
4. 95+ mm	10. 127 mm	4. 100 mm	7. 90 mm
5. 164 mm	11. 85 mm		8. 145 mm
6. 146 mm	12. 63 mm		
Cervical Vertebra 7		Right Tibia	
1. NP	7. NP	1. 693 mm	10. 262 mm
2. NP	8. NP	2. 655 mm	11. 120 mm
3. Ant = 132 mm;	9. NP	3. 332 mm	12. 143 mm
Post = 130 mm		4. 380 mm	13. 120 mm
4. Ant = 150 mm;	10. NP	5. 115 mm	14. 98 mm
Post = 151 mm	11. 64 mm	6. 88 mm	15. 228 mm
5. NP		7. 735 mm	16. 170 mm
6. NP		8. 263 mm	17. 142 mm
		9. 80 mm	18. 115 mm
Thoracic Vertebra 11		Scapula	
1. 640 mm	7. 500 mm	1. 835 mm	9. 620 mm
2. 293+ mm	8. 122 mm	2. 690 mm	10. 180 mm
3. Ant = 122 mm;	9. 58 mm	3. 680 mm	11. 252 mm
Post = 117 mm		4. 240 mm	12. 205 mm
4. Ant = 129 mm;	10. 67 mm	5. 410 mm	13. 130 mm
Post = 130 mm	11. R(w) = 36 mm;	6. 628 mm	14. 640 mm
	R(h) = 74 mm;	7. 672 mm	15. 260 mm
	L(w) = 33 mm;	8. 5000(?) mm	
	L(h) = 69 mm		
5. 57 mm	12. R(w) = 64 mm;	1. 945 mm	Left Humerus
	R(h) = 51 mm;	2. 942 mm	9. NP
	L(w) = 64 mm;	3. 720 mm	10. 375 mm
	L(h) 64 = 64 mm	4. 440 mm	11. 270 mm
		5. 340 mm	12. 116 mm
		6. 225 mm	13. 210 mm
		7. 164 mm	14. 135 mm
		8. 154 mm	15. 280 mm
6. 52 mm			
Pelvis		Left Radius	
1. NP	7. 195 mm	1. 710 mm	6. 139 mm
2. 590 mm	8. 660 mm	2. 132 mm	7. 154 mm
3. 910 mm	9. NP	3. 123 mm	8. 122 mm
4. 860 mm	10. NP	4. 70 mm	9. NM
5. 190 mm	11. NP	5. 125 mm	
6. 120 mm			
Sacrum		Right Ulna	
1. 374 mm	6. NP	1. 822 mm	7. 210 mm
2. 250+ mm	7. NP	2. 598 mm	8. 220 mm
3. NP	8. NP	3. 405 mm	9. 205 mm
4. NP	9. NP	4. 590 mm	10. 108 mm
5. 245 mm		5. 515 mm	11. 170 mm
		6. 640 mm	12. 260 mm
Right Femur			
1. 1095 mm	10. 239+ mm		
2. 1035 mm	11. 244 mm		
3. 140 mm	12. 117 mm		
4. 392 mm	13. 240+ mm		
5. 193 mm	14. 80+ mm		
6. 104 mm	15. 250 mm		
7. 555 mm	16. 117 mm		
8. 485+ mm	17. 168 mm		
9. 263 mm	18. 158 mm		

NM = Not measured
NP = Not present

Metapodials

	Length	Smallest depth of diaphysis	Smallest breadth of diaphysis	Depth of proximal end	Breadth of proximal end	Depth of distal end	Breadth of distal end
MC 1 (left)	118 mm	50 mm	42 mm	81 mm	57 mm	67 mm	55 mm
MC 2 (left)	?	58 mm	?	?	?	80 mm	?
MC 3 (left)	176 mm	58 mm	78 mm	105 mm	95 mm	86 mm	88 mm
MC 4 (left)	151 mm	56 mm	79 mm	101 mm	86 mm	90 mm	85 mm
MC 5 (left)	139 mm	73 mm	79 mm	101 mm	93 mm	102 mm	85 mm
MC 2 (right)	155 mm	58 mm	67 mm	107 mm	80 mm	92 mm	87 mm
MC 3 (right)	?	55 mm	74 mm	?	?	84 mm	103 mm
MC 4 (right)	?	?	?	?	?	?	?
MT 1 (left)	~58 mm	30 mm	29 mm	38 mm	36 mm	?	?
MT 2 (left)	98 mm	42 mm	53 mm	73 mm	54 mm	68 mm	68 mm
MT 3 (left)	115 mm	37 mm	66 mm	77 mm	69 mm	67 mm	82 mm
MT 4 (left)	115 mm	48 mm	60 mm	82 mm	86 mm	76 mm	87 mm
MT 5 (left)	65 mm	85 mm	89 mm	90 mm	79 mm	61 mm	81 mm
MT 3 (right)	?	29 mm	36 mm	51 mm	42 mm	?	?
MT 2 (right)	98 mm	43 mm	56 mm	73 mm	62 mm	64 mm	68 mm
MT 3 (right)	114 mm	36 mm	65 mm	76 mm	71 mm	67 mm	84 mm
MT 4 (right)	112 mm	48 mm	58 mm	85 mm	84 mm	74 mm	80 mm
MT 5 (right)	66 mm	78 mm	79 mm	87 mm	81 mm	65 mm	82 mm

Phalanges

	Length	Smallest depth of diaphysis	Smallest breadth of diaphysis	Depth of proximal end	Breadth of proximal end	Depth of distal end	Breadth of distal end
First CPH II (L)	78 mm	37 mm	60 mm	70 mm	74 mm	43 mm	70 mm
First CPH III (L)	85 mm	36 mm	67 mm	65 mm	66 mm	44 mm	80 mm
First CPH IV (L)	74 mm	34 mm	61 mm	65 mm	80 mm	?	?
First CPH V (L)	87 mm	40 mm	61 mm	65 mm	75 mm	41 mm	67 mm
First CPH II (R)	?	?	?	68 mm	?	?	?
First CPH III (R)	86 mm	38 mm	64 mm	67 mm	86 mm	44 mm	77 mm
First CPH IV (R)	76 mm	36 mm	63 mm	67 mm	83 mm	43 mm	76 mm
First TPH II (L)	54 mm	32 mm	47 mm	51 mm	55 mm	36 mm	50 mm
First TPH III (L)	66 mm	30 mm	64 mm	53 mm	69 mm	39 mm	67 mm
First TPH IV (L)	~57 mm	36 mm	68 mm	56 mm	71 mm	?	?
First TPH V (L)	54 mm	39 mm	52 mm	52 mm	65 mm	36 mm	51 mm
First TPH II (R)	59 mm	32 mm	46 mm	53 mm	59 mm	65 mm	48 mm
First TPH III (R)	65 mm	29 mm	65 mm	51 mm	67 mm	39 mm	68 mm
First TPH IV (R)	63 mm	41 mm	62 mm	52 mm	67 mm	39 mm	67 mm
First TPH V (R)	60 mm	39 mm	53 mm	53 mm	66 mm	38 mm	54 mm