

Congosaurus bequaerti, a Paleocene Dyrosaurid (Crocodyliformes; Mesoeucrocodylia) from Landana (Angola)

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Abstract

A complete redescription of the material of *Congosaurus bequaerti* from the Cabinda enclave (Angola), first described in 1914 by DOLLO, enables a taxonomic revision of this species. The genus *Congosaurus* was considered by BUFFETAUT (1976, 1980) as a junior synonym of the genus *Hyposaurus*. BUFFETAUT (1976, 1980) used the dorsoventral flattening of the mandible to distinguish *Hyposaurus* from the genus *Rhabdognathus*. A scatter plot comparing width/height ratio of the mandible according to the tooth position, supports that the two genera can clearly be separated by this method. On the other hand the values obtained for *Congosaurus bequaerti* are closer to *Rhabdognathus* than to *Hyposaurus*, underlining a clear difference between *Congosaurus* and *Hyposaurus*. The anatomical characteristics furnish more arguments to differentiate these two genera. In *C. bequaerti*, the lachrymal is extremely anteriorly extended and the posterior maxillary and dentary teeth are labio-lingually compressed, contrary to the condition observed in *Hyposaurus* or *Rhabdognathus*. In *Hyposaurus*, the external mandibular fenestra is large and the teeth exhibit ventrolingually “twisted” anterior carinae, contrary to the extremely reduced fenestra and the linear anterior carinae of *Congosaurus bequaerti*. The snout proportion of *C. bequaerti* (about 65 % of the total skull length) is about the same than in *Hyposaurus* (66 %) and far from *Rhabdognathus* (73 %).

All these characters suggest that *Congosaurus bequaerti* should be distinguished from *Hyposaurus* and *Rhabdognathus*, and then, the original DOLLO's genus should be retained for this species.

Key-words: *Congosaurus*, Dyrosauridae, Crocodyliformes, taxonomy, Paleocene, Angola.

Résumé

Une description complète du matériel de *Congosaurus bequaerti* de l'enclave de Cabinda (Angola), décrit pour la première fois en 1914 par DOLLO, permet une révision taxonomique de cette espèce. Le genre *Congosaurus* fut considéré par BUFFETAUT (1976, 1980) comme un synonyme plus récent du genre *Hyposaurus*. BUFFETAUT (1976, 1980) utilisa l'aplatissement dorso-ventral plus important de la mandibule pour distinguer *Hyposaurus* du genre *Rhabdognathus*. Un graphique, comparant le rapport largeur/hauteur de la mandibule en fonction de la position sur celle-ci, prouve que ces deux genres peuvent clairement être distingués par cette méthode. Par contre, les valeurs obtenues pour *Congosaurus bequaerti* sont plus proches de celles de *Rhabdognathus* que d'*Hyposaurus*, soulignant une nette différence entre *Congosaurus*

et *Hyposaurus*. Les caractéristiques anatomiques fournissent d'autres arguments pour différencier ces deux genres. Chez *Congosaurus bequaerti*, le lacrymal est extrêmement étendu antérieurement et les dents maxillaires et dentaires postérieures sont comprimées labio-lingualement contrairement à ce que l'on a observé chez *Hyposaurus* ou *Rhabdognathus*. Chez *Hyposaurus*, la fenêtre mandibulaire externe est large et les dents montrent une carène antérieure ventro-lingualement déviée, contrairement à la fenêtre très réduite et aux carènes droites de *Congosaurus bequaerti*. Les proportions du museau de *C. bequaerti* (environ 65 % de la longueur total du crâne) sont à peu près les mêmes que celles d'*Hyposaurus* (66 %) et très éloignées de *Rhabdognathus* (73 %).

Tous ces caractères suggèrent que *Congosaurus bequaerti* peut être distingué d'*Hyposaurus* et de *Rhabdognathus*, et donc le genre original décrit par DOLLO doit être conservé pour cette espèce.

Mots-clés: *Congosaurus*, Dyrosauridae, Crocodyliformes, taxonomie, Paléocène, Angola.

Introduction

In 1913, the skeletal remains of a fossil crocodyliform, discovered by J. Bequaert (BEQUAERT, 1923) during a botanical expedition in Landana (Cabinda enclave, Angola) (Fig. 1), were brought to the Musée d'Afrique Centrale in Tervuren, Belgium. These comprised the nearly complete skeleton of a dyrosaurid crocodylomorph. They were described preliminarily and named *Congosaurus bequaerti* by DOLLO (1914). Though DOLLO (1914) promised a more complete description of the individual for a later date, he was never able to finish this work. Therefore, in 1948 the director of the former “Musée du Congo belge” in Tervuren invited W. E. Swinton from London to re-examine the *Congosaurus* skeleton. SWINTON (1950) prepared an extended description of the remains of this dyrosaur species. The taxonomic status of *Congosaurus bequaerti* was questioned by ARAMBOURG (1952) and ANTUNES (1964); they regarded *Congosaurus* as a junior subjective synonym of *Dyrosaurus*. BUFFETAUT (1976, 1980) revised the material once again and, in contrast to the former authors, argued that the Cabinda dyrosaur belongs to the genus *Hyposaurus*. This remained until recently the taxonomical status for the Cabinda dyrosaur.

Studies of dyrosaur material from North Africa (JOUVE, pers. obs.) indicate that the Cabinda dyrosaur can be distinguished from the North American and North Afri-

can species of *Hyposaurus* by characters of its skull and mandible. A new taxonomic revision of this material was therefore deemed necessary. Additionally, the only extended description of the material by SWINTON (1950) contained inaccuracies. Therefore a redescription of the type material connected with a discussion of the former results are presented herein.

The remains of the Cabinda dyrosaur were discovered in a sea-cliff in Landana. The strata of the Landana cliff were deposited in a sedimentary basin that was formed during the opening of the South Atlantic (PETTERS, 1991). The succession comprises strata of early Paleocene (Selandian) and middle Eocene (Lutetian) age. The sediments mainly consist of calcareous sandstones, marly shales, conglomerates and, near the top, silicified limestones (BEQUAERT, 1923; DENAEYER, 1929; DARTEVELLE, 1938; DARTEVELLE & CASIER, 1943; VALE, 1960). The exposed strata are divided into a lower and an upper part separated into 32 lithological units ("couches" or "beds", DARTEVELLE & CASIER, 1943). The lower beds No. 1 to 26 are considered to be of Selandian age, bed No. 27 to 32 are probably Lutetian age. The age determination is based on fish and molluscan remains (DARTEVELLE, 1938; DARTEVELLE & CASIER, 1943), but these statements are uncertain and the precise age of beds 27 to 32 is doubtful (MILLER, 1951). The lower units are generally rich in fossil remains (LERICHE, 1927). The upper units mostly lack macrofossils but contain foraminifers. The

remains of *Congosaurus bequaerti* were collected from bed No. 8 and therefore determined to be of a Montian (= Selandian) age (SWINTON, 1950). Other fossil remains reported from the Montian units comprise nautiloids (MILLER, 1951), echinids (DARTEVELLE, 1952), fishes (LERICHE, 1920, 1927; DARTEVELLE & CASIER, 1943, SAINT-SEINE, 1950) and turtles (DOLLO, 1924).

The material referred to *Congosaurus* described in the present paper is housed in the "Musée d'Afrique Centrale" at Tervuren (Belgium).

Abbreviations of Institutions

MNHN – Muséum National d'Histoire Naturelle, Paris, France;
MRAC – Musée Royal d'Afrique Centrale, Tervuren, Belgique;
NJSM – New Jersey State Museum, Trenton, USA.; OCP – Office Chérifien des Phosphates, Khouribga, Maroc.

Redescription of *Congosaurus bequaerti* DOLLO, 1914

Crocodylomorpha WALKER, 1970
Cocodyliiformes HAY, 1930
Mesoeucrocodylia WHETSTONE & WHYBROW, 1983
Neosuchia BENTON & CLARK, 1988
Dyrosauridae DE STEFANO, 1903

Genus *Congosaurus* DOLLO, 1914

Emended diagnosis of genus – same as species.

Type species – *Congosaurus bequaerti* DOLLO, 1914, from the Paleocene of Cabinda, Angola.

Congosaurus bequaerti DOLLO, 1914

- 1952 *Dyrosaurus (Congosaurus) bequaerti* ARAMBOURG, p 297.
1964 *Dyrosaurus bequaerti* ANTUNES, p 189.
1976 *Hyposaurus bequaerti* BUFFETAUT, p 489.
1980 *Hyposaurus bequaerti* BUFFETAUT, p 23.

Emended diagnosis – Dyrosaurid with a fairly developed rostrum that comprises circa 65 % of the total skull length; anterior process of jugal extends anteriorly as far as the prefrontal; lachrymal extremely extended anteriorly, making the lachrymo-nasal contact more than two times the length of the prefronto-nasal one; posterior mandibular alveoli labio-lingually compressed; mandible as wide as high; 20 teeth on each maxilla and premaxilla (4 premaxillary and 16 maxillary teeth), external mandibular fenestra small.

Holotype – M.R.A.C. 1741-1743, 1745, 1796, 1797, 1802, 1803, 1806, 1809-1811, 1813-1819, 1823, 1828, 1839, 1852, 1854, 1895, 1870, 1871, 1887, 1894, an almost complete skeleton, with cranial and post cranial remains from the Paleocene of Landana (Cabinda), Angola (DOLLO, 1914, p 290).

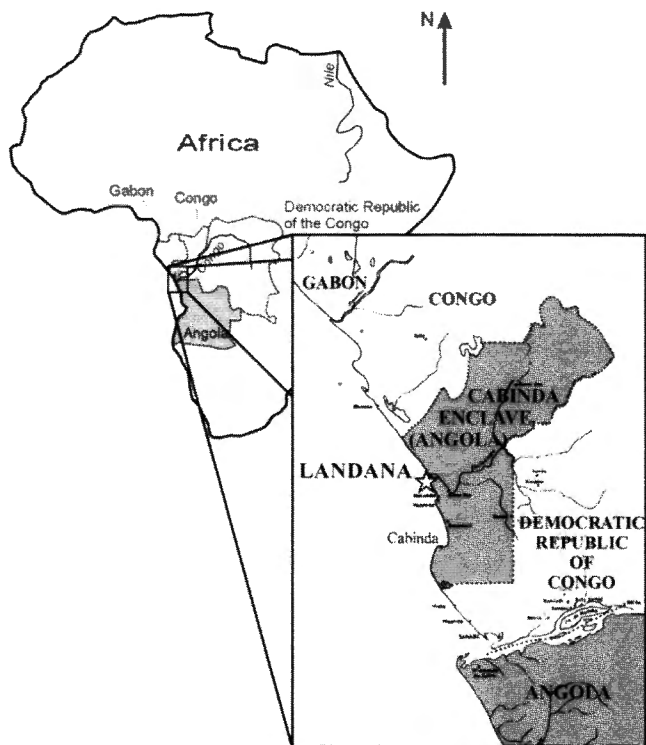


Fig. 1 — Geographical position of the Landana cliff, type locality of *Congosaurus bequaerti* DOLLO, 1914 (detailed map, modified from HOURCQ, 1966).

Preservation – The skull is broken posterior to the anterior margin of the orbit, and the braincase and skull deck are lost. The sutures of the skull have been traced by SWINTON (1950) with black ink, but those from the anterior wall of the suborbital cavity require reinterpretation (Pl. 1, Fig. 4, 5).

The mandible is almost complete and only the anterior part comprising the first six teeth is missing. The two posterior rami are dorsoventrally compressed and distorted.

The remains of the axial skeleton comprise the axis and its odontoid process, the 3rd to 9th cervical vertebrae, the 2nd prothoracic vertebra, the 1st, 4th to 8th and 10th thoracic vertebrae, the last presacral vertebra representing one lumbar vertebra as well as the 2nd to 4th, 6th, 9th to 18th and three terminal caudal vertebrae (probably the 30th, 31st and 35th). The precise positions of the caudal vertebrae were determined by a comparison of their centrum lengths. From the thoracic region one and from the caudal region four isolated neural spines are present. Remains of ribs belong to the left 2nd and the right and left 3rd to 7th cervical ribs as well as to 5th thoracic ribs and 5th haemal arches are present. The appendicular skeleton is represented by the right scapula, the right and left coracoid, the right humerus, the proximal and distal part of the right ulna, the proximal part of the right radius, a right radiale, four right metacarpals, the left ilium, the right and left femur, the left tibia, the proximal part of the left fibula, a proximal and a distal fragment of two metatarsals, six phalanges as well as three ungual phalanges, and several dorsal and ventral osteoderms.

The preservation of the remains ranges from the well-preserved and complete vertebrae, ribs and bones of the appendicular skeleton to the very fragmentary, badly damaged remains. Most of the postcranial elements suffer from mediolateral compression and distortion.

Skull – The rostrum is narrow in its anterior three-quarters and widens only in its posterior quarter, from the level of the 8th maxillary teeth, to twice its anterior width. The remains can be reconstructed to form a longirostrine skull in which the rostrum comprises 65 % of the total skull length (Fig. 2). The postorbital region being missing, this estimate must be taken with care. The dorsal surface of the preserved skull remains is lightly sculptured with shallow grooves and ridges.

In dorsal view, the external nares are anteroposteriorly oval and dorsally directed (Pl. 1, Fig. 1). Their lateral margins are lower than the posterior. In lateral view, the lateral margins are anteroventrally inclined (Pl. 1, Fig. 2).

In ventral view, the foramen incisivum is a narrow aperture in the median plane of the ventral surface of the premaxilla (Pl. 1, Fig. 3). Its anterior extremity extends slightly between the first right and left premaxillary teeth, separating these posteriorly. The foramen incisivum ends posteriorly at the level of the posterior margin of the second tooth. Contrary to the tracing of SWINTON (1950; Pl. 1B), the ventral contact of the premaxillae posterior to the foramen incisivum is not certain, and

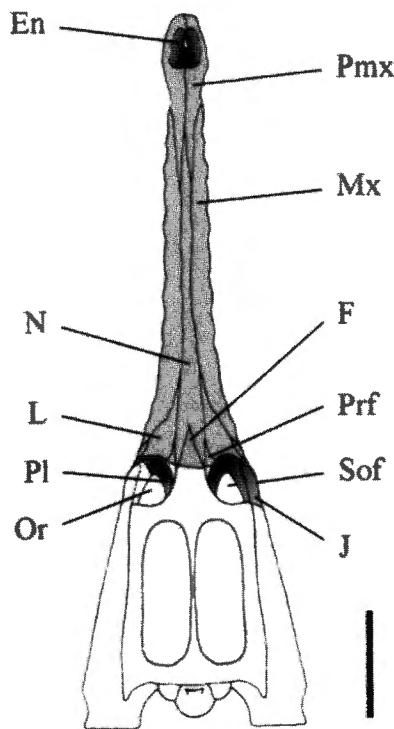


Fig. 2 — Reconstruction of the skull of *Congosaurus bequaerti* DOLLO, 1914. The skull length is estimated corresponding to the length of the mandible. The shape of the postorbital area is unknown in *C. bequaerti* and completely imagined in this figure (area in white). Scale bar: 10 cm.

the maxillae probably reach the posterior margin of the foramen incisivum.

The orbit is laterally bordered by the jugal, anteriorly by the lacrimal and anteromedially by the prefrontal. Because the skull is broken away at the level of the orbit, the anterior wall of the suborbital cavity is exposed. From the anteroventral margin of this wall, a small postnasal fenestra connects the antorbital cavity (sensu WITMER, 1995) with the suborbital cavity. The anterolateral wall of the suborbital cavity is dorsally formed by a high, anteriorly convex vertical wall of the lacrimal; the lateral wall is dorsally formed by the jugal and ventrally by the maxilla (Pl. 1, Fig. 4, 5).

The suborbital fenestra reaches anteriorly the level of the fourteenth maxillary tooth, and only its most anterior part is preserved.

The premaxillae are narrow and have a convex lateral margin (Fig. 2). The anterior suture between the right and left premaxillae forms a distinct dorsal protuberance anteriorly to the external nares. The posterodorsal process of the premaxilla reaches the level of the interalveolar space between the third and fourth maxillary teeth. The premaxilla bears four alveoli. From these alveoli, the third premaxillary alveolus is the largest, whereas the first, second and fourth premaxillary alveolus have the same diameter. Concavities for the occlusion of the man-

dibular teeth separate the premaxillary teeth, forming shallow lateral notches, slightly dorsally visible. These sulci create an irregular outline to the premaxillae in dorsal view. The alveolar border projects ventrally, below the interalveolar space, so that the lateral margin of the premaxilla is very wavy in lateral view. A deep occlusal notch for the first dentary tooth separates the first and second premaxillary alveoli. The first right and left premaxillary alveoli are positioned very close to each other.

The right and left maxillae are dorsally separated by the nasal bone over all their length (Fig. 2). The lateral margin of the maxilla is relatively linear posteriorly and only in its posterior sixth curves laterally. Several foraminae are present on the medial margin of the maxilla, located just posteriorly to the postnasal fenestra (Pl. 1, Figs. 4, 5). These openings are probably neurovascular foraminae, of which the passage of the maxillary nerve (*n. alveolaris dorsalis caudalis*). The maxilla possesses 16 separated alveoli. The right and left maxillae ventrally contact each other until the level of the 12th maxillary alveolus. From this level, the maxillae are medially separated by the palatines and diverge posterolaterally. As on the premaxilla, the alveolar border projects ventrally, below the interalveolar space, so that the lateral margin of the maxilla is strongly wavy in lateral view. The maxillary alveoli are relatively small, and the first to sixth alveoli are circular in outline whereas the more posterior alveoli are labiolingually compressed and have an anteroposterior oval outline. The interalveolar space between the first to eighth maxillary alveoli is more than twice as long as the alveoli. From the eighth maxillary alveolus the interalveolar space continuously decreases in length so that the interalveolar space between the most posterior maxillary teeth is less long than the alveoli. The width between the right and the left row of alveoli is anteriorly twice the width of a maxillary alveolus and constant from the first to the sixth maxillary alveoli. This space increases progressively posteriorly from the seventh.

The nasal is a single bone that passes deeply between the posterodorsal processes of the premaxillae (Fig. 2). It reaches anteriorly the level of the interalveolar space between the first and second maxillary alveoli, and is largely excluded from the external nares. The width of the nasal is constant from its posteriormost contact with the premaxillae to the level of the seventh maxillary alveolus, posterior to which the nasal expands to twice its anterior width. The nasal is posteriorly separated by a median projection of the frontal that reaches the level of the 12th maxillary alveolus.

Only the anteriorly directed tip of the prefrontal is preserved (Fig. 2). This tip wedges between the laterally positioned lacrimal and the medially positioned frontal, exceeds anteriorly the level of the anterior margin of the orbits on a very short length. The dorsal three-quarters of the prefrontal pillars are formed by the prefrontal whereas the basis of each pillar is formed by the palatine (Pl. 1, Fig. 4, 5). Medially, the right and the left prefrontal pillars are separated from each other by a narrow and high slit-

like opening that is interpreted as a passage for the nasal septum and the olfactory tract. The frontal forms the dorsal margin of this opening. From the frontal, a small medial process descends and probably separates the right and left olfactory nerves. A medial process on each prefrontal pillar ascends dorsally and stops at the same level as the descending process of the frontal. This process does not seem to be formed by the prefrontal, but maybe by the frontal or an ethmoidal ossification, because a long vertically oriented suture separates this process from the prefrontal pillar. The ventromedial margin of the prefrontal pillar (*sulcus septalis*) seems not to be formed by the palatine, but by another bone, perhaps the pterygoid. The prefrontal sends a small lateral hooked-shaped process from the prefrontal pillar within the postnasal fenestra, a little bit dorsal to the prefrontal-palatine suture.

The lachrymal is large and wide and nearly triangular in dorsal view (Fig. 2). Its contact with the nasal is very broad anteriorly and exceeds the prefrontal-nasal contact for more than twice of its length. The lachrymal forms the semi-circular anterior margin of the orbit.

The jugal constitutes the lateral margin of the orbit (Pl. 1, Fig. 4, 5). Its anterior process ends anterior to the prefrontal at the level of the 12th maxillary alveolus.

Mandible – The mandible is extremely elongated and narrow in its anterior preserved half. The mandibular symphysis posteriorly reaches the level of the sixteenth dentary alveolus (varying according to size and age in dyrosaurids (JOUVE, pers. obs.)). The external mandibular fenestra is reduced to a small opening, surrounded posterodorsally by the surangular, anterodorsally and anteriorly by the dentary and ventrally by the angular (Pl. 2, Fig. 1, 2). The retroarticular process is elongated and curves posterodorsally. As a result of the strongly concave medial horizontal wing of the articular, the retroarticular process is medially deeply concave (Pl. 2, Fig. 3, 4), with a 'L'-shaped cross section at mid length of the retroarticular process.

The dentary extends for three-quarters of the total length of the mandible. In lateral view, the dentary ends posteriorly with a high triangular process that forms the anterior and dorsal margin of the external mandibular fenestra (Pl. 2, Fig. 1, 2).

The splenials extend widely anteriorly and reach anteriorly the level of the interalveolar space between the ninth and the tenth dentary alveolus (varying according to the size and age in dyrosaurids (JOUVE, pers. obs.)). Thus, they meet along a symphysis. In anterior direction, both splenials tapers to a sharp wedge between both dentaries. Posteromedially, the splenials end at about mid length between the last dentary tooth and the glenoid fossa, anterior to the external mandibular fenestra (Pl. 2, Figs. 3, 4).

The angular extends along the posterior fourth of the mandible. Its ventral margin is convex. In ventral view, the angular ends anteriorly with a ventral process that reaches the level of the posteriormost dentary tooth.

Posteriorly, the angular constitutes the ventral margin of the retroarticular process and half of its height in lateral view (Pl. 2, Figs. 1, 2). It extends to the posterior end of the retroarticular process.

The surangular reaches anteriorly the posteriormost dentary alveolus with a thin dorsomedial process. The anterodorsal margin of the surangular bears two occlusal pits for the two posteriormost maxillary teeth. The surangular forms the lateral half of the glenoid fossa, and in the retroarticular process its suture with the articular curves laterally. The surangular is posteriorly long, narrow and faces dorsolaterally on the retroarticular process. Lateral to the glenoid fossa, it bears a laterally oriented longitudinal rim. The posterior part of the rim bears a large foramen aereum (Pl. 2, Figs. 5, 6).

The medial half of the glenoid fossa is formed by the articular. The articular bears an anteromedial process that gives the glenoid fossa a posteriorly concave anterior margin (Pl. 2, Figs. 5, 6). This process continues in a narrow lamina that reaches anteroventrally toward the medioventral margin of the mandible. The articular forms all of the medial part of the retroarticular process. Its medial wing is in ventral position posterior from the joint, at the same level as the ventral margin of the retroarticular process. This medial wing forms an 'L'-shaped transverse cross-section (Pl. 2, Figs. 3, 4).

No trace of the coronoid is preserved.

Dentition – The teeth are homodont, conical and slender. In labial view, the teeth are slightly curved posteriorly distally and end with an acute apex (Pl. 1, Fig. 6). The first to eleventh dentary teeth have a cylindrical cross section. The posterior dentary and maxillary teeth are lateromedially compressed in cross-section. The roots of the teeth are not much wider than the tooth crowns. The teeth are divided into asymmetrical labial and lingual surfaces by well-developed mesial and distal carinae. The lingual surface of the tooth crowns have well-developed striae that run straight from the base to the dorsal third of the crowns (Pl. 1, Fig. 7). Striae are present on labial and lingual surfaces of the teeth (Pl. 1, Figs. 6, 7).

The size of the teeth decreases from front to back. The posterior teeth are more robust than the anterior and their lingual striations are very less marked or absent.

Axial skeleton – All preserved vertebral centra are weakly amphicoelous. The odontoid process is wedge-shaped in lateral view and tapers from dorsal to ventral to one third of its dorsal length. A well-developed diapophysis is anterodorsally situated at the lateral surface of the odontoid process. The parapophysis lies with its anterior half at the lateral surface of the odontoid process and with its posterior half at the lateral surface of the axis vertebral centrum (Pl. 3, Fig. 1). The axis vertebral centrum is hourglass-shaped in ventral view. A knob-like hypapophysis is positioned centrally in the posterior fourth of the ventral surface (LANGSTON, 1995). From the hypapophysis, a median and longitudinally oriented crest runs to the anterior margin of the ventral surface. The neurocentral

suture is in its anterior two-thirds slightly dorsally convex but curves ventrally in its posterior third. The dorsal margin of the neural arch inclines in a straight line from anterior to posterior for approximately 25 degrees and forms the neural spine in its caudal third.

The anterior and the posterior surface of the vertebral centra of the third to ninth cervical slightly converge dorsally (Pl. 3, Fig. 2-6). The anterior third of the ventral surface of the vertebral centra is strongly rugose. Whereas the third cervical vertebra bears a hatchet-shaped hypapophysis in the anterior third of the ventral surface of the centrum, at the fourth and fifth cervical the hypapophysis is replaced by a rugosity (LANGSTON 1995). The hypapophysis of the sixth cervical forms a low, sharp crest in the posterior third of the ventral surface of the centrum. At the seventh and eighth cervical, the hypapophyses are low crests that continue from the anterior half of the ventral surface of the centrum posteriorly (Pl. 3, Fig. 4, 5). The hypapophysis of the ninth cervical projects ventrally from the anterior half of the vertebral centrum (Pl. 3, Fig. 6, STORRS, 1986). The anterior margin of the hypapophysis is weakly convex and rugose, and the posterior margin is linear. The ventral margin of the hypapophysis is convex.

In lateral view, the parapophysis is displaced from a position anteroventrally at the lateral surface of the vertebral centrum to a position caudomedially at the lateral centrum surface between the third and the eighth cervical (Pl. 3, Fig. 1-5). The parapophysis of the ninth cervical overlaps with its dorsal fourth the neurocentral suture. The ventral margin of the diapophysis of the third and fourth cervical is formed by the vertebral centrum. From the fifth cervical on the diapophysis lies directly dorsally to the neurocentral suture and the parapophysis.

The preserved part of the neural spine of the third cervical is positioned in the posterior half of the neural arch (Pl. 3, Fig. 1). The neural spine is rod-like and caudodorsally directed. The neural spine of the sixth cervical is straight and dorsally directed. The neural spines of the seventh and eighth cervical are slightly dorsocaudally directed and possess a weakly convex anterior and a weakly concave posterior margin, and a convex, slightly broadened dorsal margin. The height of the neural spines increases from the third to the ninth cervical vertebra (Table 1).

In lateral view, the anterior and posterior surface of the dorsal vertebral centra diverge dorsally. The preserved last presacral possesses a rugose posterior surface from which the left and right lateral fourth are bent caudolaterally. The second prothoracic bears a large hypapophysis similar in outline to the hypapophysis of the ninth cervical (Pl. 3, Fig. 7). The last preserved hypapophysis is at the first thoracic vertebra and it is positioned posteromedially at the ventral surface of the vertebral centrum and possesses a strongly convex ventral margin. The lateral surfaces of the thoracics without hypapophyses converge strongly in ventral direction so that the ventral surface is reduced to a rounded crest.

The parapophysis of the second prothoracic overlaps

with its dorsal third the neurocentral suture, whereas at the first thoracic, the parapophysis lies completely at the neural arch. From at least the fourth thoracic, parapophysis and diapophysis are united in a transverse process. Remarkably, the dorsals have a large articular surface for the elastic ligament that forms a deep groove in the ventral two thirds of the anterior and posterior margin of the neural spines (Pl. 3, Fig. 10).

The neural spines of the dorsals are slightly posterodorsally bent (LANGSTON, 1995) and decrease in height from the 2nd prothoracic to the 2nd thoracic (Pl. 3, Fig. 9, Table 1). The anterior margin of the spine is slightly convex and the posterior margin is slightly concave and broadened. The strongly broadened dorsal margin of the neural spines of the second prothoracic and the first thoracic are slightly convex. The anterior margin of the neural spines of the fourth and fifth thoracic curves modestly to the broadened dorsal margin and the dorsal margin inclines in height from anterior to posterior for 20 degrees.

At the third caudal, the ventral surface of the vertebral centrum bears a posterior articular surface for the haemal arch. From the fourth caudal in the anterior and posterior fourth of the ventral surface, articular surfaces for the haemal arches are developed. Between two lateral and longitudinal ridges, the ventral surface of the vertebral centrum is concave (STORRS 1986).

The second to fourth caudal possess caudal ribs that are positioned directly dorsal from the neurocentral suture at the neural arch. The caudal ribs are in dorsal view sword-shaped with a convex anterior and a strongly concave posterior margin. A transverse process is preserved at the sixth to seventeenth caudal. The transverse process lies medially at the lateral surface of the neural arch at the sixth caudal, and it is displaced into the caudal half in the more terminal caudal vertebrae. The preserved caudals without transverse process exhibit a rounded crest in the medial third at the lateral surface of the neural arch. The pre- and postzygapophysis is completely reduced and a rod-like process from the twelfth caudal. The neural spines of the second to sixth caudal are dorsally directed (Pl. 3, Fig. 11) whereas those of the terminal caudals are rod-like with a wide dorsal part and caudodorsally directed (Pl. 3, Fig. 13, LANGSTON, 1995). The neural spines increase in height until the sixth caudal (Table 1, Pl. 3 Fig. 11-13).

The second cervical rib (Pl. 4, Fig. 1,2; Table 2) is as long as the odontoid process plus axis. The capitulotubercular incision is v-shaped. The third to seventh cervical ribs (Pl. 4, Fig. 3-6) are one fifth longer than the vertebral centrum (Table 2). From the third to the seventh cervical rib, the part of the costal body posterior to the tuberculum decreases in length. The ventral margin of the rib is slightly convex medially and the lateral surface is centrally depressed. At the fifth to seventh cervical ribs, the medial surface of the costal body is only slightly concave.

The costal body of the eighth cervical rib (Pl. 4, Fig. 7) is oriented in the vertical plane. The preserved thoracic ribs are bow-shaped with a strongly convex anterior and a

Table 2 — Measurements of the preserved ribs of the holotype of *Congosaurus bequaerti* DOLLO, 1914. All measurements are given in mm. Abbreviations for the distances: L cc, rib length; L pc; length of cranial process (only in cervical ribs); L cap, length of capitulum; L tub, length of tuberculum; H arc, height of haemal arch.

Specimen		L cc	L pc	L cap	L tub	H arc
No. 1856	axial rib	96		6	11	
No. 1864	right 3rd cervical rib	93	27	21	25	
No. 1861	left 3rd cervical rib	88	22		23	
No. 1858	right 4th cervical rib			20	29	
No. 1860	left 4th cervical rib	90	23		23	
No. 1862	right 5th cervical rib	85	32	14	17	
No. 1884	left 5th cervical rib			15	20	
No. 1863	left 6th cervical rib				29	
No. 1857	right 6th cervical rib	100	20	23	32	
No. 1883	right 7th cervical rib					
No. 1789	left 8th cervical rib	74		14	5	
No. 1797	left 9th cervical rib	65*		22	9	
No. 1799	left thoracic rib			21	7	
No. 1745	left thoracic rib	173		25		
No. 1743	left thoracic rib	241				
No. 1877	haemal arch	144				144
No. 1876	haemal arch	127				127

strongly concave posterior margin. The ventral third of the costal body is broadened. At the anterior thoracic ribs (Pl. 4, Fig. 8,9) the capitulotubercular incision is semi-circular.

From the few preserved haemal arches (Pl. 4, Fig. 10, 11), anterior elements are three times as long as the vertebral centra. A haemal arch probably from the region of the 20th caudal reaches three quarters of the length of the vertebral centrum. In lateral view, the neural arches are medially constricted, with the more posterior haemal arches having a greater degree of constriction. Starting from the haemal foramen, a deep groove runs ventrally at the anterior and posterior margin of the haemal arch. The ventral fourth of the haemal arch is in lateral view spatulate and rugose.

Appendicular skeleton — SWINTON (1950) incorrectly described the preserved right scapula (No. 1809) as a right ischium. Its anterior margin is strongly concave whereas its posterior margin is only weakly concave (Pl. 4, Fig. 12). The dorsal margin of the scapular wing is dorsally convex and rugose. The scapular neck reaches one third of the length of the scapular wing and is ante-

Table 3 — Measurements of the scapula, coracoid and ilium of the holotype of *Congosaurus bequaerti* DOLLO, 1914. All measurements are given in mm.

Specimen		Height	Corpus length	Proximal length	distal length
No. 1809	right scapula	241	51	114	185
No. 1811	right coracoid	192	23	86	55
		Height	Length	Length of acetabulum	
No. 1806	ilium	114	181	26	

roposteriorly oval in cross-section. The glenoid fossa of the scapula is caudoventrally directed and strongly concave. The acromion forms a strong, dorsoventrally directed bulge that divides the lateral surface of the scapular head into an anterior third and posterior two thirds. Anterior to the acromion lies a rough lateral tuberosity.

The coracoid (Pl. 4, Fig. 13) reaches four fifths of the scapular height (Table 3). The posteroventrally projecting glenoid process of the coracoid head bears a humeral articular surface that is slightly posteroventrally directed and kidney-shaped in outline (LANGSTON, 1995). A dorsoventrally oval coracoid foramen is positioned slightly anterodorsally from the centre of the coracoid head. The coracoid neck is rod-like with a nearly circular cross-section. The coracoid wing is hatchet-shaped. The ventral margin of the coracoid wing is convex and broadened.

The ilium (Pl. 4, Fig. 16, 17) has a convex dorsal margin that is broadened and strongly rugose. The dorsal margin of the ilium ends anteriorly with a narrow anterodorsal tubercle that is positioned dorsally to the sacral ribs (STORRS, 1986). Posterodorsally the ilium forms a broad caudal tubercle. The anterior margin of the ilium is strongly concave. The ventral margin of the ilium is drawn out into an anterior and a posterior peduncle between which the semicircular dorsal margin of the acetabular foramen is incised (STORRS, 1986). The anterior peduncle of the ilium bears an anteroventrally directed, oval, weakly convex and rugose ischiac articular surface. The posterior iliac peduncle has an ischiatic articular surface that is divided into an anterolaterally directed, dorsal part and a posteroventrally directed, rugose ventral part. The acetabular fossa is dorsally bordered by a strong, dorsally convex supraacetabular crest.

The proximal and distal extremities of the humerus (Pl. 4, Fig. 14, 15) are not twisted against each other. The humeral shaft is circular in cross-section. The humeral head ends dorsally with a convex articular surface

that bears a median, semispheroidal lateral glenoid tubercle. The bulge-like deltopectoral crest extends at the anterior surface of the humeral parallel to the lateral margin of the proximal humeral extremity (LANGSTON 1995). The deltopectoral crest ends distally in a strongly developed rugosity. Both condyles of the distal extremity of the humerus are divided from each other by a deep intercondylar sulcus.

The right ulna (Pl. 4, Fig. 20, 21) was described as a tibia by SWINTON (1950) and is preserved in two pieces. The ulnar shaft is circular in cross-section. The anterior condyle of the proximal head is one fourth wider than the posterior condyle. At the articular surface of the ulnar head, a median circular capitular fovea is developed. The distal extremity of the ulna ends with a distally directed projection that bears the carpal articular surface. The carpal articular surface is divided by a weak median sulcus into an anterior and a posterior part from which the posterior part is a half wider than the posterior one.

In contrast to SWINTON (1950), who stated that a radius was not preserved, the head of the proximal extremity of the right radius (No. 1820) is present in *Congosaurus* (Pl. 4, Fig. 22). In proximal view, the radial head is lateromedially oval and centrally depressed. The ulnar articular surface curves from the posterior margin of the radial head to the posterior surface of the proximal extremity.

The radiale (Pl. 4, Fig. 25, Table 4) reaches one fourth of the ulnar length. The shaft of the radiale is constricted.

The femur is curved sigmoidally and one tenth longer than the humerus (Pl. 4, Fig. 18, Table 4). The proximal and distal extremity of the femur are twisted against each other with an angle of 140 degrees. The femoral shaft is semi-circular in cross-section. The fourth trochanter is a prominent tuberosity positioned at the border between the medial surface of the proximal femoral extremity and the posterior surface of the femoral shaft. A shallow, proximodistally oval paratrochanteric fossa is developed anterior to the fourth trochanter. Both condyles end with a tip at the posterior surface of the distal extremity and are separated from each other by an intercondylar fossa with a median rugosity.

The tibia, described by SWINTON (1950) as an ulna, reaches four fifths of the length of the femur (Pl. 4, Fig. 19, Table 4). The tibial shaft is circular in cross-section. The proximal extremity of the tibia is bent from the tibial shaft in a posterior direction and reaches twice the width of the shaft. The distal extremity of the tibia is one tenth wider than the tibial shaft. The astragalar articular surface is divided by an anteriorly positioned sulcus into a longer medial and a shorter lateral hemicondyle.

The shaft of the fibula is long and slender with an oval cross-section (Pl. 4, Fig. 23). A prominent fibular trochanter is developed at the anterolateral surface of the fibular shaft directly distally from the fibular head. The fibular head is irregularly rounded in proximal view and forms an anterolateral projection to the anterolateral surface of the fibula. The distal extremity of the fibula is not preserved.

Table 4 — Measurements of the limb bones of the holotype of *Congosaurus bequaerti* DOLLO, 1914. All measurements are given in mm.

Specimen		Length	proximal width	corpus width	distal width
No. 1813	right humerus	289	85	33	81
No. 1818	right ulna	169	69	32	52
No. 1815	right femur	298	74	38	69
No. 1817	left femur	300	74	37	68
No. 1816	right tibia	214	60	29	48
No. 1831	carpal	18	21		
No. 1822	metapodial	36	14	11	21
No. 1823	metapodial	48	21	12	32
No. 1825	metapodial	55	22	13	33
No. 1826	metapodial			16	28
No. 1827	metapodial	51	14	10	19
No. 1835C	metapodial		16	10	
No. 1835A	phalanx	26	14	10	18
No. 1835B	phalanx	28	16	12	21
No. 1824	phalanx	20	15	12	15
No. 1832A	phalanx	13	8	6	
No. 1832B	phalanx	17	9	7	
No. 1832C	phalanx	13	8	5	
No. 1828	ungual phalanx	52	17		
No. 1829	ungual phalanx	38	14		
No. 1830	ungual phalanx	39	12		

The metacarpals and the preserved metatarsal of *Congosaurus* have a very similar morphology. These metapodials have a constricted shaft and a spatulate basis with a convex proximal margin. The dorsal and palmar surface of the distal condyle is rugose. The lateral margins of the metapodial head are strongly broadened and form a proximodistally oval area with a median circular depression. A carpal/tarsal articular surface is well developed and divided by a median indentation into a medial and a lateral condyle. The dorsal and palmar surface of the metapodial head is fairly roughened.

The phalanges have constricted shafts (Pl. 4, Fig. 26, 27). The distal condyles of the phalanges bear proximally a kidney-shaped, concave articular surface with a convex dorsal and a concave palmar margin. The phalangeal head is bordered by a strongly broadened lateral margin with a median circular depression. The carpal articular surface consists of a lateral and a medial condyle separated from each other by a medial condyle. The preserved unguals

are strongly curved longitudinally and possess a strongly convex dorsal and a strongly concave plantar margin (Pl. 4, Fig. 22). The unguals are proximally wide and taper to a distal tip.

Osteoderms — The dorsal osteoderms belong to a medial and a lateral longitudinal row as well as an accessory dorsal series. The medial dorsal osteoderms (Pl. 4, Fig. 30, 31) are rounded rectangular in outline and slightly vaulted externally (LANGSTON, 1995). The medial margin is delicately serrated. The anterior margin of the scutes is smooth but the posterior margin is serrated or roughly jagged. The anterolateral edge of these osteoderms forms a laterally projecting process that can reach one fifth of the transverse width of the scute. The external surface of the scutes is sculptured by a few deep oval pits, but the anterior tenth of the osteoderm bears a smooth articular surface. In external view, the lateral margin of the scute is depressed and separated from the remaining external surface by a sharp edge (Pl. 4, Fig. 30, 31).

The lateral dorsal osteoderms are rounded triangular to rounded square in outline with a medial margin that is linear and slightly serrated (Pl. 4, Fig. 32). The external surface of the osteoderms is sculptured by irregular, oval pits. In internal view, the medial margin of the osteoderms is strongly bevelled in a lateral direction (Pl. 4, Fig. 33). The lateral and the medial dorsal osteoderms overlap each other at their lateral and medial margin respectively.

The lateral margin of the lateral dorsal osteoderm with square outline is strongly serrated which indicates the presence of a second accessory osteoderm in these transverse rows. These second accessory dorsal osteoderms are probably similar in outline to the rounded triangular lateral dorsal osteoderms, but possess a serrated and not laterally bevelled medial margin. The accessory and the lateral osteoderms of the dorsal armour contact each other along a serrated suture.

The preserved osteoderms of the ventral armour are rectangular in outline (Pl. 4, Fig. 29). Their lateral margins are slightly serrated and their anterior and posterior margins strongly serrated. The external surface of the ventral osteoderms is sculptured with deep and rounded pits. The internal surface of the ventral osteoderms is covered by a meshwork of narrow standing, delicate striae that cross each other with acute angles. In addition to these osteoderms, several small accessory osteoderms, probably from the limb region, are preserved. These osteoderms have a very irregular, asteroidal outline and their external surface is slightly sculptured.

Discussion

Since its introduction in literature by DOLLO (1914), the validity of the genus *Congosaurus* was in dispute. After the description of *Congosaurus bequaerti* by DOLLO (1914) and SWINTON (1950), ARAMBOURG (1952) and ANTUNES (1964) discussed a lack of diagnostic features

to distinguish between *Congosaurus* and *Dyrosaurus*. As a result, the genus *Congosaurus* subsumed into synonymy by both authors. In a compilation about the distribution of dyrosaurid fossils in Africa, BUFFETAUT (1976) mentioned the genus *Congosaurus* as a synonym to *Hyposaurus*. These assignments were discussed again by BUFFETAUT (1980), who revised *Congosaurus bequaerti* and reassigned it to the genus *Hyposaurus* on the basis of mandibular characters. A new find of the Paleocene from Tilemsi in Mali (MNHN TGE 4032) was assigned to the species "*Hyposaurus*" (*Congosaurus*) *bequaerti* (BUFFETAUT, 1980).

The genus *Hyposaurus* was erected by OWEN in 1849 and comprises North American as well as North African species. In northern Africa, *Hyposaurus* was described together with several other genera in the Paleocene of Morocco, with *H. paucidens* (ARAMBOURG, 1952), and in the Paleocene of the Sokoto Province in Nigeria, with *H. wilsoni* and *nopscai* (SWINTON, 1950). The numerous genera from this late layer were revised by BUFFETAUT (1980), with new material from the Tilemsi Valley in Mali, and only two were regarded as valid. In North America only one species, *Hyposaurus rogersii*, is recog-

nised (DENTON *et al.*, 1997), but *Rhabdognathus* is probably present too (JOUVE, pers. obs.). These two genera, *Hyposaurus* and *Rhabdognathus* can be easily distinguished from each other by their rostrum length, which represents 73 % of the skull length in *Rhabdognathus* (JOUVE, pers. obs.) and only 66 % in *Hyposaurus rogersii* (JOUVE, pers. obs.). Unfortunately, both *Hyposaurus* and *Rhabdognathus* were insufficiently diagnosed by BUFFETAUT (1980), who in his emended diagnosis gave some imprecise and blurred characters for the genus *Hyposaurus*, as "a cross dentary section variable, generally wider than high, oval to circular...". For *Rhabdognathus*, BUFFETAUT (1980) described "a long and narrow snout and the mandibular symphysis higher than wide" as diagnostic characters.

To make the differences in the width/height ratio between *Hyposaurus* and *Rhabdognathus* more precisely visible, these ratios at any position in the symphyseal region of the mandible were displayed for various *Hyposaurus* and *Rhabdognathus* species from the Maestrichtian and Paleocene of North America, Morocco, Mali and Nigeria in a diagram (Fig. 3). The diagrams showed that *Hyposaurus* and *Rhabdognathus* are clearly separated

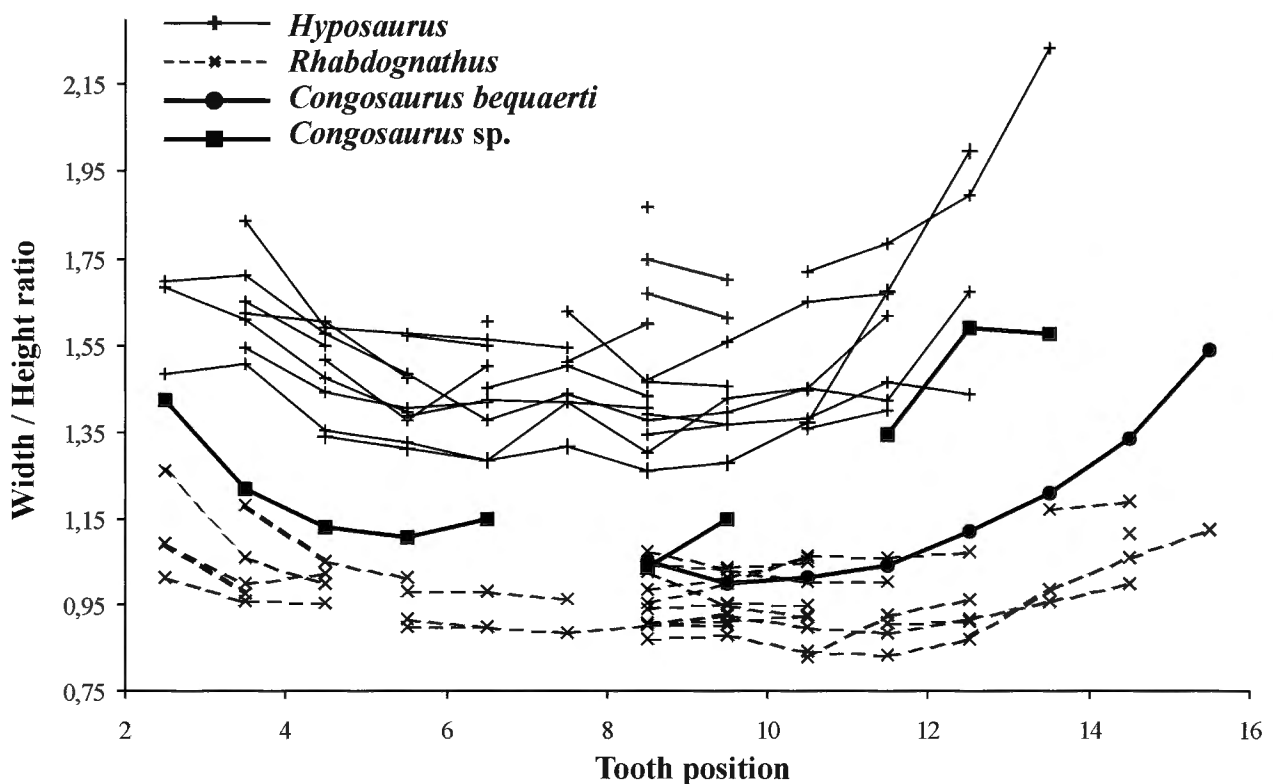


Fig. 3 — Mandibular proportions of *Hyposaurus*, *Congosaurus* and *Rhabdognathus*. The values show the width/height ratio of the mandible as taken from measurements between the teeth, according to their positions on the mandible. The material is from Mali (preserved in the MNHN), Nigeria (preserved in the NHM), and Angola (preserved in the MRAC); plus one mandibular fragment from North America (NJSM 10861, figured by DENTON *et al.*, 1997) and two from Morocco (preserved in the MNHN (*H. paucidens*, figured by ARAMBOURG, 1952); and in Geological Survey of the OCP, DEK-GE 1202).

from each other by their differences in the mandibular cross section: *Rhabdognathus* has a width-height ratio that is below 1.10 between the fourth and the thirteenth dentary alveolus, the mandibular symphysis region is therefore roughly as high as it is wide. In contrast, in *Hyposaurus* the mandibular symphysis width-height ratio exceeds a value of 1.25 – the mandibular symphysis region in this genus therefore is clearly wider than high.

Surprisingly, the holotype of *C. bequaerti* from Cabinda displays the same values as *Rhabdognathus* (Fig. 3). Also the width-height ratio of the mandibular symphysis of the Malian specimen of “*Hyposaurus*” *bequaerti* (MNHN TGE 4032) seems to be problematic. In this specimen, the mandibular width between the 4th and the 10th tooth is about equal to the height as it occurs in *Rhabdognathus*, whereas the mandible in this region is more flattened in *H. wilsoni*, *H. nopscai*, *H. rogersii* and the *H. paucidens* and *H. sp.* from Morocco (ratio superior to 1.25). In the posterior part of the mandible, the Malian “*H.*” *bequaerti* fits the values of *Hyposaurus*. However, the flattening of the posterior part of the mandible is in the holotype of *C. bequaerti* less important than in the Malian specimen and fits the values of *Rhabdognathus*.

In *Hyposaurus rogersii*, *nopscai* and *wilsoni* all dentary alveoli are circular in outline as it is the case in all other dyrosaurids, whereas the posterior dentary alveoli are laterally compressed in *C. bequaerti*. Moreover, in *H. rogersii*, some teeth bring a particular shape of their anterior carinae which is ventrolingually “twisted” (DENTON et al., 1997; JOUVE, pers.obs.). This characteristic is not observed on all the teeth of each specimen of the North American *Hyposaurus*, but it is very frequent in the Maastrichtian specimens, and, contrary to DENTON et al. (1997), have also been observed in some of the rare Paleocene forms (JOUVE, pers.obs.). In the Malian sediments, the teeth are extremely rare, and only known for one specimen (TGE 4373), exhibiting also this “twisted” carinae. In *Hyposaurus* from Morocco, the same condition is observed (JOUVE, pers. obs.). This “twisted” carinae is present in all *Hyposaurus* where the teeth are known, but is not developed at any teeth of *Congosaurus bequaerti*.

Furthermore, in *C. bequaerti*, the anterior process of the jugal extends anteriorly to reach at least the anterior end of the prefrontal. The prefrontal, in contrast to *C. bequaerti*, extends anterior to the anterior extent of the jugal in other known dyrosaurids, such as *Hyposaurus rogersii* (JOUVE, pers. obs.), *Dyrosaurus phosphaticus* (THÉVENIN, 1911; PIVETAU, 1935; BERGOUNIOUX, 1956; MOODY & BUFFETAUT, 1981; HUA, 1995), *Phosphatosaurus gavioloides* (BERGOUNIOUX, 1956; BUFFETAUT, 1978; MOODY & BUFFETAUT, 1981) and *Rhabdognathus sp.* (BROCHU et al., 2002). Likewise, the lachrymal in *C. bequaerti* is very long anteriorly and its contact with the nasal is more than twice the prefrontal-nasal suture, a proportion much more significant than observed in all other dyrosaurids. In the type species of *Hyposaurus*, (*H. rogersii*), which is the best known, the external man-

dibular fenestra forms a wide opening, contrary to the very modest one in the *C. bequaerti* mandible. *C. bequaerti* has at least 20 teeth in the premaxilla and maxilla, whereas *H. rogersii* has only 15 teeth in the upper jaw.

To summarize, *C. bequaerti* can be distinguished from all other valid *Hyposaurus* species (*Hyposaurus nopscai* and *wilsoni* from Mali and Nigeria, *H. paucidens* and sp. from Morocco, and from the type species, *H. rogersii* from North America), by a mandibular symphysis as wide as high, straight mesial and distal carinae, a strongly reduced external mandibular fenestra, a jugal extending anteriorly past the prefrontal and a lacrimo-nasal suture that is at least twice as long as the prefronto-nasal suture. Conversely, *Hyposaurus* can be diagnosed by the probably diagnostic characters of a mandibular symphysis wider than high and “twisted” anterior tooth carinae (in species where the teeth are known), but this will be the matter of a different paper (JOUVE, in prep.).

C. bequaerti has a similar rostrum length (65 % of the total skull length), as *H. rogersii* (66 %), in contrast to *Rhabdognathus rarus* (73 %). Even if the snout proportion is the same, the tooth number differs between *C. bequaerti*, which has 17 teeth anterior to the orbits, and *H. rogersii*, with only 13 teeth anterior to the orbits, and *R. rarus* having 25 teeth. *Congosaurus bequaerti* differs from *Hyposaurus* by its higher mandible, and from *Rhabdognathus* by its shorter snout.

Contrary to ARAMBOURG (1952) and ANTUNES (1964), *C. bequaerti* is also not a member of the genus *Dyrosaurus*, since its rostrum is much shorter (17 preorbital teeth; rostrum: 65 % of the total skull length) than the snout of *Dyrosaurus phosphaticus* (THOMAS, 1893) (23 preorbital teeth, and snout proportion at about 70 % (JOUVE, pers. obs.)).

It is therefore reasonable to retain DOLLO’s original genus *Congosaurus* for this species. The Malian specimen (TGE 4032) possesses a rostrum length and an anterior mandibular height like *Congosaurus bequaerti* and therefore may belong to the same genus. However, the flattening of the posterior part of the mandible makes it doubtful, if this individual belongs to the same species as *Congosaurus bequaerti*. This difference could be also an effect of an individual variation, but since no other specimen is known for comparison, it seems preferable to refer this specimen only as *Congosaurus sp.*

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Abbreviations of anatomical terms

Ang – angular; Art – articular; D – dentary; Emf – external mandibular fenestra; En – external nares; F – frontal; Fa – foramen aereum; Fo – foramen; Gc – glenoid cavity; J – jugal; L – lachrymal; Mx – maxilla; N – nasal; Npd – nasopharyngeal duct; Or – orbit; Pl – palatine; Pmx – premaxilla; Pnf – post-nasal fenestra; Prf – prefrontal; ?Pt – pterygoid; Rap – retro-articular process; Sa – surangular; Sof – suborbital fenestra; Spl – splenial; Ss – sulcus septalis.

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Explanation of plates

PLATE 1

Congosaurus bequaerti DOLLO, 1914

- Fig. 1, 2, 3 — holotype, MRAC 1741c, anterior extremity of the snout in dorsal, left lateral and ventral view.
 Figs. 4, 5 — holotype, MRAC 1741c, posterior view of the skull, anterior wall of suborbital cavity.
 Figs. 6, 7 — holotype, MRAC 1744, lingual and labial view of two mandibular teeth.

Scale bars represent 5 cm.

PLATE 2

Congosaurus bequaerti DOLLO, 1914, holotype, MRAC 1801

- Fig. 1, 2 — lateral view of the posterior part of the mandible.
 Fig. 3, 4 — medial view of the posterior part of the mandible.
 Fig. 5, 6 — dorsal view of the posterior part of the mandible.

Scale bar represents 5 cm.

PLATE 3

Congosaurus bequaerti DOLLO, 1914

- Fig. 1 — holotype, MRAC 1839 and 1879, lateral view of odontoid process plus axis.
 Figs 2, 3, 4, 5, 6 — holotype, MRAC 1840, 1871, 1869, 1872, 1873, lateral view of 3rd, 6th, 7th, 8th and 9th cervical.
 Fig. 7 — holotype, MRAC 1849, lateral view of 2nd prothoracic.
 Fig. 8 — holotype, MRAC 1854, lateral view of 1st thoracic.
 Figs 9, 10 — holotype, MRAC 1855, lateral and medial view of 5th thoracic.
 Figs 11, 12, 13 — holotype, MRAC 1852, 1892, 1895, lateral view of 6th, 9th and a terminal caudal.

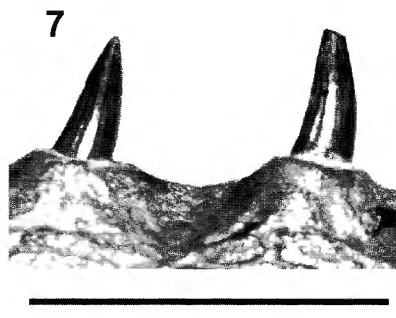
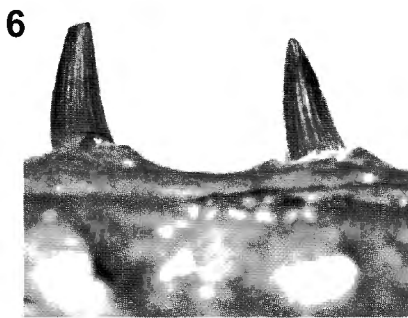
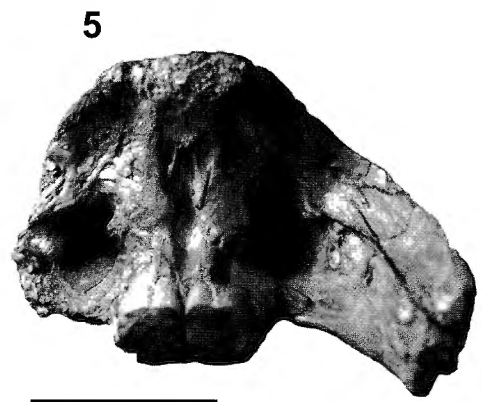
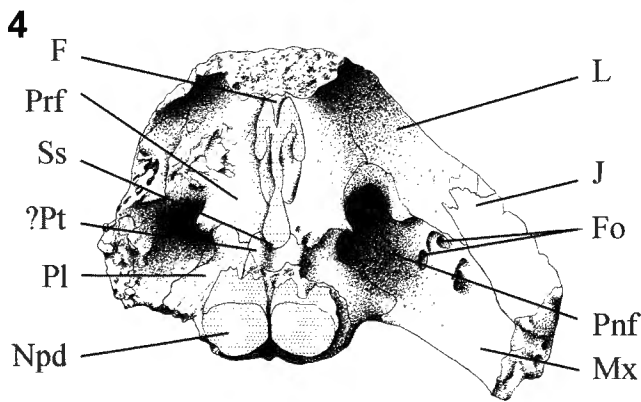
Scale bars represent 30 mm

PLATE 4

Congosaurus bequaerti DOLLO, 1914

- Figs. 1, 2 — holotype, MRAC 1856, lateral and medial view of axial rib.
Figs. 3, 4 — holotype, MRAC 1864, medial and lateral view of 3rd cervical rib.
Figs. 5, 6 — holotype, MRAC 1862, medial and lateral view of 5th cervical rib.
Fig. 7 — holotype, MRAC 1789, lateral view of 8th cervical rib.
Figs. 8, 9 — holotype, MRAC 1745, 1743, lateral view of thoracic ribs.
Figs. 10, 11 — holotype, MRAC 1881, 1876, lateral view of chevrons.
Figs. 12, 13 — holotype, MRAC 1809, 1811, lateral view of scapula and coracoid
Figs. 14, 15 — holotype, MRAC 1813, caudal and cranial view of humerus.
Figs. 16, 17 — holotype, MRAC 1806, lateral and medial view of ilium.
Figs. 18, 19 — holotype, MRAC 1817, 1815, lateral view of femur and medial view of tibia.
Figs. 20, 21 — holotype, MRAC 1818, lateral and medial view of ulna.
Fig. 22 — holotype, MRAC 1820, medial view of radius.
Fig. 23 — holotype, MRAC 1814, lateral view of fibula.
Fig. 24 — holotype, MRAC 1819, ventral view of radiale.
Figs. 25, 26 — holotype, MRAC 1823, dorsal and ventral view of phalanx.
Fig. 27 — holotype, MRAC 1828, lateral view of unguis phalanx.
Fig. 28 — holotype, MRAC 1906, external view of ventral osteoderm.
Figs. 29, 30 — holotype, MRAC 1954,1960, external view of dorsal osteoderms of the medial longitudinal row. Arrows indicate anterior direction.
Figs. 31, 32 — holotype, MRAC 1959, external and internal view of dorsal osteoderm of the lateral longitudinal row. Arrows indicate anterior direction

Scale bars represent 20 mm.



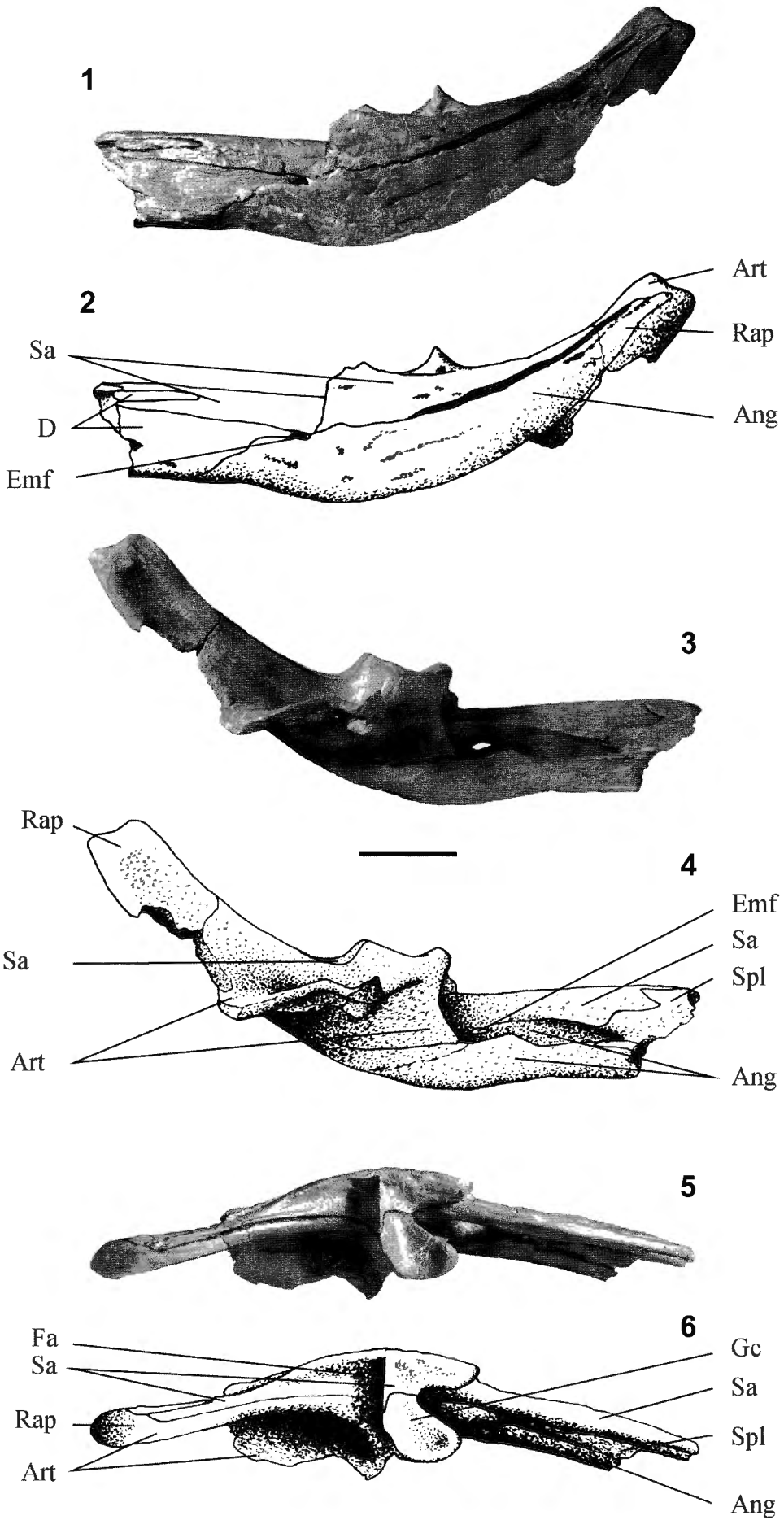


PLATE 2

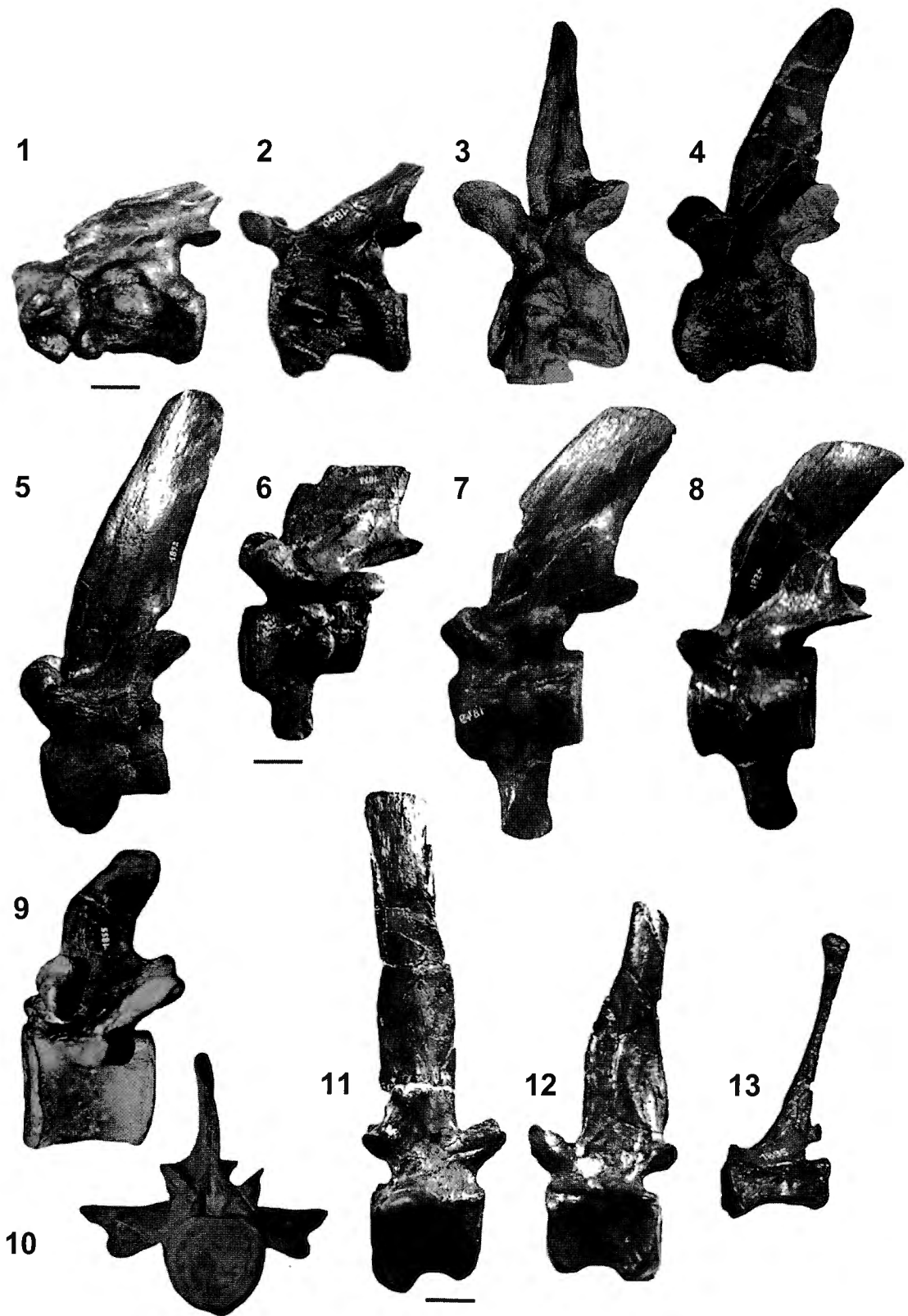


PLATE 3

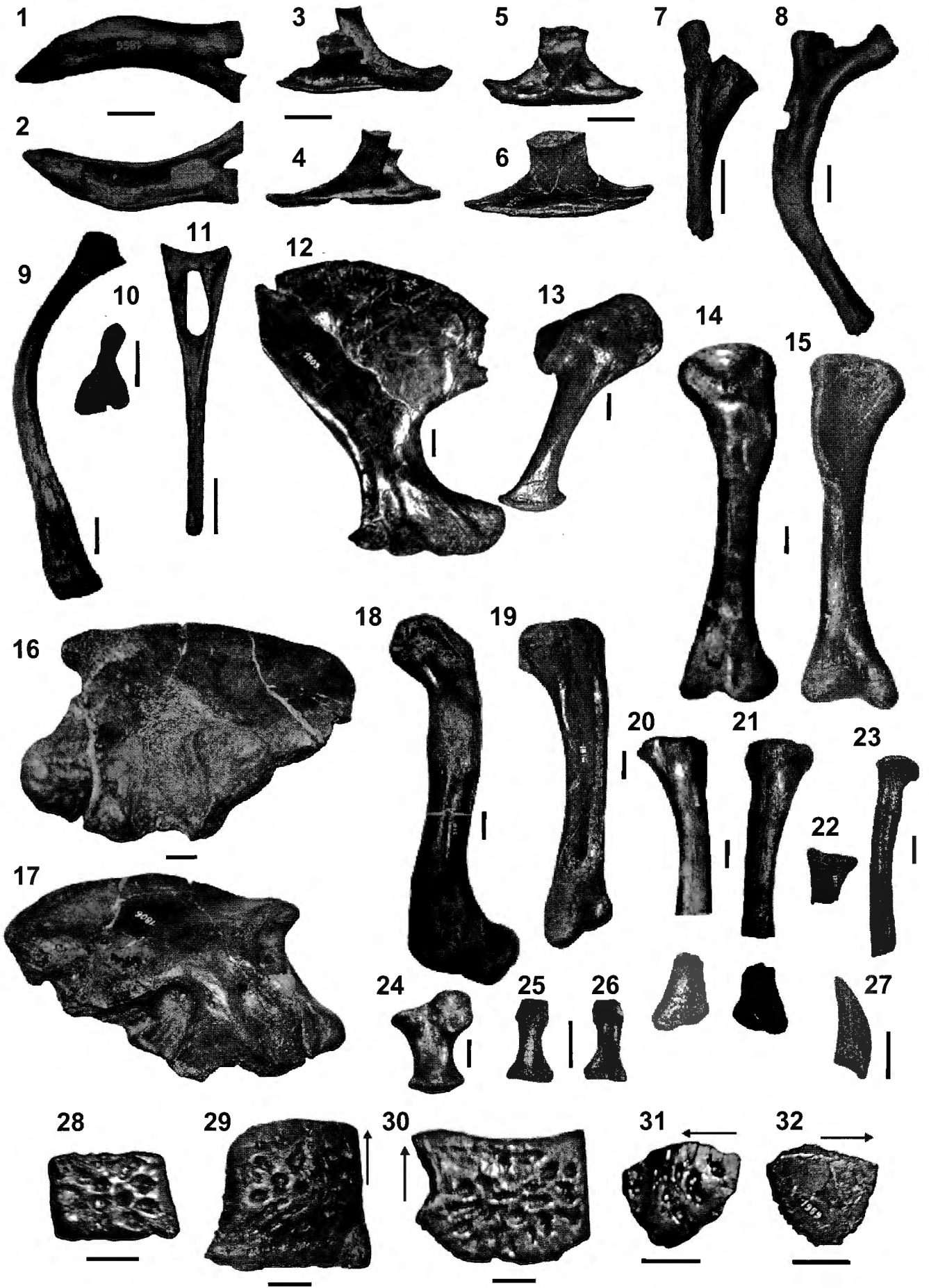


PLATE 4