GIRAFFOIDS FROM THE SIWALIKS OF PAKISTAN –

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Abstract: Although today they occur in Africa, during the Miocene Giraffoids were widespread in Eurasia. We describe the giraffoid faunas found in the Siwaliks of Pakistan. These faunas are extremely rich and provide with several new giraffoid taxa that are morphologically different to what taxa known before and give new insights in the taxa. Non-Siwalik localities that contribute key information are: Fort Ternan, Kalodirr, Tung Gur, Gebel Zelten, Gebel Hamrin and Bou Hanifia. (1) The Palaoemerycidae are distinct with ossicones and an occipital horn. The list of taxa includes five new palaeomerycids: *Tauromeryx canteroi* nov. sp., *Charis gratia* nov. gen. sp. nov., *Fovea fossata* nov. gen. sp. nov, *Goniomeryx flynni* gen. nov. sp. nov., and *Lateralia morgani* nov. gen. nov. sp. nov.; (2) new climacoceratids: *Vittoria soriae* gen nov. sp nov. *Orangemeryx badgleyi* nov. sp. We also define two new ranks within the Climacoceridae family: the Climacocerinae and the Prolibytheriinae. (3) Preliminary systematics suggest that Giraffidae can be subdivided into two clades: the long and the short neck groups. The Siwaliks sample a total of twelve different giraffids: *Progiraffa exigua*, Giraffokeryx *punjabiensis*, *Ua pilbeami*, *Orea leptia*, *Injanatherium hazimi*, *Giraffa punjabiensis, Giraffa sivalensis*, *Decennatherium asiaticum*, *Bramatherium megacephalum*, *Bramatherium perminese*, *Bamiscus micros*, and *Sivatherium giganteum*. *Palaeotragus germanii* and *Bohlinia tungurensis* are new determinations. Progiraffinae and Bramatheriinae as new subfamilies. The subfamilies of

Giraffidae seem to hold as isolated evolutionary silos. They are: Progiraffinae, Giraffokerycinae, Okapiinae, Bohlininae, Giraffinae, Palaeotraginae, Samotheriinae, Bramatheriinae and Sivatheriinae. It is hard to connect these subfamilies as they most appear around 15 Ma.

Italiano Riassunto: Sebbene oggi siano presenti in Africa, nel Miocene i Giraffoidi erano diffusi in Eurasia. Descriviamo i taxa giraffoidi trovati nei Siwalik del Pakistan. Queste faune mioceniche sono estremamente ricche e forniscono numerosi nuovi taxa di giraffoidi che sono morfologicamente diversi da quanto noto e forniscono nuovi spunti sui taxa già conosciuti. Fort Ternan, Kalodirr, Tung Gur, Bou Hanifia, Gebel Hamrin and Gebel Zelten sono ulteriori località in cui gli esemplari contribuiscono alla Siwalik species (1) I Palaoemerycidae sono distinti con ossiconi e corno occipitale. L'elenco dei taxa comprende cinque nuovi paleomericidi: Tauromeryx canteroi nov. sp., Charis gratia nov. gen. sp. nov., Fovea fossata nov. gen. sp. nov, Goniomeryx flynni gen. nov. sp. nov., e Lateralia morgani nov. gen. nov. sp. nov.; (2) nuovi climacoceratidi: Vittoria soriae gen nov. sp nov. Orangemeryx badgleyi nov. sp. Definiamo inoltre due nuovi ranghi all'interno della famiglia dei Climacoceridae: i Climacocerinae e i Prolibytheriinae. (3) La sistematica preliminare suggerisce che i Giraffidae possono essere suddivisi in due cladi: i gruppi a collo lungo e quello a collo corto. I Siwalik campione di un totale di dodici diversi giraffidi: Progiraffa exigua, Giraffokeryx punjabiensis, Ua pilbeami, Orea leptia, Injanatherium hazimi, Giraffa punjabiensis, Giraffa sivalensis, Decennatherium asiaticum, Bramatherium megacephalum, Bramatherium perminese, Bamiscus micros e Sivatherium giganteum. Palaeotragus germanii e Bohlinia tungurensis sono nuove determinazioni. Classi Progiraffinae e Bramatheriinae novae. Le sottofamiglie dei Giraffidae sembrano costituire silos evolutivi isolati. Essi sono: Progiraffinae, Giraffokerycinae, Okapiinae, Bohlininae, Giraffinae, Palaeotraginae, Samotheriinae, Bramatheriinae e Sivatheriinae. È difficile collegare queste sottofamiglie poiché compaiono principalmente intorno al 15 milioni di anni fa.

Français Résumé : Bien qu'ils soient aujourd'hui présents en Afrique, les giraffoïdes étaient répandus en Eurasie au Miocène. Nous décrivons les faunes de girafoïdes trouvées dans les Siwaliks du Pakistan. Ces faunes sont extrêmement riches et fournissent plusieurs nouveaux taxons de girafoïdes qui sont morphologiquement différents des taxons connus auparavant et donnent de nouvelles informations sur les taxons. Les localités non-Siwalik qui fournissent des informations clés sont : Fort Ternan, Kalodirr, Tung Gur, Gebel Zelten, Gebel Hamrin et Bou Hanifia. (1) Les Palaoemerycidae se distinguent par des ossicônes et une corne occipitale. La liste des taxons comprend cinq nouveaux paléomerycidés : Tauromeryx canteroi nov. sp., Charis gratia nov. gén. sp. nov., Fovéa fossata nov. gén. sp. nov., Goniomeryx flynni gen. nov. sp. nov., et Lateralia morgani nov. gén. nov. sp. nov.; (2) nouveaux climacocératidés : Vittoria soriae gen nov. sp nov. Orangemeryx badgleyi nov. sp. Nous définissons également deux nouveaux rangs au sein de la famille des Climacoceridae : les Climacocerinae et les Prolibytheriinae. (3) Une systématique préliminaire suggère que les Giraffidae peuvent être subdivisés en deux clades : les groupes à cou long et court. Les Siwaliks échantillonnent un total de douze girafes différents : *Progiraffa exigua, Giraffokeryx punjabiensis, Ua pilbeami, Orea leptia, Injanatherium hazimi, Giraffa punjabiensis, Giraffa sivalensis, Decennatherium asiaticum, Bramatherium megacephalum, Bramatherium perminese, Bamiscus micros* et *Sivatherium giganteum. Palaeotragus germanii* et *Bohlinia tungurensis* sont de nouvelles sous-familles. Progiraffinae et

Bramatheriinae sont nouveaux catégories. Les sous-familles de Giraffidae semblent constituer des silos évolutifs isolés. Ce sont : les Progiraffinae, les Giraffokerycinae, les Okapiinae, les Bohlininae, les Giraffinae, les Palaeotraginae, les Samotheriinae, les Bramatheriinae et les Sivatheriinae. Il est difficile de relier ces sous-familles car elles apparaissent pour la plupart vers 15 Ma.

INTRODUCTION

The base of all zoological investigations are the new data and the resulting new names. Establishing that base is critical for future research in animal diversity and paleoecology. This study provides such a base. The Siwalik formations found in the Indian Subcontinent consist of Miocene to Pleistocene fluvial sediments that were deposited in a sequence of basins located along the southern edge of the collision zone between Asia and peninsular India. These sediments are characterized by their thickness and abundance of fossils, including a varied collection of terrestrial and freshwater vertebrates. As a result, they have captured the attention of scientists for more than 170 years (Barry et al., 2013). Additional localities are necessary and key to the Siwalik study. The major ones are: Fort Ternan, Kalodirr, Tung Gur, Gebel Zelten and Bou Hanifia.

They are divided into three different parts: The Lower Siwaliks are the older, and include the Chinji Formation, which is mainly Middle Miocene in age, and the underlying Kamlial Formation which extends into the Early Miocene; the Middle Siwaliks are mostly Late Miocene in age and are comprised by the Dhok Pathan Formation and the underlying Nagri Formation and is where we found a high abundance of giraffoids. Finally, the Upper Siwaliks correspond to the layers that contain the Plio-Pleistocene levels (Flynn et al., 2013). In the upper layers the giraffoid diversity is low.

The Siwalik giraffids first came to knowledge thanks to the expeditions of Falconer and Cautley during the 1830's and Pilgrim during the 1900s.There provided with several examples of fossil giraffids like *Giraffokeryx punjabiensis* and *Sivatherium giganteum*, but most of the giraffids found were described based on very fragmentary or/and undiagnostic remains (e.g. *Progiraffa exigua*, *Giraffa priscilla*, *Giraffa sivalensis*) (Falconer and Cautley, 1836; Pilgrim, 1908, 1911).

Here we describe the material collected by the Yale/Harvard Geological Survey of Pakistan during the decades of the 1970s-90s, led by David Pilbeam, John Barry, Michèle Morgan, Larry Flynn, Mahmood Raza and others. These materials have accurate chronological and stratigraphic data that help with the interpretations and show us a highly rich continental faunas in which giraffoids where both abundant and morphologically diverse (Table 1).

MATERIAL AND METHODS

Material is temporarily deposited at the Peabody Museum of Harvard – It is a Yale/ Harvard and Geological Survey of Pakistan collection from 1976 to 2011. The figures show the

new taxa and a review of key older taxa. The study is a data base that will be used in the future. Ma is mega-anum – a million years.

ABBRAVIATIONS:

AMNH American Museum of Natural History, New York; GSI (IM) Indian Museum in Calcutta; MCZ, Museum of Comparative Zoology at Harvard, Cambridge; MNHNP, Museum national d'Histoire naturelle de Paris; NHM, Natural History Museum London; NHMBa, Natural History Museum of Basel; MNCN, Museo Nacional de ciencias naturales Madrid; YGSP, Yale-Geological Survey of Pakistan collections Islamabad; YPM, Yale Peabody Museum New Haven.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen 1848

Suborder Ruminantia Scopoli 1777

Infraorder Pecora Linnaeus, 1758

Superfamily Giraffoidea Simpson 1931

Pecoran ruminants with ossicone type horns. It includes three families: Palaeomerycidae, Climacoceridae and Giraffidae. Their ossicones are separate ossifications above the frontal bone. They appear as distinct little cups above the frontal in fetal life. They eventually fuse in older age to the frontal. Ossicones are commonly covered by skin which is sometimes keratinized by the apex (*Giraffa*). Ossicones can be bare at the apex and dead bone there in *Okapia* and *Samotherium*. The integument retreats and exposes the apical bone (*Okapia*). Rarely an ossicone is made from keratin instead of bone occur in *Okapia*.

Family Palaeomerycidae Lydekker, 1883

Palaeomerycids are Old World giraffoids that appeared during the early Miocene. They are characterized for the presence of frontal ossicones as in Giraffidae and an additional occipital horn, convergent but not related to the one of the north American Dromomerycidae. The confusion of dromomerycids with palaeomerycids is widespread. The dromomerycids have horns of frontal origin not ossicones. The palaeomerycids have ossicones. They both share the convergence of an occipital horn. For reference see Prothero and Litter (2007; Astibia and Morales 2006; Sánchez et al. 2015; Costeur et al. 2015).

Tauromeryx canteroi nov. sp.

Holotype- YGSP 42343, two occipital horn fragments belonging to the same individual.

Type locality - Y0502.

Age- 11,951-11,991 Mya.

Etymology- *canteroi*-Named after Enrique Cantero, preparator at the MNCN.

Diagnosis- The ossicones above the orbits are thin and long and slender curving gently back. The grooving is minimal. The horns are at the occipital edge. They are broken off, but the base is wide, and they seem to thin abruptly. They are deeply grooved. The occipital surface is remarkably flat with no details of nuchal ligament. There is distortion and the left horn is oriented more lateral than the other. The radius (Y GSP 26792) is much shorter than the metacarpal. This is the only ruminant with such a specialization (If the two specimens belong to the same individual – (J. C. Barry personal communication claims they are). The astragalus has a well-developed head with distinct ridges. Figure 1. Astibia et al. (1998) described a *Tauromeryx* specimen. It is similar to the current species but differs in the horn morphology. Fig. 1.

Dimensions: Y 42343: width and length 3.1? x 3.65; 17393 horn above orbit Y 17393 width at base the base it is 2.92 x 1.60 cm and the preserved length is 13.45 cm. That is not along the curve, which would be longer.

Charis gratia nov. gen. nov. sp.

Holotype- Y GSP 30933, partial skull, detached ossicone and maxillary fragments.

Type locality – Y0691.

Age- 13,032-13,137 Ma.

Etymology- Charis-Named after the ancient Greek muse Haris or Charis – a muse for grace, beauty and life. – as in Charming. Gratia-means thankful as for the finding of a skull in the Siwaliks is rare.

Diagnosis- The braincase is crushed lateromedially. The calvaria is flat and there are no parietal sinuses. The ossicone with surface with smooth longitudinal ridges. Blunt apex. Oval-triangular cross-section. The calvaria is flat and there are no sinuses. The ossicone is a typical shape similar to the *Okapia*. It gently curves back it is triangular in cross section with no canals. The apex is a simple round in from. The occipital has two very deep pits for the funicular ligament. The bullae are oval and large. The occipital condyles are slight merging in the median plane. The posterior basioccipital tuberosities are strongly lateral thin ridges. The anterior basioccipital tuberosities are large ovals. The glenoid fossae are large. There is a *Palaeomeryx*-fold in the molars. The four cusps are separate. The buccal cingulum is very small. The lingual cingulum is also very small and there are no basal pillars. There was an occipital horn which is broken off. The edge of the occipital shows this by the presence of two strong supporting ridges Figures 2 and 3. This species is similar to *Palaeomeryx* but it differs in the occipital horns. Similar ossicones were found at Kalodirr (undescribed). Fig. 2 and 3.

Dimensions: Y 21897: ~3.45 x ~ 2.55 (cm); Y 23715 is from Locality Y 311.

Fovea fossata nov. gen. nov. sp.

Holotype- Y GSP 21897, detached ossicone.

Other specimens- Y GSP 23715, detached ossicone from locality Y0311.

Type locality- Y0504.

Localities- Y0504 (11.6-11.6 Ma.), Y0311 (10,026-10,100 Ma.)

Age- 10.0-11.6 Ma.

Etymology- *Fovea*- is pit as in the eye, *fossata* is fossa.

Diagnosis-species with small ossicones of triangular short shape. They curve inward as most other palaeomerycid ossicones. Blunt apex. Oval cross-section. Remarkable ornamentation in the form of little fossae that cover the whole surface of the ossicone. They are slightly similar to *Triceromeryx pachecoi* in having a messy surface. Figure 4. This species resembles *Triceromeryx* in having a disorganized horn surface (Crusafont 1952).

Dimensions: YGSP 21897 basal length 4.4 mm height 6 mm. YGSP 23715 basal width 3 mm available height 6 mm. Fig. 4.

Goniomeryx flynni nov. gen. nov. sp.

Holotype- Y GSP 30608, detached ossicone.

Other specimens- Y GSP 31810, detached ossicone from locality Y0750.

Type locality- Y0758.

Localities- Y0758 (13,940-14,161 Ma.), Y0750 (12,740-12,758 Ma.)

Age- 12.7-14.1 Ma.

Etymology- Gonio-is angle as the ossicone is angled, -meryx ruminant - flynni - the trivial name after Larry Flynn who has worked in the Siwaliks.

Diagnosis- Ossicones with thin longitudinal lines in the surface and a thin oval cross section. Remarkable lateral facet at the ossicone base with a smooth surface. The holotype has a surface under the ossicone showing that it was detached in early life. The second specimen is fused to the frontal. The specimens have a strongly angular outline with two keels a mid-anterior keel the abruptly turns laterally at the base and a posterior keel which terminates 20 mm above the base. The pedicle is absent but in YGSP 31810 a little excavation with a smooth surface is visible posteriorly (like a pedicle). The ossicone is above the orbit. The orbit is typical with no specializations. There is no internal canal. The shaft of the ossicone thins abruptly. Figure 5.

Dimensions: YGSP 30608 is 35.7 X 34.4 mm; YGSP 31810 is 39.3 X 34.0 mm.

Lateralia morgani nov. gen. nov. sp.

Holotype- Y GSP 30593, ossicone and skull fragment.

Type locality- Y0500.

Age- 12- 12.1 Ma.

Etymology- *Lateralia*- refers to the lateral position of the ossicones, -*morgani* named after Michèle Morgan who has worked in the Siwaliks.

Diagnosis- The smallest palaeomerycid. The ossicone is situated laterally on the frontal behind the orbit. There is grooving on the ventral side the shaft which is straight. At the base there is a restricted sinus cranially. There are no keels and no canal internally. The lateral margin of the ossicone extends further inferiorly than the medial margin. It has a maximum length of 17.8 mm in antero-post direction. Figure 6.

Dimensions: Maximum length of 17.8 mm in antero-post direction. The width perp to the maximum length (not a cross section to max length but measuring maximum extent of ossicone in this orientation) is 15.9 mm. The width perp to the maximum length with medial point fixed at base of ossicone and lateral point measured in cross section to max length is 13.8 mm. It is possible that this taxon is related to *Orygotherium* as it is very small. But *Orygotherium* is known only from dentitions (Vislobokova 2004). A. Gentry has identified this specimen as a bovid. Fig. 6.

Family Climacoceridae Hamilton 1978

Climacocerinae new rank

Diagnosis- Taxa with ossicones that branch on the anterior part of the shaft superficially resembling those of deer. Most taxa form horn shafts rounded cross sections and do not taper going up from the base. One taxon had no branches. Another taxon had complex flat horns with branches at the edge. The rounded horns had regular fine homogeneous grooving. Grooving may be hair embedded in the bone. The flat horns were smooth with vein impressions. The fusion of the ossicone to the frontal leaves no markings or sutures. The apices are pointy.

Vittoria soriae nov. gen. nov. sp.

Holotype- NHM M.26690 (identified as a palaeomerycid by Hamilton (1973) and a female *Prolibytherium* by Sánchez et al., 2010). Curated at the NHM (London).

Siwalik specimens- Y GSP 31790, ossicone shaft fragments (loc Y0747), Y GSP 102058, horn fragment (loc. Unknown).

Type locality-Gebel Zelten (Libya).

Localities- Y0747. 17.8-17.9 Ma.

Age-Lower Miocene.

Etymology- Vittoria- refers to the V shape of the cranial appendages. V signifies victory - as used by Churchill -*soriae*- Named after. Dolores Soria, the first female vertebrate paleontologist to study giraffids.

Diagnosis- A species with straight unbranching ossicones. There are no keels on the ossicones which curve gently inward. The central canal is large and extremely oval. There is a thin cortex. The Siwalik specimens have a longitudinal groove on one side. The skull roof is very thick. The surface of the ossicones has fine grooving which is due to the excellent preservation. We hypothesize that this is fossilized hair embedded into the surface. The slope angle of the appendage relative to the cranial roof is 40°. Described as a female Prolibytherium by Sánchez et al. (2010). It differs from *Prolibytherium* in numerous horn characters. Figures 7 and 8. *Climacoceras* from the Miocene of Kenya has forked ossicones with small tines (MacInnes 1936; Hamilton 1978). The un-forked ones as (NHM M 26690) was published as a female *Prolibytherium* by Sánchez et al. (2010).

Dimensions: Holotype NHM M 26690 width at base 18 mm. We add specimens that might also be Vittoria in the sample: *Climacoceras* YGSP 31927 and YGSP 31790 both from the Chinji. Fig. 7 and 8.

Orangemeryx badgleyi nov. sp.

Holotype-Y GSP 23698.

Type locality- Y0666.

Age- 13.7-13.8 Ma.

Etymology- *badgleyi* - Named after Catherine Badgley who has worked in the Siwaliks.

Diagnosis- A base of a right ossicone and part of frontal. The surface is smooth There is a medial keel. Laterally the edge makes a flat surface which can be also considered as a broad keel. No sutures with the frontal are visible. The frontal sinus under the horn is well-developed. The sinus has several large bony cells in it. and is filled with mud. Figure 9. The current species is very similar to *Orangemeryx* (Morales et al. 1999). Fig. 9.

Dimensions: YGSP 23698: 4.15 x 3.65 (cm).

Family Giraffidae Gray 1821

Progiraffinae new rank

Progiraffa exigua Pilgrim, 1908

Holotype- Mandible with m2 and m3 (Pilgrim, 1908, Plate 1: fig. 1). Sind. Roo. Geol. Surv. Ind.- XXXVII. p. 165.

Type locality- Upper Nari beds in the Bugti Hills.

Age- Lower Siwaliks, Early Miocene.

Etymology- *Progiraffa* means early *Giraffa*, and *exigua* refers to the small size.

Diagnosis- Small giraffid. Brachydont dentition with rugose enamel, and bilobed canines with pointy larger medial lobe. Upper molars with distinct bifurcation of postmetaconule crista, postprotocrista and premetaconule crista. Anterolingual cingulum prominent. Lower molars with large metastylid well separated from metaconid, m3 with robust entoconulid, *Palaeomeryx* fold absent (modified after Pilgrim, 1911, and Barry et al., 2005). Figures 10, 11, 12.

Material: MT Y 24305 MT and Y 42342 MT are assigned to *Progiraffa*. MC 26709 and MT 4549 are also part of this taxon. Two astragali 41182 and DGK 12 and may belong to *Progiraffa*. Also, maxilla PSAP 312 and mandible PASP 41662 are *Progiraffa*. *Georgiomeryx georgalasi* skull (THB 30 MN5) form Thymiana Chios Island (de Bonis et al. 1997). Figures 1-, 11, 12, 12b.

Giraffokerycinae Solounias 2007

Giraffokeryx punjabiensis Pilgrim 1910

Holotype- a selected neotype AM 19475, a complete skull.

Paratypes-AMNH 19611, teeth; AMNH 19472, left maxilla with P3-M3; AMNH 19587, mandible right ramus with p2-m3. YGSP 19842 maxilla, 42433 astragalus, 29119 complete anterior pair of ossicones, 24306 complete metatarsal, 47198 ossicone juvenile, 1194, 51470, 42426, 27761, ossicones, 5361 m3, 8101 m1-m3.

A sample of smaller individual: MC YGSP 26790, 4505 MC 24342; 20416 RMC.

Type locality- 1,000 feet below the Bhandar bone bed, and one mile south of Nathot in the Punjab. Middle Siwaliks.

Age- Lower-Middle Siwaliks. Middle Miocene.

Etymology- *Giraffokeryx*- giraffe horn - *punjabiensis*- from the Punjab.

Diagnosis- Four ossicones. Anterior pair more anterior than the orbit and fused at the base. Posterior ossicones are more posterior than the orbit grooved with simple apex. At the base posterior ossicones have a disorganized bony mass. The ossicones are deeply grooved. No sinuses in skull. Upper premolars shortened. Palatine indentation posterior. Masseteric fossa small. Metapodials long and slender. Less elongated upper premolars than *G. primaevus*.

The original sample is mandibular fragments in Calcutta some of which are figured in Pilgrim 1911 without him selecting a type. A p4 stands out and is characteristic (Pilgrim 1911 – plate II fig. 1). Later Colbert and Brown described a nearly perfect skull AMNH 19311. Colbert 1935 selected an upper M3 as a type from the Pilgrim sample. This is not diagnostic. We take

the skull AMNH 19311 as a lectotype/neotype. Localities are the Chinji Formation for all material.

Four ossicones. Anterior pair more anterior than the orbit and fused at the base. Posterior ossicones are more posterior than the orbit deeply grooved with simple apex. The base of the posterior ossicones forms a lump of disorganized bone. Except for the basal disorganized bone, the shafts of the four ossicones are very similar. No sinuses in calvaria. Upper premolars shortened. Palatine indentation positioned posterior. Masseteric fossa small. Cervicals not short but not long either. Metapodials long and slender. Figures 13, 13b, 14, 15.

Dimensions: Metatarsal YGSP 24306 (456X32.6 mm), metatarsal YGSP 47187 (430X30), tibia YGSP 52472 (425X35 mm), radius YGSP 46575B (450X40 mm). Also see Colbert and Brown (1933) and Colbert (1935) for measurements. Fig. 13, 14, 15

Giraffokeryx primaveus from Fort Ternan. Metatarsal NHM M30210 (3108). Radius NHM M30215. C3 NHM M3078. Figure 13b.

Okapiinae Bohlin 1926

Ua pilbeami Solounias, Smith & Ríos, 2022

Holotype- Y GSP 28483, a partial skull with both ossicones, frontal, ethmoid, and left orbit preserved.

Other specimens- Y GSP 26847 ossicone fragment from locality Y 0691.

Type locality- Y0758 (13,940-14,161 Mya), Y 0691 (13,032-13,137 Mya).

Age- 13,032-14,161 Mya.

Diagnosis- *Ua pilbeami* shares with *Okapia* ossicones with an exposed apex and constriction, a large anterior frontal sinus, and a para-style on the upper pre-molars that is deeply separate from the meso-styles. The lower premolar anterior stylids and posterolingual conids are also deeply separated. It differs from *Okapia* in having long and grooved ossicones. The ossicones are slightly more anterior. In *Okapia* the metapodials are shorter. Figure 16 and 17.

Solounias N., Smith S. & Rios M. (2022).

Samotheriinae Hamilton 1978

Injanatherium Henitz and Sen 1981

Holotype: *Inajantherium hazimi* a skull in Pointers France from Gebel Hamrin Iraq. It was published without a number.

Injanatherium hazimi from the Siwaliks YGSP 8869; YGSP 24295; frontal with base of ossicone; YGSP 17891.

Diagnosis – Ossicones rounded smooth surfaced. Apex flat with small bumps. Ossicones directed back from a posterior supraorbital position. Braincase similar to *Samotherium boissieri*. Occipital condyles large and approximated. Posterior basioccipital tuberosities flat and transverse. Anterior basioccipital tuberosities rounded and robust. Bulla rounded and small. Glenoid fossa concave. Figures 21, 22. We place this taxon is Samotheriinae. The new restoration of the type horn is a right and is positioned vertically behind the orbit. The only difference from *Samotherium* is the flat apex of the ossicone. Figure 21 and 22.

Palaeotraginae Pilgrim 1911

Palaeotragus germanii as in Bou Hanifia of Algeria. YGSP 16818c, V 5639, Radius M0159, Tibia YGSP 0985, MT NS 105; MC X 0098. Arambourg C. (1959). Vertébrés continenteaux du Miocène Supérieur de l'Afrique du Nord. *Publ. Service Carte Géologique Algérie Paléontologie* 4: 1-161. 53 figs., 18 pls.

Bohlininae Solounias 2007

Bohlinia tungurensis from Tung Gur. New identification as *Bohlinia*. Skull and teeth figured in Colbert (1936). AMNH 26582 is a skull. AMNH 92306 is a metatarsal from Tung Gur. Characteristic is the parastyle and metastyle of P3. They curve in strongly towards the mesostyle. The same character is in *Bohlinia attica* and *Helladotherium duvernoyi*.

Colbert, E.H., 1936. *Palaeotragus in the Tung Gur formation of Mongolia* (pp. 1-17). American Museum of Natural History Novitates. 874, 1-17.

Giraffinae Gray 1821

Orea leptia new genus and species

Holotype- Y GSP 20415a – a left complete left metatarsal. Radius Y GSP 20415b distal tibia; Y GSP 20415c malleolar, Y GSP 20415d calcaneus, Y GSP 20415e cubonavicular.

Type locality- Y0640.

Age- 13,649-13,655 Ma.

Etymology- *Orea* is Greek for beautiful – *leptia* to denote its exceptional slenderness and length.

Diagnosis- Large giraffid with extremely slender metapodials and long neck. The ventral metapodial troughs are well-developed. The ventral metapodial ridges are rounded. The distal metapodial end is compact. The malleolar, calcaneus, cubonavicular and astragalus are small and very slender. The astragalus has two facets.

A skull fragment from Al Jadidah in Iraq may also belong to this species. There are two metatarsals in that locality which are virtually identical to the type metatarsal of *Orea* from the Chinji. Cast: AMNH 127351 B has a deep trough and it is long. Proximal width 38.07 mm; depth

38.07; min width 21.22 mm estimated total length 366 mm. Cast: AMNH 127351 A has a deep trough and it is long. min width 22.97 mm; distal width 40.03. Cast: skull fragment AMNH 127348. The dorsal side of the ossicone base is fattened. There is a posterior bulge of the ossicone base. Ossicone grooved and flat. Occipital condylar width 66.08 mm. Minimal distance of temporal lines across calvaria 36.02.

Holotype metatarsal YGSP 20416 from Y 640 - (510X24.1 mm).

The L: W ratio of the metacarpal is smaller than that of the metatarsal, at 14.9. This is still larger than the L:W ratio of *Giraffa* and *Bohlinia* metacarpals. This L:W highlights the unique slenderness of the metapodials in *Orea*.

Additional Specimens – 37187 left MT fragment, Y 494 12.377 Ma; 4021 left MC fragment Y 076, 11.410 Ma; Y 23694 mid-shaft MC Y 0666, 13.797 Ma; Y 1907 proximal left MC Y076, 11.410 Ma; Y 1168 distal MC Y076, 11.410 Ma; Y 23385 complete radius Y059, 13.62 Ma (520.7X30 mm); Y 23384 complete tibia Y059 13.652 Ma (500X34 mm). Y 20415 cubonavicular, calcaneus and fibula, fragment of astragalus and metacarpal from Y 0640 13.65 Ma. The cubonavicular, calcaneus and fibula are not studied in detail, as we do not have similar known materials from other species to compare in this size range.

The atlas' dorsal arch and ventral surface are elongated cranio-caudally. The wings are flushed to the body. The L:W ratio of the atlas is 1.39, and its length is 50.61 mm. The distal part of the wing is broken. The foramen for the vertebral artery is oval in this species, similar to the vertebral artery foramen found in *Giraffa*. Figures 18, 19, 20, 20b.

Giraffa punjabiensis Pilgrim, 1910, 1911.

Holotype- MM no. 20 dentition in Calcutta.

Type locality-Dhok Pathan

Age-Middle Siwaliks 8.1 Ma

Etymology- *punjabiensis*- from the Punjab.

Diagnosis- Ossicones placed slightly medially and posterior. No apical knobs. No epikouron. Multiple small head sinuses. Metapodials long trough reduced. Smaller size. P4 is narrower.

Early Late Miocene of the Potwar Plateau, including an 8.1-million-year-old ossicone, 9.4-million-year-old astragalus, and 8.9-million-year-old metatarsal and refer them to *Giraffa*. Left Ossicone: YGSP 16274.

Y 20415 cubonavicular, calcaneus and fibula, fragment of astragalus and metacarpal from Y 0640 13.65 Ma. The cubonavicular, calcaneus and fibula are not studied in detail, as we do not have similar known materials from other species to compare in this size range.

Giraffa punjabiensis ossicone (YGSP 16274) in lateral view. (B) *Giraffa sp*. ossicone in medial view. (C) Undersurface of *Giraffa* sp. ossicone. It is likely that this ossicone belonged to a young

adult individual, as the undersurface exhibits the characteristic pitting seen in ossicones not yet fused to the skull (Danowitz et al. 2017).

Measurements: Length x width of ossicone 30 mm above base: 50 mm x 35 mm; Length x width of ossicone at apex: 21 mm x 22 mm. Axial length of ossicone: 130 mm. Figure 23.

See: Danowitz et al. (2017).

Giraffa sivalensis Falconer & Cautley, 1843

Holotype- specimens figured in Figure 13.

Type locality- Markanda Valley.

Age-Upper Siwaliks

Etymology- *sivalensis*- from the Siwaliks.

Diagnosis-Molars and premolars very similar to *Giraffa camelopardalis*. Neck long. Metapodials with long ventral deep trough. When compared to *G. punjabiensis G. sivalensis* is larger, has proportionally lower length of upper and lower molars, and a wider p4. Intermediate between *G. punjabiensis* and the more recent *Giraffa*. Figure 13. Van Sittert, and Mitchell (2015). Studied the measurements and proportions of that species. Danowitz et al. (2015) studied the morphometric changes from this species to *Giraffa camelopardalis*. Figure 24.

Bramatheriinae new rank

A type species for the new rank is *Baramtherium perminese* at the AMNH. It includes metacarpals metatarsals a jaw, a skull and many small fragments and teeth.

Lyra sherkana Ríos & Solounias, 2023

Holotype- Y GSP 47357, braincase with both ossicones, basicranium and occipital (face and dentition missing).

Paratypes- Detached ossicone fragments (YGSP 6392- loc. Y0311, YGSP 47192-loc Y0514, YGSP 49597-loc Y0311, YGSP 20651, loc-Y0311).

Type locality- Y0647.

Age-12,352-12,402 Mya.

Etymology- The genus is named after Lyra an ancient instrument with similar shape, the specific name it's in honor of Dr. Tanya Sher Khan daughter of the woman medic assigned in Khaur. She participated in the campaigns of the Harvard Geological Survey of Pakistan Project since she was a little girl and found the holotype during the 1994 expedition.

Diagnosis- Giraffid with ossicones positioned slightly posterior to the orbit, with the anterior ossicone edge reaching the midpoint of the orbit. The ossicones are slightly posteriorly

inclined in lateral view. The ossicone surface is composed of two layers, a thinner external layer and thicker external layer. The posterior ossicone surface is lumpy with streaks of secondary bone growth. The base is smooth and devoid of secondary bone growth. There is a bulge at the base both in the posterior and the anterior side. The shaft is gently curved posteriorly, directed laterally forming a 50-degree angle with the skull roof, and is triangular in cross section. A slight clockwise torsion is present along the axis of the shaft. The apex terminates in a small knob that can be smooth or with small bumps present on its surface. The parapex is present. The frontal sinus and surface boss penetrate the base of the ossicone. There is a faint posterior keel. There is a small bulge between the two ossicones centrally on the skull. The frontal sinuses are developed anteriorly but are not well developed on the caudal part of the braincase. The braincase is short. The posterior margin of the right supraorbital foramen is situated in the middle of the antero-medial surface of the ossicone. The anterior basioccipital tuberosities are notably large. The mastoids are covered by bone thickenings resembling secondary bone growth. The anterior basioccipital tuberosities are notably large and rough on their surface. The bulla is bulbous and rounded. The occipital condyles are well separated on the ventral surface. Figures 25,26, 27.

Dimensions: See Ríos & Solounias (2023).

Decennatherium asiaticum Ríos, Danowitz & Solounias, 2021

Holotype- metatarsal YGSP 15184.

Paratype- metacarpal YGSP 11455.

Type locality- Y0311.

Age- 10,026-10,100 Ma.

Etymology- *Decennatherium*, beast of the deity Decenna; *asiaticum*- from Asia.

Diagnosis- Large giraffid. Curved ossicones ornamented by a high number of deep ridges on their surface, which run longitudinally to the apex of the ossicone. The apex is blunt, and the section is oval. Smaller than the ones of Decennatherium rex. Lower molars longer than wider where the lingual wall shows a developed metastylid. The metacarpal is longer and with a slightly slenderer diaphysis index than the other *Decennatherium* species with a value of 9.18. The lateral and medical epicondyles of the metacarpal are slightly asymmetrical with a more triangular medial epicondyle. The metacarpal palmar shaft shows rounded medial and lateral ridges. Distally, the tibia shows a large, flat, and circular ventral fibular facet and an elongated and thin medial malleolus. The distal APD/distal TD tibia index is lower than in the other Decennatherium taxa with a value of 0. 74. The astragalus intratrochlear notch is broad and shows a distinct medial scala and distal intracephalic fossa. The metatarsal shows no distinct pygmaios and has a slightly slenderer diaphysis index than the other Decennatherium species with a value of 8.44. The proximal phalanx shows a distinct notch in lateral view that separates

the lateral palmar eminence from the articular surface of the base. Figure 28. A detailed study by Ríos, Danowitz & Solounias (2021) relates to this species. Figure 28.

Libytherium proton Ríos, Abbas, Khan & Solounias, 2022

Holotype- Y GSP 46530, complete left ossicone.

Paratype- Y-GSP 49608, right hemimandible.

Type locality- Y0311.

Age- 9,596-10,100 Mya.

Etymology- *Proton* means the first.

Diagnosis- A notably large giraffid. The ossicones are cylindrical, elongated, and curving inward but not twisted. There is lateral prong near the base and no base flange. The cross section is oval near the base. The shaft is rounded and has no bumps. The ossicone extends upwards and curves gently. There is fine grooving on the surfaces (dorsal and ventral). Near the apex the there are two small dorsal bumps followed by a concave excavation. There are also two ventral bumps. The area where the bumps begin is the para-apex. Other ossicones do not have bumps. The apex is a small, flattened disc. There is a large central canal. The jaw is large and robust and with a short symphysis. There is no indentation on the jaw between the angle and ramus. The molars have a small buccal cingulum and reduced styles. The p3 has a mesolingual conid. The posterolingual and posterobuccal conids join posterolingually through the posterior stylid forming a rounded posterior fossette. The p4 is very molarized with a larger anterior lobe that represents two thirds of the tooth length, and the protoconule is labially more extended than the protocone. Enamel is very rugose and thick. The entoconid is separated from the metaconid and the posthypocristid. The protoconid is wider and rounder than the hypoconid, which is U-shaped. There is a thin buccal connection between the wide postprotocristid and the prehypocristid. The radius is large, with a large bulge on the dorsal surface distally above the lunate fossa. The styloid process of the ulna is fused to the radius and is small and round. There is a small depression dorsally for the extensor tendon. The metacarpals are longer than in *Libytherium* maurusium and *Sivatherium giganteum*. The central palmar trough is shallow. The astragalus is not squared. It is a simple rectangular in outline with a small medial crest on the trochlea. Figure 29.

Dimensions: See Ríos, Abbas, Khan & Solounias, 2022

Bramatherium megacephalum Lydekker, 1876

Holotype- AM-19670, skull.

Type locality- Dhok Pathan.

Age- 7.0-10.2 Ma. Late Miocene.

Holotype IM D 150 skull (Lewis 1939).

Etymology- *Bramatherium*, beast of the Hindu deity Brama; megacephalum, large head, regarding the large ossicones.

Diagnosis- Large size giraffid with robust limbs, a short face and a massive and relatively short neck and rugose tooth enamel. *Bramatherium* is further distinguished by two very large, transversely placed ossicones arising from a common, median frontoparietal base and two smaller, more posterior, lateral, parietal ossicones. When compared *to B. perimense, B. megacephalum* has less robust and smaller ossicones, with the anterior ossicones arising from a less developed common base and a less massive skull, plus less prominent anterior styles in the upper teeth. Described and figured by Lewis 1939.

Dimensions of the Yale specimen described by Lewis 1939: width across occipital condyles 137 mm; P3 to M3 179 mm. Neck lengths: atlas 90 mm; axis 192 mm; C3 140 mm; C4 142 mm; C5 160 mm; and C6 163 mm. Figure 30.

Bramatherium perminese Falconer 1845

Type skull figured but not named by Bettington (1845). Skull presumably still in the Royal Society of Surgeons collections. Cast of that skull at AMNH is 27016 (according to Colbert 1935; lectotype is NHM maxilla 48933 – not diagnostic). Second skull from Perim Island AMNH 197791 from Dhok Pathan figured in Colbert (1935). Massive anterior ossicone bosses. The actual ossicone was thin over the huge boss. See Colbert (1935) for more information.

Dimensions described by Lewis (1939) and Colbert (1935): width across occipital condyles 131 cm. P4 to M3 163 mm; P3 to M3 168; See Lewis (1939). Figure 31.

Bramiscus micros nanos Ríos, Abbas, Khan & Solounias, 2023

Holotype- PUPC 22/01, a small fragment frontlet bearing pair ossicones with their fused bases.

Type locality- Chinji Formation, Lower to Middle Siwaliks, Punjab, Pakistan.

Age- 9.3-13.65 Mya.

Etymology- *Bramiscus*: -*iscus* means very small in ancient Greek, means small *Bramatherium*. *Micros*- means small in size.

Diagnosis- Diagnosis. Small size giraffid with two pairs of ossicones. The anterior pair are fused at their base (Bramatherium-like). The posterior pair is straight and possibly directed laterally. All ossicones have an oval cross-section at base and tending to be circular at apex. The ossicone surface is covered with longitudinal ridges of a medium depth. The ridges are deeper and larger ventrally and laterally. The dentition is brachydont with rugose enamel. The upper molars have a postmetaconule fold and a labial cingulum, as well as a developed entostyle. The lower p2 has a crest on the anterior valley. The lower p3 has a well-developed paraconid and

parastylid. Metaconid narrower than the entoconid. Lower molars with protoconid and hypoconid slightly rounded and labially has rugose enamel and an anterolabial cingulum. *Palaeomeryx* fold absent. Lower molars with high L/W index. Metatarsal has a characteristic large medial ridge and a low lateral ridge. Figure 32.

Dimensions: See in Ríos, Abbas, Khan & Solounias (2023).

Bramiscus micros Ríos, Abbas, Khan & Solounias, 2023

Holotype- PUPC 22/01, a small fragment frontlet bearing pair ossicones with their fused bases.

Type locality- Chinji Formation, Lower to Middle Siwaliks, Punjab, Pakistan.

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Etymology- *Bramiscus: -iscus* means very small in ancient Greek, means small *Bramatherium*. *Micros*- means small in size.

Diagnosis- Diagnosis. Small size giraffid with two pairs of ossicones. The anterior pair are fused at their base (*Bramatherium*-like). The posterior pair is straight and possibly directed laterally. All ossicones have an oval cross-section at base and tending to be circular at apex. The ossicone surface is covered with longitudinal ridges of a medium depth. The ridges are deeper and larger ventrally and laterally. The dentition is brachydont with rugose enamel. The upper molars have a postmetaconule fold and a labial cingulum, as well as a developed entostyle. The lower p2 has a crest on the anterior valley. The lower p3 has a well-developed paraconid and parastylid. Metaconid narrower than the entoconid. Lower molars with protoconid and hypoconid slightly rounded and labially has rugose enamel and an anterolabial cingulum. *Palaeomeryx* fold absent. Lower molars with high L/W index. Metatarsal has a characteristic large medial ridge and a low lateral ridge. Figure 32.

Sivatheriinae Bonaparte 1850

Sivatherium giganteum Falconer & Cautley, 1843

Holotype- BM 15283, skull. (Falconer and Cautley, 1836: plate 2; Harris, 1976a,

1976b); ossicone NHM: 39524 a; ossicone 39525; 39523 female skull; 39533 metacarpal; 39752 metatarsal and a complete neck.

Type locality- Upper Siwaliks

Age-Plio-Pleistocene.

Etymology- *Sivatherium* means beast (therium) of Siva, the Hindu god of destruction, and giganteum refers to its large size.

Diagnosis- Skull where the posterior ossicones are composed of hundreds of placations and are covered with ribbons of material – not palmate but with a large bump near the base. Anterior ossicones simple cones. Nasals arched. The frontal sinuses are small but multiple. The

molars resemble bovines with additional crests. The metacarpals are shorter than the metatarsals. The neck is short with massive ventral tubercles. Figures 33 and 34. This is a new concept of a family monotypic for *Sivatherium.* Figure 33.

DISCUSSION

The Siwaliks Miocene has the highest diversity in giraffoid taxa of all the fossil record, only similar to the diversity peak found in Greece during the Late Miocene (Solounias, 2007). It has recorded a variety of giraffoids including all three families of the clade: Palaeomerycidae, Climacoceridae and Giraffidae. The earliest recorded are the climacoceratids, which disappear from the Siwalik faunas before the Middle Miocene. Palaeomerycids appear for the first time in the Siwaliks record at the beginning of the Middle Miocene disappearing before the Late Miocene. Giraffids appear first in the Lower Miocene and achieve the highest diversity during the Late Miocene, after, they gradually disappear from the Siwaliks.

Lower Siwaliks Giraffoid faunas (18.3-13.1 Mya)

The earliest giraffoids recorded are the climacocerids *Vittoria soriae* nov. gen., *Goniomeryx* flynni nov. sp. and *Orangemeryx badgleyi* nov. sp., and the giraffid Progiraffa exigua, *Ua pilbeami*, and *Orea leptia*. The earliest palaeomerycid of the Siwaliks record is *Goniomeryx flynni* nov. gen. nov. sp. followed by *Charis gratia* nov. gen. nov. sp.

Middle Siwaliks Giraffoid faunas (13.1-10.1 Mya)

The majority of plaeomerycids appear during the Middle Siwaliks, including *Lateralia morgani* nov. gen. nov. sp., *Tauromeryx canteroi* nov. sp., and *Fovea fossata* nov. sp.They coexisted with several giraffids including *Giraffokeryx punjabiensis*, *Giraffa punjabiensis*, *Lyra sherkana*, and *Bramiscus micros*.

Upper Siwaliks Giraffoid faunas (10.1-0 Mya)

The latest giraffoid faunas included the last palaeomerycids which disappeared right at the beginning of the Upper Siwaliks. The main representatives of the clade were the large Sivatheriinae giraffids *Bramatherium megacephalum, Bramatherium perimense*, Libytherium proton, and Sivatherium giganteum plus the giraffine *Giraffa sivalensis*.

THE GIRRAFFPODEA GENERAL CONSIDERATIONS

There are several families of Pecora. They have been generally classified by Janis and Theodor (2014). They are: The Cervidae and primitive cervoids have been most extensively studied (e.g., Azanza et al. 2011; Landette-Castillejos et al. 2019; Rossner et al. 2021). There is basically a persisting scientific interest in antlers their histology and antler shedding. Antlers generate above a frontal pedicle and are annually shed. The general result or am cervids have the same type of antler (Rossner and xxx). Bovidae have been extensively studied in both systematics as they include cows and sheep which are our food. The Bovidae are very diverse in body size and horn shapes (Simpson 1949; Gentry 1968; Gentry 1992; Hassanin and Douzery

1999). The bovid horns are difficult to interpret. The available studies are old but are informative (Dürst 1926; Dove 1935) and summarized by Janis and Scott (1987) and by Davis et al. (2014) Preliminary data suggest that the horn is a composite of a separate ossification externally (the os cornu), a frontal origin horn internally and a keratinous horn sheath cover.

The other Pecora have not been studied as much. The Dromomerycidae are a group of taxa where the horns are constructed by an upward growth of the frontal bone. The dentitions are primitive (Frick 1937). The Antilocapridae also have horns formed by the frontal bone but may be distinguished by the covering keratinous horn sheaths and more hypsodont teeth (O'Gara and Matson 1975). Antilocapridae have been studied very or am.

Giraffoidea (Climacoceridae, Palaeomerycidae and Giraffidae). The Giraffoidea of the Pecora is a group of taxa united by the presence of supraorbital ossicones. Ossicones are separate ossifications which later in life fuse with the frontal bone (Ganey et al. 1990; Solounias 2007; Solounias 2023).

There are three major studies of cladistic analyses. Hamilton 1978 Geraads 1986 and Rios et al. XXXX, Ríos and Morales (2019).

Climacoceridae and Palaeomerycidae

Climacoceridae is a difficult to study group from east Africa and now the Siwaliks of Pakistan (this paper) (Hamilton 1978). Presently Climacoceridae are assumed to have ossicones. This is based on two specimens. One form Moruorot Hill where the base is detached (Grossman and Solounias 2014 fig. 2 – UCMP 40461)). The other is from the Siwaliks (Y GSP 30608) and shows at the base a flat surface of a detached ossicone type as in the Moruorot one.

Palaeomerycidae have ossicones and an enigmatic occipital horn (Qiu et al. 1985; Astibia and Morales 2006; Sánchez et al. 2015). They have often been confused with Dromomerycidae. This is due to the occipital hone which is convergence. Some domesticated cows also have an occipital horn (a small one but in the same position).

Giraffidae possess ossicones only and are only or am to large-sized taxa (Bohlin 1926; Hamilton 1978; Solounias 2007; 2023). No small-sized species exist unlike Cervidae and Bovidae.

We name several new genera and species. The material is very small and one may wonder why name new taxa with such a poor record. This is because we need to know the diversity of life and there are very few changes in the near future to obtain more material. The Climacoceridae and Palaeomerycidae are particularly rare. They may have inhabited highlands as thus they lived outside of the main flood plains where deposition of bones is simpler. On the other hand, Giraffidae are more abundant and were inhabiting lowland depositional environments. These three groups differentiate before 18 Ma. There is no record then to document their original appearance. When they first appear, they are full-fledged in their three

respective groups. The sediments that record the oldest taxa are Moruorot Hill, Kalodirr, Gebel Zelten and Kalmlial.

Description of the eight Giraffidae subfamilies

The Giraffidae form a number of subfamilies which are not directly connected. They share the bilobed canine, closed orbital opening for the nasolacrimal duct, crenulated enamel, ossicones and large body size large metapodials and browsing diet (except for the *Samotherium* group).

In Giraffidae the proximal end of the metatarsal can be used as a diagnostic tool as it differs in most species. Figure 35. The ossicones are also useful in separating the subfamilies.

The Giraffidae can be subdivided into subfamilies. These are:

Progiraffinae new rank

Based on *Progiraffa exiqua* Pilgrim 1911. This includes *Progiraffa* (*Canthumeryx sirtensis*), *Georgiomeryx georgalasi* and possibly other unnamed early Miocene species. There are undescribed ossicones of this taxon form Kalodirr which were similar to the okapi. It was found in Gebel Zelten (as Canthumeryx) and Moruorot Hill (undescribed). In the Zinda Pir and lower Siwaliks, there are dental specimens. This earliest giraffid is *Progiraffa exigua* has been described by Barry at al. (2005). The material has been covered by Hamilton (1973 and 1978 as *Canthumeryx*). The cervicals of *Canthumeryx* are elongated. We know from these specimens that *Progiraffa* had a short conical ossicone and a longish cervical vertebrae. The premolars are clearly primitive with long crests and lingual valleys open (Hamilton 1978). I thank Dr. Ari Grossman for his help with the Kalodirr material. What makes these specimens giraffid is the presence of ossicones. Note that *Zarafa zelteni* from Gebel Zelten is excluded from these species as it is a palaeomerycid. In *Zarafa* the enamel is not crenulated; thus, it cannot be a giraffid. In addition, the occipital is highly suggestive that it had an occipital horn which is broken off. There is an undescribed orbital ossicone of this in the NHM which clearly point towards this taxon being a palaeomerycid.

The giraffe is close to *Progiraffa*. The true ossicone of the giraffe is short with a broad base. That is the ossicone after removing the extremal epikouron. The dentition is plesiomorphic. In these two features the giraffe is similar to *Progiraffa*. Thus, in the evolution of the giraffe directly from *Progiraffa* is plausible. The giraffe added a frontal sinus and elongated the metapodials. The cervicals of course became longer. In conclusion, as far as the fossil record can help we have *Progiraffa* as the most likely direct ancestor.

Giraffokerycinae Solounias 2007

Based on *Giraffokeryx punjabiensis*. *Giraffokeryx* punjabiensis from the Chinji of the Siwaliks and *G. primaevus* from Fort Ternan in Kenya are the two species. The second is the more primitive. They had four ossicones and no frontal sinuses. The posterior ossicones were long and deeply grooved and perhaps were covered with keratin. At the base, there is a bulge of

disorganized bone. The anterior ossicones were fused at the base. They had long metapodials. Libytherium also has basal bulges on the ossicones. They have long metapodials. The metatarsal of *Giraffokeryx* has an untypical digit III.

The short neck of the okapi is similar to *Bramatherium*. They also share the four ossicones and large anterior frontal sinuses. The second pair of ossicones of the okapi are reduced plates in pits above the orbits. The metapodials are also similar. Thus, the okapi does have affinities with *Bramatherium*. In *Giraffokeryx* and the okapi they share the four ossicones but the neck of *Giraffokeryx* and the metapodials are longer. Thus, *Giraffokeryx* less similar.

Okapiinae Bohlin 1926

Based on *Okapia johnstoni*. There is no fossil record of *Okapia*. The living species is a mystery with many unsolved issues. It is possible that there are fossil okapi-like animals in the Chinji Formation of the Siwaliks. We are currently researching these. Okapia possesses two posteriorly placed ossicones that are smooth-surfaced, conical and the bone is commonly exposed at the apices. Here may be a second rudimentary pair of ossicones over the orbital margin. The females are hornless but may have small ossicones. The females are larger-sized than the males. The ossicones may produce periodically keratinous horn sheaths. Okapia has well developed nasal and anterior frontal sinuses and inflated bullae. They have shortened necks. A compressed proximal metatarsal and cuneiforms fused to the cubonavicular. They have medium metapodials.

A Miocene species from the Baringo Basin of Kenya; namely *Afrikanokeryx leakey*. It has bulbous bullae and canals in the ossicones. It is a rare and unique taxon.

Ua pilbeami is close to the okapi. It has distal constriction in the ossicone. It also has an anterior large frontal sinus.

Bramatheriinae new rank

Based on *Bramatherium perimense*. The following group is termed Sivatheriinae but ironically, this name is not correct as we remove *Sivatherium* from the subfamily. The can be named Bramatheriinae as *Bramatherium perimense* is the more complete specimen and the older most named genus in the group. In *Bramatherium perimense* from Perim Island there is a skull, limbs and a complete mandible. *Bramatherium permimense* is a large giraffid found in the Perim Island and in Dhok Pathan. It has anterior bosses that were huge and commonly mistaken for ossicones. They were situated posterior to the orbits. The bosses may had thin ossicone on them. The posterior ossicones were straight and directed laterally. Both ossicones share a common base. Within the ossicones, there are two canals. Thus, both the back and front ossicones were formed my merging of separate ossifications. The neck was short and massive. The metatarsals display accessory digits and two well-developed ventral ridges. The medial right (digit II) is taller than the lateral. The median ridge of the metatarsals in very strong while

the lateral ridge is very weak. Bramatherium is also found in the Pliocene of Turkey and the Miocene of Samos (the oldest). They have short to medium in length metapodials.

Helladotherium duvernoyi is very similar. It probably had small posterior ossicones that have never been identified. There is a possibility that the anterior ossicones have been found. NHM M37843 is one of these specimens. It is a flattened disc-like ossicone with a rich sinus at the base. The boss of the holotype skull is long and oval as was the adhering ossicone. The surface is rounded and full of vessel impressions and irregular islands of epikouron. It is similar to the anterior ossicones of *Libytherium maurusium* form Djibouti (Geraads 1985). There may have not been posterior ossicones as there are no bosses on the type skull. I place *Vishnutherium iravadicum* in *Helladotherium*. It is a rare large taxon with extremely large parastyles metastyles and cingula and it possesses deep troughed metapodials. The premolars resemble those of *Helladotherium*.

Libytherium maurusium was widespread in the Pliocene of Africa. Many consider it to be congeneric with *Sivatherium* on the overall superficial similarity of the ossicones and the large body size. The ossicones gently curve and are positioned posteriorly on the skull in both genera. The ossicones are twisted and deeply grooved. The anterior ossicones are flattened discs. *Birgerbohlinia* and *Decennatherium* are very similar to Libytherium.

Bramiscus is a small-sized taxon similar to *Bramatherium*. The median ridge of the metatarsals in very strong while the lateral ridge is very weak.

Palaeotraginae Pilgrim 1911

Based on *Palaeotragus rouenii*. Palaeotraginae are represented by two species: *Palaeotragus rouenii* and *Palaeotragus coelophrys* (larger). A new genus (unnamed) *germanii* from Bouhanifia is a little older and can be included. The stratigraphy and morphology suggest a progressive reduction in size from a large species to a smaller one. The ossicones are simple smooth surfaced spikes positioned more internally. The apices are often bare bone. The females were hornless. The premolars were reduced. In Palaeotragus there is a gap between the external auditory meatus and the glenoid fossa that gap is filled with a bony shelf. They may specializations in their premaxillae suggesting a different type of upper lip. The metapodials are long and slender.

Samotheriinae Hamilton 1978

Based on *Samotherium boissieri*. It includes *Inajanatherium hazimi*, Samotherium, Schansitherium, and *Alicephalus*. They have long spike like ossicones that are supraorbital (posterior orbital margin). The ossicones are smooth surfaced and are often exposed at the apex. The fontal sinuses are small to absent. The premolars are reduced in size. There is a morphocline of increasing masseteric fossae and the displacement of the orbit posteriorly. The smallest masseter is in *Alcicephalus*, followed by *Samotherium boissieri* and *Schansitherium*. *Samotherium major* has an extremely large masseter and a posterior orbit. *Samotherium*

boissieri possessed a squared premaxilla for mixed feeding. Alcicephalus had a wide occiput the others had a narrow one. The females can be horned but not always. The necks are longish and the metapodials are short. *Injanatherium hazimi* Henitz et al. 1981 from Injana province Gebel Hamrin Iraq (Henitz et al. 1981). This may be congeneric with *Samotherium boissieri*.

Bohlininae Solounias 2007

Based on *Bohlinia attica*. Massive ossicones without canals. Skull roof flat without sinuses. P3 and P4 with enlarged curved inward parastyles. Cervicals long. Metapodials long. Metapodial trough deep. Medial femoral epicondyle reduced.

Bohlinia has a long neck but the C7 is not specialized (unpublished material). It is a long C7 but without ventral tubercles (where the giraffe is specialized with a C7 that is exceptional in having ventral tubercles). In other words, the C7 of Bohlinia is rather normal. What is untypical is the lack of a large and medial epicondyle on the femur. In this respect, Bohlinia is unlike other giraffids. The femur resembles more that of a dromedary. Thus, Bohlinia resembles a camel in limb posture and is rather different from the majority of the Giraffidae. Honanotherium is now know by complete skulls from Gansu. They are very similar to Bohlinia. The metapodials were ticker and shorter than in Bohlinia. Giraffa evolved in the Siwaliks of Pakistan. It migrated into Africa rather recently. Bohlinia evolved in the Pikermian Biome. Honanotherium in the Beotian Biome. The metapodials are either medium or long in this subfamily.

Giraffinae Gray 1821

Based on *Giraffa camelopardalis*. The ossicones are covered in males with epikouron which extends down the face up to the face muscles. The parietals are not covered by epikouron. There is usually a third central ossicone in males. The frontal sinuses are strongly developed. The teeth are robust and the premolars are large. The cervicals are long. C5, C6 and C7 are homogeneous in shape. T1 resembles a C7. The metapodials are long and slender and the ventral troughs are minimal. *Giraffa jumae* from Olduvai has smaller frontal sinuses and not nasal ossicones. Thus, the modern giraffe is a rather recent species. *Giraffa punjabiensis* is as large as modern *Giraffa*. It is the oldest of the genus and apparently *Giraffa* evolved in the Siwaliks of the Indian Subcontinent.

Sivatheriinae Bonaparte 1850

Based on *Sivatherium giganteum*. A difficult to interpret taxon from the Pleistocene of India. It is large, the size of *Bubalus*. The posterior ossicones are composed of thousands of horizontal laminations. The placations are covered by flat ribbons of bony material. The frontal sinuses are eight small chambers but are small in volume. Females without ossicones. The metacarpals are notably shorter than the metatarsals.

Sivatherium giganteum Pliocene of the Siwaliks of India. It is unique because of the stricture of the ossicones. They actually may not be ossicones but a unique horn. The internal anatomy of the “ossicone” is hundreds of fine horizontal plates of bone (NHM 39524a). The horizontal

plates are coved by a thin veneer of none (about 1 mm thick). They are in turn covered by flattened ribbons of external bone and a few venations. Lateral bumps are present on the edges of the twisted shaft structure. There are no internal canals. The sinuses of the skull are small. The anterior ossicones seem normal giraffid ossicones and are conical. The females were hornless (female skull NHM M 39523). The metacarpals are notably shorter than the metatarsals unlike other Giraffidae. The neck was short with massive cervical processes. The head may have been positioned down as in Bison. It was a mixed feeder and probably a browser (incisors NHM M 15288). They have short metapodials and the anterior are notably shorter like a tragulid. It may be a palaeomerycid.

Relations of Giraffidae

Gradual changes are found in many examples of evolution. For example, changes in the mammalian ear in the origin of birds from species like archaeopteryx and in numerous fish lineages where skulls and fins and body shapes can be organized is evolutionary sequences. We have good sequences in human and Cetacean evolution. You can read about sequences in many books (such as: E. Mayr 1988 p. 406 "Toward a new philosophy of biology;" G. G. Simpson 1944 "Tempo and mode of evolution)."

Alternatively, evolutionary relationships in various taxa can be with small gaps or large gaps. In addition, horizontal or vertical sequences are desired but not always available. At the phylum level, most phyla are distinct with very few intermediates. In this case the gaps are large. The baupläne is key and recognizable by morphology this is true in the classification of Phyla. At a smaller level the Giraffidae are in a similar situation. There are subfamilies but no clear way of connecting these in a coherent evolutionary fashion. Gaps do exist.

CONCLUSIONS

Lower Siwaliks Giraffoid faunas (18.3-13.1 Mya) are: The earliest giraffoids recorded are the climacoceratids *Vittoria soriae nov. gen. nov. sp.*, *Goniomeryx flynni nov. sp.*and *Orangemeryx badgleyi nov. sp.,* and the giraffid *Progiraffa exigua, Ua pilbeami*, and *Orea leptia.* The earliest palaeomerycid of the Siwaliks record is Goniomeryx flynni nov. gen. nov. sp. followed by *Charis gratia nov. gen. nov. sp.* The earliest giraffid is *Progiraffa exigua.*

Middle Siwaliks Giraffoid faunas (13.1-10.1 Mya) are: The majority of plaeomerycids appear during the Middle Siwaliks, including *Lateralia morgani nov. gen. nov. sp., Tauromeryx canteroi nov. sp.,* and *Fovea fossata nov. gen. nov. sp.* They coexisted with several giraffids including *Giraffokeryx punjabiensis, Giraffa punjabiensis, Lyra sherkana,* and *Bramiscus micros*.

Upper Siwaliks Giraffoid faunas (10.1-0 Mya) are: The latest giraffoid faunas included the last palaeomerycids which disappeared right at the beginning of the Upper Siwaliks. The main representatives of the clade were the large sivatherine giraffids Bramatherium *megacephalum, Libytherium proton, and Sivatherium giganteum* plus the *Giraffa sivalensis*.

FIGURES

Palaeomerycidae

Fig. 1 *Tauromeryx canteroi* A) occipital bone with base of horns Y 42343. White line shows possible direction of horns; B) occipital horns Y 42343 in dorsal view; C) Y 17393 frontal horns not associated specimen.

Fig. 2. *Charis gratia* holotype YGSP 30933 A) ventral view; B) right lateral view; C) dorsal view; D) occipital view; E) right maxilla; F) left maxilla.

Fig. 3. *Charis gratia* holotype YGSP 30933 A) ossicone dorsal aspect; B) ossicone ventral aspect; C) basicranium. The ossicones were oriented lateral and dorsal.

4. *Fovea fossata*. A and B) Y23715 and C) medial view of holotype Y21897; D) anterior view of holotype; E) lateral view of holotype.

Fig. 5. *Goniomeryx flynni* holotype Y 30608 A) lateral view; B) ventral view showing the detached ossiocne; C) anterior view; D) lateral view; E) posterior view; F) 31810 loc 758 14 Ma dorso-lateral view; G) lateral view; H) anterior view.

Fig. 6. *Lateralia morgani* hototype Y 50593. A) ventral view; B) medial; C) the axis of the ossicone view; D) posterior view; E) dorsal view.

Climacoceridae

Fig.7. A) *Vittoria soriae* NHM M 26690 (holotype); B) NHM M 102058 both from Gebel Zelten. C) close up of b showing a cross section. Note there is an ossicone sinus.

Fig. 8. *Vittoria or Climacoceras*. a and b) Y 31790 fragments. No sinus in the ossicone. C) Y 31927 ossicone fragment. The fine striations are hypothesized to be ossified hair; D and E) Y 47197 a large specimen where the double cortex is clearly visible in the cross section. Both from the Chinji.

Fig. 9. *Orangemeryx badgley* 23698 loc 666 13.7 Ma. A) posterior aspect; B) anterior aspect; C) lateral; medial view – note the large frontal sinus.

Giraffidae

Fig. 10. *Progiraffa exigua* A) lower m2 and m3 holotype from Pilgrim 1911 plate one; B) Progiraffa sivalensis from Pilgrim 1911 (probably also exigua) plate one; C) a similar m3 from AMNH 857 from the Chinji; D) m3 of Giraffokeryx AMNH 19317 for a hypsodonty comparison; E) Y 42342 MT.

Fig. 11. *Progiraffa exigua* A and B) dorsal and lateral view of occipital/parietal NHM M E91 26673 from Gebel Zelten Libya; C) MT YGSP 24305 from the Chinji; D, E and F) C3 vertebra

restored UCM 4220 from Moruorot Hill Kenya; G) NMK K 722- 17089 ossicone from Kalodirr Kenya.

Fig. 12. *Progiraffa exigua* Two astragali A and B) 41182 and DGK 12 and may belong to Progiraffa. C and D) maxilla PSAP 312; E and F) mandible PASP 41662 of *Progiraffa*.

Fig. 12 b. *Progiraffa exigua* skull form Chios – originally named *Georgiomeryx georgalasi*

Fig. 13. *Giraffokeryx punjabiensis* A, B, C) AMNH 19475 skull of the lectotype of *Giraffokeryx* punjabiensis; D) a p4 figured by Pilgrim 1911; E and F) anterior ossicones Y GSP 23119; G) Y GSP 47198 longitudinal section of a small ossicone assigned to this species; F) metatarsal Y GSP 24306.

Fig. 13b *Giraffokeryx primaveus* from Fort Ternan the ossicone has been lost in Nairobi - restorations of a hypothetical skull. Churcher (1970) thought that the ossicone was *Samotherium*.

Fig. 14. *Giraffokeryx punjabiensis*. A and B) the lectotype AMNH 19475. Note the bony mass at the base of the ossicone; C and D) Y GSP 15470 the base morphology connecting to the frontal is different from that of Giraffa; D) ossicone 26847; E) Y GSP 19842 upper dentition.

Fig. 15. *Giraffokeryx punjabiensis* of lectotype AMNH 19475. A) the basicranium of lectotype; B) the dentition.

Fig. 16. *Ua pilbeami* holotype Y GSP 28483. A) The complete left ossicone. B) View of the skull fragment form an anterior-dorsal aspect to show the frontals and the boss. C) The apex of the ossicone. D) Lateral aspect of the apex with the constriction and a cross section showing the internal canal. E) Medial aspect of the apex. F) A direct anterior aspect of the cranial fragment showing the enlarged frontal sinus. Scale bar: 50 mm for A, B, F; 25 mm for C, D, E.

Fig. 17. Ventral views of *Ua pilbeami* n. gen. n. sp. metatarsal and metacarpal and other selected metatarsals for comparison. A) *Ua pilbeami* n. gen. n. sp. metatarsal Y GSP 24305. B) Ua pilbeami n. gen. n. sp. metacarpal Y GSP 4505. C) *Okapia johnstoni* AMNH 1196. D) *Decennatherium asiaticum* Y GSP 15184. E) *Giraffokeryx punjabiensis* Y GSP 24306. F) *Palaeotragus rouenii* MNHNP from Pikermi 1691. G) *Orea leptia* Y GSP 20415. H) *Giraffa camelopardalis* AMNH 53543. I) *Bohlinia attica* MNHNP Pikermi 27561. All to the same scale to facilitate comparisons.

Fig. 21. *Injanatherium hazimi* cast of original holotype in MNHNP from Gebel Hamrin Iraq. Orignally described without a number (Heintz Brunet and Sen, 1981). Original in Poiters. a) *Injanatherium hazimi* type showing the erroneous restoration (A) and (B) the corrected restoration. Red line points to a pristine orbital margin. This proves that the ossicone could not be directed laterally. Green pointer shows the erroneous location of the ossicone. Black shows the correct location of the ossicone. C) dorsal view – only one ossicone is known; the right. The left ossicone is a visual duplicate. D) lateral view; F) braincase.

Fig. 22. *Injanatherium hazimi* from the Siwaliks. A, B (apex) and C (base) YGSP 8869; D and E) YGSP 24295; F and G) frontal with base of ossicone YGSP 17891.

Fig. 18. *Orea leptia* YGSP 20415. A) ventral view; B) dorsal view; C) left lateral view; D) proximal end.

Fig. 19. *Orea leptia* A) YGSP 23385 radius; B) YGSP 23384 tibia; C) same tibia proximal end; D) radius proximal end; e) tibia distal end.

Fig. 20. *Orea leptia* A) atlas cervical YGSP 32821; B) *Giraffa* AMNH 82001 C) *Okapia* AMNH 51197. The same scale to facilitate comparisons. D) YGSP 8101/443 an ossicone fragment similar to that of skull AMNH 127340 – from Al Jadidah of Iraq.

Fig.20b Three *Orea* specimens from Al Jadidah of Iraq. Top and center metapodial fragments. Bottom: three views of a skull. Notice the ossicone similarity to YGSP 8101/443.

Fig. 23. *Giraffa punjabiensis* YGSP 16274. A) lateral; B) medial; C) base. The attachment differs from that of the okapi and the giraffe.

Fig. 24. *Giraffa sivalensis* a C3 vertebra NHM M 39747.

Fig. 25. *Lyra sherkana* A and B) YGSP 43357 C) YGSP 6392; D) 49597.

Fig. 26. *Lyra sherkana* A) dorsal view; B) braincase view of YGSP 43357.

Fig. 27. *Lyra sherkana* A) lateral view; B) Close up of ossicone of YGSP 43357 showing massive boss and two surface layers of ossicone material.

Fig. 28. *Decennatherium asiaticum* A) YGSP 9472 astragalus; B) YGSP 15184 MT; C) YGSP 14580 MC; D) m3 tooth YGSP 13201. Scales in mm.

Fig. 29. *Libytherium proton* A) ossicone YGSP 46530; B) Metacarpal 16818; D) metatarsal 17918. C) YGSP 14960 showing canal, inner cortex and thick outer corstex. Scales in mm.

Fig. 30. *Bramatherium megacephalum* skull at YPM 13881 - figure from Lewis 1939.

Fig. 31. *Baramtherium perimense* Skull from the Perim Island Pliocene AMNH 19771 (Colbert 1935).

Fig. 32. *Bamiscus micros* A small-sized *Bramatherium*-like taxon. A) ossicones YGSP 20597; B) Metatarsal YGSP 14998 – red lie shows the characteristic medial large ridge; C) Metacarpal YGSP 42162.

Fig. 33. *Sivatherium giganteum* A) holotype NHM M 39524; B) occipital view; C) NHM M 15284 lateral view; D) same in palatal view.

Fig. 34. *Sivatherium giganteum* A) (anterior), B) (posterior), C) (lateral), of ossicone NHM M39525; D) MC NHM M 39533; MT NHM M 39752.

Fig. 35. A variety of proximal ends of metatarsals showing the presence of five digits. *Giraffokeryx* has an untypical digit III.

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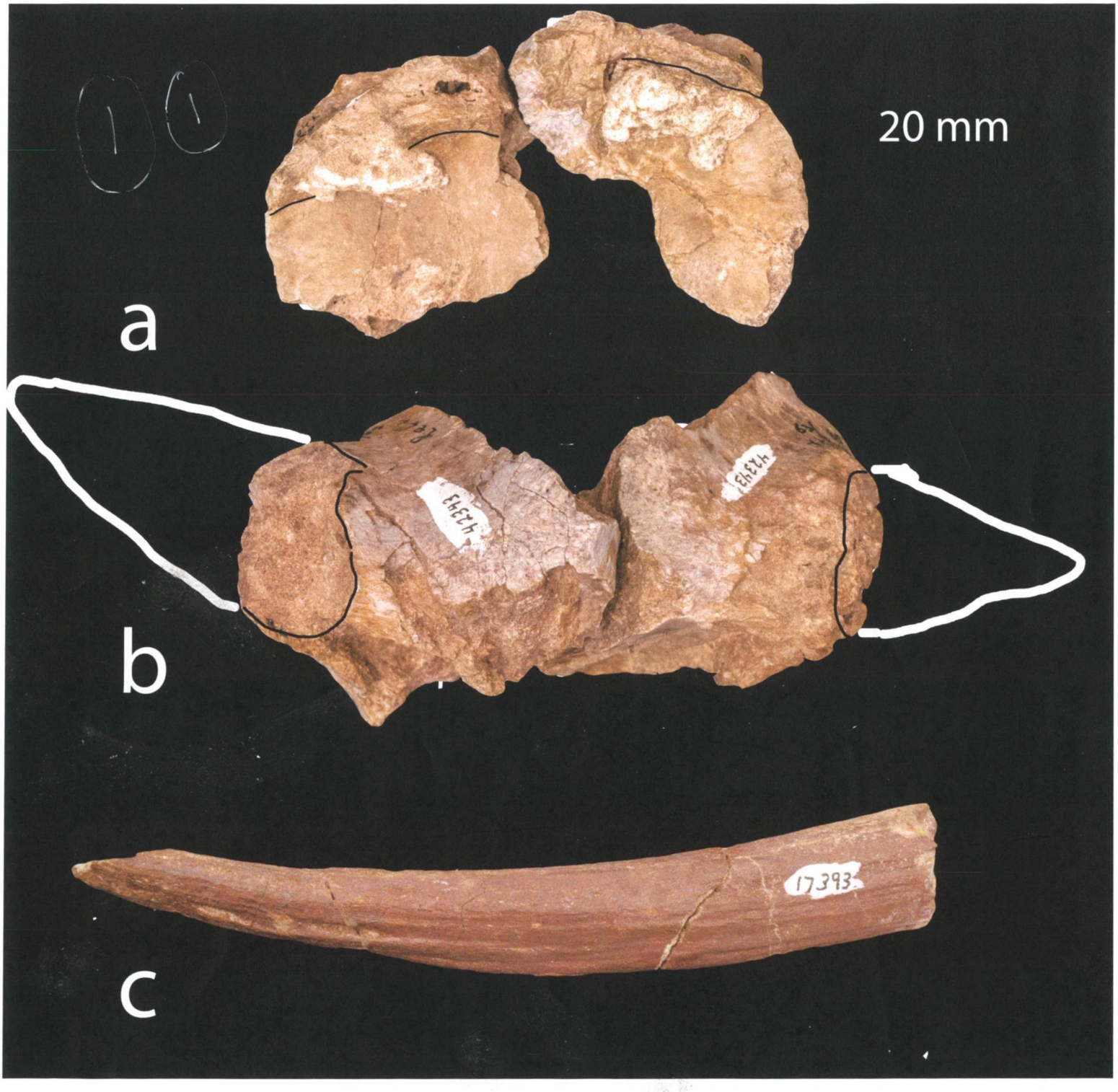
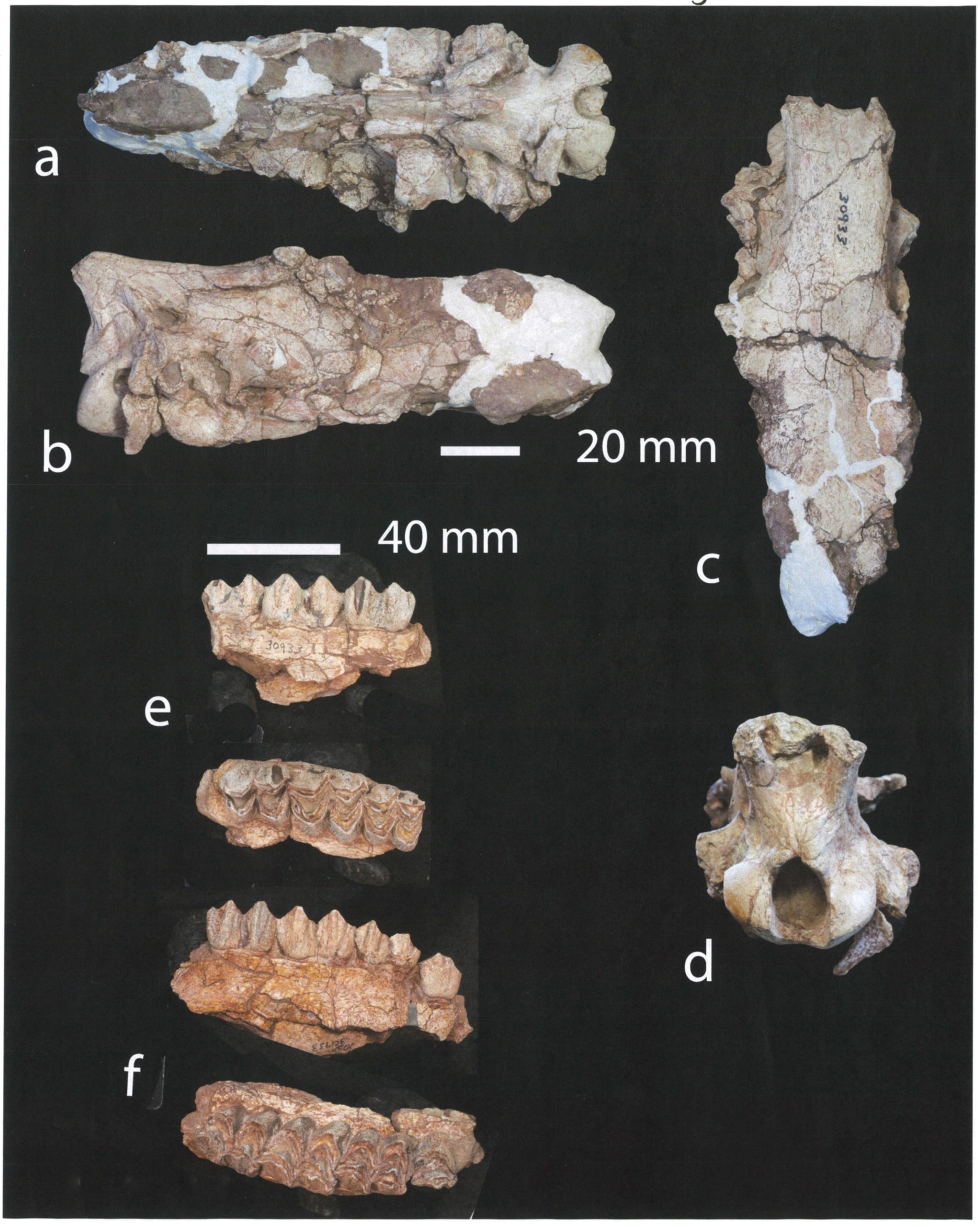
Palaeomerycidae:
Tauromeryx cauteroi



Palaeomeryidae. Charis gratia



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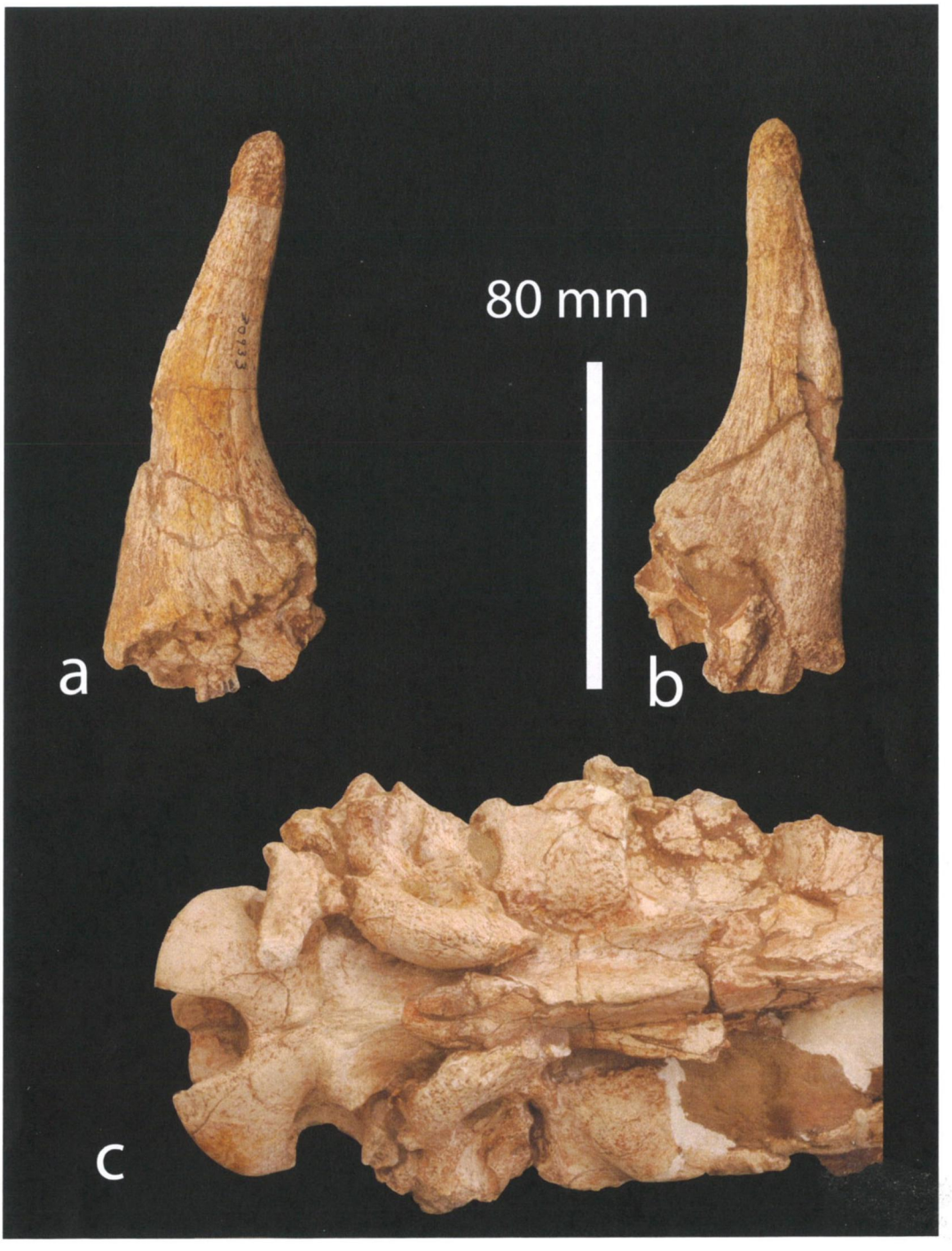
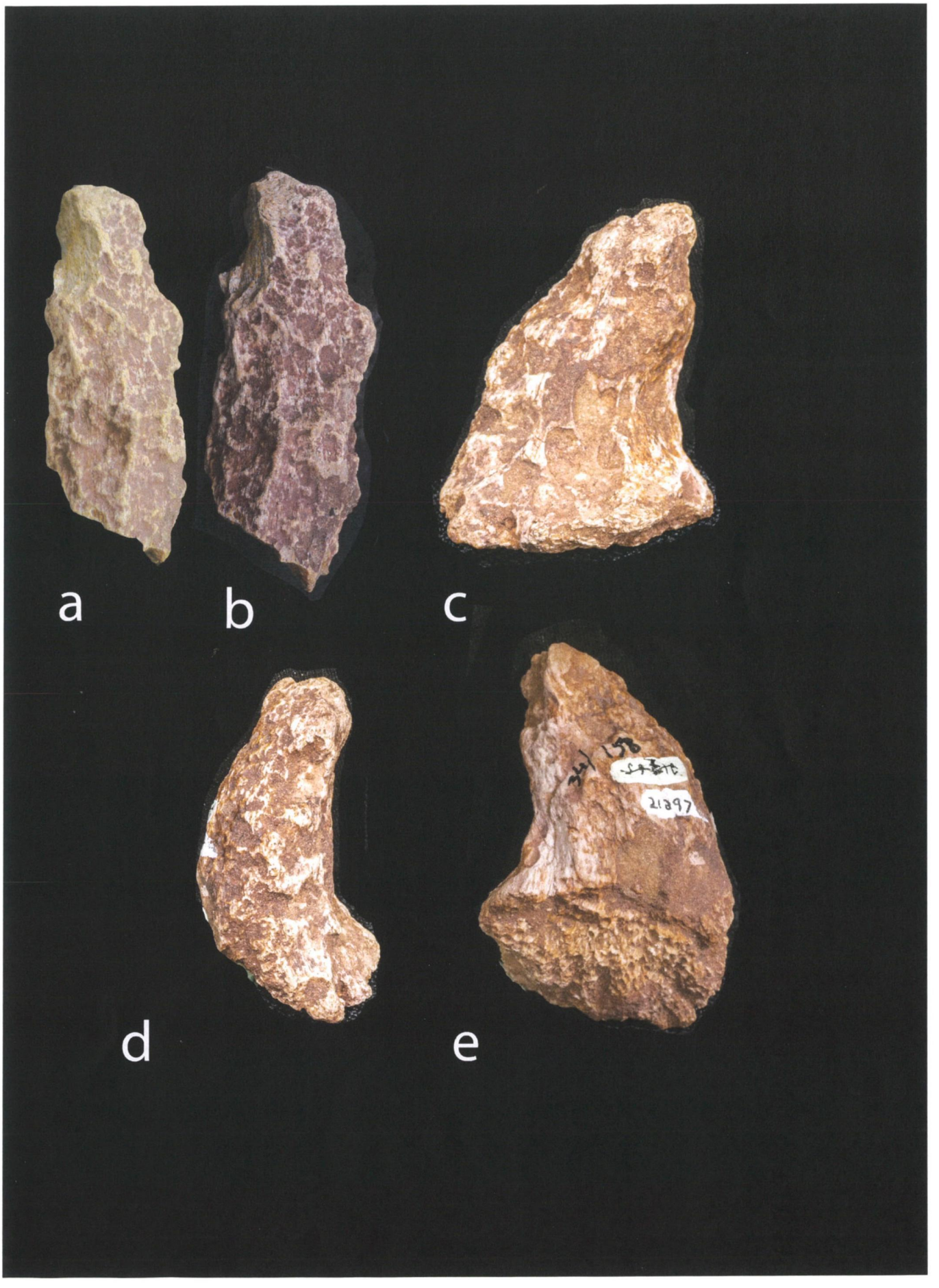
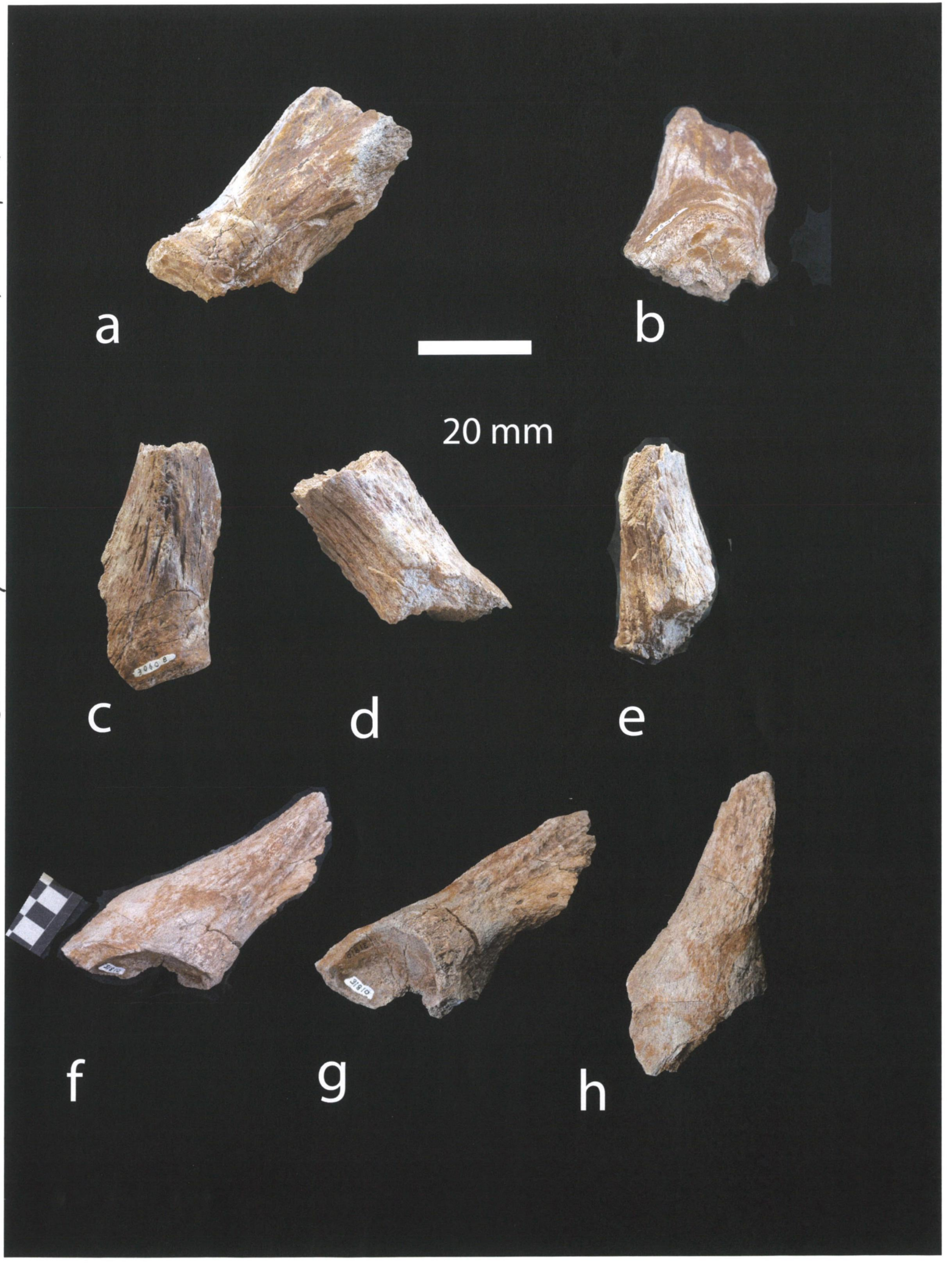


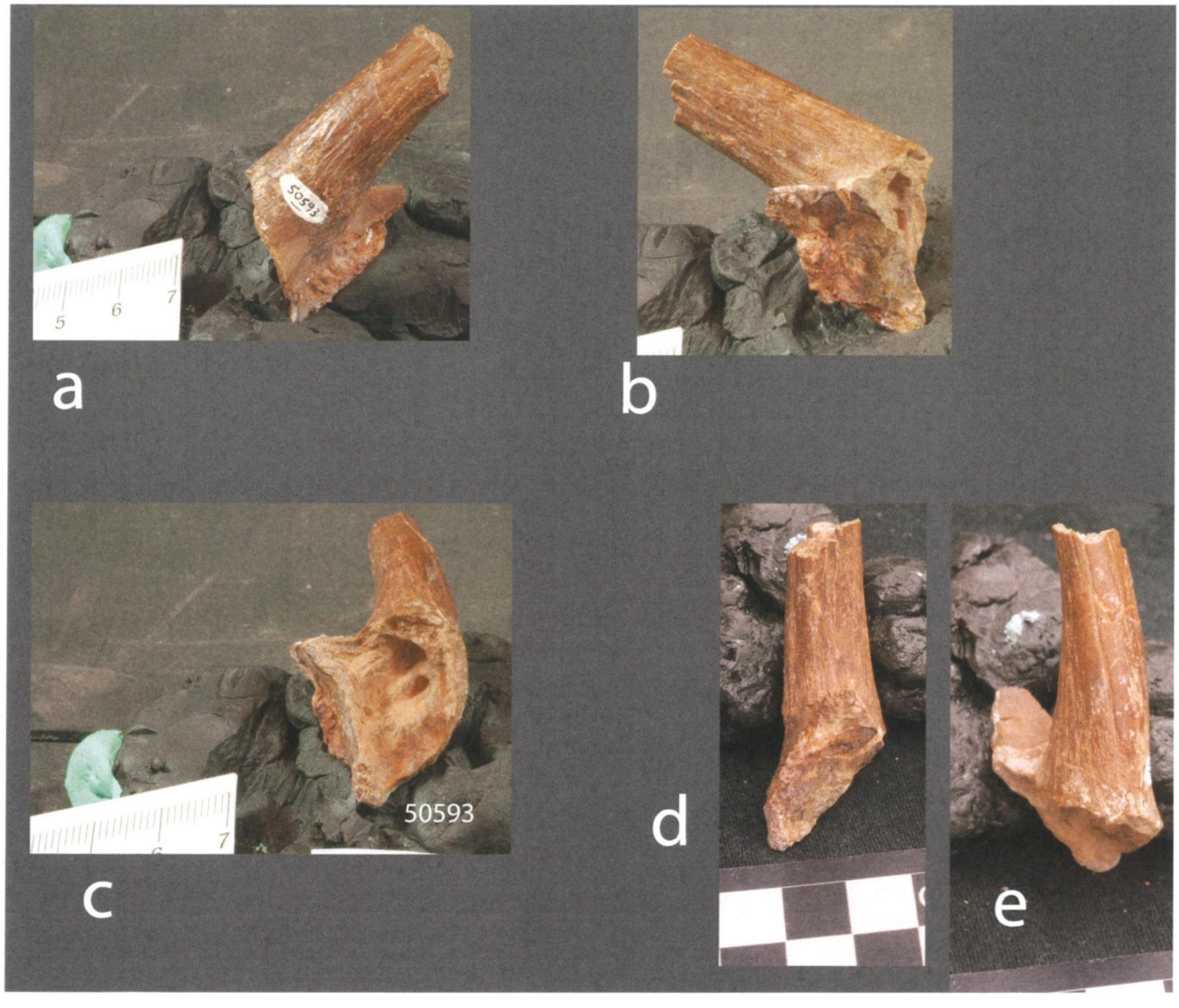
Palaeomeryidae: Fovea fossata



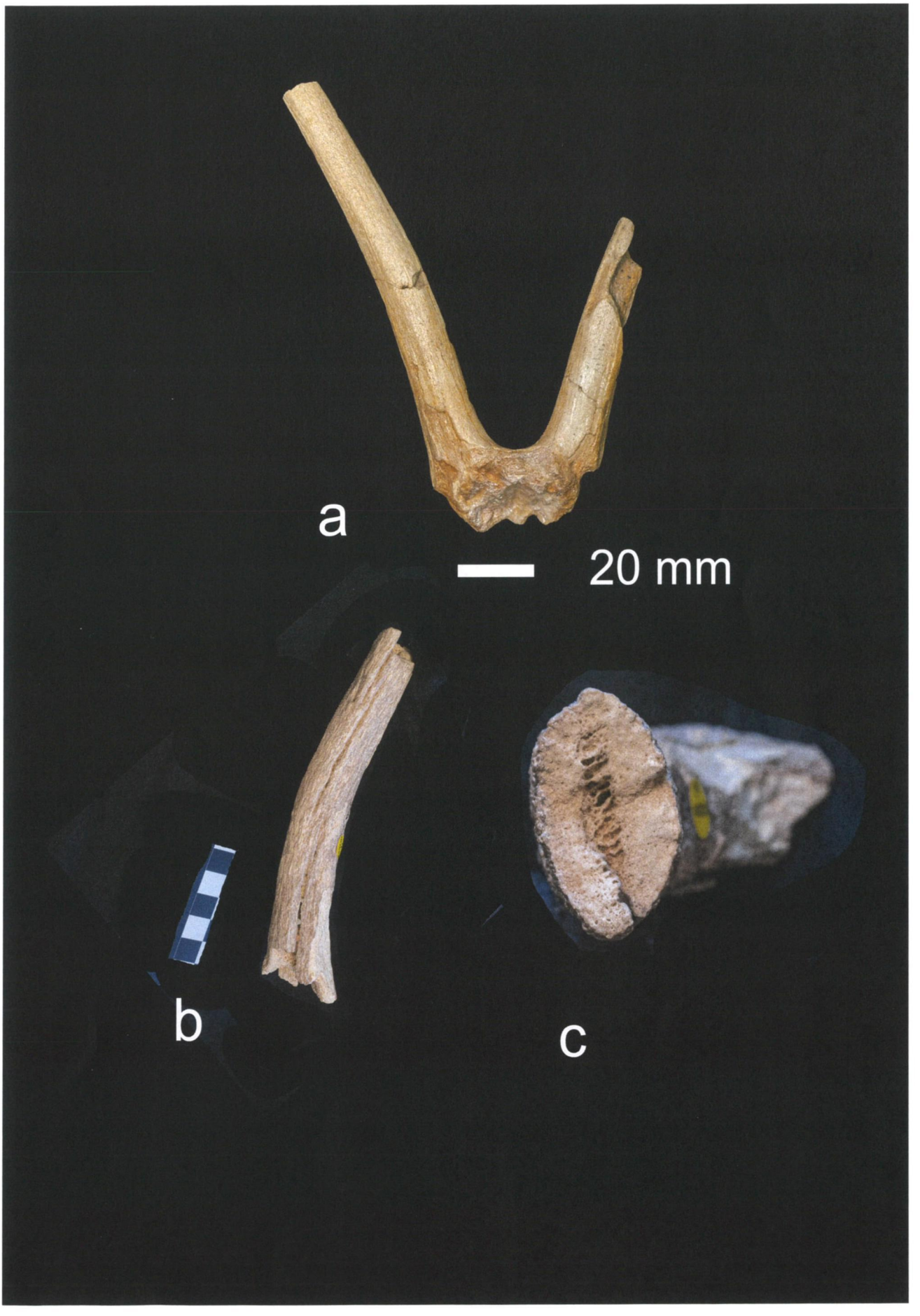
Palaeomerycidae : Goniomeryx Flynni



Palaeomerycidae: Lateralia morgani

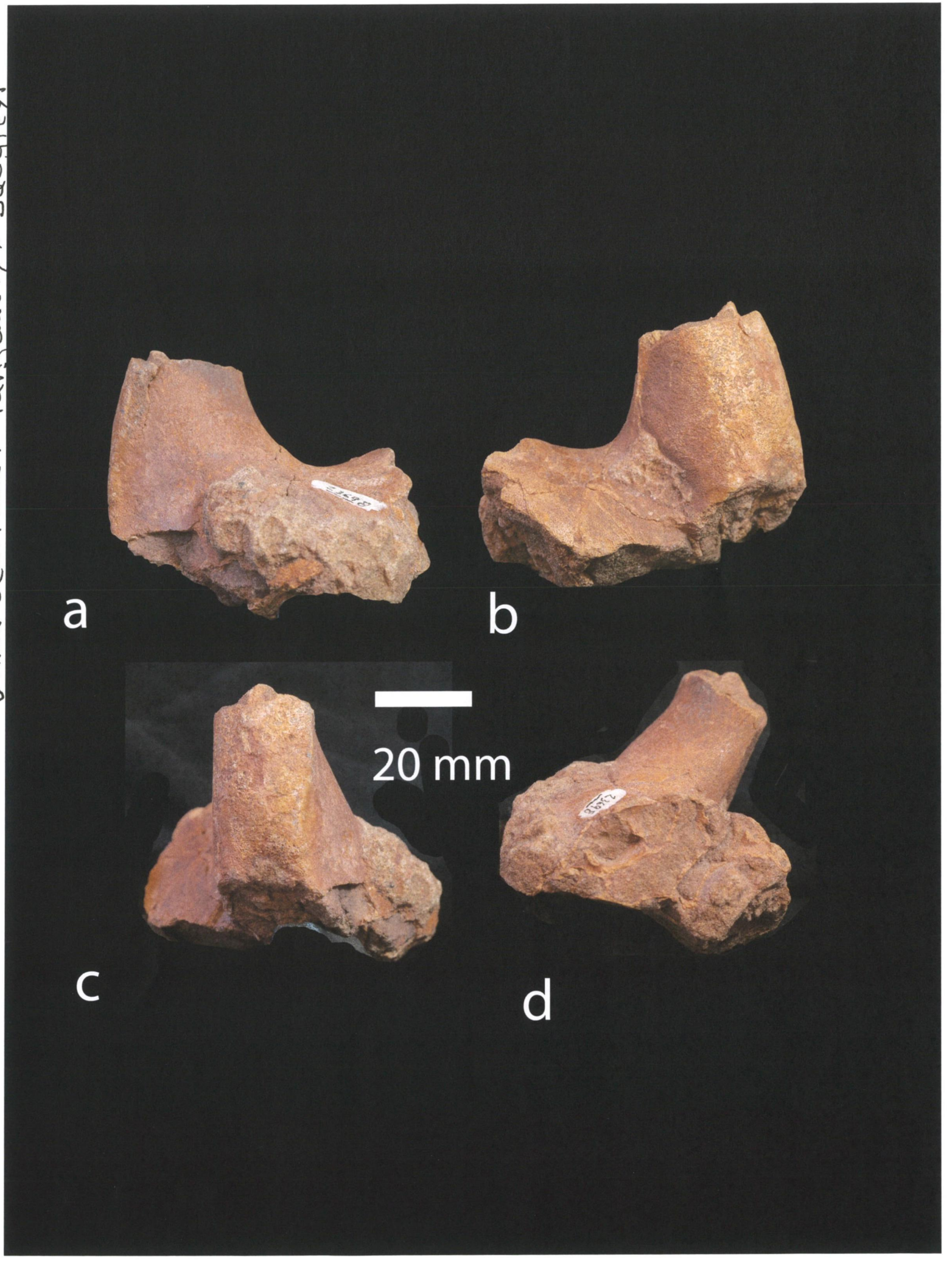


Climacoceridae : Vittoria soriae

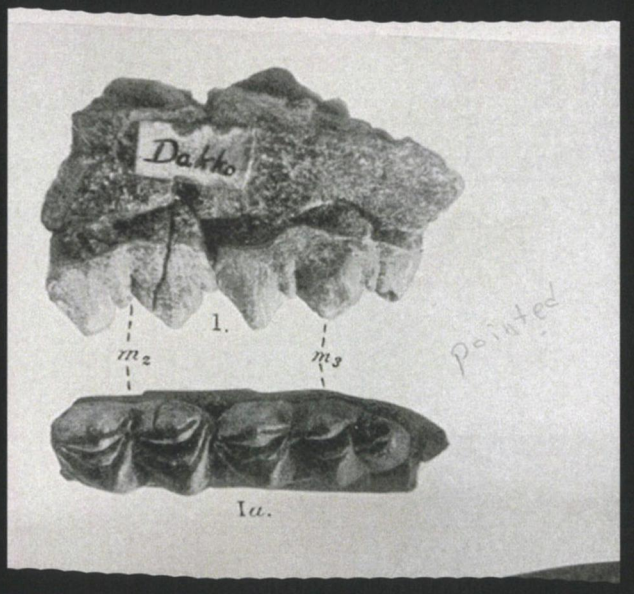


Vittoria soriae

Clima oceridae: Orangemeryx badgleyi



Giraffidae Progiraffinae Progiraffa exigua



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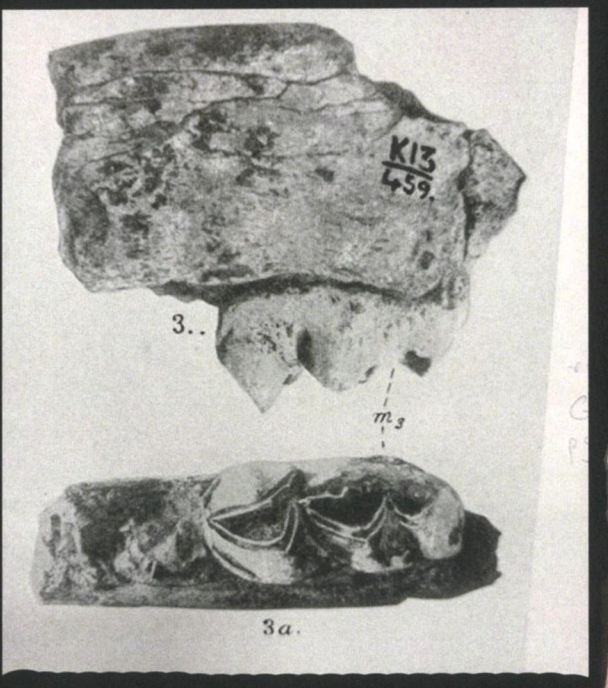


b

c

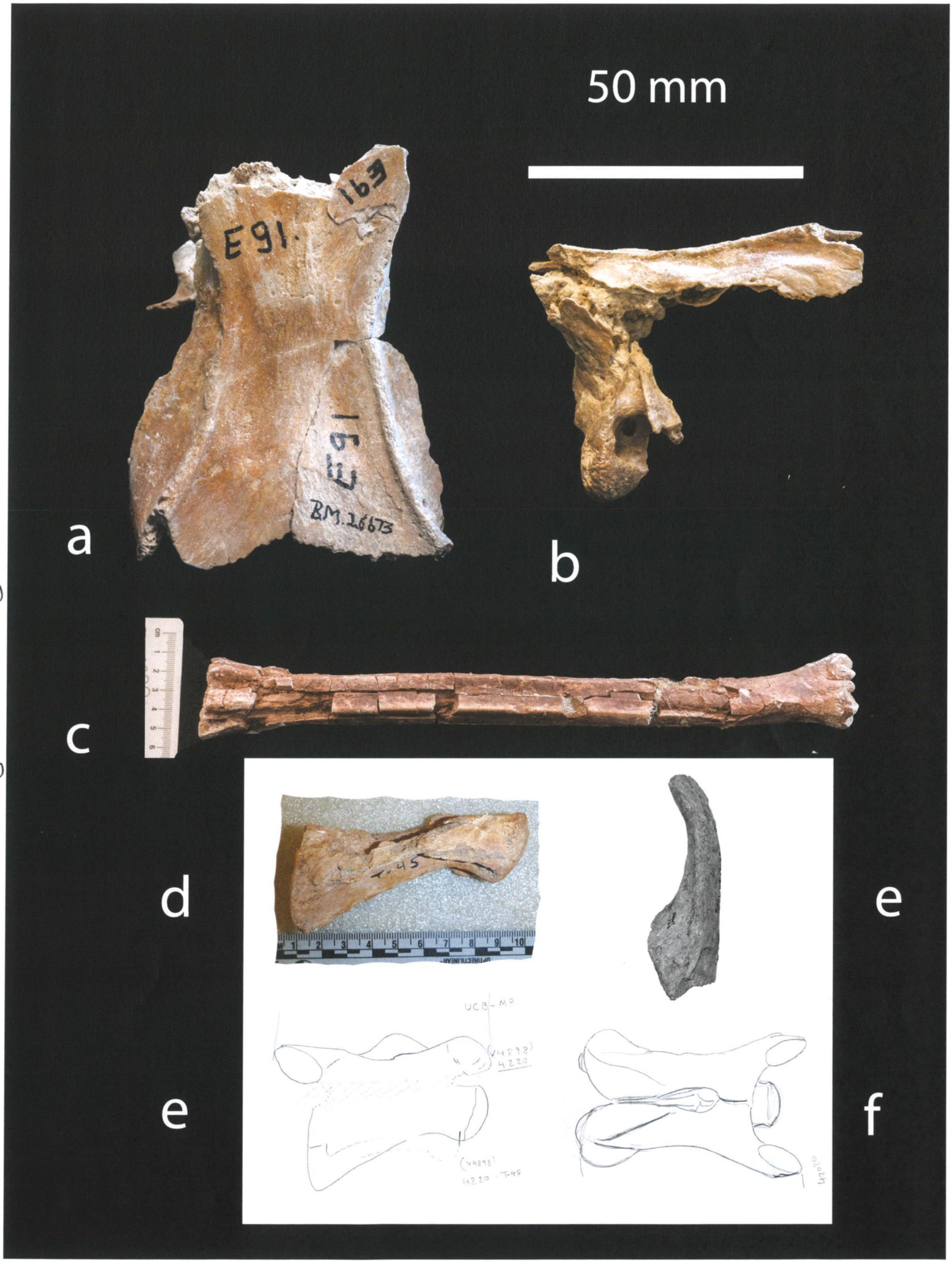
d

20 mm

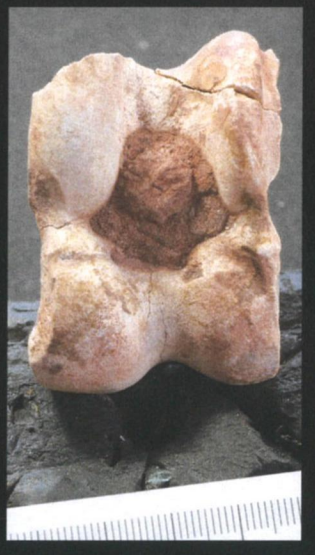
e

20 mm

Progiraffa exigua



.. Prosiratitia exigua



a

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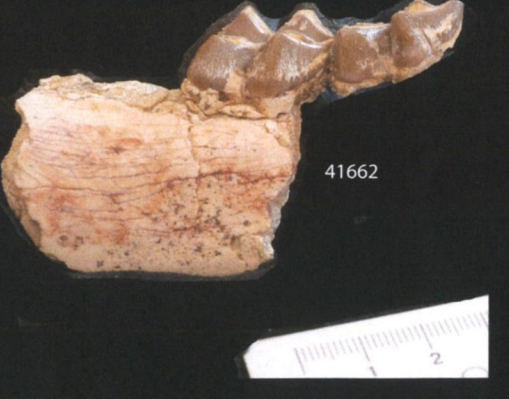

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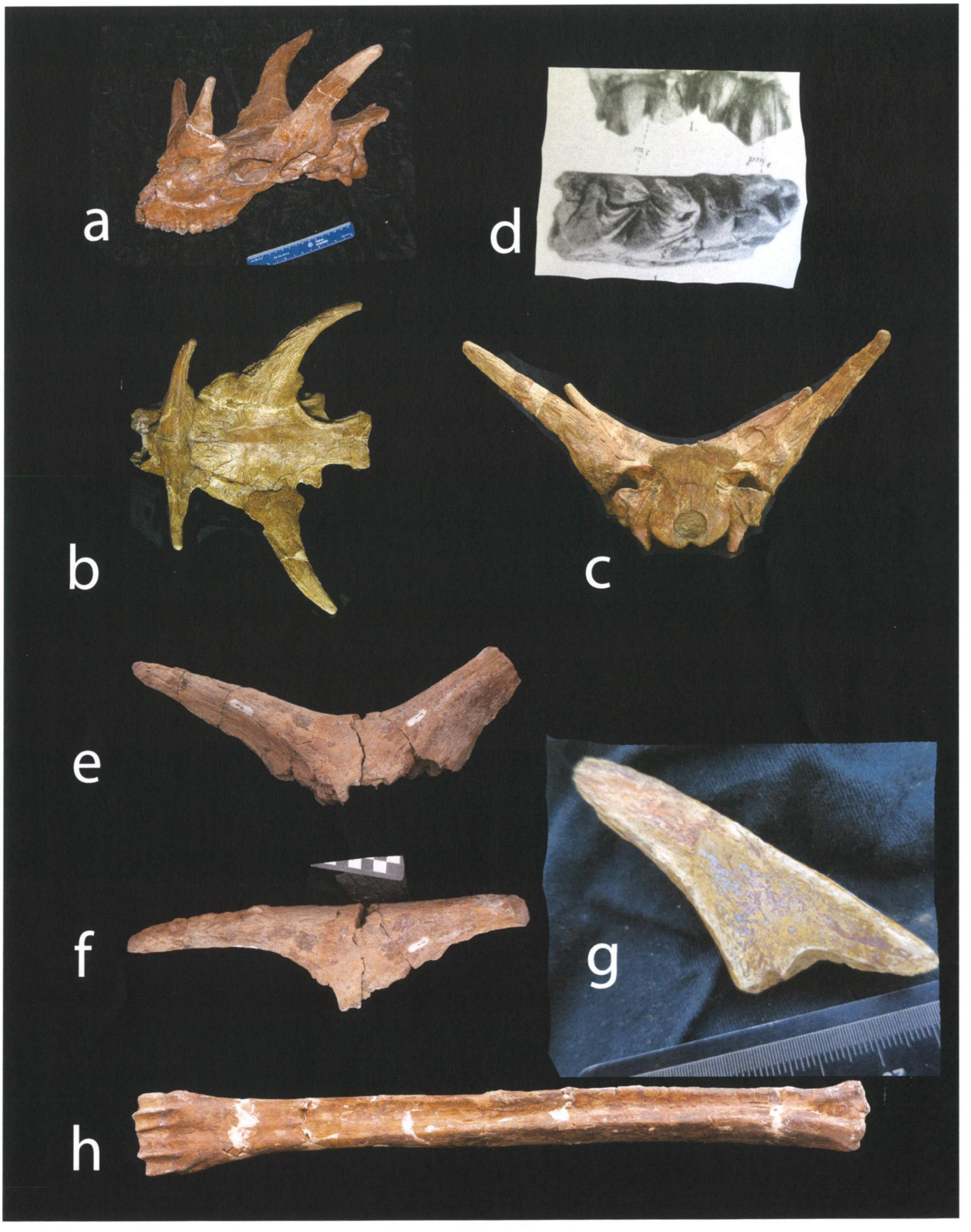
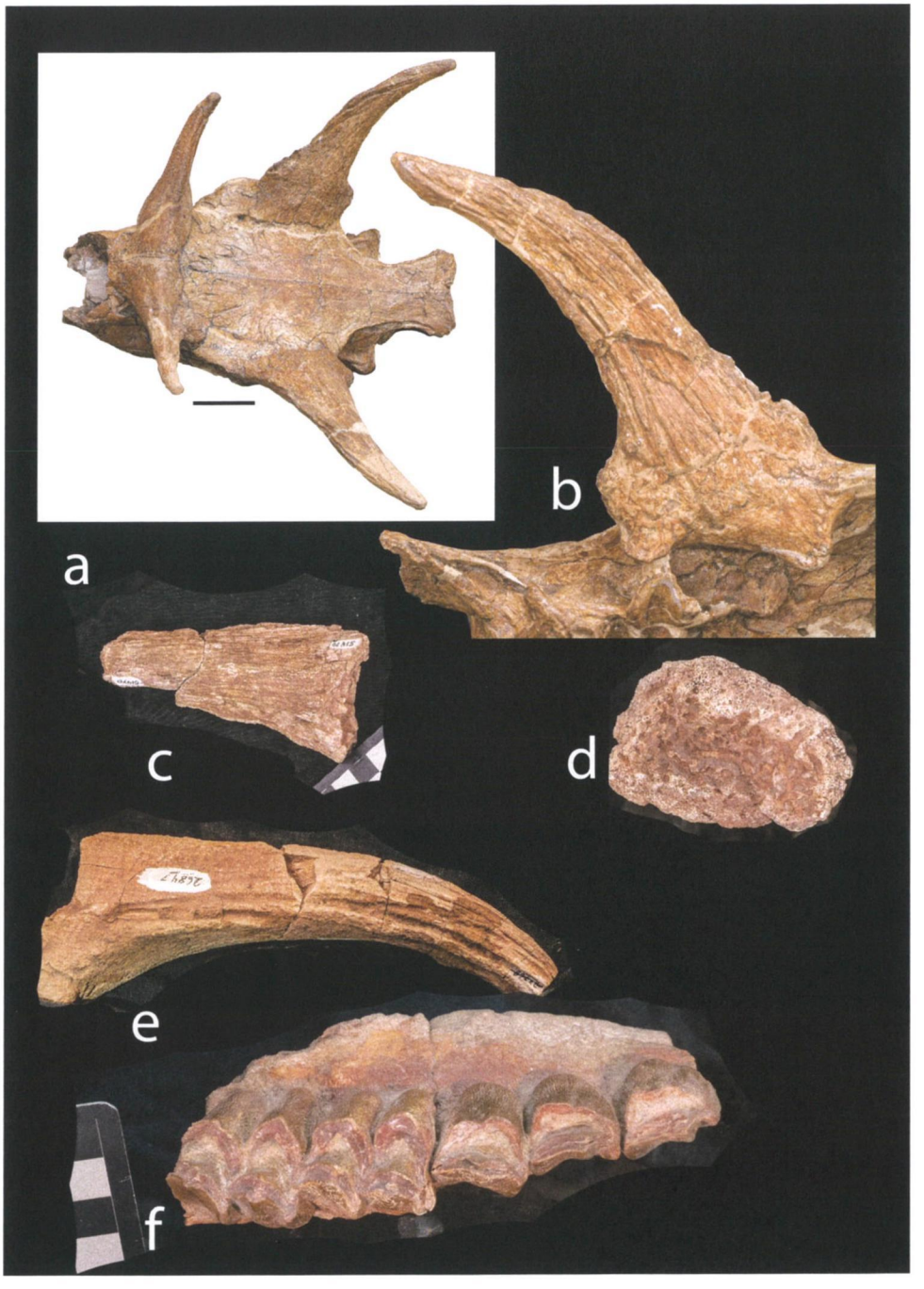
Progiraffa exigua (Georeomeryx georgalasi)

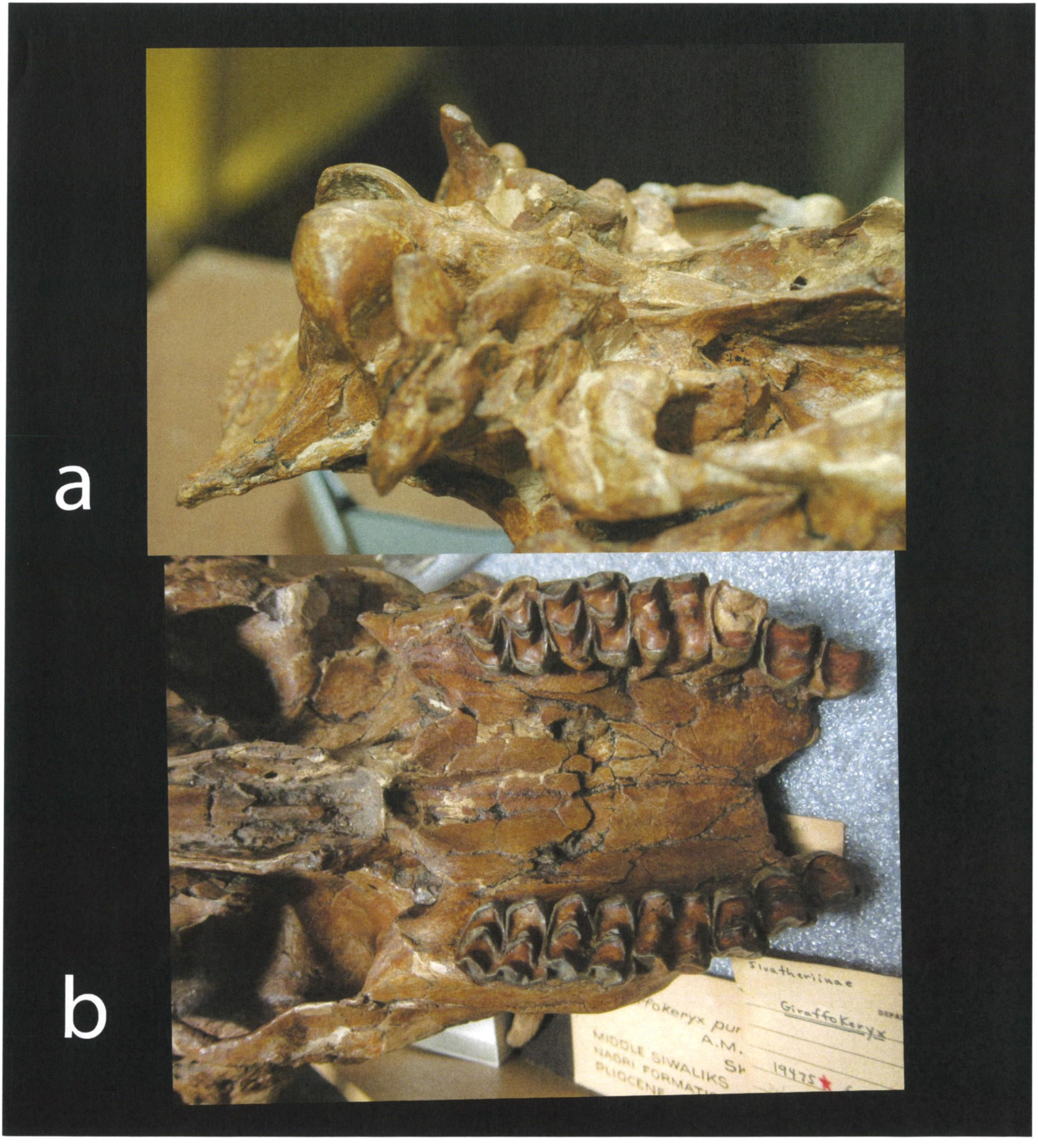
Giraffokeryx punjabiensis



Giraffokeryx punjabiensis



Giraffokeryx punjabiensis



"Giraffokeryx" primaevus

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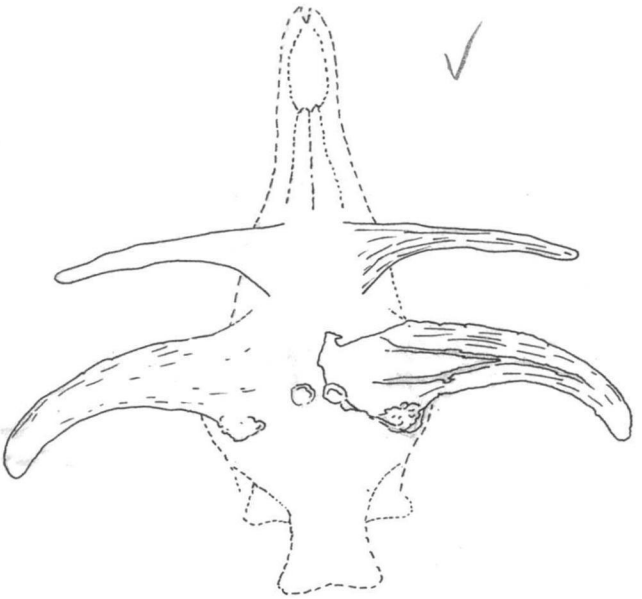

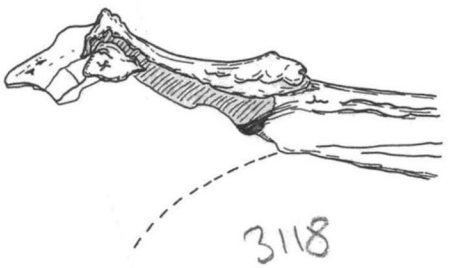

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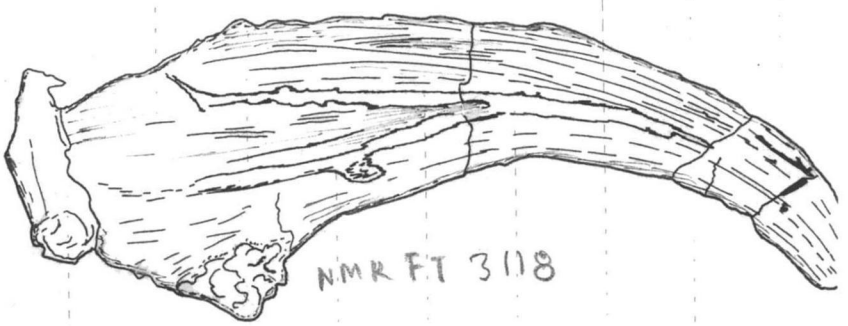
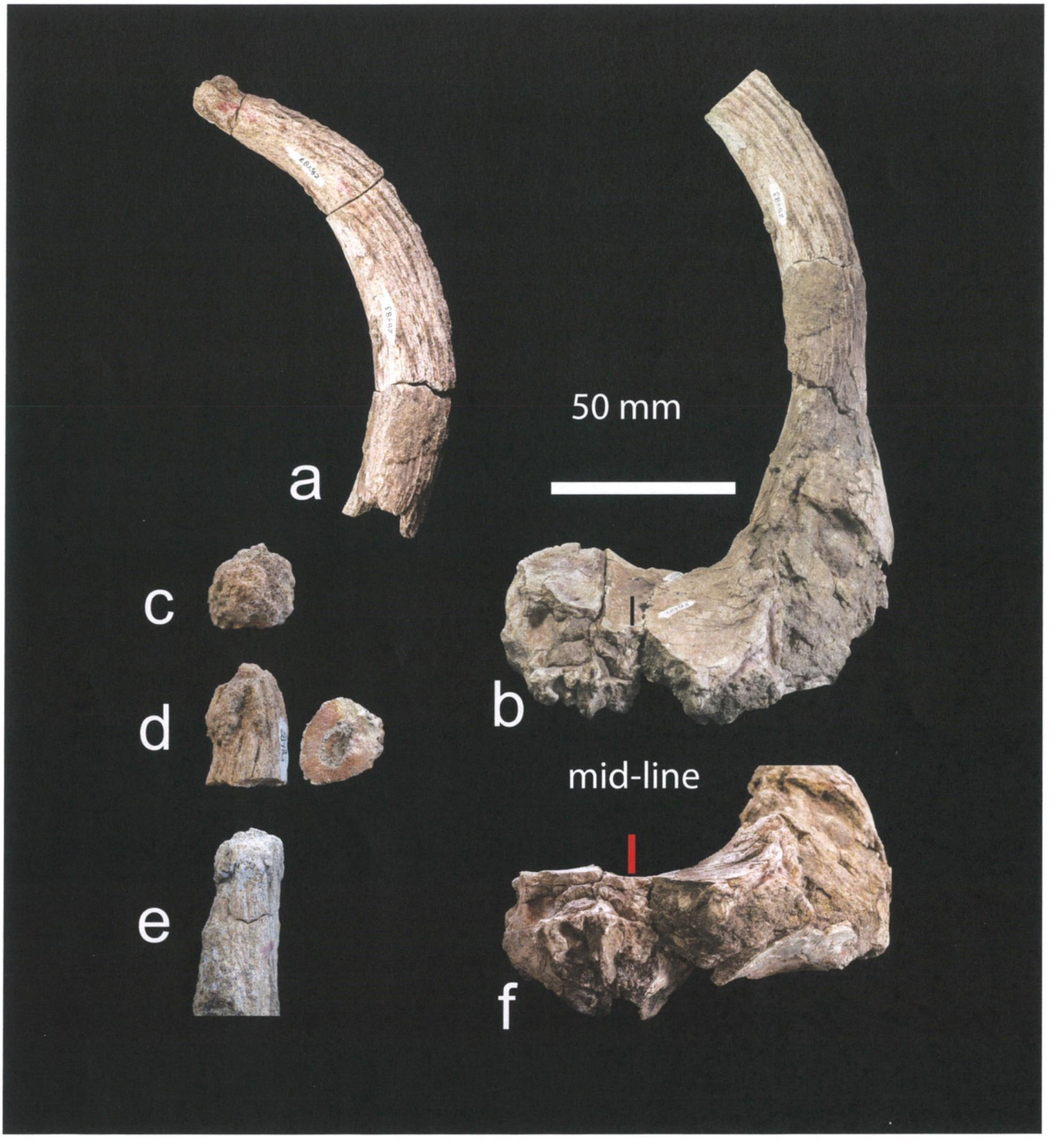


NMK FT 3118

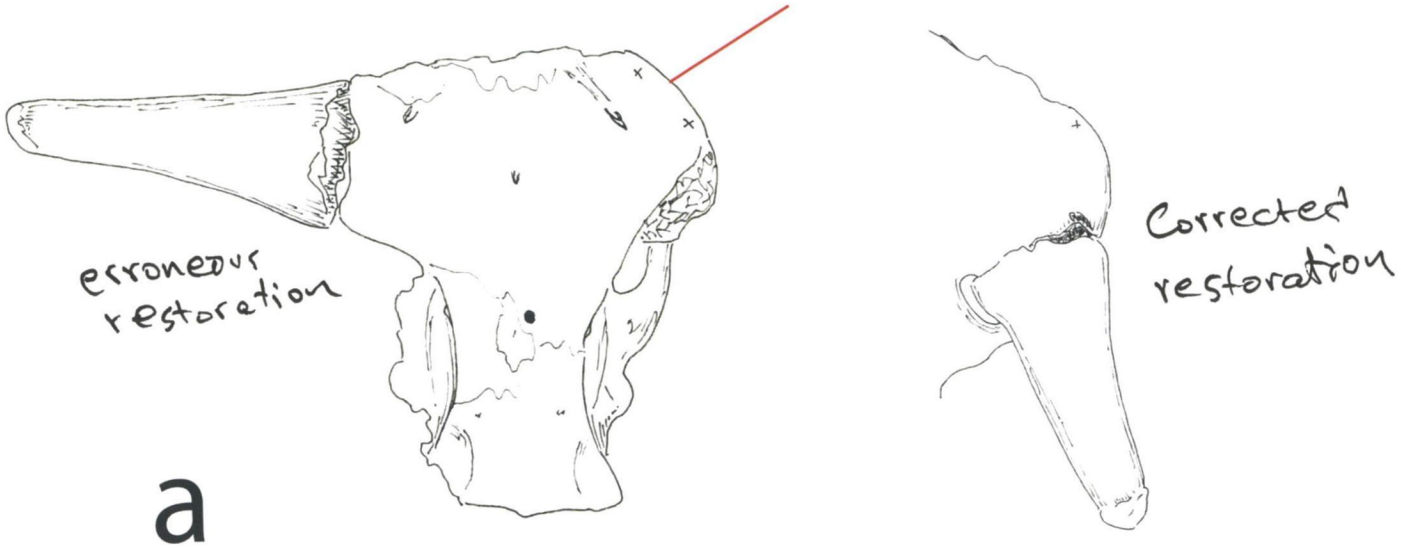
NMK FT 3119

Okapiinae : Va pilbeami



Uapilbeami
a
b
Okapia
c
Decenatherium asiaticum
d
Giraffokeryx
e
Palaeotragus rouenii
f
Orea leptia
g
Giraffa
h
Bohlinia
i
Uapilbeami

Holotype: Iujanatherium hazimi



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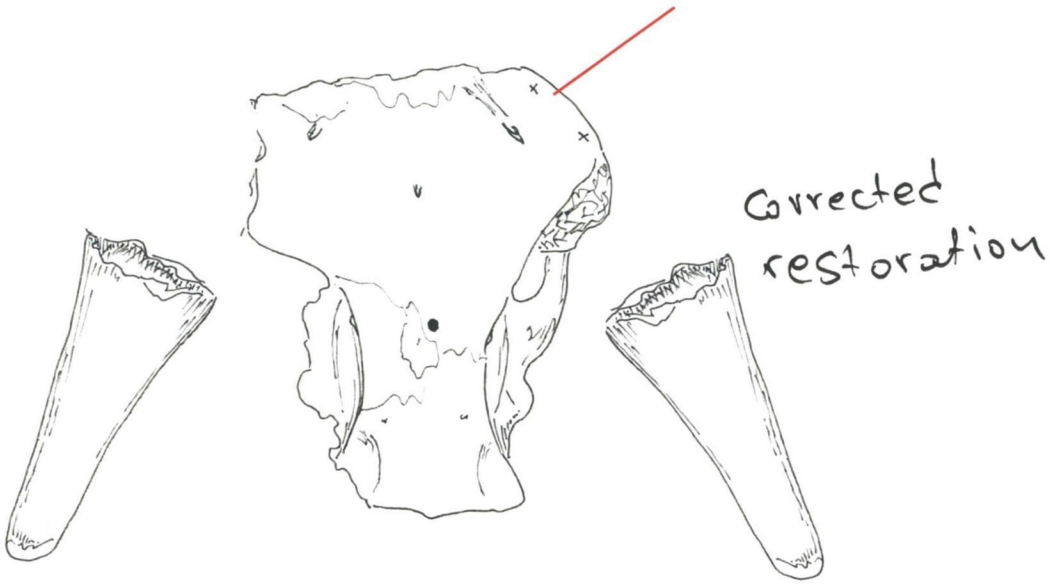

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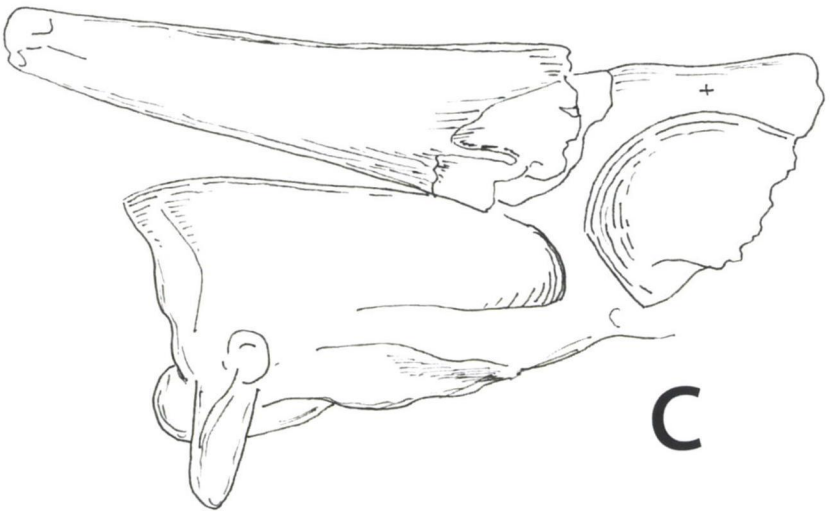

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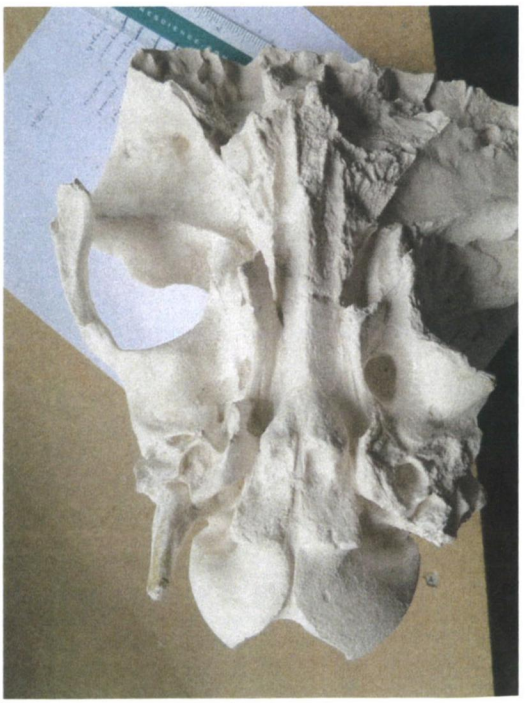
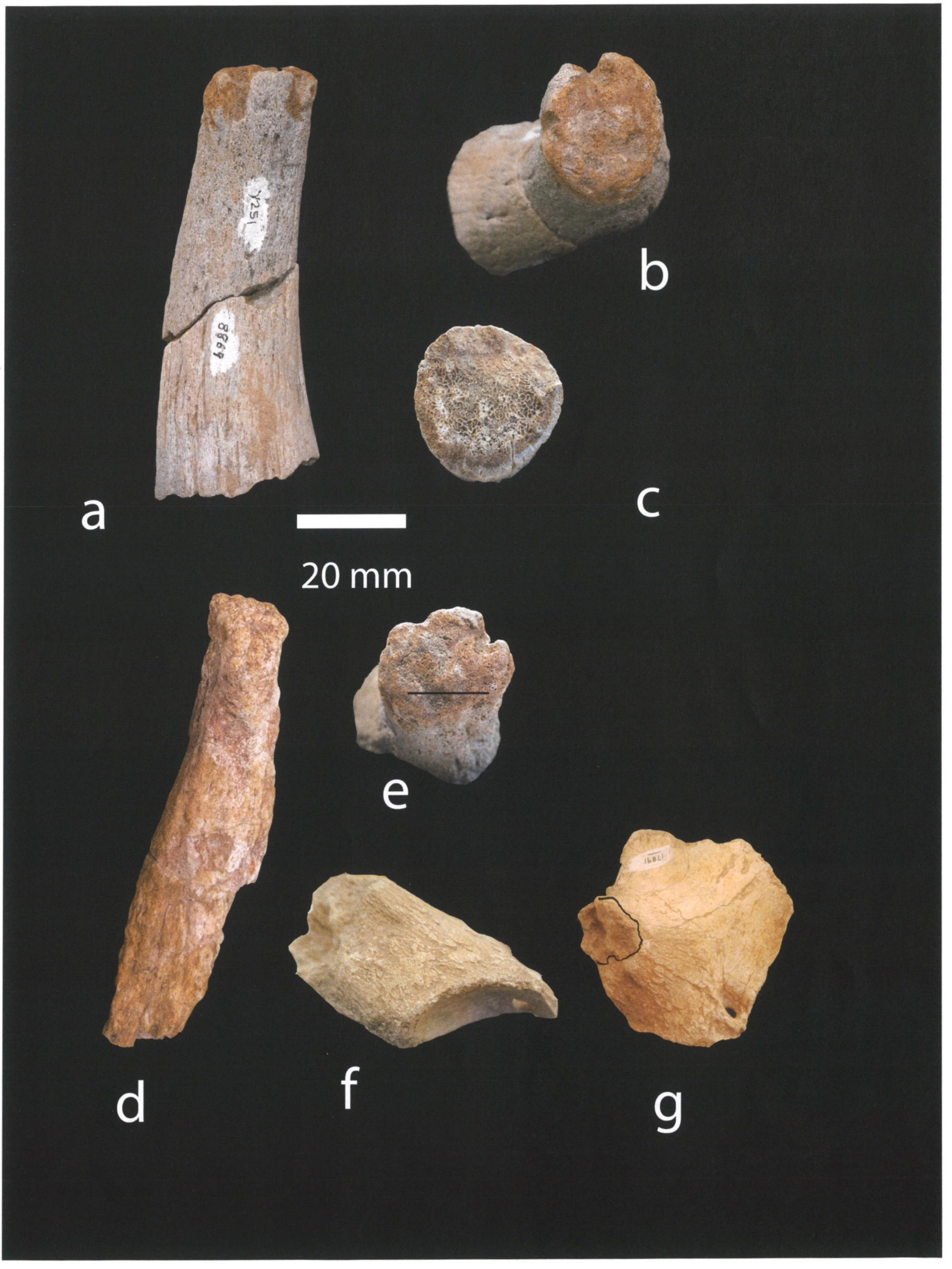
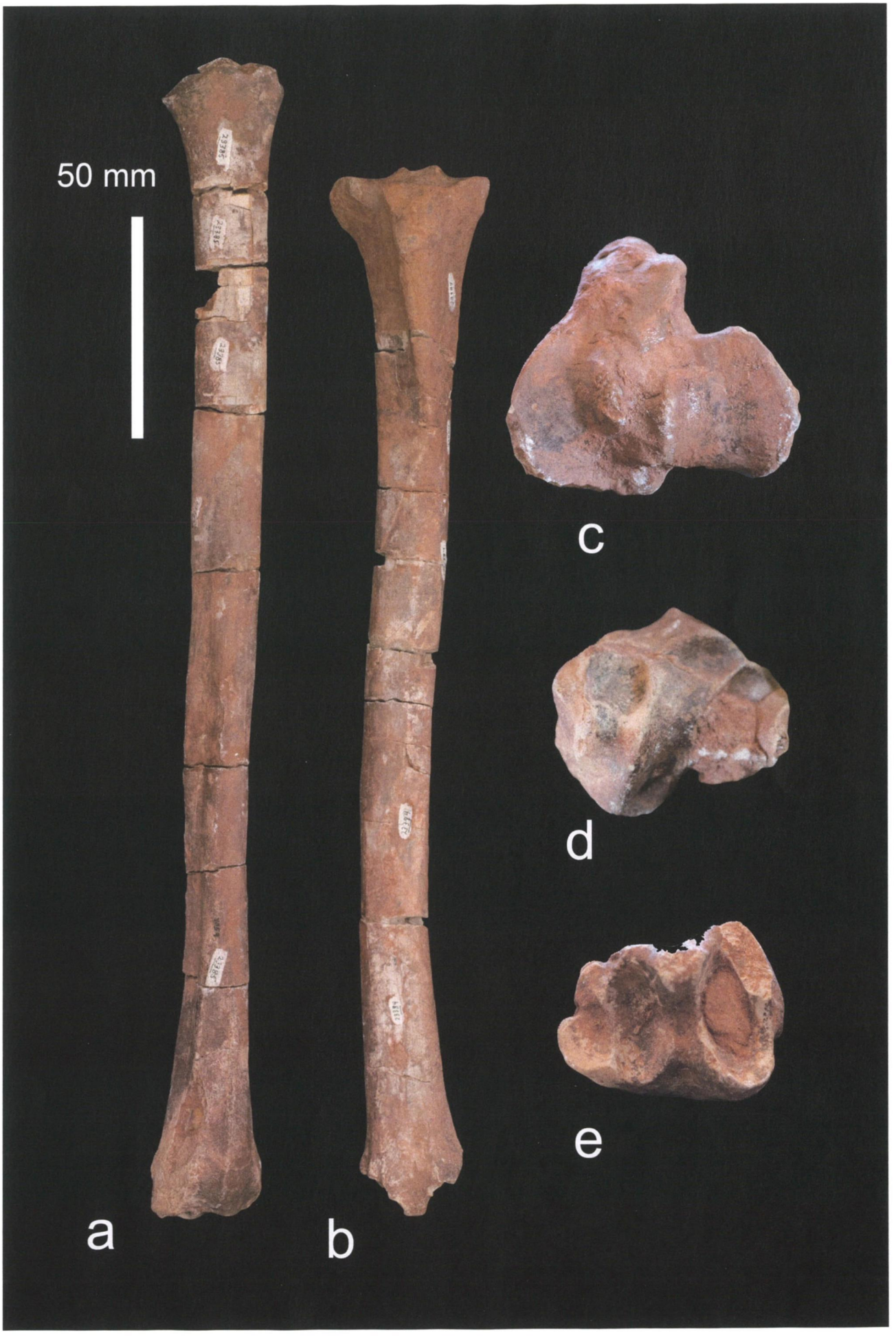


Samotheriinae: Injanatherium hazimi



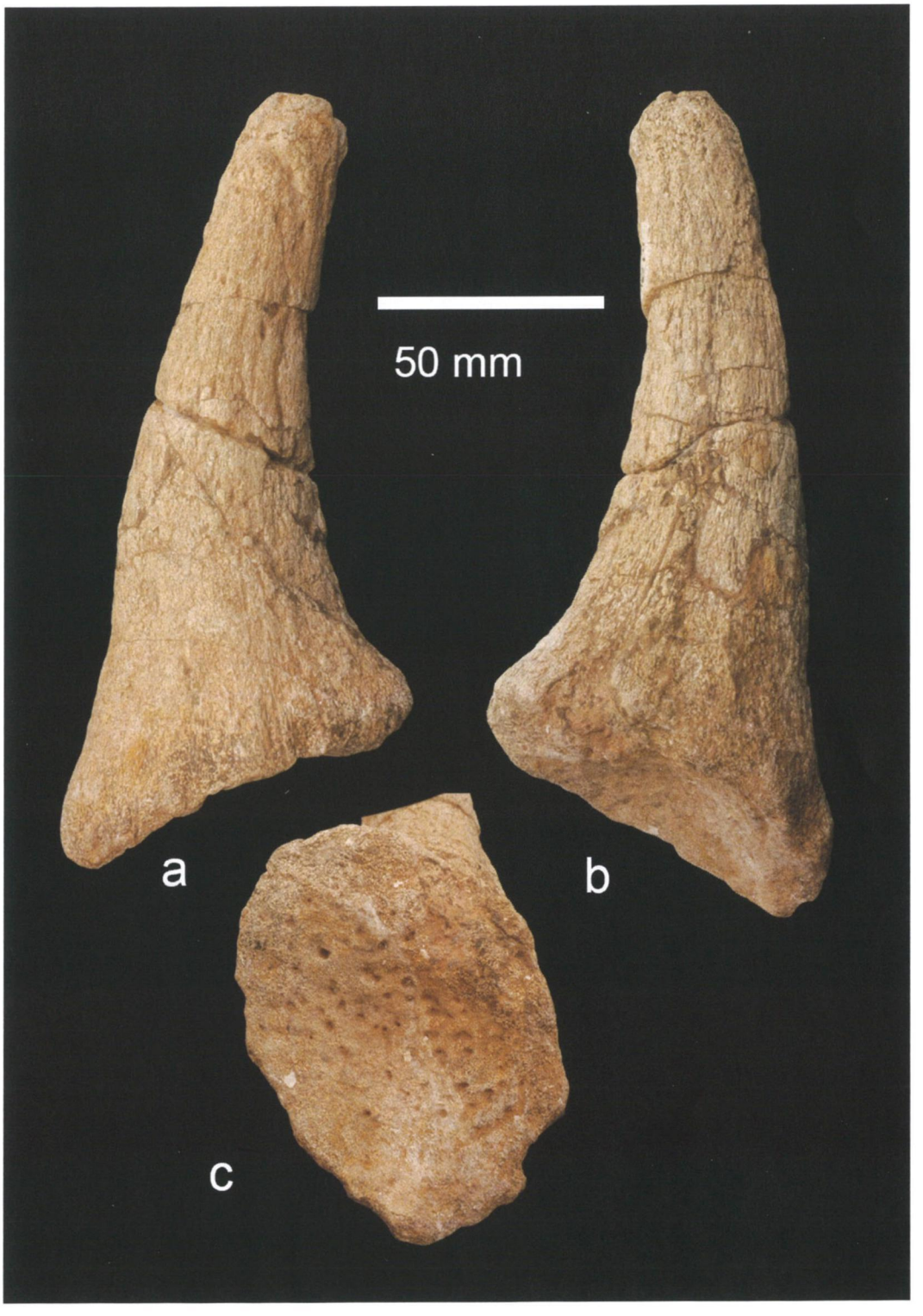
Giraffinae: Orea leptia



Orca leptia

Orca
leptica
Giraffa
Okapia
a
b
c

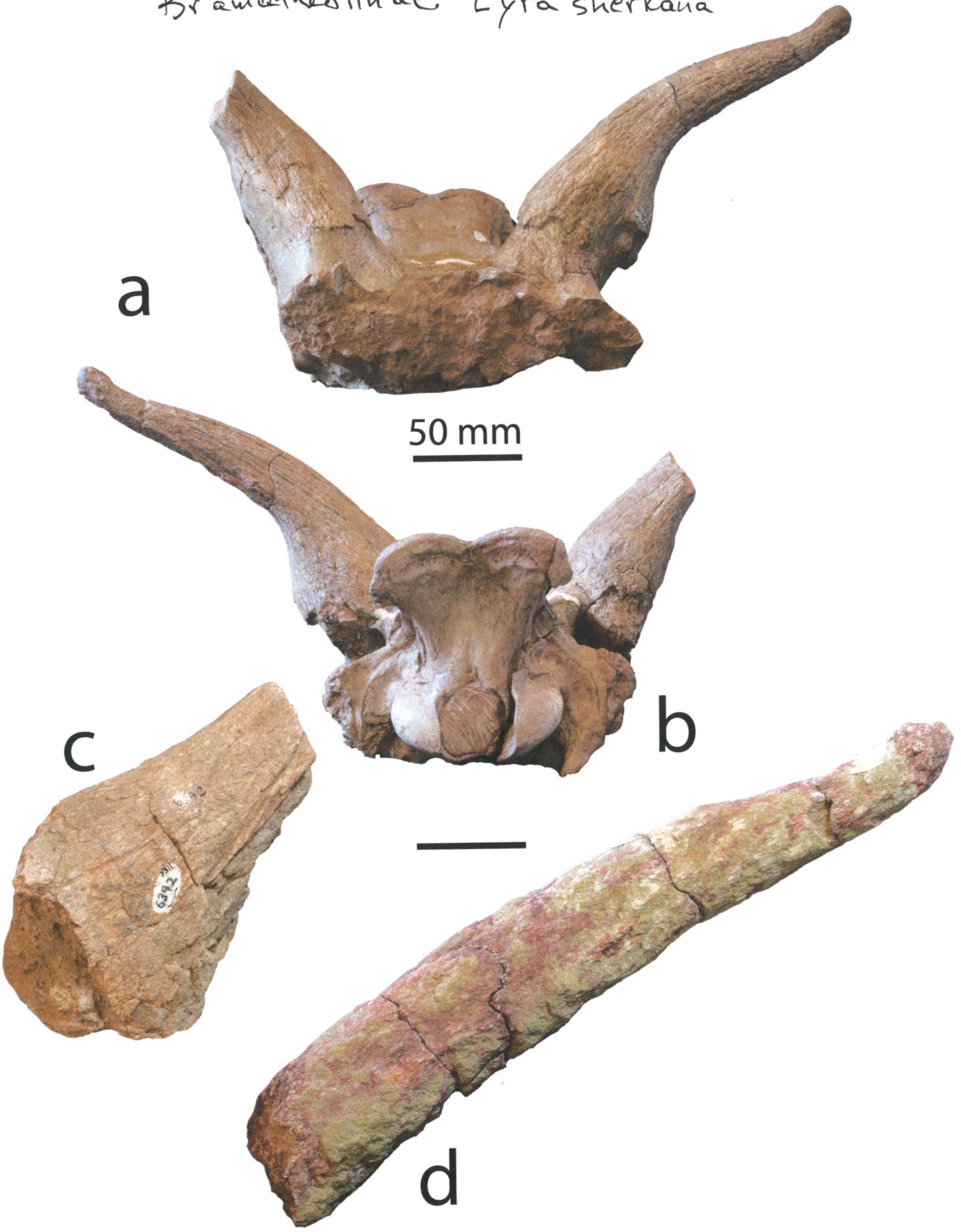
Giraffinae: Giraffa punjabiensis



Giraffa sivalensis

50 mm

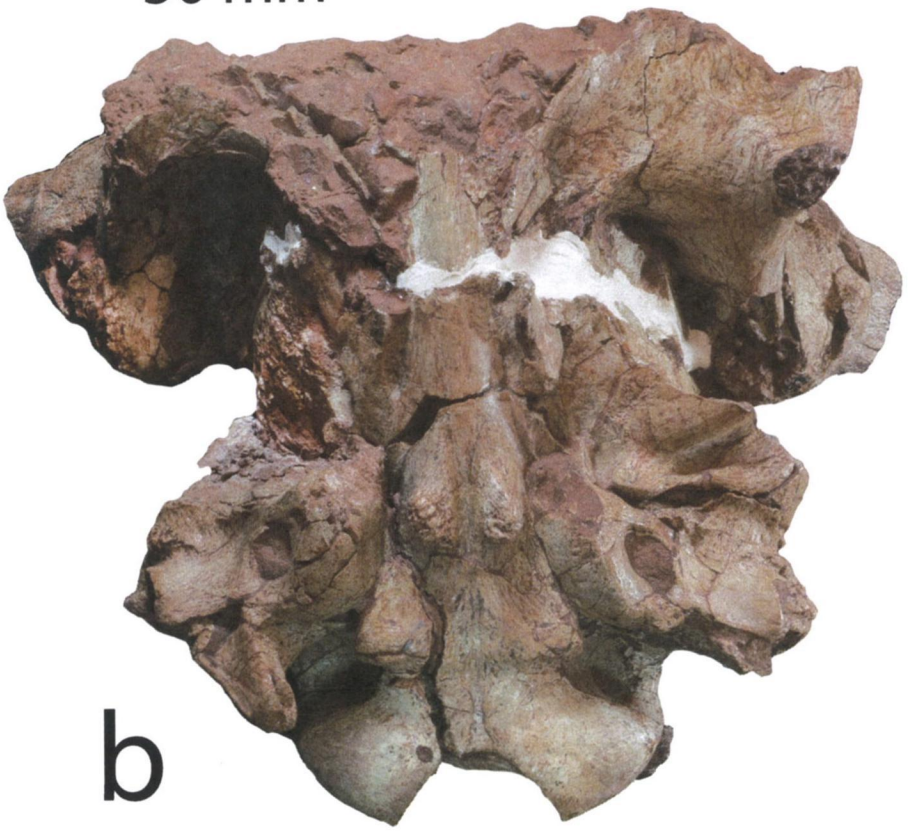
Bramatherinae: Lyra sherkana



Lyra sherkana

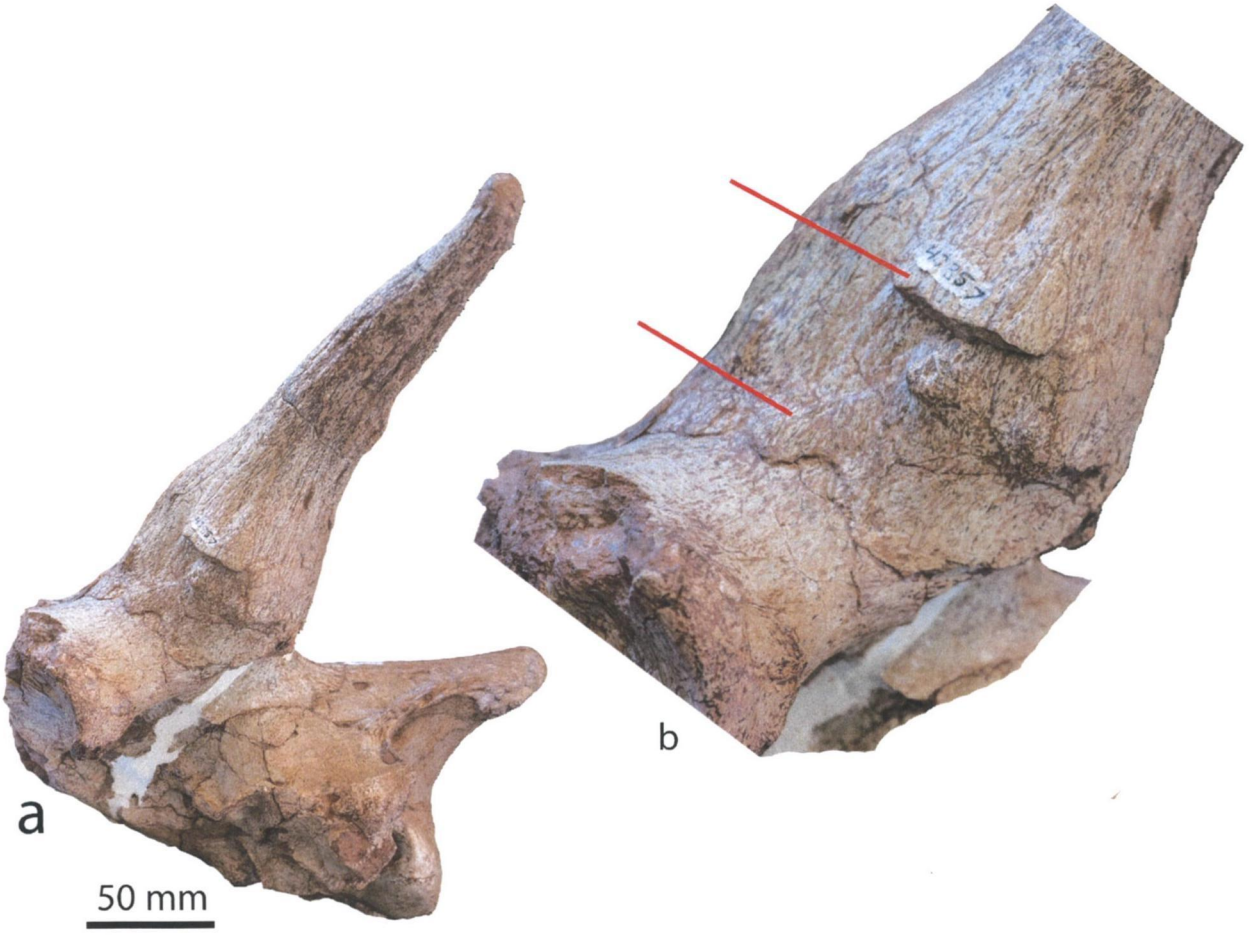
a

50 mm



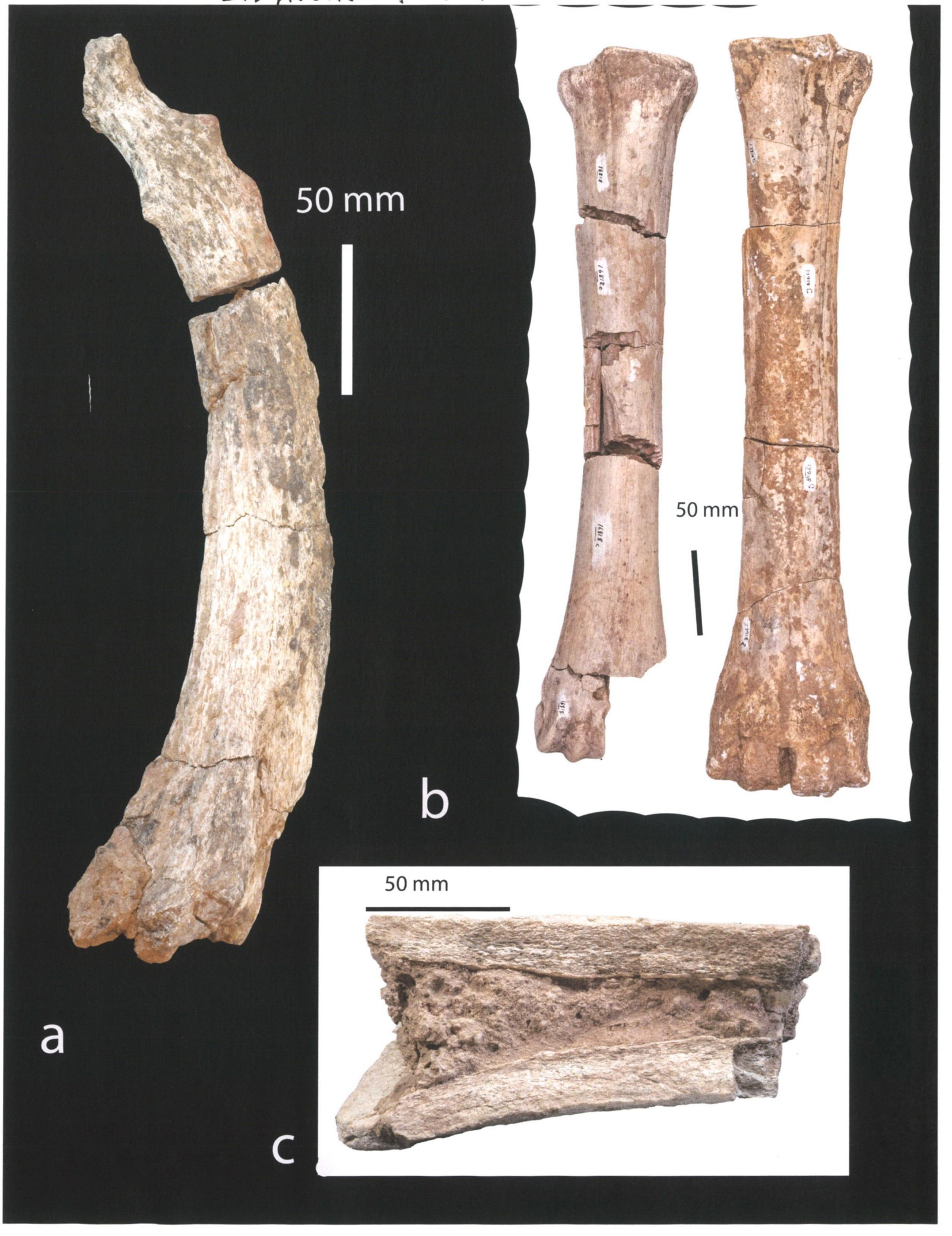
b

Lyrasherkana



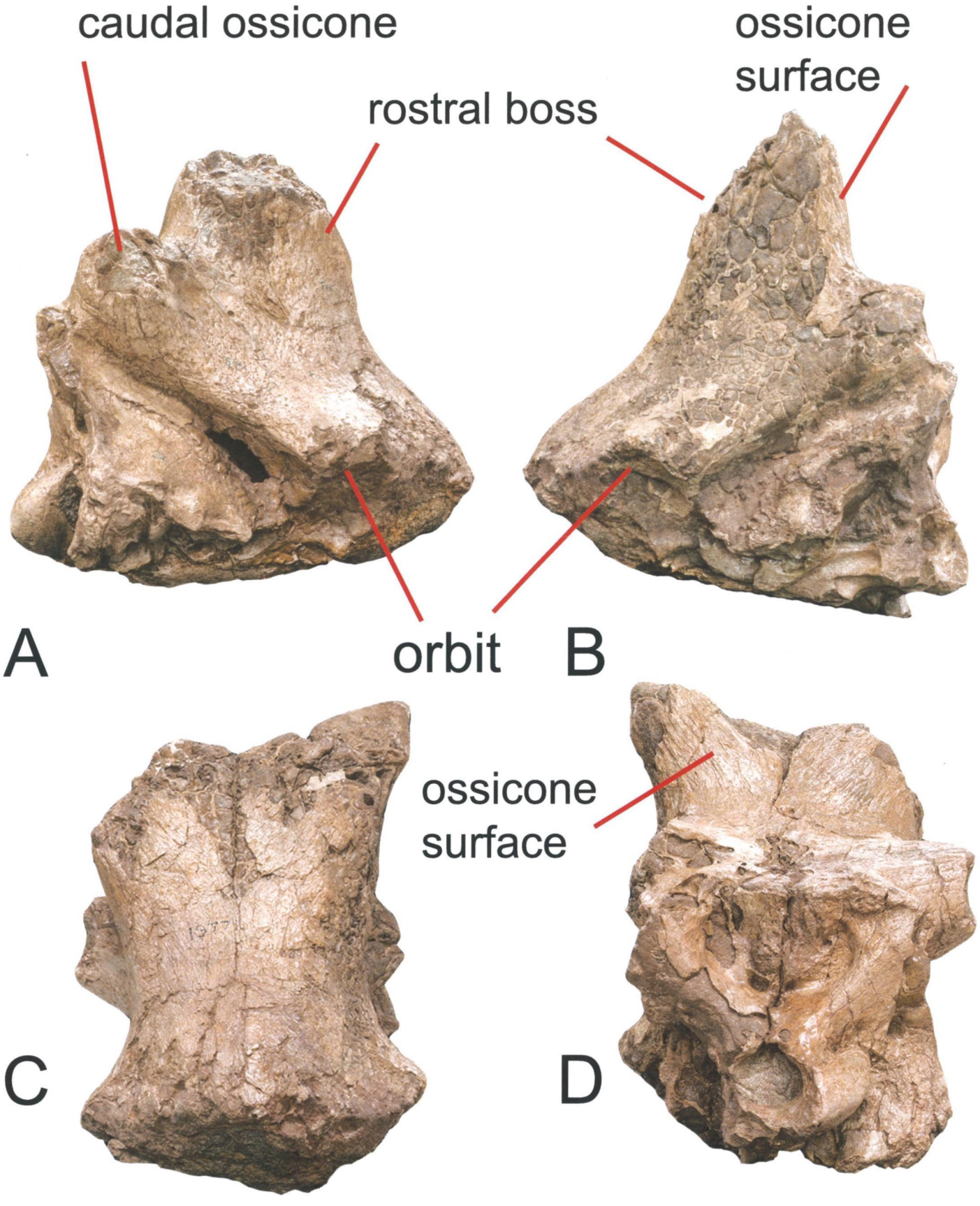
Bramatheriinae : Decennatherium asiaticum

Libytherium proton

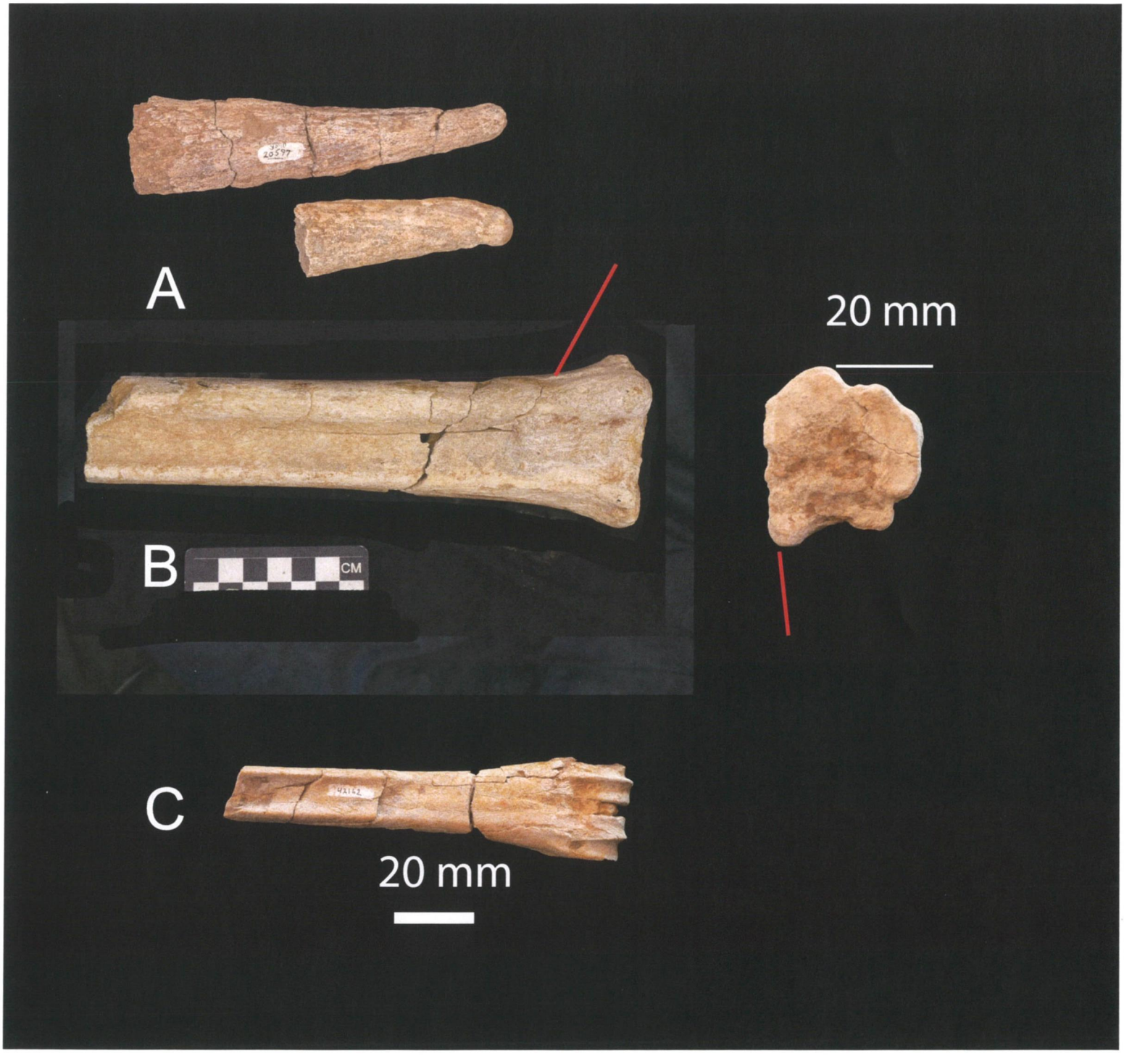


Bramatherium megacephalum

Bramatherium perimense



Bramiscus nanos or micros

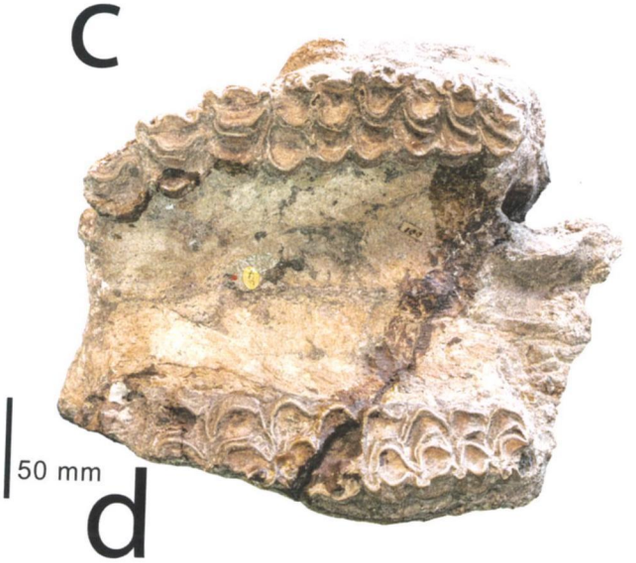


Sivatheriinae: Sivatherium giganteum

a

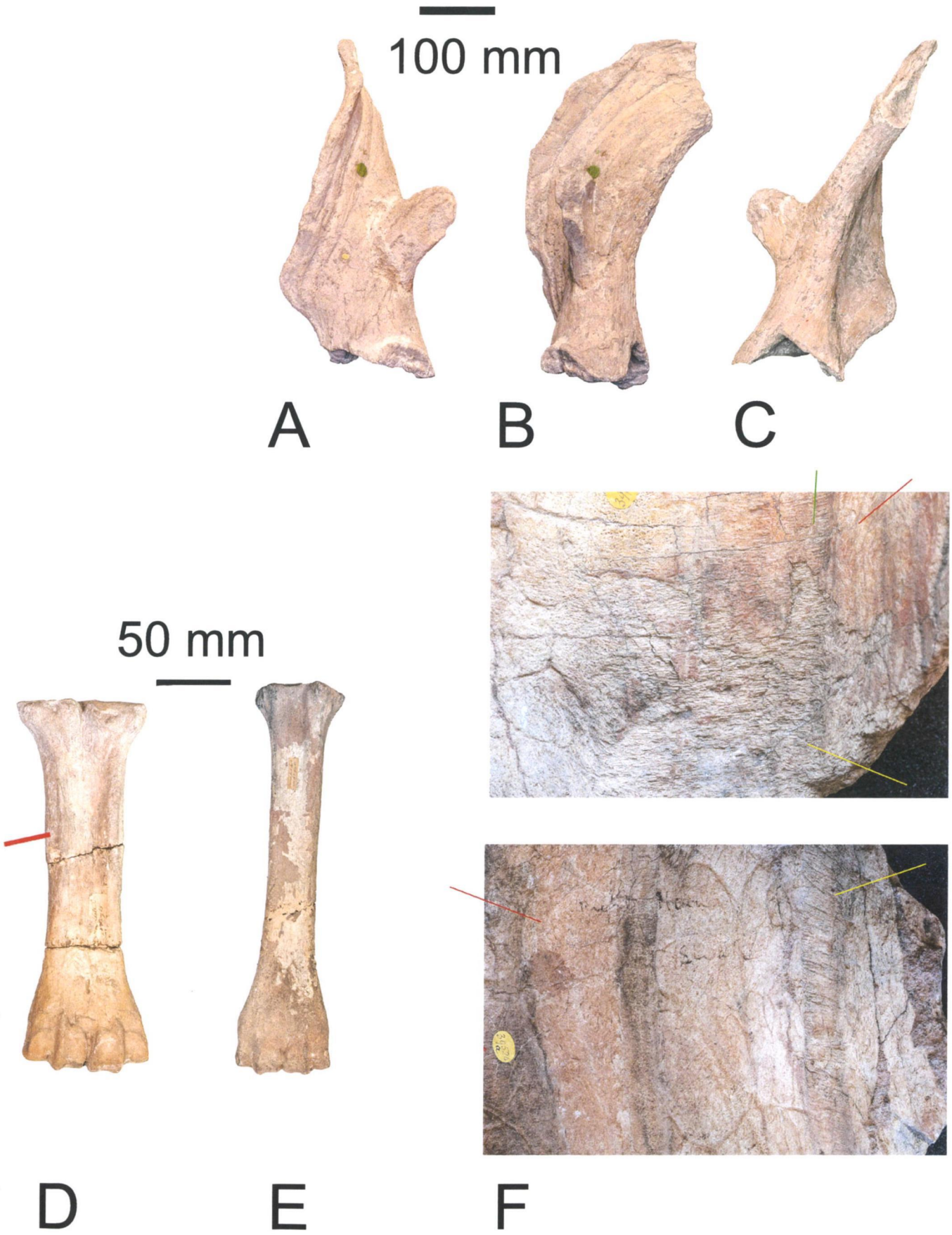
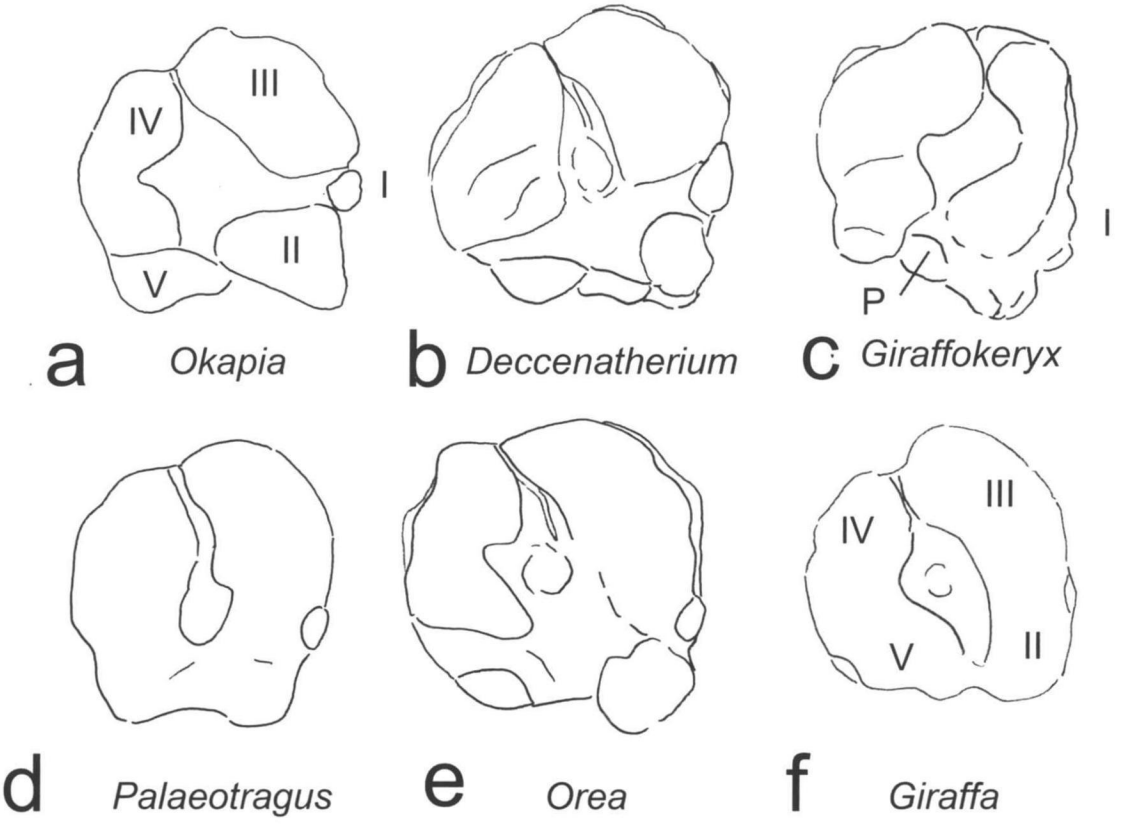
b

c



d

Sivatherium giganteum



Proximal metatarsals