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Stratigraphic context and paleoenvironmental significance of minor taxa (Pisces, Reptilia, Aves, Rodentia) from the late Early Pleistocene palaeoanthropological site of Buia (Eritrea)

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ABSTRACT

The Buia Homo site, also known as Wadi Aalad, is an East African paleoanthropological site near the village of Buia that, due to its very rich yield from the late Early Pleistocene, has been intensively investigated since 1994. In this paper, which reports on the finds of the 2010-2011 excavations, we include new fossil evidence on previously identified taxa (i.e., reptiles), as well as the very first description of the small mammal, fish and bird remains discovered. In particular, this study documents the discovery of the first African fossil of the genus *Burhinus* (Aves, Charadriiformes) and of the first rodent of the site. This latter is identified as a thryonomyid rodent (cane rat), a relatively common taxon in African paleoanthropological faunal assemblages. On the whole, the new occurrences documented within the Buia vertebrate assemblage confirm the occurrence of taxa characterized by strong water dependence. The palaeoenvironmental characteristics of the fauna is confirmed as fully

compatible with the evidences, obtained through sedimentology and facies analysis, documenting the sedimentary evolution of fluvio-deltaic and lacustrine systems

KEY WORDS: Fossil Vertebrates, Pisces, Reptilia, Aves, Mammalia, *Burhinus*, Thryonomyidae, Early Pleistocene, Buia, Eritrea

Introduction

The Buia-Dandiero area (100 Km south of Massawa, in the northern Danakil Depression, Eritrea; Figure 1A) is well known for the one-million-year-old *Homo* cranium from Buia (Abbate et al., 1998; Macchiarelli et al., 2004; Bondioli et al., 2006) discovered in 1994. It has since been the object of extensive research by a multidisciplinary international team coordinated by the Earth Sciences Department of the University of Florence and the Eritrea National Museum, thus enabling the discovery of further human remains (Abbate et al., 1998, 2004b; Rook et al., 2002), abundant fossil vertebrates (Ferretti et al., 2003; Delfino et al., 2004; Martínez-Navarro et al., 2004, 2010; Rook et al., 2010), and a rich archaeological record of Mode 1 (Oldowan) and Mode 2 (Acheulean) tool industries in a late Early Pleistocene chronological framework (Abbate et al., 2004b). The *Homo* bearing deposits (Alat Formation) of the Buia sedimentary succession have been dated through different approaches and fall within the Jaramillo Subchron (C1r.1n), at approximately 1.0 Ma (Albianelli and Napoleone, 2004; Bigazzi et al., 2004).

Previous paleontological studies have documented the presence, in the Buia faunal assemblage, of a variety of reptiles and large mammals (Delfino et al., 2004; Martínez-Navarro et al., 2004; 2010; Rook et al., 2010). In the present paper we provide the first description of fish, birds and small mammals retrieved during the recent (2010-2011) excavations of the so-called “*Homo* site” outcrop (UMTS coordinates 37P E600710 N1632638). In particular, we report the discovery of two isolated rodent incisors, one of which shows diagnostic characteristics that enable attribution to cf. *Thryonomys* sp., a cane rat, a relatively common taxon in the fossil record of Africa, often occurring in faunal assemblages from paleoanthropological sites (Geraads et al., 2004; Wesselman et al., 2009).

Geological setting

The Dandiero Basin is part of the Danakil depression (Fig. 1A) which is 300 km-long, oriented NNW-SSE, and mainly filled with Plio-Pleistocene marine evaporitic deposits. The Dandiero Basin covers an area of about 100 km² (Fig. 1B) and is filled with 900-1000 m of alluvial to lacustrine Pleistocene deposits. It is enclosed to the north by the slopes of the Alid volcano, and to the east by the fluvio-eolian sand field of the Samoti plain; the western and southern boundaries are made of Neoproterozoic basement rocks. The Dandiero Basin infill is made of three unconformably-bounded units (Abbate et al., 2004a): Maebele Synthem, Curbelu Synthem and Samoti Synthem.

The Maebele Synthem (Early to Middle Pleistocene) consists of six lithostratigraphic units (Abbate et al., 2004a): fluvial Bukra sand and gravel (150-200 m thick), fluvio-deltaic Alat Formation, (70-100 m thick), fluvial Wara sand and gravel (250 m thick), lacustrine Goreya Formation (50 m thick), fluvio-deltaic Aro sand (120 m thick) and alluvial fan Addai fanglomerate (250-300 m thick).

The Curbelu Synthem consists of late Pleistocene alluvial-fan gravel (up to 50 m thick), whereas the Samoti Synthem is made of fluvial gravel passing laterally into eolian sand accumulated during Late Pleistocene-Holocene (Abbate et al., 2004a).

The Alat Formation provided the largest amount of artefacts and fossil remains, including human bones. It reveals three main cycles shifting from a fluvial to a lacustrine environment and back to fluvial. The nomenclature used in the present paper, to indicate its different depositional units (e.g. DL, FL), is from Ghinassi et al. (2009). The lower boundary of the Alat Formation corresponds to the base of the Jaramillo Subchron (1.07 Ma), as established by the dating (1.3 ± 0.3 Ma) of an ash layer present in the lower part of the unit. The upper boundary of the Jaramillo Subchron (0.99 Ma) is located approximately 10 m below the top of the Alat Formation (Albianelli and Napoleone, 2004).

The fossil vertebrate assemblage from Buia

A preliminary faunal list describing the fossil, vertebrate, remains discovered in Buia was published in 1998 (Abbate et al., 1998). This and the discoveries made since indicate the Buia faunal assemblage falls among the typical late Early Pleistocene East African faunas. It is, in fact, characterised by the presence of the latest derived representative forms of *Elephas recki*, *Hippopotamus gorgops*, *Kolpochoerus olduvaiensis*, *Kolpochoerus majus*, *Metridiochoerus* aff. *M.*

modestus and *Bos buiaensis*, in association with taxa still present today, such as *Ceratotherium simum*, *Equus* cf. *E. grevyi*, *Tragelaphus* cf. *T. spekei*, and *Kobus* cf. *K. ellipsiprymnus*. The geological and sedimentological framework, paleomagnetism, and fission track dating (Abbate et al., 2004b; Ghinassi et al., 2009) are in good agreement with the indications obtained through mammal biochronology, and all point to the final phases of the Early Pleistocene (Martínez-Navarro et al., 2004, 2010; Rook et al., 2010). Taxa characterized by strong water dependence, such as hippopotamus, waterbuck, sitatunga, *Kolpochoerus*, crocodile, paleomedusid chelonian, Nile monitor lizard and African rock python (Delfino et al., 2004) predominate in this vertebrate assemblage. The palaeoenvironmental characteristics of the fauna are therefore fully compatible with the evidences, obtained through sedimentology and facies analysis, that document the sedimentary evolution of fluvio-deltaic and lacustrine systems (Ghinassi et al., 2009).

New vertebrate remains (Pisces, Reptilia, Aves and Rodentia) from Buia

Stratigraphic frame

The fieldwork conducted in 2010 and 2011 at the Buia *Homo* site (Wadi Aalad), allowed us to collect a sample of fossil vertebrates. The Buia *Homo* site (Wadi Aalad), is an area in which the upper part of the fluvio-deltaic Alat Formation is exposed (Fig. 2A and B). In particular, the lower part of the outcrop corresponds to 10-50 cm thick fluvial, cross-stratified sandy topset of a Gilbert-type delta (DL4 in Ghinassi et al., 2009), covered by shoalwater delta deposits (DL5 in Ghinassi et al., 2009). DL5 unit, approximately 3 m thick, shows a cyclothem architecture stemming from the interaction of high-frequency lacustrine oscillations and the autocyclic compensational stacking pattern of deltaic lobes (Ghinassi et al., 2009). At a structural level, the outcrop is marked by the vertical stacking of 30-70 cm thick packages (fig. 2C) that gradually coarsen towards the top of each layer, thus transitioning from basal mud into well-stratified sand. Within the basal mud layer, both lacustrine gastropod remains (*Melanoides tuberculata*) and fish bones are common; on the other hand, the sandy deposits only contain rare gastropod shell fragments and these are often pedogenized (Fig. 2D). The DL5 deposits are covered by fluvial deposits (FL2a in Ghinassi et al., 2009) consisting of sandy channel bodies (0.5-1 m thick and 10-15 m wide) cut in floodplain pedogenized mud. The uppermost part of the outcrop is made of fluvial sand (FL2b in Ghinassi et al., 2009) that reaches 1.5 m in thickness and that cuts into the underlying fluvio-deltaic deposits (Fig. 2A). The FL2b sand consists of well-stratified medium

sized sand bar deposits (Fig. 2E) overlaying the gravelly, and rich in bone, basal layer accumulation of the deepest part of the channel (channel lag).

Collecting methods and fossils repository

The specimens have been retrieved during the recent (2010-2011) fieldwork campaigns at the Buia *Homo* site outcrop (Wadi Aalad), with collecting methods that includes both surface screening and dry sieving of excavated sediment. The extreme environmental conditions of the Danakil depression desert hampered us to proceed with wet screen washing, a collecting method that would have - possibly - provided us with richer samples of small vertebrates for particular layers, such as the base of the channel FL2b.

Most fish remains were collected from the shell-rich deposits of unit DL5; this unit also contained one of the crocodile remains here described (UA3624). Most of the 2010-2011 fossil vertebrate collection derives from the channel lag gravel of unit FL2b; this includes most of the crocodile remains (UA2188, UA2293, UA2489, UA2513, UA2530, UA2694, UA2729, UA2750, UA2774, UA2791, UA2810, UA2875, UA2837, UA2949, UA2991, UA3014, UA3035-36, UA3125, UA2135, UA3101-3102, UA3209, UA3416, UA3418, UA3452-53, UA3458, UA3564, UA3581, UA3638, UA3666), several turtle specimens (UA2152, UA2221, UA2237, UA2480, UA3566-68, UA3644-45, UA3680, UA3693-3694), two bird remains (UA3099, UA3158), and the Thryonomyidae upper incisor (UA2195). Surface collection and section cleaning provided most of the remaining specimens.

All the specimens are housed at the National Museum of Eritrea (Asmara, Eritrea).

New fossil finds

Pisces

Order Siluriformes

Family Clariidae Günther, 1864

Genus *Clarias* Scopoli, 1777

Subgenus *Clarias (Clarias)* Teugels, 1986

Clarias (Clarias) sp.

Material – UA404 (Fig. 3), a single partially complete and articulated skull, plus at least four moderately well-preserved abdominal vertebral elements and part of the right pectoral-fin

girdle. A large number of fragmentary cranial bones exhibiting a pattern of ornamentation similar to that of the fossil documented herein has also been collected mostly from lacustrine unit DL5 and from the overlying fluviatile FL2a unit.

Description – The neurocranium is almost complete, missing a large portion of its right sector and part of the ethmoid region.

The neurocranial bones are well-developed and strongly ossified. The skull roof is flattened and rigid, with deeply interdigitating and horizontally arranged bones. The external surface of the neurocranial bones is extensively sculptured, showing the typical granular pattern of the clariid genera *Clarias* and *Heterobranchus*. Of the vomer, only a small part of the toothed plate is preserved. The lateral ethmoid is approximately as long as it is wide, with an oblique anterior margin and a Y-shaped sensory canal groove; a strong lateral process for the articulation with the second infraorbital bone emerges along the obliquely oriented anterior margin of this bone. The frontals are the largest bones of the skull roof; these are broader at the middle of their length, approximately at the level of the posterior border of the anterior fontanel. The anterior fontanel is relatively long and separates the contralateral frontals for about one half of their length. The portion anterior to the posterior cranial fontanel is the only preserved part of the parieto-supraoccipital. The sphenotic is quadrangular in outline; the lateral groove for the sensory canal is coincident with its medial contact with the frontal. Such a groove also runs on the anteromedial sector of the massive pterotic. The pterotic is an irregular and massive bone that forms part of the posterior border of the neurocranium. The fourth infraorbital bone is a thick and drop-like bone with a relatively large supraorbital process. The single suprapreopercle is broadly separated from the fourth infraorbital. The posttemporo-supracleithrum is sutured to the neurocranium at its posterolateral corner; the groove for the sensory canal is well recognizable on the outer surface of this bone.

The anterior portion of the mandible is the only element of the jaw bones found. As in other clariids, it consists of a single complex bone, the dentosplenio-mentomeckelium (see Adriaens et al., 1997; Cabuy et al., 1999; Devaere et al., 2001); the mandibular tooth battery does not extend posteriorly until what appears to be the coronoid process. Of the suspensorium, only part of the hyomandibula and quadrate are recognizable in the fossil. The opercle is roughly triangular in outline, with a sculptured outer surface and a prominent facet for the articulation with the suspensorium.

The hyoid bar is robust; its general morphology greatly resembles that of *Clarias gariepinus* described by Adriaens and Verraes (1998).

Four partially complete abdominal vertebrae are preserved. The centra are discoid, antero-posteriorly compressed, and characterized by lateral and ventral fossae of a variety of sizes; the bases of the parapophyses are relatively thin. The neural spines are thickened and laterally compressed.

The preserved pectoral girdle consists of massive and strongly ossified left cleithrum and coracoid. The outer surface of the cleithrum is extensively ornamented. An oval fenestra is visible between the cleithrum and coracoid (see Devaere et al., 2007) at their convergence close to the lateral wall of the body.

Remarks – The overall configuration of the cranial and postcranial bones of the specimen described herein clearly justify its assignment to the catfish family Clariidae. Within clariids, the flattened and strongly ossified skull roof with bones characterized by extensive sculpturing of their outer surface is exclusive of the genus *Heterobranchus* as well as of three African subgenera of the genus *Clarias* (in the sense of Teugels, 1986), namely *C. (Clarias)*, *C. (Claroides)*, and *C. (Anguilloclarias)*. The general proportions of the lateral ethmoid and its oblique anterior margin are characteristic of certain species of the subgenus *C. (Clarias)*. Moreover, the Y-shaped sensory canal groove on the lateral ethmoid has been observed exclusively in the extant species *C. (Clarias) anguillaris* and in some indeterminate Miocene fossils assigned to the subgenus *C. (Clarias)* (Otero and Gayet, 2001; Otero et al., 2010). Summarizing, the osteological structure of UA404 is consistent with that of the two extant species of the subgenus *C. (Clarias)*, *C. (Clarias) anguillaris* and *C. (Clarias) gariepinus* (see e.g., Nawar, 1954; Adriaens and Verraes, 1998; Devaere et al., 2007); reason for which, the material documented herein is referred to the subgenus *C. (Clarias)*. As a matter of fact, the inadequate preservation of the specimen does not allow a more detailed taxonomic analysis for which additional and more complete specimens would be desirable.

Clariids are relatively common in the Neogene sedimentary record of Africa. As pointed out by Stewart (2001), this is possibly due to the distinctive cranial ornamentation that renders them perhaps the most commonly reported African fossil fish remains. The oldest records from the African continent date to the lower Miocene sediments of Kenya (Van Couvering, 1977). Members of the family Clariidae occupy a variety of freshwater environments in tropical to temperate sectors of Asia and Africa. More than 30 species arranged in six subgenera inhabit the freshwaters of the African continent (Teugels and Adriaens, 2003). Clariids are characterized by the unique presence of the suprabranchial organ. An organ that enables them to withstand poorly oxygenated waters, survive out of water for many hours,

and migrate from one pond to another even though these omnivorous fishes primarily live in the well-oxygenated shallow and quiet waters of rivers and lakes.

Reptilia

Order Crocodylia

Family Crocodylidae Cuvier, 1807

Genus *Crocodylus* Laurenti, 1768

Crocodylus niloticus Laurenti, 1768

Material - isolated teeth: UA2188, UA2359, UA2530, UA2609, UA2674, UA2694, UA2729, UA2750, UA2774, UA2790-2791, UA2810, UA2875, UA2889, UA2937, UA2949, UA2991, UA3014, UA3036, UA3101-3102, UA3125, UA3135, UA3209, UA3234-3237, UA3297, UA3415-3416, UA3452-3453, UA3458, UA3503-3504, UA3564, UA3581, UA3624, UA3628, UA3743, UA3774, UA3794, UA3798-3799, UA3824-3825, UA3848-3849, UA3905 (three teeth), UA3917, UA3948, UA3954, UA3988, UA4105-4111, UA4173-4374, UA4576, UA4654, UA5089-5090, UA5161, UA5277, UA5371, UA5505, UA5545. Osteoderm fragments: UA2199, UA2287, UA2489, UA2513, UA3418, UA3666, UA3989, UA4113-4114, UA4172, UA4174, UA4404, UA4575, UA5162-5163, UA5332. Vertebral fragments: UA2293, UA3293, UA4112. Rib fragment: UA3035.

Remarks - All the teeth are isolated and most have a reabsorbed root indicating that they were shed during life. An exception is represented by UA3536 whose root was not reabsorbed indicating that the tooth fell out post mortem (for a recent discussion on shed teeth, see Frey and Monninger, 2010). This fits with the discovery in the site of skeletal remains such as osteoderm, rib and vertebral fragments, which necessarily trace back to deceased specimens. None of the remains retrieved during the excavation are taxonomically diagnostic at a species or genus level. They are therefore tentatively attributed to *Crocodylus niloticus*, the only crocodylian to have been identified, on the basis of more informative material, in the Buia region (Delfino et al., 2004). However, the diversity of the African Plio-Pleistocene crocodylian record has, just recently been enriched with the description of two new extinct species: *Crocodylus anthropophagus* from Olduvai Gorge, Tanzania (Brochu et al., 2010) and *Crocodylus thorbjarnarsoni* from the Lake Turkana Basin, Kenya (Brochu and Storrs, 2012). Given that these two species were erected on the basis of relatively complete skulls and of characters that are not preserved in the crocodylian remains from Buia, the specific

identification of the Buia crocodiles would need to be confirmed on better preserved specimens than those retrieved so far.

Order Testudines

Family Pelomedusidae Cope, 1868

Genus *Pelusios* Wagler 1830

Pelusios cf. *P. sinuatus* (Smith, 1838)

Material - shell fragments: UA2152, UA2221, UA2237, UA2480, UA2610, UA2902, UA2915, UA2939, UA2958, UA3238-3240, UA3377, UA3482, UA3566-3568, UA3644-3645, UA3680, UA3693-3694, UA3704, UA3953, UA3955-3958, UA3960, UA3962-3969, UA4015-4018, UA4176, UA4657, UA4917-4918, UA4928, UA4999, UA5160, UA5237, UA5242-5244, UA5372-5373, UA5439, UA5544.

Remarks – Different shell fragments have been identified because distinctive morphological characters render this possible on even highly fragmented samples. The morphology of the incomplete neural UA5439 and of the peripheral UA2237 fit (although not exclusively) with those of *Pelusios sinuatus*, a species previously identified in the region (as *P. cf. P. sinuatus*; Delfino et al. 2004). UA5439 is characterized by being elongated, probably hexagonal, with a deeply bent intervertebral sulcus on the external surface. UA2237 hosts the pleuro-marginal, the intermarginal, and possibly the interpleural sulci; the first of which is located at about the medial third of the external surface of the element. All the other turtle remains sharing with these the general structure and surface pattern, have been tentatively attributed to the same taxon.

Order Squamata

Suborder Serpentes

Family Boidae Gray, 1825

Genus *Python* Daudin, 1803

Python gr. *P. sebae* (Gmelin, 1789)

Material - fragmentary vertebrae: UA2920, UA4115

Remarks - two large-sized fragmentary vertebrae, fully congruent with the morphology described by Delfino et al. (2004), attributed to python.

Aves

Order Pelecaniformes

Family Anhingidae Ridgway, 1887

Genus *Anhinga* Brisson, 1760

Anhinga sp.

Material - UA4080, humerus.

Description - Shaft of a right humerus (Width of the shaft: 8.2 mm) showing some morphological characteristics of the Anhingidae; a family of the order Pelecaniformes. In particular on the cranial face of the fossil humerus, there is a strong sulcus that runs parallel to the distal portion of the crista deltopectoralis; a trait absent in Phalacrocoracidae. The crista deltopectoralis is distally elongated and has an outline that is much more regular than those observed in Phalacrocoracidae. A sulcus, present in the Anhingidae but not in the Phalacrocoracidae, is clearly detectable on the caudal side of the shaft, close to the distal part of the crista deltopectoralis. These characteristics, some already described by Becker (1986), allow the attribution of this humerus shaft from Buia to *Anhinga* sp.

Remarks – Given the familial attribution of *Protoplotus beauforti* Lambrecht is uncertain (Olson, 1985), *Anhinga* is the only certain, living or fossil, genus of the Anhingidae Family. Even though the fossil record of *Anhinga* is rich in the New World, and in particular in South America (Dyke and Walker, 2008), its Neogene African and Eurasiatic record only comprises three species: the living *A. melanogaster* from the Miocene of Chad and Ethiopia (Louchart et al., 2008) and from the Pleistocene of Ethiopia (Louchart, 2008), the extinct *A. pannonica* from the Upper Miocene of Europe and Africa (Dyke and Walker 2008; Louchart et al., 2008), and *A. hadarensis* from the Plio-Pleistocene of Ethiopia and Tanzania (Brodkorb and Mourer-Chauviré, 1982). In addition, *Anhinga* sp. has been reported from the Miocene of Sahabi in Libya (Ballmann, 1987) and from the Pliocene sites of Kanapoi in Kenya (Harris et al., 2003) and Aramis in Ethiopia (Louchart et al., 2009). Shaft width indicates that this fossil does not belong to the modern *A. melanogaster* or the fossil *A. hadarensis*, which both have narrower shafts than the remain here described. Even though *Anhinga pannonica* is larger than these two species, it is only known by very fragmentary remains (Dyke and Walker, 2008; Louchart et al., 2008) and a detailed comparison with the fossil from Buia is therefore impossible. The various species within the Aninghidae are exclusively fish-eaters, thus strictly related to aquatic environment.

Order Gruiformes

Family Rallidae Vigors, 1825

Rallidae indet.

Material - UA3158, tibiotarsus (Fig. 4A); UA5331, coracoid.

Description - Distal part of a right tibiotarsus (distal width 6.0 mm; distal depth 6.3 mm) that is attributed, on the basis of different morphological characteristics to the Rallidae. In particular, the condylus medialis is visibly smaller and thinner than the condylus lateralis; the margin of the condylus medialis is very sharp on the caudal side and much thicker on the cranial side; in distal view the cranial part of the condylus medialis is tilted medially and the epicondylus medialis well evident; the distal outline of the condylus lateralis is homogeneously thick. UA5331 is a shaft fragment of the left coracoid of a similar sized Rallidae, as suggested by the laterally pointed cotyla scapularis. Following the abovementioned characteristics, the bones can be attributed to Rallidae indet. of a middle-sized species, a little smaller than the living *Gallinula chloropus*. The bones have been attributed only at Family level because of their fragmentary status.

Remarks - The fossil record of the Rallidae is quite abundant (Cracraft, 1973; Olson, 1977, 1985). Various records are also known from Africa, most of which are attributed to Rallidae indet. (Rich, 1980; Rasmussen et al., 1987; Louchart et al., 2009; Mourer-Chauviré and Geraads, 2010); a noteworthy exception to this are the different species recognized by Prassack (2010) for the Late Pliocene of Olduvai Gorge. Most of the Rallidae are related to wet environments, either as aquatic species living in reedbeds and the floating vegetation or as species living in humid grassland around lakes or swamps.

Order Charadriiformes

Family Burhinidae Mathews, 1912

Genus *Burhinus* Illiger, 1811

Burhinus sp.

Material - UA4838, humerus (Fig. 4B).

Description - Broken proximal epiphysis of a right humerus (proximal width from the dorsal side of the incisura capitis to the tuberculum dorsale 11.4 mm; proximal depth 6.0 mm) with a sharp margo caudalis and a very evident tuberculum dorsale, both of which are

characteristics typical of Charadriiformes. Within the Order Charadriiformes, the humerus can be referred to *Burhinus*, the only living African Burhinidae, for the following characteristics: in caudal view, the margo caudalis does not reach the distal side of the caput humeri; the tuberculum dorsale is very evident and well separated from both the dorsal side of the *caput humeri* and the *crista deltopectoralis*; the transverse ridge of the incisura capitis shows a transverse ridge confined to its ventral side. This characteristic has been coded by Strauch (1978) and Mayr (2011) for *Burhinus*, but with different scores. The bone has been attributed to *Burhinus* sp. because its fragmentary nature does not allow a more precise determination.

Remarks - The fossil record of the genus *Burhinus* is very scarce (Bickart, 1981; Olson, 1985), in particular the fossil here described represents the first definitive finding from Africa and the oldest occurrence of the genus *Burhinus* (Bickart, 1981; Tyrberg, 1998). The various species of the genus *Burhinus* inhabit the open country, from the river banks to savannas or steppe, with scarce vegetation.

Aves indet.

Material - UA3099, ulna.

Remarks - Fragmentary shaft of an ulna that belongs to a middle-sized bird too poorly preserved to provide any taxonomic information.

Mammalia

Order Rodentia

Family Thryonomyidae Pocock, 1922

Genus *Thryonomys* Fitzinger, 1867

Cf. *Thryonomys* sp.

Material – UA2195 left upper incisor, UA2323 right lower incisor (Fig. 5a-h).

Description - UA2323 (Fig. 5e-h) is a right lower incisor fragment of a relatively large rodent (length 4.4 mm; breadth 7.1 mm) whose identification remains uncertain. UA2195 (Fig. 5a-d) is an left upper incisor of a relatively large rodent (length 6.1 mm; breadth 6.9 mm) that, although fragmentary, bears a peculiar feature on the enamel surface: the occurrence of three longitudinal enamel grooves.

Although scanty, the sample provides us enough morphological evidence allowing a tentative taxonomical attribution.

The occurrence of grooves on the upper incisor enamel surface is in fact the exclusive synapomorphy of the Thryonomyidae crown group. A further element pointing to the attribution to Thryonomyidae is found in the general morphology of the incisors.

Thryonomyids are characterized by their wide, massive incisors with thick enamel (cfr. Ellerman, 1940: p. 145). Both our specimens are relatively large, stoutly built, and with thick enamel (enamel thickness measured at occlusal margin being 0.7 mm for the upper incisor UA2195, and 0.5 mm for the lower incisor UA2323) markedly expanded on both distal (Fig. 5a and 5e) and medial (Fig. 5c and 5g) sides.

The upper incisor UA2195, reveals the occurrence of three longitudinal grooves on the enamel surface with a peculiar arrangement given by the fact that the deepest groove is occupying a central position whereas the other two are displaced towards the inner edge (Fig. 5b). This feature is, within the group, exclusively expressed in modern (*Thryonomys swinderianus*, *Thryonomys gregorianus*) and Plio-Pleistocene fossil *Thryonomys* (node 25 in López-Antoñanzas et al., 2004), ensuring us in attributing the tooth to the genus *Thryonomys*. The UA2195 specimen (the upper incisor) is larger than the extant species *T. gregorianus* but comparable in size to *T. swinderianus*, and one would be tempted to attribute UA2195 to the latter species. Due to the fragmentary status of the specimens and to the very limited sample we prefer, however, to maintain a cautious taxonomic attribution referring the specimens to cf. *Thryonomys* sp.

The lower incisor, on the other hand, does not show any groove on its outer enamel surface (as is the case in thryonomyids). However, on the basis of the fact that it is relatively large-sized and shows a proportionally large breadth (in addition to its overall stoutly built aspect and thick enamel), it could be tentatively attributed to this family.

Remarks - Thryonomyid phylogeny (and systematics) has been revised by López-Antoñanzas et al. (2004). The family displays its maximum diversity (and widest geographic range, expanding to the east into Pakistan) in the Miocene (Flynn and Winkler, 1994). Ever since the beginning of the Pliocene, the family is limited to the single African genus, *Thryonomys*, identified in several Pliocene sites (Chemeron Formation and Tabarin, Kenya; Wembere-Manonga Formation, and Ndolanya Beds at Laetoli, Tanzania; Members B and G of the Shungura Formation at Omo, and Middle Awash, Ethiopia; Behrensmeyer et al., 1997; Wesselman, 1984; Denys, 1987, 2011; Wesselman et al., 2009; Winkler, 1990, 1997) and in

different Pleistocene to recent sites (Dietrich, 1948; Monod, 1970; Wesselman, 1984; Peters, 1990; Behrensmeyer et al., 1997; Geraads et al. 2004; Everett, 2010).

Thryonomys swinderianus (the “greater cane rat”) is widely distributed in sub-Saharan Africa, with the exception of the arid eastern horn and much of the south-western part. *Thryonomys swinderianus* is a semiaquatic dweller of marshy areas, floodplains, and estuaries. *Thryonomys gregorianus* (the “lesser cane rat”) is, instead, distributed from Cameroon to western Ethiopia and southward to Zimbabwe; it inhabits drier ground in moist savannahs and is adapted to more open conditions (Nowak, 1999; Jenkins, 2001).

Conclusions

The 2010-2011 field-work at Buia *Homo* site, in the Danakil Depression of Eritrea, allowed the recovery and identification of different vertebrate fossils whose study allows greater insight into the paleoenvironment of this palaeoanthropological site.

The reptile remains are represented mostly by crocodylian teeth, vertebrae, rib and osteoderm fragments, as well as turtle shell fragments, and rare fragmentary snake vertebrae. These remains confirm the identifications previously obtained through the study of more representative material collected in a partially overlapping but vaster area of the Buia region (Delfino et al., 2004). Of special interest is the identification and description of the fish, birds and micromammals found.

The fish remains herein described are assigned to *Claris (Claris) sp.*, a taxon belonging to a family (Clariidae) relatively common in the Neogene sedimentary record of Africa. Members of the family Clariidae occupy a variety of freshwater environments in tropical to temperate sectors of Asia and Africa. The occurrence of abundant Clariidae within the lacustrine sediments of the Buia succession is consistent with the sedimentological interpretations (Ghinassi et al., 2009). These omnivorous fish primarily inhabit the well-oxygenated shallow and quiet waters of rivers and lakes (albeit capable of withstanding poorly oxygenated waters, surviving out of water for many hours, and migrating from one pond to another). The fossil bird taxa identified at Buia allow us to hypothesize the occurrence of both open water with reedbeds, as suggested by the exclusively fish-eating *Anhinga* and the Rallidae, and of dry areas inhabited by *Burhinus* (Del Hoyo et al., 1996). Of particular importance is the identification of *Burhinus* never observed before in African paleontological records. This find, moreover, represents the oldest occurrence of the genus because the next most ancient remains are from the Late Pleistocene of America (Bickart, 1981), The Middle Pleistocene in

Europe (Tyrberg, 1998) and in the Recent of Asia and Australia, given that there are no fossil records, to recent times.

Finally, significant is the identification of UA2195 as *cf. Thryonomys* sp. This record documents the occurrence of Thryonomyid rodents in a country (Eritrea, where the genus is absent in living assemblages) and palaeoanthropological area (the Buia basin) in which it had never been attested before, and further extends its association with early *Homo*. Since extant Thryonomyid rodents are restricted to sub-Saharan Africa, their occurrence in Eritrea during the Early Pleistocene is congruent with a less arid climate at this time. In fact, the occurrence of *cf. Thryonomys* sp. at Buia, supports previous sedimentological and paleontological evidences (Delfino et al., 2004; Martínez-Navarro et al., 2004; Ghinassi et al., 2009), indicating a paleoenvironment scenario characterised by the presence of moist grassed habitats adjacent to persistent water. Other localities from the late Early and Middle Pleistocene of the Afar/Danakil Depression, include records from Gona (Everett, 2010), and Asbole (Geraads et al., 2004) but an analysis of the differences and similarities between faunas is impossible because the record is biased by a number of effects (e.g. taphonomic, preservation) and above all because it has only rarely been sampled and remains are extremely sparse. As a matter of fact, the Eritrean record from Buia helps in providing evidence of the distribution of Thryonomyid rodents in East Africa in late Early Pleistocene times, as well as its occurrence within faunas associated with the occurrence of *Homo* in the African fossil record.

The new taxa identified at the Buia *Homo* site, some of which reported for the first time in the entire sedimentary basin, were linked to the presence of water bodies that are now absent in the region. As a whole, the present study confirms that the Buia assemblage is predominated by taxa characterized by strong water dependence (Delfino et al., 2004; Martínez-Navarro et al., 2004) and is fully compatible with the sedimentological evidences, documenting the sedimentary evolution of fluvio-deltaic and lacustrine systems (Ghinassi et al., 2009).

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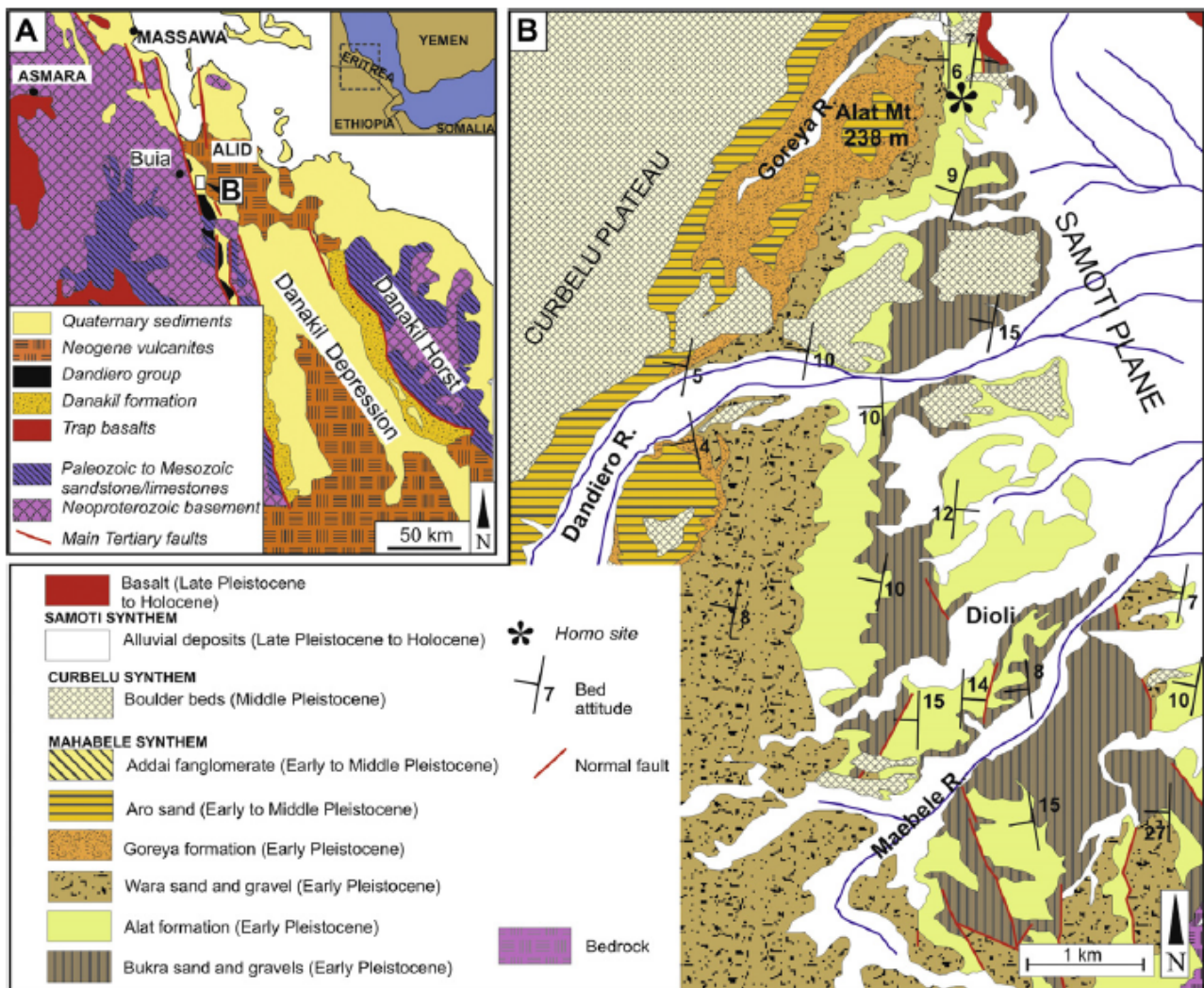


Figure 1 - (A) Geographic location and schematic geological map of the Danakil depression. (B) Schematic geological map of the Dandiero Basin (after Abbate et al., 2004a).

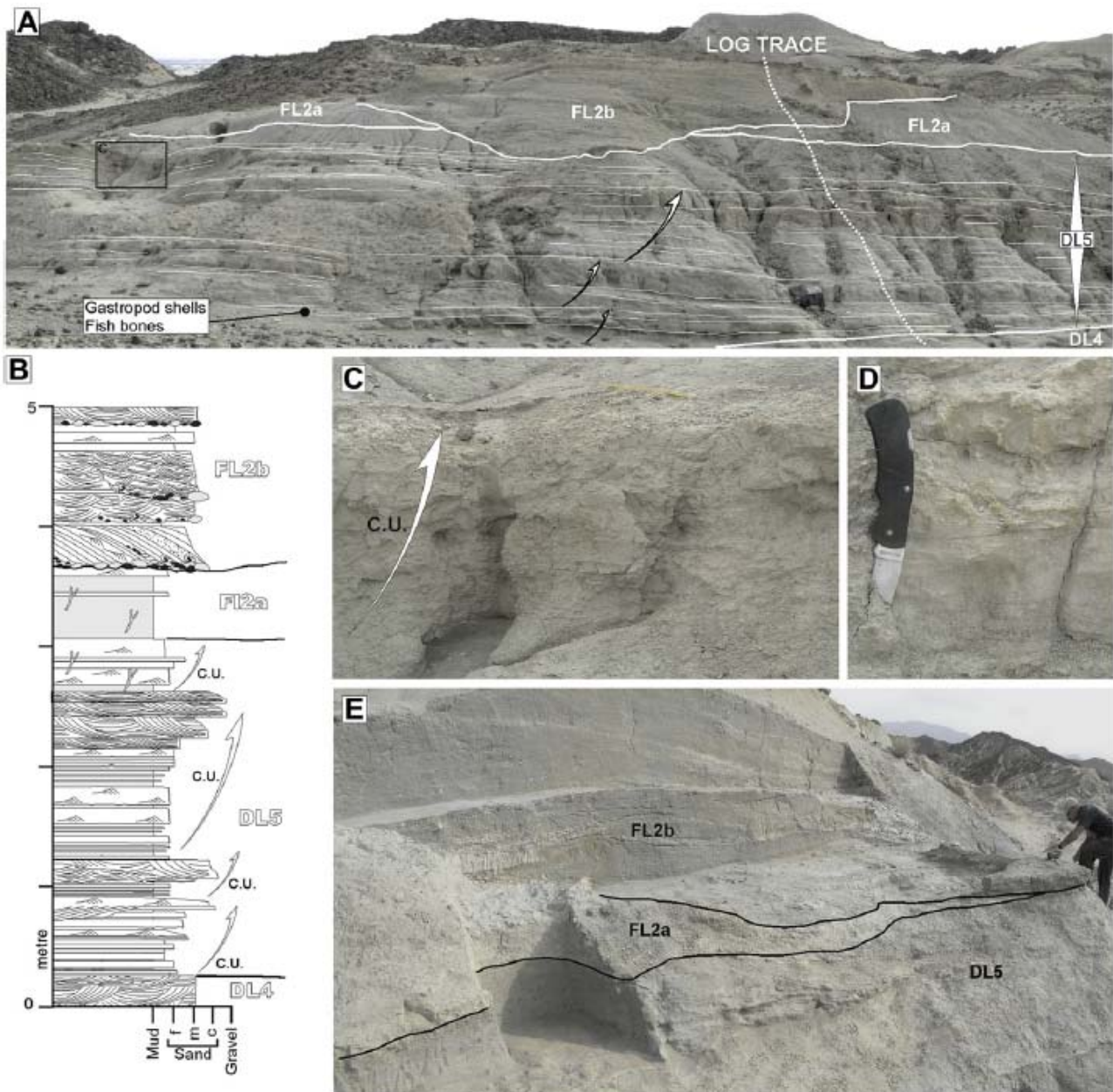


Figure 2 - The Wadi Aalad hominin site. (A) Panoramic view of the site from West. Note the erosional surface at the base of unit FL2b. (B) Sedimentological log across the site. See inset A for location of log trace. (C) Coarsening-upward delta lobe deposit (unit DL4) accumulated in a marginal, shallow-water lacustrine setting. (D) Detail from C showing root traces developed at the top of delta lobe deposit. (E) Fluvial sandy deposit of unit FL2b.

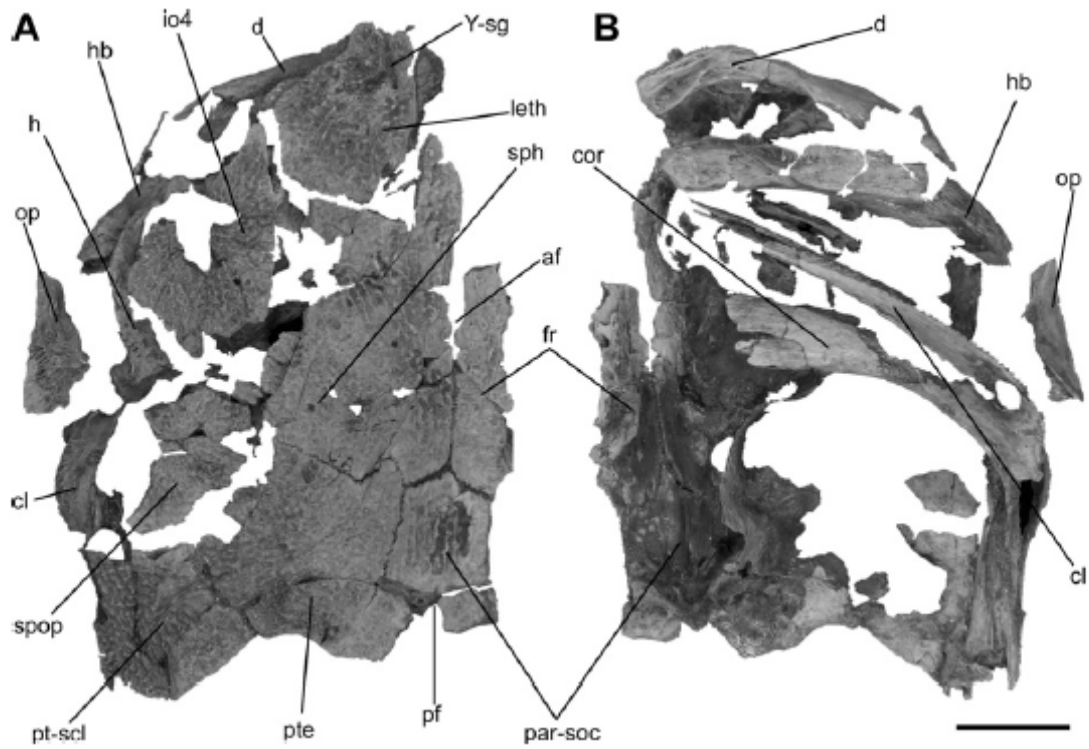


Figure 3 – *Clarias (Clarias) sp.*, UA404. Skull in dorsal (A) and ventral (B) view. Abbreviations: af, anterior fontanel; cl, cleithrum; cor, coracoid; d, dentary; fr, frontal; h, hyomandibula; hb, hyoid bar; io4, fourth infraorbital bone; leth, lateral ethmoid; op, opercle; par-soc, parietosupraoccipital; pf, posterior fontanel; pte, pterotic; pt-scl, posttemporo-supracleithrum; sph, sphenotic; spop, suprapreopercle; Y-sg, Y-shaped sensory groove. Bar scale represents 20 mm.

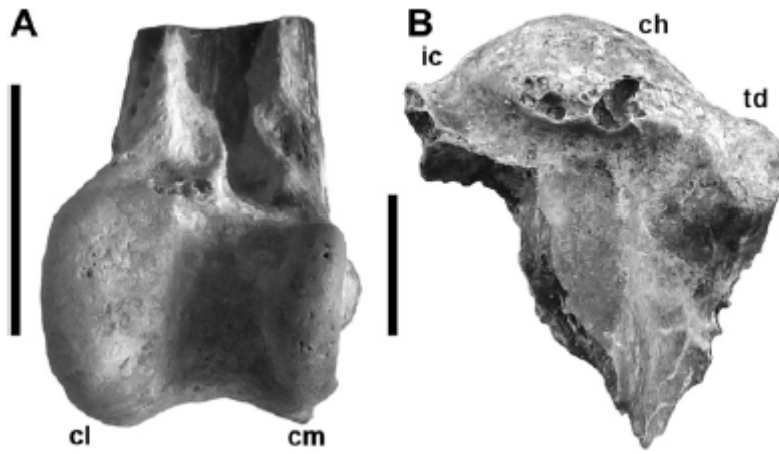


Figure 4 - Aves from Buia. A) Rallidae indet., right tibiotalus (UA3158), distal end in cranial view; B) *Burhinus* sp., right humerus (UA4038), fragmented proximal end in caudal view. Abbreviations: cm, condylus medialis; cl, condylus lateralis; ch, caput humeri; ic, incisura capitis; td, tuberculum dorsale. Bar scales represent 5 mm.

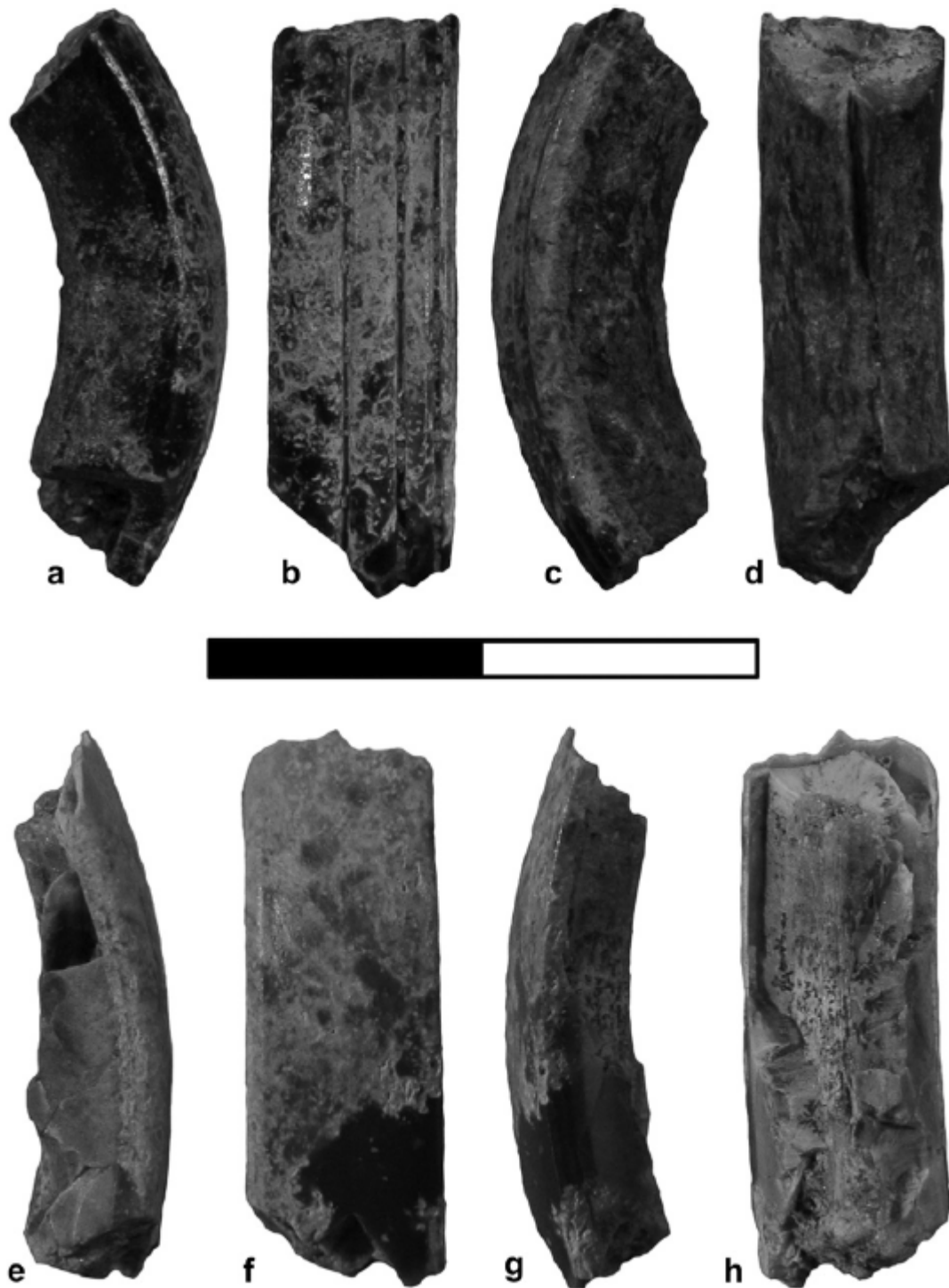


Figure 5 – cf. *Thryonomys* sp. , UA2195 left upper incisor in distal (a), labial (b), medial(c), and occlusal (d) views. Rodentia indet. (possibly attributable to Thryonomyidae), UA2323 right lower incisor in distal (e), labial (f), medial (g), and occlusal (h) views. Bar scale represents 20 mm.