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FOSSIL REPTILES FROM THE PLEISTOCENE *HOMO*-BEARING LOCALITY OF BUIA (ERITREA, NORTHERN DANAKIL DEPRESSION)

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Abstract. The Early to early-Middle Pleistocene fossil assemblage from the Buia area (Northern Danakil Depression, Eritrea) hosts, along with *Homo* and several other large mammal taxa, the following reptiles: Nile Crocodile, *Crocodylus niloticus*, Serrated Hinged Terrapin, *Pelusios* cf. *P. sinuatus*, Nile Monitor, *Varanus niloticus* and African Rock Python, *Python* gr. *P. sebae*. All the identified taxa belong to living species. At present, these taxa do not occur in the Northern Danakil depression since it is an arid area. *P. sinuatus* is not a member of the Eritrean herpetofauna. Although the marked preponderance of the crocodile remains is probably connected to the taphonomy of the sites and the collecting methods used, the ecological value of the reptile fauna corroborates that of the mammals, in indicating a lacustrine or fluvio-deltaic palaeoenvironment and a tropical/subtropical or even sub-Sahelic climate. The Buia remains represent the first reported Eritrean palaeoherpetofauna.

Riassunto. L'associazione fossile risalente al Pleistocene Inferiore – inizio del Pleistocene Medio dell'area di Buia (Depressione Dancala Settentrionale, Eritrea), contiene, oltre ai resti appartenenti al genere *Homo* e numerosi altri mammiferi di grandi dimensioni, i seguenti rettili: *Crocodylus niloticus*, *Pelusios* cf. *P. sinuatus*, *Varanus niloticus* e *Python* gr. *P. sebae*. Sebbene la netta preponderanza dei resti di coccodrillo sia probabilmente connessa alla tafonomia delle località fossilifere e alle metodologie di ricerca e raccolta del materiale fossile, la valenza ecologica dei rettili concorda con quella dei mammiferi nell'indicare un paleoambiente lacustre o fluvio-deltizio tipico di un clima tropicale/subtropicale o anche sub-saheliano. Tutti i taxa identificati sono attualmente viventi ma non abitano più la Dancalia settentrionale, poiché si tratta di una regione desertica. *P. sinuatus* non fa attualmente parte della fauna eritrea. I resti fossili di Buia rappresentano la prima paleoerpetofauna descritta per l'Eritrea.

Introduction

The fossil record of the modern herpetofauna of Africa is poorly known when compared to those of Europe or North America. Large and "attractive" taxa such as crocodylians and chelonians have received much more attention than the amphibians and squamates whose recovery, due to their smaller size, usually requires time-consuming collecting activities and whose study, due to an extraordinary complex biodiversity, calls for comprehensive comparative osteological collections.

With some exceptions, concerning mainly crocodylians and chelonians again, purely palaeontological localities are rarely studied: the majority of the fossil material comes from sites which have yielded human remains and therefore the bulk of the sites is located in Eastern or Southern Africa. Notwithstanding this, the evolution of the modern herpetofauna of Eritrea appears to be totally unknown: an extensive bibliographic search, also through the "Bibliography of the Earth Sciences for the Horn of Africa" (Kalb et al. 2000), gave no results concerning fossil amphibians or reptiles.

The research activity undertaken since 1995 by the Florence University (Earth Sciences Department and Geology and Palaeontology Museum) in collaboration with the Department of Mines (Asmara), the National Museum of Eritrea (University of Asmara) and other Eritrean and European Institutions, led to identification of several Pleistocene localities in the Buia area (Northern Danakil Depression, Eritrea) hosting a rich

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vertebrate fossil fauna. The geological setting and the fossil assemblage have been preliminary published by Abbate and co-workers (1998; see also: Ferretti et al. 2003). The following list of mammals results from a recent revision of the Buia fossil collection (see Martínez-Navarro et al. 2004):

Homo "*erectus*-like", *Theropithecus* cf. *T. oswaldi* (Andrews, 1916), cf. *Crocuta crocuta* (Erxleben, 1777), *Elephas recki* Dietrich, 1916, *Ceratotherium simum* (Burchell, 1817), *Equus* cf. *E. grevyi* Oustalet, 1882, *Hippopotamus gorgops* Dietrich, 1926, *Hexaprotodon* sp., *Kolpochoerus olduvaiensis* (Leakey, 1942), *Kolpochoerus majus* (Hopwood, 1934), *Metridiochoerus* aff. *M. modestus* (Van Hoepen and Van Hoepen, 1932), *Giraffa* cf. *G. jumae* Leakey, 1965, *Tragelaphus* cf. *T. spekei* P.L. Sclater, 1863, *Pelorovis oldowayensis* Reck, 1928, *Kobus* cf. *K. ellipsiprymnus* (Ogilby, 1833), *Hippotragus gigas* Leakey, 1965, *Gazella* sp., Caprini indet.

Although the *Homo*-bearing layers, being near the top of the Jaramillo subchron, have been dated to ~ 1 Myr before present, the chronological allocation of the fossiliferous localities ranges from Early to early-Middle Pleistocene. So far, the lower vertebrates have not been studied but the presence of fishes as well as that of crocodylians and chelonians, has been cited by Abbate et al. (1998). The description of this reptile fauna (amphibians have not been found) is the subject of the present contribution to African palaeoherpetology.

Material and Methods

The material described herein belongs to the palaeontological collections of the National Museum of Eritrea in Asmara and was collected in the Buia area during the 1995 and 1997 field seasons of the Buia Project. The fossil remains come from two different sectors of the Dandiero (Buia) Basin: South of Dandiero river (collection abbreviation: DAN) and north of Dandiero river (Wadi Alaad; collection abbreviation: UA). Moreover, a limited number of fossils seen (and not collected) during 2002 field work in the locality called Maebele will be briefly described in order to complete the knowledge of the herpetofauna of the area. For each specimen, the site GPS field code will be reported. For the sake of brevity, no differences have been made between fragmentary or well-preserved remains listed in the material section of each taxon. Traditionally, vertebrate neontologists and paleontologists use the term "skull" to denote the combined unit of the "cranium" (upper jaw) and the mandible (lower jaw). A deviation from this use has appeared in the literature both of non-mammalian and mammalian publication. In this paper the senior author opted to follow the common use in paleoherpetology to employ the term "skull" instead of "cranium" for the upper jaw.

Systematic Palaeontology

Order **Crocodylia** Gmelin, 1788
Family Crocodylidae Cuvier, 1807
Genus *Crocodylus* Laurenti, 1768

Crocodylus niloticus Laurenti, 1768

Material. Skull: DAN 158, DAN 186, DAN 225 (skull and lower jaw), DAN 226; premaxilla: DAN 58; maxilla: DAN 105-106, DAN 188; dentary: DAN 90, DAN 104, DAN 137, UA 38, UA 226, UA 236; UA 241, UA 420-421; tooth: UA 373, UA 408-411, UA 414-415; femur: DAN 36, DAN 156, metapodial: DAN 43; phalanx: UA 221; vertebra: DAN 32-33, UA 208, UA, 284, UA 395 (two remains), UA 400-401, UA 403, UA 419, UA 422, UA 427-428; rib: DAN 34; osteoderm: DAN 25-31, DAN 38-42, DAN 57, DAN 203-204, UA 128, UA 170, UA 191, UA 260, UA 416-417, UA 423-424, UA 429-431.

Crocodylians are by far the most common reptiles in the Buia Collection of the National Museum.

Description

Skull. Among the taxonomically relevant specimens, the incomplete skull DAN 186 shows several characters useful for a correct identification. The specimen, represented by the region anterior to the orbits, shows the premaxillae, maxillae, palatines and right ectopterygoid in ventral view (Fig. 1: A, C) and premaxillae, maxillae, nasals, lacrimals, jugals, prefrontals and frontal in dorsal view (Fig. 1: B, D). Some of the listed bones are nearly complete, others are fragmentary. The general preservation is good although the premaxillae are slightly separated from the maxillae (about 4 mm) and all the ventral surface is affected by partly dislocated fractures that have caused a moderate deformation. The right sector of the skull is better preserved than the left one that has suffered much more deformation. A thin arenaceous concretion partially covers the dorsal and ventral surfaces. The total length of the specimen is 191 mm, and the maximum width is 104 mm.

The left premaxilla is represented by the posterior edentulous region only; the right one is incomplete but two alveoli and the corresponding interalveolar pit are preserved in the anterior area. The remnants of the premaxillae delimit the posterior margin of the nasal cavity.

On the right lateral margin of the skull, the suture between the premaxilla and the maxilla corresponds to a deep notch for the IVth dentary tooth. The right maxilla shows 11 alveoli the dimensions of which, as well as those of the interalveolar spaces, cannot be measured with precision due to the concretion and the sediment that occludes them. The Vth alveolus is the largest and corresponds to a marked swelling on the dorsal surface. Interalveolar pits are regularly present; the IVth is particularly deep. The posteriormost extension of the premaxilla-maxilla suture is opposite the anterior margin of the IInd alveolus of the right maxilla (to its centre on the left one). The maxillo-palatine median suture extends to the level of the anterior margin of the VIIth alveolus. The anteriormost margin of the palatine fenestra points to the centre of the IXth alveolus. Taking into account the greater incompleteness and the slight deformation, the described characteristics seem to be valid for the left

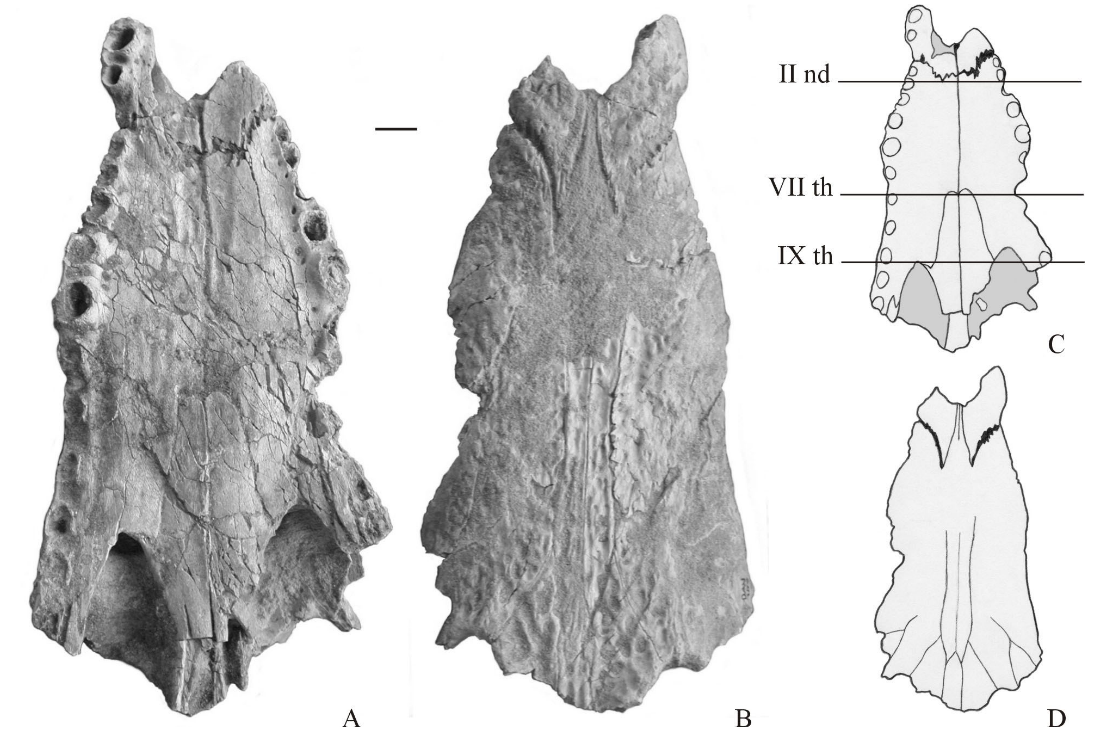

Fig. 1 - *Crocodylus niloticus*. Skull (DAN 186), total length: 190 mm. A) ventral view; B) dorsal view; C) schematic drawing in ventral view; D) schematic drawing in dorsal view. Note in C that the posteriormost extension of the premaxilla-maxilla suture reaches the IInd maxillary alveolus, the maxillo-palatine median suture reaches the VIIth alveolus and the anteriormost margin of the palatine fenestra reaches the IXth alveolus. Scale bar equals 10 mm.

maxilla also. The anterior process of the right ectopterygoid (the left one is not preserved) is deeply forked. It is not possible to ascertain how much the external margin of the maxillaries was festooned. The preserved margins of the nasal cavity and, more particularly, those of the orbits are markedly in relief. The nasals reach the nasal cavity with their anterior narrow tip.

Other skull fragments are not so well preserved and are consequently difficult to interpret. For example, specimen DAN 158 is much larger and more complete than DAN 186 (and apparently not so fractured and deformed) but, at present, it is completely covered by a thin concretion that masks every suture and fine anatomical detail.

Dentary. Several mandible fragments are available in the National Museum collection: the incomplete dentary DAN 137 is particularly well preserved and informative (Fig. 2). It is a right dentary that shows 15 tooth positions. It is rather complete: the margin of the Ist alveolus and the symphyseal area are partially eroded and the distal end of the bone is lacking. The total length is 260 mm. The majority of the alveoli do not bear teeth: an inner cast is present in the first alveolus, tooth fragments are preserved in the IVth and XIth alveoli and a small tooth is visible in the XIIth alveolus. The length of the mandibular symphysis cannot be measured accurately because it is eroded, but it can be estimated at about 55 mm, whereas its width is 34.5 mm (symphyseal length:width ratio = 0.8); the symphysis reaches posteriorly to the centre of the Vth alveolus (Fig. 2: B). The dorsal lobus symphysialis is about 9 mm longer that the ventral one. The dorsolateral margin of the dentary is deeply festooned when observed in dorsal or lateral view. The maximum thickness of the dentary corresponds to the alveoli Ist (31 mm), IVth (38 mm), XIth (40 mm) and the posterior end of the bone (45 mm).

The length/width (in mm) of the alveoli are as follows (the asterisk indicates uncertainty of the measurement):

Ist: not measurable; IInd: 10.7/9.6; IIIrd: 9.0/8.6; IVth: 11.7/10.2*; Vth: 8.3/7.9; VIth: 8.5/7.6; VIIth: 8.4/7.5; VIIIth: 8.6/7.5*; IXth: 7.1/7.0*; Xth: 9.2/8.6; XIth: 11.1/9.1; XIIth: 11.4/8.7; XIIIth: 10.0/6.6; XIVth: 11.3*/6.5; XVth: 10.1/5.3.

The interalveolar distances (in mm) are as follows:

Ist: 6.7*; IInd: 8.5; IIIrd: 3.3; IVth: 3.1; Vth: 3.9; VIth: 5.2; VIIth: 9.5; VIIIth: 17.1; IXth: 8.8; Xth: 5.4; XIth: 4.5; XIIth: 7.0; XIIIth: 10.1; XIVth: 9.5.

The largest alveolus is the IVth; the VIIIth interalveolar space corresponds to a long diastema.

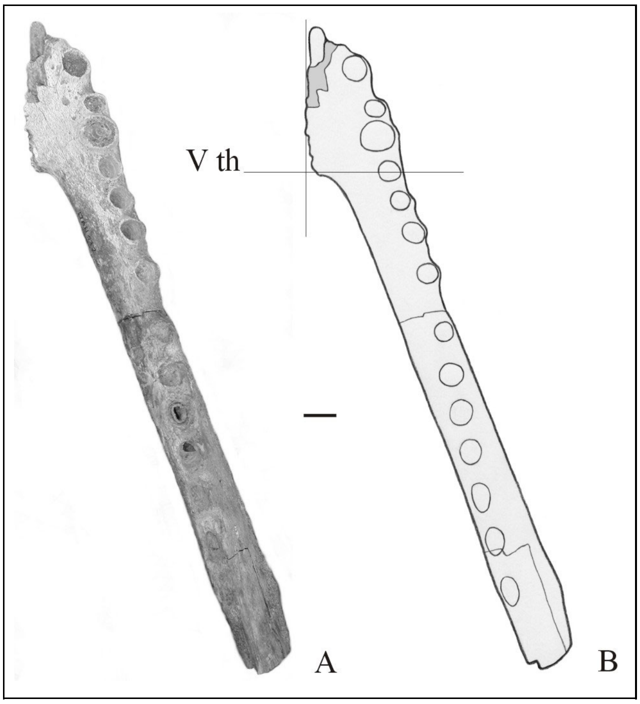

Fig. 2 - *Crocodylus niloticus*. Right dentary (DAN 137), total length: 260 mm. A) dorsal view; B) schematic drawing in dorsal view; note that the symphysis extends posteriorly to the center of the Vth alveolus. Scale bar equals 10 mm.

Although the splenial is lacking, its imprint clearly shows that it did not reach the symphysis and that its anterior tip passed ventral to Meckelian groove.

Specimen DAN 225 is a partially preserved skull and a nearly complete right lower jaw. The skull is almost completely covered by a sandy crust and therefore it is not possible to identify any relevant information of taxonomic interest. In contrast, the lower jaw is only partially englobed in sandstone. It is broken into 5 major pieces and the total length is 500 mm. The total number of alveoli is 15. The ventral surangular process is shorter than the dorsal. The foramen aereum of the articular opens relatively near to the median margin.

Teeth. Isolated teeth are characterised by the presence of evident mesial and distal keels that separate the buccal surface from the lingual one (less developed than the buccal). Those from the anterior part of the buccal cavity have a sharp shape and show small ridges on both surfaces; those from the rear of the buccal cavity are progressively more blunt and the small ridges are less evident.

Vertebrae. Several vertebrae, representing both the dorsal and the caudal tract, are also present. Specimen UA 284 seems to show a trace of a broken hypapophysis and therefore could be a cervical vertebra. Common traits of well preserved vertebrae are: procoelous body, pre- and postzygapophyses laterally directed and tilted at about 45°, pre- and postzygapophyseal facets nearly rectangular in shape. Curiously, a large vertebra (UA 208) whose centrum length is at least 53 mm (underestimated since the condyle is eroded) lacks of the neural arch because the neurocentral suture still was not closed (Fig. 3: A), while other vertebrae of comparable size (UA 400 and 401) show a closed suture.

Osteoderms. All the osteoderms show a median keel and the typical pattern of deep roundish pits. The outline varies from irregularly oval to rectangular. The biggest osteoderm (DAN 203; Fig. 3: B) is 77.3 mm long and 62 mm wide, but since it is fragmentary, its width is underestimated. Its shape suggests that it comes from the dorso-lateral district.

Discussion

All the crocodylian material seems to belong to a single taxon that, on the basis of the skull remains, is undoubtedly a brevirostrine form belonging to family Crocodylidae.

According to Tchernov (1986) the Pleistocene crocodylian of East Africa are represented by three species: *Crocodylus cataphractus* Cuvier, 1824, *Crocodylus lloydi* Fourtau, 1920 and *Crocodylus niloticus* Laurenti, 1768. *C. lloydi* has been considered by Tchernov (1986) as the forerunner of *C. niloticus*, but a close relative to *Osteolaemus* by Brochu (2001). Storrs (2003) recently placed this species in the new genus *Rimasuchus*. Apart

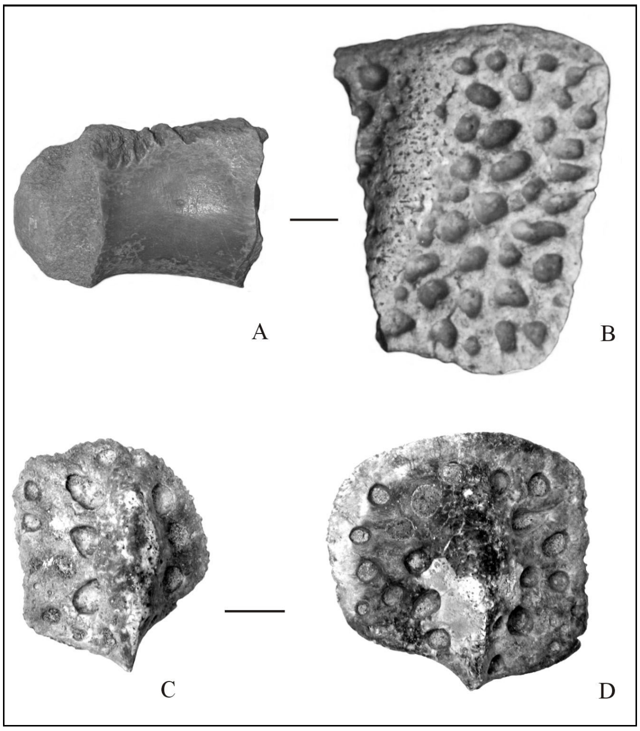

Fig. 3 - *Crocodylus niloticus*. A) dorsal vertebra (centrum only) in right lateral view (UA 208), total length: 53 mm; B) osteoderm in dorsal view (DAN 203), total length: 77.3 mm; C) osteoderm in dorsal view (DAN 29), total length: 37.7 mm; D) osteoderm in dorsal view (DAN 30), total length: 41.6 mm. Scale bar equals 10 mm.

from "*C. lloydi*", which became extinct in the Late Pleistocene or Holocene, the other species are still living, but only *C. niloticus* has been reported for the extant herpetofauna of Eritrea (Largen 1997).

Although the presence of *C. cataphractus* among the fossil materials can be excluded because it is a longirostrine crocodylian, its characters will be discussed along with those of "*C. lloydi*".

The allocation of the Buia material to *Crocodylus niloticus* rests (see Tchernov 1986, Tab. 1) on the position of the posteriormost extension of the premaxilla-maxilla suture (opposite the IInd maxillary alveolus as in *C. niloticus* and not the Ist as in "*C. lloydi*" or *C. cataphractus*), the extension of the maxillo-palatine median suture (VIIth alveolus as in *C. niloticus* and not the VIth as in "*C. lloydi*" or IXth as in *C. cataphractus*) and the position of the anteriormost margin of the palatine fenestra (VIIIth-IXth alveolus as in *C. niloticus* and not the VIIth-VIIIth as in "*C. lloydi*" or the XIth-XIIth as in *C. cataphractus*) as well as on the posterior extension of the dentary symphysis (middle of the Vth dentary alveolus as in *C. niloticus* and not the IIIrd-IVth in "*C. lloydi*" or the VIIth-VIIIth as in *C. cataphractus*). The estimated symphyseal length:width ratio of 0.8 falls in the range of *C. niloticus* published by Tchernov (1986) and Rauhe *et al.* (1999): 0.79-1.1 and 0.8-1.0 respectively.

Although many of the features discussed by Tchernov have been recently considered by Storrs (2003) as being too variable and therefore not diagnostic, the new diagnosis of "*Rimasuchus lloydi*" does not match the morphology of the Buia remains: the premaxillae are not broader than long and the palatal premaxillary/maxillary suture is not straighter than it is in *C. niloticus*.

Moreover, the identification of the Buia crocodylians as *C. niloticus* is strongly supported by one of the unambiguous synapomorphies of the genus *Crocodylus* identified by Brochu (1999, 2000; it is not possible to evaluate the other three characters due to the incompleteness -or incomplete restoration- of the remains): the anterior process of the ectopterygoid is distinctly forked (character 109, state 1). This character is not shared by "*C. lloydi*" that, according to Brochu, does not belong to this genus. Also the presence of very modest preorbital ridges (character 144, state 0), matches with *C. niloticus* and not with "*C. lloydi*".

The presence of *C. niloticus* in the fossil assemblages of the Buia area is remarkable, because, even though this species can be traced back to the Late Miocene (Rauhe et al. 1999; Storrs 2003), it has been considered an "apparently a rare element of African faunas prior to the Middle Pleistocene" (Harris 1978). Pickford (2003) described the species *Crocodylus gariepensis* from the early Middle Miocene of Arrisdrift, Namibia, and interpreted it as being ancestral to the Nile Crocodile. If this is correct, then the lineage apparently originated in southern Africa some 17 Ma and only spread northwards in the Late Miocene when environments in East Africa became more open and water bodies more unstable.

Some of the crocodile remains from Buia belonged to animals of relatively large size. Since "the ratio of skull to total length for an adult crocodile is about 1:7" (Spawls et al. 2002), the lower jaw of 50 cm (DAN 225) should belong to a specimen about 3.5 m in total length, which was not necessarily fully grown. The absence of sutural closure in dorsal vertebrae of more than 50 mm length indicates that the individuals were neither fully mature nor fully grown at the time of death (Brochu 1996). The vertebra seen in the locality R030, whose centrum was 72 mm long and sutured to the neural arch, probably belonged to a morphologically mature individual which was bigger.

Order **Chelonii** Brongniart, 1800
Infraorder Pleurodira Cope, 1864
Family Pelomedusidae Cope, 1868
Genus *Pelusios* Wagler, 1830

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

Material. Entoplastron: UA 374

Description

A perfectly preserved entoplastron (length 45.3 mm; width 46.8 mm; maximum thickness 11.3 mm) shows some seams on its external surface (Fig. 4). The longitudinal seam corresponds to the boundary between the humeral shields; the posterior seams are slightly irregular and should correspond to the boundary between the humerals and left pectoral shield. The anterior seams should correspond to the boundary between the humerals and the intergular. The absence of a longitudinal seam in the anterior area indicates the absence of paired gulars reaching the entoplastron and therefore the presence of a single intergular that fully separates the gulars.

Discussion

These characters are typical of some pleurodiran chelonians and allow us to refer the fossil to the family Pelomedusidae, the only African family that shows an intergular so developed. The fossil can be identified as *Pelusios* cf. *P. sinuatus* by the combination of the following characters: large size and shape (delimited by crests) of the sulcus border of the intergular, moderate overlap of the intergular on the entoplastron and slight overlap of the humero-pectoral sulcus on the entoplastron (see Broin 1969; Broin 1983; de Lapparent de Broin, pers. comm.).

Pelomedusid chelonians are relatively common in the African fossil record: a preliminary catalogue has been proposed by Lapparent de Broin (2000). *Pelusios*

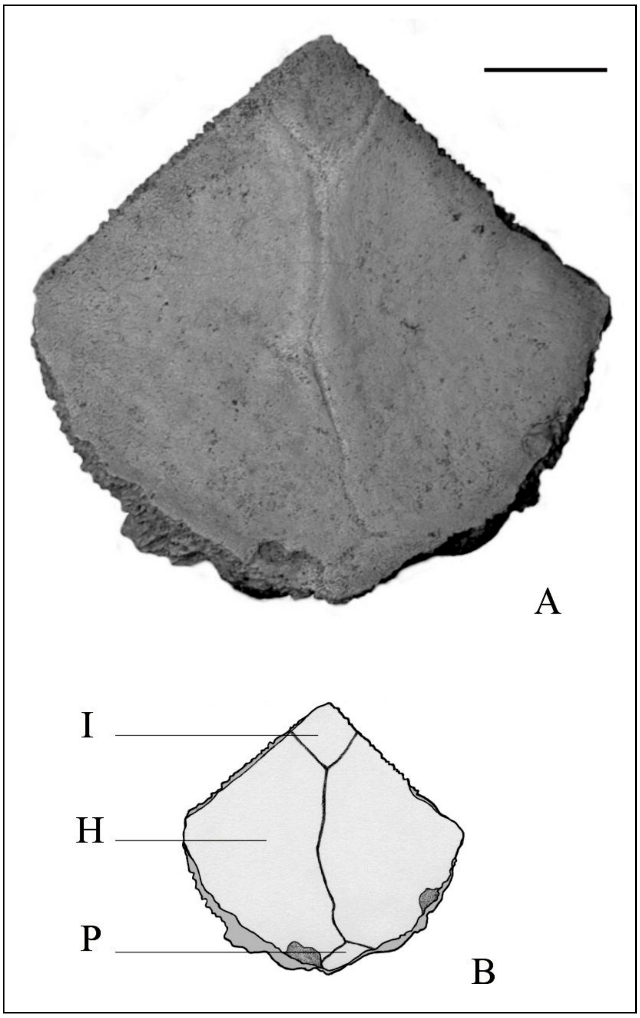

Fig. 4 - *Pelusios* cf. *P. sinuatus*. A) entoplastron in ventral view (UA 374), total length: 45.3 mm; B) idem, schematic drawing. H = humeral, I = intergular, P = pectoral. Scale bar equals 10 mm.

sinuatus is the most common chelonian of Africa since the Mio-Pliocene and genus *Pelusios* has been present north up to Libya and in the Nile Valley of Sudan during the Holocene, and in Djibouti during the Plio-Pleistocene. The only pelomedusid reported among the extant Eritrean herpetofauna (Largen 1997) is *Pelomedusa subrufa* (Lacépède, 1788).

A few other chelonian remains have been allocated only to the level of order because they are heavy damaged or are not diagnostic (DAN 224; UA 21; UA 412; UA 413; UA 418; UA 425; UA 426) or still need to be restored: this is the case of the anterior portion of a fragmentary shell of small size (UA 432; total length: 105 mm) that, although damaged in the anterior area of the plastron and partially covered by sediment, should be of some taxonomic value when fully prepared. All these remains could belong to *Pelusios* and therefore the presence of indeterminate Chelonii is tentatively not reported in the faunal list.

Order **Sauria** McCartney, 1802
Family Varanidae Gray, 1827
Genus *Varanus* Merrem, 1820

Varanus niloticus (Linnaeus, 1766)

Material. One vertebra UA 466

Description

The Buia collection of the National Museum holds a vertebra clearly belonging to a large lizard (Fig. 5). The specimen is relatively well preserved; only the left synapophysis, the neural spine apex and the ventral rims of the cotyle and the condyle are markedly eroded or damaged. It shows a centrum length of approximately 21 mm and centrum width of 12.3 mm. In anterior view, the cotyle is dorso-ventrally depressed and ventrally oriented (it faces antero-ventrally), the prezygapophyses do not show any sign of prezygapophyseal process and are dorsally tilted at 45° approximately, the neural canal is narrow (filled by sediment), the neural arch is markedly raised (pars tectiformis lower than prezygapophyses), and with no signs of a zygosphene. In caudal view, the condyle and the postzygapophyses show a morphology matching that of their anterior counterparts; there are no evidences of a zygantrum. In dorsal view, there is an evident interzygapophyseal constriction, the prezygapophyseal facets are drop-shaped and laterally directed. In ventral view, the synapophyses are laterally protruding, the centrum has a triangular shape, its surface is devoid of any ridge or groove and it is deeply constricted just before the condyle. In lateral view, the cotyle shows a marked antero-ventral orientation, the ventral surface of the centrum is flat, the neural spine is well developed and restricted to the posterior region of the neural arch and some ridges are visible on the ventro-lateral surface of the prezygapophyses.

Discussion

According to Largen (1997) two species of monitor lizards inhabit Eritrea at present: *Varanus exanthematicus* (Bosc, 1792) and *Varanus niloticus* (Linnaeus, 1766).

The vertebra can be referred to the latter (and not to the former or any other African species), because of the combination of the following characters (see Bailon & Rage 1994): precondylar constriction well developed, ventral orientation of the cotyle (Lv/LV = 0.79) and large size.

Another large vertebra has been identified in the locality called Maabale (site code N042) during 2002 fieldwork. Even if the precondylar constriction cannot be observed because of the fragmentary state of the fossil, it can be referred to the same taxon on the basis of its general morphology and large size.

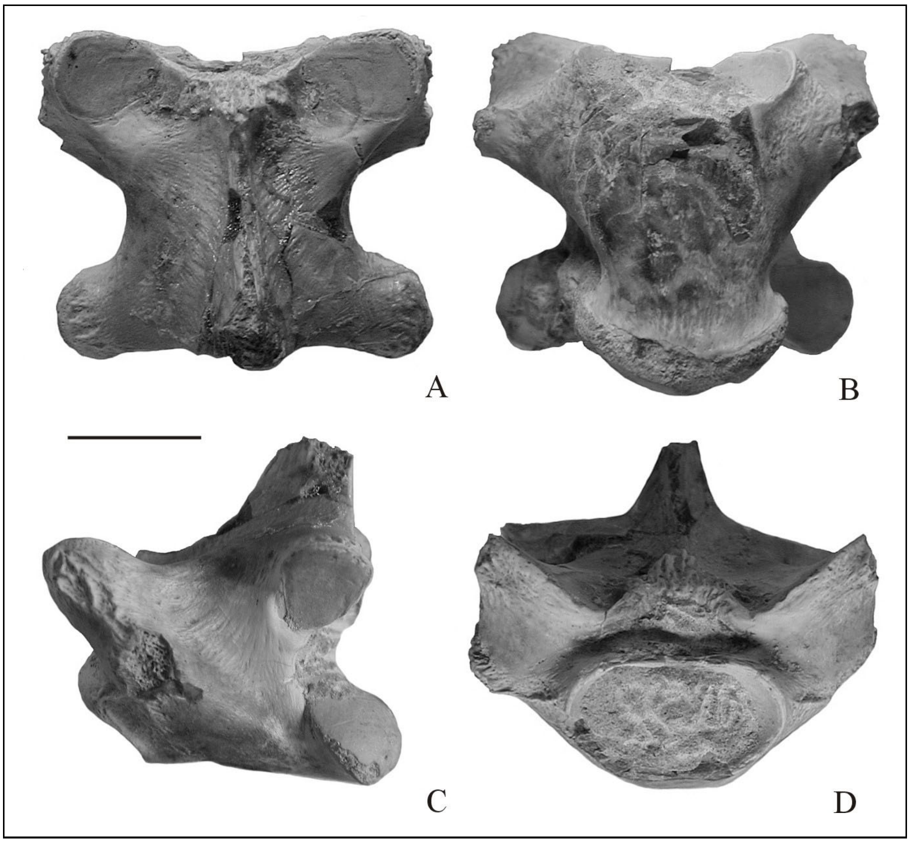

Fig. 5 - *Varanus niloticus*. Trunk vertebra (UA 466), centrum length: 21 mm approx. A) dorsal view; B) ventral view; C) left lateral view; D) anterior view. Scale bar equals 10 mm.

Order **Serpentes** Linnaeus, 1758
Family Boidae Gray, 1825
Genus *Python* Daudin, 1803

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

Material. Two vertebrae (UA 267; UA 432)

Description

The National Museum palaeontological collection includes two vertebrae of a snake. Specimen UA 432 is by far the best-preserved (Fig. 6). This vertebra is massively built and large: the centrum length is 16.2 mm but since the condyle surface is partially eroded, a length of at least 17 mm can be supposed; the centrum width is 25.7 mm.

The right prezygapophyses and the neural spine are lacking; the paradiapophyses, the left pre- and postzygapophyses, the zygosphene and the condyle are partially eroded or damaged.

In anterior view, the cotyle is slightly oval (dorsoventrally depressed and with nearly straight ventro-lateral margins), the paracotylar foramina are lacking, the left prezygapophyseal facet is slightly tilted dorsally, the neural canal is narrow, the dorsal margin of the zygosphene is convex; a small but quite distinct tubercle is perceivable at the boundary between the base of the zygosphene and the top of the neural canal: the tubercle is dorsally prolonged by a small crest.

In dorsal view, the anterior margin of the zygosphene is slightly concave, the median tubercle at the

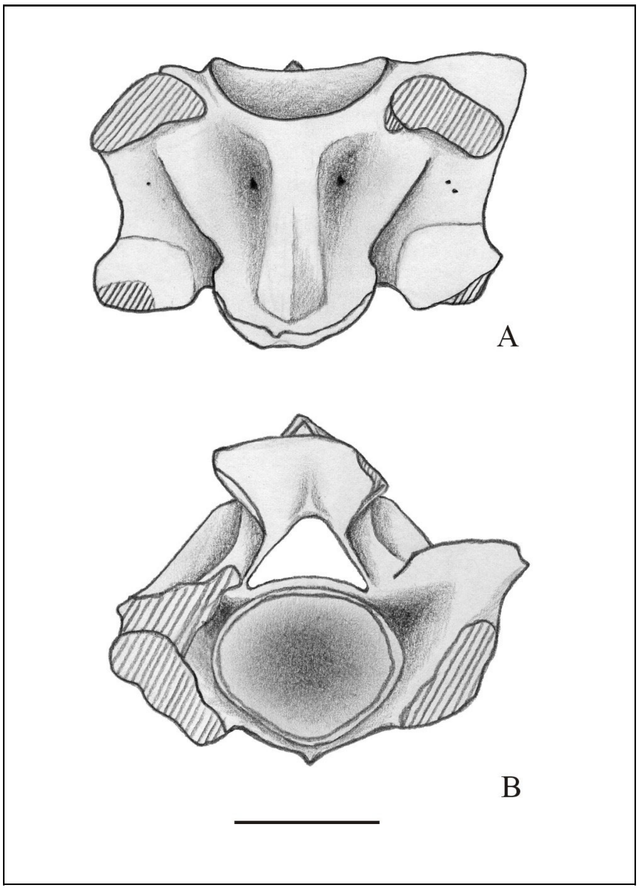

Fig. 6 - *Python* gr. *P. sebae*. Trunk vertebra (UA 432), centrum length: 16.2 mm. A) ventral view; B) anterior view. Scale bar equals 10 mm.

base of the zygosphene is distinctly visible, the left prezygapophyseal facet is laterally directed and seems to be vaguely rectangular. The interzygapophyseal constriction is moderate and located just before the beginning of the postzygapophyses.

In posterior view, the neural arch is high, massive, and its dorsal margins are nearly straight. The zygantra are wide and deep. The postzygapophyseal facets show an inclination that is complementary with that of the prezygapophyseal one.

In ventral view, the haemal keel is distinct and relatively high: its caudal end is slightly widened but latero-laterally compressed and elevated into a ridge. The subcentral foramina are evident and of average size; the lateral foramina are small (two foramina are present on the left side). The subcentral grooves are not developed. A slight precondylar constriction is present. Since the right prezygapophyses is broken off and the left one is apically damaged, it is not possible to record the presence of prezygapophyseal processes.

In lateral view, it could be noticed that the anterior margin of the neural spine, despite it being broken off, coincides with the posterior end of the zygosphene.

All the described characteristics are typical of first mid trunk vertebrae; the snake to which this vertebra belonged could have attained a total length of about 450 cm.

The second vertebra (UA 267) is much more fragmentary than the previous one because all the structures of the vertebra are damaged or broken off. An arenaceous sediment occludes the neural canal and partially covers the vertebral surface. The caudal end of the haemal keel is compressed and elevated into a ridge with some irregular small tubercles. Altogether, the morphology is basically the same as described above. It is possible to estimate that the centrum length is about 16-17 mm and the centrum width is 24 mm approximately.

Discussion

The vertebrae can be referred to a member of a family Boidae since the centra are wider than long (the ratio centrum length/centrum width is 0.66 in UA 432). The large size allows to exclude the presence of a member of the subfamily Erycine and points to the subfamily Pythoninae that is represented in Africa by the sole genus *Python*; the size of the vertebra matches only with species of the *P. sebae* group, that can reach a total length of about 5.5 m (Spawls et al. 2002). *P. sebae* has been recently split in two different species (Broadley 1999): the nominal form is widespread in central and West Africa whereas the southern populations are now considered as *P. natalensis* A. Smith, 1840. Since the comparative osteology of these two species is still undescribed, the fossil remains are simply referred to the group (consisting therefore of *P. sebae* and *P. natalensis*), even if *P. sebae* is the only python living in Eritrea at present (Largen 1997).

At least 11 vertebrae, 9 vertebral fragments and 2 rib fragments of snakes have been found, along with the above described monitor lizard, in the Maabale locality (site code N042): their morphology is very homogenous (they could belong to a single individual) and match perfectly the specimen UA 432 with the exception of the haemal keel, the caudal end of which is not always elevated into a sagittal ridge (as a small "blade-like" ridge) but is sometimes enlarged and relatively flattened with some tiny irregular ridges for muscular insertion. This difference could indicate that the vertebrae come from a more posterior trunk section.

The morphology of all the fossil remains matches well with that of the available comparative osteological material of *P. sebae*. Minor differences concern the development of the "zygosphene tubercle" and haemal keel (namely the presence of the tiny but distinct irregular ridges).

Although the fossils are quite variable, the presence of a common set of characters allows us to trace the *P. sebae* lineage into the Early Miocene of Namibia (*P.* cf. *P. sebae*, Rage 2003), an then in the latest Miocene of some localities in Uganda (*P.* cf. *P. sebae* – *P. sebae* or *P.* aff. *P. sebae*; Bailon & Rage 1994), at the Mio-Pliocene transition (*P.* aff. *P. sebae*; Brunet et al. 2000) and Late Miocene (*P.* cf. *P. sebae*; Vignaud et al. 2002) of Chad, in the Pliocene of Laetoli (*P. sebae*; Meylan 1987) and of Hadar (? *P. sebae*; Rage 1979; Bailon & Rage 1994), as well as in the Early Pleistocene of Olduvai (*P.* aff. *P. sebae*; Rage 1973).

Discussion and conclusions

The fossil herpetofauna of the Buia area is represented by four taxa: one crocodile, *Crocodylus niloticus*, one pelomedusid chelonian, *Pelusios* cf. *P. sinuatus*, one monitor lizard, *Varanus niloticus*, and one python, *Python* gr. *P. sebae*. All these taxa belong to extant species. The Pleistocene herpetofauna of North America and Europe are almost essentially represented by modern taxa (Holman 1991, 1995, 1998, 2000) and Africa is not an exception. The main difference between the Pleistocene and the modern herpetofaunas is therefore not strictly related to the taxonomic pool but to the ranges of each taxon.

Following Largen (1997), all the identified taxa, except the chelonian, live in Eritrea at present but none of them is known from the Buia area or, more generally, in the Northern Danakil Depression. This seems to confirm that the Pleistocene herpetofaunas of East Africa have also been subject to major range adjustments, related to humidity changes but not directly to periodic glaciations and deglaciations as happened in Eurasia or in North America (Holman 1991, 1995, 1998, 2000). At present, the Danakil Depression is a desert but the sands and whitish clayey silts that comprise the fossiliferous beds were deposited in a fluvio-deltaic and lacustrine environment (Abbate et al. 1998). The herpetofauna fully agrees with such a kind of environment since the Nile Crocodile and the Serrated Hinged Terrapin are restricted to all kinds of aquatic environments (river mouths and estuaries included), the Nile Monitor is usually found near water, and the African Rock Pythons are most abundant near low altitude rivers, lakes and swamps (Spawls et al. 2002).

Since the habitat of all the reptile fauna could be basically the same, the fact that crocodile remains outnumber those of the other taxa is most likely due to their larger size and their higher visibility in the field and not to peculiar ecological requirements. All the identified taxa are of relatively large size. Amphibians and small reptiles are virtually lacking: their absence is probably due not to the fact that they are absent in the deposits, but because they have not been collected. The recovered remains are all bigger than one centimetre and such kind of remains can be easily spotted during a surface survey with no need for carefully wet-sieving huge amounts of sediment.

The retrieval and study of the small herpetofauna as well as all the microvertebrates, which were most likely associated with the described taxa, should be one of the primary goals of future research in the Northern Danakil area, not only because African microvertebrates are still poorly known (among others, see Bailon & Rage -1994- for squamates and Rage & Rocek -2000- for anurans), but mainly because it could help to further characterise the environment of the Buia area at the beginning of the Pleistocene.

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