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Human consumption of turtles of the *Homo rudolfensis* site Uraha (Malawi, East Africa)

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ABSTRACT: A survey is given of the hitherto known turtle taxa from the Plio-Pleistocene of the Chiwondo Beds in Malawi. The paper includes new materials from these beds of Uraha, Karonga District of northern Malawi, collected by the «Hominid Corridor Research Project (HCRP)». The following species are discovered: *Pelomedusa subrufa* ssp., *Pelusios sinuatus* (A. Smith 1838), *Cyclanorbis senegalensis* (Duméril & Bibron, 1835) and *Cycloderma frenatum* Peters, 1854, all from the deposits which yielded *Homo rudolfensis* Alexeev, 1986. In the collection of fossils from this site also include two fragments of clavicular plates of great catfishes (Siluroidea: Clariidae) which remarkably resemble each other in the fragmented form, although they belong to evidently different individuals. The flat-shaped bones originate from the thickened joint area of the pectoral fin sting and the adjoining flat pectoral area. This combines with damages of an otherwise complete turtle shell by early humans. This evidence of consumption of aquatic animals could support an «aquatic ape hypothesis» in the sense of Morgan (1997), Verhaegen (2000) and Niemitz (2006, 2010).

KEY WORDS: *Homo rudolfensis*, ANTHROPOGENIC DAMAGES, PELOMEDUSIDAE, CYCLANORBINAE, CHIWONDO BEDS, PLIO-PLEISTOCENE, URAHA, MALAWI

RESUMEN: Se lleva a cabo una revisión de los taxones de Quelonios de la formación plio-pleistocénica de Chiwondo en Malawi conocidos hasta la fecha. El trabajo incluye la presentación de nuevos materiales procedentes del depósito de Uraha, en el distrito de Karonga en el norte de Malawi que fueron recolectados por el «Hominid Corridor Research Project (HCRP)». Las especies descubiertas han sido: *Pelomedusa subrufa* ssp., *Pelusios sinuatus* (A. Smith 1838), *Cyclanorbis senegalensis* (Duméril & Bibron, 1835) and *Cycloderma frenatum* Peters, 1854. Se trata de depósitos en los que se han encontrado restos de *Homo rudolfensis* Alexeev, 1986. En la colección de fósiles se incluyen también dos fragmentos de placas de la clavícula de peces gato (Siluroidea: Clariidae) de gran tamaño que aparecen sospechosamente fragmentados de una misma manera a pesar de pertenecer a ejemplares distintos. Los huesos planos procedían del área engrosada de la articulación del radio de la aleta pectoral en su zona de inserción con el cleitro. Este hallazgo viene a añadirse a otro realizado presumiblemente por los homínidos en un caparazón de tortuga. Toda esta evidencia de consumo de animales acuáticos podría apoyar la «hipótesis del simio acuático» defendida por Morgan (1997), Verhaegen (2000) y Niemitz (2006, 2010).

PALABRAS CLAVE: *Homo rudolfensis*, DAÑO DE ORIGEN ANTROPOGÉNICO, PELOMEDUSIDAE, CYCLANORBINAE, FORMACIÓN DE CHIWONDO, PLIO-PLEISTOCENO, URAHA, MALAWI

INTRODUCTION

East African terrestrial animal species range from 22% to 57% in 15 modern environments (Kovarovic *et al*., 2002). In contrast, the collections from the Chiwondo Beds contain nearly 90% terrestrial species – fossorial, scansorial, and (semi-) arboreal animals are absent. This places them towards modern tropical grassland or semi-arid bushland as well as to Swartkrans 1 and the Upper Ndolanya Beds which also have high percentages of terrestrial taxa. In the Chiwondo Beds small animals are underrepresented or completely absent. In modern ecosystems, species of 1 g to 10 kg range between 53% and 82%: the African tropical grassland and bushland faunas exhibit the smallest percentage (Kovarovic *et al*., 2002), but the Malawi fauna corresponds neither to the observed weight pattern of Swartkrans 1 nor to the East African localities of Kanapoi, Aramis, Laetoli Beds, or the Ndolanya Beds (Figure 1). The fauna is dominated by medium- to large-sized species, the latter being large bovids, proboscideans, and hippopotamuses. Consequently there exists an overrepresentation of herbivorous species. Grazers and browsers are dominant, in particular alcelaphin grazers are abundant like in Swartkrans 1 and the Ndolanya Beds. As far as known, stone tools are directly associated with fossils of Homo rudolfensis, contrarily to the slightly younger horizons along the western Lake Turkana. Therefore, it is not completely clear, but at rather possible that *Homo rudolfensis* was the first human species that used stone tools. Based upon dental examinations, it is assumed that *Homo rudolfensis* was predominantly herbivorous. The damages in shells of freshwater turtles described herein emphatically supports the presumption that *Homo rudolfensis* was hunting aquatic vertebrates as additional part of its diet. The oldest fossil turtles of Malawi are known from the Early Cretaceous (dinosaur beds of the Mwakasynguty area, Sive valley, Karongo District) and the Early Cretaceous Lupata Group (upper member), with new specimens of *Platycheloides nyasae* Haughton, 1828 (Pelomedusidae). Again from the Karonga District (-9° 55’ 28.99”, +33° 56’ 29.82”), fossil *Pelusios sinuatus* and *Cycloderma frenatum* were recorded from Pliocene sediments (2.5-4.8 Ma) (Meylan, 1990; Lapparent de Broin, 2000). The age of the sediments was determined as 2.3 my.

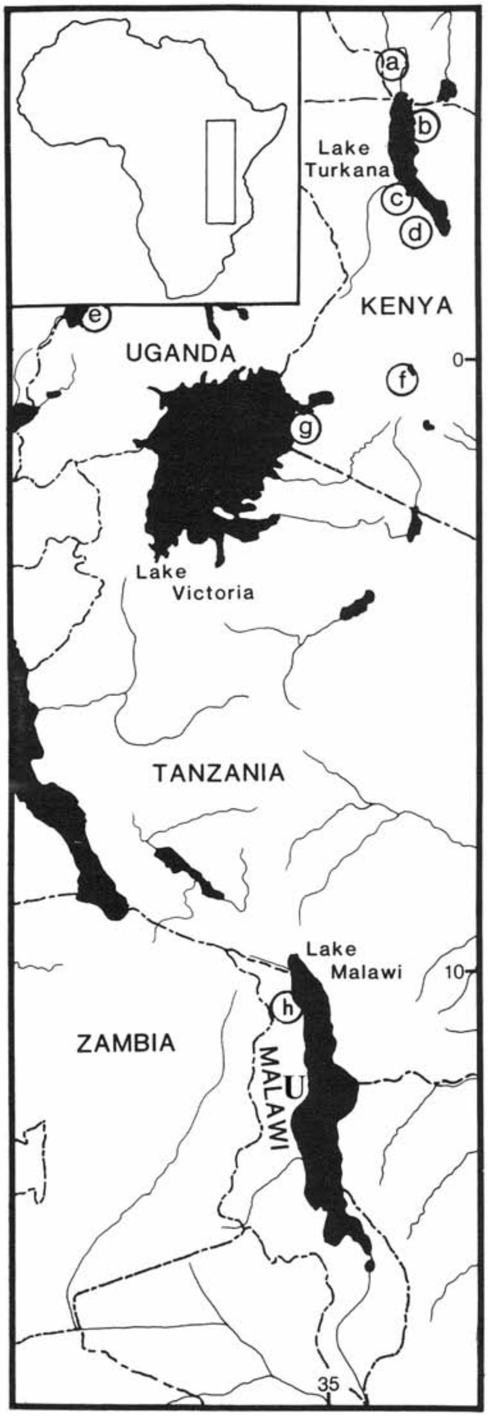

FIGURE 1

Map of the East-African rift-system with the locality Uraha; according Meylan *et al*. (1990), adapted. Fossil turtles sites: a = Omo, b = Koobi Fora, c = Lothagam, d = Kanapoi, e = Kaiso, f = Cheremon, g = Karungu, h = Chiwondo, U = Uraha.

GENERAL FAUNAL CHARACTER OF THE CHIWONDO BEDS

Fauna, taphonomy, and geology of the Plio-Pleistocene Chiwondo Beds are summarized by Bromage & Schrenk (1986), Schrenk *et al*. (1993), Wood (1993), Bromage *et al*. (1995), Stidham (2004) and Sandrock *et al*. (2005, 2007). According to these authors the vertebrate fauna of the Chiwondo Beds in Northern Malawi is heavily biased towards the preservation of large terrestrial mammals, the majority being ungulates. The faunal diversity is similar to assemblages of African short grass plains. The taxonomic diversity is nevertheless low, emphasizing an incomplete fossil record. Based on modern bovid representation in African game parks, statistical tests show that the Chiwondo bovid assemblage consists of a mixture of species found in the Somali-Masai and the Zambezian ecozones. The composition of the terrestrial fauna is similar to Swartkrans 1 and the Upper Ndolanya Beds. The fossil assemblages can be assigned to three biostratigraphic time intervals, dating from more than 4.0 Ma to less than 1.5 Ma. The occurrence of *Paranthropus boisei* at a lake margin site in the Chiwondo Beds corresponds to robust australopithecine-bearing localities near Lake Turkana, Kenya. A case study showed that the investigated death assemblage on a delta plain in the Malema region was subject to heavy modification after deposition. This has affected the size distribution, the frequencies of skeletal elements, and thus the taxonomic composition. High-density skeletal elements such as molars and partial mandibles dominate the assemblage. The *Homo rudolfensis* locality at Uraha has a different faunal composition, its preservation in a paleosol points to a different taphonomic history and the Uraha area encompasses a longer time span. According to Kullmer (2008) the southern localities at Uraha show a complex stratigraphic pattern with at least four age levels documented by the association of suid fossils. At the northern localities it seems to be slightly less complicated, since the suid remains suggest a split into two levels. Pig remains occur in two stratigraphic units. Unit 2 (Figure 2) contains *Notochoerus jaegeri*. The younger stratigraphic unit 3A can be subdivided by the suid fauna into an older zone 3A-1 containing *Notochoerus euilus* and a younger zone 3A-2 with more advanced forms as *Notochoerus scotti* and early *Metridiochoerus andrewsi*. Unit 3B contains advanced *M. andrewsi* and *M. compactus*. Furthermore, Bromage & Schrenk (1986) recorded cercopithecid specimens from the Chiwondo Beds. The majority of this material was collected from the Middle Pliocene Unit 3A, but one single specimen is allocated to the Early Pliocene Unit 2. This latter specimen belongs to a papionine of an indeterminable genus similar in size to *Parapapio ado* and *Pliopapio alemui*. Among the specimens from Unit 3A, two species can be diagnosed: an indeterminable species of *Theropithecus*, and a species of *Parapapio* similar in dental size to *P. broomi*. None of the genera from Unit 3A are exclusive to either East Africa or South Africa. Their relative abundances, however, are more similar to Middle Pliocene South African sites where *Parapapio* is the most common primate genus, and *Theropithecus* is comparatively rare. This is in contrast to similarly-aged East African sites where *Theropithecus* is by far the most abundant genus. Stidham (2004) describes extinct ostrich eggshells as

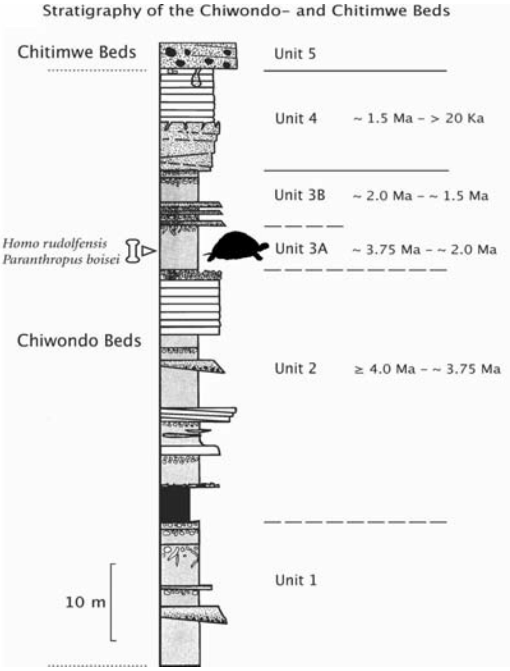

FIGURE 2

Generalized stratigraphic profile of Chiwondo and Chitimwe Beds Units 1–5 including their age ranges from Sandrock *et al*. (2007). Solid lines mark major unconformities; dashed lines mark minor unconformities. Abbreviations: Si = silt, si = silty; fs = fine sand; ms = middle sand; cs = coarse sand; s = sandy; fg = fine gravel; mg = middle gravel; cg = coarse gravel; g = gravelly; x = stone; y = boulder; quantity of sediment fraction ‘= slight, “= very slight, — = strong.

Struthio daberasensis Pickford *et al*., 1995 from the Chiwondo Beds.

TURTLE MATERIAL ANALYSIS

Abbreviations: HLMD = Hessisches Landesmuseum Darmstadt, ZSMH = Zoologische Staatssammlung München, Herpetologische Sammlung.

Terminology: Carapace plates: nuchal = nu, neural = n I – n VIII, pleural = pl I – VIII, peripheral = pe I – pe XI, metaneural = mn I – II, pygal = py; carapace scutes: cervical = ce, central = c 1 – c 5, lateral = l 1 – l4, caudal = ca. Plastron plates. epiplastral = epi, entoplastron = ento, hyoplastron = hyo, mesoplastron = meso, hypoplastron = hypo, xiphiplastron = xiphi; plastron scutes: gular = gu, humeral = hu, pectoral = pec, abdominal = ab, femoral = fe, anal = an.

Classification: Order Testudines Linnaeus, 1758

a) Infraorder Pleurodira Cope, 1864/ Family Pelomedusidae Cope, 1868/ Genera *Pelomedusa* Wagler, 1830 and *Pelusios* Wagler, 1830

b) Infraorder Cryptodira Cope, 1868/ Superfamily Trionychoidea Fitzinger, 1826/ Family Trionychidae Fitzinger, 1826/ Subfamily Cyclanorbinae Lydekker, 1889/ Tribe Cyclanorbini (Hummel, 1929)/ Genera *Cyclanorbis* Gray, 1835 and *Cycloderma* Peters, 1854

Material distribution and description:

Pelomedusa subrufa (Lacépède, 1788) - HLMD 11 (Plate 2, figures 3-4): metaneural, medial length 32.0 mm, right anterior length 35.0 mm, right posterior length 13.0 mm, maximal length 40.0 mm, maximal width 40.0 mm, posterior width 19.0 mm. HLMD without number at Plate 1, figures 1-2, nearly complete shell. Figures 3a-b

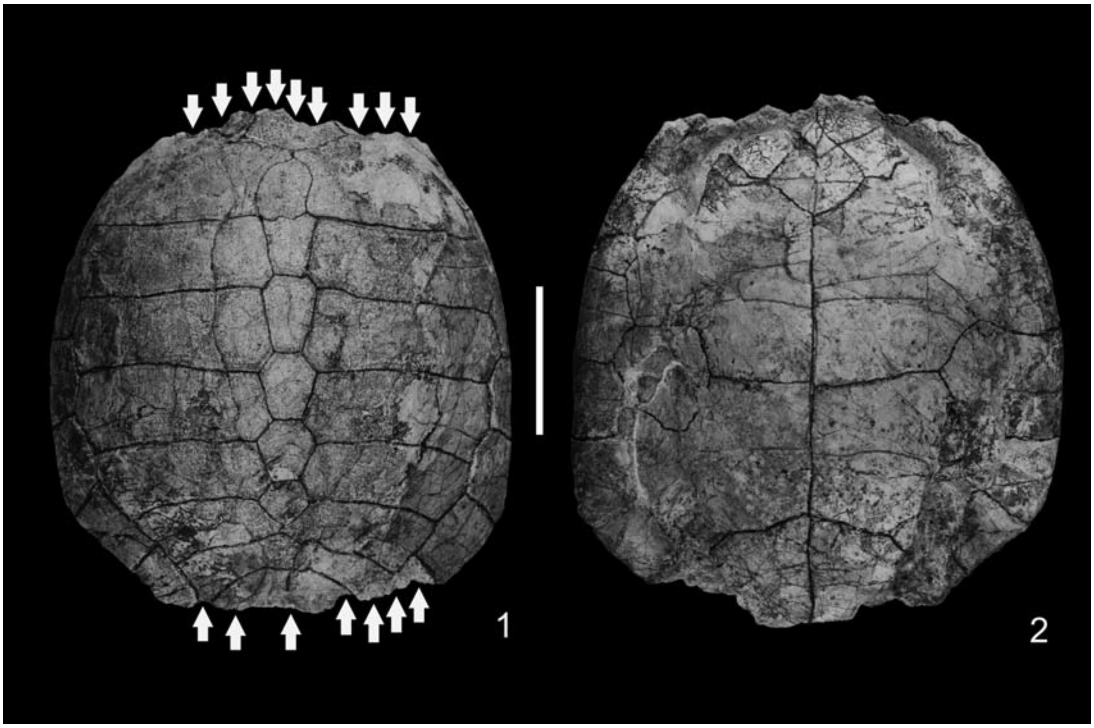

PLATE 1

Pelomedusa subrufa, Uraha, steinkern (internal mould) with nearly complete shell. Figure 1 = carapace, figure 2 = plastron. The arrows above described the percussion notches in the head and at tail in the lower range shown clearly anthropogenic damages. Scale bar 5 cm. Photo Dirk Urban, Erfurt Museum.

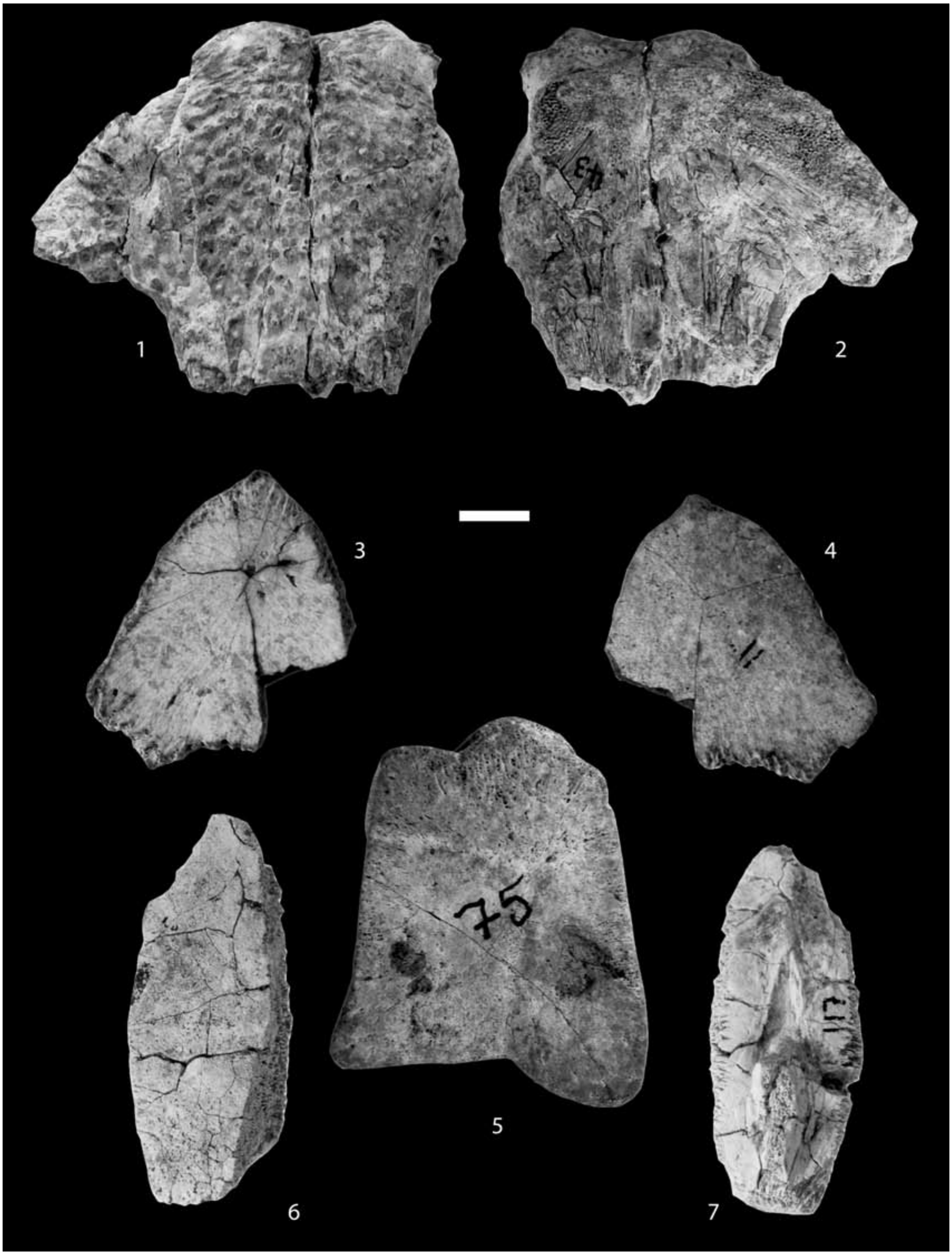

PLATE 2

Cyclanorbis senegalensis, Uraha, figure 1=HLMD 43, entoplastron ventral, 2= visceral, *Pelomedusa subrufa* figure 3 = HLMD 11, metaneural dorsal, 4 = visceral; *Pelusios sinuatus*, figure 5 = HLMD 75 dorsal; figure 6 = HLMD 117, neural plate I dorsal, 7 = visceral. Scale bar = 1 cm. Photo Dirk Urban, Erfurt Museum.

show the distribution pattern of the shell. - *Pelusios sinuatus* (A. Smith, 1838) - HLMD 117 (Plate 2, figure 6-7): neural I, anterior margin 6.0 mm thick, at the posterior 13.0 mm, left anterior length 0.0 mm, right anterior length 6.0 mm, left posterior length 35.0 mm, right posterior length 40.0 mm, maximal length 47.0 mm, maximal width 19.0 mm posterior width 10.0 mm. HLMD 16: hexagonal neural III; anterior width 9.5 mm konvex, posterior width 10.0 mm concave, left anterior length 21.5 mm, right anterior length 21.0 mm, left posterior length 13.0 mm, right posterior length 12.0 mm, anterior thickness 9.0 mm, posterior thicknesss 9.0 mm. HLMD without number, neural indet. HLMD 143: left pleural I, anterior width 39.0 mm, posterior width 66.0 mm, proximate length 45.0 mm, distal length 63.0 mm, marginal thickness 8.0 mm, pleural thickness 13.0 mm. HLMD 9: left peripheral V, median keel length 38.0 mm, length of marginal 5 sulcus 17.0 mm, length of marginal 6 sulcus 16.0 mm. HLMD 75 (Plate 2, figure 5): right peripheral VIII, length 35.0 mm, width 34.0 mm, length of marginal 8/9 sulcus 20.0 mm, length of marginal 9 sulcus 29.0 mm, distal marginal 9 sulcus length 15.0 mm, upper margin visceral 14.0 mm. Peripherals IV: [length of medial keel, length at distal anterior, length at distal posterior, high of marginal 4/5 sulcus, marginal 4 sulcus length, marginal 5 sulcus length] HLMD 134, left: 44.0 mm, 32.0 mm, 30.0 mm, 31.0 mm, 23.0 mm, 18.0 mm, HLMD 68, left: 41.0 mm, 33.0 mm, 27.0 mm, 24.0 mm, 21.0 mm, 18.0 mm, HLMD 76, left: 36.0 mm, 28.0 mm, 26.0 mm, 23.0 mm, 16.0 mm, 15.0 mm, HLMD 63, right: 35.0 mm, 23.0 mm, 22.0 mm, 28.0 mm. Figures 3c and 4a show the distribution pattern of the shell.

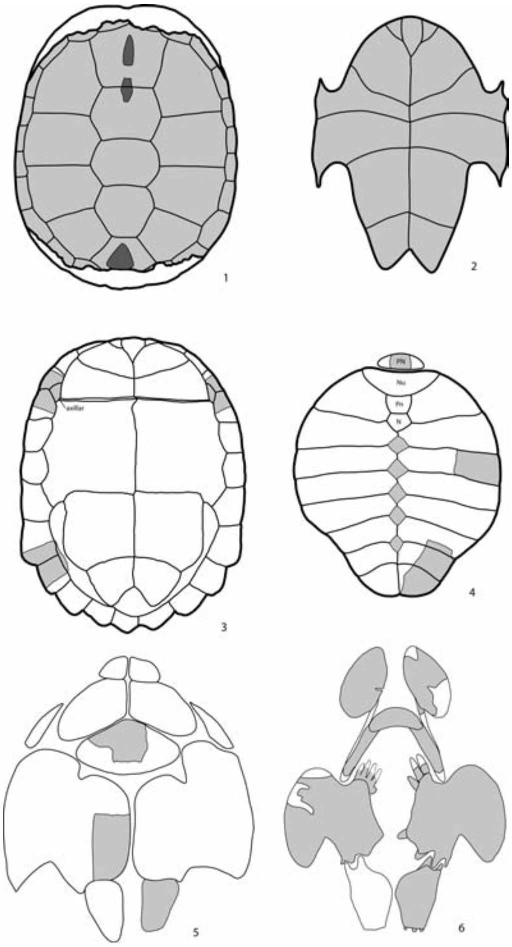

FIGURE 3

Distribution of preserved bones at the shells of different species from Uraha. 1: *Pelomedusa subrufa*, carapace (anterior two neurals of *Pelusios*, posterior the single metaneural of *Pelomedusa*); 2: *Pelomedusa subrufa*, plastron; 3: *Pelusios sinuatus*, plastron (note the position of peripherals IV with axillar scute in relation to the hinge, furthermore the single peripheral VIII); 4: *Cyclanorbis senegalensis*, carapace/discus; 5: *Cyclanorbis senegalensis*, ZSMH 2508/0, plastron of a complete body mummy missing the head; discus length/-breadth = 226 mm/ 176 mm and ZSMH 2509/0, a complete shell with a discus length/-breadth = 31.0 mm/ 25.0 mm; both not located (remark the presence of praenuchal and the distribution of preserved bone plates along the middle line and the margin), 6 = *Cycloderma frenatum*, plastron according Meylan *et al*. (1990). Line drawing Heike Künzel (TLDA).

Cyclanorbis senegalensis (Duméril & Bibron, 1835) - HLMD 53: praenuchal, 43.5 mm x 43 mm. HLMD 59: hexagonal neural, anterior width 19.0 mm convex, posterior width 16.5 mm concave, left anterior length 31.5 mm, right anterior length 32.5 mm, left posterior length 13.5 mm, right posterior length 11.5 mm, anterior thickness 7.5 mm, posterior thickness 10.5 mm. HLMD 214: hexagonal neural; anterior width 16.0 mm convex, posterior width 14.5 mm concave, left anterior length 32.0 mm, right anterior length 34.0 mm, left posterior length 14.5 mm, right posterior length 14.5 mm, anterior thickness 7.0 mm, posterior thicknesss 7.5 mm. HLMD 73: neural, anterior width 18.5 mm, length 40.0 mm. HLMD 55: possibly right pleural II, 44.5 mm x 39.0 mm. HLMD 41a: right pleural V, proximal length 56.0 mm; distal length 63.5 mm, 8.5 mm thick; at the rib 11.5 mm thick. HLMD 82: pleural indet., 69.0 mm x 43.5 mm. HLMD 56: right pleural VIII, 83.0 mm x 59.0 mm, 9.0 mm thick, at the rib 11.5 mm thick. HLMD 43

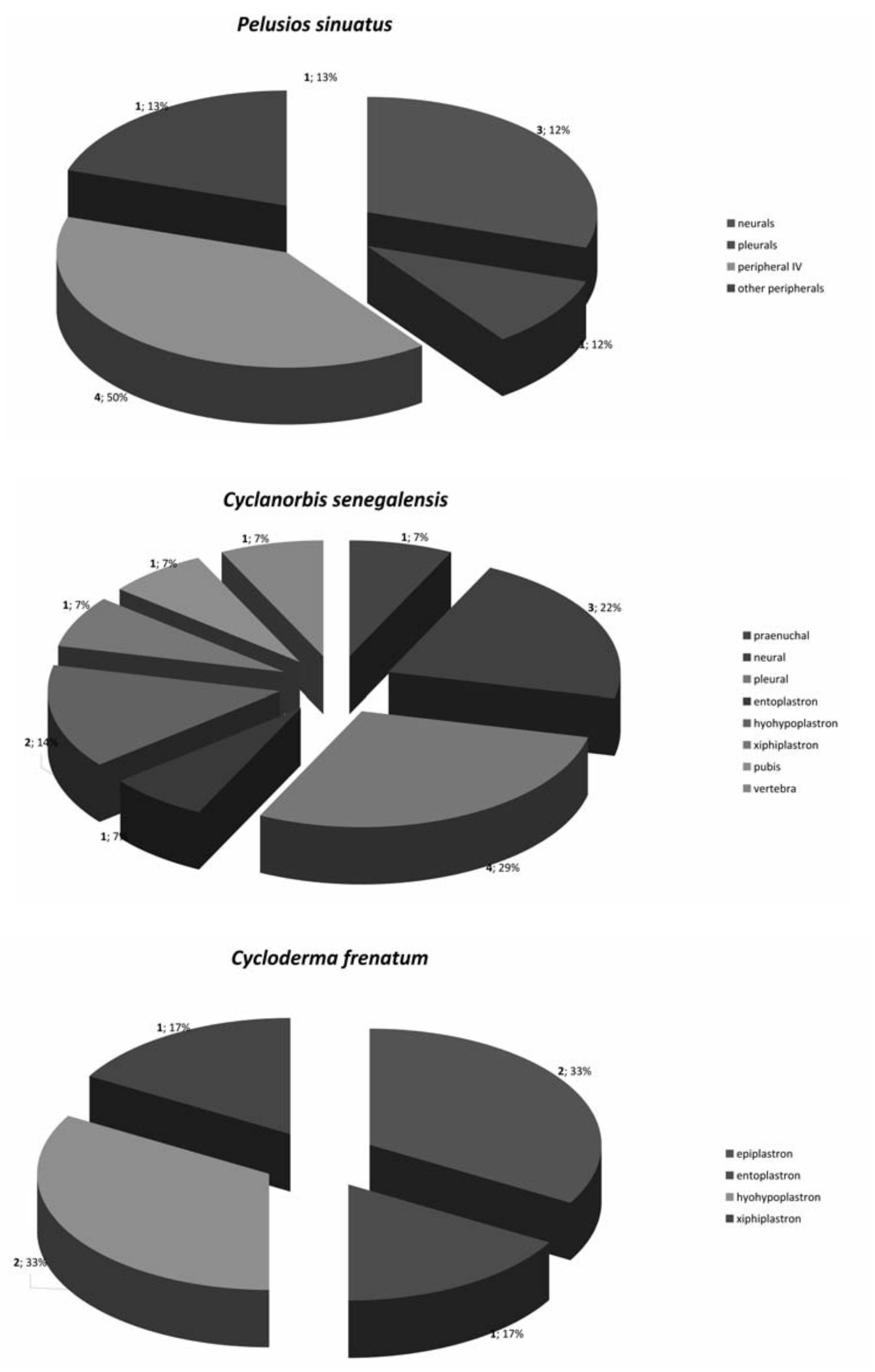

FIGURE 4

Number and percentages of the various shell elements of chelonians from Uraha.

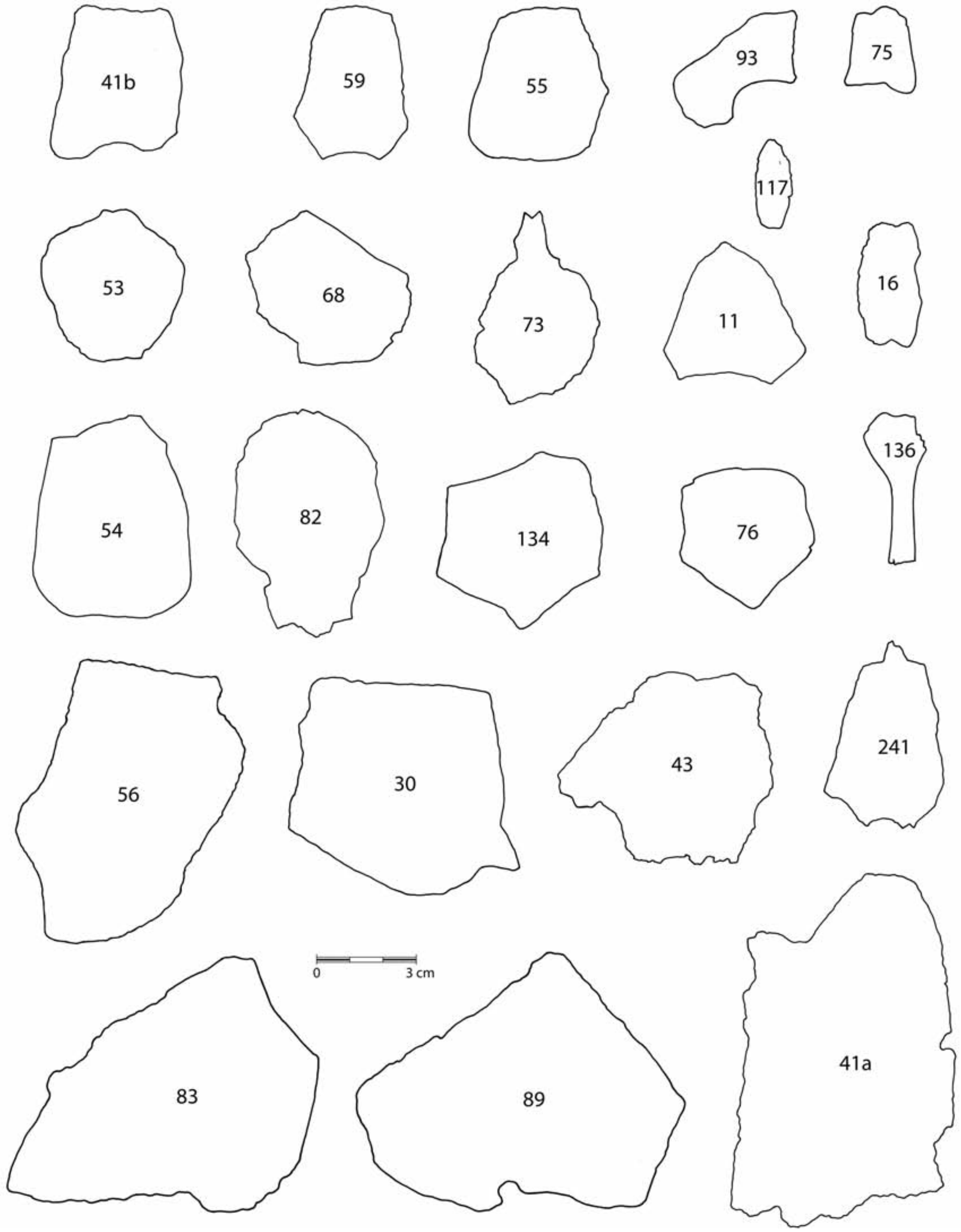

FIGURE 5

Fracture patterns of chelonians at Uraha exhibit great regularity, and suggest a hydrodynamic selection of the materials. (*Pelomedusa subrufa* = 11, *Pelusios sinuatus* = 16, 75, 117, *Cyclanorbis senegalensis* = 41b, 59, 55, 53, 68, 73, 54, 82, 13476, 136, 56, 30, 43, 241, 41a, Clariidae gen. et sp. indet. = 83, 89). Scale bar 3 cm.

(Plate 3, figures 1-2): entoplastron, length 56.0 mm, width 62.0 mm, articulation areas of the lateral processes 17.0 mm long at left and 42.0 mm at right, thickness at anterior margin 11.0 mm. HLMD 54: hyohypoplastron, 58.0 mm x 46.0 mm, 9.0 mm thick, at process 11.0 mm; HLMD 30: lateral wing, distal 12.5 mm thick, 63.0 mm x 61.0 mm (without process). HLMD 41b: xiphiplastron fragment, 58.0 mm x 36.0 mm. HLMD 136: vertebrae indet. HLMD 93: right pubis. Figures 3d-e and 4b show the distribution pattern of the shell. In *Cyclanorbis senegalensis* the presence of a praenuchal plate is the main difference to *Cycloderma frenatum* Peters, 1854 –a nearly complete plastron from Uraha was described by Meylan *et al*. (1990) and includes epiplastrals, entoplastron, hyohypoplastrals and left xiphiplastron. Figures 3f and 4c show the distribution pattern of the shell.

PATTERNS OF TURTLE CONSUMPTION AND BUTCHERY PROCESS

Blasco (2008) described evidences of the acquisition and use of tortoises (*Testudo hermanni*) for food in the form of: (1) cutmarks on limb bones

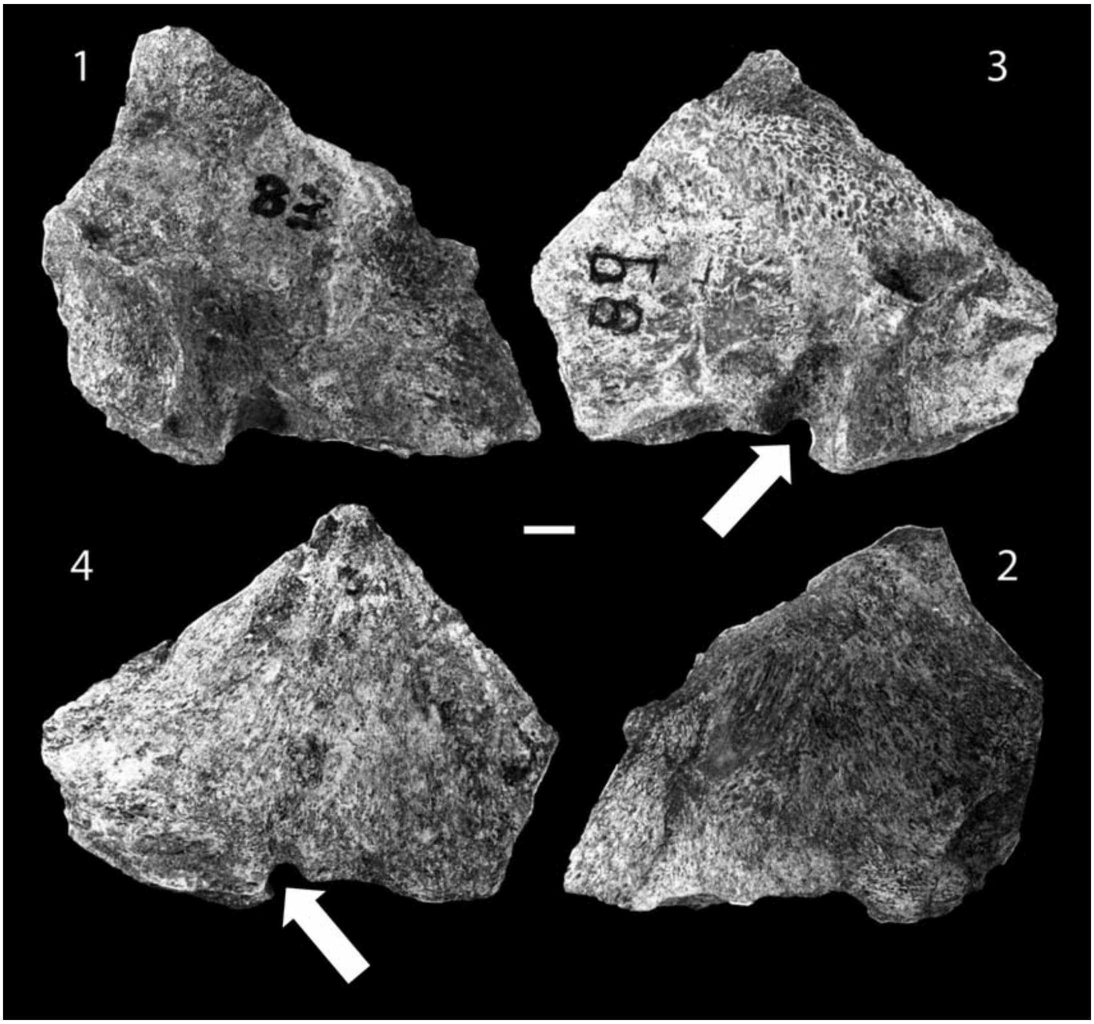

PLATE 3

Two bone tools possibly from catfish claviculae (Clariidae, Siluroidea); figure 1-2: HLMD 83; figure 3-4: HLMD 89. Scale bar = 1 cm.

and ventral surface of the carapace and plastron; (2) presence of burning traces on tortoise skeleton and shell; (3) elements of anthropogenic damages on carapace and plastron: crash pits and notches as well as impact flakes; and (4) human toothmarks on limb bones. This paper tries to examine the possible patterns in the tortoise consumption sequence from Level IV of Bolomor Cave in Spain and improves data on the butchery process and tortoise consumption in the Late Middle Pleistocene in Europe. The condition of our turtle materials described here suggests that they are food remains, too, but only evidences of class 3 are supported. All fossil specimens are fragmentary; even the most complete shell (Plate 1) shows unnaturally widened frontal and caudal openings into the shell. Double colorations in sense of burned turtle bones are hitherto unknown from the Chiwondo Beds. Two bony plates are herewith proposed for discussion as potential tools of *Homo rudolfensis* (HLMD 83: Plate 3, figures 1-2; HLMD 89: Plate 3, figures 3-4). This evidence of the consumption of aquatic animals could support an «aquatic ape hypothesis» (Morgan, 1997; Verhaegen, 2000; Niemitz, 2006, 2010). They remarkably resemble to scrapers or choppers of wood, flint or bone of other hominid localities. Kaufulub & Stern (1987) describes the attributes and sedimentary context of an assemblage of stone artefacts recovered from Plio-Pleistocene deposits in northern Malawi. The assemblage was excavated from a paleo-gully fill located within the Chiwondo Beds. It includes flaked pebbles and pebble fragments, flakes, and flake fragments. These currently provide the earliest evidence for the presence of hominids in Malawi and in the whole southern Central African region. The relevance of early stone tools and bone remains was discussed by Domínguez-Rodrigo (2009). The similar appearance in both bone tools from Uraha does not seem to be accidental or to be caused by natural fracture. The largely fragmented turtle materials also confirm this interpretation (Figure 4). Such handy osseous plates could have been used for dazing or killing the turtle or for cracking and widening the openings of the shells of the defensible *Pelusios*, *Pelomedusa* or large *Cyclanorbis*. These mud turtles could be sensed by persons wading with their feet and then be captured quickly with their hands. Smaller turtles like *Pelomedusa* (to 20.0 cm) could have been crashed and opened as shown in Plate 1 figures 1-2: The arrows point towards crash marks with negative flake scars which are unusual for fossil turtles. The occurrence of regularly broken bones in a *Homo rudolfensis* site is striking and may indicate early «fish and turtle-coshing» by early humans. Contrarily, larger turtles with lockable shell openings like *Pelusios* and Cyclanorbinae (up 50.0 cm) could have been killed by use of suitable tools (Plate 3). These tools possibly originated from a euteleostean fish, Siluriformes: Siluroidei: Siluroidea: Clariidae, with the type genus *Clarias* Scopoli, 1777. They occur from the Pliocene to Recent in South Asia and Africa. The catfish genus *Clarias* is able to move from one pond to another one by crawling across land. These animals might have been easy prey for the early humans during terrestrial crawling. Van Wassenbergh *et al*. (2006) have discovered that the 'eel catfish' *Channallabes apus*, an inhabitant of the muddy swamps of tropical Africa, too, has a remarkable ability to forage and capture prey on land. However fishing in the water without any equipment is futile. Therefore turtle hunting in the water close to shores and banks as well as catching fish on land for acquiring animal proteins might have been present in this «water ape stage» of early humans.

DISCUSSION

The almost entire shell of a female *Pelomedusa subrufa* shows a dorsal surface of the carapace damaged by preparation. The neuralia row is reduced to 5/6A/6A/6A/6A/5, without contact with the nuchal and metaneural plates; this causes the partial median contact of pleurals I and VI as well as complete median contact of pleurals VII and VIII. The general morphology of the shell is helm-like, corresponding to the common name «helmed turtle» of this species, with the length/width ratio 1.12, a length/high ratio 2.13 and a width/high ratio 1.9. This means that the carapace is almost circular, nearly twice as broad as high, and only slightly longer than the double height. The length of the plastron is 175.0 mm. The bridges are 83.0 mm long; this corresponds to a bridge ratio of 2.11. In the posterior opening the pelvis is visible; it is strongly fused with the carapace and plastron, a typical character of the pleurodires. The entoplastron is rhombiform in shape and divided by the humeropectoral suture. The polygonal mesoplastra do not extend beyond the bridge region and do not contact at midline. The plastron is convex; this is regarded as sexual character of the female. For the courses of the preserved sutures of horny plates, see the figures. Due to the sagittal contact of the humeropectoral sutures, the subspecies *Pelomedusa subrufa olivacea* is excluded here. Today *Pelomedusa subrufa nigra* is restricted to southern East Africa. A possible infraspecific position of the Uraha shell cannot be clearly confirmed because shell differences are unknown. The allocation of the metaneural plate HLMD 11 from Uraha is founded in the lengths/width ratio. In the mentioned remain of *Pelomedusa* it is 1.0, whereas in *Pelusios sinuatus* it is only 0.53. Thus there is a distinct character for differentiation between both pelomedusid turtles from Uraha. This area is not preserved in the nearly complete shell from Uraha (Plate 1, figure 1 and 6), few parts of the nuchal, pygal and right epiplastral are lacking. Pits are often closely associated with patches of striae that result from slippage of stone against bone during impact events, or they have emanated from them. Crash notches are semicircular indentations on fracture edges with corresponding negative flake scars. Impact flakes refer to shaft fragments produced by hammer stone impacts which display the same basic technical attributes of percussion as it occurs on stone flakes (Blasco, 2008). This is the type of the crash notches in the shell shown in Plate 1; it shows clearly anthropogenic damages.

The main criterion for the identification of *Pelusios sinuatus* is, as already mentioned in the description, the existence of an axillar scute on each peripheral plate IV. The presence of an axillar scute in *Pelusios sinuatus* is highly significant, whereas it is absent in all other species of *Pelusios*. A discrete axillar plate is absent in hatchlings of *P. sinuatus*, but it appears during the development of the plastral hinge; it is clearly defined in all specimens with a carapace length exceeding 70.0 mm. The other shell remains can clearly be grouped here because of their dimensions; with a maximum length of the carapace of 465.0 mm, it is by far the largest species within the genus. The peripherals IV have a key role in the articulation of the anterior plastron lobe. This would break even in a violent overstretching of the hinge to extend the shell opening. This bone is relatively common in the Uraha samples (Figure 4a).

Now we can see that the use of bones and stones for opening of turtle shells and their catch without manual tools along the river banks, was a key step in the recolonization of the land along the lakes and rivers. Turtle meat is more similar to the human proteins and fats than fish or shellfish, and may thus have been a key factor in brain evolution. Verhaegen´s hypotheses (1987, 1994, 1999) states that the ancestral population of humans, chimps and gorillas some 8 to 6 million years ago lived in mangroves in Arabia-Africa. There they could have frequently waded bipedally, comparable to extant mangrove-living proboscis monkeys. Their food, like that of extant mangrove-living capuchin monkeys, then included hard-shelled fruits and oysters. Hominids, capuchins and sea otters share tool use and thick teeth enamel. Although both *Australopithecus* and *Homo* species seem to have dwelt at the edge between land and water, the differences in palaeo-milieu, dentition, tool use and brain size suggest that both had different lifestyles. Nevertheless, there is a completely natural sequence of small behavioural innovations that could lead from early australopithecines to modern humans (Golding, 1972; Nishida, 1980; Ellis, 1991; Chadwik, 1995; Yamakoshi, 1998). According Verhaegen & Puech (2000) and own results the follow synoptic presentation is valid for the relations between ecological circumstances, lifestyle and evolution of bipedalism in humans:

<table>
<tr><td colspan="2">all hominoids
frugivory and herbivory in tropical forests</td></tr>
<tr><td>chimps and gorillas
using stones to crack hard-shelled fruits and nuts
frugi- and herbivory also in forest clearings
plus «short»-legged bipedal wading in shallow waters
plus more frequent surface-swimming</td><td>early hominids
wading and swimming also in mangrove forests
plus feeding on bivalves growing on lower tree parts
using shells or stones to crush shellfish
using bone tools and stones for opening turtles
using stone tools for various purposes
colonizing the seashores and rivers as omnivores
re-invasion of the land along the rivers</td></tr>
<tr><td colspan="2">modern humans
long- legged bipedalism on land</td></tr>
</table>

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