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Abstract: Although there are several recent works about systematics of genus *Hippopotamus* during Pleistocene, great confusion still remains. In Author's opinion *Hippopotamus incognitus* (referred to *H. amphibius*) and *Hippopotamus tiberinus* (referred to *H. antiquus*) are not valid species.

Keywords: Hippopotamidae, Hippopotamus antiquus, Hippopotamus amphibius, Paleontology, Phylogeny, Africa, Europe.

IBEX J.M.E. 3:53-55

Problems concerning the origin, the systematics and the stratigraphical distribution of the genus *Hippopotamus* have been discussed in the last years by several authors: Coryndon & Coppens, 1973; Coryndon, 1978; Pickford, 1983, 1989; Faure, 1984; Faure & Méon, 1984; Petronio, 1986; Mazza, 1991; Di Stefano *et al*, in progress.

At present the writer is involved in the morphometric study of some cranial remains, preserved at the Museum of Natural History of Paris, which were collected in several African deposits: Ternifine (Algeria), Omo Valley (Ethiopia) and Ain Hanech (Algeria). According to a preliminary study of these remains and taking into account some considerations about the phylogeny of the European hippopotamuses (Petronio, 1986; Di Stefano *et al*, in press), the following conclusions can be proposed in this note, which will be better justified and explained in a next and more descriptive paper.

1. Among all the hypotheses on the origin of the Hippopotamidae, the writer retains valid those of Pickford (1983, 1989), who assumes that Hippopotamidae originated from the Doliochoerinae and, more precisely, from the genus Xenohyus Ginsburg, a Tayassuidae of great size from the Early and Middle Miocene of Europe. The dental pattern of Xenohyus is similar to that of Kenyapotamus Pickford from the Middle and Late Miocene of Africa (Pickford, 1983) (16-8 Ma), which represents the more ancient genus of the family Hippopotamidae. Therefore, it is probable that the hippopotamuses originated from the Tayassuidae and that the genus *Kenyapotamus* gave origin to the genus *Hippopotamus*. The more archaic forms of this latter genus migrated towards Europe about 7-5 Ma ago (*Hippopotamus siculus* Hooijer and *Hippopotamus pantanelli* Joleaud in Italy, *Hippopotamus crusafonti* Aguirre in Spain and France). About 4 Ma ago, in the Kaiso Basin (Uganda) the presence of *Hippopotamus kaisensis*, the probable ancestral form of the lineage of the living *Hippopotamus amphibius* is signaled.

Hippopotamus protamphibius, the direct ancestor of this latter species is very abundant in the Omo Basin (Ethiopia) in the Shungura Formation, particularly in the levels C-H, dated between 2.5 and 1.5 Ma.

2. *H. amphibius* itself appears for the first time in the same basin in the Omo Valley in the levels G of the Shungura Formation, dated about 2 Ma ago, with more specialized forms than *H. protamphibius*.

3. In the Olduvai section (Tanzania) (Hay, 1976), about 1.8 and 0.4 Ma, hippopotamuses more adapted to an aquatical way of life have been collected from level 1 to level 4. Particularly, in the level 1 (about 1.9-1.8 Ma) some specimens referable to *H. amphibius* have been found (short and high skull, rather low orbits, long and only slightly inclined post-orbital region, reduced or absent P2-P3 diastema; high mandible with convex lower border of the horizontal ramus).

From the level 2 (about 1.7-1.6 Ma) a hippopotamus species, already more specialised for an aquatical habitat than the level 1 species, was collected, with more elongated muzzle, higher orbits, more inclined parietals, more elongated mandible with straight or concave lower border of the horizontal ramus. This form was named by Dietrich (1928) as *Hippopotamus* gorgops, a new species separated both from the african *H. amphibius* Linnaeus and from the European species *H. antiquus* Desmarest. Mazza (1991) considers *H. antiquus* from Valdarno morphologically near to *H. gorgops* of the level 2 of Olduvai.

Finally, from level 4 (about 0.7 Ma) (the level 3, according to Geraads, 1982, did not yield fossil remains) several remains of *H. gorgops* were collected with a more advanced degree of specialisation towards the aquatical environment (even more elongated skull, shortened and high neurocranium, high orbits and presence of P2-P3 diastema). According to Mazza (*op. cit.*) these remains show morphological similarities with the new European species *H. tiberinus* Mazza.

4. From the study of some cranial remains from Ternifine (Algeria) (in progress), referable to the Middle Pleistocene, it is possible to stress that the cranial structure typical of the European *Hippopotamus antiquus* is present also in the African gisements; moreover, the strict morphological similarity between the bone structures of *H. antiquus* and *H. gorgops*, leads to assign those two forms to the same species; in this case *Hippopotamus antiquus* Desmarest has the priority.

5. Besides, the writer had the opportunity to observe some skulls preserved in the Natural History Museum of Paris, coming from Ain Anech (Algeria), some of those collected and illustrated by Arambourg (1979), other still undescribed; among this material, some skulls show the cranial morphology typical of *H. anti-quus*, while a hippopotamine neurocranium perfectly fits the diagnosis of *H. tiberinus* given by Mazza (op. cit.).

6. The gisement of Ain Hanech is correlatable (Arambourg, *op. cit.*; Geraads, *op.cit.*) with the level 1 of Olduvai and corresponds approximately to the age of the Olivola faunas or, at least, to the Tasso faunas from Valdarno (Late Villafranchian).

7. What has been previously illustrated implies those more specialized forms of *H. antiquus*

(the European forms of which are referred by Mazza (*op. cit.*) to the species *H. tiberinus* and, on the contrary, are considered by the writer (Petronio, in progress) inside the intraspecific variability of *H. antiquus*) are present also in Africa in the same locality and maybe in the same levels as the archaic form of *H. antiquus*.

8. According to the writer's opinion, in Africa during the Middle Pliocene and Pleistocene, in a temporal succession to be verified, four tetraprotodont hippopotamuses species exist: H. *kaisensis* (about 4 Ma), H. *protamphibius* (about 2.5 Ma), H. *amphibius* (about 2 Ma) and H. *antiquus* (about 1.8 Ma) the derived species better adapted to the aquatical environment.

It was thought (Petronio, 1986) that, apart the insular endemic species as the Cretan Hippopotamus creutzburgi creutzburgi and H. creutzburgi parvus and the siculo-maltese Hippopotamus amphibius pentlandi and Hippopotamus melitensis, the European Pleistocene was characterized by the presence of two different species: Hippopotamus antiquus (Late Villafranchian-Galerian) and Hippopotamus amphibius, nowadays living in Africa, but present in Europe during the time interval Galerian-Late Pleistocene.

Faure (op. cit.) and Mazza (op. cit.) have recently described two new species: Hippopotamus incognitus Faure and Hippopotamus tiberinus Mazza.

The holotype of Hippopotamus incognitus is represented by a skull from Barrington (Cambridge, England) preserved in the Sedwich Museum of the Cambridge University. This species differs from *H*. *antiquus* in having a shorter muzzle and in the morphology of the postorbital and occipital region, but, according to the writer's opinion, these features fit in the intraspecific variability of the living species Hippopotamus amphibius. In fact, the same skull and mandible characters observed in the Barrington skull are also showed both in a complete Middle Pleistocene skull from Tor di Quinto (Rome) and in the living hippopotamus. Thus, as stressed in a previous work (Petronio op. cit.), H. incognitus is not to be considered a valid species, and the hippopotamus from Barrington must be referred to the living species Hippopotamus amphibius.

The holotype of *Hippopotamus tiberinus* is represented by an incomplete skull collected in a middle Galerian deposit from Maglianella (Rome), preserved in the Museum of Natural History of the Certosa di Calci (Pisa). Mazza (op. cit.) choosed as paratype the rather complete skeleton from S. Oreste (Rome) (previously considered as *H. antiquus* by Caloi *et al*, 1980), which he refers to *H. tiberinus*. According to the same Author, other specimens which must be referred to that species are the Middle-Late Pleistocene of Rhine Valley (Germany) ones.

H. tiberinus is considered a more derived form than *H. antiquus*, showing similarities, as already mentioned, with the evolution of the African *H. gorgops* lineage from Olduvai Gorge (Tanzania).

Mazza (*op. cit.*) considers that *H. tiberinus* differs from *H. antiquus* mainly in having very short post-orbital region, elevated orbits, occiput slightly inclined forward and occipital condyles strongly protruding.

The writer, considering the wide variability which characterizes the present hippopotamuses species (Arambourg, *op. cit.*; Petronio, *op. cit.*), does not consider valid the species *H. tiberinus*, because the morphological differences with its ancestral form listed by the Author seem to represent a continuum not easily separable.

Moreover, the holotype is represented only by a portion of skull on which it is impossible to observe several other morphological characters which are recognized as diagnostic by Caloi et al. (op. cit.) and Petronio (op. cit.) for the definition of the species H. antiquus. Mazza himself (op. cit.), describing the paratype skull of S. Oreste (Rome), lists other peculiar characters of H. tiberinus that can not be recognized in the holotype skull, and ignores that the S. Oreste skull is compressed and many parts of it have been reconstructed. Besides, no importance is given to the mandible characters, which instead are considered by Caloi et al. (op. cit.) as diagnostic for the specific attribution to H. antiquus. Nevertheless, whether if H. tiberinus is maintained as a valid species or, more likely, the characters of that species may be fitted those of H. antiquus, it is to be noted that hippopotamuses forms with specialized characters from other localities of different ages extend the vertical distribution of the species H. antiquus up to the Late Pleistocene.

In conclusion, it is possible to assert that in the European Pleistocene only two hippopotamuses species are present: *H. amphibius*, from the Middle Pleistocene (not better specified) to the Late Pleistocene (isotopic Stage 4 of the oceanic paleotemperature curve) and *H. anti-*

quus from the Late Villafranchian to the Late Pleistocene (Rhino terraces, Mazza, *op. cit.*).

REFERENCES

- ARAMBOURG C., (1979) Vertébrés villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). Fondation Singer Polignac, Paris, 141 pp.
- CALOI L., PALOMBO M.R. & PETRONIO C., (1980) -Resti cranici di Hippopotamus antiquus (= H. major) e Hippopomatus amphibius conservati nel Museo di Paleontologia dell'Università di Roma. Geol. Romana, Roma 19: 91-119.
- CORYNDON S.C., (1978) Hippopotamidae. In: Evolution of African Mammals. C.T. Maglio & H.B.S. Cooke (eds), Harvard University Press, Cambridge 23: 483-495.
- CORYNDON S.C. & COPPENS Y., (1973) Preliminary report on Hippopotamidae (Mammalia, Artiodactyla) from the pliocene-pleistocene of the lower Omo basin, Ethiopia. In: Fossil Vertebrates of Africa. L.S.B. Leakey, R.J.G. Savage & S.C. Coryndon (eds). Academic Press, London, 3: 139-157.
- DIETRICH W.O., (1928) Pleistozän deutsch-ostafrikanische Hippopotamusreste. Wiss. Ergebn. Oldoway-Exped., 1913: 40.
- DI STEFANO G., PETRONIO C. & SARDELLA R., in press -Il significato biocronologico e paleoecologico di alcuni taxa di mammiferi del plio-pleistocene dell'italia centrale. In: *Biostratigrafia dell'Italia Centrale*. A. Farinacci (ed.), Studi Camerti, Camerino.
- FAURE M., (1984) Les Hippopotames quaternaires non-insulaires d'Europe occidentale. *Nouv. Arch. Hist. Nat. Lyon*, 3: 13-79.
- FAURE M. & MÉON H., (1984) L'Hippopotamus crusafonti de la Mosson (près Montpellier). Première reconnaissance d'un Hippopotame néogène en France. C.R. Acad. Sci. Paris, 298, II (3): 93-98.
- GERAADS D., (1982) Paléobiogéographie de l'Afrique du Nord depuis le Miocène terminal. *Geobios*, Lyon, 6: 473-481.
- HAY Ř. L., (1976) Geology of the Olduvai Gorge. University of California Press, Berkeley.
- MAZZA P., (1991) Interrelation between Pleistocene hippopotami of Europe and Africa. Boll. Soc. Paleont. It., Modena, 30 (2): 153-186.
- PETRONIO C., (1986) Nuovi resti di Ippopotami del Pleistocene medio inferiore dei dintorni di Roma e problemi di tassonomia e filogenesi del gruppo. *Geol. Romana*, Roma, 25: 63-73.
- PICKFORD M., (1983) On the origins of Hippopotamidae togheter with descriptions of two new species, a new genus and a new subfamily from the miocene of Kenya. *Geobios*, Lyon, 16: 193-217.
- PICKFORD M., (1989) Update on hippo origins. C.R. Acad. Sci. Paris, 309 II: 163-168.