A stylohyoideum of *Palaeoloxodon antiquus* from Gesher Benot Ya'aqov, Israel: morphology and functional inferences

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SUMMARY: Among the mammal remains discovered at Gesher Benot Ya'aqov (south of the Hula Valley, Dead Sea Rift, Israel) were cranium, tusk fragments, and limb bones that were assigned to an extinct straight-tusked elephant, *Palaeoloxodon antiquus*. One stylohyoideum was also collected. Based on inferences from data on living elephants, it is hypothesized that *P. antiquus* had a tongue about 80 cm long used to grasp leaves and grasses. Further, *P. antiquus* lived in small herds, about 5-15 individuals, and that herd members could have communicated with infrasonic calls with other herds, a few kilometers away. All in all, the hyoid apparatus has been a pivotal structure for adaptation in the course of proboscidean evolution.

Gesher Benot Ya'aqov (GBY), located south of the Hula Valley, Dead Sea Rift, a segment of the Great African Rift System, is known for its early to middle Pleistocene (780,000 years ago) sedimentary sequence comprised of several Acheulian archaeological horizons, rich in lithic assemblages as well as in fauna and flora (Goren-Inbar *et al.* 2000). Material referable to extinct straight-tusked elephant, *Palaeoloxodon antiquus* (family Elephantidae, order Proboscidea) includes a cranium, tusk fragments, limb bones, and one left stylohyoideum (Goren-Inbar *et al.* 1994). Some authors prefer to use *Elephas* (*Palaeoloxodon*) *antiquus* instead of *Palaeoloxodon antiquus*.

The stylohyoid (Hebrew University catalogue no. GBY #215) was found in sediments probably originating from Layer II-6 (Trench II, Area B), the same layer where the cranium material of *P. antiquus* was found. One of a set of little studied bones, the stylohyoid is found deep in the throat (the hyoid apparatus comprised of two stylohyoidea, two thyrohyoidea, and one basihyoideum) of elephants, living and extinct (Shoshani 1986). They are rarely collected from extant or extinct proboscideans. Unfamiliarity with these bones has resulted in describing a stylohyoid as an antler of an extinct deer (Green 1956). The stylohyoid is a Y-shaped bone, one "arm" of the Y is the superior ramus, the other "arm" is posterior ramus, and the third "arm" is the inferior ramus (terminology after Inuzuka *et al.* 1975). In this specimen, the inferior ramus is broken, otherwise it is in good condition; the combined superior-posterior length is 135 mm. This specimen does not have the typical "angulus" (a depression on the superior-posterior rami as observed in side view) that has been observed on several stylohyoid bones of *P. naumanni* (Inuzuka *et al.* 1975). This difference could be a species difference between *P. naumanni* and *P. antiquus*. GBY #215 has a tubercle on the superior ramus that may be homologous to tubercles observed on some *P. naumanni* stylohyoidea. It is noted that only one stylohyoid of *P. antiquus* was exam-

ined compared to several stylohyoids of *P. naumanni*.

Based on the work of Inuzuka (1977a, b) and our morphological observations (in the context of archeological settings of GBY, as well as other observations of skeletons of *P. naumanni*), it is suggested that the genus *Palaeoloxodon* be considered a *bona fide* taxon and not a subgenus of *Elephas*. Detailed long-term study (about 25 years) of processes and grooves for muscle attachment and twisting of bones on the hyoid apparatus (mostly stylohyoidea) enables the authors to infer functionality for these bones. Elephantid taxa, for example, possess a posterior ramus which is absent in some early proboscideans, e.g., *Mammut americanum* (Tassy & Shoshani 1988; Saegusa & Shoshani 1992). This ramus serves for attachment of the digastricus muscle that helps to open the jaw (Eales 1926; Garrod 1875; Gasc 1967). Identification of GBY 215 was made by comparing it to 194 stylohyoid hyoid elements, representing 151 individuals of living and extinct proboscideans, namely: Mammoths (e.g., *Mammuthus primigenius*), Asian elephants (*Elephas maximus*), extinct elephantids (e.g., *E. recki, Palaeoloxodon naumanni*), African elephants (*Loxodonta cyclotis* and *L. africana*), stegodons (e.g., *Stegodon aurorae*), gomphotheres (e.g., *Gomphotherium productum, Amebelodon floridanus*), mammutids (*Mammut americanum*), and a deinothere (*Deinotherium giganteum*). Based on gular musculature of living elephants and morphology of hyoid apparatus (e.g., Eales 1926), it is hypothesized that the functional anatomy of hyoid of *P. antiquus* was similar to that of extant elephants. It is suggested that *P. antiquus* had a tongue about 80 cm long that could be projected a short distance from the mouth to grasp leaves and grasses. The tongue along with a flexible trunk, enabled straight-tusked elephants to graze or to browse on Pleistocene foliage about 8 meters above ground [trunk flexibility is deduced from size and position of external naris and from size and numbers of infraorbital canals (Shoshani 1986); height above ground is estimated from data on living elephants when standing on hind legs (Shoshani *et al.* 1987). It is suggested that *P. antiquus* lived in small herds, about 5-15 individuals, and that herd members could have communicated with infrasonic calls with other herds, perhaps a few kilometers away (communication hypothesis is based on hyoid and cochlear anatomy; Meng *et al.* 1997). In addition, it is proposed that the hyoid apparatus supported a pharyngeal pouch used as a resonating chamber (similar to the condition in howler monkey; Vaughan *et al.* 2000). At other periods, this pouch was used to store water for drinking or dousing in time of stress (Shoshani 1998). It appears that the hyoid apparatus has been a pivotal structure for adaptation to newly available ecological niches of in their long geological history.

References

Eales, N.B. 1926. The anatomy of the head of a foetal African elephant, *Elephas africanus (Loxodonta africana)*. Part I. *Transactions of the Royal Society of Edinburgh* 54(3): 491-551 + 12 plates.

Garrod, A.H. 1875. On the hyoid bone of the elephant. *Proceedings of the Zoological Society of London* 1875: 365-367.

Gasc, J.-P. 1967. Squelette hyobranchial. In P.-P. Grasse (ed.), *Traité de Zoologie* 16(1): 550-583, 1103-1106. Paris: Masson et Cie Editeurs.

Goren-Inbar, N., Lister, A., Werker, E. & Chech, M.A. 1994. A butchered elephant skull and associated artifacts from the Acheulian site of Gesher Benot Ya'aqov, Israel. *Paleorient* 20/1: 99-112.

Goren-Inbar, N., Feibel, C.S., Verosub, K.L., Melamed, Y., Kislev, M.E., Tchernov, E., & Saragusti, I. 2000. Pleistocene Milestones on the Out-of-Africa Corridor at Gesher Benot Ya,aqov, Israel. *Science* 289: 944-974.

Green, M. 1956. The lower Pliocene Ogallala-Wolf Creek vertebrate fauna, South Dakota. *Journal of Paleontology* 30(1): 146-169.

Inuzuka, N. 1977a. On a fossil skull of Palaeoloxodon naumanni from saruyama, Shimosa-machi, Chiba Prefecture, central Japan. *Journal of the Geological Society*

Japan 83: 523-536.

Inuzuka, N. 1977b. On the origin of *Palaeoloxodon naumanni* - A comparative osteology of the cranium. *Journal of the Geological Society Japan* 83: 639-655.

Inuzuka, N., Hasegawa, Y., Nogariya, H., & Kamei, T. 1975. On the stylohyoid bone of Naumann's elephant (*Elephas naumanni* Makiyama) from Lake Nojiri. Memoirs Faculty of Science, Kyoto University, *Series of Geology and Mineralogy* 41(1): 49-65.

Meng, J., Shoshani, J. & Ketten, D. 1997. Evolutionary evidence for infrasonic sound and hearing in proboscideans. *Journal of Vertebrate Paleontology,* 17: 64A.

Saegusa, H. & Shoshani, J. 1992. A stylohyoideum of *Stegodon* (Proboscidea, Stegodontidae) from the Pleistocene of Java and its phylogenetic significance. *Journal of Vertebrate Paleontology* 12,: 50A.

Shoshani, J. 1986. *On the phylogenetic relationships among Paenungulata and within Elephantidae as demonstrated by molecular and osteological evidence*. Ph.D. Dissertation, Wayne State University, Detroit (Michigan). Ann Arbor, Michigan University Microfilms, 649 pp.

Shoshani, J. 1998. Understanding proboscidean evolution: a formidable task. *Trends in Ecology & Evolution* 13(12): 480-487.

Shoshani, J., Hillman, J.C. & Walcek, J.M. 1987. "Ahmed", the logo of the Elephant Interest Group: encounters in Marsabit and notes on his model and skeleton. *Elephant* 2(3): 7-32.

Tassy, P. & Shoshani, J. 1988. The Tethytheria: elephants and their relatives. In M. Benton (ed.), *The phylogeny and classification of the tetrapods. 2: Mammals* (The Systematics Association, Special 35B): 283-315. Oxford: Clarendon Press.

Vaughan, T.A., Ryan, J.M. & Czaplewski, N.J. 2000. *Mammalogy* (4th edition, Fort Worth (Texas): Saunders College Publishing, Harcourt Brace Jovanovich Publishers.