

# Comparisons of stegodon and elephantid abundances in the Late Pleistocene of southern China

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**SUMMARY:** In the Pleistocene fauna of southern China, *Elephas* coexists with *Stegodon* whose molar structure is more primitive and which presumably fed on more browses than the former. I surveyed the Chinese literature of ca. 180 localities in southern China where *Stegodon* and *Elephas* occur separately or co-occur, to learn if stegodon outnumber elephants in the late Pleistocene fauna of China. I found that stegodon localities significantly outnumber those with elephants. The above results for south China seem to support the Generalist vs. Specialist hypothesis proposed by Shoshani (1992). However, because of the complexities in feeding mechanisms in *Stegodon* and *Elephas*, the definitions of the terms “grazer” and “browser” do not necessarily help to distinguish between generalist and specialist taxa. Detailed reconstruction of feeding habits of stegodons is necessary for the evaluation of the present results.

## 1. INTRODUCTION

*Elephas maximus* is the only species of the Proboscidea living in present day East Asia, but *Elephas* coexisted with extinct genus *Stegodon* throughout Pleistocene in southern China (Takahashi & Namatsu 2000). Youngest remains of *Stegodon* were found from a Neolithic site (Xiaohe Cave) in Yunnan Province, which is dated at 4100 bp (Ma & Tang 1992). Thus, extinction of the stegodons is a very recent event which occurred during Holocene.

Sympatry of two proboscidean species has been known also from the late Pleistocene of North America, where primitive taxon American mastodons coexisted with derived taxon mammoths. Shoshani (1989) examined the number of proboscidean fossils found from Michigan and found that American mastodons outnumber mammoths in forested area (diverse habitat), and vice versa in open habitat. He argued that relative abundances of proboscideans observed in the late Pleistocene of North America fits his generalist vs. specialist hypothesis (Shoshani 1992). According to this hypothesis, primitive, generalist taxon outnum-

ber derived, specialist taxon in diverse habitat, if the animals compared share same body size and close phylogenetic relationship.

Census study of the late Pleistocene proboscideans is worth to be conducted not only in North America but also in other area of the world, for instance East Asia, where stegodons and elephants coexisted during Pleistocene. Specialist vs. generalist hypothesis predicts that stegodons must outnumber elephants during late Pleistocene in China, because stegodons are primitive compared to the elephants in molar structure and they were living in forested, diverse habitat. Thus, prime motivation of this study is to test this prediction. However, as noted later, the results obtained through such census studies must have implication not only on generalist vs. specialist hypothesis but also on the of the late Pleistocene extinction of megafauna in East Asia.

## 2. LITERATURE SURVEY

### 2.1 Tong-Liang case

The objective of this study is learn if stegodons had outnumbered elephants during late

Pleistocene in China, where forested environment has been predominated. I have examined published data of southern Chinese cave fauna in attempt to see the relative abundance of stegodons and elephants.

The best snapshot of population densities of elephants and stegodons during the late Pleistocene is available from a Paleolithic site called Tong-Liang in Sichuan, China, where large number of proboscidean fossils are obtained from a fluvial bed dated at  $21550 \pm 310$  bp (Zhang *et al.* 1982). Pollens and plants macrofossils obtained from the bed suggest the vegetation was similar to present-day subtropical damp forest of Sichuan. In this habitat, *Stegodon* outnumbered *Elephas*. Dominance of *Stegodon* over *Elephas* observed in Tong-Liang is impressive but a piece of data from only one locality is not sufficient to show the general tendency of stegodons and elephants densities in the late Pleistocene of China.

## 2.2 Other localities in southern China

I examined about 130 papers on localities where *Stegodon* and *Elephas* occur separately or co-occur, to learn if the tendency seen in Tong-liang is generally the same throughout the late Pleistocene of China. Ideally, census study must be based on the number of specimens obtained from study area, but, except for Tong-liang, most of Chinese papers do not document the number of specimens found in localities. Instead of the number of specimens, that of assemblages is counted here. If assemblages from a locality are clearly distinguished bed by bed in literatures, they are counted separately.

Taxonomic status of Chinese Pleistocene proboscideans must be clarified, prior to the examination of the proboscidean localities in South China. Ideally, taxa compared must be identified at specific level. However, most of the reports on excavation in China are without the description of the specimens and the specific status of fossil taxa is not always clear. Thus, we employed only the generic name in our analysis.

In order to select reliable data for the analy-

sis, the description of the stratigraphy of the locality in the literature is examined. More than half of the reports are found not detailed in the description of the stratigraphy. Such published data are omitted together with obviously contaminated assemblage from the data set.

Late middle and late Pleistocene assemblages are selected using radiometric dating data and an index fossil. In South China,  $^{14}\text{C}$  and uranium series methods have been done only on the site from where important hominid fossils or Paleolithic tools have been excavated. Thus, limited number of the site will be remained in the data set if only the radiometric dating is used for the selection of the localities. Other means to determine the geological age of the assemblages is necessary. *Crocota crocota ultima* (Matsumoto 1915) is employed here as an index fossil, to include more assemblages in our analysis, in addition to the radiometric dates. Recent reexamination of several U-series dating of oldest localities of *Crocota crocota ultima* in South China suggests that those localities are geologically much older (ca. 240 ka) than previously thought (Shen & Jin 1991). The last record of this species was reported from in Shengxian Cave at Lishui, Jiangsu ( $11,200 \pm 1000$  bp.) (Ma & Tang 1992). Thus, the possible geological ages of assemblages analyzed here are scattered between ca. 240 ka and ca. 10 ka.

The assemblages formed under closed habitat are selected because concern here is whether forested environment is more favored by *Elephas* or *Stegodon*. In order to exclude the fossil assemblage formed under temperate or steppe vegetation from the data set, the assemblages containing genus *Equus*, which is regarded here as an indicator of open habitat, were omitted from the data set. Consequently, the list contains only the assemblages from woodland and forest environment. Another list that includes assemblage presumably came from densely forested area is also made. *Ailuropoda*, *Pongo* and *Hylobates* are considered here as indicators of densely forested area since they are found today in such area (Corbet & Hill 1992). Using those three taxa as indicators of denser forest, second list was made.

### 3. RESULTS

Two lists obtained through above procedure were subjected to a statistical test. McNemar's test was carried out here because same assemblages are counted two times in order to obtain the ratio between number of assemblages containing *Elephas* and those containing *Stegodon*. The null hypothesis is that the frequencies of the assemblages containing *Stegodon* and those containing *Elephas* are equal in both lists. I employed binomial distribution for the calculation of the one-tailed probability of the data because when samples are small, an "exact" binomial test is recommended (Sokal & Rohlf 1995). Number of assemblages containing *Stegodon* is significantly greater than that containing *Elephas* in both lists. This result may suggest that subtropical and tropical forests in south China during the period between ca. 230 ka to ca. 10 ka was more favored by *Stegodon* than by *Elephas*.

### 4. DISCUSSION

#### 4.1 Implication of the Generalist vs. Specialist hypothesis

Until detailed census study of Pleistocene proboscideans from China has been done together with additional radiometric studies, it may be premature to draw conclusion on the relative densities of stegodons and elephants. Nevertheless, the above result for south China in general, and for the Paleolithic site Tong-Liang in Sichuan in particular seems to suggest that stegodons outnumbered elephants during late Pleistocene and the former taxon did not decline until the very end of Pleistocene at least in forested areas of southern China. This result has implications for both generalist vs. specialist hypothesis and extinction pattern of stegodons in East Asia.

According to Shoshani (1989, 1992), data from *Mammuthus* vs. *Mammut* in North America supports generalist vs. specialist hypothesis. Primitive taxa *Mammut* outnumbered *Mammuthus* in diverse habitat.

Likewise, in southern Chinese case, primitive taxa stegodons outnumbered derived taxa *Elephas* in diverse forest habitat. Thus both cases in North America and China seem to support the generalist vs. specialist hypothesis.

However, there remain some problems concerning the distinction between generalist and specialist in extinct taxa. Shoshani (1989, 1992) suggested that *Mammuthus* is a specialized grazer whereas *Mammut* is a primitive browser. However, there still remain uncertainties concerning feeding habit of American mastodons. American mastodons have traditionally been considered to be typical browsers, because of their primitive molar structure. Following this traditional view, Haynes (1991) considered American mastodons selective feeder who travel between clumps of dicotyledonous plants. However, Gobetz & Bozarth (2001) suggested that mammutid fed on grass as well as browse based on the analysis of opal phytoliths in tooth calculus of *Mammut* molars. Intestinal contents and coprolite from mastodont remains also suggest a mixture of browsing and grazing habits (Lepper *et al.* 1991, Harington *et al.* 1993). Thus, those recently obtained data suggest that American mastodons were mixed feeder.

The above arguments suggest exact diet of the American mastodons is still hard to be determined and the primitive nature of molar structure alone can not specify specialist or generalist nature of the extinct animal. Obviously, we still need some means other than molar structure to estimate food selection even in the case of well studied American mastodon, much more in the case of stegodons. Structural difference between stegodons and elephants in molar is less than that between mastodons and mammoths, and what is even worse, there has been nearly no report on plant material associated with stegodons remains from southern Chinese cave fauna. Until we obtain reliable picture of feeding habits of stegodons, it seems to be quite premature to consider that southern Chinese case fits generalist vs. specialist hypothesis.

#### 4.2 Implication on extinction pattern of stegodons

Present result cast doubt on my previous idea that most of stegodons already declined before the late Pleistocene (Saegusa 1996). My previous idea on the extinction pattern of stegodons is provably very biased because when I prepared a chronological range chart of stegodons, I employed only the fossil records accompanied with radiometric data and the magnetostratigraphy of continuous geological sections. Late survival of stegodons into the very end of the late Pleistocene may not be specific to southern China but also in other areas in Asia. Recent radiometric study done on Ngangdong, central Java (Swisher *et al.* 1996) suggests that stegodons still survived until the very end of Pleistocene in Java. Therefore, chronological range of stegodons and its abundance during Pleistocene must be revised not only in China but also India or Indonesia, based on published data, which are not used in my previous revision of stegodons.

#### 5. CONCLUSION

Based on literature survey on ca. 180 localities in southern China, a data set of stegodons and elephants is constructed, to learn if stegodon outnumber elephants in the late Pleistocene fauna of China. McNemar's test on this data set suggests that stegodon outnumber elephants in the late Pleistocene fauna of China. This results seem to support the Generalist vs. Specialist hypothesis proposed by Shoshani (1992). Note, however, that because of the complexities in feeding mechanisms in *Stegodon* and *Elephas*, the definitions of the terms "grazer" and "browser" do not necessary help to distinguish between generalist and specialist taxa. Detailed reconstruction of feeding habits of stegodons is necessary for the evaluation of the present results. Present result also suggests late survival of stegodons into the very end of the late Pleistocene may not be specific, to southern China but also in other areas in Asia.

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