Memoir of the Fukui Prefectural Dinosaur Museum 7: 105–108 (2008)

COMPUTED TOMOGRAPHY OF A HYPSODONT TROGOSINE, *HIGOTHERIUM HYPSODON* (MAMMALIA, TILLODONTIA): A PHYLOGENETIC IMPLICATION

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ABSTRACT

The tooth morphology in the holotype (NSM-PV 20118) of *Higotherium hypsodon* Miyata and Tomida, 1998, a highly hypsodont trogosine tillodont from the early Middle Eocene in Japan, was examined by using images reconstructed from X-ray computed tomography data. The CT images reveal the two roots at m2 and the incomplete root at m3 inside the mandible of the specimen, suggesting a great morphological difference from the ever-growing and rootless molars in *Chungchienia* from the Middle Eocene of China. This result does not support a previously proposed monophyletic clade consisting of *Higotherium* and *Chungchienia*.

Key words: Tillodontia, *Higotherium*, *Chungchienia*, hypsodonty, Middle Eocene

宮田和周・冨田幸光（2008） 高歯冠のトロゴサス亜科裂歯類 *Higotherium hypsodon*（哺乳綱，裂歯目）のＸ線 CT 画像：その系統的意義について． 福井県立恐竜博物館紀要 7：105–108.

Higotherium hypsodon Miyata and Tomida, 1998 は日本の中期始新世初期から知られる高歯冠を持つトロゴサス亜科の裂歯類であり，Ｘ線 CT 装置を使用してその模式標本（NSM-PV 20118）に保存された大臼歯の形態を調査した．Ｘ線 CT 画像は第二大臼歯においては２本の歯根を，第三大臼歯においては歯根が未形成であることを示し，中国の中期始新世から知られる *Chungchienia* の成長を続ける無歯根歯とは異なる．Ｘ線 CT 画像が明らかにした *Higotherium* の大臼歯の形態は，以前提唱された *Higotherium* と *Chungchienia* からなる単系統群を支持しない．

INTRODUCTION

The subfamily Trogosinae Gazin, 1953, is a derived group of the order Tillodontia and includes five genera known from the late Early to early Middle Eocene in North America and the Middle Eocene in East Asia: *Trogosus* Leidy, 1871, from the United States, Canada, and Japan; *Tillodon* Gazin, 1953, from the United States; *Kuanchuanius* Chow, 1963a, from China; *Higotherium* Miyata and Tomida, 1998, from Japan; and *Chungchienia* Chow, 1963b, from China (Russell, 1935; Chow et al., 1996; Miyata, 2007a). Trogosine tillodonts are characterized by having large rootless second incisors (I2s and i2s), which possibly reflect a rhizophagous diet (Lucas and Schoch, 1998; Miyata, 2007b). The first three genera have rooted cheek teeth with high (hypsodont) or low (brachydont) crowns. A recent phylogenetic analysis based on dental characters shows close affinities between the three genera, but the phylogenetic positions of other two genera (*Higotherium* and *Chungchienia*) are still unclear (Miyata, 2007b). Further materials clarifying the interrelationships among trogosines are required.

Higotherium and *Chungchienia* are known only from fragmentary jaws with lower cheek teeth, but the great degree of hypsodonty in the two genera is unusual and clearly distinguishes them from other tillodont genera. All lower cheek teeth in *Chungchienia* are rootless, ever-growing with unilateral enamel coverings (Chow, 1963b; Chow et al., 1996). Miyata and Tomida (1998) proposed a sister-group relationship between *Higotherium* and *Chungchienia* in their phylogenetic tree, based on the possible synapomorphic character, “much more hypsodont molars with expanded enamel extending into dentary.” This suggests an unusual degree of hypsodonty in the two genera compared with other trogosines but does not mean that *Higotherium* has rootless and ever-growing molars as in *Chungchienia*. Actually, Miyata and Tomida (1998) provided an x-ray image of the mandible of *Higotherium*, but it does not clarify the molar structures inside the mandible. This paper aims to examine the molar structure of *Higotherium* using X-ray computed tomography and to discuss the phylogenetic position of *Higotherium*.

Received March 5, 2008. Accepted October 6, 2008.
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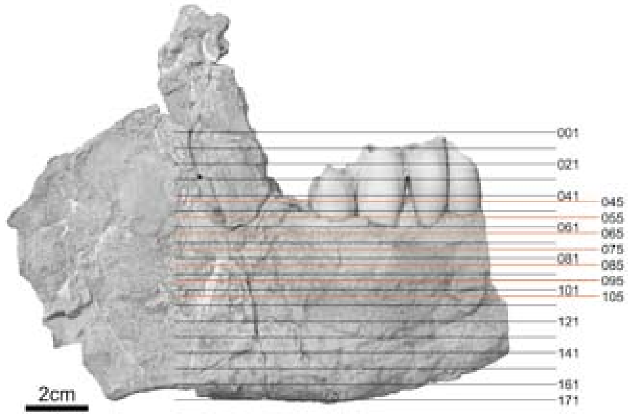

FIGURE 1. Holotype of *Higotherium hypsodon*, NSM-PV 20118, a right mandibular fragment with incomplete m2 and nearly unworn m3 in labial view, with index lines showing the positions of the reconstructed CT images in horizontal (coronal) plane. The images on the red lines (045, 055, 065, 075, 085, 095, and 105) are shown in Figure 2.

METHOD

Because *Higotherium* is a monotypic genus consisting of *H. hypsodon*, which is known only from the holotype (Fig. 1, NSM-PV 20118), a nondestructive method using X-ray computed tomography (CT) was carried out to examine the molar structures inside the mandible. The CT scanning was performed at the Department of Diagnostic Radiology, Fukuiken Saiseikai Hospital (7-1, Funabashi, Wadanaka-cho, 918-8503), Fukui Prefecture, Japan, using a medical CT, Aquilion-16 (Toshiba, Tokyo, Japan), under the control of the department.

The original data set comprises 530 slices of the whole specimen, which were taken in the original vertical plane orthogonal to the anteroposterior axis of the mandible (i.e., parallel to the transverse plane). The field of view (FOV) was 161.25 mm. Each slice has a thickness of 0.5 mm, and the inter-slice spacing is 0.3 mm. Each original image was saved as a 512 by 512 pixel bitmap image with a 24-bit gray-scale depth. To provide more accessible images, multi-planar reconstruction (MPR) images were processed from the original CT data, using a workstation (AquariusNet workstation; Terarecon, San Mateo, CA) at Fukuiken Saiseikai Hospital. Two reconstructed serial images were obtained: one in the horizontal plane (i.e., the coronal planes; 171 images, Fig. 1) orthogonal to the mandibular ramus, the other in the vertical plane (57 images) parallel to the mandibular ramus (see also Appendices 1 and 2). Figures 1 and 2 respectively show the approximate positions of the reconstructed images in the horizontal plane and selected images with our interpretations. The outline of molars inside the mandible is shown in Figure 3. The Appendices provide two animations showing the serial images in the horizontal and vertical planes through the web site of Fukui Prefectural Dinosaur Museum (http://www.dinosaur.pref.fukui.jp/archive/memoir/memoir007.html).

DESCRIPTION AND RESULT

The CT images indicate the presence of dividing m2 root (= two roots at m2) and incompletely formed m3 root in the specimen (Figs. 2, 3). The total dorsoventral height of the m2 is estimated to be approximately 51 mm, and the m2 root becomes clearly divided around 29 mm from the top of crown (around position 061 in Figure 1). The m2 posterior root is longer and stouter (estimated as about 22 mm long from the bifurcation) than the anterior one (about 17.5 mm long). In cross section, each root of m2 is oval-shaped with long labiolingual axis and becomes rather circular near the bottom (Fig. 2). The serial coronal images from the positions 031 to 060 in Figure 1 show the concave lingual surface at the unexposed part of m2 (A' and B' in Fig. 2); on the m2 lingual surface, there is a groove running from the dentine under the metaconid to the bifurcation of the root. The CT images do not provide any clues of the enamel distribution on the unexposed part of m2. However, given the position of the exposed labial enamel on the talonid (Fig. 3), the labial enamel in the m2 likely extends more downwardly below the position of root bifurcation than in *Trogosus* molars (cf., fig. 18 in Gazin, 1953; fig. 10E in Gunnell et al., 1992).

The total height of m3 is about 50 mm, including 24 mm of the unexposed part at the labial side. There is no bifurcate structure in m3 root, and the lingual part near the bottom is ambiguous in the serial coronal CT images, but the outline of the double columnar labial wall can be traced (Fig. 2). This indicates that the root formation at m3 is not complete; the m3 seems to have an open root inside the mandible at this immature stage. There is no posterior elongation of the third lobe in the mandible, unlike in other tillodonts. The enamel layer presumably covers most of the m3 labial surface inside the mandible, considering the pattern of the enamel distribution in the m2.

CONCLUSION

Molar hypsodonty in *Higotherium* is a derived state compared with moderately hypsodont trogosines such as *Trogosus* (Miyata and Tomida, 1998), but it had been unknown whether or not *Higotherium* had ever-growing molars as in *Chungchienia*. As shown in the X-ray CT images, the two roots of m2 in *Higotherium* are closed as in other trogosines except *Chungchienia*. The m3 root is probably open in the immature stage, but it must be formed to be closed finally as in the m2. The result supports *Higotherium* has a delayed eruption of molars as Miyata and Tomida (1998) mentioned, but it never has ever-growing molars, unlike in *Chungchienia*.

Miyata and Tomida (1998) suggested that *Higotherium* and *Chungchienia* formed a monophyletic clade based on having "expanded enamel extending into dentary (=higher degree of hypsodonty)". However, we admit that this synapomorphic character proposed by Miyata and Tomida (1998) should be inadequate, because there is still a morphological gap between *Higotherium* with rooted molars and *Chungchienia* with ever-growing molars. The both genera show a higher degree of hypsodonty than in other tillodonts, but no character undoubtedly supporting the affinity between *Higotherium* and *Chungchienia* has been known so far. In addition, the m3 of *Higotherium* differs from that of *Chungchienia* in absence of the posterior elongation of m3 third lobe (Miyata and Tomida, 1998). Further

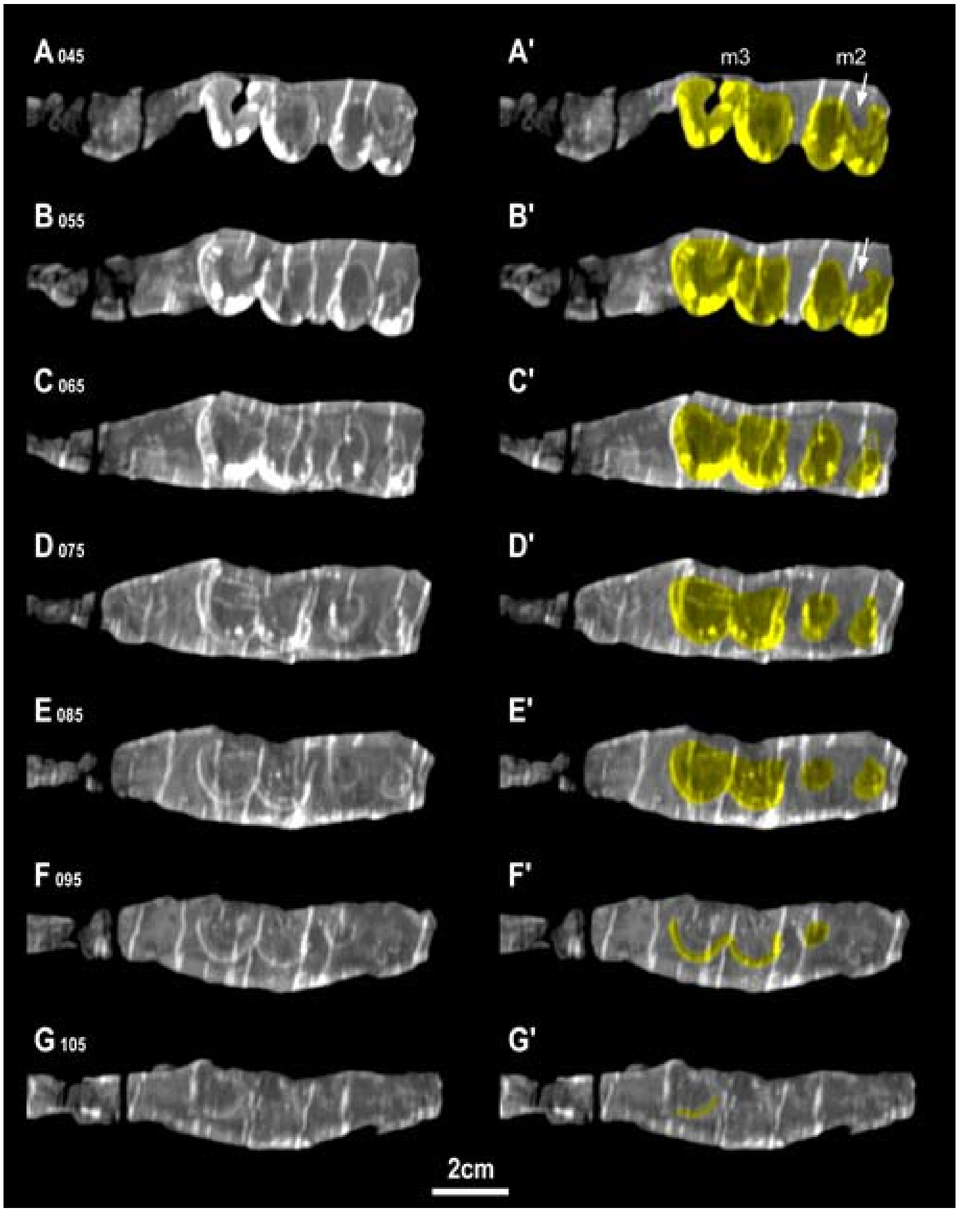

FIGURE 2. Reconstructed CT images (**A**–**F**) of NSM-PV 20118, *Higotherium hypsodon*, in horizontal (coronal) plane, and the interpretations (**A'**–**F'**) indicating the tooth positions in yellow. Arrows in A' and B' show a groove on the lingual surface of m2 inside the mandible.

materials of *Higotherium* and *Chungchienia* are required to clarify their phylogenetic positions among the trogosines and to examine whether their higher degree of hypsodonty is correlated to the phylogeny. At the present stage, it is possible to consider that *Higotherium* seems not to be the best candidate sharing a common ancestor with *Chungchienia*, giving a hypothesis of advanced hypsodonty independently occurred in other trogosines.

We know of many cases of hypsodont patterns changing to rootless cheek teeth in various herbivorous mammal groups, in conjunction with changing diet (e.g., taeniodonts, Schoch, 1986; equid perissodactyls, MacFadden, 1992; various families of rodents and notoungulates, MacFadden, 2000). The possible parallel evolution of the high hypsodonty seen in Asian tillodont species might suggest that their rhizophagous habits, or the ingestion with soil, proceeded during the Middle Eocene.

ACKNOWLEDGMENTS

We would like to thank all staff in Department of Diagnostic Radiology, Fukuiken Saiseikai Hospital, for helping to take the X-ray CT images. Dr. Fumiaki Kono, Fukuiken Saiseikai Hospital, kindly worked on the operation of the medical CT. Our special thanks are due to Drs. Tetsuya Minami and Shiro Miyayama for working on the processing of CT images and the animations to help our examination. We gratefully acknowledge Dr. Gregg F. Gunnell, University of Michigan, Museum of Paleontology, for critical reading of the manuscript and

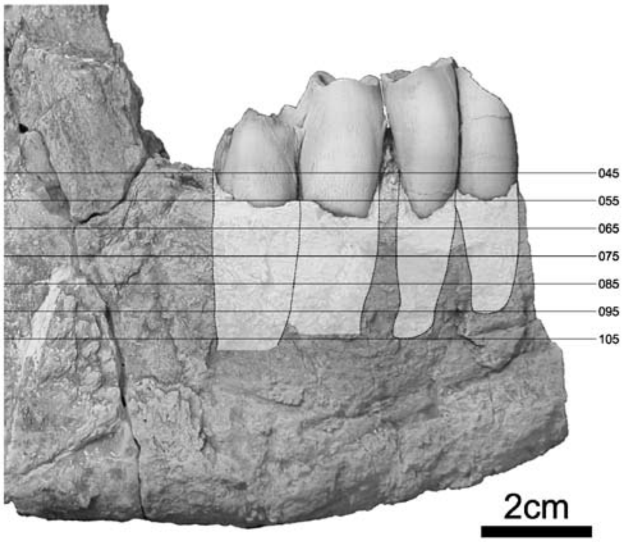

FIGURE 3. Reconstructed outline of the molars inside the mandible, NSM-PV 20118, *Higotherium hypsodon*.

providing valuable suggestions that improved the manuscript. We thank Drs. Kenneth D. Rose, Johns Hopkins University and Naoko Egi, Primate Research Institute, Kyoto University, who also gave us helpful suggestions and critical comments for the manuscript as the reviewers.

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