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# Verhoeven's giant rat of Flores (*Papagomys theodorverhoeveni*, Muridae) extinct after all?

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## Abstract

Recently *Papagomys theodorverhoeveni* was reported to be still extant on the basis of a single museum specimen. Based on comparison with extensive zooarchaeological material from Liang Bua, the identification of this specimen is refuted.

## Contents



## Introduction

The genus *Papagomys* consists of giant rats from the island of Flores, Indonesia. It was defined by Sody (1941) on the basis of *Mus armandvillei* Jentink, 1892, the only recent species of giant rat inhabiting the island. Palaeontological studies, however, made it clear that in the past the diversity of giant murids was far larger. Hooijer (1957) described a second species of *Papagomys*, *P. verhoeveni*, and also a second genus of giant rat, *Spelaeomys*, from Liang Toge. Musser (1981) added to these the genus *Hooijeromys* and several genera of smaller rats. He agreed with Hooijer that a second species of *Papagomys* had been present on Flores. Unfortunately, Hooijer had selected a specimen of *P. armandvillei*, of which fossils had been found in the same deposit, as the holotype. Therefore, based mostly on the same material, Musser (1981) defined the species *Papagomys theodorverhoeveni*.

Some years ago a recent specimen of *Papagomys theodorverhoeveni* was reported from the island of Flores (Suyanto and Watts, 2002). The specimen, consisting of a skull and mandibles, had been collected in 1974 at Ruteng, Manggarai, West Flores and was stored in the collections of the Museum Zoologicum Bogoriense (MZB 12716). Based on the comparison with four specimens of *P. armandvillei*, to which species MZB 12716 had originally been attributed, Suyanto and Watts concluded that it concerned a recent specimen of *P. theodorverhoeveni*. The main reasons for this re-identification were the somewhat smaller size of the specimen and the presence of an anterocentral cusp on the m1 of MZB 12716.

Recent excavations at the cave Liang Bua on Flores have yielded a large number of fossils of murids, among which many mandibles, maxillaries and isolated teeth of both *Papagomys armandvillei* and *P. theodorverhoeveni*. The site became renowned for the find of a small-bodied hominine, *Homo floresiensis*, which is considered to be a descendant of *H. erectus* that became dwarfed under insular conditions (Brown *et al.,* 2004). The *Papagomys* assemblage from the cave allows us a far better estimate of the range of variation of the two known species, both morphologically and metrically. The large sample, which includes all age classes from juvenile to senile, also allows us to get a better grip on how the morphology and dimension of the molars change with wear.

The initial description of *Papagomys theodorverhoeveni* was based on eleven specimens in comparison to a not much larger sample of *P. armandvillei*. This may have created the false impression that differences were clear-cut. In our much larger sample we found that some characters are variable, though the character states differ markedly between the species. Identification was primarily based on size. In case molars were preserved in mandibles, the robustness of the jaw helped in the identification, as the jaw of *P. armandvillei* is much more robust than that of *P. theodorverhoeveni*. The presence of the anterocentral cusp of the m1, the presence of the anterolabial cusp in m2, m3 and the presence of labial cusplets on m1 and m2, were only used as secondary characters. Understanding the morphological variation is needed to re-evaluate the identification of MZB 12716 as *P. theodorverhoeveni*. The Liang Bua collection contains 409 specimens identified as *Papagomys*, among which are 149 *P. theodorverhoeveni* and 191 *P. armandvillei*. The remaining part of the material could not be identified at species level.

## Material and methods

The fossil material consists of isolated teeth as well as fragments of maxillaries and mandibles. Most of the material was obtained by dry sieving sediment from the Liang Bua Cave, although part was excavated directly. All molars were measured using a Leica Ortholux measuring microscope. Length and with were measured at right angles. Four characters employed by Musser (1981) in his diagnosis of *P. theodorverhoeveni* were scored (Fig. 1). These are: the presence of an anterocentral cusp on m1 (AC) (1 in Fig. 1), the presence

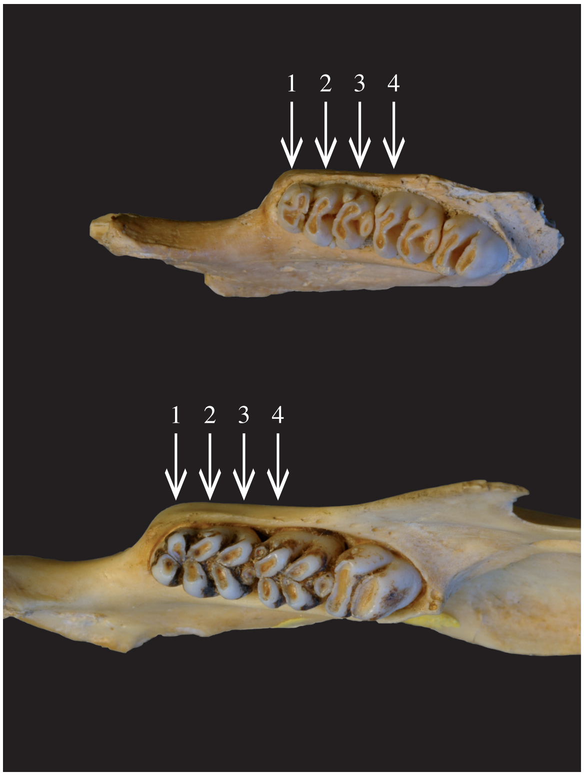



*Fig. 1*. Holotypes of *Papagomys armandvillei* (RMNH 18301, below) and *P. theodorverhoeveni* (RGM 195620, above) indicating the elements mentioned in the text (anterocentral cusp, 1; anterolabial cusplet, 2; posterolabial cusplet, 3; anterolabial cusp, 4).

*Table 1*. Measurements of *Papagomys* molars from Liang Bua and from MZB 12716 (Mean ± SD, observed range in parentheses, number of individuals measured). For the lower molars of MZB 12716 the estimated length is given in square brackets.

| | *P. armandvillei* | | *P. theodorverhoeveni* | | MZB 12716 |
|---|---|---|---|---|---|
| | L | W | L | W | W [est.] |
| m1 | 6.16 ± 0.33<br>(5.57-6.96)<br>*n* = 66 | 4.21 ± 0.27<br>(3.82-5.03)<br>*n* = 65 | 5.08 ± 0.35<br>(4.25-6.15)<br>*n* = 79 | 3.48 ± 0.26<br>(2.83-3.92)<br>*n* = 78 | 4.2 [6.7] |
| m2 | 4.67 ± 0.36<br>(4.03-5.68)<br>*n* = 62 | 4.51 ± 0.28<br>(4.03-5.14)<br>*n* = 62 | 3.75 ± 0.21<br>(3.25-4.39)<br>*n* = 78 | 3.58 ± 0.24<br>(3.00-4.07)<br>*n* = 78 | 4.5 [5.2] |
| m3 | 4.99 ± 0.37<br>(4.20-5.65)<br>*n* = 39 | 4.12 ± 0.28<br>(3.59-4.60)<br>*n* = 39 | 3.75 ± 0.29<br>(3.06-4.44)<br>*n* = 55 | 3.19 ± 0.30<br>(2.65-3.79)<br>*n* = 55 | 4.2 [4.4] |
| M1 | 7.72 ± 0.60<br>(6.66-9.06)<br>*n* = 41 | 5.01 ± 0.32<br>(4.39-5.80)<br>*n* = 41 | 6.02 ± 0.35<br>(5.18-6.66)<br>*n* = 36 | 3.80 ± 0.29<br>(3.31-4.50)<br>*n* = 36 | 4.9 |
| M2 | 5.03 ± 0.36<br>(4.18-5.66)<br>*n* = 31 | 4.68 ± 0.30<br>(4.27-5.69)<br>*n* = 31 | 3.91 ± 0.27<br>(3.36-4.56)<br>*n* = 20 | 3.51 ± 0.23<br>(3.50-3.98)<br>*n* = 20 | 4.7 |
| M3 | 4.65 ± 0.32<br>(4.09-5.28)<br>*n* = 20 | 3.97 ± 0.26<br>(3.52-4.52)<br>*n* = 20 | 3.37 ± 0.43<br>(2.73-4.26)<br>*n* = 17 | 3.06 ± 0.17<br>(2.71-3.37)<br>*n* = 17 | 4.1 |

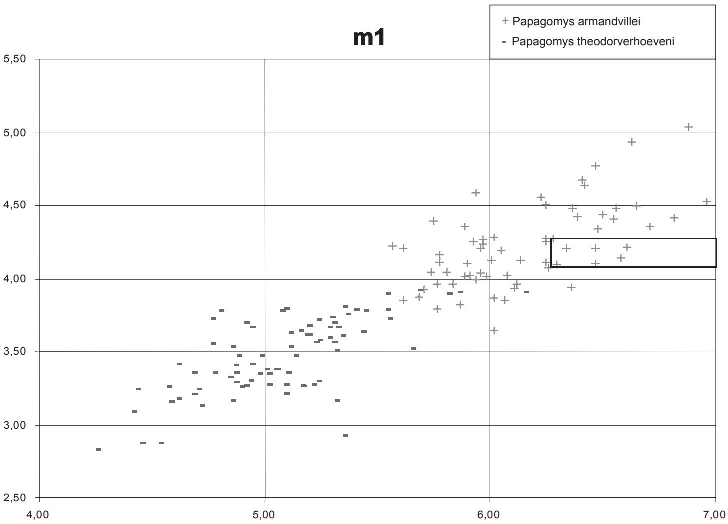



*Fig. 2*. Length/width diagram of the m1 of *Papagomys* species from Liang Bua. The estimated measurements of MZB 12716 are indicated by a rectangle.

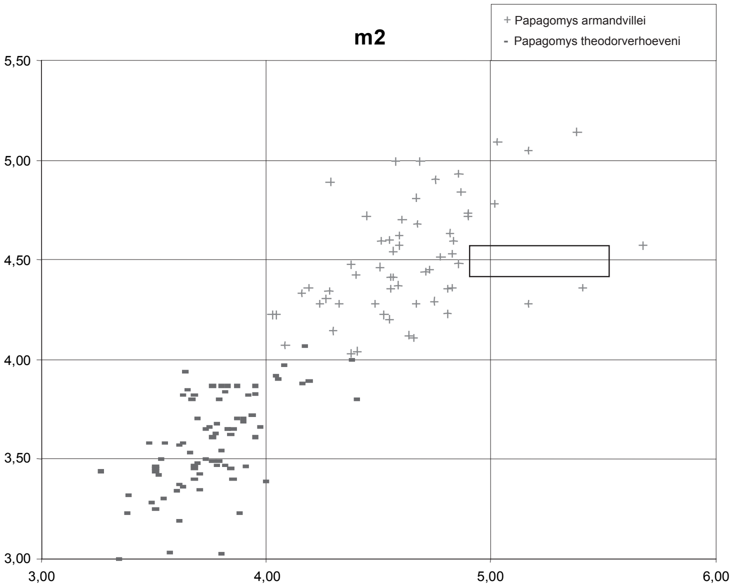



*Fig. 3*. Length/width diagram of the m2 of *Papagomys* species from Liang Bua. The estimated measurements of MZB 12716 are indicated by a rectangle.

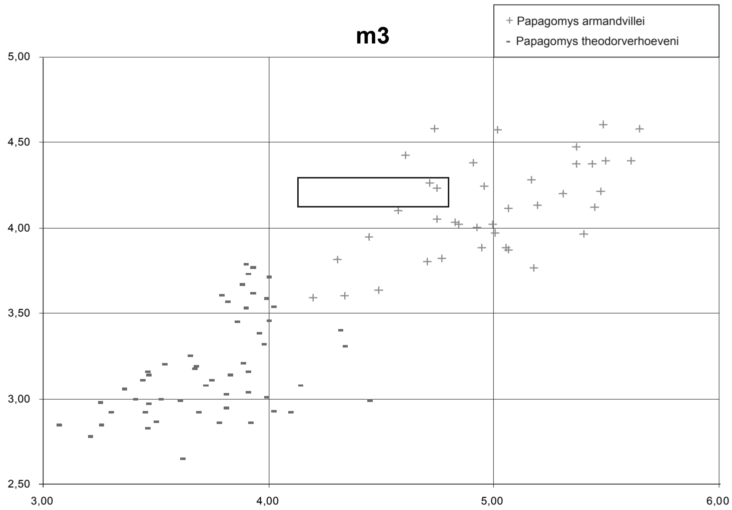



*Fig. 4*. Length/width diagram of the m3 of *Papagomys* species from Liang Bua. The estimated measurements of MZB 12716 are indicated by a rectangle.

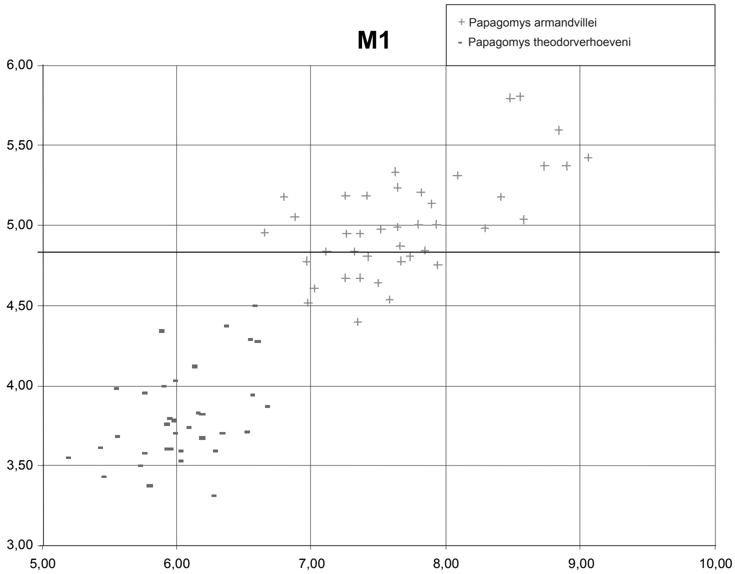



*Fig. 5*. Length/width diagram of the M1 of *Papagomys* species from Liang Bua. The width given by Sayunto and Watts (2002) is indicated by a line.

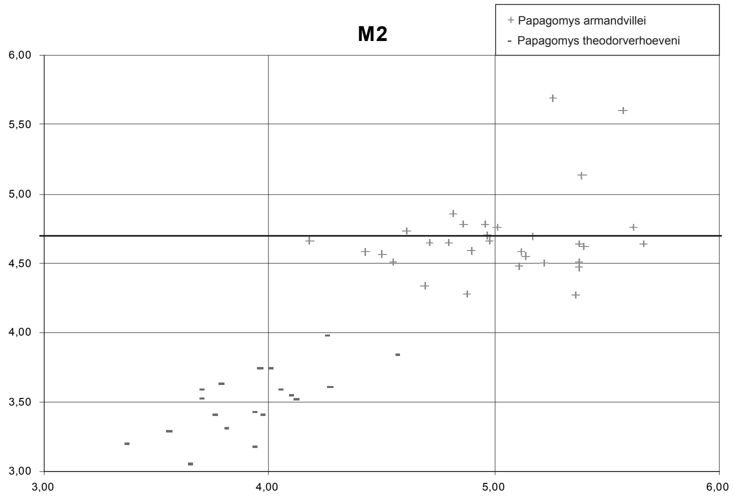



*Fig. 6*. Length/width diagram of the M2 of *Papagomys* species from Liang Bua. The width given by Sayunto and Watts (2002) is indicated by a line.

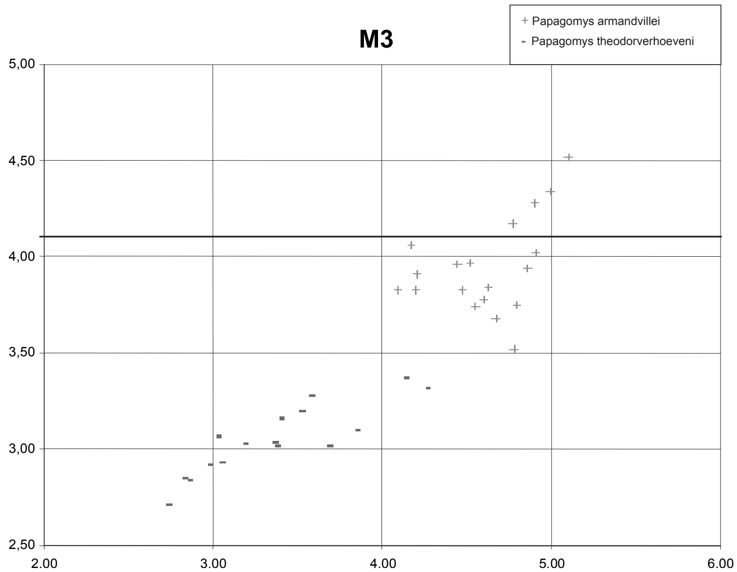



*Fig. 7*. Length/width diagram of the M3 of *Papagomys* species from Liang Bua. The width given by Sayunto and Watts (2002) is indicated by a line.

*Table 2.* Summary of morphological variation in *Papagomys* material from Liang Bua. For each character, the first column outlines the number of specimens with a certain state and the second the percentage of specimens with that state. Abbreviations: WS = wear stage, AC = anterocentral cusp, AL = anterolabial cusp, Cv3 = anterolabial cusplet, Cv5 = posterolabial cusplet.

| Species | WS | State | AC | % | AL | % | Cv3 | % | Cv5 | % |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. armandvillei* | **1** | Present | 5 | 33.3 | 2 | 28.6 | 1 | 6.7 | 1 | 6.7 |
| | | Absent | 10 | 66.7 | 5 | 71.4 | 14 | 93.3 | 14 | 93.3 |
| | | Unobservable | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | **2** | Present | 2 | 4.8 | 20 | 34.5 | 5 | 10.4 | 10 | 19.2 |
| | | Absent | 46 | 95.8 | 38 | 65.5 | 42 | 87.5 | 41 | 78.8 |
| | | Unobservable | 0 | 0 | 0 | 0 | 1 | 2.1 | 1 | 1.9 |
| | **3** | Present | 1 | 12.5 | 0 | 0 | 2 | 25 | 1 | 10 |
| | | Absent | 7 | 87.5 | 11 | 84.6 | 5 | 62.5 | 8 | 80 |
| | | Unobservable | 0 | 0 | 2 | 15.4 | 1 | 12.5 | 1 | 10 |
| | **All** | **Present** | **8** | **11.3** | **22** | **28.2** | **8** | **11.3** | **12** | **15.6** |
| | | **Absent** | **63** | **88.7** | **54** | **69.2** | **61** | **85.9** | **63** | **81.8** |
| | | **Unobservable** | **0** | **0** | **2** | **2.6** | **2** | **2.8** | **2** | **2.6** |
| *P. theodorverhoeveni* | **1** | Present | 3 | 20 | 17 | 100 | 4 | 25 | 20 | 95.2 |
| | | Absent | 11 | 73.3 | 0 | 0 | 12 | 75 | 0 | 0 |
| | | Unobservable | 1 | 6.7 | 0 | 0 | 0 | 0 | 1 | 4.8 |
| | **2** | Present | 11 | 24.4 | 36 | 78.3 | 25 | 56.8 | 47 | 94 |
| | | Absent | 32 | 71.1 | 10 | 21.7 | 19 | 43.2 | 3 | 6 |
| | | Unobservable | 2 | 4.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| | **3** | Present | 1 | 6.7 | 6 | 33.3 | 8 | 53.3 | 10 | 66.7 |
| | | Absent | 11 | 73.3 | 11 | 61.1 | 6 | 40 | 4 | 26.7 |
| | | Unobservable | 3 | 20 | 1 | 5.6 | 1 | 6.7 | 1 | 6.7 |
| | **All** | **Present** | **15** | **20** | **59** | **72.8** | **37** | **49.3** | **77** | **89.5** |
| | | **Absent** | **54** | **72** | **21** | **25.9** | **37** | **49.3** | **7** | **8.1** |
| | | **Unobservable** | **6** | **8** | **1** | **1.3** | **1** | **1.3** | **2** | **2.3** |

of an anterolabial cusplet on m1 (Cv3) (2 in Fig. 1), presence of a posterolabial cusplet on m1 (Cv5) (3 in Fig. 1), and presence of an anterolabial cusp on m2 (AL) (4 in Fig. 1). These cusps are according to Musser present in *P. theodorverhoeveni*, but absent in *P. armandvillei*. Furthermore, the laminae are more upright positioned in *P. theodorverhoeveni*.

Because morphology is affected by wear, we defined three wear stages. In wear stage 1, the wear facets of all individual cusps are separated. Wear stage 2 is defined by merger within laminae, whereas molars in which mergers of wear facets between laminae occur were placed in wear stage 3.

We estimated the lengths of the lower molars of MZB 12716 from Suyanto and Watts (2002, figure 1), using as a reference the values given in their table 1 for m1-m3 length and width of the various lower molars. The estimated lengths are given in Table 1. The measurements are indicated by a rectangle in Figs. 2-4, allowing a 5% margin of error.

All multivariate and statistical analyses were performed using SPSS 15.0.

The material from Liang Bua described in this paper is currently kept in Naturalis, Leiden, but will be stored in the Pasat Arkeologi Nasional Indonesia, Jakarta.

## Results

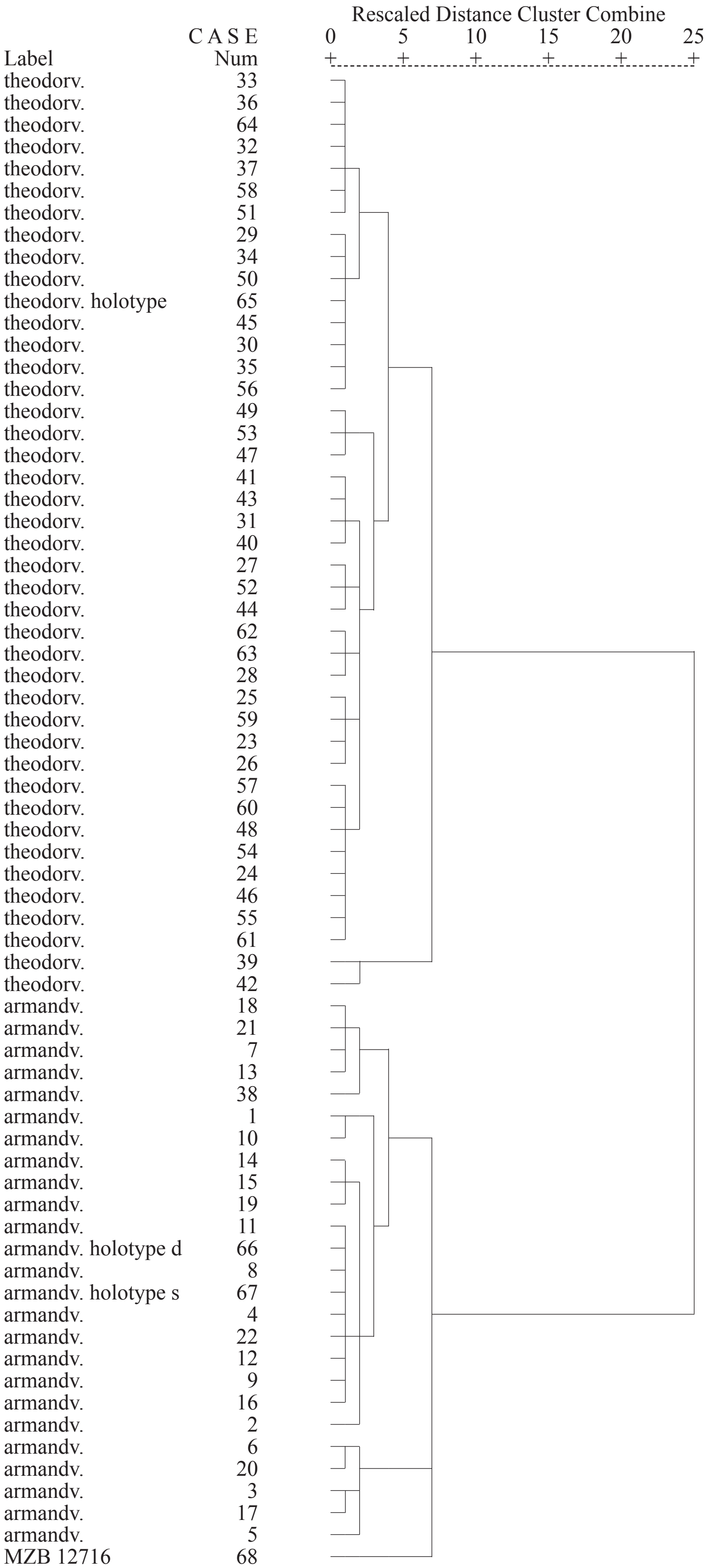
Given the large variation in size, it is clear that two species of *Papagomys* are present in the Liang Bua material. There is a certain amount of overlap, particularly in length of the m1 (Fig. 2). This is in itself not very surprising, since the length is more influenced by wear than the width. Therefore it seems peculiar that the overlap in the m3 is larger in the width than in the length. This may well be a result of the more slanting plates in *P. armandvillei*, which results consistently in a longer last molar in this species.

Plotting the data for MZB 12716 in the various diagrams (Figs. 2-7) shows that in the lower molars, even allowing for a margin of error because of the estimation, the various elements fall within the range of *Papagomys armandvillei*. The width given by Suyanto and Watts (2002) for the upper molars has been indicated in Figs. 5-7 as a line, which lies well above the maximum width for *P. theodorverhoeveni*, and again within the range of *P. armandvillei*.

Apart from the metrical overlap, it is also clear that most of the diagnostic characteristics noted by Musser (1981) show, in fact, a certain degree of variation. Actually, this was already clear, since the holotype of *P. armandvillei* does possess an anterolabial cusp on the m2 (Fig. 1), one of the characters deemed diagnostic for *P. theodorverhoeveni*.

The range of variation in the Liang Bua material (Table 2) indicates that all four morphological characters examined are actually variable within both species. The best differential character is the presence of the posterolabial cusplet, which is present in 90% of *P. theodorverhoeveni*, but in only 7% of *P. armandvillei*. We found an anterolabial cusp in 73% of our *P. theodorverhoeveni* material, but in only 27% of our *P. armandvillei* material. The anterolabial cusplet is present in about half of *P. theodorverhoeveni* examined and in 11% of *P. armandvillei*. The presence or absence of an anterocentral cusp is evidently the least distinctive character. This cusp is present in only 10% of our *P. armandvillei* material, but also in only 21% percent of our *P. theodorverhoeveni* material. The absence of all cusps seems to be quite strongly related to wear. For example, the anterolabial cusp was present in all our *P. theodorverhoeveni* material in wear stage 1, but in only 33% of the molars in our wear stage 3.

There is a strong difference in size between the two species of *Papagomys* (Figs. 2-7). There is substantial overlap only for m1. Nevertheless, Student's T-test performed separately on the lengths and widths of all the elements show a significant difference in size at a 99 % confidence level. The size difference is also apparent




◀ *Fig. 8*. Dendrogram showing a cluster analysis (Average linkage, squared Euclidean distance) of Liang Bua complete lower dentitions in combination with the holotypes of *Papagomys armandvillei* (including the holotype: d = dextral, s = sinistral), *P. theodorverhoeveni* and MZB 12716.

from a cluster analysis (average linkage, squared Euclidean distance) performed on the lengths and widths of molars from *Papagomys* mandibles from Liang Bua that preserve the entire molar row. To these we have added data of the holotypes of both species and of MZB 12716. The dendrogram (Fig. 8) shows that *P. theodorverhoeveni* and *P. armandvillei* are divided neatly into to clearly separated clusters. MZB 12716 clearly clusters with the *armandvillei* specimens, albeit as a bit of an outlier, which may be due to the way the measurements were estimated.

## Discussion

However surprising Suyanto and Watts' (2002) conclusion was that a species known from fossils only was still living, it was certainly not unlikely. Another rat that had been described from fossils by Musser has in fact been recently recognised in the Recent fauna. Musser (1981) had described *Floresomys naso* on the basis of Holocene dentaries and lower teeth from Liang Toge. As the genus name was preoccupied, he proposed the replacement name *Paulamys* (Musser *et al.,* 1986). A living specimen of a murid at least closely related to *P. naso* was collected in 1989 (Kitchener *et al.,* 1991).

Nevertheless, we do not agree with Suyanto and Watts (2002), that specimen MZB 12716 represents *P. theodorverhoeveni*. MZB 12716 is a young animal - on the basis of the photograph (o.c., fig. 1) we would place it in wear stage 1 - and therefore, most diagnostic characteristics of *P. theodorverhoeveni* should be easily visible. MZB 12716 does have an anterocentral cusp on m1, as does 10% of our *P. armandvillei* material and 21% of our *P. theodorverhoeveni* material. According to Suyanto and Watts (2002), an anterolabial and posterolabial cusplet are also present on m1. However, we cannot recognize the presence of either cusplet from the photograph they provide, and in our experience the posterolabial cusplet is almost invariably clearly present in young *P. theodorverhoeveni* (it is present in 95% of our wear stage 1 *P. theodorverhoeveni* material). MZB 12716 does not have an anterolabial cusp on m2 either. This cusp is present in all our wear stage 1 *P. theodorverhoeveni* material. According to Suyanto and Watts (2002), MZB 12716 is somewhat smaller than another *Papagomys* found in the MZB collection. However, the molar breadth measurements they provide fall well within the range of variation in our *P. armandvillei* material, and well above even the largest specimens of *P. theodorverhoeveni*. In conclusion, all evidence suggests that MZB 12716 is not an example of *P. theodorverhoeveni*, but of *P. armandvillei*. K.M. Helgen, who has seen the specimen, kindly informed us that he had come to the same conclusion (Helgen, pers. comm. 2007). Therefore, *P. theodorverhoeveni* should still be considered an extinct species.

## Acknowledgements

We are most grateful to the directorate of the Pasat Arkeologi Nasional Indonesia for the opportunity to study the Liang Bua material. This material was excavated by an Indonesian/ Australian team as part of the program "Astride the Wallace Line: 1.5 million years of human evolution, dispersal, culture and environmental change in Indonesia." under the direction of Mike Morwood. Together with Gert van der Bergh he enticed the study of the Liang Bua micromammal assemblage. Eelco Kruideniers made the photographs in Fig. 1. Israel Garcia Paredes assisted with the statistical analyses, and commented on our manuscript. The help of all these colleagues is gratefully acknowledged.

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