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Abstract

Excavations at Liang Bua Cave yielded a large amount of micromammal remains, the major part of which are murids, and some can be referred to three different species of giant rats. Whilst *Papagomys armandvillei* is still living on Flores, the other two species, *Papagomys theodorverhoeveni* and *Spelaeomys florensis* went extinct late during the Holocene. In this paper, the fossil record of these species at Liang Bua Cave is discussed. These giant murids are a clear example of insular gigantism, and can be seen as end members of the Island Rule. Opposition against the general applicability of this 'rule' is mainly based on a scale perspective. The study of giant rats at Liang Bua cave provides new insights in the understanding of human behavior, diet and environment. A strong acme in the number of giant rats in the cave during the Holocene may represent a taphonomical artifact, resulting from Palaeolithic hunting activity.

Keywords

giant, pleistocene, extinctions, survivors, holocene, indonesia, flores, bua, liang, rats, CAS

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Giant rats from Liang Bua cave...when the Island Rule cannot be broken

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Keywords

Liang Bua; Flores; insularism; gigantism; rats

Abstract

Excavations at Liang Bua Cave have yielded a large amount of micromammals remains, the major part of which are murids, and some of them can be referred to three different species of giant rats. Whilst *Papagomys armandvillei* (Jentink, 1892) is still living on Flores, the other two species, *P. theodorverhoeveni* (Musser, 1981) and *Spelaeomys florensis* (Hooijer, 1957) went extinct during Late Holocene. In this paper the fossil record of these species at Liang Bua Cave, together with the morphological differences between lower and upper molars of these two species, are discussed. Furthermore, the study of giant rats at Liang Bua cave provides new insights in the understanding of human behavior, its diet and its environment.

Giant rodents, together with dwarf elephants, have always been considered one of the main and first products of insularism. When Foster wrote the paper considered one of the manifests of the Island Rule, giant rodents were already alimentering the scientific debate, so much that the first sentence says (Foster, 1964: 234): “Workers in Europe have been debating whether isolation of

rodent populations, either on islands or as alpine isolates, results in a tendency toward gigantism, or whether the large size commonly found in these insular populations is the consequence of their being relicts of a once more widely spread large form”.

Still, the presumed tendency of small mammals to attain large size on islands (and the tendency of insular dwarfing in large mammals) is hotly debated. The Indonesian island of Flores is very much at the centre of this debate, as is clear from the paper of Meiri et al. (2008), one of the most important documents arguing against the Island Rule being a general tendency. This paper starts with mentioning *Papagomys armandvillei*, the giant rat of Flores, and, of course, the dwarfed insular hominin of the island, *Homo floresiensis*. The latter, of course, forms the main reason for all of the attention that the island has been given by scholars working on insular evolution. However, it is just one example in a fauna in which the typical characteristics of island evolution are clearly present (Van der Bergh et al., 2008; Meijer et al., 2010). Apart from *Papagomys*, southeast Asia has yielded more very large rodents on islands, such as the genera *Phloeomys* (Waterhouse, 1839) and *Crateromys* (Thomas, 1895) on the Philippines, and the extinct *Coryphomys buehleri* Schaub, 1937 from Timor, of which remains have recently been extensively re-described (Aplin and Helgen, 2010). All these Southeast Asian rats can be considered the product of insular gigantism. This phenomenon is by no means restricted to the region. For instance, the Late Miocene faunas of the palaeoisland Gargano showed a wide radiation of giant rats of the genus *Mikrotia* (Freudenthal, 1976), as well as a giant dormouse (Daams & Freudenthal, 1985), giant hamster (Freudenthal, 1985) and giant gymnure (Butler, 1980).

Giant rats living on islands today can be seen as survivors from the endemic Pleistocene faunas. The arrival of man has had profound effect of insular faunas all over the world, leading to many extinctions. This also holds true for giant insular murids. We already noted that *Coryphomys* from Timor has become extinct, and also on the island of Flores, two giant species, *Spelaeomys florensis* and *Papagomys theodorverhoeveni* died out during the Holocene (Hooijer, 1957, Musser, 1981). The latter actually was reported to be still living (Suyanto & Watts, 2002), but Zijlstra et al. (2008) demonstrated this was based on a misidentification. The possibility that a second species of *Papagomys* is still present on Flores can, however, not be excluded. After all, also *Paulamys naso*, after having been described from fossils, was later found to be still living on the island (Kitchener et al., 1991, 1998; Locatelli et al., submitted).

Unfortunately, the fossil record of the insular endemics in Southeast Asia is poor. Flores is a favourable exception. The first remains of giant rats from the island, recovered by Dr. Verhoeven at Liang Toge, were described by Hooijer (1957). Musser (1981), in his monograph on the Flores fossil rodents, gave full descriptions of giant rats remains recovered from fossil sites in Flores. Apart from the three species known from Holocene deposits, he also noted a very large murid from the island's Middle Pleistocene, *Hooijeromys nusatenggara*, as well as some ordinary sized endemics from the

Holocene. Still, up to 2000, the number of published fossil murid specimens from the island was round about thirty.

New excavations at Liang Bua cave, as well as the study from material excavated in the 1980s have dramatically increased the number of rodent fossils. Although the giant murids were already relatively well known through the work of Hooijer (1957) and Musser (1981), this new material provides important new information. This is because 1) for the first time, also material is available from the Late Pleistocene, dating back to 95 ka; 2) we are now better able to record the variation in the different species, including descriptions from the upper dentition; 3) a detailed geochronology of the section in the Liang Bua cave is available (Roberts et al., 2009), allowing us to study changes in the fauna in time; 4) carefully recorded archaeological finds from the section allow us to study changes in fauna in relation to human behaviour. The study of the variation in the species of *Papagomys* has been largely dealt with by Zijlstra et al. (2008), in their attempt to differentiate *P. armandvillei* and *P. theodorverhoeveni* in the vast fossil record from the cave. After providing detailed descriptions of the various species, we will therefore focus in this paper on the changes in relative abundance of the giant rodents, and see how these relate to climate and/or human behaviour.

Material and Methods

Liang Bua is a limestone cave in western Flores, about 13 km north-west of Ruteng, the Manggarai District capital (Fig. 1). Discovered as an archaeological site in 1950 by Father Theodor Verhoeven, the same carried out the first systematic excavation in 1965. Between 1978 and 1989, the National Centre for Archaeology, Djakarta excavated ten sectors in the cave under direction of Prof. Soejono, focussing on the Holocene parts of the stratigraphy. A joint Indonesian-Australian team, led by Mike Morwood (University of Wollongong), started in 2001 to extend the excavation to the Pleistocene. When this resulted in the find of insular hominine, *Homo floresiensis*, in Sector VII, a new sector, Sector XI was dug out directly adjacent to Sector VII.

1: Location map

The material in this paper encompasses both the fossils from the Soejono and Morwood excavations. We focus on sector IV, the sector of which the faunal remains have been most extensively studied (Van den Bergh et al., 2009; Meijer et al., 2010; Locatelli et al., [in prep](#) a, b), but also includes material from sectors III and VII. The material was excavated along 10 cm spits. Much of the rodent material was obtained by dry sieving sediment from the excavations. A detailed stratigraphy of the various Liang Bua sectors was given by Westaway et al. (2009); the geochronology of the cave is given in Roberts et al. (2009).

544 mandibular and maxillary remains of giant rats were recovered. Among them, 352 are lower remains and 172 are upper ones; 20 are incisive fragments. The list of the number of specimen per species and dental portion is reported in Table 1.

LOWER	n	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
<i>Papagomys armandvillei</i>	159	6.10	4.18	4.57	4.46	4.78	4.10
<i>Papagomys theodorverhoeveni</i>	118	5.03	3.45	3.72	3.56	3.70	3.16
<i>Spelaeomys florensis</i>	17	5.72	4.12	4.37	4.17	4.08	3.59
<i>Papagomys</i> sp. Indet.	58			5.56	4.84		

UPPER	n	LM1	WM1	LM2	WM2	LM3	WM3
<i>Papagomys armandvillei</i>	75	7.69	5.04	5.16	4.67	4.59	3.89
<i>Papagomys theodorverhoeveni</i>	69	5.90	3.86	3.94	3.55	3.35	3.10
<i>Spelaeomys florensis</i>	9	6.27	4.25	4.12	4.08		
<i>Papagomys</i> sp. Indet.	19					5.28	4.51

Table 1: total number of remains per species and mean value of measurements. W=width; L=length; minuscule=lower tooth; capital= upper tooth

Measurements of length and width of all molars have been taken, according to the method used for small and middle size murids (Fig. 2). Of every measurement, descriptive analysis has been performed, using the Analysis Toolpak of Microsoft Office Excel.

2: Plan of measurements

Mean measurements of teeth recovered at Liang Bua have been compared with those of sub-fossil teeth of *Papagomys armandvillei*, *P. theodorverhoeveni* and *Spelaeomys florensis* from Liang Toge and recent of *Papagomys armandvillei* (the only Giant rat still living on Flores). All these measurements are reported in Musser (1981).

On lower tooth rows, PCA has been performed using PAST Software (Hammer et al., 2001). Since complete series are necessary to perform multivariate analysis, only complete tooth rows have been analysed with multivariate analysis. PCA has not been performed on upper tooth rows because of the low number of complete specimens (none of *Spelaeomys florensis* and only 29 of *Papagomys*).

Systematic Palaeontology

Class: Mammalia Linnaeus, 1758

Order: Rodentia Bowdich, 1821

Family: Muridae Illiger, 1811

Subfamily: Murinae Illiger, 1811

Genus: *Papagomys* Sody, 1941

Papagomys armandvillei Jentink, 1892

Synonymy:

Mus armandvillei, Jentink 1892

Mallomys armandvillei, Thomas 1898; Tate 1936

Holotype: Young adult, RMNH 18301, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis)

Distribution: Flores, Indonesia. Fossil material has been recovered from Liang Bua (Upper Pleistocene and Holocene) and Liang Toge (Holocene). First occurrence, Liang Bua cave Sector IV spit 60 (Late Pleistocene); last fossil occurrence Sector IV spit 9 (ca.500 years). The species still occurs on Flores today.

Morphological description:

Upper tooth row: Molars robust; the widest molar is M1, but M2 can be as large as M1; the last molar is the narrowest. All the cusps are high and slant distally, so that there is overlapping among teeth: M1 covers the mesial part of M2 and the latter covers the mesial part of M3 (characteristic of species without t7).

I: massif, curved, with mesial enamels with yellowish/orange pigmentation.

M¹: The molar is anchor by five roots: a large mesial one, two small median ones, a small linguo-distal and a large distal root. The M¹ has three rows of cusps. All the medial cusps (t2, t5 and t8) are large and circular in occlusal view. The first row, formed by t1, t2 and t3, is almost transversal; only t1 is located a bit distally compared to the other cusps. t1 is circular in cross section and large; t3 is smaller and flattened. The second row is less transverse; the central and the labial cusps (t5 and t6) look like the corresponding ones in the first row, but t4 is not as cylindrical as t1, is more inclined

and the shape in cross section is not circular, but elongated toward the first row. The third row is formed only by a large, almond-shaped t8, connected with a vestigial t9. There is no t7.

M²: The molar is anchored by four roots, two mesial and two distal ones. The M² formed by a t1 and two distal rows of cusps. t1 is cylindrical, large or drop shaped; except for a thin connection with t5, this cusp is separated from the first row. This row, formed by t4, t5 and t6, is transverse or a bit arched in worn teeth; t3 slants distally. The third row is made by a very large t8; t9 is very small, reduced to a small labial appendix of t8.

M³: The molar is anchored by three roots: two mesial ones and a large distal one. t1 is large, cylindrical and well separated from the first toothrow. t3 is only a vestigial small mesial protuberance of the first row, which is mainly formed by t4, t5 and t6, arranged in a transverse row, which becomes arched with wear. All the cusps of the first row are about of similar size, the central one (t5) being the bigger. The second row is transverse and formed by the confluence of t8 and t9. The molar has a squarish outline.

Lower tooth row: lower molars are wide and the occlusal pattern is simple; subsidiary cusplets are rarely present. As in the upper tooth row, the cusps of the molars are slanted backwards. The M₂ is the wider molar.

M₁: this molar is anchored by four roots, a large mesial one, two small central (one lingual and one labial) and a large distal one. The outline of the tooth is rectangular. Cusps are arranged in three laminae. The first lamina is made up of two cusps, the antero-labial cusp (a-lab) and the antero-lingual cusp (a-ling). These cusps are widely confluent; in young individuals the lamina is V shaped, with the cusps merging along the midline; in worn teeth the area of confluence increases and the lamina becomes elliptical. Since a-ling is slightly bigger than a-lab, the lamina looks inclined. The second lamina is formed by two oblong cusps, the protoconid and the metaconid, which merge in the midline. The third lamina is formed by two oblong cusps, the hypoconid and entoconid, which fuse together in the midline. The second and third laminae are very similar and are arched. A massive and cylindrical posterior cingulum is present. Subsidiary cusplets (anterior labial cusplet and anterocentral cusp) are present only in few specimens (around 10%), and are poorly developed; a posterior labial cusplet is more frequent (almost 30%).

M₂: the M₂ is anchored by three roots, two small mesial and a large distal one. The occlusal outline is squarish, since length and width are about the same. Cusps are arranged in two laminae. The first lamina has a straight mesial margin; the labial and lingual cusps are oblong and merge in the midline, so that distal margin is arched. The protoconid is larger than the metaconid. In around 10% of specimens there is a small anterolabial cusp. The second row is made up of two cusps, hypoconid and entoconid, which are oblong and merge in the midline. This lamina is arched, assuming a boomerang shape. A large cylindrical posterior cingulum is located at the distal margin of the tooth.

M₃: this is the smallest and simplest among molars. It is anchored by three roots, two small mesial ones (labial and lingual) and a large distal one. The occlusal surface is made up by two chunky transverse laminae; the first is straight, the second is oval.

Measurements

The results of the descriptive statistical analysis are reported in **Table 2**.

<i>Papagomys armandvillei</i>	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	LM1	WM1	LM2	WM2	LM3	WM3
Mean	6.10	4.18	4.57	4.46	4.78	4.10	7.69	5.04	5.16	4.67	4.63	3.94
Standard deviation	0.35	0.27	0.35	0.28	0.53	0.28	0.60	0.29	0.57	0.25	0.28	0.23
Sample Variance	0.12	0.07	0.13	0.08	0.28	0.08	0.36	0.09	0.33	0.06	0.08	0.05
Range	1.46	1.39	1.76	1.20	2.01	1.01	2.40	1.40	3.09	1.33	1.01	1.00
Minimum	5.50	3.64	3.93	3.94	3.64	3.59	6.66	4.39	4.18	4.27	4.09	3.52
Maximum	6.96	5.03	5.68	5.14	5.65	4.60	9.06	5.79	7.27	5.60	5.10	4.52
Count (n)	87	86	82	82	54	54	46	47	36	37	21	21
Confidence Interval (95,0%)	0.07	0.06	0.08	0.06	0.14	0.08	0.18	0.09	0.19	0.08	0.13	0.11

Table 2 : descriptive analysis of *Papagomys armandvillei*

Papagomys theodorverhoeveni Musser, 1981

Holotype: Right dentary with M₁ – M₃, RGM 195620, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis)

Distribution: Flores, Indonesia. Known only from fossil remains from Liang Toge and Liang Bua caves. First occurrence at Liang Bua cave, Upper Pleistocene, Sector IV spit 64 (Late Pleistocene). Last occurrence Liang Bua cave, sector IV, spit 1 (sub-recent).

Morphological description:

Upper tooth row: robust relative to the maxillary bone; the widest molar is M1, but M2 can be as large as M1; the third is the narrowest. All the cusps are high and slant distally, so that the molars overlap: M1 covers the mesial part of M2 and the latter covers the mesial part of M3, as is typical for species lacking t7.

I: massif, curved, with mesial enamels with yellowish/orange pigmentation.

M¹: five roots anchor this tooth: one large mesial root, two small medial, a small lingual distal and a large distal one. Each tooth has three rows of cusps. Central cusps (t2, t5 and t8) are large and circular in cross section. The first row, formed by t1, t2 and t3, is straight and transversal along t2

and t3, but bends abruptly near the t1, which lies linguodistal to the other cusps. t1 is cylindrical, circular in cross section and large; t3 is smaller and oblong. The second row is arched and formed by triangular cusps in younger specimens and flattened in worn teeth. The third row, lacking t7, is formed only by a large, almond-shaped t8, connected with t9, which is oblong and well defined in young individuals.

M²: the molar is anchored by four roots, two mesial and two distal. The M2 is formed by a t1 and two distal rows of cusps. t2 sometimes is absent or very small and sometimes cylindrical, well defined, but always clearly smaller than the other cusps. t1 is cylindrical and stout; it is circular or drop shaped in cross section. Except for a thin connection with t5, this cusp stands apart from the first row. This row, formed by t4, t5 and t6, is transverse or slightly arched in worn teeth; t3 slants distally. The third row is made by a very large t8; t9 is very small, reduced to a small labial appendix of t8.

M³: the last molar is anchored by three roots, two mesial ones and one large distal. t1 is large, cylindrical; t3 is small, usually connected to the first row. With wear, t1 and t3 merge widely with the first row in a single field. The first row is formed by t4, t5 and t6, arranged in row, which becomes progressively more arched with wear. All the cusps of the first row are about of similar size, the central one (t5) being slightly bigger. The second row is transverse and formed by the confluence of t8 and t9. The tooth has a general squarish outline.

Lower tooth row: lower molars are wide and the occlusal pattern is simple (few subsidiary cusplets and reduction of cusps). The wider molar is the second.

M₁: this molar is anchored by four roots, one large mesial, two small central (one lingual and one labial) and a large distal one. Like in *Papagomys armandvillei*, cusps are arranged in three laminae. The anterolabial and anterolingual cusps, forming the first lamina, are widely confluent, merging along the axis. In worn molars, the area of confluence increases and the lamina becomes elliptical. Since the anterolingual cusp is slightly larger than the anterolabial one, the lamina is asymmetrical. In around 20% of the specimens, a small anteroventral cusp is present. The second and third laminae are formed by two oblong cusps (protoconid and metaconid in the second, hypoconid and entoconid in the third one), which merge at the midline. The second and third laminae are very similar and are arcuate. In around 90% of the specimens, a posterior labial cusplet is present, standing against hypoconid. About half the specimens also has a small anterior labial cusplet. A massive and cylindrical posterior cingulum is present.

M₂: the second molar is anchored by three roots, two small mesial and a large distal one. The occlusal outline is squarish, since length and width are about the same. Cusps are arranged in two laminae. The first lamina has a straight mesial margin, slanting in about 70% of the specimens due to the presence of a cylindrical anterolabial cusp; protoconid and metaconid are oblong and merge in the midline, making the distal margin of the lamina arched. The protoconid is larger than the

metaconid. The second row is made by two cusps, hypoconid and entoconid, which are oblong and merge in the midline. This lamina is arcuate, assuming a boomerang shape. In few cases a posterior labial cusplet is visible in young individuals, lying against the hypoconid. A large cylindrical posterior cingulum is located at the distal margin of the tooth.

M₃: the molar is anchored by three roots, two small mesial ones (labial and lingual) and a large distal one. The occlusal surface is made up by two chunky transverse laminae; the first is straight or lobated; in some cases a small anterolabial cusp lies against the protoconid. The second lamina is oval.

Measurements

The results of the descriptive statistical analysis are reported in Table 3.

<i>Papagomys theodorverhoeveni</i>	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	LM1	WM1	LM2	WM2	LM3	WM3
Mean	5.03	3.45	3.72	3.56	3.70	3.16	5.90	3.86	3.94	3.55	3.35	3.10
Standard deviation	0.39	0.27	0.24	0.25	0.34	0.30	0.52	0.38	0.33	0.30	0.50	0.28
Sample Variance	0.15	0.07	0.06	0.06	0.12	0.09	0.27	0.14	0.11	0.09	0.25	0.08
Range	2.01	1.09	1.22	1.07	1.65	1.24	2.25	2.09	1.21	1.21	1.89	1.19
Minimum	4.14	2.83	3.17	3.00	2.79	2.55	4.41	3.10	3.35	3.05	2.37	2.54
Maximum	6.15	3.92	4.39	4.07	4.44	3.79	6.66	5.19	4.56	4.26	4.26	3.73
Count (n)	88	87	82	82	57	57	56	56	29	29	24	24
Confidence Interval (95,0%)	0.08	0.06	0.05	0.05	0.09	0.08	0.14	0.10	0.13	0.11	0.21	0.12

Table 3 descriptive statistical analysis of *Papagomys theodorverhoeveni*

Differences between *Papagomys armandvillei* and *Papagomys theodorverhoeveni*:

The striking difference between these species is the size: *P. armandvillei* is larger. However, the size variation is gradual, and morphological differences are needed to make the species discrimination stronger.

Musser (1981), on the basis of Liang Toge material, defined the morphological difference between *P. theodorverhoeveni* and *P. armandvillei*. Nevertheless, as it often happens in palaeontology, because of the limited number of specimens retrieved, some differences were not interspecific, but represented local variations in the sample considered. Zijlstra et al. (2008) made an accurate analysis on some mandibular characters that were considered diagnostic by Musser (1981). In particular, they focused on the presence/absence of cusps and subsidiary cusplets on molars, the frequencies in their presence/absence and the relationship between them and wear. These characters proved to be variable, but could still be of some use as some of the frequencies varied between the two species. The presence of an anterocentral cusp in m1 is not diagnostic at all, with

only 10% of difference in frequencies between the species; the anterior lingual cusplet on m1 and anterolabial cusp on m2 are show a far larger difference in the frequencies (around 50%, being more frequently present in *Papagomys theodorverhoeveni*). The most diagnostic character was the presence of the posterior labial cusplet on m1 (90% in *P. theodorverhoeveni*, only 7% in *P. armandvillei*). In general, even if both these species are characterized by a very simple occlusal pattern, *P. theodorverhoeveni* has more subsidiary cusplets and cusps, and consequently the molar pattern is more elaborate.

Apart from these characters, the rows in the upper molars are thinner in *P. theodorverhoeveni* than in *P. armandvillei*. In general, cusps have a tendency to look more rounded and circular in *P. armandvillei* and angular or triangular in *P. theodorverhoeveni*.

Genus: *Spelaeomys* Hooijer, 1957

Spelaeomys florensis Hooijer, 1957

Holotype: RGM 629580, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis)

Distribution: Flores, Indonesia. *Spelaeomys* is only known from fossil remains recovered from Liang Toge (Holocene) and Liang Bua (Upper Pleistocene; Holocene).

Morphological description:

Upper tooth row: teeth pattern is much elaborated, with developed subsidiary cusps and cusplets and a complicated arrangement of main cusps. M^1 is the larger tooth. In the Liang Bua fossil material, no M^3 has been recovered.

M^1 : the first molar is anchored by four roots (a large mesial, a small centro-lingual and two small distal ones). Central cusps (t2, t5 and t8) are the biggest and are semicircular or triangular in occlusal view. Lingual cusps (t1, t4 and t7) are oval, labial ones (t3, t6 and t9) are drop-shaped or oblong. Between t1 and t2 and between t1 and t4 there can be two lingual subsidiary cusplets. A small one is present on the labial side between t6 and t9. Cusps are well separated among each other; with wear, distal cusps merge together before mesial ones. A small posterior cingulum is present.

M^2 : the molar is anchored by four roots, two mesial and two distal. The outline is squarish. t1 is triangular in occlusal view, pointing lingually. t2 is large and triangular. t3 is smaller and cylindrical. t5 is semicircular, labial and lingual cusps (t4, t6, t7 and t9) are oblong. The posterior cingulum is cylindrical and connected to t8 by the labio-distal corner.

Lower tooth row: m1 is the widest molar, m3 is the narrowest. Lower molars, like the upper ones, have an elaborated pattern, with main cusps flanked by well-developed subsidiary cusplets.

M₁: the molar is anchored by three roots (large mesial one and two distal ones). Next to the six main cusps - three lingual (anterolingual cusp, metaconid and entoconid) and three labial (anterolabial cusp, protoconid and hypoconid) - and posterior cingulum, there are many subsidiary cusplets. Main cusps are drop-shaped and meet along the midline of the tooth. The posterior cingulum is triangular in occlusal view. Six subsidiary cusplets are present: one large and circular anterocentral cusp; one very small cusplet flanks the mesial margin of the anterolabial cusp; a cylindrical one flanks the labio-distal margin of the same cusp; one large drop shaped anterior labial cusplet; a very large oval posterior labial cusplet, located mesially to the hypoconid; a cylindrical disto-labial cusplet, opposite to the posterior cingulum.

M₂: its outline is squarish. The cusps pattern is the same of the distal part of M₁: protoconid and hypoconid are triangular/semicircular in occlusal view; metaconid and entoconid are oblong and drop shaped. The posterior cingulum is cylindrical. Four subsidiary cusps are present along the labial margin. From the mesial to distal these are the cylindrical anterolabial cusp and a smaller cusplet that merges in early wearstages; an oval to drop-shaped posterior labial cusplet and a small cylindrical distal cusp opposite to the posterior cingulum.

M₃: the last molar is anchored by two roots (mesial and distal); its outline is rectangular. There are four drop-shaped main cusps: metaconid, protoconid, entoconid and hypoconid. Beside the anterolabial cusp, which is semicircular, there are two tiny cylindrical mesial cusplets.

Measurements

The results of the descriptive statistical analysis are reported in **Table 4**.

<i>Spelaeomys florensis</i>	<i>Lm1</i>	<i>Wm1</i>	<i>Lm2</i>	<i>Wm2</i>	<i>Lm3</i>	<i>Wm3</i>	<i>LM1</i>	<i>WM1</i>	<i>LM2</i>	<i>WM2</i>
Mean	5.72	4.12	4.37	4.17	4.08	3.59	6.27	4.25	4.12	4.08
Standard deviation	0.31	0.20	0.15	0.22	0.08	0.29	0.23	0.08		0.02
Sample Variance	0.09	0.04	0.02	0.05	0.01	0.08	0.05	0.01		0.00
Range	1.02	0.65	0.51	0.67	0.21	0.77	0.60	0.22	0.00	0.03
Minimum	5.30	3.77	4.04	3.82	3.99	3.18	6.00	4.16	4.12	4.06
Maximum	6.32	4.42	4.55	4.49	4.19	3.95	6.60	4.38	4.12	4.09
Count (n)	13	13	10	10	7	7	5	5	1	2
Confidence Interval (95,0%)	0.18	0.12	0.11	0.15	0.07	0.27	0.29	0.10		0.18

Table 4: descriptive statistical analysis of *Spelaeomys florensis*

Results

3: Scatter plots of molar measurements

The scatter plots (Fig. 3) show the distribution of measurements of lower and upper molars of giant rats. The results of PCA analysis are reported in Table 5-6 and Fig. 4.

Axis	Eigenvalue	Variation
1	5.3718	89.53
2	0.304875	5.0812
3	0.135038	2.2506
4	0.0898026	1.4967
5	0.0665627	1.1094
6	0.031927	0.53212

Table5: Eigenvalues and Variation of PCA applied to large murids from Liang Bua

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
LM/1	-0.4113	0.1526	-0.6071	0.498	0.4099	0.1512
WM/1	-0.41	0.4018	0.03918	-0.6034	0.3783	-0.4021
LM/2	-0.4149	-0.1921	-0.4386	-0.1531	-0.7146	-0.2542
WM/2	-0.4193	0.2647	0.2485	-0.1812	-0.2194	0.7819
LM/3	-0.3801	-0.8303	0.1849	-0.1299	0.3295	0.08078
WM/3	-0.4125	0.1376	0.5845	0.561	-0.1467	-0.3647

Table 6: Eigenfactors of PCA

Figure6: PCA of large murids

The ordination of the PCA successfully separates the different species. The separation is clearest on the first axis, which is mainly related to size variation (all variables are directly correlated, and the first axis describes almost the 90% of the entire variation). This also explains why *Papagomys armandvillei* and *Spelaeomys florensis* result to be closer than the two cogenetic species. On second and third axis there is no separation among different taxa. As already noticed by the morphological analysis, *P. armandvillei* and *P. theodorverhoeveni* are morphometrically very similar, but can be mostly distinguished on the basis of size differences.

Discussion

The Giant rats' fossil remains of *Papagomys armandvillei*, *P. theodorverhoeveni* and *Spelaeomys florensis* from Liang Bua cave represent the first fossil occurrence of these species. As the giant rats are already found in the oldest, Late Pleistocene, deposits of the cave, and are endemic to the island, we must assume that they had already dwelled the island for a while. It is difficult to establish how long ago they originated, since there is a huge gap in the fossil documentation between the Middle Pleistocene deposit of the Ola Bula Formation and the Liang Bua site. In this time, the faunal composition of the assemblages changed, but not so much if we consider that more than half million years passed (Meijer et al., 2010). The Komodo dragon, *Varanus komodoensis*, survived all Quaternary climatic fluctuations and is still living today; *Stegodon florensis*, underwent some modifications, and appears in Liang Bua as a separate subspecies, *Stegodon florensis insularis* (van den Bergh et al., 2008). Its extinction is recorded at Liang Bua, just before the end of the Pleistocene. The only known Middle Pleistocene rodent of the island is *Hooijeromys nusatenggara* (Musser, 1981). It was a large-sized rat, larger than *Paulamys naso* and *Komodomys rintjanus*, but smaller than the true giant forms *Papagomys armandvillei*, *P. verhoeveni* and *Spelaeomys florensis*. Only two maxillaries from Ola Bula are known of these species, plus four isolated molars tentatively associated with *H. nusatenggara* from Boa Leza. The similarities between the species of *Papagomys* and *H. nusatenggara* have been thoroughly analysed by Musser (1981), on the basis of the few remains known. They share the general structure of upper molars, with low cusps in transverse rows, the lack of t7 and posterior cingula and the absence of t3 in M2, as well as the same number of roots. The lower molars that have tentatively been attributed to the species show a even greater resemblance to those of *Papagomys*. Musser (1981) placed *Hooijeromys nusatenggara* in its own genus based on some differences in the maxillary bone and in the arrangement of cusps on upper teeth. Nevertheless, *Hooijeromys* represents a plausible ancestor of Late Pleistocene murids of Flores. Thus, the scanty evidence suggests that the phylogenetic continuity between early Middle Pleistocene and Late Pleistocene faunal assemblages from Flores as observed by Meijer et al. (2010) also applies to the giant rodents of the genus *Papagomys*.

The phylogenesis of *Papagomys armandvillei* has been studied by means of Microcomplement Fixation of Albumin (Watts and Baverstock, 1994). The Microcomplement Fixation of Albumin placed *Papagomys* in the *Rattus*-like clade, as had already been suggested in a morphological study by Musser and Newcomb (1983). In the analyses, *Papagomys* turned out to be in the same clade as another Flores endemic, *Komodomys rintjanus*. Unfortunately, the other two endemics, *Paulamys* and *Rattus hainaldi* were not included in the study.

Within the Flores murids, *Spelaeomys florensis* is clearly the odd one out. While all the other native rodents (with the exception of the shrew rat) seem to belong to the same clade and seem to be more related among them than with any other species outside Flores (Musser, 1981), *Spelaeomys florensis* displays more similarities with murids from New Guinea and nearby Timor. From the latter, Quaternary remains of *Coryphomys buehleri* Schaub, 1937 have been recently thoroughly re-described (Aplin and Helgen, 2010). These species share many characters. The mandible shape, that is so different from the ones of the native rats of Flores, with the deepening under the first lower molar; the complex structure of molars; the presence of t7 on upper molars is a feature shared only by few species, together with the presence of a massif posterior cingulum. Although *Spelaeomys florensis* has many more accessory cusplets than the Timor giant rat, the morphology of the main cusps is very similar. Timor is quite a near island, particularly if we consider the island range directly east of Flores. These islands, which during glacials were probably connected to Flores, have a shortest distance to Timor of about 20 km. Thus, a close phylogenetic relationship between Flores and Timor species is hardly surprising.

Since there is no fossil record of *Spelaeomys* predating the Liang Bua deposits, its arrival (or of its ancestors) on the island is unknown. The first occurrence at Liang Bua can be recorded at spit 46 of Sector IV, in the first part of Late Pleistocene. In sector IV it is scarce; on the contrary its abundance is far higher in sector VII (Late Glacial). The relatively high number of fossils found in Liang Toge suggests that the species was also more common in that area. Overall, this rare species is still enigmatic. A deeper analysis of skeletal and dentary features may provide more clues on the origin of this species.

Fig. 5 shows the changes in the relative distribution of the various murids in Sector IV. Sample sizes between the various spits vary greatly, and are indeed very low for some of the spits. In order to reduce the effect of these low sample size, we have constructed a three point weighted average curve to illustrate the main trends. Spits below spit 57 yielded at the most only one murid fossil per spit, and have not been taken into account here.

4: weighted distribution of murids remains at Liang Bua Cave. On the vertical axes there are the spits; on the horizontal axis the relative abundance

The graph clearly shows the introduction of the commensals *Rattus exulans* (Locatelli et al., in prep. a) and *Rattus* sp. (= *R. rattus* or *R. argentiventer*; Locatelli et al., in prep. b). It also shows the two peaks of *Komodomys* in the lower and upper parts of the section, believed to represent relatively dry periods in the Late Pleistocene and Late Holocene, respectively.

The distribution of the three species of giant rat shows a remarkable curve. These large murids are present in the lower part of the section, where they constitute about 10 % of the entire murid assemblage. Around spit 37, there is a sharp increase in the number of giant rat fossils, with values varying between 50% and 90% up to spit 16. The rise in giant rodents is bracketed by C14 dating of spit 39 with calibrated ages of 10.7 and 11.0 ka on the one side, and calibrated C14 dating for spit 34 with calibrated ages of 9.2 and 9.8 ka (Roberts et al., 2009). Thus, the beginning of the peak closely coincides with the beginning of the Holocene. The drop in number of giant rats is bracketed by C14 dating from spit 17 (4.18 ka) and spit 15 (3.62 ka). This is not only the period in which there is a massive reorganisation of the murid assemblages, with the first introduction of commensals, but also a period in which the climate around the Indian Ocean became drier (Locatelli et al., in prep. b). Thus, two scenarios can be formulated for this change in distribution, climatic change or human intervention.

Westaway et al. (2009) used speleothem data to follow climate evolution between 49 ka and 5 ka, defining a series of stages. Their phase 6 (11 ka – 5 ka) is characterized by wet conditions and the return of moist forests. The rich environment would certainly have provided an ample food supply for the Flores Giant Rats. The acme in this large murids ends around the time that there are indications for a re-opening of the landscape. This may have had a negative effect on the resources for rodents on the island. Although the dating place the acme in a climatic period which would certainly have been favourable, we deem it unlikely, that this is directly responsible for the high number of giant murid remains in the cave. After all, an increase in resources would not only have been favourable to the large species, but also for the small and middle-sized endemics that dwelled the islands. Thus, it cannot explain a change in the relative abundance, and certainly not in which the majority of the fossils belongs to the largest species, as smaller species are usually more abundant in natural assemblages.

The same dating given above, also bracket two important events in the human colonization of Flores. The oldest remains of *Homo sapiens* have been found in the early Holocene layers of Liang Bua, whereas the first traces of Neolithic man are found around spit 15. Therefore, the acme in giant rats coincides with the presence of a culture of hunter/gatherers on the island. At the time of arrival of *Homo sapiens*, the stegodon had already become extinct (van den Bergh et al., 2009). In other words, *Papagomys armandvillei* was at the time the largest mammal on the island. Assuming human nature has not basically changed since the Palaeolithic, it would be logical that the new inhabitants went for the big prey first. This may account for the initial peak in *Papagomys armandvillei* remains. As this would put a certain stress on the local population, the humans at a

certain point had to do with the much smaller *P. theodorverhoeveni*. The scenario of human influence would also account for the unnatural size distribution in the Liang Bua taphanocoenosis, which in part can be explained as the dinner remains. Careful analysis of the postcranial remains of the giant rats in this period is needed to confirm this hypothesis.

***Papagomys*, *Spelaeomys* and the Island Rule**

As we noted in our introduction, *Papagomys armandvillei* was specifically mentioned by Meiri et al. (2008) in their paper arguing against the generality of the Island Rule. The Flores Giant Rat is certainly a prime example of a giant insular form, and as we have seen above, it is only one out of three examples from Flores alone, if we also take the fossil record into account. This makes at first sight the conclusion by Meiri et al. (2008) that gigantism among rodents is not a general rule very surprising. Instead, these authors conclude that the island rule is clade related. Admittedly, murids are one of these clades in which they found a tendency to enlarged size on islands. But the size-increase they found was minor, when compared to the increase necessary to evolve into a giant rat. Thus, there seems to be a gap between palaeontologists, who embrace the Island Rule as a main mechanism behind the peculiar mammals found in islands, and neontologists, who in part doubt the general tendency predicted by the rule.

Mostly, however, this discussion is semantical, as different scholars work on different scales. The study of Meiri et al. (2008) is based on comparison of conspecific individuals on the island and the mainland. As such, they record only the initial stage of size increase. Though *Papagomys* is mentioned, endemic taxa like the Flores Giant Rat are not used in the analyses. In contrast, palaeontologists recognize mainly the end members of insular evolution. And there are the giant forms among the micromammals, which have received the most attention over the years.

So are *Papagomys* and *Spelaeomys* proving that the Island Rule cannot be broken? In combination with other insular giant rodents, they certainly show that gigantism is a very common phenomenon. However, we have to bear in mind, that not all murids on Flores attained giant size. *Paulamys* and *Komodomys* are presumably of similar size as their mainland ancestor, and should *Rattus hainaldi* be proven to be part of the same clade, we would even have to assume a size decrease for that lineage. We strongly agree with Lomolino (2005), who stated that the “The island rule remains a very general pattern – in one sense a relatively complex combination of patterns across a range of spatial and temporal scales, but in another sense relatively simple in that the emergent pattern results from predictable differences in selective pressures among species of different size, and from a tendency for convergence toward phenotypes that seem optimal for particular bau plans and ecological strategies” Thus, we cannot claim that *Papagomys* and *Spelaeomys* form prove of the island rule. They are merely examples, which need to be assessed in a larger context. At the same time we note that examples such as these should be taken into account when discussing the generality of the

island rule, and that the study of Meiri et al. (2008) is in this respect too limited for definitive conclusions.

Conclusion

Large sized murids recovered at Liang Bua Cave (Flores, Indonesia) could be assigned to at least three different species, all endemic to Flores: *Papagomys armandvillei*, *P. verhoeveni* and *Spelaeomys florensis*. Only the former is still living, while the other ones got extinct in recent times. While *Papagomys* species are similar to the Middle Pleistocene rat that lived on Flores (*Hooijeromys nusatenggara*) and to ones of middle size murids (*Komodomys rintjanus* and *Paulamys naso*), *Spelaeomys naso* denotes a different origin. The three large species are clear examples of insular gigantism, which is a well-known phenomenon in island rodents.

The relative abundance of giant rats increases abruptly during Holocene; this event could be related to a better adaptation of these species to wetter environments, but considering the recent extinction of the only large mammal present on the island and the lack in the increase of the relative abundance of the other species, this interpretation sounds unlikely. On the other hand, since giant rats are also still eaten nowadays, they could have become an important element in the diet of “the new arrival”, *Homo sapiens*. In order to confirm this interpretation, an analysis of cutmarks on the postcranial bones is necessary; nevertheless, the presence of burnt mandibles strengthens further this hypothesis.

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