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Pleistocene survivors and Holocene extinctions: The giant rats from Liang Bua (Flores, Indonesia)

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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.

1. Introduction

Giant rodents, together with dwarf elephants, have always been considered one of the first and main products of insularism. When Foster wrote the paper considered one of the manifestos of the Island Rule, giant rodents were already feeding the scientific debate, so much so 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*".

Ever since Foster made this observation, the presumed tendency of small mammals to attain large size on islands (and the tendency of insular dwarfing in large mammals) has been hotly debated (e.g., Van Valen, 1973; Case, 1978; Heaney, 1978; Lomolino, 1985, 2005; Köhler et al., 2008; Meiri et al., 2008; Lomolino et al., 2011). The Indonesian island of Flores is nowadays 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 both *Papagomys armandvillei*, the giant rat of Flores, and the dwarfed insular hominin of the island, *Homo floresiensis*. The latter is, of course, 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 of a fauna in which the typical characteristics of island evolution are clearly present (Van den 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 and Freudenthal, 1985), giant hamster (Freudenthal, 1985) and giant gymnure (Butler, 1980).

Giant rats living on islands today can be seen as survivors of the endemic Pleistocene faunas. The arrival of humans has had profound effects on insular faunas all over the world, leading to many extinctions, including giant insular murids. *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 was actually reported to be still living (Suyanto and Watts, 2002), but Zijlstra et al. (2008) demonstrated this was

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based on a misidentification. However, the possibility that a second species of *Papagomys* is still present on Flores cannot be excluded. *Paulamys naso*, after having been described from fossils, was later found to be still living on the island (Kitchener et al., 1991; Kitchener and Yani, 1998).

Although the fossil record of the insular endemics in Southeast Asia generally 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. Nevertheless, up to the turn of the century, the number of published fossil murid specimens from the island was only 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, material from the Late Pleistocene, dating back to 95 ka, is also available; 2) better records of the variation in the different species, including descriptions from the upper dentition, are available; 3) a detailed geochronology of the section in the Liang Bua cave is available (Roberts et al., 2009), allowing study of faunal changes in time; 4) carefully recorded archaeological finds from the section allow study of changes in fauna in relation to interferences by humans and their commensals. 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* from *P. theodorverhoeveni* in the vast fossil record from the cave. After providing detailed descriptions of the various species, the focus in this paper is on the changes in relative abundance of the giant rodents, to see how these relate to climate and/or human behaviour.

2. Material and methods

Liang Bua is a limestone cave in western Flores, about 13 km northwest of Ruteng, the Manggarai District capital (Fig. 1). It was discovered as an archaeological site in 1950 by Father Theodor Verhoeven, who, in 1965, carried out the first systematic excavation. Between 1978 and 1989, the National Centre for Archaeology in Djakarta excavated ten sectors within the cave focussing on the Holocene parts of the stratigraphy under the direction of Prof. R.P. Soejono. In 2001, a joint Indonesian–Australian team, led by Mike Morwood (University of Wollongong), extended the excavation to the Pleistocene. When this resulted in the discovery of an insular hominin, *H. floresiensis*, in Sector VII, the adjacent Sector XI was also dug out.

Table 1
Total number of remains per species; lower case = lower tooth; capital = upper tooth.

Number of identified teeth	m1	m2	m3	M1	M2	M3
Papagomys armandvillei	87	82	54	47	37	21
Papagomys theodorverhoeveni	88	82	57	56	29	24
Spelaeomys florensis	13	10	7	5	2	
Papagomys sp. Indet.		2				1
Total	188	176	118	108	68	46

The material in this paper encompasses the fossils from both the Soejono and Morwood excavations. The focus is on sector IV, the sector in which the faunal remains have been most extensively studied (Van den Bergh et al., 2009; Meijer et al., 2010), 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 wet sieving sediment from the excavations. A detailed stratigraphy of the various Liang Bua sectors was given by Westaway et al. (2009), and the geochronology of the cave is given in Roberts et al. (2009).

The studied sample includes 544 mandibular and maxillary remains of giant rats. Among them, 352 are lower remains and 172 are upper ones; 20 are incisor fragments. Molar sample sizes per species are reported in Table 1. The material is stored at the National Research and Development Centre for Archaeology in Djakarta.

The length and width of all molars have been measured, according to the method outlined in Fig. 2. Descriptive analysis has been performed on each measurement, using the Analysis Toolpak of Microsoft Office Excel.

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

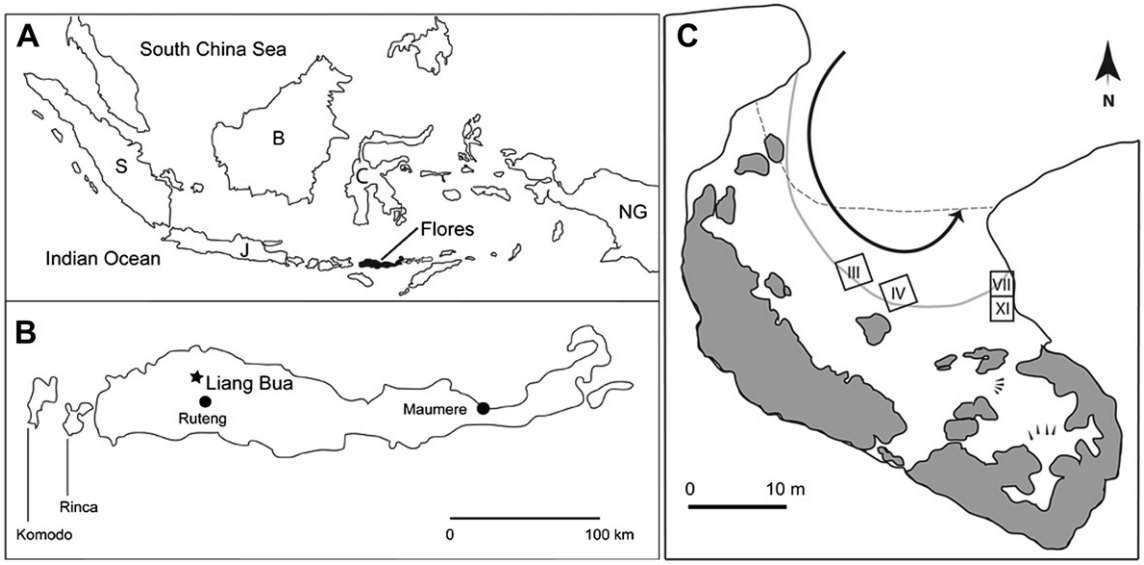

Fig. 1. Location map. A. Location of Flores. B. Location of Liang Bua. C. Map of Liang Bua cave.

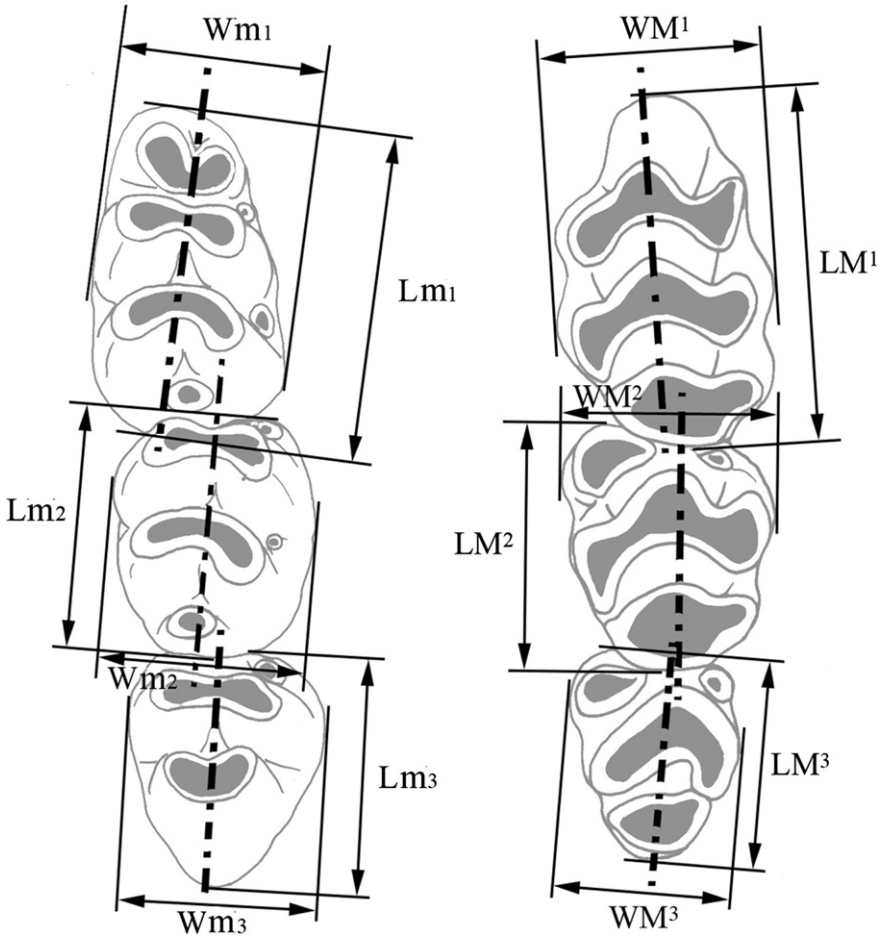

Fig. 2. Plan of measurements.

On lower tooth rows, PCA has been performed using PAST Software (Hammer et al., 2001). Multivariate analysis has been performed only on complete mandibular tooth rows. PCA has not been performed on upper tooth rows because of the low number of complete specimens (none of *S. florensis* and only 29 of *Papagomys*).

3. Systematic palaeontology

Class: Mammalia Linnaeus, 1758
Order: Rodentia Bowdich, 1821
Family: Muridae Illiger, 1811
Subfamily: Murinae Illiger, 1811
Genus: *Papagomys* Sody, 1941

3.1. P. armandvillei (Jentink, 1892) Fig. 3g–m

3.1.1. Synonymy

Mus armandvillei Jentink 1892.
Mallomys armandvillei Thomas 1898; Tate 1936.

3.1.2. Holotype

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

3.1.3. 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.

3.1.4. Morphological description

3.1.4.1. Upper tooth row. Molars robust; the widest molar is M1, but M2 can be as wide as M1; the last molar is the narrowest. All the cusps are high and slant distally, so that molars overlap in occlusal view: 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 anchored 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 similar to 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 in the direction of 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.

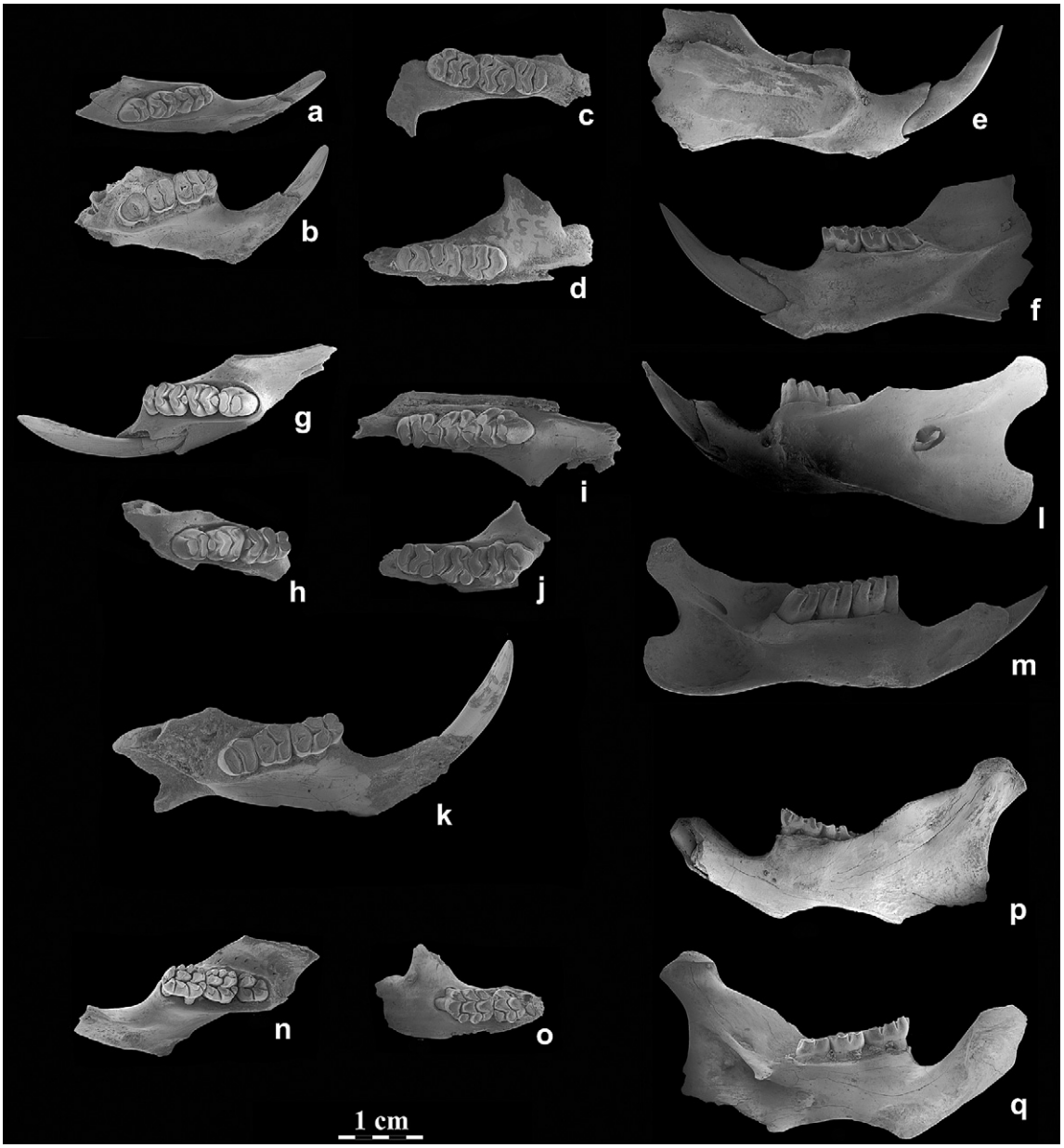

Fig. 3. SEM pictures of the remains. a–f – *Papagomys theodorverhoeveni*; a–b: lower tooth rows; c–d: upper tooth rows; e: mandible in labial view; f: mandible in lingual view. g–m – *Papagomys armandvillei*; g–i: lower tooth rows; j–k: upper tooth rows; l: mandible in labial view; m: mandible in lingual view. n–q – *Spelaeomys florensis*; n: lower tooth row; o: upper tooth row; p: mandible in labial view; q: mandible in lingual view.

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 tooth row. 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.

3.1.4.2. 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. As a-ling is slightly bigger than a-lab, the lamina appears 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 are also fused 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 the 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.

3.1.5. Measurements

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

3.2. *P. theodorverhoeveni* Musser, 1981 Fig. 3a–f

3.2.1. Holotype

Right dentary with m1–m3, RGM 195620, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis) from Liang Toge, Flores.

3.2.2. 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).

3.2.3. Morphological description

3.2.3.1. Upper tooth row. Robust relative to the maxillary bone; the widest molar is the M1, but the M2 can be as wide as the M1; the third molar 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, mesial enamel 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 linguo-distal 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 is sometimes absent or very small; 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, formed by t4, t5 and t6 arranged in line, 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.

3.2.3.2. 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. As in *P. 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 about 20% of the specimens, a small anterocentral 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 about 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.

Table 2
Descriptive statistical analysis of *Papagomys armandvillei*.

Papagomys armandvillei	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

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 lobate; in some cases a small anterolabial cusp lies against the protoconid. The second lamina is oval.

3.2.4. Measurements

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

3.3. Differences between *P. armandvillei* and *P. theodorverhoeveni*

The striking difference between the two species of *Papagomys* is the size: *P. armandvillei* is larger. However, the size variation is gradational, and additional morphological differences are required for more robust species discrimination (Zijlstra et al., 2008).

On the basis of Liang Toge material, Musser (1981) defined morphological differences between *P. theodorverhoeveni* and *P. armandvillei*. Nevertheless, as often happens in palaeontology, because of the limited number of specimens retrieved, some differences appeared to represent only local variations in the sample considered. Zijlstra et al. (2008) made an accurate analysis of some mandibular characteristics that were considered diagnostic by Musser (1981). In particular, they focused on the frequencies of presence/absence of cusps and subsidiary cusplets on molars at different stages of wear. Although these characters proved to be variable, some of these cusplets seem to be clearly more frequently present in one species, whereas others showed similar frequencies in both taxa. In contrast to the diagnosis of Musser (1981), the presence of an anterocentral cusp in m1 is not diagnostic, with only 10% of difference in frequencies between the species. The anterior lingual cusplet on m1 and anterolabial cusp on m2 show a far larger difference in the frequencies (around 50%, being more frequently present in *P. 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 though 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

3.4. *S. florensis* Hooijer, 1957 Fig. 3n–q

3.4.1. Holotype

RGM 629580, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis) from Liang Toge, Flores.

3.4.2. Distribution

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

3.4.3. Morphological description

3.4.3.1. Upper tooth row. Teeth pattern is much elaborated, with developed subsidiary cusps and cusplets and a complicated arrangement of main cusps. M1 is the larger tooth. In the Liang Bua fossil material, no M3 has been recovered.

M1: 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 from each other; with wear, distal cusps merge together before mesial ones. A small posterior cingulum is present.

M2: 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.

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

m1: The molar is anchored by three roots (a 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 a 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 resembles 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 wear stages; 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:

Table 3
Descriptive statistical analysis of *Papagomys theodorverhoeveni*.

Papagomys theodorverhoeveni	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

metaconid, protoconid, entoconid and hypoconid. Beside the anterolabial cusp, which is semicircular, there are two tiny cylindrical mesial cusplets.

3.4.4. Measurements

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

4. Results

Scatter plots for the lower and upper molars of the various species of giant rats are shown in Fig. 4. These scatter plots show the size difference between *P. armandvillei* and *P. theodorverhoeveni*. The *r*- and *p*-values have been calculated for the two species separately. The notably high *p*-value for the M2 of *P. armandvillei* is mainly the result of one outlier, presumably a very young individual. Omitting this point lowers the *p* to 0.026.

The overlap between the *P. theodorverhoeveni* and *P. armandvillei* is small, and notably, the two species represent a near continuum, giving *Papagomys* as a genus a wide size range. *Spelaeomys* has a completely different morphology, which suggests a different niche than either *Papagomys* species. It is somewhat remarkable that in size it has a position exactly intermediate between the two species of that genus. The consistently higher *p*-values for *S. florensis* can be explained by the much lower sample sizes for this species.

The results of a PCA based on the length and width of the different elements in complete tooth rows are reported in Tables 5 and 6 and Fig. 5. The first axis, explaining 89.53% of the total variation, has equal negative loadings for all measurements. Given the strong correlation between its components, axis 1 is mainly related to size, with the largest specimens having the largest negative values. As in the scatter diagrams, the two species of *Papagamys* are separated with *Spelaeomys* holding a central position. The high correlation between variables also suggests that the proportions within the tooth row are similar for the giant rats. Though certainly true for *Papagomys*, the molars of *Spelaeomys* do have a different outline c.q. L/W ratio. Given the low number of complete tooth rows of *Spelaeomys*, these differences did not have a large influence on the PCA. The second axis, explaining 5.08% of the variation, does not give a separation for the different species, but notably all *Spelaeomys* mandibles hold positive values on this axis, which is mainly based on the length of the m3 and width of the m1.

5. Discussion

The giant rat fossil remains of *P. armandvillei*, *P. theodorver hoeveni* and *S. florensis* from Liang Bua cave represent the oldest fossil record 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, it must be assumed that they had already dwelled on 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. At this time, the faunal composition of the assemblages changed, but not by very much, considering that more than half million years had 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 *H. nusatenggara* (Musser, 1981). It was a large-sized rat, larger than *P. naso* and *Komodomys rintjanus*, but smaller than the true giant forms *P. armandvillei*, *Papagomys verhoeveni* and *S. 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 known remains. 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 an even greater resemblance to those of *Papagomys*. Musser (1981) placed *H. 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. The scanty evidence therefore 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 *P. 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 by a morphological study by Musser and Newcomb (1983). In the analyses, *Papagomys* turned out to be in the same clade as another Flores endemic, *K. rintjanus*. Unfortunately, the other two endemics, *Paulamys* and *Rattus hainaldi* were not included in the study.

Within the Flores murids, *S. florensis* is clearly the odd one out because of its peculiar morphology. Although all the other native rodents (with the exception of the shrew rat) seem to belong to the same clade and to be more related to each other than to any other species outside Flores (Musser, 1981), *S. florensis* displays more similarities with murids from New Guinea and nearby Timor. From the latter, Quaternary remains of *C. 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 massive posterior cingulum. Although *S. florensis* has many more accessory cusplets than the Timor giant rat, the morphology of the main cusps is very

Table 4
Descriptive statistical analysis of *Spelaeomys florensis*.

Spelaeomys florensis	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	LM1	WM1	LM2	WM2
Mean	5.72	4.12	4.37	4.17	4.08	3.59	627	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

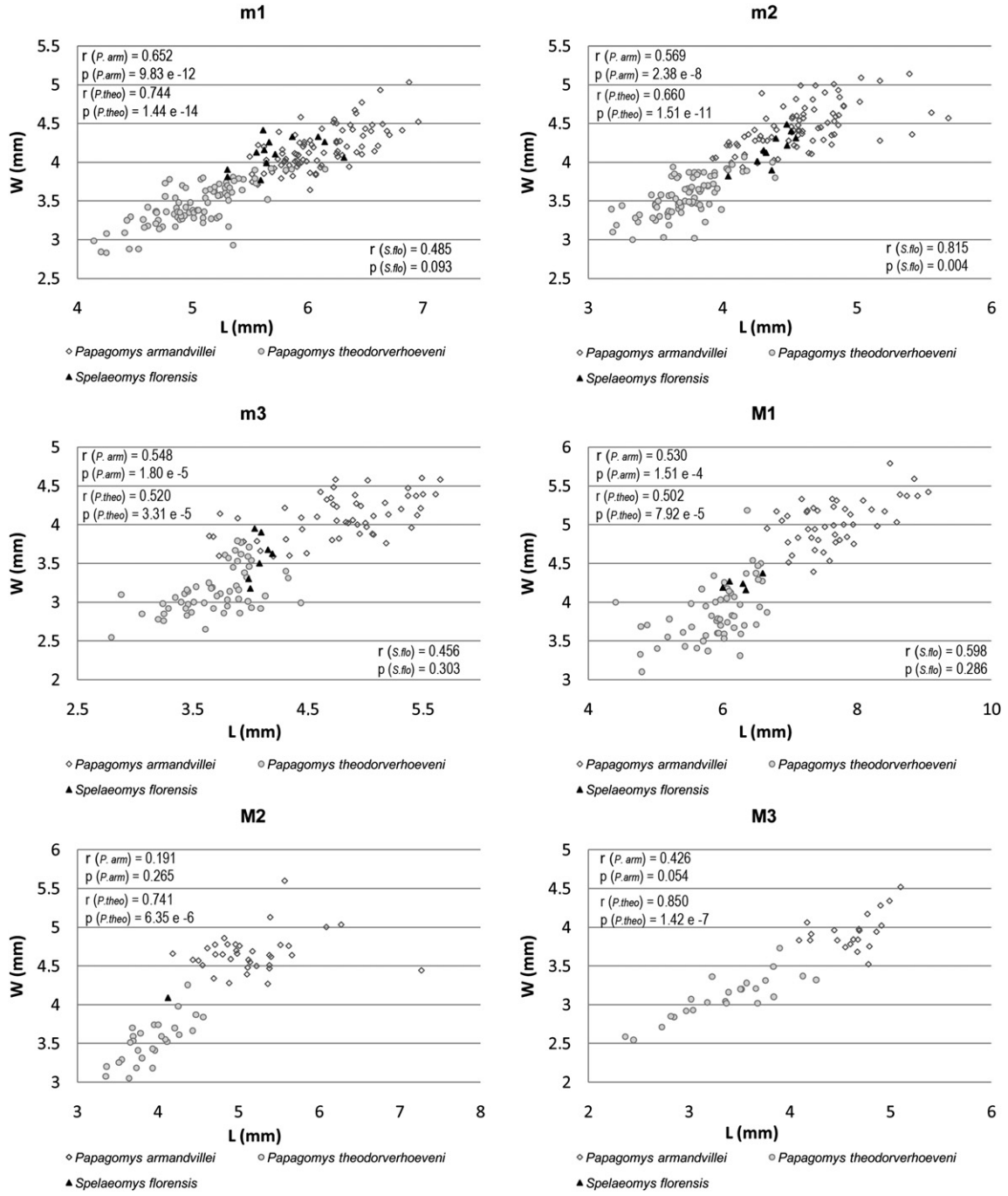

Fig. 4. Scatter plots of molar measurements.

similar. Timor is quite close to Flores, particularly considering the island chain 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.

As there is no fossil record of *Spelaeomys* predating the Liang Bua deposits, its arrival (or that 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 early Late Pleistocene. In sector IV it is scarce; on the other hand, its abundance is 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. 6 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, a three point weighted average curve was constructed 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.

The graph clearly shows the introduction of the commensals *Rattus exulans* and *Rattus* sp. (=*Rattus rattus* or *Rattus argentiventer*). 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.

Table 5
Eigenvalues and Variation of PCA applied to large murids from Liang Bua.

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

Table 6
Eigenfactors of PCA.

	Axis 1	Axis 2
Lm1	−0.4113	0.1526
Wm1	−0.41	0.4018
Lm2	−0.4149	−0.1921
Wm2	−0.4193	0.2647
Lm3	−0.3801	−0.8303
Wm3	−0.4125	0.1376

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 20–30% 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. 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 for large murids ends at a time when 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 places the acme in a climatic period which would certainly have been favourable, it is unlikely that this is directly responsible for the high number of giant murid remains in the cave. An increase in resources would not only have been favourable to the large species, but also to the small and middle-sized endemics that dwelled on the islands. It cannot therefore explain a change in the relative abundance. Furthermore, it is peculiar to have the majority of the fossils belonging to the largest species, as smaller species are usually more abundant in natural assemblages.

The same dating also brackets 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 *H. sapiens*, *Stegodon* had already become extinct (Van den Bergh et al., 2009). Therefore, *P. armandvillei* was at the time the largest mammal (besides humans) on the island. Assuming human nature has not basically changed since the Palaeolithic, it would be logical that the new inhabitants went for the biggest prey first. This may account for the initial peak in *P. armandvillei* remains. As this would put a certain stress on the local population of *P. armandvillei*, the humans would have turned to the much smaller *P. theodorverhoeveni*. The scenario of human influence would also account for the unnatural size distribution in the Liang Bua taphocoenosis, which can in part be explained as resulting from food remains. Careful analysis of the postcranial remains of the giant rats in this period is needed to test this hypothesis.

5.1. *Papagomys, Spelaeomys and the island rule*

As noted in the introduction, *P. 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 discussed above, if the fossil record is taken into account it is only one of three examples from Flores alone. This seems in contradiction to the conclusion by Meiri et al. (2008) that gigantism among rodents is not a general rule. Instead, these authors conclude that the island

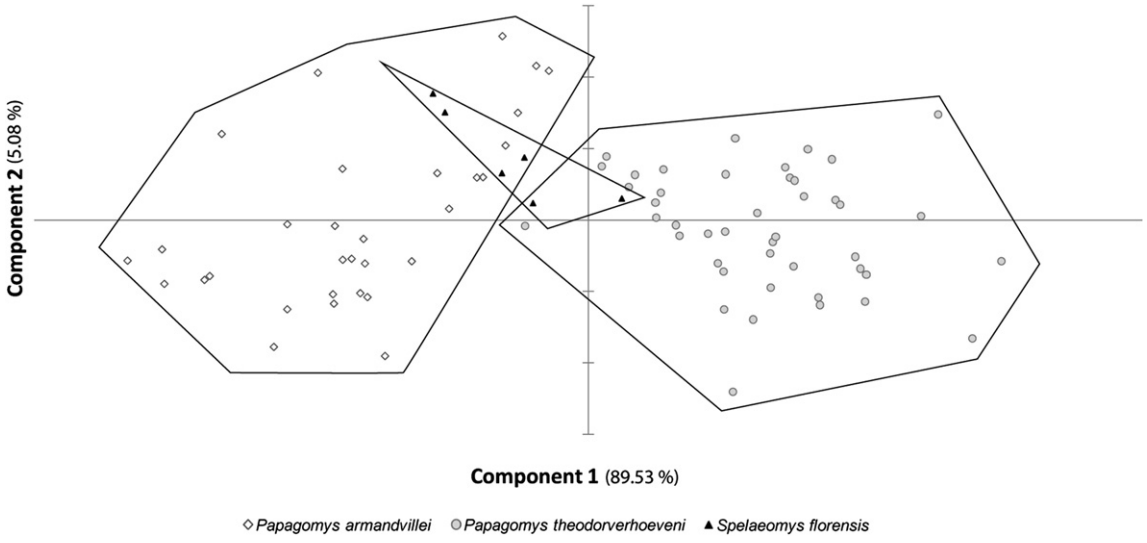

Fig. 5. PCA of large murids.

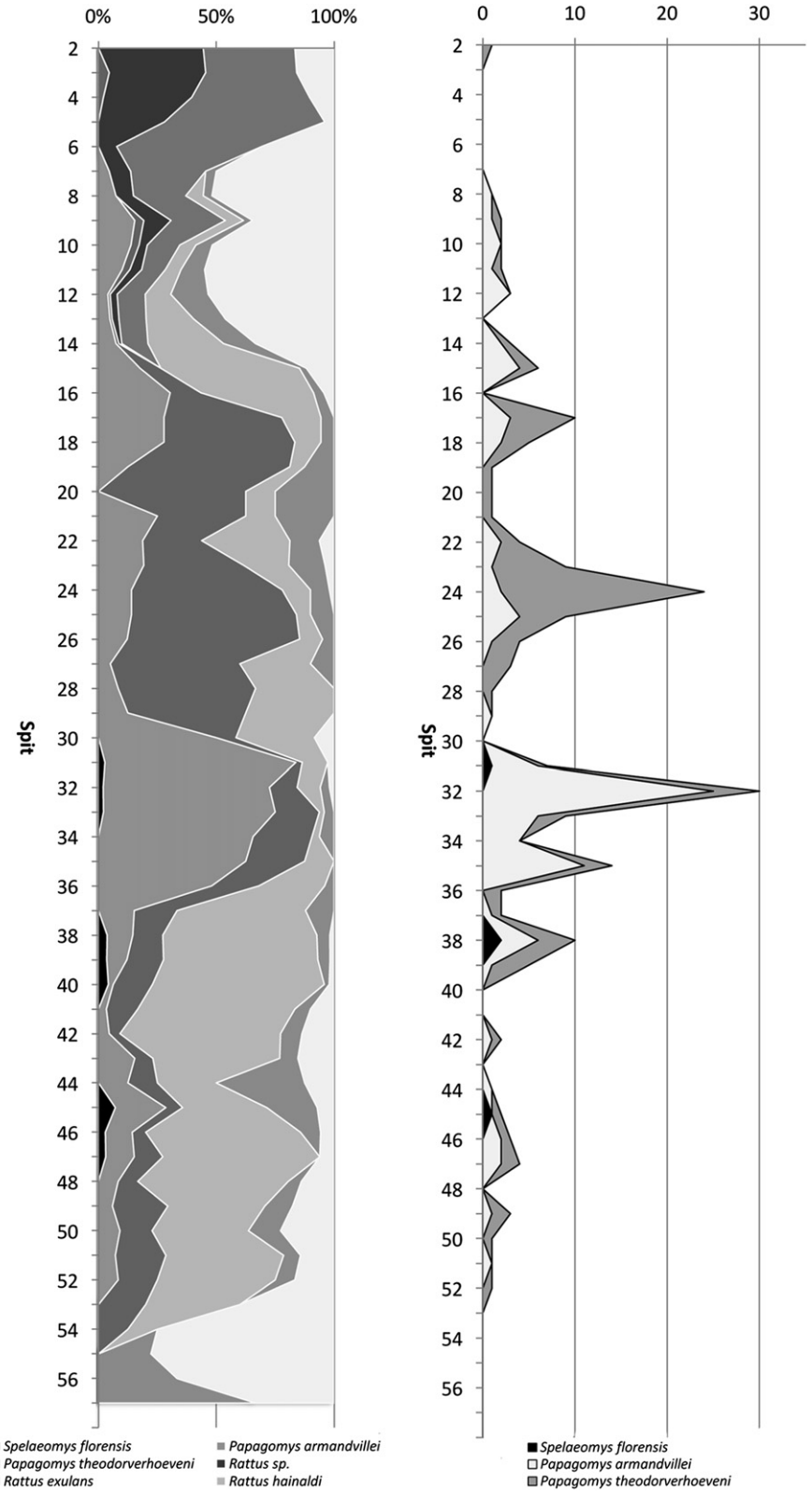

Fig. 6. Weighted distribution of murids remains at Liang Bua Cave. On the vertical axes are the spits; on the horizontal axis the relative abundance (left) and the number of remains (right).

rule is clade related. Admittedly, murids are one of these clades in which they found a tendency to become larger on islands. However, the size-increase they found was minor, when compared to the increase necessary to evolve into a giant rat. Most island taxa included in Meiri's et al. study originate from continental islands that had been connected to mainland areas during the last glacial maximum, and one could argue that size changes have not yet fully reached their maximum potential. Thus, there seems to be

a conceptual difference 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 semantic, as different scholars work on different scales. The study of Meiri et al. (2008) is based on a comparison of individuals on islands with conspecifics from 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. These are the giant forms among the micromammals, which have received the most attention over the years.

So, do *Papagomys* and *Spelaeomys* prove 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, not all murids on Flores attained giant size. *Paulamys* and *Komodomys* are presumably of a size similar to that of their mainland ancestor, and should *R. hainaldi* be proven to be part of the same clade, a size decrease would be assumed for that lineage. The authors strongly agree with Lomolino (2005, page 1696), 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, it cannot be claimed that *Papagomys* and *Spelaeomys* prove the island rule. They are merely examples, which need to be assessed in a larger context. At the same time, 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.

6. Conclusion

Large-sized murids recovered at Liang Bua Cave (Flores, Indonesia) could be assigned to at least three different species, all endemic to Flores: *P. armandvillei*, *P. verhoeveni* and *S. florensis*. Only the former is still extant, while the other ones became extinct in recent times. While *Papagomys* species are similar to the Middle Pleistocene rat that lived on Flores (*H. nusatenggara*) and presumably related to the endemic middle size murids (*K. rintjanus* and *P. 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 the Holocene. This event could be related to a better adaptation of these species to wetter environments, but given the recent extinction of the only large mammal present on the island (*S. florensis insularis*) and the lack of increase in the relative abundance of other species (middle and small sized murids), this interpretation sounds unlikely. On the other hand, they could have become an important element in the diet of "the new arrival", *H. sapiens*, since giant rats are still eaten today. In order to test this interpretation, an analysis of cutmarks on the postcranial bones is required. Nevertheless, the presence of burnt mandibles further strengthens this hypothesis.

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