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THREE NEW GIANT PREHISTORIC RATS FROM FLORES LESSER SUNDA ISLANDS

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With pls. XIV—XV

The specimens described in the present paper have been collected by Dr. Th. L. Verhoeven at Liang Toge, a cave near Warukia, 1 km south of a hamlet called Lepa, in Manggarai, western Flores. This cave, as well as many others explored in the island by Verhoeven (1952, 1953), contains a Mesolithic flake and blade industry (Van Heekeren, 1957, p. 107). The faunal remains obtained from Liang Toge consist almost exclusively of jaws and bones of large rats, and it is of interest to place these specimens on record as they represent forms that are new to science, different from the one and only giant rat that is still living on Flores, *Papagomys armandvillei* Jentink).

The discovery of new giant rats in a comparatively recent cave deposit such as that of Liang Toge in Flores, which is definitely post-Pleistocene, is not very surprising. The Lesser Sunda Islands are almost a blank as far as prehistoric mammals are concerned, and the first prehistoric fauna of this area to become known, viz., that of Timor, likewise in a Mesolithic context (Sarasin, 1935), proved to contain a distinct genus and species of giant rat, *Coryphomys bühleri* Schaub (1937). Like the living *Papagomys armandvillei* of Flores, the subfossil Timor form belongs to the Muridae with complexly folded molars, subfamily Phloeomyinae (see Simpson, 1945, p. 91). This group, the member genera of which exist for the most part high in the mountains of the remoter islands of the Malay Archipelago, presents the appearance of a relict fauna (Tate, 1936, p. 505). As in other murid groups extending into the area east of Wallace's Line, a physiological shift in the direction of giantism is apparent (Tate, l.c., p. 612). Simpson (1945, p. 208) holds the center of murid evolution to have been in the tropical and largely insular regions of the Old World, adding "that the family really is of relatively recent origin and differentiation and, if it existed at all as yet, was highly localized and not abundant until the Pliocene". The finds reported upon in the present paper tend to show that in early post-Pleistocene times there was a richer murid fauna in the Lesser Sunda Islands area than there is at present.

Part of the material collected by Dr. Verhoeven at Liang Toge originates from the deepest layer; these specimens are marked as such in each case. The remainder of the collection was made without regard to the stratification of the cave deposit. All specimens had to be treated with acetic acid in order to remove the matrix from even the tiniest folds of the teeth.

Before passing on to the prehistoric cave rats it is necessary to say a few words about the recent endemic giant rat of Flores. "*Mus*" *armandvillei* Jentink (1892, p. 79, pl. V figs. 1-7) has been held to belong to *Mallomys* Thomas (1898a, p. 2; see also Mertens, 1936, p. 311, and Tate, 1936, p. 635), but has been raised to distinct generic rank, *Papagomys,* by Sody (1941, p. 322). The distinguishing characters given by Sody are aptly taken. Unlike *Mallomys, Papagomys armandvillei* is *Rattus*-like in the configuration of the skull, lacking the inflation and convexity of the anterior portions of the frontals, and the depression of the frontals between the ridges that are characteristic of *Mallomys.* Although the palate is narrowed both in *Papagomys* and *Mallomys* the difference is again marked in the molars.

In *Papagomys* the last molars, both above and below, present the tendency to form plain and straight transverse laminae, as in *Rattus*; the sharp anterior enamel infoldings between the median and lingual tubercles of the two lophs of M^3, and the deep posterior infoldings between the median and lingual tubercles of the two lophs of M_3 seen in *Mallomys* do not occur in *Papagomys.* The buccal tubercles related to lophs 1 and 2 of M^1, and to loph 1 of M^2 are less well separated from the median tubercles in *Papagomys* than in *Mallomys.* On the other hand, *Papagomys* possesses buccal tubercles in the form of extensions of the median tubercles of loph 3 of M^1 and of loph 2 of M^2; these extensions do not occur in *Mallomys.* The number of lingual tubercles (two to M^1, two to M^2, and three to M^3) is the same in both. In the lower jaw, M_1 and M_2 are much alike in *Papagomys* and *Mallomys,* forming lophs that are deeply notched in behind between the median and lingual tubercles. The anterior loph of M_1 consists of two imperfectly separated tubercles of which the lingual is the larger. There is a posterior tubercle in the notch of the last loph of M_1 and M_2 forming the "talonid". These poster'or tubercles are more developed in *Papagomys* than in *Mallomys.* Moreover, in *Papagomys* there are antero-buccal tubercles in M_2 and M_3 that do not show in *Mallomys*. The lower dentitions of the two genera are at once distinguished by the characters of M_3, which has simple, uncleft lophs in *Papagomys*, and distinctly bicuspid lophs in *Mallomys*, as already stated above.

Papagomys armandvillei besar nov. subsp.

Diagnosis: Teeth larger than those of recent *Papagomys armandvillei armandvillei* (Jentink) but identical in specific characters.

Holotype: The left mandibular ramus with M_{1-3} described and figured in the present paper (pl. XIV fig. 1).

Locality: Liang Toge near Warukia, Manggarai, western Flores.

Age: Early post-Pleistocene.

Name: Besar (Malay) means large.

In the Liang Toge collection there are various mandibular rami with the full complement of teeth, and a right M^{1-2}. These specimens agree with the holotype of *Papagomys armandvillei* (Jentink) in the Leiden Museum (cat. ost. a) in every detail of their structure. The two upper molars possess the critical buccal extensions of the median tubercles of the last lophs (loph 3 in M^1, loph 2 in M^2) by which they can be distinguished from their homologues in *Mallomys*. Of the lower jaw the following specimens are available: 1, left mandibular ramus with M_{1-3} (holotype, pl. XIV fig. 1); 2, right ramus with M_{1-3} (pl. XIV fig. 2); 3, right ramus with M_{1-3} (pl. XIV fig. 3); 4, left ramus with M_{1-3}; 5, right ramus with M_{1-3}; 6, left ramus with M_{1-2}; 7, left ramus with M_{1-2}; 8, left ramus with M_1; 9, right ramus with M_1. Of these rami, nos. 1-3 and 6 originate from the deepest layer of the cave deposit.

TABLE 1

Measurements of recent and subfossil teeth of
Papagomys armandvillei (in mm)

	recent	*Papagomys armandvillei besar*								
Length M^{1-2}	11.3	11.9								
Width of M^1	4.7	5.3								
Width of M^2	4.5	5.1								
No. of specimen		1	2	3	4	5	6	7	8	9
Length M_{1-3}	14.7	16.4	16.3	15.7	—	15.8	—	—	—	—
Width of M_1	4.1	4.6	4.8	4.4	4.2	4.4	4.1	4.3	4.2	4.2
Width of M_2	4.3	4.8	4.9	4.6	5.0	4.7	4.7	4.7	—	—
Width of M_3	4.2	4.6	4.7	4.5	4.7	4.6	—	—	—	—
Lower I, ant. post.	2.8	3.8	—	—	—	—	—	—	—	—
Idem, transverse	2.0	2.7	—	2.6	—	—	2.7	—	—	—

Nos. 1-3, figured on pl. XIV figs. 1-3 of the present paper, represent successive stages of wear: no. 1 is the least worn, and in no. 3 wear is most advanced. The antero-buccal tubercle of M_2 is shown by an enamel fold in no. 1 only; in the more advanced stages of wear it has fully merged with the first loph of M_2, which is much produced forward buccally. The antero-buccal tubercle of M_3 leaves a trace only in no. 1. The two tubercles forming the anterior loph of M_1 are still separated by a groove in no. 1; in nos. 2 and 3 they have become confluent. The posterior tubercles of $M_{1\text{-}2}$, relatively larger than those in *Mallomys*, are distinct in stages 1 and 2; in stage 3 these "talonids" are confluent with the hind lophs, the posterior notches of these lophs being shown by triangular enamel islets. The last molars (damaged antero-buccally in no. 2) show the simple undivided second loph characteristic of *Papagomys*. Very tiny buccal tubercles related to loph 2 of M_2, blocking the entrance to the valley between lophs 1 and 2, are seen in specimens 5 and 8; in the former there is also a tiny enamel point related to loph 3 of M_1, and placed at the buccal entrance to the valley between lophs 2 and 3. These accessory buccal tubercles do not show in the single recent specimen available for comparison.

The difference in size between the recent and the cave teeth will be seen from table 1. All the cave specimens present dimensions larger than the recent, and evidently belonged to individuals that exceed the recent in size. This is quite in harmony with the general rule that subfossil and fossil remains of recent species average larger than their recent homologues (Hooijer, 1949, 1950). I have no doubt that *Papagomys armandvillei besar* nov. subsp. should be regarded as directly ancestral to the living *Papagomys armandvillei armandvillei* (Jentink). The amount of time that has elapsed since the deposition of the remains in the cave deposit has been sufficient for a subspecific differentiation to have taken place.

There is a second species of *Papagomys* in the Liang Toge collection that differs from the living form in its lesser size as well as in various structural characters, as follows:

Papagomys verhoeveni nov. spec.

Diagnosis: Smaller in size than *Papagomys armandvillei* (Jentink), but agreeing in dental characters except in the following particulars: buccal tubercles related to loph 3 of M_1 and to loph 2 of M_2 always present; buccal tubercles related to lophs 2 and 1 of M_1 developed in the great majority of the specimens. Anterior fold of loph 1 of M_1 of greater relative depth than that in *P. armandvillei*. M_3 narrower in relation to $M_{1\text{-}2}$ than in *P. armand-villei*.

Holotype: The right maxillary with $M^{1\text{-}3}$ described and figured in the present paper (pl. XIV fig. 4).

Locality: Liang Toge near Warukia, Manggarai, western Flores.

Age: Early post-Pleistocene.

Name: I have named this species after its discoverer, Dr. Th. L. Verhoeven.

The present species is twice as abundant in the cave collection as is the larger *Papagomys armandvillei besar* nov. subsp. There are eighteen mandibular rami and one entire upper dentition, from the right side and perfectly preserved (pl. XIV fig. 4). It is smaller than *Papagomys armandvillei*; the length M^{1-3} is 14.2 mm as opposed to 15.4 mm on the right, and 15.6 mm on the left side of the holotype of *P. armandvillei* in the Leiden Museum, and 15.0-16.1 mm in three specimens of the same species in the Bogor Museum recorded by Sody (1941, p. 322). Structurally, the subfossil upper molars closely resemble recent *Papagomys*: there are buccal extensions to the median tubercles of the last lophs of M^1 and M^2; the lophs of M^3 are not cut into in front between the median and lingual tubercles, and the buccal tubercles of lophs 1 and 2 of M^1 and of loph 1 of M^2 are less well separated from the median tubercles than are the lingual. In all these points the subfossil specimen differs from *Mallomys* as well as recent *Papagomys armandvillei* does. The two lingual tubercles of M^1 are related to lophs 1 and 2. Of the two lingual tubercles of M^2 the first is anterior to loph 1, the second is related to loph 1. In M^3 the first lingual tubercle is anterior to loph 1, the second and third relate to lophs 1 and 2. This condition obtains both in *Papagomys* and in *Mallomys*, but in the latter the lingual tubercles of M^3 are as well separated from the median tubercles as are those of M^{1-2}, whereas in *Papagomys* they are not. In other gigantic rats the numbers of lingual tubercles to the upper molars are different, as related further on in the present paper.

It is not without interest to note that in *Rattus* we find the same numbers of buccal and lingual tubercles in the same relation to the lophs of the upper molars as in *Papagomys*. The lophs in *Rattus* molars, however, are less high and less angular, more simply built than those in *Papagomys*. The first loph of M^3 in *Rattus* is curved backward buccally, and soon merges with the second loph so as to close off the buccal entrance to the main transverse valley of M^3 (occasionally the valley between lophs 1 and 2 of M^3 becomes isolated lingually earlier than buccally, as seen in a specimen of *Rattus whiteheadi* (Thomas) figured by Tate, 1936, p. 569 fig. 15B). Moreover, none of the species of *Rattus* attains the size of *Papagomys*: the largest *Rattus* species in existence belong to the *edwardsi-sabanus* group (Tate, 1936, p. 575; Ellerman, 1941, p. 53), and their length M^{1-3} is only about 10 mm at most.

Therefore, the upper dentition just described, and figured on pl. XIV fig. 4, belongs to *Papagomys*. The lower dentition of the present species is represented by the following specimens: 1, left mandibular ramus with $M_{1\text{-}3}$ (pl. XV fig. 1); 2, left ramus with $M_{1\text{-}3}$ (pl. XV fig. 2); 3, right ramus with $M_{1\text{-}3}$ (pl. XV fig. 3); 4, right ramus with $M_{1\text{-}3}$; 5, left ramus with $M_{1\text{-}3}$ (first loph of M_1 incomplete); 6, right ramus with $M_{1\text{-}3}$ (M_3 incomplete antero-buccally); 7, left ramus with M_1 and M_3; 8, left ramus with $M_{1\text{-}2}$; 9, left ramus with M_1; 10, left M_1; 11, left ramus with $M_{1\text{-}3}$; 12, right ramus with $M_{1\text{-}3}$; 13, right ramus with $M_{1\text{-}3}$ (slightly damaged buccally); 14, right ramus with $M_{1\text{-}3}$ (M_3 incomplete antero-lingually); 15, left ramus with $M_{1\text{-}2}$; 16, right ramus with $M_{1\text{-}3}$ (much worn down, $M_{2\text{-}3}$ incomplete lingually); 17, left ramus with M_1; 18, right ramus with M_1. Of this series, nos. 1-10 are from the deepest layer of the cave deposit, as is also the upper dentition of pl. XIV fig. 4. The measurements are presented in table 2.

TABLE 2

Measurements of teeth of *Papagomys armandvillei* (recent) and of *Papagomys verhoeveni* nov. spec. (in mm)

	recent	*Papagomys verhoeveni*						
Length $M^{1\text{-}3}$	15.0-16.1		14.2					
Width of M^1	4.7		4.6					
Width of M^2	4.5		4.4					
Width of M^3	3.9		3.8					
No. of specimen		1	2	3	4	5	6	7
Length $M_{1\text{-}3}$	14.7	13.2	13.9	13.7	13.8	—	14.2	—
Width of M_1	4.1	3.7	4.1	3.9	3.9	4.0	4.0	3.7
Width of M_2	4.3	4.0	4.2	4.0	4.0	4.2	4.1	—
Width of M_3	4.2	3.5	3.7	3.8	3.7	3.7	—	3.3
Lower I, ant. post.	2.8	3.1	—	—	—	—	—	—
Idem, transverse	2.0	2.0	—	2.1	2.2	2.0	—	—
No. of specimen		8	9	10	11	12	13	14
Length $M_{1\text{-}3}$		—	—	—	13.2	13.2	14.0	12.5
Width of M_1		3.9	4.2	3.8	3.8	3.8	3.9	3.6
Width of M_2		4.0	—	—	3.9	4.0	4.0	3.7
Width of M_3		—	—	—	3.4	3.7	3.7	—
Lower I, ant. post		—	—	—	—	—	3.2	—
Idem, transverse		—	—	—	2.1	—	2.2	—
No. of specimen		15	16	17	18			
Length $M_{1\text{-}3}$		—	—	—	—			
Width of M_1		3.7	3.7	3.9	4.1			
Width of M_2		3.9	—	—	—			
Width of M_3		—	—	—	—			
Lower I, ant. post.		3.2	—	—	—			
Idem, transverse		2.0	—	—	—			

Nos. 1-3, figured in pl. XV figs. 1-3 of the present paper, illustrate successive stages of wear of the lower dentition. The best developed buccal tubercles are those related to loph 1 of M_2 and M_3; these antero-buccal tubercles also show in the larger *Papagomys armandvillei*. In *Papagomys verhoeveni* there are also buccal tubercles related to loph 3 of M_1 and to loph 2 of M_2; these form the main distinguishing character of the present species, as they develop only very exceptionally in *P. armandvillei*. The tubercles in question are entire in no. 1, worn to enamel rings in no. 2, and confluent with the last lophs of M_1 and M_2, though still showing as looped folds, in no. 3. They are present in all of the specimens of *Papagomys verhoeveni* listed above; it is only in the most worn dentitions (nos. 14 and 16) that they can hardly be recognized.

Next in importance is a buccal tubercle that is related to loph 2 of M_1; it is almost invariably present (lacking only in nos. 9 and 18), and is always smaller than that related to loph 3 of M_1. It is less well separated from the loph to which it belongs, and unites with the enamel margin of the loph earlier than does the tubercle related to loph 3, as shown in no. 2 (pl. XV fig. 2).

Finally, there is a third buccal tubercle that can be distinguished in the M_1 of *Papagomys verhoeveni*. It is very small, and placed in front of the median tubercle of loph 1. Usually it becomes confluent with this tubercle upon a slight amount of wear; in no. 2 (pl. XV fig. 2) it is still distinct, whereas in no. 3 (pl. XV fig. 3) it has merged with the median tubercle of loph 1 of M_1. The anterior buccal tubercle shows up in every specimen of M_1 of *P. verhoeveni* that is entire and not too much worn in front, with the exception only of no. 10.

Neither the buccal tubercle related to loph 2 nor that related to loph 1 of M_1 do occur in recent *Papagomys armandvillei*, and these tubercles do not show up in *P. armandvillei besar* nov. subsp. either.

The anterior groove of loph 1 of M_1, separating the median from the larger lingual tubercle, is more developed in *Papagomys verhoeveni* than in *P. armandvillei;* because of its greater relative depth it remains visible as an anterior enamel infolding in all but the most advanced stages of wear, whilst in *Papagomys armandvillei* this fold is soon worn off.

In possessing a greater number of buccal tubercles in its lower molars than does the larger *Papagomys armandvillei* (both recent and subfossil), *Papagomys verhoeveni* appears to represent a more primitive stage than does *P. armandvillei,* at least if we accept Ellerman's view that the more complex dental pattern is the primitive one. Ellerman (1941, p. 44) considers the "simple-toothed" *Rattus*-like murids to be specializations from "complex-toothed" types such as those described in the present paper. The opposite view is held by Tate (1936, p. 509), who assumes the teeth of *Rattus* to represent the archaic murid tooth form.

In table 3 are presented the ranges of variation and the means of the dimensions of the lower teeth of the two cave forms of *Papagomys*; it is evident from these figures that the larger form has a relatively wider M_2 than has the smaller, while in *Papagomys verhoeveni* the last molar is more reduced in width as compared with $M_{1\text{-}2}$ than is the case in *Papagomys armandvillei.* The tendency to third molar reduction in the smaller, extinct, form of *Papagomys* more likely than not is a specialized trait of the present species.

TABLE 3

Ranges of variation and means of dimensions of lower teeth of *Papagomys* from Liang Toge

	Papagomys armandvillei besar		*Papagomys verhoeveni*	
	range	mean	range	mean
Length $M_{1\text{-}3}$	15.7-16.4	16.1	12.5-14.2	13.5
Width of M_1	4.1-4.8	4.4	3.6-4.2	3.9
Width of M_2	4.6-5.0	4.8	3.7-4.2	4.0
Width of M_3	4.5-4.7	4.6	3.3-3.8	3.6
Lower I, ant. post.	3.8	3.8	3.1-3.2	3.2
Idem, transverse	2.6-2.7	2.7	2.0-2.2	2.1

The giant rat occurring most abundantly in the Liang Toge collection is an extremely complex-toothed form representing a new genus, the diagnosis of which is presented below.

Spelaeomys nov. gen.

Diagnosis: A genus of phloeomyine murids characterized by the large numbers of buccal and lingual tubercles to the molars, the upper molars having the following numbers of tubercles; buccal 4 - 4 - 2, lingual 4 - 3 - 3; the lower molars: buccal 4 - 4 - 2, lingual 5 - 3 - 2. Lophs of M^3 notched in front, those of M_3 notched in behind. M^3 consists of two lophs and a single talon, M_3 has two lophs without a talonid.

Genotype: *Spelaeomys florensis* nov. spec.

Spelaeomys florensis nov. spec.

Diagnosis: A species of *Spelaeomys* intermediate in size between *Mallomys rothschildi* Thomas and *Lenomys meyeri* (Jentink).

Holotype: The right maxillary with $M^{1\text{-}3}$ described and figured in the present paper (pl. XIV fig. 5).

Locality: Liang Toge near Warukia, Manggarai, western Flores.

Age: Early post-Pleistocene.

The M^{1-3} dext. hereby designed as the holotype of *Spelaeomys florensis* is only slightly worn. The left M^{1-3} represented on pl. XIV fig. 6 is moderately worn, and, like the type, originates from the deepest layer of Liang Toge. The pattern of the two series of upper molars is so similar that they may be described together.

Of the buccal tubercles, there are four in M^1 and M^2 , and two in M^3. Those of M^1 are each related to one of the three lophs, while the fourth is merely a postero-external extension of the median tubercle of loph 3. In M^2 the first buccal tubercle stands anterior to loph 1, the second and third are related to lophs 1 and 2, while the fourth is an extension of the median tubercle of loph 2. Of the two buccal tubercles of M^3 the first stands anterior to loph 1, the second is an extension of the median tubercle of loph 1. The second loph of M^5 has no buccal tubercle, and neither has the talon.

On the lingual side there are four tubercles in M^1, three in M^2 and M^3. In M^1 the first and second lingual tubercles belong to loph 1, the third belongs to loph 2, and the fourth to loph 3. In M^2 the first lingual tubercle is anterior to loph 1, the second and third are related to lophs 1 and 2. The first lingual tubercle of M^3 is anterior to loph 1, the second and third relate to lophs 1 and 2.

The present cave specimens clearly belong to the "Muridae with complexly folded molars", the Phloeomyinae (see Tate, 1936, p. 612). As noted by Ellerman (1941, p. 292), this subfamily name is not appropriate, as *Phloeomys* has the molar lophs plain and straight, and is the most strictly simple-toothed form in the whole Indo-Malayan area, but Simpson (1945, pp. 91 and 208) adopts Tate's usage. Beside *Phloeomys* (which needs not concern us at present) the subfamily Phloeomyinae includes the genera *Mallomys, Lenomys, Crateromys, Pogonomys, Chiropodomys* (all recent; only *Lenomys* is also known in the subfossil state: Hooijer, 1950, p. 77, pl. III fig. 11), *Coryphomys* (known only in the subfossil state: Schaub, 1937), and, of course, *Papagomys* dealt with above. It is with all of these complex-toothed rats that I shall compare our new *Spelaeomys florensis* in the following pages. For the sake of convenience the numbers of buccal and lingual tubercles to the upper and lower molars of the complex-toothed phloeomyine rats are given in table 4.

It will be easy to see from the figures of the upper dentitions of *Papagomys* and *Spelaeomys* (pl. XIV figs. 4-6) that *Spelaeomys* differs from *Papagomys*. In the latter genus the buccal tubercles are only three in number in M^1 (the postero-external is absent), two in M^2 (the anterior and the postero-external missing), whereas the M^3 of *Papagomys* is much more simply built than that of *Spelaeomys,* consisting of two lophs that are not cut into in front, and without buccal tubercles at all. The lingual tubercles also are fewer in number in *Papagomys* than in *Spelaeomys,* viz., two in

TABLE 4

Numbers of buccal and lingual molar tubercles
in the genera of phloeomyine murids

	buccal tubercles								lingual tubercles							
	Spelaeomys	*Papagomys*	*Mallomys*	*Lenomys*	*Crateromys*	*Pogonomys*	*Chiropodomys*	*Coryphomys*	*Spelaeomys*	*Papagomys*	*Mallomys*	*Lenomys*	*Crateromys*	*Pogonomys*	*Chiropodomys*	*Coryphomys*
M^1	4	3	2	4	2	4	4	—	4	2	2	3	3	3	3	—
M^2	4	2	1	4	1	4	4	—	3	2	2	3	3	3	3	—
M^3	2	0	0	2	0	1	0	—	3	3	3	3	3	3	3	—
M_1	4	1-3	0	2	0	cingulum	cingulum	0	5	4	4	4	4	5	5	5
M_2	4	1-2	0	2	0	cingulum	cingulum	0	3	3	3	3	3	3	3	3
M_3	2	1	0	1	0	cingulum	cingulum	0	2	2	2	2	3	2	2	2

M^1 (only one relating to loph 1, one to loph 2, and none to loph 3), and two in M^2 (the tubercle anterior to loph 1 missing). In M^3 the number of lingual tubercles is three in both genera, but the median tubercle of the third loph (or talon) present in *Spelaeomys* is not developed in *Papagomys.*

In *Mallomys* (four skulls of *Mallomys rothschildi* Thomas in the Leiden Museum) the number of buccal tubercles to M^1 and M^2 is smaller than that in *Papagomys;* the M^3 of *Mallomys* resembles that of *Spelaeomys* in having anterior enamel infoldings between the median and lingual tubercles of lophs 1 and 2, although in the absence of buccal tubercles (there may be a trace of a buccal tubercle related to loph 1 in slightly worn specimens), and of a talon the M^3 of *Mallomys* differs from that of *Spelaeomys* just as much as does that of *Papagomys* .

In *Lenomys* (four skulls of *Lenomys meyeri* (Jentink), including the type, in the Leiden Museum) the number of buccal tubercles of M^1 and M^2 is the same as that in *Spelaeomys.* In M^3 of *Lenomys* there even are three buccal tubercles; the second loph has an external extension as marked as that of the first. However, the talon so clearly shown in M^3 of *Spelaeomys* is either absent or incipient in *Lenomys.* Further, the antero-lingual tubercle of M^1 seen in *Spelaeomys* does not occur in *Lenomys,* the number of lingual tubercles to M^1 thus being reduced to three.

In *Crateromys* (two skulls of *Crateromys schadenbergi* (Meyer) in the Leiden Museum) the buccal tubercles of the upper molars are almost entirely suppressed; a young specimen shows that lophs 1 and 2 of M^1, and loph 2 of M^2 only possess external extensions to the median tubercles that may be counted as tubercles. M^3 of *Crateromys* is of the same build as that of *Mallomys*, with notched lophs and no talon; it is wider in relation to M^{1-2} than that of *Mallomys* (table 5). The numbers of lingual tubercles to the upper molars of *Crateromys* are the same as those of *Lenomys*, three to each of the molars.

TABLE 5

Measurements of upper molars of *Spelaeomys* and other large complex-toothed rats (in mm)

	Spelaeomys florensis		*Mallomys rothschildi*	*Lenomys meyeri*	*Crateromys schadenbergi*
Length M^{1-3}	13.4	14.6	16.4	12.2	14.8
Width of M^1	4.0	4.3	5.2	3.5	4.1
Width of M^2	3.9	4.1	4.9	3.3	4.3
Width of M^3	3.1	3.2	4.3	2.6	4.0

In *Pogonomys*, the species of which are much smaller than those of the other genera of complex-toothed rats dealt with above (length M^{1-3} 4.1-6.7 mm; Rümmler, 1938, p. 14), M^3 has only one buccal tubercle (that anterior to loph 1); the two lophs join buccally upon wear (as in *Rattus*), and there is no talon. Moreover, the anterior lingual tubercle of M^1 developed in *Spelaeomys* does not occur in *Pogonomys* either.

Even smaller in size is *Chiropodomys* (including *Insulaemus*) (length M^{1-3} 3.3-4.7 mm; Tate, 1936, pp. 720-722); the number of buccal tubercles to M^1 and M^2 is four, as in *Spelaeomys, Lenomys* and *Pogonomys,* but M^3 appears to lack even the anterior buccal tubercle; it has, however, a talon. The lingual tubercles are three to each of the upper molars, as in *Pogonomys* (that anterior to loph 1 of M^2 is duplicated in a specimen figured by Tate, 1936, p. 631 fig. 30B).

The upper dentition of *Coryphomys* is unknown; its lower dentition will be dealt with presently.

The lower dentition of *Spelaeomys florensis* is shown in thirty rami of the mandible, as follows: 1, right mandibular ramus with M_{1-3} (pl. XV fig. 4); 2, right ramus with M_{1-3} (pl. XV fig. 5); 3, left ramus with M_{1-3} (pl. XV fig. 6); 4-7, four left rami with M_{1-3}; 8, right ramus with M_{1-2};

9-10, two left rami with M_{1-2}; 11, right ramus with M_1; 12, right M_1; 13-19, seven right rami with M_{1-3}; 20-23, four left rami with M_{1-3}; 24, right ramus with M_{1-3} (M_1 incomplete anteriorly); 25, left ramus with M_{1-3} (idem); 26, left ramus with M_{1-3} (M_3 incomplete buccally); 27, left ramus with M_{1-2}; 28, left ramus with M_{1-2} (M_1 incomplete anteriorly); 29, left ramus with M_{2-3}; 30, left ramus with M_1. Of this series, nos. 1-12 are from the deepest layer of the Liang Toge deposit.

Nos. 1-3 (pl. XV figs. 4-6) illustrate successive stages of wear. The lower dentition, as shown by these figures, is characterized by the large numbers of buccal and lingual tubercles. Of the buccal tubercles there are four in M_1 and M_2, and two in M_3. The first buccal tubercle of M_1 is merely an extension of the median tubercle of loph 1; the second and third are related to lophs 2 and 3, and the fourth is posterior to loph 3. In M_2 and M_3 the first and second buccal tubercles are related to loph 1, the third and fourth of M_2 belong to loph 2. In M_3 the second loph has no buccal tubercle; it is deeply cut into behind, between the median and lingual tubercles, and, therefore, is bicuspid. The posterior notch in the hind loph of M_3 remains distinct even in the most advanced stages of wear, and readily serves to distinguish the mandibles of *Spelaeomys* from those of *Papagomys* with which they are intermingled in the Liang Toge deposit.

The lingual tubercles are five in number in M_1, three in M_2, and two in M_3. The foremost of the lingual tubercles of M_1 stands anterior to the second lingual tubercle and the median tubercle of loph 1. The second, third, and fourth lingual tubercles belong to lophs 1, 2, and 3, whereas the fifth lingual tubercle of M_1 is posterior to loph 3, and forms the "talonid". Of the three lingual tubercles of M_2 the first and second relate to lophs 1 and 2, the third is behind loph 2, the "talonid". In M_3 the two lingual tubercles are related to lophs 1 and 2; there is no "talonid".

As shown in the lower dentition of *Papagomys verhoeveni* (pl. XV figs. 1-3) the fourth buccal tubercle of M_1, posterior to loph 3, does not occur, and neither does that posterior to loph 2 of M_2. The buccal tubercle related to loph 1 of M_2 is single instead of duplicated as in *Spelaeomys*, thus reducing the number of buccal tubercles of M_2 of *Papagomys* to two. In M_3 of *Papagomys* there is only one buccal tubercle, corresponding to the two related to loph 1 in *Spelaeomys*. On the lingual side the numbers of tubercles are less different in the two genera: only the foremost lingual tubercle of M_1 seen in *Spelaeomys* does not develop in *Papagomys*. The two genera, however, are at once distinguished by the lophs of M_3, which are deeply notched in behind in *Spelaeomys*, and simple, undivided, in *Papagomys*. The talonids of M_1 and M_2 are relatively larger in *Papagomys* than in *Spelaeomys*.

Mallomys resembles *Spelaeomys* more closely in the characters of the lower molars than does *Papagomys,* for it has the bicuspid lophs of M_3 as well as the small talonids of $M_{1\text{-}2}$ that we find in *Spelaeomys.* However, in *Mallomys* buccal tubercles are absent in all of the lower molars, and the anterior lingual tubercle of M_1 seen in *Spelaeomys* does not develop either.

Buccal tubercles do develop in the lower molars of *Lenomys,* but are fewer in number than those in *Spelaeomys*: only two to M_1, two to M_2, and one to M_3. The last loph of M_3 is only weakly notched in behind, not sharply as in *Spelaeomys* and in *Mallomys;* the talonids of $M_{1\text{-}2}$ are small, as in the last-mentioned genus. In *Lenomys* the numbers of lingual tubercles are the same as those in *Mallomys.*

Crateromys, like *Mallomys,* lacks the buccal tubercles in the lower molars; there are four lingual tubercles to M_1 and three to M_2, as in *Papagomys, Mallomys,* and *Lenomys,* but, in contradistinction to these genera as well as to *Spelaeomys, Crateromys* has three lingual tubercles to M_3, the third being that placed behind the last loph, the talonid (omitted in the figure presented by Thomas, 1898b, pl. XXXVI fig. 2). The lophs of M_3 of *Crateromys* have deep posterior enamel infoldings just as those of *Spelaeomys* and *Mallomys.*

In *Pogonomys* as well as in *Chiropodomys* buccal tubercles are replaced by a weak cingular ledge that extends along M_1 and M_2, but does not continue behind loph 1 of M_3. I have not been able to ascertain the exact numbers of buccal cusps to each of the molars; they do not show clearly in any of the six specimens in the Leiden Museum. There may, however, be as many as four to M_1 and M_2, and two to M_3, as in *Spelaeomys,* but I have not recorded these figures in table 4. The accessory loph in front of loph 1 of M_1, corresponding to the anterior lingual tubercle of *Spelaeomys,* appears to be bicuspid when slightly worn; it is, at any rate, relatively wider, and stands out more prominently to the front than in *Spelaeomys.* The lingual tubercles show very clearly in the lower molars both of *Pogonomys* and of *Chiropodomys,* and conform in numbers and positions to those of *Spelaeomys,* viz., five to M_1, three to M_2, and two to M_3. The last lop' of M_3 is not cut into behind; in this respect *Pogonomys* and *Chiropodomys* resemble *Papagomys.*

There remains for comparison only *Coryphomys,* known from a subfossil mandibular ramus with $M_{1\text{-}3}$ found in a cave near Nikiniki, Timor, and described and figured by Schaub (1937). In this specimen, buccal tubercles are absent, just as in *Mallomys* and *Crateromys.* The anterior end of M_1 is more complicated than that in *Spelaeomys,* for it shows a bicuspid loph in front of loph 1, resembling that seen in *Pogonomys* and *Chiropodomys.* The numbers of lingual tubercles agree with those of the two last-mentioned genera (five to M_1, three to M_2, and two to M_3). The last loph of M_3 is straight, not notched in behind as is that in *Spelaeomys*; in this respect *Coryphomys* agrees with *Papagomys*.

TABLE 6

Measurements of lower teeth of *Spelaeomys florensis* (in mm)

No. of specimen	1	2	3	4	5	6	7	8	9	10
Length M_{1-3}	14.9	14.1	14.4	14.7	15.1	15.0	13.8	—	—	—
Width of M_1	4.2	4.1	4.1	4.1	4.5	4.3	4.1	4.2	4.2	4.3
Width of M_2	4.3	4.3	4.3	4.2	4.6	4.5	4.3	4.4	4.4	4.5
Width of M_3	3.8	3.8	3.7	3.7	3.7	3.9	3.7	—	—	—
Lower I, ant. post	3.0	—	—	—	—	3.3	—	—	—	—
Idem, transverse	2.2	—	—	—	—	2.2	2.2	2.4	—	—
No. of specimen	11	12	13	14	15	16	17	18	19	20
Length M_{1-3}	—	—	14.3	15.3	13.8	15.4	15.1	14.0	14.2	15.2
Width of M_1	4.1	4.1	4.0	4.5	4.2	4.3	4.3	4.1	4.1	4.2
Width of M_2	—	—	4.2	—	4.3	4.5	4.5	4.2	4.3	4.4
Width of M_3	—	—	3.7	4.0	3.7	—	3.9	3.7	3.6	3.7
Lower I, ant. post.	—	—	2.8	—	—	—	3.2	—	—	—
Idem, transverse	—	—	1.9	—	—	—	2.3	—	2.4	—
No. of specimen	21	22	23	24	25	26	27	28	29	30
Length M_{1-3}	14.0	13.9	15.0	—	—	14.7	—	—	—	—
Width of M_1	4.3	4.1	4.2	4.2	4.3	4.2	4.1	4.2	—	4.2
Width of M_2	4.6	4.1	4.5	4.3	4.4	4.3	4.2	4.3	4.1	—
Width of M_3	3.8	3.7	3.9	3.7	3.8	—	—	—	3.6	—

TABLE 7

Measurements of lower molars of *Spelaeomys* and other large complex-toothed rats (in mm)

	Spelaeomys florensis		*Mallomys rothschildi*	*Lenomys meyeri*	*Crateromys schadenbergi*	*Coryphomys bühleri*
	range	mean				
Length M_{1-3}	13.8-15.4	14.6	16.4	11.5	15.6	19.9
Width of M_1	4.0-4.5	4.2	4.4	3.5	4.0	5.4
Width of M_2	4.1-4.6	4.3	4.3	3.4	4.2	6.2
Width of M_3	3.6-4.0	3.8	4.2	3.1	4.3	5.6

As shown in table 7, *Coryphomys bühleri* is the largest of the complex-toothed rats, while *Spelaeomys florensis* is intermediate in size between *Mallomys rothschildi* and *Lenomys meyeri* as regards both the upper (table 5) and the lower teeth (table 7).

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EXPLANATION OF THE PLATES

PLATE XIV

Figs. 1-3, *Papagomys armandvillei besar* nov. subsp., Liang Toge, Flores; fig. 1, left M_{1-3} (holotype); figs. 2-3, right M_{1-3}.

Fig. 4, *Papagomys verhoeveni* nov. spec., Liang Toge, Flores, right M^{1-3} (holotype).

Figs. 5-6, *Spelaeomys florensis* nov. gen. nov. spec., Liang Toge, Flores; fig. 5, right M^{1-3} (holotype); fig. 6, left M^{1-3}.

All figures 5 2/3 natural size.

PLATE XV

Figs. 1-3, *Papagomys verhoeveni* nov. spec., Liang Toge, Flores; figs. 1-2, left M_{1-3}; figs. 3, right M_{1-3}.

Figs. 4-6, *Spelaeomys florensis* nov. gen. nov. spec., Liang Toge, Flores; figs. 1-2, right M_{1-3}; fig. 3, left M_{1-3}.

All figures 5 2/3 natural size.


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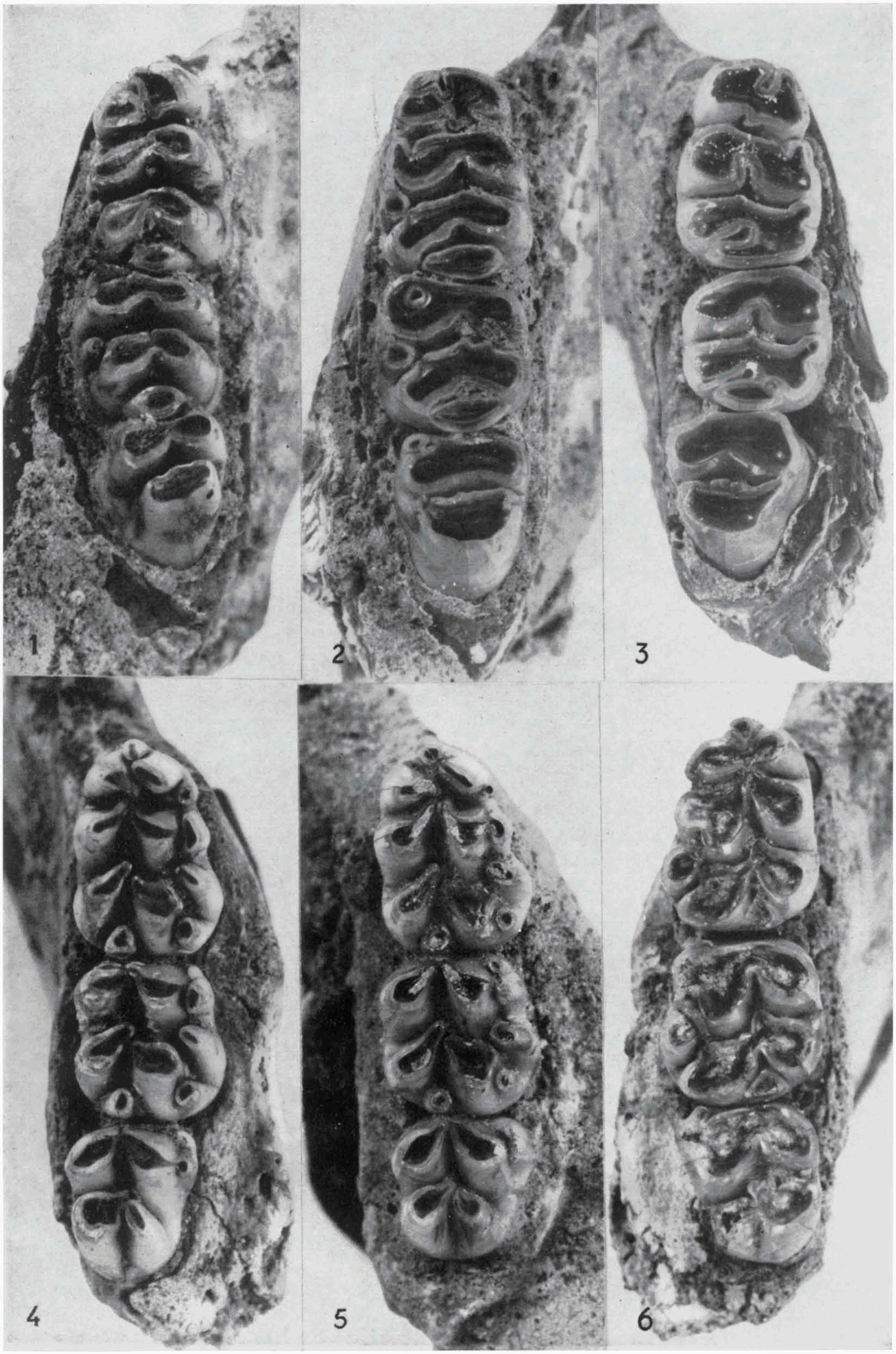
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