

The taxonomic Status of small Fossil Wombats (Vombatidae: Marsupialia) from Quaternary Deposits, and of related modern Wombats

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The taxonomic value of characters of the upper and lower incisors and premolars, of the anterior region of the palate, and of the nasals and frontals has been verified for modern species of *Vombatus* and *Lasiorchinus*. However, characters of the lower dentition and the mandible reliably distinguish between *Vombatus* and *Lasiorchinus* at the generic level only, and are inadequate for identification of species within these genera.

Three modern subspecies of *Vombatus ursinus* are recognized; *V. u. ursinus* (Shaw, 1800), *V. u. tasmaniensis* (Spencer & Kershaw, 1910), and *V. u. platyrhinus* (Owen, 1853). *Vombatus ursinus mitchellii* (Owen, 1838) is recognized as a fossil subspecies from Pleistocene deposits of Wellington Caves, New South Wales. *Phascolomys parvus* Owen, 1872, *Phascolomys pliocenae* McCoy, 1866, and *Phascolomys thomsoni* Owen, 1872 have been placed in the synonymy of *Vombatus ursinus* (Shaw, 1800). *Vombatus hacketti* Glauert, 1910 is recognized as a fossil species from Pleistocene deposits of Mammoth Cave, Western Australia. *Phascolomys gillespiei* De Vis, 1900 and *Lasiorchinus latifrons barnardi* Longman, 1939 have been placed in the synonymy of *Lasiorchinus krefftii* (Owen, 1872). *Lasiorchinus angustidens* (De Vis, 1891) is recognized for a fossil species from the eastern Darling Downs, Queensland. The relationships of the plesiomorphic species *Warendja wakefieldi* Hope & Wilkinson, 1982 have not yet been established.

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INTRODUCTION

Classification of living and fossil wombats has long been the source of considerable confusion. Kirsch and Calaby (1977: 23), who listed three species of two genera of living wombats, stated that '... the nomenclature of wombats has an arbitrary element.' The confusion is partly due to the complex historical background of the nomenclature, and partly due to poor understanding generally of the taxonomic value of skeletal and dental characters of wombats.

Modern wombats were first known from Flinders Island in Bass Strait, and from Tasmania, and given a variety of names by early workers (see Thomas, 1888). The earliest name for the southern island form is *Didelphis ursina* Shaw, 1800. Although the name *Opossum hirsutum* Perry, 1811 probably applied to the mainland Common Wombat (see Troughton, 1941), a mainland form was not known to the British palaeontologist, Richard Owen, when he named a wombat fossil from Pleistocene deposits at Wellington Caves, New South Wales as *Phascolomys mitchellii* (Owen in Mitchell, 1838). The island form was known to Owen as *Phascolomys vombatus* Leach, 1815. Owen (1845) was the first to recognize the modern Southern Hairy-nosed Wombat as a distinct species, *Phascolomys latifrons* Owen, 1845. Owen later had access to skulls of the modern mainland Common Wombat and his study of cranial bones led him to describe this form as a fourth species, *Phascolomys platyrhinus* Owen, 1853. He considered this modern species to be very similar to, but distinct from, the fossil species

P. mitchellii. In both papers (Owen, 1845, 1853) Owen defines characters of the skull bones to distinguish between these 'species', which he assigned to two groups — the 'platyrhine' (= common or forest wombats) and 'latifrons' (= hairy-nosed) wombats. Murie (1865) placed Owen's species *latifrons* in *Lasiorhinus*. The generic distinction of *latifrons* was never recognized by Owen, nor by other 19th century writers who referred all wombats (except the giant *Phascolonus gigas*) to the genus *Phascolomys*.

In 1872 Owen produced two large treatises on fossil wombats, the first (Owen, 1872a) bearing on species similar in size to existing wombats, and the second (Owen, 1872b) being confined to species exceeding the present in size. Owen (1872a) described three more fossil species very similar to living forms: *Phascolomys krefftii*, from Wellington Caves, and *Phascolomys thomsoni* and *Phascolomys parvus* from Pleistocene deposits of the eastern Darling Downs, Queensland.

Since then three other small fossil species have been described in the genus *Phascolomys*: *Phascolomys pliocen* McCoy, 1866 from Dunolly, Victoria; *Phascolomys angustidens* De Vis, 1891 from the eastern Darling Downs; and *Phascolomys hacketti* Glauert, 1910 from Mammoth Cave, Western Australia. Another unique small wombat, *Warendja wakefieldi* Hope & Wilkinson, 1982 has been described for jaw fragments from Pleistocene deposits in McEacherns Cave in southwestern Victoria.

It is necessary to review current opinion on the taxonomy of modern wombats before discussion of the status of fossil species. In the most recent review of living and fossil wombats Tate (1951) recognized three geographically separate forms of the living Common Wombat as subspecies of *Vombatus ursinus*: a Tasmanian form, *V. u. tasmaniensis* (Spencer & Kershaw, 1910); a continental form, *V. u. platyrhinus* (Owen, 1853); and the Flinders Island form, *V. u. ursinus* (Shaw, 1800). He also considered the fossil form *V. u. mitchellii* from Wellington Caves, to be a subspecies most similar to *V. u. platyrhinus*. Ride (1970) and Kirsch and Calaby (1977) did not recognize these subspecies and included all living forms in a single species *Vombatus ursinus*. Tate (1951) considered *Phascolomys hacketti* from Western Australia to be a synonym of *V. u. platyrhinus*, and listed *thomsoni*, *parvus* and *pliocen* as fossil species of *Vombatus* without further comment.

Classification of the geographically separate forms of the modern hairy-nosed wombats has also been uncertain. Tate (1951) listed three modern subspecies of *Lasiorhinus latifrons*: *L. l. latifrons* (Owen, 1845) from South Australia, *L. l. gillespiei* (De Vis, 1900) from Moonie River, Queensland, and *L. l. barnardi* Longman, 1939 from Clermont, Queensland. He considered the fossil forms, *L. krefftii* and *L. angustidens*, to be distinct species. Ride (1970) listed each of the three modern forms of hairy-nosed wombat as full species. Kirsch and Calaby (1977) recognized *L. latifrons* from South Australia at the specific level, but followed Wilkinson (quoted in Merrilees, 1973), in placing *L. barnardi* and *L. gillespiei* in the synonymy of *L. krefftii* although no data were given by Wilkinson to support this suggestion.

In this study dental nomenclature follows Archer (1978). Accordingly, the dental formula of wombats is $I_1^1, P_3^3, M_{2-5}^{2-5}$. All measurements are in millimetres.

TAXONOMIC CHARACTERS OF THE SKULL AND TEETH OF WOMBATS

Until 1967 there had been no reassessment of the taxonomic value of characters used by Owen and others to distinguish between the various species of fossil wombat, nor had any study been made of inter- and intraspecific variation in living wombats. Two studies published in that year (Merrilees, 1967; Crowcroft, 1967) represent the first important steps in the clarification of vomatid taxonomy.

Merrilees (1967) reassessed the taxonomic value of many characters of the skull and teeth described by Owen between 1846 and 1872 to distinguish between

TABLE 1

Non-metric character states diagnostic at the generic level for modern wombats

No.	Description of Character	<i>Vombatus</i>	<i>Lasiorhinus</i>
1.	Proportions of nasals	Narrow relative to length	Wide relative to length
2.	Shape of upper incisors	Wider than deep	Deeper than wide
3.	Wear angle on upper incisors	Near transverse	Near vertical
4.	Upper premolars	Anterolingual groove	No anterolingual groove
5.	Palate width between posterior lobe of M ²⁻²	Narrow	Wider
6.	Depth of 'ectalveolar plate' of maxilla*	Shallow	Deep
7.	Shape of anterior palate	Narrow, less concave	Flares anteriorly
8.	Premaxillary/nasal suture	Much longer than maxillary/nasal suture	Shorter than maxillary/nasal suture
9.	Cross-sectional shape lower incisor	Triangular	Spatulate
10.	Upper symphyseal surface between P ₃₋₃	Flat base	Concave base
11.	Shape of lower premolars	Oval in T.S.	Subrectangular in T.S.
12.	Foreward extent of 'ectalveolar groove'**	To anterior edge M ₅	To anterior edge M ₄
13.	Upper surface mandibular diastema	Convex	Flat
14.	Maximum depth ramus	Below M ₄	Below M ₃
15.	Masseteric fossa	Deep, large masseteric canal	Shallow, masseteric canal absent or small

* Term introduced by Owen (1872a) for the portion of the maxilla directly below the anterior origin of the zygomatic arch.

** Name introduced by Owen (1872a) for the labial valley between the posterior molars and the base of the ascending ramus of the coronoid process of the dentary.

'platyrrhine' and 'latifront' wombats (i.e. between species of *Vombatus* and *Lasiorhinus*). He noted high variability in most of Owen's characters in modern populations of *Lasiorhinus latifrons* and *Vombatus ursinus* (= *V. hirsutus*). This variability occurred even within a single population of one species. Merrilees (1967) concluded, particularly, that non-metric morphological characters of the molar teeth do not suffice to distinguish modern taxa, even at the generic level. He also confirmed that absolute tooth size is unreliable as a taxonomic character in wombats due to the open-rooted continuously growing nature of the teeth. Characters of the incisor and premolar teeth and of the palate, cranial bones and mandible were found by Merrilees (1967) to be adequate to identify specimens from the modern fauna at the generic level only. He made no attempt to distinguish between taxa within *Lasiorhinus* using these characters.

A study by Crowcroft (1967) of variation in some cranial characters of geographically separate populations of *Lasiorhinus latifrons* from South Australia also indicated great intraspecific variability. However, he demonstrated some consistent differences between these populations on the basis of the configuration of the naso-frontal sutures and other skull features. He also considered these characters and some other cranial features as adequate to distinguish between *L. latifrons* and the Queensland hairy-nosed wombats, probably at the specific level.

Further assessment of intergeneric and intraspecific variation of cranial and dental characters of wombats has been undertaken in this study. Table 1 presents a summary of the non-metric characters used in this study for the assignment to genera

TABLE 2

Metric characters of the skull and teeth of wombats

NUMBER	
1.	Basicranial length
4.	Maximum length nasals
5.	Maximum length frontals
6.	Maximum posterior width nasals
7.	Width nasals at anterior edge of premaxilla
8.	Mid-line length of anterior nasal projection
9.	Depth of premaxillary suture between incisors
10.	Length of premaxillary/nasal suture
12.	Maxilla depth below origin of zygomatic arch (= ectalveolar plate of Owen 1872).
14.	Length upper cheek tooth row at level of alveolus
16.	Width of palate between posterior lobes M ²
17.	Maximum diameter of P ³
18.	Minimum diameter of P ³
19.	Width of enamel on upper incisor
20.	Depth of upper incisor
21.	Width of enamel of lower incisor
22.	Vertical depth of lower incisor
23.	Minimum diameter of P ₃
24.	Maximum diameter of P ₃
25.	Length of lower cheek tooth row at level of alveolus

TABLE 3

*Cranial and dental dimensions (mm) of modern Vombatus ursinus. Numbered characters are described in Table 2.
Specimens are from the collections of the Australian Museum*

CHARACTER	M2258	S 799	M7485	M3378	M3709	M3360	M3044	M2958	M2339
1	131.0	140.0	135.0	160.0	162.0	162.0	150.0	140.0	161.0
4	57.5	66.0	58.0	67.0	73.5	71.5	69.5	65.0	73.0
5	54.0	56.0	53.0	64.0	—	69.0	65.0	61.0	—
6	36.5	41.5	46.0	51.0	47.0	51.0	48.0	47.0	53.0
7	11.0	14.5	12.0	17.0	17.5	17.0	17.0	20.0	19.0
8	6.5	8.0	9.0	11.0	10.0	10.0	8.0	12.0	10.0
9	7.0	7.0	6.0	7.0	8.0	8.0	10.0	7.0	8.0
10	33.5	40.5	36.5	43.0	50.0	48.5	44.0	37.0	47.5
12	12.0	12.0	11.0	12.5	12.5	13.0	12.5	13.5	12.0
14	44.0	45.5	43.0	51.5	50.0	52.0	48.0	46.0	53.0
16	5.5	4.5	5.5	7.0	7.0	7.0	6.0	5.0	5.0
17	7.5	6.0	5.5	7.0	7.5	7.5	7.5	6.2	7.0
18	5.3	4.8	4.8	6.5	6.2	6.0	6.0	4.6	6.5
19	9.3	10.0	8.6	11.5	10.7	11.0	10.0	10.2	11.3
20	4.7	5.3	5.2	6.5	6.2	6.5	5.8	5.8	6.1
21	7.0	7.2	6.5	8.8	8.1	8.5	7.0	8.3	8.3
22	5.5	6.2	6.0	8.0	7.3	6.6	6.8	7.0	7.0
23	5.5	5.5	5.5	6.5	6.7	6.5	6.5	6.0	6.4
24	4.0	4.0	3.9	5.0	5.0	5.0	4.5	4.5	4.8
25	45.5	45.5	—	52.0	53.3	53.0	49.0	47.5	54.5
	Flinders Is., SA 1919	Tasmania	Flinders Is., SA 1929	Oberon, NSW	Oberon, NSW	Mittagong, NSW	Mt Darrah, Cooma, NSW	Mt Darrah, Cooma, NSW	Batlow, NSW

TABLE 4

Cranial and dental dimensions (mm) of modern Lasiorhinus latifrons from South Australia
Specimens are from the collections of the Australian Museum. Numbered characters are described in Table 2

CHARACTER	M8024	M8026	M8027	M8028	M8029	S 801	S 787
1	148.0	157.0	156.0	149.0	136.0a	—	158.0
4	54.0	60.0	61.0	55.0	52.0a	60.0	60.0
5	69.0	—	67.0	65.0	58.0a	66.0	63.0
6	59.0	59.0	59.0	51.0	57.0	63.0	58.0
7	30.0	25.0	24.0	26.0	28.0	25.0	26.0
8	15.5	16.3	14.5	14.8	11.5	15.0	18.0
9	16.0	16.0	16.0	16.0	14.0	15.5	16.0
10	26.0	26.0	24.0	22.0	20.0	23.5	21.0
12	18.5	20.0	20.0	20.0	15.0	18.5	18.5
14	45.0	49.0	51.0	49.0	43.0	50.0	52.5
16	12.0	11.0	12.0	11.0	8.0	10.0	9.0
17	8.0	7.0	7.8	7.0	7.0	8.0	—
18	5.5	6.0	5.7	6.0	5.0	6.1	—
19	9.0	9.8	9.7	9.8	8.5	—	10.0
20	7.0	7.2	7.2	7.5	6.5	—	7.5
21	5.7	6.0	5.9	5.9	4.7	6.1	5.8
22	6.8	7.6	7.2	7.4	5.8	7.1	8.0
23	5.1	5.9	5.5	5.0	5.5	5.7	5.8
24	5.5	6.0	6.0	5.1	4.8	5.5	6.2
25	45.0	—	52.0	49.0	43.0	48.0	50.0
	Portee, SA	Portee, SA	Portee, SA	Portee, SA	Portee, SA	No location	South Australia

of incomplete fossil fragments. These have been selected from those used by Owen (1846, 1872a), Merrilees (1967) and Crowcroft (1967). In addition, 19 metric characters have been defined in Table 2.

Tables 3 and 4 present data for these characters for modern *V. ursinus* and *L. latifrons*. Measurements were made on skulls in the collection of the Australian Museum. These data are summarized with the sample mean (\bar{X}), standard deviation(s), and coefficient of variation (CV) for each character in Table 5. The relatively high values obtained for CV of *V. ursinus* reflect the geographic heterogeneity of the sample, as well as the high degree of intraspecific variability noted by Merrilees (1967). Skulls of modern Queensland wombats in the collections of the Queensland Museum were also measured. These include the type of *Lasiorhinus barnardi* from Clermont (QM 6239) and three syntypes of *L. gillespiei* from Moonie River (QM J13145, J13144, J13143). Three wombat skulls from Deniliquin, New South Wales, were measured from the collections of the National Museum of Victoria. These data are presented in Table 6.

The diagnostic value, at the species level, of some of these characters is suggested by the separation of the species of modern wombats into clusters in bivariate scattergrams, some examples of which are shown in Fig. 1. The data indicate that several of the characters measured here distinguish between at least two modern species of *Lasiorhinus*. Thus, the wombats from Clermont, Moonie River, and Deniliquin can be distinguished from *L. latifrons* from South Australia by having the nasals longer relative

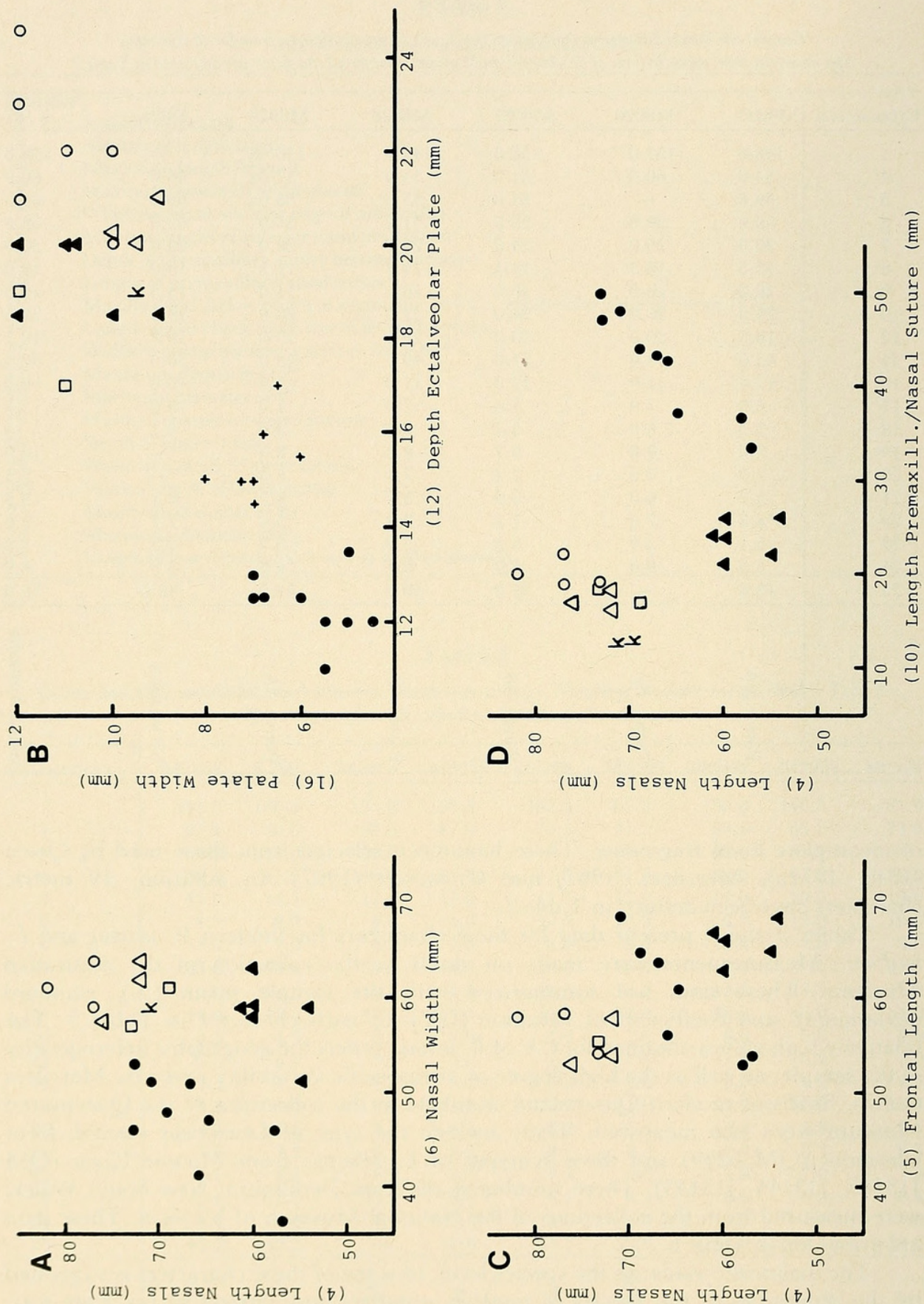


Fig. 1. Bivariate scattergrams illustrating clustering of three species of modern wombats, and some fossil specimens, using selected skull characters. The species are indicated as follows: • *Vombatus ursinus*, + *V. ursinus mitchellii* (Wellington Caves), ▲ *Lasiorhinus latifrons* (South Australia), △ *L. krefftii* (Moonie R.), ○ *L. krefftii* (Clermont), □ *L. krefftii* (Deniliquin), 'k' *L. krefftii* (Wellington Caves). Data from Tables 3, 4, 5, 6.

TABLE 5

Statistical summary of cranial and dental dimensions (mm) of modern *Lasiiorhinus latifrons* and *Vombatus ursinus*
Data are from Tables 3 and 4. Numbered characters are described in Table 2

CHARACTER	N	\bar{X}	<i>Vombatus ursinus</i>			N	\bar{X}	O.R.	S	C.V.
			O.R.	S	C.V.					
1	9	149.0	131.0-162.0	12.7	8.8	6	150.7	136.0-158.0	8.3	5.8
4	9	66.8	57.5-73.5	5.9	9.1	7	57.4	52.0-61.0	3.6	6.7
5	7	60.3	53.0-69.0	6.1	10.4	6	64.7	58.0-69.0	3.8	6.1
6	9	46.8	36.5-53.0	5.1	11.3	7	58.0	51.0-63.0	3.6	6.5
7	9	16.1	11.0-20.0	3.0	19.4	7	26.3	24.0-30.0	7.8	8.1
8	9	9.4	6.5-12.0	1.7	18.1	7	15.1	11.5-18.0	2.0	13.6
9	9	7.6	6.0-10.0	1.1	15.3	7	15.6	14.0-16.0	0.8	5.0
10	9	42.3	33.5-50.0	5.8	14.2	7	23.2	21.0-26.0	2.3	10.5
12	9	12.3	11.0-13.5	0.7	6.0	7	18.6	15.0-20.0	1.8	9.9
14	9	48.1	43.0-50.0	3.7	7.9	7	48.5	43.0-52.5	3.4	7.2
16	9	5.8	4.5-7.6	1.0	17.2	7	10.4	8.0-12.0	1.5	15.1
17	9	6.9	5.5-7.5	0.8	11.1	6	7.5	7.0-8.0	0.5	7.2
18	9	5.6	4.8-6.5	0.8	13.9	6	5.7	5.5-6.1	0.4	7.7
19	9	10.3	8.6-11.5	0.9	9.4	6	9.5	8.5-10.0	0.6	6.4
20	9	5.8	4.7-6.5	0.6	10.9	6	7.2	6.5-7.5	0.4	5.4
21	9	7.7	6.5-8.8	0.8	10.7	7	5.7	4.7-6.1	0.5	8.6
22	9	6.7	5.5-8.0	0.7	11.1	7	7.1	5.8-8.0	0.7	10.2
23	9	4.5	3.9-5.0	0.5	10.5	7	5.6	4.8-6.2	0.5	9.6
24	9	6.1	5.5-6.7	0.5	8.5	7	5.5	5.0-5.9	0.3	6.5
25	8	50.3	45.5-54.5			6	47.8	43.0-52.0		

to their width (characters 4, 6) and relative to the length of the frontals (character 5); by the longer anterior projection of the nasals (character 8); by the shorter premaxillary/nasal suture (character 10); and by the wider I^1 (character 19). The Moonie River and Deniliquin wombats agree with each other and differ from *L. latifrons* in consistently having a backward projection of the nasals at their median suture with the frontals, although the form of this suture differs considerably in detail between individuals (e.g. QM J13143 and QM J13144). A median backward projection of the nasals into the frontals was not observed in any specimen of *L. latifrons* in either the Australian Museum or the South Australian Museum.

Skulls of the Clermont wombats are slightly larger than those from Moonie River and Deniliquin, but cluster close to those populations in the bivariate scattergrams. However, they differ consistently from the other two populations in all having a forward projection of the frontals into the nasals at their median suture. All Clermont specimens also possess a narrow posterior extension of the maxillae to form a short suture with the frontals. However, this character is not diagnostic for the Clermont wombats, having been observed as a rare variant in *L. latifrons* (e.g. SAM M8029) and in the Deniliquin wombats (e.g. NMV C6228).

Very few characters of the mandible could be shown to have taxonomic value at the species level. Merrilees (1967) has pointed out the great variability within *L. latifrons* in the depth of the masseteric fossa and presence or absence of a masseteric canal, as well as the level of origin of the coronoid process. These are all characters used by Owen. Although these characters are diagnostic at the generic level in modern wombats, the degree of intraspecific variability is insufficiently understood at the species level. No clear distinguishing features could be found between the mandibles of *L. latifrons* from South Australia and the Queensland and Deniliquin wombats. For example, depth of the masseteric fossa was variable in the specimens from Moonie

TABLE 6

Cranial and dental dimensions (mm) of modern Lasiorhinus krefftii from New South Wales and Queensland. Specimens are from the collections of the Queensland Museum and the National Museum of Victoria. Numbered characters are described in Table 2

CHARACTER	QM J6239	QM J14051	QM J20354	QM J6283	QM J6284	QM J6240	QM J13143	QM J13145	QM J13144	NMV C6230	NMV C6228	NMV
1	169.0	171.0	172.0	—	171.0	162.0	156.0	160.0	158.0	155.0	155.0	155.0
4	77.0	77.0	82.0	73.5	—	—	76.0	72.5	72.0	—	73.0	69.0a
5	58.0	58.0	58.0	54.5	55.5	60.0	53.0	54.0	58.0	55.0	55.0	—
6	64.0	59.0	61.0	—	52.0a	52.0	57.5	62.0	64.0	60.0	57.5	61.0a
7	43.5	35.6	37.0	—	34.0	34.0	31.0	35.0	34.0	30.0	28.0	30.0
8	27.0	25.0	25.0	25.0	—	—	23.0	23.0	24.0	—	22.0	23.0
10	19.2	22.2	20.0	19.0	23.5	17.0a	17.5	18.0	16.0	18.0	19.0	17.5
12	24.8	21.0	22.0	23.0	22.5	20.0	20.0	21.0	20.0	19.0	17.0	18.0
14	58.0	54.5	57.0	—	56.5	56.0	47.0	51.0	50.0	48.5	53.0	52.0
16	12.0	12.0	11.0	12.3	10.0	10.0	10.0	9.0	9.5	12.0	11.0	14.0
17	7.5	7.2	—	—	—	—	—	—	6.8	7.5	—	7.0
19	10.3	11.0	11.5	10.5	11.0	10.0	9.5	10.0	9.5	10.5	—	11.4
20	8.5	7.3	7.5	8.8	8.0	9.0	7.7	8.5	7.8	7.3	—	8.0
21	7.7	7.4	7.7	7.5	—	—	—	—	6.3	6.5	—	7.0
22	9.1	9.0	9.2	8.2	—	—	—	—	7.2	7.4	—	8.5
23	5.8	5.9	5.8	5.5	—	—	—	—	5.3	4.8	5.3	5.1
	Clermont, Qld	Clermont, Qld	Clermont, Qld	Clermont, Qld	Clermont, Qld	Clermont, Qld	Moynie R., SE Q.	Moynie R., SE Q.	Moynie R., SE Q.	Deniliquin, NSW	Deniliquin, NSW	Deniliquin, NSW

River, being very shallow and non-perforate in QM J13145, but deeper and possessing a small masseteric canal in QM J13144. The ectalveolar groove extended as far forward as the posterior lobe of M_4 in the Queensland wombats studied here, agreeing with the majority of specimens of *L. latifrons* from South Australia (Merrilees, 1967). It extended slightly further forward, to the anterior lobe of M_4 , in the three specimens examined from Deniliquin. It is concluded that it is not possible to use these mandibular characters to distinguish species within either genus of living wombats.

It must be assumed that the difficulties encountered in using characters of the teeth and jaws of modern wombats for taxonomic purposes also apply to fossil genera and species especially those most closely related to modern forms. With few exceptions, fossil taxa have been described from incomplete and unassociated jaw fragments only, however some cranial bones are known. Postcranial bones have not been studied. At present, fossil wombat taxonomy is heavily dependent on morphological features of the incisor and premolar teeth, the shape and proportions of the palate, and the morphology and proportions of the most anterior bones of the cranium.

In this study the status is reviewed of fossil vombatid species similar to living wombats in size. For two of these, *Phascolomys mitchellii* Owen and *Phascolomys krefftii* Owen, relatively large samples are available from their type locality, Wellington Caves, New South Wales. These samples have permitted detailed study of variability in the fossil taxa under review.

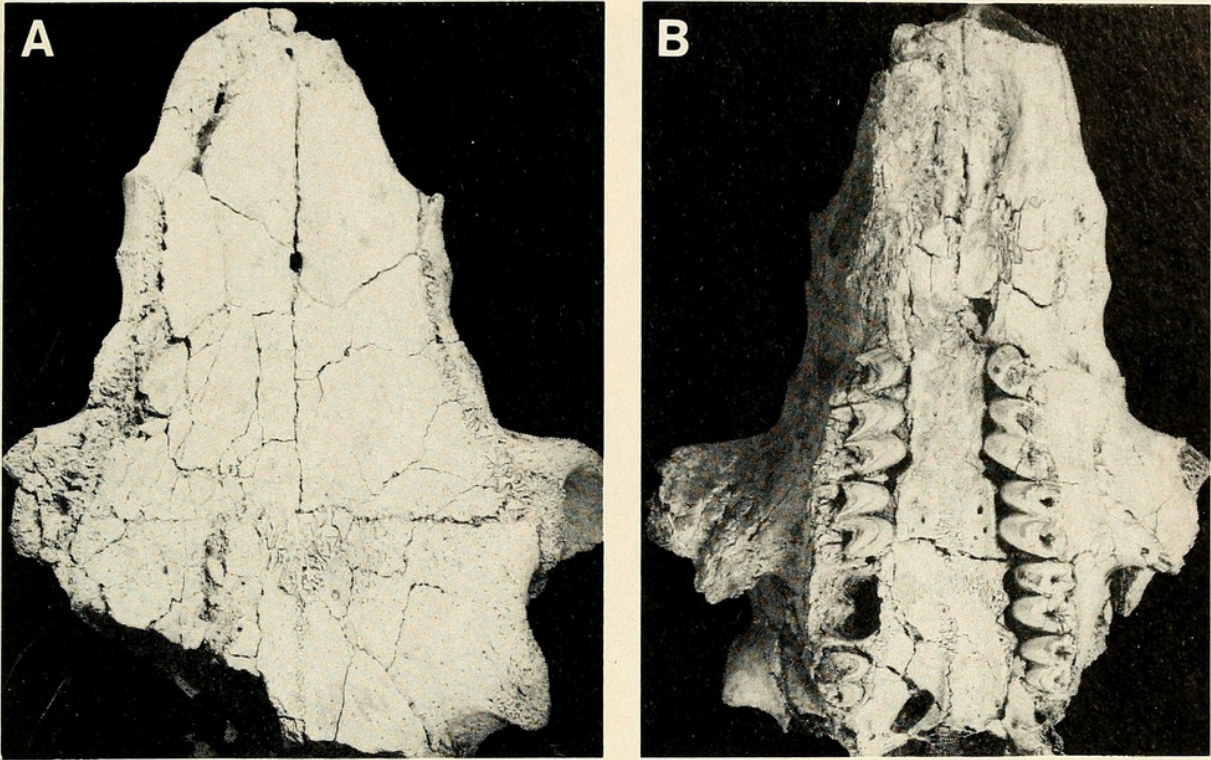


Fig. 2. Skull, AM F58703 of *Vombatus ursinus mitchellii* (Owen, 1838) from Wellington Caves. A. Dorsal view. B. Palatal view, with alveoli for left and right P^3 , M^{2-5} .

SYSTEMATICS

Genus *VOMBATUS* Geoffroy, 1803

Vombatus ursinus (Shaw, 1800)

Synonymy: Fossil taxa in the synonymy of *Vombatus ursinus* Shaw are *Phascolomys mitchellii* Owen, 1838, *Phascolomys parvus* Owen, 1872, *Phascolomys pliocen* McCoy, 1866 and *Phascolomys thomsoni* Owen, 1872.

i) *Phascolomys mitchellii* Owen, 1838

The type locality of *Phascolomys mitchellii* is given as 'Wellington Valley', New South Wales (Owen in Mitchell, 1838). However, Owen (1872a) is more specific, listing the origin of the syntypes as the Breccia-cavern, Wellington Valley. The four syntypes of *Phascolomys mitchellii* are present in the Sir Thomas Mitchell Collection of the British Museum (Natural History). Mahoney and Ride (1975) have discussed at length the problem of the exact origin of specimens in this collection, and have concluded that the possibility that some of them originated from Buree (or Boree), also in the Wellington Valley, cannot be discounted. One syntype, BM M10791, a mutilated cranium (figured Mitchell, 1838, pl. 30, fig. 4) has been selected here as the lectotype of *Phascolomys mitchellii* Owen. Paralectotypes are BM M10792, a partial right mandibular ramus (ibid. fig. 5); BM M10793, a right maxillary tooth row (ibid. fig. 6); and BM M10794, a right mandibular fragment with I_1 broken off, P_3 - M_5 (ibid. fig. 7). Three other specimens from Wellington caves referable to this subspecies were noted by Owen (1872a). These are BM 42598, a mutilated cranium (ibid. pl. 17, figs 1, 3, 4, 5); BM 42612, an edentulous right maxillary fragment (ibid. pl. 17, figs 7, 8); and BM 42604, a left mandibular fragment (ibid. pl. 19, fig. 5; pl. 21, figs 5, 6). The Australian Museum collection from Wellington Caves includes six fragments of the skull and upper jaws: AM F58703 (Fig. 2A-B), F5372, F5398, F5380, F5378, MF730; and

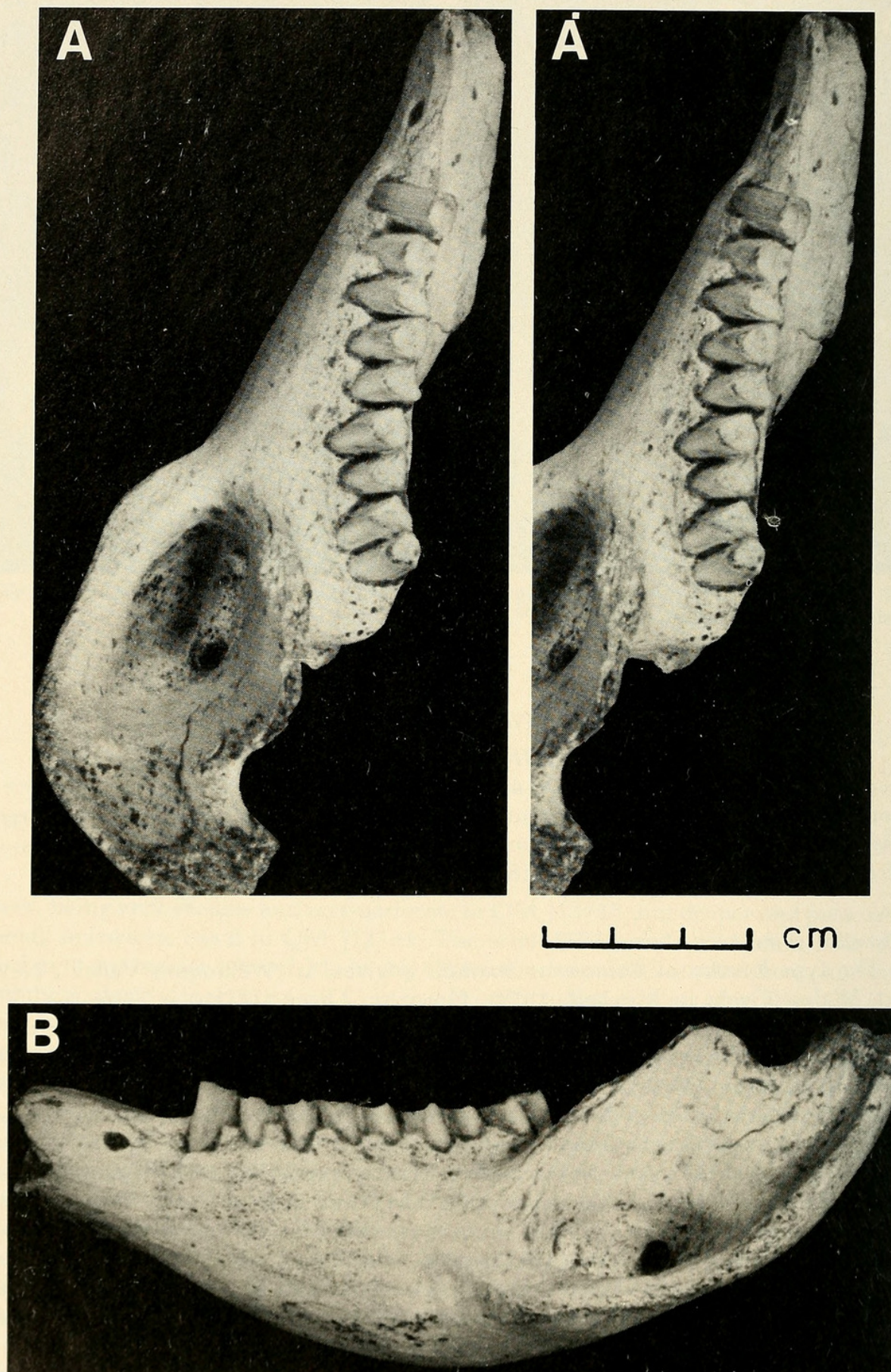


Fig. 3. A left mandibular ramus, AM F31055 of *Vombatus ursinus mitchellii* (Owen, 1838) from Wellington Caves. A, A'. Stereopair of occlusal view with P₃, M₂₋₅. B. Labial view.

TABLE 7

List of specimens of Vombatus ursinus mitchelli from Wellington Caves in the Australian Museum (AM numbers)
The Table indicates the characters which are present in each specimen in the state diagnostic for the genus Vombatus. These characters are described in Table 1

SPECIMEN NUMBER	DESCRIPTION	CHARACTERS DIAGNOSTIC FOR <i>VOMBATUS</i>
F58703	Crushed cranium, I ¹ broken, edentulous	1, 5, 7
F5372	Partial skull, with left and right P ³ -M ⁵	4, 5, 7
F5398	Partial palate, with left P ³ -M ⁵	4, 5
F5380	Partial palate, edentulous	5
F5378	Palate fragment, edentulous	4, 5, 6
F5383	Right maxillary fragment M ²⁻⁵	5
MF730	Right maxillary fragment M ²	6
F35406	Left mandibular ramus, I ₁ , P ₃ -M ₅	9, 11, 12, 13, 15p
F58707	Right mandibular ramus, I ₁	9, 10, 12, 13, 15p
F18866	Left and right mandibular rami, I ₁₋₁	9, 10, 12, 13
F31055	Left mandibular ramus, I ₁ , P ₃ -M ₅	9, 10, 12, 15p
MF720	Right mandibular ramus, P ₃ -M ₅	11, 12, 13, 15np
F58705	Left mandibular ramus, I ₁ , M ₂₋₅	9, 12, 15np
F5390	Right mandibular ramus, P ₃ -M ₅	11, 12, 14, 15p
MF721	Right mandibular ramus P ₃ -M ₅	11, 12, 15p
MF723	Right mandibular ramus, M ₂₋₅	12, 15p
F35404	Left mandibular ramus M ₂₋₅	12, 15p
F5386	Right mandibular ramus, M ₄	12, 15p
F5381	Right mandibular ramus, M ₄₋₅	12, 15np
F5373	Left mandibular ramus, edentulous	12, 15np
MF105	Left mandibular ramus I ₁	9, 11, 13, 14, 15np
F5382	Left mandibular ramus, M ₂₋₄	12, 15np
F58706	Right mandibular ramus, edentulous	9, 10, 12, 15np
F5401	Left mandibular ramus, I ₁ , M ₃₋₅	9, 12, 14, 15np
F5387	Right mandibular ramus, edentulous	12, 15p
F53719	Left mandibular fragment, P ₃ -M ₄	11, 12, 15p
F5377	Left mandibular ramus I ₁ , M ₃₋₅	9, 12, 15p
F5332	Right mandibular fragment, P ₃ -M ₅	11, 12, 14, 15p

p = perforate, np = non-perforate.

twenty two mandibular fragments: AM F35406, F58707, F18866, F31055 (Fig. 3A-B), MF720, F58705, F5390, MF723, MF721, F35404, F5386, F5381, F5373, MF105, F5382, F58706, F5401, F5387, F5315, F5332, F53719, F5377, which are referable to a species of *Vombatus*. These specimens are described in Table 7, in which the characters enabling each to be referred to a species of *Vombatus* are noted.

Measurements and Comparisons. Fossil material from Wellington Caves has been compared with a sample of 9 skulls of modern *jvombatus ursinus* from New Sout Wales, Tasmania, and South Australia (Table 3), and with observations of that species by Merrilees (19673). Metric data of taxonomic importance for the modern species are summarized in Table 5. The corresponding data for the fossil sample are presented in Table 8 and 9.

Data for the fossil sample generally fall within, or close to, the observed ranges for the same characters in modern *V. ursinus* with the exception of the values for character 12, the depth of the ectalveolar plate of the maxilla. This is deeper in all of the fossil specimens (see Fig. 1B). Thus fossil specimens form a discrete cluster in all bivariate

TABLE 8

Dimensions (mm) of the upper dentition, palate and cranial bones of Vombatus ursinus mitchelli from Wellington Caves. Numbered characters are described in Table 2. Specimen numbers refer to the Australian Museum collection (AM)

CHARACTER	MF730	F58703	F5372	F5398	F5380	F5378	F5383
6	—	50.0	—	—	—	—	—
10	—	47.0	—	—	—	—	—
12	14.5	17.0	15.3	16.0	15.5	15.0	15.0
14	49.0	50.0	44.5	47.3	—	54.5	49.0
16	7.0a	6.5	7.3	5.8	6.0	8.0	7.0a
19	—	9.0	—	—	—	—	—
20	—	6.5	—	—	—	—	—

(a) approximate measurement.

comparisons involving character 12. The fossil specimens cluster with *V. ursinus* in all other bivariate comparisons. Only two cranial specimens, F58703 (Fig. 2A-B) and BM 42598 Owen 1872a, pl. 17, figs 1, 3, 4, 5), exhibit the taxonomically important maxillae, frontals and premaxillae. In both these specimens the form and estimated length of the nasals and the proportional lengths of the premaxillary/nasal and maxillary/nasal sutures agree closely with the condition in modern *V. ursinus*. The extremely short maxillary/frontal suture, which was noted by Owen (1872a), appears to be more characteristic of modern mainland *V. ursinus* than the Tasmanian or Flinders Island races, although the full range of possible variation in these characters has not been studied here. The dentition and palate of the fossil specimens are indistinguishable morphologically from modern *V. ursinus*.

While the mandibular fragments from Wellington Caves have been referred to the genus *Vombatus* on the basis of the character states listed in Table 7, they are extremely fragmentary and exhibit no characters that indicate significant variation from modern *V. ursinus*. All measurements (Table 9) fall within, or close to the observed ranges of values for modern *V. ursinus*.

Discussion. Owen (1872a) recognized close similarity between the extinct *Phascolomys mitchellii* and the 'platyrrhine' wombats (i.e. the mainland Common Wombat and the Tasmanian Wombat) in most features of the dentition and anterior cranial bones. However, he considered them to be specifically distinct on the basis of possession of certain character states typical of 'latifront' (i.e. *Lasiorhinus* sp.) wombats. These include a supposed shorter maxillary/nasal suture, the more deeply concave anterior palate, and the greater vertical depth of the maxilla beneath the anterior root of the zygomatic arch (the 'ectalveolar plate'). Similarly, he considered that the mandibular fragments exhibited a slightly more anterior origin for the coronoid process, and more forward posterior termination of the symphysis relative to the molar teeth, features that he considered to be more characteristic of 'latifront' wombats. However, the present study and the work of Merrilees (1967) have indicated that such variability is characteristically found both within and between modern populations of *V. ursinus*, with the exception of character 12, the depth of the ectalveolar plate of the maxilla, which is consistently greater in the fossils than in any modern specimens.

In view of the high degree of variability found in this study for a geographically heterogeneous sample of modern *V. ursinus* (Table 5) Tate's (1951) decision to recognize the following subspecies may be justified: *Vombatus ursinus ursinus* (Shaw, 1880) from Flinders Island; *V. u. tasmaniensis* (Spencer & Kershaw, 1910) from

TABLE 9

Dimensions (mm) of the mandible and lower teeth of Vombatus ursinus mitchelli from Wellington Caves
Numbered characters are described in Table 2. Specimen numbers refer to the Australian Museum collection (AM)

SPECIMEN	CHARACTER				
	21	22	23	24	25
F35406	9.0	8.0	4.5	6.7	51.0
F58707	7.9	7.2	—	—	47.5
F18866	8.5	8.0	—	—	—
F31055	—	—	4.7	6.8	53.5
MF721	—	—	4.3	5.7	47.0
F5373	—	—	—	—	56.5
MF720	—	—	4.5	—	52.0
F5390	—	—	3.7	—	47.0
F5401	—	—	—	—	53.0
F35404	—	—	—	—	44.0
F332	—	—	—	—	51.0
F58706	—	—	4.5	6.7	51.0
F58705	—	—	—	—	46.0
MF105	—	—	4.3	6.7	54.0
F5379	—	—	4.5	—	47.5

Tasmania, and *V. u. platyrhinus* (Owen, 1853) from eastern mainland Australia. However, a more comprehensive study, possibly considering serological, isozyme or chromosomal characters, is needed to clarify the taxonomic status of modern wombat populations. The present study has demonstrated at least one distinctive morphological character (depth of the ectalveolar plate of the maxilla) in the Wellington Caves fossils. Thus it is considered here that recognition of the fossil population from Wellington Caves as a subspecies, *V. ursinus mitchellii* (Owen, 1838), is warranted on the basis of present knowledge.

Although the mandibular fragments from Wellington Caves are indistinguishable from modern *V. ursinus* they have also been referred here to *V. u. mitchellii* as part of the topotypical sample, since the sparse data do not justify the recognition of more than one subspecies of *V. ursinus* in this fauna.

Specimens referable to species of *Vombatus*, and similar in size to modern *V. ursinus* have been reported from many other Pleistocene deposits in mainland Australia and from Tasmania. Since it has not been possible to include them in this study their specific or subspecific status is unknown.

ii) *Phascolomys parvus* Owen, 1872

Merrilees (1967) selected BM No. 32893, a partial left mandibular ramus from the eastern Darling Downs, Queensland, as a lectotype of *P. parvus* from four mandibular syntypes described and figured by Owen (1872). While Owen (1872) regarded these as specifically distinct because of their small size, Merrilees (1967) has shown that they represent juvenile specimens, and as such has demonstrated that *P. parvus* Owen is a junior synonym of *Vombatus ursinus* (as *V. hirsutus*). That BM 32893 is referable to a species of *Vombatus* is confirmed by the anterior extent of the 'ectalveolar groove' and deep masseteric fossa (characters 12 and 15, respectively in Table 1). The fossil material exhibits no taxonomic characters sufficient for further identification. It is concluded that *P. parvus* Owen is a junior synonym of *Vombatus ursinus* (Shaw).

iii) *Phascolomys pliocenus* McCoy, 1866

The holotype of *P. pliocenus* McCoy is a mandibular ramus, NMV P7422 from Dunolly, Victoria (see Mahoney and Ride, 1975). This specimen has been redescribed and refigured by Wilkinson (1978) who has presented evidence supporting the correct reference of this specimen, and others referred to *P. pliocenus* by McCoy (1874) to *Vombatus ursinus* (as *V. hirsutus*). According to criteria described in the present study NMV P7422 agrees with *V. ursinus* in size, and with a species of *Vombatus* according to characteristics of the masseteric fossa (characters 12, 14, 15 of Table 1). Other diagnostic characters are obscured by adhering matrix in this specimen. Two other specimens were referred to *P. pliocenus* by McCoy (1874), these being two partial mandibles, NMV P7441 and NMV P7442 from Lake Bullenmerrie, Victoria. Wilkinson (1978) has refigured these specimens, but they are mislabelled in plate 17 of that paper. The correct labelling should show pl. 17, figs 1 and 2 to represent NMV P7441, while pl. 17, figs 3 and 4 represent NMV P7442. These specimens have been examined by me. Both exhibit character states of the masseteric fossa and premolar and incisor teeth diagnostic for a species of *Vombatus* (characters 10-15, Table 1), probably *V. ursinus*, as suggested by Wilkinson (1978). The lower incisors of NMV P7442 vary slightly from *V. ursinus* as described here and by Merrilees (1967) in that they are somewhat more spatulate in cross section, and in that the enamel does not entirely cover the outer face of the tooth. Dimensions of I_1 of NMV P7442 are width = 0.8 mm, depth = 7.5 mm. Reference to Table 5 indicates these are within the range of *Vombatus ursinus*.

The name *Phascolomys pliocenus* McCoy is therefore considered to be a junior synonym of *Vombatus ursinus* Shaw. However, the holotype and other mandibular fragments described by McCoy (1874) cannot be referred to any subspecies of *V. ursinus* on the basis of present understanding of the characters they exhibit.

iv) *Phascolomys thomsoni* Owen, 1872

The holotype of *P. thomsoni* is a partial right mandibular ramus, probably from the eastern Darling Downs, Queensland (Mahoney and Ride, 1975), figured by Owen (1872, pl. 18, figs 8, 9; pl. 21, fig. 7). Owen (1872) recognized the similarity of this specimen to the modern 'platyrrhine' wombat, but diagnosed the species solely on its possession of narrower molars than *P. mitchellii* and *P. platyrrhinus*. Merrilees (1967) has demonstrated that this character does not distinguish between modern wombat species, even at the generic level. It cannot, therefore, suffice to describe a species of *Vombatus*. It is concluded, therefore, that *P. thomsoni* Owen is a junior synonym of *Vombatus ursinus* Shaw, supporting De Vis (1891) who had suggested its synonymy with *P. mitchellii*.

Vombatus hacketti Glauert, 1910

The holotype of *Phascolomys hacketti* Glauert is an incomplete skeleton including a cranium and mandible, no. 60.10.3 in the Western Australian Museum. The specimen is from the Pleistocene 'Le Soeuf deposit' of Mammoth Cave, Western Australia (Archer *et al.*, 1980). The skull, mandible and postcranial elements have been described in Glauert's original diagnosis of the species (Glauert, 1910). It was only possible to examine the edentulous skull (Fig. 4A-C) during the present study. The dimensions of the skull for numbered characters described in Table 1 are as follows: 1) Basicranial length = 163.0 mm; 4) Maximum length nasals = 80.0 mm; 5) Maximum length frontals = 56.0 mm; 6) Maximum posterior width nasals = 48.0 mm; 7) Anterior width nasals = 11.0 mm; 8) Length anterior nasal projection = 10.5 mm; 10) Length premaxillary/nasal suture = 39.0 mm; 12) Depth ectalveolar plate of

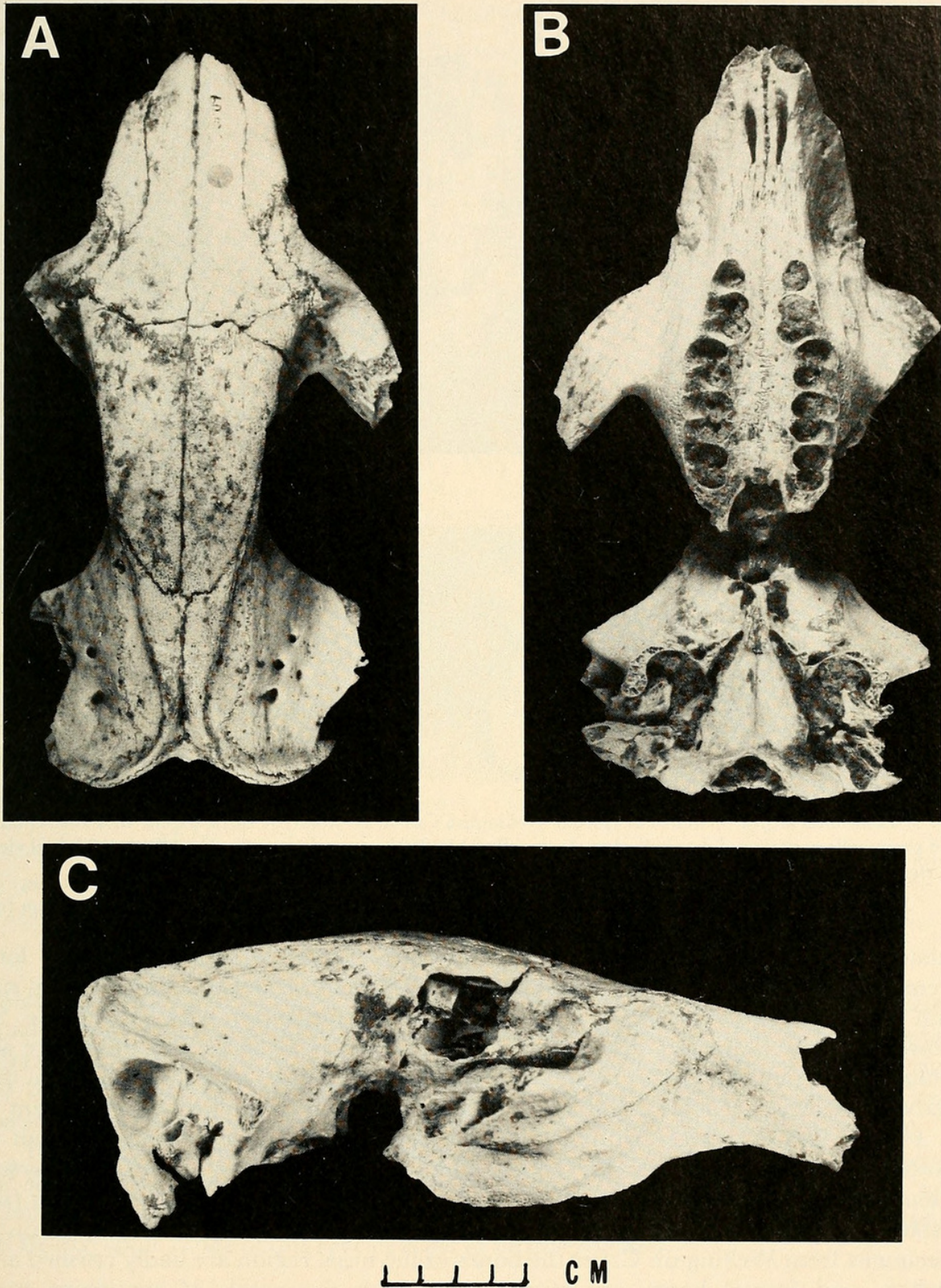


Fig. 4. Holotype skull of *Vombatus hacketti* (Glauert, 1910), Western Australian Museum No. 0.10.3 from Mammoth Cave, Western Australia. A, Dorsal view. B, Ventral view. C, Right lateral view.

maxilla = 17.5 mm; 14) Length upper cheek tooth row = 54.5 mm; 16) Width palate between posterior lobes of M_2 = 6.0 mm.

That this skull is referable to a species of *Vombatus* is supported by the following characters, as described in Table 1: 1) long narrow nasals; 4) grooved P^3 ; 5) narrow

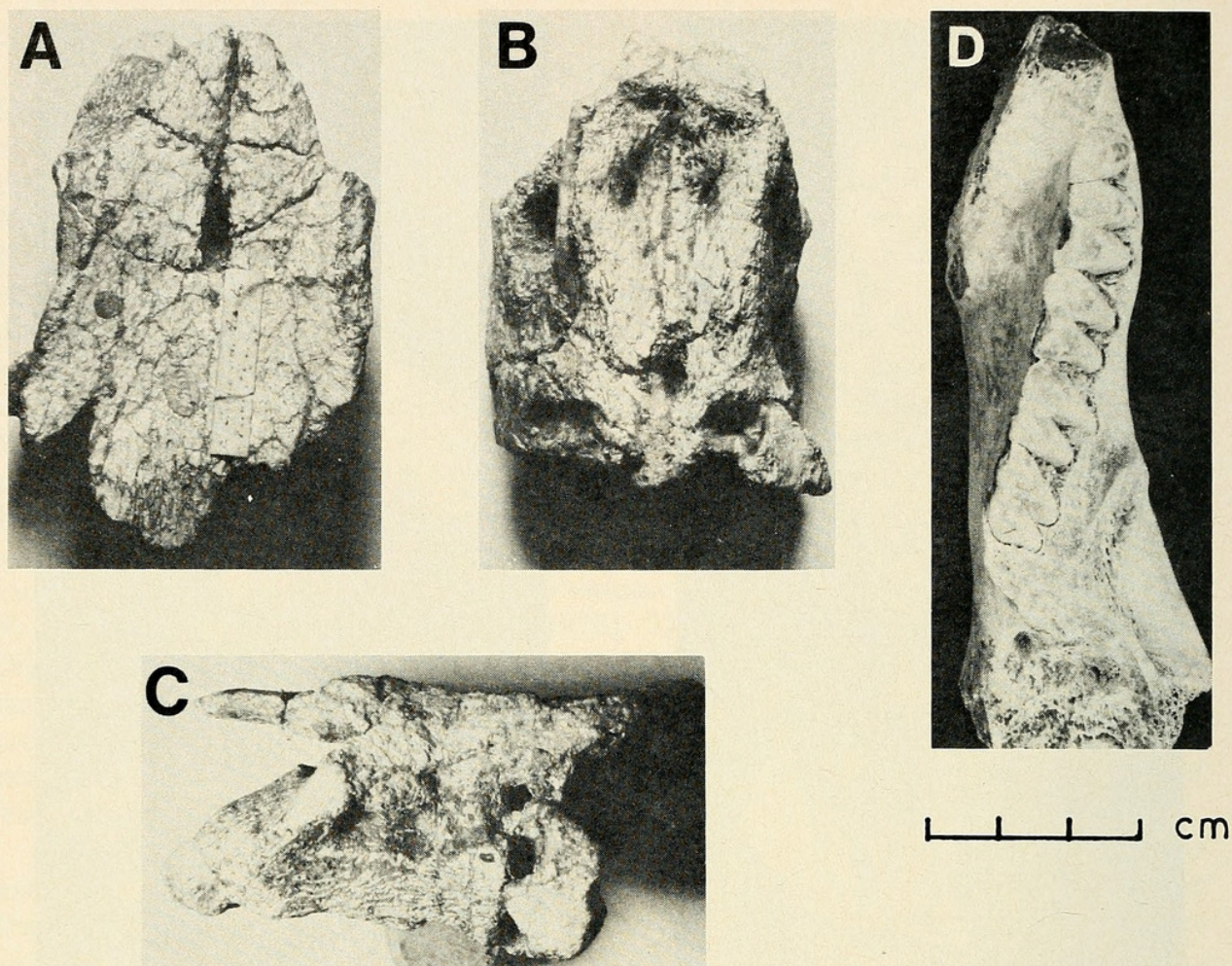


Fig. 5. *Lasiorhinus krefftii* (Owen, 1872) from Wellington Caves. **A**, holotype of *L. krefftii*, BM 42601, nasal and premaxillary region of the skull, dorsal view. **B**, BM 42601, ventral view. **C**, BM 42601, left labial view. **D**, right mandibular ramus, AM F35405, with P₃, M₂₋₅, occlusal view.

palate between M²⁻²; 7) narrow flat anterior palate; 8) proportionately long premaxillary/nasal suture. The Mammoth Cave skull shows general agreement in size with modern *Vombatus ursinus* in most characters measured here (see Table 5). However, three characters distinguish it from modern *V. ursinus*. The nasals are absolutely and relatively longer than in any modern or fossil *V. ursinus* measured in this study (character 4, Tables 2 and 3); postorbital processes of the frontals are absent in *V. hacketti*; and the depth of the ectalveolar plate of the maxilla is greater than in modern *V. ursinus* (character 12, Tables 2 and 3). In this latter character *V. hacketti* resembles specimens from Wellington Caves, here ascribed to *V. ursinus mitchellii* (see Table 8). Further comparison between the two fossil forms is difficult, since in all specimens from Wellington Caves the bones of the nasal region are badly crushed and broken, and frontal bones are missing. Although the nasals of specimens from Wellington Caves cannot be measured, their estimated length is not greater proportionately than nasals of modern *V. ursinus*. Thus it appears that the Mammoth Cave skull is unique in having nasals which are much longer, both absolutely and relative to their width and to the length of the frontals. Glauert (1910) also noted that the skull of *V. hacketti* was characterized by greater intertemporal constriction than modern *V. ursinus*. There are no teeth in the holotype skull. The alveoli for I¹ suggest that these teeth are less triangular in cross-section than I¹ of modern *V. ursinus* or of *V. u. mitchellii* from Wellington Caves. Glauert (1910: 18) has described loose incisor teeth from

TABLE 10

List of specimens of Lasiorhinus krefftii (Owen) from Wellington Caves in the Australian Museum (AM numbers)
The table indicates the characters present in each specimen in the state diagnostic for the genus Lasiorhinus. These characters are described in Table 1

SPECIMEN NUMBER	DESCRIPTION	CHARACTERS DIAGNOSTIC FOR <i>LASIORHINUS</i>
F35405	Right mandibular ramus, P ₃ , M ₂₋₅	10, 11, 12, 14, 15p
F51851	Left and right mandibular rami, I ₁ (broken), right P ₃ , M ₂₋₅	10, 11, 14
F58704	Right mandibular ramus, I ₁ (broken), P ₃ , M ₂₋₅	9, 10, 12, 14
F5400	Anterior symphysis of mandible, edentulous	10, 13
F5389	Right mandibular fragment, edentulous	12
F5393	Right mandibular fragment, M ₃₋₅	12, 15p
F5394	Right mandibular fragment, P ₃ , M ₂₋₄	11, 12
F5385	Right mandibular fragment, M ₄₋₅	12, 15np
F5392	Right mandibular fragment, edentulous	12
F5388	Left mandibular fragment, P ₃ , M ₂₋₅	11, 12
F5391	Right mandibular fragment, edentulous	12, 15np
F51853/4	Left and right rami, right P ₃ , M ₂₋₄	11, 12, 14, 15np
F5331	Right mandibular fragment, P ₃ , M ₂₋₅	11, 12, 15np
F5323/97	Left mandibular ramus, M ₂₋₅	12
F5309	Right mandibular fragment M ₃₋₅	12, 15p
F5320	Right mandibular fragment, P ₃ , M ₂₋₅	11, 12, 15np
MF719	Crushed rostral region of skull with right I ¹ , left and right P ³ , M ²⁻⁵	1, 2, 4, 5, 6, 8
F5403/4	Palate with left P ³ , M ²⁻⁵ , right P ³ , M ²⁻³	4, 5, 6
F58702	Palate fragment, right P ³ , M ²⁻⁵ , left M ²⁻⁴	4, 5, 6

(p) perforate.

(np) non-perforate.

Mammoth Cave that '... have no sharp anterior edge, ... their section, too, being broad and oval', supporting the suggestion from the holotype that I¹ of *V. hacketti* differs from that tooth in *V. ursinus*. Glauert (1910) has noted features of the sacrum and scapula which he considers to be uniquely characteristic of *V. hacketti*. These characters have not as yet been studied sufficiently to support their taxonomic value.

It is considered that the differences noted here between the Mammoth Cave skull and skulls of modern *V. ursinus* and the Wellington Caves fossil subspecies are sufficient for its recognition as a distinct species, *Vombatus hacketti* Glauert. The geographic and stratigraphic range of this species is yet to be investigated.

Genus *LASIORHINUS* Gray, 1863

Lasiorhinus krefftii (Owen, 1872)

Synonymy: *Phascolomys gillespiei* De Vis, 1900, *Lasiorhinus latifrons barnardi* Longman, 1939, *Phascolomys krefftii* Owen, 1872.

The holotype of *Phascolomys krefftii* Owen is a partial cranium with broken upper incisors, from the 'Breccia Cave', Wellington Caves, New South Wales, BM 42601 (Fig. 5A-C) (Mahoney and Ride, 1975). Paratypes are three mandibular fragments,

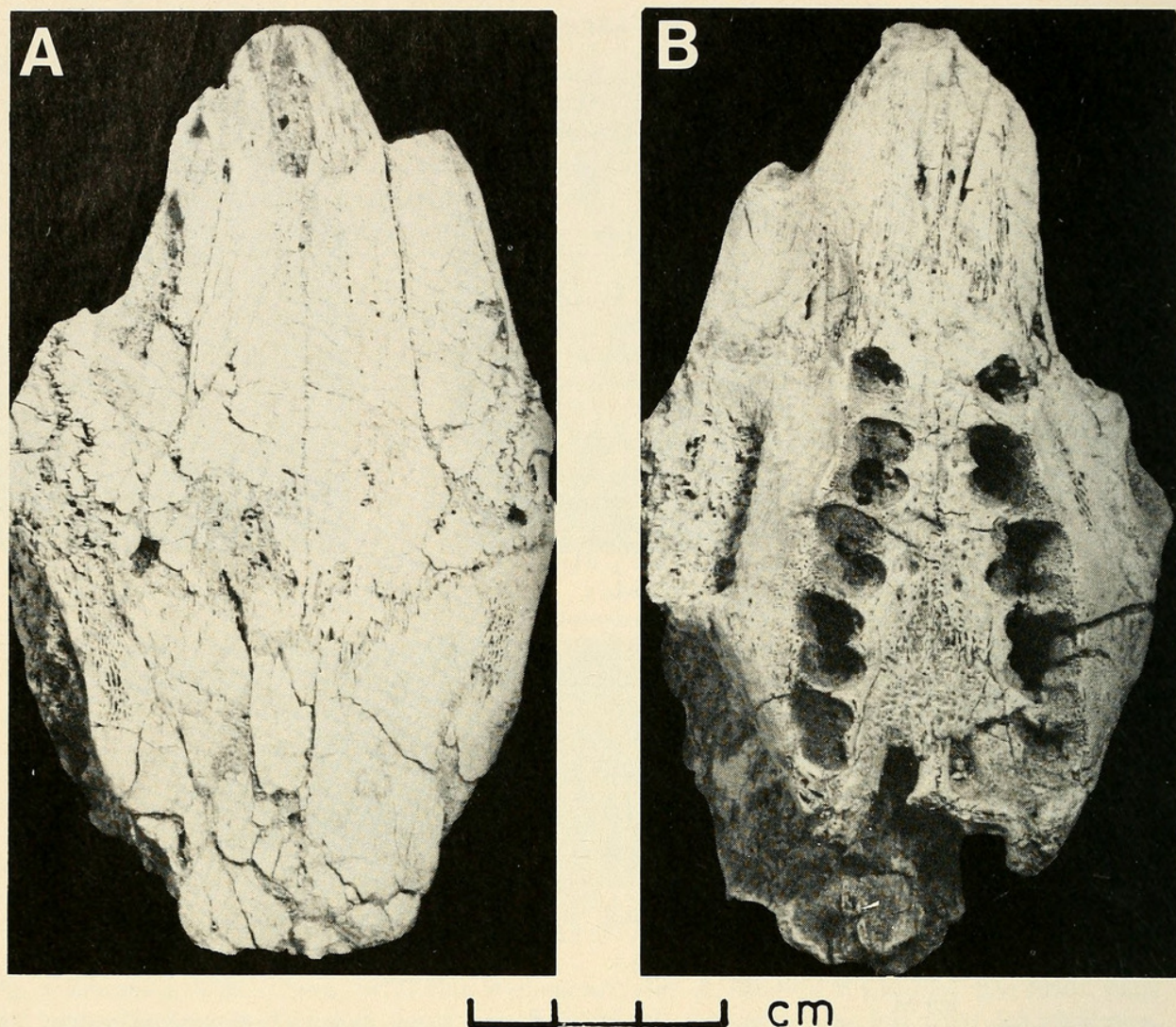


Fig. 6. The skull, AM MF719, of *Lasiorhinus krefftii* (Owen, 1872) from Wellington Caves. **A**, dorsal view. **B**, palatal view, with left and right P_3 , M_{2-3} , left M_4 , and left and right M_5 .

BM 42609 Owen 1872a pl. 19, fig. 4; pl. 21, fig. 4; pl. 22, fig. 4), BM 42610 *ibid.* pl. 19, fig. 3; pl. 22, fig. 6; pl. 23, fig. 5), and BM 42602 (*ibid.* pl. 20, fig. 2; pl. 23, fig. 4; pl. 22, fig. 7). The Australian Museum collection from Wellington Caves contains a further three fragments of the skull and maxilla: AM MF719 (Fig. 6A-B), F5403/4 and F58702; and sixteen mandibular fragments: AM F35405 (Fig. 5D), F51851, F58704, F5400, F5389, F5393, F5394, F5385, F5392, F5388, F5391, F51853/4, F5331, F5323/F5397, F5309, F5320, which have been referred to *L. krefftii*. These specimens are described in Table 10 which also lists the characters by which each has been identified as belonging to a species of *Lasiorhinus*.

Measurement and comparisons. Fossil material referable to *Lasiorhinus krefftii* (Owen) from Wellington Caves has been compared with skulls of modern hairy-nosed wombats from Clermont and Moonie River in Queensland and from Deniliquin in New South Wales (see Table 5) and with a sample of seven skulls of modern *L. latifrons* from South Australia (Table 4). Measurements for all metric characters of taxonomic importance evident in the fossil sample are given in Tables 11 and 12.

The fossil specimens, BM 42601 and AM MF 719, exhibit the taxonomically important nasal, maxillary and premaxillary bones, and the naso-frontal suture (Figs 5

TABLE 11

Dimensions (mm) of the cranium and upper dentition of Lasiorhinus krefftii (Owen) from Wellington Caves
Numbered characters are described in Table 2

CHARACTER	AM MF719	BM 42601	AM F58702	AM F5403/4
4	71.5	70.0a	—	—
6	59.0	—	—	—
7	38.5	36.0a	—	—
8	23.0	21.0	—	—
10	13.0	13.0a	—	—
12	16.0	—	19.0	21.0
14	52.5	—	48.0	48.5
16	10.5	—	9.5	8.5
17	—	—	7.5	8.0
18	5.6	—	5.0	5.0
19	10.8	—	—	—

(a) approximate measurement.

and 6). Both agree with specimens from Clermont, Moonie River, and Deniliquin and are distinct from *L. latifrons* from South Australia in the greater length, relative to the width, of the nasals (characters 4 and 6, Table 2); in the longer anterior projection of the nasals (character 8, Table 2); and the greater enamel width of I¹ (character 19, Table 2). In both fossil skulls the naso-frontal suture runs perpendicular to the long axis of the skull laterally, but is directed posteriorly toward the midline (i.e. there is a median backward projection of the nasals into the frontals) and is extremely convoluted toward the midline. AM MF719 shows the maxilla to have a narrow posterior extension which forms a short, convoluted suture with the frontal, as is found in one specimen from Deniliquin (NMV C6228), in all skulls from Clermont, and as occasionally found in *L. latifrons* from South Australia (e.g. AM M8092). The anterior projection of the nasals (character 8, Table 2) is relatively longer in the fossils than in *L. latifrons*, within the observed range of values for specimens from Moonie River and Deniliquin, but shorter than in specimens from Clermont. Neither specimen from Wellington Caves exhibits any downward deflection of the anterior nasal projection, a character state found in the skulls from Queensland and Deniliquin.

Of the fragmentary fossil mandibular specimens here referred to *L. krefftii* (see Table 10) few possess taxonomically useful metric characters. All available data are presented in Table 12. One specimen, F58704, has I₁ deeper and wider (characters 21 and 22, Table 2) than observed in modern *L. latifrons*, but within the observed range of Clermont wombats. Other data fall within the observed range of *L. latifrons* from South

TABLE 12

Dimensions (mm) of the lower teeth of Lasiorhinus krefftii (Owen) from Wellington Caves
Numbered characters are described in Table 2

CHARACTER	AM F35405	AM F51851	AM F58704	AM F5331	AM F5320
21	—	—	7.5a	—	—
22	—	—	9.0a	—	—
23	5.3	5.7	—	5.1	4.6
25	52.0	50.0	54.0	47.5	47.1

(a) approximate measurement.

Australia. The ectalveolar groove of the fossil specimens extends forward to the anterior lobe of M_4 (as observed in the Deniliquin wombats) except in F51853/4, where it only reaches the posterior lobe of that tooth. The masseteric fossa is relatively shallow in the fossils and non-perforate, except in AM F35405, F5393, and F5309, in which a small masseteric foramen is present.

Discussion. Owen (1872a) named the species *Phascolomys krefftii* on the basis of a single crushed cranium (the holotype), and several mandibular fragments from the Wellington Caves. He recognized the close similarity of the holotype to the modern species, *Lasiorhinus latifrons* and noted, as the sole distinguishing feature of this cranium, the posteriorly-directed projection of the nasals at their median suture with the frontals (Owen, 1872a: 178). He distinguished the referred mandibular fragments from *L. latifrons* by the more backward extent of the symphysis, by the slightly longer and deeper ectalveolar groove, by some slight variations in the shape of the ridges bounding the non-perforate masseteric fossa, and on his assessment that the molar teeth were narrower than in *L. latifrons*. In the same publication he stated that other mandibular fragments from Wellington Caves were indistinguishable from modern *L. latifrons*. The larger sample available in the present study supports the distinction of the Wellington Caves fossils from modern South Australian *L. latifrons*, the only living species of *Lasiorhinus* known to Owen.

Wilkinson (in Merrilees, 1973) proposed the synonymy of *Lasiorhinus krefftii* and the modern Queensland species, *L. barnardi* and *L. gillespiei*, but presented no supporting data. While some differences in size and anatomical detail have been recorded here between the skulls of the hairy-nosed wombats from Clermont, Moonie River, and Deniliquin, this is comparable in degree to differences found by Crowcroft (1967) between geographic races of *L. latifrons* from South Australia and to the differences indicated here, and by Merrilees (1967) between sub-species of *Vombatus ursinus*. Therefore the modern hairy-nosed wombats from Queensland and from Deniliquin are considered conspecific. The synonymy of this modern species with *L. krefftii* from Wellington Caves, and its distinction from *L. latifrons* is supported by the following characteristics comparable in fossil and modern skulls: length of nasals relative to their width, greater anterior width of nasals, the longer anterior projection of the nasals, and the greater enamel width of I^1 . Fossils of *L. krefftii* share a tendency with modern *L. krefftii* to have a shorter premaxillary/nasal suture than *L. latifrons*. However, this suture is absolutely shorter in the Wellington Caves specimens than in any modern wombat. A median backward projection of the nasals at their suture with the frontals, not observed in *L. latifrons*, was found in *L. krefftii* from Wellington Caves, Moonie River and Deniliquin, but not in specimens from Clermont, all of which have a median forward projection of the frontals into the nasals. Crowcroft (1967) indicated that variation in this character distinguished between geographic races of modern *L. latifrons*.

Mandibular fragments from Wellington Caves exhibit few taxonomically useful characters. The single lower incisor available (AM F58704) is wider and deeper than I_1 of *L. latifrons*, and similar in size to I_1 of the Clermont wombats. Other dental dimensions are within, or only slightly greater than the observed ranges of *L. latifrons*. The fossils resemble wombats from Deniliquin in the more anterior origin of the coronoid process (ectalveolar groove) at the level of the anterior lobe of M_4 . Other characters, such as the depth of the masseteric fossa and presence or absence of a masseteric foramen, are variable and have been shown to have no taxonomic value at the species level. Thus the data from mandibles alone would not exclude the possibility that *L. latifrons* was present in the Wellington Caves deposits, as suggested by Owen

(1872a). However, there are insufficient data to support the recognition of more than one species in that deposit. All mandibular specimens from Wellington Caves which are referable to a species of *Lasiorhinus* have here been referred to *L. krefftii* as part of the topotypical sample.

Wilkinson (in Merrilees, 1973) has reported *L. krefftii* from late Pleistocene deposits at Lake Tandou, Lake Menindee and Lake Victoria in New South Wales. These specimens were not available for this study. The present disjunct distribution of *L. krefftii* in the modern fauna supports the hypothesis that these populations represent relicts of a previously greater range from southeastern Queensland, through inland New South Wales, to northern Victoria as suggested by Wilkinson (in Merrilees, 1973).

?Lasiorhinus angustidens De Vis, 1891

Phascolomys angustidens was named by De Vis (1891) for three mandibular fragments (see Mahoney and Ride, 1975) from the eastern Darling Downs, Queensland. De Vis (1891) only compared this material with Owen's fossil *Phascolomys mitchelli*, shown here to be a subspecies of *Vombatus ursinus*. That the material referred by De Vis (1891) to *angustidens* represents a species of *Lasiorhinus* is indicated by the proportions of the alveolus of I_1 (character 9, Table 1), by the shape of P_3 (character 11, Table 1), and the anterior extent of the 'ectalveolar groove' (character 12, Table 1) in QM F2921, selected here as the lectotype of *Phascolomys angustidens* De Vis, 1891. The present study has indicated that characters of the mandible alone are generally insufficient to distinguish between species of *Lasiorhinus*.

Wilkinson (in Hope and Wilkinson, 1982) has suggested that *angustidens* belongs in *Phascolonus*, although he has given no justification for this decision. Several features of *Lasiorhinus angustidens* argue against such allocation. It does not have a vertical labial groove on P_3 , considered by Dawson (1981) to be a derived feature in *P. gigas*, nor are the molar lobes of *L. angustidens* separated by a deeply U-shaped median valley, as in *Phascolonus gigas*.

Dawson (1983) has pointed out that '*Phascolomys*' *medius* is dentally very similar to species of *Lasiorhinus*, although features of its palate differ greatly from species of *Lasiorhinus*. With this in mind it is conceivable that the mandibular fragments here assigned to *L. angustidens* could represent '*Phascolomys*' *medius*. They are much smaller than mandibles referred to '*P.*' *medius* by Owen (1872b), but could represent juveniles of that species, as *Phascolomys parvus* Owen represented juveniles of *Vombatus ursinus* (Merrilees, 1967). There is, however, no way to test this hypothesis at present. Until more conclusive evidence becomes available the name *angustidens* must be considered to be available for a species of *Lasiorhinus*.

Genus *WARENDJA* Hope & Wilkinson, 1982

Warendja wakefieldi Hope & Wilkinson, 1982

This species is known from two mandibles, and some isolated upper teeth (premolars and molars) from Pleistocene deposits in McEacherns Cave, Victoria. The characters of the mandible and its ascending ramus, as described by Hope and Wilkinson (1982) are atypical of other known wombats, but are apparently plesiomorphic among diprotodonts. With one exception (the depth of I_1 relative to its width) all dental characters of *W. wakefieldi* are plesiomorphic for vombatids according to the criteria described by Dawson (1981, 1983). Because of the preponderance of plesiomorphic characters in material described so far it is not yet possible to establish the phylogenetic relationships of *W. wakefieldi* to other Pleistocene or Tertiary vombatids.

GENERAL DISCUSSION

The preceding study has clarified taxonomic concepts of small fossil wombats from the Pleistocene, at least as far as possible with current understanding of the taxonomy of related modern forms. The Northern Hairy-Nosed Wombat, now extant only at Clermont, Queensland, apparently represents a relict population of *Lasiorhinus krefftii*, once widely distributed throughout New South Wales and southern Queensland. However, there is, as yet, no indication of the origin, or past distribution of the modern Southern Hairy-nosed Wombat, *Lasiorhinus latifrons*.

The correct taxonomic status of geographic variants of the Common Wombat, *Vombatus ursinus*, both fossil and modern, has yet to be established. Preliminary studies of variation in *V. ursinus* (Merrilees, 1967, and the present study) indicate the possibility that the geographically and stratigraphically isolated groups recognized here and by Tate (1951) as subspecies of *V. ursinus* could represent full species. A comprehensive study of modern populations, based on characters such as chromosome number and morphology, serology, or allozymes is needed before the taxonomic significance of morphological variation in these wombats can be fully understood. If such a study supported the recognition of more than one species of *Vombatus* in the modern fauna, it is likely that *V. mitchellii* from Wellington Caves could represent a distinct species of *Vombatus* rather than a sub-species of *V. ursinus* as designated here. Recognition here of *Vombatus hacketti* from Mammoth Cave as a full species is a reflection of the more complete cranial material available for that species.

The poor understanding of morphological variation in both 'common' and hairy-nosed wombats obscures knowledge of the stratigraphic range and the phylogeny of these small vombatids. Tooth and jaw fragments in the size range of species of *Lasiorhinus* and *Vombatus* are known from many Pleistocene deposits throughout Australia, but without cranial material (at least) their specific status cannot be confidently established, at present.

As yet no representatives of *Vombatus*, *Lasiorhinus* or *Warendja* are known from Tertiary faunas. The only record of any Tertiary vombatid resembling the modern species in size is a partial molar recorded by Rich (1980) from the Pliocene Hamilton fauna of Victoria. Large species representing at least three other vombatid genera (*Phascolonus*, *Ramsayia* and *Rhizophascolonus*) have been described from Tertiary faunas (Archer and Bartholomai, 1978; Dawson, 1981). However, the phylogenetic relationships of these genera, and of *Lasiorhinus* and *Vombatus* are still obscure (see Dawson 1983). Cladistic analysis of vombatid dental and palatal characters (Dawson, 1981, 1983) has indicated that *Vombatus ursinus* is the most plesiomorphic species of Quaternary and modern faunas. *Warendja wakefieldi* was not included in those analyses. The scant material so far described suggests that this species is so far removed from other fossil and modern wombats that it may even represent a distinct subfamily.

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