QUATERNARY GIBBONS FROM THE MALAY ARCHIPELAGO

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CONTENTS

INTRODUCTION

In the years 1888-1890 Eug. Dubois explored a number of limestone caves in the Padang Highlands, central Sumatra, and made a large collection of teeth of a great variety of mammals. The fauna is characterized by the relative abundance of orang-utan (more than 3000 teeth: Hooijer, 1948), and contains no extinct species. The cave teeth differ from their homologues in recent skulls of the same species only by their greater average size; in several cases examined the differentiation has proceeded to the stage of good temporal subspecies [1]). The Sumatran cave fauna has been referred to the prehistoric portion of the Holocene by Dubois (1891, p. 93), and so far no more precise statement can be made; a few thousand years would suffice for the subspecific advance shown by various recent Sumatran mammal species over their representatives in the cave fauna of the same island.

1) For summaries of and references to the cases of the orang-utan, porcupine, tiger, tapir, and rhinoceroses, see Hooijer, 1949; for the elephant, see Hooijer, 1955, and for the bovids, see Hooijer, 1958.

The object of the present paper is the collection of gibbon teeth from the prehistoric caves of Sumatra in the Dubois collection. Dubois has never even mentioned that his collection from the Sumatran caves contained any gibbon material; no reference to these is found in his papers. In 1940 Von Koenigswald gave a list of the fossil Primates from Pleistocene deposits in Java, comprising *Symphalangus syndactylus,* and *Hylobates "leuciscus"* as well as *Hylobates* spec. (Von Koenigswald, 1940, p. 63). The first and second of these are stated to occur both in the Djetis and in the Trinil faunas, the last is recorded from the Djetis fauna exclusively. The age of these two faunas is Middle Pleistocene (Hooijer, 1952b). Finally, Pleistocene teeth from two fissure deposits in Java have been recorded by Badoux (1959) as *Symphalangus syndactylus,* and *Hylobates* cf. *"leuciscus"*. These deposits are regarded by Badoux (l.c., p. 136) as transitional between the Middle and the Upper Pleistocene.

While no material of gibbons has ever been recorded from the cave deposits of Java, and no further material has been collected in the Sumatran caves since Dubois explored them seventy years ago, gibbon material has recently been found at Niah Great Cave in Sarawak, Borneo (Medway, 1959). This material, which will be described by me in a forthcoming issue of The Sarawak Museum Journal, will be referred to in the present paper for the sake of completeness.

Recent material of Southeastern Asiatic gibbons has been examined in the Leiden Museum (registered below as L.M.), in the Zoological Museum at Amsterdam (A.M.), and in the British Museum (Natural History) in London (B.M.). The following measurements have been taken:

Calvarium

1. Greatest length (prosthion—opisthocranion).
2. Basal length (prosthion—basion).
3. Length of cranial cavity (from basion).
4. Greatest width of brain case.
5. Biorbital width.
6. Postorbital constriction.
7. Height of calvarium (projective height from basion to vertex, perpendicular to ear-eye horizon).

Mandible

8. Total length (infradentale—gonioncaudale).
9. Length of ramus ascendens.

10. Bicondylar width (across outer edges).
11. Height of symphysis.
12. Height of ramus horizontalis (a) at middle of P_3.
13. Idem (b) at middle of M_3.
14. Height of ramus ascendens (from deepest point of incisura semilunaris to gonionventrale).

These measurements will be indicated by the above numbers in the tables of skull measurements. In addition, I have taken dental measurements, which are self-explanatory, and I have employed some statistics: n = the number of variates; R = range of variation; M = mean; σ = standard deviation; C = coefficient of variation. The standard deviation, σ, is $\sqrt{\frac{\Sigma e^2}{n-1}}$ in which e is the deviation of every single variate from the mean. The variation coefficient, C, is $\frac{\sigma \cdot 100}{M}$. The standard error of a difference, $E_{diff.} = \sqrt{E_{M rec.}{}^2 + E_{M subf.}{}^2}$. These standard errors ($E_M = \frac{\sigma}{\sqrt{n}}$) are necessary to determine whether the difference in average size found between two series of variates has statistical significance; differences between the means more than two times greater than the standard error of the difference may be considered significant for subspecific differentiation (see Hooijer, 1950, p. 11).

All measurements recorded in the present paper are in mm.

Order PRIMATES Linnaeus
Family PONGIDAE Elliot
Genus SYMPHALANGUS Gloger

Symphalangus syndactylus syndactylus (Raffles)

Material examined:

Infants

1. Skull. Deli, N.E. Sumatra, coll. L. P. de Bussy. A.M.
2. Mounted skin of female. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. h.

Juveniles

3. Skull. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. d.
4. Skull. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. e.
5. Skull of male. Tandjoeng Morawa, N.E. Sumatra, coll. B. Hagen. L.M., cat. ost. l.
6. Mounted skin and skull of male. Telok Betong, S. Sumatra, from the Rotterdam Zoo, 11-5-1923. L.M., reg.no. 1223.

7. Mounted skin of female (skull inside). Padang, W. Sumatra, from C. G. C. Reinwardt, 1823. L.M., cat. syst. e.
8. Mounted skin of male. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. f.
9. Mounted skin of female. Padang, W. Sumatra, from S. Müller, 1834. L.M., cat. syst. g.
10. Flat skin of male. Palembang, S. Sumatra, from the Rotterdam Zoo, 3-7-1924. L.M., reg.no. 1326.

Subadults

11. Skeleton of male. "Java", from S. Müller. L.M., "*Hylobates leuciscus*", cat. ost. b.
12. Skull. Padang Highlands, central Sumatra, coll. J. F. Snelleman, 1878. L.M., cat. ost. n.
13. Flat skin and skeleton of male. From the Rotterdam Zoo, 29-9-1925. L.M., reg.no. 1421c.
14. Skull of female. From the Amsterdam Zoo, 3-9-1928. A.M.
15. Skull of female. Sumatra, from the Amsterdam Zoo, 6-7-1931. A.M.
16. Skull of male. Boekit Simpang, Moeara Laboe, W. Sumatra, from the Amsterdam Zoo, 11-8-1931. A.M.
17. Flat skin and skeleton of female. From the Rotterdam Zoo, 12-12-1935. L.M., reg.no. 2403.

Adults (sex not recorded)

18. Skull. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. b.
19. Skull. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. c.
20. Skull. Padang Highlands, central Sumatra, coll. J. F. Snelleman, 1878. L.M., cat. ost. m.
21. Incomplete skull. Boea, Padang Highlands, central Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 5021.
22. Sixteen teeth of an animal that died in captivity in Soerabaja, Java, in 1929. Coll. W. C. van Heurn. L.M., reg.no. 2688.
23. Flat skin (skull inside). Achin, N. Sumatra, coll. Rookmakers, 10-10-1930. L.M., reg.no. 5100.

Adult males

24. Skeleton. Batang Singalang, central Sumatra, from S. Müller. L.M., cat. ost. a. Supernumerary premolar in left maxillary.
25. Skull. Marolam, N.E. Sumatra, coll. B. Hagen, 15-10-1880. L.M., cat. ost. g.
26. Skull. Tandjoeng Morawa, N.E. Sumatra, coll. B. Hagen, 24-2-1880. L.M., cat. ost. k.
27. Mounted skin and skeleton. Pangkalan Brandan, N.E. Sumatra, from the Rotterdam Zoo, 3-5-1923. L.M., reg no. 1220.
28. Skull. Ajer Poetih, Padang Highlands, central Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4614.
29. Skull. Ogan Oeloe, Palembang, S. Sumatra, from the collection of E. Dubois, 1941. L.M., reg no. 4617.
30. Skull. Upper Bintoehan, S. of Benkoelen, S. Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4618.
31. Skull. Goenoeng Sago, Boekit Nantiga, central Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4620.
32. Calvarium. Telok Betong, S. Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4676.
33. Skull. Ajer Poetih, Padang Highlands, central Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4615.

34. Skull. Tandjoeng Morawa, N.E. Sumatra, from the Amsterdam Zoo, 26-12-1930. A.M.
35. Mounted skin. Padang, W. Sumatra, from S. Müller, 1837. L.M., cat. syst a.
36. Mounted skin (skull inside). Padang, W. Sumatra, from S. Müller, 1837. L.M, cat. syst. c.
37. Flat skin. Poeloe Sangkar, Korinchi, central Sumatra, coll. E. Jacobson, 1-6-1920. L.M., reg.no. 991.

Adult females

38. Skull. Tandjoeng Morawa, N.E. Sumatra, coll. B. Hagen, 2-8-1880. L.M., cat. ost. f.
39. Skull. Marolam, Deli, N.E. Sumatra, coll. B. Hagen, 20-9-1880. L.M., cat. ost. h. Malformed M^3 and M_3 sin.
40. Skull. Tandjoeng Morawa, N.E. Sumatra, coll. B. Hagen, 1-4-1880. L.M., cat. ost. i.
41. Skull. Bander Laboean, Deli, N.E. Sumatra, coll. B. Hagen, 1-11-1880. L.M., cat. ost. j.
42. Mounted skin and skeleton. Tandjoeng Johore, N.E. Sumatra, from R. van Prehn Wiese, 29-12-1904. L.M., cat. syst. m, cat. ost. o.
43. Stuffed skin and skull. N.W. slope of Mt. Ophir, central Sumatra, coll. E. Jacobson, 19-5-1917. L.M., reg.no. 1013.
44. Skull. Soengei Karang, N.E. Sumatra, coll. F. C. van Heurn, 15-6-1919. L.M. There is a fourth molar in the left maxillary.
45. Stuffed skin and skull. From the Rotterdam Zoo, 22-5-1935. L.M., reg.no. 2332.
46. Skull. Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 2682.
47. Skull. Ogan Oeloe, Palembang, S. Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4619.
48. Calvarium. Benkoelen, W. Sumatra, from the collection of E. Dubois, 1941. L.M., reg.no. 4675.
49. Skull. From the Amsterdam Zoo, 29-4-1934. A.M.
50. Mounted skin (skull inside). Padang, W. Sumatra, from S. Müller, 1837. L.M., cat. syst. b.
51 Mounted skin (skull inside). Padang, W. Sumatra, from S. Müller, 1837. L.M., cat. syst. d.

Symphalangus syndactylus continentis Thomas

Material examined:

Adult males

1. Skin and skull (type). Semangko Pass, Selangor-Pahang Boundary, Malay Peninsula, coll. H. C. Robinson, 26-1-1908. B.M., no. 8.7.20.1.
2. Skin and skull. Goenoeng Tahan, Pahang, Malay Peninsula, coll. H. C. Robinson, 1906. B.M., no. 6.10.4.1.

Adult females

3. Skin and skull. Semangko, Selangor. B.M., no. 10.10.1.4.

Thomas (1908, p. 301) noted that there are no external differences between the subspecies from Sumatra and the Malay Peninsula, but that the size of the peninsular form would be rather less than that of the Sumatran *syndactylus*. I have measured a series of Sumatran skulls, and compared them with the British Museum skulls only to find trifling differences, as will be seen from tables 1 and 2. But there is no doubt a tendency for the peninsular specimens to be smaller than their Sumatran relatives, and Thomas's subspecies may be maintained for the sake of convenience. I have not found any significant differences in the quality of the fur of the Sumatran specimens, but it should be noted that Pohl (1911) found skins from animals living at about 1500 m altitude to have longer and fuller fur than those from lowland animals.

TABLE 1

Skull measurements of adult males of *Symphalangus syndactylus*

		syndactylus (Sumatra)				*continentis* (Malaya)	
No.	n	R	M	σ	C	1	2
1	11	122-138	129	6.4	5.0	127	123
2	11	90-109	100	5.8	5.8	93	93
3	11	62-73	69	3.9	5.7	63	66
4	11	62-70	68	2.7	3.9	62	68
5	11	66-80	74	4.9	6.6	70	70
6	11	42-52	48	3.0	6.3	43	47
7	11	50-59	55	2.9	5.3	50	53
8	10	82-100	90	5.4	6.0	86	84
9	10	31-40	35	3.0	8.6	35	30
10	10	61-77	70	6.0	8.6	69	72
11	10	23-29	26	2.1	8.0	25	24
12	10	18-23	20	1.9	9.5	18	18
13	10	14-19	17	1.5	8.8	16	14
14	10	28-37	31	3.3	10.6	32	28

TABLE 2

Skull measurements of adult females of *Symphalangus syndactylus*

		syndactylus (Sumatra)				*continentis* (Malaya)
No.	n	R	M	σ	C	3
1	12	112-126	121	3.8	3.1	116
2	12	85-95	91	3.2	3.5	87
3	12	60-69	66	2.5	3.8	68
4	12	62-71	66	2.8	4.2	65
5	12	62-73	67	3.2	4.8	—
6	12	46-52	49	2.0	4.1	45
7	12	48-56	54	2.4	4.4	53
8	11	77-84	80	2.3	2.9	79
9	11	27-34	31	2.5	8.1	30
10	11	62-69	65	2.2	3.4	—
11	11	21-27	23	1.9	8.3	19
12	11	16-20	18	1.8	10.0	16
13	11	13-17	15	1.1	7.3	14
14	11	24-31	28	2.2	7.9	31

As already related in a previous paper (Hooijer, 1952a) there are marked differences in size and proportions between the male and the female skulls of *Symphalangus syndactylus syndactylus*; the male skull is, on an average, larger than the female, with a proportionally narrower brain case, more projecting orbits, deeper postorbital constriction, and lesser height. The mandible as a whole is relatively larger in the male than in the female, but proportionally narrower. From the few data at present available on the continental siamang it would seem that the sexual differences in the skull of this subspecies are as marked as those in the Sumatran form. In the species of *Hylobates* examined the sexual differences in the skull are less pronounced than those in *Symphalangus*; this is, perhaps, a primitive trait in the larger form as compared with the gibbons of the genus *Hylobates*.

There are no skull remains either of *Symphalangus* or of *Hylobates* in the fossil collections available to me at present, and consequently we may now pass on to the teeth, of which there are a fair number in the cave collections from Sumatra made by Dubois. The difference in size between the sexes that we found in the skulls of *Symphalangus* is also manifest in the teeth: the male teeth average larger than the female, and the difference is most pronounced in the canines, although even in these elements the ranges of variation of dimensions do overlap to some extent (tables 3 and 4).

TABLE 3

Measurements of upper teeth of males and of females of *Symphalangus syndactylus syndactylus*

		males					females				
		n	R	M	σ	C	n	R	M	σ	C
I^1	tr.	7	4.7-5.7	5.3	0.35	6.6	3	5.2-5.6	5.4	0.21	3.9
	ap.	8	4.2-4.8	4.5	0.23	5.1	7	3.9-5.0	4.5	0.41	9.1
I^2	tr.	6	4.2-5.0	4.8	0.30	6.2	6	4.1-5.0	4.5	0.35	7.8
	ap.	10	4.4-5.5	5.0	0.36	7.2	8	4.2-5.3	4.7	0.43	9.1
C	ap.	7	8.9-11.5	10.1	0.90	8.9	8	7.4-9.1	8.4	0.61	7.3
	tr.	10	6.2-7.8	6.9	0.67	9.6	11	5.0-6.7	5.9	0.56	9.5
P^3	ap.	10	5.5-6.4	5.9	0.32	5.4	11	4.9-6.0	5.5	0.46	8.4
	tr.	11	6.0-7.2	6.6	0.37	5.6	11	5.4-7.2	6.2	0.51	8.2
P^4	ap.	10	5.4-6.3	5.9	0.27	4.6	10	4.7-6.1	5.4	0.49	9.2
	tr.	11	6.1-7.2	6.7	0.27	4.0	11	5.7-7.4	6.3	0.57	9.1
M^1	ap.	14	6.8-8.2	7.6	0.39	5.1	8	6.9-8.3	7.6	0.46	6.0
	tr.	13	6.2-7.8	7.2	0.47	6.2	10	6.2-7.8	7.0	0.45	6.4
M^2	ap.	13	7.8-9.0	8.4	0.37	4.4	10	6.9-9.0	8.0	0.69	8.6
	tr.	11	6.9-8.8	8.1	0.52	6.4	10	7.0-8.6	7.6	0.58	7.6
M^3	ap.	7	6.4-8.3	7.7	0.64	8.3	7	6.5-8.0	7.2	0.63	8.7
	tr.	6	7.6-8.4	7.9	0.29	3.6	8	7.1-9.1	7.6	0.66	8.7

The statistical data on the teeth of both sexes of the siamang show further that the lateral upper incisor, I^2, is smaller relative to I^1 in the females than in the males. There is no difference in the relative sizes of the two upper premolars between the two sexes, but the upper molars do show some interesting sexual differences in relative size: M^2 is larger relative to M^1 in the males than in the females, and M^3 is also less reduced in size as compared with M^1 in the males than in the females. In the mandible, we note that M_2 is again larger relative to M_1 in the males than in the females; in the males M_2 is just exceeded in size by M_3, whereas in the females M_3 averages

TABLE 4

Measurements of lower teeth of males and of females of

Symphalangus syndactylus syndactylus

		males					females				
		n	R	M	σ	C	n	R	M	σ	C
I_1	tr.	9	3.1-4.0	3.5	0.27	7.8	5	3.0-4.0	3.5	0.36	10.3
	ap.	9	3.6-4.3	4.0	0.23	5.7	6	3.5-4.5	3.9	0.36	9.2
I_2	tr.	9	3.4-4.3	3.8	0.25	6.7	7	3.2-4.4	3.7	0.38	10.2
	ap.	9	4.3-5.0	4.6	0.25	5.5	9	3.9-5.2	4.4	0.45	10.3
C	ap.	9	7.1-9.6	8.7	0.78	8.9	10	6.8-8.3	7.7	0.53	6.8
	tr.	9	6.1-8.0	6.8	0.59	8.7	10	5.2-6.5	5.7	0.47	8.3
P_3	ap.	6	8.2-9.5	8.9	0.44	5.0	10	7.4-9.2	8.1	0.70	8.6
	tr.	8	4.6-5.5	5.1	0.35	6.8	10	4.0-5.5	4.7	0.41	8.8
P_4	ap.	8	6.3-8.0	7.2	0.47	6.5	10	5.6-8.0	6.5	0.67	10.3
	tr.	8	4.7-5.3	5.1	0.19	3.6	10	4.4-5.2	4.8	0.30	6.2
M_1	ap.	10	7.7-8.6	8.2	0.37	4.5	7	7.5-8.5	8.1	0.40	4.9
	tr.	11	5.5-6.9	6.4	0.40	6.2	6	6.1-6.6	6.3	0.21	3.3
M_2	ap.	9	8.6-9.8	9.0	0.36	4.0	8	7.8-9.2	8.5	0.48	5.7
	tr.	8	6.8-7.5	7.2	0.25	3.5	9	6.1-7.4	6.7	0.41	6.2
M_3	ap.	4	8.6-9.8	9.2	0.51	5.5	6	7.7-9.5	8.4	0.65	7.7
	tr.	7	6.4-7.7	7.1	0.40	5.6	7	6.0-7.5	6.5	0.49	7.6

smaller than M_2. These tendencies toward reduction of I^2 and M^3 stamp the female as more progressive than the male; this is a feature also shown in the greater brachycephalization of the skull. The predominance in size of M^2 over the other molars is a characteristic of the pongid dentition; as shown by Remane (1921, p. 27, table X) the second molar is most often the largest in the series in the gorilla, chimpanzee, orang-utan, and gibbons (*Symphalangus* and *Hylobates*), with the exception only of the female chimpanzee, in which M^1 is the largest of the upper molars in more than 50 per cent. of the cases examined. In the males, the percentages of occurrence of M^3 as the largest molar are higher than in the females (Remane, l.c.), the females displaying the more advanced condition.

The comparison between the dentition of the subfossil orang-utan from the Sumatran caves and that of the living orang-utan has shown (Hooijer, 1948) that the excess in size of the second molar over the other molars is more pronounced in the prehistoric form than it is in the recent, whereas further the lateral incisors are less reduced in relative size, and the male canines are larger relative to the female in the prehistoric as compared with the recent orang-utan. On an average, the prehistoric teeth are sixteen per cent. larger than the recent. These results were based on a study of material much richer than that available in the case of the gibbons. It seems reasonable to suppose that the gibbons, too, have undergone significant changes in the relative proportions of the elements of their dentition during the time which has elapsed since the deposition of the teeth in the Sumatran caves. How much of these evolutionary trends are we going to find in our gibbon material? The following chapters will provide the answer to this question.

First of all, we have to separate the teeth of *Symphalangus* from those of *Hylobates* in the Sumatran cave collections. Both the dark-handed *Hylobates agilis* Cuvier and the white-handed *Hylobates lar* (L.) occur today in Sumatra beside the large siamang *Symphalangus syndactylus* (Raffles). Although the teeth of *Hylobates* are generally smaller than those of *Symphalangus* the ranges of variation of dimensions overlap: the upper ranges of the gibbon incisors, canines, premolars, and first molars overlap with siamang ranges. Fortunately, in addition to size, there are morphological differences; those pertaining to the post-canine dentition have been dealt with by Remane (1921) and Eckardt (1929). The following is a summary of their findings:

In the first and second upper molars of *Symphalangus* the length (ap.) exceeds the width (tr.). In *Hylobates* the reverse condition is found.

In *Symphalangus* the cusps of the molars are less marginal in position, less well defined, and relatively lower than those in *Hylobates*.

In the upper molars the protocone is always the largest cusp; then follow, in order of diminishing crown surface area: in *Symphalangus* metacone and paracone, but in *Hylobates* paracone and metacone. The metacone is relatively larger in *Symphalangus* than in *Hylobates*. The hypocone is the smallest cusp; it is smaller relative to the other cusps in *Symphalangus* than in *Hylobates*.

In order of decreasing height the paracone always comes first; it is the highest cusp. The second highest cusp is the metacone in *Symphalangus*, but the protocone in *Hylobates*, while the hypocone always is the lowest cusp. Thus, in *Symphalangus* the metacone is higher than the protocone; in *Hylobates* the protocone is higher than the metacone.

In *Symphalangus* there is a depression on the crown surface between paracone and protocone as well as between metacone and hypocone; in *Hylobates* the area between paracone and protocone is not depressed, but there is a valley between metacone and hypocone.

In the lower molars the hypoconid is more forward in position in *Symphalangus* than in *Hylobates*; in *Symphalangus* it is placed in front of the entoconid, whereas in *Hylobates* it is often opposite to the entoconid.

The anterior cusps of the lower molars (protoconid and metaconid) are much larger than the others; in *Symphalangus* the metaconid is the largest cusp both in M_1 and M_2; in *Hylobates* the protoconid is the largest in M_1, and the metaconid is the largest in M_2.

In *Symphalangus* the highest cusp in the lower molar is the hypoconid; the others are about equally high. In *Hylobates* the metaconid is the highest cusp; then follow hypoconid and entoconid; the protoconid is the lowest cusp.

The most conspicuous ridge in the upper molars is the crista obliqua, which runs from the tip of the protocone to the tip of the metacone. It is more strongly developed in *Symphalangus* than in *Hylobates*, and often reduced in M^3 of *Hylobates*, but rarely so in *Symphalangus*.

The anterior transverse ridge in the upper molars, connecting paracone and protocone, ends lingually in front of the protocone in *Symphalangus*, whereas in *Hylobates* it runs to the tip of the protocone.

The most constant ridge in the lower molars is the posterior trigonid ridge between protoconid and metaconid; in *Symphalangus* it is more rounded off apically than in *Hylobates*, and cut into by a median cleft.

In *Symphalangus* there is no ridge between entoconid and hypoconulid (mesoconid in Remane and Eckardt), but in *Hylobates* this connecting ridge is rather often present.

The cingulum is less well developed in *Symphalangus* than in *Hylobates*, in which latter it may be seen at the protocone, passing backward into the hypocone. In the lower molars the cingulum is much reduced; a trace is sometimes seen between protoconid and hypoconid, and only in *Hylobates*.

Accessory cusps occur more frequently in *Hylobates* than in *Symphalangus* (Eckardt even negates their occurrence in the latter genus), and may be found between metacone and hypocone in the upper, and between hypoconid and entoconid, or between metaconid and entoconid in the lower molars.

The boundary between crown and root is much less distinct in *Symphalangus* than in *Hylobates*. In *Hylobates* the neck of the molars is constricted at the crown-root junction, most markedly so in the upper jaw; this constriction is less pronounced in *Symphalangus*.

CAVE MATERIAL OF SYMPHALANGUS AND HYLOBATES FROM SUMATRA

The incisors and canines of *Symphalangus* do not show structural differences from their homologues in *Hylobates*; there is only a difference in size, and one of averages only, as stated above. This being the state of affairs, there is no way of establishing even the generic identity of the isolated specimens in the collections from the limestone caves in the Padang Highlands, central Sumatra. But this is no reason to exclude them from the present study, for they yield important information just the same.

INCISORS

There are fifteen specimens of the central upper incisor, I^1, in the Sumatran collection, Coll. Dub. no. 11669/1-15. Nos. 1-7 are from the right side, nos. 8-15 from the left. Nos. 1, 2, 4, 7-9, 11-13 and 15 are from the Sibrambang cave, nos. 3, 6 and 14 from the Lida Ajer cave, no. 10 from the Djamboe cave, whereas the cave from which no. 5 was obtained is unknown. These subfossil specimens are indistinguishable from those of recent *Symphalangus*, but likewise indistinguishable from those of *Hylobates;* it is, however, easy to separate them from their narrower and higher homologues in *Presbytis* and *Trachypithecus,* while the stout hypsodont *Macaca* I^1 does not even remotely resemble them. There is, in this subfossil series, variation in the relative development of the lingual cingulum (tuberculum dentale), as shown in pl. I figs. 1-2, as well as in size; the measurements are given in table 5.

With the exception only of five specimens (nos. 5, 7, 11, 14 and 15) the cave I^1 are larger than the largest recent male I^1 of *Symphalangus* that I have seen; two cave specimens (no. 4: pl. I fig. 1, and no. 12) represent just this recent maximum size, 5.7 by 4.8 mm. The smallest subfossil specimens (nos. 14 and 15) are still within the variation limits of recent male and female *Symphalangus* (smallest male 4.7 by 4.2 mm; smallest female 5.2 by 4.0 mm), but they are also within the limits of *Hylobates;* the largest (male) I^1 of *Hylobates agilis* measures 5.5 by 4.3 mm, the smallest, 4.4 by 3.8 mm. It is, therefore, evident that the cave incisors are larger than the recent, on an average; the largest cave specimens undoubtedly represent *Symphalangus,* while possibly *Hylobates* is represented among the smaller teeth.

TABLE 5

Measurements of subfossil I^1 of *Symphalangus* and *Hylobates*

No. of specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Transverse	6.5	6.0	6.3	5.7	5.6	5.8	5.7	6.6	6.8	7.0	5.9	5.7	5.4	5.3	5.0
Anteroposterior	5.0	5.0	5.4	4.8	4.2	4.8	4.7	5.4	5.2	4.6	4.4	4.8	5.2	4.0	4.3

There are only six specimens of the lateral upper incisor, I^2, in the cave collections from Sumatra, Coll. Dub. no. 11670/1-6, of which nos. 1-2 are from the right, nos. 3-6 from the left side. Nos. 1, 2 and 5 originate from the Sibrambang cave, no. 6 from the Djamboe cave; the locality of nos. 3-4 is not recorded. This is a narrower, but usually anteroposteriorly thicker tooth than I^1, more distinctly asymmetrical, with the cutting edge rising into a blunt tip, the lateral slope of which is invariably longer and more steep than the medial. The lingual cingulum may or may not be swollen, but is always present. The measurements given in table 6 indicate that the cave teeth fall right in the upper end of the range of variation for the recent specimens of *Symphalangus* with the exception of one (no. 5) that is above this range. All are larger than the recent I^2 of *Hylobates*, the largest (male) I^2 of *Hylobates agilis* measuring only 4.2 by 4.6 mm. It is highly probable that most, if not all, of the cave specimens actually represent *Symphalangus*.

TABLE 6

Measurements of subfossil I^2 of *Symphalangus* and *Hylobates*

No. of specimen	1	2	3	4	5	6
Transverse	4.7	4.9	4.4	4.8	5.1	5.0
Anteroposterior	5.0	5.1	5.2	5.0	5.6	5.0

No specimens of the central lower incisor, I_1, appear to be referable to gibbons, but of the lateral lower incisor, I_2, there are two specimens that can confidently be referred to either *Symphalangus* or *Hylobates*, one right and one left, Coll. Dub. no. 11671/1-2. The crown bulges out markedly above the root (a distinction from *Presbytis* and *Trachypithecus*), and varies much individually in the development of the cutting edge, straight (incisiform) or pointed (caniniform), as lateral incisors usually do (see Remane, 1921, p. 107, fig. 24). The right I_2 is from the Sibrambang cave, and measures 4.0 mm transversely against 5.0 mm anteroposteriorly, that is, within the limits of *Symphalangus* (table 4) but above the range of *Hylobates* as far as the anteroposterior diameter is concerned (at most 4.5 mm in *Hylobates agilis*; 4.7 mm in *Hylobates moloch abbotti* Kloss from Borneo). The other, the left I_2, is not much wider (4.2 mm) but much thicker anteroposteriorly (5.7 mm) than the right I_2; the cave from which it came is not recorded. This is almost certainly a *Symphalangus* specimen. The recent I_2 of *Symphalangus* that comes nearest to it as to size (in a female, no. 47) is 5.2 mm anteroposteriorly.

CANINES

The gibbon canine is numerically the best represented dental element in the Sumatran collection, but the quality of many specimens is rather poor because of (natural) wear or damage. The full height can be taken only in comparatively few specimens; this measurement can be taken for the upper canine only in eight out of forty recent skulls of *Symphalangus,* viz., those in which the canine is not yet worn. ,

In table 7 are given the anteroposterior length at the base of the crown, the basal width, and the full height of the unworn crowns of upper canines of recent *Symphalangus,* the height measured in a straight line on the posterior side of the tooth from the base of the enamel to the tip. For comparative purposes I have included in this table the identical measurements of a series of six unworn upper canines of *Hylobates agilis,* likewise of both sexes. This table shows in the first place that there is no difference in the relative height of the unworn crown of the upper C between the two sexes; although the male canine is the highest it is also longer and wider at the base, and in the ratio of the height to the basal length or to the basal width it falls well into the range of the females. In *Hylobates* there are no sexual differences in the proportions of the upper C either. Further, table 7 shows that the height of the crown, in relation to its basal diameters, is much the same in *Symphalangus* and in *Hylobates*; in other words, there is no way of telling the upper canines of the two genera apart in collections of isolated specimens. There only remains a difference in average size, not in proportions.

TABLE 7

Measurements and ratios of unworn upper C of *Symphalangus syndactylus* and of *Hylobates agilis*

Symphalangus no.	33	22	17	43	45	47	48	12
	♂	?♂	♀	♀	♀	♀	♀	?♀
1. Basal length	10.6	10.4	8.7	8.3	7.4	8.8	9.1	7.4
2. Basal width	7.8	6.8	6.7	6.0	5.3	5.4	5.7	5.0
3. Total height	22.3	21.4	16.8	20.0	15.2	18.6	19.3	17.6
4. Ratio 3 : 1	2.1	2.1	1.9	2.4	2.1	2.1	2.1	2.4
5. Ratio 3 : 2	2.9	3.1	2.5	3.3	2.9	3.4	3.4	3.5

Hylobates agilis no.	9	14	15	21	25	26
	♂	♂	♂	♂	♀	♀
1. Basal length	7.0	8.0	7.2	6.7	6.2	7.5
2. Basal width	4.8	5.1	5.5	4.8	4.8	4.8
3. Total height	17.0	18.4	14.5	17.0	13.0	16.2
4. Ratio 3 : 1	2.4	2.3	2.0	2.5	2.1	2.2
5. Ratio 3 : 2	3.5	3.6	2.6	3.5	2.7	3.4

The gibbon upper canine (both sexes), being three times as high as wide at the base, is a much more hypsodont tooth than its homologue in the males of the other living pongids. The upper canines of the male *Presbytis* and *Trachypithecus* are about equally high but differ in their peculiar twist and grooving of the root, while the *Macaca* male upper C, which also resembles that of *Symphalangus* and *Hylobates,* may be distinguished by its more marked anterior lingual groove, which extends on to the root, the ridging of the convex labial surface, and the absence of a lingual cingulum. In the gibbons the high and slender crown of the upper canine has no ridge on the labial surface; this surface is gently rounded throughout, and the anterior lingual groove, which follows the gentle backward curvature of the crown, fades away near the tip and does not extend quite to the base of the enamel, which is marked by a low cingulum internally forming a point at the posterior edge. The posterior edge of the crown, which is only slightly concave from above downward, is sharp already in the unworn state, and becomes a true cutting edge when the lingual enamel is worn away against the labial surface of P_3. The lingual ridge behind the vertical groove, as well as the anterior, blunt edge of the crown, both touch the lower canine and are worn away so that in old specimens the groove is no longer shown. By the process of wear the height of the crown is much reduced, the tip being beveled internally, eventually becoming so thin transversely that it is easily broken off intra vitam.

In the collections from the Sumatran caves there are 136 specimens of upper canines of gibbons, but only eleven teeth are unworn or so slightly worn that the height may be taken. Their measurements will be found in table 8. Of this series, Coll. Dub. no. 11672/1-11, four are from the right, and seven from the left side. Nos. 1-3, 5-7, 10 and 11 originate from the Sibrambang cave, no. 9 from the Djamboe cave, while the cave of nos. 4 and 8 is unknown. No. 5, a beautifully preserved crown of a left upper C, is shown in pl. I fig. 8.

TABLE 8

Measurements and ratios of unworn subfossil upper C of *Symphalangus* and *Hylobates*

No. of specimen	1	2	2	4	5	6
1. Basal length	10.7	10.0	8.1	8.6	9.5	8.9
2. Basal width	7.6	6.5	5.1	5.6	7.3	6.4
3. Total height	22.8	20.0	17.0	18.7	21.2	17.6
4. Ratio 3 : 1	2.1	2.0	2.1	2.2	2.2	2.0
5. Ratio 3 : 2	3.0	3.1	3.3	3.3	2.9	2.8

No. of specimen	7	8	9	10	11
1. Basal length	8.9	8.7	9.1	7.8	7.4
2. Basal width	6.0	6.5	6.4	5.7	5.3
3. Total height	18.3	17.8	19.4	16.7	17.1
4. Ratio 3 : 1	2.1	2.0	2.1	2.1	2.3
5. Ratio 3 : 2	3.1	2.7	3.0	2.9	3.2

The subfossil upper canine listed in the first column of table 8 is slightly higher than any of the recent presented in table 7, and none of the subfossil canines is as small as the female canines of *Hylobates;* this tends to show, again, that the cave teeth are larger than the recent. The degree of hypsodonty of the cave canines is within recent limits, however; there is no difference in relative crown height between the recent and the subfossil upper C. The subfossil collection no doubt comprises male as well as female canines both of *Symphalangus* and of *Hylobates;* whether the sexual difference in size was any greater in prehistoric times than it is now (as was the case in the orang-utan: Hooijer, 1948) we do not know. The size difference is more marked in recent *Symphalangus* (almost no overlap of dimension ranges) than in recent *Hylobates* (with widely overlapping ranges).

The remaining 125 subfossil specimens of upper C are all worn, and the majority is incomplete at the base due to posterior wear, damage, or rodent gnawing. Only twenty upper canines remain of which the basal diameters of the crown can be taken, seven right and thirteen left (Coll. Dub. no. 11673/1-20). Nos. 1, 2 and 8-16 are from the Sibrambang cave, no. 3 is from the Lida Ajer cave, nos. 4 and 17-19 are from the Djamboe cave, nos. 5-7 and 20 are without a record for the cave in which they were found. They vary in anteroposterior length at base from 7.8 to 11.3 mm, and in transverse width at base from 5.5 to 8.2 mm, thereby slightly extending the upper limits of the ranges already found for the unworn subfossil upper C (table 9).

TABLE 9

Measurements of subfossil upper C of *Symphalangus* and *Hylobates*

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	8.3	9.0	10.7	8.5	10.7	9.7	9.0	11.3	9.7	9.0
Transverse	6.1	6.7	8.2	6.4	7.4	6.5	6.8	7.7	6.1	6.1

No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	9.0	8.3	9.4	8.7	8.8	8.2	7.8	8.9	9.0	8.1
Transverse	5.8	6.4	6.6	6.6	5.7	6.0	6.1	6.6	6.5	5.5

The lower canines of *Symphalangus* and *Hylobates* that are not yet noticeably worn at the tip, and of which, beside the basal diameters, the total height of the crown can be given (table 10), tend to be larger and higher-crowned in males than in females. This tendency is more marked in *Symphalangus* than in *Hylobates agilis.*

TABLE 10

Measurements and ratios of unworn lower C of *Symphalangus syndactylus* and of *Hylobates agilis*

Symphalangus no.	26	28	33	22	17	40	43	45
	♂	♂	♂	?♂	♀	♀	♀	♀
1. Basal length	8.8	8.6	8.9	8.2	8.4	8.1	7.9	6.8
2. Basal width	6.3	6.7	7.2	6.5	6.3	5.8	5.8	5.3
3. Total height	15.7	14.0	15.8	16.6	12.6	14.1	13.2	10.0
4. Ratio 3 : 1	1.8	1.6	1.8	2.0	1.5	1.7	1.7	1.5
5. Ratio 3 : 2	2.5	2.1	2.2	2.6	2.0	2.4	2.3	1.9

Symphalangus no.	47	12
	♀	?♀
1. Basal length	8.1	7.9
2. Basal width	6.5	5.0
3. Total height	13.0	12.0
4. Ratio 3 : 1	1.6	1.5
5. Ratio 3 : 2	2.0	2.4

Hylobates agilis no.	9	14
	♂	♂
1. Basal length	6.4	7.0
2. Basal width	5.2	5.5
3. Total height	11.3	12.9
4. Ratio 3 : 1	1.8	1.8
5. Ratio 3 : 2	2.2	2.3

Hylobates agilis no.	15	20	21	24	10	25	26	32
	♂	♂	♂	♂	?♂	♀	♀	♀
1. Basal length	6.8	7.0	6.7	7.3	7.4	6.2	6.6	7.0
2. Basal width	5.0	4.9	4.7	5.9	5.0	4.2	5.0	5.2
3. Total height	10.7	12.3	12.0	12.3	13.0	9.0	11.6	10.4
4. Ratio 3 : 1	1.6	1.8	1.8	1.7	1.8	1.5	1.8	1.5
5. Ratio 3 : 2	2.1	2.5	2.6	2.1	2.6	2.1	2.3	2.0

The total height of the crown, measured in a straight line on the posterior side of the tooth from the base of the enamel to the tip, averages 15.2 mm in three males of *Symphalangus syndactylus* against only 12.6 mm in five females; in *Hylobates agilis* these figures are 11.9 mm (six males) and 10.3 mm (three females). The difference in relative crown height between the sexes is more pronounced in the lower C than in the upper, the highest-crowned lower C belonging to males, and the lowest-crowned to females. However, it is further clear from table 10 that there is no difference in relative crown height between *Symphalangus* and *Hylobates,* so that we shall not be able to definitely establish the generic identity of the lower canines as isolated specimens either.

Lower canines of gibbons are easily distinguished from those of *Presbytis* and *Trachypithecus* males by their much less transversely compressed crowns and better developed posterior cingular development; in *Macaca* the lower canine is also narrower transversely, and in the males shows a characteristic vertical groove in the middle of the medial surface of the crown not seen in the gibbons. The roots in male *Macaca* lower canines are longitudinally grooved on the medial surface, whereas the medial surface of the roots of gibbon lower C is convex or flattened, not grooved.

As wear advances on the lower C the tip and the posterior prominence at the base of the crown are spared for a longer period than those in the upper canine; skulls in which the upper C is heavily worn internally (mainly against the anterior lower premolar; anteriorly against the lower canine) may still show lower canines without appreciable wear at tip or base behind. Therefore, although the number of isolated lower gibbon canines in the Sumatran cave collection is equal to that of the upper, viz., 136, there are many more lower canines of which the height can be taken, and fewer specimens unfit for measurement at the base. In table 11 are found the measurements and ratios of twenty-eight lower canines, fifteen from the right

TABLE 11

Measurements and ratios of unworn subfossil lower C of *Symphalangus* and *Hylobates*

No. of specimen	1	2	3	4	5	6	7
1. Basal length	8.9	8.0	8.5	8.7	7.9	8.3	7.8
2. Basal width	6.7	5.7	6.1	6.2	6.3	6.6	6.4
3. Total height	15.0	14.4	14.3	14.2	13.3	15.2	14.4
4. Ratio 3 : 1	1.7	1.8	1.7	1.6	1.7	1.8	1.8
5. Ratio 3 : 2	2.2	2.5	2.3	2.3	2.1	2.3	2.3
No. of specimen	**8**	**9**	**10**	**11**	**12**	**13**	**14**
1. Basal length	8.5	9.1	8.3	8.3	8.7	7.8	7.7
2. Basal width	6.3	6.8	5.8	6.2	6.7	6.0	5.4
3. Total height	13.7	15.1	14.8	12.3	14.3	14.9	13.7
4. Ratio 3 : 1	1.6	1.7	1.8	1.5	1.6	1.9	1.8
5. Ratio 3 : 2	2.2	2.2	2.5	2.0	2.1	2.5	2.5
No. of specimen	**15**	**16**	**17**	**18**	**19**	**20**	**21**
1. Basal length	8.2	10.0	8.4	7.7	8.2	9.2	8.5
2. Basal width	6.4	7.5	6.4	6.1	6.1	7.0	6.5
3. Total height	14.6	15.8	12.7	15.2	15.0	15.0	16.3
4. Ratio 3 : 1	1.8	1.6	1.5	2.0	1.8	1.6	1.9
5. Ratio 3 : 2	2.3	2.1	2.0	2.5	2.5	2.1	2.5
No. of specimen	**22**	**23**	**24**	**25**	**26**	**27**	**28**
1. Basal length	7.8	9.0	7.8	8.8	9.0	9.0	7.2
2. Basal width	6.2	6.7	6.1	6.7	6.9	6.8	5.6
3. Total height	12.6	14.7	13.4	15.8	15.4	16.7	12.8
4. Ratio 3 : 1	1.6	1.6	1.7	1.8	1.7	1.9	1.8
5. Ratio 3 : 2	2.0	2.2	2.2	2.4	2.2	2.5	2.3

side and thirteen from the left (Coll. Dub. no. 11674/1-28). No. 6 is shown in pl. I fig. 10. Nos. 1-9 and 16-25 are from the Sibrambang cave, nos. 10 and 11 from the Lida Ajer cave; the name of the cave of nos. 12-15 and 26-28 is not recorded. A few subfossil specimens exceed the recent lower C of *Symphalangus syndactylus* in dimensions, while none are as small as the female lower C of *Hylobates agilis,* signifying the greater average size of the cave specimens as compared with the recent, but the height ratios of the cave teeth vary between the same limits as do those of the recent canines. The remaining specimens of lower canines of gibbons in the Sumatran cave collections, all incomplete apically, vary in basal anteroposterior length from 6.5 to 9.8 mm, and in width from 5.1 to 7.2 mm, slightly extending the lower limits of the ranges already found for the unworn specimens of table 11.

CAVE MATERIAL OF SYMPHALANGUS FROM SUMATRA

PREMOLARS

The upper premolars are bicuspids; the labial cusp (paracone) is larger than the lingual (protocone), and the anteroposterior valley between them is crossed by a ridge, which runs from the tip of the paracone to the marginal ridge in front of the protocone, both in *Symphalangus* and in *Hylobates.* This ridge, the anterior transverse ridge (vordere Trigonleiste in Remane, 1921, p. 71) exceptionally (in P^4) runs to the tip of the protocone (as in upper molars of *Hylobates*). In front of the anterior transverse ridge, enclosed by the marginal ridge of the crown, is the anterior fossa; behind the ridge is the much larger posterior fossa of the crown. The anterior fossa extends lower down on the crown in the anterior upper premolar (P^3) than in the posterior (P^4), making the anterior edge of the paracone longer, and the labial surface of the crown more produced rootward anteriorly in P^3 than in P^4.

The upper premolars of *Presbytis* and *Trachypithecus* as well as those of *Macaca* differ from their homologues in the gibbons in their higher crowns, narrower and deeper fossae, and by the roots (two buccal and one lingual) being separate, not fused to a considerable extent as they are in gibbons. The protocone in the monkey P^{3-4} is more distinctly marked off behind, too.

The P^3 of *Symphalangus syndactylus* differs from that of *Hylobates* not only in size but also in proportions: the former is relatively wider than the latter. In table 12 are given the measurements of four recent P^3 of *Symphalangus* and those of four recent P^3 of *Hylobates*; the variation in anteroposterior length is the same in both series, but the *Symphalangus* specimens are significantly wider than those of *Hylobates.*

TABLE 12

Measurements of recent P^3 of *Symphalangus* and of *Hylobates*

	Symphalangus				*Hylobates agilis*			
No. of specimen	40	44	41	33	15	19	23	14
Anteroposterior	4.9	5.0	5.1	5.5	4.9	5.0	5.1	5.5
Transverse	6.7	6.4	6.1	6.8	5.3	5.4	5.3	5.4

It is, therefore, possible to distinguish between the P^3 of the two genera of gibbons. There are nineteen specimens of P^3 in the Sumatran cave collection all of which appear to belong to the larger siamang gibbon; ten from the right and nine from the left side (Coll. Dub. no. 11675/1-19). Nos. 1-6 and 11-18 originate from the Sibrambang cave, no. 7 from the Lida Ajer cave (pl. II fig. 1), and nos. 8-10 and 19 from caves the name of which is not on record. The cave specimens, doubtless including males as well as females, nevertheless average larger than do the recent male P^3 of *Symphalangus;* the mean anteroposterior length of the subfossil *Symphalangus* P^3 is 6.1 mm, the mean transverse width is 6.7 mm, against 5.9 and 6.6 mm, respectively, in recent males (5.5 and 6.2 mm, respectively, in recent females: table 3). The difference would have been more marked had we been able to sex the cave specimens, and compare them for each sex separately. Since this proves to be impossible I have assembled the data on the recent P^3 of *Symphalangus syndactylus,* twenty-two specimens, eleven of either sex, which average 5.7 mm anteroposteriorly, and 6.4 mm transversely, and compared them with the series of nineteen subfossil P^3 presented in table 13.

TABLE 13

Measurements of P^3 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	6.1	6.5	7.0	6.4	6.3	5.7	6.0	5.7	6.4	6.2
Transverse	6.7	7.0	7.7	6.7	6.5	6.8	6.4	6.8	6.7	6.6
No. of specimen	11	12	13	14	15	16	17	18	19	
Anteroposterior	6.1	5.8	6.0	5.7	6.2	5.7	6.3	6.0	6.4	
Transverse	6.3	6.3	6.8	6.4	7.3	6.5	6.7	6.9	6.7	

TABLE 14

Statistical data on P^3 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	21	5.7	0.45	7.9	0.13	3.1
Idem, subfossil	19	6.1	0.35	5.7		
Transverse, recent	22	6.4	0.48	7.5	0.13	2.3
Idem, subfossil	19	6.7	0.34	5.1		

Notwithstanding the overlap of dimensions, the difference between the means of the anteroposterior diameters of the recent and the subfossil specimens is three times the standard error of this difference, and it is two times the standard error of the difference for the transverse diameters. Therefore, the difference in size between the recent and the subfossil P^3 of *Symphalangus syndactylus* is statistically significant; it is justifiable to regard the cave siamang as a large temporal race of the living species under the name *Symphalangus syndactylus subfossilis* nov. subsp., the formal diagnosis of which will be given at the end of the present chapter. It is further worthy of note that the sample of the cave siamang P^3 has lower variation coefficients, and thereby is less variable than the recent sample used for comparison, as might be expected in a local population as compared with a sample consisting of specimens from widely separated localities on the island of Sumatra.

The P^4 of *Symphalangus syndactylus* gradually pass into those of *Hylobates*, the smallest *Symphalangus* P^4 being indistinguishable from the largest *Hylobates* P^4 as to size and proportional width (table 15).

TABLE 15

Measurements of recent P^4 of *Symphalangus* and of *Hylobates*

	Symphalangus syndactylus				*Hylobates agilis*		
No. of specimen	41	45	38	46	23	14	19
Anteroposterior	4.7	4.9	5.0	5.0	4.6	4.8	5.0
Transverse	5.8	6.0	5.7	6.0	5.6	5.6	5.7

The difference in average size between the P^4 of the two genera is very great, however. In the Sumatran cave collections there are fifty-one specimens of P^4, which fall into two distinct groups, forty-nine specimens varying from 5.3 to 6.8 mm anteroposteriorly, and from 6.2 to 7.8 mm transversely, and two specimens of which the dimensions are 4.4-4.6 mm anteroposteriorly, and 5.1-5.4 mm transversely. Moreover, one of the small specimens is in situ in a fragment of the maxillary with M^{1-2} displaying *Hylobates* characters; this is doubtless a specimen of *Hylobates*. I shall deal with the two small specimens later, under the genus *Hylobates*, and refer all of the larger specimens to *Symphalangus*. They are registered as Coll. Dub. no. 11676/1-49, nos. 1-26 being from the right, the others from the left side. Nos. 1-20 and 27-45 are from the Sibrambang cave, nos. 21, 22 and 46 from the Lida Ajer cave, and nos. 23-26 and 47-49 from an unknown cave. The subfossil specimens average larger than the recent, and, as shown in table 17, the difference in size does stand the statistical test. The cave P^4 is significantly larger than the recent P^4 of *Symphalangus syndactylus syndactylus* (twenty-two specimens, eleven male and eleven female).

TABLE 16

Measurements of P^4 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	5.8	5.9	5.8	5.6	5.8	5.6	5.4	6.0	5.6	6.1
Transverse	7.1	6.5	6.4	7.0	7.5	6.4	6.6	6.9	6.2	6.7
No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	6.2	6.0	6.1	6.0	5.5	5.5	5.4	6.6	6.2	6.0
Transverse	7.8	6.8	7.2	6.9	7.0	6.8	6.5	7.5	6.9	7.3
No. of specimen	21	22	23	24	25	26	27	28	29	30
Anteroposterior	5.8	5.8	6.0	5.3	5.8	6.1	5.5	6.5	5.9	6.8
Transverse	7.0	6.7	6.3	6.7	6.7	6.8	6.6	7.3	7.4	7.7
No. or specimen	31	32	33	34	35	36	37	38	39	40
Anteroposterior	6.0	5.9	6.0	6.2	5.5	6.2	6.7	5.9	6.3	5.8
Transverse	7.1	7.7	7.0	7.1	6.9	7.4	7.1	6.5	7.3	6.8
No. of specimen	41	42	43	44	45	46	47	48	49	
Anteroposterior	5.6	6.4	5.6	6.1	6.1	5.7	6.4	5.7	5.9	
Transverse	6.8	7.7	7.0	6.6	7.0	7.1	6.6	6.7	6.8	

TABLE 17

Statistical data on P^4 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	20	5.6	0.47	8.3	0.11	2.7
Idem, subfossil	49	5.9	0.34	5.8		
Transverse, recent	22	6.5	0.49	7.5	0.12	3.3
Idem, subfossil	49	6.9	0.31	4.5		

The anterior lower premolar (P_3) is an anteroposteriorly elongated tooth with a strong pyramidal cusp, the protoconid. The buccal surface is convex and produced rootward anteriorly; this surface shears against the upper canine during transverse movements of the mandible. Three ridges descend from the tip of the protoconid, one anteriorly, one lingually, and one posteriorly. The anterior and posterior ridges both curve inwards near the base, joining the lingual cingulum, and enclosing a depressed area on the lingual surface of the crown that is divided by the transverse ridge, the metaconid ridge, into an anterior trigonid fossa and a posterior talonid fossa. As pointed out by Remane (1921, p. 78) the two genera of gibbons differ in the development of the metaconid ridge, which joins the lingual cingulum in *Symphalan-*

gus but often fails to do so in *Hylobates* (cf. Remane, l.c., p. 74, fig. 18 m-o), in which case there is a continuous lingual basal ledge not elevated in the middle of its course. The reduction of the metaconid ridge, and thereby that of the metaconid, is a good character to distinguish the *Hylobates* P^3 from that of *Symphalangus,* in which the metaconid is occasionally present as a distinct cusp just lingually of the protoconid and not much inferior to it in height (*Symphalangus syndactylus syndactylus,* nos. 12 and 17).

The gibbon P_3 (as well as P_4) is distinguished from that of the monkeys *Presbytis, Trachypithecus,* and *Macaca* by its lower crown, less well developed antero-external downward protrusion of the enamel, and by its fused roots. In the monkeys, especially in the male *Macaca* in which the downward extension of the antero-external enamel is very striking indeed, the crowns are higher and the anterior and posterior roots separate along their entire length; in *Symphalangus* and in *Hylobates* only the root tips are free.

Eleven cave specimens of P_3, three right and eight left, all from the Sibrambang cave, have transverse ridges from the protoconid joining the lingual cingulum. In one specimen (no. 4) the base of the anterior ridge descending from the tip of the crown is thickened, forming a kind of cusp (pl. I figs. 5), whereas in another (no. 5) there is a distinct metaconid only slightly less high than the protoconid (pl. I fig. 9). All of these specimens represent *Symphalangus* (Coll. Dub. no. 11677/1-11).

TABLE 18

Measurements of P_3 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10	11
Anteroposterior	8.7	9.7	8.8	9.6	9.0	—	9.4	8.5	—	8.2	10.0
Transverse	5.0	5.1	4.9	5.7	5.0	5.5	5.6	5.2	5.6	5.0	5.6

Comparison of the subfossil P_3 with a series of twenty recent P_3 of the siamang (six male, ten female, and four of unknown sex) as given in table 19 proves the difference in size to be significant.

TABLE 19

Statistical data on P_3 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	20	8.5	0.66	7.8	0.25	2.4
Idem, subfossil	9	9.1	0.61	6.7		
Transverse, recent	20	4.8	0.40	8.4	0.13	3.8
Idem, subfossil	11	5.3	0.31	5.9		

The subfossil P_3 is, again, less variable than its recent homologue, as shown by the low variation coefficients.

The last lower premolar, P_4, is represented in the Sumatran cave collections by ten specimens, five from each side (Coll. Dub. no. 11678/1-10), all from the Sibrambang cave. The metaconid varies from a cusp fully as high as the primary protoconid to a small point lingually of the protoconid, but it is always readily seen; in *Hylobates* it seems generally smaller relative to the main cusp than in *Symphalangus*. There is much individual variation in size of the anterior fossa, the trigonid fossa in front of protoconid and metaconid, as well as in the anteroposterior extent of the talonid fossa behind the pair of cusps. The talonid fossa is much shortened in a number of *Hylobates* premolars; such abortive specimens are rare in *Symphalangus* (no. 45). The posterior marginal ridge connecting the posterior ridges from protoconid and from metaconid, enclosing the talonid fossa, often shows a cusp-like elevation behind the protoconid representing the hypoconid, and less frequently a cusp behind the metaconid, which is the entoconid. In *Hylobates* these supernumerary cusps are exceptionally seen. Two subfossil specimens, both P_4 sin., no. 7 with a distinct hypoconid, and no. 10 showing the entoconid, are presented in pl. I figs. 3-4. The former specimen is much shorter than the latter.

TABLE 20

Measurements of P_4 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	7.1	6.6	6.8	7.7	6.6	7.7	7.1	7.2	7.2	7.8
Transverse	5.2	4.8	4.7	5.5	5.0	5.1	5.0	4.7	5.2	5.3

The subfossil P_4 averages just as large as does the recent male P_4 of *Symphalangus syndactylus syndactylus* (table 4), but larger than the average of a series of seven male, ten female, and three of unknown sex (table 21). The difference between the means of the anteroposterior diameters of the subfossil and the recent P_4, as well as that of the transverse diameters, is just two times the standard error of the difference, and, therefore, only just great enough for the subfossil teeth to be significantly larger than the recent. As we have seen above, the upper premolars and the anterior lower premolar of *Symphalangus syndactylus subfossilis* nov. subsp. stood the statistical test very well indeed. This indicates that in the posterior lower premolar the diminution in size since the time of the deposition of the teeth in the Sumatran caves was somewhat less marked than that in the other premolars. In the subfossil race the anterior lower premolar is larger relative to the posterior lower premolar than it is in the recent Sumatran race, a feature doubtless correlated with the comparatively large size of the canines in the extinct cave form.

TABLE 21

Statistical data on P_4 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	20	6.8	0.63	9.3	0.20	2.0
Idem, subfossil	10	7.2	0.44	6.1		
Transverse, recent	20	4.9	0.28	5.7	0.10	2.0
Idem, subfossil	10	5.1	0.27	5.3		

MOLARS

It is an easy matter to separate gibbon molars from the bilophodont cercopithecoid molars of *Presbytis, Trachypithecus,* and *Macaca* in the Sumatran cave collections. The distinction between the molars of *Symphalangus* and those of *Hylobates* is also made without much trouble; the distinguishing features given by Remane (1921) and Eckardt (1929) have already been listed above (pp. 9-10). Now there remains the determination of the serial position of the isolated cave molars as either first or second or third or even fourth molars (fourth molars occur in two out of fifteen *Symphalangus* skulls: Schultz, 1933, p. 236; only in one out of my series of thirty *Symphalangus* skulls, viz., in no. 44).

With the exception of the last, which is exceptional anyway, the upper molars of *Symphalangus* can be classed fairly well. The first upper molar is peculiarly trapezoidal in outline, projecting much more forward buccally than lingually due to the advanced position of the paracone. It its wider behind than in front. In the second upper molar, which is wider than the first, the protocone has shifted forward somewhat, making the crown a little more regularly quadrate. It tends to be widest in front. The third upper molar, with the protocone placed still more forward, shows retrogressive tendencies in the reduction of the posterior cusps, in particular the metacone. The crown is wider than long, and widest anteriorly.

There are 68 specimens of the first upper molar of *Symphalangus* in the cave collections from Sumatra, Coll. Dub. no. 11679/1-68. Nos. 1-35 are from the right side, nos. 36-68 from the left. Nos. 1-22 and 36-58 originate from the Sibrambang cave; nos. 23-30 and 59-67 are from the Lida Ajer cave; nos. 31-33 are from the Djamboe cave; the cave from which nos. 34, 35 and 68 were obtained is not recorded. A few specimens are figured to show the characteristic crown shape of M^1 in the siamang, two from the right side (nos. 1 and 23: pl. II figs. 2-3) and one from the left (no. 60: pl. II fig. 4). Only two specimens, nos. 29 and 61, are in situ in small maxillary fragments also holding part of the alveoli of M^2, but the M^2 belonging to these M^1 have not been found; the remaining specimens are isolated.

TABLE 22

Measurements of M^1 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	7.7	9.1	8.4	8.1	8.2	7.7	8.1	8.6	8.0	8.3
Transverse	7.3	9.0	8.2	7.6	7.7	7.5	8.0	8.2	7.0	8.2
No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	7.8	8.7	8.3	9.3	9.0	8.6	8.9	8.2	9.0	8.0
Transverse	7.0	8.4	7.9	8.6	8.4	7.9	7.8	7.7	8.4	7.8
No. of specimen	21	22	23	24	25	26	27	28	29	30
Anteroposterior	8.9	9.2	8.2	8.5	8.8	8.1	9.0	8.5	8.1	8.6
Transverse	8.3	8.5	7.7	7.9	8.6	7.2	8.0	7.9	7.4	8.2
No. of specimen	31	32	33	34	35	36	37	38	39	40
Anteroposterior	8.7	8.8	8.2	8.7	8.7	8.3	9.0	8.0	8.7	8.4
Transverse	8.0	8.1	8.0	8.1	8.2	8.0	8.8	7.5	8.5	7.8
No. of specimen	41	42	43	44	45	46	47	48	49	50
Anteroposterior	8.2	8.1	9.0	8.4	8.2	8.8	8.3	9.1	8.8	8.1
Transverse	7.8	7.2	8.5	8.3	7.7	8.6	8.0	8.2	8.1	7.9
No. of specimen	51	52	53	54	55	56	57	58	59	60
Anteroposterior	8.0	7.9	8.2	8.8	8.4	8.0	7.8	8.2	9.2	8.3
Transverse	8.3	8.6	8.2	8.2	8.2	7.6	7.4	8.0	8.4	7.8
No. of specimen	61	62	63	64	65	66	67	68		
Anteroposterior	8.3	8.5	8.3	8.9	8.9	8.2	8.6	8.2		
Transverse	8.5	7.8	7.5	8.8	9.1	7.9	8.5	7.7		

The crista obliqua, connecting protocone and metacone, is distinct in all except the heavily worn specimens; the anterior transverse ridge terminates lingually in front of the tip of the protocone, and the cingulum at the lingual side of the protocone occurs only in a few specimens, including the figured no. 60. Accessory cusps between metacone and hypocone were observed only in two or three cases, including the figured no. 1; these very tiny elevations of the posterior marginal ridge were seen in one recent skull (no. 47), and only in the right M^1, not in the left. The measurements of the subfossil M^1 are given in table 22.

For comparison with the subfossil series I have used all the recent M^1

available, 13 male, 8 female, and 7 of unknown sex; 28 specimens in all. Table 23 shows that the cave molars decidedly exceed the recent in dimensions: the difference between the means is almost three times the standard error of this difference both for the anteroposterior and for the transverse diameter of the crown.

TABLE 23

Statistical data on M^1 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	28	7.7	0.39	5.1	0.28	2.9
Idem, subfossil	68	8.5	0.40	4.7		
Transverse, recent	28	7.2	0 40	5.5	0.29	2.8
Idem, subfossil	68	8.0	0.45	5.7		

The second upper molar of *Symphalangus* is even more abundantly represented in the Sumatran cave collections than is the first: 79 specimens, 41 of which from the right side. These specimens, Coll. Dub. no. 11680/1-79, originate from the following caves: nos. 1-28 and 42-64, Sibrambang cave; nos. 29-38 and 65-74, Lida Ajer cave; nos. 39, 40 and 75, Djamboe cave; nos. 41 and 76-79, no record. Two specimens from the Sibrambang cave, one right (no. 1) and one left (no. 45), as well as one left M^2 (no. 79) are shown in pl. I fig. 6, pl. II figs. 7-8.

TABLE 24

Measurements of M^2 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	9.1	8.5	8.8	9.7	8.4	8.9	8.7	8.0	8.9	8.5
Transverse	8.6	8.6	9.0	9 0	8.5	9.0	9.0	7.9	8.8	8.3
No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	9.4	9.2	8.3	9.0	10.0	9.3	8.7	9.0	9.0	9.3
Transverse	9.0	8.8	8.2	8.7	9 0	8.7	8.8	9.2	8.7	9.1
No. of specimen	21	22	23	24	25	26	27	28	29	30
Anteroposterior	9.1	8.4	9.5	8.8	9.3	8.7	8.3	8.3	7.9	8.5
Transverse	9.7	8.2	9.1	9 2	8.7	9.0	8.4	8.7	8.2	8.5
No. of specimen	31	32	33	34	35	36	37	38	39	40
Anteroposterior	9.2	8.5	8.8	8.1	8.4	8.3	8.0	8.5	9.1	9.1
Transverse	8.5	9.5	9.0	8.5	8.8	8.3	8.4	8.2	8.9	8.7
No. of specimen	41	42	43	44	45	46	47	48	49	50
Anteroposterior	8.0	9.2	8.6	9.0	9.2	8.7	8.8	9.2	9.6	9.4
Transverse	8.1	8.5	8.5	8.7	9.0	8.8	8.6	9.1	8.9	8.7

No. of specimen	51	52	53	54	55	56	57	58	59	60
Anteroposterior	9.0	9.6	9.1	9.7	9.3	9.3	9.1	9.3	9.3	9.3
Transverse	8.5	9.1	8.4	9.3	9.3	9.5	9.4	9.0	8.8	9.1
No. of specimen	61	62	63	64	65	66	67	68	69	70
Anteroposterior	8.1	8.5	8.7	8.5	9.6	8.4	9.2	8.0	8.2	9.1
Transverse	7.8	8.2	8.3	8.5	8.7	8.7	8.9	8.5	8.5	9.0
No. of specimen	71	72	73	74	75	76	77	78	79	
Anteroposterior	9.6	8.9	9.5	9.0	9.2	8.9	8.3	8.1	9.0	
Transverse	9.7	8.3	9.3	9.0	8.3	8.4	8.2	8.7	8.5	

No. 79 is the only one which has a noticeable posterior accessory cusp. It will be observed (table 24) that in no less than 27 out of the 79 subfossil M^2 the width exceeds the length, and that in 5 specimens the width equals the length. Although as a rule in recent *Symphalangus* the length exceeds the width in M^2 as well as in M^1, in my series of 26 recent skulls in which M^2 can be measured both ways the width exceeds the length in 4, and equals the length in 2 more. Thus, the tendency for M^2 to be wider than long is present both in the living and in the subfossil siamang, but more marked in the cave form than in the recent.

The statistical data presented in table 25 show that the subfossil M^2, on an average, has a relatively greater width than the recent. The difference in size, as may be expected, is statistically significant: M^2, indeed, passes the test with flying colours, one might say.

TABLE 25

Statistical data on M^2 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	26	8.2	0.55	6.7	0.12	5.8
Idem, subfossil	79	8.9	0.49	5.5		
Transverse, recent	26	7.9	0.56	7.1	0.12	6.7
Idem, subfossil	79	8.7	0.40	4.6		

The third upper molar of *Symphalangus* is represented in the Sumatran cave collections by 64 specimens, nos. 1-34 from the right, nos. 35-64 from the left side (Coll. Dub. no. 11681/1-64). The posterior pair of cusps is much reduced relative to the anterior pair in most specimens; a small-sized but typical specimen, no. 1, is shown in pl. II fig. 5 above a very wide and short specimen, no. 11 (pl. II fig. 6); both are from the right side and originate from the Sibrambang cave. Nos. 1-24 and 35-54 are from the last-mentioned cave, which furnished the bulk of the Sumatran cave material; nos. 25-32 and 55-61 originate from the Lida Ajer cave, no. 62 is from the

Djamboe cave, and the name of the cave from which nos. 33, 34, 63 and 64 were obtained is not recorded. The measurements are presented in table 26.

TABLE 26

Measurements of M^3 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10	11
Anteroposterior	7.2	7.9	7.9	8.7	8.0	7.0	7.5	8.1	8.2	8.6	7.5
Transverse	8.1	8.5	8.4	8.8	8.5	8.2	9.1	8.5	8.8	8.9	9.6

No. of specimen	12	13	14	15	16	17	18	19	20	21	22
Anteroposterior	8.2	8.0	7.9	9.0	7.4	7.7	7.5	7.5	8.7	7.6	7.9
Transverse	8.8	9.2	8.9	9.7	8.2	8.5	8.0	7.8	9.0	8.5	8.3

No. of specimen	23	24	25	26	27	28	29	30	31	32	33
Anteroposterior	8.4	9.3	7.5	7.4	7.8	7.3	8.4	7.8	7.8	8.0	7.6
Transverse	8.9	8.8	8.2	8.0	8.4	9.3	9.1	8.0	8.5	8.2	8.2

No. of specimen	34	35	36	37	38	39	40	41	42	43	44
Anteroposterior	7.5	8.2	8.3	8.4	7.4	8.6	8.5	7.6	7.6	8.1	7.5
Transverse	7.8	8.2	8.8	9.0	8.9	8.7	9.2	8.2	8.1	8.7	9.3

No. of specimen	45	46	47	48	49	50	51	52	53	54	55
Anteroposterior	8.4	7.9	8.7	7.8	7.3	7.9	7.6	8.0	7.2	8.6	8.2
Transverse	7.8	8.6	8.9	7.8	8.0	8.1	8.4	8.1	8.2	8.9	9.0

No. of specimen	56	57	58	59	60	61	62	63	64
Anteroposterior	7.2	7.7	8.4	7.8	7.7	7.4	7.4	7.8	7.4
Transverse	8.4	8.8	8.6	8.0	8.1	8.5	8.4	8.2	8.7

The great majority of the subfossil specimens are wider than long, as is the rule in the recent M^3 of *Symphalangus,* although the difference appears to be more marked in the subfossil than in the recent specimens. Only in nos. 24 and 45 the length is greater than the width, but both of these are worn and lack a posterior contact facet so that they doubtless represent last molars. No. 45, a left M^3, is shown in pl. II fig. 10; it closely resembles in shape the sole elongated specimen of M^3 in my recent series of skulls (no. 33). It has an accessory tubercle on the posterior marginal ridge between metacone and hypocone. Such posterior accessory cusps are rather frequently observed among the subfossil specimens, in contradistinction to the recent: nos. 10, 13, 25, 34, 35, 38, 40, 45, 47, 54 and 60 possess posterior accessory cusps. In one out of these eleven subfossil M^3, viz., no. 35 (pl. II fig. 9) there are even two extra cusps between metacone and hypocone. I have not found any posterior extra cusps on M^3 of recent *Symphalangus,* not even in the skull no. 47 in which the right M^1 bears such a cusp. Remane (1921, p. 53) observed posterior extra cusps only in one out of ten recent

M^3 of *Symphalangus,* and found none in M^2 or M^1. The frequency of occurrence of these cusps in the subfossil M^3 of *Symphalangus* is one in six.

TABLE 27

Statistical data on M^3 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	16	7.4	0.63	8.5	0.17	2.9
Idem, subfossil	64	7.9	0.49	6.2		
Transverse, recent	16	7.8	0.55	7.1	0.15	4.7
Idem, subfossil	64	8.5	0.44	6.2		

The data given in table 27 show that the subfossil M^3 is significantly larger and also relatively wider than the recent. The subfossil series is less variable than the recent, as usual.

In the lower molar series of *Symphalangus,* M_1 is characterized by the buccal anterior cusp (protoconid) being more advanced in position than the lingual (metaconid), making the anterior transverse valley oblique in its course. The width over the talonid portion of the crown is invariably greater than that over the anterior cusps (trigonid width). M_2 is a larger and wider tooth, with the anterior cusps more nearly opposite each other; the trigonid width may exceed the talonid width. In M_3 the talonid portion may be reduced in width and length, but the crown may also be longer than that of M_2 in the same skull. The entoconid is smaller, however, and the hypoconulid more centrally placed. The greatest width is usually in front.

We have got 35 specimens of M_1 in the Sumatran cave collections; nos. 1-19 from the right, and nos. 20-35 from the left side (Coll. Dub. no. 11682/1-35). Nos. 1-18 and 20-32 are from the Sibrambang cave, no. 33 is from the Lida Ajer cave, and the cave from which nos. 19, 34, and 35 were obtained is unknown. Nos. 1 and 20 (pl. II figs. 11-12) have an accessory internal cusp between metaconid and entoconid; such extra cusps occur in a few recent M_1 (of skulls nos. 47 (both sides) and 28 (left side only)) as well. In recent skull no. 43 the metaconid is split in both M_1. Splitting of cusps of molars in gibbons, further cases of which will be given below, was found by Remane (1921, p. 57) only in M_1 (entoconid).

The measurements of the subfossil M_1 of *Symphalangus syndactylus* are recorded in table 28. For comparison I have used a total of 19 recent M_1, 9 male, 6 female, and 4 of unknown sex. The statistics (table 29) show that the subfossil M_1 is significantly larger than the recent, and more variable, especially in its anteroposterior diameter.

TABLE 28

Measurements of M_1 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	9.0	8.3	9.1	9.2	8.8	8.2	8.0	9.1	7.7	8.7
Transverse	7.1	6.7	7.3	6.7	6.9	6.4	6.4	7.4	6.0	6.9
No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	8.6	8.6	8.7	8.3	8.8	8.7	8.4	8.3	9.0	9.0
Transverse	6.7	6.8	7.0	6.8	6.4	6.9	7.0	6.8	7.2	6.6
No. of specimen	21	22	23	24	25	26	27	28	29	30
Anteroposterior	8.1	8.2	8.9	8.5	8.3	8.4	8.2	8.0	8.7	8.9
Transverse	6.8	6.6	6.9	6.5	6.5	6.4	6.6	6.4	6.9	7.2
No. of specimen	31	32	33	34	35					
Anteroposterior	9.7	9.6	7.7	8.3	9.1					
Transverse	7.2	7.3	6.0	6.7	6.6					

TABLE 29

Statistical data on M_1 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	19	8.2	0.32	3.9	0.11	3.6
Idem, subfossil	35	8.6	0.47	5.5		
Transverse, recent	19	6.3	0.31	4.9	0.09	5.6
Idem, subfossil	35	6.8	0.34	5.0		

The second lower molar, M_2, is represented in the Sumatran cave collections by 45 specimens (Coll. Dub. no. 11683/1-45), the first 23 of which are from the right side. Nos. 1-19 and 24-42 are from the Sibrambang cave, nos. 20-22, 43 and 44 from the Lida Ajer cave, no. 23 from the Djamboe cave, and no. 45 is from an unknown cave. No. 41 only is anomalous in showing an accessory cusp split off from the entoconid; it is almost a "tuberculum intermedium" as figured in the two M_1 recorded above. Remane (1921, p. 56) found this tubercle in 3 M_1 and 1 M_2 of *Symphalangus*; it does not occur in the recent M_2 of *Symphalangus* which I have seen.

A statistical comparison between the subfossil M_2 (table 30) and 20 recent M_2 (including 7 male and 8 female specimens) shows that the cave specimens average decidedly larger than the recent, and that the difference between the means is more than four times the standard error of this difference, and, therefore, significant (table 31).

The last lower molar of *Symphalangus,* of which there are 60 specimens in the Sumatran cave collections, is rather variable in shape; short and

TABLE 30

Measurements of M_2 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	10.2	10.3	9.9	9.2	9.6	9.3	8.9	9.9	9.4	9.7
Transverse	7.8	8.0	7.6	7.0	7.1	7.1	7.3	7.5	7.4	7.7
No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	9.5	9.2	9.8	9.4	9.2	8.8	9.2	8.8	9.6	10.2
Transverse	7.3	7.2	7.2	7.7	7.3	7.0	7.3	7.1	7.2	7.8
No. of specimen	21	22	23	24	25	26	27	28	29	30
Anteroposterior	10.0	8.9	10.4	9.7	10.0	10.3	9.9	9.8	9.4	9.2
Transverse	7.8	7.3	7.8	8.2	7.4	8.0	7.9	7.8	7.5	7.0
No. of specimen	31	32	33	34	35	36	37	38	39	40
Anteroposterior	10.4	8.9	9.4	9.9	9.4	9.8	9.3	8.7	9.1	9.7
Transverse	8.1	7.6	7.4	7.6	7.7	7.5	7.2	7.2	7.3	7.3
No. of specimen	41	42	43	44	45					
Anteroposterior	9.2	9.4	8.9	9.3	10.2					
Transverse	7.4	7.3	7.7	7.2	7.7					

TABLE 31

Statistical data on M_2 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	20	8.8	0.56	6.4	0.15	4.7
Idem, subfossil	45	9.5	0.47	5.0		
Transverse, recent	20	7.0	0.44	6.3	0.11	4.5
Idem, subfossil	45	7.5	0.31	4.1		

wide crowns (e.g., no. 57: pl. II fig. 14) occur beside long and narrow specimens. The roots are mostly fused, and are recurved backward. There are 31 right specimens against 29 from the left side (Coll. Dub. no. 11684/1-60). Nos. 1-28 and 32-56 originate from the Sibrambang cave, nos. 29, 57 and 58 from the Lida Ajer cave, no. 59 from the Djamboe cave; the cave from which the remaining nos. 30, 31 and 60 were obtained is unknown. No. 1 (pl. II fig. 13), a rather elongated specimen, has a split hypoconid, not observed among the recent molars one of which, however, has a split entoconid (the right M_3 in skull no. 33). Accessory tubercles between metaconid and entoconid, or tubercula intermedia, occur in various specimens, and are either large as in nos. 2 and 3, or small as in nos. 12, 49 and 54. One of the cave specimens, no. 4, has a tiny posterior contact facet not seen in the others; this indicates that the mandible to which this molar belonged had a supernumerary molar. Fourth molars do occur in the recent siamang gibbon, but only rarely; one case of M_4 on both sides of the mandible is cited by Remane (1921, p. 10), and in the material examined by me there is only one instance of M^4 (skull no. 44). Schultz (1933, p. 236) records fourth molars to occur in two out of fifteen skulls of *Symphalangus,* but does not state whether they are maxillary or mandibular.

The cave specimens (table 32) have been compared with 14 recent M_3 (4 male, 6 female, and 4 of unknown sex). As is clear from table 33 the subfossil last lower molars, less variable than their recent homologues as is the case in most of the premolars and molars, are decidedly larger than the recent as well.

TABLE 32

Measurements of M_3 of *Symphalangus syndactylus subfossilis* nov. subsp.

No. of specimen	1	2	3	4	5	6	7	8	9	10
Anteroposterior	9.8	10.7	10.3	9.2	8.4	8.6	9.2	9.8	8.7	9.0
Transverse	7.7	8.2	7.8	7.1	6.9	7.5	7.2	8.0	7.7	7.4
No. of specimen	11	12	13	14	15	16	17	18	19	20
Anteroposterior	10.1	9.0	9.4	9.5	9.2	9.9	8.5	8.7	8.8	9.0
Transverse	8.1	7.4	7.5	7.1	7.5	7.8	7.6	7.1	7.5	7.6
No. of specimen	21	22	23	24	25	26	27	28	29	30
Anteroposterior	10.1	8.6	10.1	10.0	8.9	9.6	8.7	8.9	9.0	9.3
Transverse	6.9	7.2	8.1	7.8	7.0	7.5	7.0	6.8	7.0	7.3
No. of specimen	31	32	33	34	35	36	37	38	39	40
Anteroposterior	9.5	10.5	9.7	9.7	9.7	10.5	8.2	9.0	8.6	8.5
Transverse	8.3	8.0	7.8	7.7	8.0	7.9	6.8	7.5	6.7	7.1
No. of specimen	41	42	43	44	45	46	47	48	49	50
Anteroposterior	8.3	8.9	9.5	8.5	9.7	8.7	9.7	8.5	9.3	9.4
Transverse	7.5	7.8	7.8	7.4	7.5	7.4	7.7	6.9	7.2	7.5
No. of specimen	51	52	53	54	55	56	57	58	59	60
Anteroposterior	9.1	9.5	9.8	10.0	9.8	9.3	8.4	9.1	8.6	9.4
Transverse	7.0	7.7	7.1	7.3	7.3	7.4	7.5	7.5	7.5	—

TABLE 33

Statistical data on M_3 of *Symphalangus syndactylus*

	n	M	σ	C	$E_{diff.}$	$\frac{M_{subf.}-M_{rec.}}{E_{diff.}}$
Anteroposterior, recent	14	8.8	0.74	8.4	0.20	2.5
Idem, subfossil	60	9.3	0.36	3.9		
Transverse, recent	14	6.9	0.50	7.2	0.14	4.3
Idem, subfossil	59	7.5	0.38	5.1		

As we have seen above, the subfossil siamang gibbon averages decidedly larger in tooth dimensions than the living form from Sumatra. There can be no doubt that the cave teeth belong to a subspecies directly ancestral to the extant *Symphalangus syndactylus syndactylus* (Raffles) from the same island. From the measurements given in tables 13-33 it is evident that the premolars and molars have not been reduced in size to exactly the same extent (the incisors and canines unfortunately must be left out of account since the possibility of admixture of *Hylobates* elements cannot be excluded). Table 34 gives the average „robustnesses" (a measure of the crown surface: the product of the anteroposterior and the transverse crown diameters) of the cave and the recent teeth as well as the ratios of size. It will be seen from this table that the crown surface in the subfossil siamang is from 10

TABLE 34

Robustness of P and M of *Symphalangus syndactylus*

	S.s. subfossilis	*S.s. syndactylus*	Ratio
P^3	40.87	36.48	112 : 100
P^4	40.71	36.40	112 : 100
M^1	68.00	55.44	123 : 100
M^2	77.43	64.78	119 : 100
M^3	67.15	57.72	116 : 100
P_3	48.23	40.80	118 : 100
P_4	36.72	33.32	110 : 100
M_1	58.48	51.66	111 : 100
M_2	71.25	61.60	116 : 100
M_3	69.75	60.72	115 : 100

to 23 per cent. larger than that in the homologous recent teeth. The P_3 has been reduced in size to a greater extent than the P_4; in the subfossil race M^1 is larger than M^3, and has been reduced to a greater extent than any of the other molars; in the living form it averages slightly smaller than M^3. In the mandible, the molar most reduced in size is M_2, whereas the reduction in size of M_3 is only very slightly less. If this does represent a process of reduction starting from the back of the tooth row it would seem that the process is more advanced in the upper jaw than in the lower, in which M_1 is comparatively slightly affected, as is P_4. The reduction in size of P_3 is rather marked (15 per cent.); this, as already mentioned, is no doubt a process of adjustment to the diminishing size of the upper canine which, too, must have been much larger in the extinct cave form than in the recent.

It is now possible to present the following diagnosis of the subfossil race of *Symphalangus syndactylus* from the prehistoric Sumatran caves:

Symphalangus syndactylus subfossilis nov. subsp.

Diagnosis: Teeth identical in specific characters with those of recent *Symphalangus syndactylus* (Raffles) but of larger average size; the difference in tooth size is statistically significant. The anterior lower premolar is larger relative to the posterior than in the living form; in the upper tooth row the first molar averages larger than the third, in the lower the second molar is larger relative to the first and third than in the living form.

Holotype: The right upper second molar, Coll. Dub. no. 11680/1, represented on pl. I fig. 6 of the present paper.

Locality: Sibrambang cave, Padang Highlands, Central Sumatra. The bulk of the material is from this cave; other specimens are from the Lida Ajer and the Djamboe cave in the Padang Highlands.

Age: Early Holocene.

PLEISTOCENE MATERIAL OF SYMPHALANGUS FROM JAVA

From the Pleistocene of Java, in which island the siamang gibbon is now extinct, teeth of *Symphalangus* have been recorded by Von Koenigswald (1940) as well as by Badoux (1959). The left lower (second?) molar from a fissure deposit at Patjitan figured by Von Koenigswald (1940, pl. III fig. 8) appears to be within recent limits (dimensions of crown approximately 9 by 7 mm). Badoux (1959, pp. 90-93, pl. VIII figs. 1-15) records 40 isolated teeth from two fissure deposits at Punung only two of which are not within the range of their recent homologues, viz., an M^3 6.0 by 6.5 mm in diameters, which is smaller, and an M_3 10.1 by 8.0 mm in diameters, which is larger than the corresponding molar in the recent *Symphalangus*. On the whole, it seems to me that the fossil Javan gibbon was smaller-toothed than the subfossil Sumatran race. It might upon further study prove to present a case parallel to those of the orang-utan, porcupine, tiger and tapir, which are represented in the Pleistocene of Java by forms smaller-toothed than those from the cave fauna of Sumatra (see Hooijer, 1949). There is no material referable to *Symphalangus* in the Dubois collection from Java.

Genus HYLOBATES Illiger

Hylobates agilis Cuvier

Material examined:

Juveniles

1. Skull. W. Sumatra, from the Amsterdam Zoo, August, 1923 (a). A.M.
2. Skull. W. Sumatra, from the Amsterdam Zoo, August, 1923 (b). A.M.
3. Mounted skin and skeleton of female. Sumatra, from the Rotterdam Zoo, 7-4-1931. L.M., reg. no. 1945.

4. Stuffed skin and skull of male. Sumatra, from the Rotterdam Zoo, 29-8-1919. L.M., reg. no. 930.
5. Mounted skin of male. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. f.
6. Mounted skin of female (skull inside). Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. i.
7. Mounted skin of female (skull inside). Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. j.

Subadults

8. Skull of female. Soeliki, W. Sumatra, from the Amsterdam Zoo, 10-8-1823. A.M.
9. Mounted skin and skull of male. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. g.

Adults (sex not recorded)

10. Skull. Padang, W. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. d.
11. Skull. N. Sumatra, purchased from Schlüter and Mass. Coll. Sody no. 3. L M.
12. Skull. Padang, W. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. b.
13. Skull. Padang, W. Sumatra, from C. G. C. Reinwardt. L.M., cat. ost. c.

Adult males

14. Mounted skin and skeleton. Sumatra, from the Rotterdam Zoo, 18-6-1932. L.M., reg. no. 2085.
15. Skull. From the collection of E. Dubois, 1941. L.M., reg. no. 4608.
16. Skeleton. Batang Singalang, central Sumatra, from S. Müller. L.M., cat. ost. a.
17. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. b.
18. Mounted skin and skeleton. Padang, W. Sumatra, from the Rotterdam Zoo, 25-8-1922. L.M., reg. no. 1166.
19. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. h.
20. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. k.
21. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. m.
22. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. n.
23. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. p. M_3 sin. congenitally absent.
24. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. q.

Adult females

25. Stuffed skin and skull. W. Sumatra, coll. E. Jacobson, 1935. L.M., reg. no. 2372.
26. Skull. From the Rotterdam Zoo, 22-11-1938. L.M., reg. no. 3716.
27. Mounted skin and incomplete skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. c.
28. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. d.
29. Mounted skin and incomplete skull. Padang, W. Sumatra, coll. Henrici, 1838. L.M., cat. syst. e.
30. Mounted skin and skull. E. of Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. a.

31. Mounted skin. Padang, W. Sumatra, from C. G. C. Reinwardt. L.M., cat. syst. l.
32. Mounted skin and skull. Padang, W. Sumatra, from S. Müller, 1836. L.M., cat. syst. o.
33. Mounted skin and skeleton. From the Rotterdam Zoo, 18-8-1931. L.M., reg. no. 1987.

This, the dark-handed gibbon, is one of the species of *Hylobates* today living in Sumatra, the other being *Hylobates lar albimanus* (Vig. et Horsf.). Both *agilis* and *lar* also occur in Malaya, but subspecific distinction has been made only in the latter species and not in *agilis* (although Chasen, 1940, p. 63, cites the Malayan and Sumatran form as *Hylobates agilis agilis* no other subspecific name of *H. agilis* is mentioned in his work). Kloss (1929, p. 113/14) states to have attempted to treat the gibbons of Java and Borneo, together with *agilis*, as allied subspecies, but finally to have kept *agilis* as

TABLE 35

Skull measurements of adult males and females of *Hylobates agilis*

	males					females				
No.	n	R	M	σ	C	n	R	M	σ	C
1	11	102-108	105	2.0	1.9	7	99-109	104	4.4	4.2
2	11	72-75	74	1.3	1.8	7	69-81	73	3.9	5.3
3	11	56-61	59	1.4	2.4	7	57-62	59	1.9	3.2
4	11	58-64	62	2.1	3.4	7	58-62	60	1.4	2.3
5	11	62-68	65	1.8	2.8	8	59-64	62	1.7	2.8
6	11	45-52	49	1.8	3.7	8	45-50	48	1.8	3.8
7	11	49-57	52	2.3	4.4	7	48-55	51	2.6	5.1
8	11	60-69	66	3.0	4.5	8	61-69	64	2.4	3.8
9	11	21-28	25	2.0	8.0	8	22-25	24	1.4	6.0
10	11	51-58	55	2.7	5.0	8	52-59	55	2.4	4.4
11	11	18-21	19	1.3	6.8	8	17-20	19	1.1	5.8
12	11	14-17	16	1.2	7.5	8	12-18	15	1.7	11.3
13	11	9-13	12	1,2	10.0	8	9-13	11	1.7	15.5
14	11	18-23	21	1.8	8.6	8	18-22	20	1.7	8.5

a species in its own right, placing the others under "*cinereus*" (recte: *moloch*). Pocock (1927, p. 725) regarded *agilis* as a subspecies of *lar*, but he stands alone in this, and in the most recent classification by Fiedler (1956, p. 219) *H. agilis* is listed as a distinct species.

The skull measurements given in table 35 show that the sexual difference in average skull size is very small in *agilis*, much smaller than in *Symphalangus syndactylus* (tables 1 and 2). It stands to reason that the sexual differences in tooth size are also slight in *Hylobates*; tables 36 and 37 bear this out. The sexual differences are most marked in the anteroposterior diameters of the upper canine and the anterior lower premolar. The last lower molar averages larger in the females than in the males instead of smaller as most other teeth do; the central upper incisor is also larger in the females than in the males.

TABLE 36

Measurements of upper teeth of males and of females of *Hylobates agilis*

		males					females				
		n	R	M	σ	C	n	R	M	σ	C
I^1	tr.	7	4.4-5.5	4.9	0.41	8.4	4	4.9-5.4	5.1	0.24	4.7
	ap.	6	3.8-4.3	4.0	0.23	5.8	5	3.7-4.2	4.0	0.21	5.3
I^2	tr.	8	3.5-4.2	3.9	0.22	5.6	5	3.7-4.0	3.9	0.14	3.6
	ap.	8	3.7-4.6	4.2	0.37	8.8	6	3.7-4.3	4.0	0.24	6.0
C	ap.	8	6.4-8.5	7.5	0.69	9.2	7	6.2-7.5	7.0	0.45	8.5
	tr.	9	4.4-5.9	5.3	0.47	8.9	7	4.7-5.5	5.1	0.29	5.9
P^3	ap.	11	4.5-5.7	5.0	0.39	7.8	6	4.4-5.0	4.7	0.21	4.5
	tr.	11	4.8-5.4	5.1	0.24	4.7	6	4.5-5.3	4.8	0.28	5.8
P^4	ap.	9	3.8-5.0	4.3	0.43	9.8	6	4.1-4.3	4.2	0.06	1.4
	tr.	10	4.8-5.7	5.2	0.36	6.9	7	4.6-5.2	4.9	0.19	3.9
M^1	ap.	10	5.5-6.7	5.9	0.36	6.1	6	5.7-6.3	5.9	0.21	3.5
	tr.	10	5.7-6.7	6.2	0.31	5.0	6	5.9-6.6	6.3	0.29	4.6
M^2	ap.	11	5.8-6.5	6.1	0.22	3.6	6	5.7-6.1	5.9	0.16	2.7
	tr.	11	5.8-6.8	6.4	0.32	5.0	6	6.2-6.6	6.4	0.14	2.2
M^3	ap.	11	4.9-6.0	5.4	0.40	7.4	5	5.2-5.6	5.4	0.16	3.0
	tr.	11	5.2-6.9	6.0	0.41	6.8	6	5.8-6.6	6.2	0.28	4.5

TABLE 37

Measurements of lower teeth of males and of females of *Hylobates agilis*

		males					females				
		n	R	M	σ	C	n	R	M	σ	C
I_1	tr.	9	3.2-3.5	3.4	0.13	3.8	6	3.3-3.5	3.3	0.09	2.7
	ap.	9	3.2-4.0	3.6	0.29	8.1	7	3.1-3.9	3.4	0.30	8.8
I_2	tr.	9	3.3-4.1	3.6	0.24	6.7	7	3.4-4.0	3.6	0.19	5.3
	ap.	9	3.8-4.5	4.1	0.30	7.3	7	3.8-4.2	4.0	0.15	3.8
C	ap.	11	6.2-7.3	6.9	0.33	4.6	8	6.2-7.0	6.7	0.34	5.1
	tr.	11	4.6-5.9	5.1	0.38	7.5	8	4.2-5.3	4.9	0.38	7.8
P_3	ap.	10	5.9-7.8	7.0	0.59	8.4	7	6.2-6.9	6.4	0.25	3.9
	tr.	11	3.7-4.8	4.0	0.31	7.7	7	3.8-4.6	4.1	0.29	7.1
P_4	ap.	10	4.6-5.5	5.0	0.36	7.2	7	4.6-5.2	4.8	0.21	4.4
	tr.	10	3.8-4.8	4.2	0.36	8.6	7	4.0-4.5	4.2	0.21	5.0
M_1	ap.	10	5.6-6.8	6.3	0.37	5.9	6	6.1-6.6	6.3	0.18	2.9
	tr.	10	4.9-5.6	5.1	0.27	5.3	6	5.0-5.3	5.2	0.13	2.5
M_2	ap.	11	5.9-6.9	6.4	0.33	5.2	6	6.0-6.3	6.1	0.13	2.1
	tr.	10	5.2-6.4	5.6	0.34	6.1	6	5.3-5.8	5.6	0.16	2.9
M_3	ap.	10	5.5-6.6	6.0	0.36	6.0	6	5.8-6.8	6.3	0.38	6.0
	tr.	11	4.8-5.8	5.2	0.34	6.6	6	5.5-5.9	5.6	0.15	2.7

CAVE MATERIAL OF HYLOBATES FROM SUMATRA

In sharp contrast to *Symphalangus*, *Hylobates* is very poorly represented in the collections from the Sumatran caves. The best specimen is a set of teeth, P^4-M^2 dext., in a calcareous concretion, originating from the Lida Ajer cave (Coll. Dub. no. 11685; pl. I fig. 7). This truly remarkable specimen (in view of the rarity of *Hylobates* in the caves) is fully within the limits of recent males of *H. agilis*, and above the range of the females in the dimensions of P^4 and M^2 (table 38). The only further upper tooth of *Hylobates* from Sumatran caves is an isolated P^4 dext. from the Sibrambang cave (Coll. Dub. no. 11686) very similar to that in the Lida Ajer specimen and only slightly longer and narrower (table 38). Whether these cave specimens represent *H. agilis* or perhaps *H. lar* (one subspecies of *H. lar* is found today in Sumatra: *H. lar albimanus*) cannot be established as the few (male) skulls of the Sumatran race of *H. lar* available to me are indistinguishable in dental characters from those of *H. agilis*. The same applies to two lower molars, both from the Sibrambang cave (Coll. Dub. no. 11687), which appear to be the only elements of the lower dentition referable to *Hylobates*. They represent M_2 sin. and M_3 dext., and they are only a trifle longer than their homologues in recent *H. agilis* (table 38).

TABLE 38

Measurements of subfossil teeth of *Hylobates* spec.

Coll. Dub. nos.	11685	11686	11687
P^4 ap.	4.4	4.6	—
tr.	5.4	5.1	—
M^1 ap.	5.8	—	—
tr.	6.5	—	—
M^2 ap.	6.5	—	—
tr.	6.7	—	—
M_2 ap.	—	—	7.1
tr.	—	—	5.9
M_3 ap.	—	—	7.0
tr.	—	—	5.7

In view of the extreme scarceness of *Hylobates* premolars and molars in the Sumatran caves (4 uppers against 279 of *Symphalangus*, and 2 lowers against 161 of *Symphalangus*) it would seem unlikely that any *Hylobates* incisors are included among the 23 gibbon incisors recorded above, but a few *Hylobates* canines may be present among the rich material of canines (136 uppers and 136 lowers). However, as there is no way of telling *Hylobates* incisors and canines apart from those of *Symphalangus* these elements must be left generically undetermined. We have seen that the *Symphalangus* of prehistoric Sumatra was distinctly larger-toothed than the extant form of the island, and the same would seem to hold good for the prehistoric *Hylobates* spec., which is either in the upper end of the range of variation for the recent specimens, or even above this range in dental dimensions. Since the species of the subfossil *Hylobates* teeth cannot be determined, they must be recorded as *Hylobates* spec.

PLEISTOCENE MATERIAL OF HYLOBATES FROM JAVA

There is neither Pleistocene nor prehistoric cave material of *Hylobates* in the Dubois collection from Java. Von Koenigswald (1940, p. 64, pl. II fig. 15) figures a tooth from the Pleistocene of Sangiran in Java as belonging to *Hylobates "leuciscus"*. The earliest available valid name of the Javanese gibbon, as Cabrera (1930) has pointed out, is *Simia moloch* Audebert, 1797, and the correct name of the Javanese gibbon is *Hylobates moloch moloch* (Audebert); see Chasen, 1940, p. 64. Among 40 isolated teeth from two fissure deposits at Punung in Java recorded by Badoux (1959, pp. 90-93) there is only one specimen, an M^3, that is stated to be within the range of *Hylobates "leuciscus"*; the others are larger and are referred to *Symphalangus syndactylus*. It is not quite clear whether Badoux considers this molar to represent the living gibbon of Java, for in his diagram on p. 98 it is represented as *Symphalangus* spec. If the small specimen really belongs to *Hylobates* this would indicate that *Hylobates* is very rare at Punung, making up just about the same very small percentage of the total number of gibbon teeth as at the Sumatran caves, in which, as we have already seen, *Symphalangus* is about seventy-five times more abundantly represented than is *Hylobates*.

CAVE MATERIAL OF HYLOBATES FROM BORNEO

A left ramus of the mandible with P_4-M_3, originating from an alluvial deposit in Sarawak, Borneo, has been recorded as *Hylobates* spec. by Lydekker (1887, p. 298). I have examined the specimen in the British Museum (Natural History), and found it to belong to a langur, *Presbytis* spec. However, remains of *Hylobates* have recently been found at the Great Cave of Niah, in Sarawak, during explorations of the cave by the Sarawak Museum under the direction of Mr. T. Harrisson (Medway, 1959, p. 632). Through the courtesy of Mr. Harrisson I have been able to examine these remains, which will be reported upon elsewhere. Suffice it to say that the cave specimens are indistinguishable from, and either within the limits or slightly above the range of recent *Hylobates moloch abbotti* Kloss today inhabiting the western parts of Borneo. Hence, the picture appears to be the familiar one of a cave form differentiated from the living form of the same region only in its slightly greater average size.

PLEISTOCENE MATERIAL OF HYLOBATES FROM CHINA

Although this does not strictly come within the purview of the present paper, dealing as it does with the Malay Archipelago exclusively, mention may be made here of a fragment of the left ramus of the mandible with M_{2-3} from out the limestone fissures of Yenchingkou, Szechwan, the only *Hylobates* found in situ so far beyond the present range of the gibbons. It was described by Matthew and Granger (1923, p. 588, fig. 18) as *Bunopithecus sericus* Matthew et Granger, but later referred to *Hylobates* by Colbert and Hooijer (1953, p. 27). The Pleistocene molars are indistinguishable from those of recent *Hylobates*; the last molar in this single specimen is longer and wider than the second, as is the case in 3 out of 18 mandibles of *H. agilis* (and in 3 out of 13 mandibles of *Symphalangus*), and in size they are near or within the limits of the living *Hylobates hoolock* (Harlan) from Burma as given by Remane (1921, p. 25). Whether or not the Pleistocene Chinese gibbon merits a distinct specific name cannot be made out on the basis of the material at present available.

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EXPLANATION OF THE PLATES

Plate I

Figs. 1 and 2, *Symphalangus* c.q. *Hylobates* spec., I^1 dext.; fig. 1, Coll. Dub. no. 11669/4, Sibrambang cave, Sumatra, lingual view; fig. 2, Coll. Dub. no. 11669/3, Lida Ajer cave, Sumatra, lingual view.

Figs. 3-6, *Symphalangus syndactylus subfossilis* nov. subsp., Sibrambang cave, Sumatra; fig. 3, P_4 sin., Coll. Dub. no. 11678/7, crown view; fig. 4, P_4 sin., Coll. Dub. no. 11678/10, crown view; fig. 5, P_3 sin., Coll. Dub. no. 11677/4, lingual view; fig. 6, M^2 dext. (holotype), Coll. Dub. no. 11680/1, crown view.

Fig. 7, *Hylobates* spec., P^4-M^2 dext., Coll. Dub. no. 11685, Lida Ajer cave, Sumatra, crown view.

Fig. 8, *Symphalangus* c.q. *Hylobates* spec., upper C sin., Coll. Dub. no. 11672/5, Sibrambang cave, Sumatra, lingual view.

Fig. 9, *Symphalangus syndactylus subfossilis* nov. subsp., P_3 sin., Coll. Dub. no. 11677/5, Sibrambang cave, Sumatra, lingual view.

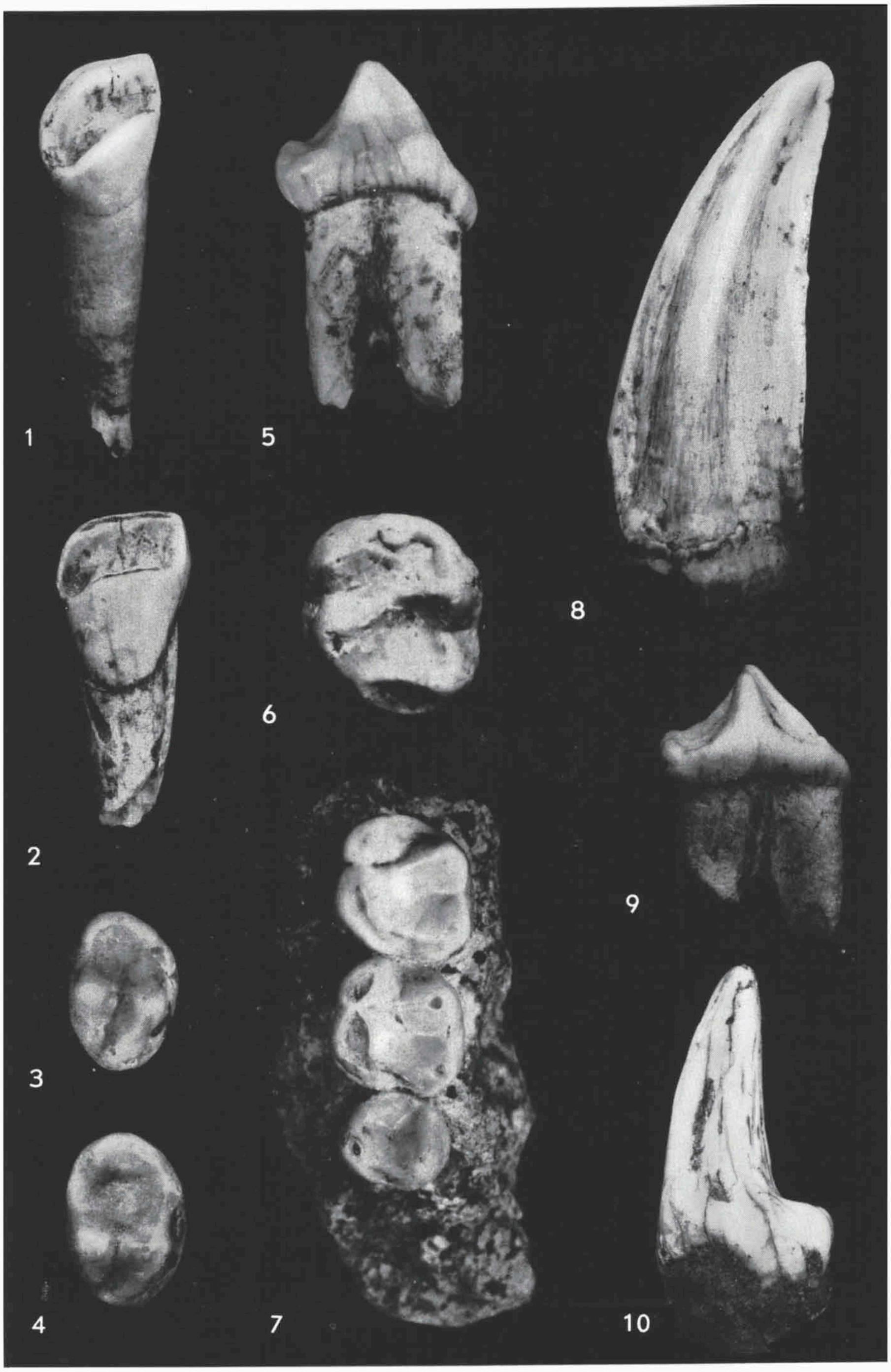
Fig. 10, *Symphalangus* c.q. *Hylobates* spec., lower C dext., Coll. Dub. no. 11674/6, Sibrambang cave, Sumatra, lingual view.

All figures 3 × natural size.

Plate II

Crown views of teeth of *Symphalangus syndactylus subfossilis* nov. subsp. from Sumatran caves; fig. 1, P^3 dext., Coll. Dub. no. 11675/7, Lida Ajer cave; fig. 2, M^1 dext., Coll. Dub. no. 11679/1, Sibrambang cave; fig. 3, M^1 dext., Coll. Dub. no. 11679/23, Lida Ajer cave; fig. 4, M^1 sin., Coll. Dub. no. 11679/60, Lida Ajer cave; fig. 5, M^3 dext., Coll. Dub. no. 11681/1, Sibrambang cave; fig. 6, M^3 dext., Coll. Dub. no. 11681/11, Sibrambang cave; fig. 7, M^2 sin., Coll. Dub. no. 11680/45, Sibrambang cave; fig. 8, M^2 sin., Coll. Dub. no. 11680/79, no record; fig. 9, M^3 sin., Coll. Dub. no. 11681/35, Sibrambang cave; fig. 10, M^3 sin., Coll. Dub. no. 11681/45, Sibrambang cave; fig. 11, M_1 dext., Coll. Dub. no. 11682/1, Sibrambang cave; fig. 12, M_1 sin., Coll. Dub. no. 11682/20, Sibrambang cave; fig. 13, M_3 dext., Coll. Dub. no. 11684/1, Sibrambang cave; fig. 14, M_3 sin., Coll. Dub. no. 11684/57, Lida Ajer cave.

All figures 3 × natural size.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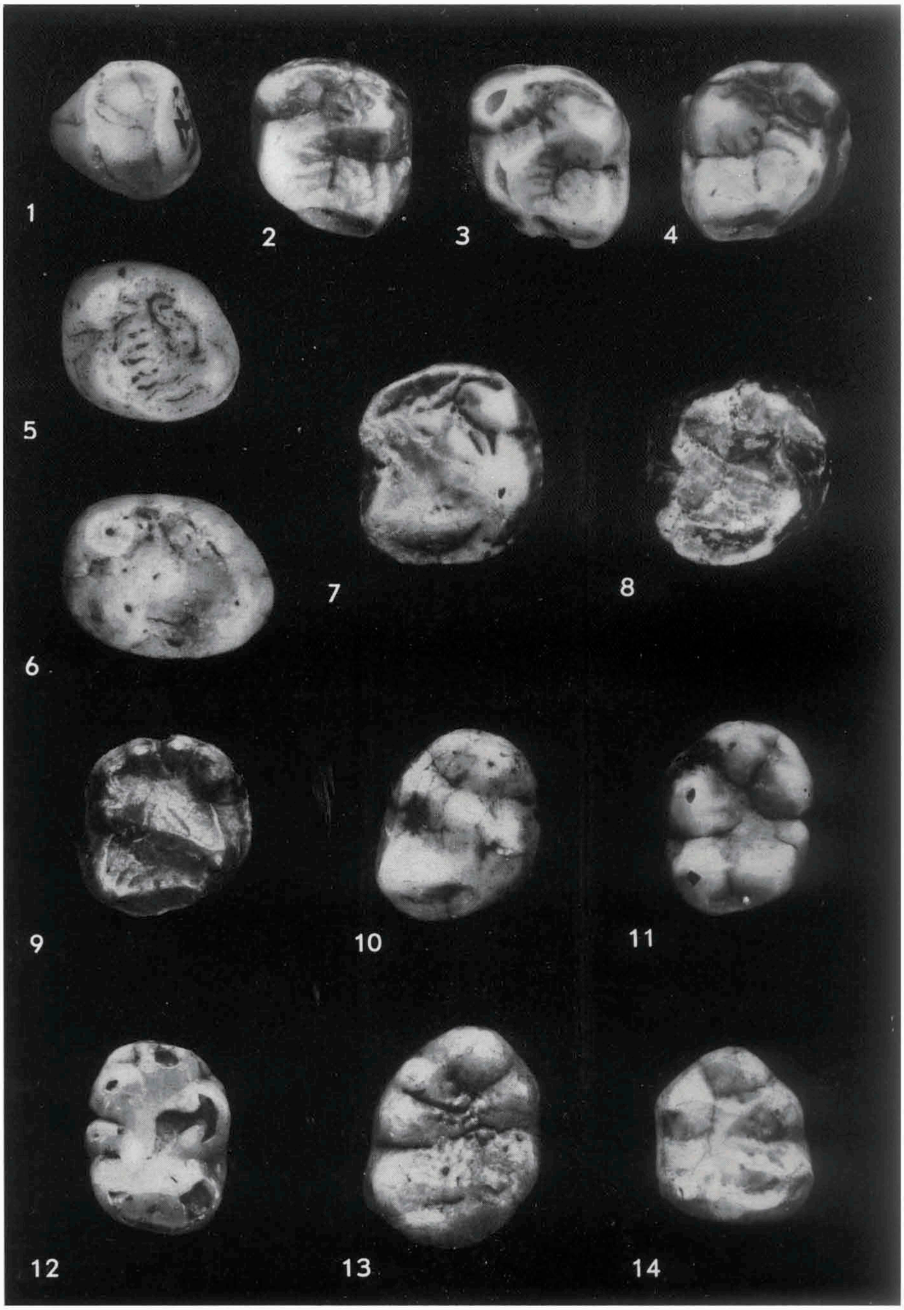
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