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A LOWER MANDIBLE OF *ZYGOMATURUS GILLI* FROM THE SANDRINGHAM SANDS, BEAUMARIS, VICTORIA, AUSTRALIA

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Introduction

Stirton (1957) described three diprotodontid specimens which had been recovered from the Black Rock Sandstone of the Brighton Group (Kenley 1967), on the shore of Port Phillip Bay near Beaumaris, Victoria. One of the specimens, M.U.G.D. No. 2020, subsequently became the type of *Zygomaturus gilli* (Stirton 1967) and the second, N.M.V. P15905, was also assigned to that species (*ibid.*). The third specimen, a fragment with the symphysis and part of the horizontal ramus containing the alveoli of P_3, base of M_1, and most of M_2, was also discussed by Stirton (1957), but at that time information on Tertiary diprotodontids was insufficient for a close determination of its affinities. In 1967, Mr Colin Macrae found the rear portion of a mandible containing M_3 and M_4 which proved to fit perfectly onto the former specimen. With this surprising discovery, a nearly complete mandible is represented, lacking only the angle, coronoid process, and anterior tip of the symphysis. Now that this individual is more completely represented, it is possible to compile a sufficiently adequate description to allow an analysis of its affinities. Such is the purpose of the present report. The specimen originally described by Stirton is catalogued as N.M.V. P15911A; the portion collected by Macrae is P15911B. The complete specimen will be designated here as N.M.V. P15911A-B.

I am grateful to Mr H. E. Wilkinson, Assistant Curator of Fossils, National Museum of Victoria, for giving me the opportunity to describe this specimen. The manuscript has been read and criticized by R. H. Tedford, Department of Vertebrate Paleontology, American Museum of Natural History, New York, and by W. A. Clemens, Department of Paleontology, University of California, Berkeley. D. E. Savage, Director of the Museum of Paleontology, University of California, Berkeley, gave permission for the specimen to be illustrated by Owen J. Poe, staff artist. Responsibility for any statements made in this report rests on me alone. Such measurements as could be made are presented in Table 1.

Gill (1957) has summarized the evidence showing that the specimen described herein was derived from rocks of the Black Rock Sandstone which also yielded the invertebrate fossils used by Singleton (1941) in defining the Cheltenhamian Stage. Stirton, Tedford and Woodburne (1968) present a summary of the age determinations proposed for the Cheltenhamian, and conclude that it is probably early Pliocene, but Kenley (1967), Darragh in Wilkinson (this memoir) and other authors cited in Stirton, Tedford, and Woodburne (*op. cit.*) support a late Miocene age for this Stage. N.M.V. P15911A-B apparently represents the lower mandible of *Zygomaturus gilli*. The general stage of evolution displayed by the lower mandible and dentition is similar to that of the previously described upper dentition of this species, i.e. more advanced than the Alcoota zygomaturines (Woodburne 1967a, b) and more primitive than those from the Palankarinna fauna (Stirton 1967).

This tends to corroborate the post Alcoota-pre Palankarinna age assigned to the Beaumaris fauna, as based on the phyletic position of *Zygomaturus gilli* (see Stirton, Tedford, and Woodburne 1968, for a review). If the age of the Cheltenhamian, and therefore that of the Beaumaris fauna, is late Miocene, the temporal position of the older faunas found in the Northern Territory and South Australia may need to be revised downward somewhat. It is also possible that both the Alcoota and Beaumaris faunas could be late Miocene in age, with the Alcoota being the older of the two.

Both parts of the specimen have a rich brown to yellowish brown colour, the lingual surface of the symphysis is stained a deep maroon. Remnants of the drab brown siltstone matrix are found on the antero-lingual surface of the symphysis and partially filling the anteroventral portion of the pterygoid fossa above the antero-lingual edge of the angular process. A small remnant of matrix remains on the internal surface of the coronoid process lateral to the postalveolar shelf. The bony surface of the mandible bears numerous small cracks and pits, and a large piece of bone is missing from the ventral surface below M_2 and M_3. Most of the projecting edges of the specimen are abraded and rounded to a variable extent. In particular, abrasion has affected the anterior tip of the symphysial portion, the leading edge of the coronoid process, the rear of the preserved portion of the angular process and, to a lesser extent, the lingual edge of the postalveolar shelf and the entire lingual side of the ventral edge of the horizontal ramus. A chip of bone about 22 mm long has been lost from this edge of the ramus immediately antero-ventral to the pterygoid fossa. Another, flat, shallow flake of bone nearly 24 mm long is missing from the ventral surface of the angle immediately ventral to the fossa. The edges of the break along which the two parts of the mandible fit together are still sharp, however, so it appears that most postmortem abrasion of the specimen was sustained while it was all in one piece. There can be no doubt that the two pieces form the partial right mandible of a single individual diprotodontid.

Zygomaturus gilli

Mandible. When the two parts are fitted together (Fig. 1A, C) the mandible is of rather normal diprotodontid construction. The alveolar border and ventral edge of the horizontal ramus are both moderately convex ventrally. Below M_2 and M_3 the lateral surface is dorsoventrally convex, but becomes flatter anterior to M_2. A nearly circular mental foramen is located about 9 mm below and slightly anterior to the exposed anterior root of P_3. The vertically elongate, narrow, and slightly concavo-convex posterior portion of the incisor root is visible immediately below and medial to the mental foramen (see Stirton 1957, text-figure 5D). The incisor root is open at this point which, to judge from most other Tertiary diprotodontids, is not far from the tip. There is no evidence as to the nature of the pre-cheek tooth diastema above the mental foramen, but below it the ventral edge of the symphysis extends downward approximately 4 mm below the ventral edge of the horizontal ramus. The masseteric fossa is partly preserved posteroventral to M_4, and although its leading edge is not preserved the coronoid process probably rose past the posterior half of M_4. The angle at which this took place is not determinable, however. The ventrolateral surface of the ramus slopes sharply ventromedially below the masseteric fossa. The faintly developed digastric process and post-digastric sulcus is not visible in lateral view.

In occlusal view (Fig. 1B) both the labial and lingual surfaces of the horizontal ramus are nearly straight, although they converge slightly anteriorly. The postal-
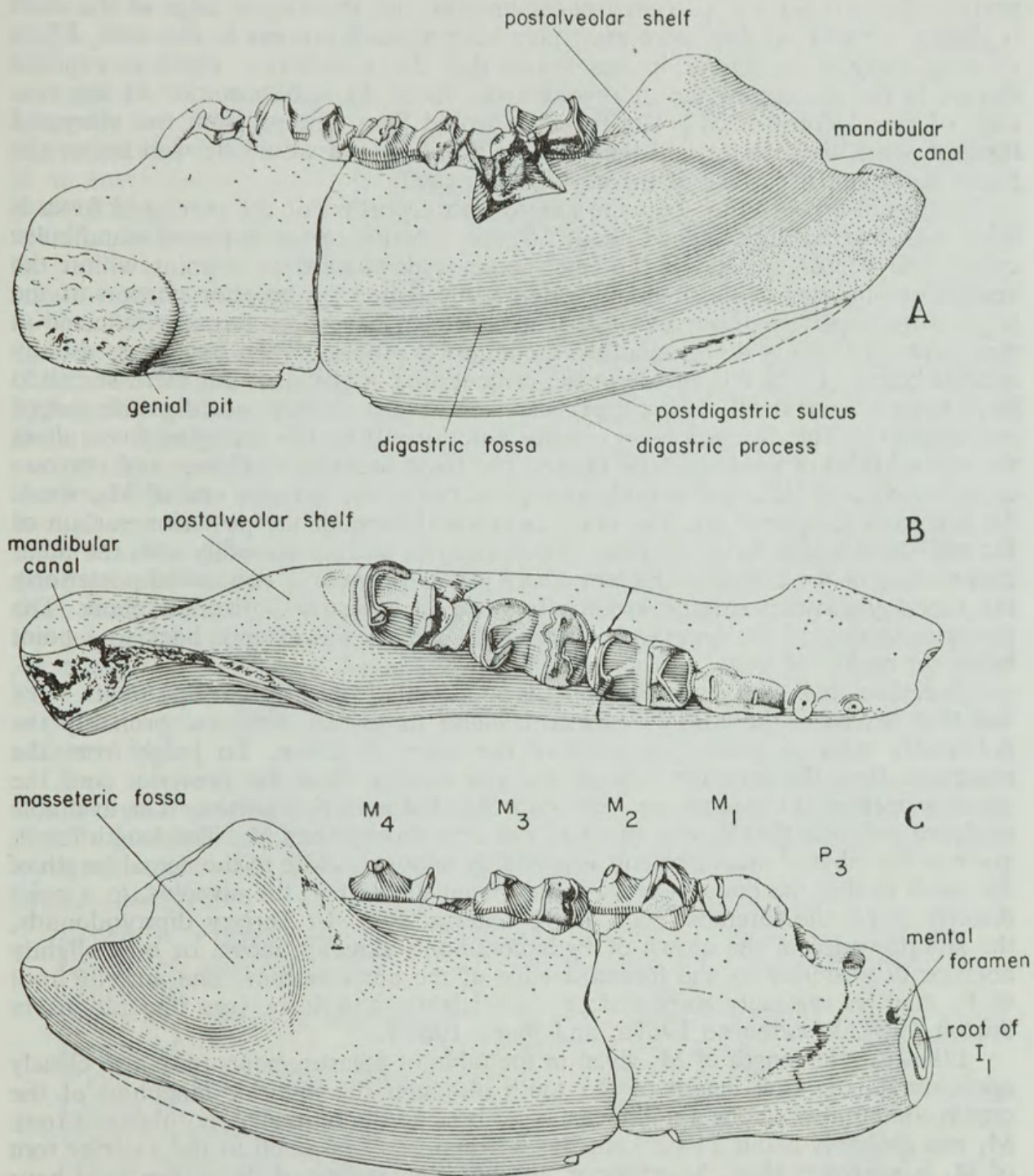
Fig. 1—*Zygomaturus gilli*, right mandible with symphysial and angular portions partly preserved, three fourths natural size. Nat. Mus. Vict. P15911A (symphysis) and P15911B (horizontal ramus). A. Lingual view. B. Occlusal view. C. Labial view.

veolar shelf has a nearly flat upper surface posterior to M_4; its lingual surface is smoothly continuous with that of the rest of the mandible, and curves gradually posteromedially toward the area of the pterygoid fossa. A strongly developed postalveolar process was probably never present, but the lingual edge of the shelf is slightly abraded so that there may have been a small process in this area. Upon clearing away some matrix it was found that the mandibular canal is exposed medial to the surface of the pterygoid fossa about 41 mm posterior to the rear edge of the alveolus of M_4. The foramen would then emerge from the pterygoid fossa at some distance beyond the point in question and would lie well below the plane of the upper surface of the postalveolar shelf.

In lingual aspect (Fig. 1A) the anteroventral portion of the pterygoid fossa is filled with matrix, and extends about 15 mm anterior to the exposed mandibular canal. The ventral border of the fossa extends downward to a point within the ventral one-quarter of the mandible. Below the fossa, the anterior portion of the angle is incompletely preserved; it does not seem to have been strongly inflected at this point. In Tertiary diprotodontids, the digastric process, when present, is usually located below M_4. In this specimen the critical area is abraded, but there seems to have been a very small digastric process and a very shallow postdigastric sulcus posterior to it. The digastric fossa extends anteriorly from the pterygoid fossa along the ventral third of the horizontal ramus. The fossa becomes shallower and narrower anteriorly and fades out entirely at a point below the anterior end of M_3, about 30 mm from the genial pit. The latter is exposed beneath the posterior portion of the mid-sagittal symphysial surface. The symphysis merges smoothly with the adjacent surface of the mandible. Except where it begins to curve downward posteriorly the supra-symphysial surface extends forward in a nearly horizontal plane. The posterior surface of the symphysis is smoothly convex and extends back to a point below the middle of M_1.

Dentition. It is unfortunate that P_3 is represented only by the tips of its roots and that M_1 lacks the coronal surface because these two teeth are probably the potentially most diagnostic elements of the lower dentition. To judge from the preserved tips, the anterior root of P_3 was smaller than the posterior and the anterior portion of the tooth was narrower than the posterior portion. The available evidence indicates that P_3 was about 17 per cent shorter than M_1. The length for P_3 given in the table of measurements is probably relatively close to the actual length of the tooth in that the dimension was taken from the rear of the alveolus, to a point directly above the foremost edge of the anterior root. In Teriary diprotodontids, the anterior edge of the crown of P_3 is commonly directly above, or only slightly anterior or posterior to, the foremost edge of the anterior root. The anterior root of P_3 may be vertically emplaced or slant slightly anteriorly (see illustrations in Stirton 1967, Woodburne 1967a, and Plane 1967).

Likewise, the length of M_1 given in the table of measurements may also closely approximate the true length of the tooth although the anterior cingulum of the crown commonly extends a millimetre or so beyond the immediately subjacent root. M_1 was probably about 21 per cent shorter than M_2. Inasmuch as the anterior root of M_1 is narrower than the posterior, the anterior moiety of the crown may have been narrower than the posterior.

The surface of M_2 is the most completely preserved of all of the cheek teeth, but the labial and lingual surfaces of the protolophid and the lingual surface of the hypolophid are abraded. However, I estimate that the actual widths of the protolophid and hypolophid were approximately equal. The tooth is constricted at the

transverse valley and apparently had a bilobed occlusal outline. An anterior cingulum is present, but it is not thick anteroposteriorly. The presence of a weakly developed paralophid is suggested by a slight bulge in the anteriolabial quadrant of the protolophid. This is more pronounced in M_2 than in the corresponding part of M_3. The protolophid was apparently aligned transversely although it probably had an anteriorly concave occlusal pattern. It is separated from the hypolophid by a broadly V-shaped transverse valley in which the anterior wall is directed more vertically than the posterior wall. This can be best seen in lingual view (Fig. 1A). A moderately developed metalophid descends the anterior face of the hypolophid in an anteromedial orientation, but is aligned more anteriorly when it reaches the transverse valley. The metalophid blends into the posterior base of the protolophid near the longitudinal midline of the tooth. The hypolophid is aligned slightly posteromedially, rather than transversely as for the protolophid, and has an anteriorly concave occlusal pattern. The posterior cingulum is highest at the longitudinal midline of the tooth, but makes no conspicuous connection to the hypolophid.

The third molar is about 11 per cent longer than M_2, and has a bilobed occlusal outline. Although the labial end of the protolophid and the lingual end of the hypolophid are abraded, I estimate that the protolophid was at least 2 mm wider than the hypolophid. As in M_2, the anterior cingulum in M_3 is narrow anteroposteriorly and apparently did not extend around to the labial or lingual sides of the protolophid. Although much of the enamel is missing from the protolophid, enough remains to show that the paralophid, if present, was not as well developed as in M_2. The transverse valley separating the anterior and posterior moieties of the tooth is broadly V-shaped with the anterior wall being more nearly vertical than the posterior. If the features of the dentine reflect the basic configuration of the enamel, the protolophid was aligned transversely to the long axis of the tooth. As in M_2, the hypolophid is aligned somewhat posterolingually. The metalophid of M_3 is similar to that in M_2 except for more clearly demonstrating its anterior orientation as it approaches the transverse valley. The posterior cingulum is similar to that in M_2.

Only the posterior moiety is adequately preserved in M_4 although it is probable that the greatest width of the tooth would have been measured across the protolophid. Except for being about 5 per cent longer, the construction of M_4 is apparently not significantly different from that of M_3.

MEASUREMENTS:

Length P_3 (approximate)	12·8 mm
Length M_1 (approximate)	15·4
Length M_2	19·5
Width M_2 (posterior, minimum)	12·9
Length M_3	21·9
Width M_3 (anterior, minimum)	15·1
Length M_4	23·0
Width M_4 (posterior, minimum)	14·5
Length P_3-M_4 (measured at the alveoli)	93·1
Depth below alveolar border, anterior edge M_1	42·6
Depth below alveolar border, between M_3 and M_4	46·5

Comparisons. N.M.V. P15911A-B is a zygomaturine diprotodontid. This is shown by its relatively long P_3 and by its rather close resemblance to *Kolopsis torus, Plaisiodon centralis,* and *Zygomaturus keanei,* as detailed below. Tertiary

nototherine diprotodontids have a characteristically short P_3 and labial cingula on the lower molars which are incipiently or markedly developed depending upon the genus in question. Palorchestine diprotodontids typically have relatively non-bilobate lower molars, all of which have prominently to well developed paralophids and metalophids, at least in faunas of late Miocene or later age.

The Beaumaris mandible closely resembles that of *Kolopsis torus*, described (Woodburne 1967a) from the late Miocene Alcoota fauna of the Northern Territory. This similarity includes the position and orientation of the masseteric fossa and leading edge of the coronoid process, the shape and configuration of the labial and lingual surfaces of the horizontal ramus and symphysis, the position of the mental foramen, the configuration of the digastric and pterygoid fossae, the horizontal alignment of the supra-symphysial surface, the development of the postalveolar shelf, the probable position of the mandibular foramen, the poorly developed digastric process and postgastric sulcus, and the general outline of the molars, as represented.

Points in which the Beaumaris specimen differs from the Alcoota species are the better developed metalophid and the asymmetrically V-shaped rather than symmetrically U-shaped transverse valley of the molars, the relatively narrower molar proportions, the more anterior position of the genial pits, the smaller development of the postalveolar process and the flattened, concavo-convex cross section of the proximal root of the incisor.

The Beaumaris specimen also shows similarities to *Plaisiodon centralis* of the Alcoota fauna. *P. centralis* differs from N.M.V. P15911A-B in that the ventral border of the angle is straight in lateral view and rises sharply posterodorsally from the ventral surface of the horizontal ramus. In the Beaumaris specimen this area of the angle is smoothly curved. In addition, the mandibular canal would lie below a horizontal line drawn along the lingual alveolar border below M_2-M_4 in the Beaumaris specimen, rather than at or slightly above such a line in *P. centralis*. Moreover, the anteroventral edge of the pterygoid fossa reaches down only to a point located about midway between the dorsal and ventral edges of the ramus in *P. centralis*, while in the Beaumaris mandible this part of the fossa lies well down in the lower one quarter of the ramus.

The dentition of N.M.V. P15911A-B resembles that of *P. centralis* in the general occlusal outline, the relative development of the metalophid, the shape of the transverse valley, and in the somewhat narrower, more elongate proportions of the molars. The posterior root of the lower incisor of *P. centralis* is bi-concave in cross section, and the posterior tip is closed.

Kolopsis rotundus, of the middle Pliocene Awe fauna, New Guinea (Plane 1967), has the same relative molar proportions as *K. torus* and thus differs from the Beaumaris specimen. *K. rotundus* is also distinguished from N.M.V. P15911A-B in that the lower incisor displays a widely open root and extends posteriorly to the rear of the symphysis. Further, in *K. rotundus*, the sulcus between the rear of M_4 and the anterolingual surface of the coronoid process is broad, the postalveolar process, digastric process and postdigastric sulcus are prominent, the ventral edge of the pterygoid fossa reaches downward only to a point about halfway between the dorsal and ventral edges of the mandible, the supra-symphysial surface rises anterdorsally, genial pits are absent, and the metalophid is essentially straight, although obliquely oriented. *K. rotundus* resembles the Beaumaris specimen in the degree of development of the metalophid on the molars.

Kolopsoides cultridens (Awe fauna) differs sharply from the Beaumaris speci-

men in that the jaws are more massive, the symphysis extends posteriorly to below M_2, the digastric process is stronger, the genial pit is flat, and the metalophid of the molars is formed from the protolophid as well as from the hypolophid. The lower incisor has a subovate posterior cross section and the tip of the tooth is closed.

The mandible of *Zygomaturus keanei* (Palankarinna fauna, Stirton 1967) is considerably larger than the Beaumaris specimen, but if the dorsoventrally crushed nature of the former is taken into account, it resembles the Beaumaris mandible in general shape as well as in the position and nature of the genial pits, the slightly developed postalveolar process, the occlusal proportions of the molars, the curved metalophid, the absence of labial cingula and in the general shape and degree of closure of the posterior tip of the incisor root.

TABLE 1

| | | *Kolopsis torus* | | | | | *Zygomaturus gilli* | |
	N	OR	$\overline{X}$	s	V	"$\overline{X}$"	"S"	"$\overline{X}$"±2"s"
P³								
Length	14	17·1-20·5	18·7 ± 0·28	1·05 ± 0·20	5·60 ± 1·05	23·0a	1·28	20·4-25·6
Width across paracone and protocone	13	13·7-15·8	15·1 ± 0·20	0·73 ± 0·14	4·83 ± 0·95	17·4	0·83	15·7-19·1
M²								
Width, post.	9	17·8-21·4	19·3 ± 0·38	1·15 ± 0·27	5·96 ± 1·40	20·7	1·23	18·2-23·6
M³								
Length	16	21·5-25·0	23·6 ± 0·25	1·00 ± 0·18	4·24 ± 0·75	27·7	1·17	25·4-30·0
Width, ant.	15	20·4-23·2	21·9 ± 0·22	0·87 ± 0·16	3·97 ± 0·73	25·7	1·02	23·7-27·7
M⁴								
Length	16	21·2-25·3	23·6 ± 0·27	1·08 ± 0·19	4·58 ± 0·81	27·0	1·10	24·8-29·2
Width, ant.	15	20·1-23·5	21·7 ± 0·23	0·90 ± 0·16	4·15 ± 0·76	23·5	0·97	21·6-25·4

| | | *Kolopsis torus* | | | | | N.M.V. P15911A-B | |
	N	OR	$\overline{X}$	s	V	"$\overline{X}$"	"S"	"$\overline{X}$"±2"s"
P₃								
Length	21	12·3-15·5	14·0 ± 0·17	0·78 ± 0·12	5·57 ± 0·86	12·8	0·71	11·4-14·2
M₁								
Length	12	17·2-19·0	18·0 ± 0·16	0·54 ± 0·11	3·00 ± 0·61	15·4	0·46	14·5-16·3
M₂								
Length	19	18·7-21·6	20·2 ± 0·19	0·83 ± 0·13	4·11 ± 0·67	19·5	0·80	17·9-21·1
Width, post.	17	13·8-16·0	15·1 ± 0·13	0·55 ± 0·09	3·64 ± 0·62	12·9	0·47	12·0-13·8
M₃								
Length	14	21·8-25·8	23·3 ± 0·35	1·30 ± 0·24	5·58 ± 1·05	21·9	1·22	19·5-24·3
Width, ant.	13	16·4-19·7	18·2 ± 0·25	0·90 ± 0·17	4·95 ± 0·97	15·1	0·75	13·6-16·6
M₄								
Length	19	22·1-27·0	24·2 ± 0·32	1·43 ± 0·23	5·91 ± 0·96	23·0	1·36	20·3-25·7
Width, post.	15	15·6-20·0	17·2 ± 0·28	1·10 ± 0·20	6·40 ± 1·17	14·4	0·94	12·5-16·3

"$\overline{X}$" ± 2"s" = range of two standard deviations on either side of the "mean". The "mean" is taken as the dimension measured on *Z. gilli* and N.M.V. P15911A-B, "s" being computed from V of *K. torus*. All measurements in mm.

a = approximate, ant. = anterior, post. = posterior, N = number of specimens, OR = observed range, $\overline{X}$ = mean, s = standard deviation, V = coefficient of variation.
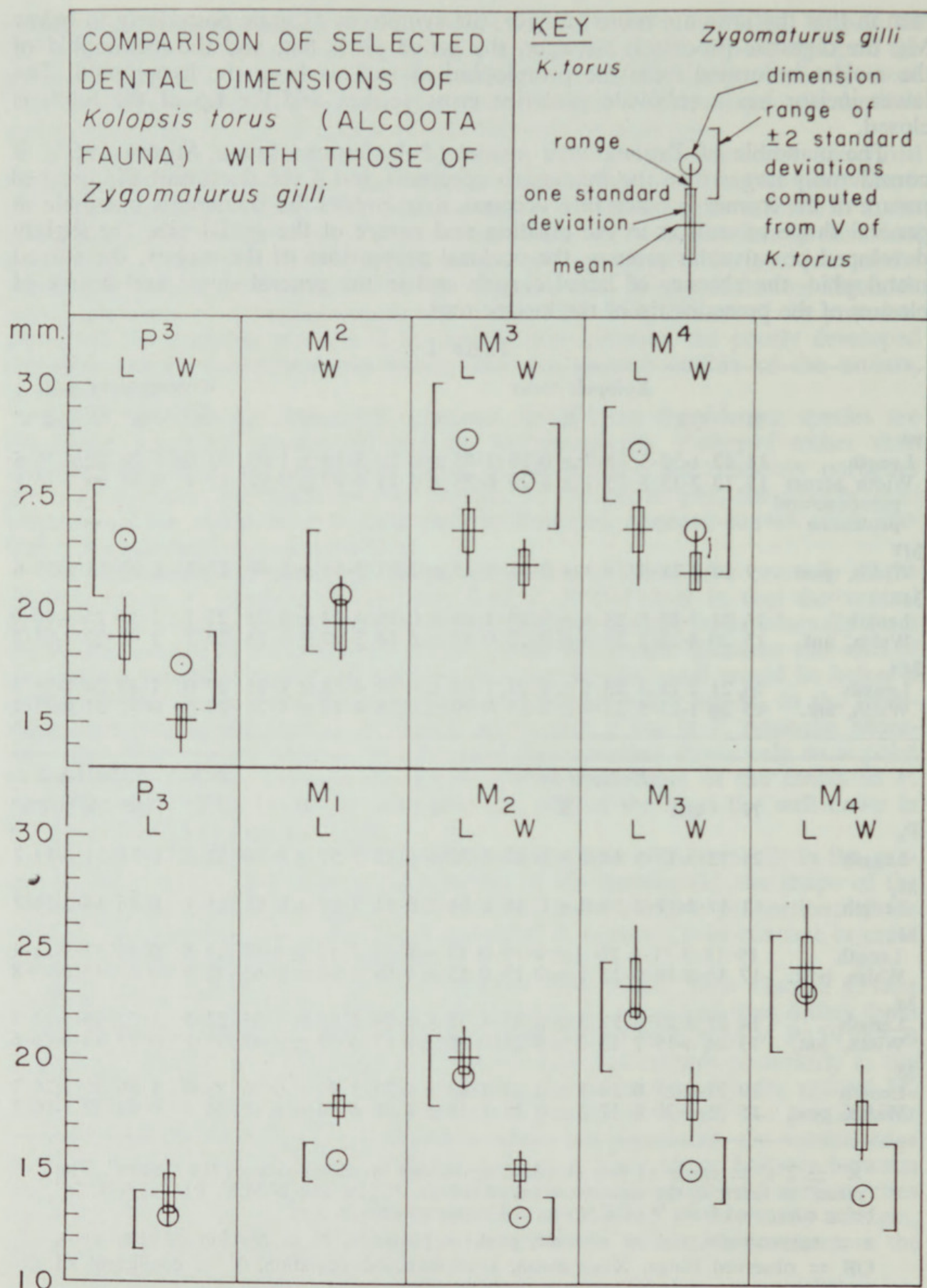
Fig. 2—Comparison of selected dental dimensions of *Kolopsis torus* (Alcoota fauna) with those of *Zygomaturus gilli* and a theoretical estimate of the range of these dimensions for a population of *Z. gilli*.

Z. keanei differs from the Beaumaris specimen in its stronger digastric process and postdigastric sulcus, anterodorsally inclined supra-symphysial surface, less bilobate basal outline of its molars, and the fact that both the protolophid and hypolophid contribute to the metalophid on M_4.

As shown in Table 1 and Fig. 2, the upper teeth of *Z. gilli* are conspicuosly larger than those of *K. torus*, except for the posterior width of M^2. The lower teeth of N.M.V. P15911A-B are generally smaller than those of *K. torus*, but overlap does occur in the lengths of P_3, M_2, M_3, and M_4.

Following procedures such as those indicated in Simpson, Roe, and Lewontin (1960), the hypothetical value of the standard deviation (s) for the population to which *Z. gilli* belongs can be computed from the coefficient of variation (V) calculated for the *K. torus* sample. These values are presented in the statistical summary below. The above procedure assumes that the dimensions observed for *Z. gilli* represent the 'mean' for its population, and that the coefficient of variation of the population would be similar to that of the closely related species, *K. torus*. Simpson, Roe, and Lewontin (1960, p. 212) indicate that over 95 per cent of all specimens in a population would theoretically fall within a range of plus or minus two standard deviations from the mean.

As shown in Fig. 2, the hypothetical range in dental dimensions of a 'population' of *Z. gilli* would completely or nearly overlap the observed ranges of analogous dimensions of the Alcoota population of *K. torus*. The fact that N.M.V. P15911A-B is too small to occlude satisfactorily with the upper teeth of *Z. gilli* is insufficient for taxonomic separation of the two groups of specimens. They could represent individuals pertaining to different parts of a 'normal' population curve of *Z. gilli*. Such a population would have approximately the same dental dimensions as those of *K. torus*. In the absence of definitive contrary evidence, and in view of its geographic and geologic proximity to the other specimens of *Z. gilli*, and because it has a similar evolutionary position, N.M.V. P15911A-B is referred to that species.

Conclusions

From the data summarized above, the mandible N.M.V. P15911A-B pertains to *Zygomaturus gilli*. Although its tooth proportions are close to *Plaisiodon*, the mandibular characters of the Beaumaris specimen are sufficiently divergent to warrant separation from that genus. The mandible of N.M.V. P15911A-B is closely similar to *Kolopsis torus* and, to a lesser degree, to *K. rotundus*. Except for its narrower tooth proportions, the Beaumaris specimen is relatively close, dentally, to *K. rotundus*. *Kolopsoides cultridens* is sufficiently divergent from the Beaumaris specimen to be excluded from further discussion.

Allowing for the dorsoventral crushing of the specimen of *Zygomaturus keanei* (late Pliocene), some of the features in which it differs from the Beaumaris mandible, e.g. the deeper pterygoid and digastric fossae and prominent digastric process and postdigastric sulcus, could be correlated with its large size. Such features are commonly found in the larger more massive Tertiary diprotodontids such as *Pyramios alcootense, Meniscolophus mawsoni*, and *Z. keanei*, but are not as prominently developed in some of the smaller species.

The remaining differences between *Z. keanei* and N.M.V. P15911A-B, the anterodorsal slope of the supra-symphysial surface and the somewhat less bilobate basal occlusal outline of the molars, would not preclude referral of the Beaumaris

specimen to the genus *Zygomaturus*. The high, laterally compressed, and somewhat open cross section of the proximal end of the incisor in the Beaumaris specimen differs in detail from that of *Z. keanei*, but the proportions of the incisor cross section, and the fact that the root remains open close to (if not at) the tip, is similar in both. Of the Tertiary diprotodontids surveyed, a high narrow proximal incisor cross section was also found in *Plaisiodon centralis* and *Pyramios alcootense*, the latter being a nototheriine. In both of these, however, the root is closed, and although the posterior cross section is bi-concave, it differs in detail from that in *Z. keanei* (Stirton 1967, fig. 4B), and the Beaumaris specimen.

In summary, the combination of its mandibular characters, coupled with the elongate proportions of the molars, the well developed arcuate metalophid, and laterally compressed, but open proximal cross section of the lower incisor, permit referral of N.M.V. P15911A-B to the genus *Zygomaturus*; for reasons presented previously, the specimen is assigned to *Z. gilli*.

N.M.V. P15911A-B presents a mosaic of characters. Those which are more advanced than *K. torus* are the more strongly developed and curved metalophid and asymmetrically V-shaped transverse valleys of the molars, and the flattened, essentially open posterior root of the lower incisor. The more primitive position of the Beaumaris mandible with respect to *Z. keanei* is shown in its considerably smaller size, the lack of a strong protolophid contribution to the metalophid of M_4 and possibly the less prominent development of the pterygoid and digastric fossae, and the smaller digastric process and shallower postdigastric sulcus.

The post *K. torus*—pre *Z. keanei* stage of evolution of the Beaumaris mandible thus substantiates the post Alcoota-pre Palankarinna age assignment proposed for the Beaumaris fauna, as based on evidence of the upper dentition of *Z. gilli* (Stirton, Woodburne, and Plane 1967; Stirton, Tedford and Woodburne 1968).

Tentative expanded diagnosis of Zygomaturus gilli

Referral of N.M.V. P15911A-B to *Z. gilli* allows the diagnosis of the species to be expanded beyond that given in Stirton (1967, p. 135) subject of course to future discoveries: Size much smaller than Palankarinna species, roughly similar to that of *Kolopsis torus*; mandible less robust than *Z. keanei*, with shallower pterygoid and digastric fossae; less prominent digastric process, postdigastric sulcus, and postalveolar process; supra-symphysial surface nearly horizontal; lower molars with more bilobate occlusal outline; no protolophid contribution to the metalophid on M_4.

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