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GENERIC AND SPECIFIC DIAGNOSES IN THE GIGANTIC MACROPODID GENUS *PROCOPTODON*

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Figures 1-10

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ABSTRACT

A revised diagnosis of the Pleistocene genus *Procoptodon* is presented. The species also are revised and diagnosed. Numerous diagnostic characters have been found in the patterns and construction of the teeth. Owen's species *Procoptodon goliah* (Owen), 1846, *Procoptodon rapha* Owen, 1873, and *Procoptodon pusio* Owen, 1873, are recognized. As indicated by Owen, 1874, *Pachysiagon otuel* is a synonym of *Procoptodon pusio*. All of these are from late Pleistocene faunas. No specimens of *Procoptodon* are now known from older faunas. It is thought that a common ancestry of *Procoptodon* and *Sthenurus* in the Sthenurinae is much farther back in the Tertiary than has been previously assumed.

INTRODUCTION

The largest and most bulky of all kangaroos is *Procoptodon goliah*. *Procoptodon rapha*, although also large, is smaller than *P. goliah*. Other late Pleistocene macropodids like *Protemnodon* and *Macropus ferragus* have skulls of equal length but they are not as deep as in *Procoptodon*. Nor does the evidence from the limbs indicate that the other large macropodids were as large as the largest *Procoptodon* species.

Procoptodon is currently classified in the subfamily Sthenurinae. R.H. Tedford (Ph.D. dissertation), as based on his Lake Menindee specimens, has revealed that *Procoptodon* is monodactyl in the hind foot, having reduced even the fifth metatarsal to a vestige, the forelimbs are proportionally much longer than in the macropodines and the basicranium is so shortened that the skull is as deep as it is long.

The other genus of the Sthenurinae is, of course, *Sthenurus*. Tedford has in press a revision of that genus. It is our purpose here to present revised diagnoses of the genus and species of *Procoptodon*. We have recognized Owen's species *P. goliah*, *P. rapha* and *P. pusio* (syn. *Pachysiagon otuel*). Our diagnoses are based primarily on the dentition. All three species are represented in the late Pleistocene Bingara fauna which was found in Bone Camp Gully, a tributary of Ironbark Creek, 15 miles east of Bingara, New South Wales. The collection has been loaned to us from the Australian Museum for a faunal report (Marcus, Ph.D. dissertation). Our detailed information is based primarily on those specimens as compared with casts of the holotypes. It seems desirable to present the diagnoses prior to the appearance of the longer report so they will be available to others working on fossil macropodids.

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PROCOPTODON Owen, 1873

The genotype of *Procoptodon*, a maxilla fragment with three molars, was discovered in the Darling Downs of Queensland and presented to Richard Owen by Sir Thomas L. Mitchell in 1844. A brief preliminary description was written by Owen and was communicated to George R. Waterhouse, who at that time was writing his book on "The Natural History of the Mammalia." Consequently, Owen's first account of the specimen, which he named *Macropus goliah*, appeared with an illustration as early as 1846. Some subsequent confusion arose concerning recognition of the type specimen, because, in the original description, it was stated there were two upper molars. This evidently was an error in printing. As a result, however, Lydekker (1891) stated that the type had been lost. Fortunately this is not true. The type M1896 is in the British Museum (Natural History) and the teeth are M¹, M² and M³ not M², M³ and M⁴ as recorded by Owen and Lydekker.

The generic name *Procoptodon* as well as the species names *Procoptodon rapha* and *Procoptodon pusio* were introduced in abstract form by Owen in 1873, but the specimens were fully described in his memoir in 1874. In the memoir he also described part of a mandible as *Pachysiagon otuel* which three years later (1877) he realized was a synonym of *Procoptodon pusio*. All of these types came from the Darling Downs and in so far as we know are late Pleistocene in age.

Most of the generic characters used by Owen (1874; 1876; 1877) and Lydekker (1887; 1891) are equally applicable to one or another species of *Sthenurus*. These are: large palatine vacuities extending far forward; anterior position of masseteric process; ankylosis of symphysis of mandible; deep short ramus; short canine $-P_3$ diastema; molars with complex enamel patterns; premolars resemble those in *Sthenurus*.

In attempting to correct Owen's identification of the specimens Lydekker (1887) incorrectly identified specimens resembling the type of *P. pusio* as *P. rapha* and used characters that are not diagnostic of the species. He also ignored Owen's (1877) earlier synonymy and used the name *Procoptodon otuel* for the lower dentitions of *P. pusio*. The specimens from Victoria that were figured by McCoy (1879) as *P. goliah* are apparently *P. rapha*.

In comparing what he considered to be transitional characters between *P. pusio* and *Sthenurus oreas*, DeVis (1895) synonymized *Procoptodon* with *Sthenurus*. Tate (1948) partly subscribed to DeVis' conclusions by recognizing *Procoptodon* and *Sthenurus* as subgenera.

The dental and mandibular characters in *P. pusio* are on the whole more like those in *Sthenurus* than are the characters in the other species of *Procoptodon*. This persuaded DeVis and others to believe that there must be an early Pleistocene or late Tertiary ancestral relationship in common for the genera. This phyletic relationship has not been confirmed in any of the older faunal assemblages. It is true, however, that we know of no *Procoptodon* specimen older than those that we have thought to be late Pleistocene in age. The presence of strong midlinks and forelinks in the molars of *Procoptodon* and their great reduction in *Sthenurus* does not support a close relationship of the genera. Obviously these genera are more closely related than either are to any of the other genera in the Macropodidae, but if, as so frequently seems to be indicated in herbivorous mammals, the molars are less subject to accelerated evolution than the incisors, premolars, feet or gross morphology, the *Procoptodon* and *Sthenurus* lineages may well extend much farther back into the Tertiary than we can visualize on the basis of the evidence available.

Revised Generic Diagnosis: I¹ larger than I³; I² small; I³ slightly compressed laterally but not as much so nor as elongate as in S. occidentalis; labial surface slightly convex anteroposteriorly and without groove. P³ more bulbous at base of crown than in all species of Sthenurus, except S. occidentalis.

Upper molars: anterior cingulum shelf less blade-like than in Sthenurus, anterolabial end usually not connected to base of paracone; anterior transverse valley crossed by forelink and by accessory spurs from protoloph (no forelink in P. pusio); high midlink sharply defined, connects anteriorly and slightly labially of anteroposterior midline across protoloph; spur from posterior surface of protoloph on midline and at lingual side of anterior part of midlink and parallel to it; no protoconal spur; area between midlink and labial end of middle transverse valley relatively narrow and not elevated; posterior paraconal spur and anterior metaconal spurs well defined in P. goliah and P. rapha but curve lingually toward midlink and sometimes connect to it, forming pockets, and do not form anteroposterior crest across labial end of middle transverse valley; in P. pusio, however, these spurs have strong tendency to form anteroposterior labial crest across middle transverse valley, especially on $M^{\frac{1}{2}}$ and $M^{\frac{4}{2}}$; metaconal spur as well developed or more so than in any species of *Sthenurus*: posterior surface of metaloph with vertical V-shaped grooves and adjacent ridges; transverse lophs appear less sharply crested because of prominent connection of links and spurs, relatively narrower than in *Sthenurus* and without scoop-like posterior surfaces; teeth higher crowned than in all species of Sthenurus, except S. atlas.

Mandible: horizontal ramus massive and wide transversely, lower border rounded in *P. goliah* and less sharply crested throughout its length even in *P. rapha* than in *Sthenurus*; relatively narrow digastric fossa descends from postdigastric sulcus at posterior base of ascending ramus anteroventrally to lower border of horizontal ramus below posterior end of M_4 ; prominent digastric process; deep postdigastric sulcus; wide pterygoid fossa becomes narrow anteroventrally and passes below and anterior to masseteric foramen; medial angular crest passes anteroventrally where it connects with upper ridge of digastric fossa, medial surface below crest narrow and rounded; condyle and angle relatively and actually much higher above molars than in *Sthenurus*.

Lower incisor relatively smaller than in *Sthenurus*, especially in vertical depth of blade. P_3 relatively shorter and more bulbous at base than in *Sthenurus*, except in *S. occidentalis*.

Lower molars: bulbous or tend to be bulbous at bases of crowns; anterior cingulum shelf relatively and actually wider transversely than in *Sthenurus*; high curved forelink connects transverse crest of anterior cingulum shelf with protolophid at lingual base of protoconid; small but conspicuous anterior cingulum in front of transverse crest at anterior edge of tooth; midlink high and sharply crested; prominent or subdued spur extends into middle transverse valley from hypolophid parallel and linguad to posterior part of midlink (also present in *S. oreas*); no tendency for elevation of middle area of middle transverse valley; lophids with spurs and vertical ridgelets; posterior surface of hypolophid with wide triangular grooves (except in *P. pusio*); transverse occlusal crests relatively narrower than in *Sthenurus*; lophids without scoop-like anterior surfaces; molars higher crowned than in all species of *Sthenurus*, except possibly *S. atlas*.

Procoptodon goliah (Owen), 1846

Holotype: Part of right maxilla with M^1 - M^3 . BMNH M1896.

Type locality: Darling Downs, Queensland.

Revised diagnosis: On the average animals slightly larger than P. rapha; lophs, links, spurs, ridgelets and grooves on molars not as sharply crested and on the whole less numerous on the checkteeth than in P. rapha, but always more so than in P. pusio.

 $P^{\underline{3}}$ with shorter, less sharply crested posterolabial crest than in *P. rapha*; slightly shorter than $M^{\underline{1}}$; main and lingual crest not as high and serrate as in *P. rapha*; occlusal basin open anteriorly; anterior moiety only slightly narrower than posterior moiety; base of crown bulbous posteriorly and tends to be so anteriorly.

Upper molars: crowns slightly lower and wider than in *P. rapha*; lophs slanting toward centre of crown from lingual bases (except in holotype) and some other specimens; anterior cingulum not sharply crested and closely appressed against base of anterior loph; slight emargination of link between end of cingulum and paracone on anterolabial corner of tooth; pocket on anterolabial surface of anterior loph; pocket on posterolabial surface of anterior loph and on anterolabial surface of posterior loph not opening into labial end of middle transverse valley; pit in middle transverse valley on lingual side of midlink seldom developed, but when present only on one or two upper molars (compare with *P. rapha*); posterior paraconal and anterior metaconal spurs not sharply crested, but enclose pockets; forelink less sharply crested than in *P. rapha*.

Ventral border of mandible below $M_{\overline{2}\cdot\overline{4}}$ broadly rounded. Lower incisor relatively short and vertically wide.

 P_3 triangular in outline, with posterior moiety much wider than anterior moiety; crescentic posterolabial crest connected anterolabially and posterlingually to main crest, therefore occlusal basin closed at both ends; anterior outline as viewed from above with rounded vertical edge; slightly shorter than M_T .

Lower molars: crowns frequently relatively wider than in *P. rapha*, lophids usually slanting toward centre of crown from lingual and labial bases; anterior transverse valley on each side of forelink tend to be shallower than in *P. rapha* or *P. pusio*; crescentic midlink directed anterolabially across middle transverse valley; protolophid spur of midlink relatively much longer than in *P. pusio*; three or more ridgelets on lingual side of midlink greatly subdued; pits in bottoms of middle transverse valley on one or both sides of midlink less frequent than in *P. rapha*, these features when present occur on one or possibly two lower molars in *P. goliah*; spur on anterior surface of hypolophid at lingual side of midlink and parallel to it well developed; pocket not formed on posterior surface of protolophid on lingual side of midlink; three prominent ridges and two wide grooves on posterior surface of hypolophid.

Procoptodon rapha Owen, 1873

Holotype: Part of immature left mandible with base of incisor, diastema from $I-P_{\overline{2}}$, roots and alveoli of $P_{\overline{2}}$ and $DP_{\overline{3}}$, $P_{\overline{3}}$ unerupted. BMNH 32885.

Type locality: Condamine River, Darling Downs, Queensland.

Revised diagnosis: On the average animals slightly smaller than P. goliah; lophs, links, spurs, ridgelets and grooves on molars sharper crested and on the whole more numerous on the checkteeth than in P. goliah, and always more than in P. pusio. $P^{\underline{3}}$ with prominent, sharp, posterior labial, crescentic crest; slightly longer than $M^{\underline{1}}$; main crest and lingual crest high and serrate; occlusal basin open anteriorly; anterior moiety much narrower than posterior moiety; base of crown bulbous posteriorly but less so anteriorly.

Upper molars: crowns slightly higher and narrower than in *P. goliah*; crowns nearly vertical at lingual ends of lophs; anterior cingulum sharply crested and projected anteroventrally; deep emargination of link between end of cingulum and paracone on anterolabial corner of tooth; pocket on anterolabial surface of anterior loph; pocket on posterolabial surface of anterior loph and on anterolabial surface of posterior loph usually open into labial end of transverse valley; pit formed on all four upper molars in middle transverse valley between base of midlink and low ridge which is half-way between midlink and lingual mouth of valley (this low ridge not to be confused with midline protoloph spur that is parallel and on same level as anterior part of midlink); posterior paraconal and anterior metaconal spurs sharply crested, but seldom enclose pockets; forelink more sharply crested than in *P. goliah*.

Ventral border of mandible below $M_{\overline{2}\cdot\overline{4}}$ rather sharply defined vertically. Lower incisor relatively short and vertically wide.

 P_3 triangular in outline, with posterior moiety much wider than anterior moeity; crescentic posterolabial crest separated from main crest anterolabially and posterolingually, therefore occlusal basin open at both ends; anterior outline as viewed from above with rather sharp vertical edge; slightly shorter than M_T .

Lower molars: crowns relatively narrower than in *P. goliah*; nearly vertical at labial and lingual ends of lophids; anterior transverse valley on each side of forelink deeper than in *P. goliah*; midlink usually directed anterolabially across middle transverse valley; protolophid spur of midlink relatively much longer than in *P. pusio*; three or more ridgelets on lingual side of midlink usually more prominent than in *P. goliah*; pits in bottom of middle transverse valley on one or both sides of midlink more frequent than in *P. goliah*—these features on all lower molars in *P. rapha*; spur on anterior surface of hypolophid at lingual side of midlink and parallel to it well developed; pocket formed on posterior surface of protolophid on lingual side of midlink; three prominent ridges and two grooves on posterior surface of hypolophid.

Procoptodon pusio Owen, 1873

Synonym—Pachysiagon otuel Owen, 1874

Holotype: Pair of maxillae with $P^{\underline{3}}$ unerupted, $DP^{\underline{3}}$, $M^{\underline{1}}$ - $M^{\underline{3}}$, most of right $M^{\underline{1}}$ now destroyed as well as labial side of anterior cingulum of left $M^{\underline{1}}$. BMNH 39996.

Type locality: King Creek, Darling Downs, Queensland.

Revised diagnosis: Animals much smaller than *P. goliah* or *P. rapha*; lophs, links, spurs, ridgelets and grooves on molars greatly reduced in numbers and not sharply crested.

 $P^{\underline{3}}$ with or without slight indication of posterolabial crest; slightly shorter than M¹; main crest high and sharply crested but not as serrate as in *P. goliah* or *P. rapha*, lingual crest lower and also less serrate; occlusal basin closed anteriorly; anterior moiety much narrower than posterior moiety; base of crown somewhat bulbous posteriorly and less so anteriorly.

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Upper molars: crowns nearly vertical at lingual ends of lophs; posterior labial paraconal and anterior labial metaconal spurs with strong tendency to form anteroposterior labial crest across middle transverse valley especially on M³ and M⁴, posterior paraconal spur also connects across to midlink forming smaller anterior pocket, this connection then forms anterior border of larger posterior pocket that encloses labial third of middle transverse valley (although these features do not occur in the holotype); pocket on posterior surface of metaloph present or absent; no pocket formed on anterolabial surface of anterior loph; no forelink; no pit in middle transverse valley at lingual base of midlink.

Ventral border of mandible below M_{2-4} inflected and sharply defined on lingual edge of ramus. Lower incisor relatively long and vertically narrower than in *P. goliah.*

 $P_{\overline{3}}$ elongate with posterior moiety only slightly wider than anterior moiety; relatively short crescentic posterolabial crest separated from main crest anterolabially and posterolingually by narrow clefts similar to *P. rapha*, occlusal basin relatively short; anterior outline as viewed from above with rather rounded vertical edge; much shorter than $M_{\overline{T}}$.

Lower molars: crowns relatively narrow, nearly vertical at lingual and labial ends of lophids; anterior transverse valley on each side of forelink deeper than in *P. goliah*; midlink directed anterolingually then anterolabially across middle transverse valley in early stages of wear and nearly straight in later stages; protolophid spur of midlink relatively much shorter than in *P. goliah* or *P. rapha*; one to three ridgelets on lingual side of midlink more reduced than in *P. rapha*; no pits in bottom of middle transverse valley on lingual side of midlink; spur on anterior surface of hypolophid at lingual side of midlink and parallel to it only slightly developed; pocket not formed on posterior surface of protolophid on lingual side of midlink; posterior surface of hypolophid with numerous small ridgelets and shallow grooves, area slightly depressed, short but more prominent ridgelet at middle near base of crown.

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EXPLANATION OF FIGURES

- Fig. 1. Procoptodon pusio Owen, 1873; holotype, Darling Downs, Qld.; *a*, occlusal view of left P^3 , twice natural size; *b*, occlusal view of left DP^3 and $M^1 M^2$ in maxilla, natural size, partly redrawn from Owen 1874 (Pl. LXXVII, 6) and 1877 (Pl. XC, 6); BMNH 39996.
- Fig. 2. Procoptodon rapha Owen, 1873; referred specimen, Bingara fauna, N.S.W.; occlusal views of P³ M¹, natural size; Aust. Mus. MF1048.
- Fig. 3. Procoptodon goliah (Owen), 1846; holotype, Darling Downs, Qld.; a, occlusal views of right $M^{\underline{1}} M^{\underline{3}}$ in maxilla; b, $M^{\underline{3}}$, posterior view; natural size; drawn from cast; BMNH M1896.
- Fig. 4. Procoptodon goliah (Owen), 1846; referred specimen, Bingara fauna, N.S.W., a, occlusal views of left P³, M¹ M² in maxilla; b, M³, posterior view; natural size; Aust. Mus. MF890.
- Fig. 5. Procoptodon rapha Owen, 1873; holotype, Condamine River, Darling Downs, Qld.; a, labial view showing base of incisor, diastema and unerupted $P_{\overline{3}}$, natural size; b, occlusal view, and c, labial view of $P_{\overline{3}}$; natural size; drawn from cast; BMNH 32885.
- Fig. 6. Procoptodon pusio Owen, 1873; holotype of Pachysiagon otuel, King Creek, Darling Downs, Qld.; part of right mandible with occlusal view of $M_{\overline{2}} M_{\overline{4}}$; natural size; drawn from cast; BMNH 46310.
- Fig. 7. Procoptodon pusio Owen, 1873; referred specimen, Bingara fauna, N.S.W.; a, occlusal and b, labial views of right $P_{\overline{s}}$; twice natural size; drawn from nearly complete mandible; UCMP 60053.
- Fig. 8. Procoptodon pusio Owen, 1873; referred specimen, Bingara fauna, N.S.W.; left mandible with occlusal views of $P_{\overline{s}}$, $M_{\overline{s}} M_{\overline{s}}$, diastema partly restored; natural size; UCMP 60053.
- Fig. 9. Procoptodon rapha Owen, 1873; referred specimen, Bingara fauna, N.S.W.; left mandible with occlusal views of $P_{\overline{s}}$, $M_{\overline{s}}$ missing, $M_{\overline{s}} M_{\overline{s}}$; natural size; Aust. Mus. MF886.
- Fig. 10. Procoptodon goliah (Owen), 1846; referred specimen, Bingara fauna N.S.W.; right mandible with occlusal views of $P_{\overline{3}}$, $M_{\overline{1}}$ missing, $M_{\overline{2}} M_{\overline{4}}$ (drawn in reverse); natural size; Aust. Mus. MF953.







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